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

Order Hadromerida Topsent, 1894

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Hadromerida Topsent (Demospongiae), including Clavulina Vosmaer and Astromonaxonellida Dendy, contains 23 nominal families or subfamilies of which 13 families are recognised here (two allocated as *incertae sedis*). The order includes sponges with monaxonic megascleres (tylostyles, subtylostyles, oxeas or derivatives) producing radiate or subradiate skeletal arrangement, although this arrangement may be obvious only in the peripheral skeleton in some, often with scarce spongin and consequently firm, non-elastic consistency. Ectosomal spicules are often smaller than choanosomal ones, and where present these may form a prominent cortical skeleton. Microscleres may include various forms of euasters, spirasters, rhabds, microxeas and/or raphides, although many hadromerids lack microscleres altogether. Hadromerid sponges are known from all oceans at all depths.

Keywords: Porifera; Demospongiae; Hadromerida; Acanthochaetetidae; Alectonidae; Clionaidae; Hemiasterellidae; Placospongiidae; Polymastiidae; Sollasellidae; Spirastrellidae; Stylocordylidae; Suberitidae; Tethyidae; Timeidae; Trachycladidae.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

[suborder] Hadromerina Topsent, 1894. [order] Hadromerina Topsent, 1928c. Hadromerida de Laubenfels, 1936a. Clavulina Vosmaer, 1885b (part). Astromonaxonellida Dendy, 1905.

Definition

Demospongiae with monaxonic megascleres (tylostyles, subtylostyles, oxeas or derivatives) forming radiate or subradiate skeletal arrangement, sometimes only obvious in the peripheral skeleton; ectosomal spicules usually smaller than choanosomal ones, and where present they may produce a cortical skeleton; spongin often sparse producing firm non-elastic consistency; microscleres may include various forms of euasters, spirasters, rhabds, microxeas and/or raphides in trichodragmata, or absent in many taxa.

Diagnosis

Sponges with uniform spiculation of monaxonic megascleres (monactinal or diactinal, most often tylostyles or subtylostyles, but also including exotyles, strongyloxeas, oxeas or modified forms of these). Sponges are frequently massive with megascleres radially arranged throughout the entire skeleton (e.g., Tethyidae), or with this arrangement only obvious at surface (e.g., Polymastiidae), but typical growth forms also include excavating forms (Clionaidae), thinly encrusting (e.g., Timeidae), spherical (Tethyidae), stipitate (Tethyidae, Polymastiidae, Stylocordylidae, Suberitidae), vasiform and arborescent branching forms (e.g., Hemiasterellidae, Trachycladiidae). Megascleres usually consist of more than one size class, with ectosomal spicules often smaller than choanosomal spicules, usually standing perpendicular to the surface, protruding through the ectosome and forming a hispid palisade or cortical skeleton. Spongin fibres are generally poorly developed (if at all present), frequently producing a firm, non-elastic, friable consistency, although in several genera (e.g., *Caulospongia*, *Suberites*) spongin is abundant and these taxa are more compressible and elastic. Bright colours are common (yellows, oranges, reds) but generally not diagnostic, and in some cases (e.g., encrusting forms), colouration may be produced by symbionts. Where known choanocytes have a periflagellar sleeve. Microscleres may consist of euasters, sterrasters, streptasters and derivatives, spherasters, micrasters, anthasters, lophasters, pseudasters (amphiasters), spirasters, spiraster-like spirules, microrhabds, microxeas or microstrongyles, but are absent in several families. Most groups are oviparous (where known), with eggs extruded and development of parenchymella larvae (in one case a blastula larva) directly in seawater. Budding is common in Tethyidae.

