

# SPHINCTOZOAN AND INOZOAN HYPERCALCIFIED SPONGES: AN OVERVIEW

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## INTRODUCTION

Many sponges that secrete a rigid skeleton composed of calcium carbonate, which may be aragonite or calcite (high- or low-Mg calcite), are included in the hypercalcified sponges in TERMIER and TERMIER (1973, 1977). Additionally, different types of spicular skeletons of calcite or siliceous mineralogy may be embedded within the rigid skeletons. Sponges with chambered construction are included in the group, termed Sphinctozoa, and those nonchambered representatives are included in the group termed Inozoa. These two groups were united in classic works in the Pharetronida (a division now regarded as obsolete; see Glossary, p. 410). Because of the polyphyletic nature of both of these groups, these terms cannot be used as systematic categories for classification of these sponges. The terms Sphinctozoa and Inozoa are used here for morphologically chambered or nonchambered sponges, respectively, without taking their systematic position into consideration.

The chambered Sphinctozoa and nonchambered Inozoa have been previously assigned to the Calcarea but are now largely included in the Demospongiae. They represent polyphyletic hypercalcified sponge groups and range stratigraphically from the Cambrian to the Recent. Their external and internal morphology, occurrence of spicules, mineralogy and microstructure of their rigid skeletons, their roles as reef builders, their stratigraphic record and geographic distribution, patterns of evolution and extinction, and a short review of the classification are discussed. A list of known sphinctozoa and inozoa genera, with their stratigraphic occurrences, are also presented here (p. 387–395).

Hypercalcified sponges, including sphinctozoa, inozoa, stromatoporoids,

archaeocyaths, and chaetetids are important groups of carbonate-producing invertebrates occurring in Phanerozoic reef ecosystems and in shallow-water biotopes. Archaeocyaths in the Cambrian, stromatoporoids in the Ordovician to Devonian, and inozoa, sphinctozoa, and chaetetids in the late Paleozoic and Mesozoic, particularly in the Permian and Triassic, are the main inhabitants of shallow-water biotopes and reef-building organisms.

The evolution of inozoa and sphinctozoa hypercalcified sponges was influenced by two significant events, one at the end of the Paleozoic era and the other at the end of the Triassic period, and by several other relatively minor extinction events. More than 90% of sponge genera became extinct during both of those major events, and no described Permian sponge species have been recognized in pioneer Middle Triassic reefs. However, several morphologically identical or similar genera, the so-called Lazarus taxa (JABLONSKI, 1986), reappear in the Upper Triassic (Norian) record. The event at the end of the Triassic was also dramatic for both the inozoa and sphinctozoa, for almost all documented sponge taxa in those groups became extinct. Only one genus of sphinctozoa, *Stylothalamia*, survived the Triassic-Jurassic boundary event. Again, morphologically identical or similar sphinctozoa and inozoa taxa reappear in the Upper Jurassic record.

## HISTORY

Because most Recent sponges bear skeletal components composed of spongin or spicules, fossil sponges with a rigid skeleton but without spicules (due to their initial lack or to loss related to recrystallization) have been assigned to different groups of

organisms. For example, the stromatoporooids have been assigned to hydrozoans. Some have been classified as a separate phylum (phylum Archaeocyatha) or to other fossil groups, like the Chaetetida. All of these groups are now included in the Porifera (HOOPER, VAN SOEST, & DEBRENNE, 2002; Stromatoporoidea: STEARN, 1972, 1975a, 2010b; VACELET, 1985; WOOD, 1987, 1990a; STEARN & PICKETT, 1994; STEARN & others, 1999; COOK, 2002; Archaeocyatha: HARTMAN & GOREAU, 1970, 1975; GRAY, 1980; DEBRENNE & VACELET, 1984; RIGBY & others, 1993; DEBRENNE & ZHURAVLEV, 1994; DEBRENNE, ZHURAVLEV, & KRUSE, 2002; Chaetetida: REITNER & WÖRHEIDE, 2002; and see Classification and Evolution of the Fossil and Living Hypercalcified Chaetetid-Type Taxa, p. 105–114).

The so-called Pharetronida [including the chambered Sphinctozoa STEINMANN (1882) or Thalamida DE LAUBENFELS (1955), and nonchambered Inozoa STEINMANN (1882), sponges with a rigid calcareous skeleton] were generally attributed to the Calcarea in the past. No special attention was paid to their spicular skeletons, which may have been embedded within the calcareous rigid skeleton in some representatives of both groups. Detailed investigations during the last half-century, especially those investigations including scanning electron microscopy, have shown that both the sphinctozoan and inozoa groups are polyphyletic in origin. Both appeared for the first time in the Cambrian and occur in the geologic record up to the Recent. Because of their significantly different morphologies, the Sphinctozoa and Inozoa are treated separately on the following pages.

## SPHINCTOZOANS

Chambered skeletal construction, with or without spicular skeletons, and with different skeletal mineralogy (aragonitic and calcitic) and microstructure, has developed independently several times in different sponge groups during the geologic past. For example, archaeocyathan chambered

sponges are known from the Cambrian and later (e.g., *Archaeosycon*, *Cerbicanicyathus*: DEBRENNE, ZHURAVLEV, & ROZANOV, 1989; DEBRENNE & WOOD, 1990; DEBRENNE, 1992; ZHURAVLEV, 1989). Other examples include the Silurian agelasid demosponges *Nematosalpinx* and *Aphrosalpinx* (MYAGKOVA, 1955a, 1955b; RIGBY, NITECKI, & others, 1994; FINKS & RIGBY, 2004d), the Cambrian heteractinid chambered sponges *Nucha*, *Wagima*, and *Jawonya* (PICKETT & JELL, 1983; KRUSE, 1987; PICKETT, 2002), the Jurassic–Cretaceous calcarean chambered sponges *Barroisia* MUNIER-CHALMAS in STEINMANN, 1882, and *Muellerithalamia* REITNER, 1987c, among others, along with the hexactinellid chambered sponges (*Casearia* QUENSTEDT, 1858, *Dracolychnos* WU & XIAO, 1989; RIGBY, WU, & FAN, 1998, Triassic–Jurassic), and demosponge chambered sponges (e.g., *Celyphia* POMEL, 1872; *Radiocella* SENOWBARI-DARYAN & WURM, 1994). These may be the majority of late Paleozoic and Mesozoic chambered sponges. Because of the lack of rigid calcareous skeletons, representatives of chambered hexactinellids and lithistid demosponges (*Radiocella*) are not treated in this section, though chambered archaeocyaths are discussed below (see systematic descriptions of the Archaeocyatha, p. 1025–1035).

## EXTERNAL MORPHOLOGY

We include in the term external morphology all features of sphinctozoan sponges that are visible and recognizable from the skeletal exterior. External features of sphinctozoan sponges include: (1) outer segmentation; (2) sponge shape; (3) chamber shape; (4) arrangement of the chambers; (5) inhalant canals or ostia in exowalls and their patterns; and (6) exhalant canals or oscula. The major morphological elements of sphinctozoan sponge skeletons are shown in Figure 215.

### Outer Segmentation

Chambered organization is the most important characteristic feature of sphinctozoan sponges, separating them from other hyper-

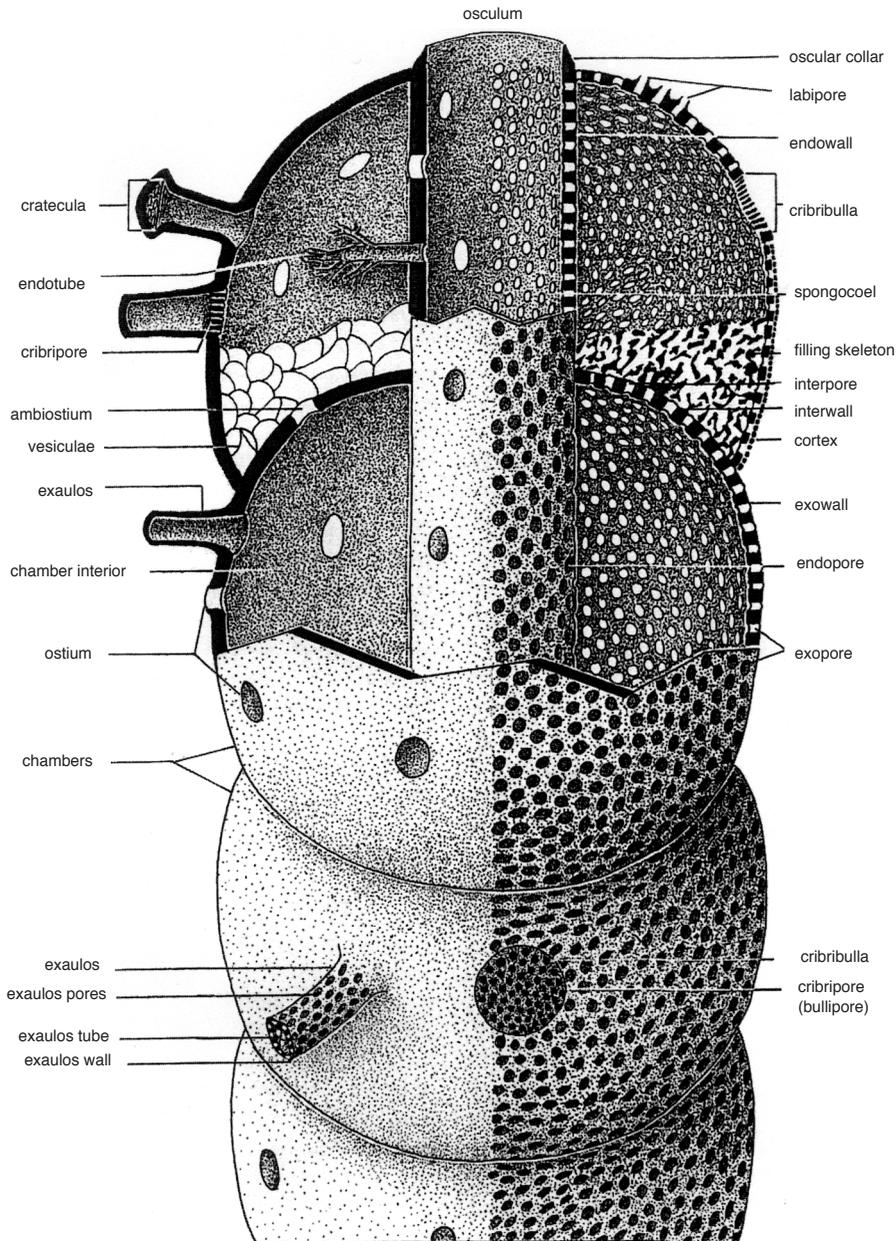


FIG. 215. Major morphological skeletal elements of sphinctozoan sponges. On the right, main characteristic features of the porate forms, and on the left, aporate forms. Of the filling skeleton structures, only the reticular type, on the right, and the vesicular type, on the left, are shown in the interior of the last chamber. Skeletal elements like those in the aporate sponges may also occur in porate representatives (adapted from Senowbari-Daryan, 1990).

calcified sponge groups. Outer segmentation corresponds generally to internal segmentation. However, due to overlap of earlier chambers by younger, later chambers in some

representatives, especially those taxa with crescentlike chambers (e.g., the Triassic genus *Senowbaridaryana*, Fig. 216–217, or *Zardinia*, Fig. 218), outer segmentation may be totally

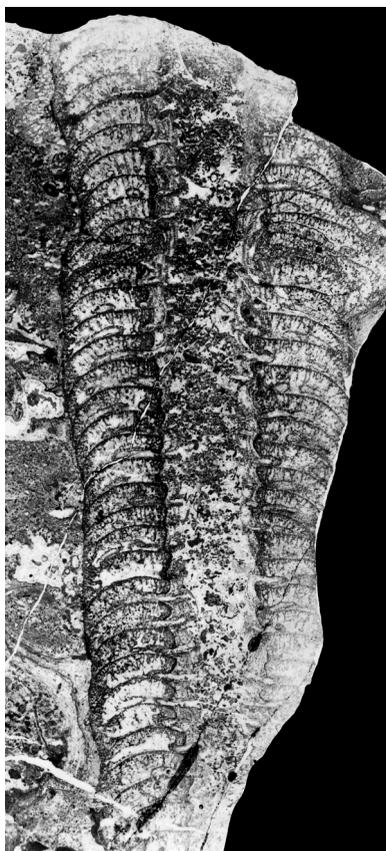


FIG. 216. *Senowbaridaryana hydriotica* SENOWBARI-DARYAN, 1990. Outer segmentation of this porate and siphonate sphinctozoan is totally lacking, but the chambered construction can be seen after cutting the specimen in longitudinal section. Crescentlike chambers contain reticular filling skeleton; Carnian, Triassic, Hydra, Greece,  $\times 1.7$  (Senowbari-Daryan & Schäfer, 1983).

lacking or hard to recognize. The chambered sphinctozoan construction of such sponges is recognizable only after cutting into their skeletons in longitudinal sections. Transverse sections of such sponges appear as several concentric circular walls arranged one inside the other. Outer annulation of skeletons, which generally reflects growth stages, does not consistently indicate internal segmentation.

Single-chambered sphinctozoans are very rare, but have been reported from the Cambrian of Australia (*Nucha* PICKETT & JELL, 1983; *Blastulospongia* PICKETT & JELL, 1983; *Jawonya* KRUSE, 1983; *Wagima* KRUSE,

1987; and later only from the Upper Triassic of Vancouver Island, Canada, as the species *Nucha? vancouverensis* STANLEY, 1998).

### Sponge Shape

Those multichambered sphinctozoan sponges with a constant chamber diameter are usually cylindrical in shape (Fig. 219.3–219.7). Club-shaped skeletons occur in some taxa (e.g., the Permian species *Lemonea conica* SENOWBARI-DARYAN, 1990, or *Senowbaridaryana conica*, Fig. 217, Fig. 220), where the sponge or chamber diameters increase during sponge growth. Representatives of sheetlike or flattened forms also occur with hemispherical chambers arranged in one layer (e.g., the Permian genus *Neogualupia* ZHANG, 1987) or two layers (e.g., *Platythalmiella* SENOWBARI-DARYAN & RIGBY, 1988), or occur with tubelike chambers (e.g., the Permian genus *Subascosymplegma* DENG, 1981) (Fig. 219.10, Fig. 221). Aggregate forms composed of clusters of chambers (e.g., Permian *Exaulipora* RIGBY, SENOWBARI-DARYAN, & LIU, 1998; see Fig. 219.8, Fig. 222), or irregularly shaped sphinctozoans (e.g., *?Polysiphonaria* FINKS, 1997) occur also in Permian and Triassic deposits. Sphinctozoans are usually single, unbranched stems. Dichotomously branched taxa (e.g., *Nevadathalamia ramosa* SENOWBARI-DARYAN & REID, 1987) or rejuvenated skeletons are rare (e.g., *Panormida priscae* SENOWBARI-DARYAN, 1980b; Fig. 223). Marginal displacements of chamber walls have been observed, for example, in the Triassic species *Vesicocaulis reticuliformis* JABLONSKY, 1972 (SENOWBARI-DARYAN, 1990).

### Shape of Chambers

Spherical to hemispherical chambers are the most common shapes in sphinctozoan sponges, as, for example, in some species of *Colospongia* or *Sollasia* (Fig. 224–225). Other chambers may be barrel shaped, as in some species of *Amblysiphonella*, or crescentlike, as in *Cryptocoelia* (Fig. 226) or *Zardinia* (Fig. 218). Chambers that are flattened rectangular (*Enoplocoelia*, *Tolminothalamia*),

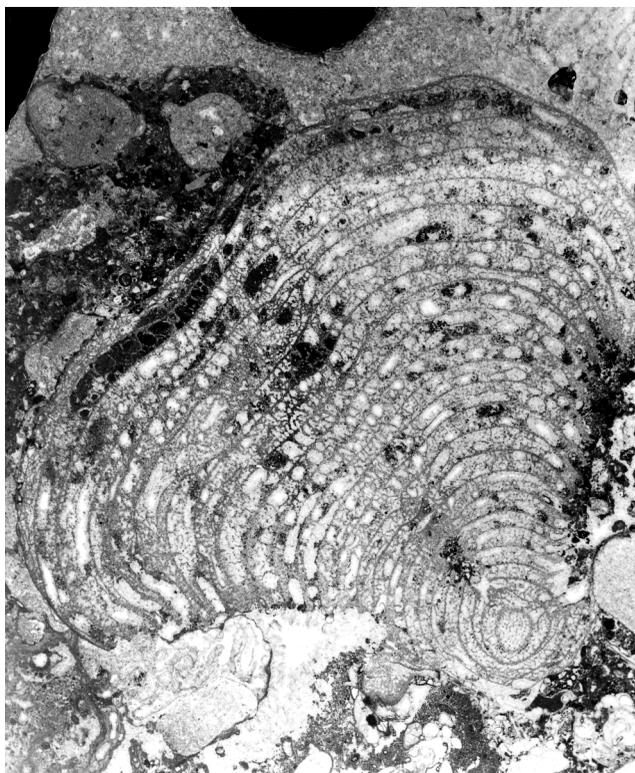


FIG. 217. *Senowbaridaryana conica* (SENOWBARI-DARYAN & SCHÄFER, 1986). Marginal axial section through the conical sponge. Diameters of crescentlike chambers increase rapidly during growth of the sponge. The chamber interiors contain small tubes that are more or less parallel to the axis of the sponge; Norian, Triassic, Sicily,  $\times 3$  (Senowbari-Daryan & Schäfer, 1986).

funnel shaped (*Panormida*, Fig. 223) or tubelike (*Cinnabaria* or *Subascosymplegma*, Fig. 221) occur also in other chambered sponges.

#### Arrangement of Chambers

The arrangement of chambers in multi-branched sphinctozoans may be moniliform. In asiphonate species, hemispherical to subspherical chambers are arranged one above the other, as, for example, in the porate genus *Colospongia* (Fig. 224) or the aporate genus *Sollasia* (Fig. 225). Chamber arrangement may be catenulate, where ringlike chambers are stacked one above the other in siphonate species, as in the porate genera *Amblysiphonella* (Fig. 227) and *Polytholusia* or in the aporate genus *Girtyocoelia* (Fig. 228). Occurrences of

several egg-shaped or cystlike chambers, arranged in one or more glomerate layers (like kernels of an ear of corn) around a spongocoel, are known from chambered sponges with either aragonitic or Mg-calcitic skeletons (Fig. 219.5–219.6, Fig. 220, Fig. 229–230). A glomerate arrangement of the chambers was developed very early in calcitic chambered sponges, in the Cambrian chambered archaeocyath genus *Polythalamia* DEBRENNE & WOOD (1990; see also FINKS & RIGBY, 2004d, p. 695, fig. 459, 2a–c; and see also Fig. 82.3) and as well in the Silurian genera *Palaeoscheda* MYAGKOVA (1955a) and *Aphrosalpinx* MYAGKOVA (1955b; see RIGBY, NITECKI, & others, 1994). Arrangement of cystlike chambers in one or more layers around the spongocoel occurs also in Carboniferous



FIG. 218. *Zardinia cylindrica* SENOWBARI-DARYAN & SCHÄFER, 1983. Longitudinal section of sponge, with Mg-calcite mineralogy, exhibiting a retrosiphonate type of spongocoel and crescentlike chambers; because of overlap of older chambers by younger ones, the exowalls are thicker than interwalls and endowalls; *Z. cylindrica*, like other species of the genus, is characterized by tubular canals that diverge upward and outward through internal filling skeleton and chamber walls, to open in exterior of sponge; Carnian, Triassic, Hydra, Greece,  $\times 3$  (Senowbari-Daryan & Schäfer, 1983).

and Permian taxa and again, once more, in Norian forms. For example, the Carboniferous and Permian genus *Discosiphonella* INAI, 1936, is characterized by one layer of cystlike chambers around the spongocoel, and the contemporaneous *Cystothalamia* GIRTY (1908a) or *Diecithalamia* SENOWBARI-DARYAN (1990; Fig. 229) by more layers of chambers around the spongocoel (GARICÍA-BELLIDO, SENOWBARI-DARYAN, & RIGBY, 2004). *Discosiphonella*, as an example of a so-called Lazarus fauna (JABLONSKI,

1986), is not known from the Lower and Middle Triassic but appears again in the Norian Upper Triassic (SENOWBARI-DARYAN & LINK, 1998). The Ladinian–Carnian, Mg-calcitic sphinctozoan genus *Alpinothalamia* SENOWBARI-DARYAN, 1990 (Fig. 230) is also characterized by chambers that are arranged in more than one layer around the spongocoel. Glomerate arrangement of the cystlike chambers around the spongocoel occurs also in the Jurassic calcarean genus *Thalamopora* (ROEMER, 1840).

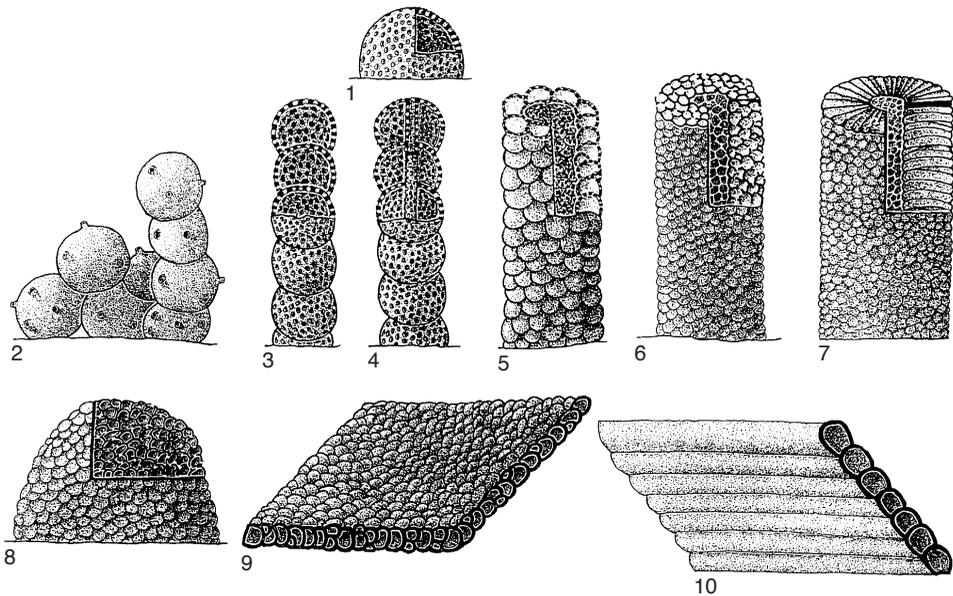


FIG. 219. Main growth shapes of sphinctozoan sponges. 1, Single chambered (e.g., the heteractind genus *Blastospongia* PICKETT & JELL); 2, moniliform (e.g., *Celyphia* POMEL); 3, moniliform (e.g., *Colospongia* LAUBE); 4, catenulate (e.g., *Amblysiphonella* STEINMANN); 5, monoglomerate (e.g., *Discosiphonella* INAI); 6, polyglomerate (e.g., *Cystothalamia* GIRTY); 7, stratiform (e.g., *Lemonea* SENOWBARI-DARYAN); 8, uviform (e.g., *Uvanella* OTT); 9, platyform, stratiform (e.g., *Neogadalupeia* ZHANG); and 10, platyform, tubular (e.g., *Subascosymplegma* DENG) (adapted from Senowbari-Daryan, 1990).

### Inhalant Canals or Ostia in Exowalls and Their Patterns

Two kinds of inhalant canal systems are recognized in sphinctozoan sponges, based on their sizes and their distribution patterns in the exowall. These systems were termed porate and aporate by SEILACHER (1962). The porate type is characterized by small openings, termed pores (or exopores), that are usually less than 1 mm in diameter and are evenly distributed in the external wall. The numbers of such pores may reach 100 or more in a single chamber. These pores may have circular or oval cross sections. In some genera, such as in the Triassic genus *Nevadathalamia* or the Recent *Vaceletia*, spinelike elements may extend into the interior of the pores. Most pores, however, are simple, though dichotomously branched, multibranched, and labyrinthic-branched pore systems occur in some genera (Fig. 231).

The Permian species *Follicatena permica* SENOWBARI-DARYAN, 1990 (Fig. 232), which has a chamber construction like that of *Colospongia*, has chamber walls with screenlike cribribulla, each with numerous small openings termed cribripores (bullipores). Pores combined with ostia, sometimes termed ostial pores (as in the Upper Triassic species *Colospongia dubia* LAUBE, see SENOWBARI-DARYAN, 1990, pl. 40, 8–9; FINKS & RIGBY, 2004d, fig. 462, 2a), or pores combined with cribribulla with cribripores (as in the Upper Triassic species *Colospongia wahleni* SENOWBARI-DARYAN & STANLEY, 1988), are known from exceptional examples.

Aporate sphinctozoans are characterized by chamber walls with large openings, termed ostia, which are usually larger than 1 mm in diameter, and usually fewer than 10 ostia occur per chamber. The ostia may be depressed or have elevated rims, or even have rims that are extended, tubelike, as, for example, in *Girtyocoelia* (Fig. 228). The

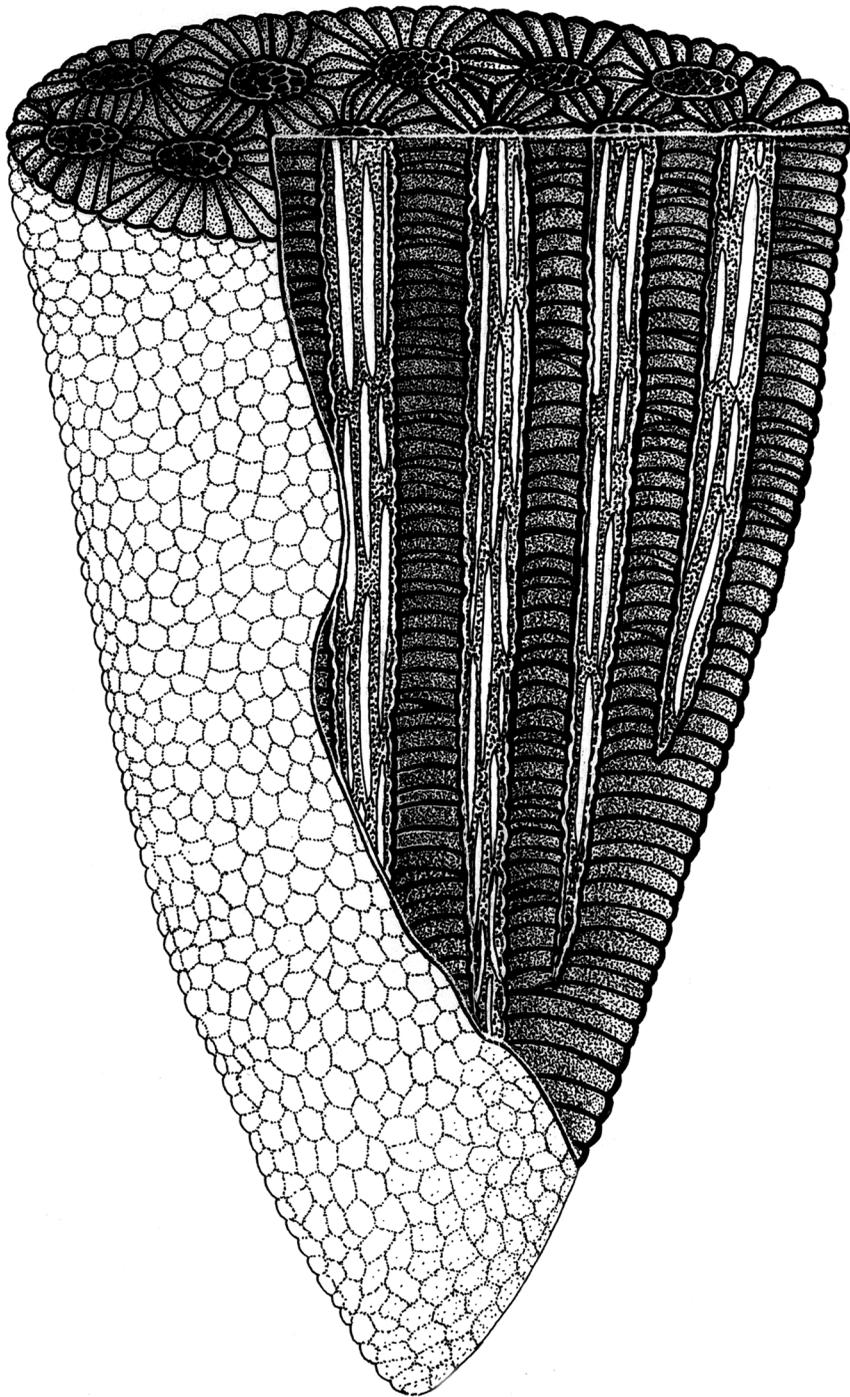


FIG. 220. Reconstruction of *Lemonea conica* SENOWBARI-DARYAN showing the conical shape of the sponge, bundles of spongocoels, and the stratiform chambers arranged radially around the spongocoels; chamber walls are perforated, but the pores are not shown; schematic, not to scale (Senowbari-Daryan, 1990).

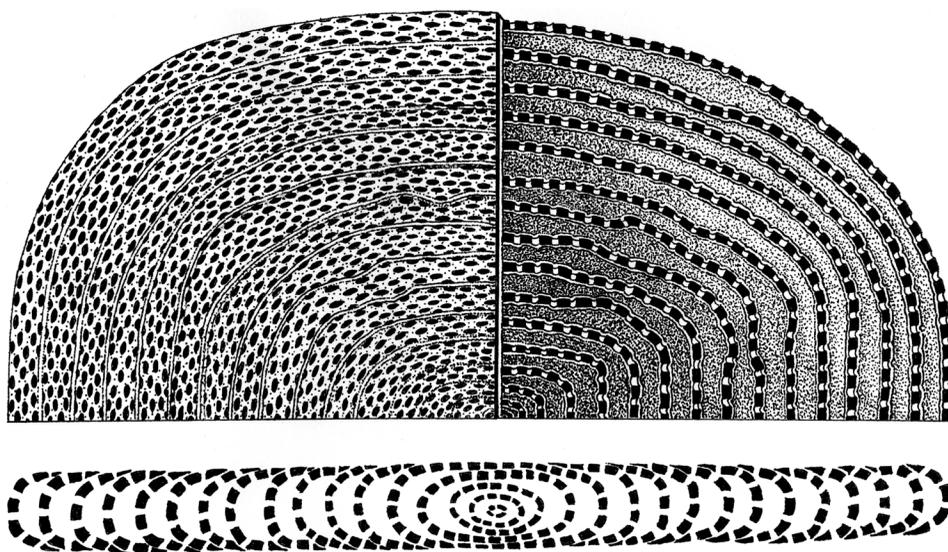


FIG. 221. Reconstruction of *Subascosymplegma oussifensis* (TERMIER & TERMIER, 1977b). The sheetlike or hemispherical sponge is composed of arcuate, tubelike chambers, and the younger chambers overlap preceding chambers; upper Permian, Djebel Tebaga, Tunisia; schematic, not to scale (Senowbari-Daryan & Rigby, 1988).

latter openings are called exaulos (sing., exaulos). The exaulos tube may be perforated with exaulos pores, as, for example, in the Permian genus *Exaulipora* RIGBY, SENOWBARI-DARYAN, & LIU, 1988 (Fig. 222), or it may be aporate, as in *Girtyocoelia* (Fig. 228). The inner end of some exaulos in aporate forms may have screenlike cribribulla, like those in some of the porate sphinctozoans, such as in *Exaulipora* (Fig. 222).

#### Exhalant Canals or Oscula

The tops of some siphonate sphinctozoan sponges, like *Amblysiphonella*, may have a single large opening, an osculum, or several openings, or oscula, grouped as canal bundles and commonly located axially. Such axial canal bundles may occupy more than 70% of the whole sponge diameter, as, for example, in the Triassic species *Diecithalamia polysiphonata* DIECI, ANTONACCI, & ZARDINI, 1968 (Fig. 229). Where a retrosiphonate axial tube or spongocoel is formed by downward extension of upper chamber walls (Fig. 233), the diameter of the osculum commonly appears larger than the diameter of the spongocoel. In

most other types of constructions (Fig. 233), the diameter of the osculum corresponds to the diameter of the spongocoel.

The spongocoel wall (endowall) may have pores or openings of the same size as those in the exowalls or interwalls, but they also may be different (Fig. 227–228). Several individual spongocoels may be present in large, laterally extended sphinctozoan sponges, as in the Triassic species *Cryptocoelia lata* SENOWBARI-DARYAN & SCHÄFER, 1983 (Fig. 234), or separate spongocoel bundles may be developed, as in the Permian species *Lemonea conica* SENOWBARI-DARYAN, 1990 (Fig. 220). In the Triassic *Zanklithalamia multisiphonata* SENOWBARI-DARYAN, 1990, such bundles may pass through the whole sponge body.

Starlike exhalant canal openings, an astrorhizal system, may be developed in a variety of stromatoporoid and inozoan sponges, and have been observed in a few genera of sphinctozoan sponges. In the Ordovician genus *Cliefdenella* WEBBY, 1969, or in the Triassic genus *Tabasia* SENOWBARI-DARYAN, 2005a, exhalant canals end in a starlike astrorhizal system (see WEBBY, 1969, 1979a,

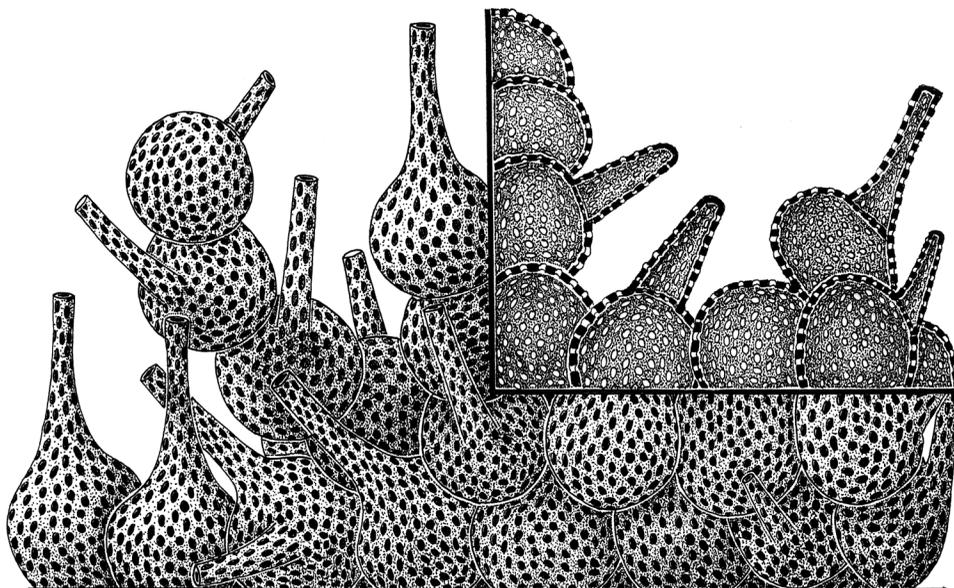


FIG. 222. Reconstruction of *Exaulipora permica* (SENOWBARI-DARYAN), Permian, Guadalupe Mountains, Texas and New Mexico, United States, showing perforated exaulos walls and the cribribulla with cribripores at the base of the exaulos; vesiculae occur within the interior of the segment, but they are not shown (Senowbari-Daryan, 1990).

1986; STOCK, 1981; WEBBY & LIN, 1988). In the Permian sheetlike or funnel-shaped species *Guadalupia explanata* (KING, 1943), one side of the sheets commonly has several astrorhizal canals that served as exhalant canals (Fig. 235).

#### INTERNAL MORPHOLOGY

Internal morphologic elements are characteristic features that can be observed after cutting the skeleton. These features include the internal segmentation and chamber shape, internal walls (interwalls and endowalls) and their characteristics, such as whether they are double or single layered, their thickness, and patterns of perforation. Also included are spongocoels and their formation type, and the types of filling skeletons within chamber interiors.

##### Internal Segmentation

The internal segmentation, a most important feature of sphinctozoan sponges, usually corresponds to outer segmentation.

However, a few taxa, especially those with crescentlike chamber shapes (Fig. 216, Fig. 218), have distinct internal segmentation (see also *Cassianothalamia* REITNER, 1987b; *Uvothalamia* SENOWBARI-DARYAN, 1990), but their outer segmentation is poorly developed, or even totally lacking.

Interwalls, the walls between chambers, may have the same thickness as exowalls of the same chambers, but they also may be different. Perforation patterns of interwalls usually correspond to those of the exowalls, but they also may be different in some taxa, as in some species of *Amblysiphonella* or in *Girtyocoelia* (Fig. 227–228).

##### Internal Canal System

There are three types of exhalant canal systems in sphinctozoan sponges. These were called the *Colospongia*-type, *Sphaerocelesia*-type, and *Amblysiphonella*-type by SENOWBARI-DARYAN (1990) (Fig. 236). The *Colospongia*-type (Fig. 224, Fig. 236.3) system is without a separate siphon or spongocoel and was called asiphonate by SEILACHER (1962). It is assumed

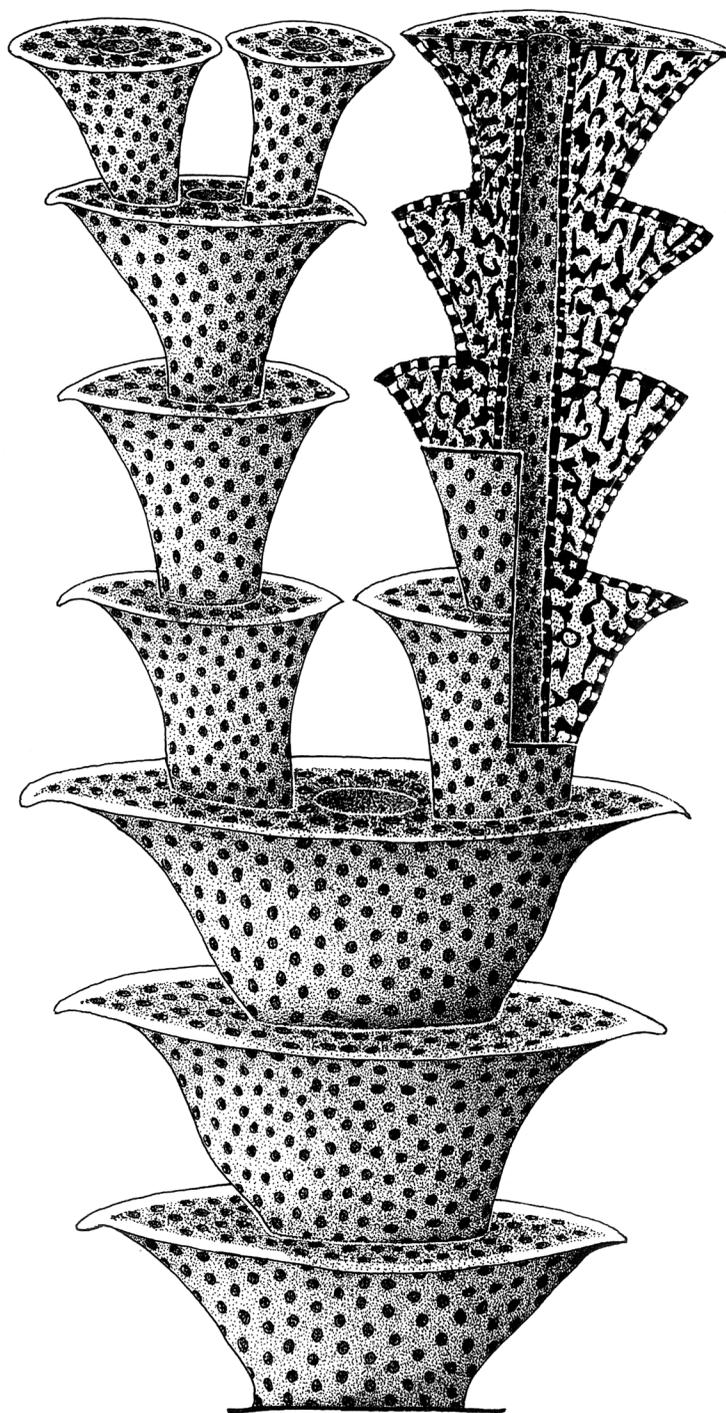


FIG. 223. Reconstruction of *Panormida priscae* SENOWBARI-DARYAN. The porate and siphonate sponge is characterized by funnel-shaped chambers and rejuvenescence; chamber interiors are filled with reticular filling structure; Norian, Triassic, Sicily; schematic, not to scale (Senowbari-Daryan, 1990).



FIG. 224. *Colospongia catenulata* OTT, 1967. Longitudinal section through five spherical-hemispherical chambers arranged in a moniliform series, one above another; chamber walls are pierced by uniform, equal-sized, and evenly distributed pores; chamber interiors contain some vesiculae; Ladinian–Carnian, Triassic, Wetterstein Limestone, Austria,  $\times 5$  (Senowbari-Daryan & Rigby, 2011).

that pores in the exowalls (exopores) served as the inhalant canal system, and that pores at the top of chambers (interpores) served as exhalant openings. In the *Sphaero-coelia*-type, each chamber top is pierced by a single large pore or osculum that served as the exhalant opening (Fig. 225, Fig. 236.2). This system was called cryptosiphonate by SEILACHER (1962). The siphonate *Amblysiphonella*-type (Fig. 227, Fig. 236.1) system is characterized by development of a true spongocoel, separated from the chamber by its own wall (endowall). The exhalant system types of SEILACHER (1962), thus, are largely characterized by the type of spongocoel formation. In retrosiphonate sponges, the chamber roofs are curved downward, growing until they merge with roofs of preceding chambers, as, for example, in *Amblysiphonella* (Fig. 233.4). In ambisiphonate sponges, chamber roofs

grew upward and arched horizontally toward the osculum. That system is recognizable by a large pore in the middle of the endowall, as, for example, in *Barroisia* (Fig. 233.5). Pro-siphonate sponges are characterized by upward growth of chamber roofs, as, for example, in *Girtyocoelia* (Fig. 233.6). It should be mentioned that recognition of the spongocoel type is not always easy, sometimes it is virtually impossible.

Thicknesses and perforation patterns of the spongocoel wall (endowall) may be the same as, or different from, those of the interwalls or exowalls (Fig. 227–228).

In some taxa, as in the Triassic species *Zardinia cylindrica* SENOWBARI-DARYAN, 1990, for example, numerous additional inhalant canals converge inward through the internal filling structure and chamber walls from the outside of the sponge, and coarser exhalant canals open into the spongocoel through the inner part of the wall (Fig. 218). Some of the inhalant canals have small convergent branches near the dermal surface.

### Filling Skeleton

Chamber interiors of some sphinctozoan sponges lack any internal structures, but many others have skeletal elements within chambers formed while the chambers were functional parts of the biologic activity of the sponges. These special kinds of skeletal elements are called filling skeletons or filling structures. Six types of filling skeletons have been recognized in chambered sphinctozoan sponges, including: reticular, trabecular, tubular, septate, sporelike, and pisolitic skeletons (Fig. 237). A combination of two filling skeletons (septate + reticular) is an exceptional case and has been reported only in the Triassic genus *Ceotinella* PANTIC, 1975 (Fig. 237). Vesiculae may occur with (*Cryptocoelia*) or without (*Colospongia*, *Sollasia*) other internal structures within the same sponge (SENOWBARI-DARYAN, 1990). Vesiculae are not considered here to be elements of a filling skeleton, because they sealed off older chambers or parts of chambers and pores that were no longer occupied or used

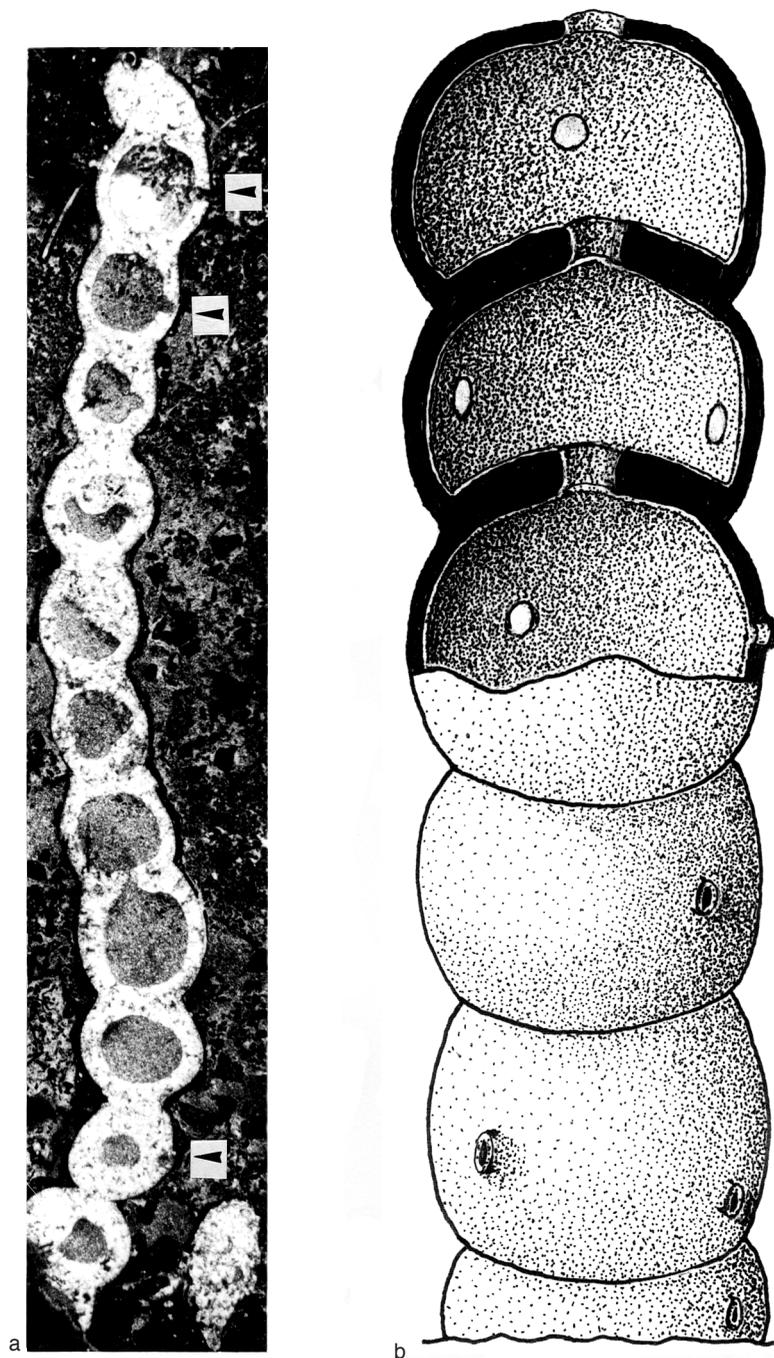


FIG. 225. *Sollaia ostiolata* STEINMANN, 1882, an abundant and cosmopolitan sphinctozoan sponge in Carboniferous and Permian deposits; *a*, longitudinal section cuts through numerous moniliform cryptosiphonate chambers with thick, aporate chamber walls; *arrows* indicate large openings (ostia) in few chambers cut by the section; lower Permian, Sosio valley, Sicily,  $\times 4.6$  (adapted from Senowbari-Daryan & Di Stefano, 1988a); *b*, reconstruction showing large opening in the roofs of the chambers and weakly rimmed ostia in the exowalls (adapted from Senowbari-Daryan, 1990).

