

Suborder Myxillina Hajdu, Van Soest & Hooper, 1994

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Suborder Myxillina Hajdu *et al.* (Demospongiae, Poecilosclerida) are characterized by possession of tridentate chelae and absence of toxas. Most Myxillina have differentiated choanosomal and ectosomal megascleres, but this may be lost secondarily. Eleven families are distinguished based on microsclere morphology, megasclere types, and skeletal architecture. A key to the families is provided.

Keywords: Porifera; Demospongiae; Poecilosclerida; Myxillina; Chondropsidae; Coelosphaeridae; Crambeidae; Crellidae; Dendoricellidae; Desmacididae; Hymedesmiidae; Iotrochotidae; Myxillidae; Phellodermidae fam. nov.; Tedaniidae.

DEFINITION, DIAGNOSIS, SCOPE

Definition

Poecilosclerida with tridentate or polydentate chelae microscleres; palmate chelae absent; toxas absent; sigmas usually present. Differentiated ectosomal and choanosomal megascleres, although either or all may be lost secondarily. Ectosomal megascleres typically diactinal, commonly with aniso-terminations. Choanosomal megascleres usually styles, rarely oxeas or strongyles.

Diagnosis

Myxillina basically have encrusting shape and soft consistency; some are very thinly encrusting; occasionally branching or of firm consistency, or bladder-like and fistular. They share a distinction with Microcionina in having separate ectosomal and choanosomal megascleres.

Description of characters

Ectosomal megascleres. Ectosomal megascleres, called 'tornotes' in this suborder, are most frequently arranged as palisades or bouquets; their shape is basically diactinal (oxea-, strongyle- or tylote-like), but very frequently shape and ornamentation of both ends are slightly different (then called 'anisotornotes'). In one family their shape is so nearly a subtylostyle that these are likely to be truly monactinal and their homology with other tornotes is doubtful; in this case the name 'tornote' is avoided. The tornote shafts are smooth almost without exception; their endings may be variously sharply pointed, mucronate, blunt, swollen, microspined or bearing one or several larger spines. The extent to which the tornotes penetrate into the choanosomal skeleton varies considerably and in some families they replace partly or wholly the choanosomal megascleres. In some families the tornotes are grouped palisade-like around slightly raised rounded pore-fields called areolated porefields or 'areolae' (in French: 'cribles').

Choanosomal megascleres. Choanosomal megascleres are basically styles (occasionally oxeas or strongyles), which may be smooth, lightly or more heavily spined on and around the head, or entirely spined. Like in many Microcionina these are often of two categories: main and auxiliary, usually differentiated in size, ornamentation and location within the skeleton. Main megascleres tend to be smooth or lightly spined, usually longer and thicker forming the basic

skeletal plan or – in thinly encrusting forms – perpendicular to and penetrating the surface, and macroscopically hispid. The auxiliary megascleres tend to be smaller, usually entirely spined, echinating the skeletal tracts, the nodes of the skeletal reticulum or – in thinly encrusting forms – arranged in groups ('bouquets') around a single main megasclere. In one family they simulate ectosomal spicules to form a surface crust. Auxiliary megascleres are frequently lost or in some cases undifferentiated in shape from the main megascleres. Several groups have their choanosomal skeleton partly or wholly replaced by a reticulation of sand grains and other foreign material.

Chelae. Chelae deviate from the typical poecilosclerid palmate chelae in having at least three clearly developed alae: a median fluke and two flanking alae. These 'tridentate' chelae may be further differentiated into 'arcuate' chelae (which have their flanking alae still partly attached to the shaft without visible development of further alae on the shaft) and 'anchorate' chelae (which have incipient extra alae, called 'fimbriae', which also may extend a long way along the shaft). The alae of both arcuate and anchorate chelae are normally rounded blades (called 'spatulate') but may be occasionally pointed, looking like predator's teeth (called 'unguiferate'). Both spatulate and unguiferate chelae often develop extra alae (called 'polydentate'). In one family species possess probable derivations of polydentate anchorate chelae in the shape of 'double-umbrella' microscleres (called 'birotulas'). Arcuate chelae may become deformed to shapes dissimilar to the original type (e.g., 'abyssochelae'). Chelae also often occur in two size categories, which frequently differ slightly in shape. Occasionally, they may be asymmetrical, twisted, or otherwise deformed. In a few genera chelae occur with spines or hooks on their shaft. Chelae may occasionally be lost in species which otherwise share convincing similarities with various Myxillina. One family lacks chelae entirely and its membership of Myxillina is tentative based on similarities of its tornotes with those of other Myxillina.

Other microscleres. Sigmas (shared with Mycalina, but lacking in Microcionina) are frequent, often in two size categories, but lacking entirely in one family. Toxas are absent. Trichodragmas and single raphides are occasionally found. One family has special raphide-like microspined microscleres (called 'onychaetes').

