PALEOZOIC DEMOSPONGEA: MORPHOLOGY AND PHYLOGENY

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INTRODUCTION

The demosponges have essentially as ancient a fossil record as the hexactinellids. The oldest fossils of the class were considered for many years to be from the Lower Cambrian (Rigby, 1987b), but more recent discoveries have extended that record back into Ediacaran-age Precambrian (Brasier, Green, & Shields, 1997; Li, Chen, & Hua, 1998). Demonstration of their existence alongside hexactinellids in the lowermost Cambrian and earlier sequences is hindered by the form of their earliest spicules, which are oxeote monaxons. These are indistinguishable in normal preservation from rhabdodiactines of hexactinellids. The minute axial cross of the rhabdodiactine axial canal is rarely preserved or at least rarely observed in older fossils, and the SEM work necessary to distinguish the square cross section of the hexactinellid axial canal from the triangular one of the demosponge (Reiswig, 1974) has not yet been done. Because no coherent skeleton of demosponge morphologic type has been found in Lower Cambrian strata, their existence at that time must still be conjectural.

SKELETAL MORPHOLOGY

The principal skeleton of living demosponges is composed most often of spongin (collagen) fibers in which variable numbers of spicules may be embedded, ranging from none at all to so many that the spongin is reduced to a mere cement between the spicules. This is termed a fibrous skeleton. Other demosponges may contain only spicules scattered without apparent order throughout the flesh, a condition often referred to as confused, although diffuse might be a better term. Combinations of the two arrangements are also known. Microscleres usually have a diffuse organization, even in sponges with a fibrous skeleton containing megascleres. Although diffusely arranged, microscleres may be concentrated in some parts of the sponge, especially in a differentiated outer zone or cortex when such exists in the soft parts. Microscleres are not properly part of the principal skeleton, however, nor are the specialized megascleres that are associated with the dermal layers. A few demosponges lack spicules altogether but are supported by variable amounts of the mesohyl (or **mesoglea**) found in all demosponges. This is a nonliving gel permeated with microscopic spongin fibers and motile amoebocytes.

FIBER TYPES

Among the sponges with a fibrous skeleton, several types of fiber may be recognized, although these are best thought of as end members of a graded series. Where each fiber is coextensive with a single monaxon, a simple isodictyal net is formed in which the spicules are united tip to tip and chiefly outline triangular interspaces. This may be developed in three dimensions, but often the isodictyal net is developed only in a plane or planes parallel to the outer surface. If more than one spicule lies side by side, yet nevertheless the side of each mesh space is but one spicule long, the net is compound **isodictyal.** Where many spicules lie along the length of a fiber in succession there is a net of spiculofibers (if the spicules dominate in volume) or of spicule tracts (if the spongin dominates). Almost always these fibers or tracts consist of several spicules side by side; it is rare to have a train of single spicules end to end. The spicules may all be parallel to the longitudinal axis of the fiber, or they may diverge outward and upward from the center of the fiber. The latter is termed a plumose fiber. An outer layer of spicules directed at a higher angle to the fiber axis may be present; these are said to be echinating, while the inner layer of more parallel spicules are said to be coring. A substantial fiber of spongin may bear only echinating spicules or may contain none at all but be cored by foreign sand grains (as in many keratose sponges). The principal spiculofibers are usually arranged as upwardly and outwardly diverging ascending fibers (or tracts) connected laterally by more slender fibers. A particular species or genus is often characterized by its fiber type, but sometimes more than one type is present in a single sponge.

SKELETAL TYPES

Among Paleozoic demosponges common as fossils there are several skeletal types that are particularly widespread: 1. hazeliid; 2. heliospongiid; 3. dystactospongiid; 4. anthaspidellid; 5. chiastoclonellid; 6. anthracosyconid; 7. astylospongiid; 8. haplistiid; 9. hindiid; and 10. *Belemnospongia* types. Each of these is characteristic of a particular family, except for the somewhat doubtful *Belemnospongia.*

Hazeliid type

Anastomosing subparallel spiculofibers of plumosely arranged oxeas characterize the main skeleton. A dermal layer of tangential oxeas may also be present. The Middle Cambrian genus *Hazelia* includes the species *H. delicatula* WALCOTT, 1920 (not the type species), which has spiculofibers of parallel (not plumose) oxeas arranged in a nearly isodictyal net (that is, with triangular mesh spaces one spicule-length long rather than subparallel and anastomosing). Further study of more specimens will be required to demonstrate whether the two types are to be considered end members of an intergrading sympatric series. Until such time, it is better to consider the hazeliid type as the former alone. Note that the spicules are oxeas rather than the styles that seem to characterize most plumose spiculofibers.

Heliospongiid type

Spiculofibers composed of bundles of parallel oxeas form the main skeleton. The quadrangular mesh spaces are more or less one spicule length wide, and the spiculofibers are typically radial and concentric in orientation. This skeleton approaches the form of a compound isodictyal net, but the successive overlapping of spicules and their curvature around the fiber junctions accord more with properties of a spiculofiber. A dermal layer of tangentially arranged oxeas not organized in bundles may be present. The haplistiid type is similarly organized but with the oxeas replaced by rhizoclones.

Dystactospongiid type

Spiculofibers forming the principal skeleton are composed typically of styles in plumose to parallel arrangement coated with heloclonid desmoids through which echinating styles may protrude. The desmoids may, however, form the entire spiculofiber, as in *Dystactospongia* itself; and the presence of such spicules in a spiculofibrous skeleton must be considered diagnostic of the type. The principal spiculofibers are usually subparallel and connected by lateral spiculofibers or by anastomosis. Oxeas may substitute for styles, but this is uncertain. This is a sublithistid type of skeleton and resembles a hazeliid with a coating of desmoids. The possibility that *Dystactospongia,* with desmoids alone, is actually a murrayonid calcisponge with flaky spherulites cannot be totally dismissed.

Anthaspidellid type

This type is characterized by a lithistid skeleton in which the dendroclone desmas form a simple isodictyal net with triangular interspaces parallel to the upper surface. The sponge grows by adding successively such layers, with the dendroclones occupying corresponding positions so that ladderlike, vertical series of dendroclones are formed. Terminal zygoses of the dendroclones interlock to form vertical columns or trabs that may be cored by oxeas. A few dendroclones have the external form of tetraclones. An imperforate basal layer may be aspicular.

Chiastoclonellid type

This type is characterized by a lithistid skeleton in which most spicules are chiastoclones and tetraclone-like forms with some dendroclones. The spicules interlock by terminal zygoses in a three-dimensional net of irregular but obscurely concentrically layered form. Radially oriented smooth monaxons may be present. An imperforate basal layer, like that of anthaspidellids, may be present.

Anthracosyconid type

This type is characterized by a lithistid skeleton in which dendroclones are oriented perpendicular to the upper surface in concentric layers. They may be grouped in bundles and may intergrade with rhizoclones. The bundles may be regarded as short spiculofibers more or less one spicule-length long. They are similar to those of the haplistiids, but unlike the haplistiids they are rarely throughgoing from one layer to the next. Instead they are often partition-like within the layer and form the wall between one horizontal canal and its neighbor. These partition-like spiculofibers may themselves be penetrated by pores. The spicules are rhizoclone-like, that is, with lateral zygoses, only when they occur in bundles.

Haplistiid type

This type is characterized by a lithistid skeleton in which radial spiculofibers are connected by usually thinner horizontal fibers to form quadrangular mesh spaces in the radial plane and more often quadrangular than triangular mesh spaces in the tangential plane. The mesh spaces are close to one spicule length long. The horizontal fibers occupy corresponding positions in successive layers so as to outline radial canals. The spiculofibers are porous and hollow to varying degrees in different genera. They are composed of subparallel rhizoclones and smooth monaxons (oxeas and strongyles); the smooth monaxons tend to occupy a more peripheral or coating position on the fiber. In some genera the fibers are cored by larger smooth monaxons. Dendroclones occasionally occur within the fibers and may substitute for horizontal fibers in the young parts of the sponge. A dermal layer of tangential smooth monaxons may be present, which may be organized in a finer mesh of fibers. This differs from the heliospongiid skeleton in the presence of rhizoclones and from the anthracosyconid in the dominance of rhizoclones, presence of smooth monaxons, and presence of well-defined radial and horizontal spiculofibers. A subtype in which the spiculofibers are flattened sheets is sometimes called radiate-lamellate and occurs in *Chaunactis* and *Mortieria* as well as in many post-Paleozoic rhizomorines.

Astylospongiid type

This is possibly a third way in which dendroclones can be organized, namely as a simple isodictyal net with triangular interspaces in three dimensions. This interpretation was first proposed by ZITTEL (1884). It is favored herein but is not yet firmly established. The alternative interpretation of this skeletal type, proposed by HINDE (1888) and RAUFF (1894), is that of concentric layers of six-armed anapodal desmas (dichotriders). See Volume 3 for a fuller discussion (*Treatise Part E (Revised),* vol. 3, in press). In addition to the principal skeleton of desmas, there are radially arranged, long, smooth monaxons that may have supported a dermal layer analogous if not homologous to protriaenes in other groups. The individual skeletal elements, be they dendroclones or spicule arms, resemble closely anthaspidellid dendroclones except that they are oriented in three dimensions rather than parallel to separate, successive sheets.

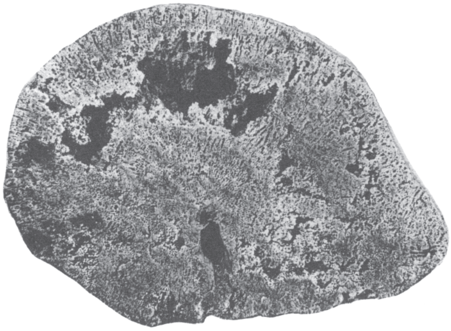

FIG. 31. *Multistella porosa* FINKS, 1960, in vertical section, with mold of a brachiopod shell just above base, and with spicule series radiating from mold surface; brachiopod was original hard surface to which sponge attached, and was subsequently overgrown, AMNH 28089, Cherry Canyon Formation, AMNH Locality 21SW, Guadalupe Mountains, Texas, USA, ×1 (Finks, 1960).

Hindiid type

This type is characterized by a lithistid skeleton composed of concentric layers of three-armed, anapodal desmas (tricranoclones). The spicules occupy corresponding positions in alternating layers so as to outline radial canals. A dermal layer of probably diffusely arranged, tangential, smooth monaxons is present as well as larger, radial, smooth monaxons that probably supported the dermal layer. These are analogous and possibly homologous to protriaenes of the Dicranocladina. In late Paleozoic genera, four-armed anapodal desmas and **megarhizoclones** may also be present. The megarhizoclones are associated with a more irregular arrangement of the spicules in the layers and occupy spaces between the desmas.

FIG. 32. Magnified view of surface of *Scheiia tuberosa* TSCHERNYSCHEW & STEPANOV showing monaxial spicules of possible dermal layer overlying main internal structure where spicules outline skeletal pores of hindiid skeleton, AMNH 28072, Leonard Formation, AMNH Locality 666, Guadalupe Mountains, Texas, USA, ×5 (Finks, 1960).

Belemnospongiid type

In this type, the entire skeleton consists of radial spiculofibers of long oxeas. It is possible that these are root tufts of a sponge whose principal skeleton was less coherent and more easily dispersed. The typical *Belemnospongia* with well-defined spicule bundles is late Paleozoic. In the Burgess Shale of the Cambrian there are radial masses of oxeas not grouped in bundles. Whether they are related, are root tufts, or are demosponges is equally uncertain.

BASAL ATTACHMENTS

Root tufts, that is, masses of elongate spicules that anchor the sponge in or above a soft mud bottom, are less common among demosponges of all geologic periods than among hexactinellids. Among living sponges they are best developed in such deeper water forms as *Thenea.* No Paleozoic demosponge with a well-developed root tuft is definitely known. The earliest group of demosponges to achieve widespread abundance, the anthaspidellid lithistids of the Ordovician, commonly have a short basal stalk that directly encrusts a shell or other hard object. Beginning with the Silurian *Aulocopium,* many members of this group and of the related chiastoclonellids, developed a characteristic concentrically wrinkled, imperforate, apparently aspicular but mineralized basal layer that resembles the holotheca of a compound rugose coral. This appears to have covered the part of the sponge that was sunk into soft mud. A shell at the initial ends of the ascending trabeculae and completely enclosed within the lower part of the sponge above the basal layer has been found in one specimen (Fig. 31), indicating that the initial attachment was by the usual encrusting of a hard object. The imperforate layer was a later development as the sponge sank under its own increasing weight. This is confirmed by the discovery of sponges that lack the usual imperforate layer attached to a rooted crinoid stem above the sea bottom.

Another early group, the tricranocladine Hindiidae, includes Ordovician and later *Hindia sphaeroidalis* that had no attachment whatever. These are usually perfectly spherical sponges. Since they have no structural polarity in oscules or anything else, they may have actually rolled about freely on the sea floor. A few individuals, especially in Permian species or in Australian Ordovician genera, are nonspherical and may have evidence of basal encrustation or attachment.

Although members of the genus *Astylospongia* usually live up to their name by lacking a stalk and, indeed, any signs of a basal attachment, they do have structural polarity in the presence of an osculum or exhalant pore cluster in a depression at the upper end. It is possible that the lowered center of gravity produced by the upper depression in their otherwise spheroidal bodies enabled them to right themselves automatically. Some related genera may have rolled about (*Carpospongia, Caryospongia*), while other genera had stalks and basal encrustations (*Palaeomanon*).

Stalks or basal encrustation are the rule in all other Paleozoic lithistids. *Belemnospongia,* as remarked earlier, may have been a root tuft of a nonlithistid demosponge, but it is entirely possible that it is the whole sponge.

DERMAL SPECIALIZATION

The simplest dermal specialization is a layer of small monaxons, usually smooth oxeas, that are tangential to the surface and in diffuse orientation. Such a spiculation, embedded in the exopinacoderm, is common in living demosponges. In fossils it is preserved as tangent monaxons scattered over the surface of the sponge. Where these spicules differ from those of the principal skeleton and also do not occur in the matrix the identification as a dermal layer is fairly certain. Otherwise there is a possibility that they are foreign or are internal flesh spicules. Such a dermal skeleton is known with fair certainty in the Hindiidae (Fig. 32). It is probably also present in the Haplistiidae, for loose, small oxeas are commonly concentrated at surfaces of specimens of *Haplistion* (Fig. 33); however, because similar spicules also coat the spiculofibers, one cannot be certain there was a separate dermal layer. Nevertheless, in the related genus *Chaunactis,* there is a definite dermal layer of a more elaborate sort. There, small, smooth oxeas are organized into a quadrate mesh of

FIG. 33. Small oxeas on surface of *Haplistion sphaericum* FINKS, 1960 probably represent remnants of a dermal layer, although such spicules also coat spiculofibers of main skeleton, USNM 127632, Magdalena Formation, USNM Locality 518q, Otero Coumnty, New Mexico, USA, ×10 (Finks, 1960).

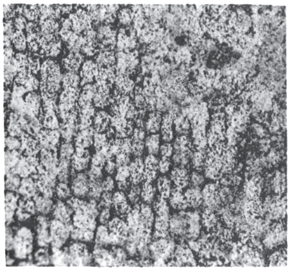

FIG. 34. Magnified view of fine, dermal mesh made of small, smooth oxeas in *Chaunactis foliata* FINKS, 1960, which has a desma-dominated, principal, internal skeleton, USNM 127640, Gaptank Formation, USNM Locality 700, Glass Mountains, Texas, USA, ×10 (Finks, 1960).

FIG. 35. Small frond of *Hazelia palmata* WALCOTT, 1920, showing obliquely crossing skeletal strands of spicules, USNM 66491, Burgess Shale, British Columbia, Canada, ×4 (Walcott, 1920).

spiculofibers finer than the desma-dominated fibers of the internal skeleton (Fig. 34). Also in *Mortieria* subparallel oxeas form a dermal layer. It is likely, therefore, that some sort of dermal layer is characteristic of other genera in the family.

Many specimens of *Hazelia* from the Burgess Shale are coated with a continuous layer of diffusely oriented, tiny, tangential monaxons. This layer is essentially continuous and the dermal pores must have been small (see Fig. 35). Thus, a dermal specialization goes back to some of the earliest known demosponges of the Cambrian. In the later Paleozoic heliospongiids a tangential dermal layer of oxeas is also developed. Here, the spicules are of the same size and form as those making up the spiculofibers of the principal skeleton, but the dermal layer is organized into a flat tangential sheet pierced by the large, circular inhalant pores (Fig. 36).

Not all Paleozoic demosponges had such a dermal skeleton. It is seemingly absent from the earliest lithistids, namely the anthaspidellids and the related chiastoclonellids. So far as can be determined, these families, however, had a nonspicular, imperforate dermal layer on the underside, as has been discussed above in the section on basal attachments.

Another form of dermal support aside from the tangential monaxons, occurs in the hindiids and in the astylospongiids. Long, smooth monaxons, much larger than desmas of the main skeleton or of the tangential dermal oxeas, are radially oriented within some of the radial skeletal canals and protrude above the outer surface. Similar spicules occur in living demosponges, for example *Spongilla* and *Ephydatia,* where they support the exopinacoderm above a subdermal space or vestibule (see also FINKS, 1971b). It is likely that the radial monaxons of the hindiids and astylospongiids had a similar function. Many living sponges have this function performed by triaenes instead of monaxons, including such common genera as *Steletta, Tetilla,* and *Geodia,* as well as many lithistids ranging from the Mesozoic to the present day. Isolated protriaenes, such as might have come from a nonlithistid sponge, are known as early as the Visean, and together with associated calthrops are the earliest record of definite tetraxonic spicules.

SPICULE FORMS

A brief review of the kinds of demosponge spicules found in Paleozoic rocks follows, for the moment without discussion of origins. The simplest and the first to appear is the oxea. The entire skeleton of the Middle Cambrian *Hazelia* is formed of smooth oxeas, larger in the main skeleton and smaller in the dermal layer. They may be diffusely arranged in the dermal layer, in an isodictyal net, or in plumose spiculofibers. The first two arrangements are typical of the occurrence of oxeas up to the Holocene; the last is more often associated with styles. From the Ordovician *Saccospongia* to the present day, styles occur characteristically in plumose spiculofibers with their blunt ends inward and their pointed ends facing outward and upward. The association of particular spicule shapes with occurrence in a specific larger organization is true of most spicule forms and points to a functional origin of spicule shapes.

The earliest lithistid desmas are the dendroclones of anthaspidellids. They appear in the Middle Cambrian. They are essentially smooth oxeas with arborescent zygoses confined to the two ends. The terminal position of the zygoses is appropriate for the isodictyal net in which they occur; the spicules are in mutual contact only at their ends. In the later (Permian) anthracosyconids, in which dendroclones often occur side by side in bundles, lateral zygoses are developed along the shaft on the side facing another spicule. The finer nature of the zygoses in such spicules distinguishes them from the similar rhizoclones of the haplistiids. It must be admitted that the distinction is sometimes difficult to make, and it is best to call all such spicules rhizoclones. In general, haplistiid rhizoclones have coarser and less finely branched zygoses. A third type of rhizoclone is found in the chiastoclonellids as well as in the anthracosyconids and haplistiids. It is a curved spicule that outlines partially a skeletal pore or canal. It is smooth on the concave side facing the pore and bears lateral zygoses on the convex side that articulates with other spicules.

In some dendroclones of Ordovician and later anthaspidellids, the smooth main shaft splits into three short, smooth branches at one end of the spicule, and these bear the terminal zygoses at their ends. Such a spicule resembles a tetraxial tetraclone, but axial canals are not demonstrable in the branches. Such spicules are more common than typical dendroclones in the anthracosyconids; the branched end uniformly faces upward or outward. Similar spicules are abundant in the chiastoclonellids and are present in smaller numbers in the haplistiids.

Another spicule that intergrades with dendroclones is the chiastoclone, characteristic of the chiastoclonellids. It has two or three branches with terminal zygoses at both ends of the spicule; the intervening shaft is very short or absent so that the spicule has an X-shaped profile. The presence of chiastoclones and tetraclone-like forms in the chiastoclonellids, rather than the more typical dendroclones of the anthaspidellids, is associated with a much more irregular skeletal net. The net may be considered isodictyal in that the spicules articulate end to end and outline mesh spaces one spicule-length wide between them. It is much denser, however, than the anthaspidellid net and is not organized into distinct layers, nor are spicules in corresponding positions in each layer to form radial series. A highly irregular or asymmetrical form of chiastoclone with many arms and no shaft occurs in the Silurian chiastoclonellids *Anomoclonella* and *Pycnopegma* and was called an anomoclone by Rauff (1895); it is here considered a variant chiastoclone. In the Permian species assigned to the Chiastoclonellidae the tetraclone-like spicules are actually more numerous than true chiastoclones.

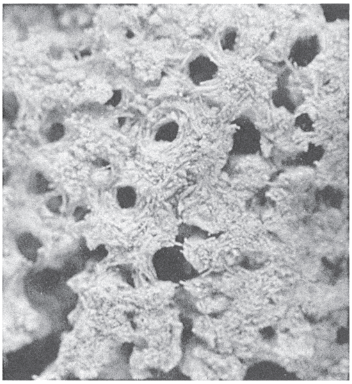
Fig. 36. Inhalant surface of *Heliospongia excavata* King, 1933, with distinct dermal layer of spicules surrounding circular skeletal pores, USNM 127580b, Rock Hill Lithology Member of Graford Formation, USNM Locality 518g, Wise County, Texas, USA, ×10 (Finks, 1960).

It is doubtful whether true tetraclones occur in the Paleozoic. Tetraclone-like spicules of the Devonian to Permian *Jereina* superficially resemble true tetraclones of the Cretaceous *Jerea,* including the characteristically inflated junctions of the spicules. The peculiar arrangement of the canal system is also similar in the two genera. Nevertheless, axial canals are not known from the Paleozoic forms, and it is not known therefore if the branches are true rays. The presence of chiastoclones in *Jereina,* along with the tetraclone-like spicules, relates it clearly to the chiastoclonellids. On the other hand, the reported presence of chiastoclones in the Cretaceous genus suggests that the two may be related after all.

Another type of desma, superficially similar to rhizoclones but almost certainly of independent origin, are the megarhizoclones or megarhizoclonids, of the Permian hindiid *Scheiella.* These are antlerlike spicules with coarse, curving branches without the finely arborescent terminations of the dendroclone-rhizoclone type of desma. As a matter of fact, branches of the megarhizoclones do not serve primarily for articulation. They occupy spaces between tricranoclone desmas of the principal skeleton; the latter are intimately interlocked among themselves, and the megarhizoclones only loosely interlock with them, rather more like vines perhaps, twining about their supports. They are associated with the more open and irregular principal skeleton of *Scheiella,* which is in turn associated with a greater number of four-rayed tricranoclones than in its earlier relative, *Scheiia.* Before discussing tricranoclones, however, we will look at other, more clearly monaxial desmas and related simple spicules.

The strongyle, with two blunt ends, appears later in the fossil record than the oxea, although at times one may be hard pressed to distinguish between a blunt oxea and a strongyle. Like the oxea and to a lesser extent the style, strongyle-like forms also occur in the Hexactinellida. Consequently, isolated spicules cannot be identified with certainty as being of demosponge origin. The Carboniferous and later haplistiids seem to be the earliest demosponges in which strongyles are demonstrably part of the skeleton. There they comprise the spiculofibers along with oxeas and rhizoclones. Like the oxeas they often have a superficial position in the fibers. They are also sometimes concentrated on the surface of the specimen or in the immediately adjacent matrix, suggesting that they were part of a tangent dermal layer. They also occupy a corresponding dermal position and probable function in the Permian hindiid *Scheiia* and *Scheiella,* along with oxeas that apparently take their place in the early Paleozoic *Hindia.* Dermal strongyles and oxeas are also present in the Permian Anthracosyconidae.

There is a group of monaxial and possibly tetraxial desmas and desmoids that possess articular facets or cups, rather than sharp-ended and finely branched arborescent zygoses of the rhizoclone-like spicules. The group with articular facets includes heloclones and various types of anapodal spicules such as megaclones, tricranoclones, dicranoclones, sphaeroclones, and didymoclones. The simplest of these are the desmoids that coat spiculofibers of *Saccospongia* and other Ordovician dystactospongiids. They are sinuous bodies of irregular outline with one or more subcircular notches that surround partly a neighboring spicule. They are termed heloclonid desmoids because they resemble the **heloclones** of Mesozoic Helomorina.

The remaining members of this group are anapodal spicules (Finks, 1971b), that is, desmas in which the arms are all on one side of the spicule, the inward or proximal side in relation to the whole sponge. Sponges with this type of spicule build their skeletons in successive layers parallel to the sponge surface. The spicules of the latest-formed layer articulate with those of the preceding layer by means of terminal facets on their proximally directed arms to form what may be termed a simple enspicular isodictyal net, that is, one whose mesh spaces are outlined by single arms or branches of spicules.

The simplest of these are megaclones, which are clearly monaxial. Several stout, smooth arms arise from one side of a smooth monaxial central body and terminate in cuplike articular facets. The only published example from the Paleozoic of this predominantly Mesozoic group is the lower Carboniferous *Archaeodoryderma* REID, 1968b. It is known only from isolated spicules that are associated with heloclones and ophirhabds (the latter being sinuous monaxons that lack articular facets). It is assumed that all these spicules came from the same sponge, which had a relatively incoherent and perhaps sublithistid skeleton.

Anapodal spicules of the hindiids, called tricranoclones (REID, 1963b), have similar terminal articulating cups, but the distal surface of the spicule is tuberculate. In the widely occurring early Paleozoic *Hindia* and in the Australian *Belubulaspongia, Palmatospongia,* and *Arborohindia,* there are three proximal arms tetrahedrally arranged and a short fourth arm (**brachyome**) that is directed distally. The tubercles are apparently concentrated around the edge of the articular cups, encircle the brachyome, and lie along the distal side of the proximal arms. In the skeletal net the articular cups rest on the distal sides of arms of the spicule beneath, adjacent to the brachyome. The tubercles appear to interlock. The net is so arranged that spicules occupy corresponding positions in alternating layers such that each of the proximal arms of a single spicule rests upon three different spicules in the layer beneath. The corresponding spicules of alternative layers form radial series that outline radial canals between them. In the late Paleozoic *Scheiia* the brachyome is missing, the tubercles are distributed over the entire distal surface, and a few spicules have four instead of three proximal arms. This is continued in the Late Permian *Scheiella,* in which it is clearly associated with a more irregular and open skeletal net, one in which regular radial series of spicules are difficult to recognize. As noted earlier, megarhizoclones occupy interstitial positions in this irregular net. The tubercles interlock demonstrably, and their more general distribution over the distal surface, as well as the absence of the brachyome, would seem to be associated with the less regular placement of the articular facets on the underlying distal surfaces, which in turn is related to the less regular net. It is not known whether the tricranoclone is a monaxial or tetraxial form. If it is tetraxial, the earlier *Hindia* form is closer to a tetraxon in shape than the later *Scheiia-Scheiella* form.

