

Class Hexactinellida Schmidt, 1870

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Hexactinellida Schmidt (Porifera) are deep-water marine sponges defined by their production of siliceous spicules of hexactinic, triaxonic (cubic) symmetry, or shapes clearly derived from such forms by reduction of primary rays or terminal branches added to the ends of primary rays. They lack calcareous minerals and sclerified organic spongin as skeletal components. Siliceous spicules may be entirely loose, or partially fused to form a rigid basal and choanosomal framework. Their living tissues are mainly syncytial, with distinctive porous plugs joining differentiated regions of the syncytium to each other or to discrete cellular components. Flagellated-collar units are anucleate. Hexactinellids are viviparous and, from detailed study of a single species, produce distinctive trichimella larvae. Two subclasses are recognized by different microsclere forms – amphidiscs and hexasters. Hexactinellids include about 500 described species, 7% of all Porifera, distributed in 5 orders, 17 families and 118 genera.

Keywords: Porifera; Hexactinellida; Amphidiscophora; Hexasterophora; Amphidiscosida; Aulocalycoida; Hexactinosida; Lyssacosida; Lychniscosida.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Hexactinellidae Schmidt, 1870. *Coralliospongia* (in part) Gray, 1867a. *Vitrea* Thomson, 1868. *Hyalospongiae* (in part) Claus, 1872. *Sextradiatospongia* Gray, 1874. *Triaxonia* Schulze, 1886.

Definition

Porifera with siliceous spicules of triaxonic (cubic) symmetry or derivations of that basic form. Typical spicules are hexactine in form, the three axes intersecting at right angles; loss of one or more rays results in spicules of pentactine, tetractine, triactine, diactine or monactine form. The axial filament is square in section.

Diagnosis

Body form variable, including monomeric tube-, cup-, funnel-, cap-, club-, lobate- and blade-forms, with or without lateral diverticula, and branching tubule or solid cylinders, with or without anastomoses; encrusting forms unknown. Entirely marine on hard or soft substrate; attached directly to hard substrate either firmly by basal disc cementation (basiphytous) or loosely by grappling anchor spicules (lophophytous); attached to soft substrate by rooting spicules (lophophytous) or rarely by solid roots (rhizophytous). Skeletons of (mineral) siliceous spicules, as separate elements or joined by silica deposition and (organic) thin lattice of collagen; dense spongin, calcareous deposition and aspicular forms unknown. Siliceous spicules generally divisible into megascleres and microscleres on basis of form, size, and function; intermediate-size surficial spicules sometimes distinguished as mesoscleres. Megascleres basically hexactins but reduction of one or more rays results in pentactins, tetractins (usually stauractins), triactins (usually tauactins), diactins and monactins (usually basal anchors, sceptrales, or sceptres); megasclere ray branching is rare. Rigid skeletal frames of hexactine megascleres often fused at or soon after spicule formation along parallel rays or at ray crossing points

are known as dictyonal frameworks; rigid frames formed by fusion of non-hexactine megascleres (usually diactins) long after spicule formation in more basal body regions of sponges with otherwise separate spicules are not considered dictyonal frameworks. Living tissues are mainly syncytial, including dermal and atrial membranes, internal trabeculae and flagellated chamber walls with anucleate collar bodies. Discrete nucleate cellular components embedded in pockets or capsules of the syncytium may be joined together or to syncytium by distinctive porous plugs or may be entirely separate. Cellular differentiation is slight. Translocation of intrasyncytial materials is by symplastic flow transport across plugs and cytoplasmic streaming within open syncytia; stimuli are disseminated throughout entire individuals by membrane conduction. The flagellated chambers are large and eurypylous, arranged between very thin-walled inhalant and exhalant water conducting canals in syconoid, sylleibid or leuconoid pattern. All known members are active water pumpers and particle filterers; food particle acquisition by passive flow and sedimentation appears minor or non-existent. Larval form, the trichimella, is well-known for only one species; among many distinctive features it has an equatorial, subepidermal sheath of multiflagellate cells, the flagella of which project through pores of the overlying syncytial epidermis to provide motility. Reproductive strategy is viviparous in the few forms where known.

Remarks

Hexactinellida presently contains about 500 Recent species or 7% of all described Recent Porifera. They have been reported from depths of 5–6770 m and are unknown in freshwater or intertidal habitats. They constitute important members of deep-water marine communities, many of which remain unsampled or poorly sampled, and in those regions that have supposedly been well sampled, new species continue to be discovered. It is likely that the total number of species will exceed 1000 when present institution collections are reviewed and unsampled areas are surveyed. In early taxonomic treatments (e.g., Schulze, 1886), the class was divided on presence or absence of a fused dictyonal framework – present in Dictyonina and absent in Lyssacina. Realization that