Scope

Twenty three family or subfamily taxa have been included in Hadromerida at one time or another, although only 13 families are recognised in this work (two *incertae sedis*): Acanthochaetetidae Fischer, 1970; Alectonidae Rosell, 1996b; Clionaidae d'Orbigny, 1851; Hemiasterellidae Lendenfeld, 1889b; Placospongiidae Gray, 1867a; Polymastiidae Gray, 1867a; Sollasellidae Lendenfeld, 1887a (*incertae sedis*); Spirastrellidae Ridley & Dendy, 1886; Stylocordylidae Topsent, 1928c; Suberitidae Schmidt, 1870; Tethyidae Gray, 1848; Timeidae Topsent, 1928c; Trachycladidae Hallmann, 1917c (*incertae sedis*). Other nominal families are synonymised as follows: [Astraxinellidae] Dendy, 1905 and Leptosastrinae Topsent, 1928c are synonyms of Hemiasterellidae; [Spirophorellinae] Lendenfeld, 1889b (*nomen nudum*) and Rhaphidistiinae de Laubenfels, 1936a are synonyms of Trachycladidae; Thoosidae Rosell & Uriz, 1997 is a synonym of Alectonidae; Choanitidae de Laubenfels, 1936a is a synonym of Spirastrellidae; Tabulospongiidae Mori, 1976 is a synonym of Acanthochaetetidae; Donatiadae Carter, 1875c and Xenospongiidae Carter, 1882b are synonyms of Tethyidae. Chondrosiidae Schulze, 1877 (emend. Chondrosiidae Wiedenmayer, 1977; =Chondrillidae Gray, 1872a) is allocated to its own order.

Remarks

Topsent (1898a) initially included nine families into his suborder Hadromerina, and further proposed to subdivide the taxon into two Sections, Aciculida (as Aciculides) with diactinal megascleres (containing Coppatiidae, Strepasteridae, Tethyidae, Stylocordylidae) and Clavulida (as Clavulides) with monactinal megascleres (containing Clionaidae, Spirastrellidae, Polymastiidae, Suberitidae, Mesapidae). In his 1904 monograph Topsent also included some genera now allocated to Desmoxyidae (e.g., *Heteroxya*) in his group Aciculides. Hentschel (1923) and Wilson (1925) adopted Topsent's scheme, and added the families Chondrosiidae and some other genera of [Astraxinellidae] (=Hemiasterellidae). Topsent (1928c: 33) subsequently elevated Hadromerina to ordinal status, and also abandoned his earlier subdivision of the order given that Tethyidae had monactinal megacleres (but otherwise conformed with Aciculida, which was characterized by diactinal megascleres), and that Chondrosiidae 'suppressed' its megascleres making its allocation to one or the other group equivocal. In this revision Topsent (1928c) included Spongosoritidae (now in Halichondrida), Coppatiidae (now in Astrophorida) and Chondrosiidae (now in its own order Chondrosida), together with seven 'typical' families (Clionidae [now Clionaidae], Polymastiidae, Spirastrellidae, Stylocordylidae, Suberitidae, Tethyidae, Timeidae). He admitted (p. 34) that Chondrosiidae, in particular, was not a straightforward allocation to Hadromerida, and he also reallocated [Astraxinellidae] (=Hemiasterellidae) to the Halichondrida, although again with some reservations (pp. 38–39) about the validity and affinities of this family.

Some 19th and 20th century authors did not follow Topsent's (1898a, 1904, 1928c) system (e.g., Dendy, 1922b; Burton, 1932b, 1959a), preferring instead the earlier classifications, such as those proposed by Ridley & Dendy (1887) and Sollas (1888), in which hadromerids were often assigned to a suborder Clavulina Vosmaer, 1885b, or sometimes to a family Clavulidae. In this latter scheme, as modified by Ridley & Dendy (1887) two families were recognised: Suberitidae (which included genera now assigned to Stylocordylidae, Polymastiidae, Clionaidae) and Spirastrellidae (which also included Latrunculiidae). Ridley & Dendy (1887) also remarked on the probable relationship between these taxa and the Halichondrida, notably the common possession of radially arranged tylostyles; cork-like granular 'ground substance'; presence of a distinct fibrous cortex; and absence of spongin in the skeleton.

