Subclass CHORISTIDA
Sollas, 1880

Demospongea with triactinal, tetractinal, or pentactinal megascleres but without any spicules developed as desmas, and similar sublithistid, monaxonoid, microspiculate, and askeletose sponges. Megascleres usually including both tetractines and monaxons; the latter oxeas in most genera, but other diactines (e.g., strongyles) or monactines (e.g., styles) in some; tetractinal megascleres calthrops, triaenes, or both, intergrading or not; either calthrops or triaenes accompanied in some genera by variants with more or fewer rays; a few genera with triactinal or pentactinal (centrotetraia) megascleres but no tetractines; triaenes typically arranged radially. Choanosomal megascleres of forms with triaenes may be mainly or all monaxons, which are felted without order or arranged radially; spicules of microspiculate genera diactinal to polyactinal, with triactines or tetractines always present and tetractines predominant in most genera; principal microscleres of forms with megascleres may be streptoscleres, euasters, or sigmaspires, which are not found together, except that simple euasters may accompany streptoscleres; additional microrhabds or spiny variants in some genera; a few genera with these microscleres only, or no microscleres although megascleres are present. Canal systems of modern forms eurypylous, aphodal, or diplodal; their ectsosome a dermis or a cortex. Cortex sometimes packed with microscleres to form an external armor. Reproduction mainly unknown and then presumably oviparous or asexual, but a few with incubated amphiblastulae or parenchymelloid embryos. Spongin typically absent, but reportedly rarely present and then cementing megascleres. Included monaxonid genera agree closely with various choristid genera except for having only monaxon megascleres. Ordovician–Holocene.

This taxon, here ranked as a subclass, is used sensu Sollas (1880d, 1888) as including all nonlithistid genera with tetractinal megascleres, irrespective of whether these are calthrops or triaenes, and comparably microspiculate sponges in which typical megascleres are absent. It is not used sensu De Laubenfels (1936, p. 166), as restricted to forms in which tetractines are long-shafted triaenes, or in the further restricted sense of Bergquist and Hogg (1969, p. 217), which excludes Choristida sensu De Laubenfels in which the microscleres are sigmaspires.

The division by De Laubenfels (1936, p. 166, 177; 1955, p. 42–43) of Sollas’s order Choristida into orders Choristida sensu De Laubenfels and Carnosa Carter sensu De Laubenfels (not sensu Carter), with the latter comprising forms that typically lack long-shafted triaenes, was effectively a reversion to Sollas’s (1886) provisional distinction between the suborders Triactina Sollas and Tetractina Sollas. This arrangement was rejected by Sollas (1888) after study of the microscleres, which he used for his final distinctions between the suborders Sigmatophora Sollas, Astrophora Sollas, and Microsclerophora Sollas. De Laubenfel’s use of the megascleres is here rejected as inconsistent with probable relationships among the Choristida, which were more correctly understood by Sollas (1888), and with both the intergradation of megasclerous calthrops and short-shafted and long-shafted triaenes and the presence of long-shafted triaenes in some Carnosa sensu De Laubenfels. The name Choristida Sollas is
also preferred for the subclass to the alternative Tetractinellida Marshall sensu Zittel (1878b), because the latter taxon has been used by various authors, including Marshall (1876) and Sollas (1888), as including the Lithistida.

Division of the subclass into orders is based mainly on the methods used by Sollas (1888) to distinguish suborders of his order Choristida with the following differences: (a) suborders are raised in rank to orders; (b) names based on spicular characters are replaced by names based on type genera; and (c) a division (Demus, Sollas) of Sollas’s suborder Astrophora is made a separate order. Equivalents are as follows: suborder Microsclerophora Sollas: order Plakinida Reid, herein; suborder Signatophora Sollas: order Craniellida Reid, herein; suborder Astrothora Sollas in part (Demus Euastrosa Sollas, Demus Sterrostosa Sollas): order Ancorinida Reid herein; and suborder Astrothora Sollas in part (Demus Streptastrosa Sollas): order Pachastrellida Reid, herein.

A few modern monaxonids are so similar to various sponges with tetractinal megascleres that their inclusion in this subclass seems well justified; but their treatment as Choristida depends on soft parts and microscleres, not available for study in the fossils. These forms are mentioned in diagnoses of the subclass and orders, but no attempt is made here to identify fossil examples. The most likely fossil examples are monaxonids placed here in the family Ophiraphiditidae Schrammen of the order Epipolasida Sollas, subclass Monaxonida, which agree with the choristid Cephaloraphiditidae Reid except for absence of tetractines.

Order PLAKINIDA Reid, 1968

[Plakinida Reid, 1968a, p. 22] [=Microsclerophora Sollas, 1887, p. 423; Megasclerophora von Lendenfeld, 1903, p. 28; Homosclerophora Dendy, 1905, p. 64]

Microspiculate sponges with tetractinal or triactinal spicules, to which diactines or forms with more than four rays may be added, and askeleose sponges with amphiblastular embryos like those seen in some forms with spicules; tetractine spicules simple, partly or all lophose, or developed as candelabras; triactine spicules typically triodal, often linked with diactine spicules morphologically by intermediates with one short ray and two larger ones more or less straightened into line; some with diactines and triactines only, with either predominant; triaenes absent in most but some with short-shafted triaenes, which may be varied as diænes or tetaænes; one modern species with triaenes and very small amphiasters. ?Upper Jurassic, Lower Cretaceous (?Albian), Upper Cretaceous (?Cenomanian, ?Santonian, Campanian)–Holocene.

This order includes forms regarded as similar to Plakina Schulze (Plakinidae) and others (Thrombidae, Acanthastrellidae) having spicules of similar size, although genera are not certainly allied to Plakina. The latter applies specially to Thrombus Sollas (Thrombidae; Eocene, Holocene), in which shafts of small triaenes may have a swelling suggesting a spicular center that does not correspond with the center from which the rays radiate.

Because of the small size of the spicules, the fossils ascribed to this order are rare and mainly from deposits yielding microscleres. The oldest are small, isolated calthrops and lophose calthrops from the Carboniferous (Visean) of Ireland, not ascribed to any genus but similar to those of some living Plakinidae. Spicules like those of Acanthasterella Schrammen occur in the Upper Jurassic (Kimmeridgian) of Germany, and this genus occurs in the Upper Cretaceous of Germany. Spicules like those of modern species of Plakina and Thrombus occur in the Eocene of New Zealand, and some other loose Cretaceous spicules may be plakinid.

The family Helobrachiidae Schrammen, 1910, which was included in this order (as Homosclerophora Dendy, 1905) by Rezvoin, Zhuravleva, and Koltun (1962), comprises one genus with large megascleres and is here referred to the order Pachastrellida.

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Family PLAKINIDAE Schulze, 1880

[Plakinidae SCHULZE, 1880, p. 441] [=Corticilae VOSSAER, 1885, p. 323]

Microspiculate sponges, without triaenes unless a subtriaene occurs as a variant of a calthrops; spicules typically including tetractines, which are often predominant, although diactines, triactines, pentactines, or forms with more rays may occur; some genera with triactines and diactines only, with either predominant. Diactines commonly irregular, intergrading with triactines. Tetractines all simple or some lophose, then sometimes candelabras (s.s.).

One modern genus viviparous, with amphiblastula embryos. [Monolophose and trilophose tetractines have triaenose symmetry but are not classed as triaenes, being simply two forms in a series from monolophose to tetralophose; this type of variation does not occur in triaenes s.s. The doubtful records above are based on isolated spicules, not identified generally. The Carboniferous (Mississippian) record is acceptable as genuine, since spicules concerned include small, lophose calthrops.] Lower Cretaceous (?Albian), Paleogene (upper Eocene)–Holocene.

Plakina SCHULZE, 1880, p. 448 [*P. monolopha; SD DE LAUBENFELS, 1955, p. 44]. Simple, encrusting sponges with thin dermis or no ectosome; coralliform; spicules simple diactines, triactines, and tetractines, and monolophose to tetralophose tetractines; embryos incubated amphiblastulae. Lower Cretaceous (?Albian), Paleogene (upper Eocene)–Holocene: England, ?Albian, New Zealand, upper Eocene; cosmopolitan, Holocene.——Fig. 127,1a–i. *P. monolopha, Holocene, Mediterranean Sea; a–e, various diactine to tetractine megascleres; f–i, monolophous tetractines, ×400 (Schulze, 1880).——Fig. 127,1j–l. P. trilopha SCHULZE, Holocene, Mediterranean Sea; trilophose tetractines, ×400 (Schulze, 1880).——Fig. 127,1m–p. P. australi HINDE & HOLMES, Oamaru Formation, upper Eocene, New Zealand; m, monolophose calthrops; n, dilophose calthrops; o–p, trilophose calthrops, last placed with this species by HINDE and HOLMES, 1892, ×600 (Hinde & Holmes, 1892).