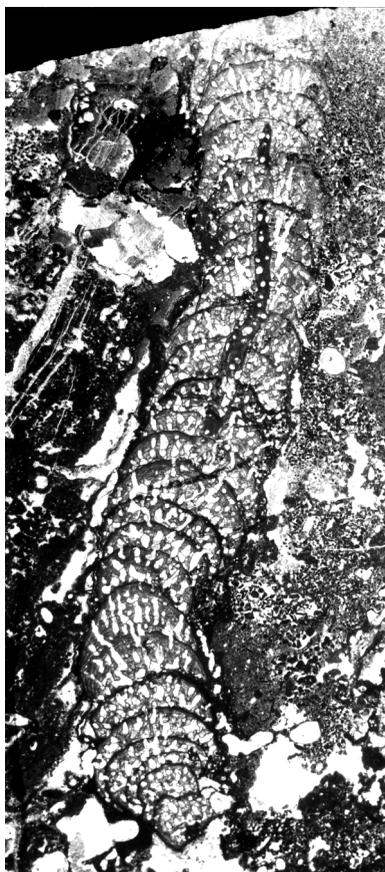


FIG. 226. *Cryptocoelia zitteli* STEINMANN, 1882, an abundant sponge within the Ladinian–Carnian reefs in the western Tethys. Longitudinal section through the sponge shows numerous crescentlike chambers in a moniliform arrangement; spongocoel is cut in upper part of the sponge; chamber interiors are filled with trabecular (pillarlike) filling skeleton showing distinct lamination (see Fig. 234); Carnian, Triassic, Slovenia,  $\times 3.3$  (Senowbari-Daryan, 1981).

by the sponge. Vesiculae, their secretion processes in several stages, and the sealing of pores by vesiculae are shown in Figure 238, in the Triassic genus *Jablonskyia* SENOWBARI-DARYAN, 1990.

A filling skeleton has not been reported from Cambrian sphinctozoans. Cambrian segmented sponges with different filling skeletons, described in the literature as archaeocyaths, are not considered in this section. Most Ordovician representatives of

sphinctozoans also lack a filling skeleton. The oldest type of internal filling skeleton seems to be the tubular type, where tubes extend into the chamber interiors from exopores of the exowall in the Ordovician species *Amblysiphonelloides tubulara* RIGBY & POTTER, 1986, from the Klamath Mountains, northern California. Similar tubes may also occur in *Girtyocoelia canna*, described by the same authors from the same locality. The large, coarse, pillar-like vertical tubes in *Cliefdenella* WEBBY, 1969, extend through several flattened low chambers and with the small vertical tubes that pierce only a few layers serving as exhalant tubes. They provide good examples of fine and coarse exhalant structures in the basic water vascular system and are not classified as filling structures. They are totally different from the tubular elements that are more or less horizontal, running perpendicular to the sponge axis in *Amblysiphonelloides* RIGBY & POTTER, 1986 (see WEBBY, 1969; WEBBY & MORRIS, 1976; RIGBY & POTTER, 1986). Later tubular filling skeleton elements occur in several genera, in the Permian genus *Pseudoamblysiphonella* SENOWBARI-DARYAN & RIGBY, 1988, and in the Triassic genus *Polytholusia* RAUFF, 1938. Tubular filling skeletons are not known from Jurassic and younger sphinctozoans.

Trabecular (pillar-like) filling skeletons (Fig. 237, Fig. 239) appear first in the Silurian genus *Rigbyspongia* DE FREITAS, 1987, from Cornwallis Island, Canadian Arctic. This type of filling skeleton is common in Permian to Triassic sphinctozoans, as well as in Cretaceous–Paleogene/Neogene representatives, and in the modern *Vaceletia crypta* (VACELET, 1977b; PICKETT, 1982).

Reticular filling skeletons (Fig. 237, Fig. 240) seem to have developed originally in the Ordovician species *Amblysiphonella reticulata* RIGBY & POTTER (1986), but are well known in the Middle Devonian genus *Hormospongia*, described by RIGBY and BLODGETT (1983) from central Alaska. This type of filling skeleton is common in Permian and Triassic representatives, but in the post-Triassic record it is known only



FIG. 227. *Amblysiphonella* sp. Marginal axial section exhibiting hemispherical chambers with perforated exowalls; interwalls are aporate and double layered; endowall is thinner than the exo- and interwalls and is pierced by large and unevenly distributed openings; Norian–Rhaetian, Triassic, Nayband Formation, Iran,  $\times 4$  (Senowbari-Daryan & Rigby, 2011).

from the Jurassic calcarean genus *Muellerithalamia* REITNER, 1987b.

Sporelike filling skeletons (Fig. 237) are not common and, until now, have been described only from Permian examples, such as *Intrasporeocoelia* (FAN & ZHANG, 1985; RIGBY, FAN, & ZHANG, 1988), and from the Triassic genus *Delijania* SENOWBARI-DARYAN, 2005a.

A pisolitic-like filling skeleton (Fig. 237) is only known from the genus *Pisothalamia*, described from the upper Permian of southern Tunisia by SENOWBARI-DARYAN and RIGBY (1988).

Septate-type filling skeletons (Fig. 237) occur in the Devonian genus *Radiothalamos* PICKETT & RIGBY, 1983, and in the Triassic genus *Phragmocoelia* OTT, 1974.

Two kinds of filling skeleton do not normally occur within the same sponge. The Triassic genus *Ceotinella* PANTIC (1975), however, is exceptional, for in that genus peripheral septate and axially reticular filling skeletons (Fig. 237) occur in the same sponge chambers.

It should be mentioned that internal filling skeletons are more common in porate than in aporate representatives of sphinctozoans.

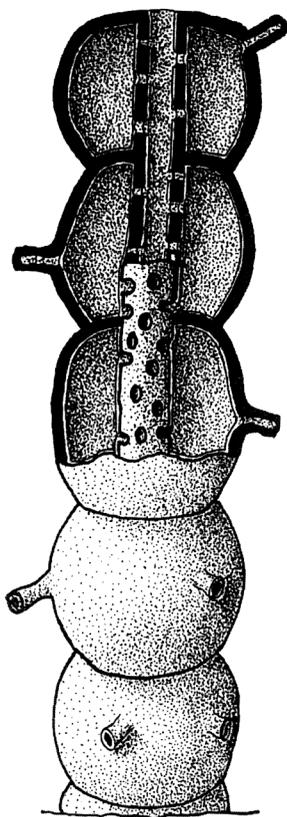


FIG. 228. Reconstruction of *Girtyocoelia beedei* (GIRTY, 1908b) showing unevenly perforated endowall of the spongocoel, and aporate exowalls with sporadic ostia with tubular exaulos; similar to *Sollasia*, *Girtyocoelia* is also an abundant and cosmopolitan sponge in Carboniferous and Permian deposits; schematic, not to scale (adapted from Senowbari-Daryan, 1990).

This is probably related to the lesser skeletal resistance of the porate construction, caused by perforation of the chamber walls. It was probably a benefit for these sponges to stabilize their skeletons by secreting the internal filling structure.

### Spicules

The only living sponge with sphinctozoan construction, *Vaceletia* (VACELET, 1977b), does not have a spicular skeleton. Fossil sphinctozoan sponges commonly lack spicules, possibly because they were not preserved, or they were initially rare.

There are no reports of occurrences of spicules in sphinctozoan archaeocyaths. However, REITNER (1991b, 1992) reported spicules in close proximity to the nonchambered coscinocyathid and other archaeocyaths in lower Cambrian reefs of South Australia, suggesting the spicules were either entrapped during secondary skeletal-forming processes of the archaeocyaths, or secreted from within their primary skeletons. DEBRENNE and ZHURAVLEV (1992b), however, considered it more likely that the spicules, like certain trilobite fragments, were entirely incorporated in archaeocyathan secondary skeletons from debris that lay close by on the sea floor. Indeed, none had a primary skeletal origin, as confirmed by DEBRENNE, ZHURAVLEV, and KRUSE's more general statement that "no undoubted spicules have been recorded from the primary skeleton of archaeocyaths" (see p. 885). Polyactines have been reported in the single-chambered Cambrian sphinctozoan heteractinid sponge *Jawonia* (KRUSE, 1987; DEBRENNE & WOOD, 1990; REITNER, 1992; PICKETT, 2002). Sphinctozoan hexactinellid sponges have chambered skeletons composed of hexactine spicules arranged in a latticelike structure, as shown in an Upper Triassic Iranian species of *Casearia* (Fig. 241). Sphinctozoan construction with both spicular and rigid skeletons is not known in the hexactinellids. Lithistid demosponges with skeletons composed of tetractine spicules arranged in a lattice-like structure, without a rigid skeleton, are known only in the Upper Triassic genus *Radiocella* (SENOWBARI-DARYAN & WÜRME, 1994) from the Alps.

In so-called classic sphinctozoan sponges, *sensu* STEINMANN (1882), spicules have been reported from only a few upper Paleozoic and Triassic representatives. Monaxon siliceous spicules, replaced by calcite, pyrite, or other minerals, were reported from some Permian forms, including *Pisothalamia spiculata* SENOWBARI-DARYAN & RIGBY, 1988, and *Subascosymplesma oussifensis* (TERMIER & TERMIER, 1977b), and from some Triassic genera with aragonitic skeletal microstruc-

ture, such as in *Colospongia* LAUBE, 1865, *Celyphia* POMEL, 1872, *Thaumastocoelia* STEINMANN, 1882, or with Mg-calcitic skeletal mineralogy, as in *Cassianothalamia* REITNER, 1987b (SENOWBARI-DARYAN, 1989, 1990, 1991; SENOWBARI-DARYAN & GARCÍA-BELLIDO, 2002a; SENOWBARI-DARYAN & RIGBY, 1988; REITNER, 1987c, 1990, 1992). The spicular skeletons of all these taxa are composed of monactine macroscleres (Fig. 242). Possible microscleres are known only from the Carnian species *Cassianothalamia zardini* REITNER, 1987b, which has a Mg-calcitic rigid skeleton (REITNER, 1987c, 1990). However, ENGESER and APPOLD (1988) did not find microscleres in *Cassianothalamia*. The identification of some cavities within the pillar-filling structures as spicules in some Mesozoic sphinctozoan sponges (*Murguiathalamia* REITNER & ENGESER, 1985, or *Vascothalamia* REITNER & ENGESER, 1985) by REITNER and ENGESER (1985) and REITNER (1990, 1992) seems to be a misinterpretation, as discussed in detail by SENOWBARI-DARYAN (1990, p. 23). Calcitic triactine spicules have been found in several Jurassic and Cretaceous genera: in *Barroisia* MUNIER-CHALMAS, 1882 (QUENSTEDT 1858; SEILACHER, 1962; SENOWBARI-DARYAN & ABATE, 1996; SENOWBARI-DARYAN & GARCÍA-BELLIDO, 2002a); *Sphaeroceelia* STEINMANN, 1882; and *Muellerithalamia* REITNER, 1987c (REID, 1967, 1968; DEBRENNE & LAFUSTE, 1972; SENOWBARI-DARYAN, 1989, 1990; REITNER, 1990, 1992). The different basic spicules present in skeletons of hypercalcified sphinctozoan sponges indicate the polyphyletic nature of this group.

#### Mineralogy and Microstructure of the Rigid Skeleton

Because of strong recrystallization, the original mineralogy of the rigid skeleton of early Paleozoic sphinctozoans is not known (RIGBY & POTTER, 1986). However, the granular microstructure of those Silurian chambered sponges, described as archaeocyaths by previous authors and redescribed by RIGBY, NITECKI, and others (1994) as



FIG. 229. *Diecithalamia polysiphonata* (DIECI, ANTONACCI, & ZARDINI, 1968). The longitudinal section exhibits cystlike chambers arranged in two or more layers (polyglomerate) around an axial spongocoel that is composed of several individual tubes; Carnian, Triassic, Hydra, Greece,  $\times 3$  (Senowbari-Daryan & Rigby, 2011).

sphinctozoans, strongly suggests an original skeletal mineralogy of high-Mg calcite. The similarities of mineralogy and microstructure of sphinctozoan sponges and archaeocyaths were discussed by KRUSE and DEBRENNE (1989) and ZHURAVLEV (1989). The skeletal mineralogy of representatives of these sponges is not discussed in detail in this section.

The primary skeletal mineralogy (now aragonite or neomorphic calcite) of the majority of upper Paleozoic and Mesozoic sphinctozoans was aragonite, like in the Recent *Vaceletia* (VEIZER & WENDT, 1976; WENDT, 1977, 1978, 1979, 1984, 1990; GAUTRET, 1985; SENOWBARI-DARYAN, 1990). Sphinctozoans with Mg-calcitic mineralogy (up to 11 Mol%  $\text{MgCO}_3$ ; RUSSO & others, 1991) appeared in the Middle Triassic (Anisian), became abundant in the Ladinian and Carnian (*Alpinothalamia* SENOWBARI-DARYAN, 1990;



FIG. 230. *Alpinothalamia bavarica* (OTT, 1967), a porate-aporate sponge, with Mg-calcite skeletal mineralogy, composed of numerous cystlike chambers arranged in two or more layers around an axial spongocoel that has a thick endowall; Carnian, Triassic, Sicily,  $\times 1.5$  (Senowbari-Daryan & Abate, 1986).

*Cassianothalamia* REITNER, 1987b; *Stylothalamia* OTT, 1967), and became extinct at the end of the Triassic. However, the only documented sphinctozoan sponge that survived beyond the Triassic–Jurassic boundary, *Stylothalamia columnaris* (LE MAITRE, 1935), is known from several localities (see SENOWBARI-DARYAN & HAMEDANI, 1999). The high-Mg calcite of its skeleton is not proven, and the skeletal preservation suggests that the primary skeletal mineralogy of this sponge seems to have been aragonite. Both aragonitic and high-Mg-calcitic mineralogy of the rigid

skeleton also occurs in Jurassic–Cretaceous sphinctozoan sponges, some of which were described as hydrozoans (e.g., *Actinostromaria* CHALMAS in DEHORNE, 1920; this genus is now considered to be an agelasid demosponge of stromatoporoid type; see the introduction to post-Devonian hypercalcified demosponges, p. 201 and 206).

The processes of biomineralization in hypercalcified sponges in general were discussed by SIMKISS (1986), and STEARN and PICKETT (1994), and of sphinctozoans and inozoans in particular, by GAUTRET (1985), GAUTRET and CUIF (1989), CUIF and GAUTRET (1991), WENDT (1979, 1990), FINKS (1990), and REITNER and others (1997). Figure 243 shows these processes of calcification in the Triassic genus *Jablonskyia* SENOWBARI-DARYAN, 1990; for a detailed description see SENOWBARI-DARYAN (1997).

The six principal types of microstructures known in sphinctozoan sponges include (Fig. 244): (1) spherulitic, (2) irregular, (3) orthogonal, (4) clinogonal, (5) lamellar, and (6) microgranular (DEBRENNE & LAFUSTE, 1972; CUIF, 1973, 1974, 1979; CUIF & others, 1979; CUIF & others, 1990; SENOWBARI-DARYAN, 1990, 1991; SENOWBARI-DARYAN & GARCÍA-BELLIDO, 2002a; WENDT, 1979, 1984, 1990).

The earliest known microstructure of sphinctozoan sponges seems to be of lamellar type, reported from the Ordovician genus *Angullongia* by WEBBY and RIGBY (1985) and RIGBY and POTTER (1986). WENDT (1984), in contrast to JONES (1979), concluded that lamellar microstructure was caused by a diagenetic process and was not developed as a primary structure in the sponges. However, the excellent aragonitic preservation of the rigid skeleton of *Celyphia submarginata* MÜNSTER, 1841 (Fig. 242), from the Cassian Formation (Dolomite, Italy), suggests that the lamellar microstructure in this sponge is primary (SENOWBARI-DARYAN, 1990, 1991; REITNER, 1992). Lamellar microstructure is also known from the other Triassic genus *Montanaroa* RUSSO (1981).

The spherulite type of microstructure in sphinctozoans is known from several

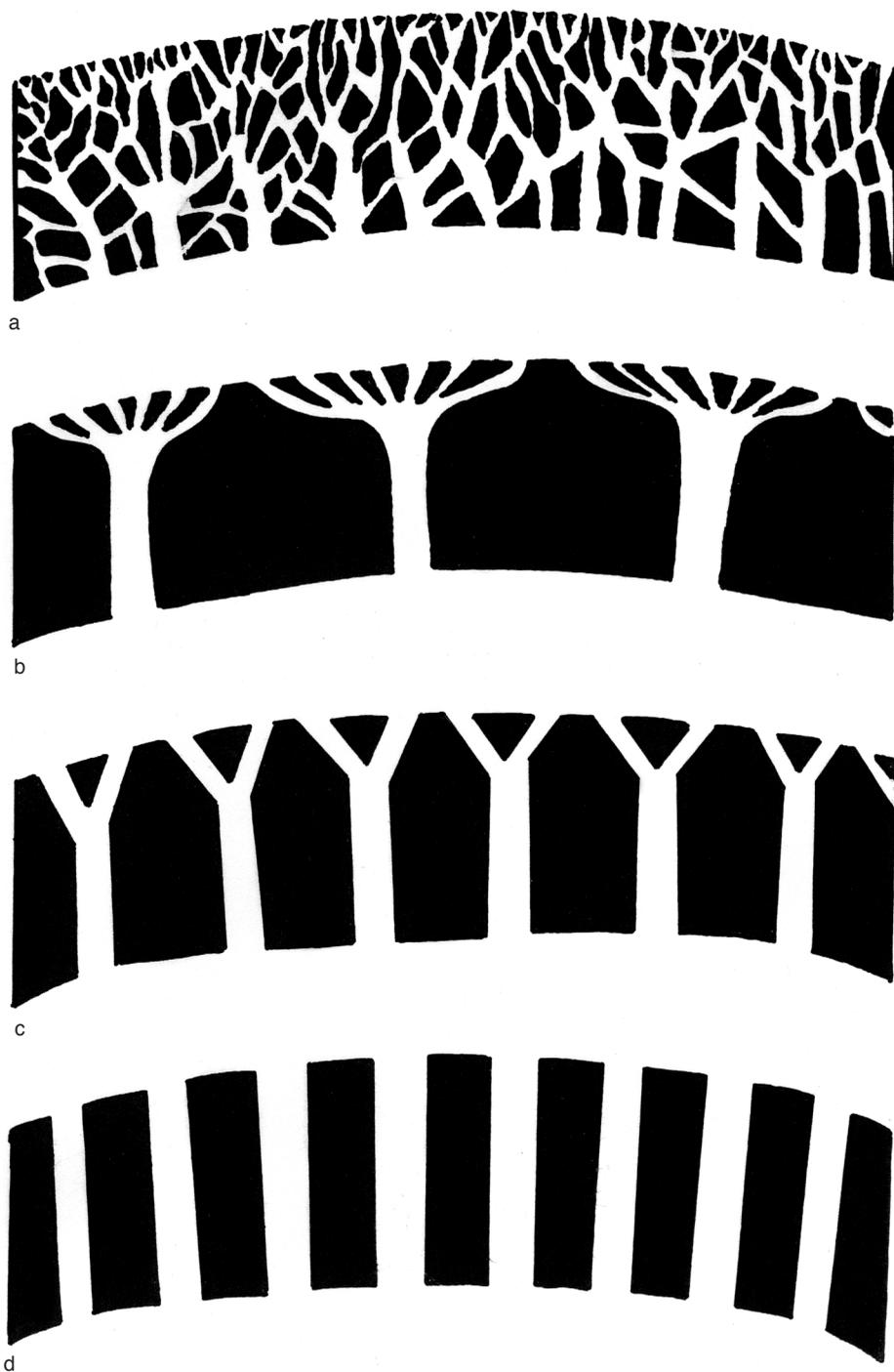


FIG. 231. Perforation pattern in porate sphinctozoans; *a*, labyrinthic branched pores, *b*, multibranching pores, *c*, dichotomously branched pores, and *d*, single pores; schematic, not to scale (Senowbari-Daryan, 1990).

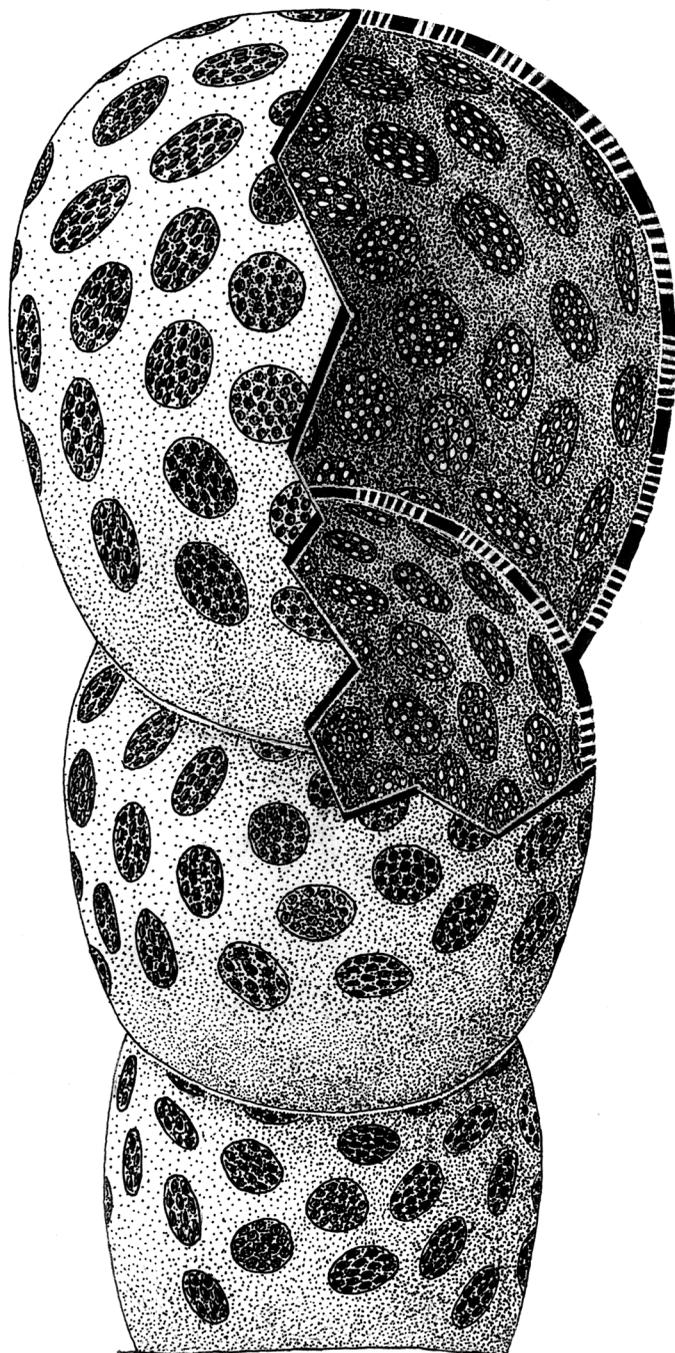


FIG. 232. Reconstruction of *Follicatena permica* SENOWBARI-DARYAN, 1990. The exowall and interwalls of this moniliform and *Colospongia*-like sponge contains numerous openings in the chamber walls of cribribulla with cribripores; cribribulla are not developed near bases of the chambers; species is known from the Permian of Sicily; schematic, not to scale (Senowbari-Daryan, 1990).

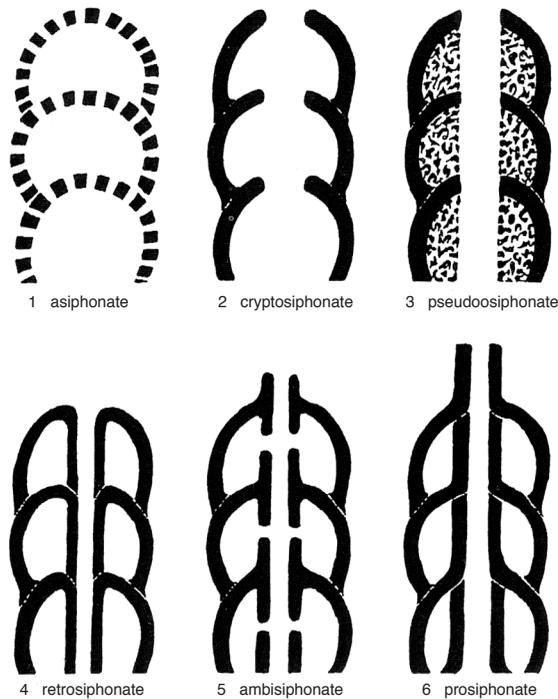


FIG. 233. Theoretical consideration of SEILACHER (1962) for the formation of canals in sphinctozoan sponges. 1, Asiphonate, *Colospongia*; 2, cryptosiphonate, *Sollasia*; 3, pseudosiphonate, *Senowbaridaryana*; 4, retrosiphonate, *Amblysiphonella*; 5, ambisiphonate, *Barroisia*; and 6, prosiphonate, *Girtyocoelia*. The recognition of retrosiphonate, ambisiphonate, and prosiphonate types is not always easy (adapted from Seilacher, 1962).

Carboniferous and Permian genera, such as *Sollasia* and *Girtyocoelia*. Spherulitic microstructure is the most common type in upper Paleozoic and Triassic sphinctozoans with an aragonitic skeletal mineralogy (GAUTRET, 1985; WENDT, 1990; MASTANDREA & RUSSO, 1995). These spherulites are of different sizes in various taxa.

Granular microstructure (irregular micritic, MÜLLER-WILLE & REITNER, 1993) is typical of sphinctozoan sponges with high-Mg-calcite mineralogy, such as the Triassic genera *Cassianothalamia* REITNER, 1987b, *Uvanella* OTT, 1967, or *Alpinothalamia* SENOWBARI-DARYAN, 1990. Granular microstructure is also developed in some Jurassic and Cretaceous chambered sponges, such as in *Boikothalamia convexa* (BOIKO, 1981), and other sponges described as hydrozoans in the literature

(the Upper Jurassic genus *Actinostromaria* CHALMAS in DEHORNE, 1920), although this genus is now regarded as an agelasid demosponge of stromatoporoid type (see p. 201, 206).

The aragonitic rigid skeleton of modern *Vaceletia* is composed of irregularly arranged needles of aragonite (GAUTRET, 1985; WENDT, 1990; CUIF & GAUTRET, 1991; WOOD, 1991b; MASTANDREA & RUSSO, 1995). Irregular microstructure is known also from some fossil representatives with aragonitic skeletal mineralogy, such as the Triassic genera *Colospongia* LAUBE, 1865, or *Solenomia* POMEL, 1872.

Clinogonal microstructure has been reported from the secondary (internal) layer of the skeletal wall in the Triassic species *Thaumastocoelia cassiana* STEINMANN, 1882 (see FINKS & RIGBY, 2004d, p. 664).

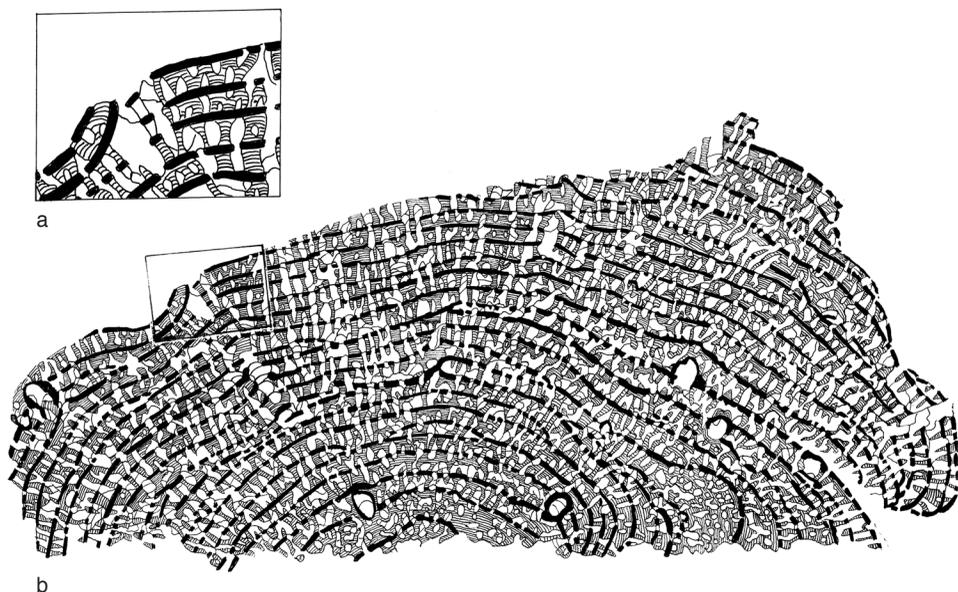


FIG. 234. *Cryptocoelia lata* SENOWBARI-DARYAN & SCHÄFER, 1983. Drawing of a longitudinal thin section exhibiting laterally extended chambers, numerous upward and outward radiating exhalant canals, and the lamellar structured trabecular (pillarlike) filling skeleton within the chamber interiors, as in *Cryptocoelia zitteli* STEINMANN, 1882; Carnian, Triassic, Hydra, Greece; a,  $\times 6$ , b,  $\times 3$  (Senowbari-Daryan & Schäfer, 1983).

#### PALEOBIOLOGY, PATTERNS OF WATER CIRCULATION, AND PALEOECOLOGY

In the living chambered sponge *Vaceletia*, only the last added, or youngest, chambers are occupied with living soft body (VACELET, 1979b). This is also true in some other hypercalcified sponges, such as *Ceratoporella* HICKSON, 1911, in which only about 1 mm is occupied by the soft body (HARTMAN & GOREAU, 1966, 1970), or in *Astrosclera willeyana* LISTER, 1900, in which only about 1 cm of the youngest part of the skeleton is occupied by the soft body (WÖRHEIDE & others, 1997). This suggests that in fossil chambered sponges, the living sponge body, perhaps, was also limited to the last chambers. This assumption is supported by observations of some internal skeletal structures. For example, vesiculae are interpreted as a type of secondary skeletal element that may occur more abundantly within older chambers. They may partially or entirely, internally, seal off the inhalant

pores of the exowalls (Fig. 238). In addition, other kinds of internal skeletal structures, which are interpreted as support organs of the skeleton, are commonly observed within the older chambers. The rigid exoskeleton (chamber walls) was probably covered by a thin organic membrane, like in modern *Vaceletia*.

As discussed above in the section on Internal Canal System (p. 330), there were principally three types of exhalant canal systems in sphinctozoan sponges (Fig. 236). These were termed *Colospongia*-type, *Sphaerocoelia*-type, and *Amblysiphonella*-type by SENOWBARI-DARYAN (1990). The *Colospongia*-type, called asiphonate by SEILACHER (1962), is without a separate spongocoel. Thus, it is assumed that the lateral pores of the exowalls served as inhalant canals. Water entered via these inhalant canals and then circulated through the small choanocyte chambers, located within the chamber interiors, and then exited through the interpores that served as exhalant canals. The large openings in chamber interwalls in the *Sphaerocoelia*-type

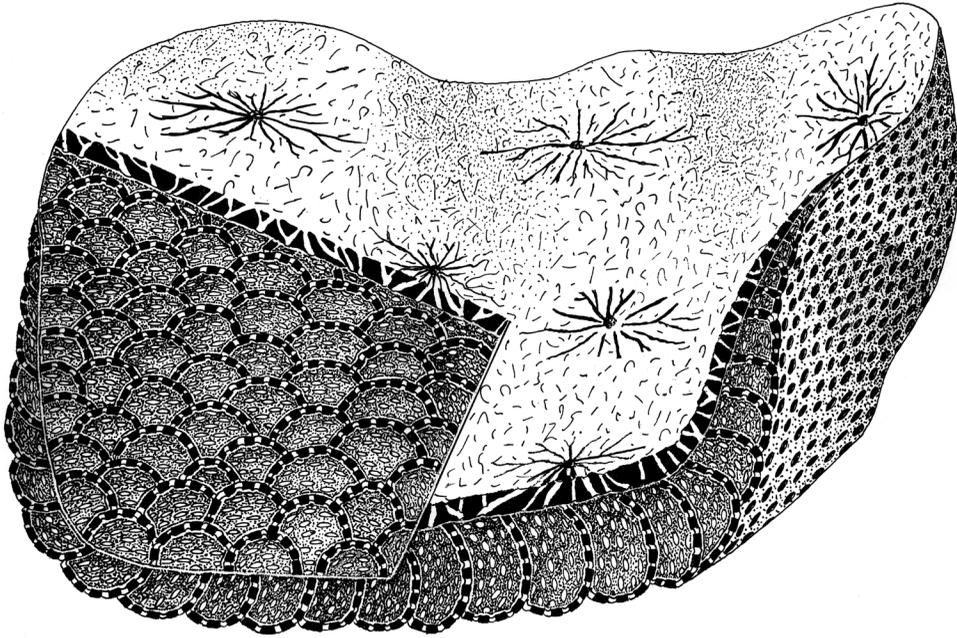


FIG. 235. Reconstruction of *Guadalupia explanata* (KING, 1943) is characterized by numerous hemispherical chambers arranged beside and above one another. Exowalls on the lower outside are perforated (inhalant pores), and the opposite upper surface bears several astrothrizal canal systems that served as exhalant canals. The sponge is abundant in Permian reefs, Guadalupe Mountains, Texas and New Mexico, United States; schematic, not to scale (Senowbari-Daryan, 1990).

system likely served as exhalant canals. A spongocoel was most probably developed, which extended as a tubular large opening through the whole sponge and was bounded by soft tissue within the chamber interiors. The *Amblysiphonella*-type system had an axial canal (or a bundle of axial canals). Water passed through exopores into the chamber interiors, and after circulation in choanocyte chambers, exited through the axial canals and osculum. Similar occupation of the main chambers by smaller choanocyte chambers and the passage of water through the skeleton in some chambered archaeocyaths were reconstructed by ZHURAVLEV (1989).

According to KRUSE (1987), Cambrian sphinctozoans did not live in reef environments. Ordovician to Carboniferous hypercalcified sphinctozoans are commonly found in what were shelf sediments. Sedimentological and paleontological data indicate that during the latest lower Permian

to the middle Permian, sphinctozoans changed their biotope. Middle and upper Permian and Triassic sphinctozoans inhabited shallow-water environments, mainly reef or reefal biotopes. Cretaceous sphinctozoans are also found in deposits of similar environments (REITNER & ENGESER, 1985). Sedimentological and paleontological data indicate that sphinctozoans lived mostly in low-energy environments, below wave base, in the photic zone, usually at depths of 15–50 m (SENOWBARI-DARYAN & RIGBY, 1988; SENOWBARI-DARYAN, 1991). According to FAGERSTROM (1984), the different shapes and growth types of Permian sphinctozoans suggest they functioned in three different ways in the reef communities: as bafflers and sediment traps, as frame builders, and as sediment binders.

The modern sphinctozoan sponge *Vaceletia* lives in cryptic habitats on outer slopes of coral reefs in the Indo-Pacific region

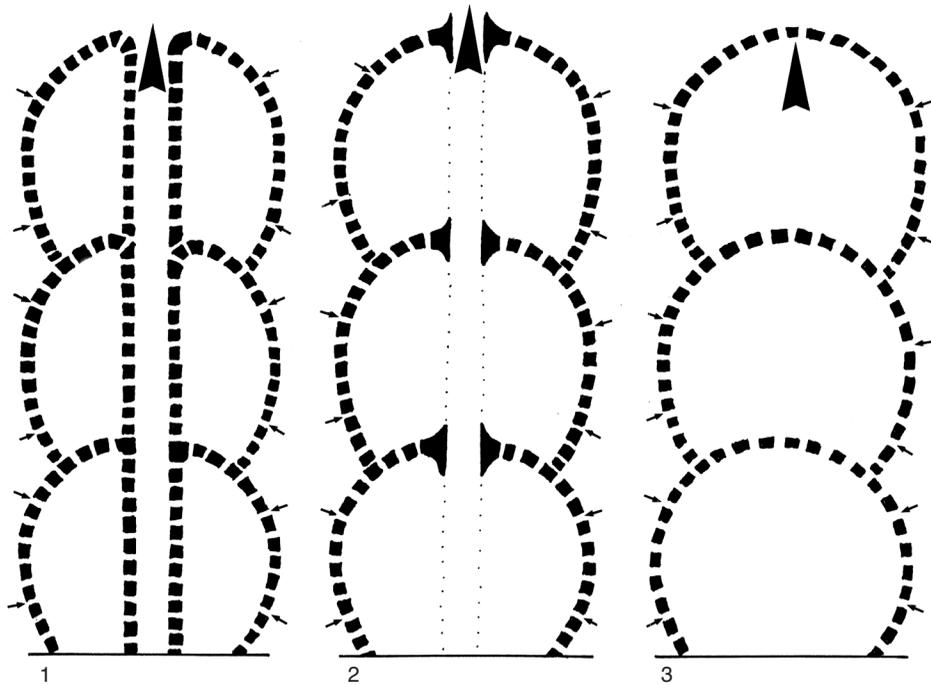


FIG. 236. Three principal types of water circulation in sphinctozoan sponges. 1, *Amblysiphonella*-type, 2, *Sphaero-coelia*-type, and 3, *Colospongia*-type; small arrows indicate direction of inhalant water motion; large arrows indicate direction of exhalant water currents (Senowbari-Daryan, 1990).

at depths of 15–38 m (VACELET, 1979b; BASILE, CUFFEY, & KONICH, 1984). However, the majority of Permian and Triassic sphinctozoan sponges were upright, growing organisms attached to hard substrates on the sea bottom. The observation and interpretation of WOOD, DICKSON, and KIRKLAND-GEORGE (1994, 1996) that most sphinctozoans of the Permian Capitan reef were cryptobionts inhabiting cavities made by other organisms were not confirmed by other workers (RIGBY, SENOWBARI-DARYAN, & LIU, 1998; FAGERSTROM & WEIDLICH, 1999a; NEWELL, 2001; NOÉ, 2003).

#### REVIEW OF CLASSIFICATION

STEINMANN (1882) was the first author to classify chambered sponges. He placed them in four families, based on the combination of the presence or absence of a spongocoel and the type of filling skeleton within the chamber interiors. GIRTY (1908a) added

two additional families to STEINMANN's (1882) families. DE LAUBENFELS (1955) was the next author to add two more families to the sphinctozoan sponges. Based on the external pattern of perforation (porate or aporate), SEILACHER (1962) created two superfamilies (Porata and Aporata) and assigned all known families to these superfamilies. Later, SEILACHER's superfamilies were raised to suborder ranks by PICKETT and RIGBY (1983). The SEILACHER (1962) classification was also modified by OTT (1967). Based on the presence or lack of a spicular skeleton, and its chemical composition (siliceous or carbonate) and on the mineralogical composition of the rigid skeleton (aragonite or Mg calcite), SENOWBARI-DARYAN (1990) classified the chambered sponges into six orders (compare RIGBY & others, 1993).

1. Sphaerocoeliida WENDT, 1979. Calcareous spicular skeleton, calcitic rigid skeleton primary aragonite? Calcareous? Jurassic.

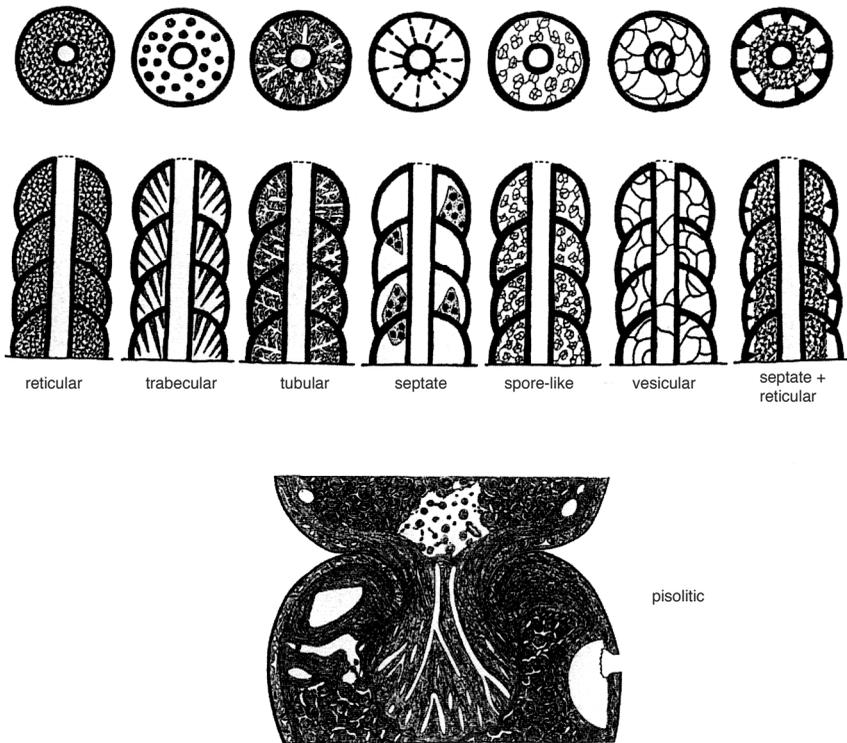


FIG. 237. Appearance of different types of filling skeleton known in the sphinctozoans, as seen in longitudinal and transverse sections. Vesiculae may occur separately or in combination with other types of filling skeleton (adapted from Senowbari-Daryan, 1990).

2. Verticillitida TERMIER & TERMIER (in H. TERMIER, G. TERMIER, & VACHARD, 1977). With or without primary siliceous spicules, rigid skeleton composed of aragonite. Demospongiae; Triassic–Recent.

3. Permosphincta TERMIER & TERMIER, 1974. Aragonitic rigid skeleton lacking spicules. Demospongiae? Calcarea?; Cambrian–Cretaceous.

4. Pisolthalamida SENOWBARI-DARYAN & RIGBY, 1988. Siliceous spicular skeleton composed of primary monaxons, with an aragonitic rigid skeleton and pisolitic internal filling structure. Demospongiae; Permian.

5. Hadromerida (*partim*), according to REITNER (1987c). Probably monactine megascleres and sphaeraster microscleres. Demospongiae, Triassic (the only genus of this taxon—*Cassianothalamia*—was assigned to the new family Cassianothalamiidae

by REITNER (1987b), order Hadromerida. MÜLLER-WILLE and REITNER (1993) moved the genus *Cassianothalamia* to the family Geoiidae within the order Astrophorida.

6. Guadalupiida TERMIER & TERMIER (in H. TERMIER, G. TERMIER, & VACHARD, 1977). Without spicules, calcitic rigid skeleton (according to FINKS, 1983, rigid skeleton is primary aragonite). Demospongiae; Permian.

Finally, chambered sponges without a spicular skeleton but with rigid skeletons composed of high-Mg-calcite mineralogy were united in the order Uncertain by SENOWBARI-DARYAN (1990). These fossils range in age from Middle to Upper Triassic.

WU (1991, 1995) classified the sphinctozoan sponges into five suborders, based on differences in their exhalant canal systems: Asiphonata (without a spongocoel); Siphonata (with an axial canal or an axial canal bundle); Vasculata (with a central conduit

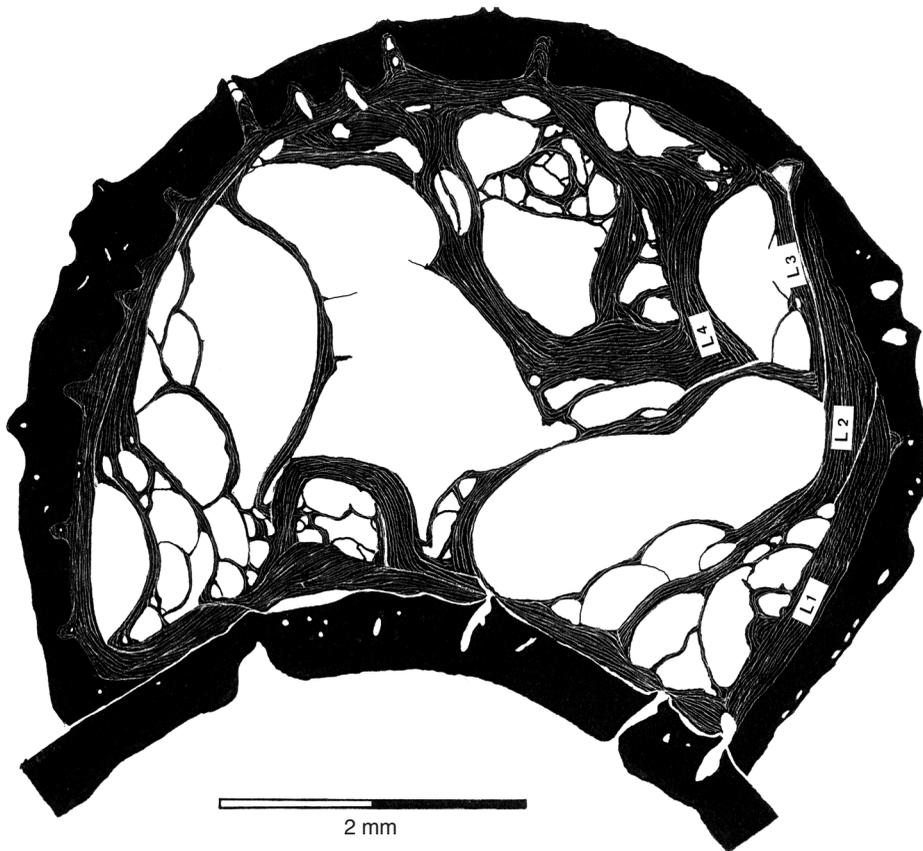


FIG. 238. A chamber of *Jablonskyia andrusovi* (JABLONSKY) showing vesiculae secreted in at least four stages (L1–L4). The exopores are sealed off by different stages of vesiculae (Senowbari-Daryan, 1990).

or central conduit bundle); Polysiphonata (having more than one exhalant tube or vertical tube bundle scattered in the whole sponge); and Polyvasculata (having more than one vertical conduit or vertical conduit bundle scattered in the whole sponge). Numerous old and new families established by WU (1991) were assigned by him to these suborders.

Because of their polyphyletic nature, the chambered sponges were assigned to different sponge classes, including Heteractinida, Demospongiae, Calcarea, Hexactinellida, and Archaeocyatha, Hexactinellida, and Archaeocyatha by SENOWBARI-DARYAN and GARCÍA-BELLIDO (2002a). Most sphinctozoans are classified into different orders within the demosponges. In addition, a sepa-

rately listed bibliography of fossil sphinctozoans was provided by SENOWBARI-DARYAN and GARCÍA-BELLIDO (2002b).

FINKS and RIGBY (2004d) followed the frame of the classification of SENOWBARI-DARYAN and GARCÍA-BELLIDO (2002a), with some revision and modification. They assigned most hypercalcified chambered sponges to the class Demospongia (=Demospongiae), subclass Ceractinomorpha, orders Agelasida and Vaceletida; and subclass Tetractinomorpha, order Hadromerida.

In summary, because of the polyphyletic nature of chambered sponges, their preservation problems, and because of gaps in their occurrences and documented evolution during Earth history, the systematic

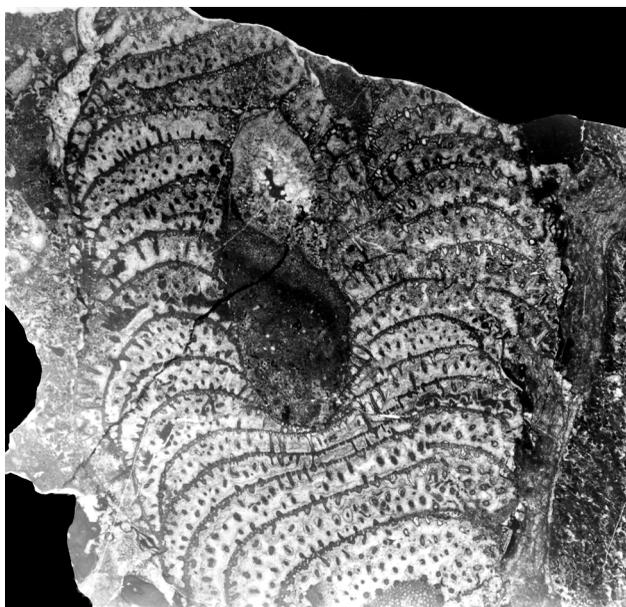


FIG. 239. *Stylothalamia hydriotica* SENOWBARI-DARYAN, 1990. This retrosiphonate sponge exhibits the trabecular (pillarlike) filling skeleton within the chamber interiors; pillars appear as points when cut transversely; Carnian, Triassic, Hydra, Greece,  $\times 2.2$  (Senowbari-Daryan, 1990).

classification of this group of sponges is still unsatisfactory. There is limited agreement about the importance of different features of hypercalcified sphinctozoan sponges among different workers, thus leading to different classifications. Also, there is not an exact boundary between the sphinctozoans and sponges with other similar fossils, described as stromatoporoids, hydrozoans, or archaeocyaths. There are numerous Cambrian genera, described as archaeocyaths, that have internal and external constructions like those of upper Paleozoic or Mesozoic representatives. Also, the mineralogy and microstructure of the rigid skeletons of some of them are apparently the same. For example, the lower Cambrian chambered *Gerbicanicyathus* BELYAEVA (see DEBRENNE, ZHURAVLEV, & KRUSE, 2002, fig. 52/G, I) and *Clathrioscinus popovi* VLASOV, 1961, described as archaeocyaths, have the same construction and the same perforation of chamber walls as that in the Paleozoic and Triassic *Amblysiphonella* (see ZHURAVLEV, 1989). Their difference from *Amblysiphonella* is in skeletal

mineralogy. However, an *Amblysiphonella*- or *Gerbicanicyathus*-type sponge with the same skeletal mineralogy (high-Mg calcite) is also known as *Leinia* SENOWBARI-DARYAN (1990) from Upper Triassic (Carnian) deposits. Also, the internal filling structures (especially of trabecular type) in several Cambrian archaeocyaths and Mesozoic sphinctozoans are identical. For example, the Cambrian species *Nochoroicyathus mirabilis* ZHURAVLEVA and the Jurassic species *Boikothalamia convexa* (= *Verticillites convexus* BOIKO, 1981) can hardly be differentiated (compare ZHURAVLEVA & MYAGKOVA, 1987, pl. 1, I; BOIKO in ZHURAVLEVA & MYAGKOVA, 1981, pl. 40, 2; BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, pl. 64, 3b). Numerous other analogous examples could be added to this list. The phylogeny of archaeocyaths was discussed by ZIEGLER and RIETSCHEL (1970) and ROWLAND (2001), and the possible connection of chambered archaeocyaths and sphinctozoan sponges has been previously discussed by ZHURAVLEVA (1970) and DEBRENNE and VACELET (1984).



