

Order Poecilosclerida Topsent, 1928

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Poecilosclerida Topsent (Demospongiae) contains the highest diversity of species and possibly the greatest range of morphometric characters of all Porifera, with 25 families, 129 genera and 50 subgenera recognised as valid, and several thousands of described species worldwide, distributed from intertidal to abyssal depths. Four suborders are delineated based primarily on: chelae geometry (palmate-arcuate-anchorate forms, and diancistra derivatives); presence/absence of discate microrhabds; presence/absence and geometry of other microscleres; ectosomal megasclere geometry; and choanosomal megasclere diversity, geometry and regionalisation of megascleres within the skeleton. The order is defined as containing demosponges with discrete organic and inorganic skeletons, with discrete siliceous spicules, a skeletal organisation commonly localized to particular regions (at a minimum ectosomal and choanosomal skeletons but potentially containing up to five regionally differentiated megasclere morphologies), microscleres consisting of meniscoid spicules (sigmas and derivatives such as chelae, sigmancistras, diancistras, etc., with chelae synapomorphic for the order, although not all taxa contain them), in addition to diverse other forms such as toxas, forceps, onychaetes, raphides (in trichodragmata), microrhabds, acanthomicrorhabds, anisodiscorhabds, isochiadiscorhabds, spinorhabds, thraustoxeas, spirosigmata, thraustosigmata and microstyles.

Keywords: Porifera; Demospongiae; Poecilosclerida; Microcionina; Myxillina; Mycalina; Latrunculina.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Poeciloscleridae Topsent, 1894c: 5. Poecilosclerina Topsent, 1928c: 41, 43. Poecilosclerida Topsent (*nomen correctum* de Laubenfels, 1955b: E21).

Definition

Demospongiae with skeleton composed of discrete siliceous spicules; main skeleton composed of megascleres (monactinal, diactinal or both) and spongin fibres in various stages of development; both fibre and mineral skeletons always show regional differentiation such that megascleres are often differentiated into distinct ectosomal and choanosomal components; microscleres include meniscoid forms such as chelae (unique to the order), sigmas and sigmancistra-derivatives, and other diverse forms such as toxas, raphides, microxeas and discate microrhabds; the order is predominantly viviparous with incompletely ciliated parenchymella larvae (one oviparous family (Raspailiidae), and another suspected oviparous family (Rhabderemiidae), is also included).

Diagnosis

Sponges characterized by a skeleton of both spicule and spongin elements, usually well-developed, either sometimes vestigial, in which megascleres are monactinal, diactinal or both, and spongin development varies from well-developed horny fibres enclosing spicules to an interspicular collagen cement (Bergquist, 1978; Hartman, 1982). A few groups have a fused (hypercalcified) basal calcitic skeleton or an articulated siliceous skeleton composed of desmas ('lithistid' or 'sublithistid'), along with free siliceous skeletons, with clues as to their identities provided by these free spicules, and these desmas are interpreted as ancestral features, more commonly observed in the Mesozoic faunas. Simpson (1984) suggested that the order was characterized by at least two distinctly localized

types of megascleres (with or without distinctive geometries): the larger usually choanosomal megascleres embedded in spongin fibres (=principal megascleres), and often smaller ones which are free in the mesohyl (=subectosomal auxiliary megascleres), or localized at the surface (=ectosomal megascleres), or protruding from spongin fibres in which they are embedded (=echinating megascleres) – sometimes all the latter categories are present. Conversely, various mycalid poecilosclerids have only a single category of megasclere ('mycalostyles'), with the presumption that the differentiated ectosomal and echinating megascleres have been secondarily lost (Van Soest, 1984b), or alternatively, that their presence in most other poecilosclerids is an evolutionary achievement (Hajdu *et al.*, 1994a). Poecilosclerids usually have an abundantly collagenous mesohyl, and microscleres include chelae (a synapomorphy for the order), although not all taxa have them. Sexual reproduction is predominantly viviparous, oviparous in two families (Raspailiidae, and possibly Rhabderemiidae), and in those species incubating larvae they are parenchymella with uniform flagellum size and bare posterior poles.

Remarks

Poecilosclerida is the most diverse of all orders of Porifera (Bergquist, 1978; Hartman, 1982), both in terms of numbers of species and the range and diversity of morphological characters (Bergquist & Fromont, 1988; Hajdu *et al.*, 1994a). This diverse morphology is certainly also reflected in the many different opinions concerning interpretation of character importance, character polarity, and indeed character homology itself, producing a proliferation of systematic schemes for the group (discussed in detail by Bergquist & Fromont, 1988).

