MICROSCLERES IN DEMOSPONGE CLASSIFICATION

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ABSTRACT

A critical assessment of the value of microscleres in zoological classification of spiculate Demospongia is undertaken. Microscleric criteria are judged to be an acceptable basis for primary (ordinal) classification of nonlithistid demosponges, but not of lithistids from which they are too sparsely available. A classification on this basis is offered, and discussed together with some relevant phylogenetic concepts.

INTRODUCTION

This paper has been written in connection with revision of the *"Treatise on Invertebrate Paleontology"* Part E, to which I am contributing. The paper is zoological, but its subject is fundamental to discussion of demosponge classifications and phylogeny.

In ZITTEL's (1878) classification of the sponges now grouped as Demospongia (SOLLAS, 1885), those with spicules were divided into orders (Tetractinellida, Monactinellida, Lithistida) by reference to their megascleres only, in accordance with his judgment that microscleres are too variable to be significant at this level (ZITTEL, 1877). In contrast, the microscleres were used taxonomically by the *Challenger* authors (RIDLEY & DENDY, 1887; SOLLAS, 1888), and especially by SOLLAS who was influenced by SCHULZE's (1885, 1887) reports on the Hexactinellida. All later zoological classifications, including SCHRAMMEN's (1910, 1924) used in paleontology, have made use of microscleres, though with varying emphasis. At one extreme is the practice started by HENT- SCHEL (1909), and adopted by DENDY (1916-22) and BURTON (e.g., 1956, 1959), of arranging all forms but the Homosclerophora (=Microsclero- phora of SOLLAS; Megasclerophora of LENDENFELD and SCHRAMMEN) on the basis of their micro-

scleres only. At the other extreme are the views of DE LAUBENFELS (1936), who held that ". . . microscleres have taxonomic value (but much less than do megascleres and general structure) . . ." (1936, p. 166), and did not use taxa at any level based on microscleres alone. Between these extremes lie the methods of TOPSENT (e.g., 1928), SCHRAMMEN's classifications (1910, 1924) and LAGNEAU-HÉRENGER's variant (1962) of it, the "HERDMAN" classification of DENDY (1905), HENTSCHEL's later classification (1925), and the HENTSCHEL-SCHRAMMEN hybrid used by REZVOI *et al.* (1962) in the *Osnovy Paleontologii*.

This paper attempts a critical assessment of the value of microscleres in classification, and sets out my approach to their use. Readers not familiar with demosponge microscleres will find it useful to refer to DENDY's paper of 1921, which contains good illustrations as well as its author's conclusions up to that date, but it should be noted that I do not accept DENDY's concept of diactinal (or, sigmatose) microscleres as a homologous series.

PROBLEMS ENCOUNTERED

NATURE OF PROBLEMS

The use of microscleres in taxonomy undoubtedly involves several problems, which need to be stated at the outset.

First, some morphological types of microscleres have clearly been evolved more than once, and this applies to some of the types which have been used taxonomically. In particular, 1) morphological euasters can be either euasters *s.s.* or pseudasters derived from various spiny monaxons (Fig. 1); 2) spirasters may be either streptoscleres (="dichotriacts," DENDY, 1924; streptasters *sensu* BURTON) or spinispiras (Fig. 2-3); 3) amphiasters can be streptoscleres, variants of sanidasters (=streptasters *sensu* DE LAUBENFELS), or variants of spinispiras (Fig. 2-4); 4) sigmas *s.l.* (e.g., DENDY, 1921) may be either sigmaspires (Fig. 5) or sigmas *s.s.* (SOLLAS, 1888; TOPSENT, 1928). In some cases, different homologies can be inferred readily from markedly different patterns of morphological variation (cf. DENDY, 1921, 1924) or from differences in ontogeny; but microscleres of

types having more than one origin can also occur without evidence of how they should be interpreted. Examples are the euaster-like microscleres of various monaxonid sponges, or the isolated amphiasters of the lithistid *Callipelta* SOLLAS.

Second, nomenclature of individual types of microscleres is based generally on morphology, not homology, so that convergent forms of the same morphological type are called by the same name. This can be a problem, especially for paleontological workers unfamiliar with what types may be convergent and with criteria of homology. On the other hand, use of one name for spicules of identical form is unavoidable, and as noted, homology may be unknown.

Third, various authors may name the same type of spicule differently or use the same name with different meanings. The following are relevant examples:

1) DENDY (1921) distinguished euasters *s.s.* from pseudasters of monaxon origin, some of which have the form of true euasters; but
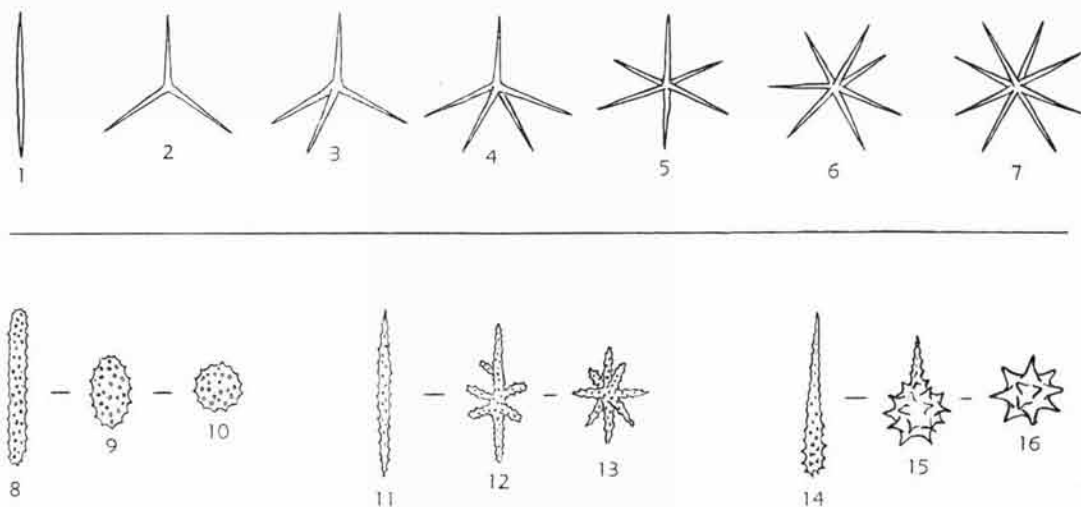

FIG. 1. Meristic variation in euasters s.s. *(1-7)* contrasted with passages from monaxon to pseudoeuaster *(8-16)*.

1-7. Ancorinid oxyasters ranging diactin to octactin, also showing characteristic shapes of these types. The diactin form (1) is morphologically a microrhabd, though homologically an oxyaster.

8-16. Monaxon to pseudoeuaster transitions in species of *Pseudastrella* DENDY *(8-10)*, *Dosilia* GRAY *(11-13)* and *Raspailia* NARDO *(14-16)*.
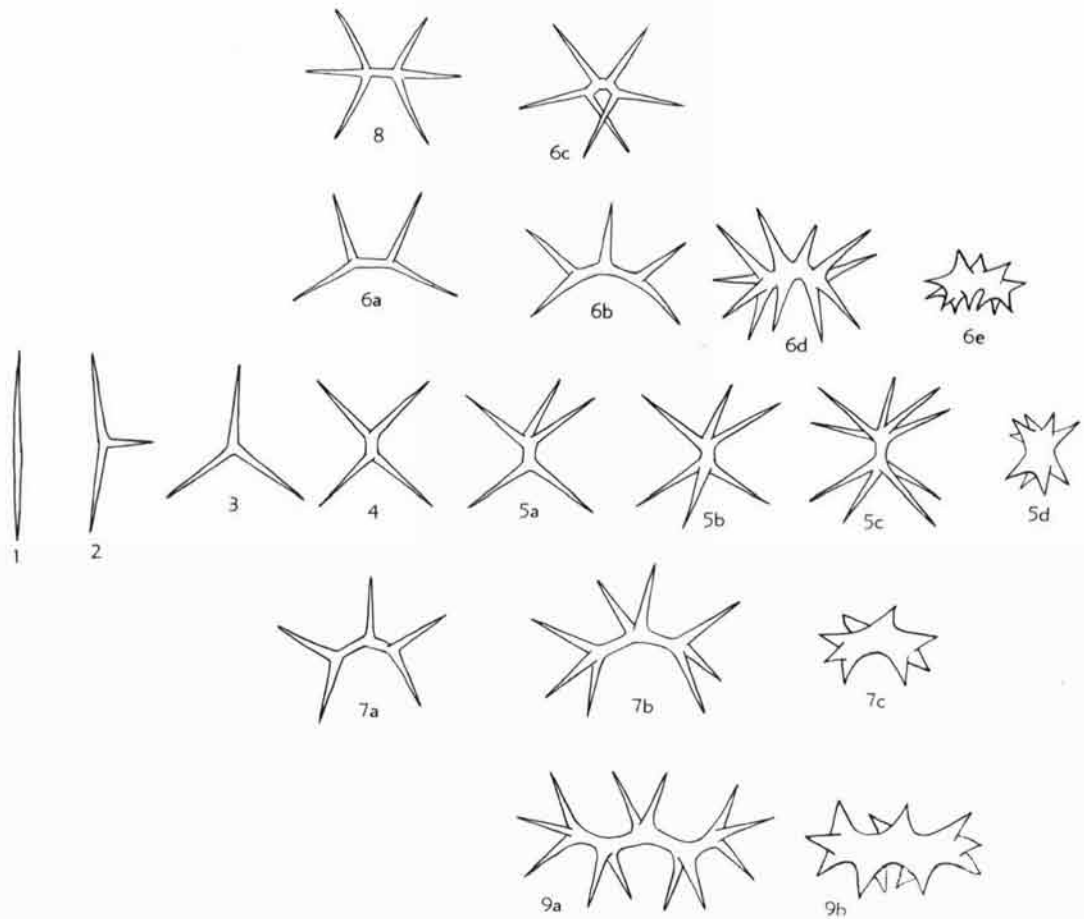
Fig. 2. Shape variations in streptoscleres.

Examples showing sequences from plesiasters to amphiasters and spirasters; *1-8* from one specimen of *Poecillastra tenuilaminaris* Sollas, and 9 from a *Thenea* sp.

1. Microxea.——*2*. Irregular triactin.——*3*. Regular triactin (microtriod).——*4*. Simplest typical plesiaster, interpreted by DENDY as dichotriactin (compare *3*).—— *5a-d*.——Amphiasters.——*6a-e, 7a-c*. Metasters, some *(6d,e)* approaching spirasters.——*8*. Amphiaster related to metasters of type *6a*.——*9a,b*. Spirasters.

Effects of thickening in *5d, 6e, 7c, 9b*. Spicules of this group comprise streptasters *sensu* BURTON and are the characteristic microscleres of his taxon Streptastrosclerophora (=Streptosclerophora DENDY; Poecillastrida herein). Compare with Fig. 4, showing streptasters *sensu* DE LAUBENFELS.

"euaster" is often still used morphologically for spicules which DENDY called pseudasters. "Astrose microscleres" *sensu* DENDY (1921) are euasters *s.s.*; but this term as used by DE LAUBENFELS (1936, 1955) means all asters *sensu* SOLLAS (1888), including euasters *s.s.*, streptoscleres, and monaxial pseudasters. The pseudasters of *Placospongia* GRAY called sterrasters by SOLLAS (1888) but sterrospirae by DENDY (1921) were at first called sterrasters by DE LAUBENFELS (e.g., 1936), but later called selenasters by him (e.g., 1955). BUR-

TON, whose work continued DENDY's, sometimes used "pseudaster," but may give pseudasters individual names which are also applicable morphologically to euasters *s.s.* (e.g., 1956, p. 123, spicules of *Vibulinus* GRAY called both pseudasters and tylasters), or use a name applicable to either without saying which is represented (e.g., 1959, p. 210-211, spicules of *Timea* GRAY called spherasters).

2) SOLLAS's term streptaster (1888, p. lxiii) was defined to take in "asters" in which "the
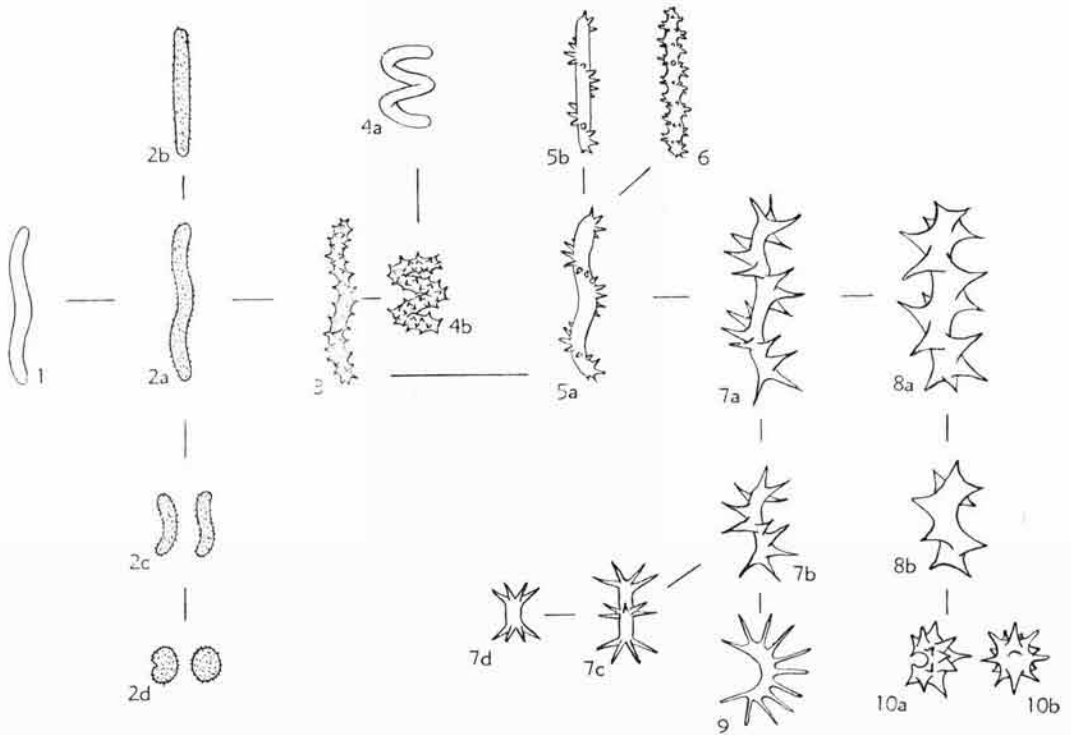
FIG. 3. Spinispiras and variants.

From spicules of *Cliona* GRANT, *Spirastrella* SCHMIDT, *Timea* GRAY, *Trachycladus* CARTER, *Anthosigmella* TOPSENT, and *Dotonella* DENDY.

1. Smooth strongylospire.
2. Strongylospires and variant types, with fine spinules which are not arranged spirally; *2a*, typical microspinulate strongylospire; *2b*, straight variant (microstrongyle); *2c*, short strongylospire, analogous to sigmaspire; *2d*, comparable pseudospheraster of *Timea spiniglobata* (CARTER), showing C-shape in one view.
3. Spinispira with larger spinules still not arranged spirally.
4. Open spiral forms characteristic of *Trachycladus* CARTER; *4a*, smooth form; *4b*, spinulate form.
5. Spicules with small spines arranged in single spiral series; *5a*, spinispira; *5b*, straight variant.
6. Polyspiral form from *Dotonella* DENDY comparable to 5.

7. Spirasters and variants; *7a,b*, long and short variants of spiraster; *7c,d*, variants of this type developed as discaster (*7c*) and amphiaster (*7d*).
8. Massive spirasters resembling *7a,b* but more thickened; *8a,b*, long and short variants.
9. Sigmaster of slender type characteristic of *Anthosigmella* TOPSENT.
10. Massive sigmasters as seen in *Timea curvistellifera* DENDY, *Spirastrella tristellata* TOPSENT, or *Cliona aethiopica* BURTON; *10a*, C-shaped view; *10b*, spheraster-like view at right angles to *10a*.

[Sterrospiras (=selenasters) omitted.] [Compare the pattern of variation from strongylospires (*1,2a,c*) and microrhabds (*2b*) to spirasters (*7a,b; 8a,b*) and amphiasters (*7d*) with that seen in streptoscleres (Fig. 2), in the ranges from microrhabd (microxea, Fig. 2,*1*) through plesiasters (Fig. 2,*2-4*) to metasters (Fig. 2,*6a-e; 7a-c*), spirasters (Fig. 2,*9a,b*) and amphiasters (Fig. 2,*5a-d*).]

actines do not proceed from a center, but from a longer or shorter axis, which is usually spiral." The spicules so grouped included streptoscleres (Fig. 2), spinispiras (Fig. 3), and sanidasters (Fig. 4) as now understood. Following DENDY's characterization (1924) of the metasters, plesiasters and spirasters of Pachastrellidae and Theneidae (=streptoscleres, REID, 1963) as "dichotriacts," BUTON used "streptasters" as applying to

these spicules only (e.g., 1959, fig. 1), and took them as the characteristic microscleres of his taxon Streptastrosclerophora (1929; =Streptoclerophora DENDY, 1924). For DE LAUBENFELS, however, a streptaster was a "straight rod with long spines or rays" (1955, p. 30), i.e., a sanidaster (cf. *ibid.*, p. 27, fig. 17,11, and SOLLAS, 1888, p. lxiv); he also included some spicules called microrhabds (*not* streptasters) by SOLLAS (in, e.g., *Halina*

BOWERBANK: cf. DE LAUBENFELS, 1955, p. 43, and SOLLAS, 1888, p. cxxxiii, 108). There are thus two contrasting restricted usages of "streptaster," and streptasters *sensu* DE LAUBENFELS are not the distinctive microscleres of BURTON's Streptastrosclerophora. As a further complication, DE LAUBENFELS sometimes used "streptaster" for spicules which are streptoscleres (i.e., streptasters *sensu* BURTON), not sanidasters or spined microrhabds (in, e.g., *Corallistes* GRAY; DE LAUBENFELS, 1955, p. 45).

In passing, it is not appropriate to restrict the term to straight forms, when the root "strept-"
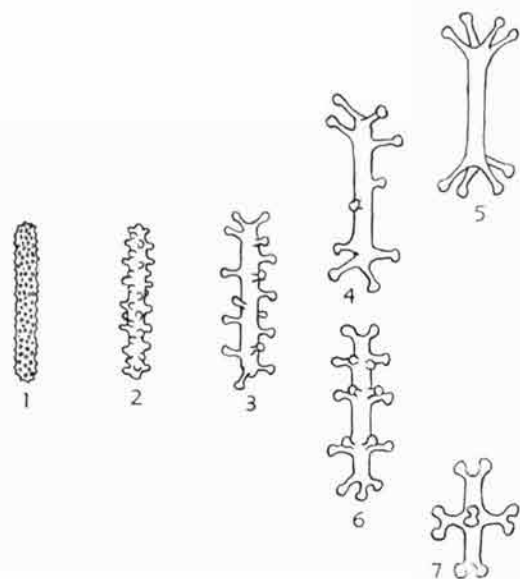
means "twisted," and SOLLAS's taxon Streptastrosa (1888) was originally called Spirastrosa (1887).

3) The sigmaspire (Fig. 5) of SOLLAS (1888, p. lxii) was equated by DENDY (1905, 1921, 1916-22) with the sigma *s.s.*, and called a sigma accordingly. But TOPSENT regarded these spicules as distinct morphologically and homologically (1928, p. 26), and is followed in this view by BURTON (e.g., 1959). DE LAUBENFELS agreed that the two had different origins (1936, p. 166), but sometimes he still called sigmaspires sigmas. SCHRAMMEN called sigmaspires sigmas in non-lithistid sponges (1910, p. 31; 1924, p. 34), but used sigmaspires in rhizomorine lithistids (1910, p. 30, 135).

Lastly, some modern sponges have no microscleres, or none which are useful taxonomically; these forms can only be arranged by comparison with the others, and some (e.g., *Vetulina* SCHMIDT) have no counterparts with microscleres. There are also many fossil lithistids from which microscleres are almost unknown, and some of these have no modern counterparts (e.g., Anthaspidellidae, Cylindrophymatidae) or none of known position (e.g., Astylospongiidae).

