Class Demospongiae Sollas, 1885

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Demospongiae (Porifera) have discrete cellular elements, parenchymella or blastula larvae, with either viviparous or oviparous reproductive strategies. The skeleton is composed of monaxonic or tetraxonic siliceous spicules (never triaxonic) bound together with spongin in discrete fibres or loosely aggregated, and ubiquitous collagenous filaments forming the ground substance of the intercellular matrix. Spicules and/or fibres, or both, may be absent in some taxa, and several other groups with solid calcitic or siliceous skeletons are also included ('sclerosponges', 'sphinctozoans', 'lithistids') rendering the class morphologically heterogeneous. Three subclasses are recognised based on larval morphology, reproductive strategy, tetraxonid versus monaxonic megascleres, and microsclere geometries, although these divisions require further refinement, and as such they are often ignored by contemporary authors. Demosponges include about 85% of all described Recent species, some are freshwater but predominantly they are marine species living from the intertidal to the deepest seas, with around 15 orders (the exact number still in contention), 88 families, and about 500 valid genera.
Keywords: Porifera; Demospongiae; Homoscleromorpha; Tetractinomorpha; Ceractinomorpha.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Demospongiae Sollas, 1885c.

Definition

Porifera with siliceous spicules and/or a fibrous skeleton, or occasionally without a skeleton. Spicules are either monaxonic (either monactine or diactine) or tetraxonic (tetractine), never triaxonic. The axial filament is embedded in a triangular or hexagonal cavity.

Diagnosis

Encrusting, massive, lobate, tubular, branching, flabellate, cup-shaped or excavating sponges. Skeleton composed of spongin fibres alone or together with siliceous spicules which are usually divided into megascleres and microscleres. Megascleres are basically monaxonic or tetraxonic; microscleres are diverse, polyaxial or monaxone, often quite elaborate in shape and ornamentation. Spongin is almost universally present, forming discrete fibres or binding the skeletal elements. In most cases the spicular skeleton and fibrous skeleton form a combined reinforcement. Fibrils of collagen are ubiquitous. Some groups lack spicular skeletons, but compensate that by building an elaborate fibre skeleton. A few (unrelated) groups have no skeletal elements other than diffuse fibrillar collagen. Other minor groups have developed a hypercalcified basal skeleton in addition to other skeletal elements, or have a solid aragonitic structure lacking free spicules. In total these skeletal variants contribute to a heterogenous morphological concept of Demospongiae, although there are other (non-morphometric) characters that provide more valuable clues as to their phylogenetic affinities (e.g., possession of viviparity, parenchymella larvae). The cellular elements are discrete, never syncytial, and cellular diversity may be considerable. The aquiferous system is of the leucon-type, although one family of deep-water Poecilosclerida (Cladorhizidae) has lost its aquiferous system and has assumed a carnivorous lifestyle, and dependent on fibroblastic flow (archaeocyte/pinacocyte). Choanocyte chambers may be eurypylous, diplodal or aphodal. Larvae are mostly parenchymella, but in some groups there are cinctoblastula or blastula forms produced. Both oviparous and viviparous reproductive strategies occur.

Remarks

Demospongiae contains about 85% of all living sponges, with about 6000 'valid' living species of demosponges already described in the literature. There are potentially double this number of species, with the extant poriferan fauna estimated to comprise at least 15,000 species worldwide (Hooper & Lévi, 1994; based on surveys of unpublished museum collections). Furthermore, this estimate is probably conservative as it largely neglects the grossly under-sampled and under-studied encrusting, cryptic, sciaphilic and other small taxa that pervade the many crowded marine communities, such as the coral reefs (Hooper *et al*., 1998). Most demosponges are marine, but several dozens of species occur in freshwater habitats all over the world (so far excluding Antarctica).

Within Demospongiae three subclasses are recognized (Homoscleromorpha, Tetractinomorpha, Ceractinomorpha), although there is an increasing number of anomalies and exceptions between otherwise closely allied family groups – based on putative morphological similarities and their differing reproductive strategies – signaling that some subclass taxa require tighter definition based on new data. Nevertheless, a rough division is possible based on the mutually exclusive presence of aster microscleres and reticulate skeletal elements. These might be equated with Tetractinomorpha and Ceractinomorpha, respectively (although the original contents of these subclasses were different, e.g., based on reproductive strategies, larval morphology). Homoscleromorpha is homogeneous, with a single order and family (Homosclerophorida, Plakinidae). Thus, although some taxa do not appear to fit this model this subclass system offers an hypothesis to evaluate the diverse demosponge orders and families.