Acanthoplakina BURTON, 1959, p. 156 [*Plakinolopha spinosa KIRKPATRICK, 1900, p. 350; OD]. Spicules diactines, triactines, and calthrops, with strong, lateral spines, repeatedly branched (polycallosed) tips, or both; successive divisions of tips in planes rotating at right angles; rays of calthrops often with whorl of large spines near their origins; diactines may be larger than other spicules. Paleogene (upper Eocene)–Holocene: New Zealand, upper Eocene; Indian Ocean, Western Pacific, Holocene.——Fig. 127,3a. *P. monolopha, Holocene: Otago, New Zealand; characteristic spiny calthrops, ×600 (Hinde & Holmes, 1892).

Corticium SCHMIDT, 1862, p. 42 [*C. candelabrum; OD]. Aphodal to dipodal; spicules simple calthrops and subtriaenas, lophose calthrops and candelabras (tetralophose calthrops, with one branching ray distinct from others, and its branches often spiny). Paleogene (upper Eocene)–Holocene: New Zealand, upper Eocene; cosmopolitan, Holocene.——Fig. 127,2a–c. C. spp., upper Eocene, Otago, New Zealand; candelabra spicules, ×600 (Hinde & Holmes, 1892).

Family THROMBIDAE Sollas, 1887

[Thrombidae SOLLAS, 1887, p. 428]

Microspiculate sponges whose characteristic spicules are short-shafted, spiny triaenes, sometimes having a central or subcentral enlargement of axial filament of rhabdome; sometimes also with monaene, diatena, tetraene, or mesotriaene variants of characteristic triaenes; one modern species with very small, additional amphitetraenes (possible amphitetraenes). [The group is sometimes included with Plakinidae, but axial enlargement in rhbdomes suggests a spicular center; if this is correct, the seeming triaenes are trichodiactines, not tetractines. This feature does not occur in Plakinidae s.s.] Upper Cretaceous, Paleogene (upper Eocene)–Holocene.

Thrombus SOLLAS, 1886, p. 179 [*T. challengeri; OD]. Encrusting to nodular; spicules sometimes trichothriaienes or mesotriaene variants of this type (mesothriaienes), to which other variants (e.g., monaenes, diatieae) or very small amphitetraenes (possible amphitetraenes) may be added; sometimes partly or all sigmatriaienes (short-shafted prototriaienes with cladal tips flexed outwardly) and monaene to tetraene variants; central enlargement of rhabdal axis sometimes marked by external annulation; second rhabdal ray of mesotriaenes up to about half length of primary one. Upper Cretaceous, Paleogene (upper Eocene)–Holocene: northern Germany; Upper Cretaceous; New Zealand, upper Eocene; Indian Ocean, Western Pacific, Caribbean, Atlantic, Holocene.——Fig. 127,3a. T. spp., upper Eocene, Otago, New Zealand; characteristic spicules, ×50 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).——Fig.
Porifera—Demospongea

Porifera—Demospongea

**Family ACANTHASTRELLIDAE**

Schrammen, 1924

[Schrammen, 1924a, p. 37]

Spicules small, spiny, grading from calthrops into short-shafted triaenes, some approaching size of true megascleres; other characters unknown. [The relationships of this group are doubtful, possibly with recent families Plakinidae, Pachastrellidae, or Plakinastrellidae (no known fossils). The axial enlargement seen in triaenes of Thrombidae is not developed. Similarly shaped calthrops to triaenes from Carboniferous (Mississippian, Ireland) are of megascleric size and occur with apparently related pentaactines (tetraenes) and hexactines.] ?Upper Jurassic, Upper Cretaceous (Campanian).

**Acanthastrella** Schrammen, 1924a, p. 44 ['A. panniculosa', OD]. Encrusting or nodular; rays of spicules unbranched; spines without order or locally with more or less annular or spiral arrangement. ?Upper Jurassic, Upper Cretaceous (Campanian): southern Germany [loose spicules only], ?Upper Jurassic: northern Germany, Campanian.—Fig. 127, 5. *A. panniculosa*, Mucronatenkreide, Campanian, Misburg; isolated triaenes with spinose rays, ×50 (Schrammen, 1924; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
Order PACHASTRELLIDA
new order

Choristid sponges whose characteristic microscleres are streptoscleres (pleiasters, metasters, and related forms of spirasters and amphasters), having triaenes, calthrops, or both among their megascleres, and similar sponges having euasters or diactinal microscleres but no typical triaenes; streptoscleres often accompanied by microrhabds and in some forms by simple oxyasters having 4 to 6 rays. Carboniferous–Holocene.

Due to absence of microscleres in fossils, recognition of genera referred to this order is based on comparison of their megascleres with those of modern examples and especially on occurrence of megascleric calthrops or comparable spicules (atriactines, centrotriaenes). These calthrops and comparable spicules are confined to this order in the modern Choristida; the same is here assumed to be true of the fossils, although without direct knowledge of their microscleres.

Genera with streptoscleres were formerly placed by REID (1968a) in an order Poecillastrida REID, equivalent to DENDY’s (1924a) Streptosclerophora. Because of the absence of microscleres in fossils, it is here more convenient to follow SOLLAS in including forms with calthrops, with euasters or diactinal microscleres, in the family Pachastrellidae CARTER. This also seems consistent with their probable relationships. The order name is changed to allow for this difference in concept, and because (a) the name Poecillastrida can be criticized as resembling Poecillosclerida TOPSSENT, which refers to the Desmacidontida of this classification, and (b) Poecillastra SOLLAS is not the type genus of a family and is also regarded by some authors as a synonym of Pachastrella SCHMIDT.

The order appears to be first represented by loose calthrops or subtriaenes from the Upper Ordovician of Sweden (REIF, 1968), assuming that these did not belong to other unknown forms. Branching calthrops like those of some modern Pachastrella species (e.g., P. abyssi SCHMIDT) occur from the Carboniferous (Visean) of Ireland.

Family PACHASTRELLIDAE
Carter, 1875

Megascleres typically include calthrops, replaced sometimes by subtriaenes or centrotriaenes; some genera with both calthrops and typical triaenes, intergrading or not; monaxon megascleres present or absent; microscleres of modern examples include either streptoscleres or euasters, to which microrhabds or variants may be added, or microrhabds only. Subtriaenes may be nearly triactinal, with one ray represented by a rudiment. [This family includes the zoological families Pachastrellidae CARTER and Calthropellidae VON LENDENFELD, united for convenience. Because these families cannot be distinguished without reference to microscleres, the reference of fossils without microscleres to living genera is always doubtful.] Carboniferous–Holocene.

Haliniidae DE LAUBENFELS, as used in the previous Treatise Part E (DE LAUBENFELS, 1955), is a junior synonym of five older family names based on included genera: Pachastrellidae CARTER, 1875; Plakinidae SCHULZE, 1880; Corticidae VOSSMAER, 1885; Calthropellidae VON LENDENFELD, 1907; and Acanthastrellidae SCHRAMMEN, 1924a. Here Plakina SCHULZE and Corticium SCHMIDT are in the Plakinidae and Acanthastrella SCHRAMMEN in the Acanthastrellidae.

The following key shows pachastrellid genera suggested by a number of types of megasclerous skeletons, including some not recorded below.

A. With calthrops or subtriaene variants, or both intergrading; sometimes also with other variants having more or fewer rays.


a. No distinct category of dichotriaene megascleres; branching rays uncommon or absent in calthrops etc.; Halina BOWERBANK...
Subfamily PACHASTRELLINAE
Carter, 1875

[nom. correct: REID, herein, ex Calthropellidae von Lendenfeld, 1907, p. 301]

Characteristic microsceleres of modern species are euasters; streptoscleres absent. †Cretaceous, Holocene.

Calthropella Sollas, 1888, p. 107 [*C. simplex; SD von Lendenfeld, 1903, p. 83] [=Corticellopsis Bergquist, 1968, p. 62 (type, Corticella

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Fig. 128. Pachastrellidae (p. 180–183).
Porifera—Demospongea

Pachastrellidae

holocene. (Albian), Paleogene (upper Eocene)–Holocene. The oldest genus included; here adopted in new sense for Pachastrellidae grouped with family type should be family name Pachastrellidae Carter, 1875, sometimes also with euasters or toxas.

