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# REVIEW



# The terminology of sponge spicules

Magdalena Łukowiak<sup>1</sup> | Rob Van Soest<sup>2</sup> | Michelle Klautau<sup>3</sup> Thierry Pérez<sup>4</sup> | Andrzej Pisera<sup>1</sup> | Konstantin Tabachnick<sup>5</sup>

<sup>1</sup>Department of Environmental Paleobiology, Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland

<sup>2</sup>Naturalis Biodiversity Center, Dept. Marine Biodiversity, Leiden, The Netherlands

<sup>3</sup>Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

<sup>4</sup>IMBE, Aix Marseille Univ, Avignon Univ, CNRS. IRD. Station Marine d'Endoume. Marseille, France

<sup>5</sup>Shirshov Institute of Oceanology of Academy of Sciences of Russia, Moscow, Russian Federation

#### Correspondence

Magdalena Łukowiak, Institute of Paleobiology, Polish Academy of Sciences, ul. Twarda 51/55, 00-818 Warszawa, Poland, Email: mlukowiak@twarda.pan.pl

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# Abstract

Sponges (Porifera) are a diverse and globally distributed clade of benthic organisms, with an evolutionary history reaching at least the Ediacaran-Cambrian (541 Ma) boundary interval. Throughout their research history, sponges have been subjects of intense studies in many fields, including paleontology, evolutionary biology, and even bioengineering and pharmacology. The skeletons of sponges are mostly characterized by the presence of mineral elements termed spicules, which structurally support the sponge bodies, though they also minimize the metabolic cost of water exchange and deter predators. The description of the spicules' shape and the skeleton organization represents the fundamental basis of sponge taxonomy and systematics. Here, we provide an illustrated catalogue of sponge spicules, which is based on previous works on sponge spicules, for example, and gathers and updates all terms that are currently used in sponge descriptions. Each spicule type is further illustrated through high quality scanning electron microscope micrographs. It is expected to be a valuable source that will facilitate spicule identification and, in certain cases, also enable sponge classification.

#### KEYWORDS

Porifera, spicule names, spicule nomenclature

# **1** | INTRODUCTION

The form and organization of spicules in the sponge skeleton, sometimes combined with spongin fibers, are crucial for sponge taxonomy, systematics and phylogeny. Spicule shapes and morphology are genetically controlled (Uriz et al., 2003). Spicule evolution has been discussed since long (e.g., Cárdenas et al., 2011, 2012; Dendy, 1925; Dohrmann et al., 2017; Reid, 1968, 1970; Schuster et al., 2015) and, recently, it was confirmed that there is a relatively good agreement between molecular phylogenies and taxonomy based on morphology (including spicules) especially in Hexactinellida and Calcarea (subclass Calcinea) in comparison to other sponge groups (Dohrmann et al., 2017; Klautau et al., 2013). Homoplasies appear in several levels of sponge classification. In Calcarea, some characters of the skeleton architecture are highly homoplastic, as are characters of the aquiferous system (Manuel et al., 2003).

The tetractinal symmetry of spicules of Demospongiae and Homoscleromorpha seems to have originated independently (Gazave et al., 2012; Uriz, 2006). Also, within demosponges several sponge groups established (among others), on spicule morphology, turned out to be polyphyletic (e.g., Cárdenas et al., 2011; Erpenbeck et al., 2006). It is especially in Astrophorina that convergent evolution and secondary loss occurred frequently in spicule evolution and took place many times in all major clades, for both megascleres and microscleres (Cárdenas et al., 2011). For example, it is assumed that calthrops, mesocalthrops and mesodichotriaenes have originated independently many times in these groups (Cárdenas et al., 2011). The same is true for phyllotriaenes, which are only known in some lithistid families. They may have evolved independently at least twice in Phymaraphiniidae and Theonella (Cárdenas et al., 2011). Also, sigmas (C-shaped spicules) evolved more than once, i.e., in Biemnida, Poecilosclerida and Haplosclerida (Morrow et al., 2013). In other

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cases, close relationships between some sponge groups can be difficult to infer due to the highly autapomorphy morphologies of their spicules, like in the orders Halichondrida and Agelasida (Erpenbeck et al., 2006). Despite these reservations, systematics based on spicules has proven its usefulness in identification, classification, and reconstructions of sponges phylogenetic relationships.

The aim of this catalogue is to gather, define, and illustrate all types of sponge spicules described in various taxonomic studies (e.g., Bergquist, 1978; Borojevic et al., 1968; Boury-Esnault & Rützler, 1997; Gadea Buisán, 1947; Green, 1991; Hooper, 2003; Hooper & Soest, 2002; Lundbeck, 1902; Reid, 1970; Ridley & Dendy, 1887; Schulze & Lendenfeld, 1889; Sollas, 1888; Reiswig & Kelly, 2011, 2018; Tabachnick & Reiswig, 2002; Vacelet, 2012; de Vos et al., 1991; Wiedenmayer, 1944, 1977 and the references cited therein; van Soest, 2021) using high resolution scanning electron microscope (SEM). Some terms were adopted or modified from the Thesaurus of Sponge Morphology (Boury-Esnault & Rützler, 1997).

This comprehensive source of information about the occurrence of various spicule types, both in living sponges and in fossil representatives, will allow sponge specialists and non-specialists, dealing with isolated spicules, to recognize and name them. It will be thus of great interest for taxonomists, ecologists, and paleontologists.

The text is divided in two sections: (1) General spicule terms includes basic terms concerning spicule structure and shortcuts used in the text; (2) Spicule names—lists all current spicule names. Each term is preceded by the abbreviation of the sponge class name or of a sponge informal name (D. for Demospongiae, DL. for lithistid demosponges, H. for Hexactinellida, Ho. for Homoscleromorpha, and C. for Calcarea). In this section, for every spicule type, there is an example of a characteristic sponge species (family or group) bearing this particular spicule type and a reference for the spicule SEM picture placed at the end of the text. The term provided in italics in "general spicule terms" and "spicule names" can be found as defined separately in the glossary. Spicule types known exclusively from the fossil record are marked by "†."

# 2 | PORIFERAN TISSUE AND SKELETON

The mesohyl is an extracellular matrix that contains specialized and pluripotent sponge cells, symbiont prokaryotes and other endobionts, as well as organic material (mainly proteins such as collagen fibrils and sometimes spongin), spicules, inorganic foreign material, and inorganic material produced by sponge cells. Most sponges possess skeletons composed of spicules usually organized in architectural networks. In some groups, they are arranged into rigid (fused) skeletal structures. Siliceous spicules are biocomposites that incorporate organic material in their structure—a special protein complex forming an axial filament situated in the interior of most siliceous spicules (Ehrlich et al., 2022; Görlich et al., 2020; Uriz, 2006; Uriz et al., 2003). Collagen or chitin matrix may be also present inside the silica spicules (Ehrlich et al., 2007, 2017, 2018; Fromont et al., 2019;

Pisera et al., 2021). So far, the axial filament has never been observed in the spicules of Calcarea (Uriz, 2006). Calcareous spicules, despite the absence of an axial filament, show low amounts of an organic matrix between the crystals and an organic envelope surrounding the spicules (Rossi et al., 2014). Some sponges belonging to both Demospongiae and Calcarea also have a notable rigid, massive aragonite or calcite basal skeleton (Hajdu & van Soest, 2002; Manuel et al., 2002). These massive structures are not composed of spicules, but spicules can be associated with this kind of skeleton, being present in the mesohyl. In lithistids, an informal group within Demospongiae, a hypersilicified skeleton occurs (Pisera & Lévi, 2002; Pisera, 2003).

# 3 | SHORT CHARACTERISTICS OF THE SPONGE CLASSES

## 3.1 | Demospongiae Sollas (1885)

The class Demospongiae is the largest, morphologically most diverse, and successful group of the phylum Porifera. It is the only sponge class that is distributed in marine, brackish as well as in fresh water environments. It comprises 83% of all accepted living sponges, with 7873 (including 268 freshwater species) species worldwide (de Voogd et al., 2022). Demospongiae includes three subclasses and 22 extant orders (Morrow & Cárdenas, 2015). In the ocean, they are known worldwide from the hadal to the eulittoral zone (Van Soest et al., 2012). They are filter feeding animals as all other sponge groups, but also include some peculiar carnivorous representatives in the family Cladorhizidae (Hestetun et al., 2017; Vacelet & Boury-Esnault, 1995).

Demosponges produce a skeleton of opaline spicules, frequently supplemented with spongin fibers. In some cases, they have only fibers of spongin or chitin (Ehrlich et al., 2018; Fromont et al., 2019). Solid, calcified (aragonite) skeletons, sometimes complemented by free-spicules, also occur in various modern sponge groups (Clionaida, Haplosclerida, Merliida, and Agelasida), and in the fossil sphinctozoans which are actually a polyphyletic group (Senowbari-Daryan & García-Bellido, 2002; Vacelet, 1985). The demosponge spicules are mainly monaxons and tetraxons (triaenes) but never triaxons. Spicules in Demospongiae never fuse with each other. Only lithistids have a solid hypersilicified skeleton formed by articulated siliceous spicules called desmas. The articulation means that there is always a thin space that separates particular desmas at places at which they connect. As such, in contrast to hexactinellids, no additional siliceous cement is involved. Desmas may have variable geometry (anaxial, monaxial, tetraxial, spheraxial) and shape being smooth or strongly sculptured. Lithistid sponges, due to their heavy silicification and articulation of desmas, dominate the demosponge fossil record. The earliest reliable demosponges are early Cambrian (515 Ma) disassociated fossil spicules (Botting et al., 2015 and discussion therein) but the origin of this class is estimated from sponge mitochondrial genomes to be in the Neoproterozoic (Dohrmann & Wörheide, 2017; Plese et al., 2021; Schuster et al., 2018).

## 3.2 | Hexactinellida Schmidt (1870)

Only 698 hexactinellid species are known today, which comprises slightly over 7% of all known living sponges (de Voogd et al., 2022). Sponges of this class are characterized by the lack of dissolvable spongin as skeletal component, although the collagen matrix is seen on Transmission Electron Microscopy. This group is characterized by the presence of thin mesohyl and multinucleated syncytium which is a major tissue component (Leys, 2003). Hexactinellid sponges are inhabitants of waters with oceanic salinity. They are psychrophilic and live mainly in bathyal and abyssal ecosystems (down to about 7000 m; Tabachnick et al., 2017). In favorable conditions of low temperatures (below 14°C), high dissolved silicate and low light, they can inhabit shallow-waters (about 8 m depth; Goodwin et al., 2012). Loose spicules of some dead hexactinellids sometimes accumulate into spicule mats (Barthel, 1992), while hexactinellids with rigid frameworks may produce various reef constructions known in both recent and fossil state.

Siliceous (opaline) spicules may be loose or partially or completely fused. The latter condition (fused spicules) may result in the formation of a rigid choanosomal framework (Schulze, 1887). Such framework consists of specific dictyonal strands (Reid, 1963). Hexactinellids produce siliceous spicules of hexactinic or triaxonic (or cubic) symmetry or shapes clearly derived from such spicules by reduction of primary rays or branching of the primary rays. A loss of one or more rays results in pentactines, tetractines, triactines, diactines, and monactines. The earliest reliable sponge fossils are hexactinellid spicules from Iran dated to c. 535 Ma. (Hamdi et al., 1989), but some hexacts are known also from Ediacaran-Cambrian (541 Ma) cherts from South China (Chang et al., 2019).