FIG. 240. *Solenolmia manon* (MÜNSTER, 1841). Longitudinal and oblique sections exhibiting reticular filling skeleton in chamber interiors; axial canal is cut in one specimen, on the left; Ladinian–Carnian, Triassic, Dolomites, Italy,  $\times 2.5$  (Senowbari-Daryan & Rigby, 2011).

#### PATTERNS OF EVOLUTION AND EXTINCTION

During the last few decades, numerous papers have been published about mass extinction or bio-events during Phanerozoic time. Numerous papers have treated the different groups of marine and nonmarine organisms. However, no extinction data about the sponges in general, nor about the sphinctozoan sponges in particular, are available in either RAUP and SEPKOSKI (1982, 1984) or SEPKOSKI (1986, 1990), nor in publications of other workers treating extinctions at the Permo–Triassic boundary or the Triassic–Jurassic boundary (Permo–Triassic: RAUP & BOYAJIAN, 1988; ERWIN, BOWRING, & YUGAN,

2002; Triassic–Jurassic: BENTON, 1986, 1988, 1991; HALLAM, 1990, 1996, 2002; HALLAM & GOODFELLOW, 1990; HALLAM & WIGNALL, 1997), although the chambered sponges were the main reef builders in late Paleozoic and in Triassic time. Some general observations about the evolution, extinction, and diversification of sphinctozoan sponges in Phanerozoic time are presented below.

To date, about 160 genera of various types of hypercalcified, chambered sponges have been described. Chambered archaeocyaths and hexactinellids are excluded here. For details see the summary, below, of classification and stratigraphic occurrences (p. 386–395) and SENOWBARI-DARYAN & GARCÍA-BELLIDO (2002a).

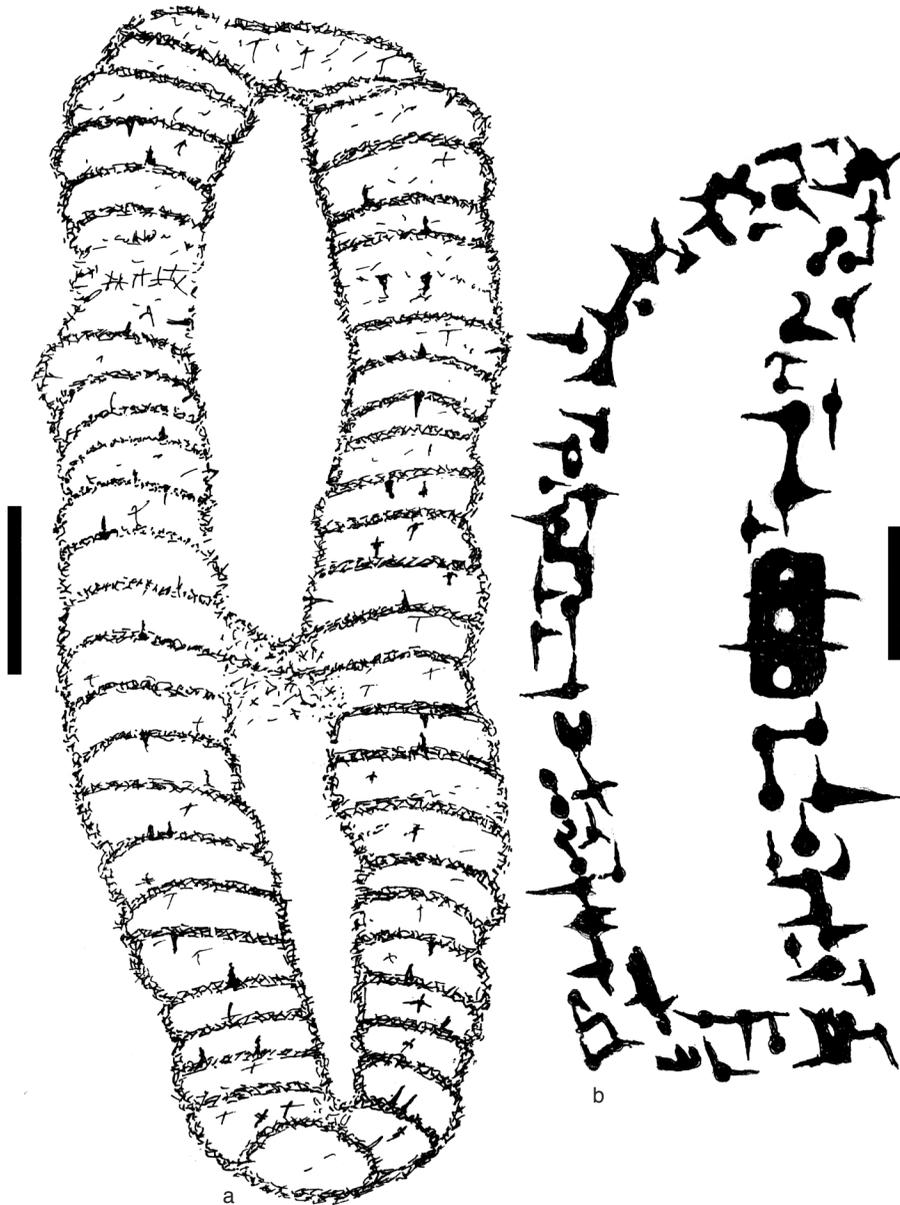


FIG. 241. Lattice skeleton of chambered hexactinellid sponge *Casearia* sp., upper Norian, Triassic, Nayband Formation, Iran. *a*, Longitudinal section showing lattice arrangement of hexactine spicules forming chamber walls, scale bar, 1 cm; *b*, magnification of one chamber showing arrangement of individual hexactines within the chamber and spongocoel walls, scale bar, 1 mm (Senowbari-Daryan & Rigby, 2011).

### Cambrian

Six genera have been reported from the Cambrian (Fig. 245). Five of them are limited to the Cambrian, and only the genus *Amblysi-*

*phonella* continued into the Ordovician. Fifty percent of Cambrian genera (three genera: *Jawonia*, *Nucha*, and *Wagima*; see PICKETT, 2002) belong to the heteractinid sponges.

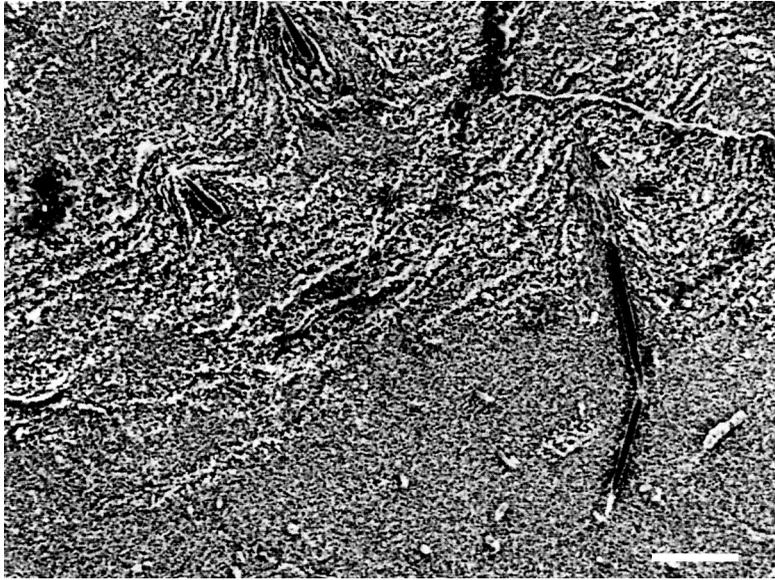


FIG. 242. Monaxon spicules imbedded in the chamber wall of the Triassic species *Celyphia submarginata* (MÜNSTER, 1841). Spicules are located in the center of wavy lamellar microstructure; Carnian, Triassic, Cassian Formation, Dolomites, Italy, scale bar, 30  $\mu$ m (Senowbari-Daryan, 1990).

### Ordovician

Fifteen genera have been reported from the Ordovician, and 14 of them are new in the Ordovician. Only the genus *Amblysiphonella* survived from the Cambrian assemblage. The Ordovician marked the first radiation of sphinctozoan sponges. However, of these 15 Ordovician genera, only the genus *Cystothalamiella* survived the Ordovician–Silurian boundary event, which also affected many other benthic organisms (see BRECHLEY, 1989). *Amblysiphonella* has been reported from the Cambrian and Ordovician and also occurs in the Carboniferous, Permian, and Triassic, but it has not been reported from the Silurian or Devonian. *Amblysiphonella* could be another genus that survived the Ordovician–Silurian event but still has not been reported from the Silurian. *Pseudoimperatoria* is another genus reported from the Ordovician and Permian but not from the Silurian–Carboniferous. The possible extinction of 14 genera produced a generic extinction rate of 93%. Ordovician sponge

diversification was summarized, in general, by CARRERA and RIGBY (2004).

### Silurian

Five genera of sphinctozoans are known from the Silurian (Fig. 245), and four of them are new. Only *Cystothalamiella* survived from the Ordovician.

### Devonian

Only two hypercalcified sphinctozoan sponges, *Hormospongia* and *Radiothalamos*, are known from the Devonian. Both of them are new in the Devonian, and they are limited to this period.

### Carboniferous

The Carboniferous (Fig. 245) marked the second diversification period of hypercalcified sphinctozoan sponges. Eight genera, with numerous species, are known from deposits at many different localities of this period. Six of these eight genera first appear in the Carboniferous. Only *Amblysiphonella* ranges

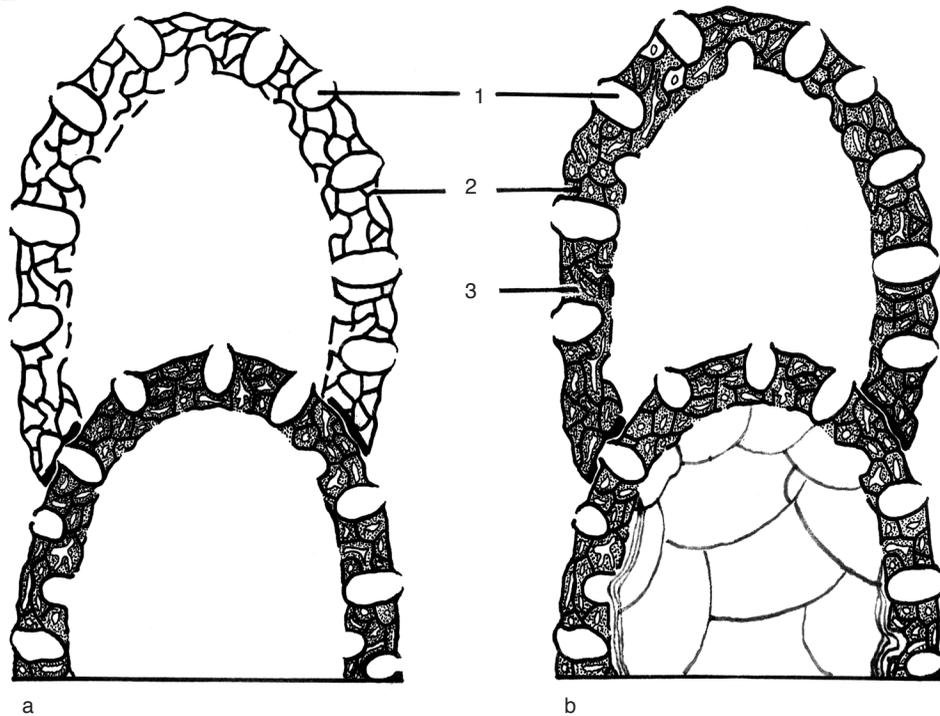


FIG. 243. Biomineralization process of the chamber walls in *Jablonskyia adrusovi* (JABLONSKY). The initial calcification started the thin labyrinthine lines within the wall (a) and proceeded from these lines into the interspaces (b); rodlike or labyrinthine systems of spaces remained free from calcification and may be changed with spicules. 1, exopores, 2, lines of initial calcification of the first mineralization stage, and 3, full calcification of the spaces between lines of initial calcification; schematic, not to scale (Senowbari-Daryan, 1997).

up from the Cambrian and *Girtyocoelia* has been reported also from the Ordovician.

### Permian

The Permian is the third and most significant diversification period of hypercalcified sphinctozoan sponges in Paleozoic time. At least 60 genera are known; of these 52 appear in the Permian as new. Six genera range up from the Carboniferous and 2 genera range up from the Ordovician.

The Permian–Triassic boundary event was the second and most significant extinction event for hypercalcified sphinctozoan sponges at the end of Paleozoic time. Of the known 60 genera in the Permian, 38 genera became extinct and only 22 genera survived the Permian–Triassic boundary event, for an

extinction rate of approximately 63% at the genus level. However, it should be noted that no Permian species have been reported from deposits of the Lower Triassic and Anisian time (SENOWBARI-DARYAN & others, 1993).

### Triassic

The Triassic was the fourth diversification period for chambered sponges. About 83 genera, with more than 200 species, have been described from the Triassic. The diversification of the hypercalcified sphinctozoans with rigid aragonitic skeletons increased rapidly in the Triassic. Chambered sponges with high-Mg-calcite mineralogy appeared in the Anisian, and the number of these taxa also increased during Ladinian and Carnian time. Sphinctozoan hexactinellids with

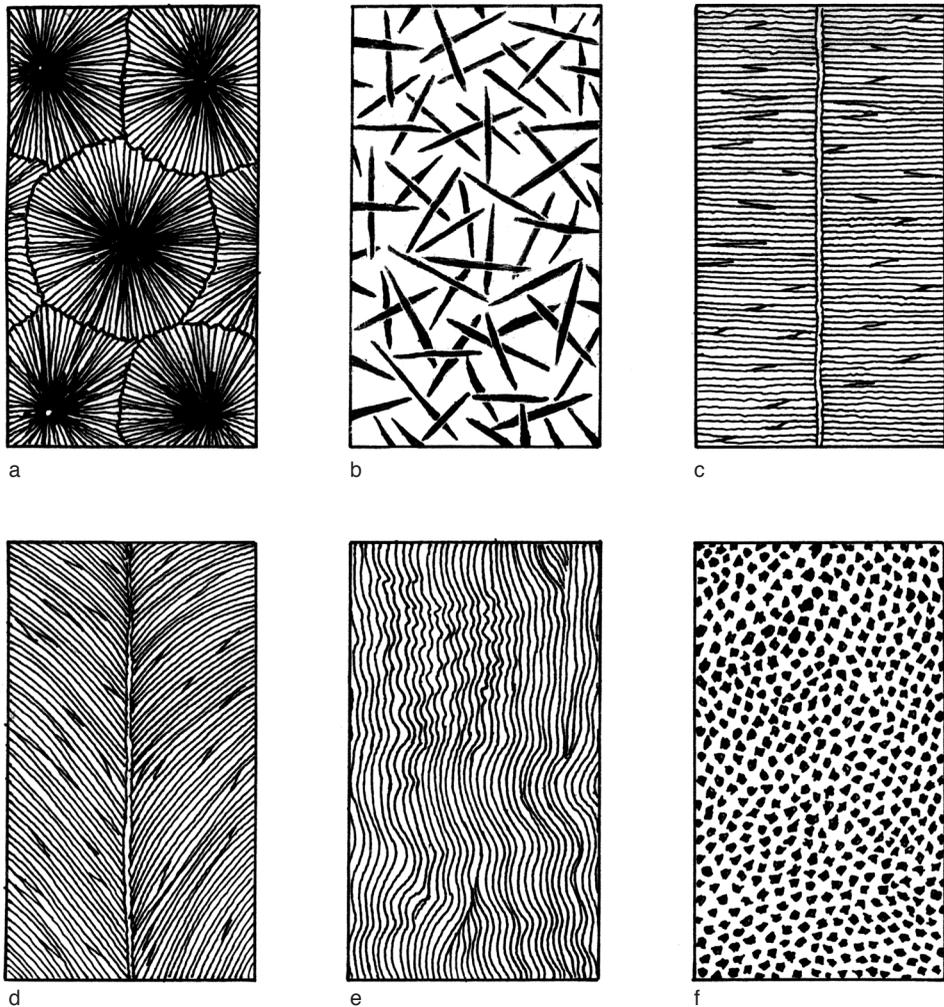


FIG. 244. Different microstructures known in sphinctozoan sponges. *a*, Spherulitic, *b*, irregular, *c*, orthogonal, *d*, clinogonal, *e*, lamellar, and *f*, microgranular; note that spherulitic, clinogonal, and granular types of microstructure also apply to certain inozoans (see p. 362–366); schematic, not to scale (Senowbari-Daryan, 1990).

hexactine spicular skeletons appeared for the first time in the Carnian. Only one genus of chambered lithistid demosponge is known from the Norian, and it was reported from Gosaukamm, Austria (SENOWBARI-DARYAN & WÜRME, 1994).

Of the 83 hypercalcified sphinctozoan genera known from the Triassic, 61 genera are new and 22 genera survived from the Paleozoic. However, there is a major break in the record, for no sphinctozoan sponges have been reported from the Lower Triassic

(Scythian), and no Paleozoic chambered species have been found in Anisian reefs (SENOWBARI-DARYAN & others, 1993).

The number of sphinctozoan taxa greatly increased during the Middle and Upper Triassic (Carnian). In addition to aragonitic sphinctozoans, a large number of sphinctozoans with high-Mg-calcite mineralogy appeared. At the Carnian–Norian boundary, or in the lower Norian, some 12–17 million years before the end of the Triassic (STANLEY, 2001a), another extinction event changed the

radiation of sphinctozoan sponges considerably. Almost all representatives with high-Mg-calcite mineralogy became extinct; those with aragonitic skeletons were less affected by this extinction. According to FLÜGEL and SENOWBARI-DARYAN (2001), about 50% of sphinctozoan sponges, at the generic level, disappeared during upper Carnian–lower Norian time. However, few of the so-called conservative taxa, such as *Colospongia* and *Amblysiphonella*, survived this extinction event. The Norian diversification produced many new taxa with both simple and complex constructions. The number of taxa seems to have decreased during the uppermost Triassic, which ended with a significant extinction event at the Triassic–Jurassic boundary.

Comparing Triassic sphinctozoan assemblages with those of the Permian, the Ladinian and Carnian sponge faunas exhibit few similarities to those of the upper Paleozoic sphinctozoans. On the other hand, the similarity of Permian and Norian–Rhaetian assemblages is much greater. For example, the genera *Discosiphonella*, *Polycystocoelia*, and *Platythalamella* are known from Permian and Norian–Rhaetian deposits, but not from Lower and Middle Triassic and Carnian occurrences. Most of the conservative Carboniferous–Permian genera, like *Discosiphonella*, *Sollasia*, *Colospongia*, and *Amblysiphonella*, survived, but only a few of the so-called progressive genera survived beyond the Permian–Triassic extinction event. Similar Norian reappearances of taxa from other phyla that seemed to have disappeared at the end of the Paleozoic have been reported by other authors: for example, the Paleozoic strophomenid brachiopod *Gosaukammerella* (SENOWBARI-DARYAN & FLÜGEL, 1996) and phylloid algae (R. P. REID, 1986).

The Triassic–Jurassic event terminated the major evolutionary burst of Triassic sphinctozoan sponges. Of the 83 known Triassic genera, 82 genera became extinct at the Carnian–Norian, or at the end-Norian extinction event, which is a generic extinction rate of about 98%. Only the genus

*Stylothalamia* survived beyond the Triassic–Jurassic boundary. *Stylothalamia columnaris* LE MAITRE, 1935, is the only sphinctozoan species known from the Lower Jurassic (Liassic) at several localities in the world (South America: HILDEBRANDT, 1971, 1981; SENOWBARI-DARYAN & STANLEY, 1994; North Africa: SCHROEDER, 1984; Europe: BECCARELLI BAUCK, 1986; see SENOWBARI-DARYAN & HAMEDANI, 1999).

### Jurassic

As noted above, only one species of sphinctozoan sponge, *S. columnaris*, is known from the Lower Jurassic. Both the hypercalcified sphinctozoans with various filling structures (e.g., *Boikothalamia*), and the hexactinellid representative, e.g., *Casearia*, appear again in the Middle and Upper Jurassic. Calcarean sphinctozoans, including *Barroisia*, *Thalamopora*, *Sphaerocoelia*, and *Muellerithalamia*, also appear in the Upper Jurassic. Only four genera of hypercalcified chambered sponges are known from the Upper Jurassic. Some of these genera continued into the Cretaceous.

### Cretaceous

To date, only ten Cretaceous hypercalcified sphinctozoans are known from several combined localities, especially from Europe (REITNER & ENGESER, 1985, 1989b; ENGESER & NEUMANN, 1986; HILLMER & SENOWBARI-DARYAN, 1986). Apparently, only two genera survived the Cretaceous–Tertiary boundary, which is an extinction rate of 90%.

### Paleogene–Neogene

Only two or three Paleogene–Neogene sphinctozoan sponge genera are known. *Vaceletia* (PICKETT, 1982) is the only living sphinctozoan sponge. For more information see SENOWBARI-DARYAN, 1990; SENOWBARI-DARYAN and GARCÍA-BELLIDO, 2002a.

### Holocene

Only one genus of chambered sponge, *Vaceletia*, has been reported as occurring in the Holocene.

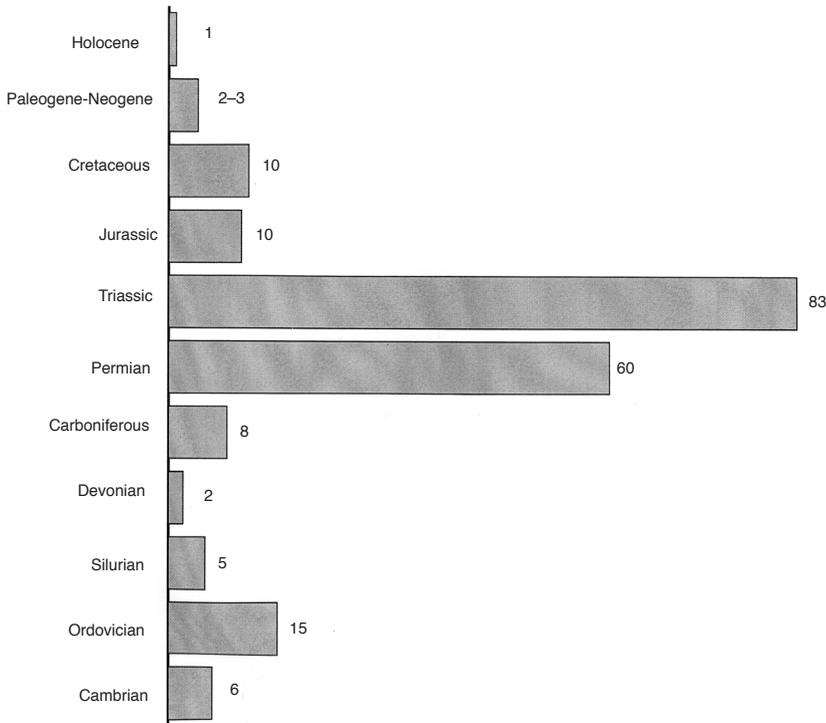


FIG. 245. Number of hypercalcified sphinctozoan genera per geologic period through the Phanerozoic (chambered hexactinellid genera are not considered in this diagram; Senowbari-Daryan & Rigby, 2011).

Figure 245 shows the number of sphinctozoan sponge genera occurring per period through Earth history.

## INOZOANS

Like sphinctozoan sponges, the inozoans (Inozoa STEINMANN, 1882) are polyphyletic. Although some Triassic taxa, such as *Sestrostomella* (see REITNER, 1992) and Jurassic inozoan sponges like *Peronidella* HINDE, 1893, secreted spicular skeletons, almost all Triassic and Permian representatives of the group lack a spicular skeleton. For that reason, RIGBY and SENOWBARI-DARYAN (1996a) suggested separation of inozoan sponges without spicular skeletons into the Inozoida, and those with a spicular skeleton into the Inozoa. Without taking spicular skeletons differences into consideration, the morphologic features of both groups are discussed here.

## EXTERNAL MORPHOLOGY

### Sponge Shape

Shapes of inozoan sponges are usually cylindrical, like *Peronidella* HINDE, 1893, for example, or *Stollanella* BIZZARINI & RUSSO, 1986; but club- or mushroom-shaped taxa, as, for example, *Permocorynella* RIGBY & SENOWBARI-DARYAN, 1996a, or sheetlike taxa, such as *Auriculospongia* TERMIER & TERMIER, 1974, or irregularly massive to hemispherical taxa, such as *Estrellospongia* RIGBY & SENOWBARI-DARYAN, 1996a, are also known. Figure 246 shows the principal general shapes of inozoans.

Both single and multibranched growth types also occur, such as the Upper Triassic multibranched species *Peronidella iranica* SENOWBARI-DARYAN, 2003 (Fig. 247). Inozoan sponges are commonly less than

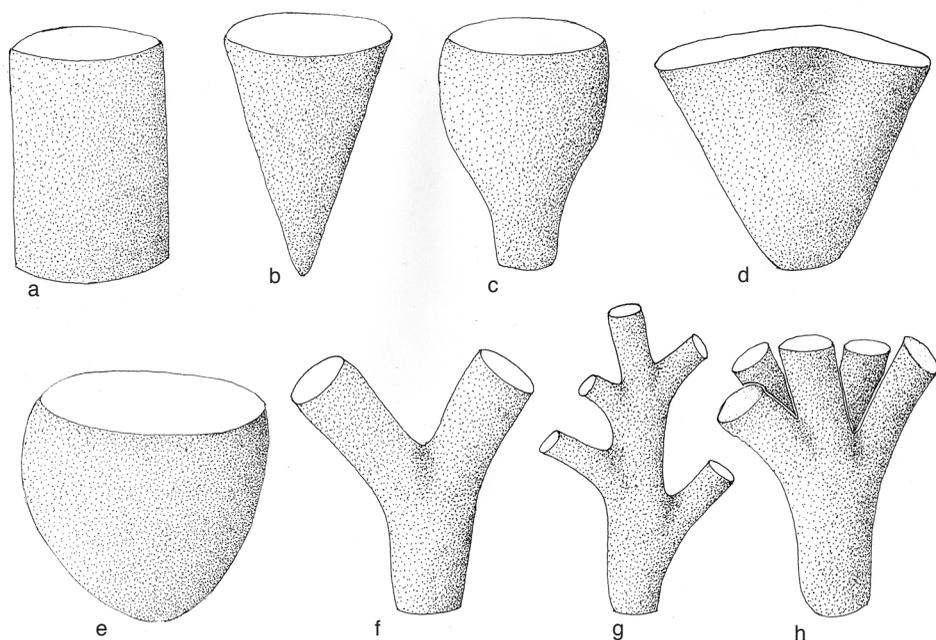


FIG. 246. General shapes of skeletons of inozoan sponges. *a*, cylindrical, *b*, arcuate conical, *c*, conical to club shaped, *d*, tabular, *e*, hemispherical, *f*, single dichotomously branched, *g–h*, dichotomously multibranched; schematic, not to scale (Senowbari-Daryan & Rigby, 2011).

10 cm in diameter, although large species, up to 2.5 m diameter, like the platelike Permian *Gigantospongia discoforma* RIGBY & SENOWBARI-DARYAN, 1996b, are exceptional. Annulated, screwlike, or externally segmented forms also occur, as, for example, the Permian genera *Imperatoria* DE GREGORIO, 1930, and *Minispongia* RIGBY & SENOWBARI-DARYAN, 1996a. Outer dermal surfaces of inozoans may be smooth or characterized by having distinct growth lines. The major skeletal elements of inozoans are shown in Figure 248.

#### External Inhalant Canals

Outer surfaces of inozoans may totally lack perforations, but the majority of these sponges are perforated by numerous small pores, or by less abundant large openings, termed ostia (Fig. 249–250). Sponges with a distinct cortex or dermal layer commonly have pores or ostia, but in representatives without a dermal layer, communication from the outside to

the sponge interior is accomplished through spaces between skeletal fibers, as, for example, in *Peronidella* HINDE, 1893. Pores or ostia may have circular or oval cross sections. Ostia are usually separated, single, circular openings, as in the Permian genus *Djemelia* RIGBY & SENOWBARI-DARYAN, 1996a, but starlike ostia or two or more combined ostia that may be united into groups, also occur, as, for example, in some species of the genus *Dabarella* RIGBY & SENOWBARI-DARYAN, 1996a. Both ostia types may be rimmed or have tubelike projections, termed exaules. Exaules of inozoans are usually less than 1 mm long, and exaules, like those observed in some sphinctozoan representatives, such as in *Girtyocoelia* COSSMAN, 1909 (Fig. 228), have not been reported in inozoans. The two types of openings (pores and ostia) of inhalant canals usually do not occur together in the same sponge.

In sheetlike representatives of inozoan sponges, the opposite surfaces may have similar porosity, or be different. For example, in the

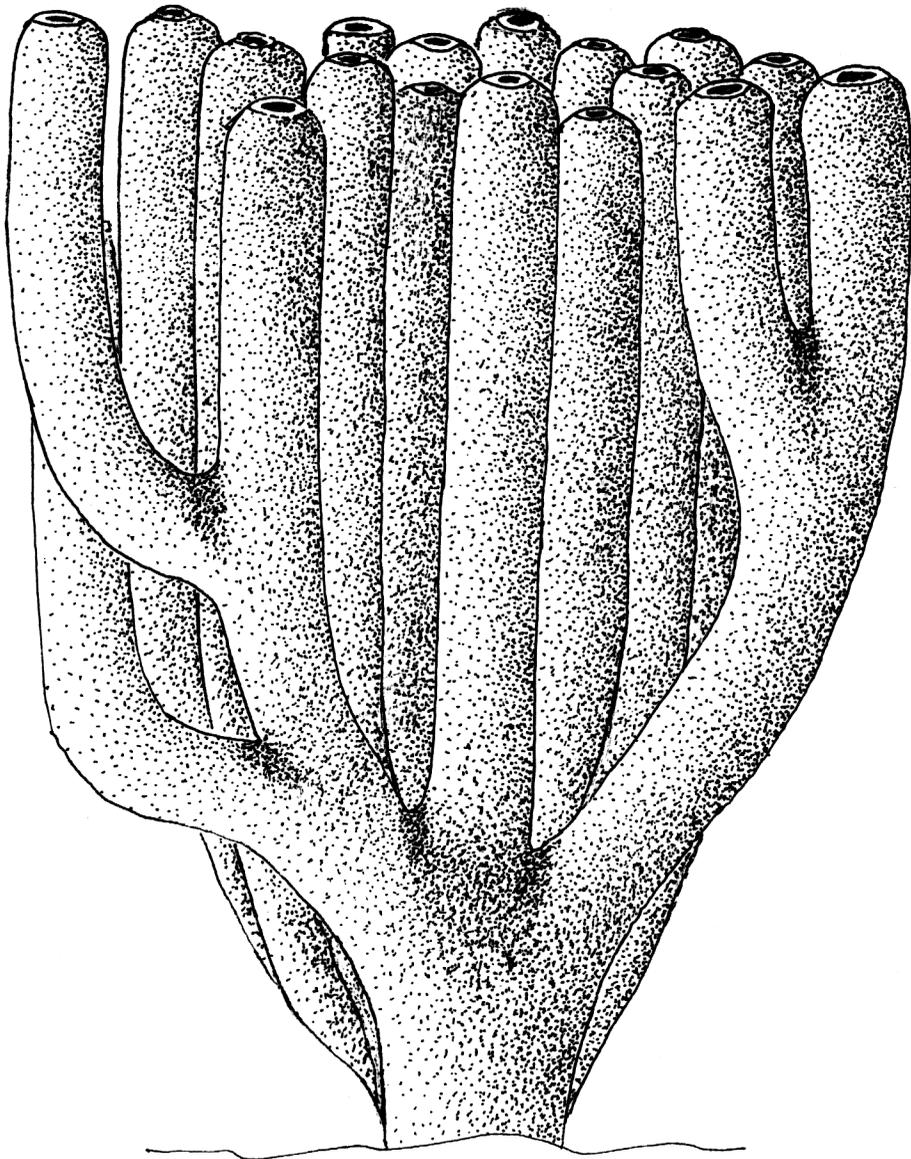


FIG. 247. Reconstruction of multibranched inozoan sponge *Peronidella iranica* SENOWBARI-DARYAN, 2003; Norian–Rhaetian, Triassic, reefs within Nayband Formation, Iran (Senowbari-Daryan, 2003).

Permian genus *Auriculospongia* TERMIER & TERMIER, 1974 (see Fig. 259.1), or in the Triassic genus *Aliabadia* SENOWBARI-DARYAN (2005a), the opposite sides are totally different.

#### External Exhalant Canals

As mentioned above, some inozoan sponges lack an axial spongocoel, espe-

cially those with sheetlike construction, but representatives of cylindrical- or club-shaped taxa may also be without distinct exhalant canals, as, for example, the Permian genus *Daharella* RIGBY & SENOWBARI-DARYAN, 1996a (Fig. 249) or the Triassic genus *Molengraaffia* VINASSA DE REGNY, 1915.

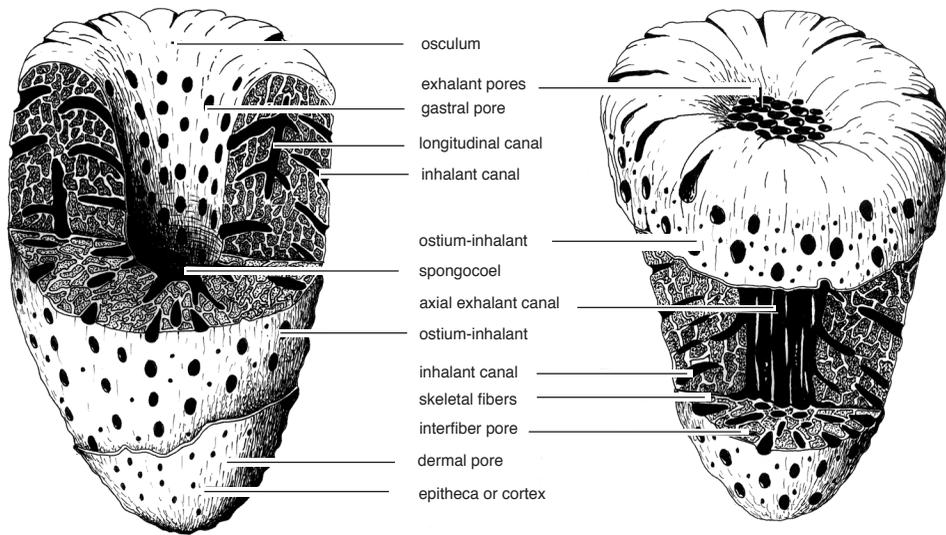


FIG. 248. Major skeletal elements of inozoan sponges; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

Some inozoans are characterized by only one osculum (e.g., *Peronidella* HINDE, 1893), and others by several oscula (e.g., *Sestrostomella* ZITTEL, 1878; Fig. 251), which are visible as one or several openings at the top of the sponge (Fig. 251; see also DIECI, ANTONACCI, & ZARDINI, 1968, pl. 25–26). In representatives with a single spongocoel, that spongocoel may be circular, oval, or starlike in cross section. Oscula of spongocoels may be located in depressions or on elevations. Upper surfaces of some inozoans may have numerous oscula across the top of the sponge (e.g., the Permian genera *Polytubispongia* RIGBY & SENOWBARI-DARYAN, 1996a [Fig. 250], or *Medenina* RIGBY & SENOWBARI-DARYAN, 1996a). These and other types of oscula extend as spongocoels into the sponge interior.

Starlike arrangements of exhalant canals in an astrophthal system are developed in a variety of genera in inozoan sponges. For example, tops of the Permian sponge *Prestellispongia lobata* (PARONA, 1933), which has a conical shape, are occupied by one or more astrophthal systems (see DIECI, ANTONACCI, & ZARDINI, 1968; RIGBY & SENOWBARI-DARYAN, 1996a). Several astrophthal systems cover the outer surface of the

cylindrical and massive genus *Stellispongiella* WU (see TERMIER & TERMIER, 1955; RIGBY & SENOWBARI-DARYAN, 1996a). The astrophthal systems may be located on elevations (mamelons) (Fig. 252, Fig. 259.4) or not.

## INTERNAL MORPHOLOGY

### Spongocoels

Some inozoans possess only one axial spongocoel (e.g., *Peronidella* HINDE, 1893) (Fig. 259.2), and others have several axial spongocoels (e.g., *Sestrostomella* ZITTEL, 1878 [Fig. 251], or *Stollanella* BIZZARINI & RUSSO, 1986 [Fig. 253]). These spongocoels may pass vertically or longitudinally through the whole sponge from near the base up to the summit (e.g., *Sestrostomella*), or it may be limited to only the upper part of the sponge (e.g., the Permian genus *Pseudohimatella* RIGBY & SENOWBARI-DARYAN, 1996a). The spongocoel may have its own skeletal wall (Fig. 254), or it may be surrounded by the fibrous skeleton of the entire sponge wall, without a distinct separate inner layer (Fig. 255). Several sponges possess numerous vertical spongocoels that are distributed through the whole sponge (see Fig. 259.3) (e.g., the Permian genera *Preeudea* TERMIER & TERMIER, 1977a, or *Polytubifungia* RIGBY & SENOWBARI-DARYAN, 1996a; Fig.

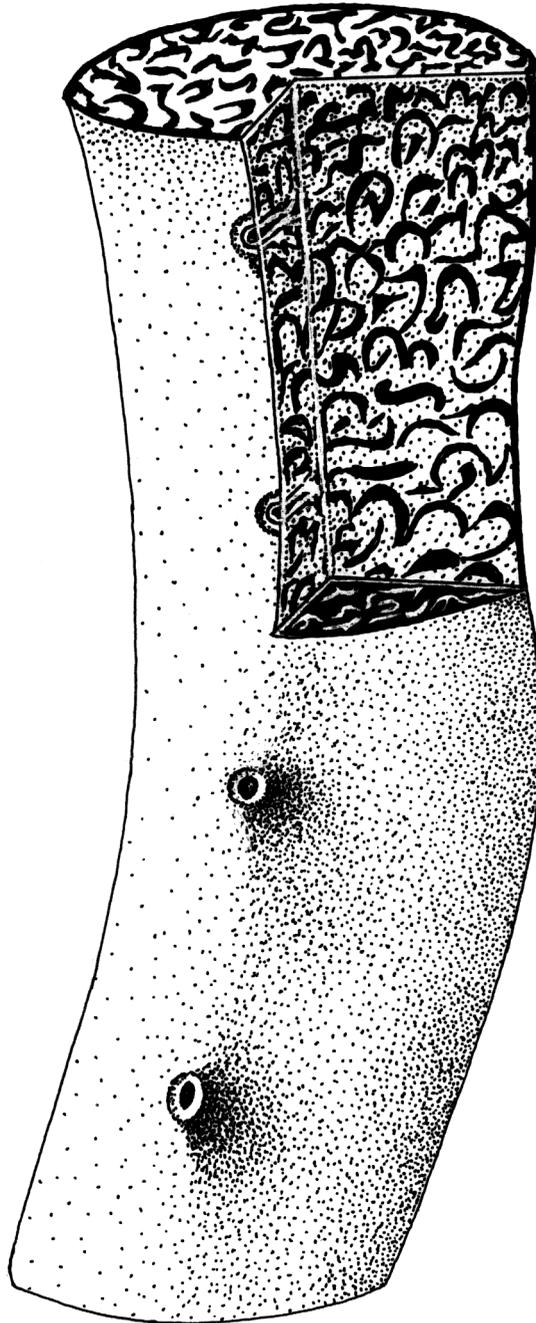


FIG. 249. Reconstruction of asiphonate inozoan sponge *Daharella micella* RIGBY & SENOWBARI-DARYAN, 1996a. Water passed through rimmed ostia and out through interfiber spaces; sponge is known from upper Permian, Djebel Tebaga, Tunisia; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

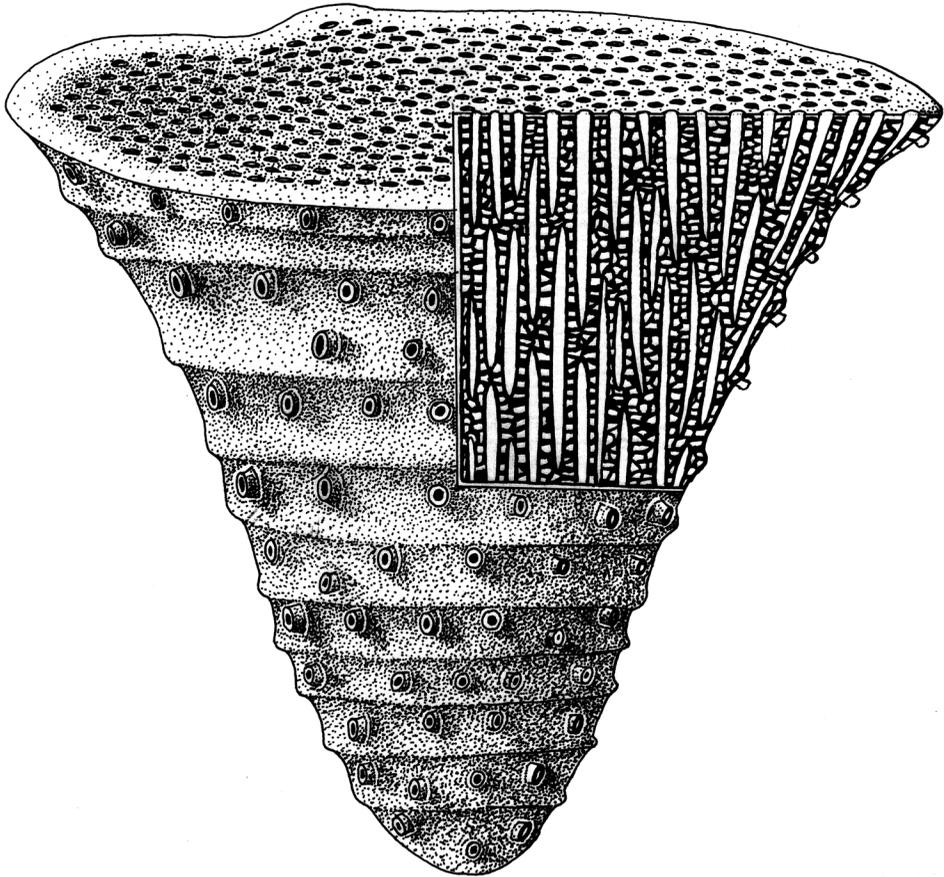


FIG. 250. Reconstruction of *Polytubispongia maxima* RIGBY & SENOWBARI-DARYAN, 1996a; externally annulate conical sponge bearing numerous rimmed ostia on the dermal surface that serve as inhalant canals; exhalant canals are numerous, more or less parallel tubes that are distributed through whole sponge; sponge is known from upper Permian, Djebel Tebaga, Tunisia; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

250). The Permian genus *Pseudohimatella* RIGBY & SENOWBARI-DARYAN, 1996a, is characterized by a shallow axial spongocoel and numerous additional small spongocoels that pass vertically through the whole sponge. The Triassic genus *Marawandia* SENOWBARI-DARYAN, SEYED-EMAMI, & AGHANABATI, 1997, possesses several spongocoels that are usually located near the periphery of the sponge (Fig. 254). In the Permian genus *Exotubispongia* RIGBY & SENOWBARI-DARYAN, 1996a, the interior of the sponge is filled with a reticular fibrous skeleton, but the more outer part of the sponge is marked by numerous vertical canals (Fig. 256).

#### Internal Inhalant and Exhalant Canals

Outer ostia continue as tubes into the relatively thick sponge wall in some inozoans, as, for example, in the Permian genus *Permo-corynella* RIGBY & SENOWBARI-DARYAN, 1996a (Fig. 255, Fig. 257), or in the Jurassic genus *Endostoma* ROEMER, 1864 (= *Corynella* ZITTEL, 1878). These tubes may be called inhalant tubes or canals (Fig. 255). Spongocoels of these sponges may have a distinct, separate wall that is pierced by openings called gastral pores. Gastral pores may continue into the sponge wall as radial tubes, which are termed exhalant tubes, or canals. Inhalant



FIG. 251. *Sestrostomella robusta* ZITTEL; oblique sections; sponge is characterized by a bundle of axial tubes that may range up to 20 individual tubes. Additional small tubes are also present, and they diverge upward and outward to dermal surface of sponge; concentric lines in sponge wall reflect growth lines; Norian–Rhaetian, Triassic, Nayband Formation, Iran,  $\times 2.5$  (Senowbari-Daryan, Seyed-Emami, & Aghanabati, 1997).

and exhalant tubes are usually not connected directly with each other. These tubes may have a pierced wall or may be surrounded by the fibrous skeleton of the sponge wall. Inhalant and exhalant canals are usually oriented horizontally, but they are also commonly longitudinal and parallel to the axial spongocoel (Fig. 255). In some genera, the exhalant canals may converge upward and open into the spongocoel, as in *Sestrostomella* ZITTEL, 1878 (Fig. 251), or they may be outwardly divergent within the sponge wall and open at the sponge surface, as in *Permocorynella* RIGBY & SENOWBARI-DARYAN, 1996a (Fig. 255, Fig. 257), or in *Stollanella* BIZZARINI & RUSSO, 1986 (Fig. 235).

Astrorhizal systems, common in stromatoporoids and Recent hypercalcified sponges such as *Ceratoporella*, occur in a variety of inozoan sponges. For example, the Permian–Triassic genus *Stellispongiella* WU, 1991, is a massive, rodlike sponge that is characterized by astrorhizal exhalant canals, which in some specimens are located within mamelon-like elevations (Fig. 252). Also, summits of some other genera, such as the Permian–Triassic genus *Prestellispongia* RIGBY & SENOWBARI-DARYAN, 1996a, and the Triassic genus *Stellispongia* D'ORBIGNY (see DIECI, ANTONACCI, & ZARDINI, 1968), have several astrorhizal exhalant canal systems.