Our present understanding of the concept of Poecilosclerida stems from Ridley & Dendy's (1887) order Monaxonida, in which poecilosclerid genera were placed in two families of the suborder Halichondrina (Heterorrhapididae, lacking chelae; and Desmacidonidae with chelae). Topsent (1894c) refined this scheme, although splitting the non-cheliferous and cheliferous

poecilosclerids into separate families Haploscleridae and Poeciloscleridae, respectively. Hentschel (1923) also provided a major contribution to the present concept of Poecilosclerida in establishing a number of families, many of which are still recognised today, but he persisted in retaining a subordinal distinction between taxa with or without chelae, and placed primary emphasis on the presence or absence of spiny megascleres ('acanthostyles') in his subordinal classification. Topsent (1928c) established Poecilosclerida to emphasize the unique possession of chelae microscleres, and his definition and families included have been maintained more-or-less intact up to the present. De Laubenfels (1936a) purposefully, or otherwise, destabilised this phylogenetic system in an attempt to simplify the poriferan nomenclature and classification, while explicitly acknowledging little heed for phylogenetic relationships among family-level taxa. His classification has been adopted by a few authors, at family and sometimes higher taxonomic levels, up until the 1980s (e.g., Hoshino, 1981a, b; Pulitzer-Finali, 1983), but this is now mostly rejected by contemporary authors who have more-or-less returned to Topsent's (1928c) scheme, following the lead of Lévi (1973) and Bergquist (1978) in particular. Bergquist & Fromont (1988) provide a comprehensive historical analysis of this systematics and the characters emphasized by the various authors in their respective classifications.

Subsequent development of the Poecilosclerida systematics has mostly concerned the allocation of genera to various families, with these appearing and disappearing between the various schemes. Hajdu *et al.* (1994a) provide a brief outline of these family-level changes, and also proposed a subdivision of the order based on recognizing monophyletic taxa within the vast and diverse assemblage of Poecilosclerida (see summary below).

There are now many contemporary monographic publications on regional poecilosclerid faunas, each differing slightly in the families and genera contained within, reflecting differences in opinions between authors as to the importance of certain diagnostic characters over others: e.g., Lévi (1963) (South Africa); Wiedenmayer (1977b) and Van Soest (1984b) (Caribbean); Bergquist & Fromont (1988) (New Zealand); Wiedenmayer (1989) (Bass Strait, Victoria), Hooper & Lévi (1993a) and Hooper & Battershill (1998) (New Caledonia). There are also many contemporary publications that have reviewed or revised various families of poecilosclerids, together reflecting the ecological importance, the phylogenetic significance and the huge challenge of defining this order within a phylogenetic framework: e.g., Raspailiidae (Hooper, 1991), Microcionidae (Hooper, 1996a), Rhabderemiidae (Hooper, 1990a; Van Soest & Hooper, 1993), Acarnidae, Desmacididae and Myxillidae (Desqueyroux-Faundez & Van Soest, 1996, 1997; Van Soest, 1998), Latrunculiidae (Kelly-Borges & Vacelet, 1995), Crambeidae (Maldonado & Uriz, 1996b), Desmacellidae (Van Soest, 1984b; Hooper *et al.*, 1991; Hooper, 1984b, 1996b), Mycalidae (Hajdu, 1999). Despite this growing literature, however, it is true that poecilosclerid systematics is still far from resolved. Building on Hajdu *et al.* (1994a) proposal to develop a systematics for Poecilosclerida based on monophyletic clades the following chapters constitute major revisions of the order, focusing on subordinal, family and generic and subgeneric levels of classification. In many cases subgeneric taxa are proposed

as 'convenient' clades to manage large suites of taxa, whereas higher taxa are based on more sound phylogenetic principles, including published character analyses.

Scope

The number of families recognised in the order varies according to different authors (e.g., Lévi, 1973; Wiedenmayer, 1977b; Bergquist, 1978; Hartman, 1982; Van Soest, 1984b; Bergquist & Fromont, 1988). Recently, Hooper & Wiedenmayer (1994) included 16 families in the order (although these were based solely on the published Australian fauna, with several families not yet 'officially' recorded for this fauna): twelve with chelae microscleres, three without chelae, and one of uncertain placement. Hajdu *et al.* (1994a) presented a more global view, recognising 17 families: Anchinoidae, Cladorhizidae, Coelosphaeridae, Crambidae (=Crambeidae), Crellidae, Desmacellidae, Guitarridae, Hamacanthidae, Hymedesmiidae, Iophonidae (=Acarnidae), Microcionidae, Mycalidae, Myxillidae, Phoriospongiidae, Raspailiidae, Rhabderemiidae, Tedaniidae.

Latrunculiidae, included in Poecilosclerida by Lévi (1973) and Van Soest (1984b), has also commonly been assigned to Hadromerida (Reid, 1968d; Bergquist, 1978; Hartman, 1982). There is now more substantial evidence to support its inclusion in Poecilosclerida (e.g., Kelly-Borges & Vacelet, 1995), but as demonstrated in this work, it is now considered to be polyphyletic based on ontogenetic differences in microrhabd morphology ('chessman spicules') between groups of taxa within the 'latrunculiids'. *Diacarnus* and related genera (family Podospongiidae), bearing spinose microrhabd (spinorhabd) microscleres, have suggested affinities with the Mycalidae based on possession of a sigmoid protorhabd with presumed homology to diancistra derivatives. Conversely, *Latrunculia* and related genera have discate microrhabds (acanthomicrorhabds or discorhabds) (family Latrunculiidae), with a straight protorhabd, and remain uncertain as to their affinities within Poecilosclerida, and consequently are allocated here to a new monophyletic suborder Latrunculina. Although this proposal is a preliminary phylogenetic hypothesis, as yet with little (published) empirical support, it does have merit in recognizing distinct ontogenetic differences in microrhabd morphologies between Podospongiidae and Latrunculiidae (Samaai, unpublished data).