De Laubenfels (1936a) was probably the first to formally adopt Topsent's scheme, and was followed by most contemporary authors working on hadromerids (e.g., Bergquist, 1968 *et seq*.). De Laubenfels' (1936a) treatment of the order is a useful précis of hadromerid apomorphies, noting that the possession of a radiate or subradiate architecture, the total, or almost total, lack of spongin, and a pronounced cortical specialization in the ectosome were indicative of affinities with the 'tetraxon sponges' (now assigned to the orders Astrophorida, Spirophorida and Chondrosida, and including many 'Lithistida'), and he suggested that they differ from these 'tetraxon' orders principally in having tylostyles as their chief megascleres. Conversely, his speculation that this latter feature, together with the possession of spongin in some taxa, indicated that they may be more closely related to Poecilosclerida, is now discounted and supported by non-morphological evidence (e.g., common possession of oviparous reproductive strategy), and to a large degree validates a 'tetraxon sponge' clade (e.g., Bergquist, 1978). De Laubenfels (1936a) recognised only five families, differentiated primarily by their microsclere composition: Spirastrellidae (as Choanitidae), which included Timeidae (as a subfamily); Suberitidae (including Polymastiidae); Placospongiidae; Clionidae (now Clionaidae); and Gastrophanellidae (for a small group of 'lithistids' with tylostyles or exotyles). Other taxa that we now include in Hadromerida were mostly assigned to his order Epipolasida, such as Tethyidae, Stylocordylidae (which he included in Podospongiidae), and Trachycladidae.

Major contemporary syntheses of the sponge classification (e.g., Lévi, 1973; Bergquist, 1978; Hartman, 1982; and others) agree on a core component of Hadromerida (containing eight families: Tethyidae, Polymastiidae, Suberitidae, Spirastrellidae, Clionidae (=Clionaidae), Placospongiidae, Timeidae and Stylocordylidae). Conversely, there are several other families disputed by contemporary authors as having Hadromerida affinities. Some of these have been recently settled based on additional non-morphological evidence. Chondrosiidae (=Chondrillidae) was elevated to full ordinal status (Boury-Esnault & Lopes, 1985), and is now allocated to its own order Chondrosida. Latrunculiidae was found to be polyphyletic, now subdivided into two families, both allocated to the Poecilosclerida (see chapters by Kelly & Samaai and Samaai & Kelly, this work). Acanthochaetetidae are hypercalcified sponges ('sclerosponge' grade of construction) which show clear morphological (spicular) affinities to the Spirastrellidae (e.g., Van Soest, 1984a; Wood, 1990), with additional recent molecular support from 28S rRNA sequences to support this hypothesis (Chombard *et al*., 1997). Sollasellidae is *incertae sedis* within Hadromerida, showing (perhaps) superficial similarities to some 'true' hadromerids. It is similar to Polymastiidae in having a cortical skeleton, especially to *Pseudotrachya* with which it shares the combination of choanosomal styles and ectosomal oxeas. Similarly, it shows similarities with some Suberitidae, such as *Homaxinella*, and Stylocordylidae, sharing a stalked habit and axially condensed skeleton (see chapter by Van Soest, this volume). However, Sollasellidae remains poorly known and these affinities are relatively speculative.

The allocation of Hemiasterellidae and Trachycladidae to Hadromerida is more controversial, and to date lacks any definitive molecular or other non-morphological support. These families are remnants of the now dismantled order Axinellida, with both assigned to Hadromerida based on megasclere and microsclere morphologies and skeletal structure, whereas other families once assigned to the axinellids are allocated to Poecilosclerida and Halichondrida (see respective chapters in this volume). Assigning Hemiasterellidae to Hadromerida is fairly straightforward using morphological criteria, with the common possession of euasters, monactinal megascleres and radial skeletal architecture, at least at the surface (Voultsiadou-Koukoura & Van Soest, 1991a). Chemotaxonomic support for this hypothesis (Hooper *et al*., 1992), however, is equivocal. Hemiasterellids differ from other hadromerids, such as Polymastiidae and Spirastrellidae, in having axially compressed choanosomal skeletons (sometimes loosely constructed or hymedesmoid, e.g., *Paratimea*) and an ectosomal palisade which appears to be homologous to the 'typical' hadromerid cortical skeleton. Hemiasterellids also show similarities to *Aaptos* (Suberitidae) and *Tethya* (Tethyidae) in having predominantly style megascleres, rather than tylostyles found in many hadromerid taxa, although some hemiasterellids retain long oxeas in the extra-axial skeleton (see chapter by Hooper, this volume).