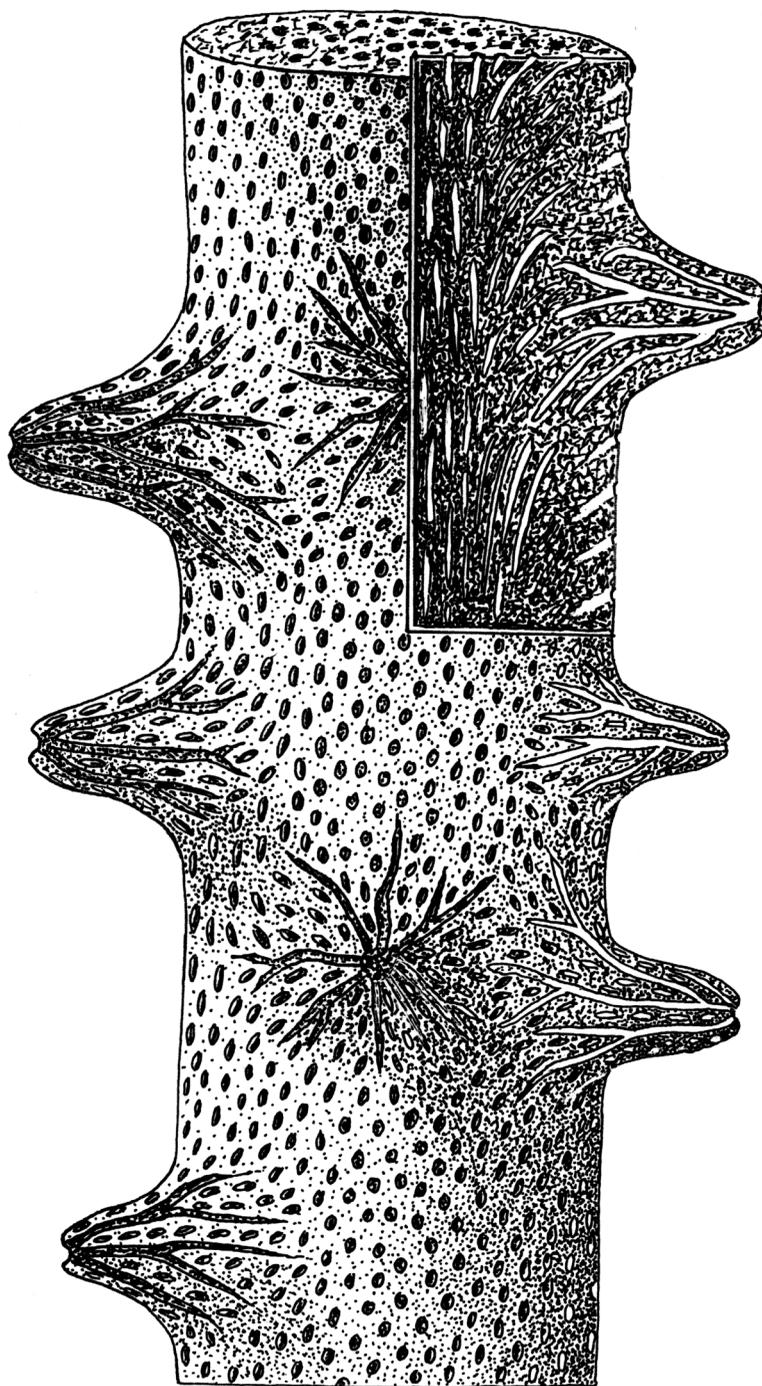


FIG. 252. Reconstruction of *Stellispongiella bacilla* (TERMIER & TERMIER, 1977b), a cylindrical inozoan sponge from upper Permian, Djebel Tebaga, Tunisia; astrorhizal systems served as exhalant canals and are located on sharp moundlike elevations; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

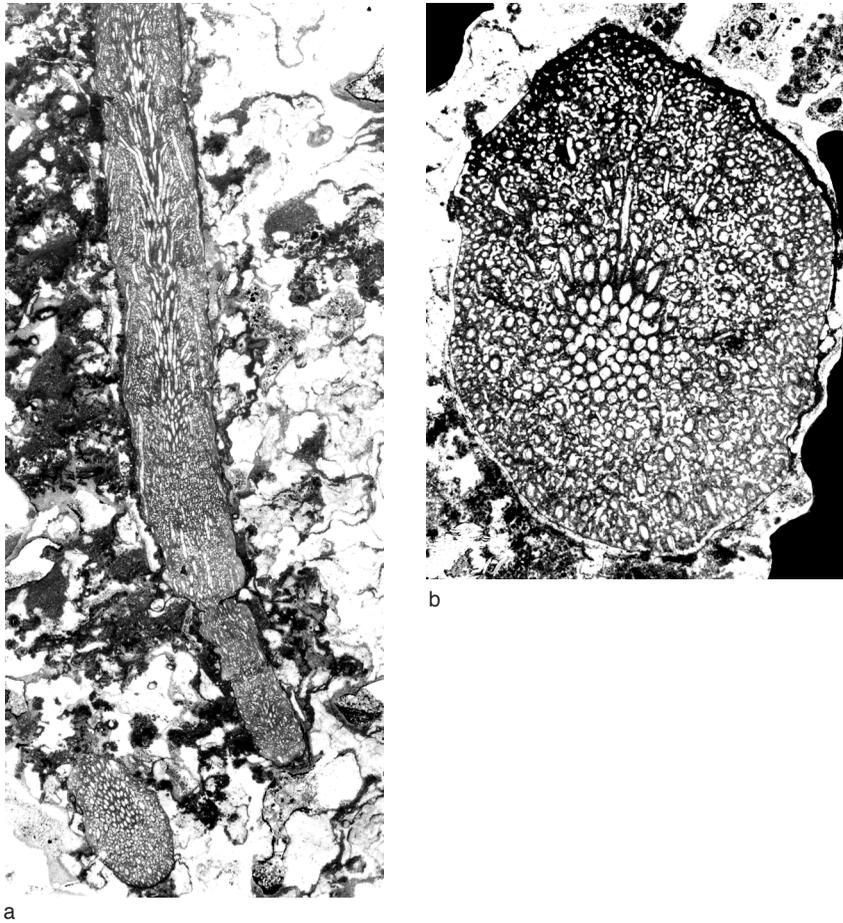


FIG. 253. *Stollanella diecii* BIZZARINI & RUSSO, 1986. *a*, Longitudinal,  $\times 1.5$ , and *b*, transverse,  $\times 5$ , sections of cylindrical inozoan sponge. It has Mg-calcite skeletal mineralogy and is characterized by an axial canal bundle composed of up to approximately 50 individual tubes; additional smaller tubes around axial bundle diverge upward and outward toward dermal surface of sponge; Ladinian–Carnian, Triassic, Dolomites, Italy (Senowbari-Daryan & Rigby, 2011).

### Structure of Rigid Skeleton

Walls of the majority of inozoan sponges are composed of reticulate skeletal fibers. Thicknesses and orientations of such skeletal fibers may vary across different parts of the same sponge skeleton. Fibers in *Auriculospongia* TERMIER & TERMIER, 1974, are linearly arranged parallel to the growth direction and may be associated with some transverse fibers, but they appear unoriented in sections perpendicular to the growth direction (see RIGBY & SENOWBARI-DARYAN, 1996a, fig. 12). In the Triassic genera

*Molengraaffia* VINASSA DE REGNY, 1915, and *Anguispongia* SENOWBARI-DARYAN, 2005b, orientations of fibers are totally different in sections cut parallel or perpendicular to the growth direction (see SENOWBARI-DARYAN, 2005b). Walls around axial spongocoels in some Triassic sponges are composed only of tubes that diverge upward and outward. These tubes are interconnected with other tubes by numerous intertubular pores.

### Spicules

Investigations of well-preserved Permian inozoan sponges from Djebel Tebaga, Tunisia

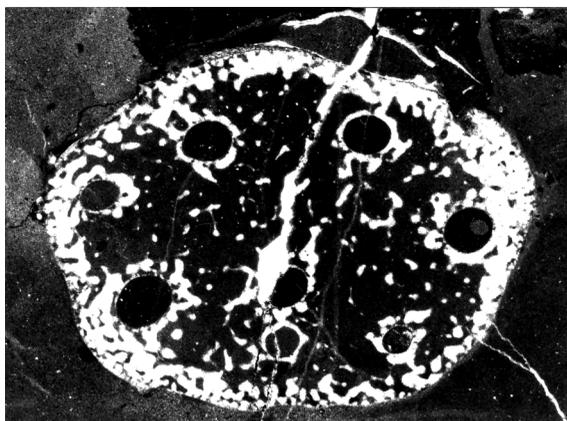


FIG. 254. *Marawandia iranica* SENOWBARI-DARYAN, SEYED-EMAMI, & AGHANABATI, 1997. Cylindrical inozoan sponge, seen here in transverse section, has several (6–8) usually peripherally located spongoecol tubes with more or less distinct exowalls pierced by labyrinthic branched pores; Norian–Rhaetian, Triassic, Nayband Formation, Iran,  $\times 12$  (Senowbari-Daryan, Seyed-Emami, & Aghanabati, 1997).

by scanning electron microscopy by WENDT (1977, 1978, 1979, 1984) and RIGBY and SENOWBARI-DARYAN (1996a) show that these sponges lack calcareous or siliceous spicular skeletons. Detailed discussion of whether the spicules were originally lacking, or were lost secondarily during diagenesis, was given by RIGBY and SENOWBARI-DARYAN (1996a).

In contrast to the Permian inozoans, spicules have been found in some Triassic and Jurassic inozoan sponges. For example, spicules occur in the Triassic genera *Sestrostomella* ZITTEL, 1878, and *Stellispongia* D'ORBIGNY, 1849b, and in the Jurassic genus *Peronidella* ZITTEL in HINDE, 1893 (see REITNER, 1992).

#### Mineralogy and Microstructure of the Rigid Skeleton

Modifications of calcite, aragonite, and Mg calcite are known from fossil inozoan representatives. Because of replacement of aragonite by calcite, primary skeletal mineralogy is not known for lower Paleozoic (Cambrian–Carboniferous) inozoans. However, traces of spherulitic microstructure, like those in Paleozoic stromatoporoids that point to an original primary aragonite composition (STEARN, 1972), are also preserved in some Carboniferous inozoans,

suggesting a primary aragonitic mineralogy of these taxa (WENDT, 1984). Certain aragonitic skeletal mineralogy was reported from upper Permian inozoans of Djebel Tebaga, Tunisia (WENDT, 1977, 1979; RIGBY & SENOWBARI-DARYAN, 1996a). The majority of inozoan sponges from other Permian localities of the world are recrystallized. As a result, the primary skeletal mineralogy of sponges from these localities is not known.

Aragonite skeletal mineralogy is known also from numerous Triassic taxa, such as *Eudea polymorpha* (KLIPSTEIN), *Leiospongia involuta* (KLIPSTEIN), and *Peronidella lorenzi* ZITTEL, or *Sestrostomella robusta* ZITTEL (DIECI, RUSSO, & RUSSO 1974a; WENDT, 1974, 1975, 1979, 1990; MÜLLER-WILLE & REITNER, 1993; MASTANDREA & RUSSO, 1995).

Mg-calcitic mineralogy is very rare in Triassic inozoans but does seem to be present. For example, it is present in *Stollanella* BIZZARINI & RUSSO, 1986, which, according to the authors, has a micritic, irregular, or homogenous skeletal texture, as described in examples from the Carnian Cassian Formation (Dolomites, northern Italy). It is also present in some as yet undescribed Norian–Rhaetian species from southern Turkey.

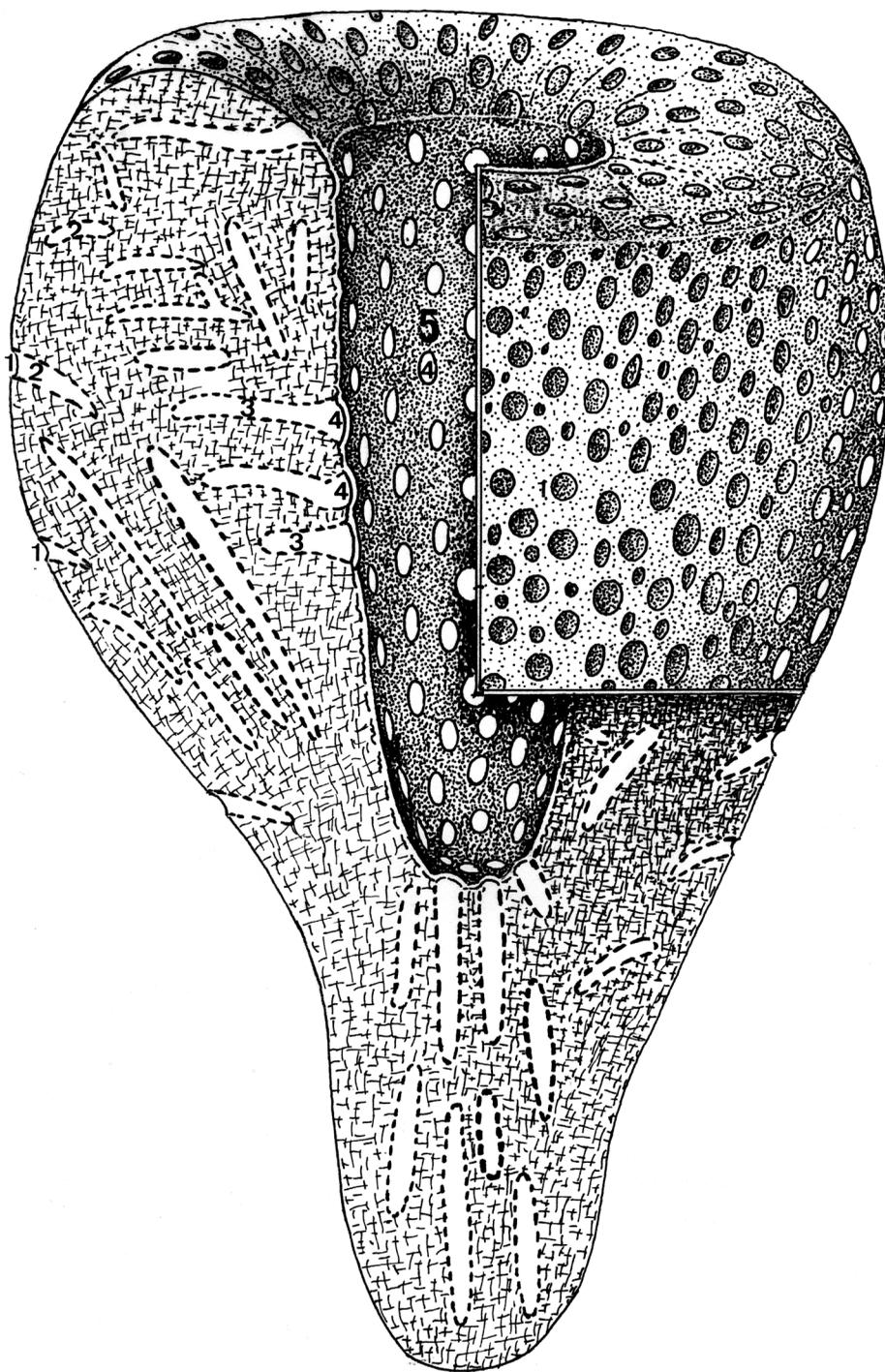


FIG. 255. Reconstruction of *Permacorynella* RIGBY & SENOWBARI-DARYAN, 1996a, showing 1, exopores or ostial pores, 2, inhalant canals, 3, exhalant canals, 4, endopores, and 5, deep spongocoel. Spaces between the inhalant and exhalant canals are filled with reticular fiber skeleton; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

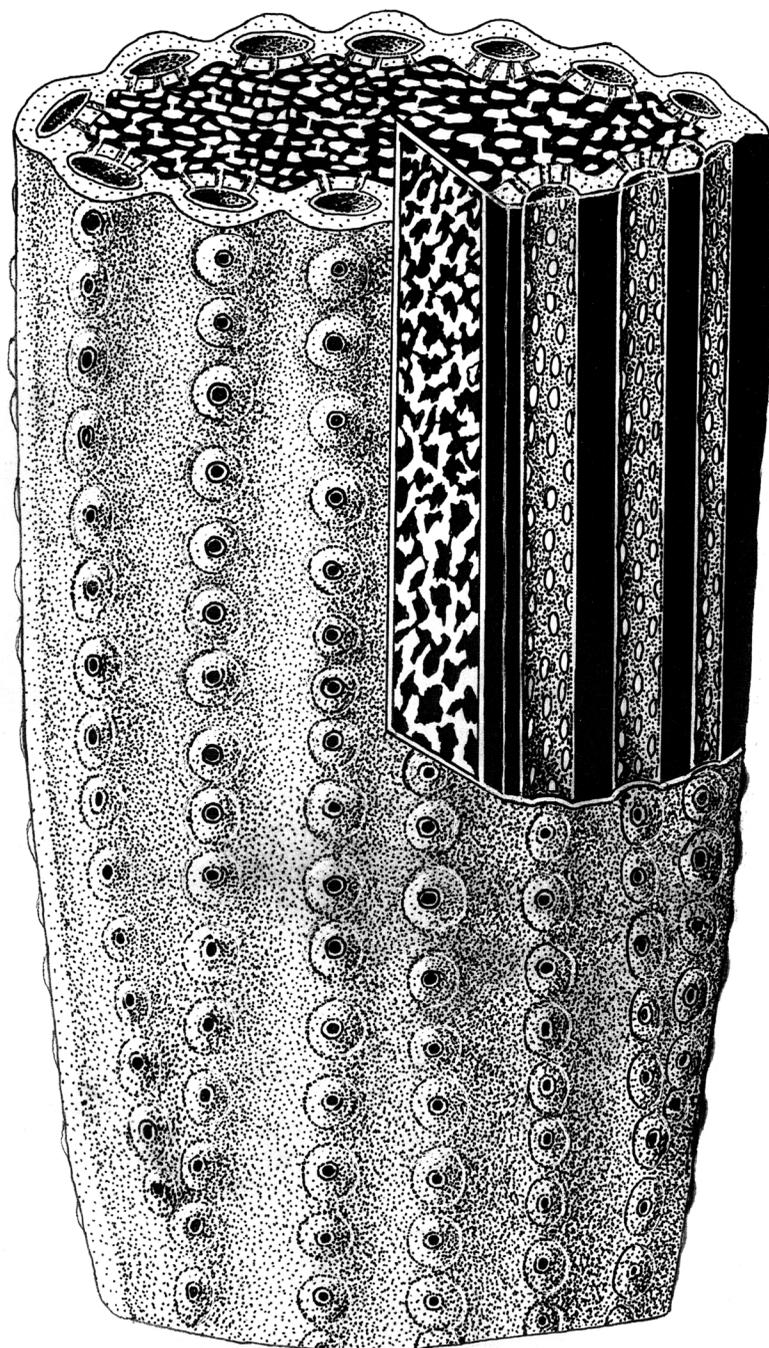


FIG. 256. Reconstruction of *Exotubispongia pustulata* RIGBY & SENOWBARI-DARYAN, 1996a; sponge has numerous vertical peripheral tubes that are connected by pores to spaces in the internal reticular skeleton and to the dermal surface through numerous ostia located on pustulelike elevations. The sponge is known, to date, only from upper Permian, Djebel Tebaga, Tunisia; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

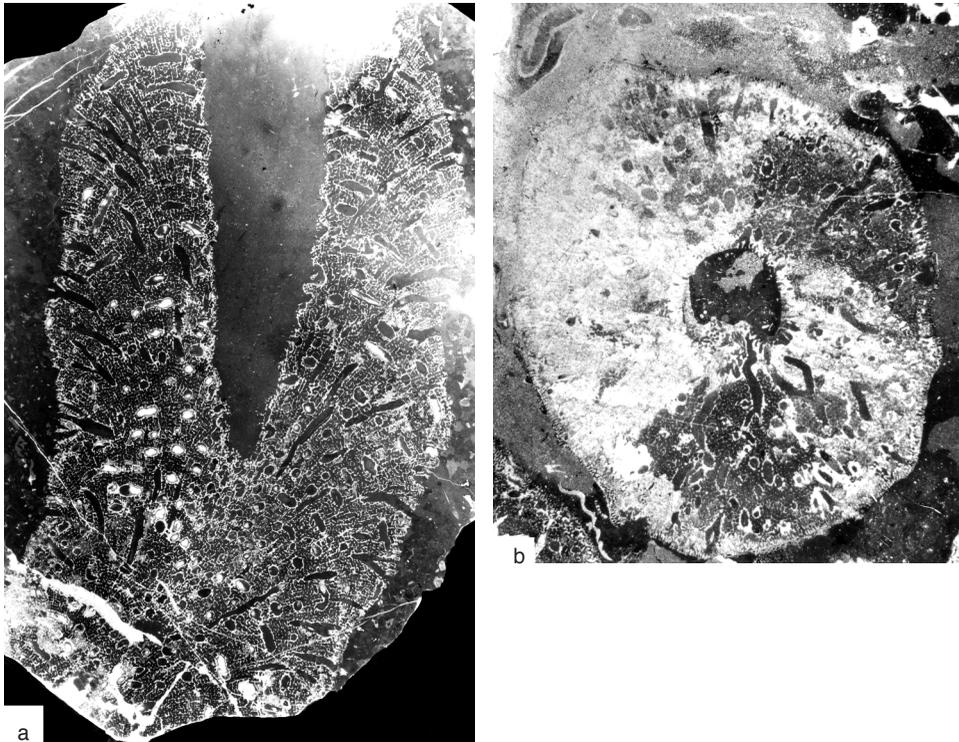


FIG. 257. *Permacorynella maxima* SENOWBARI-DARYAN, SEYED-EMAMI, & AGHANABATI, 1997, as seen in *a*, longitudinal and *b*, transverse sections. Sponge is characterized by an axial spongocoel and numerous additional branched tubes that diverge upward and outward to become perpendicular to dermal surface of sponge; Norian-Rhaetian, Triassic, Nayband Formation, Iran,  $\times 2$  (Senowbari-Daryan & Rigby, 2011).

WENDT (1979, 1984, 1990) concluded that principally five types of microstructure occur within the inozoan sponges. He listed them as: (1) granular; (2) irregular; (3) spherulitic; (4) clinogonal; and (5) orthogonal. More than one microstructure type may occur in primary and secondary skeletons within the same sponge skeleton.

A granular microstructure (Fig. 244) was observed, for example, in the Permian–Triassic genus *Himatella* ZITTEL, 1878 (WENDT, 1979), and an irregular microstructure is known from the Triassic genus *Eudea* (WENDT, 1979, 1990; MASTANDREA & RUSSO, 1995).

Spherulitic microstructure (Fig. 244), the most common microstructure in inozoan sponges, is known from the majority of Permian and Triassic genera. It has been recog-

nized, e.g., in Permian *Sphaeropontia* RIGBY & SENOWBARI-DARYAN, 1996a (Fig. 258), and in the Triassic genera *Sestrostomella* ZITTEL, 1878 (DIECI, ANTONACCI, & ZARDINI, 1968; WENDT, 1979; MASTANDREA & RUSSO, 1995), or *Peronidella* (DIECI, ANTONACCI, & ZARDINI, 1968; MÜLLER-WILLE & REITNER, 1993). A list of Permian inozoan sponges with spherulitic microstructure from Djebel Tebaga, Tunisia was given by RIGBY and SENOWBARI-DARYAN (1996a), with sizes of spherulites in those sponges ranging from 30–100  $\mu\text{m}$ .

Clinogonal microstructure (Fig. 244) occurs in the Triassic species *Stellispongia variabilis* (WENDT, 1979, 1984). According to WENDT (1975, 1979, 1984), the Triassic sponge *Cassianostroma küpperi* FLÜGEL has a clinogonal microstructure. *Cassianostroma* was originally described as a hydrozoan by

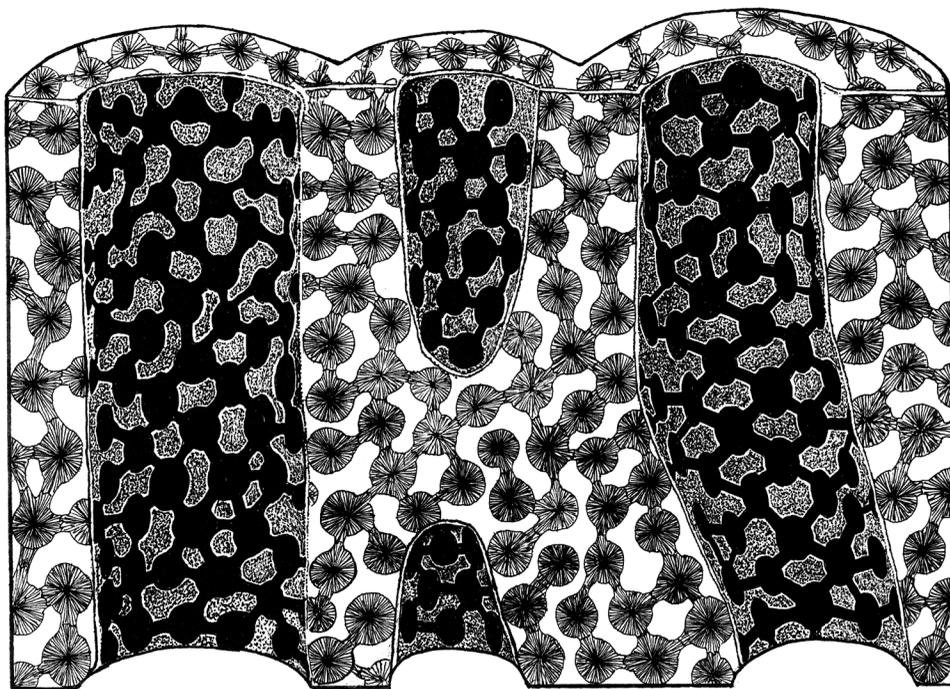


FIG. 258. Spherulitic microstructure of *Sphaeropontia regulara* RIGBY & SENOWBARI-DARYAN, 1996a, upper Permian, Djebel Tebaga, Tunisia. This type of microstructure is most abundant in aragonitic inozoan and sphinctozoan sponges; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

FLÜGEL (1960), but it also may be considered as an inozoan sponge. However, according to FLÜGEL (1960, p. 55) the “radial-strahligen Bau der ‘Radial-Struktur’” should be classified as spherulitic. Similar (or identical) sponges from the same horizon and locality, but with irregular microstructure, were described as *Stromatowendtia* RUSSO, MASTANDREA, & BARACCA, 1994.

The occurrence of an orthogonal type microstructure (Fig. 244) is not proven in Triassic inozoans.

#### PALEOBIOLOGY, PATTERNS OF WATER CIRCULATION, AND PALEOCOLOGY

Possible water circulation patterns in Permian inozoan sponges of Djebel Tebaga, Tunisia, were discussed by RIGBY and SENOWBARI-DARYAN (1996a). They differentiated four main patterns (Fig. 259).

1. *Auriculospongia*-type: in these sheetlike sponges, water moved essentially horizontally.

2. *Peronidella*-type: cylindrical or club-shaped sponges with inhalant openings on side surfaces, and with one or several spongocoels open at the summit; passage of water was horizontal and then vertical.

3. *Pseudohimatella*-type: cylindrical or club-shaped sponges without differentiated inhalant openings on side surfaces, but at the top of the sponge, and associated there with one or several spongocoels; passage of water was vertically downward, then horizontal, and then vertically upward.

4. *Stellispongiella*-type: sponges where inhalant and exhalant openings are both located on side surfaces; passage of water was horizontal, then vertical, and then horizontal.

Similar water movement patterns also may have been present in Mesozoic inozoan sponges.

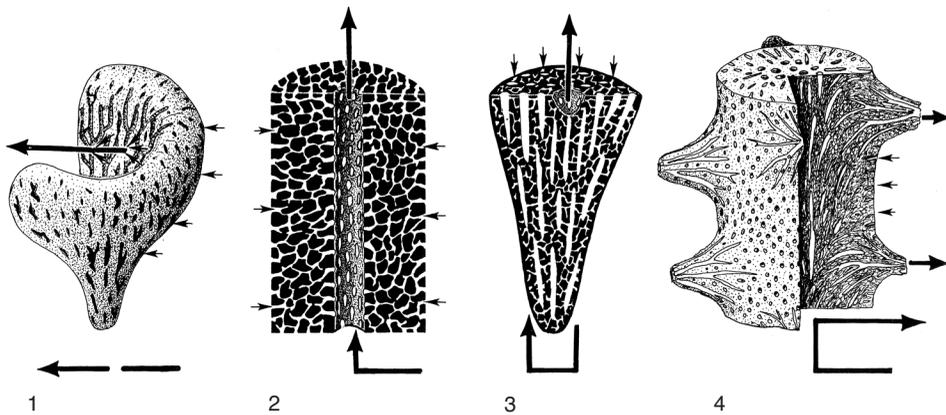


FIG. 259. Pathways of water movement in inozoan sponges. *Small arrows* indicate inhalant current directions; *large arrows* indicate exhalant directions. 1, *Auriculospongia*-type (pathway: inhalant = horizontal, exhalant = horizontal); 2, *Peronidella*-type (pathway: inhalant = horizontal, exhalant = vertically upward); 3, *Pseudohimatella*-type (pathway: inhalant = vertically downward, exhalant = vertically upward); 4, *Stellispongiella*-type (pathway: inhalant = horizontal, exhalant = horizontal); schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

Inozoan sponges, as important late Paleozoic and Triassic reef builders, lived in the same biotopes as the sphinctozoan sponges and likely had functions similar to those of the sphinctozoans, discussed previously (see p. 341–342).

#### REVIEW OF CLASSIFICATION

A summary of the review of classification of inozoan sponges by earlier authors was given by RIGBY and SENOWBARI-DARYAN (1996a). In the same publication, they subdivided the inozoans of STEINMANN (1882) into two orders: the Inozoa, which includes those with a spicular skeleton; and the Inozoida, which includes those without a spicular skeleton. Sponges from both the Inozoa and the Inozoida were placed in the classes Demospongea (=Demospongiae), and Calcarea by FINKS and RIGBY (2004d). They subdivided the hypercalcified sponges and placed them into the following subclass to ordinal level groupings.

##### Class Demospongiae

Subclass Ceractinomorpha LÉVI, 1953

Order Agelasida VERRILL, 1907

Order Vaceletida FINKS & RIGBY, 2004d

Subclass Tetractinomorpha LÉVI, 1953

Order Hadromerida TOPSENT, 1898

##### Class Calcarea

Subclass Calcinea BIDDER, 1898

Order Clathrinida HARTMAN, 1958

Order Murrayonida VACELET, 1981

Subclass Calcaronea BIDDER, 1898

Order Leucosolenida HARTMAN, 1958

Order Sycettida BIDDER, 1898

Order Stellispongiida FINKS & RIGBY, 2004d

Order Sphaerocoeliida WENDT, 1979

Order Lithonida DÖDERLEIN, 1892

#### PATTERNS OF EVOLUTION AND EXTINCTION

Inozoans, like the sphinctozoans, had pulses of major diversification separated by times of extinction during the late Paleozoic and Mesozoic, and had reduced records, to near total extinction, in the Cenozoic. These records have not been widely published, although the prominence of both of these groups in the Permian and Triassic records is well known. Currently, approximately 100 genera of various hypercalcified inozoan sponges have been described, including forms now placed dominantly in the Demospongiae, but including several Mesozoic and Cenozoic genera placed in the Calcarea as well.

Figure 260 shows the abundance and number of inozoan genera reported to date from each geologic period through the Phanerozoic.

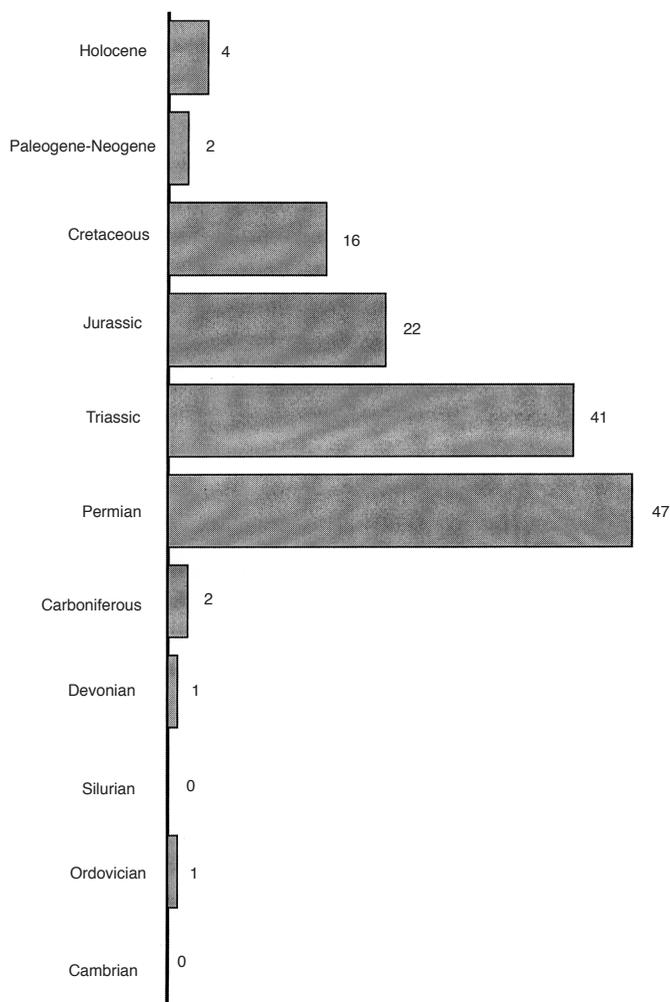


FIG. 260. Number of inozoan genera per geologic period through the Phanerozoic. Genera that have been described as hydrozoans are not considered in the diagram (Senowbari-Daryan & Rigby, 2011).

**Cambrian**

No inozoan sponges have been described from the Cambrian.

**Ordovician**

The single genus *Imperatoria*, based on the species *I. mega* has been reported as inozoan by RIGBY and POTTER (1986) from the Upper Ordovician Kangaroo Creek Formation, Klamath Mountains, northern California. This sponge was attributed to the sphinctozoan genus

*Pseudoimperatoria* by SENOWBARI-DARYAN and RIGBY (1988).

**Silurian**

No Silurian inozoan sponges have been documented to date.

**Devonian**

The genus *Fissispongia* KING, 1938, is the only inozoan sponge currently reported from the Devonian. The genus is a moderately long-ranging form that first appeared in the Middle Devonian (?Eifelian), of Alaska

(RIGBY & BLODGETT, 1983), but which ranges up through the Carboniferous into the lower Permian in the south-central United States.

### Carboniferous

Only two genera of inozoan sponges have been reported from the Carboniferous, including *Fissispongia*, cited above, and the somewhat similar long-ranging genus *Maeandrostia* GIRTY, 1908b. These sponges marked the base of major expansions of the inozoans that took place during the Permian, for *Maeandrostia* also ranges from the upper lower Carboniferous, through the Permian, into the lower Middle Triassic.

### Permian

The Permian marks the first major pulse of diversification of the hypercalcified sponges with inozoan skeletal structure. Presently, 47 genera of inozoans have been described from the Permian, and 46 of these genera appear in the Permian as new forms. With that taxonomic expansion, the inozoans also became more geographically widespread, as noted in Stratigraphic and Geographic Occurrences (p. 371).

The Permian–Triassic boundary extinction event had a major impact on the inozoan sponges, as it did on the sphinctozoan forms, and fossils of other phyla too. Of the 47 inozoan genera reported from the Permian, only 15 or 16 survived into the Triassic, so that the extinction rate was approximately 70%.

### Triassic

Of the 41 inozoan genera known from the Triassic, 25 or 26 genera are new and 15 or 16 genera survived from the Permian. As with the sphinctozoans, there is a major break in the record, for no inozoans are known from the Lower Triassic (Scythian), and only *Maeandrostia* GIRTY, 1908b, see above, has been found in Anisian reefs of northern Italy (SENOWBARI-DARYAN & others, 1993). Inozoan sponge taxa increased greatly in number during the

Middle and Upper Triassic, and a second pulse of sponge diversification was produced. As with the inozoans, however, the number of taxa decreased sharply toward the end of the Triassic, and a second major extinction event occurred at the Triassic–Jurassic boundary. Only *Sestrostomella*, and questionably *Stellispongiella*, among the demosponges, and *Stellispongia*, *Pareudea*, *Eudea*, and *Oculospongia* among the Calcarea, and *Cornuasporgia* and ?*Trameria* among the class and order Uncertain inozoans, survived into the Jurassic beyond the boundary event. From the Triassic on through the Cenozoic, the Calcarea play an ever increasingly significant role in the evolutionary development of the inozoans.

### Jurassic

A third pulse of inozoan diversification resulted in the documented occurrence of 22 new inozoan genera, along with 6 genera that survived beyond the boundary extinction event into the Jurassic, which had an extinction rate of about 73%. This has resulted in a known Jurassic inozoan fauna of 22 genera. Of these, the 5 genera, *Sestrostomella*, *Epitheles*, *Winwoodia*, *Aulocopagia*, and *Stellispongiella* are classed with the Demospongiae, and the remainder are classed with the Calcarea (FINKS & RIGBY, 2004a, 2004d). Except for *Sestrostomella*, which was reported from the Canadian Atlantic Shelf, all other Jurassic inozoan genera have been reported from localities in Europe, around the western end of the Tethyan seaway, an area that continued as a major locus of evolution of these forms.

### Cretaceous

A total of 16 to 18 genera of inozoan sponges have been reported, and 2 more are questionably reported from the Cretaceous. Of these, 10 or 12 genera are new forms and 6 are carry-over elements from the Jurassic. Only *Trachytila*, *Pharetrospongia*, and *Elasmopagia* are demosponge forms, and the remainder of these Cretaceous inozoans are

genera of the moderately rapidly evolving family Stelligeridae, of the Calcarea (FINKS & RIGBY, 2004a, 2004d). All of these Cretaceous inozoans have been reported from localities in Europe, which, again, was the locus of inozoan evolution for the period.

#### Paleogene–Neogene

Only two inozoan genera are documented from deposits of these ages. *Elasmotoma* has been reported from the Eocene of Mexico, and *Tretocalia* from the Miocene of Australia (FINKS & RIGBY, 2004d, p. 741, 748). The lower and mid-Cenozoic record of inozoans is one of near extinction of sponges with this skeletal structure.

#### Holocene

Four genera of inozoans have been reported as occurring in the Holocene. These include: *Trachysphacion* POMEL, 1872; *Eudea* LAMOUROUX, 1821; *Mammillopora* BRONN, 1825, and *Peronidella* ZITTEL in HINDE, 1893, all from the Mediterranean Sea near France, and all are now included in the Calcarea (FINKS & RIGBY, 2004d, p. 743–747). These inozoans are living representatives of genera that first appeared in the early Mesozoic.

### TEMPORAL AND SPATIAL DISTRIBUTION OF SPHINCTOZOANS AND INOZOANS

#### STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCES

In general, sphinctozoan and inozoan sponges have a lower and mid-latitude distribution throughout their history and have relatively limited geographic distributions through much of the early Paleozoic. However, they became more widely distributed and considerably more diverse during the Permian and Triassic and became increasingly less diverse and more geographically limited during the later Mesozoic and Cenozoic (Fig. 245, Fig. 261–272).

The heteractinids *Jawonya* and *Wagima*, which occur in the lower and lower middle Cambrian in the Northern Territory (KRUSE, 1983, 1990) of Australia, are the oldest forms included by some in the sphinctozoans. Moderate faunules of early sphinctozoans, including *Blastulospongia* and *Amblysiphonella*, and the heteractinid *Nucha*, are also the earliest sphinctozoan forms and have been reported from middle Cambrian rocks of New South Wales (PICKETT & JELL, 1983). Other documented Cambrian occurrences are the single-genus records of *Polythalamia* from the lower Cambrian of Alaska and Nevada, in western North America (DEBRENNE & WOOD, 1990), and the upper Cambrian occurrence of *Blastulospongia* from Hubei, China (CONWAY MORRIS & CHEN, 1990), and from Queensland, Australia (BENGTSON, 1986; Fig. 261).

Sponges described as archaeocyaths from the Cambrian could be attributed to the inozoans, but they are not discussed here. The inventory of sphinctozoan and inozoan sponges treated here is based on cited publications and on the works of FINKS and RIGBY (2004a, 2004b, 2004d).

The oldest nonarchaeocyath sponge, *Imperatoria mega* (RIGBY & POTTER, 1986), was described as being an inozoan from Ordovician rocks of the eastern Klamath Mountains of northeastern California. This sponge was attributed to the sphinctozoan genus *Pseudoimperatoria* by SENOWBARI-DARYAN and RIGBY (1988).

Five genera of Ordovician sphinctozoans, *Cliefdenella*, *Angullongia*, *Belubulaia*, *Nibiconia*, and *Rigbyetia* (Fig. 262), have been documented from New South Wales, Australia by WEBBY (1969), WEBBY and RIGBY (1985), RIGBY and WEBBY (1988), and WEBBY and LIN (1988). From western North America, nine Ordovician genera have been reported from northern California and Oregon (RIGBY & POTTER, 1986; WEBBY & LIN, 1988), including *Amblysiphonella*, *Amblysiphonelloides*, *Angullongia*, *Corymbospongia*, *Cystothalamiella*, *Exaulipora*, *Porefieldia*, *Pseudoimperatoria*, and *Rigbyetia*.

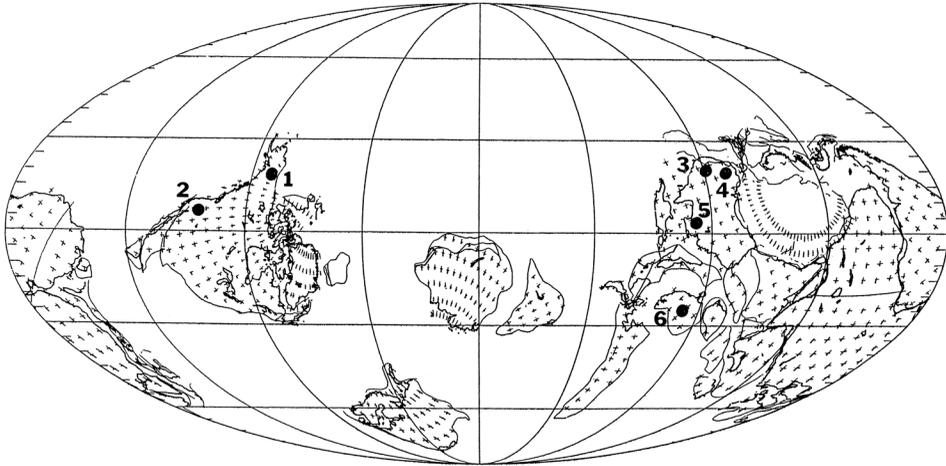


FIG. 261. Paleogeographic distribution of localities from where Cambrian sphinctozoans have been reported: 1, Tatonduk River, eastern Alaska, United States; 2, Antler Peak quadrangle, Nevada, United States; 3, Queensland, Australia; 4, New South Wales, Australia; 5, Northern Territory, Australia; 6, Hubei, China (base map adapted from Scotese & McKerrrow, 1990).

Five genera of Ordovician sphinctozoans, including *Alaskaspongia*, *Angullongia*, *Cliefdenella*, *Corymbospongia*, and *Pseudoporefieldia*, have been documented from Alaska and the Yukon Territory (STOCK, 1981; RIGBY, POTTER, & BLODGETT, 1988). These are the most diverse Ordovician sphinc-

tozoan faunules documented to date, and they mark an early period of diversification of sponges with these types of chambered skeletons. *Khalfinaea* WEBBY & LIN, 1988, has been reported from the Shaanxi and Xinjiang provinces of China and the Altai Sayan region of Russia, and it is the only

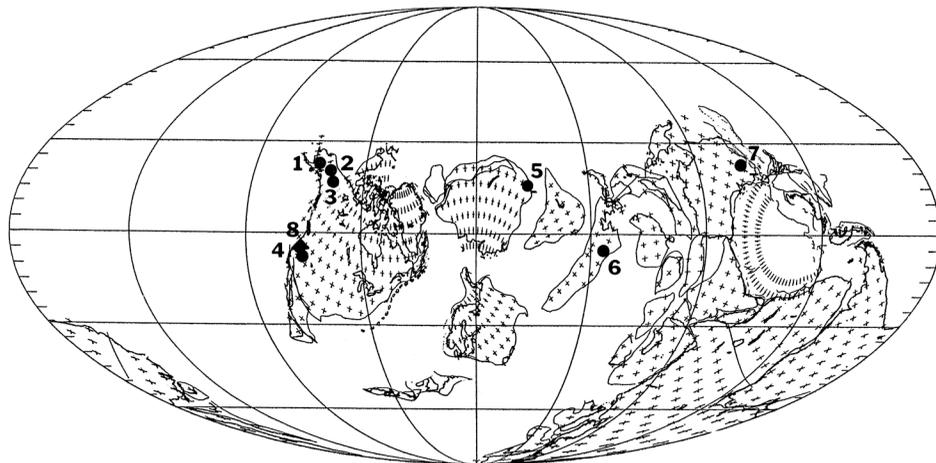


FIG. 262. Paleogeographic distribution of localities from where Ordovician sphinctozoan (circles) and inozoan (triangle) sponges have been reported. Sphinctozoans occur at localities: 1, McGrath A-4 and A-5 quadrangles, west-central Alaska, United States; 2, Livengood quadrangle, east-central Alaska, United States; 3, Jones Ridge, Yukon Territory, Canada; 4, Antler Peak quadrangle, Nevada; 5, Altai Sayan, eastern Kazakhstan, Russia; 6, Hubei, China; 7, New South Wales, Australia. Inozoans have been reported from locality 8, Klamath Mountains, Oregon (base map adapted from Scotese & McKerrrow, 1990).

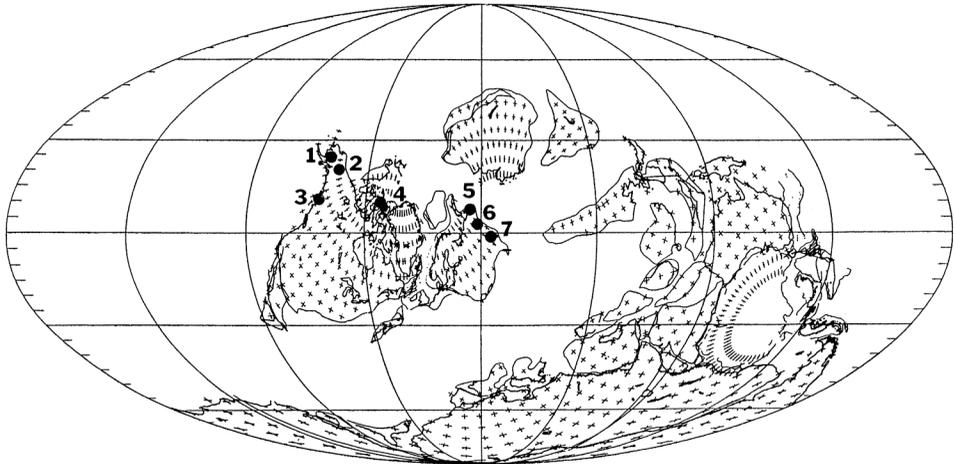


FIG. 263. Paleogeographic distribution of localities from where Silurian sphinctozoan sponges have been reported: 1, Taylor Mountains D-2 quadrangle, southwestern Alaska, United States; 2, White Mountain area, McGrath A-4 and A-5 quadrangles, west-central Alaska, United States; 3, Seaotter Sound area, southeastern Alaska, United States; 4, Cornwallis Island, District of Franklin, Northwest Territories, Canada; 5, Pay-Khoy, Cape Belyi Nos, northern Russia; 6, western slope of Northern Ural Mountains, Russia; 7, eastern slope of Central Ural Mountains, Russia; no inozoans have been reported from the Silurian (base map adapted from Scotese & McKerrow, 1990).

Ordovician sphinctozoan sponge described from these areas (Fig. 262).