The skeletal net of the astylospongiids was interpreted by RAUFF (1894) as similar to that of *Hindia,* and its principal spicule as similar to a tricranoclone except that it had six anapodal arms instead of three. The arms are straight rather than bowed as in the hindiids, and they are long, slender, and smooth. The center of the spicule where they meet is somewhat inflated and spheroidal, hence the name sphaeroclone. Each arm resembles in size and shape an anthaspidellid dendroclone. This was the first interpretation given to these spicules (ZITTEL, 1884). If so, the spheroidal centra would be merely inflated and possibly secondarily cemented junctions of dendroclones in a three-dimensional, simple isodictyal net. There exists no specimen or published illustration (excluding drawn reconstructions) that permits a critical rejection of one of these alternative interpretations. In some illustrations (e.g., PICKETT, 1969, pl. 10,*4*) the ends of the arms appear arborescent in the manner of dendroclones but details always seem to be at the limit of visibility or preservation.

Tricranoclones, megaclones, and sphaeroclones (if they exist) are the only anapodal spicules known so far from Paleozoic rocks. Other types are known from Mesozoic and later deposits. Of the Paleozoic forms, only the tricranoclone is possibly tetraxial.

Tetraxons of a nonlithistid type are known definitely from Paleozoic rocks beginning with the Lower Carboniferous. Isolated calthrops and various forms of triaenes are known. These include protriaenes and anatriaenes. The more elaborate dermal supporting dichotriaenes and phyllotriaenes are apparently not reported from the Paleozoic.

REID (1963c) has interpreted the supposed branching hexactines ornamented with spiral ridges of the Carboniferous *Spiractinella* as pseudohexactines of a demosponge because they intergrade with similarly ornamented but much rarer apparent tetraxons. The occurrence of similar spicules in the undoubted hexactinellid *Arakespongia,* which is roughly contemporaneous with *Spiractinella,* however, favors a hexactinellid assignment, which is followed herein. The known propensity of hexactinellid spicules for suppression of rays and variation in the angles between rays is not inconsistent with interpreting the tetraxons of *Spiractinella* as pseudotetraxons.

Finally it must be said that microscleres, of either the sigmatose or astrose variety, are so far unknown from Paleozoic rocks. Microrhabds are also unknown, but it would be hard to distinguish between a very small oxea and a microrhabd.

CANAL SYSTEMS

Herein we deal with the skeletal canals, which probably correspond only to the larger of the true canals and may be broader than these. In general, inhalant canals tend to follow the ascending tracts of the skeleton inward and downward, while the exhalant canals tend to parallel the accretionary layers of the skeleton at right angles to the inhalant passages. If a cloaca or spongocoel is present, exhalant canals run upward and inward along the accretionary layers toward the cloaca. Large exhalant canals perpendicular to the accretionary layers, however, may take the place of the cloaca. In massive sponges without a cloaca, exhalant canals may still follow the accretionary layers but converge upon numerous local exhalant centers, while inhalant canals are perpendicular to the accretionary layers as before. The simplest type of canal system is one in which both inhalant and exhalant canals are radial and perpendicular to the accretionary layers.

Although the upper depression of a cup-shaped sponge is often homologized with a cloaca, there is some evidence that this may not always be correct. The inner surface of the cup frequently bears local exhalant centers (as in *Anthaspidella*) just like the surface of a massive sponge. Truer homologues or at least structural analogues of the cloaca are exhalant canals that are perpendicular to the accretionary layers of the skeleton and therefore at right angles to the other exhalant canals. They are often grouped in the axial region of the sponge and sometimes lead into a true cloaca from below. They may also lead into local exhalant centers.

The simplest canal system or more specifically the most uniform and symmetrical is that associated with the spherical and probably unattached *Hindia* and *Scheiia* among the hindiids. All canals are radial, and the exhalant ones are distinguished, if at all, only by their greater diameter. Porelike passages between the spicule arms connect adjacent radial canals. Some of these canal-like spaces may have been occupied by choanocyte chambers, for there is no other open space in the sponge. The living flesh of the sponge may have occupied only the outer layers of the skeleton; disintegration of the interior of the skeleton has occurred in some specimens.

The spherical astylospongiid *Carpospongia* has a canal pattern like that in *Hindia* (Rigby, 1986b). *Caryospongia,* although similar to *Hindia* in external outline, has a more complex canal system. Smaller inhalant and perhaps some exhalant canals are straight and radial. Most large exhalant canals, however, curve upward toward the outer surface and cut across the accretionary layers of the skeleton. As in all astylospongiids, the skeleton has more open space between the spicules than in the hindiids. This type of canal system is like that found in many massive sponges of less regular outline, for example the anthaspidellid *Multistella.*

Many massive chiastoclonellids (for example, *Defordia*) and anthracosyconids (for example, *Collatipora*) have this type of canal system. Often the single exhalant opening of each center (really a short cloaca) is replaced by a cluster of exhalant pores that are the termini of short radial exhalant canals (really a multiple cloaca). The species *Heliospongia excavata* also has this type of canal system, as does the cup-shaped *Anthaspidella,* although the form of the sponge is flabellate and subramose.

A variant of this form of canal system occurs in the genus *Anthracosycon.* Here the exhalant pore cluster is spread over one surface of the sponge (usually the top). The horizontal exhalant canals that converge upon the cluster are confined to the periphery of the surface, usually rising a short distance up the sides and running in a short distance toward the center of each accretionary layer. In this variant the dominant exhalant canals are now the short cloacas that run perpendicular to the accretionary layer.

Another type of canal system in which the exhalant canals are largely perpendicular to the accretionary layers is one in which these canals open into grooves on the surface of the sponge. In the spheroidal astylospongiid *Caryospongia* the grooves are meridional as they are also in the cup-shaped *Phialaspongia.* In the massive anthaspidellid *Phacellopegma* the grooves anastomose over the entire surface.

Exhalant canals perpendicular to the accretionary layers may be scattered over the sponge surface in complete isolation from one another. This is true in the haplistiid *Haplistion* and the hindiid *Scheiella.* Here we are brought back essentially to the simple condition of *Hindia* but without the spherical symmetry.

The relation of exhalant pore clusters to a cloaca occurs in a number of intermediate forms. In the astylospongiids *Astylospongia* and *Palaeomanon,* exhalant canals run parallel to the accretionary layers and open into a cup-shaped depression on the top of the sponge, which cuts down into these layers. This cup-shaped depression is homologous to a true cloaca that cuts down even deeper into the interior of a cylindrical sponge, as in *Heliospongia* and *Coelocladia* among the heliospongiids; *Exochopora, Lissocoelia, Aulocopium, Rhopalocoelia,* and *Nevadocoelia* among the anthaspidellids; *Columellaespongia* among the haplistiids; *Saccospongia* among the dystactospongiids; and *Camellaspongia, Devonoscyphia,* and *Attungaia* among the astylospongiids, in which exhalant canals follow the accretionary layers horizontally to the cloacal surface. In many of these, vertical exhalant canals perpendicular to the accretionary layers enter the cloaca from below, just as in an exhalant pore cluster. The anthaspidellid *Zittelella* is another intermediate form in which the homology between an exhalant pore cluster and a cloaca is clearly shown. Here an axial cluster of vertical exhalant canals perpendicular to the accretionary layers opens into a cup-shaped depression on the top of the sponge, where they are joined by converging exhalant canals following each accretionary layer.

For the horizontal exhalant canals to coalesce vertically to form slitlike spaces traversing several accretionary layers is a common tendency among anthaspidellids and is especially well developed in *Archaeoscyphia.* It occurs also in the astylospongiid *Devonospongia.* Indeed, it is not confined to canal systems with a cloaca, for it is also found to some extent in the anthracosyconid *Anthracosycon* and in the chiastoclonellid *Actinocoelia;* in the latter, the slitlike spaces converge upon local exhalant centers. It occurs also in the haplistiids *Chaunactis* and *Mortieria,* where it gives rise to the radiate-lamellate skeletal structure found also in many Mesozoic rhizomorines.

The axial cluster of exhalant canals that leads into the cloaca of many sponges can itself become a principal feature of the canal system, as in the chiastoclonellid *Jereina.* Each of the axial canals is essentially a separate cloaca and may even diverge from the axial region to open on the side of the sponge. This confirms the homology to a true cloaca of exhalant canals that are perpendicular to the accretionary layer.

Unlike the cup-shaped upper surfaces of *Astylospongia* and *Zittelella,* which are true homologues of a cloaca, the cup-shaped surfaces of the anthaspidellid *Anthaspidella* and the astylospongiid *Phialaspongia* are like the outer surface of a massive sponge. The former bears exhalant centers with converging canals; the latter bears meridional grooves containing exhalant pores. Nevertheless, the accretionary layers of *Anthaspidella* are transected by this cuplike surface. In this respect it is like a true cloaca and therefore may also be homologous, even though the structural correspondence with a true cloaca is not complete.

It remains to be noted that in some later Paleozoic species of anthracosyconids (*Anthracosycon auriforme*) and haplistiids (*Chaunactis*), there appears to be the first development of differentiated inhalant and exhalant surfaces on a noncloacate, sheetlike, or flabelliform sponge.

PHYLOGENY

It is apparent from the foregoing discussion that the form of the spicules and the form of the skeletal net are closely correlated, while both are relatively uncoupled from the pattern of the canal system. Families can be defined to a large extent by the form of the skeletal net. Individual spicule forms are more widely distributed, but the shape of particular spicules is often related to their spatial occurrence in the skeletal net. Thus it is likely that the evolution of spicule form is tied, in most instances if not in all, to a function of an architectural sort. Convergent evolution of spicule shape is therefore a possibility. Reconstruction of phylogeny can be based most securely on the interpenetration of spicule morphology, skeletal net morphology, and the unique sequence of these forms through time.

As is shown by their early occurrences, oxeote spicules, a spiculofibrous skeleton, and a differentiated dermal layer of tangent spicules are primitive features. These are all found in the mid-Cambrian *Hazelia,* which is one of the oldest completely preserved demosponge skeletons; several species, all sharing the enumerated features, are known. This is a nonlithistid form, preserved only because of the special conditions of the Burgess Shale. Black shales of Late Cambrian age in Quebec may give us a later glimpse of the same group in the form of the species *Lasiothrix flabellata* Dawson & Hinde, 1889, which may be a *Hazelia* or a related genus. (It is not the type species of *Lasiothrix,* which may be considered a hexactinellid.) Among the Burgess Shale specimens assigned to the various species of *Hazelia* there are different forms of the skeletal net and of the whole sponge. Perhaps some of these should be recognized as separate genera. The type species, *H. palmata,* has a skeletal net of anastomosing ascending spiculofibers; the spicules are somewhat plumosely arranged within the fibers. The entire sponge is apparently flabellate and without a cloaca. There may be a continuous brush of dermal spicules perpendicular to the surface. *H. delicatula,* on the other hand, appears to be cylindrical and branching, with a probable cloaca and distinct, circular inhalant pores. The principal net is compound isodictyal and the tangent dermal layer is simple isodictyal, at least in part.

From *Hazelia delicatula* it is possible to derive geometrically (which, of course, is not the same as saying they must of necessity have been so derived phylogenetically) several Paleozoic demosponge families by the following structural transformations. By making the compound isodictyal skeletal net more regularly rectangular, formed in accretive layers, and in general thickening both the tracts and the body wall, one can produce the structure of the late Paleozoic family Heliospongiidae. If, in addition, one converts some of the oxeas to rhizoclones by development of lateral zygoses, one arrives at the structure of some of the earliest completely preserved Haplistiidae, the Devonian genera *Columellaespongia* and *Varneycoelia,* which have a cloaca that is absent from most Paleozoic rhizomorines. Loss of the cloaca would produce their massive Devonian contemporaries (and Australian counterparts) *Crawneya* and *Oremo,* as well as the later Paleozoic haplistiids.

In another direction entirely, one can structurally derive the Anthaspidellidae from the simple isodictyal surface net of *Hazelia delicatula* by developing terminal zygoses on the oxeas, thus transforming them into dendroclones, and by building the skeleton of successive layers of these simple, isodictyal nets of dendroclones. Early anthaspidellids, possibly the Late Cambrian *Gallatinospongia* and certainly the early Ordovician *Archaeoscyphia,* also have the cloacate form of *Hazelia delicatula.*

If the skeleton of astylospongiids is composed truly of dendroclones or even of dichotriders (sphaeroclones) that are formed by the fusion of dendroclone elements, they could be derived from the earliest anthaspidellids (or directly from a *Hazelia delicatula*) by development of a three-dimensional arrangement of the simple isodictyal net. The earliest astylospongiids (*Astylospongia, Caliculospongia, Camellaspongia, Phialaspongia*) appear in the later middle Ordovician (Trentonian). They are cup shaped or cloacate with the exhalant pores arranged in vertical rows. These features are also characteristic of the earliest anthaspidellids, such as the Early Ordovician *Archaeoscyphia;* and the time relationships are such that an origin from an *Archaeoscyphia*-like sponge is quite plausible.

One can also derive the structure of the Silurian and later Chiastoclonellidae from the anthaspidellid structure. The transformation involved here is development of a three-dimensional net of rodlike elements by more elaborate branching of the dendroclone zygoses, forming chiastoclones, and the still more irregular anomoclones. This type of net (see above) is termed herein an enspicular isodictyal net, for the individual mesh elements are parts of spicules rather than entire spicules. The relationship is supported by the continued presence of dendroclones in chiastoclonellids, as well as by the characteristic concentrically wrinkled imperforate basal layer found in many chiastoclonellids and anthaspidellids. A possible connecting link is the mid-Silurian massive anthaspidellid *Dendroclonella,* which is very close in form to the contemporaneous and sympatric chiastoclonellid *Chiastoclonella* from the Niagaran of Tennessee. The latter, more than the other early chiastoclonellids, retains the radial rows of spicules that occur in the anthaspidellids. The former is unusual (although not unique) among anthaspidellids in being massive in shape. It is what one would expect for an ancestor of the uniformly massive chiastoclonellids. The greater irregularity and complexity of the late Paleozoic chiastoclonellids as compared to the Silurian forms supports the theory that the mode of origin of the chiastoclonellids was due to the decrease in the symmetry of an anthaspidellid.

Another group that contains dendroclones is the Permian Anthracosyconidae. Their structure is quite different from that of the anthaspidellid-chiastoclonellid group. Their dendroclones are arranged perpendicular to the surface in concentric shells, rather than parallel to the surface as in the anthaspidellids. In many species they are grouped into pillarlike bundles and in some species these may coalesce laterally to form wall-like structures outlining horizontal canals. The dendroclones in these bundles often develop lateral zygoses, so they become more or less rhizoclone-like. Most of them, however, are tetraclone-like. It would be possible to derive this group from the haplistiids by eliminating the transverse spiculofibers and decreasing the size, spacing, continuity, and regularity of the remaining radial spiculofibers, even to the point of rendering them single dendroclones. The fact that single dendroclones substitute for spiculofibers in juvenile parts of *Haplistion aeluroglossa* (although there for transverse fibers and not radial ones) makes this plausible. Nevertheless, the dominance of dendroclones and the absence of the coarser haplistiid-type of rhizoclone requires a reversion to a more ancestral spicule type, although perhaps this should be regarded as an example of neoteny. The absence of smooth monaxons in the anthracosyconids (except for a local patch on a specimen of *Dactylites micropora*) argue for a derivation from the haplistiids rather than to them, if one accepts the origin of the haplistiids from a hazeliid-heliospongiid lineage in which smooth monaxons are primitive. This would be consistent also with the late Paleozoic occurrence of the anthracosyconids. They could also have been developed from chiastoclonellids by reorganizing the isotropic skeleton into layers of perpendicularly oriented spicules. Forms of the spicules themselves are very similar in the two groups. The origin of the anthracosyconids must remain more problematical than some of the families discussed here, but it is clear that they belong somewhere in the complex of lineages that includes the Orchocladina and Rhizomorina and that ultimately goes back to hazeliimorph ancestors.

To return to *Hazelia,* one can derive another set of lineages from the type species, *H. palmata.* In this species ascending spiculofibers are subparallel and anastomosing, and the net is distinctly anisotropic, with mesh spaces being elongate parallel to the axis of growth. First of all, it is possible that the haplistiids were derived from this species directly rather than from *H. delicatula* via a heliospongiid-like intermediate as outlined above. One could produce the haplistiid structure by replacing the anastomoses of *H. palmata* with regularly spaced transverse spiculofibers and by developing lateral zygoses on some of the oxeas. In this connection, it may be significant that the ascending fibers in haplistiids are always thicker than the transverse fibers (unlike in the heliospongiids). It may also be significant that in the earliest haplistiids from the Devonian this distinction is more emphasized, and the mesh spaces are less quadrangular than in later forms.

A more clearly related group is *Saccospongia* and the other Ordovician dystactospongiids. All that is needed is to turn the oxeas into styles, arrange them in a more plumose fashion in the fibers, and coat the fibers with a layer of heloclone-like desmoids. Gross morphology of the net is essentially the same in both groups. Within the dystactospongiids there is a certain amount of variety. The extent of desma coating of fibers is variable in *Saccospongia* itself, a feature also of living desmacidontids with similar morphology, such as *Helophloeina* and *Desmatiderma* (see Finks, 1967a). In *Dystactospongia* the fibers seem to be composed entirely of desmoids without the styles (see Rigby, 1966b). In *Heterospongia* they are composed of desmoids together with seemingly nonplumose monaxons (styles or oxeas). The last two genera have a massive, subdigitate habit like *Hazelia palmata; Saccospongia* is tubular (cloacate) and branching. In *Dystactospongia* and *Heterospongia* thin transverse connecting fibers seem to dominate over true anastomosis as a means of joining the ascending fibers. This is close to the gross structure of the haplistiids, and a third possible origin of that group would be through a dystactospongiid similar to *Heterospongia;* here there is a possibility of the rhizoclones arising from the desmoids rather than from the oxeas directly.

Many living genera of sponges with chelate microscleres and stylote megascleres (and therefore belong to the natural group of the desmacidontids) have a sublithistid skeleton of often plumose spiculofibers of styles invested with monaxonic desmoids (see discussion by Finks, 1967a). The correspondence of their structure with that of *Saccospongia* is so close that an origin from *Saccospongia* and ultimately *Hazelia palmata* of the entire closely knit group of sigma-bearing monaxonic sponges and the similar but spiculeless Keratosa is quite plausible. The axinellids, with plumose spiculofibers of styles, and even the Clavulina (hadromerids), with tylostyles, might also have had their origin from this lineage; such a hypothesis permits a one-time origin of styles, together with a functional reason for their origin, namely their participation in plumose spiculofibers where the blunt end provides an attachment surface for the spongin.

The spicule complement assigned by Reid (1968b) to the Carboniferous megamorine *Archaeodoryderma* includes heloclones similar to the desmoids of *Saccospongia,* true anapodal megaclones, and ophirhabds. He considered the sponge to be sublithistid. This could conceivably have descended from a dystactospongiid, especially if still sublithistid, and thus lead ultimately from *Hazelia* to the post-Paleozoic Megamorina and Helomorina. This can have far-reaching implications, for the Megamorina share the presence of streptosclere microscleres and dermal triaenes with two other post-Paleozoic lithistid groups, the Dicranocladina and the Tetracladina, as well as with the nonlithistid theneids (pachastrellids). If these are truly related, then some tetraxon-bearing sponges could have descended from *Hazelia.*

Some light is shed on this possibility by the last remaining major lineage of Paleozoic sponges, the hindiids. At their first appearance in the Ordovician their principal spicules resemble those of no other group of sponges, not even the contemporaneous astylospongiids, even if the spicules of the latter are considered anapodal. By Late Devonian and Carboniferous time these had been transformed into the distinctive *Scheiia* spicule, which is joined in the Late Permian *Scheiella* by megarhizoclones. The combination of megarhizoclones and tuberculate anapodal spicules is characteristic of the post-Paleozoic Dicranocladina. Transformation of the *Scheiia* anapodal spicule into a dicranoclone is no greater a change than the earlier transformation of the *Hindia* anapodal spicule into the *Scheiia* one. Another transformation, however, is also necessary. This is the conversion of radial oxeas into radial dichotriaenes. Some sponge specialists find this harder to accept despite the fact that it is known to occur in ontogeny (Watanabe, 1957; Sollas, 1887). Reiswig's (1971) discovery that the axial canal of demosponges has a triangular cross section indicates how such a transformation could have taken place; the structural organization that favors the addition of three equally spaced rays is present in every oxea. It is no more mysterious to add three rays than to lose them. The possible functional morphological reasons for these transformations is discussed in greater detail elsewhere (Finks, 1971b) to provide fuller support for a more irregularly curved dermal membrane. What is important here is the likelihood, based on the *Hindia* lineage, that sponges with tetraxons can arise from ancestors that have only monaxons. It also makes more plausible the origin of tetraclones from the expansion of tripartite dendroclone zygomes and the descent of the Tetracladina from late Paleozoic Chiastoclonellidae.

True tetraxons, in the form of isolated calthrops and triaenes, are known from Carboniferous (Visean; Hinde, 1888) and later rocks. These must have originated independently from the hindiid line. They are not known to occur as part of specimens of any of the other lithistid and sublithistid lineages previously discussed. Thus they represent a separate lineage or lineages that was probably, though not necessarily, always nonlithistid. The living choristids and possibly homosclerophorids with **euastrose** microscleres may be part of this lineage.

Tracing the post-Paleozoic descendants of these Paleozoic lineages is rendered more difficult by the poor Triassic demosponge record. Nevertheless, Late Paleozoic beginnings can be seen for some later groups. The tendency to form a radial-lamellar architecture of rhizoclones in some late-Paleozoic haplistiids (*Mortieria, Chaunactis*) makes likely the descent of the Mesozoic rhizomorines, such as *Cnemidiastrum,* from them. The presence of megarhizoclones together with tuberculate anapodal spicules of variable arm number in the Late Permian hindiid *Scheiella* makes likely the descent from them of Jurassic and later Dicranocladina, such as *Dicranoclonella, Pachycothon,* and the living *Corallistes* (Finks, 1971b). The Permian chiastoclonellid *Jereina* has mostly tetraclone-like desmas with inflated junctions; the presence of similar tetraclones in the Cretaceous tetracladine *Jerea,* which also contains the chiastoclones of the Permian genus and an axial cluster of parallel apochetes, suggests a descent of at least some Tetracladina from the chiastoclonellids. The similarity of the Ordovician *Saccospongia* to living sublithistid desmacidontids (Finks, 1967a) renders almost superfluous the

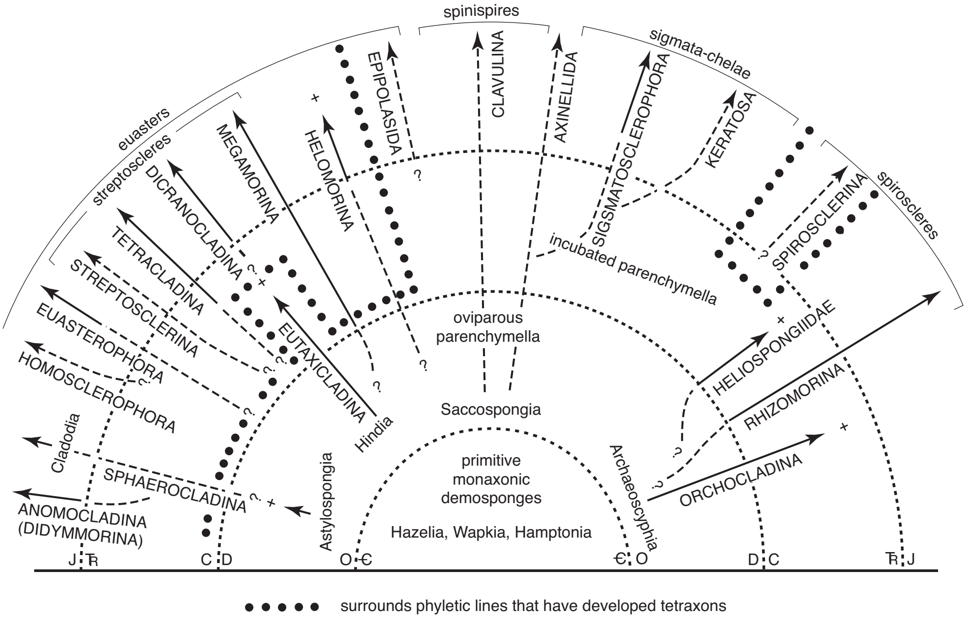

FIG. 37. Suggested phylogeny of major noncalcareous groups of the Demospongia (Finks, 1967a).

absence of an intermediate fossil record. (Here I might add that recent acceptance of the episodic nature of evolution renders less effective those objections based on the long time span involved.) If one wishes to accept a one-time origin of styles and plumose architecture one may derive the axinellids, hadromerids, and tethyids (epipolasids) from the same basic stock. If one accepts a one-time origin of sigmatose microscleres, then all the Poecilosclerida (including the desmacidontids in the narrower sense of sponges with chelae and styles) together with the related (according to many authorities) monaxonid groups Haplosclerida and Halichondrida and the similar but nonspicular Keratosa, would all go back to *Saccospongia* and its close relatives. WIEDENMAYER (1977a, 1977b), however, noted the similarity between *Heliospongia* and the living haplosclerids *Petrosia, Xestospongia,* and *Cribrochalina* with respect to radial-reticulate skeletal architecture and spiculation and suggested an origin of the sigma-bearing groups through *Heliospongia* and ultimately *Hazelia,* separate from *Saccospongia.* This is discussed further below. Finally, if one accepts a one-time origin of heloclones, as well as a connection between heloclones, **ophirhabds,** and **megaclones** as cited by REID (1968b), then *Saccospongia* may also be the source of Carboniferous and later Megamorina, the Mesozoic Helomorina, and the Mesozoic to Holocene Ophiraphiditidae (Fig. 37).

Some Paleozoic lineages seem to have become extinct. The anthaspidellids and chiastoclonellids appear not to have survived the Permian, although the Tetracladina may possibly have descended from the chiastoclonellids. The anthracosyconids appear to be a side branch without issue. The haplistiids did not survive the Paleozoic, but they lead directly into the later Rhizomorina so that the lineage did not die out. The hindiids likewise did not survive, but they seem to lead directly into the Dicranocladina. The astylospongiids appear to have died out in the Devonian. Forms with sphaeroclones, however, such as the Cretaceous *Cladodia* and the Tertiary to Holocene *Vetulina,* as well as forms with didymoclones, such as the Jurassic *Cylindrophyma* and *Melonella,* may have descended from them if the astylospongiids indeed had sphaeroclones. It is also possible that these groups descended from one of the other lineages with anapodal spicules, such as the Dicranocladina or Megamorina.

