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PART E, REVISED, VOLUME 4, CHAPTER 7: 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 Webby, 2010: *Treatise Online,* Chapter 8, Glossary, p. 14). 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 Calcispongiae 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 sphinctozoan and inozoan genera, with their stratigraphic occurrences, are also presented here (p. 67–75).

Hypercalcified sponges, including sphinctozoans, inozoans, 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 inozoans, sphinctozoans, 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 inozoan and sphinctozoan 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 inozoans and sphinctozoans, for almost all documented sponge taxa in those groups became extinct. Only one genus of sphinctozoan, *Stylothalamia,* survived the Triassic-Jurassic boundary event. Again, morphologically identical or similar sphinctozoan and inozoan 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

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to loss related to recrystallization) have been assigned to different groups of organisms. For example, the stromatoporoids 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, 1975, 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; WEST, 2011).

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 Calcispongiae 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 sphinctozoans and inozoans 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 might include the Silurian agelasid demosponges *Nematosalpinx* and *Aphrosalpinx* (MYAGKOVA, 1955a, 1955b; RIGBY, NITECKI, & others, 1994; FINKS & RIGBY, 2004c), the Cambrian heteractinid chambered sponges *Nucha, Wagima,* and *Jawonya* (PICKETT & JELL, 1983; KRUSE, 1987; PICKETT, 2002), the Jurassic–Cretaceous calcisponge chambered sponges *Barroisia* MUNIER-CHALMAS in STEINMANN, 1882, and *Muellerithalamia* REITNER, 1987b, 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 chapter, nor are chambered archaeocyaths discussed here.

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 1.

Outer Segmentation

Chambered organization is the most important characteristic feature of sphinctozoan sponges, separating them from other hypercalcified sponge groups. Outer segmentation corresponds generally to internal segmentation. However, due to overlap of earlier

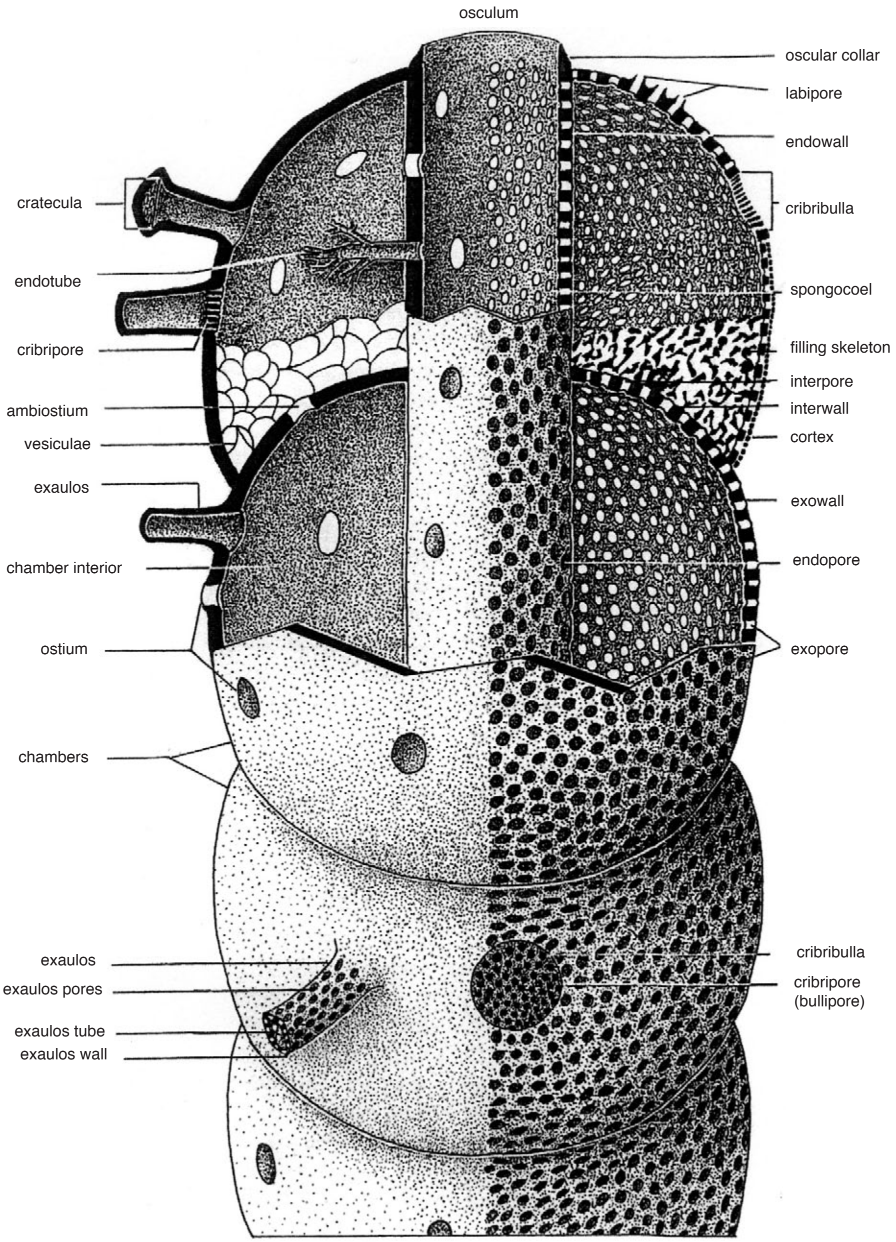


FIG. 1. Major morphological skeletal elements of sphinctozoan sponges. On the right, main characteristic features of the porate forms, and on the left, aporate forms. Of the filling skeleton structures, only the reticular type, on the right, and the vesicular type, on the left, are shown in the interior of the last chamber. Skeletal elements like those in the aporate sponges may also occur in porate representatives (adapted from Senowbari-Daryan, 1990).

chambers by younger, later chambers in some representatives, especially those taxa with crescentlike chambers (e.g., the Triassic genus *Senowbaridaryana,* Fig. 2–3, or *Zardinia,* Fig. 4), outer segmentation may be totally lacking or hard to recognize. The chambered sphinctozoan construction of such sponges is recognizable only after cutting into their skeletons

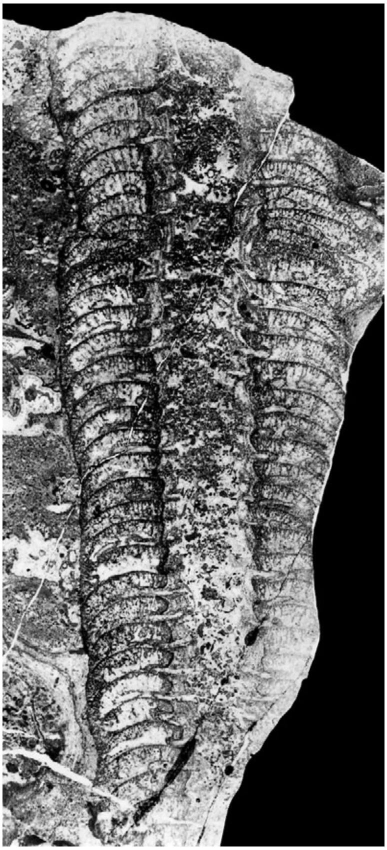


FIG. 2. *Senowbaridaryana hydriotica* SENOWBARI-DARYAN, 1990. Outer segmentation of this porate and siphonate sphinctozoan is totally lacking, but the chambered construction can be seen after cutting the specimen in longitudinal section. Crescentlike chambers contain reticular filling skeleton; Carnian, Triassic, Hydra, Greece, ×1.7 (Senowbari-Daryan & Schäfer, 1983).

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. 5.3–5.7). Club-shaped skeletons occur in some taxa (e.g., the Permian species *Lemonea conica* SENOWBARI-DARYAN, 1990, or *Senowbaridaryana conica,* Fig. 3, Fig. 6), 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 *Neoguadalupia* 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. 5.10, Fig. 7). Aggregate forms composed of clusters of chambers (e.g., Permian *Exaulipora* RIGBY, SENOWBARI-DARYAN, & LIU, 1998; see Fig. 5.8, Fig. 8), 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. 9). 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. 10–11). Other chambers may be barrel shaped, as in some species of *Amblysiphonella,* or crescentlike, as in *Cryptocoelia* (Fig. 12) or *Zardinia* (Fig. 4). Chambers that are flattened rectangular (*Enoplocoelia, Tolminothalamia*), funnel shaped (*Panormida,* Fig. 9) or tubelike (*Cinnabaria* or *Subascosymplegma,* Fig. 7) occur also in other chambered sponges.

FIG. 3. *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, ×3 (Senowbari-Daryan & Schäfer, 1986).

Arrangement of Chambers

The arrangement of chambers in multibranched 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. 10) or the aporate genus *Sollasia* (Fig. 11). Chamber arrangement may be catenulate, where ringlike chambers are stacked one above the other in siphonate species, as in the porate genera *Amblysiphonella* (Fig. 13) and *Polytholosia* or in the aporate genus *Girtyocoelia* (Fig. 14). 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. 5.5–5.6, Fig. 6, Fig. 15–16). 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, 2004c, p. 695, fig. 459,*2a–c*) and 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 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*

FIG. 4. *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, ×3 (Senowbari-Daryan & Schäfer, 1983).

GIRTY (1908a) or *Diecithalamia* SENOWBARI-DARYAN (1990; Fig. 15) 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. 16) 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 calcisponge genus *Thalamopora* (RÖMER, 1840).

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

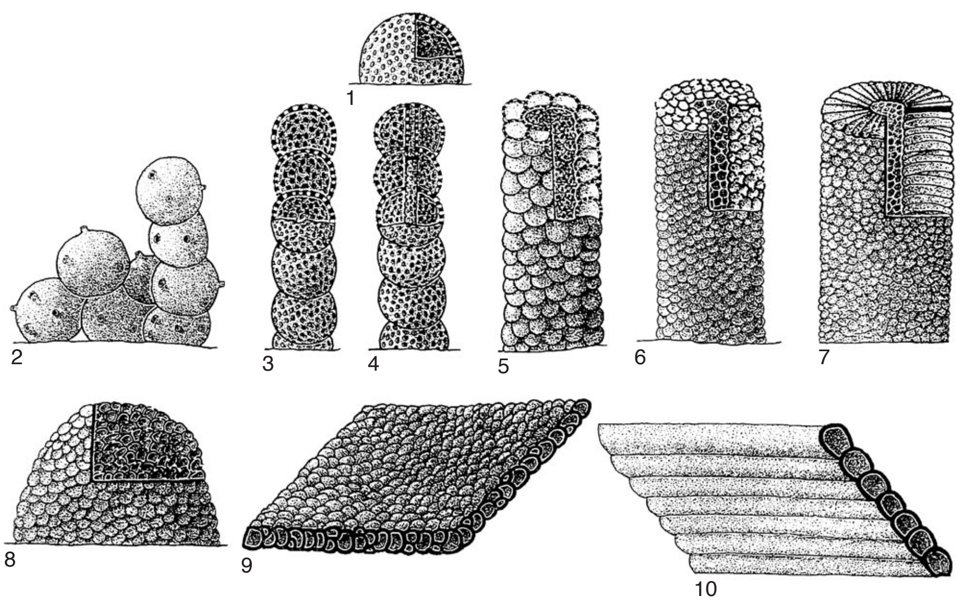


Fig. 5. Main growth shapes of sphinctozoan sponges. *1,* Single chambered (e.g., the heteractind genus *Blastulospongia* Pickett & Jell); *2,* moniliform (e.g., *Celyphia* Pomel); *3,* moniliform (e.g., *Colospongia* Laube); *4,* catenulate (e.g., *Amblysiphonella* Steinmann); *5,* monoglomerate (e.g., *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., *Neoguadalupia* Zhang); and *10,* platyform, tubular (e.g., *Subascosymplegma* Deng) (adapted from Senowbari-Daryan, 1990).

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. 17).

The Permian species *Follicatena permica* Senowbari-Daryan, 1990 (Fig. 18), 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, 2004c, 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. 14). The latter openings are called exaules (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. 8), or it may be aporate, as in *Girtyocoelia* (Fig. 14).

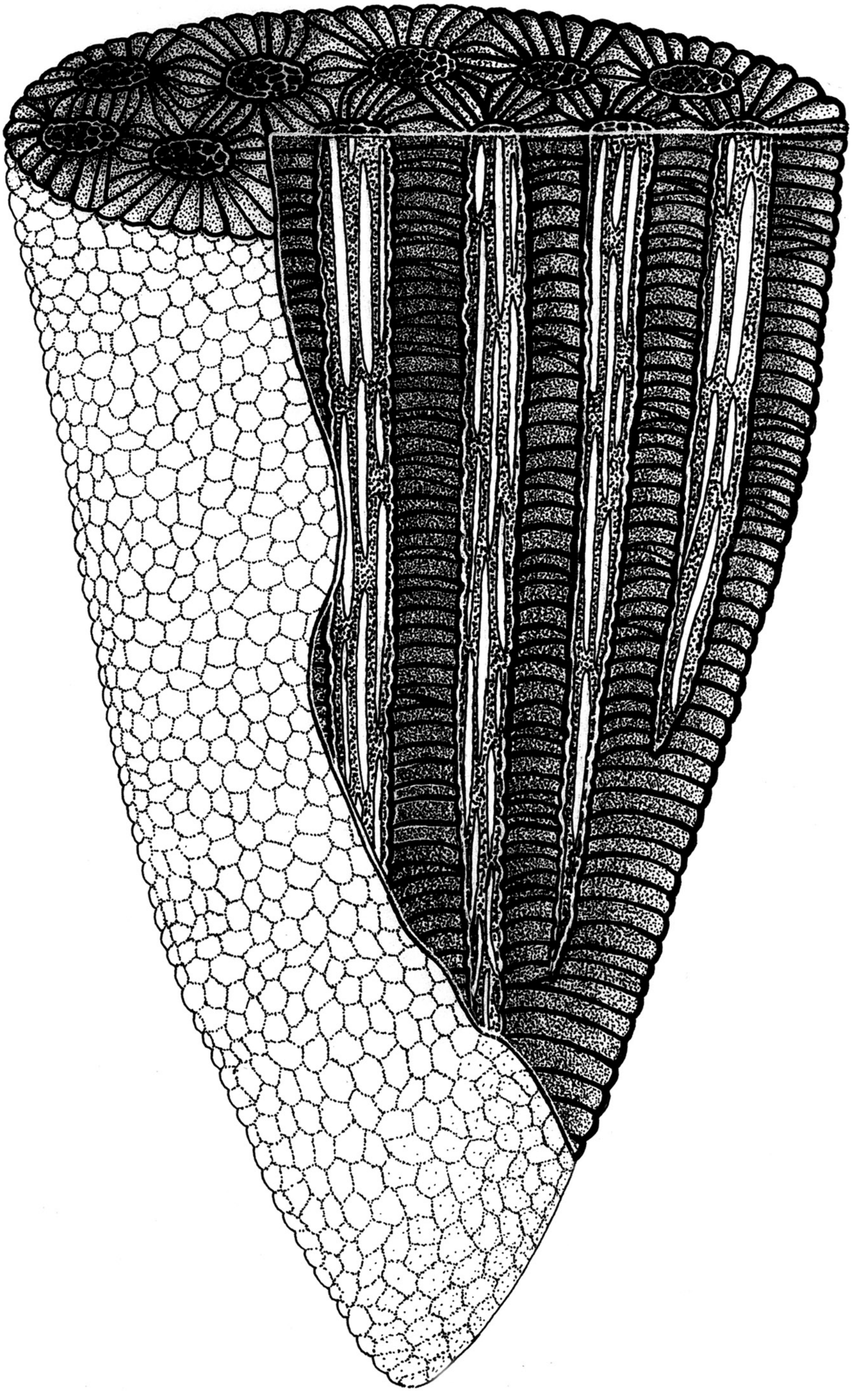


Fig. 6. Reconstruction of *Lemonea conica* Senowbari-Daryan showing the conical shape of the sponge, bundles of spongocoels, and the stratiform chambers arranged radially around the spongocoels; chamber walls are perforated, but the pores are not shown; schematic, not to scale (Senowbari-Daryan, 1990).

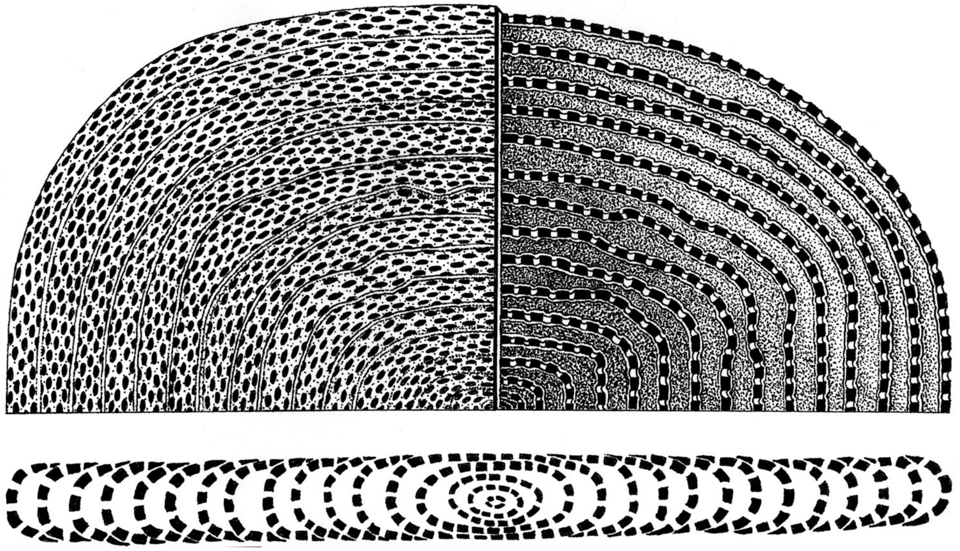


FIG. 7. Reconstruction of *Subascosymplegma oussifensis* (Termier & Termier, 1977). The sheetlike or hemispherical sponge is composed of arcuate, tubelike chambers, and the younger chambers overlap preceding chambers; upper Permian, Djebel Tebaga, Tunisia; schematic, not to scale (Senowbari-Daryan & Rigby, 1988).

The inner end of some exaules in aporate forms may have screenlike cribribulla, like those in some of the porate sphinctozoans, such as in *Exaulipora* (Fig. 8).

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. 15). Where a retrosiphonate axial tube or spongocoel is formed by downward extension of upper chamber walls (Fig. 19), the diameter of the osculum commonly appears larger than the diameter of the spongocoel. In most other types of constructions (Fig. 19), 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. 13–14). Several individual spongocoels may be present in large, laterally extended sphinctozoan sponges, as in the Triassic species *Cryptocoelia lata* Senowbari-Daryan & Schäfer, 1983 (Fig. 20), or separate spongocoel bundles may be developed, as in the Permian species *Lemonea conica* Senowbari-Daryan, 1990 (Fig. 6). 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, 1979, 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. 21).