In this present volume we recognise 25 families, 129 genera, 50 subgenera and several thousands of described species, allocated among four suborders: Microcionina (four families), Myxillina (eleven families), Mycalina (nine families) and Latrunculina *incertae sedis* (one family) (see below). Poecilosclerids have been recorded from all marine environments, from the shallow intertidal to the abyssal depths (Hartman, 1982).

Recent reviews

Lévi, 1973; Wiedenmayer, 1977b, 1989; Bergquist, 1978; Hartman, 1982; Van Soest, 1984b; Bergquist & Fromont, 1988; Hajdu *et al.*, 1994a; Hooper & Wiedenmayer, 1994; Kelly Borges & Vacelet, 1995.

KEY TO SUBORDERS

- (1) Chelae microscleres are absent 2
 Chelae microscleres are present 6

- (2) Microscleres are absent (apart from raphides (trichodragmata) in a few genera) **Microcionina** (Raspailiidae)
 Microscleres are present, although not chelae 3
- (3) Microscleres include sigmoid morphologies 4
 Microscleres include acanthose microrhabds 5
- (4) Microscleres may include sigmas, microxeas, commata and raphides **Mycalina** (Desmacellidae)
 Microscleres are peculiar sigmoid-like (spirosigmata, thraustosigmata), toxiform (thraustoxea) and rugose
 microstyles **Microcionina** (Rhabderemiidae, *incertae sedis*)
- (5) Microscleres are distinctive acanthomicrohabds with discate modifications (acanthose discorhabds), with single perpendicular
 spicules typically arranged in a compact palisade, their bases buried in the ectosomal membrane and projecting
 outside of the ectosome **Latrunculina** (Latrunculiidae, *incertae sedis*)
 Microscleres are distinctive spinorhabds, often in two size categories, disposed in a dense crust or scattered in a band within the
 ectosome **Mycalina** (Podospongiidae)
- (6) Chelae microscleres are exclusively palmate isochelae, toxas often present 7
 Chelae microscleres are tridentate-derived (arcuate, anchorate forms); toxas never present **Myxillina**
- (7) Ectosomal megascleres monactinal with small terminal spines; choanosomal megascleres include at least 2 morphologies localized
 to distinct regions within the body, often spined **Microcionina**
 In addition to palmate chelae (iso- and aniso-morphologies), microscleres include sigmas or sigmancistra-derivatives; megascleres
 consist only of a single smooth style with faintly constricted neck and/or faintly swollen tyle ('mycalostyles') **Mycalina**

SUBORDINAL CLASSIFICATION OF POECILOSCLERIDA

Key characters

Differentiation of suborders within Poecilosclerida fundamentally rests on the presence/absence and morphology of chelae microscleres (palmate versus tridentate-derived forms (arcuate and anchorate chelae)). The classification also relies on other characters, such as the presence or absence of toxa microscleres, the presence/absence, geometry and spination of ectosomal megascleres, and the number and localization of choanosomal megascleres within the skeleton (Hajdu *et al.*, 1994a).

Chelae. Chelae morphotypes have been discussed in detail by Hajdu *et al.* (1994a) based on a detailed SEM examination of all reported forms in most nominal genera. These authors suggest that there are three fundamental morphologies, differentiated by the degree of fusion of alae to the shaft and the torsion of the shaft itself. Unfortunately, this distinction is not always clear-cut, sometimes being one of 'grade', with the consequence that intermediary forms may make allocation to palmate, arcuate or anchorate categories difficult (e.g., Hooper, 1996a). Nevertheless, in most cases these categories hold up and their diagnostic utility as phylogenetic markers remains highly informative. Palmate isochelae (Fig. 1) are defined as having two incomplete lateral alae extensively fused with the shaft, and a frontal ala of varying width. Arcuate chelae (Fig. 2) have a well-formed frontal ala and more completely formed lateral alae which in most cases are separated from the shaft. Intermediary forms may have their lateral alae partially separated from the shaft (and hence they may be potentially confused between either category), but arcuate chelae are usually recognizable as having 'teeth-like' alae, irrespective of the degree to which the lateral alae are attached. Anchorate chelae (Fig. 3) have at least three completely formed alae, with the lateral ones (i.e., those adjacent to the frontal ala) completely detached from the shaft, in addition to which there are two other lateral alae totally fused to the shaft and resembling ridges. Modifications to these basic plans (such as unguiferous forms; Figs 2D, 3B) are generally recognizable as belonging to one of these three categories based on the presence or absence of lateral ridges (anchorate vs. palmate forms, respectively). Other modifications to chelae are common amongst Poecilosclerida: e.g., birotules (Fig. 3D), anisochelae (Fig. 1F), placocheles (Fig. 4A),

cleistochelae (Fig. 4K), tetrapocilli (Fig. 4L), coelodisc (Fig. 4G), clavidisc (Fig. 4J), etc., some of which are diagnostic for particular taxa.