Problems of the second and third types are, of course, artificial, but can nonetheless cause incorrect assessment of the value of microscleres. For instance, the basis and value of BURTON's taxon Streptastrosclerophora is not apparent if the diagnostic microscleres are pictured as streptasters *sensu* DE LAUBENFELS, instead of with reference to DENDY's "dichotriact" concept.

FIG. 4. Sanidasters and variants: spicules of the ancorinids *Ancorina* SCHMIDT, *Sanidasterella* TOPSENT, *Tribrachium* WELTNER, and *Disyringa* SOLLAS showing variation from spinulate microstrongyle *(1)* to amphiaster *(5)* and pseudochiaster *(7)*. *1.* Microstrongyle with small pointed spinules.——*2.* Microstrongyle with larger strongylote spinules, approaching a sanidaster.——*3.* Typical sanidaster, with tylote spinules.——*4.* Variant of *3* showing passage toward *5*.——*5.* Amphiaster.——*6.* Verticillate (or discaster) variant of *3*.——*7.* Unusual variant of *6*, resembling a chiaster.

[Compare variation in these spicules, which are streptasters *sensu* DE LAUBENFELS (1955, p. 30), with those seen in streptoscleres (Fig. 2), which are streptasters *sensu* BURTON (e.g., 1959). According to DE LAUBENFELS (1936, p. 167), an ancorinid sanidaster (this figure, *3*) only differs from a *Thenea* spiraster (Fig. 2.9*b*) in being "much less bent." According to DENDY (1924) and REID (1963 and herein), these spicules belong to different series of microscleres, distinguished by quite different patterns of variation, though individual shapes are sometimes comparable.]

DIAGNOSTIC MICROSCLERES

In this and following sections, the terms choristid, monaxonid and lithistid refer to Demospongia with the types of megascleric skeleton seen in forms referable to the taxa Choristida SOLLAS (*sensu* SOLLAS, *not* DE LAUBENFELS), Monaxonida SOLLAS and Lithistida SCHMIDT, but are used in their descriptive sense only, without reference to classification.

One may first exclude all microrhabds from diagnostic status. These forms are clearly polyphyletic, and may evidently have three different origins; in some forms they are identifiably or probably diactinal euasters or streptoscleres, but in others they appear to be related to diactinal megascleres.
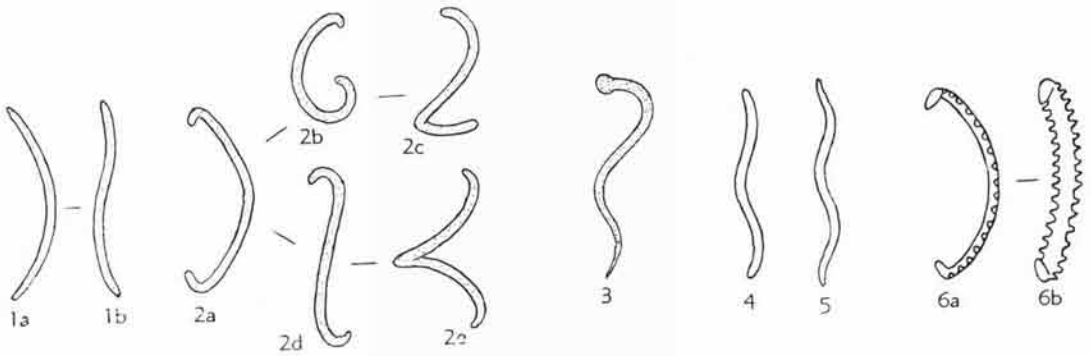
Fig. 5. Sigmaspires and variants from spicules of species of *Craniella* SCHMIDT and *Chrotella* SOLLAS.

1a,b. C-shaped and S-shaped views of a simple sigmaspire without hooked ends.——*2a-e.* Typical sigmaspire showing different appearances in 5 views.——*3.* Sigmaspire variant developed as sinuous microtylostyle.——*4,5.* Toxaspires.——*6a,b,* Chela-like dentate sigmaspire with C-shaped shaft and teeth in two opposite lateral rows, in two views.

[Compare with figures of streptoscleres developed as spirasters (Fig. 2,9*a,b*) and spinispiras developed as strongylospires (Fig. 3,*1,2a,c*). According to DE LAUBENFELS (1936, p. 173), sigmaspires are "very probably" reduced spirasters; according to REID (herein), the only comparable "spirasters" are spinispiras (Fig. 3), which are sometimes called spirasters collectively, and which pass into sigmaspire-like forms when developed as strongylospires (Fig. 3.2*a,c*).

Five main types of microscleres are found as the characteristic microscleres of contrasting groups of nonlithistid demosponges. DENDY (1905, 1921), at first referred all microscleres to two major series termed "polyact" or astrose (*sensu* DENDY) and "diact" or sigmatose, consisting respectively of euasters *s.s.* and sigmas *s.l.* with related types. Later he added a third group "dichotriacts" (DENDY, 1924), comprising streptoscleres. Nonlithistids with "dichotriacts" are all choristids (Pachastrellidae, Theneidae) acceptable as closely related. The forms with euasters may be choristid or monaxonid, but these types show no difference in their microscleres, architecture, or soft parts. But those with "diact" microscleres include three contrasting groups of sponges: 1) the choristid Craniellidae (Tetillidae DENDY), whose characteristic microscleres are sigmaspires; 2) the monaxonid Spirastrellidae and Clionidae, whose characteristic microscleres are spinispiras; and 3) the monaxonid Desmacidontidae and similar sponges, whose characteristic microscleres are sigmas and related forms, or both, e.g., diancistras, clavidiscs, chelas, bipocilli, and others. The last group in particular is considerably different from the others in typical examples and has generally more in common with the keratose sponges. A few of the lithistids have microscleres which are otherwise characteristic of one of these five groups of nonlithistids (e.g., streptoscleres in

Corallistes SCHMIDT, sigmaspires in *Taprobane* DENDY, sigmas and chelas in *Desmatiderma* TOPSENT); but others have no special microscleres (e.g., *Theonella* GRAY) or simply no microscleres (e.g., *Vetulina* SCHMIDT).

A fivefold grouping of these microscleres is therefore appropriate, though the third and fourth types (sigmaspires, spinispiras) are comparable morphologically and may be homologous. Their distribution in choristids, monaxonids and lithistids is summarized in Table I. It is also convenient to consider certain other types of microscleres, which occur as associates of the main ones.

1) EUASTERS s.s. AND ASSOCIATES

Euasters *sensu* DENDY (1921) are the characteristic microscleres of the choristid Ancorinidae *s.s.* (i.e., Stellettidae of SOLLAS, DENDY, BURTON; not Ancorinidae *sensu* DE LAUBENFELS, i.e., taking in Theneidae) and Geodiidae, also found in some simpler forms (*Calthropella* SOLLAS) and monaxonids (e.g., *Tethya* LAMARCK, *Jaspis* GRAY). The simplest and basic euasters, comprising oxyasters and variants of this type (e.g., "chiasters"), are meristically varying radiates with the number of rays varied in the sequence 3, 4, 5, 6, 7 . . . etc., up to several dozens. There may also be diactinal and rarely monactinal variants. This pattern of variation (Fig. 1,*1-7*) is characteristic

of euasters *s.s.*, and distinguishes them from various euaster-like pseudasters which do not show it (e.g., Fig. 1,*8-16*). As shown by DENDY (1921), it is comparable with variation shown by spicules of the plakinid *Dercitopsis* DENDY, with positive variation (i.e., multiplication of rays) carried further. The group also includes comparable spherasters and the solidified sterraster and aspidaster; the two latter do not show pauciradiate variants, but occur with simple euasters which do.

Some sponges with euasters *s.s.* possess microscleres having the form of spined monaxons. These may be simply finely spined microxeas or miscrostrongyles (e.g., *Ecionemia* BOWERBANK), but, when they have fewer and larger spines, they are called sanidasters (=straight "streptasters," DE LAUBENFELS; e.g., *Ancorina* SCHMIDT, *Sanidastrella* TOPSENT). By restriction of spines to the ends, this spicule can pass into an amphiaster. These forms are often regarded as based on diactinal euasters (e.g., SOLLAS, 1888); they are also relevant in discussion of the sigmaspire and spinispira.

Euasters *s.s.* are almost confined to the types of sponges cited, though apparently genuine oxyasters occur in a few other forms.

2) STREPTOSCLERES

This name was proposed by me (REID, 1963) for "streptasters" comprising the plesiaster, metaster, spiraster, and amphiaster microscleres of the choristid Pachastrellidae (*sensu* BURTON, not SOLLAS) and Theneidae which were called "dichotriacts" by DENDY (1924), because of the varying usage of the term "streptaster," because some streptasters *sensu* SOLLAS (1888) are not streptoscleres, and because most streptoscleres are not morphologically dichotriactins.

Streptoscleres are the characteristic microscleres of Pachastrellidae and Theneidae, and are otherwise found only in a few lithistids (e.g., *Corallistes* SCHMIDT). They are forms which show meristic variations on a pattern of branching (Fig. 2), and appear to be based on a microtriod prototype (DENDY, 1924). Classification as plesiasters, metasters, amphiasters, or spirasters is a simplification of the variations which occur. The simplest typical streptoscleres are plesiasters with two "rays" at each end of a shaft, in the same or different planes. This type is commonly accompanied by microtriods of similar size, and forms which show gradational passage from triod to microxea. Since the last may be more or less irregular, they seem to be derived from the triods. By comparison, the basic type of plesiaster appears to be a dichotriactin, with a single ray branched dichotomously. The remaining more complex types fall into several series, with progressive complication by addition of further branches or repeated heterotomous branching, with the latter producing sympodial spiral axes composed of a succession of branches. These are the relationships implied by DENDY's term "dichotriact." By thickening of the central part or axis, examples assume a resemblance to monaxial amphiasters or to spinispiras.

DENDY (1924) held that streptoscleres ("dichotriacts") are unrelated to euasters *s.s.*, and never occur with them. This has been questioned by myself (REID, 1963), on the grounds that microtriods are widely distributed as triactinal euasters, and that other pauciradiate euasters occur in some theneids. Some apparent microcalthrops may in fact be plesiasters, with one ray of a basic microtriod branched near the point of its origin; but this does not seem to be true of the four- to six-rayed microscleres of *Thenea wrightii* SOLLAS (1888, pl. viii, figs. 14, 15) which are regular oxyasters.

DE LAUBENFELS (1936) placed *Thenea* GRAY in the Ancorinidae, and held that the genus ". . . differs from *Ancorina* SCHMIDT only in that the streptasters of the latter are much less bent than those of the former" (*ibid.*, p. 167); but this seems incorrect to me. Ancorinid sanidasters (=streptasters, DE LAUBENFELS) may be bent, producing a resemblance to a metaster, but they do not show the variations characteristic of streptoscleres, and the axis is apparently or observably monaxial (Fig. 4). In contrast, the axial part of a theneid metaster or spiraster is evidently not a bent monaxon, but a sympodial axis due to spiral branching (Fig. 2). A comparison might be made with the unusual branching microrhabds of *Tethyorraphis* LENDENFELD, which falls in DE LAUBENFELS' Epipolasida; but these could only be compared with the simplest type of plesiaster, and the genus is monaxonid. BURTON (1934, p. 568) did not figure the spicules of *T. oxyaster* BURTON which he described as spirasters; but his slide preparation of spicules of the holotype (Brit. Mus. (Nat. Hist.), Zool. no. 30.8.13.30a) contains irregularly bent spiny microrhabds, which might be compared with a spinispira.

Against this, at least one form with typical streptoscleres has additional spirasterlike spicules which seem to be simply monaxons. In *Pachastrella monilifera* SCHMIDT, intergrading plesiasters and metasters are accompanied by slender spinulated strongyles, which may be sinuous or roughly spiral. In spiral form, this spicule resembles the type of spinispira shown at Fig. *3,3,* which some authors call a spiraster, though it does not have truly raylike spines. Since spinispiras show gradation from finely spinulated strongylospires to true spirasters (Fig. *3,2a,3,7a,8a*), it might be argued that spirasters treated here as streptoscleres (i.e. "dichotriacts") are in fact forms analogous (or homologous) with spinispiras; and, since spinispiras appear to be genuine monaxons, that the spiraster here has the character maintained by DE LAUBENFELS. Material studied in preparation for this paper, confirmed the sequence of "dichotriact" forms described by DENDY, however, including forms that pass from metaster to spiraster. The "spiraster" of *P. monilifera,* on the other hand, shows no evident relationship to metasters it accompanies. I therefore interpret it as probably of independent origin from a spinulated microrhabd, unless it is possible for a spicule which appears to be a simple monaxon to originate from a sympodial spiraster.

3) SIGMASPIRES

The sigmaspire is the characteristic microsclere of the choristid Craniellidae (=Tetillidae *sensu* SOLLAS, DENDY, BURTON; not Tetillidae *sensu* DE LAUBENFELS, in which microscleres are lacking); it is also found in some monaxonids (e.g., *Tentorina* BURTON) and rhizomorine lithistids (e.g., *Taprobane* DENDY). It is typically a spirally twisted monaxon of about one revolution, appearing C-shaped or S-shaped (Fig. *5,1-2*) according to how it is viewed, but may pass into forms which are C-shaped without being spiral or approach this condition. The two ends are blunt and either strongylote or tylote. Many examples are spinulate, having spines which range from prominent ("sigmospirasters") to minute; in the latter case, the spicule may seem smooth unless highly magnified. The only special variants are occasional toxaspires (in, e.g., *Chrotella macellata* SOLLAS), and C-shaped forms with toothlike spines in opposite lateral rows, which can mimic a chela by restriction of teeth to its ends (in, e.g.,

Chrotella amphiacantha TOPSENT).

The blunt ends and common spinulation distinguish the sigmaspire from the sigma *s.s.,* which is characteristically sharp-ended (oxeote), and almost never spinulate. The most nearly comparable microscleres are the clionid and spirastrellid spinispira, which can pass into sigmaspires, and the spinulate microrhabds and sanidasters of ancorinids and some other forms.

4) SPINISPIRAS AND VARIANTS

Spinispira is the name used by DENDY (1921, 1922) and BURTON (e.g., 1934) for characteristic microscleres of the monaxonid Spirastrellidae and Clionidae ("Clavulidae" DENDY, BURTON; Hadromerina TOPSENT) These are often called spirasters as a group (e.g., by DE LAUBENFELS), but some are not spirasters morphologically. A spinispira is a spirally twisted monaxon of one to several revolutions, with an ornament of spinules or raylike spines which may also be spirally arranged. The spiral is usually "solid," not open as in sigmaspires. Examples from one sponge may vary in the number of revolutions, or be more or less constant. In different sponges, they range from microspinulate strongylospires lacking spiral arrangement of the spinules, to stout spirasters homeomorphic with those found as streptoscleres; between these extremes are slender spirasters, with a line of spinules following the outside of the spiral (Fig. 3). The ends are typically blunt when not spined. The principal variants are occasional smooth polyspires, forms in which the spiral twist is lacking, and two sorts of pseudoeuasters. A straight variant may be a spinulate microrhabd, a sanidaster-like spicule with the spinules arranged spirally, an amphiaster with spines in terminal whorls, or a verticillate discaster. In *Placospongia* GRAY, a pseudosterraster (=sterrospira, DENDY; selenaster, DE LAUBENFELS) develops from an initial spinispira, by solidification after growth of numerous spines. Some species of *Timea* GRAY (e.g., *T. curvistellifera* DENDY) have very short "spirasters" (or sigmasters), which may have a C-shaped axis or resemble a spheraster according to how they are viewed; in other species (e.g., *T. stellivarians* CARTER), these are replaced by euaster-like spicules, which cannot be distinguished morphologically from ancorinid spherasters. A comparable sigmaster accompanies normal spinispiras

in *Spirastrella tristellifera* Topsent, and a slender spined form (Fig. 3,9) is characteristic of *Anthosigmella* Topsent.

No sharp morphological distinction can be made between spinispiras and craniellid sigmaspires; the two are not certainly homologous (*see* Discussion below), but both are forms of one type morphologically. Both are spirally twisted monaxons, with ends typically blunt when not spined; many sigmaspires are spinulate, and some spinispiras have minute spinules lacking spiral arrangement. Moreover, a spinispira with but one revolution, and microspinulate only, is essentially similar in character to a cranellid sigmaspire, though usually different in appearance through the latter being typically a slender open spiral.

Spinispiras do not appear to be related to streptoscleres, although both may be spirasters. Members and variants of both types can be arranged in series from spiraster to microrhabd, but the patterns of these series are different (Figs. 2-3). In streptoscleres (Fig. 2), morphological transition from spiraster to microrhabd occurs through intermediate metasters, plesiasters, and microtriods, the forms of which imply the pattern of branching pictured by Dendy (1924). Axial filaments are rarely detectable except in some large plesiasters; but similar branching can affect the rays of megascleric caltrops in *Pachastrella abyssi* Schmidt, and the cladi of mesotriaenes in *Yodomia perfecta* Dendy. In contrast, transition from a spinispira-spiraster to a microrhabd (Fig. 3) occurs through forms with progressively more numerous but smaller lateral spinules, with the spinules lacking spiral arrangement in finely microspinulate examples. Further, some spinispiras are observably monaxial, or may share microspinulation or central annulation or both (in, e.g., *Cliona vastifica* Hancock) with a megascleric oxea which is clearly monaxial. These facts point to streptosclere and spinispira spirasters being not homologous spicules, but convergent types of different origins. This conclusion is supported by general comparison of pachastrellids and theneids with spirastrellids and clionids, which have nothing specially in common to suggest derivation of either group from the other.

It was argued by Dendy (1921) that the spinispira group must derive from a sigma *s.s.* through a discaster, because 1) discasters of *Sigmosceptrella* Dendy arise ontogenetically from C-shaped protorhabds, 2) discasters occur with palmate chelas in *Barbozia* Dendy, and 3) true discorhabds occur in the comparable *Didiscus* Dendy (see also Dendy, 1922, p. 129-138). I cannot agree with this opinion. *Barbozia* and *Didiscus* are best placed with the sigma-bearing sponges, as was done by de Laubenfels (1936), since the former has true chelas, and the latter much spongin and some echinating megascleres. The *Barbozia* discorhabd is probably not even related to a sigma *s.s.*, since intermediate forms link it with a megascleric oxea directly (see Dendy, 1922, p. 133). In contrast, the typical spirastrellids have generally more in common with choristids, in spite of their monaxonid spiculation, and some of the clionids are certainly oviparous. *Sigmosceptrella* can be placed with spirastrellids, but the C-shaped protorhabd of its discasters ("discorhabds," Dendy, but see Dendy, 1922, pl. 18, fig. 4a,b) need not represent a sigma prototype, if (following Topsent, 1928) sigmas *s.s.* and sigmaspires are differentiated. It need not even represent a sigmaspire, if the C-shaped sigmaster is interpreted as a spinispira derivative.

Sigmaspires and spinispiras are therefore best interpreted as simply what they appear to be, namely, spirally twisted monaxons, with a tendency to pass into spirasters (or sigmasters) by progression from finely microspinulate to coarsely spinous scleres. Their prototype should then be a microrhabd, derived in different forms from a diactinal euaster, a megascleric oxea, or possibly both. The two types and their variants have been called spiroscleres by me (Reid, 1963), without homological implication, though the group may be homologous (*see* Discussion, below).

5) SIGMATOSCLERES AND ASSOCIATES

The term sigmatoscleres (Reid, 1963) designates sigmas *s.s.* and related forms, which are the characteristic microscleres of the monaxonid Desmacidontidae and similar sponges (Haplosclerida and Poecilosclerida, Topsent, de Laubenfels). They do not occur in other sponges, if sigmaspires are referred to a separate category of microscleres. A sigma is monaxial and may be markedly spiral, but is typically C-shaped to S-shaped with hooked ends faced toward each other on opposite sides or in some intermediate position. Examples between the extreme forms are C-shaped or S-shaped according to how they

are viewed. The spicule is characteristically sharp-ended (oxeote) and nonspinulate, in contrast to sigmaspires which are blunt-ended (strongylate or tylote) and commonly spinulate. The other forms included as sigmatoscleres comprise diancistras, clavidiscs, chelas, chelasters, canonchelas, spherancoras, chela-variant amphidiscs, and bipocilli, which either develop from an initial C-shaped sigma, or intergrade with a form (e.g., a chela) which develops in this manner. These forms are interpreted as specialized sigma derivatives, in which ontogeny represents phylogeny when the protohabd is C-shaped.

