HEXACTINELLIDA: GENERAL MORPHOLOGY AND CLASSIFICATION

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INTRODUCTION

The Hexactinellida are sponges distinguished by siliceous spicules that are characteristically either simple orthotriaxial hexactines or variants of this type and by adult nonchoanocytal soft parts in the form of a trabecular **syncytium**, without either mesenchyme or pinacoderm. The characteristic spicules are either the only forms present or are sometimes accompanied by diactinal monaxons whose relationship to them is not always demonstrable. Tetraxial and polyaxial spicules do not occur.

Hexactinellida are recognized in paleontology by the form of the spicules or by some forms having characteristic skeletal frameworks formed by fused spicules (not united by zygosis, as in lithistid Demospongea). Skeletal remains occur certainly from the Lower Cambrian upward but also may occur in the somewhat older Ediacaran beds of Australia.

HEXACTINELLIDA AND HYALOSPONGES

The name Hexactinellida is preferred to hyalosponges, which was used by de Laubenfels (1955). Schmidt (1870) was the first to characterize the Hexactinellida as a distinct group of Porifera separated completely from Demospongea and stated the character of the spicules correctly. The taxon Hyalospongiae of Claus (1872), attributed by de Laubenfels (1955) to Vosmaer (1887), was intended to include lithistid Demospongea as well as Hexactinellida. The Hyalospongiae was based on the supposed diagnostic value of (a) the so-called fibrosiliceous skeleton thought by Bowerbank (1862) to exist in lithistid Demospongea and some Hexactinellida but now considered as imaginary and (b) the type of hexactinellidan framework known to Claus from *Euplectella aspergillum* Owen, 1841 (the Venus flower basket). Such a framework does not even occur in all species of *Euplectella.* The only other character mentioned was frequent occurrence of beardlike roots, which occur in only some Hexactinellida and demosponges. It was also claimed later by de Laubenfels (1958) that fusion of spicules, which he wrongly thought was regarded by Claus as the diagnostic character, is always significantly present at some stage in Hexactinellida. In fact, it is unknown from one entire subclass (Amphidiscophora Schulze), and not known from all members of the other.

de Laubenfels (1958) also included as hyalosponges the Heteractinida of this volume, which were unknown to Claus. These forms are clearly distinct from the Hexactinellida; their spiculation is not triaxial in basis, and their spicules were calcareous.

Finally, the spicules of Hexactinellida are no more glassy than those of Demospongea. They simply happen to be conspicuously glassy in some well-known glass sponges (e.g., *Euplectella*); equally glassy structures occur in some less well-known lithistids, e.g., *Theonella* Gray, which are also the forms that Bowerbank and Claus failed to separate from the Hexactinellida.

SOFT PARTS

Soft parts of adult Hexactinellida consist of a reticulate choanocytal membrane, which forms an internal layer of flagellated chambers, and inner and outer networks of syncytial filaments or trabeculae in which the chambers are suspended. Interspaces of the structure are filled by the external medium (i.e., seawater), which presumably circulates through them. The choanocytal membrane consists of flat choanocytes linked syncytially by lateral processes; the chambers formed by it are typically separate but joined together at their open (**apopylar**) ends by a trabecular **connecting membrane. Trabeculae** of inner and outer networks have no regular direction internally but form tangential networks at the two bounding surfaces. These are the **dermal** and **gastral membranes.** Here the terms dermal and gastral are used simply conventionally, referring to the external and paragastral sides of the wall without other homological implications. Trabecular parts immediately under the two bounding membranes, in which chambers are absent, are termed subdermal and subgastral respectively. The inner and outer networks are sometimes called the **epirhysome** and **aporhysome.**

It was argued by Bidder (1929) that the special character of the soft parts point to the Hexactinellida originating from branching colonial Choanoflagellata, independently of sponges with a mesenchyme (Gelatinosa Bidder). Hexactinellidan embryos are, however, much like those of Demospongea, with a cellular layer at the surface and a gelatinous interior. The post-embryonic change by which the adult type of soft parts must originate is more likely to represent their origin in phylogeny.

Hexactinellida may have a chamber system only or also possess a canal system, consisting of exhalant canals only or with additional inhalant canals. In the simplest instance, all chambers face the gastral membrane directly and are thimble shaped or modified by development of lateral diverticula. There may be no other special circulatory features, or enlarged intertrabecular lacunae may occur between the open ends (apopyles) of the chambers and the gastral bounding membrane or between their summits and under the dermal membrane. The condition of these sponges is essentially rhagonlike, although with partial transition to leuconlike if the chambers have diverticulation. More commonly a layer of simple chambers is locally protruded to form radial to branching diverticula, which may intercommunicate if their branches grow together. Occasionally, the chamber layer is convoluted to form labyrinths of chamber-lined passages, which may be open under the dermal membrane as well as on the gastral side. Interiors of structures formed by convolution of the chamber layer may form exhalant canals directly or have a trabecular lining around an intertrabecular canal, the wall of which may be formed by a canalar membrane similar to the dermal and gastral membranes. Exhalant canals may end under the gastral membrane or open directly through it because of secondary fenestration. The bounding membrane of the gastral surface may then appear to pass into the exhalant canals through becoming continuous with a lining **canalar membrane,** but the origin of this condition can be seen by comparison of young and old parts. Between diverticula of the chamber layer, there are usually corresponding inhalant canals formed as specially differentiated intertrabecular spaces. Again a lining canalar membrane may be present. These canals begin under the dermal membrane and normally never pierce it.

It needs to be noted that formation of the chamber and canal systems is not based on diverticulation or any sort of folding of the wall as a whole but on internal convolutions of the **choanocytal membrane** or the chamber layer only. There is never any outgrowth of the type seen in sycettoid Calcarea, and formation of inhalant canals involves no folding of any kind. These facts are important because various paleontologists have tried to explain features of fossil skeletons that represent the positions of chambers or canals as due to the wall being folded. This idea was first stated in the pioneer work of J. T. Smith (1847, 1848), who attributed such features to longitudinal plications called plaits, which were supposed to fuse together laterally to produce canal-like spaces in the skeleton. Smith believed he was describing Bryozoa and had no knowledge of sponge canal systems, let alone that of the Hexactinellida, which were first described adequately by Schulze (1887a, 1887b). Despite this, the idea has persisted to the present, in the work of Moret (1926b), for example, who sometimes pictured the folding as running transversely. For correct interpretation, features related to the canal system must not be attributed to folding of the wall as a whole, and features related to true folding are not related to the canal system. True modes of formation of canalar interruptions of the skeleton are by progressive displacement of loose spicules as the corresponding soft features are enlarged (again demonstrable by comparison of young and old parts) or by direct interruption of developing skeletal meshwork in a growing marginal region.

Various Hexactinellida have soft parts that are secondary additions to the basic wall structure. Many that are fixed directly to the substratum have a secondary basal expansion, which may be purely trabecular or contain chamber-bearing structures. Some forms have terminal oscula covered by porous diaphragms, termed sieve plates; these are usually simply trabecular but may also contain flagellated chambers like those of the lateral wall (e.g., in *Aphrocallistes* Gray). The living *Callicyclix zitteli* (Marshall & Meyer, 1879) has a body of dividing and anastomosing tubes enclosed in a peripheral capsule without flagellate chambers, and skeletal structures imply presence of a similar capsule in various fossils.

SPICULES

Spicules of Hexactinellida are formed from opaline silica with some mixture of organic matter, deposited around organic axial filaments or in various ways to form additional anaxial structures. They arise in all parts of the trabecular network and are secreted by multinucleate scleroblast-syncytia, in instances where their origin is known.

Spicules in which axial filaments extend to tips of normal rays, without raylike or branchlike anaxial prolongations, are called **holactines** and take names ending -actine. The central morphological type is the orthotriaxial hexactine, with six rays arranged as though following the axes of a cube and with their axial filaments meeting at a central axial cross. Primary variants of this type are spicules with fewer than six rays, linked with either hexactines or one another morphologically by intermediates with one ray or more short to rudimentary by comparison with the others. In many such spicules, a six-rayed axial cross is still present, with the undeveloped rays represented by axial rudiments. These forms, however, grade into spicules without axial rudiments, which may then be diaxons or monaxons. The spicules take names from pentactine to monactine according to the number of rays. Forms with four or three rays may, however, be either cross- or T-shaped stauractines (stauracts of some authors) and **tauactines,** with rays following two of the three triaxon axes only, or **orthotetractines** and orthotriactines with all three represented. Diactines may similarly be **orthodiactines,** with two rays at right angles, or rhabdodiactines with the two in line.

This group of variations is usually regarded as due to secondary reduction of a basic hexactine or similar reductions of its derivatives. It cannot be demonstrated that this view is correct, but reduction from a central type is more likely than convergence to it from multiple prototypes. Minchin (1905) thought that stauractines may have preceded hexactines in phylogeny because of their occurrence as the first spicules formed in ontogeny and supposed suitability for the support of thin-walled structures. This could be correct, but is not clearly demonstrable stratigraphically. The embryonic stauractines are also homologically members of one division of the adult megascleric skeleton (autodermalia: see below), not prototypes of the spicules in general, and are explicable alternatively as simply an embryonic specialization.

Holactines may be modified further by distortion of the regular triaxial pattern. Rays may be bent near their origins or curve progressively away from the ideal cubic axes. This can occur with a genetic basis or simply by growth of spicules in restricted situations, e.g., between closely spaced canals. Pentactine megascleres supporting dermal or gastral membranes often have the paired rays slightly bent toward a fifth proximal ray, directed inward. This condition is carried further in spicules that some forms protrude for attachment, in which small paired rays are bent strongly toward a large proximal ray to form grapnels that function as such. These spicules are described as anchorate. Some recent authors have called them anatetraenes by analogy with demosponge anatriaenes; but the triaenes and analogous polyaenes of Demospongea and Heteractinellida are not basically triaxial and have meristically variable cladomes in which interactinal angles depend on the number of rays. Such spicules do not occur in Hexactinellida. An anchorate pentactine with a distal axial rudiment is also not properly an anatetraene but an anisomesoanatetraene, if this nomenclature were used. In another development, specially distorted pentactines of one family (Rossellidae) have the interactinal angle between two of the paired rays more than 90°, up to more than 270°, and the rays arranged in the remaining arc at subequal intervals. These are **paratropal pentactines** or **paratropes.** Fossil examples have sometimes been mistaken for dermalia of lithistids.

Modification of holactines may occur by growth of solid (anaxial) lateral spines on the rays. These may simply grow outward but are commonly curved toward the tip of the ray. Some forms have such spines specially developed on an outwardly directed (distal) ray of pentactine or hexactine megascleres of which four paired rays support a bounding membrane; these are pinular pentactines or hexactines or simply **pinuli.** In rhabdodiactines called uncinates, thornlike spines are all directed toward one end of the spicule. In anchoring rhabdodiactines of some genera, groups of recurved spines at the end of a protruded shaft form grapnel-like **umbels,** analogous functionally with the grapnels of anchorate spicules although different in origin. Amphidisc microscleres and their variants bear similar umbels without apparent function. In microscleres called sceptrules, the cross-containing end of a monactine or a strongly unequal-rayed diactine with one ray rudimentary bears spines in forms varying from a brushlike, centrifugal cluster to an umbel-like ring of recurved teeth.

In a special group of microscleres called **rosettes,** and distinguished from holactines as astral, the true rays bear anaxial, branchlike prolongations or terminals or are replaced by anaxial outgrowths. These spicules take names ending -aster or -come, with the most common type being six-rayed hexasters. Further nomenclature of hexasters is based on the form of the terminals, which are simple, sharp spines in **oxyhexasters,** bear terminal knobs, discs or recurved teeth in **tylohexasters, discohexasters,** and onychohexasters, or are petal-like in floricomes. Some have the true rays or principals much shorter than the terminals, and some of these forms sometimes grade into triaxial **pseudopolyactines** in which the terminals radiate directly from a spherical centrum containing a six-rayed axial cross. **Octasters** are a special mutant form in which the six normal principals are replaced by eight raylike and terminal-bearing pseudoactines, which arise from the eight three-dimensional angles of an axial cross in the central part.

In anchorate pentactines or tauactines the axial filaments of the grapnel rays are sometimes rudimentary, although a solid anchor fluke is well developed. This development is not related to formation of hexaster terminals but a separate modification in the spicules concerned, which grade into normal forms through intermediates.

The rays of spicules of all sorts are normally not branched in living genera, although branching may be seen in rare abnormal examples. The fossil *Acanthocoryna* FINKS, 1960, has pentactines with a branchlike outgrowth on the outside of each paired ray; but examples from the Irish Carboniferous, at least, can have an axial canal in the typical ray but not the branch, which seems to be simply a secondary spine homologically. In *Docoderma* FINKS, 1960, massive development of tangentially radiating spines converts pentactines into spicules resembling the polyaenes of some Heteractinellida.

Some Hexactinellida have megascleres united to form rigid skeletal frameworks. The union is characteristically by fusion (not by articulation as in Demospongea), very probably because of the syncytial character of the soft parts. There are several modes of union. First, where they cross or lie side by side, rays may fuse together but still remain recognizable as individual rays. Rays close together but not in contact may then also be united by transverse siliceous bridges or **synapticula.** Second, pairs of rays apposed side by side may be enclosed in a common siliceous envelope to form beams in which individual rays are not apparent except by the presence of their axial filaments. These main modes of union may occur separately or in the same skeleton. Third, megascleres arranged with four paired rays supporting a dermal or gastral membrane (or arranged correspondingly, although the soft parts are unknown) may be connected by branching and anastomosing siliceous filaments in the meshes enclosed by the paired rays. The relationship of these filaments to the soft parts is unknown, but their pattern is typically similar to that of the trabeculae forming bounding membranes.

In many Paleozoic Hexactinellida with apparently unconnected spicules, the skeleton retains its organization in a manner that is very unusual in later comparable forms. This simply may be due to conditions of burial, but might instead indicate the presence of something like spongin.

MEGASCLERES

The lateral wall of Hexactinellida is characteristically supported by three series of megascleres. Two support the dermal and gastral bounding membranes; the third occurs in the interior and supports the wall as a whole as well as its internal choanocytal and canalar structures. The dermal and gastral megascleres or **dermalia** and **gastralia** are commonly pentactines, arranged with four paired rays in or under the bounding membrane and the fifth directed inward. The paired rays are called **tangentials** or, more strictly, **paratangentials** because their orientation is seldom truly tangential. Pentactines arranged in this manner may be replaced by stauractines, by hexactines with a projecting distal ray as well as an inwardly directed proximal ray, or by pentactines with the unpaired ray distal. Distal rays are often pinular when present. Very rarely, the gastralia are rhabdodiactines, which lie in the plane of the surface. The internal parenchymal megascleres vary from hexactines to diactines or may rarely include monactines.

There are two types of **parenchymal skeletons.** In **lyssacine** Hexactinellida, the megascleres are typically loose and of types from hexactine to rhabdodiactine, occurring in various combinations and being all rhabdodiactines in some genera. As fossils, the latter may appear falsely to be monaxonid sponges since the triaxon character of rhabdodiactines is apparent only if the axial crosses can be seen. The main supporting elements are **principalia** against which may lie smaller comitalia. The megascleres are sometimes fused together as a secondary development in the whole of the body or the older parts only. In dictyonine Hexactinellida the parenchymal megascleres or **dictyonalia** are characteristically all hexactines and are fused to form a rigid dictyonal framework as part of their normal development. In lyssacines, union between the spicules is usually more or less haphazard, but in dictyonines some or all skeletal beams are typically of the sort enclosing pairs of rays together.

Some lyssacine Hexactinellida have two series of dermalia with autodermalia whose tangential rays lie in the bounding membrane and different hypodermalia whose tangentials lie under it. The difference may be striking; *Rossella* CARTER, 1872, and related forms have small stauractine, pentactine, or hexactine **autodermalia,** contrasting with **hypodermalia** in the form of paratropal pentactines whose rays may be more than ten times longer. Where ontogeny is known, the autodermalia correspond with the embryonic stauractines, and the hypodermalia are a separate development; they seem sometimes to derive homologically from the parenchymal megascleres.

The names autodermalia and hypodermalia were originally introduced by SCHULZE (1887a, 1887b) to designate any dermalia that lie with the tangentials in the bounding membrane or under it, without necessary presence of two distinct series. Similar names were applied to the gastralia on this basis (**autogastralia, hypogastralia**). But the terms have their principal usage in instances where two systems are present, and SCHULZE himself called the outer set autodermalia even though some of its members may lie under the membrane when numerous. In paleontology, the terms are useful only if two series of dermalia are present or if apparent dermalia also seem to be special external members of a parenchymal skeleton.

Some lyssacine Hexactinellida protrude megascleres termed **prostalia** from external or marginal surfaces. The megascleres are usually either rhabdodiactines, or pentactines with a long proximal ray and may originate as hypodermalia or members of the parenchymal principalia. They are classed as **pleuralia** if protruded from lateral surfaces; marginalia, if arranged around an osculum; and basalia if protruded from the base and used for attachment. The last are typically either anchorate or provided with a terminal umbel. If a sieve plate is present, its megascleres may be special oscularia related to dermalia and gastralia but differently developed.

Last, several instances are known in which larval Hexactinellida with adult-type soft parts possess a special internal basal skeleton in the form of small, ankylosing hexactines termed **basidictyonalia.** These are distinct from the normal adult parenchymal megascleres and may have a peculiar mode of union in which fusion by their tips is preceded by zygosis-like articulation (e.g., in *Rhabdocalyptus mirabilis* SCHULZE). The ankylosing tips may also be anaxial for some distance from the end. This mode of union does not occur in adult parenchymal structures and certainly not in dictyonine frameworks, whose description as consisting of spicules fused tip-to-tip is not correct (e.g., DE LAUBENFELS, 1955).

MICROSCLERES

The spicules classed as microscleres are all those not referable to some division of the megascleres. They are typically small by comparison but sometimes reach equal or even larger sizes. Most of the main types have been noted above (see Spicules, p. 129).

The most common microscleres are small parenchymal triaxons. In the subclass Amphidiscophora these are always holactines; in the subclass Hexasterophora they are characteristically rosettes, although holactines sometimes also occur. Other microscleres are less widely distributed.

The characteristic microscleres of the subclass Amphidiscophora are amphidiscs with equal terminal umbels at the ends of a short shaft. These spicules are monaxons, but variants with four or six rays (**staurodiscs, hexadiscs**) are diaxons or triaxons. Asymmetric amphidiscs with one umbel larger than the other have been called hemidiscs (or hemiamphidiscs). The amphidiscs are typically found at right angles to bounding or canalar membranes, with one half protruded through the membrane. They are never produced by forms with rosettes.

The sceptrule group of microscleres is characteristic of one group of dictyonine Hexactinellida (suborder Hexactinosa) but unknown in another (suborder Lychniscosa) or in lyssacines. The end containing the axial cross and usually bearing spinous outgrowths is protruded through a bounding membrane with the single ray proximal, or similarly through a canalar membrane.

Uncinates occur as microscleres in dictyonines with sceptrules (Hexactinosa), in the sense of being accessory elements that take no part in formation of the main supporting skeleton. Some are small raphides, but others range up to strongly barbed forms larger than the true megascleres. These uncinates are monaxons, whose relationship to triaxons cannot be demonstrated. Uncinates present as megascleres in some forms with amphidiscs (Amphidiscophora) are, in contrast, sometimes clearly triaxial.

The Paleozoic Dictyospongiidae are reticulosids, some of which have paraclavule microscleres (umbels *sensu* HALL & CLARKE, 1899) resembling amphidiscs with one umbel missing or like a nail-like form of sceptrule called a **clavule.** The nature of these spicules is unknown, but they seem to be monaxons.

Microscleres are almost absent from fossil Hexactinellida but are sometimes found loose in sediments.

CLASSIFICATION

The classification used here above family-group level is based on the method of MORET (1926b), adopted in agreement with LAGNEAU-HÉRENGER (1962) and REZVOI, ZHURAVLEVA, and KOLTUN (1962). The reason for using this method is the absence of microscleres in the fossils and especially in lyssacines, modern representations of which may have amphidisc or rosette microscleres but similar megascleres. There is no implied rejection of the zoological use of microscleres when these are fully available. The taxa distinguished are ranked as orders (Lyssacida, Hexactinosa, and Lychniscosa).

Early attempts at classification of Hexactinellida were by KENT (1870), CARTER (1875), and MARSHALL (1876). KENT divided Hexactinellida as an order into suborders Coralliospongiae GRAY and Callicispongiae KENT, with connected spicules and loose spicules only, respectively. The first group in fact included lithistids (*Macandrewia* GRAY) as well as Hexactinellida. These were removed by CARTER, who changed the names to Vitreohexactinellida and Sarcohexactinellida, now called families, and added a third group, Sarcovitreohexactinellida, for forms with spicules united in only part of the body. His Sarcohexactinellida is of interest because of microscleric divisions Birotulifera and Rosettifera, adopted by SCHULZE (1887b) as Amphidiscophora and Hexasterophora. MARSHALL thought that some dictyonines are distinguished by a continuous system of axial canals in the beams of the skeletal framework and called these Synauloidea, as opposed to other Hexactinellida comprising Asynauloidea. In fact, the canals originate in dead specimens by secondary internal solution, enlarging the true axial canals of incorporated spicules to the point of coalescence.

ZITTEL (1877b) rejected these classifications and proposed suborders Dictyonina and Lyssakina, distinguished by the dictyonine and lyssacine types of parenchymal skeleton. These morphological terms derive from the names of his taxa, with spelling Lyssakina changed to Lyssacina by SCHULZE (1887a, 1887b).

In SCHULZE's *Challenger* system, ZITTEL's Dictyonina and Lyssacina (in this spelling) were accepted but subdivided on the basis of microscleres. The Lyssacina comprised tribes Hexasterophora and Amphidiscophora having, respectfully, hexasters (rosettes) but not amphidiscs and amphidiscs but not hexasters. The Dictyonina, with hexasters but not amphidiscs, were divided into Uncinataria and Inermia according to the presence or absence of uncinates; and the Uncinataria were divided into subtribes Clavularia and Scopularia, with sceptrules in the form of nail-like clavules and broomlike **scopules**, respectively. In later work (1899, 1904), SCHULZE gave up ZITTEL's taxa, dividing all Hexactinellida directly into Amphidiscophora and Hexasterophora. These are the main divisions currently accepted by zoologists, and they were ranked as subclasses by REID (1958a), as they are herein.

Another innovation by SCHULZE (1887a, 1887b) was the introduction of the name Triaxonia as a substitute for Hexactinellida. The diagnostic concept implied is the same in both instances, since the triaxon character of the spicules is the basis of SCHMIDT's (1870) original diagnosis; but the name Triaxonia was used by SCHULZE in connection with his theory of sponge phylogeny, in which two stocks of siliceous sponges called

Triaxonia (Hexactinellida) and Tetraxonia (choristid Demospongea) were supposed to have arisen independently from sponges without spicules. These names were used in SCHRAMMEN's work (1910, 1912, 1924a, 1936), and more recently by LAGNEAU-HÉRENGER (1962) and REZVOI, ZHURAVLEVA, and KOLTUN (1962), but the theory they depended on is doubtful; tetraxons do not occur in Hexactinellida, but triaxons occur in various demosponges, as shown long ago by SOLLAS (1888).

SCHULZE's (1899) rejection of ZITTEL's taxa left the lyssacine Hexasterophora and former Dictyonina grouped together without separation above family-group level. IJIMA (1903) suggested a division into unnamed tribes A, B, and C, consisting respectively of the lyssacines and SCHULZE's Inermia and Uncinataria. He also rejected derivation of dictyonines from the lyssacines as claimed by SCHULZE (1887a, 1887b) on grounds that parenchymal megascleres of the latter are of various types, always including rhabdodiactines, whereas those of dictyonines are normally all hexactines and never include rhabdodiactines.

SCHRAMMEN (1902) had suggested dividing the Hexactinellida (Triaxonia) into suborders Stauraktinophora, Hexaktinophora, and Lychniskophora, with the parenchymal megascleres typically stauractines in the first, including simple hexactines and their variants in the second, and specially modified hexactines called lychniscs in the third. The last group (Lychniskophora) depends on the fact that some dictyonines have the central parts of dictyonalia enclosed by an octahedral framework of 12 anaxial buttresses, which grow across the angles between the rays from points equidistant from the center. These dictyonalia are called lantern-spicules or lychniscs. No comparable structures are known in other Hexactinellida. Shortly afterward, SCHRAMMEN (1903) dropped the first group and renamed the others Hexactinosa and Lychniscosa as divisions of SCHULZE's Hexasterophora. Lyssacines, then included as Hexactinosa, were removed in 1912 so that this group then consisted of dictyonines only. This scheme was accepted by IJIMA (1927), whose last work, published six years posthumously, also characterized the lyssacine Hexasterophora as Lyssacinosa. A similar scheme given by SCHRAMMEN (1924a) used independently the new termination -aria (e.g., Hexactinaria), now used by REZVOI, ZHURAVLEVA, and KOLTUN (1962). SCHRAMMEN also divided Amphidiscophora into Amphidiscaria and Hemidiscaria, the former comprising forms with typical amphidiscs, the latter based on fossil occurrence of hemidisc microscleres, unknown in the modern forms. REID (1958) used this arrangement with the Amphidiscophora and Hexasterophora ranked as subclasses, with the orders Amphidiscosa and Hemidiscosa in the former and Hexactinosa, Lychniscosa, and Lyssacinosa in the latter. That classification scheme is followed herein, with the exception that the additional order Reticulosa is used to include many Paleozoic dictyosponges. MORET (1926b), however, preferred to retain ZITTEL's taxa in paleontology, because classification of fossils by microscleres is not normally possible, and he used the Lyssacida and Dictyonida. The Hexactinosa and Lychniscosa, however, can be recognized from their megascleres only, and they are used as subdivisions of the Hexasterophora.

DE LAUBENFELS (1955) accepted the Hexactinosa and Lychniscosa as separate orders, using the names Dictyida ZITTEL and Lychniskida SCHRAMMEN for them. While these are acceptable as separate orders on grounds of their supposed separate origin (IJIMA, 1927), equation of ZITTEL's Dictyonina (as Dictyida) with SCHRAMMEN's Hexactinosa is contrary to usual practice and is not thought desirable.

PALEOZOIC HEXACTINELLIDA: MORPHOLOGY AND PHYLOGENY

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ORGANIZATION OF THE PALEOZOIC RETICULOSID SKELETON

The simplest reticulosids, which constitute most of the early forms from the Cambrian, are conical to spherical with a very thin body wall surrounding a large interior space or cloaca. In the conical forms the wider end is open as a broad osculum; in some spheroidal forms there is seemingly no osculum at all. The body wall is most often composed of stauractines, in some sponges of pentactines or hexactines, that lie parallel to one another in the plane of the body wall. They are of several sizes and usually organized as follows: the largest are quincuncially arranged, tip to tip in vertical and horizontal series, so that **quadrules** are formed, outlined by the length of one ray. A stauractine one-half the diameter of the largest occupies each such quadrule, dividing it into four smaller quadrules. Each of the smaller quadrules is similarly occupied by a third order of stauractine, and so on to a fourth or fifth order. Spicules of each size, except the largest, have their centers quadrately arranged. Sometimes the rays overlap within each order rather than being tip to tip. RIGBY (1966a, p. 554) has noted a species of *Protospongia* in which the largest spicules are quadrately arranged or, in other words, as though the largest, quincuncially arranged series were missing. This nearly monolayered sheet of stauractine spicules in parallel arrangement persists as a dermal (**autodermal**) layer in most Paleozoic reticulosids, even in those forms in which a layer of irregularly arranged parenchymal spicules forms most of the thickness of the body wall. There are some genera of thick-walled sponges in which this outer quadrate layer seems to be missing, but whether the loss is phylogenetic or merely taphonomic cannot always be ascertained.

It is worth noting that spicules of any one size in these quadrate sheets lie in linear series parallel to their rays. This seems to be a fundamental relationship, for it reappears in the Mesozoic and later dictyonine skeleton, where, as REID (1958a, p. xxv) pointed out, the unit of construction is a fused, linear series of equally sized hexactines. There is some evidence that this may reflect a fundamental morphogenetic process, even in the unfused spicules of the Paleozoic reticulosid sponges. Some specimens of *Hydnoceras* and other dictyosponges have healed injuries in which the new growth includes long, curving lines of stauractines at variance with the original quadrate mesh that must have been formed as a linear series by addition of spicules at one end (Fig. 49). This suggests that the normal quadrate mesh described above grows by addition of spicules of like size at the upper end of each vertical series and that as the sponge expanded upward, new series were formed by branching or were intercalated between the old. It would be of interest to investigate, in specific groups of sponges, whether this was accomplished by addition of the next smaller order of size, or whether new series of several sizes are intercalated. The suggestion of FINKS (1960, p. 104, 134) that in some species smaller spicules have been inserted in each quadrule as the sponge expanded, would be a completely different mode of growth involving growth over the entire body rather than at the upper or growing edge. It is possible that both kinds of growth occurred in different species or even in the same species. The ultimate cause of the rectangularity of hexactinellid spicules and spicular meshes appears to be the

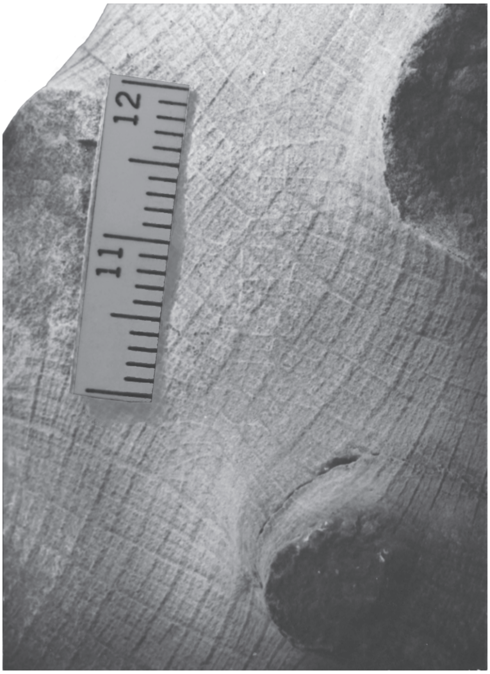

FIG. 49. *Hydnoceras tuberosum* HALL & CLARKE, 1899; healed section of skeleton with curved lines of spicules at angles to original skeletal structure to right of scale, Queens College No. 4, topotype, Devonian, New York, USA, ×2 (new).

crystallization in a cubic or tetragonal symmetry of the protein making up the axial fibers of the spicules (the fibers are square in cross section) formed within the scleroblast cells and genetically determined (REISWIG, 1971). Their formation in long lines, however, seems to require an independent cause at the cellular or syncytial level.

