HYPERCALCIFIED SPONGES

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INTRODUCTION

Many sponges belonging to the subphylum Gelatinosa (i.e., the classes Demospongea and Calcarea) secrete a massive skeleton of calcium carbonate in addition to any spicules, siliceous or calcareous, that they may produce (see summaries by VACELET, 1991; WOOD, 1990; REITNER, 1991; SENOWBARI-DARYAN, 1991; MASTANDREA & RUSSO, 1995). Most of these have been assigned to special groups based on the gross morphology of this nonspicular skeleton, such as the Sphinctozoa, Archaeocyatha, Inozoa, Stromatoporoidea, Chaetetida, and possibly Favositida (=Thallocorallia). The calcium carbonate may be either aragonite or calcite, of various microstructures, and secreted either intracellularly or extracellularly. (Intracellular secretion, corresponding to their mode of siliceous spicule production, may be a synapomorphy of the class Demospongea, although extracellular production by various methods almost always accompanies it.) The term basal skeleton (HARTMAN & GOREAU, 1975, p. 3) has been applied generally to this nonspicular calcium carbonate framework, although the earlier term sclerosome (RAUFF, 1913) is available for the material itself, and in some instances (e.g., Sphinctozoa, and probably Archaeocyatha) the skeleton is not confined to the base of the living tissue. The term hypercalcified (TERMIER & TERMIER, 1977a, 1977b) is convenient to use for all sponges that secrete nonspicular calcium carbonate and can include forms that cement spicules together with a calcium-carbonate coating without producing a separate basal skeleton, as in most Heteractinida as well as in many Inozoa of the class Calcarea. It has been suggested (CUIF & GAUTRET, 1991; WOOD, 1990) that ocean chemistry drives the production and mineralogy of the nonspicular carbonate and that symbiotic cyanobacteria may induce or support its precipitation (VACELET, 1983). Nevertheless, the rigid skeleton is adaptive to high wave-energy environments, and the hypercalcified sponges have been significant members of reef communities throughout Phanerozoic time. They have been major reef builders when not outcompeted by other sessile benthos with massive skeletons (WOOD, 1991).

SECRETION, MINERALOGY, AND MICROSTRUCTURE

The massive calcium carbonate is secreted by several processes, which often characterize particular taxonomic groups. Some groups use more than one process. The mineralogy may also characterize groups, some secreting aragonite, others calcite with variable amounts of magnesium substituting for calcium. It was formerly thought that aragonite and calcite were secreted alternatively or together in the same species or even in the same individual, but recent studies indicate that this is not so (MASTANDREA & RUSSO, 1995). The microstructure of the secreted material also seems to be characteristic of particular groups, inasmuch as it results from the process of secretion. The secretory process is often related to the mode of secretion of the spicular skeleton. For example, demosponge spicules are secreted uniformly intracellularly, and this is also the initial locus of secretion of one type of hypercalcified skeleton, namely that of spherulitic aragonite, although the spherules, following their extrusion from the parent cell, may be enlarged by extracellular secretion. In the Calcarea, on the other hand, both spicules and the hypercalcified skeleton are secreted extracellularly by multiple cells, and both are made of magnesian calcite.

The principal microstructures and mineralogies recognized (see especially

WOOD, 1990; CUIF & GAUTRET, 1991; MASTANDREA & RUSSO, 1995) are as follows.

Spherulitic Aragonite

Also called compound spherulitic, this is characteristic of the living demosponge *Astrosclera* and its relatives, which have stromatoporoid morphology, as well as of a large number of Permo-Triassic genera of inozoan, sphinctozoan, and chaetetid morphology. The spherulites are first produced intracellularly then transported to their skeletal location and simultaneously enlarged by extracellular secretion. Most of the living astrosclerids have acanthostyle spicules, which might place them with the ceractinomorph order Poecilosclerida (SOEST, 1991) except that the spines are verticillate as in the living *Agelas,* with which VACELET (1983, 1985) and WOOD (1990) placed them, as the order Agelasida, which is presumably also ceractinomorph, although WIEDENMAYER (1994) suggested a tetractinomorph affinity.

Penicillate Aragonite

Also called clinogonal aragonite, elongate spherulitic, or water-jet structure, this is characteristic of the living demosponge *Ceratoporella,* of chaetetid morphology, which is assigned to the order Agelasida for the same reasons as *Astrosclera.* The aragonite is secreted extracellularly by pinacoderm cells. This morphologic type intergrades with the spherulitic type, inasmuch as spherulites are often extended asymmetrically by extracellular secretion so as to become penicillate. Many Triassic genera of chaetetid as well as inozoan morphology have this structure.

Irregular Aragonite

Also called microgranular aragonite, this is found in the living sphinctozoan demosponge *Vaceletia,* a ceractinomorph that cannot be assigned to any order owing to its absence of spicules, as well as a number of Triassic genera of sphinctozoan, inozoan, and stromatoporoid morphologies. The irregularly arranged aragonite needles are secreted over a collagen fiber framework and may be grouped in membrane-bounded, mineralization units with a center of organic matter (GAUTRET, 1985; MASTANDREA & RUSSO, 1995).

Homogeneous-Granular Mg Calcite

Also called microgranular Mg calcite, this is not known in any living species but is found in a number of Triassic genera of sphinctozoan and inozoan morphology, the best known of which is *Cassianothalamia,* assigned by REITNER (1987a, 1991) to the tetractinomorph demosponge order Hadromerida on the basis of the presence of tylostyles, spirasters, and euasters. The Cambrian Archaeocyatha also have this microstructure (KRUSE & DEBRENNE, 1989). Whether this indicates a relationship of the Archaeocyatha to the Tetractinomorpha and Hadromerida must, for the present, remain an open question.

Lamellar Mg Calcite

Characteristic of the living *Acanthochaetetes,* also assigned to the order Hadromerida on the basis of the presence of tylostyles and spirasters, this microstructure is formed of microcrystals of magnesian calcite aligned in one plane, secreted extracellularly over a matrix of collagen fibers. It is found in a number of euaster-bearing Cretaceous to recent genera of chaetetid morphology as well as a Cretaceous genus *Calcichondrilla* REITNER, 1991, of encrusting, nonchaetetid morphology.

Penicillate Mg Calcite

Also called clinogonal calcite or fascicular fibrous calcite, this structure is found in the Mississippian and later genus *Chaetetes,* as well as in other Paleozoic and Mesozoic genera of chaetetid morphology, such as *Stromatoaxinella* WOOD & REITNER, 1988. It also includes the living chaetetid genus *Merlia.* The presence of subtylostyles in most of these genera supports an assignment to the ceractinomorph demosponge order Poecilosclerida (SOEST, 1991), also favored by the resemblance of *Merlia* clavidiscs to the diancistras of some poecilosclerids. Vacelet and Uriz (1991), however, favored an assignment of *Merlia* to the tylostyle-bearing tetractinomorph order Hadromerida on histologic grounds, questioning the relation of clavidiscs to diancistras.

Spherulitic Mg Calcite

The only demosponge that clearly has this microstructure is the Cretaceous genus *Euzkadiella* Reitner, 1987c, of stromatoporoid or quasi-inozoan morphology. It possesses subtylostyles in plumose arrangement, rather similar to many of the chaetetid types with penicillate calcite discussed above. The spicules relate *Euzkadiella* to the Poecilosclerida (Soest, 1991), but Reitner (1987c) assigned it to the related order Haplosclerida on the basis of spicule arrangement. The Pennsylvanian stromatoporoid *Newellia,* which likewise has plumose bundles of subtylostyles, was considered to be related to *Euzkadiella* by Wood, Reitner, and West (1989). The microstructure of *Newellia,* however, is microgranular calcite (Wood, Reitner, & West, 1989), at least as preserved. If spherulitic calcite is as related to penicillate calcite as the corresponding aragonitic microstructures are, *Euzkadiella* and perhaps *Newellia* may be related to *Chaetetes. Petrobiona* Vacelet & Levi, 1958, a lithonid calcaronean genus of the class Calcarea, also has a penicillate to spherulitic calcite basal skeleton but is associated with typical calcarean spicules. *Murrayona* Kirkpatrick, 1910a, a murrayonid calcinean genus of Calcarea, also has calcite spherulites associated with calcarean spicules.

Fibrous Mg Calcite

Also called orthogonal Mg calcite, this is characterized by fibers of calcite perpendicular to the surface of the skeletal elements. It is found in several groups of the subclass Calcaronea of the class Calcarea, largely as interspicular cement: in the minchinellids, in the typically inozoan Mesozoic stellispongiids, in the sphaerocoeliid sphinctozoan *Barroisia* (but not in *Tremacystia,* which is granular [Reid, 1968d], perhaps diagenetically), and probably in the class Heteractinida.

There may be a large-scale taxonomic significance to basal skeleton mineralogy that is somewhat obscured by current taxonomic disagreements. Aragonite is associated with ceractinomorph demosponges (Types 1–3), assuming the Agelasida to be ceractinomorph, as Vacelet (1983, 1985) and Wood (1990) maintain. Magnesian calcite, on the other hand, is associated with a tetractinomorph demosponge group in two (Types 4 and 5) and possibly three (Type 6) instances, as well as with the class Calcarea (Types 7 and 8). This suggests that *Merlia* (Type 6) is in fact a tetractinomorph as Vacelet and Uriz (1991) maintained and that *Euzkadiella* (Type 7) is also a tetractinomorph. It may not be without significance that cladistic analysis (in which basal skeleton mineralogy is not one of the characters) shows the Tetractinomorpha to be a sister-group of the Calcarea or Homoscleropora (Soest, 1991). This line of reasoning supports the assignment of the Agelasida to the Ceractinomorpha.

MORPHOLOGIC TYPES

As seen from the foregoing discussion, the gross morphology of the basal skeleton is not correlated closely with the microstructure. The microstructure appears to have some taxonomic value at the class and order levels. That is, it is often correlated with spicule form and cytologic or embryologic characters that have been used to establish some of the commonly accepted class-order taxa. The gross morphology, however, may have some significance at the family level. It seems reasonable that major patterns of growth should be genetically controlled and indicate common ancestry. The major morphologic types of hypercalcified sponges are as follows.

Sphinctozoan

The basal skeleton (in this instance not really basal) forms a perforated cortex around the soft tissue. The soft tissue grows to a characteristic size and shape and then secretes a calcareous envelope about itself, forming a so-called chamber. After several further chambers are formed in successive bouts of growth, the soft tissue gradually withdraws from the earlier chambers, often forming vesicles to seal off the abandoned spaces. These vesicles, together with pillars, fibers (trabeculae), and tubes that seem to have been formed within the living soft tissue, are referred to collectively as filling tissue. At least some of the tubes and intertrabecular spaces appear to have surrounded major canals in the soft parts. The filling tissue is often indistinguishable from inozoan structure or from the pillars of stromatoporoid structure.

Inozoan

This morphologic type is characterized by a basal skeleton of fibrous (trabecular) or anastomosing, tubular form. In many instances the fibers (trabeculae) appear to have been bundles of spicules cemented together and coated by the calcium carbonate. In instances where there are no spicules or only a few scattered, often partly protruding ones, it is likely that the basal skeleton invested spongin fibers previously laid down. The trabeculae usually have a characteristic pattern, often radiating upwardly and outwardly with cross connections between them, as do the spongin fibers and spicule bundles of many nonhypercalcified sponges. They also may anastomose irregularly. A perforated cortex is developed often, and major canal systems may interrupt the trabecular net. The soft tissue of the sponge appears to have occupied the intertrabecular spaces to a significant depth below the upper surface, and the presence of epizoans and inhalant pores well down on the sides of the sponge imply that some of them stood well above the sea floor.

Stromatoporoid

This morphology consists of narrow, closely spaced pillars perpendicular to the upper surface of the sponge, with irregular cross connections. Regular enlargements of the cross connections at more or less the same level occur at closely spaced intervals parallel to the upper surface (latilaminae). Major canal systems, usually exhalant systems about an oscule (astrorhizae), may interrupt the pillars and latilaminae. An imperforate epitheca bearing concentric growth lines may coat the under surface of the entire skeleton. The living tissue of the sponge occupied probably primarily the spaces between the pillars above the last-formed latilamina. The pillars may contain bundles of spicules as in inozoan types, and indeed the only difference between inozoans and stromatoporoids is the larger size and wider spacing of the trabeculae or pillars in inozoans, their less perpendicular relation to the outer surface, and the absence of latilaminae. Inozoan trabeculae outline usually more elaborate and deeper canal systems, implying a greater depth of living tissue within the skeleton as well as a possible absence of periodic growth. Combinations of the stromatoporoid and sphinctozoan type of skeleton are known: the family Guadalupiidae is characterized by a layer of sphinctozoan morphology (the thalamidarium) coated on the exhalant side by a layer of stromatoporoid morphology complete with astrorhizae (the trabecularium). It is possible that the supposed instance of a sphinctozoan coated by a chaetetid (*Fistulispongina* TERMIER & TERMIER, 1977a) is in fact a single organism as originally proposed.

Chaetetid

This morphology consists of spaces of meandriform to polygonal cross section (calicles) outlined by relatively thin walls of calcium carbonate perpendicular to the outer surface of the sponge that may incorporate spicules. Grooves corresponding to exhalant systems about an oscule (astrorhizae) may indent the outer edges of the calicle walls. The walls may be perforated by pores (mural pores) or bear spines projecting into the lumen of the calicle. In most genera horizontal cross partitions (tabulae) occur at intervals in the calicles. (In the ceratoporellids the calicles may also be filled in below with solid skeletal material.) A thin, imperforate epitheca bearing concentric growth lines may coat the entire under surface of the sponge skeleton, being added to at the point where the base meets the upper layer of living tissue. It is apparent that this morphology corresponds not only to that of *Chaetete,* which has been accepted as a sponge because of the presence of astrorhizae and incorporated spicules (D. I. Gray, 1980), but also to that of the favositids, which have so far yielded neither astrorhizae nor undisputed spicules, but which may also be sponges (Kirkpatrick, 1912; Hartman & Goreau, 1975; Kazmierczak, 1984, 1991). Living genera of chaetetid morphology include *Merlia* Kirkpatrick, 1908; *Ceratoporella* Hickson, 1911; and *Acanthochaetetes* Fischer, 1970. In the living forms the soft tissue extends across the entire upper surface above the basal skeleton and fills also each calicle down to the uppermost tabula (or to the solid backfill in some ceratoporellids). In addition, each tabula may have a central pore (in *Merlia*) or be initially incomplete (in *Acanthochaetetes*), and the spaces beneath the upper few tabulae may be filled with storage cells that can regenerate the sponge if the surface tissue is destroyed (Vacelet, 1991).

Other Morphologies

The class Calcarea includes several additional morphologic types confined to one or a few genera each that differ to varying degrees from the foregoing. The living *Petrobiona* Vacelet & Levi, 1958, has a massive basal skeleton with a deeply and irregularly pitted surface. The pits are analogous to the calicles of the chaetetid morphology, and the sponge tissue occupies the pits as well as forming a coating over the entire upper surface. Thin, branching canals, ending blindly, extend into the basal skeleton from the lower part of each pit. They contain storage cells and are analogous to the subtabular spaces of chaetetids (Vacelet, 1991).

Several genera have a cortex of overlapping scales or flakes derived from the enlargement of triradiates. Except for the osculum and a limited area of inhalant pores, the cortex is imperforate as in many *Sphinctozoa.* In the living calcinean *Murrayona* Kirkpatrick, 1910a such a cortex is underlain by an *inozoan* trabecular skeleton built of spherulitic to penicillate calcite. Between the principal trabecular basal skeleton and the cortex are unfused spicules of several calcarean types including bundles of tuning fork spicules. In the related *Paramurrayona* Vacelet, 1967a, the inozoan skeleton is completely absent, but the cortical skeleton has an additional layer of irregular, imbricated flakes beneath the outer layer of scales. Loose, calcarean spicules are also present. In the living calcaronean *Lepidoleucon* Vacelet, 1967a the cortex of scales is the only rigid skeleton, the flesh beneath containing only loose spicules of calcarean types. Each of these genera resembles a single chamber of a sphinctozoan, the first having inozoan filling tissue.

In the Jurassic to Holocene calcaronean family Minchinellidae the basal skeleton consists of layers of tetraradiates with the distal ray uniformly directed upwardly, the three proximal rays curving downwardly with clasping terminations, and the whole cemented together with fibrous calcite. Loose calcarean spicules of several types occur in the flesh above the basal skeleton. Except for the regularly layered arrangement and the absence of smaller, coating spicules, this type of basal skeleton is not too different from that of the Jurassic and Cretaceous inozoa with calcarean spicules here assigned to the family Stellispongiidae. It is even closer geometrically to the siliceous, lithistid, dicranoclone skeleton of the Paleozoic demosponge family Hindiidae, presumably a homeomorph inasmuch as (apart from the mineralogic difference of the skeletal material) the megarhizoclones found in some genera (e.g., *Scheiella* Finks, 1971b) are not known in any Calcarea.

In the *Heteractinida,* the principal skeleton of octactines (to which are added triactines, tetractines, and polyactines in the Wewokellidae) is almost always fused together by calcite cement. It is not certain whether this is original or diagenetic. Two Cambrian genera, however, *Jawonya* Kruse, 1987, and *Wagima* KRUSE, 1987, have a cortical, partly imperforate, sphinctozoan type of calcareous basal skeleton that incorporates silicified (or possibly siliceous) octactine or polyactine spicules (or possibly hexactines with extra rays) in what resembles a single sphinctozoan chamber that is certainly original and not diagenetic (KRUSE, 1990).

The archaeocyathan type of skeleton, which will not be discussed further herein, resembles the sphinctozoan type (with some differences in filling tissue) but lacks the repeated units of growth.

TAXONOMY

Living species of hypercalcified sponges have demonstrated that similar morphologies of the basal skeleton may occur in different classes and orders (WOOD, 1991). The same may be said of mineralogy and microstructure, although these have somewhat greater fidelity to taxa established originally by other means. Cladistic analysis has confirmed that the presence of specific spicule types provides useful synapomorphies for demosponge classification at the ordinal level (SOEST, 1991) and subordinal level (HAJDU, SOEST, & HOOPER, 1994), and it is fortunate that spicules are occasionally preserved in the fossils. A consensus is gradually emerging based on a combination of these characteristics together with data on living forms (VACELET, 1985, 1991; WOOD & REITNER, 1988; BOROJEVIC, BOURY-ESNAULT, & VACELET, 1990; DEBRENNE & WOOD, 1990; WOOD, 1990, 1991; CUIF & GAUTRET, 1991; GAUTRET, VACELET, & CUIF, 1991; REITNER, 1991; SENOWBARI-DARYAN, 1991; SOEST, 1991; DEBRENNE & ZHURAVLEVA, 1994; HAJDU, SOEST, & HOOPER, 1994; STEARN & PICKETT, 1994; WIEDENMAYER, 1994; MASTANDREA & RUSSO, 1995). The classification adopted here is an outgrowth of this consensus.

Because the morphological types called stromatoporoid, chaetetid, and archaeocyathid will be treated in separate volumes of the *Treatise,* those hypercalcified sponges dealt with here are confined to the morphologic types called inozoan and sphinctozoan. The entire class Heteractinida might be regarded as hypercalcified, inasmuch as primary cementation of spicules to one another by calcium carbonate occurs in most genera, but those sponges are treated in a separate section in this volume.

Those assigned to the class Demospongea include the orders Agelasida (both inozoan and sphinctozoan types), Vaceletida (sphinctozoan and inozoan types), Hadromerida (inozoan and sphinctozoan types), and an inozoan group (family Pharetrospongiidae) of uncertain ordinal position. The Agelasida also include genera of chaetetid (e.g., *Ceratoporella* HICKSON, 1911) and stromatoporoid (e.g., *Astrosclera* LISTER, 1900) morphologies not dealt with in this volume. Likewise, the Vaceletida include stromatoporoid types (e.g., *Burgundia*), and the Hadromerida include chaetetid types (e.g., *Acanthochaetetes* HARTMAN & GOREAU, 1975), also dealt with elsewhere.

Those assigned to the class Calcarea include the orders Murrayonida (inozoan type with quasisphinctozoan elements), Stellispongiida (inozoan type), Sphaerocoeliida (sphinctozoan type), and Lithonida (inozoan type).

HYPERCALCIFIED DEMOSPONGEA

ORDER AGELASIDA VERRILL, 1907

Assignment to this group is based on verticillate acanthostyle spicules when present and a basal skeleton of spherulitic or penicillate (clinogonal) aragonite. Among living species verticillate acanthostyles are associated with both spherulitic microstructure (e.g., *Astrosclera*), which is initially produced intracellularly but enlarged extracellularly, and penicillate microstructure (e.g., *Ceratoporella*), which is produced extracellularly. Spherulitic skeletons may include later-formed penicillate parts. Although most of the fossil species lack the spicules and are assigned on the basis of skeletal mineralogy and microstructure only, their generally consistent association when both are present supports the assignment (WOOD, 1990;

MASTANDREA & RUSSO, 1995). Some fossil species contain smooth monaxons that are calcite pseudomorphs (presumably) after the original silica (e.g., *Thaumastocoelia cassiana* STEINMANN, 1882, see MASTANDREA & RUSSO, 1995, fig. 4.6; and *Sestrostomella robusta* ZITTEL, 1878b, see WENDT, 1974, fig. 6), and the loss of spines may be diagenetic. On the other hand, the living *Hispidopetra* HARTMAN, 1969, has only smooth styles associated with a spherulitic aragonite basal skeleton of inozoan type (HARTMAN, 1969). The living *Calcifibrospongia* HARTMAN, 1979, of stromatoporoid morphology, has smooth strongyles, associated with a spherulitic, aragonite, basal skeleton. It is possible, therefore, that not all hypercalcified sponges with a spherulitic, aragonite, basal skeleton are agelasiids. There is no other basis for assigning the fossils to a different order, however. WIEDENMAYER (1994, p. 66) considered the styles of *Hispidopetra* to have lost their spines and assumed a relationship to the astrosclerid or ceratoporellid group. Indeed, although smooth, they do have the same long, slender form of typical agelasid acanthostyles; so do the strongyles of *Calcifibrospongia.* The vertical trabeculae of *Hispidopetra,* bristling with plumosely arranged, smooth styles, are almost identical in diameter and spacing to those of the Permian inozoan *Catenispongia* FINKS, 1995, which likewise has spherulitic microstructure and may have echinating or plumose, smooth monaxons; the vertical trabeculae of *Hispidopetra,* although long (7 mm) for a living hypercalcified sponge, are considerably shorter than those of *Catenispongia,* and the encrusting habit of *Hispidopetra* is quite different from the large, fungiform, osculebearing *Catenispongia.* Nevertheless, the similarities make a relationship plausible. The Catenispongiidae, as well as other families with smooth monaxons embedded in a spherulitic, basal skeleton, may belong to another order than the Agelasida. One possibility, the Poecilosclerida, is characterized by subtylostyles (SOEST, 1991), but the styles of *Hispidopetra* are not even slightly tylote. The monaxons, perhaps styles, of *Thaumastocoelia, Sestrostomella,* and *Catenispongia* (if this last genus has true spicules) are less slender and more stubby than either the styles of *Hispidopetra* or the acanthostyles of typical agelasids.

Apart from the sclerosponge genera included in the Astroscleridae and Ceratoporellidae, the living species of the Agelasida are confined to the single genus *Agelas,* which is difficult to place among the demosponges (SOEST, 1991). Its only spicules are the slender, verticillate acanthostyles echinating the spongin fibers, whose presence in *Astrosclera, Ceratoporella, Goreauiella,* and *Stromatospongia,* in a similar position relative to the calcareous skeletal elements, are the principal basis for associating them with *Agelas,* the similar *Hispidopetra* being also included despite the smoothness of its styles. VACELET (1985, p. 8) was apparently the first to assign them definitely to the family Agelasiidae (with a query in VACELET, 1983) on the basis of spicule and soft tissue affinities. HARTMAN and GOREAU (1970, p. 220), on the other hand, pointed out that the spines are recurved toward the head of the style in the sclerosponges and are not so in *Agelas.*

Nonverticillate acanthostyles are a relatively neat synapomorphy for the order Poecilosclerida, in particular for the suborders Myxillina and Microcionina (HAJDU, SOEST, & HOOPER, 1994). WIEDENMAYER (1994, p. 66), on the other hand, has stressed the resemblance of the verticillate styles of the sclerosponges to the discasters of *Latrunculia* and the verticillate sanidasters of *Sceptrintus,* which two genera he would place in the family Latrunculiidae, near the families Agelasidae and Astroscleridae (=Ceratoporellidae), in the order Hadromerida (WIEDENMAYER, 1994, p. 64, 69, 70, 119). Because of the large number of fossil hypercalcified sponges that have basal skeletons of originally intracellularly produced spherulites of aragonite, similar to those of the Astroscleridae, as well as the uncertainties of the placement of *Agelas,* it seems appropriate to keep them all in a separate order Agelasida as has been done by VACELET, Wood, Reitner, and other investigators. The Agelasida are assigned here to the subclass Ceractinomorpha following the opinions of Vacelet (1985) and Soest (1991).

The evidence for intracellular production of the spherulites is the presence of a core to each spherulite that is delimited by a physical break and that may be mineralogically different from the outer layers of the spherulite, often replaced by iron oxide or sulfide, giving it a dark-colored appearance (Cuif & Gautret, 1991). The later extracellularly added layers of aragonite may render the spherulite asymmetrical, or the skeleton may be exclusively produced extracellularly as in some or all living Ceratoporellidae. The asymmetrical spherulites (flaky spherulites of Finks, 1983a, 1990) are more strongly developed in the secondary filling of original, tissue-filled spaces, and seem characteristic of particular families. Other families (e.g., Ceratoporellidae, Pharetrospongiidae) are characterized by largely, or wholly, penicillate microstructure. In general, however, the families are also defined by common features of gross morphology.

ORDER VACELETIDA FINKS & RIGBY, HEREIN

This group is defined by the characteristic microstructure of the basal skeleton, namely, irregular-aragonitic (microgranular aragonitic). It is secreted extracellularly over a collagen matrix (Vacelet, 1979; Wood, 1990). The living *Vaceletia* Pickett, 1982, of sphinctozoan morphology, lacks spicules, as do the fossil genera that have the same microstructure. Its histology and embryology place it in the subclass Ceractinomorpha (Vacelet, 1983, 1985) to which the order Vaceletida is here assigned. The families recognized here are defined by gross morphology.

ORDER HADROMERIDA TOPSENT, 1898

The hadromerids belong to the subclass Tetractinomorpha and are characterized by the presence of tylostyles but no tetraxons and usually some form of astrose microsclere (Soest, 1991). The hypercalcified species have a basal skeleton of calcite; in those of chaetetid morphology, such as the recent *Acanthochaetetes* Hartman & Goreau, 1975, it is of lamellar microstructure (Wood, 1990) or alternatively of penicillate microstructure if *Chaetetes* Fischer de Waldheim, 1829, and its relatives, or *Merlia* Kirkpatrick, 1908, are hadromerids; in those of sphinctozoan and inozoan morphology it is of homogeneous-granular, magnesian-calcite microstructure (Mastandrea & Russo, 1995). The families recognized here are defined by gross morphology.

HYPERCALCIFIED CALCAREA

ORDER MURRAYONIDA VACELET, 1981

This is the only certain order of hypercalcified sponges in the subclass Calcinea (Borojevic, Boury-Esnault, & Vacelet, 1990). As in all members of the class Calcarea, the mineralogy of all skeletal elements is calcite. In the family Murrayonidae there is an inozoan-like, trabecular, aspicular, basal skeleton, plus a cortical skeleton of overlapping scales derived developmentally from triradiate spicules. Isolated spicules of particular form also occur around the osculum, on the inhalant surface, and beneath the cortex. In the family Paramurrayonidae there is a similar cortex of scales, interior bundles of tuning-fork spicules but no aspicular basal skeleton. In the family Lelapiellidae there is a cortex of enlarged, anapodal triradiates (tripods), plus internal bundles of straight biradiates, plus a basal layer of curved biradiates.

ORDER STELLISPONGIIDA FINKS & RIGBY, HEREIN

This Mesozoic group includes the typical inozoa with spicules characteristic of the class Calcarea. There is considerable doubt concerning their assignment to one or the other of the two well-established subclasses of the Calcarea (Calcinea and Calcaronea), which are based on characters unobservable in fossils, namely, the position of the choanocyte nucleus and the type of larva. The presence of regular triactines (i.e., with rays of equal length and angle) is almost distinctive of the subclass Calcinea (VACELET, 1991, p. 255), but the same author (VACELET, 1991, p. 253) allowed some nonsagittal (i.e., regular) triradiates into the subclass Calcaronea. The Stellispongiida frequently have both types of spicule in the same species. They have a principal skeleton composed of fibers built around one or more triradiates or tetraradiates (including tuning-fork spicules) cemented side by side with calcite that at least in some instances has a radial structure (CUIF & others, 1979) and may be coated by a layer of filiform spicules (HINDE, 1893b). Because the living Calcaronea belonging to the order Lithonida often have spicules cemented together with calcite, the Stellispongiida are here placed tentatively in the subclass Calcaronea. The two Mesozoic families (Stellispongiidae and Endostomatidae) are separated according to whether the spicule bundles consist of a larger spicule or spicules coated by smaller ones (Stellispongiidae) or of several subequal spicules (Endostomatidae). The recent family Lelapiidae is also included because it too has spicule bundles (including tuning-fork spicules), although they are not cemented; this last family is clearly calcaronean. The presence of spicule bundles and the tuning-fork spicules commonly found within them is not confined to the Calcaronea. They are also present in the living order Murrayonida, which is clearly calcinean (VACELET, 1983, 1985).

ORDER SPHAEROCOELIIDA VACELET, 1979

These sponges, so far known only as fossils, are characterized by a sphinctozoan morphology. The spicules (variably tetraradiates, triradiates, and derived forms, sagittal where clearly visible) are embedded in a variable amount of fibrous or granular calcite (most thoroughly described by REID, 1968d). The predominance of sagittal spicules in at least two genera (*Tremacystia* HINDE, 1884a, and *Sphaerocoelia* STEINMANN, 1882) favors but does not require an assignment to the Calcaronea. The triradiates of *Barroisia* MUNIER-CHALMAS, 1882, on the other hand, "appear to be simply equiradiate where their character can be recognized" (REID, 1968d, p. 7), as in typical Calcinea. The presence in this last genus of tylostyles similar to those of the demosponge order Hadromerida (or Poecilosclerida if they are considered to be subtylostyles), together with the fibrous (rather than granular as in *Tremacystia*) microstructure of the aspicular calcite, might suggest an assignment elsewhere; but if true triradiates are present, an assignment to the Calcarea and not Demospongea seems to be required. It is worth noting, however, that almost all hypercalcified sponges referred to either the Hadromerida or the Poecilosclerida on the basis of spicules have a calcitic basal skeleton: penicillate in the chaetetids (Hadromerida); lamellar in the acanthochaetetids (Hadromerida); and microgranular in *Cassianothalamia* and its relatives (Hadromerida), as well as in the stromatoporoid *Newellia* (Poecilosclerida on the basis of its subtylostyles) (see WOOD, REITNER, & WEST, 1989; CUIF & GAUTRET, 1991; MASTANDREA & RUSSO, 1995). *Barroisia* is herein retained provisionally in the Sphaerocoeliidae in the absence of more definitive evidence for its relationships.

ORDER LITHONIDA DOEDERLEIN, 1892

This Jurassic to recent group is clearly assignable to the Calcaronea on the basis of the choanocyte cytology and the larval morphology of the living species. Originally coterminous with the family Minchinellidae, in which the principal skeleton consists of tetraradiates fused together with fibrous calcite, it was expanded by VACELET (1981) to include two other recent, hypercalcified, calcaronean families: the Petrobionidae, in which the principal skeleton is an aspicular mass of spherulitic and penicillate calcite, and the Lepidoleuconidae, in which there is an external armor of overlapping scales derived from the enlargement of equiangular triradiates as in the calcinean order Murrayonida. One might argue that each should be in its own order, but for convenience they are retained here in the order Lithonida.

SYSTEMATIC DESCRIPTIONS

Class DEMOSPONGEA Sollas, 1875

[*nom. correct.* DE LAUBENFELS, 1955, p. 37, *pro* Demospongiae SOLLAS, 1875, p. 421]

Spicules of opaline silica are monaxonic or tetraxonic with axial canal of triangular cross section; spongin and mesohyl commonly abundant; architecture of aquiferous system of rhagon type, with small, choanocyte chambers and small choanocytes. *Cryogenian–Holocene.*

Subclass CERACTINOMORPHA Lévi, 1953

[*nom. correct.* BERGQUIST, 1967, p. 167, *pro* Céractinomorphes LÉVI, 1953, p. 855]

Skeleton generally reticulate and anisotropic; megascleres, when present, monaxonic, never tetraxonic; microscleres, when present, generally sigmas or chelae, never asters; basal skeleton, when present, usually (possibly always) aragonite. *Cambrian–Holocene.*

Order AGELASIDA Verrill, 1907

[Agelasida VERRILL, 1907, p. 333]

Spicules (if present) long, slender, verticillate acanthostyles (or rarely, smooth styles or strongyles of similar proportions) in plumose or echinating position embedded in spongin fibers or in basal skeleton ; basal skeleton (if present) of spherulitic or penicillate aragonite. [RIGBY & SENOWBARI-DARYAN (1996, p. 26) proposed the new superorder Aspiculata and the new order Inozoida in the class Calcarea to include the following families: Auriculospongiidae TERMIER & TERMIER, 1977; Stellispongiellidae WU, 1991; Peronidellidae WU, 1991; Virgulidae TERMIER & TERMIER, 1977; and the new families Sphaeropontiidae and Exotubispongiidae. They observed (p. 20), however, that their higher classification is an artificial or form classification of these Paleozoic sponges, whose skeletons are made of spherulitic aragonite. Those families are included here in the Agelasida.] *Ordovician–Triassic.*

Family CATENISPONGIIDAE Finks, 1995

[Catenispongiidae FINKS, 1995, p. 1]

Aspicular skeleton composed of meandriform, anastomosing trabeculae, outlining anastomosing, tubular spaces of irregular orientation; trabecular microstructure of large (50 to 400 μm), isodiametric spherulites of aragonite; larger canals and oscules commonly present; imperforate cortex variably developed; no spicules known with certainty. [This family is separated from the Virgolidae TERMIER & TERMIER, 1977a, on the basis of the irregular rather than radial arrangement of the trabeculae.] *Permian (Artinskian)–Triassic.*

Catenispongia FINKS, 1995, p. 1 [**C. agaricus;* OD]. Conical-fungiform with strongly convex, upper surface overhanging sides; rugose sides invested with finely porous cortex that bears numerous large, circular pores; interior with meandriform, longitudinal sheets of finely porous trabeculae; sheets outlining longitudinal, laterally anastomosing, canal-like spaces that open on top surface as circular to meandriform, coarse pores; trabecular sheets porous with fine, anastomosing, tubular spaces of circular cross section that open laterally into longitudinal canals as well as on top surface, where they form chains of fine, circular pores between larger, meandriform spaces; large, circular oscules with well-defined margins scattered over top surface, being larger than largest meandriform spaces, and connected to them internally; trabeculae composed of large, isodiametric spherulites; spicules apparently absent but surface of trabeculae showing echinating protrusions, some thin sections showing smooth, strongyle-like, or possibly stylelike (more probably bladed) structures (possibly diagenetic), and large, presumably foreign, monaxon fragments occasionally partly embedded in trabeculae. *Permian (Kungurian–Capitanian):* USA (Texas).——FIG. 384,*2a–c.* **C. agaricus; a,* side view of holotype with lipped ostia in lower, dense, dermal layer and coarse skeleton with larger, exhalant ostia in upper part, Cherry Canyon Formation, Guadalupian, Guadalupe Mountains, ×0.5; *b,* view from above

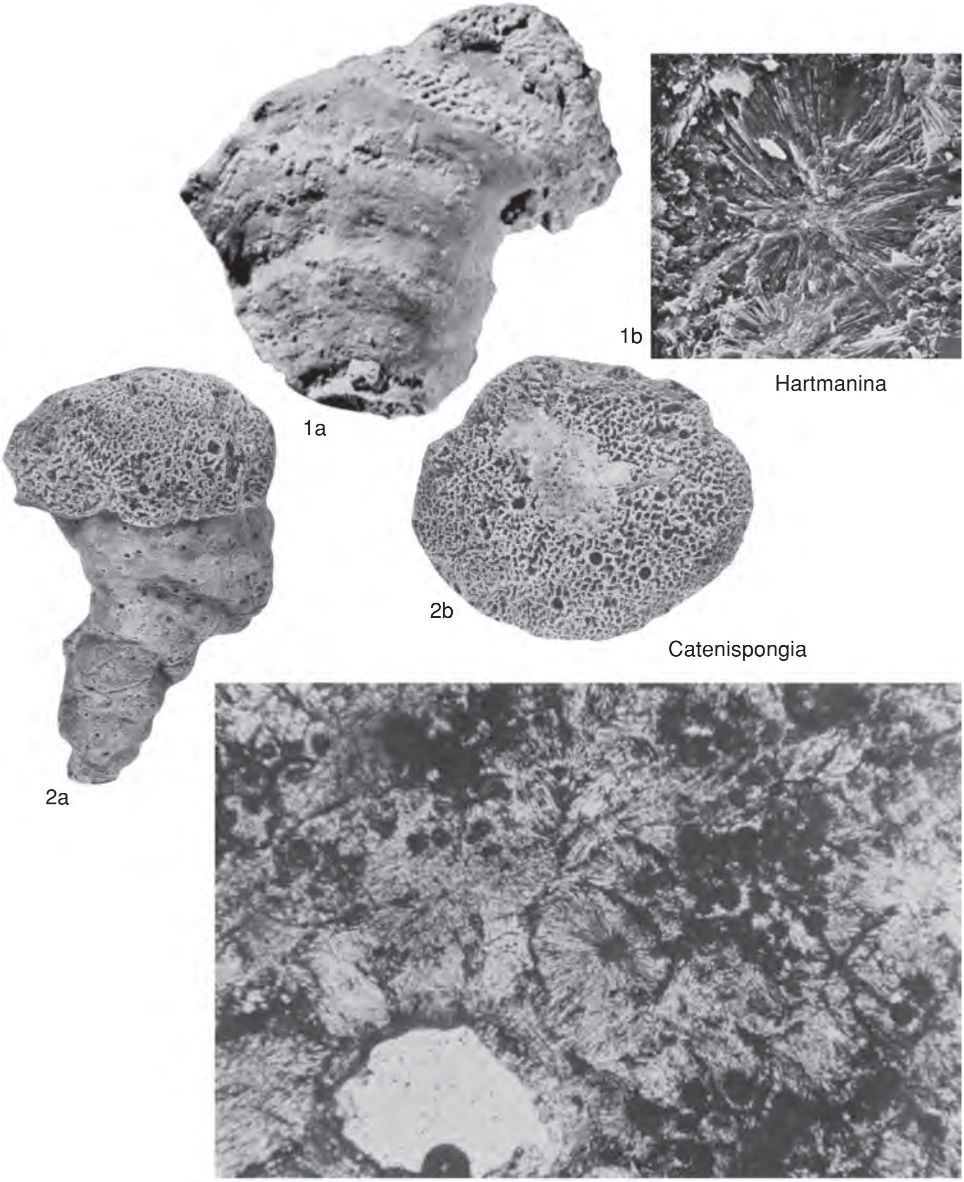


FIG. 384. Catenispongiidae (p. 594–596).

with coarse, exhalant ostia interrupting meandering trabeculae and with fine, intertrabecular spaces, Cherry Canyon Formation, Guadalupian, Guadalupe Mountains, USNM 128060, ×0.5; *c,* photomicrograph showing spherulites in a paratype section, Rhodes Canyon Formation, Leonardian, Glass Mountains, AMNH 44295, ×75 (Finks, 1995).

Hartmanina DIECI, RUSSO, & RUSSO, 1974b, p. 141 [**Achilleum verrucosum* MÜNSTER, 1841, p. 26; OD] [?=*Leiospongia* D'ORBIGNY, 1849, p. 548, *partim,* obj.; *Leiofungia* FROMENTEL, 1860a, p. 49, *partim,* obj.]. Conical-fungiform with flat to convex upper surface, overhanging sides; sides covered with rugose, imperforate cortex; top surface bearing circular to meandriform, intertrabecular spaces; no oscules, canals, or pores on sides; trabeculae anastomosing but internal arrangement otherwise unknown; trabeculae composed of medium to large, isodiametric spherulites; spicules absent. [Absence of pores on the sides, as well as absence of pores larger than the regular, intertrabecular spaces on the top distinguishes this genus from *Catenispongia* FINKS, 1995.] *Triassic:* Europe.——FIG. 384,*1a–b.* **H. verrucosum* (MÜNSTER), San Cassiano Formation, Carnian, Dolomite Alps, Italy; *a,* side view of holotype with dense, dermal layer and irregular, radial, trabecular spaces on top, ×2; *b,* spherulite of medium dimensions from holotype, SSPHG AS VII 383, ×500 (Dieci, Russo, & Russo, 1974b).

Ossimimus FINKS, 1995, p. 2 [**O. robustus;* OD]. Large, cylindroid branches bearing scattered, large, circular oscules; surface widely covered with imperforate, dermal layer, the remainder showing small, meandriform, intertrabecular spaces; trabeculae outline uniformly small, anastomosing tubes of circular cross section interpenetrating in every direction but frequently subparallel to outer surface; oscules open into canals of same diameter as oscule and perpendicular to surface, canals penetrate some distance into sponge and communicate with intertrabecular spaces; trabeculae composed of medium-sized, isodiametric spherulites; spicules absent. *Permian (Kungurian–Roadian):* USA (Texas).——FIG. 385,*2a–b.* **O. robustus,* Road Canyon Formation, Leonardian, Glass Mountains; *a,* subcylindrical, branched, holotype with irregularly distributed oscula over dense, dermal surface, ×0.5; *b,* photomicrograph of internal, skeletal structure of anastomosing trabeculae, USNM 128066, ×10 (Finks, 1995).

Stratispongia FINKS, 1995, p. 2 [**S. cinctuta;* OD]. Conical, stipitate, broadly expanding, sometimes branching; concentrically rugose sides semi-corticate, bearing small, meandriform pores and few large, circular ones; top surface bearing small, meandriform, intertrabecular spaces and numerous larger, circular pores; trabeculae solid (but pierced laterally by small, circular pores), meandriform, dominantly vertical and closely spaced; horizontal layers produced by zones of horizontal canals; trabeculae composed of large, isodiametric spherulites; spicules absent. *Permian (Artinskian–Capitanian):* USA (Texas).——FIG. 385,*1a–b.* **S. cinctuta,* Road Canyon Formation, Leonardian, Glass Mountains; *a,* side view of holotype with smooth, dermal surface and rough top, AMNH 44287, ×1; *b,* photomicrograph of paratype showing trabeculae outlining anastomosing, tubular spaces, AMNH 44294, ×10 (Finks, 1995).

Family VIRGOLIDAE Termier & Termier, 1977

[*nom. correct.* FINKS & RIGBY, herein, *pro* Virgulidae TERMIER & TERMIER, 1977a, p. 31] [=Tubulispongiidae WU Ya Sheng, 1991, p. 35, *partim;* Acoelidae WU Ya Sheng, 1991, p. 57, *partim;* Paracorynellidae WU Ya Sheng, 1991, p. 64]

Trabeculae of aspicular skeleton dominantly radial and longitudinal, outlining spaces of subpolygonal to meandriform cross section that may communicate by large, lateral pores; trabecular microstructure of large (50 to 350 μm), isodiametric spherulites, but not demonstrated in type genus; sides covered with imperforate cortex in some genera, including types; calcitic (originally siliceous) monaxons present in some genera but not in type. This family has chaetetid morphology. *Permian–Triassic.*

Subfamily VIRGOLINAE Termier & Termier, 1977

[*nom. transl. et correct.* FINKS & RIGBY, herein, *ex* Virgulidae TERMIER & TERMIER, 1977a, p. 31]

Obconical to massive sponges with reticular skeletal net, numerous coarse longitudinal exhalant canals more or less diverge upward into spongocoel, where present; inhalant canals subhorizontal and converge from inhalant pores. *Permian (Kungurian)–Triassic.*

Virgola DE LAUBENFELS, 1955, p. 55, *nom. nov. pro Virgula* GIRTY, 1909, p. 73, *non* SIMPSON, 1900 [**Virgula neptunia* GIRTY, 1909, p. 74; OD] [=?*Pseudovirgula* GIRTY, 1909, p. 75, obj.; ?*Conosclera* WU Ya Sheng, 1991, p. 37 (type, *C. vermicula,* OD); *Ramospongia* WU Ya Sheng, 1991, p. 59 (type, *R. minor,* OD)]. Narrow cylinders branching at acute angles; sides covered with rugose, imperforate cortex; top surface unknown; fine trabeculae outlining narrow, tubular spaces of circular to meandriform cross section that anastomose but are dominantly longitudinal and radial; no larger oscules or canals; trabecular microstructure unknown; spicules unknown. [Genus differs from *Ossimimus* FINKS, 1995, in the dominantly longitudinal and radial arrangement of the trabeculae; in the absence of larger canals and oscules, in the continuous, imperforate, dermal layer; and in the smaller size of all parts; in addition spherulites are not yet observed. *Pseudovirgula* GIRTY, 1909, differs in having large pores on the sides at the end of short, tubular projections of the dermal layer leading into short canals of comparable size that interrupt the trabecular mesh; it may also have sphinctozoan-like segmentation; mesh spaces and branch diameter are approximately half that of *Virgola.*] *Permian (Kungurian–Changhsingian):* China (Guangxi), *Kungurian;* USA (Texas), *Guadalupian;* ?China (Hubei), Tunisia, *Changhsingian.*——FIG. 386,*1a–b.* **V. neptunia* (GIRTY), Capitan Formation, Guadalupian, Guadalupe Mountains, Texas; *a,* transverse section of holotype showing nature of skeleton and lack of spongocoel, USNM 118130, ×4; *b,* oblique section through branched reference specimen showing coarse, skeletal structure largely uninterrupted by canals or a spongocoel in either branch, USNM 35009, ×4 (Rigby, Senowbari-Daryan, & Liu, 1998).

Dactylocoelia CUIF, 1979, p. 476 [**D. cylindrocoelia;* OD]. Simple, cylindrical sponges 10 to 12 mm in

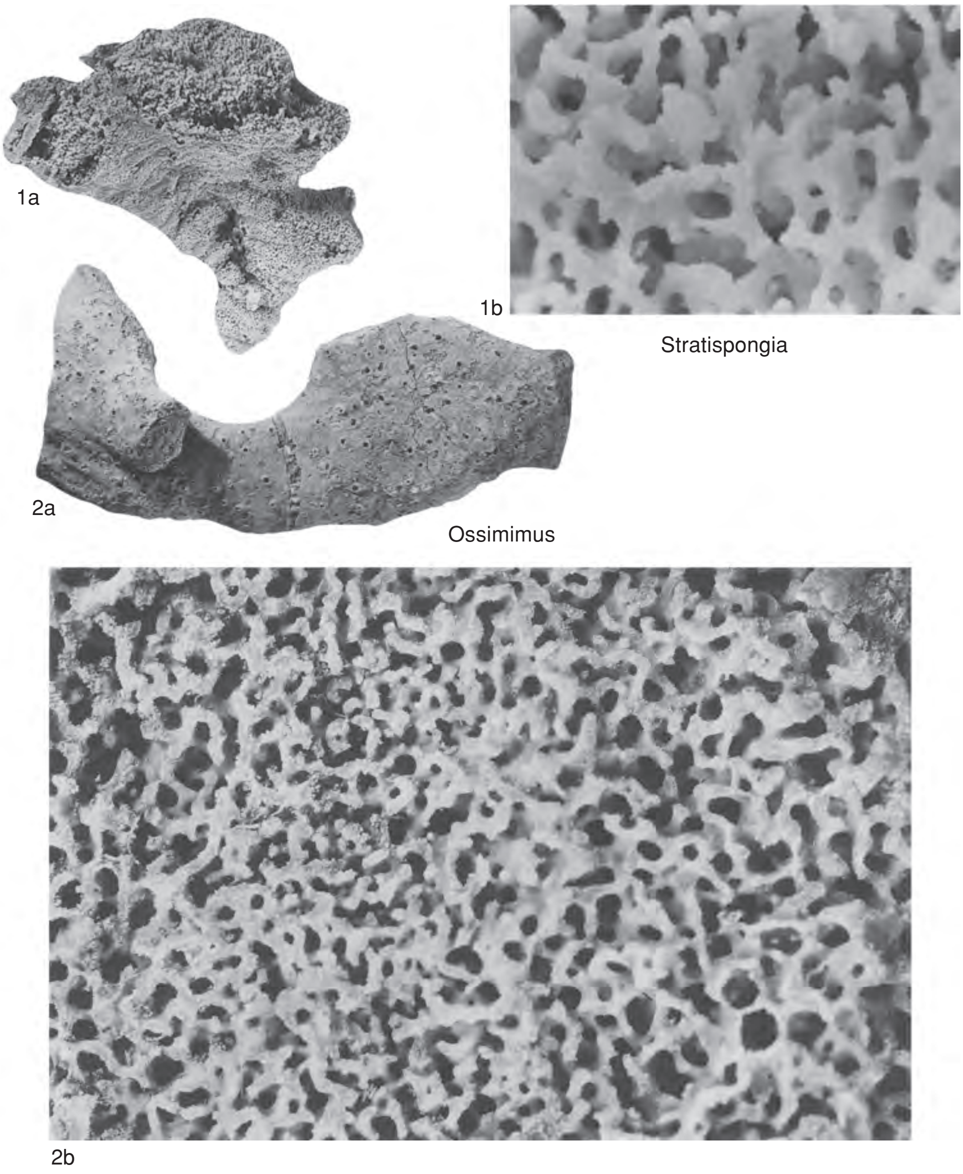


Fig. 385. Catenispongiidae (p. 596).

diameter and several centimeters high, with exterior marked only with small, shallow depressions of canal ostia; axial region with moderately open, reticular structure composed of isodiametric, aragonitic spherulites; outer region distinctly more massive, perforated only by horizontal, reticular canals, and composed of aragonite spherulites that are somewhat eccentric in inner part but in outer, massive, distinctive part of skeleton spherulitic fibers oriented toward periphery. *Triassic:* Turkey.——Fig. 386,*2a–b*. **D. cylindrocoelia,* Nappes d'Antalya, Taurus lycien; *a,* longitudinal, fractured sponge, ×1; *b,* transverse section across reticulate skeleton of axial region, on left, and through outer wall, on right, showing differences in spherulite structure, approximately ×50 (Cuif, 1979).

Intratubospongia Rigby, Fan, & Zhang, 1989b, p. 790 [**I. typica;* OD] [=*Dendrosclera* Wu Ya Sheng, 1991, p. 46 (type, *D. irregularis,* OD); *Paracorynella* Wu Ya Sheng, 1991, p. 64 (type, *P. flexa,* OD); *Paristellispongia* Wu Ya Sheng, 1991, p. 71 (type, *P. parallelica,* OD); *Cystospongia* Wu Ya Sheng, 1991,

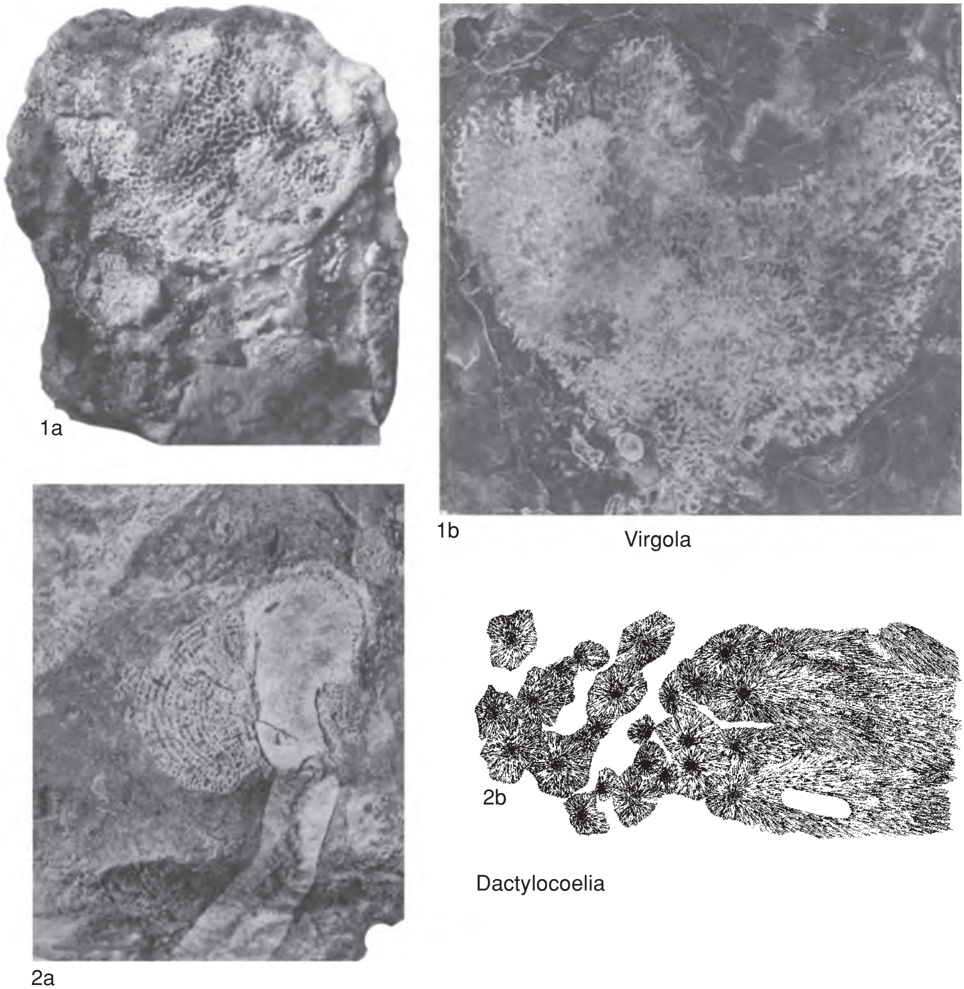


FIG. 386. Virgolidae (p. 596–597).

p. 84 (type, *C. guangxiensis,* OD)]. Cylindrical to club-shaped sponges that lack a spongocoel but with many large, longitudinal, exhalant canals of various diameters irregularly distributed; inhalant canals essentially horizontal; skeleton of fine fibers; axial cluster of exhalant canals absent. Microstructure and spicules unknown. *Permian (Guadalupian–Lopingian):* China (Guangxi, Guizhou).——FIG. 387,*1a–b.* **I. typica,* Changxing Formation, Changhsingian, Guangxi; *a,* longitudinal section of holotype with numerous discontinuous, vertical canals throughout fine, skeletal net, IG 5096, ×2; *b,* irregular, fibrous, fine-textured skeletal net with dense interruption of skeleton (*arrow*) in upper part and canals filled with dark matrix below, IGASBA 5247, ×20 (Rigby, Fan, & Zhang, 1989b).

Keriocoelia CUIF, 1974, p. 149 [**K. conica;* OD]. Small, flabellate-conical and stipitate; sides covered with imperforate layer; top surface with circular to submeandriform, intertrabecular spaces or calicles; top edges of trabeculae denticulate; intertrabecular spaces filled in from below by secondary material; trabeculae composed of large, isodiametric spherulites, secondary filling is penicillate in structure; styles present, embedded in spherulitic skeleton. *Triassic:* Europe.——FIG. 388*a–c.* **K. conica,* San Cassiano Formation, Carnian, Dolomite Alps, Italy; *a,* general morphologic aspect of type specimen, ×3; *b,* photomicrograph of distal surface with alveolar reticulation showing dentate appearance produced by small spherulite, ×20; *c,* spherulites in transverse section, ×30 (Cuif, 1974; courtesy of *Geobios*).

Reticulocoelia CUIF, 1973, p. 124 [**R. arborescens;* OD]. Ramose, branches somewhat flattened and lobate; surface bearing only circular to

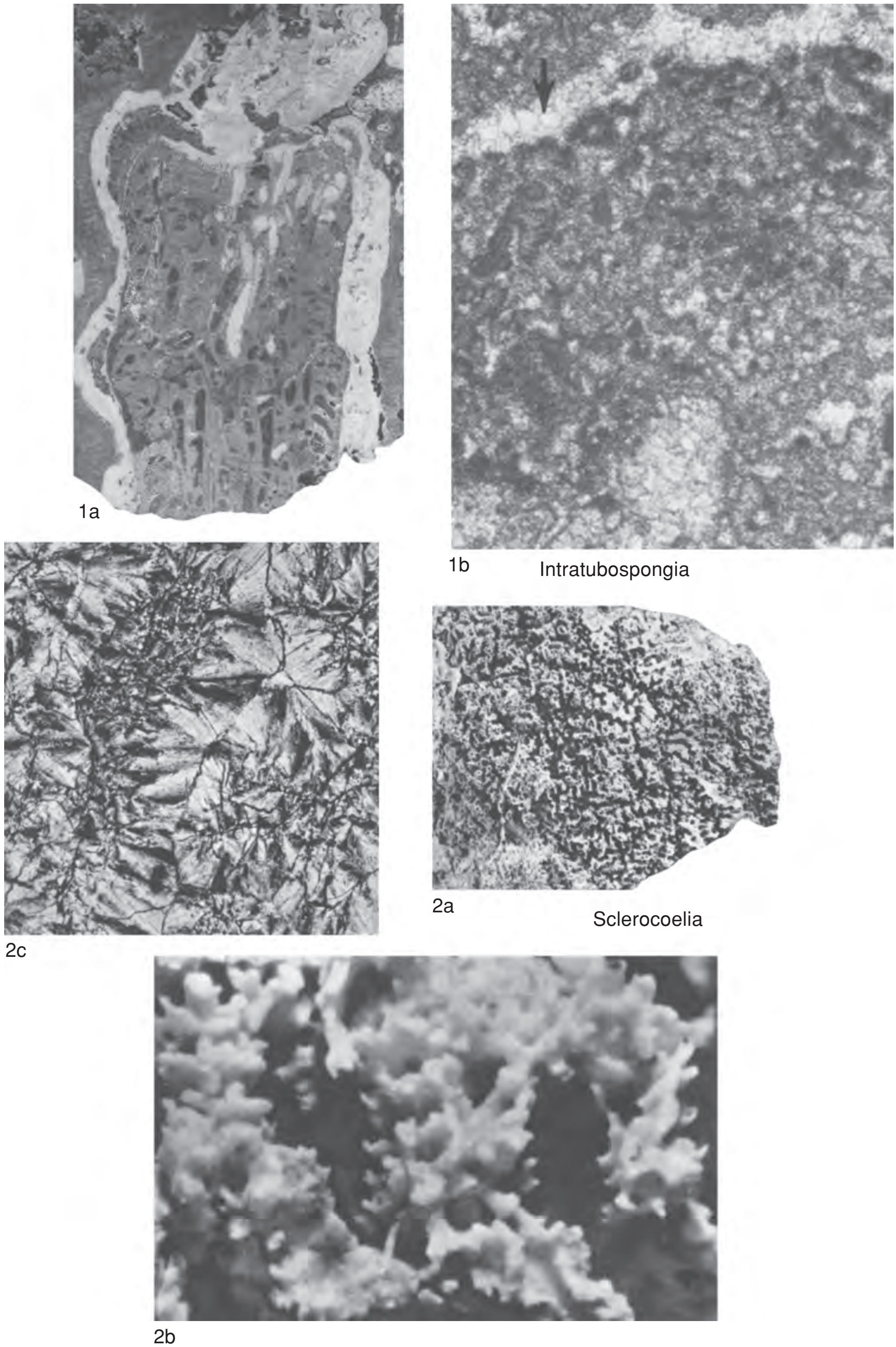


FIG. 387. Virgolidae (p. 597–601).