A sigma is essentially a specially curved form of oxea. According to Dendy (1921), it derives from a primitive toxa, which in turn can be compared with an angled plakinid diactin. The latter are identified (Schulze, 1880) as spicules produced by reduction of triactins, because every transition occurs between triactin (triod) and oxea, and many oxeas in this sequence are markedly irregular at the middle. Dendy (1922, p. 25) also supposed that monaxonid sponges with sigmas are "epipolasid" derivatives of the choristid Craniellidae (=Tetillidae Dendy), produced by loss of triaenes in phylogeny. In fact, there is no certain evidence that desmacidontids and their allies are related to tetraxon-bearing sponges, or have ever possessed any form of true radiate spicule. They are generally sponges which have most in common with the dictyoceratid Keratosida, which they closely approach in some forms with reticulate spongin. Apart from the resemblance of sigmas and sigmaspires, they have nothing else specially in common with craniellids, or any other choristid with toxas (e.g., *Halina* Bowerbank), unless it is significant that some craniellids are viviparous (e.g., *Craniella schmidtii* Sollas, *C. elegans* Dendy). Craniellids, in contrast, are typical radiate choristids, many also markedly corticate, and generally much like some

ancorinids apart from the different microscleres. Further, microscleres inherited from a craniellid ancestor, with the characters of living craniellids, would be typical sigmaspires, not sigmas. Even if one postulates origin of the sigma-bearing monaxonids from plakinids, there is still the objection that their embryos are always parenchymulas, while those known from plakinids are amphiblastulas. Lévi (1957) even argued that the group has arisen from the keratose sponges, independently of forms with tetraxons, and has always been monaxonid (*see* Ideas on Phylogeny, below).

If sigmas are judged instead in terms of the actual spiculation of the sponges in which they occur, without hypothetical reference to other Demospongia, the obvious comparison is with ordinary oxeas. The latter are widely distributed in sigma-bearing sponges, as both megascleres and microscleres. I know no reason why sigmas should not be directly related to them, and produced independently of any comparable microsclere in other sponges.

Some authors (e.g., de Laubenfels, 1936, p. 166) have suggested that sigmas may be simplified chelas. This is certainly possible as a secondary reversion, since chelas develop from sigmas, but it does not seem probable as origin of sigmas in general. A sigma, apart from its curvature, is a normal diactinal monaxon. A chela, a diancistra, or other form developing from a sigma is, in contrast, a diactin specially modified by formation of nonactinal outgrowths. The origin of these spicules as various types of specialized sigma derivatives is intrinsically more probable than the origin of sigmas from any one of them, except by reversion.

The term sigmatoscleres introduced by me (1963) is not equivalent to Dendy's "sigmatose microscleres," which also take in sigmaspires, spinispiras, and related forms.

DISCUSSION

GENERAL COMMENTS

At the outset, one must agree with de Laubenfels (1936, p. 166) that uncritical reliance on microscleres, and particularly "sigmas" *sensu* Dendy, can lead to incorrect conclusions. Megascleres and soft parts must certainly be considered; it is also necessary for basic assessment

of the value of the microscleres to take account of the overall characters of the sponges they occur in. But, if this is done, it still emerges that some types of microscleres are characteristic of a number of groups of sponges, and that those characteristic of one group are either rare or absent in the others. Moreover, one cannot call Topsent or Burton

TABLE 1.—*Distribution of Microscleres Identified as Streptoscleres, Euasters s.s., Sigmaspires, Spinispiras and Sigmatoscleres in Demospongia with Choristid, Monaxonid, Sublithistid and Lithistid Megascleric Skeletons.*

[Explanation.—For the types of specified microscleres which occur in Demospongia with a given type of megascleric skeleton, read across. For the distribution of given types of specified microscleres in Demospongia with the cited types of megascleric skeletons, read downward. Other types of microscleres (microrhabds, sanidasters, etc.) are omitted.]

Type of megascleric skeleton	Type of microclere				
	Streptoscleres	Euasters s.s.	Sigmaspires	Spinispiras	Sigmatoscleres
Choristid	×	×	×	—	—
Monaxonid	—	×	×	×	×
Sublithistid	—	—	—	—	×
Lithistid	×	—	×	—	×

uncritical, or say that they failed to take account of megascleres and soft parts. BURTON followed DENDY in basing his taxonomic grouping on microscleres, and in various other ways, but long has placed craniellids (tetillids of BURTON) and "clavulids" (spirastrellids, etc.) in his Astrosclerophora (e.g., BURTON, 1937). DENDY himself drew attention to the different general characters of "tetillids" and monaxonids with sigmas, though he thought these differences less important than the presence of "sigmatose" microscleres (1922, p. 25).

One may criticize DENDY for his general assumption that ontogeny indicates phylogeny. This is clearly not always true. For instance, DENDY (1921, p. 126) held that tetraxial and monaxial desmas are independent phylogenetically, because of their ontogenetic origin from tetraxons and monaxons respectively. The same idea had previously been stated by SCHRAMMEN (1910, p. 29). Some monaxial desmas are clearly of monaxon origin (e.g., in *Desmatiderma* TOPSENT), but tetraxial and monaxial desmas are completely intergrading in species of *Macandrewia* GRAY (SOLLAS, 1888; TOPSENT, 1904). Whichever direction is ascribed to phylogeny in these desmas, the ontogenetic prototype of the phylogenetic end form does not correspond with the phylogenetic prototype. On the other hand, DENDY's assump-

tion seems generally justified in his treatment of the microscleres. For instance, there are no grounds for thinking that the ontogenetic origin of a sterraster from a polyactinal oxyaster, or of a chela from a sigma, do not correspond with phylogeny.

The main issue needing discussion is the lack of correspondence between groups based on microscleres and divisions based on megascleres, including both the general distinctions between choristids, monaxonids, and lithistids (Table 1), and the various further divisions of DE LAUBENFELS' classifications (1936, 1955). The distribution of microscleres through the relevant taxa are shown in Table 2 (the divisions of which, however, also take in forms lacking microscleres). Nonlithistids and lithistids need separate discussion, and genera with streptosclere microscleres are the most convenient starting point.

NONLITHISTIDS WITH STREPTOSCLERES

Nonlithistids with streptoscleres comprise DENDY's (1924) Streptosclerophora (=Streptastrosclerophora BURTON), and are placed by BURTON (1956, 1959) next after DENDY's (1905) Homosclerophora (=Microsclerophora SOLLAS; Megasclerophora VON LENDENFELD). They are choristids comprising the families Pachastrellidae SOLLAS, *sensu* VON LENDENFELD (1907) (not including Calthropellidae, e.g., *Calthropella* SOLLAS, *Halina* BOWERBANK), and Theneidae GRAY *sensu* SOLLAS (not including, e.g., *Ancorina* SCHMIDT). Tetraxial megascleres may include calthrops only or both calthrops and triaenes in the former, but only triaenes in the latter. In DE LAUBENFELS' classification, the choristids as understood here (i.e., Choristida *sensu* SOLLAS, not DE LAUBENFELS) are divided into Choristida *sensu* DE LAUBENFELS (not *sensu* SOLLAS, =Choristida + Carnosida DE LAUBENFELS) and Carnosa CARTER *sensu* DE LAUBENFELS (not *sensu* CARTER), the former comprising forms which contain only triaenes. Accordingly, pachastrellids fall in the Carnosa, but *Thenea* GRAY falls in the Choristida. DE LAUBENFELS (1936, p. 167) held that the "streptasters" of *Thenea* differ from those of *Ancorina* only in being more bent, and he asked "Where then is there any justification for a separate family for *Thenea*?".

The "streptasters" of *Ancorina* are spinulate microrhabds or sanidasters (Fig. 4,*1-3*), as in other ancorinids *s.s.* Those of *Thenea* are typical streptoscleres (Fig. 2), exactly like those of pachastrellids, and including plesiasters with the characteristic "dichotriact" branching which shows that these forms are not monaxons. *Pachastrella* Schmidt lacks triaenes and radiate architecture, but gradation to the triaenose and radiate conditions occurs in other pachastrellids, e.g., *Poecillastra* Sollas. Further, even if spirasters of *Thenea* are regarded as spiral monaxons, instead of as streptoscleres, still they would correspond to spicules of this type, which may occur in *Pachastrella*.

By comparison, *Thenea* is evidently nothing but a fully radiate relative, with additional specializations related its lophophytous habit. Oxyasters which may be present in addition to streptoscleres may have several more rays than a pachastrellid microcalthrops, which is equally an oxyaster; but the genus does not have typical polyactinal euasters, and normal ancorinids *s.s.* with these microscleres (e.g., *Ancorina, Stelletta* Schmidt) do not have streptoscleres. *Tethyopsis dubia* Wilson might possibly be thought an exception, since polyactinal oxyasters are accompanied by microscleres resembling plesiasters and metasters (Wilson, 1925, pl. 45, fig. 12), though strongylate where streptoscleres are always oxeate. But these spicules cannot be claimed to be related to sanidasters, not present in other *Tethyopsis* species, in which the second form of aster is a chiaster. The otherwise ancorinid character and special morphology of *Tethyopsis* Stewart also clearly support Wilson's view (1925, p. 301) that these spicules have arisen independently of theneid streptoscleres. Anatriaenes, present in *Thenea*, are lacking in pachastrellids, but can occur in forms placed in the Carnosa (e.g., *Chelotropella* Lendenfeld; de Laubenfels, 1936, p. 181).

This leaves only the absence in *Thenea* of a megascleric calthrops, which the oxyasters may represent, to justify reference of this genus and the others with streptoscleres to different orders. The absence of a calthrops is a dubious basis for even family distinction; Sollas (1888) made the reverse one, restricting Pachastrellidae to forms without triaenes.

In the same way, ancorinids *s.s.* were placed in the Choristida by de Laubenfels, but euaster-bearing forms containing calthrops (e.g., *Chelo-*tropella, Calthropella* Sollas) were referred to the Carnosa.

Discussing separation of these "orders," de Laubenfels referred to *Poecillastra,* but argued: "So many intermediate forms exist among the Porifera, however, that to amalgamate all so connected would leave inconveniently few categories, consequently it is here advocated that Carter be followed to the extent of using his order, Carnosa" (1936, p. 177). But this arrangement does not follow Carter. The only tetraxon-bearing sponges placed by Carter in his order Carnosa (1875, p. 128, 188, 191) were the microspiculate Plakinidae (i.e., Homosclerophora Dendy). All known genera with megascleric calthrops and triaenes, including *Thenea* and *Pachastrella,* were placed in the Pachytragidae and Pachastrellidae of Carter's order Holoraphidota (1875, p. 130, 183-185, 190, 198-199).

EUASTERS

Turning to euasters, these are specially characteristic of 1) the choristid Ancorinidae *s.s.* (=Stellettidae of Sollas and others), Erylidae and Geodiidae, tetraxons of which are triaenes, and 2) monaxonids such as *Tethya* Lamarck and *Jaspis* Gray. These forms can either be separated on a basis of the presence or absence of tetraxial megascleres or placed in a single group characterized by euastrose microscleres. Dendy (1916) adopted the latter arrangement from Hentschel (1909), with the general assumption that monaxonids are forms derived from choristids by suppression of triaenes. He included both choristids and monaxonids in the Ancorinidae (=Stellettidae of Dendy) and even together in the genus *Aurora* Sollas, *sensu* Dendy (1916, p. 242-251). In de Laubenfels's scheme the two are separated. The choristids fall in the Choristida *sensu* de Laubenfels, with genera having microscleres which are streptoscleres (*Thenea*) or sigmaspires (*Craniella*). The monaxonids fall in the Epipolasida de Laubenfels, with others (e.g., Rhaphidistiinae, Jaspidae) in which special microscleres are sanidasters, sigmaspires (e.g., *Trachygellius* Topsent) or spinispiras (e.g., *Trachycladus* Carter).

Comparing these arrangements in terms of other characters, no general difference is seen between choristids and monaxonids (epipolasids) with euasters except for the presence of tetraxial

megascleres in the former. The supposed "diag-nostic" concrescence of choanocyte collars in choristids, relied on by SOLLAS (1888, p. 411) in dividing the monaxonids between his "Epipo-lasidae" and Monaxonida, has been found to be imaginary. The soft parts are generally similar and both choristids and monaxonids may be corticate or not, with a fully developed fibrous cortex in the monaxonid *Tethya*. Skeletal archi-tecture ranges confused to fully radiate in both types; the euasters are identical in character, how-ever one interprets them, and of one to several kinds in both cases, with forms up to sterrospher-aster in monaxonids. The presence of triaenes in the choristids but not the monaxonids is a genuine difference; but some of the choristids have mainly monaxial megascleres, and very few triaenes. An example strongly suggesting that transition can occur is *Stellettinopsis corticata* (CARTER), origi-nally thought to be monaxonid, in which sparse triaenes, first seen by SOLLAS (1888), have also very small cladomes, with the length of cladi less than the thickness of the rhabdome.

In other words, here it is separation based on the megascleres, not the grouping based on micro-scleres, which fails to gain support from other evidence. There is no direct proof of the origin of monaxonids from choristids (or the opposite); but some of the choristids show seemingly transi-tional characters, and the two types are so similar in other ways that taxonomic separation cuts across what is readily acceptable as a natural assemblage. It is true that some monaxonids with euasters (e.g., *Tethya*) have features not matched among choristids, or show (e.g., *Hemiasterella*) no close resemblance to any living choristid. This does not debar them, however, from having arisen earlier or simply diverged farther than others.

SIGMASPIRES AND SPINISPIRAS

Sigmaspires and spinispiras pose a more diffi-cult problem. They are comparable forms mor-phologically, but are different if not sharply dis-tinct, and are typical of contrasting types of sponges. Craniellids are triaenose choristids, but spirastrellids and clionids are monaxonids with tylostyles. Both types are also found, however, in monaxonids lacking tylostyles (e.g., *Trachycladus* CARTER, *Tentorina* BURTON).

Relying on the megascleres, DE LAUBENFELS (1936) referred craniellids to his Choristida, but

spirastrellids and clionids to the Hadromerida (*sensu* DE LAUBENFELS; =Hadromerida *sensu* TOPSENT, less Epipolasida DE LAUBENFELS), and the other monaxonids to his Epipolasida. BURTON (e.g., 1956, 1959), in contrast, referred all these sponges to his Astrosclerophora, together with euaster-bearing genera, and even placed all mon-axonids in a single family "Clavulidae"—this name, based on Clavulina VOSMAER (*fide* DENDY, 1922, p. 129), is invalid taxonomically, having no generic type. BURTON did not state how he inter-prets the spiroscleres, but presumably he took forms containing them as derived from those with euasters. His comment (1956, p. 113) on TOP-SENT's (1928) arrangement of the "clavulids" (i.e., next to the Coppatiidae (=Jaspinae DE LAU-BENFELS) and Tethyidae (cf. TOPSENT, 1928, p. 34-35, 70), however, should imply that he re-lated them to the euaster-bearing monaxonids (e.g., *Tethya*) and not to craniellids directly. I formerly (REID, 1963) suggested the inclusion of craniellids and "clavulids" in a separate order Spirosclerophora, with sigmaspires and spinispiras taken as the characteristic microscleres but not cer-tainly claimed to be homologous.

Discussing craniellids, DE LAUBENFELS (1936, p. 173) held that the fine spinulation of sigma-spires ". . . very probably proves them to be re-duced spirasters with spines only vestigial." I see no connection between sigmaspires and spir-asters, except that the sigmaspire is a form from which spinispiras could be developed. The true spirasters known from choristid sponges (e.g., Pachastrellidae, *Thenea*) are streptoscleres, with a spiral axis which clearly appears to be sympodial on comparison with the metasters and plesiasters. In contrast, nothing suggests that a sigmaspire is anything but a twisted monaxon. The curvature is continuous, except when the ends are markedly hooked. The spinules are typically small and numerous and are only arranged regularly when relatively large and few. The forms in which spinules are most prominent are not spirasters, but chela-like spicules, for example in *Craniella australiensis* (CARTER) and *Chrotella amphiac-antha* TOPSENT. Moreover, for spinules to be small does not mean that they are vestigial; this is just as consistent with their marking an incipient stage of spinulation, which is also more probable when small examples are numerous and arranged without order.

If the sigmaspire is taken as simply a spirally twisted monaxon, the obvious comparison is with microrhabds; these are uncommon, but spinulate examples accompany sigmaspires, e.g., in *C. australiensis*. These appear identical in character with the spinulate microrhabds of various euaster-bearing sponges (e.g., *Pachymatisma* BOWERBANK, *Rhabdodragma* DENDY). In these sponges microrhabds have no known connection with spirasters, which do not occur, and they should be related to euasters if to any aster. This is clearly their status (e.g., in *Pachymatisma johnstonia* BOWERBANK) where they share microspinulation with comparable oxyasters (cf. BOWERBANK, 1872, pl. 8, fig. 6-8). No apparent difference distinguishes spinulation in such microrhabds and in megascleres, in which it is clearly a secondary ornament.

Following this argument, it is tempting to homologize the sigmaspire with microrhabds of comparable sponges with euasters, and accordingly to picture craniellids as forms in which euasters have been lost in phylogeny and replaced by a new kind of microsclere. This idea fits the arrangement made by BURTON, which is also required if the sigmaspires are supposed to represent reduced (or, diactinal) euasters. But I know no certain evidence that this is correct. A microrhabd could just as well arise by reduction of a megasclere, without relation to euasters. In *Acanthotetilla* BURTON, acanthorhabds which BURTON (1959, p. 202) thought may represent missing sigmaspires are essentially of megascleric size (0.4 mm. long), though smaller than the triaenes. Craniellids also seem sharply distinct from the euaster-bearing sponges, unless the doubted spherasters of *"Tetilla" japonica* LAMPE were in fact not intrusive. In addition, some are eurypylous sponges; these, and hence presumably the others, can not be derived from a typical aphodal ancorinid, unless the eurypylous condition is a simplification and not primitive, as is generally assumed.

If Burton's placement of Craniellidae with euaster-bearing sponges is rejected, it might still be thought possible to see a choristid prototype of sigmaspires, and also of spinispiras, in the "spiraster" of *Pachastrella monilifera* SCHMIDT, which resembles a spinulated spinispira. This spicule could also be regarded as evidence in support of the opinion of DE LAUBENFELS, if it is interpreted as derived from a spiraster strepto-

sclere; though I think that it is simply a spinulated monaxon. The microscleres now supposed to have been lost in phylogeny would be streptoscleres, or at least the forms grading from plesiaster to metaster or amphiaster which identify this series. But neither craniellids nor "clavulids" have anything else specially in common with *Pachastrella* SCHMIDT, which is a nonradiate choristid without either triaenes or tylostyles, and again has an aphodal canal system. In addition, there is evidence that the "clavulid" spinispira has arisen directly in that group, from a megascleric oxea (Fig. 6,*1-4*).

The "clavulids" of BURTON consist chiefly of the Hadromerida *sensu* DE LAUBENFELS, but also include some forms referable to the Epipolasida DE LAUBENFELS (Jaspidae, Rhaphidistiinae) when the microsclere is a sigmaspire (e.g., *Tentorina* BURTON) or a spinispira (e.g., *Trachycladus* BURTON). In TOPSENT's scheme (1928, p. 36, 70) referred to by BURTON (1956), these sponges were grouped with euaster-bearing monaxonids (Coppatiidae, Tethyidae) in the order Hadromerina *sensu* TOPSENT (=Hadromerida + Epipolasida DE LAUBENFELS), with a family Timeidae based on *Timea* GRAY between the euaster-bearing Tethyidae and the spinispira-bearing Spirastrellidae. The megascleres do not prohibit this arrangement, since styles may be present in *Tethya*; but some of the forms containing tylostyles are eurypylous (e.g., *Cliona* GRANT) where *Tethya* is aphodal to diplodal. The microscleres either support it or not, according to how they are interpreted.