OKADA (1928) has shown that juvenile sponges of the living *Farrea occa* have the form of a thinly walled sphere with a skeleton of stauractines. The choanocyte membrane lines the inner cavity; that is, the sponge is asconoid. In shape and spiculation the juvenile *Farrea* resembles many Cambrian reticulosids, and it is not unreasonable to conjecture that these were also asconoid, as DE LAUBENFELS (1955) suggested. Persistence of a quadrate skeleton of stauractines as the outermost layer in thickly walled forms, in which an inner parenchymal layer of different organization may be present, suggests that the entire skeleton of the early forms is homologous to a dermal skeleton. This has been suggested by SOLLAS (1880a), REID (1958a, p. xlii), and RIGBY (1969, 1983b, 1986a).

It is possible that thinly walled forms in which the spicules are hexactines were no longer asconoid, for the proximal rays might have helped to support diverticula of the choanocyte membrane. This seems certainly to be true for species like *Multivasculatus ovatus* HOWELL & VAN HOUTEN, 1940 of the Late Cambrian (see FINKS, 1970), in which the skeleton is composed of several layers of hexactines. It is probably true of some thinly walled mid-Cambrian forms as well. Such a structure could have supported the simple or compound thimblelike diverticula of the choanocyte membrane characteristic of adult living hexactinellids. *Hintzespongia* RIGBY & GUTSCHICK, 1976 almost certainly has such diverticula, for beneath an outer layer of stauractines there is a thin layer of hexactines that are arranged irregularly about circular openings that were either exhalant canals leading from the choanocyte chambers or else contained the chambers themselves.

In most Paleozoic reticulosid hexactinellids the principal skeleton is a parenchymal one that lies beneath the dermal quadrate layer. There are so many variants that to list all the known arrangements is less than clarifying . Nevertheless some broad groupings of structure can be recognized and may indicate phylogenetic relationships. (It must be confessed, however, that we are not certain as to how much convergent evolution there has been.) In one such group the spicules of the parenchymal skeleton lack a parallel arrangement but are irregularly disposed about radial tubes, which appear to be inhalant and exhalant skeletal canals. These tubes may branch and often connect with smaller, more irregular skeletal canals; but for the most part they are straight, parallel, subequal, and penetrate completely or nearly the entire sponge wall. The simplest form of this skeletal type occurs in the mid-Cambrian *Hintzespongia* Rigby & Gutschick, 1976 (probably also in the Ordovician *Cyathophycus* Walcott, 1879 and *Teganium* Rauff, 1893), in which the canalized parenchymal layer is approximately one spicule thick, beneath a similarly monolayered quadrate dermal layer. In the mid-Ordovician *Brachiospongia* Marsh, 1867 the parenchymal layer is not only many spicules thick but also is bounded by enlarged hypodermal and hypogastral spicules. In the Devonian *Pelicaspongia* Rigby, 1970a and a number of similar genera, the outer quadrate dermal layer seems to be missing, and in the Pennsylvanian and Permian *Stioderma* Finks, 1960 the hypodermal spicules develop sutured interlocking and fusion that forms a rigid net. The Ordovician *Pyruspongia* Rigby, 1971 appears to be a related type that possesses hypodermalia but lacks skeletal canals and the quadrate dermal layer.

In another type, the parenchymal skeleton consists of a cubic mesh of hexactines, scarcely to be distinguished from the dermal layer. The Late Cambrian *Multivasculatus* Howell & Van Houten, 1940 and the Permian *Microstaura* Finks, 1960 have this type of skeleton and are two genera that are probably not closely related.

In a third type the parenchymal skeleton consists of bundles of spicules, vertical and horizontal, in alternating layers. In many Devonian and Mississippian dictyosponges there is but one vertical and one horizontal layer, seemingly of rhabdodiactines. In the Pennsylvanian and Permian *Stereodictyum* Finks, 1960 there are numerous such layers, and they seem to be composed of long-rayed hexactine derivatives in which two or more rays are suppressed.

In a fourth type, related to the preceding, enlarged hypodermal pentactines or hexactines are present between the autodermal quadrate mesh and the underlying layer of spicule bundles. They are parallel to the other spicules and their rays are accompanied by smaller **comitalia,** usually monaxonic. Some Devonian and Mississippian dictyosponges and possibly also some Permian genera are of this type, such as *Endoplegma* Finks, 1960 and *Carphites* Finks, 1960, in which the inner layer of bundles is composed of tauactines. The Permian docodermatids may be secondarily irregular derivatives of this type, with some species developing interlocking and fusion of the hypodermalia to form a rigid net.

A fifth type, represented only by the Permian *Pileolites* Finks, 1960, has linear series of fused hexactines, the series in nonparallel arrangement, and connected by synapticulae. This may not be a reticulosid at all, but rather an aulocalycid hexactinosan.

The Ordovician *Hydriodictya* Rigby, 1971 is a primitive, thinly walled form in which a second quadrate mesh lies beneath the dermal layer but at an angle to it. It is not clear whether this inner layer should be considered parenchymal or gastral. The Ordovician *Dierespongia* Rigby & Gutschick, 1976 is a similarly two-layered form, but the inner layer is irregular rather than quadrate.

FIG. 50. Enlarged part of dermal surface of holotype of *Docoderma papillosum* FINKS, 1960, showing small, star-shaped dermalia with numerous stubby, branching, tangential rays, between larger papillate hypodermal pentactines, PU 78885, Leonardian Bone Springs Limestone, Apache Canyon, Van Horn quadrangle, Texas, USA, ×2 (Finks, 1960).

SPECIALIZED SPICULES

Most spicules in Paleozoic reticulosids are hexactines or derivatives by reduction with simple, smooth rays. They may be accompanied by more elaborate spicules that, in many instances, appear to have been modified for special functional needs. These specialized spicules are of the following sorts: (1) enlarged hypodermal and hypogastral spicules, (2) small comitalia, (3) microscleres, (4) prostalia, including root-tuft spicules (basalia), pleuralia, and marginalia.

HYPODERMALIA AND HYPOGASTRALIA

These are usually pentactines in which the ray facing the bounding membrane (gastral or dermal) has been suppressed or reduced. They are almost always larger and stouter-rayed than the parenchymal spicules, and they frequently bear species-characteristic protuberances on the outward-facing surfaces of the tangential rays. The dermal and gastral varieties may be identical, but often the dermal are larger, and the protuberances, if any, are different on the two sorts. The function of these spicules seems to be supportive and protective, which accounts for their large size and external projections. In some late Paleozoic species they may develop special interlocking processes, sometimes accompanied by actual fusion, which results in a rigid skeleton. In the two genera in which this is known (*Stioderma, Docoderma*) the interlocking is accomplished by branching processes in the tangential plane, which are external to the regular paratangential rays. Sometimes two different forms of enlarged hypodermalia occur together as in *Docoderma papillosum* FINKS, 1960 from the Permian (Fig. 50).

COMITALIA

These smaller spicules parallel and accompany the rays of the hypodermal, hypogastral, and parenchymal spicules. They are most often monaxonic. They may be simple, smooth rhabdodiactines with pointed ends. In many members of the Dictyospongiidae described by HALL and CLARKE (1899) they include curved monaxons with blunt ends, like strongyles of the demosponges, although presumably derived from hexactines by suppression of rays. Some are so stout as to resemble beans. They have also been found in genera belonging to other families, such as the Permian *Docoderma* and *Carphites.* Tauactines also occur as comitalia in the last two genera. Another group of spicules occurring as comitalia are small or undeveloped varieties of specialized prostalia found in the same individual. These include **clemes**, normally occurring in root tufts, where they have anchorate terminations. They also include anchor-shaped anadiaenes with short shafts. Such spicules may also occur in more elongate form in root tufts, but more often they seem to be pleuralia, in which function they protrude from the sponge surface in closely packed masses. As reported from some dictyosponges by HALL and CLARKE (1899), however, they accompanied internal spicule bundles. Like microscleres, comitalia may occur throughout the sponge even though they may have originated to perform a localized special function.

MICROSCLERES

Restudy of the type specimens of dictyosponge genera of HALL and CLARKE has revealed that **paraclavule** microscleres occur in closely packed masses at the sponge surface, with the umbellate ends facing outward (Fig. 51). This is especially well illustrated in the holotype of *Cleodictya mohri* HALL, 1884 but occurs also in the original specimen of one of HALL and CLARKE's illustrations of *Physospongia dawsoni* (WHITFIELD) (HALL & CLARKE, 1899, pl. 62,*9*). It appears that these spicules formed a protective dermal armor. Amphidiscs of living hexactinellids occur in the same position (REID, 1958a, p. xxx). This discovery strengthens the inference that paraclavules are ancestral to amphidiscs and explains their original asymmetry. If they were selected originally to serve a protective function the umbel would be needed on one side only. (They may have served chiefly to discourage the settling of larvae, like other small protruding spicules, a need that has given rise to pedicellariae and avicularia in other phyla.) The oldest known paraclavules are Mississippian. By the Pennsylvanian, both **hemidiscs** (a paraclavule with a smaller umbel at the other end) and amphidiscs (equal umbels at both ends) appeared. *Microhemidiscia* KLING & REIF, 1969 has hemidiscs, *Uralonema* LIBROVICH, 1929 has amphidiscs, and *Itararella* KLING & REIF, 1969 has both (see their fig. l*f*). Paraclavules went extinct in the Permian (see FINKS, 1960, p. 127), hemidiscs until the Cretaceous (see SCHRAMMEN, 1924a; ORTMANN, 1912). Why amphidiscs should have persisted is difficult to explain; perhaps they save the sponge energy in the process of protruding an umbellate end (the spicule would never need to be rotated through more than 90 degrees).

FIG. 51. Photomicrograph of part of dermal surface of holotype of *Cleodictya mohri* HALL, 1884, with closely spaced paraclavule microscleres at dermal surface, with umbellate ends facing outwardly, between vertical megasclere tracts, Carboniferous Keokuk Group, Crawfordsville, Indiana, USA, ×40 (new).

If paraclavules are accepted as ancestral to amphidiscs, a possibility originally suggested by REID (1958a, p. xxxii), it may aid us in reconstructing phylogenetic relationships. REID (1968b, p. 1,247) has pointed out that *Hyalostelia* ZITTEL, 1878c resembles the living amphidiscophoran family Pheronematidae in having "large pentactine hypodermalia, and parenchymal megascleres which are mainly hexactines or pentactines." He continued, ". . . but these forms have pinular autodermalia and autogastralia, and the basalia are bidentate monactines whose shafts may be developed as 'clemes'." The Dictyospongiidae are now interpreted to have paraclavules (i.e., protoamphidiscs), tripinuli (HALL & CLARKE, 1899), clemes and bidentate anchors (anadiaenes) (HALL & CLARKE, 1899), as well as large pentactine hypodermalia in some genera (*Acloeodictya, Lebedictya*). The Permian *Eudoplegma ("Carphites") diabloense* (FINKS, 1960, p. 127) has large pentactine hypodermalia, bidentate anchors, and paraclavules and, like the related cleme-bearing *Dococderma,* has the curved, strongyle-like comitalia also found in the dictyosponges. Thus the dictyosponges, the Permian dococdermatids, and perhaps such other late Paleozoic hexactinellids as *Hyalostelia* and *Stioderma* may not be so far removed from the living Amphidiscophora as once thought.

There are other complications, however; *Griphodictya* HALL & CLARKE, 1899, *Itararella* KLING & REIF, 1969, and *Endoplegma ("Carphites")* (FINKS, 1960, p. 127) have paraclavules (amphidiscs in *Itararella*) occurring with hexasters. It is possible, as suggested originally by the authors of the last two genera, that the co-occurrence is fortuitous (i.e., one or both washed in). It is also possible that the present mutual exclusion of the two microsclere types was not true of some Paleozoic groups and also that the pheronematid characters cited above were once more widespread.

The hypothesis that paraclavules are precursors to the amphidiscs is supported or at least not contradicted by the geologic history of other siliceous spicule types. Among the demosponges the monaxon is the first spicule type to appear in the geologic record even though the potentiality to form tetraxons was present from the beginning in the triangular cross section of the axial canal (REISWIG, 1971). Likewise, among the hexactinellids the first spicules to appear are stauractines, the fully developed hexactines not appearing until later. Thus there seems to be a pattern of initially not realizing fully, or perhaps suppressing the potentialities of a given spicule form.

PROSTALIA

The earliest hexactinellids preserved whole from the Cambrian bristle with protruding spicules. Thus, the presence of prostalia is a fundamental feature of the class. Because they cover the entire body as pleuralia, they seem to provide protection, probably discouraging both predation and settlement of larvae. A fringe of **marginalia** about the osculum is also present in Cambrian forms and seems to have evolved so as to prevent entrance into the cloaca by commensals. The marginalia may also enclose the stream of waste-water issuing from the cloaca, preventing its premature dispersion and recycling by the sponge. They, thus, might function as an oscular chimney in the manner analyzed by BIDDER (1923). Basalia or root-tuft spicules are also found in these early sponges. Unlike later forms, they seem to consist of only a few spicules, although they may be very long. All varieties of prostalia in these Cambrian hexactinellids (that is, pleuralia, marginalia, and basalia) appear to be simple rhabdodiactines without special terminations, spines, or other modifications. It is possible that some pleuralia may have been pentactines with an elongate distal ray. The only specialized spicules in these sponges are the stout elements twisted together like strands of rope, known as *Kiwetinokia* WALCOTT, 1920, that were probably basalia (see also *Palaeosaccus* HINDE, 1893a).

Stouter bundles of basalia are known from the Ordovician on. The oldest seem to be *"Hyalostelia" explanatum* (HICKS, 1869) from the Tremadoc (HINDE, 1888, p. 110). (*Pyritonema* M'COY, 1850, *Acestra* ROEMER, 1861, and *Hyalostelia* ZITTEL, 1878c were founded wholly or partly on isolated Paleozoic root tufts.) By the Trentonian very large root-tuft bundles of *Pattersonia* MILLER, 1882 occupy much of the sponge. Examination of similar root tufts of near topotypes with excellent preservation, which may belong to *Pattersonia,* have a few clemate spicules with a quadrianchorate termination, apparently the first appearance of specialized basalia; most of the spicules in these tufts are smooth, presumably rhabdodiactines, and have simple pointed terminations where the tips are visible. Large root tufts with accompanying hexactines are also known from a perireefal facies of the earlier Chazy Series (FINKS & TOOMEY, 1969 and unpublished). It is of interest to note that *Pattersonia* occurs in the same beds as *Brachiospongia,* which supported itself above the same soft sea floor on fingerlike, hollow, radiating protuberances of the body wall, rather resembling mangrove roots. Apparently root tufts were not the only successful hexactinellid response to identical conditions; in the later Paleozoic root tufts remained common, while the *Brachiospongia* type of adaptation did not occur again until the Mesozoic and Tertiary.

Among the diverse Devonian and Mississippian dictyosponges, surprisingly few genera have been found with root tufts, although the general shape and spiculation suggest their presence. Only *Dictyospongia* Hall & Clarke, 1899 and *Retifungus* Rietschel, 1970 have been found with root tufts attached, but the rather similar *Prismodictya* Hall & Clarke, 1899 and *Hydnoceras* Conrad, 1842 have not, despite their local occurrence in great numbers. Furthermore, no unattached root tufts have been found associated with them. Nevertheless, the strong inner vertical bundles of long spicules found in most dictyosponge genera could be the upper ends of root-tuft basalia as they seem to be in *Retifungus,* but we must also accept the strong possibility that in most of the dictyosponge genera they were not. One additional feature that suggests the connection of the vertical bundles with root tufts is the occurrence in some of them of clemes and short, bidentate anchors (*Physospongia, Cleodictya, Acloeodictya,* and *Lyrodictya*), which in other genera are specifically root-tuft spicules with obviously functional anchorate ends. It is possible, however, that they are vestigial in their occurrences with the dictyosponges.

Two dictyosponge genera, *Thysanodictya* Hall & Clarke, 1899 and *Phragmodictya* Hall, 1884, had definitely flat putative bases, surrounded by an outwardly and supposedly downwardly directed frill or **periloph,** which in this interpretation would have served in place of a root tuft. This structure is not, however, composed of basalia but is an apronlike extension of the quadrate mesh of autodermalia and apparently composed of stauractines. There is a possibility that these genera have been restored upside down, and that the supposed basal disc is rather an oscular sieve surrounded by a frill as in some species of the living *Euplectella.* This is certainly a possibility in the instance of *Thysanodictya hermenia* (Hall & Clarke, 1899, pl. 40) and *T. scyphina* (Hall & Clarke, 1899, pl. 42,*8*) in which the supposed upper end is strongly contracted rather like a basal apex.

The short-shafted bidentate anchors (anadiaenes) in the dictyosponges could have been pleuralia. They seem to serve this function in a Permian species ("Lyssacine, species 1" of Finks, 1960, p. 112) known only from fragments, where they occur over large areas of the sponge surface, closely packed together as a kind of dermal armor rather like the paraclavules in some dictyosponges. Their anchorate ends, which lack axial canals and are therefore not rays, are perpendicular to the sponge surface and often parallel to one another in local clusters with larger anchors in the center of the cluster. Such anchorate pleuralia are obviously homologous with anchorate basalia. It is likely that this spicule type was originally selected for its anchoring function in basalia but that its equal usefulness in a protective function caused shorter-shafted versions to be selected as pleuralia.

Reid's (1958a, p. xxxiii) suggestion that the continuity of basalia with a lateral covering of pleuralia is a primitive condition seems to be borne out by the fossil record. The earliest whole hexactinellids (mid-Cambrian) have a more or less continuous covering of simple rhabdodiactine prostalia with the basalia distinguished from the pleuralia solely by their greater length. Reid's further suggestion (1958a) that basalia arose by modification for attachment of some members of an original covering of pleuralia in an originally basiphytous sponge may not be correct, however. It is certainly not likely to be so in the instance of anchorate pleuralia, for their shape is obviously related to an original function as basalia. Even among the simplest rhabdodiactine prostalia, the earliest

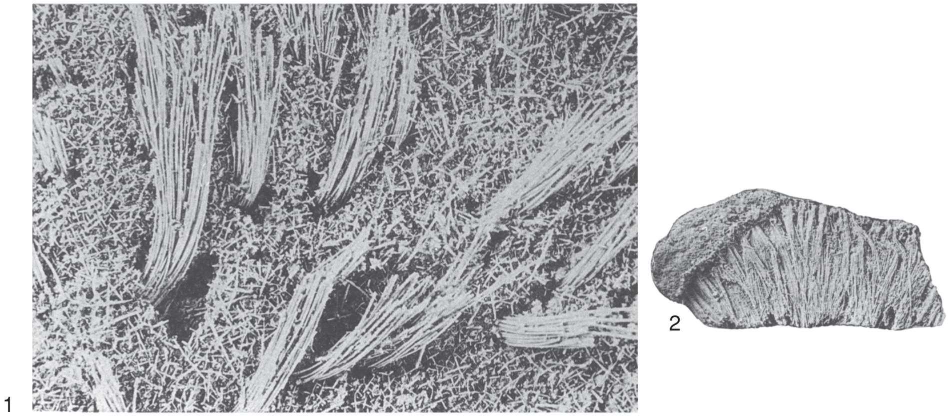

FIG. 52. *1,* Enlarged part of exterior of paratype of *Polylophidium discus* FINKS, 1960, showing dermal layer of pentactines and stauractines of various sizes pierced by tufts of monaxon pleuralia, ×5; *2,* fragmentary specimen with part of dermal layer removed to show coalesced, continuous, radiating mass of spicules in sponge interior, AMNH 28076:1, Word Formation, Word Ranch, Glass Mountains, Texas, USA, ×1 (Finks, 1960).

mid-Cambrian sponges either have longer basalia already differentiated, or the prostalia are of equally great length.

In some later forms, such as the Permian *Polylophidium* FINKS, 1960, the pleuralia are gathered into local tufts all over the sponge surface (Fig. 52.1), with a much wider, ring-like tuft providing attachment; all the tufts coalesce on the sponge interior into a continuous radiating mass of spicules (Fig. 52.2), and it is evident that the pleuralia and basalia had a common origin. The numerous tufts of the Devonian *Polylophalis* REIMANN, 1945a appear to be all basalia. HALL and CLARKE (1899) stated that many of the dictyosponges have tufts of pleuralia arising either from nodes, as in *Hydnoceras,* or from the intersections of vertical and horizontal spicule bundles, as in *Physospongia.* Examination of the type specimens indicates that in at least some of these it is not clear whether they are truly pleuralia or simply sprung-out portions of the internal horizontal spicule bundles brought about by crushing of the specimen due to burial.

The erect lamella that HALL and CLARKE (1899) interpreted as being present on the surface of such dictyosponges as *Clathrospongia* HALL, 1884 need comment. These are supposed to be extensions of the dermal quadrate mesh of stauractines perpendicular to the sponge surface along the traces of the major and minor quadrules. HALL and CLARKE believed that these, in turn, had lamella perpendicular to them, so that a three-dimensional cubic boxwork of lamella existed above the original dermal surface of the sponge (HALL & CLARKE, 1899, pl. 49,*6–7*). The evidence for these structures appears to be two-fold: (1) the surfaces of the specimens have pronounced ridges along the major and to a lesser extent along the minor quadrules; (2) at the sides of some specimens the dermal quadrate mesh seems to be prolonged as a kind of flange about one major quadrule wide that lies flat on the enclosing matrix rather than arching over the sediment filling the sponge interior, as the rest of the dermal mesh does. Close examination of many of the type specimens raises questions regarding the interpretation of HALL and CLARKE. The flanges are indeed present, but they could be interpreted as crushed edges of the specimen in which the two sides of the thin body wall were flattened together without sediment between them (or alternatively as flaps laid back along a vertical split). The ridges are also present, but they are nowhere nearly as high as the flanges they are supposed to represent. In at least one instance, the syntype of *Acloeodictya marsipus* illustrated by HALL and CLARKE (1899, pl. 55,*4*)

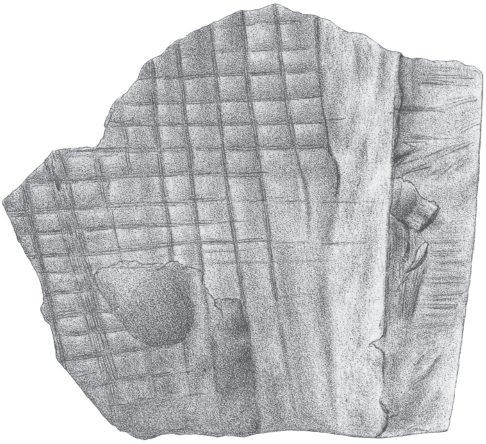

FIG. 53. Enlarged view of part of syntype of *Acleodictya marsipus* HALL & CLARKE, 1899, in which one of larger ridges is formed of vertical rays of large hypodermal pentactines or stauractines with underlying comitalia, Carboniferous Keokuk Group, Crawfordsville, Indiana, USA, ×1 (Hall & Clarke, 1899).

in which the spicules are preserved as pyrite rather than as the more usual impressions in matrix, the largest ridges are formed by the rays of large hypodermal pentactines or stauractines together with underlying bundles of comitalia (Fig. 53). It is possible that all the ridges in the genera considered by HALL and CLARKE to have erect, reticulating lamella (*Clathrospongia, Acloeodictya, Thysanodictya, Lebedictya*) are formed by the rays of large hypodermalia or internal spicule bundles. Because the usual preservation of these sponges is as impressions on the matrix, it is not always possible to be sure of the form of the spicules.

EVOLUTIONARY RELATIONSHIPS AND CLASSIFICATION

It is not unreasonable to regard the thinly walled Middle Cambrian sponges, which are the oldest whole hexactinellids preserved, as a coherent group close to the basic stock of the class. They all have in common a thin outer layer of stauractines or pentactines in parallel orientation that persists as a dermal layer in most later reticulosids. Thus, parallel orientation and lack of fully developed hexactines seem to be primitive features. Distribution of choanocytes that can be inferred from this thin skeletal wall, namely either lining the central cavity or else forming rather short choanocyte chambers between the proximal rays of the pentactines, is what one expects as a primitive feature. The nearly continuous covering of simple, rhabdodiactine prostalia is not necessarily expected but on the evidence of these sponges is also a primitive feature. Most of these early genera (*Protospongia* SALTER, 1864; *Acanthodictya* HINDE in DAWSON & HINDE, 1889; *Palaeosaccus* HINDE, 1893a; and *Diagoniella* RAUFF, 1894) are vase shaped (ranging from spheroidal to conicocylindrical) with an open osculum and with a few of the rhabdodiactine prostalia greatly elongated as basalia. Root tufts would, therefore, also seem to be primitive.

A second group, contemporary with the above, appears to represent a more advanced state. Inside the pentactine layer is an equally thin layer of hexactines not in parallel orientation but arranged irregularly about large, closely spaced circular openings that were probably exhalant skeletal canals. This is the first appearance of a parenchymal layer distinct from the dermal layer. *Hintzespongia* RIGBY & GUTSCHICK, 1976 is the only named genus, but *Ratcliffespongia* RIGBY, 1969 is probably the denuded inner layer of such a sponge. The extent to which a similar layer may have been present but not preserved in sponges of the *Protospongia* group is an open question.

All these early thinly walled hexactinellids have been found in shaly sediments. One might argue that more elaborate hexactinellids also existed at that time in less quiet-water environments but were destroyed prior to burial. It is also possible that the various features of these thinly walled forms were specifically adapted to quiet-water environments. There is some evidence for one or both of these conclusions because very similar thin-walled species not only persisted into the Ordovician Utica Shale, contemporaneous with the very elaborate, thickly walled *Brachiospongia* and *Pattersonia* of other facies but are found also as late as Pennsylvanian in a black shale (Mecca Quarry Shale) above a coal seam. No mid-Cambrian sponges of the complexity of a *Brachiospongia,* however, have been found in nonshale facies, nor have any isolated modified hypodermal spicules been found. The earliest thickly walled Cambrian sponge, *Multivasculatus* HOWELL & VAN HOUTEN, 1940 from nonshaly beds of the Upper Cambrian is still relatively simple and built of unmodified hexactines. Furthermore, even if some features of the thinly walled forms are specific adaptations to quiet water and muddy bottoms, the evident simplicity of their organization and spiculation accords well with their early appearance in the fossil record, in support of their being truly primitive.

Persistent descendants of *Protospongia* with monolayered body walls of stauractines or pentactines may include the late Silurian *Plectoderma* HINDE, 1884a, in which the larger spicules may be superposed to form bundles of parallel rays. Another such descendant may be *Actinodictya* HALL, 1890b from the Upper Devonian, in which the stauractines are extremely large, some more than half the sponge diameter, which itself is considerable; in this genus the stauractines lose their parallel arrangement.

Dierespongia RIGBY & GUTSCHICK, 1976 is an Ordovician form from a limy facies and has developed a separate layer of parallel hexactines. Some other poorly preserved Ordovician sponges may also be related, such as *Stephanella* HINDE, 1891; *Polyplectella* RUEDEMANN, 1925; *Foerstella* RUEDEMANN, 1925; and *Sycodictya* RUEDEMANN, 1925, all from the Utica Shale. Whether the Permian *Polylophidium* FINKS, 1960 is an ultimate descendant of this lineage is not certain, but its general organization is very similar although more complex in its separate tufts and thicker wall.

The special structure seen in the Cambrian *Hintzespongia* RIGBY & GUTSCHICK, 1976 seems to be continued in the equally thinly walled Ordovician genera *Cyathophycus* WALCOTT, 1879 and *Teganium* RAUFF, 1894 from the Utica Shale. There can be no doubt that topotype specimens of the type species of *Teganium* (*Cyathophycus subsphaericus* WALCOTT, 1879) that were illustrated by HALL and CLARKE (1899, pl. 1,*14–22*) under the name of *Sphaerodictya subspherica* (WALCOTT) have exactly the same basic structure as *Hintzespongia,* with an inner layer of hexactines arranged irregularly around circular openings overlain by a quadrate mesh of stauractines. The outer layer of bristling prostalia seen in these specimens of *Teganium* is not known in *Hintzespongia;* but, as discussed above, it is a primitive feature of many Cambrian forms. (The actual type specimens of *Teganium* have no spicules; see FINKS, 1960, p. 111.) *Cyathophycus* is closer to *Hintzespongia* in external form, being conicocylindrical rather than spherical. The spicules of the inner layer are not known, but HALL and CLARKE (1899, pl. 1,*1–13*) showed beneath the outer quadrate mesh a layer of granular pyrite outlining circular openings of the same relative size and distribution as those in the inner layers of *Hintzespongia* and *Teganium.* It is worth noting that all these thinly walled forms are from shales. Thickening of the inner layer with its circular openings and nonparallel hexactines results in a wall structure like that of *Brachiospongia* and *Pattersonia.* As will be discussed below, *Hintzespongia* may have given rise by such a process to these thickly walled contemporaries of *Teganium* and *Cyathophycus,* which were perhaps adapted to a rougher-water environment.