Other microscleres. Meniscoid spicules, sigmas and derivatives (including chelae, sigmancistras, diancistras), are sympleiomorphic for the clade Haplosclerida + Poecilosclerida (Van Soest, 1987a). Conversely, sigma-derivatives are only found in Poecilosclerida and many of these morphologies are apomorphic for particular taxa (e.g., placocheles for taxa such as Guitariidae; Fig. 4A). Unmodified sigmas are also present in some poecilosclerids (e.g., Desmacellidae; Fig. 4E). Similarly, sigmancistra-derivatives such as diancistras (*Hamacantha*; Fig. 4I) and clavidiscs (*Merlia*; Fig. 4J) are apomorphic for Mycalina (Hamacanthidae

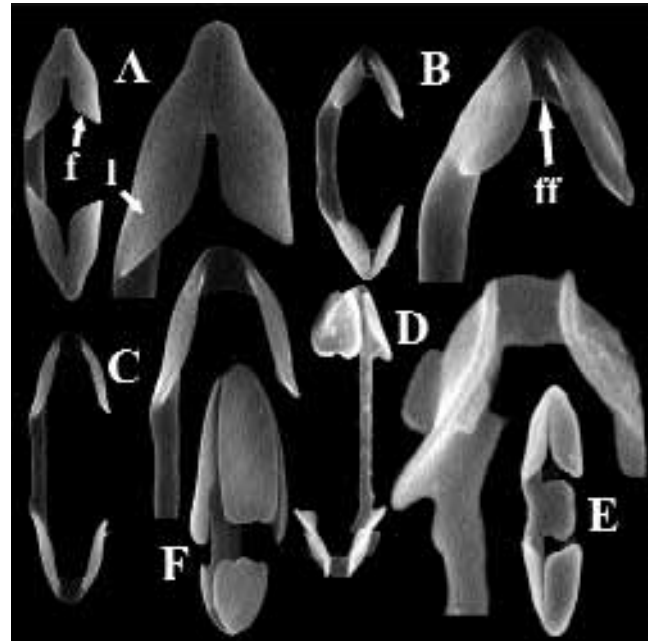


Fig. 1. Palmate-derived isochelae (abbreviations: f, frontal ala fully-formed; l, lateral ala, incompletely formed, fused with shaft by its longest axis; ff, lateral and frontal alae nearly completely detached from each other). A–C, palmate isochelae with alae of variable length and thickness. D, fluted alae. E, winged shaft. F, anisochela. (A, C, *Clathria australiensis*; B, C. *oxyphila*; D, C. *macropora*; E, C. *toxipraedita*; F, *Mycale* sp.).

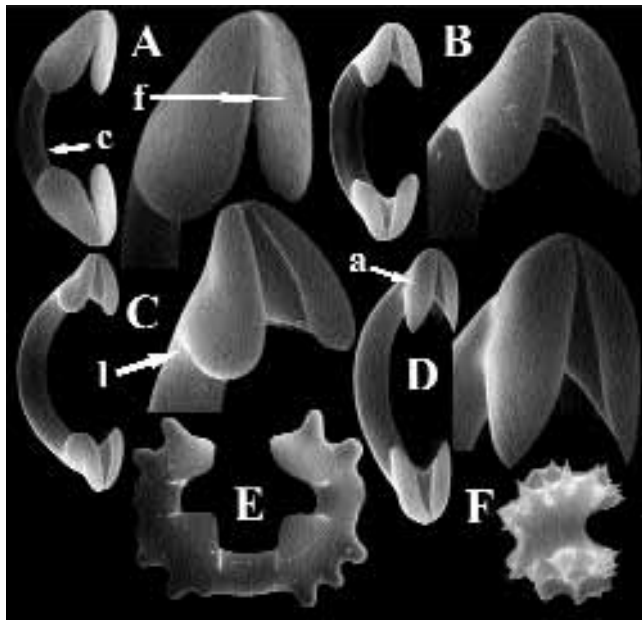


Fig. 2. Arcuate-derived isochelae (abbreviations: c, curved shaft; f, frontal alae well-formed; pf, partially fused frontal and lateral alae; l, lateral alae partially separated from shaft; a, alae teeth like). A–C, arcuate isochelae with alae of varying length. D, unguiferous arcuate isochelae. E, highly modified displaster-like arcuate-derived chela. F, strongly deformed bluntly spined arcuate-derived chela. (A, '*Clathria*' *grisea*; B, *Ectyodoryx* sp.; C, *Hamigera dendyi*; D, '*Clathria*' *scabida*; E, *Acanthancora clavilobata*; F, *Acanthancora cyanocrypta*.)