# 3.3 | Homoscleromorpha Bergquist (1978)

This is the smallest class of Porifera with a worldwide distribution in only marine environments, with three oceanic regions representing current hotspots of Homoscleromorpha occurrences: the Pacific Ocean, the Tropical Western Atlantic Ocean and the Mediterranean Sea (Lage et al., 2018). Homoscleromorphs are mainly distributed in cryptic semi-dark and dark habitats, from intertidal to bathyal depths. There are 130 valid species in this group representing about 1.5% of all sponges known so far (de Voogd et al., 2022). Although all Homoscleromorpha share common traits allowing to distinguish them from all other sponge classes (e.g., basal membrane under pinacoderm and choanoderm, flagellate pinacocytes, specific siliceous spicules when they exist; Gazave et al., 2012; Maldonado & Riesgo, 2007), the taxonomy and systematics within this class is a challenging issue because of the lack of obvious diagnostic characters and a rather high plasticity in some cases. However, this class has known one of the highest rates of new descriptions over the last two decades through the use of integrative taxonomy (e.g., Boury-Esnault et al., 2013). Still containing only one order, this sponge class has

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seen its systematics overturned in the last 10 years, with its separation from the Demospongiae, the resurrection of one family (Oscarellidae) and the redefinition of the family Plakinidae (Ruiz et al., 2017). Among the two known families, all Oscarellidae are skeletal-less, cytological traits being used for their identification: vacuolar and spherulous cells, organized in clusters in some cases, or harboring very peculiar paracristalline inclusions in some other cases. Recently, it has been shown that the choanocyte kinetids structure strongly supported the division of the Oscarellidae family in two clades (Pozdnyakov et al., 2020). In Plakinidae, three genera are also known to be skeletal-less (Ruiz et al., 2017; Ruiz et al., submitted), but in general this family lacks cytological descriptions. When present, spicules are rather small (100 µm on average) and not differentiated into mega- and microscleres (Van Soest et al., 2012). They are peculiar tetractines (calthrops, 10-300 µm) and derivatives after ramification (lophose spicules) or reduction of the number of actines (triods,  $10-300 \,\mu$ m, diods  $25-750 \,\mu$ m). Their ramifications can be homogeneous (homolophose spicules) or heterogeneous (heterolophose) in variable positioning along the actines. Homoscleromorph spicules are known in the fossil record from at least early Carboniferous (Mehl-Janussen, 1999; Reid, 1970).

#### 3.4 | Calcarea Bowerbank (1862)

The class Calcarea corresponds to about 8.5% (801 species) of the phylum Porifera (de Voogd et al., 2022). The species within this class are all marine and can be found from the intertidal zone to, less frequently, the abyssal zone (some even in a depth range of 1120–4400 m; Janussen & Rapp, 2011). The skeleton in Calcarea is composed exclusively of calcium carbonate (spicules of Mg-calcite) (Rossi et al., 2014).

Nowadays, the diversity of spicule types in this class is reduced, with only three basic forms: diactines, triactines, and tetractines (Manuel et al., 2002; Van Soest et al., 2012) with a variety of derivatives/variants within them. The plane of the actines (basal or apical), the angle between them (equiangular or sagittal), their shape (conical, slightly conical, or cylindrical), and the character of the tips (rounded, blunt, or sharp), are some of the characteristics that differentiate the spicules of Calcarea. Pentactines, which are mainly found in fossil Calcarea, have also been found in extant species, but they are rare (Chagas & Cavalcanti, 2017; Rossi et al., 2006). There is no differentiation in micro- and megascleres. Solid, hypercalcified (calcite) skeletons, complemented by free calcite spicules, also occur in some extant groups (orders Murrayonida, Lithonida) with affinities to fossil taxa (Vacelet et al., 2002).

The oldest fossils of Calcarea are specimens of *Eiffelia* Walcott, 1920 (Order Heteractinida) from the middle Cambrian Burgess Shale. However, some doubts remain if *Eiffelia* was indeed a genus of Calcarea (Botting & Butterfield, 2005). The first unchallenged fossil record of a calcareous sponge is that of *Leucandra walfordi* Hinde, 1893 from the Middle Jurassic, King's Sutton, Northamptonshire (Pickett, 2002).

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# 4 | GENERAL SPICULE TERMS

Acanth(o)—spined; the spines may regularly or irregularly cover the spicule surface; for example, *acanthostyle*, *-oxea*, *-rhabd*.

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Acerate-pointed like a needle; with a gradual thinning of the spicule tip; for example, *acerate oxea*.

Aciculo—with thorn or spine-like projections; for example, aciculospinorhabd.

Actine—a ray of a spicule; it is also used as suffix in general nomenclature of spicules; for example, *monactine*, *diactine*, *tetractine*, *hexactine*; see also *ray*.

Ala (pl. alae)—in *chela* a flake-like structure that in different number (usually three) and arrangement ends the chela shaft; anterior ala is the one that is facing the *shaft*; others are called lateral alae (Figure 3.7, 22).

Amphi—with identical structures on both sides, for example, rays, discs, usually radiating from both ends of the shaft; for example, *amphidisc*, -oxea, -tyl, -torn.

Ana-with *clads* directed backward; for example, *anatriaene*.

Anaxial-without an axis; for example, anaxial desma.

Anchorate—having a shape of an anchor; with two or more clawor grapnel-like spines; for example, anchorate isochela; compare with palmate and arcuate; see also anchor.

Aniso—of unequal form or size; for example, *anisohexaster*, *-chela*, *-discohexaster*, *-strongyle*, *-strongyloxea*.

Antho-of flower (thorn) shape/pojections; for example, anthosigma, -spheraster.

Apex–D.; a rosette or crown of spines in the top of *rhabd* of Latrunculiidae (Figure 2.3).

Apical actin(e) – the fourth ray (*actine*) of a *tetractine* in C., which is frequently in a plan perpendicular to the basal *triradiate* system and that protrudes from the center; it can be smooth or covered with spines (Figure 11.17,21).

Apical cone—H.; a conical structure of outer (upper) ends of a *basalia* which protrude inside or over the atrial cavity (e.g., genus *Hyalonema* and some pedunculated Hexactinellida); or a rounded and often widened outer ray tip in pinnular rays.

Aster (astro-)—of star shape; for example, *astrotylostyle*, *sterrasters*.

Axial—having an axis/axes or situated around/in the direction of, or along an axis; for example, *tetraxial desma*.

Axial filament—organic proteinaceous construction situated in the central part of most siliceous spicules; it determines the geometry of a spicule.

Brachyome-a shortened arm of a trider (Figure 8.2, 3).

Calyco—a type of branching when the secondary rays begin from cup-like outer ends of primary rays; for example, *calycocome*.

Capitulum—an enlargement or a swelling at the distal end of primary rays of a microsclere; for example, *calycocome*, *plumicome*; or the area of junction of *scopule tines* with *shaft*.

Centro(a)-indicating center, for example, centrotylote.

Centrotylote—indicating median swelling/tyle; for example, centrotylote oxea. Chia(sto)-cross-like; for example, chiastoclone.

Clad(us) (pl. cladi)—in *triaenes* a ray or axial branch within the *cladome*; *c*. possesses (is based on) axial canal or axis and is usually shorter than the *rhabd*.

Cladome–a part of a *triaene* consisting of the three *cladi*; see *rhabdome* (Figures 4.2, 8, 25 and 5.4).

Clavate-club-shaped; for example, cusped clavate clavule.

Clone—in DL.; a ray-like arm of a *desma* in which the number of clones is governed by the *crepis* geometry.

Conical—of shape of a cone; compare with *hastate*; for example, *conical oxea*.

Crepis—in DL.; a basal form (early stage of development) based on axial filament of body of a *desma* before modification and deposition of multiple layers of silica.

Cri(co)—with spiral or annulate ornamentation; for example, cricorhabd, -style, -xea.

Dendro-of tree shape; for example, *dendroclone*.

Desmoid-approaching the form of *desma*; for example, desmoids of *Crambe crambe*.

Deuteroclad—an actinal branch or a distal, branched portion of a ray.

Disco-of shape of a disc; in H. when several-numerous teeth have a common base; for example, *discohexaster*, *-rhabd*.

Epirhabd—a part of developed *desma*; it is formed by the deposition of layers of silica around the *crepis*.

Falx (pl. falces)—in *chela*; a web- or a sickle-shaped structure connecting the anterior *ala*/each ala/tooth with the *shaft* on the inside.

Fimbriae (pl.)-paired, narrow, wing-like structures flanking the *shaft* of *anchorate chela* distally or throughout (Figure 3.19).

Flexuous-with curves, turns, or windings; for example, *flexuous oxea*.

Fringe—a narrow unpaired structure located in the inner side of a *shaft* of *chela*, *sigmancistra* and *diancistra*; compare with *fimbriae*.

Fusiform-tapering regularly toward both ends; the tapering is followed by a light curve, for example, *fusiform oxea*, *f*. (*tylo*)*style*.

Hastate—with a pointed tip; the tapering is neatly more abrupt close to the spicule tip, isometric and of equilateral triangle shape; for example, *hastate oxea*; compare with *conical* (Figure 6c).

Hemi(y)—prefix for hexasterous spicules with irregular number of secondary rays, when one or more (but not all) primary rays carry a single secondary ray; for example, *hemidiscohexaster*, *-hexaster*, *-onychohexaster*, *-oxyhexaster*, and *-oxystauraster*.

Hexa-indicating six; for example, hexaster.

Hilum—in geodiids and placospongiids; a depression on the ellipsoidal forms of *sterraster*, *selenaster*, and *aspidaster* (Figure 1.2, 6).

Iso—of equal length or form; it refers to the ends of a spicule; for example, isochela, -strongyloxea.

Lanceolate-spear-like; for example, lanceolate oxea.

Lopho—with rays/tips forked or branched like a tuft; for example, *lophocalthrop*, *-triaene*, *-discohexaster*.

Manubrium–D.; a base of *rhabd* of Latruculiidae, which is embedded in the ectosomal membrane (Figure 2.3).



FIGURE 1 Asters and spherical spicules. 1–3. Selenasters; 4–6. Sterrasters; 7. Sterrospheraster; 8–11. Aspidasters; 12, 16, 17. Spherasters; 13. Spherule; 14. Microsphere; 15. Pycnaster; 18. Anthospheraster; 19, 20. Spheroxyasters; 21. Megaster; 22. Oxyspheraster; 23, 24. Oxyasters; 25. Tylaster; 26. Strongylaster; 27, 28. Strongylospherasaters; 29. Micraster/Tylaster; 30. Anthaster; 31. Pseudospheraster; 32. Pseudoeuaster. H, hilum.



**FIGURE 2** Rhabd-derived microscleres. 1, 2. Acanthodiscorhabds (anisodiscorhabds); 3, 4. Spinorhabds; 5. Trochirhabd; 6. Subtrochirhabd; 7. Spirorhabd; 8–14. Spirasters; 11, 12. Diplaster; 15. Plesiaster; 16. Metaster; 17–22. Amphiasters; 20, 22. Strongyloamphiasters; 23. Centrotylote acanthomicroxea; 24. Microacanthostrongyle; 25. Microtylostyle; 26. Raphides (in trichodragma); 27. Microxea; 28. Acanthorhabd; 29. Microstrongyle; 30, 31. Ataxasters; 32. Didiscorhabd; 33. Sanidaster. Ap, apex; aw, apical whorl; mn, manubrium; mw, whorl; sh, shaft; sw, subsidiary whorl.



FIGURE 3 Sigma-derived spicules. 1. Rosette of anisochelae; 2. Birotule; 3–10. Isochelae; 6. Unguiferate arcuate isochelae; 7, 8. Unguiferate anchorate chelae; 4, 9. Abyssochelae; 10. Spined isochela; 11–18. Anisochelae; 11. Anomochela; 12. Unguiferate anisochela; 13–15. Palmate anisochelae; 16, 17. Naviculichela front view (16) and side view (17); 18. Diastrophochela; 19, 20. Sphaerancoras; 21. Bipocillum; 22. Cleistochela; 23. Diancistra; 24. Clavidisc; 25. Canonochela; 26. Cercichela; 27–29. Placochelae; 30. Dischela; 31. Naviculichela; 32. Biplacochela; 33. Tetrapocillum; 34. Chiastosigma; 35. (Centrangulate) Cyrtancistra; 36. Sigmancistra; 37-39. Sigmas; 40. Croca; 41. Toxa; 42. Thraustoxea; 43. Comma; 44. 45. Forceps; 46, 48. Thraustosigmas; 47. Spirosigma; 49. Sigmaspire; 50, 51. Colloscleres. Al, ala; fm, fimbria; sh, shaft.

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**FIGURE 4** Triaenes: 1–4, 6. Anatriaenes; 5, 7–10, 13, 17, 23, 25. Dichotriaenes; 7–12. Orthotriaenes; 13–15, 17, 19. Plagiotriaenes; 16. Fragment of protriaene; 18. Fragment of mesotriaene; 20–23, 25. Protriaenes; 24. Promonaene; 26, 27. Prodiaenes. Cl, cladome; rbd, rhabd.



