GENERAL FEATURES OF THE PORIFERA

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INTRODUCTION

Sponges are simple, multicellular, sedentary, marine, and nonmarine aquatic animals that feed and respire by drawing water through their bodies. Circulating water is propelled by the uncoordinated flagella of cells termed choanocytes, unknown in true metazoans and resembling individual choanoflagellates. An internal skeleton is usual and typically consists of calcareous or siliceous **spicules;** but siliceous spicules may be accompanied or replaced by an organic skeletal material (**spongin**). A few modern sponges have no skeleton.

Modern and most fossil sponges generally have been referred to four or five classes: Calcarea BOWERBANK, Demospongea SOLLAS, Hexactinellida SCHMIDT, Heteractinida HINDE, and Sclerospongia HARTMAN & GOREAU. The Calcarea are sponges with a skeleton of calcareous spicules. The Demospongea have soft parts like those of the Calcarea, but their skeletons consist of siliceous spicules, of siliceous spicules and spongin together, or of spongin fibers only; or sometimes a skeleton may be absent. The Hexactinellida also have siliceous spicules but are distinguished from the Demospongea by the form of the spicules, by absence of spongin, and by histological differences. The recently rediscovered Sclerospongia have been considered by some to represent an additional class that includes modern forms and fossils, such as the stromatoporoids and chaetetids. Other workers include these sponges in the Demospongea. Modern sclerosponges have a skeleton of siliceous spicules, spongin, and basal massive calcareous structures. A small extinct group with distinctively shaped spicules of uncertain but probable calcareous original composition is placed herein into a separate class, the Heteractinida HINDE. Its strati-graphic range is Lower Cambrian to Lower Permian.

ANATOMY AND HISTOLOGY

The general organization of sponges is centered on their water circulation. There are many variations in detail, but all types can be explained as having some modification of a simple basic pattern. This basic sponge has a simple cup-shaped or tubular body attached to a substratum by a closed base but is open at the top (Fig. 1). The part of the body, termed the **lateral wall,** that bounds the central cavity above the fixed base is pierced by many small pores. The central cavity, called the **paragaster** or **spongocoel,** is lined with **choanocytes;** their beating flagella cause water to be drawn in through the small lateral pores and expelled through the large open top, the osculum. Food particles are ingested by choanocytes as the water passes through; digestion is not extracellular, and respiration occurs also.

This very simple pattern is not known as an adult condition in modern sponges, although the simplest Calcarea form branching tubes with simple porous walls and develop from an unbranched tubular larva, the **olynthus.** In most Calcarea and all Demospongea and Hexactinellida, choanocytes do not line the paragastral surface but are restricted to lateral **flagellated chambers.** These are sometimes simply free diverticula of the lateral wall but are usually located within it and not visible externally. Water circulation is more complex, correspondingly, with two main patterns (see below). There are also two main types of histological organization: one in Calcarea and Demospongea, the other in Hexactinellida.

In Calcarea and Demospongea, the lateral wall (Fig. 2) has a gelatinous internal groundmass or **mesenchyme,** which is
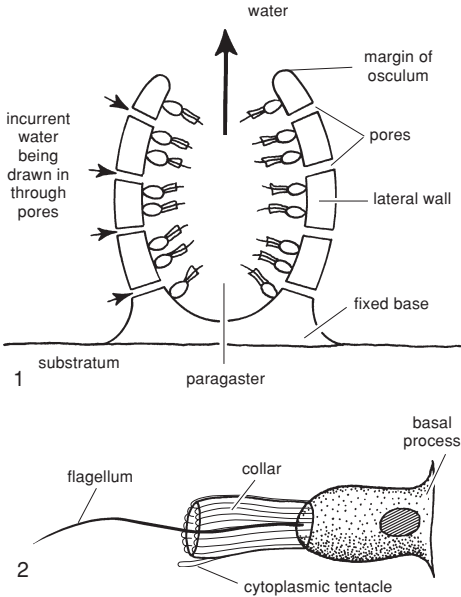
FIG. 1. Basic morphology and water circulation of sponges; *1,* longitudinal section through a simple asconoid sponge to show basic morphological features and water circulation; the section does not correspond with the adult state of any modern sponge, although represented briefly by the olynthus larvae of some Calcarea, and initially asconoid rhagons of a few Demospongea; *2,* single choanocyte, with collar made of cytoplasmic tentacles, and long flagellum (new).

typically coated by flattened dermal cells or **pinacocytes** where choanocytes are absent. The mesenchyme contains cells of various types, some of which are able to move within it, such as the generalized **archaeocytes.** It also includes the cells that secrete the spicules (**scleroblasts** or **sclerocytes**) or spongin (**spongioblasts** or **spongocytes**).

The Calcarea have three grades of circulatory organization (Fig. 3). In ascons, the adult body forms branching, thin-walled tubes, with choanocytes on the paragastral surface. The walls are perforated by intracellular pores that pierce cells termed **porocytes.** Circulating water enters the paragastral cavity directly by way of the pores in this simple condition, which is termed **asconoid** (Fig. 3.1). In **sycons,** choanocytes are restricted to flagellated chambers arranged radially around an axial paragaster (Fig. 3.2). In the simplest or **sycettoid** type,

the chambers are separate, lateral diverticula of a central, paragastral tube. In **grantioid** sycons, they are internal spaces in a compact lateral wall, which appears to represent fusion of the separate chambers. Radial passages for ingress of water are left between the chambers and are called **inhalant canals** or **prosochetes;** together, they comprise a **canal system.** The condition of these sponges, in which chambers discharge to the paragaster directly, is called **syconoid.** In **leucons,** internal flagellated chambers are grouped around exhalant canals, the **apochetes,** which carry the excurrent water to the paragastral cavity, and this type of circulation is **leuconoid** (Fig. 3.3). All the known Demospongea are leucons as adults, although some develop from a larval rhagon with internal chambers arranged in the syconoid manner and no canals of either sort. In SOLLAS's (1887) pre-*Challenger* account of the Porifera, the leuconoid type of canal system was described as the rhagon type, because some of the leuconoid Demospongea develop from rhagons. But a rhagon as such (SOLLAS, 1887, 1888) is the larval form only, with chambers,
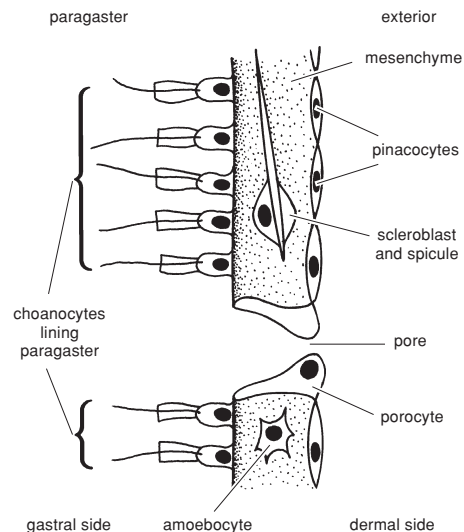

FIG. 2. Longitudinal section of lateral wall in an asconoid member of class Calcarea showing cytological and other features; choanocyte layer at left corresponds with thick lines of Figures 3–4 (new).
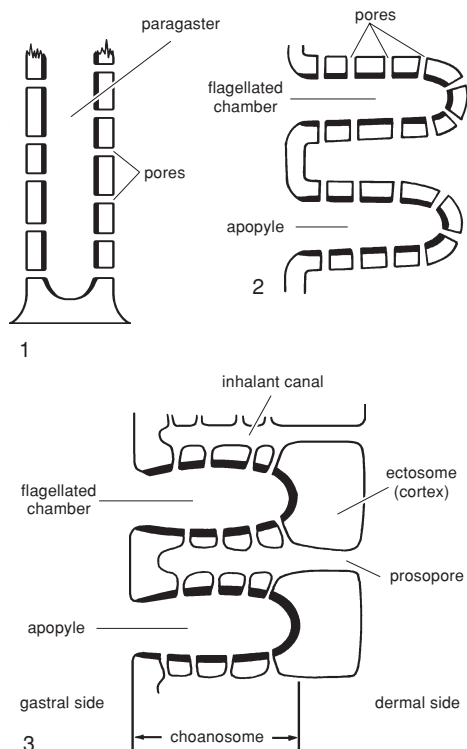
FIG. 3. Asconoid and syconoid Calcarea, in diagrammatic longitudinal sections; *thick lines* refer to choanocyte layer (Fig. 2, left side); *1,* tubular asconoid sponge; *2,* radial diverticula of a sycettoid sycon; *3,* lateral wall of a grantioid sycon, with an ectosome developed as a thick cortex (new).

but without a canal system; and other leucons do not develop from rhagons.

In most Calcarea and Demospongea with enclosed inhalant canals, the external or dermal surface of the body is formed by a compact chamberless layer, the ectosome (Fig. 4–7). The internal part containing the chambers is then called the **choanosome.** An ectosome may be either a thin, skinlike dermis or a thicker, rindlike cortex. Inhalant canals may extend through an ectosome but more commonly begin from larger subdermal spaces underlying it, which the water enters through pores or canals in the ectosome. A similar structure on the exhalant or **gastral** side of the wall is the **endosome.**

This term was proposed as the name of an ectosome-like stratum on the exhalant side

of the choanosome, with the inner trabecular network of Hexactinellida (SOLLAS, 1887) and a demosponge structure (SOLLAS, 1888) as examples. Accordingly it must not be used as equivalent to choanosome (e.g., see BURTON, 1963 for correct usage).

Larvae of Hexactinellida are much like those of some Demospongea, but the adults have no mesenchyme and no covering pinacocytes. Flattened choanocytes are connected together syncytially by lateral processes to form a **reticulate** choanocytal membrane, diverticular outgrowths of which form the flagellated chambers (Fig. 5–6). The chambers are supported from both sides by a three-dimensional network of syncytial filaments, the **trabeculae,** comprising a trabecular network. The outer (inhalant) and inner (exhalant) surfaces are formed by **dermal** and **gastral membranes** composed of trabeculae netted and flattened in the plane of the surface. Interspaces of the trabecular network are filled with water from outside, which presumably circulates through them. The spicules are formed in the trabeculae by multinucleate **scleroblast-syncytia.** The arrangement of chambers may be syconoid (Fig. 5) or leuconoid (Fig. 6), with the latter more usual. Simple examples have neither inhalant nor exhalant canals, so that water must reach and leave the chambers entirely
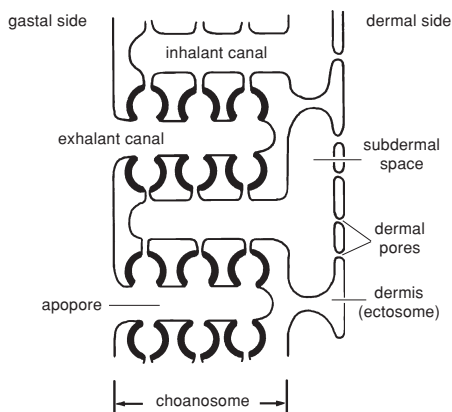

FIG. 4. Diagrammatic longitudinal section of wall of a leuconoid sponge, with ectosome developed as thin, porous dermis covering subdermal spaces (new).
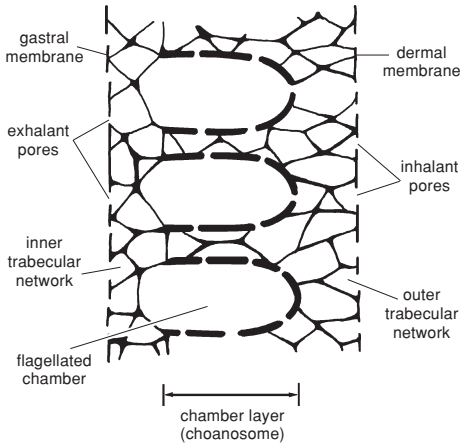
FIG. 5. Diagrammatic longitudinal section of lateral wall in Hexactinellida; choanocytal membrane (*thick lines*) forms radial flagellated chambers; in adult modern Hexactinellida this simple pattern is modified by diverticulation of chambers or folding of chamber layer (see also Fig. 6) (new).

through spaces between trabeculae; in the others, chambers are grouped around exhalant canals, and inhalant canals may also be present between them. Both types of canals are produced by special enlargement of the ordinary intratrabecular spaces and are, thus, not directly related to the similar prosochetes and apochetes of Calcarea and Demospongea. Inhalant canals begin under the dermal membrane or start from larger subdermal spaces underlying it; the **exhalant canals** end under the gastral membrane, end in larger subgastral spaces underlying it, or open through the membrane directly due to secondary fenestration. The external membranes are thus comparable morphologically to the ectosome and endosome of Calcarea and Demospongea, although different histologically.

The internal anatomy of sponges is not significantly modified by differences in **habitus** (i.e., form of the body), but leuconoid types may have modifications of the basic pattern pictured above. In the basic type of sponge body, the inhalant and exhalant (or dermal and gastral) surfaces are external and internal respectively, with the latter forming the lining of a paragastral cavity (Fig. 7.1). In

several conditions there is no paragaster. First, expansion of a basically cuplike body can produce a plate- or mushroomlike growth, with the upper surface being homologically gastral and the underside dermal. Water discharged from exhalant canals thus leaves the body directly instead of through an axial paragaster. If the openings or **apopores** of exhalant canals are prominent features of the surface they are often then called **oscula** and function as such, although not homologous with a primary osculum. In **flabellate** sponges, the body is fanlike, tonguelike, or bladelike, with opposite surfaces being dermal and gastral respectively. In other forms the paragastral cavity is suppressed so that no true gastral surface exists. Exhalant canals then open at the top of the body or at various points in the sides. In encrusting forms, water is usually discharged through numerous oscula in an otherwise inhalant upper surface (Fig. 7.2).

It is worth noting here that the term **pore** can have several meanings when applied to Porifera. Pores of the soft parts may be (1)
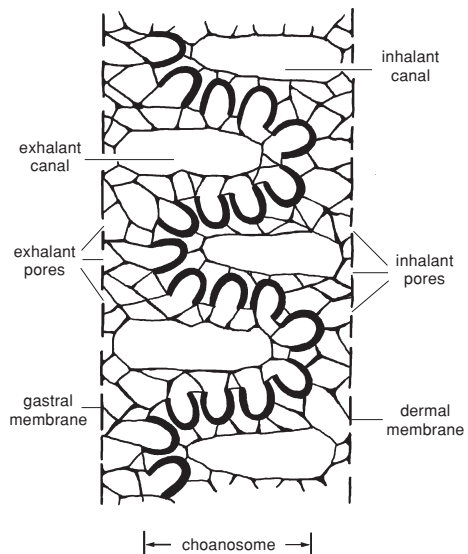

FIG. 6. Diagrammatic longitudinal section of lateral wall in Hexactinellida with chamber layer radially convoluted, and with intertrabecular inhalant and exhalant canals (new).

intracellular perforations of the walls of ascons; (2) perforations in the walls of flagellated chambers, through which water is received from inhalant canals or intertrabecular spaces; (3) external openings (**prosopores**) of inhalant canals or apertures (apopores) of exhalant canals; (4) perforations in the surface of an ectosome or endosome, not related directly to canals of the choanosome; or (5) perforations in the dermal and gastral membranes of Hexactinellida. The same name or variants may also be used for features of skeletal surfaces, in the form of special apertures, where flagellated chambers or canals have entered a skeletal framework. In other words, this term is vernacular and is used to mean any small aperture or perforation without homological implication. It is important not to confuse the different features for which it may be used.

In the first edition of *Treatise Part E* (DE LAUBENFELS, 1955), skeletal pores and canals were called by the same names as the true canals (prosochetes, apochetes) and their apertures (prosopores, apopores). There are several objections to this terminology. First, the skeletal features are not the canals of the soft parts and represent them only imperfectly. In some Hexactinellida, skeletal apopores or apochetes are related to flagellated chambers (e.g., in *Cyclostigma* SCHRAMMEN, *Aphrocallistes* GRAY) instead of to exhalant canals (i.e., apochetes). In genera with no modern species, they could represent either. A skeletal framework may have no canalization in a sponge with both prosochetes and apochetes in the soft parts. Last, many fossils have features of uncertain function. The present authors, therefore, use skeletal pore and skeletal canal as general designations and when function is unknown. Similarly the terms **ostia** and **epirhyses** are used as they were by RAUFF (1893, 1894, 1895), SCHRAMMEN (e.g., 1910, 1912), and IJIMA (1927) when such specific terms can be used.

SPICULES

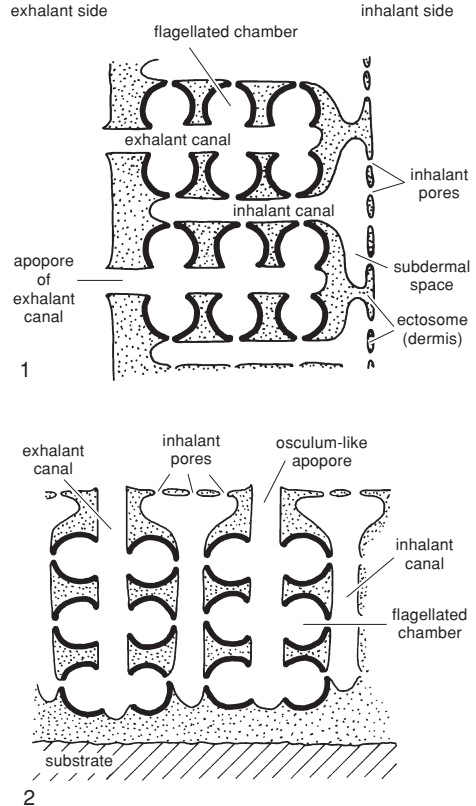Typical sponge spicules are produced by secretion of calcite or opaline silica around

FIG. 7. Diagrams of eurypylous types of canal system; *1,* sponge with separate (and opposite) inhalant and exhalant surfaces; *2,* encrusting form with inhalant pores and apopores on one surface; both examples shown with ectosome developed as a porous dermis covering subdermal spaces from which inhalant canals run inwardly; *thick lines* represent choanocytal linings of flagellated chambers; other parts *finely outlined* and *stippled;* canals, shown here diagrammatically as straight and simple, are normally branched more or less extensively in practice (new).

organic **axial filaments** and are either needle-like or pinlike with a single coring axial filament, or they are stellate bodies consisting of three or more radiating rays cored by filaments that radiate from a spicular center (Fig. 8.4, 8.5, 8.9). **Rays** formed in this manner are **actines,** and their mode of formation is actinal. In other types, initial actinal bodies are modified in various ways by **nonactinal secretion,** producing, for example, regular or irregular outgrowths without organic axes. Some spicules are formed wholly by nonactinal secretion. A raylike
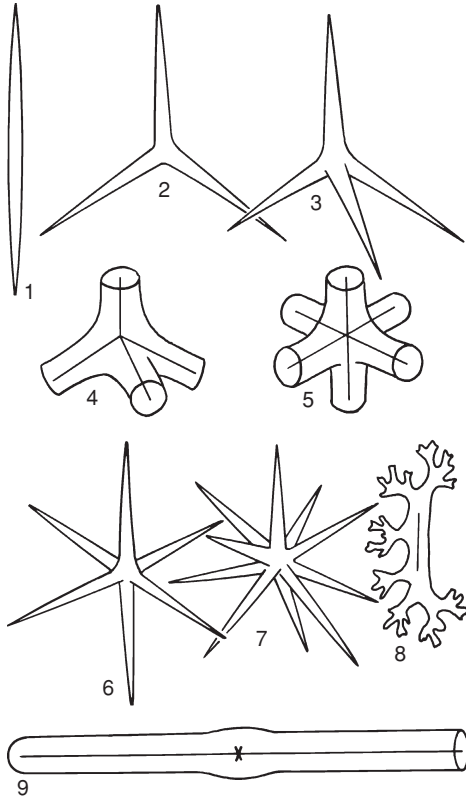
FIG. 8. Examples of sponge spicules; *1,* monaxon, classed as a diactine because both ends are pointed; *2,* triactine classed as a triod, has three rays in one plane at 120° intervals; called triaxon by some authors (not herein) but of different symmetry from hexactinal triaxon in views *5* and *6; 3,* tetraxial tetractine, with 4 rays disposed as though along tetrahedral axes; equiradiate form called a calthrops as a demosponge spicule; *4,* central part of view *3,* with 4 axial filaments (or canals) that radiate from spicular center; *5,* central part of triaxial hexactine, with central axial cross formed by 6 axial filaments, the central part of view *6; 6,* triaxial hexactine with 6 rays that follow 3 axes that intersect at right angles; triod in view *2* is not a variant of this type of spicule; *7,* polyactine, also a polyaxon; *8,* irregularly shaped spicule (desma of a lithistid demosponge), with monaxial character shown by single axial canal; *9,* central part of triaxial diactine from hexactinellid sponge (also called a rhabdodiactine), having triaxial center; 4 aborted rays represented by axial rudiments only (new).

structure without an axial filament is a **pseudoactine,** and individual outgrowths or complete spicules without organic axes are **anaxial.** Actinal calcite or silica secretion often begins while the axial filament is still growing so that this filament projects terminally from a mineral sheath. The end (or each end) is finally covered after ceasing to grow. After death, decay of an axial filament produces a hollow **axial canal,** which is often enlarged by internal solution of the surrounding mineral matter. Such canals may be open at the ends, due to secondary perforation or to growth of the spicule having been incomplete. In fossils, the canals may be lost in diagenesis. Internal solution may also produce misleading **pseudoaxial canals** in originally solid anaxial structures.

The length or diameter of spicules that occur within the body is usually between several micrometers and several centimeters, although larger spicules may occur. Much larger sizes, however, are reached by spicules that some sponges protrude from their bases to form anchoring structures, in which one ray imbedded in the body continues to grow. In the largest known example, the modern hexactinellid *Monoraphis chuni* SCHULZE is supported by a single basal needle reaching more than two meters long and a centimeter thick.

Modern nomenclature of spicules is based generally on that of the authors of the *Challenger* reports (POLÉJAEFF, 1883; RIDLEY & DENDY, 1887; SCHULZE, 1887a; SOLLAS, 1888), with additions by various later authors (e.g., RAUFF, 1893, 1894, 1895). The names used are of various types as described below.

a. Names ending -**actine** (or -act or -actin in some literature) refer usually to the number of rays. Stellate spicules are **triactines, tetractines, pentactines, hexactines,** and others, according to number of rays present, or they are simply called polyactines if the number is more than six (Fig. 8). Pinlike or needlelike spicules are called **monactines** or **diactines** according to whether they are sharp at one end only or both, assuming that this implies growth in one direction or two. Adjectives referring to the number of rays are formed similarly with the termination -actinal, for example, monactinal or hexactinal.

In some types of spicules, the number of axial filaments and the number of rays are identical; but in others, some axial filaments cease to grow shortly after inception, so that no corresponding rays are formed. The rudimentary axial filaments persist at the spicular center as **axial rudiments.** The spicule takes its name from the number of rays developed and not from the number of axial filaments (Fig. 8.9), for example as in the **octactines** that characterize some **heteractinid** sponges where axial filaments are not known.

b. Names ending -**axon** refer to the orientation of rays and axial filaments, which are pictured as following a varying number of growth axes. There are four main types.

1. **Monaxons** are spicules with a single axial filament, in which actinal growth occurs at one end only or both and thus along one axis in one or both directions (Fig. 8.1).

2. **Tetraxons** have four axial filaments arranged as though following tetrahedral axes or in some distorted form of this pattern and have four or fewer rays (Fig. 8.3).

3. **Triaxons** have axial filaments following three axes that intersect at right angles and have six or fewer rays (Fig. 8.5–8.6).

4. **Polyaxons** comprise all spicules in which rays grow in five or more unrelated directions (Fig. 8.7). **Pentiradiate** and **sexiradiate** spicules occur in the heteractinid sponges and are spicules in which five and six rays, respectively, radiate from a center and occur in a single plane.

The term **diaxon** is also used for less important spicules in which rays or axial filaments follow two axes only, which intersect or meet at an angle. This aspect of the character of spicules is expressed adjectivally with terms ending -axial, for example, **monaxial** or **tetraxial.**

The use of terms based on hypothetical growth axes is partly conventional, not literal. In the strictest sense, tetraxons and triaxons are four- and six-rayed spicules, in which the rays follow the ideal tetrahedral and rectangular patterns, but the same terms are applied to distorted variants of these types. Thus, an anchorlike variant of the regular tetraxon, with three rays bent back toward a fourth, is still called a tetraxon, and an irregular variant of a regular triaxial hexactine is similarly still a triaxon. But triaxons and tetraxons do not comprise simply any types of spicules in which growth of rays can be said to follow three or four axes. In particular, spicules with three rays in one plane at equal angles (120°) are literally triaxial, but they are not variants of the six-rayed rectangular triaxon and are called triods, not triaxons.

The status of spicules as monaxons, tetraxons, and so on is not altered by suppression of rays if the axial filaments persist or by formation of secondary anaxial outgrowths that may alter their overall form. For instance, many Hexactinellida contain needlelike spicules with the outward form of monaxons, in which a **spicular center** at some point between the two ends has a six-rayed and triaxial axial cross, with four rays represented by axial rudiments (Fig. 8.9). Such a spicule is not a monaxon but a diactinal triaxon or **rhabdodiactine.** In a group of Demospongea called **lithistids,** articulated spicules that form a skeletal framework may begin their development as obvious monaxons or anaxial corpuscles but come to resemble tetraxons or polyaxons through formation of solid, raylike outgrowths (Fig. 8.8); these spicules are **monaxial** and **anaxial,** not **tetraxial** or **polyaxial.**

Arrangement of spicules according to the number of axes has often been given first place in their classification. Herein the class of Porifera in which particular spicules occur is taken as the first consideration, because similar morphological types can have different relationships in different classes.

c. Many names of individual types of spicules are based on various aspects of their form, including resemblances to other objects. A regular tetraxon with four equal rays is called a **calthrops,** from its resemblance to a caltrop; but a tridentlike tetraxon, with one ray long and three short, is a triaene. The
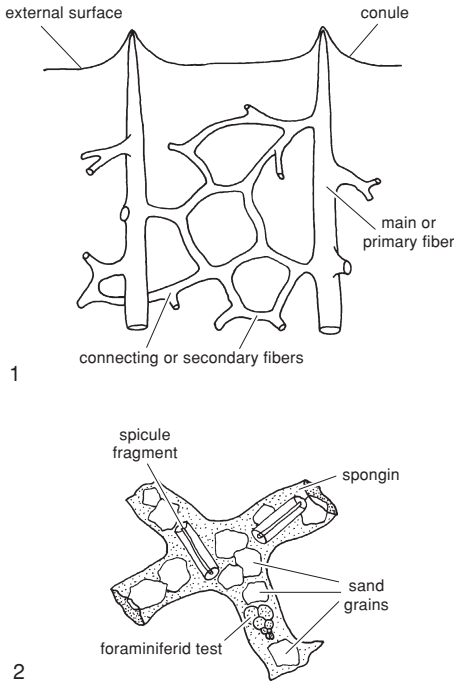
FIG. 9. Keratose skeletons of dictyoceratid type; *1,* section showing primary (main) and secondary (connecting) fibers, and conules where surface is raised by ends of primary fibers; *2,* fibers cored by foreign bodies, here shown as mainly sand grains but also includes spicule fragments and a foraminifer test; spongin *stippled* (new).

monaxon-like triaxial diactines of Hexactinellida are rhabdodiactines, in contrast to **orthodiactines** in which two rays meet at right angles. A cross-shaped tetractine is a **stauractine.** Various starlike spicules are called **asters** and given individual names ending -aster. In monaxons, nomenclature is based on the form of the ends; for instance, a monaxon is an **oxea** if both ends are sharp, a **style** if one is sharp but one blunt, and a **strongyle** if both are blunt. The form of the rays in other spicules may be shown by adding prefixes (e.g., oxy-, sharp, in oxyhexactine; **acanth-,** in **acanthostyle,** implies a spiny ornament).

d. In some instances, different names have come to be used for similar spicules of different classes. In particular, triactines and tetractines of Calcarea are often called **triradiates** and **quadriradiates** but are simi-

lar morphologically (though not ontogentically) to spicules called **triods** and **triaenes** in Demospongea. Some terminology used herein is different from that of the first edition of *Treatise Part E* (DE LAUBENFELS, 1955), for example, **triaxial** and **triaxon.** The term triaxial was introduced by SCHMIDT (1870) to distinguish from demosponge tetraxons the spicules of the Hexactinellida in which up to six rays follow three axes at right angles. This is the meaning of triaxial and triaxon in the *Challenger* volumes (SCHULZE, 1887a; SOLLAS, 1888) and in most later literature (e.g., RAUFF, 1893, 1894, 1895); but earlier VON LENDENFELD (1887) and SOLLAS (1887) used triaxon to include triods. This was an error pointed out by SOLLAS (1888) himself but copied by DE LAUBENFELS (1955). Herein we give the term triaxon its usual meaning. The triod and triaxon are both literally triaxial but need to be distinguished as having entirely different symmetries; the triod is not found in Hexactinellida, and those of Calcarea and Demospongea show relationship to tetraxons.

