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

Order Astrophorida Sollas, 1888

John N.A. Hooper[1] & Rob W.M. Van Soest[2]

[1]Queensland Museum, P.O. Box 3300, South Brisbane, Qld, 4101, Australia. (JohnH@qm.qld.gov.au)
[2]Zoological Museum, University of Amsterdam, P.O. Box 94766, 1090 GT, Amsterdam, Netherlands. (soest@science.uva.nl)

Astrophorida Sollas (Demospongiae), also sometimes known as Choristida Sollas, include sponges with asterose microscleres and tetractinal megascleres (either sometimes lost), together with microxeas, microrhabds and oxeas, and skeletal architecture always radial, at least at the surface, but more confused towards the centre of the body. Five families are currently included (with 38 genera and two subgenera), and species are known from all oceans and at all depths.
Keywords: Porifera; Demospongiae; Astrophorida; Ancorinidae; Calthropellidae; Geodiidae; Pachastrellidae; Thrombidae.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

[Asterophora] Sollas, 1887 (*nomen nudum*). Astrophora Sollas, 1888. Astrophoridae Brien, 1968. Astrophorina Wiedenmayer, 1977b. Choristidae Sollas, 1880 (part). Choristida Sollas, 1885b (part). Tetractina Vosmaer, 1885b (part). Not Tetractinellida Marshall, 1876. Epipolasida *sensu* de Laubenfels, 1936a (in part).

Definition

Demospongiae with asterose microscleres, sometimes with microxeas and microrhabds, and with tetractinal megascleres and oxeas radially arranged at least peripherally.

Diagnosis

Sponges usually have a coarse texture emphasizing silica content over spongin in the skeleton. Microscleres are asters in one or more categories (sometimes lost), sometimes accompanied by microxeas and microrhabds. Megascleres are tetractinal, usually triaenes, calthrops, or short-shafted triaenes, together with oxeas, always with some radial skeletal architecture obvious at least in the peripheral skeleton, and with architecture often more confused towards the centre of the body. In genera that have lost tetractinal megascleres, leaving only oxeas, there is always some radial skeletal organisation remaining. Reproduction is oviparous although gametes are so far described for very few species. Larval stages are not yet known.

Scope

Five families, 38 genera and two subgenera are currently included in this order: Ancorinidae Schmidt, 1870 (with 15 genera: *Stelletta, Tethyopsis, Cryptosyringa, Rhabdastrella, Jaspis, Ancorina, Disyringa, Stryphnus, Ecionemia, Psammastra, Penares, Melophlus, Asteropus, Tribrachium, Holoxea*), Calthropellidae Lendenfeld, 1907 (with four genera: *Calthropella, Chelotropella, Pachastrissa, Pachataxa*), Geodiidae Gray, 1867a (with six genera: *Erylus, Caminus, Geodia, Isops, Pachymatisma, Sidonops*), Pachastrellidae Carter, 1875b, including Theneidae Carter, 1883 (with 12 genera and two subgenera: *Acanthotriaena, Ancorella, Brachiaster, Characella, Cladothenea, Halina, Pachastrella, Poecillastra, Stoeba, Thenea, Triptolemma, Vulcanella, Vulcanella (Annulastrella), Vulcanella (Vulcanella)*, and Thrombidae Sollas, 1888 (monotypic: *Thrombus*).

Remarks

Sollas's (1888) early concept of suborder Astrophora was defined as "*Choristida in which one or more of the microscleres is an aster*", with order Choristida defined as Tetractinellida lacking 'lithistid' desmas, and in turn the Tribe Tetractinellida defined to include Demospongiae with triaene or tetraxon megascleres, or desmas. Disassembling this hierarchy of taxa into an inclusive definition for the order Astrophorida we arrive exactly at the definition presented by Hartman (1982), repeated above. That this concept has survived over a century of revisions is perhaps testimony to its robustness amongst the Porifera. Early histories of the order are provided by Sollas (1888: cii) and Topsent (1928c: 25).