A nominal supraordinal group, 'Keratosa', was proposed by early authors for sponges lacking a siliceous skeleton. Such a group, if it had any plausibility today, would contain the orders Dictyoceratida, Dendroceratida, Verongida and Halisarcida, but

these groups in reality are quite disparate, and hence the taxon has no real basis for support (Bergquist *et al*., 1998).

Several species of 'living fossils' previously assigned to 'Sphinctozoa' (now included in the order Verticillitida) and 'Sclerospongiae' are also undoubted Demospongiae, possessing a viviparous reproductive strategy and producing parenchymella larvae, in Recent species at least (Vacelet, 1979b). These species presently sit uneasily within a homogeneous concept of Demospongiae, based on a poriferan bauplan.

Lévi (1953a, 1956a, 1957b, 1973) provides an outline and discussion of the various proposals subdividing the Demospongiae at suprafamily levels, and he was also the first to provide a comprehensive synthesis of the 'modern' sponge classification.

Scope

We recognize three subclasses of demosponges with extant representatives, distributed amongst 15 orders, 88 families and ca. 1000 nominal genera (although only about 500 genera are presently considered valid). Most of these genera are marine but there are also about 40 genera confined to freshwater. Orders included at this time are: (1) Homoscleromorpha: Homosclerophorida; (2) Tetractinomorpha: Astrophorida, Chondrosida, Hadromerida, most 'lithistids' (polyphyletic), Spirophorida; (3) Ceractinomorpha: Agelasida, Dendroceratida, Dictyoceratida, Halichondrida, Halisarcida, Haplosclerida, Poecilosclerida (which includes some 'lithistids'), Verongida, and Verticillitida (the latter a fossil order to which a single Recent genus is currently assigned). Several other widely employed ordinal taxa are allocated to existing orders, following contemporary revisions of these groups, although not presently universally accepted (e.g., Axinellida (see Halichondrida), Ceratoporellida (see Agelasida), Choristida (see Astrophorida), Petrosida, also known previously as Nepheliospongida (see Haplosclerida)).

Recent reviews

Lévi, 1973; Bergquist, 1978; Hartman, 1982; Hooper & Wiedenmayer, 1994.

SUBCLASSES OF DEMOSPONGIAE

Subclass Homoscleromorpha Lévi, 1973

Other names. Microsclerophora Sollas, 1887. Carnosa Carter, 1875c.

Definition. Demospongiae with cinctoblastula larvae and viviparous reproduction; skeleton composed of tetraxonic siliceous spicules and derivatives with equal rays (diods, triods, lophate spicules), arranged around choanocyte chambers reflecting the canal structure; no differentiation between megascleres and microscleres although size differences do occur between types of spicules; spicules usually small (100 μm or less), not localised to any particular region; choanocyte chambers with large numbers of choanocytes.

Remarks. The subclass presently contains a single order and family.

Subclass Tetractinomorpha Lévi, 1953a

Other names. Chondrospongiae Lendenfeld, 1886. Spiculispongiae Gray, 1867. Tetractinellida Marshall, 1876.

Tetractinellidae Sollas, 1880. Tetraxonia Dendy, 1905. Astrotetraxonida Hentschel, 1909.

Definition. Demospongiae with parenchymella or blastula larvae, predominantly oviparous reproduction (although in some genera young sponges are apparently incubated within the parent and set free as small adults; Bergquist, 1978). Megascleres are tetraxonic and monaxonic, occurring together or separately; microscleres are asterose forms and derivatives; skeletal structure is usually radial or axially compressed.

Remarks. Tetractinomorpha was recognised as a polyphyletic taxon several decades ago (Bergquist, 1978), but it has nevertheless persisted in the contemporary classification in a slightly modified form to the present. Four 'well established' orders are traditionally included within the concept of Tetractinomorpha: Astrophorida (also known as Choristida) and Spirophorida – both of which continue to be treated as a single order Tetractinellida by a few authors (with a shared character of tetractines; Chombard *et al*., 1998) – Hadromerida, and Chondrosida. A fifth order Lithistida is clearly polyphyletic, with many taxa showing major affinities to Astrophorida and some to Hadromerida, to which they may be eventually allocated. Despite recent attempts (e.g., Kelly, 2000), resolving the systematic affinities of most 'lithistids' remains elusive, especially those that lack free spicules that may provide phylogenetic clues (see also Remarks for Ceractinomorpha). The order is herein abandoned (Pisera & Lévi, this volume).