Tetraxons, as defined by the *Challenger* authors (SCHULZE, 1887a; SOLLAS, 1888), who followed SCHMIDT (1870) and VOSMAER (1882, 1883, 1884, 1885, 1887), and by nearly all later authorities (e.g., RAUFF, 1893, 1894, 1895), comprise spicules of the types of the demosponge calthrops and triaene, with four rays arranged as though following tetrahedral axes. They do not include the cross-shaped stauractines of Hexactinellida, which are properly triaxons or diaxons according to whether there are axial rudiments of the two additional rays of a hexactine (SCHULZE, 1887a; RAUFF, 1893, 1894, 1895; IJIMA, 1927).

SPONGIN

Spongin is a protein material secreted by some Demospongea but not found in other Porifera. Forms whose principal spicules are monaxons may have them cemented together by spongin or imbedded in reticulate spongin fibers. In **keratose** sponges only

spongin is secreted, and the skeleton consists of reticulate spongin fibers or of branching fibers that are separate except at a common base (Fig. 9). The two types of spongin skeleton are distinguished as **dictyoceratid** and **dendroceratid**. The secreted skeleton is sometimes reinforced with foreign material, comprising a **xenoskeleton.**

Spongin may also occur in nonskeletal roles as fine filaments or membranes.

OTHER SKELETAL CHARACTERISTICS

Spicular skeletons of sponges vary widely in character and in various ways. Different types of spicules occur in different classes, and not all the types that occur are found in any one genus. Spicules are sometimes all similar but commonly vary in form, size, or both. When two or more types are present in one skeleton, they are often distributed differently. The spicules of some sponges are simply embedded in the soft parts without other connection, but others have spicules cemented, articulated, or fused together to form a rigid skeletal framework. Flagellated chambers or a canal system may then cause interruption of skeletal meshwork and sometimes other modifications. Some sponges have special types of spicules protruded from their surfaces, and these may take part in formation of anchoring structures.

When spicules of a sponge are of two or more sorts that differ in form, size, function, or some combination of these factors, each sort present is a category of spicules. As simple examples, the spicules may consist of monaxons and tetraxons of similar or different sizes or of monaxons of two or three sizes that do not intergrade. Herein names of the categories are those of the spicules themselves. Further terms are used where spicules differ in distribution and function. For instance, a spicule may occur in all parts of the body or be restricted to the choanosome or to an ectosome; it is then correspondingly somal, choanosomal, or ectosomal. Protruded spicules forming anchoring structures are classed as **radical** or called **basalia.** Details

of the types of spicules present with their distribution and function are termed the **spiculation.**

In most Demospongea and all Hexactinellida, the spicules are differentiated into two main functional categories comprising main supporting elements, or **megascleres,** and accessory elements, or **microscleres.** As implied by the names, these are typically of large and small sizes, respectively. It is difficult to generalize, but the lengths or diameters of many examples fall in ranges above and below about 0.1 mm. Sometimes, however, a spicule that is normally a microsclere grows to megascleric size; it is usually then still called a microsclere homologically, although some authors call it a megasclere simply because of its size. The types of spicules found as megascleres and microscleres vary widely in different sponges. The two may be similar in form but are commonly different, and some types of spicules occur only as megascleres or microscleres. For instance, the demosponge triaene is always a megasclere; on the other hand, many-rayed spicules occur as microscleres in some Demospongea but never as demosponge megascleres. Megascleres are often differentiated further into different types supporting the interior (choanosome) and surface parts (e.g., dermis, dermal membrane), and different types of microscleres may also be differently distributed.

Spicules forming rigid skeletal frameworks are united by calcareous cement (**sclerosome**) in the Calcarea (Fig. 10.1), by articulation (**zygosis**) in the Demospongea (Fig. 10.2), and by fusion in the Hexactinellida (Fig. 10.3). They are always megascleres in the two latter classes, in which distinct microscleres are present, and are typically those of the choanosome, although megascleres supporting the surfaces may also be united. A skeletal framework remains intact after death unless physically broken, although other loose spicules that occur are usually lost with the soft parts unless trapped in the meshes. In forms with loose spicules only, the skeleton collapses as the soft parts
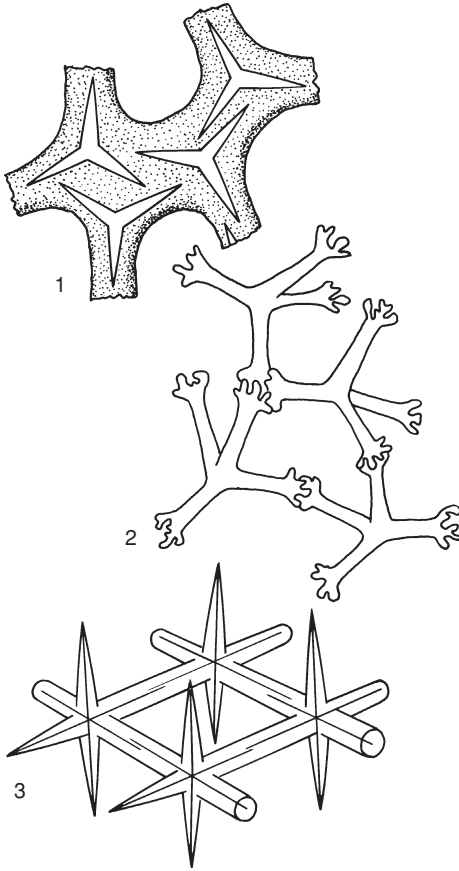
Fig. 10. Rigid spicular skeletons; *1,* triactines of a member of class Calcarea embedded in calcareous cement (sclerosome); *2,* tetraxial desmas of a member of class Demospongea, order Lithistida, united by articulation (zygosis); *3,* parenchymal hexactines of a member of class Hexactinellida, united by fusion during development (ankylosis) to form part of a rigid dictyonal framework; positions of individual dictyonal hexactines indicated by their axial filaments (new).

decay, and the spicules are dispersed by current action. In consequence, most fossil Porifera are forms with **skeletal frameworks.**

In some forms with skeletal frameworks, flagellated chambers and inhalant and exhalant canals are small enough to lie within the meshes of continuous skeletal meshwork. But in other forms canals and sometimes chambers are larger than the normal skeletal meshes and cause interruption of meshwork that develops around them. This modification of the skeleton is skeletal canalization. It

is also seen in keratose sponges with reticulate skeletons producing, for instance, the larger holes and channels in a bath sponge. The features produced may be restricted to meshwork at the surface or penetrate the skeleton deeply, with inhalant and exhalant features overlapping within it. These features persist when the soft parts decay and give an indication of their character, although not a complete one. An internal cavity, for instance, may represent only the principal trunk of a canal whose smaller branches pass out through the lining skeletal meshes. Apertures in skeletal surfaces due to canalization are called **skeletal pores** herein, and internal canal-like passages are **skeletal canals.** Skeletal pores and canals are ostia and epirhyses (Rauff, 1893, 1894, 1895; Schrammen, 1910, 1912; Ijima, 1927), if identified certainly as inhalant, and **postica** and **aporhyses,** if certainly exhalant. Some special types of internal features are also distinguished (Ijima, 1927). But many fossil sponges have skeletal pores or canals that cannot be identified functionally so that use of these terms only is more convenient. Absence of canalization in a fossil skeletal framework does not mean that the sponge lacked flagellated chambers or even a canal system; on the contrary, chambers must always be assumed to have been present, with, for example, inhalant and exhalant canals in any instance in which the modern examples are leucons.

Skeletal pores and canals that arise by internal interruption of growing skeletal meshwork are classed as **intraskeletal.** Accounts that represent canalization in some fossil Hexactinellida (e.g., *Ventriculites* Mantell) as produced by plication of the wall are incorrect and are badly inconsistent with the nature of the soft parts of modern forms. The skeletal canals of these sponges are true intraskeletal features, produced as in other Porifera. Diverticulation of the choanocytal membrane to form flagellated chambers and of the basic chamber layer producing leuconoid conditions are purely internal occurrences, involving no folding of the wall as

a whole. The inhalant and exhalant canals of Hexactinellida are enlarged intertrabecular spaces, produced without folding of any sort.

FORM AND ATTACHMENT

The external form or habitus of sponges varies widely. Simple examples form cups or hollow cylinders or expand into funnel-like or mushroomlike shapes. In others, hollow tubes branch dendritically, divide and anastomose repeatedly, or radiate from the outside of an axial tube or funnel. Longitudinal folding of the wall or a basically funnel-like growth can produce features ranging from closely spaced plications to radiating, finlike flanges. Some forms with no paragaster or spongocoel are massive, taking globular, pyriform, cushionlike or irregular shapes; others are tuberlike or bushlike or are flabellate sponges, of fanlike or similar shapes, with opposite sides inhalant and exhalant, or with exhalant apertures on both sides. Another sponge forms thin crusts, with oscula of a number of separate paragaster-like cavities. Some sponges grow in forms intermediate between various types now described. There is also a variety of minor and special developments. For instance, the main mass of the body may be raised on a stalk, or a lateral wall may be pierced by local apertures called **parietal gaps.** In some sponges outward form is modified by secondary structures, which arise at the end of normal growth; in Hexactinellida, a terminal osculum may be covered by a porous transverse **diaphragm** or **sieve plate,** or a body consisting of dividing and anastomosing tubes may be enclosed in a capsule.

Many sponge species conform to one habitus, although individuals may vary in their detailed development. Others are more variable and may have gradations through two or more of the types that are distinct in other sponges. Variation in form is presumably genetic in basis, but environment may also have an influence, and one species may then take different forms under different conditions (see Variability and Variation, p. 223).

Sponges are attached to the substratum by an encrusting base, by imbedded rootlike outgrowths of the basal part of the body, or by protruded spicules imbedded in an underlying sediment and typically forming a beardlike or ropelike **root tuft.** They are then classed accordingly as **basiphytes, rhizophytes,** or **lophophytes.** A few have no type of attachment and are simply anchored by their weight or capable of drifting (see also Functional Morphology and Adaptation, p. 219–220; and Ecology and Paleoecology, p. 243).

INDIVIDUALITY

Sponges have less distinct individuality than true Metazoa, and what comprises an individual may be problematical. Forms with regular shapes have a generally individual character; but sometimes a group of what are normally distinct individuals are produced from a single common base. Closely spaced sponges of one species may also grow together basally or so as to form a single composite mass when branching, massive, or encrusting. Sponges with more than one osculum are often interpreted as colonies, from an argument (MINCHIN, 1900) that each osculum marks an individual; but multiple oscula can arise in a variety of ways, for example, by transverse constriction and division of a single primary osculum, by lateral budding, or by apopores assuming the status of oscula.

APPENDIX: TERMINOLOGY

Some of the terminology in sections of this volume may be different from that of the first edition of the *Treatise Part E* (DE LAUBENFELS, 1955).

triaxial, triaxon. The term triaxial was introduced by SCHMIDT (1870) to distinguish spicules of the Hexactinellida, in which up to six rays follow three axes at right angles, from demosponge tetraxons. This is the meaning of triaxial and triaxon in the *Challenger* volumes (SCHULZE, 1887a; SOLLAS, 1888) and in most later literature (e.g., RAUFF, 1893, 1894, 1895); but

earlier VON LENDENFELD (1887) and SOLLAS (1887) used triaxon to include triods. This was an error, pointed out by SOLLAS himself (1888) but copied by DE LAUBENFELS (1955). The present authors give the term triaxon its usual meaning. The triod and triaxon are both literally triaxial but need to be distinguished as having entirely different symmetries; the triod is not found in Hexactinellida, and those of Calcarea and Demospongea are related to tetraxons.

tetraxon. Tetraxons, as defined by the *Challenger* authors (SCHULZE, 1887a; SOLLAS, 1888), who followed SCHMIDT (1870) and VOSMAER (1882, 1883, 1884, 1885, 1887), and by nearly all later authorities (e.g., RAUFF, 1893, 1894, 1895), comprise spicules of the types of the demosponge calthrops and triaene, with four rays arranged as though following tetrahedral axes. They do not include the cross-shaped stauractines of Hexactinellida, which are properly triaxons or diaxons according to whether there are axial rudiments of the two additional rays of a hexactine (SCHULZE, 1887a; RAUFF, 1893, 1894, 1895; IJIMA, 1927).

rhagon. In SOLLAS's (1887) pre-*Challenger* account of the Porifera, the leuconoid type of canal system was described as the rhagon type because some of the leuconoid Demospongea develop from rhagons. But a rhagon as such (SOLLAS, 1887, 1888) is the larval form only, with chambers but without a canal system; and other leucons do not develop from rhagons.

endosome. This term was proposed as the name of an ectosome-like stratum on the exhalant side of the choanosome, with the inner trabecular network of Hexactinellida (SOLLAS, 1887) and a demosponge structure (SOLLAS, 1888) as examples. Accordingly, it must not be used as equivalent to choanosome and is used correctly, for example, by BURTON (1963).

skeletal pores and canals. In the first edition of *Treatise Part E* (DE LAUBENFELS, 1955), these features of the rigid skeleton were called by the same names as the true canals (prosochetes, apochetes) and their apertures (prosopores, apopores), which are soft part structures in living sponges. There are several objections to this method. First, the skeletal features are not the canals of the soft parts and represent them only imperfectly. In some Hexactinellida, skeletal apopores or apochetes are related to flagellated chambers (e.g., in *Cyclostigma* SCHRAMMEN, *Aphrocallistes* GRAY), instead of exhalant canals (i.e., apochetes). In genera with no modern species, they could represent either. A skeletal framework may have no canalization in a sponge with both prosochetes and apochetes in the soft parts. Last, many fossils have features of uncertain function. Herein, therefore, the terms skeletal pore and skeletal canal are used both as general designations and when function is unknown. In addition, terms (ostia, epirhyses, etc.) used by RAUFF (1893, 1894, 1895), SCHRAMMEN (1910, 1912), and IJIMA (1927) are used herein when specific terms can be used.

CLASSIFICATION

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The outline classification presented below is principally of fossil sponges treated in the systematic volume of *Treatise Part E (Revised),* vol. 3 (in press). It summarizes taxonomic relationships and presents stratigraphic ranges of the various taxa. Numbers in parentheses indicate the number of recognized fossil genera in each suprageneric group, from family to class, with the number of subgenera included being the second number, listed after the semicolon.

The order of taxa in the outline represents taxonomic relationships and may be different from the order presented in the systematic volume because taxa in those sections are generally separated into Paleozoic and Mesozoic-Cenozoic occurrences. As a result, some major categories may be represented in two or three systematic sections. For example, the section treating hypercalcified sponges documents sponges strictly included in the class Calcarea and also some demosponges (noted by the symbol ** after the stratigraphic ranges) that have calcareous skeletons. In other sections, a family with a long stratigraphic range may be represented in both Paleozoic and Mesozoic sections or chapters where those demosponges or hexactinellid sponges are treated.

SUMMARY OF CLASSIFICATION

Phylum Porifera Grant, 1836 (1,183;30)
  Class Demospongea Sollas, 1875 (615;11)
    Subclass Clavaxinellida Lévi, 1956 (54)
      Order Protomonaxonida Finks & Rigby, herein (39)
      Order Clavulina Vosmaer, 1887 (15)
    Subclass Choristida Sollas, 1880 (52;2)
      Order Plakinida Reid, 1968 (5)
      Order Pachastrellida Reid, herein (13)
      Order Ancorinida Reid, 1968 (19;2)
      Order Craniellida Reid, 1968 (2)
      Order Uncertain (12)
      Order and Family Uncertain (1)
    Subclass Tetractinomorpha Lévi, 1953 (30)
      Order Streptosclerophorida Dendy, 1924 (13)
        Suborder Eutaxicladina Rauff, 1894 (13)
      Order Hadromerida Topsent, 1898** (17)
    Subclass Ceractinomorpha Lévi, 1953 (479;9)
      Order Dictyoceratida Minchin, 1900 (5)
      Order Dendroceratida Minchin, 1900 (0)
      Order Verongida Bergquist, 1978 (3)
      Order Halichondrida Topsent, 1898 (2)
      Order Poecilosclerida Topsent, 1928 (16)
      Order Haplosclerida Topsent, 1898 (18)
      Order Sigmatosclerophorida Burton, 1956 (4)
      Order Agelasida Verrill, 1907** (145)
      Order Vaceletida Finks & Rigby, herein** (51)
      Order Lithistida Schmidt, 1870 (114)
        Suborder Orchocladina Rauff, 1895 (114)

Order Tetralithistida Lagneau-Hérenger, 1962 (93;9)
  Suborder Tetracladina Zittel, 1878 (70;9)
  Suborder Dicranocladina Schrammen, 1924 (16)
  Suborder Pseudorhizomorina Schrammen, 1901 (2)
  Suborder Didymmorina Rauff, 1893 (5)
Order Megalithistida Reid, herein (28)
  Suborder Helomorina Schrammen, 1924 (6)
  Suborder Megamorina Zittel, 1878 (22)
Order Axinellida Bergquist, 1967 (1)
Order Uncertain (1)
Order and Family Uncertain (5)
Order Monolithistida Lagneau-Hérenger, 1955 (18)
  Suborder Megarhizomorina Schrammen, 1924 (2)
  Suborder Sphaerocladina Schrammen, 1910 (16)
Order and Suborder Uncertain (1)
Order Spirosclerophorida Reid, 1963 (114;9)
  Suborder Rhizomorina Zittel, 1878 (88;9)
  Suborder Uncertain (26)
Class Hexactinellida Schmidt, 1870 (432;19)
  Subclass Amphidiscophora Schulze, 1887 (160)
  Order Amphidiscosa Schrammen, 1924 (41)
  Order Reticulosa Reid, 1958 (118)
  Order Hemidiscosa Schrammen, 1924 (1)
  Subclass Hexasterophora Schulze, 1887 (272;19)
  Order Lyssacinosa Zittel, 1877 (36)
  Order Hexactinosa Schrammen, 1903 (134;8)
  Order Lychniscosa Schrammen, 1903 (81;11)
  Order and Family Uncertain (6)
  Order Uncertain (15)
Class and Order Uncertain (2)
Class Heteractinida de Laubenfels, 1955 (32)
  Order Octactinella Hinde, 1887 (26)
  ?Order Hetairacythida Bedford & Bedford, 1937 (4)
  Order and Family Uncertain (2)
Class, Order, and Family Uncertain (3)
Class Calcarea Bowerbank, 1864 (57)
  Subclass Calcinea Bidder, 1898 (3)
  Order Clathrinida Hartman, 1958 (???)
  Order Murrayonida Vacelet, 1981 (3)
  Subclass Calcaronea Bidder, 1898 (54)
  Order Leucosolenida Hartman, 1958 (0)
  Order Sycettida Bidder, 1898 (4)
  Order Stellispongiida Finks & Rigby, herein (32)
  Order Sphaerocoeliida Vacelet, 1979 (5)
  Order Lithonida Doederlein, 1892 (12)
  Order and Family Uncertain (1)
Class and Order Uncertain (29)
Class Uncertain (13)
Unrecognizable Genera (235)

CLASS DEMOSPONGEA:
GENERAL MORPHOLOGY AND CLASSIFICATION

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The Demospongea are sponges with mesenchyme and **pinacoderm,** as in Calcarea, but with a skeleton of siliceous spicules, of organic matter (spongin), of both, or with no skeleton. The spicules are monaxial to polyaxial or anaxial, and four-rayed spicules are characteristically tetraxial. Spicules with more than four rays occur normally only as microscleres.

No single skeletal character distinguishes all Demospongea from other sponges. The spicules vary widely, and different kinds occur singly or in numerous different combinations. Most living genera with spicules have either both megascleres and microscleres or megascleres only; but a few have microscleres only or small spicules not regarded as properly either megascleres or microscleres. Megascleres and microscleres may be similar but are often of different types so that megascleres are diactines or tetractines, for example, but microscleres are polyactines. Three main types of skeletons occur in forms containing megascleres. In **choristid** Demospongea, the **choristids,** some or all the megascleres are tetractinal or triactinal, although monaxons (usually diactines) may also be present, and all megascleres are loose in the soft parts without articulation or connection by spongin. In **monaxonids** the megascleres are monaxons only, developed as diactines or monactines, and may be loose in the soft parts, cemented together by spongin, or embedded in spongin fibers.

Lithistids have some or all the megascleres in the form of articulated **desmas,** which form a stony skeletal framework. The desmas are usually developed from initial monaxons or tetraxons but have articulatory parts (**zygomes**) and sometimes raylike arms (**clones**) that are characteristically anaxial. Some desmas are entirely anaxial. The anaxial structures of lithistid desmas do not

occur in megascleres of choristid or monaxonid sponges. In keratose sponges with a skeleton composed of spongin only, the skeleton consists of dendritic or reticulate fibers or may also include loose spongin spicules when the fibers are dendritic.

Fossil Demospongea are recognized by occurrence of one of the three main types of megascleric skeletons, by traces of a spongin skeleton, or by dissociated megascleres or microscleres of types only found in Demospongea. Nearly all forms containing megascleres are distinguished from Hexactinellida by the absence of triaxial examples (hexactines and variants), and some are distinguished further by occurrence of tetraxons (calthrops, triaenes, tetraxial desmas), which do not occur in Hexactinellida. Union of megascleres solely by articulation (zygosis) distinguishes lithistid skeletal frameworks from structures formed in Calcarea or Hexactinellida by cementation or fusion of spicules. Very rarely, some megascleres of Hexactinellida may be articulated, but lithistid desmas are never triaxial.

Some fossil sponges are known that may be either Hexactinellida or monaxonid Demospongea. This taxonomic problem arises because the principal megascleres of some hexactinellids are monaxon-like diactines (or rhabdodiactines), which cannot be recognized as hexactinellidan spicules from their outward form only. In living examples other spicules are obvious triaxons (hexactines and others: see class Hexactinellida, *Treatise Part E (Revised),* vol. 3, in press), and an **axial cross** between the ends of most diactinal megascleres has rudimentary axial filaments of two or four undeveloped rays; but most fossils have the main megascleres only, and the character of their axial systems is often not demonstrable. If a sponge with diactinal megascleres of
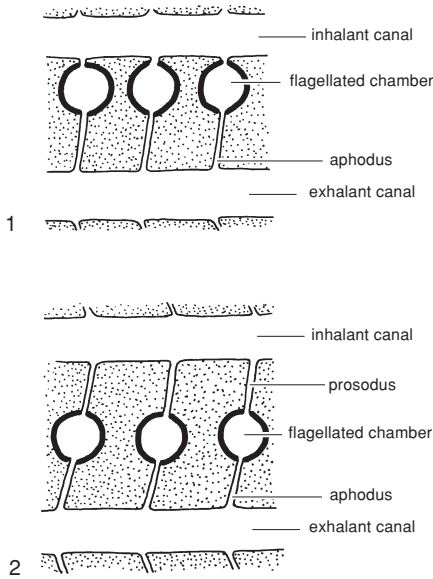
FIG. 11. Aphodal and diplodal canal systems; *1,* aphodal type, in which flagellated chambers discharge to exhalant canals proper by fine ducts termed aphodi; *2,* diplodal type, with aphodi as in *1,* and with additional fine ducts termed prosodi through which water is led to flagellated chambers from inhalant canals proper; as in eurypylous sponges (see Fig. 7), the canals are branching passages in practice, and incurrent and excurrent water may pass through different surfaces of the body or different parts of the same surface; *thick lines* represent choanocytal linings of flagellated chambers; other parts *finely outlined and stippled* (new).

undetermined character has the spicules united by fusion or by lateral **synapticula,** often running like the rungs of a ladder between parallel diactines, it belongs to the Hexactinellida. If, however, the spicules are unconnected, there is strictly no way of deciding which class is represented; but comparisons with forms of known position sometimes suggest that such sponges may be Hexactinellida. No sponge with loose diactines only, however, can be shown conclusively to be a hexactinellid unless the megascleres are demonstrably diaxial or triaxial.

The apparent stratigraphic range of the class Demospongea is Lower Cambrian to recent, although the oldest forms included are supposed monaxonids without certainly diagnostic spicules.

SOFT PARTS

The soft parts of adult Demospongea are broadly similar to those of leuconoid Calcarea, with various special features. As in the Calcarea, a mesenchymal groundmass is present. Choanocytes are restricted to flagellated chambers, which are typically globular, and always receive water from inhalant canals and discharge it through exhalant canals. External and canalar surfaces are coated by a layer of discrete pinacocytes, by a syncytial **epithelioid membrane,** or, in some keratose sponges, apparently by membranous spongin. There is nearly always an ectosome, developed as a thin, skinlike dermis or as a thick and often tough and fibrous cortex. In some forms, a dermislike endosome forms an exhalant surface. In **euryphylous** sponges, the chambers receive water directly from the main trunks or branches of inhalant canals, and their **apopyles** open directly into exhalant canals. **Aphodal** sponges (Fig. 11.1) have fine ducts termed **aphodi** between the chambers and larger exhalant canals proper. **Diplodal** sponges (Fig. 11.2) have similar fine **prosodi** between inhalant canals and chambers. The euryphylous and aphodal conditions are the common ones. An ectosome developed as a **dermis** is typically porous and underlain by subdermal spaces, from which the inhalant canals run into the interior. Inhalant canals may pass inward through a **cortex** from the surface but more often start from subdermal spaces under or within it. If the spaces lie under the cortex, they are **subcortical,** and water reaches them through short **intracortical** canals sometimes called **chones.** Less commonly, subdermal spaces interrupting a cortex are roofed by a thin porous surface layer. In either instance, pores seen at the surface may form concentrations in special poriferous areas. Within a cortex, chones or true canals may have musclelike sphincters for closure.