FUNCTIONAL REASONS FOR THE EVOLUTION OF PALEOZOIC DEMOSPONGES

Unlike the Hexactinellida and Calcarea, demosponges appear to have always had leuconoid architecture. This is supported by their fossil record as well as by their rhagon juvenile stage. A few of the earliest whole fossil demosponge skeletons are thin walled, but most, such as *Hazelia,* are thick bodied and suited for the support of scattered choanocyte chambers. Even the tubular, cloacate species of *Hazelia* are thick walled and bear pores that imply the presence of a well-developed canal system.

The earliest fossil demosponges were from quiet-water environments, such as *Hazelia* of the Burgess Shale. A skeleton of simple, slender monaxons held together by spongin is adequate for support, and the delicate nature of the spicules reflects the relative scarcity of dissolved silica in seawater. *Hazelia* also had two ways of achieving maximal strength with minimal material. *H. delicatula* has an isodictyal net with triangular interspaces. A triangular framework has maximum resistance to deformation and uses the least material. *H. palmata* has a skeleton of ascending fibers of plumose bundles of monaxons. The greater flexibility of such a skeleton is not disadvantageous in quiet waters.

The first lithistids appear in the Cambrian but become common in the Ordovician and are associated with shallow-water, often reefy limestones. It is hard to avoid the conclusion that the development of interlocking spicules was adaptive to higher wave-energy conditions. Among the hindiids, astylospongiids, and anthaspidellids, the skeleton consists of an isotropic (hindiids, astylospongiids) or anisotropic (anthaspidellids) triangulated net that supplements the rigidity produced by lithistid interlocking. The isotropic triangulated net (triangular in all directions) is attained by multirayed spicules; the anisotropic triangulation (triangular parallel to the surface) uses the basic monaxons. A sublithistid type is developed out of the skeleton of ascending fibers in the dystactospongiids. Here the plumose skeleton of *Hazelia palmata* is coated with desmoids that confer rigidity.

The anthaspidellids are the dominant lithistids in the reefy facies of the Ordovician and Silurian. The triangulated net is parallel to the upper and outer growing surface of the sponge, like a succession of superposed geodesic domes. Because spicules in successive layers occupy corresponding positions, the triangulation is carried downward through the entire skeleton as radial or ascending triangular compartments. The triangulated dome resists compression from above, and the longitudinal triangular compartments resist lateral compression. Such a structure is especially appropriate for the elongate tubular or conical shapes assumed by most anthaspidellids, particularly the earliest ones of the Ordovician such as *Archaeoscyphia.* It is not without significance that such anthaspidellids are important constituents of Ordovician reefs, particularly in the Arenig-Llandeilo interval.

The fibrous structure of the dystactospongiids is less strong and also less sparing of silica than that of the anthaspidellids. They are more abundant in the later Ordovician (Caradoc–Ashgill) and in somewhat deeper or at least nonreefy facies. They also tend to be smaller.

The astylospongiids, with their rigid, three-dimensionally triangulated net that is as delicate and sparing of silica as that of the anthaspidellids, reached their acme in the Silurian (Tennessee and Gotland) and Devonian (Australia). The Devonian taxa are of larger size and parallel the Ordovician anthaspidellids in shape.

In the later Paleozoic the dominant lithistids have a skeleton of bundled parallel monaxons with regular radial or ascending fibers connected by partly triangulated concentric shells of fibers. The triangulation is not carried down through the skeleton as in the anthaspidellids, and the dominant mesh space in both longitudinal and tangential view is quadrangular. Such skeletons include those of the heliospongiids, haplistiids, and anthracosyconids. Here strength is achieved by thickness of the bundled fibers, which is a more wasteful way of using silica. One may wonder whether silica may have been in better supply than in the earlier Paleozoic. This bit of speculation is not wholly unfounded, for many late Paleozoic sponges of all classes are hypersilicified and hypercalcified in the form of either heavy, excrescence-covered spicules (the siliceous hexactinellids *Stioderma, Docoderma, Carphites, Endoplegma,* and *Stereodictyum* and the calcareous heteractinids *Asteractinella* and *Wewokella*) or massive calcareous sclerosome (the sphinctozoans *Girtyocoelia, Amblysiphonella, Stylopegma* and the inozoans *Maeandrostia, Fissispongia, Catenispongia, Stratispongia*).

There is a tendency through the Paleozoic to break down or decrease the regular symmetry of these concentric and radial types of skeleton, apparently accommodating large canals and **cavaedial spaces,** and thereby shortening distances that narrower canals have to traverse between surfaces in contact with the ambient medium. The chiastoclonellids appear to be such a development out of probable anthaspidellid ancestors. Late Paleozoic genera within the hindiids (*Scheiella*) and haplistiids (*Mortieria, Chaunactis*) have similar development. In all these sponges the partial or complete triangulation of the ancestral skeleton is almost wholly lost. The more irregular skeletal net is built of such more complex spicules as chiastoclones and various rhizoclone-like forms.

POST-PALEOZOIC DEMOSPONGEA

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INTRODUCTION

The main general features of post-Paleozoic demosponge faunas may be summarized in the following ways.

1. Mesozoic demosponge genera are predominantly lithistids, a group that reached its greatest diversity in the Cretaceous period. There are no reliable Mesozoic records of modern nonlithistid genera, but some may have existed, since some lithistids (e.g., *Discodermia* Barboza du Bocage) have survived since the Early Cretaceous.

2. Cenozoic demosponges include fewer lithistids, most of which are Miocene, but there are more supposed occurrences of modern nonlithistid genera, and some of these are probably genuine.

3. Modern demosponges are mainly nonlithistids, which greatly outnumber both all the known modern lithistids and all the known nonlithistid fossils. Cenozoic and modern lithistids appear to be mainly survivors of the large Cretaceous lithistid fauna. The large modern nonlithistid fauna may have existed at least as early as the Eocene epoch since material from the Eocene of New Zealand suggests an Indo-Pacific fauna as diverse as the modern one and includes many living genera.

4. The fossil nonlithistid Demospongea fall mainly into two categories, a) a minority comprising purely fossil genera, whose relationships to modern forms are unknown, and b) a majority comprising supposed fossil examples of modern genera recorded on the basis of isolated megascleres or microscleres that resemble those of some modern species, but which are not diagnostic of the recorded genus. A few modern genera are more or less reliably recorded from material with both megascleres and microscleres (e.g., *Ecionemia* Bowerbank, Eocene [Plantagenet Beds], Western Australia) or from spicules found in only one modern genus (e.g., *Thrombus* Sollas, Eocene, New Zealand).

5. There are very few acceptable records of keratose sponges and none of askeletose genera (myxosponges).

6. Isolated microscleres include a) euasters from oxyaster to sphaeraster and sterraster, from the Upper Jurassic; b) the same forms plus plesiasters, spheres, spinispiras, discasters, sigmas, diancistras, clavidiscs, and various types of chelas, from the Upper Cretaceous; and c) the same from the Eocene (New Zealand), including many chela forms like those of various modern genera and sometimes species.

Because of its character, the nonlithistid record throws almost no useful light on the classification or phylogeny of modern forms. The record is not only sparse and unsatisfactory but probably also extremely incomplete. It is possible that the present large fauna evolved mainly in the Cretaceous period, but some of its origins appear to be much older. For instance, geodiid choristids, with long-shafted triaene megascleres and sterraster microscleres, were apparently already in existence in the Early Carboniferous (Ireland, Scotland). Other spicules of the same age resemble megascleres of some modern monaxonids.

The general characters of the modern nonlithistid demosponges have already been described, but an outline of those of characteristics of some families will be useful here.

1. Plakinidae. Microspiculate sponges, without triaenes; spicules usually mainly tetractinal but sometimes triactinal or diactinal; some with lophose tetractines (e.g., type genus *Plakina* Schulze); incubated amphiblastulae in *Plakina.*

2. Thrombidae. Microspiculate sponges, whose spicules are small, spiny triaenes (often trichotriaenes).

3. Pachastrellidae. Streptosclere microscleres; megascleres oxeas and calthrops, centrotriaenes, or both; aphodal canal system.

4. Poecillastridae. Streptosclere microscleres; megascleres oxeas, calthrops, and triaenes, with the last two intergrading; usually eurypylous.

5. Theneidae. Specialized deep-sea sponges, like Poecillastridae but all tetraxon megascleres long-shafted triaenes; often fixed by a root tuft.

6. Calthropellidae. Microscleres euasters or spiny microrhabds; megascleres calthrops or subtriaenes; sterrasters and aspidasters absent.

7. Ancorinidae. Microscleres euasters ranging from oxyaster to sterrosphaeraster (not sterraster or aspidaster), or with additional microrhabds or sanidasters; megascleres oxeas and triaenes, except in rare monaxonid species; aphodal.

8. Geodiidae. Similar to Ancorinidae but with sterrasters or aspidasters that pack a cortex to form a dermal armor.

9. Tetillidae. Microscleres sigmaspires when any special form is present; megascleres oxeas and triaenes, the latter almost never dichotriaenes.

10. Samidae. Microscleres sigmaspires; megascleres amphitriaenes with branched cladi; sometimes said to bore but may live in foreign borings.

Most living choristid species belong to genera of the Plakinidae, Poecillastridae, Theneidae, Ancorinidae, Geodiidae, and Tetillidae. The further nominal families Corticidae, Craniellidae, Ectyonillidae, Erylidae, Plakinastrellidae, and Halinidae also comprise choristids but are regarded here as synonyms.

The following families are monaxonid unless otherwise stated.

11. Coppatiidae. Ancorinid-like sponges without triaenes; skeleton radiate or not; megascleres diactines; microscleres euasters, sanidasters, or both.

12. Tethyidae. Sponges with a cortex and radiate skeletal structure; microscleres euasters, in forms from oxyaster to sphaeraster; megascleres typically strongyloxeas, arranged with pointed ends outward.

13. Epallacidae. Megascleres oxeas, styles, or tylostyles, arranged in columns and cemented with spongin; microscleres simple euasters.

14. Sollasellidae. Megascleres oxeas, arranged radially; no microscleres.

15. Spirastrellidae. Spinispira microscleres; predominant megascleres tylostyles, but may also have simple styles or oxeas, or these types only; monactines arranged point outward; not boring.

16. Placospongiidae. Similar, with additional sterraster-like sterrospiras.

17. Clionidae. Spirastrellid-like sponges that bore in calcareous substrata, excavating small, hemispherical lime pellets that are expelled through oscula.

18. Suberitidae, Polymastiidae, and allies. Spirastrellid-like sponges without spinispiras; microscleres are microrhabds or are absent.

19. Latrunculidae. Spirastrellid-like sponges with no microscleres but characteristic discasters that hispidate ectosome.

20. Timeidae. Spirastrellid-like sponges without typical spinispiras; characteristic microscleres sphaerasters, replaced in some by sigmasters.

21. Chondrillidae. No megascleres; only spicules typically sphaerasters, replaced in some by sigmasters.

22. Thoosidae. Megascleres styles, spiny oxeas, or lacking; microscleres are a) tuberculate microrhabds (*Alectona* CARTER) or special amphitylasters (*Thoosa* HANCOCK); b) diactinal to tetractinal oxyasters; larva may have dermal armor of tetraxial or monaxial plates, which rarely persists in adults; said to bore, and often placed in Clionidae, but lack spinispiras and tylostyles.

23. Axinellidae *sensu lato.* No microscleres in typical examples, although some may have microrhabds; predominant megascleres styles, although diactines (oxeas, strongyles, ophirhabds) may occur; the megascleres typically arranged in plumose columns, in

some forms with a distinct axial skeleton from which plumose fibers run to the surfaces; some crustose, with tangentially arranged diactines, and monactines that echinate the substratum; spongin more or less abundant.

24. Sigmaxinellidae. Axinellid-like sponges with sigma microscleres.

25. Rhabderemiidae. Axinellid-like sponges whose megascleres include hockey-sticklike rhabdostyles; microscleres toxas and contorted sigmas.

26. Raspailiidae. Axinellid-like sponges with additional spiny styles.

27. Cyamonidae. Similar forms with spiny styles replaced by diactinal to pentactinal pseudoradiates, which arise from monactines in ontogeny.

28. Chalinidae. Spicules typically diactinal and usually megascleres only, although sigmas or toxas may occur; spongin cementing to reticulate; some species with few spicules, or falsely appearing as keratose sponges; no dermal skeleton.

29. Spongillidae. Chalinid-like freshwater sponges that form gemmules; gemmule spicules typically amphidiscs.

30. Lubomirskiidae. Similar freshwater forms without gemmules or microscleres; spicules usually spiny.

31. Hamacanthidae. Megascleres oxeas or styles; characteristic microscleres diancistras; some also with sigmas.

32. Halichondriidae. Megascleres slender oxeas or styles, often matted without order; a tangential dermal skeleton usual, but no special dermal megascleres; spongin inconspicuous or lacking; no microscleres.

33. Desmacidontidae, Ectyonidae, and allies. Characteristic microscleres are chelas, often accompanied by sigmas; megascleres often of more than one type, and usually one or more of three sorts: a) principal monactines, b) echinating monactines, c) dermal diactines; spongin cementing to fibrous, with few spicules in some; fibers echinated, or cored only.

34. Astroscleridae, Ceratoporellidae, and Merliidae. Monaxonids that secrete a nonspicular aragonitic basal skeleton, resembling those of some Stromatoporoidea (Astroscleridae) or Chaetetida and favositid Tabulata (Ceratoporellidae, Merliidae); megascleres monactines; clavidisc microscleres in Merliidae; none in others.

These diagnoses should be read as outlines only, and different usages of the same names may be found elsewhere. An incorrect usage of note is use of Tethyidae for the choristid Tetillidae in some work by VON LENDENFELD (e.g., 1907), which resulted from identification of *Tethya* LAMARCK with *Tetilla* SCHMIDT. In paleontology, this error was copied in SCHRAMMEN's late monographs (1924a, 1936). Zoologists place living monaxonids into many more families than those cited above. The most useful detailed systematic accounts are in monographs by TOPSENT (1928b) and DE LAUBENFELS (1936). Of these accounts, that given by TOPSENT is in some ways the more satisfactory, but DE LAUBENFELS listed and classified almost every known modern genus.

Some nonlithistid fossils are worth notice here. *Discispongia* KOLB and *Prostolleya* LAGNEAU-HÉRENGER from the Jurassic of Europe have megascleres suggesting ancorinids or geodiids. Sterrasters may occur in *Discispongia* but are possibly foreign. The same families may be represented in the Upper Cretaceous by *Stolleya* SCHRAMMEN and *Geodiopsis* SCHRAMMEN, but smooth sterraster-like bodies ascribed to the latter could be spheres, not sterrasters. *Theneopsis* SCHRAMMEN and *Tetillopsis* SCHRAMMEN have megascleres suggesting a theneid and a tetillid.

A few fossil choristids do not correspond with any known modern forms. *Acanthastrella* SCHRAMMEN (Jurassic–Cretaceous) has small, spiny calthrops or subtriaenes, which do not have the branching of the axial enlargement of those of the living *Thrombus* SOLLAS. *Helobrachium* SCHRAMMEN (Upper Cretaceous) has triactinal megascleres with long, curved or hooked rays and a buttonlike rudiment of a fourth ray. The hooking of rays makes the skeleton loosely coherent, although no zygosis is present. In the Cephaloraphiditidae (Upper Cretaceous), the choanosomal megascleres are intertwined ophirhabds (sinuous oxeas), which are sufficiently coherent for skeletons to retain canalar features. Subtriaenes and oxeas or styles were also present. These sponges have been called Ophiraphiditidae by SCHRAMMEN (1910, 1912), because of VON ZITTEL's (1878b) identification of *Ophiraphidites* CARTER with Cretaceous sponges with subtriaenes; but the modern type species *O. tortuosus* CARTER was based on a fragment having ophirhabds only, and spicules of this type occur in various monaxonid sponges.

Helminthophyllum SCHRAMMEN is a Jurassic sublithistid with dichotriaene dermalia. The choanosomal megascleres, called **kyphorhabds**, are short, curved strongyles with transverse, weltlike swellings on the convex side and sometimes small terminal facets where the spicules were in contact.

Rhaxella HINDE is a Jurassic sponge supposed to have no spicules but sterrasters, but it may be based on partly rotted remnants of a thick geodiid cortex.

Fossil monaxonids are even more difficult to assess because of the number of modern families whose members have similar megascleres. *Opetionella* VON ZITTEL from the Jurassic and Cretaceous comprises sponges with oxea megascleres and could be coppatiids. *Stramentella* GERASIMOV (Upper Jurassic) has oxeas and styles occurring in an upwardly expanding tuft, which suggests an axinellid. The first possibly genuine examples of modern genera are supposed Upper Cretaceous species of *Axinella* SCHMIDT (Axinellidae) and *Halichondria* FLEMING (Halichondriidae). *Rhizopsis* SCHRAMMEN of the same age is a possible desmacidontid. Clavidisc and diancistra microscleres from the Upper Cretaceous suggest the existence of *Merlia* KIRKPATRICK (Merliidae) and *Hamacantha* GRAY (Hamacanthidae). Some supposed Cretaceous stromatoporoids (e.g., *Stromatoporellina* KUEHN) could be Astroscleridae.

A number of Mesozoic genera have ophirhabds as their principal megascleres, although other diactines or monactines may also be present. It is possible that sponges of this sort may be cephaloraphiditids that have lost their tetraxons before fossilization or allied forms in which the tetraxons were lost in phylogeny, but the oldest (i.e., *Euleraphe* SCHRAMMEN, *Ophiodesia* SCHRAMMEN) are Jurassic forms, considerably older than the known cephaloraphiditids. Several modern genera with ophirhabds lack tetraxons in life. The modern forms also have varied relationships. *"Jaspis" (Ophiraphidites?) serpentina* WILSON, with ophirhabds and oxeas, has euaster microscleres and is otherwise a normal coppatiid; but *Bubaris* GRAY, with styles and ophirhabds, is close to *Axinella* SCHMIDT of the family Axinellidae, and some fossil spicules ascribed to *Axinella* are ophirhabds like those of *Bubaris.*

Both Jurassic and Cretaceous sediments yield strongly annulated megascleres of the types called criccalthrops, **cricotriaenes,** cricotylotes, and cricostyles. These may represent one genus, as suggested by their ornament, or several. They are sometimes found together (in, e.g., the upper Greensand (Albian), England), and Upper Cretaceous cricotriaenes and cricostyles may be intergradational, but curved cricotylotes, as the Albian examples known as *Monilites* CARTER, occur alone in the living thoosid *Alectona higgini* CARTER. The sediments of both systems have also yielded **trachelotriaenes** with swollen rhabdomes and small dichotriaene cladomes. The form of these spicules suggests an ancorinid or a geodiid. If all fossil examples are from one genus, it existed from at least the Early Carboniferous (Visean, Ireland).

The Cenozoic records of nonlithistids are based mainly on isolated spicules ascribed to modern genera. Many are from the Eocene of New Zealand or the Miocene of Western Australia and represent Indo-Pacific faunas. Identifications of genera are often dubious, but some seem to be genuine. In the Eocene, plakinids are represented by lophose tetractines like those of living species of *Plakina* SCHULZE and *Corticium* SCHMIDT. *Thrombus* SOLLAS is represented by typical spiny trichotriaenes. These are the first sure examples of members of these families, although spicules that may represent them are known from rocks as old as the Early Carboniferous. The geodiids are represented by loose sterrasters and by such aspidasters as those of the living *Erylus* GRAY and *Triate* GRAY. An Eocene *Ecionemia* with associated megascleres and microscleres is acceptable as a genuine ancorinid. Some Eocene sphaerasters are like those of living *Tethya* species. Eocene spinispiras are presumably from spirastrellids or clionids, and the spirastrellid *Dotonella* DENDY is suggested by a special form. Some discasters correspond with those of living *Latrunculia* DU BOCAGE (Latrunculiidae). Rhabderemiids are probably represented by characteristic rhabdostyles and *Discorhabdella* DENDY by distinctive pseudastrose megascleres. There are many supposed generic records based on chelas, but none of these spicules is truly distinctive. Diancistras and clavidiscs again suggest *Hamacantha* and *Merlia*. A supposed record of *Melonanchora* CARTER (HINDE & HOLMES, 1892) was based on a clavidisc, not the typical sphaeranchora of this genus.

Spongillids and lubomirskiids, related to modern forms inhabiting Lake Baikal, are known from Miocene sedimentary rocks of that region. Spongillids are similar to the marine chalinids and point to their previous existence, if interpreted as relict derivatives of a former marine fauna. There are various supposed earlier records of spongillids (e.g., Upper Jurassic, England), but these record monaxons found in sediments with freshwater faunas.

A few apparent demosponges are known only from loose spicules that occur in both past and modern sediments. *Ditriaenella* HINDE & HOLMES is based on unusual amphimesotriaene megascleres, known from Eocene rocks (New Zealand) and the modern Indian Ocean (Seychelle Islands). An unknown sponge is represented by distinctive discs, called **pinakids**, found loose in sediments of the Upper Jurassic (Europe), the Albian and Upper Cretaceous (Europe), the Eocene (New Zealand), and the modern Indian Ocean.

Although most Cenozoic nonlithistids are poorly known, those identified with reasonable certainty are scattered through the spectrum of modern forms in a way that suggests that all the main existing groups had already existed for some time by the Eocene. As noted already, some stocks may be very much older. In particular, the choristid Geodiidae, which have the most specialized development of euaster microscleres, appear to have existed as early as the Early Carboniferous (Visean).

In dealing with the lithistids, it is helpful to begin by recalling those from Paleozoic systems (see Paleozoic Demospongea, above, p. 63). The predominant Paleozoic lithistids were the Orchocladina, with dendroclones and related forms of desmas, and the Sphaerocladina, with sphaeroclones. The remainder comprise a) the moderately diverse Tricranocladina; b) the somewhat more diverse Rhizomorina (e.g., *Haplistion* YOUNG & YOUNG); and c) some possible Tetracladina (e.g., *Jereina* FINKS), with tetraclone-like desmas but no triaenes. There are also a few sublithistid sponges, of which *Archaeodoryderma* REID (Lower Carboniferous) may be related to later forms with heloclones and megaclones.

The predominant Mesozoic lithistids are the typical Tetracladina, with both tetraclones and triaenes, and the Rhizomorina, which have rhizoclones but no tetraxons. There are several minor groups possessing triaenes: a) the Dicranocladina, whose desmas are dicranoclones or related forms grading into rhizoclones; b) the Jurassic Didymmorina, whose characteristic desmas are didymoclones; and c) the Helomorina and Megamorina, with heloclones and megaclones, which appear to be allied and to be unrelated to other forms with triaenes. The Didymmorina have been thought to lack tetraxons, but triaenes that seem to be *in situ* have been found in *Cylindrophyma milleporata* (GOLDFUSS). The name Megarhizomorina has one Cretaceous genus, *Megarhiza* SCHRAMMEN, with large rhizoclone desmas that may lack zygosis or have only loose zygosis. There are also some Sphaerocladina.

Tetracladina with triaenes appear first in the Upper Jurassic and are forms with spiny tetraclones or triders that may grade into rhizoclone-like desmas. The dermalia of these sponges (Sontheimiidae) are dichotriaenes where known. There are also some Jurassic forms with smooth desmas, which appear to be Siphoniidae, although triaenes are not recorded, and loose annulated desmas seem to represent the Phymaraphiniidae. The group became abundant and diverse in the Cretaceous Period, when it included forms with smooth and tuberculate desmas and with triaenes that range from dichotriaenes to phyllotriaenes. These spicules occur in various combinations, which are used as the basis of families (e.g., smooth desmas, dichotriaenes in Siphoniidae; smooth desmas, phyllotriaenes in Theonellidae; tuberculate desmas, phyllotriaenes, or discotriaenes in Discodermiidae). The Phymaraphiniidae, with phyllotriaenes, are especially distinguished by smooth tetraclones with prominent epicrepid annulations at the base of each clone. The peculiar family Plinthosellidae has tuberculate triders of dipodal forms as desmas and anaxial plates as dermalia. A variety of genera have more or less extensive development of anaxial supplemental rhizoclonids, which sometimes formed a supplemental cortex, the so-called **deckschicht** or **epitheca.**

Few fossils of this group are known above the Upper Cretaceous and Cenozoic and modern forms appear to be Mesozoic relicts. One of the most widespread modern forms, *Discodermia* DU BOCAGE, is reliably recorded from the Aptian (Spain) and presumably evolved earlier. Some extant genera have no microscleres but microrhabds (e.g., *Discodermia* [Discodermiidae], *Theonella* GRAY [Theonellidae]), but others have metasters and plesiasters indistinguishable from choristid streptoscleres, occurring in *Neosiphonia* SOLLAS (Siphoniidae) and *Racodiscula* VON ZITTEL (Discodermiidae).

Dicranocladine lithistids with triaenes and dicranoclones (Corallistidae) evolved in the Upper Jurassic, and one Jurassic genus (*Leiocarenus* SCHRAMMEN) is closely similar to the living *Corallistes* SCHMIDT. The desmas of this group are mainly dipodal to tetrapodal dicranoclones, but irregular forms also occur, the latter predominated in the Campanian *Procorallistes* SCHRAMMEN. Those of the two modern genera, *Corallistes* SCHMIDT and *Heterophymia* POMEL, are usually irregular, although typical dicranoclones also occur but are less massive than in the fossils. The microscleres vary from plesiasters through metasters to spirasters and are presumably streptoscleres. Some fossils and the living *Heterophymia* have supplemental rhizoclonids.

Macandrewia GRAY of the living Macandrewiidae has dermal phyllotriaenes and mainly irregular and tetraclone or rhizoclone-like desmas. The occurrence of a few tetraxial desmas among the others suggests affinity with the tetracladine family Discodermiidae. *Macandrewia* has only microrhabds as microscleres, but *Daedalopelta* SOLLAS has also streptoscleres. Another living family Neopeltidae, in which dermalia are monaxial discs, has no fossil record.