Silurian sphinctozoan sponges have somewhat more limited diversity and geographic occurrences than those of the Ordovician (Fig. 263). Silurian sphinctozoans have been reported from Pay-Khoy, Cape Belyi Nos,

and the Northern and Central Ural Mountains of Russia (MYAGKOVA, 1955a, 1955b; ZHURAVLEVA & MYAGKOVA, 1974a, 1974b, 1981, 1987), and from southeastern, south-central, and southwestern Alaska in North America, where *Aphrosalpinx*, *Nematosalpinx*, and *Palaeoscheda* have been recovered (RIGBY,

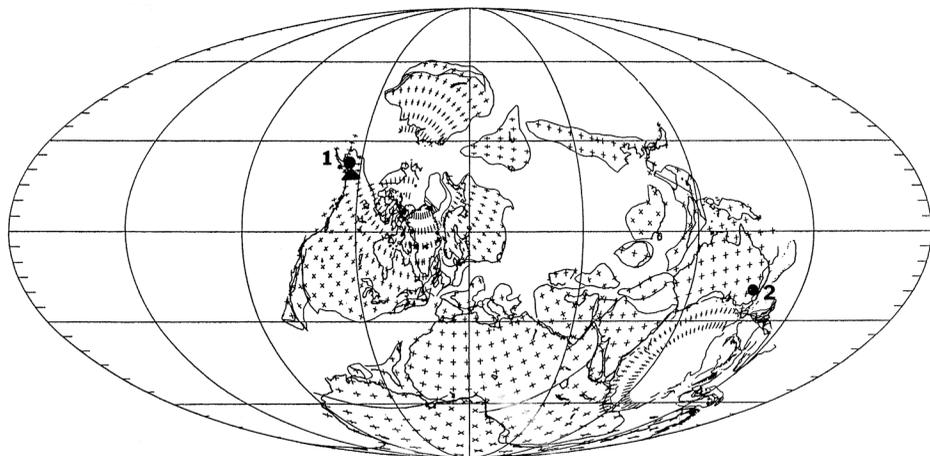


FIG. 264. Paleogeographic distribution of localities from where Devonian sphinctozoan (circles) and inozoan (tri-angle) sponges have been reported: 1, McGrath area, west-central Alaska, United States, where both sphinctozoan and inozoan sponges occur; 2, New South Wales, Australia (base map adapted from Scotese & McKerrow, 1990).

NITECKI, & others, 1994). The marked similarity of aphasalpingid sphinctozoan sponges of Alaska and Russia suggests significant paleobiogeographic relationships between the Alexander terrane of southeastern Alaska and the Nixon Fork terrane of west-central Alaska with that of the Ural Mountains, as was earlier suggested by RIGBY, NITECKI, and others (1994). *Aphrosalpinx* MYAGKOVA, 1955b, and *Palaescheda* MYAGKOVA, 1955a, are known from the Silurian of both the northern Ural Mountains and southeastern Alaska. *Nematosalpinx* MYAGKOVA, 1955a, is known from both the Ural Mountains and southwestern Alaska. It is associated with *Cystothalamiella* RIGBY & POTTER, 1986, in the latter area.

*Rigbyspongia* DE FREITAS, 1987, was described from Ludlovian rocks from Cornwallis Island, Arctic Canada. It is the only sphinctozoan reported from that region.

Sphinctozoans were markedly restricted, both geographically and taxonomically, in the Devonian (Fig. 264). *Hormospongia* RIGBY & BLODGETT, 1983, has been reported from the Eifelian of the McGrath area of southwestern Alaska, the type area, and from New South Wales, Australia (PICKETT & POHLER, 1993). *Radiothalamos* PICKETT & RIGBY, 1983, the other known Devonian sphinctozoan, was described from the earlier Lower Devonian of New South Wales. The questionable inozoan, *Fissispongia*, has been reported from the Devonian of Alaska (RIGBY & BLODGETT, 1983). It is the only possible Devonian inozoan known to date, and *Fissispongia* is considered to be a sphinctozoan by some workers.

Carboniferous sphinctozoans are known principally from lands bordering the Tethyan Seaway (Fig. 265), but no major diverse sphinctozoan Carboniferous assemblages have been reported from the region. Three genera, *Amblysiphonella*, *Colospongia*, and *Sollasia*, have been reported from Austria (LAUBE, 1865; PELZMANN, 1930; LOBITZER, 1975; KÜGEL, 1987), and five genera, *Amblysiphonella*, *Cystothalamia*, *Discosiphonella*, *?Sebergasia*, and *Sollasia* from Spain (STEINMANN, 1882; GARCÍA-BELLIDO,

2002; GARCÍA-BELLIDO, SENOWBARI-DARYAN, & RIGBY, 2004). *Sollasia* has recently been reported from the United Kingdom (RIGBY & MUNDY, 2000), and *Amblysiphonella* and *Discosiphonella* from China (INAI, 1936). *Amblysiphonella* and other sponges have also been reported from the upper Carboniferous of Nebraska and Texas (CLARKE, 1897; GIRTY, 1908b, 1915; KING, 1933, 1938, 1943; TOOMEY, 1979), at some distance from the Tethyan region. As in earlier occurrences, these fossil localities were also at tropical to subtropical paleolatitudes.

Carboniferous inozoans are also limited geographically and taxonomically. *Maeandrostia* GIRTY, 1908b, was first described from the Pennsylvanian of Kansas, but it has also been reported from Texas and Oklahoma (Fig. 265), as has the questionable inozoan *Fissispongia* (KING, 1938; RIGBY & MAPES, 2000). *Maeandrostia* has also been reported as occurring in Carboniferous deposits of Sicily and the former Yugoslavia, along the western margin of the Tethyan seaway (FINKS & RIGBY, 2004d, p. 644).

Sphinctozoans are significant faunal elements in Permian assemblages from around the margin of the Tethyan seaway and in isolated lower latitude areas in western North and South America (Fig. 266; RIGBY & SENOWBARI-DARYAN, 1995). Several major assemblages have been described from the Tethyan seaway area, and these occurrences have been documented in FINKS and RIGBY (2004d). For example, 20 genera have been documented from Sicily (PARONA, 1933; SENOWBARI-DARYAN, 1980a, 1990; SENOWBARI-DARYAN & DI STEFANO, 1988a), 27 genera from Tunisia (TERMIER & TERMIER, 1955; H. TERMIER, G. TERMIER, & VACHARD, 1977; SENOWBARI-DARYAN & RIGBY, 1988, 1991) in the western part of the Tethyan seaway margin, and 15 genera from Oman (WEIDLICH & SENOWBARI-DARYAN, 1996), on the southern seaway margin. Sphinctozoans are also significant faunal elements from various localities in China, where 34 genera have been described (HAYASAKA, 1918; DENG, 1982a, 1982b; ZHANG, 1983,

1987; FAN & ZHANG, 1985; REINHARDT, 1988; RIGBY, FAN, & ZHANG, 1988, 1989a; FLÜGEL & REINHARDT, 1989; RIGBY, FAN, & others, 1994; BELYAEVA, 2000; FAN, WANG, & WU, 2002).

Sphinctozoan sponges of Russia have been extensively documented in the major work by BOIKO, BELYAEVA, and ZHURAVLEVA (1991), where faunas from the different regions were treated in separate chapters in the volume. Permian sponges from Middle Asia (southern Tian-Shan, Karatchatyr Mountains), from North Pamir (Darwaz and Piotr I Mountains), from the Far East (southern Primorsky Krai), from Armenia, and from the Crimea are documented in separate chapters, along with later chapters on Triassic and Jurassic sphinctozoans.

Less diverse sphinctozoan assemblages are known from the Permian of Greece (GUERNET & TERMIER, 1969; FLÜGEL & REINHARDT, 1989), Pakistan (WAAGEN & WENTZEL, 1888), Iran (SENOWBARI-DARYAN & HAMEDANI, 2002; SENOWBARI-DARYAN, RASHIDI, & HAMEDANI, 2005), India (DE KONINCK, 1863), Thailand (SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994), Indonesia (WILCKENS, 1937), Cambodia (MANSUY, 1913, 1914), and Japan (HAYASAKA, 1918; AKAGI, 1958; IGO, IGO, & ADACHI, 1988), as occurrences are traced around the Tethyan seaway margin. In most of these areas, only one or two sphinctozoan genera have been reported, although seven genera have been reported from Thailand and six from Tajikistan in Russia.

In North America, nine sphinctozoans, including *Amblysiphonella*, *Cystothalamia*, *Exaulipora*, *Guadalupia*, *Lemonea*, *Parauvanella*, *?Polysiphonaria*, *Preverticillites*, and *Tristratocoelia*, have been reported as being part of the sponge assemblage from the Permian reef complex of the Guadalupe Mountains and related areas in Texas and New Mexico (GIRTY, 1908a; KING, 1943; SENOWBARI-DARYAN, 1990; FINKS, 1995, 1997; RIGBY, SENOWBARI-DARYAN, & LIU, 1998).

A modest faunule of five sphinctozoan genera has been described from western

Venezuela (RIGBY, 1984), as the only suite of Permian sphinctozoans documented to date from South America. This assemblage includes *Colospongia*, *Cystothalamia*, *Guadalupia*, and *Girtyocoelia*.

The Permian marked a major expansion, both taxonomically and geographically, in the occurrence of inozoan sponges (Fig. 267). Major inozoan assemblages have been collected and described from Permian rocks in Tunisia (TERMIER & TERMIER, 1955, 1974; H. TERMIER, G. TERMIER, & VACHARD, 1977; RIGBY & SENOWBARI-DARYAN, 1996a), where approximately 30 genera have been described. Somewhat less extensive inozoan faunas have been described from various localities in eastern and southeastern China (RIGBY, FAN, & ZHANG, 1989b; FAN, RIGBY, & ZHANG, 1991; WU, 1991; RIGBY, FAN, & others, 1994), and from the Texas–New Mexico region in the United States (GIRTY, 1908a; KING, 1943; FINKS, 1995; RIGBY, SENOWBARI-DARYAN, & LIU, 1998), where 12 genera are documented. In a major addition to the Guadalupe Mountain assemblage, RIGBY and BELL (2006), described 5 additional genera from Guadalupian Permian rocks of the Guadalupe Mountains.

Less diverse Permian inozoan faunules have been documented from Italy (Sicily), (PARONA, 1933; ALEOTTI, DIECI, & RUSSO, 1986; SENOWBARI-DARYAN & DI STEFANO, 1988a), Thailand (SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994), Iran (SENOWBARI-DARYAN, RASHIDI, & HAMEDANI, 2005), around the western end of the Tethyan seaway, where four genera have been documented in each of those localities, and where one genus, *Peronidella*, has been reported from the Permian of Hungary (H. W. FLÜGEL, 1973).

In the western part of North America, a single Permian inozoan genus, *Radiotrabeulopora*, has been reported from east-central California (RIGBY, LINDER, & STEVENS, 2004). This genus has been interpreted as a disjectopoid-type hypercalcified sponge that has possible inozoan relationships (see p. 319).

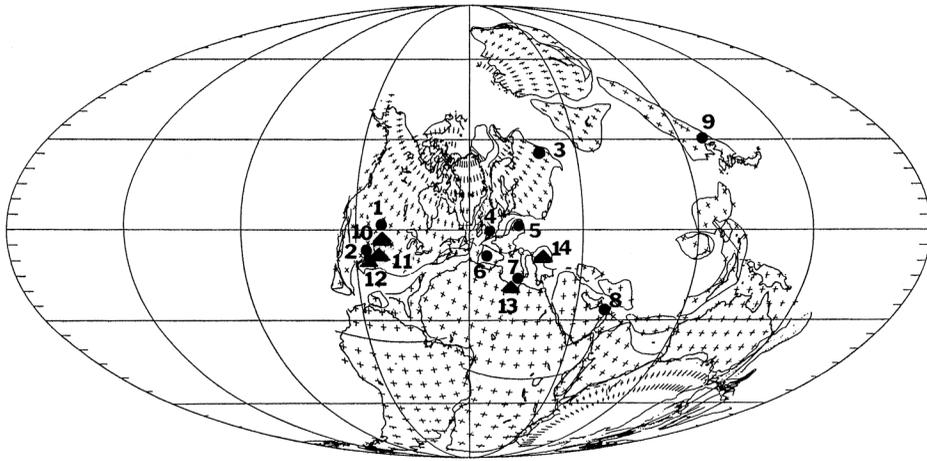


FIG. 265. Paleogeographic distribution of localities from where Carboniferous sphinctozoan (circles) and inozoan (triangles) sponges have been reported. Sphinctozoan sponges have been reported from localities: 1, Nebraska, United States; 2, Texas, United States; 3, Russia, in general; 4, Yorkshire, United Kingdom; 5, Austria; 6, Spain; 7, Sicily, Italy; 8, Oman; 9, Manchuria, China. Inozoans have been reported from localities: 10, Kansas, United States; 11, Oklahoma, United States; 12, Texas, United States; 13, Sicily, Italy; 14, former Yugoslavia (base map adapted from Scotese & McKerrrow, 1990).

Triassic sphinctozoans underwent a major taxonomic burst, and they have been reported from a greater number of localities than sphinctozoan faunas from any earlier period of geologic time (Fig. 268). These occurrences

are cited in FINKS and RIGBY (2004c). Like Permian faunas, Triassic sphinctozoans have been reported widely from margins of the Tethyan seaway and from the western parts of North and South America. The most diverse

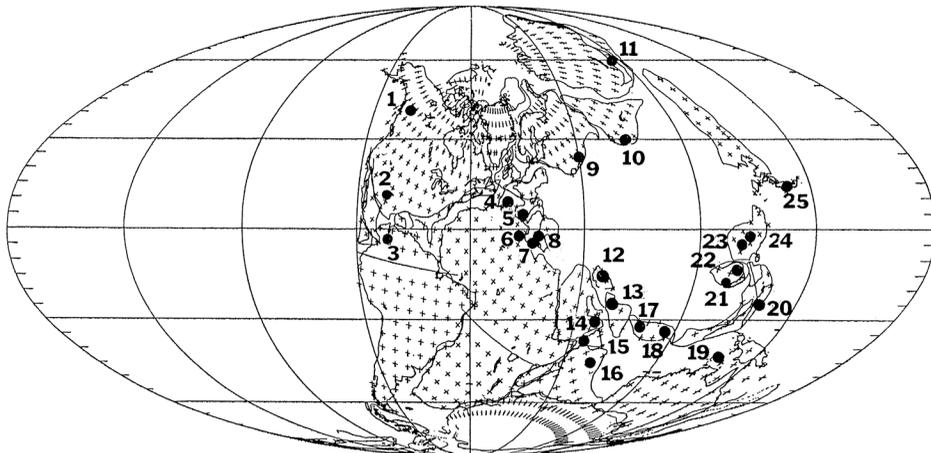


FIG. 266. Paleogeographic distribution of localities from where Permian sphinctozoan sponges have been reported: 1, British Columbia, Canada; 2, Guadalupe Mountain region, Texas and New Mexico, United States; 3, western Venezuela; 4, Spain; 5, Sicily; 6, Tunisia; 7, Greece; 8, former Yugoslavia; 9, Ukraine; 10, Tajikistan; 11, Russian Far East; 12, Turkey; 13, Iran; 14, Oman; 15, Pakistan; 16, India; 17, Caucasus, Russia; 18, Tibet; 19, Timor; 20, Indonesia; 21, Thailand; 22, Cambodia; 23, Sichuan-Guizhou, China; 24, Hubei, China; 25, Japan (base map from Scotese & McKerrrow, 1990).

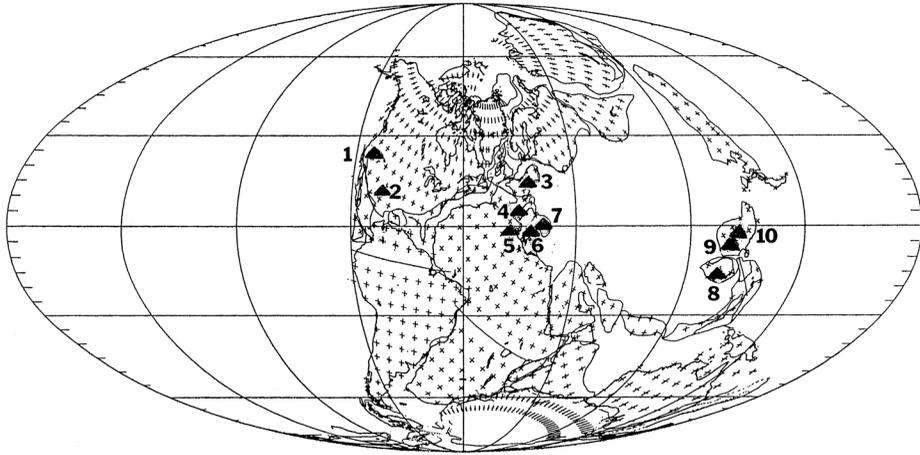


FIG. 267. Paleogeographic distribution of localities from where Permian inozoan sponges have been reported: 1, east-central California, United States; 2, Guadalupe Mountain region, Texas and New Mexico, United States; 3, Europe in general; 4, Sicily, Italy; 5, Tunisia; 6, former Yugoslavia; 7, Hungary; 8, Thailand; 9, Guangxi and Guizhou area, southeastern China; 10, Hubei area, eastern China (base map adapted from Scotese & McKerrow, 1990).

faunas are those from southeastern European and Middle Eastern countries.

North American assemblages were mainly collected from the western part of the United States, Canada, and Mexico. SENOWBARI-DARYAN and REID (1987)

described a moderate assemblage of sphinctozoans from the Stikine terrane, from the southern Yukon, in westernmost Canada. Sphinctozoans there are part of sponge reefs and interreef accumulations, and the occurrence of 14 sphinctozoan genera has been

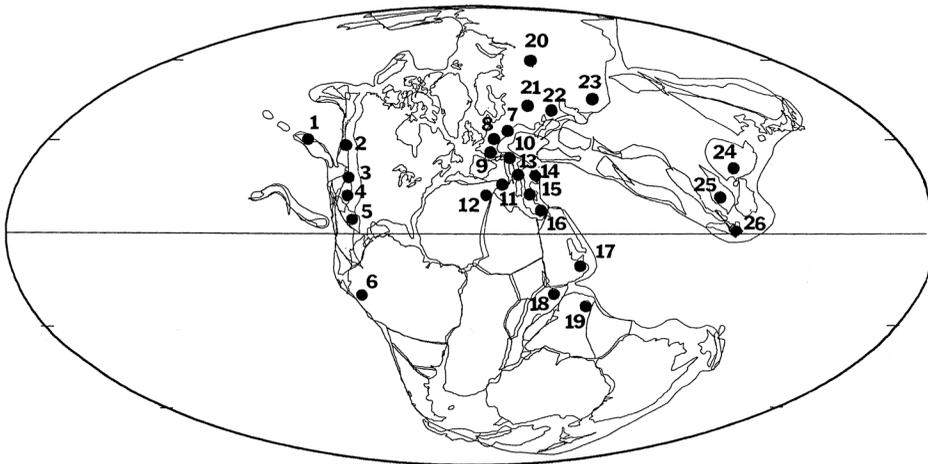


FIG. 268. Paleogeographic distribution of localities from where Triassic sphinctozoan sponges have been reported: 1, Stikine terrane, southern Yukon Territory, Canada; 2, Quesnel Range, southern British Columbia, Canada; 3, Willowa Mountains, eastern Oregon, United States; 4, Mineral County, western Nevada, United States; 5, Sonora, Mexico; 6, central Peru; 7, former Czechoslovakia; 8, Germany; 9, France; 10, northern Italy; 11, Sicily; 12, Tunisia; 13, former Yugoslavia; 14, Hungary; 15, Greece; 16, Turkey; 17, Oman; 18, Iran; 19, Himalayan Mountains, northern, India; 20, Northern Ural Mountains, Russia; 21, Ukraine; 22, Caucasus region, Russia; 23, Tajikistan and Pamir regions; 24, Sichuan, China; 25, Thailand; 26, Timor (base map from Scotese, 2001).

documented from the area. An additional genus, *Fanthalamia*, has been documented from Triassic rocks in the Quesnel Range, in southern British Columbia (STANLEY & SENOWBARI-DARYAN, 1999). Farther to the southeast, in eastern Oregon, three sphinctozoan genera, *Polycystocoelia*, *Neogudalupia*, and *Nevadathalamia*, have been reported from the Triassic of the Wallowa Mountains by SENOWBARI-DARYAN and STANLEY (1988). *Fanthalamia* SENOWBARI-DARYAN & ENGESER (1996), and *Cinnabaria* SENOWBARI-DARYAN (1990) occur in Triassic deposits in Nevada and British Columbia. The close tie of these assemblages with Chinese faunas is suggested because some of these genera are characteristic of Tethyan faunas and, as suggested by SENOWBARI-DARYAN and REID (1987), some of the genera documented in Yukon suites had been previously reported only from Tethyan localities, and others from both American and Tethyan localities. They suggested that such a mixture might reflect the origin of the Stikine terrane as an island in the ancestral Pacific Ocean, between the Tethys region and North America.

The occurrence of *Nevadathalamia* SENOWBARI-DARYAN, 1990, in Nevada, is geographically intermediate between occurrences of that sponge in the Yukon region of Canada, to the north, and from Sonora, Mexico, to the south, where it occurs with *Fanthalamia* and *Cinnabaria*, as reported by SENOWBARI-DARYAN (in STANLEY & others, 1994) and SENOWBARI-DARYAN, STANLEY, and GONZALEZ-LEON (2001).

The only Triassic sphinctozoans thus far reported from South America are from Peru (RAUFF, 1938; SENOWBARI-DARYAN, 1994b), where occurrences of *Amblysiophonella*, *Discosiphonella*, and *Polytholusia* have been documented. Generically diverse major faunas of Triassic sphinctozoans have been reported from southeastern Europe (Fig. 268), with 29 genera of sponges from the Alps (MÜNSTER, 1841; LAUBE, 1865; POMEL, 1872; STEINMANN, 1882; OTT, 1967; DIECI, ANTONACCI, & ZARDINI, 1968; SENOWBARI-DARYAN, 1978, 1981,

1990; SENOWBARI-DARYAN & SCHÄFER, 1979; SENOWBARI-DARYAN & RIEDEL, 1987). From Austria, 27 genera have been reported (MÜNSTER, 1841; STEINMANN, 1882; OTT, 1967; DIECI, ANTONACCI, & ZARDINI, 1968; OTT in KRAUS & OTT, 1968; WOLFF, 1973; OTT, 1974; SENOWBARI-DARYAN, 1978, 1990; SENOWBARI-DARYAN & SCHÄFER, 1979; DULLO, 1980; ENGESER & NEUMAN, 1986; SENOWBARI-DARYAN & RIEDEL, 1987; SENOWBARI-DARYAN & WÜRME, 1994). From Italy, primarily Sicily, 15 genera have been reported (SENOWBARI-DARYAN, 1980b; SENOWBARI-DARYAN & ABATE, 1986; SENOWBARI-DARYAN & SCHÄFER, 1986; SENOWBARI-DARYAN & DI STEFANO, 1988b); and from southern Italy (Calabria) where 6 genera have been described by SENOWBARI-DARYAN and ZAMPARELLI (1999, 2003), and SENOWBARI-DARYAN, ABATE, and others (1999). Sphinctozoan sponge faunas from the Carpathians include 17 genera (MÜNSTER, 1841; STEINMANN, 1882; VINASSA DE REGNY, 1901, 1908; SCHOLZ, 1972; MELLO, 1975; BALOGH & KOVACS, 1976; KOVÁCS, 1978a; SENOWBARI-DARYAN, 1978, 1990; SENOWBARI-DARYAN & RIEDEL, 1987; RIEDEL & others, 1988; FLÜGEL & others, 1991 in 1991–1992); and those from southern European countries (Greece, Romania, and the former Yugoslavia) include 16 genera (PANTIC, 1975; SENOWBARI-DARYAN, 1981, 1982, 1990; SENOWBARI-DARYAN & SCHÄFER, 1983; SENOWBARI-DARYAN & RIEDEL, 1987; RIEDEL & SENOWBARI-DARYAN, 1989).

Diverse sphinctozoan assemblages are known from Turkey, where at least 18 Triassic genera have been documented (RIEDEL, 1990; SENOWBARI-DARYAN, 1990, 1994a; SENOWBARI-DARYAN & LINK, 1998; SENOWBARI-DARYAN, LINK, & GARCÍA-BELLIDO, 2003), and from Tajikistan, where 22 genera have been cited in Triassic faunas (BOIKO, 1984a, 1990; BOIKO, BELYAEVA, & ZHURAVLEVA, 1991). Primary sources for Tajikistan occurrences of most of these genera are not cited, but the genera are listed from Tajikistan in FINKS and RIGBY (2004d).

Less diverse Triassic sphinctozoan collections have also been documented from various areas in western Russia, including the Caucasus (MOISEEV, 1944; BOIKO, 1990; BOIKO, BELYAEVA, & ZHURAVLEVA, 1991), where 10 genera have been documented; and from the Pamir region (BOIKO, 1986), where 3 genera are cited. Single Triassic sphinctozoan genera are known from the Northern Urals (MYAGKOVA, 1955a) and from the Ukraine–Crimea region (BOIKO, BELYAEVA, & ZHURAVLEVA, 1991). In addition, 11 different genera are listed as occurring in Russia, presumably western Russia, by FINKS and RIGBY (2004d) (MYAGKOVA, 1955a, 1955b; SENOWBARI-DARYAN, 1990; BOIKO, BELYAEVA, & ZHURAVLEVA, 1991).

Less diverse faunules are known from Romania, where 4 Triassic sphinctozoan genera are cited in FINKS and RIGBY (2004d), including *Amblysiphonella*, *Enoplocoelia*, *Solenolmia*, and *Stylothalamia* (STEINMANN, 1882; SENOWBARI-DARYAN & RIEDEL, 1987; RIEDEL & SENOWBARI-DARYAN, 1988; SENOWBARI-DARYAN, 1990). The 2 genera *Solenolmia* and *Vesicocaulus* have been identified from the Triassic of the former Czechoslovakia (JABLONSKY, 1972; SENOWBARI-DARYAN & RIEDEL, 1987; SENOWBARI-DARYAN, 1990). In the area around the southwestern part of the Tethyan seaway, Triassic sphinctozoans have also been collected from Iran, where the occurrence of 25 genera has been reported (SENOWBARI-DARYAN & HAMEDANI, 1999; SENOWBARI-DARYAN, 2005a; FINKS & RIGBY, 2004d). Triassic sphinctozoans reported from Oman include 10 genera (SENOWBARI-DARYAN, 1990; BERNECKER, 1996; SENOWBARI-DARYAN, BERNECKER, & others, 1999; FINKS & RIGBY, 2004d). Only the genus *Cinnabaria*, described as *Colospongia catenulata* by BHARGAVA and BASSI (1985), has been reported from India.

In the southeastern part of the seaway margin, reported occurrences of Triassic sphinctozoans from China include *Dracolychnos* WU & XIAO, 1989, and *Casearia*; both genera are now included in the Hexactinellida (REID, 2004, p. 486). These genera

and other hexactinellids are not included in this presentation. From the Moluccas (Indonesia), five genera of Triassic sphinctozoans have been described (WILCKENS, 1937) and four genera from Timor (VINASSA DE REGNY, 1915; SENOWBARI-DARYAN, 1990).

Triassic inozoan occurrences are primarily focused around the Tethyan margin (Fig. 269). Large faunules of Triassic inozoans have been reported from Italy, where ten genera have been documented from the Dolomite Alps of northern Italy (DIECI, ANTONACCI, & ZARDINI, 1968; CUIF, 1974; RUSSO, 1981; BIZZARINI & RUSSO, 1986; ENGESER & TAYLOR, 1989; RIEDEL & SENOWBARI-DARYAN, 1991), and two genera from the Island of Sicily (SENOWBARI-DARYAN & SCHÄFER, 1986).

Elsewhere in Europe, 2 genera are known from the Triassic of Austria (KLIPSTEIN, 1843–1845; HAAS, 1909), and 10 from several countries in Europe in general (FINKS & RIGBY, 2004d). A single Triassic inozoan genus, *Himatella*, has been reported from Tunisia (H. TERMIER, G. TERMIER, & VACHARD, 1977). Three genera, *Dactylocoelia*, *Reticuloceelia*, and *Peronidella*, have been documented from the Triassic of Turkey (CUIF, 1973; RIEDEL, 1990), and at least 12 genera from Iran (SENOWBARI-DARYAN, SEYED-EMAMI, & AGHANABATI, 1997; SENOWBARI-DARYAN, 2005b). *Peronidella* is the only inozoan genus reported from Oman (BERNECKER, 1996), but 4 inozoan genera have been reported from Timor, including *Ateloracia*, *Himatella*, *Leiospongia*, and *Precorynella* (WILCKENS, 1937; FINKS & RIGBY, 2004d). In contrast to the rich sphinctozoan fauna known from the Pamir Mountains and the Caucasus, the inozoan fauna of this region is poorly known. However, MOISEEV (1944) reported the occurrence of 2 genera (*Molengraaffia* and *Hodsia*) from Caucasus, and DORONOV, GAZDZICKI, and MELNIKOVA (1982) reported the occurrence of 3 genera (*Precorynella*, *Corynella*, and *Molengraaffia*) from the southeastern Pamir Mountains.

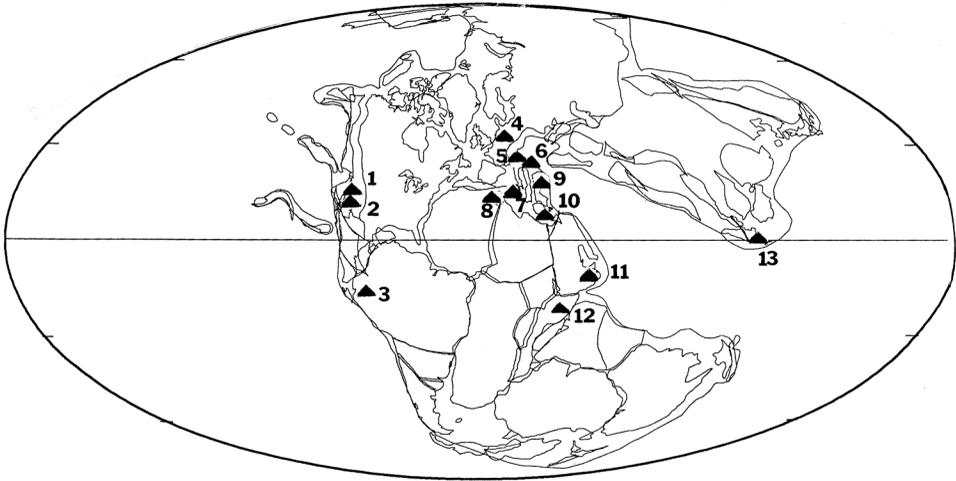


FIG. 269. Paleogeographic distribution of localities from where Triassic inozoan sponges have been reported: 1, Wallowa Mountains, eastern Oregon, United States; 2, Mineral County, western Nevada, United States; 3, Peru; 4, Europe, in general; 5, Dolomite Alps, northern Italy; 6, Austria; 7, Sicily; 8, Tunisia; 9, Hungary; 10, Turkey; 11, Oman; 12, Iran; 13, Timor (base map adapted from Scotese, 2001).

*Preperonidella* is the only Triassic inozoan genus reported from Oregon, in the western United States. *Stellispongia* has been described from the Triassic of Peru (RAUFF, 1938), where *Preperonidella*, as *Peronidella*, has also been reported (SENOWBARI-DARYAN, 1994b). *Corynella* and *Eusiphonella* (treated in FINKS

& RIGBY, 2004d, p. 743, 748, as junior synonyms of *Endostoma* and *Pareudea*, respectively), as well as questionable *Stellispongiella*, were also listed as inozoan sponges from Peru (SENOWBARI-DARYAN, 1994b, p. 57) and are now considered to belong to the Calcarea, rather than to the Demospongiae like most

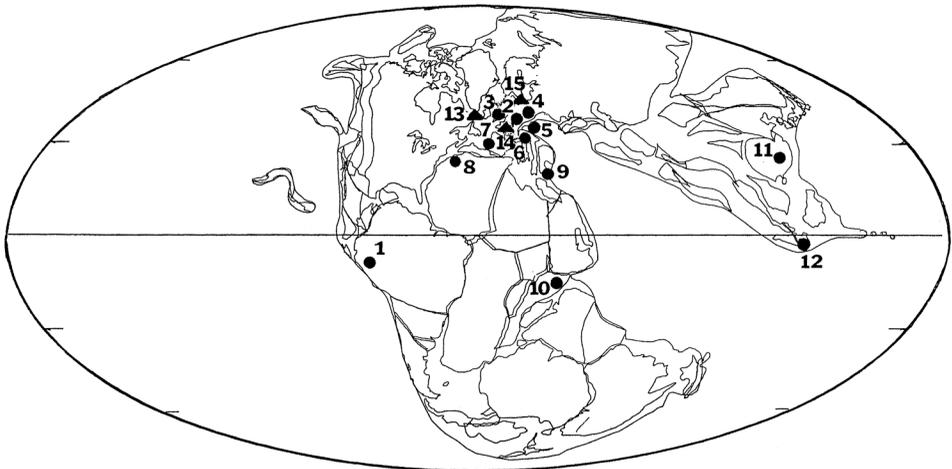


FIG. 270. Paleogeographic distribution of localities from where Jurassic spongiactinozoan (circles) and inozoan (triangles) sponges have been reported. Spongiactinozoans occur at localities: 1, Peru; 2, England, United Kingdom; 3, Germany; 4, Poland; 5, former Czechoslovakia; 6, Italy; 7, Portugal; 8, Morocco; 9, Greece; 10, China; 11, Moluccas; 12, Cambodia. Inozoans occur at localities: 13, eastern Atlantic shelf, Canada; 14, France; 15, Germany (base map adapted from Scotese, 2001).

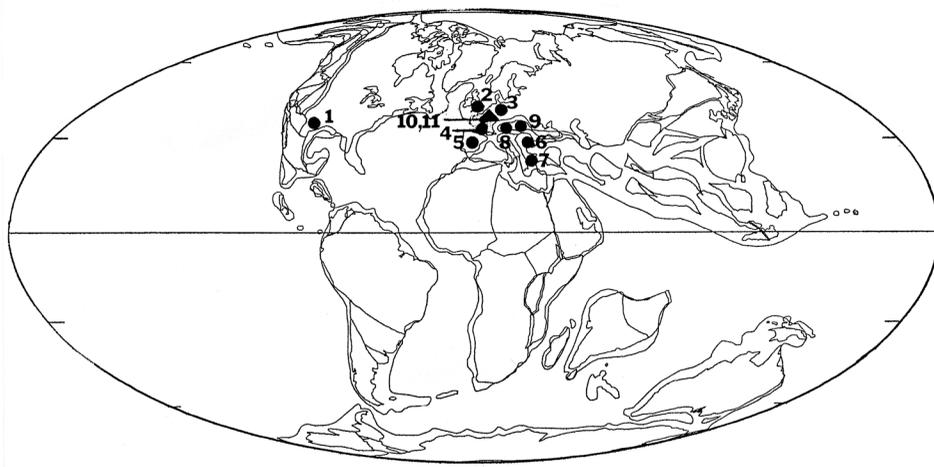


FIG. 271. Paleogeographic distribution of localities from where Cretaceous sphinctozoan (*circles*) and inozoans (*triangles*) sponges have been reported. Sphinctozoans occur at localities: 1, Texas, United States; 2, United Kingdom; 3, Germany; 4, France; 5, Spain; 6, Romania; 7, Greece; 8, Switzerland; 9, Austria. Inozoans occur at localities: 10, Germany; and 11, France (base map adapted from Scotese, 2001).

other inozoans. *Cornuaspongia* and *?Trammeria* were also described from the Triassic of Peru by SENOWBARI-DARYAN (1994b). They are also considered as probable inozoans, but their taxonomic positions in class and order are uncertain (FINKS & RIGBY, 2004d, p. 762, 764).

Diversity and geographic spread of sphinctozoan sponges in the Jurassic record is markedly reduced from that of the Triassic, although the major focus of occurrences is still along western margins of the Tethyan seaway (Fig. 270). For example, *?Deningeria* and *Sphinctonella* have been reported from

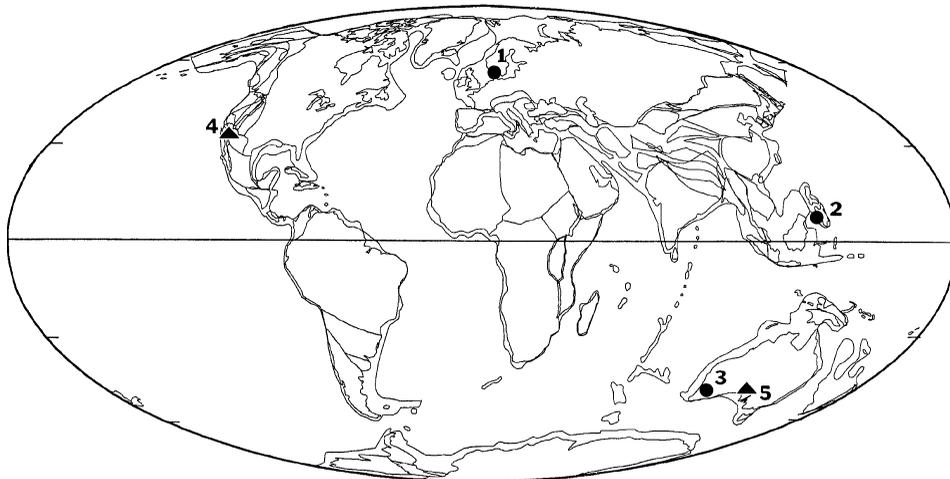


FIG. 272. Paleogeographic distribution of localities from where Paleogene–Neogene sphinctozoan and inozoan sponges have been reported. Sphinctozoan sponges (*circles*) have been reported from: 1, Denmark (Paleocene); 2, Marinduque, Philippine Islands, (Eocene); 3, southwestern Australia (Eocene); and inozoan sponges (*triangles*) have been reported from: 4, Mexico (Eocene); and 5, Australia (Miocene) (base map adapted from Scotese, 2001).

Poland (HURCEWICZ, 1975); *Barroisia* and *Muellerithalamia* from Germany (QUENSTEDT, 1858; REITNER, 1987c), the latter two genera included in the Calcarea (FINKS & RIGBY, 2004d). *Barroisia*, *Sphaerocelesia*, and *Thalamopora* have been reported from the Czech Republic and Slovakia (ZEISE, 1897) and *Thalamopora* from Portugal (G. TERMIER, H. TERMIER, & RAMALHO, 1985). *Barroisia* has also been reported from the United Kingdom (KEEPING, 1883) and from Italy (SENOWBARI-DARYAN & ABATE, 1996), and *Boikothalamia* has been reported from Spain (REITNER & ENGESER, 1985). *Casearia*, a hexactinellid chambered sponge, is not treated in detail here, but it has been reported from along the eastern margin of the Tethyan realm from China (WU & XIAO, 1989; RIGBY, WU, & FAN, 1998), from central Iran, the western Tethys (Germany), and northern Tethys (Pamir Mountains) (MÜLLER, 1974; BOJKO, 1990; SENOWBARI-DARYAN & HAMEDANI, 1999).

Only a single Lower Jurassic sphinctozoan, *Stylothalamia*, has been reported from the American continents (Fig. 270) and that was from Peru (HILDEBRANDT, 1971; SENOWBARI-DARYAN & STANLEY, 1994). *Stylothalamia* has also been reported from European countries (RADOIČIĆ, 1966; PALLINI & SCHIAVINOTTO, 1981; SCHIAVINOTTO, 1984; BECCARELLI BAUCK, 1986; BROGLIO LORIGA & others, 1991), and from northern Africa (SCHROEDER, 1984). From the Upper Jurassic, the genera *Barroisia*, *Boikothalamia*, *Sphaerocelesia*, *Thalamopora*, and *Verticillites* have been reported from several different European countries by various authors (see SENOWBARI-DARYAN & GARCÍA-BELLIDO, 2002a). The occurrence of ?*Cryptocoeliopsis* WILCKENS, 1937, or ?*Deningeria* WILCKENS, 1937, has been reported from Poland (HURCEWICZ, 1975).

Jurassic inozoans are more diverse than contemporaneous sphinctozoans, but they are still less geographically extensive and less diverse than those of the Triassic (Fig. 270). Several calcareous sponges that are considered as inozoans, including *Endostoma*, ?*Elas-*

*mostoma*, *Enaulofungia*, *Pareudea*, and *Eudea*, have been reported from the Jurassic of Germany (WAGNER, 1964; MÜLLER, 1984); from Italy (BIZZARINI, BRAGA, & MASTANDREA, 1987); and from Greece (BONNEAU & TERMIER, 1975). The single genus *Epitheles*, based on species included in *Myrmecium*, has been reported from France, along with the questionable *Aulocopagia* POMEL, 1872. *Winwoodia* (RICHARDSON & THACKER, 1920) has been documented from England. An additional 12 genera of the family Stellispongiidae, within the Calcarea, are included in the list of inozoans appended below, and all are reported as occurring in the Jurassic deposits of Europe. Undescribed inozoan sponges are abundant in Jurassic deposits of the Sotori Mountains in northeastern Iran (SENOWBARI-DARYAN, personal observation). The only reported inozoan from the Jurassic of North America is *Sestrostomella*, from the Canadian Atlantic Shelf (FINKS & RIGBY, 2004d, p. 611). Six genera were reported by RAUFF (1938) and SENOWBARI-DARYAN (1994b) from Peru in South America.

Cretaceous geographic spread of sphinctozoan sponges is even more restricted than that of the Jurassic, but the focus is still in western European countries (Fig. 271). The most diverse faunas have been found in Spain (SCHROEDER & WILLEMS, 1983; SCHROEDER, 1984; REITNER & ENGESER, 1985; REITNER, 1987c), where five genera have been reported, followed by faunules from Germany (STEINMANN, 1882; DUNIKOWSKI, 1883; WELTER, 1911; HILLMER & SENOWBARI-DARYAN, 1986) and France (DELEMATTE, TERMIER, & TERMIER, 1986; TERMIER & TERMIER, 1985a, 1985b), where four genera have been documented from both countries. Single genera have been reported from other European localities, including *Stylothalamia* from Austria (ENGESER & NEUMANN, 1986; SENOWBARI-DARYAN, 1990), *Stylothalamia* from Greece (SENOWBARI-DARYAN & GARCÍA-BELLIDO, 2002a), and *Barroisia* from Romania, Switzerland (STEINMANN, 1882), and England (HINDE, 1882, 1884; REID, 1968).

*Stylothalamia* is the only sphinctozoan genus reported from the Cretaceous of North America, where specimens of the genus were recovered from central Texas by WELLS (1934).

Cretaceous inozoans are more diverse than contemporaneous sphinctozoans, but they are certainly more geographically limited than in the Jurassic record, for Cretaceous occurrences have been reported principally from European localities (Fig. 271). *Pharetrospongia strahani* SOLLAS, 1877, for example, was reported from England, as the figured specimen in FINKS and RIGBY (2004d, p. 614), although the genus is cited there as occurring in Europe, which would suggest a broader distribution. *Elasmopagia* POMEL, 1872, is the only Cretaceous inozoan-type demosponge reported to date from France, and it was not illustrated when proposed. *Trachytila* WELTER, 1911, is likewise the only Cretaceous inozoan demosponge reported from Germany.

Sixteen genera that are included in the family Stelligeridae DE LAUBENFELS, 1955, class Calcarea, by FINKS and RIGBY (2004d, p. 739–747) are considered to have inozoan skeletal structure (see appended list below, p. 383). Twelve of these genera are documented from Cretaceous deposits of Europe, and two more are reported as questionably present there in the Cretaceous (LAMOUROUX, 1821; BRONN, 1825; DE FROMENTEL, 1860a; ROEMER, 1864; POMEL, 1872; ZITTEL, 1878; HINDE, 1884, 1893; ZEISE, 1897; WELTER, 1911; FINKS & RIGBY, 2004d).

Cenozoic sphinctozoans are certainly geographically and taxonomically limited, for they have been described from only three localities (Fig. 272). Only two genera have been documented from a European country: *Verticillites* and *Wienbergia* from Denmark (RAVN, 1899; CLAUSEN, 1982). In addition to the European occurrence, only the single genus *Marinduqueia* has been described from the Eocene of the Philippine Islands (YABE & SUGIYAMA, 1939), and an Eocene species of the living genus *Vaceletia* has been reported from Western Australia (PICKETT, 1982).

Reported Paleogene–Neogene inozoans are limited to the occurrence of *?Elasmostoma* DE FROMENTEL, 1860a, from the Eocene of Mexico (FINKS & RIGBY, 2004d, p. 741), and *Tretocalia* HINDE, 1900, from the Miocene of Australia (PICKETT, 1983). Four inozoan genera of the class Calcarea, including the stelligerid *Trachysphercion* POMEL, 1872, and the holcospongiid *Eudea* LAMOUROUX, 1821, and *Mammillopora* BRONN, 1825, have been reported from the Holocene (FINKS & RIGBY, 2004d, p. 743–747).

## ROLES OF SPHINCTOZOANS AND INOZOANS AS CONTRIBUTORS TO REEFS

Hypercalcified inozoan and sphinctozoan sponges (including archaeocyaths, stromatoporoids, and chaetetids) were the most abundant metazoan contributors to the formation of invertebrate reefs during the Paleozoic and early Mesozoic (WOOD, 1990b, 1991b; KIESSLING, 2001b). Only the roles of sphinctozoans and inozoans as contributors to reefs and reefal deposits, and their abundance, are treated in the following discussions.

### CAMBRIAN–CARBONIFEROUS

In contrast to abundant archaeocyaths in the Cambrian and stromatoporoids in Ordovician to Devonian reefs, inozoan and sphinctozoan sponges were not abundant reef builders during this time interval, but both groups are known from reefs or reefal deposits from some localities (Ordovician: WEBBY & RIGBY, 1985; RIGBY & POTTER, 1986; RIGBY, POTTER, & BLODGETT, 1988; RIGBY & WEBBY, 1988; WEBBY & LIN, 1988; Silurian: DE FREITAS, 1987; RIGBY, NITECKI, & others, 1994; RIGBY & CHATTERTON, 1999; Devonian: RIGBY & BLODGETT, 1983; see also RIGBY & CHATTERTON, 1999).

Contemporary with the chaetetids, inozoan and sphinctozoan sponges became more important contributors among the sponge

association in the upper Carboniferous. Individually rich, but with low diversity, sponge faunas have been described from bedded shallow-water carbonates from the Carnic Alps, Austria (PELZMANN, 1930; LOBITZER, 1975; KÜGEL, 1987), from Spain (STEINMANN, 1882; VAN DE GRAAF, 1969; GARCÍA-BELLIDO & RIGBY, 2004; GARCÍA-BELLIDO, SENOWBARI-DARYAN, & RIGBY, 2004); and from Kansas, Texas, and Oklahoma (GIRTY, 1908b; KING, 1933, 1938, 1943; RIGBY & MAPES, 2000) in the United States.

### PERMIAN

Sphinctozoan and inozoan sponges are among the most significant contributors in Permian metazoan reefs (KIESSLING, 2001b; WEIDLICH, 2002). Both groups are abundant in lower Permian sponge *Tubiphytes-Archaeolithoporella* reef boulders of Sicily (SENOWBARI-DARYAN & DI STEFANO, 1988a), or in bedded reefal bioconstructions of Iran (SENOWBARI-DARYAN, RASHIDI, & HAMEDANI, 2005).

Inozoan- and sphinctozoan-dominated middle and upper Permian reefs occur worldwide (for a summary, see RIGBY & SENOWBARI-DARYAN, 1995; WEIDLICH, 2002). Both groups have been described from reefs or reefal limestones from several localities in Texas and New Mexico, in the United States (for a summary, see FAGERSTROM & WEIDLICH, 1999a, 1999b; NOÉ, 2003; sponges described by GIRTY, 1908b; FINKS, 1960; RIGBY & SENOWBARI-DARYAN, 1996a, 1996b; RIGBY, SENOWBARI-DARYAN, & LIU, 1998); from Venezuela (RIGBY, 1984); from Sicily (PARONA, 1933; ALEOTTI, DIECI, & RUSSO, 1986; SENOWBARI-DARYAN, 1990; FLÜGEL, DI STEFANO, & SENOWBARI-DARYAN, 1991); from Tunisia (TERMIER & TERMIER, 1974; H. TERMIER, G. TERMIER, & VACHARD, 1977; SENOWBARI-DARYAN & RIGBY, 1988; RIGBY & SENOWBARI-DARYAN, 1996a); from Pakistan (WAAGEN & WENTZEL, 1888); from Japan (HAYASAKA, 1918; AKAGI, 1958; IGO, IGO, & ADACHI, 1988); from China (FAN & ZHANG, 1985; FLÜGEL & REINHARDT, 1989; RIGBY, FAN, & ZHANG, 1989a, 1989b; FAN, RIGBY,

& JINGWEN, 1990; FAN, RIGBY, & ZHANG, 1991; WU, 1991; RIGBY, FAN, & others, 1994; RIGBY, FAN, & NAIREN, 1995; BELYAEVA, 2000; FAN, WANG, & WU, 2002); from Oman (WEIDLICH & SENOWBARI-DARYAN, 1996); from Iran (SENOWBARI-DARYAN & HAMEDANI, 2002; RIGBY, SENOWBARI-DARYAN, & HAMEDANI, 2005; SENOWBARI-DARYAN, RASHIDI, & HAMEDANI, 2005); from Caucasus (see BOIKO, BELYAEVA, & ZHURAVLEVA, 1991); from Thailand (SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994); and from the former Yugoslavia (FLÜGEL, KOCHANSKY-DEVIDE, & RAMOVŠ, 1984; SREMAC, 2005).