**FIGURE 5** Ectosomal triaenes. 1–3. Calthrops; 2. Acanthocalthrop; 3. Dichocalthrop; 4–17. Triaenes; 4. Mesotriaene; 5. Triaene; 6, 7. Mesodichotriaenes; 8. Branched triaene; 9. Acanthotrichotriaene; 10. Dichotriaene; 11–13. Phyllotriaenes; 14. Pseudophyllotriaene; 15, 16. Discotriaenes; 17. Pseudodiscotriaene; 18, 19. Triactines; 20–22. Polyactines; 23, 24. Amphitriaenes. Cl, cladome; rbd, rhabd.

Mega—having large size (relative term); for example, *megaclone*, *megasclere*; compare with *micro*.

Micro—of a small size (relative term); compare with *mega*. Mucronate—ended with a spur-like projection; for example, *mucronate tylostyle*.

Meso-of intermediate size and/or shape, a middle size; for example, *mesoamphidisc*; see also *mesotriaene*.

Nodulose-being knobby; for example, nodulose amphiaster.



FIGURE 6 Monaxone megascleres. 1-17. Diactines; 1, 2. Strongyles; 3, 4. Tylotes; 5. Subtylote; 6. Tylostrongyle; 7-16. Oxeas; 8. Fusiform oxea; 9. Anisoxea; 10. Oxea with blunt tips; 11. Oxea with mucronate tips; 12. Oxea with symmetrical tips; 13, 14. Acanthoxea; 15. Strongyloxea; 16. Thin oxea; 17. Tornote; a. Tornote tip; b. Asymmetrical tip; c. Hastate (symmetrical) tip; d. Blunt tip; e. Stepped tip; f. Acerate tip; g. Conical tip; h. Mucronate tip; 18-34. Monactines; 18-21. Acanthostyles; 22. Rhabdostyle; 23. Strongyloxea; 24-26. Styles; 26. Mycalostyle; i. Developed tyle; j. Developed tyle; k. Faintly developed tyle; l. Polyactine tip; 28. Polytylote; 29. Subtylostyle; 30-32. Tylostyles; 34. Verticillate style.



FIGURE 7 "Auxiliary" spicules. 1. Flexous strongyle, 2. Onychaete; 3–5. Flexuous oxeas; 6. Flexuous strongyle; 7. Crooked acanthoxea; 8. Verticillated strongyle; 9. Acanthoxea; 10. Tuberculated oxea; 11. Spiral strongyle; 12. Cladotoxa; 13. Acanthostrongyle; 14. Kyphorhabd; 15. Spined microxea; 16. Cladotylote; 17. Spherostyle; 18, 19. Exotyles; 20. Pinakid; 21. Polyactine; 22-25. Gemmuloscleres; 22. Pseudobirotule; 23-25. Birotulate gemmuloscleres.

Ortho-in triaenes; when clads form with the rhabd an angle of about 90°; for example, orthotriaene.

Oxy-having acute tips; for example, oxydiaster, -diactine, -hexaster, -pentactine.

Paired actin(e)-C.; in triactines and in the basal triradiate system of tetractines, always in sagittal or parasagittal spicules; the ray(s) opposed to the unpaired one. (Figure 11.3, 12, 17, 21).

Paratropal-an intersection of spicule rays at angles notably differing from 90°; for example, hypodermal pentactines of some Rossellidae.

Primary-in H.; the central part of a spicule, for example, rays which are centrally connected at the node of the spicule and distally

give rise to secondary structures (e.g., rays); compare with secondary (Figure 9.35, 36).

Pro-in triaenes; when clads are directed forward away from the rhabd; for example, protriaene.

Proto-indicating first, ancestral, early or basic; proximal, unbranched portion of a branched ray; for example, protoclad, -rhabd.

Pseudo-approaching or attaining the shape of other spicule/ structure; for example, pseudoaster, -phyllotriaene.

Ray-analogous term for act(ine) used for microscleres or in C.; in H. used for both micro- and megascleres.

Rhabd(ome)-the longest ray of tetractinal spicule such as phyllotriaene or discotriaene penetrating choanosome perpendicularly;

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**FIGURE 8** Lithistid desmas and articulated skeletons. 1. Trider framework; 2, 3. Triders; 4. Megaclone framework; 5. Megaclone; 6. Rhizoclone framework; 7, 8. Rhizoclones; 9. Dendroclone framework; 10. Dendroclones; 11. Dicranoclone framework; 12, 13. Dicranoclones; 14. Tetraclone framework; 15. Tetraclone; 16. Pseudotetraclone framework; 17. Astroclone; 18. Sphaeroclone; 19. Heloclone; 20. Didymoclone; 21. Mesotrider. Fused Hexactinellida skeletons. 22. Dictyonal framework–lychniscosid skeleton (Lychniscosida); 23. Dictyonal framework–euretoid skeleton (Euretidae); 24. Dictyonal framework–euretoid skeleton (Tretodictyidae); Calcarea skeleton. 25. Skeleton of *Plectroninia* (Calcarea).

see also *rhabdosclere* in spicule names and *cladome* (Figures 4.2, 8, 25 and 5.4).

Sclere—unused term for spicule, but occurs in compound terms; for example, macro-, micro-, sigmatosclere.

Sigmoid(al)—curved like a sigma; crescent or S-shaped, for example, sigmoid chela; also shape of secondary rays in plumicome.

Secondary—in H.; a structure of a spicule (e.g., a ray or a terminal branch) starting from a primary structure, for example, a ray; compare with *primary* (Figure 9.20, 27, 28, 30, 35a, 35b).

Shaft—a straight part connecting two distal regions of a *microsclere*; for example, in *amphiaster*, *dendroclone*, and *chela* (Figures 2.3 and 3.7, 19, 22, 24).

Spur-in H.; a free (unfused) ray of a *dictyonal* framework at the margin.

Sph(a)er(o)—of spherical shape; for example, *sphaeroclone*; in H. prefix indicating type of ray termination of *microscleres* with spherical knobs.

Spir(o)-of spiral shape; for example, spiraster.

Stauro(a)—in H.; cross-shaped; with four rays in one plane; for example, *stauractine*; compare with *chiasto*-.

Stellate-star-shaped; in H. used for (*disco*)hexaster secondary rays grouped in clusters resulting in a star-shaped microsclere.

Strongylo(te)—a spicule resembling a strongyle; for example, strongylote megascleres of Petrosia (Strongylophora).

Sub-not completely developed; for example, subtylostyle.



FIGURE 9 (See caption on next page)



FIGURE 10 Hexactinellida spicules II. 1. Anchor; 2–6. Sceptrules; 2. Pilate clavule; 3. Tyloscopule; 4. Strobiloscopule; 5. Aspidoscopule; 6. Sarule; 7. Diactine; 8. Uncinate; 9. Oxyhexaster; 10. Scepter; 11. Sword hexactine; 12. Tauactine; 13. Fragment of hypodermal pentactine with paratropal tangential rays; 14. Paratetractine; 15. Onychodiaster; 16. Fibule; 17. Paradisc; 18-20. Amphidiscs; 21. Tetradisc; 22. Pentadisc.

FIGURE 9 Hexactinellida spicules I. 1-4. Pentactines; 5. Pinular pentactine; 6, 7. Pinular hexactines; 8. Stauractine; 9. Discostauractine; 10. Onychohexaster; 11. Discohexaster; 12. Discohexactine; 13. Oxyhexactine; 14. Tylohexaster; 15. Discohexactine; 16. Hexactine; 17. Discohexaster; 18. Lophodiscohexaster; 19. Discoctaster; 20. Microhexaster; 21. Oxystauraster; 22, 23. Oxyhexasters; 24. Onychohexactine; 25. Plumicome; 26. Hemioxyhexaster; 27. Strobiloplumicome; 28. (Disco)plumicome; 29. Spirodiscohexaster; 30. Floricome; 31. Discaster; 32. Calycocome; 33. Drepanocome fragment; 34. Codonhexaster with two anchorate ends preserved; 35. Graphicome; a. Graphicome secondary ray; b. Springohexaster secondary ray; 36. Springohexaster.

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**FIGURE 11** Calcarea spicules. 1. Tripod; 2. Regular triactine; 3. Sagittal triactine; 4. Pseudosagittal triactine; 5. Aliactine; 6. Subregular triactine; 7–9. Tetractines; 10. Parasagittal triactine; 11. Nail-shaped triactine; 12. Diapason; 13. Trichoxea; 14. Diactine; 15, 16. Grapnel (15) and detail of the upper part (16); 17. Microdiactine; 18. Chiactine; 19. Tetrapod; 20. Scale; 21. Anchor; 22. Pugiole. A, apical actine; p, paired actine; u, unpaired actine.

Tine–H.; a branch/prong/spine emanating from a scopule, sceptrule or lonchiole head.

Toxiform–D.; bow-shaped; for example, *toxiform oxeas*, *t*. *raphids*.

Trochi-equipped with disc/s; for example, trochirhabd.

Tyle(o)—with one or more rounded, spherical tip/s; for example, tylostyle, rhabdotylostyle.

Typh(oid(al)—in H.; with abrupt elongate cylindrical inflation (rod) in the ray axis; for example, *typhahexaster*.

Umbel—in H.; a *disc* or *rotule* with teeth at margin of *amphidisc* shaft; *u*. can be toothed, anchorate, or discoidal (e.g., Amphidiscophora).

Unpaired actin(e)—in C.; in *parasagittal* or *sagittal triactines* and in the *basal triradiate* system of sagittal *tetractines*; the actine (ray) opposed to the *paired* actines (Figure 11.3, 12, 17, 21).

Whorl-D.; parallel circular discs or spines along the shaft of a spicule; in Latrunculiidae a w. is placed immediately beneath the apex of spines (apical w.), in the middle of shaft (median w.), and next to *manubrium* (subsidiary w.) of a *rhabd* (Figure 2.3).

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Vermicular-resembling the form or a track of a worm; for example, vermicular oxea, v. style.

Verticillate—ornamented by whorls; for example, *verticillate oxea*, v. style, v. sanidaster (Figure 6.34).

Zygome—in DL.; a part of a *desma* that interlocks with another spicule.

# 4.1 | Spicule names

# 4.1.1 | A

Abyssochela–D.; an arcuate *isochela* with frontal teeth touching or nearly touching, and usually a height and width ratio close to one (e.g., *Abyssocladia tecta*) (Figure 3.4, 9).

Acanthodiscorhabd—called also chessman spicule; D.; a kind of *discorhabd* equipped with spines arranged in whorls (e.g., Latrunculiidae); compare with *didisco-*, *spino-*, and *trochirhabd* (Figure 2.1, 2).

Acanthophore—H.; a spicule surrounding the point of insertion of the tuft of a *basalia* into the sponge body; usually a *hexactin* to *monactin* (with often short thick and/or spined rays) or *sphere* (pearl) (e.g., Hyalonematidae).

Acanthorhabd-an ornamented rhabd (Figure 2.28).

Acanthotriaene – D.; a *triaene* with spined surface (e.g., genus *Acanthotriaena*); it may posses divided *clads* (e.g., acanthotrichotriaene of *Thrombus abyssi*) (Figure 5.9).

Acanthostrongyle–D.; a *strongyle* with spined surface (e.g., genus *Plocamione*). (Figures 2.24 and 7.13).

Acanthostyle–D; a style with spined surface (e.g., *Lissodendoryx* [*Ectyodoryx*] *antarctica*) (Figure 6.18–21).

Aciculodiscorhabd—see *discorhabd*.

Aciculospinorhabd-see spinorhabd.

Aliactine–C.; a specialized butterfly-shaped *tetractine* lining apopylar chambers (e.g., *Paragrantia waguensis*) (Figure 11.5).

Ambuncinat(e)-see uciante.

Amphiaster–D., DL.; a *microsclere* with microspined rays radiating from both ends of a *shaft* (e.g., *Neoaulaxinia zingiberadix*); it can be, for example, *strongyloamphiaster*; compare with *streptaster* (Figure 2.17–22).

Amphichel-see chela.

Amphiclad-see amphitriaene.

Amphidisc—called also discodiactin; D., H.; in some H. (all Amphidiscophora and some Hexasterophora) spicule characterized by a *shaft* (may be spinose) with discoidal or anchorate ends (e.g., *Monorhaphis chuni*); compare with *birotule* (Figure 10.18–20).

Amphistrongyl(e)-see strongyle.

Amphitorn—see *tornote*.

Amphitriaene-called also amphiclad; D.; a *triaene* in which the *cladomes* protrude from both ends of the *rhabd(ome)* (e.g., genera *Samus, Amphitethya*) (Figure 5.23, 24).

Amphitylote-see tylote.

Anadiaene-see anatriaene.