This order is sometimes referred to as Choristida, a taxon which is still occasionally used by some contemporary authors. However, 'Choristida', as originally proposed by Sollas (1880) and subsequently refined by Vosmaer (1882b) and Sollas (1886a), differs from Astrophorida in both its content and definition. Conversely, usage of 'Choristida' by contemporary authors (e.g., Bergquist, 1978) generally refers to Astrophorida *s.s*. and not to Choristida *s.s*., because under Sollas's (1886a) definition the latter taxon contained families currently assigned to Astrophorida (Pachastrellidae, Theneidae, Stellettidae and Geodiidae) + Homosclerophorida (Corticiidae) + Spirophorida (Tetillidae). Tetractinellida *sensu* Zittel (1879), which explicitly excluded 'Lithistida', essentially mirrors that of Choristida, and for this reason the taxon was renamed Tetractina by Vosmaer (1885b).

In the 'Challenger' report on the Tetractinellida Sollas (1888) again revised Choristida and proposed three suborders: (1) Sigmatophora Sollas, 1887 (containing Tetillidae and Samidae), which we now know as order Spirophorida; (2) Microsclerophora Sollas, 1887 (containing Plakinidae, Corticiidae and Thrombidae), which is clearly polyphyletic; and (3) Astrophora Sollas, 1888 (with three 'Demi' containing Theneidae, Pachastrellidae, Stellettidae, Epipolasidae (with question), Geodiidae and Placospongiidae) (see below). Bergquist (1968) employed 'Choristida' in the sense of Lendenfeld (1903), Hentschel (1923), Topsent (1928c), de Laubenfels (1936a) and others, all of who

contributed to refining the taxon to a point where it became nearly synonymous with our present understanding of Astrophorida (although Bergquist retained Tetillidae in the order but relegated *Pachastrella* to the Homosclerophorida).

Thus, the concept of the taxon Choristida has now nearly merged with that of Astrophorida, and the choice of one name over another might be decided by the Rules of Priority (Choristida has seniority over Astrophorida). However, suprafamilial taxa are not bound by the rules of the ICZN (Anon., 1999), and consequently we follow Lévi (1973) and Hartman's (1982) usage of Astrophorida. This decision is justified on the basis that its present usage is nearly identical to the original concept of Sollas (1887), whereas Choristida, as used by contemporary authors, bears little resemblance to the original taxon. Furthermore, as far as we can ascertain there has never been a genus 'Choristes', so in effect Choristidae Sollas, 1880 could also be construed as a *nomen nudum*.

This present understanding of Astrophorida follows Lévi (1973: 595), who elevated it to ordinal status. He excluded [Epipolasidae] Sollas, 1888 (which he placed in an order *incertae sedis*) and Placospongiidae (which he referred to Hadromerida), and added the families Thrombidae and Calthropellidae. The most recent comprehensive treatment of Astrophorida, that of Hartman (1982), included seven families (Stellettidae, Geodiidae, Calthropellidae, Pachastrellidae, Theneidae, Thrombidae and Jaspidae (also known as Coppatiidae)), and some of these are merged here to form a revised ordinal taxon that contains only five families.