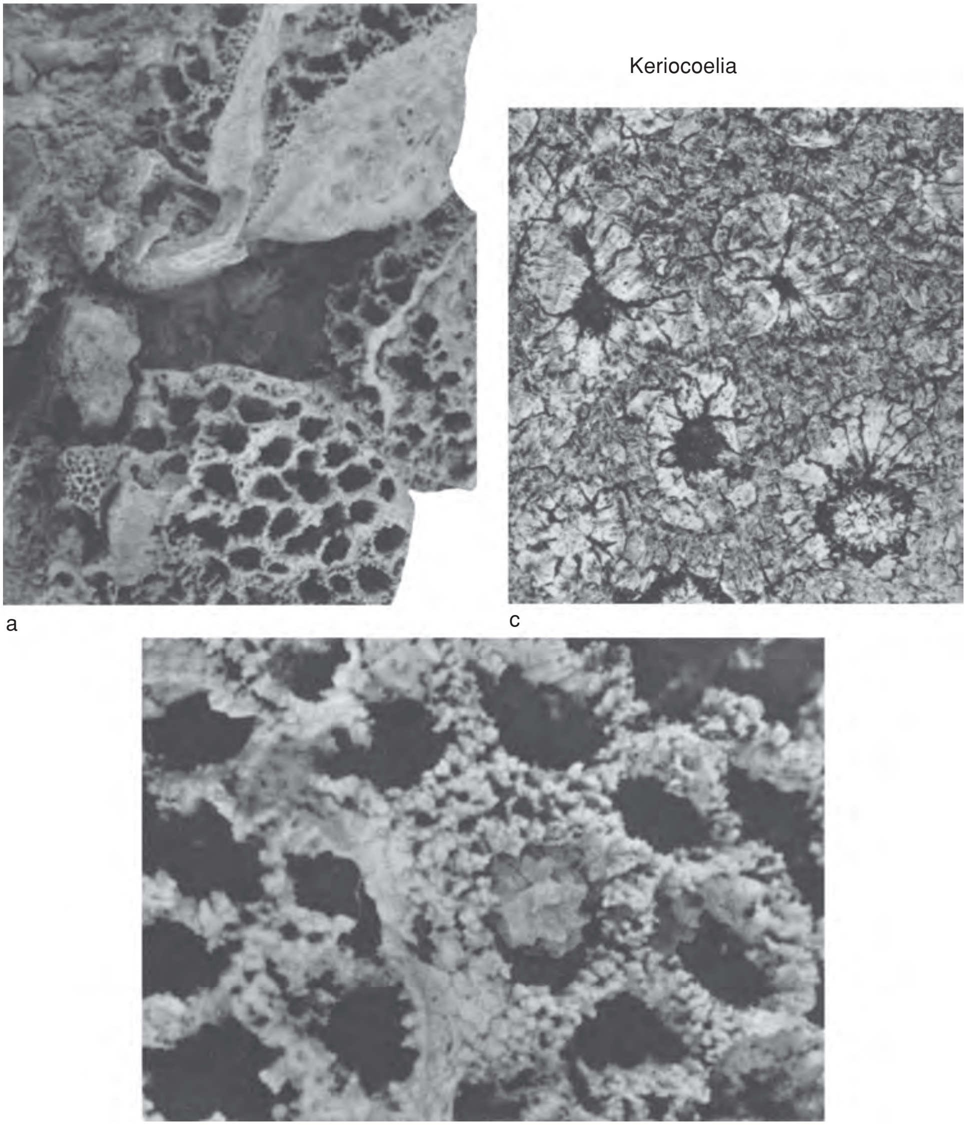


FIG. 388. Virgolidae (p. 598).

meandriform, small, intertrabecular spaces; no larger pores, oscules, or cortex; trabeculae and intertrabecular spaces anastomosing but dominantly longitudinal and distally divergent; trabeculae composed of large, isodiametric spherulites. *Triassic (Carnian–Norian):* Turkey.——FIG. 389*a–b*. **R. arborescens,* Triassic deposits, Korkuteli; *a,* transverse section of branch of type specimen, ×5; *b,* surface with alveolar development corresponding to homogenous, internal structure, magnification unknown (Cuif, 1973; courtesy of *Geobios*).——FIG. 390*a–b*. **R. arborescens,* Triassic deposits, Korkuteli; *a,* spherulite showing irregular orientations in internal, skeletal net, ×100; *b,* drawing of microstructure of skeletal net, with spherulite in interior of trabeculae with layered crust over exterior, scale indicated by bar (Cuif, 1973; courtesy of *Geobios*).

Sclerocoelia CUIF, 1974, p. 147 [**S. hispida;* OD]. Thick, encrusting masses whose upper surface bears palmately branched ends of trabeculae that outline meandriform, intertrabecular spaces; intertrabecular spaces below current upper surface completely filled by secondary, trabecular material; primary trabeculae composed of moderately large, isodiametric spherulites that subsequently expand asymmetrically to fill intertrabecular spaces. Calcite (originally silica) acanthostyles embedded in spherulitic skeleton. [This genus differs from others included in this family and was compared by CUIF (1974, p. 149) to the living sclerosponge *Goreauiella* HARTMAN, 1969, by HARTMAN and GOREAU (1970).] *Triassic:* Europe.——FIG. 387,*2a–c*. **S. hispida,* San Cassiano Formation, Dolomite Alps, Italy; *a,* general morphology of upper surface of type specimen, ×2; *b,* photomicrograph showing general morphology of outer, vertical processes, ×60; *c,* photomicrograph under crossed nicols showing large spherulite, ×100 (Cuif, 1974; courtesy of *Geobios*).

Subfamily PREEUDINAE Rigby & Senowbari-Daryan, 1996

[Preeudinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 88]

Virgulid sponges lacking large osculum or depression on summit. *Permian (Kungurian–Changhsingian).*

Preeudea TERMIER & TERMIER, 1977a, p. 33 [**P. minima;* OD]. Subcylindrical to subspherical, small sponges lacking a spongocoel but with numerous vertical-walled, tubelike, exhalant canals that may be clustered in axial area or distributed throughout sponge; exterior with dense, dermal layer marked by ostia with raised rims; skeleton very fine net of fibers that may be interrupted by obscure, horizontal, inhalant canals; microstructure spherulitic. *Permian (Lopingian):* Tunisia.——FIG. 391,*1a–d*. **P. minima,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* top of spherical specimen with central bundle of tubular, exhalant canals and dermal surface with rimmed, canal ostia, USNM 463734, ×2; *b,* side view of conicocylindrical sponge with rimmed, possible inhalant canals, ×2; *c,* summit of same sponge with cluster of axial canals in shallow, rimmed depression, USNM 463735, ×2; *d,* restoration showing general canal and skeletal pattern, and tubular or rimmed, inhalant ostia in dermal layer, not to scale (Rigby & Senowbari-Daryan, 1996a).

Medenina RIGBY & SENOWBARI-DARYAN, 1996a, p. 89 [**M. laterala;* OD]. Single to branched or club-shaped sponges, may be annulate, with numerous longitudinal, exhalant canals clustered side by side in axial area but separation between them increasing toward periphery; horizontal canals developed between exhalant tubes and in outer part of skeleton; walls of both vertical and horizontal canals with numerous small pores; skeletal microstructure spherulitic. *Permian (Lopingian):* Tunisia.——FIG. 392*a–f*. **M. laterala,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* summit view of branched holotype with spongocoels into which empty numerous small, exhalant pores, ×1; *b,* side view of holotype, USNM 463728, ×1; *c,* summit view of paratype, half of which shows ostia of numerous longitudinal, exhalant canals,

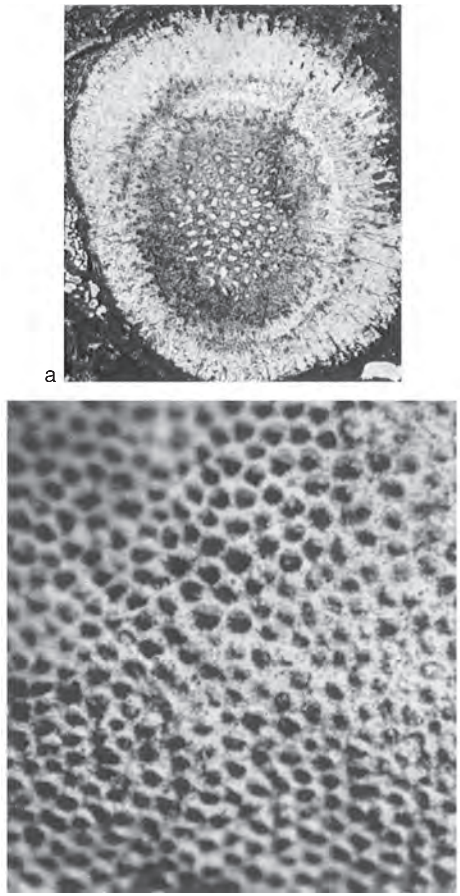


FIG. 389. Virgolidae (p. 598–600).

USNM 463730, ×2; *d,* side view of weathered paratype with outer, stacked, horizontal canals exposed in upper part, ×2; *e,* micronodose, dense, dermal layer produced by rounded tips of outwardly divergent, skeletal fibers, USNM 463732, ×10; *f,* reconstruction showing relationships of vertical and horizontal canals in interior of obconical sponge, not to scale (Rigby & Senowbari-Daryan, 1996a).

Microsphaerispongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 92 [**M. polyarteria;* OD]. Small, spherical sponges with several relatively shallow spongocoels distributed over surface and with low rims; dermal layer perforated by numerous small pores; skeleton of reticulate, relatively coarse fibers; may be attached. *Permian (Lopingian):* Tunisia.——FIG. 391,*2a–d*. **M. polyarteria,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* paratype with diagnostic sieve plate in exhalant opening, USNM 480227, ×5; *b,* spherical paratype with rimmed, exhalant openings in

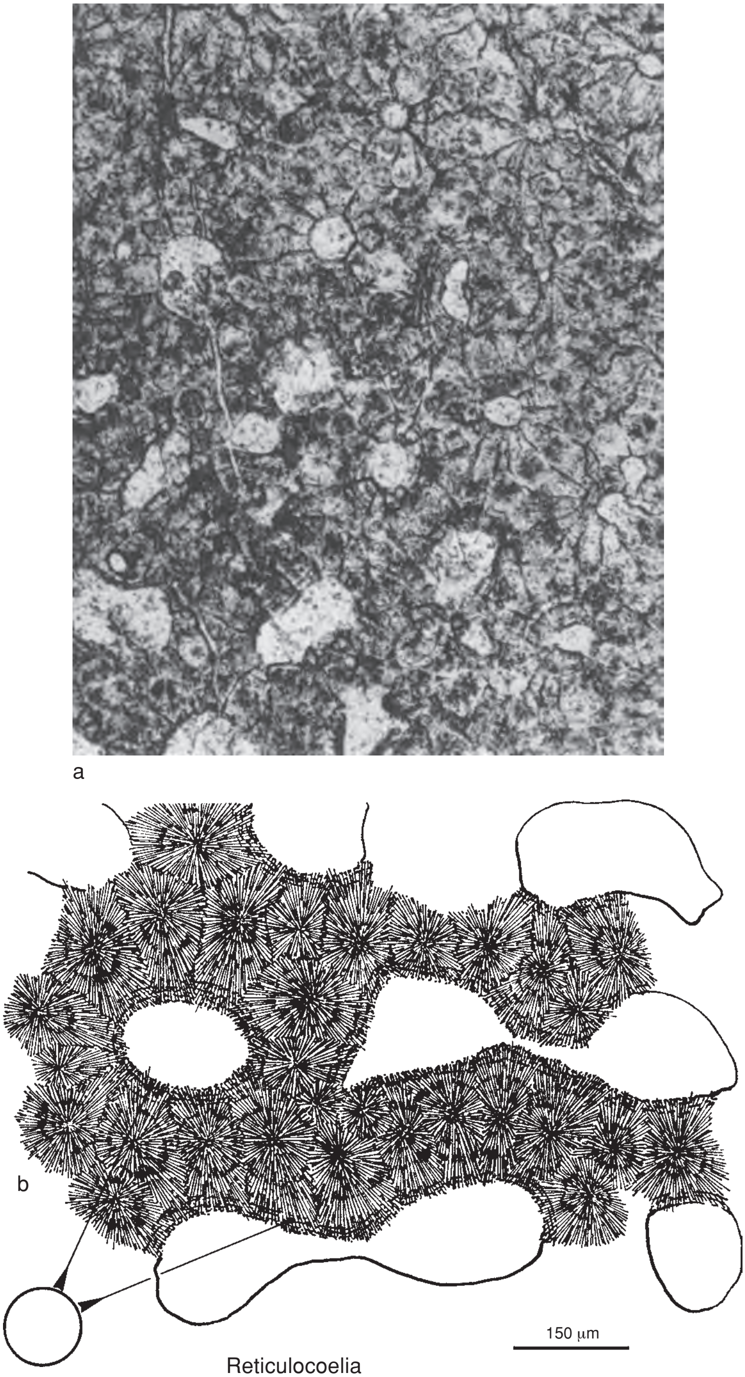


FIG. 390. Virgolidae (p. 598–600).

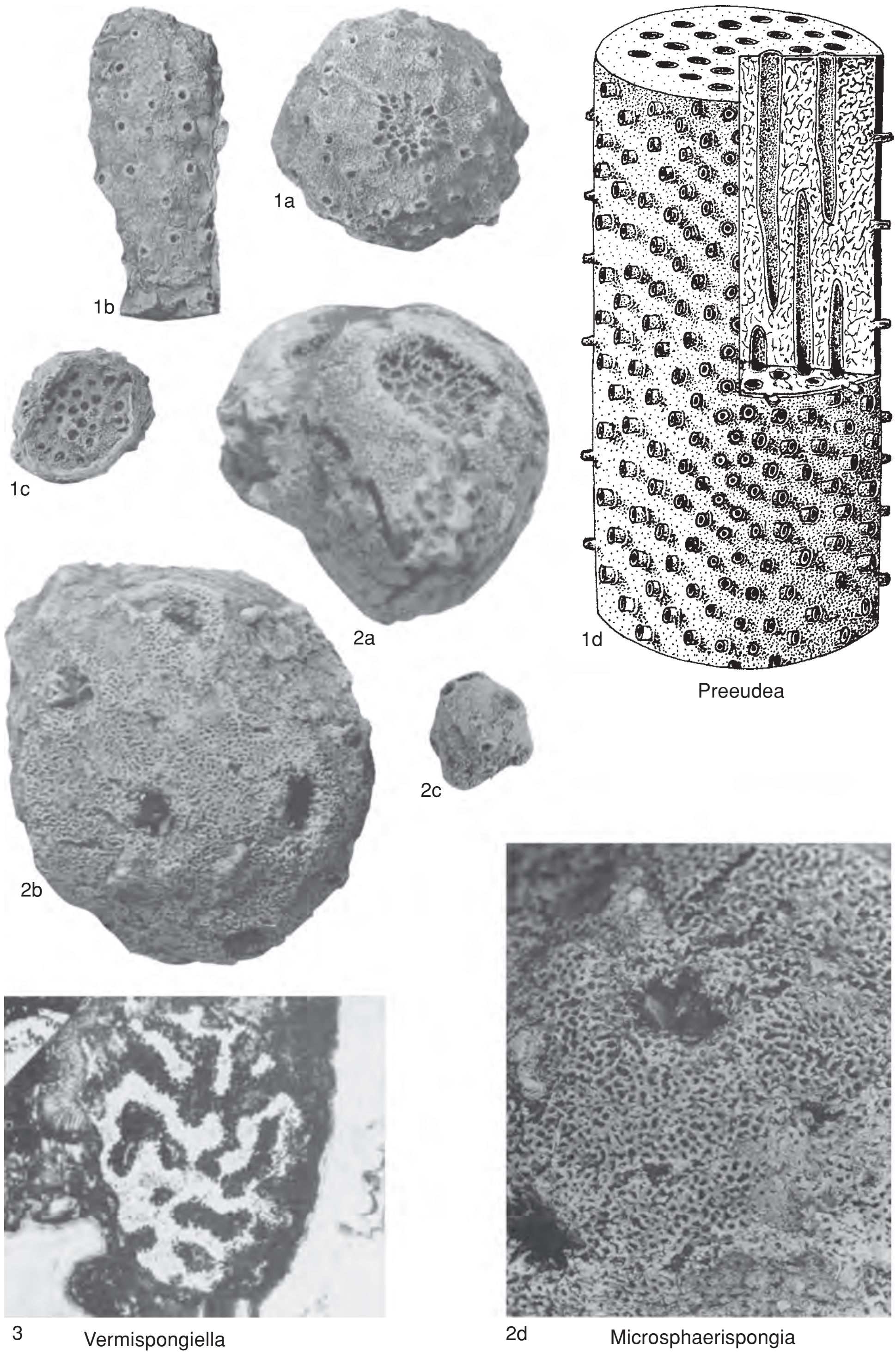


FIG. 391. Virgolidae (p. 601–607).

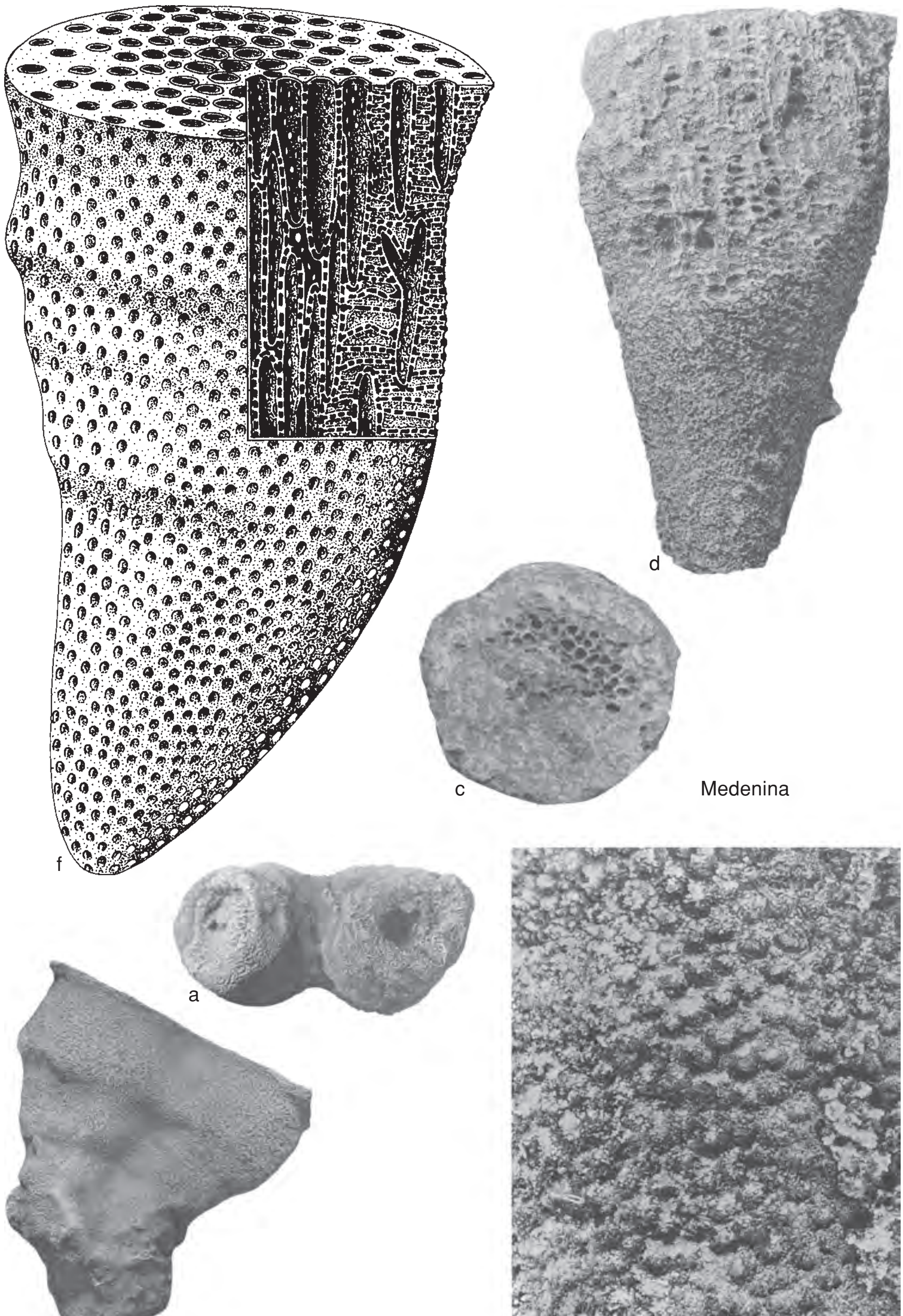


FIG. 392. Virgolidae (p. 601).

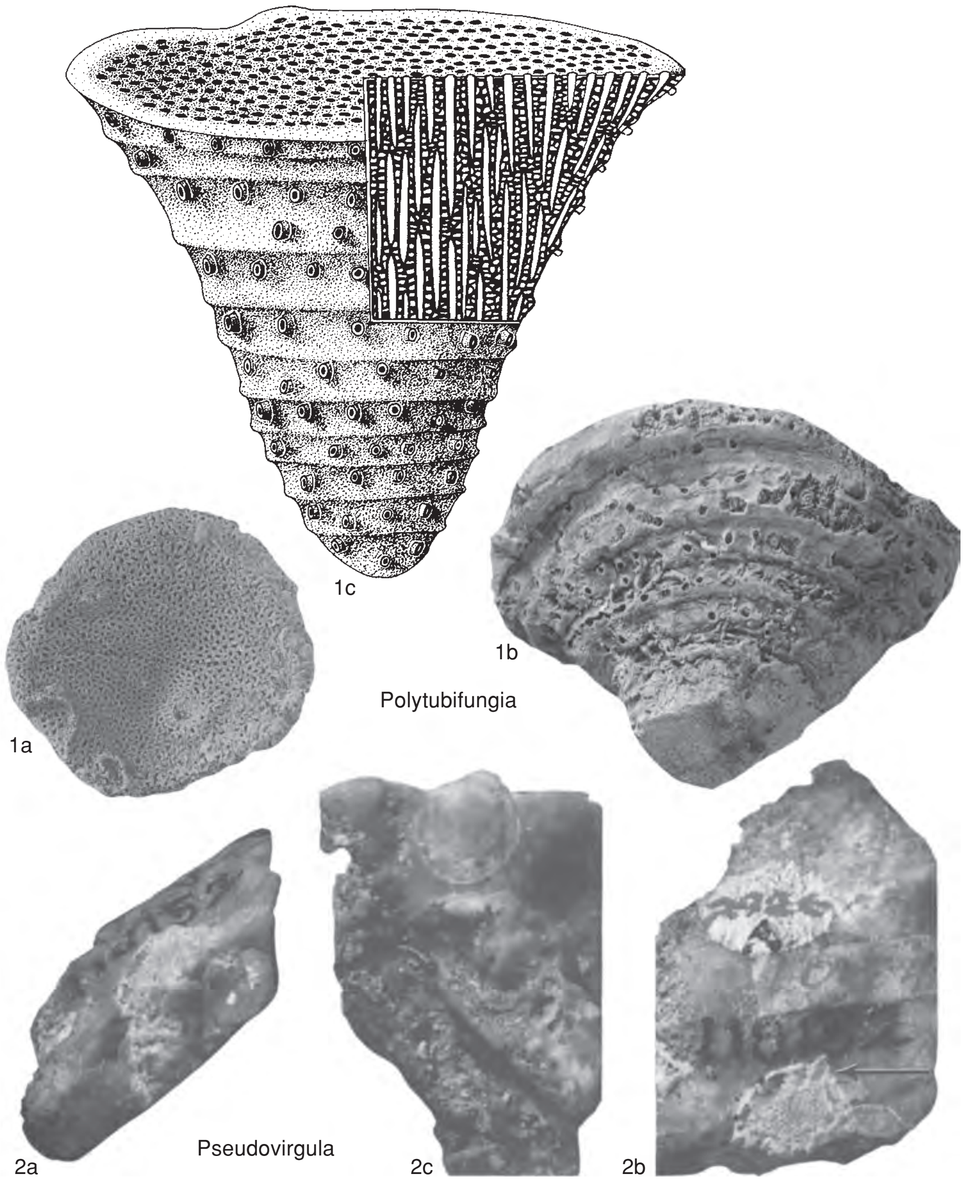


FIG. 393. Virgolidae (p. 605–606).

porous, skeletal net, USNM 480228, ×5; *c,* subspherical holotype with rimmed oscula, USNM 480226, ×1; *d,* photomicrograph of paratype with scattered, coarse, exhalant ostia and smaller, inhalant ostia and skeletal pores, USNM 480228, ×10 (Rigby & Senowbari-Daryan, 1996a).

Polytubifungia RIGBY & SENOWBARI-DARYAN, 1996a, p. 90 [**P. maxima;* OD]. Mushroom-shaped sponges without large, deep spongocoel but with numerous unwalled, coarse, vertical, exhalant canals distributed more or less uniformly throughout entire sponge; fibrous skeleton between canals very fine textured; inhalant canals absent or ill defined in interior but with raised rims on exterior; growth lines clearly developed in dense, dermal layer; microstructure unknown. *Permian (Lopingian):* Tunisia.——FIG. 393,*1a–c.* **P. maxima,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* summit of holotype with shallow, broad depression and numerous exhalant ostia, ×1.5; *b,*

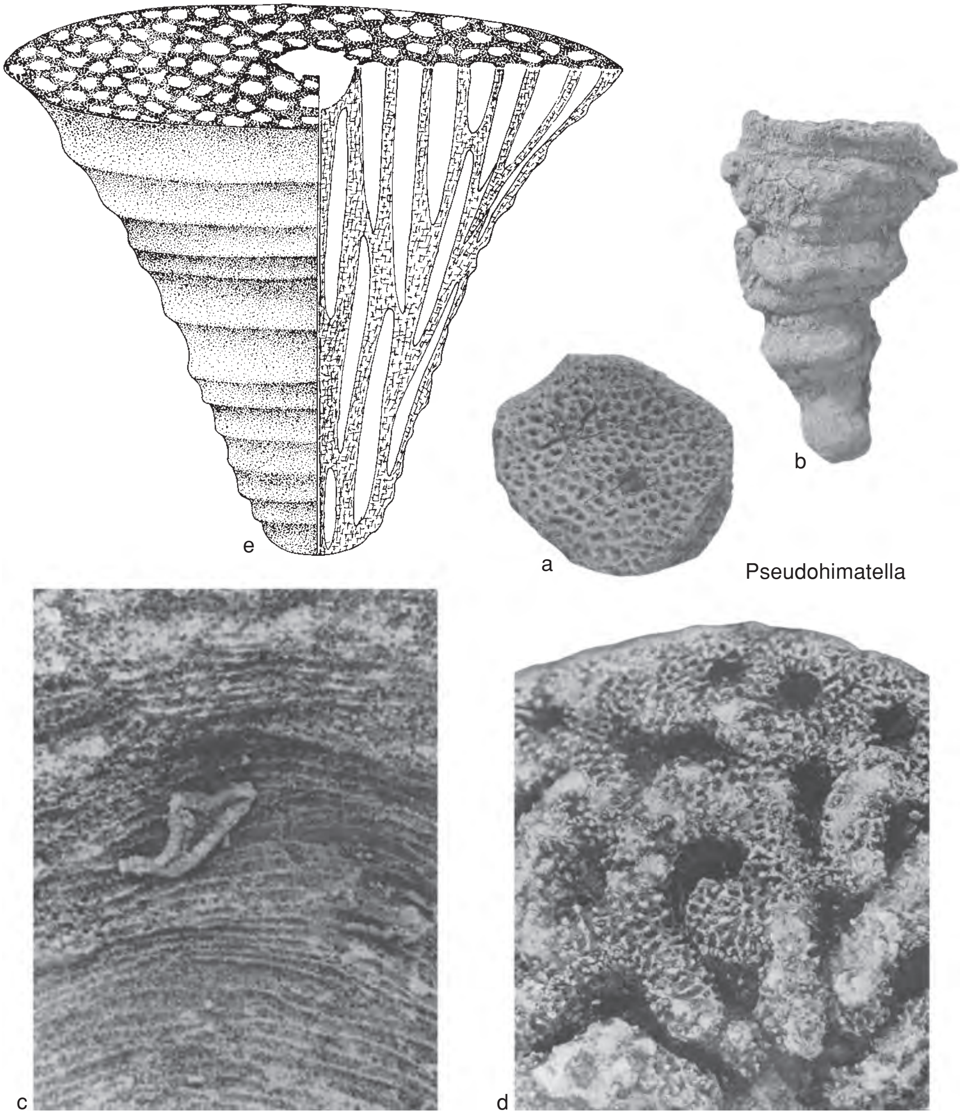


FIG. 394. Virgolidae (p. 608).

oblique side view with numerous inhalant ostia in dense, annulate, dermal layer, USNM 480215, ×2; *c,* reconstruction showing dense, dermal layer with rimmed ostia and skeletal and canal patterns of interior, not to scale (Rigby & Senowbari-Daryan, 1996a).

Pseudovirgula GIRTY, 1909, p. 75 [**P. tenuis;* OD]. Small, stemlike, cylindrical sponges without a spongocoel but with central region of delicate, reticulate skeleton surrounded by outer, open zone that lacks skeletal net but with irregularly spaced and developed, uparched laminae that subdivide this part of sponge into irregular chambers; open area also with well-developed, coarse, radiating, tubular exaules that extend out from central skeletal region to or beyond the well-defined dermal layer. *Permian (Guadalupian):* USA (Texas).——FIG. 393,*2a–c.* **P. tenuis,* Capitan Limestone, Guadalupe Mountains; *a,* side view of small, cylindrical holotype, ×4; *b,* upper transverse section with prominent exaulos (*arrow*) and dark, unskeletonized layer between light, dermal layer and interior, fibrous skeleton, ×4; *c,* lower surface showing central, fibrous skeleton and outer moat inside well-defined, dermal layer, USNM 118152, ×4 (Rigby, Senowbari-Daryan, & Liu, 1998).

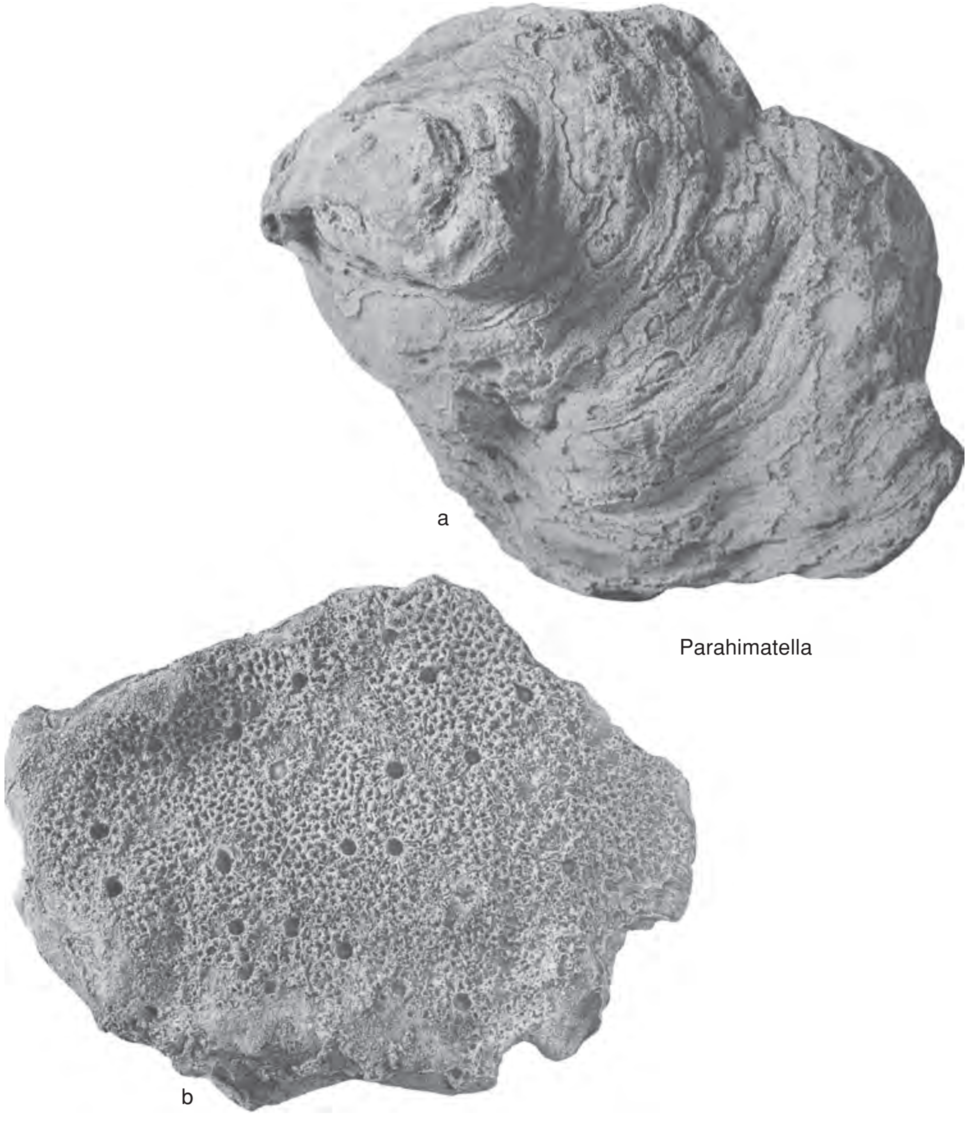


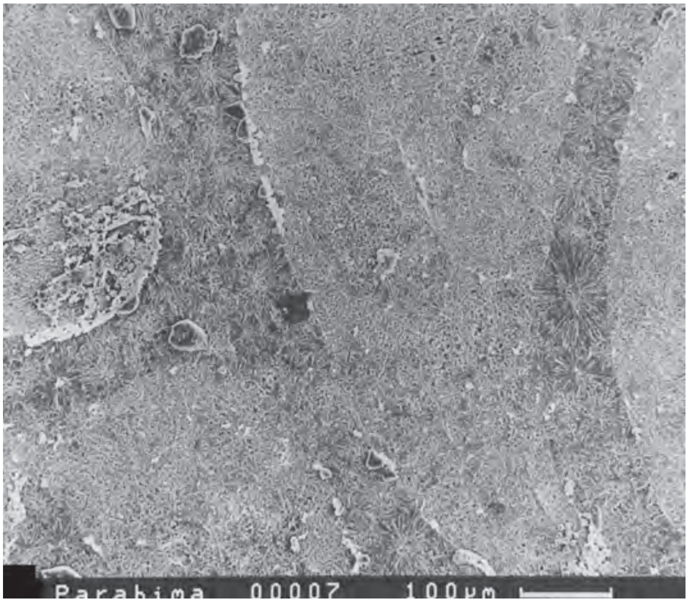
FIG. 395. Virgolidae (p. 608).

Vermispongiella FINKS & RIGBY, herein, *nom. nov. pro Vermispongia* WU Ya Sheng, 1991, p. 68, *non* QUENSTEDT, 1878, p. 171, *nec* WHITFIELD, 1905, p. 298 [**Vermispongia spiniformis* WU Ya Sheng, 1991, p. 68; OD]. Ovate sponges with moderately coarse canals vermiform and interconnected throughout entire sponge; short, excurrent canals not differentiated; skeletal tracts coarse and composed of fibers in irregular structure or in regular lattice; free ends of fibers extending into canals to form spinose-appearing surfaces of skeletal tracts. *Permian (Kungurian):* China (Guangxi).——FIG. 391,*3*. **V. spiniformis* (WU), Maokou Formation, Kungurian, Reef of Xiangbo; longitudinal section of holotype, IGASB xb37-2-12, ×2 (Wu Ya Sheng, 1991).

Subfamily PSEUDOHIMATELLINAE Rigby & Senowbari-Daryan, 1996

[Pseudohimatellinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 93]

Virguliid sponges club to mushroom shaped with large osculum in axial part of summit; vertical, exhalant canals not ending in osculum but distributed across summit. *Permian.*



Parahimatella

FIG. 396. Virgolidae (p. 608).

Pseudohimatella RIGBY & SENOWBARI-DARYAN, 1996a, p. 93 [**Himatella pauciporata* PARONA, 1933, p. 37; OD]. Club to mushroom shaped or pearlike without an axial spongocoel but generally one or more large, shallow, osculum-like depressions in axial area of summit; numerous long, coarse, vertical, exhalant canals distributed throughout entire sponge; canals circular to polygonal or irregular in transverse sections; limited horizontal, inhalant canals; rigid skeleton between canals fine, reticulate, fibrous net; dense, dermal layer may have growth lines in lower part; spherulitic microstructure. *Permian:* Tunisia, Italy (Sicily).——FIG. 394*a–e*. **P. pauciporata* (PARONA), Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; *a,* summit view showing two large, exhalant oscula and numerous coarse, exhalant ostia, ×1; *b,* side view of annulate, obconical sponge with dense, dermal layer, USNM 480248, ×1; *c,* photomicrograph of dermal surface with fine microsculpture uninterrupted by canals, USNM 480254, ×10; *d,* photomicrograph of upper surface with micronodose, broad, skeletal tracts between coarse ostia, USNM 480251, ×10; *e,* restoration showing canal pattern and dense, dermal layer of obconical sponge, not to scale (Rigby & Senowbari-Daryan, 1996a).

Subfamily PARAHIMATELLINAE Rigby & Senowbari-Daryan, 1996

[Parahimatellinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 94]

Virguliid sponges with fibrous skeleton of coarse spherulites; fibers in vesiculate-appearing network; numerous deep, widespread spongocoels with oscula on upper surface. *Permian (Lopingian).*

Parahimatella RIGBY & SENOWBARI-DARYAN, 1996a, p. 94 [**P. vesiculata;* OD]. Broadly obconical or flaring, mushroomlike to annulate, subcylindrical sponges lacking a major axial spongocoel, but with numerous vertical, walled spongocoels with oscula at surface; exhalant canals converging to bases or sides of spongocoels; distinct, small, vertical, inhalant canals extending down from surface into skeleton; skeleton vesiculate of bubblelike chambers arranged in either vertically stacked series or *en echelon* between canals, each chamber with one or two pores; walls coarsely spherulitic; rodlike elements, possibly foreign, common throughout skeleton. *Permian (Lopingian):* Tunisia.——FIG. 395*a–b*. **P. vesiculata,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* side and bottom view of sheetlike holotype with dermal surface marked by growth lines, ×1; *b,* summit view showing numerous irregularly distributed, circular oscula separated by coarse, fibrous skeleton and small, inhalant ostia, USNM 480261, ×1 (Rigby & Senowbari-Daryan, 1996a).——FIG. 396. **P. vesiculata,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; paratype, SEM photomicrograph of cystlike walls are 50 to 100 µm thick and composed of large spherulites approximately 80 µm in diameter, scale indicated by bar at base, USNM 480261 (Rigby & Senowbari-Daryan, 1996a).

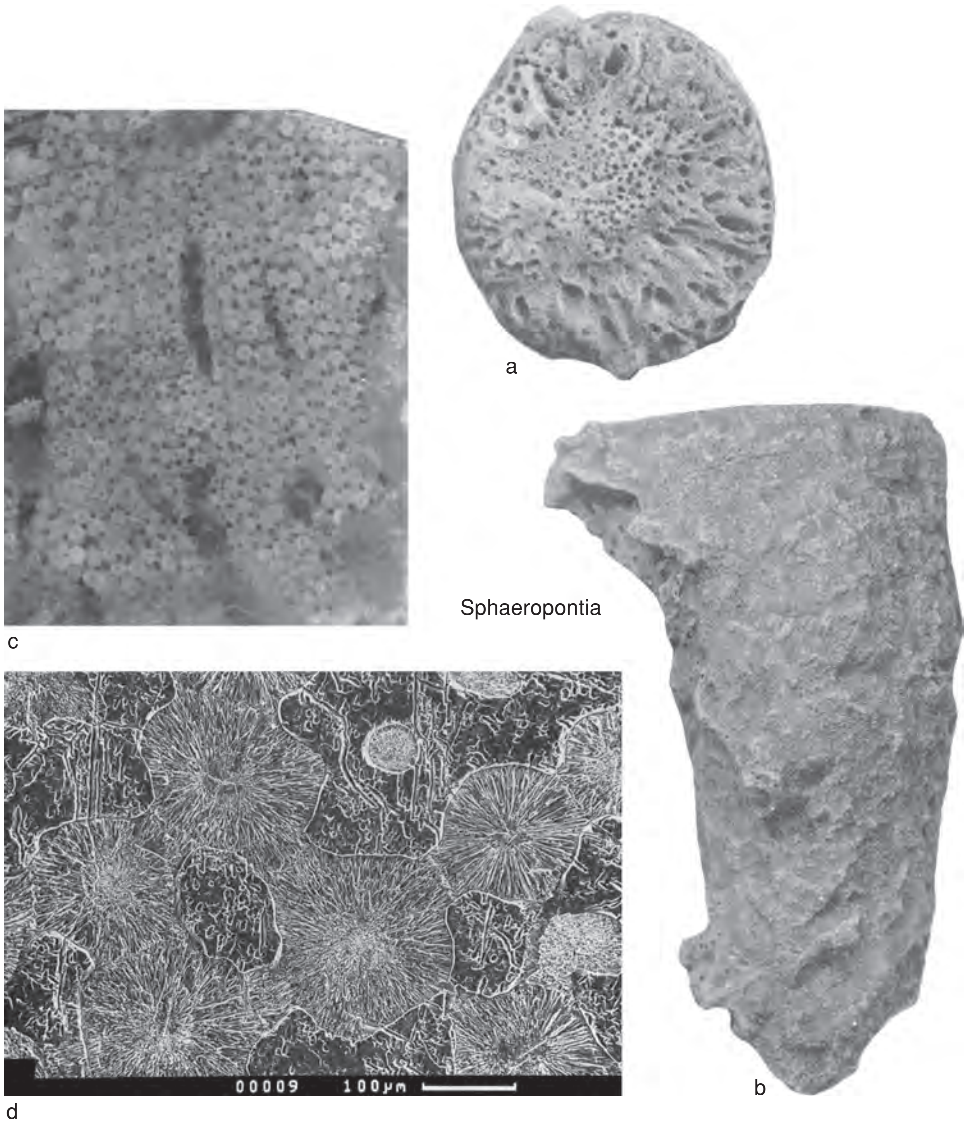


FIG. 397. Sphaeropontiidae (p. 609–610).

Family SPHAEROPONTIIDAE Rigby & Senowbari-Daryan, 1996

[Sphaeropontiidae RIGBY & SENOWBARI-DARYAN, 1996a, p. 95]

Spherulites separated from one another and connected only by extensions between to form a loosely packed, quasicubic, three-dimensional net. [This type of skeleton shows some resemblance to the filling tissue of *Intrasporeocoelia* FAN & ZHANG, 1985. The authors of the family (RIGBY & SENOWBARI-DARYAN, 1996a, p. 96) suggest that the sphaeroclone desmas of the lithistid family Astylospongiidae may prove to be spherulites of the type found here, rather than desmas.] *Permian (Lopingian).*

Sphaeropontia RIGBY & SENOWBARI-DARYAN, 1996a, p. 96 [**S. regulara;* OD]. Conicocylindrical with large, upwardly and outwardly diverging, exhalant canals penetrating spherulitic, skeletal net. *Permian*

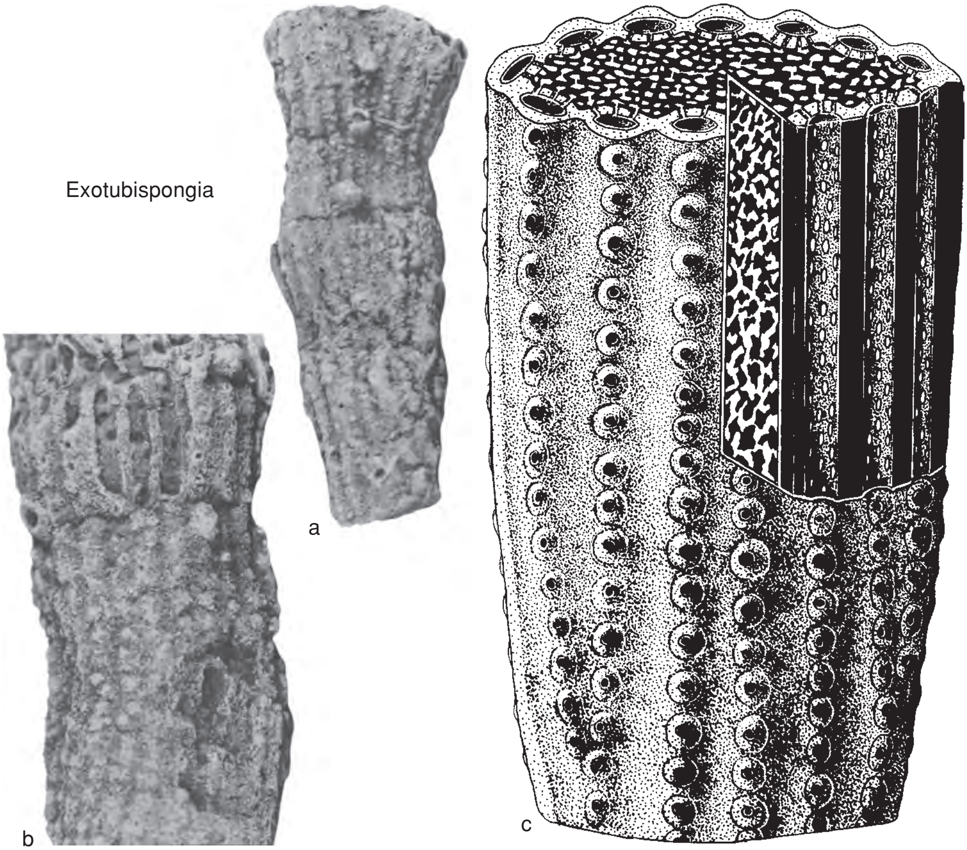


FIG. 398. Exotubispongiidae (p. 610–611).

(Lopingian): Tunisia.——FIG. 397*a–d.* **S. regulara,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* summit view of conicocylindrical holotype with numerous radially divergent, exhalant canals and some smaller, nearly vertical, ones in axial area, USNM 480321, ×2; *b,* side view of weathered paratype, USNM 480229, ×2; *c,* polished surface of paratype into nearly transparent calcium carbonate showing spherical spherulites connected by rays in skeletal tracts interrupted by canals, ×10; *d,* SEM photomicrograph of same paratype showing several spherulites and interconnecting, beamlike elements, USNM 480230, scale indicated by bar at base (Rigby & Senowbari-Daryan, 1996a).

Family EXOTUBISPONGIIDAE Rigby & Senowbari-Daryan, 1996

[Exotubispongiidae RIGBY & SENOWBARI-DARYAN, 1996a, p. 97]

Cylindrical to branched, inozoid sponges with several vertical, exhalant, tubelike canals forming part of periphery in dermal part of sponge; inner part with reticular, fibrous skeleton; outer surface with numerous small, pustular pores arranged either in vertical lines along canals or irregularly. *Permian (Lopingian).*

Exotubispongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 97 [**E. pustulata;* OD]. Small, cylindrical or branched sponges with several vertical, tubelike canals in outer ring near periphery; central spongocoel absent; skeleton of upwardly divergent, reticulate fibers; microstructure unknown; vertical canals connect to exterior by numerous small pores that may be pustular and arranged in linear series on ribs along vertical canals or irregularly over dermal surface. *Permian (Lopingian):* Tunisia.——FIG. 398*a–c.* **E. pustulata,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* side view of incipiently branched holotype with pustular pores in lines, USNM 480231, ×5; *b,* enlarged side view of paratype with vertically aligned, pustulose pores over vertical canals exposed in upper part, USNM 480235, ×10; *c,* reconstruction showing exterior and vertical and horizontal sections; coarse, longitudinal canals near periphery have large canals on pustular nodes on surface; inner area with reticular, skeletal fibers, not to scale (Rigby & Senowbari-Daryan, 1996a).

Family SESTROSTOMELLIDAE de Laubenfels, 1955

[Sestrostomellidae DE LAUBENFELS, 1955, p. 97; *emend.*, FINKS & RIGBY, herein] [=Sestrostomellidae DE LAUBENFELS, 1955, p. 97, *partim;* Stellispongiidae DE LAUBENFELS, 1955, p. 97, *partim;* Polysiphonellidae BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 92; Polysiphonellidae WU Ya Sheng, 1991, p. 65]

Sponges of inozoan morphology with vertical canals perpendicular to upper surface and radial canals parallel to it; central cloaca often present; microstructure of spherulitic and clinogonal aragonite with sparse monaxons. *Triassic–Lower Cretaceous.*

Sestrostomella ZITTEL, 1878b, p. 40 [**S. robusta;* SD DE LAUBENFELS, 1955, p. 97] [=?*Palaeoierea* LAUBE, 1865, p. 233 (type, *Manon? gracilis* MÜNSTER, 1841, p. 28, OD); *Sestromostella* ZITTEL, 1903, p. 62, obj.]. Conical to cylindrical (occasionally with horizontal constrictions) with central cluster of parallel, subequal, exhalant canals that extend deeply into sponge along its axis; canals closely apposed and circular to subpolygonal in cross section; subhorizontal, radial canals empty into them and may be present as radial grooves on convex, top surface; central canals open into shallow, upper depressions. Exterior surface smooth with small, circular to meandriform, inhalant openings between skeletal fibers; imperforate, dermal layer may cover basal part of sponge. Larger, inhalant canals arch inwardly and upwardly parallel to top surface; internal trabeculae forming obscure layers parallel to top surface; intertrabecular spaces circular to meandriform in cross section. Occasional (calcitic, presumably after silica) monaxons may be present among (aragonitic) regular or flaky spherulites composing trabeculae (WENDT, 1974; FINKS, 1983a). Frequently forming bushy colonies of subparallel individuals fused basally and laterally. [Jurassic and Cretaceous homeomorphs with trabeculae composed of a large, central triradiate coated by small, sinuous spicules should not be assigned to this genus; they might be accommodated in *Enaulofungia* FROMENTEL, 1860a. *Palaeoierea* LAUBE, 1865, is senior to *Sestrostomella* if it is indeed a synonym. It is, however, more likely a *Thaumastocoelia* STEINMANN, 1882 (see p. 664, herein). It can be suppressed under the 50-year rule of the *Code* (ICZN, 1999).] *Triassic–Jurassic:* Europe, Iran, *Triassic;* Canadian Atlantic Shelf, *Jurassic.*——FIG. 399,*1*. **S. robusta,* Cassian Formation, Carnian, southern Alps, Italy; *a,* near longitudinal section of branched, partially recrystallized example showing reticulate structure and axial tubes of spongocoel on left, ×1 (Riedel & Senowbari-Daryan, 1991; courtesy of Springer-Verlag GmbH & Co.).

Ateloracia POMEL, 1872, p. 228 [**Cnemidium manon* MÜNSTER, 1841, p. 30; SD RAUFF, 1893, p. 71]. Broadly conical, convex, upper surface with central, shallow, cloacal depression, toward which radial, exhalant grooves converge; interior, exhalant canals parallel to upper surface or obliquely convergent on cloaca; inhalant canals perpendicular to upper surface; trabecular mesh fine; sides of sponge invested by dermal layer; trabecular microstructure (WENDT, 1974, p. 503, 507, fig. 1) irregular (aragonitic), partly spherulitic with occasional (calcitic, presumably after silica) monaxons. [Genus differs from *Precorynella* DIECI, ANTONACCI, & ZARDINI, 1968, in absence of large, radially arranged ostia on the upper surface, in the finer trabecular net, narrower internal canals, and especially the absence of large, axial, vertical, exhalant canals. This name is available for the spherulitic Triassic species usually assigned to *Stellispongia* D'ORBIGNY, 1849, provided that *Cnemidium manon* is considered congeneric with the noncloacate, polyosculate species similar to *Cnemidium variabile* MÜNSTER, 1841. Suitable illustrations for this genus are unavailable.] *Triassic:* Europe, Timor.

Brevisiphonella RUSSO, 1981, p. 5 [**B. longirima;* OD]. Small, compound sponge composed of conicoclavate individuals fused laterally; large, elongate-oval osculum opening into shallow, funnel-shaped cloaca at center of each individual, approximately one-third diameter of individual; remainder of surface with fine, meandriform, intertrabecular spaces without dermal layer; skeletal trabeculae outlining anastomosing, tubular spaces; microstructure clinogonal; no spicules known. *Triassic (Carnian):* Italy.——FIG. 399,*4a–e*. **B. longirima,* San Cassiano Formation, Cortina d'Ampezzo, Dolomite Alps; *a,* side view of holotype; *b,* diagonal view illustrating several elongate oscula, IPUM 19274; *c,* side view of branched paratype, IPUM 19275, ×4; *d,* transverse paratype section showing elliptical spongocoel and lack of defined dermal layer, IPUM 19276, ×8; *e,* transverse paratype section showing clinogonal microstructure, IPUM 19277, ×200 (Russo, 1981).

Epitheles FROMENTEL, 1860a, p. 35 [**Myrmecium hemisphaericum* GOLDFUSS, 1826, p. 18; OD] [=*Myrmecidium* VINASSA DE REGNY, 1901, p. 10, *nom. van., nom. nov. pro Myrmecium* GOLDFUSS, 1826, p. 18, *non* LATREILLE, 1825; ?*Gymnomyrmecium* POMEL, 1872, p. 203 (type, *Myrmecium gracile* MÜNSTER, 1841, p. 26)]. Typically hemispherical with broadly conical base covered by concentrically wrinkled, dermal layer; narrow, central cloaca opening onto top surface and fed by vertical, central, and upwardly and inwardly curving, lateral, exhalant canals that may crenulate oscular rim; inhalant ostia cover top surface and lead inwardly and downwardly; intertrabecular spaces small and mostly circular in cross section. [Trabecular microstructure of a specimen (AMNH 1281/1) identified by ZITTEL as the type species appears to be small, sinuous bodies, parallel to trabecular surfaces, of the type called by HINDE (1893b, p. 214 *et passim.*,

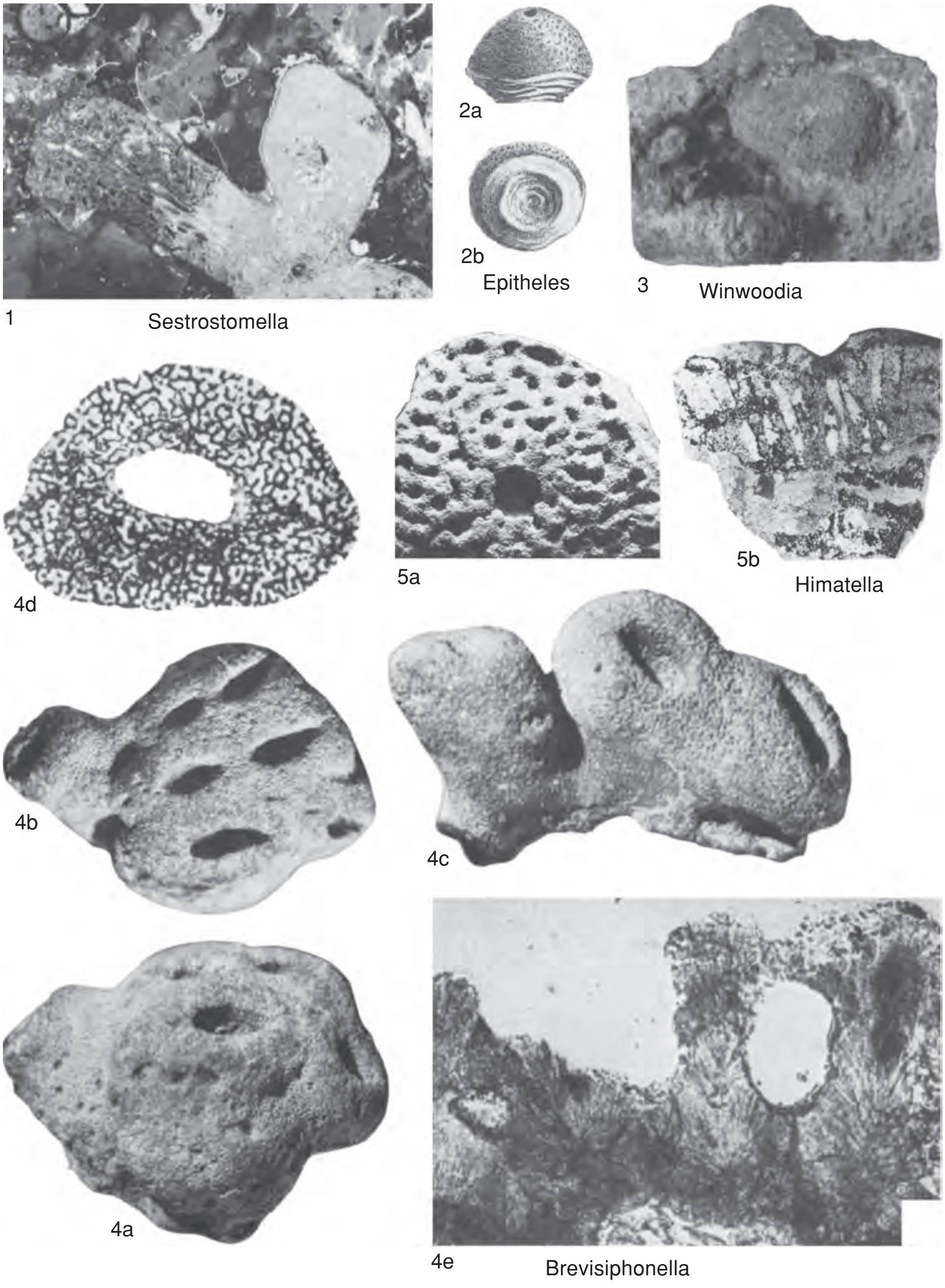


FIG. 399. Sestrostomellidae (p. 611–614).