Allocation of Latrunculiidae has also oscillated between Tetractinomorpha (close to Hadromerida) and Ceractinomorpha (close to Poecilosclerida) throughout its long and tortuous taxonomic history. The family is now recognised as two separate taxa (with the resurrection of Podospongiidae), and currently referred to Ceractinomorpha (with some support from molecular and biochemical evidence).

The tetractinomorph order Axinellida Bergquist is also considered polyphyletic by most contemporary authors (although not universally accepted by all), with families distributed amongst the predominantly viviparous Ceractinomorpha and the predominantly oviparous Tetractinomorpha. This treatment is followed in the present volume because it has a more sound morphometric base (e.g., asterose vs. non-asterose taxa), but there is currently no published corroboratory molecular support one way or the other. Hemiasterellidae and Trachycladidae are the only 'axinellid' families that now remain in this subclass, with suggested affinities to the Hadromerida.

Subclass Ceractinomorpha Lévi, 1953a

Other names. Cornacuspongiae Vosmaer, 1887, Monaxonidae Sollas, 1882b, Monaxonida Ridley & Dendy, 1887.

Definition. Demospongiae with parenchymella larvae and predominantly viviparous sexual reproduction; generally with both a spicule skeleton and well-developed spongin fibres forming a diversity of skeletal structures (although siliceous spicules are lost altogether in three orders and in several other genera, and spongin fibres are lost or greatly reduced in several genera scattered throughout the subclass). Spicules are monaxonic (either monactinal (styles) or diactinal (oxeas-strongyles)), never tetractinal (although modifications to the ends of some monaxonic spicules occur and may appear to be superficially tetractinal); microscleres are diverse (meniscoid (chelae), oxeote, toxote, spheres) but never asterose.

Remarks. Acceptance of the concept of subclass Ceractinomorpha has diminished in the contemporary literature, largely due to the declining acknowledgement that viviparity is a pivotal phylogenetic character to differentiate the taxon from the oviparous Tetractinomorpha. An increasing number of oviparous taxa have been found in Ceractinomorpha (e.g., Petrosiidae, Verongida), with sound biological, biochemical or other evidence to support this scheme (e.g., Bergquist, 1980a). In contrast, the allocation of some other oviparous (or suspected oviparous) taxa to Ceractinomorpha remains controversial.

Of the families formerly included in the polyphyletic order Axinellida six are now included in Ceractinomorpha. Axinellidae and Desmoxyidae are included by some authors in the Halichondrida (e.g., Van Soest *et al*., 1990), even though they may be exclusively oviparous (although data are still rudimentary for most genera). In the case of Axinellidae there is molecular support from 28S rDNA analyses that shows the family is (a) polyphyletic but (b) indeed close to Halichondriidae (Alvarez *et al*., 2000a). In the case of Desmoxyidae this relationship is far more speculative. Desmacellidae demonstrate both modes of reproduction. For example, viviparity has been recorded for several species of *Biemna* (with some also producing gemmule-like asexual bodies, similar to asexual resting bodies seen in some *Mycale*), whereas *Neofibularia nolitangere* is clearly oviparous (e.g., see reviews by Fell, 1993; Boury-Esnault & Jamieson, 1999, and literature contained therein). The likelihood that the family is polyphyletic (i.e., their phylogeny is erroneously based on morphological convergence) is negligible as similarities between *Desmacella*, *Biemna* and *Neofibularia* are convincing, and it can only lead to the conclusion that there is a discrepancy in the interpretation of mode of reproduction as phylogenetic markers for otherwise very closely related sponges (i.e., concepts of 'vivipary' and 'ovipary' are non-homologous within the sponge phylogeny). Raspailiidae (oviparous, where known) is also assigned to Poecilosclerida based on morphological similarities to the viviparous family Microcionidae. While this relationship is supported by character analysis and chemotaxonomic data (Hooper *et al*., 1992), no sequence data is yet available to support this hypothesis. Rhabderemiidae (reproduction unknown) is less confidently included in Poecilosclerida. It possesses diverse microscleres that are assumed homologues of poecilosclerid microscleres (with this assumption supported by possession of true toxas in three species of *Rhabderemia*), but most of these microscleres are unique and therefore potentially analogues of typical poecilosclerid morphologies. Agelasidae also theoretically belong to Tetractinomorpha (oviparous), but its allocation has oscillated between Ceractinomorpha and Tetractinomorpha. The family is now assigned to its own monophyletic order (Agelasida), and its inclusion within Ceractinomorpha has some molecular support

(Alvarez *et al*., 2000a). Further literature citations are provided in the respective family chapters below as evidence in support of these allocations, but nonetheless, they remain contentious by some authors.