Bowerbank, 1858, p. 288; SD de Laubenfels, 1934, p. 288, SD de Blainville, 1830 (type, H. bucklandi Bowerbank, 1858, p. 288); Battersby Bowerbank, 1874b, p. 343 (type, Hymeniacidon bucklandi Bowerbank, 1864, p. 234). Encrusting to nodular, with a cortex; megascleres typically regular calthrops or slightly subtriactineous variants, with unbranched rays, not accompanied by monaxons; other variants unusual; microscleres toxas and spiny microharchs, which may pass into sanidasters or strongylasters plus oxeas; microscleres spiny microharchs, spinuspira-like strongylasters, or amphiated. [Diagnosis by de Laubenfels, 1955, in which he cited calthrops as megascleres, does not fit characters of type or any species.] Paleogene (upper Eocene)–Holocene: New Zealand, upper Eocene; eastern Atlantic, Indonesia, Holocene.——Fig. 128,9a. *T. cladosus (Sollas), Holocene, Indonesia; centrotriactinae, ×150 (Sollas, 1888).——Fig. 128,9b. T. australis (Hinde & Holmes), upper Eocene, Otago, New Zealand; characteristic centrotriactinae, showing one of rhinal rays only, ×40 (Hinde & Holmes, 1892).

Subfamily HALININAE

De Laubenfels, 1934

[nom. transl. Reed, herein, ex Halinidae de Laubenfels, 1934, p. 1] Characteristic microscleres of modern species are spiny microharchs or variants; sometimes also with euasters or toxas. [Originally invalid (junior) substitute for family name Pachastrellidae Carter, 1875, based on the idea that family type should be oldest genus included; here adopted in new sense for Pachastrellidae grouped with Halina Bowerbank.] Lower Cretaceous (?Albian), Paleogene (upper Eocene)–Holocene.

Dercitus Gray, 1867, p. 542 [*Hymeniacidon bucklandi Bowerbank, 1858, p. 288; SD de Laubenfels, 1936, p. 43], [=Halina Bowerbank, 1858, p. 288, non de Blainville, 1830 (type, H. bucklandi Bowerbank, 1858, p. 288); Battersby Bowerbank, 1874b, p. 343 (type, Hymeniacidon bucklandi Bowerbank, 1864, p. 234)]. Encrusting to nodular, with a cortex; megascleres typically regular calthrops or slightly subtriactineous variants, with unbranched rays, not accompanied by monaxons; other variants unusual; microscleres toxas and spiny microharchs, which may pass into sanidasters or amphiated. [Engeser and Mehl (1993) considered Dercites and Dercitus as the same genus. They have different type species and probably should be kept separate, with Dercites as the unidentifiable form as treated by de Laubenfels (1955, p. 105).] Lower Cretaceous (?Albian), Holocene: southern England, ?Albian; cosmopolitan, Holocene.——Fig. 128,6a–c. *D. bucklandi (Bowerbank), Holocene, Europe; a, calthrops, ×50; b, spiny microxea; c, toxas, ×300 (de Laubenfels, 1955).

Triptolemma de Laubenfels, 1955, p. 43, nom. nov. pro Triptolemus Sollas, 1888, p. 93, obj., non Peckham, 1885 [*Triptolemus cladosus Sollas, 1888, p. 93; OD]. Characteristic megascleres centrotriactinae, with rhinal rays short, equal, conical, and cladi irregularly polycladose; sometimes also with oxes, but no calthrops or other tetractins; microscleres spiny microharchs, spinispira-like strongylasters, or amphiated. [Diagnosis by de Laubenfels, 1955, in which he cited calthrops as megascleres, does not fit characters of type or any species.] Paleogene (upper Eocene)–Holocene: New Zealand, upper Eocene; eastern Atlantic, Indonesia, Holocene.——Fig. 128,9a. *T. cladosus (Sollas), Holocene, Indonesia; centrotriactinae, ×150 (Sollas, 1888).——Fig. 128,9b. T. australis (Hinde & Holmes), upper Eocene, Otago, New Zealand; characteristic centrotriactinae, showing one of rhinal rays only, ×40 (Hinde & Holmes, 1892).

Subfamily UNCERTAIN

Fossil Pachastrellidae s.l. with megascleres comparable to those of living species or more than one subfamily above, or with no living species.

Acanthophora Sollas, 1873, p. 79 [*A. bartogii; OD]. Massive, lobose with oxas megascleres and tornote, triradiate to hexiradiate microscleres, but poorly known. [No known suitable figures.] Lower Cretaceous: Europe.

Helobrachium Schrammen, 1910, p. 128 [*H. consecutum; OD]. Encrusting to irregularly lobate; principal megascleres subtriactines with three long, curved to terminally hooked rays, and a fourth ray represented by a buttonlike rudiment; hooked ends may intermesh so that skeleton is loosely coherent without zygosis; oxes also present; micropisculation unknown (no exact modern counterpart, but comparable subtriactines occur in Nethea Sollas of Pachastrellinae and Pachastrella von Lendenfeld of Calthropellinae). [The genus was placed in the lithistid suborder Megamorina by de Laubenfels (1955, p. 50–51) and said to have “typical megaclone desmas,” with additional triactines; but spiculation as given by Schrammen (1910) and above are to the present author’s knowledge.] Upper Cretaceous (Coniacian–Maastrichtian): northern Germany.——Fig. 128,2a–b. *H. consecutum, Quadratenkreide, Senonian, Oberberg; a, triactine spicules with long, curved rays that have axial canals; b, part of small spicule with node that has short canal suggesting centrotriaene, showing one of rhinal rays only, ×40 (Schrammen, 1910).

Paropites Počta, 1884, p. 40 [*P. hindei; OD]. Sponge basin shaped with a thick, basal stalk, thick walled with well-developed, radial, canal system; gastric surface with round, exhalant ostia; spicules are oxes with associated, small spheres, and calthrops with tips of rays finely branched. Creta-
ceous: Europe.—Fig. 128, 3a-c. *P. hindei*, Malmätzer Schichten, Bohemia; a, side view of typical sponge, ×0.5; b, skeletal fragment with small spheres and calthrops; c, isolated, small spicule with ringlike structures on rays, ×50 (Počta, 1884).

**Propachastrella** Schrammen, 1910, p. 71 [*Pachastrella primaeva von Zittel*, 1878b, p. 9; OD]. Lamellar, leaf or ear shaped to irregularly lobate or nodular; principal megascleres simple and branching calthrops; distinct dichotriaenes also present, sometimes forming an ectosomal skeleton; terminal branches of branched calthrops may resemble zygomes of desmas, although not articulated; some examples also with calthrops in which unbranched rays are shortened and swollen, or with pentactinal to polyactinal calthrops variants; no oxea megascleres, microspiculation unknown (no exact counterpart in living sponges, and calthrops and dichotriaenes found together in both Pachastrellinae and Calthropellinae). [Comparable modern forms include *Pachastrella chuni* von Lendenfeld, 1907 (Pachastrellinae), *Chelotropella sphaerica von Lendenfeld*, 1907 (Calthropellinae), calthrops and dichotriaenes in both, although oxeas also present.]

*Cretaceous* (Turonian–Maastrichtian): dichotriaenes in both, although oxeas also present.]

**Family THENEIDAE** Gray, 1872

[**[nom. correct. Sollas, 1886, p. 178, pro Theneidae Gray, 1872a, p. 460]**

Sponges with triaene and oxea megascleres and streptosclere microscleres; no megascleritic calthrops, triactines, or centrotriaenes; triaenes usually long shafted; architecture radiate or not; some anchored by protruded anatriaenes, or rarely by distally knobbled pseudotylostyles, in which terminal knob may contain axial rudiments of anatriaene cladi; modern examples eurypylous and noncorticate. [Diagnoses were sometimes based on soft parts and microscleres (e.g., *Sollas*, 1888), which then would include some genera with calthrops, which here are included in the family Pachastrellidae (subfamily Pachastrellinae). Malandro (2002, p. 141) included the Theneidae in the Pachastrellidae, but they are retained here as separate families. Sponges considered here as within the Theneidae were included with Ancorinidae by de Laubenfels (1936, 1955) through identification of streptoscleres with ancorinid sanidasters.] **Upper Cretaceous** (?Turonian, Coniacian–Holocene.