The quadrate mesh of parallel stauractines that forms the principal skeleton of *Protospongia* is not only homologous with the outer layer of *Hintzespongia, Teganium, Cyathophycus,* and their thicker-walled descendants such as *Brachiospongia* and *Pattersonia;* but it also persists as the principal skeleton of another lineage, the great group known as the Dictyospongiidae HALL & CLARKE, 1899. In this family a different type of inner parenchymal layer is developed, namely vertical and horizontal bundles of long spicules, perhaps rhabdodiactines, that parallel the outer quadrate mesh. The beginning of this structure is perhaps seen in the Cambrian *Acanthodictya,* in which vertical bundles of spicule rays, perhaps including rhabdodiactines, run the length of the sponge and are prolonged into the root tuft. This sponge, at least as reconstructed, has a prismatic appearance because of the prominent vertical bundles. It is probably not without significance that the oldest true dictyosponge, *Prismodictya* HALL & CLARKE, 1899 from the upper Silurian (in the form of *Dictyophytra* RAUFF, 1894 and *Phormosella* HINDE, 1889b, *nomina oblita*) has a similar, prismatic, conicocylindrical form.

In the Lower Devonian *Retifungus* RIETSCHEL, 1970 the upper part of the sponge resembles *Prismodictya,* but the lower part is cylindrical and nonprismatic, passing downward into a long root tuft. This may mark the beginning of an evolutionary side branch that led to the cylindrical *Dictyospongia* HALL & CLARKE, 1899 of the Late Devonian and early Mississippian by a process of neoteny, for it is the lower, first-formed part of *Retifungus* that is cylindrical. The order of succession in time is right, and, moreover, the upper ends of large specimens of *Dictyospongia* may have incipient prism faces (HALL & CLARKE, 1899, p. 72). *Microstaura* FINKS, 1960 from the Permian may be a last descendant of this lineage. It, too, is cylindrical with a faint suggestion of prism faces in the largest specimens. The body well is thicker than in earlier dictyosponges by multiplication of the layers of parallel hexactines to form a cubic mesh. Whether this is, in turn, ancestral to Mesozoic dictyonines by fusion of the mesh is an open question. The dictyonines may have had another origin, in a nonparallel mesh, to be discussed below. It should be noted that only in this *Retifungus-Dictyospongia-Microstaura* group have root tufts been found attached to dictyosponges.

Hydnoceras CONRAD, 1842, the first of the dictyosponges to be described and probably the best known, is another likely derivative of *Prismodictya* in which the eight-sided prismatic shape is retained. *Hydnoceras* has horizontal expansions and contractions, each expansion bearing a whorl of eight nodes. The nodes are located at the interfacial angles and vary in size from low peaks to large, pendant, saccular protuberances. They tend to be consistent in form, not only within a single individual but among individuals at a given locality, suggesting either genetically differentiated local demes, a certain amount of environmental control, or both. One might expect that the more elaborately protruded nodes formed in quieter water, where mechanical strength was less necessary and where the need for more intake surface was greater (or perhaps where mechanical considerations did not forbid the packing of more sponge into a given volume of space).

Genera of related shape include *Rhabdosispongia* HALL & CLARKE, 1899, which lack the nodes but have the annular expansions and contractions as well as the prismatic sides that are initially eight in some species but generally more. This genus may have arisen, like *Hydnoceras,* directly from *Prismodictya. Ceratodictya* HALL & CLARKE, 1899 has only the annular expansions and contractions without trace of either prismatic sides or nodes. *Hydnocerina* CLARKE, 1918a is another Late Devonian member of the *Hydnoceras* group, as are the others so far discussed; it lacks prismatic sides but bears whorls of nodes that are more rounded and more closely spaced than those of

Hydnoceras. The Mississippian *Cleodictya* Hall, 1884 resembles a *Hydnocerina* with but one whorl of nodes and may have been derived from it.

Botryodictya Hall & Clarke, 1899 is a Late Devonian to Mississippian nonprismatic sponge with large, saccular protuberances like the most extreme ones seen in *Hydnoceras* but that often split further into two or four subprotuberances. The lower part of the body of *Botryodictya* is a narrow cylinder like *Dictyospongia* (some specimens of *Dictyospongia* might be juveniles of *Botryodictya*), but it expands abruptly into the protuberance-bearing main part of the sponge. It is possible that it arose from *Dictyospongia,* acquiring its resemblances to *Hydnoceras* by convergence; but an origin from *Hydnoceras* by suppression of prism faces (a common change) and elaboration of nodes is more direct.

Interfacial ridges between prism faces in *Prismodictya* and *Hydnoceras* seem to be emphasized by extra large, internal, vertical spicule bundles. Enlargement of these bundles and the similar horizontal bundles may have led to another group of dictyosponges derived from *Prismodictya.* In the one that is closest to *Prismodictya,* namely the late Devonian *Gongylospongia* Hall & Clarke, 1899, each prism face bears a vertical series of alternate protuberances and depressions, separated by the unbroken and rather strong interfacial angles; unlike *Hydnoceras,* the entire sponge does not have expansions and contractions, nor do the nodes occur on the interfacial angles.

Another Late Devonian genus has both vertical and horizontal spicule bundles that outline rectangular spaces. Every alternative horizontal space in alternative vertical rows was occupied by what may have been either a protuberance of the dermal mesh or a parietal gap. If it were a protuberance then the vertical rows would resemble the vertical rows of *Gongylospongia* minus the depressions. It must be admitted that the interpretation of this genus, *Uphantenia* Vanuxem, 1842, is open to doubt. That of the Mississippian *Physospongia* Hall, 1884 is not, however, and its resemblances to *Uphantenia* help in the reconstruction of the latter. In *Physospongia* strong horizontal and vertical spicule bundles outline rectangles that contain alternating protuberances and depressions in both vertical and horizontal directions so as to form a checkerboard pattern. Each vertical row resembles those of *Gongylospongia,* and the pattern of *Uphantenia* would be produced by the omission of alternating vertical rows. These alternating vertical rows that lack protuberances in *Uphantenia* are narrower than the rows that bear protuberances. If they are made narrower still so that they become an interfacial ridge, they produce the pattern of *Gongylospongia.* The sequence *Prismodictya-Gongylospongia-Uphantenia-Physospongia* forms a graded morphological series that is consistent with their occurrence in time, and it may represent an actual phylogenetic sequence.

The presence of vertical and horizontal spicule bundles outlining quadrules larger than the small squares of the stauractine mesh leads to another group of dictyosponges characterized by large quadrules bounded by coarse ridges. The genera of this group in which spicules are actually preserved reveal two kinds of structure: in the Late Devonian *Arystidictya* Hall & Clarke, 1899 and in the early Mississippian *Thamnodictya* Hall, 1884 the large quadrules are outlined by bundles of spicules, possibly rhabdodiactines; in the early Mississippian genera *Lebedictya* Hall & Clarke, 1899 and *Acloeodictya* Hall & Clarke, 1899 the large quadrules are outlined by large stauractines or pentactines whose rays are underlain by bundles of comitalia, possibly rhabdodiactines. The first type of structure may represent merely the second type from which the stauractines have been lost. (Many of the specimens are internal molds from which the entire dermal layer has been lost.) Alternatively the stauractines may have been added in the course of evolution, inasmuch as the second type appears later in time. Hall and Clarke (1899) interpreted the structural elements outlining the large quadrules in *Lebedictya* and *Acloeodictya,* as well as in the similar Late Devonian to early Mississippian genera *Thysanodictya* Hall & Clarke, 1899 and *Clathrospongia* Hall, 1884, to have been erect lamella formed of the stauractine mesh. This has been discussed above and reasons given for doubting their interpretation. Examination of many of the type specimens shows that the large quadrules of *Arystidictya, Thamnodictya, Lebedictya,* and *Acloeodictya* are outlined by spicule bundles, whatever the further contributions of other structures may have been. Thus the whole group may be related to and perhaps descended from the *Gongylospongia-Uphantenia-Physospongia* group.

The Permian genera *Endoplegma* Finks, 1960 and *Carphites* Finks, 1960 have a structure of large pentactines or hexactines in parallel orientation underlain by vertical and horizontal bundles of tauactines. This structure is similar to that of *Acloeodictya* and *Lebedictya,* although the pentactines are very much coarser, as are the inner bundles. Nevertheless, the presence in *Endoplegma "Carphites" diabloense* of a paraclavule, bidentate anchor, and short, curved strongyle-like spicules (Finks, 1960, p. 127), all of which are characteristic dictyosponge accessory spicules (bidentate anchors are known from *Acloeodictya,* paraclavules and strongyles from *Lebedictya*), suggest that *Endoplegma* and *Carphites* arose from this group of dictyosponges by a kind of gigantism. Of the two Mississippian genera cited, *Acloeodictya* is most similar to the Permian sponges, both in its larger pentactines and in its external shape, which is like that of *Endoplegma.*

Mattaspongia Rigby, 1970a from the Late Devonian may be related to this group of dictyosponges. Its large parallel hexactines, occurring in a single layer, are similar in size and arrangement to the large hypodermal pentactines of *Lebedictya* and *Acloeodictya,* and they are similarly accompanied by comitalia of rhabdodiactines.

Another genus from the late Pennsylvanian and Early Permian, *Stereodictyum* Finks, 1960, consists of horizontal and vertical spicule bundles in multiple layers, without any dermalia or hypodermalia. (The type species lacks them, but the early Pennsylvanian *S. proteron* Rigby & Washburn, 1972 is reported to have a fine surficial mesh of hexactines on one specimen.) The sponge occurs in broad, curving sheets, and perhaps the explanate *Thamnodictya* from the Mississippian is near its ancestry. Its origin from this group of dictyosponges involves the loss of dermal and hypodermal spicules and the multiplication of spicule bundle layers. The spicules making up the bundles in *Stereodictum* appear to be largely reduced hexactines in which at least one ray is developed in each of the three axes. Thus the origin might involve the addition of rays to the bundle spicules. Inasmuch as we are not certain that the spicules in the bundles of dictyosponges are rhabdodiactines, there may not be a very great difference in spicule form, after all.

Another group of dictyosponges has a smooth surface without protuberances, ridges, or flat faces. Wherever they are known from sufficiently complete material, the body is cylindrical, often narrowest in the middle, with a wide, sometimes flat base and a wide upper end; they are sometimes vertically fluted. They may have evolved from the *Hydnoceras* group by subduing of annulations and protuberances, comparable to a progression from *Hydnocerina* through *Cleodictya* to *Calathospongia.* Late Devonian members are *Hydriodictya* Hall & Clarke, 1899 and *Corticospongia* Caster, 1939. Mississippian genera are *Calathospongia* Hall & Clarke, 1899; *Lyrodictya* Hall, 1884; *Phragmodictya* Hall, 1884; and *Griphodictya* Hall & Clarke, 1899. In addition, the Mississippian *Ectenodictya* Hall, 1884 appears to be based on a fragment of one of these sponges, according to Hall and Clarke (1899, p. 164–165), probably *Calathospongia.* Two other supposed dictyosponges, *Hallodictya* Hall & Clarke, 1889 and *Cryptodictya* Hall, 1890 from the Upper Devonian, may be similar fragments, but the paucity of spicules makes them somewhat dubious even as sponges. This whole group may be heterogeneous.

Griphodictya, in particular, seems to be different from the other dictyosponges in that its interior is filled with a continuous mass of rhabdodiactines or similar long spicules not organized into separate bundles, at least as preserved. *Phragmodictya* is another special instance with its supposed basal disk and frill; it could be descended from *Botryodictya* by the loss of stalk and protuberances, especially if the diaphragm between body and stalk in *Botryodictya* is homologous to the basal disk of *Phragmodictya.*

Griphodictya brings us to another problem, namely the origin of the Hexasterophora and Amphidiscophora. As mentioned above, *Griphodictya* was reported to contain numerous hexasters along with paraclavules. Oxyhexasters and small hexactine microscleres occur with clemes as early as in the middle Silurian *Corticulospongia* RIGBY & CHATTERTON (1989, p. 41) in the thin-walled euplectellid from Arctic Canada. The Late Carboniferous *Itararella* and the Permian *Endoplegma ("Carphites")* contain what may be adventitious hexasters together with amphidiscs and a paraclavule, respectively. In addition, the Early Carboniferous *Erythrospongia* HUDSON, 1929 apparently contains hexasters along with such dictyosponge-like spicules as bidentate anchors, curved strongyles and possibly clemes, although not paraclavules. If paraclavules are homologous to amphidiscs, which seems probable, then either the supposed hexasters are not true hexasters, or there were sponges in Carboniferous and possibly in Silurian times that contained two types of microscleres that today are mutually exclusive. If so, the two groups, Amphidiscophora and Hexasterophora, may not yet have differentiated one from the other. The Early Carboniferous *Uralonema* LIBROVICH, 1929 is the earliest known sponge to contain true amphidiscs. It is approximately contemporaneous with the hexaster-bearing forms *Griphodictya* and *Erythrospongia* and for that matter with the earliest paraclavule-bearing forms. *Uralonema* seems to be assignable not only to the true Amphidiscophora (that is, the Amphidiscosa) but specifically to the Pheronematidae or close to them due to its possessing dermal and gastral pinules and parenchymal hexactines. Perhaps the true Amphidiscophora arose at this time alongside a persistent earlier group in which amphidiscophoran and hexasterophoran characteristics were still combined.

As for the earliest Hexasterophora, the Early Carboniferous *Erythrospongia* is a possible candidate, but its complement of dictyosponge-like accessory spicules, as well as its somewhat obscure gross morphology, raise some doubts. The Permian *Pileolites* FINKS, 1960 may be a better candidate, but no hexasters have been found in it. Isolated hexasters have been recovered from the sediment associated with the type specimens, however; see FINKS, 1960, p. 142, and pl. 33*b.* Nevertheless, its gross morphology is hexasterophoran-like. Originally described as a euplectelloid (FINKS, 1960), it seems to have even more interesting hexasterophoran affinities. REID's emphasis (1964, p. lxxiii ff.) on the dictyonal strand as the primary unit of organization in dictyonines requires a reexamination of earlier interpretations of its structure.

Pileolites is built of horizontal layers of irregularly crisscrossing, long, spicular strands apparently joined by synapticulae. These strands can be demonstrated in a few places to be composed of more than one hexactine and fused together seriatim with overlapping rays. The strands were originally interpreted as composed of a few hexactines at most, with very greatly elongated rays in the horizontal plane. An interpretation as a fused linear series of many small hexactines with nearly equidimensional rays, however, avoids the assumed discrepant length between horizontal and vertical rays and also accounts for some of the supposed synapticulae as actually hexactinal rays. (Some suppression of rays may have to be invoked, however; for six-rayed crossings are not common.) This permits each horizontal strand to be considered as a dictyonal strand unit. The nonparallel arrangement of such strands occurs in the small, supposedly aberrant, dictyonal group of the Aulocalycidae. It is possible that this group is primitive and that *Pileolites* is the ancestor of the dictyonine Hexasterophora. If so, one should look for still earlier roots among Paleozoic lyssacinosans of irregular spicular arrangement, such as the Brachiospongioidea, and not among the parallel-spiculed protosponge-dictyosponge lineage. It may be that the dictyosponges are closer to the Amphidiscophora and the brachiospongioids to the Hexasterophora.

REID's description of the aulocalycoid skeleton (1964, p. xcii) agrees with the structure of *Pileolites* in almost every detail. In his discussion (p. xciii–xciv) he pointed out the similarities with the euplectellid lyssacinosan skeleton but noted that they lack the parenchymal rhabdodiactines that both he and IJIMA (1927) accepted as diagnostic of Lyssacinosa. By this criterion *Pileolites* could be accepted as a lyssacinosan, since it has such rhabdodiactines along with the aulocalycoid skeleton, and the aulocalycoids could be regarded as descendants that had lost the rhabdodiactines. With this point of view, the aulocalycoids would not be dictyonines, not even the degenerate dictyonines envisaged by REID (1964, p. xciv), but rather a side branch of the Lyssacinosa: degenerate euplectelloids. It may be of heuristic value, however, even if not absolutely compelled by present evidence, to regard *Pileolites* as the Permian beginning of an aulocalycoid grade of dictyonine organization, which ultimately led to the first mid-Triassic dictyonines of euretoid grade.

It is now worth returning to the earliest amphidiscosan, *Uralonema.* The hypodermal and hypogastral hexactines of the Early Carboniferous genus, with their swollen distal and paratangential rays, are nearly identical in size and shape with the corresponding spicules of the Pennsylvanian and Permian *Stioderma* FINKS, 1960, although *Stioderma* lacks the hypogastralia. Both genera possess a large, stout root tuft and possibly also the inward rolling of the dermal layer at the oscular rim (see LIBROVICH, 1929, fig. 1, p. 14, 46). *Uralonema* does not possess the large, circular, parietal gaps characteristic of *Stioderma,* but it is well to remember that specimens of *Uralonema* are only as large as juveniles of *Stioderma* and that in these small individuals of *Stioderma* the parietal gaps are quite small. The pinuli of *Uralonema* do not occur in *Stioderma,* nor do the spinose parenchymal hexactines of *Stioderma* occur in *Uralonema.* Of more interest in the present context, amphidiscs have not been found in *Stioderma.* Nevertheless, the resemblances are sufficient to suggest a close relationship, which would also include the Early Carboniferous *Hyalostelia* ZITTEL, 1878c, as interpreted by REID (1968c), who has likewise suggested such a relationship. The Late Carboniferous *Itararella* KLING & REIF, 1969 also belongs here; it has amphidiscs, but its external form is poorly known. If these four late Paleozoic genera are indeed true Amphidiscosa and, as mentioned earlier here, close to the Pheronematidae of the present day, what can be said of their origins?

Brachiospongia and *Pattersonia,* from the Trentonian (Caradoc), are the earliest known lyssacinosans with differentiated hypodermal spicules. Those of *Brachiospongia* somewhat resemble the hypodermalia of *Stioderma* and *Uralonema* in having a spherical knob in place of the distal ray and in having a distal tubercle on each tangential ray. These enlargements are much less strong than in the later genera; furthermore similar enlargements of varying degree are known from other genera, such as the Silurian *Astroconia* SOLLAS, 1881 and the Permian *Docoderma.* The hypodermal spicules of *Pattersonia* are less well known but were said by BEECHER (1889, p. 26), in describing the junior synonym *Strobilospongia,* to resemble those of *Brachiospongia. Pattersonia* is closer to the late Paleozoic Amphidiscosa in having a well-developed root tuft, which *Brachiospongia* lacks. Indeed, among the thickly walled Paleozoic lyssacinosans with nonparallel parenchymal and hypodermal spicules and with large skeletal canals or parietal gaps, one can distinguish two sorts: open, cup-shaped forms with root tufts and vaselike forms with flat bases and no root tuft. Among the former there are, including *Pattersonia;* the Devonian *Pelicaspongia* Rigby, 1970a; *Pseudohydnoceras* Reimann, 1945a; *Bayviewia* Reimann, 1945a; *Polylophalis* Reimann, 1945a; and *Calicispongia* Reimann, 1945a (the last is not reported to have basalia but resembles the others in form); and the Pennsylvanian *Arakespongia* Rigby, Chamberlain, & Black, 1970. Among the latter there are, including *Brachiospongia;* the Ordovician *Rhaeaspongia* Lamont, 1935; *Colpospongia* Lamont, 1935; and *Pyruspongia* Rigby, 1971; and the Silurian *Malumispongium* Rigby, 1967b; and *Oncosella* Rauff, 1894.

Microscleres are not known from any of these sponges. (The oxyhexaster reported from *Arakespongia* by Rigby, Chamberlain, & Black [1970, p. 829 and fig. 12U] seems too large to be a microsclere and resembles in its spiral ornamentation the spicules of *Spiractinella* Hinde, 1888.) On the basis of the cup shape and root tuft, however, the Devonian *Pelicaspongia* group and perhaps the Pennsylvanian *Arakespongia* may represent a lineage connecting *Pattersonia* with the Carboniferous and Permian Amphidiscosa (*Uralonema, Hyalostelia, Stioderma*). The quadranchorate ends of the basalia in *Pattersonia, Uralonema, Hyalostelia,* and *Arakespongia* are another common feature. If true, the roots of the Amphidiscosa, and perhaps amphidiscs themselves, go back to the Ordovician *Pattersonia.*

In this view, the dictyosponges and their possible dococdermatid descendants represent a sister lineage with some amphidiscophora-like features, especially the homologous paraclavules, but would not be directly ancestral to the Amphidiscosa.

The forms not bearing root tufts also make rather a coherent group. The Ordovician *Pyruspongia,* and the Silurian *Malumispongium* and *Oncosella* are very similar in shape although the Ordovician genus lacks skeletal canals. *Brachiospongia,* also Ordovician, with its radial, rhizophytous protuberances, resembles the contemporary *Rhaeaspongia. Colpospongia,* with its strong radial flutings, is intermediate between its contemporaries, the radially protuberant *Brachiospongia* on the one hand and the slightly fluted *Pyruspongia* on the other. This lineage cannot be traced clearly beyond the Silurian. The Permian *Pileolites* resembles in external form nothing so much as the tip of a *Brachiospongia* protuberance. It is the only Late Paleozoic hexactinellid with a flattish base and no root tuft. As mentioned earlier, it is also characterized by irregularly arranged parenchymal spicules and prominent skeletal canals perpendicular to the surface. The distal ray of its dermal (or hypodermal) spicules is reduced to a spherical knob. If all these similarities to *Brachiospongia* signify a true relationship of descent, it may be that the roots of the true Hexasterophora go back to *Brachiospongia.* Only the recovery of microscleres from these genera can settle the matter. Thus the hypothesis that *Pileolites* is a protodictyonine may make it possible to trace their source to the Ordovician.

The following is a proposed phylogeny that will embody so far as possible these working hypotheses. The line of descent from protospongiids like *Acanthodictya* to the dictyosponges and from them to the stereodictyids and dococdermatids of the Late Paleozoic will have to be accommodated in a single high-level taxon. The order Reticulosa Reid, 1958a is available for this group and was essentially defined for them. (The two Permian families here included were not yet published at that time.) The presence of paraclavules and the principal skeleton consisting of a quadrate mesh of spicules of dermal or partly dermal origin were among the original diagnostic features. As discussed above, this group has strong amphidiscophoran affinities, not the least of which are the paraclavules, here considered homologues of the amphidiscs. For this reason it is here placed into the subclass Amphidiscophora. The possible presence of hexasters in this group necessitates a redefinition of the subclass Amphidiscophora. The order Hemidiscosa may have originated during the mid-Paleozoic from dictyosponges like *Griphodictya* through hemidiscosans like *Microhemidiscia.* (The presence of a hemidisc in the amphidisc-bearing *Itararella* KLING & REIF, 1969, if it is not adventitious from the co-occurring *Microhemidiscia,* suggests an alternative origin by reduction from the Amphidiscosa.)

The remaining order of the Amphidiscophora, the Amphidiscosa, with true amphidiscs, seems to have had a separate origin, going back to the protospongiids by a different lineage. The Late Paleozoic Stiodermatidae appear to be true Amphidiscosa, based on the inclusion therein of *Uralonema,* which has demonstrable amphidiscs. A related group of mid-Paleozoic forms, which can be accommodated in the Pelicaspongiidae RIGBY, 1970a, carry this lineage back ultimately to *Pattersonia* of the Ordovician and probably to still earlier forms known only by their stout root tufts (see HINDE, 1888, p. 110) from at least as far back as the Tremadoc. Both *Pattersonia* and *Brachiospongia* have as their most similar, simpler predecessor the mid-Cambrian *Hintzespongia,* which shares with them the characteristics of a parenchymal layer of nonparallel hexactines organized around prominent skeletal canals. *Hintzespongia,* the very similar Ordovician *Cyathophycus,* and the mid-Cambrian *Ratcliffespongia,* which has only the parenchymal layer and may be a *Hintzespongia* denuded of its dermal layer, can be accommodated in the family Hintzespongiidae FINKS, 1983b.

Where to place the Hintzespongiidae is to some extent a matter of choice. Because they seem equally related both to the pattersoniid line leading to the Amphidiscosa, and to the brachiospongiid line leading to the Hexasterophora, including them in either does not seem appropriate. Their greater similarity to the equally thinly walled Protospongiidae favors their inclusion in the order Reticulosa. The closely similar, spherical Teganiidae would be placed alongside them.

As shown above, the interpretation of *Pileolites* as having an aulocalycoid skeleton enables us to connect the hexactinosan Hexasterophora with *Brachiospongia.* The order Lychniscosa probably originated from the Hexactinosa in Triassic times as suggested by the incomplete development of lychnisc nodes in the first lychniscosan, *Triadocoelia* VINASSA DE REGNY, 1901 from the Carnian. *Brachiospongia* itself and related forms with nonparallel parenchymalia enlarged hypodermalia and no root tuft, which are the Pyruspongiidae RIGBY, 1971 and the Malumispongiidae RIGBY, 1967b, would be included in a revised Brachiospongioidea and would be the earliest members of the order Lyssacinosa. The order Hexactinosa would commence with the Permian *Pileolites.*

Several other Paleozoic forms are not yet accommodated in this scheme. One is the Late Cambrian *Multivasculatus,* which is the first hexactinellid with a cubic mesh of hexactines. Although similar to the protospongiids in its parallel spicules (but not in its encrusting habit) it does not seem to be related to the line that led to the dictyosponges, with their internal spicule bundles and thin walls. It may be ancestral to the Devonian *Titusvillia* CASTER, 1939, which, with its curiously reversed flanges on the branches, might be taken for a *Scalarituba* or other ichnofossil, as CASTER (1939, p. 7) originally did, were it not for the presence of hexactines. The connection with *Titusvillia* is based on the presence in the latter of a cubic mesh of hexactines. CASTER himself expressed reservations concerning a three-dimensional cubic mesh. It is not present in the externally similar *Annulispongia* RIGBY & MOYLE, 1959, which has only a dermal and cloacal layer. Other genera related by external shape include *Armstrongia* CLARKE, 1920; *Protoarmstrongia* CASTER, 1941; and possibly *Aglithodictya* HALL & CLARKE, 1899 and *Iowaspongia* THOMAS, 1922. On the last, I could find no spicules on the holotype, and it may be a burrow. The Multivasculatiidae de Laubenfels, 1955 and the Titusvilliidae Caster, 1939 will accommodate these genera respectively, although if *Aglithodictya* is included with the *Titusvillia* group, the family Aglithodictyiidae Hall & Clarke, 1899 (*nomen translatum*) has priority.

Another early Paleozoic form may be related to the titusvilliids in that it possesses a skeleton composed solely of a dermal and a gastral quadrate mesh, as in *Annulispongia* and possibly *Titusvillia.* This is the Ordovician *Hydnodictya* Rigby, 1971, the sole member of the Hydnodictyiidae Rigby, 1971. Unlike the titusvilliids, the paratangential spicule rays of the gastral mesh are orientated at 45° to those of the dermal mesh.

Still another group characterized by two layers of quadrate mesh, at least in some species, is that including *Dierespongia* Rigby & Gutschick, 1976 and possibly *Stephanella* Hinde, 1891; *Polyplectella* Ruedemann, 1925; *Foerstella* Ruedemann, 1925; *Sycodictya* Ruedemann, 1925; and *Polylophidium* Finks, 1960. These are all characterized by a spheroidal shape and large rhabdodiactine prostalia that extend from the center of the sponge to well past the dermal layer. Rigby and Gutschick (1976) was of the opinion that the spicules of the inner layer in *Dierespongia* were not in parallel orientation. It should be noted that original parallelism of spicules may not be preserved when a small, spheroidal surface is compressed flat upon a bedding plane. In any event, the inner layer of *Dierespongia* is not organized around large, circular openings as in *Hintzespongia, Cyathophycus,* or *Teganium.* Inasmuch as the latter type of organization points toward another line of development, it is desirable to separate such forms from those in which the inner layer is continuous, whether perfectly parallel or not. Thus the concept of the Dierespongiidae should be revised to encompass those spheroidal forms with large rhabdodiactine prostalia radiating from the center of the sponge and with the inner layer not organized about circular openings. For this reason, *Hintzespongia* is here removed from the Dierespongiidae and placed with *Ratcliffespongia* and *Cyathophycus.* The Dierespongiidae, Hydnodictyiidae, and Titusvilliidae seem somewhat related in that they tend to emphasize a dermal and a gastral layer rather than a parenchymal one. They also seem in their prevailingly quadrate arrangement of spicules to be clearly derivable from the Protospongiidae and therefore to find a place among the Reticulosa.

It remains to discuss *Vauxia* Walcott, 1920. This eminently spongelike object, whose elegant colonies grace many museum dioramas of the Burgess Shale sea floor, was originally considered a hexactinellid by Walcott (1920, p. 316). The type specimens and topotype material collected by D. H. Krinsley do not have anything resembling a hexactinellid spicule (see also Rigby, 1986a). Where best preserved, the structure consists of a hexagonal to rectangular net somewhat elongate parallel to the longitudinal axis of the branch. If the hexagons or rectangles are not elongate then the zigzag lines parallel to the longitudinal axis are more strongly impressed into the matrix than the cross connections (see also Walcott, 1920, pl. 82,*1b;* Rigby, 1986a, pl. 1,*4,* pl. 2,*3,* fig. 8–10). This structure seems to be the basis for Walcott's diagram (1920, p. 319, fig. 9) in which one zigzag and its cross connection are taken to be three paratangential rays of a reduced hexactine. In most places the regular hexagonal structure breaks down into smaller, more irregular patterns that have a more curving than polygonal outline. Some of this may be due to superimposition of two layers of skeletal net, but some appear to be the irregular wrinkling due to shrivelling or flexing of a semirigid layer. The pattern is outlined by either grooves or ridges, which have been taken to be the impressions of spicules or the spicules themselves. The entire organism has the form of a branching, tubular sponge. These organisms were interpreted to be keratose sponges by Rigby (1986a).