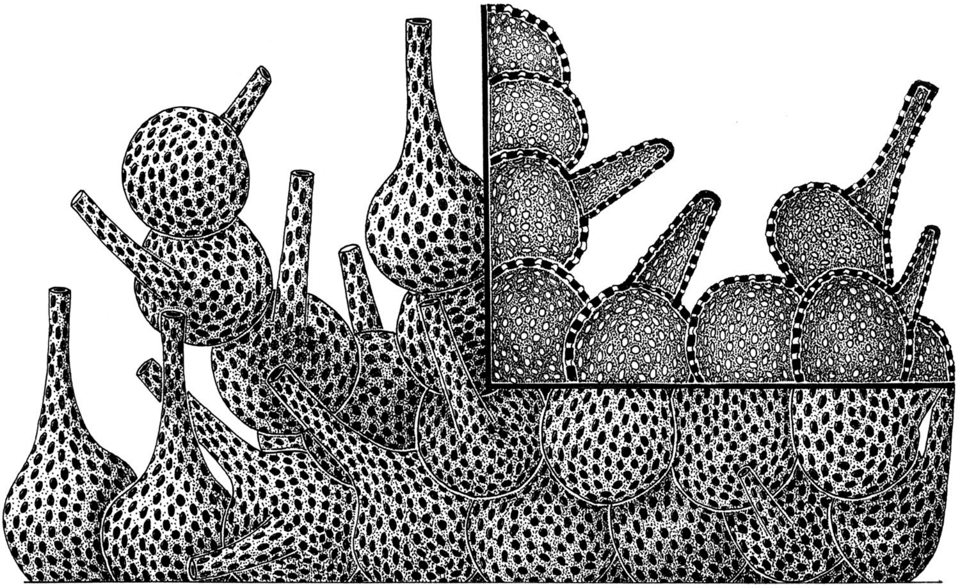


FIG. 8. Reconstruction of *Exaulipora permica* (SENOWBARI-DARYAN), Permian, Guadalupe Mountains, Texas and New Mexico, United States, showing perforated exaulos walls and the cribribulla with cribripores at the base of the exaules; vesiculae occur within the interior of the segment, but they are not shown (Senowbari-Daryan, 1990).

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, have distinct internal segmentation (e.g., *Cassianothalamia* REITNER, 1987a; *Uvothalamia* SENOWBARI-DARYAN, 1990), but their outer segmentation is poorly developed, or even totally lacking (Fig. 2, Fig. 4).

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. 13–14).

Internal Canal System

There are three types of exhalant canal systems in sphinctozoan sponges. These were called the *Colospongia*-type, *Sphaerocoelia*-type, and *Amblysiphonella*-type by SENOWBARI-DARYAN (1990) (Fig. 22). The *Colospongia*-type (Fig. 10, Fig. 22.3) system is without a separate siphon or spongocoel and was called asiphonate by SEILACHER (1962). It is assumed 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 *Sphaerocoelia*-type, each chamber top is pierced by a single large pore or osculum that served as the exhalant

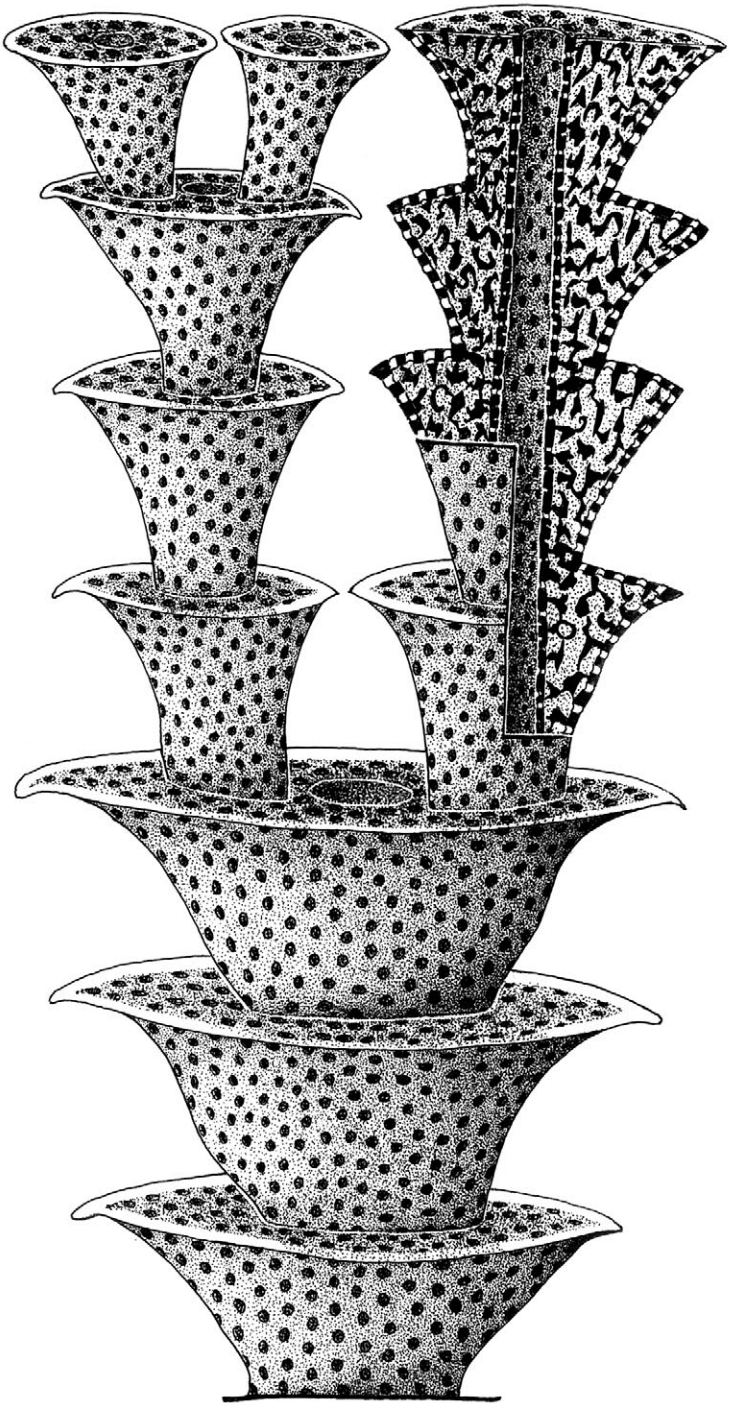


Fig. 9. Reconstruction of *Panormida priscae* Senowbari-Daryan. The porate and siphonate sponge is characterized by funnel-shaped chambers and rejuvenescence; chamber interiors are filled with reticular filling structure; Norian, Triassic, Sicily; schematic, not to scale (Senowbari-Daryan, 1990).

FIG. 10. *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, ×5 (new).

opening (Fig. 11, Fig. 22.2). This system was called cryptosiphonate by SEILACHER (1962). The siphonate *Amblysiphonella*-type (Fig. 13, Fig. 22.1) 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. 19.4). 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. 19.5). Prosiphonate sponges are characterized by upward growth of chamber roofs, as, for example, in *Girtyocoelia* (Fig. 19.6). 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. 13–14).

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. 4). 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. 23). 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. 23). 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 by the sponge. Vesiculae, their secretion processes in several stages, and the sealing of pores by vesiculae are shown in Figure 24, in the Triassic genus *Jablonskyia* SENOWBARI-DARYAN, 1990.

A filling skeleton has not been reported from Cambrian sphinctozoans. Cambrian

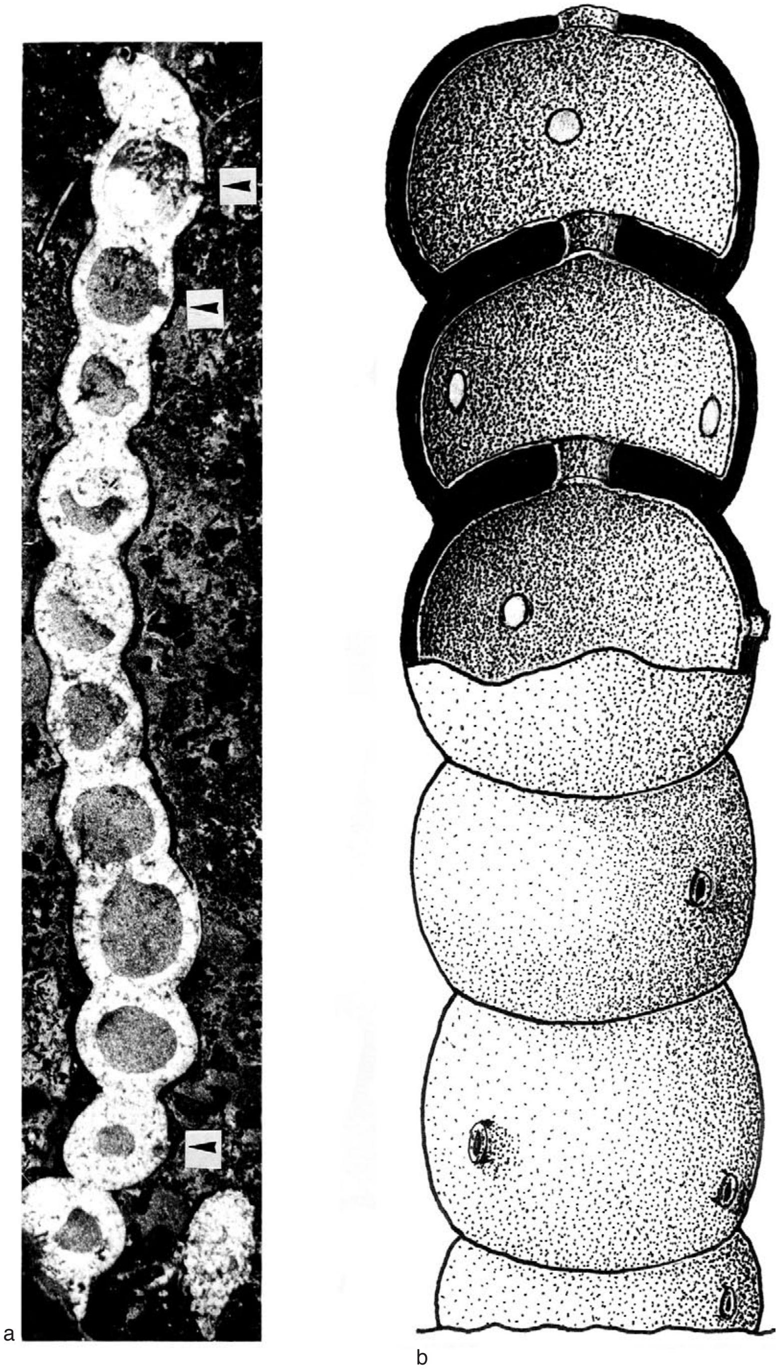


FIG. 11. *Sollasia ostiolata* STEINMANN, 1882, an abundant and cosmopolitan sphinctozoan sponge in Carboniferous and Permian deposits; *a,* longitudinal section cuts through numerous moniliform cryptosiphonate chambers with thick, aporate chamber walls; *arrows* indicate large openings (ostia) in few chambers cut by the section; lower Permian, Sosio valley, Sicily, ×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. 12. *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. 20); Carnian, Triassic, Slovenia, ×3.3 (Senowbari-Daryan, 1981).

segmented sponges with different filling skeletons, described in the literature as archaeocyaths, are not considered here. 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 *Polytholosia* RAUFF, 1938. Tubular filling skeletons are not known from Jurassic and younger sphinctozoans.

Trabecular (pillar-like) filling skeletons (Fig. 23, Fig. 25) 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, 1977; PICKETT, 1982).

Reticular filling skeletons (Fig. 23, Fig. 26) 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 from the Jurassic calcisponge genus *Muellerithalamia* REITNER, 1987a.

Sporelike filling skeletons (Fig. 23) 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.

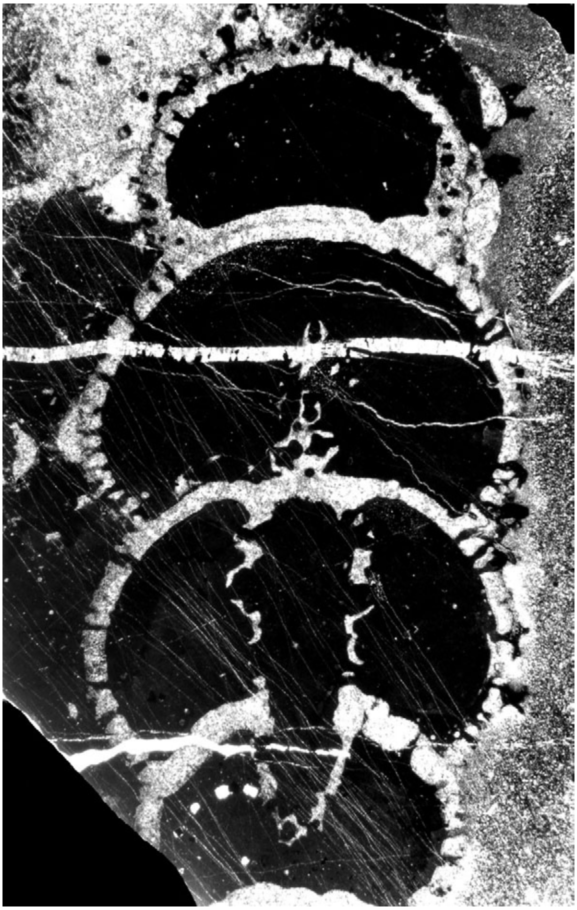


FIG. 13. *Amblysiphonella* sp. Marginal axial section exhibiting hemispherical chambers with perforated exowalls; interwalls are aporate and double layered; endowall is thinner than the exo- and interwalls and is pierced by large and unevenly distributed openings; Norian–Rhaetian, Triassic, Nayband Formation, Iran, ×4 (new).

A pisolitic-like filling skeleton (Fig. 23) 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. 23) 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. 23) 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. This is probably related to the less 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,

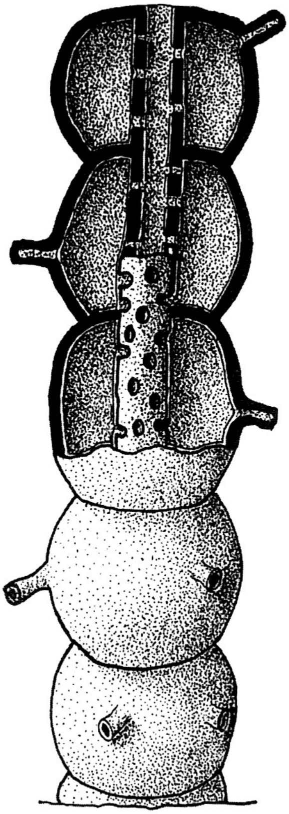


FIG. 14. Reconstruction of *Girtyocoelia beedei* (GIRTY, 1908b) showing unevenly perforated endowall of the spongocoel, and aporate exowalls with sporadic ostia with tubular exaulos; similar to *Sollasia, Girtyocoelia* is also an abundant and cosmopolitan sponge in Carboniferous and Permian deposits; schematic, not to scale (adapted from Senowbari-Daryan, 1990).

1977), 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 (1991, 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 (1992), 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, in the *Treatise Online*, Part E, Revised Chapter 18A, p. 41, that "No undoubted spicules have been recorded from the primary skeleton of archaeocyaths." 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. 27). 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 latticelike structure, without a rigid skeleton, are known only in the Upper Triassic genus *Radiocella* (SENOWBARI-DARYAN & WÜRM, 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 *Subascosymplegma oussifensis* (TERMIER & TERMIER, 1977), and from some Triassic genera with aragonitic skeletal microstructure, such as in *Colospongia* LAUBE, 1865, *Celyphia* POMEL, 1872, *Thaumastocoelia* STEINMANN, 1882, or with Mg-calcitic skeletal mineralogy, as in *Cassianothalamia* REITNER, 1987a (SENOWBARI-DARYAN, 1989, 1990, 1991; SENOWBARI-DARYAN & GARCÍA-BELLIDO, 2002a; SENOWBARI-DARYAN & RIGBY, 1988; REITNER, 1987b, 1990, 1992). The spicular skeletons of all these taxa are composed of monactine macroscleres (Fig. 28). Possible microscleres are known only from the Carnian species *Cassianothalamia zardinii* REITNER, 1987a, which has a Mg-calcitic rigid skeleton (REITNER, 1987b, 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 & GARCIA-BELLIDO, 2002a); *Sphaerocoelia* STEINMANN, 1882; and *Muellerithalamia* REITNER, 1987b (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 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 paper.

FIG. 15. *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, ×3 (new).

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; VACELET, 1979a; GAUTRET, 1985; SENOWBARI-DARYAN, 1990). Sphinctozoans with Mg-calcitic mineralogy (up to 11 Mol% $MgCO_3$; RUSSO & others, 1991) appeared in the Middle Triassic (Anisian), became abundant in the Ladinian and Carnian (*Alpinothalamia* SENOWBARI-DARYAN, 1990; *Cassianothalamia* REITNER, 1987a; *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

FIG. 16. *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, ×1.5 (Senowbari-Daryan & Abate, 1986).

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 by WOOD, 2011, p. 9, to be a demosponge agelasid stromatoporoid).

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 29 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. 30): (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. 28), 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 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)

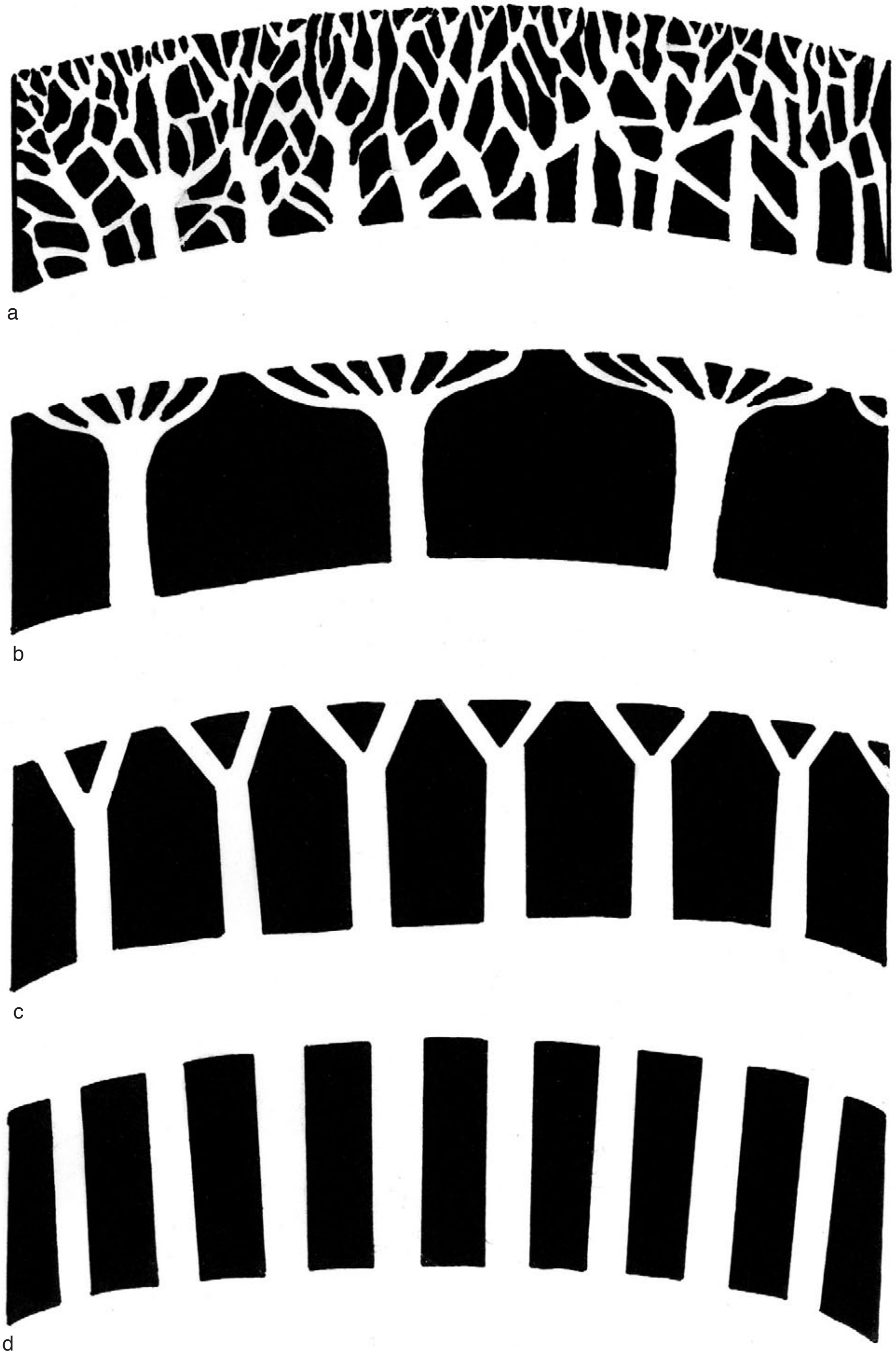


FIG. 17. Perforation pattern in porate sphinctozoans; *a,* single pores, *b,* dichotomously branched pores, *c,* multibranched pores, and *d,* labyrinthic branched pores; schematic, not to scale (Senowbari-Daryan, 1990).