For TOPSENT (1928, p. 35), as for DE LAUBENFELS (1936), the asters of *Timea* were simply euasters. In most *Timea* species, they are polyactinal euasters (commonly spherasters) morphologically; but in *T. curvistellifera* DENDY an apparent spheraster grades into a sigmaster, with stout spines arising from a short C-shaped axis (cf. DENDY, 1921, fig. 40f-h). Similar spicules are unknown in typical euaster-bearing sponges, but can occur as known spinispira variants. In *T. spiniglobata* (CARTER), apparent spherasters with a finely spined globular centrum show comparable passage into kidney-shaped (i.e., C-shaped) variants with similar fine spinulation. These occurrences led DENDY (1921, p. 30-31) to argue that the seeming euasters of *Timea* are properly pseudasters, derived from spinispiras by shortening of the axis. This seems probably correct to me from
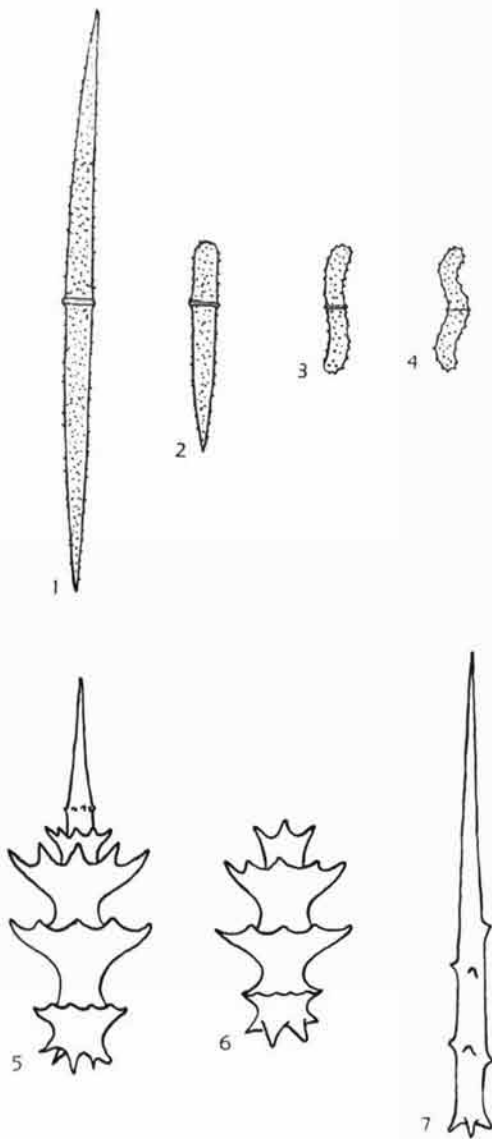
FIG. 6. Sequences suggesting homology between megascleres and microscleres.

1-4. Cliona vastifica HANCOCK.——*1*. Megascleric oxea. ——*2*. Short stylote variant.——*3,4*. Two strongylospires. All *(1-4)* share fine spinulation and a central annulation. The presence of similar ornament in these spicules suggests that spinispiras *(See* Fig. 3) are microscleres derived from a megascleric oxea, with finely and nonspirally spinulate strongylospires (Fig. 3,2) as the prototypes from which more specialized types have arisen. An opposite direction of phylogeny, e.g., from a spiraster (Fig. 3,8*a*) to a megascleric oxea, seems improbable.

5-7. Latruncula apicalis RIDLEY & DENDY.——*5-6*. Typical dicasters, with and without apical spine.——*7*. Variant

evidence provided by comparison of *Timea* spicules with various forms taken by spinispiras in *Cliona* GRANT.

In *C. aethiopicus* BURTON (1932, fig. 40d) they are stout sigmasters, with heavy spines as in the microscleres of *T. curvistellifera;* at the other extreme (e.g., in *C. vastifica* HANCOCK) they are microspinulate strongylospires, which may pass into C-shaped variants or short microstrongyles which approach forms seen in *T. spiniglobata.* Other examples show every intermediate gradation, through spirasters with spinules arranged spirally or not. Moreover, spinispiras may share microspinulation (e.g., in *C. vastifica*) to which central annulation may be added, with a megascleric oxea (Fig. 6), with which there is therefore good reason to think them homologous; supporting this, variants of the oxeas may be strongylote at one end or both, with the strongylote ray of a stylote form reduced by comparison with the other (e.g., HARTMAN, 1958, fig. 5). If these forms correspond with stages in an evolutionary sequence, as is likely, since all are from one genus, the direction will be almost certainly from oxea to sigmaster, not the opposite.

From *Timea* alone, it might be claimed that the forms intergrading with apparent spherasters have arisen from the latter, by a secondary distortion; but the evidence from *Cliona* points clearly in the opposite direction. By comparison, what is seen in *T. spiniglobata* is reduction of a strongylote microrhabd to a sphere, with microspinulation persisting to produce a "spheraster"; and *T. curvistellifera* shows the same process affecting a coarsely spined sigmaster.

It is emphasized that this interpretation of "euasters" of *Timea* as pseudasters does not depend on DENDY's (1921, p. 124) claimed origin of spinispiras from "sigmodiscorhabds," which is rejected. What is envisaged (Fig. 6) is reduction of an oxea to a microstrongyle, with spination and spiral twisting as additional developments, and further reduction of the axis of a resulting spinispira in some microscleres leading to euaster-like conditions. The spines are regarded as a

developed as larger simple acanthostyle. Since discasters typically occur at the surface in this genus, with the apical end outward, the occurrence of 7 suggests that the discasters represent small styles or tylostyles, arranged pointed end outward, which form cortical "palisades" in similar genera without discasters.

secondary ornament, and microspinulation as representing the inceptional condition, with fewer but larger spines and spiral arrangement as more advanced developments. Nonspiral microscleres corresponding with the prototype envisaged are, for example, the centrotylote microrhabds of *Suberites ficus* (JOHNSTON); their gradation from microstrongyles to rather larger microstyles and microxeas, with microspinulation in some examples, is strongly suggestive of the seeming relationship between oxeas and microspinulate spinispiras (or strongylospires) in *Cliona vastifica* (e.g., HARTMAN, 1958, fig. 1, 5). Comparison of *S. ficus* with *S. domunculus* (OLIVI) *sensu* HARTMAN also plainly suggests that the microrhabds of the former are the homologues of the megascleric oxeas of the latter (cf. HARTMAN, ibid.).

Even if *Timea* "euasters" are accepted as pseudasters, a different connection with euaster-bearing sponges might be claimed on a basis of equating spinispiras with the spinulate microrhabds of various ancorinids and coppatiids (i.e., streptasters *sensu* DE LAUBENFELS). The monaxonid *Asteropus* SOLLAS has oxea megascleres, and euasters and spinulate microrhabds or sanidasters as microscleres; by loss of the euasters and spiral twisting of the microrhabds, the result would resemble the spiculation of *"Rhaphidistia* CARTER" *sensu* DE LAUBENFELS (1936; not the unrecognizable *Rhaphidistia* CARTER, *s.s.,* which was Lower Carboniferous and possibly a *Haplistion*). But this leaves the problem of whether commonly eurypylous sponges (e.g., *Cliona*) can derive from forms which are aphodal or diplodal. I can see no grounds for claiming this connection, except that it is possible. In contrast, the evidence cited above is direct, from "clavulids" either with tylostyles *(Suberites)* or both tylostyles and spinispiras *(Cliona),* and can only be avoided if the oxeas are supposed to be derived from spinispiras.

On these grounds, the microscleres support exclusion of Coppatiidae and Tethyidae from the Hadromerida (DE LAUBENFELS, 1936), if this taxon is used. There is no proof that forms with spinispiras are not related to euaster-bearing sponges; but *Timea* is not an intermediate between Tethyidae and spirastrellids, in the sense of comprising a form with both tylostyles and genuine euasters. There is no proof of relationship between spinispiras and ancorinid or coppatiid sanidasters, but there are grounds for thinking them related to a megascleric oxea. This is why

I (REID, 1963) did not follow BURTON's (e.g., 1956) inclusion of the "clavulids" in his Astrosclerophora. On the other hand, it does not seem correct to exclude forms with spiroscleres but not tylostyles from treatment as Hadromerida, or "clavulids." In some (e.g., *Trachycladus* CARTER), their exclusion (DE LAUBENFELS, 1936) depends on the small difference between simple styles and tylostyles. These are related types of spicules, found together and intergrading in various genera (e.g., *Spirastrella* SCHMIDT, *Quasilina* NORMAN, *Polymastia* BOWERBANK). Conversely, if BURTON (1959) is right in his placing of *Trachycladus tethyoides* BURTON, a species of *Trachycladus* can have tylostyles instead of styles. In *Tentorina* BURTON, the microscleres are sigmaspires morphologically; but spinispiras take the form of sigmaspires in forms with and without tylostyles (e.g., *Cliona topsenti* LENDENFELD, *Trachycladus cervicornis* BURTON). The *Trachycladus* spinispira is more open-spiral than in most spirastrellids and clionids, but is matched in *Spirastrella spinispirulifer* (CARTER) or by the smaller type of spinispira in *Dotonella mirabilis* DENDY. Accordingly, BURTON's treatment as "clavulids" of forms containing styles but not tylostyles seems well justified. From the microscleres, at least some forms with oxea megascleres could be included; for instance, *"Rhaphidistia" spectabilis* CARTER has oxeas only, but the microsclere is a polyspiral spinispira, approaching the larger *Dotonella* form.

If BURTON's "clavulids" are not forms related to the euaster-bearing monaxonids (Tethyidae, etc.), the obvious alternative is relationship to the choristid Craniellidae. The sigmaspire and spinispira are essentially similar microscleres, and spinispira-variants may be sigmaspires morphologically (cf. Fig. 3, 5). The soft parts are no problem, since various craniellids are eurypylous. At least two monaxonids with sigmaspires appear to be of craniellid origin. *Trachygellius* TOPSENT and *Raphidotethya* BURTON are stipitate sponges, resembling *Amphitethya* LENDENFELD but with oxea megascleres only. *Amphitethya* is choristid, but may have triaenes in only the stalk, and the main body megascleres all oxeas. By comparison, these monaxonids appear to be reduced craniellids, with the triaenes lost completely. Triaenes may also be uncommon in typical craniellids; *"Trachygellius" cinachyra* DE LAUBENFELS has even proved (LITTLE, 1963, p. 61) to be a *Craniella,* in which DE LAUBENFELS did not find triaenes. It is not

claimed that these forms prove a craniellid origin of "clavulids," of which those with tylostyles and spinispiras are obviously not simply epipolasid craniellids; but it does seem that they could have had this origin before evolving tylostyles and spinispiras. For instance, strongyloxea megascleres of *Tentorina* BURTON, the microscleres of which are sigmaspires morphologically, are transitional between oxeas and styles, and the skeletal structure is like that of *Tentorium* VOSMAER. The open-spiral spinispira typical of *Trachycladus* CARTER, also seen in some spirastrellid species, compares directly with the craniellid toxaspire of *Chrotella macellata* SOLLAS; in *Trachycladus cervicornis* BURTON, which is otherwise a typical *Trachycladus*, it is replaced by an amphitylote sigmaspire, which resembles those figured by LITTLE (1963, fig. 30) from *Craniella cinachyra*. This suggests distinctly that these spicules are not simply convergent.

The status of "discorhabds," thought by DENDY (1921) to link spinispiras with sigmas, is best discussed after the sigmatoscleres.

The sigma group of microscleres (sigmatoscleres, REID, 1963) presents no special problem, except that it cannot be sharply defined morphologically. A sigma *sensu* TOPSENT may be spirally contort, like a sigmaspire; a craniellid sigmaspire may be smooth so far as is detectable, C-shaped rather than spiral, or sometimes not blunt- but sharp-ended. The chela-like sigmaspire variants are similarly not sharply separable from genuine chelas. A microsclere may thus be called a sigma, a chela or a sigmaspire according to the sponge it occurs in, not according to its shape. The differences emphasized by TOPSENT (1928, p. 26) are also entirely insufficient to show any fundamental difference between sigmaspires and sigmas; the grounds for placing them in separate series, and for thinking them probably convergent, depend essentially on the sponges.

Taxonomically, sigmatoscleres are the characteristic microscleres of VOSMAER's (1882-87) Halichondrina (not Halichondrina *sensu* TOPSENT, DE LAUBENFELS,) though not specially cited by VOSMAER in characterization; of DENDY's (1905) Sigmatomonaxonellida, though the sigmas were thought to equate with craniellid sigmaspires; of the Cornacuspongida VOSMAER as defined by HENTSCHEL (1925, p. 378-379) and ZHURAVLEVA (1962, p. 59); and BURTON's Sigmatosclerophora as used in his later work (e.g., 1956, 1959, not

1932). TOPSENT and DE LAUBENFELS, however, placed these forms in several orders. In TOPSENT's scheme (1928), most, and all with chelas, are placed as Poecilosclerina, but a few as Halichondrina *sensu* TOPSENT (e.g., *Sigmaxinella* DENDY) or Haplosclerina (e.g., *Gellius* GRAY, *Oceanapia* NORMAN), in his subclass Monaxonellida (=Monaxonida SOLLAS, in DENDY's 1905 spelling). These taxa were based on overall characters, with emphasis on megaspiculation. DE LAUBENFELS (1936) used TOPSENT's taxa as orders of the class Demospongia, but altered their contents; in particular, some genera (e.g., *Desmacidon* BOWERBANK, *Guitarra* CARTER) were moved from the Poecilosclerina to the Haplosclerina, making both include forms containing chelas. TOPSENT's Haplosclerina was discussed as though based on lack of microscleres (*ibid.*, p. 33-34), though this was not its basis (cf. TOPSENT, 1928, p. 66). Other genera moved oppositely from the Haplosclerina to the Poecilosclerina (e.g., *Oceanapia* NORMAN, *Petrosia* VOSMAER) or Halichondrina (e.g., *Rhaphisia* TOPSENT), or from Halichondrina to Poecilosclerina (e.g., *Sigmaxinella* DENDY), Hadromerina (e.g., *Cerbaris* TOPSENT) or the new Epipolasida DE LAUBENFELS (e.g., *Trachycladus* CARTER, *Topsentia* BERG). The order Halichondrina is omitted in his later *"Treatise"* classification (1955); this may be due to lack of fossil examples, but a family (Hamptoniidae DE LAUBENFELS, 1955, p. 39) compared with axinellids (i.e., Halichondrina) is in the Poecilosclerida. BURTON united TOPSENT's orders as Sigmatosclerophora (e.g., 1956, 1959), except for removing some Halichondrina to the Astrosclerophora as "Clavulidae" (e.g., *Trachycladus* CARTER) or "Astraxinellidae" (e.g., *Hemiasterella* CARTER); but his families Axinellidae, Desmacidontidae and "Haploscleridae" are otherwise essentially TOPSENT's orders.

I prefer BURTON's arrangement for at least TOPSENT's Haplosclerina and Poecilosclerina. It is generally agreed that these groups comprise related types of sponges; they have sigmas in common, and chelas if defined as by DE LAUBENFELS. In contrast, the megaspiculation shows nothing more distinctive than these microscleres, and no unmistakable basis for subdivisions. DE LAUBENFELS moved genera from each of TOPSENT's taxa to the other, and in various other ways. The scheme used by HENTSCHEL (1925, p. 406-408) and REZVOI *et al.* (1962, p. 30-31) is even

more different, dividing Topsent's Poecilosclerina into Protorhabdina (e.g., *Biemna* Gray, *Mycale* Gray) and Poikilorhabdina (e.g., *Desmacidon* Bowerbank, *Guitarra* Carter), but uniting most Haplosclerina and Halichondrina as Phthinorhabdina (e.g., *Gellius* Gray, *Axinella* Schmidt, *Halichondria* Fleming). Two genera (e.g., *Mycale, Desmacidon*) may even fall in one subfamily in Topsent's scheme (1928, p. 45), but different and differently characterized orders or suborders in those of both de Laubenfels (Poecilosclerina, Haplosclerina) and Hentschel (Protorhabdina, Poikilorhabdina).

The Halichondrina of Topsent have, however, no characteristic microscleres, and many have megascleres only (e.g., *Halichondria, Axinella*). Those with microscleres have various sorts. *Sigmaxinella* Dendy and *Sigmaxia* Hallmann have typical sigmas; but *Trachycladus* Carter has spinispiras, and *Hemiasterella* Carter and *Vibulinus* Gray euastriform asters. Various genera have acanthoxeas as megascleres (e.g., *Acanthoxifer* Dendy) or microscleres (e.g., *Halicnemia* Bowerbank) or called megascleres by some authors but microscleres by others (e.g., *Higginsia* Higgin). Dendy last (1922) regarded the forms without asters as derived from the "Haploscleridae" and Desmacidontidae (i.e., Haplosclerina, Poecilosclerina Topsent) polyphyletically, but *Hemiasterella* as a "clavulid" with pseudasters. Topsent instead derived the Halichondrina from his Hadromerina (1928, p. 37), and the Poecilosclerina and Haplosclerina from the Halichondrina. Dendy's views and Topsent's are thus opposite, since Dendy (1922, p. 130) derived "clavulids" from desmacidontids. De Laubenfels (1936) used Topsent's taxon, but moved forms with sigmas and some others (e.g., *Rhabdoploca* Topsent) to the Poecilosclerina, various genera to the Hadromerina *sensu* de Laubenfels (e.g., *Cerbaris* Topsent, *Halicnemia* Bowerbank), and *Hemiasterella, Trachycladus* and *Vibulinus* to his Epipolasida. This left only forms with no microscleres (e.g., *Axinella, Halichondria*), or with microrhabds which are usually acanthoxeas (e.g., *Higginsia*); but the last are also seen in *Halicnemia*, which was removed. Burton (e.g., 1956, 1959) placed many Halichondrina *sensu* Topsent in his Sigmatosclerophora as Axinellidae (*Axinella, Phakellia, Sigmaxinella, Halichondria*) or Desmacidontidae (e.g., *Higginsia*), but *Trachy-*

cladus and *Halicnemia* in the Astrosclerophora as "Clavulidae," and *Hemiasterella* and *Vibulinus* as "Astraxinellidae." In contrast, *Halicnemia* and *Higginsia* were both Axinellidae for Dendy (1922), both "Astraxinellidae" for Topsent (1928), but respectively axinellid and spirastrellid ("choanitid") for de Laubenfels (1936).

I see little clear evidence of how most of these sponges should be classified. *Sigmaxinella* has typical sigmas (e.g., Dendy, 1922, pl. 16, fig. 6b), and links the Axinellidae with the sigma-bearing sponges if placed in that family.

Against this, *Trachycladus* has spinispiras, matched in various clionids and spirastrellids, and needs to be regarded as a "clavulid." *Hemiasterella* and *Vibulinus* also link with this group, if the microscleres are accepted as pseudasters like those of *Timea* Gray (cf. Dendy, 1921, p. 125; 1922, p. 144; Burton, 1956, p. 123, fig. 1); but they do not pass into or accompany spinispiras. Those of *Hemiasterella* are simply typical oxyasters morphologically, with pauciradiate variants down to microcalthrops in *Hemiasterella typus* Carter, and to monactin if *Epallax callocyathus* Sollas is a *Hemiasterella* (cf. Sollas, 1888, p. 423-425, 434; Dendy, 1922, p. 144); this should imply direct connection with euaster-bearing sponges, not "clavulids." *Halicnemia* typically has only spiny microrhabds, though a species with euastriform asters was included by Topsent (*Halicnemia constellata* Topsent); it does not resemble "*Choanites* Mantell," i.e., *Ficulina* Gray (=*Suberites* Nardo), as was stated by de Laubenfels (1936, p. 144), but might be compared with *Radiella* Schmidt (=*Trichostemma* Sars) on the basis of the type *H. patera* Bowerbank. The microscleres were reduced asters for Topsent (1928, p. 39), but were equated by Dendy (1922, p. 126-129) with the small acanthoxeas of *Higginsia*, called microscleres by de Laubenfels (1936, p. 132) and Burton (1959, p. 255-256, *H. robusta* Burton), and megascleric acanthoxeas of *Acanthoxifer* Dendy.