The name *Neohindia* SCHRAMMEN was based on a species of the Cretaceous corallistid *Pachinion* VON ZITTEL, now called *P. cylindratum* (SCHRAMMEN), but withdrawn by its author (SCHRAMMEN, 1910, 1912) after study of the type species of *Pachinion, P. scriptum* (F. A. ROEMER). This misleading name has led several authors to suppose a relationship between "*Neohindia*" and the Paleozoic *Hindia* DUNCAN. These nominal genera were even placed by DE LAUBENFELS (1955) in two families, with "*Neohindia*" assigned to the sphaerocladine family Astylospongiidae. *Pachinion* has no special resemblance to hindiids, and the species *P.*

scriptum and *P. cylindratum* are so similar that they could be based on individual variants of one biological species. *Pachinion* resembles the tetracladine sponge *Plinthosella* VON ZITTEL especially in the character of its desmas, which cannot be distinguished by any external feature from those of *Plinthosella.*

The Isoraphiniidae or Helomorina in which desmas are heloclones comprise a few genera scattered from the Upper Jurassic to the present. The dermalia are usually dichotriaenes in the fossils, which are Jurassic and Cretaceous, but are simple plagiotriaenes in the living *Costifer* WILSON. The Megamorina, with megaclones, have a limited Paleozoic record, but most genera are known from the Upper Cretaceous with a single modern genus (*Pleroma* SOLLAS). Most can be placed into one family, the Pleromatidae, but the Cretaceous *Heterostinia* VON ZITTEL is distinguished by having supplemental rhizoclonids. The dermalia are usually dichotriaenes but may be varied as simple triaenes. No member of these groups has phyllotriaenes, discotriaenes, or dermal discs. *Costifer* and *Pleroma* have amphiaster and spiraster microscleres of uncertain homology and additional microrhabds that are irregularly nodular in *Costifer.*

The Didymmorina comprise one small Jurassic family of uncertain affinity. The characteristic didymoclones have been thought sometimes to comprise two linked sphaeroclones (e.g., SCHRAMMEN, 1910, 1912; *not* 1936) grading morphologically into rhizoclones and developed from a crepidal strongyle. They resemble some desmas of Paleozoic Anonoclonellidae, which were also called didymoclones by RAUFF (1893, 1894, 1895), but can also be compared with dicranoclones having grouped clones at the ends of a central shaft (in e.g., *Leiocarenus* SCHRAMMEN). The dichotriaenes found in a species of *Cylindrophyma* VON ZITTEL are like those of Jurassic corallistids (REID, 1963d).

The Rhizomorina, with rhizoclone desmas and no tetraxons, have many Jurassic and Cretaceous genera. They dominate the known Jurassic fauna. There are forms possessing all types of rhizoclones and compact or fibrous skeletons. The radiate type of rhizoclone, in which three or more clones are emitted from a center, is usually subordinate or absent but occasionally predominant. The Jurassic Cnemidiastridae have predominantly bipolar desmas, analogous with simple forms of orchocladine dendroclones and also resemble some anthaspidellid Orchocladina in canalar features. Because of intergrading variations in external form, canalization, and the character of the desmas, many genera are difficult to arrange into clear-cut families.

A number of modern Rhizomorina (e.g., *Azorica* CARTER) appear to be Cretaceous relicts, and other Cretaceous genera (e.g., *Jereopsis* POMEL (*non* SCHMIDT); *Verruculina* VON ZITTEL) survived at least until the Miocene. It is difficult to relate the modern genera to nonlithistid sponges. The Scleritodermidae have sigmaspires like those of the choristid Tetillidae but are otherwise so different that relationship seems doubtful. The others have microrhabds only or no microscleres.

The Sphaerocladina have several Jurassic and Cretaceous genera and a single living genus. There is a major break in the record of the suborder between the abundant Silurian and Devonian occurrences and the Mesozoic forms (RIGBY, 1991a). No sphaerocladines are known from the Carboniferous and *Ellesmerespongia* RIGBY, 1970b, described as a Permian astylosponge from Arctic Canada, may be a didymmorine sponge instead (RIGBY, 1991a).

The fossil Mastosiidae have desmas like those of the Paleozoic Astylospongiidae but with a vermiform canal in the centrum. The centrum of sphaeroclones of the living *Vetulina* SCHMIDT (Vetulinidae) contains a granular nucleus that arises as a hilum-like pit during ontogeny. There are various similar fossils in which neither feature is known. Subordinate astroclones are commonly also present, and a Cretaceous mastosiid

(*Ozotrachelus* DE LAUBENFELS) has anaxial dermal plates. The living *Vetulina* has no microscleres. The Cretaceous mastosiids *Ozotrachelus* and *Macrobrochus* SCHRAMMEN are strikingly like Astylospongiidae, but the last surely known astylospongiid is Devonian. The long gap from Devonian to Jurassic also makes it uncertain whether the Paleozoic and later families are directly related.

The Jurassic and Cretaceous Lecanellidae comprise two genera with large desmas, which are astroclones (*Lecanella* VON ZITTEL) or forms approaching sphaeroclones (*Regnardia* MORET). No nuclear features are known, although desmas of *Regnardia* may have an internal solution cavity (moelle of LAGNEAU-HÉRENGER, 1962). The desmas of these sponges may possibly have arisen independently of typical sphaeroclones and might correspond with those of the living sublithistid *Crambe* VOSMAER.

There are various modern lithistids and sublithistids with no certain relationship to any fossils. Some of these (e.g., *Petromica* TOPSENT) may be related to the Cretaceous Megarhizidae, which they resemble in the form and loose zygosis of their desmas. These genera and some others (e.g., *Tetranthus* VON LENDENFELD, *Lophacanthus* HENTSCHEL) have features suggesting relationships to axinellid or similar sponges. Four genera with chelas appear to be related to the Desmacidontidae. *Desmatiderma* TOPSENT and *Helophloeina* TOPSENT are sublithistids with megaclone-like intergrading with normal monaxons. They do not have triaenes and do not appear to be allied to the Megamorina in which chelas are unknown. *Lithochela* BURTON has dipolar desmas set transversely to cored skeletal fibers, with a pattern like that seen in the anthaspidellid Orchocladina. *Crambe* VOSMAER has astroclone and sphaeroclone-like desmas, with multiple granular inclusions corresponding with the number of clones. These genera are not known as fossils, but some may in fact be represented by loose Cenozoic (Eocene) desmas that have been thought to belong to Megamorina or Sphaerocladina (cf. HINDE & HOLMES, 1892).

Jurassic to recent forms, in general, repeat types of canalization and skeletal growth of the Paleozoic lithistids. For instance, the type of canalization typical of Astylospongiidae was repeated in some Cretaceous Siphoniidae (Tetracladina) in which it presumably evolved independently. Its development in various Cretaceous genera was related to reduction of the paragastral cavity, with the growth plan of the skeleton showing correlated change from mainly marginal to concentric. The astylospongiid-like character of some Cretaceous Sphaerocladina (Mastosiidae) presumably evolved independently, if these forms were not direct descendants of the Astylospongiidae. The variant of this type of canal system in which the axes of elongate sponges are traversed by bundles of longitudinal aporhyses crossed by radial epirhyses recurs in various Tetracladina (e.g., *Jerea* VON ZITTEL), Megamorina (e.g., *Doryderma* VON ZITTEL), and Rhizomorina (e.g., *Jereopsis* POMEL). Ennomoclonar grouping of clones, as in desmas of the Tricranocladina (Hindiidae) and Sphaerocladina, was repeated by Tetracladina (e.g., *Plinthosella* VON ZITTEL), Dicranocladina (e.g., *Gignouxia* MORET, *Pachinion* VON ZITTEL), and Megamorina (e.g., *Heterostinia* VON ZITTEL, *Propleroma* MORET). A structure like that of the Anthaspidellidae (Orchocladina) recurs in the living *Lithochela,* which especially resembles forms in which the skeletal fibers are cored by oxeas (e.g., *Climacospongia* HINDE). The radial canalization and related skeletal structure of Tricranocladina is, however, not paralleled in any post-Paleozoic lithistids, although almost exactly reproduced in a Cretaceous minchinellid (class Calcarea: *Porosphaera* STEINMANN).

CLASSIFICATION

The classification adopted here for ordinal arrangement of the post-Paleozoic Demospongea is a hybrid of neontological and paleontological methods intended for use by both zoologists and paleontologists. In general, the nonlithistids are treated by neontological methods, but lithistids are treated by methods evolved in paleontology.

As noted already, most genera of nonlithistids recorded as post-Paleozoic fossils are represented by loose spicules, which resemble spicules found in modern species. Unless these forms are treated empirically—for instance, by methods analogous with those used for dissociated conodonts—the genera supposedly represented can be defined only in terms of modern material, which also provides the only basis for assessing their relationships. It seems best, therefore, to treat these forms by zoological methods. This means that purely fossil genera must usually be treated as forms of uncertain position, but this seems permissible because these forms are not numerous and because this is their factual status.

In contrast, the lithistids are known chiefly from articulated skeletons and greatly outnumber their living relatives. The latter have also so far yielded no useful alternative to the taxonomic methods initiated by VON ZITTEL and very little evidence of how they are related to nonlithistids. The methods used in paleontology provide a workable classification that is also applicable to many modern forms and which seems, at least in part, to correspond with biological relationships.

A similar combination of neontological and paleontological methods was used by DE LAUBENFELS (1955). The classification used here, however, differs widely from that of DE LAUBENFELS in the treatment of nonlithistid sponges and in some aspects of the treatment of lithistids.

For further explanation, a number of subheadings are convenient.

STATUS OF PHYLOGENETIC CONCEPTS

The fundamental purpose of the classification presented herein is to provide a useful, orderly arrangement of the forms that are classified without further implications. The only proper primary criteria are accordingly observable characters. In practice, a phylogenetic concept is also involved when the subordinate members of any higher taxon are thought to be related biologically. In consequence, a classification can be partly or wholly a picture of inferred relationships. The closest correspondence between taxonomic and phylogenetic divisions can be thought a desirable objective, provided that the artificial nature of taxonomy is remembered. It is also true that classification can be used for the expression of a preconceived picture of phylogeny. Phylogenetic implications are properly a secondary attribute of classification, but not its primary purpose. Furthermore, nothing requires that a classification be based on an overall picture of phylogeny, or, especially, that inadequate evidence should be stretched to provide one for this purpose.

Moreover, from a practical viewpoint, it is not currently possible to give any clear picture of demosponge phylogeny. There are two major problems: a) the almost total lack of useful paleontological data on the nonlithistid sponges; and b) the ambiguous character of comparative zoological data. Reconstruction of phylogeny from stratigraphic sequences of genera is ruled out by the very sparse and plainly incomplete fossil record, by the dubious character of many of the nonlithistid records, and by the unknown relationships of all purely fossil genera. There is not even one instance in which the relationship of two modern genera can be traced through fossil species. The modern forms allow detailed study of all parts of the skeleton and also, for example, gross soft anatomy, embryology, cytology, or biochemistry, but all of them are phylogenetically end forms, and they represent only whatever stocks have survived to the present. On both these counts there is doubt regarding the status ascribed by some zoologists to a few modern genera, which are supposed to be primitive (see p. 101–102 below).

The classification adopted, accordingly, is not based on any overall picture of phylogeny nor intended to imply one. Some taxa distinguished at order or suborder level are envisaged as natural assemblages or at least as including one main natural assemblage from which possibly convergent forms cannot yet be separated. Others, however, comprise forms grouped solely in terms of morphological characters, which cannot be assumed to be distinctive of one natural assemblage, and are sometimes assessed as convergent in unrelated sponges. The choice between these methods has been based on which seemed the more appropriate in particular instances. There is no objection to the use of both methods herein, provided that what is intended is made clear in diagnosis.

CRITERIA OF CLASSIFICATION

The classification is traditional in being based chiefly on the skeleton. It is not claimed that only the skeleton can provide taxonomic criteria, but at present only skeletal data are available on a scale permitting classification of the class as a whole. In addition, only skeletal characters are apparent in the fossils.

In dealing with modern nonlithistids, there is more reliance herein on the character of the microscleres than in DE LAUBENFELS's classification (1936) but only to the level at which some families are grouped into orders. DENDY's (1921) concept of sigmatose microscleres is not accepted herein nor is the homology of all euasters assumed.

The taxonomic use of microscleres by SOLLAS (1888) was based on their successful use by SCHULZE (1887a) in dealing with the Hexactinellida. It is now clear that demosponge microscleres do not have the clearcut significance of their hexactinellidan counterparts. There are various instances in which similar microscleres, which have sometimes been used in taxonomy, occur in sponges otherwise so different that no special relationship should be assumed (e.g., the choristid Tetillidae and lithistid Scleritodermidae). There are also many forms without microscleres and instances in which morphologically similar microscleres have clearly implied different origins.

It is nonetheless a fact that some main types are characteristic microscleres of a number of groups of nonlithistids, which can be judged to be natural assemblages in terms of their overall characters. Those typical of one such group are also unusual in or absent from the others. To this extent, the microscleres seem to me to provide a real basis for the characterization of taxa, provided that their various limitations are remembered. I also think that DENDY (1921, 1924b) was well justified in distinctions that he made between asters (euasters) *sensu stricto;* dichotriacts (streptoscleres), and pseudasters. Some objections to use of the microscleres are removed by rejecting his views on how sigmatose forms are related: in particular, a) the supposed homology of tetillid sigmaspires with sigmas *sensu stricto;* and b) the alleged origin of spinispiras from sigmas through sigmodiscasters.

In dealing with lithistids, I follow SCHRAMMEN's (1910, 1912, 1924a) use of three criteria: a) the character of the desmas, in terms of the methods of VON ZITTEL (1884) and RAUFF (1893, 1894, 1895); b) the presence or absence of dermal triaenes or related types of spicules; and c) the microscleres of modern forms. The last have, however, little value, except in support of the conclusion that lithistids are polyphyletic (SCHRAMMEN, 1910, 1912; BURTON, 1929; DE LAUBENFELS, 1936).

NAMES OF TAXA

Most names proposed for divisions of the class Demospongea above family-group level have not been based historically on those of type genera, although Chalinida GRANT, Halichondrina VOSMAER, and Axinellida LÉVI are exceptions.

Names based on morphological features are open to various objections, and names based on demosponge microscleres involve special problems. A given type of microsclere may be characteristic of a taxon in the sense that this type is the main or only special form developed, but in no instance in which the names of taxa have been based on such microscleres are the characteristic forms present in all genera included. Some groups in which special microscleres occur in some genera (e.g., spinispiras in some of VOSMAER's Clavulina) contain more genera that lack them. If axinellid sponges and their allies are regarded as comprising an order, they cannot be named in terms of microscleres, which are typically absent and include no distinctive type when present. In addition, some names are misleading. The characteristic microscleres implied by the names Sigmatophora SOLLAS and Spirophorida LÉVI are sigmaspires, not sigmas *s.s.* or spires in general. The microscleres characteristic of the Streptastrosa of SOLLAS and the Streptastrosclerophora of BURTON are DENDY's dichotriacts (1924b), i.e., streptoscleres, not all forms classed as streptasters by SOLLAS (1888) and especially not the ancorinid sanidasters called streptasters by DE LAUBENFELS (1936). Names not based on microscleres (e.g., Poecilosclerina TOPSENT) may avoid this type of problem but again refer to no general feature of all forms included.

Names used here for orders of choristid and monaxonid sponges are based on those of type genera, except in one (Epipolasida) where the taxon is thought to be composite. The conceptual basis of such taxa is relationship to a fixed type genus and does not change if some included genera are later removed elsewhere. Such names can be criticized as expressing a concept of relationship—or phylogeny—that cannot be established conclusively; but their use is fixed practice in family-group nomenclature and seems an acceptable principle when relationship is what is envisaged. This method is not used, however, for taxa regarded as simply convenient assemblages of forms of uncertain or varying relationships or for any of the lithistid suborders. Some lithistid groups (e.g., Helomorina, Megamorina) are probably natural assemblages, but all consist chiefly of fossils whose relationships to even one another are strictly uncertain, and there seems to be no advantage in changing the traditional nomenclature.

RANKS OF TAXA

Taxa distinguished above family-group level are ranked as subclasses, orders, and suborders. Use of suborders is restricted to the lithistids, except for one monaxonid order (Chalinida GRANT), which unites two contrasting although apparently related groups of sponges.

SUBCLASSES

The class Demospongea SOLLAS is divided here into four subclasses: Choristida SOLLAS, Monaxonida SOLLAS, Keratosida GRANT, and Lithistida SCHMIDT. The principal members of these taxa are the sponges whose skeletons have choristid, monaxonid, keratose, and lithistid conditions, respectively; and all fossil genera are arranged on this basis. A few modern sponges that do not have the typical conditions are, however, regarded as members of the first three subclasses because of apparent relationships to typical genera. These atypical forms include sublithistids (e.g., *Crambe* VOSMAER, *Lithochela* BURTON), askeletose genera (e.g., *Oscarella* VOSMAER, *Chondrosia* NARDO, *Halisarca* DUJARDIN), some with microscleres only (e.g., *Chondrilla* SCHMIDT), and a very few monaxonids that are thought to be close allies of choristids. For instance, *Raphidotethya* BURTON is considered to be a monaxonid member of the normally choristid family Tetillidae SOLLAS, closely allied to the choristid *Amphitethya* VON LENDENFELD. One fossil sublithistid, *Helminthophyllum* SCHRAMMEN, is placed in the subclass Choristida, because the skeleton is choristid in character apart from its sublithistid features.

Each subclass includes two or more orders, whose relationships do not seem to be currently demonstrable, although grounds may exist for regarding them as probably related. The subclass that seems nearest to comprising a natural assemblage is the subclass Choristida, whose orders (Plakinida, Poecillastrida, Ancorinida, Craniellida) can be thought to have shared a common origin, although these orders, and the Ancorinida especially, may have shared the same origin as some which are classed as Monaxonida. The subclass Lithistida, in contrast, is regarded as certainly composite although convenient taxonomically. The concepts that are used in distinguishing orders and suborders are derived mainly from the methods of the following authors.

i. Choristida: SOLLAS (1888); DENDY (1905, 1924b).

ii. Monaxonida: VOSMAER (1882, 1883, 1884, 1885, 1887); TOPSENT (1928b); DE LAUBENFELS (1936); LÉVI (1955).

iii. Keratosida: MINCHIN (1900).

iv. Lithistida: SCHRAMMEN (1910, 1912, 1924a, 1936); LAGNEAU-HÉRENGER (1962).

These subclasses do not fit some major divisions of the class that have been made by zoologists and certainly not the current Tetractinomorpha and Ceractinomorpha of LÉVI (1957b). Some reasons these were not adopted are examined below (p. 101–102). For paleontology, however, it is also a matter of convenience to have at least primary divisions fit observable skeletal characters of the fossils. In addition, if most of the monaxonids have arisen independently of choristids with megascleres, which seems likely, the use of the subclasses Choristida and Monaxonida has at any rate some basis in phylogeny.

SUBCLASS CHORISTIDA

Most modern choristids can be arranged in four groups, as follows.

a. In microspiculate sponges comprising the family Plakinidae SCHULZE, the spicules are not differentiated into typical megascleres and microscleres, although meristic calthrops variants of some genera can be regarded as simple oxyasters. In the three remaining groups, there are typical megascleres and microscleres, of which the microscleres are of one of three main types.

b. In the families Pachastrellidae CARTER, Poecillastridae *nov.,* and Theneidae GRAY, the characteristic microscleres are streptoscleres (metasters *sensu* VON LENDENFELD; dichotriacts, DENDY). When others are present, they are microrhabds or simple oxyasters found as plesiaster variants.

c. In Calthropellidae VON LENDENFELD, Ancorinidae SCHMIDT, and Geodiidae GRAY the characteristic microscleres are polyactinal euasters to which sterrasters or aspidasters may be added. There may also be microrhabds or sanidasters but not streptoscleres.

d. In the Tetillidae and Samidae, the microscleres are sigmaspires or variants when any special forms are present. Some tetillids are also distinguished by occurrence of distinctive trichodal protriaenes or of incubated parenchymelloid embryos.

These groups, with some further additions, comprise the four orders Plakinida, Poecillastrida, Ancorinida, and Craniellida. The corresponding type genera are *Plakina* SCHULZE, *Poecillastra* SOLLAS, *Ancorina* SCHMIDT, and *Craniella* SCHMIDT. Each type genus is also the type of a nominal family, although Craniellidae DE LAUBENFELS is here regarded as a synonym of the older Tetillidae SOLLAS. *Tetilla* SCHMIDT was not taken as type of the order Craniellida because the type species *T. euplocamos* SCHMIDT is not known to have microscleres. Except for minor differences in the allocation of particular genera, the orders are equivalent to the following older taxa, whose names were not based on those of genera.

i. Plakinida: Carnosa CARTER (*sensu* CARTER, *not* DE LAUBENFELS); Microsclerophora SOLLAS; Megasclerophora VON LENDENFELD (*sensu* 1903); Homosclerophora DENDY.

ii. Poecillastrida: Metastrosa VON LENDENFELD; Streptosclerophora DENDY; Streptastrosclerophora BURTON; Streptastrosa SOLLAS minus Calthropellidae VON LENDENFELD (herein order Ancorinida).

iii. Ancorinida: Astrophora SOLLAS minus Poecillastrida (Metastrosa, etc.).

iv. Craniellida: Sigmatophora SOLLAS; Spirophorida LÉVI.

Inclusion of modern sponges, in addition to the typical members of the families cited, is restricted to the following instances.

a. The myxosponge *Oscarella* Vosmaer is accepted as a member of the Plakinida, closely allied to *Plakina,* which has similar amphiblastula embryos. *Thrombus* Sollas, the only genus of family Thrombidae Sollas, is placed in this order because of the small size of its spicules, although it does not seem closely related to any typical Plakinidae.

b. *Aurora* Sollas of the order Ancorinida, family Ancorinidae, is accepted as having apparently both choristid and monaxonid species on the basis of Dendy's (1916) demonstration of several pairs of similar species, in each of which one species is distinguished chiefly from the other by the absence of triaenes. Some purely monaxonid genera with euaster microscleres may also be monaxonid Ancorinida biologically but are excluded here for reasons given below (second paragraph).

c. The monaxonids *Raphidotethya* Burton and *Trachygellius* Topsent appear to be close allies of the choristid genus *Amphitethya* von Lendenfeld, of the otherwise choristid family Tetillidae Sollas (order Craniellida) and do not seem to be related to any typical Monaxonida.

The inclusion of even a few forms as Choristida that do not have choristid morphology might be criticized as inappropriate but such inclusion follows Sollas's (1888) usage and seems justified biologically. There appear to be genuine instances in which literal taxonomic reliance in the principal conditions of the skeleton would cut across relationships. The best known instance is that of the pseudoceratosa, in which different individuals of one species may either have or lack spicules and thus differ in a way by which genera would be placed in different subclasses (Monaxonida and Keratosida). At least one sponge normally classed as a monaxonid can sometimes have choristid characters. The megascleres of *Alectona* Carter (family Thoosidae, order Spirastrellida) are normally spiny oxeas; but those of the type species *A. millari* Carter, as seen in Carter's own material, may also include a few regular triactines, and intermediates that link these with the normal diactines (oxeas) morphologically. The transition between these triactines and diactines follows the same pattern as in plakinid Choristida. In literal terms, a specimen with triactines is morphologically a choristid, although these spicules are normally absent; and the genus has often been placed in the purely monaxonid family Clionidae. Here again, a difference that is normally of high taxonomic significance can occur between species of one genus and even different individuals of one species.

The order Ancorinida is restricted here by removal of most of the monaxonids that were originally included (Reid, 1968a) but which are now placed in the order Epipolasida of the subclass Monaxonida. Those comprising the family Coppatiidae Topsent were regarded by Dendy (1916) as monaxonid Ancorinidae (=Stellettidae, Dendy), in which triaenes or other tetraxons had been lost in phylogeny. This practice extended the concept implied by Sollas's (1888) family Epipolasidae and was influenced by Dendy's observations on *Aurora* (see above). It is reasonably likely that some genera grouped here as Coppatiidae are monaxonid Ancorinida biologically; but this cannot be established firmly. Some others could be allied just as well to plakinids like *Dercitopsis* Dendy, in which the largest spicules present are oxeas. In addition, monaxonids comprising the Tethyidae Gray and Epallacidae Topsent are not close to any living choristid and are thought by current authors to be allied to spirastrellid and axinellid Monaxonida. It seemed best to move these forms elsewhere, which is also more convenient for paleontological arrangement.

de Laubenfels (1936, 1955) placed choristids into two orders that cut across the present classification.

1. Choristida *sensu* DE LAUBENFELS (*not* SOLLAS) (=Triaenina SOLLAS): Poecillastrida, Ancorinida, and Craniellida in which tetraxon megascleres are typically long-shafted triaenes and never calthrops;

2. Carnosa *sensu* DE LAUBENFELS (*not* CARTER) (=Tetradina SOLLAS): all other choristids, including (i) Plakinida; (ii) Poecillastrida and Ancorinida having calthrops, with or without additional triaenes, or with calthrops replaced by triactines or centrotriaenes; and (iii) *Samus* GRAY, of the order Craniellida, in which the megascleres are short-shafted amphitriaenes. The arrangement used herein is regarded as clearly nearer to the probable relationships of these sponges than that used by DE LAUBENFELS. It is least satisfactory in dealing with forms that lack triaenes, which can be difficult to classify; but nearly all genera with triaenes—comprising most Poecillastrida and Ancorinida and all Craniellida—fall clearly in one of three groups that require being distinguished taxonomically. By comparison, the classification of DE LAUBENFELS both cuts across probable relationships and unites forms that need to be separated. His treatment of *Thenea* GRAY, which he dissociated from other Poecillastrida as a supposed ancorinid is especially problematic. He relied on the argument (DE LAUBENFELS, 1936, p. 167) that *Thenea* ". . . differs from *Ancorina* SCHMIDT only in that streptasters of the latter are much less bent than those of the former." The microscleres of *Thenea* are streptoscleres, developed mainly as plesiasters, metasters, or spirasters; but the only streptasters that occur in *Ancorina* are spinulated microrhabds, like those of *Ecionemia* BOWERBANK, that may grade toward sanidasters. The simple oxyasters of some *Thenea* species are also clearly related to the three- or four-rayed forms common as plesiaster variants in other Poecillastrida.

THE OLDEST CHORISTIDA

In the text above, which discusses the possible relationships of the choristid and monaxonid Demospongea, and elsewhere (REID, 1970), there is agreement with FINKS (1967b, 1971b) in considering the oldest known choristid spicules to be of Early Carboniferous (Visean) age. It was, nonetheless, thought likely that their Visean diversity must imply that the group is far older, unless its pre-Visean evolution was much faster than from then to the present.