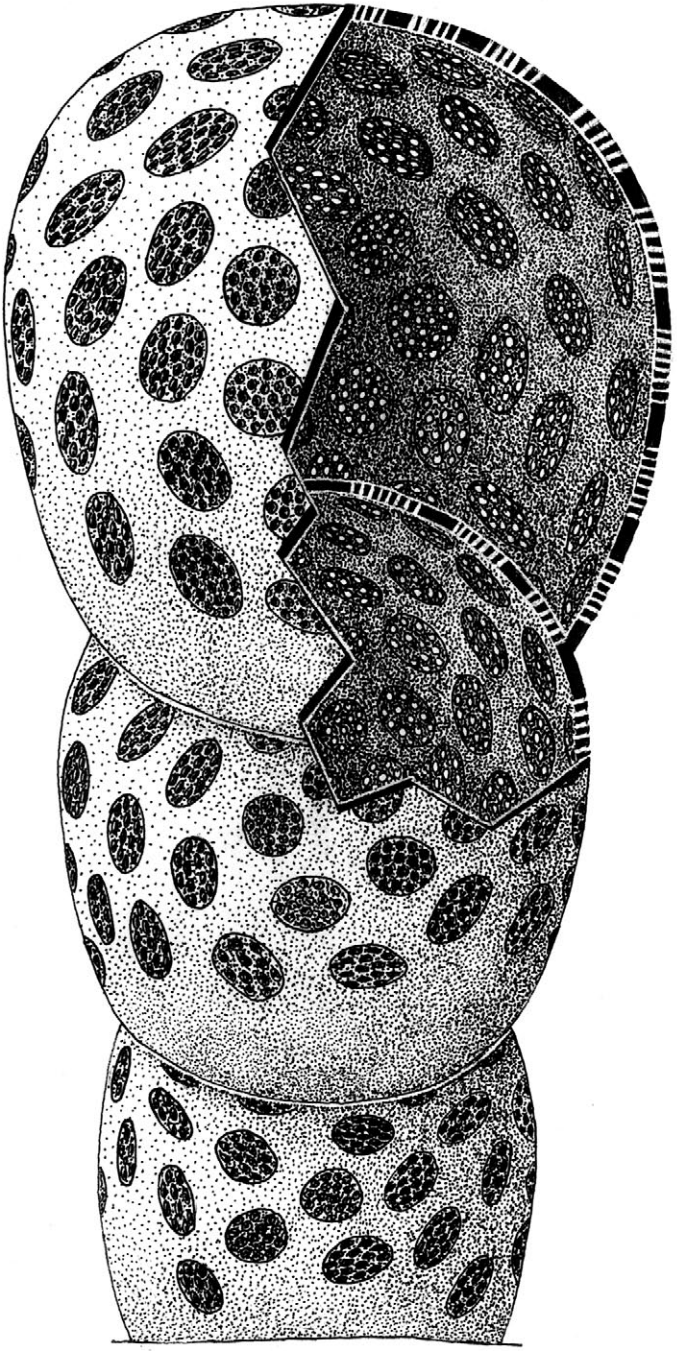
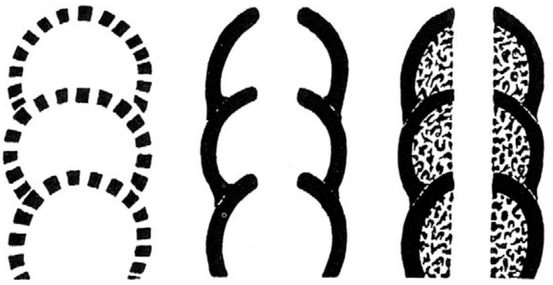
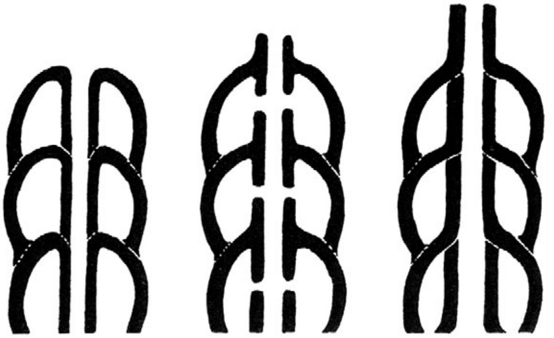


FIG. 18. Reconstruction of *Follicatena permica* SENOWBARI-DARYAN, 1990. The exowall and interwalls of this moniliform and *Colospongia*-like sponge contains numerous openings in the chamber walls of cribribulla with cribripores; cribribulla are not developed near bases of the chambers; species is known from the Permian of Sicily; schematic, not to scale (Senowbari-Daryan, 1990).



1 asiphonate 2 cryptosiphonate 3 pseudoosiphonate



4 retrosiphonate 5 ambisiphonate 6 prosiphonate

Fig. 19. 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).

is typical of sphinctozoan sponges with high-Mg-calcite mineralogy, such as the Triassic genera *Cassianothalamia* Reitner, 1987a, *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, 1979), and other sponges described as hydrozoans in the literature (the Upper Jurassic genus *Actinostromaria* Chalmas in Dehorne, 1920), although this genus is now regarded by Wood (2011, p. 9) as a demosponge: interpreted as an agelasid stromatoporoid.

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 *Solenolmia* 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, 2004c, p. 664).

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

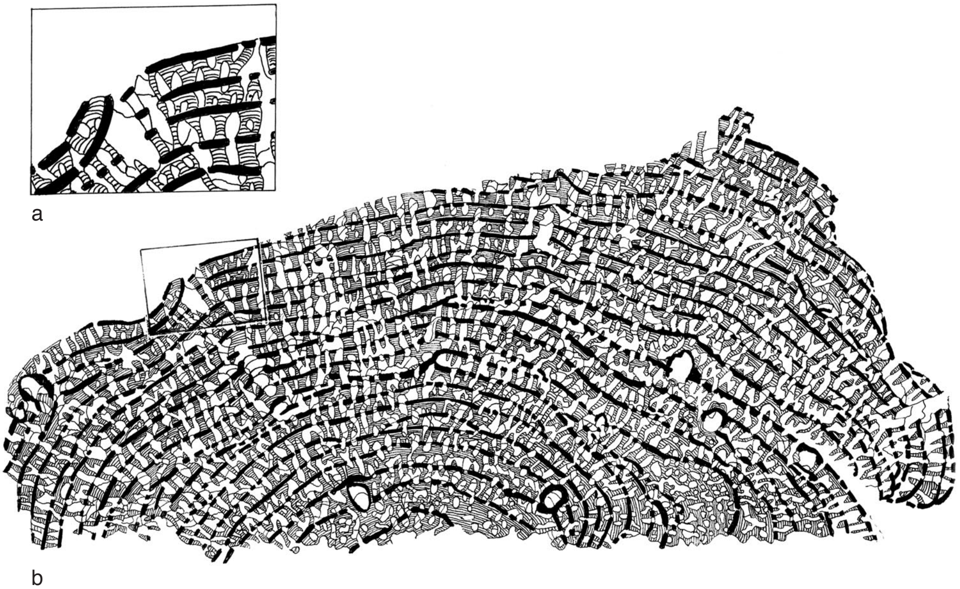


FIG. 20. *Cryptocoelia lata* SENOWBARI-DARYAN & SCHÄFER, 1983. Drawing of a longitudinal thin section exhibiting laterally extended chambers, numerous upward and outward radiating exhalant canals, and the lamellar structured trabecular (pillarlike) filling skeleton within the chamber interiors, as in *Cryptocoelia zitteli* STEINMANN, 1882; Carnian, Triassic, Hydra, Greece; *a,* ×6, *b,* ×3 (Senowbari-Daryan & Schäfer, 1983).

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. 24). 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. 10), there were principally three types of exhalant canal systems in sphinctozoan sponges (Fig. 22). 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 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

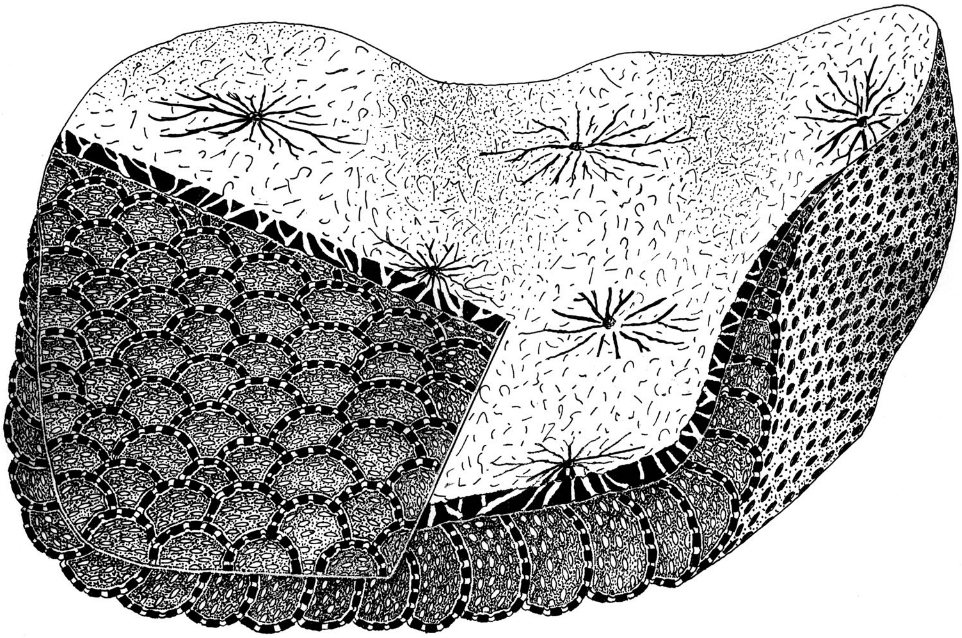


FIG. 21. Reconstruction of *Guadalupia explanata* (KING, 1943) is characterized by numerous hemispherical chambers arranged beside and above one another. Exowalls on the lower outside are perforated (inhalant pores), and the opposite upper surface bears several astrorhizal canal systems that served as exhalant canals. The sponge is abundant in Permian reefs, Guadalupe Mountains, Texas and New Mexico, United States; schematic, not to scale (Senowbari-Daryan, 1990).

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 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

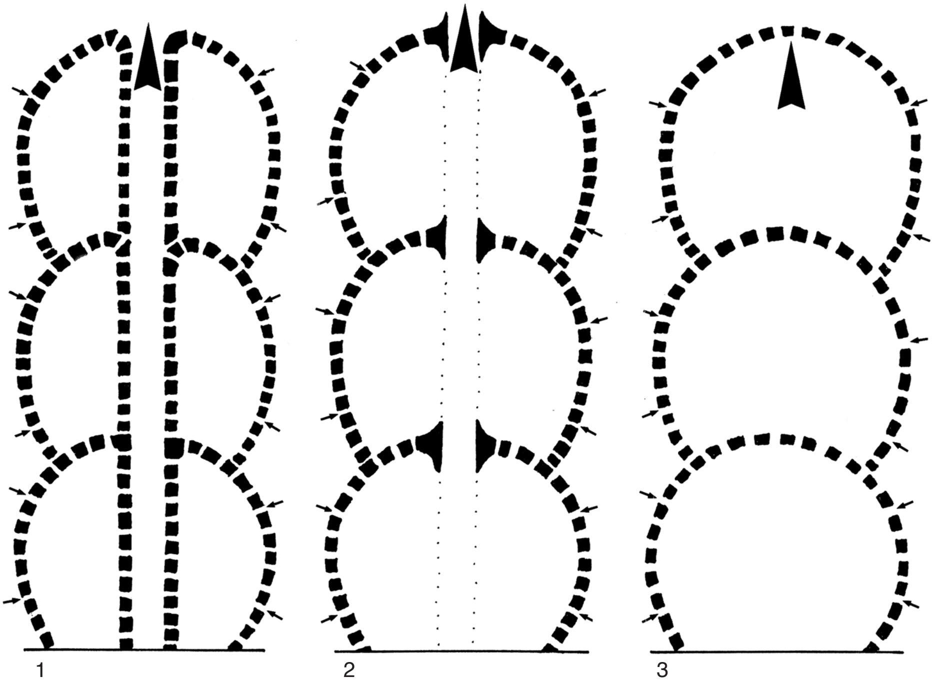


FIG. 22. Three principal types of water circulation in sphinctozoan sponges. *1, Amblysiphonella*-type, *2, Sphaerocoelia*-type, and *3, Colospongia*-type; *small arrows* indicate direction of inhalant water motion; *large arrows* indicate direction of exhalant water currents (Senowbari-Daryan, 1990).

(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 of 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 VACELET, 1979b. Calcareous spicular skeleton, calcitic rigid skeleton primary aragonite? Calcispongiae; Jurassic.

2. Verticillitida TERMIER & TERMIER (in TERMIER, 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? Calcispongiae?; Cambrian–Cretaceous.

4. Pisothalamida SENOWBARI-DARYAN & RIGBY, 1988. Siliceous spicular skel-

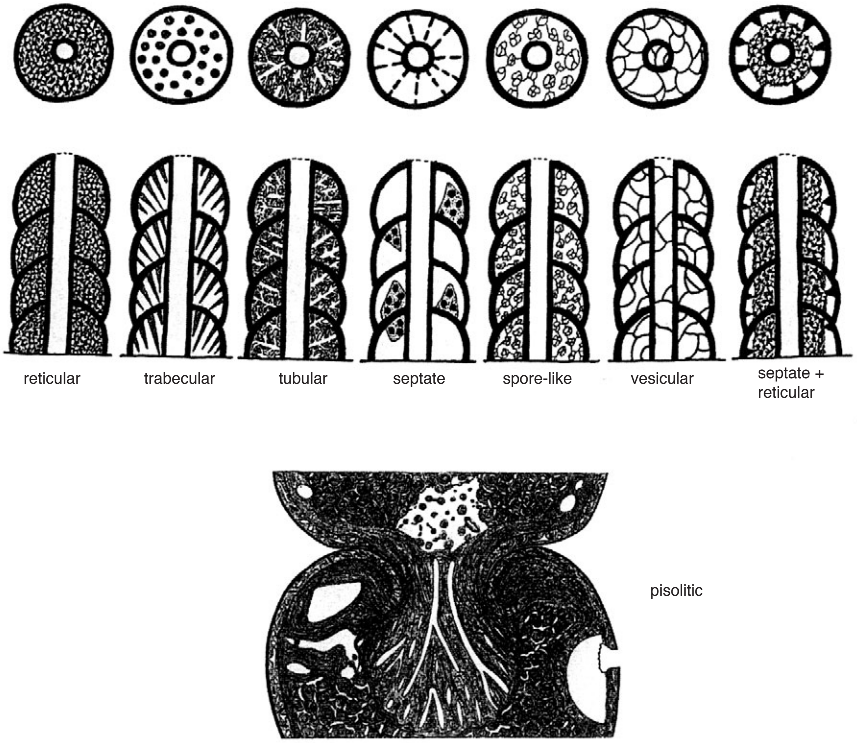


FIG. 23. Appearance of different types of filling skeleton known in the sphinctozoans, as seen in longitudinal and transverse sections. Vesiculae may occur separately or in combination with other types of filling skeleton (adapted from SENOWBARI-DARYAN, 1990).

eton composed of primary monaxons, with an aragonitic rigid skeleton and pisolitic internal filling structure. Demospongiae; Permian.

5. Hadromerida (*partim*), according to REITNER (1987b). Probably monactine megascleres and sphaeraster microscleres. Demospongiae, Triassic (the only genus of this taxon—*Cassianothalamia*—was assigned to the new family Cassianothalamiidae by REITNER (1987a), order Hadromerida. MÜLLER-WILLE and REITNER (1993) moved the genus *Cassianothalamia* to the family Geoiidae within the order Astrophorida.

6. Guadalupiida TERMIER & TERMIER (in TERMIER, 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 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

FIG. 24. 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).

sponge classes, including Heteractinida, Demospongiae, Calcarea (=Calcispongiae), Hexactinellida, and Archaeocyatha, Calcispongiae, Hexactinellida, and Archaeocyatha by SENOWBARI-DARYAN and GARCÍA-BELLIDO (2002a). Most sphinctozoans are classified into different orders within the demosponges. In addition, a separately listed bibliography of fossil sphinctozoans was provided by SENOWBARI-DARYAN and GARCÍA-BELLIDO (2002b).

FINKS and RIGBY (2004c) 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 Demospongea (=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 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

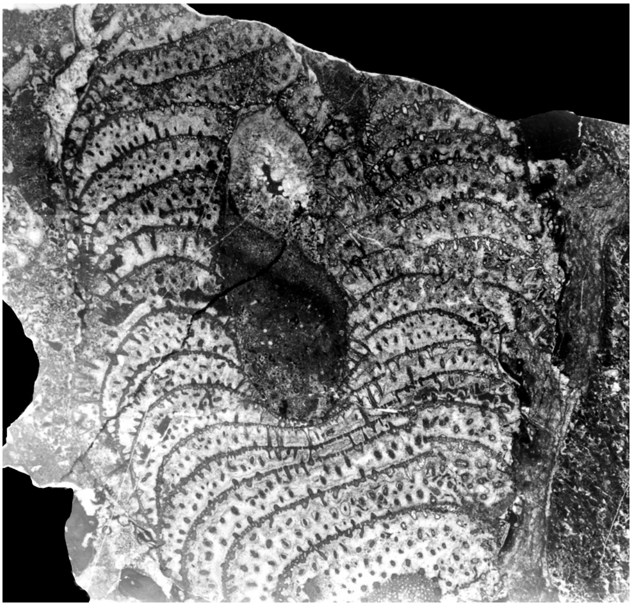


FIG. 25. *Stylothalamia hydriotica* SENOWBARI-DARYAN, 1990. This retrosiphonate sponge exhibits the trabecular (pillarlike) filling skeleton within the chamber interiors; pillars appear as points when cut transversely; Carnian, Triassic, Hydra, Greece, ×2.2 (Senowbari-Daryan, 1990).

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 *Clathricoscinus 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 *Nochoroiocyathus mirabilis* ZHURAVLEVA and the Jurassic species *Boikothalamia convexa* (=*Verticillites convexus* BOIKO, 1979) can hardly be differentiated (compare ZHURAVLEVA & MYAGKOVA, 1987, pl. 1,*1;* 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).