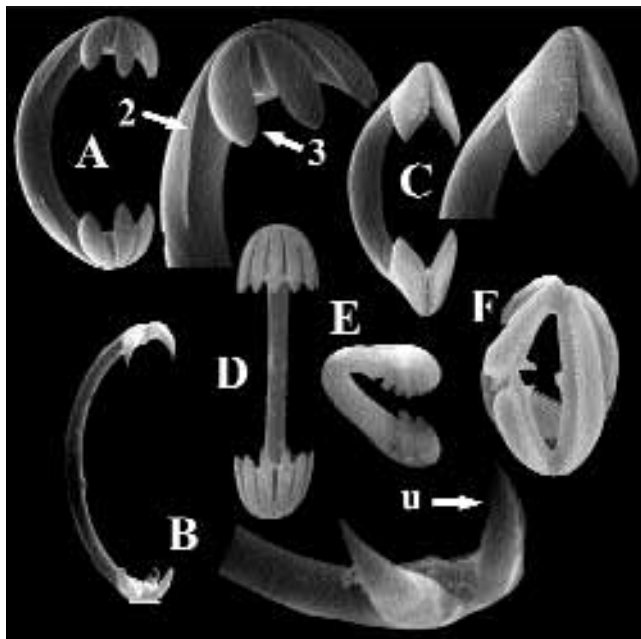


Fig. 3. Anchorate-derived chelae (abbreviations: 3, three completely formed alae, with the lateral ones completely detached from the shaft; 2, two rudimentary lateral alae completely fused to the shaft resembling ridges; u, unguiferous teeth-like alae). A, fully formed lateral and frontal alae. B, unguiferous arcuate isochelae with teeth-like alae (and enlarged view). C, reduced frontal teeth-like alae, but with persistent ridge on shaft. D, birotule. E, polydentate anchorate spatulate chela. F, spherancora. (A–B, *Monachora unguiculata*; C, *Crella incrustans*; D, *Iotrochota acerata*; E, *Ectyonopsis hartmani*; F, *Melonancora elliptica*.)

and Merliidae). Birotules (Fig. 3D) are many-toothed chelae with alae encircling the shaft, and thought to have originated from anchorate chelae (Van Soest, 1987a). These are characteristic of the myxillinid family Iotrochotidae. Toxas (Fig. 4B) are also sympleiomorphic for Poecilosclerida + Haplosclerida. Their absence from Myxillina is considered to be a derived character. Forceps, recurved pincer-like rods (Fig. 4C–D), occur in both Mycalina and Myxillina and their possession has been interpreted as independently derived in both, assuming they are indeed homologous (Hajdu *et al.*, 1994a). Onychaetes (Fig. 4F) are synapomorphic for Tedaniidae, although their origin, and the affinities of this family, are still equivocal (Hajdu *et al.*, 1994a). Likewise, raphides (often in trichodragmata; Fig. 4M) are homoplastic with a broad occurrence in most poecilosclerid assemblages and also found in several taxa outside the Poecilosclerida (e.g., Halichondrida).

Two families have acanthomicrohabds ('chessman spicules') occurring in a surface crust. Previously these taxa were amalgamated in a single family (Latrunculiidae), but Kelly & Samaai and Samaai & Kelly (this volume) demonstrate fundamental ontogenetic differences between two morphotypes of 'chessman' spicules, indicating their homoplastic ontogenetic development and negating any homology as previously thought. Podospongiidae have spinorhabds (Fig. 4N), bearing two whorls of spines arranged serially around the spicule, between a proximal and distal whorl of