In some Demospongea, the young sponge developed first from the newly settled larva is a transitory **rhagon** that has flagellated chambers but no canal system and no

ectosome. A rhagon takes the form of a thinly walled, hollow cone with an oscular opening at the top (Fig. 12.1–12.2). The lateral wall of the upper part (**spongophare**) contains globular flagellated chambers, whose apopyles open directly into the paragastral cavity; but the basal part (**hypophare**) applied to the substrate has no chambers. Small pores in the external surface lead into the chambers of the upper part. The adult leuconoid condition, which is often correspondingly eurypylous, is produced by complication of the wall, which in some instances is comparable to the diverticulation of sycettoid Calcarea. In one instance (LÉVI, 1957b), an even simpler rhagonlike larva has an asconoid condition, with choanocytes lining the whole paragaster, and no flagellated chambers. In other Demospongea, however, the canals are developed first within a solid larva, and aphodi may be present before an osculum appears. For many, no embryos or larvae are known.

INFLUENCE OF SOFT PARTS ON THE SKELETON

Two main results of the influence of the soft parts on the skeleton may be noted within fossil material.

First, division of the soft parts into external ectosome and internal choanosome can result in restriction of some spicules to one of these parts of the body or in special arrangement of megascleres in relation to an ectosome, although they do not lie entirely within it. There are two important instances. In choristid sponges, tetractinal megascleres are often developed as triaenes (see p. 20–21), arranged so that three similar rays lie in or under an ectosome, and a fourth layer ray extends into the choanosome. In massive (e.g., globular) choristids with triaenes, this leads to arrangement of megascleres in a radiating (radiate) manner. In lithistids, the desmas of the skeletal framework are characteristically choanosomal megascleres. At the surfaces, however, there may be separate ectosomal megascleres in the form of loose
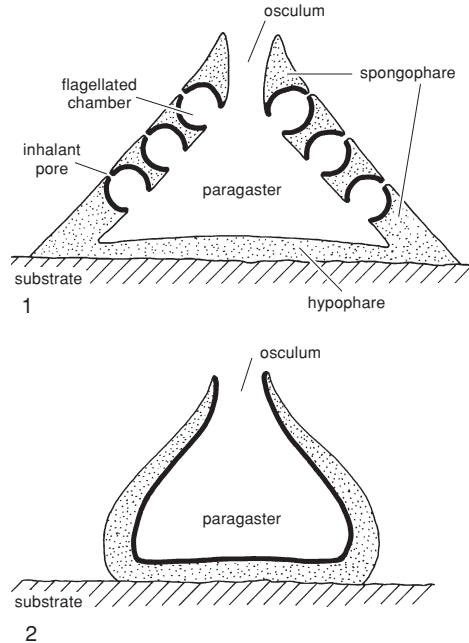

Fig. 12. Rhagons shown in vertical section; *1,* rhagon in original sense (SOLLAS, 1888), with upper part (spongophare) containing flagellated chambers but no canal system, and a chamberless basal part (hypophare); *2,* asconoid larva of *Halisarca dujardini* JOHNSTON, Holocene, also currently called a rhagon; *thick lines* represent choanocytal linings of flagellated chambers or paragastral cavity; other parts *finely outlined and stippled;* substrate *crosshatched* (new).

triaenes, loose monaxons, or special desmas different from those of the interior.

Second, growth of skeletal meshwork around canals that are larger than ordinary skeletal meshes results in production of skeletal pores or canals (p. 4). These features occur in many lithistid and keratose sponges, but only the former are common as fossils. The skeletal pores or canals may be outlined by specially enlarged meshes only but involve more typically interruptions equal in width to several or many meshes. In lithistids, the desmas forming meshwork surrounding them are distorted often by curvature or in other ways.

Judging from modern forms, the general construction of connected skeletal frameworks is not normally controlled by the arrangement of canals or flagellated chambers
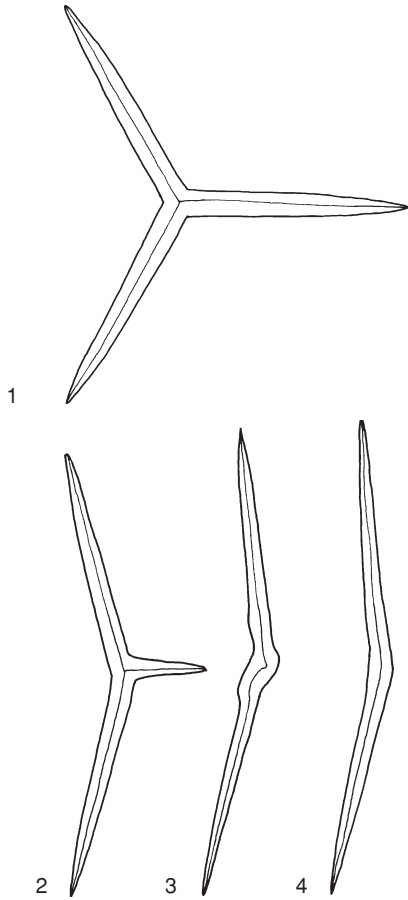
apparent skeletal canals were produced by special arrangements of the spicules, although how such features were related to the soft parts is unknown.

SPICULES

Demosponge spicules consist of hydrated (opaline) silica with some content of organic material that is secreted concentrically around organic axial filaments or partly or entirely without control by distinct axial structures. Megascleres may be formed by groups of scleroblasts, but many microscleres arise inside single ones. Axial filaments are usually present in megascleres, although lithistid desmas and some lithistid ectosomal spicules are partly or entirely anaxial. In microscleres, axial filaments occur rarely, except in especially large examples; their evident occurrence in some suggests their presence in the others, but this cannot be asserted.

Variations in form and other characters of demosponge spicules result from a number of developments, found singly or in various combinations. Some developments occur only in megascleres or microscleres, but others occur apparently in both, although, strictly, the rarity of detectable axial filaments in microscleres can make apparently similar features not certainly identical in origin. The small spicules forming the skeletons of some Demospongea (Plakinidae, Thrombidae, Samidae) and noted as microscleres have variations similar to those of some choristid megascleres, although sometimes with special developments.

For further description, the following arrangement is convenient.

1. Number of rays. The number of rays (or, in microscleres, apparent rays) may be varied meristically in a sequence 1, 2, 3, 4, 5, etc. (Fig. 13–18). In the simplest instance, all the rays are similar in length, without occurrence of spicules with some rays partially developed. The angles between the rays vary according to their number and are usually subequal or equal, although exceptions may occur. The symmetries of diactinal,

FIG. 13. Spicules of types intergrading from triactine to diactine; *1,* triod, or regular triactine, with three equal rays at 120% intervals; *2,* triactine with two equal rays, which meet at a wider angle than corresponding rays in view *1,* and 1 short ray; *3,* angled diactine, irregularly bent near center and with axial filament kinked centrally at point corresponding with position of short ray in view *2; 4,* more regular diactine with rays still angled; irregular or angled character of diactines (views *3–4*) is thought to imply derivation by reduction of 1 ray of a triactine (views *1–2*); these transitions are seen chiefly in spicules of choristid Plakinidae but also occur in monaxonid *Alectona* Carter, whose megascleres are normally of types shown in views *3–4* (new).

in the soft parts, as might be imagined, but seems to be essentially independent unless modified by canalization. Correspondingly, various fossil lithistids have similar types of canalization in skeletons that are differently constructed, and formed from different kinds of desmas. Nonetheless, in some fossils

triactinal, tetractinal, and hexactinal spicules are typically monaxial (with two rays in line), triodal (three rays at 120° intervals in one plane), and tetraxial (four rays following three axes at right angles), respectively. This type of variation occurs mainly in microscleres called **euasters** (p. 30), in which the number of rays may vary from one to more than 100 and is typically more than four; but it also occurs among megascleres and small analogous spicules with two to six rays and then usually among individual variants of a normal tetractine.

There may also be intergradation between monactinal and tetractinal spicules through intermediates in which some rays are relatively short, rudimentary, or represented only by internal axial rudiments. Transitions between diactines, triactines, and tetractines are often accompanied by reorientation of rays, so that, for example, two rays in line in a diactine correspond with two at 120° in a triod (triactine). This style of variation occurs mainly in small, megasclere-like spicules of Plakinidae (Fig. 13) but sometimes in megascleres of typical choristids or the initial bodies (**crepides**) of some desmas. It is usually interpreted as being due to a process of reduction (SCHULZE, 1880), because diactines intergrading with regular triactines can be markedly irregular in their middle parts.

Monaxons are usually considered as having either one or two rays according to whether the two ends are different (e.g., sharp and blunt respectively) or similar; but a so-called monactine can originate by secondary rounding of one end of an initial diactine.

2. Branching rays. Rays may divide into true actinal branches due to branching of the axial filament during growth (Fig. 14). Branching is usually dichotomous, with division occurring once only in each ray affected, but may sometimes result in production of three or more branches at one division or may be repeatedly dichotomous.

Clear actinal branching occurs mainly in loose megascleres and small analogous spi-
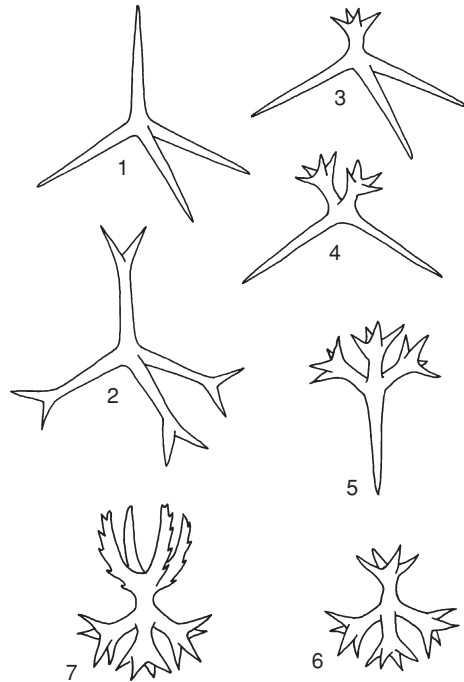

Fig. 14. The calthrops (or regular tetractine) and branched variants; *1,* simple calthrops with unbranched rays; *2,* dichocalthrops with each ray branched dichotomously; *3–7,* lophose tetractines with rays divided into groups of 4 branches; *3,* monolophose tetractine; *4,* dilophose tetractine; *5,* trilophose tetractine; *6,* tetralophose tetractine with all rays developed similarly; *7,* candelabrum, or tetralophose tetractine with branches of 1 ray especially developed (new).

cules, which are usually tetractinal and never normally monactinal or diactinal. The number of rays affected may be any number of those present, for example, one to four in a tetractine; or branching may be restricted to rays grouped as a cladome (see point 5 below, triaenose symmetry). Occasionally, branching may occur in the initial body (crepis) of a tetraxial or related type of desma (p. 52) or in axial canals representing it.

In microscleres, repetitive branching appears to occur in a series of forms (**streptoscleres,** p. 31) that typically have sympodial spiral axes, although axial filaments can be detected rarely.

3. Terminal features. The ends of monaxons or individual rays are generally finely pointed (**oxeote**) but sometimes
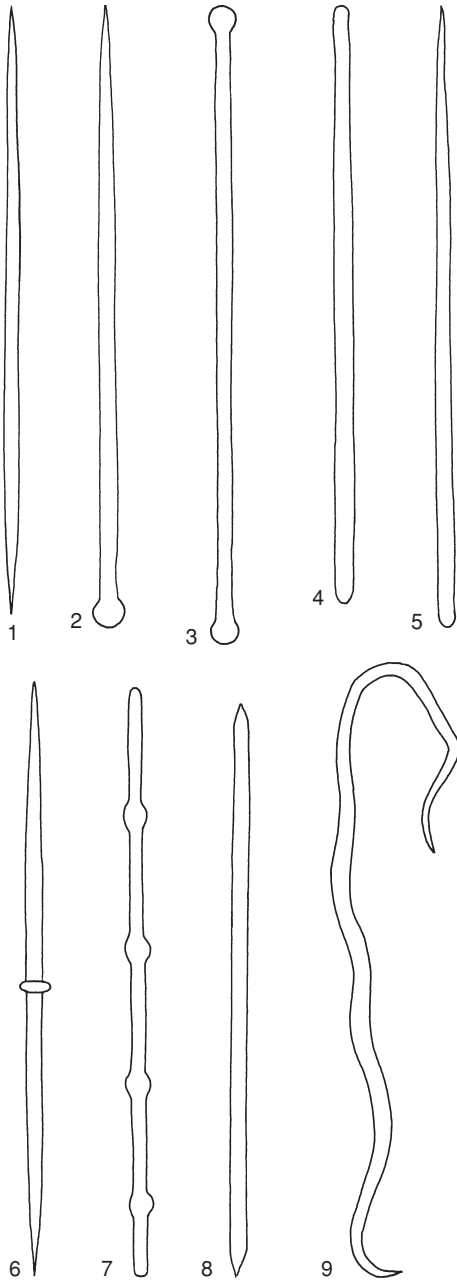
FIG. 15. Nomenclature of demosponge monaxons; *1,* oxea (or, amphioxea), sharply pointed at both ends; *2,* tylostyle, with 1 end sharp, other swollen; *3,* tylote (or amphitylote), with swollen ends; *4,* strongyle (or amphistrongyle), with blunt ends; *5,* style, with 1 end blunt, 1 sharply pointed; *6,* centrotylote oxea, with annular central tylus; *7,* polytylote strongyle; *8,* tornote (or, amphitornote), abruptly pointed at both ends; *9,* ophirhabd with pointed (oxeate) ends (new).

abruptly pointed (**tornote**), rounded (**strongylote**), or spherically knobbed (**tylote**) (Fig. 15). In monaxons, the two ends may be similar or differently developed. In monaxial megascleres with one end only strongylote or tylote, the corresponding end of the axial filament may also have a rounded enlargement; this is usually interpreted as marking the spicular center, that is, the point from which growth began, so that spicules with this feature are regarded as genuine monactines.

4. Curvature and torsion. Curvature of individual rays is a feature of various loose megascleres and small analogous spicules. A monaxial megasclere may be curved along its length, bent centrally, or sometimes irregularly sinuous. Some apparently diactinal microscleres are bent centrally, bow shaped, or rarely bent like a forceps with the two ends converging. Others have continuous torsion in a range from C-shaped or S-shaped to polyspiral and spring or screwlike. These shapes may also occur in the axial parts of microscleres whose final shape is modified further by various types of outgrowths (see point 6 below).

5. Triaenose symmetry. Many loose tetractinal megascleres and some small analogous spicules are developed as triaenes, in which three rays are similar but are distinguished in some way from the fourth (Fig. 16). The three similar rays are called **cladi** and together form a **cladome,** while the fourth ray is the **rhabdome.** This nomenclature was based on the idea (SOLLAS, 1888) that the cladi are branches of a primary monaxon or rhabdus; in practice such spicules may develop from regular tetractines, but the terms have been generally adopted. The cladi may differ from the rhabdome (a) by being shorter or, less commonly, longer; (b) by curvature or displacement away from the regular tetraxial positions, either away from or toward the rhabdome; (c) by branching, which is normally single and usually dichotomous, though trichotomous branching may occur; (d) in lithistids, by production of lateral expansions, which may form leaflike features or coalesce as a sili-

ceous disc; or (e) by some combination of two or more of these developments. The rhabdome is normally a simple straight ray and is commonly longer, sometimes much longer, than the cladi, although shorter or even rudimentary in some sponges. These spicules are characteristically arranged with the cladi toward or in an ectosome or occasionally an endosome and with the rhabdome directed inwardly.

In some sponges, triaenes and occasional variants have meristic variation in the number of cladi, of which one to four may be present (Fig. 17–18). The variants with one, two, or four cladi are called **monaenes, diaenes,** and **tetraenes.** The angles between the cladi are varied in accordance with their number; hence a tetraene occurring as a variant of a triaene with cladi at right angles to the rhabdome (orthotriaene, see p. 25) can have the triaxon symmetry of a hexactinellidan pentactine, although this is very uncommon.

Two other types of loose megascleres or analogous spicules, both uncommon, have a triaene-like symmetry (Fig. 19). **Mesotriaenes** are forms in which the rhabdome is diactinal, with equal or unequal rays in line, and a cladome arising from a point between the ends. Forms with the rhabdal rays equal occur as choanosomal megascleres and appear to be special, five-rayed variants of equiradiate tetractines (calthrops), which they occasionally accompany. The cladi are emitted at right angles to the rhabdome; they may be simple, branched once dichotomously, or repeatedly dichotomous. This type can be distinguished conveniently by SOLLAS's (1888) original name centrotriaene. Mesotriaenes with unequal rhabdal rays occur as occasional variants of some normal triaenes with the rhabdal ray much longer than the cladi; the extra ray may be similar to the cladi in length, shorter, or represented only by an axial rudiment. **Amphitriaenes** are spicules resembling a triaene with a cladome at both ends of the rhabdome. The cladi of the two ends may be simple or dichotomously or trichotomously branched, in any combination. It is not clear how these
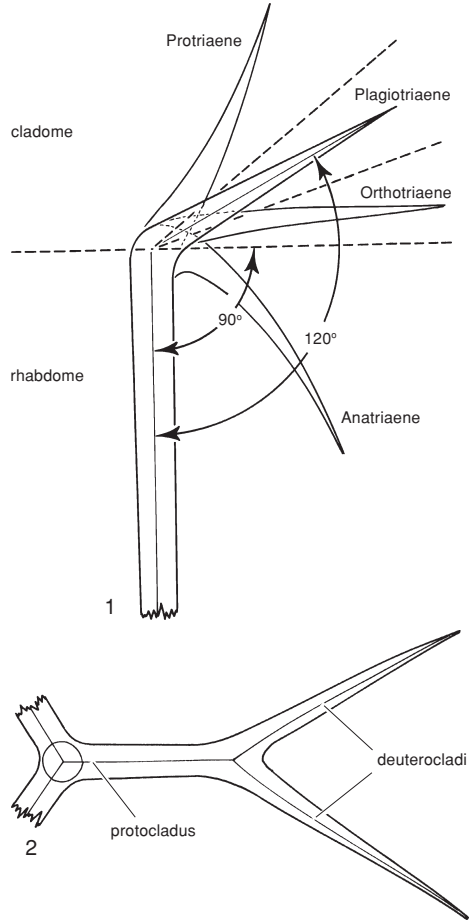
FIG. 16. Nomenclature of triaenes; *1,* nomenclature based on attitude of cladi; figure shows part of rhabdome (long ray) of a long-shafted triaene and 1 cladus of cladome oriented as in plagiotriaenes (strong outline) and protriaenes, orthotriaenes, and anatriaenes (finger outlines); *2,* part of cladome of dichotriaene seen in plan view showing protocladus and deuterocladi of 1 cladus; fine internal lines in both figures are axial filaments (new).

spicules are related to the others. There is sometimes an enlargement at the middle of the axial filament of the rhabdome; if this is regarded as a spicular center, the cladomes should then comprise true branches arising from the ends of a diactine.

In lithistid desmas, the initial body (crepis) is occasionally a triaene, a centrotriaene, or an amphitriaene, although this may not be apparent from the shape of the

FIG. 17. Calthrops and meristic variants; *1–5,* spicules of *Calthropella* SOLLAS; *1,* diactine with angled rays; *2,* triactine (triod);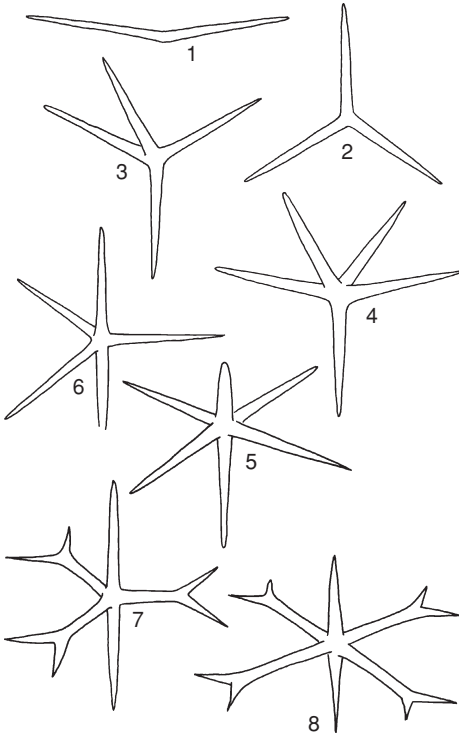 *3,* calthrops (tetractine); *4,* pentactine, of type in which 2 pairs of rays are set at different angles to a fifth, here pointed downward; this type grades into forms in which the 4 upper rays make equal angles with the fifth and which tend to take orthotetraene shape (see Fig. 18,*4,8*); *5,* hexactine with triaxon symmetry; this example also having 5 equal rays and one that is shorter and terminally blunted; *6–8,* spicules of *Yodomia* LEBWOHL; *6,* pentactine developed as a centrotriaene; compare with view *4,* from which this type may originate by straightening of 2 rays into line; *7,* centrotriaene with simple rhabdal rays (here vertical) but dichotomously branched cladi; *8,* hexactine variant of view *7,* with 4 branched cladi and with triaxon symmetry; this type may be called a centrotetraene or dichocentrotetraene (new).

fully formed desma (see point 9 below). On the other hand, some desmas have triaene-like shapes (e.g., with three raylike arms similar and one differently developed) unrelated to the form of the crepis, which may then be an equiradiate tetractine, a monaxon, or an anaxial corpuscle.

6. Ornament and secondary rays. Ornamentation of rays or of the shaft of a monaxon is a feature of some spicules. In megascleres, the only common ornament consists of small spines or spinules arranged without order, less commonly in regular whorls, and rarely in spiral series. A few megascleres have annular or spiral ridging. Ornamented microscleres are mainly monaxons (or, apparent monaxons) with straight to spiral axes (see point 4 above), having simple to spiral spinulation or various special shapes due to outgrowths that are spinelike, bladelike, or leaflike or form simple or serrated transverse flanges.

In some monaxonids, **spinules** ornamenting megascleres contain axial filaments, which begin some distance from the primary axial filament. These spinules are thus comparable with true cored rays, although clearly secondary additions. Occasionally, megascleres, which are normally spiny monactines (**acanthotylostyles**), are replaced by apparently diactinal to pentactinal spicules, with one to four extra rays arising as outgrowths from one end of an initial monaxon. The extra rays contain axial filaments that begin at some distance from the end of the primary filament instead of meeting it at a center as in true radiate megascleres; these rays are therefore regarded as secondary, corresponding with the cored type of spinule, and presumably evolved by enlargement of spinules at the base of a monactine.

In various microscleres, gradation from spiny monaxon to apparent polyactine suggests analogous developments, but no axial filaments are detectable.

7. Epicentric secretion. In a few instances, spicules are formed or initiated by secretion around a center. Microscleric spheres of some genera consist of silica secreted around a central granule, which seems to be organic. Sometimes a sphere passes morphologically into a short, round-ended monaxon (strongyle), implying its origin from the latter by further shortening unless the opposite is imagined. In some anaxial desmas (**sphaeroclones,** see p. 57) the initial body (crepis) is a siliceous corpuscle, apparently with no organic center, although a granular nucleus may appear during growth.

8. Central and axial thickening. Secondary secretion of silica may occur around the center of a radiate spicule. This is seen mainly in some euaster microscleres, in which secretion around the center of an initial polyactine can produce a spherical mass, with the ends of rays projecting (in **sphaeraster,** see p. 30–31), or solid spherical to discoidal spicules (**sterrasters, aspidasters,** see p. 30–31) with no trace of separate rays but a fine surface granulation.

Analogous secondary thickening may occur along the axial parts of monaxial microscleres, producing changes in form. In extreme instances, forms with a spiral or C-shaped axis are converted into spicules (**sterrospiras, chelasters,** see p. 32–34) resembling solidified euasters.

9. Special features. The character and form of the desmas of lithistids and a few other sponges with partly lithistid characters (**sublithistids,** see p. 49) result from secretion of silica either partly or entirely without control by growing axial filaments. The articulatory parts (zygomes) of the desmas are characteristically anaxial, and some have additional anaxial raylike arms (clones) or are wholly anaxial. Desmas are typically of various irregular shapes with the zygomes being often branching, rootlike outgrowths but sometimes handlike, cuplike, or tonguelike and with clones arranged in various ways when present. The overall form of a desma may be more or less clearly determined by that of an initial body of crepis, which may be tetractinal, triactinal, or monaxial or have little or no obvious relationship to it. In some types, accretion of silica at the ends of a monaxial crepis or around an anaxial initial corpuscle produces spherical masses (centra) from which clones radiate. In addition to features peculiar to a number of main types of desmas (p. 49–51), individual desmas may have further variations related to orientation or location in the skeleton or distortions due to canalization.

Some lithistids also have ectosomal megascleres that are formed either partly by nonactinal secretion or are wholly anaxial. In the former, siliceous outgrowths from an
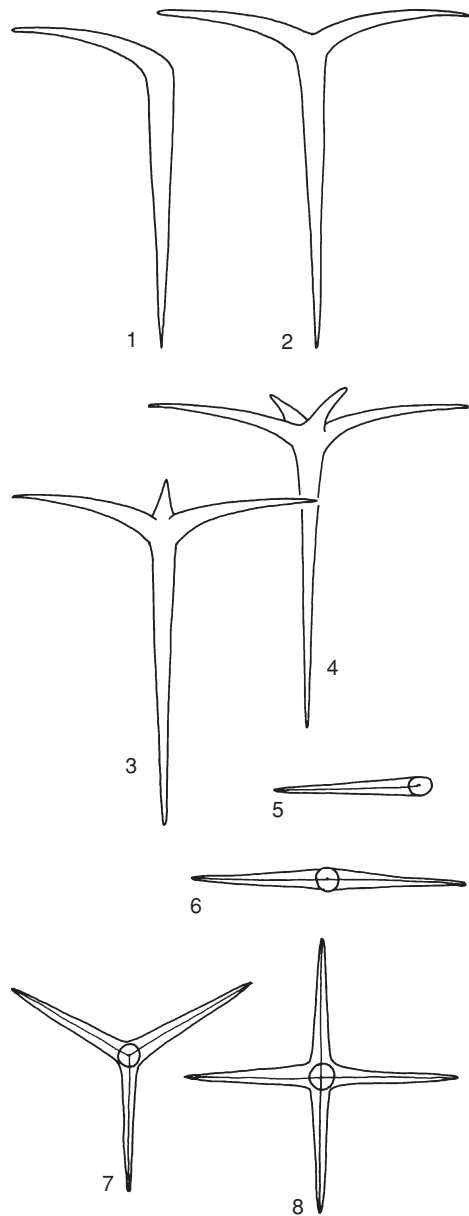
FIG. 18. Nomenclature and form of meristic triaene variants, which differ in number of cladi; illustrated by variants of simple orthotriaene (views *3, 7*); *1–4,* side views, rhabdome downward; *1,* monaene; *2,* diaene; *3,* triaene; *4,* tetraene. *5–8,* views with cladome in plan, and the rhabdome toward front; *5,* monaene; *6,* diaene; *7,* triaene; *8,* tetraene; also illustrates resemblance of demosponge orthodiaenes (views *2, 6*) and orthotetraenes (views *4, 8*) to hexactinellidan tauactines and pentactines (new).
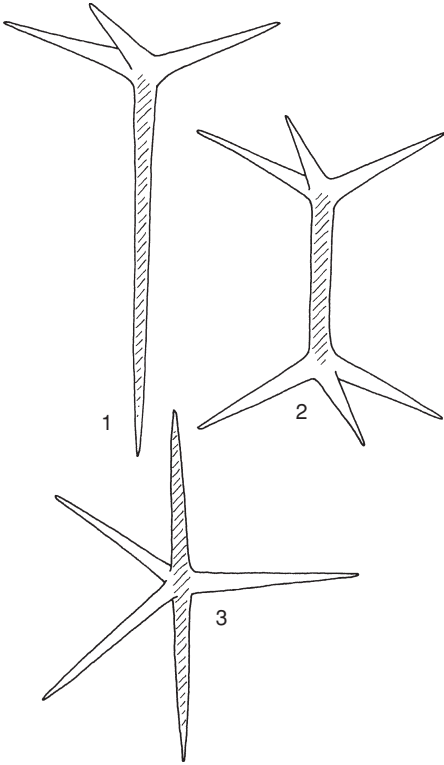
F_IG._ 19. Megascleres with triaenose symmetry, classed as triaenes *s.l.,* in which rays are contrasted as forming a rhabdome (*crosshatched shading*) and a cladome or 2 cladomes (unshaded rays); *1,* triaene *s.s.,* with a single rhabdal ray and 3 cladi; the rhabdome (rhabdal ray) of this type is typically longer than cladi, as here, and cladi are also often displaced from regular tetraxial positions (here, slightly toward rhabdome); *2,* amphitriaene with central rhabdal shaft bearing cladomes at both ends; this type can be compared with some amphiaster microscleres, to which it was related by T_OPSENT_ (1928b); *3,* mesotriaene of centrotriaene type with 2 opposite rhabdal rays (or, a diactinal rhabdome), and 3 central cladi that meet rhabdal axis at right angles (new).

initial tetractine or monaxon form leaflike expansions or siliceous discs. Anaxial, ectosomal megascleres range from finely branching bodies to scalelike plates.