In fact, REIF (1968) has recorded what seem to be older examples from the Upper Ordovician of Borehole, Estonia. The spicules occur with other types ascribed to Hexactinellida and Heteractinellida and, therefore, cannot be identified certainly as those of true choristids; but their shapes would be regarded as marking them as choristid spicules if found for example, in the Carboniferous. Morphologically they are calthrops or short-shafted triaenes or in one instance what seems to be a broken, long-shafted protriaene. In addition, a peculiar spicule (**dodecaactine**), ascribed by REIF (1968) to a hexactinellid, could also be interpreted as a tetralophose calthrops with one ray branched near its origin and compared with the candelabra spicules of the living *Corticium.*

These spicules seem to establish the existence of Ordovician choristids, which already had both calthrops and long-shafted triaenes. This in turn should imply that the group must be older than Late Ordovician, if the triaenes and calthrops are assumed to be related types of spicules. They are also almost as old as the oldest known *Hindia,* whose desmas are noted above as suggesting derivation from a pre-existing choristid.

SUBCLASS MONAXONIDA

Modern monaxonids are divided into six orders: the Epipolasida, Spirastrellida, Axinellida, Astrosclerida, Chalinida, and Desmacidontida. Fossils are referred to these orders when any arrangement is possible. The order Epipolasida is regarded as composite and is used for convenience. The remaining five orders are not known to be composite although all include genera that are nearer than others to the central type genus. The corresponding type genera are *Spirastrella* Schmidt, *Axinella* Schmidt, *Astrosclera* Lister, *Chalina* Grant, and *Desmacidon* Bowerbank, each of which is also type of a family. No microscleres occur in *Axinella, Astrosclera,* or *Chalina* (also called *Haliclona* Grant), but *Spirastrella* and *Desmacidon* have the characteristic microscleres of their orders.

The order Epipolasida comprises various monaxonid sponges that have euaster microscleres like those of the choristid Ancorinidae and some similar forms that have microrhabds, sanidasters, or no microscleres. It is also a convenient position for some of the fossils. I do not include genera with spinispira microscleres, some of which were included by de Laubenfels (1936) but are here placed in the order Spirastrellida. The name Epipolasida is not meant to imply derivation from choristid Ancorinidae (="Stellettidae"), as was Sollas's Epipolasidae (1888), and in this sense is used as by de Laubenfels. Modern forms included are mainly those comprising the families Coppatiidae Topsent (=Jaspidae (Jaspinae), de Laubenfels), Tethyidae Carter, Epallacidae Topsent, and Sollasellidae von Lendenfeld.

The mutual relationship of the families of this order are not known with certainty, and they may be allied to members of various other orders. They are grouped together generally on the basis of having (a) true meristically varying euasters like those seen in Ancorinidae and (b) mainly oxeas as megascleres and no tylostyles except as minor variants of a style (or strongyloxea). All such sponges were regarded by Dendy (1916) as derivatives of ancorinid (stellettid) Choristida, which had lost tetraxon megascleres in phylogeny. In reality, as de Laubenfels (1936) emphasized, it is not known whether their condition is secondary or primitive or whether they are allied to choristids or other monaxonids or to both in different instances. The possible relationship of coppatiids to Ancorinidae has been noted already. The Tethyidae have similar microscleres, but the megascleres are typically strongyloxeas, sometimes passing into variants developed as true styles or even tylostyles arranged radially and pointing outward as in members of the order Spirastrellida. Topsent (1928a) grouped these sponges with the spinispira-bearing Spirastrellida in his order Hadromerina, and this view is supported by biochemical evidence (Bergquist & Hogg, 1969). On the other hand, Topsent's view depended on the presence of apparent euasters in the family Timeidae; and Dendy (1921) seems to have been right in interpreting these microscleres as pseudoeuasters derived from spinispiras because of their replacement by sigmasters in several species of *Timea* Gray. Typical Spirastrellida never have euastriform microscleres, and the spinispiras found in some families appear to be related to megascleres. Hence the Tethyidae seem less closely related to the forms with spinispiras than Topsent thought, at least in terms of their skeletal characters.

The Epallacidae (*Epallax* Sollas and *Hemiasterella* Carter, sometimes thought to be identical) were placed by Sollas (1888) in the family Axinellidae Ridley and Dendy and recently in the order Axinellida by Lévi (1955). Sollas (1888) thought that these forms are also close to the choristid Plakinidae from which the axinellids could thus have arisen directly; but Dendy (1922) regarded their euasters as pseudasters analogous with the pseudoradiate megascleres of *Cyamon* Gray. Examining material that was previously studied by these authors indicates that the euasters of *Epallax callocyathus* Sollas are closely similar to spicules of the supposed plakinid *Astroplakina* Dendy, which was claimed to justify Dendy's own views on the origin of true euasters in choristids.

Fossils with ophirhabd megascleres have been placed into the family Ophiraphiditidae Schrammen, which should fall in the subclass Choristida because most of the genera have subtriaenes in addition to ophirhabds. A Cretaceous sponge with subtriaenes was identified by von Zittel

(1878b) as a species of the modern genus *Ophiraphidites* CARTER; but the type species *O. tortuosus* CARTER was based on a macerated fragment having ophirhabds only, and similar spicules occur in the basal parts of several Axinellida, e.g., *Bubaris* GRAY. The fossils with subtriaenes were accordingly removed to a family Cephaloraphiditidae REID (1970), herein placed in the subclass Choristida. But ophirhabds, oxeas, and euasters are the only spicules present in the recent *"Jaspis" serpentina* WILSON, which is a typical coppatiid apart from having ophirhabds. This suggests a position in this family for *Ophiraphidites, sensu* CARTER and for purely monaxonid fossils such as *Euleraphe* SCHRAMMEN and *Heteroraphidites* SCHRAMMEN.

The Chondrillidae SCHMIDT normally have no spicules except euasters, which are usually sphaerasters and are often regarded (e.g., DENDY, 1916; TOPSENT, 1928a) as derived from coppatiids or tethyids by loss of megascleres. The Chondrosiidae SCHULZE appear to be allies in which all spicules have been lost. If these origins are accepted, these families can be placed into the Epipolasida. On the other hand, the sphaerasters of *Chondrilla* SCHMIDT are sometimes replaced by sigmasters, for example in *C. phyllodes* SCHMIDT. This suggests a relationship to the Timeidae TOPSENT of the order Spirastrellida unless *Chondrilla* is composite.

The order Spirastrellida comprises the Clavulina of VOSMAER (1882, 1883, 1884, 1885, 1887) or the Hadromerina *sensu* TOPSENT (1928a; not DE LAUBENFELS, 1936), which remain after removal of some families to the Epipolasida. The characteristic microscleres of the Spirastrellida are spinispiras and related forms; but these microscleres are almost restricted to the central families Spirastrellidae SCHMIDT, Clionidae D'ORBIGNY, and Placospongiidae GRAY. Other forms may have microrhabds, some of which may be homologous with spinispiras, or no microscleres. The Timeidae TOPSENT have euastriform microscleres that, however, appear to be pseudasters because sigmasters sometimes replace them (e.g. in *Timea curvistellifera* DENDY). Genera whose reproduction is known are usually oviparous, with parenchymella or parenchymella-like embryos. Spinispiras are related to megascleric oxeas, with which they sometimes share a fine spinulation or a central annulation (e.g., both in *Cliona vastifica* HANCOCK). Many genera of the order have tylostyles, but styles or oxeas may also occur and genera that lack tylostyles are not excluded herein.

The Thoosidae COCKERELL (*Thoosa* HANCOCK and *Alectona* CARTER) appear to be allied to the boring Clionidae, with which they are sometimes included, but are not typical of the order. Neither genus has spinispiras, and *Thoosa* has no megascleres. The oxea megascleres of *Alectona* are sometimes varied as triactines, and *Thoosa* may have slender triactinal or tetractinal oxyasters or dermal plates that develop from small tetractines. The inclusion of these forms in the order Spirastrellida could be doubted; but they may be archaic forms, which point to its origin (cf. below, p. 111).

A few forms with spinispira microscleres (e.g., *Trachycladus* CARTER) are axinellid according to LÉVI (1955). This could mean either than spinispira microscleres have evolved independently in axinellids or that megascleric skeletons can take on an axinellid aspect in sponges that are not Axinellida.

The order Axinellida comprises the family Axinellidae RIDLEY and DENDY and various similar sponges removed by LÉVI (1955) from the Halichondrina *sensu* TOPSENT (1928b) or the Poecillosclerina TOPSENT. These removals were made as a result of his division of the class Demospongea SOLLAS into subclasses Ceractinomorpha LÉVI and Tetractinomorpha LÉVI (1955, 1957a), which requires all forms grouped as Ceractinomorpha to be viviparous. This in turn depends on a picture of phylogeny that derives the Ceractinomorpha with spicules (orders Chalinida and Desmacidontida herein) from the keratose sponges and these from viviparous halisarcid myxosponges. Axinellida whose reproduction is known are oviparous, although with embryos of the same type as in Ceractinomorpha.

The central family Axinellidae comprises sponges without microscleres. The predominant megascleres are styles and are sometimes the only megascleres, although diactines may also occur. Plumose spicular fibers are frequent, and there may be a special axial skeleton. Spongin is more or less abundant and may form continuous fibers. Some similar sponges have microrhabds, toxas, or sigmas as microscleres, but no cheloid forms occur. Other genera have additional acanthostyle megascleres or related pseudastrose forms of megascleres or microscleres. In some genera, diactines are blunt-ended ophirhabds. Some are encrusting forms, with monactine megascleres arranged vertically so as to echinate the substratum. In addition to normal monaxonids, *Monocrepidium* TOPSENT and the fossil *Scolioraphis* VON ZITTEL have sublithistid modification of ophirhabds, which are developed as irregularly annulated scoliorhabds. A few modern lithistids with large megaclone or rhizoclone-like desmas (e.g., *Petromica* TOPSENT, *Lithobubaris* VACELET) are possibly of axinellid origin and could be placed in this order instead of the artificial subclass Lithistida. The fossil Megarhizidae SCHRAMMEN, placed here in the lithistid suborder Megarhizomorina SCHRAMMEN, have analogous desmas.

The order Astroscleridae is new and contains sponges with a monaxonid spicular skeleton and a nonspicular aragonitic basal skeleton. In the Astroscleridae LISTER, this structure resembles the skeletons of typical **astrorhiza**-bearing stromatoporoids; but in *Ceratoporella* HICKSON and *Merlia* KIRKPATRICK, sole genera of the Ceratoporellidae HICKSON and Merliidae KIRKPATRICK, it suggests those of fossil Chaetetida or favositid Tabulata. *Ceratoporella* was also mistaken for a coenothecalian octocoral before the soft parts were known (MONTANARO-GALLITELLI, 1956, p. 194). Astroscleridae and *Ceratoporella* lack microscleres and have spiny styles as megascleres, some of which have the spines arranged in whorls as in various Axinellida. On the other hand, *Merlia* has smooth megascleres only and has clavidisc microscleres that are usually regarded as related to the diancistra microscleres of hamacanthid Chalinida (e.g., DENDY, 1921; TOPSENT, 1928b). This is why the order is placed between the Axinellida and the Chalinida, although either or both of these resemblances, in fact, may be illusory.

HARTMAN and GOREAU (1970) placed these sponges into a new class Sclerospongiae and suggested that the fossil Chaetetidae and the astrorhiza-bearing Stromatoporoidea were also similar sponges. The class was so named because aragonite is commonly secreted in the form of spherulitic bodies, which they called sclerodermites; although, in general usage, the term **sclere** means spicule, as in megasclere. The few modern genera are, nonetheless, typical Demospongea apart from the special basal skeleton, and a form that lost this structure in phylogeny would appear to be a normal monaxonid. Their reference to an order of the subclass Monaxonida therefore seems more appropriate, if the modern forms only are considered. A subclass Sclerospongida would, however, be appropriate if accepted as including the fossils, and consisting for example of the orders Stromatoporida and Chaetetida. These groups are to be treated in a subsequent volume of the *Treatise.*

LECOMPTE (1956, p. 121) rejected any relationship of Stromatoporoidea to sponges without mention of *Astrosclera,* whose status as a demosponge has been known since 1910 (KIRKPATRICK, 1910b). He ruled out a relationship between **astrorhizae** and the canals of a rhagon (i.e., leuconoid) canal system on the grounds that a lamellar distribution of canals is not observed in Porifera. The radial groups of exhalant canals that occur at the surface in Astrosclerida are disposed horizontally, and corresponding astrorhiza-like channels are characteristic of *Astrosclera.* In *Ceratoporella,* the surface tissue is so thin that the canals raise the dermis, like veins under skin. The siliceous spicules lie loose in the soft tissues, and do not form part of the basal skeleton unless included incidentally. The impassable obstacle is, thus, an expected condition if the Stromatoporoidea are sponges.

A loose Campanian microsclere called a psyllium by SCHRAMMEN (1924a, pl. 4,*14*) is a clavidisc like those found in *Merlia,* which may, thus, have been a contemporary of the latest accepted stromatoporoids.

The order Chalinida comprises the Halichondrina *sensu* LÉVI (1957b; i.e., members of the Halichondrina *sensu* TOPSENT (1928b) not removed to the order Axinellida) and Haplosclerida *sensu* TOPSENT (i.e., not including chela-bearing sponges included by DE LAUBENFELS, 1936), which are placed in suborders Halichondrina and Chalinida respectively. The order Desmacidontida comprises the Poecillosclerina of TOPSENT (1928b) except for genera removed to the Axinellida by LÉVI (1955). These orders appear to have a special relationship to one another and to keratose sponges.

TOPSENT (1928a) and DE LAUBENFELS (1936) placed the orders Halichondrina and Haplosclerida on opposite sides of an order Poecillosclerina. This arrangement was based on (a) the inclusion of the present Axinellid as Halichondrina and their resemblance to some Spirastrellida (=Hadromerina, TOPSENT); and (b) resemblances between some Haplosclerida (=Chalinida herein) and dictyoceratid Keratosida. The removal of the Axinellida from the Halichondrina *sensu* TOPSENT leaves this group much restricted. Sample genera studied biochemically by BERGQUIST and HOGG (1969) are grouped as follows:

i. Halichondrina *sensu* LÉVI and Haplosclerida (=Chalinida);

ii. Poecillosclerina (=Desmacidontida) and Keratosida.

The Halichondrina *sensu* LÉVI and the marine Haplosclerida (Chalinida) are also similar in (1) the simplicity of the megascleric skeleton and (2) the frequent lack of microscleres, which never include cheloids when present (although these occur in some Haplosclerida *sensu* DE LAUBENFELS, 1936). These forms, therefore, are placed herein into one order, called Chalinida, with suborders retained for consistency with previous classifications. The name Chalinida GRANT is used as senior to Halichondrina VOSMAER. *Chalina* GRANT is currently regarded as a synonym of *Haliclona* GRANT; but herein an analogy is assumed with family-group nomenclature, which permits only a change in name when the type genus is a homonym. This analogy seems to be required by the use of a type genus.

The Chalinida and Desmacidontida are viviparous in forms whose reproduction is known, with large parenchymella embryos. They share this condition with the keratose sponges and Halisarcidae, with which they were united as Ceractinomorpha by LÉVI (1957b). The orders are distinguished by different developments of the skeleton, which is generally simpler in the Chalinida than in Desmacidontida. The Chalinida typically have megascleres of a single sort only, which are commonly diactines, and have no special dermal megascleres, echinating spicules, or cheloid microscleres. There are often no microscleres, although toxas or sigmas occur in some marine forms, and amphidiscs and other pseudasters occur in some freshwater genera (Spongillidae GRAY).

The Desmacidontida are typically forms with chelas or related forms of microscleres, although these are absent from some genera. The term lipochelous has been used by some zoologists to imply that the absence of chelas is due to their loss in phylogeny, although this is strictly an assumption. The megascleric skeleton is sometimes as simple as in Chalinida (and forms of this sort were included in TOPSENT's Haplosclerida by DE LAUBENFELS), but it typically includes two or more sorts of megascleres. In addition to the principal megascleres, which may be either diactines or monactines, there may be echinating spicules, special dermal megascleres, or both. Dermal megascleres are often diactines. Echinating spicules are typically monactines and often acanthostyles. Examples of this type may echinate skeletal fibers or be scattered through the mesenchyme but are commonly described as echinating in either instance. A few forms with chelas are sublithistids (e.g., *Helophloeina* Topsent, *Lithochela* Burton), with various types of desmas (p. 88). Spongin occurs in both orders; and both include genera ranging from some without spongin or with inconspicuous amounts to others in which the main skeleton is formed by reticulate spongin fibers.

SUBCLASS KERATOSIDA

This subclass is restricted to keratose sponges and is divided into Minchin's orders Dictyoceratida and Dendroceratida. The halisarcid myxosponges are acceptable as askeletose Dendroceratida.

The Dictyoceratida appear to be allied certainly to the Chalinida and Desmacidontida, but how they are related is uncertain. The older view, held by von Lendenfeld (1889a), Minchin (1900), and Topsent (1928b), is that dictyoceratids were derived from forms with spicules; but Lévi (1957b) regarded the latter as derived from Dictyoceratida. The older view is followed herein, although solid evidence is lacking. Biochemical evidence (Bergquist & Hogg, 1969) related the dictyoceratids to the Desmacidontida, although based on two genera from families that von Lendenfeld (1889a) related to the Chalinida.

SUBCLASS LITHISTIDA

Lithistids are divided here into suborders that correspond to taxa called Tribus by Schrammen in his two final monographs (1924a, 1936) but equivalent to suborders because they formed divisions of his orders. The arrangement is generally based on two characteristics: (i) the character of the desmas and (ii) the presence or absence of triaenes or related types of dermalia and their character, when present. The characters of suborders distinguished may be summarized as follows:

A. Dermal triaenes are usually present and range from dichotriaenes through phyllotriaenes to discotriaenes; some genera have monaxial or anaxial discs instead:

1. Suborder Tetracladina von Zittel: desmas typically tetraclones or triders, although accessory monaxial forms may also occur (e.g., as radical desmas).

2. Suborder Dicranocladina Schrammen: desmas dicranoclones, large rhizoclone-like forms (megarhizoclonids, Schrammen) or intermediates to which a few tetraxial desmas may be added.

B. Dermal triaenes are usually dichotriaenes, rarely simple triaenes; no phyllotriaenes, discotriaenes, etc.

3. Suborder Helomorina Schrammen: desmas heloclones.

4. Suborder Megamorina von Zittel: desmas megaclones.

5. Suborder Didymmorina Rauff: desmas didymoclones, rhizoclones, and intermediates.

C. Dermal triaenes unknown and lacking in living examples.

6. Suborder Megarhizomorina Schrammen: large rhizoclone-like desmas, loosely or sometimes not articulated.

7. Suborder Rhizomorina von Zittel: desmas rhizoclones only.

8. Suborder Sphaerocladina Schrammen: desmas sphaeroclones, astroclones, or intermediates.

The use of this method of classification does not imply that all named types of desmas are sharply distinct or that every named type is found in one suborder only. Some named types are completely intergrading (e.g., didymoclones and rhizoclones); others are not (e.g., didymoclones and heloclones). The type of desma cited as characteristic of a given suborder is usually a predominant type of desma and may be present in all included genera; but it may also grade in some or even all genera into some different nominal type, which may sometimes predominate or replace it. For instance, true tetraclones are present in most Tetracladina; but they may be accompanied by subordinate monaxial desmas or replaced by triders. In Dicranocladina, the desmas may be (i) dicranoclones; (ii) megarhizoclonids; (iii) both together; or (iv) part or all intermediates. The sphaeroclones of Sphaerocladina are often accompanied by astroclones and sometimes replaced by them. A given type of desma, which is characteristic in one suborder (e.g., rhizoclones in Rhizomorina) may also occur as a subordinate form in others (Dicranocladina, Didymmorina). On the other hand, some types have not been found together (e.g., tetraclones, megaclones, sphaeroclones). These facts were well known to SCHRAMMEN, but are partly disguised in his monographs (1910, 1912, 1924a, 1936) by his habit of naming desmas taxonomically (by e.g., use of rhizoclone for desmas of Rhizomorina only, irrespective of morphology).

This method provides a satisfactory arrangement of most of the post-Paleozoic fossils as well as most modern genera. The most important problematical fossils are genera with desmas like those found in various groups with triaenes, although the latter are absent. These genera are usually allocated according to the form of the desmas, although the absence of triaenes could be due to a, original absence; b, loss in phylogeny; or c, loss in fossilization.

The suborders cited are grouped into orders as follows.

1. Order Tetralithistida LAGNEAU-HÉRENGER, *sensu nov.:* Tetracladina, Dicranocladina, and (?) Didymmorina.

2. Order Megalithistida *nov.:* Helomorina and Megamorina.

3. Order Monalithistida LAGNEAU-HÉRENGER, *sensu nov.:* Megarhizomorina, Rhizomorina, and Sphaerocladina.

The Tetracladina and Dicranocladina and the Helomorina and Megamorina are interpreted herein as contrasting groups of sponges whose desmas are reasonably certain to have had different prototypes (calthrops and ophirhabds, respectively). They are placed in separate orders accordingly. The Didymmorina were classified as lithistid Monaxonia by SCHRAMMEN (1936); but there are small dichotriaenes, which do not appear to be intrusive, in a *Cylindrophyma milleporata* (GOLDFUSS) identified by SCHRAMMEN himself, and the desmas are comparable with some found in Dicranocladina. The order Monalithistida is envisaged as a composite grouping, convenient for lithistid types with monaxial megascleres only, or thought to have been of monaxonid origin. The Paleozoic Orchocladina also fall in this order. No separate order is envisaged for the Sphaerocladina, which were very probably derived from the Orchocladina and which may have normal monaxons in addition to the desmas (e.g., in the living *Vetulina* SCHMIDT).

The Paleozoic Tricranocladina (=Eutaxicladina *sensu* SCHRAMMEN: *not* RAUFF or DE LAUBENFELS) have desmas of uncertain character, regarded as tetraxons by SCHRAMMEN. If this is correct, they could be classified as Tetralithistida; but they are not related to the typical Tetracladina and Dicranocladina, whose relationships seem to lie with the choristid Poecillastrida.

ALTERNATIVE CLASSES OR SUBCLASSES

Phylogenies suggested by both DENDY (1905) and LÉVI (1957b) envisage the class Demospongea as comprising two major groups of sponges, descended independently from different myxosponge ancestors. In LÉVI's scheme, the taxa distinguished on this basis are subclasses Tetractinomorpha LÉVI and Ceractinomorpha LÉVI of the class Demospongea; but DENDY's were treated as the orders Tetraxonida VOSMAER and Euceratosa DENDY of a class non-Calcarea, which also included the Hexactinellida as an order Triaxonida SCHULZE. It might be asked why neither of these schemes is used here for division of the class Demospongea into subclasses or its replacement by two classes. This question specifically applies to the scheme of

Lévi (1957b), which is currently widely, although not universally, accepted.

First, Dendy's views are not now acceptable because of his insistence (a) that monaxonid sponges are all forms derived from choristids by loss of tetraxons in phylogeny; and (b) that no true keratose sponges (hence Euceratosa) are related to any forms with spicules. In current perspective, a very large proportion of monaxonids have no known or likely relationship to choristid sponges, in the sense required by Dendy. The Chalinida and Desmacidontida (=Halichindrina, Poecilosclerina, and Haplosclerida Lévi) also seem to be genuinely allied to the keratose sponges, in terms of the current biochemical and embryological evidence.

The factual basis of the subclasses proposed by Lévi (1957b) is the embryology of their members and especially of genera grouped as Ceractinomorpha (here Chalinida, Desmacidontida, Keratosida). The latter are always viviparous with parenchymella embryos when sexual reproduction is known (although this uniformity is due partly to removal of forms that disturb it).

Sexual reproduction is uncommon in Tetractinomorpha and some forms that have it are oviparous. On the other hand, this group has no general uniformity because embryos recorded may be (a) incubated amphiblastulae (*Oscarella* Vosmaer, *Plakina* Schulze of Plakinida); (b) nonincubated parenchymellae (e.g., *Tethya* Lamarck of Epipolasida); or (c) parenchymelloid types, incubated (e.g., Tetillidae, Craniellida; *Stylocordyla* Thomson of Spirastrellida) or not (e.g., *Polymastia* Bowerbank of Spirastrellida). It has also been found recently (Bergquist & Hartman, 1969) to be diverse biochemically, with four major patterns of amino-acid groupings, one of which can be subdivided further. Tetractinomorpha in effect means little more than Demospongea that are not Ceractinomorpha unless Lévi's picture of phylogeny is also considered.

The critical evidence for Lévi's picture (1957b) is derived from the early development of two modern sibling species of the myxosponge *Halisarca* Dujardin, which resembles dendroceratid Keratosida in the character of its soft parts. In *H. dujardini* Johnston the larva developed from the embryo is an asconoid rhagon; in *H. metschnikovi* Lévi, however, it is a syconoid rhagon like that of the dendroceratid *Aplysilla sulfurea* Schulze. According to Lévi (1957b), this implies that the Dendroceratida were derived from halisarcids; the Dictyoceratida from the Dendroceratida; and the orders with spicules (Halichondrina, Poecillosclerina, Haplosclerida Lévi; Chalinida and Desmacidontida herein) are derived from the dictyoceratids. Thus, spicules of monaxonid Ceractinomorpha are supposed to have evolved independently of those of Tetractinomorpha.

This idea may be correct but certainly can also be doubted for a number of reasons.

i. The general character of the spicules appears to be identical in both instances, and all types of megascleres found in Ceractinomorpha (except the desmas of *Crambe*) can be matched in Tetractinomorpha. The toxa and sigma types of microscleres occur also in some Axinellida, and sigmaspire-variants that are chelas morphologically occur in some Craniellida (e.g., *Chrotella amphiacantha* Topsent, *Tetilla sigmoanchoratum* Koltun). No difference in the mode of secretion of the spicules has yet been demonstrated. Last, desmas are identical in character and mode of union whether in Tetractinomorpha (e.g., *Pleroma* Sollas) or Ceractinomorpha (e.g., *Desmatiderma* Topsent). All these resemblances suggest that the spicules did not have different origins.

ii. Derivation of the spiculate Ceractinomorpha from keratose sponges implies replacement of spongin by spicules during phylogeny. On the other hand, if axinellid sponges are put into the Tetractinomorpha their spongin has presumably evolved as a replacement for spicules. Such opposite developments seem unlikely.

iii. Both Dendy (1905) and Lévi (1953, 1957b) based their pictures of phylogeny on modern sponges only. Although they provide the only realistic basis for speculation, the modern forms are all end forms phylogenetically and have no chronological sequence. Their morphology alone, hence, provides no certain measure of phylogenetic direction. It is unknown whether the simplicity of forms like *Oscarella* and *Halisarca* is primitive or due to regression, e.g., by neotenous retention of larval characters, or which type of *Halisarca* rhagon was derived from the other. Furthermore, no modern taxon can ever be ancestral to another, although they may share common origin. Moreover, the fact that a series of modern taxa can be arranged into a sequence from simplest to most complex need not imply that this sequence represents their phylogeny. For example, such a pattern could also arise by the iterative divergence of retarded stocks from a primary progressive one, with the oldest divergent stock then retaining the most primitive characters.