"filiform sinuous spicules." HURCEWICZ (1975, p. 254, fig. 20 and pl. 30, fig. 1), in a specimen assigned to the same species, identified subequal triactines with subordinate tetractines and diactines, with the basal, dermal layer composed of paratangential diactines underlain by a layer of short diactines perpendicular to the surface. The taxonomic position of this genus will have to be determined by a microscopic study of the type specimen. WAGNER (1964, p. 26) placed this genus (as

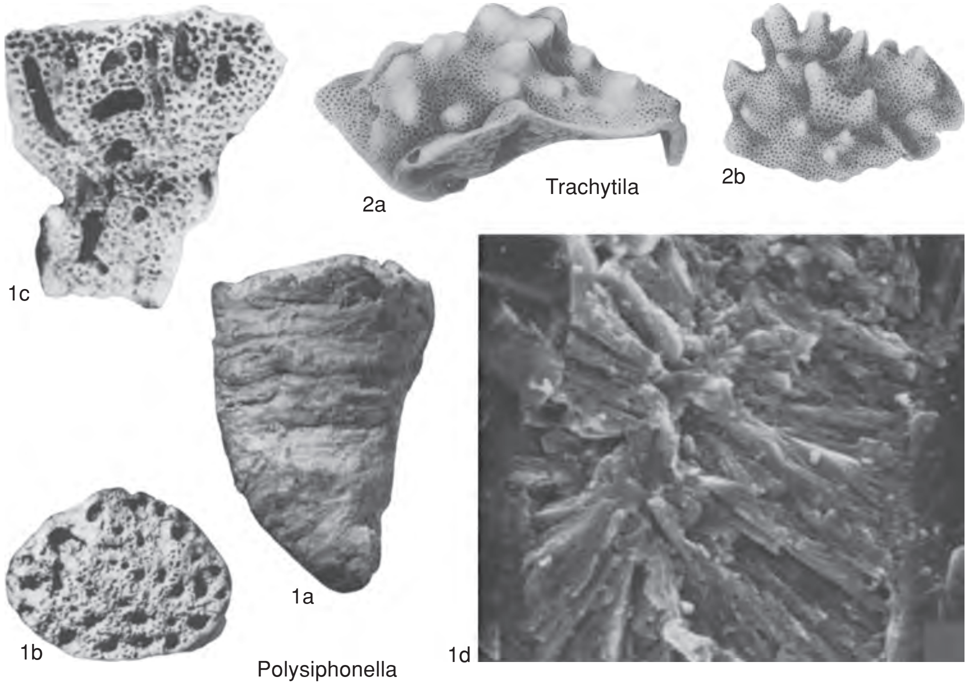


FIG. 400. Sestrostomellidae (p. 613–614).

Myrmecium GOLDFUSS, 1833 and *Myrmecidium* VINASSA DE REGNY, 1901) in subjective synonymy with *Eusiphonella* ZITTEL, 1878b, but the trabecular microstructure is different.] *Jurassic:* Europe.——FIG. 399,*2a–b.* **E. hemisphaerica* (GOLDFUSS), ?Corallian Limestone, ?Oxfordian, Upper Jurassic, Thurnau, France; *a,* side view of small, hemispherical sponge with small osculum at summit and irregularly wrinkled, lower, dermal layer, magnification unknown; *b,* view of same sponge from below showing dense, wrinkled, dermal layer, magnification unknown (Fromentel, 1860a).

Himatella ZITTEL, 1878b, p. 29 [**Tragos milleporatum* MÜNSTER, 1841, p. 29; OD]. Broadly conical, flaring upwardly from a narrow base to a width approximately equal to height; top surface gently convex, meeting sides in sharp rim; sides covered with dermal layer, sometimes horizontally rugose; narrow cloaca penetrating most of sponge, opening on center of top surface; top surface showing meandriform, intertrabecular spaces and scattered ostia; some ostia on sides; internal, meandriform, trabecular net often showing periodic thickening parallel to top surface; no interior canals other than intertrabecular spaces. Trabecular microstructure possibly (aragonitic) penicillate or spherulitic with occasional (calcitic, originally siliceous) monaxons (WENDT, 1974, p. 503, 507). *Triassic:* Europe, Tunisia, Timor.——FIG. 399,*5a–b. H. meandrina* TERMIER & TERMIER, Series of Merbah el Oussif, Changhsingian, Djebel Tebaga, Tunisia; *a,* view from above with central osculum and surrounding skeleton with ostia of vertical canals, ×2; *b,* axial section with prominent, vertical canals in upper part, some of which empty into shallow spongocoel, ×2 (Termier, Termier, & Vachard, 1977b; courtesy of *Géologie Méditerranéenne*).

Polysiphonella RUSSO, 1981, p. 10, *non* BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 93 [**P. diecii;* OD]. Small, conical sponge with flat top covered with ovoid, exhalant openings that communicate with subvertical (possibly anastomosing) canals of interior; intervening skeletal tissue finely trabecular, outlines anastomosing tubular spaces, whose openings are visible on top surface between larger, exhalant pores; sides covered with horizontally rugose epitheca; trabecular microstructure penicillate; no spicules known. *Triassic (Carnian):* Italy.——FIG. 400,*1a–d.* **P. diecii,* San Cassiano Formation, Cortina d'Ampezzo, Dolomite Alps; *a,* side view of holotype with dense, dermal layer; *b,* view of holotype summit with numerous, exhalant oscula, IPUM 19285, ×5; *c,* vertical section of paratype showing several subvertical, exhalant canals in reticulate skeleton, IPUM 19290, ×8; *d,* paratype, SEM showing irregular, skeletal microstructure, IPUM 19293, ×500 (Russo, 1981).

Trachytila WELTER, 1911, p. 64 [**T. tuberosa;* OD]. Sponges with many branches with sharp, wart- or club-shaped expansions that may have oscula at their ends, intervening dermal area with smaller, probably inhalant, round ostia; basal attachment surface may be irregularly wrinkled or with small, wartlike nodes; vertical canals interrupted by common tabulae; skeletal fibers include poorly preserved, scattered, three-rayed spicules. [Included in the family with some question.] *Lower Cretaceous:* Germany.——FIG. 400,*2a–b*. **T. tuberosa,* Essener Grünsand, Cenomanian, Essen; *a,* side view showing encrusting base and nodular, upper parts of sponge; *b,* view from above of moderately lobate form of genus, ×1 (Welter, 1911).

Winwoodia RICHARDSON & THACKER, 1920, p. 178 [**W. porula* RICHARDSON & THACKER, 1920, p. 179; OD]. Massive sponges, lacking surficial grooves, with or without terminal oscula on summit; numerous inhalant ostia in dermal surface, which lacks a dermal cortex, except possibly present around base. [Included in the family with question.] *Middle Jurassic:* England.——FIG. 399,*3*. **W. porula,* upper Inferior Oolite, Gloucestershire; side view of relatively massive, though small, type specimen, ×2 (Richardson & Thacker, 1920).

Family PHARETROSPONGIIDAE de Laubenfels, 1955

[Pharetrospongiidae DE LAUBENFELS, 1955, p. 98, *partim; emend.,* FINKS & RIGBY, herein]

Basal skeleton of penicillate microstructure of inozoan morphology, consisting of anastomosing trabeculae that outline meandriform, anastomosing, tubular spaces; it is not known if mineralogy is aragonite or calcite; monaxons parallel to length of trabeculae said by earlier authors to be present in type genus and in some others, but they may be referring to penicillate needles. *Permian (Guadalupian)–Cretaceous.*

Subfamily PHARETROSPONGIINAE de Laubenfels, 1955

[*nom. transl.* FINKS & RIGBY, herein, *ex* Pharetrospongiidae DE LAUBENFELS, 1955, p. 98]

Trabeculae and their interspaces not dominantly vertical and subparallel. *Triassic (Carnian)–Cretaceous.*

Pharetrospongia SOLLAS, 1877a, p. 249 [**P. strahani;* OD]. Sponge body curving or convoluted plates that may anastomose or form funnel-shaped or subcylindrical bodies; exhalant surface smoother than inhalant, and may have small, circular oscules; otherwise no pores other than intertrabecular spaces, which are circular to meandriform. [Trabeculae of a referred specimen identified by R. E. H. REID and examined by the present author (RMF) has solid, penicillate microstructure with no trace of spicules; supposed parallel monaxons that HINDE (1884a, p. 202) described may have been the penicillate needles.] *Cretaceous:* Europe.——FIG. 401,*2a–b*. **P. strahani; a,* side view of cup-shaped specimen with thin walls and reticulate, inner surface, Upper Chalk, Kent, England, ×1; *b,* camera lucida drawing of fibers showing traces of spicules, Upper Greensand, Cambridge, England, ×50 (Hinde, 1884a).

Euepirrhysia DIECI, ANTONACCI, & ZARDINI, 1968, p. 123 [**E. montanaroae;* OD]. Massive (but small) sponge composed of laterally fused, conical individuals; upper surface flat or gently convex, pustulose, with circular, often lipped pore in center of each pustule; much larger, circular oscule in center of each component individual (diameter approximately one-fifth that of individual) surrounded by radiating, dendritic, exhalant canals; upper surface meeting sides in sharp rim or edge; sides covered with horizontally wrinkled epitheca; cylindrical cloaca extending to base of sponge from each oscule; horizontal, exhalant canals enter cloaca from side at regular vertical intervals to produce laminated appearance; closely spaced, vertical canals (possibly inhalant) extend downwardly from each pustule pore on upper surface; remainder of skeleton dense; microstructure unknown; spicules not known. [A second species, *E. pusilla* (LAUBE, 1865), is represented by solitary, conical individuals; pores of the upper surfaces are largest at the periphery where they form a distinct ring.] *Triassic (Carnian–Norian):* Italy.——FIG. 401,*1a–c*. **E. montanaroae,* San Cassiano Formation, Norian, Dolomite Alps; *a,* view of holotype from above with axial spongocoel in each branch and surface marked by rimmed, possibly inhalant ostia, ×2; *b,* view from below showing convergent, exhalant canals around three spongocoels, and openings of vertical, possibly inhalant canals, all within dense, dermal layer, ×2; *c,* vertical section with axial spongocoel and walls with regularly spaced levels of exhalant, canal development and vertical canals producing reticulate-appearing skeleton, IPUM 17543, ×2 (Dieci, Antonacci, & Zardini, 1968).

Subfamily LEIOFUNGIINAE new subfamily

[Leiofungiinae FINKS & RIGBY, herein] [type genus, *Leiofungia* FROMENTEL, 1860a, p. 49]

Conical, imperforate cortex on sides; skeleton dense, with trabeculae subparallel in direction of growth, thin, and outlining narrow, subequal spaces of dominantly meandriform cross section; trabecular microstructure penicillate where known. [The morphology of this subfamily is quasistromatoporoid.] *Permian (Guadalupian)–Cretaceous.*

Leiofungia FROMENTEL, 1860a, p. 49 [**Achilleum milleporatum* MÜNSTER, 1841, p. 26; OD]. Conicocylindrical with convex, upper surface; sides

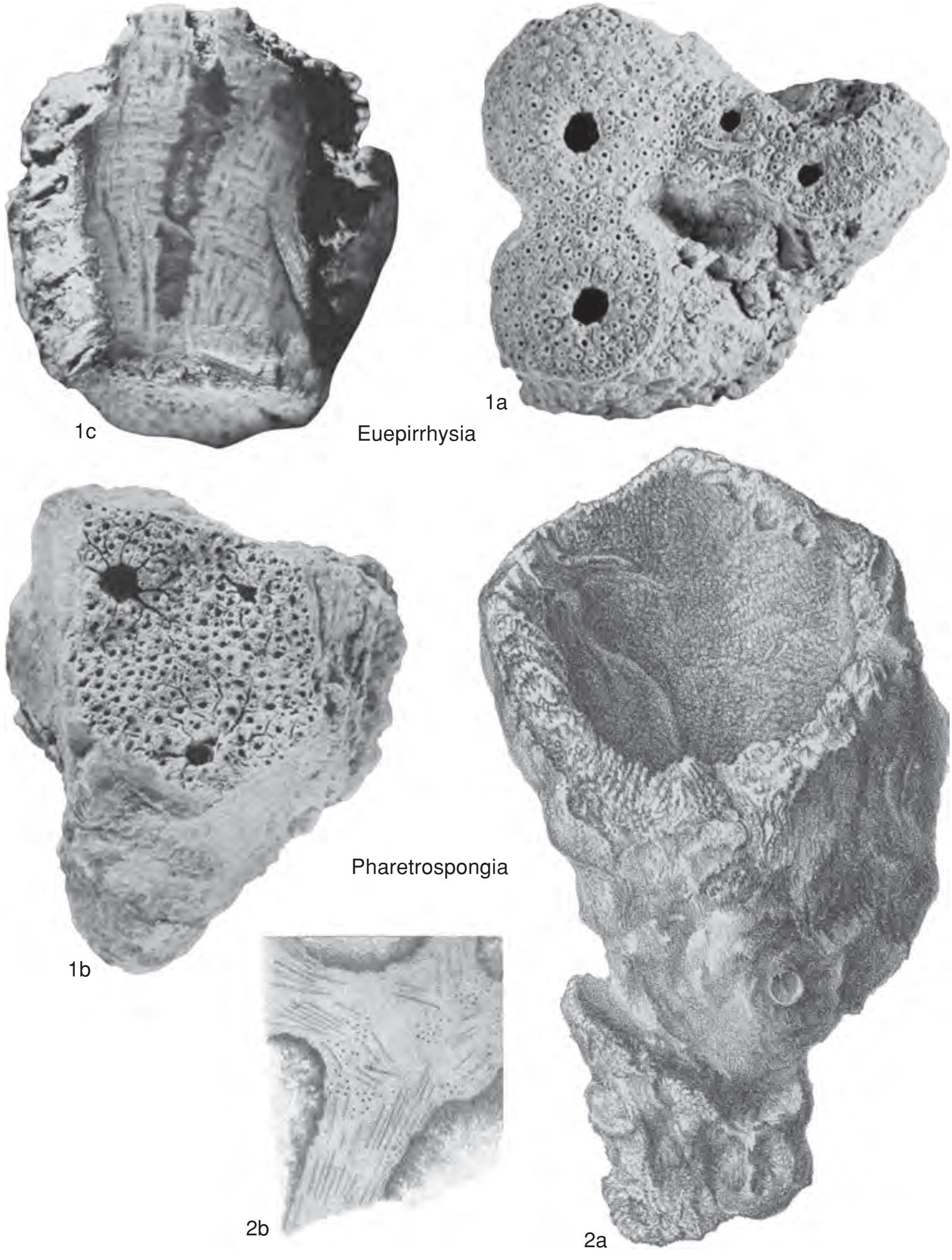


FIG. 401. Pharetrospongiidae (p. 614).

covered with imperforate, dermal layer; pores on upper surface very small, closely spaced, some circular or subpolygonal, but mostly meandriform, as openings of closely spaced, vertical-radial canals separated by thin trabeculae that have penicillate microstructure; it is not known whether type specimens have horizontal cross partitions, as in many sclerosponges; no spicules known. [This genus corresponds to *Leiospongia sensu* DIECI, RUSSO, & RUSSO (1974b, p. 138) *non* D'ORBIGNY (1849, p. 548).] *Triassic:* Europe.——FIG. 402,*2a–b*. **L. milleporata* (MÜNSTER), San Cassiano Formation,

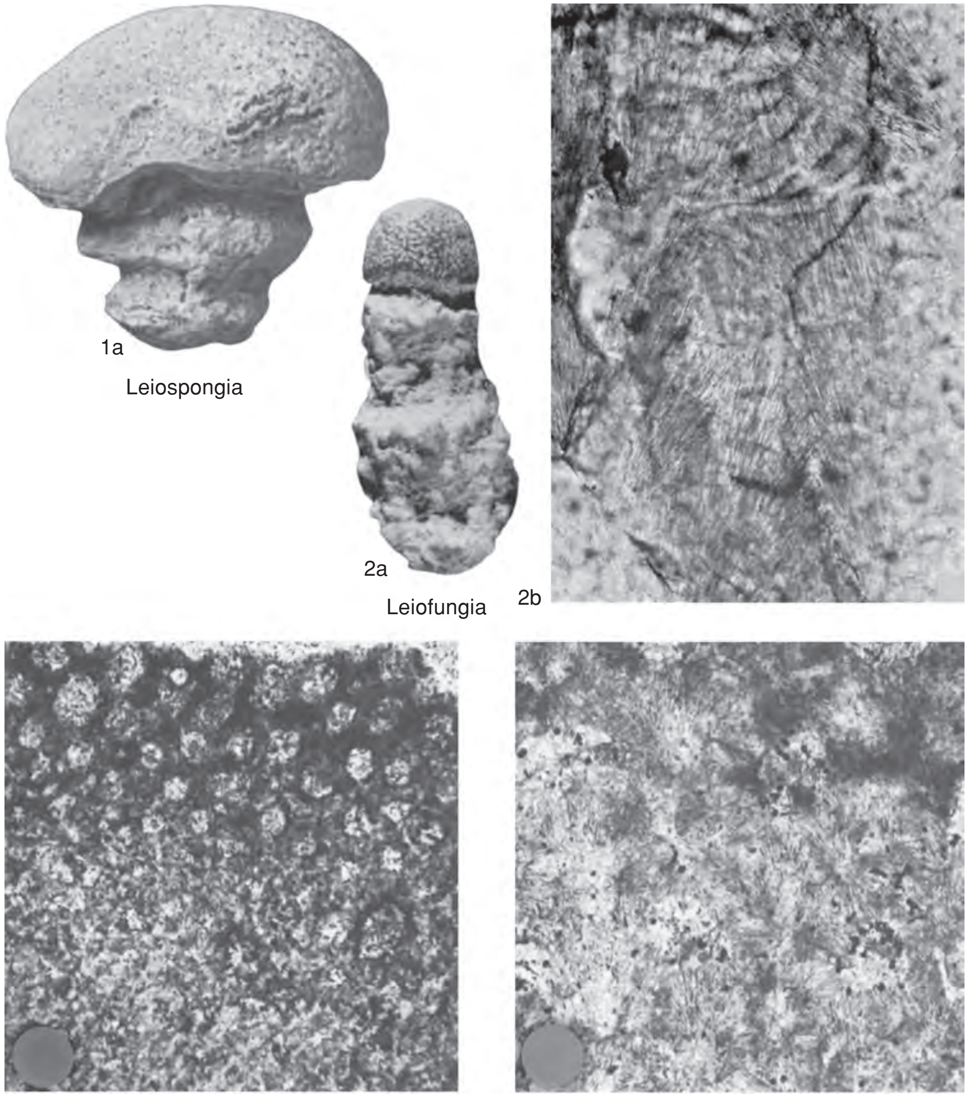


FIG. 402. Pharetrospongiidae (p. 614–618).

Carnian, Dolomite Alps, Italy; *a,* side view of holotype with imperforate, dermal layer and porous, upper surface, ×5; *b,* photomicrograph of longitudinal section with penicillate, crystalline fibers, SSPHG AS VII 445, ×250 (Dieci, Russo, & Russo, 1974b).

Aulacopagia POMEL, 1872, p. 245 [**Leiospongia maeandrina* D'ORBIGNY, 1850, vol. 1, p. 295; OD]. Resembles *Leiofungia* FROMENTEL, 1860a, but upper surface bearing meandriform furrows; internal structure unknown and may not be related. [No known suitable figures.] *Jurassic:* Europe.

Elasmopagia POMEL, 1872, p. 246 [**E. anomala;* OD]. Possibly flabellate or vertically laminar sponge with concentrically wrinkled, dermal layer covering sides, porous, skeletal net visible only at top. [Otherwise genus resembles "*Leiospongia* D'ORBIGNY, 1849" (i.e., *Leiofungia* FROMENTEL, 1860a, or *Hartmanina* DIECI, RUSSO, & RUSSO, 1974b) of which it was proposed as a subgenus. It was not illustrated and the internal structure is not known.] *Cretaceous:* France.

Grossotubenella RIGBY, FAN, & ZHANG, 1989b, p. 794 [**G. parallela;* OD]. Cylindrical to subcylindrical

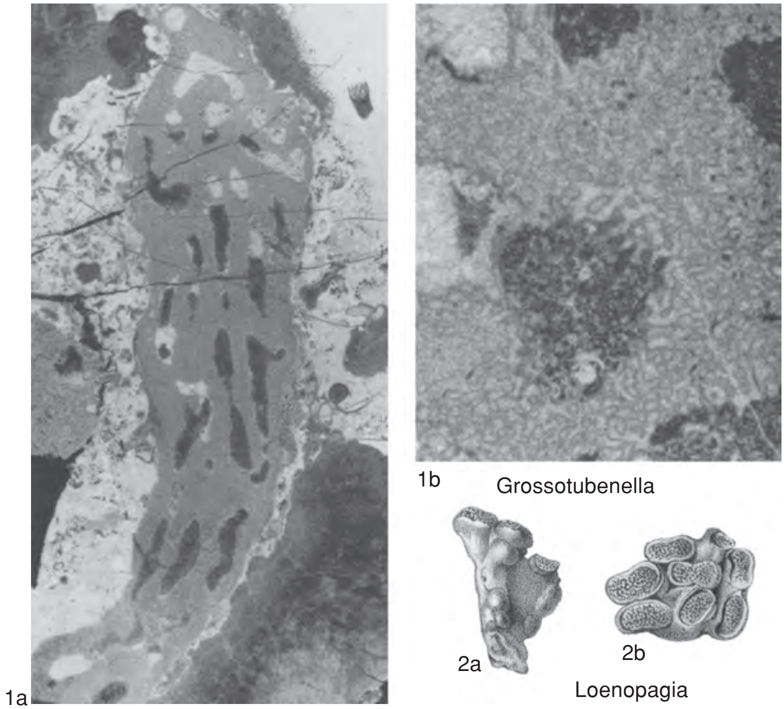


FIG. 403. Pharetrospongiidae (p. 616–618).

sponges without a spongocoel but with a weakly annulate exterior; interior with many coarse, nearly equally spaced, subvertical, subparallel to sinuous, exhalant canals that branch upwardly, infrequently; incurrent canals not evident. Skeleton even textured, composed of fine, vermiform fibers, pierced throughout by small, irregular, skeletal pores; spicules unknown. [Included in the family and subfamily with some question.] *Permian (Guadalupian):* China (Guangxi).——FIG. 403,*1a–b*. **G. parallela,* Maokou Formation, Kungurian, Longlin County; *a,* vertical section of holotype showing cavernous interior with coarse, vertical canals separated by coarse tracts of fine, fibrous skeleton, ×2; *b,* photomicrograph showing fine, fibrous skeleton in tracts between unlined canals, IGASB 5216, ×20 (Rigby, Fan, & Zhang, 1989b).

Leiospongia D'ORBIGNY, 1849, p. 548 [**Achilleum granulosum* MÜNSTER, 1841, p. 26; SD FINKS & RIGBY, herein] [=?*Hartmanina* DIECI, RUSSO, & RUSSO, 1974b, p. 141 (type, *Achilleum verrucosum* MÜNSTER, 1841, p. 25)]. Spheroidal or hemispherical to encrusting sponges with almost straight calicles, divided irregularly by tabulae; walls and tabulae of penicillate, aragonitic structure; distinct dermal layer absent; surface bearing closely spaced, fine, equidimensional pores of subequal size, and edges of intervening trabeculae bearing fine granules; spicules fusiform styles or acanthostyles irregularly present and parallel to growth direction. [Only two species, *Achilleum granulosum* and *A. verrucosum,* KLIPSTEIN, 1843 in 1843–1845, were cited (as examples) in connection with *Leiospongia* when D'ORBIGNY established the genus in November, 1849 (p. 548). *Prodrome de Paleontologie,* sometimes cited as the first publication of the genus, was published in January, 1850 according to ENGESER and TAYLOR (1989, p. 41–42). According to Article 67.2 of the *Code* (ICZN, 1999), a nominal species that was not included when a new nominal genus was established cannot be validly designated or indicated as the type species of that genus. Thus the subsequent designation of *Achilleum milleporatum* MÜNSTER, 1841 as type of *Leiospongia* D'ORBIGNY, 1849 by DE LAUBENFELS (1955, p. 100) is not valid. *Achilleum verrucosum* was chosen by DIECI, RUSSO, and RUSSO (1974b, p. 141) as type of their new genus *Hartmanina,* which they separated from *Leiospongia* on the basis of its possession of a spherulitic skeleton rather than a penicillate one, among other features. If one is not to sink *Hartmanina* into synonymy with *Leiospongia,* one must choose the remaining species originally included by D'ORBIGNY, namely *Achilleum granulosum* MÜNSTER, 1841 (the ascription to KLIPSTEIN by D'ORBIGNY is to a subsequent description of MÜNSTER's species) as the type species for *Leiospongia.* So far as we know, the microstructure of *L. granulosum* has not been published, nor have we seen the holotype. Hopefully for the retention of

Hartmanina, it is not spherulitic, but the finer pores and denser skeleton would justify a separation in any case.] *Triassic:* Europe, Timor.——Fig. 402,*1a–c. L. alpina* (Klipstein), Cassian Formation, lower Carnian, St. Cassian, Italy; *a,* side view of holotype, BMNH S10462, ×1; *b,* transverse section through calicles, ×35; *c,* spherulitic structure of wall, ×130 (Engeser & Taylor, 1989).

Loenopagia Pomel, 1872, p. 245 [**Tragos ramosum* Klipstein, 1843 in 1843–1845, p. 283; OD]. Partly fused, subparallel, conicocylindrical branches, covered laterally by dermal layer; rounded, finely porous upper surface of each branch forming knob on colony surface. [Genus resembles a compound *Leiofungia* Fromentel, 1860a, and could well be that genus, but nothing is known of the internal structure, microstructure, or spicules of *Loenopagia.*] *Triassic:* Europe.——Fig. 403,*2a–b.* **L. ramosum* (Klipstein), Cassian beds, Tyrol area, Austria; *a,* side view of branched, small sponge with dense, dermal layer and porous summit, ×1; *b,* view down onto summit of sponge showing porous, exhalant surfaces of branch tips, ×1 (Klipstein, 1843 in 1843–1845).

Radicanalospongia Rigby, Fan, & Zhang, 1989b, p. 798 [**R. normala;* OD]. Encrusting, commonly forming cylindrical, budding growths with dense, basal layer; pseudocentral, spongocoel-like tube may form where sponges encrusted soft-bodied organisms; many regularly stacked, cylindrical, exhalant canals piercing fibrous skeleton and may assume radial pattern in cylindrical growths; less common and smaller, longitudinal and radial, incurrent canals connecting exhalant canals; skeletal fibers evenly spaced around skeletal canals to produce fine-textured skeleton between coarse canals; spicules and microstructure unknown. *Permian (Guadalupian):* China (Guangxi).——Fig. 404*a–c.* **R. normala,* Maokou Formation, Kungurian; *a,* oblique section of subcylindrical, encrusting holotype with imperforate base over dark, central matrix and stacked, regular series of radial canals, IGASN 5090, ×2; *b,* encrusting bases of paratype showing radial canals in walls around dark matrix, IGASB 5088, ×2; *c,* photomicrograph of fine, fibrous, skeletal net between uniform, radiating canals in holotype, IGASB 5090, ×10 (Rigby, Fan, & Zhang, 1989b).

Family AURICULOSPONGIIDAE Termier & Termier, 1977

[Auriculospongiidae Termier & Termier, 1977a, p. 29] [=Tubulispongiidae Wu Ya Sheng, 1991, p. 35]

Sheet- or platelike sponges with one side inhalant and other side exhalant surface, with or without prominent canals; skeleton of fibers parallel to growth direction, with spherulitic microstructure, probably aragonitic. *Permian (Asselian–Changhsingian).*

Subfamily AURICULOSPONGIINAE Termier & Termier, 1977

[*nom. transl.* Rigby & Senowbari-Daryan, 1996a, p. 26, *pro* Auriculospongiidae Termier & Termier, 1977a, p. 29]

Auriculospongiids without inhalant canals but with exhalant canals on one side; interfiber spaces serving as inhalant openings. *Permian (Asselian–Changhsingian).*

Auriculospongia Termier & Termier, 1974, p. 247 [**Phacellopegma auriculata* Termier & Termier, 1955, p. 625; OD]. Earlike to palmate, bladed sponges with both inhalant and exhalant surfaces marked by tangential, moderately deep furrows that are smaller on inhalant side; skeletal fibers dominantly parallel growth direction and composed of spherulites. *Permian (Lopingian):* Tunisia.——Fig. 405*a–b.* **A. auriculata* (Termier & Termier), Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* inhalant side showing irregular, small pores and larger, mounded ostia, ×1; *b,* diagram of arrangement of skeletal fibers within a club-shaped specimen, not to scale (Rigby & Senowbari-Daryan, 1996a).——Fig. 406*a–c.* **A. auriculata* (Termier & Termier), Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* exhalant upper surface with a prominent system of divergent furrows in which exhalant ostia are situated, USNM 463571, ×1; *b,* photomicrograph of upper surface with indented canals separated by irregular nodes of light, skeletal fibers around dark, skeletal pores, USNM 463574, ×10; *c,* SEM photomicrograph of rigid skeleton composed of spherulites, USNM 463577, scale indicated by bar at base (Rigby & Senowbari-Daryan, 1996a).

Cavusonella Rigby, Fan, & Zhang, 1989b, p. 796 [**C. caverna;* OD]. Cylindrical, uneven to undulating exteriors; interiors pierced by coarse, irregular openings that may bifurcate upwardly and may make up to one-half sponge volume; prominent, continuous, longitudinal canals and continuous central spongocoel absent; skeleton of irregular fibers in loose, upwardly and outwardly expanding pattern. *Permian (Guadalupian–Lopingian):* China (Guangxi), *Guadalupian;* Tunisia, *Lopingian.*——Fig. 407,*1a–d.* **C. caverna; a,* sublongitudinal section of holotype with irregular, coarse canals in relatively fine, upwardly divergent, fibrous skeleton, Maokou Formation, Kungurian, Guangxi, IGASB 5201, ×2; *b,* transverse section of paratype with coarse canals in interior, Maokou Formation, Kungurian, Guangxi, IGASB 5195, ×2 (Rigby, Fan, & Zhang, 1989b); *c,* side view of club-shaped sponge with small, inhalant ostia on ridges between large, exhalant ostia, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia, ×2; *d,* weathered exterior with uniform, skeletal net in coarse tracts between coarse canals, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia,

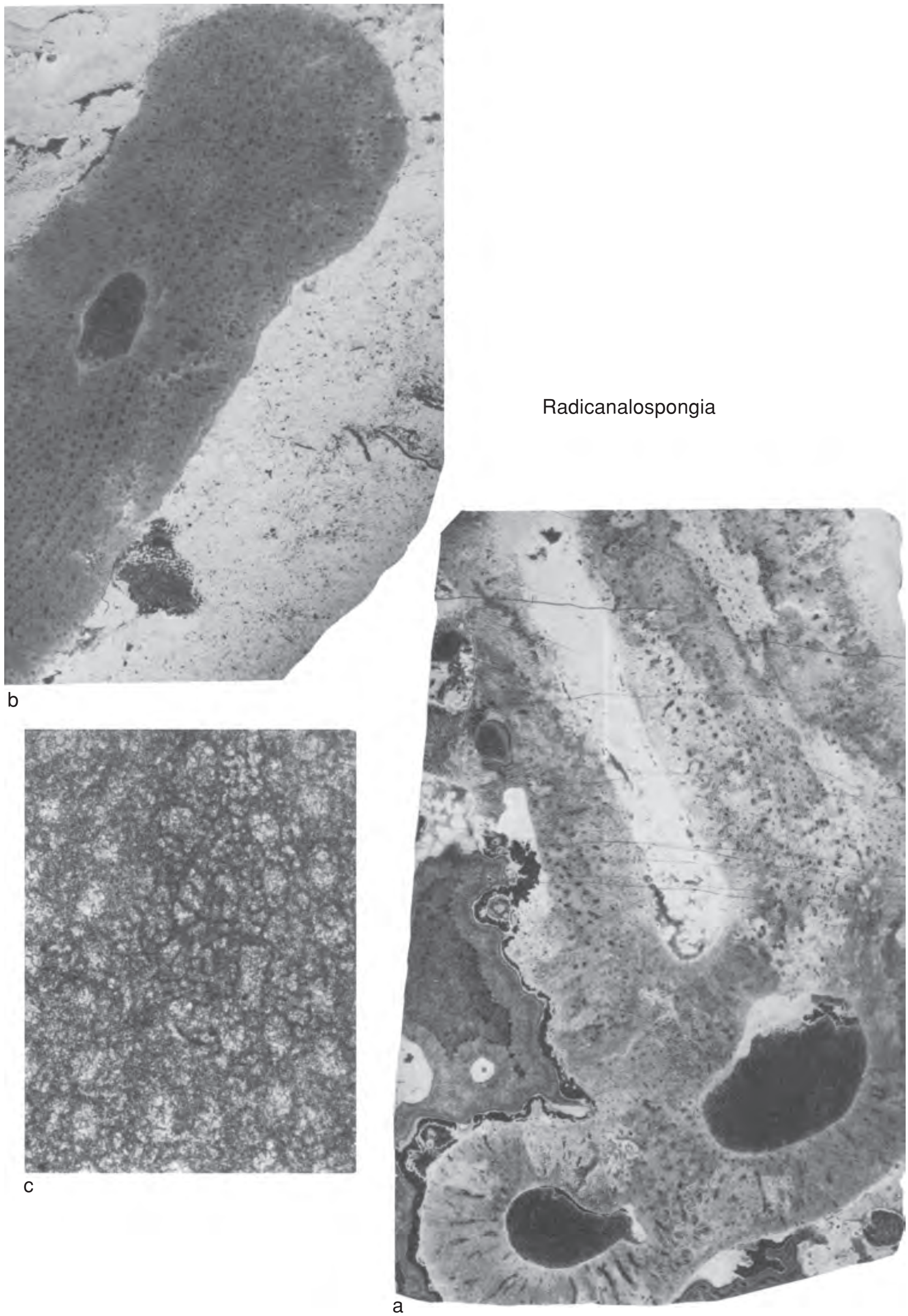


FIG. 404. Pharetrospongiidae (p. 618).

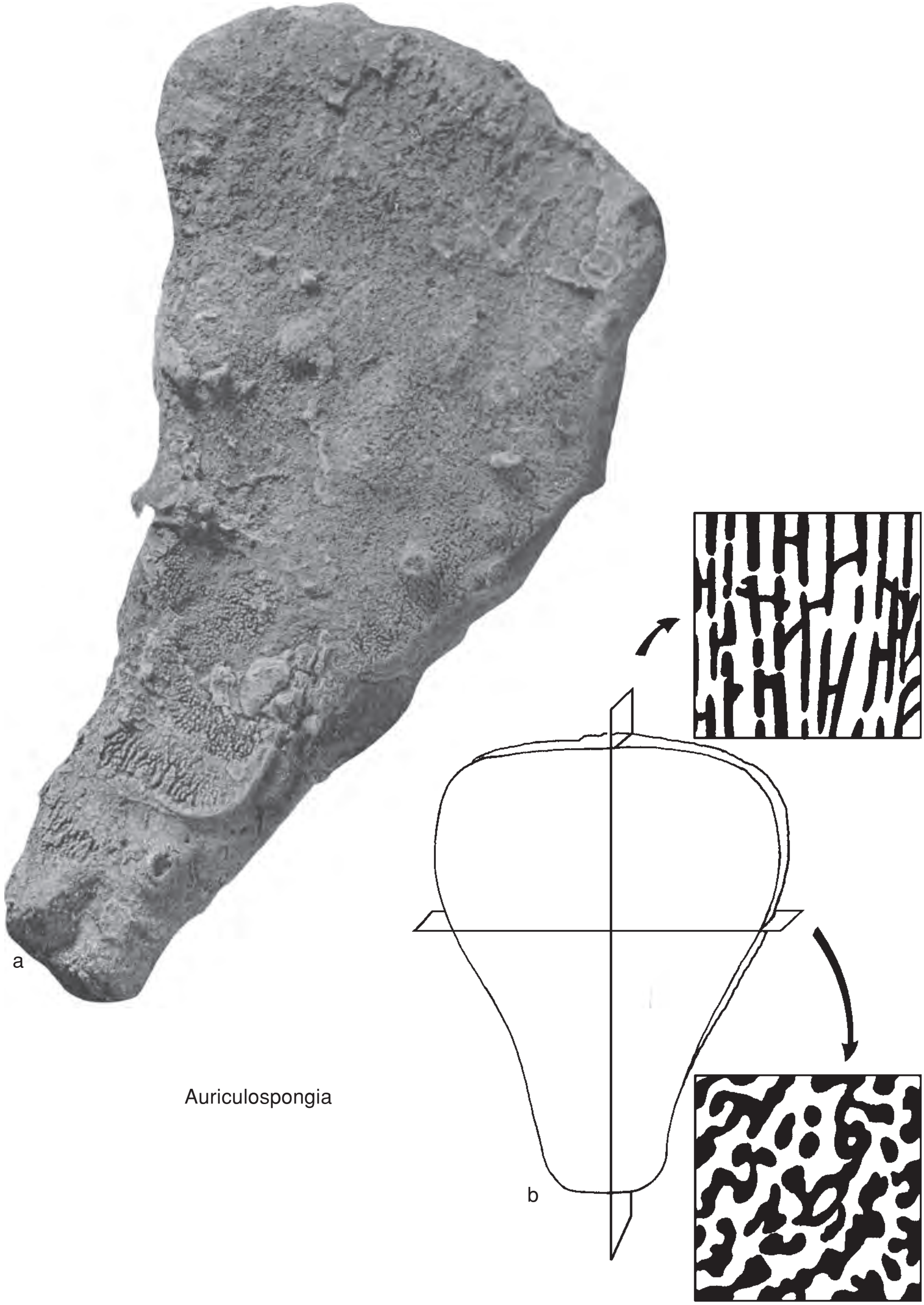
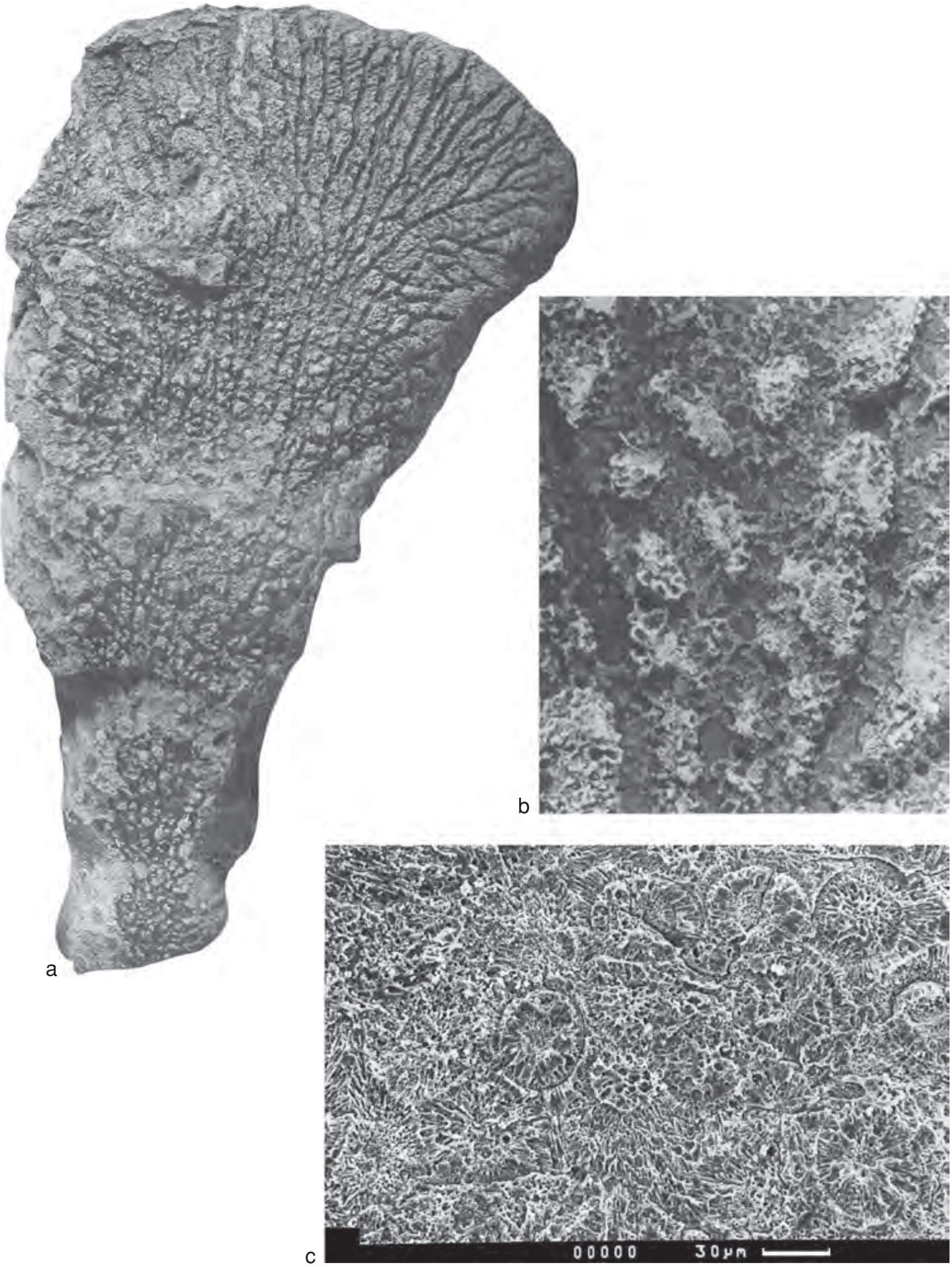


FIG. 405. Auriculospongiidae (p. 618).



Auriculospongia

FIG. 406. Auriculospongiidae (p. 618).

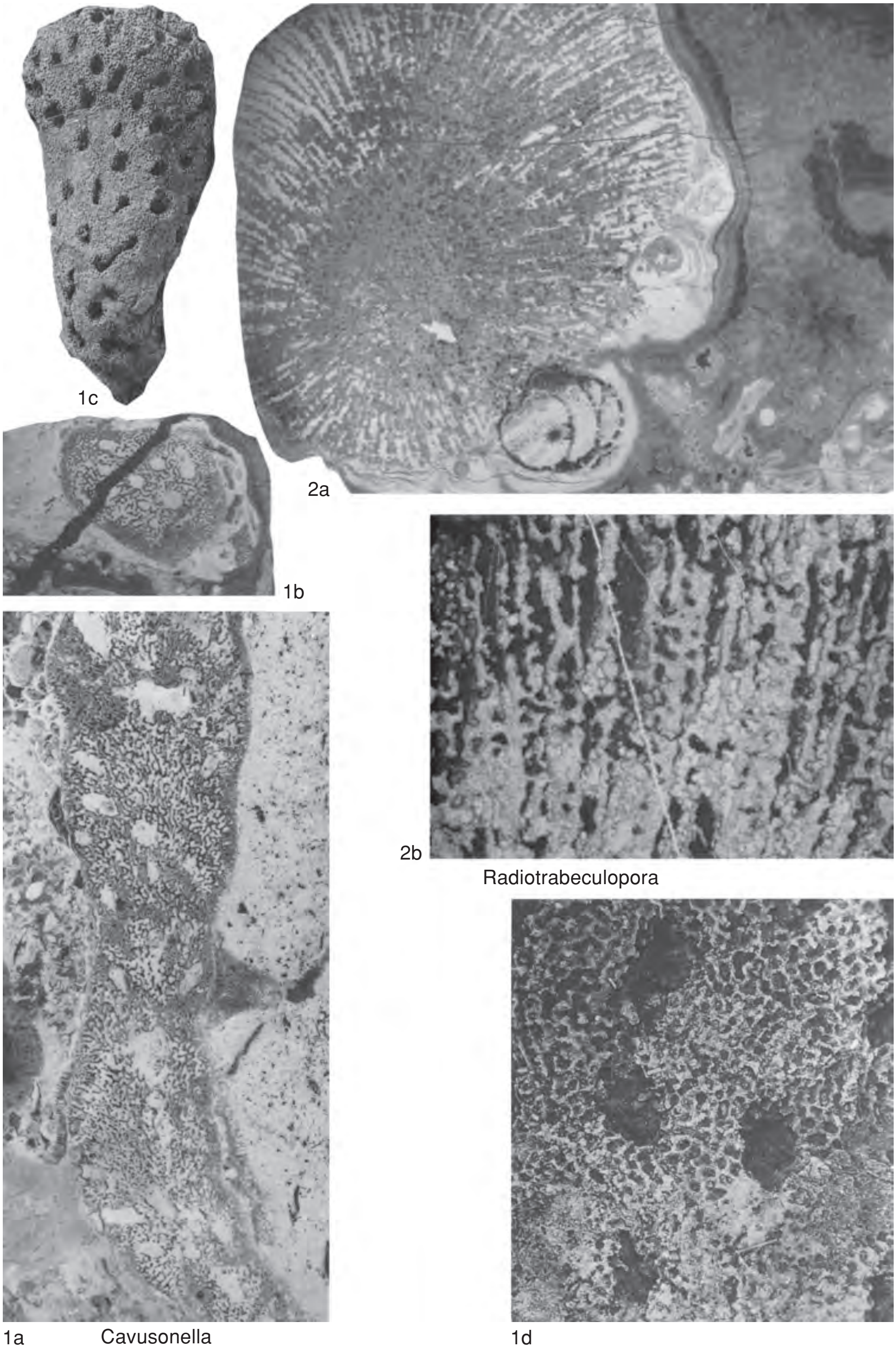


FIG. 407. Auriculospongiidae (p. 618–624).

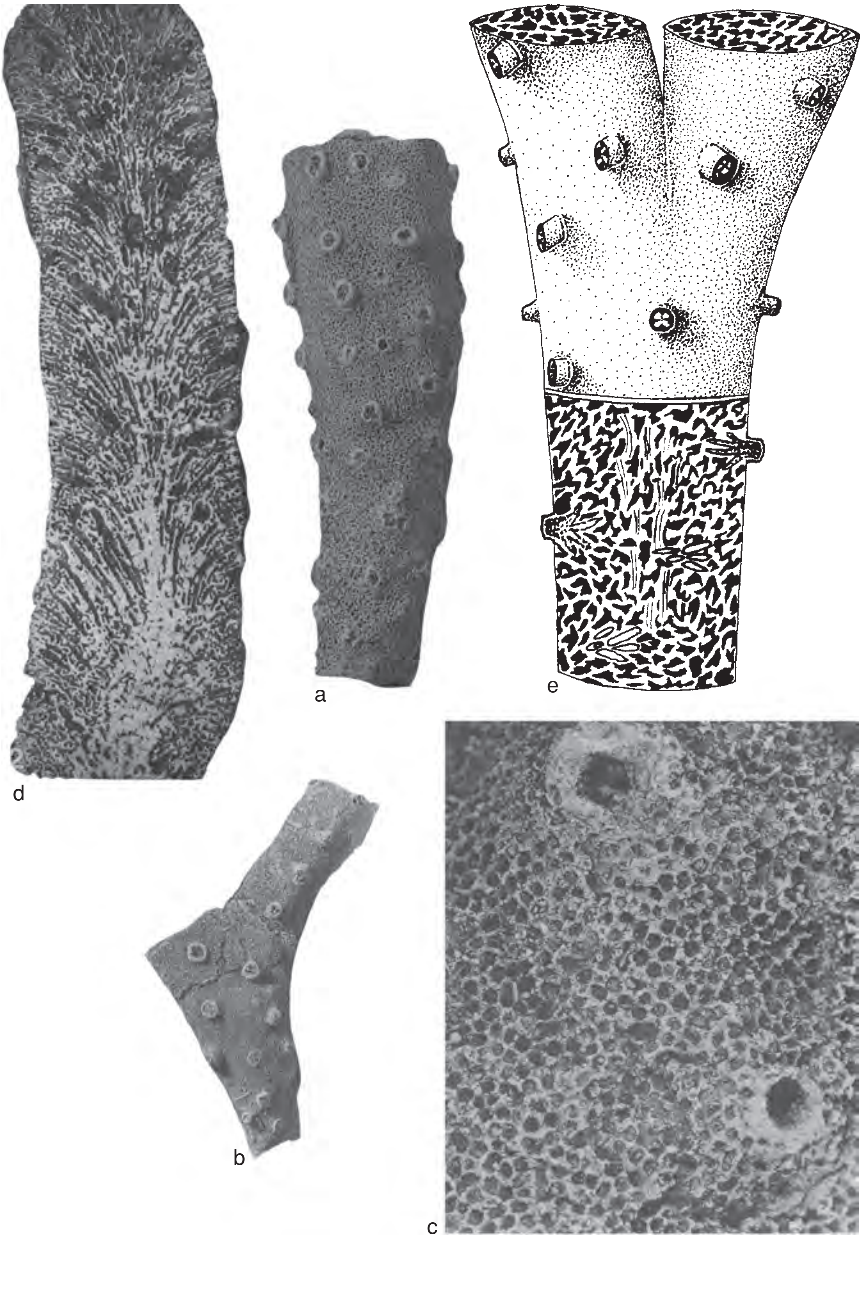


FIG. 408. Auriculospongiidae (p. 624).

USNM 463589, ×10 (Rigby & Senowbari-Daryan, 1996b).

Radiotrabeculopora Fan, Rigby, & Zhang, 1991, p. 56 [**R. xiangboensis;* OD] [=*Tubulispongia* Wu Ya Sheng, 1991, p. 35 (type, *T. concentrica,* OD); *Flabellisclera* Wu Ya Sheng, 1991, p. 36 (type, *F. discreta,* OD); *Gigantosclera* Wu Ya Sheng, 1991, p. 38 (type, *G. deformis,* OD); *Gracilitubulus* Wu Ya Sheng, 1991, p. 39 (type, *G. perforatus,* OD); *Fungispongia* Wu Ya Sheng, 1991, p. 39 (type, *F. circularis* Wu Ya Sheng, 1991, p. 40, OD)]. Cylindrical to massive, obconical or mushroom- to club-shaped sponges with skeleton of many trabeculae of various diameters that are essentially longitudinal and parallel to each other; trabeculae may merge into single, coarse elements or coarse ones may divide into slender ones; canals between trabeculae diverging upwardly with moderate range of diameters; many smaller pores irregularly interrupting trabeculae; skeletal structure aragonitic with spherulitic microstructure. *Permian (Asselian–Changhsingian):* USA (California), *Asselian–Sakmarian;* China (Guangxi, Yunnan), *Guadalupian;* China (Guangxi, Hubei), Tunisia, *Lopingian.*——Fig. 407,*2a–b.* **R. xiangboensis,* Maokou Formation, Kungurian, Xiangbo, Guangxi, China; *a,* cross section of spheroidal holotype with irregular, radial trabeculae and canals, which has overgrown sphinctozoan sponge at base, projection print of thin section, IGASB 5154, ×2; *b,* thin section parallel to radial skeleton showing coarse, radial and horizontal trabeculae, coarse pores, and larger canals, IGASB 5154, ×5 (Fan, Rigby, & Zhang, 1991).

Subfamily DAHARELLINAE Rigby & Senowbari-Daryan, 1996

[Daharellinae Rigby & Senowbari-Daryan, 1996a, p. 34]

Auriculospongiids without exhalant canals, but with distinct, tubelike, inhalant canals; spaces between fibers serving as exhalant openings. *Permian (Changhsingian).*

Daharella Rigby & Senowbari-Daryan, 1996a, p. 34 [**D. ramosa;* OD]. Branched to unbranched, cylindrical to palmate sponges that lack a continuous spongocoel or axial bundle of exhalant canals; exterior with numerous circular to starlike, inhalant ostia on tips of tubelike canals; sievelike plate may be developed at base of each ostium, openings may continue into interior as separate, inhalant tubes; skeleton fibrous reticulate. [*Daharella* lacks an axial spongocoel or common, through-going, longitudinal, exhalant canals. The co-occurring and externally similar-appearing *Preeudea* has numerous, vertical, exhalant tubes and *Djemelia* has a well-defined, axial spongocoel.] *Permian (Changhsingian):* Tunisia.——Fig. 408*a–e.* **D. ramosa,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* side view of branched holotype in which exhalant pores have distinct rims, USNM 463593, ×1; *b,* side view of simple paratype with characteristic dermal surface and rimmed ostia, USNM 463952, ×2; *c,* photomicrograph of exterior with rimmed, coarse, exhalant ostia in uniform net of fine fibers around skeletal pores, USNM 480411, ×10; *d,* longitudinal section showing arrangements of skeletal fibers and canals ending at surface, USNM 463594, ×3; *e,* schematic diagram showing skeletal and canal structure of genus, not to scale (Rigby & Senowbari-Daryan, 1996a).

Subfamily GIGANTOSPONGIINAE Rigby & Senowbari-Daryan, 1996

[Gigantospongiinae Rigby & Senowbari-Daryan, 1996b, p. 351]

Sheetlike to palmate auriculospongiids with both inhalant and exhalant, transverse canals and major, longitudinal, exhalant canals; spongocoels and oscula absent. *Permian (Guadalupian).*

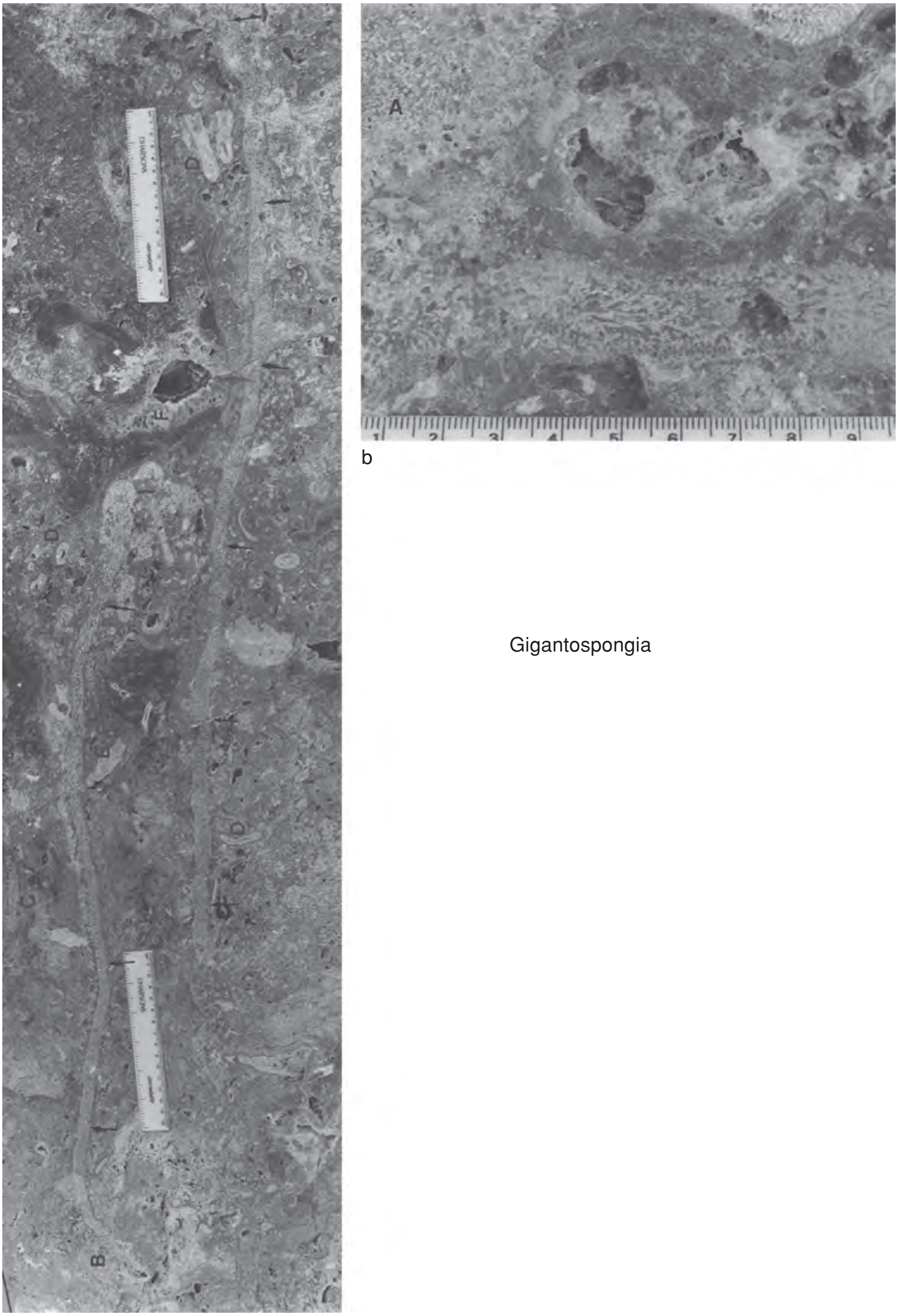
Gigantospongia Rigby & Senowbari-Daryan, 1996b, p. 353 [**G. discoforma;* OD]. Large, discoidal, inozoid sponges with distinct and prominent, divergent to parallel, longitudinal-radial canals, with more irregular, transverse canals generally at right angles or steep angles to dermal-gastral surfaces; limited, astrorhizal development may occur on dermal surface; skeletal tracts subhorizontally and radially divergent, parallel to tubular canals, tracts cross connected by irregular to columnar, vertical, subparallel elements in transverse sections. Skeletal microstructure unknown. *Permian (Guadalupian):* USA (New Mexico).——Fig. 409*a–b.* **G. discoforma,* Capitan Limestone, Guadalupian, Guadalupe Mountains, New Mexico; *a,* part of large horizontal holotype, below (left), and reference specimen, above, in field exposure (*arrows*), scales in inches and centimeters; *b,* vertical section through holotype showing differentiated, upper and lower layer and canals divergent in direction of growth, scale in centimeters (Rigby & Senowbari-Daryan, 1996b).

Subfamily SPINOSPONGIINAE Rigby & Senowbari-Daryan, 1996

[Spinospongiinae Rigby & Senowbari-Daryan, 1996a, p. 37]

Cylindrical to club-shaped auriculospongiids lacking inhalant and exhalant canals; skeleton with prominent, thornlike spines. *Permian (Changhsingian).*

Spinospongia Rigby & Senowbari-Daryan, 1996a, p. 37 [**S. radiata;* OD]. Cylindrical to club-shaped sponges lacking a central spongocoel or other coarse, exhalant and inhalant canals; exterior marked by tips of spinelike, skeletal elements that



b

Gigantospongia

a

FIG. 409. Auriculospongiidae (p. 624).