**Thenea** Gray, 1867, p. 541 [*Tethea muriatica* Bowerbank, 1858, p. 308; OD]. Typically symmetrical, usually globular, hemispherical, or mushroomlike, and attached by a diffuse root tuft or by a group of more compact, rootlike processes; often hispid or with a prominent equatorial fringe of hispading spicules; pores mainly in special lateral areas; internal skeleton radiate; triaenes typically including dichotriaenes, with short, primary cladi and long branches, additional prototriaenes, and small anatriaenes; radical megascleres usually large anatriaenes, to which a few pseudotylostyles may be added, but occasionally all pseudotylostyles; with streptoscleres only, or with plesiaster-variant oyster having four or one to several more rays (supposed records based on isolated megascleres).

**Pachastrellida** Mostler, 1986

[Costamorphidae Mostler, 1986, p. 343]

**Family COSTAMORPHIIDAE**

Mostler, 1986

Sponges whose megascleres are composed of diverse calthrops, asterlike triaenes or of calthrops-derived needles and diverse triders, all showing outer sculpture of riblike halffrings with irregular margins; known only from isolated spicules. **Upper Triassic.**

**Costamorpha** Mostler, 1986, p. 343 [*C. zlambachensis*; OD]. Sponges whose skeleton is composed of calthrops and associated mesotriaenes with characteristic outer sculpture of irregular half rings, **Upper Triassic** Austria.—Fig. 129, 1a–b. *C. zlambachensis*, Zlambach Formation, Rhaetian, St. Agatha; a, holotype calthrop; b, drawing of characteristic calthrop, scale not given but approximately ×100 (Mostler, 1986).

**Family THENEIDAE** Gray, 1872

[**[nom. correct. Sollas, 1886, p. 178, pro Theneidae Gray, 1872a, p. 460]**

Sponges with triaene and oxea megascleres and streptosclere microscleres; no megascleritic calthrops, triactines, or centrotriaenes; triaenes usually long shafted; architecture radiate or not; some anchored by protruded anatriaenes, or rarely by distally knobbled pseudotylostyles, in which terminal knob may contain axial rudiments of anatriaene cladi; modern examples eurypylous and noncorticate. [Diagnoses were sometimes based on soft parts and microscleres (e.g., *Sollas*, 1888), which then would include some genera with calthrops, which here are included in the family Pachastrellidae (subfamily Pachastrellinae). Malandro (2002, p. 141) included the Theneidae in the Pachastrellidae, but they are retained here as separate families. Sponges considered here as within the Theneidae were included with Ancorinidae by de Laubenfels (1936, 1955) through identification of streptoscleres with ancorinid sanidasters.] **Upper Cretaceous** (?Turonian, Coniacian–Holocene.

**Thenea** Gray, 1867, p. 541 [*Tethea muriatica* Bowerbank, 1858, p. 308; OD]. Typically symmetrical, usually globular, hemispherical, or mushroomlike, and attached by a diffuse root tuft or by a group of more compact, rootlike processes; often hispid or with a prominent equatorial fringe of hispading spicules; pores mainly in special lateral areas; internal skeleton radiate; triaenes typically including dichotriaenes, with short, primary cladi and long branches, additional prototriaenes, and small anatriaenes; radical megascleres usually large anatriaenes, to which a few pseudotylostyles may be added, but occasionally all pseudotylostyles; with streptoscleres only, or with plesiaster-variant oyster having four or one to several more rays (supposed records based on isolated megascleres).

**Cretaceous** (?Turonian, Coniacian–Maastrichtian), Paleogene (?upper Eocene), Holocene: Czech Republic, Slovakia, England, *Pachastrella* chuni von Lendenfeld, 1907 (Pachastrellinae), *Chelotropella sphaerica von Lendenfeld*, 1907 (Calthropellinae), calthrops and dichotriaenes in both, although oxeas also present.]

**Family COSTAMORPHIIDAE**

Mostler, 1986

[Costamorphidae Mostler, 1986, p. 343]

Sponges whose megascleres are composed of diverse calthrops, asterlike triaenes or of calthrops-derived needles and diverse triders, all showing outer sculpture of riblike halffrings with irregular margins; known only from isolated spicules. **Upper Triassic.**

**Costamorpha** Mostler, 1986, p. 343 [*C. zlambachensis*; OD]. Sponges whose skeleton is composed of calthrops and associated mesotriaenes with characteristic outer sculpture of irregular half rings, **Upper Triassic** Austria.—Fig. 129, 1a–b. *C. zlambachensis*, Zlambach Formation, Rhaetian, St. Agatha; a, holotype calthrop; b, drawing of charac-
FIG. 129. Costamorphiidae and Theneidae (p. 183–185).
Pachastrellida—Ancorinida

(Sollas, 1888).—Fig. 129, 2f–g. T. delicata Sollas, Holocene, South Indian Ocean; f, radical pseudotylostyle, \( \times 15 \); g, terminal knob (tylus) of same, showing axial rudiments, \( \times 180 \) (Sollas, 1888).

?Theneopsis Schrammen, 1910, p. 54 [*Tethyopsis steinmanni von Zittel, 1878b, p. 9, OD] [=Tethyopsis von Zittel, 1878b, p. 9, obj., non Stewart, 1870, p. 281]. Nodular or tuberlike, some examples lacunar internally; megascleres large oxeas, smaller orthotriaenes and delicate, but long-shafted anatriaenes arranged perpendicular to external surface or to surfaces of internal lacunae; microscleres unknown. [Name suggests relationship to Thenea, but compared with Sphincterella de Laubenfels (as Sphinctrella Schmidt, non Schmarda) by original author; could equally be ancorinid or geodiid.] Cretaceous (upper Campanian): northern Germany.—Fig. 129,3a–d. *T. steinmanni (von Zittel), Quadratenkreide, Misburg; a, irregular, tuberlike sponge with internal lacunae, \( \times 1 \); b–d, spicules including orthotriaenes, anatriaenes, incomplete, and oxea, incomplete, \( \times 10 \) (Schrammen, 1910).

Order ANCORINIDA Reid, 1968

[Ankorinida Reid, 1968a, p. 22; emend., Reid, herein]

Choristid sponges with triaenes and euaster microscleres, or with additional spinulated microrhabds or sanidasters or these types of microscleres only, and similar monaxonoids that differ only in absence of triaenes; some with sterrasters or aspidastera in addition to normal euasters; most choristid with oxea megascleres in addition to triaenes, and some with strongyles or styles. Carboniferous (Mississippian)—Holocene.

Recognition of fossils referred to this order may be based on comparison of microscleres with those of modern examples or recognition of sterraster or aspidaster microscleres, which occur in some sediments. The oldest apparent sterrasters are Carboniferous (Mississippian), and occur with dichotriaene megascleres like those of various modern Geodiidae, of which these microscleres are characteristic. Since this family is the most specialized of the order, both the family and the order are likely to be older than the known record.

The order Ancorinida was originally taken as including all choristids with microscleres of the above types and all monaxonoids with true euasters (i.e. not pseudoeuasters; Reid, 1968a). The choristid Calthropellidae v. Lendenfeld and Halinidae de Laubenfels are now included in the order Pachastrellida (family Pachastrellidae) following Sollas (1888), and most of the monaxonoids are placed in the order Epipolasida de laubenfels. This change is partly for convenience in paleontology; but it also seems clear that the monaxonoids have varied affinities and that some, at least, are allied to the Spirastrellida, although the latter have spinispira microscleres when any distinctive forms are present. Tethya Lamarck in particular agrees closely with the typical Spirastrellida biochemically (Bergquist & Hogg, 1969), although the microscleres are euasters like those of typical Ancorinida. Biochemical agreement is thought here to be probably more significant than occurrence of similar microscleres, which should be seen as representing parallel developments.

Some modern monaxonoids do, however, seem likely to belong with the order Ancorinida, and Dendy (1916) claimed a series of pairs of similar choristid and monaxonoid species within the genus Aurora Sollas. Some fossils placed here in the artificial order Epipolasida could be monaxonid Ancorinida; but there is no way by which they can be recognized as such.

Family ANCORINIDAE Schmidt, 1870

[Ankorinidae Schmidt, 1870, p. 64] [=Stellettidae Sollas, 1888, p. cxxxiv, nom. transl. et correct. Sollas, 1888, p. cxxxiv, ex group (=subfamily) Stellettina Carter, 1875, p. 184]

Sponges with triaene and oxea microscleres and with euaster microscleres that do not include sterrasters or aspidastera; no megascleretic calthrops or triactines; some genera with typical microscleres accompanied by microrhabds or sanidasters; may also have diaenes or monaenes as subordinate variants of triaenes, or diaenes as typical megascleres of special oscular outgrowths; styles or strongyles sometimes present as oxea variants; whole skeleton commonly

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radiate; but some have choanosomal oxees irregularly felted and only triaenes radial; modern examples typically aphodal, with cortex or not; euasters in forms from oxyaster to sterrospheraster, alone or in various combinations; few with dermal armor formed by cortex packed with spherasters or sterrospherasters; triaenes sometimes inconspicuous or vestigial, so that sponge may at first seem monaxonid (some purely monaxonid sponges included in zoology, on basis of detailed resemblance in soft parts and microscleres, not available in paleontology). Jurassic–Holocene.