Anamonaene-see anatriaene.

Anatriaene–D.; a triaene with clads curved backward, toward the rhabd (e.g., family Tetillidae, Ancorina cerebrum); special derivatives of a. are anadiaene and anamonaene which are characterized by reduced number of cladi (by 1 and 2, respectively); compare with hexactinellid anchor (Figure 4.1–4, 6).

Anchor-C., H.; in H. *basalia* megascleres with one end of anchor shape (e.g., genus *Hyalonema*); it can be dianchorate (e.g., *Holascus tasmanensis*); in C. a *triactine* or *tetractine* present at the base of the calcareous sponge that helps the individual to attach to the substrate (e.g., *Amphoriscus ancora*, A. *synapta*); compare with demosponge *anatriaene* (Figures 10.1 and 11.15, 21)

Anchorate chela—D.; an *(iso)chela* with three or more free *alae* (at each end) in the form of recurved processes shaped like anchor claws or blades and with two incipient lateral alae fused with the *shaft* over their entire length; the shaft is usually gently curved, not abruptly arched (e.g., genus *Crambe*); compare with *palmate* and *arcuate chela* (Figure 3.7, 8).

Anchorate clavule—H.; a *clavule* with anchorate head; may be spiroanchorate (e.g., *Aspidoscopulia bisymmetrica*).

Ancora-see chela.

Ancora unguifera—see unguiferous-anchorate chela.

Anisodiscorhabd—called also cricophalangaster; see *discorhabd*. Anisochela—D.; a *chela* with differently developed *alae* (e.g.,

genus Mycale, Asbestopluma vaceleti) (Figure 3.11–18).

Anomochela–D.; a modified *palmate anisochela* with a very large, twisted and wide frontal *ala* at the smaller end of the chela (e.g., *Mycale* [Anomomycale] titubans) (Figure 3.11).

Anthaster–D.; an *euaster* with sculptured, branched, or divided ray tips (e.g., *Diplastrella megastellata*) (Figure 1.30).

Anthosigma—D.; an arc-shaped *microsclere* with tuberculate projections on the convex side and on the ends of the spicule (e.g., genus *Cliona*); sometimes referred to *spirasters* of *Placospongia anthosigma* (Figure 2.13).

Anthospheraster–D.; a *spheraster* possessing sculptured, branched, or divided ray tips (e.g., *Chondrilla sacciformis*) (Figure 1.18).

Arcuate chela–D.; an *(iso)chela* with usually bow-shaped *shaft* and three free (separated from the shaft) *alae* at each spicule end (e.g., *Phorbas claviger*) (Figure 3.6).

Aspidaster–D.; an elongated and flattened, sometimes discshaped *microsclere* possessing numerous fused rays which end with minute spinose projections (e.g., genus *Erylus*) (Figure 1.8–11).

Aspidoplumicome-see plumicome.

Aspidoscopule–H.; a *scopule* (originally strobiloscopule) with snake-like tines (e.g., genus *Aspidoscopulia*) (Figure 10.5).

Astroclone–DL.; a *desma* made of arms radiating from the center (e.g., genera *Lecanella*, *Vetulina*) (Figure 8.17).

Astrose microsclere-see aster.

Ataxaster–D.; a microspined, ovoid *microrhabd* with many forms branched or irregular; shapes may be termed centrotylote rhabds, rods with side branch(es), round balls, cross-shaped, or rarely polyangular/aster-like (e.g., subgenus *Calthropella* [*Pachataxa*]) (Figure 2.30, 31).

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**FIGURE 12** Homoscleromorpha spicules. 1–3. Diods; 2, 3. Lophose diods; 4–8. Triods; 5. Microtriod; 6. Monolophose triod; 7. Dilophose triod; 8. Trilophose acanthotriod; 9–15. Calthrops; 11. Monolopho(u)s(e) calthrop; 12. Dilopho(u)s(e) calthrop; 13. Trilopho(u)s(e) calthrop; 14, 15. Tetralopho(u)s(e) calthrops; 16. Candelabra; 17. Pseudolophose spicule.

Atrialia (pl.)—called also *gastralia*; H.; spicules associated with the atrial surface (e.g., genus *Lophophysema*).

Autodermalia (pl.)–H.; *dermalia* with one ray protruding outside the sponge body.

Autogastralia (pl.)-H.; gastralia with one ray protruding into the atrium.

# 4.1.2 | B

#### Bacillus-see microstrongyle.

Barbule-see uncinate.

Basalia (pl.)–H.; a type of *prostalia* represented by basal spicules protruding from lower sponge surface and serving for attachment (e.g., genus *Monorhaphis*).

Bihamate-no longer in use; see sigma.

Biplacochela–D.; a strongly modified *chela*-derived *microsclere* consisting of two discs bearing numerous *fimbriae* connected eccentrically by a smooth *shaft* (e.g., genus *Guitarra*) (Figure 3.32).

Bipocillum—D.; a *chela* with short curved *shaft* and fused serrated *alae*; the alae may be also claw-like (e.g., *lophon unicorne*, *l. timidum*) (Figure 3.21).

Birotula(te)/e–D.; a *microsclere* characterized by a *shaft* with discoidal or anchorate ends (e.g., genus *lotrochota*); compare with *amphidisc* (Figure 3.2).

Bistellate-see amphiaster.

Bogen-not in use; see toxa.

# 4.1.3 | C

Calt(h)rop—called rarely chelotrop; D., Ho.; a symmetrical *tetractin* with four rays of equal length not situated in the same plane and with the angle of 120° between each ray (e.g., *Dercitus bucklandi*, genus *Calthropella* and several genera of Ho.) (Figures 5.1–3 and 12.9–15).

Calycocom(e)—H.; a stellate *discohexaster* with *secondary rays* distributed in close tufts; unlike in *lophodiscohexaster*, the secondary rays are not numerous and primary rays are widened distally to a calyx-like structure (e.g., genus *Rossella*) (Figure 9.32).

Canalaria (pl.)–H.; spicules associated with or usually lining canals (e.g., genus *Semperella*), often similar to *dermalia*.

Candelabrum (pl. Candelabra)—Ho.; a heterolophose *calthrop* with branched rays and usually with one, more developed upper ray (diagnostic trait of single Ho. genus *Corticium*) (Figure 12.15).

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Canon(o)chela–D.; a modified derivative of *(iso)chela* with *alae* fused together (e.g., *Isodictya lankensteri*); compare with *cercichela* (Figure 3.25).

Centrangulate spicule—any monaxonic spicule possessing sharp bend in the middle of the spicule, for example, *centrangulate (micro) oxea* (e.g., genus *Plakortis*), *c. sigma*; compare with *thraustoxea* (Figure 3.30).

Centrotylote oxea-D.; an *oxea* possessing median swelling/tyle (e.g., genus *Polymastia*) (Figure 2.23).

Centrotriaene–D.; a *triaene* with three *clads* and shorter *rhabds* (e.g., genus *Triptolemma*); *c*. include *mesotriaenes* and *mesocalthrops* (Figure 5.4).

Cercichela—D.; a modified derivative of *chela* in which *alae* fuse together (e.g., *Cercicladia australis*); very similar in shape to *canonochelae* but in contrast to them, *c*. are microacanthose; compare also with *clavidisc* (Figure 3.26).

Chela—rarely called amphichel; D.; a *microsclere* with curved *shaft* and recurved *alae* or teeth on each end (e.g., Poecilosclerida); it can be, for example, *iso-*, *naviculi-*, diastropho-, *sigmoid* (Figure 3.2–18, 31).

Chelotrop-invalid term, see *calthrop*.

Chessman spicule-see acanthodiscorhabd.

Chiaster-see strongylaster.

Chiactine–C.; a *tetractine* in which the *apical actine* is almost perpendicular to the basal triradiate system, curving to the opposite direction of the unpaired actine ("cruciform" spicules) (e.g., family Achramorphidae) (Figure 11.18).

<sup>†</sup>Chiastoclone–DL.; a *desma* resembling a *dendroclone* but with a very short central *shaft* (e.g., fossil suborder Orchocladina).

Chiastosigma–D.; a microsclere composed of two crossed sigmas (e.g., genera Acanthancora, Hymenancora, Chiastosia) (Figure 3.34).

Cladotoxa–D.; a monaxonic *microsclere* with hook-like *clads* at the end of a bent (sometimes spinose) *shaft* (e.g., *Acanthoclada prostrata*); compare with *cladotylote* (Figure 7.12)

Cladotylote—D.; a *monaxon* with smooth or spined *shaft*, with one end provided with three or four (exceptionally five) large hooks and the other end provided with a thick smooth knob or with smaller hooks (e.g., genus *Acarnus*) (Figure 7.16).

Clavidisc—D.; an oval, ring-shaped *microsclere* with small indents at the inner side of the ring (e.g., genus *Merlia*); not circular but rather droplet-shape in any orthogonal section (excluding the idents); *c*. are fused C-formed spicules (e.g., *diancistras*); compare with *cercichela* (Figure 3.24).

Clavule—H.; a *sceptrule* with one terminal *umbel* (anchorate) or discoidal head (e.g., genus *Farrea*); *c*. may be anchorate; unlike *tylodisc*, *c*. are megascleres (Figure 10.2).

Cleistochela—D.; a palmate (*iso*)*chela* with the anterior *alae* nearing or touching and provided with an inward directed plate-like extension of the *shaft* partially or entirely filling the space between the shaft and the anterior *alae* (e.g., common in Microcionidae); compare with *naviculichela* (Figure 3.22).

Codondiactin-see amphidisc.

Codonhexaster—H.; a *hexaster* with umbel-shaped and anchorate ray tips (e.g., *Chaunoplectella megapora*) (Figure 9.34).

Codonhexactin—H.; a *hexactin* with long ray ended with umbellike projections; in contrast to *discohexactin* with discoidal rays, same to *discohexactin* with anchorate discs (e.g., genus *Bolosoma*, *Advhena magnifica*) (Figure 9.11).

Coelodischela-see dischela.

Collosclere–D.; probably derivation of a *chelae*; a sclere entirely enveloped in a siliceous thin coat (e.g., *Clathria* [*Thalysias*] *collosclera*) (Figure 3.50, 51).

Comitalia (pl.)—H.; accessory spicules closely associated with principalia (e.g., Euplectella aspergillum).

Comma (pl. commata)–D.; a comma-shaped *microstyle* (e.g., *Biemna omanensis*) (Figure 3.43).

Cricophalangaster—other name for anisodiscorhabd; see discorhabd.

<sup>†</sup>Cricorhabd–D.; a *rhabd* with annulate ornamentation and swollen, usually spined and slightly asymmetric apices; homology is associated either with Recent *anisodiscorhabd* or *didiscorhabd*.

Croca-D.; a J-shaped microsclere (e.g., subgenus Antho [Jia]) (Figure 3.40).

Cuspidate—H.; a spiny nonuncinate megasclere of Pheronematidae; a type of *sceptre* likely originated from *uncinate* with several enlarged spines on one end (e.g., *Platylistrum platessa*).

Cyrtancistra-D.; a *sigma* with semilanceolated endings; it is considered related to/a reduced form of *diancistra* (e.g., genus *Pozziella*) (Figure 3.35).

## 4.1.4 | D

†Dendroclone–DL.; a *desma* with long central *shaft* and branched ends; term used in fossil lithistids (e.g., fossil suborder Orchocladina) (Figure 8.9, 10).

Dermalia (pl.)—H.; spicules associated with the dermal surface of a sponge body (e.g., family Euplectellidae).

Desma–DL.; any choanosomal, more or less irregular *megasclere* of DL. that is articulated (rarely unarticulated) with other spicules of the same type; *d*. may be anaxial, polyaxial, monaxial, or tetraxial and include e.g., *dicrano-*, *rhizo-*, *sphaero-*, *mega-*, *tetraclone* (Figures 8.5, 7, 15).

Deuteroclad-see dichotriaene.

Diact(in(e)—C., D., H., Ho.; any spicule with two diverging rays; *d*. may be monaxonic (e.g., *oxeas*, *strongyles*, *diods*) or be reduced forms of *calthrops*, *triods*, *tetraxons* or *hexacts*; in C. spicule similar to *oxeas* of D. but with two *actines* (at least the initial growth is bidirectional); the tips in *d*. can be identical or not (Figures 6.1–17, 7.7–10, 10.7 and 11.13, 14, 17).