Nine orders are potentially allocated to Ceractinomorpha based on the predominance of viviparity, and/or the production of parenchymella larvae, and/or they possess close morphological similarities with other viviparous ceractinomorphs. These include: Agelasida (oviparous), Dendroceratida, Dictyoceratida, Halichondrida, Halisarcida, Haplosclerida, Poecilosclerida (with one (Raspailiidae) or possibly two oviparous families (Rhabderemiidae)), Verongida (oviparous), Verticillitida, with another (Petrosiidae, oviparous) family included within the predominantly viviparous Haplosclerida. Axinellidae is also included within the viviparous Halichondrida, and despite recent molecular support for this allocation it is still not universally accepted by all contemporary authors.

Several genera with exclusively or predominantly 'lithistid' or 'sublithistid' skeletons are also included in various ceractinomorph families (i.e., *Crambe*, *Desmatiderma*, *Desmanthus*, *Lithochela*, *Petromica*), and a few 'sublithistid' species are found in genera with a predominantly 'non-lithistid' grade of construction (e.g., *Esperiopsis*). This issue is still controversial. One school of thought suggests that the 'lithistid' grade of construction may have 'persisted' from a once more-widespread fauna (e.g., Ordovician and Devonian sponge reefs), with free spicules indicative of phylogenetic affinities (e.g., Van Soest & Zea, 1986; Hooper & Lévi, 1989; Van Soest *et al*., 1990). Another school suggests that desmas are indicative of phylogenetic affinities and taxa possessing them are recognisable at least at the family level (e.g., Kelly, 2000; Pisera, pers. comm.; Pisera & Lévi, this volume). These arguments remain unresolved without other supporting evidence, except in cases like *Esperiopsis* and *Crambe* which have clear affinities to Poecilosclerida based on the possession of microscleres that are unique to this order.

Conclusions

Given all of these anomalies it is questionable whether reproductive strategy is a suitable biological criterion to formulate a phylogenetic hypothesis at the level of subclass, or indeed if the subclass classification is necessary at all. For this reason many contemporary authors prefer not to group the different orders into subclasses, but we suggest that these higher taxa have value as working hypotheses to reconstruct evolutionary relationships between the diverse orders and families of demosponges. It therefore remains a challenge for the future to re-evaluate and perhaps expand this subclass classification for the Demospongiae, incorporating new datasets.

KEY TO ORDERS OF RECENT DEMOSPONGIAE

This key may not always result in the assignment of each individual sponge specimen to its proper order due to the imperfectness of juvenile or growth stages, phenomena like reduced spiculation in carbonate environments, or deviating species associated with orders only through circumstantial similarity with species showing a full complement of ordinal characters. Consequently, several redundancies are deliberately included in the key, but it is necessary to use it with care.

(1) Skeleton absent 2
  Skeleton present 7
(2) Firm sponges with cartilaginous consistency 3
  Soft sponges 4

(3) With leuconoid aquiferous system and diplodal choanocyte chambers; ectosome thick ... **Homosclerophorida** (*Pseudocorticium*)
       With a well developed cortex made of thick fascicles of fibrillar collagen, numerous spherulous cells, and inhalant apertures localised in special structures .... **Chondrosida** (*Chondrosia*)

(4) With fibrillar collagen only 5
       With a nodular spongin fibre skeleton .... **Chondrosida** (*Thymosia*)

(5) Choanocyte chamber eurypylous, simple 6
       Choanocyte chambers tubular and branched, size about 100 μm; ectosomal and subectosomal collagen highly organised and structurally diversified .... **Halisarcida**

(6) Ectosome thin, with sylleibid-like aquiferous system; choanocyte chambers eurypylous, rounded, less than
       60 μm diameter .... **Homosclerophorida** (*Oscarella*)
       With a thin cortex enriched with fibrillar collagen parallel to the surface, a superficial cuticle and pore-sieves
       may be present .... **Chondrosida** (*Thymosiopsis*)
       Ectosome strongly collagen-reinforced and bounded by a distinct skin, with spherulous cells ~10 μm in diameter are common throughout the mesohyl but particularly concentrated in the ectosome; sponge attaining a thickness of only about 5 mm; choanocyte chambers large and sac-shaped .... **Verongida** (*Hexadella*)