An outline of the classification of Paleozoic hexactinellids proposed by Finks (1983, p. 109–112) and herein in Table 1.

This scheme of phylogeny and classification differs from that proposed by Rigby (1976b, p. 56, fig. 5) in only two essential features. The Pyruspongiidae are here placed with the Malumispongiidae (because of their similar special shape, nonparallel spicules, and enlarged hypodermalia), while Rigby put them with the Hydnodictyidae. He considered the lack of parietal gaps (that is, circular skeletal canals) more diagnostic of relationship and the development of enlarged hypodermalia (his armored) as a convergent feature. Also the Dierespongiidae are here divided among two families, the Hintzespongiidae, including *Hintzespongia,* and placed with the Teganiidae as Rigby did his Dierespongiidae, and the restricted Dierespongiidae; including *Dierespongia* and *Choia,* and here placed with the Hydnodictyidae. Rigby did not deal with the Amphidiscophora nor with the problem of the origin of the Hexasterophora, two major problems with which the present classification and phylogeny are intimately bound.

The present scheme differs from that of Reid (1958a, p. xlvi, fig. 24) in placing the Reticulosa with the Amphidiscophora and in deriving the Hemidiscosa and the Amphidiscosa from two separate lineages within the Reticulosa, the second from an earlier offshoot that also gave rise to the Hexasterophora Lyssacinosa, and through the latter to the Hexactinosa and Lychniscosa.

A radically different hypothesis of hexactinellid phylogeny could be proposed if elements of the dictyosponge quadrate mesh were regarded as protodictyonine strands. It has been pointed out above (p. 135) that specimens of *Hydnoceras* and other dictyosponges with repaired injuries sometimes have curving strands of the quadrate mesh connecting horizontal with vertical elements of the regular mesh, as though the linear series of spicules were the unit of construction. In all dictyosponges where the individual spicules have been seen (usually as pyritized replacements of the original opal) they have been separate and unfused. Thus dictyosponges seem not to possess true dictyonal strands. In most Devonian forms, however, including *Hydnoceras,* no spicules have been preserved, only their impressions in the sediment. Observations of these molds, including those of the injured areas referred to above, neither confirms nor denies a fusion of the spicules into strands. Even if they were fused, the dictyosponge quadrate mesh would differ from the similarly monolayered farreoid hexactinosan mesh (see Reid, 1964, p. lxxv ff.) in having strands of differing thickness outlining the several orders of quadrules.

Table 1. Outline of classification of Paleozoic Hexactinellids as proposed by Finks (1983b).

TAXON NAME AND LEVEL
Class Hexactinellida Schmidt
Subclass Amphidiscophora F. E. Schulze
Order Reticulosa Reid
Superfamily Protospongioidea Hinde
Family Protospongiidae Hinde
Superfamily Dierespongioidea Rigby & Gutschick
Family Dierespongiidae Rigby & Gutschick
Family Hydnodictyidae Rigby
Family Multivasculatidae de Laubenfels
Family Titusvilliidae Caster
Family Aglithodictyiidae Hall & Clarke
Superfamily Dictyospongioidea Hall & Clarke
Family Dictyospongiidae Hall & Clarke
Subfamily Prismodictyinae de Laubenfels
Subfamily Dictyospongiinae Hall & Clarke
Subfamily Hydnoceratinae Finks
Subfamily Calathospongiinae Hall & Clarke
Subfamily Physospongiinae Hall & Clarke
Subfamily Thysanodictyinae Hall & Clarke
Family Docodermatidae Finks
Family Stereodictyidae Finks
Superfamily Hintzespongioidea Finks
Family Hintzespongiidae Finks
Family Teganiidae de Laubenfels
Order Hemidiscosa Schrammen
Family Microhemidisciidae Finks
Order Amphidiscosa Schrammen
Family Pattersoniidae Miller
Family Pelicaspongiidae Rigby
Family Stiodermatidae Finks
Subclass Hexasterophora F. E. Schulze
Order Lyssacinosa Zittel
Superfamily Brachiospongioidea Beecher
Family Brachiospongiidae Beecher
Family Pyruspongiidae Rigby
Family Malumispongiidae Rigby
Order Hexactinosa Schrammen
Family Pileolitidae Finks

In the Carboniferous dictyosponges, where spicules are often preserved, as well as in the Cambrian and Ordovician

Protospongiidae, the larger quadrules are formed by larger individual stauractines or pentactines. Thus, the whole basis of the dictyosponge skeleton seems to be a nested set of spicules of different size, and it stands in contrast to the uniformly fine **farreoid** mesh. On the basis of presently available evidence, considering the dictyosponge mesh to be ancestral to that of the hexasterophoran dictyonines seems unwarranted. The tendency of spicules of similar size to be produced in linear series seems best regarded as a characteristic of Hexactinellida in general.

Earlier suggestions that cubic-meshed dictyosponges of nearly uniform spicule size, such as the Permian *Microstaura,* could have given rise directly to the dictyonine sponges by fusion of spicules (e.g., FINKS, 1960, p. 102) involve the implicit hypothesis that the dictyosponges were ancestral to at least some of the Hexasterophora. REID's placement of the Reticulosa as a possible offshoot of the Hexasterophora (REID, 1958a, fig. 24, p. xlvi) does not put the dictyosponges into the direct ancestry of the dictyonines but suggests a closer relationship than that of the hypothesis proposed here. REID, however, regarded the quadrate mesh of the Reticulosa as dermal or partly dermal, while the dictyonine skeleton is parenchymal (1958a, p. xliv–xlv); thus, they would not be closely homologous, and any common tendencies to form linear series of spicules would not indicate direct ancestry.

POST-PALEOZOIC LYSSACINOSA

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Post-Paleozoic **lyssacines** are known mainly from modern examples on which this account is based. In zoological classification, they are representatives of the order Amphidiscosa Schrammen of the subclass Amphidiscophora Schulze and the order Lyssacinosa Zittel, as restricted by Schrammen, of the subclass Hexasterophora.

Living Amphidiscosa are exclusively lophophytous sponges with amphidisc microscleres, to which staurodisc or hexadisc variants are occasionally added. Parenchymal megascleres vary from hexactines to rhabdodiactines and may be all of the latter type. Both autodermalia and hypodermalia are normally present. Autodermalia are usually pentactines, with the unpaired ray distal and **pinular;** hypodermalia are larger pentactines, with the unpaired ray proximal and running into the choanosome. The gastral skeleton consists of autogastralia like the autodermalia. Canalaria corresponding with the autodermalia or gastralia may also occur. Basalia are monactinal where their character is known, with a four- or six-armed axial cross at the distal end and a varying number (usually 2 to 8) of solid anchor teeth. Recurved spines are also often present along the shafts of these spicules. Monactinal or diactinal pleuralia or marginalia may also occur.

Three living families of Amphidiscosa are currently distinguished (Ijima, 1927). The Pheronematidae are sponges whose principal parenchymal megascleres are hexactines or pentactines, although other types may also occur, including smaller rhabdodiactines. The basalia are characteristically bidentate, with two recurved flukes only, in line with axial rudiments of a four or six-armed axial cross. Uncinates are common among minor spicules present internally, and spiny monactines called scepters occur as pleuralia or marginalia. The scepters have the axial cross distal and the spines directed distally (not recurved as in the basalia), with a special distal whorl sometimes present.

The Hyalonematidae are sponges whose parenchymal megascleres include prominent rhabdodiactines, although hexactines may also be present. The basalia have grapnel-like ends with four or more recurved teeth in most instances and are usually arranged in a compact glass rope. Uncinates are nearly always absent, and no scepters occur, although the place of the latter may be taken by spiny rhabdodiactines with a central ring of buttonlike rudiments of the four reduced rays.

The third family, the Monoraphididae, comprises *Monoraphis* Schulze, which is distinguished by parenchymal megascleres that are mainly tauactines and by being supported by a single, very large, basal needle, the end of which is unknown.

Fossil Amphidiscosa are known mainly from occasional finds of loose amphidiscs in Mesozoic or Cenozoic sediments. No modern genera have been identified certainly as fossils, although some have been identified by inference from isolated megascleres (e.g., by Hinde & Holmes, 1892).

The living Lyssacinosa were divided by Ijima (1927) into four families, the Leucopsacadidae Ijima, Euplectellidae Gray, Caulophacidae Ijima, and Rossellidae Gray. This arrangement is accepted herein, although with some reservations and with the name Caulophacidae replaced by the senior synonym Asconematidae Schulze. The four families form two groups, with two families in each. Both groups include both basiphytous and lophophytous genera. The Leucopsacadidae and Euplectellidae are united by having simple **dermal skeletons** only, without distinct autodermalia and hypodermalia, and by basalia that are typically umbel-bearing diactines in lophophytous genera. The Asconematidae and Rossellidae have both autodermalia and hypodermalia, and the basalia of lophophytous genera (Rossellidae only) are anchorate pentactines.

The Euplectellidae are generally thin-walled sponges of normally tubular habitus that are either lophophytous or basiphytous. The dermalia are characteristically hexactinal, with a prolonged proximal ray that gives the spicules a swordlike appearance. IJIMA (1903, 1927) distinguished the subfamilies Euplectellinae GRAY and Corbitellinae IJIMA, the latter being a junior synonym of Taegerinae SCHULZE (1887a). The Euplectellinae are lophophytous sponges in which the basalia are typically rhabdodiactines with a terminal umbel at the distal end. The distal ray of the two that lie in line to form the shaft is always shorter than the proximal and sometimes is so short that the spicule is nearly a monactine. The shaft often bears recurved lateral spinules with which the umbel teeth appear to be homologous.

In simple Euplectellinae, e.g., *Holascus* SCHULZE, the wall is imperforate, with a simple parenchymal spiculation. The principalia may be all hexactines, pentactines, or stauractines, arranged in a regular manner with four tangential rays oriented longitudinally and transversely so that these apposed rays enclose square meshes. Rhabdodiactines are present, but only as comitalia.

In more advanced genera, e.g., *Euplectella* OWEN, the wall is pierced by numerous parietal oscula and has a more complex parenchymal spiculation, in which the rays of some spicules may intersect in diagonal directions. In both advanced and simple genera, the terminal osculum may be covered by a secondary sieve plate, which is formed at the end of normal growth and contains special megascleres called oscularia. In some forms, which may have advanced spiculation, all the megascleres are permanently separate. In others they may be fused, either in basal parts only or to varying extents through the upper parts or the whole body. Fusion occurs, in part, by union of the megascleres where they cross and contact one another but, in part, also by formation of synapticula where rays are close together but not in contact. Fusion may affect oscularia, as well as the parenchymal megascleres, but never the dermalia or gastralia.

The Taegerinae (=Corbitellinae IJIMA) are basiphytous sponges, with an encrusting basal skeleton composed of small fused hexactines (basidictyonalia, IJIMA). The parenchymal megascleres are mainly hexactines and rhabdodiactines, the latter generally being predominant. Some (e.g., *Regadrella* SCHMIDT) are thin-walled sponges with parietal oscula and a sieve plate, resembling some Euplectellinae although having the parenchymal skeleton formed mainly from diagonally crossing rhabdodiactines; but others have different habits. The parenchymal megascleres of the basal part are fused to one another and to the basidictyonalia; higher up they may be free or partly or entirely fused. If they are fused up to the oscular margin, the sieve plate if present becomes rigid.

The Leucopsacadidae of IJIMA (1903, 1927) are lophophytous sponges with similar basalia and no hypodermalia, but with autodermalia and gastralia that are all simple pentactines. According to IJIMA (1927), the parenchymal megascleres should be hexactines and rhabdodiactines with the former predominant; but in some of the genera he included the megascleres are mainly or all rhabdodiactines (*Caulocalys* SCHULZE, *Placopegma* SCHULZE, *Chaunangium* SCHULZE).

The Rossellidae are mainly lophophytous, but some are basiphytous sponges with both autodermalia and hypodermalia. The autodermalia are small hexactines, pentactines, or stauractines that may be spiny but never truly pinular and that have the unpaired ray proximal when pentactinal. The hypodermalia are typically much larger pentactines that may be normal pentactines with tangential rays meeting at right angles or partly or all paratropal. The parenchymal megascleres are usually mainly rhabdodiactines, with some additional hexactines or with rhabdodiactines only. The basalia of lophophytous genera are anchorate pentactines with the anchor flukes formed by true rays (not umbel teeth) and with the unpaired ray forming a long shaft that is embedded in the body. Some genera have additional pleuralia that correspond in form with the hypodermalia and originate as hypodermalia that are later protruded through the surface. The overlapped tangential rays of these pentactinal pleuralia then form an external veil outside the dermal membrane. In lophophytes, such spicules may be mixed with the typical basalia, with which they may also intergrade morphologically; correspondingly, the basalia develop with their anchors beneath the dermal membrane and are protruded later. In basiphytous sponges, the base contains a rigid basidictyonal skeleton, with which the lowermost parenchymal megascleres are united; but rigidity does not spread through the rest of the body. Some are stalked sponges, with a rigid stalk supporting a body with loose megascleres only.

Paratropal spicules and octaster microscleres, which have sometimes been found loose in sediments, occur only in the Rossellidae, although not in all genera. The presence or absence of two forms of the rosette group of microscleres (**plumicomes,** octasters) is used by zoologists (Schulze, 1897, 1904; Ijima, 1904, 1927) to distinguish the subfamilies Lanuginellinae, Rossellinae, and Acanthascinae. There are no correlated general differences in the megaspiculation, but paratropal megascleres are restricted to the Rossellinae and Acanthascinae and octasters to the Acanthascinae only.

The Asconematidae are basiphytous sponges with pentactinal hypodermalia, which are not paratropal, and with autodermalia and gastralia that are typically pinular hexactines, sometimes varied as pentactines with the unpaired ray distal and pinular. The parenchymal megascleres are rhabdodiactines and hexactines or the former only, as in Rossellidae. The encrusting base has a rigid basidictyonal network with which parenchymal megascleres of the lower parts are also united; or there may be a stalk with a rigid union of the parenchymal megascleres, although these remain loose in the body above.

An alternative arrangement (Ijima, 1904, 1927; Schulze, 1904) removes the type genus, *Asconema* Kent, to the Rossellidae (-inae), leaving specialized stalked asconematids as a family Caulophacidae (*ex* Caulophacinae Schulze, 1887a). This can be justified on the grounds that the two groups are closely related and that the autodermalia and gastralia of *Asconema* are properly only subpinular; but those of the typical Rossellidae are nonpinular, and rossellids may also be stalked (e.g., *Crateromorpha* Gray).

There are very few post-Paleozoic fossils of the Lyssacinosa, although the group almost certainly ranges back into the Paleozoic (see below). *Stauractinella* Zittel of the Upper Jurassic has been thought to be a euplectellid (Schrammen, 1936) but is known only from hexactine megascleres without diagnostic value. Sponges apparently identical with the living *Regadrella* (Euplectellidae, Taegerinae) appear in the Upper Cretaceous (Cenomanian), with *Proeuplectella* Moret, which is probably an allied form, although incompletely known. *Purisiphonia* Bowerbank comprises thick-walled forms like *Regadrella,* but with the parietal gaps in the form of perforating radial canals. de Laubenfels (1955) included this genus in the Dictyonida (Hexactinosa, Staurodermatidae), but the skeleton is very clearly that of a taegerine euplectellid. Paratropal pentactines like those of some existing Rossellidae (Rossellinae or Acanthascinae) are known from the Turonian and Senonian. Otherwise the group is known chiefly from loose Cenozoic spicules, some of which, although not diagnostic, have been referred to modern genera (e.g., by Hinde & Holmes, 1892).

From Cretaceous sediments, there is evidence of an otherwise unknown group of Amphidiscophora. Microscleres obtained loose from sediments include so-called hemidiscs or **hemiamphidiscs** that resemble amphidiscs but have one umbel larger than the other. In zoological classification the group has been made an order, the Hemidiscosa of the Amphidiscophora (SCHRAMMEN, 1924a; REID, 1958a). How large a group is represented is unknown; there could have been only one species from the evidence available.

Because of the almost blank record, assessment of the past evolution of existing Lyssacida depends on comparative evidence. The first point to note is that division of the Hexactinellida into forms possessing amphidiscs or hexasters is, so far as is known, completely sharp. All living Amphidiscosa have amphidiscs, not hexasters or any other rosette form; all living Lyssacinosa have hexasters, but never amphidiscs. In addition, the Dictyonida agree with the Lyssacida in possession of hexasters but not amphidiscs. Hence, the division into two stocks possessing either amphidiscs and hexasters, respectively, is inferred to be the primary phylogenetic division among forms now surviving. This, however, does not imply that there may not have been other stocks.

Living Amphidiscosa are all evidently closely related, although divisible into two main families, and a third comprising *Monoraphis* only. They share occurrence of pentactinal hypodermalia and of monactinal basalia whose character implies origin from pentactines. By analogy with rossellid Lyssacinosa, the basalia probably arose from hypodermalia. The Pheronematidae can be regarded as relatively primitive, because of the greater importance of hexactines or pentactines as parenchymal microscleres. In the Hyalonematidae the rhabdodiactines are often predominant and also have specialization of basalia to form glass ropes (e.g., in *Hyalonema* GRAY). Concentration of basalia as an anchor rope is correlated with increase in size but reduction in number of spicules (REID, 1958a). The family also lacks the scepter (see the Pheronematidae, *Treatise Part E (Revised),* vol. 3, in press). *Monoraphis* carries basal specialization to the extreme but seems to be closely related to the Pheronematidae because scepters are present.

The Lyssacinosa include two groups of sponges that have no obvious point of contact. The Euplectellidae and Leucopsacadidae lack hypodermalia, and basalia of lophophytes are typically umbel-bearing rhabdodiactines. Similar spicules may occur in the parenchymal skeleton, e.g., in *Euplectella* OWEN. The Rossellidae and Asconematidae have pentactinal hypodermalia (except in some genera, e.g., *Aulochone* SCHULZE, in which their absence is supposed to be secondary), and the lophophytes have pentactinal basalia that are homologous to the hypodermalia. The two groups, thus, seem to have evolved lophophytous attachment independently, using different types of spicules. In the Euplectellidae, one can probably assume evolution from forms like the simpler Euplectellinae with imperforate walls (e.g., *Euplectella*) and Taegerinae (e.g., *Regadrella*), although with the usual reservation that the genera cited are all modern. Even the simplest Euplectellinae, however, are not really primitive morphologically because their parenchymal megascleres include sharply distinct principalia and comitalia. The Rossellidae and Asconematidae are generally specialized sponges, having most advance characters in genera with paratropal hypodermalia and octaster microscleres (e.g., *Rhabdocalyptus* SCHULZE). Beyond this, it is difficult to comment, except that occurrence of taegerine euplectellids and Rossellidae with paratropal spicules in the Upper Cretaceous suggests a much longer history.

With few exceptions, no certain relationships can be claimed between Paleozoic and later Lyssacida. Almost no diagnostic microscleres are known from the Paleozoic sponges, and some of those recorded (as hexasters) are only doubtfully genuine. This leaves only the megaspiculation as a basis for assessment, but most types of megascleres and various conditions of the skeleton occur in both living series. Both include forms with the parenchymal megascleres varying from mainly hexactines to all rhabdodiactines. Pinular autodermalia are shared by most Amphidiscosa and the asconematid Lyssacinosa, and pentactinal hypodermalia by the Amphidiscosa and the rossellid and asconematid Lyssacinosa. Only euplectellid and leucopsacadid Lyssacinosa have basalia that are umbel-bearing rhabdodiactines; but external form alone, which is all that can be seen in most fossils, does not distinguish these spicules from basalia of some Hyalonematidae, and they sometimes pass into monactines. True pentactinal basalia are now seen normally only in rossellid Lyssacinosa; but the axial crosses of hyalonematid monactines imply origin from pentactines, and the normal monactines have occasional pentactinal variants. Hence none of these types can be cited as implying the occurrence of either amphidiscs or hexasters; and no useful purpose is served by comparison with a member of the Amphidiscosa, when an equally comparable genus exists in the Lyssacinosa. This leaves little but restriction of uncinates and scepters to the Amphidiscosa (although uncinates also occur in the order Dictyonida) and restriction of paratropal hypodermalia and fusion of the parenchymal megascleres to the Lyssacinosa.

A second problem is that some Paleozoic sponges have spicules of types unknown in any modern Lyssacida. This applies especially to the paraclavule microscleres of some Dictyospongiidae (*Treatise Part E (Revised),* vol. 3, in press). These sponges have often been thought to be allied to the living Euplectellidae, which they broadly resemble, and SCHULZE (1887b) accepted them as fossil euplectellids; but no existing euplectellid, or any other lyssacine, is known to have paraclavules. When compared with other microscleres the latter resemble most an amphidisc with one umbel missing. The megascleric basalia can also be matched in the Pheronematidae or Hyalonematidae, as well as in the Euplectellidae. REID (1957a) has suggested that these sponges are not members of any living order but of an extinct one.

Because of these problems, I do not postulate herein origins of the two groups of modern Lyssacida (Amphidiscosa and Lyssacinosa) among the Paleozoic sponges. But the Amphidiscosa and probably the Lyssacinosa existed in the Late Paleozoic. First, the Carboniferous *Uralonema* LIBROVICH has recognizable amphidiscs, and was placed in the Hyalonematidae by REZVOI, ZHURAVLEVA, and KOLTUN (1962). Second, in Permian *Pileolites* FINKS the parenchymal megascleres are united as in various Lyssacinosa. As shown by FINKS (1960), the genus comes closest to the living Euplectellidae, although as he also showed, it is not a euplectellid. In particular, the outermost fused megascleres appear to be dermalia, which are never united in modern forms. For further comments on these sponges, see chapter on Paleozoic Hexactinellida: Morphology and Phylogeny (p. 135).

WORKING KEYS TO SOME LYSSACINOSID FAMILIES

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Because of problems dealing with material lacking diagnostic microscleres, when sponges in different families distinguished by the microscleres have similar megascleres, some guidance may be helpful.

When microscleres are present, as in modern material, most Lyssacinosa (other than some rossellids that lack hypodermalia) can be placed correctly on the following basis.

A. Amphidisc microscleres present; no hexasters or other rosettes.

1. Principal parenchymal megascleres hexactines or pentactines, although rhabdodiactines may also occur; basalia monactinal and typically bidentate; scepters often present: **Pheronematidae.**

2. Fixed by a single large needle; principal parenchymal megascleres tauactines: **Monoraphididae.**

3. Principal parenchymal megascleres mainly or all rhabdodiactines; basalia monactines that have usually four or more anchor teeth; no scepters: **Hyalonematidae.**

B. Hexaster microscleres present; no amphidiscs.

1. Dermal megascleres not differentiated into distinct autodermalia and hypodermalia.

a. Dermalia swordlike hexactines: **Euplectellida.**

b. Dermalia pentactines, with unpaired ray proximal: **Leucopsacadida.**

2. With distinct autodermalia and hypodermalia.

a. Autodermalia stauractines, pentactines with the unpaired ray proximal, or nonpinular hexactines: **Rossellidae.**

b. Autodermalia pinular hexactines, or subpinular pentactines with the unpaired ray distal: **Asconematidae.**

Most genera can also be placed correctly by using the following keys, which do not rely first on microscleres, provided that megaspiculation is complete.

A. Dermal megascleres not differentiated into distinct autodermalia and hypodermalia; lophophytous genera with basalia that are umbel-bearing rhabdodiactines; parenchymal megascleres may be fused together in lower parts or throughout the body (hexaster microscleres).

1. Dermalia hexactines; generally thin-walled sponges, with megascleres all loose or fused in the lower parts or the whole body; lophophytous or basiphytous; wall with parietal oscula in some genera: **Euplectellidae.**

2. Dermalia pentactines, with the unpaired ray proximal; thick walled lophophytes, without fusion of megascleres in most instances: **Leucopsacadidae**.

B. Dermal megascleres differentiated into distinct autodermalia and hypodermalia; lophophytous genera with basalia that are monactines or pentactines; fusion of parenchymal megascleres restricted to lower parts of basiphytes (hexaster or amphidisc microscleres).

1. Basiphytous sponges, and lophophytes whose basalia are pentactines with paired rays forming four recurved anchor flukes; hypodermalia usually large pentactines, which may be paratropal, but sometimes tangentially lying rhabdodiactines; megascleres fused in the lower parts of basiphytous genera, but not in lophophytes (hexaster microscleres).

Autodermalia hexactines, pentactines with the unpaired ray proximal, or stauractines; sometimes spiny, but hexactines not pinular;

hypodermalia may be paratropal when pentactinal; lophophytous or basiphytous: **Rossellidae.**

b. Autodermalia pinular hexactines, or pentactines with a subpinular distal ray; basiphytous: **Asconematidae.**

2. Lophophytous sponges whose basalia are monactines, with two, four, or more recurved teeth arising from distal end; or sponge fixed by a single basal needle; hypodermalia pentactines with unpaired ray proximal, never paratropal; autodermalia usually pentactines with unpaired ray distal and pinular; no fusion of megascleres in any part (amphidisc microscleres).

a. Principal parenchymal megascleres hexactines or pentactines, although rhabdodiactines may also occur; basalia typically with two recurved anchor teeth only, and not arranged to form a glass rope; sceptres often present: **Pheronematidae.**

b. Sponge fixed by a single giant needle; principal parenchymal megascleres tauactines: **Monoraphididae.**

c. Principal parenchymal megascleres mainly or all rhabdodiactines; basalia monactines, which usually have four or more recurved anchor teeth at distal end, usually emitted in single tuft only and sometimes forming a glass rope; no sceptres, although diactinal pleuralia may occur: **Hyalonematidae.**

Isolated spicules are usually not diagnostic of any single genus, but particular families or groups of families may be indicated by some types.

1. Pinular hexactines; particularly **Asconematidae,** but also occur in some Dictyonida (e.g., *Bathyxiphus* SCHULZE).

2. Pinular pentactines: characteristic autodermalia of Amphidiscosa (**Peronematidae**, **Monoraphidae, Hyalonematidae**); but comparably subpinular pentactines occur in *Asconema* Kent (**Asconematidae**).

3. Paratropal pentactines: **Rossellidae** (**Rossellinae** or **Acanthascinae**).

4. Unequal-rayed rhabdodiactines, with an umbel at end of shorter ray: characteristic basalia of lophophytous **Euplectellidae** and **Leucopsacadidae.**

5. Anchorate pentactines: characteristic basalia of **Rossellidae**, also sometimes occurring as pleuralia.

6. Anchorate monactines with two anchor teeth only: characteristic basalia of **Pheronematidae.**

7. Anchorate monactines with four or more recurved anchor teeth: characteristic basalia of **Hyalonematidae.**

8. Octasters: **Acanthascinae (Rossellidae).**

DICTYONINE HEXASTEROPHORA

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INTRODUCTION

Post-Paleozoic fossil Hexactinellida are predominantly **dictyonines,** here included with the Lyssacinosa in the subclass Hexasterophora Schulze, 1887b as in zoological classification. Dictyonine sponges are members of the orders Hexactinosa Schrammen and Lychniscosa Schrammen. In some paleontological classifications the Hexactinosa and Lychniscosa are combined into the order Dictyonida, with Hexactinosa and Lychniscosa treated as suborders. In this volume, however, the zoological classification is followed.

Dictyonine sponges are Hexactinellida with a parenchymal skeleton that is always a rigid dictyonal framework. The component megascleres or **dictyonalia** are united as part of their normal development and are hexactines except in some species in which there is suppression of rays that would otherwise project freely from skeletal surfaces. The framework is never composed of a mixture of different kinds of megascleres or partly or entirely of diactines, as in lyssacines with rigid skeletal frameworks.

The Hexactinosa and Lychniscosa are distinguished by occurrence of different kinds of dictyonalia. In Hexactinosa, the spicular centers or nodes have no special modifications except that they may sometimes be swollen. In Lychniscosa, the centers of typical dictyonalia are enclosed within an octahedral framework of **interactinal buttresses,** which extend across the twelve interactinal angles from points equidistant from the center. The buttresses of these **nodal octahedra** originate from siliceous fibers that grow across the **interactinal angles** before union of the spicules. After this union, further thickening of skeletal beams and nodal buttresses does not affect the enclosed central part of the spicule, which remains delicate. Although Lychniscosa may also have dictyonalia that lack nodal octahedra, the latter are altogether absent in Hexactinosa.

Most modern dictyonines have dermalia and gastralia, which are usually pentactines with the unpaired ray proximal, but some are hexactines. In one genus (*Aphrocallistes* Gray) the **gastralia** are **rhabdodiactines.** Such spicules are usually absent from fossils, presumably through being unconnected, as in most modern species. Some fossils (e.g., *Craticularia* Zittel, *Porospongia* d'Orbigny, *Cypellia* Pomel) and one living genus (*Fieldingia* Kent), however, have connected dermalia or gastralia that are pentactines or stauractines. Hexasters are present in all living species but two (*Cyrtaulon sigsbeei* (Schmidt); *C. solutus* Schulze), and most of the Hexactinosa have additional **uncinates** and **sceptrules,** although either or both may be absent. These microscleres are unknown in fossils although sceptrules have been found loose in sediments with fossil Hexactinosa.