Diaene–D.; a *triaene* with number of *clads* reduced to two; for example, *pro-*, *anadiaene* (part of a series: -triaene, -diaene, -monaene) (e.g., *Cinachyrella apion*) (Figure 4.26, 27).

Diancistra-D.; a *microsclere* with hook, knife-shaped ends, notched where they join the *shaft* (e.g., genus *Hamacantha*); compare with *cyrtancistra* (Figure 3.23).

Diapason—called also tuning-fork spicule; C; a *triactine* with paired *actines* parallel to each other, as they are opposite to the unpaired one (e.g., *Murrayona phanolepis*) (Figure 11.12).

Diaster—H.; a *diactin* with astrose outer ends (e.g., genus *Aphrocallistes*); it can be, for example, *disco-* or *onychodiaster*; compare with demosponge *amphiaster* and *diplaster* (Figure 10.15).

Dichotriact-see streptosclere.

Dichotriaene–D., DL.; a *triaene* with dichotomously divided *clads* (e.g., genus *Thenea*) (Figures 4.5, 7–10, 13, 17, 23, 25 and 5.6, 7, 10).

Dichocalthrop–D.; a *calthrop* with dichotomously divided clads/ rays (e.g., *Dercitus* (*Stoeba*) *lesinensis*); often confused with *dichotriaene* (Figure 5.3).

Dicranoclone–DL.; an anaxial arched *desma* bearing well developed tubercles (e.g., family Corallistidae) (Figure 8.11–13).

Dictyonalia (pl.)—H.; rigid frameworks of choanosomal spicules or *principalia* that originated from fused *hexactins* (in Sceptrulophora, Lychniscosida and likely Fieldingiidae); often growing as dictyonal strands, otherwise from simple spicule fusion.

Didiscorhabd—D.; a *microrhabd* equipped with two or more similar discs along the *shaft* (e.g., genus *Didiscus*); compare with *trochi*- and *discorhabd* (Figure 2.32).

†Didymoclone–DL.; a *desma* resembling two *sphaeroclones* united by a horizontal *shaft*; clones directed downwards (e.g., Late Jurassic genus *Cylindrophyma*) (Figure 8.20)

Diloph-see dilophose calthrop.

Dilopho(u)s(e) calthrop–Ho.; a *lophocalthrop* with two rays dichotomous to polytomous (e.g., *Plakina corticioides*); compare with *mono-*, *tri-*, and *tetralophose c*. (Figure 12.16).

Diplospinorhabd-see spinorhabd.

Diod—Ho.; a *diactine* with a central kink; *d*. (and triods) of various sizes may develop from reduced calthrops; *d*. may be lophate (e.g., genera *Plakinastrella*, *Plakortis*, *Placinolopha*, *Plakina*); see also *lophodiod* (Figure 12.1, 3, 4).

Diplaster–D.; an astrose *microsclere* in which *rays* or spines radiate from two near points; compare with *amphiaster* and *diaster* (e.g., genera *Placospherastra*, *Diplastrella*) (Figures 2.11, 12).

Disc-see umbel.

Dischela—D.; a *chela* composed of two *alae*, which are parallel, disc-shaped, and concave on the inside (usually with an aperture/ s in the center of the ala) connected with each other on their margins by short pillar-like *shafts* (e.g., genus *Coelodischela*) (Figure 3.30).

Discaster–H.; like a *discohexaster* but with *primary rays* subsumed into the expanded and common siliceous center (e.g., genus *Nodastrella*) (Figure 9.31).

Discodiactin-see amphidisc.

Discoctaster—H.; a stellate discoidal *microsclere* (*octaster*) with more than six (usually eight) *primary rays* in which *secondary rays* (rarely one) are situated in close tufts (similar to *calycocome*) (e.g., *Acanthascus* [*Staurocalyptus*] *dowlingi*) (Figure 9.17).

Discohexact(in)—H.; a hexact(in) with discoidal ends (e.g., Calyptorete ijimai, Crateromorpha [Neopsacas] krinovi) (Figure 9.14).

Discostauractin-see tetradisc.

Discohexaster—H.; a discoidal *hexaster* with numerous thin and long *secondary rays*; the *primary rays* are well distinguished (e.g., *Aspidoscopulia bisymmetrica*) (Figure 9.11, 17, 18).

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Discoplumicome-see disco- and plumicome.

Discorhabd—called also sceptrum; D.; a rod-shaped *microrhabd* bearing several similar discs (usually serrated) situated along the *shaft*; frequently with unequal tips (anisodiscorhabd), or additional apical projection (aciculodiscorhabd) (e.g., family Latrunculiidae); other derivatives of *d.* are, for example, isospinodiscorhabd or isochiadiscorhabd; compare with *trochi-*, *didiscorhabd* (Figure 2.1, 2).

Discostauractine—H.; in Hexasterophora a *microsclere* consisting of four *rays* with discoidal outer ends; compare with *tetradisc* of Amphidiscophora (Figure 9.9).

Discotauactine–H.; a three-rayed *diaxon* with *rays* situated in a single plane, with disc-like ends (e.g., *Bolosoma meridionale*); see *tauactine* and *discostauractine*.

Discotriaene–DL.; an ectosomal *triaene* with tangential discshaped (flat or slightly concave or convex) *cladome* with a tetraxial axial canal (e.g., family Theonellidae); see also *pseudodiscotriaene* (Figure 5.15, 16).

Dragma–D.; a bundle of *microscleres*; there can be, for example, *sigmo-*, *toxo-*, or *trichodragma* (Figure 2.21).

Drepanocome-H.; a *hexaster* with sickle- or hook-like *secondary rays* terminal that are situated on six *primary rays* (e.g., genera *Saccocalyx*, *Dictyaulus*); in some cases hardly distinguished from *sigmatocome*, which have smaller *sigma*-like *secondary rays* and *springohexaster* whose secondary rays are differently curved (Figure 9.33).

# 4.1.5 | E

Euaster–D.; every astrose *microsclere* in which the rays radiate from the spicule center; *e*. are, for example, *oxyasters*, *oxyspherasters* and *anthasters*; see also *aster* (Figure 1.22–24, 26).

Exotyle–D.; a (*tylo*)*style* possessing ornamented or enlarged distal end (e.g., *Mycale* [*Rhaphidotheca*] *loricata*); see also *spherostyle* (Figure 7.18, 19).

# 4.1.6 | F

Fibul(a)—H.; a microsclere consisting of two bent rays derived from greatly reduced oxyhexaster (e.g., Holascus fibulatus); compare with sigma and sigmaspire (Figure 10.16).

Flexuous oxea–D; an (*aniso*)oxea of a wavy shape (e.g., genera Monocrepidium and Bubaris) (Figure 7.3-5).

Flexuous strongyle–D.; an (*aniso*)strongyle of a wavy shape (e.g., genus *Bubaris*) (Figure 7.1, 6).

Floricome—H.; a specific type of *discohexaster* with rather thick sshaped *secondary rays* ended with a plate provided with teeth, claws, or in other words *secondary rays* carrying asymmetrical discs (e.g., *Malacosaccus coatsi*) (Figure 9.30). WILEY-morphology

Forceps—called also labis; D.; an U-shaped microsclere (e.g., genus Forcepia) (Figure 3.44, 45).

Fusiform oxea—D.; an *oxea* tapering regularly toward both ends (e.g., *Asteropus arenosus*) (Figure 6.8).

Fusiform (tylo)style–D.; a (tylo)style tapering regularly toward one end (e.g., *Spheciospongia tentorioides*) (Figure 6.27).

# 4.1.7 | G

Gastralia (pl.)-see atrialia.

Gemmulosclere–D.; spicules forming the case (armor) of gemmules; in freshwater sponges (e.g., genus *Ephydatia*) (Figure 7.22–25).

Graphicom(e)—called also graphi(o)hexaster; H.; an *oxyhexaster* in which the *secondary* oxyoidal *rays* are very numerous, situated in close tufts; during spicule preparations *primary rays* and tufts of secondary rays are found almost always separately (e.g., *Waltheria flemmingi*) (Figure 9.35).

Graphi(o)hexaster-see graphicome.

Grapnel—C.; a *triactine* or *tetractine* with reduced paired or basal actines (respectively) and long unpaired or *apical actines* (respectively); they can be present in the atrium (e.g., *Leucandra rudifera*) or at the base, helping to attach the sponge to the substrate (e.g., *Sycon ancora*) (Figure 11.16).

#### 4.1.8 | H

Harpoon-like tetractine-see pugiole.

Helicographiocome-see pappocome.

Heloclone–DL.; an elongated monocrepidial *desma* with sinuous *shaft*, no branches, and *zygomes* as lateral notches; axial canal usually present along the whole desma length (e.g., family Isoraphiniidae) (Figure 8.19).

Hemidisc-H.; an amphidisc with umbells of different size (e.g., Pheronema raphanus, fossil genus Microstaurella minima).

Hemioxyhexaster—H.; an oxyhexaster with some primary rays which carry one secondary ray (e.g., Euplectella sanctipauli) (Figure 9.25).

Hemiuncinate—H.; a *monaxon* with finely pointed outer end, and the opposite one rounded with one to several spines; the *shaft* is covered by small spines which are directed towards the rounded outer end; compare with *uncinate* and *ambuncinate* (e.g., *Hyalonema* [*Hemiuncinata*] comanchei).

Hexact-see hexactine.

Hexactin(e)—called also hexact; H.; a spicule with six unbranched *rays*/triactinal symmetry, perpendicular to one another (e.g., *Hyalonema* [*Hyalonema*] *proximum*); building block of dictyonal framework in Hexactinosida; in *h*. microscleres, it can be, for example, *oxy-*, *discohexaster* (Figure 9.13, 14, 16).

Hexadisc-H.; a microsclere consisting of six rays with discoidal outer ends spicule with discoidal outer ends; compare with *tetradisc*.

Hexaster–H.; a *microsclere* with six branched *rays* (e.g., genus *Dictyaulus*) (Figure 9.18, 20, 21).

Hypodermalia (pl.)—H.; spicules which supplement *dermalia* and which are notably larger than the latter; with one *ray* protruding inside the body; the other rays situated in the dermal plane; the tangential rays may be situated over the dermal surface.

Hypogastralia (pl.)—H.; spicules analogous to *hypodermalia* but connected with atrial surface; with one *ray* protruding inward; the other rays situated in atrial plane.

# 4.1.9 | |

Intermedia (pl.)–H.; *parenchymalia* situated among *principalia* or *dictyonalia*.

Isochela-D.; a *chela* with equal ends (*alae*) (e.g., *Esperiopsis koltuni*) (Figure 3.3-10).

# 4.1.10 | K

†Kyphorhabd—a thick, monaxial, curved spicule with inner side concave and weakly sculptured or smooth; outer side is convex and regularly covered with semi-annular ridges; articulation weak at the tips (e.g., Jurassic demosponge genus *Helminthophyllum*) (Figure 7.14).

# 4.1.11 | L

Labis-see forceps.

Lateralia (pl.)-see prostalia.

Lophocome-see lophodiscohexaster.

Lonchiole—H.; a monaxon with a single tine or a distal ray (in contrast to sarule and scopule which have more than one tine) or a diactin with rays of significantly different length (e.g., Lonchiphora ijimai, Lonchiphora antarctica).

Lopho(u)s(e)calt(h)rop—Ho.; a *calthrop* with lophate-ended *rays*; prefixes mono-, di-, tri-, and tetra- show how many rays of the *l. c.* are lophate, for example, *mono-* (e.g., genus *Placinolopha*), *tetralophose calthrop* (e.g., *Plakina kanaky*) (Figure 12.10–13).

Lophocome-see sigmatocome.

Lophodiod-Ho.; a lophate-ended *diactin* (e.g., *Placinolopha spinosa*) (Figure 12.2, 3).

Lophodiscohexaster—H.; a *discohexaster* with thin and usually numerous *lophate secondary rays* (e.g., *Hexactinella carolinensis*) (Figure 9.18).

Lophotetract—Ho.; a lophate-ended *tetractin*; compare with *tetraloph* (Figure 12.15, 16).

Lophotriaene–Ho.; a *triaene* with branched tips (like a *candelabrum*), one branch being longer than the others (e.g., *Corticium candelabrum*) (Figure 12.12–15).

Lychnisc—H.; a *hexactin* with a center that resembles a perforated octahedron; *l*. is building block of fused dictyonal framework in Lychniscosida and never observed separately from the dictyonal skeleton (Figure 8.22–24).