In addition, the survival to the present of two groups of supposedly primitive genera (plakinids and *Oscarella;* halisarcids) does not mean that others have not existed or were the true ancestral sources of the orders with megascleres. A persistence of primitive characters, if genuine, implies in itself a nonprogressive status. In other words, the true ancestral stocks of most or all advanced modern orders may, in fact, have disappeared as completely and in the same manner as mammal-like reptiles or thecodont archosaurs.

iv. If the *Halisarca* species are siblings their status has two implications that can count against Lévi's (1957b) conclusions.

a. Their speciation must be too recent to bear directly on demosponge origins, or even nearly so.

b. If siblings can be distinguished by their embryology, this is *ipso facto* evidence that embryological characters can change cenogenetically and can be less stable phylogenetically than adult characters at even speciation level.

In addition to these problems, it should probably not be assumed that all lithistids are Tetractinomorpha. In particular, the Anthaspidellidae of the Paleozoic Orchocladina have a structure suggesting their origin from a chalinoid monaxonid, now found only among the Chalinida and Desmacidontida. It also seems likely that the Sphaerocladina are of orchocladine origin.

The classification used here makes the compromise of basing subclasses on the skeleton but adopting Lévi's order Axinellida. There is no implied rejection of his concept of a special relationship between Ceractinomorpha, and their division between the Monaxonida (as Chalinida and Desmacidontida) and Keratosida is acceptedly artificial.

SKELETAL EVOLUTION

In attempting an assessment of demosponge phylogeny, it seems best to ask first whether any general patterns can be demonstrated. One is then at once confronted by the fact that most directions of evolutionary changes cannot be firmly established, even when they can be fairly presumed.

First, no critical data are provided by the fossils, at least with respect to nonlithistids. The fossil Demospongea, unlike those now living, are predominantly lithistids, and all the nonlithistids together are considerably less numerous than the genera distinguished by zoologists. Most fossils have nothing but megascleres. Furthermore, most supposed fossil occurrences of existing genera are based on isolated megascleres or microscleres, many of which have no diagnostic value. No extinct genus or family can be classified more certainly than as choristid or monaxonid. There are very few reliable records of keratose sponges and none of myxosponges. With the evidence suggesting that the record is probably also extremely incomplete, these facts rule out normal reliance on stratigraphic sequences as a basis for establishing phylogeny.

Comparative zoological data are, therefore, the main source of evidence; but the modern forms have no chronological sequence and include only whatever stocks have survived to the present. In consequence, such data are generally of uncertain significance.

One general assumption that seems safe at present is that lithistid sponges are derivatives of nonlithistids, produced by conversion of some normal type of megasclere into a desma. This conclusion is unopposed thus far. It seems to be supported by the characters of the sublithistids at least, in which a desma intergrades with a simple monaxon, although the direction of change is not strictly demonstrable.

The most important problem is the relationship of choristid and monaxonid sponges. This can be approached by considering three contrasting possibilities.

1. The primitive demosponge spicules were tetraxons, and all monaxons are derived from them. All monaxonids have arisen from choristids by loss of tetraxons in phylogeny.

2. The primitive spicules were monaxons, and all tetraxons are derived from them. All choristid sponges have arisen from monaxonids by evolving tetraxons in phylogeny.

3. Choristid and monaxonid sponges have had separate origins.

In instances (1) and (3) tetraxons found in lithistids will have been inherited from choristids; but in instance (2) they could either be inherited or evolved from monaxons after the lithistid condition was developed.

The first of these concepts corresponds with the views held by Dendy (1905, 1916), which were based on those of Schulze (1887b). These authors also thought that small spicules like those of plakinids were primitive and assumed that loss of tetraxons has occurred in forms with megascleres. The principal arguments for this view are (i) the transitions from triactines or tetractines to diactines seen in plakinids and some other forms, which seem to show clearly that the diactines are produced by reduction; (ii) the apparently central status of triactines or tetractines in relation to spicules as different as oxeas, long-shafted triaenes, lithistid discotriaenes and discs, tetraxial and some monaxial desmas, sterrasters, and spiraster streptoscleres; and (iii) the close resemblance of some monaxonids to choristids, which may even be so close that both types can be regarded as species of one genus (*Aurora* Sollas; Dendy, 1916). The main objections are (a) the general lack of demonstrable relationships between choristids and most monaxonids and (b) the existence of evidence suggesting an opposite picture.

The second possible picture of phylogeny, deriving choristids from monaxonids, has been almost ignored except by Finks (1967b), although hinted at by Sollas (1888). It is suggested by several sorts of evidence:

i. The development of long-shafted triaenes of various modern sponges from initial monaxons during ontogeny.

ii. The occurrence in *Paratetilla* Dendy (Tetillidae, Craniellida) of subtriaenes, which appear to be modified derivatives of a normally long-shafted type (as accepted by Dendy himself: Dendy, 1922).

iii. The occurrence of diactinal to pentactinal spicules that appear to be derived from monactines (echinating acanthostyles) in the axinellids *Cyamon* Gray and *Trikentrion* Weltner.

iv. The geological appearance of monaxonid sponges in the Cambrian Period, long before the oldest known choristids, which are Late Ordovician.

The closely similar choristids and monaxonids, used by Dendy (1905) in support of his opinions, could also be cited in this context with an opposite significance.

The objections are that none of this evidence is conclusive and some of it is certainly unreliable.

1. There is no guarantee that the ontogeny of spicules must represent their phylogeny. In the instances of (i) lithistid discs related to dermal triaenes and (ii) related tetraxial and monaxial desmas, it is clear that ontogenetic prototypes can alter cenogenetically in a way that leaves the adult form as the main indication of homology. This conclusion is independent of the direction ascribed to

phylogeny in these instances. In the instances of (a) monaxial discs related to triaenes and (b) monaxial radical desmas related to tetraclones, the change in phylogeny implied by their functional adaptations is tetraxon to monaxon, not the opposite.

In long-shafted triaenes, delay in formation of the cladi could also be cenogenetic if it is related to hypertrophy of the rhabdome. It might also lead ultimately to their suppression, with replacement of tetraxons by monaxons. This would fit DENDY's picture of phylogeny.

2. The subtriaenes of *Paratetilla* occur at or near the surface and may only be an ectosomal specialization in this genus.

3. The axinellid sponges have no certain relationship to any choristids in terms of any known evidence. The occurrence of secondary radiates in some genera has also depended presumably on their prior possession of echinating acanthostyles. There is nothing in the characters of choristids to suggest that their tetraxons were ever echinating spicules.

4. Lower Carboniferous choristids had spicules including small simple and lophose calthrops, large simple and branching calthrops, subtriaenes, long-shafted plagiotriaenes, protriaenes and anatriaenes, mesotriaene variants of protriaenes, typical dichotriaenes, trachelotriaenes, and unusual pentactinal and hexactinal megascleres. There are also rounded bodies that appear to be sterrasters. The choristids must already have existed for long enough to evolve this range of different types of spicules, which include some like those of plakinids and every major type of tetraxial megasclere found in modern forms. Unless the innovation of new types was initially much faster than since the Carboniferous Period, the time involved could be up to several times longer than that from the Early Carboniferous to the present.

5. The existence of choristids before at least the Ordovician Period is suggested by the typically tetraxial form of the desmas of *Hindia* DUNCAN and related genera and by the structural resemblance of hindiids to the minchinellid *Porosphaera* STEINMANN, in which the spicules were certainly tetractinal.

6. The pre-Carboniferous monaxonids are known only by their megascleres, and whether they are related to choristids or any later sponges is unknown. They could, in fact, represent monaxonid stocks that have descended independently of choristids or have no later relatives. If LÉVI's views are followed, such monaxonids need to be identified as Tetractinomorpha before they can be cited in evidence.

7. If choristid and monaxonid stocks have descended independently from plakinid-like microspiculate sponges, as envisaged by SOLLAS (1888), their first geological appearance will almost surely have depended on evolution of megascleres; so that which appeared first in an adequate geological record would indicate only which stock first evolved megascleres, without implication that either is derived from the other.

The concept of separate descent of most choristids and monaxonids (point 3 above) fits their general lack of evident relationship; but monaxonid stocks that were ancestral to choristids may not have living representatives. SOLLAS's (1888) concept of the descent of most choristids and monaxonids from plakinid-like sponges, by development of megascleres from tetraxons or from monaxons only, fits with the fact that the largest spicules present in plakinids may be either tetraxons (e.g., *Plakinastrella* SCHULZE) or monaxons (e.g., *Dercitopsis* DENDY). The small size of spicules in plakinids is not known to be primitive, however.

Thus, none of the three possibilities suggested above can be shown to be the truth, and some of the evidence can in fact support opposite views, according to how it is interpreted.

The most likely possibility is the third, envisaged by SOLLAS (1888), with his further conclusion that a few monaxonids only are true derivatives of choristids with megascleres. It seems clear that DENDY was badly mistaken in his concept of sigmatose microscleres, which formed the chief basis of his view that monaxonids are all derived from choristids. But the origin of choristids from monaxonids, although certainly possible, is not currently supported by any reliable evidence. In particular, it need not be implied by the development of some modern triaenes from monaxons in ontogeny. The paleontological data are also mainly of unknown significance, except for clear evidence that choristids had undergone substantial evolution before their first known appearance. On the other hand, DENDY's explanation of the skeletal evolution of choristids fits their characters sufficiently well to suggest that it is probably correct, at least for the Plakinida, Poecillastrida, and Ancorinida. There is no evidence that this applies also to the Craniellida, in which all tetraxon megascleres are triaenes; but his principal mistake was in assuming that, because a few monaxonids appear to be genuinely allied to typical choristids, this must also apply to all the others.

In attempting to reconstruct the pattern of skeletal evolution, several general points may first be considered.

1. The numerous occurrences of similar features (e.g., presence of both megascleres and microscleres or radial arrangements of megascleres) in sponges that appear to have no direct relationship implies widespread occurrence of parallel or convergent developments.

2. Assuming that the spicules were originally all of one sort, a trend toward differentiation of spicules into separate categories is implied by all instances in which two or more categories are present. On comparative grounds, size, form, or both may be affected, and there may be a correlated functional development (for instance, the arrangement of triaenes for support of the ectosome).

3. Once different categories of spicules have become differentiated, they usually evolve independently. For instance, in lithistids the megascleres developed as desmas may be accompanied by normal oxeas and triaenes; so that modification into desmas can be seen in one category of megascleres without others being affected. Once established, any category of spicules can undergo apparently further differentiation, for instance so that several sorts of triaenes are developed.

4. It is reasonably likely that spicules were initially little or no larger than the cells that secreted them. This implies that the occurrence of megascleres is a secondary development, resulting from enlargement of spicules in phylogeny. Its significance is probably functional, indicating correlation between increase in size of the spicules and their efficiency as supporting elements. Unless all the groups possessing megascleres have an orthogenetic relationship, which does not seem likely, their development has occurred independently in various lines of descent.

5. Many microscleres have shapes that do not occur in megascleres. This may be because the shapes restricted to microscleres are not suited to the supporting function of megascleres. Many shapes of microscleres have no obvious functional significance, and the microscleres themselves have often no apparent function. It was DENDY's view that most variation in the shape of sponge spicules has no primary functional significance, although types that are suited to some function may be put to it.

6. In various instances, related types of microscleres found together have an inverse relationship between size and complexity in shape. For instance, when several sorts of streptoscleres are present, it is common for the simplest (plesiasters) and most complex (spirasters) to be also the largest and smallest, respectively. This suggests that the difference in size between megascleres and microscleres can involve a reduction in the size of the microscleres in phylogeny as well as an increase in the size of the megascleres.

7. Many instances are known in which similar sponges differ only in the presence or absence of one of several categories of spicules. In addition, examples occur in which those of one category are abnormally rare, although present. This seems to represent a trend to secondary simplification of the skeleton by suppression of categories of spicules.

8. Differentiation of spicules into two or more orders of size during early phylogeny

can be pictured as the primary origin of microscleres, but they seem also sometimes to originate as secondary derivatives of megascleres. This applies especially to the spinispira series of microscleres, which seem to be related to megascleric oxeas (p. 96). Unless it is thought that a typical oxea megasclere can be derived from a spiraster, the direction of phylogeny implied is from megasclere to microsclere. The loss of some categories of megascleres (e.g., calthrops of Choristida) in phylogeny might sometimes have been due to their conversion into microscleres.

These principles apply to all types of demosponges that have spicules and do not depend on how choristids and monaxonids are related. They can, therefore, form a general background to any attempted reconstruction of demosponge phylogeny, irrespective of which of the main possibilities is envisaged.

Next, if choristids and monaxonids are related as envisaged by SOLLAS (1888), the prototypes of both would be simple, plakinid-like sponges with small spicules of a single size grade only. In some at least, the spicules would then be expected to vary from diactines to simple polyactines (e.g., five- or six-rayed); but others could have had diactines only. It does not matter what type of spicule is considered to be primitive. *A priori,* monaxons (diactines) could be thought to be the most likely prototypes, with the primitive scleroblast then forming one protorhabd only. Later, multiplication of protorhabds and their union in radial groups could have led to production of spicules with three or more rays, as seems likely to have happened in Calcarea and Heteractinellida. On the other hand, diactines of the living plakinids appear to be derived from triactines by suppression of one ray. The small size of the spicules can be pictured as related to the size of the scleroblasts or perhaps to the size of the flagellated chambers, as envisaged by SCHULZE (1887b).

If this picture is correct, the evolution of megascleres could then have the functional basis of providing more efficient support for the body, in general, and for the chambers and canal system against compression by its weight. This in turn could permit the evolution of increased size and new shapes in the body with increased physiological efficiency or new modes of function. The primary origin of microscleres would then be the retention of smaller spicules for the local support of the tissues and the circulatory system; although whether this function would account for their whole evolution is debatable. On loss of function, they might either persist as nonfunctional structures or be lost altogether. Alternatively, the development of microscleres might also have occurred as a means of controlling the number of spicules that grow to megascleric size, preventing overproduction of megascleres.

The first step in further evolution of the prototypes postulated would be differentiation of the spicules into two or more size grades, with the larger forms assuming the function of megascleres. In a stock with spicules varying meristically in the number of rays, the selective enlargement of tetractines or both tetractines and diactines would yield suitable prototypes for the typical choristid sponges. Why these shapes should be selected for enlargement is unknown; but presumably a functional adaptation would select the types best suited to the large-scale support of the body and to the movement of spicules within it. Smaller varying spicules, ranging from diactines to pentactines or hexactines for example, would be simple euasters in effect and would include the appropriate prototypes of all choristid euasters and of streptoscleres. The type of spiculation envisaged would be similar to that of the living plakinid *Plakinastrella* SCHULZE. In addition, enlargement of tetractinal to hexactinal spicules would account for the aberrant spiculation of *Spiractinella* HINDE.

On the other hand, enlargement of diactines only into megascleres would lead directly to monaxonid sponges, again with simple euaster microscleres. SOLLAS (1888) envisaged this origin for the axinellid sponges, with the root stock represented by the living Epallacidae in which simple euasters are present. The occasional occurrence of triactines as variants of *Alectona* oxeas has a similar implication if the prototype diactines are supposed to be derived from triactines. In plakinids, the largest spicules present may be oxeas in *Dercitopsis* DENDY, although this genus was supposed to establish his views (e.g., 1921) about the origin of choristid microscleres.

When euasters or related forms are absent from genera with megascleres, this could represent the loss of such microscleres in phylogeny; but this need not be postulated in monaxonids, at least. If some of the demosponge prototypes had only diactinal spicules as a primary or secondary condition, their descendants with megascleres will never have had any spicules with more than two rays, unless these have arisen from diactines as a secondary development.

Evolution on all of these lines seems to be a likely explanation of the spicular characters of the living nonlithistid Demospongea if allowance is made for some further developments. There have probably been at least some instances of monaxonids evolving from choristids by loss of tetraxial megascleres and of microscleres arising from megascleres as a secondary occurrence. No grounds exist, however, for insisting on a single unvarying pattern proceeding orthogenetically from either choristid to monaxonid or the opposite. Both extreme views are equally unlikely. There is also, then, no implication that either choristids or monaxonids should appear first stratigraphically or that whichever does so in practice must be ancestral to the other; this will simply have depended on which stocks were first to evolve spicules large enough to be preserved and recognized.

If primitive sponges were crustose, the first tetraxial megascleres could well have been short-shafted triaenes with three cladi directed to the surface. A tendency to orthotriaene shape would be likely, so that cladi could underlie the ectosome tangentially. The symmetrical calthrops, on the other hand, would be better adapted to support of a choanosome several times the depth of spicules supporting it. The triaene can be pictured also as arising as an ectosomal modification of a primary calthrops (DENDY, 1921). Either picture or both could be correct, and these spicules are certainly intergrading in the modern forms with calthrops as megascleres. The triaenes (or subtriaenes) of such sponges may be very little different from calthrops and oriented to the surface or at random. In the living *Pachastrella* SCHMIDT, a calthrops is accompanied by a separate category of oxeas; these could be envisaged as evolved independently, but diactines occur as minor variants of a calthrops in *Calthropella* SOLLAS for example.

The initial type of megascleric skeleton developed in choristids can be pictured, thus, as consisting of subtriaenes, calthrops, or both together or of these types plus oxeas. Megascleres from the choanosome would always include tetractines, and no special ectosomal skeleton would be present. The fossil *Propachastrella* SCHRAMMEN (Upper Cretaceous) has a minor advance on this condition, with choanosomal calthrops and variants accompanied by distinct ectosomal dichotriaenes.

The predominant type of modern choristid can be pictured as having developed from prototypes with diactines and tetractines as megascleres and with triaenes developed at the surface for support of the ectosome. Such triaenes are oriented with the cladi in or under the ectosome and with the rhabdome running radially inward. The triaenes could intergrade initially with a choanosomal calthrops but might also become differentiated. The prevalent condition in modern forms would then be produced by the loss of the choanosomal calthrops, leaving only the oxeas (diactines) as choanosomal megascleres. This could happen by simple suppression of a choanosomal calthrops or by its conversion into triaenes or microscleres. A more or less gradual replacement of calthrops by triaenes is suggested by the characters of the living *Poecillastra* SOLLAS. In addition, two minor trends are needed: (a) progressive replacement of short-shafted by long-shafted triaenes and (b) diversification of triaenes into more than one category, e.g., dichotriaenes and anatriaenes. A sponge of this type, without special arrangement of the oxeas, would have the felted type of choristid skeleton; but arrangement of the oxeas in parallel with the shafts of the triaenes would lead to radiate sponges. The adoption of globular habit might encourage this development.

As a final stage, sponges of this type could give rise to monaxonids, by loss of triaenes. Some modern forms have very few triaenes and have been mistaken for monaxonids before these spicules were discovered in their skeletons (e.g., "*Trachygellius*" [=*Craniella*] *cinachyra* de Laubenfels). There could also be conversion of triaenes into monaxons by loss of their cladi. In *Stellettinopsis* Carter, first thought to be monaxonid, the length of cladi may be less than the thickness of the rhabdome. If the formation of the rhabdomes of some long-shafted triaenes before their cladi is cenogenetic, as this picture of phylogeny requires, a final step could be their total suppression.

Description of evolution of sponges that are primary monaxonids needs minor further comment. Principal changes in megascleres are from oxea to style and then to tylostyle, with other forms (strongyles, amphitylotes, ophirhabds) as side products. The variously patterned types of skeletons (radiate, fibrous, reticulate) are presumably more advanced than the felted type, although secondary reversion is also possible. Spongin seems best regarded as sparsely developed, initially, and becoming fibrous later. Arrangement of spicules into fibers would encourage presumably this development. The pseudoceratosa with fibrous spongin and few spicules, or none in different specimens, should then represent sponges in the process of losing the spicules and becoming purely keratose. I prefer this view to Lévi's (1957b) implication that Ceractinomorpha with spicules have evolved from purely keratose sponges with progressive reduction of spongin. His picture of phylogeny also does not permit this explanation for fibrous spongin in the axinellid sponges.

It is not implied, however, that all keratose sponges must be derived from monaxonids with megascleres. If the spiculate Ceractinomorpha are derived from microspiculate sponges with diactines only, it is possible that spongin or its prototype (e.g., disseminated mesenchymal fibers) was evolved before megascleres in either some or all instances; a keratose sponge could then evolve by loss of the spicules at this stage, without spongin ever having connected spicules. If spicules were evolved in some primitive forms but not others, modern keratose sponges could be forms in which spicules have never existed at any stage of phylogeny. These different postulates could represent the histories of the Dictyoceratina and Dendroceratina, which are grouped biochemically with the megasclere-bearing Desmacidontida and the askeletose Halisarcidae, respectively.

Lithistids appear to have arisen from nonlithistid sponges by conversion of one category of choanosomal megasclere into desmas. If this is correct, their primary pattern of megaspiculation must depend on the kinds of megascleres present in their nonlithistid prototypes. There are four main possibilities, assuming that the prototypes of desmas are the principal choanosomal megascleres.

1. A choristid with choanosomal calthrops and no distinct triaenes gave rise to a lithistid with tetraxial desmas but no triaenose dermalia. An additional oxea, not converted into desmas could persist as a supplemental oxea.
2. A choristid with choanosomal calthrops and ectosomal triaenes differentiated gave rise to a lithistid with tetraxial desmas and triaenes.
3. A choristid with tetraxial megascleres restricted to ectosomal triaenes and with all choanosomal forms monaxons (e.g., oxeas) yielded a lithistid with triaenes and monaxial desmas.
4. A lithistid derived from a purely monaxonid sponge had monaxial desmas and perhaps supplemental monaxons but no triaenes.

These predicted patterns correspond with those of various major groups of lithistids as well as some sublithistid sponges.

a. The Tricranocladina (or Hindiidae) could be lithistids of the first sort if their desmas were tetraxial, since no other megascleres but oxeas appear to have been present. The small size of the desmas could imply a microspiculate prototype, but this would not alter the relationship envisaged.

b. The ontogenetic development of typical tetraclones from an initial calthrops suggests the second mode of origin for the triaene-bearing Tetracladina.

c. Although ectosomal triaenes are present, the monaxial desmas of the Helomorina and Megamorina (heloclones, megaclones) have no sign of derivation from tetraxons and are probably ophirhabd derivatives. The desmalike spicules of the sublithistid *Helminthophyllum* SCHRAMMEN, which are accompanied by triaenes, are also probably of monaxon origin.

d. The Rhizomorina and Orchocladina have monaxial desmas but lack triaenes and have nothing to suggest derivation from tetraxon-bearing sponges. The Anthaspidellidae of the Orchocladina have a structure suggesting derivation from a chalinoid monaxonid, corresponding with forms now seen only among the monaxonid Chalinida and Desmacidontida. The modern *Desmatiderma* TOPSENT, *Helophloeina* TOPSENT, and *Lithochela* BURTON are sublithistid Desmacidontida with characters intermediate between monaxonids and lithistids.

On the other hand, these are not the only possibilities. In Tetracladina, the typical tetraclones may be accompanied by variants with triactinal, diactinal, or monaxial crepides found in varying abundance, of which forms with triactinal crepides may outnumber or entirely replace true tetraclones. A similar replacement of tetraclones by related monaxial desmas could result in evolution of a sponge with monaxial desmas and triaenes, not produced in the manner envisaged above, as in the Helomorina for example. This mode of origin is suggested for the Dicranocladina by their general resemblances to discodermiid and similar Tetracladina and by the presence in *Macandrewia* GRAY of tetraxial variants of the normally monaxial desmas. The two groups are not sharply separable when this genus is considered.

Anaxial desmas have no evident nonlithistid prototypes, but progressive reduction of axial structures in transitions from monaxons to desmas (e.g., in *Desmatiderma*) suggests that the anaxial type of desma has a culminating stage of this process. This could then be the origin of the Sphaerocladina. If the shortening of the axial shaft seen in transitions from dendroclones to chiastoclones of the Orchocladina is supposed to represent progressive shortening of monaxon crepis, the sphaeroclone could then be essentially a modified chiastoclone with an ennomoclonar shape correlated with growth of the skeleton in layers.

Thus, in these instances, origins of some groups of lithistids can be pictured as involving a secondary change in the desmas, whose monaxial or anaxial character does not represent that of a nonlithistid megasclere. A further possibility for secondary change is loss of triaenes, producing forms with tetraxial or monaxial desmas but no triaene dermalia. This is possibly represented in the Didymmorina, in which triaenes that appear to be intrinsic have so far only been found in one specimen of *Cylindrophyma milleporata* (GOLDFUSS).

Simple triaenes and dichotriaenes of lithistids are indistinguishable from those of choristids; but phyllotriaenes and discotriaenes have no choristid counterparts. These forms seem to represent a special lithistid modification of the ectosomal skeleton, resulting in production of an armor of overlapping megascleric scales. At the end of this sequence, discotriaenes with rudimentary cladi intergrade with monaxial discostrongyles, with an axis in a rhabdal ray only. These are not of separate origin, since their intergradation may be seen in the spicules of one specimen. This presumably represents progressive reduction of the crepis from tetraxial to monaxial unless a normal dichotriaene can be derived from a monaxial disc. The apparently anaxial dermal plates of *Plinthosella* VON ZITTEL suggest an ultimate stage in this sequence.

This suggested picture of spicular evolution can explain all the principal developments seen in demosponge megaspiculation. There is no certainty of its correctness because of its comparative basis, and other pictures are possible. In particular, some parts could require to inversion if tetraxial megascleres can originate as triaenes derived from monaxons. It is, therefore, essentially a personal impression of what seems currently most likely. On the other hand, there is no current evidence that development of tetraxons from monaxons is in any case more than simply possible, except at the most primitive level in ancestral microspiculate Demospongea.

Whether one looks at biochemical or traditional spicular evidence, by far most modern monaxonids have no evidence of special relationship to choristids, of a type implying origin of either from the other. There are especially no known choristids that have features suggesting derivation from the typically monaxonid orders (Spirastrellida, Axinellida, Chalinida, Desmacidontida; or, in other nomenclature, Hadromerina, Axinellida, Haplosclerida, Halichondrina, and Poecilosclerina). This suggests strongly evolution on the lines first suggested by SOLLAS (1888), with choristids and monaxonids arising by selection of different types of spicules for enlargement into megascleres. This could very well apply to even most supposed epipolasids (*sensu* SOLLAS), of which many coppatiids could, in fact, share no more with ancorinids than a common microspiculate ancestry.

