Systema Porifera: A Guide to the Classification of Sponges, Edited by John N.A. Hooper and Rob W.M. Van Soest

Order Haplosclerida Topsent, 1928

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Haplosclerida Topsent (Demospongiae) is characterized by possession of an isodictyal skeleton of diactinal megascleres. The megascleres are relatively short fusiform oxeas, or short compact strongyles. Microscleres are restricted to microxeas/strongyles, sigmas, toxas, raphides and amphidiscs. The sigmas and toxas may be interpreted as a trait shared with the order Poecilosclerida. A large number of common shallow-water marine sponges and all sponges occurring in freshwater are considered members of this order. To accommodate the high diversity of groups and habitats, and in acknowledgement of the continuing debate about monophyly of the order, three suborders are now recognized: Haplosclerina with families: Callyspongiidae, Chalinidae and Niphatidae; Petrosina with families Calcifibrospongiidae Petrosiidae and Phloeodictyidae; and Spongillina with families Spongillidae, Malawispongiidae, Metaniidae, Metschnikowiidae, Palaeospongillidae, Potamolepiidae and Lubomirskiidae. Haplosclerina and Petrosina appear closely related morphologically and are controversial higher taxa. They may be conveniently separated by the absence of a clear anisotropic skeletal structure and the apparent oviparous reproduction in Petrosina. Spongillina appear more distantly related and are characterized by absence of a tangential ectosomal skeleton, possession of spined megascleres and unique amphidisc microscleres, and gemmules with an elaborate anatomy and physiology.
Keywords: Porifera; Demospongiae; Haplosclerida; Haplosclerina; Petrosina; Spongillina subord.nov.

DEFINITION, DIAGNOSIS, SCOPE

Definition

Demospongiae in which the main skeleton is partially or entirely composed of an isodictyal anisotropic or isotropic, occasionally alveolate reticulation of spongin fibres and/or spicules, with uni- to multispicular tracts of diactinal spicules forming triangular, rectangular or polygonal meshes. Megascleres are exclusively oxeote or strongylote, bonded together with collagenous spongin or enclosed within spongin fibres; microscleres, if present, may include sigmas and/or smooth toxas (both frequently centrangulate), microxeas or microstrongyles, and in one group amphidiscs.

Diagnosis

Encrusting, massive, lobate, tubular, arborescent, flabellate or excavating sponges. Habit, colour and oscular features broadly variable. Consistency generally compressible to soft, brittle or hard and incompressible in one group. Ectosomal skeleton usually unispicular, tangential, regular reticulation of single spicules, bundles or spongin enforced fibres. It may be frequently absent or occasionally developed into a thick impenetrable crust. Choanosomal skeleton a regular isodictyal reticulation of megascleres encased in variable amounts of spongin. The reticulation may take the form of a strictly unispicular-isotropic skeleton. Frequently it is anisotropic with thicker or thinner ascending tracts interconnected by single spicules or thin tracts. In some groups the skeletal tracts are arranged in thickly alveolar fashion in which meshes may become rounded and result in a disoriented reticulation. Spicules usually are relatively short fusiform sharply pointed oxeas ('cigar-shaped'), which in general may be easily differentiated from oxeas in other orders. Strongyles are also common and it is not infrequent that they derive from juvenile oxeote stages. Oxeas and strongyles may also occur together, then often in different size categories, the smallest of which may be functional microscleres and then are dubbed microxeas or microstrongyles. These are usually concentrated in the ectosome. Megascleres are usually smooth, but in one suborder are frequently finely spined. Microxeas occurring in that same group are also invariably spined. Further microscleres in the order are sigmas, toxas and raphides. In one suborder there is a unique microsclere type, the amphidiscs, associated with the gemmule resting stage. Sigmas and toxas are often characteristically angularly bent, making them distinct from such microscleres in other orders. Two of the three suborders share secondary metabolites of the pyridine and acetylene compound types. One monotypical genus has a sclerosponge basal skeleton.

Scope

Three suborders and 13 families are recognized. Together these sponges occur in all habitats, including freshwater, in all seas and on all continents. The order comprises the highest biodiversity of all sponges in terms of species and habitats.

Taxonomic history

Synonymy. Haplosclerina Topsent, 1928c. Haplosclerida de Laubenfels, 1955b. Nepheliospongida Bergquist, 1980. Petrosida Boury-Esnault & Van Beveren, 1982.