10. Teratological variants. Individual spicules sometimes have irregular modification by contortion, branching of rays, or addition of extra rays. The axial filaments of extra rays may be continuous with the normal axial system or separate from it. Very rarely, com-

posite spicules may form where two or more have grown together.

All the main types of variations in the character of the spicules are represented in fossils. Only those present in megascleres are seen for the most part, but a few unusual deposits have yielded examples of nearly all the known kinds of microscleres.

The nomenclature of spicules is based simply on various aspects of their form or partly on inceptional characters when changes occur during growth. The last applies specially to lithistid megascleres. Microscleres, desmas, and some other forms are dealt with in sections below, but the following may be noted at this point.

a. Spicules are termed generally as monactines, diactines, triactines, tetractines, etc., according to the number of rays, or simply as polyactines if more than six are present. A regularly tetraxial and equiradiate tetractine is distinguished from triaenes as a calthrops (Fig. 14, 20). A triactine may be a triod, if it has three rays in one plane at 120° intervals, or a tripod, if it has the three arranged pyramidally. Any radiate microsclere or form with raylike outgrowths arising from an axial portion is an aster.

b. The prefixes **dicho-** and tricho- imply dichotomous or trichotomous branching, affecting one to all rays in, for example, a dichocalthrops or only the cladi of a dichotriaene (Fig. 20). Branching producing a regular cluster of three or more branches is lophose, and a lophose tetractine may be monolophose to tetralophose according to how many rays are affected. Repetitive branching is polycladose.

c. Monaxons with the two ends finely pointed (oxeote), abruptly pointed (tornote), rounded (strongylote), or knobbed (tylote) are called oxeas, tornotes, strongyles, and tylotes respectively (Fig. 15–16), or alternatively given the extra prefix amphi-, as in, for example, amphioxea or amphitylote. Those with only one end oxeote are styles if the other is strongylote, **tylostyles** if it is tylote. A strongyloxea has one end oxeote, the other

at first tapering as in an oxea but rounded at the tip. A hairlike monaxon is a **raphide.** Some further types take names with the termination -rhabd, e.g., ophirhabd for megascleres that are sinuous oxeas or strongyles.

d. The nomenclature of triaenes is based mainly on the form and attitude of the cladi (Fig. 16). The central type of triaene morphologically is the **plagiotriaene,** with straight or nearly straight unbranched cladi meeting the rhabdome at angles between about 110° and 135°, and regularly tetraxial when the angle is 120°. If the cladi are instead markedly curved toward the rhabdome or grow out at a lesser angle to it, the spicules are **orthotriaenes** until the angle between cladi and rhabdome is 90°, and anatriaenes when it is less than 90°. Triaenes with simple cladi curved markedly away from the rhabdome or meeting it at angles more than 135° are **protriaenes** (Fig. 21.1). Meristic triaene variants with a different number of cladi are named similarly, for example as prodiaenes or anadiaenes. If the cladi are dichotomous or trichotomous, a triaene is a **dichotriaene** or a **trichotriaene;** the primary cladal rays are then the protocladi, and their branches are deuterocladi. If the shape is otherwise similar to that of orthotriaenes or protriaenes, the names orthodichotriaene and prodichotriaene have sometimes been used. Lithistid triaenes with the cladi leaflike or forming a disc are **phyllotriaenes** and **discotriaenes.** The nomenclature of mesotriaenes and amphitriaenes follows similar principles when any special names are given; for instance, a mesotriaene found as a variant of a normal anatriaene can be called an anamesotriaene. Amphitriaenes have also been called homopolar or heteropolar, according to whether the two ends are similar or differently developed.

There is some variation in usage of the names given to simple triaenes. These were based originally by SOLLAS (1888) on the angle between the cladi and the axis of the rhabdome; but later authors (e.g., VON
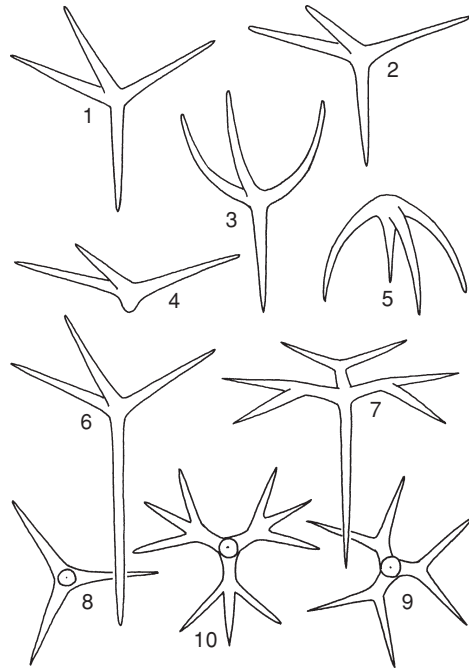

FIG. 20. Short-shafted triaenes, including subtriaenes (views *2–5*); *1,* calthrops oriented as a triaene; included for comparison with others, and because it may intergrade with spicules shown in views *2–6; 2,* equal-rayed (or equiradiate) orthotriaene, with triaenose symmetry occurring only in displacement of 3 rays (at top) toward fourth as compared with true calthrops (view *1*); *3,* equiradiate protriaene, with 3 rays curved away from fourth; *4,* subtriactine, with 3 equal rays arranged as in view *2,* and the fourth (or, rhabdal ray) represented by a rudiment; may occur as a variant of views *1, 2,* or *6; 5,* anatriaene with 3 equal rays (cladi), and a shorter fourth (rhabdal) ray; this type may grade to forms with rhabdal ray reduced to a rudiment, which may be termed anatripods; *6,* typical plagiotriaene, with rays arranged as in a calthrops (view *1*), but with a rhabdal ray longer than 3 others that are taken as cladi; as drawn here, this form is approaching a long-shafted triaene into which it passes gradationally; *7,* dichotriaene, with an unbranched rhabdal ray (pointed downward) little longer than branched cladi; *8–10,* cladome of triaenes (or subtriaenes), as seen with the rhabdal ray toward front; *8,* simple triaene; *9,* dichotriaene; *10,* trichotriaene (new).

LENDENFELD, 1903; DE LAUBENFELS, 1955) have varied some of his concepts, placing emphasis on curvature of the cladi, or citing different angular relationships. In practice, it is difficult to maintain a consistent
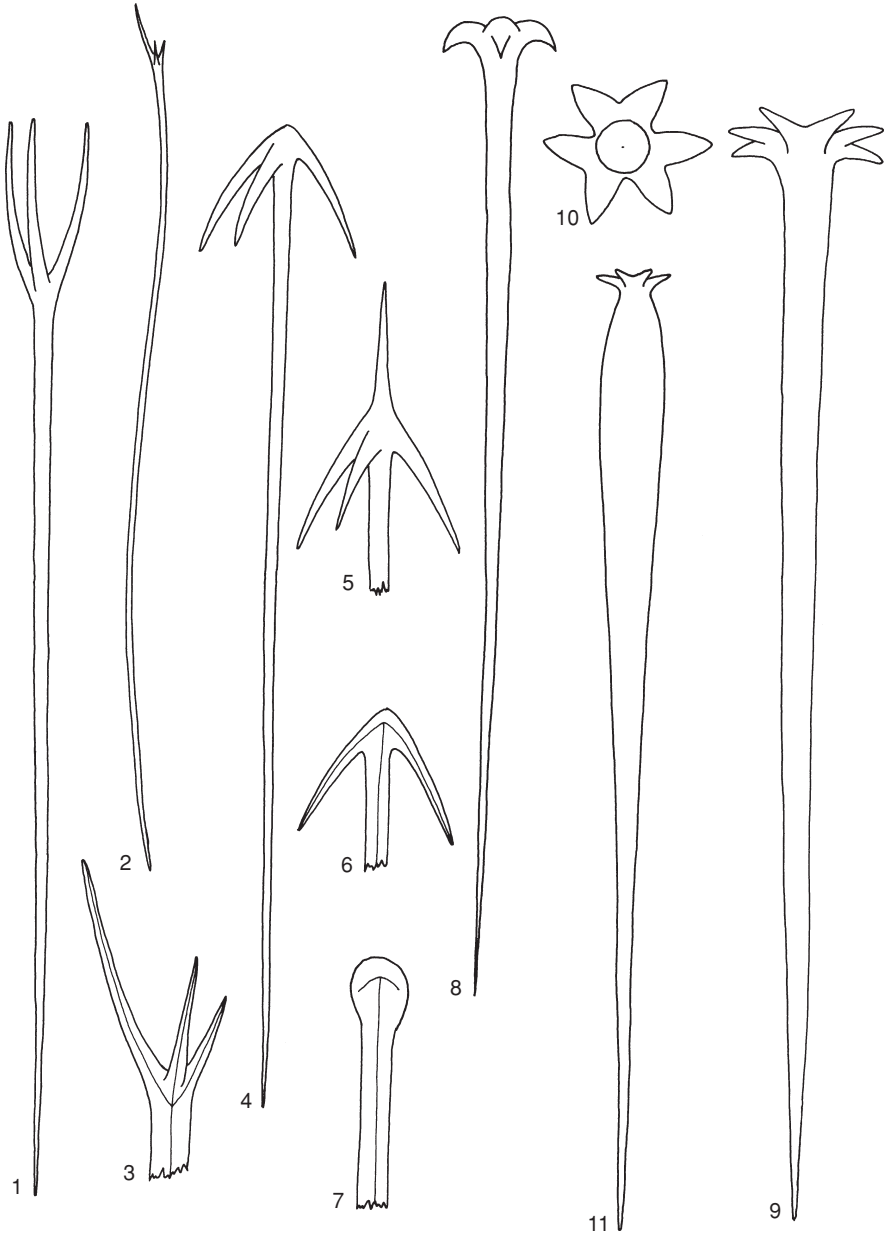
FIG. 21. Long-shafted triaenes and some variants; *1,* long-shafted protriaene, with rhabdome (i.e., long rhabdal ray) about 6 times as long as cladi; *2,* hairlike (trichodal) protriaene of *Tetilla* SCHMIDT with unequal (1 long, 2 short) cladi; *3,* cladal end of same spicule, showing the axial filaments; *4,* typical anatriaene; *5,* mesotriaene variant of view *4* with a second rhabdal ray (pointing upwardly) about same length as cladi; *6,* anadiaene variant of view *4; cladal* end, showing axial filaments; *7,* pseudotylostyle variant of view *6; cladal* (or, tylote) end, showing axial filaments; *8,* long-shafted orthotriaene with recurved cladi, not strictly an anatriaene but approaching that type (see view *4*); *9,* long-shafted dichotriaene, with cladi little longer than maximum diameter of rhabdome; *10,* cladome of view *9* with rhabdal ray (or, rhabdome) toward front; *11,* trachelotriaene, with swollen, clublike rhabdome; cladome as in view *10* but its total diameter little greater than maximum diameter of rhabdome (may be less in some examples) (new).

nomenclature. The problem is partly that the four types distinguished intergrade so that any distinction is arbitrary and partly that the two criteria cited (angle between cladi and the rhabdome; curvature of cladi) vary independently. Some triaenes do not fit readily any named category; for instance, the cladi may begin at an angle of more than 135° to the rhabdome, as in some protriaenes, but curve back toward it or grow out initially as in orthotriaenes but curve strongly away from it. The principal differences are in usage of the terms plagiotriaene and orthotriaene; the writer uses these essentially in the sense they were given by VON LENDENFELD (1903, 1907).

Triaenes are also described as long- or short-shafted, according to the length of the rhabdome; but, again, authors differ in what they mean by long and short. Herein triaenes are called long-shafted if the rhabdome is twice or more than twice as long as the cladi. It is also convenient to make a further distinction between triaenes *s.s.,* with the rhabdome longer than the cladi, and subtriaenes in which it is not longer or is shorter.

e. Spicules with a conspicuous ornament but otherwise simple shapes are named by addition of a prefix to a general name. The main instance is that of spiny spicules, called **acanthoxeas** or **acanthostyles.** The prefix **cric-,** as in **criccalthrops** and **cricostyle,** implies strong annulation, which occurs mainly in some fossil spicules. A strongly annulated monaxon with both ends tylote is a **cricorhabd.**

Another development in monaxons, conveniently treated as ornament, is development of annular to spherical enlargements at the center or at several points between the two ends, without continuous ornamentation. These spicules are **centrotylote** if a single central feature is present and polytylote if there is more than one. The latter type is uncommon and is usually a variant of a tylostyle.

f. The prefix **micro-** designates small spicules, as in microcalthrops or microxea. This usage is restricted here to microscleres but has sometimes been applied to the small spi-

cules of Plakinidae or to small crepides of lithistid desmas.

TETRAXONS AND TRIAXONS

The regular tetraxon, the calthrops, is the central type of demosponge spicule from which all other types have arisen according to a concept due principally to SCHULZE (1880, 1887a) and DENDY (1905, 1916, 1921). A sponge without tetraxons as megascleres or in any form is supposed to have lost them in phylogeny. These ideas are based mainly on the characters of some simple Demospongea with small spicules, comprising the family Plakinidae SCHULZE. The spicules of these sponges are mainly tetractinal but occasionally diactinal, triactinal, or pentactinal, with diactines or triactines predominant in some genera. Diactinal spicules intergrade with triactines or sometimes tetractines through forms in which one or two rays are rudimentary. They may be either angled centrally or markedly irregular when strictly diactinal; this is regarded as showing the origin of monaxons as secondary diactinal derivatives of triactines or tetractines. Tetractinal spicules may be modified by branching but are never true triaenes. In *Plakina* SCHULZE the soft parts are unusually simple: a eurypylous adult develops by diverticulation of a rhagon (SCHULZE, 1880) and may sometimes lack an ectosome (*P. monolopha* SCHULZE). If these sponges are interpreted as primitive, their simple diactinal to pentactinal spicules can be seen as representing the prototypes of all spicules of other Demospongea whether megascleres or microscleres. The primary basis of different types of spiculation then seems to be meristic variation, with all other developments secondary. In megascleres, triaenes are explicable as functional calthrops derivatives that support the ectosome, to which the cladome is typically directed.

In addition, some choristids with tetractinal megascleres in the form of triaenes only have the latter much subordinate to monaxons (usually oxeas) and resemble closely some monaxonids with similar microscleres (euasters or sigmaspires, see p.

19, 30). In a few forms, the triaenes are so inconspicuous that until their discovery a sponge (e.g., *Stellettinopsis* CARTER) has been supposed to be monaxonid. Hence it has been argued that some (SOLLAS, 1888) or all (DENDY, 1916, 1922) monaxonids are forms derived from choristids with triaenes by loss of these spicules. The designation epipolasid has this implication as used by SOLLAS and DENDY though not by DE LAUBENFELS (1936, 1955).

These ideas can provide a complete explanation of demosponge spiculation (see DENDY, 1921) but are not certainly correct. Their basis is comparative study of modern sponges, which are all end forms phylogenetically, without stratigraphic evidence. In fact, the oldest monaxonids are Cambrian in age, but the oldest certain choristids are Late Ordovician. This may be due only to incompleteness of the stratigraphic record, which is very sporadic, or to forms with monaxons being simply the first to develop spicules large enough to be preserved. SOLLAS (1888), however, regarded at least some triaenes as derived from monaxons because long-shafted triaenes can develop ontogenetically from an initial monaxon. This can be thought to be more consistent with the paleontological evidence, although this involves assuming that ontogeny follows phylogeny, which is clearly not always correct; SOLLAS also admitted that some triaenes have no sign of this origin. DE LAUBENFELS (1936) noted loss of triaenes as a possible mode of origin of monaxonids in his order Epipolasida but thought that the calthrops as a megasclere is usually derived from a triaene by shortening of the rhabdome. Even DENDY (1922) held that some subtriaenes seem to be derivatives of normal, long-shafted triaenes (*Paratetilla* DENDY). Further, various authors since VOSMAER (1882, 1883, 1884, 1885, 1887) have seen no close connection, or none in DENDY's sense (e.g., TOPSENT, 1928b), between one group of monaxonids (those with sigmatosclere microscleres, p. 35) and sponges with tetraxons, and LÉVI (1957b) has suggested that their spicules are

of independent origin. Last, *Plakina* has embryos of a type (**amphiblastulas**) unknown in any true choristid or any other form possessing megascleres.

As a brief assessment, before full discussion, herein the calthrops is regarded as being acceptable, morphologically, as a central type of spicules in Plakinidae, in most choristids, in monaxonids with euaster microscleres, and in some lithistids; but it does not certainly follow that its symmetry is not secondary or even that all tetraxons are homologous. There are various instances in which the ideas of SOLLAS or DE LAUBENFELS fit the facts at least as well as those of DENDY. Some monaxonids seem to be genuinely allied to choristids, but most have no demonstrable relationship to sponges with tetraxons; though, equally, it does not seem demonstrable that any are of independent origin. More generally, most of the evidence available is from modern forms, which can give no objective indication of the direction of phylogeny, whatever may seem likely. Herein, therefore, the SCHULZE-DENDY picture of phylogeny is not taken as a basic assumption, although parts of it seem justified.

It is also often said that hexactinal triaxons occur only in Hexactinellida and never in Demospongea. This idea is fundamental to SCHULZE's (1887b) picture of phylogeny in siliceous sponges; it is argued of tetraxons and triaxons that neither can give rise to the other, so that each must have arisen independently in separate stocks. The orders Tetraxonia (-ida) and Triaxonia (-ida) used by SCHULZE (1887b), SCHRAMMEN (1912), and others (LAGNEAU-HÉRENGER, 1962; REZVOI, ZHURAVLEVA, & KOLTUN, 1962) express this concept taxonomically.

In fact, triaxial spicules occur in many living Demospongea, although not normally as megascleres. They occur mainly in forms possessing euaster microscleres (p. 30), in which six-rayed euasters are usually triaxial in form. These spicules cannot be dismissed as really anaxial, because large examples may have an observable axial system (e.g., VON LENDENFELD, 1907, pl. 28, *13*). A four-rayed

euaster, however, is usually a calthrops and thus a tetraxon. The relationships of tetraxial and triaxial euasters is simply that of four- and six-rayed members of a meristically varying series, with the rays arranged at equal angles that depend on their number. Occasional triaxial megascleres have also been recorded as abnormal hexactinal variants of a normal calthrops (*Calthropella simplex* Sollas, 1888) or centrotriaene (*Yodomia perfecta* Dendy, 1916); in addition, a pentactinal triaxon is known as a variant of a normal orthotriaene (*Sphinctrella cribrifera* Sollas, 1888). The fossil *Spiractinella* Hinde with mainly triaxial megascleres also seems to be a demosponge, since less common, four-rayed spicules are calthrops and triaenes (Reid, 1963c).

It cannot be claimed, therefore, that tetraxons and triaxons must have independent origins or that triaxon spicules are only found in Hexactinellida. The true distinctive feature of hexactinellidan spiculation is that all the spicules present are either hexactinal triaxons or variants of this type with fewer rays, excepting only some monaxons whose relationship to triaxons is not demonstrable. I am unaware of any grounds for asserting the homology of hexactinellidan triaxons with those of Demospongea; the latter seem more likely to have arisen independently in various demosponges, and this must be so if tetraxons are the central type of demosponge spicule.

MICROSCLERES

Because of their bearing on the relationships of choristids, monaxonids, and lithistids, a knowledge of the microscleres is desirable before megaspiculation is considered.

Demosponge microscleres vary widely in form and have many shapes that do not occur in megascleres. For several reasons, they are difficult to treat systematically. A purely morphological treatment is unsatisfactory because of numerous instances in which forms that are similar morphologically appear to be convergent homeomorphs; but a true homological treatment is even more dif-

ficult because of the number of examples involved, and because evidence of homologies is often lacking in those examples that are disputable. There are also various artificial problems, due to differences in opinion or usage, resulting, for example, in the same spicule taking different names or a given name having different meanings in the works of different authors.

Some examples of these problems are as follows.

1. In the *Challenger* nomenclature, Sollas (1888) grouped all polyactinal and pseudopolyactinal choristid microscleres as asters and divided these further into (a) euasters, with rays (or, apparent rays, emitted from a center), and (b) **streptasters,** with rays arising from an axial part, which is usually spiral (hence the prefix strept-, twisted). A variety of further named types were distinguished within these groups. Later work (Dendy, 1924b) demonstrated that some types included (**plesiasters, metasters,** and **spirasters** of the choristid Pachastrellidae and Theneidae) as streptasters have sympodial axes produced by repetitive branching. A nonspiral type called a **sanidaster** is restricted to the first group, but de Laubenfels (1955, p. 30) defined it as comprising straight spiny monaxons and also included forms with fine spinulation called spiny microrhabds (not streptasters) by Sollas (*Halina (Dercitus) bucklandi* Bowerbank per de Laubenfels, 1955, p. 43, fig. 23,*lb*). Sollas's (1888) streptasters thus included two types of spicules, each of which has since been called streptasters in different restricted senses. In addition, the spiraster type of choristid streptaster is homeomorphic with some monaxonid microscleres that appear to be spiral monaxons, called spinispiras by Dendy and Burton (and herein, p. 32–33) but spirasters by de Laubenfels.

2. In Dendy's (1916, 1917, 1921, 1922) nomenclature, a microsclere regarded as a spiny monaxon or as derived from this type even if euastriform morphologically, is called a pseudaster. This usage has been followed by some authors (e.g., Burton) but not others

(e.g., DE LAUBENFELS, 1955). The term has also been used for euastriform spicules of various monaxonid sponges in which evidence of homology is lacking, on a basis of subjective assessment of other characters irrespective of the form of the microscleres. Furthermore, even if a seeming euaster intergrades with a monaxon, there is no certainty that either is the prototype phylogenetically, although DENDY's view seems generally more likely.

3. Some choristid sponges (Craniellidae) have twisted monaxial microscleres called **sigmaspires** by SOLLAS (1888), with a spire of about one revolution and appear C-shaped or S-shaped, according to how they are viewed. These were regarded (SOLLAS, 1888) as distinct from similar sigmas of various monaxonid sponges (e.g., Desmacidontidae). Various later authors have equated these spicules as sigmas (e.g., VON LENDENFELD, 1904b; HENTSCHEL, 1909), and DENDY's classification (1916, 1917, 1921, 1922) depends on assuming their homology. But TOPSENT (1928b), since followed by BURTON, rejected the identity of these microscleres and the picture of phylogeny DENDY based on it. DENDY's ideas were rejected by DE LAUBENFELS (1936) but still called both types sigmas. As a further complication, some sigmaspires pass into spicules that would be called chelas if found in Desmacidontidae but were called sigmaspires by TOPSENT (1928b) because of their evident homology with that type.

It is therefore not possible to give an account of the microscleres that conforms with all previous usages. The attempt is made herein to combine the best features of the previous literature with some original views where this seemed desirable. In part, a homological treatment is attempted, in that some types of microscleres are noted as characteristic of various groups of sponges in which they can be thought to be homologous. If, however, a morphological type recurs sporadically in sponges with no evident special relationship, it is usually considered as repetitive.

Fossil Demospongea having the megascleric skeleton contain rarely microscleres, but most of the main types are known from some sedimentary rocks.

a. EUASTERS

Defined morphologically, a euaster is any microsclere in which rays or apparent rays radiate from a center. Euasters occur mainly as the characteristic microscleres of the choristid Calthropellidae, Ancorinidae, and Geodiidae and the monaxonid Coppattiidae and Tethyidae in which they have similar characters. The euasters of these sponges are meristically varying spicules with up to a hundred rays or more and are typically polyactinal, although tetractines or triactines may be present. Diactines or monactines may also occur as further meristic variants, although not strictly euasters morphologically. Tetractinal and hexactinal examples are usually tetraxons (microcalthrops) and triaxons respectively, although they may also have other shapes. The simplest euasters are **oxyasters,** with finely pointed rays and no central swelling. In variants in which the rays have developed differently, the latter are blunt or flat ended in strongylasters, knobbed terminally in tylasters, or spiny in anthasters. The tylaster type is also sometimes called a chiaster, because four-rayed examples with curved rays can be *chi*-shaped. An anthaster with spines developed mainly at the tips of the rays is called an acanthotylaster by some authors. Any of these types may be modified by occurrence of a central enlargement, the centrum, whose diameter may be less or greater than the lengths of the parts of the rays that project from it. Some authors use the term sphaeraster for any such spicules, but others restrict the term to forms in which the centrum is conspicuous (according to SOLLAS, 1888, when the diameter equals or is greater than one third the length of the rays). In specialized sterrasters, restricted to the choristid Geodiidae, a highly polyactinal initial oxyaster solidifies from the center outward, until the rays are marked only by fine surface granulation. A smooth

depression, the hilum, on one side of the spicule often marks the position of the secreting scleroblast, within which the sterraster was formed. Some sterrasters are markedly kidney shaped rather than spherical, a type sometimes called a rhax by paleontologists (following RAUFF, 1893). A flattened discoidal variant of the sterraster is an aspidaster. A spicule intermediate between a sphaeraster and a true sterraster is a sterrospheraster.

If DENDY (1921) is followed, these euasters may be seen as comprising meristic variants of a central tetraxon (microcalthrops), with variation mainly in a positive direction though negative variants also occur (triactines, diactines, monactines). In fact, there is no sure indication that any type is central, although four is the maximum number of rays in normal megascleres.