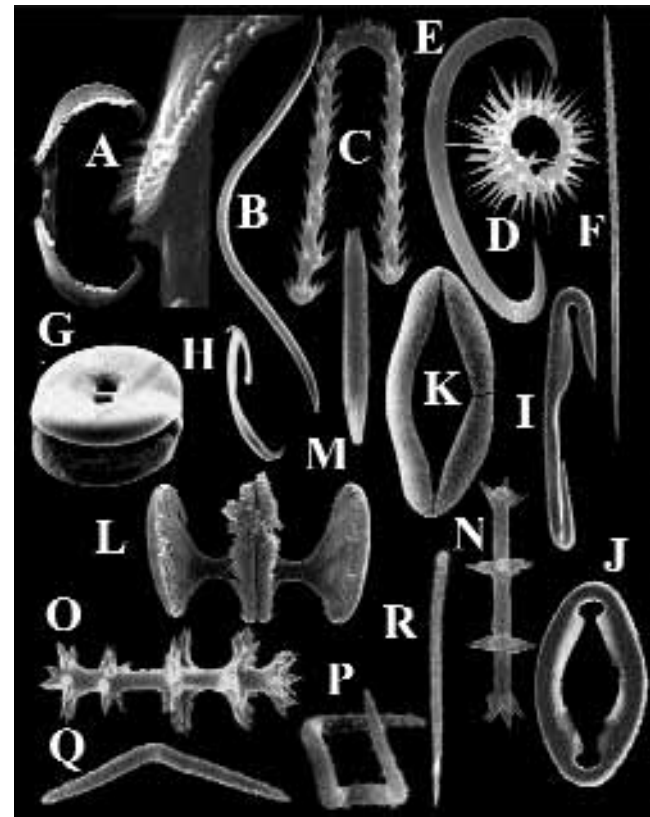


Fig. 4. Examples of other Poecilosclerida microscleres. A, spined chela, including view of ala (*Guitarra*). B, wing-shaped toxas (*Acarnus*). C, forceps (*Forcepia*). D, small incurled forceps (*Forcepia* (*Leptolabis*)). E, sigma (*Mycale*). F, onychaete (*Tedania*). G, coelodisc (*Coelodischela*). H, sigmancistra (*Euchelipluma*). I, diancistra (*Hamacantha*). J, clavidisc (*Merlia*). K, cleistochela (*Clathria*). L, tetrapocilla (*Tetrapocillon*). M, trichodragmata (bundle of raphides; *Raspailia*). N, spinorhabd (*Diacarnus*). O, discorhabd (*Latrunculia*). P, thraustosigma (*Rhabderemia*). Q, thraustoxea (*Rhabderemia*). R, microstyle (*Rhabderemia*).

spines, one of which may be longer than the other. This family has suspected Mycalina affinities based on the fact that the prorhabd of spinorhabds is sigmoid, thus with presumed homology to sigmancistra derivatives, and with corroboratory support for this assertion from other skeletal and non-morphological characters. Latrunculiidae, of uncertain affinity within Poecilosclerida, have discate acanthorhabds (discorhabds) (Fig. 4O), bearing apical and basal whorls of spines and several crenulate discs in between these, with the prorhabd lacking any sigmoid modification. Further, within Latrunculiidae there are several different morphologies of acanthodiscorhabds, each apomorphic for various genera: anisodiscorhabds or 'typical chessman spicules' (in *Latrunculia*), isoconidiscorhabds or 'sceptres' (in *Sceptrella*), and isochiadiscorhabds or truncate discorhabds (in *Tsitsikamma* gen. nov.; Samaai & Kelly) (refer to respective chapters in this volume).

Similarly, the affinities of Rhabderemiidae based on their microsclere morphologies remains enigmatic, with oxea- or toxalike microscleres (thraustoxeas; Fig. 4Q), sigma-like spicules (spirosigmata, thraustosigmata; Fig. 4P) and microstyles (Fig. 4R) possibly analogous to toxas, sigmas and rhabds of other poecilosclerids (refer to chapter Rhabderemiidae, this volume). Rhabderemiidae remains *incertae sedis* within Poecilosclerida. They may have affinities with Raspailiidae, based on characters other than microscleres (skeletal structure similar to *Aulospongos*, for example), although the possession of true toxas in some species (Van Soest & Hooper, 1993) possibly supports a closer relationship with Acarnidae. Alternatively, Rhabderemiidae may be a completely independent line within Poecilosclerida, but there is so far no molecular support to corroborate any relationship within Poecilosclerida in general, or affinities with any family in particular.

Ectosomal megascleres. Ectosomal spicules are fundamental to the subclass classification, with Microcionina having predominantly monactinal ectosomal megascleres. (1) Raspailiidae have special bundles of styles or oxeas surrounding larger protruding spicules; Microcionidae have basally spined ectosomal styles tangential or paratangential; Acarnidae have tangentially arranged tyloles or anisostyles with spined bases tangential or paratangential; Rhabderemiidae lack special ectosomal spicules, as do certain genera of the other families (refer to chapters by Hooper in this volume). (2) Myxillina have predominantly diactinal ectosomal megascleres without basal spination, or with rare, irregular or coarse spines (ectosomal spicules absent in several families) (refer to chapters by Van Soest in this volume). (3–4) Mycalina and Latrunculina lack ectosomal spicules altogether (presumed secondary losses; or alternatively, independent evolutionary acquisitions on the part of the other suborders) (refer to chapters by Hadju *et al.*, Van Soest *et al.*, Kelly & Samaai and Samaai & Kelly in this volume).

Acanthostyles. Acanthostyles are widespread but not universal amongst Poecilosclerida, with their absence from various taxa (e.g., Mycalina, Latrunculina) interpreted as either derived or primitive features (Hooper, 1991, 1996a; Hajdu *et al.*, 1994a, respectively). These spicules echinate spongin fibres (e.g., Raspailiidae, Microcionidae), core fibres (e.g., Myxillidae) or both (e.g., Crellidae). Their diverse geometries (including patterns of spination) (Figs 5–6) may be highly diagnostic for particular lower-level taxa (e.g., spatulate versus sharply pointed spines in the genus *Echinodictyum* (Raspailiidae)), but these phylogenetic patterns are unclear at higher taxonomic levels (Refer to Hooper, 1991, 1996a for additional illustrations).

Diversity of megascleres. By definition Poecilosclerida has at least two categories of megascleres, coring fibres and occurring

interstitially, in the ectosome, and/or echinating skeletal tracts. Microcionina can have up to five categories (with the exception of Rhabderemiidae), whereas at the opposite end of the continuum, Mycalina and Latrunculina have only one category.