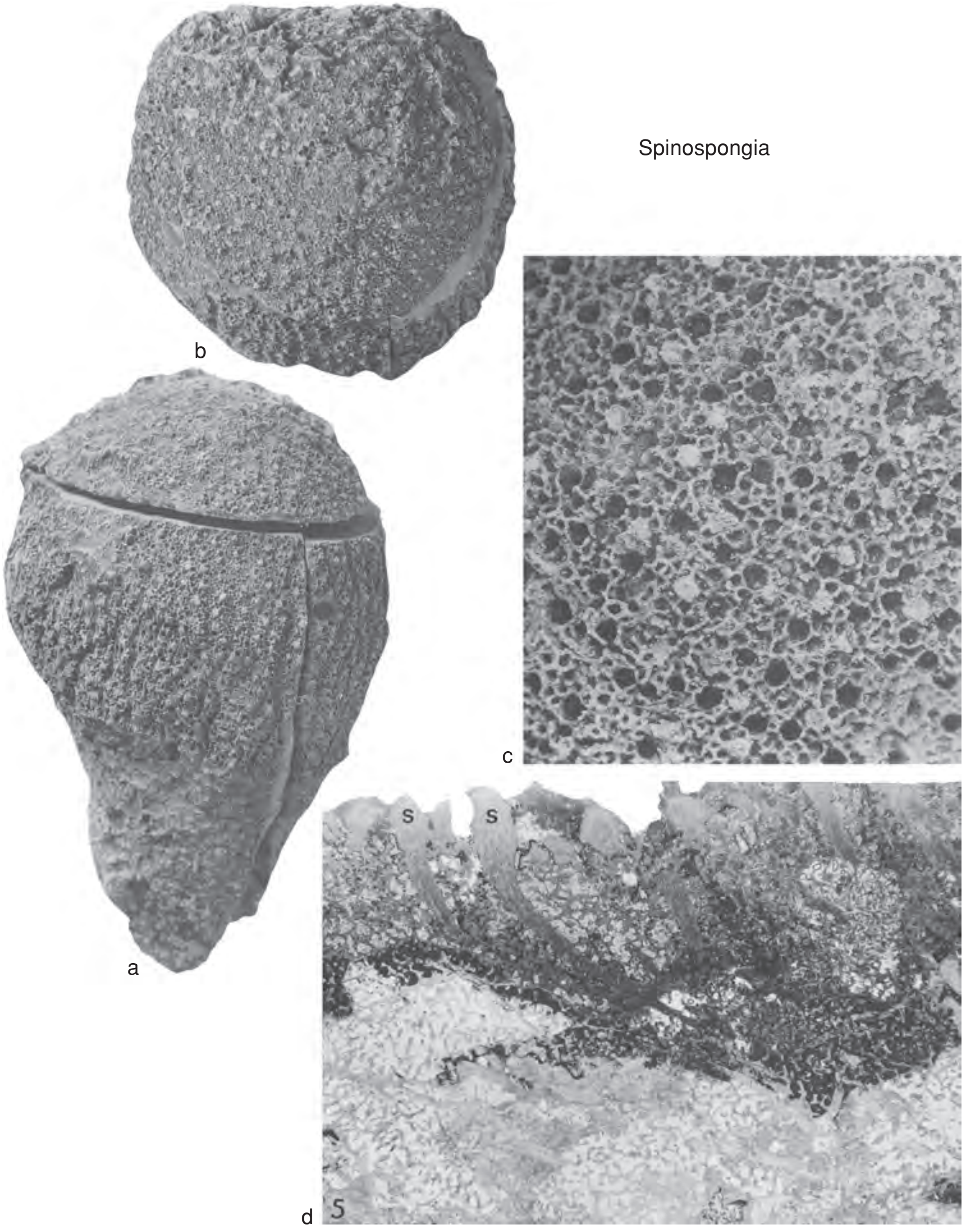


FIG. 410. Auriculospongiidae (p. 624–627).

continue into interior and help form skeleton; coarse, discontinuous openings between spines; interior with reticulate, fibrous skeleton composed of spherulites. *Permian (Changhsingian):* Tunisia.——FIG. 410*a–d*. **S. radiata,* Djebel Tebaga Biohermal Complex, Djebel Tebaga; *a,* side view of rounded, obconical holotype, spherical tips of spinose, skeletal rods show as light dots, small openings between spines do not extend far into interior as canals, ×2; *b,* top view of holotype, spongocoel absent, USNM 464611, ×2; *c,* prominent spines are light, elevated areas in dermal surface of paratype, with skeletal fibers outlining skeletal pores and round, inhalant openings, USNM 463613, ×10; *d,* photomicrograph of section showing spines (*s*) that diverge upwardly and outwardly to dermal surface, internal

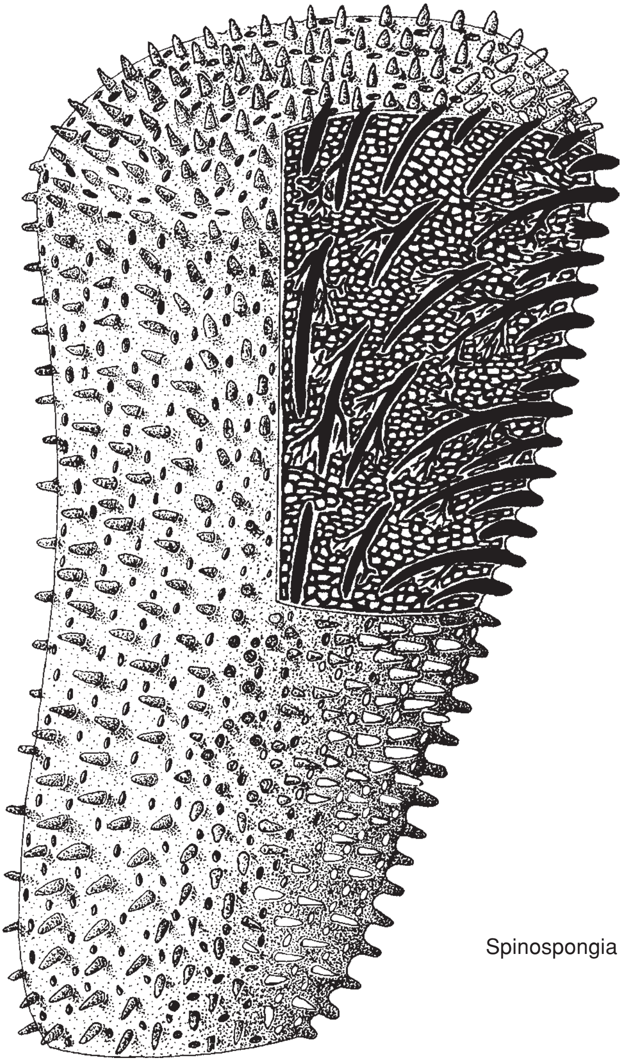


FIG. 411. Auriculospongiidae (p. 624–627).

spaces between spines filled with bubblelike, skeletal tracts, USNM 463615, ×5 (Rigby & Senowbari-Daryan, 1996a).——FIG. 411. **S. radiata,* Djebel Tebaga Biohermal Complex, Djebel Tebaga; schematic diagram showing outer morphology and structure of skeleton in longitudinal section, not to scale (Rigby & Senowbari-Daryan, 1996a).

Subfamily ACOELIINAE Wu, 1991

[*nom. transl.* FINKS & RIGBY, herein, *ex* Acoeliidae WU Ya Sheng, 1991, p. 57]

Cylindrical to club-shaped or obconical sponges lacking a spongocoel or significant inhalant and exhalant canals in spherulitic, fibrous, skeletal net. *Permian (Guadalupian–Lopingian).*

Acoelia WU Ya Sheng, 1991, p. 57 [**A. ruida;* OD]. Sponges moderately large, obconical, curved, with skeleton of thick fibers that are somewhat discontinuous and of moderately uniform diameters; interconnected spaces between fibers circular in longitudinal sections; dermal layer not developed. *Permian (Guadalupian):* China (Guangxi).——FIG. 412,*1. *A. ruida,* reef of Xiangbo, Guadalupian; holotype section of irregular, thick fibers lacking coarse canals and dermal layer, xb27-6-2, ×3 (Wu Ya Sheng, 1991).

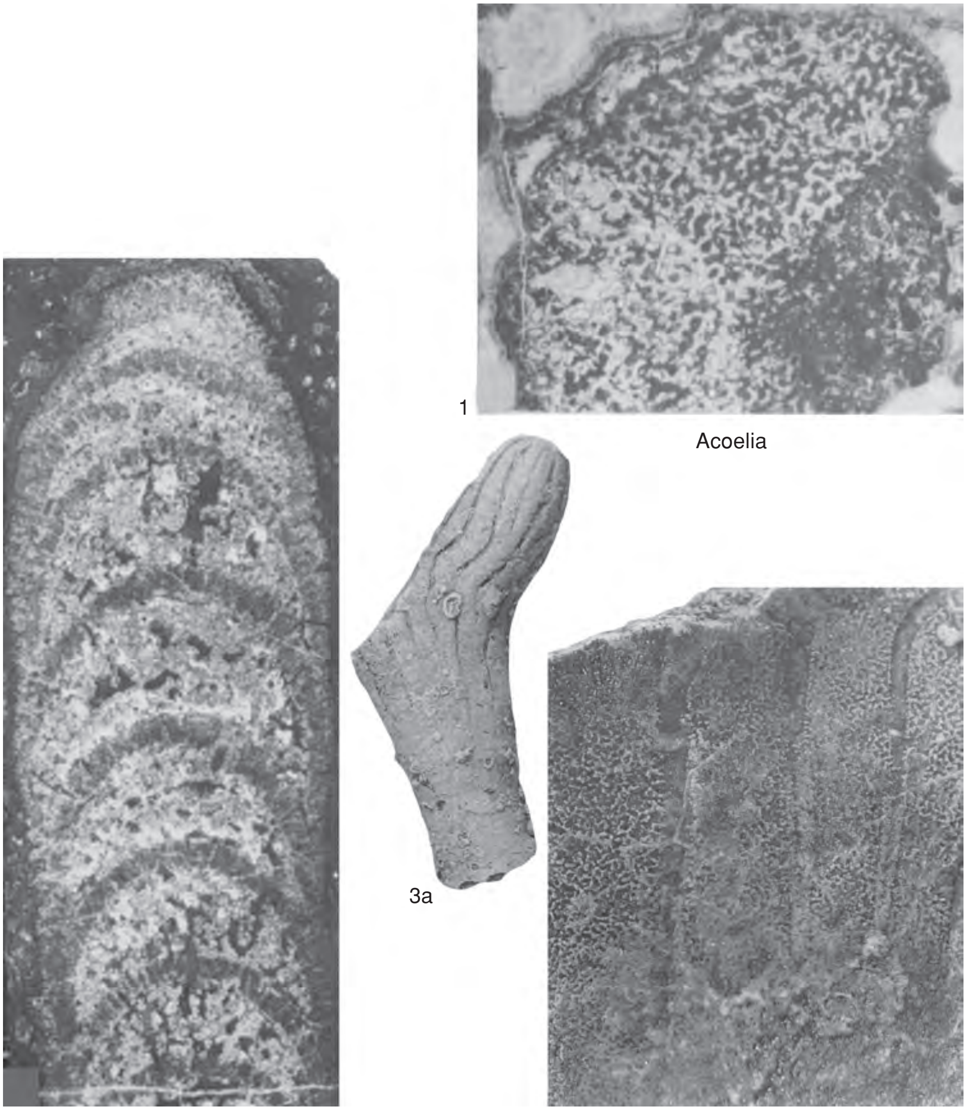


FIG. 412. Auriculospongiidae (p. 627–629).

Solutossaspongia SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994, p. 25 [**S. crassimuralis* SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994, p. 26; OD]. Cylindrical, unbranched sponges with distinct, thick, outer wall; skeleton of interior composed of loose, reticular fibers; spongocoel absent. [SENOWBARI-DARYAN and INGAVAT-HELMCKE (1994) concluded that the family Acoeliidae and the genus *Acoelia* WU Ya Sheng, 1991, were based on inadequate samples that may have been only tangential sections of other sponges. *Solutossaspongia* differs from WU's genus in having a thick, outer wall and a loosely packed, fibrous, internal skeleton. They were reluctant to include the genus in the Acoeliidae and instead included it in the inozoa but in family Uncertain.] *Permian (Lopingian):* Thailand.——FIG. 412,*2.* **S. crassimuralis,* upper Permian limestone, Dorashamian, Phrae; holotype section with thick, outer wall and open, endosomal, reticulate skeleton, BSPGM R15, ×3.5 (Senowbari-Daryan & Ingavat-Helmcke, 1994).

Thallospongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 38 [**T. reticulata;* OD]. Branching, solid, small, twiglike sponges lacking spongocoel or major internal, canal system in uniform, upwardly divergent skeleton; upper exterior with impressed, subvertical canals that converge to upper tip. *Permian (Lopingian):* Tunisia.——FIG. 412,*3a–b.* **T. reticulata,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* side view of holotype showing branching form, ×2; *b,* photomicrograph of exterior of holotype showing indented, vertical canals in fine, skeletal net, USNM 4480358, ×10 (Rigby & Senowbari-Daryan, 1996a).

Family STELLISPONGIELLIDAE Wu, 1991

[Stellispongiellidae WU Ya Sheng, 1991, p. 65]

Massive to hemispherical or stemlike to obconical sponges lacking a spongocoel but upper or outer surface including one to several oscula or astrorhizal clusters of exhalant canals; canals of cluster may extend into interior; fibrous skeleton aspiculate, commonly reticulate, with spherulitic microstructure; dense, dermal layer may be present on base. *Permian (Guadalupian)–Triassic (Norian).*

Subfamily STELLISPONGIELLINAE Wu, 1991

[*nom. transl.* FINKS & RIGBY, herein, *ex* Stellispongiellidae WU Ya Sheng, 1991, p. 65]

Stellispongiellids in which starlike, oscular clusters of convergent, exhalant canals may be developed on mamelon-like mounds or impressed into generally smooth, upper or outer surface; sponges commonly ramose. *Permian (Guadalupian)–Triassic (Norian).*

Stellispongiella WU Ya Sheng, 1991, p. 65 [**Stellispongia bacilla* TERMIER & TERMIER, 1955, p. 622; OD] [=*Stellispongia* TERMIER & TERMIER, 1955, p. 620, obj., *non* D'ORBIGNY, 1849]. Cylindrical, stemlike to branched or palmate to irregularly encrusting sponges with numerous uniformly distributed oscula to which converge exhalant canals in a stellate pattern; oscula may be on nodes, on smooth exteriors, or impressed into stems; exterior with numerous inhalant pores to short canals that may be lost in skeletal net or may lead to upwardly divergent, axial canals, which connect to radial, exhalant canals and ostia that may occur in tangential, oscular canals or on exterior between oscula; microstructure spherulitic; spongocoel absent. [These Permian sponges were grouped early with similar-appearing species in *Stellispongia* and the Stellispongiidae. Once the spiculate nature of the skeleton of Triassic and probably younger species of *Stellispongia* became known (REITNER, 1992), however, it was considered important that these aspiculate sponges be separated at generic and family levels.] *Permian (Guadalupian–Lopingian):* China (Guangxi), Tunisia; *Triassic (Norian):* ?Peru.——FIG. 413*a–d.* **S. bacilla* (TERMIER & TERMIER), Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; *a,* side view showing coarse, exhalant, astrorhizal canals on nodes with fine skeleton, USNM 480276, ×2; *b,* branched sponge with astrorhizal canal system on low nodes, USNM 480278, ×1; *c,* photomicrograph of node with indented, convergent, astrorhizal canals in reticulate, skeletal net, USNM 480412, ×10; *d,* generalized drawing showing canal patterns in skeleton and general morphology, not to scale (Rigby & Senowbari-Daryan, 1996a).——FIG. 413*e. S. reticulata* RIGBY & SENOWBARI-DARYAN, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; side view of holotype with well-preserved, astrorhizal, canal net, USNM 4464648, ×2 (Rigby & Senowbari-Daryan, 1996a).

Subfamily PRESTELLISPONGIINAE Rigby & Senowbari-Daryan, 1996

[Prestellispongiinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 49]

Massive to fungiform stellispongiellids with one to several exhalant openings on the summit that extend into interior as clusters of canals; smaller inhalant canals commonly from upper surface and between canals of surficial, starlike, astrorhizal, oscular clusters; skeleton a regular reticulation to one with longitudinally dominant fibers. *Permian (Lopingian).*

Prestellispongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 49 [**Stellispongia lobata* PARONA, 1933, p. 31; OD]. Irregularly obconical to hemispherical or mushroomlike sponges with one to several stellate, oscular clusters of exhalant canals on summit; numerous smaller, vertical or longitudinal inhalant canals in intervening spaces; skeletal structure regular reticulation of small fibers with spherulitic microstructure; spicules absent. *Permian (Lopingian):* Tunisia.——FIG. 414*a–d.* **P. lobata* (PARONA), Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* summit of sponge with several starlike, exhalant, canal clusters and small, inhalant ostia between, USNM 480369; *b,* side view of irregular, obconical sponge with encrusted, dense, dermal layer; *c,* summit view of same specimen with exhalant, canal clusters and small, circular, inhalant ostia, USNM 480366, ×1; *d,* schematic drawing of type (Rigby & Senowbari-Daryan, 1996a).——FIG. 414*e. P. permica* (PARONA); schematic drawing (Rigby & Senowbari-Daryan, 1996a).——FIG. 414*f. P. scapulata* RIGBY & SENOWBARI-DARYAN; schematic drawing (Rigby & Senowbari-Daryan, 1996a).

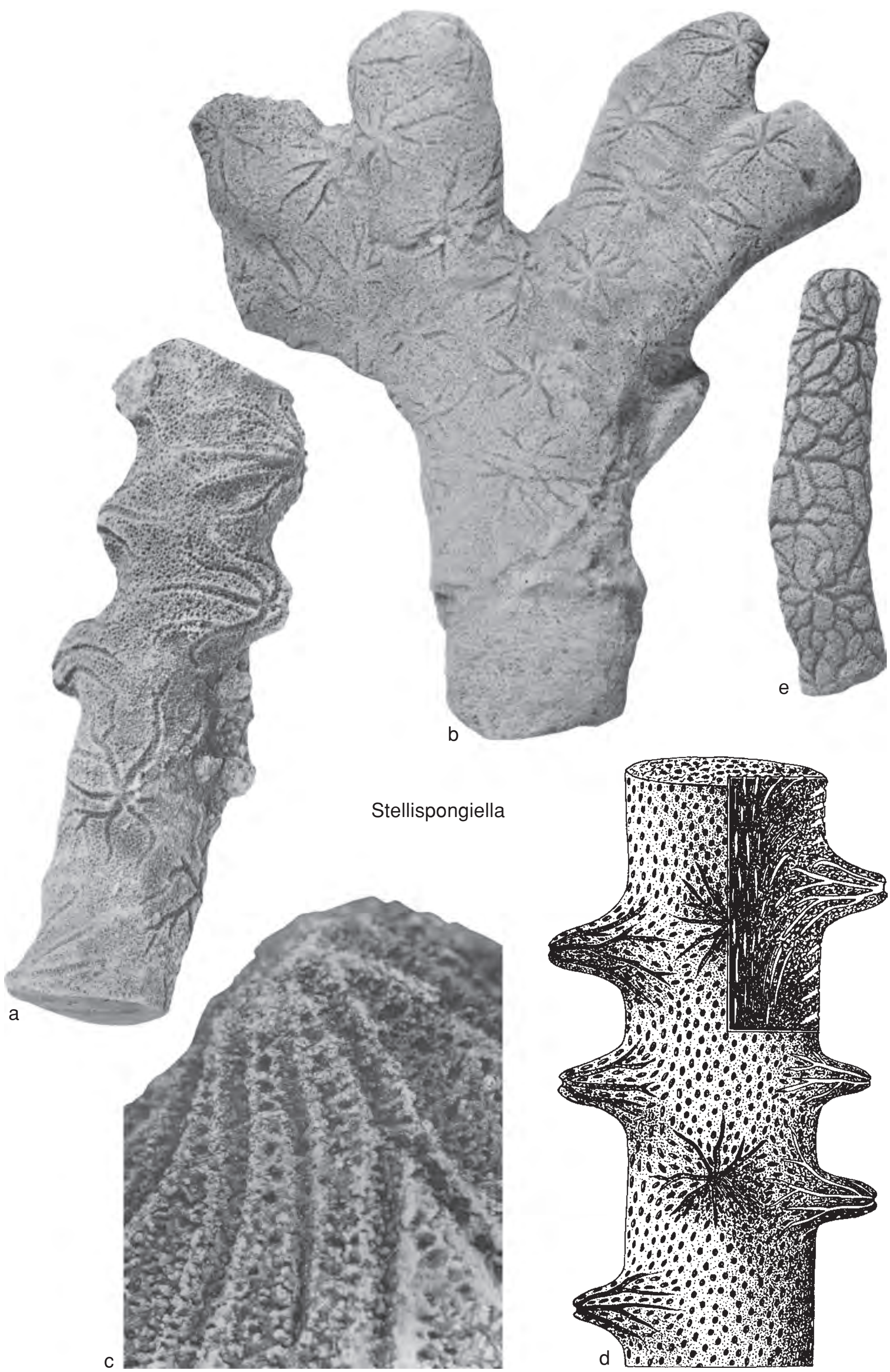


FIG. 413. Stellispongiellidae (p. 629).

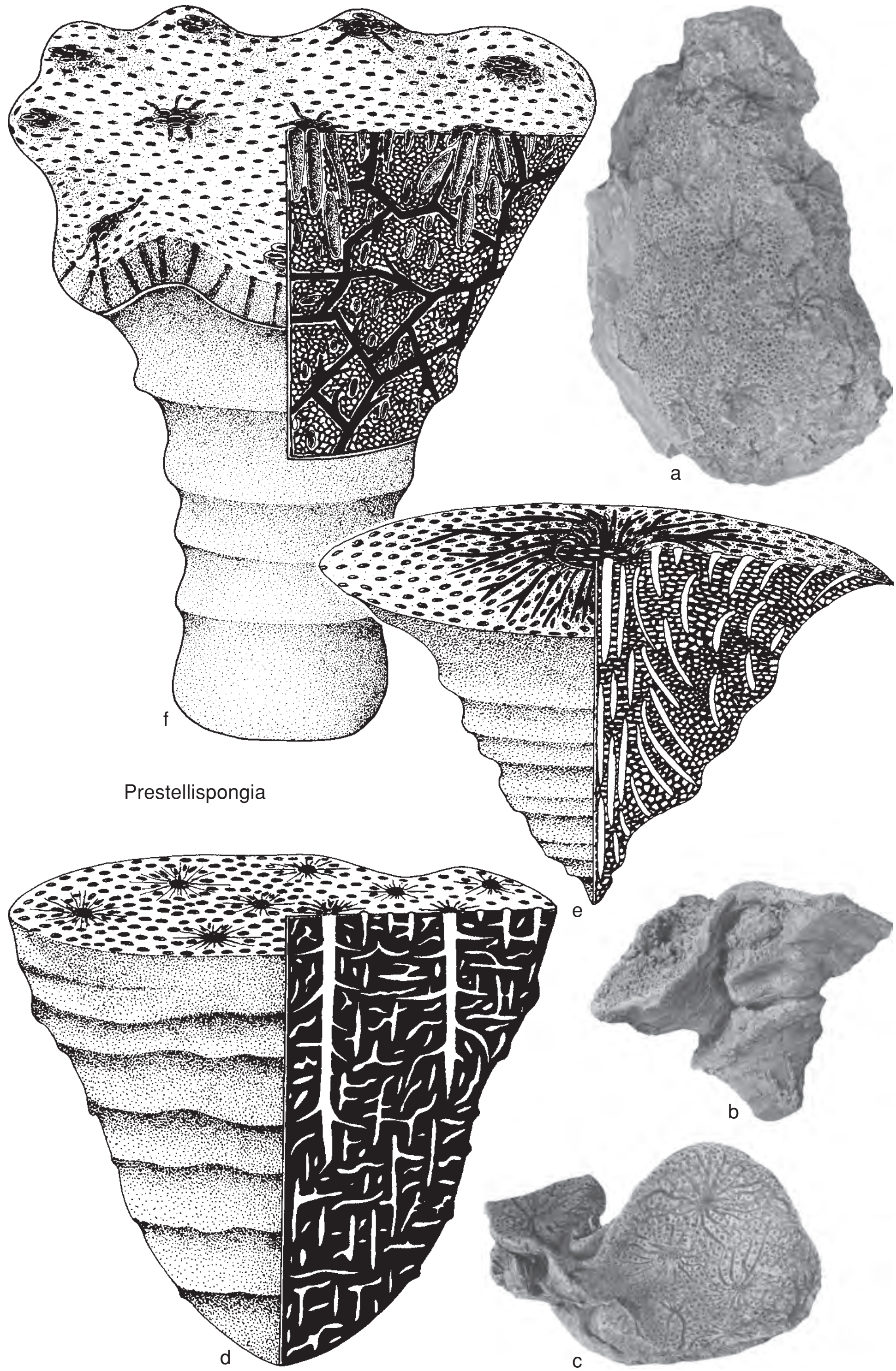


FIG. 414. Stellispongiellidae (p. 629).

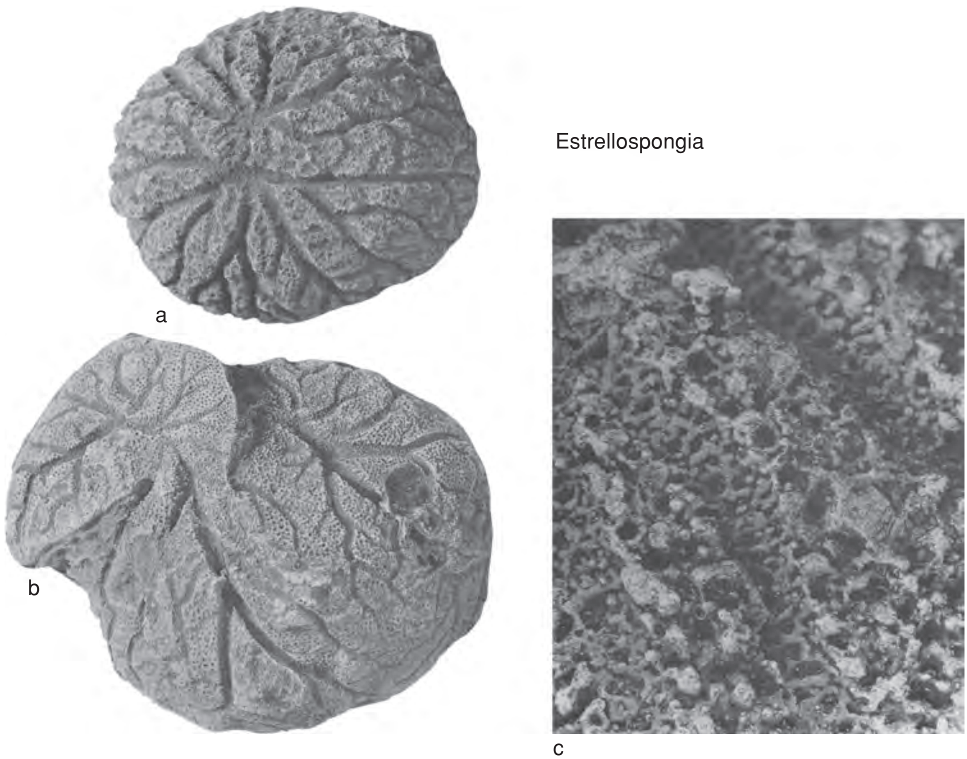


FIG. 415. Stellispongiellidae (p. 632).

Subfamily ESTRELLOSPONGIINAE Rigby & Senowbari-Daryan, 1996

[Estrellospongiinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 56]

Massive prestellispongiids that lack oscula and spongocoels but with several astrorhizal clusters of convergent, largely surficial, exhalant canals; coarse openings lacking in fibrous, skeletal net. *Permian (Lopingian).*

Estrellospongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 56 [**E. grossa;* OD]. Irregularly massive, hemispherical to lobate sponges with upper surface marked by one or more astrorhizal systems of coarse, convergent, exhalant canals that are tangential to dermal surface; lacking coarse, vertical, exhalant canals to oscular ostia but with numerous irregularly upward, divergent canals in irregularly but prominently divergent, ladderlike, fibrous skeleton; microstructure spherulitic. *Permian (Lopingian):* Tunisia.——FIG. 415*a–c.* **E. grossa,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel, Tebaga; *a,* holotype summit with multibranched, exhalant canals, USNM 463639, ×1; *b,* paratype with irregular growth but characteristic canals on summit, USNM 464645, ×1; *c,* paratype, coarse fibers exposed in canal grooves of surficial, exhalant canals, with skeletal pores on ridges between, USNM 463644, ×10 (Rigby & Senowbari-Daryan, 1996a).

Family PREPERONIDELLIDAE new family

[Preperonidellidae FINKS & RIGBY, herein] [=Peronidellidae WU Ya Sheng, 1991, p. 56, *partim;* Corynellidae WU Ya Sheng, 1991, p. 69] [type genus, *Preperonidella* FINKS & RIGBY, herein]

Sponges in which exhalant system consists of only spongocoel or cluster of several coarse canals in axial region of sponge; other differentiated canal systems may be absent or well developed; skeletal microstructure spherulitic. *Upper Ordovician–Upper Triassic.*

Subfamily PREPERONIDELLINAE new family

[Preperonidellinae FINKS & RIGBY, herein] [type genus, *Preperonidella* FINKS & RIGBY, herein]

Sponges with axial spongocoel but without distinct inhalant and exhalant canals;

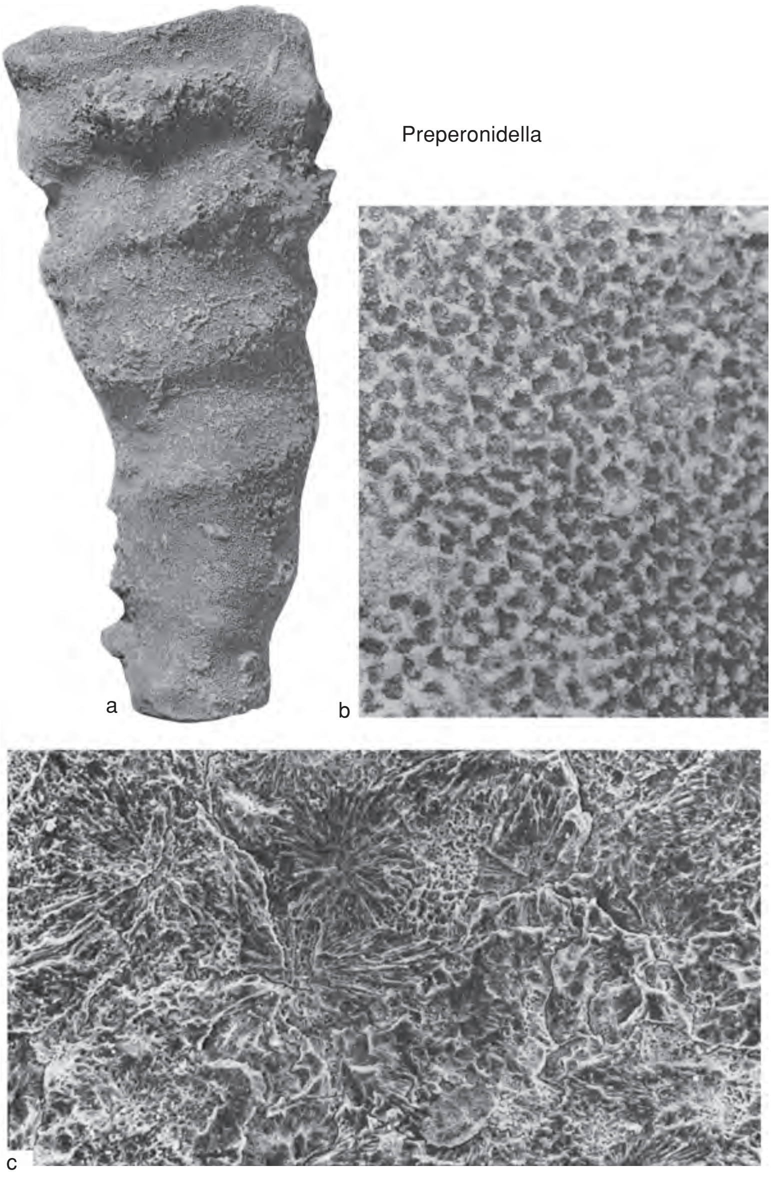


FIG. 416. Preperonidellidae (p. 633–635).

skeletal microstructure spherulitic. *Permian (Guadalupian)–Upper Triassic.*

Preperonidella FINKS & RIGBY, *nom. nov.* herein [**Peronidella magna* RIGBY & SENOWBARI-DARYAN, 1996a, p. 58; OD] [=*Peronidella* ZITTEL in HINDE, 1893b, p. 213, *partim* (type, *Spongia pistilliformis* LAMOUROUX, 1821, p. 88; SD DE LAUBENFELS, 1955, p. 99). Sponges smooth to annulate, columnar to branched, with exhalant canal system only tubular axial spongocoel, although endowall may be pierced by circular endopores in longitudinal rows, dermal layer pierced by small, inhalant ostia; skeletal fibers thin and uniform to variable and thick, and commonly in irregular, reticulate structure; fibers with spherulitic microstructure; dense, dermal layer may be present. [Part of the original *Peronidella* has spicules and is now included in *Paronadella* RIGBY &

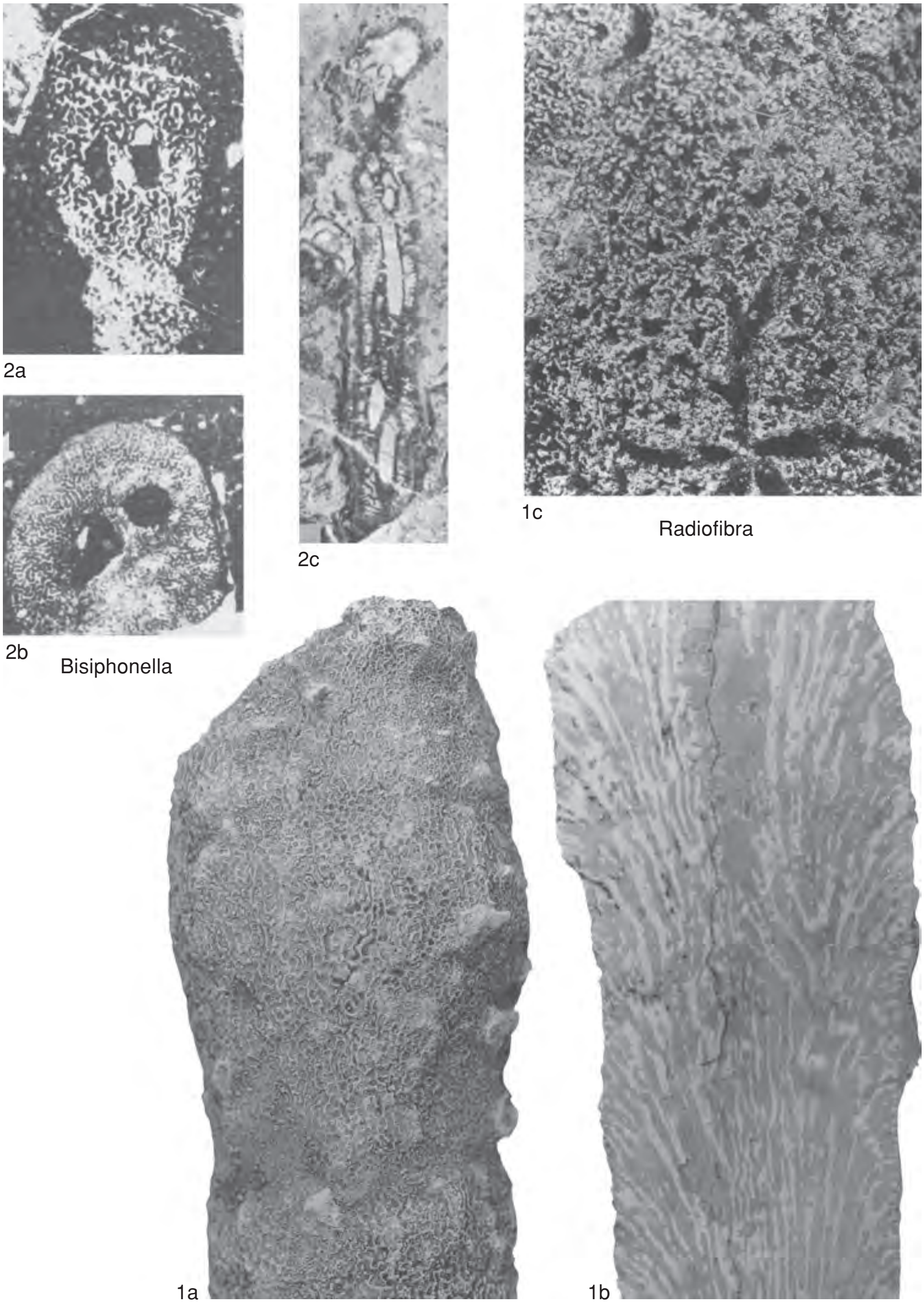


FIG. 417. Preperonidellidae (p. 635).

SENOWBARI-DARYAN, 1996a (see p. 743, herein). Part of *Peronidella* lacks spicules and is renamed *Preperonidella* herein, and the family and subfamily names are based on that new name; the original *Peronidella* and *Paronadella* are now included in the subfamily Stellispongiinae, p. 739, herein.] *Permian (Guadalupian)–Upper Triassic:* China (Guangxi, Sichuan), Tunisia, Thailand, USA (Texas, New Mexico), *Guadalupian–Lopingian;* USA (Oregon), Oman, Peru, *Upper Triassic.*——FIG. 416*a–c.* **P. magna* (RIGBY & SENOWBARI-DARYAN), Lopingian, Upper Biohermal Complex, Djebel Tebaga, Tunisia; *a,* side view of annulate, columnar holotype with dermal layer with numerous inhalant pores, USNM 463663, ×1; *b,* photomicrograph of dermal layer of holotype with numerous skeletal pores defined by relatively robust fibers in almost rectangular, skeletal structure lacking canals, ×10; *c,* SEM photomicrograph of paratype showing densely packed, large, partially recrystallized spherulites of skeletal fibers, USNM 480422, ×4,500 (Rigby & Senowbari-Daryan, 1996a).

Bisiphonella WU Ya Sheng, 1991, p. 60 [**B. cylindrata;* OD]. Cylindrical, stemlike sponges with two parallel, axial, walled spongocoels of essentially same size that extend through much of sponge; skeletal fibers in regular to irregular, but relatively uniformly spaced, reticulate net; with or without dermal cortex; short, exaulos-like tubules may extend from spongocoel wall into interior of chambers. *Permian (Guadalupian–Lopingian):* China (Guangxi), Thailand.——FIG. 417,*2a–c.* **B. cylindrata; a,* holotype, diagonal section with double, spongocoel tubes in fibrous, reticulate skeleton, Reef of Xiangbo, Guadalupian, Guangxi, IGASB xb27-B-2a, ×2; *b,* transverse section with two spongocoels in fibrous skeleton, Reef of Xiangbo, Guadalupian, Guangxi, IGASB xb34-2-2, ×2 (Wu Ya Sheng, 1991); *c,* longitudinal section with two walled, tubular spongocoels cut in lower part, Lopingian, Phrae Province, Thailand, BSPGM R9, ×2 (Senowbari-Daryan & Ingavat-Helmcke, 1994).

Radiofibra RIGBY & SENOWBARI-DARYAN, 1996a, p. 61 [**R. lineata;* OD]. Cylindrical to subcylindrical sponges that may be branched, all with narrow, deep, axial spongocoel; fibrous skeleton of interior with poorly defined arrangement in transverse sections, but divergent upwardly and outwardly in longitudinal section; spaces between fibers probably canals that diverge upwardly and outwardly toward periphery; short, lateral canals may also occur; microstructure spherulitic. *Permian (Lopingian)–Upper Triassic:* Tunisia, *Lopingian;* Iran, *Upper Triassic.*——FIG. 417,*1a–c.* **R. lineata,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; *a,* side view of holotype with coarse, skeletal net, ×2; *b,* polished, longitudinal section with matrix-filled spongocoel and coarse, upwardly divergent fibers, ×2; *c,* photomicrograph of surface showing coarse, skeletal net around smaller inhalant and larger exhalant openings, USNM 463675, ×10 (Rigby & Senowbari-Daryan, 1996a).

Subfamily PERMOCORYNELLINAE Rigby & Senowbari-Daryan, 1996

[Permocorynellinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 65]

Sponges in which the axial spongocoel is deep, extending virtually through sponge; inhalant and exhalant canals present as regular or irregular tubes. *Permian (Lopingian)–Upper Triassic.*

Permocorynella RIGBY & SENOWBARI-DARYAN, 1996a, p. 65 [**Corynella ovoidalis* PARONA, 1933, p. 36; OD]. Spherical, mushroom- or club-shaped sponges with one or two oscula on summit as upper ends of deep spongocoels; radiating and starlike grooves may surround osculum; several vertical, exhalant canals in basal part of sponge empty into base of spongocoel and other higher ones empty into sides of spongocoel, although other upwardly and outwardly divergent, exhalant canals may also occur; horizontal, inhalant canals well defined near periphery of sponge and inhalant pores may be arranged in vertical or horizontal rows; relatively fine, skeletal fibers in regular to reticulate net fill space between canals; skeleton originally primarily aragonite with spherulitic microstructure; lower, dermal surface of mushroom-shaped sponges without pores but with distinct growth lines. *Permian (Lopingian)–Upper Triassic:* Tunisia, *Lopingian;* Iran, *Upper Triassic.*——FIG. 418,*2a–d.* **P. ovoidalis* (PARONA), Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; *a,* side view with inhalant ostia on ridges between indented, radial, inhalant canals, USNM 463682; *b,* side view of conicocylindrical form with prominent, inhalant ostia, ×2; *c,* summit view showing large, central spongocoel and radial canals, with inhalant ostia on ridges between canals, USNM 463685, ×2; *d,* schematic drawing showing form and canal development, not to scale (Rigby & Senowbari-Daryan, 1996a).

Djemelia RIGBY & SENOWBARI-DARYAN, 1996a, p. 71 [**D. amplia;* OD]. Single to branched, cylindrical to club-shaped sponges with deep, axial spongocoel; dermal surface with numerous ostia, some of which are on exaules; ostia lead to branched, tubular canals that pass into reticular, fibrous skeleton in interior of wall; spongocoel with distinct wall perforated by well-developed exhalant canals leading into spongocoel. *Permian (Lopingian):* Tunisia.——FIG. 418,*1a–d.* **D. amplia,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* side view of holotype, ×1; *b,* transverse section showing axial spongocoel and convergent, exhalant canals, USNM 463692, ×2; *c,* side view of paratype, ×2; *d,* top view into large, central

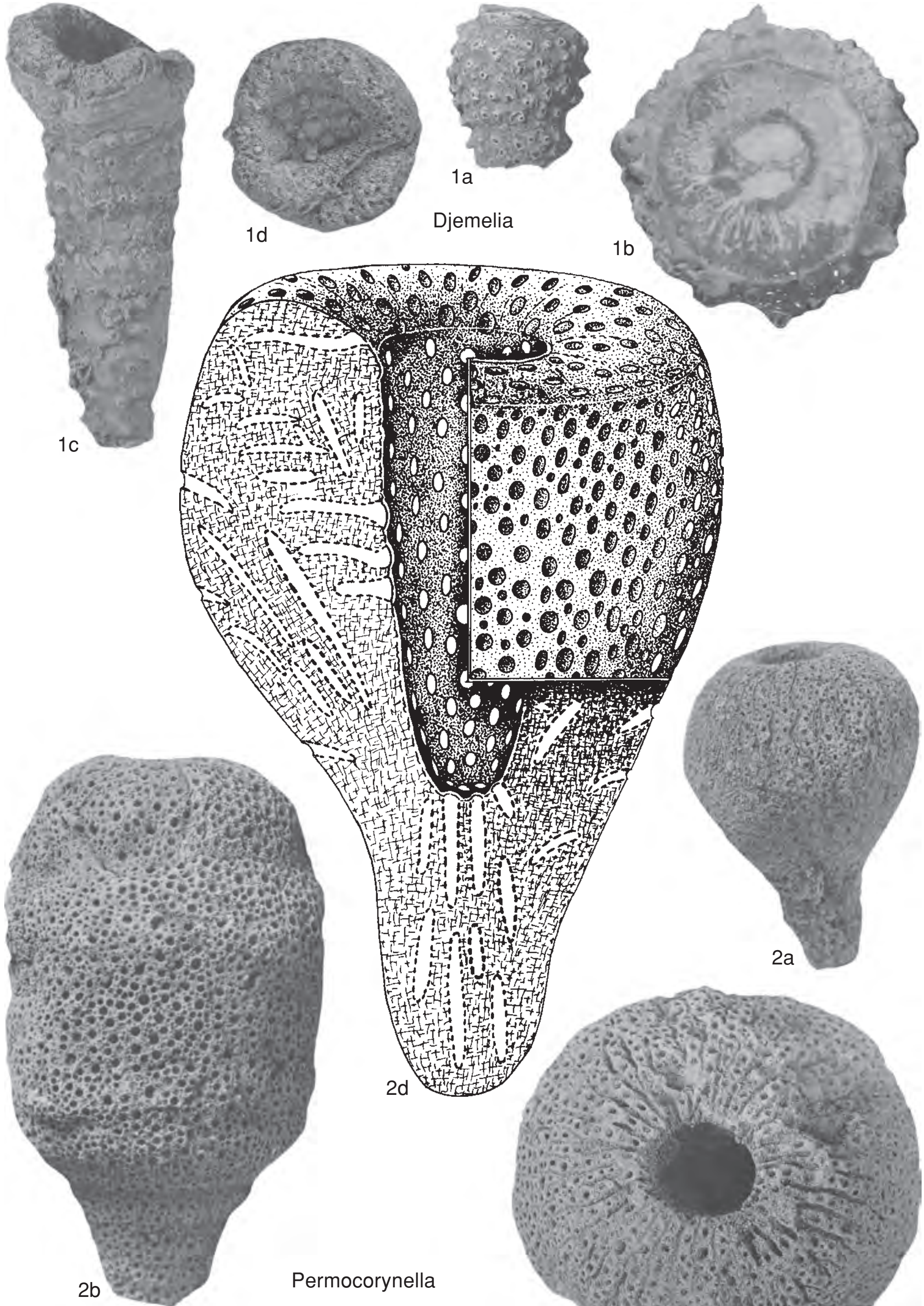


FIG. 418. Preperonidellidae (p. 635–637).

spongocoel, USNM 463693, ×2 (Rigby & Senowbari-Daryan, 1996a).

Saginospongia Rigby & Senowbari-Daryan, 1996a, p. 69 [*S. angusta; OD]. Cylindrical to branched sponges with deep spongocoel in coarse, massive skeleton that appears with radial structure in transverse sections and upwardly divergent in longitudinal sections; internal skeleton of very fine, reticulate or sievelike fibers; microstructure unknown. *Permian (Lopingian):* Tunisia.——Fig. 419*a–c*. *S. angusta,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* side view of coarse, textured holotype, ×2; *b,* photomicrograph showing moderately coarse ostia and canals with broad, skeletal tracts with coarse structure, USNM 463677, ×10; *c,* schematic diagram of skeletal and canal patterns, not to scale (Rigby & Senowbari-Daryan, 1996a).

Subfamily PRECORYNELLINAE Termier & Termier, 1977

[*nom. transl.* Finks & Rigby, herein, *ex* Precorynellidae Termier & Termier, 1977a, p. 45]

Sponges with two or more axial spongocoels or clusters of parallel, coarse, axial, exhalant canals that may be continuations of radial canals; inhalant canals present or absent. *Upper Ordovician–Upper Triassic.*

Precorynella Dieci, Antonacci, & Zardini, 1968, p. 126 [*Cnemidium pyriformis Klipstein, 1843 in 1843–1845, p. 291; OD] [=?*Holosphecion* Pomel, 1872, p. 224 (type, *H. tuberosum,* OD)]. Stipitate-spheroidal to obconical or clavate; solitary or laterally fused in small colonies; well-defined, shallow cloaca on top surface surrounded by numerous closely spaced, radial, exhalant grooves that extend well down sides of sponge, alternating with meridional rows of large, inhalant ostia; bottom of cloacal depression covered by radially arranged, closely spaced, large openings of exhalant canals that extend deeply into axial region of sponge; sides of cloaca bearing similar openings of canals that arch upwardly and inwardly parallel to top surface of sponge, being former radial surface grooves. Sponge exterior with small, circular to meandriform, intertrabecular spaces between larger, inhalant ostia, except for imperforate, dermal layer near base; trabeculae of interior layered parallel to top surface with upwardly and outwardly divergent, connecting elements; exhalant canals of interior parallel to arcuate layers except for central, longitudinal group; inhalant canals extending inwardly and downwardly from ostia parallel to connecting elements. Trabecular microstructure of type species spherulitic and penicillate, according to Wendt (1974, p. 503). [Differs from *Sestrostomella* in presence of cloaca, large canals parallel to top surface, and large ostia on sides.] *Permian–Triassic:* North America, South America, Europe, Tunisia, Timor.——Fig. 420,*2a–c*. *P. pyriformis* (Klipstein), San Cassiano Formation, Norian, Dolomite Alps, Italy; *a,* side view of obconical, globose hypotype with dermal surface perforated by numerous inhalant ostia, ×2; *b,* view from above of oscular margin with axial osculum and rows of inhalant ostia, hypotype IPUM 17563, ×2; *c,* longitudinal section showing cluster of vertical, exhalant canal leading to central osculum shallow spongocoel, each canal with an uparched lower part, smaller downwardly arched, inhalant canals showing near dermal layer, IPUM 17565, ×2 (Dieci, Antonacci, & Zardini, 1968).

Bicoelia Rigby, Senowbari-Daryan, & Liu, 1998, p. 72 [*Bisiphonella tubulara Senowbari-Daryan & Ingavat-Helmcke, 1994, p. 24; OD]. Cylindrical sponges with two parallel, axial spongocoels, each with separate wall pierced by pores or tubular canals connected to pores in surrounding, reticulate skeleton; distinct, perforated, dermal layer; skeleton between dermal layer and spongocoel walls loose, textured, and partially radially arranged, fibrous network; some horizontal tabulae may occur within spongocoels. *Permian (Guadalupian–Lopingian):* Thailand, China, USA (New Mexico).——Fig. 420,*1a–b*. *B. guadalupensis* Rigby & Senowbari-Daryan, Capitan Limestone, Capitanian, Guadalupe Mountains, New Mexico; *a,* holotype (*arrow*) in a polished section with several other large examples of sponge, all with double spongocoel in axial region, USNM 35175-1, ×2; *b,* paratype with several transverse sections, each with double spongocoel and coarsely reticulate wall, USNM 35175, ×2 (Rigby, Senowbari-Daryan, & Liu, 1998).

Imperatoria De Gregorio, 1930, p. 39 [*I. marconii; OD] [?=*Bisiphonella* Wu Ya Sheng, 1991, p. 60 (type, *B. cylindrata,* OD)]. Sponge with turriculate form, branched to unbranched; each cup- to funnel-shaped, segmentlike element with a horizontal to sloping ramp across its summit and with sharp, outer edge; interior unsegmented, but with upwardly and outwardly directed, moderately coarse, fibrous reticulate skeleton; lacking axial tubes or through-going spongocoel but individual segments may have small oscula above short, coarse, exhalant tubes; upper and lateral, dermal layers smooth and with numerous small pores or with numerous ostia on exaules of outer wall in species questionably included in genus, which also has irregular, horizontal and vertical canals that are largely wanting in other species in genus. *Upper Ordovician–Permian:* USA (California), *Upper Ordovician;* Italy (Sicily), Tunisia, ?China, *Permian.*——Fig. 421,*2a*. *I. marconii,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; side view of annulate sponge, USNM 463711, ×1 (Rigby & Senowbari-Daryan, 1996a).——Fig. 421,*2b–d*. *I. voluta* Rigby & Senowbari-Daryan, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; *b,* side view of holotype showing annulate, turriculate form, ×2; *c,* view from above with two adjacent, walled oscula in relatively coarse,

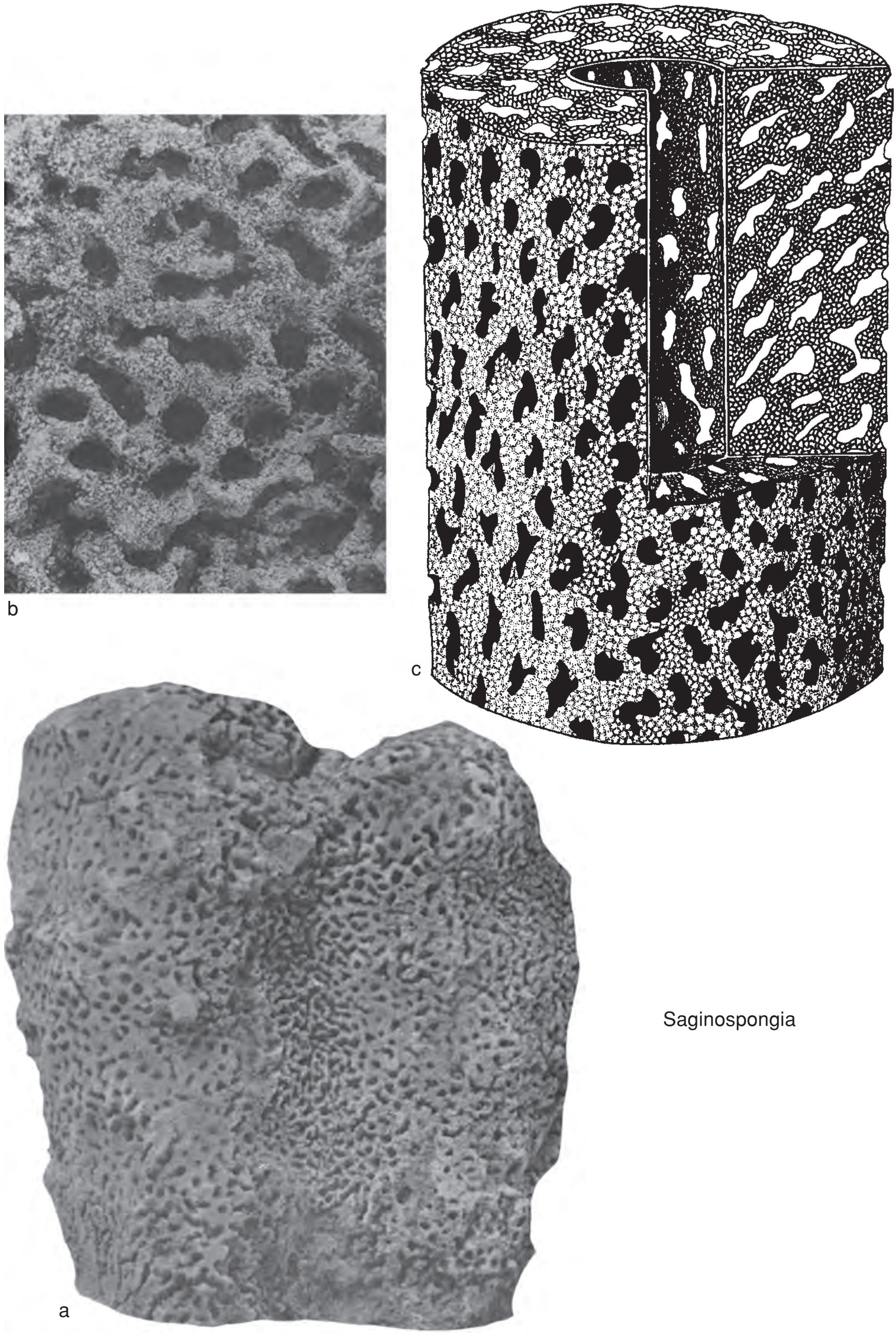


FIG. 419. Preperonidellidae (p. 637).

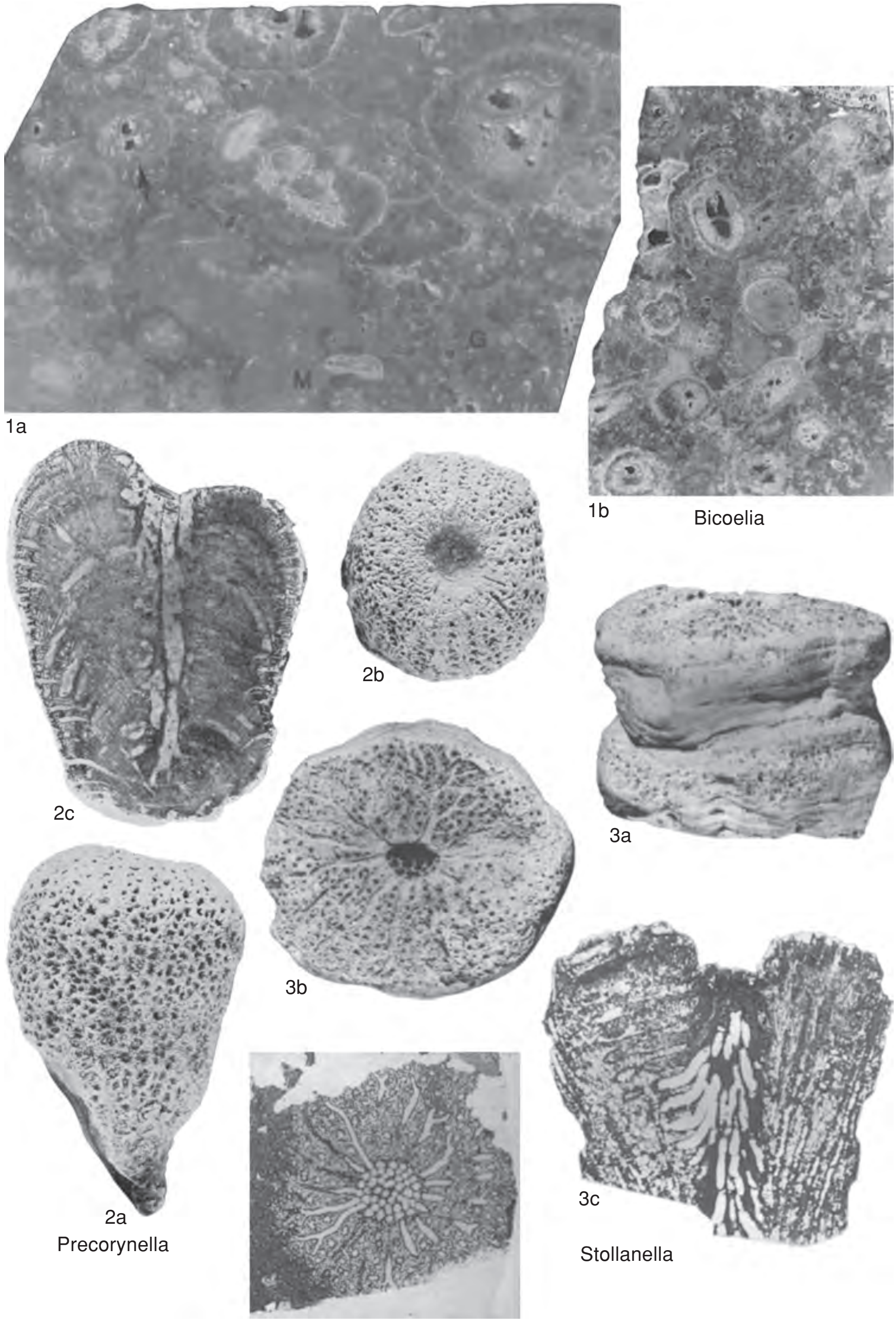


FIG. 420. Preperonidellidae (p. 637–642).

FIG. 421. Preperonidellidae (p. 637–641).