Subfamily ANCORININAE
Schmidt, 1870

[nom. transl. de Laubenfels, 1936, p. 167, ex Ancorinidae Schmidt, 1870, p. 64; emend., Reid, herein]

Euaster microscleres of modern examples typically accompanied by differentiated microrhabds that are rough, finely spined, or developed as sanidasters; these microrhabds often intergrading with diactinal, euaster variants, from which they are only distinguished by slightly further modification (e.g., thickening, shortening), or with a typical, radiate euaster through irregular intermediates. [The subfamily is emended by removal of genera with microscleres identified as streptoscleres, that are here placed in Pachastrellidae (Pachastrellinae) or Theneidae, because identification of streptoscleres with ancorinid strellinae) or Theneidae, because identification of stubs as streptoscleres, that are microrhabds that are allied to oxea megascleres homologically; these microscleres are retained here accordingly.

Sanidasters (De Laubenfels, 1936) is reification of streptoscleres with ancorinid strellinae) or Theneidae, because identification of doublets as streptoscleres, that are microrhabds that seem to be allied to oxea megascleres homologically; these genera are here placed in the Stellettinae.

Jurassic–Holocene.

Ancorina Schmidt, 1862, p. 51 [*A. cerebrum; SD de Laubenfels, 1936, p. 167]. Sponges spherical, of moderate size with skeleton containing oxees, anatriaenes, dichotriaenes, and three kinds of asters; dermal layer consisting of bundles of anchorate spicules and main web of fibers including those and other kinds of spicules. Holocene; cosmopolitan. —Fig. 130,2a–f. *A. cerebrum, Zara and Quarnero, Adriatic Sea; various spicules from fibrous skeleton of type sponge, including large anatriaenes and dichotriaenes, b,e,f, x60; a,c,d, x125 (Schmidt, 1862).

Discispongia Kolb, 1910 in 1910–1911, p. 251 [*D. unica; OD]. Discoidal to cup-shaped form with skeleton of oxees and various triaenes; canal system not developed. Jurassic: Europe.—Fig. 130,6a–d. *D. unica, Weiss Jura, Kimmeridgian, Sontheim, Germany; a, discoidal holotype from above with marginal ring, ×0.5; b, proatriaene; c, dichotriaene, ×25; d, anatriaene, ×50 (Kolb, 1910–1911).

Ecionemia Bowerbank, 1862, p. 1,101 [*E. acervus; OD] [=Ecionema Sollas, 1886, p. 192, nom. null.]. Massive, lobate, pyriform, cup-shaped, or related shapes; megascleres oxees and orthotriaenes, plagiotriaenes, or prototriaenes, or with additional anatriaenes; radiate architecture; euasters are tyasters, spherasters, or both; microrhabds smooth, finely spined, or developed as sanidasters; cortex typically absent. [Separation from Ancorina Schmidt controversial, here based chiefly on absence of dichotriaenes, oxysters, cortex. Paleogene (Eocene)–Holocene: Western Australia, Miocene, Miocene; cosmopolitan, Holocene.—Fig. 130,1. E. glauteri Chapman & Crespin, Miocene, Western Australia; rodlike specimen with expanded base, possibly a stalk, preserving oxees, prototriaenes and spherasters, sanidasters, WAGS, X1 (Chapman & Crespin, 1934, courtesy of The Royal Society of Western Australia).

Subfamily STELLETTINAE Carter, 1875


Microscleres of modern examples are typically euasters only, without microrhabds except as otherwise unmodified, diactinal, euaster variants; rarely, also with smooth microxeas. [The Stellettinae sensu von Lendenfeld comprises the Ancorinidae without special oscular tubes, seen in forms grouped as Tethyopsidineae von Lendenfeld (1907, p. 253), without reference to microscleres. Emendation of Stellettinae sensu de Laubenfels allows inclusion of Penares Gray, in which microxeas are thought to be related to oxea megascleres, not to microrhabds typical of the Ancorinidae.] Jurassic–Cretaceous, Cretaceous (?Albian, Turonian)–Holocene.
Ancorinidae (p. 186–188).

Fig. 130. Ancorinidae (p. 186–188).
Porifera—Demospongia

Stelletta Schmid, 1862, p. 46 [*S. boglicii; SD Sollas, 1888, p. cxxxix, not S. grubii Schmid, 1862, p. 46, SD de laubenfeld, 1955, p. 42]. Massive, spherical, cylindrical, cuplike, or related shapes; surface hispid in some species or rarely conulose; megascleres radially arranged oxeas and plagiotremae, orthotremae, or dichotremae, or also including anatraeae; euasters typically oxyasters and tyasters (chisters), found mainly in choanosome and ecosome respectively, but sometimes lacking oxyasters or with tyasters replaced by strongylasters or sperasters; strongly corticate, with cortex two layered, the inner layer fibrous (supposed fossil records based on isolated megascleres).

Lower Jurassic, Cretaceous (?Coniacian–Maastrichtian), Cretaceous (?Albian), Paleogene (?Eocene), Holocene.——Fig. 130, a–e. S. argulana von lendenfeld, Holocene, Arghulas Bank, South Africa; a, side view of whole sponge, ×5; b, anatraeae, ×100; c–d, plagiotremae; e, dichotremae, ×25 (von Lendenfeld, 1907).——Fig. 130, f. S. sp., upper Eocene, Otago, New Zealand; triaene ascribed to S. sp., ×40 (Hinde & Holmes, 1892).

Penares Gray, 1867, p. 542 [*Stelletta belleri Schmid, 1864, p. 32; OD]. Nodular or massive; megascleres oxeas and dichotremae, arranged more or less radially or also with styles or subtylostyles; microscleres oxyasters and smooth microxeas, the latter centrotylote or not; ecosome thin, packed with tangentially arranged microxeas (doubtful record based on megascleres). Cretaceous (?Campanian), Holocene; northern Germany, ?Campanian; South Africa, Holocene.——Fig. 130, a–e. P. sp., Quadratenkreide, Oberg; triaene spicules of genus, ×10 (Schrammen, 1910).——Fig. 130, f–h. P. obtusus von lendenfeld, Holocene, Arghulas Bank, South Africa, megascleres; f–g, dichotremae; h, oxeae, ×20 (von Lendenfeld, 1907).

?Stolleya Schrammen, 1889, p. 7 [*S. microtulipa; SD de laubenfeld, 1955, p. 42]. Form of body uncertain; collapsed examples nodular or crustlike, or with traces of rounded elevations with osculum-like pits at their summits; megascleres large oxeas and smaller, long-shafted dichotremae with small cladomes, or also with subordinate plagiotremae or protriremae as variants of typical dichotremae; cladal branches of most dichotremae more or less in one plane; microscleres unknown. [Compared with Anthiastra Sollas of Stellitinae by original author but could represent several other genera: e.g., see Penares Gray.] Cretaceous (Turonian–Maastrichtian); England, northern Germany.——Fig. 130, a–d. *S. microtulipa, Quadratenkreide, upper Campanian, Oberg, northern Germany, spicules of type species; a, dichotrema; b, clade of dichotremae; c, cladal ends of further dichotremae; d, oxeae, incomplete, ×10 (Schrammen, 1910).

Family GEOIDIDAE Gray, 1867

[nom. correct. Reid, herein, pro Geodina Sollas, 1888, p. cdliii, pro Geodiidae Gray, 1867, p. 504] [=Stellettina Sollas, 1888, p. 209; Euyidae von lendenfeld, p. 11]

Sponges similar to Ancorinidae but distinguished by having a cortex that is densely packed with sternasters or aspidasters to form a stony, dermal armor. Most with other euasters in choanosome, their forms ranging as in Ancorinidae; some also with microrhabds or spheres, or with spheres as sole choanosomal microscleres. [Dermal sternasters and aspidasters are formed in the choanosome, but moved outwardly and accumulated in the cortex. Sterrasters originate from highly polyactinal oxyasters, whose rays grow in all directions equally; aspidasters from similar prototypes with rays all in one plane. The Carboniferous (Mississippian) record from loose triaenes and sternasters is not determinable at the generic level.] Carboniferous (Mississippian–Holocene).

Subfamily GEOIDIINAE Gray, 1867

With sternasters but not aspidasters. Carboniferous (Mississippian–Holocene).