Skeletal architecture. The gross organic and inorganic skeletal architecture, the structural differentiation of the inorganic skeleton, and the distribution of mineral components in that structure are primary diagnostic features for many taxa (Lévi, 1960b, 1973; Bergquist, 1978; Hartman, 1982). However, when used alone skeletal architecture is not necessarily a reliable indicator of phylogenetic affinities. Choanosomal skeletal structures such as hymedesmioid, plumose, plumo-reticulate, regularly reticulate, isodictyal reticulate, renierioid reticulate, axially compressed and halichondroid arrangements may be characteristic of various genera, or sometimes of certain families, but higher taxa can rarely be defined by these features alone, with the presumption that they are more susceptible to adaptive pressures than are characters such as microsclere morphology (Ridley & Dendy, 1887; Dendy, 1905; see

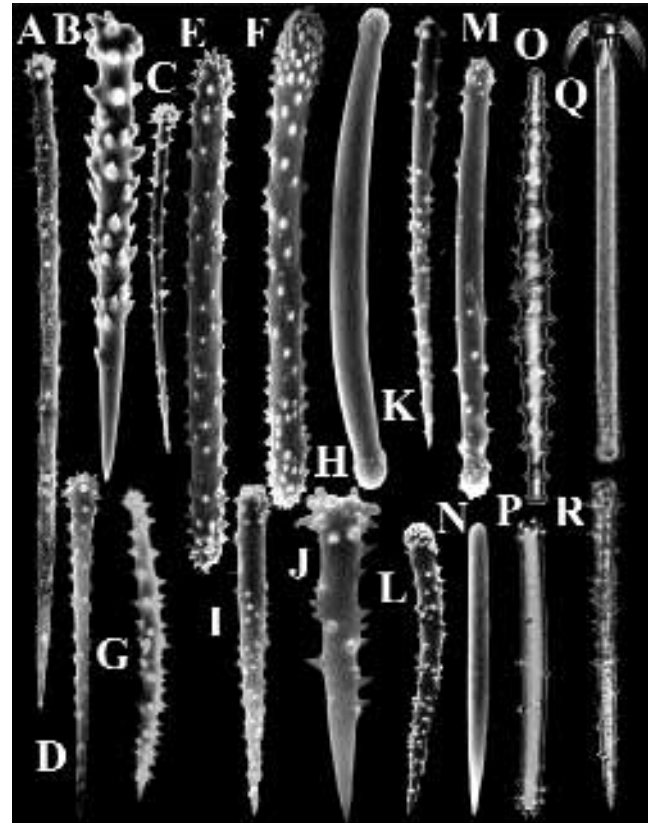


Fig. 5. Examples of poecilosclerid acanthostyle geometries. A–D, G, I–L, R, echinating acanthostyles. E, F, H, M, P, 'plocamiform' acanthostyles. N, echinating style. O, acanthorhabd. Q, cladotylote. A, *Chaetodoryx richardi* (Coelosphaeridae). B, *Hymedesmia zetlandica* (Hymedesmiidae). C, *Phorbis perarmatus* (Hymedesmiidae). D, *Plocamionida ambigua* (Hymedesmiidae). E, *Ectyonopsis ramosus* (Myxillidae). F, *Ectyonopsis hartmani* (Myxillidae). G, *Crellomyxilla intermedia* (Myxillidae). H, *Plocamiancora igzo* (Myxillidae). I, *Clathria (Clathria) crassa* (Microcionidae). J, *Clathria (Thalysias) rubra* (Microcionidae). K, *Clathria (Thalysias) darwinensis* (Microcionidae). L, *Clathria (Thalysias) phorbisiformis* (Microcionidae). M, *Antho (Acarnia) ridleyi* (Microcionidae). N, *Holopsamma arborea* (Microcionidae). O, *Acanthorhabdus fragilis* (Acarnidae). P, *Wigginsia wigginsii* (Acarnidae). Q, *Acarnus innominatus* (Acarnidae). R, *Dolichacantha macrodon* (Acarnidae).