(7) Megascleres present 8
       Only asterose microscleres present .... **Chondrosida** (*Chondrilla*)
       Siliceous spicules absent (or secondarily lost) 17

(8) Spicules exclusively verticillate-spined styles or oxeas .... **Agelasida**
       Spicules may be spined or smooth but are not exclusively verticillate- spined 9
       Megascleres always include articulated siliceous desmas, with or without free
       spicules .... **Demospongiae 'lithistids'** (polyphyletic)

(9) Megascleres are all monaxones 10
       Megascleres include diods and/or triods, megascleres and microscleres undifferentiated, sometimes spicules are lost completely and sponge may be superficially confused with compound ascidians .... **Homosclerophorida**
       Megascleres include triaenes 16

(10) Megascleres exclusively diactines (oxeas and/or strongyles) 11
       Megascleres diverse or exclusively monactinal (tylostyles, styles, strongyloxeas) 15

(11) Asterose microscleres .... **Astrophorida**
       No asterose microscleres 12

(12) Megascleres arranged in an isodictyal or anisodictyal reticulation 13
       Megascleres arranged in a confused manner or plumose or plumo-reticulate 14

(13) Microscleres include chelae, megascleres often localized to distinct regions (e.g., inside fibres), sand/detritus may replace megascleres completely .... **Poecilosclerida**
       No chelae; microscleres absent or restricted to sigmas, toxas, raphides, amphidiscs or microspined oxeas, megascleres diactinal usually producing well-formed structures such as triangular, rectangular or polygonal meshes .... **Haplosclerida**

(14) Microscleres include chelae and or sigmas or toxas .... **Poecilosclerida**
       No chelae, sigmas or toxas .... **Halichondrida**

(15) Microscleres may be absent or may include asterose and monaxonic forms (microxeas, spirasters); skeleton peripherally radiate forming palisades of spicules at the surface .... **Hadromerida**
       Microscleres include chelae and/or sigmas, occasionally microscleres are absent .... **Poecilosclerida**
       No asters, and no other microscleres other than trichodragmas (or raphides); skeleton peripherally tangential or undifferentiated, main skeleton composed of a criss-cross of spicules, or compressed into a distinct axis, or with plumose, plumo-reticulate or dendritic mineral skeleton, fibre system poorly developed or absent .... **Halichondrida**

(16) Microscleres sigmaspires (rugose c- or s-shaped), spherical growth form usual, radial pattern of
       triaenes and oxeas .... **Spirophorida**
       Microscleres rugose sigmaspires, no oxeas, no radial skeleton, no spherical growth form .... **Spirophorida** (Samidae)
       Microscleres asters or streptoscleres, large oxeas always present, sometimes with triaenes, skeleton only obviously radial at the surface .... **Astrophorida**

(17) Solid carbonate skeleton, lacking free spicules, with a solid cortex producing a series of chambers on top of each other, the youngest (uppermost) chambers lined with living tissue .... **Verticillitida**
       Skeleton of discrete spongin fibres 18

(18) Fibres generally well laminated, containing a cellular mass visible as a dark pith in transmitted light, without differentiation of primary or secondary elements, many taxa aerophobic (darken in contact with air) .... **Verongida**
       Fibres contain a core of sand or spicule fragments or are entirely free of inclusions 19

(19) Skeleton an anastomosing system of interconnected fibres, often well developed and relatively homogeneous fibre construction with 2–3 different sized networks, consistency not collagenous .... **Dictyoceratida**
       Skeleton consists of dendritic fibres arising from basal attachment, with fibres strongly laminated .... **Dendroceratida**
       Skeleton with reticulate, plumoreticulate or plumose fibres containing sand or spicule fragments, with vestigial spicules (check for microscleres or echinating spicules) or occasionally no spicules at all .... **Poecilosclerida**
       Fibre skeleton well-developed, more-or-less regularly reticulate, and also with a tangential ectosomal (tertiary) network of fine aspicular fibres and foreign material, whereas choanosomal fibres are aspicular and with only foreign material (or sometimes extremely vestigial oxeas) .... **Haplosclerida** (*Dactylia*)