Other families included in Astrophorida at one time or another are now allocated elsewhere as follows: Stellettidae Carter, Coppatiidae Topsent and Jaspidae de Laubenfels are included here in Ancorinidae; Erylidae Lendenfeld is included in Geodiidae; [Epipolasidae] Sollas, 1888, is also a *nomen nudum* with the genus *Epipolasis* de Laubenfels, 1936a (not erected until half a century after the family was established), now included in Halichondriidae while the other genera included in [Epipolasidae] by Lévi (1973) (*Jaspis, Stelletinopsis, Asteropus*) are referred in Ancorinidae (see chapter by Uriz, this volume). Theneidae Carter is included here in Pachastrellidae, although this allocation remains controversial (see chapter by Maldonado, this volume). Corticiidae is a junior synonym of Plakinidae, and now allocated to order Homosclerophorida, and Tetillidae belongs to the order Spirophorida. There have been several proposals to subdivide the order Astrophorida, based on aster morphology. The earliest of these schemes was that of Sollas (1888: cxiii) who proposed three clades. (1) Demus Streptastrosa Sollas, 1888 ("*in which one of the microscleres is a spiraster, or when this is not the case one of the megascleres is a calthrops*"), containing Theneidae and Pachastrellidae. (2) Demus Euastrosa Sollas, 1886a ("*in which euasters are always present, but never spirasters nor sterrasters… Triaenes are present but not calthrops*"; Sollas, 1887), containing the Stellettidae (and [Epipolasidae]). (3) Demus Sterrastrosa Sollas, 1887 ("*in which the characteristic microsclere is a sterraster*"), containing the Geodiidae (and Placospongiidae). These three 'Demi' were united by the common possession of some form of aster, and also frequently possessing a second distinctive category of aster (forming the clade Astrophorida). This scheme was 'unnatural' (polyphyletic) and has long since been abandoned.

By comparison, the most recent of these schemes was suggested by Reid (1963a, 1968d), and reiterated by Lévi (1991) and Chombard *et al*. (1998), who recognised two orders, Euasterophorida Reid, 1963a and Streptosclerophorida Dendy, 1924, to remove the traditional barrier between the astrophorids and lithistids. (1) Euastrophorida (with euasters – including sterrasters, oxyasters, aspidasters, strongylasters etc.), contained Geodiidae, Ancorinidae and Calthropellidae. (2) Streptosclerophorida (with streptosclere microscleres – including sanidasters, metasters, amphiasters, plesiasters etc.) (refer to Chombard *et al*., 1998, for illustrations of microsclere morphology), contained Pachastrellidae (including Theneidae) and Thrombidae, in addition to many desma-bearing 'lithistid' taxa with obvious astrophorid affinities (i.e., those bearing triaenes: Tetracladina Zittel, 1878c; Megamorina Zittel, 1878c; Dicranocladina Schrammen, 1924a and Streptosclerina Reid, 1963a (also known as Asterostreptidae Topsent, 1902)). This proposal has potential merit, and as such the Key to Families, provided below, was constructed based on this fundamental subdivision of the order Astrophorida. However, it requires further morphological and molecular resolution, particularly with regard to the question of incorporating 'Lithistida' into the present concept of Astrophorida (see below), and as such it is not been progressed further here. Furthermore, there appears to be an overlap between the groups Euastrophorida and Streptosclerophorida. Genera such as *Stryphnus* and *Asteropus* (and to a lesser extent *Ancorina* and *Ecionemia*), have both euasters and streptasters. It may be significant that sanidasters and amphiasters of these genera appear to be based on a straight rod, and appear at first glance not to be spiral, as are the spirasters and metasters of Pachastrellidae. But this problem of homology is indeed contentious and needs further study.

Discussion of the concepts of Astrophorida and Choristida also requires consideration of the nominal order Tetractinellida, proposed by Marshall (1876) and further developed by Sollas (1888) and Lendenfeld (1907) in particular. Sollas (1888: xcix) defined the order as "*Demospongiae in which some or all of the scleres are tetraxons, triaenes, or desmas*". Tetractinellida contains what we now know as Astrophorida + Spirophorida + 'Lithistida', sharing the possession of tetraxon spicules as its only apomorphy. Inclusion of 'Lithistida' into this clade, based on this apomorphy at least, is questionable given that not all 'lithistids' contain triaene megascleres, but this observation merely supports the already well-espoused hypothesis that 'Lithistida' are polyphyletic (e.g., Kelly Borges & Pomponi, 1994), whereas the majority of 'lithistid' taxa are probably true astrophorids (or tetractinellids). In this regard, Reid's (1963a) proposal to subdivide the 'Lithistida' into several orders and suborders (based on both the desma and free spicule morphologies) may have some merit, although his allocation of other non-lithistid taxa to this scheme is highly contentious and not accepted by most contemporary authors. Interestingly, Sollas (1888: c) adopted a contrary position, arguing that 'Lithistida' lacking tetraxons (or triaxons) had probably lost them, and he strongly supported the possession of desmas as a phylogenetically informative character to unite the clade 'Lithistida'. This position is one to which we have returned to in this volume (see chapters on 'Lithistida' by Pisera & Lévi, this volume) – but one that is perhaps based more on ignorance rather than on any substantial new knowledge of this taxon since the early 20th century. Resolving the 'lithistid' dilemma remains a future challenge that might best be resolved from molecular datasets.