Geodia Lamarck, 1815, p. 333 [*G. gibberosa; OD] [=Cydonium Fleming, 1828, p. 516 (type, C. nulleri, OD); Silicophaera Hughes, 1985, p. 603 (type, S. asteroderma, OD), described from isolated sternaster microscleres]. Massive, globose, lobate, forming thick-walled cups or related shapes; intracortical canals (chones) cribiporal or with exhalant chones opening through single apertures (uniporal); exhalant, pore sieves or other apertures usually localized, in a small, central cavity in some uniporal forms, mainly on inner face if body is cup shaped, or in special lateral areas; typical microscleres oxeas and orthotremae or dichotremae, to which anatraeae, protriremae, or both may be added; sometimes with subordinate, triaene variants (e.g., diaeaeae) or oxea variants (e.g., strongyles; some with additional small oxeas (e.g., 0.10 as large as main ones), distributed generally or localized in cortex; microscleres other than sternasters are smaller euasters in range of oyster to speraster, of one sort only or more than one; no microrhabds; some species with spherasters of choanosome entering cortex in walls of chones, or with protruded megascleres (supposed fossil records based chiefly on loose megascleres). Lower Jurassic, Cretaceous (?Aptian, Albian)—Holocene: Austria, Lower Jurassic;
southern England. *Aptian, Albian;* England, Germany, Poland, *Upper Chalk*; USA (Alabama), *Paleocene;* New Zealand, *Upper Eocene;* Western Australia, Spain, *Miocene;* cosmopolitan, *Holocene.* ——Fig. 131, 1a–g. *G. stellata* von Lendenfeld, Holocene, Holocanus, Arghulas Bank, South Africa; *a* vertical or axial section through sponge with radiate structure, ×0.5; *b–c,* small diaene and triaene, with short, extra, rhodal ray, pointing upward, ×50; *d,* dichotriaene, ×33; *e–f,* small anatriaenes (shown with rhodamb ine incomplete), ×50; *g* group of elliptical sterrasters, ×150 (von Lendenfeld, 1907).

**Caminus** Schmidt, 1862, p. 48 [*C. vulcani;* OD]. Globular to massive or lobate; inhalant chones as in *Geodia,* but exhalant water leaving through oscula of a few local, paragastral cavities; typical megascleres strongyles and orthotriaenes, but latter may be varied as dichotriaenes and strongyles may grade into oxea or amphistylole (=stylonygyle) variants; no anatriaenes; accessory microscleres euasters and spheres or spheres only. *Upper Cretaceous* (*Turonian–* *Maasrichtian*), *Paleogene* (*Eocene*)— *Holocene,* Czech Republic, Slovakia, England (supposed records based on loose megascleres), *Turonian–* *Maasrichtian; Western Australia,* *Eocene;* cosmopolitan, *Holocene.* ——Fig. 131, 2a–d. *C. sphaeroconia* Sollas, Holocene, Brazil, South Atlantic; *a* side view of complete sponge, ×0.5; *b* vertical section showing exhalant canals and paragastral cavity, ×11; *c* exceptionally large, somal sphere; *d* compound spheres, ×400 (Sollas, 1888).

**Concliasspongia** Robinson & Haslett, 1995, p. 199 [*C. rarus;* OD]. Sponge characterized by oblong to oval, siliceous microscleres whose surfaces are covered with pentameral pores except for single small, barren patch that has an X standing out in relief, which is interpreted as hilum; two larger pores occur in areas between greatest angles of X. [Taxonomic placement of these isolated microscleres is uncertain, but they are grouped here with apparently related forms such as *Geodia.*] *Paleogene* (*middle lower Miocene*) Ecuador. ——Fig. 131, 3. *C. rarus,* Dos Bocas Formation, 3 km south of San Pedro; holotype microsclere with characteristic surface sculpture, Slide JW 199, BMNH, ×200 (Robinson & Haslett, 1995; courtesy of Journal of South American Earth Sciences).

**Cydonium** Fleming, 1828, p. 516 [*C. mulleri;* OD]. Distinguished from *Geodia* Lamark in usage of Sollas (1888), restricting *Geodia* to forms with a distinct, paragastral cavity when young, sometimes also when adult, and with spincntrate, uniporal, exhalant chones; this usage now generally rejected since characters relied upon are not constant. [There is one record under Sollas’s usage.] *Paleogene* (*Eocene*); Western Australia.

**Geodiopsis** Schrammen, 1910, p. 117 [*Geodia cretacea* Schrammen, 1899, p. 8; SD de Laubenfels, 1955, p. 42]. Form unknown; megascleres stout oxees and proatriaenes, slender anatriaenes, and variants, the last with a short, sec-
Fig. 131. Geodiidae (p. 188–189).
Ancorinida

132.1a–d. *R. perforata*, Lower Calcareous Grit, Oxfordian, Scarborough, Yorkshire; a, side view of subpalmate sponge with labyrinthine upper end, \( \times 0.5 \); b, transverse section showing complex, canal pattern of interior, \( \times 1 \); c, drawings of several sterrasters showing range of size and shape, \( \times 40 \); d, globular sterraster with minute points of surface produced by tips of radial fibers, \( \times 100 \) (Hinde, 1890).

Rhaxelloides Trejo, 1967, p. 37 [*R. sphaerica; OD*]. Isolated microscleres star shaped, spherical to cylindrical; spherical forms 80 to 170 microns in diameter and of two types: hollow with small and irregularly distributed protuberances, and solid with large, conical, regularly distributed protuberances. Upper Cretaceous: Mexico.——Fig. 132, 3a–b. *R. sphaerica*, Malpaso, Chiapas; a, typical solid, spherical spicule with large protuberances; b, typical hollow, spherical spicule with small, surficial protuberances, \( \times 205 \) (Trejo, 1967).

Subfamily ERYLINAE Sollas, 1888

[nom. correct: Reid, herein, pro Erylina Sollas, 1888, p. cxlvii]

With aspidasters. *Upper Jurassic–Holocene.*

Erylus Gray, 1867, p. 549 [*Stelletta mammillaria Schmidt, 1862, p. 48; OD*]. Encrusting to massive, lobate, spheroidal or cylindrical; inhalant chones with single apertures only (uniporal); exhalant apertures oscula or pores of single chones; megascleres oxeas, strongyles, or both, and orthotriaenes or dichotriaenes; no anatriaenes; internal architecture not radiate except near cortex; accessory microscleres microrhabds and euasters, latter of a single sort or more in range from oxyaster to spheraster; microrhabds centrotylote or not, sometimes forming a layer at surface of cortex; aspidasters range from thin discs with radial canals or ridges to thicker, tubercululate bodies, like flattened sterrasters. Paleogene (upper Eocene)–Holocene: New Zealand, upper Eocene; Western Australia, ?Miocene; cosmopolitan, Holocene.

E. (Erylus). Adult aspidaster resembles a flattened sterraster, with tubercululate surfaces; tubercles without order or in groups, sometimes stellate in form; opposite sides may be ornamented differently. Paleogene (?upper Eocene), Neogene (?Miocene), Holocene: New Zealand, ?upper Eocene; Western Australia, ?Miocene; cosmopolitan, Holocene.——Fig. 133, 3a–f. E. (E.) lendenfeldi Sollas, Holocene, Indian Ocean, aspidasters; a–b, adult examples with opposite sides differently ornamented, \( \times 200 \); c–e, developmental stages, \( \times 770 \) (Dendy, 1916; courtesy of Academic Press Ltd.).

E. (Triate) Gray, 1867, p. 549 [*Stelletta disco-phora Schmidt, 1862, p. 47; OD*]. Adult aspidaster a very thin disc or elliptical plate,
finely granulate or smooth; may be radially ridged along tracks of original rays (resembles young stages of *E. (Erylus)* aspidasters). *Paleogene (upper Eocene)—Holocene:* New Zealand, upper Eocene; East Atlantic, Mediterranean, Indian Ocean, *Holocene.*—Fig. 133, 2. *E. (T.)* sp., upper Eocene, Otago, New Zealand; aspidaster, ×200 (Hinde & Holmes, 1892).