The occurrence of forms in which triaenes are abnormally rare is also clearly comparable with instances in which various other types of spicules (e.g., monaxonid acanthostyles, chelas; spicules of pseudoceratosa) are abnormally uncommon or absent in some species, populations, or individual sponges. These instances are generally regarded as showing a process by which categories of spicules can be lost in phylogeny and cannot be interpreted differently unless the spicules concerned are all supposed to be arising *de novo.* By comparison, the choristids with rare triaenes seem almost certain to have a condition that would lead ultimately to production of monaxonid sponges and not an opposite process of production of choristids from monaxonids. In the lithistid sequence from dichotriaenes to monaxial discs, it seems almost certain, again, that the spicules have evolved from tetraxon to monaxonids and not in the opposite direction. Unless these comparisons are misleading, the development of some long-shafted triaenes from monaxons in ontogeny is probably cenogenetic and related to hypertrophy of their rhabdomes, not a feature implying that triaenes have arisen from monaxons in phylogeny.

As stated, however, this is the opinion of the author, from which others are entitled to differ. All that can strictly be insisted upon is that any assessment or opinion should always consider all the relevant possibilities and evidence and should always be adjustable, if necessary, in the light of new evidence.

As a footnote, there is some possibility that some nonlithistid sponges could be forms derived from lithistids by reduction or loss of the desmas. For example, *Crambe* VOSMAER of the Desmacidontida has a mainly monaxonid spiculation but possesses basal desmas that resemble those of some Sphaerocladina. Since Sphaerocladina may contain supplemental monaxons, *Crambe* might show a stage in reduction toward a purely monaxonid condition, although this does not seem probable.

PHYLOGENY

As emphasized already, no reliable picture of demosponge phylogeny can be given at present because of the virtual restriction of critical evidence to modern comparative data. The following suggestions are based on skeletal, biochemical, and embryological data on the general basis that the skeleton has evolved along the lines suggested above.

1. It seems likely that the primitive Demospongea were simple microspiculate sponges, some of which at least had spicules that varied meristically from diactines to simple polyactines. Others may have had diactines only, either as a primitive condition or because other forms were eliminated.

2. The orders Plakinida through Axinellida (i.e., LÉVI's Tetractinomorpha) may have descended from prototypes with spicules that varied meristically. The Plakinida, then, are to be regarded as persistently primitive in having only small spicules not differentiated into typical megascleres and microscleres but in having some differentiation, with specialized features that do not occur in typical choristids (candelabra spicules, amphiblastula embryos), and they may include forms that are not, in fact, closely related. The Poecillastrida and Ancorinida appear to be stocks of common origin, both possessing true megascleres but with different types of characteristic microscleres. The Craniellida seem to be a separate series, not related to other forms with megascleres.

3. Some monaxonids grouped here as Epipolasida (Coppatiidae) are either derived from choristid Ancorinida by loss of triaenes or other tetraxons or from allied forms with megascleres developed from monaxons only. Other Epipolasida seem to belong with the Spirastrellida (Tethyidae) or Axinellida (Epallacidae, Sollasellidae).

4. The Spirastrellida and Axinellida are two series of primary monaxonids with megascleres developed from diactines only. Euastriform microscleres are typically absent, presumably through loss in phylogeny, but have persisted in the Tethyidae and Epallacidae if these forms are included. Spirastrellida can then be pictured as including two divergent series: (a) the Tethyidae, with euasters retained and developed in parallel with those of choristid Ancorinida; and (b) other forms, with euasters lost and sometimes replaced by secondary microscleres (microrhabds, spinispiras) derived from megascleres.

5. The Chalinida and Desmacidontida are primary monaxonids, derived from primitive sponges with diactinal spicules only. According to LÉVI, their spicules were evolved independently of those of Tetractinomorpha, but this need not be correct. These forms and the keratose sponges were derived from a stock in which incubated parenchymella were an early development, and some forms may have lacked or lost spicules before any developed megascleres. The Chalinida include two main stocks with different skeletal features that are, nonetheless, similar biochemically and in having generally simple spiculation. The Desmacidontida are more nearly allied to the dictyoceratid Keratosida and are distinguished from Chalinida by more specialized spiculation and the occurrence of chelas. The reticulate structure of Dictyoceratida suggests that they once possessed spicules, although this need not be conclusive. They could also be polyphyletic, for example, if various Desmacidontida lost their spicules in different periods. The Dendroceratida and Halisarcidae may be persistently primitive or degenerate.

6. The Astrosclerida have features (verticillate spicules, clavidiscs) suggesting affinities with Axinellida or Chalinida but are too poorly known for further comment.

7. The Lithistida are polyphyletic, and their relationships are largely unknown. The following derivations are suggested.

a. Tetracladina: from pachastrellid Poecillastrida, with triaenes and choanosomal calthrops by conversion of calthrops into tetraclone desmas.

b. Dicranocladina: from Tetracladina by reduction of the crepides of desmas from tetraxons to monaxons; source stock most nearly represented by Jurassic Sontheimiidae, and probably shared with Cretaceous to recent Discodermiidae.

c. Didymmorina: unknown but perhaps as suggested for Dicranocladina.

d. Helomorina, Megamorina: from a choristid with ophirhabds and triaenes;

perhaps from a stock also leading to theneid Poecillastrida.

e. Tricranocladina (=Eutaxicladina sensu SCHRAMMEN): unknown; from an early microspiculate choristid if *Hindia* desmas were tetraxial.

f. Orchocladina: from a chalinoid monaxonid, perhaps of order Chalinida.

g. Rhizomorina: in part at least from Orchocladina by replacement of dendroclones by rhizoclones but may also include convergent forms of different (e.g., craniellid, axinellid) origin.

h. Megarhizomorina: unknown; but possibly axinellid, if regarded as including, for example, *Petromica* TOPSENT of extant forms.

i. Sphaerocladina: unknown but possibly from chiastoclonellid Orchocladina by conversion of chiastoclones into sphaeroclones and astroclones.

DEMOSPONGE PHYLOGENY

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INTRODUCTION

Two treatments of demosponge phylogeny are presented in this volume, one by Finks (p. 63, Paleozoic Demospongea: Morphology and Phylogeny) and the present chapter. The views expressed may differ radically, but this serves to emphasize how little is really known and how subjective are the expressed views. Finks (1967a, 1971b) has accepted the concept that tetraxial megascleres can arise from monaxial megascleres, a concept not accepted herein. In addition, Finks's discussions (1967a, 1971b) are centered on single genera, whereas, herein the approach is to begin from the totality of all available evidence and try to work inward toward some acceptable common starting point. Moreover, while genera relied on by Finks are fossils, herein the belief is that only modern forms, excepting some lithistids, are well enough known to be a basis for useful speculations.

In the following text, nonlithistids and lithistids are discussed separately because they present different problems.

NONLITHISTID PROBLEMS

Fossil and modern nonlithistids present different problems of interpretation. The sparse and sporadic fossil record is probably very incomplete, and nearly all fossil material is incomplete. Modern forms present problems because phylogenetic end forms from a single time plane can yield no objective indication of phylogenetic directions. These problems interact, because the fossils throw almost no light on what courses phylogeny may have followed.

Starting with the fossils, one may note first that the total of recorded fossil genera is much smaller than the total known from modern seas, while the total of purely fossil forms is smaller still. This is an unlikely picture of the true relative abundance of nonlithistids in the past and the present; and it is, at least in part, due to the spicules being loose in the tissues and hence scattered after death. Indeed, loose spicules from some deposits (e.g., cricorhabd from the Upper Jurassic and Cretaceous or trachelotriaenes from the Lower Carboniferous and Upper Jurassic) have occurrences of sponges not known from associated megascleres; and there are frustratingly rare glimpses of faunas that were probably as large as any modern ones (e.g., the lower Tertiary of Oamaru, New Zealand: Hinde & Holmes, 1892).

A further major cause of the poor fossil record is that only some formations yield material, while in other formations fossils do not occur at all. Those that do yield material are mostly limestones, such as the Irish Glencar Limestone (Visean) and the Malm and Chalk of Germany, and some sandstones (e.g., the Upper Greensand of southern England); and, even here, remains may be limited to drifted spicules occurring in only some localities. The problem seems to be that even large siliceous megascleres are preserved only under certain physicochemical conditions and otherwise are either dissolved before fossilization can occur or rendered inextractable by later calcification. But, nonlithistid sponges almost certainly lived in many environments whose sediments have no trace of their spicules. In the Oxford Clay of England, for instance, large *Gryphaea dilatata* may be riddled with borings of the type made by *Cliona,* although spicules of the latter do not occur; and, while much of the English Chalk has no trace of spicules, the internal meal of hollow flints may be packed with them. Thus the record plainly has been subject to diagenetic deletions, and there probably have been many species that have left no trace whatever.

Because the record is restricted mostly to forms with large megascleres, this problem also goes farther, for microscleres and small megascleres are found only in rare deposits (e.g., the Oamaru sponge earth) or in protected situations (e.g., in flints). This has several consequences. First, it makes it likely that another large segment of the nonlithistid record is missing and that the apparent order in which major groups first appear in the record may depend upon when they first evolved large megascleres. The stratigraphic order of such apparent first appearances, thus, cannot be trusted as a key to phylogeny, quite apart from the possible effects of fortuitous preservation.

Second, virtual restriction of associated spicules to megascleres means that no fossil species can be referred certainly to a modern taxon, at even the generic level; and this problem is complicated further by occurrences of similar megascleres or similar skeletal architecture (e.g., radiate, plumose, or reticulate patterns) in members of different modern orders. This makes it doubtful how far back modern orders can be traced, when possible representatives might belong to more than one of them, and similar megascleres or architecture might also have evolved in extinct groups.

Third, another result is a very sparse record of microspiculate sponges, from which forms with megascleres probably derived (DENDY , 1921). Their first known occurrence in the Lower Carboniferous (REID, 1970) is probably a result of fortuitous preservation with no bearing on demosponge phylogeny.

Last, a further defect in the record is its almost complete restriction to spicular material. There are very few sure records of keratose sponges and none of dendroceratids or askeletose myxosponges. One might suspect that cementing spongin was present in the Burgess Shale monaxonids, for example, because they have well-preserved, complex, reticular arrangements of monaxial megascleres (in e.g., *Takakkawia* WALCOTT, 1920); but this excellent preservation also could have been due simply to the absence of physical disturbance and scavengers. There is also a complete lack of embryological data, used increasingly in zoology since its introduction by LÉVI (1957b), and of biochemical data of sorts used by BERGQUIST and HARTMAN (1969), for example. The first deficiency is especially relevant. For instance, were the Burgess Shale monaxonids oviparous sponges to which oviparous choristids could they be allied, or were they viviparous Ceractinomorpha with no bearing on choristid ancestry?

In summary, it is evident the fossil record is highly lacunar, recording only a tiny minority of past species and mostly forms whose relationships are either uncertain or unknown. Even the order in which they appear stratigraphically may depend upon the size of their spicules or simply on fortuitous preservation. Such a record cannot provide an adequate basis for assessing phylogeny, using any of the arguments traditional in paleontology. It could be highly misleading, for instance, to assume that some apparently younger group must have evolved from some apparently older one. In fact they may have evolved in the opposite order, without such a development being evident, or perhaps neither arose from the other. For such reasons, working backward from data provided by modern forms seems preferable, in general using the present as a key to the past. The only exception, in which the past could be the key to the present, is in the idea (e.g., VACELET, 1979, 1981) that monaxonid groups evolved polyphyletically from sclerosponges, by losing the calcareous basal skeleton. In this instance, the fossil record provides suggestive evidence (WOOD, REITNER, & WEST, 1989).

Some minor problems can also be noted here. First, some supposed fossil records of extant genera have been based on loose spicules, which may not represent the genus claimed. Some are highly dubious, as for example the records of *Thenea* GRAY, 1867, or *Geodia* LAMARCK, 1815, which have been based on triaenes, and might belong to these genera or to others. Other records have been based on apparently distinctive spicules, such as the aspidasters of *Erylus* GRAY, 1867, the discasters of *Latrunculia* BARBOZA DU BOCAGE, 1869, or the diancistra of *Hamacantha* GRAY, 1867. While these are less doubtful, there is no conclusive evidence that the sponges represented could be referred to these genera if known fully. Second, there can also be problems if microscleres appear to be preserved as well as megascleres. For instance, sterrasters occur in examples of *Discispongia* KOLB, 1910 in 1910–1911, that have associated megascleres and have been thought to belong to that genus (e.g., by SCHRAMMEN, 1936); but they may also occur within the skeletons of other Malm sponges, including hexactinellids in which they are presumably foreign or intrusive. It is therefore not certain that these spicules belong to *Discispongia.*

In modern forms, in contrast, a large amount of information on soft parts and spicules is available, due mainly to the work of such authors as VON LENDENFELD, RIDLEY, SOLLAS, HENTSCHEL, DENDY, TOPSENT, and their successors, but also in part to older authors (e.g., GRAY, BOWERBANK, CARTER). Until recently, classification has been based almost wholly on their spicular data; but in the last few decades embryology and biochemistry have made new evidence available and will continue to do so as more forms are investigated. Again, until recently, speculations on phylogeny have been centered on the spicules, most notably by DENDY (e.g., 1921); but, since 1957, embryology has assumed a major role, with LÉVI's (1957b) picture of an early division of the class into two major groups (his Tetractinomorpha and Ceractinomorpha) on this basis.

Most such data, however, are badly flawed as a basis for assessing phylogeny, because all modern species are phylogenetic end forms and because comparative study of species that are effectively all from one time can yield no objective indications of phylogenetic direction. Some examples illustrate this problem.

a. *Oscarella* VOSMAER and *Plakina* SCHULZE, 1880, are simple sponges with similar soft parts and unique amphiblastula larvae. *Oscarella* is askeletose, but *Plakina* is microspiculate. Does *Oscarella* represent a stock from which *Plakina* has arisen, or is it a plakinid that has lost its spicules?

b. "*Trachygellius cinachyra*" DE LAUBENFELS (1936) was thought to be purely monaxonid by DE LAUBENFELS but was later found to have a few triaenes by LITTLE (1963). Is this species a choristid in process of losing triaenes or an ex-monaxonid in process of becoming a choristid?

c. Various pseudokeratose monaxonids and the sclerosponge *Astrosclera* LISTER can occur in forms with or without spicules. Are they in process of losing or acquiring them?

d. The sclerosponge *Merlia normani* KIRKPATRICK can occur in forms with or without a calcareous basal skeleton. Is it a monaxonid in process of becoming a sclerosponge, or a sclerosponge becoming a monaxonid?

e. LÉVI's (1957b) concept of a subclass Ceractinomorpha was based on the presence of an asconoid larva in one of two sibling species of *Halisarca* DUJARDIN, this being assumed to be more primitive than a normal secant rhagon seen in the other. But what evidence is there that the asconoid form is not simplified rather than primitive?

f. The simplicity of such genera as *Oscarella* and *Halisarca* has led to their being seen widely as primitive; but is their simplicity a retained primitive condition or due to paedomorphic simplification?

g. In some choristids, long-shafted triaenes arise from monaxons in ontogeny, through the cladi being added at one end of an initially monaxial shaft. Does their ontogeny recapitulate phylogeny or have cenogenetic delay in formation of the cladi?

In none of these examples can the question be answered except on the basis of inference.

Different kinds of comparative evidence can also point to opposite conclusions. Most notably, LÉVI (1957b) pictured the initial evolution of his Ceractinomorpha as proceeding from askeletose *Haliscara*-like sponges through the keratose dendroceratids to dictyoceratids and, thus, in the direction of increasing morphological complexity; but the only oviparous forms among these sponges are the dictyoceratid Verongiidae, all the others including *Halisarca* having incubated parenchymellae. Assuming that oviparous sponges are unlikely to be derived from viviparous ones, embryology then points to the simplicity of *Halisarca* being secondary and not primitive. This problem cannot be solved by removing the verongiids, as suggested by BERGQUIST (1978), unless dictyoceratids have evolved from two different sources.

In any case, no modern species can have any direct bearing on the origins of major clades in demosponge phylogeny. All are phylogenetic end forms that may retain clues to their ancestry but are living long after all major divergences must be judged to have occurred. We do not know the dates of these divergences; but chela microscleres have the Desmacidontida as existing in the Late Cretaceous, for example, and sterrasters have the most specialized Ancorinida (the Geodiidae) as present by the Late Jurassic. Further, if reticulate skeletal architecture is trusted as evidence of affinity, a ceractinomorph stock must have existed by the Cambrian. Use of modern forms as keys to phylogeny, hence, needs very cautious treatment.

Moreover, if any pair of modern orders is thought to have evidence of common origin, they must still have had independent histories since divergence occurred, even if one is thought to retain primitive characters. For instance, the living plakinids may represent the type of sponges from which choristids with large megascleres were evolved, as SCHULZE (1887a) and DENDY (e.g., 1921) thought; but, if so, they have had a separate history since at least Ordovician times. Finally, it has to be realized that living forms may give a distorted picture of the overall radiation of nonlithistids as it would be seen if past faunas were known as well as modern ones. It has long been known, for instance, that modern lithistids give only a glimpse of even the Cretaceous diversity of these sponges; and there is an emerging possibility (VACELET, 1981) that monaxonid groups with no obvious evolutionary precursors may have arisen from sclerosponges by loss of the calcareous skeleton.

The extant nonlithistid fauna is, thus, also defective as a basis for assessing phylogeny, despite the fact that most speculations by zoologists are based on it. It can, of course, be hoped that cladistic analysis of biochemical data will provide clearer answers when enough forms have been studied; but even this method could be misleading. Most vertebrate specialists, for instance, do not see cladistics as proving a common origin for birds and mammals but only that extensive biochemical resemblances can arise by convergence. In the instance of birds and mammals, the fossil record is good enough to confirm their separate origins, but nonlithistids have no comparable record against which biochemical results can be checked.

In consequence, reliance still has to be placed mainly on comparative methods and on subjective assessment of which of any two alternative hypotheses is more probably correct. For example, *Merlia normani* could be in the process of either losing or gaining a calcareous accessory skeleton; but since such a complex structure, which resembles a cerioid tabulate skeleton with centrally perforated tabulae, seems an unlikely product of a single *de novo* mutation, a process of loss seems more likely. As another instance, choristids whose microscleres include euasters, streptoscleres, or both are least distinct in form with only calthrops as megascleres (pachastrellids) and most distinct in those with only long-shafted triaenes and no calthrops (theneids and geodiids). If divergence of forms with euasters and streptoscleres, respectively, from a single source is then thought more likely than convergence to pachastrellids from two sources, the direction of spicular phylogeny implied is from calthrops to triaene and not from triaene to calthrops. Furthermore, if that is correct, the development of some triaenes from monaxons in ontogeny must be cenogenetic and not reflect their phylogeny. Such judgments must also be weighted in terms of the quantity of evidence available. For these choristids, there are enough modern species available for comparative study for the conclusions just stated to be rated as probably correct. While the evidence from *M. normani* does point to loss of the calcareous skeleton, however, it does not demonstrate that all monaxonids to which sclerosponges have affinities have arisen in this manner.

HISTORICAL BACKGROUND

This section does not attempt to cover fully all the relevant literature, but as a background to the interpretation presented below outlines main lines of thought that some authors have followed.

First, in the late nineteenth and early twentieth centuries, zoological speculations on lineages were based mainly on the idea that all demosponge spicules are derived from the regular tetraxon or calthrops. This view first clearly emerged in work by SCHULZE (1880, 1887a), who saw intergradations in spicules of *Plakina* SCHULZE as showing that diactines of that genus arose from calthrops. In this and similar forms, intermediates are apparently reduced by one or two rays occurring as rudiments only, and no triaenes are present. This led SCHULZE to postulate the origin of monaxonids from choristids (his order Tetraxonia) and that of keratose sponges from monaxonids (Fig. 38). He explained the tetraxial form of the calthrops as functionally adapted to supporting tightly packed, globular, flagellated chambers arranged in a tetrahedral manner (Fig. 39). This implies that the calthrops arose as a choanosomal spicule and, hence, that triaenes are derivatives adapted to supporting the ectosome.

SOLLAS (1888), in contrast, thought that tetraxons could arise from monaxons in phylogeny, as some triaenes do in ontogeny. While following this view in interpreting spicular phylogeny, he was unsure of its validity, however, and took a different view in interpreting demosponge phylogeny. After noting his treatment of the spicules as hypothetical, he continued: ". . . there is a good deal to be said for an opposite hypothesis which would derive the triaene from the microcalthrops . . . indeed, the simplicity which at once follows the adoption of this view is so great that nothing but the stubbornness of the ontological data prevents me from adopting it" (1888, p. lxxi–lxxii). In view of this, he suggested two alternative pictures of spicular relationships, with

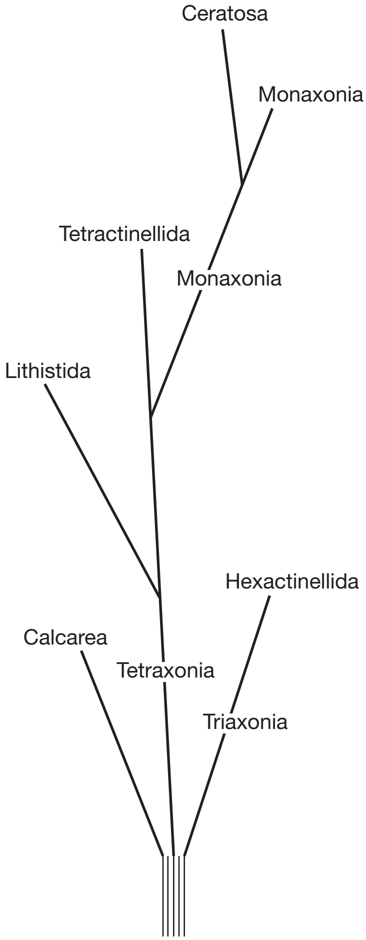

FIG. 38. Schulze's view of sponge phylogeny, with regular tetraxons assumed to be the basic type of demosponge spicule (adapted from Schulze, 1887b).

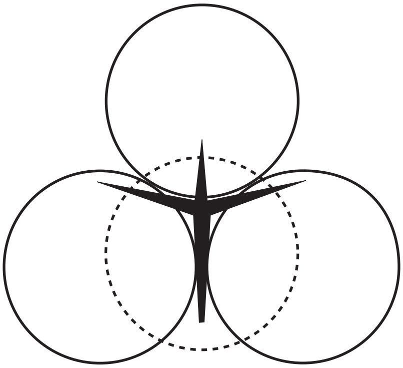

FIG. 39. Schulze's concept of the regular tetraxon as evolved to fit between closely packed, globular, flagellated chambers (adapted from Schulze, 1887b).

phylogeny proceeding in opposite directions (Fig. 40); and he also saw monaxial desmas as derived from tetraxial prototypes, despite the evidence from triaenes. Thus, while SOLLAS was influenced by the then general idea that ontogeny recapitulates phylogeny, he did not apply it rigidly and recognized contrary evidence.

SOLLAS's (1888) taxonomic groupings are more important, as having formed the basis of concepts developed by DENDY (1905, 1921, 1924b) and HENTSCHEL (1909), as well as SOLLAS's view on phylogeny. SOLLAS divided choristids as follows.

1. Microsclerophora, for microspiculate genera.
2. Astrophora, for forms with megascleres and astrose microscleres (euasters or streptoscleres).
3. Sigmatophora, with megascleres and sigmaspires but never astrose microscleres.

The Astrophora were divided into a) Streptastrosa, with streptoscleres (streptasters of SOLLAS); b) Euastrosa, with euasters not including sterrasters; and c) Sterrastrosa, with sterrasters. In addition:

4. A few monaxonids (e.g., *Asteropus* SOLLAS), called Epipolasidae, were regarded as Euastrosa in which tetraxons (triaenes) had been lost.
5. Most other monaxonids were divided into Spintharopora and Meniscophora, distinguished by having astrose and sigmatose microscleres respectively.

A few others with no microscleres were placed in a further group Asemophora.

Much in contrast to his treatment of spicular morphology, SOLLAS (1888, p. clx) based his two main pictures of demosponge phylogeny (Fig. 41) on the view that the triaene is derived from a calthrops or microcalthrops. The two schemes differ only in the pacing of monaxonids with sigmatose microscleres (Meniscophora); and he also thought that these might have been derived from both the sources suggested. The only scheme he could suggest to allow triaenes to originate from monaxons required descent from primitive sponges with only sigmaspires (Fig. 42); and he recognized this picture as improbable because of its wide separation of the Microsclerophora and Astrophora. His assessment of demosponge phylogeny, thus, did not follow the pattern of his treatment of the spicules, as one might suppose from reading it.

DENDY (1905, 1921) followed SCHULZE (1880, 1887b) in regarding tetraxons as central to demosponge spiculation, but saw only a few keratose sponges (pseudoceratosa, DENDY) as derived from monaxonids. Besides evidence relied on by SCHULZE, he emphasized meristic variation in the number of spicular rays, occurring especially in *Dercitopsis* DENDY, as a key to spicular phylogeny. This pattern (a 2, 3, 4, 5, 6 . . . sequence) is sometimes repeated in variants of a megascleric calthrops and can explain the origin of polyactinal euasters. On this basis, SOLLAS's Microsclerophora, renamed Homosclerophora, were interpreted as primitive demosponges with spicules not differentiated into megascleres and microscleres; while his Astrophora and Sigmatophora were regarded as two derived stocks with megascleres, distinguished by different types of microscleres. In addition, all monaxonids, grouped as Astromonaxonellida (=Spintharophora SOLLAS) and Sigmatomonaxonellida (=Meniscophora + Asemophora, SOLLAS), were regarded as

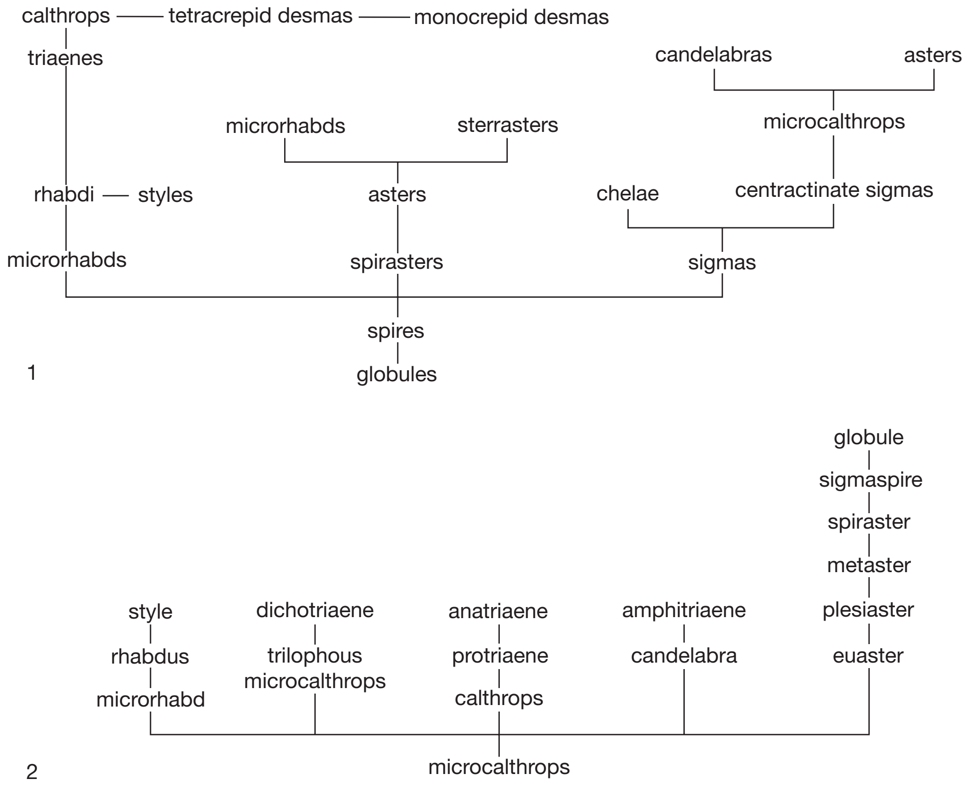

FIG. 40. Sollas's alternative interpretations of spicular phylogeny in demosponges, *1,* taking spheres as a starting point, *2,* and with microcalthrops; there are variants of modern sponges that have only microcalthrops and variants but none with only spheres (globules) (adapted from Sollas, 1888).

epipolasids, derived respectively from Astrophora and Sigmatophora (Fig. 43). DENDY thus differed radically from SOLLAS (Fig. 41), who regarded some or all monaxonids as derived from microspiculate sponges.