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

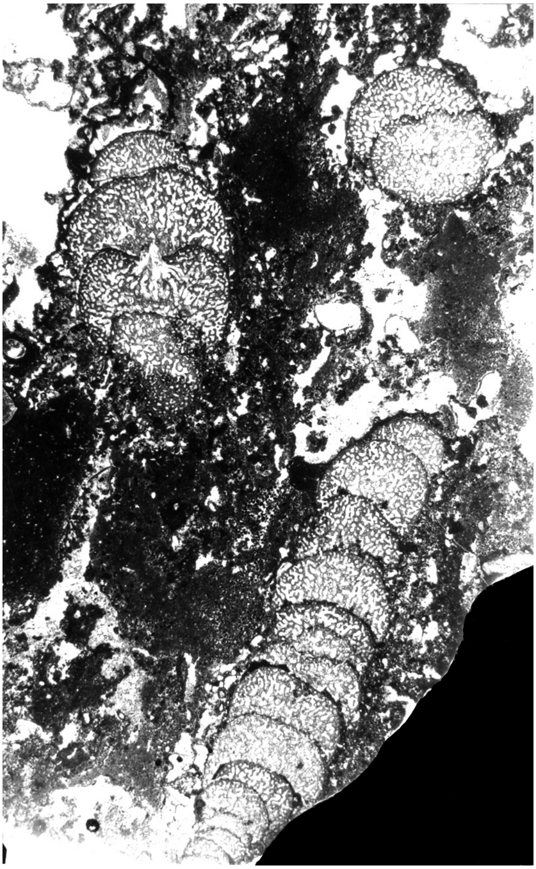


FIG. 26. *Solenolmia manon* (MÜNSTER, 1841). Longitudinal and oblique sections exhibiting reticular filling skeleton in chamber interiors; axial canal is cut in one specimen, on the left; Ladinian–Carnian, Triassic, Dolomites, Italy, ×2.5 (new).

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 SENOWBARI-DARYAN & GARCÍA-BELLIDO (2002a) and the Summary of Classification and Stratigraphic Occurrences (p. 66–75 herein).

Cambrian

Six genera have been reported from the Cambrian (Fig. 31). Five of them are limited to the Cambrian, and only the genus *Amblysiphonella* continued into the Ordovician. Fifty percent of Cambrian genera (three genera: *Jawonia, Nucha,* and *Wagima*; see PICKETT, 2002) belong to the heteractinid sponges.

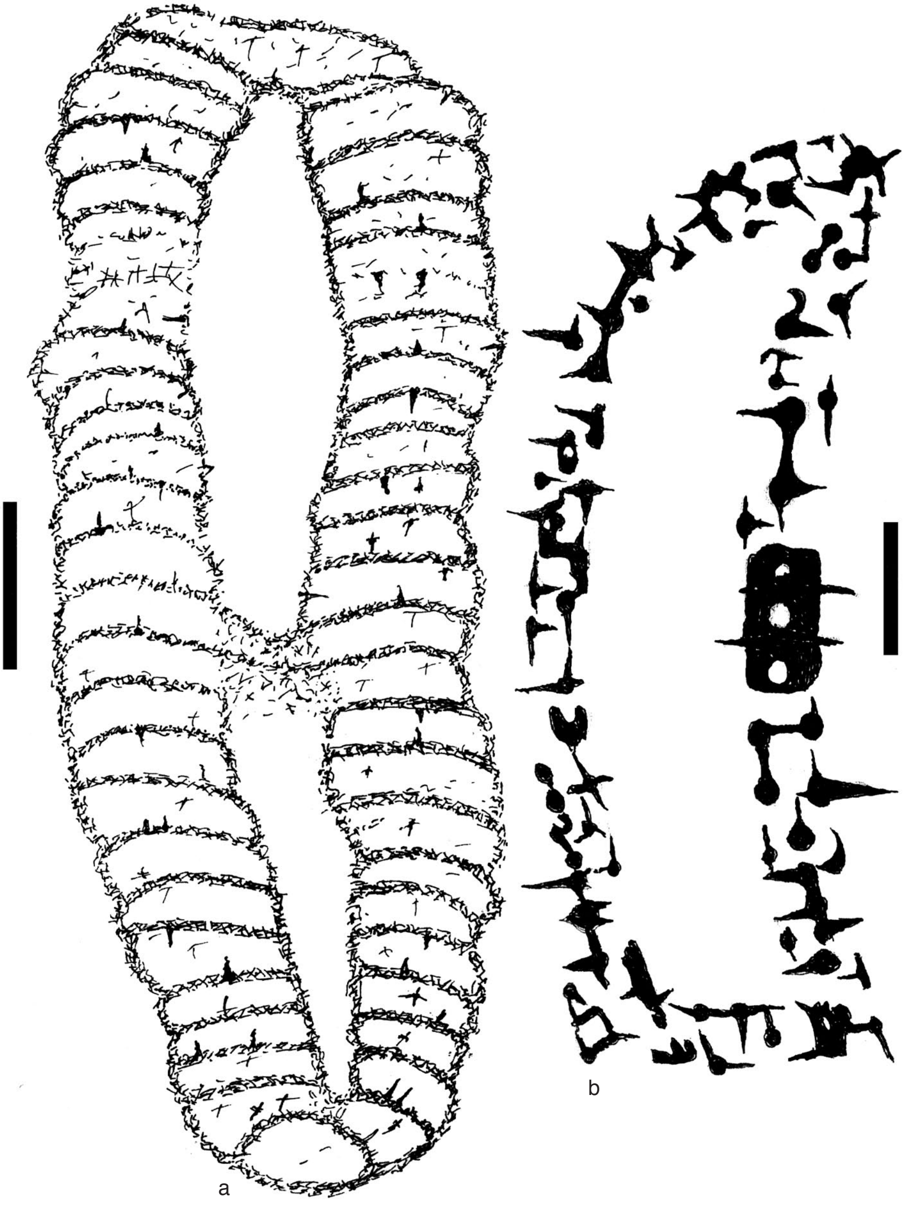


FIG. 27. Lattice skeleton of chambered hexactinellid sponge *Casearia* sp., upper Norian, Triassic, Nayband Formation, Iran. *a,* Longitudinal section showing lattice arrangement of hexactine spicules forming chamber walls, scale bar, 1 cm; *b,* magnification of one chamber showing arrangement of individual hexactines within the chamber and spongocoel walls, scale bar, 1 mm (new).

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

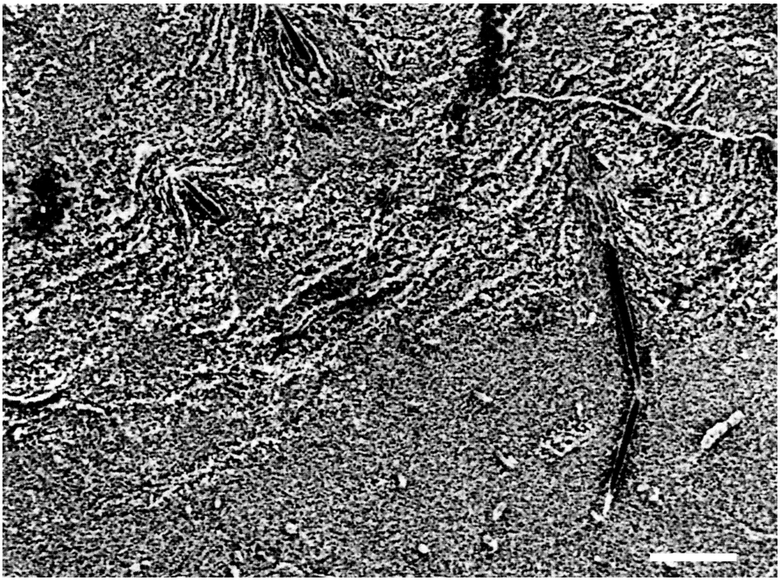


FIG. 28. Monaxon spicules imbedded in the chamber wall of the Triassic species *Celyphia submarginata* (MÜNSTER, 1841). Spicules are located in the center of wavy lamellar microstructure; Carnian, Triassic, Cassian Formation, Dolomites, Italy, scale bar, 30 µm (Senowbari-Daryan, 1990).

other benthic organisms (see BRENCHLEY, 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. 31), 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. 31) 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 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 extinc-

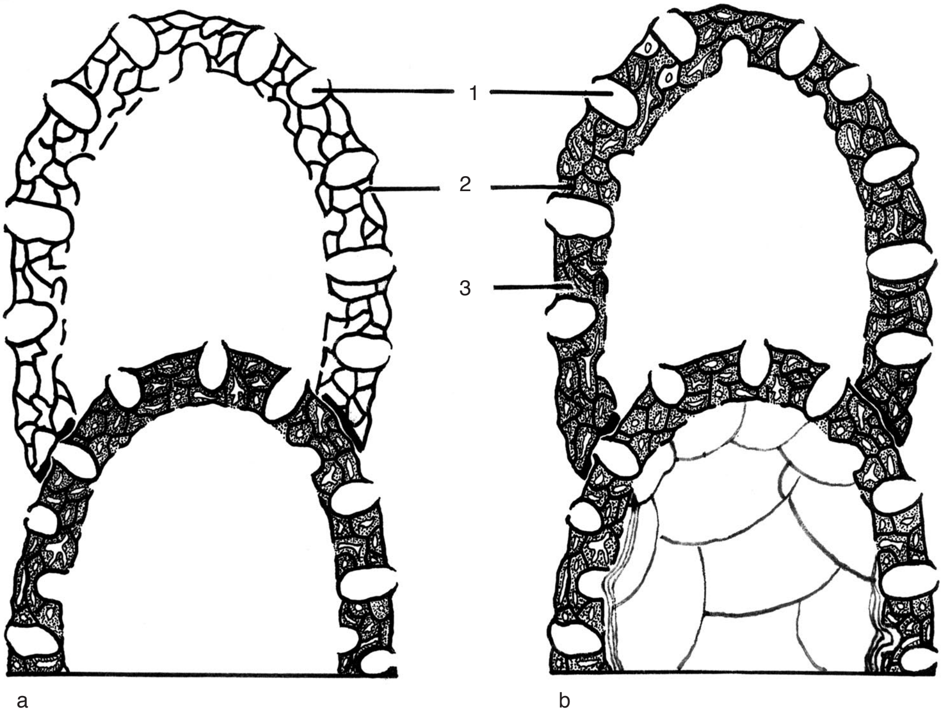


FIG. 29. Biomineralization process of the chamber walls in *Jablonskyia adrusovi* (JABLONSKY). The initial calcification started the thin labyrinthic lines within the wall (*a*) and proceeded from these lines into the interspaces (*b*); rodlike or labyrinthic systems of spaces remained free from calcification 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).

tion 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 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 & WÜRM, 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

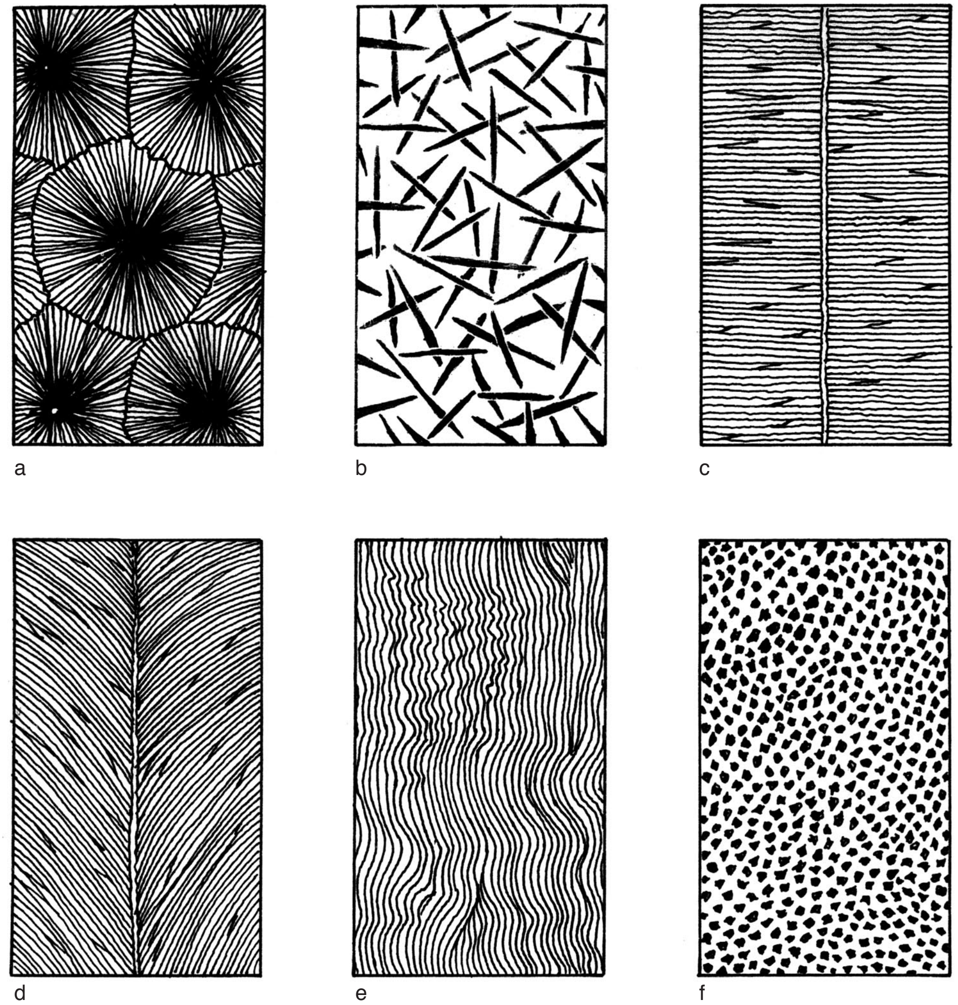


Fig. 30. Different microstructures known in sphinctozoan sponges. *a,* Spherulitic, *b,* irregular, *c,* orthogonal, *d,* clinogonal, *e,* lamellar, and *f,* microgranular; note that spherulitic, clinogonal, and granular types of microstructure also apply to certain inozoans (see p. 40–44); schematic, not to scale (Senowbari-Daryan, 1990).

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, 2001), 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 *Platythalamiella* are known from Permian and Norian–Rhaetian deposits, but not from Lower and Middle Triassic and Carnian ones. 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. Calcisponge 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, 1989; 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.

Figure 31 shows the number of sphinctozoan sponge genera occurring per period through Earth's 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

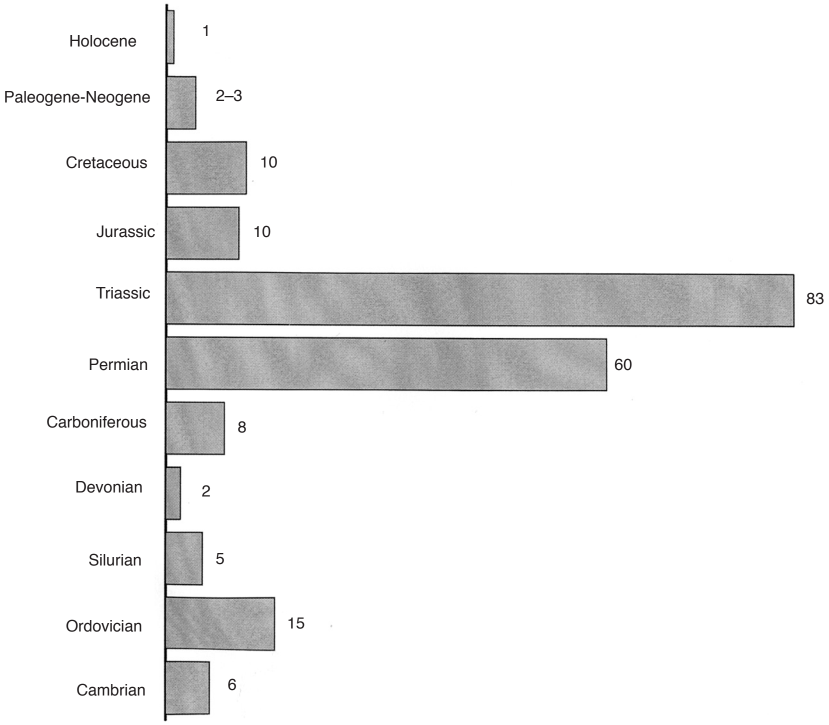


FIG. 31. Number of hypercalcified sphinctozoan genera per geologic period through the Phanerozoic (chambered hexactinellid genera are not considered in this diagram; new).

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 32 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. 33). Inozoan sponges are commonly less than 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 34.

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. 35–36). Sponges with a distinct cortex or dermal layer commonly

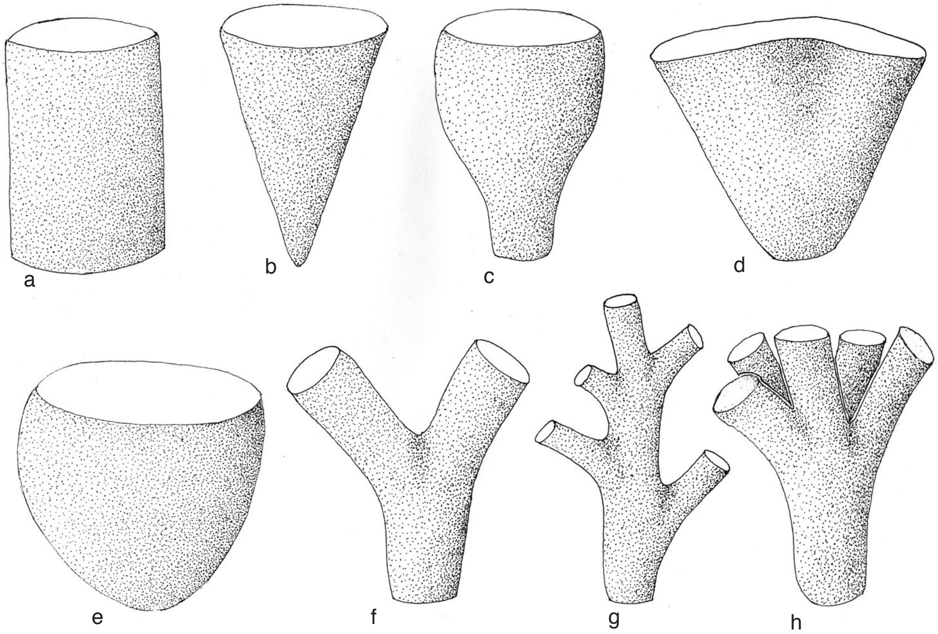


FIG. 32. General shapes of skeletons of inozoan sponges. *a,* cylindrical, *b,* arcuate conical, *c,* conical to club shaped, *d,* tabular, *e,* hemispherical, *f,* single dichotomously branched, *g–h,* dichotomously multibranched; schematic, not to scale (new).

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 *Daharella* 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. 14), 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 Permian genus *Auriculospongia* TERMIER & TERMIER, 1977 (see Fig. 45.1), 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, especially 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. 35) or the Triassic genus *Molengraaffia* VINASSA DE REGNY, 1915.