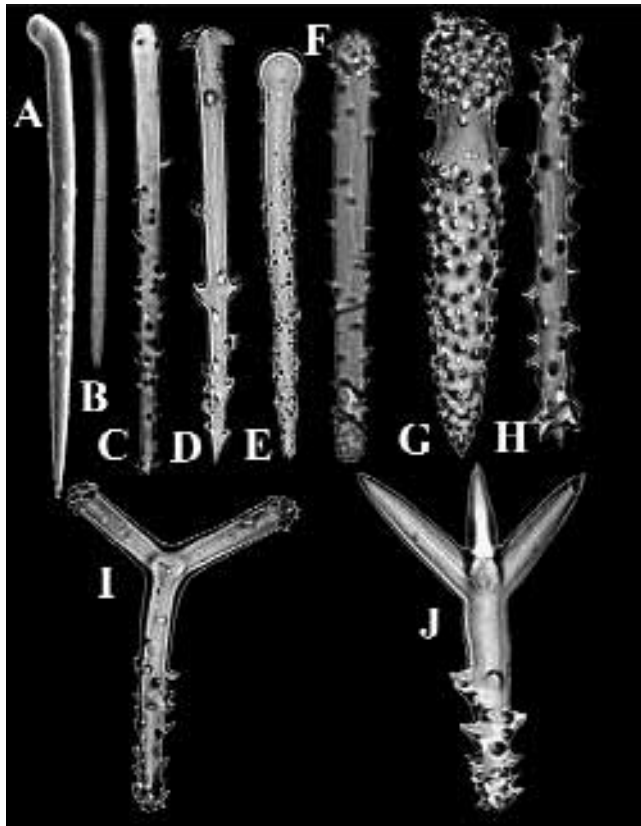


Fig. 6. Examples of poecilosclerid acanthostyle geometries (cont.). A–B, rhabdostyles. C–D, clavulate acanthostyles. E, G, bulbous acanthostyles. F, spatulate acanthostyle. H, ‘plocamiform’ acanthostongyle. I–J, sagittal triacts/tetracts (acanthoplagiotriaenes). A, *Rhabderemia sorokiniae* (Rhabderemiidae). B, *Rhabderemia pusilla* (Rhabderemiidae). C, *Ectyoplasia tabula* (Raspailiidae). D, *Endectyon fruiticosa aruensis* (Raspailiidae). E, *Raspailia (Hymeraphiopsis) irregularis* (Raspailiidae). F, *Echinodictyum mesenterinum* (Raspailiidae). G, *Lithoplocamia lithistoides* (Raspailiidae). H, *Plocamione pachysclera* (Raspailiidae). I, *Cyamon vickersi* (Raspailiidae). J, *Trikenrion flabelliforme* (Raspailiidae).

discussion in Hajdu *et al.*, 1994a, and Hooper, 1996a) (refer to illustrations contained within the various poecilosclerid families in this volume). A contrary approach was taken by Berquist & Fromont (1988) who recognised the validity of different skeletal structures as primary diagnostic characters, in addition to, and in some cases equal with other features such as microsclere morphology, resulting in a proliferation of genera that confused their phylogenetic relationships. Chelae microsclere geometry, as a primary apomorphy, provides a partial resolution of these discrepancies. Choanosomal skeletal architectures (e.g., hymedesmioid, microcionid, renieroid, isodictyal, axially compressed etc.) are suspected to be homoplastic developments largely incongruent with phylogenies based on microsclere geometries (palmate – arcuate – anchorate origins),

although there are still no substantial molecular data to corroborate this hypothesis.

Incorporation of detritus into skeleton. This feature is widespread over a variety of otherwise unrelated taxa, including various Poecilosclerida (Microcionina, Myxillina), Haplosclerida, Dictyoceratida, Dendroceratida, Verongida etc., and is not attributed much significance above the species-level, or occasionally genus-level of classification.

Microcionina Hajdu, Van Soest & Hooper, 1994a

Four families, with terminally spined ectosomal monactinal megascleres (occasionally modified to quasidiactinal forms, always asymmetrical); choanosomal megascleres diverse, consisting of at least two categories localized to distinct regions within the skeleton, or sometimes up to five categories including spicules echinating fibres in many taxa; isochelae exclusively of palmate origin, with diverse forms of toxas but lacking sigmas. Families: Acarnidae, Microcionidae, Raspailiidae, Rhabderemiidae.

Myxillina Hajdu, Van Soest & Hooper, 1994a

Eleven families, with ectosomal megascleres basically diactinal, although aniso-terminations are widespread, and terminal spination of ectosomal megascleres rare or if present usually coarse or irregular, with tridentate-derived chelae (iso- or aniso-, arcuate, anchorate or birotulate), but lacking toxas. Families: Chondropsidae, Coelosphaeridae, Crambeidae, Crellidae, Dendoricellidae, Desmacididae, Hymedesmiidae, Iotrochotidae, Myxillidae, Phellodermiidae fam. nov., Tedaniidae.

Mycalina Hajdu, Van Soest & Hooper, 1994a

Nine families, with megascleres almost always a single smooth category, never echinating the skeletal tracts, consisting of (sub-)(tylo-)styles with faintly constricted neck and/or faintly swollen tyle (‘mycalostyles’), with microscleres sigmancistra derivatives and chelae which are mostly palmate; Podospongiidae, with spinorhabds (‘chessman spicules’), is also allocated to this suborder based on skeletal and other characters (see Kelly & Samaai, below). Families: Cladorhizidae, Desmacellidae, Esperioptidae, Guitarridae, Hamacanthidae, Isodictyidae, Merliidae, Mycalidae, Podospongiidae.

Latrunculina Kelly & Samaai, subord. nov.

Monotypic (Latrunculiidae), with wispy wide-meshed reticulate to reinforced reticulate choanosomal skeleton composed of anisostyles or strongyles, ectosomal skeleton compact tangential, microscleres are discate acanthorhabds typically arranged vertically in a palisade on the outside of ectosome; without chelae, sigmas or toxa microscleres.