These examples illustrate a case in which microscleres are of little help in classification; but the principal problem is not the uncertainty as to how certain types should be interpreted, but the resemblance of forms with no microscleres, or none of value, to sponges with three different significant types (i.e., sigmas, spinispiras, euasters).

DISCORHABDS

Last, several problems arise from DENDY's (1921, 1922) views on his "discorhabds" (=discorhabds *s.s.* + discasters), and from TOPSENT's (1928) views on these spicules and on chelas and sigmas. DENDY (1922, p. 129-131) placed genera with "discorhabds" (*Barbozia* DENDY, *Didiscus* DENDY, *Sigmosceptrella* DENDY, *Latrunculia* DU BOCAGE) in his "Clavulidae" with the typical spirastrellids, and saw them as linking the latter with the Desmacidontidae. The grounds for this were 1) occurrence of both chelas and "discorhabds" in *Barbozia,* 2) development of a discaster from a C-shaped protorhabd in *Sigmosceptrella,* and 3) passage of a spinispira into a verticillate sanidaster or discaster in *Spirastrella corticata* (CARTER). TOPSENT (1928) instead placed these sponges in his Poecilosclerina, regarding the "discorhabds" as either amphiasteriform isochelas (isoancres, TOPSENT) in *Barbozia* (1928, p. 45-46), or, in his Latrunculiidae, as amphiaster-derivatives which could be related to chelas (*ibid.,* p. 47), which he thought of similar origin (*ibid.,* p. 44). On the other hand, sigmas were interpreted as simply reduced diactinal oxyasters (*ibid.,* p. 44).

There are several objections to these notions. First, it is doubtful whether discorhabds are either homologous spicules or forms related to chelas. Those of *Sigmosceptrella* could represent a "spiny chela," or chelaster, but the others have straight protorhabds. Those of *Barbozia* and *Didiscus* are modified oxeas morphologically (cf. DENDY, 1922, pl. 18, fig. 1d, 3b-c), develop from oxeas in ontogeny, and accompany oxea megascleres, overlapping them in size in *Didiscus;* these facts suggest direct relationship to megascleric oxeas, not to chelas. The *Latrunculia* "chessman" can be thought related to spinispiras, if interpreted in terms of the microscleres of *S. corticata,* which was made a *Latrunculia* by CARTER (1879, p. 298) and TOPSENT (1928, p. 47). Against this, typical discasters (Fig. 6, right) of *Latrunculia apicalis* RIDLEY & DENDY, which do not pass into or accompany spinispiras, may have a stylote or tylostylote axis (cf. RIDLEY & DENDY, 1887, pl. 45, fig. 9a, c; pl. 51, fig. 1b), and in imperfectly developed examples are irregularly spined styles (e.g., KIRKPATRICK, 1908, pl. 15, fig. 5-7); taken with their typical arrangement at the surface with the stylote end inward (RIDLEY & DENDY, 1887, pl. 51, fig. 1b), this suggests correspondence with the cortical styles or tylostyles seen in various "clavulids." If *Sigmosceptrella* correctly is included in the "clavulids," the most likely prototype of its so-called "sigmodiscorhabd" is not a sigma or a chela but a spinispira varied as a sigmaster.

Second, TOPSENT's (1928) concept of chelas as amphiaster-derivatives does not seem correct to me. This idea depends on derivation of the dentate type of chela from the toothed "birotulate" of *Iotrochota* RIDLEY, by curvature of the shaft and resorption of teeth on the convex side (TOPSENT, 1928, p. 44), and on comparison of *Iotrochota* birotulates with spicules of *Samus anonymus* GRAY, which TOPSENT (1928, p. 28) also called amphiasters, as grounds for regarding the former as the prototype of chelas. For me the spicules of *Samus* GRAY are genuine amphitriaenes, with true actinal cladi identified by axial filaments continuous with that of the rhabdome (cf. CARTER, 1879, p. 351, pl. 29, fig. 3; SOLLAS, 1888, p. liv, fig. x,o). The toothed ends of dentate chelas, including the "birotulates," are not comparable cladomes. Chelas, like diancistras and clavidiscs, develop from sigmas (cf. DENDY, 1921, p. 107-113), and some are essentially ornamented sigmas even when adult. The different development of the ends in anisochelas is comparable with markedly different curvature of the ends in some sigmas; the "contortion" common in sigmas is unusual in chelas, but occasionally present (e.g., HENTSCHEL, 1911, p. 349, fig. 32f). These facts point strongly to homology of sigmas and chelas, not to different origins.

SUMMARY AND CONCLUSIONS

Returning to general assessment, the main points above may now be correlated. First, DENDY was mistaken in assuming the homology of sigmaspires and sigmas *s.s.,* which are probably if not certainly convergent; even if this is not accepted, the sponges they occur in can scarcely be related as he claimed (1922, p. 12, 25; cf. TOPSENT, 1928, p. 31). The homology of his "discorhabds," and his views on the origin of spinispiras, are also not acceptable. On the other hand, he seems to have been right in interpreting the asters of *Timea* as pseudoeuasters, in at least the species he cited (1921), and the "dichotriact" (streptosclere) series of microscleres as not simply spiral monaxons.

TOPSENT (1928) and DE LAUBENFELS (1936) were justified in rejecting parts of DENDY's conclusions; but DE LAUBENFELS at least went too far in the opposite direction, if classification is judged by correspondence with probable relationships. He described the microscleres as having "much less" value than do megascleres and general structure (1936, p. 166); but divisions of his classification which cut across groupings based on microscleres may in fact depend solely on occurrence of particular megascleres, without support from other evidence. This applies specially to 1) division of Choristida *sensu* SOLLAS into Carnosa and Choristida *sensu* DE LAUBENFELS, on the basis of presence or absence of a megascleric calthrops; 2) reference of some genera to his Epipolasida on a basis of absence of triaenes, which even led to inclusion of some with euasters (*Stellettinopsis corticata* CARTER) or sigmaspires ("*Trachygellius*" *cinachyra* DE LAUBENFELS) whose triaenes were simply unknown to him; and 3) reference of genera with spinispiras to the Hadromerina *sensu* DE LAUBENFELS or his Epipolasida, according to whether the megascleres include tylostyles or simple styles only. In none of these cases are there good grounds for claiming

that megascleres provide better evidence of relationships than the microscleres. More generally, the megascleres also provide no sure basis for arrangement of the sponges with sigmatoscleres (sigmas *s.s.*, chelas, etc.) in more than a single major taxon. The microscleres are generally acceptable as reflecting relationship; but the megascleres allow the different methods of HENTSCHEL (1925), TOPSENT (1928) and DE LAUBENFELS (1936), and even their three different treatments of *Desmacidon* and *Mycale*.

Therefore, I can see no grounds for DE LAUBENFELS's emphasis on megascleres, unless the aim of classification is seen as comprehensive arrangement, without emphasis on relationships. This is an acceptable method, if the number of forms without microscleres is thought to make "natural" arrangement impracticable. But, even if this view is taken, there is still little justification for distinctions between 1) Haplosclerina and Poecilosclerina *sensu* DE LAUBENFELS, 2) Hadromerina *sensu* DE LAUBENFELS and Epipolasida, and 3) Choristida *sensu* DE LAUBENFELS and Carnosa, which in each case comprise intergrading forms which might just as well be placed in one taxon.

CLASSIFICATION RECOMMENDED

First, I follow BURTON in preferring classification in terms of inferred relationships where this is practicable. It is not desirable, however, to emphasize phylogeny (cf. BURTON, 1956, p. 113), unless this means simply that forms grouped together are supposed to be related.

Next, classification of the spiculate nonlithistids should be based on initial recognition of six groups of sponges:

1) Microspiculate Plakinidae (e.g., *Plakina* SCHULZE, *Corticium* SCHMIDT), in which typical megascleres are absent, plus the "myxosponge" *Oscarella* VOSMAER, in which the amphiblastula embryos agree with those of *Plakina*.

2) Choristid sponges, characteristic microscleres of which are streptoscleres, though microrhabds or simple euasters may also occur.

3) Choristid and monaxonid sponges, characteristic microscleres of which are polyactinal euasters, with solidified derivatives (sterrasters, aspidasters) added, not accompanied by streptoscleres though microrhabds or sanidasters may occur.

4) Choristid sponges, characteristic microscleres of which are sigmaspires, without streptoscleres or euasters though microrhabds sometimes occur.

5) Monaxonid sponges, characteristic microscleres of which are spinispiras, though these may pass into sigmaspires, microrhabds, amphiasters, sanidasters or pseudoeuasters.

6) Monaxonid sponges, characteristic microscleres of which are sigmastoscleres.

These are the only groups acceptable as a basis for major taxonomic divisions, if arrangement of the forms containing megascleres (groups 2-6) is based on microscleres. The main questions are how these groups should be treated, and what others need to be added.

Historically, the groups defined above have been the basis of taxonomic use of the microscleres, from the classifications of the *Challenger* authors (RIDLEY & DENDY, 1887; SOLLAS, 1888) to BURTON's current system (e.g., 1959), arranged in various combinations and with further variations in treatment of euaster-bearing sponges of

Group 3. The main relevant taxa and combinations are as follows (see also Table 2):

1) Group 1. Microsclerophora SOLLAS, Homosclerophora DENDY, Megasclerophora LENDENFELD.

2) Group 2. Streptastrosa SOLLAS; Metastrosa LENDENFELD; "Asterostreptidae" TOPSENT; Streptosclerophora DENDY; Streptastroclerophora BURTON.

3) Group 2 + Group 3 less monaxonids. Astrophora SOLLAS *sensu* DENDY, 1905.

4) Group 2 + Group 3 less Tethyidae. Astrophora SOLLAS, *sensu* SOLLAS.

5) Group 2 + Group 3. Astrotetraxonida HENTSCHEL, *sensu* DENDY, 1916.

6) Groups 2 + 3 + 5. Astrotetraxonida HENTSCHEL, *sensu* HENTSCHEL.

7) Group 3 less Tethyidae. Euastrosa SOLLAS + Sterrastrosa SOLLAS.

8) Group 3. Astrotetraxonida HENTSCHEL, *sensu* DENDY, 1924; Astrosclerophora BURTON in original (1929) sense.

9) Monaxonids of Group 3 + Group 5. Astromonaxonellida DENDY; Hadromerina TOPSENT, *sensu* TOPSENT.

10) Groups 3 + 4 + 5. Astrosclerophora BURTON in current (e.g., 1959) sense.

11) Group 4. Sigmatophora SOLLAS.

12) Groups 4 + 5 + 6. Sigmatotetraxonida HENTSCHEL, *sensu* DENDY, 1922; Sigmatosclerophora BURTON in original (1929) sense.

13) Groups 4 + 6. Sigmatotetraxonida HENTSCHEL, *sensu* HENTSCHEL.

14) Group 5. Clavulina VOSMAER; "Clavulidae" *sensu* BURTON.

15) Group 6. Halichondrina VOSMAER, *sensu* VOSMAER (not DE LAUBENFELS, TOPSENT); Sigmatomonaxonellida DENDY; Sigmatosclerophora BURTON in current sense (e.g., 1959).

The solution now suggested is that each of the six groups above, plus forms considered referable to groups 2-6 though lacking characteristic microscleres, should comprise a separate order, without further grouping except as Demospongia. Each of these orders is pictured basically as simply a workable taxonomic assemblage; but it also seems acceptable that the typical members, possessing the characteristic microscleres in groups 2 to 6, comprise natural assemblages. Nothing shows that the microscleres relied on are convergent in unrelated sponges, except for the probable convergence of craniellid sigmaspires (Group 4) and

sigmas *s.s.* (Group 6), and possible convergence of the former and similar spinispiras (Group 5). By comparison, there is little clear evidence of further relationships. It would probably be correct to associate Groups 2 and 3, since streptoscleres and polyactinal euasters both seem to be derived from simple (=pauciradiate) euasters, and genera whose megascleres are calthrops (e.g., *Pachastrella* SCHMIDT, *Calthropella* SOLLAS) are similar apart from the microscleres; but the two groups would still need to be regarded as divergent and distinguishable series. It is possible to argue for various other relationships (cf. above); but none of these seems certainly demonstrable, and some claimed by DENDY (1905, 1916-22) are untenable. The simplest solution thus also seems the most realistic for this type of classification.

Next, names of taxa characterized by microscleres have generally been based on the latter (e.g., Astrophora, Euastrosa, etc.; cf. e.g., SOLLAS, 1888); but this seems inappropriate when numbers of genera included may lack the characteristic microscleres, and some types (euasters, sigmaspires) are not in fact confined to one order. It is therefore proposed to base names on the name of an included type genus, with characteristic spiculation. The names proposed are:

Group 1. Order Plakinida (type, *Plakina* SCHULZE).

Group 2. Order Poecillastrida (type, *Poecillastra* SOLLAS).

Group 3. Order Ancorinida (type, *Ancorina* SCHMIDT).

Group 4. Order Craniellida (type, *Craniella* SCHMIDT).

Group 5. Order Spirastrellida (type, *Spirastrella* SCHMIDT.)

Group 6. Order Desmacidontida (type, *Desmacidon* BOWERBANK).

The last is subjectively synonymous with Halichondrina (-ida) VOSMAER if *Halichondria* BOWERBANK is included in the Desmacidontida; but microscleres are lacking in *Halichondria* (see also next paragraph), and ordinal nomenclature need not follow strict priority.

These six orders appear generally adequate for arrangement of the spiculate nonlithistids. Certainly some genera are difficult to allocate, but this is so with most classifications including that of DE LAUBENFELS. The only large group for which a further order could be thought appropriate are the Halichondrina *sensu* DE LAUBENFELS; but it

seems best at present to follow Burton in regarding them as Desmacidontida (=Sigmatosclerophora restr., Burton).

The most acceptable arrangement of the lithistid sponges is that given by de Laubenfels in his *"Treatise"* classification (1955, p: 44-66), though some of the suborders need revision. It is now well established that these sponges are polyphyletic (Schrammen, 1910; Topsent, 1928; Burton, 1929a; de Laubenfels, 1936; Reid, 1963), but insufficient is known for their general allocation to the orders above. Significant microscleres (streptoscleres, sigmaspires, chelas) occur in a few living species; but more have no microscleres or none of value, and almost nothing is known from the numerous fossils. There are also several groups with no modern representatives (Orchocladina, Didymmorina), or none with microscleres (Sphaerocladina) or diagnostic microscleres (Megamorina). Formerly, I (Reid, 1963) grouped lithistid suborders with nonlithistids when diagnostic microscleres are known from some species, but this involves reliance on the desmas of the others, and at least one type of desma (rhizoclones) appears to have had more than one origin (Reid, *ibid.*). All true lithistids are therefore now placed in the order Lithistida, retaining this name because the order is known to be composite. An exception, however, may be made for sublithistids with chelas (e.g., *Desmatiderma* Topsent, *Lithochela* Burton), which are too clearly Desmacidontida to need placing elsewhere.

In passing, the "sigmas" relied on by Hentschel (1925, p. 407) and Rezvoi *et al.* (1962, p. 62) in placing the Rhizomorina ("Rhizomorinidae" Hentschel) in Vosmaer's Cornacuspongida (i.e., as Desmacidontida, herein) are not sigmas *s.s.* but typical sigmaspires, as correctly stated by Topsent (1928, p. 22-26; cf. also Sollas, 1888, p. 346-347; Dendy, 1922, p. 8).

The keratose sponges are not sharply separable from the Desmacidontida, because of occurrence of "pseudoceratosa" (Dendy, 1905) with spicules or none in different specimens (e.g. *Spinosella, Siphonochalina* spp.), but are typically entirely aspiculate, and include forms with little resemblance to any with spicules. It is convenient to place them in an order Keratosida, though admitting that this separation is partly artificial. The order is also presumably composite, if some

or all keratose sponges have arisen from various Desmacidontida (cf. e.g., Ridley & Dendy, 1887; Minchin, 1904; Topsent, 1928; de Laubenfels, 1936).

This classification may be summarized as follows:

Order PLAKINIDA

Microspiculate Demospongia, with amphiblastula embryos where any are known, and askeletose Demospongia with similar embryos; spicules mainly tetractinal, triactinal or diactinal, though forms with more rays may occur. Examples: *Plakina* Schulze, *Plakortis* Schulze, *Roosa* de Laubenfels, *Corticium* Schmidt.

Order POECILLASTRIDA

Choristid Demospongia whose characteristic microscleres are streptoscleres, though microrhabds or pauciradiate euasters may also occur; without sigmaspires or typical polyactinal euasters. Examples: *Poecillastra* Sollas, *Thenea* Gray, *Pachastrella* Schmidt.

Order ANCORINIDA

Choristid or monaxonid Demospongia whose characteristic microscleres are polyactinal euasters, though microrhabds or sanidasters may also occur, and similar sponges with euasters only or no spicules; without streptoscleres or sigmaspires. Examples: *Ancorina* Schmidt, *Stelletta* Schmidt, *Calthropella* Sollas, *Plakinastrella* Schulze, *Erylus* Gray, *Geodia* Lamarck, *Asteropus* Sollas, *Jaspis* Gray, *Tethya* Lamarck, *Hemiasterella* Carter, *Chondrilla* Schmidt, *Chondrosia* Nardo.

Order CRANIELLIDA

Choristid Demospongia whose characteristic microscleres are sigmaspires, sometimes varied as toxaspires or chela-like spicules, and similar monaxonid sponges; without streptoscleres or euasters, though microrhabds sometimes occur. Examples: *Craniella* Schmidt, *Tetilla* Schmidt, *Paratetilla* Dendy, *Amphitethya* Lendenfeld, *Samus* Gray, *Raphidotethya* Burton.

Order SPIRASTRELLIDA

Monaxonid Demospongia whose characteristic microscleres are spinispiras, sometimes varied as microrhabds, sigmaspires, amphiasters, sanidasters or pseudoeuasters; some with euastriform asters of uncertain homology; without sigmatoscleres. Cementing spongin rarely present, but spongin fibers absent. Examples: *Spirastrella* SCHMIDT, *Cliona* GRANT, *Placospongia* GRAY, *Trachycladus* CARTER, *Timea* GRAY, *Suberites* NARDO, *Polymastia* BOWERBANK, *Diplastrella* TOPSENT.

Order DESMACIDONITIDA

Monaxonid and sublithistid Demospongia whose characteristic microscleres are sigmatoscleres, though discasters or other pseudasters may also occur; without spinispiras. Spongin frequent as cement or skeletal fibers; occasional species pseudoceratose, with spongin but no spicules in some specimens. Examples: *Desmacidon* BOWERBANK, *Haliclona* GRANT, *Siphonochalina* SCHMIDT, *Gellius* GRAY, *Mycale* GRAY, *Crambe* VOSMAER, *Desmatiderma* TOPSENT, *Myxilla* SCHMIDT, *Lithochela* BURTON, *Tedania* GRAY, *Clathria* SCHMIDT, *Microciona* BOWERBANK, *Higginsia* HIGGIN, *Axinella* SCHMIDT, *Sigmaxinella* DENDY, *Halichondria* BOWERBANK.

Order KERATOSIDA

Demospongia with a spongin skeleton only, unless this is supplemented by foreign inclusions, and similar askeletose sponges. Examples: *Spongia* LINNÉ, *Dysidea* GRAY, *Aplysilla* SCHULZE, *Halisarca* JOHNSTON.

Order LITHISTIDA

Demospongia whose main or only megascleres are desmas, which are typically united by zygosis to form a skeletal framework. Loose monaxons, dermal triaenes or analogous spicules, or microscleres may also occur.

Suborder TETRACLADINA

Lithistida whose characteristic desmas are tetraclones, sometimes varied as triders, though monaxial radical desmas or supplemental rhizoclonids may also occur. Often with dermalia in the form of dichotriaenes, phyllotriaenes or discotriaenes, replaced in a few by discotriaene-like spicules which are monaxial or anaxial. Examples: *Theonella* GRAY, *Discodermia* DU BOCAGE, *Neosiphonia* SOLLAS, *Kaliapsis* BOWERBANK, *Siphonia* GOLDFUSS, *Jerea* ZITTEL, *Prokaliapsis* SCHRAMMEN, *Plinthosella* ZITTEL.