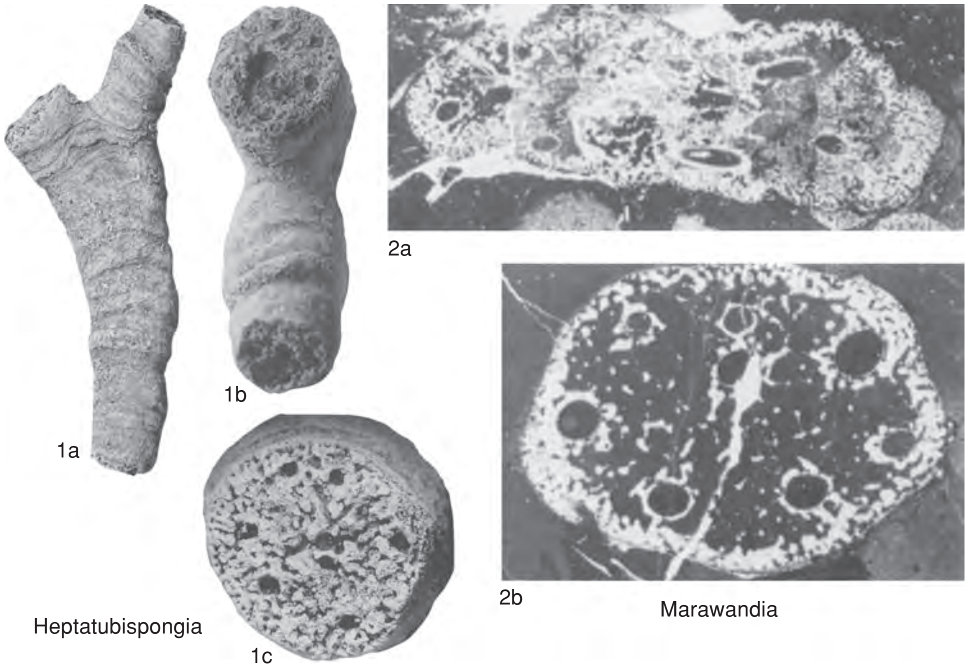


FIG. 422. Preperonidellidae (p. 642).

fibrous skeleton, USNM 463715, ×4; *d,* turriculate paratype, side view, USNM 613712, ×2 (Rigby & Senowbari-Daryan, 1996a).

Minispongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 78 [**M. carinata;* OD]. Tiny, dichotomously branched or cylindrical sponges with one to several united or parallel spongocoels; dermal layer without perforations but with prominent annulations or ridges that may merge laterally in zigzag fashion; skeleton of reticulate fibers. *Permian (Guadalupian–Lopingian):* Tunisia, USA (New Mexico, Texas). ——FIG. 421,*3a–c.* **M. carinata,* Djebel Tebaga Biohermal Complex; Changhsingian, Djebel Tebaga, Tunisia; *a,* side view of small, annulate to ridged holotype, USNM 463704, ×5; *b,* side view of branched paratype, USNM 463705, ×5; *c,* top view showing spongocoel with several parts and surrounding, fibrous wall, USNM 463708, ×5 (Rigby & Senowbari-Daryan, 1996a).——FIG. 421,*3d–e. M. constricta* (GIRTY), Capitan Limestone, Capitanian, Guadalupe Mountains, Texas; *d,* side view of small, annulate holotype, USNM 118132, ×2; *e,* diagonal section through small sponge with relatively coarse, skeletal structure of thin wall, USNM 35175, ×10 (Rigby, Senowbari-Daryan, & Liu, 1998).

Ramostella RIGBY & SENOWBARI-DARYAN, 1996a, p. 79 [**R. stipulata;* OD]. Cylindrical to branched, small sponges generally with axial cluster of coarse, exhalant canals; lacking transverse, inhalant canals in interior other than moderately coarse, skeletal pores; skeleton upwardly and outwardly expanding reticulation of fine fibers; upper surface with surficial grooves that converge toward axial, exhalant, canal cluster and that continue longitudinally as undulating and subparallel grooves some distance down in dermal surface of cylindrical flanks; microstructure spherulitic. *Permian (Lopingian):* Tunisia.——FIG. 421,*1a–c.* **R. stipulata,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* top view of holotype showing summits of three short branches, ×2; *b,* side view showing triangular, palmate form and short branches marked with irregular grooves, but lacking inhalant ostia, USNM 480354, ×2; *c,* photomicrograph of upper, lateral slope of paratype with subvertical grooves, coarse exhalant ostia, and finer, skeletal pores defined by coarse, skeletal fibers, USNM 480377, ×10 (Rigby & Senowbari-Daryan, 1996a).

Stollanella BIZZARINI & RUSSO, 1986, p. 131 [**S. diecci;* OD]. Sponges simple or branched, steeply obconical with broad base and wrinkled epitheca; axial cluster of subvertical, exhalant canals, as inner, abruptly uparched ends of subhorizontal parts of canals in inner part of wall; oscular surface with shallow spongocoel and several radial furrows; aligned prosopores of subvertical, inhalant canals occurring between furrows; microstructure is micritic. [Aligned, relatively straight, subvertical, inhalant canals penetrate down into the sponge wall from the upper surface in *Stollanella,* in contrast to *Precorynella* where most inhalant canals feed from the lateral, dermal surface. Vertical, inhalant canals are unknown in *Sestrostomella,* and in addition it has a spherulitic microstructure, as does *Precorynella.*] *Upper Triassic:* Italy.——FIG. 420,*3a–d.* **S. diecci,* San Cassiano Formation, Carnian, Dolomiti di Braies; *a,* side view of holotype, ×2; *b,* view of summit with central spongocoel that has numerous exhalant ostia in gastral wall, ×2; *c,* longitudinal section showing large, exhalant canals and smaller, subvertical, inhalant canals, ×2; *d,* transverse section with convergent and axial cluster of exhalant canals in holotype, MCSNV 10150, ×3 (Bizzarini & Russo, 1986).

Subfamily HEPTATUBISPONGIINAE Rigby & Senowbari-Daryan, 1996

[Heptatubispongiinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 83]

Sponges in which an axial spongocoel is present with several coarse, longitudinal, exhalant canals regularly spaced in one ringlike layer near periphery. *Permian (Lopingian)–Upper Triassic.*

Heptatubispongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 83 [**H. symmetrica;* OD]. Cylindrical to branched sponges with axial spongocoel or relatively large, axial canal, and usually seven smaller, collateral, vertical canals uniformly spaced in ring near periphery, although numbers of such canals range from six to eight; outer surface with a few ostia; internal skeleton composed of relatively coarse, reticulate fibers; growth lines prominent on exterior. *Permian (Lopingian):* Tunisia.——FIG. 422,*1a–c.* **H. symmetrica,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* side view of branched holotype, ×2; *b,* summit of left branch, above showing minor, axial, exhalant canals and symmetrically placed, collateral, vertical canals near margin, ×4; *c,* base of holotype with ring of exhalant canals near margin and radial canals around central spongocoel, USNM 463724, ×8 (Rigby & Senowbari-Daryan, 1996a).

Marawandia SENOWBARI-DARYAN, SEYED-EMAMI, & AGHANABATI, 1997, p. 312 [**M. iranica;* OD]. Cylindrical, branched sponge with several separated, exhalant tubes, usually of same size and not axially located, that pass through sponge; each tube with distinct wall pierced by openings from sponge interior; outer surface with distinct wall perforated by labyrinthic canal system; loosely packed, skeletal fibers of reticular type fill interior; microstructure and spicular structure not known. *Upper Triassic:* Iran.——FIG. 422,*2a–b.* **M. iranica,* reefs within the Nayband Formation, Norian–Rhaetian, Marawand, Iran; *a,* oblique section of holotype showing several internal, exhalant canals surrounded by skeletal fibers, outer wall with labyrinthic canal system, SPIE M/73, ×5; *b,* transverse section with eight peripheral, exhalant canals, each with perforated wall, and dense, fibrous, outer wall, SPIE P/324/1, ×10 (Senowbari-Daryan, Seyed-Emami, & Aghanabati, 1997; courtesy of *Revista Italiana di Paleontologia e Stratigraphia*).

Family FISSISPONGIIDAE new family

[Fissispongiidae FINKS & RIGBY, herein] [type genus, *Fissispongia* KING, 1938, p. 499]

Cylindroid; multiple, narrow, central cloacae; trabecular tissue between exowall and endowall outlines anastomosed, tubular spaces that converge inwardly and upwardly to cloacae; interwalls and segmentation variably developed; segments often conical, flaring upwardly; type genus has small ostea and lipped exopores; microstructure of type genus (others not known) very small, isodiametric spherulites (15 to 20 µm). *Devonian (Eifelian)–Permian (Roadian).*

Fissispongia KING, 1938, p. 499 [**F. jacksboroensis;* OD] [=?*Hormospongia* RIGBY & BLODGETT, 1983, p. 773 (type, *H. labyrinthica,* OD)]. Conicocylindrical, branching, ranging from strongly segmented to unsegmented; segments, when present, strongly conical, expanding upwardly; cloaca narrow, central, and double or very rarely multiple; one cloaca circular in cross section and internally tangent to the second, which wraps around it; endowall of circular cloaca thicker than that of other, which may be locally absent; exowall with very small, closely spaced exopores, together with more widely spaced, larger, circular pores that have strong lips or are at end of spoutlike projections; interwalls absent, even in strongly segmented forms, except for peripheral, incurved part of exowall; interior filled with fine net of trabeculae that outline anastomosed, tubular spaces that tend to be directed inwardly and upwardly, coalescing to enter cloacas through large, circular endopores; endowall between circular cloaca and surrounding one usually imperforate, except where trabecular tube crosses outer cloaca to enter circular one; trabeculae and walls composed of very small, isodiametric spherulites; no spicules. *Middle Devonian (?Eifelian), Carboniferous (Middle Pennsylvanian–Roadian):* USA (Alaska), *?Eifelian;* southcentral and southwestern USA, *Middle Pennsylvanian–Upper Pennsylvanian, Asselian–Roadian.*——FIG. 423,*2a–e.* **F. jacksboroensis,* Graham Formation, Virgilian, Jack County, Texas; *a–c,* three syntypes showing obconical to branching habit and rimmed ostia characteristic of type species, UTBEG K-1467, ×1 (King, 1938); *d,* side view of annulate, incipiently branched specimen, ×2; *e,* enlarged part of same sponge showing small, inhalant pores and larger, rimmed pores in dermal layer, OUZC 3013, ×10 (Rigby & Mapes, 2000).

?Hormospongia RIGBY & BLODGETT, 1983, p. 775 [**H. labyrinthica;* OD]. Conicocylindrical, branching sponge composed of superposed, conical to discoid segments; one to three narrow, central, vertical cloacae pass through at least several segments; remainder of chamber interior filled with meandri-

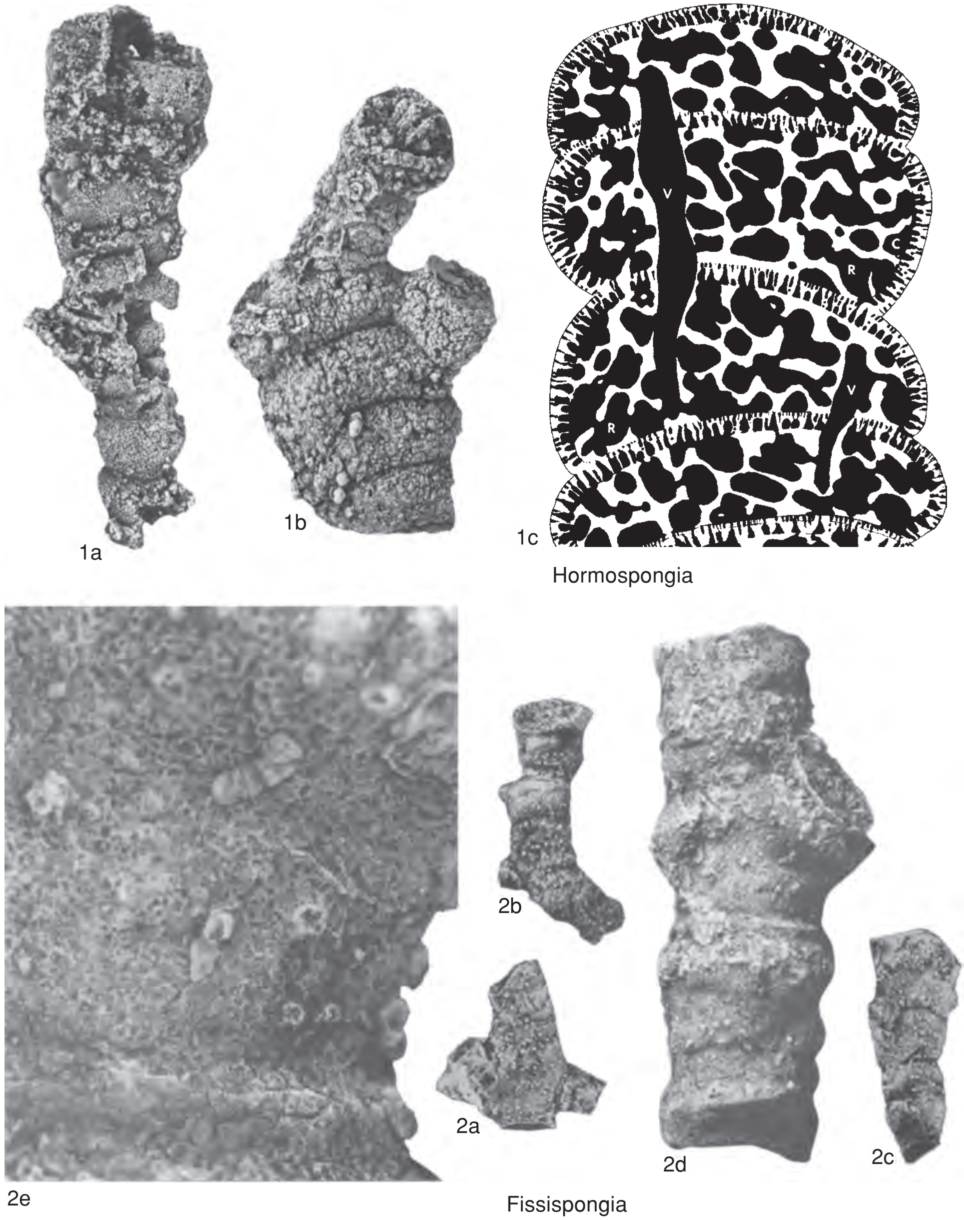


FIG. 423. Fissispongiidae (p. 642–644).

form trabeculae that outline anastomosed, tubular spaces that rise inwardly toward central cloacae; exopores small, circular, and closely spaced on exterior of exowall but merging into wider canals in interior of exowall and communicating with internal, intertrabecular spaces; interwall a continuation of exowall at top of chamber; endowalls incompletely developed; microstructure not known; no spicules known. [This genus is similar to *Fissispongia* KING, 1938, but differs in the more variable number of central cloacae, in complexity of canal and pore development, lack of lipped ostia in the dermal layer, and in possibly better developed interwalls.] *Devonian (Eifelian):* USA (Alaska), Australia (New South Wales).——FIG. 423,*1a–c*. **H. labyrinthica,* Cheeneetnuk Limestone, Eifelian, Cheeneetnuk River, McGrath Quadrangle, Alaska; *a,* side view of holotype showing uniserial, porous chambers in holotype, UAF 2459, ×2; *b,* branched paratype, UAF 2460, ×2; *c,* generalized vertical section showing vertical (*V*), concentric (*C*), and dominantly radial (*R*) canals within globular chambers and branched pores in walls, approximately ×5 (Rigby & Blodgett, 1983).

Family MAEANDROSTIIDAE Finks, 1971

[Maeandrostiidae FINKS, 1971a, p. 292]

Cylindroidal, cloacate sponges with aspicular skeleton of large, isodiametric spherulites (40 to 140 μm); external cortex with circular, lipped pores, usually large, and, in type genus, meandriform; internal skeleton of meandriform, anastomosing trabeculae outlining radial, upwardly divergent, tubular spaces in Carboniferous and Early Permian species, becoming reduced to radially elongate, vertical pillars between interwalls with radially elongate interpores in some later forms; endowall present; vesicles present in some genera. [This family includes both inozoan-like and sphinctozoan-like forms; the transition between the two types, shown by Early Permian species of *Stylopegma* KING, 1943, as well as the commonly shared characters of circular, lipped exopores and large, isodiametric spherulites, argues for a phylogenetic unity. The Verticillitidae differ in having a nonspherulitic aspicular skeleton and polygonal exopores in a netlike exowall. *Fissispongia* KING, 1938, and its relatives differ in having much smaller spherulites and in the multiple, confluent, central cloacae.] *Carboniferous (Middle Pennsylvanian)–Triassic.*

Maeandrostia GIRTY, 1908, p. 284 [**M. kansasensis;* OD]. Conicocylindrical to broadly conical, with domical, top surface and central osculum, often branching to form small, flabellate clusters; external cortex may be present locally or widely, pierced by large, circular to meandriform, lipped openings that reveal edges of internal trabeculae, as do areas that are free of cortex; trabeculae outlining anastomosed tubes of circular to meandriform cross section that have prevailingly radial and longitudinal (upwardly diverging) orientation; central cloaca of approximately one-third diameter of sponge lined by cortex or endowall, which truncates intertrabecular spaces and is pierced by pores smaller than these spaces; trabeculae composed of large, isodiametric spherulites; spicules absent. [This genus is a homeomorph of the Mesozoic *Eudea* LAMOUROUX, 1821, which lacks isodiametric spherulites.] *Carboniferous (Middle Pennsylvanian)–Triassic (Anisian):* USA (Texas, Oklahoma, Kansas), Italy (Sicily), Yugoslavia (Slovenia), *Middle Pennsylvanian–Upper Pennsylvanian, Permian;* ?China, *Permian;* Italy, *Anisian.*——FIG. 424,*2a–c.* **M. kansasensis,* Plattsburg Limestone, Desmoinesian–Virgilian, Chanute, Kansas; *a,* side view of cylindrical syntype, ×1; *b,* transverse thin section of syntype showing axial spongocoel and vesicular, skeletal material, ×2; *c,* longitudinal polished section of syntype showing irregularly chambered walls and axial spongocoel, USNM 53468, ×2 (Girty, 1908).

Adrianella PARONA, 1933, p. 14 [**A. distefanoi;* OD]. Conical; central, possibly cloacal depression on slightly domed, top surface; exterior smooth, pores not preserved; interior composed of meandriform trabeculae that outline anastomosed, tubular canals; trabecular mesh has obscure, concentric layering; trabecular microstructure unknown; spicules unknown. *Permian:* Sicily.——FIG. 424,*1a–c.* **A. distefanoi,* Permian limestone, Palazzo Adriano; *a,* side view of obconical holotype; *b,* holotype from above with shallow, axial spongocoel, ×1; *c,* transverse section showing meandriform trabeculae and small canals that become more common in outer part, all part of syntype suite, ×5 (Parona, 1933).

Eurysiphonella HAAS, 1909, p. 162 [**E. steinmanni;* OD]. Conicocylindrical; cloaca somewhat more than one-third sponge diameter; chambers high and apparent from segmentation of exterior; exopores, interpores, and endopores small, circular, and closely spaced, endopores a bit larger and interpores a bit smaller than exopores; chambers either completely hollow, contain vesicles, or are filled with irregular, trabecular network; trabecular microstructure unknown; no spicules known. *Triassic:* Austria.——FIG. 424,*4a–c.* **E. steinmanni,* Hallstätter Kalke, Rhaetian, Fischerwiese by Alt-Aussee; *a,* side view of exterior of type specimen showing segmentation and perforated, chamber walls; *b,* longitudinal section showing central spongocoel or cloaca with thin walls and hollow, bulbous chambers; *c,* view from below of broken surface showing central spongocoel and perforate interwall between chambers, ×1 (Haas, 1909).

Polysiphonaria FINKS, 1997, p. 352 [**Polysiphonia flabellata* FINKS, 1995, p. 4; OD]. Cylindrical branches fused laterally to form flabellate or reticulate shapes; branched at acute angles; no external annulation; closely spaced, moderately large, circular labripores in exowall, with very small exopores between them; multiple, narrow, vertical cloacae with small, vertically elongate endopores; cloacae widely separated and circular in cross section; horizontal interwalls closely spaced with moderately large, closely spaced, radially elongate or

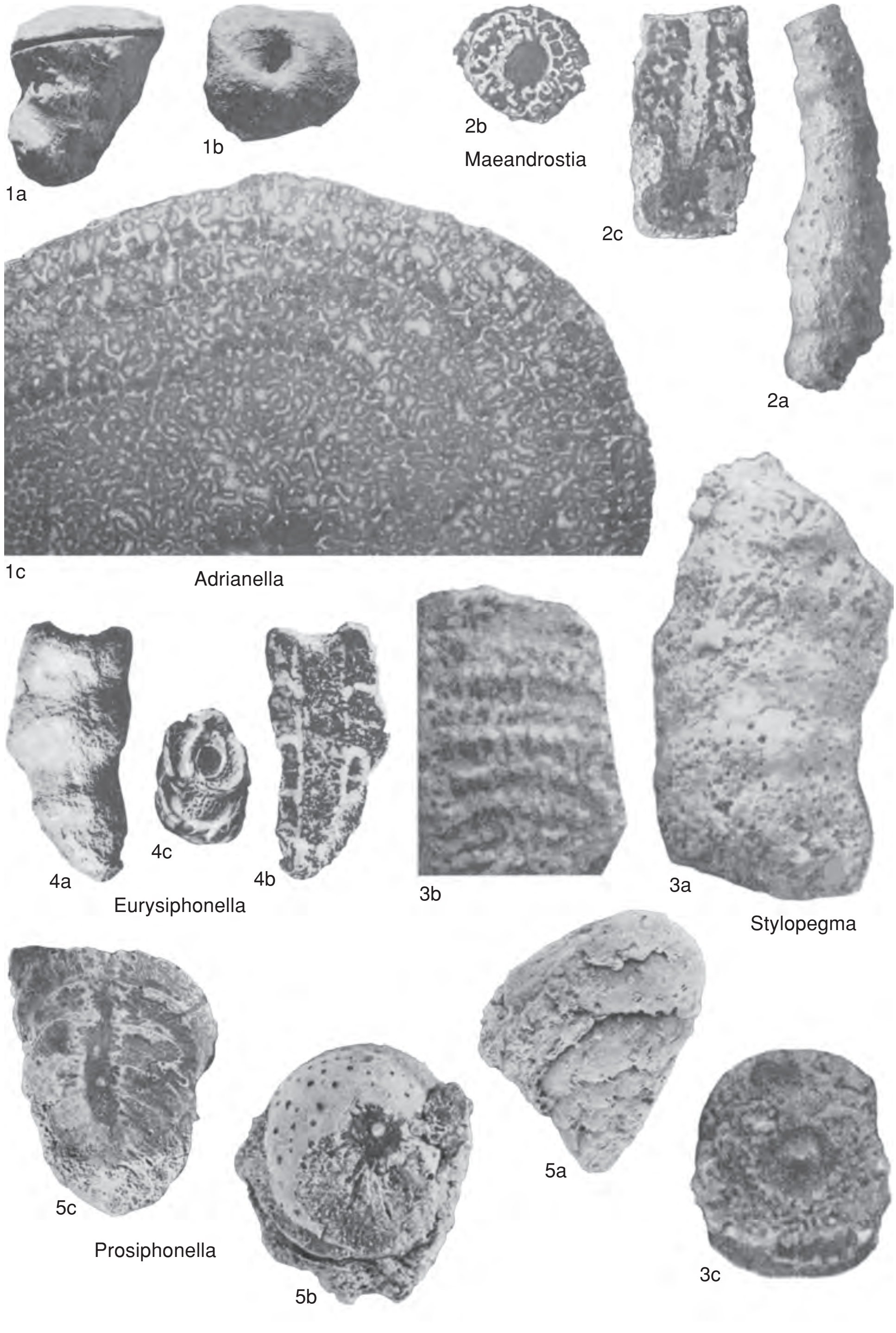


FIG. 424. Maeandrostiidae (p. 644–646).

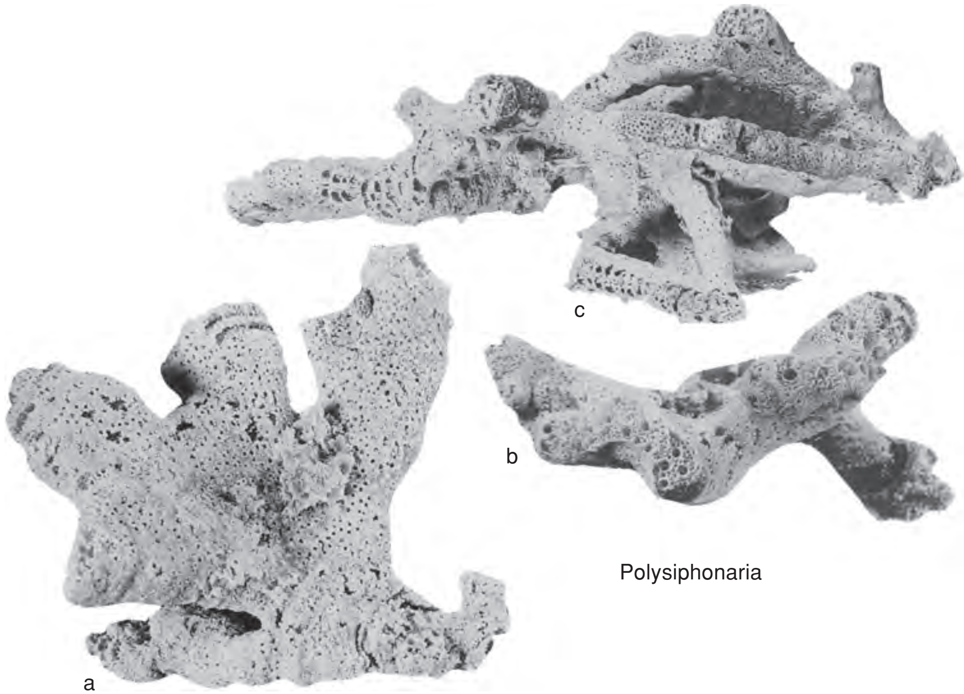


FIG. 425. Maeandrostiidae (p. 644–646).

submeandriform interpores; numerous closely spaced, often coalescent, vertical pillars connect interwalls across low chambers; trabecular microstructure not known; no spicules known. *Permian:* USA (Texas).——FIG. 425*a–c.* **P. flabellata* (FINKS), Road Canyon Formation, Leonardian, Glass Mountains; *a* side view of flabellate, branched holotype; *b,* top view showing multiple branched, tubular spongocoels, AMNH 44309; *c,* paratype with anastomosing branches and parallel, flabellate branches with chambers separated by arched interwalls, AMNH 44316, ×1 (Finks, 1995).

Prosiphonella DIECI, ANTONACCI, & ZARDINI, 1968, p. 138 [**P. amplectens;* OD]. Conical; numerous large, circular exopores, larger exopores lipped; osculum relatively narrow, central; endowall discontinuous because of large endopores; interwall and interpores presumably similar to exowall and exopores; each chamber partially enveloping chamber beneath; chambers low, filled with slender trabeculae forming fine, meandriform mesh in which larger, horizontal canals empty into cloaca; similar large canals perpendicular to exowall extending inwardly and downwardly from large exopores and may branch; trabecular microstructure unknown; no spicules known. *Triassic:* Europe.——FIG. 424,5*a–c.* **P. amplectens,* San Cassiano Formation, Norian, Dolomite Alps, Italy; *a,* side view of holotype with overlapping chambers; *b,* top of holotype with central spongocoel and rounded summit perforated by coarse, inhalant exopores; *c,* longitudinal section through uparched chambers and prosiphonate spongocoel, IPUM 17596, ×2 (Dieci, Antonacci, & Zardini, 1968).

Stylopegma KING, 1943, p. 18 [**S. dulce;* OD]. Branching cylinders or cones; external segmentation present or absent; prominent, central cloaca (absent in earliest chambers); porous interwalls always present (interpores may be radially elongate); chambers contain vertical, radially elongate, somewhat meandriform and anastomosing trabeculae or vertical, cylindrical pillars (most trabecula-like near interwalls and in earlier species); vesicles may also be present; porous endowall (endopores may be vertically elongate); continuous exowall with circular exopores of one or more sizes, larger usually strongly lipped (labripores); trabeculae, pillars, and walls composed of large, isodiametric spherulites; spicules absent. *Permian:* USA (Texas).——FIG. 424,3*a–c.* **S. dulce,* Leonard Formation, Leonardian, Baylor Mountains; *a,* side view of holotype exterior with pores in dermal layer, YPM 16594, ×2; *b,* eroded surface of holotype showing prominent, horizontal, and less regular trabeculae of skeletal net, YPM 16594, approximately ×10; *c,* transverse section of paratype with prominent, tubular spongocoel and walls with irregular trabeculae, YPM 16597, ×2 (King, 1943).

Family ANGULLONGIIDAE Webby & Rigby, 1985

[Angullongiidae WEBBY & RIGBY, 1985, p. 211]

Cylindroid with central cloaca; superposed, toroidal chambers containing radial tubes or trabeculae; vesicles may be present; exopores small and numerous; endopores may be locally concentrated; ostia generally present at ends of mamelon-like protrusions; type genus has lamellar secondary lining to wall but microstructure of primary wall not known. [This family bears some resemblance to the Girtyocoeliidae with its ostia and, in some genera, endopores concentrated in a ring, but differs in the presence of numerous exopores and internal, filling tissue in the chambers.] *upper Lower Ordovician–upper Upper Ordovician.*

Angullongia WEBBY & RIGBY, 1985, p. 212 [**A. vesica;* OD]. Conicocylindrical, moderately large sponge with superposed, toroidal chambers visible externally; wide, central cloaca approximately one-half sponge diameter; mamelon-like protuberances of exowall may terminate in long ostia; exopores small, circular, widely spaced, lipped; very fine exopores may occur between larger ones; interwall a continuation of exowall, with interpores similar to exopores; endowall (inner spongocoel wall of original authors) continuous with (retrosiphonate) and similar to interwall; dendritic, tubular canals extending inwardly and upwardly from chamber interior to endowall (said to be saclike but peripheral ends may have been intersected obliquely); endowall with fine endopores covering their inner ends; chamber interior lined with thick, secondary, lamellar deposits, through which larger exopores and interpores pass as canals, as is frequently the case with such deposits; remainder of chambers filled with very small vesicles, near walls are subparallel to them; occasional vesicles may occur within cloaca. *Middle Ordovician–upper Upper Ordovician:* USA (Alaska), *Middle Ordovician;* New South Wales, *upper Upper Ordovician.*——FIG. 426,*3a–c.* **A. vesica,* Angullong Tuff, Ashgill, Cliefden Caves area, New South Wales, Australia; *a,* longitudinal section of holotype with broad spongocoel and chambers filled with vesiculae, ×2; *b,* transverse section of holotype where central spongocoel has a distinct endowall and chambers filled with fine vesiculae and saclike sections of tubular canals, SUP51000, ×2; *c,* generalized reconstruction showing form and skeletal structure of sponge, approximately ×2 (Webby & Rigby, 1985).

Alaskaspongia RIGBY, POTTER, & BLODGETT, 1988, p. 740 [**A. nana;* OD]. Small, conical sponge with superposed, spheroidal to hemispheroidal chambers; narrow, central cloaca one-fifth sponge diameter or less; closely spaced, very small exopores; inner half of interwall formed of trabeculae radiating from endowall and outlining triangular interpores; endopores concentrated in inner part of each chamber; one or more pointed, saclike extensions of chamber drape over exterior of preceding chamber and taper to an exaulos-like tube with terminal opening. *upper Lower Ordovician:* USA (Alaska).——FIG. 426,*2a–b.* **A. nana,* unnamed Middle Ordovician sequence, White Mountain area, McGrath Quadrangle; *a,* side view of holotype showing general obconical form with sagging, adnate chambers increasing upwardly in size, ×2; *b,* diagonal view into broken chamber showing porous, retrosiphonate, central tube and interwalls, draped exaules showing on lower part of sponge, USNM 417201, ×2 (Rigby, Potter, & Blodgett, 1988).

Amblysiphonelloides RIGBY & POTTER, 1986, p. 19 [**A. tubulara;* OD]. Conicocylindrical, small, with superposed, discoid chambers; segmentation visible externally; cloaca approximately one-third sponge diameter; exopores small, closely spaced, circular, uniform; exowall continuous with interwall but interpores somewhat smaller than exopores; endopores elongate vertically and same size as interpores; radial tubes, apparently imperforate, lead inwardly from many exopores, occasionally branching inwardly, most end short of endowall but some connect with endopore; microstructure not known; no spicules known. *upper Lower Ordovician–upper Upper Ordovician:* USA (California).——FIG. 427,*2a–d.* **A. tubulara,* Kangaroo Creek Formation, Llandeilo–Ashgill, Klamath Mountains; *a,* side view of holotype with low, annular, moniliform chambers, BMNH S10172; *b,* side view of paratype with porous chamber walls, BMNH S10175, ×2; *c,* vertical section of silicified sponge showing porous, retrosiphonate, central tube and interwalls, BMNH S10177, ×2; *d,* diagonal section through paratype showing irregular, tubular, filling structures and porous chamber walls, BMNH S10178, ×10 (Rigby & Potter, 1986).

Belubulaia WEBBY & RIGBY, 1985, p. 217 [**B. packhami;* OD]. Conicocylindrical, small, occasionally branching sponge with superposed, spheroidal to hemispheroidal segments visible externally; central cloaca one-third to one-fifth sponge diameter; small, circular, closely spaced exopores of varying size; in addition, large ostia are present on ends of mamelon-like protrusions of exowall; interwall continuous with exowall and bearing same pores; endopores somewhat larger than exopores, circular, lipped on chamber side, concentrated in ring at upper end of chamber; occasional vesicles in chambers; microstructure not known; no spicules known. *lower Upper Ordovician:* Australia (New South Wales).——FIG. 426,*1a–c.* **B. packhami,* Belubula Limestone, Belubula River; *a,* side view of holotype with superposed, spheroidal chambers, SUP5105, ×2; *b,* longitudinally broken paratype showing chambers around central tube with endopores confined to upper parts of chambers, SUP51020, ×5; *c,* side view of small, paratype

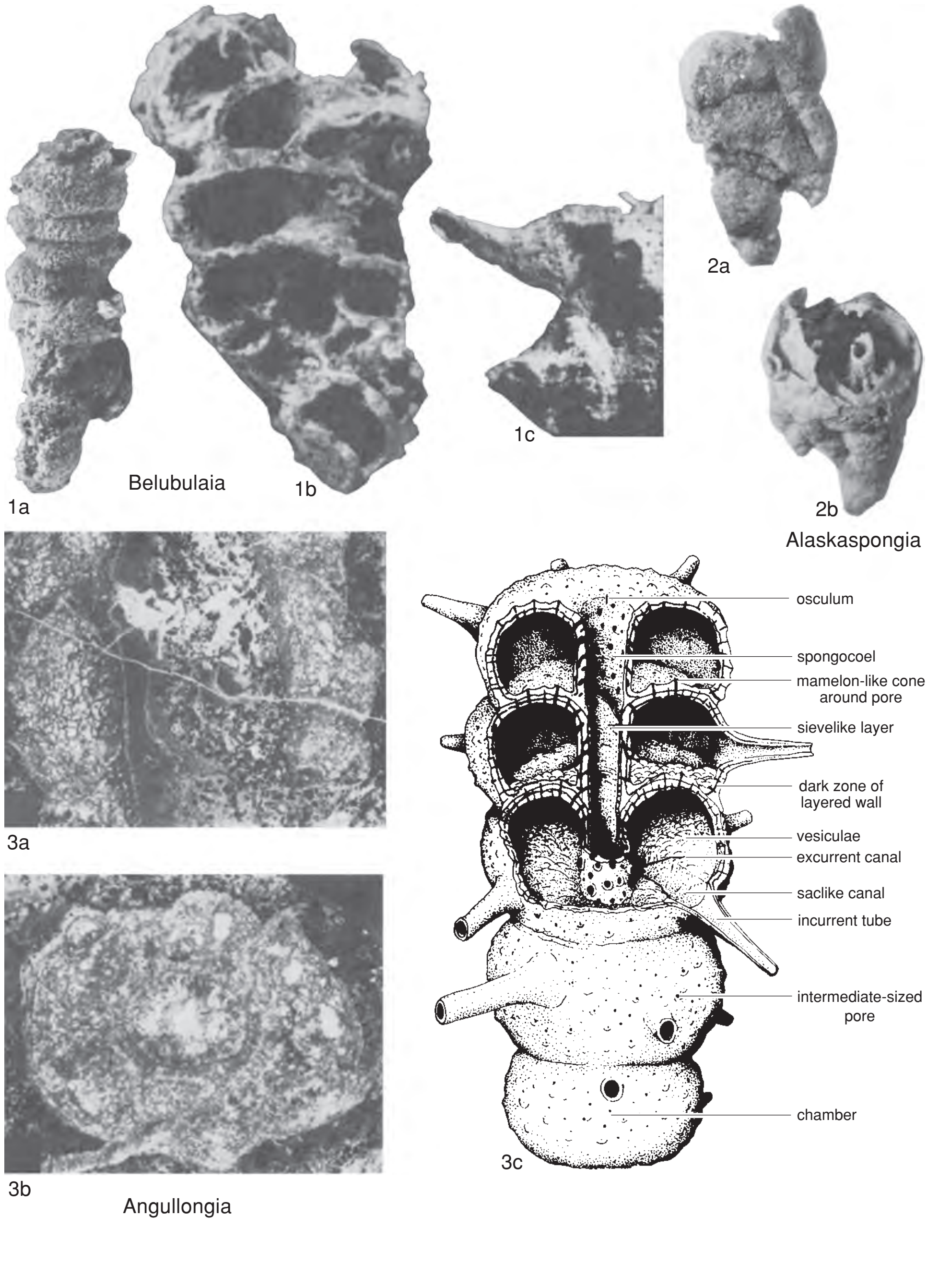


FIG. 426. Angullongiidae (p. 647–650).

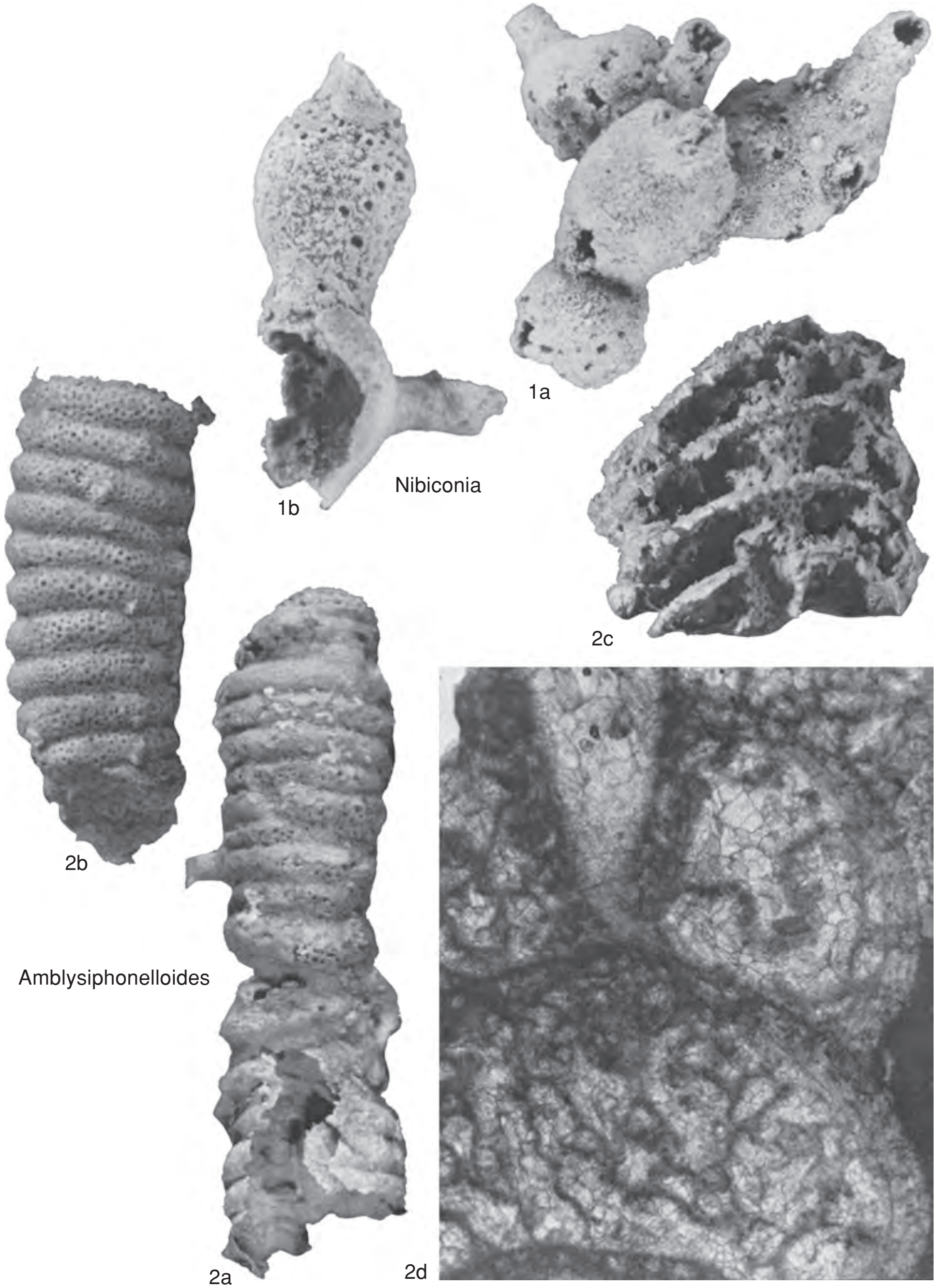


FIG. 427. Angullongiidae (p. 649–650).

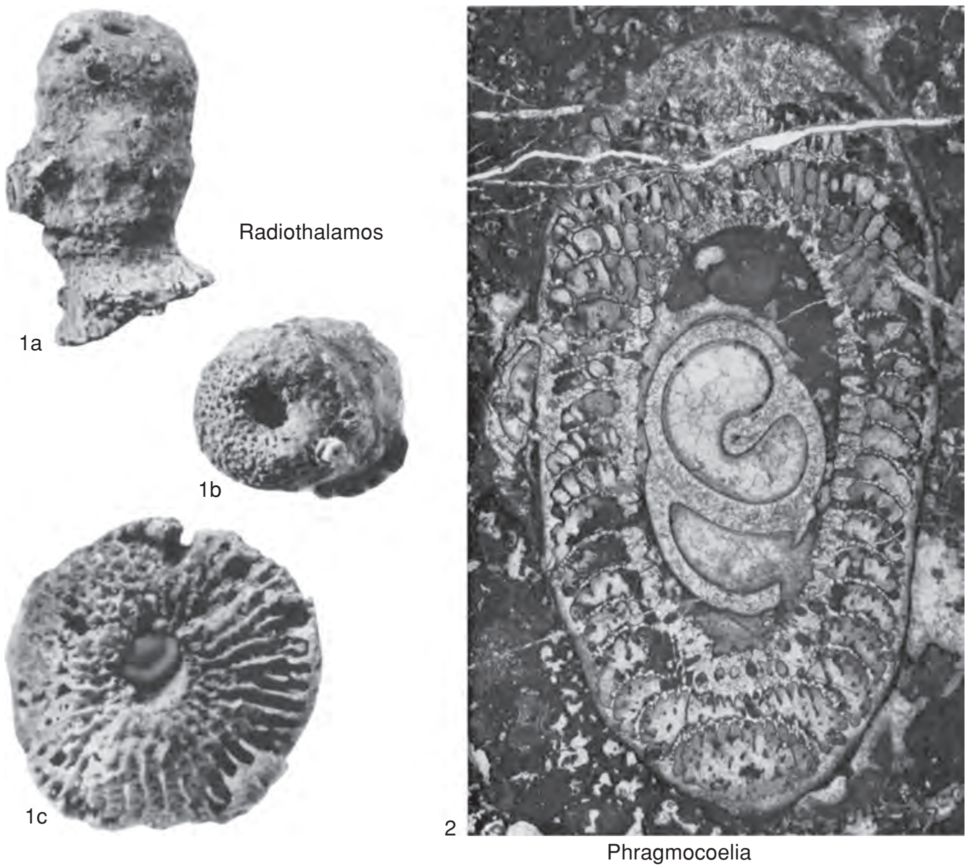


FIG. 428. Phragmocoeliidae (p. 650–651).

fragment with tubular ostia on two chamber exowalls, SUP51024, ×4 (Webby & Rigby, 1985).

Nibiconia RIGBY & WEBBY, 1988, p. 90 [**N. adnata;* OD]. Irregularly branching sponge of adnate to moderately isolated, swollen chambers with cylindrical Axel, but ill-defined, central spongocoel; chambers lacking vesiculae or other filling structures; chamber walls perforate. *lower Upper Ordovician:* Australia (New South Wales).——FIG. 427,*1a–b.* **N. adnata,* Sugarloaf Creek breccia of Malongulli Formation, Cliefden Caves area; *a,* holotype of adnate, spindle-shaped chambers with prominent exaules, AMu F66917, ×8; *b,* paratype with distinctly porous walls and necked connection between chambers, with tubular exaulos on right, AMu F66919, ×8 (Rigby & Webby, 1988).

Family PHRAGMOCOELIIDAE Ott, 1974

[Phragmocoeliidae OTT, 1974, p. 715]

Porate sphinctozoans with septate chamber fillings. *Devonian (Lochkovian)–Triassic (Carnian).*

Phragmocoelia OTT, 1974, p. 715 [**P. endersi;* OD]. Cylindrical, not externally segmented; cloaca broad with well-developed endowall; endopores circular, closely spaced, and arranged in horizontal rows just above each interwall; additional, smaller endopores irregularly arranged; interpores small, of similar size to smaller endopores except near periphery where they may be same size as exopores; exopores similar in size to larger endopores; chamber height low; chambers containing radial, closely spaced, septalike trabeculae that may break up into radially elongate pillars; trabecular microstructure not known; no spicules observed. *Triassic (Carnian):* Europe (northern Calcareous Alps).——FIG. 428,*2.* **P. endersi,* Wettersteinkalk, Autrichian Calcareous Alps, Austria; *a,* diagonal section of holotype with chambers in single layer around thick-walled, coarsely perforate, axial spongocoel, chambers with septal, filling structures, porous exowall showing near base, BSPGM, ×5 (Ott, 1974; courtesy of *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*).

Radiothalamos PICKETT & RIGBY, 1983, p. 738 [**R. uniramosus;* OD]. Conicocylindrical, with superposed, low, toroidal chambers visible externally; central cloaca approximately one-fifth to one-sixth sponge diameter; interwall continuous with exowall of preceding chamber; exopores small, circular, closely spaced and of one size, interpores somewhat larger and subangular; endowall incompletely preserved but may be meshlike with large endopores; chambers bearing closely spaced, radial, vertical septa pierced by large, vertically elongate pores; microstructure not known; spicules not known. [Genus somewhat resembles *Stylopegma* KING, 1943, but the latter has trabeculae that are straight and more regularly radial.] *Devonian (Lochkovian–Pragian):* Australia (New South Wales).——FIG. 428,*1a–c*. **R. uniramosus,* Garra Formation, Wellington; *a,* side view of small, silicified holotype with subcylindrical form, ×2; *b,* view from above showing osculum of central spongocoel and canals of relatively thick walls, MMF 23738, ×2; *c,* silicified paratype from above showing radial chambers and prospores in thick wall around central spongocoel, MMF 23737, ×2 (Pickett & Rigby, 1983).

Family INTRASPOREOCOELIIDAE Fan & Zhang, 1985

[Intrasporeocoeliidae FAN & ZHANG, 1985, p. 17] [=Polysiphonellidae BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 93, *non* Polysiphonellidae WU Ya Sheng, 1991, p. 65]

Cylindrical, often branched sponges composed of superposed, overlapping, hemispheroidal chambers with porate walls that apparently lack ostia; central spongocoel absent although chambers may be pierced by longitudinal, open tubes; chamber interiors filled by anastomosing trabeculae that have upward and outward organization; in type genus trabeculae formed of fused spheroidal bodies (possible spherulites). *Permian (Guadalupian–Lopingian).*

Intrasporeocoelia FAN & ZHANG, 1985, p. 18 [**I. hubeiensis;* OD]. Cylindrical, branching or spheroidal sponges, composed of superposed, hemispheroidal or meniscoidal, overlapping chambers; exowall-interwall a single unit pierced by closely spaced, small, circular exopores-interpores; outer-upper surface microspinose (or microridged, as material is only known from sections); narrow, cloaca-like, vertical tubes, defined by discontinuous endowall, may penetrate a few successive chambers and their interwalls; they are not central and more than one may be present; chambers, especially earlier ones, may be filled by secondary structures analogous to lamellar lining and vesicles of other sphinctozoans, but consisting of spheroidal (or possibly rodlike) bodies fused laterally to form a lining to inner surface of chamber, as well as to form curving, anastomosing trabeculae, with an upward and outward organization, that locally outline circular, horizontal, canal-like spaces within chambers that are interrupted by larger canals of interwalls; original wall microstructure unknown, but illustrations suggest small, isodiametric spherulites; it is possible that sporelike bodies of filling tissue are abnormally large spherulites; no spicules known. *Permian (Guadalupian–Lopingian):* China, Tunisia, Italy (Sicily), Greece, Oman, Thailand, Russia.——FIG. 429,*3a–b*. **I. hubeiensis,* Maokou Formation, Guadalupian, Kefeng, Guangxi, China; *a,* longitudinal section of subcylindrical form with low, arcuate chambers with porous interwalls and sporelike, filling structures that produce stippled-appearing filling on left, IGASB 5099, ×1; *b,* photomicrograph of sporelike, filling structure in chambers between lighter, porous interwalls, IGASB 5059, ×2 (Rigby, Fan, & Zhang, 1989a).

Belyaevaspongia SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994, p. 10 [**Polysiphonella insolita* BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 93; OD] [=*Polysiphonella* BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 93, obj., *non* RUSSO, 1981; WU Ya Sheng, 1991, p. 65]. Moniliform imperforate sphinctozoan lacking a spongocoel, but with numerous small tubes that extend through one or two chambers; interiors of chambers hollow or filled with vesiculae. *Permian (Lopingian):* Thailand, Russia (Primoria, Far East), China.——FIG. 429,*1a–b*. **B. insolita* (BELYAEVA), Upper Permian limestone, Dorashamian, Phrae Province, Thailand; *a,* reference section through chambered sponge with some vesiculae and small tubes that commonly lead to branching points, ×1; *b,* enlargement of part of same specimen showing perforate, chamber walls and small, perforate tubes (*arrows*), BSPGM R1, ×2 (Senowbari-Daryan and Ingavat-Helmcke, 1994).

Rahbahthalamia WEIDLICH & SENOWBARI-DARYAN, 1996, p. 39 [**Amblysiphonella? bullifera* SENOWBARI-DARYAN & RIGBY, 1988, p. 181; OD]. Single or branched stems of ringlike chambers around axial spongocoel; chambers filled with bubblelike, filling structures; individual bubbles may be interconnected by tubelike or rodlike elements; chamber walls perforated by numerous unbranched pores, which may be oriented obliquely to wall. *Permian (Lopingian):* Oman, Tunisia, China.——FIG. 430*a–b*. **R. bullifera* (SENOWBARI-DARYAN & RIGBY), Djebel Tebaga reef complex, Changhsingian, Djebel Tebaga, Tunisia; *a,* holotype section with central, tubular spongocoel with coarser pores than in exowalls and interwalls, chambers with bubblelike, filling structures, USNM 427282, ×3; *b,* enlarged, single chamber of section from holotype with interconnected, bubblelike, filling structures, USNM 427283, ×1 (Senowbari-Daryan & Rigby, 1988).

Rhabdactinia YABE & SUGIYAMA, 1934, p. 179 [**R. columnaria;* OD] [=*Guangxispongia* WU Ya Sheng, 1991, p. 83 (type, *G. spinalis,* OD)]. Columnar sponges of superimposed, low, concentric chambers; chambers hollow or with scattered, sporelike, filling structures; vertical, exhalant tubes well developed and widely distributed but prominent, central

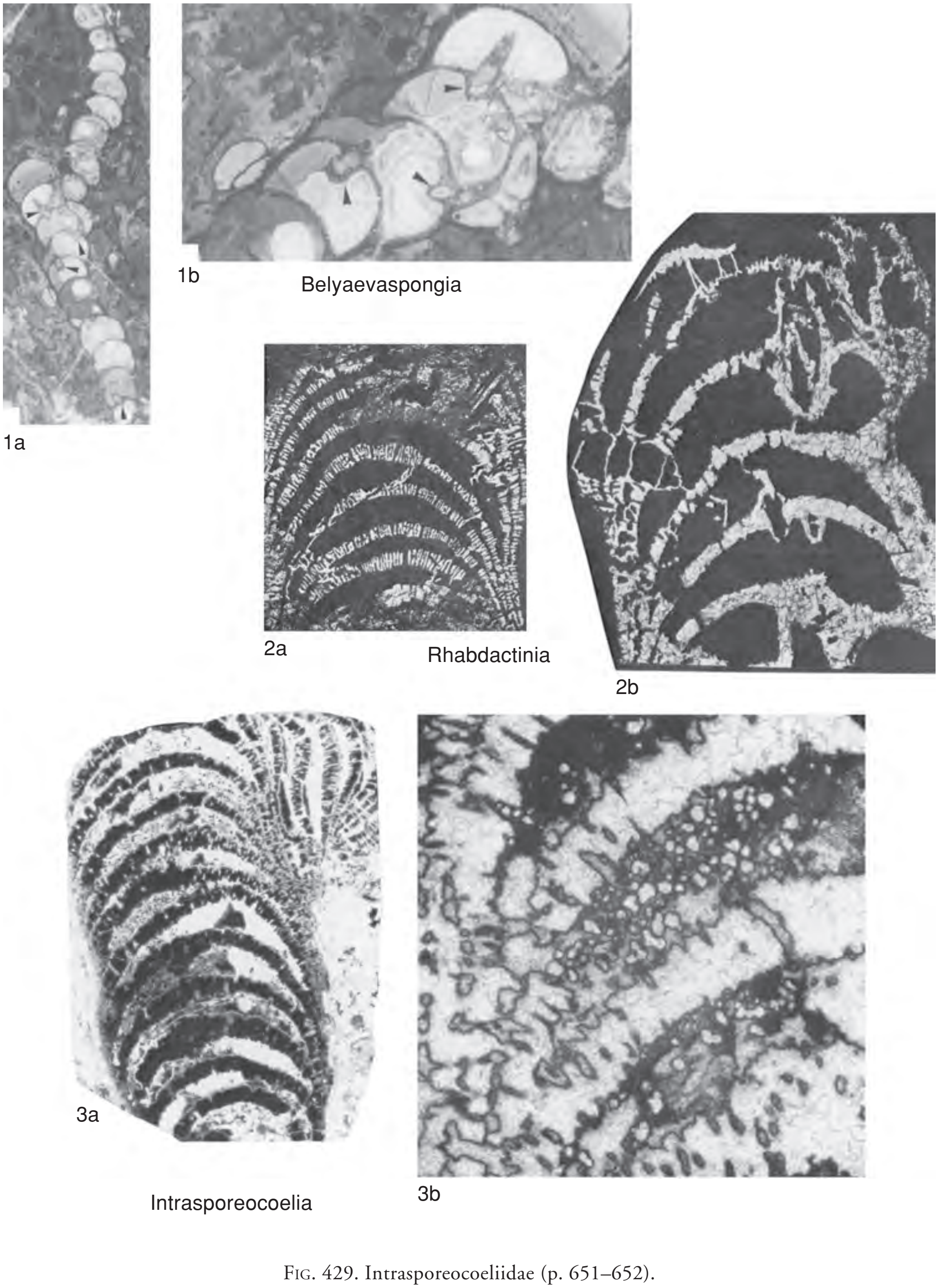


FIG. 429. Intrasporeocoeliidae (p. 651–652).

tube or spongocoel not developed; walls with numerous pores. *Permian (Guadalupian–Lopingian):* Japan, China (Hubei, Guangxi, Zhejiang), Tunisia, Oman, Russia.——FIG. 429,*2a–b.* **R. columnaria,* Mimikiri Limestone, Tosa Province, Sikoku, Japan; *a,* longitudinal section of type sponge with arcuate chambers and coarsely porous interwall, ×1; *b,* longitudinal section with numerous vertical, exhalant tubes cutting light gray interwalls, ×2 (Yabe & Sugiyama, 1934).

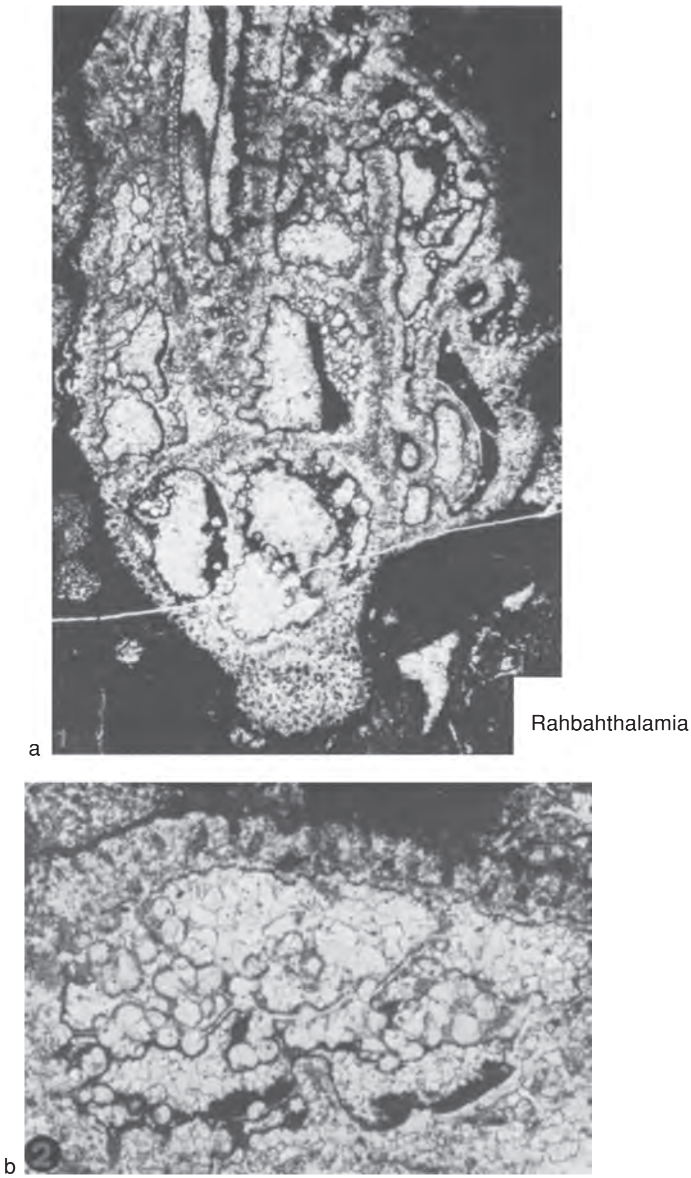


FIG. 430. Intrasporeocoeliidae (p. 651).

Family CRYPTOCOELIIDAE Steinmann, 1882

[Cryptocoeliidae STEINMANN, 1882, p. 175]

Porate permosphinctans with aragonitic, basal skeleton and trabecular, filling structure; spicular skeleton unknown. *Silurian (Ludlow)–Upper Triassic.*

Cryptocoelia STEINMANN, 1882, p. 176 [**C. zitteli;* OD]. Cylindrical, composed of overlapped, hemispheroidal or caplike segments, more or less visible on exterior; exowall bearing closely spaced, small, subpolygonal (possibly lobate) exopores, as well as occasional, somewhat larger, lipped, circular exopores; no cloaca or endowall; interwall a continuation of exowall of underlying chamber, doubled by trabecular coating of chamber above;

interior of low chambers filled by dominantly vertical, pillarlike trabeculae that show limited, lateral anastomosis and expand laterally at top and bottom of each chamber; they may also outline occasional, large, vertical canals of circular cross section; thin vesicles may occupy spaces between pillars in earlier segments; trabecular microstructure an irregular horizontal lamination, within which STEINMANN (1882) observed irregular, branching bodies of unknown nature. *Permian–Upper Triassic:* China (Sichuan), *Permian;* Europe, Iran, Canada (Yukon), *Middle Triassic–Upper Triassic;* Caucasus region, Russia, *Norian;* Tajikistan, *Carnian–Rhaetian.*——FIG. 431,*1a–b.* **C. zitteli,* Cassian beds, Triassic, Seelande Alps, Austria; *a,* side view of exterior of holotype made of overlapping, caplike chambers with porous exowalls, ×1; *b,* vertical section of holotype showing chamber structure and vertical, pillarlike trabeculae, ×2 (Steinmann, 1882).