HABITUS AND GENERAL SKELETAL MORPHOLOGY

Although the Hexactinosa and Lychniscosa appear to have evolved independently from at least an early stage of their history (see Phylogeny, p. 174), they have many common features in both habitus and skeletal morphology. The implied parallel evolution is presumably the result of possession of the same type of skeleton.

Dictyonine sponges vary widely in habitus, but many are funnel-like, branched and tubular, or of some related shape. They are mainly thinly walled sponges with a lateral wall or skeletal framework, generally about 1 to 10 mm thick. Many with walls less than 5 mm thick (e.g., species of *Farrea* Bowerbank, *Eurete* Semper, *Calyptrella* Schrammen, *Brachiolites* Smith) form branching and anastomosing tubes, which presumably are stronger mechanically than simple free branches. Genera in which the wall exceeds 10 mm thick are usually funnel-like or flabellate (e.g., *Stauroderma* Zittel, *Rhizoporterion* Zittel, *Porospongia* d'Orbigny) or sponges that form solid branches with no paragastral cavity (e.g., *Sclerothamnus* Marshall). The body may be supported by an encrusting base or by rootlike basal outgrowths.

In sponges in which the body consists partly or entirely of dividing and anastomosing tubes, it encloses two systems of passages, within and between the tubes respectively. These enclosed passages, termed **cavaedia,** are lined by the soft gastral and dermal membranes in life and by the corresponding skeletal surfaces in fossil examples. The same term has also sometimes been used for spaces enclosed between plications of the wall (Ijima, 1927) or for enclosed spaces that more probably represent a canal system (see below and p. 174).

In the simplest dictyonines (e.g., *Farrea, Calyptrella*), the skeletal framework consists of a single layer of rectangular meshwork or of a single primary layer (in *Farrea* and related forms) on which a further layered or irregular meshwork is built up by accretion of new dictyonalia (Fig. 54). The beams of the primary meshwork each contain rays of two dictyonalia laid together side by side and enclosed in a common siliceous envelope. When additional meshwork is layered, the secondary beams are also formed in this manner, and the three-dimensional meshes are roughly cubic. Irregularly oriented secondary components are fused together haphazardly where their rays come into contact with the primary beams or with one another.

In most forms, however, the dictyonal meshwork is initially three dimensional and is not constructed in layers (Fig. 55–56). Series of dictyonalia are united by the rays of one axis to form parallel or subparallel dictyonal strands with a longitudinal to radial orientation, which are connected together laterally by beams formed from the other rays. The beams forming the dictyonal strands each contain two apposed spicular rays, as in the beams of the primary meshwork of the simplest type of skeleton. The lateral connecting beams may be formed in this manner, by fusion of their tips with beams or nodes in adjacent strands, or by haphazard unions where they happen to

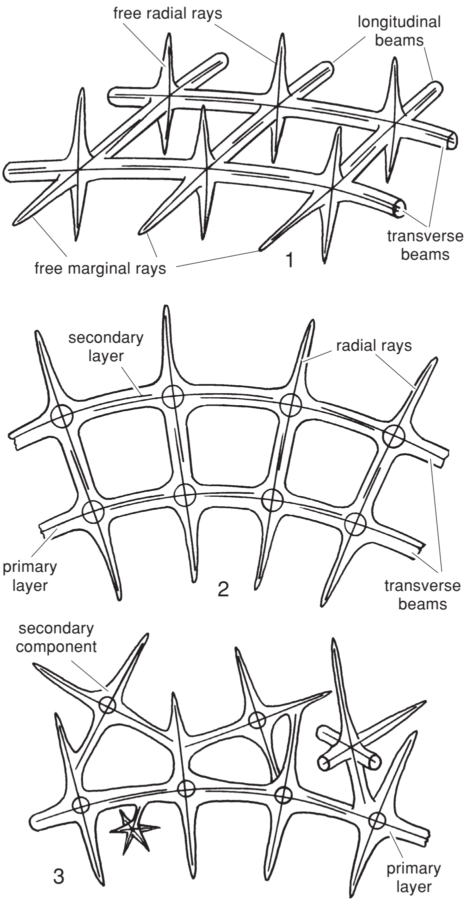

Fig. 54. Order Dictyonida, suborder Hexactinosa; farreoid structure; figures oriented dermal side upward, gastral side downward; *circles* in views *2* and *3* represent skeletal beams cut at their origins; *1,* marginal part of farreoid primary layer, with margin and free longitudinal rays toward front: each skeletal beam includes 2 oppositely directed rays of adjacent dictyonal hexactines, apposed side by side and enclosed in common siliceous envelope [not united tip-to-tip]; free rays of radially oriented spicular axes project on either side of each skeletal node; *2,* transverse section of regular three-dimensional meshwork, in which single secondary layer of meshwork is superimposed on primary layer (seen below: see view *1*); *3,* transverse section of skeleton with irregular secondary meshes, in which secondary hexactines have random orientation (new).

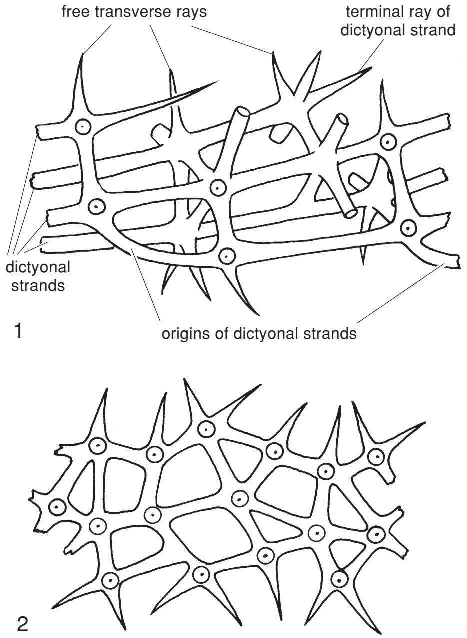

FIG. 55. Order Dictyonida, suborder Hexactinosa; sectional views of simple euretoid structure; *circles* with central spot mark beams cut at origins; *1,* simple euretoid skeleton, 1 to 2 meshes deep, in longitudinal section; dermal side upward; growth left to right; *2,* transverse section of simple euretoid skeleton, of type in which transverse (connecting) beams form regular transverse lamellae, having characteristic irregularly variable form and orientation of meshes, and lack of layered construction. Compare with Figure 54.1–54.3 (farreoid structure), and note that three-dimensional meshwork represented here corresponds with farreoid primary layer (Fig. 54.1) only; based on recent *Periphragella elisae* MARSHALL (new).

cross one another. The shape of meshes between the strands varies correspondingly from generally rectangular to mainly or all triangular or irregular.

Two genera (*Aulocalyx* SCHULZE, *Rhabdodictyum* SCHMIDT), placed in the Hexactinosa as Aulocalycidae (IJIMA, 1927), have skeletal frameworks composed of large hexactines united in an altogether haphazard manner. It is possible, however, that these are not true dictyonine sponges (see Phylogeny, p. 174).

The common type of skeleton, which is three dimensional initially, has often been wrongly assumed to have the same type of structure as the layered type that occurs only in the hexactinosan *Farrea* and some related genera. This mistake arose because skeletons of the common type are misleadingly like cubic structures if the meshes between dictyonal strands are regularly rectangular. The difference is seen easily in sections at right angles to the strands in which meshes enclosed by the connecting beams have irregularly variable shapes and orientations.

In many examples of such skeletons, the outermost meshwork at dermal or gastral surfaces differs from that of the interior and then comprises a **dictyonal cortex** (Fig. 57). This may arise by secondary accretion of dictyonalia to the primary structure or by various modifications of the outermost primary meshwork. Either type may form a thin surface layer only or be several meshes deep.

Another common development is **skeletal canalization,** here described as **intradictyonal,** representing the canal system or sometimes the flagellated chambers. As usual, this results from the skeleton growing around preexisting soft parts. The simplest development is formation of small skeletal pores (ostia, postica) or short canals (epirhyses, aporhyses) in secondary cortical meshwork, representing the positions of small inhalant canals on the dermal side and of flagellated chambers on the gastral side. This type of canalization may also occur in the secondary meshwork of *Farrea* and related genera and is the only type of canalization they exhibit. More advanced canalization affecting primary meshwork of skeletons that are initially three dimensional may be either intracortical only or affect the whole interior. In the latter, there may be two systems of skeletal canals (epirhyses, aporhyses) that typically open on the dermal and gastral sides, respectively, or a single system of canals that open on both sides. Skeletal canals of either type may be radial and separate, branching and intercommunicating from radial trunks, or irregularly labyrinthine. When two distinct systems are present, sometimes one but not the other is open through both skeletal surfaces.

Labyrinthine canalization can cause difficulties in interpretation. First, in some instances it may be difficult or almost impossible to determine whether one or two systems of skeletal canals are present. This applies especially to fossils preserved as pseudomorphs, as for example in many Cretaceous specimens. Second, in other sponges such canals are much wider than intervening skeletal partitions, and in these the skeleton may appear to consist of dividing and anastomosing tubes. Canalization can be inferred to be intradictyonal in some fossils that have this condition and have existing relatives in which the soft parts are known. But in others that have no living relatives the wall structure might be interpreted in either way.

Various canalized genera have circulatory apertures in the surfaces of the dictyonal framework spanned externally by **superficial meshwork** that are formed by union of the dermalia or gastralia, by union of adventitious dictyonal hexactines, or from siliceous filaments that grow out from the skeletal surface. Two or all of these types of superficial structures may also occur in one sponge. When dermalia or gastralia are fused together, this may happen by simple cementation of paratangential rays that lie side by side or by growth of branching and anastomosing siliceous filaments across the paratangential meshes.

Some Hexactinosa and Lychniscosa with intradictyonal epirhyses and aporhyses have longitudinal furrowing of the dermal or gastral surface, along the lines of series of ostia (e.g., *Sphenaulax* Zittel) or postica (e.g., *Leiostracosia* Schrammen), or irregularly reticulate furrowing of the dermal surface (*Ventriculites* Mantel). When longitudinal, this **superficial furrowing** suggests longitudinal folding of the wall but is spanned by superficial meshwork when this is present, as in all the genera cited. It presumably represents the courses of subdermal channels on the dermal side, and subgastral channels or plications of the chamber layer on the gastral side.

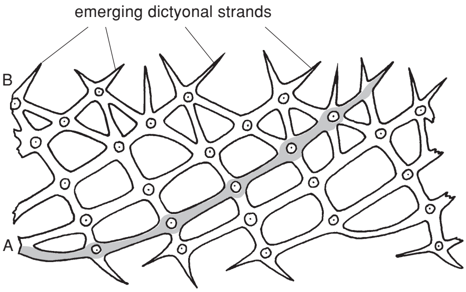

Fig. 56. Order Dictyonida, suborder Hexactinosa, euretoid structure; longitudinal section of euretoid meshwork; *A,* dermal emergence of dictyonal strands (1 *shaded*), which begin on gastral side (below) and have marked outward curvature; *B,* change in form of meshes from quadratic to triangular toward dermal side; orientation and style as in Figure 57 (new).

Species of the living lychniscosan *Callicyclix* Schrammen (=*Aulocystis* Schulze, 1887b; *non Aulocystis* Schlüter, 1885 [Coelenterata, Anthozoa, Tabulata, Auloporidae]) have a body composed of dividing and anastomosing tubes enclosed in a **peripheral membrane** that extends across the terminal openings of the tubes and the spaces between them. This membrane may be supported by loose spicules resembling the dermalia, as in *C. zitteli sibogae* (Ijima), or additionally by secondary dictyonal meshwork formed after the end of normal growth, as in *C. zitteli zitteli* (Marshall & Meyer). Some fossils have similar capsular or annular

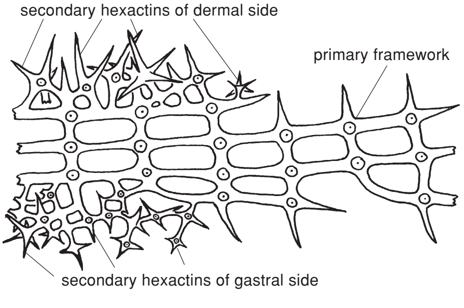

Fig. 57. Order Dictyonida, suborder Hexactinosa; simple euretoid skeleton with cortical meshwork formed by secondary accretion of dictyonal hexactines at primary surfaces; longitudinal section, dermal side upward, growth left to right; *circles with central dot* mark transverse beams cut at origins; secondary meshwork seen in older part only (left); secondary hexactines larger on dermal side; for convenience dictyonal strands are drawn as though vertically superimposed; based on Upper Cretaceous *Eurete (Aulodomus) prolatum* Reid (new).

peripheral structures that imply the existence of a similar membrane in life, e.g., *Tremabolites* ZITTEL, *Coeloptychium* GOLDFUSS. Structures resembling lyssacine **sieve plates** sometimes occur (e.g., *Coeloptychium, Aphrocallistes* GRAY) but may differ in containing flagellated chambers in living sponges (*Aphrocallistes*).

The basal skeleton is always internal and rigid and consists of secondary dictyonal hexactines or of anastomosing siliceous filaments that grow downward from the dermal surface of the dictyonal framework. In some forms, e.g., *Laocoetis* POMEL, an upward extension of the basal skeleton forms a superficial meshwork far above the basal parts. Meshwork like that of the basal skeleton may also be formed on the lower parts of the paragastral surface, although it takes no part in basal fixation. Basal and analogous meshwork of the gastral side may lack canalization or have skeletal canals like those of the dictyonal framework or of a different type.

In using older literature, it is useful to note that the **Deckschichten** of ZITTEL (1877b, 1878a, 1878b) and the dermal layers of HINDE (1884a, 1887a, 1888, 1893b, 1912) may be (i) a dictyonal cortex of primary or secondary origin, (ii) superficial meshwork of any sort, or (iii) a peripheral structure. In SCHRAMMEN's work (1912, 1924a, 1936), however, a Deckschicht is nearly always a **dictyonal cortex.** In MORET's (1926b) usage, a **cortex dépendant** may be a dictyonal cortex, a superficial structure arising from the dictyonal surface, or in some sponges an upward extension of the basal skeleton. A **cortex indépendant** is the dermal or gastral skeleton or is a connected superficial meshwork developed from them. **Ectosomal** as used by IJIMA (1927) means the dermal or gastral skeleton. This was apparently not understood by DE LAUBENFELS (1955), who sometimes used ectosomal for dictyonal structures, called Deckschicht by SCHRAMMEN, e.g., in the Eubrochididae DE LAUBENFELS, 1955, p. 79).

HEXACTINOSA

The Hexactinosa are dictyonines in which **nodal octahedra,** distinctive of the Lychniscosa, are never developed at any stage of ontogeny. In most genera, the living examples are also distinguished by possession of uncinate and sceptrule microscleres.

In most Hexactinosa, the component dictyonalia of the primary dictyonal meshwork are united to form regular parallel or subparallel dictyonal strands. These occur in two main types of skeleton.

In the **farreoid** type, which occurs only in few Farreidae, the primary meshwork is formed in a single layer only (Fig. 54) apart from local irregularities, with the dictyonal strands running longitudinally (i.e., from the base to the skeletal margin). The meshes are typically rectangular, with the beams each enclosing two rays of adjacent dictyonalia. The remaining two rays of each dictyonal hexactine project at right angles on opposite sides of each intersection of the meshwork. The skeleton may retain this condition throughout life, except in the basal parts, where meshwork of the basal skeleton covers it, or have more or less extensive accretion of secondary components to form further layered or irregular meshwork. This accretion may occur in the older parts only or extend to the skeletal margin.

In **euretoid** skeletons, which occur in all other Hexactinosa except the doubtfully included Aulocalycidae (see *Treatise Part E (Revised),* vol. 3, in press), the meshwork is primarily three dimensional with a depth of one to many meshes and is not formed in layers (Fig. 55). In simple examples, the skeletal meshwork is only one to several meshes deep. The dictyonal strands then run almost longitudinally but with a gradually spreading arrangement so that many of them end at the dermal or gastral surface of the skeleton instead of at the skeletal margin (Fig. 56). This migration of strands to the surfaces is **emergence.** In more advanced skeletons that are several to many meshes thick, the strands spread out more rapidly and have more or less marked outward curvature emerging at both surfaces at angles up to 90° or begin on the gastral side and run to the dermal side. Thus, emergence of the strands may be bilateral or unilateral, according to whether they run to both surfaces or to one only. Their direction may be radial from some distance under the surface, and in some forms (*Aphrocallistes* spp., *Leptophragma pusillum* Schrammen) they are radial or subradial for most or all of their length. In all instances, the emerging dictyonal strands are continually replaced by new ones. The whole thickness of this type of three-dimensional meshwork is homologous with the single primary layer of farreoid skeletons, not with the layered or cubic type of farreoid meshwork with which it has been identified formerly.

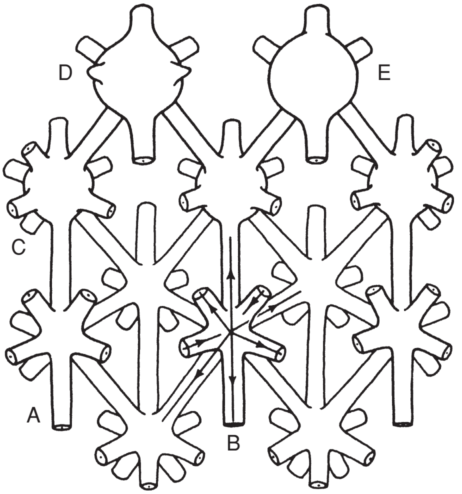

Fig. 58. Order Dictyonida, suborder Hexactinosa, euretoid structure; skeletal meshwork with multiradiate nodes and triangular meshes regularly developed, in part also with nodes spherically enlarged; plan view, top part tilted slightly away from front (hence triangular meshes are not equilateral as in true plan view); outermost meshwork at top of figure, internal meshwork below; *A,* meshwork of interior, with 10 beams radiating from each skeletal node; *B,* node with axial canals drawn in; *arrows* show direction of rays; spicular axes follow same pattern as all other nodes except 2 surface nodes at top (views *D–E*); *C,* similar meshwork with nodes spherically swollen, although less so than at surface (views *D–E*); *D,* node at surface, with projecting tips of reduced free rays that do not follow orientations seen in interior (see view *B*); *E,* similar node with free rays suppressed (or engulfed) (new).

Euretoid skeletons have four main but intergrading conditions in the form of the meshes between dictyonal strands. First, meshes between strands may be typically rectangular, apart from local irregularities. The connecting beams then form successive, platelike, transverse lamellae of irregular meshwork, through which the strands run at right angles. Because of the spreading arrangement of the strands, these lamellae are typically convex toward the skeletal margin and may overlap marginally if the spreading of the strands is pronounced. Second, meshes between the strands may have a mixture of rectangular, trapezoidal, rhomboidal, and triangular meshes in varying proportions; some connecting beams are then formed from single rays instead of pairs of rays. Third, the meshes may all be triangular and the connecting beams all formed from single rays that are attached by their tips to the centers of adjacent dictyonalia (Fig. 58). The skeletal nodes are then said to be **multiradiate** since more than six beams (typically 8–10) radiate from each of them. In this type of skeleton, dictyonal strands are often difficult to identify since the meshwork has a similar appearance in all directions. Last, the connecting beams may be formed in a haphazard manner, where the rays that form them happen to meet other strands or individual rays.

The types of euretoid skeleton in which meshes between dictyonal strands are mainly rectangular and mainly triangular were distinguished by Moret (1926b) as type *Craticularia* and type *Eurete* respectively, but both occur in both genera and may intergrade from one part of the skeleton to another in both genera.

In interpreting the structure of a euretoid skeleton, the orientation of dictyonal strands

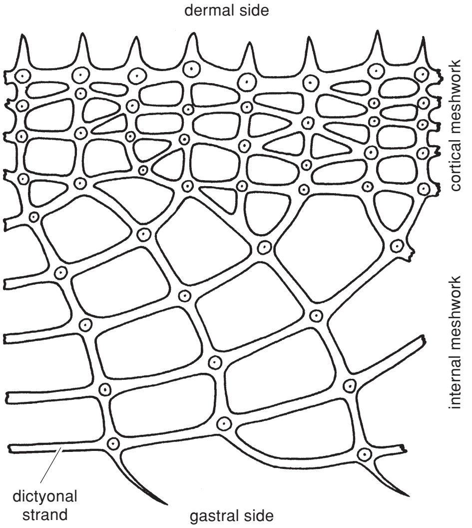

FIG. 59. Order Dictyonida, suborder Hexactinosa, euretoid structure; longitudinal section of skeleton in which dictyonal strands emerge radially on dermal side (top), and beams connect their radial parts to form roughly stratified primary cortical meshwork; also with outermost beams of dermal side differentially thickened: note that beams having stratification in cortex correspond structurally with those that connect dictyonal strands transversely in interior, and that only some radial strands of cortex are continuations of those seen internally (below cortex); orientation and style as in Figure 57; based on examples of recent *Leptophragmella choanoides* (SCHULZE & KIRKPATRICK) having minimal canalization (new).

should be established first. This is because the same type of structure may look different according to their orientation or that of sections in relation to them. In particular, a skeleton with rectangular meshes between the strands will have regular meshwork in sections roughly parallel to them but irregular meshwork in sections transverse to them. A similar difference occurs between plan views or tangential sections of skeletons in which the orientation of strands is mainly longitudinal in one instance but radial or subradial in another. Failure to understand this has led to description of imaginary differences between regular and irregular construction in various fossils.

Many euretoid skeletons have some type of dictyonal cortex (Fig. 57, 59). In the simplest, this results only from special thickening of beams or skeletal nodes at the surfaces. In others, there are structural changes as the surface is approached. Meshes between strands may change shape from rectangular in the interior to irregularly variable or triangular in the cortex (Fig. 57). Skeletons, with markedly convex transverse lamellae may have their margins overlapped and united to form irregular cortical meshwork. If strands are radial or subradial from some distance below the surface, a thickly layered cortex may result. The meshwork seen at the surface is irregular and may have diagonally intersecting series of beams running through it. Last, various developments may occur in combination.

In addition to primary developments, a cortex also may be produced by accretion of secondary dictyonalia. This type passes downward into the basal skeleton.

Farreoid and euretoid skeletons both may have a state of dictyorhysis, in which all circulation occurs through ordinary meshes. In others there is canalization of secondary meshwork or primary canalization of the euretoid type of skeleton. The simplest canalar features are small ostia or postica or short intracortical **epirhyses** or **aporhyses,** which open internally into uncanalized meshes. Fully developed intradictyonal canals may be **diplorhytic,** comprising separate series of epirhyses and aporhyses, or form single systems of **diarhyses** or **schizorhyses** that open through both skeletal surfaces. Diarhyses are oblique to radial tubular or prismatic skeletal canals, each of which contains a complex flagellated chamber in living examples. Schizorhyses are intercommunicating cleftlike features or labyrinthine tunnels that contain corresponding chamber-lined canals. Some other special developments also occur.

Some advanced euretoid Hexactinosa have a superficial meshwork that is developed outside the dictyonal skeleton proper and across canalar apertures. This is usually formed either from dictyonal hexactines, from connected dermalia and gastralia, or both together. Siliceous filaments growing out from the dictyonal skeleton also occur in some genera (e.g., *Nemarete* REID) but are less common than in Lychniscosa.

The basal skeleton is always composed of dictyonal hexactines. These have been called basidictyonalia (IJIMA, 1927) but do not appear to be homologous with lyssacine basidictyonalia. The basal meshwork may pass upward into secondary meshwork of the dictyonal framework proper in farreoids or into dictyonal superficial meshwork in euretoids (e.g., *Laocoetis* POMEL).

The **aulocalycoid** skeletons of the Aulocalycidae are composed of large, haphazardly united hexactines whose rays are interwoven diagonally (Fig. 60). True dictyonal strands seem to be absent, although strandlike series of beams may occur.

Turning to families, the Farreidae are simple Hexactinosa with farreoid skeletons and no canalization or with secondary ostia or postica only. The sceptrules of living sponges are all **clavules** or clavules and **lonchioles** or **sarules.**

The Euretidae are simple euretoid Hexactinosa that may lack canalization entirely, have intracortical features in primary or secondary meshwork, or have vague development of deeper epirhyses or aporhyses with no regular pattern. One modern genus (*Tretochone* REID) has special accessory **amararhyses** that are additional to the true canal system. These consist of longitudinal tunnels that open through slits in the gastral surface and through branch tunnels leading to the tops of papillae on the dermal side. The sceptrules of modern euretids are typically scopules but are sarules in one genus (*Sarostegia* TOPSENT) and are absent from some others (e.g., *Myliusia* GRAY).

The Craticulariidae and Cribrospongiidae are advanced euretoid Hexactinosa with deep epirhyses and aporhyses having different characteristic arrangements. In Craticulariidae, they typically occur in separate longitudinal series and represent inhalant canals and choanocytal outgrowths formed in alternating segments of the growing sponge margin. The epirhyses are often also arranged in transversely corresponding positions so that their ostia form a quadratic pattern. The aporhyses are then arranged similarly with each aporhysis located quincuncially in the center of a group of four epirhyses. A quincunx pattern then occurs if the wall is sectioned or eroded tangentially. In Cribrospongiidae with canals in longitudinal series, epirhyses and aporhyses occur alternately in the same series and often in alternating positions in adjacent series. The patterns of ostia and postica are consequently quincuncial, and the pattern that occurs in tangential section is quadratic. These patterns have often been confused through reliance on eroded material or on genera in which one set of canals perforates both surfaces (e.g., epirhyses in *Guettardiscyphia* DE FROMENTEL; aporhyses in *Andreaea* SCHRAMMEN).

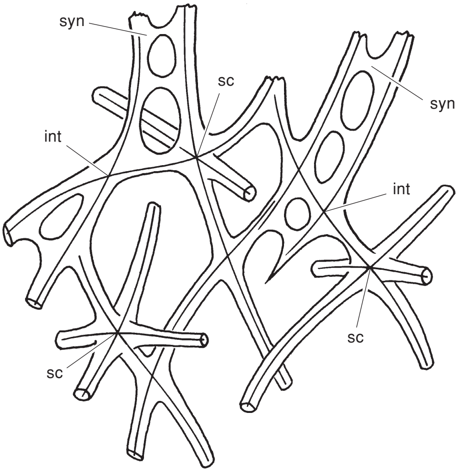

FIG. 60. Order Dictyonida, aulocalycoid structure that may occur in suborder Hexactinosa; meshwork formed by irregular union of 3 hexactines and rays from 4 others; positions of rays shown by their axial filaments; *syn,* synapticulae; *int,* intersection of rays; *sc,* spicule center (new).

In Craticulariidae, some genera (e.g., *Sphenaulax* ZITTEL) have longitudinal furrowing of one skeletal surface. Some Cribrospongiidae have modification by multiplication of the number of epirhyses, which may become arranged in hexagonal groups (*Andreaea*), or development of internal labyrinths from one or both systems of skeletal canals (e.g., *Polyopesia* SCHRAMMEN). Both families include genera with and without a superficial meshwork of dictyonal or dermal origin when present. These families are mainly extinct, scopule microscleres are known only from one living craticulariid (*Leptophragmella* REID).

The Aphrocallistidae and Tretodictyidae are advanced euretoids distinguished by canalization in the form of diarhyses and schizorhyses, respectively. The living forms have scopules. In Aphrocallistidae (one genus, *Aphrocallistes* GRAY), the dictyonal strands also run radially or subradially, when any are present, and dictyonalia in thin partitions between closely spaced diarhyses may be distorted so that all six rays lie roughly in one plane. In some species, oscula become covered by sieve-platelike structures, which contain flagellated chambers in a living sponge (*A. beatrix* GRAY). In Tretodictyidae, the schizorhyses vary from narrow, intercommunicating clefts to large, labyrinthine tunnels, separated by narrow partitions. A superficial meshwork composed of connected dermal pentactines occurs in one fossil and one modern genus (*Placotrema* HINDE, *Fieldingia* KENT).

The families Staurodermatidae and Cystispongiidae and the subfamily Caseariinae of the Craticulariidae comprise advanced euretoid sponges whose relationships to other forms are uncertain. All are fossils. Nothing is known of the microscleres, but the sceptrules would probably be scopules as in the previous families.

Stauroderma ZITTEL has complicated diplorhytic canalization, which may be a specialized form of the cribrospongiid type. Alternating ostia in the dermal skeletal surface lead into branching epirhyses, which unite to form a labyrinth of fine passages. Similar passages in the interspaces form an aporhytic labyrinth, arising from branching aporhyses whose openings are in pitlike depressions in the gastral skeletal surface. The epirhytic labyrinth also opens on this side through small apertures and sinuous grooves in the areas between the aporhytic depressions. This surface is usually densely coated by a superficial meshwork formed from gastral pentactines and siliceous filaments, which extends into but not over the depressions.

Casearia QUENSTEDT is a sponge with rejuvenescent growth like that of sphinctozoan demosponges, although with solid segments. A deep, narrow paragaster extends through the successive segments. The canal system, when apparent, is diplorhytic, either with no recognizable pattern or approaching the craticulariid type. The external surface of each segment is covered by paratangential meshwork, which seems to consist of fused dermalia.

Porospongia D'ORBIGNY and related genera are sponges with obscure canalization, which has been said to consist of epirhyses and aporhyses but may be schizorhytic. The dermal surface of the skeleton bears superficial meshwork formed from cemented stauractines or pentactines. On the gastral side, similar gastralia are united by siliceous filaments in the paratangential meshes to form a finely porous membrane pierced at intervals by round or ovate apertures.