**Prodactylocalycites** Reid, nom. nov. herein, nom. nov. pro *Dactylocalycites* Carter, 1871, p. 123 (invalid, Code Art. 20, ICZN, 1999), sensu De Laubenfels, 1955, p. 58 [*Dactylocalycites callodiscus* Carter, 1871, OD]. Sponge unknown; represented by spicules called pinakids, in form of thin discs with marginal notches or submarginal perforations, located between fine, tubular canals that radiate from center. [Spicules sometimes thought to be dermalia of a lithistid, by comparison with phyllotriaenes and discotriaenes, but distinguished from known lithistid dermalia by the multiple radial canals; here compared with aspidasters of *Triate* Gray. The invalid name *Dactylocalycites* Carter (1871, p. 123) was proposed to refer to spicules, not entire sponges; phyllotriaenes, discotriaenes, and pinakids were referred to *Dactylocalyx Stutchbury,* 1842, p. 87.] *Upper Jurassic—Holocene:* southern Germany, *Upper Jurassic:* southern England, Germany, Albanian–Campanian; New Zealand, upper Eocene; West Atlantic (Barbados), *Paleogene—Neogene:* Indian Ocean, *Holocene.*—Fig. 133, 1a. *P. callodiscus* (Carter), Quadratenkreide, Campanian, Oberg, Germany; pinakid disc showing canals, ×50 (Schrammen, 1924a; courtesy of E. Schweizerbart’sche Verlagsbuchhandlung).—Fig. 133, 1b. *P.* sp., upper Eocene, Otago, New Zealand; dermal disc (pinakid) with submarginal perforations, ×200 (Hinde & Holmes, 1892).—Fig. 133, 1c–d. *P. ellipticus* (Carter), Upper Greensand, Upper Cretaceous, Exeter, England; modified pinakids, ×75 (Carter, 1871).

**Family PAELOSPONGIIDAE**

Mostler, 1986

*Paelospongia* Mostler, 1986, p. 337 [*P. longiradiata; OD*. Spicules are mesotriaenes with rhabds of variable length and strong, spinose cladi. *Upper Triassic:* Italy, Austria.—Fig. 134, 1a–b. *P. longiradiata,* Zlambach Formation, Rhaetian, St. Agatha, Austria; *a,* photomicrograph of holotype mesotriaene, ×100; *b,* drawing of spinose mesotriaene characteristic of genus, scale not given but approximately ×50 (Mostler, 1986).
Ancorinida—Craniellida

Actinospongiella Reid, herein, nom. nov. pro Actinospongia Mostler, 1986, p. 342, non d’Orbigny, 1849 [*Actinospongia hexagona Mostler, 1986, p. 342; OD]. Spicules are strongly spinose dichotriaenes with rhabd missing or reduced to button. Upper Triassic: Austria. — Fig. 134.2. *A. hexagona (Mostler), Zlambach Formation, Rhaetian, St. Agatha; photomicrograph of characteristic dichotriaene, scale not given but approximately ×100 (Mostler, 1986).

Order CRANIELLIDA Reid, 1968

[Craniellida Reid, 1968a, p. 22] [=suborder Sigmatophora Sollas, 1887, p. 423; suborder Spiroscletina Reid, 1963d, p. 199; “Spirophorides” (or rank given) Borojevic, Cabioch, & Levi, 1968, p. 4]

Choristid sponges that typically have sigmaspire microscleres, although a few have only microrhabds or no microscleres, and monaxonids that resemble choristids except for absence of tetraxial megascleres (triaenes); some choristids with sigmaspires accompanied by microrhabds, spheres, or cheloids, or rarely replaced by toxaspires; most choristids with long-shafted triaenes, which are typically prototriaenes and anatriaenes; prototriaenes of some with unequal cladi and varied as diaenes and monaenes; single genera with additional subtriaene or amphitriaene megascleres and one with amphitriaene only; dichotriaenes absent in most, and may be polycladose when present; additional oxea megascleres in most choristids, and oxeas only in monaxonids; megascleric calthrops unknown; euasters and streptoscleres absent. Upper Cretaceous (Campanian)—Holocene.

Recognition of possible fossil examples of this order is based entirely on occurrences of megascleres like those of modern species. Slender prototriaenes and mesotriaene variants, like those of various living Tetillidae, first appear in the Carboniferous (Visean) of Ireland. Polycladose dichotriaenes, like those of Tetilla infrequens (Hentschel), occur in the lower Cenomanian of southern England.

This order has no obvious relationship to the other Choristida, although it shares possession of tetraxial megascleres. Modern examples can commonly be recognized by the general aspect of their megascleres, of which asymmetrical (anisocladose) prototriaenes are peculiar to this order. They are also unusual in the rarity of dichotriaenes that, when present, are prodichotriaenes whose cladi may branch more than once. The latter forms do not occur in Pachastrellida or Ancorinida, although similar branching occurs in the spicules of some Plakinida.

Two modern monaxonids, Trachygellius Topsent and Raphidotethya Burton, are so much like the typical choristids, apart from lacking triaenes, that their inclusion in the order seems appropriate; but no fossils of this type can be recognized in the absence of microscleres and soft parts.

Family TETILLIDAE Sollas, 1886


Sponges with triaene and oxea megascleres and, typically, with sigmaspire microscleres, no megascleric calthrops; some with typical microscleres accompanied by microrhabds or spheres or with microrhabds only or no microscleres; triaenes typically long-shafted prototriaenes and anatriaenes, although either may be absent; often including hairlike (trichodal) prototriaenes with unequal cladi (commonly one long, two short), which are distinctive in absence of sigmaspires; all types sometimes vary as diaenes or monaenes, which predominate in some species; a few with additional orthotriaenes, subtriaenes, amphitriaenes, or
vestigial triaenes only; no typical dichotriaenes, although rarely a triaene may have cladi branching once or more often; main skeleton typically radiate, rarely plumose; some with special, cortical oxeas, arranged radially or tangentially; most anchored by protruded anatriaenes, replaced rarely by distally knobbed pseudotylostyles; no microscleres known. [Position uncertain, but megascleres are comparable with those of living Tetilla sandalina Sollas, for example, that lacks anatriaenes.] Upper Cretaceous (Campanian): Germany.—Fig. 135, 2a–b. T. longitridens Schrammen, Quadratenkreide, Oberg; oxea and protariaenes, ×10 (Schrammen, 1910).

Craniella Schmidt, 1870, p. 66 [*C. tethyoides; SD De Laubenfels, 1936, p. 175; not Alcyonium cranium Muller, 1776, p. 255, as cited in De Laubenfels, 1955, p. 42]. Megascleres typical of family; main skeleton radiate; ectosome developed as a cortex with radial, cortical oxeas in an inner, fibrous layer and a cavernous, outer layer; sigmaspires present and rarely accompanied by chelalike variants. [The genus was also treated by De Laubenfels (1936) as including noncorticate sponges, here regarded as species of Tetilla Schmidt, 1868, by restriction of that genus to forms lacking sigmaspires. Doubtful Eocene records (Hinde & Holmes, 1892, p. 235; Chapman & Crespin, 1934, p. 110) are based on loose triaenes only. Muller’s article cited by De Laubenfels, as listed above, was published in 1776.] Paleogene (?Eocene), Holocene: Australia, New Zealand, ?Eocene; cosmopolitan, Holocene. ——Fig. 135, 1a–b. C. cranium; loose protriaenes similar to those of living Craniella cranium (Muller), ×50, ×40 (Hinde & Holmes, 1892).

Order UNCERTAIN

Choristid and sublithistid sponges with modern counterparts, but possessing tetraxial megascleres; no microscleres known.

Family CEPHALORAPHIDITIDAE
Reid, 1968

[Cephaloraphiditidae Reid, 1968c, p. 1,252]

Megascleres include sinuous monaxons (ophirhabds), to which oxeas, strongyles, amphitrylostyles, or styles may be added, and short-shafted triaenes or subtriaenes with unbranched cladi; ophirhabds typically intertwined to form a loosely coherent, skeletal framework, without formation of zygomes; tetraxial megascleres arranged ra-
dially with their cladi at surface of skeleton or scattered among ophirhabds; no microscleres known. [Members of this family were placed by SCHRAMMEN (1903, p. 17) in the family Ophiraphiditidae SCHRAMMEN; but the type genus, Ophiraphidites CARTER, 1876, is known only from fragmentary material, in which tetraxial megascleres are absent. ZITTEL (1878b) had previously identified Ophiraphidites with Cretaceous forms possessing triaenes, and was followed by SCHRAMMEN in this usage; but the most nearly similar modern sponge, "Jaspis" serpentina WILSON, has no tetraxial megascleres in life. It seems better to place the forms with monaxons only in the order Epipolasida of the subclass Monaxonida, therefore, which is also appropriate because the microscleres of J. serpentina are euasters.]

If that species is a so-called epipolasid derivative of a form with tetraxons, its euasters should place the Cephaloraphiditidae in the order Ancorinida.