Some inozoans are characterized by only one osculum (e.g., *Peronidella* HINDE, 1893), and others by several oscula (e.g., *Sestrostomella* ZITTEL, 1878; Fig. 37), which are visible as one or several openings at the

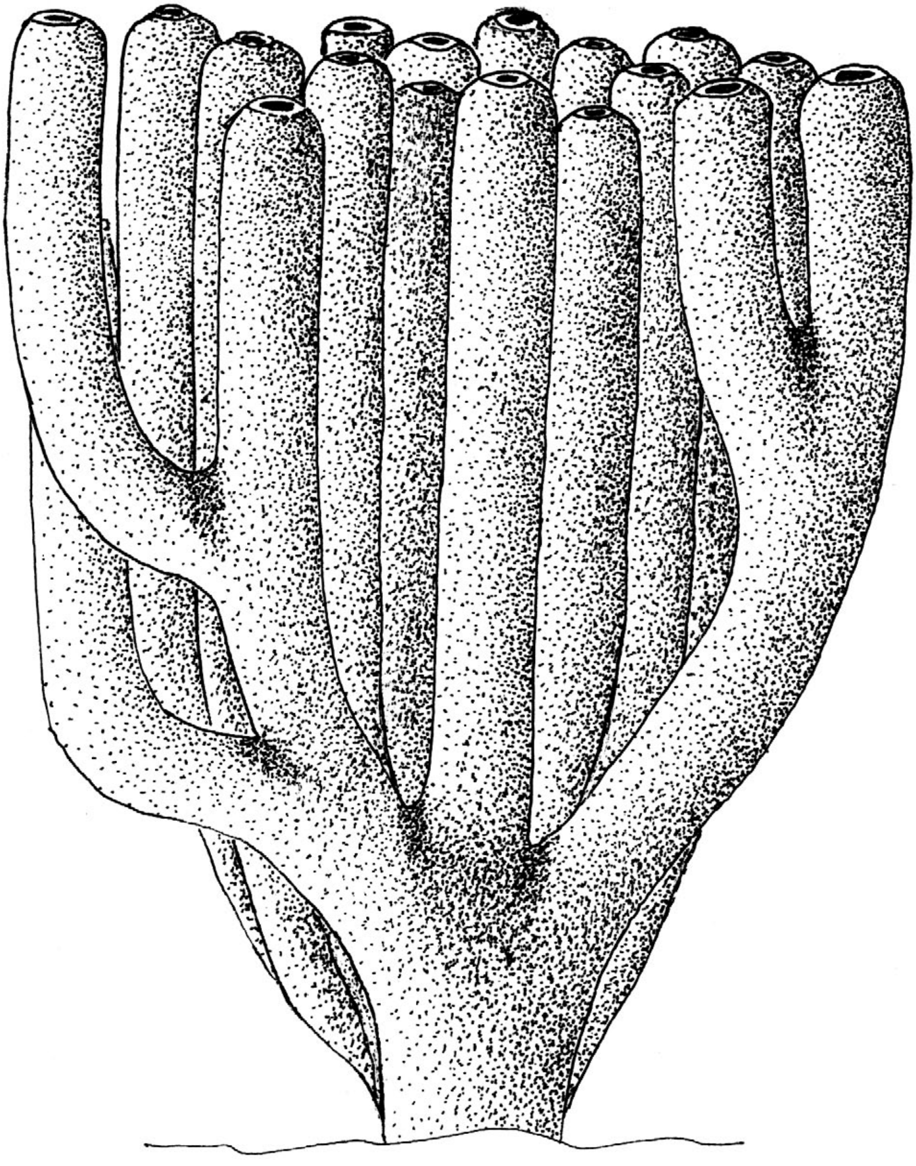


FIG. 33. Reconstruction of multibranched inozoan sponge *Peronidella iranica* SENOWBARI-DARYAN, 2003; Norian–Rhaetian, Triassic, reefs within Nayband Formation, Iran (Senowbari-Daryan, 2003).

top of the sponge (Fig. 37; 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. 36], 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 astrorhizal system are developed in

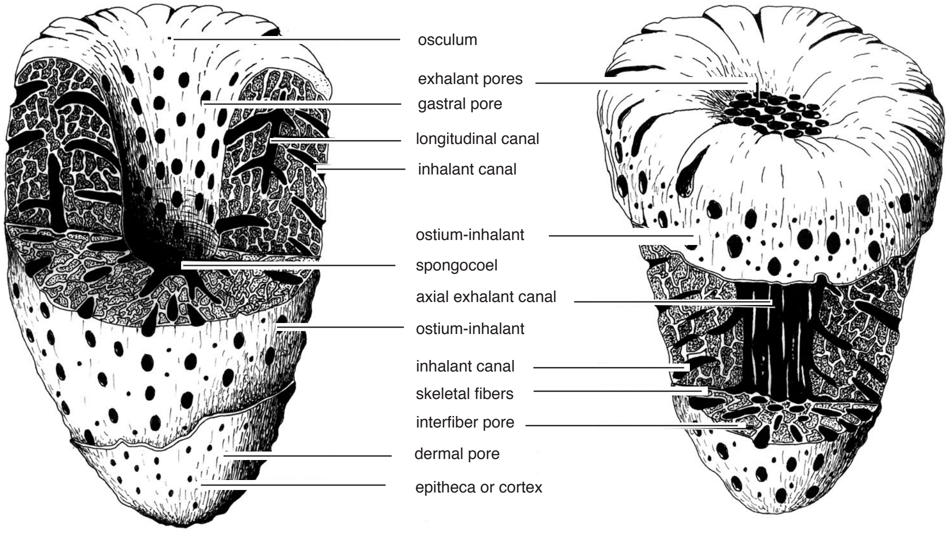


FIG. 34. Major skeletal elements of inozoan sponges; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

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 astrorhizal systems (see DIECI, ANTONACCI, & ZARDINI, 1968; RIGBY & SENOWBARI-DARYAN, 1996a). Several astrorhizal systems cover the outer surface of the cylindrical and massive genus *Stellispongiella* WU (see TERMIER & TERMIER, 1955; RIGBY & SENOWBARI-DARYAN, 1996a). The astrorhizal systems may be located on elevations (mamelons) (Fig. 38, Fig. 45.4) or not.

INTERNAL MORPHOLOGY

Spongocoel(s)

Some inozoans possess only one axial spongocoel (e.g., *Peronidella* HINDE, 1893) (Fig. 45.2), and others have several axial spongocoels (e.g., *Sestrostomella* ZITTEL, 1878 [Fig. 37], or *Stollanella* BIZZARINI & RUSSO, 1986 [Fig. 39]). 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. 40), or it may be surrounded by the fibrous skeleton of the entire sponge wall, without a distinct separate inner layer (Fig. 41). Several sponges possess numerous vertical spongocoels that are distributed through the whole sponge (see Fig. 45.3) (e.g., the Permian genera *Preeudea* TERMIER & TERMIER, 1977, or *Polytubifungia* RIGBY & SENOWBARI-DARYAN, 1996a; Fig. 36). 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. 40). 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. 42).

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 *Permocorynella* RIGBY & SENOWBARI-DARYAN, 1996a (Fig. 41, Fig. 43), or in the Jurassic genus

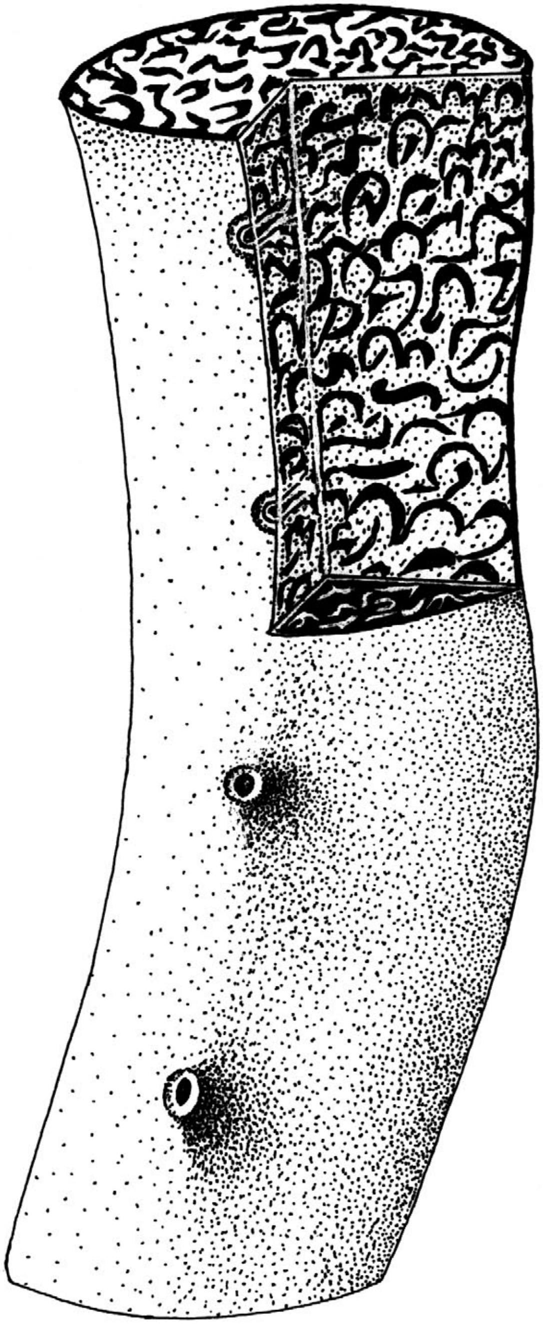


FIG. 35. Reconstruction of asiphonate inozoan sponge *Daharella micella* RIGBY & SENOWBARI-DARYAN, 1996a. Water passed through rimmed ostia and out through interfiber spaces; sponge is known from upper Permian, Djebel Tebaga, Tunisia; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

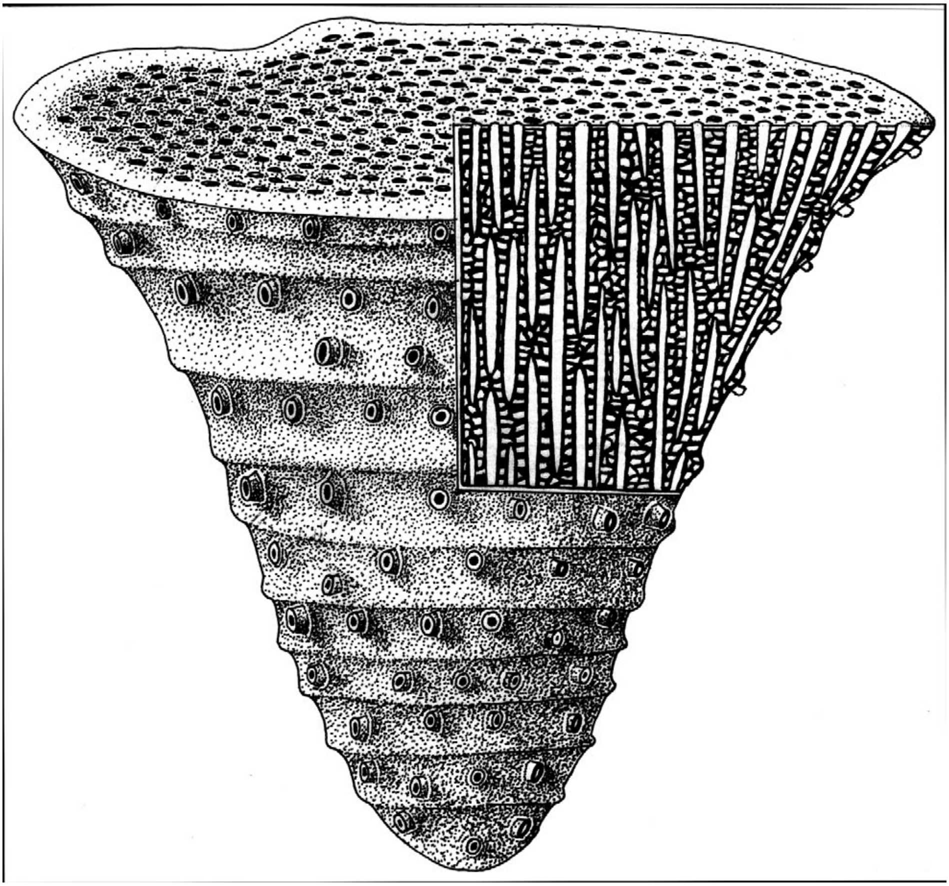


FIG. 36. Reconstruction of *Polytubispongia maxima* RIGBY & SENOWBARI-DARYAN, 1996a; externally annulate conical sponge bearing numerous rimmed ostia on the dermal surface that serve as inhalant canals; exhalant canals are numerous, more or less parallel tubes that are distributed through whole sponge; sponge is known from upper Permian, Djebel Tebaga, Tunisia; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

Endostoma RÖMER, 1864 (=*Corynella* ZITTEL, 1878). These tubes may be called inhalant tubes or canals (Fig. 41). 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 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. 41). In some genera, the exhalant canals may converge upward and open into the spongocoel, as in *Sestrostomella* ZITTEL, 1878 (Fig. 37), or they may be outwardly divergent within the sponge wall and open at the sponge surface, as in *Permocorynella* RIGBY & SENOWBARI-DARYAN, 1996a (Fig. 41, Fig. 43), or in *Stollanella* BIZZARINI & RUSSO, 1986 (Fig. 39).

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

FIG. 37. *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, ×2.5 (Senowbari-Daryan, Seyed-Emami, & Aghanabati, 1997).

by astrorhizal exhalant canals, which in some specimens are located within mamelon-like elevations (Fig. 38). 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 canals systems.

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 be different in 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.

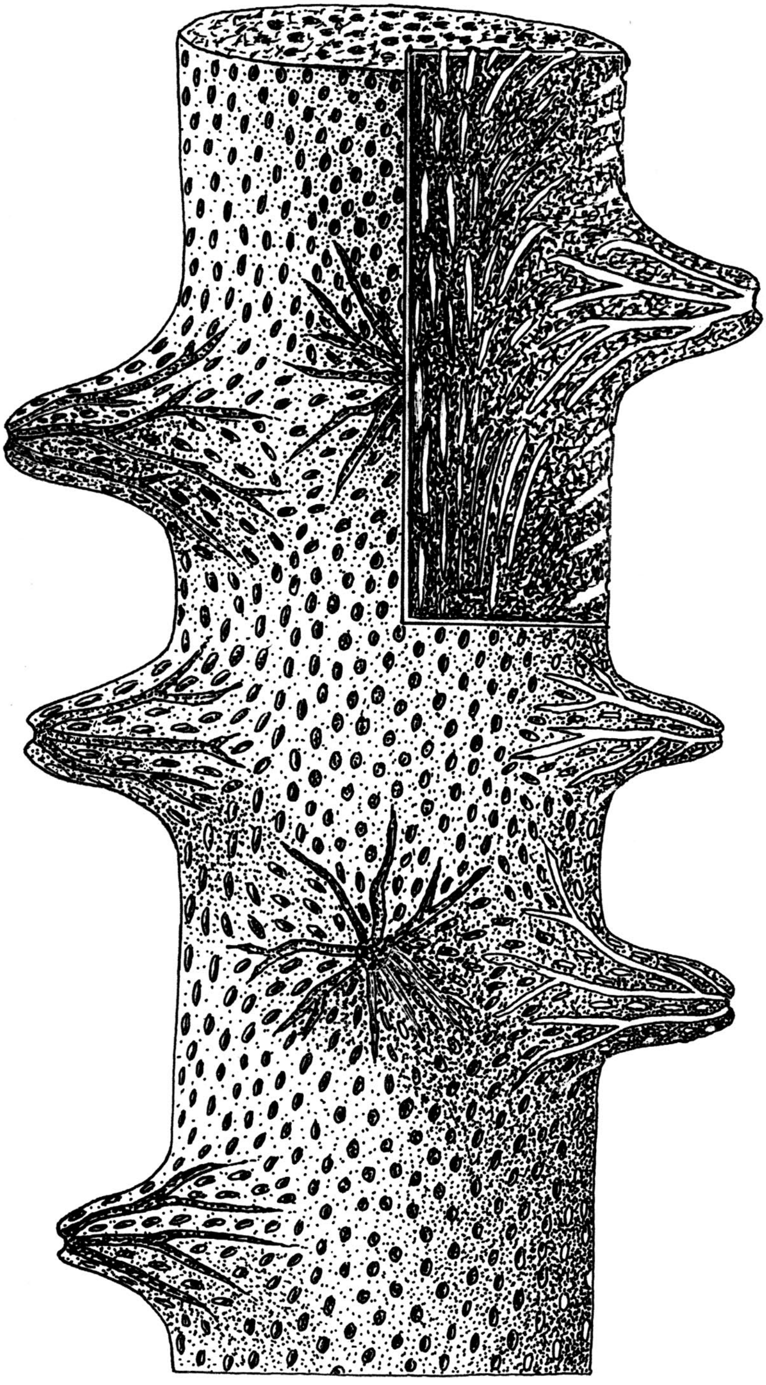


FIG. 38. Reconstruction of *Stellispongiella bacilla* (TERMIER & TERMIER, 1977), a cylindrical inozoan sponge from upper Permian, Djebel Tebaga, Tunisia; astrorhizal systems served as exhalant canals and are located on sharp moundlike elevations; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

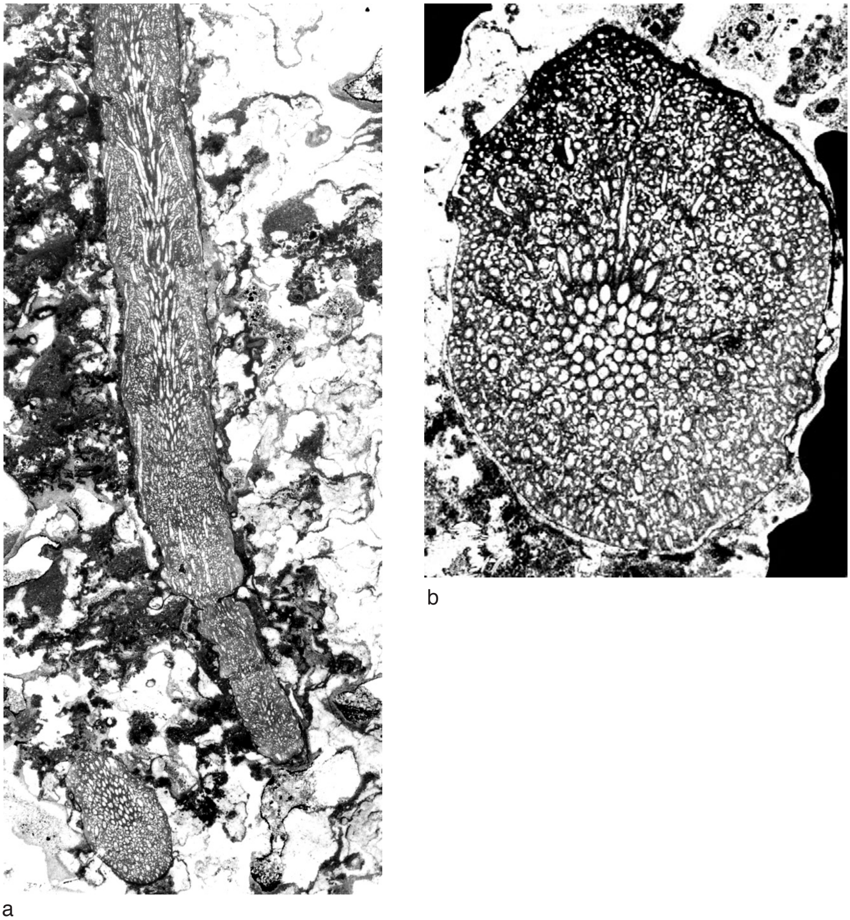


FIG. 39. *Stollanella diecii* BIZZARINI & RUSSO, 1986. *a,* Longitudinal, ×1.5, and *b,* transverse, ×5, sections of cylindrical inozoan sponge. It has Mg-calcite skeletal mineralogy and is characterized by an axial canal bundle composed of up to approximately 50 individual tubes; additional smaller tubes around axial bundle diverge upward and outward toward dermal surface of sponge; Ladinian–Carnian, Triassic, Dolomites, Italy (new).