Cystispongia ROEMER is a sponge with a pyriform body, composed of thinly walled lamellae enclosing labyrinthine passages that are enclosed externally by a capsulelike structure. The internal passages can be interpreted as either cavaedia or schizorhyses. The genus is a true hexactinosan, although the name *Cystispongia* has often been misapplied to similar Lychniscosa.

Last, the doubtfully included Aulocalycidae have aulocalycoid skeletal structure and either no canalization or vague ostia or postica. No uncinates or sceptrules are present.

LYCHNISCOSA

The name Lychniscosa is based on the term **lantern-spicule** or **lychnisc,** applied to dictyonalia with nodal octahedra or lanterns that are distinctive of this suborder (Fig. 61).

In typical Lychniscosa, most or all dictyonalia have nodal octahedra except sometimes in a secondary meshwork. In some forms, however, octahedra occur in only parts of the skeleton or even in only parts of some individuals. This is due either to solidification of the octahedra after formation or sometimes to simple failure to develop them in much of the skeleton. Genera of this kind (e.g., *Dactylocalyx* STUTCHBURY, *Stauronema* SOLLAS) have been mistaken for Hexactinosa although they need to be placed in this suborder.

A simple type of dictyonal framework, which occurs only in *Calyptrella* SCHRAMMEN, consists of a single layer of rectangular meshwork. This is comparable to the single primary layer of the hexactinosan Farreidae but lacks distinct **dictyonal strands.**

Other Lychniscosa have euretoid-like conditions, with dictyonal strands that are not arranged in layers and that spread and emerge comparably. The meshes between these strands are commonly predominantly rectangular, and the main variation from this condition occurs by loss of the regular arrangement of the spicules so that dictyonal strands are absent. The hexactinosan condition with regularly triangular meshes and **multiradiate nodes** is not reproduced.

Although the dictyonal strands of these forms resemble those of Hexactinosa, there seems to be a fundamental difference in the way in which their orientation is controlled. In Hexactinosa that consist of dividing and anastomosing tubes, the dictyonal strands follow the local direction of growth and pass from one tube to another at points of branching or anastomosis. An axial section of a similar lychniscosan, instead, has strands spreading out from an axis or center irrespective of the local directions of the walls of the tubes. These types of structure may be contrasted as **concordant** in Hexactinosa but **discordant** in Lychniscosa. The discordant lychniscosan type causes difficulties in interpreting some fossils because interruption of the strands by circulatory passages of doubtful character cannot be taken as a criterion of **intradictyonal** canalization (as in Hexactinosa).

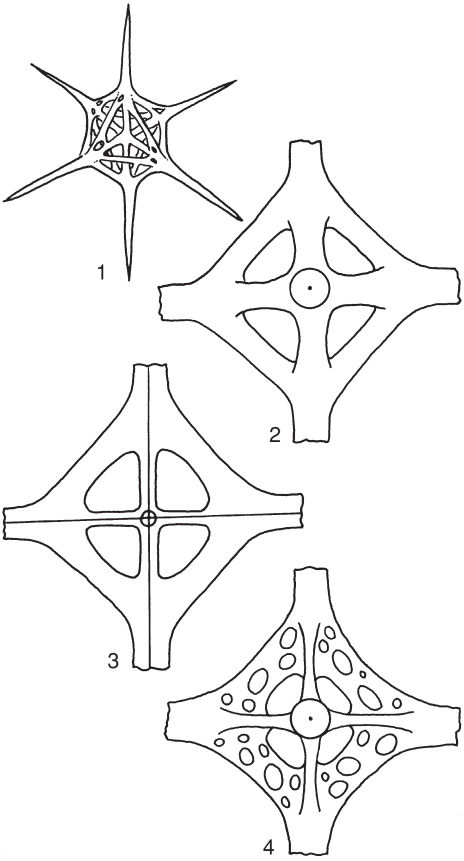

FIG. 61. Order Dictyonida, suborder Lychniscosa, lychniscs; *1,* young lychnisc, not yet incorporated into dictyonal framework, showing octahedral form of nodal lantern; at this stage 12 interactinal buttresses of lantern are more delicate than spicular rays (see view *3*); *2,* nodal part of typical adult lychnisc, drawn with 1 beam of dictyonal framework toward front, showing 8 of 12 interactinal buttresses (in this view, others are hidden behind); *circle with central dot,* cut skeletal beam facing front; *3,* section through adult lychnisc developed as in view *2* showing relatively unthickened central part; *lines* that intersect at center are axial canals of sectioned rays; *4,* nodal part of adult lychnisc, in which solid nodal buttresses are replaced by perforated plates; same view as view *2* (new).

Lychniscosa other than *Calyptrella* may have a dictyonal cortex, produced either by secondary accretion or by modification of the outermost primary meshwork. If primary meshwork is modified, this usually happens in one of three ways. First, lychnisc octahedra may be solidified at the surface although

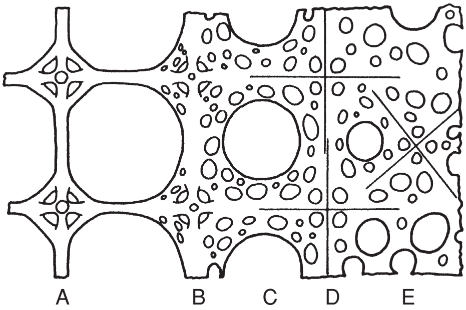

FIG. 62. Order Dictyonida, suborder Lychniscosa; cortical modification of external lychniscs to form a porous cortical membrane, seen in external view of skeletal surface; different conditions represent stages in development of this type of cortex in different sponges; *A,* unmodified lychniscs, like those of internal meshwork except that unattached rays (*central circles*) project freely from surface; *B,* lychnisc buttresses in plane of surface are replaced by perforated plates; at left, those of adjacent lychniscs are just confluent; at right, a continuous porous lamella extending between adjacent spicules; *C,* surface is formed by a porous siliceous membrane, with large pore at center of each interspicular mesh; *D,* distal rays and outer half of each nodal lantern are aborted, positions of spicules are shown by their axial canals; spicular centers indicated by axial crosses, around each of which are grouped 4 small pores that reflect underlying half-lantern structure; *E,* cortex is porous siliceous membrane with axial canals of spicules oriented irregularly (not united to form continuous meshwork, as in view *D*); positions of centers as in view *D* (new).

remaining open structures in the interior. Second, surface layers may have an irregular structure, contrasting with regular internal meshwork. Third, the meshes at the surface may be covered by a finely porous siliceous membrane that is produced by expansion of the buttresses of nodal octahedra to form perforated plates, which grow together, or by union of branching siliceous filaments that grow across the meshes (Fig. 62). Distally directed rays of dictyonalia at the surface and the corresponding halves of their nodal octahedra are then often aborted. This type of cortical membrane is pierced by small ostia or postica but often extends into larger canals if these are present.

Canalization of the skeleton may be present or absent and intracortical only or fully developed. The simplest features are small ostia or postica outlined by secondary meshwork as in *Callicyclix meandrina* (SCHRAMMEN) or by piercing a primary cortex as in *Callodictyon* ZITTEL. These presumably represent small inhalant canals and flagellated chambers like those of living *Callicyclix* species. Other fossils have diplorhytic canalization (i.e., epirhyses and aporhyses) or single systems of skeletal canals resembling diarhyses or schizorhyses. Epirhyses and aporhyses may represent inhalant and exhalant canals, respectively, although modern examples are unknown; but the nature of the soft parts is uncertain in the others. In Hexactinosa, diarhyses and schizorhyses are distinct, but skeletal canals that resemble them in fossil Lychniscosa are instead intergrading. Various fossils could have either intradictyonal canalization or cavaedial passages enclosed by anastomosing tubes or lamellae, according to how they are interpreted. The discordance between skeletal organization and local directions of growth does not permit these states to be distinguished by evidence from skeletal structure.

Superficial meshwork occurs in some genera and usually consists either of connected dermalia (in Cypelliidae) or of adventitious siliceous filaments that grow out from the surface of the dictyonal framework (Fig. 63). These filaments commonly grow from the ends of projecting dictyonal rays or from their positions when projecting rays are aborted, especially on the gastral side. They occasionally form paratangential networks that probably mark the position of the soft gastral membrane. Superficial meshwork formed from dictyonal hexactines is uncommon but occurs in some genera (e.g., *Stauronema* SOLLAS).

The basal skeleton may be formed from dictyonal hexactines, with or without nodal octahedra, or from siliceous filaments that grow downward from the skeletal surface in the lower parts of the body. The latter type occurs especially in sponges from the chalk of western Europe, in which it forms rootlike outgrowths. It seems to be an adaptation to fixation on soft sediment. Some Cretaceous

Ventriculitidae with dictyonal framework canalized by radial to labyrinthine epirhyses and aporhyses have their basal meshwork canalized by tubular longitudinal canals that run down from the positions of ostia in the dermal surface proper, as in *Rhizopoterion* ZITTEL.

The peripheral capsule of the living *Callicyclix zitteli* (MARSHALL & MEYER) may be supported entirely by loose pentactines resembling dermalia or, additionally, by a secondary dictyonal meshwork that grows into it from margins of the tubular branches at the end of normal growth. Various fossil genera (e.g., *Tremabolites* ZITTEL) have similar, rigid but usually denser structures produced by an initial growth of typical dictyonalia covered externally by a layer of smaller components and an external siliceous membrane formed from anastomosing siliceous filaments. Axial crosses of spicules that appear to be **stauractines** may occur in this membrane; but sometimes these are dictyonalia with distal rays aborted. In some forms (e.g., *Stamnia* POMEL) a similar membrane coats the marginal surface of a sponge with intradictyonal epirhyses and aporhyses.

In *Coeloptychium* GOLDFUSS the upper surface of a radially plicated funnel is covered by a sieve plate formed from siliceous filaments that grew out from the tops of upward facing plications. In *Cameroptychium* LEONHARD, a comparable sieve plate is formed from unmodified adventitious lychniscs.

Lychniscosa are difficult to classify due to our lack of knowledge of their soft parts. Consequently, the arrangement used here in some of the accepted divisions is more or less arbitrary.

The family Calyptrellidae comprises only *Calyptrella* SCHRAMMEN, with a simple netlike skeleton. The Callodictyonidae comprise all Lychniscosa with euretoid-like skeletons and no canalization or with simple ostia and postica only except for some specialized genera referred to the family Coeloptychidae. A soft peripheral capsule or a rigid **peripheral skeleton** may be present in genera with the body composed of dividing and anastomosing tubes (*Callicyclix, Tremabolites*); but the presence or absence of soft capsules is not determinable in fossils. The Coeloptychidae are comparable but specialized sponges in which an annular peripheral skeleton truncates either plications of a funnel-like body or radiating tubes that arise from plications of an axial funnel. The upper surface of the body or the inside of an axial funnel may be covered by a sieve plate.

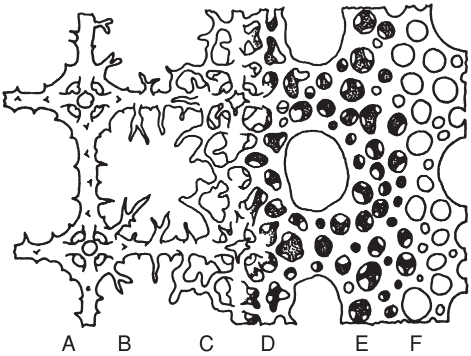

FIG. 63. Order Dictyonida, suborder Lychniscosa; formation of finely porous, cortical membrane from branched and anastomosed, siliceous filaments, which grow out from lychniscs at surface; conditions represent those of different genera or stages in development; *A,* meshwork at surface is similar to that of interior, skeletal beams ornamented with small spines; *B,* branched, siliceous filaments project into and over outermost spicular meshes; *C,* filaments are now anastomosed, although spicular meshwork is still visible under them; *D–F,* spicular meshwork covered externally by dense, three-dimensional meshwork of anastomosed, siliceous filaments; *D,* mesh spaces between filaments of irregular shapes; *E,* external filaments form a smooth, external membrane, with rounded pores; *F,* this is shown alone, with underlying structure omitted; between views *D* and *E,* an intracortical, skeletal pore opens into each underlying mesh of dictyonal framework; similar structures may occur in peripheral skeletons (new).

The Ventriculitidae are Lychniscosa with radial to labyrinthine epirhyses and aporhyses and no special marginal structures. In some, the skeletal canals are arranged in longitudinal series, similar to the arrangement in cribrospongiid Hexactinosa. In others, this pattern is modified by multiplication of epirhyses; by furrowing of skeletal surfaces that may replace epirhyses on the dermal side; by development of internal labyrinths, although the ostia and postica retain their alternating arrangement; or in other special ways. The surfaces are usually coated by a siliceous cortical membrane, and a superficial meshwork may occur. The latter is usually formed from siliceous filaments, but sometimes from dictyonal hexactines. The body is nearly always funnel-like.

The Camerospongiidae include some sponges similar to the Ventriculitidae with a flattened oscular margin coated by an annular siliceous membrane and other sponges in which the wall resembles an axial tube with lateral outgrowths or a cavaedial labyrinth, with an annular membrane at the summit. Researchers interpret the latter types as showing the effects of coalescence of inhalant canals around radial chamber-bearing structures.

Coeloscyphia TATE (=*Polyblastidium* ZITTEL), the only genus of the Polyblastidiidae, is a sponge in which an axial tube or group of tubes emits budlike lateral outgrowths. The latter have rows of epirhyses on the outside and longitudinal aporhytic furrows on the inside. This sponge is possibly but not certainly a specialized ventriculitid.

The Pachyteichismatidae are funnel-like or toplike sponges, with a canal system of uncertain type. In some genera the wall is excavated from both sides by alternating clefts that may intercommunicate internally. These forms grade into others in which the wall is labyrinthically cavernous. Small ostia or short radial canals may occur in the walls of internal passages. The dictyonal framework is characteristically very regular, with little or no cortex. The clefts or internal passages were regarded as cavaedia by SCHRAMMEN (1936) but seem more probably intradictyonal.

Dermal surfaces of Sporadopylidae have alternating apertures of radial skeletal canals, which either pass directly through the skeleton or into a labyrinth before opening on the gastral side. The canals are, thus, comparable with both diarhyses and schizorhyses. In the Dactylocalycidae a single system of anastomosing tubular canals opens through both skeletal surfaces. Both families have extensive suppression of lychnisc octahedra in some genera (e.g., *Dactylocalyx*), which have been mistaken for hexactinosa.

The Cypelliidae have canalization that seems like that of Dactylocalycidae, but the Cypelliidae are older and have the dermal surface coated by a porous superficial membrane in which the dermalia are imbedded.

PHYLOGENY

Nothing is known of the origin of this order, which is first represented in the record by specialized Devonian *Pillaraspongia* RIGBY, 1986b from western Australia and possibly *Pseudopemmatites* FRAIPONT, 1911 and *Pachyspongia* TERMIER & TERMIER, 1981 from the Devonian of Belgium, along with figured but undescribed sponges from the Upper Devonian of Poland (RIGBY, RACKI, & WRZOLEK, 1982). Until recently the specialized hexactinosid *Cribrospongia* (=*Tremadictyon*) and *Casearia* from the Middle Triassic (Anisian) were the oldest known representatives of the order. A supposed Ordovician example (*Okulitchina* WILSON: DE LAUBENFELS, 1955) is a lithistid demosponge (FINKS, 1960). IJIMA (1927) believed that Hexactinosa and Lychniscosa had different origins because nodal octahedra of the latter are formed before the spicules unite; if this corresponds with phylogeny, the lychniscs existed in proto-Lychniscosa before the dictyonine condition was developed.

A similar problem exists in the deciphering of further phylogeny. Complex forms appear in the geologic record without apparent simpler prototypes and are also the predominant types in the earlier faunas. Most of the simple types do not appear until the Early or Late Cretaceous. These types appear primitive morphologically by comparison with earlier complex sponges but appear in the opposite stratigraphic order to what might be expected. On the other hand, forms appearing suddenly were evidently immigrants and complex forms presumably evolved from simpler ancestors. Perhaps the original dictyonines were deep-water sponges whose simple descendants were unable until at least the Devonian in some lines and later in their history in other lines to extend into depths approaching wave base, which their thicker-walled derivatives could colonize.

The theoretical prototype of Hexactinosa is a lyssacine sponge with hexactinal dermalia, principalia, and gastralia and with hexaster microscleres and some prototypes of uncinates and sceptrules. The sponge is **basiphytous** (not **lophophytous**), with a basal skeleton composed of hexactines like the **principalia.** Prototypes of sceptrules could have been small pinular hexactines that gave rise first to sarules (see IJIMA, 1927) by loss of paratangential rays and then to clavules or scopules. Uncinates do not appear to correspond with the comitalia of Lyssacinosa because the latter take part in formation of rigid frameworks and uncinates are not fused. The principalia are arranged in a single layer, with a longitudinal and transverse orientation. The prototype of Lychniscosa is a similar sponge with loose lychniscs as principalia if ontogeny follows phylogeny in modern forms. The prototypes of uncinates and sceptrules need not have been present, but the absence of these spicules in the few modern species may be due to their loss in phylogeny, as appears to be true in some Hexactinosa. This sponge is presumably derived from an older one without lychniscs.

The fossil of pre-Triassic age that comes closest to these prototypes is the Permian dictyospongiid *Microstaura* FINKS (FINKS, 1960), although nothing is known of the microscleres and most dictyospongiids are lophophytes. This middle Permian genus also seems to have evolved far too late.

If the phylogeny of Hexactinosa is assessed from the comparative evidence, the primitive stock are sponges with farreoid skeletons and sarules or some other prototypes of clavules and scopules. The Farreidae are more or less unaltered descendants of these sponges. The euretoid skeleton was presumably evolved from the farreoid type, resulting in a dictyonal framework that was three dimensional initially; this in turn allows further evolution of thicker-walled sponges and more efficient circulatory systems. Interaction of the later developments leads to canalization of the skeleton on lines determined by previous evolution of the canal or chamber systems. The simple Euretidae, in which sceptrules are normally **scopules,** represent the stock from which higher forms originated since the sceptrules of the latter are scopules in all known instances. The Craticulariidae and Cribrospongiidae are canalized sponges that retained a canal system with both inhalant and exhalant canals but diverged into forms having contrasting serial patterns. Their prototypes are forms like the living *Chonelasma* SCHULZE and *Tretochone* REID that have similar canal systems but only **intracortical** canalization. The craticulariid pattern compares with linear series of ostia and postica that occur in various euretids; the cribrospongiid type has no known euretid counterpart and, thus, seems more specialized. The Aphrocallistidae and Tretodictyidae represent independent evolutionary series of different but still euretid origin. The other families are enigmatic, but *Stauroderma* and Porospongiidae are probably derivatives of the Cribrospongiidae and Tretodictyidae, respectively.

As noted, this picture does not fit the stratigraphic sequence of first appearances, but these clearly do not correspond with any probable evolutionary sequence. Although sponges with dictyonal skeletons are known from the Devonian of Australia and Europe, the earliest known Hexactinosa are the specialized *Cribrospongia* and *Casearia* of Middle Triassic (Anisian) age. Even allowing for initially rapid evolution, the specialization and divergence of these genera imply a long previous history, perhaps from a period very much older than Permian. The most specialized genus, *Stauroderma,* appeared suddenly in the Middle Jurassic with the fully evolved Craticulariidae (*Craticularia*) and the first known euretids (*Pseudocavispongia* LAGNEAU-HÉRENGER). The first known (Oxfordian) tretodictyid, *Nitidus* de Laubenfels had already wide cavernous schizorhyses like those of the living *Psilocalyx* Ijima. The canalized Aphrocallistidae and very simple Farreidae appeared in the Cretaceous. In none of these families is there evidence of major evolutionary progress after their first appearances.

The Aulocalycidae, included doubtfully as Hexactinosa following Ijima (1927), lack the dictyonal strands, uncinates, and sceptrules that occur in farreoid and euretoid genera. They could be forms derived from simple Hexactinosa by loss of these features. They do not appear to belong with the Lyssacinosa because the parenchymal megascleres are all hexactines and all fused together as in true dictyonines. But they could mark an independent line of descent from the same source as true Dictyonida without closer relationship.

The Lychniscosa have a similar history of sudden appearance of already specialized genera, with simple forms making late appearances. The Cretaceous *Calyptrella,* with a simple netlike skeleton, is probably a late survivor of the primitive stock of the suborder. The first step in further evolution are appearances of farreid-like and euretid-like sponges, whose most direct descendants would be the Callodictyonidae. From this stock originated various canalized families. The Ventriculitidae, with diplorhytic canalization (epirhyses and aporhyses), appear to have existed by the Middle Jurassic (*Calathiscus* Sollas; although nodal octahedra are not clearly developed in most instances, and no good material is known). The Pachyteichismatidae, Sporadopylidae, and Cypelliidae, all of which flourished in the Late Jurassic, mark three further lines of specialization. The Cretaceous abundance of Callodictyondiae and Ventriculitidae should mark further evolution in these families. The Cretaceous Coeloptychidae were essentially highly specialized callodictyonids. The Dactylocalycidae, first appearing stratigraphically in the Lower Cretaceous, should represent a further line of descent, unless they are related to the earlier Cypelliidae.

GLOSSARY OF MORPHOLOGICAL TERMS

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INTRODUCTION

Parts of speech of terms, where not obvious, is indicated: (n), noun; (n pl), plural noun; (adj), adjective. Obsolete terms are in italics, and terms applied mainly or exclusively to members, spicules, or features of specific classes are indicated by (Cal) for Calcarea, (Dem) for Demospongea, (Hex) for Hexactinellida, and (Het) for Heteractinida.

GLOSSARY

acantho-. Ornamented with spinules.

acanthorhabd (n). Any monaxon with spinules.

acanthostrongyle (n). Strongyle with spinules (Dem).

acanthostyle (n). Style with spinules (Dem).

acanthotriaene (n). Triaene with spinules (Dem).

acanthotylostyle (n). Monaxon with swollen knob on one end and sharply pointed at the other end, with spines along the shaft.

acanthoxea (n). Oxea with spinules (Dem).

acerate (adj). Needle shaped, oxeate, referring to the extremities of megascleres.

acrepid (adj). Anaxial, refers to development from an anaxial initial body, or crepis (Dem).

actin, -e (n). True spicular ray, produced by secretion of mineral matter around an organic axial filament.

-actin, -e (n). Signifies ray in names of spicules referring to number, character, or absence of rays; in Hexactinellida, also designates holactines.

-actinal (adj). termination signifying ray.

afferent (adj). Inhalant.

agglutinating (adj). Sponge that creates its own substratum by cementing together a mixture of foreign material.

amararhysis (n). Skeletal canal in the form of a longitudinal tunnel with slitlike gastral openings, also open dermally at the ends of branch tunnels leading to the tops of papilliform external outgrowths; condition in which such skeletal canals are present (Hex).

ambiostium (n). A large exopore at the junction of two chambers that communicates with both chambers (Dem).

ambisiphonate (adj). Condition in a sphinctozoan in which an axial tube is formed by growth from both the floor and the roof of each skeletal chamber, with the two parts growing together so that a ring of perforations is left (Dem).

ambucinate (adj). Diactine with spines pointed back toward the center.

amoebocyte (n). Mesenchymal cell capable of amoeboid movement.

amphiaster (n). Microsclere with a group of raylike centrifugal spines at each end of a straight central shaft (Dem).

amphiblastula (n). Sponge embryo or free larva in which the surface is flagellate except in a small area at one pole.

amphidisc (n). Monaxial microsclere in which the ends of a straight shaft bear discoidal transverse expansions or whorls of recurved teeth (umbels) (Dem, Hex).

amphitriaene (n). Spicule similar to a triaene with a cladome at both ends of the rhabdome (Dem).

amphitrider (n). Amphitriaene-like desma, with three clones like those of a clonome at each end of a central shaft (centrome); or desma developed from an amphitriaene crepis, not retaining an obvious amphitriaene-like form (Dem).

amphityle, -ote (n). Tylote.

ana-. Designates grapnel or anchorlike spicules, with cladi recurved toward a rhabdome.

anactinal (adj). Without true cored rays.

anapolyaenes (n pl). Grapnel-like polyaenes, with the cladi recurved toward the rhabdome (Het).

anatriaene (n). Triaene with cladi recurved toward the rhabdome.

anaxial (adj). Mineral secretion in spicules not formed around an organic axial filament; see also cryptaxial.

anaxon (n). Spicule formed without organic axial structures, and hence also lacking true rays; see also cryptaxon.

anchora (n). Dentate anchor similar to chela (Dem).

anchorate (adj). With paired rays recurved toward a shaft formed by an unpaired ray, so that the spicule is anchorlike (Hex, Dem).

aniso-. Unequal; asymmetrically developed.

anisochela (n). Chela with ends developed differently (Dem).

ankylosis (n). Union of spicules by fusion.

anomoclad (n). Sphaeroclone (Dem).

anomoclone (n). Variably shaped desma intergrading with chiastoclones but not resembling an amphitrider, in some forms like a stoutly built arched rhizoclone or approaching a didymoclone; nature of the crepis unknown (Dem).

aphodal (adj). Leuconoid with aphodi but not prosodi.

aphodus (n). Fine tubular duct connecting a flagellated chamber with a main trunk or branch of an exhalant canal (apochete).

apical (adj; of choanocyte nuclei). At the end of the cell that bears the flagellum and collar (Cal).

apochete (n). Exhalant canal.

apopore (n). Exhalant pore.

apopyle (n). Open and exhalant end of a flagellated chamber.

apopylar (adj). Of or with an apopyle.

aporate (adj). Lacking pores.

aporhysis (n). Skeletal canal corresponding with a flagellated chamber or an exhalant canal of the soft parts.

aporhysome (n). Inner trabecular network (Hex).

archaeocyte (n). Reproductive cell, capable of converting into other types of cells.

ascon (n). Sponge in which choanocytes line the paragaster, without flagellated chambers or a canal system.

asconoid (adj). With the character of an ascon; as in ascons; see also homocoelous.

asiphonate (adj). Condition of thalamid sphinctozoans that lack any form of axial channel (Dem).

aspidaster (n). Discoidal microsclere with the structure of a flattened sterraster (Dem).

aster (n). Any polyactinal or seemingly polyactinal microsclere.

-aster. Designates some form of aster.

astral (adj). With anaxial terminal outgrowths of the type characteristic of rosettes (Hex).

astroclone (n). Anaxial desma with radiating clones, which are not all directed to one side as in sphaeroclones; zygomes rootlike to cuplike. Includes anomoclones *sensu* Schrammen (not Rauff) (Dem).

astrorhiza (n). traces of excurrent canal system on or within a rigid skeleton that appears as a radial or star-shaped structure.

astrose (adj). Comprising asters (Dem).

atrium (n). The spongocoel of a sponge.

aulocalycoid (adj). With diagonally interwoven or intersecting, strandlike series of skeletal beams through the whole depth of the dictyonal framework, in which typical subparallel dictyonal strands are not present (Hex).

autodermal (adj). Of or comprising autodermalia (Hex).

autodermalia (n pl). Megascleres that support the dermal membrane directly (Hex).

autogastral (adj). Of or comprising autogastralia (Hex).

autogastralia (n pl). Megascleres that support the gastral membrane directly (Hex).

axial canal (n). Intraspicular cavity left by decay of an axial filament, or the same enlarged by internal solution of mineral matter.

axial cross (n). Feature seen at the spicular center of triaxons, where axial filaments of rays arranged in opposite pairs appear to intersect (Hex).

axial filament (n). Organic coring filament, around which the mineral part of a spicular ray is deposited; see also axone.

axial rudiment (n). Rudimentary axial filament.

axial tube (n). Skeletal structure developed in the axial part of a series of skeletal chambers in some thalamid sphinctozoans, consisting of a series of discontinuous structures like the septal necks of chambered Cephalopoda, or of a single continuous tube (Dem).