Suborder DICRANOCLADINA

Lithistida whose desmas are dicranoclones, to which triaene dermalia may be added, or with rhizoclone desmas and triaenes; supplemental rhizoclonids or occasional tetraxial desmas may also occur. Triaenes dichotriaenes or phyllotriaenes. Examples: *Corallistes* SCHMIDT, *Daedalopelta* SOLLAS, *Macandrewia* GRAY, *Pachinion* ZITTEL, *Leiocarenus* SCHRAMMEN.

Suborder MEGAMORINA

Lithistida whose desmas are heloclones or megaclones, to which dermal triaenes or supplemental rhizoclonids may be added. Triaenes protriaenes, plagiotriaenes or dichotriaenes. Examples: *Costifer* WILSON, *Isoraphinia* ZITTEL, *Pleroma* SOLLAS, *Doryderma* ZITTEL.

Suborder DIDYMMORINA

Lithistida whose characteristic desmas are didymoclones, though rhizoclones may also occur. Dermal triaenes (dichotriaenes) may also be present. Example: *Cylindrophyma* ZITTEL (no modern examples).

Suborder RHIZOMORINA

Lithistida without dermal triaenes whose desmas are all rhizoclones. Examples: *Scleritoderma* SOLLAS, *Taprobane* DENDY, *Azorica* CARTER, *Aciculites* SCHMIDT, *Seliscothon* ZITTEL, *Verruculina* ZITTEL, *Scytalia* ZITTEL, *Petromica* TOPSENT, *Megarhiza* SCHRAMMEN.

Suborder ORCHOCLADINA

Lithistida without dermal triaenes whose characteristic desmas are dendroclones, chiastoclones or anomoclones, though rhizoclones or pseudotetraclones may also occur. Examples: *Anthaspidella* ULRICH, *Aulocopium* OSWALD, *Archaeoscyphia* HINDE, *Phacellopegma* GERTH, *Pycnopegma* RAUFF (no modern examples).

Suborder SPHAEROCLADINA

Lithistida without dermal triaenes whose desmas are sphaeroclones or astroclones, to which

anaxial dermal bodies may be added. Examples: *Vetulina* SCHMIDT, *Lecanella* ZITTEL, *Regnardia* MORET, *Ozotrachelus* DE LAUBENFELS, *Astylospongia* ROEMER.

Suborder TRICRANOCLADINA

Lithistida without dermal triaenes whose desmas are tricranoclones. Example: *Hindia* DUNCAN (no modern examples).

IDEAS ON PHYLOGENY

It does not seem possible to give any sure picture of demosponge phylogeny at present. The group is extremely frustrating for the paleontologist, used to thinking in terms of stratigraphical evidence. The record of nonlithistid sponges is clearly extremely incomplete, and microscleres are almost never associated with macroscopic material. Many fossil lithistids are recorded, but their microscleres are again almost unknown. Ideas on phylogeny must thus be based essentially on comparative study of the modern forms. This is a legitimate method, provided it is realized that comparison of forms from one time-plane furnishes no objective evidence of the direction of change in phylogeny. It must also be recognized that all modern genera and species are phylogenetic end forms, and that this applies especially to any forms claimed to be primitive. Some zoological speculators have badly lost sight of these principles.

The most important problem is lack of unequivocal evidence of the primitive character of demosponge spicules. According to SCHULZE (1887) and DENDY (1921), the central type of demosponge spicule is the regular tetraxon, or calthrops, and all Demospongia (SCHULTE, 1887) or all with spicules (DENDY, 1921) are supposed to have a choristid ancestry. The Plakinida (Homosclerophora, DENDY) are supposed to show a type of spiculation which represents the primitive condition. On comparative grounds, the picture of the calthrops as a central type of spicule seems well founded; in particular, it forms a common point in morphological series leading to types as distinct as oxeas, discotriaenes, tetraxial and monaxial desmas, spirastral streptoscleres, and sterrasters and aspidasters. Radiation to these types from a central one is surely more likely than the opposite. On the other hand, this need not be conclusive.

First, the oldest known choristids are only Lower Carboniferous in age, but monaxonids date from the Cambrian. This could be regarded as evidence for evolution of megascleres from monaxon (oxea) to calthrops, by way of long and short-shafted triaenes. Second, the supposedly primitive Plakinida are not certainly known below the Miocene. Third, the reason why the cladi of triaenes are called cladi is apparent origin (SOLLAS, 1888) of some long-shafted triaenes from initial monaxons in ontogeny, so that the cladi appear to be branches of a primary rhabdus. If it is assumed, following DENDY (1921), that ontogeny follows phylogeny, this again should point to the origin of tetraxons from monaxons through triaenes. These points were not noted by DENDY (1921), nor by BURTON (1956) in attacking DE LAUBENFELS's (1936) inversion of TOPSENT's (1928) order of taxa.

On the other hand, this evidence needs critical assessment. First, nothing is known of microscleres of the pre-Carboniferous monaxonids, which may in fact not have been related to any choristids. Second, Carboniferous choristid material includes tetraxons ranging from regular calthrops to long-shafted trachelotriaenes, suggesting a long previous history. Third, spicules of Plakinida are characteristically of microscleric size, and cannot be expected to be commoner as fossils than microscleres. Fourth, spicular ontogeny need not always follow phylogeny, but may show instead nonphyletic patterns due to caenogenetic evolution. The desmas already cited (Discussion, para. 2) in this context show caenogenetic change in the crepis, however phylogeny is interpreted. Lithistid dermalia grading from dichotriaene to discotriaene provide another example; although the discotriaene is presumably the end form in this series, the crepis is usually a simple orthotriaene, without deuterocladi. This reduction is carried further in discostrongyles, if these are accepted as derived from discotriaenes. If the origin of triaenes from monaxons is seen in this context, it could represent caenogenetic retardation of formation of the cladi, correlative with hypertrophy of the rhabdome, and possibly ultimately leading to their total suppression. There is nothing to show that this picture is less likely

characteristic microscleres

Ancorinida

Poecillastrida

polyactinal
euasters

streptoscleres

triaene

oxea only

oxea

simple

euasters

calthrops

+

oxea

microscleres
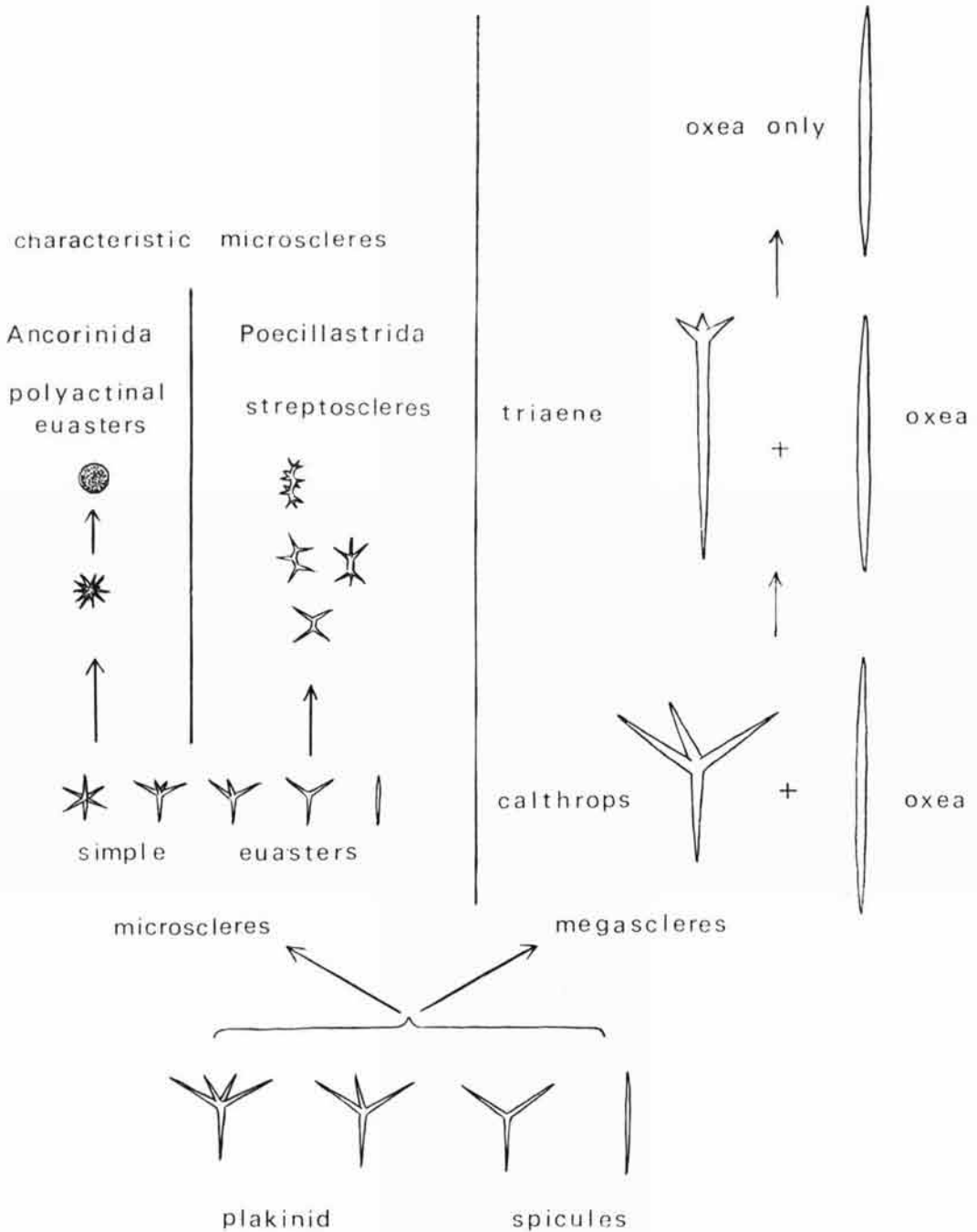
megascleres

plakinid

spicules

FIG. 7. Spicular phylogeny in Plakinida, Ancorinida and Poecillastrida, if typical megascleres and microscleres were both evolved from spicules like those of *Dercitopsis* DENDY. This explanation is based wholly on observed spiculations.

than the palingenetic one, and, on balance, it seems the more probable. These objections to the SCHULZE-DENDY theory are thus also far from conclusive.

What also seems relevant, moveover, is to ask how the microscleric calthrops is related to the megascleric calthrops. DENDY's (1921) picture of spicular phylogeny allows the two to be homologous, since both are envisaged as derived from plakinid tetraxons (Fig. 7). But if all tetraxons are derived from monaxial megascleres, by way of long-shafted triaenes, it is difficult to give any simple explanation of the present spiculation of the Poecillastrida and Ancorinida. Since long-shafted triaenes are megascleres, and triaenes are in general never microscleres, it seems that evolution of a microscleric calthrops, and any related type of microsclere, could only follow previous evolution of a megascleric calthrops from a triaene (Fig. 8). Yet most of the choristids with streptosclere or euaster microscleres are forms without megascleric calthrops (Theneidae, Geodiidae, most Ancorinidae); and the Coppatiidae and Tethyidae have euasters, but are purely monaxonid. If the choristid ancorinids are supposed to be derived from the monaxonid coppatiids, instead *of vice versa* as envisaged by DENDY (1916, 1921), the coppatiids must in turn be derivatives of other unknown choristid sponges, in which triaenes and calthrops must have existed to permit the evolution of euasters. This paradoxical conclusion seems hard to avoid, except by claiming that the megascleres and microscleres had independent origins.

In detail, if the megascleres and microscleres are thought to be homologous, a coherent explanation can be given for the spiculations seen in the orders Plakinida, Ancorinida and Poecillastrida. The Plakinidae can first be envisaged as surviving descendants of a stock which once gave rise to the two other orders, but has since had a separate and long evolutionary history. The lophose type of calthrops (or candelabra spicules *sensu lato*) and the amphiblastula embryos of *Plakina,* which do not occur in true choristids, can be cited as probably products of this separate plakinid evolution. Assuming, with DENDY (1921), an initial spiculation like that now seen in *Dercitopsis* DENDY, the first step towards evolution of higher forms should be differentiation of the spicules into several size grades, e.g. as is now seen in *Plakinastrella copiosa* SCHULZE. This would then lead to the largest spicules present becoming large

enough to qualify as megascleres. At this stage, the megascleres should be either all calthrops or a mixture of calthrops and oxeas, and the microscleres simple euasters, in the form of small calthrops or other pauciradiate variants.

From this stage on, the megascleres and microscleres could evolve independently, with two main stocks characterized by development of polyactinal euasters (Ancorinida) and streptoscleres (Poecillastrida) respectively. In the megascleric skeleton, production of triaenes as an ectosomal specialization could be followed by restriction of tetraxons to triaenes, with monaxons persisting as the principal or only choanosomal megascleres. Choanosomal calthrops could be lost by simple suppression, by conversion into triaenes, or possibly by conversion into further euasters; the last could explain the occurrence of large simple euasters in some *Thenea* species. The last stage, in the ancorinid series, could be loss of the triaenes with production of monaxonid sponges, by simple suppression of triaenes as envisaged by DENDY (1916, 1921), or by proterogenetic loss of the cladi following caenogenetic delay in their formation (see above). With the microscleres, progressive complication in form could be accompanied by progressive diminution in size, as seen now in, e.g., the two different sizes of euasters in *Corticella stelligera* (SCHMIDT), or in the streptosclere series in which the plesiaster, metaster and spiraster types are often progressively smaller.

As stated above, it is difficult to give a comparable picture which inverts the direction of phylogeny. If the choristid Ancorinidae are derived from monaxonid copatiids, and tetraxons in general are derived from monaxons via triaenes, the coppatiids must themselves be derivatives of triaene-bearing sponges, and the latter of further unknown monaxonids. That is, the Ancorinidae must have twice been monaxonid and choristid alternately in the course of their history, with the first two stages wholly hypothetical. The Theneidae may either have had a similar history, with three previous stages (monaxonid, choristid, monaxonid) unknown, or they may be, e.g., ancorinid derivatives showing loss of polyactinal euasters and development of streptoscleres. In either case, the two groups should converge toward forms with only calthrops as megascleres, and beyond these to plakinids as degenerate end forms (see DE LAUBENFELS, 1936, p. 177). Alternatively, hypothetical generations of monaxonids
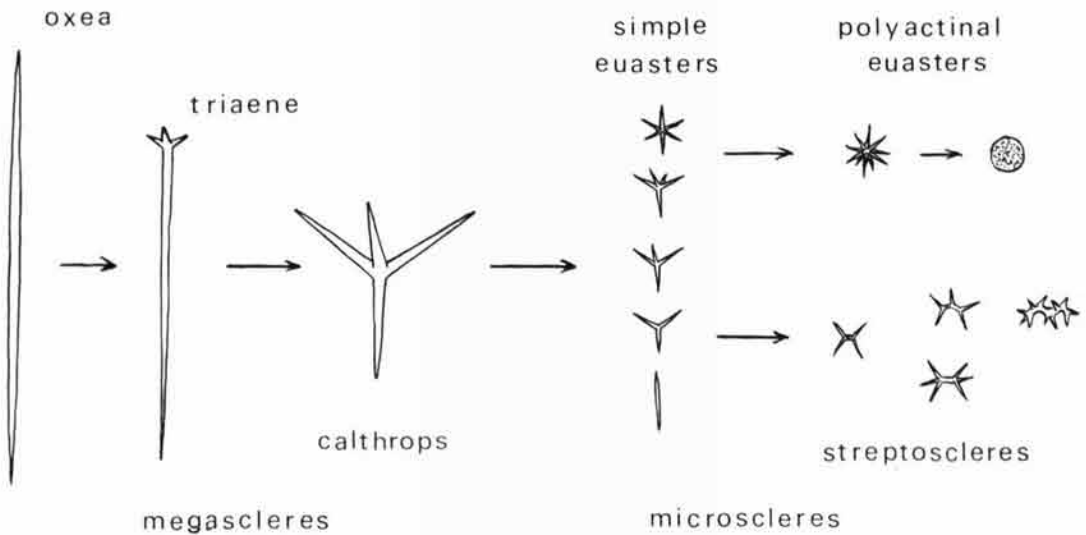
Fig. 8. Spicular phylogeny in Ancorinida and Poecillastrida if all tetraxons arose from monaxial megascleres as triaenes. If this is correct, a monaxonid sponge having euaster microscleres must be derived from an earlier choristid, derived in turn from an earlier monaxonid.

and choristids can be avoided by claiming that the megascleres and microscleres had some kind of independent origins, though again they must be pictured as merging at the end of their evolution. If microscleric calthrops and triactins are also claimed to be end-forms, they must have been derived independently from polyactinal euasters in the Ancorinida, and from spirasters, amphiasters, or both in the Poecillastrida. Further unknown prototypes must then be pictured for these specialized microscleres.

There is no certain evidence whether any of these pictures is correct; but only DENDY's notions allow a coherent explanation of the known spiculation of these sponges, without assumptions other than that seemingly homologous spicules are homologous in fact. With the microscleres, it also seems distinctly more likely that polyactinal euasters and amphiastrose or spirastrose streptoscleres are phylogenetic end forms, not prototypes from which microscleric tetractins and triactins have arisen at the end of phylogeny. If plakinids are seen as end-forms, they might be explained as being simplified in relation to forming thin crusts, though this habit is not general in them. *Samus* GRAY, and perhaps *Thrombus* SOLLAS, might be pictured as comparable end forms in a craniellid series. But this notion still leaves the other problems noted, and would also have the further im-

plication that the rhagon type of larva, as seen in *Plakina,* is not a primitive feature. In addition, the sponges to be pictured as most primitive, among members of these orders now living, would be the coppatiid and tethyid Ancorinida, with complex types of euaster microscleres (spherasters, sterrospherasters), and sometimes radiate architecture and a massive or distinctly fibrous cortex, as in e.g., *Tethya* LAMARCK. These highly organized sponges give a very strong impression of being anything but primitive, and more probably having the status ascribed to them by DENDY (1916, 1921).

In contrast, the three remaining orders of nonlithistid sponges (Craniellida, Spirastrellida, Desmacidontida) have no obvious connections with the others. Choristids only occur in the order Craniellida. BURTON (e.g. 1956) presumably regards them as of ancorinid origin, since he groups them in his Asterosclerophora. The sigmaspires could represent microrhabds (or sanidasters) of ancorinid sponges, assuming loss of normal euasters. But this leads to the problem that craniellids may be eurypylous, while the choristid ancorinids are typically aphodal or diplodal. In addition, craniellids are sometimes viviparous, with large parenchymula larvae. Since calthrops are absent, one could argue that the triaenes must, here at least, be oxea derivatives;

though absence of calthrops in modern forms does not prove this, and irregular development of cladi in triaenes showing passage into diaenes and monaenes (in e.g., protriaenes, etc., of *Craniella* and *Cinachyra* species) suggests reduction of cladi. But the only monaxonids which seem fairly certain allies are again highly organized sponges (*Trachygellius* TOPSENT, *Raphidotethya* BURTON).

The monaxonid Spirastrellida, or "clavulids," again seem more or less isolated. TOPSENT (1928) arranged them with monaxonid Ancorinida in his Hadromerina. Styles and sometimes tylostyles occur in *Tethya* species; but the spinispira does not appear to be a modified euaster. On the contrary, it seems to be directly related to oxea megascleres, of which it is not a likely prototype (p. 15). At least some spirastrellid "euasters" also seem to be modified spinispiras (p. 14). DENDY's derivation of the spinispira from a sigma, through a discorhabd, appears altogether fanciful. The other possibility is relationship to craniellid choristids, because the characteristic microscleres (sigmaspires, spinispiras) are comparable, and at least some monaxonid "clavulids" have sigmaspire microscleres (e.g. *Tentorina sigmatophora* BURTON, *Trachycladus cervicornis* BURTON). *Stylocordyla* WYVILLE THOMSON is specially like a craniellid, though neither type of microsclere is present. But, again, there is no indication of phylogenetic direction, except that a choristid derived from a typical spirastrellid would presumably inherit both spinispiras and tylostyles.