Various further monaxonids have microscleres in the form of polyactinal euasters, without pauciradiate (few-rayed) variants (pentactines, tetractines, triactines, etc.), which have no demonstrable relationship to the euasters described above. Other similar spicules are gradational with intermediates into a monaxial microsclere (e.g., a spinispira, p. 33) or megasclere (e.g., an acanthostyle) and may then be called **pseudoeuasters** if supposed to have been derived from the monaxons. There may be sometimes comparative evidence that a seeming euaster is really a pseudoeuaster, for instance, if an apparently related species contains forms that pass into monaxons.

b. STREPTOSCLERES

This name was adopted (REID, 1963b) for the streptaster microscleres of the choristid Pachastrellidae and Theneidae, also called dichotriacts by DENDY (1924b), because of confusion in usage of the term streptaster and because most of these spicules are not dichotriactines morphologically.

Streptoscleres are streptasters *sensu* SOLLAS (1888) that appear to have meristic variations on a pattern of dichotomous or more complex branching. The simplest typical streptosclere is a spicule that appears to have two branches at the ends of a short central shaft, either in the same plane or in different planes. This type is often accompanied by simple triactines, which in turn grade into oxeas through various irregular intermediates; by comparison, it seems to be a dichotriactine, with one ray branched dichotomously. Other typical streptoscleres have more complex branching (e.g., trichotomous) or repeated heterotomous branching with production of composite (sympodial, DENDY, 1924b) spiral axes. Individual types distinguished are (i) plesiasters, with a short straight axis; (ii) metasters, with a spiral axis making less than one revolution; (iii) spirasters, with an axis making one to several turns; and (iv) amphiasters, with branches in whorls at the ends of a straight central shaft. In practice the picture is more complex, since these types intergrade in all directions. Other complications are (a) that morphological spirasters and amphiasters need not be streptoscleres (see sanidasters, p. 29, and spinispiras, p. 32–33); and (b) that VON LENDENFELD (1907) used metaster as a general name for streptoscleres.

DENDY (1924b) regarded streptoscleres as unrelated to euasters, but VON LENDENFELD (1907) regarded them as aster-derivatives. VON LENDENFELD's view seems more probably correct; microscleric triactines, regarded as the central type (DENDY, 1924b), are widely distributed as pauciradiate euasters; and some forms with streptoscleres (e.g., *Thenea wrightii* SOLLAS) have other oxyasters with up to six rays. There are also several instances in which Ancorinidae have euasters passing into spicules resembling plesiasters (e.g., *Tethyopsis dubia* WILSON), although these forms can also be compared with sanidasters.

By thickening of the axial part, a streptosclere of spiraster or amphiaster type may pass into a spicule resembling a monaxial spinispira (p. 32–33) or a type of amphiaster related to sanidasters. These forms can be identified usually as streptoscleres by association with typical examples but could not be recognized as such if found dissociated.

c. MICRORHABDS, SANIDASTERS, AND VARIANTS

A typical **microrhabd** is a straight monaxial microsclere without raylike spines, although fine spinulation may be present, and is usually an oxea (or microxea) or a strongyle (microstrongyle). These same names may also be used for curved specimens unless there are grounds for regarding these as forms of a sigmaspire (p. 32) or a spinispira (p. 33–34). A short microstrongyle may be almost as thick as it is long or pass into a sphere (p. 36); if spinulate, this type has sometimes been called a phalangaster. A spinulate microrhabd with relatively few, large, raylike spines is a sanidaster or an **amphiaster** if the spines occur in whorls at the ends. The relationships of these spicules may be shown by mutual replacement in species of one genus (e.g., *Sanidasterella* Topsent) or intergradation in one species.

In forms with euasters or streptoscleres, a microrhabd may be identifiable as a diactinal euaster or streptosclere. Microrhabds and sanidasters accompanying euasters but not directly comparable to each other are often assumed to be their homologues, and a sanidaster may pass into a euaster through intermediates. But microrhabds also occur in many other sponges without euasters, and comparative evidence may then suggest that, for example, a microxea in one species is equivalent to a megascleric oxea in another. Thus microrhabds appear to have several different origins and have probably arisen independently in many different sponges.

Spiny microxeas and sanidasters are streptasters *sensu* De Laubenfels (e.g., 1955), at least by that author's definition; but he also sometimes used the name for streptoscleres with composite axes. They are not the streptasters of Burton (1959), which are streptoscleres. A spiny microxea is a streptaster *sensu* De Laubenfels but not in Sollas's original (1888) sense.

d. SIGMASPIRES AND VARIANTS

Sigmaspires are arcuate to spiral monaxial microscleres that occur especially in the choristid Craniellidae (Tetillidae auctt.), although indistinguishable spicules also occur in some monaxonids and lithistids. A typical sigmaspire is a blunt-ended, spiral monaxon of about one revolution, appearing C-shaped or S-shaped according to how it is viewed. Many examples are spinulate, although the spinules may be seen only at high magnification. Simple variants range toward a true, flat C-shape or pass into **toxaspires** making rather more than one revolution and appearing bow-shaped in some aspects. A strongly spined spiral sigmaspire has sometimes been called a sigmaspiraster. In *Chrotella* Sollas, C-shaped variants have spines in two opposite lateral rows along their length or restricted to the ends; the latter type resembles the chelas of some Desmacidontidae (*Treatise Part E (Revised),* vol. 3, in press) but have still been called sigmaspires (Topsent, 1928b) because of their evident homology.

Various authors have termed sigmaspires as **sigmas** (e.g., von Lendenfeld, 1904c; Dendy, 1924b; De Laubenfels, 1936), although the latter name was based (Ridley & Dendy, 1887) on partly comparable microscleres of monaxonid sponges (e.g., Desmacidontidae) with no evident relationship to craniellids. Herein Sollas (1888) and Topsent (1928b) are followed, as by Burton (e.g., 1959), who thought these types distinct. Their homology was also rejected by De Laubenfels (1936), although he still called both sigmas (1936, 1955). In von Lendenfeld's (1904c) nomenclature, the term sigmaspire was expanded to take in the spiraster type of streptosclere, which, however, he later called a metaster (von Lendenfeld, 1907).

e. SPINISPIRAS AND VARIANTS

Spinispiras and their variants are the characteristic microscleres of the monaxonid Spirastrellidae and Clionidae, which appear to be closely related. Typical spinispiras are blunt-ended (strongylote) monaxons of one to several revolutions bearing spines of varied size that may also have spiral arrangement. They vary from finely microspinulate strongylospires, with many small spinules

that are not arranged spirally, to stoutly spined forms homeomorphic with a spiraster streptosclere. Intermediates between these extreme forms have spines of moderate size along the outside of the spiral. Coiling is usually tight in polyspiral examples, although some springlike forms occur; but short forms may resemble a sigmaspire, although usually stouter. In other variations, a spinispira may pass into (i) a smooth strongylospire; (ii) a C-shaped or straight microstrongyle, with small spinules that are not arranged spirally; (iii) a C-shaped form, strongly spined externally, called a sigmaster herein; (iv) a straight monaxon with spines arranged spirally; (v) a straight amphiaster, with spines in whorls at the ends; or (vi) a similar discaster with further whorls between the ends. In *Placospongia* Gray, a short, long-spined, initial spinispira solidifies, producing a spicule resembling a sterraster, although distinguished by its different ontogeny. Initially mistaken for a genuine sterraster (Sollas, 1888), this form is now called a sterrospira (Dendy, 1921, and herein) or a selenaster (de Laubenfels, 1955).

Because coarsely spined spinispiras resemble the spiraster form of streptosclere, all spinispiras are sometimes called spirasters (e.g., de Laubenfels, 1936, 1955); but a finely microspinulate strongylospire is not a spiraster morphologically in the sense of possessing raylike spines. The coarsely spined forms are streptasters *sensu* Sollas (1888), but the group does not seem to be related to the streptosclere series (above, p. 31). The spiraster forms are homeomorphic, but the range of variation in the two groups follows different patterns. In particular, the characteristic morphological passage from spiraster to microtriod through intermediate metasters and plesiasters, as in streptoscleres, never occurs in spirastrellids or clionids. There are no other grounds for believing that these families are closely related.

The homology of the spinispira group is debatable. A spinispira is essentially similar to the spinulate sigmaspire, although typically polyspiral; but no sure connection can be demonstrated between the choristid Craniellidae and the monaxonid Spirastrellidae and Clionidae. In *Timea* Gray, usually classified as a spirastrellid, the microscleres are typically euastriform (usually sphaeraster) but sometimes pass into sigmasters; this was read by Dendy (1921) as meaning that the seeming euasters are pseudasters but could also be taken as suggesting derivation of spinispiras from euasters. Some spinispiras have observable axial filaments, however, and thus seem to be genuine monaxons. A finely spinulate form may also share identical spinulation, a central annulation, or both with a megascleric oxea, which is the most likely prototype.

f. SIGMATOSCLERES

This name was adopted by Reid (1963b) for sigmas and other forms that are the characteristic microscleres of the monaxonid Desmacidontidae, also occurring in some other monaxonids and sublithistids.

A typical sigma is a smooth, sharp-ended (oxeote), C-shaped monaxon or a similar form with the ends out of line, and then C-shaped or S-shaped in different views. If the ends are markedly out of line, it is said to be contort. In variant conditions, a sigma may (i) have one end reversed, producing a genuine S-shape; (ii) approach a true spiral shape; or (iii) bear a short external spine centrally or two opposite central spines directed inward and outward. Sigmas of some genera have hooked ends of markedly different sizes or in one instance have sawtooth external serrations on the hooked ends. A rare chiastosigma, apparently related to centrally spined sigmas, resembles two sigmas crossed centrally and is *chi*-shaped in some aspects.

The other types included as **sigmatoscleres** are mainly forms developed from a flat, C-shaped sigma in ontogeny, with the initial shape modified by secondary outgrowths. A **diancistra** has bladelike expansions, the fimbriae, on the inside of the curve and looks like a penknife with a partly opened blade at each end. A **clavidisc** is a similar spicule with the ends grown together, producing an ovate disc with a median slit running lengthwise. A canonchela is like a

clavidisc with additional lateral fimbriae growing out from the central parts and is larger on one side than on the other. The rest form a group known as cheloids, comprising chelas and apparently related types, with various types of lateral outgrowths at the ends or sometimes with spines on the convex side. **Chelas** occur in two main forms, called dentate and palmate. A **dentate chela** has grapnel-like ends, with inwardly curving thorn- or toothlike lateral outgrowths arranged in opposite pairs. The ends of the central shaft may also bear small lateral expansions or alae. Terminology of these spicules is sometimes further refined according to the number of terminal flukes, as in tridentate or quinquedentate (the number is odd because the end of the initial sigma forms a single central fluke). A few forms pass from this type of chela into so-called **amphidiscs,** with a symmetrical ring of recurved flukes at each end of a straight shaft. A palmate chela has inwardly facing ends and further lateral teeth when these are present, expanded to form leaflike palms; the alae are strongly developed and sometimes form hoodlike expansions. Either type of chela may have similar ends or one end larger than the other and is then an **isochela** or an **anisochela,** respectively. The two types are also intergrading, through dentate forms with terminal flukes markedly flattened, which are sometimes called arcuate. An unusual spheranchora resembles two clavidiscs intersecting at right angles but develops from a tridentate chela in ontogeny. A placochela has alae meeting in the middle to give the shaft a figure-of-eight shape and palms forming circular expansions on the inward facing ends. A **bipocillus** has lobate leaflike expansions at the ends or spoonlike expansions with the concave sides faced together. Forms often called spiny chelas, herein called **chelasters,** may lack the typical features of chelas but have stout spines developed on the convex side. The spines may occur without order or in partial transverse whorls. Most chelasters are obviously C-shaped, but short stout examples can resemble a sphaeraster in some aspects.

In other developments, a sigma may pass into a simple microxea, with one or more bends along its length, or a toxa with a central bend and the ends curved in the opposite direction. Spicules of these types are, however, found in many other sponges, in which they cannot be considered as sigmatoscleres. A tonglike forceps, found only in the Demospongea, is essentially a toxa with the two ends bent together. Some examples are smooth, but other bear spinules and small terminal expansions.

There are several different views of how these spicules are related. According to DENDY (1921) the central type is the sigma, derived from an oxea by way of a toxa, and the prototype from which the more specialized forms have arisen in phylogeny, as well as in ontogeny. For TOPSENT (1928b), a sigma was supposed to be derived from a simple euaster with the lost rays represented by the central spines of some examples; but a chela was a spicule derived from an amphiaster through an amphidisc. DE LAUBENFELS (1936) suggested that some sigmas are chela derivatives. There is no way of testing these contentions, but DENDY's view seems generally most likely. There is no objective evidence that sigmas and chelas had separate origins. The two types are often found together, apart from the chela arising from a sigma; and a chela may have the two ends out of line, as in the contort type of sigma. Moreover, the general spiculation of the sigma-bearing sponges is normally entirely monaxonid, and the supposed amphiasters of *Samus anonyma* GRAY that TOPSENT (1928b, p. 44) cited in this context are, in fact, amphitriaenes with true actinal cladomes. The same sponge has otherwise no special resemblance to the chela-bearing desmacidontids. Reversion to a sigma from, for example, a chela would certainly be possible, however.

DENDY (1916, 1917, 1921, 1922) also held that the sigma is homologous with the craniellid sigmaspire; but TOPSENT (1928b) and DE LAUBENFELS (1936) both rejected this idea and were followed by BURTON (e.g., 1959). As pointed out by TOPSENT, the two

are not identical morphologically: a sigmaspire is typically blunt ended, finely spinulate, and more spiral than C-shaped, but a sigma is typically sharp ended, unornamented and more C-shaped than spiral. There is also no evident relationship between the choristid craniellids and the sigma-bearing monaxonids, whose only close relatives appear to be the keratose sponges. A relationship imagined by Dendy (1922) is, again as said by Topsent (1928b), essentially based on preconviction. Sigmas and sigmaspires are, therefore, held herein to be convergent.

In alternative nomenclature, the dentate type of chela is called anchorate (e.g., de Laubenfels, 1955) or is called an **anchora** (ancre in Topsent, 1928b) with the term chela then restricted to the palmate type.

g. OTHER PSEUDASTERS

Some monaxonid sponges have further types of pseudastrose microscleres, which seem to have varying homologies.

In **discasters,** sometimes called **discorhabds** (Dendy, 1921), a monaxial shaft bears whorls of separate spines or discoidal flanges between the ends. The best known discaster is the so-called **chessman spicule** of *Latruncalia* du Bocage, in which the shaft typically bears a varying number of marginally serrated flanges, although separate spines may occur. Whorls of spines may also occur at the ends, or one end may be stylote or tylote. In *Sigmosceptrella* Dendy, a discaster with whorls of spines at the ends and between them develops from a sigma-shaped prototype, whose inward facing ends are engulfed by a thickened shaft during development. In *Barbozia* Dendy, a sharp-ended monaxon has two whorls or separate spines between the ends, and *Didiscus* Dendy has two simple discs.

Dendy (1921) interpreted these spicules as homologous and as pointing to the origin of the spinispira series from chelas; but this is not believed by other authors (e.g., Topsent, 1928b; de Laubenfels, 1936) nor followed herein. The genera cited have nothing else in common except that all are monaxonids. A spiraster-type spinispira passes into a spined discaster in *Spirastrella corticata* (Carter); but none of the other discasters pass into spinispiras and no spinispira or any other discaster develops from a sigma. Occasional imperfect variants of the *Latruncalia* discaster, or chessman spicule, are spiny styles or tylostyles and this spicule typically occurs at the surface of the body, where apparently related forms have small ectosomal styles or tylostyles. While not conclusive, this suggests its homology with the latter. The *Sigmosceptrella* discaster may be a chelaster homologically, but that of *Barbozia* is simply a modified oxea, and occurs in a sponge in which abnormal variants of a megascleric oxea may have comparable modification (Dendy, 1921). In *Didiscus,* the young forms of discasters and megascleric oxeas are initially indistinguishable. It seems likely, therefore, that these microscleres include forms with several different origins.

A euastriform microsclere with the form of a polyactinal sphaeraster may intergrade rarely with a spiny monaxial megasclere, which appears to be its prototype unless the opposite is imagined. The megasclere may be a diactinal oxea or strongyle, or a monactinal style or tylostyle, and the linking intermediates are shorter monaxons. This transition seems to correspond with occurrence of short variants of various smooth megascleres, for example, very short strongyles whose length is little more than their thickness, but with shortening carried to the extreme, and persistent spination producing a euastriform spicule. This type of passage from megasclere to microsclere in apparently homologous spicules does not occur in typical microscleres (although spinispiras may share ornament with a megasclere: see p. 32–33), and treatment of the present type as microscleres is essentially arbitrary. In another instance, short, finely spined tylostrongyles, corresponding to forms found as short variants of a typical tylostyle have sometimes been called korynasters (e.g., Schrammen, 1924a), although they are properly megascleres.

Various freshwater Spongillidae have amphidisc spicules, with a simple or serrated

transverse disc at each end of a straight shaft, or amphiaster variants with spines in two irregular clusters. These types may occur with a small acanthoxea and be linked with it by intermediate spicules. In *Dosilia* GRAY, a spiny-shafted amphidisc is accompanied by spicules with passage from acanthoxea to pseudoeuaster, by shortening of the monaxon shaft and growth of many secondary rays from its center, and also by double variants with secondary rays growing from two centers. The amphidisc itself may have variants with secondary rays on the shaft. Spongillid amphidiscs are similar morphologically to those found as uncommon variants of the dentate type of chela (*Iotrochota* RIDLEY; see also p. 34), with which they have sometimes been associated (e.g., DE LAUBENFELS, 1936); but no sure connection can be made between these spicules or the sponges in which they occur.

h. DRAGMAS

Some forms have very fine monaxial microscleres secreted in bundles, each bundle being formed within one scleroblast. These are called **dragmas** and may be straight orthodragmas or take the form of toxas or sigmas. Their hairlike fineness is sometimes described as trichodal. They are not known as fossils.

i. SPHERES

A number of choristid sponges contain microscleric spheres consisting of silica secreted around an initial granule or of two or more such bodies fused together. These forms appear to originate by abortion of a microrhabd, since occasional variants of composite examples may have one component replaced by a normally cored spicular ray. A short microstrongyle may also pass into a sphere by gradation.

DISTRIBUTION OF MICROSCLERES

The distribution of different types of microscleres discussed above, is difficult to summarize completely, but a number of general points are worth restating.

1. The most widespread microscleres are microrhabds, which occur in many choristids, monaxonids, and lithistids. They may occur either alone or with some other type (e.g., euasters or streptoscleres).

2. Euasters, streptoscleres, sigmaspires, spinispiras, and sigmatoscleres are each the characteristic microscleres of particular groups of demosponges, and the type characteristic of each of these groups is either rare or absent in the others. Forms with euasters or sigmatoscleres as the characteristic microscleres have none of the other types, unless sigmas are equated with sigmaspires. Streptoscleres, typical spinispiras, and sigmatoscleres are restricted to the groups they characterize, unless chelalike sigmaspire variants are equated with true chelas.

3. Any of these major types of microscleres may be present in one form only or in two or more differing in size, shape or both. Different forms of one main type may also be differently distributed anatomically; for instance, a sponge with euasters may have small oxyasters in the choanosome and large spherasters or sterrasters packing a cortex.

4. Other pseudasters and further minor types (dragmas, spheres) are distributed sporadically in various demosponge genera. Dragmas that are sigmas are restricted to sigma-bearing sponges.

5. Various Demospongea have no microscleres, although spicules identifiable as megascleres are present. Some of these sponges are otherwise identical or similar to various other forms with microscleres, but some are not.

The occurrence of the five main types of microscleres restricted to some groups of demosponges may be outlined as follows.

6. Typical euasters, in which pauciradiate examples have recognizable meristic variation, occur mainly in the choristid Calthropellidae, Ancorinidae, and Geodiidae, and the monaxonid Tethyidae and Coppatiidae. Simple euasters may occur in some forms with streptoscleres (Theneidae) and some

other sponges. Spherasters and sterrasters have recently been recorded in some fossil lithistids (Megamorina; Hurcewicz, 1966) but may be intrusive since a similar modern form has only spirasters (possible streptoscleres).

7. Streptoscleres occur mainly in the choristid Pachastrellidae and Theneidae but also in some members of two groups of lithistids (Tetracladina, Dicranocladina).

8. Sigmaspires are characteristic of the choristid Craniellidae but also appear to be present in a few monaxonids and lithistids. An apparent sigmaspire, which may not be homologous with these spicules, may also occur as a variant of a spinispira.

9. Spinispiras are restricted to the monaxonid Spirastrellidae and Clionidae, unless spirasters found in some lithistids are thought to be spinispiras.

10. Sigmatoscleres are characteristic of the monaxonid Desmacidontidae and some similar sponges and are otherwise found only in several desmacidontid-like sublithistids.

Occurrence of these five types as the characteristic microscleres of different groups of demosponges has led many since the *Challenger* authors (Ridley & Dendy, 1887; Sollas, 1888) to use them in classification, as either subordinate to the megascleres (see also Rauff, 1893; Schrammen, 1910, 1912; Topsent, 1928b) or providing the principal criteria of classification (e.g., Hentschel, 1909; Dendy, 1916, 1917, 1921, 1922; Burton, 1959; Reid, 1963b). But their use involves interpretative problems, in dealing with homologies (see previous section) and with forms that lack microscleres. The occurrence of five types as characteristic of groups of nonlithistids, which can also be thought to be homogeneous, and distinct in terms of their other characters, is here considered to be acceptable grounds for using these microscleres in the characterization of taxa. It is acceptable provided that such characterization is understood to rest firmly on this basis and not simply on a basis of occurrence of particular types of microscleres. Too little is known about most lithistids for them to be treated in this manner, however. The method is also unsuitable for general paleontology, because microscleres are nearly always lacking in fossil material, and because many fossil lithistids do not resemble modern forms with microscleres or distinctive microscleres.

SPICULAR ONTOGENY AND PHYLOGENY

In description of the microscleres, several instances have been noted if a specialized type of adult spicule is developed from a different prototype in ontogeny by secondary modification of its initial form. Examples include development of a sterraster from a polyactinal oxyaster (p. 30), of a sterrospira from a spinispira (p. 32–33), or of a diancistra or a chela from a sigma (p. 33). It is reasonably likely, although not surely demonstrable, that such changes in ontogeny correspond with an earlier change in phylogeny.

There are, nonetheless, occurrences that have an ontogenetic prototype need not represent a phylogenetic prototype. Because some lithistid desmas develop from initial tetraxons but others from initial monaxons or anaxial corpuscles, it was argued by Schrammen (1910) and Dendy (1921) that these types must have arisen independently. But in *Macandrewia* Gray there is intergradation between normally monaxial desmas and occasional tetraxial variants (Schmidt, 1880; Sollas, 1888; Topsent, 1904). This points to origin of one of these types from the other; moreover, whichever direction is ascribed to phylogeny, the ontogenetic prototype of the phylogenetic end form does not correspond with its phylogenetic prototype. In another example, intergrading phyllotriaenes and discotriaenes of some lithistids may develop from either a dichotriaene or a simple triaene. In turn, a discotriaene with simple and short to rudimentary axial filaments in the cladal disc may pass into a monaxial spicule, in which these filaments are lacking.

The ontogenetic prototypes of some demosponge megascleres, thus, seem to have
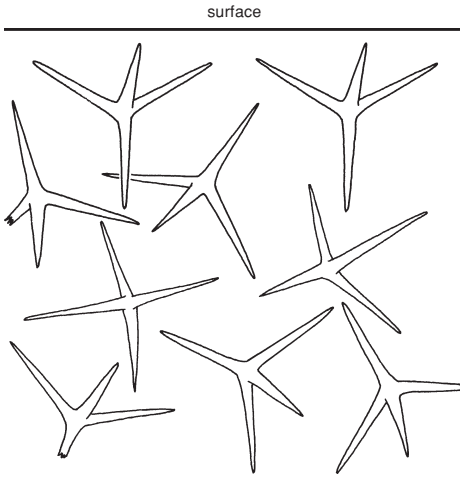
surface

Fig. 22. Choristid skeletons (type 1): all megascleres calthrops, oriented irregularly except that those near surface (top here) may have 3 rays pointing outwardly, 1 inwardly (new).

been subject to caenogenetic alterations in phylogeny, assuming that transitions in these spicules represent evolutionary sequences. This was not understood by SCHRAMMEN and DENDY, although shown earlier by SOLLAS (1888). Presumably the same principle may apply to microscleres. In particular, typical streptoscleres do not appear to develop from triactines, although their adult variations point to this prototype in phylogeny unless an opposite derivation (i.e., spiraster to triactine) is postulated.

MEGASPICULATION:
1. CHORISTIDS

The choristid Demospongea, the choristids, are nonlithistid sponges that either have megascleres with three or more rays, although monaxons may also occur, or have small analogous spicules not of megascleric size. The predominant form in the characteristic spicules is four-rayed (tetractinal) and tetraxial, although this type is sometimes replaced by triactines or rarely outnumbered by spicules with more than four rays. Tetraxial examples may be calthrops, subtriaenes, or true triaenes; and these types may occur alone or in any com-

bination. When triaenes are present as megascleres, one to several different sorts may occur. Monaxial megascleres are usually oxeas, but sometimes strongyles or styles. Additional microscleres may be present or absent; those of modern forms include euasters, streptoscleres, sigmaspires, microrhabds, sanidasters, and spheres but not spinispiras or sigmatoscleres.

The typical choristids are those with megascleres and greatly outnumber the others. It is difficult to generalize, but the megascleres are usually spicules with rays from 0.2 mm long to many times longer. The largest tetraxons are triaenes, in which the rhabdome may reach lengths of 10 to 20 mm or more in the body and may be considerably longer (e.g., 40 to 50 mm) in examples protruded for anchorage. The length of monaxons is comparable with that reached by the rhabdomes of triaenes, though either type may be larger than the other in a given sponge. Calthrops or monaxons may occur without regular arrangement, producing an irregular feltwork of interwoven rays; but triaenes are typically arranged with the cladi toward a dermal or gastral surface and the rhabdome running radially inward. Many massive forms whose megascleres are triaenes and monaxons have generally radiate architecture with all the megascleres following lines that radiate from a point within the body.

To distinguish three intergrading subtypes is useful for further description in which tetraxial megascleres are (i) all calthrops or subtriaenes or both; (ii) the latter intergrading with true triaenes; or (iii) all triaenes. As usual with nonlithistids, these can be illustrated best by reference to living examples, but some fossils are also relevant.

The first group is typified by *Halina* BOWERBANK, *Pachastrella* SCHMIDT, and similar genera. The megascleres may all be forms with three or more rays (*Halina*) or include monaxons (*Pachastrella*). The skeleton is never truly radiate and is sometimes entirely irregular; but calthrops or subtriaenes next to the surface may have three rays directed to-

ward it and the fourth inward, as is usual in triaenes (Fig. 22). Megascleres other than monaxons are most commonly tetractinal calthrops or subtriaenes, with other types (triactines, pentactines) either absent or present as only minor variants; but some forms have only triactinal megascleres or spicules with more than four rays as a characteristic feature. The fossil *Helobrachium* SCHRAMMEN has triactinal but tetraxial megascleres (**helotriaenes,** SCHRAMMEN, 1910), with the fourth ray represented by a buttonlike rudiment and the other rays hooked at the ends; because of these hooked ends the skeleton is loosely coherent, although lithistid features are absent. In the living *Yodomia* LEBWOHL, calthrops or subtriaenes are accompanied by smaller pentactinal centrotriaenes with occasional hexactinal variants.