The combination of ophirhabds and triaenes are also appropriate in a source stock of the lithistid order Megalithistida; but the known cephaloraphiditids occur too late in time, and the microscleres of living megalithistids are microrhabds and spirasters.] Jurassic–Neogene.

Cephaloraphidites SCHRAMMEN, 1899, p. 6 [*C. cavernosum; SD DE LAUBENFELS, 1955, p. 43]. Thick-walled cup with shallow, paragastral cavity; external and paragastral surfaces with numerous small, skeletal pores (ostia, postica), from which radiate skeletal canals; principal megascleres ophirhabds and clublike styles (rhopalostyles); additional oxeas and short-shafted triaenes in meshes of skeletal framework; microscleres unknown. [The type species was based on a fragment; but the habit is known from C. milleporatus SCHRAMMEN, 1899, which has similar spicules.] Cretaceous (Campanian); Germany.

——FIG. 136,3a–d. C. milleporatus SCHRAMMEN, Quadratenkreide, Oberg; spicule suite including a, ophirhabds; b, rhopalostyles; c, triaenes; and d, an oxea, ×10 (Schrammen, 1910).

Euleraphe SCHRAMMEN, 1937, p. 82 (SCHRAMMEN, 1936, p. 184, nom. nud.) [*E. incrustans; OD]. Thin crusts on other sponges; canal system barely developed in inner part; spicules short and sinuous, termed eulerhabds, forming thick blanket. Jurassic: Germany.—FIG. 136,1a–b. *E. incrustans, Weiss Jura, Gerstetten; a, sinuous eulerhabd with associated acanthotriaene; b, strongly curved eulerhabd, ×50 (Schrammen, 1937).

Heteroraphidites SCHRAMMEN, 1901, p. 17 [*H. spongiosus SCHRAMMEN, 1901, p. 18; OD]. Globose or tuberose, attached sponges with skeleton largely of strongyles and tylostyles, with large
Fig. 137. Cephaloraphitidae (p. 197).
amphioxas; tetractine spicules rare; microscleres unknown. **Upper Cretaceous–Neogene: cosmopolitan.**—*Fig. 136.4a–f.* *H. spongiosus,* Quadratenkreide, Campanian, Oberg, Germany; representative spicules (Schrammen, 1901).

**Megaloraphium** Schrammen, 1910, p. 127 [*M. auriforme*; OD]. Irregularly ear shaped; skeletal pores typically absent although a few small examples may occur; no skeletal canals; main megascleres very large ophirhabds (e.g., 10 mm long); oxeas and small triaenes in skeletal meshes; microscleres unknown. **Cretaceous (Campanian): Germany.**—*Fig. 137.2a–e. *M. auriforme,* Quadratenkreide, Oberg; a, young individual without skeletal pores but with well-preserved, spicular structure; b, example with a few small pores in parts, ×1; c–e, spicule suite including ophirhabd, triaenes, oxea, ×16 (Schrammen, 1910).

**Ophiodesia** Schrammen, 1937, p. 70 (Schrammen, 1936, p. 183, nom. nud.) [*O. solivaga; OD]. Flat ear-shaped sponges with moderately thick wall; megascleres are sinuous ophirhabds and lumpy styles. **Upper Jurassic:** Germany.—*Fig. 136.2a–b. *O. solivaga,* Weiss Jura, Streitberg; a, ophirhabds; b, nodular styles, ×10 (Schrammen, 1937).

**Polytretia** Schrammen, 1910, p. 126 [*P. seriatopora*; OD]. Ear-shaped; convex side more or less smooth with large, skeletal pores from which short canals run inwardly; concave side irregularly sculptured with large postica in depressed parts, typically in groups of 5 to 10; main megascleres ophirhabds; oxeas and triaenes in skeletal meshes; microscleres unknown. **Cretaceous (Campanian): Germany.**—*Fig. 137.1a–c. *P. seriatopora,* Quadratenkreide, Oberg; a, convex surface with large, skeletal pores; b, concave surface with large, exhalant postica, ×1; c, triaenes as seen from below, ×16 (Schrammen, 1910).

**Rhabdospongia** Sollas, 1873, p. 79 [*R. cummunis; OD]. Sponges more or less rodlike, megascleres are sinuose oxeas. [No known suitable figures.] **Lower Cretaceous:** Europe.

**Family HELMINTHOPHYLLIDAE**

Schrammen, 1937

Sublithistid sponges whose principal megascleres are short, curved monaxons (kyphorhabds), with successive, semiannular swellings interrupted on concave sides, and with weakly developed, zygomelike expansions at ends in some examples; dichotriaenes occur as dermalia; no other spicules known. [The kyphorhabds are arranged so that their ends abut on other examples and are loosely coherent when zygomelike ends are developed. The sublithistid character of the single known genus was recognized by Schrammen (1937, p. 70).] **Upper Jurassic (Kimmeridgian).**

**Helmintophyllum** Schrammen, 1937, p. 69 (Schrammen, 1924a, p. 150, nom. nud.; Schrammen, 1936, p. 183, nom. nud.) [*H. feifeli; OD]. Earlike or platelike; no skeletal pores or canals; main megascleres kyphorhabds; dermalia short- shafted dichotriaenes; no other spicules known. **Upper Jurassic (Kimmeridgian): Germany.**—*Fig. 138.2. *H. feifeli,* Weiss Jura; kyphorhabds, ×20 (Schrammen, 1937).

**Family SCOLIORAPHIDIDAE**

Zittel, 1879

[**nom. corrupt. de Laubenfels, 1955, p. 42, pro Scolioraphidae Zittel, 1879, p. 2**]

Some spicules strikingly annulate; microscleres unknown. **Cretaceous.**

**Scolioraphis** Zittel, 1878b, p. 4 [*S. cerebriformis; SD de Laubenfels, 1955, p. 42]. Meandridform leaves or irregular shapes containing dense masses of annulate, lumpy spicules. **Upper Cretaceous:** Europe.—*Fig. 138.4. *S. cerebriformis,* Quadratenkreide, Campanian, Suttermberges, Germany; characteristic spicules, ×25 (de Laubenfels, 1955).

**Condylacanthus** Fischer, 1867, p. 237 [*C. gaudryi; OD]. Spicules elongate, needlelike with regular, prominent annulations; head with three short branches, each of which is trilobed and tuberculate. **Cretaceous:** France.—*Fig. 138.5. *C. gaudryi,* sandstone of Chalk, Pontavesnes by Beauvais, Oise; isolated spicule, ×40 (Fischer, 1867).**

**Family UNCERTAIN**

**Arthaberia** Siemiradzki, 1913, p. 190 [*A. balinensis; OD]. Semilithistid, top-shaped sponge with thick walls and numerous oval ostia on upper surface; lower surface finely porous; skeleton of very long but thin, rodlike spicules that have curved nodes scattered here and there on their sides; these are sometimes associated with same size rhizomorines in upper layer, but latter were not observed in interior where rodlike spicules form closely packed fibers that are radially arranged; outer, dermal layer formed by growth of nodose, triaene, anchorlike spicules whose ephirhabd follows fiber trend, but whose zygosmes occur singly or generally form three-rayed structures. **Jurassic:** Poland.—*Fig. 138.6a–b. *A. balinensis,* Krakau; a, side view, ×1; b, section through outer part of wall with radially oriented, monaxial spicules in interior and three-rayed spicules in outer wall, ×3 (Siemiradzki, 1913).**
**Fusiferella** De Laubenfels, 1955, p. 43, *nom. nov. pro Atractophora Schrammen, 1924a, p. 76, non Stall, 1853 [*Atractophora armata Schrammen, 1924a, p. 76; OD]*. Sponge elongate, with skeleton composed of spindle-shaped, straight to curved amphioxeas that form thick bundles that are radially arranged in wall and form a fur of slanting spicules on surface. *Upper Cretaceous*: Germany. ——Fig. 138, 1a–b. *F. armata* (Schrammen), Mukronatenkreide, Campanian, Misburg; *a*, holotype with skeletal bundles, ×0.5; *b*, amphioxeas, ×10 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

**Ungulaspongia** Mostler, 1996c, p. 157 [*U. permica; OD*]. Isolated, anatriaene spicules whose three reflexed clads have expanded radially spinose or nodose, pawlike tips. *Permian (Roadian)*: USA (Texas). ——Fig. 138, 3. *U. permica*, Road Canyon Formation, Glass Mountains; isolated, holotype anatriaene with clads having characteristic, pawlike tips, ×150 (Mostler, 1996c).

**Fig. 138.** Helminthophyllidae, Scolioraphididae, and Uncertain (p. 197–198).