Lyssacine—H.; a spicular framework formed by loose spicules: *hexactins* and their derivatives up to *diactins* (e.g., family Euplectellidae).

# 4.1.12 | M

Macramphidisc-H.; a large *amphidisc* (e.g., *Monorhaphis chuni*) (Figure 10.19, 20).

Marginalia (pl.)—called also oscularia; H.; prostalia forming a fringe around main osculum (e.g., Pheronema carpenteri).

Megaclone—DL.; an arch-shaped *desma*, usually branched with two to four arms directed downward; may be smooth or more rarely tuberculate (with an uneven surface), with short monaxial *crepis*; *zygomes* terminal (articulating with lateral and/or upper part of other *m*.; articulation "hand to shoulder") (e.g., family Pleromidae); *m*. form articulated skeleton (Figures 8.4, 5).

Megasclere–D., H.; a generally large spicule; rather variable in form, but not as much as microscleres; usually with a structural role in sponge architecture/anatomy; compare with *microsclere*.

Megaster—D.; a type of astrose *microsclere* of exceptionally large size (e.g., *Tethya seychellensis*) (Figure 1.21).

Melonchela—see sphaerancora.

Meniscoid—every microsclere derived from *sigma* (e.g., *chela*, *diancistra*, *bipocilla* etc.).

Meso(dicho)triaene–D.; a (*dicho*)triaene with rhabd extended beyond the *cladome* (e.g., genus *Pachataxa*) (Figures 4.18 and 5.6, 7).

Mesotrider-DL.; an articulated *desma*-like spicule based on *mesotriaene* geometry (e.g., genus *Brachiaster*); compare with *trider* (Figure 8.21).

Metaster—D.; a microsclere with a short twisted shaft and longer spines; intermediate form between *plesiaster* and *spiraster* (e.g., genus *Sphinctrella*) (Figure 2.16).

Micraster–D.; a smaller type of *aster* in the family Tethyidae, which may be *tylaster*, *strongylaster* or *oxyaster* (Figure 1.29).

Microdiactine–C.; a small *diactine*, which can be fusiform or have different tips (e.g., *Leucandra globosa*) (Figure 11.17).

Microdichocalthrop-see micro-, calthrop, and dichocalthrop.

Microholactin—see microhexactine.

Microparadisc-see paradisc.

Microrhabd—D., Ho.; a diactine microsclere (e.g., genus Theonella, Plakinastrella globularis); see rhabd (Figure 2.23, 24).

Microsclere—D., H.; a generally small spicule attributed to this type; *m*. usually do not form the main architecture of the skeleton but appear auxiliary; compare with *megasclere*.

Microsphere—H.; a small globular microsclere that may have a lumpy or smooth surface (e.g., *Malacosaccus microglobus*); in D. and Ho. usually called *sphere* or *spherule* (Figure 1.14).

Microstrongyle—called also bacillus (not in use today); D.; a strongyle microsclere (e.g., Erylus niger); m. can be centrotylote (e.g., Suberites ficus) (Figure 2.29).

Microtriod—Ho.; a *triod* microsclere derived from (*micro*)*calthrop* (e.g., *Plakinastrella clippertonensis*) (Figure 12.5).

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Microxea–D., DL.; an oxea microsclere (e.g., Petrosia [Petrosia] microxea) (Figure 2.27).

Monact(ine)–D., H.; any one-rayed spicule; the ray grows from one end only and possesses ends fundamentally different in form, for example, *style*, *tylostyle* (Figure 6.18–34).

Monaene–D.; reduced *triaene* with only one *clad* (e.g., family Tetillidae) (Figure 4.24).

Monaxon—any spicule with one axis (or *ray*) and a central canal; *m*. include both *mono-* and *diactinal* spicules, for example, *oxea*, *style*, *strongyle*.

Monoloph-see monolophose calthrop.

Monolopho(u)s(e) calthrop—Ho.; a *calthrop* with one ray dichotomous to polytomous (e.g., *Plakina corticioides*); compare with *tetra*-, *tri*-, and *dilophose c* (Figure 12.11).

Mycalostyle–D.; a (*sub*)(*tylo*)*style*, usually more or less fusiform in shape, with faintly constricted neck and/or faintly swollen *tyle*; characteristic for families Mycalidae and Cladorhizidae (e.g., *Chondrocladia* (*Meliiderma*) *turbiformis*) (Figure 6.26).

# 4.1.13 | N

Nail-shaped spicule—C.; a *triactine* or *tetractine* with tiny, reduced, paired or basal (when tetractine) actines contrasting with the very long unpaired or apical actine (e.g., genus *Kebira*) (Figure 11.11).

Naviculichela–D.; a modified *anisochela* in which the upper and lower frontal *alae* are fused and the *shaft* develops a plate-like extension filling in the space between shaft and alae (e.g., genus *Mycale* [*Naviculina*]) (Figure 3.16, 17, 31).

Needle-like diactine—C.; a *diactine* with a hole near one of the tips (e.g., *Kuarrhaphis cretacea*).

# 4.1.14 | O

Octaster—H.; a *microsclere* with eight primary-like *rays* originated from a *hexaster* with a fusion of six *primary rays* in a common center to *aster*, giving rise to usually eight pseudo primary rays; terminal rays project from these; usually *secondary rays* have discoidal outer ends (*discoctaster*); rarely they are oxyoidal (e.g., genus *Acanthascus*) (Figure 9.17).

Onychaete(a)—D.; a thin monaxonic *microsclere* with small spines (most frequently looking like barbs) that are gradually suppressed at the thinner end, and usually with a discernible subterminal swelling (e.g., *Tedania* [*Tedania*] *strongylostyla*) (Figure 7.2).

Onychaster-see onychohexactine and onychohexaster.

Onychodiactin(e)-see onycho- and diactin.

Onychodiaster-H.; see onycho- and diaster (e.g., Regadrella phoenix) (Figure 10.15).

Onychohexaster—H.; a *hexaster* with onychoidal *secondary ray* terminals (anchorate and with claws partially or wholly bent inwardly)

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(e.g., Crateromorpha [Neopsacas] variata, Gymnorete alicei) (Figure 9.10).

Onychohexactin(e)–H.; a *hexactine* with onychoidal secondary ray terminals (anchorate and with claws partially or wholly bent inwardly) (Figure 9.24).

Orthotriaene–D., DL.; a *triaene* in which the *clads* are directed at right angles to the *rhabd* (e.g., *Geodia rex*) (Figure 4.7–12).

Oscularia (pl.)-see marginalia.

Oxyaster–D.; an *euaster* with long pointed *rays* that are longer than two-thirds of the total diameter (e.g., *Jaspis johnstonii*) (Figure 1.23, 24).

Oxea—rarely called amphioxea; D.; a *monaxon* (diactinal); usually a symmetrical spicule pointed at both ends (e.g., genus *Xestospongia*); o. may be *acantho-*, *tricho-*, angulate, asymmetrical, *centrotylote*, curved, *flexuous*, *fusiform*, or polytylote; the tips can be *acerate*, *asymmetrical*, *blunt*, *conical*, *hastate*, *mucronate stepped*, or *symmetrical* (Figures 6b–h, 7–16 and 7.7, 9, 10, 15).

Oxyhexaster—called also holoxyhexaster; H.; a *hexaster* with *rays* tapering to a point (e.g., *Hexactinella carolinensis*) (Figure 9.22, 23, 26). Oxystauraster—see oxy- and *stauraster*.

Oxysph(a)eraster—D.; an *euaster* with centrum that is more than one-third of the total diameter (e.g., *Tethya seychellensis*); compare with *spheroxyaster* (Figure 1.22).

Oxytylote-unused term for a spicule shaped like a common pin.

## 4.1.15 | P

Parasagittal spicule—C.; an equiangular *triactine* with the *unpaired actine* longer than the *paired actines* (e.g., *Paragrantia waguensis*) (Figure 11.10).

Palmate (an)isochela–D.; a chela with lateral alae at each end fused with shaft by its longer dimension and the anterior alae standing free (e.g., Amphilectus ovulum and genera Mycale and Clathria); see also arcuate and anchorate chela (Figure 3.13–15).

Pappocome—called also trichaster/helicographicome/lophohexaster; H.; a graphicome-like hexaster with long secondary rays arranged in broadly radiating brushes unlike graphicomes (e.g., genus Trichasterina).

Paraclavule-see tylodisc.

Paradisc—H.; an *amphidisc* with umbels placed asymmetrically, in contrast to umbels in amphidisc (e.g., *Pheronema raphanus*) (Figure 10.17).

Paratetractin(e)—H.; a four-rayed *triaxon* with two rays in one axis and the other two perpendicular to them (e.g., *Euplectella paratetractina*) (Figure 10.14).

Parenchymalia comitalia (pl.)–H.; accessory spicules physically associated with *principalia*; see *comitalia*.

Parenchymalia intermedia (pl.)—H.; microscleres or accessory spicules of choanosomal skeleton found among principalia and/or dictyonalia; see intermedia.

Parenchymalia principalia (pl.)—see *principalia*. Pearl—see *sphere*. Pentact(ine)—C., H.; five-rayed spicule; in. C. it can be a basal *triactine* with a bifurcated apical actine or a basal *tetractine* with an apical actine (e.g., *Sycon pentactinalis*); in H. a *triaxon* with perpendicular *rays* (e.g., *Staurocalyptus dowlingi*); see also *pinule* (Figures 9.1–4 and 10.13).

Pentadisc—H.; a *microsclere* consisting of five *rays* with discoidal outer ends (e.g., *Trychella kermadecensis*); compare with *tetradisc* (Figure 10.22).

Pentaster-H.; see pentactine and aster (e.g., genus Farrea).

Phyllotriaene—DL.; a *triaene* with a leaf-shaped, irregular, or branching *cladome* and one *ray* called *rhabdome*, usually perpendicular to the sponge surface and penetrating it (e.g., family Theonellidae) (Figure 5.11–13).

Pile(a)te clavule—H.; a *clavule* with a pileate disc on one end (e.g., *Aspidoscopulia bisymmetrica*) (Figure 10.2).

<sup>†</sup>Pinakid—a flat, elliptical, disc-shaped spicule of unknown origin; with various peripherally arranged gaps (that can be marginally open), sometimes with several radial canals (Figure 7.20).

Pinular hexactine—sometimes called pinule; H.; a *hexactine* with one ray having a fir-tree shape (e.g., *Aphrocallistes vastus*) (Figure 9.6, 7).

Pinular pentactine—sometimes called pinule; H.; a *pentactine* with one *ray* having a fir-tree shape (e.g., *Pheronema raphanus*) (Figure 9.5).

Pinule-see pinular hexactine and p. pentactine.

Placochela–D.; an *isochela* with internally ornamented *alae* and *shaft*; alae are plate-like (e.g., genus *Guitarra*); compare with *dischela* (Figure 3.27–29).

Plagiotriaene–D., DL.; a *triaene* with *clads* directed forward and forming an angle of about 45<sup>°</sup> with the *rhabd* (e.g., *Ecionemia solida*) (Figure 4.13–15, 17, 19).

Plesiaster-D., DL.; a spiny streptaster with very short shaft and usually smaller number of rays (e.g., genus Thenea) (Figure 2.15).

Pleuralia (pl.)-see lateralia.

Plumicome—H.; an oxyoidal *hexaster* with sigmoidal *secondary rays* situated on the edge of the discoidal outer end of the *primary ray* (e.g., *Chaunangium crater*); *p*. with snake-like *secondary rays* emanating from the edge of a shield-like disc in a single whorl of *primary rays* is called aspidoplumicome (e.g., *Saccocalyx careyi*); see *strobiloplumicome* (Figure 9.25, 28).

Polyact(ine)—called also polyaxon; D.; a radiate spicule with two up to six *cladi* or actines; in amphipolyactines the number of cladi can vary between five and ten (e.g., *Cyamon amphipolyactinum*) (Figures 5.20–22 and 7.21).

Polyaxon-see polyactine.

Polytylote—D.; a megasclere with two or more annular swellings along the *shaft* (e.g., *Sphaerotylus bouryesnaultae*); compare with *tylote* (Figure 6.28).

Polyspire-see spirula.

Principalia (pl.)—H.; main spicules of choanosomal skeleton; form the principal component of skeletal support; include also *dictyonalia* (e.g., *Rossella antarctica*).

Prodiaene–D.; a reduced *protriaene* with only two *cladi* (e.g., *Cinachyrella arabica*) (Figure 4.26, 27).