-axon. General termination of names based on the number of axes of growth that rays follow.

axone (n). Axial filament.

azygose (adj). Without zygomes (Dem).

basal (adj; of choanocyte nuclei). At the end of the cell that is attached to the mesenchymal surface (Cal).

basal (adj; of body or spicules). Attached to or next to the substratum; corresponds with initial in sponges attached at one point only.

basal plate (or lamina) (n). Special skeletal layer or structure developed next the substratum in basiphytous sponges.

basal ray (n). The third ray of a sagittal triradiate, contrasted with the two similar rays (Cal).

basal skeleton (n). Any spicules or structure specially concerned with basal attachment.

basalia (n pl). Prostalia of the dermal part of the body, by which the sponge is anchored (Hex).

basidictyonalia (n). Small hexactines fused to form a special basal skeleton in some lyssacine Hexactinellida.

basiphyte (n). Sponge attached by an encrusting base.

basiphytous (adj). Attached by an encrusting base.

beam (n). Rodlike element in hexactinellid skeletons formed of merged rays of adjacent spicules.

bihamate (n). Diancistron (Dem).

bipocillate (n). Bipocillus (Dem).

bipocillus (n). Monaxial microsclere whose ends bear spoonlike or leaflike expansions, with concave sides facing together; see also diaspid (Dem).

birotulate (n). Amphidisc; an amphidisc, staurodisc, hexadisc, or hemidisc (Hex).

bispatulate (n). Palmate chela (Dem).

brachyome (n). The fourth arm of a trider when shorter than the clones of the brachyome, comprising a short clone, a clone-rudiment, or a crepidal ray from which no clone is produces (Dem).

bullipore (n). Pore within a cribribulla.

calthrops (n). Regular tetraxon with four equal rays; see also chelotrope (Dem).

canal (n). Internal passage to carry circulating water.

canal system (n). Inhalant or inhalant and exhalant canals of sycons and leucons.

canalar (adj). Related to the canal or chamber system.

canalar membrane (n). Trabecular membrane lining an inhalant or exhalant canal (Hex).

canalaria (n pl). Spicules occurring in the linings of inhalant or exhalant canals (Hex).

candelabrum (n). Tetralophose calthrops in which the branches of one ray may differ from those of the others (Dem).

capstan tubercles (n pl). Stalked tubercles, with a constricted neck and an expanded head, which may be bifid or trifid, arising by thickening of simple or branching lateral spinules (Dem).

category (of spicules) (n). One of the main types of spicules found in a sponge or a group of sponges, distinguished by form, size, location, function, or some combination of these characters.

cateniform (adj). Catenulate or moniliform (Dem).

catenulate (adj). With skeletal chambers arranged in a linear series (Dem).

cavaedia (n pl). External spaces enclosed within a body consisting of dividing and anastomosing tubes, or between folds of a plicated wall; not part of the canal system proper; see also intercanals.

cavaedial space (n). Large, deep indentations of the sponge's dermal surface.

centrifugal (adj). Directed away from the spicular center.

centrome (n). The central shaft of an amphitrider (Dem).

centrotylote (n). Monaxon with a central enlargement (Dem).

centrum (n). A differentiated central part of a spicule.

chamber (n). One of the regular juxtaposed hollow structures formed by the skeleton in sphinctozoan sponges (Dem).

chamber system (n). The flagellated chambers to which choanocytes are restricted in syconoid and leuconoid sponges.

chela (n). Microsclere developed from a C-shaped sigma, in which the ends bear inward-facing, toothlike or bladelike, lateral appendages, arranged in opposite pairs (see dentate chela, palmate chela) (Dem).

chelaster (n). Pseudaster developed from a chela (Dem).

cheloids (n). Microscleres resembling chelas and related forms.

chelotrope (n). Calthrops (Dem).

chessman spicule (n). Discaster (Dem).

chiastoclone (n). Name applied to desmas of Orchocladina having the form of an amphitrider with the central shaft shorter than the clones, or with clones emitted radially from a center; nature of the crepis uncertain (Dem).

choanocytal (adj). Lined by or composed of choanocytes.

choanocytal membrane (n). Reticulate internal membrane, diverticula of which form the flagellated chambers, composed of choanocytes connected by lateral processes (Hex).

choanocyte (n). Flagellated cell with a single flagellum, enclosed basally by a tubular protoplasmic collar; see also collar cell.

choanosomal (adj). Of the choanosome.

choanosome (n). The part of the body of a syconoid or leuconoid sponge containing flagellated chambers, when covered externally by a stratum (e.g., an ectosome) without choanocytal structures.

chondrenchyma (n). Stiff, cartilage-like mesenchyme.

chone (n). Intracortical inhalant canal, extending through a cortex from the external surface to a subdermal space underlying it (Dem).

choristid (adj). (1) With tetractinal or triactinal megascleres, to which other types may be added, but without desmas; (2) of choristids (Dem).

choristid (n). Demosponge with a choristid skeleton; member of the order Choristida.

clad (n). Any ray or axial branch in a spicule. The term is used chiefly in triaenes or tetraenes.

cladi (n pl). The similar rays of a triaene or similar spicule (e.g., diaene, tetraene).

cladocalthrops (n). Calthrops with repeatedly branching rays (Dem).

cladome (n). Group of similar rays, arranged radially in relation to a monactinal or diactinal rhabdome.

clathrate (adj). Structure resembling an open latticework.

clavidisc (n). Microsclere in the form of an ovate disc with a central perforation, produced by ingrowth and union of the ends of a diancistron-like prototype; see also psellium.

clavule (n). Pinlike or nail-like sceptrule in which the end of the spicule containing the axial cross is more or less swollen (tylote), or bears a marginally denticulate transverse disc or a ring of recurved teeth (Hex).

cleme (n). Long monactine with alternating thornlike lateral spinules arranged in two opposite rows (Hex).

cloaca (n). See spongocoel.

cloacal (adj). Of the cloaca, paragaster, or spongocoel.

clone (n). Raylike arm of a desma, partly or wholly anaxial (Dem).

clonome (n). Group of three similar clones, analogous (not homologous) with a cladome (Dem).

collar cell (n). Choanocyte.

collenchyma (n). Mainly gelatinous mesenchyme.

collencyte (n). Typically stellate mesenchymal cell, the points of which emit fine branching filaments that may be connected syncytially with those from other examples (Cal, Dem).

collosclere (n). Spicule composed of colloidal silica (Dem).

comital (adj). Comprising comitalia (Hex).

comitalia (n pl). Accessory parenchymal megascleres, occurring apposed to principalia in some lyssacine Hexactinellida (Hex).

concordant structure (n). In dictyonine Hexactinellida, condition in which the orientation of dictyonal strands is related to the local direction of growth.

connecting beams (n pl). In dictyonine Hexactinellida, skeletal beams that connect adjacent dictyonal strands laterally.

connecting membrane (n). Trabecular membrane extending between the open ends (apopyles) of flagellated chambers (Hex).

coring (adj). Running longitudinally in the core of a skeletal fiber.

coronal (adj). Fringing an osculum.

cortex (n). Thick, rindlike ectosome.

cortex (*sensu* Moret) (n). Any external part of the skeleton that differs from that of the interior, irrespective of homology.

cortex dépendant (*sensu* Moret) (n). Any specially modified external part of a skeletal framework, or superficial structure arising from the surface of such a framework.

cortex indépendant (*sensu* Moret) (n). Ectosomal triaenes of Demospongea, dermalia and gastralia of Hexactinellida.

cortical (adj). Of the cortex; of the skeletal cortex.

corynaster (n). Finely spinulate, clublike tylostrongyle (Dem).

craticula (n). A screenlike element across the outer end of an exaulos (Cal).

craticular pore (n). A pore in the craticula.

crepidal (adj). Of the crepis (Dem).

crepis (crepides, pl.) (n). Initial body in a spicule that then grows substantially by anaxial secretion (Dem).

cribribulla (n). Inward-facing, blisterlike sieve at the inner end of an exaulos.

cribripore (n). Small pores in sievelike cribribulla (Dem).

cric- (cricc-). With a typically strong annular ornament (Dem).

criccalthrops (n). Annulated calthrops (Dem).

cricophalangaster (n). Small cricorhabd with spinulate annulations (Dem).

cricorhabd (n). Strongly annulated monaxon (Dem).

cricostyle (n). Annulated style, with the annulations sometimes dying out toward the sharp end (Dem).

cricotriaene (n). Annulated triaene (Dem).

cryptaxial (adj). Anaxial (Dem).

cryptaxon (n). Anaxon (Dem).

cryptosiphonate (adj). Condition of thalamid sphinctozoans in which skeletal chambers communicate through an aperture or a group of apertures at the top of each chamber, without an axial tube (Dem, Cal).

cyathiform (adj). Cup shaped.

cystenchyma (n). Mesenchyme in which the most common cells contain conspicuous vacuoles.

Deckgespinnst (n). Superficial meshwork (Hex).

Deckschicht (n). *Sensu* Zittel, a skeletal cortex, superficial meshwork, or a peripheral skeleton (cf. dermal layer *sensu* Hinde); *sensu* Schrammen, a skeletal cortex.

dendritic (adj). Forming branching growths.

dendro-. Treelike.

dendroceratid (adj). Type of spongin skeleton consisting of dendritically branched fibers, which are unconnected except where they arise from a common basal plate (Dem).

dendroclone (n). Name applied to desmas of Orchocladina with the form of an amphitrider or a dipolar rhizoclone, in the former with a centromelike shaft roughly equalling or longer than the clones; nature of the crepis uncertain (Dem).

dentate chela (n). Chela in which the lateral appendages are toothlike, with one to several pairs at each end (Dem).

dermal (adj). (1) external or inhalant; (2) consisting of pinacocytes; (3) non-choanocytal; (4) comprising a dermis; (5) supporting a dermis or a dermal membrane; (6) comprising a special external stratum of a skeletal framework; (7) peripheral.

dermal layer (histological) (n). (1) Epidermis and mesenchyme; (2) an ectosome (Cal, Dem).

dermal layer (skeletal). Name applied to various external parts of skeletal frameworks, or to a peripheral skeleton, irrespective of whether related to a true dermal skeleton.

dermal membrane (n). Membranous trabecular network forming the dermal (outer, inhalant) surface of the body (Hex).

dermal skeleton (n). Skeleton of an ectosome or an endosome; the dermalia in Hexactinellida, or any rigid structure formed by their union.

dermal surface (n). The external and inhalant surface of the lateral wall surrounding an axial paragaster, or any equivalent surface.

dermalia (n pl). (1) Spicules supporting an ectosome or an endosome (Dem); (2) a dermal membrane (Hex); (3) (n) specialized spicule of outer or dermal part of skeleton.

dermis (n). Thin, skinlike ectosome.

desma (n). Articulating megasclere; see also desmone (Dem).

desmal framework (n). The skeletal framework of lithistid demosponges, consisting of articulated desmas (Dem).

desmoid (n). Desmalike spicule, not regarded as a true desma, or supposed to derive from a pseudaster (not a normal megasclere) (Dem).

desmone (n). Desma (Dem).

diact (n). Diactine.

diactin, -e (n). Spicule with two rays; two-rayed holactine (Hex).

diactinal (adj). Two-rayed.

diactinose (adj). Comprising diactines and modified derivatives, which are initially diactinal (Dem).

diaene (n). Triaene-like spicule with only two cladi.

diancistron (n.; pl. -a). C-shaped microsclere with bladelike lamellae developed along the inside curve, hence appearing like a partly opened penknife (Dem).

diaphragm (n). More or less rigid internal plate subdividing chambers (Cal).

diarhysis (n). Oblique to radial skeletal canal that is open at both ends, marking the position of a complex flagellated chamber, not accompanied by epirhyses; condition in which diarhyses are present (Hex).

diaspid (n). Bipocillus.

diaxon (n). Spicule with rays following two growth axes that meet at an angle or intersect.

diaxial (adj). With rays following two growth axes that meet at a point or intersect; containing two angled axial filaments.

dicho-. Signifies dichotomous branching of rays.

dichocalthrops (n). Calthrops with one or more rays branched dichotomously.

dichohexactin, -e (n). Hexactine with rays branched dichotomously.

dichotriaene (n). Triaene with the cladi branched dichotomously.

dichotetraene (n). Tuberculate monaxial desma of dipodal to polypodal or irregular form, with rootlike, terminal zygomes.

dicranoclone (n). Tuberculate monaxial desma of dipodal to polypodal or irregular form, with rootlike, terminal zygomes.

dicrepid (adj). With a diactinal crepis (Dem).

dictyoceratid (adj). Type of spongin skeleton consisting of reticulate fibers (Dem).

dictyonal (adj). Of the dictyonal framework (Hex).

dictyonal cortex (n). Specially modified external part of a dictyonal framework (Hex).

dictyonal framework (n). The rigid, parenchymal skeletal framework of dictyonine Hexactinellida.

dictyonal strand (n). Longitudinal to radial, strandlike series of skeletal beams, formed by union of a series of dictyonalia (Hex).

dictyonalia (n pl). Parenchymal megascleres that fuse to form the skeletal framework in dictyonine Hexactinellida (Hex).

dictyonine (adj). (1) With a parenchymal skeleton that is always a rigid skeletal framework, composed of fused megascleres that are always hexactines except when rays are lost at skeletal surfaces; (2) of dictyonines (Hex).

dictyonine (n). Hexactinellid sponge with a dictyonine parenchymal skeleton; member of the orders Hexactinosa or Lychniscosa.

didymoclone (n). Monaxial desma in which zygome-bearing clones are emitted from spherical swellings at the ends of an epirhabd, and are typically directed to one side of the desma; zygomes rootlike, or cuplike with denticulate margins (Dem).

dilophose (adj). With two lophose rays.

diploclone (n). Sublithistid desma with incipient to digitate expansions of the ends of an epirhabd, also grading into a normal strongyle; the zygomelike ends do not articulate as in lithistids proper (Dem).

diplodal (adj). Leuconoid with both prosodi and aphodi.

diplorhysis (n). Condition in which the skeletal framework contains both epirhyses and aporhyses.

dipolar rhizoclone (n). Rhizoclone with rootlike zygomes or distinct clones at the ends of a smooth central shaft, which is the epirhabd (Dem).

discaster (n). Microsclere with discoidal flanges or whorls of raylike spines surrounding a straight nonaxial shaft. Also called a sceptrella, discorhabd, or chessman spicule (Dem).

discohexact (n). Hexactinoid hexaster with terminal discs or umbels (Hex).

discohexaster (n). Hexaster in which the ends of the terminal outgrowths are capped by transverse discs or denticulate umbels (Hex).

discordant structure (n). In dictyonine Hexactinellida, condition in which the orientation of dictyonal strands is not related to the local direction of growth.

discorhabd (n). Discaster (Dem).

discostrongyle (n). Monaxial disc, with or without a rhabdome-like central stalk, arising from an initial strongyle (Dem).

discotriaene (n). Triaene with a specially modified cladome that consists of a siliceous disc with the axial filaments or canals of short initial cladi in the central part; see also symphyllotriaene (Dem).

distal ray (n). One of rays of a spicule, when directed outwardly at right angles to an external surface.

dodecaactine (n). Spicules with six equally spaced initial rays that diverge from a common point, but three alternating rays are shorter and the three intervening rays are longer and have trifurcate tips so that the spicule has 12 outer rays.

dragma (n). Monaxial microsclere that occurs in bundles (Dem).

dragmata (n pl). Monaxial microscleres occurring in sheaves and produced by a single scleroblast (Dem).

echinating (adj). Projecting from the surface of a skeletal fiber; used for monaxons occurring with one end imbedded in spongin fibers, which are said to be echinated by them (Dem).

ectosomal (adj). Of the ectosome.

ectosome (n). Chamberless and porous external stratum, extending across the outer ends of inhalant canals; developed as a thin dermis or a thick cortex (Cal, Dem).

efferent (adj). Exhalant.

emergence (n). In dictyonine Hexactinellida, migration of dictyonal strands to the dermal or gastral surface of a three-dimensional dictyonal framework.

endocameral (adj). Within the skeletal chambers of thalamid sphinctozoans (Dem).

endolithic (adj). Cavity-dwelling sponge occupying cavities in hard substrates.

endopore (n). Opening through the wall of a central tube, the endowall (Dem).

endopsammic (adj). Sand-dwelling sponge living in soft substrates.

endosomal (adj). Of the endosome.

endosome (n). Chamberless stratum between the choanosome and gastral or other exhalant surface. May also be misused as meaning choanosome (Cal, Dem).

endotube (n). Tube that pierces the endowall or extends into the chamber from the endowall in a sphinctozoan (Dem).

endowall (n). Wall of a central tube, cloaca, or siphon (Dem, Cal).

ennomoclone (n). Spicule with short, distal arm and three or six proximal, longer arms or rays directed symmetrically away from it; a tricranoclone or sphaeroclone (Dem).

epicrepid (adj). Formed directly around the crepis (Dem).

epidermis (n). Layer of pinacocytes or equivalent syncytial membrane, coating mesenchymal surfaces where choanocytes are absent (Cal, Dem).

ephirabd (n). The epicrepid part of a monaxial desma (Dem).

epirhysis (n). Skeletal canal corresponding with an inhalant canal in the soft parts.

epirhysome (n). Outer trabecular network (Hex).

epitheca (n). Thin, wrinkled layer different in structure from the normal skeleton.

epithelioid membrane (n). Epidermis consisting of a syncytial membrane (Dem).

epochete (n). Canal-like space that is properly an external depression, additional to true canal system.

equianchorate (n, adj). Isochela (Dem).

euaster (n). Radiate microsclere in which rays proceed from a genuine center (not from a monaxial shaft, as in pseudasters), also typically polyactinal; some with rays partly or completely enveloped by secondary silica that grows outward from the spicular center (see also sphaeraster, sterraster) (Dem).

euastrose (adj). Comprising euasters (Dem).

eulerhabd (n). Stout form of ophirhabd, often U-shaped (Dem).

euretoid (adj). With subparallel dictyonal strands spreading through three-dimensional primary meshwork (Hex).

eurypylous (adj). Leuconoid with chambers opening directly through the walls of exhalant canals (apochetes), without intervening aphodi.

eutaxiclad (n). Dicranoclone (note: this desma is not eutaxicladine, i.e., an ennomoclone, *sensu* Rauff, being based on a form of his rhizoclone) (Dem).

excurrent (adj). Flowing out.

exaulos (n). Spoutlike tube in sponge wall (Cal).

excurrent canal (n). Exhalant canal.

exhalant (adj). Through which water passes out; see also efferent.

exhalant area (n). Part of the surface of a sponge without paragaster or spongocoel, where exhalant canals open.

exhalant canal (n). Internal passage leading water from a group of flagellated chambers to the paragaster, or to an external exhalant area if a paragaster is lacking; see also apochete.

exopore (n). Pore that pierces the outer wall of a chamber (Cal).

exowall (n). External skeleton of a chamber (Cal).

farreoid (adj). With dictyonal strands restricted to a single layer or primary meshwork, to which further secondary meshwork may be added (Hex).

fiber (n). Column of spongin forming part of skeleton may or may not contain spicules or foreign materials.

filling structures (n pl). Endocameral skeletal structures of thalamid sphinctozoans (Dem).

flabellate (adj). Fanlike or tonguelike.

flagellated chamber (n). Choanocyte-lined lateral diverticulum or rounded internal cavity from which water is discharged to the paragaster directly (in sycons) or through an exhalant canal (in leucons) (Cal, Dem); diverticulum of the choanocytal membrane, which opens into meshes of the inner trabecular network (aporhysome) or into an exhalant canal (Hex).

floricome (n). Hexaster in which terminal outgrowths arranged in several whorls are S-shaped and petallike or plumelike, with the ends facing outward (Hex).

florule (n). Scopule-like spicule with a shaft shorter than the terminal spines, which form a flowerlike ring (?Hex).

forceps (n). Monaxial microsclere shaped like a sugar tongs (Dem).

furcula (n). Spicule shaped like a wishbone (Hex).

fusiform (adj). Tapered toward both ends and in oxeate spicules.

gastral (adj). Refers to (1) choanocytes; (2) the internal surface of the sponge wall surrounding an axial paragaster, to a corresponding surface when an axial paragaster is lacking, or to spicules or any other structure specially associated with this surface.

gastral cavity (n). See spongocoel..

gastral layer (n). Choanocyte layer.

gastral membrane (n). Membranous trabecular network forming the gastral (inner, exhalant) surface of the body (Hex).

gastral skeleton (n). The gastralia in Hexactinellida or any rigid structure formed by their union.

gastral surface (n). The internal and exhalant surface of the lateral wall surrounding an axial paragaster, or an equivalent surface.

gastralia (n pl). Spicules supporting the gastral membrane (Hex).

gemmule (n). Asexually produced regenerative body.

glass sponge (n). Member of the class Hexactinellida.

globostellate (n, adj). Sphaeraster or sterraster (Dem).

glomerate (adj). With skeletal chambers arranged like the seeds in an ear of corn or like grapes in a cluster (Dem).

grantioid (adj). Syconoid, with true enclosed inhalant canals in a compact wall.

graphiocome (n). Hexaster whose rays bear brushlike clusters of fine terminals; see also graphiohexaster (Hex).

graphiohexaster (n). Graphiocome (Hex).

habitus (n). External form.

hastate (n, adj). Tornote or oxea (Dem), a spicule remaining of uniform diameter for most of its length, but which has abrupt tapering tips.

heloclone (n). Sinuous monaxial desma with zygomes in the form of lateral facets or notches, sometimes digitate at the ends but without true zygome-bearing clones; axial canal often almost as long as desma; see also megaclad, megaclone, rhabdoclone (Dem).

helotriaene (n). Tripod with three long, curved rays and a tubercle-like rudiment of a fourth (Dem).

hemiamphidisc (n). Hemidisc (Hex).

hemiaster (n). Imperfect hexaster in which some rays are holactinal (Hex).

hemidisc (n). Asymmetrical amphidisc, with one terminal umbel much larger than the other; see also hemiamphidisc (Hex).

heteractine (n). Spicule of heteractinid sponge, commonly octactine based but may be polyactine.

heteractinid (adj). Referring to heteractine sponges.

heterocoelous (adj). With choanocytes restricted to flagellated chambers, the paragaster having a pinacocytal lining (Cal).

hexact (n). Hexactine (but some so-called hexacts of Hexactinellida are hexactinoid hexasters).

hexactin, -e (n). Spicule with six rays; six-rayed holactine (Hex).

hexactinal (adj). Six-rayed.

hexactinellid (adj). Normally taxonomic, but sometimes used of spicules meaning hexactinal.

hexactinoid (adj). Hexactine-like, in the instance of hexactine-like microscleres that are properly hexasters with a single anaxial terminal continuing the line of each true ray (Hex).

hexactinose (adj). (1) of hexasters, hexactinoid; (2) of a dictyonal framework, without lychniscs (Hex).

hexadisc (n). Hexactinal amphidisc-variant (Hex).

hexaene (n). Triaene-like spicule with six cladi (Het).

hexaster (n). Six-rayed (hexactinal) and triaxial microsclere, in which the end of each ray bears a group of anaxial, branchlike, and centrifugal outgrowths, or rarely a single anaxial extension of the true cored ray (Hex).

hiloid pit (n). Hilum-like pit in the basal part of a ray (Het).

hilum (n). Smooth pit in the surface of a sterraster marking the position of the scleroblast nucleus.

hispid (adj). With a bristly appearance, due to protrusion of spicules.

hispidating (adj). Giving a bristly appearance.

holactin, -e (n). Spicule without the special terminal outgrowths of hexasters (Het).

holactinal (adj). Without terminal outgrowths of the type seen in hexasters.

holaster (n). Rosette in which all rays bear terminals (Hex).

homocoelous (adj). Asconoid (Cal).

hypercalicified sponges (n). Sponges that secrete nonspicular calcium carbonate, and may include forms that cement spicules together with coatings of calcium carbonate, as well as inozoans and related forms whose principal skeletal structure is calcium carbonate, either aragonite or calcite.

hypodermal (adj). Subdermal.

hypodermalia (n pl). Megascleres that support the dermal membrane but underlie autodermalia from which they differ (Hex).

hypogastral (adj). Subgastral (Hex).

hypogastralia (n pl). Megascleres that support the gastral membrane but underlie autogastralia, from which they differ (Hex).

hypophare (n). Basal layer of the body, apposed to the substratum (Dem).

incurrent (adj). Flowing in.

incurrent canal (n). Inhalant canal.

inequianchorate (n, adj). Anisochela (Dem).

infundibuliform (adj). Funnel shaped.

inhalant (adj). Through which water enters; see also afferent.

inhalant canal (n). Internal passage, leading water to flagellated chambers.

inner trabecular network (n). The trabeculae on the gastral side of the choanocytal and connecting membranes (Hex).

interactinal (adj). Between rays.

interactinal angle (n). Angle between two rays.

interactinal buttress (n). Anaxial strut or plate forming one of the edges of a nodal octahedron in a lychnisc (Hex).

interactinal suture (n). Joint between the bases of rays of the same spicule, which are not continuous as in normal sponge spicules (Cal, Het).

intercanals (n pl). Cavaedia.

intermedia (n pl). Smaller spicules occurring between principalia or dictyonalia, excluding lyssacine comitalia (Hex).

interpore (n). Pores that pierce the wall between chambers in sphinctozoans (Dem).

intertrabecular (adj). Between trabeculae.

interwall (n). Upwardly convex partitions between chambers in sphinctozoans (Dem).

intracortical (adj). Extending through a cortex or a skeletal cortex, but not beyond it.

intradictyonal (adj). Refers to intraskeletal canalization of a dictyonal framework (Hex).

intraskeletal (adj). Within the skeleton; designates features produced by interruption of developing skeletal meshwork, as distinct from enclosed but essentially external cavaedia.

iso-. Equal; symmetrically developed.

isochela (n). Chela with similar ends (Dem).

isodictyal (adj). With the sides of skeletal meshes formed by terminally connected monaxons, cemented together with spongin (Dem).

keratode (n). Spongin.

keratose (adj). Composed of spongin; with a spongin skeleton only (Dem).

kieselhaut (n) (*sensu* Schrammen). Dense but porous siliceous membrane, usually a peripheral structure but sometimes coating a marginal surface only (Hex).

kyphorhabd (n). Stout, curved monaxon with transverse swellings on the convex side, which may have small articulatory facets at its ends (Dem).

labid (n). Forceps.

labripore (n). Exopores surrounded by a distinct external lip (Cal).

lantern node (n). Nodal octahedron of a lychnisc (Hex).

lantern spicule (n). Lychnisc (Hex).

lateral wall (n). The part of a sponge body surrounding an axial paragaster.

leucon (n). Sponge in which flagellated chambers discharge via exhalant canals (apochetes) and inhalant canals are also present.

leuconoid (adj). With the characters of a leucon; as in leucons.

lithistid (adj). (1) With the main internal megascleres developed as articulated desmas, which form a coherent to rigid skeletal framework; (2) of lithistids (Dem).

lithistid (n). Demosponge with a lithistid skeleton; member of the order Lithistida.

lonchiole (n). Sceptrule with a single anaxial spine opposite the single ray (Hex).

long-shafted triaene (n). Triaene with the rhabdome several to many times longer than the rays of the cladome (Dem).

lophophyte (n). Sponge anchored by a root tuft.

lophophytous (adj). Anchored by a root tuft.

lophose (adj). With rays dividing into clusters of branches.

lychnisc (n). Dictyonal hexactine in which the central part is enclosed by an octahedral framework of 12 interactinal buttresses, which cross the interactinal angles from points equidistant from spicular center; see also lantern node and lantern spicule (Hex).

lychniscose (adj). Having lychniscs (Hex).

lyssacine (adj). (1) With parenchymal megascleres primarily or permanently unfused and of various sorts, often partly or all forms with less than six rays, which may be all rhabdodiactines; if secondary fusion occurs, the resultant skeletal framework retains the characteristic composition; (2) of lyssacines (Hex).

lyssacine (n). Hexactinellid sponge with a lyssacine parenchymal skeleton; member of the order Lyssacida.

marginal (adj). At the margin of an osculum, or at some other corresponding growing margin (e.g., of a funnel-like sponge).

marginalia (n pl). Prostalia of an oscular margin (Hex, Dem).

massive (adj). Forming a solid mass.

mega-, megalo-. Large.

megaclad (n). Megaclone (Dem).

megaclone (n). Monaxial desma, not of rhizoclonar type, in which distinct clones have zygomes in the form of longitudinal facets of cuplike, tonguelike, or hand-like terminal expansions; see also heloclone, rhabdoclone, megaclad (Dem).

megalome (n). The fourth clone of a trider when longer than the clones of the clonome (Dem).

megarhizoclone (n). Large rhizoclone, sometimes passing into desmas approaching a megaclone (Dem).

megarhizoclonid (n). Desma with the form of a rhizoclone, occurring in a lithistid whose typical desmas are dicranoclones (Dem).

megasclere (n). Major skeletal element, forming part of the main supporting skeleton when accompanied by accessory microscleres.

megascleric (adj). Of or comprising megascleres.

megaspiculation (n). The megascleres present in a given species, genus, etc.

membrana reticularis (n). Choanocytal membrane (Hex).

mesenchymal (adj). Of the mesenchyme (Cal, Dem).

mesenchyme (n). The gelatinous internal groundmass of Calcarea and Demospongea; see also mesoglea, parenchyma.

mesoglea (n). Mesenchyme.

mesohexaene (n). Mesopolyaene with six cladi, also called an octactine (Het).

mesopentaene (n). Mesopolyaene with five cladi (Het).

mesopolyaenes (n pl). Mesotriaene-like spicules with 4 to 6 cladi (Het).

mesotetraene (n). Mesotriaene-like spicule (or mesopolyaene) with four cladi.

mesotriaene (n). Spicule with three cladi and a diactinal rhabdome, the rays of which may be equal or unequally developed.

mesotrider (n). Tetraclonar desma in which the crepis is a mesotriaene (Dem).

metaster (n). Microsclere (streptosclere) in which raylike spines are emitted from a spiral axis of less than one turn (Dem).

micro-. May designate (1) a microsclere; (2) a small form of a particular microsclere; or (3) a spicule of microscleric size, not a microsclere homologically.

microrhabd (n). Any rodlike monaxial microsclere (Dem).

microsclere (n). Accessory skeletal element, typically but not always smaller than megascleres.

microscleric (adj). Of or comprising microscleres.

microspiculate (adj). With very small spicules, not identified as megascleres or microscleres (Dem).

microspiculation (n). The microscleres present in a given species, genus, etc.

monact (n). Monactine.

monactin, -e (n). Spicule with a single ray only; monaxon with one end sharply pointed; single-rayed holactine.

monactinal (adj). Single rayed.

monaene (n). Triaene-like spicule with only one cladus.

monaxon (n). Spicule in which rays grow along a single growth axis, in one or two directions.

monaxial (adj). With rays following a single growth axis only; containing a single axial filament.

monaxonid (adj). (1) With monaxial megascleres only, unless pseudoradiates are present, and without desmas; (2) of monaxonoids (Dem).

monaxonid (n). Demosponge with a monaxonid skeleton; member of the order Monaxonida.

moniliform (adj). Linear, threadlike growth; see also cateniform.

moniliform acuate (n). Cricostyle (Dem).

monocrepid (adj). With a monaxial crepis; see also rhabdocrepid (Dem).

monolophose (adj). With one lophose ray.

multiradiate node (n). Skeletal node from which more than six beams radiate (Hex).

myocyte (n). Contractile cell.

myxosponge (n). Demosponge with no skeleton.