### TRIASSIC

Hypercalcified sponges, including the group of spongiomorphid fossils described as hydrozoans by early workers (now considered to be sponges, such as *Spongiomorpha* FRECH, 1890, and *Disjectopora* WAAGEN & WENTZEL, 1888; see also Summary of Classification, p. 386, below), and chaeteterids were among the most significant contributors to Middle and Late Triassic reefs (FLÜGEL & SENOWBARI-DARYAN, 2001; FLÜGEL, 2003). FLÜGEL (2003) concluded that hypercalcified sponges made up to 50–75% of the bulk of Late Triassic reefs. Inozoans and sphinctozoans are particularly abundant in Upper Triassic reefs. Of these, the sphinctozoans seem to be more abundant than the inozoans. Sponges with aragonitic and Mg-calcitic mineralogy are both represented. Generic diversity, complexity, and the dimensions of both groups increased from the Anisian to the Carnian and reached its maximum development during the Norian. The diversity of both groups seems to have decreased during the uppermost Norian or Rhaetian stage, and their importance as principal contributors, bafflers, and framebuilders was taken over by scleractinian corals.

Middle Triassic sphinctozoan- and inozoan-dominated reefs or reefal carbonates are known from numerous localities in the western Tethys (Alps: OTT, 1967; DULLO & LEIN, 1980; BRADNER & RESCH, 1981; FOIS & GAETANI, 1981, 1984; HENRICH,

1982; SENOWBARI-DARYAN & others, 1993; RÜFFER & ZAMPARELLI, 1997; EMMERICH & others, 2005; for more information, see FLÜGEL & SENOWBARI-DARYAN, 2001), and from the Apennines (SENOWBARI-DARYAN, ABATE, & others, 1999). Sphinctozoans have been reported from the Middle to Upper Triassic of the western Tethys (from the Alps of Austria: ZANKL, 1969; SENOWBARI-DARYAN, 1978, 1980a, 1990; SENOWBARI-DARYAN & SCHÄFER, 1979; SCHÄFER, 1979; DULLO & LEIN, 1980; for more information, see FLÜGEL, 1981, 2003; FLÜGEL & SENOWBARI-DARYAN, 2001); from northern Italy (MÜNSTER, 1841; DIECI, ANTONACCI, & ZARDINI, 1968; RUSSO, 1981; BIZZARINI & RUSSO, 1986); from southern Italy (MASTANDREA & RETTORI, 1989; SENOWBARI-DARYAN & ZAMPARELLI, 1999, 2003); from the Carpathians (JABLONSKY, 1971, 1972, 1975; BALOGH & KOVÁCS, 1976; KOVÁCS, 1978a, 1978b; FLÜGEL & others, 1992 in 1991–1992); from the former Yugoslavia (SENOWBARI-DARYAN, 1981, 1982; RAMOS & TURNSEK, 1984; TURNSEK, BUSER, & OGOR-ELEC, 1987); and from Greece (SCHÄFER & SENOWBARI-DARYAN, 1982; SENOWBARI-DARYAN, 1982; SENOWBARI-DARYAN & SCHÄFER, 1983; SENOWBARI-DARYAN, MATARANGAS, & VARTIS-MATARANGAS, 1996).

Triassic sphinctozoan- and inozoan-dominated reefs and reefal limestones are also known from the southern Tethys (Sicily: SENOWBARI-DARYAN, 1980b; SENOWBARI-DARYAN, SCHÄFER & ABATE, 1982; SENOWBARI-DARYAN & ABATE, 1986; SENOWBARI-DARYAN & SCHÄFER, 1986; SENOWBARI-DARYAN & DI STEFANO, 1988b; from Turkey: CUIF, 1973; SENOWBARI-DARYAN, 1994a; SENOWBARI-DARYAN & LINK, 1998; SENOWBARI-DARYAN, LINK, & GARCÍA-BELLIDO, 2003, and from Oman: BERNECKER, 1996; SENOWBARI-DARYAN, BERNECKER, & others, 1999). These types of deposits are also known from the northern Tethys (Caucasus: MOISEEV, 1944; BOIKO, BELYAEVA, & ZHURAVLEVA, 1991), and from the central Tethys (SENOWBARI-DARYAN, 1996, 2005a; SENOWBARI-DARYAN, SEYED-EMAMI, & AGHANABATI, 1997).

Sphinctozoan and inozoan sponges have been described from other Norian–Rhaetian reefs from the western Tethys (VINASSA DE REGNY, 1915; WILCKENS, 1937; RÖHL & others, 1991), and from around the Panthalassian ocean from North America (Nevada: STANLEY, 1979; British Columbia, Canada: STANLEY & SENOWBARI-DARYAN, 1999; Yukon, Canada: SENOWBARI-DARYAN & REID, 1987) and South America (SENOWBARI-DARYAN, 1994b).

Occurrences of approximately 16 sphinctozoan genera in Middle Triassic reefs and 55 genera in Upper Triassic reefs have been recorded. Inozoan sponges of Triassic deposits are not well known. They are represented by approximately 41 genera, but there are many more undescribed taxa.

In Jurassic deposits and reefs, siliceous sponges are more abundant than hypercalcified sponges in general, and especially the sphinctozoan and inozoan sponges. Based on the abundance of reef builders, LEINFELDER (2001) described three types of Jurassic reefs, and discussed them as coral reefs, siliceous sponge reefs, and pure microbiolite reefs. Although some sphinctozoan sponges are known from Upper Jurassic reefs, they do not play an important role in shallow-water environments. Inozoans, excluding those just described as stromatoporoids, are significantly more abundant than sphinctozoans in Jurassic deposits, and especially in Upper Jurassic deposits.

Jurassic sphinctozoans and inozoans are known in reef associations from Italy (SCHIAVINOTTO, 1984; BECARELLI BAUCK, 1986; BIZZARINI, BRAGA, & MASTANDREA, 1987; BROGLIO LORICA & others, 1991), Germany (QUENSTEDT, 1858; ZITTEL, 1879; WAGNER, 1964; LANG, 1985; REITNER, 1987c), Switzerland (OPPLIGER, 1929), France (POMEL, 1872), the former Yugoslavia (RADOIČIĆ, 1966), Greece (BONNEAU & TERMIER, 1975), Morocco (SCHROEDER, 1984), Poland (HURCEWICZ, 1972, 1975), and Peru (HILDEBRANDT, 1971, 1981; SENOWBARI-DARYAN, 1994b).

The abundance of both sphinctozoans and inozoans increased during the Cretaceous.

Several taxa have been described, especially from the Cretaceous of Spain (SCHROEDER & WILLEMS, 1983; REITNER & ENGESER, 1985; REITNER, 1987d), and Germany (HILLMER & SENOWBARI-DARYAN, 1986).

In summary, the hypercalcified sponges (including archaeocyaths, stromatoporoids, chaetetids, sphinctozoans, and inozoans) are the dominant metazoan fossil groups in Cambrian to Permian reefs. Among the invertebrates, sphinctozoan and inozoans were the main reef builders of Permian and Triassic reefs. In the uppermost Triassic (Rhaetian), scleractinian corals became more abundant than the hypercalcified sponge groups. The role of corals as the main reef builders continued to rise until Recent times, with the exception of the Cretaceous, when rudist bivalve reefs developed.

### TECHNIQUES FOR STUDY

Sphinctozoans and inozoans are calcareous forms where both external and internal structures are critical for taxonomic evaluation. As a result, these fossils are prepared for examination and description much like bryozoans or stromatoporoids. Thin sections or polished sections of the skeletons provide primary information on those structures. Vertical axial sections that show the internal and dermal elements, coupled with similarly complete transverse sections, are normally important for analysis of elongate forms. Sections at high angles to and parallel to surfaces in platelike forms are also both necessary for adequate documentation of their structure, as in other fossil groups. In some forms, it may be helpful to prepare tangential or oblique sections to show chamber patterns and structures. Sections or polished surfaces should be prepared large enough to show the general structure of the fossil, rather than only a small part.

It is sometimes helpful to etch polished surfaces or sections with very dilute (3–5%) or concentrated (100%) acetic acid. Etched surfaces should be frequently checked during processing, compared to see which preparation is most productive on the particular

samples, and that technique then applied for final preparation. Low-relief etched surfaces are necessary for examination of microstructure and spicules by scanning electron microscopy.

Silicified fossils of these groups are normally prepared for study by etching them in dilute hydrochloric or acetic acids. This allows encasing matrix to be removed so that details of the individual skeletons can be examined. Where the skeletons are very delicate, they may be embedded in epoxy, and after cutting the skeletons, they can be examined.

### SUMMARY OF CLASSIFICATION AND STRATIGRAPHIC OCCURRENCES

The following is a list of all the currently recognized chambered (Sphinctozoa) and nonchambered (Inozoa) hypercalcified sponge genera and their stratigraphic occurrences.

Most aspects of the systematic classification proposed by FINKS and RIGBY (2004d, p. 585–764) have continued to be used here, but there are some important changes, as follows.

1. Demospongiae SOLLAS, 1885, is here maintained as class group name, given its widespread use and general acceptance by zoologists and paleontologists. The ICZN Code (1999) has not stipulated a consistent form of ending for class group names, although one attempt was made in the first *Treatise* Part E volume (MOORE, 1955), including the change DE LAUBENFELS (1955) made to poriferan class divisions, viz., “Demospongea, Hyalospongea and Calcispongea.”
2. Subclasses Tetractinomorpha and Ceractinomorpha LÉVI, 1953, have proven to exhibit polyphyletic relationships, and this has led to suggestions that use of these two traditional subclasses should be abandoned (BOURY-ESNAULT, 2006).
3. Order Vaceletida FINKS & RIGBY (2004d, p. 691) is broadly constituted to incor-

porate many families and a wide scope of stratigraphic records but does not have priority over order Verticillitida TERMIER & TERMIER, 1977a; note also the recent common usage of this ordinal subdivision by VACELET, 2002b, p. 1097, and SENOWBARI-DARYAN and GARCÍA-BELLIDO, 2002a, p. 1521, is preferred here.

4. Calcispongiae DE BLAINVILLE, 1830, p. 494, and Calcarea BOWERBANK, 1864, p. 160, have been widely used as alternative class-level group names. The original spelling of DE BLAINVILLE (1830) was Calcispongia, but most subsequent authors have preferred to use the class-level name Calcarea for sponges with calcareous spicules (see more detailed discussion on p. 293).
5. In the FINKS and RIGBY (2004d) classification, the two subclasses of the Calcarea are the Calcinea and Calcaronea, with the former including two orders (Murrayonida and Clathrinida), and the latter with five orders (Leucosolenida, Sycet-

tida, Stellispongiida, Sphaecoeliida, and Lithonida). This contrasts with the new classification presented in this section, which only involves subclass Calcinea, with mainly sphinctozoan types grouped into two orders (Sphaeroceeliida and Lithonida) and inozoan types grouped within one order (Stellospongiida). The subclass Calcaronea is no longer considered to contain sphinctozoan or inozoan sponges.

The list of hexactinellid, lithistid, and heteractinid sphinctozoans are included, as well as the demosponge and calcarean representatives. For references that are not listed in this presentation, see FINKS, REID, and RIGBY (in KAESLER, 2004, p. 812–855). Stratigraphic abbreviations: C, Cambrian; O, Ordovician; S, Silurian; D, Devonian; Ca, Carboniferous; P, Permian; T, Triassic; J, Jurassic; Cr, Cretaceous; Ce, Cenozoic; R, Recent. A question mark before the genus name means either the family affiliation or the validity of the genus is uncertain.

## SPHINCTOZOA

Class Demospongiae SOLLAS, 1885

Order Agelasida VERRILL, 1907

Family Angullongiidae WEBBY & RIGBY, 1985

*Angullongia* WEBBY & RIGBY, 1985 (O)

*Alaskaspongia* RIGBY, POTTER, & BLODGETT, 1988 (O)

*Amblysisphonelloides* RIGBY & POTTER, 1986 (O)

*Belubulaia* WEBBY & RIGBY, 1985 (O)

*Nibiconia* RIGBY & WEBBY, 1988 (O)

Family Phragmocoeliidae OTT, 1974

*Phragmocoelia* OTT, 1974 (T)

?*Baghevangia* SENOWBARI-DARYAN, RASHIDI, & HAMEDANI, 2005 (P)

*Radiothalamos* PICKETT & RIGBY, 1983 (D)

Family Intrasporeoceliidae FAN & ZHANG, 1985

*Intrasporeocelia* FAN & ZHANG, 1985 (P)

*Belyaevaspongia* SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994 (P)

*Delijania* SENOWBARI-DARYAN, 2005a (T)

*Rahbahthalamia* WEIDLICH & SENOWBARI-DARYAN, 1996 (P)

*Rhabdactinia* YABE & SUGIYAMA, 1934 (P)

Family Cryptocoeliidae STEINMANN, 1882

*Cryptocoelia* STEINMANN, 1882 (P–T)

*Anisothalamia* SENOWBARI-DARYAN & others, 1993 (T)

*Antalythalamia* SENOWBARI-DARYAN, 1994a (T)

?*Calabrispongia* SENOWBARI-DARYAN & ZAMPARELLI, 2003 (T)

- Rigbyspongia* DE FREITAS, 1987 (S)  
*Sphaerothalamia* SENOWBARI-DARYAN, 1994a (T)  
 Family Palermocoeliidae SENOWBARI-DARYAN, 1990  
*Palermocoelia* SENOWBARI-DARYAN, 1990 (T)  
 Family Thaumastocoeliidae OTT, 1967  
 Subfamily Thaumastocoeliinae OTT, 1967  
*Thaumastocoelia* STEINMANN, 1882 (P–T)  
 ?*Calymenospongia* ELLIOTT, 1963 (Ce)  
 ?*Follicatena* OTT, 1967 (P–T)  
*Henricellum* WILCKENS, 1937 (P–T)  
*Pamirothalamia* BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991 (T)  
*Pamiroverticillites* BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991 (T)  
*Porefieldia* RIGBY & POTTER, 1986 (O)  
*Pseudoporefieldia* RIGBY, POTTER, & BLODGETT, 1988 (O)  
 ?*Solenocoelia* CUIF, 1973 (T)  
*Sollasia* STEINMANN, 1882 (Ca–T)  
*Sphaeroverticillites* BOIKO, 1990 (T)  
 Subfamily Enoplocoeliinae SENOWBARI-DARYAN, 1990  
*Enoplocoelia* STEINMANN, 1882 (P–T)  
*Girtyocoelia* COSSMANN, 1909 (O–T)  
*Girtyocoeliana* RIGBY & others, 2005 (O)  
*Naybandella* SENOWBARI-DARYAN, 2005a (T)  
*Phraethalamia* SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994 (P)  
 Family Amphorithalamiidae SENOWBARI-DARYAN & RIGBY, 1988  
*Amphorithalamia* SENOWBARI-DARYAN & RIGBY, 1988 (P)  
 Family Polyedridae TERMIER & TERMIER, 1977a  
*Polyedra* TERMIER & TERMIER, 1977a (P)  
 Family Aphrosalpingidae MYAGKOVA, 1955b  
 Subfamily Fistulospongiinae TERMIER & TERMIER, 1977a  
 ?*Fistulosponginina* TERMIER & TERMIER, 1977a (P)  
*Aphrosalpinx* MYAGKOVA, 1955b (S)  
*Cystothalamiella* RIGBY & POTTER, 1986 (O–S)  
*Nematosalpinx* MYAGKOVA, 1955a (S)  
*Uvacoelia* KÜGEL, 1987 (Ca)  
 Subfamily Vesicocauliinae SENOWBARI-DARYAN, 1990  
*Vesicocaulis* OTT, 1967 (T)  
*Russospongia* SENOWBARI-DARYAN, 1990 (T)  
*Tolminothalamia* SENOWBARI-DARYAN, 1990 (T)  
*Yukonella* SENOWBARI-DARYAN & REID, 1987 (T)  
 Subfamily Palaeoschadinae MYAGKOVA, 1955a  
*Palaeoscheda* MYAGKOVA, 1955a (S)  
 Family Glomocystospongiidae RIGBY, FAN, & ZHANG, 1989a  
*Glomocystospongia* RIGBY, FAN, & ZHANG, 1989a (P)  
*Huayingia* RIGBY, FAN, & others, 1994 (P)  
 Family Sebergasiidae DE LAUBENFELS, 1955  
 ?*Sebergasia* STEINMANN, 1882 (Ca)  
*Amblyisphonella* STEINMANN, 1882 (?C, ?O, Ca–T)  
*Calabrisiphonella* SENOWBARI-DARYAN & ZAMPARELLI, 2003 (T)  
*Chinaspongia* BELYAEVA, 2000 (P)

- Crymocoelia* BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991 (P)  
 ?*Laccosiphonella* ALEOTTI, DIECI, & RUSSO, 1986 (P)  
 ?*Lingyunocoelia* FAN, WANG, & WU, 2002 (P)  
*Minisiphonella* BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991 (T)  
 ?*Oligocoelia* VINASSA DE REGNY, 1901 (T)  
 ?*Paramblysiphonella* DENG, 1982c (P)  
*Polycystocoelia* ZHANG, 1983 (P–T)  
*Pseudoamblysiphonella* SENOWBARI-DARYAN & RIGBY, 1988 (P)  
*Pseudogadalupeia* TERMIER & TERMIER, 1977a (P)  
*Stylocoelia* WU, 1991 (P)  
*Vesicorubularia* BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991 (P)
- Family Olangocoeliidae BECHSTÄDT & BRANDNER, 1970  
*Olangocoelia* BECHSTÄDT & BRANDNER, 1970 (T)
- Family Cliefdenellidae WEBBY, 1969  
*Cliefdenella* WEBBY, 1969 (O)  
*Khalfinaea* WEBBY & LIN, 1988 (O)  
*Rigbyetia* WEBBY & LIN, 1988 (O)
- Family Guadalupiidae GIRTY, 1908a  
*Guadalupia* GIRTY, 1908a (P)  
 ?*Cystauletes* KING, 1943 (Ca–T)  
*Cystothalamia* GIRTY, 1908a (Ca–T)  
*Diecithalamia* SENOWBARI-DARYAN, 1990 (T)  
*Discosiphonella* INAI, 1936 (Ca–T)  
*Lemonea* SENOWBARI-DARYAN, 1990 (P)  
*Praethalamopora* RUSSO, 1981 (T)
- Family Tabasiidae SENOWBARI-DARYAN, 2005a  
*Tabasia* SENOWBARI-DARYAN, 2005a (T)  
 ?*Madonia* SENOWBARI-DARYAN & SCHÄFER, 1986 (T)
- Order Verticillitida TERMIER & TERMIER, 1977a
- Family Solenolmiidae ENGESER, 1986
- Subfamily Solenolmiinae ENGESER, 1986  
*Solenolmia* POMEL, 1872 (P–T)  
 ?*Adrianella* PARONA, 1933 (P)  
*Ambithalamia* SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994 (P)  
 ?*Cryptoceeliopsis* WILCKENS, 1937 (T, ?J)  
 ?*Deningeria* WILCKENS, 1937 (T, ?J)  
*Hormospongia* RIGBY & BLODGETT, 1983 (D)  
*Panormida* SENOWBARI-DARYAN, 1980b (T)  
*Paradeningeria* SENOWBARI-DARYAN & SCHÄFER, 1979 (P–T)  
 ?*Polysiphonaria* FINKS, 1997 (P)  
*Polythalamia* DEBRENNE & WOOD, 1990 (C); described as a capsulocyathid archaeocyath by DEBRENNE, ZHURAVLEV, & KRUSE (see p. 918)  
*Preverticillites* PARONA, 1933 (P)  
*Prosiphonella* DIECI, ANTONACCI, & ZARDINI, 1968 (T)  
*Sabraja* MOISEEV, 1944 (T)  
*Senowbaridaryana* ENGESER & NEUMANN, 1986 (T)  
 ?*Seranella* WILCKENS, 1937 (T)  
*Welteria* VINASSA DE REGNY, 1915 (P–T)
- Subfamily Battagliinae SENOWBARI-DARYAN, 1990

- Battaglia* SENOWBARI-DARYAN & SCHÄFER, 1986 (T)  
 Family Colospongiidae SENOWBARI-DARYAN, 1990  
 Subfamily Colospongiinae SENOWBARI-DARYAN, 1990  
*Colospongia* LAUBE, 1865 (Ca–T)  
*Blastulospongia* PICKETT & JELL, 1983 (C)  
*Pseudoimperatoria* SENOWBARI-DARYAN & RIGBY, 1988 (O–P)  
*Subascosymplegma* DENG, 1981 (P)  
*Tristratocoelia* SENOWBARI-DARYAN & RIGBY, 1988 (P)  
*Uvothermalia* SENOWBARI-DARYAN, 1990 (P)  
 Subfamily Corymbospongiinae SENOWBARI-DARYAN, 1990  
*Corymbospongia* RIGBY & POTTER, 1986 (O, ?P)  
*Exaulipora* RIGBY, SENOWBARI-DARYAN, & LIU, 1998 (?O, P)  
*Imbricatocoelia* RIGBY, FAN, & ZHANG, 1989a (P)  
*Lichuanospongia* ZHANG, 1983 (P)  
*Neogualdalupea* ZHANG, 1987 (P–T)  
*Parauvanella* SENOWBARI-DARYAN & DI STEFANO, 1988a (P–T)  
*Platythalamiella* SENOWBARI-DARYAN & RIGBY, 1988 (P–T)  
*Shotorispongia* SENOWBARI-DARYAN, RASHIDI, & HAMEDANI, 2006  
 Subfamily Kashanelliinae SENOWBARI-DARYAN, 2005b  
*Kashanella* SENOWBARI-DARYAN, 2005a (T)  
 Family Gigantothalamiidae SENOWBARI-DARYAN, 1994a  
*Gigantothalamia* SENOWBARI-DARYAN, 1994a (T)  
*Zanklithalamia* SENOWBARI-DARYAN, 1990 (T)  
*Lucaniaspongia* SENOWBARI-DARYAN, ABATE, & others, 1999 (T)  
 Family Tebagathalamiidae SENOWBARI-DARYAN & RIGBY, 1988  
*Tebagathalamia* SENOWBARI-DARYAN & RIGBY, 1988 (P)  
*Graminospongia* TERMIER & TERMIER, 1977a (P)  
 Family Annaecoeliidae SENOWBARI-DARYAN, 1978 (T)  
*Annaecoelia* SENOWBARI-DARYAN, 1978 (T)  
 Family Cheilosporitiidae FISCHER, 1962  
*Cheilosporites* WÄHNER, 1903 (T)  
 Family Salzburgiidae SENOWBARI-DARYAN & SCHÄFER, 1979  
*Salzburgia* SENOWBARI-DARYAN & SCHÄFER, 1979 (P–T)  
 Family Cribrothalamiidae SENOWBARI-DARYAN, 1990  
*Cribrothalamia* SENOWBARI-DARYAN, 1990 (T)  
 Family Verticillitidae STEINMANN, 1882  
 Subfamily Verticillitinae STEINMANN, 1882  
*Verticillites* DEFRANCE, 1829 (J–Ce)  
*Boikothalamia* REITNER & ENGESER, 1985 (J)  
*Marinduqueia* YABE & SUGIYAMA, 1939 (Ce); this genus has recently been given an alternative assignment to that presented here and classified within the Order Dictyoceratida, Family Vaceletiidae (see discussion, p. 273–275)  
 ?*Menathalamia* REITNER & ENGESER, 1985 (Cr)  
*Murguiathalamia* REITNER & ENGESER, 1985 (Cr)  
*Stylothalamia* OTT, 1967 (P–Cr)  
*Vaceletia* PICKETT, 1982 (Cr–R) this genus has recently been given an alternative assignment to that presented here and classified within the Order Dictyoceratida, Family Vaceletidae (see discussion, p. 273–275).  
*Vascothalamia* REITNER & ENGESER, 1985 (Cr)

- ?*Wienbergia* CLAUSEN, 1982 (Ce)
- Subfamily Polytholosiinae SEILACHER, 1962
  - Polytholusia* RAUFF, 1938 (P–T)
  - ?*Ascosymplegma* RAUFF, 1938 (T)
  - Nevadathalamia* SENOWBARI-DARYAN, 1990 (T)
  - ?*Tetraproctosia* RAUFF, 1938 (T)
- Subfamily Fanthalamiinae SENOWBARI-DARYAN & ENGESER, 1996
  - Fanthalamia* SENOWBARI-DARYAN & ENGESER, 1996 (T)
  - Cinnabaria* SENOWBARI-DARYAN, 1990 (T)
  - Iranothalamia* SENOWBARI-DARYAN, 2005a (T)
- Subfamily Polysiphospongiinae SENOWBARI-DARYAN, 1990
  - Polysiphospongia* SENOWBARI-DARYAN & SCHÄFER, 1986 (T)
- Family Uncertain
  - Platysphaero-coelia* BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991 (T)
- Order Hadromerida TOPSENT, 1898
  - Family Celyphiidae DE LAUBENFELS, 1955
    - Celyphia* POMEL, 1872 (P–T, Cr)
    - Alpinothalamia* SENOWBARI-DARYAN, 1990 (T)
    - Cassianothalamia* REITNER, 1987b (T)
    - Jablonskyia* SENOWBARI-DARYAN, 1990 (T)
    - Leinia* SENOWBARI-DARYAN, 1990 (T)
    - Loczia* VINASSA DE REGNY, 1901 (T)
    - Montanaroo* RUSSO, 1981 (T)
    - Pamirocoelia* BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991 (T)
    - Paravesicocaulis* KOVÁCS, 1978a (T)
    - Pisothalamia* SENOWBARI-DARYAN & RIGBY, 1988 (P)
    - Pseudovanella* SENOWBARI-DARYAN, 1994a (T)
    - Tongluspongia* BELYAEVA, 2000 (P)
    - Uvanella* OTT, 1967 (P–T)
  - Family Ceotinellidae SENOWBARI-DARYAN in FLÜGEL, LEIN, & SENOWBARI-DARYAN, 1978
    - Ceotinella* PANTIC, 1975 (T)
  - Family Polysiphonidae GIRTY, 1908a
    - Polysiphon* GIRTY, 1908a (P)
    - Arbusculana* FINKS & RIGBY, 2004d (P)
    - ?*Zardinia* DIECI, ANTONACCI, & ZARDINI, 1968 (T)
- Subclass Lithistida SCHMIDT, 1870
  - Order Tetralithistida LAGNEAU-HÉRENGER, 1962
    - Suborder Tetracladina ZITTEL, 1878
      - Family Radiocelliidae SENOWBARI-DARYAN & WÜRM, 1994
        - Radiocella* SENOWBARI-DARYAN & WÜRM, 1994 (T)
- Class Calcarea BOWERBANK, 1869
  - Subclass Calcinea BIDDER, 1898
    - Order Sphaerocoeliida VACELET, 1979b
      - Family Sphaerocoeliidae STEINMANN, 1882
        - Sphaerocoelia* STEINMANN, 1882 (P–Cr)
        - Barroisia* MUNIER-CHALMAS, 1882 (J–Cr)
        - Sphinctonella* HURCEWICZ, 1975 (J)
        - Thalamopora* ROEMER, 1840 (J–Cr)
        - Tremacystia* HINDE, 1884 (Cr)

- Order Lithonida DÖDERLEIN, 1892  
 Family Minchinelliidae DENDY & ROW, 1913  
*Muellerithalamia* REITNER, 1987c (J)
- Class and Order Uncertain  
*Pseudodictyoelia* BOIKO, 1984a (T)
- Class Hexactinellida SCHMIDT, 1870  
 Subclass Hexasterophora SCHULZE, 1887  
 Order Hexactinosa SCHRAMMEN, 1903  
 Family Craticulariidae RAUFF, 1893  
 Subfamily Caseariinae SCHRAMMEN, 1937  
*Casearia* QUENSTEDT, 1858 (T–J)  
*Caucasocoelia* BOIKO, 1990 (T)  
*Dracolychnos* WU & XIAO, 1989 (T)  
*Innaecoelia* BOIKO, 1990 (J)  
*Pseudoverticillites* BOIKO, 1990 (T)
- Class Heteractinida DE LAUBENFELS, 1955  
 Order Octactinellida HINDE, 1887  
 Family Nuchidae PICKETT, 2002  
*Nucha* PICKETT & JELL, 1983 (C)  
*Jawonya* KRUSE, 1987 (C)  
*Wagima* KRUSE, 1987 (C)

### INOZOA

The following list contains only the confirmed fossil inozoan sponges. Representatives of modern calcareous algae, including some inozoan taxa described as algae, are not listed here.

- Class Demospongiae SOLLAS, 1885  
 Order Agelasida VERRILL, 1907  
 Family Catenispongiidae FINKS, 1995  
*Catenispongia* FINKS, 1995 (P)  
*Hartmanina* DIECI, RUSSO, & RUSSO, 1974b (T); described as an obj. syn. of *Leiospongia* D'ORBIGNY, 1849b, a chaetetid as per ENGESER & TAYLOR, 1989, and classified by West and Wood as an agelasid (see p. 264).  
 demosponge  
*Ossiminus* FINKS, 1995 (P)  
*Stratispongia* FINKS, 1995 (P)
- Family Virgolidae TERMIER & TERMIER in H. TERMIER, G. TERMIER, & VACHARD, 1977  
 Subfamily Virgolinae TERMIER & TERMIER in H. TERMIER, G. TERMIER, & VACHARD, 1977  
*Virgola* DE LAUBENFELS, 1955 (P)  
*Dactylocoelia* CUIF, 1979 (T)  
*Intratubospongia* RIGBY, FAN, & ZHANG, 1989b (P)  
*Keriocoelia* CUIF, 1974 (T); described as a chaetetid as per DIECI & others, 1977, and classified by West and Wood as an agelasid demosponge (see p. 262)  
*Reticuloceelia* CUIF, 1973 (T)  
*Scleroceelia* CUIF, 1974 (T); described as a chaetetid as per DIECI & others, 1977, and West and Wood classified as an agelasid demosponge (see p. 264)
- Subfamily Preeudinae RIGBY & SENOWBARI-DARYAN, 1996a  
*Preeudea* TERMIER & TERMIER in H. TERMIER, G. TERMIER, & VACHARD, 1977 (P)  
*Medenina* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
*Microsphaerispongia* RIGBY & SENOWBARI-DARYAN, 1996a (P)

- Polytubifungia* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
*Pseudovirgula* GIRTY, 1908a (P)  
*Vermispongiella* FINKS & RIGBY, 2004c (P)  
 Subfamily Pseudohimatellinae RIGBY & SENOWBARI-DARYAN, 1996a  
*Pseudohimatella* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
 Subfamily Parahimatellinae RIGBY & SENOWBARI-DARYAN, 1996a  
*Parahimatella* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
 Family Sphaeropontiidae RIGBY & SENOWBARI-DARYAN, 1996a  
*Sphaeropontia* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
 Family Exotubispongiidae RIGBY & SENOWBARI-DARYAN, 1996a  
*Exotubispongia* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
 Family Sestrostomellidae DE LAUBENFELS, 1955  
*Sestrostomella* ZITTEL, 1878 (T–J)  
*Brevisiphonella* RUSSO, 1981 (T)  
*Epitheles* DE FROMENTEL, 1860a (J)  
*Himatella* ZITTEL, 1878 (P–T)  
*Polysiphonella* RUSSO, 1981 (T)  
*Trachytila* WELTER, 1911 (Cr)  
*Winwoodia* RICHARDSON & THACKER, 1920 (J)  
 Family Pharetrospongiidae DE LAUBENFELS, 1955  
 Subfamily Pharetrospongiinae DE LAUBENFELS, 1955  
*Pharetrospongia* SOLLAS, 1877 (Cr)  
*Euepirrhysia* DIECI, ANTONACCI, & ZARDINI, 1968 (T)  
 Subfamily Leiofungiinae FINKS & RIGBY, 2004d  
*Leiofungia* DE FROMENTEL 1860a (T)  
*Aulacopagia* POMEL, 1872 (J)  
*Elasmopagia* POMEL, 1872 (Cr)  
*Grossotubenella* RIGBY, FAN, & ZHANG, 1989b (P)  
*Leiospongia* D'ORBIGNY, 1849b (T); described as a chaetetid, as per ENGESER & TAYLOR, 1989, and classified by West and Wood as an agelasid demosponge (see p. 264)  
*Loenopagia* POMEL, 1872 (T)  
*Radicanalospongia* RIGBY, FAN, & ZHANG, 1989b (P)  
 Family Auriculospongiidae TERMIER & TERMIER, 1977b  
 Subfamily Auriculospongiinae RIGBY & SENOWBARI-DARYAN, 1996a  
*Auriculospongia* TERMIER & TERMIER, 1974 (P)  
*Anguispongia* SENOWBARI-DARYAN, 2005b (T)  
*Cavusonella* RIGBY, FAN, & ZHANG, 1989b (P)  
*Molengraaffia* VINASSA DE REGNY, 1915 (T)  
*Radiotrabeulopora* RIGBY, FAN, & ZHANG, 1989b (P); described as belonging to the family Disjectoporidae (order ?Inozoa) by Stearn (see p. 319)  
 Subfamily Daharelliinae RIGBY & SENOWBARI-DARYAN, 1996a  
*Daharella* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
*Aliabadia* SENOWBARI-DARYAN, 2005b (T)  
 Subfamily Gigantospingiinae RIGBY & SENOWBARI-DARYAN, 1996a  
*Gigantospingia* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
 Subfamily Spinospongiinae RIGBY & SENOWBARI-DARYAN, 1996a  
*Spinospongia* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
 Subfamily Acoeliinae WU, 1991  
 ?*Acoelia* WU, 1991 (= *Molengraaffia* VINASSA DE REGNY, 1915) (P)

- Solutossaspongia* SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994 (P)  
 Family Stellispongiellidae WU, 1991  
 Subfamily Stellispongiellinae WU, 1991  
*Stellispongiella* WU, 1991 (P–T)  
*Lutia* SENOWBARI-DARYAN, 2005a (T)  
 Subfamily Prestellispongiinae RIGBY & SENOWBARI-DARYAN, 1996a  
*Prestellispongia* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
 Subfamily Estrellospongiinae RIGBY & SENOWBARI-DARYAN, 1996a  
*Estrellospongia* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
 Family Preperonidellidae FINKS & RIGBY, 2004d  
 Subfamily Preperonidellinae FINKS & RIGBY, 2004d  
*Preperonidella* FINKS & RIGBY, 2004d (P–T)  
*Bisiphonella* WU, 1991 (P)  
*Radiofibra* RIGBY & SENOWBARI-DARYAN, 1996a (P–T)  
 Subfamily Permocorynellinae RIGBY & SENOWBARI-DARYAN, 1996a  
*Permocorynella* RIGBY & SENOWBARI-DARYAN, 1996a (P–T)  
*Djemelia* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
*Saginospongia* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
 Subfamily Precorynellinae TERMIER & TERMIER, 1977b  
*Precorynella* DIECI, ANTONACCI, & ZARDINI, 1968 (P–T)  
*Bicoelia* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
*Imperatoria* DE GREGORIO, 1930 (O, P)  
*Minispongia* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
*Ramostella* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
*Stollanella* BIZZARINI & RUSSO, 1986 (T)  
 Subfamily Heptatubispongiinae RIGBY & SENOWBARI-DARYAN, 1996a  
*Heptatubispongia* RIGBY & SENOWBARI-DARYAN, 1996a (P)  
*Marawandia* SENOWBARI-DARYAN, SEYED-EMAMI, & AGHANABATI, 1997 (T)  
 Family Fissispongiidae FINKS & RIGBY, 2004d  
*Fissispongia* KING, 1938 (D–Ca)  
 Family Maeandrostiidae FINKS, 1971  
*Maeandrostia* GIRTY, 1908b (Ca–T)  
*Stylopegma* KING, 1943 (P)  
 Class Calcarea BOWERBANK, 1869  
 Subclass Calcinea BIDDER, 1898  
 Order Stellispongiida FINKS & RIGBY, 2004d  
 Family Stellispongiidae DE LAUBENFELS, 1955  
 Subfamily Stellispongiinae DE LAUBENFELS, 1955  
*Stellispongia* D'ORBIGNY, 1849b (?J, Cr)  
*Amorphospongia* D'ORBIGNY, 1849b (J)  
*Blastinoidea* RICHARDSON & THACKER, 1920 (J)  
*Conocoelia* ZITTEL, 1878 (Cr)  
*Diaplectia* HINDE, 1884 (J)  
*Elasmoierea* DE FROMENTEL, 1860a (Cr)  
 ?*Elasmostoma* DE FROMENTEL, 1860a (J, Cr–Ce)  
*Euzittelia* ZEISE, 1897 (J–Cr)  
 ?*Heteropenia* POMEL, 1872 (Cr)  
*Lutia* SENOWBARI-DARYAN, 2005a (T)  
*Pachymura* WELTER, 1911 (Cr)

- Pachytilodia* ZITTEL, 1878 (Cr)  
*Pareudea* ÉTALLON, 1859 (T–J)  
*Paronadella* RIGBY & SENOWBARI-DARYAN, 1996a (P–J)  
*Peronidella* ZITTEL in HINDE, 1893 (J–Cr, R)  
*Steinmanella* WELTER, 1911 (Cr)  
*Trachypenia* POMEL, 1872 (Cr)  
*Trachysinia* HINDE, 1884 (J)  
*Trachysphecion* POMEL, 1872 (J, R)  
Subfamily *Holcospongiinae* FINKS & RIGBY, 2004d  
*Holcospongia* HINDE, 1893 (J)  
*Actinospongia* D'ORBIGNY, 1849b (J)  
*Astrospongia* ÉTALLON, 1859 (J)  
*Calicia* DULLO & LEIN, 1980 (T)  
*Enaulofungia* DE FROMENTEL, 1860a (?T, J, ?Cr)  
*Eudea* LAMOUROUX, 1821 (T–J, R)  
*Mammillopora* BRONN, 1825 (J, ?Cr, R)  
*Oculospongia* DE FROMENTEL, 1860a (P, ?T, J–Cr)  
*Tremospongia* D'ORBIGNY, 1849b (Cr)  
*Tretocalia* HINDE, 1900 (Ce)  
Class and Order Uncertain  
*Bortepesia* BOÏKO, 1984a (T)  
*Cornuaspongia* SENOWBARI-DARYAN, 1994b (T–J)  
?*Corynospongia* DENG, 1990 (P)  
*Lamellispongia* BOÏKO, 1984a (T)  
?*Trammeria* SENOWBARI-DARYAN, 1994b (T–J)

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# GLOSSARY OF TERMS APPLIED TO THE HYPERCALCIFIED PORIFERA

B. D. WEBBY, Compiler

With contributions by F. DEBRENNE, S. KERSHAW, P. D. KRUSE, H. NESTOR,  
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This glossary covers all the major groups of hypercalcified sponges, including the fossil representatives of the Archaeocyatha, Stromatoporoidea, Chaetetida, Sphinctozoa, and Inozoa, and as well the living hypercalcified members of the classes Demospongiae and Calcarea. It includes the terms used to describe the wide range of morphological types of nonspiculate basal calcareous skeletons. It also includes relevant spicule terminology for the well-preserved fossil skeletons exhibiting spicule traces and for describing the spicules associated with the living hypercalcified basal skeletons, as well as those loosely aggregated in soft tissues of their upper growing surfaces. The glossary reflects the scope and wide-ranging progress made in research on the various hypercalcified sponge groups over the past 40 years. Many of the terms defined in the glossary are discussed and illustrated in the introductory chapters of this volume.

Parts of this compilation are based significantly on the following works: (1) BOURY-ESNAULT and RÜTZLER's (1997) *Thesaurus on Sponge Morphology* (with its terminology focused on extant forms); (2) parts of HOOPER and VAN SOEST's (2002a) *Systema Porifera* that deal with the terminology of fossil Sphinctozoa (contributed by SENOWBARI-DARYAN and GARCIA-BELLIDO) and the Archaeocyatha (with its separate glossary contributed by DEBRENNE, ZHURAVLEV, and KRUSE); (3) the contribution on Paleozoic stromatoporoids by STEARN and others (1999), also with a separate glossary; and (4) the fossil sponge glossary in the *Treatise on Invertebrate Paleon-*

*tology*, Part E, Revised, vol. 2, contributed by REID and RIGBY (2003). An etymology of the Greek words used in the formation of sponge terminology, nomenclature, and taxon names by BOURY-ESNAULT and RÜTZLER (1997) and HOOPER and VAN SOEST (2002a) is presented in VOULTSIADOU and GKELIS (2005).

The terms defined here in alphabetical order as being of greater importance in this *Treatise* volume are listed in bold and singular, and the groups of hypercalcified sponges to which they apply are denoted at the end of each entry by abbreviations in bold and square brackets. These latter are identified (special interests of authors are included in parentheses) as follows: **Ar**, archaeocyaths (Debrenne, Zhuravlev, Kruse); **Ch**, chaetetids (West); **Cr**, cribricyaths (Zhuravlev, Kruse); **Di**, disjectoporids (Stearn); **Ex**, extant forms (Vacelet, Willenz); **In**, inozoans (Senowbari-Daryan, Rigby); **Ms**, Mesozoic stromatoporoids (Wood); **Ps**, Paleozoic stromatoporoids (Stearn, Webby, Nestor, Stock, Kershaw); **Pu**, pulchrilaminids (Webby); **Ra**, radiocyaths (Kruse, Zhuravlev, Debrenne); **Sp**, sphinctozoans (Senowbari-Daryan, Rigby). Some nonspiculate stromatoporoid-like forms (Stearn, Stock) from the Mesozoic are also denoted by **Ms**.

Each entry in the alphabetically arranged glossary list includes the specific term, then one or more sentences defining the term, followed by a listing of additional terms that are included for comparative purposes to the defined term. Other terms that are viewed as having lesser importance are also

listed as synonyms (syn.); these are mainly regarded as superfluous (or obsolete). A few other terms are entered in the glossary with italics, and contributing authors regard these as obsolete; consequently they are not recommended for continued use by workers on hypercalcified sponges. Two examples are (1) the so-called coralline sponges, a term that is more or less synonymous with hypercalcified sponges but inappropriately named, even allowing for some that show a superficial resemblance to corals; and (2) the Sclerospongiae, an artificial (polyphyletic) grouping of living forms exhibiting demosponge affinities, with solid calcareous skeletons and, as well, fossil stromatoporoids and chaetetids.

The presentation of this consolidated glossary has involved entering terminology across a number of different hypercalcified sponge groups, and this has resulted in some multiple listings with a term having been introduced independently by workers in a number of different groups. Consequently, the definitions vary greatly: in some cases they describe very similar structures, and in other examples the features given a common name represent entirely unrelated structures. For example, whereas the term *astrorhiza* seems to define homologous structures across a number of different groups, the term *tabula* appears to represent completely unrelated types of structures across various groups. In preparing this consolidated glossary, we maintain the separated multiple entries for each term using an italicized *or* between each successive entry. The only other alternative was to present separate glossaries for each group, but this seemed a less satisfactory approach, given the longer-term aim to produce an entirely unified nomenclature for the hypercalcified sponges.

Though the archaeocyathan terms used here derive mainly from the summary in DEBRENNE, ZHURAVLEV, and KRUSE (2002), they were originally proposed by a number of workers, most notably DEBRENNE, ROZANOV, and ZHURAVLEV (1990, p. 205); ZHURAVLEV,

DEBRENNE, and WOOD (1990); WOOD, ZHURAVLEV, and DEBRENNE (1992); and DEBRENNE and ZHURAVLEV (1992b, p. 34, 58). In addition, some general terms were taken from VLASOV (1962); ROZANOV (1973, p. 62–77); WENDT (1980); WOOD (1987); and MEYEN (1988).

The Paleozoic stromatoporoid terms compiled here have been compiled from the glossary list in STEARN and others (1999, p. 5–10). This was the first attempt since the late 1950s (GALLOWAY, 1957, p. 350–360) to produce a concise, simplified, yet comprehensive list of morphological terms in English. BOGOYAVLENSKAYA (1968, 1984), KHALFINA (1972), and BOL'SHAKOVA (1973) provided other morphological summaries.

A glossary of Mesozoic stromatoporoid terms was compiled by WOOD (1987), and, prior to the summary of morphological terminology in SENOWBARI-DARYAN and GARCIA-BELLIDO (2002a), there was a comprehensive coverage of the morphological terminology of sphinctozoans assembled by SENOWBARI-DARYAN (1990).

A divergence of opinion exists between the usages of the term stromatoporoid among authors of the chapters dealing with Mesozoic taxa. Wood (p. 193–208, 209–292) has treated the term stromatoporoid as representing a grade of organization of the hypercalcified skeleton, and so the term is viewed as having little or no taxonomic significance. The spiculate relationship is considered by Wood to have prime importance in classifying the Mesozoic taxa and in assigning them to the class Demospongiae; or, where spicules are lacking, the taxa are placed in *incertae sedis* of the Porifera. The second opinion stems from the long-standing perception among Paleozoic workers that the term stromatoporoid is taxonomically important: it remains the basis for recognition of the Ordovician–Devonian class Stromatoporoidea as an independent, unified, and exclusively nonspiculate group. Given this background, Stearn and Stock (p. 307–310) regarded the comparatively limited and uncertain record of nonspic-

ulate, upper Paleozoic–Mesozoic forms as being stromatoporoid-like taxa, with uncertain links to early to mid-Paleozoic Stromatoporoidea.

It should be noted that the list of Paleozoic stromatoporoid terms presented in this glossary is additionally classified into those terms that are: (1) related to skeletal form and structure (skeleton = sk); (2) structures parallel to growth surfaces (tangential = ts); (3) structures normal to growth surfaces (longitudinal = ls); (4) related to the aquiferous filtration system (aquiferous = aq); and (5) related to microstructural type (microstructure = mi). One of the supplementary categories in parentheses (above) has been added to each Paleozoic stromatoporoid term listed in the glossary.

It is important also to distinguish growth orientations within laminar, domical, and bulbous stromatoporoid skeletons, as well as to the different orientations of thin sections used to study them. In particular, growth takes place *longitudinally* as the organism extends outwardly through successive growth surfaces, and *tangentially* as it extends laterally, parallel to successive growth surfaces. For studying columnar and dendroid skeletons, three different orientations are used: *longitudinally*, in the direction of the long axis of the column or branch; *transversely*, at right angles to the long axis; and *tangentially*, in the direction of the long axis, but offset to near the outer margin of the column or branch. In the *transverse* cut, structures are parallel to growth toward the periphery of branch, but normal to growth in the axial region.

Thin sections used in studying archaeocyaths and chaetetids are typically cut in two main orientations: *longitudinally* and *transversely* (perpendicular to and parallel to the growth surface, respectively).

Other abbreviations used in the Glossary are listed below.

S2a: *Systema Porifera*, vol. 2, DEBRENNE, ZHURAVLEV, and KRUSE, 2002, p. 1539–1699, Class Archaeocyatha BORNEMANN, 1884.

S2b: *Systema Porifera*, vol. 2, SENOWBARI-DARYAN and GARCIA-BELLIDO, 2002a, p. 1511–1533, Fossil sphinctozoan: chambered sponges (polyphyletic).

Th: *Thesaurus on Sponge Morphology* (edited by BOURY-ESNAULT & RÜTZLER, 1997, Smithsonian Contributions to Zoology 596:1–55).

Tr: *Treatise on Invertebrate Paleontology*, Part E, Revised, Volume 2 (REID & RIGBY, 2003), glossary for Porifera, p. 177–190.