Anisothalamia SENOWBARI-DARYAN & others, 1993, p. 216 [**A. minima;* OD]. Unbranched to rarely branched stems that lack a spongocoel, with porate interwalls of chambers but aporate exowalls; chambers with some pillar filling structures; skeleton originally aragonite without spicules. [Sections of *Anisothalamia* may appear similar to tangential sections of *Enoplocoelia,* but the latter has a spongocoel, which is wanting in *Anisothalamia.*] *Triassic (Anisian):* Italy.——FIG. 431,*3a–b.* **A. minima,* Recoaro to Serla Formation, Olang Dolomite Alps; *a,* longitudinal section of holotype with thick exowall and arched, perforated interwalls, with pillar structures in chambers (*arrows*), SPIE 229b, ×20; *b,* section of reference specimen with partial, secondary calcification of lower walls and perforate interwalls in upper chambers, SPIE R1.5, ×10 (Senowbari-Daryan & others, 1993).

Antalythalamia SENOWBARI-DARYAN, 1994a, p. 418 [**A. riedeli;* OD]. Moniliform sponges with spherical chambers that lack a spongocoel but have porate walls; large and unbranched pores give sponge exterior a rough, honeycomb-like appearance; filling structure consisting of few but relatively massive columns; numerous vesiculae occur in chamber interiors. [*Antalythalamia* may appear very similar to *Colospongia,* but the latter lacks the pillarlike filling structures that are characteristic of the genus and the Cryptocoeliidae. *Antalythalamia* also appears somewhat similar to the pillar-bearing *Amblysiphonella? polyformis* SENOWBARI-DARYAN & SCHÄFER, 1986, but the latter has a spongocoel.] *Triassic (Norian):* Turkey.——FIG. 431,*2a–b.* **A. riedeli,* Cipit limestone blocks, Taurus Mountains; *a,* holotype, longitudinal thin section with pillars and vesiculae in seven perforate chambers, SPIE 19 G 11/2, ×10; *b,* drawing of holotype showing vesiculae and dark pillars in chambers, bar scale 3 mm long (Senowbari-Daryan, 1994a).

Rigbyspongia DE FREITAS, 1987, p. 840 [**R. catenulata;* OD]. Cateniform, porate, trabeculate sphinctozoan with multisiphonate, axial region; shallow spongocoel into which most equal-sized canals converge and empty; other similar canals exit through exopores around margin of osculum; numerous vertical pillars are common filling structures in all chambers. [*Rigbyspongia* was originally included in the family Polysiphoniidae (DE FREITAS, 1987), but that family consists of unsegmented sponges and is not included in the thalamid sponges (SENOWBARI-DARYAN, 1990, p. 104), but in the latter work the genus was included in the Cryptocoeliidae, as it is here.] *Silurian (Ludlow):* Canada (Cornwallis Island).——FIG. 432,*2a–d.* **R. catenulata,* Silurian limestone, District of Franklin; *a,* side view of exterior of holotype, with numerous exopores, ×2; *b,* longitudinal section with shallow spongocoel in upper part above several vertical, exhalant canals, numerous pillars showing in chambers; *c,* transverse section showing pillars in outer chambers, GSC 85330, ×2; *d,* schematic reconstruction showing skeletal and canal patterns with pillars in outer chamber layer, not to scale (De Freitas, 1987; courtesy of *Canadian Journal of Earth Sciences*).

Sphaerothalamia SENOWBARI-DARYAN, 1994a, p. 420 [**S. vesiculifera;* OD]. Asiphonate, moniliform sponge composed of spherical to hemispherical chambers that increase upwardly in size; chamber walls with dichotomously branching pores; pillarlike elements extending out from chamber interwalls and ectowalls and function as bases for later developing vesiculae, which partially or entirely fill chambers; skeleton possibly aragonitic with irregular microstructure; spicular skeleton composed of monaxons and possible tylostyles, which were incorporated into basal skeleton. [*Sphaerothalamia* is similar to *Antalythalamia* but has branching pores in the chamber walls and a spicular skeleton of monaxons.] *Triassic (Norian):* Turkey.——FIG. 432,*1a–b.* **S. vesiculifera,* Cipit limestone blocks, Taurus Mountains; *a,* holotype, thin section through three chambers with thick, vesicular, filling structures based in part on pillarlike extensions out from walls, bifurcating pores show on exowalls, SPIE 19 G 78/1, ×10; *b,* drawing of transverse section of paratype showing bifurcating exopores and filling structure pillars in black and vesiculae stippled, SPIE 16 G 49, scale bar, 3 mm (Senowbari-Daryan, 1994a).

Family PALERMOCOELIIDAE Senowbari-Daryan, 1990

[Palermocoeliidae SENOWBARI-DARYAN, 1990, p. 109]

Porate permosphinctans with radial framework parallel to a well-developed, tubular, canal system in chamber or segment walls. *Upper Triassic.*

Palermocoelia SENOWBARI-DARYAN, 1990, p. 109 [**P. tubulifera;* OD]. Permosphinctans with development of a radial, parallel, tubular pore system in chamber walls, which in longitudinal section are composed of trabecular, filling structures simulating that of *Stylothalamia;* skeleton with microgranular

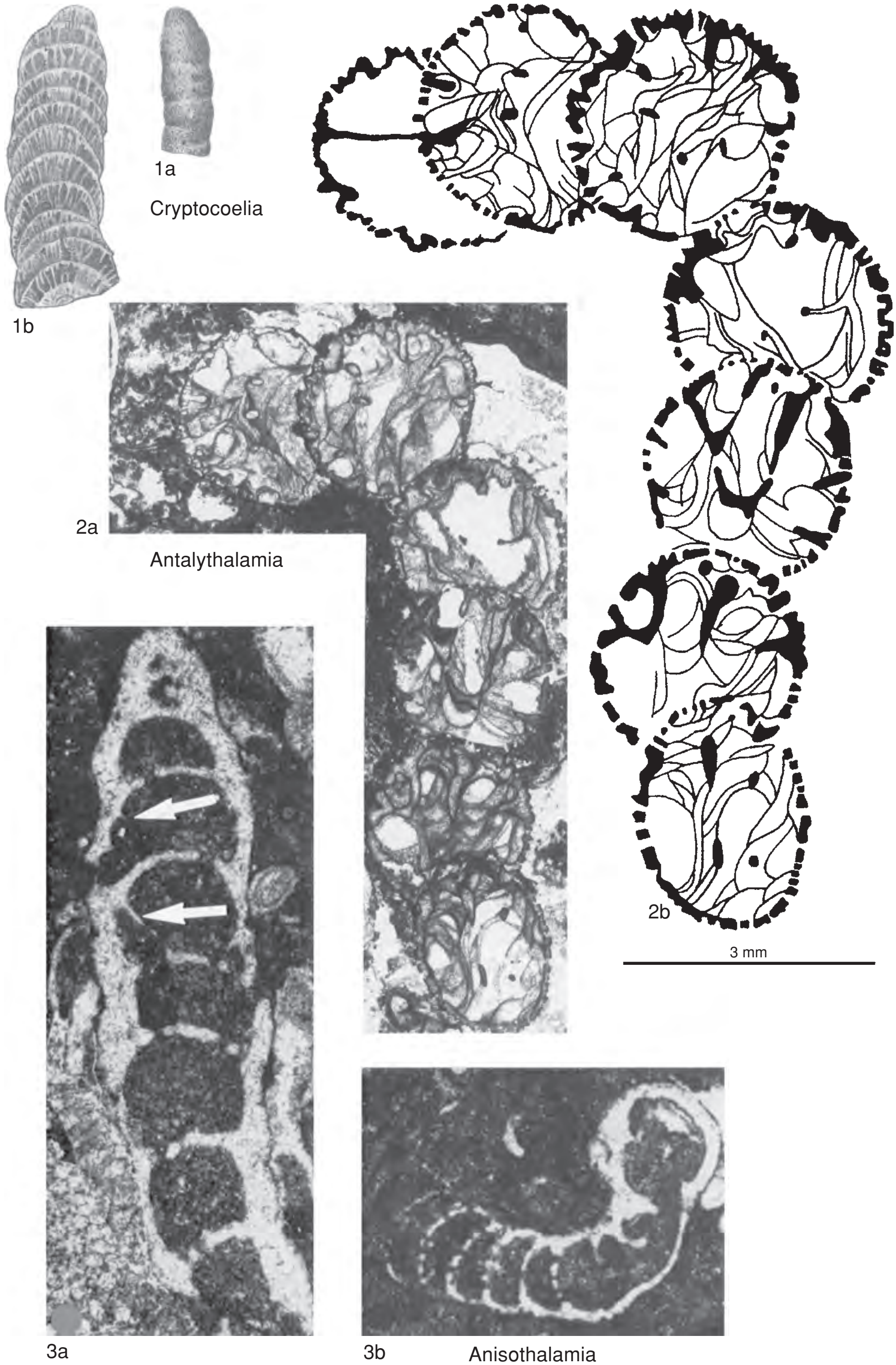


FIG. 431. Cryptocoeliidae (p. 653–654).

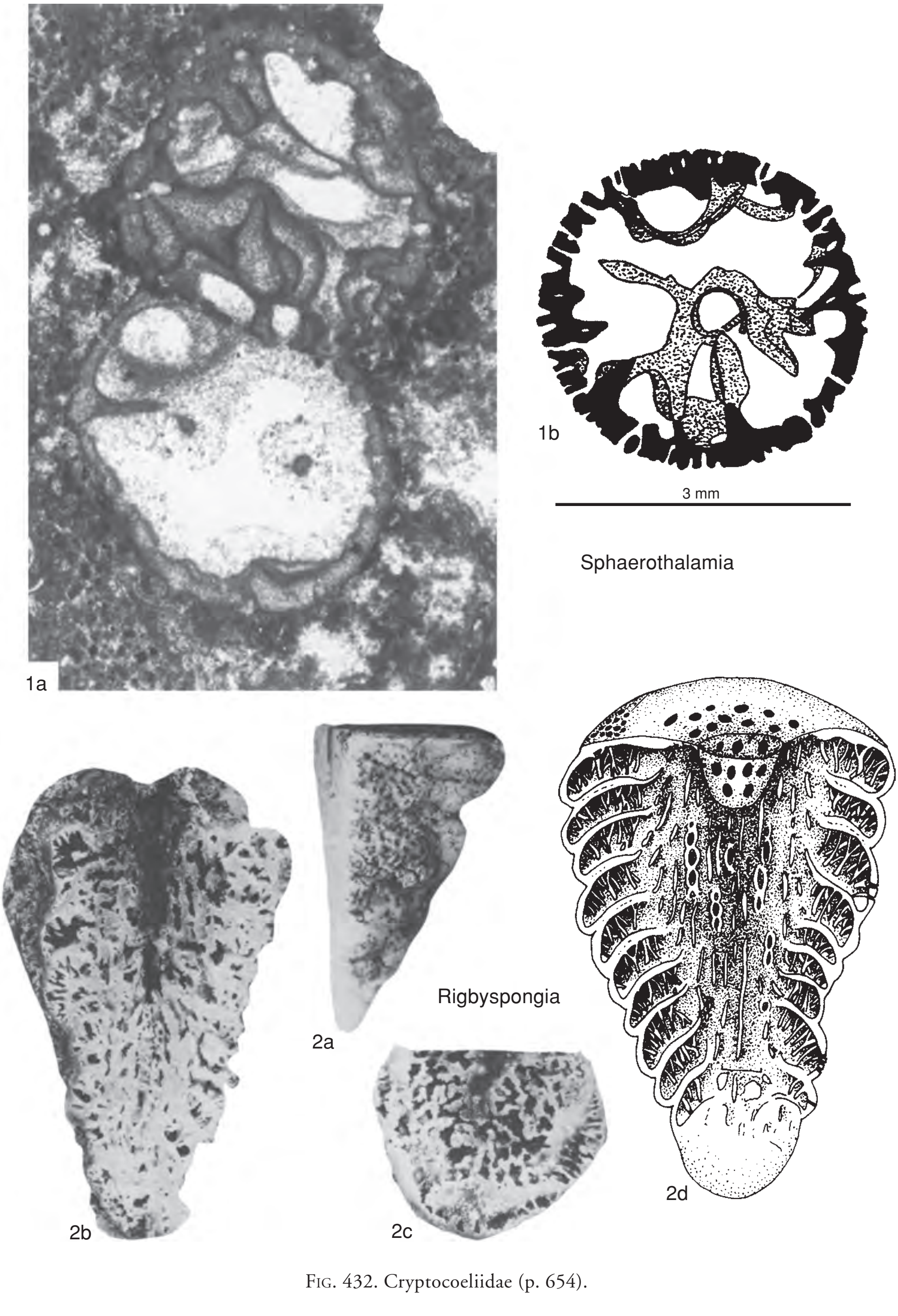


FIG. 432. Cryptocoeliidae (p. 654).

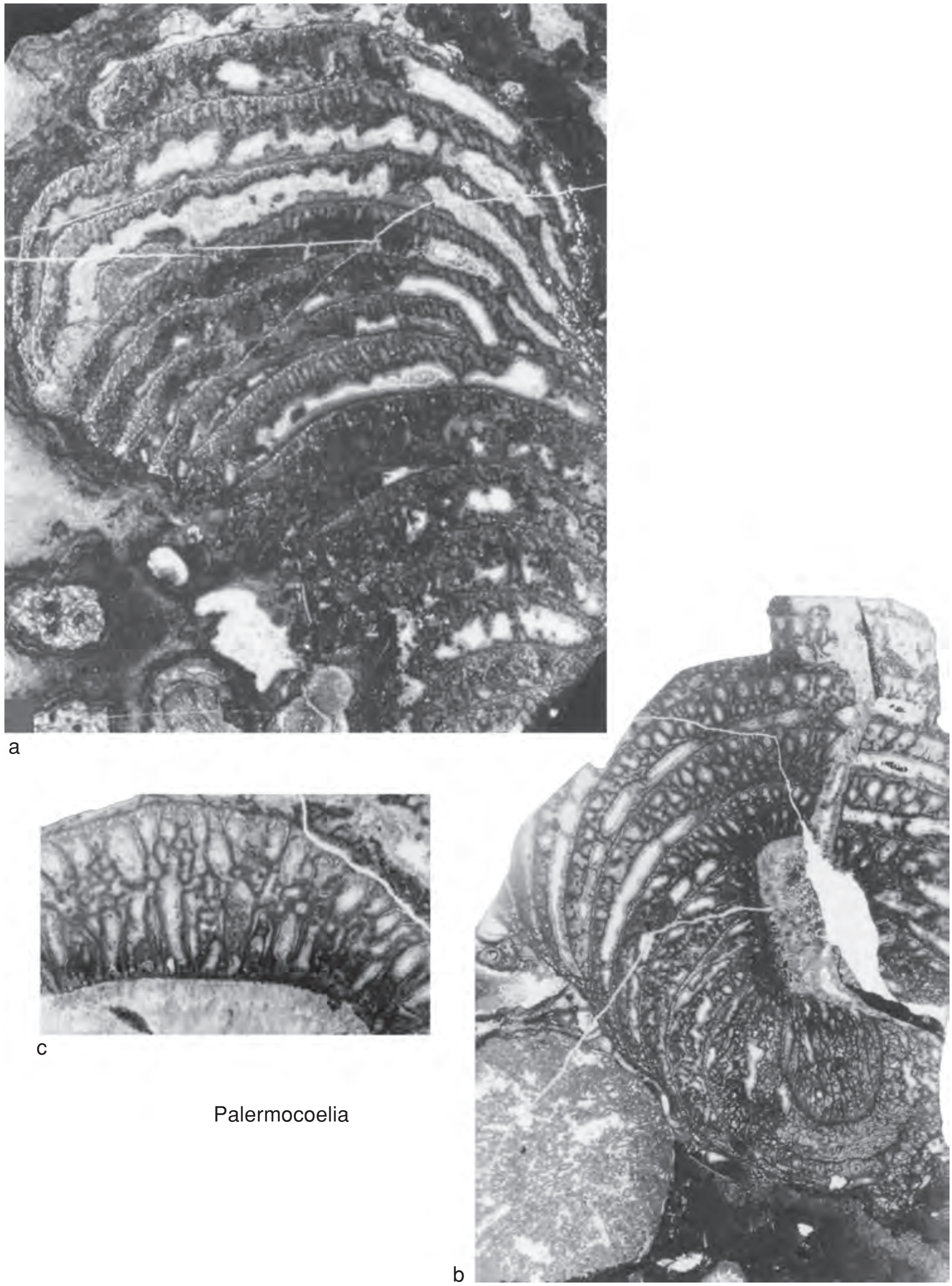


FIG. 433. Palermocoeliidae (p. 654–658).

microstructure, perhaps produced by diagenesis; reticular filling structures developed here and there in older chambers; vesiculae are limited to peripheral parts of older chambers. *Upper Triassic:* Italy. ——FIG. 433*a–c*. **P. tubulifera,* Triassic reef limestone, Norian–Rhaetian, Palermo, Sicily; *a,* longitudinal section of holotype with low chambers partially filled with calcite or matrix; tubular pores showing in middle and upper chamber walls, SPIE D/361/2, ×4; *b,* transverse section through lower part of holotype with central spongocoel and thick walls with tubular pores, SPIE D/361/3, ×2; *c,* photomicrograph of spongocoel wall showing tubular structure and intervening filling structure, SPIE D/361/6, ×5 (Senowbari-Daryan, 1990; courtesy of *Münchner Geowissenschaftliche Abhandlungen,* Verlag Dr. Friedrich Feil).

Family GIRTYOCOELIIDAE new family

[Girtyocoeliidae FINKS & RIGBY, herein] [=Amphorithalamiidae SENOWBARI-DARYAN & RIGBY, 1988, p. 201] [type genus, *Girtyocoelia* COSSMANN, 1909, p. 67]

Spheroidal chambers; exowall generally imperforate, with well-developed exauli, that may contain internal cribribulla, in equatorial ring; cloaca present except in juveniles (protocysts), with endopores often concentrated in a ring; filling structures sparse to absent, but vesicles or trabeculae may occur. *Ordovician–Triassic.*

Girtyocoelia COSSMANN, 1909, p. 67 [**Heterocoelia beedei* GIRTY, 1908, p. 284; OD] [=*Heterocoelia* GIRTY, 1908, p. 282, obj., *non* DAHLBOM, 1854; *Apocoelia* RIGBY, 1984, p. 1,453 (type, *A. sphaera* RIGBY, 1984, p. 1,456, OD)]. Spherical segments, or spheroidal when in contact, arranged in subparallel, branching, occasionally anastomosing, linear series; segments in each series connected by continuous, narrow, central tube or cloaca that is frequently visible externally between segments and protrudes beyond last segment (prosiphonate); juveniles (protocysts) adnate on shells and other sponges, and initially lack cloaca, although not osculum, and their exauli may be very short or very long; exowall imperforate except for equatorial ring of large, circular exopores at ends of spoutlike exauli or sometimes merely strongly rimmed; at inner end of each exaulos is a hemispherical sieve of smaller, circular pores (cribribulla) that bulges into chamber; inner surface of exowall may have anastomosing network of fibers applied to it, but no fibers are known from lumen of chamber itself; vesicles may be present in lumen; endowall pierced by small to large, circular endopores, often concentrated into two sievelike rings, one near lower and one near upper end of chamber; these rings may bulge into chamber; when successive segments are in contact, interwall double, being two exowalls; cloaca of new branch arising through exowall; exauli of successive segments may occasionally join; long exauli of protocysts may invade other sponges; wall microstructure consists of small (20 to 60 μm), isodiametric spherulites; laminar, secondary layer of clinogonal (penicillate) structure may be present on inside of walls lining chamber; no spicules known. [Early protocysts in which the cloaca has not yet appeared were named *Apocoelia* by RIGBY (1984, p. 1,453).] *Ordovician–Triassic (Carnian):* Australia, *Ordovician;* Austria, *upper Bashkirian–Gzhelian;* southcentral to southwestern United States, *Upper Pennsylvanian, Wordian;* Tunisia, Spain, Italy (Sicily), Oman, Venezuela, Thailand, China, *Lopingian;* Russia, *Wordian–Capitanian;* Austria, Yugoslavia, Greece, Italy (Sicily), *Ladinian–Carnian.*——FIG. 434,*1a–e*. **G. beedei* (GIRTY), Plattsburg Limestone, Desmoinesian–Virgilian, Chanute, Kansas; *a,* cluster of several individuals showing growth form, ×1; *b,* section showing axial spongocoel and globular chambers in branching specimen, ×2; *c,* section showing chambers separated along axial spongocoel, all part of syntype suite, USNM 53471, ×2 (Girty, 1908); *d,* silicified specimen with prominent, tubular exaules on each globular chamber, USNM, Glass Mountains, Texas, ×1.5; *e,* reconstruction showing globular chambers around porous, central tube and with prominent exaules, not to scale (Senowbari-Daryan, 1990; courtesy of *Münchner Geowissenschaftliche Abhandlungen,* Verlag Dr. Friedrich Feil).

Amphorithalamia SENOWBARI-DARYAN & RIGBY, 1988, p. 201 [**A. cateniformis;* OD]. Spheroidal chambers encrusting other surfaces and connected by long, sometimes branching tubes that may be regarded as exauli; one or usually more oval clusters of polygonal pores, surrounded by a low rim, occurring on upper surface of each chamber and may be regarded as cribribulla flush with surface; interior of each chamber filled with fine, meandriform, trabecular net that outlines anastomosing, tubular spaces; exowall aporate; no cloaca; microstructure unknown; no spicules known. [These appear to be protocysts of an unknown adult form (unless paedomorphic); they differ from the protocysts of *Girtyocoelia* COSSMANN, 1909, in having trabecular, filling tissue and in development of cribribulla-like structures at the surface. They also lack the prominent, central tube distinctive of adult *Girtyocoelia.* The overall organization, however, is similar to that of *Girtyocoelia* and they would seem to be related. There are, in fact, traces of trabeculae on the inner surface of the *Girtyocoelia* exowall. The spelling given here is that used consistently in the original description of the genus and type species. The alternate spelling *Amphorothalamia,* used in the figure captions, table of contents, and elsewhere in the original publication, is to be regarded as a *lapsus calami.*] *Permian (Lopingian):* Tunisia.——FIG. 435,*1a–c*. **A. cateniformis,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* attached, flasklike chambers connected by tubes in holotype, ×2; *b,* two chambers of holotype showing distinct ostia, several per chamber, and interior, reticulate, filling structure, ×5; *c,* sketch of holotype,

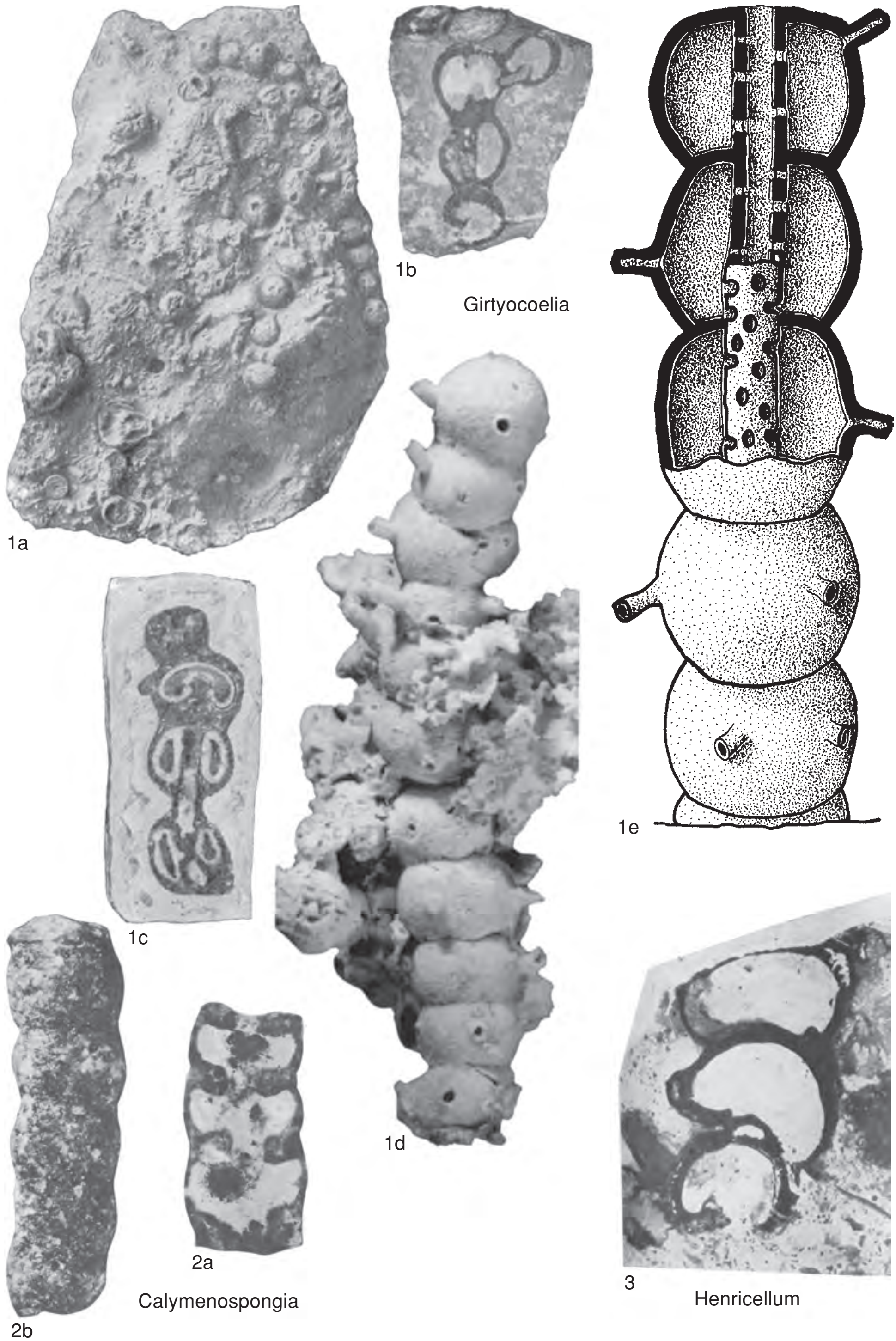


FIG. 434. Girtyocoeliidae (p. 658–660).

either branched stem or two individuals, USNM 427414, approximately ×2 (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

Calymenospongia ELLIOTT, 1963, p. 295 [**C. kurdistanensis:* OD]. Small, uniserial calcisponge, chambers nearly spherical, hollow, fused, double interwalls producing thick layer between chambers; chambers interconnected in interior by single, large osculum through interwalls; exowall with few scattered, relatively coarse, irregularly placed, inhalant ostia. *Paleogene (Paleocene):* Iraq.——FIG. 434,*2a–b*. **C. kurdistanensis,* Kolosh Formation, Bekhme, Erbil Liwa, northern Iraq; *a,* holotype showing uniserial growth form, BM S8335; *b,* vertical section through paratype showing chambers, fused thick interwalls, and thin exowalls, BMS8336, ×25 (Elliott, 1963).

Enoplocoelia STEINMANN, 1882, p. 166 [**Scyphia? armata* KLIPSTEIN, 1843 in 1843–1845, p. 284; OD]. Cylindrical, not clearly segmented externally; central cloaca about one-fourth sponge diameter; exowall finely porous with circular to vertically elongate, slitlike, meandriform spaces, partly obscured by imperforate cortex, as well as a horizontal row, for each internal segment, of larger, circular exopores with strong lips, or more precisely, a volcano-like protrusion of exowall; chambers low; interwalls sievelike, being pierced by closely spaced, circular interpores of two sizes that are intermediate between sizes of large and small exopores; endopores circular to vertically elongate and size of larger interpores; vertical, trabecular ridges may be attached to chamber side of endowall; chamber lumen free of skeletal structures; walls composed of primary layer of isodiametric spherulites of small to large size; older parts of chambers and cloaca may be largely filled with secondary deposit of clinogonal (penicillate) aragonite; spicules not known. [The specimens of species from the Permian of Sicily are incomplete and questionable.] *Permian–Triassic:* Tunisia, Italy (?Sicily), *Permian;* Greece, Italy (Sicily), Austria, Romania, *Triassic.* ——FIG. 435,*3a–b*. **E. armata* (KLIPSTEIN), San Cassiano Formation, Carnian–Norian, Dolomite Alps, Italy; *a,* side view of branched type specimen with lipped exopores, ×2; *b,* tangential polished section of holotype showing uniformly porous interwalls of low chambers, ×4 (Steinmann, 1882).

Henricellum WILCKENS, 1937, p. 194 [**H. insigne;* OD]. Spheroidal to hemispheroidal chambers attached in linear series; small, blisterlike chamber attached to outside of each principal chamber and communicates with it by one (or possibly more) small canals through exowall, but there is probably not communication between principal chambers; a few large exopores present on each segment, but wall otherwise imperforate; chamber interior has no skeletal elements; microstructure and spicules not known; outer surface appearing somewhat rough. [Genus is known only from sections and the structure is not well understood. It is conceivable that the blisterlike chambers with their associated canals are exauli with cribribulla, seen in partial view, but this is conjecture.] *Permian (?Wordian–?Capitanian), Triassic:* Russia, *?Wordian–?Capitanian;* Indonesia, Canada (Yukon), *Triassic.*——FIG. 434,*3*. **H. insigne,* Pharetrone Limestone, Upper Triassic, Seran, Moluccas, Indonesia; longitudinal section of holotype with spheroidal chambers lacking filling structures and with rare exopores, S 194, ×2 (Wilckens, 1937; courtesy of *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abt. B*).

Phraethalamia SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994, p. 21 [**P. tubulara;* OD]. Stemlike, aporate, thalamid sponges with two or more parallel, axial spongocoels that penetrate ringlike, stacked chambers; numerous branched tubes extending from spongocoel wall laterally into hollow chamber interiors, which lack vesiculae and filling structures. [In general size and chamber arrangement, *Phraethalamia* is similar to *Girtyocoelia,* but the latter has only a single, axial spongocoel and it lacks the distinctive tubes that extend from the spongocoel wall into the chambers. Such tubes are known in the Permian demosponge *Pseudoamblysiphonella* SENOWBARI-DARYAN & RIGBY, 1988, and in *Barroisia lehmani* HILMER & SENOWBARI-DARYAN, 1986, from the Cretaceous of Germany, but both those genera have perforated outer walls.] *Permian (Lopingian):* Thailand.——FIG. 435,*2a–b*. **P. tubulara,* upper Permian limestone, Dorashamian, Phrae; *a,* holotype, longitudinal section through several chambers and two wide, axial canals, ×2; *b,* drawing of holotype showing spherical, imperforate, chamber walls, double axial canals, and smaller tubes that extend from spongocoel wall into interior of chambers, BSPGM R8, ×1 (Senowbari-Daryan & Ingavat-Helmcke, 1994).

Polyedra TERMIER & TERMIER, 1955, p. 615 [**P. tebagaensis;* OD]. Cylindrical sponge composed of superposed, spheroidal segments; central cloaca one-third to one-fifth sponge diameter; outer surface of each segment divided into large, polygonal, flat or concave areas, each area bounded by raised rim containing large, circular labripore (or short exaulos) at its center; external surface of sponge, both inside and outside polygonal areas, bearing fine, reticulate sculpture, which is obscurely radial about each labripore; original description states that an internal chamber corresponds to each polygonal area, that these chambers communicate with each other by pores, and that the cloaca is sometimes partitioned longitudinally. [Redescription of topotypes by SENOWBARI-DARYAN and RIGBY (1988, p. 196 ff.; pl. 37,*1–8*) shows a single chamber for each segment, a cribribulla over the internal end of each exaulos, and small, scattered endopores in the endowall; microstructure not known; no spicules known. As redescribed, this genus differs from *Girtyocoelia* COSSMANN, 1909, in the polygonal facets and reticulate surface sculpture.] *Permian (?Artinskian, Lopingian):* Tajikistan, *?Artinskian;* Tunisia, *Lopingian.*——FIG. 436,*1a–d*. **P. tebagaensis,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; *a,* side view of specimen with one rimmed ostium per flattened

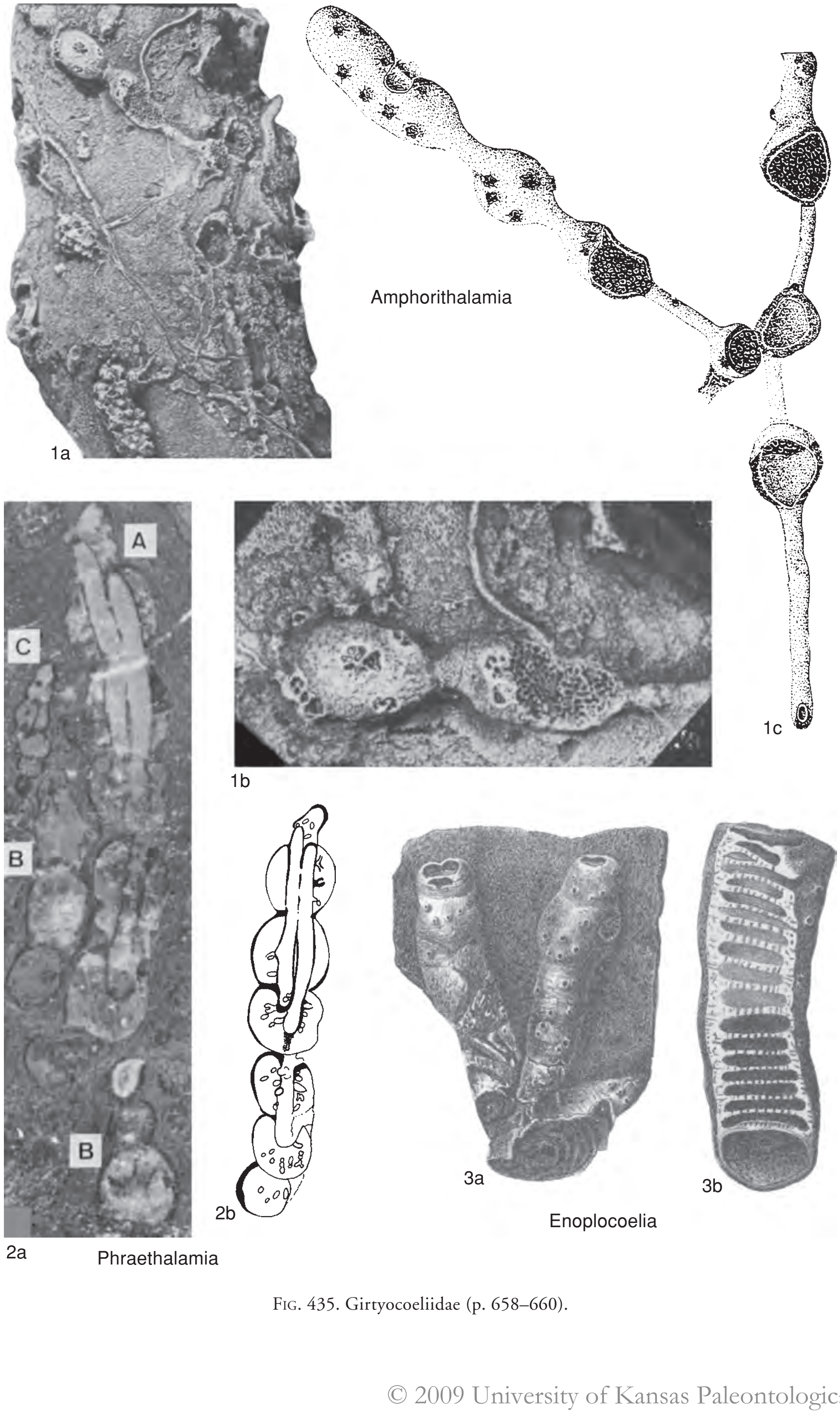


FIG. 435. Girtyocoeliidae (p. 658–660).

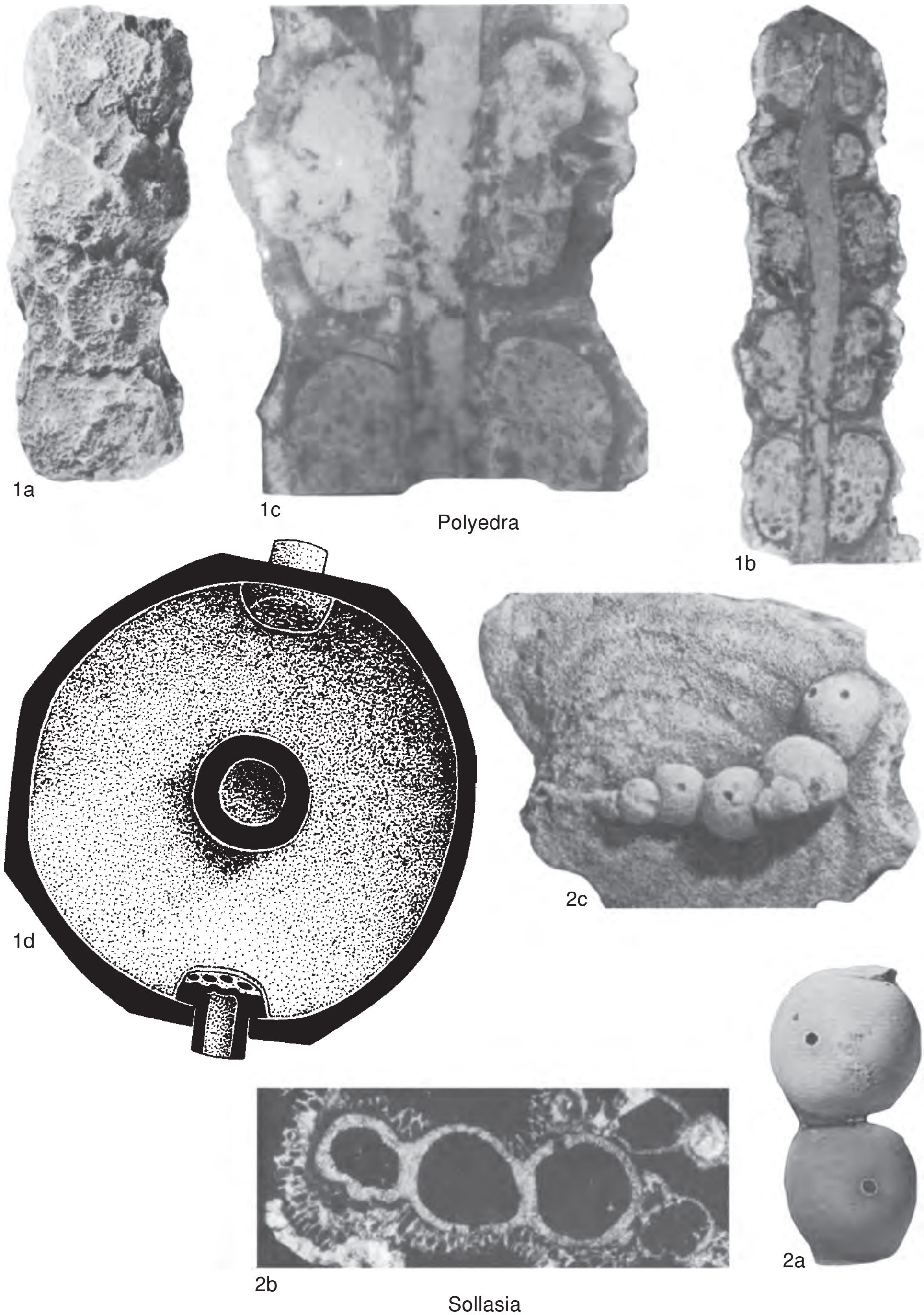


FIG. 436. Girtyocoeliidae (p. 660–664).

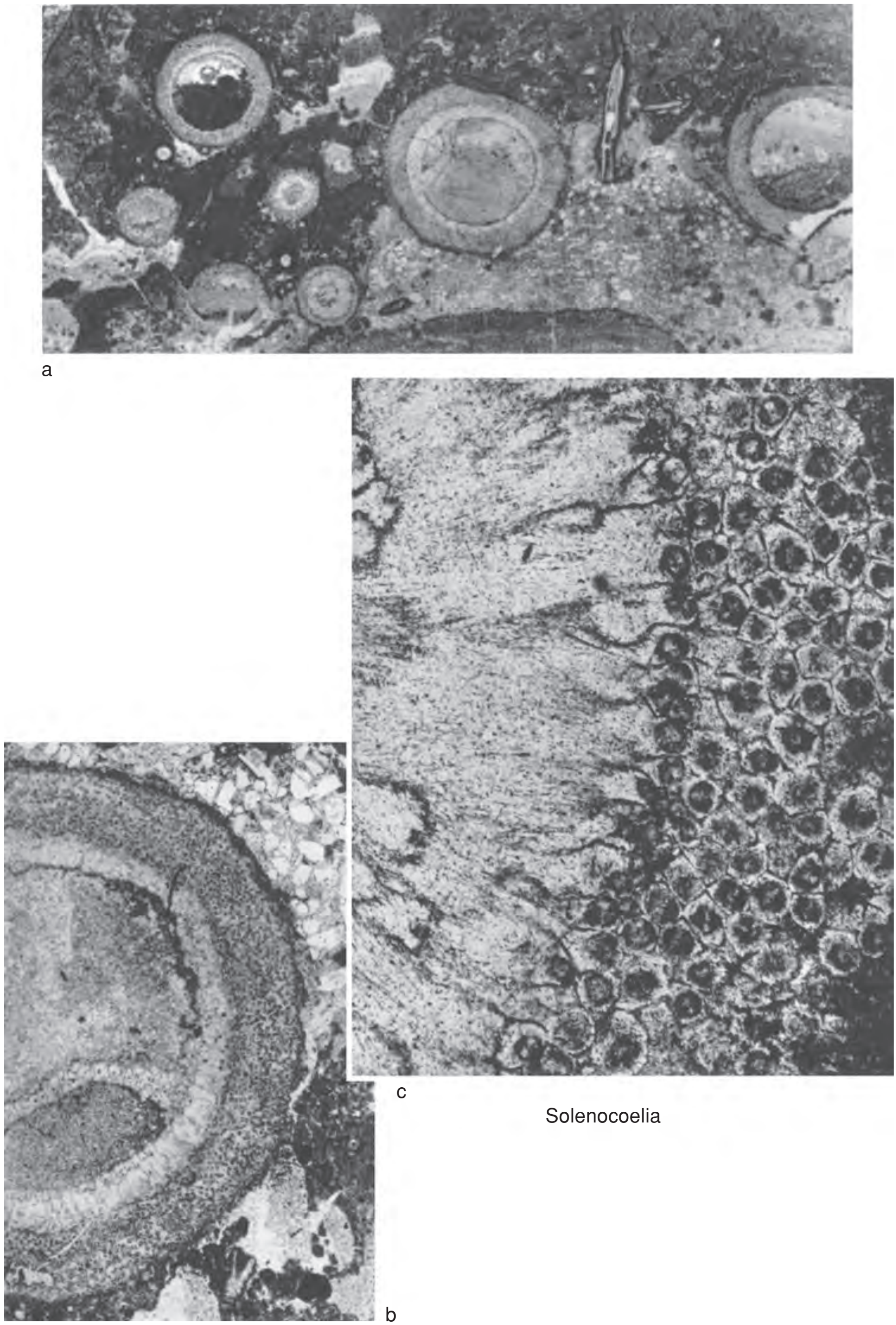


FIG. 437. Girtyocoeliidae (p. 664).

chamber face, which have reticulate, radial sculpture, USNM 427375, ×2; *b,* polished, axial section showing growth form and axial tube, as well as cribribulla on right exowall of second chamber from bottom, ×2; *c,* photomicrograph of lower part of same specimen, with cribribulla at midheight in right exowall of upper chamber, USNM 427377, ×5; *d,* diagram of transverse section showing two ostia with sievelike, cribribulla plates at internal end of short exaules in exowall, and central tube, not to scale (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

?Solenocoelia CUIF, 1973, p. 122 [**S. cylindracea;* OD]. Conical; so-called exowall imperforate; interior without skeletal structures except for occasional thin, curved, tabula-like partition; no pores; primary layer of outer wall and all of tabulae built of small, isodiametric spherulites; outer wall has inner, clinogonal layer; no spicules. [It is doubtful that this is a sponge.] *Triassic:* Turkey.——FIG. 437*a–c.* **S. cylindracea,* Triassic deposits, Carnian–Norian, Korkuteli; *a,* type, transverse sections of a group of organisms, ×4; *b,* transverse section with spherulitic structure in both layers of outer wall and in arched plate in interior, ×18; *c,* photomicrograph showing spherulites in outer wall and strongly asymmetrical ones in interior, ×100 (Cuif, 1973; courtesy of *Geobios*).

Sollasia STEINMANN, 1882, p. 151 [**S. ostiolata;* OD]. Spheroidal to barrel-shaped segments in contact in linear series; exowall imperforate except for equatorial ring of large, circular, lipped exopores; no cloaca or endowall, but central osculum at top of each segment; primary layer of exowall of next segment beginning peripherally so that primary interwall is formed by exowall of preceding segment; secondary layer lining lumen of each chamber, coating both sides of interwall; primary layer of exowall or interwall containing fine, anastomosing canals that may be filaments of endolithic fungi or algae; spherulites or spicules not observed. [Permian species in literature poorly known and doubtful.] *Carboniferous (Bashkirian)–Triassic (Rhaetian):* Spain, *Bashkirian;* Austria, *upper Bashkirian–Gzhelian;* Tunisia, Italy (Sicily), Oman, United States (Texas), China and southeastern Asia; Russia, Tajikistan, *Guadalupian–Lopingian;* ?Hungary, *Anisian;* Caucasus region, Russia, *Carnian–Rhaetian;* Italy (Sicily), *Norian.*——FIG. 436,*2a–c.* **S. ostiolata,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; *a,* side view of fragment with two chambers, smooth walls, and well-developed ostia, USNM 4427384, ×2; *b,* section through a fragment with three chambers showing double interwalls, lack of filling structures, and granular, spherulitic microstructure in walls that are overgrown with a chaetetid, USNM 427390, ×5; *c,* specimen illustrating increase in chamber size in early stages of growth, USNM 427394, ×3 (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

Family THAUMASTOCOELIIDAE Ott, 1967

[Thaumastocoeliidae OTT, 1967a, p. 15, *partim; emend.,* FINKS & RIGBY, herein]

Cateniform, without cloaca; cribribulla-like pore fields, approximately flush with surface of exowall and surrounded by low rims, occurring equatorially and also forming osculum and interpores. *Middle Ordovician–Triassic.*

Thaumastocoelia STEINMANN, 1882, p. 153 [**T. cassiana;* OD] [=?*Follicatena* OTT, 1967a, p. 20 (type, *F. cautica* OTT, 1967a, p. 22, OD); ?*Palaeoierea* LAUBE, 1865, p. 233 (type, *Manon? gracilis* MÜNSTER, 1841, p. 28, OD)]. Cylindrical, segmented; segments spheroidal or barrel shaped; no cloaca; exowall aporate except for a few circular, lipped exopores or circular, sievelike clusters of small, circular exopores (see DIECI & others, 1968, pl. 27,*8*), clusters depressed below surface and surrounded by external, raised rim (essentially a cribribulla and very short, wide exaulos) [unless the specimen of DIECI and others is a *Follicatena*]; interpores (and terminal oscular field) grouped in large, sievelike cluster bowed down into lower chamber; interior of chambers without skeletal structures; interwall a continuation of exowall of lower chamber covered by secondary layer only of upper chamber; exowall or interwall composed of primary layer of very large, isodiametric spherulites of subpolygonal outline, lined internally by secondary layer of clinogonal (penicillate) structure; supposed, large, calcareous spicules (monaxonic and branching) in secondary layer may be random sections of larger filaments of endolithic fungi or algae, whose finer, irregularly branching filaments have been observed both in secondary layer and also perforating spherulites of primary layer. [*Palaeoierea* LAUBE, 1865, resembles *Thaumastocoelia* externally, but its interior structure is unknown; the surface was said to be finely porous, but the large, granular spherulites may have given this impression. It is the senior synonym if truly congeneric. See also *Sestromella,* p. 611 herein.] *Permian (?Cisuralian–?Guadalupian, Lopingian)–Triassic:* Oman, China; USA (Texas), *?Permian;* Italy, Hungary, Turkey, Tajikistan, *Triassic.*——FIG. 438,*1a–d.* **T. cassiana,* San Cassiano Formation, Carnian–Norian, Dolomite Alps, Italy; *a,* side view with lipped exopores on barrel-shaped chambers of type specimen, ×2; *b,* longitudinal section of type showing porous interwalls and impervious outer walls, ×1; *c,* view from above of coarsely perforate interwall, ×10; *d,* section through chamber wall showing large, isodiametric spherulites and supposed spicules that may be penicillate, calcareous elements, ×25 (Steinmann, 1882).

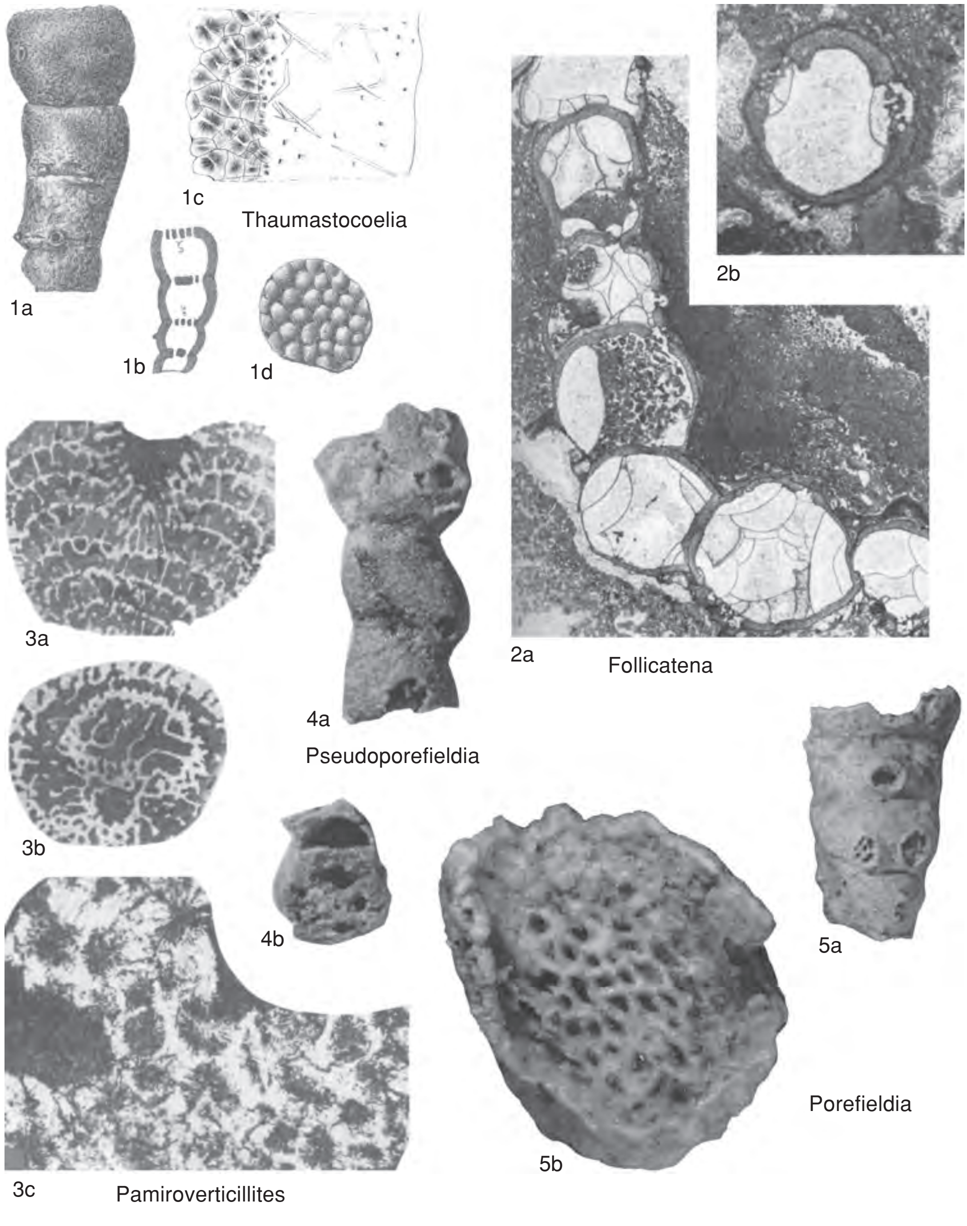


FIG. 438. Thaumastocoeliidae (p. 664–667).

?Follicatena OTT, 1967a, p. 20 [**F. cautica* OTT, 1967a, p. 22; OD]. Spheroidal segments forming chains; cloaca absent; exowall imperforate except for sievelike groups of exopores (cribribullae possibly flush with surface); similar groups of interpores pierce double interwall, pores in wall of lower chamber, with wall of upper chamber absent over entire sievelike group; interior of chambers often filled with numerous vesicles, but no other interior skeletal structures; microstructure unknown; no spicules known. *Permian–Triassic:* Italy (Sicily), Russia Pamir region, Tajikistan, China, *Permian;* Alpine-Mediterranean region, USA (Oregon), Canada (Yukon), *Triassic.*——FIG. 438,*2a–b*.

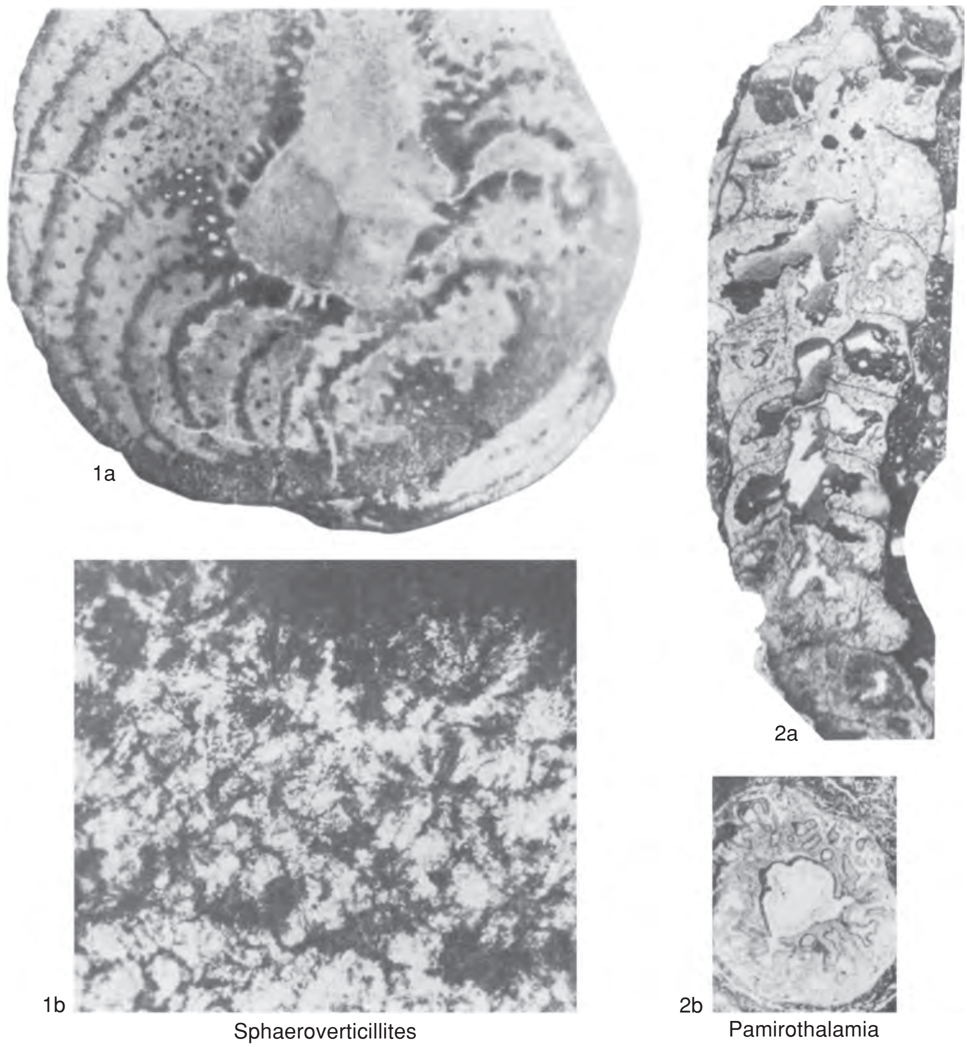


FIG. 439. Thaumastocoeliidae (p. 666–667).

F. cautica, Wettersteinkalk, reef facies, Ladinian, Kaisergebirge, Austria; *a,* longitudinal section of holotype with spheroidal chambers and imperforate walls with cribribullae, best seen in upper and lower chambers, BSPGM G 396 a/67, ×2.5; *b,* transverse section of holotype chamber with two distinct cribribulae, BSPGM G 397 a/67, ×5 (Ott, 1967a; courtesy of *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*).

Pamirothalamia BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 135 [**P. originalis;* OD]. Catenulate sponge with spherical chambers around axial canal that is cryptosiphonate; ostia in distal parts of chambers and on lateral surfaces; chamber walls fragile, in form of possible bars; interwalls double where two chambers juxtaposed and each chamber with complete wall. [*Pamirothalamia* is similar to *Sollasia* but has thin, chamber walls and endowall of axial, exhalant structure, somewhat similar to that in *Battaglia* SENOWBARI-DARYAN & SCHÄFER, 1986.] *Triassic:* Tajikistan.——FIG. 439,*2a–b*. **P. originalis,* Triassic limestone, between Aksu River and Dzhilgakochusu River; *a,* longitudinal section through large sponge with thick exowalls and double interwalls, central, exhalant canal or spongocoel ill defined, MIGT 793-15 116/53, ×4; *b,* transverse section showing complex, inhalant canals in thick walls, MIGT 793-16 116/54, ×4 (Boiko, Belyaeva, & Zhuravleva, 1991).

Pamiroverticillites BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 153 [**Sphaeroverticillites conicus* BOIKO, 1990, p. 123, *partim;* OD]. Spherical to cup-shaped sponges composed of low, circular chambers that are overlapping, without visible constrictions on dermal surface; dermal surface with equally distributed, round pores; axial spongocoel cylindrical with retrosiphonate chamber walls; chambers with vertical, trabecular filling structures; skeletal structure spherulitic with small spherulites in lower chamber walls, directed downwardly, in possibly parallel rows; spherulites in upper walls large, upwardly directed, and nearly parallel. [Differs from *Sphaeroverticillites* in growth form and *Preverticillites* in type of filling structures.] *Triassic (Norian):* Tajikistan.——Fig. 438,*3a–c.* **P. conicus* (Boiko), southeastern Pamir; *a,* vertical section showing low, overlapping chambers with vertical, trabecular filling structures and shallow, axial spongocoel, ×1; *b,* transverse section with small, axial spongocoel in lower part, and porous chamber walls, ×2; *c,* photomicrograph of part of wall showing spherulites in wall, MIGT 793-25 116/76, ×50 (Boiko, Belyaeva, & Zhuravleva, 1991).