A possible clue to the origins of these sponges is the occurrence of simple oxyasters in some species of *Thoosa* HANCOCK (e.g., *T. fischeri* TOPSENT), which is usually placed as a clionid though it lacks spinispiras and has aberrant amphiastriform spicules. The oxyasters are slender triactins or tetractins, showing passage into diactins. While these forms might represent either a plakinid tetraxon or a degraded megascleric calthrops, they could also point to the origin of "clavulids" from the same primitive euaster-bearing stock as the order Ancorinida, perhaps also near the source of the "astraxinellids." The latter do not seem to be derived from the typical monaxonid Ancorinida (Coppatiidae and Tethyidae), though some possess polyactinal euasters. This suggestion would also fit the occurrence of eurypylous sponges among both "clavulids" and "astraxinellids," assuming this condition to be primitive; it could also suggest that the nominal genus *Timea* may

be composite biologically, comprising forms in which the asters are sometimes pseudoeuasters derived from spinispiras, but sometimes true euasters. Last, if TOPSENT (1928) was right to associate *Samus* with *Thoosa*, the presence in *Samus* of sigmaspires and small amphitriaenes would support the common origin of "clavulids" and craniellids, though this would involve taking the boring clionids as the most primitive "clavulids."

This leaves the problem of how the Desmacidontida are related to other forms with spicules. Once DENDY's notions are rejected, there is nothing to connect them certainly with any tetraxon-bearing sponges, unless the central spines of some sigmas are thought to point to origin from triactinal or tetractinal spicules (cf. TOPSENT, 1928). This suggests either a very long-standing separation, or, assuming that tetraxons are the primitive spicules in forms which possess them, that the Desmacidontida are of independent origin and primitively monaxonid.

The idea of independent origin of two groups of spiculate demosponges from myxosponge ancestors has recently been argued by LÉVI (1953, 1957), from embryological evidence. LÉVI divides Demospongia into Tetractinomorpha and Ceractinomorpha, with the latter comprising Halisarcidae, the keratose sponges and the typical Desmacidontida. The spiculate Ceractinomorpha (i.e., Desmacidontida herein) are supposed to derive from Keratosida, and the latter from the myxosponge *Halisarca*. The basis of this is general embryological agreement between *Halisarca* and other Ceractinomorpha, and occurrence of a *Halisarca* species in which the larva is an asconoid "rhagon," regarded as marking the genus as the most primitive demosponge known. The Plakinida are placed at the center of the Tetractinomorpha (as Homosclerophora), with *Oscarella* cited as possibly near to the ancestral type.

LÉVI's ideas are attractive, but are open to several objections.

1) *Halisarca* is a modern sponge, which cannot be directly ancestral to any supposed derivative, yet must also be assumed to have existed for longer than any forms supposed to derive from some past *Halisarca*. Chela-bearing Desmacidontida have existed since at least the Jurassic, implying a long enough earlier history for evolution of chelas. Further, if common origins are implied by

resemblance between a) some Orchocladina and the living *Lithochela,* or b) desmas of the Sphaerocladina and those of *Crambe* VOSMAER (LÉVI, 1960), this history goes beyond the Ordovician. In contrast, LÉVI's (1957) *Halisarca* evidence is based on a pair of sibling species, due presumably to recent speciation. In addition, the longer a supposed ancestral form must be thought to have persisted, the longer it has had for subsequent evolution of nonancestral characters.

2) No proof exists that morphologically simple sponges must be primitive, and not regressive types produced, e.g., by retarded development of adult characters. Here again it is relevant that *Halisarca* and *Oscarella* are modern, and thus objectively phylogenetic end forms.

3) *Halisarca* and *Oscarella* are both forms with incubated embryos, and therefore not primitive embryologically, assuming the normal relationship between oviparity and viviparity; on the contrary, both should be advanced types, derived from oviparous ancestors. The contrast between simple adult morphology but advanced embryology is also at any rate consistent with their being degraded forms, in which simplification has affected adult organization but not reproduction.

4) The main embryological schism in the Demospongia does not fall between the Tetractinomorpha and Ceractinomorpha, but between the Plakinida with amphiblastula embryos and other Tetractinomorpha, in which the few embryos known are always parenchymulas, as in Ceractinomorpha. This seems much more significant than whether the embryo is incubated or not, and is large or small in consequence.

5) As pointed out by BURTON (1963, p. 26), there is no proof of the common idea that a sycon must derive from an ascon, and not vice versa. An asconoid rhagon could just as well be derived from the normal syconoid type as "ancestral" to it. Considering a) the normal character of rhagons b) the late speciation implied by sibling status, this could be thought more likely than the opposite.

6) Inversion of the usual picture of origin of the Keratosida from Desmacidontida by loss of spicules involves the complication of assuming that the spicules were first imbedded in spongin, and only became free of it by reduction of the spongin. This seems inherently less likely than the picture of progression from local cementation to development of reticulate skeletons, with loss of spicules following.

7) There is no apparent difference between spicules of "tetractinomorphs" and "ceractinomorphs," apart from their different ranges in shape. Lithistid specialization, in particular, is identical in character in forms as far distant as tetraxon-bearing lithistids (Tetracladina, Dicranocladina, Megamorina) and sublithistid Desmacidontidae. This seems more consistent with inheritance of common potentialities by forms of common origin, than with independent origins of identical specializations.

It therefore seems premature to hold that embryology points to independent origin of tetraxon- and monaxon-bearing series of spiculate demosponges. Probably the only sure conclusion to be drawn from the *Halisarca* siblings is that sibling species differing mainly in the character of their larvae show that embryological characters can be less stable phylogenetically than adult characters, at even speciation level.

DENDY (1905) also thought that Demospongia include two stocks derived independently from myxosponge ancestors, but took these as comprising all spiculate forms together as Tetraxonida, and the Keratosida as Euceratosa. The only keratose sponges related to Tetraxonida were "pseudoceratosa," which are keratose examples of species in which the skeleton consists of spicules and spongin or spongin only in different individuals; true keratose sponges, with spicules never present, must be of different origin. This concept is not convincing. The agreements between Keratosida and Desmacidontida are genuine, however they ought to be interpreted. Further, if the Keratosida are iterative (i.e., repetitive) derivatives of Desmacidontida, of varying ages in different cases, transitional characters can only be expected in forms now in process of losing the spicules. The "euceratosa" are then explicable as simply of earlier origin, with characters often more or less modified by further evolution, or perhaps sometimes due to derivation from sponges unlike any now living. This picture seems to fit the facts at least as well as any other.

Therefore I see no sure evidence that existing Demospongia represent two main lines of descent from myxosponge ancestors, in either LÉVI's sense or DENDY's, or even that the myxosponges cited have any connection with demosponge ancestry.

The Desmacidontida are certainly difficult to relate to other forms with spicules, and seem to have a special relationship to keratose sponges; but relationships of some of the other groups (e.g., Craniellida) are just as enigmatic, and lack of transition among modern forms is not a criterion of lack of relationship. For instance, no transitions exist between modern birds and mammals, but this does not mean that their bones were evolved independently.

At least two possibilities exist for independent descent in phylogeny of stocks with tetraxons or no spicules but monaxons, from the same primitive source. First, diactinal spicules occur in some living plakinids, apparently as triactin-variants. In *Roosa* DE LAUBENFELS (1936, p. 178, pl. 19, fig. 2) the spicules are mainly diactinal, though triactins and transition forms occur. A plakinid-like root stock could thus have included forms with monaxial spicules only, long before evolution of megascleres and microscleres. Second, one should also ask how radiate spicules arose in the first case. In Calcarea, formation of rays as initially separate units suggests the origin of triactins and tetractins from assembled groups of primitive monaxons. Though the spicules are formed differently in modern Demospongia, this could explain the origin of radiate types in phylogeny. In particular, it could be the basis of meristic variation in the spicules, which was emphasized by DENDY (1921) as the primary mode of variation. The primitive spiculation would then consist of small monaxons only. If these were assembled into radiates in some forms but not others, one or more stocks could descend to the present without ever possessing tetraxons. In either case, descendants of forms with tetraxons could evolve as was envisaged by DENDY.

This picture has a bearing on the paleontological record. If stocks with tetraxons and only monaxons descended independently, whichever stock first developed megascleres would probably appear first stratigraphically, with no implication of being ancestral to the others. Thus monaxonid sponges could have megascleres before the evolution of choristids, with no implication that monaxonids are ancestral to choristids. If radiate spicules arose by compounding from primitive monaxons, monaxonids with megascleres could exist before plakinid-like sponges existed.

To sum up, it does not, first, seem possible to show any single general pattern in the phylogeny of forms now discussed. On comparative grounds, DENDY's picture of spicular phylogeny (1905, 1916, 1921, 1922, 1924) is acceptable as explaining the characters of the Plakinida, Ancorinida and Poecillastrida (DENDY's Homosclerophora, Astrotetraxonida restr., and Streptosclerophora); but it cannot be shown to apply to the Craniellida, Spirastrellida, or Desmacidontida (i.e., DENDY's Sigmatotetraxonida). The craniellid sponges are choristids, but have no sure connection with the others, and have features which suggest no close relationship in the sense implied by BURTON. There are no real grounds for claiming that either Spirastrellida or Desmacidontida are derived from any choristid sponges. The former may be allied to the craniellid choristids; but the latter have no probable relatives but the keratose sponges.

These findings do not, however, call for total inversion of DENDY's whole picture of phylogeny. First, lack of apparent relationship between groups known almost solely from their modern phylogenetic end forms is not proof of lack of relationship. It may only mean that groups have been separated for too long for connections to be evident. Second, evidence that a pattern of phylogeny is probably in one major line of descent is not affected by evidence that other lines may have existed, and may not have followed this pattern. Once separated, different stocks may then follow quite different phylogenies. Third, monaxonid sponges need not be derived from any choristid, if plakinid-like ancestral forms sometimes had only monaxial spicules (Fig. 9). There are two ways in which this can be envisaged, one based on the observed spiculation of living plakinids.

It seems very likely that a picture on this basis is the right one. The Plakinida have some features not repeated in the Ancorinida and Poecillastrida; but, the fish *Latimeria* has features not repeated in tetrapod vertebrates, without precluding crossopterygians from being ancestral to tetrapods. The whole spiculation and anatomy of the Plakinida, Ancorinida and Poecillastrida gives a very strong impression of morphological radiation from simple sponges, with the calthrops as a central type of spicule. This pattern also extends to the lithistid Tetracladina, Dicranocladina and Megamorina, in which tetraxon megascleres are present, and microscleres are streptoscleres when any distinctive form is seen. The apparent radiation is readily explicable phylogenetically, in
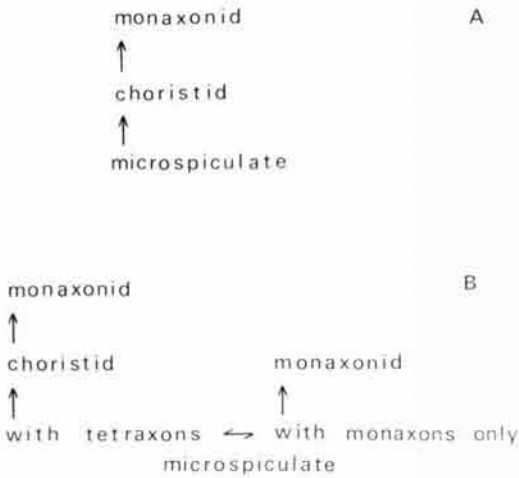
monaxonid   A

↑

choristid

↑

microspiculate

monaxonid   B

↑

choristid   monaxonid

↑   ↑

with tetraxons ⟷ with monaxons only
microspiculate

Fig. 9. Relationship of microspiculate, choristid, and monaxonid sponges, as inferred by Dendy *(A)* and Reid *(B)*. Under Dendy's picture of phylogeny (1905, 1916, 1921), all monaxonid sponges must be forms derived from choristids. According to Reid's different picture, monaxonids may be forms derived either from choristids, or from sponges with no spicules but monaxons before the evolution of megascleres. The latter mode of origin is thought probable for the Desmacidontida (compare also Reid, 1963, fig. 2: Sigmatosclerophora=Desmacidontida).

terms of observed characters only. To claim derivation of all calthrops from long-shafted triaenes involves inventing hypothetical generations of choristids and monaxonids to account for monaxonid sponges which have microscleric calthrops as euasters. To picture the calthrops as always a phylogenetic end form would require its derivation independently from spicules as different as long-shafted triaenes, polyactinal euasters, amphiastrose or spirastrose streptoscleres, rhizoclone or dicranoclone desmas, and lithistid discotriaenes or discostrongyles; and a different prototype is required for each of these various types of spicules, and the sponges they occur in. Any of these notions could, in fact, be correct; but none is convincing, and none is even needed if some monaxonids descended independently. If this view still leaves the phylogeny of some forms uncertain, this is not grounds for inverting the probable part of Dendy's picture to try to account for them.

The classification recommended above is not based on a picture of phylogeny, except that forms placed in orders with type genera are supposed to be related. My ideas on further rela-

tionships are as follows, but any other picture which fits the facts is also admissible (Fig. 10).

1) The Plakinida may be persisting representatives of a primitive choristid series, once ancestral to the other types of choristids. But they must have had a long independent history since at least the Carboniferous Period, and probably earlier, and some of their features may be due to regressive simplification. They are also not primitive embryologically, and are distinguished by a special type of embryo (amphiblastulas) unknown in other choristids, or any other demosponges.

2) The Poecillastrida and Ancorinida are probably groups of common origin, divergent in the character of the microscleres, but showing largely parallel evolution in the megaspiculation (though with loss of tetraxons in Ancorinida only).

3) The Craniellida and Spirastrellida are either groups of independent origin showing partial convergence in the microscleres, or groups of common origin divergent in both mega- and microspiculation. It is possible, but not demonstrable, that either group or both had an ancorinid origin, perhaps near the source of the "astraxinellids."

4) The Desmacidontida and Keratosida are related types of sponges, of which the latter have probably arisen repeatedly from the former by loss of spicules. There is no sure connection between the Desmacidontida and any tetraxonbearing sponges, but also no sure evidence that their spicules are of independent origin.

5) The Lithistida are polyphyletic derivatives of various nonlithistid sponges, and some have microscleres found otherwise in Poecillastrida, Craniellida or Spirastrellida (and Desmacidontida, if sublithistid forms are included). The origins of most groups (suborders herein) are uncertain. There is evidence (Reid, 1963) that the Tetracladina (not Orchocladina herein, grouped formerly as Tetracladina) arose from the same source as the pachastrellid Poecillastrida, and the Dicranocladina from the Tetracladina by reduction of the crepides of desmas from tetraxons to monaxons; but other types of desmas are probably all monaxon-derivatives, as in sublithistid Desmacidontida (e.g., *Desmatiderma* Topsent).

In conclusion, it seems a fair comment that the problem of demosponge phylogeny is largely a matter of having to rely almost solely on the
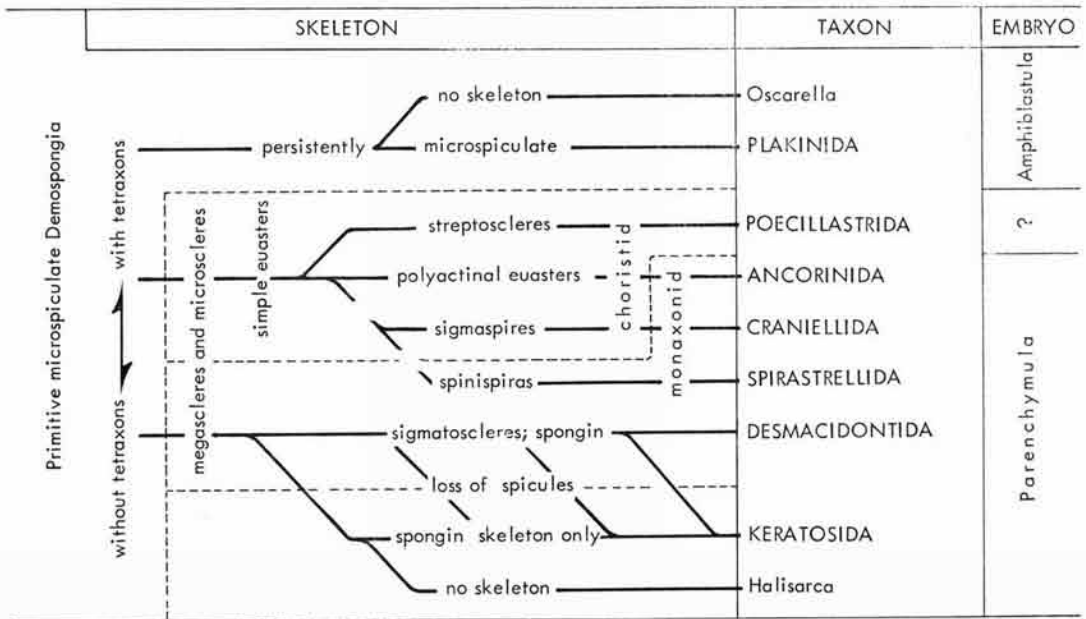
Fig. 10. Suggested relationships of living Demospongia, except Lithistida. The proposed classification does not depend on this picture of relationships.

skeleton for working data. In this respect Lévi's attempt to add embryological evidence is a welcome step forward; but, as shown above, this evidence is of doubtful significance, and sexual products are unknown in many Demospongia. The canal system might be considered to provide further evidence, but again its significance is uncertain because the direction of phylogenetic change is not demonstrable (see Discussion, above). The eurypylous state can be thought to be more primitive than the aphodal condition, and certainly sometimes arises by direct complication of the wall of a rhagon; but this does not prove that it cannot arise from the aphodal type in phylogeny, as a simplification, if a broadly lacunar structure is best suited to the sponge's living conditions or ability to circulate water. As seen above, some pictures of phylogeny suggest origin of eurypylous sponges from aphodal stocks, and if this is correct it also follows that the rhagon itself could be secondary. In other words, the rhagon type of larva may not represent any adult stage in demosponge evolution. This leaves only biochemical or cytological evidence as likely to provide data on a useful scale; but, until this is available, one can only rely on the spicules.

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TABLE 2.—*Distribution of Microscleres Identified as Streptoscleres, Euasters s.s., Sigmaspires, Spinispiras and Sigmatoscleres in Suprafamilial Assemblages of Demosponges Recognized by Different Authors.*

[Explanation.—The occurrence of the specified kinds of microscleres in demosponge groups distinguished by cited authors is indicated by letters, as follows.——A. Present as the characteristic microscleres of the relevant taxon, found in some or all families.——B. Present as the characteristic microscleres of some included families, though other cited types are characteristic of other families.——C. Present in isolated genera or species only.——D. Examples with up to six rays, developed as oxyasters, may accompany the characteristic streptoscleres.——E. Present only in included sublithistids.——F. Present only in lithistids. For the types of specified microscleres found in members of any given taxon, read across. For the distribution of a given type of microsclere in the taxa recognized, read vertically. Taxa comprising Demospongia without spicules are omitted.]