Spicules

Investigations of well-preserved Permian inozoan sponges from Djebel Tebaga, Tunisia 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, 1849, 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

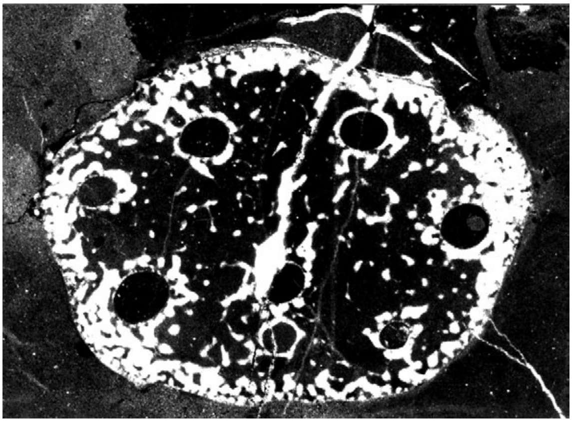


FIG. 40. *Marawandia iranica* SENOWBARI-DARYAN, SEYED-EMAMI & AGHANABATI, 1997. Cylindrical inozoan sponge, seen here in transverse section, has several (6–8) usually peripherally located spongocoel tubes with more or less distinct exowalls pierced by labyrinthic branched pores; Norian–Rhaetian, Triassic, Nayband Formation, Iran, ×12 (Senowbari-Daryan, Seyed-Emami, & Aghanabati, 1997).

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.

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. 30) 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. 30), the most common microstructure in inozoan sponges, is known from the majority of Permian and Triassic genera. It has been recognized, e.g., in Permian *Sphaeropontia* RIGBY & SENOWBARI-DARYAN, 1996a (Fig. 44), and in the Triassic genera *Sestrostomella* ZITTEL, 1878 (DIECI, ANTONACCI, & ZARDINI, 1968;

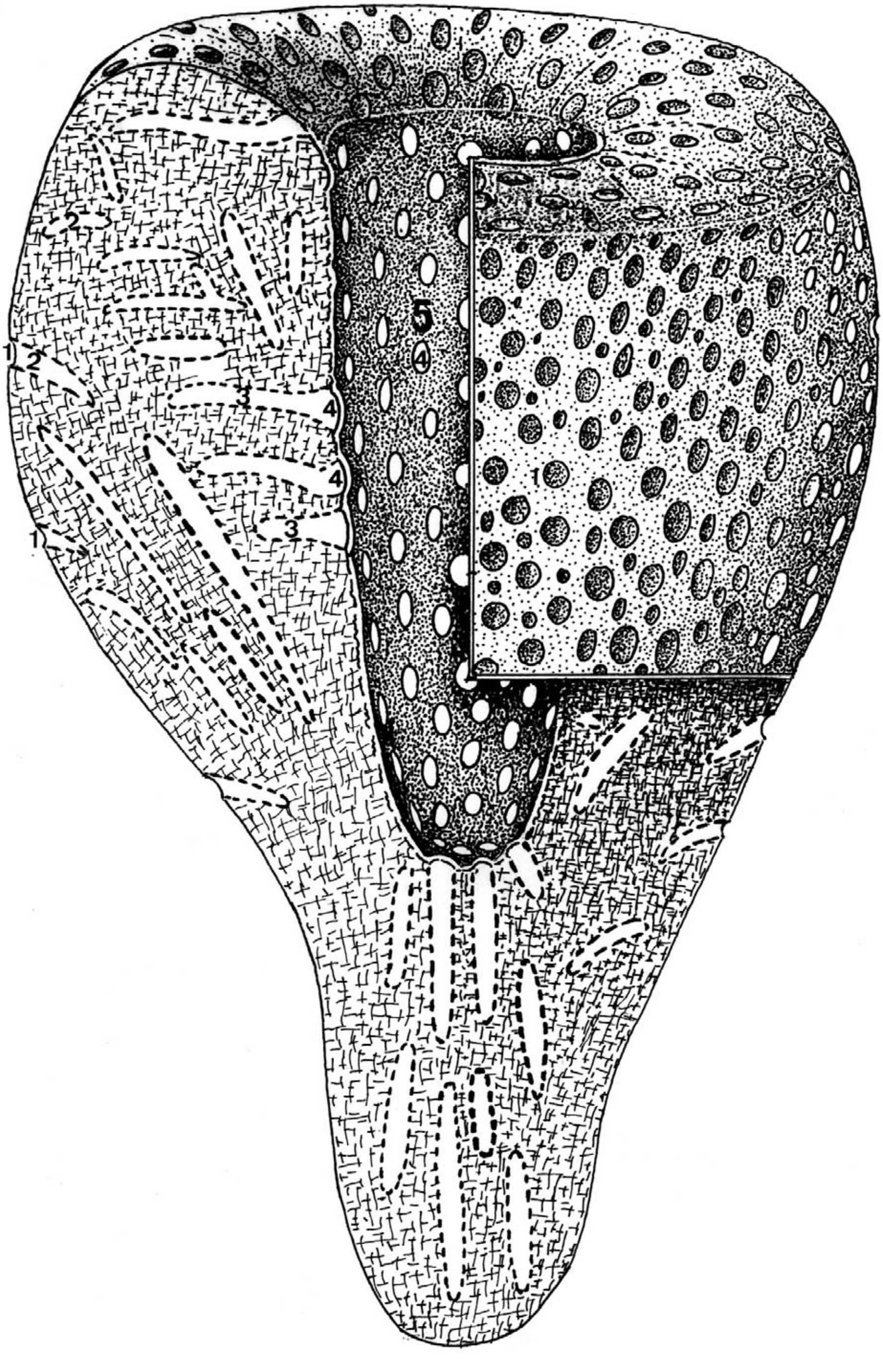


FIG. 41. Reconstruction of *Permocorynella* RIGBY & SENOWBARI-DARYAN, 1996a, showing *1,* exopores or ostial pores, *2,* inhalant canals, *3,* exhalant canals, *4,* endopores, and *5,* deep spongocoel. Spaces between the inhalant and exhalant canals are filled with reticular fiber skeleton; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

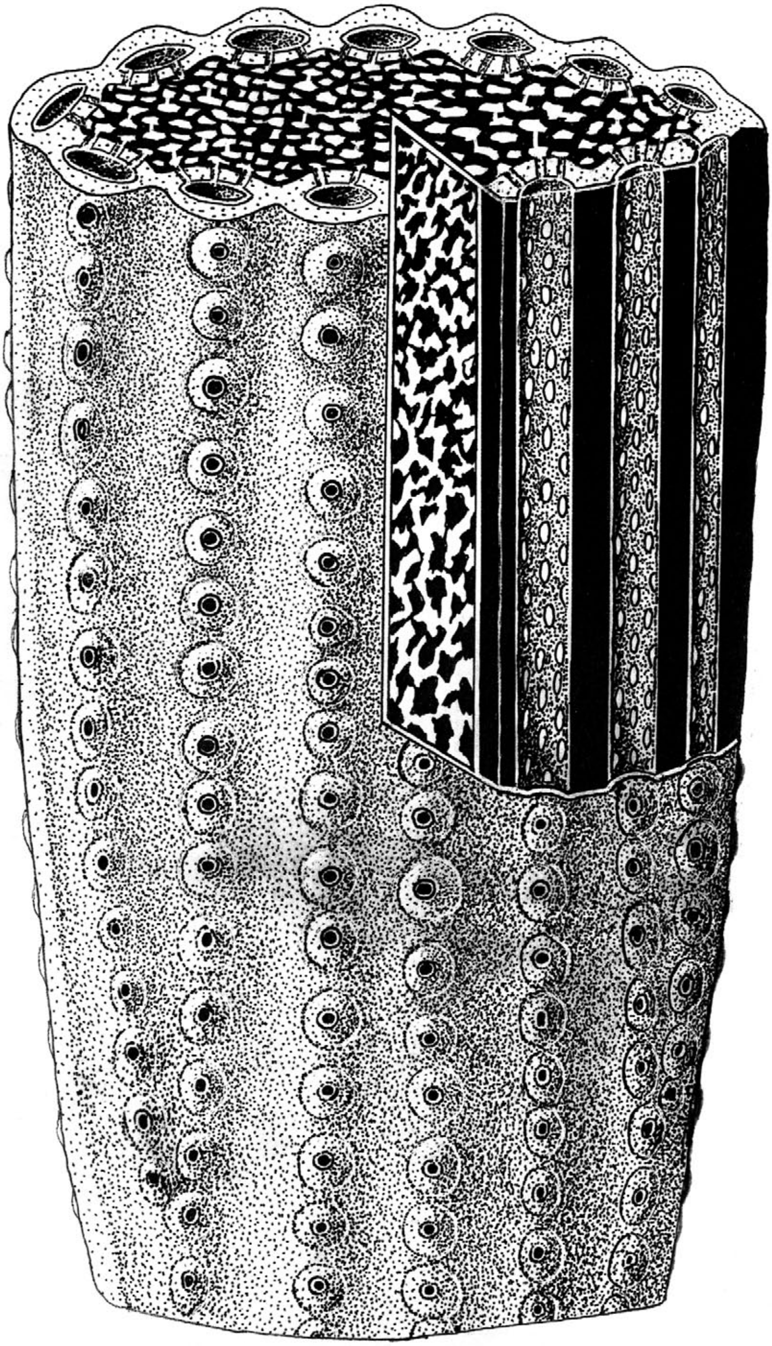


FIG. 42. Reconstruction of *Exotubispongia pustulata* RIGBY & SENOWBARI-DARYAN, 1996a; sponge has numerous vertical peripheral tubes that are connected by pores to spaces in the internal reticular skeleton and to the dermal surface through numerous ostia located on pustulelike elevations. The sponge is known, to date, only from upper Permian, Djebel Tebaga, Tunisia; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

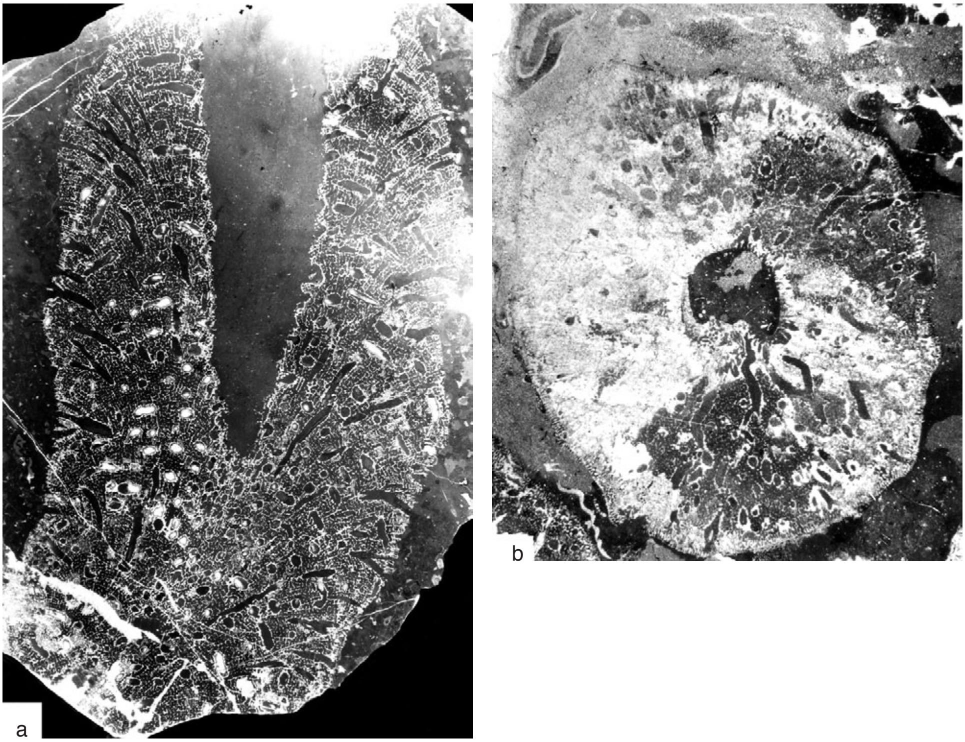


FIG. 43. *Permocorynella maxima* SENOWBARI-DARYAN, SEYED-EMAMI, & AGHANABATI, 1997, as seen in *a,* longitudinal and *b,* transverse sections. Sponge is characterized by an axial spongocoel and numerous additional branched tubes that diverge upward and outward to become perpendicular to dermal surface of sponge; Norian–Rhaetian, Triassic, Nayband Formation, Iran, ×2 (new).

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 µm.

Clinogonal microstructure (Fig. 30) 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 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. 30) 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. 45).

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

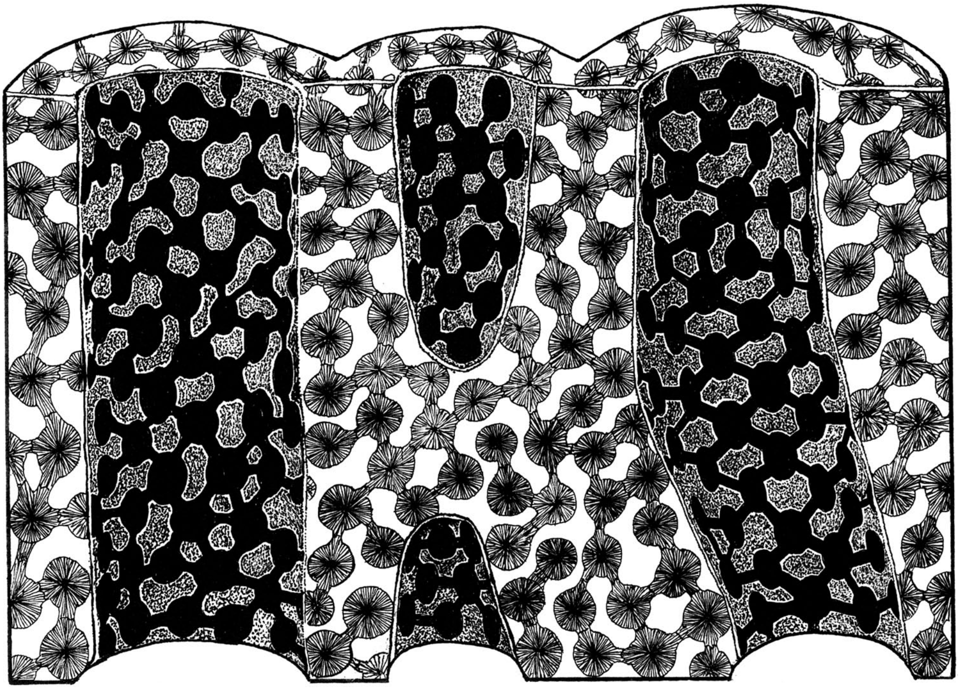


FIG. 44. Spherulitic microstructure of *Sphaeropontia regulara* RIGBY & SENOWBARI-DARYAN, 1996a, upper Permian, Djebel Tebaga, Tunisia. This type of microstructure is most abundant in aragonitic inozoan and sphinctozoan sponges; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

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.

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 under Paleobiology, Patterns of Water Circulation, and Paleoecology, above, p. 21.

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 (=Calcispongiae) by FINKS and RIGBY (2004c). They subdivided the hypercalcified sponges and placed them

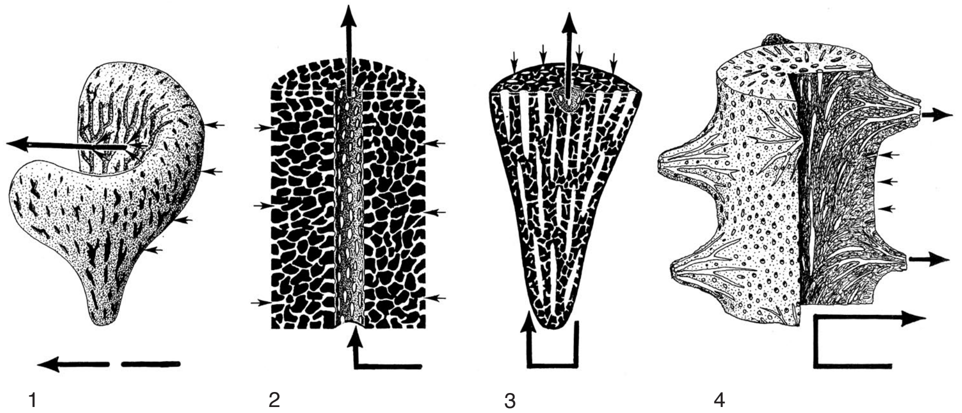


FIG. 45. Pathways of water movement in inozoan sponges. *Small arrows* indicate inhalant current directions; *large arrows* indicate exhalant directions. *1, Auriculospongia*-type (pathway: inhalant = horizontal, exhalant = horizontal); *2, Peronidella*-type (pathway: inhalant = horizontal, exhalant = 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).

into the following subclass to ordinal level groupings.

Class Demospongiae
  Subclass Ceractinomorpha Lévi, 1953
    Order Agelasida Verrill, 1907
    Order Vaceletida Finks & Rigby, 2004c
  Subclass Tetractinomorpha Lévi, 1953
    Order Hadromerida Topsent, 1898
Class Calcispongiae
  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, 2004c
    Order Sphaerocoeliida Vacelet, 1979a
    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 Calcispongiae as well.

Figure 46 shows the abundance and number of inozoan genera reported to date from each geologic period through the Phanerozoic.

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.

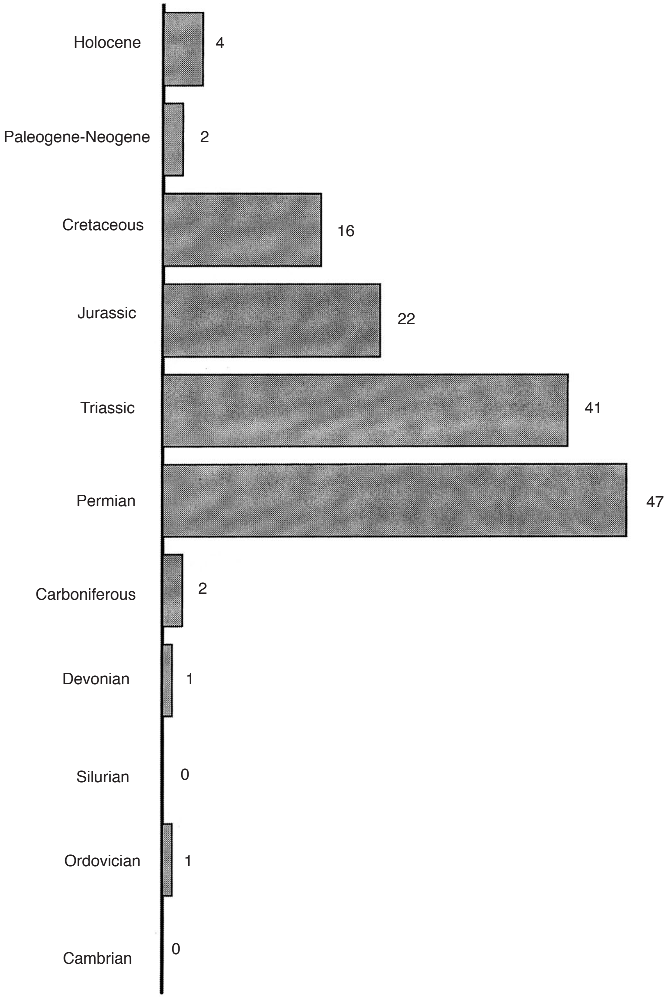


FIG. 46. Number of inozoan genera per geologic period through the Phanerozoic. Genera that have been described as hydrozoans are not considered in the diagram (new).

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 *Maeandostia* 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, below (p. 51).