History of Haplosclerida. An extensive historical account of ideas of classification of marine sponges now united in this order may be found in De Weerdt (1985: 16). For the freshwater sponges, a survey of ideas on classification are presented elsewhere (Manconi & Pronzato, this volume). It is beyond the present chapter to repeat these, and only a few major ideas are here elaborated. The marine sponges were originally distributed among two groups, chalinid sponges with spongin as a major component of the skeleton, and renierid sponges without visible spongin. Such a subdivision was already employed by Schmidt (1870), and was also used by Vosmaer (1887) and Ridley & Dendy (1887), for example, Renierid sponges were frequently associated with the genus

Halichondria and some other halichondrid genera. Topsent (1928c) was the first to include both types of sponges into a single group, and to disassociate them from halichondrids. This was followed by most major authors since then. De Laubenfels (1936a) attempted to compromise the integrity of Haplosclerida by adding a group of chelae-bearing poecilosclerid genera into it, which he called 'Desmacidonidae'. The contents of his Desmacidonidae are at present distributed over many different suborders and families of Poecilosclerida and all have been excluded from Haplosclerida long since. A recent attempt (Hajdu *et al*., 1994b) to reintroduce a chela-bearing family (Isodictyidae) into Haplosclerida likewise was refuted (Samaai *et al*., 1999) and is not adopted in the present volume. Chalinid and renierid sponges continued to be recognized within Haplosclerida as basal stemgroups representing two diverging lines of evolution (cf. Griessinger, 1971; Lévi, 1973). They were employed as 'families' Haliclonidae and Renieridae, with a third family Gelliidae for taxa with microscleres. Independently, a fourth overlapping family Adociidae was employed by some authors. Subsequently the classification was refined and diversified (Van Soest, 1980; Bergquist & Warne, 1980; Bergquist, 1980; De Weerdt, 1985). Van Soest, followed by De Weerdt, recognized five families among marine haplosclerids, three of which may be regarded to belong in the 'chalinid' group, and two in the 'renierid' group. However, continuation of the terms chalinid and renierid for the two groups was demonstrated to be impossible, as it was made clear that *Reniera* itself belonged to the chalinid group. Bergquist (1980) proposed to subdivide the order into two distinct (and according to her unrelated) orders, viz., Haplosclerida *s.s.* and Nepheliospongida, again more or less covering the chalinid vs. the renierid lines. The name Nepheliospongida was later replaced by Petrosida (see Boury-Esnault & Van Beveren, 1982; Hartman, 1982), because the fossil genus *Nepheliospongia* could not be linked with the recent members of the group on convincing evidence (amongst others, the presence of spicules in *Nepheliospongia* could not be demonstrated). The first order, Haplosclerida *s.s.* was postulated to incubate their larvae, the second, Petrosida was postulated to be oviparous. So far this distinction is upheld in various studies (e.g., Wapstra & Van Soest, 1987; Ilan & Loya, 1990; Fromont, 1994; Fromont & Bergquist, 1994). In addition, the second group would have unique chemistry by exclusively possessing sterols with a cyclic sidebranch. Subsequent studies have failed to substantiate the chemical distinctness of the Petrosida (cf. Fromont *et al*., 1994), and other chemical characters (notably 3-alkyl piperidine derivatives, cf., Andersen *et al*., 1996 and straight-chain acetylenes, cf. Van Soest *et al*., 1998) have been found to occur over both groups, re-establishing their close relationship. Nevertheless, the two groups are recognizable and definable on the basis of skeletal architecture in addition to the difference in reproductive strategy. Since both show many similarities in spicule form and size, and share unique chemistry, they are here recognized as suborders, along with the freshwater sponges. The sclerosponge genus *Calcifibrospongia* is newly assigned to Petrosina in a family of its own, Calcifibrospongiidae.

Biology. Marine Haplosclerida are typical inhabitants of shallow-water and intertidal habitats, reefs and mangroves, where they form a colourful and striking element of the filter-feeding community. Several species may reach a large size and presumably these represent long-lived microhabitats for a large variety of symbionts. One genus is excavating limestone substrates (corals, shells) and several groups may live buried in the sediment. Larvae of at least one suborder have a characteristic ciliation pattern consisting of a 'skirt' of longer cilia surrounding a bare posterior pole. Freshwater sponges with few exceptions have gemmules as a resting stage to tide them over adverse conditions (ice, drought). The gemmules also enable them to cross large areas of dry land by means of wind transport or bird's feet.

Previous reviews. Griessinger (1971), Bergquist & Warne (1980), Van Soest (1980), Desqueyroux-Faúndez (1984, 1987), de Weerdt (1985, 1986), Fromont (1991, 1993), Penney & Racek (1968).

KEY TO THE SUBORDERS OF HAPLOSCLERIDA

(1) Marine sponges 2
Freshwater sponges ..... **Spongillina**

(2) Skeleton anisotropic, i.e., consists of clearly recognizable ascending spicule tracts or fibres interconnected at regular distances by secondary spicule tracts or fibres. Larvae are incubated ..... **Haplosclerina**
Skeleton isotropic, i.e., consists of a reticulation without a clear orientation and without distinction in primary ascending and secondary interconnecting spicule tracts or fibres, skeleton densely confused. Larvae unknown, presumably oviparous ..... **Petrosina**