Promonaene–D.; a reduced *protriaene* with only a single *clad* (e.g., *Isabella mirabilis*) (Figure 4.24).

Prostalia (pl.)—called also supradermalia; H.; spicules whose parts protrude outside the sponge body; distinguished to: *basalia*, *lateralia*, and *oscularia*.

Protriaene—D.; a *triaene* with *clads* directed (or sharply curved) forward, away from the *rhabd* (e.g., *Cinachyrella arabica*) (Figure 4.16, 20–23, 25).

Pseudo(eu)aster—D.; a nonastrose *microsclere* approaching the shape of an (*eu*)*aster* (e.g., *Crambe talliezi*, genus *Pseudoastrella*) (Figure 1.32).

Pseudobirotule–D.; a *microsclere* of similar morphology to *birotule* characteristic for freshwater sponges (e.g., *Corvoheteromeyenia* heterosclera) (Figure 7.22).

Pseudodiscotriaene—DL.; an ectosomal *megasclere* resembling a *discotriaene* but monaxial with the axial filament located in the *rhabd* or *cladome* (e.g., genus *Neopelta*) (Figure 5.17).

Pseudolophose spicule—Ho.; a spicule with 2–4 actines ramifying in 2–8 conical fused *rays* (e.g., *Plakinastrella pseudolopha*) (Figure 12.17).

Pseudophyllotriaene—DL.; an ectosomal spicule closely resembling a *phyllotriaene* but being monaxial, with crepis located in the *rhabd* or *cladome* (e.g., genus *Sollasipelta*) (Figure 5.14).

Pseudotetraclone—DL.; a monaxial *desma* with elongate *clones* resembling *tetraclone* or *rhizoclone* (e.g., *Macandrewia spinifoliata*) (Figure 8.16).

Pseudosagittal spicule—C.; a subcortical *triactine* or *tetractine* whose paired actines have different lengths; besides, the cortex is supported by the shortest *paired actine* and the *unpaired actine*, while the longest paired actine penetrates the choanosome (e.g., *Grantessa borojevici*) (Figure 11.4).

Pseudospheraster—DL.; a *microsclere* with slightly eccentrically projecting massive spiny *rays* and a swollen centrum, that resembles *spheraster* but is most probably a modified *amphiaster* (e.g., *Manihinea lynbeazleyae*) (Figure 1.31).

Pugiole—called also dagger-like tetractine or harpoon-like tetractine; C.; a *tetractine* whose apical actine is opposed to the *unpaired* one, that is, the four actines are in the same plane (e.g., *Petrobiona massiliana*) (Figure 11.22).

Pycnaster–D.; a *spheraster* in which the rays are merely low conules, usually densely arranged on the spicule surface and with indistinct bases (e.g., *Geodia cylindrica*) (Figure 1.15).

# 4.1.16 | Q

Quadriradiate-C.; synonym of tetractine; compare with calthrop.

# 4.1.17 | R

Raphide—called also trichite; D., DL.; a *rhabd* or an *oxea*, sometimes wavy, sinuous, or toxiform; may occur in bundles called *trichodragma*;

*r*. occur, for example, in some lithistids with rhizoclone *desmas*. Figure 2.26

Regular spicule—C.; a triactine or tetractine spicule with basal rays of equal length, and with equal angles (120°) between them, when projected onto a plane perpendicular to the optic axis (e.g., *Clathrina clathrus*, *Ernsta tetractina*) (Figure 11.2).

Rhabd(o(sclere))—D.; any monaxonic spicule; see also, for example, micro-, disco-, stylo-, acantho-, cricorhabd; see also rhabd (ome) in general spicule terms.

Rhabdodiactin(e)—H.; to be rejected; a two rayed *monaxon*, usually all *diactines* of hexactinellids fall within the definition.

Rhabdodragma-see trichodragma.

Rhabdostyle-D.; a *style* with strongly curved basal end; the basal/upper part may be spirally curved (e.g., genus *Rhabderemia*, *Raspailia* [*Raspaxilla*] *hymani*) (Figure 6.22).

Rhizoclone–DL.; an anaxial irregular *desma*, usually with numerous spines and or/pointed tubercles which serve as *zygomes* (mostly lateral) (e.g., family Azoricidae, rhizomorine lithistids) (Figure 8.6–8).

Rosette—D., H.; in D. a regular globular arrangement of *palmate* (*an*)*isochelae* (e.g., subgenus *Clathria* [*Cornulotrocha*] and genus *Mycale*) and star-shaped pattern on the surface of *sterrasters* and *aspidasters*; in H. a central portion of microsclere *hexasters*, *hexactins* (and their derivatives) is called primary rosette (e.g., *Rossella antarctica*) (Figures 3.1 and 9.30).

# 4.1.18 | S

Sagittal spicule–C.; a *triactine* or *tetractine* with two equal (paired) angles and one dissimilar (unpaired) angle at the center, when projected onto a plane perpendicular to the optic axis (e.g., *Sycon ciliatum*) (Figure 11.3).

Sanidaster—D.; a *microsclere* with spines along the straight *shaft* (e.g., *Disyringa dissimilis*); the spines may be or may not be spirally arranged; in freshwater sponges there are sanidasters gemmulo-scleres (e.g., *Corvoheteromeyenia sanidosclera*); s. can be *verticillate* (Figures 2.33 and 7.15).

Sarule—H.; a *sceptrule* with tuft of spines (tines) emanating from the top of the head (e.g., genus *Sarostegia*) (Figure 10.6).

Scale–C., D.; in D. a flat, half-oval, disc-shaped *microsclere* (e.g., genus *Lepidosphaera*); in C. a *triactine* whose actines are not well individualized, giving it the appearance of a circular or almost circular spicule (e.g., family Murrayonidae) (Figure 11.20).

Scepter–H.; a *monaxon* with partly spiny shaft acerated at central or apical tip, which is also partly ornamented with short conical spines (e.g., family Pheronematidae) (Figure 10.10).

Sceptrule—H.; a special *monaxon* with secondary developments *tines* at one end (e.g., many Hexactinosida); for example, *scepter*, *scopule* (Figure 10.2–6).

Sceptrella—see *sanidaster*, *discaster*; also a genus within Latrunculiidae.

Sceptrum-see discorhabd.

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Scopule—H.; a fork-like *sceptrule* with few (usually three to four) *tines* extending from the head (e.g., *Aphrocallistes vastus*); see *aspidoscopule* (Figure 10.3–5).

Selenaster—called also sterrospira; D.; a large spherical, kidneyshaped or ellipsoidal monaxial *microsclere* with numerous, irregular short *rays* and/or the rounded-polygonal (usually triangular) plates between the grooves (e.g., genus *Placospongia*); *s.* is monaxial; often confused with *sterrasters* (Figure 1.1–3).

Sigma—called also bihamate (not in use today); D.; a C- or S-shaped *microsclere*, usually smooth (e.g., genus *Mycale*); the ends of a *s*. may be equipped with an external serration (e.g., serrated sigma of subgenus *Mycale* [*Paresperella*] *serrulata*) or microspination (e.g., genera *Biemna*, *Neofibularia*, *Sigmaxinella*); s. can be flagellated (e.g., *Mycale* [*Naviculina*] *diversisigmata* and subgenus *Haliclona* [*Flagellia*]); compare with *anthosigma* (Figure 3.37–39).

Sigmancistra–D.; a modified *sigma* with droplet-like orthogonal section (e.g., genus *Cladorhiza*) (Figure 3.36).

Sigmaspire–D.; a C- or S-shaped often microspined *spirosclere* (e.g., family Scleritodermidae and Spirophorina: Tetillidae, Samidae); compare with *spirosigma(ta)* (Figure 3.49).

Sigmatocom(e)—called also lophocome, tylfloricome; H.; a *hexa-ster* with sigmoidal, s-shaped, or aspid-like *secondary rays* (arranged in a single circle on each *primary ray*), which are similar in size to those of *strobiloplumicome* and *plumicome*, but unlike *drepanocome* and *springohexaster* which are noticeably larger (e.g., Lyssacinosida).

Sigmatosclere–D.; a collective term (i.e., why it should be avoided) for any *sigma*, *chela*, *toxa*, or *forceps*; *s*. as opposed to, for example, astrose, rhabdose and oxeote microscleres. Should be avoided as with no descriptive precision.

Sigmodragma–D.; a bundle of *sigmas*; see also *trochidragma* and *toxodragma*.

Sinuous microstrongyle-see spiral strongyle.

Sphaerancora—D.; an ellipsoidal unguiferous anchorate chela that is formed by the fusion of the three upper and lower unguiferous alae of an anchorate isochela (e.g., Melonanchora elliptica); compare with dischela (Figure 3.19, 20).

Sphaeraster-see spheraster.

Sph(a)ere—called also pearl; D., H., Ho.; a smooth rounded, spherical silica formation; silica spheres may accompany normal spicules (e.g., *Guitarra flamenca*, *Tethya seychellensis*, *Walteria flemmingi*, *Plakortis quasiamphiaster*); compare with *spherule* and *micraster* (Figure 1.14).

Sphaeroclone–DL.; an anaxial *desma* with a globular center; covered with spines on one side and with ray-like arms extending in opposite direction (e.g., genera *Vetulina*, *Astylospongia*) (Figure 8.18).

Sph(a)erostrongylaster—D.; a spherical microslere with blunt rays which are more than one-third of the total diameter (e.g., *Timea clandestina*); compare with *strongylaster* (Figure 1.26).

Sph(a)eroxyaster—D.; an *euaster* with rays which are more than one-third of the total diameter (e.g., *Erylus incrustans*); compare with *oxyspheraster* (Figure 1.19, 20).

Spherancora-see sphaerancora.

Spheraster–D.; an *aster* possessing short *rays* of diameter usually equal or smaller than the diameter of a thick center (e.g., *Chondrilla nucula*) (Figure 1.12, 16, 17).

Sph(a)erostrongyloaster—see strongylospheraster.

Sph(a)ero(s)tyle–D.; a *style* with one end club-shaped (sometimes sculptured) and the other end usually pointed (e.g., genus *Sphaerotylus*); see *exotyle* (Figure 7.17).

Spheroclone-see sphaeroclone.

Spherule–D.; a spherical *microsclere* with minute spines densely covering the whole spicule (e.g., *Caminus primus*) (Figure 1.13).

Spinispira-see spiraster.

Spinispirula-see spiraster.

Spinorhabd—D.; a spinulate acanthomicrorhabd (also the term "rod" is used) with four whorls of (sometimes reduced) spines arranged serially along the spicule (e.g., family Podospongiidae and genus *Diacarnus*); *s.* may develop dumbbell- or diplaster-shaped apices, often slightly asymmetrical (diplospinorhabd; e.g., *Diplopodospongia teliformis*); or as whorl of long spines with center and spines clustering at one or both ends of the rhabd (aciculospinorhabd; e.g., *Neopodospongia pagei*); compare with *discorhabd* (Figure 2.3, 4).

Spiral strongyle–called also sinuous strongyle; D; a sinuous, smooth or finely spined *microsclere* (e.g., *Cliona vermifera*, *Spiroxya levispira*) (Figure 7.11).

Spiraster—called also spinispira(e) or spinispirula; D.; a spiral, rodshaped *microsclere* with spines arranged spirally around the rod (e.g., genera *Cliona*, *Trachycladus*); compare with *diplaster* (Figure 2.8–14).

Spirodiscohexaster—H.; a *discohexaster* with a bunch of terminal, spirally twisted secondary rays (e.g., genus *Rhabdodictyum*) (Figure 9.29).

Spirosclere—any spiral sclere with twisted axis; for example, sigmaspire, spirula, spirorhabd.

Spirorhabd–D.; a spicule similar to *acanthoxea* but with spirally arranged axis (e.g., *Spirorhabdia vidua*) (Figure 2.7).

Spirosigma(ta)—D.; a rugose *sigma*-like *microsclere* with a strongly contorted, spiral twist (e.g., genus *Rhabderemia*); compare with *sigmaspire* (Figure 3.47).

Springohexaster—H.; a *hexaster* with sigmoidal, bow-, or springshaped *secondary rays* arranged in a single circle on each *primary ray* (e.g., Lyssacinosida); compare with *sigmatocome* and *drepanocome* (Figure 9.35b, 36).

Stauract(in(e)—H.; a cross-like spicule which consists of four rays situated in one plane; their axes are perpendicular to one another; derived from a *hexaster* by ray reduction (e.g., *Staurocalyptus dowlingi*) (Figure 9.8).