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 Calcispongiae, and *Cornuaspongia* and *?Trammeria* among the class and order Uncertain inozoans, survived into the Jurassic beyond the boundary event. From the Triassic on through the Cenozoic, the Calcispongiae 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 Calcispongiae (FINKS & RIGBY, 2004a, 2004c). 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 Stellispongiidae, of the Calcispongiae (FINKS & RIGBY, 2004a, 2004c). 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. *?Elasmostoma* has been reported from the Eocene of Mexico, and *Tretocalia* from the Miocene of Australia (FINKS & RIGBY, 2004c, 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: *Trachyspecion* 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 (=Calcispongiae) (FINKS & RIGBY, 2004c, 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. 31, Fig. 47–58).

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. 47).

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, 2004c).

The oldest nonarchaeocyath sponge, *Imperatoria mega* (RIGBY & POTTER, 1986), was described as being an inozoan from Ordovician rocks of the eastern Klamath Mountains of northestern 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. 48), 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.* 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 sphinctozoan 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 Ordovician sphinctozoan sponge described from these areas (Fig. 48).

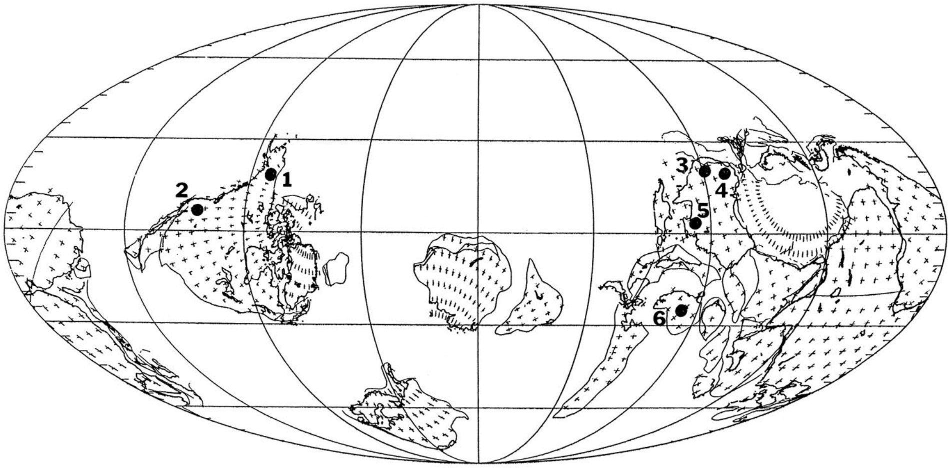


FIG. 47. Paleogeographic distribution of localities from where Cambrian sphinctozoans have been reported: *1,* Tatonduk River, eastern Alaska, United States; *2,* Antler Peak quadrangle, Nevada, United States; *3,* Queensland, Australia; *4,* New South Wales, Australia; *5,* Northern Territory, Australia; *6,* Hubei, China (base map adapted from Scotese & McKerrow, 1990).

Silurian sphinctozoan sponges have somewhat more limited diversity and geographic occurrences than those of the Ordovician (Fig. 49). 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, Nitecki, & others, 1994). The marked similarity of aphrosalpingid sphinctozoan sponges

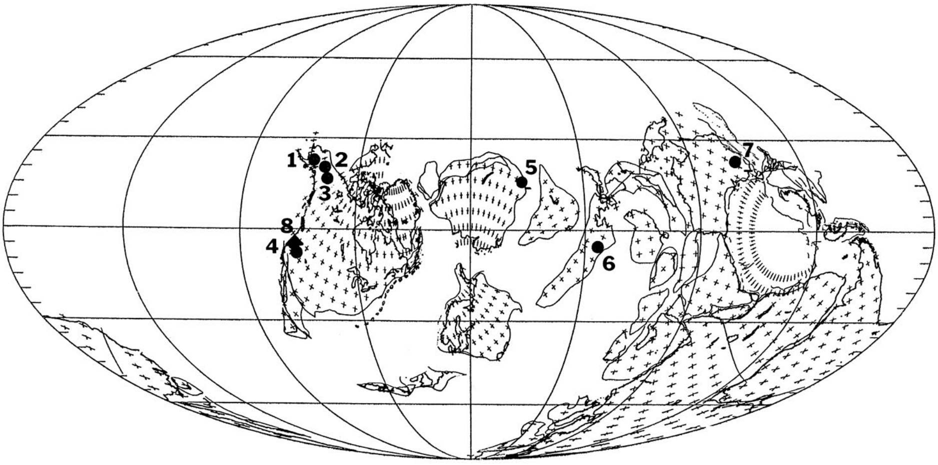


FIG. 48. Paleogeographic distribution of localities from where Ordovician sphinctozoan (*circles*) and inozoan (*triangle*) sponges have been reported. Sphinctozoans occur at localities: *1,* McGrath A-4 and A-5 quadrangles, west-central Alaska, United States; *2,* Livengood quadrangle, east-central 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 & McKerrow, 1990).

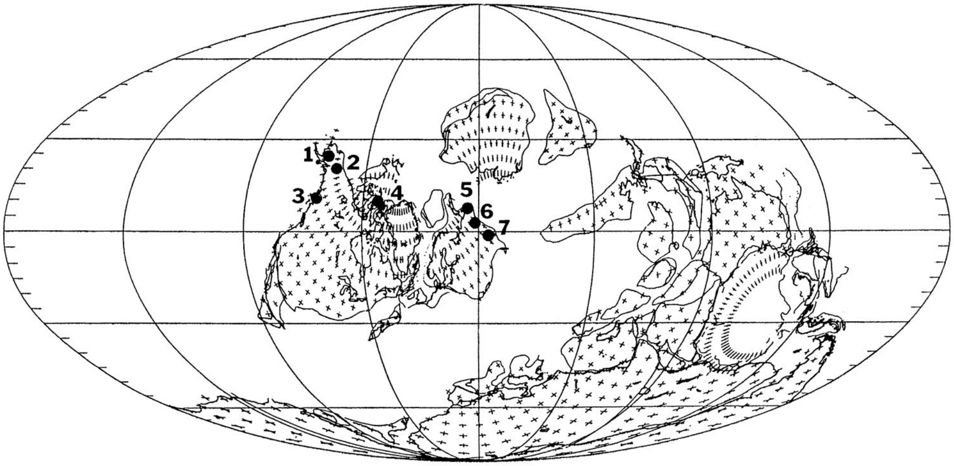


FIG. 49. Paleogeographic distribution of localities from where Silurian sphinctozoan sponges have been reported: *1,* Taylor Mountains D-2 quadrangle, southwestern Alaska, United States; *2,* White Mountain area, McGrath A-4 and A-5 quadrangles, west-central Alaska, United States; *3,* Seaotter Sound 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).

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 *Palaeoscheda* 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.

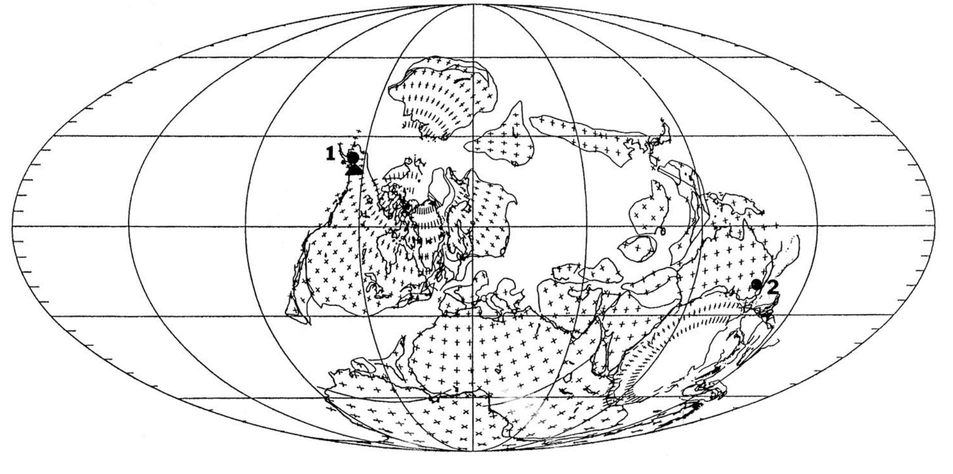


FIG. 50. Paleogeographic distribution of localities from where Devonian sphinctozoan (*circles*) and inozoan (*triangle*) sponges have been reported: *1,* McGrath area, west-central Alaska, United States, where both sphinctozoan and inozoan sponges occur; *2,* New South Wales, Australia (base map adapted from Scotese & McKerrow, 1990).

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. 50). *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. 51), 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, ?Sebargasia,* 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. 51), 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, 2004c, 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. 52; 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 (2004c). 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; Termier, 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 Pimorje), 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, 1971; 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. 53). Major inozoan assemblages have been collected and described from Permian rocks in Tunisia (Termier & Termier, 1955, 1974; Termier, 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, *Radiotrabeculopora,* has been reported from east-central California (Rigby, Linder, & Stevens, 2004). This genus has been interpreted as a disjectoporid-type hypercalcified sponge that has possible inozoan relationships (see Stearn, 2010a: *Treatise Online,* Part E, Revised, Chapter 6, p. 9).

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. 54). 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 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.

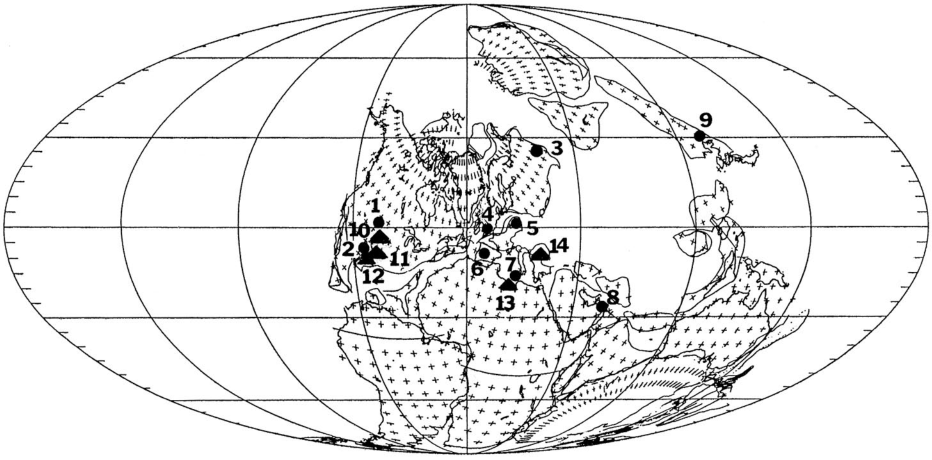


FIG. 51. Paleogeographic distribution of localities from where Carboniferous sphinctozoan (*circles*) and inozoan (*triangles*) sponges have been reported. Sphinctozoan sponges have been reported from localities: *1,* Nebraska, United States; *2,* Texas, United States; *3,* Russia, in general; *4,* Yorkshire, 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 & McKerrow, 1990).

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 documented from the area. An additional genus, *Fanthalamia,* has been documented from Triassic rocks in the Quesnel Range,

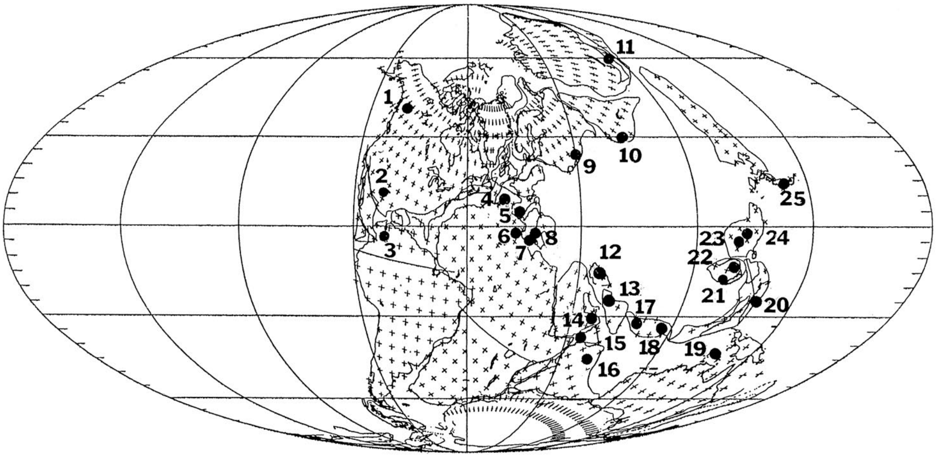


FIG. 52. Paleogeographic distribution of localities from where Permian sphinctozoan sponges have been reported: *1,* British Columbia, Canada; *2,* Guadalupe Mountain region, Texas and New Mexico, United States; *3,* western Venezuela; *4,* Spain; *5,* Sicily; *6,* Tunisia; *7,* Greece; *8,* former Yugoslavia; *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 & McKerrow, 1990).

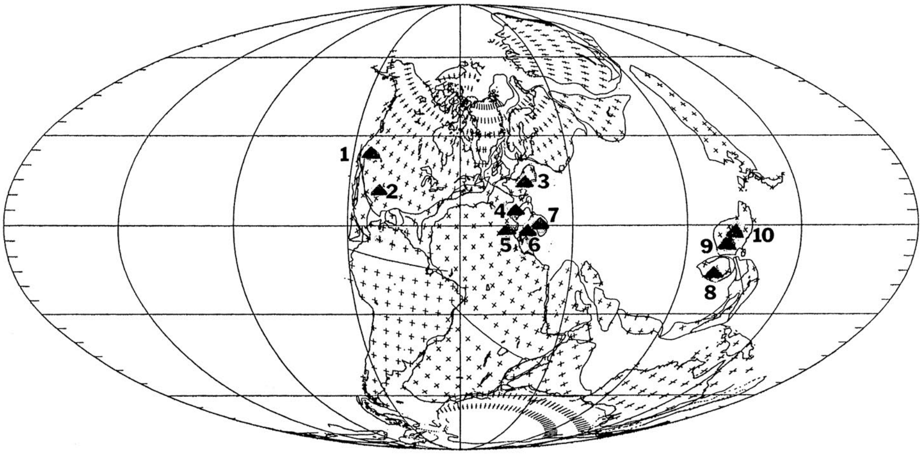


Fig. 53. Paleogeographic distribution of localities from where Permian inozoan sponges have been reported: *1,* east-central California, United States; *2,* Guadalupe Mountain region, Texas and New Mexico, United States; *3,* Europe in general; *4,* Sicily, Italy; *5,* Tunisia; *6,* former Yugoslavia; *7,* Hungary; *8,* Thailand; *9,* Guangxi and Guizhou area, southeastern China; *10,* Hubei area, eastern China (base map adapted from Scotese & McKerrow, 1990).

in southern British Columbia (Stanley & Senowbari-Daryan, 1999). Farther to the southeast, in eastern Oregon, three sphinctozoan genera, *Polycystocoelia, Neoguadalupia,* 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

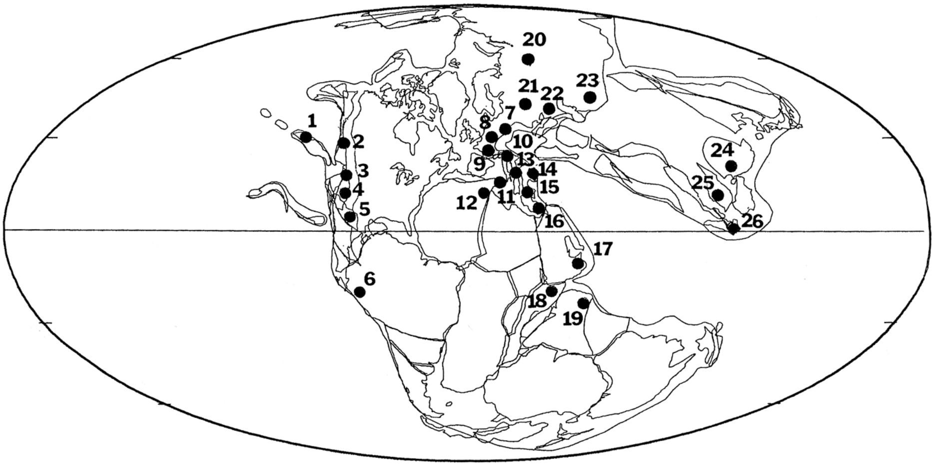


Fig. 54. Paleogeographic distribution of localities from where Triassic sphinctozoan sponges have been reported: *1,* Stikine terrane, southern Yukon Territory, Canada; *2,* Quesnel Range, southern British Columbia, Canada; *3,* Wallowa Mountains, eastern Oregon, United States; *4,* Mineral County, western 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).

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 *Amblysiphonella, Discosiphonella,* and *Polytholosia* have been documented. Generically diverse major faunas of Triassic sphinctozoans have been reported from southeastern Europe (Fig. 54), 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 & WÜRM, 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, 1984, 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 (2004c).

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 (2004c) (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 (2004c), 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 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, 2004c). Triassic sphinctozoans reported from Oman include 10 genera (Senowbari-Daryan, 1990; Bernecker, 1996; Senowbari-Daryan, Bernecker, & others, 1999; Finks & Rigby, 2004c). 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 Molluccas, five genera of Triassic sphinctozoans have been described (Wilckens, 1937); from Timor, four genera (Vinassa de Regny, 1915; Senowbari-Daryan, 1990); and from Indonesia, six genera (Wilckens, 1937).

Triassic inozoan occurrences are primarily focused around the Tethyan margin (Fig. 55). 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, 2004c). A single Triassic inozoan genus, *Himatella,* has been reported from Tunisia (Termier, Termier, & Vachard, 1977). Three genera, *Dactylocoelia*, *Reticulocoelia,* 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, 2004c). In contrast to the rich sphinctozoan fauna known from the Pamir Mountains and Caucasia, the inozoan fauna of this region is poorly known. However, Moiseev (1944) reported the occurrence of 2 genera (*Molengraaffia* and *Hodsia*) from Caucasia, and Doronov, Gazdzicki, and Melnikova (1982) reported the occurrence of 3 genera (*Precorynella, Corynella,* and *Molengraaffia*) from the southeastern Pamir Mountains.