Sponges with megascleres ranging from calthrops to true triaenes are exemplified by *Poecillastra* SOLLAS, in which they vary continuously from regular calthrops to plagiotriaenes or orthotriaenes, with the rhabdome up to several times longer than the cladi. The skeleton may be more or less irregular or have triaenes arranged radially near the surface but an irregular feltwork of calthrops internally (Fig. 23). If oxeas (monaxons) are present they may form radial bundles, and calthrops of the interior may then occur with one ray aligned with the oxeas and the other three directed outward. This condition approaches that of true radiate choristids, in which all the tetraxons are triaenes. In another development, the fossil *Propachastrella* SCHRAMMEN has irregularly felted calthrops and variants accompanied at the surface by presumably ectosomal dichotriaenes.

The fossil *Spiractinella* HINDE (Fig. 24) appears to have aberrant development of this type of skeleton, with the megascleres mainly of types having five or six rays. The most common megascleres are hexactines, **dichohexactines,** and two kinds of dichotetraenes; but others include calthrops intergrading with simple triaenes and rare **dichotriaenes.** The sponge is known mainly
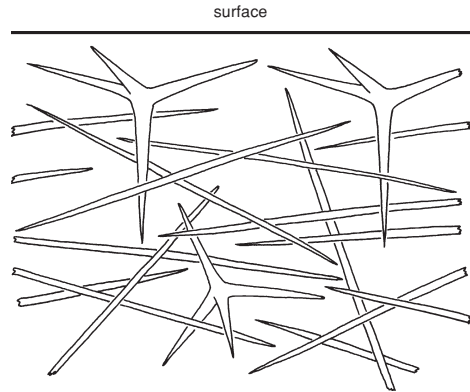

FIG. 23. Choristid skeletons (type 2): example with ectosomal triaenes and choanosome oxeas and calthrops; triaenes are short-shafted orthotriaenes arranged with 3 cladal rays toward surface and fourth (rhabdal) ray pointing inwardly; under their cladomes, presumed here to lie in ectosome, choanosomal skeleton consists of irregular feltwork of oxeas and subordinate calthrops (new).

still from dissociated spicules, but these occur together and share a distinctive spiral ornament. The dichotriaenes and one type of dichotetraene also share a peculiar style of branching, in which one large cladal branch stands roughly at right angles to the rhabdome, and a small branch is directed away from it but parallel with its axis (REID, 1963b). By analogy with later forms, the symmetrical hexactines, dichohexactines, and calthrops were probably spicules of the interior, with the triaenes and tetraenes underlying an external surface. This sponge was long thought to belong to the Hexactinellida, but the calthrops and triaenes require its reference to the class Demospongea. The dichohexactines, although outwardly similar to hexactinellidan **hexasters,** are megascleres (not microscleres) and have genuine actinal branching, as in demosponge dichotriaenes. The genus is also of interest because a similar sponge without tetraxons could not be identified as a demosponge from its spicules. A possible example is the contemporaneous (Carboniferous) *Stromatidium* GIRTY, whose known spicules are **polycladose** dichotetraenes with a strong spiny ornament; in genera from the
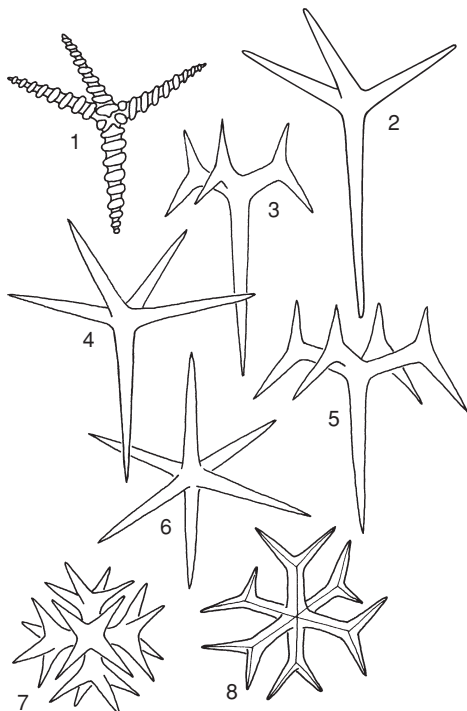
Fig. 24. Unusual choristids: *Spiractinella* Hinde (Lower Carboniferous); *1,* calthrops shows characteristic spiral ornament, omitted in other figures; *2,* short-shafted plagiotriaene, which intergrades with 1; *3,* dichotriaene, with cladal branches (or deuterocladi) arranged in vertical planes; *4,* tetraene, with 2 pairs of opposite cladi (= upper 4 rays as shown) making different angles with the fifth ray; *5,* tetraene with cladi developed as in 3; this type also grades into forms with the branches (deuterocladi) horizontal or recurved toward rhabdome (here pointed downward); *6,* regular hexactine; *7,* dichohexactine, with branches of opposite rays in different planes; *8,* lophose hexactine; this type grades into euaster-like forms by further shortening of primary rays; types 1 and 2 are less common than 5–8, and 3 and 4 are uncommon; because of prevalence of triaxons (view *6–8*), this sponge was mistaken for a member of class Hexactinellida before discovery of other types of spicules (new).

Carboniferous in Ireland, such spicules occur with similarly ornamented calthrops, although no clear relationship is demonstrable. Branching rays are also abnormal in hexactinellidan megascleres. But *Stromatidium* spicules may have union by fusion, which is known in many Hexactinellida but only found teratologically in proven Demospongea.

Typical triaenose choristids have all tetraxons developed as triaenes, which are often long shafted (Fig. 25). The triaenes are typically arranged with the cladome in or under an ectosome and the rhabdome running into the choanosome at right angles to the surface; their arrangement is, hence, radiate in forms of massive habitus. They are sometimes all of one kind but more often of two or three, in the range protriaene to anatriaene or also including dichotriaenes. Some forms have mesotriaenes with a short extra distal ray as variants of a normal triaene (usually an **anatriaene**). Triaenes of different types may also differ markedly in size in one sponge; hence forms of different types and sizes found loose in a sediment need not represent separate species. Accompanying monaxons (usually oxeas) may form an irregular choanosomal feltwork or have radiate arrangement; in the latter instance they may be grouped into radiating bundles that may radiate spirally in some sponges. Fully radiate sponges may have some triaenes in the interior as well as in their typical position. At the surface, either triaenes or oxeas may protrude through an ectosome, which is then **hispidated** (i.e., bristly) externally, and some forms protrude very long-shafted triaenes (usually anatriaenes) to form beardlike rooting structures. The proportion of triaenes and monaxons is also varied. In some forms the triaenes are so few that the sponge at first appears to be monaxonid, and some modern species (e.g., *Craniella cinachyra* (De Laubenfels), *Stellettinopsis corticata* Carter) were initially described as monaxonids. The triaenes of *S. corticata* are also still more readily overlooked because the length of the cladi is less than the thickness of the rhabdome.

This family has been called Ophiraphiditidae (Schrammen, 1910); but *Ophiraphidites* Carter was based on a macerated fragment with **ophirhabds** only, which could represent several monaxonids, see for example *Bubaris* Gray. The fossil Cephaloraphiditidae (Ophiraphiditidae auctt.) are peculiar choristids, whose choanosomal

megascleres are sinuous oxeas or ophirhabds intertwined to form a loosely coherent skeletal framework without true lithistid articulations. Tetraxons found at the surface and presumably ectosomal are mainly subtriaenes, which grade into calthrops or true triaenes with the rhabdome barely longer than the cladi. These forms are unusual in the absence of long-shafted triaenes, which are otherwise normally present when the internal megascleres are monaxial.

Sponges with small spicules analogous with true choristid megascleres are conveniently termed microspiculate. The length of spicular rays is generally less than 0.2 mm, down to less than a tenth of this. The spicules are usually mainly tetractinal but sometimes mainly triactinal (*Plakortis* Schulze) or diactinal (*Roosa* de Laubenfels) without including tetractines. The latter, when present, may have variants with more than four rays. In Plakinidae, tetractines may be normal or lophose calthrops but never triaenes. Simple lophose calthrops are typical of *Plakina* Schulze and may be monolophose to fully **tetralophose. Candelabrum** spicules of *Corticium* Schmidt are special tetralophose calthrops in which the branches of one ray are larger than those of the others and also bear spines on their external faces. In alternative usage, all forms of lophose calthrops are called candelabra. The arrangement of the spicules is generally like that of choristids with calthrops as megascleres, except that a candelabrum may occur with the major branches directed toward a surface or canal. Two other genera of doubtful relationship to plakinids have triaenose spicules. *Thrombus* Sollas (Fig. 26.1–26.2) has small spiny triaenes, sometimes varied as diaenes or tetraenes, with cladi unbranched or branched dichotomously or trichotomously. *Samus* Gray has comparable amphitriaenes with the cladi branched in one cladome only or both. The rhabdome of these spicules may have a central swelling of the axial filament, suggesting that they are really diactines with branching rays.
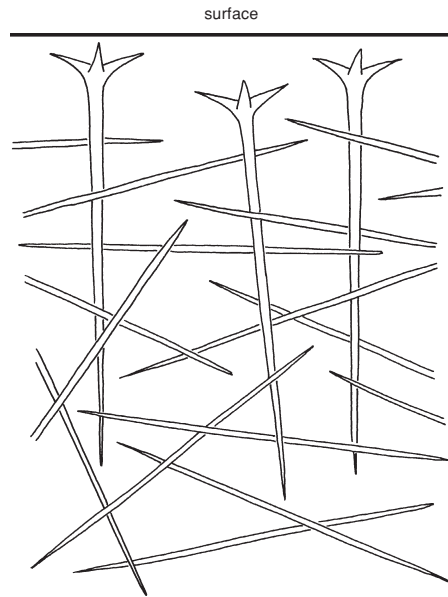

surface

Fig. 25. Choristid skeletons (type 3): with triaenes and oxeas only and radial arrangement of megascleres restricted to triaenes; triaenes are long-shafted orthotriaenes, arranged more or less radially with their cladi in or under an ectosome; choanosomal megascleres are irregularly felted oxeas (new).

Most living choristids, and all with megascleres, have an ectosome developed as a dermis or a cortex. The canal system is eurypylous to diplodal in different forms, with this range in both forms with megascleres and in microspiculate sponges. There may also be further complications, for example presence of chones (p. 16) in corticate sponges. A cortex may be soft or toughly fibrous; when euaster microscleres are present, the cortex may be packed with spherasters, sterrasters, or aspidasters to form a stony rind (Fig. 27).

Living choristids with megascleres include three main groups whose characteristic microscleres are euasters (Calthropellidae, Ancorinidae, Geodiidae), streptoscleres (Pachastrellidae, Theneidae), or sigmaspires (Craniellidae). There are none with spinispiras or sigmatoscleres. The commonest accessory microscleres are microrhabds, although sanidasters, related amphiasters, or
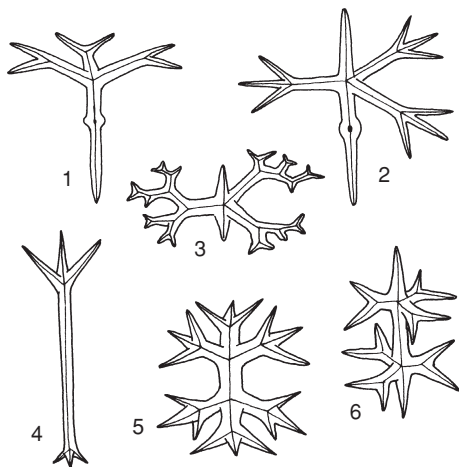
FIG. 26. Unusual choristids: *1–2,* spicules of *Thrombus* SOLLAS (Eocene–Holocene), with rhabdal rays showing a swelling of ray and axial filament that suggests a spicular center; 1, dichotriaene; 2, mesotriaene with trichotomous cladi (or, mesotrichotriaene); spiny ornament omitted in both; 3, centrotriaene of *Triptolemma* DE LAUBENFELS (Eocene–Holocene), with polycladose cladi; 4, heteropolar amphitriaene of *Amphitethya* VON LENDENFELD (Holocene); 5, equipolar amphitriaene of *Samus* GRAY (Holocene) with trichotomous cladi; 6, amphimesotriaene of *Ditriaenella* HINDE (Eocene–Holocene), with dichotomous cladi, and extra rhabdal rays at both ends of central shaft (new).

members of different families (or orders in some classifications). In addition, many members of three groups of lithistids (Tetracladina, Dicranocladina, Megamorina) have ectosomal dichotriaenes, which may be lost after death, and cannot be distinguished from choristid dichotriaenes; hence isolated dichotriaenes need not represent choristids and are especially open to suspicion in rocks that also yield triaene-bearing lithistids. On the other hand, very few lithistids have triaenes with unbranched cladi, and none have anatriaenes.

The oldest known choristids are Early Carboniferous, but their spicules range from calthrops or dichocalthrops to typical long-shafted triaenes, suggesting a longer history. Sediments containing these spicules may also yield apparent sterrasters, now found only as the characteristic microscleres of Geodiidae. Most fossil choristids resemble forms now living but are difficult to allocate with certainty because similar megascleres can occur in modern genera with different types of microscleres (e.g., euasters or sigmaspires). Exceptionally, specimens with microscleres preserved can be referred to modern genera (e.g., CHAPMAN & CRESPIN, 1934). A few fossil genera (e.g., *Helobrachium* SCHRAMMEN, *Cephaloraphidites* SCHRAMMEN) have megascleres with no modern counterparts.

MEGASPICULATION: 2. MONAXONIDS

The monaxonid Demospongea, the monaxonids, are nonlithistid sponges with megascleres that are all monaxons, except in some instances in which spicules with secondary rays replace a normal monaxon. Accompanying microscleres may be monaxial (microrhabds; sigmatoscleres), triactinal to polyactinal (euasters), or pseudopolyactinal (spinispiras; other pseudasters); or they may be absent. Spongin may be absent or may supplement the megascleric skeleton or largely replace it.

Existing monaxonids have very diverse characters and range generally from sponges

simple spheres are sometimes present. Some genera have no microscleres or none but microrhabds but are otherwise like forms in which distinctive types are present. The microspiculate Plakinidae have no microscleres, unless all of their spicules are referred to this category; this was done by SOLLAS (1888), but the lophose types do not occur as microscleres in any forms with megascleres. *Thrombus* has microscleres in the form of minute toothed amphidiscs, and *Samus* has sigmaspires.

Some choristids are preserved intact as fossils, but they are more often represented by dissociated megascleres. These should not be made the basis for erection of species or genera, unless they are especially distinctive. As seen from discussions above, several types of tetractines of different sizes may occur in one species; on the other hand, indistinguishable megascleres can be present in

that are otherwise almost identical with various choristids with mainly monaxial megascleres to forms in which the skeleton is produced mainly by reticulate spongin fibers and different individuals have a few spicules present or none. Between these extremes fall many other types, having various lesser resemblances to choristid or keratose sponges or with nothing markedly in common with either. The canal system varies from eurypylous to diplodal, as in choristid sponges. There is always an ectosome, which is sometimes a cortex but more often a simple dermis. The monaxial megascleres may be diactines (oxeas, strongyles), monactines (styles, tylostyles), or both; and any type of megasclere may occur in one or more forms. Many genera have smooth megascleres only, but in others some or all are conspicuously spiny. The spiny megascleres again may be diactines, monactines, or both. A few forms have pseudastrose megascleres. The arrangement of megascleres may be radiate, irregularly felted, or follow various patterns related to the presence of spongin. Megascleres of the choanosome and ectosome may be similar or different in form, arrangement, or both.

For further description, modern forms are conveniently divisible into three major groups, as follows:

i. more or less choristid-like sponges with euaster or sigmaspire microscleres, mainly diactinal megascleres, and normally no spongin;

ii. sponges with spinispira microscleres when any distinctive forms are present, with typically monactinal megascleres, and with spongin normally absent although occasionally small amounts occur; and

iii. sponges with sigmatoscleres or no distinctive microscleres, with diactinal or monactinal megascleres and with spongin commonly present and often conspicuous.

The last group also takes in nearly all forms containing spiny megascleres. These groups have various overlaps in the characters of the megascleric skeleton but do not represent intergrading types of organization,

surface

FIG. 27. Choristid skeletons (type 4): example with radiate structure, 2 kinds of triaenes, and cortical armor; spherical bodies beneath surface are sterraster microscleres, produced in choanosome but exported to cortex, where they accumulate to form stony armor; triaenes found under this layer are long-shafted orthotriaenes (4 shown) and smaller anatriaenes (1, at center); choanosomal megascleres are radially oriented oxeas (new).

as with groups distinguished above in description of the choristid sponges. In particular, forms with the contrasted types of microscleres are essentially nonintergrading, and how they are related is unknown.

In the first group, the Coppatiidae and Tethyidae are euaster-bearing monaxonids, of which some are closely similar to various ancorinid choristids apart from the absence of triaenes. The arrangement of megascleres

varies from confused, irregularly felted to fully radiate with the spicules grouped in bundles. The megascleres are usually oxeas, although exceptions occur. *Jaspis (?) serpentina* WILSON (1925) has oxeas of normal *Jaspis* species replaced by ophirhabds, like those of the choristid Cephaloraphiditidae. This sponge resembles the fossil *Heteroraphidites* SCHRAMMEN in which, however, absence of tetraxons could be due to their loss before burial. In *Tethya* LAMARCK, with a radiate skeleton, the megascleres are typically strongyloxeas (p. 25), sometimes passing into styles or even tylostyles, which are arranged with the pointed ends outward. Euasters of these sponges are similar to those of ancorinids with a range from simple oxyaster to sterrospheraster, and one sort or more may be present. As in ancorinids, a microrhabd or sanidaster may also occur. The ectosome is commonly a cortex and may be packed with spherasters or sterrospherasters, as in the choristid *Aurora* SOLLAS.

Trachygellius TOPSENT and *Raphidotethya* BURTON are comparable sponges, with oxea megascleres in radiating bundles but with sigmaspire microscleres like those of the choristid Craniellidae. The latter are triaenose sponges with radiate skeletons; among them, *Trachygellius* and *Raphidotethya,* which are both stalked sponges, come closest to *Amphitethya* VON LENDENFELD, which may have triaenes restricted to a stalk. The monaxonid *Stylocordyla* THOMSON, in which microscleres are absent, has a spirally radiate skeleton, reproducing a pattern that occurs in species of the choristid *Craniella* SCHMIDT.

Because such monaxonids can resemble closely various choristids in all characters but the absence of triaenes, some authors have regarded them as forms derived from triaenose choristids by loss of the triaenes. Genera for which this is claimed are sometimes called epipolasid, from SOLLAS's (1888) use of a family Epipolasidae. This name was not based on that of any genus included and is therefore invalid. The genus *Epipolasis* DE LAUBENFELS was established 48 years later, for such forms grouped with choristids in his taxon Choristida. The principal grounds for this idea are the rarity of triaenes in similar triaenose choristids, suggesting partial loss of the ability to produce this type of spicule, which could lead to its being lost completely. There is also good evidence of comparable losses of various other types of spicules, both megascleres and microscleres (e.g., BURTON, 1932). This idea was especially emphasized by DENDY (1905, 1916, 1917, 1921, 1922), who believed that all monaxonid sponges are derivatives of choristid ancestors. On the other hand, DE LAUBENFELS (1936) regarded derivations claimed by DENDY as either simply possible among other alternatives or unacceptable; the latter applies specially to alleged origin of monaxonids with sigmatosclere microscleres from craniellids with sigmaspires (DENDY, 1922), also rejected by TOPSENT (1928b). Close relationship of choristid and monaxonid sponges is probably genuine in the forms described above, although no evidence points objectively and certainly to the direction even of phylogeny. Some choristids with mainly monaxial megascleres and only rare triaenes can be so like the monaxonids cited that identification can depend on an author's observation. A relevant example is *Craniella cinachyra* (DE LAUBENFELS); initially thought to be monaxonid and described as a species of *Trachygellius* (DE LAUBENFELS, 1936), this sponge has since proved to have rare triaenes, even in DE LAUBENFELS's holotype (LITTLE, 1963). Here it seems likely that an otherwise similar sponge with monaxon megascleres only is a genuine relative. But other monaxonids have generally no comparable resemblance to any known choristid, and many have spicules or other features (e.g., spongin fibers) unknown in any choristid. While it is possible that such sponges are choristid derivatives, no general assertion is justified from the evidence available. There is, especially, no clear evidence that forms with sigmatosclere microscleres are related to any choristids except as demosponges.

A second group of modern monaxonids comprises forms with spinispira microscleres (Spirastrellidae, Clionidae) and similar

sponges with microrhabds only or no microscleres (Suberitidae, Polymastiidae). In this group, the megascleres are mainly monactinal and most typically tylostyles, although simple styles or oxeas may also occur. A few forms have the latter types only. The arrangement of the megascleres ranges from confused to fully radiate; in the latter instance, monactines are arranged with the pointed ends outward. The canal system varies from eurypylous to diplodal. The ectosome is often a cortex; it may then have a special ectosomal skeleton of small monactines arranged radially to form a cortical palisade. In some forms, the surface is made hispid by protrusion of ectosomal or choanosomal megascleres. In a special development of this condition, the hemispherical to discoidal *Radiale* SCHMIDT has a prominent equatorial fringe of large protruded spicules. A few forms (e.g., some *Polymastia* species) protrude long monactines in which the distal end is tylote, in contrast to normal internal tylostyles in which the outward end is azote. Very rarely, small amounts of spongin may occur cementing megascleres together (e.g., in *Suberites* species), but spongin fibers do not occur.

Typical examples of this group can again have some resemblances to triaenose choristids in radiate arrangement of the megascleres or in the presence of a cortex, but none resembles any known choristid in a manner suggesting origin by simple loss of triaenes. The spinispira microscleres are comparable with the sigmaspires of the choristid Craniellidae, but it cannot be asserted that these types are homologous (see p. 35).

Most other living monaxonids form a third group consisting of sponges with sigmatosclere microscleres and similar forms with only toxas, microrhabds, or no microscleres. These forms are several times more numerous than all other monaxonids together. Sigmatoscleres, when present, may be sigmas, more complex types (e.g., diancistras, chelas), or both. The megascleres may be diactines, monactines, or both, which may be smooth or conspicuously spiny. The canal system varies from eurypylous to diplodal, and the ectosome is usually a thin dermis, although rarely a cortex.

Spongin is commonly present, as either a cementing material or forming skeletal fibers that supplement the megascleric skeleton or largely replace it (Fig. 28). A few forms with fibrous spongin have sparse megascleres in some individuals but none in others, thus passing into keratose sponges. The arrangement of megascleres ranges generally from wholly confused to various special patterns related to the presence of spongin. When a skeleton has distinct meshes enclosed by cemented megascleres or by skeletal fibers, it is reticulate; it is isodictyal if the sides of the meshes are regularly subequal to equal (Fig. 28.1). A radiate arrangement of megascleres occurs occasionally.

When spongin is present, the skeleton may have a variety of conditions. If spongin fibers are absent, the arrangement of megascleres varies from wholly confused to a regular isodictyal pattern, in which individual megascleres are cemented together by their tips to enclose three-sided or four-sided meshes. Distinct spongin fibers are divisible into primary fibers, which radiate to the surface from a central or axial part of the body and secondary fibers that join primary fibers transversely. In forms with skeletal fibers, some of all megascleres are typically either embedded in the fibers or attached to them externally, as either coring spicules that are wholly enclosed within the fibers and aligned longitudinally (Fig. 28) or as **echinating** spicules (Fig. 29) attached externally by one embedded tip and directed obliquely forward. Most commonly, coring spicules are diactinal (oxeas or strongyles), and echinating spicules are monactinal (styles, tylostyles, acanthostyles); but exceptions can occur in both directions. Monactinal echinating spicules occur with the blunt (stylote or tylote) end imbedded in the fiber and the oxeote end outward.

Three types of spicule and fiber combinations are distinguished: (i) chalinid, in which only coring megascleres are present; (ii) axinellid, with echinating megascleres only
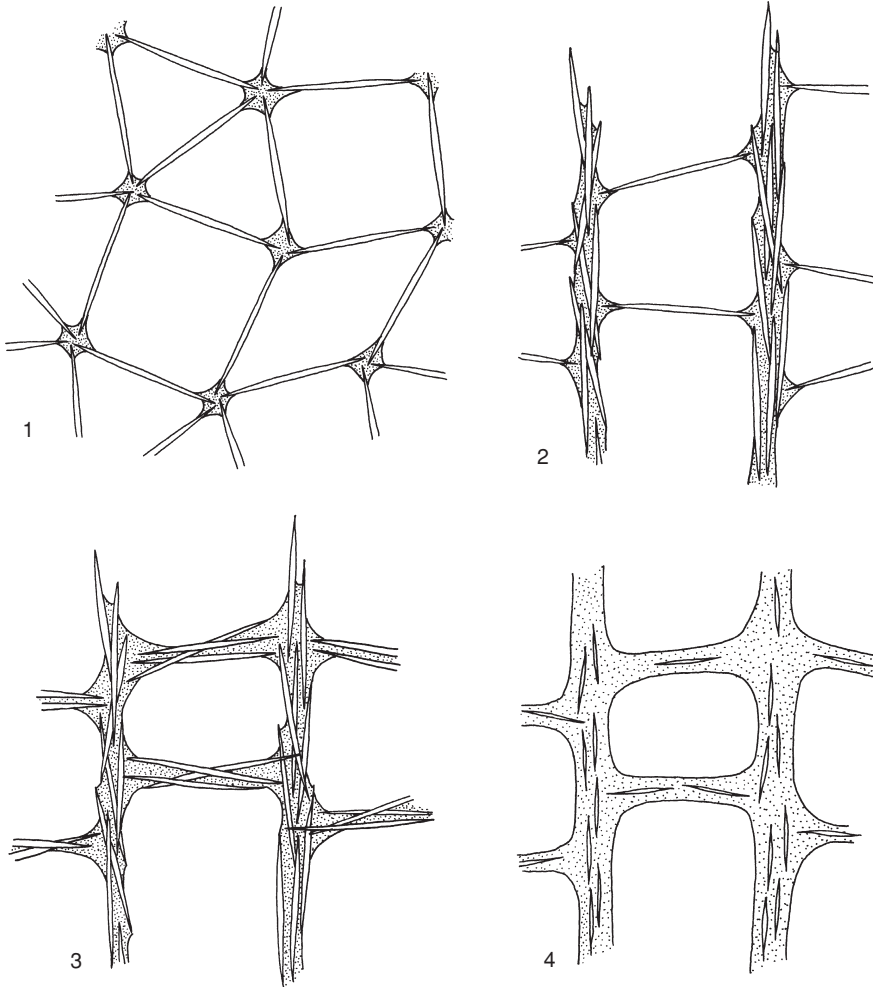
FIG. 28. Reticulate monaxonid structures, in which spicules are united by cementing or fibrous spongin; spicules oxeas in all figures; spongin *stippled; 1,* unispicular latticework of spicules united at their tips, with mainly three- and four-sided meshes; amount of spongin small; *2,* skeleton with multispicular fibers, formed by bundles of cemented spicules, and connected transversely by single spicules whose tips are imbedded in fibers; spongin more important than in view *1* but still subordinate to spicules; *3,* structure similar to view *2* but transverse connections also formed by multispicular fibers; *4,* skeleton formed chiefly by reticulate spongin fibers, which are cored by subordinate spicules; this type grades into forms in which spicules are locally or entirely absent; all structures represented are three-dimensional but are drawn as two-dimensional for simplicity; fibers of chalinid type (new).