References herein are to figures and terms used within these two volumes of the *Treatise on Invertebrate Paleontology*, Part E, Revised, Volumes 4 and 5. This glossary represents a comprehensive listing of terms used for fossil hypercalcified poriferans. Less complete are the set of terms compiled for extant representatives of the hypercalcified poriferans—a more complete listing of these is contained in BOURY-ESNAULT and RÜTZLER (1997), available online ([http://www.sil.si.edu/smithsoniancontributions/zoology/pdf\\_hi/sctz-0596.pdf](http://www.sil.si.edu/smithsoniancontributions/zoology/pdf_hi/sctz-0596.pdf)).

**acanthostyle.** Single-axis spicule that bears small spines (or spinules), one blunt end and one pointed end; normally a megasclere (Th, fig. 216; Tr, p. 177) [Ms, Ch, Ex].

**acosmoreticular (mi).** A microreticulate microstructure where the orientation of micropillars and microcolliculi is without order [Ps].

**allotube (ls).** An elongate space within the skeleton aligned normal to the growth surface, meandriform or irregular in tangential section, bounded by amalgamate net of pachysteles and pachystromes, internally divided by dissepiments in orders Stromatoporida and Syringostomatida (Fig. 324.4; Fig. 329.3–329.4 (syn., pseudozooidal tube, coenotube) [Ps].

**altoid wall.** In Kazachstanicyathida, a simple outer wall of lintels linking distal ends of pillars to form a continuous plate pierced by frequent polygonal pores (Fig. 516c) (syn., simple wall of *Altaicyathus*-type; DEBRENNE & ZHURAVLEV, 1992b) [Ar].

**amalgamate structure (sk).** Three-dimensional network in which discrete, persistent, tangential structural elements are poorly defined (Fig. 321.5–321.6) [Ps].

**ambiostrium.** A large exopore in interwall at the junction of two chambers, that opens into both chambers (S2b, fig. 1) [Sp, In].

**ambisiphonate.** Condition in which a spongocoel or axial tube is formed by growth upward from the chamber floor and downward from the roof. Usually the two parts do not grow completely

- together, leaving a ring of perforations or exopores (S2b, p. 1515, fig. 10) [Sp, In].
- ambitopic mode of life.** Like a number of other Paleozoic benthic organisms (JAANUSSON, 1979a, p. 269), many stromatoporoids were capable of maintaining markedly different types of substrate preferences, first as attached forms during early growth stages, and then switching to live essentially freely on unconsolidated substrates, like level-bottom muddy settings, through their remaining life history [Ps].
- amphiaster.** A microsclere with rays radiating from both ends of a shaft. The rays are shorter than the shaft (Th) [Ex].
- amphiblastula.** Hollow, ovoid larva, with anterior (flagellated) and posterior (nonflagellated) groups of cells, typical of Calcaronea (Th) [Ex].
- annulation.** A ringlike structure marked by either a constriction or expansion in the outer wall of the skeleton [Sp, In].
- annulus** (pl., **annuli**). Ring-shaped (annular) plate separating horizontal files of wall openings (alone or in combination with other wall types); develops on external surface of outer walls or internal (central cavity) surface of inner walls; may be of planar, S-shaped, or V-shaped section (Fig. 501; S2a, p. 1689, fig. 19–21) [Ar].
- anthoid wall.** In Anthomorpha, a simple outer wall comprising transverse lintels linking adjacent pseudosepta to form a single row of slightly subquadrate large pores; additional lintels may delineate additional, discontinuous pore rows (Fig. 516a–516b) (syn., simple wall of *Anthomorpha*-type; DEBRENNE & ZHURAVLEV, 1992b) [Ar].
- apical actine (ray).** Fourth actine of a tetractine that is joined to the basal triradiate system (Th) [Ex].
- apochete.** Exhalant canal [Sp, In].
- apopore.** Exhalant pore [Sp, In].
- apopyle.** Opening of a choanocyte chamber into an exhalant canal (Th, p. 8, fig. 37) [Ex].
- aporate.** Without pores [Sp, In].
- aporoze septum.** Septal pores absent. See septum (S2a, p. 1692, fig. 39H) [Ar].
- aquiferous system.** Whole water-conducting system of a sponge between the ostia and the osculum, comprising the inhalant system, choanocyte chambers, and exhalant system (Th, p. 8, fig. 37) [Ms, Ch, Ex].
- aquiferous unit.** Portion of the sponge that is a more or less functionally independent water-conducting system, comprising associated ostia, inhalant system, choanocyte chambers, and exhalant system, and has its drainage converging on a single osculum. See functional unit and module, which are treated as equivalents) (S2a, p. 1689, fig. 3) [Ar, Ms, Ch, Ex].
- archaeocyathan architecture.** Skeletal structure with radial-longitudinal and/or radial-transverse partitions in intervallum. See architecture (Fig. 491b; S2a, p. 1689, fig. 2A, C) [Ar].
- architecture.** Type of primary skeletal structure. See archaeocyathan architecture, chaetetid architecture, stromatoporoid architecture, thalamid architecture (Fig. 491; S2a, p. 1689, fig. 1); syn., growth pattern [Ar].
- asiphonate.** Without a spongocoel or axial canals (S2b, p. 1519, fig. 10) [Sp, In].
- asiphonate exhalant system.** Condition in sphinctozoan sponges where any form of axial canal is lacking (S2b, p. 1513) [Sp].
- aster.** Any polyactinal (multi-rayed) microsclere in which the processes diverge from a common center or axial shaft (Tr, p. 178; HOOPER & WIEDENMAYER, 1994, p. 38, fig. 117–131) [Ms, Ch, Ex].
- astrorrhiza** (pl., **astrorrhizae**) (aq). A set of radiating (stellate) and branching canals, grooves, ridges, and openings of exhalant canal system of primary skeleton, as imprints converging to a single osculum (or closely spaced oscula) on terminal growth surface of skeleton; the structures may be associated with mamelons (Fig. 326.1–326.5; Fig. 327.2–327.4; Fig. 328.1–328.4; S2a, p. 1689, fig. 61F; Th, p. 36, fig. 203, 210; Tr, p. 178); syn., excurrent canal traces, astrosystem, stellate venations [Ar, Ps, Ms, Ch, Ex, Sp, In].
- astrorrhizal canal** (aq). Part of a stellate, radiating, and/or branching, exhalant canal system within the skeleton (both longitudinally and tangentially oriented), composed of walled tubes, or where preserved without walls, as astrorrhizal paths. In chaetetids, they are confined to the external surface. Canals may be partitioned by tabulae or dissepiments (syn., lateral tube, transverse astrotube, lateral canal) [Ps, Ms, Ch, Ex].
- astrorrhizal path.** See astrorrhizal canal (Fig. 327.2–327.3) [Ps].
- astrotube.** The terms lateral and axial astrotubes have been applied to distribution of oscula on Mesozoic stromatoporoids (HUDSON, 1958); now obsolete [Ms].
- atrium.** An exhalant aquiferous cavity receiving water from one or more exhalant canals or apopyles and conducting it to one or more oscula (Th, p. 8, fig. 40; Tr, p. 178); syn., spongocoel, preoscular cavity, cloaca [Ms, Ch, Ex]; or spongocoel (Th, p. 8, fig. 40) [Sp, In].
- attached microporous sheath.** Microporous sheath attached directly to carcass pore lintels; may be continuous (covering entire surface of carcass) or discontinuous (covering each carcass pore separately). See microporous sheath (Fig. 504.2–504.3; S2a, p. 1690, fig. 44D, G) [Ar].
- autotube** (ls). An elongate space between pachystyles with circular to subcircular outline in tangential section [Ps].
- axial.** The central (older) part of a skeletal branch [Ms, Ch].
- axial canal** (aq). Longitudinally oriented median structure of the astrorrhizal system in domical, laminar, bulbous, and irregular skeletons that may be analogous to the axial canal in some columnar to dendroid stromatoporoids; may be tabulated (Fig. 329.1; Fig. 349.2; Fig. 476a) [Ps]; or spongocoel [Sp, In].

- axial tube.** Spongocoel, or a combination of discontinuous but aligned tubelike structures in interwalls [Sp, In].
- backfill.** Secondarily secreted calcareous filling material that grows syntaxially over the primary calcareous skeleton. Backfill may partially or fully occlude the primary pore space. See secondary calcareous skeleton [Ms, Ch].
- baculus** (pl., **baculi**). Longitudinal, rodlike element on external surface of outer wall [Cr].
- bar.** Radial-transverse lintel separating pores in a uniporous septum; biconcave in plan and with elongate cross section. See rod, uniporous septum (Fig. 496.3; S2a, p. 1689) [Ar].
- barrel-shaped chamber shape.** Chambers with nearly flat interwalls, but with bulging sides at midheight in subcylindrical structure [Sp, In].
- basal calcareous skeleton.** Hypercalcified sponges composed of either a rigid aspiculate or rigid spiculate skeleton, or a combination of both; the basal skeleton of calcium carbonate is considered by analogy with living hypercalcified sponges to have underlain a mantling layer of living tissue during its upward and outward growth. See rigid aspicular skeleton, rigid spicular skeleton [Ps, Ms, Ch, Ex].
- basal layer** (ts). A thin, dense, initial investment of skeletal material at the base of a stromatoporoid or chaetetid skeleton, with associated basal surface with either smooth or concentrically arranged, wrinkled, fine to coarse striae; basal layer is typically confined to undersides of laminar-domical shaped skeletons but may extend to lateral surfaces of small, cup-shaped skeletons; may be synonymous with epitheca of corals and extant hypercalcified sponges but is not of secondary origin; the basal layer was produced in an initial stage of the growth process, as part of the basal phase of STEARN (1989a); in chaetetids, the basal layer appears to be organic [Ps, Ch].
- basal phase** (ts). A unit distinguished by structures different from those of the mature skeleton, formed in the initial growth of skeletal material across the surface of the sediment or hard substrate, or resumption of growth at the base of a latilamina (Fig. 329.2; Fig. 330.3) [Ps].
- basic wall.** Wall constructed only of marginal interwall structures with additional lintels between. See rudimentary wall (Fig. 514c; Fig. 515b; S2a, p. 1689, fig. 60L) [Ar].
- bisiphonate.** Sponges with two spongocoels [Sp, In].
- bowl-like cup.** Widely conical cup. See cup (Fig. 581.2; S2a, p. 1690, fig. 69A) [Ar].
- bract.** S-shaped, cupped, or tubular plate incompletely covering a single pore; develops on external surface of outer wall or internal (central cavity) surface of inner wall. See fused bract, scale, pore tube (Fig. 500a–500b; S2a, 1689, fig. 44C) [Ar].
- branching canal.** Canal completely divided at a point along the length into two or more subsidiary canals. See canal (Fig. 503a; S2a, p. 1689, fig. 22J) [Ar].
- branching gross morphology.** Spreading out in branches; syn., dendritic, dendroid, foliose, fasciculate, ramose, digitate, phaceloid [Ms, Ch, Ex].
- branching modular organization.** Type of modular organization generated either by longitudinal subdivision or by external or interseptal budding. See modular organization; syn., dendroid, ramose (Fig. 492; S2a, p. 1691, fig. 60F–G) [Ar].
- budding.** Type of asexual reproduction in which parent cup is distinct from its progeny, though contiguous with them. [This budding terminology does not apply to chaetetids.] See external budding, intercalicular budding, interseptal budding (Fig. 522; S2a, p. 1689, fig. 9) [Ar].
- bulbous growth morphology.** Having the form of bulbous calcareous skeleton [Ms, Ch, Ex].
- bullipore.** Pore of a cribribulla (S2b, fig. 1) [Sp, In].
- buttress.** Complex, aporose structure of secondary skeleton consisting of several lamellar elements and extending from outer surface of primary skeleton to connect it with any firm substrate. See exocysthoid buttress, tersioid buttress (Fig. 552; S2a, p. 1689) [Ar].
- calcareous skeleton.** The calcareous skeletal material of hypercalcified demosponges and calcareans, both aspiculate and spiculate. See basal calcareous skeleton, skeleton; syn., coenosteum [Ms, Ch, Ex].
- calicle.** Longitudinal, tubelike, interwall structure that can be hexagonal or tetragonal in cross section. See facet (Fig. 510a; S2a, p. 1689, fig. 71A–B) [Ar]; or *calicle*. Not recommended as a chaetetid morphological term because of its cnidarian connotations; replaced by tubule (see definition, p. 415) [Ch].
- calthrop.** Equiangular tetraxon with equal rays, so-called from resemblance to the four-pointed weapon known as a calthrop; may be a mega- or microsclere (Th, p. 42, fig. 228) [Ms, Ch, Ex].
- cambroid wall.** In Loculicyathina, a simple outer wall consisting of a continuous plate pierced by simple pores; pores may be rounded, irregularly rounded, or irregularly quadrate (Fig. 515c–515f); syn., simple wall of *Cambrocyathellus*-type; DEBRENNE & ZHURAVLEV, 1992b) [Ar].
- canal.** Wall opening of length greater than diameter. See branching canal, communicating canal, noncommunicating canal, S-shaped canal, subdivided canal, V-shaped canal, spongiouse wall [S2a, p. 1689] [Ar]; or internal passage for water circulation, may be single or dichotomously to multidichotomously branched, or labyrinthic branched. See groovelike canal, fully roofed canal, exopore (S2b, p. 1519, fig. 8) [Sp, In].
- canal system.** Inhalant and exhalant canals for water circulation within the sponge [Sp, In].
- carcass.** Layer of otherwise simple pores and intervening lintels, the latter supporting microporous sheath in walls of microporous sheath type (S2a, p. 1689, fig. 27B) [Ar].
- cassicate structure** (sk). Formed by oblique skeletal elements joined to enclose diamond-shaped galleries in a network like that of a chainlink fence (Fig. 322.1) [Ps].
- cateniform.** Catenulate or moniliform structure [Sp, In].

- catenulate.** Arrangement of ringlike chambers in moniliform structure around one or more spongocoels (S2b, p. 1515, fig. 4) [Sp, In].
- catenulate modular organization.** Chainlike modular organization consisting of individuals united laterally with one or two others; generated by incomplete longitudinal subdivision. See modular organization (Fig. 495b; S2a, p. 1691, fig. 41K) [Ar].
- cavaedia** (pl.). Large, deep indentations between folds in a plicate dermal surface of a sponge [Sp, In].
- cellular** (mi). Speckled skeletal material filled with closely spaced, irregularly distributed, subspherical, clear areas (cellules) that appear to have been voids in the structural element (Fig. 338.1; Fig. 339.1; Fig. 343.2) [Ps].
- cellules** (mi). See cellular [Ps].
- cemented (fused) spicule.** Interlocked or adjacent spicules firmly linked by calcareous cement; the cement may be restricted to the junction area or may progressively encase the entire spicule (Th, p. 36, fig. 204) [Ms, Ch, Ex].
- central cavity.** Space within two-walled cup, bounded externally by inner wall (S2a, p. 1690) [Ar].
- chaetetid architecture.** Skeletal structure consisting of calices in archaeocyaths. [Use of the term tubules is preferred in chaetetids.] See architecture (Fig. 491e; S2a, p. 1689, fig. 2D) [Ar].
- chamber.** Space in a thalimid cup bounded by adjacent arched tabulae and their contiguous walls (S2a, p. 1690) [Ar]; *or* hollow, superposed, or laterally attached, major structures in sphinctozoan skeleton (S2b, fig. 1) [Sp].
- chamber shape.** Form of hollow major structures of the sponge skeleton. See barrel-shaped chamber shape, crescentic chamber shape, flattened chamber shape, funnel-shaped chamber shape, hemispherical chamber shape, tubular chamber shape, spheroidal chamber shape, rectangular chamber shape [Sp].
- chamber wall.** The skeletal structure that defines an individual chamber and may be subdivided into an exowall, interwall, and endowall [Sp, In].
- chimney.** Vertically developed mamelons bearing oscula, both of which protrude beyond the general growth surface [Ms, Ch, Ex]; *or* see exaulos [Ar, Sp, In].
- clathrate wall.** Wall consisting of a carcass of slitlike pores supporting a layer of more closely spaced, longitudinal ribs with or without transverse linking lintels. See pseudoclathrate wall (S2a, p. 1690, fig. 38E, J, 50F, H) [Ar].
- clavidisc.** Specialized microscelere, comprising an ovate disc with an elongate central perforation [Ms, Ch, Ex].
- clinogonal microstructure.** Elongate microstructural elements are divergent from a common axis at angles of less than 45° and may be penicillate, of thin pencil-like elements, or water-jet of divergent, irregular, linear elements or trabecular, of rods of anastomosing filaments, which may form an irregular mesh or web. Penicillate and water-jet are confirmed as basic types of clinogonal microstructure in sponges, but trabecular represents a cnidarian condition (not known in sponges), consequently an obsolete term in relation to sponges. Note also fascicular fibrous microstructure is broadly synonymous with clinogonal microstructure (WENDT, 1984; BOURY-ESNAULT & RÜTZLER, 1997) [Ch, Sp, In, Ms, Ex].
- clinoreticular** (mi). A microreticulate microstructural type where micropillars are inclined upward and outward from subcolumn axes; note that subcolumns in the syringostomatids have been referred to as pillars [Ps].
- cloaca.** See spongocoel [Sp, In].
- cloacal.** Of the cloaca or spongocoel [Sp, In].
- coarsely porous porosity.** Pore diameter greater than lintel width; pores rounded to polygonal in outline. See porosity (Fig. 494b; Fig. 509a; S2a, p. 1691, fig. 56F) [Ar].
- coeloblastula** (blastula). Hollow larva composed of an envelope of morphologically similar equipotent cells, to which a few, larger, nonflagellated cells may be added at the posterior pole (Th) [Ex].
- coenosteie** (ls). Not recommended because of its cnidarian connotations. See pachysteie [Ps].
- coenosteum** (sk). See skeleton. The term is not recommended for continued use in describing the solid calcified skeleton of stromatoporoid sponges. [It remains applicable to cnidarians that exhibit a common colonial skeleton, and to Bryozoa with vesicular or solid skeletal material between zooecia.] [Ps, Ms].
- coenostrome** (ts). Not recommended because of its cnidarian connotations. See pachystrome; syn., coenostrom [Ps].
- coenotube** (ls). Not recommended because of its cnidarian connotations. See allotube [Ps].
- collencyte.** Cell with branching pseudopods, involved in the secretion of collagen (Th, p. 12, fig. 49) [Ex].
- colliculus** (pl., **colliculi**) (ts). A rod attached to a pillar that joins other such rods to form a net parallel to the growth surface in the order Actinostromatida; hence the laminae in this group are composed of colliculi (Fig. 321.1–321.2) [Ps].
- column** (ls). Skeletal structure (of macrostructure level) in which the arrangement of skeletal elements differs from that of intercolumn areas. The difference is commonly in the concentration and width of astrorhizae, pillars, or other longitudinal structures. See mamelon column (Fig. 325.5) [Ps]; *or* radial structural element of the calcareous skeleton, which appears vertical in longitudinal section. Greater degree of continuity and size than pillars; syn., vertical element, radial pillar, vertical lamella [Ms].
- columnar gross morphology.** Elongate forms with a circular or subcircular cross section; syn., cylindrical [Ms, Ch, Ex].
- comma** (pl., **commas**). A curved microstyle (Th) [Ex].
- communicating canal.** Canal connected to its neighbors either by pores piercing mutual canal walls or by anastomosing. See canal (Fig. 503b; S2a, p. 1689, fig. 25E, 31E–F, 37E–F); syn., perforate canal [Ar].

- compact** (mi). Specks are distributed evenly throughout the skeletal elements so that the elements have no regular internal microstructure [Ps].
- compensation**. Morphogenetic process involving the addition of a microporous sheath-screen or other elements in response to oligomerization (S2a, p. 1690) [Ar].
- completely porous septum**. Septal pores distributed frequently and uniformly over entire septum. See septum (Fig. 496a–496b; S2a, p. 1691, fig. 22H, 24B) [Ar].
- compound wall**. Wall in which component pores or cells bear spinelike elements projecting inward from their lintels; spines may unite across pore orifice to form micropores (complete pore subdivision) or remain incompletely connected (incipient pore subdivision) (Fig. 516d; S2a, p. 1690, fig. 67F, 68F, respectively) [Ar].
- concentrically porous wall**. Wall in which pores are grouped into more or less discrete clusters corresponding to cells bounded by adjacent radial-longitudinal partitions and tangential synapticulae (Fig. 514d; Fig. 516e); syn., centripetal wall of GRAVESTOCK, 1984) [Ar].
- conical cup**. Cup in form of inverted cone. See cup (S2a, p. 1690, fig. 13C) [Ar].
- conical gross morphology**. Having the form of an inverted cone [Ms, Ex].
- contemporary phase** (ls). A unit of skeletal growth of characteristic structure that displaces others, tangentially reflecting different structures formed contemporaneously along the growth surface (e.g., areas exhibiting structures unique to those formed by the superposition of mamelons) (Fig. 322.5, Fig. 325.5) [Ps].
- coralline sponges**. So named because of their superficial resemblances to groups of skeletonized, colonial organisms like tabulate corals in the Paleozoic and scleractinian corals in the Mesozoic to Recent; and also because of the many associations where sponges occur in reef-building habitats. Both these connotations are misleading, however: coralline is not a sponge-derived morphological term, and it has no place in the broader taxonomic classification and/or evolutionary development of sponges, either hypercalcified or otherwise. Consequently, the expression coralline, even as part of a general informal usage, should be discontinued. The term *coralline demosponges* is similarly a misnomer [Ps, Ms, Ch, Sp, In, Ex].
- corallite**. Not recommended because the term has cnidarian connotations [Ms, Ch].
- corolla**. Star-shaped, convex-downward, umbrella-like structure projecting from external surface of a cup and consisting of hollow, closed shafts and their connecting membranes; part of primary skeleton (Fig. 493e–493f; S2a, p. 1690, fig. 53J–L) [Ar].
- cortex** (pl., cortices). Thin, rindlike external layer of the rigid skeleton, usually with a structure different from that of the interior part of the skeleton (S2b, fig. 1) [Sp, In].
- cortical**. Of the cortex [Sp, In].
- craticula** (pl., craticulae). A screenlike element across the outer end of an exaulos (S2b, fig. 1) [Sp, In].
- craticular pore**. An opening or pore in a craticula [Sp, In].
- crenulate**. Wall in which each intersept is individually folded to form smoothly rounded bulge directed away from the intervallum (S2a, p. 1690, fig. 74A–B); syn., turgescens [Ar].
- crenulation** (ls). A small, upward inflection of a cyst plate or lamina (Fig. 387, 2a–b) [Ps].
- crenate chamber shape**. Chambers that are C-shaped, or shaped like the moon in its first quarter [Sp, In].
- cribribulla** (pl., cribribullae). Blisterlike sieve at the inner end of an exaulos (S2b, fig. 1) [Sp, In].
- cribripore**. Pores in sieve-like or screenlike cribribulla (S2b, fig. 1) [Sp, In].
- cryptosiphonate**. Condition in sphinctozoan sponges in which chambers communicate through an aperture or group of apertures through the interwall between chambers (S2b, p. 1513, 1519, fig. 10) [Sp].
- cryptosiphonate exhalant system**. Condition in sphinctozoan sponges where skeletal chambers communicate through an aperture or group of apertures in chamber interwalls, without an axial tube (S2b, p. 1513) [Sp].
- cup**. Calcareous archaeocyathan skeleton. See bowl-like cup, conical cup, cylindrical cup, domal cup, juvenile cup, multichambered cup, platelike cup, sheetlike cup, single-chambered cup (S2a, p. 1690, fig. 1) [Ar].
- cyathiform**. Cup shaped [Sp, In].
- cylindrical cup**. Narrowly conical cup approaching form of cylinder. See cup (Fig. 502c; Fig. 509c; S2a, p. 1690, fig. 12J) [Ar].
- cyst** (ts). The space enclosed by the cyst plate [Ps].
- cyst plate** (ts). An upwardly and outwardly convex (in a few taxa, flat or concave) skeletal plate parallel to the growth surface in the order Labechiida, with most family representatives exhibiting cyst plates of variable sizes and shapes (rarely very large), and in places showing denticles on their tops. Branching to columnar members of family Aulaceratidae exhibit two types of cyst plates—large, stacked to overlapping cyst plates within axial columns; and much smaller, commonly imbricated, structural elements in lateral zones that COPPER, STOCK, and JIN (2013, p. 671) have now chosen to call “microcyst plates.” This unfortunately has wider implications, given the bulk of labechiids exhibit smaller to medium-sized cyst plates and that a stabilized nomenclature for recording all these structures has existed for more than a half century (see GALLOWAY, 1957). (Fig. 318.5; Fig. 391g; Fig. 392e); syn., microcyst plate [Ps].
- denticle**. Flattened, toothlike projection from free edge of an annulus (Fig. 501.5; S2a, p. 1690, fig. 20A,C) [Ar]; or short, solid, skeletal rod raised above the surface of cyst plates, and may extend from flanks of some pillars in the order Labechiida (incorporates villi of GALLOWAY, 1957) (Fig. 321.4; Fig. 322.5) [Ps].

- dermal.** Outer surface or part of a sponge [Sp, In].
- desma.** Typically an interlocking megasclere of varied geometry that contributes to the main body of skeleton of lithistid demosponges (Th) [Ex].
- diapason** (tuning-fork spicule). Sagittal triactine with parallel, paired rays (Th) [Ex].
- diaphragm.** Thin, flat, or convex membrane narrowing orifice of a simple pore (Fig. 499.1; S2a, p. 1690, fig. 19C, left) [Ar]; *or* more or less rigid plate subdividing chamber interiors [Sp, In].
- dichotomous exopore.** A pore that subdivides once into two branches in the outer part of the wall [S2b, fig. 8] [Sp, In].
- dictyonal network.** Three-dimensional intervallar structure comprising radial and longitudinal lintels of taeniae (in which pores are subtetragonal) linked by tangential synapticalae at each interpore node to form an orthogonal, scaffoldlike network of equidimensional units (Fig. 509b–509c; S2a, p. 1690, fig. 60J, M) [Ar].
- diploaster.** An astrose microsclere in which the rays or spines radiate from two slightly distant points (Th) [Ex].
- dissepiment** (ts). An upwardly convex or inclined plate occupying interlaminae space; the term is also applied to partitions in allotubes, autotubes, and astrorhizal canals; not always easy to distinguish from tabulae in astrorhizal canals and interlaminae spaces; also dissepiments in places partition some peripheral vesicles of the amphiporids (Fig. 319.1; Fig. 319.3; Fig. 325.3) [Ps].
- domal cup.** Cup in form of domelike plate. See cup (S2a, p. 1690, fig. 61A) [Ar].
- domical growth morphology.** Having a calcareous skeleton with a domical growth form [Ms, Ch, Ex].
- echinating.** Megascleres that protrude from the spongin plate, a fiber, or a spicule tract (Th, p. 30, fig. 173) [Ms, Ch, Ex].
- encrusting growth habit.** Forms with a low height-to-width ratio that demonstrably encrust a substrate or another organism; syn., matlike gross morphology [Ms, Ch, Ex].
- encrusting growth morphology.** Exhibiting a matlike skeletal form seen to encrust substrate or other organism [Ms, Ch, Ex].
- encrusting mode of life.** These types of stromatoporeoid organisms may be distinguished from their ambitopic counterparts by remaining in occupation of hard substrates throughout most of their life history; they are especially commonly associated with reef habitats [Ps].
- encrusting modular organization.** Modular organization in the form of a multioscular plate whose lower surface is attached to substrate. See modular organization (Fig. 492; S2a, p. 1691, fig. 61A) [Ar].
- endocameral.** Within the chambers of sphinctozoan (or informally termed thalamid) sponges [Sp].
- endopore.** Opening through the wall of a spongocoel or endowall (S2b, fig. 1) [Sp, In].
- endotube.** Tube that pierces the endowall and extends into the chamber interior from the endowall in a sphinctozoan sponge (S2b, fig. 1) [Sp].
- endowall.** The wall between the spongocoel and surrounding chamber (S2b, fig. 1) [Sp, In].
- entrapped spicules.** Calcareous or siliceous spicules that are not part of the primary spicule framework but are enclosed progressively within the calcareous solid skeleton during growth (Th, p. 36, fig. 205) [Ms, Ch, Ex].
- enveloping skeletal growth** (sk). This condition occurs where growth of a succeeding latilamina (or lamina) overlaps the previous latilamina when the living tissue was able to entirely mantle the calcareous skeleton from its top to lower lateral extremities, and to remain free from any contamination from associated sediment [Ps].
- epitheca** (pl., **epithecae**) (ts). Thin, wrinkled, calcareous covering of the basal surface of the skeleton of fossil hypercalcified sponges, probably representing initial growth. Problematic term, given its long-established cnidarian and bryozoan connotations; preferentially replaced by descriptive term basal layer for fossil stromatoporeoids and chaetetids, whereas epitheca continues to be used by specialists on extant hypercalcified taxa [Ps, Ch]; *or* thin, wrinkled, calcareous basal layer of finer structure than the superjacent, normal skeleton that covers the dead basal part of the rigid calcareous demosponge skeleton, and considered to be of secondary origin (Th, p. 36, fig. 203) [Ms, Ex].
- euaster.** A collective term for astrose microscleres in which the rays radiate from a central point (Th, p. 44, fig. 223, 258, 275, 276, 279, 291) [Ms, Ch, Ex].
- exaulos** (pl., **exaulos**). Protruding, spoutlike extension of outer walls. See chimney in *Retilamina* (DEBRENNE & JAMES, 1981) (Fig. 495.5; S2a, p. 1690, fig. 61A, 75H; S2b, fig. 1) [Ar, Sp, In].
- excurrent.** See exhalant [Sp, In].
- excurrent canal.** See exhalant canal (Th, p. 8, fig. 37) [Sp, In].
- exhalant.** Allowing the outward flow of water (syn., excurrent) [Sp, In].
- exhalant canal.** Canal that forms a part of the exhalant system and is lined by the apopinocoderm; allows discharge of water from the sponge interior; syn., excurrent canal [Sp, In].
- exhalant canal system.** Part of the aquiferous system between the apopyle and oscule (Th, p. 8, fig. 37) [Ms, Ch, Ex].
- exhalant opening.** Opening through which water exits; may be through an exhalant or gastral pore, if larger, or an exopore, if smaller [Sp, In].
- exhalant system.** Arrangement of canals or other openings through which water exits a sponge or a chamber. See asiphonate exhalant system, cryptosiphonate exhalant system, siphonate exhalant system; syn., excurrent canal system) [Sp, In].
- exocyathoid buttress.** Zoned buttress encrusting primary cup, in which each zone consists of concentric plates connected by radial plates. See buttress (Fig. 522a; S2a, p. 1689, fig. 56C, D) [Ar].
- exopore.** Pore that pierces the outer wall of a chamber. Several types of openings are included here,

- including single, dichotomous, multidichotomous, and labyrinthic exopores (S2b, fig. 1) [Sp].
- exowall.** External wall of a chamber (S2b, fig. 1) [Sp].
- external budding.** Bud on outer wall of parent cup. See budding (Fig. 492; S2a, p. 1689, fig. 60G) [Ar].
- facet.** Any flat face of a calicle or syrinx (Fig. 510a–510d; S2a, p. 1690, fig. 72A–D) [Ar].
- fascicular fibrous microstructure.** General term for microstructure of crystal fibers fanning outward and radiating upward. See clinogonal microstructure (Th, p. 36, fig. 206) [Ms, Ch, Ex].
- fiber.** A column (strand, thread) of spongin forming a reticulate or dendritic skeleton, with or without indigenous spicules or foreign material (Th, p. 30, fig. 160, 170) [Ms, Ch, Ex].
- fiber skeleton.** Aragonitic or calcitic rigid skeleton of inozoans and sphinctozoans [Sp, In].
- fibrous (mi).** Specks and crystal boundaries aligned. In laminae, this alignment is transverse; in pillars, it may curve upward and outward from the axis in a water-jet or feather structure (Fig. 336.1; Fig. 345.1) [Ps].
- filling material (filling tissue).** Secondary calcareous skeleton that partitions or fills abandoned parts of the skeleton (Th, p. 38, fig. 207) [Ms, Ch, Ex].
- filling structure (or skeleton).** Elements of the skeleton filling within chambers of sphinctozoan sponges; may be reticulate, trabecular, tubular, radially septate, sporelike, pisolitic, vesicular, or a combination, such as septate-reticulate (S2b, p. 1513, fig. 1, 11) [Sp].
- finely porous porosity.** Pore diameter less than lintel width. See porosity (Fig. 494c; S2a, p. 1691, fig. 62D) [Ar].
- first-order intervallar structure.** Intervallar structure directly connecting both walls. See intervallar structure, pseudoseptum, septum, taenia (S2a, p. 1690) [Ar].
- flattened chamber shape.** Chambers with relatively low heights as compared to their diameters [Sp].
- foramen (pl., foramina).** Circular aperture in tabulae of chaetetid skeletons, allowing interconnection between adjoining intertabular spaces (Th, p. 38, see label “fo” shown on fig. 208) [Ch]; or *foramen* (ts). See pore [Ps, Ms].
- fully roofed canal.** Canal enclosed within the skeleton [Sp, In].
- functional unit.** The portion of water-conducting system of a sponge draining a single osculum; comprised of ostia, the inhalant system, choanocyte chambers, and exhalant system [Ms, Ch, Ex].
- fungiform.** Shaped like a mushroom [Sp, In].
- funnel-shaped chamber shape.** Chambers that are like an inverted cone, with a hole or small tube at the lower or narrow end [Sp].
- fused bract.** Neighboring bracts of the same horizontal file, incompletely amalgamated to form a single structure covering two or more openings in a wall, rarely forming a complete circle. Fused bracts are planar or S-shaped in longitudinal profile (S2a, p. 1690, fig. 61B–C); syn., pseudoannulus [Ar].
- gallery (sk).** The three-dimensional interlaminar space between adjacent pillars and bounded above and below by laminae or pachystromes; may contain other structural elements (e.g., dissepiments). The term is not usually applied in the Labeciida [Ps].
- gastral.** Inner surface or part of a sponge wall around a spongocoel [Sp, In].
- globular gross morphology.** Exhibiting a globular-shaped calcareous skeleton [Ms, Ch, Ex].
- glomerate.** Arrangement of the chambers like the seeds in an ear of corn or the grapes in a cluster [Sp, In].
- granular (or microgranular) microstructure.** Composed of irregular grains or granules [Sp, In].
- groovelike canal.** Canal impression in the skeleton as a groove in the dermal layer, marking the position of a canal that was not covered by skeletal material [Sp, In].
- gross morphology.** The overall shape of the calcareous skeleton. Often subject to considerable environmental control. See nodular gross morphology, branching gross morphology, columnar gross morphology, conical gross morphology, encrusting gross morphology, laminar gross morphology, domical gross morphology. It does not include other parts of external morphology, such as surface features (e.g., mamelons, traces of astrorhizae) [Ms, Ch, Ex].
- growth axis.** Represents the direction the skeleton grew in nodular, branching, columnar, conical, and domical forms, perpendicular to the growth surface [Ms, Ch, Ex].
- growth banding.** Banding in skeleton of some hypercalcified sponges reflects variations in growth due to a range of external and possibly internal controls. Three styles of banding are recognized: (1) density banding; (2) growth interruption banding; (3) postmortem banding (YOUNG & KERSHAW, 2005); the first two styles reflect periodic changes in growth (syn., latilaminae), but the third style is produced by secondary processes of diagenesis and compaction [Ps].
- growth form (sk).** Overall shape or morphotype; may be laminar, domical, bulbous, irregular, columnar, dendroid, digitate, or digitolaminar. Laminar, domical, irregular, bulbous, and digitolaminar forms may interfinger (in places giving ragged skeletal outlines) at their outer edges with surrounding sediment, whereas columnar, dendroid, and digitate forms tend to have smooth outer margins. Among Paleozoic stromatoporoids, the domical to laminar shapes are most common (and include the largest), and the other main shapes, arranged in decreasing order of abundance, are: irregular, bulbous (moderately common), columnar, digitate, dendroid to digitolaminar (less common to rare). [Ps, Ch].
- growth habit.** The growth habits reflect different levels of skeletal integration of the modular organization and may be associated with the growth morphologies (given in parentheses) and defined in separate entries. See pseudocolonial growth habit (branching), multiserial erect growth habit (branching), multiserial encrusting-encrusting growth habit (laminar, encrusting), multiserial

- encrusting-massive growth habit (nodular, conical, hemispherical) [Ms, Ch, Ex].
- growth module.** See module [Ps].
- growth surface** (ts). Any level in the skeleton where addition to the surface is contemporaneous; basal and terminal refer to the first and last surfaces of skeletal growth (Fig. 318.1; Fig. 352.1–352.2) [Ps]; or any contemporaneous surface on or within the skeleton [Ms, Ch, Ex].
- hemispherical chamber shape.** Chambers with relatively flat bases but spheroidal roofs [Sp].
- hemispherical gross morphology.** Having a flat base and a convex upper surface; syn., massive gross morphology, domical gross morphology [Ms, Ch, Ex].
- hypercalcified sponges.** The original term hypercalcified sponges (TERMIER & TERMIER, 1973) is a generalized, informal name to describe sponges that have secreted excessive amounts of solid, nonspiculate, calcium carbonate to their basal skeletons. The name has been used for nearly four decades to recognize a wide variety of fossil sponges—groups that include the archaeocyaths, stromatoporoids, chaetetids, sphinctozoans, and inozoans, as well as a relatively small number of questionable related lines of living Demospongiae and Calcarea; in most cases, the skeletons were confined more or less entirely to the bases of the living tissue, but this was not always so in the sphinctozoans, nor in all probability, in the archaeocyaths. Additionally the term hypercalcified has for convenience been applied to certain spiculate groups, those where the spicules have been cemented together with calcium carbonate coatings without producing a completely fused basal skeleton, as in the class Heteractinida, and in some inozoans (FINKS & RIGBY, 2004c, p. 585) of the class Calcarea. In the interests of stability in sponge nomenclature, it is important that the informal term **hypercalcified sponges** be maintained exclusively for the combined living and fossil members of both formal classes Demospongiae and Calcarea. To avoid confusion, it must be clearly distinguished from the terms **calcareous sponges** or **calcifying sponges** that are rather informal names, usually reserved by zoologists for use in describing members of the class Calcarea. See *coralline sponges* [Ar, Ps, Ms, Ch, Sp, In, Ex].
- incurrent.** See inhalant [Sp, In].
- incurrent canal.** See inhalant canal [Sp, In].
- independent microporous sheath.** Microporous sheath supported above carcass by short rods arising from carcass pore lintels; this sheath type is invariably continuous. See microporous sheath (Fig. 504a; Fig. 505h–505i; S2a, p. 1690, fig. 27B, 54G, I) [Ar].
- individual.** A single skeleton, composed of one or more functional units, representing one individual. In biological terms, this represents all the cellular components and all the interactions of their components within the pinacocyte envelope [Ms, Ch, Ex].
- inhalant.** Through which water enters [Sp, In].
- inhalant canal.** Any canal forming part of the inhalant system and lined by the prosopinacoderm (Th, p. 8) [Ms, Ch, Ex]; or any canal for passage of inhalant water leading into sponge interior, which would have initially had a lining of prosopinacoderm [Sp, In].
- inner cavity.** Space within one-walled cup, bounded externally by the wall (S2a, p. 1690) [Ar].
- inner wall.** Inner of two concentric walls in two-walled cups (S2a, p. 1690) [Ar].
- Inozoa** (STEINMANN, 1882) or **inozoans.** Nonchambered, usually cylindrical or club-shaped sponges with both rigid and additionally spiculate skeleton (calcareans, demosponges) [In].
- Inozoida** (RIGBY & SENOWBARI-DARYAN, 1996a), or **inozoides.** Nonchambered, usually cylindrical or club-shaped sponges with rigid skeletons but without spicules; hence assignments to calcarean or demosponge groups remain uncertain [In].
- intercalicular budding.** Bud inside a single calicle. See budding (Fig. 492; S2a, p. 1689, fig. 62F) [Ar].
- interlaminar space.** Area or space enclosed between two successive laminae [Ps, Ms].
- internal filling skeleton.** See filling structure [Sp, In].
- interpore.** Pore in interwalls between chambers (S2b, fig. 1) [Sp, In].
- intersept.** That part of a wall or intervallum bounded by adjacent radial-longitudinal partitions (septa, taeniae) (S2a, p. 1690) [Ar].
- interseptal budding.** Bud in intervallum. See budding (Fig. 492; S2a, p. 1689, fig. 62F); syn., interparietal [Ar].
- interseptal plate.** Second-order intervallar structure in form of porous plate linking adjacent radial-longitudinal partitions (septa, taeniae) (Fig. 555.3; S2a, p. 1690, fig. 29D–E) [Ar].
- interskeletal space.** Referring to the spaces between any skeletal elements. See gallery, chamber, coenospace, coenotube [Ms, Ex].
- intertabula** (pl., **intertabulae**). That part of a wall or intervallum bounded by adjacent tabulae (S2a, p. 1690) [Ar].
- intertube.** Small tube that connects chambers through interwalls [Sp, In].
- intertubular increase.** Budding of the rigid calcareous skeleton involves the separation of tubule walls where they meet at an angle (at each intersection) and gradual expansion to full-sized tubule size with upward growth; syn., intercalicle budding [Ch].
- intervallar cell.** Part of intervallum bounded by adjacent radial-longitudinal partitions and tangential synapticalae (S2a, p. 1690) [Ar].
- intervallar structure.** Any skeletal element in the intervallum. See first-order intervallar structure, second-order intervallar structure (S2a, p. 1690) [Ar].
- intervallum.** Space enclosed between walls of a two-walled cup (S2a, p. 1690) [Ar].

- interwall.** The wall or walls between two adjacent chambers (S2b, fig. 1) [Sp, In].
- invaginated wall.** Inner wall closed at base and contiguous with tabula (S2a, 1690) [Ar].
- irregular gross morphology.** Having an irregularly shaped calcareous skeleton [Ms, Ch, Ex].
- irregular microstructure.** Irregular (felt) microstructure in which tangled linear crystal fibers have no preferred orientation (e.g., *Vaceletia*). Shape and nature of crystal fibers may be diverse or with unaligned and irregularly spaced elements (Th, p. 38, fig. 209); syn., granular, compact, freely micritic [Ms, Ch, Sp, In, Ex].
- Ischyrospongiae* (TERMIER & TERMIER, 1973). Introduced originally as a class to accommodate the extant *Calcarea* and *Demospongiae* with a solid calcareous skeleton and the fossil stromatoporoids and chaetetids, but the group name was seldom used, as it initially lacked priority over the *Sclerospongiae* HARTMAN & GOREAU (1970), only remaining applicable to extant calcareans. However, use of the TERMIERs's name has been discontinued since VACELET (1985) established the group as polyphyletic; hence the term is obsolete [Ps, Ms, Ch, Sp, Ex].
- isodiametric.** Of equal diameter, as in isodiametric spherulites in some skeletal structures [Sp, In].
- isodictyal.** An isodictyal skeleton exhibits an arrangement of spicules in simple, triangular meshes with single monaxons united tip to tip around each side (Th, p. 32; Tr, p. 183) [Ms, Ch, Ex].
- juvenile cup.** That portion of a cup generated prior to complete development of all mature structures. See cup (Fig. 497a; Fig. 497c; S2a, p. 1690, fig. 62G–H) [Ar].
- labriopore.** Exopores surrounded by a distinct external lip or rim [S2b, fig. 1] [Sp, In].
- labyrinthic exopore.** A pore that subdivides several times into a labyrinth or network of interconnected branches in the wall (S2b, fig. 8) [Sp, In].
- lamella.** A term introduced by LECOMPTE (1956), for lamina, but now obsolete [Ps].
- lamellar microstructure.** Laminar microstructure of thin layers that may be smooth and more or less uniform, to undulating and irregular [Sp, In].
- lamina** (pl., **laminae**) (ts). A tangentially extensive skeletal plate or net parallel to the growth surface; it may be single-layered or tripartite; i.e., with a less opaque central zone, a line of cellules in the central zone (ordinicellular) or an opaque central microlamina, or it may be composed of multiple microlaminae (Fig. 317.2; Fig. 320.1) [Ps]; or a continuous, concentric, calcareous sheet parallel to the growth surface, and perpendicular to radial skeletal elements, e.g., the long axes of chaetetid tubules. Laminae in chaetetids are bounded above and below by growth interruptions, and in that sense they are more analogous to latilaminae of stromatoporoids than to stromatoporoid laminae; syn., lamella *pars*, coenosteal lamella, thecal lamella [Ms, Ch].
- laminar gross morphology.** Forms with a low height-to-width ratio that are free living, i.e., that do not appear to be attached to a hard substrate; syn., tabular gross morphology [Ms, Ch, Ex].
- laminar-encrusting gross morphology.** Exhibiting overall shape as matlike or tabular growth form that may be free-living or encrusting [Ms, Ch, Ex].
- latilamina** (pl., **latilaminae**). A tangentially continuous set of layers of skeletal material of the calcareous skeleton, visible as periodic growth bands bounded above and below by phase changes or growth interruption surfaces (Fig. 329.2; Fig. 330.3) [Ps, Ms].
- leuconoid.** Aquiferous system in which the choanocytes are restricted to discrete choanocyte chambers, which are dispersed in the mesohyl (Th) [Ex].
- lintel.** Skeletal structure separating and bounding adjacent pores (S2a, p. 1690) [Ar].
- lipped pore.** Labriopore [Sp, In].
- loculus** (pl., **loculi**). That part of an intervallum delimited by two adjacent septa-taeniae and two adjacent tabulae (S2a, p. 1690) [Ar].
- longitudinal fission.** Increase in the rigid calcareous skeleton by the development of one or more pseudosepta that subdivide the tubule into equal or unequal parts; commonly the subdivision is across the shortest transverse dimension of the tubule (WEST & CLARK, 1984) [Ch].
- longitudinal fold.** In a two-walled cup, the fold of one wall or mutual folds of both walls to impart a succession of more or less regular transverse annulations of the cup (Fig. 534.5; S2a, p. 1690, fig. 16A) [Ar].
- longitudinal subdivision.** Type of asexual reproduction by which the parent cup divides into two or more cups of equal sizes; syn., longitudinal fission (Fig. 492; S2a, p. 1690, fig. 9, 59F, 60F–G) [Ar].
- louver.** Plate incompletely covering two or more adjacent pores or intercepts in the same horizontal file; intermediate between fused bract and annulus (Fig. 500c–500d; Fig. 500f; S2a, p. 1691, fig. 18B) [Ar].
- macrostructure.** Pertains to visible internal skeletal structures in low magnification (up to  $\times 10$ ) using oriented thin sections. See lamina, pillar, cyst plate, dissepiment [Ps]; wall, tubule, tabula, lamina, pseudosepta [Ch].
- mamelon** (ts). An updomed area of skeletal material on the terminal growth surface (Fig. 326.1; Fig. 326.3) [Ps]; or rounded regular or irregular elevation of the skeleton surface; may or may not show correlation with astrorhizae; syn., monticule [Ms, Ch, Ex].
- mamelon column** (ls). A structure composed of upwardly inflected laminae, cyst plates or pachystromes formed by superposition of mamelons (Fig. 325.4–325.5) [Ps].
- massive.** Solid mass (a skeleton of relatively large bulk but not specifically shaped) [Sp, In].
- massive gross morphology.** Characteristically showing a bulky, nondescript type of calcareous skeleton [Ms, Ch, Ex].