Stauraster–H.; a reduced *hexaster*; an *aster* with four rays arranged in one plane (e.g., *Crateromorpha* [*Caledochone*] *caledoniensis*) (Figure 9.21).

Staurodisc-see tetradisc.

Staurographicome–H.; a *graphiocome* with only four primary rays.

Sterraster–D.; a big spherical or ellipsoidal astrose *microsclere* with numerous short tidily arranged rays with stellate tips in form of

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rosettes (e.g., genus Geodia); it may be confused with selenaster; compare with aspidaster (Figure 1.4–6).

Sterrospheraster–D.; not in use today; a *spheraster* with numerous conical or flattened (denticulate or tuberculate) projections (Figure 1.7).

Sterrospira-see selenaster.

Streptaster—D.; any *aster* microsclere (e.g., *plesiaster* or *spiraster*) with rays proceeding from usually spiral axis (e.g., genus *Thenea*); in some pachastrellids (e.g., *Pachastrella nodulosa*); *s*. are long rhabd-like; compare with *amphiaster* (Figure 2.11).

Streptosclere—called also dichotriact; D.; any spicule with a twisted rhabd.

Strobilocome-see strobiloplumicome.

Strobiloplumicome—H.; a *plumicome* with strobilate or clavate ends of *primary rays* from which sigmoidal terminal rays emanate in several concentric circles; *secondary rays* may vary in length (e.g., *Lophocalyx biogasi*) (Figure 9.27).

Strobiloscopule-see scopule.

Strongylaster—called also chiaster; D.; an *aster* without a centrum and with free, isodiametric, blunt rays (e.g., *Asteropus moolenbeeki*); compare with *spheraster* and *spherostrongylaster* (Figure 1.26).

Strongyle—called also amphistrongyl; D., DL.; a *diactinal* spicule, usually symmetrical, with rounded ends (e.g., genus *Petrosia*) (Figures 2.28, 6.1, 2, and 7.1, 6, 8, 11, 13).

Strongyloamphiaster–DL.; an *amphiaster* with blunt strongyle ends (e.g., *Neoaulaxinia zingiberadix*) (Figure 2.20, 22).

Strongylodiscorhabd - see discorhabd.

Strongylospheraster-D.; a spheraster with blunt strongyle ends

(e.g., Timea clippertoni); compare with tylospheraster (Figure 1.27, 28). Strongylospire—see spiral strongyle.

Strongyloxea(on)–D.; a *fusiform oxea* with one end bluntly ended; it resembles a *strongyle* (e.g., *Tethya seychellensis*, *Aaptos aaptos*); it may be iso- or anisostrongyloxea (Figure 6.15).

Style–D., DL.; a monaxon spicule with one end pointed and the other blunt (e.g., *Clathria* (*Thalysias*) *hermicola*); it can be, for example, *verticillate, acantho-, rhabdo-, subtylo-, tylostyle* (Figure 6.22, 24–26, 29–32, 34).

Subhexactin-see sword hexactine.

Subpinlike acuate-see subtylostyle.

Subregular spicule—C.; an equiangular *triactine* or *tetractine*, but with all the actines with different lengths (Figure 11.6).

Subtylostyle–D.; a *tylostyle* with faintly developed tyle/swelling (e.g., *Mycale* [*Mycale*] *laevis*) (Figure 6.29).

Subtylote–D.; a *tylote* with faintly developed tyles (e.g., *Clathria* [*Thalysias*] *reinwardti*) (Figure 6.5).

Supradermalia (pl.)-see prostalia.

Subtrochirhabd—D.; a spear-like spicule with a *tyle* at one end and the other end acerate (e.g., *Chondrocladia* [*Meliiderma*] *stipitata*) (Figure 2.6).

Sword hexactin–called also subhexactin; H.; a *hexactine* with enlarged distal ray, tangential and proximal rays or ends shorter, tapering like a sword (e.g., genus *Euplectella*) (Figure 10.11).

# 4.1.19 | T

Tauactine—H.; a *triactin* with all rays situated in one plane (e.g., genus *Monorhaphis*) (Figure 10.12).

Tetraclone–DL.; a *desma* of tetraxial (but not triaenose) symmetry (e.g., family Theonellidae) (Figure 8.14, 15).

Tetract(in(e))—C., D., H.; in D. any spicule with four rays ordered in different planes (e.g., *calthrop*, *triaene*); in C. any spicule with four rays; most of them have three actines in the same plane and the fourth one (apical) is perpendicular to them, however all the four actines can be in the same plane, the fourth being opposite to the unpaired actine (see *pugiole*); *T*. may be fused by their basal actines creating a fused skeleton (e.g., genus *Plectroninia*); Figure 8.25; in H. any spicule with four rays (Figure 11.7–9).

Tetradisc—called also discostauractin and staurodisc; H.; a microsclere consisting of four rays with discoidal outer ends (e.g., Amphidiscophora); for Hexasterophora the term *discostauractin* seems preferable (Figure 9.21).

Tetraloph-see tetralophose calthrop

Tetralopho(u)s(e) calthrop—Ho.; a *calthrop* with four rays bearing *lophose* tips (e.g., *Placinolopha acantholopha*); compare with *mono-*, *di-*, and *triloph* (Figure 12.14).

Tetrapocillum–D.; a strongly modified *biplacochela*-derived *microsclere* consisting of a *shaft* connecting four fimbriae-bearing discs of which the middle two are fused (e.g., genus *Tetrapocillon*); compare with *dischela* (Figure 3.33).

Tetrapod–C.; a *tetractine* with an elevated center and stout or thickened rays (e.g., *Borojevia tetrapodifera*); compare with *calthrop* (Figure 11.19).

Tetraxon—D.; any spicule with four axes (rays) and with a central (axial) canal; for example, *triaene*, *calthrop*.

Tignule–H.; a large, thick, spindle-shaped *diactin* (e.g., genus *Hyalonema*).

Thraustosigma–D.; an irregularly curved, crooked, thick sigmalike microsclere (several species of *Rhabderemia*) (Figure 3.46, 48).

Thraustoxea—D.; a smooth or spinose zigzag-shaped double bent *microsclere*, often with central swelling (see *centrotylote*) (e.g., genus *Rhabderemia*) (Figure 3.42).

Tornote–called also amphitorn; D.; a thin, (aniso)diactinal, or monactinal *megasclere* of some Poecilosclerida (e.g., *Myxilla brunnea*) (Figure 6.17, 17a).

Toxa-called also *bogen*; D.; a bow-shaped *microsclere* (e.g., *Acarnus oaxaquensis*) (Figure 3.41).

Toxiform raphide–D.; a long irregularly curved *raphide* which may approach the form of long thin *toxa* with shallow curve (e.g., families Mycalidae and Microcionidae).

Toxodragma–D.; a bundle of very fine spicules; see also *trochidragma* and *sigmodragma*.

Tox(on)-see toxa.

Triact(in(e))–C., D., Ho.; any spicule with three rays ordered in one plane (e.g., genus *Clathrina*); in C., they may be regular, *sagittal*, and *parasagittal* or can be a *tripod* (e.g., genus *Borojevia*); in Ho. triods are called *triactins* (Figures 11.2-4, 6, 9 and 5.18, 19).

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Triaene–D., DL.; any tetraxial, tetractinal *megasclere* with one, unequal, usually longer ray (called *rhabd*) and other three rays termed *clads* (e.g., genera *Acanthotetilla*, *Stelletta*) together forming the *cladome*; there are different kinds of triaenes, for example, *pro-*, *dicho-*, *meso-*, *ana-*, *phyllo-*, *orthotriaene* (Figures 4.1–23, 25 and 5.4–17).

Triaxon(e)—H.; any spicule with three axes; see also *hexactine*. Trichaster—see *pappocome*.

Trichite—see raphide.

Trichodragma–D.; a bundle of *raphides*; see also *toxodragma* and *sigmodragma* (Figure 2.26).

Trichox(ea)—C.; a very thin, hair-like straight *diactine* generally present around the osculum or protruding from the cortex (e.g., *Leucascus neocaledonicus*) (Figure 11.13).

Tridentate chela—D.; a collective term for *arcuate, anchorate, unguiferate chelae,* and derived forms with three or more *alae* on each extremity, or additional modifications. Should be avoided as with no descriptive precision.

Trider–DL.; a *tetraclone desma* with triaenose symmetry; one ray in the form of spine or knob and not articulating with other desmas (e.g., genus *Exsuperantia*); compare with *mesotrider* (Figure 8.1–3).

Triloph-see trilophose calthrop.

Trilopho(u)s(e) calthrop—Ho.; a *calthrop* with three dichotomous or polytomous rays (e.g., *Plakina corticioides*); compare with *mono-*, *di-*, and *tetralophose c*. (Figure 12.11).

Triod-Ho.; a triactine with all rays in one plain (e.g., Plakortis angulospiculatus) (Figure 12.4-8).

Tripod—C.; a *triactine* with elevated center or with the actines in the same plane, but always with stout actines and found only on the surface of the sponge (e.g., genera *Borojevia*, *Lelapiella*) (Figures 11.1, 2).

Trochirhabd—D.; a *rhabd* bearing a mushroom-shaped cap on one end, and a subspherical bulge on the other, and up to three discs in the middle (e.g., *Chondrocladia* [*Meliiderma*] *turbiformis*); compare with (*aniso*)*discorhabd*, *cricorhabd*, and *subtrochirhabd* (Figure 2.5).

Truncaster–D.; not in use today; an *aster* with abundant, blunt rays.

Tuning-fork spicule—see *diapason*.

Tylaster—D.; an *euaster* with tylote rays and a small center (e.g., *Ecionemia solida*); the rays may be equipped with spines (e.g., *Ecionemia cinerea* and *Geodia globostellifera*) (Figure 1.25, 29).

Tylfloricome-see sigmatocome.

Tylodisc—called also paraclavule; H.; a *diactin* or *monactin* with one tip developed as *umbel* and spherical or rounded opposite tip; interpreted as an *amphidisc* with one umbel reduced (e.g., *Monorhaphis chuni, Sericolophus reflexus*).

Tylohexaster—H.; a *hexaster* with tyloid ray tips (e.g., *Claviscopulia facunda*, *Tretodictyum reiswigi*) (Figure 9.14).

Tyloscopule-see scopule.

Tylospheraster–D.; a spheraster with tylote ray ends (e.g., Stelletta makushina).

Tylostrongyle—D.; a *strongyle* with a globular swelling (*tyle*) at one end of the spicule (e.g., *Antho* [*Acarnia*], *Cliothosa tylostrongylata*) (Figure 6.6).

Tylostyle–D.; a *style* with a globular swelling at one end of the spicule (e.g., genus *Spirastrella*, *Cliona mucronata*) (Figures 2.25 and 6i–k, 30–32).

Tylote—rarely called amphitylote; D., DL.; a diactinal *megasclere* with knob-like swellings at both ends; the ends may be smooth, spined or microspined (e.g., genera *Acarnus*, *Antho* [*Plocamia*], *Tedania*) (Figures 6.3, 4).

Tylotornote-see tornote.

Typhahexaster—H.; a *hexaster* with *typhoidal* ray tips (e.g., *Hyalostylus dives*).

# 4.1.20 | U

Uncinate(ed)-called also barbule; H.; a *monaxon* with finely pointed outer ends and spines directed toward one end (e.g., *Pheronema carpenteri*); in *ambuncinate* the spines cover the spicule inclined towards its center (e.g., subgenus *Hyalonema* [*Pteronema*]) (Figure 10.8).

Unguifer/ous/ate-anchorate chela—called also ancora unguifera; D.; an *anchorate chela* with claw- or sickle-like *alae* (e.g., *Nullarbora caillieti*) (Figures 3.7, 8).

Unguifer/ous/ate-arcuate chela—D.; an *arcuate chela* with clawor sickle-like *alae* (e.g., genus *Strongylacidon*) (Figure 3.6).

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This information applies to a review paper. All data are included in the manuscript.

#### ORCID

Magdalena Łukowiak D http://orcid.org/0000-0002-5282-5341 Rob Van Soest D http://orcid.org/0000-0002-4623-0093 Michelle Klautau D http://orcid.org/0000-0002-5959-0776 Thierry Pérez D http://orcid.org/0000-0003-1826-9318 Andrzej Pisera D http://orcid.org/0000-0001-7112-6063

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# SUPPORTING INFORMATION

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