This picture of phylogeny led HENTSCHEL (1909) to place members of the two supposed main stocks into single taxa, named Astrotetraxonida and Sigmatotetraxonida. DENDY (1916, 1922) adopted this practice but moved forms with spinispira microscleres to the latter group on the grounds that their microscleres were related to sigmas and later (1924a) moved choristids with streptoscleres to a third group named Streptosclerophora. Figure 44 shows the pattern of skeletal evolution implied by this classification.

Reviewing the work of these authors, one may especially note SOLLAS's (1888) treatment as ambivalent and partly contradictory. Having written much of his test on the basis that ontogeny in triaenes is the key to spicular phylogeny, he first expressed doubts of this idea and then abandoned it in favor of seeing microspiculate sponges as ancestral to all forms with megascleres (Fig. 41). In these schemes, he is also to be noted as having regarded some or all monaxonids as derived directly from microspiculate sponges. DENDY, in contrast, was notable for treating all monaxonids as epipolasid derivatives of choristids with megascleres and for uncritical treatment of all diactinal (sigmatose) microscleres as the forms he took as diagnostic have had not less than four separate origins. Reaction against his views has also led

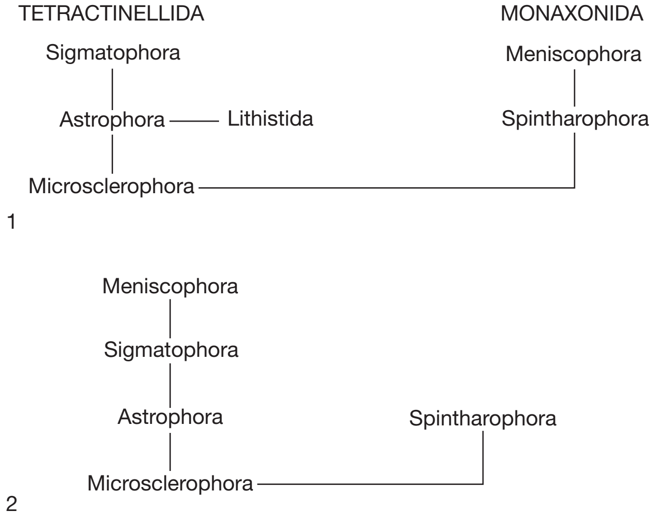

Fig. 41. Sollas's final preferred view of demosponge phylogeny, taking triaenes as derived from calthrops and not monaxons and some or all monaxonids as derived from microspiculate sponges (adapted from Sollas, 1888).

some later writers (e.g., de Laubenfels, 1936; Bergquist, 1978) to abandon the use of microscleres in taxonomy.

Burton (e.g., 1932) followed essentially Dendy, apart from changing names of taxa; but most later writers have used other methods. Hentschel (1923–1924) himself switched to a variant of Vosmaer's (1887) classification, removing most of the sigmatose monaxonids to Vosmaer's Cornacuspongida; and this arrangement was followed by Rezvoi, Zhuravleva, and Koltun (1962) in the *Osnovy Paleontologii.* The author most followed by later writers, however, is Topsent (e.g., 1892, 1904, 1928b), who followed Sollas (1888) in grouping choristids and lithistids as Tetractinellida but placed monaxonids into a subclass Monaxonellida with orders Hadromerina, Halichondrina, Poecilosclerina, and Haplosclerina based on various features of the skeleton. These taxa, with their contents reshuffled, were adopted by de Laubenfels (1936), who added a further monaxonid order Epipolasida and treated choristids as Choristida or Carnosa, based on the presence or absence of long-shafted triaenes. These changes were based on the idea that megascleres are more important than microscleres in taxonomy; and his treatment of choristids divides members of Sollas's Streptastrosa and Euastrosa between two orders. Regarding phylogeny, he noted various individual possibilities, but regarded most of them as unsubstantiated. The lithistids were seen as polyphyletic, as earlier by Schrammen (1910), and referred to various orders. The classifications of Lévi (1973) and Bergquist (1978) are nearer to Topsent's, with an order Axinellida added and with subclasses based on Lévi's picture of phylogeny (see below).

After Dendy's time, phylogenetic speculation stagnated until Lévi (1957b) introduced new concepts based on embryological evidence (Fig. 45). After noting that various past authors had seen the Demospongea as comprising two main assemblages (e.g., Vosmaer, 1887: Spiculispongiae and Cornacuspongiae), Lévi cited embryology as implying their separate descent from a very early stage of phylogeny. He began from the askeletose *Oscarella* and *Halisarca,* noting incubated larvae of different types. Those of *Oscarella* are hollow amphiblastulae, as in the microspiculate choristid *Plakina;* but those of *Halisarca* and all other forms whose larvae are known are solid parenchymellae. Further, those of Vosmaer's Cornacuspongiae

(=Meniscophora Sollas plus the keratose sponges) but no other forms were also incubated; and, while the rhagon of *H. dujardina* JOHNSON was asconoid, that of its sibling *H. metschnikovi* LÉVI was normally secant and like rhagons of keratose sponges. Oviparity, in contrast, was the rule in other forms whose reproduction was known. On this basis, he proposed subclasses Ceractinomorpha for *Halisarca* and conacuspongids and Tetractinomorpha for all other forms. In the former (Fig. 46, left), successive stages in evolution were represented by halisarcids, dendroceratids, dictyoceratids, and the spiculate orders. The Tetractinomorpha were divisible into three groups: a) true tetractinellids (=lithistids plus choristids with megascleres), with reproduction unknown; b) the Homosclerophora and *Oscarella,* with incubated amphiblastulae; and c) oviparous monaxonids grouped as Clavaxinellida (=Spintharophora, SOLLAS). In his figure (Fig. 46, right), the Homosclerophora appear as a central stock; but he expressed doubts of their having this status, and later (LÉVI, 1973) removed them to a separate subclass. The Clavaxinellida of this system revised SOLLAS's (1888) Spintharophora, which had the same contents (spirastrellids, axinellids). An incubated choristid embryo was figured by SOLLAS (1888, pl. 40,*5*), but this does not affect the main argument.

This classification has been widely accepted in zoology but still involves several problems.

1. The two *Halisarca* siblings are likely to be products of recent speciation whose divergence can have no direct bearing on that of the two main subclasses. Judged from evidence from fossils, this divergence was probably at least early Paleozoic and while there are Cambrian monaxonids that could be Ceractinomorpha, there is no way of telling whether these were viviparous or oviparous.

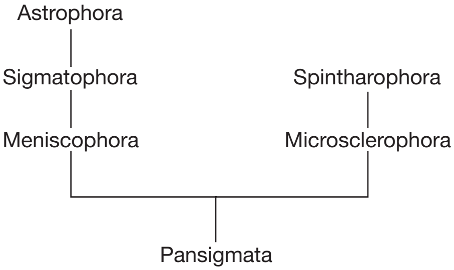

FIG. 42. Sollas's alternative to the scheme shown in Figure 41, deriving all spiculate forms from hypothetical sponges with sigmaspires only. This phylogeny was thought improbable because of wide separation of the Astrophora and Microsclerophora (adapted from Sollas, 1888).

2. The argument assumes anatomical progression from simple to complex and does not consider possible regressive evolution, for example, from dictyoceratids to halisarcids. Furthermore, while *Oscarella* and *Halisarca* appear primitive due to having simple soft parts as adults, they are less primitive than oviparous sponges in being viviparous. This could be due to their being regressive forms.

3. Although it is conventional to assume that an ascon is more primitive than a sycon, there is no objective evidence that an ascon cannot arise from a sycon. Furthermore, all that the *Halisarca* siblings show objectively is that embryological characters can be less stable than adult characters in phylogeny, even at the species level.

4. LÉVI's (1957b, 1973) picture of phylogeny requires the spicules of his subclasses to

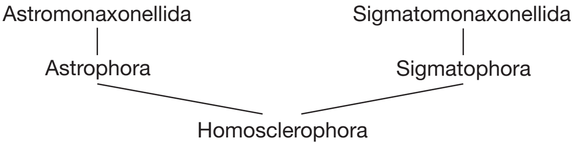

FIG. 43. Dendy's interpretation of phylogeny in spiculate demosponges, as rendered by Hentschel, 1909 (adapted from Dendy, 1905).

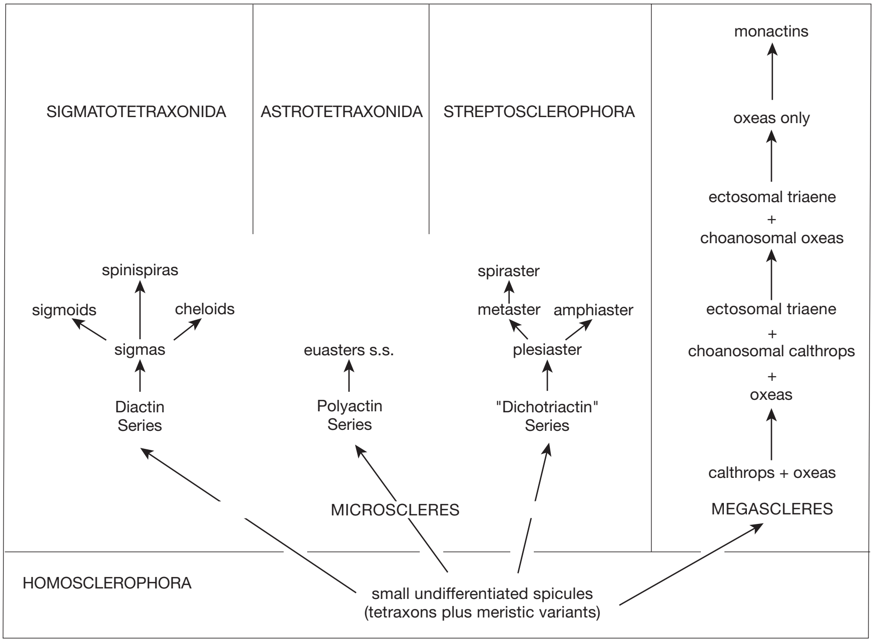

FIG. 44. Skeletal evolution in spiculate Demospongea as envisaged by Dendy in his final works (1921, 1922) (adapted from Reid, 1970; courtesy of Zoological Society of London).

have evolved independently. There is nothing in the character of the spicules themselves to suggest this, and conversion into desmas follows the same pattern in both groups.

5. The dictyoceratid verongiids are now known to be oviparous. This does not fit LÉVI's picture, unless dictyoceratids have evolved from two different sources.

6. There is no derived character by which a clade Tetractinomorpha can be defined, oviparity being a primitive character.

For reasons 1 through 4 above, REID (1968a, 1970) did not follow LÉVI in attempting a picture of phylogeny.

In the first of these papers (REID, 1968a), a critical review of the microscleres led to the conclusion that DENDY's (1921, 1924b) views were correct in some instances but mistaken in others. He was right in distinguishing his dichotriact series of microscleres (DENDY, 1924b), here called streptoscleres, from other so-called streptasters and in seeing various euaster-like spicules as

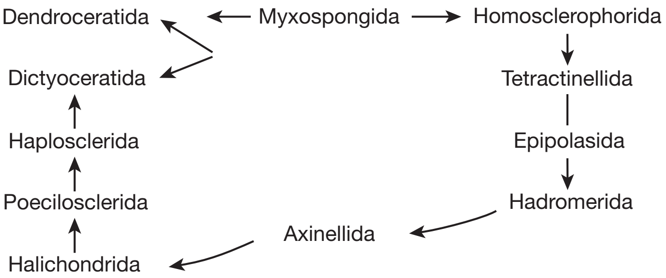

FIG. 45. Lévi's interpretation of how demosponge evolution had been viewed to that date (adapted from Lévi, 1957b).

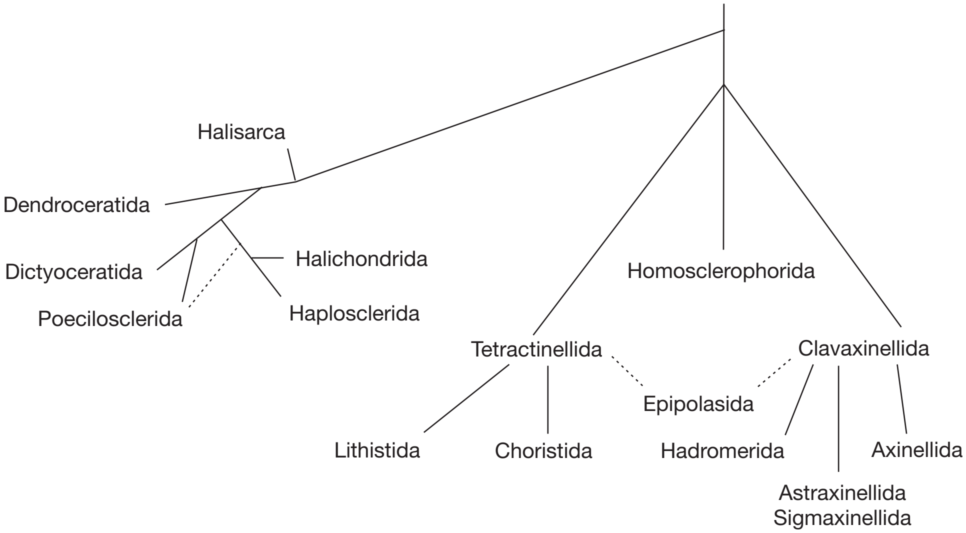

FIG. 46. Lévi's revised interpretation of demosponge phylogeny, based on embryological criteria (adapted from Lévi, 1957b).

pseudoasters; but he was badly mistaken in his concept of diactinal of sigmatose microscleres, which includes three major types with different origins (sigmaspires, spinispiras, sigmatoscleres) as well as various minor ones. Microspiculate sponges were thought the most likely prototypes of groups with megascleres, as by SOLLAS (cf. Fig. 41), with no assertion as to whether tetraxons or monaxons were primitive. DENDY's views were thought applicable to the plakinids and choristids with megascleres, in which microscleres were streptoscleres or polyactinal euasters; but choristids with sigmaspires, the Hadromerina of TOPSENT, and ceractinomorph group had no evident relationship to plakinids or astrophorous choristids. Forms with sigmaspires and the Hadromerina (Spirastrellida, REID) might be related to the euaster-bearing choristids (Ancorinida, REID); but this could not be asserted, and they could have arisen as primary monaxonids. The latter was thought to be probable for the spiculate ceractinomorphs, and keratose forms of halisarcids were thought to derive from them.

Biochemical studies by BERGQUIST and HOGG (1969) and BERGQUIST and HARTMAN (1969) on free amino acids showed further problems. These authors found a general homogeneity in the Ceractinomorpha, but not in the Tetractinomorpha, which fell into five biochemical groups and would be seen better as five separate orders (BERGQUIST & HARTMAN, 1969, p. 266). They also found no special affinity between spirastrellids and axinellids, grouped by LÉVI (1973) as Clavaxinellida and thought that even the Axinellida could be composite. In other findings, the monaxonid Epipolasida of DE LAUBENFELS (1936) were thought to belong partly with the choristids and partly with the monaxonid spirastrellids (Hadromerina in their terms). New placings of various genera were suggested, and the dictyoceratid verongiids were noted as differing from other ceractinomorphs. In a later textbook study, BERGQUIST (1978) used the term Tetractinomorpha taxonomically for a subclass but noted it as certainly polyphyletic. Her picture of ceractinomorph evolution is similar to REID's (1968a), with keratose forms and halisarcids derived from spiculate sponges. Most ceractinomorphs were seen as products of a relatively recent radiation, because of biochemical homogeneity, with verongiids

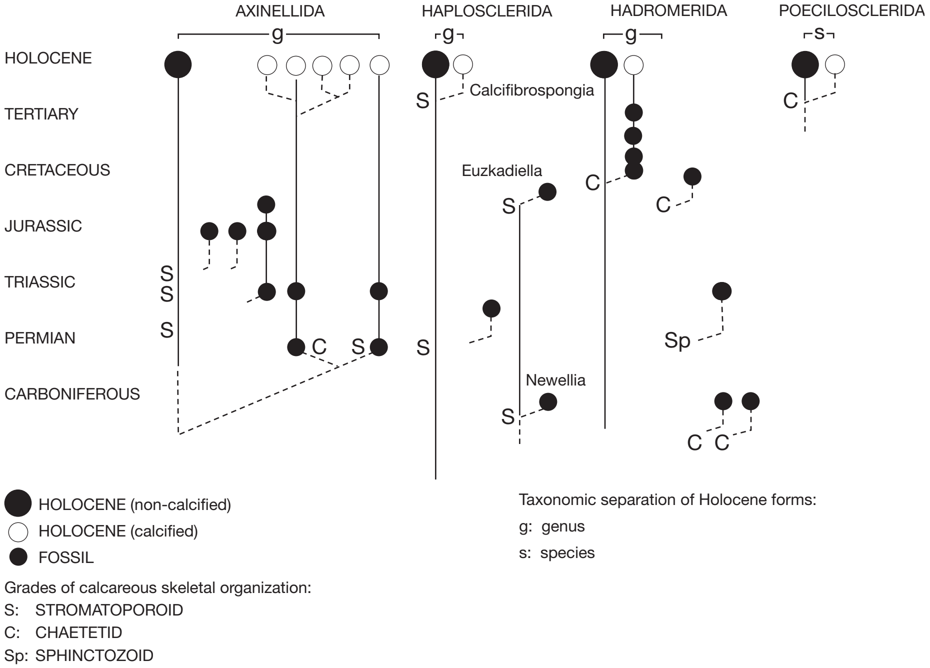

FIG. 47. Affiliation of modern and fossil sclerosponges as of 1990; for Haplosclerida, Hadromerida, Poecilosclerida, read Chalinida, Spirastrellida, and Desmacidontida (adapted from Wood, Reitner, & West, 1989).

an ancient stock with a long independent history. REID's parallel views were not mentioned, but are relevant in showing that critical study of the spicules and of microscleres especially had already led to similar suggestions. If RIGBY (1986a) is right in his placing of *Vauxia,* verongiids have existed since at least the Middle Cambrian.

In the same general period, two papers by FINKS (1967a, 1971b) revived SOLLAS's (1888) original idea that triaenes are derived from monaxons, in studies based on an Ordovician monaxonid and a Permian lithistid (*Saccospongia* ULRICH, *Scheiella* FINKS). FINKS has discussed this elsewhere in this volume (p. 77), but brief comments seem permissible here. First, *Saccospongia* could be an axinellid, an ectyonine ceractinomorph, or an unrelated convergent form with no modern relatives. Second, *Scheiella,* supposedly ancestral to dicranoclad lithistids, would need to have had monaxial desmas; but those of the related *Scheiia pumili* (HINDE), found by the hundreds in the Irish Glencar Limestone, appear to be entirely anaxial. Third, FINKS relied on no choristids being known before the Early Carboniferous; but even at that date, the diversity of their spicules (microcalthrops to long-shafted trachelotriaenes; REID, 1970) implied a much longer history, and the Ordovician record leaves only the Cambrian monaxonids as significantly older. If these are ceractinomorphs, moreover, they are not likely choristid ancestors.

The last major idea to emerge is that some or many monaxonids could have been derived from sclerosponges in phylogeny by loss of the calcareous skeleton (VACELET, 1979, 1981). This is clearly possible. The soft parts, spicules, and reproduction of known living examples are entirely like those of normal monaxonids; and *Merlia* KIRKPATRICK is known to occur in both sclerosponge and monaxonid forms (Vacelet, 1980). The modern forms are also clearly polyphyletic, having affinities to spirastrellids (hadromerids), axinellids, chalinids (haplosclerids), and desmacidontids (poecilosclerids) (Vacelet, 1985); and apparently allied fossils are known in each instance (Fig. 47), some dating as far back as Carboniferous. These are also all groups with no evident relationship to choristids. But, while related modern monaxonids could be descended from such sclerosponges, the latter could be calcified derivatives of uncalcified forms, which have not been preserved and have no modern descendants. A final verdict on these ideas is not possible at present.

Last, a final thread in demosponge phylogeny was identified by Vacelet's (1977b) discovery of a living sphinctozoid with demosponge soft parts. This line may go back to the Cambrian, where the oldest sphinctozoids are known; but their characteristic morphology is also known from Calcarea (*Sphaerocoelia, Tremacystia*), and which class most belong to is unknown.

CONCLUSIONS

In review of these various ideas, biochemistry, embryology, and microscleres are all seen as having useful data to contribute. Microscleres need critical assessment. Only streptoscleres and cheloids appear to be truly diagnostic and some (e.g., euasters) have parallel developments in different groups. Their total rejection by some authors has been as uncritical as Dendy's excessive trust in them, and some have not been understood. For instance, those of *Placospongia* Gray, called sterrasters by Bergquist (1978), make this type seem to occur in two different orders (Ancorinida, Spirastrellida). The spicules are sterrospirae, however, as stated by Dendy (1921), and indicate placing this sponge with the spirastrellids. Megascleres and skeletal architecture are unhelpful due to parallel developments in different groups, but restriction of typical dichotriaenes and large calthrops to Pachastrellida and Ancorinida fits with microscleric evidence of relationship.

Herein it is argued that only modern forms are likely to yield useful data despite their limitations and that no trust should be placed in stratigraphic sequence in fossils. There are various fossils that might be early members of modern groups, with a bearing on phylogeny; but they also might not be, and could appear in a fortuitous order. The only fossils that seem likely to be genuinely useful are the sclerosponges, but what they will yield remains to be seen.

With this background, the following suggestions are offered.

1. Judged from spicular evidence, the most likely prototypes of spiculate demosponges are oviparous microspiculate sponges, with spicules varying meristically in some but all monaxial in others. Choristids and monaxonids with megascleres should then represent various lines of descent from different parts of this spectrum, with some monaxonids never having had tetraxial spicules, as either megascleres or microscleres.
2. The Plakinida (Homosclerophora) can be seen as retaining a primitive condition in being microspiculate; but some of their features are not primitive (amphiblastula larvae, lophose calthrops), and they must have been separate from other choristids since at least the Ordovician.
3. The Pachastrellida and Ancorinida are probably related groups descended from sponges with calthrops megascleres and simple euasters, from which they have since evolved streptoscleres and polyactinal euasters, respectively.
4. The Craniellida, with sigmaspire microscleres, show no sign of relationship to other choristids and may have originated separately. In this group, the origin of triaenes from calthrops cannot be asserted since the latter are unknown.
5. The Spirastrellida have probably evolved independently of choristids from an early form with monaxon megascleres and simple euasters. In one stock leading to tethyids, polyactinal euasters were evolved;

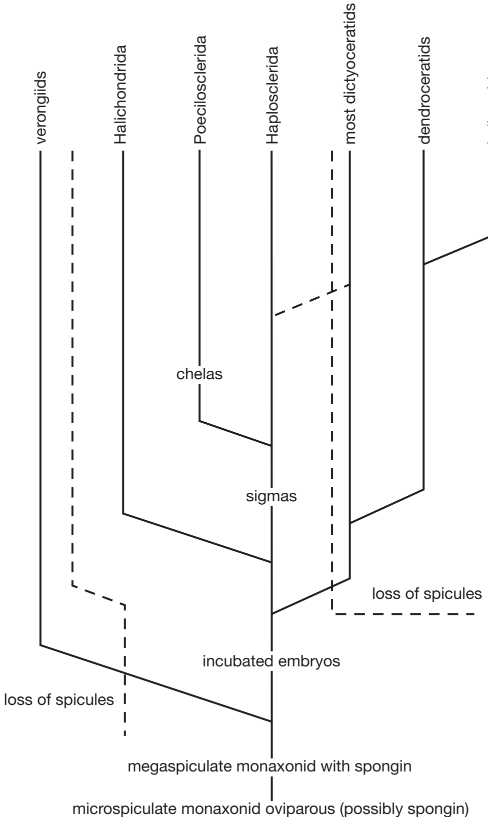

FIG. 48. Alternative interpretation of ceractinomorph evolution, using Topsent's nomenclature (1904, 1928b) (new).

but in the other, such euasters were never developed, and spinispiras arose from the megascleres.

6. The Axinellida are a second group of primary monaxonids, in some of which euasters or sigmas have evolved independently of those seen in other groups. This group may also be polyphyletic.

7. The ceratinomorph orders form a genuine clade and, except for verongiids, are likely to represent a later radiation than other groups. Their phylogeny could have followed the pattern suggested by LÉVI (1973) or some partly or wholly different one (e.g., Fig. 48).

8. The sclerosponges are polyphyletic demosponges related to the Spirastrellida, Axinellida, Chalinda, and Desmacidontida. Some fossil chaetetids and stromatoporoids are members of these taxa, but their relationships to modern forms are uncertain.

9. Some, many, or most fossil sphinctozoids may be demosponges.

Last, it might be worth noting that all groups of monaxonids include sponges with monactines, which are typically arranged with points distad, whereas, monactines are rare in choristids and have points proximad when seen. One wonders whether this could be significant.