This concept of Tetractinellida, including Reid's (1963a) proposed classification, was recently revisited using both morphological and 28s rRNA molecular data (Chombard *et al*., 1998), lending support to the recognition of a monophyletic clade, Tetractinellida, containing [(Astrophorida + 'Lithistida') and Spirophorida]. These authors noted that some pivotal astrophorid characters, such as sanidaster and amphiaster microscleres, were not necessarily

homologous amongst putative astrophorid taxa, and their use in phylogenetic analysis required more careful evaluation. They also suggested that the family Ancorinidae was polyphyletic, with two genera (*Penares* and *Stelletta*) indicated as being closer to Geodiidae and Calthropellidae, respectively, implying that the genus *Penares* should be reallocated from Ancorinidae to Geodiidae (even though there was little obvious morphological support for this allocation). However, as noted by Uriz (see family Ancorinidae, this volume), future phylogenetic analyses might better evaluate these discrepancies (and the validity of an order Tetractinellida), with the addition of further astrophorid taxa and other genes, but for the present these hypotheses are contentious. In this work we define Astrophorida to contain only non-lithistid aster-bearing taxa, with tetraxon megascleres and oxeas, and a skeleton that retains at least a peripheral radial arrangement. Astrophorids lacking asters or tetraxons are presumed secondary developments.

Previous reviews

Lévi, 1973; Bergquist, 1978; Hartman, 1982; Hooper & Wiedenmayer, 1994; Chombard *et al*., 1998.

KEY TO FAMILIES

(1) Microscleres include euasters 2
Microscleres are never euasters 3
(2) Microscleres are euasters, sanidasters or microrhabds; megascleres are long-rhabdome triaenes (sometimes absent) and oxeas ..... **Ancorinidae**
Microscleres are euasters, usually spheraster, sometimes also with microrhabds; megascleres are irregularly arranged calthrops or short-rayed mesotriaenes forming the deeper choanosomal skeleton, and radially orientated mesotriaenes or dichocalthrops forming a peripheral skeleton, mostly short-rayed; with or without oxeas ..... **Calthropellidae**
Microscleres are sterrasters, together with euasters, spherules or microrhabds; megascleres large oxeas, protriaenes, anatriaenes, and plagiotriaenes/orthotriaenes, some of which may be almost calthrops ..... **Geodiidae**
(3) Microscleres are streptasters and (in most cases) microxeas, microrhabds; megascleres include a variety of tetraxons (i.e., calthrops, short-shafted triaenes, mesotriaene, mesotriaenes-derived desmas, or long-shafted triaenes) ..... **Pachastrellidae**
Microscleres are metasters; sponge with special aquiferous openings; megascleres include long-shafted triaenes ..... **Pachastrellidae** (*Thenea* + *Cladothenea*)
Microscleres are amphiaster streptasters; megascleres are small spiny triaenes (acanthotriaenes) with simple, bifurcate and trifurcate clads ..... **Thrombidae**
Microscleres only microrhabds ..... **Ancorinidae** (*Holoxea*)
Microscleres only sanidasters ..... **Ancorinidae** (*Tribrachium*)