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, 2004c, 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 Calcispongiae, rather than to the Demospongiae

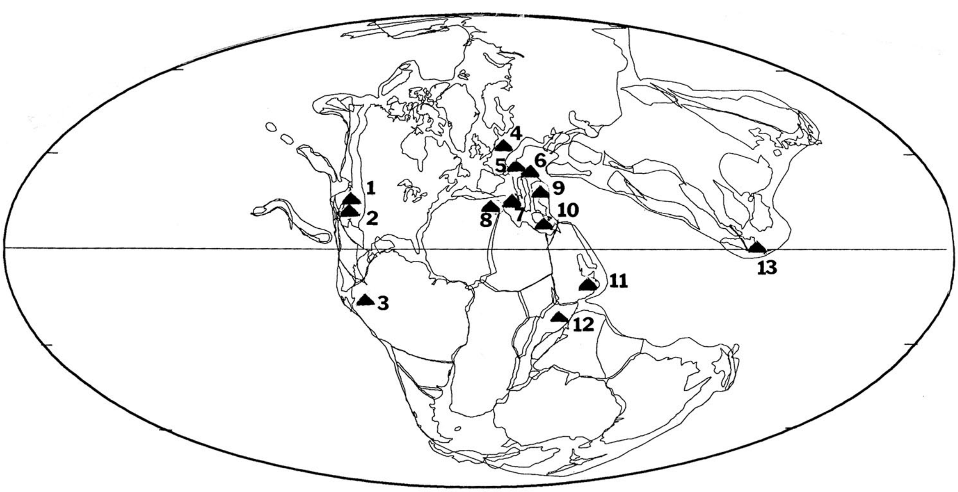


FIG. 55. Paleogeographic distribution of localities from where Triassic inozoan sponges have been reported: *1,* Wallowa Mountains, eastern Oregon, United States; *2,* Mineral County, western Nevada, United States; *3,* Peru; *4,* Europe, in general; *5,* Dolomite Alps, northern Italy; *6,* Austria; *7,* Sicily; *8,* Tunisia; *9,* Hungary; *10,* Turkey; *11,* Oman; *12,* Iran; *13,* Timor (base map adapted from Scotese, 2001).

like most 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, 2004c, 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. 56). For example, *?Deningeria* and *Sphinctonella* have been reported from

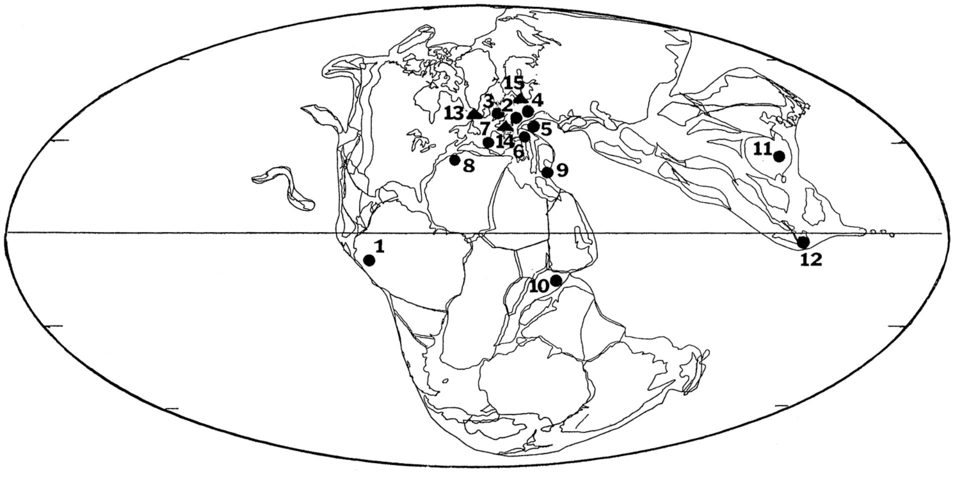


FIG. 56. Paleogeographic distribution of localities from where Jurassic sphinctozoan (*circles*) and inozoan (*triangles*) sponges have been reported. Sphinctozoans occur at localities: *1,* Peru; *2,* England, United Kingdom; *3,* Germany; *4,* Poland; *5,* former Czechoslovakia; *6,* Italy; *7,* Portugal; *8,* Morocco; *9,* Greece; *10,* China; *11,* Molluccas; *12,* Cambodia. Inozoans occur at localities: *13,* eastern Atlantic shelf, Canada; *14,* France; *15,* Germany (base map adapted from Scotese, 2001).

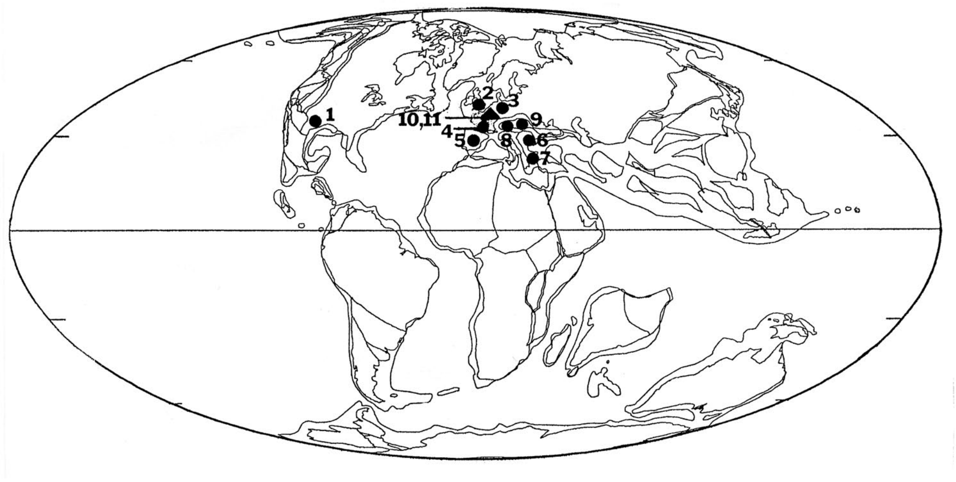


FIG. 57. Paleogeographic distribution of localities from where Cretaceous sphinctozoan (*circles*) and inozoans (*triangles*) sponges have been reported. Sphinctozoans occur at localities: *1,* Texas, United States; *2,* United Kingdom; *3,* Germany; *4,* France; *5,* Spain; *6,* Romania; *7,* Greece; *8,* Switzerland; *9,* Austria. Inozoans occur at localities: *10,* Germany; and *11,* France (base map adapted from Scotese, 2001).

Poland (HURCEWICZ, 1975); *Barroisia* and *Muellerithalamia* from Germany (QUENSTEDT, 1858; REITNER, 1987b), the latter two genera included in the Calcispongiae (FINKS & RIGBY, 2004c). *Barroisia, Sphaerocoelia,* and *Thalamopora* have been reported from the Czech Republic and Slovakia (ZEISE, 1897) and *Thalamopora* from Portugal (TERMIER, 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).

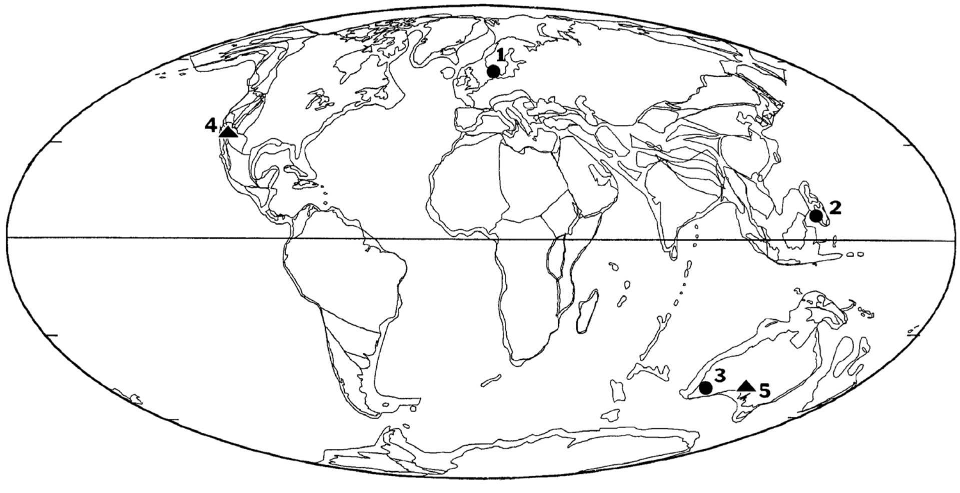


FIG. 58. Paleogeographic distribution of localities from where Paleogene–Neogene sphinctozoan and inozoan sponges have been reported. Sphinctozoan sponges (*circles*) have been reported from: *1,* Denmark (Paleocene); *2,* Philippine Islands, Marinduqueia (Eocene); *3,* southwestern Australia (Eocene); and inozoan sponges (*triangles*) have been reported from: *4,* Mexico (Eocene); and *5,* Australia (Miocene) (base map adapted from Scotese, 2001).

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; Boiko, 1990; Senowbari-Daryan & Hamedani, 1999).

Only a single Lower Jurassic sphinctozoan, *Stylothalamia,* has been reported from the American continents (Fig. 56) and that was from Peru (Hildebrandt, 1971; Senowbari-Daryan & Stanley, 1994). *Stylothalamia* has also been reported from European countries (Radoicic, 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, Sphaerocoelia, 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 that those of the Triassic (Fig. 56). Several calcareous sponges that are considered as inozoans, including *Endostoma, ?Elasmostoma, 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 Calcispongiae, 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 Shotori 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, 2004c, 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. 57). The most diverse faunas have been found in Spain (Schroeder & Willems, 1983; Schroeder, 1984; Reitner & Engeser, 1985; Reitner, 1987b), where five genera have been reported, followed by faunules from Germany (Steinmann, 1882; Dunikowsky, 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. 57). *Pharetrospongia strahani* Sollas, 1877, for example, was reported from England, as the figured specimen in Finks and Rigby (2004c, 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 demosponge inozoan reported to date from France, and it was not illustrated when proposed. *Trachytila* Welter, 1911, is likewise the only Cretaceous demosponge inozoan reported from Germany.

Sixteen genera that are included in the family Stellispongiidae de Laubenfels, 1955, class Calcispongiae, by Finks and Rigby (2004c, p. 739–747) are considered to have inozoan skeletal structure (see appended list below, p. 72). 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, 1860; Römer, 1864; Pomel, 1872; Zittel, 1878; Hinde, 1884, 1893; Zeise, 1897; Welter, 1911; Finks & Rigby, 2004c).

Cenozoic sphinctozoans are certainly geographically and taxonomically limited, for they have been described from only three localities (Fig. 58). Only two genera have been documented from a European country: *Verticillites* and *?Wienbergia* from Denmark (Ravn, 1899; Clausen, 1982). In addition to the European occurrences, 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, 1860, from the Eocene of Mexico (Finks & Rigby, 2004c, p. 741), and *Tretocalia* Hinde, 1900, from the Miocene of Australia (Pickett, 1983). Four inozoan genera of the class Calcispongiae, including the stellispongiinids *Trachysphecion* Pomel, 1872, and *Peronidella* Zittel in Hinde, 1893, and the holcospongiinids *Eudea* Lamouroux, 1821, and *Mammillopora* Bronn, 1825, have been reported from the Holocene (Finks & Rigby, 2004c, 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, 2001). 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, 2001; Weidlich, 2003). 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, 2003). 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; Termier, 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 Caucasia (see Boiko, Belyaeva, & Zhuravleva, 1991); from Thailand (Senowbari-Daryan & Ingavat-Helmcke, 1994); and from the former Yugoslavia (Flügel, Kochansky-Devide, & Ramovs, 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, herein p. 66), and chaetetids 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, & Ogorelec, 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 (Caucasia: Moissev, 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 Panthalassia 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).

Our present knowledge confirms the occurrence of approximately 16 sphinctozoan genera in Middle Triassic reefs and 55 genera in Upper Triassic reefs. 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, 1987b), Switzerland (Oppliger, 1929), France (Pomel, 1872), the former Yugoslavia (Radoicic, 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, 1987c), 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 up to today, 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 (2004c, 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 LEVI, 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 (2004, p. 691) is broadly constituted to incorporate many families and a wide scope of stratigraphic records but does not have priority over order Verticillitida TERMIER & TERMIER, 1977; note also the recent common usage of this ordinal subdivision by VACELET, 2002, p. 1097, and SENOWBARI-DARYAN and GARCÍA-BELLIDO, 2002a, p. 1521, and consequently this usage 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 present the name with the addition of an -iae termination, that is, as class Calcispongiae for the sponges with calcareous spicules.
5. In the FINKS and RIGBY (2004) classification, the two subclasses of the Calcispongiae (=Calcarea) are the Calcinea and Calcaronea, with the former including two orders (Murrayonida and Clathrinida), and the latter with five orders (Leucosolenida, Sycettida, Stellispongiida, Sphaerocoeliida, and Lithonida). This contrasts with the new classification of SENOBARI-DARYAN and RIGBY (herein), which only involves subclass Calcinea, with mainly sphinctozoan types grouped into two orders (Sphaerocoeliida 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 calcisponge 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)
      - *Amblysiphonelloides* 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 Intrasporeocoeliidae FAN & ZHANG, 1985
      - *Intrasporeocoelia* 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 in Termier, Termier, & Vachard, 1977
  - *Polyedra* Termier & Termier in Termier, Termier, & Vachard, 1977 (P)
- Family Aphrosalpingidae Myagkova, 1955b
  - Subfamily Fistulospongiinae Termier & Termier in Termier, Termier, & Vachard, 1977
    - ?*Fistulosponginina* Termier & Termier in Termier, Termier, & Vachard, 1977 (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 Sebargasiidae de Laubenfels, 1955
  - ?*Sebargasia* Steinmann, 1882 (Ca)
  - *Amblysiphonella* 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)
Pseudoguadalupia TERMIER & TERMIER, 1977 (P)
Stylocoelia WU, 1991 (P)
Vesicotubularia 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, 1977
Family Solenolmiidae ENGESER, 1986
Subfamily Solenolmiinae ENGESER, 1986
Solenolmia POMEL, 1872 (P–T)
?*Adrianella* PARONA, 1933 (P)
Ambithalamia SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994 (P)
?*Cryptocoeliopsis* 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, in *Treatise Online,* Part E, Revised, Vol. 4, Chapter 18A, p. 73
Preverticillites PARONA, 1933 (P)
Prosiphonella DIECI, ANTONACCI, & ZARDINI, 1968 (T)
Sahraja MOISSEV, 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)
Uvothalamia 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)
Neoguadalupia 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 in Termier, Termier, & Vachard, 1977 (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 De France, 1829 (J–Ce)
Boikothalamia Reitner & Engeser, 1985 (J)
Marinduqueia Yabe & Sugiyama, 1939 (Ce)
?*Menathalamia* Reitner & Engeser, 1985 (Cr)
Murguiathalamia Reitner & Engeser, 1985 (Cr)
Stylothalamia Ott, 1967 (P–Cr)
Vaceletia Pickett, 1982 (Cr–R)
Vascothalamia Reitner & Engeser, 1985 (Cr)
?*Wienbergia* Clausen, 1982 (Ce)
Subfamily Polytholosiinae Seilacher, 1962
Polytholosia 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
  - *Platysphaerocoelia* 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, 1987a (T)
    - *Jablonskyia* Senowbari-Daryan, 1990 (T)
    - *Leinia* Senowbari-Daryan, 1990 (T)
    - *Loczia* Vinassa De Regny, 1901 (T)
    - *Montanaroa* Russo, 1981 (T)
    - *Pamirocoelia* Boiko in Boiko, Belyaeva, & Zhuravleva, 1991 (T)
    - *Paravesicocaulis* Kovács, 1978a (T)
    - *Pisothalamia* Senowbari-Daryan & Rigby, 1988 (P)
    - *Pseudouvanella* 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, 2004c (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 Calcispongiae de Blainville, 1830
  - 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* Römer, 1840 (J–Cr)
        - *Tremacystia* Hinde, 1884 (Cr)
    - Order Lithonida Döderlein, 1892
      - Family Minchinelliidae Dendy & Row, 1913
        - *Muellerithalamia* Reitner, 1987b (J)
- Class and Order Uncertain
  - *Pseudodictyocoelia* Boiko, 1984 (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 Octactinella 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 inozoans 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, 1849, a chaetetid as per ENGESER & TAYLOR, 1989, and classified by WEST & WOOD in *Treatise Online*, Part E, Revised, Chapter 4B, as an agelasid demosponge
    Ossiminus FINKS, 1995 (P)
    Stratispongia FINKS, 1995 (P)
   Family Virgolidae TERMIER & TERMIER in TERMIER, TERMIER, & VACHARD, 1977
    Subfamily Virgolinae TERMIER & TERMIER in TERMIER, 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 & WOOD, in *Treatise Online*, Part E, Revised, Chapter 4B, as an agelasid demosponge
    Reticulocoelia CUIF, 1973 (T)
    Sclerocoelia CUIF, 1974a (T); described as a chaetetid as per DIECI & others, 1977, and WEST & WOOD, in *Treatise Online*, Part E, Revised, Chapter 4B, classified as an agelasid demosponge
    Subfamily Preeudinae RIGBY & SENOWBARI-DARYAN, 1996a
    Preeudea TERMIER & TERMIER in TERMIER, 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, 1860 (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, 2004c
  Leiofungia DE FROMENTEL 1860 (T)
  Aulacopagia POMEL, 1872 (J)
  Elasmopagia POMEL, 1872 (Cr)
  Grossotubenella RIGBY, FAN, & ZHANG, 1989b (P)
  Leiospongia D'ORBIGNY, 1849 (T); described as a chaetetid, as per ENGESER & TAYLOR, 1989, and classified by WEST & WOOD, in *Treatise Online*, Part E, Revised, Chapter 4B, as an agelasid demosponge
  Loenopagia POMEL, 1872 (T)
  Radicanalospongia RIGBY, FAN, & ZHANG, 1989b (P)
Family Auriculospongiidae TERMIER & TERMIER, 1977
Subfamily Auriculospongiinae TERMIER & TERMIER, 1977
  Auriculospongia TERMIER & TERMIER, 1974 (P)
  Anguispongia SENOWBARI-DARYAN, 2005b (T)
  Cavusonella RIGBY, FAN, & ZHANG, 1989b (P)
  Molengraaffia VINASSA DE REGNY, 1915 (T)
  Radiotrabeculopora RIGBY, FAN, & ZHANG, 1989b (P); described as belonging to the family Disjectoporidae (order ?Inozoa) by STEARN (2010a) in *Treatise Online*, Part E, Revised, Chapter 6, p. 9
Subfamily Daharelliinae RIGBY & SENOWBARI-DARYAN, 1996a
  Daharella RIGBY & SENOWBARI-DARYAN, 1996a (P)
  Aliabadia SENOWBARI-DARYAN, 2005b (T)
Subfamily Gigantospongiinae RIGBY & SENOWBARI-DARYAN, 1996a
  Gigantospongia 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, 2004c
Subfamily Preperonidellinae Finks & Rigby, 2004c
Preperonidella Finks & Rigby, 2004c (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, 1977
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, 2004c
Fissispongia King, 1938 (D–Ca)
Family Maeandrostiidae Finks, 1971
Maeandrostia Girty, 1908b (Ca–T)
Stylopegma King, 1943 (P)
Class Calcispongiae de Blainville, 1830
Subclass Calcinea Bidder, 1898
Order Stellispongiida Finks & Rigby, 2004c
Family Stellispongiidae de Laubenfels, 1955
Subfamily Stellispongiinae de Laubenfels, 1955
Stellispongia d'Orbigny, 1849 (?J, Cr)
Amorphospongia d'Orbigny, 1849 (J)
Blastinoidea Richardson & Thacker, 1920 (J)
Conocoelia Zittel, 1878 (Cr)
Diaplectia Hinde, 1884 (J)
Elasmoierea de Fromentel, 1860 (Cr)
?*Elasmostoma* de Fromentel, 1860 (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, 2004c
Holcospongia Hinde, 1893 (J)
Actinospongia d'Orbigny, 1849 (J)
Astrospongia Étallon, 1859 (J)
Calicia Dullo & Lein, 1980 (T)
Enaulofungia de Fromentel, 1860 (?T, J, ?Cr)
Eudea Lamouroux, 1821 (T–J, R)
Mammillopora Bronn, 1825 (J, ?Cr, R)
Oculospongia de Fromentel, 1860 (P, ?T, J–Cr)
Tremospongia d'Orbigny, 1849 (Cr)
Tretocalia Hinde, 1900 (Ce)
Class and Order Uncertain
Bortepesia Boiko, 1984 (T)
Cornuaspongia Senowbari-Daryan, 1994b (T–J)
?*Corynospongia* Deng, 1990 (P)
Lamellispongia Boiko, 1984 (T)
?*Trammeria* Senowbari-Daryan, 1994b (T–J)

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APPENDIX

After this manuscript was completed, several important papers were published dealing with the hypercalcified sponges. Some are listed below.

Finks, R. M. 2010. The sponge family Guadalupiidae in the Texas Permian. Journal of Paleontology 84(5):821–847.

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