(Fig. 30); and (iii) ectyonid, with both coring and echinating megascleres (Fig. 29). The number of spicules can vary considerably. Coring spicules may be present in bundles in both primary and secondary fibers or in the primaries only with the secondaries then containing only single spicules or none; or only a single line of spicules may be present along the axes of both types of fibers or of the primaries only. Echinating spicules vary in numbers from densely crowded examples to occasional isolated spicules, occurring several to many meshes apart in a mainly keratose skeleton. The amount of spongin may also vary; in axinellid fibers it ranges from barely enough to connect the bases of the spicules to so much that most of the spicules are buried in

spongin with only the tips of some project-
ing. In other variations primary fibers may
be connected transversely by spicules imbed-
ded at both ends, without true secondary fi-
bers. In axinellid skeletons, free primary fi-
bers radiate often to the surface from a
reticulate central or axial skeleton. Such fi-
bers, with small amounts of spongin, are
sometimes called plumose from the
featherlike appearance produced by their
echinating megascleres.

Some sponges in this group have
megascleres with secondary rays or pseud-
astrose megascleres, although still classed as
monaxonids. *Acarnus* GRAY has cladotylote
spicules with a tylote knob at one end of a
monaxial shaft and a group of recurved
teeth, typically four, at the other. The teeth
contain small axial filaments, which, how-
ever, are not continuous with the main axial
filament. This kind of spicule seems to be a
modified tylostyle with a grapnel-like group
of secondary rays added at the normally
oxeote end. *Cyamon* GRAY has normal
echinating monaxons replaced by diactinal
to pentactinal spicules, with equal or
subequal rays. These spicules are outwardly
similar to diactinal to pentactinal spicules of
choristid sponges. In ontogeny, however,
extra rays are developed from the basal (i.e.,
blunt, imbedded) end of an initial mon-
actine, and in some at least their axial fila-
ments are not continuous with the primary
axial filament. By comparison with other
forms, these spicules appear to be derived
from a normal acanthostyle, with some basal
spines enlarged as secondary rays. The spi-
cules have hence been called pseudo-
tetractines and other names. *Trikentrion*
EHLERS is a similar sponge with echinating
spicules mainly **triactinal** (or pseudo-
triactinal) and the other megascleres
diactinal. In *Discorhabdella* DENDY, an initial
monactine gives rise to pseudastrose
megascleres with a massive spiny basal en-
largement and a smaller one at the other end.

A variety of other monaxonids, some with
microscleres, have characters that do not fit
well in any of the main groups described.
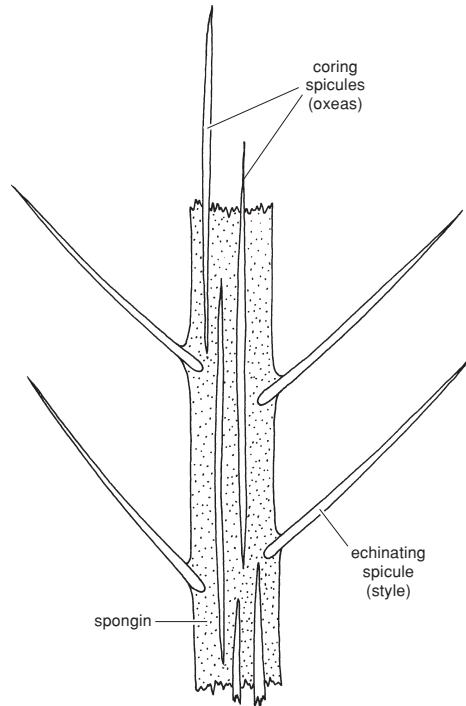The most important forms here are the

FIG. 29. Coring and echinating spicules; longitudinal
section of a skeletal fiber that is cored by oxeas and
echinated by styles; this type is termed ectyonid (new).

freshwater Spongillidae, with a typically con-
fused arrangement of simple or spiny
diactines. Microscleres may be absent or
present in the form of amphidiscs or
euastriform or other pseudasters (p. 36–37)
related to spiny diactines. The amphidisc
microscleres are found especially in repro-
ductive gemmules, although not confined to
these structures. These microscleres have
sometimes been regarded as related to chelas
(e.g., DE LAUBENFELS, 1936), but there is not
sufficient evidence to establish conclusively
this relationship.

MEGASPICULATION:
3. LITHISTIDS AND
SUBLITHISTIDS

The lithistid Demospongea, the lithistids,
are sponges in which the main choanosomal
megascleres are articulated desmas, whose
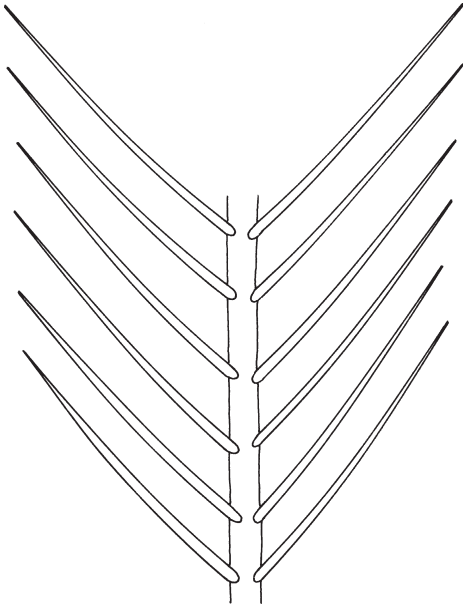union produces a loosely coherent to rigid

Fig. 30. Axinellid type of skeletal fiber with a plumose arrangement of monactines (styles) (new).

and stony skeletal framework. In addition to this desmal framework there may also be other types of megascleres comprising a supplemental skeleton. These may be of types also present in choristids or monaxonids or found only in lithistids. Microscleres may be present in living lithistid sponges and, when present, may be (i) microrhabds; (ii) recognizable streptoscleres; (iii) unidentified amphiasters or spirasters; or (iv) sigmaspires.

Existing lithistid sponges are considerably less abundant than choristids and monaxonids and seem generally to represent remnants of stocks that were formerly more abundant. In paleontology, however, the lithistids are considered to be the most important Demospongea. Only lithistid sponges are normally preserved as macrofossils, other types being rare in this condition; the skeleton does not collapse on decay of the soft parts, as in choristids and monaxonids, or decay as in keratose sponges. Further, many lithistid genera and some families and higher groups are known only

from fossil material. This is in contrast to choristid and monaxonid sponges, which are known best from their modern representatives. Methods used in studying lithistids, as a consequence, have been mainly developed in paleontology (ZITTEL, 1878a; RAUFF, 1893, 1894, 1895; SCHRAMMEN, 1910), with zoology lagging behind.

Fossil material has, however, two major limitations by comparison with modern material. First, the most important character in the identification and classification of lithistids is usually the nature of the desmas, of which there are a number of types. A desma is identified partly by its form when fully grown but in part by the nature of the initial body or crepis from which it develops. The latter is important because crepides are of more than one type and because outwardly similar adult desmas may have different types of crepides. In modern material, the nature of the crepis can be determined by tracing the ontogeny of the desmas or recognized from axial canals (p. 19) that occur in the fully grown desmas. In fossils, however, these criteria may not be available. The articulation of desmas occurs at the end of their ontogeny in modern forms, and crepides are often of microscleric size; correspondingly, developmental stages cannot be studied often in the fossils. Canal-like spaces seen in fossil desmas may be genuine axial canals but may also be pseudaxial features produced by internal solution or diagenesis. In a modern form, the absence of axial canals marks a desma as anaxial; in a fossil, this condition may be genuine or due to diagenesis. Thus assessment may need to be based on comparison with better material or even modern material. Identification on this basis can never be certain and none may be possible if a desma is equally similar to two forms having different types of crepides. Some fossils have also desmas (**didymoclones, tricranoclones**) with no modern counterparts, although in one of these (didymoclones; p. 54–56) the nature of the crepis is known from ontogeny (REID, 1963b).

Second, the absence of loose spicules in fossils presents several types of problems. The absence of microscleres means that classification must be based on the megascleres only; but, as is usual in fossil Demospongea, forms with similar megascleres may in fact have had different types of microscleres. Modern lithistids may lack microscleres, supplemental megascleres, or both during life; but their absence in fossils may be due either to absence in life or to loss after death. This may be unimportant sometimes, so far as is known, although involving some uncertainty. For instance, if supplemental triaenes are present or absent in specimens that are otherwise apparently conspecific, and are similar in age, it is reasonably likely that those without the triaenes lost these spicules after death. In some modern forms, however, the presence or absence of triaenes in forms having comparable desmas corresponds with occurrence of different types of specialized microscleres (streptoscleres, sigmaspires). Hence supplemental triaenes may be relevant as evidence of relationships, if no microscleres are known. Their absence in fossils may be of doubtful significance, because of being possibly not genuine and especially if sponges of possible but uncertain relationship are of markedly different ages. For instance, some late Paleozoic lithistids without triaenes resemble Jurassic or Cretaceous sponges in which triaenes are present.

These limitations of fossil material must always be kept firmly in mind and are especially important in discussion of relationships between different groups of lithistids. But the absence of distinctive types of microscleres is also a problem in the study of modern forms, in which they are rarely present.

The sublithistid sponges comprise a few genera that either lack a truly articulated skeletal framework in some or all individual sponges, although desmalike spicules are present or in which either desmas or loose, desmalike spicules are less abundant than simple monaxons. In the latter instance, gradation may be seen from a simple monaxon

to a desma. Though numerically few, these sublithistids provide suggestive evidence of the origin of lithistid sponges.

For further description of the spicules of these sponges, several subheaded sections are convenient.

General Features of Desmas

Despite wide variations in detail, the desmas of different types of lithistids have a number of features in common.

1. The ontogeny of any type of desmas begins with the formation of an initial body, the crepis, which lacks the form of the fully grown desma. In most types in which any crepis is known, it is usually a regular tetraxon (e.g., a calthrops) or a monaxon (e.g., a strongyle); but in variants of the tetraxon type it may be a triaene, a triactine, an angled diactine, a centrotriaene, or an amphitriaene. In one type of desma (sphaeroclones of *Vetulina* Schmidt; see p. 57) the crepis is instead an anaxial corpuscle. After inception, the desma then grows by formation of anaxial outgrowths, comprising articulatory structures (or zygomes) or both these and anaxial raylike arms (clones). In formation of these outgrowths, silica is secreted in successive layers, as in formation of typical rays; but no axial rod or protorhabd is present. A desma may be classified as tetraxial, triodal, diaxial, centrotriaenose, amphitriaenose, monaxial, or anaxial according to the nature of the crepis. Its status as belonging to one of these types is not affected by changes in form produced by post-inceptional formation of anaxial outgrowths.

In some publications (e.g., Sollas, 1888), desmas of tetraxial, triodal, monaxial, or anaxial types are called tetracrepid, tricrepid, monocrepid, and **acrepid** respectively. These terms are misleading if read literally, since a single crepis is present in each type so described. The anaxial type of desma or forms that resemble it and are supposed to be anaxial have sometimes been called cryptaxial (e.g., Schrammen, 1924a, 1936). The terms tetraxial, monaxial, etc. are,

Porifera

however, most convenient to convey a direct indication of the nature of the crepis.

The crepis is inevitably smaller than the fully grown desma, ranging from a little to much smaller according to how much of the desma is formed by anaxial outgrowth. The part of the desma enclosing the crepis may be termed epicrepid and is also called the epirhabd in monaxial desmas. The epicrepid part of a desma cannot normally be recognized by any external feature but can be identified if axial features are present internally. With fossils, one needs to remember that absence of the latter may be due to diagenesis as well as to their absence during life and, conversely, that pseudaxial canals may be produced by internal solution. In the living *Corallistes* SCHMIDT, this may even occur during life, so that arms of desmas become cored by a granular marrow that does not represent the crepis. It is also unsafe to identify the epicrepid region with the part of a desma from which growth seems to have started. This may be correct if the desma is tetraxial, triodal, or anaxial; but raylike clones may be emitted from one end of a monaxial crepis, producing a misleading suggestion that the crepis was a radiate (e.g., tetraxial) body.

The form of the crepis may correspond with a phylogenetic prototype. It is difficult to generalize, but probably the larger the crepis compared with the fully formed desma, the more likely is ontogeny to correspond with phylogeny. This is because transitions from normal megascleres to desmas that occur in sublithistid sponges have a progressive diminution of the crepis. But several instances are known in which, for example, a tetraxial desma intergrades with a monaxial desma; whichever direction is ascribed here to phylogeny, the ontogenetic prototype of the phylogenetic end form does not correspond with the phylogenetic prototype. Judged on this basis, it seems likely that tetraxial desmas and their variants are forms derived from simple tetraxons but that monaxial desmas may either be related to tetraxial desmas (e.g., dicranoclones and

some rhizoclones) or to simple monaxons (e.g., heloclones, megaclones, or other **rhizoclones**).

Nothing is known of the origin of anaxial desmas; but reduction of the crepis in passage from normal monaxons to desmas suggests that they represent the ultimate stage in reduction (see SOLLAS, 1888).

2. The articulation of desmas is affected by features known collectively as zygomes or described as **syzygial.** The simplest zygomes are terminal or lateral notches developed at points where monaxial desmas are in contact and without formation of appreciable outgrowths (e.g., in heloclones, p. 56). More commonly, however, they are outgrowths of tonguelike, handlike, or rootlike appearance; zygosis then results from the zygomes interlocking. There is no essential difference between these modes of zygosis; both may be shown by different desmas of one sponge or different zygomes of one desma when the zygomes are rootlike. According to the form of the zygomes, the skeletal framework varies from loosely coherent to so rigid that the desmas are inseparable without breakage.

3. In addition to zygomes, many desmas have raylike arms or clones that are partly or entirely anaxial. If the crepis is radiate (e.g., tetraxial or triodal), the growth of a clone may continue in the line of a crepidal axis, as in tetraclones (p. 52); the basal part of the clone is then epicrepid in character, but the rest is anaxial. Other clones have no relationship to crepidal rays or axes, arising, for example, from the sides of an epirhabd or from an epicrepid central part in an anaxial desma.

When clones are present, the zygomes are commonly located at their ends; but rootlike zygomes or similar outgrowths may also arise laterally. No fundamental distinction can be made between zygomes and clones, although these terms are convenient. On the contrary, the two are homologous, as produced by one process, and also intergrading. For instance, some desmas of one sponge may have simple clones only, with a group of rootlike terminal zygomes; but in others the zygomes arise from two main terminal branches, or the

clones themselves divide into zygome-bearing branches at any point down to their roots.

Clones are called rays, cladi, or clads by some authors; but these terms are misleading. A clone, being partly or entirely anaxial, is not a true spicular ray. Cladi or clads should refer to branches of true spicular rays and particularly the similar rays of triaenes. When authors use these terms, there is generally no implication that the spicules are related to triaenes. The description of a desma as having three, four, or more radiating rays should also identify it as triodal, tetraxial, or polyaxial; but many such desmas are monaxial, and some are anaxial.

4) It is usual for all clones of a desma to have zygosis with other desmas, irrespective of how desmas are oriented or added to the skeleton. To permit this, examples may have various distortions that vary with the orientation and spacing of adjacent individual desmas. The growing parts of young desmas thus seem to have a tendency to grow toward pre-existing desmas, ensuring construction of a continuous framework. This in turn is probably related to the anaxial character of the postcrepidal parts. Desmas may also have further variations in relation to (i) random, layered, or other constructional patterns in the skeletal framework; (ii) longitudinal or transverse orientations; or (iii) canalization of the skeleton (p. 16–17). Again, this plasticity is probably due to their partly anaxial character or to their being entirely anaxial.

NOMENCLATURE AND CLASSIFICATION

The nomenclature and classification of desmas is based generally on the form of the crepis and the fully grown desma. It is sometimes convenient, however, to use certain terms homologically, for instance in dealing with desmas in which the crepis is unknown. This applies specifically to the desmas of Paleozoic lithistids.

The nomenclature adopted here is based on that of RAUFF (1893, 1894, 1895) with additions by SCHRAMMEN (1910) and some

further modifications. The following types are distinguished:

1. tetraclonar desmas (p. 52), comprising tetraclones and associated variants;

2. rhizoclonar desmas (p. 54), comprising rhizoclones, dicranoclones, and didymoclones;

3. megaclonar desmas, comprising heloclones and megaclones (p. 56);

4. sphaeroclonar desmas (p. 57), comprising sphaeroclones *s.s.* and astroclones;

5. orchocladine desmas (p. 57), comprising dendroclones, chiastoclones, and anomoclones; and

6. tricranocladine desmas (p. 58), or tricranoclones.

The two last groups comprise Paleozoic types of desmas in which the nature of the crepis is unknown or uncertain.

The division of desmas into named types and the use of different types in the taxonomic grouping of lithistids (e.g., ZITTEL, 1878b; RAUFF, 1893, 1894, 1895; SCHRAMMEN, 1910) may give an impression that each named type is sharply distinct. On the contrary, some named morphological types are completely intergrading, although others are not. For instance, no transitions are known between tetraclones and megaclones, but dicranoclones and didymoclones both pass into rhizoclones. Such intergradations have been recognized by specialists from ZITTEL (1878b) onward but are not mentioned often in textbooks. There are also grounds for thinking that a given morphological type may sometimes have had more than one origin. For instance, the living Corallistidae, with desmas passing from dicranoclones to rhizoclones, have supplemental triaenes and streptoscleres microscleres; but the Scleritodermidae, with rhizoclones only and no triaenes, have sigmaspire microscleres. A desma with the form of a megaclone may occur (1) in a true lithistid sponge, without other types of desmas; (2) as a sublithistid spicule, intergrading with a simple monaxon with or without an intermediate heloclone; or (3) as an occasional variant of a late tricranoclone.

The classification of desmas on a basis of their morphology and of lithistids on a basis of their desmas (e.g., Zittel, 1878b; Rauff, 1893, 1894, 1895) is thus evidently partly artificial. This has led to taxonomic emphasis on other types of spicules by some authors (e.g., Schrammen, 1910; Reid, 1963b), in particular microscleres and supplemental triaenes. But often the form of the desmas is the only available basis for classification.

TETRACLONAR DESMAS

Tetraclonar desmas comprise tetraclones *s.s.* and variant types of desmas found with tetraclones or sometimes replacing them in which the crepis is a calthrops, a triaene, a triactine, an angled diactine, a monaxon, a centrotriaene, or an amphitriaene. Typical examples have an outwardly tetraxial form, a tetraxial crepis, and clones bearing zygomes in the form of rootlike terminal outgrowths. The monaxial forms included are occasional tetraclone variants or special radical desmas. The tetraclonar group by definition (Rauff, 1893, 1894, 1895) comprises desmas that are characteristic of lithistids grouped as Tetracladina (Paleozoic and Mesozoic and Cenozoic Lithistid Demosponges, *Treatise Part E (Revised),* vol. 3, in press).

The most important tetraclonar desmas are tetraclones *s.s.,* which are always tetraxial, and triders, which differ from tetraclones in showing a triaenose symmetry and may have a triactinal crepis.

A tetraclone *s.s.* is a tetraxial desma, which is not outwardly triaene-like. The crepis is commonly a calthrops but may be a short-shafted triaene. The simplest type of regular tetraclone has four equal, radiating clones that continue from the four crepidal rays and are unbranched before the terminal zygomes. In more advanced conditions the clones are branched at any point down to their origins. In irregular tetraclones the clones are unequally developed, and some may be aborted, although the desma remains tetraxial. In all types, the clones may be smooth to the zygomes, tuberculate, or beset with branching, zygomelike outgrowths.

A **trider** is a triaene-like or tripod-like desma in which the crepis is tetraxial or triactinal. When four clones are present, three are similar, comprising a **clonome** that is analogous but not homologous to the cladome of a triaene. These clones may be longer than or shorter than the fourth or may differ, for example, by being branched. The fourth may be a longer megalome or a shorter brachyome; in the latter instance it may lack a zygome or be replaced by an unmodified crepidal ray. This type passes into tripodal forms in which the fourth clone is absent. As in tetraclones, the clones may be smooth, tuberculate, or spinulated.

The triaene-like character of triders is not determined by the form of the crepis. The crepis of a desma with a **megalome** or a brachyome may be regular calthrops; while, conversely, a regular tetraclone may develop from a crepidal triaene. A trider with the brachyome aborted may still be tetraxial, with the corresponding crepidal ray rudimentary to fully developed; but a desma with four clones, bearing terminal zygomes, may have one clone entirely anaxial and the crepis triactinal. Accordingly, clonome and megalome or brachyome should not be equated with cladome and rhabdome as has been done by some authors.

Triders with a megalome or with the clonome distinguished by branching occur in forms with tetraclones, to which they are usually subordinate; but triders with a brachyome or three clones only may replace tetraclones completely in some genera (e.g., *Plinthosella* Zittel).

In forms with irregular tetraclones, these desmas may pass into variants in which the crepis is a triactine, an angled diactine, or sometimes a monaxon. The passage is gradational through forms in which one to three crepidal rays or axes are rudimentary. These desmas, which are minor variants only, are not given special names. Similar diactinal or monaxial forms may occur when the principal desmas are tripodal triders.

Mesotriders and **amphitriders** are rare types of desmas, in which the crepis is a

mesotriaene (=centrotriaene) and an amphitriaene respectively; in the former, it may be dichomesotriaene, with dichotomizing cladi but with the rhabdal rays unbranched (in *Brachiaster* WILSON) and occur as a variant of a dichotrider with a dichotriaene crepis. In either type, the form of the desma may follow the form of the crepis or disguise it by irregular growth. The central shaft of an amphitrider, corresponding with that of the crepidal amphitriaene, is called herein a **centrome.**

Zygosis between tetraclonar desmas occurs in various ways, depending on their form and arrangement. When the desmas are regular tetraclones, they may all be united by interlocking of their terminal zygomes to form syzygial nodes. These are sometimes conspicuous spherical features. Alternatively, some or all zygomes may clasp individual clones or the central parts of other desmas with no regular pattern. If so, the zygomes are more or less clawlike. All three modes of zygosis may occur among zygomes of one desma. A mixture of modes of zygosis is usual in forms with irregular tetraclones. In spiny tetraclones, branching spinules that grow laterally from the clones may form zygomes.

When the desmas are triders with a short brachyome or no fourth clone, they often have a regular arrangement in which converging clones from three desmas are applied to the brachyome or central parts of each desma, which is clasped here by the zygomes, from the side opposite the clonome. The desmas are then typically oriented with the clonome facing inward and the brachyome outward when present. This type of orientation is recurrent in various types of desmas with clones grouped directionally on one side of a center (see also dicranoclones, p. 54; sphaeroclones, p. 57).

The more irregular types of tetraclones or tetraclone variants may vary in ways related to orientation or to canalization of the skeleton. On the other hand, desmas that are regular tetraclones or triders may be united in regular patterns or quite irregularly. The form of the desmas is thus clearly not determined solely by their arrangement; on the contrary, the form of some desmas, presumably controlled genetically, determines the modes of zygosis that are possible.

In tuberculate tetraclones and other forms, the tubercles arise as lateral spinules that are subsequently thickened. When developed fully they are often capstanlike, with a constricted neck below a buttonlike head. The head may be bifid or trifid, due to corresponding branching of the original spinule. The spinules are comparable with the outgrowths forming terminal zygomes, whose branches may develop into comparable tubercles; in some, tubercles become replaced irregularly by adventitious zygomes or zygomelike outgrowths that do not form articulating zygomes. Zygomes applied to the clones or central parts of tuberculate desmas may grasp the tubercles rather than the clones bearing them; hence the tubercles are sometimes called syzygial tubercles.

Some forms with tetraclone desmas in the body proper are supported by a stalk or by root processes containing special monaxial radical desmas. These have a fiberlike shaft, a typical zygome at each end, and a short axial canal in the middle part. They may intergrade with the typical tetraclones through triders with a long megalome and a small clonome or through forms with reduction and abortion of two clones, while the two that persist are rearranged into line.

Two possible sources of confusion are worth noting here. First, all types of tetraclonar desmas are called tetraclones by some authors (e.g., MORET, 1926b; LAGNEAU-HÉRENGER, 1962), so that a genus or species said to have tetraclones may in fact have only triders. Second, monaxial or anaxial desmas (rhizoclones, p. 54; astroclones, p. 57) may also have tetraclone-like shapes, so that a desma with the form of a tetraclone need not always be a tetraclone. This leads to problems in interpreting some fossils of uncertain character. The presence of a supplemental triaene suggests that such desmas are true tetraclones, but this may not

be correct, since tetraclone-like desmas that are monaxial occur with triaenes in the living *Corallistes bowerbanki* (JOHNSON). Tuberculate desmas that are irregular tetraclones, triders, or their variants are also externally indistinguishable from monaxial dicranoclones, which again occur in forms possessing triaenes (Corallistidae). Separation of such desmas, thus, depends on recognition of the nature of the crepis, which may not be possible.

RHIZOCLONAR DESMAS

This term designates all monaxial desmas, except those grouped with tetraclones, in which the zygomes are branching, rootlike processes. Raylike anaxial clones may be present or lacking. The desmas placed in this group have probably had more than one origin.

The types of desmas included are rhizoclones, dicranoclones, and didymoclones. Both the latter types intergrade with true rhizoclones, although they are distinct when typically developed.

Rhizoclones are nontuberculate desmas, with or without distinct clones, in which the zygomes are typically branching, rootlike outgrowths. Other simple or branching spinules, which do not take part in zygosis, may also be present. These features are often present on the whole desma, although not always so. There are three main types of rhizoclones morphologically. In linear rhizoclones, the zygomes arise from a simple unbranched shaft, which may be mainly or entirely epicrepid. The shaft may be straight with the zygomes on all sides or curved with zygomes only on the convex side. In dipolar rhizoclones, the zygomes arise from the two ends of an epicrepid or partly epicrepid shaft that may be spined or smooth. The terminal zygomes are sometimes markedly bifid or carried by short clones that arise from the ends of the epirhabd. In some forms such desmas can resemble an amphitrider (p. 53) or a **dendroclone** (p. 58). In pseudoradiate rhizoclones, three or more equal or unequally developed raylike clones appear to radiate from a center, although one of the

clones contains the crepis and the others are emitted from one end of it. Desmas of this type may resemble triders or tetraclones when three or four clones are present. With all three types, zygosis is usually zygome to zygome, with the apposed zygome branches having small articulatory facets or terminal expansions in some instances.

Rhizoclones may unite to form either a dense irregular structure, without interruptions unless skeletal canals are developed, or a network of composite skeletal fibers. These types of structures are called confused and fibrous respectively. The rhizoclones may all be linear forms or a mixture of different types with any type predominating. In fibrous skeletons, variation between linear and dipolar rhizoclones may depend on orientation. For instance, in *Seliscothon* ZITTEL, skeletal fibers with a longitudinal direction may contain straight linear rhizoclones; but desmas connecting these fibers transversely are typically dipolar. Skeletal fibers may also be formed largely from the zygomes or dipolar rhizoclones, arranged transversely in ladderlike series like the dendroclones of Anthaspidellidae (Paleozoic Demosponges, *Treatise Part E (Revised),* vol. 3, in press). The curved type of linear rhizoclone is often associated with canalization of the skeleton, occurring curved around the walls of the canals with the zygomes facing outwardly.