accessory spicules, mainly microscleres, were shared by some members of both lyssacine and dictyonine groups led Schulze (1899) to create a new primary division based upon microsclere form: Amphidiscophora bearing amphidiscs and Hexasterophora bearing hexasters. These remain the two well-differentiated subclasses of Hexactinellida today despite recent discovery (Tabachnick in Tabachnick & Lévi, 1997b) of amphidiscs among hexasters in some Hexasterophora and hexadiscs (not hexasters) among typical amphidiscs in some typical Amphidiscophora. This shared similarity is believed to be a recent convergent feature and the two subclasses are still considered to have a long independent evolution since the Paleozoic (Mostler & Mehl, 1990). Tests of the distinction between the two subclasses by genetic sequence analysis have not yet been carried out but may be expected shortly. Such analyses using Hexasterophora sequences (Collins, 1998; Kruse *et al.*, 1998; Adams *et al.*, 1999; Borchellini *et al.*, 2001; Medina *et al.*, 2001) have not yet generated consistent strongly-supported relationships among Porifera classes, and are unlikely to influence systematic organization at high taxonomic levels for some time.

Scope

In its Recent composition, the class contains two subclasses, five orders with 17 families and 118 valid genera, 111 of which are placed to family and seven of which remain *incertae sedis* in two orders. Recent orders are: (1) Amphidiscophora: Amphidiscosida; (2) Hexasterophora: Aulocalycoidea, Hexactinosida, Lychniscosida, Lyssacosida.

Recent reviews

Reid, 1958a; Hartman, 1982; Mehl, 1992; Hooper & Wiedenmayer, 1994.

SUBCLASSES OF HEXACTINELLIDA

Subclass Amphidiscophora Schulze, 1886

Other names. None.

Definition. Lophophytous Hexactinellida which always contain amphidisc microscleres or some variant of them, and triaxon microscleres which never bear terminal ray branching (never astral microscleres); choanosomal skeleton of loose megascleres, never fused together, in the form of hexactins, pentactins, stauractins,

tauactins, diactins or some combination of these; hypodermalia usually as pentactins, rarely hexactins and stauractins.

Remarks. The subclass presently contains a single Recent order with three families.

Subclass Hexasterophora Schulze, 1886 (emend. Schulze, 1899)

Other names. None.

Definition. Basiphytous, rhizophytous or lophophytous Hexactinellida in which microscleres are mainly or all astral, typically hexasters; amphidiscs occur rarely as variants of discohexactins; choanosomal skeletons may consist of entirely loose spicules, sometimes irregularly joined by synaptulae or silica cement at contact points, or of regularly fused hexactins forming a dictyonal framework; dictyonal nodes, where present, may be entirely simple or lychniscid (lantern nodes).

Remarks. Hexasterophora was first erected by Schulze (1886) as a tribe of the suborder Lyssacina Zittel, containing only the hexaster-bearing lyssacine hexactinellids; he assigned the hexaster-bearing dictyonine hexactinellids to a separate suborder, Dictyonina Zittel. After considering a reorganization of the entire Hexactinellida (Schulze, 1893), Schulze (1899) finally abandoned Zittel's (1877) primary division of hexactinellids on the basis of lyssacine vs. dictyonine parenchymal skeletons, citing the presence of dictyonal tendencies at the attachment of some lyssacine Hexasterophora (basidictyonalia in *Rhabdocalyptus mirabilis*) and the existence of some hexaster-bearing genera that could be regarded as intermediates between lyssacine and dictyonine forms (e.g., *Euryplegma*) for his action. He joined all hexaster-bearing lyssacine and dictyonine hexactinellids into one of two major subdivisions (hierarchy level unspecified) of Hexactinellida as his emended Hexasterophora, and retaining his original tribe Amphidiscophora as the other major subdivision. His early insight has stood the test of time and remains the basis for subclass definitions.

Conclusions

Present subclass division of Hexactinellida has been and remains stable and non-controversial. Should evidence be discovered that amphidisc and hexaster microscleres are not independently evolved characters (from new fossil developmental information sources), or that some members of Hexactinosida share a more recent common ancestry with Amphidiscophora than with other Hexactinosida (e.g., through genetic sequence analysis), the relationships between the two subclasses would need reconsideration.

KEY TO ORDERS OF RECENT HEXACTINELLIDA

- (1) Amphidisc microscleres present; hexaster microscleres absent **Amphidiscosida**
Astral (hexasters) microscleres present; amphidisc microscleres rare (2)
- (2) Dictyonal framework formed of hexactins fused by secondary silicification (3)
Dictyonal framework of fused hexactins absent; fusion of non-hexactine megascleres (diactins, triactins, tetractins) may occur in older parts **Lyssacosida**
- (3) Dictyonal nodes mainly lychniscid, but some may be simple **Lychniscosida**
Dictyonal nodes simple (4)
- (4) Dictyonal meshes consistent in size and shape; dictyonal rays one mesh in length; dictyonal strands as serially aligned beam pairs **Hexactinosida**
Dictyonal rays irregular in size and shape; dictyonal rays exceed mesh length; dictyonal strands as long single rays or multiple (>2) overlapping rays **Aulocalycoidea**