Porefieldia Rigby & Potter, 1986, p. 37 [**P. robusta;* OD]. Small, conicocylindrical sponges composed of superposed segments, visible on exterior, without cloaca; exowall imperforate but containing two to five, cribribulla-like or craticula-like, elliptical pore fields approximately flush with surface and surrounded by prominent rim; pores subangular and separated by narrow trabeculae; interwalls with interpores of similar shape to craticular (cribribullar) pores, but larger; intervening trabeculae may be crusted on upper surface; thin vesicles may be present in chambers; microstructure not known; no spicules known. [Genus is very similar to *Follicatena* Ott, 1967a, and *Thaumastocoelia* Steinmann, 1882, both from the Triassic.] *upper Upper Ordovician:* USA (California).——Fig. 438,*5a–b.* **P. robusta,* Kangaroo Creek Formation, Ashgill, Klamath Mountains; *a,* side view of silicified, steeply obconical holotype with prominent pore fields, which may occur several per chamber, as rimmed clusters of ostia, ×2; *b,* vertical view of broken summit with coarse, sievelike interwalls and moderately thick exowalls, USNM 395885, ×5 (Rigby & Potter, 1986).

Pseudoporefieldia Rigby, Potter, & Blodgett, 1988, p. 741 [**P. micella;* OD]. Differs from *Porefieldia* Rigby & Potter, 1986, in that the exowall bears small, widely spaced exopores, in addition to pore fields, rather than being imperforate; there is but one lobate pore or pore field per chamber. *Middle Ordovician–Upper Ordovician:* USA (Alaska).——Fig. 438,*4a–b.* **P. micella,* unnamed Middle to Upper Ordovician sequence, White Mountains, McGrath Quadrangle; *a,* side view of small holotype with irregular growth form and prominent pore fields as inhalant openings, generally one per chamber, ×5; *b,* view down onto broken upper surface showing large, circular interpores in interwall, USNM 417203, ×5 (Rigby, Potter, & Blodgett, 1988).

Sphaeroverticillites Boiko, 1990, p. 122 [**S. glomeratus* Boiko, 1990, p. 123; OD]. Sponges large, spherical to cup shaped, with cylindrical, retrosiphonate, axial canal; chambers ringlike, overlapping, without visible constrictions on surface, and with trabecular filling structures; mesostructure spherulitic. *Triassic (Norian):* Tajikistan.——Fig. 439,*1a–b.* **S. glomeratus,* southwestern Pamir Mountains; *a,* vertical section of holotype showing globose sponge with thick-walled, retrosiphonate, axial canal and porous walls of low, overlapping, chambers that contain vertical, rodlike, trabecular, filling structures, MIGACT 15/I, specimen 173, ×2; *b,* photomicrograph showing spherulitic, skeletal structure in holotype, ×100 (Boiko, Belyaeva, & Zhuravleva, 1991).

Family APHROSALPINGIDAE Myagkova, 1955

[Aphrosalpingidae Myagkova, 1955a, p. 478] [=Spicidae Termier & Termier, 1977a, p. 41, *partim;* Fistulosponginidae Termier & Termier, 1977a, p. 38, *partim;* Vesicocaulidae Wu Ya Sheng, 1991, p. 91]

Aporate sphinctozoan sponges with deep spongocoel and surrounding chambers either glomerate or catenulate; steeply obconical to subcylindrical with single or branched stems; central tube or spongocoel open or occupied by cluster of axial, exhalant canals; chamber walls may be a single layer or multilayered; exaules, filling structures and intertubes may be present or absent. *upper Upper Ordovician–Triassic.*

Subfamily FISTULOSPONGININAE Termier & Termier, 1977

[*nom. transl.* Finks & Rigby, herein, *ex* Fistulosponginidae Termier & Termier, 1977a, p. 38] [=Spicidae Termier & Termier, 1977a, p. 41, *partim*]

Cylindroid with central cloaca about which a single layer of spheroidal or subpolygonal, single-walled chambers cluster; craticularia at outer end of short exaulos present in each chamber; type genus bearing small exopores as well; endowall has longitudinal canals or ridges. *upper Upper Ordovician–Permian (Lopingian).*

Fistulosponginina Termier & Termier, 1977a, p. 38 [**F. elegans;* OD] [=*Spica* Termier & Termier, 1977a, p. 41 (type, *S. spica,* OD), *non* Swinhoe, 1890, *nec* Sacco, 1892]. Cylindrical sponge with single layer of spheroidal to subpolygonal chambers surrounding narrow, central cloaca; exowall pierced by cluster of polygonal pores surrounded by low to prominent rim or scattered, large, circular labripores; remainder of exowall minutely porous; interwalls double and penetrated by fine pores as in exowall; endopores larger than fine exopores; endowall said to contain longitudinal canals; no interior structures in chamber except internal lips around large exopores; wall microstructure spherulitic; no spicules known. [*Fistulosponginina* TERMIER & TERMIER, 1977a, is *Spica* overgrown by a thin layer of a chaetetid (SENOWBARI-DARYAN & RIGBY, 1988, p. 200), unless this is part of the sponge itself, inasmuch as the agelasid Ceratoporellidae have chaetetid morphology and a spherulitic, aragonite wall structure (WOOD, 1991; MASTANDREA & RUSSO, 1995) (compare also the stromatoporoid-like trabecularium above the sphinctozoan thalamidarium in the Guadalupiidae).] *Permian (Lopingian):* Tunisia, Oman.——FIG. 440,*3a–c*. **F. elegans,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; *a,* side view of typical specimen with single, starlike ostia on ends of egglike chambers arranged in vertical rows, ×2; *b,* enlarged side view showing ostia on chamber ends, USNM 427402, ×5; *c,* polished, vertical section with cross sections of chambers around axial spongocoel, USNM 427405, ×2 (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

Aphrosalpinx MYAGKOVA, 1955b, p. 639 [**A. textilis;* OD]. Steeply obconical, cylindrical or gobletlike stems, or branched, monoglomerate sponges with generally open, axial spongocoel in middle and upper part, but with axial cluster of small, exhalant tubes in lower part; numerous outer chambers radially arranged, some with prominent, tubular, inhalant exaules in outer wall that may extend inwardly as tubules into chambers; small endopores in inner wall, locally with S-shaped, exhalant canals forming part of reticulate or vermiculate, gastral layer intermediate between cortexlike lining in upper part and axial canal complex in lower part; vesiculae may occur in chambers, particularly in lower part of sponge. *Silurian (Ludlow):* Russia (northern Urals), USA (Alaska).——FIG. 441,*1a–c*. **A. textilis; a,* transverse section showing tubular spongocoel surrounded by radial, cellular layer with prominent, distal exaules, middle Silurian limestone, Ludlovian, McGrath Quadrangle, Alaska, UCG 5592 SD, ×3; *b,* tangential section through radial chambers showing scalelike sections, with transverse sections of a few exaules showing as small rings in upper left, Heceta Formation, Ludlovian, Tuxekan Island, southeastern Alaska, UCG YP58-3AFL-92, ×4; *c,* generalized reconstruction showing chamber and exaules development, as well as axial cluster of small, exhalant canals in lower part, not to scale (Rigby & others, 1994; courtesy of *Acta Palaeontographica Polonica, Polska Akademia Nauk*).

Cystothalamiella RIGBY & POTTER, 1986, p. 32 [**C. ducta;* OD]. Conicocylindrical sponge composed of spheroidal chambers, polygonal where mutually interfering, clustered about central cloaca that is one-third sponge diameter; exowall imperforate except for short exauli that arise from low mounds and terminate in a craticula; craticular pores subpolygonal; chambers do not communicate with one another, interpores absent; endopores are relatively large, circular to subpolygonal, and closely spaced; endowall bearing irregular, longitudinal ridges on its inner surface, somewhat similar to rudimentary trabecularium of *Cystauletes* KING, 1943; vesicles may occur within chambers; microstructure not known; no spicules known. [Genus is similar to the Permian *Spica* TERMIER & TERMIER, 1977a, except that the latter has sparsely porous exowalls.] *upper Upper Ordovician–Silurian (Ludlow):* USA (California), *upper Upper Ordovician;* USA (southeastern Alaska), *Ludlow.*——FIG. 440,*2a–b*. **C. ducta,* unnamed limestone, Ashgill, Klamath Mountains, California; *a,* side view of holotype with circular to polygonal chambers in vertical cluster, each with pronounced exaulos, ×2; *b,* vertical view showing crescentic chambers around central tube and with short but pronounced exaules, USNM 395880, ×2 (Rigby & Potter, 1986).

Nematosalpinx MYAGKOVA, 1995a, p. 478 [**N. dichotoma* MYAGKOVA, 1995a, p. 479; OD]. Small, cylindrical, dichotomously branched, composed of single layer of globular chambers around axial cluster of exhalant canals that extends through sponge; irregularly curved exaules and intertubes may be developed in outer parts of chambers; endopores prominent, moderately coarse openings in endowall opening into exhalant canal cluster. *Silurian (Ludlow):* Russia (northern Urals), USA (southeastern and southwestern Alaska).——FIG. 441,*2a–c*. **N. dichotoma; a,* monoglomerate, radial chambers around axial cluster of thick-walled, exhalant canals, Silurian beds, Vishera River, Russia, ×10; *b,* longitudinal section with well-defined, outer, cellular layer and inner, exhalant, canal cluster, Silurian beds, Vishera River, Russia, FM PE39869, ×10; *c,* weathered sample with transverse and longitudinal sections through branched specimens, Silurian limestone, Taylor Mountain D-2 Quadrangle, southwestern Alaska, CUG 83RB40, ×2 (Rigby & others, 1994; courtesy of *Acta Palaeontographica Polonica, Polska Akademia Nauk*).

Uvacoelia KÜGEL, 1987, p. 146 [**U. schellwieni;* OD]. Catenulate to glomerate, circular chambers arranged around prosiphonate, central canal or spongocoel; outer, chamber walls not perforated by pores, but each chamber connected to central canal through apopore; growth of new chambers sometimes resulting in lateral displacement of wedges of older chambers. *Carboniferous (Pennsylvanian):* Austria.——FIG. 440,*1a–c*. **U. schellwieni,* Auernig beds, Westphalian–Stephanian, Carnic Alps; *a,* holotype section of spherical chambers with elongate exaules and coarse endopores to central spongocoel, SPIE GP 54, ×5; *b,* longitudinal section of spherical chambers with elongate exaules, SPIE GP54, ×3; *c,* generalized restoration, not to scale (Kügel, 1987; courtesy of *Facies*).

Subfamily VESICOCAULIINAE Senowbari-Daryan, 1990

[Vesicocauliinae SENOWBARI-DARYAN, 1990, p. 120]

Spiciid sponges with catenulate arrangements of their chambers. *Triassic.*

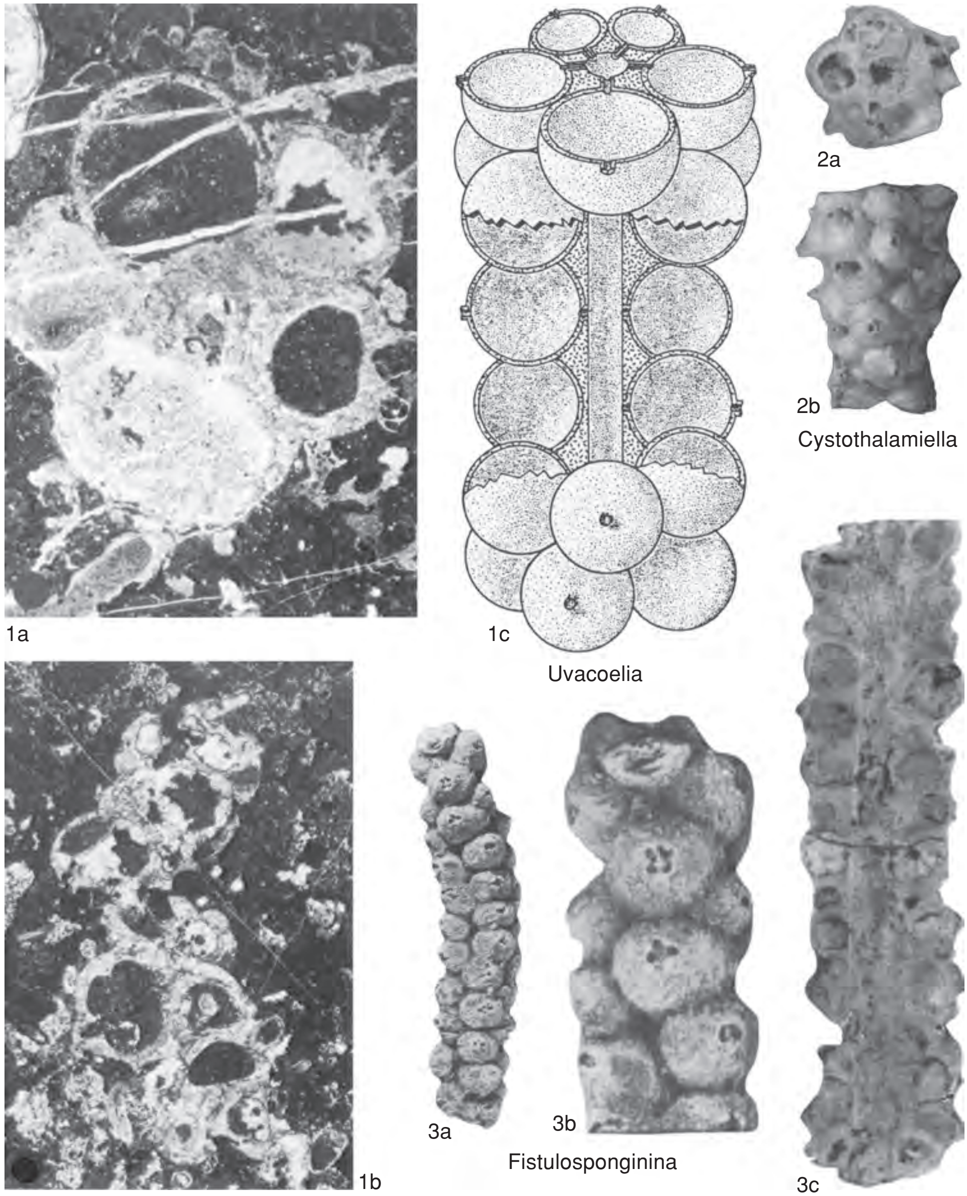


FIG. 440. Aphrosalpingidae (p. 667–668).

Vesicocaulis OTT, 1967a, p. 25 [**V. alpinus;* OD]. Hemispheroidal segments overlapping in chains; exowall imperforate except for sievelike groups of small exopores, each group underlain by a plaque of trabecular tissue (perhaps a cribribulla-like structure); endowall of narrow, central cloaca surrounded by, and continuous with, broad zone of similar trabecular tissue, whose meandriform, anastomosing, small canals tend to run parallel with cloaca, but also opening into it as small, circular endopores, and also communicate with lumen of chamber; remainder of lumen filled with small, thin-walled vesicles that are elongate parallel to exowall; interwall a continuation of exowall of preceding chamber; microstructure unknown; no spicules known. *Triassic:* Austria, Carpathian region, Czech Republic, Slovakia, Italy (Dolomite Alps, Sicily), Greece, Yugoslavia, Hungary.——FIG.

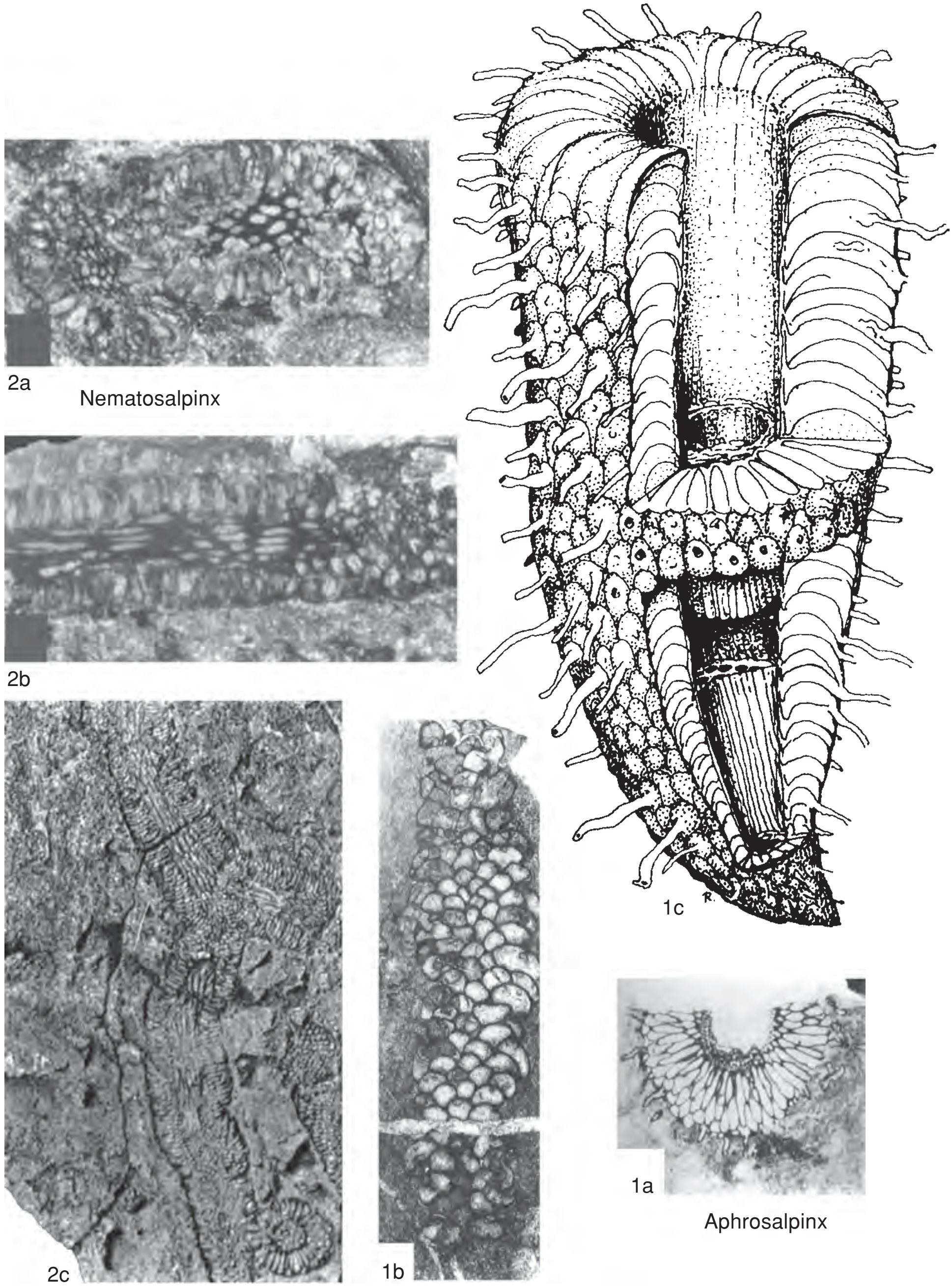


FIG. 441. Aphrosalpingidae (p. 668).

442,*1a–b*. **V. alpinus,* Wettersteinkalk, Ladinian, Karwendel, Austria; *a,* holotype, oblique section through older chambers, filled with vesiculae, and narrow, tubular spongocoel, blanketed with anastomosing, small canals, chamber walls with sievelike clusters of exopores, A 161 a/67, ×5; *b,* transverse section through parts of two chambers filled with vesiculae around narrow, axial spongocoel, and with cribribulla-like pore clusters in upper exowalls, A 161 a/67, ×5 (Ott, 1967a; courtesy of *Neues*

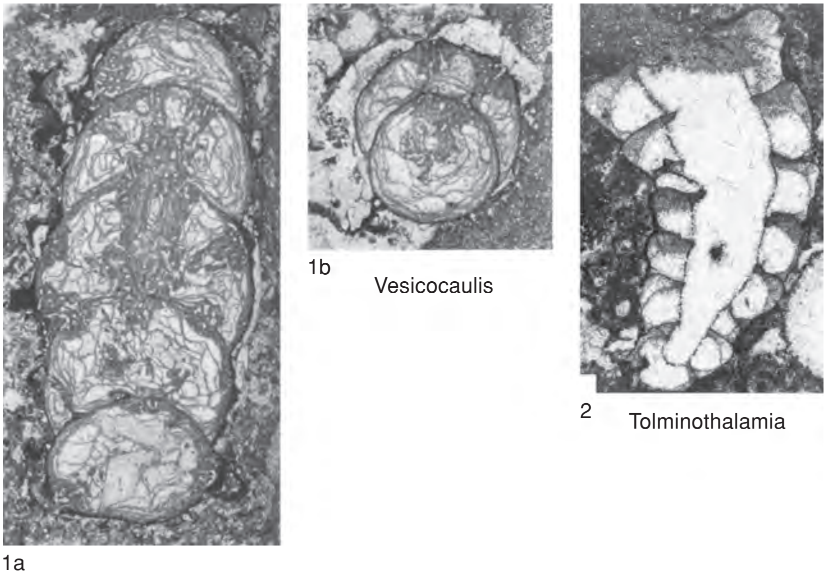


FIG. 442. Aphrosalpingidae (p. 669–671).

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Russospongia SENOWBARI-DARYAN, 1990, p. 125 [**Cryptocoelia lupensis* SENOWBARI-DARYAN, 1980, p. 182; OD]. Aporate, stemlike sponges with hemispherical chambers in catenulate arrangements; stems with a possible pro- or retrosiphonate spongocoel that extends through entire length of sponge; chambers or segments containing possible septal to trabecular, filling structures; both wall and filling structures have lamellar microstructure; isolated-appearing ostia are common in basal parts of segments; vesiculae also occur; microstructure and spicular skeleton are unknown. [*Russospongia* differs from *Vesicocaulis* OTT in having laminate-appearing septal to reticulate, filling structures and from other similar-appearing sponges in having aporate, chamber walls and radially arranged, filling structures.] *Triassic (Norian–Rhaetian):* Italy (Sicily).——FIG. 443,*2a–b*. **R. lupensis* (SENOWBARI-DARYAN), Triassic reef limestone; *a,* holotype, longitudinal, cylindrical section of chambers with septal to trabecular, filling structures, Cozzo de Lupo, SPIE P/l84, ×2; *b,* transverse section showing thin, chamber walls and radial, septal, filling structures, Piano di Bataglia, Sicily, SPIE P/438/1, ×2 (Senowbari-Daryan, 1990; courtesy of *Münchner Geowissenschaftliche Abhandlungen,* Verlag Dr. Friedrich Feil).

Tolminothalamia SENOWBARI-DARYAN, 1990, p. 123 [**Girtyocoelia carnica* SENOWBARI-DARYAN, 1981, p. 109; OD]. Aporate sponges with a retrosiphonate spongocoel with very thin, perforated walls; segment interwalls thicker that outer ectowalls; ostia hardly developed; microstructure of skeleton probably irregular; spicular skeleton not known. *Triassic (Carnian):* Italy (Sicily), Yugoslavia (Slovenia).——FIG. 442,*2*. **T. carnica* (SENOWBARI-DARYAN), reef limestone, Huda Juzna, Yugoslavia; longitudinal section with large, thin-walled spongocoel and chambers with somewhat thicker, largely imperforate walls, SPIE thin section 13, ×5 (Senowbari-Daryan, 1990, courtesy Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).

Yukonella SENOWBARI-DARYAN & REID, 1987, p. 900 [**Y. rigbyi;* OD]. Sphinctozoans with catenulate chambers around an ambi- to prosiphonate, central canal consisting of several small canals; some ostia, but not pores, present in outer or ectowall of sponge, but pores are abundant in chamber interwalls; chambers lack filling structures, although a few vesiculae may be present. *Triassic (Norian):* Canada (Yukon).——FIG. 443,*1a–b*. **Y. rigbyi,* Lime Peak reef, Lake Laberge area; *a,* longitudinal section showing porous, chamber interwalls that become imperforate toward exterior, and bundled, exhalant tubes in axial area (top to left), GSC 74608, ×2; *b,* generalized reconstruction showing dermal surface and skeletal and canal development, not to scale (Senowbari-Daryan & Reid, 1987; courtesy of *Canadian Journal of Earth Sciences*).

Subfamily PALAEOSCHADINAE Myagkova, 1955

[*nom. transl.* FINKS & RIGBY, herein, *ex* Palaeoschadidae MYAGKOVA, 1955a, p. 480]

Skeletons with double-layered, thick-walled chambers in which outer layer is

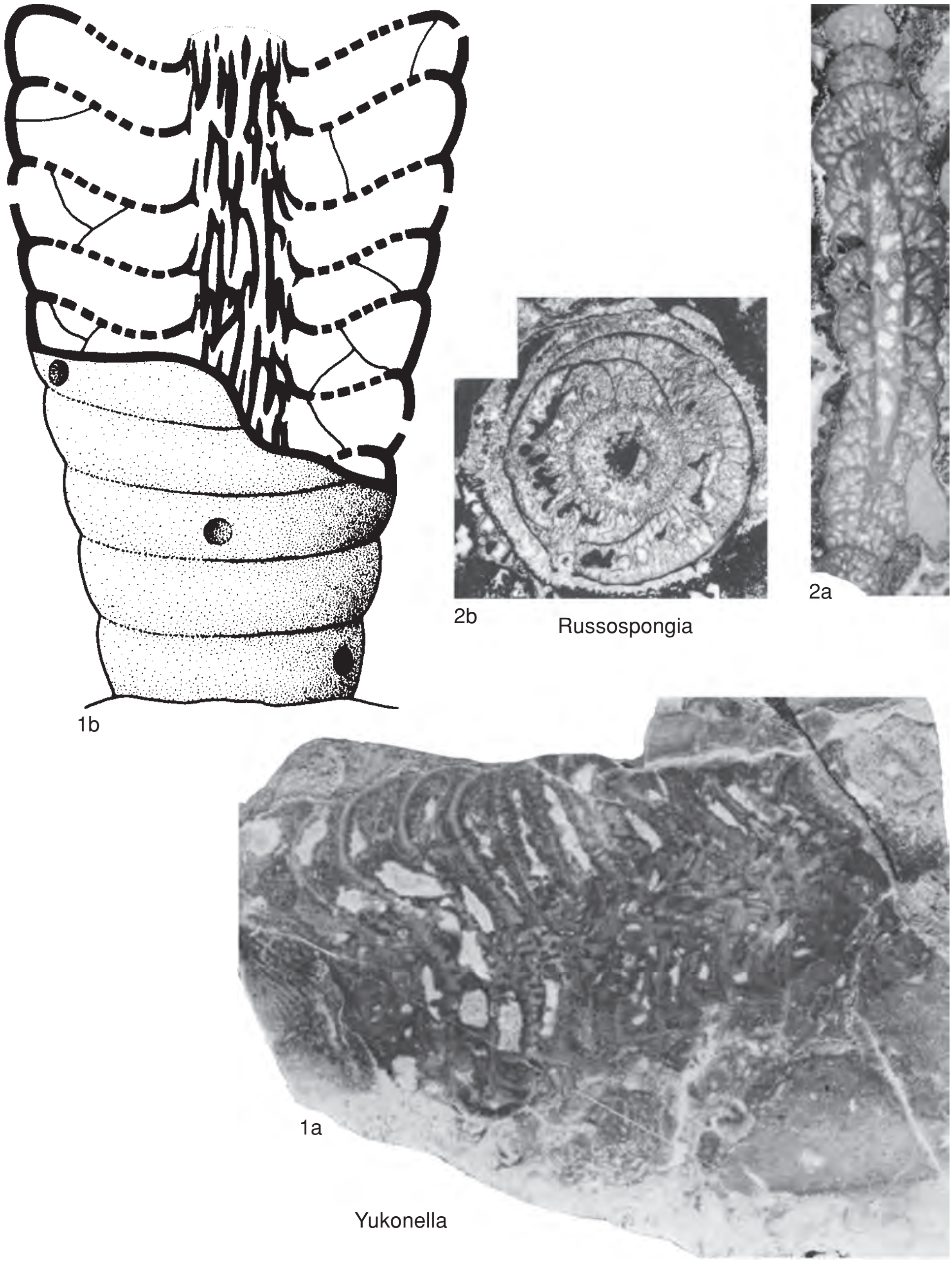

FIG. 443. Aphrosalpingidae (p. 671).

distinctly porous but inner, laminated layer largely lacks pores. *Silurian (Ludlow).*

Palaeoscheda MYAGKOVA, 1955a, p. 480 [**P. crassimuralis;* OD]. Irregularly steeply obconical to cylindrical sphinctozoans with one layer of globose, upwardly arcuate, cystlike chambers around irregular, central tube of several exhalant canals; interwalls and ectowalls double layered with inner, dense layer with only fine, scattered pores, but outer layer with coarse, abundant pores; ectowalls with large, circular ostia from which intertubes extend irregularly

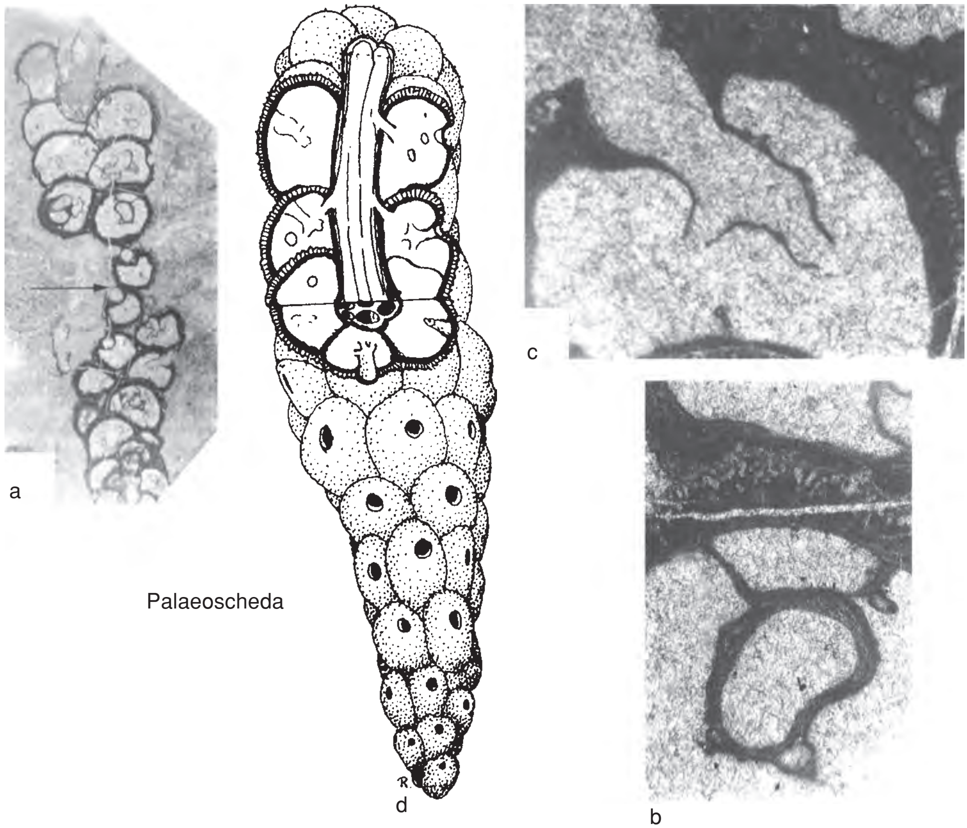

FIG. 444. Aphrosalpingidae (p. 672–673).

into chamber interiors and possibly branch; exaules not developed; endopores obscure to irregular. [The outer layer of chamber walls has coarse pores, but thin sections indicate that these do not penetrate the dense, inner, microcrystalline layer. For this reason the subfamily and genus are tentatively placed here among the aporous sponges but into a distinct subfamily.] *Silurian (Ludlow):* Russia (northern Urals), USA (southeastern Alaska), Canada (?Northwest Territories).——FIG. 444*a–d.* **P. crassimuralis,* Heceta Formation, Prince of Wales Island, southeastern Alaska; *a,* nearly complete, longitudinal section showing globose chambers around spongocoel, in lower part, with intertube connections and ostia (*arrow*) in chamber walls, ×2; *b* photomicrograph of coarsely porous interwall, with later added, laminated, upper and lower layers, and vesicula or intertube section below, ×20; *c,* photomicrograph of intertube interrupting interwall, CUG SB3-7EFL1-90, ×25; *d,* generalized reconstruction showing relationships of canals to globose chambers, not to scale (Rigby & others, 1994; courtesy of *Acta Palaeontographica Polonica,* Polska Akademia Nauk).

Family GLOMOCYSTOSPONGIIDAE Rigby, Fan, & Zhang, 1989

[Glomocystospongiidae RIGBY, FAN, & ZHANG, 1989a, p. 436; *emend.,* FINKS & RIGBY, herein]

Spheroidal to hemispheroidal, aporate chambers arranged in sheets about cavaedial, or perhaps differentiated inhalant and exhalant, spaces with which they communicate by a pore; occasionally, adjacent chambers may communicate by a similar pore, but there are no other pores. [The Triassic *Henricellum* WILCKENS, 1937, was included by the original authors of the family, in addition to the type genus. It, however, does not have the peculiar cavaedial spaces seen in *Glomocystospongia,* and shows more resemblance to the Girtyocoeliidae, with which it is here included (RMF).] *Permian (Lopingian).*

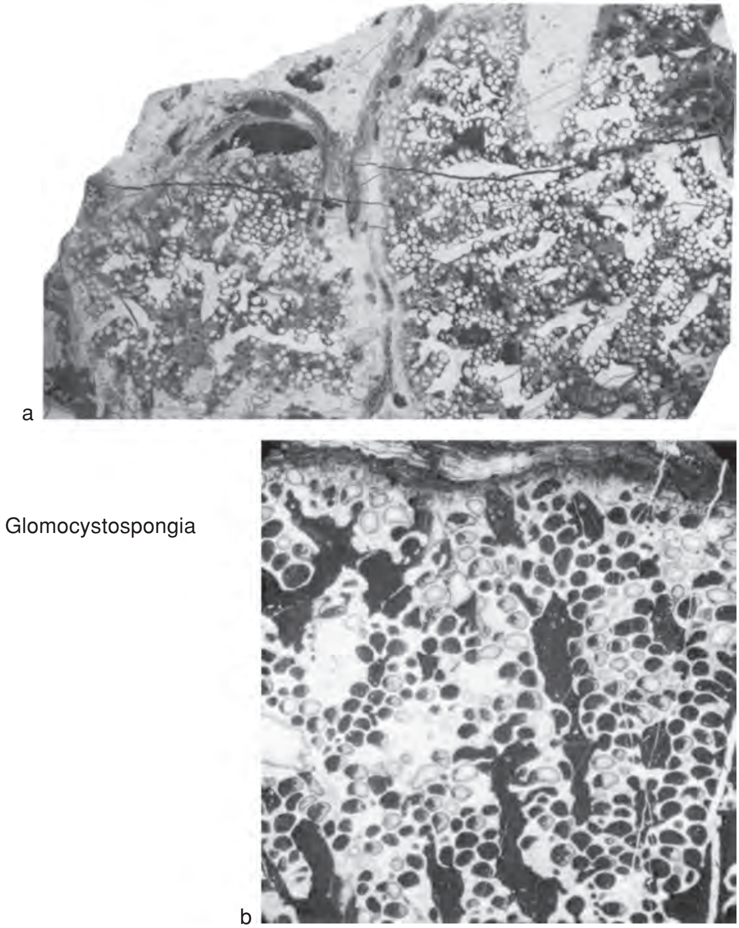

Fig. 445. Glomocystospongiidae (p. 674).

Glomocystospongia Rigby, Fan, & Zhang, 1989a, p. 436 [**G. gracilis;* OD]. Sponge massive, explanate or branching-cylindrical, containing subparallel, slitlike, occasionally anastomosing, or dendritic and somewhat radially arranged, possible cavaedial spaces, between which are anastomosing sheets of small, hemispheroidal chambers; convex surfaces of chambers face outwardly and upwardly; each chamber opens by a single, large pore into nearest cavaedial space; very rarely chambers communicate with an adjacent one by a single pore; there are no other pores. [There is a suggestion that spaces may be differentiated into inhalant and exhalant systems, rather than being cavaedia, because some extend radially in from the exterior and end blindly, while other, interior ones are centripetally dendritic, as if exhalant; this is supported by the presence of vesicle-like partitions in some dendritic spaces similar to those that close off disused parts of a cloaca; if so, there must be two openings in each chamber. A referred specimen from Tunisia (Senowbari-Daryan & Rigby, 1991) contains oxea-like spicules embedded within the sclerosomal skeleton; they are radial with respect to the sponge, therefore parallel to the surface in the cavaedial walls, but perpendicular and protruding in the chamber walls. The spicules, now calcified or pyritized, are inferred to have been originally siliceous.] *Permian (Lopingian):* China (Sichuan), Tunisia.——Fig. 445*a–b.* **G. gracilis,* Changxing Formation, Changhsingian, Sichuan; *a,* irregular growth form of glomerate chambers around coarse, inhalant-exhalant openings in hemispherical, possibly lobate, branched holotype, ×2; *b,* photomicrograph showing small, clustered chambers, each with one opening, in single layer around coarse, inhalant-exhalant openings in holotype, IGASB 4021, ×5 (Rigby, Fan, & Zhang, 1989a).

Huayingia Rigby & others, 1994, p. 98 [**H. glomerata;* OD]. Nodular, aggregate, foliate to tabular, composed of numerous small, crescentic chambers in vertical section and arched, triangular to spatulate or crescentic in horizontal section; walls imperforate with single large, tubular, retrosiphonate-

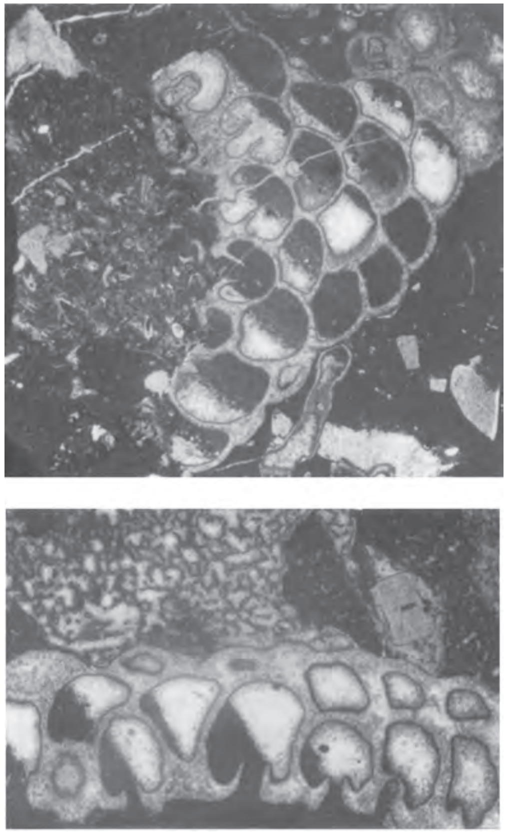

FIG. 446. Glomocystospongiidae (p. 674–675).

appearing ostium per chamber; vesiculae rare within chambers; cribribulla absent. *Permian (Changhsingian):* China (Sichuan, Guizhou).——FIG. 446*a–b.* **H. glomerata,* Changxing Formation, Changhsingian, Huaying City, Sichuan, China; *a,* subhorizontal section through holotype plate showing cystose chambers with tubular ostium, in chambers on left, JS0055, ×5; *b,* vertical section through paratype with arcuate chambers and reflexed, ostial tube in base, JS0056, ×5 (Rigby & others, 1994).

Family SEBARGASIIDAE de Laubenfels, 1955

[Sebargasiidae DE LAUBENFELS, 1955, p. 101; *emend.,* FINKS & RIGBY, herein] [=Sebargasiidae DE LAUBENFELS, 1955, p. 101, *partim;* Sphaerosiphonidae STEINMANN, 1882, p. 163, *nom. van., partim*]

Cylindroid; central cloaca (retrosiphonate); small, circular, closely spaced exopores; wall microstructure spherulitic; no spicules known; vesicles may be present in chambers but not pillars or trabeculae. [Sphaerosiphonidae STEINMANN, 1882, was not based on a nominate genus.] *?Ordovician, Carboniferous–Triassic.*

Sebargasia STEINMANN, 1882, p. 171 [**S. carbonaria;* OD]. Cylindrical, superposed segments visible externally; central cloaca one-third sponge diameter; exopores small, circular, closely spaced; interwall a continuation of exowall of preceding segment with its pores; endowall in continuity with interwall of same segment (retrosiphonate) but with coarse endopores mainly near upper and lower ends of chamber; chambers empty; wall microstructure not known; no spicules known. *Carboniferous (Bashkirian):* Spain.——FIG. 447,6*a–b.* **S. carbonaria,* upper Carboniferous limestone, Sebargas, Asturia, northwestern Spain; *a,* side view of type subcylindrical type specimen, ×1; *b,* longitudinal section with chambers around tubular spongocoel with moderately coarse endopores, interwalls and exowalls with finer pores, ×2 (Steinmann, 1882).

Amblysiphonella STEINMANN, 1882, p. 169 [**A. barroisi* STEINMANN, 1882, p. 170; OD] [?=*Laccosiphonella* ALEOTTI, DIECI, & RUSSO, 1986, p. 226 (type, *Amblysiphonella merlai* PARONA, 1933, p. 43,

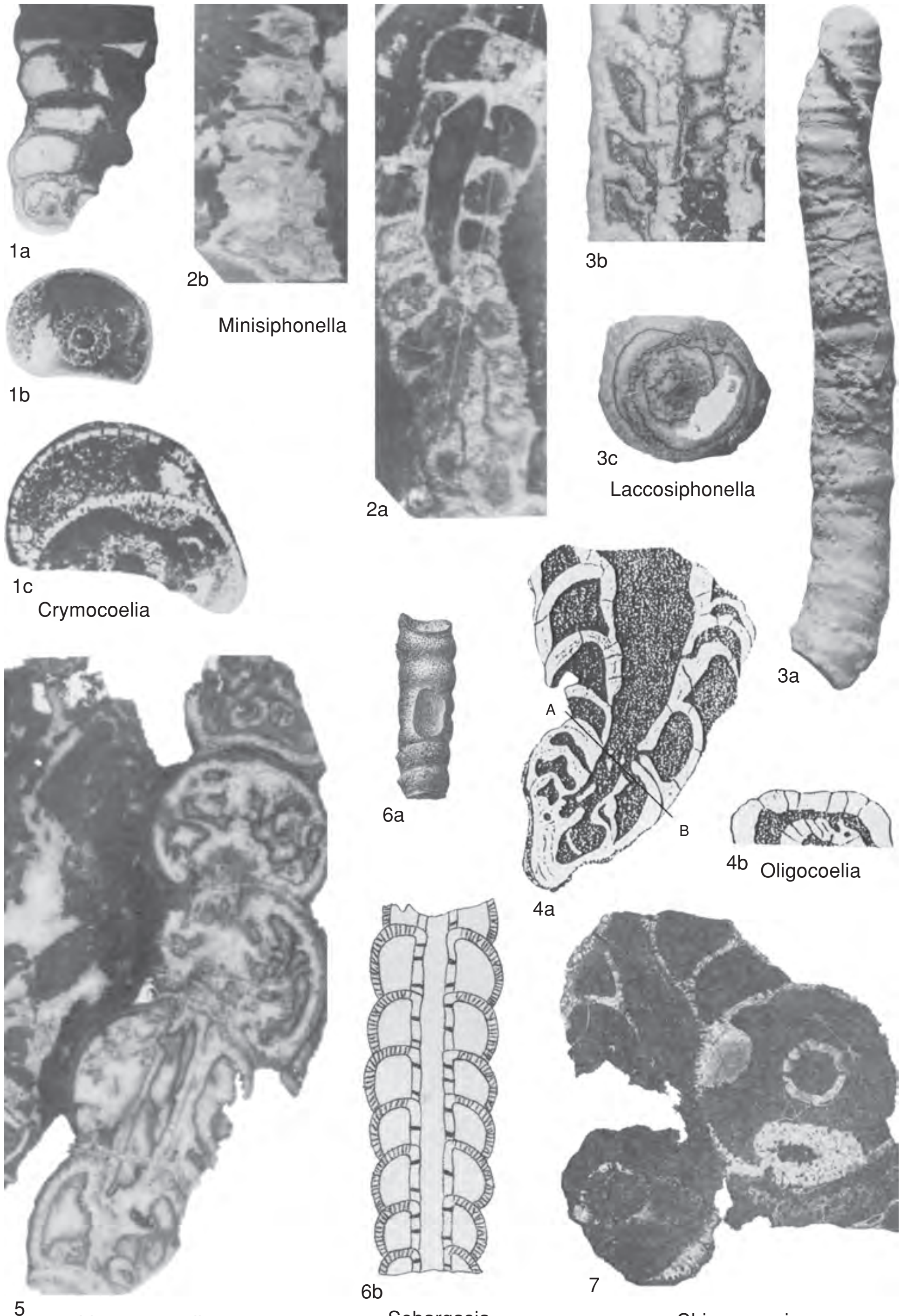

FIG. 447. Sebargasiidae (p. 675–678).

OD); ?=*Sebargasia* STEINMANN, 1882, p. 171 (type, *S. carbonaria;* OD); ?=*Paramblysiphonella* DENG, 1982, p. 254 (type, *P. amblysiphonelloides,* OD); ?=*Lingyunocoelia* FAN, WANG, & WU, 2002, p. 339 (type, *L. spherica*)]. Cylindrical, sometimes subparallel branched segments correspond externally to interior chambers that are in linear series; central cloaca about one-third sponge diameter; exowall with numerous small, circular, closely spaced exopores; interwall a continuation of exowall, below, with similar pores; endowall somewhat thinner and endopores somewhat larger and more widely spaced; interior of chamber and sometimes cloaca may contain imperforate vesicles; wall microstructure small, isodiametric spherulites that may expand asymmetrically into lumens of pore canals and chambers; no spicules known except for a single, possible triradiate (VAN DE GRAAF, 1969, pl. 2,*2*) that may be foreign. [Because of homeomorphy, the range and distribution are uncertain; the genus should be used only for spherulitic, aspicular forms with only vesicles, and no trabeculae, in the chamber interiors. *Sebargasia* STEINMANN, 1882, differs chiefly in its fewer, larger endopores, and its smaller exopores; it should probably be considered a junior (page priority) synonym.] *?Cambrian, ?Ordovician, Carboniferous–Triassic:* Australia, *?Cambrian;* USA (California), *?Ordovician;* Kyrgyzstan, *Carboniferous;* Spain, China, Austria, *Bashkirian, Moscovian;* USA (Texas), *Upper Pennsylvanian;* Japan, China, USA (Texas, New Mexico), Tunisia, Italy (?Sicily), Oman, Tajikistan, Armenia, *Permian;* USA (Oregon), Italy (Sicily), Greece, Iran, Indonesia, China, Peru, Tajikistan, Russia (Caucasus region), *Triassic.*——FIG. 448,*2a–b.* **A. barroisi,* Carboniferous limestone, Sebargas, Asturia, northwestern Spain; *a,* side view of type specimen, ×1; *b,* longitudinal section showing porous chambers with scattered vesiculae, around perforate tubular spongocoel, exowalls and interwalls are also finely and uniformly perforate, ×2 (Steinmann, 1882).

Chinaspongia BELYAEVA, 2000, p. 156 [**C. fani;* OD]. Catenulate sponge, porate, forming colonies where adjoining sponges, at a particular phase in development, have common outer walls; in addition to central tubes, lateral ones pass through two or three neighboring chambers; locally these are contiguous with the outer chamber wall. *Permian (Lopingian):* China.——FIG. 447,*7.* **C. fani,* Maokou Formation, Tonglu, Zhejiang Province; holotype, diagonal section through two subcylindrical branches, each with prominent, central tube and branched, lateral tubes, thin, chamber walls with common, circular, inhalant ostia, FEGI no. 15-MB, thin section 21(1), ×2 (Belyaeva, 2000).

Crymocoelia BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 118 [**C. zacharovi;* OD]. Uniserial, chambered sponges, subcylindrical lower part and globose upper chambers; retrosiphonate central canal with thin, inner, perforate layer surrounded by outer layer of thin-walled, convergent, exhalant canals to make complex wall; porous chamber interwalls nearly flat but downflexed near margins where walls overlap; walls porous and relatively thin; early chambers with vesicular filling structures, later ones hollow but uppermost ones with reticular, skeletal material from walls; microstructure with granular, relict texture. *Permian (Wordian–Capitanian):* Russia (Ukraine).——FIG. 447,*1a–c.* **C. zacharovi,* Midian, Crimea, River Marta; *a,* near-vertical section showing uniserial growth form, MFGI 923-5 3a; *b,* transverse section showing porous exowall of axial spongocoel, MFGI 923-8 4a, ×1; *c,* oblique section showing porous exowalls and interwalls, with porous, thick endowall of spongocoel in lower center, MFGI 923-5 1, ×2 (Boiko, Belyaeva, & Zhuravleva, 1991).

?Laccosiphonella ALEOTTI, DIECI, & RUSSO, 1986, p. 226 [**Amblysiphonella merlai* PARONA, 1933, p. 43; OD]. Cylindrical; externally segments correspond to low, superposed chambers; cloaca approximately one-third sponge diameter; exopores, interpores, and endopores subequal, small, and closely spaced; endowall thick, in which endopores form short canals that may possibly anastomose; vesicles may be present in chambers; microstructure unknown; no spicules observed. [The only characters that may distinguish this from *Amblysiphonella* STEINMANN, 1882, assuming the microstructure to be spherulitic aragonite, are the thick endowall and the possibly anastomosing endoporal canals. Anastomosing, poral canals (in all walls), however, are seen in well-preserved specimens of many sphinctozoan genera, especially if the wall is thick. The thickened endowall is probably not appropriate by itself as a generic distinction.] *Permian:* Italy (Sicily).——FIG. 447,*3a–c.* **L. merlai* (PARONA), Permian limestone, Palazzo Adriano, Sosio; *a,* side view of cylindrical type specimen with weak annulae that correspond to chambers in interior, ×1; *b,* longitudinal section showing thick, porous endowall of spongocoel and chambers in outer part; *c,* transverse section showing thin, chamber walls and thick wall of spongocoel, ×2 (Parona, 1933).

?Lingyunocoelia FAN, WANG, & WU, 2002, p. 339 [**L. spherica;* OD]. Moniliform sponge of stacked, spheroidal chambers with an axial spongocoel or cloacal tube; chamber interiors filled with vesiculae or irregular filling material; neither exowalls nor endowalls of central tube have well-defined pores, exowalls also lack tubular exauli. [*Lingyunocoelia* has the general form of *Amblysiphonella* or *Girtyocoelia* with spheroidal chambers and a central, tubular cloaca or spongocoel. *Lingyunocoelia* is reported to lack pores in both the exowalls and endowalls of the skeleton, but those structures may have been lost because of diagenesis, for faint impressions of pores in both the exowall and endowall are visible in the published figure of the holotype. The holotype appears strikingly similar to *Amblysiphonella merla* PARONA, 1933.] *Permian (Guadalupian):* China (Guangxi).——FIG. 447,*5.* **L. spherica*, Maokou Formation; subvertical section of holotype showing stacked, linear series of spheroidal chambers and axial, central tube, with filling structures in chambers, faint pores showing in both exowalls and endowalls, particularly in lower chambers, JO651-2, ×2 (Fan, Wang, & Wu, 2002).

Minisiphonella Boiko in Boiko, Belyaeva, & Zhuravleva, 1991, p. 149 [**M. cribrata;* OD]. Catenulate, chambered colonies in which round to subspherical chambers are very small; axial canal siphonate; outer surface of chambers with distinctive, horizontal ribs. *Triassic:* Tajikistan.——Fig. 447,*2a–b*. **M. cribrata,* Triassic limestone, Norian, southeastern Pamir; *a,* somewhat oblique, longitudinal section of small sponge showing stacked chambers with siphonate, axial spongocoel; coarse, exhalant ostia and finer, more common, inhalant canals in ribbed outer wall, MIGT 191-10 116/50, ×10; *b,* tangential, vertical section through chamber walls showing ribbed exterior and simple, inhalant ostia throughout walls, MIGT 191-11 116-51, ×10 (Boiko, Belyaeva, & Zhuravleva, 1991).

Oligocoelia Vinassa De Regny, 1901, p. 17 [**O. zitteli* Vinassa De Regny, 1901, p. 18; OD]. Conical, curved, not segmented externally; broad, upwardly expanding, central cloaca; some segments possibly incompletely toroidal; exowall bearing small, closely spaced, circular exopores; interwall an upward continuation of exowall, but interpores may be larger and more widely spaced than exopores; endowall a downward continuation of interwall (retrosiphonate) with endopores similar to possible interpores; chamber interior empty; microstructure unknown; spicules not known. *Triassic (Carnian):* Hungary. ——Fig. 447,*4a–b. O. zitteli,* Veszprém, Jeruzsálemhegy; *a,* longitudinal section showing form of sponge, its chambers, and central spongocoel, all with thick walls, ×2; *b,* transverse section showing pores in outer wall and spongocoel wall, along line A-B of view *a,* ×2 (Vinassa de Regny, 1901).

?Paramblysiphonella Deng, 1982, p. 254 [**P. amblysiphonelloides;* OD]. Straight, cylindrical sponge with more or less annulate exterior produced by subequal chambers, all pierced by central spongocoel; upper wall of each chamber strongly arched upwardly but locally laterally discontinuous in longitudinal sections; wall perforated by numerous small pores, almost circular in cross section; outer walls also pierced by small canals; vesiculae not developed. [Whether this genus is distinct from *Amblysiphonella* is questionable. A new, detailed description to better document its morphology is necessary (Senowbari-Daryan, 1990, p. 63).] *Permian (Cisuralian):* Tibet.——Fig. 448,*4a–b*. **P. amblysiphonelloides; a,* longitudinal section showing broad spongocoel and chambered walls with discontinuous chamber interwalls, NIGPAS 35355; *b,* transverse section with large spongocoel and some interrupted chamber walls, NIGPAS 35356, ×1 (Deng, 1982).

Polycystocoelia Zhang, 1983, p. 11 [**P. huajiaopingensis;* OD] [=*Sinocoelia* Zhang & Fan in Fan & Zhang, 1985, p. 15 (type, *S. lepida,* OD); *Stromatocoelia* Zhang & Fan in Fan & Zhang, 1985, p. 16 (type, *S. asiatica* Zhang & Fan in Fan & Zhang, 1985, p. 17, OD)]. Cylindrical to cup shaped to single or branched stems with retrosiphonate, central spongocoel, which may be poorly developed; superposed chambers flattened and caplike, arranged with scalelike appearance; vesiculae and filling structures absent; walls of single layer pierced by numerous interpores and exopores, but coarser ostia not present. *Permian (Lopingian)–Triassic (Norian):* China (Guangxi), Tunisia, Canada (Yukon), Russia, *Lopingian;* Tajikistan, *Norian.*——Fig. 449,*1a–b*. **P. huajiaopingensis,* Changxing Formation, Changhsingian, Lichuan, Hubei, China; *a,* holotype section with spongocoel in upper part and remainder with coarsely perforate interwalls and exowalls, 0148, ×1.5 (Fan & Zhang, 1985); *b,* characteristic interwalls pierced by moderately coarse interpores, thin, netlike endowall showing in upper left and exowall on right, IG5070, ×10 (Rigby, Fan, & Zhang, 1989a).

Pseudoamblysiphonella Senowbari-Daryan & Rigby, 1988, p. 186 [**P. polysiphonata;* OD]. Conicocylindrical series of superposed, toroidal to fusiform chambers; segmentation visible externally; four to six narrow cloacae clustered in axial region and generally of circular, cross section; exopores small, closely spaced, and circular to submeandriform; exowall curving inwardly at top of chamber to form interwall, which may be partially doubled by succeeding chamber exowall; chambers filled with trabecular tissue that outlines anastomosed tubes that converge dendritically inwardly and upwardly to enter one of axial cloacae; trabeculae appear to be absent from peripheral part of each chamber; microstructure unknown; no spicules known. [This genus differs from *Fissispongia* King, 1938, in the larger number of axial cloacae (although rare individuals of *Fissispongia* have multiple cloacae), in the apparent absence of larger lipped exopores, and in the toroidal form of the chambers.] *Permian (Lopingian):* Tunisia.——Fig. 448,*3a–c*. **P. polysiphonata,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a,* holotype of ringlike, partially agglomerate chambers, USNM 427307, ×2; *b,* paratype, transverse section showing branched tubes in interior and perforate exowall, USNM 427309, ×5; *c,* restoration showing ringlike chambers with branched canals and multiple, exhalant, axial canals, not to scale (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

Pseudoguadalupia Termier & Termier, 1977a, p. 40 [**Guadalupia alveolaris* Parona, 1933, p. 49; OD]. Cylindrical sponge composed of superposed, spheroidal chambers; central cloaca approximately one-third sponge diameter; outer surface of exowall bearing closely spaced, circular to polygonal pits with large, circular exopore at bottom of each pit; entire exowall microporous with fine, circular pores; interwall questionably double (i.e., two exowalls in contact); interpores similar to exopores; endopores circular, widely spaced, larger than large exopores; vesicles and small, spherical bodies (as in *Intrasporeocoelia* Fan & Zhang, 1985) may be present in chambers; microstructure not known; no spicules known. [Genus is similar to

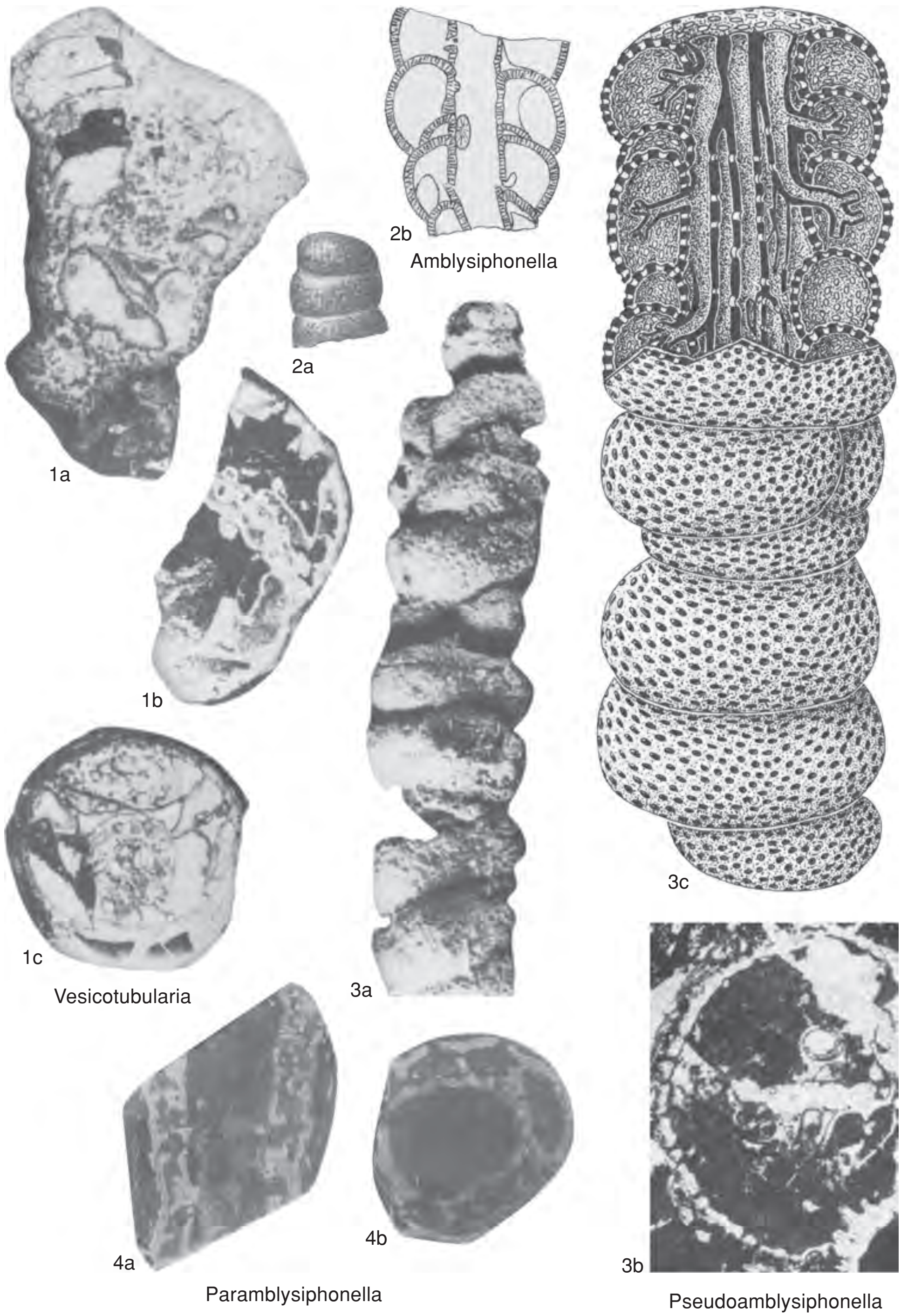

FIG. 448. Sebargasiidae (p. 675–681).