Conversely, the affinities of Trachycladidae remain unclear. There are no reproductive, molecular or chemical data to support any morphological hypotheses. Brøndsted (1924b) suggested a close relationship between *Trachycladus* and Spirastrellidae, given fundamental similarities in their microsclere geometries, although with equally fundamental differences in patterns of spination of these microscleres. Peripheral skeletal architecture of trachycladids is plumoreticulate; the axial skeleton is compressed (both composed of oxeas or modified oxeote megascleres); and the ectosomal skeleton is composed of a cortical skeleton of microscleres (spined vermiform spinispirae), together with smooth microrhabds scattered throughout the skeleton (see chapter by Hooper and Van Soest this volume). These characteristic spinispirae resemble spirasters, common to some hadromerids, but the homology of these two forms of spicules remains to be determined. Trachycladidae is *incertae sedis* within Hadromerida.

Several more recent publications provide new insights on the affinities of Hadromerida, although none of these treatments include all the families assigned here, with most concerning only the 'typical' families of hadromerids. These works include: (1) new alkaloids as taxonomic markers for the order (Bergquist *et al*., 1991a); (2) structure of the aquiferous system (Bavestrello *et al*., 1998b); (3) 28S rRNA sequence data (Chombard *et al*., 1999) – which hypothesised the inclusion of family Halichondriidae in the Hadromerida (supporting Topsent's (1928c) earlier proposal to include Spongosoritidae in this order), and proposed further to recognise four suborders: Spirastrellina, Timeina, Polymastiina and Suberitina; (4) 18S rRNA sequence data (Kelly-Borges *et al*., 1991), which apparently were insufficiently informative to resolve the phylogeny at the higher taxonomic level (Chombard *et al*., 1999); (5) the phylogenetic significance of an excavating habit amongst hadromerids (Rossell & Uriz, 1997); (6) an analysis of the phylogenetic significance of skeletal architecture (including presence or absence of axial compression), megasclere geometry (presence, absence and secondary loss of triaenes), microsclere geometry (including euaster geometries and their derivatives), reproductive strategy (ovipary versus vivipary), and other features used to assess the relationships of Hadromerida within a tetractinellid clade (amongst others) (Van Soest, 1991); (7) an evaluation of chemistry used as chemotaxonomic markers (Van Soest & Braekman, 1999) – who evaluated the approximately 185 secondary metabolites described from Hadromerida and concluded that there were no distinct compounds that could be used reliably as taxonomic markers for the order, although several appeared to be useful for family-level taxa.

Distribution

Recorded from all oceans at all depths.

Previous reviews

Lévi, 1973; Bergquist, 1978; Hartman, 1982; Chombard *et al*., 1999.

KEY TO FAMILIES

(1) Microscleres euasters 2
Microscleres sterrasters 3
Microscleres streptasters and/or microstrongyles or microrhabds 4
Microscleres spined 'corkscrew shaped' spinispirae 6
Asterose microscleres absent 7

(2) Megascleres styles, oxeas or both, forming compressed axial (or basal) skeletons and plumo-reticulate or radial peripheral skeletons; growth forms commonly arborescent, massive and vasiform, occasionally encrusting; microscleres euasters with smooth and/or partially microspined rays .... **Hemiasterellidae**
Megascleres stylote, mainly strongyloxeas (but sometimes subtylostyles, tylostyles or anisostrongyles) forming radial bundles or sometimes parallel tracts, and frequently with a well-developed ectosomal cortical skeleton; growth forms commonly spherical, globular or massive; microscleres often include two categories of euasters (micrasters and megasters), sometimes also with microrhabds, microstrongyles, exotyles and spheres .... **Tethyidae**
Megascleres single or tracts of tylostyles running to the surface; growth forms predominantly encrusting; microscleres are euasters (including anthasters and lophasters) or pseudasters (amphiasters) forming a densely packed cortical skeleton .... **Timeidae**