- massive modular organization.** Type of modular organization (bulky skeleton) generated by contiguous addition of new aquiferous units. See modular organization (Fig. 492; S2a, p. 1691, fig. 71A, 75A, E) [Ar].
- meandroid.** A flexuous pattern shown by tubules in transverse section as opposed to discrete, regular, or irregular polygons [Ch].
- megapillar (ls).** A rodlike structure of a larger order of magnitude than a pillar. Megapillars can be distinguished in taxa having two sizes of pillars, such as *Bifariostroma*, *Oslodictyon*, *Yabeodictyon*, *Actinodictyon*, *Belemnostroma* [Ps].
- me gasclere.** Major supporting spicule; the larger size group where two distinct size categories exist. Generally with a length greater than 100  $\mu\text{m}$  [Ms, Ch, Ex].
- melanospheric (mi).** Specks are concentrated in closely spaced, irregularly distributed, subspherical opaque areas separated by clear areas (Fig. 338.2–338.3) [Ps].
- membrane tabula.** Second-order intervallar structure developed in same plane in one or several intersepts by fusion of spines. See tabula (Fig. 511; S2a, p. 1692, fig. 10) [Ar].
- mesohyl.** Part of sponge enclosed in pinacoderm and choanoderm (Th, p. 12) [Ex].
- microcolliculus (pl., microcolliculi) (ts).** A very fine, tangentially oriented rod that with other such rods forms a network joining micropillars within microreticulate microstructure [Ps].
- microcyst plate (ts).* A term proposed by COPPER, STOCK, and JIN (2013, p. 671), but its use should be discontinued as it contributes little towards achieving a more simplified and unified nomenclature of cyst plate terminology within the Labechiida. See cyst plate [Ps].
- microgranular microstructure.** Diverse microstructure composed of equant micrite-sized grains or crystals; in some cases, anhedral crystals have randomly oriented c-axes (Fig. 521; Th, p. 8, fig. 211; S2a, p. 1691) [Ar, Ms, Ch, Ex].
- microlamellar microstructure.** Structure in which the crystal fibers are disposed in crisscross layers, mostly parallel to the growing surface of the skeleton (e.g., *Acanthochaetetes*) (Th, p. 41, fig. 212) [Ch, Ms, Ex].
- microlamina (pl., microlaminae) (ts).** A thin, compact, laterally persistent plate that may be part of a lamina, or a single element parallel to the growth surface, or may consist of microcolliculi (Fig. 322.3) [Ps].
- micropillar (ls).** A very fine, rodlike, longitudinal structural element within microreticulate microstructures [Ps].
- microporous sheath.** Thin skeletal plate supported by lintels of carcass pores and pierced by micropores of lesser diameter; develops on external surface of outer wall or internal (central cavity side) surface of inner wall. See attached microporous sheath, independent microporous sheath (Fig. 504; S2a, p. 1690); syn., microporous membrane [Ar]; or an external layer of nesasters in some radiocyath genera; comprises anastomosing rays and tangential linking cross pieces (Fig. 658, 1a) [Ra].
- microreticulate (mi).** Structural elements composed of micropillars and microcolliculi giving a three-dimensional network of fine posts and beams. See acosmoreticular, clinoreticular, orthoreticular (Fig. 339.3) [Ps].
- microsclere.** Accessory spicule of often ornate shape; the smaller size group where two size categories exist. Spicules generally smaller than 100  $\mu\text{m}$  (Th, p. 44) [Ms, Ch, Ex].
- microstructure.** Crystal arrangement of calcareous skeleton that forms the skeletal elements, as seen under high power using a light microscope and/or an SEM. See irregular microstructure, microgranular microstructure, microlamellar microstructure, penicillate microstructure, clinogonal microstructure, orthogonal microstructure, spherulitic microstructure, trabecular microstructure, water-jet microstructure, fascicular fibrous microstructure, lamellar microstructure (Fig. 521; S2a, p. 1690; S2b, p. 1520, fig. 12); syn., ultrastructure, skeletal material, skeletal tissue [Ar, Ms, Ch, Sp, In, Ex]; or see compact, fibrous, striated, tubulate, cellular, melanospheric, microreticulate (three types), ordinocellular, vacuolate [Ps].
- modular organization.** Skeleton incorporating two or more aquiferous units united by common intervallar structures. See branching modular organization, catenulate modular organization, encrusting modular organization, massive modular organization, pseudoceroid modular organization (Fig. 492; Fig. 495; S2a, p. 1691, fig. 9) [Ar].
- module.** Functional unit of the poriferan aquiferous filtration system, serving a fixed volume of cells. A sponge module consists of incurrent pores (ostia), a connective canal system of incurrent and excurrent canals, and a common exhalant opening (osculum). In fossil sponges, a module is defined by the extent and influence of each osculum that may be expressed by the catchment area of the astrophorhizae. See functional unit, aquiferous unit [Ar, Ms, Ch, Ex]; or fundamental construction unit of the skeleton of Stromatoporellida and Clathrodictyida consisting of a floor that becomes the upper layer of a tripartite lamina (and is absent in the clathrodictyids), a roof that becomes the lower layers of the succeeding lamina, and the pillars and other structures enclosed between these layers; alternatively termed a growth module. Note that this concept of a sponge module relates to the secretion of successive structural elements (floors and posts) rather than the organization of aquiferous units (Fig. 353.2; Fig. 354.1–354.2) [Ps].
- monaxon.** Linear, nonradiate spicule, or a spicule type not having more than two rays along one axis (Th, p. 44) [Ms, Ch, Ex].
- moniliform.** Linear arrangement of the chambers in asiphonate sphinctozoans (S2b, p. 1512, 1515, fig. 4) [Sp].

- monoglomerate.** Arrangement of several cystlike chambers in a single layer around one or more axial spongocoel(s) (S2b, p. 1512, 1515, fig. 4) [Sp, In].
- monoplatyform.** Chambers forming plates a single chamber layer thick, with chambers laterally adjacent to one another (S2b, p. 1512, 1515, fig. 4) [Sp, In].
- monticule** (ts). A small mamelon in Paleozoic stromatoporoids. See mamelon [Ps].
- multichambered cup.** Cup incorporating two or more chambers. See cup (Fig. 491c; S2a, p. 1690, fig. 2B2, 52G–H) [Ar].
- multidichotomous exopore.** A pore that subdivides once into several branches in the outer part of the wall (S2b, fig. 8) [Sp, In].
- multiperforate tumulus.** Tumulus with several pores, each pore surmounting a small papilla. See tumulus (Fig. 506c–506e; S2a, p. 1692, fig. 31N) [Ar].
- multiserial encrusting-encrusting growth habit.** A form with a low height-to-width ratio, composed of many laterally connected modules. See laminar-encrusting gross morphology [Ms, Ch, Ex].
- multiserial encrusting-massive growth habit.** A form with a high height-to-width ratio that is composed of many modules. The modules are often bound both laterally across the growth surface and along the growth axis of the skeleton, with no skeletal separation between them. Often the skeleton consists of many superposed modules, though only surficial modules will be active. See nodular gross morphology, columnar gross morphology, conical gross morphology, hemispherical gross morphology [Ms, Ch, Ex].
- multiserial erect growth habit.** Where more than one laterally connected functional module is present on each skeletal branch at any one time. See branching gross morphology [Ms, Ch, Ex].
- nesaster.** Primary constituent of inner or outer wall; solid, starlike structure consisting of 6 to 20 coplanar rays radiating from a central boss. In some genera, nesasters additionally bear an external microporous sheath. See microporous sheath (Fig. 658, 1b; Fig. 659b; Fig. 660, 2a–c); syn., aster, rosette [Ra].
- netlike porosity.** Pore diameter much greater than lintel width; pores polygonal in outline. See porosity (Fig. 499i; S2a, p. 1691, fig. 49D, 62A, C); syn., retiform porosity, reticulate porosity [Ar].
- nodular gross morphology.** Almost spherical, often composed of a number of nodular growths. See globular gross morphology, irregular gross morphology, subspherical gross morphology, bulbous gross morphology, massive gross morphology [Ms, Ch, Ex].
- noncommunicating canal.** Canal lacking connecting pores or any other communication with adjacent canals. See canal (Fig. 502; S2a, p. 1689, fig. 23H); syn., imperforate canal [Ar].
- non-enveloping skeletal growth (sk).** A type of growth condition that occurs where a succeeding latilamina (or lamina) fails to completely overlap the preceding latilamina, giving a smooth appearance in cases where comparatively rapid upward growth was maintained, or it develops a ragged appearance when sediment spreads across lower parts of lateral margins of the skeleton [Ps].
- oligomerization.** Morphogenetic process involving decrease in number of pores or pore rows per intersept with accompanying increase in size of individual pores (S2a, 1691) [Ar].
- ontogeny.** The development during the course of an individual's life history; has not been recognized in either stromatoporoids or chaetetids; probably the term should be regarded as obsolete in these groups [Ms, Ch]. Skeletal ontogeny is recognized in archaeocyaths, however. See skeletal ontogeny [Ar].
- orbicyathoid.** See transverse fold (Fig. 494c; S2a, p. 1691, fig. 16D–E) [Ar].
- ordinicellular (mi).** Axial planes of laminae are marked by a layer of subspherical clear areas (cellules), giving laminae a three-layered, or tripartite, appearance in longitudinal section. Where divisions between these cellules are missing, the semicontinuous, clear middle layer accentuates this tripartite appearance. In some tripartite laminae, the central layer may be more opaque than those above and below (Fig. 320.1; Fig. 434e) [Ps].
- organic skeleton.** Spongin or collagenous part of mechanical support found in demosponges [Ms, Ch, Ex].
- orthogonal microstructure.** Microstructure in which the crystal fibers are in perpendicular and radial orientation relative to a central axis (Th, p. 40, fig. 213) [Ms, Ch, Ex]; *or* elongate microstructural elements diverging from a common axis at high angles to produce a radial, fibrous microstructure (Th, p. 40, fig. 213) [Sp, In].
- orthoreticular (mi).** Microreticulate microstructure where micropillars are normal to laminae-pachystromes and the microlaminae are parallel to the laminae [Ps].
- oscule.** See osculum [Sp, In].
- osculum** (pl., **oscula**). One (or more) openings through which water discharges from a sponge to the exterior; usually located at top of sponge (Th, p. 8, fig. 8, 38; S2b, fig. 1); syn., lateral astrotube, axial astrotube [Ar, Ms, Ch, Sp, In, Ex].
- ostial pore.** Proposed as new term for small inhalant apertures through external wall of calcarous skeleton [Sp, In].
- ostium** (pl., **ostia**). Any opening in the exopinacoderm through which water enters the living sponge. The term should be reserved for small inhalant apertures through living tissue. For inhalant apertures through calcareous walls of fossil skeletons, for example, the exowall of sphinctozoans, the general term pore remains available, or more specifically, ostial pore may be applied (Th, p. 8, fig. 45) [Sp, Ex].
- outer wall.** Outer of two concentric walls in two-walled cups (S2a, p. 1691) [Ar].
- pachysteale** (ls). A wall-like part of the amalgamate net, either meandriform or fused to form a closed, continuous network in tangential section of orders

- Stromatoporida and Syringostromatida (Fig. 321.5–321.6); syn., coenostele [Ps].
- pachystrome** (ts). A part of the amalgamate net that parallels the growth surface in the orders Stromatoporida and Syringostromatida (Fig. 321.5–321.6); syn., coenostrome [Ps].
- palmate**. With palms or with handlike structure [Sp, In].
- papilla** (pl., **papillae**) (ls). A raised, rounded extension of a pillar on the terminal growth surface [Ps].
- paragaster**. Spongocoel [Sp, In].
- paralamina** (pl., **paralaminae**) (ts). A planar skeletal plate that traverses single-layered, chevron-shaped laminae of a few genera of the order Clathrodictyida (NESTOR, 1966a) [Ps].
- pectinate tabula**. Second-order intervallar structure developed in same plane in all or most intersepts and consisting of bolster(s) and centripetal spines in mutually opposed, comblike arrangement. See tabula (Fig. 534, 4c; S2a, p. 1692, fig. 15H) [Ar].
- pellis**. Simple, aporose structure of secondary skeleton externally enveloping outer wall (S2a, p. 1691, fig. 59A) [Ar].
- pelta** (pl., **peltae**). In Monocyathida, a transverse, convex or concave primary skeletal structure, the direct extension of the wall, roofing inner cavity, and with central sag bearing an orifice (Fig. 507.1–507.2a–b; S2a, p. 1691, fig. 2G, 12H) [Ar].
- penicillate microstructure**. Crystal fibers fanning outward and radiating upward in a freely divergent manner (e.g., *Ceratoporella*). This microstructure is a subdivision of the broader clinogonal and fascicular fibrous microstructural types. See fascicular fibrous microstructure, clinogonal microstructure (Th, p. 40) [Ch].
- periloph**. Raised rim around an exopore or inhalant pore (formerly ostium); shorter than tubular exalos. See labriopore [Sp, In].
- peripheral**. Outer (younger) part of a skeletal branch [Ms, Ch].
- peripheral expansion**. Increase in the rigid calcareous skeleton by the development from the thin growing edge (soft tissue), of new, full-sized tubules on a preexisting substrate that fuse with preexisting tubules of the skeleton (WEST & CLARK, 1983) [Ch].
- peripheral membrane*. See sheath [Ps].
- peripheral vacuole**. A cellule that occupies a space between a pillar-pachystele, small interconnecting processes, and an adjacent, thin, curved plate resembling a dissepiment (previously termed peripheral membrane and cyst plate) of a few truptostromatid genera (e.g., *Hermatostroma*, *Hermatoporella*) (Fig. 323.2; Fig. 324.2) [Ps].
- peripheral vesicle** (ls). Elongated, bubble-like, gallery space forming part of a sporadically developed row along the inner side of the sheath of amphiporid stromatoporoids; in some cases partitioned by dissepiments (Fig. 476b) [Ps].
- peripterate**. Ribbonlike element spirally coiled along cup axis to form outer wall (Fig. 665, 2) [Cr].
- Pharetronida* (ZITTEL, 1878). Former grouping for sphinctozoan and inozoan sponges (polyphyletic) [Sp, In].
- phase** (sk). A part of the skeleton characterized by a change of growth structure either longitudinally (successive) or tangentially (contemporary). Divided into basal phase, contemporary phase, spacing phase, successive phase, and terminal phase (Fig. 329.5; Fig. 330.1) [Ps].
- pillar** (ls). A skeletal rod (rarely a plate); may be long, columnar, continuous through laminae and interlaminae spaces, or may be confined to an interlaminae space, upwardly conical, spool shaped, grading into upwardly or downwardly inflected laminae in Paleozoic stromatoporoids. Pillars of order Labechiida may be circular, irregular, meandriform, or bladed (with or without flanges) in tangential section. A series of short, superposed interlaminae pillars in families Truptostromatidae and Gerronostromatidae that may be difficult to distinguish from long, continuous pillars unless the traces of laminae cross them. See ring pillar (Fig. 317.3; Fig. 319.5; Fig. 321.2; Fig. 322.2; Fig. 323.3–323.4) [Ps]; *or* pillars are relatively short and discontinuous. See column; syn., vertical lamella, radial pillar [Ms]; *or* rodlike structure connecting adjacent tabulae and may extend through tabulae (Fig. 656, 1a–b; Fig. 657; S2a, p. 1691, fig. 2F, 51F, 75G–H) [Ar]; *or* rodlike elements extending between interwalls of successive chambers [Sp].
- pillar-lamellae**. Horizontal elements that are part of the primary calcareous skeleton; short, discontinuous, concentric elements, contiguous with pillars or columns; syn., horizontal lamellae, concentric lamellae, lamellae *pars*, transverse lamellae [Ms].
- pinacocyte**. Cell delimiting the sponge from the external milieu and always in a layer one-cell deep only (Th, p. 14, fig. 49, 51, 59) [Ex].
- pinacoderm**. Surface lined by pinacocytes (Th, p. 14, fig. 49) [Ex].
- pisolitic filling structure** (or **skeleton**). Composed of small, round-to-ellipsoidal calcium carbonate bodies with concentric and radial internal structure [Sp, In].
- platelike cup**. Conical cup in which apical angle of cone approaches 180°. See cup (Fig. 615, 1a–b; S2a, p. 1690, fig. 58A) [Ar].
- plate tabula**. First-order intervallar structure in form of porous plate. See tabula (Fig. 498; S2a, p. 1692, fig. 40C, 43F) [Ar].
- plicate wall**. Wall in which each intersept is individually folded to form sharp, mid-interseptal longitudinal ridge, directed away from intervallum and separating planar to subplanar lateral flanks (Fig. 493a; S2a, p. 1691, fig. 42A); syn., asteroid, stellate [Ar].
- plumose**. A type of skeletal construction made of primary fibers or spicule tracts from which skeletal elements radiate obliquely (Th, p. 34, fig. 192) [Ms, Ch, Ex].

- polyactine.** A spicule with many growth axes [Ms, Ch, Ex].
- polyglomerate.** Arrangement of chambers around one or more axial spongocoel(s) in two or more layers (S2b, p. 1512, 1515, fig. 4) [Sp, In].
- polyplatyform.** Chambers forming plates composed of two or more flat layers, with chambers laterally adjacent to one another (S2b, p. 1512, 1515, fig. 4) [Sp, In].
- polysiphonate.** Sponges with more than two spongocoels [Sp, In].
- porate.** With pores. Sphinctozoans whose chamber walls (at least the exowall) contain small and equally distributed openings of the same size [Sp].
- pore.** General term for any small opening of a calcareous wall through which water passes. On external walls of hypercalcified sponges, such pores may represent inhalant apertures (the term ostia was previously applied to these structures but should be reserved for inhalant openings through the exopinacoderm of living sponges). See ostial pore [Sp, In]; *or* restricted to openings piercing any primary skeletal structure, of diameter greater than thickness of that structure. See slitlike pore, stirrup pore, subdivided pore (S2a, p. 1691) [Ar]; *or* an opening of rounded section through a lamina (foramen of GALLOWAY, 1957, is a large pore) [Ps, Ms].
- pore field.** Cluster of pores, particularly if in flat area surrounded by a low rim, in an exowall [Sp, In].
- pore tube.** Structure of elongate, scooplike to tubular shape, completely or almost completely covering a single pore (Fig. 520a–520b; S2a, p. 1691, fig. 64A–D, 70C) [Ar]; *or* longitudinally oriented, canal-like tubes that developed by the superposition of pores, which were first pierced by the original cyst plates or laminae. The pore tubes are considered to be primary structures and typically have sparry calcite infills; see labechiid genus *Forolinia* (NESTOR, COPPER & STOCK, 2010, p. 57, pl. 2a–b, 4a–b). However, this same type of structure has been inferred to be a product of selective dissolution of pillarlike elements by diagenetic processes and secondary infilling of the “tube” with sparry calcite, as seems likely in many examples of the labechiid genus *Stromatocerium*; see discussion in the Labechiida (p. 710–711) and illustrations of the so-called “pore tubes” (hollow pillars or wall-less “rods”) in KAPP and STEARN (1975, fig. 3) and Webby (1979b, p. 248, fig. 5A–D) [Ps].
- porosity.** Character of pore arrangement in a primary skeletal structure. See coarsely porous porosity, finely porous porosity, netlike porosity, slitlike porosity, septum, pseudoseptum, taenia (S2a, p. 1691) [Ar].
- primary calcareous skeleton.** Initially formed calcareous skeleton and well differentiated from an enveloping secondary calcareous skeleton. [Paleozoic stromatoporoids do not show such a clear-cut differentiation into primary and secondary skeletal growth, and to some extent this applies to chaetetids as well.] (Th, p. 40, fig. 207) [Ms, Ch, Ex]; *or* that part of skeleton formed during ontogeny (primary growth of individual) by biologically controlled processes and serving as the locus for principal life functions (Fig. 521a–521c; S2a, p. 1691, fig. 4) [Ar].
- primary spicule framework.** Framework of arranged spicules around which the predominantly primary calcareous skeleton is precipitated (Th, p. 40, fig. 207) [Ms, Ch, Ex].
- prosiphonate.** A type of spongocoel in which individual chamber roofs or interwalls grew upward to form the spongocoel (S2b, p. 1519, fig. 10) [Sp].
- prospore.** Inhalant pore [Sp, In].
- prosopyle.** Opening of an inhalant canal into a choanocyte chamber (Th, p. 8, see label “pro” in fig. 37) [Ex].
- pseudocerioid modular organization.** Massive type of modular organization consisting of individuals united laterally with two or more other individuals; generated by incomplete longitudinal subdivision. See modular organization (Fig. 495c; Fig. 523c; S2a, p. 1691, fig. 25A) [Ar].
- pseudoclathrate wall.** Wall consisting of a layer of closely spaced, longitudinal ribs and transverse linking lintels supported by short rods above quadrate intervallar cells. See also clathrate wall (Fig. 612, *Ib*; S2a, p. 1691, fig. 55D) [Ar].
- pseudocolonial growth habit.** Having only one active functional module present on each skeletal branch. See branching gross morphology [Ms, Ch, Ex].
- pseudogemmule.** Accumulation of gemmular archaeocytes in basal cavities of a solid skeleton or hypercalcified skeleton (Th) [Ex].
- pseudolamellar microstructure.** Diagenetic alteration of the microstructure, producing parallel plates of recrystallized crystals and giving an internally layered appearance in transverse section [Ms].
- pseudoseptum** (pl., **pseudosepta**). Radial-longitudinal first-order intervallar structure formed by irregularly porous, planar-to-subplanar partition, developed during ontogeny from initial taenial structure; may be coarsely porous or finely porous. See porosity (Fig. 494; S2a, p. 1691, fig. 57E, 59G) [Ar]; *or* calcareous structure that subdivides (or longitudinally partitions) tubules; pseudosepta are associated with the growth and expansion of the rigid calcareous skeleton. See longitudinal fission [Ch].
- pseudosiphonate.** A type of spongocoel that lacks a true axial tube but with a tubular axial passage that may or may not be outlined by an endocameral structure (S2b, p. 1519, fig. 10) [Sp, In].
- pseudospicules.** Linear, spicule-like elements of spongin or spongin-related materials in living forms, or of secondary mineral fillings of primary or secondary linear openings within skeletal structures in fossil examples [Sp, In].
- pseudotaenial network.** Three-dimensional intervallar structure, comprising taeniae linked by synapticulae at each interpore node (Fig. 509; S2a, p. 1691, fig. 64A–D, 66F–G, 67D–E) [Ar].

- pseudozooidal tube*. A term introduced by GALLOWAY (1957) but because of its hydrozoan and/or bryozoan connotations, it is here replaced by allotube [Ps].
- puigole tetractine**. Dagger-shaped, cruciform, or harpoonlike tetractine (BOROJEVIC, BOURY-ESNAULT, & VACELET, 2000) [Ex].
- pustula** (pl., **pustulae**). Wall structure covering an individual wall pore, in form of low cone or hemispherical dome pierced by a single central orifice (Fig. 517d; S2a, p. 1691, fig. 59K) [Ar].
- radial**. Elements radiating outward from a central point or area [Ms, Ch].
- radial canal**. Radially directed inhalant or exhalant canal [Sp, In].
- radiate**. Spicule with three or more radiating growth axes, or referring to radiating arrangement of megascleres [Ms, Ch, Ex].
- radiate skeleton**. A type of skeleton in which the structural components diverge from a central region toward the sponge surface (Th, p. 34, fig. 194) [Ms, Ch, Ex].
- radicatus** (pl., **radicati**). Dense lamellar structure of secondary skeleton anchoring the cup to a substrate (ZHURAVLEVA & MYAGKOVA, 1981, fig. 7; S2a, p. 1690, fig. 1); syn., *epithec*a [Ar].
- raphide**. A very thin, hairlike microscle, often in bundles called trichodragmas (Th) [Ex].
- rectangular chamber shape**. Chambers that have four sides and are quadrangular [Sp].
- recurrence**. Morphogenetic polymorphic set of features regularly repeating along the same vector in each series of homologous variability (S2a, p. 1691) [Ar].
- redimiculus** (pl., **redimiculi**). Narrow, aporose, radial-longitudinal plate projecting externally or internally from a wall (Fig. 499f–499g; S2a, p. 1691, fig. 51B) [Ar].
- regular spicule**. Triactine or tetractine spicule with basal rays of equal length and with equal angles (120° between them, when projected into a plane perpendicular to the optic axis) (Th) [Ex].
- reticular**. Endocameral structure consisting of an irregularly three-dimensional network of beams of skeleton (S2b, fig. 11) [Sp, In].
- reticulate filling structure** (or **skeleton**). Composed of a three-dimensional network of fibers or other linear elements [Sp, In].
- reticulate skeleton**. General organization of skeleton consists of a three-dimensional network of fibers, tracts, lines, and/or individual spicules (Th, p. 34, fig. 155–158, 163, 175, 176, 180, 195); syn., *reticulum* [Ms, Ch, Ex].
- retrosiphonate**. A type of spongocoel formed by downward or backward extension of the chamber walls in sphinctozoans (S2b, p. 1519, fig. 10) [Sp, In].
- rhagon**. Earliest functional stage with multiple choanocyte chambers and aquiferous canals, typical for Demospongiae (Th, p. 18, fig. 86) [Ms, Ch, Ex].
- rib**. Narrow longitudinal plate linking annuli to wall (S2a, p. 1691, fig. 19G–H) [Ar].
- rigid aspicular skeleton**. A skeleton that originates from the direct secretion of aspiculate elements made of calcium carbonate; siliceous or calcareous spicules may be secondarily entrapped in the skeleton during the growth process. See basal calcareous skeleton (Th, p. 40, fig. 208) [Ms, Ch].
- rigid skeleton**. Skeleton of hypercalcified sponges that is not flexible; either aspiculate, spiculate, or both, and irrespective of whether it developed initially from a completely fused basal calcareous skeleton or not [Sp, In].
- rigid spicular skeleton**. Skeleton in which the main framework is first made up of fused or linked spicules that may later be invested by an aspiculate cement (Th, p. 40, fig. 204) [Ms, Ch].
- rim**. In two-walled cups, a planar-to-convex primary skeletal structure developed by the direct extension of one wall to unite with the other, creating intervallum roofing (Fig. 507.3–Fig. 507.4; S2a, p. 1691, fig. 26B) [Ar].
- ring pillar**. Short pillar that appears as a hollow cone formed by upward inflection of a lamina (e.g., *Stromatoporella*) [Ps].
- rod**. Radial-transverse lintel separating pores in a uniporous septum; of uniform diameter and circular cross section. See bar, uniporous septum (S2a, p. 1691) [Ar]; *or* rodlike skeletal elements for disjunctopores, either longitudinal or tangential, forming the three-dimensional skeletal network (Fig. 208, I–2); syn., *trabecula*, *concentriferod*, *radirod* [Di].
- rudimentary wall**. Wall constructed only of marginal intervallum structures. See basic wall (Fig. 515a; S2a, p. 1691, fig. 71C–D) [Ar].
- sagittal spicule**. Triactine or tetractine with two equal angles (paired angles) and one dissimilar angle (unpaired angle) at the center, when projected into a plane perpendicular to the optic axis (Th) [Ex].
- scale**. Triangular or circular spicule derived from a triactine (Th) [Ex]; *or* curved, S-shaped or V-shaped plate spanning and incompletely covering two or more laterally adjacent pores; develops on external surface of outer wall or internal (central cavity) surface of inner wall. See bract, spine [Ar].
- scalenohedral structure**. Diagenetic pseudostructure caused by recrystallization. Forming a sawtooth arrangement of fibers that appear darker in thin section [Ms, Ch].
- sclere**. Spicule [Sp, In].
- sclerocyte**. Cell involved in spicule formation. In demosponges with intracellular secretion, sclerocytes are characterized by numerous mitochondria and the presence of spicule-axial filaments. In calcareans, where secretion is extracellular, sclerocytes have septate junctions between them (Th, p. 14, fig. 49, 69) [Ex].
- sclerodermite**. Aggregate of crystals forming a microstructural unit of the calcareous skeleton (Th, p. 40, fig. 215) [Ms, Ch, Ex].
- sclerosome**. Calcareous cement or nonspiculate calcium carbonate that unites spicules or forms skeletal fibers that then become imbedded (Tr p. 187) [Sp, In].

- Sclerospongiae* (HARTMAN & GOREAU, 1970). This group was introduced as a separate class to include extant Demospongiae with solid calcareous skeletons and fossil counterparts (stromatoporoids, chaetetids, and sphinctozoans), but this combination proved to include polyphyletic relationships (VACELET, 1985); hence the term is obsolete. No hypercalcified calcareans were associated with this group [Ps, Ms, Ch, Sp, Ex].
- secondary calcareous skeleton.** Skeletal components formed after the deposition of the primary skeleton, enveloping and/or infilling space between the initial elements; not easy to distinguish in chaetetids (Fig. 521.1d; Th, p. 40, fig. 207; S2a, p. 1691, fig. 4) [Ar, Ms, Ch].
- secondary thickening.** A type of secondary calcareous material that precipitates as simple aporose structures in multiple layers of enveloping elements upon the primary skeleton; difficult to differentiate in chaetetids (S2a, p. 1691, fig. 4) [Ar, Ms, Ch].
- second-order intervallar structure.** Intervallar structure developed upon first-order structures. See intervallar structure (S2a, p. 1690) [Ar].
- segment.** Term used by some authors for a chamber of a sphinctozoan [Sp].
- segmentation.** Subdivision of some linear sphinctozoan sponges into chambers, often marked by annulations of outer walls at chamber junctions [Sp].
- segmented tabula.** Plate tabula being a direct extension of outer and/or inner walls. See tabula (Fig. 512; S2a, p. 1692, fig. 66D–E) [Ar].
- septate filling structure (or skeleton).** Composed of vertical, bladeli-like elements that are commonly radially arranged [Sp, In].
- septate-reticulate filling structure (or skeleton).** Composed of a combination of two types of filling structures: septate and reticulate. Such combinations of these and other filling structures are rare [Sp, In].
- septum (pl., septa).** Radial-longitudinal, first-order intervallar structure in form of planar partition, ontogenetically fully developed (apart from porosity) from its inception. See aporose septum, completely porous septum, sparsely porous septum, uniporous septum (S2a, p. 1692); syn., paryeti [Ar].
- shaft.** Radial-transverse element linking one nesaster of outer wall with corresponding nesaster of inner wall; of uniform diameter and circular cross section (Fig. 658, 1a) [Ra].
- sheath (ls).** Imperforate, calcified, commonly discontinuous, thin outer wall that bounds the stem fragments of the order Amphiporida and the family Stachyoditidae; has contact with and is supported by outer extensions of the skeletal network (pillars with lateral processes, amalgamate, or pachystele-like structural elements) (Fig. 349.2; Fig. 476a–b); syn., peripheral membrane [Ps].
- sheetlike cup.** Cup in form of vertical or horizontal plate. See cup (Fig. 615, 1a–b; S2a, p. 1690) [Ar].
- sieve plate.** Screenlike or perforated plate in an osculum or across a spongocoel below the level of the osculum [Sp, In].
- simple tumulus.** Tumulus with a single, typically downwardly oriented pore. See tumulus (Fig. 506a–506b; S2a, p. 1692, fig. 30L, 47B) [Ar].
- single-chambered cup.** Cup incorporating one chamber only. See cup (Fig. 491d; S2a, p. 1690, fig. 2B1, 52A) [Ar].
- single exopore.** A single, tubular, unbranched opening (S2b, fig. 8) [Sp, In].
- siphon.** Spongocoel [Sp, In].
- siphonate.** Having a distinct spongocoel [Sp, In].
- siphonate exhalant system.** Condition in sphinctozoan sponges where skeletal chambers communicate through an axial tube (S2b, p. 1513) [Sp, In].
- skeletal ontogeny.** Development of the primary skeleton through the lifetime of the organism, from juvenile to adult [Ar].
- skeletal structure (sk).** Frameworks (laminae, pillars, and other elements) of the basal calcareous skeleton dominated by gridlike combinations of structural elements that characterize the main orders of the class Stromatoporoidea: (a) domes (cyst plates) and pillars in order Labechiida; (b) floors (laminae) and pillars in order Clathrodictyida and order Stromatoporellida; (c) beams (colliculi) and pillars in order Actinostromatida; and (d) an amalgamate structure composed of floors (pachystromes) and walls (pachysteles) in orders Stromatoporida and Syringostromida (Ps).
- skeletal tracts.** A column of aligned megascleres (Th, p. 34, fig. 201) [Ms, Ch].
- skeleton.** All hard parts secreted by the living organism in support and protection of itself above the substrate, thus avoiding mantling sediment and/or overgrowth by competitors (Th, p. 34); syn., coenosteum, colony, coenosarcal tissue, coenochyme. Given the connotations these five synonyms have with colonial organisms (in particular cnidarians), their continued use in sponge terminology should not be maintained [Ps, Ms, Ch, Ex].
- slitlike pore.** Pore in form of a transversely oriented slit. See pore (Fig. 498e; Fig. 499); Fig. 512c; S2a, p. 1691, fig. 21M, 40G, J) [Ar].
- slitlike porosity.** Pores elongate-elliptical in outline. See porosity (Fig. 498e; Fig. 499); Fig. 512c; S2a, p. 1691, fig. 40J) [Ar].
- spacing phase (ts).** A unit distinguished by changes in the spacing of laminae, cysts, or pachystromes (Fig. 317.4; Fig. 329.5) [Ps].
- sparsely porous septum.** Septal pores distributed frequently and uniformly over part of septum only or irregularly or infrequently distributed. See septum (Fig. 496d–496e; S2a, p. 1692, fig. 21G) [Ar].
- speck (mi).** An equidimensional opaque body in skeletal material of a stromatoporeid a few micrometers across that is the smallest (microgranule size) unit of microstructure seen in the light microscope (Fig. 335.2) [Ps].
- spheroidal chamber shape.** Chambers that are globose or essentially spherical [Sp].
- spherulite.** Skeletal microstructure composed of spherulites that are composed of crystals radiating

- from a common center (Th, p. 40, fig. 215; S2b, fig. 12) [Sp, In, Ch].
- spherulitic microstructure.** Globular (centric or excentric) arrangement of crystal fibers or skeletal elements radiating from a common center (e.g., *Astrosclera*) (Th, p. 40, fig. 215); syn., spheroidal microstructure [Ms, Ch, Sp, In, Ex].
- Sphinctozoa** (STEINMANN, 1882; =Thalamida DE LAUBENFELS, 1955), or **sphinctozoans.** General terms applied to chambered sponges. Because of polyphyletic nature of chambered sponges, the terminology is not taxonomically valid (demosponges, calcareans) [Sp].
- spicular.** Of or pertaining to spicules [Ms, Ch, Sp, In, Ex].
- spiculate.** Consisting of spicules, or spicule-bearing [Ms, Ch, Sp, In, Ex].
- spiculate skeleton.** Framework of arranged spicules [Ms, Ch, Ex].
- spicule.** A discrete, mineralized skeletal element, generally composed of silica or calcium carbonate, and secreted by sclerocytes. Spicules typically formed as more or less elongated rays with pointed, rounded, or more elaborated terminations, arranged along one or more axes (Th, p. 34, fig. 195) [Ms, Ch, Sp, In, Ex].
- spine.** Skeletal structure comprising a narrow, elongate, and typically tapering process projecting freely from any skeletal element; a spine is distinguished from a bract by the relatively small, circular-to-subcircular attachment area and a needlelike-to-thornlike shape (acicular to flattened) of the former. For inner walls, spines are considered as ornamental elements of simple walls; whereas bracts, together with scales, are a family diagnostic character. The distinction is difficult to appreciate, as there are no distinct morphological boundaries in the continuum from spines to cupped bracts (e.g., in the *Anaptycyathus-Erugatocyathus* group, in which the whole continuum of structures may be seen). See bract, scale (S2a, p. 1692, fig. 67K) [Ar].
- spinose rod** (ls). A slender, upwardly tapering rod, usually with spar-replaced center and resembling a spine (Fig. 487) [Pu].
- spongin.** Skeletal substance in Demospongiae consisting of collagen microfibrils of approximately 10 nm diameter (Th, p. 34, fig. 160, 170, 176, 185, 200) [Ms, Ch, Ex].
- spongiouse wall.** Massive inner wall consisting of elaborately waved, communicating canals (Fig. 556, 1a–b; Fig. 556,2; S2a, p. 1692, fig. 39E–F) [Ar].
- spongocoel.** Large central canal or canals for exhalant (or excurrent) water. If only a single spongocoel is present, it is usually axially situated. If more spongocoels are present, they may be grouped in axial bundles or distributed throughout the sponge body [Sp, In, Ex].
- spongocyte.** Cell secreting spongin fibers (Th, p. 14, fig. 49, 71, *spo* = spongin) [Ex].
- spore-like filling structure or skeleton.** Composed of hollow sporelike structures that may be attached to one another or arranged in a network [Sp, In].
- S-shaped canal.** Canal with S-shaped aspect in longitudinal section. See canal (Fig. 502c; S2a, p. 1689, fig. 28K–L, 59L) [Ar].
- stem** (sk). Term applied to fragmentary parts of branches of dendroid-shaped skeletons of the order Amphiporida [Ps].
- stipule.** Leaflike appendage arising from canal-bract junction in a wall with a longitudinal, V-shaped appearance, or subdividing subspherical chambers in outer walls of some Ethmophylloidea (Fig. 503c; S2a, p. 1692, fig. 32F, 34C–F, 36C–E, 49C) [Ar].
- stirrup pore or canal.** Pore or canal located at the junction of a wall and a septum or tabula. Typically, a stirrup pore or canal is accompanied by a semicircular indentation in the septal or tabular margin. See pore, canal (Fig. 496c; S2a, p. 1691, fig. 17A) [Ar].
- stratiform.** Sheetlike growth form consisting of single layer of chambers. Also, arrangement of tubelike chambers around one or more spongocoels (S2b, p. 1512, 1515, fig. 4) [Sp, In].
- stratocyst** (ts). A term introduced by BOGOYAVLENSKAYA (1984, p. 11) for long and low cyst plates resembling microlaminae. Not recommended for continued use, as it duplicates more commonly accepted usages of “long and low cyst plates,” and “long-low cyst plates,” especially in the Labechiida [Ps].
- streptaster.** Aster in which the rays proceed from an axis that is usually spiral (Th) [Ex].
- striae** (pl.). Transverse platelike elements of inner wall (Fig. 664,2c) [Cr].
- striated** (mi). Specks concentrated in short, rodlike bodies; a microstructure apparently unique to *Stachyodes* (Fig. 474d–e) [Ps].
- stromatoporoid architecture.** Skeletal structure with mattresslike chambers containing pillars, bearing superficial resemblance to some stromatoporoids. See architecture (Fig. 516c; Fig. 656, 1a–b; Fig. 657; S2a, p. 1689, fig. 2E) [Ar].
- strongyle.** An isodiametric, diactinal megasclere with rounded ends (Th, p. 46, fig. 280) [Ms, Ch, Ex].
- style.** Monaxon spicule with one end pointed, the other (head or base) blunt; normally a megasclere (Th, p. 46, fig. 282) [Ms, Ch, Ex].
- subcolumn** (ls). A structure of subcircular cross section that consists of micropillars and microcolliculi arranged in an acomoreticular or clinoreticular pattern; in syringostromatids, the term pillar has been used as an alternative [Ps].
- subdivided canal.** Canal bearing processes projecting inward from its wall. See canal (Fig. 517e–517f; S2a, p. 1689, fig. 70A–E) [Ar].
- subdivided pore.** Pore with more or less well-developed subdivision, ranging from radially directed spines to complete microporous sheath. See pore, compound wall (Fig. 516d; Fig. 517a; S2a, p. 1691, fig. 67G–H, 69A) [Ar].
- subspherical growth morphology.** Having a subspherically shaped calcareous skeleton [Ms, Ch, Ex].
- successive phase** (ts). A unit of growth distinguished and bounded by longitudinal changes in structure

- within the skeleton; the phase may be terminal, basal, or spacing (Fig. 330.1) [Ps].
- superposed astrorrhizae.** Successive generations of astrorrhizae that have formed along the same radial axis (Fig. 323.4; Fig. 328.2); syn., stacked astrorrhizae, astrorrhizal cylinders, astrorrhizal columns, astrorrhizal corridors, astrocolumns [Ps, Ms].
- synaptacula** (pl., **synaptaculae**). Second-order intervallar structure comprising narrow tangential rod linking adjacent, longitudinally oriented first-order intervallar structures (Fig. 560a; S2a, p. 1692, fig. 32A) [Ar].
- syrinx** (pl., **syringes**). First-order intervallar structure comprising porous radial tube of hexagonal or tetragonal cross section (Fig. 510.2a–d; S2a, p. 1692, fig. 72A–D) [Ar].
- tabellar wall.** Wall consisting of longitudinal ribs linked by flattened transverse lintels (S2a, p. 1692, fig. 70H–I) [Ar].
- tabula** (pl., **tabulae**). Transverse porous partition linking both walls of a two-walled cup. See membrane tabula, pectinate tabula, plate tabula, segmented tabula (Fig. 498; Fig. 511–512; S2a, p. 1692) [Ar]; *or* flat to gently curved plates that partition astrorrhizal canals (Fig. 325.1; Fig. 329.1) and localized areas of interlaminar space; they commonly develop tangentially and may be difficult to distinguish from dissepiments. Also, irregular, complete to incomplete plates within the axial canal of the order Amphiporida and other dendroid to columnar growth forms (*Stachyodes*, *Idiostroma*) (Fig. 325.1; Fig. 329.1; Fig. 349.2) [Ps]; *or* a discrete calcareous plate, generally flat or slightly curved parallel to the growth surface, which, as a floor, partitions the basal part of the skeletal cavity; this plate may or may not be perforated by a foramen that may or may not be subsequently infilled and is commonly thinner than the tubule walls. These distinctive features, which are present in both Mesozoic stromatoporoids and chaetetids, do not appear to be homologous with tabulae of archaeocyaths or Paleozoic stromatoporoids [Ms, Ch, Ex].
- tabular.** Platelike [Sp, In].
- tabular wall.** Wall that is an outward or inward extension of a tabula or chamber-forming segment (Fig. 498c; S2a, p. 1692, fig. 54C) [Ar].
- tabulate osculum.** Osculum in stromatoporoids that has been repeatedly partitioned by secondarily deposited tabulae; syn., zooidal tube, superposed galleries, zooidal tubule, major autotube [Ms].
- tabulum.** Platelike elements that divide skeletal cavity. Relationship between the term tabulum and the tabulae of other hypercalcified groups remains unknown [Sp, In].
- taenia** (pl., **taeniae**). First-order intervallar structure; nonplanar, often dichotomous, radial-longitudinal partitions in intervallum; may be coarsely or finely porous. See porosity (Fig. 508; S2a, p. 1692) [Ar].
- terminal phase** (ts). Consists of the last units of skeletal growth that preserve a change in structure [Ps].
- tersioid buttress.** Tubular buttress consisting of concentric envelope and infilling platy elements. See buttress (Fig. 522; S2a, p. 1689, fig. 42B) [Ar].
- tetractine.** A spicule with four rays (Th, p. 26, fig. 144) [Ex].
- Thalamida* (DE LAUBENFELS, 1955). Former grouping of sphinctozoans [Sp].
- thalamid architecture.** Skeletal structure with subspherical chambers. See architecture (Fig. 491; S2a, p. 1689, fig. 2B1–B2) [Ar].
- thalamidarium.** Single layer of chambers in a stratiform or sheetlike sphinctozoan sponge in which chambers are convex toward the growing edge [Sp].
- toroidal.** Growth form having an open or doughnut-shaped coil [Sp, In].
- trabeculae** (pl.). Filling structure composed of regular rodlike or beamlike pillars supporting roof over the bottom of chambers in sphinctozoans; in living hexactinellid sponges, the same term is used for divided and anastomosed, protoplasmic filaments that form a network of water-filled interspaces (S2b, fig. 11) [Sp, In].
- trabecular filling structure of skeleton.** Composed of parallel or slightly diverging, rod- or beamlike elements supporting chamber walls [Sp, In].
- trabecular microstructure.* Where the crystal fibers are symmetrically arranged around the growth axis and axial fibers are absent (a cnidarian condition that is unknown in sponges).
- transverse fold.** In a two-walled cup, fold of one wall or mutual folds of two walls to impart a succession of more or less regular, longitudinal annulations of cup (Fig. 494c; S2a, p. 1692, fig. 58A); syn., orbicyathoid [Ar].
- triactine.** A spicule with three rays (Th, p. 26, fig. 148, 150–153) [Ms, Ch, Ex].
- tubercule.** Small, slightly raised calcareous projections, like tiny spines, that occur at the junction between two or more tubules at the top of the basal calcareous skeleton, where the thin soft tissue is presumed to have been in contact with the skeleton [Ch].
- tubiform.** Polyplatyform with tubelike chambers, laterally or vertically adjacent, forming platelike structures (S2b, p. 1513) [Sp, In].
- tubular.** Arrangement of skeletal elements with appearance of closely packed tubes [Ms, Ch]; *or* endocameral filling structure usually consisting of branched tubes between the openings of exowalls and endowalls (S2b, fig. 11) [Sp, In].
- tubular chamber shape.** Chambers that are linear and pipelike [Sp].
- tubular filling structure of skeleton.** Composed of small, tubelike elements that may be curved, irregularly oriented, and often bifurcated [Sp, In].
- tubulate** (mi). Clear, vermiform areas extending irregularly through the speckled skeletal material; best shown in *Clathrocoilon* (Fig. 337.2) [Ps].
- tubule.** The tubes that constitute the basal calcareous skeleton of chaetetid hypercalcified demosponges; exhibiting meandroid- to irregularly polygonal-shaped outlines in tangential section; syn., calicle, pseudocalyx (pl., pseudocalices) [Ch].

- tubulus** (pl., **tubuli**). Complex structure of secondary skeleton consisting of tubular structure in central cavity (S2a, p. 1692, fig. 66G) [Ar].
- tumulus** (pl., **tumuli**). Outer wall structure in shape of a discrete, hollow subspherical dome covering an individual wall opening. See multiperforate tumulus, simple tumulus (Fig. 506; S2a, p. 1692) [Ar].
- tylostyle**. A style with a tyle (globular swelling) at the base (Th, p. 48, fig. 493) [Ms, Ch, Ex].
- uniporous septum**. Septum with single longitudinal row of pores of diameter subequal to intervallum width; pores separated by bars or rods. See septum, bar, rod (Fig. 496c; S2a, p. 1692, fig. 13B–C) [Ar].
- unpaired actine**. The ray of a triactine or of a triradiate basal system of a tetractine, lying in the plane of bilateral symmetry of sagittal spicules (not the basal ray) (Th) [Ex].
- uviform**. Sponges with chambers clustered to form irregular aggregates (S2b, p. 1512, fig. 4) [Sp, In].
- vacuolate** (mi). Scattered subspherical voids larger than cellules (about 100  $\mu\text{m}$ ) within compact laminae and pillars, as in *Trupetostroma* (Fig. 340.3; Fig. 481a) [Ps].
- vermiculate**. Irregularly sinuous [Sp, In].
- verticillately spined style**. Acanthostyle with spines arranged in regular rows; the term is used for the spicules of Astroscleridae and Agelasidae (VACELET, 2002a) [Ex].
- vesicle**. Simple, aporose, bubble-like structure of secondary skeleton (Fig. 521.3; S2a, p. 1692, fig. 4, 59L–M) [Ar].
- vesicle** or **vesicular skeleton**. Filling structure of bubblelike imperforate diaphragms, usually within chambers, but rarely in a spongocoel, or in exhalant and inhalant canals (S2b, fig. 11) [Sp, In].
- vesicular filling structure** (or **skeleton**). Composed of small, blister- or bubblelike elements that are upwardly or laterally convex [Sp, In].
- villi**. An obsolete term used by GALLOWAY (1957) that is incorporated in the definition of denticle [Ps].
- V-shaped canal**. Canal with V-shaped aspect in longitudinal section; may be upright or inverted. See canal (Fig. 502d; S2a, p. 1689, fig. 49C–D); syn., geniculate [Ar].
- wall**. The calcareous element, or elements, that define(s) the basal skeleton of the individual in solitary hypercalcified demosponges, or the constituent modules of modular hypercalcified demosponges. In chaetetids, the microstructure is commonly fascicular, but may be either water jet, penicillate, or spherulitic when unaltered [Ch]; *or* see altoid wall, anthoid wall, basic wall, cambroid wall, concentrically porous wall, clathrate wall, compound wall, inner wall, outer wall, plicate wall, pseudoclathrate wall, rudimentary wall, spongiose wall, tabellar wall, tabular wall [Ar].
- water-jet microstructure**. Where crystal fibers progressively fan outward around the growth axis (e.g., *Merlia*). This microstructure is a subdivision of the broader clinogonal and fascicular fibrous microstructural types. See fascicular fibrous microstructure, clinogonal microstructure (Th) [Ch, Ex].
- zygosis**. Mode of junction between siliceous desmas or calcareous tetractines by the interlocking of their terminal or lateral expansions. A secondary cement may be present (Th) [Ex].