Authors	Streptoscleres	Euasters s.s.	Sigmaspires	Spinispiras	Sigmatoscleres
VON ZITTEL, 1878					
Monactinellida	—	B	C	B	B
Tetractinellida	B	B	B	—	—
Lithistida	C	—	C	—	E
Challenger authors (RIDLEY & DENDY, 1887; SOLLAS, 1888)					
Tetractinellida	B	B	B	—	—
Choristida	B	B	B	—	—
Sigmatophora	—	—	A	—	—
Astrophora	B	B	—	—	—
Microsclerophora	—	—	—	—	—
Lithistida	C	—	C	—	—
Monaxonida	—	—	C	B	B
Halichondrina	—	—	—	—	A
Clavulina	—	—	C	A	—
DENDY, 1905					
Tetractinellida	B	B	B	—	—
Homosclerophora	—	—	—	—	—
Astrophora	B	B	—	—	—
Sigmatophora	—	—	A	—	—
Lithistida	C	—	C	—	—
Monaxonellida	—	B	C	B	B
Astromonaxonellida	—	B	—	B	—
Sigmatomonaxonellida	—	—	C	—	A
DENDY, 1916+1925					
Homosclerophora	—	—	—	—	—
Astrotetraxonida	—	A	—	—	—
Sigmatotetraxonida	F	—	B	B	B
Streptosclerophora	A	D	—	—	—
DE LAUBENFELS, 1936					
Haplosclerina	—	—	—	—	A
Poecilosclerina	—	—	—	—	A
Halichondrina	—	—	—	—	—
Hadromerina	—	C	—	A	—
Epipolasida	—	B	C	C	—
Choristida	B	B	B	—	—
Carnosida	B	B	C	—	—
BURTON, 1959					
Streptastrosclerophora	A	D	—	—	—
Astrosclerophora	—	B	B	B	—
Sigmatosclerophora	—	—	**—**	—	A
Lithistida	C	—	C	—	E
REID, this paper					
PLAKINIDA	—	—	—	—	—
POECILLASTRIDA	A	D	—	—	—
ANCORINIDA	—	A	—	—	—
CRANIELLIDA	—	—	A	—	—
SPIRASTRELLIDA	—	—	C	A	—
DESMACIDONTIDA	—	—	—	—	A
LITHISTIDA	C	—	C	—	—

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APPENDIX: TECHNICAL GLOSSARY

This glossary is intended for nonspecialist readers, to whom terms used above are unfamiliar, but may also be useful to specialists who wish to check my usages.

acanthostyle (n.). Spiny monaxial spicule, with one blunt and one pointed end (e.g., Fig. 1,*14*); normally a megasclere.

acanthoxea (n.). Spiny monaxial spicule, which is sharp at both ends (e.g., Fig. 1,*11*); may be either a megasclere or a microsclere.

actinal (adj.). Appertaining to or consisting of true rays.

amphiaster (n.). Microsclere with radiating spines at both ends of a straight monaxial shaft (e.g., Fig. 2, *5a-d, 3,7d,* 4,5); recurrent in three main groups of microscleres (Fig. 2-4), as well as in individual developments.

amphidisc (n.). Monaxial spicule with a simple transverse disc, serrated transverse disc, or ring of recurved spines, at each end of a straight shaft; usually a microsclere, but a megasclere functionally in some fresh-water sponges. Also called a birotulate, some related to a chela and some to an oxea or acanthoxea.

asconoid (adj.). With choanocyte cells lining a central cavity (paragaster, or spongocoel) and no flagellated chambers.

aster (n.). Any polyactinal or seemingly polyactinal microsclere, in which rays or apparent rays are emitted from a center (e.g., Fig. 1,*2-7,13,16*) or from an axial shaft, which may be straight, C-shaped or spiral (e.g. Fig. 2,*4-9b;* 3,*5a-10b;* 4,*3-7;* 6,*5,6*).

astrose microscleres. Term used variably as meaning either 1) all microscleres which are asters in the above sense, or 2) euasters only, as distinct from pseudasters (*see* euaster, pseudaster). The restricted usage is due specially to DENDY (1921, p. 103). In other works, the terms can mean euasters, streptoscleres (Fig. 2), spinispiras (Fig. 3), sanidasters (Fig. 4), and various unrelated forms with a monaxon basis (e.g., Fig. 1,*10, 13,16;* 6,*5,6*).

bipocillus (n.). C-shaped microsclere in which the ends expand into inwardly concave spoonlike features, or comparable but bilobed or trilobed expansions; classed here as a sigmatosclere.

birotulate (n.). Same as amphidisc.

calthrops (n.). Four-rayed spicule with rays of similar length, arranged as though following the axes of a tetrahedron; so-called from resemblance to the four-pointed weapon called a calthrop (sometimes spelled caltrop); megasclere or microsclere.

candelabrum (n.). Lophose calthrops in which the branches of one ray are larger than those of the other three; or used meaning any lophose calthrops (*see* lophose). Found only in Plakinidae; not properly a microsclere, but of microscleric size (*see* microspiculate).

canonchela (n.). Specialized microsclere resembling a clavidisc, but with inward-arching lateral expansions in two opposite pairs; classed as a sigmatosclere.

centrotylote (adj. or n.). Condition in which a monaxon has a spherical to annular swelling between its ends, typically centrally or subcentrally; spicule of the above type.

chela (n.). C-shaped microsclere in which the two ends bear regular groups of inward-facing thorn to blade-like teeth; classed here as a sigmatosclere. Develops from a simple C-shaped sigma. Some forms also called anchorates or anchors.

chelaster (n.). An aster which develops from or inter-grades with a chela.

chiaster (n.). Euaster developed as a tylaster; so-called from a supposed "*chi*-shaped" form in some examples, which, however, is commonly not apparent.

choristid (n. or adj.). Demosponge with tetractinal mega-scleres, or some other radiate type (e.g., triactins) if tetractins are lacking, though monaxial megascleres are usually also present; appertaining to choristids; in taxo-nomic usage, member of the order Choristida SOLLAS. First two usages only in this paper.

cladi (n. pl.). *See* cladome.

cladome (n.). The three similar rays (cladi) of a triaene (*see* triaene).

clavidisc (n.). Specialized sigmatosclere microsclere, com-prising an ovate disc with an elongate central perfora-tion; develops from a C-shaped sigma.

crepis (n.). *See* desma.

desma (n.). Articulating megasclere, characteristic of lithistid demosponges, though also found in sublithistids. The initial body in ontogeny, called the crepis (pl., crepides), is a tetraxon, a monaxon, or an anaxial corpuscle in different types.

diactin (n.). Spicule with two rays, in line or at an angle.

diancistra (n.). C-shaped sigmatosclere microsclere, with inward facing bladelike expansions, resembling a partly opened penknife.

dichotriactin, dichotriact (n.). In a broad sense, any triactin showing branching of rays; in a special sense, term used by DENDY (1924), in the form dichotriact, to designate the streptosclere series of microscleres (Fig. 2), on a basis of envisaging this series as arising from branching triactins. Equivalent to streptaster in BURTON's restricted sense.

dichotriaene (n.). Triaene with cladi branched dichoto-mously.

discaster (n.). Microsclere with whorls of spines or with serrated discs between the ends of a monaxial shaft (e.g., Fig. 3,7*c*; 6,5,6).

discorhabd (n.). Strictly, a microsclere with transverse discs between the ends of a monaxial shaft; also used by DENDY (e.g., 1921) for all discasters.

discostrongyle (n.). Specialized dermal megasclere of cer-tain lithistid sponges, in which a siliceous disc arises from a blunt-ended initial monaxon (i.e., a strongyle).

discotriaene (n.). Specialized dermal megasclere of certain lithistid sponges, in which the cladome of an initial triaene gives rise to a siliceous disc.

euaster (n.). In a broad sense, any microsclere in which rays or apparent rays arise from a center (not an axis); in DENDY's sense, followed here, meristically varying spicules of this type, found in sponges grouped here as Ancorinida (Ancorinidae, Geodiidae, Coppatiidae, Tethy-idae) (e.g., Fig. 1,*1-7*).

lithistid (n. or adj.). Demosponge with the main internal skeleton composed of articulated megascleres (desmas), though normal types may also be present; appertaining to lithistids; in taxonomic usage, member of the order Lithistida SCHMIDT.

lophose (adj.). Style of branching in which rays divide into clusters of three or more branches, seen in spicules (lophose calthrops, candelabra) of some Plakinidae.

megasclere (n.). Major supporting spicule. Monaxial, radi-ate, or, in lithistids, some anaxial; usually an oxea, style, tylostyle, calthrop, triaene, or desma. Length of rays usually in the range 0.2-20 mm, but protruded ex-amples grow larger.

mesotriaene (n.). Triaene-like spicule with the cladome at the center of a diactinal shaft, or with an extra short ray opposite a long rhabdome.

metaster (n.). Streptosclere microsclere with raylike spines arising from a curved axis making less than one revolu-tion (Fig. 2,6*a-e*,7*a-c*). Also used (after VON LENDEN-FELD, 1907) to mean any type of streptosclere.

metastrose microscleres. Streptoscleres (Fig. 2).

microcalthrops (n.). Microscleric calthrops.

microrhabd (n.). Microscleric monaxon.

microsclere (n.). Accessory spicule, typically much smaller than megascleres; may be a euaster (Fig. 1,*1-7*), strepto-sclere (Fig. 2), spinispira (Fig. 3), microrhabd (e.g., Fig. 4,*1*), sanidaster (Fig. 4,*3*), sigmaspire (Fig. 5), sigmatosclere, or of special types (e.g., Fig. 1,*10,13,16;* 6,5,6). These types of spicules are characteristically not found as megascleres, though random examples may approach the size of typical megascleres. Other micro-scleres include simple monaxons, which are widely dis-tributed (e.g., Fig. 2,*1*).

microspiculate (adj.). Condition of Plakinidae, in which the spicules are of microscleric size, but do not include forms which are characteristically microscleres, and are megascleres functionally.

microstrongyle (n.). Straight monaxial microsclere with blunt ends (e.g., Fig. 4,*1*, showing an ornamented ex-ample).

microtriod (n.). Microscleric triactin of triod type, with three rays at angles of 120° in one plane (e.g., Fig. 2,*3*).

microxea (n.). Microscleric oxea, i.e., a monaxon with both ends pointed (e.g., Fig. 2,*1*).

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

monaxonid (n. or adj.). Demosponge with monaxial megascleres but no radiate megascleres, except rarely as a secondary development; appertaining to monaxonids; in taxonomy, member of the order Monaxonida SOLLAS.

orthotriaene (n.). Triaene with the angle between the cladi and the rhabdome about 110° to 90°; or used meaning only forms with this angle about 90°. Authors vary in their usage.

oxea (n.). Monaxon with both ends sharply pointed; may be a megasclere or a microsclere, but usually called a microxea in the latter case.

oxeote (adj.). Sharply pointed. Also used as a noun, equivalent to oxea.

oxyaster (n.). Euaster with sharply pointed rays (e.g., Fig. 1,*1-7*).

plesiaster (n.). Streptosclere microsclere with spines arising from a short straight axis. The simplest type (Fig. 2,*4;* compare SOLLAS, 1888, fig. xii,v,w) could also be called

an amphiaster (compare Fig. 2,*4-5d*); but more complex types (not figured) resemble euasters, except in views showing the axis. The simple plesiaster (Fig. 2,*4*) can be taken as a dichotriactin (DENDY, 1924; compare Fig. 2,*3*), and regarded as a starting point in evolution of more complex 'amphiasters and metasters (*compare* Fig. 2,*5a-7c*). Associated diactinal and triactinal spicules (Fig. 2,*1-3*) are sometimes also classed as plesiasters (or metasters, *sensu* VON LENDENFELD), because of apparent homology with plesiasters *s.s.*

protorhabd (n.). Initial rod from which a ray develops.

pseudoeuaster (n.). Spicule with the form of a euaster, which is regarded as a modified monaxon, because intergrading with a monaxon (Fig. 1,*10-16*) or arising from one in ontogeny. Does not show meristic variations as in Fig. 1,*1-7*.

pseudaster (n.). Term used specially by DENDY, comprising any aster in which raylike outgrowths arise from a monaxial shaft (e.g., Fig. 3,*5a-10b; 6,5,6*), or in which such a spicule intergrades with a monaxon which appears to be its prototype (e.g., Fig. 1,*8-16*). Roughly equivalent to streptaster *sensu* SOLLAS (1888).

pseudosterraster (n.). Pseudaster with the form of a sterraster (*see* sterraster).

radiate (n.). Spicule with three or more radiating rays.

radiate (adj.). Two unrelated usages: 1) referring to radiates; 2) referring to a radiating arrangement of megascleres (as radiate architecture), which may be monaxons and triaenes or all monaxons.

rhabdome (n). The dissimilar ray of a triaene (sometimes shortened to rhabd but properly this means a monaxon).

rhagon (n.). Demosponge larva with the form of a thin-walled hollow cone, the walls of which contain chambers but no canal system. Also misused (e.g., DE LAUBENFELS, 1955) as meaning any sponge with a leucon canal system, because some demosponge leucons develop from rhagons.

sanidaster (n.). Microsclere with raylike spines, commonly knobbed (tylote) terminally, along a straight monaxial shaft (Fig. 4,*3*). Accompanies euasters in some forms grouped here as Ancorinida; intergrades with spiny microrhabds (e.g., Fig. 4,*1*) and also passes into amphiasters (Fig. 4,*5*). Streptasters *sensu* DE LAUBENFELS (1955, p. E30; *not* SOLLAS, 1888, p. lxiii, of which this is one of five forms listed).

selenaster (n.). Same as sterrospira.

sigma (n.). C-shaped to S-shaped diactinal microsclere, often showing both shapes in different views, which typically has pointed ends and no ornament; found in forms grouped here as Desmacidontida. In other usage, here rejected, includes sigmaspires (e.g., DENDY, 1921). Central type of the sigmatosclere group of microscleres.

sigmaspire (n.). Spirally twisted monaxial microsclere, appearing C-shaped or S-shaped in different views, and typically blunt-ended and finely ornamented with granules or spinules (e.g., Fig. 5,*1a-2e*); also certain forms which are variants of this type (e.g., Fig. 5,*3,6a,b*); found in forms grouped here as Craniellida, and a few grouped as Spirastrellida. This spicule is similar to a sigma *s.s.* and is often equated with it (e.g., DENDY, 1905, 1921); but homology is rejected here following TOPSENT (1928), because sigmaspires and sigmas *s.s.* occur in contrasting types of sponges, with no demonstrable relationship. The sigmaspire may be homologous

with the spirastrellid spinispira, which is sometimes developed in a sigmaspire-like form (e.g., Fig. 3,*2c*).

sigmaster (n.). Strongly spined C-shaped spicule, related to spinispiras (Fig. 3,*9,10a,b*).

sigmospiraster (n.). Strongly spined sigmaspire, with spinules along the outside of the spiral.

sigmatoscleres (n. pl.). Group of microscleres found in Desmacidontidae and allied sponges (Desmacidontida herein), comprising the sigma *s.s.*, diancistra, chela, and allied types (e.g., clavidiscs, bipocilli, chelasters); called sigmoids and cheloids by some authors (e.g., HENTSCHEL, 1925; but with sigmoids including sigmaspires).

sigmatose microscleres. In DENDY's usage (1905, 1921), the sigmaspire, sigma *s.s.*, and allied types, considered as a homologous series; but sometimes used meaning sigmatoscleres. The term sigmatosclere avoids this confusion.

spherancora (n.). Specialized sigmatosclere microsclere, with four segments like the halves of a clavidisc meeting at right angles. Develops from a chela with three teeth at each end.

spheraster (n.). Euaster with a globular centrum, produced by secretion of silica around the spicular center, which, however, leaves parts of the rays projecting freely. May also be used only for forms in which the centrum is prominently developed, or applied to any spicule with this shape even if not a euaster *s.s.* (e.g., Fig. 1,*10*).

spinispira (n.). Monaxial microsclere with a spirally twisted axis, making one to several revolutions, ornamented with fine spinules which are not arranged spirally, or larger ones spirally arranged (Figs. 3,*3,4b,5a,6,7a,b,8a,b*), with a range from finely spinulated strongylospires (Fig. 3,*2a*) to strongly spined spirasters (Fig. 3,*7a,8a*); passes into other forms including smooth strongylospires (Fig. 3,*1*), straight microstrongyles (Fig. 3,*2b*), sigmaspire-like spicules (Fig. 3,*2c*), straight forms with spines arranged spirally (Figs. 3,*5b,6*), discasters (Fig. 3,*7c*), amphiasters (Fig. 3,*7d*), sigmasters (Figs. 3,*9,10a,b*) or other spheraster-like variants (Fig. 3,*2d*). Sometimes called spirasters even when spines are not prominent (as in Fig. 3,*2a*). Characteristic of Clionidae and Spirastrellidae (order Spirastrellida herein).

spiraster (n.). Aster with raylike spines arising from a spiral axis making one or more revolutions (e.g., Fig. 2,*9a,b; 3,5a,7a,8a*), along the outside of the spire. May be either a streptosclere (Fig. 2) or a spinispira (Fig. 3), and thus recurrent homeomorphically in two series of microscleres. Spiraster may also be used as meaning spinispira, and then taking in forms without raylike spines.

spiroscleres (n. pl.). Sigmaspires and spinispiras, grouped together as morphologically comparable and possibly homologous (REID, 1963).

sterraster (n.). Specialized form of euaster, in which an initial form with many fine sharp rays becomes solidified to form a globular to kidney-shaped spicule. This has a granular ornament corresponding with tips of the rays, and typically a local smooth depression, or hilum, which marks the position of the nucleus of the scleroblast which secreted the spicule. Found only in the family Geodiidae (order Ancorinida).

sterrospheraster (n.). Microsclere intermediate between a spheraster and true sterraster.

sterrospira (n.). Microsclere with the form of a sterraster, which develops from an initial spinispira; characteristic of *Placospongia* GRAY (order Spirastrellida); also called a selenaster (e.g., DE LAUBENFELS, 1955).

streptaster (n.). In original usage (SOLLAS, 1888), any aster with rays (or, apparent rays) arising from an elongate axis, which is usually spiral (hence strept-); but all types listed by SOLLAS were from choristid sponges, and comprised streptoscleres and sanidasters. In BURTON's usage (e.g., 1959), streptoscleres only (Fig. 2). In DE LAUBENFELS' usage (1955, p. E30), sanidasters and comparable spiny monaxons (Fig. 4).

streptoscleres (n. pl.). Microscleres comprising the plesiasters, metasters, amphiasters and spirasters of Pachastrellidae and Theneidae, plus triactins and diactins found with them, regarded as a homologous series (Fig. 2); similar forms also occur in certain lithistids (e.g., *Corallistes* SCHMIDT). Term introduced (REID, 1963) because of confusion in the usage of the term streptaster (*see* streptaster), and because amphiasters and spirasters need not be streptoscleres (*compare* Fig. 3,7a,d; 4,5). Metastrose microscleres in some literature. The group was interpreted by DENDY (1924) as arising by spiral branching of one ray of a triactin (*compare* Fig. 3,3-9b) (hence his term "dichotriacts").

strongylospire (n.). Spirally twisted monaxon of one to several turns, with blunt (strongylate) ends, either smooth or with spinules which are not arranged spirally (e.g., Fig. 3,1,2a,3-4b). This form is usually a spinispira homologically, and is hence called a spiraster by some authors, though not a true spiraster morphologically (*compare* SOLLAS, 1888).

strongylate (adj.). Blunt-ended.

style (n.). Monaxon with one blunt end and one sharp end; normally a megasclere.

sublithistid (n. or adj.). Demosponge in which desmas are incipiently developed or are fully developed but form only a minor part of the skeleton; appertaining to sublithistids.

tetraxon (n.). Spicule in which growth of rays follows four axes, arranged as in a tetrahedron or in some modified form of this pattern; megasclere or microsclere, megascleric forms being calthrops or triaenes.

toxa (n.). Bow-shaped diactinal microsclere; commonly but not always a sigmatosclere homologically.

toxaspire (n.). Microsclere similar to a sigmaspire, of which it occurs as a variant, making rather more than one revolution, and appearing bow-shaped in some views (Fig. 5,4).

trachelotriaene (n.). Long-shafted dichotriaene with a very small cladome and rhabdome swollen in a clublike manner just below it.

triaene (n.). Tetraxial megasclere, in which three similar rays, called cladi, differ from the fourth, called rhabdome. The rhabdome is commonly though not always, longer than the cladi, up to many times longer. The cladi may be bent away from or toward the rhabdome or show branching which is usually dichotomous (in dichotriaenes). The rhabdome is characteristically unbranched. Rhabdome is sometimes shortened to rhabd, but properly this means a monaxon. Triaene-like spicules may also occur in plakinids, as variants of the lophose type of calthrops.

triod (n.). Triactin with three rays in one plane disposed at 120° angles.

tylaster (n.). Euaster with rays knobbed terminally.

tylostyle (n.). Monaxon with one pointed end and one knobbed end; normally a megasclere.

tylote (adj.). With rays knobbed terminally.