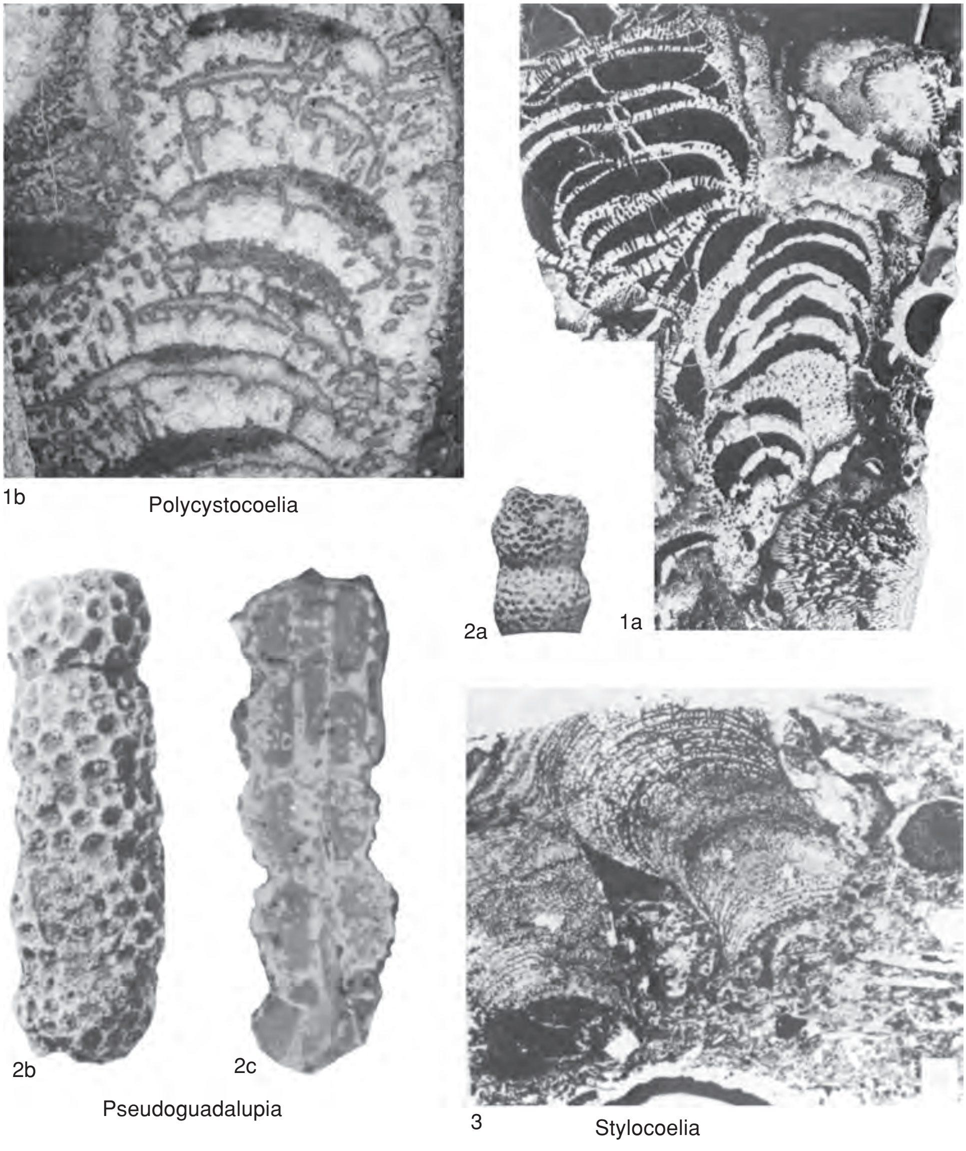

FIG. 449. Sebargasiidae (p. 678–681).

Amblysiphonella STEINMANN, 1882, except for the surface pits.] *Permian:* Italy (Sicily), Tunisia.——FIG. 449,*2a–c*. **P. alveolaria* (PARONA); *a,* side view of small, two-chambered, type fragment with surficial pits and coarse exopores, Permian limestone, Palazzo di Adriano, Sosio, Sicily, ×1 (Parona, 1933); *b,* side view of characteristic specimen with coarse exopores inside external pits in catenulate, small sponge, Djebel Tebaga reef, Lopingian, Djebel Tebaga, Tunisia, USNM 427381, ×4; *c,* polished, vertical section showing prominent, central tube and well-defined chambers, Djebel Tebaga reef, Lopingian, Djebel Tebaga, Tunisia, USNM 427383, ×2.5 (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

Stylocoelia WU Ya Sheng, 1991, p. 86 [**S. circopora;* OD]. Sponges cylindrical, of stacked, low chambers with perforate walls; central spongocoel narrow with perforate walls, chambers with pillar-filling structures that are normal to walls and confined to chambers. *Permian (Kungurian):* China (Guangxi, Guizhou), Italy (Sicily).——FIG. 449,*3*. **S. circopora,* Maokou Formation, Reef of Xiangbo, Kungurian, Longlin, Guangxi, China; longitudinal section showing low chambers with pillar-filling structures, IGASB xb31-2-1, ×2 (Wu Ya Sheng, 1991).

Vesicotubularia BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 116 [**V. prima;* OD]. Catenulate, chambered sponges with porous walls; chambers initially infilled with vesiculae and later with vesicle-like canals; central spongocoel possibly retrosiphonate and infilled with reticulate tissue; vesiculae participate in construction of chamber walls. [*Vesicotubularia* is similar to *Vesicocaulis* OTT, in having all porous walls and vesicle-like canals.] *Permian:* Russia (Ukraine).——FIG. 448,*1a–c.* **V. prima,* Permian limestone, Wordian–Capitanian, Crimea, River Marta; *a,* vertical section showing growth form and large chambers, MFGI 923-8, 2g, ×2; *b,* section of exowalls and interwalls showing canals and some vesicular filling structures, MFGI 923-8, 4a, ×5; *c,* transverse section with vesicular filling structures, MFGI 923-8, 2a, ×5 (Boiko, Belyaeva, & Zhuravleva, 1991).

Family OLANGOCOELIIDAE Bechstädt & Brandner, 1970

[Olangocoeliidae BECHSTÄDT & BRANDNER, 1970, p. 67]

Spherical aporate chambers, with overlapping to irregularly isolated walls, in series that outline and enclose both spinelike canals or openings. *Middle Triassic.*

Olangocoelia BECHSTÄDT & BRANDNER, 1970, p. 67 [**O. otti;* OD]. Spherical, overlapping, attached to isolated, thin-walled chambers, with sizes measured in millimeters, chambers with isolated pores. [Chambers may also be bound together by stolenlike tubes, according to SENOWBARI-DARYAN (1990, p. 133), who also concluded that the poriferan nature of the fossils is uncertain. Classification with the Foraminifera cannot be ruled out.] *Middle Triassic:* Italy.——FIG. 450,*5a–b.* **O. otti,* Olanger Dolomite, upper Anisian, southern Tyrols, Austria; *a,* holotype, thin section showing sections through thin-walled, irregular chambers filled and surrounded by dark matrix, GII thin section III 17, approximately ×2; *b,* tangential slice through chambers showing irregular nature of chamber walls, ×20 (Bechstadt & Brandner, 1970; courtesy of Institute für Geologie und Paläontologie, Universitet Innsbruck).

Family CLIEFDENELLIDAE Webby, 1969

[Cliefdenellidae WEBBY, 1969, p. 655]

Sphinctozoans with low, flat to convex-upward chambers with imperforate walls; interwalls penetrated by continuous, subvertical, porous, pillarlike tubes; complex, astrorhizae-like, clustered, excurrent, canal system separate from pillarlike, incurrent system and occurring between thin, imperforate interwalls; skeletons of aspicular calcium carbonate (RIGBY & POTTER, 1986, p. 41). *Middle Ordovician–Upper Ordovician.*

Cliefdenella WEBBY, 1969, p. 655 [**C. etheridgei;* OD]. Sphinctozoan sponges composed of low, platelike, hollow chambers with imperforate interwalls pierced by porous, vertical, pillarlike tubes produced by downward deflection of interwall in retrosiphonate-like, incurrent, canal system; excurrent system or astrorhizal-like canals that converge laterally from chambers and curve vertically into clusters of subvertical, tubelike openings; vertical, incurrent and excurrent tubes not interconnected; vesiculae may occur in early chambers, vertical, porous, incurrent tubes, and in excurrent canals; interwalls may be three layered, with lower and upper, clear layers separated by a medial, dark layer; upper surface commonly denticulate (RIGBY & POTTER, 1986, p. 41). *Middle Ordovician–Upper Ordovician:* Australia (New South Wales), USA (Alaska).——FIG. 451*a–c.* **C. etheridgei,* Cliefden Caves Limestone, Caradoc, Belubula River, New South Wales, Australia; *a,* holotype with prominent, coarse, exhalant, canal clusters through platelike chambers whose interwalls are also pierced by smaller, inhalant canals, SUP 24157, ×4; *b,* transverse section of part of paratype across exhalant, canal cluster with convergent canals, SUP 24154, ×4; *c,* transverse section of part of paratype with coarse, exhalant opening and numerous small, inhalant, pillarlike canals through chambers, SUP 24155, ×4 (Webby, 1969).

Khalfinaea WEBBY & LIN, 1988, p. 152 [**K. sinensis;* OD]. Conicocylindrical or rarely branching, aporate sphinctozoan with low and elongate, gently upwardly arched and stacked chambers, bounded by narrow, ringlike, imperforate exowalls and laminar, uparched interwalls; upper surfaces of interwalls may be denticulate and locally downwardly inflected into regular, nearly vertical, continuous, sometimes porous, incurrent tubes; single, large, central, excurrent tube defined by thickened endowall pierced by small tubes, giving a honeycomb-like appearance; infilled with irregular mesh of primarily randomly oriented, astrorhizal canals of varying sizes, and secondary vesiculae and other thickened (trabecular) tissue, suggesting successive, rather complex, growth interrelationships; vesiculae developed in chambers, incurrent canals and central tubes hollow, rootlike, bracing structures not known. [*Khalfinaea* is similar to *Rigbyetia* but has a large, central, excurrent tube with irregular, labyrinthine, astrorhizal canals, vesiculae, or trabecular filling tissue, and is bounded by a well-defined endowall.] *Upper Ordovician:* China (Xinjiang, Shaanxi), Russia (Altai Sayan).——FIG. 452*a–b.* **K. sinensis,* Bulongor Formation, Ashgill, Bulongor River, Xinjiang, China; *a,* longitudinal section showing upwardly arched chambers with honeycomb-like endowall defining a central tube and

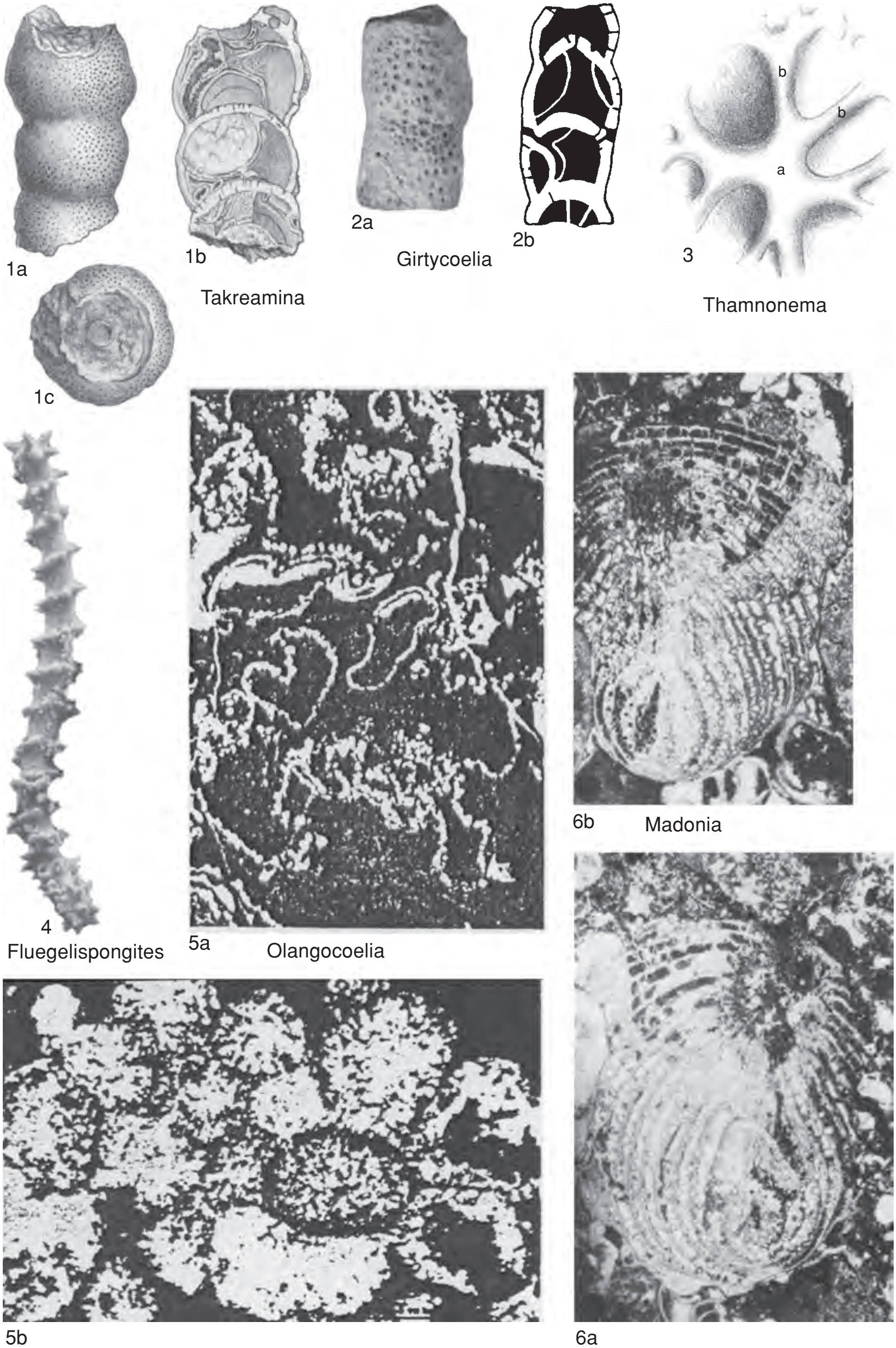

FIG. 450. Olangocoeliidae, Girtycoeliidae, and Uncertain (p. 681–691).

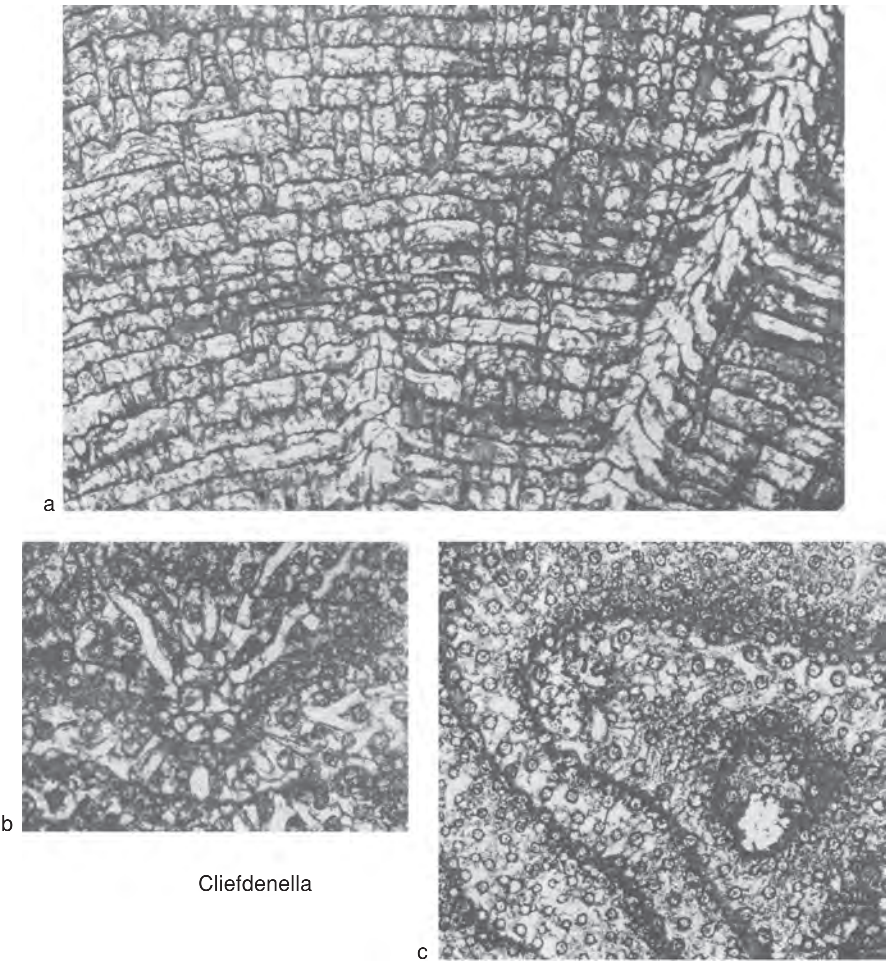

FIG. 451. Cliefdenellidae (p. 681).

with downwardly flexed, inhalant tubes, IGP 18, ×4; *b,* transverse section of paratype with central, exhalant cluster and prominent, central tube surrounded by thick walls of ringlike chambers with vesiculae and other filling structures, with sections of radial, inhalant canals, IGP 21, ×3 (Webby & Lin, 1988).——FIG. 452*c. K. shaanxiensis* WEBBY & LIN, Beiguoshan Formation, Ashgill, Longxian County, Shaanxi, China; longitudinal section of holotype with axial spongocoel surrounded by low chambers with imperforate exowalls, with fine vesiculae and downwardly inclined, inhalant canals, IGP 1, ×4 (Webby & Lin, 1988).

Rigbyetia WEBBY & LIN, 1988, p. 152 [**Cliefdenella obconica* RIGBY & POTTER, 1986, p. 42; OD]. Obconical to subcylindrical, occasionally branching, aporate sphinctozoan; chambers of low, ringlike, annulated appearance with imperforate exowalls; laminate, gently domed, imperforate interwalls with upper surfaces denticulate and locally downwardly inflected into vertical to subvertical, porous, incurrent tubes, internally; single, large, central tube of vertically continuous clusters of astrorhizal-like, excurrent canals; this seemingly interconnected with radiating, nearly horizontal, astrorhizal canals of chambers; no clearly defined endowall or endopores developed; vesiculae small and only rare in chambers, not developed elsewhere; hollow, rootlike, bracing structure may be developed. *Upper Ordovician:* USA (Oregon, California), Australia (New South Wales).——FIG. 453*a–d.* **R. obconica* (RIGBY & POTTER), Horseshoe Gulch limestone, Ashgill, Horseshoe Gulch, Klamath Mountains, California; *a,* side view of exterior of branched holotype with annulate, aporous, dermal layer, ×2; *b,* other side of holotype with clearly defined, low chambers pierced by tubular, inhalant system where dermal layer has been removed, USNM 395897, ×2; *c,* view from below of chamber interwall with central cluster of

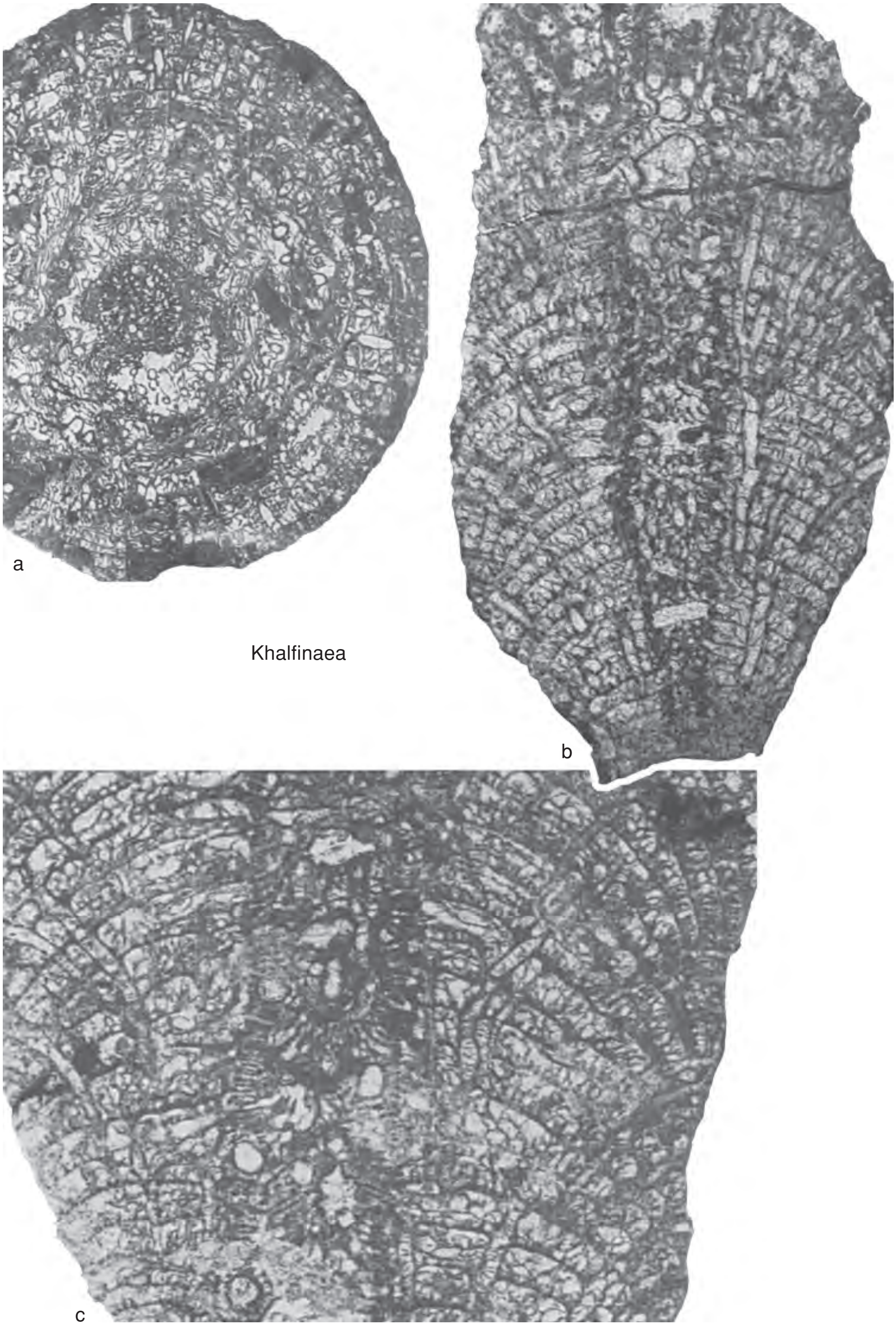

FIG. 452. Cliefdenellidae (p. 681–683).

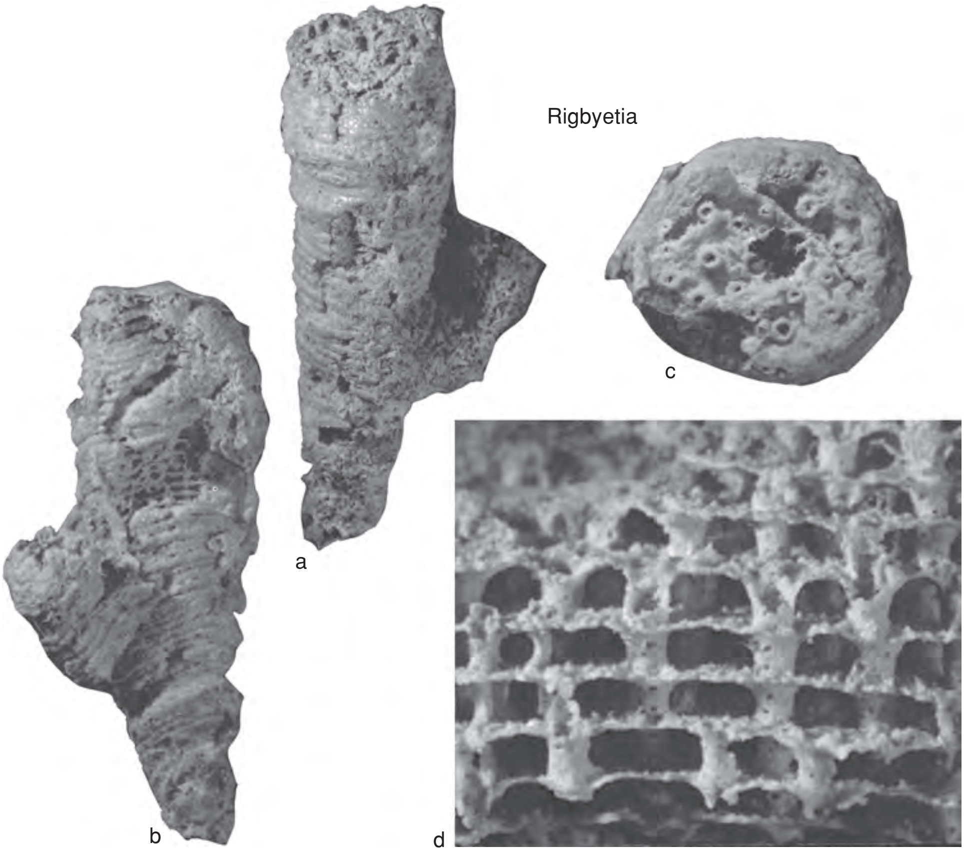

FIG. 453. Cliefdenellidae (p. 683–685).

exhalant canals surrounded by rings of smaller, inhalant canals, USNM 395903, ×5; *d,* enlarged view of paratype showing horizontal interwalls pierced by reflected, inhalant canals, BMNH S10169, ×10 (Rigby & Potter, 1986).

Family GIRTYCOELIIDAE new family

[Girtycoeliidae FINKS & RIGBY, herein] [type genus, *Girtycoelia* KING, 1933, p. 79]

Cylindroid; cloaca absent; superposed chambers with small, closely spaced, circular exopores; primary walls composed of small (20 to 50 µm in *Girtycoelia*) isodiametric spherulites; a secondary lamellar, possibly clinogonal, lining inside of chambers, continuous with vesicles associated with distal withdrawal of sponge tissue from chambers. *Carboniferous (Upper Pennsylvanian)–Triassic.*

Girtycoelia KING, 1933, p. 79 [**G. typica;* OD]. Spheroidal or hemispheroidal, subequal segments in linear series that frequently produce subparallel branches that may fuse laterally; no cloaca; exowall with closely spaced, small, subpolygonal to circular exopores of two sizes, as well as occasionally very large, circular ones with raised rims, usually near intersegment suture; imperforate, dermal layer often formed in patches, obliterating small exopores and forming a strong rim about very large ones; imperforate layer may be covered with fine, transverse wrinkles; interwalls continuous with exowall of underlying chamber and interpores same size as small exopores; chamber interiors may contain large vesicles subparallel to exowall and continuous with succession of secondary, imperforate deposits that line chamber interior and mark progressive, distal withdrawal of sponge tissue; walls built of small, isodiametric spherulites, secondary lining lamellar and possibly clinogonal; no spicules known. *Carboniferous (Upper Pennsylvanian)–Triassic (Norian):* USA (southcentral states), *Upper Pennsylvanian;* Italy (Sicily), Tajikistan, *?Permian;* Russia (Caucasus region), *Norian.*——FIG. 450,*2a–b.* **G. typica,* Graford Formation, upper Pennsylvanian, Bridgeport, Wise County, Texas; *a,* side view of cotype showing porous exowalls of hemispherical chambers in cylindrical sponge, ×2; *b,* tracing of polished section of cotype showing lack of central, tubular spongocoel in chambers with both exopores and interpores, and scattered vesiculae, ×2 (King, 1933).

?Takreamina FONTAINE, 1962, p. 205, *nom. nov. pro Steinmannia* WAAGEN & WENTZEL, 1888, p. 979, *non* FISCHER, 1886 [**Steinmannia salinaria* WAAGEN & WENTZEL, 1888, p. 980; OD] [?=*Colospongia* LAUBE, 1865, p. 237 (type, *Manon dubium* MÜNSTER, 1841, p. 28, OD); *Waagenium* DE LAUBENFELS, 1957, p. 249, *nom. nov. pro Waagenella* DE LAUBENFELS, 1955, p. 102, obj., *non* DE KONINCK, 1883, *nec* YABE & HAYASAKA, 1915]. Spheroidal, subequal segments in linear series, sometimes as subparallel branches that fuse laterally to form flabellate masses; narrow, central, circular osculum in each segment but no endowall (cloaca); exopores small, circular, closely spaced, and of two sizes; interwall a continuation of underlying exowall with its pores and osculum; chambers containing large vesicles but no other skeletal structures; microstructure unknown; no spicules known. [Except for the central osculum and the absence of the large, circular exopores, this genus resembles *Girtycoelia* KING, 1933. It may also be considered an *Amblysiphonella* STEINMANN, 1882 that lacks an endowall.] *Permian–Triassic:* Pakistan, Cambodia, Italy (Sicily), Tunisia, USA (?Texas), China (Guangxi), *Permian;* Europe, Indonesia (Timor), *Triassic.*——FIG. 450,*1a–c.* **T. salinaria* (WAAGEN & WENTZEL), Productus Limestone, Bilote, Salt Range, India; *a,* side view of fragmental holotype showing porous exowall of stacked, subspherical chambers, ×1; *b,* vertical section showing irregularly distributed vesicles of different sizes and central osculum in upper chamber, ×1; *c,* view from above showing central osculum of upper chamber and porous exowalls, ×1 (Waagen & Wentzel, 1888).

Family GUADALUPIIDAE Girty, 1909

[Guadalupiidae GIRTY, 1909, p. 79; *emend.,* FINKS & RIGBY, herein] [=Guadalupiidae GIRTY, 1909, p. 79, *partim;* Cystothalamiidae GIRTY, 1909, p. 88, *partim;* Tebagathalamiidae SENOWBARI-DARYAN & RIGBY, 1988, p. 192, *partim;* Cystauletidae BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 102, *partim;* Cystauletidae WU Ya Sheng, 1991, p. 87; Polycystothalamiidae WU Ya Sheng, 1991, p. 92]

Sponges consisting of a sheet (thalamidarium) of similar chambers, whose walls have closely spaced, small, circular pores; on one side of this sheet (exhalant side) is a variably developed layer (trabecularium) of delicate, anastomosing trabeculae, mostly perpendicular to surface, with cross connections, rather similar to those of a stromatoporoid, which may include astrorhizal systems converging on circular, lipped oscules; this double sheet may assume various topological forms, including cylinders, partial cylinders, open cups and palmate branches; chamber interiors hollow except for occasional diaphragms; wall composed of small (20 to 50 μm in *Guadalupia*) isodiametric spherulites. *Carboniferous–Triassic (Norian).*

Guadalupia GIRTY, 1909, p. 79 [**G. zitteliana* GIRTY, 1909, p. 80; OD] [=*Polyphymaspongia* KING, 1943, p. 24 (type, *P. explanata* KING, 1943, p. 25, OD); ?*Platythalamiella* SENOWBARI-DARYAN & RIGBY, 1988, p. 184 (type, *P. newelli,* OD)]. Auriform, cup shaped, infundibuliform, conicocylindrical, or flat, branching strips (sometimes on different parts of one individual, but also species specific); chambers of thalamidarium quincuncially arranged, elongate between exowall and endowall, cross section cuspate proximally and convex distally (similar to lava pillows), bulging outwardly on exowall (inhalant) side; chambers may be crossed internally by one or more flat, imperforate diaphragms, but otherwise hollow; size and proportions of chambers species specific and constant within individuals; trabecularium on inner or upper side of sponge (exhalant surface), with anastomosing trabeculae dominantly perpendicular to surface, causing it to be hispid; prominent, branching grooves (exhalant or astrorhizal systems) deeply sunk into trabecularium and converging on large, circular oscules with elevated rims, or sometimes on more obscure, central areas; exopores, interpores, and endopores small, circular, and closely spaced, exopores somewhat smaller, and endopores somewhat larger than interpores; interpores may be secondarily closed; microstructure of walls and trabeculae consisting of small, isodiametric spherulites; no spicules observed. [*Polyphymaspongia* KING, 1943, is a species of *Guadalupia* with large chambers. *Cystothalamia* GIRTY, 1909, differs from *Guadalupia* chiefly in its peculiar growth form; it is here maintained as a separate genus.] *Permian (Wordian–Changhsingian):* USA (southwestern states), northern Mexico, Italy (Sicily), China, Venezuela, *Wordian–Capitanian;* Tunisia, China, ?Thailand, *Lopingian.*——FIG. 454,*1a–c.* **G. zitteliana,* Capitan Formation, Guadalupian, Guadalupe Mountains, Texas; *a,* side view of holotype showing subcylindrical to obconical form, ×1; *b,* tangential view of section through chambers, ×5; *c,* section longitudinally through chambers, USNM 118135, ×5 (Girty, 1909).

?Cystauletes KING, 1943, p. 31 [**C. mammilosus;* OD]. Long cylinders with multiple branches; broad, central cloaca; chambers quincuncially arranged about cloaca, distally convex and proximally cuspate, forming slight bulges on exterior; no diaphragms observed; exopores, interpores, and endopores small, circular, and closely spaced, approximately equal in size, but endopores more closely spaced than other pores; thin trabecularium lining cloacal surface, consisting of narrow, meandriform ridges separating similar grooves into which endopores open; microstructure small, iso-

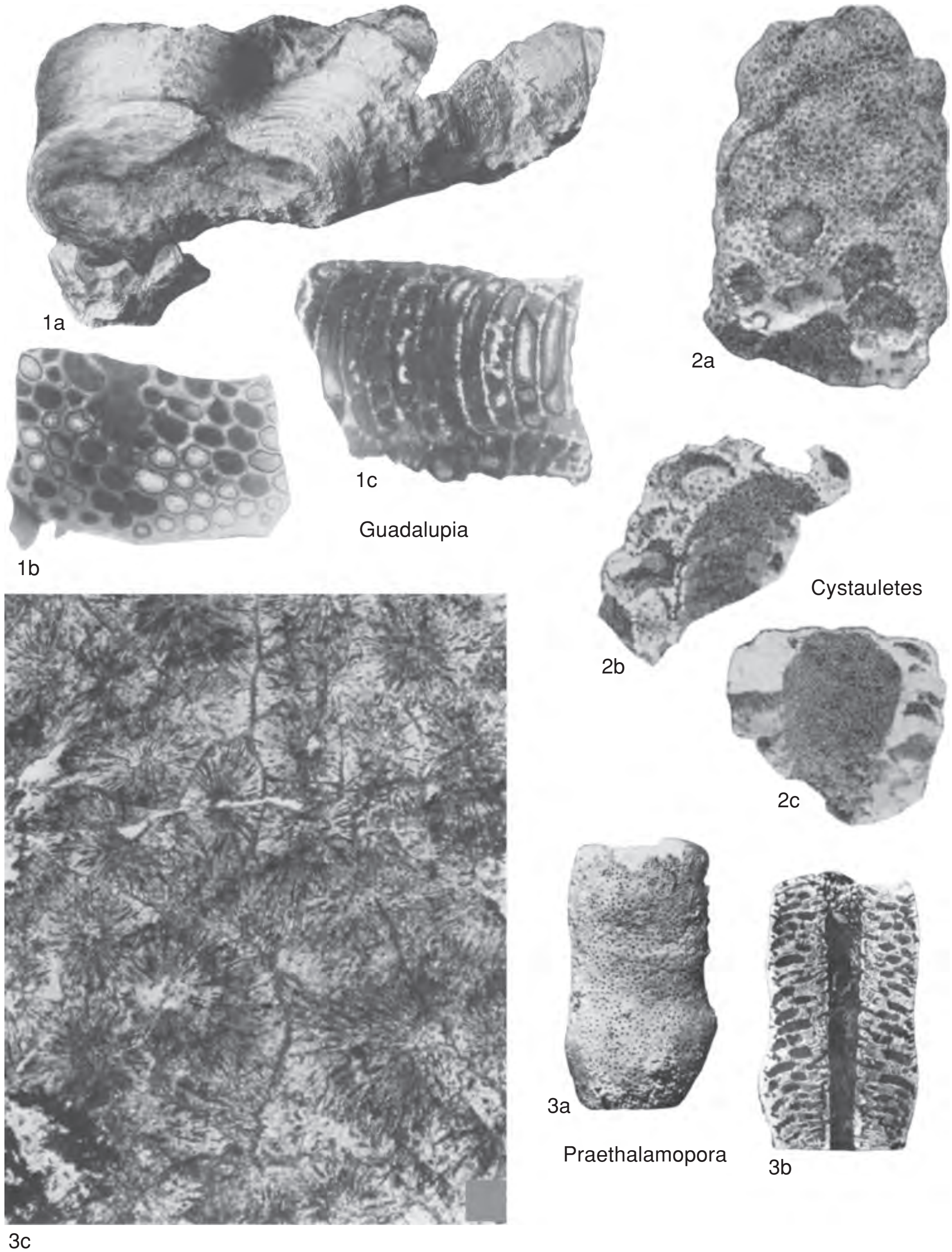

FIG. 454. Guadalupiidae (p. 686–691).

diametric spherulites; no spicules known. [Genus resembles *Discosiphonella.* SENOWBARI-DARYAN (1990, p. 56) has synonymized the two genera but *Discosiphonella* is poorly known and *Cystauletes* should be retained for tubular, branching forms (RMF).] *Carboniferous (Middle Pennsylvanian)–Triassic (Norian):* USA (Oklahoma), *Middle Pennsylvanian;* Spain, *Moscovian;* Italy (Sicily), Japan, *Cisuralian;* China (Hubei), Russia, Tunisia, *Changhsingian;* Russia (Northern Caucasus), *Norian.*——FIG. 454,*2a–c.* **C. mammilosus,* Pawnee Limestone, Desmoinesian, Nowata, Oklahoma;

a, side view of subcylindrical holotype with mammilose chamber exteriors perforated by common exopores, KU 74131, ×2; *b,* oblique section through part of spongocoel and wall, showing upwardly arcuate interwalls and porous nature of all walls in paratype, KU 74133 ×2; *c,* vertical section through large spongocoel and walls of upwardly arcuate chambers, KU 74132, ×2 (King, 1943).

Cystothalamia GIRTY, 1909, p. 89 [**C. nodulifera;* OD] [=*Racemina* TERMIER & TERMIER in TERMIER, TERMIER, & VACHARD, 1977a, p. 41 (type, *R. conica* TERMIER & TERMIER in TERMIER, TERMIER, & VACHARD, 1977a, p. 42, OD); *Polycystothalamia* WU Ya Sheng, 1991, p. 92 (type, *P. sinuolata,* OD)]. Branching, hollow cylinders, with a series of elliptical to slitlike openings from hollow interior along one side of cylinder, that may expand into cuplike, side branches; interior hollow space about half diameter of cylinder and lined by trabecularium; parallel, longitudinal, exhalant grooves and astrorhizal systems occasionally developing on this inner surface, in some instances forming parallel, exhalant tubes that partly or wholly fill portions of inner hollow as in *Lemonea* SENOWBARI-DARYAN, 1990; chambers of thalamidarium globose, making prominent bulges on exterior; exopores, interpores, and endopores small, circular, and closely spaced, endopores (exhalant) about twice size of exopores (inhalant), and interpores of intermediate size; imperforate diaphragms occasionally present in chambers that are otherwise completely hollow; microstructure spherulitic; no spicules known. [This is essentially a *Guadalupia* that has been rolled up to form a tube with gaps along one side. The foregoing is based upon the lectotype (USNM 118146, GIRTY, 1909, pl. 31,*20;* the lateral openings are present on the side not illustrated) plus numerous well-preserved topotypes and near topotypes. The Triassic species in the literature (e.g., OTT, 1967a; DIECI, ANTONACCI, & ZARDINI, 1968) without lateral openings and in which the central hollow is very narrow, possibly without a trabecularium, or in which the hollow is completely filled with a bundle of longitudinal tubes formed from the trabecularium (*viz., C. polysiphonata* DIECI, ANTONACCI, & ZARDINI, 1968, p. 147) should be referred to other genera. The other fragmentary and poorly preserved cotypes of GIRTY, 1909, are also probably not congeneric with the lectotype.] *Carboniferous–Triassic (Ladinian):* Kyrgyzstan, *Carboniferous;* Russia, *Permian;* USA (Texas), Italy (Sicily), Russia, China (Hubei), Venezuela, ?Cambodia, *Guadalupian;* China (Hubei, Zhejiang), Tunisia, *Changhsingian;* Greece, Italy (Sicily), Tajikistan, *Carnian–Norian;* Germany, Yugoslavia, *Ladinian.*——FIG. 455,*1a–b.* **C. nodulifera,* Delaware Mountain Formation, Guadalupian, Glass Mountains, Texas; *a,* two silicified specimens showing glomerate chambers with porous walls, ×2; *b,* polished, longitudinal section through outer wall showing cystose chambers of wall, ×3 (Girty, 1909).——FIG. 455,*1c–e. C. guadalupensis* (GIRTY), Capitan Formation, Guadalupian, Guadalupe Mountains, Texas; *c,* longitudinal, oblique section showing cystose chambers around central spongocoel; *d,* weakly annulate, cylindrical lectotype with low nodes produced by arcuate, chamber walls; *e,* lectotype from above showing central spongocoel and chambers of wall, USNM 118150, ×1 (Girty, 1909).

Diecithalamia SENOWBARI-DARYAN, 1990, p. 58 [**Cystothalamia polysiphonata* DIECI, ANTONACCI, & ZARDINI, 1968, p. 147; OD]. Porate, cylindrical sponge with aragonitic, basal skeleton of irregular microstructure; outer layer of chambers with glomerate arrangement around thick bundle of vertical, axial canals; filling skeleton of reticular type only in area of bundled canals; canal structure prosiphonate; spicular skeleton not known. *Triassic (Carnian):* Italy, Austria, Italy (Sicily), Greece (Island of Hydra), Yugoslavia.——FIG. 456,*1a–b.* **D. polysiphonata* (DIECI, ANTONACCI, & ZARDINI), San Cassiano Formation, Carnian, Dolomite Alps, Italy; *a,* side view of paratype showing glomerate, outer chambers, IPUM 17625, ×2 (Dieci, Antonacci, & Zardini, 1968); *b,* longitudinal section showing outer, glomerate chambers and inner cluster of vertical, exhalant canals, G/233/1, ×5 (Senowbari-Daryan, 1990; courtesy of *Münchner Geowissenschaftliche Abhandlungen,* Verlag Dr. Friedrich Feil).

Discosiphonella INAI, 1936, p. 169 [**D. manchuriensis;* OD] [?=*Ascosymplegma* RAUFF, 1938, p. 195; ?*Cystauletes* KING, 1943, p. 31 (type, *C. mammilosus,* OD); ?*Lichuanospongia* ZHANG, 1983, p. 8 (type, *L. typica,* OD)]. Sponge as restored resembles a semicircular pocket (or half a pita), long, straight edge open and presumably osculum; sides of pocket are each a thalamidarium of single layer of globose, subpolygonal chambers that bulge externally but are flat on cloacal surface; trabecularium not clearly evident but endowall thicker than exowall; interwalls consistently bulging toward aperture; exopores, interpores, and endopores are subequal and closely spaced; exopores circular but others seen only in section; cloaca traversed by irregular, imperforate partitions, mostly concave toward aperture; chambers may contain imperforate lamellae (diaphragms or possibly vesicles); microstructure unknown; no spicules known. [Genus resembles a compressed, nontubular *Cystauletes* KING, 1943, in which the aperture is the widest dimension. SENOWBARI-DARYAN (1990, p. 56) has synonymized the two genera but *Discosiphonella* is poorly known and *Cystauletes* should be retained for tubular, branching forms (RMF).] *Carboniferous (Pennsylvanian)–Triassic (Norian):* Manchuria, *Pennsylvanian;* Thailand, China, Sicily, *Lopingian;* Peru, *Norian.*——FIG. 455,*2a–c.* **D. manchuriensis,* Hsiao-shih Series, Tai-tzu-ho System, Pennsylvanian, Pen-hsi-hsein, Manchuria; *a,* side view of weathered exterior of holotype, ×1; *b,* transverse section near and almost parallel to osculum, ×1; *c,* diagrammatic restoration showing chambers and osculum at upper margin, ×1 (Inai, 1936; courtesy of *Proceedings of the Imperial Academy of Japan*).

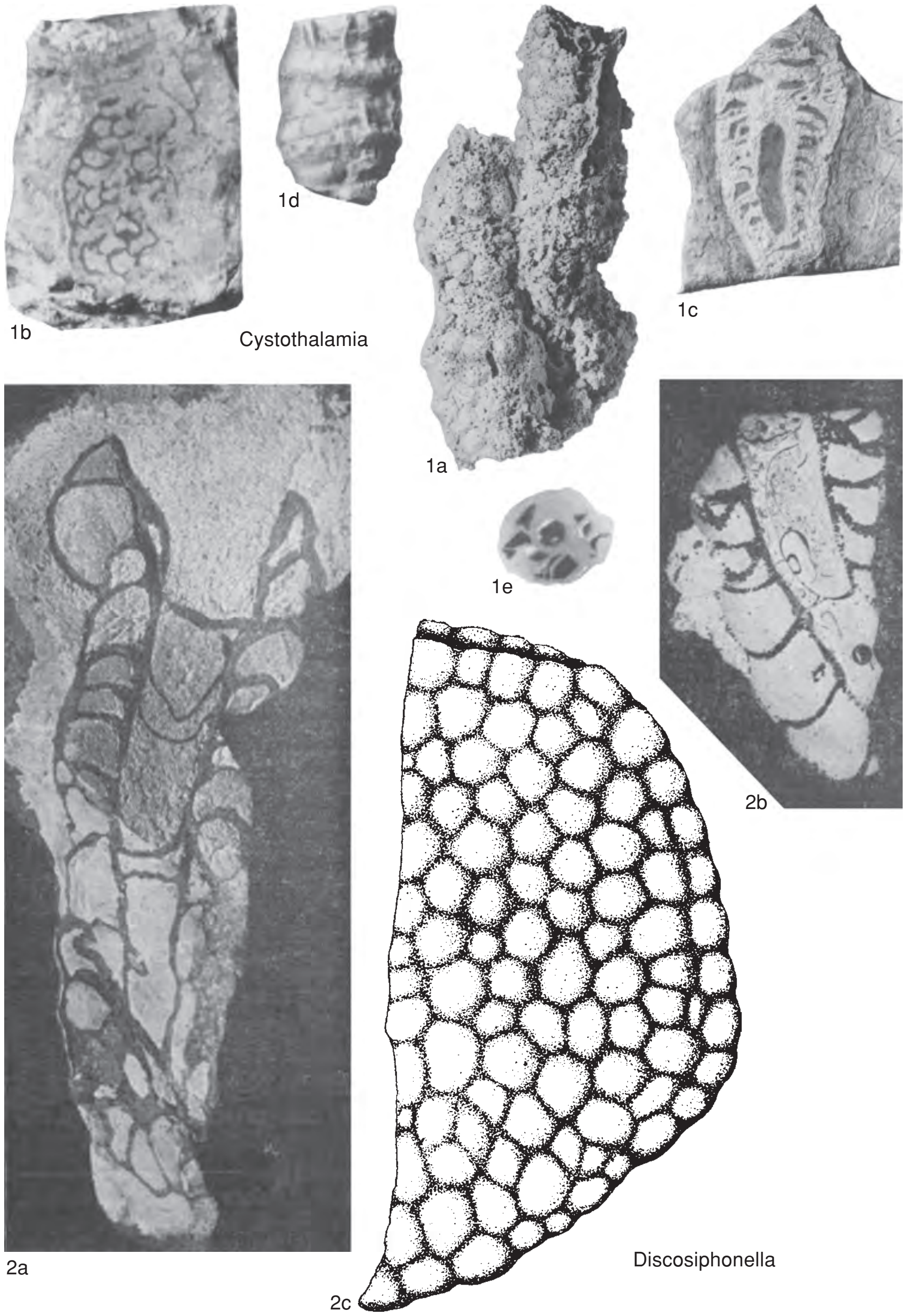

Fig. 455. Guadalupiidae (p. 688).

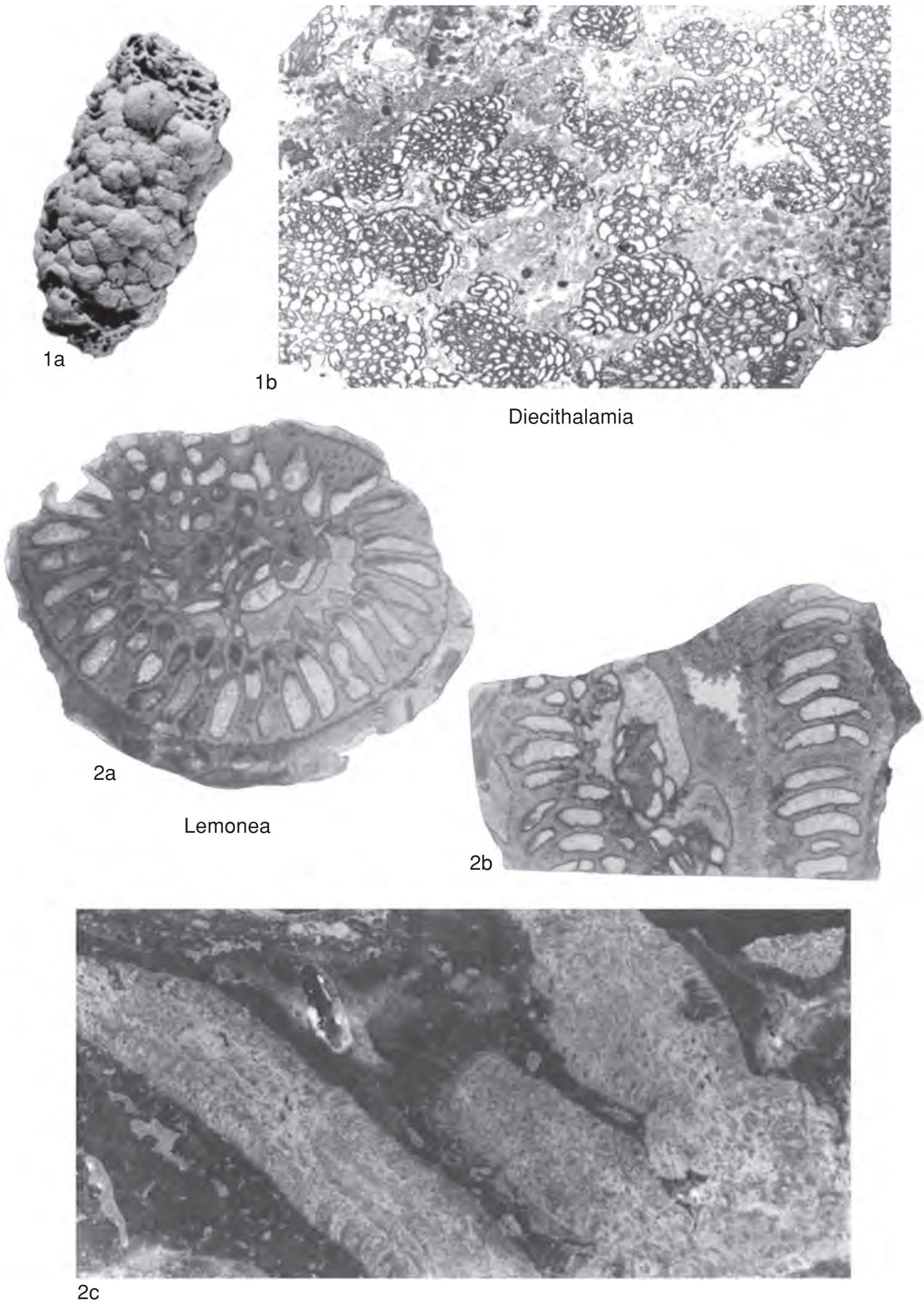

FIG. 456. Guadalupiidae (p. 688–691).

Lemonea Senowbari-Daryan, 1990, p. 151 [**Guadalupia cylindrica* Girty, 1909, p. 81; OD]. Conical to cylindrical with central cloaca partly or completely filled with parallel, exhalant canals formed from expansion of trabecularium; surrounding thalamidarium as in *Guadalupia* Girty, 1909, with which this intergrades. *Cystothalamia* Girty, 1909, also may have parallel, exhalant canals partly filling cloaca. [*Lemonea conica* Senowbari-Daryan, 1990, has multiple bundles of parallel, exhalant tubes, each bundle surrounded by a thalamidarium, but the whole forming a single, continuous, conical individual. It probably should be made a separate genus.] *Permian (Wordian–Guadalupian):* USA (Texas, New Mexico), Tunisia, Italy (Sicily), Yugoslavia, China.——Fig. 456,*2a–c*. **L. cylindrica* (Girty), Capitan Limestone, Guadalupian, Guadalupe Mountains, Texas; *a,* transverse section of holotype showing radial chambers around broad spongocoel that contains vesiculae, ×5; *b,* longitudinal section showing arcuate, radial chambers and vesiculae in spongocoel, ×5 (Girty, 1909); *c,* polished surface with longitudinal sections of three cylindrical specimens that have characteristic chamber development in their walls and vesiculae of their broad spongocoels, USNM 35019, ×1 (Rigby, Senowbari-Daryan, & Liu, 1998).

Praethalamopora Russo, 1981, p. 14 [**P. zardinii;* OD]. Cylindrical, chambers not apparent externally; exterior covered with small, closely spaced, circular pores; central cloaca narrow, diameter approximately one-fifth that of sponge; chamber height less than diameter; chambers more or less radially arranged around cloaca and ovoid in section (or alternatively, superposed discoid chambers subdivided by radial partitions); chamber walls perforated by pores; trabecularium not evident; microstructure spherulitic (isodiametric). *Triassic (Carnian):* Italy.——Fig. 454,*3a–c*. **P. zardinii,* San Cassiano Formation, Cortina d'Ampezzo, Dolomite Alps; *a,* side view of holotype exterior; *b,* longitudinal section with a tubular spongocoel and slightly arched chambers on margins, ×2; *c,* transverse section illustrating spherulitic microstructure, IPUM 19291, ×200 (Russo, 1981).

Family UNCERTAIN

Fluegelispongites Mostler, 1994, p. 345 [**F. trettoensis;* OD]. Agelasid sponges characterized by isolated, slender, C- to S-shaped acanthostrongyles that have their spines arranged in spirals. *Middle Triassic:* Italy.——Fig. 450,*4*. **F. trettoensis,* Buchensteiner Schichten, Trettoe; isolated holotype, s-shaped acanthostrongyle with spines arranged in spiral, ×300 (Mostler, 1994).

Madonia Senowbari-Daryan & Schäfer, 1986, p. 251 [**M. conica;* OD]. Porate sphinctozoan with tubular filling structure where tubes are more or less regularly developed; tubes penetrating chamber or segment roofs and more or less bind segments together; shield-shaped, overlapping chambers arranged around retro- to pseudosiphonate spongocoel; outer segmentation barely visible. [The genus was originally included in the Polytholosidae Seilacher but the tubes and their orientation in the chamber walls separate the genus from other forms in the family. Segment development and their structure are similar to the cliefdenellids of the Ordovician, but those forms do not have porous walls as in *Madonia.* For the present *Madonia* is considered to be of uncertain family relationship.] *Triassic (Norian):* Italy (Sicily).——Fig. 450,*6a–b*. **M. conica,* Reef limestone, Norian, Madonie Mountains, Sicily; *a,* transverse section of holotype showing low, shield-shaped chambers with tubular connections and central canal cut marginally in upper right, SPIE P/244/2, ×2; *b,* parallel, transverse section showing tubular structures well in lower part and their connections between chamber walls in upper part, SPIE P/244/1, ×2 (Senowbari-Daryan & Schäfer, 1986).

Thamnonema Sollas, 1883, p. 549 [**T. pisiforme;* OD]. Small, globular sponge without central cavity; skeleton a network of fibers radiating and branched upwardly from base where three equally spaced, basic fibers originate; summit with larger meshes that appear as small oscules; sides ridged meridionally. *Middle Jurassic:* England.——Fig. 450,*3*. **T. pisiforme,* Great Oolite, Hampton Down; arrangement of fibers of base; *a,* primary and, *b,* secondary fibers radiating from base, *c,* ×15 (Sollas, 1883).

Order VACELETIDA new order

[Vaceletida Finks & Rigby, herein]

Basal skeleton of microgranular aragonite organized in small, irregular units bounded by organic membrane and with organic center, the whole forming a cortex of sphinctozoan morphology, secreted at intervals over newly formed unit of soft tissue; no spicules present in living *Vaceletia* Pickett, 1982, but some fossils contain imbedded monaxons, as well as dubious spicules of more elaborate form; exopores usually lobate or polygonal in outline. *Lower Cambrian–Holocene.*

Family SOLENOLMIIDAE Engeser, 1986

[Solenolmiidae Engeser, 1986, p. 589] [=Deningeriidae Boiko, Belyaeva, & Zhuravleva, 1991, p. 156]

Superposed spheroidal segments; chambers in type genus filled with trabeculae that