(3) Microscleres sterrasters (selenasters or amphiaster-like (amphinolasters)) forming a strong cortical skeleton of polygonal plates, and with accessory microscleres being spirasters, spherasters and spherules; megascleres are tylostyles in tracts radiating from the base toward the surface and supporting the margins of the cortical plates .... **Placospongiidae**

(4) Megascleres tylostyles 5
Megascleres styles, oxeas or strongyles (occasionally absent completely), being smooth or spiny and kinked or sometimes branched; microscleres amphiasters (streptasters), usually microspined with spines arranged uniformly, clustered, or spiraled, and/or microrhabds (straight, bent, or spiral); growth forms mostly excavating, forming chambers .... **Alectonidae**

(5) Megascleres sparse tylostyles forming ascending radial tracts and protruding through the surface; microscleres streptasters (spirasters, diplasters, spiny microstrongyles) forming a dense cortical skeleton and also a basal crust; early stages may be excavating but adults are only encrusting or submassive, not endolithic, with the aquiferous system confined to the external surface and consisting of meandering vein-like structures converging on oscula .... **Spirastrellidae**
Megascleres tylostyles, styles or oxeas; skeletal arrangement varies depending on stage of development, confused in excavating (alpha) growth forms, or confused and with ill-defined tracts in encrusting (beta) and massive (gamma) forms; ectosomal skeleton a cortical skeleton of megascleres in a palisade; microscleres streptasters and/or microrhabds of different types .... **Clionaidae**
Megascleres erect tylostyles and microscleres relatively large streptasters both reinforcing a thin veneer of soft tissue covering a hypercalcified ('sclerosponge') basal skeleton .... **Acanthochaetetidae**

(6) Megascleres oxeas, strongyles and/or (tylo-)styles, forming a compressed axial region and a plumose or plumo-reticulate extra-axial region; microscleres spined 'corkscrew shaped' spinispirae and smooth microrhabds .... **Trachycladidae**

(7) Cortical skeleton well-developed 8
No well-developed cortical skeleton 9

(8) Ectosome with a more-or-less complicated cortical skeleton, always with an outer palisade of ectosomal spicules (tylostyles, or oxeas and/or exotyles); megascleres tylostyles, subtylostyles, strongyloxeas, styles or oxeas forming a radiating choanosomal skeleton; microscleres absent apart from occasional centrotylote microxeas, acanthose microxeas or raphides in trichodragmata .... **Polymastiidae**

(9) Ectosomal skeleton with bouquets or a palisade of spicules 10
Ectosomal skeleton composed of oxeas or stylotes 11

(10) No ectosomal cortical skeleton present but megascleres are arranged in bouquets or a palisade in the peripheral skeleton; megascleres usually tylostyles, often with a pronounced or modified tyle, but occasionally styles, strongyloxeas or centrotylote oxeas; choanosomal structure may be strictly radial, or show a strong axial orientation; more massive species become progressively more confusedly arranged towards the interior; microscleres absent apart from occasional microrhabds or trichodragmas .... **Suberitidae**

(11) Megascleres centrotylote oxeas or strongyles forming radial tracts in the sponge ‘body’, also often with smaller oxeas or stylotes at the surface, partly arranged in a tangential layer both on the main body and lining the stalk; stipitate habit, with a thin stalk and globular-oval ‘body’ flattened at the top (confined to deep water) .... **Stylocordylidae**
Megascleres long styles and short oxeas forming three distinct zones: a confused mass in the centre of the body; a subcortical region with low spicular density traversed by bundles of a single style surrounded by a mass of oxeas bound by spongin; and an external cortical skeleton strengthened by short oxeas; growth form is stalked, ramose with polygonal ornamentation of lines of inhalant openings on the surface .... **Sollasellidae**