neoasters (n pl). Radiate or floriform polyactines, often without distinct rhabdome and cladome but linked with true polyaenes by intermediates (Het).

nodal octahedron (n). The octahedral framework enclosing the central part of a lychnisc (Hex).

non-actinal secretion (n). Any condition in which mineral matter forming spicules or parts of spicules is not secreted concentrically around an organic axial filament.

octactin, -e (n). Spicule with eight rays; mesohexaene (Het).

octactinal (adj). Eight rayed.

octactinellid (adj). Octactinal, with the form of a mesohexaene (Het).

octaster (n). Triaxial microsclere in which eight anaxial, raylike pseudoactines are emitted from a center containing a six-rayed axial cross as though along the diagonal axes of a cube, and bear anaxial terminal outgrowths like those of a hexaster (Hex).

olynthus (n). Initial ascon formed in the early ontogeny of Calcarea, after larval fixation.

onychohexaster (n). Hexaster in which the ends of the terminal outgrowths bear umbels in the form of prominent and separate barblike teeth (Hex).

ophirhabd (n). Irregularly sinuous oxea (Dem).

orthodiactin, -e (n). Holactine with two rays growing at right angles (Hex).

orthotetractin, -e (n). Four-rayed holactine in which rays follow three growth axes, intersecting at right angles (Hex).

orthotriaene (n). Triaene in which the angle between the rhabdome and each cladus is 90 to 130°.

oscular (adj). Of an osculum.

oscule (n). Osculum.

osculum (n.; pl. -a). Aperture through which water is discharged to the exterior from a paragaster or a pseudogaster.

ostia (n pl). Inhalant skeletal pores.

ostium (n., pl. -ia). Any opening through which water enters a sponge; sometimes applied to an opening larger than a pore; used in older literature as a synonym of posticum.

outer trabecular network (n). Trabeculae on the dermal side of choanocytal and connecting membranes (Hex).

oxea (n). Monaxon sharply pointed at both ends, regarded as a diactine; see also oxeote.

oxeate (adj). Sharp ended.

oxeote (n). Oxea.

oxy-. Sharp ended.

oxyaster (n). Euaster with sharply pointed rays, the central part of which may have a small spherical mass of silica from which the rays emerge (Dem).

oxyhexaster (n). Hexaster in which the terminal outgrowths are sharply pointed (Hex).

paired rays (n pl). (1) Rays of a triaxon occurring in opposite pairs (Hex); (2) the two similar rays of a sagittal triradiate (Cal).

palm (n). One of the paired lateral processes at the ends of a chela when of bladelike form (Dem).

palmate (adj). With palms (Dem).

palmate chela (n). Chela in which the lateral appendages comprise a single pair of bladelike expansions at each end of the spicule (Dem).

paraclavule (n). Apparently monaxial microsclere with a terminal umbel at one end, resembling a short-shafted clavule or an amphidisc with one umbel missing; has also been called an umbel (Hex).

paragaster (n). See spongocoel.

paragastral (adj). Of the paragaster.

paratangential (adj). Nearly tangential; implies that the orientation of rays following the plane of a sponge surface is not strictly tangential (Hex).

paratangential (n). Tangential ray (Hex).

paratropal pentactin, -e (n). Pentactine in which the arrangement of the paired rays is distorted so that one interactinal angle is greater than the other three, which are subequal, and may exceed 180° (Hex).

paratrope (n). Paratropal pentactine (Hex).

parenchyma (n). (1) Mesenchyme; (2) mesenchyme in which cells are numerous (cf. collenchyma, with few); (3) in Hexactinellida, the trabecular network between the dermal and gastral membranes.

parenchymal (adj). Of the parenchyma.

parenchymal skeleton (n). The megascleres of the parenchyma, or any rigid structure formed by their union; hypodermalia or hypogastralia, although strictly parenchymal, are not included (Hex).

parenchymalia (n pl). Spicules of the interior, excluding the dermalia and gastralia (Hex).

parenchymella (n). Sponge embryo or free larva in which an appreciable part of the surface (up to approximately half) is formed by nonflagellate cells, the rest being flagellate.

parietal (adj). Of the lateral wall surrounding an axial paragaster.

parietal gap (n). Perforation in the lateral wall of a paragastral cavity.

parietal osculum (n). Parietal gap identified homologically as osculum.

pavement cell (n). Pinacocyte (Cal, Dem).

pentact (n). Pentactine.

pentactin, -e (n). Spicule with five rays; five-rayed holactine (Hex).

pentactinal (adj). Five rayed.

pentaene (n). Triaene-like spicule with five cladi (Het).

pentiradiate (n). Spicule with five radial rays within a single plane (Het).

periloph (n). A raised rim around an ostium or pore, a rim shorter than a tubelike exaulos (Dem).

peripheral (adj). At the periphery of a body consisting of radiating tubes, or of a radially folded disc or funnel; extending across a succession of marginal surfaces in such a body (Hex).

peripheral membrane (n). Membrane developed across and/or between a succession of marginal surfaces (Hex).

peripheral skeleton (n). Loose megascleres or rigid skeletal meshwork formed in a peripheral structure (Hex).

phalangaster (n). Very short but stout spinulate microstrongyle (Dem).

phyllopentactin, -e (n). Pentactine with bladelike lamellar expansions along the sides of the paired rays, in the plane in which they lie, so that each ray has a leaflike appearance (Hex).

phyllotriaene (n). A triaene spicule in which the three more or less equal rays are expanded into flattened, leaflike, sometimes digitate structures (Dem).

pillar (n). Rodlike skeletal structures that extend from interwall to interwall in chambers of sphinctozoan sponges (Dem).

pinacocyte (n). Cell marking limit of sponge, usually occurring in layer one cell thick.

pinacocyte layer (n). Layer of pinacocytes coating surfaces where choanocytes are lacking (Cal, Dem).

pinacoderm (n). Outer layer of a sponge.

pinakid (n). Siliceous disc with many radiating axial canals (Dem).

pinular (adj). With centripetal lateral spinules producing a resemblance to a fir tree; with a pinular ray or rays (Hex).

pinulus (n). Pinular hexactine or pentactine, with a pinular ray that is unpaired in pentactines; sometimes with less developed spinules on other rays (Hex).

plagiotriaene (n). Triaene in which the angle between the rhabdome and each cladus is about 135°.

plesiaster (n). Microsclere (streptosclere) in which raylike outgrowths are emitted from a short straight axis, sometimes grading into simple euasters with no central axis (Dem).

pleuralia (n pl). Prostalia of the sides of the body (Hex).

plumicome (n). Hexaster with S-shaped terminals, the free ends of which face outward and are arranged in several tiers (Hex).

plumose (adj). Plumelike; refers to the axinellid type of echinated skeletal fiber, without coring monaxons (Dem).

polyactin, -e (n). Spicule with many rays (in practice, any form with more than six).

polyactinal (adj). Many rayed.

polyaenes (n pl). Triaene-like spicules with 2 to 9 (typically 5 or more) rays in the cladome (Het).

polyaxon (n). Spicule with rays following more than four growth axes, arranged at subequal angles or in other ways.

polyaxial (adj). With rays following more than four growth axes.

polycladose (adj). Repeatedly branched.

porate (adj). Possessing pores.

pore (n). Any small aperture through which water passes.

pore field (n). A cluster of pores, particularly if flat and surrounded by a low rim, in an exowall.

porocyte (n). Cell perforated by an intracellular pore, through which water passes, that functions as an inhalant canal.

postica (n pl). Exhalant skeletal pores.

principalia (n pl). The main parenchymal megascleres of lyssacine Hexactinellida (Hex).

prosiphonate (adj). Condition in which the individual segments of an axial tube grow upward from the floor of each skeletal chamber, i.e. from the roof of the chamber below (Dem).

prosochete (n). Inhalant canal.

prosodus (n). Fine tubular duct leading from a main trunk of an inhalant canal (prosochete) to a flagellated chamber.

prosopore (n). Inhalant pore.

prosopyle (n). Pore through which water enters a flagellated chamber.

prostalia (n pl). Megascleres protruded from a dermal or marginal surface (Hex).

prothalmus (n). A cluster of initial few chambers of an individual sphinctozoan sponge that lacks a cloaca and is, thus, different from subsequent chambers (Dem, Cal).

protocyst (n). A chamber in a protothalus (Cal).

protriaene (n). Triaene in which the angle between the rhabdome and each cladus is more than 135°.

proximal ray (n). One of the rays of a spicule, when directed inward at right angles to an external surface.

psellium (n). Clavidisc (Dem).

pseudaster (n). Any pseudopolyactinal microsclere developed from a monaxial type (Dem).

pseudastrose (adj). Comprising pseudasters (Dem).

pseudo-. False.

pseudoactin, -e (n). Raylike structure containing no axial filament.

pseudoactinal (adj). Resembling a ray but lacking an axial filament.

pseudoaxial canal (n). Cavity resembling a true axial canal, but produced by internal solution of the axial part of an originally solid (anaxial) structure.

pseudoderm (n). Peripheral ectosome-like covering, enclosing a tubular labyrinth in some asconoid Calcarea (Cal).

pseudoeuaster (n). Oxyaster-like, sphaeraster-like, or sterraster-like microsclere, developed from a monaxial prototype (usually a spinispira) (Dem).

pseudogaster (n). Local paragaster-like cavity in a sponge with no single axial paragaster, homologically an external depression (epochete) or the trunk of an exhalant canal (apochete).

pseudohexactinose (adj). With nodal octahedra solidified so that lychniscs appear to be absent (Hex).

pseudopolyactin, -e (n). Apparently polyactinal spicule in which true cored rays are lacking (Hex).

pseudoradiate (n). Secondary diactine, triactine, tetractine, or pentactine, derived from a monactine by enlargement of spinules to the size of rays (Dem).

pseudosiphonate (adj). Condition of thalamid sphinctozoans that lack a true axial tube, but have a tubular axial passage that may or may not be outlined by an endocameral structure (Dem).

pseudospicule (n). Spicule-like body composed of spongin (Dem).

pseudotetraclone (n). Monaxial or anaxial desma with the outward form of tetraclone (Dem).

pycnaster (n). Euaster with short conical rays, which may also be a sphaeraster (Dem).

quadriradiate (n). Tetractine.

quadrule (n). Square mesh with sides formed by tangential rays of four hexactines, pentactines, or stauractines, whose centers are located at the corners, or produced by subdivision of such a square by smaller spicules within it (Hex).

radial canal (n). (1) Radially directed inhalant or exhalant canal; (2) radially directed skeletal canal; (3) a flagellated chamber of a sycon.

radiante (n). That point in the skeletal end of an anthaspidellid sponge from which the trabs radiate (Dem).

radiate (adj). (1) With radiating rays; (2) with megascleres (long-shafted triaenes or monaxons) arranged radially (Dem).

radical (adj). Rooting.

ramose (adj). Branched.

raphide (n). Hairlike monaxon.

raphidial (adj). Hairlike.

ray (n). Any portion of a spicule formed by concentric secretion of mineral matter around a centrifugal organic axial filament.

recurved (adj). Bent toward a monactinal or diactinal shaft, in the manner of spokes of a grapnel.

reticular (endocameral structure) (adj). Consisting of a three-dimensional network of skeletal beams (Cal).

reticulate (adj). Netted; in monaxonid Demospongea, refers to skeletons with spicules cemented together with spongin or imbedded in a network of spongin fibers.

retrosiphonate (adj). Condition in which an axial tube is formed by backward extensions of the wall of each skeletal chamber in sphinctozoans (Dem).

rhabd or rhabdus (n). General name for any form of monaxon; also misused in place of rhabdome.

rhabdal (adj). Of the rhabdome.

rhabdoclone (n). Megaclone or heloclone (Dem).

rhabdocrepid (adj). Monocrepid (Dem).

rhabdodiactin, -e (n). Holactine in which two opposite rays follow a single growth axis (Hex).

rhabdome (n). Axial (dissimilar) ray or pair of opposite rays, in spicules in which other rays form a cladome.

rhagon (n). Sponge with syconoid flagellated chambers but no canal system; larval demosponge having this condition; sometimes also used incorrectly as equivalent to leucon.

rhagonoid (adj). With syconoid flagellated chambers but no canal system.

rhax (n). Kidney-shaped sterraster (Dem).

rhizoclad (n). Rhizoclone (Dem).

rhizoclonar desmas (n pl). Monaxial desmas, with or without distinct clones, in which the zygomes are simple spinules or rootlike outgrowths (Dem).

rhizoclone (n). Generalized rhizoclonar desma, with or without distinct clones, without tubercles, and without spherical swellings at the ends of the epirhabd; see also rhyzoclad (Dem).

rhizoclonid (n). Anaxial supplemental desma, of rhizoclone-like form (Dem).

rhizophyte (n). Anaxial supplemental desma, of rhizoclone-like form (Dem).

rhizophytous (adj). Anchored by root processes.

rhopalostyle (n). Clublike or spindle-like style (Dem).

rhyses (n.). Canal or opening in the sponge.

root process (n). Rootlike basal outgrowth, by which a sponge is anchored.

root tuft (n). Beardlike, ropelike, or stalk-like group of protruded spicules, by which sponge is anchored.

rosettes (n pl). Hexasters and their variants, e.g., hemiasters, octasters (Hex).

sagittal triradiate (n). T- to Y-shaped triactine, with two equal interactinal angles (Cal).

sanidaster (n). Microsclere with raylike spines distributed along the length of a straight monaxial shaft (Dem).

sarcenchyma (n). Mesenchyme with many granular cells.

sarcode (n). Soft parts.

sarule (n). Brushlike sceptrule, in which a short, raylike rudiment opposite the single true ray bears numerous centrifugal spines, which are not arranged in regular whorls (Hex).

sceptrella (n). Discaster (Dem).

sceptrule (n). Monactinal but triaxial microsclere with a six-rayed axial cross at one end, which usually bears some form of anaxial outgrowth(s) externally (Hex).

schizorhyses (n pl). Intercommunicating cleftlike to labyrinthine skeletal canals, open at both skeletal surfaces (Hex).

schizorhysis (n). Condition in which schizorhyses are present (Hex).

sclere (n). Spicule.

scleroblast (n). Spicule-secreting cell.

scleroblast syncytium (n). Multinucleate syncytial mass within which a spicule is secreted (Hex).

sclerocyte (n). Scleroblast.

sclerosome (n). Calcareous cement uniting spicules or forming skeletal fibers in which they are imbedded (Dem, Cal).

sclerosomal trabeculae (n). Anastomosing skeletal elements that form the unchambered upper, exhalant, canalled layer in stratiform guadalupiid sphinctozoans (Dem).

scoliorhabd (n). Sinuous and irregularly annulated monaxon (Dem).

scopule (n). Brushlike or forklike sceptrule, with a pair or regular ring of centrifugal spines opposite the single ray (Hex).

sexiradiate (n). Spicule in which the six radiating rays occur in a single plane (Het).

short-shafted triaene (n). Triaene with the rhabdome shorter to not markedly longer than the rays of the cladome (Dem).

sieve plate (n). Perforated diaphragm extending across an osculum or across a paragaster below the level of its osculum.

sigma (n; pl. -ata). Typically C-shaped but sometimes S-shaped microsclere with sharply pointed ends, and without spinules (Dem).

sigmaspire (n). Spiral monaxial microsclere of about one revolution, C- to S-shaped in different views, typically blunt-ended, smooth or finely to markedly spinulate (Dem).

sigmatoscleres (n pl). Microscleres comprising sigmata *s.s.* and related types, including diancistra, clavidiscs, canonchelae, chelae, chelasters, chela-derivative amphidiscs, bipocilli (Dem).

sigmatose microscleres (n pl). General name given to diactinal demosponge microscleres, particularly sigmata, sigmaspires, and their variants.

siliceofibrous skeleton (n). Imaginary structure supposed to consist of a network of siliceous fibers, attributed to lithistid Demospongea and dictyonine Hexactinellida by Bowerbank (1869) and Claus (1872).

silicoblast (n). Silica-secreting scleroblast (Dem).

siphon (n). The axial tube of thalamid sphinctozoans (Dem).

skeletal canal (n). Canal-like internal cavity in a skeletal framework.

skeletal canalization (n). Interruption of skeletal meshwork, at surfaces or internally, by spaces larger than ordinary skeletal meshes, and marking the positions of canals or flagellated chambers.

skeletal cortex (n). Specially dense external part of a skeletal framework.

skeletal framework (n). Coherent internal framework, consisting of spicules united by a calcareous or spongin cement, by articulation (zygosis), or by fusion (ankylosis), or of spongin fibers with or without imbedded spicules.

skeletal node (n). Point at which beams of a skeletal framework come together.

skeletal pore (n). Canalar aperture in a skeletal surface, of inhalant, exhalant, or unknown function.

somal (adj). Found equally in the choanosome and ectosome (or endosome); distinguishes spicules with this distribution from other restricted to these regions (see ectosomal, choanosomal).

spathidorhabd (n). Spinulate oxea or strongyle, with spinules in regular whorls (Dem).

sphaeraster (n). Euaster in which the rays radiate from a spherical central part, the diameter of which is one third or more of their length (Dem).

sphaeroclonar (adj). Comprising sphaeroclones and astroclones (Dem).

sphaeroclone (n). Anaxial desma with clones radiating to one side of a center with the other side spinose, inflated to form globular centrum, or both; zygomes rootlike to cuplike; see also anomoclad (Dem).

sphaerohexaster (n). Tylohexaster (Hex).

sphaerule (n). See spherule.

sphere (n). Anaxial siliceous spherule produced by concentric secretion around a center (Dem).

spherical (adj) (of hexasters). With numerous terminals radiating to a spherical periphery, and arising from short actinal rays or from a central sphere containing a six-rayed axial cross (Hex).

spherule (n). Spherical body, commonly microscopic and of acicular crystals radiating from a common center, that may form part of skeletal fibers in calcareous sponges (also sphaerule, spherulite, sphaerulite) (Cal, Dem).

spherulitic (adj). Skeletal texture composed of spherulites (also sphaerulitic) (Cal, Dem).

sphinctozoan (n). Demosponge with a calcareous skeleton composed of straight, curved, branched, or glomerate series of hollow spheroidal chambers or bodies.

spicular (adj). Of spicules.

spicular center. Point within a spicule from which growth has commenced.

spiculation (n). The assemblage of spicules present in a given species, genus, etc.

spicule (n). Discrete mineral skeletal element; see also sclere.

spiculin (n). Organic substance forming axial filaments and sometimes also mixed with spicular silica.

spike (n). Unattached ray projecting freely from a surface of a dictyonal framework (Hex).

spinispira (n). Spiral monaxial microsclere of typically more than one revolution, which is finely microspinulate or developed as a spiraster, and may grade into a spinulate microstrongyle, a sigmaspire, a pseudoeuaster, or a discaster (Dem).

spinulate (adj). With spinules.

spinulate (n). Tylostyle (not spinulate in the sense of bearing spinules) (Dem).

spinule (n). Any small spine, not large enough to be called raylike.

spiraster (n). Microsclere in which raylike spines are emitted from a spiral axis making one turn or more; may be either a streptosclere or a spinispira (Dem).

spire (n). Any microsclere that is a spirally twisted monaxon (Dem).

spiroscleres (n pl). Microscleres comprising sigmaspires, toxaspires, spinispirae, and related pseudasters (Dem).

spongin (n). Horny skeletal substance, cementing spicules together or forming continuous skeletal fibers with or without imbedded spicules; sometimes also present in other forms (Dem).

spongioblast (n). Spongin-secreting cell.

spongocoel (n). Large, central exhalant opening, commonly obconical to rounded subcylindrical, without digestive function, also termed a cloaca, gastral cavity, or paragaster in zoological and paleontological literature.

spongocyte (n). Spongioblast.

spongophare (n). The chamber-containing upper part of a rhagon, which gives rise to the adult choanosome (Dem).

statoblast (n). Reproductive bud.

stauractin, -e (n). Cross-shaped tetractine (Hex).

staurodisc (n). Tetractinal amphidisc variant, with the rays arranged as in stauractines (Hex).

sterraster (n). Globular or kidney-shaped microsclere with a granular surface, formed by solidification of a many-rayed initial oxyaster (Dem).

sterrosphaeraster (n). Euaster intermediate between typical sterrasters and sphaerasters (Dem).

sterrospira (n). Sterraster-like microsclere developed from a spinispira (Dem).

stratiform (adj). Sheetlike growth form consisting of a single layer of chambers (Cal).

streptasters (n pl). (1) Originally (*sensu* Sollas) all types of pseudopolyactinal microscleres in which raylike spines are emitted from a linear axis rather than a center as in euasters, including plesiasters, metasters, spirasters, amphiasters, sanidasters, and discasters, irrespective of homology; (2) *sensu* Burton, streptoscleres only; (3) *sensu* de Laubenfels, spinulate microxeas and sanidasters (Dem).

streptoscleres (n pl). Microscleres comprising intergrading plesiasters, metasters, spirasters, and amphiasters, of which the first may pass into simple euasters from which this series appears to derive; dichotriacts of Dendy; streptasters *sensu* Burton (not de Laubenfels) (Dem).

strongylate (-ote) (adj). Round ended.

strongyle (n). Round-ended monaxon.

style (n). Monaxon with one end rounded, the other sharply pointed.

subcortical crypt (n). Subdermal space underlying a cortex (Dem).

subdermal (adj). Beneath the dermal surface, but outside the choanosome; see also hypodermal.

subdermal space (n). Internal space underlying an ectosome (Cal, Dem) or a dermal membrane (Hex) but outside the choanosome.

subgastral (adj). Beneath the gastral surface, but outside the choanosome; see also hypogastral (Hex).

subhexactin, -e (n). Hexactine with one ray markedly shorter than the rest (Hex).

sublithistid (adj). (1) With an incipient or imperfect development of the lithistid condition, or with a mixture of lithistid and nonlithistid characters; (2) of sublithistids (Dem).

sublithistid (n). Sublithistid demosponge (Dem).

subtriaene (n). Triaene in which differentiation of a cladome is limited to curvature or displacement of three rays toward or away from the fourth from the regular tetraxial positions; to shortening of the fourth ray; or to two of these developments together (Dem).

summit diaphragm (n). Sieve-platelike structure that forms the upper surface of the body in *Coeloptylum* Goldfuss and similar genera (Hex).

superficial furrowing (n). Furrowing of the surface of a skeletal framework, related to the positions of subdermal or subgastral channels in the soft parts, or to some other feature of a canal or chamber system; not related to folding of the sponge wall, as has sometimes been alleged when furrows run longitudinally.

superficial meshwork (n). Rigid skeletal meshwork, of various origins, developed outside the true surface of a dictyonal framework; distinguished by extending across ostia or postica of the skeletal surface proper (Hex).

supplemental (adj). Occurring in addition to desmas in lithistid demosponges.

sycettoid (adj). Syconoid with inhalant canals formed by interspaces between free radial diverticula of the wall of an axial paragaster.

sycon (n). Sponge with choanocytes restricted to radial flagellated chambers that discharge to the paragaster directly, with partially enclosed or distinct inhalant canals (prosochetes) but no exhalant canals (apochetes).

syconoid (adj). With the characters of a sycon; as in sycons.

symphyllotriaene (n). Discotriaene (Dem).

synapticula (n pl). Anaxial siliceous bridges uniting adjacent spicules (Hex).

synapticular filaments (n pl). Anaxial siliceous filaments growing out from spicular rays or skeletal beams (Hex).

syncytium (n). A mass of protoplasm that contains scattered nuclei but lacks distinct cells.

syzygial (adj). Taking part in or formed by zygosis (Dem).

syzygial node (n). Skeletal node formed by intergrowth of zygomes from two or more desmas (Dem).

tabulum (n). Plate or floor that divides skeletal cavity.

tangential (adj). Lying in or parallel with the plane of an external surface. This orientation is also called paratangential, as not truly tangential.

tangential rays (n pl). Rays that are oriented tangentially; used mainly of hexactinellidan dermalia and gastralia, or which four rays of two intersecting axes are typically tangential; see also paratangential ray.

tauactin, -e (n). T-shaped triactine (and holactine) (Hex).

terminal (n). Anaxial, branchlike centripetal outgrowth arising from the end of a true cored ray of a hexaster (Hex).

tetraclad (n). Tetraclone (Dem).

tetraclone (n). Tetraxial (tetracrepid) desma with four clones developed similarly or differently, without a differentiated clonome; crepis a small calthrops or short-shafted triaene; see also tetraclad (Dem).

tetraclonar desmas (n pl). Typically tetraxial desmas with zygomes in the form of anaxial rootlike outgrowths, including tetraclones, triders, and minor variants of these types (Dem).

tetracrepid (adj). With a tetraxial crepis (Dem).

tetract (n). Tetractine.

tetractin, -e (n). Spicule with four rays; four-rayed holactine.

tetractinal (adj). Four rayed.

tetraene (n). Triaene-like spicule with four cladi (Dem, Het).

tetralophose (adj). With four lophose rays.

tetraxial (adj). With rays following four growth axes, arranged tetrahedrally or in some distorted form of this arrangement.

tetraxon (n). Spicule in which rays follow four growth axes, arranged tetrahedrally or in some distorted form of this arrangement.

thalamidarium (n). Single layer of chambers in a stratiform sphinctozoan sponge in which chambers are convex toward the growing edge, commonly overlain by an unchambered, canalled trabecularium (Dem, Cal).

theca (n). Skeletal cortex in the form of a dense, sheathlike secondary covering (Dem).

tibiella (n). Tylote (Dem).

torno-. With rays abruptly pointed.

tornote (n). Monaxon with ends abruptly pointed (Dem).

toxaspire (n). Monaxial microsclere similar to a sigmaspire but making rather more than one revolution, and hence appearing bow shaped in some views (Dem).

toxon (n.; pl. -a). Bow-shaped, monaxial microsclere (Dem).

trab (n). Rodlike skeletal element in ladderlike anthaspidellid skeletons, formed by fusion of ray tips of runglike dendroclones, may be cored with monaxons (Dem).

trabeculae (n pl). Dividing and anastomosing syncytial filaments forming a network with water-filled interspaces (Hex); or any other rodlike or beamlike skeletal element other than a ray or branch of a single spicule, especially a structure of sclerosome.

trabecular network (n). The network of syncytial trabeculae in which the flagellated chambers of Hexactinellida are suspended, also forming the bounding (dermal and gastral) membranes.

trabecularium (n). Upper unchambered layer composed of anastomosing trabeculae, interrupted by groovelike canals, in the stratiform guadalupiid sphinctozoans (Dem).

trabeculae (endocameral structure) (adj). Consisting of regular pillars supporting the roofs of low chambers (Dem).

trabecular skeleton (n). Skeleton made of nonspicular, branching filaments.

trachelotriaene (n). Long-shafted dichotriaene with a very small cladome and a clublike rhabdome, with its maximum diameter just below the cladome and then tapered away from it (Dem).

triact (n). Triactine.

triactin, -e (n). Spicule with three rays; three-rayed holactine; see also triact, triradiate (Hex).

triactinal (adj). Three rayed.

triaxial (n). With rays or axial rudiments following three growth axes, which intersect at right angles.

triaxon (n). Spicule in which rays, axial rudiments, or both follow three growth axes, which intersect at right angles.

triaene (n). Regular or modified tetraxon with three similar rays (cladi) differing from the fourth.

trichotriaene (n). Triaene with cladi branched trichotomously.

tricranoclone (n). Triderlike desma of Tricranocladina, with three tripodally grouped clones bearing terminal zygomes in the form of simple or marginally denticulate expansions, and with or without a knobbed brachyome-like outgrowth on its opposite side; nature of the crepis unknown (Dem).

tricrepid (adj). With a triactinal crepis (Dem).

trider (n). Tetraclonar desma with three similar clones, comprising a clonome, and a fourth developed differently or lacking; crepis tetractinal or triactinal (Dem).

trifid spicules (n pl). Triaene (Dem).

trilophose (adj). With three lophose rays.

triod (n). Triactine with the rays arranged in one plane at 120° intervals.

triodal (adj). With three rays arranged in one plane at 120° intervals.

tripod (n). Triactine with rays arranged pyramidally.

tripodal (adj). With three rays or clones arranged pyramidally.

tripinulus (n). Spicule with pinular spines on a distal ray and the outward turned ends of two tangential rays (Hex).

triradiate (n). Triactine (Cal).

tubular (endocameral structure) (adj). Consisting of interconnected calcareous tubes, which open through pores of the external and internal walls (Dem).

tylo-. Terminally knobbed.

tylohexaster (n). Hexaster with knobbed terminals; see also sphaerohexaster (Hex).

tylostrongyle (n). Monaxon with one end knobbed, the other bluntly rounded (Dem).

tylostyle (n). Monaxon knobbed at one end, sharply pointed at the other.

tylote (n). Monaxon knobbed at both ends; see also amphityle.

tylote (adj). Terminally knobbed.

umbel (n). Whorl of recurved toothlike spicules at the end of a spicular ray or an anaxial pseudoactine.

umbel (n). Spicule with a single umbel at one end of a short shaft, now called a paraclavule (Hex).

uncinate (n). Diactinal monaxon with thornlike, lateral spinules, all directed toward one end (Hex).

unpaired ray (n). Ray of a triaxon when the opposite ray is suppressed.

vermiculate (adj). Irregularly sinuous.

verticillate (adj). With spinules in regular whorls.

vesicular (endocameral structure) (adj). Consisting of imperforate diaphragms (Dem).

wandlucken (n). Parietal gaps or oscula (Hex).

xenoskeleton (n). Foreign objects taken into the body, sometimes cemented by or imbedded in spongin (Dem).

xylotyle (n). Sceptre-like, prostal monactine (Hex).

zygome (n). Articulatory part of the desma (Dem).

zygosis (n). Coherent articulation of spicules, without fusion.