Dicranoclones are tuberculate desmas of generally rhizoclonar type, which have tubercles and zygomes like those seen in tetraclonar desmas, and are sometimes tripodal to polypodal in form. The central type, morphologically, is a bow or arch-shaped desma with branching, clawlike zygomes at each end and the tubercles strongest on the convex side. At the center of this side of the desma there is often an especially prominent tubercle or a tuberculate brachyome-like outgrowth; or two of these features may be present. The curved shaft consists of two clones growing in opposite directions from the center. Variations on this central dipodal type occur in two main ways. First, growth of additional clones from one or both sides of the central part produces tripodal,

tetrapodal, or sometimes polypodal desmas, which are the most distinctive type of dicranoclones. Second, clones may branch before the emission of terminal zygomes and may lack the directional grouping of dipodal to polypodal forms; the desmas then pass into irregularly shaped forms resembling irregular tetraclones. The tubercles originate in the same way as those seen in tuberculate tetraclones; thus immature desmas are morphologically rhizoclones, since the tubercles originate as spinules. Dicranoclones also grade into rhizoclone forms, in which spinules on the clones do not develop into tubercles, and may form zygomes.

In modern examples of these desmas, the crepis is typically minute (e.g., 0.02 mm long in a desma several millimeters in length). It may also be destroyed by internal solution, which causes the desma to be cored by a granular marrow extending into its clones and even zygomes. In fossils, there is often no trace of it, presumably due to diagenesis but perhaps due to the desmas sometimes having become wholly anaxial. In modern forms, the crepidal axis lies in the line of the two clones of a dipodal form, and in a comparable position in others; in *Schrammeniella* BREISTOFFER (=*Phalangium* SCHRAMMEN, *non* LINNÉ; *Iouea* DE LAUBENFELS); however, the tripodal type may have the crepidal canal in a brachyome-like feature, with the clones radiating from one end.

In RAUFF's original terminology (1893, 1894) of lithistid desmas, dicranoclones were included with rhizoclones *s.s.* as rhizoclones. Their present treatment as a distinct type follows SCHRAMMEN (1910), who, however, regarded the type that occurs in *Schrammeniella* as typical. The usual position of the crepis, when any is detectable, is as stated above; but this type of desma occurs also in *Schrammeniella;* and SCHRAMMEN (1910) in practice called both types dicranoclones. Accompanying desmas, which are rhizoclones morphologically, he called megarhizoclonids.

Dicranoclones are the characteristic desmas of lithistids grouped as Dicrano-cladina (Mesozoic and Cenozoic Lithistid Demosponges, *Treatise Part E (Revised),* vol. 3, in press), although not well developed in all genera. They appear to be related to the tetraclones of some Tetracladina. The two groups differ chiefly in that desmas are typically tetraxial in the Tetracladina but monaxial in Dicranocladina. Except when polypodal, dicranoclones are externally indistinguishable from desmas or from the tetracladines *Discodermia* DU BOCAGE, *Plinthosella* ZITTEL, and *Acrochordonia* SCHRAMMEN, in which variants of tetraclones or triders may have a diactinal or monaxial crepis. In the dicranocladine *Macandrewia* GRAY, the normally monaxial desmas intergrade with minor variants in which the crepis is a triaene with short to rudimentary cladi. There is no conclusive evidence of the direction of phylogeny, but indirect evidence is provided by the size of the crepis. In dicranocladine desmas, this is often minute; in tetracladine desmas it is usually larger and may sometimes exceed half the size of the fully formed desma. Since transition from normal megascleres to desmas is accompanied by reduction of the crepis in observed instances, the likely direction of phylogeny is from tetraclones to dicranoclones.

Didymoclones are monaxial desmas in which simple or branching clones arise from spherical swellings at the ends of a short straight **epirhabd.** They are typically directed in groups toward one side of the desma. The zygomes are formed by spinular outgrowths at the ends of the clones or by expansions with digitated margins and a central syzygial facet. Simple or branching spines often occur on the terminal swellings of the epirhabd, on the side opposite the grouped clones. Zygosis results from application of the zygomes to this part of other desmas or to their clones in its vicinity. The typical didymoclones are accompanied by desmas with various stages of passage into dipolar rhizoclones, with irregularly branching clones spreading from each end of the epirhabd and no epirhabdal swellings.

A structure formed from typical didymoclones is similar in appearance to one

formed from sphaeroclones (p. 57), in which grouped clones are emitted from one side of a spherical centrum, and the opposite side may be spiny. This resemblance has led to the two types being confused sometimes. In Zittel's classification (1878a), his family Anomocladina was defined in terms of sphaeroclones, which occur in *Mastosia* Zittel; but the included genera *Cylindrophyma* Zittel and *Melonella* Zittel have didymoclones. Later (1884), he redefined the family in terms of didymoclones but still included *Mastosia,* which was removed only after two types of desmas (called didymoclones and **ennomoclones**) had been recognized by Rauff (1893, 1894, 1895). In addition, some authors have thought that didymoclones may be bodies formed from linked pairs of sphaeroclones (e.g., Schrammen, 1910, *not* 1936). This cannot, however, be correct, because the desma develops from a crepidal strongyle (Reid, 1963b) represented by the shaft between the two swollen ends in the adult form.

Didymoclones are the typical desmas of the Jurassic Cylindrophymatidae or Didymmorina, but desmas approaching didymoclones occur in the Ordovician-Silurian Anomoclonellidae. The didymoclone-like desmas of the latter are classed here as orchocladine desmas and may be of different origin.

MEGACLONAR DESMAS

This group comprises monaxial desmas not of rhizoclonar types in which the zygomes range from simple lateral facets to tonguelike or handlike terminal expansions. They are characteristic of lithistids grouped as Megamorina, but similar desmas occur in some sublithistid sponges (p. 60). The two types included are heloclones and megaclones.

A **heloclone** is a monaxial desma that normally lacks distinct clones, in which the zygomes are simple lateral facets or notches. The crepis is a more or less sinuous monaxon that in many instances is almost as long as the fully formed desma. The desma is typi-cally sinuous with the ends markedly twisted, hooked, or sometimes digitate. The syzygial facets or notches occur mainly at the ends of the desma but may also occur at any point between the ends if two desmas cross one another. In incipient form, they are simply shallow indentations with no syzygial function. In abnormal examples, clonelike outgrowths may occur but bear no zygomes. The desmas are smooth, without spines or tubercles.

Megaclones are desmas in which distinct clones are present. They bear zygomes ranging from longitudinal facets to tonguelike or handlike expansions. The crepis is typically short and located near the center of the desma. The simplest type of megaclone is dipodal, with two opposite clones curving to one side from the ends of a short epirhabd. Other types arise by branching of the primary clones, by emission of further clones from the sides of the epirhabd, or in both ways together. The clones may lie along the side of other desmas and have zygomes in the form of longitudinal facets, or expanded terminal zygomes may clasp the epirhabds or clones of other desmas. All the clones then tend to be curved toward one side, which faces inward in relation to the skeletal surface. The desmas are normally smooth; fine tubercles may occur on the epirhabd but are never capstanlike.

Heloclones and megaclones are typical of different families (Isoraphiniidae, Pleromatidae) but are linked by intermediates in some sponges (e.g., *Nematinion* Hinde). They do not appear to be related to rhizoclonar desmas, except that some rhizoclones (megarhizoclones; Schrammen, 1910) may be forms derived from megaclones; some megaclones pass toward rhizoclone-like desmas by repeated branching of the clones. Both types are typically large desmas, reaching lengths of several millimeters in some examples. The large crepis, simple zygomes, and lack of clones point to heloclones as being relatively primitive and probably derived from a sinuous oxea (or ophirhabd) directly. The megaclone

then seems to be a more advanced desma with the crepis reduced, and true clones developed. A passage from ophirhabds through heloclones to megaclones is known from a fossil sublithistid (*Archaeodoryderma* REID, 1968c; Paleozoic Demosponges, *Treatise Part E (Revised),* vol. 3, in press), which may have been ancestral to the typical megamorine lithistids.

A heloclone with digitate ends may resemble the radical desmas of some tetracladine sponges, as first noted by ZITTEL (1878a). No genetic connection seems likely, since the latter are obviously specialized; but at least one form supposed to have heloclones, *Inodia* MORET, may in fact be based on radical desmas of a tetracladine lithistid.

SPHAEROCLONAR DESMAS

This group comprises the desmas of the living genus *Vetulina* SCHMIDT, which are anaxial, and fossil desmas, which appear to be of the same type.

In sphaeroclones, a group of clones with terminal zygomes is typically emitted from one side of a globular **centrum,** which may be spined on the opposite side. The zygomes vary from branching rootlike outgrowths to cuplike expansions with digitated margins and are applied to the centra or clones of other desmas. Spines on a centrum may be few and large or small and numerous; when small, they may branch and interlock with zygomes applied to the centrum. In some forms a centrum is absent but replaced by a group of large spines. The number of clones is variable and usually three or more. The desmas are often arranged with the centrum facing outward and the clones directed inward in relation to a skeletal surface.

In *Vetulina,* the crepis is an anaxial corpuscle. During development of the clones and centrum, a depression in the surface of the developing centrum, on the side opposite the grouped clones, becomes enclosed to form an internal nucleus. The spines on the centrum are homologous with the clones, although formed later. The crepis is poorly known in fossils. In several genera, the centrum may contain a contorted tubular canal, which looks like an axial structure (*Ozotrachelus* DE LAUBENFELS, *Mastosia* ZITTEL, *Exodictydia* MORET), but the desmas do not seem to develop from a corresponding contort monaxon. Nothing is known of the crepis in Paleozoic forms.

The *Vetulina* sphaeroclone also passes into desmas in which clones are emitted from a center without directional grouping. Similar desmas accompany sphaeroclones in some fossils (e.g., *Cladodia* MORET) or may be the only type present (e.g., *Lecanella* ZITTEL). Herein these desmas are called **astroclones.** They have also been called **anomoclones** (SCHRAMMEN, 1936), but this name was proposed for desmas not certainly related to sphaeroclones. In some forms, an astroclone can resemble a tetraclone or have zygomes like those of a megaclone; it is possible that such desmas had a different origin from true sphaeroclones.

ORCHOCLADINE DESMAS

This group comprises desmas of lithistids grouped as Orchocladina (Paleozoic Demosponges, *Treatise Part E (Revised),* vol. 3, in press) in which the nature of the crepis is uncertain. These lithistids were formerly grouped as Tetracladina (RAUFF, 1895) because some of the desmas were interpreted as tetraclones or amphitriders. The desmas included are dendroclones, chiastoclones, tetraclone-like variants of these types, and anomoclones (*sensu* RAUFF, 1895; *not* SCHRAMMEN, 1936).

Dendroclones are sometimes forms resembling a tetraclonar amphitrider, except that the number of clones at the two ends may be two, three, or four (e.g., in *Dendroclonella* RAUFF). The central shaft and clones are smooth, and the zygomes are branching or nodular processes. This type may pass into tetraclone-like desmas, with clones at one end of a primary shaft. In simpler forms, however, the dendroclone resembles a dipolar rhizoclone (e.g., in *Calycocoelia* BASSLER, *Nevadocoelia* BASSLER). The shafts of the

desmas extend transversely between skeletal fibers, termed **trabs** by RIGBY and BAYER (1971), formed mainly or entirely by their interlocked zygomes; the zygomes at the ends are not trifid but simply grow up and down the columns. The ends may, however, be bifid, as in dipolar rhizoclones. By shortening of the shaft, this type of desma passes into cross-shaped variants or into tetraclone-like desmas if the branches at one end are at right angles to those at the other. This can occur through the branches extending to two different skeletal columns at one end of the desma. There may also be passage into forms resembling linear or pseudoradiate rhizoclones.

Chiastoclones appear to be comparable with the amphitrider-like form of dendroclones, with the central shaft shortened so that the clones radiate from a very short shaft or from a center. They occur mixed with forms that are dendroclones or tetraclone-like desmas.

The nature of these desmas is uncertain. RAUFF (1893, 1894, 1895) considered them as tetraclonar desmas, and this view has been widely accepted until recently; but the simplest type of dendroclone, which is typical of the earliest genera (FINKS, 1960), appears to be monaxial. Tetraclone-like desmas occur, but their shape, at least in one type, seems related to skeletal structure, not the form of a crepis. It would be possible for all types to be monaxial or perhaps anaxial in some chiastoclones. For the present, it seems best to treat them as a separate group of desmas. Even if they prove to be monaxial generally, the names used will still be convenient, since location of the zygomes at the ends of clones is not typical of rhizoclones. For further discussion of the Orchocladina, see Paleozoic Demosponges (*Treatise Part E (Revised),* vol. 3, in press).

Anomoclones are irregularly shaped desmas of the Paleozoic Anomoclonellidae that may resemble chiastoclones, dicranoclones, or didymoclones in some examples. These desmas were interpreted by RAUFF (1893, 1894, 1895) as irregular forms of his ennomoclones comprising desmas here called sphaeroclones and tricranoclones. Because of more probable close relationship of anomoclonellids to Chiastoclonellidae (FINKS, 1960, 1967a), the desmas are interpreted herein as being irregular chiastoclone variants.

TRICRANOCLADINE DESMAS

This group comprises the desmas of the Paleozoic Hindiidae or Tricranocladina, called tricranoclones herein (REID, 1963b).

The hindiids are small spherical sponges in which fine, canal-like passages radiate from the center of the skeleton. The passages are enclosed by a very regular arrangement of triderlike desmas, arranged with three clones directed inward. In typical *Hindia* tricranoclones, the desma has a short brachyome-like feature on the side opposite the clones; in the skeleton this points radially outward. The outwardly facing sides of the clones may be markedly tuberculate, and the brachyome has a terminal knob or ring of tubercles. The zygomes are elongate terminal expansions of the clones and are applied to the outward facing sides of the clones of other desmas. When the latter are tuberculate, the zygomes are marginally digitated. Their ends may also grasp the shaft of the brachyome, below the terminal swelling. In addition to desmas with a brachyome, as in *Hindia* DUNCAN, the type includes desmas without this feature, as in *Scheiia* TSCHERNYSCHEV & STEPANOV. These are arranged in the same way as desmas in *Hindia.*

Nothing is known of the nature of the crepis in tricranoclones. RAUFF (1893, 1894, 1895) took the *Hindia* tricranoclone and the sphaeroclones of the Paleozoic Astylospongiidae as trider and dichotrider forms of a single type of desma, called ennomoclones; but he recognized that *Vetulina* desmas are anaxial. The relationship of these two types does not seem demonstrable. SCHRAMMEN (1910, 1936) interpreted the *Hindia* desma as tetraxial, because of its consistently triderlike shape. The most nearly similar desma in which the crepis is known is a

tetraxial trider found in *Kaliapsis* Bower-bank, but this is a special basal desma of a modern sponge with nothing else especially in common with *Hindia.* Finks (1960) compared desmas of *Scheiia* with dicranoclones; but herein dicranoclones are related to tetraclones and the pachastrellid calthrops (Reid, 1963b).

SUPPLEMENTAL MEGASCLERES

There are three main types of supplemental megascleres and several minor ones. The most common supplemental megascleres are supplemental monaxons, which occur in most modern lithistids and many fossils. They are commonly oxeas but may be strongles, styles, or tylostyles. They are usually found within the meshes of the skeletal framework; aligned radially, at random, or more or less in the local direction of growth; or found at the surface of the skeleton and lying tangentially. Monaxons occurring on the surface may differ from those of the interior; in modern forms, such spicules are located in the ectosome. In a few genera (e.g., *Climacospongia* Hinde), simple monaxons core skeletal fibers formed by the union of desmas. Such coring spicules are common in trabs of several genera in the Paleozoic Anthaspidellidae.

Some groups of lithistids (Tetracladina; Dicranocladina; Megamorina; Didymmorina; *Treatise Part E (Revised),* vol. 3, in press) have simple or specialized ectosomal triaenes, here called triaenose dermalia. These are sometimes simple triaenes (e.g., plagiotriaenes, in *Costifer* Wilson) but usually dichotriaenes or specially modified forms (phyllotriaenes or discotriaenes). Trichotriaenes replace dichotriaenes in some genera. All types typically lie with the cladome outside the skeletal framework with the rhabdome running into its meshes (not clasped by zygomes). The simple triaenes and dichotriaenes are like those of choristid sponges, except that dichotriaenes may have the rhabdome bent to one side or the cladi spined in ways that do not occur in choristids (e.g., in *Phrissospongia* Moret). In

phyllotriaenes, normal cladi are replaced by digitate leaflike expansions that lie in one plane and arise as lateral outgrowths from the cladi of an initial dichotriaene or simple triaene. This type grades into discotriaenes, in which the cladome becomes a simple or marginally indented siliceous disc; the initial cladi are usually unbranched and sometimes rudimentary. The last type may pass into monaxial **discostrongyles** without cladal axes. Both of these types may occur loose or have some degree of connection in a zygosis-like manner. In phyllotriaenes, zygomelike facets are occasionally present on the cladi. In discotriaenes, the margins of overlapping cladal discs may grow around the rhabdomes of other spicules. The rhabdome is not modified in either; in both types of spicules it is typically short and may be lacking.

Some lithistids whose primary desmas are tetraclones, dicranoclones, or megaclones have small accessory desmas that unite within the primary meshes or outside them to form an external secondary covering. The desmas, described as rhizoclonids, resemble small, finely branched rhizoclones but appear to be anaxial. The origin of these bodies is unknown; they do not intergrade with the typical desmas and cannot be identified with any other skeletal element.

Other types of ectosomal megascleres that occur in occasional genera include monaxial discs with an axis in the plane of the disc (*Neopelta* Sollas); scalelike anaxial plates (e.g., *Plinthosella* Zittel); and flat, branching, desmalike bodies (e.g., *Siphonidium* Schmidt, *Ozotrachelus* de Laubenfels). The status of these spicules is uncertain, although the first two may be degenerate discotriaenes homologically.

SUBLITHISTID SPONGES

Sublithistid sponges are known from both fossil and modern examples. They are mainly forms having monaxial spicules only. Their resemblance to true lithistid sponges ranges from slight to almost complete.

The Cretaceous *Megarhiza* Schrammen resembles true lithistids but with partial

failure of zygosis. The principal megascleres, called megarhizoclones by SCHRAMMEN, resemble large rhizoclones or take shapes intermediate between rhizoclones and megaclones. They may either articulate by small facets or syzygial expansions, where their parts are in contact, or be quite unconnected. The skeleton may then still have some coherence, although their branches may be only loosely interlocking. The extant genus *Petromica* TOPSENT has a similar condition and similar desmas.

Desmatiderma TOPSENT, *Helophloeina* TOPSENT, and *Lithochela* BURTON are modern sponges in which the skeleton consists of a mixture of simple monaxons and desmas, and these spicules are also intergrading. *Desmatiderma* is a finely ramified sponge in which the principal megascleres are styles with additional strongyles, but a layer of desmas is present at the surface. The desmas are elongate bodies with numerous small syzygial outgrowths and intergrade with the styles through irregularly nodular intermediates. The desmas also pass into spicules like those in the basal parts of *Megarhiza* and are here united firmly. *Helophloeina* is a comparable sponge, with the main spicules being oxeas, styles, and subtylostyles but with desmas in the basal parts. The desmas intergrade with the oxeas and approach the form of some megaclones or astroclones. In both genera, progression from simple monaxon to the most complex desmas corresponds with reduction in length of the crepis. In *Lithochela,* a modified ectyonid skeleton has the fibers cored by styles but connected transversely by desmalike spicules with irregular zygomelike expansions at each end (**diploclones,** REID, 1963b). The expanded ends are imbedded in the spongin of the fibers without true zygosis. At the surface, some desmalike spicules take on rhizoclonelike shapes. The desmalike spicules intergrade with styles like those that core the fibers, with their crepidal bodies again being reduced by comparison.

These sponges are of interest as evidence of the origin of desmas from normal megascleres and of lithistids from nonlithistid sponges. The principal evidence is the intergradation of normal monaxons with desmas or desmalike spicules and the correlated reduction of the crepidal bodies of the desmas. The latter reduction supports SOLLAS's (1888) idea that desmas originate by loss of control over silica secretion by normal axial structures, which are formed initially but cease growth before silica secretion ceases. This agrees with TOPSENT's (1928a) observation on *Desmatiderma* that the shorter the crepidal axis, the more complex the desma. It is, of course, possible to think that phylogeny had an opposite direction; but an origin of normal monaxons from desmas seems far less likely than the opposite. A further implication is that if two intergrading types of desmas also differ in the size of the crepis (e.g., tetraclones and dicranoclones; heloclones and megaclones) the form in which the crepis is larger is more likely to be phylogenetically primitive.

Crambe VOSMAER has a mainly monaxial spiculation but has anaxial desmas in the basal parts. These resemble astroclones or sphaeroclones morphologically but do not have the secondary nucleus of *Vetulina* sphaeroclones; instead, they have a number of small granular inclusions corresponding with the number of clones. In *C. crambe* (SCHMIDT), these inclusions are clustered at the center of the desma, suggesting the rudiments of spicular axes; but in *C. chelastra* LÉVI, they occur near the ends of the clones and thus must have been formed late in ontogeny. The zygomes are more like those of astroclones of *Lecanella* ZITTEL than sphaeroclones of *Vetulina* SOLLAS. There is no gradation from normal monaxons to desmas. The desmas arise from euaster-like bodies in ontogeny and here called asteroid by LÉVI (1960); but, as stated, in fact they are anaxial. Just possibly, this sponge might be an ally of the older Lecanellidae, which has almost lost its desmas.

Tetranthella LENDENFELD is an incompletely known modern form in which apparently radiate desmas or desmalike bodies occur on the surface of ectyonid skeletal fibers. This sponge should possibly be related

to *Cyamon* and *Trikentrion,* in which echinating spicules are replaced by **pseudoradiates.**

Helminthophyllum SCHRAMMEN, of Jurassic age, is unusual among sublithistids in having tetraxons as ectosomal megascleres. The main internal megascleres are short, stout, and blunt-ended monaxons, slightly arcuate, and with semiannular transverse swellings on the convex side. The ends of these spicules rest on other kinds and may have very rudimentary syzygial expansions. The dermalia are small dichotriaenes.

The Carboniferous *Archaeodoryderma* REID is an apparently sublithistid sponge, known only from dissociated spicules. These spicules grade from blunt-ended ophirhabds through heloclone-like desmas to desmas with the form of simple megaclones. They decrease in size from the ophirhabds to the megaclone-like desmas, in a way that is comparable with what is seen in *Desmatiderma.* This sponge has been responsible for a supposed Carboniferous record of a megamorine lithistid (*Doryderma* ZITTEL; HINDE, 1884a). Supplemental triaenes, which occur in true Megamorina, are not known to have been present.

DISSOCIATED SPICULES

Dissociated megascleres of lithistid or sublithistid sponges may occur loose in a sediment due to scattering of unarticulated spicules after death or to disarticulation of desmas. The latter is most common with types that have lax articulation (e.g., heloclones and megaclones). Desmas may be taken as lithistid spicules unless transitions to a nonlithistid megasclere (e.g., an ophirhabd) imply a sublithistid. With one modern exception, phyllotriaenes, discotriaenes, and similar bodies occur only in lithistids. A simple dichotriaene with the rhabdome bent markedly to one side is likely to be from a lithistid. Otherwise, however, loose spicules from lithistid or sublithistid sponges are not distinguishable from those of nonlithistids. Thus, loose dichotriaenes, oxeas, strongyles, styles, or tylostyles may be supplemental megascleres of lithistids, not

spicules of choristids or monaxonids. This should always be remembered in dealing with formations in which lithistids are known to occur.

KERATOSE SPONGES

The keratose sponges are Demospongea in which the skeleton consists of spongin only, unless foreign material is incorporated. The spongin is typically secreted in the form of skeletal fibers but may also form other structures. The fibers may be reticulate or simply dendritic. The canal system is usually eurypylous or diplodal, and the ectosome is a thin dermis.

The skeletal fibers are typically cylindrical and are formed from concentric layers of spongin secreted by cells called spongoblasts. The fibers may appear homogeneous or have a distinct granular axial medulla or pith that may form a minor or major part of the fiber. In some forms, the fibers are more or less hollow or may contain living tissue in life (*Ianthella* GRAY). The axial parts may also be packed with inclusions.

Reticulate or dictyoceratid skeletons may resemble those of monaxonids with spongin fibers. They are closely similar to the chalinid type (p. 46) in which spicules may be present or absent in different individuals of some pseudoceratose species. The fibers are then often divisible into primary fibers, which radiate to the surface of the body, and secondary fibers, which connect them transversely. The ends of the fibers may raise the dermis to form conules, producing a spiny or conulose appearance. In some forms, the axes of the primary fibers or all fibers contain foreign inclusions comprising a supplementary xenoskeleton. This type passes into forms with a skeleton composed of foreign bodies, cemented together with spongin. The inclusions may be siliceous sponge spicules, sand grains, radiolarian tests, foraminifera, or shell fragments.

In dendritic or dendroceratid skeletons, branching fibers arise from a common basal plate but are otherwise typically unconnected. Occasional transverse connections may occur, however, in some species. Foreign

inclusions are commonly absent, but may be present. *Darwinella* Lendenfeld has additional loose, spicule-like bodies, composed of spongin; these pseudospicules are often hexactinal, though the number of rays is not constant.

Spongin is not resistant to decay, and keratose sponges are correspondingly rare as fossils. Recognition should be based on occurrence of one of the types of skeletons that occur in modern forms or on chemical recognition of spongin. Some alleged fossil records of keratose sponges are not based on these criteria.

OTHER DEMOSPONGEA

A few Demospongea do not fit in any of the main categories now considered. Some may be degenerate relatives of various typical demosponges.

The so-called **myxosponges** (slime-sponges) are askeletose sponges that appear to be Demospongea. *Oscarella* Vosmaer is an aphodal or diplodal sponge with amphiblastula embryos like those of the microspiculate genus *Plakina* (p. 27). *Halisarca* Dujardin and some similar genera are eurypylous sponges with large flagellated chambers and parenchymula embryos like those of dendroceratid sponges.

Chondrilla Schmidt is a diplodal and corticate sponge with spherasters but no other spicules. The body is supported chiefly by a stiff mesenchyme. *Chondrosia* Nardo is a similar sponge with no spicules. The fossil *Rhaxella* Hinde has sterraster spicules only. *Epoudenoplax* Topsent (=*Lepidospongia* Dendy, *non* Roemer; =*Lepidothenea* de Laubenfels) is encrusting with discotriaenes but no other spicules.

The status of these sponges is debatable. *Oscarella* and *Halisarca* have been interpreted as primitively askeletose, although related to forms (e.g., *Plakina*), in which a skeleton is present (e.g., Dendy, 1905), or to degenerate forms with the skeleton lost (e.g., Minchin, 1900). The close resemblance of *Chondrilla* spherasters to those of some choristids (e.g., *Aurora* Row) and monaxonids suggests an origin by loss of megascleres in phylogeny and of *Chondrosia* by loss of the spherasters (Dendy, 1916). The spicules of *Rhaxella* correspond similarly with the sterrasters of the choristid Geodiidae, unless they are really sterrospiras like those of *Placospongia*. The spicules of *Epoudenoplax* are of a type found otherwise only as dermalia in some lithistid sponges (e.g., *Discodermia* du Bocage), suggesting origin by loss of the desmal skeleton. But none of these relationships is demonstrable.