Scope

Eleven families are presently assigned to Myxillina: Chondropsidae Carter, 1886: 122; Coelosphaeridae Dendy, 1922: 95; Crambeidae Lévi, 1963: 16; Crellidae Dendy, 1922: 92;

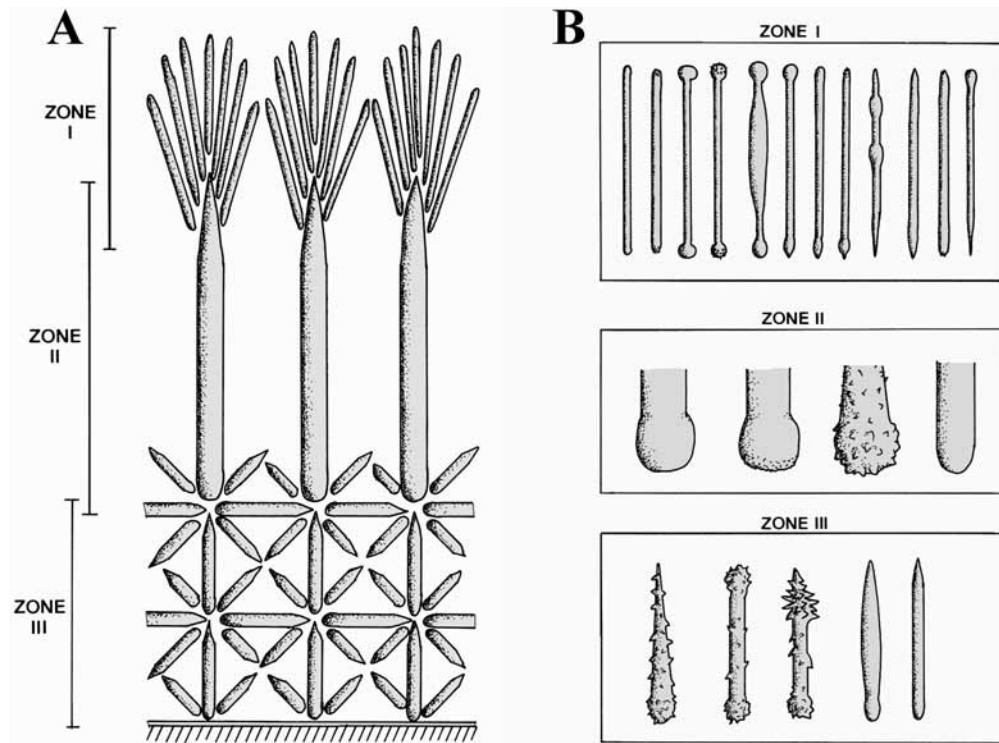


Fig. 1. A, Idealized skeletal 'bauplan' of Myxillina, consisting of three distinct zones. I, ectosomal skeleton. II, subectosomal skeleton. III, choanosomal (or basal) skeleton. B, megasclere types characteristic for the three zones.

Dendoricellidae Hentschel, 1923: 406; Desmacididae Schmidt, 1870: 52; Hymedesmiidae Topsent, 1928c: 250; Iotrochotidae Dendy, 1922: 96; Myxillidae Dendy, 1922: 85; Phellodermidae fam. nov.; Tedaniidae Ridley & Dendy, 1886: 335.

TAXONOMIC HISTORY

The suborder was only recently erected from a re-evaluation of all poecilosclerid characters (Hajdu *et al.*, 1994a). The possession of 'tridentate' chelae (Tedaniidae excepted) and lack of toxas are pivotal independent characters that distinguish the taxonomy, forming a strong set of synapomorphies that complement the possession of other shared non-exclusive characters (such as diactinal tornotes, frequent occurrence of sigmas in more than one size category, and spined auxiliary styles). Previous attempts to classify the large numbers of Poecilosclerid genera (Topsent, 1928c; de Laubenfels, 1936a; Van Soest, 1984b; Bergquist & Fromont, 1988), although arriving at widely diverging schemes, emphasized skeletal architectural features, but disregarded, to a large extent, microsclere morphology. Only de Laubenfels (1936a) formalized his ideas at the suprafamilial level and erected several suborders, including the Myxilliformes. This name has not been adopted here because of extensive differences in content between that group and the Myxillina (allowed by the ICZN Article 1; Anon., 1999).

REMARKS

Spicule morphology versus skeletal architecture

Hajdu *et al.* (1994a) discussed the distribution of the various characters amongst poecilosclerid sponges over the established

taxa, concluding that there was no concordance between broad sets of characters such as habit, skeletal architecture, surface characters and spicule complement. This lack of consistency has led to a proliferation of proposed families and genera: currently 189 nominal genera belong to the suborder Myxillina as recognized here. Debate continues over the validity of such characters as the precise nature of chelae morphology, ornamentation of the megascleres, absence or presence of categories of megascleres and microscleres, plumose versus reticulate architecture, etc. It is stressed here that there is no single classification that has gained wide acceptance. The classification presented here introduces changes and novelties to the established classifications (including the most recent summaries) based on re-examination of type and other specimens, and from a thorough survey of literature. However, this proposed scheme is not static, and serves as a sound objective basis for future proposals investigating non-skeletal characters such as histology, reproduction, nucleic acid sequences and secondary metabolite content.

Basic skeleton

An idealized view of basic Myxillina skeletal types and their likely development from an ancestral skeleton is presented in Figure 1A. This ancestral skeleton 'bauplan' is based on a combination of skeletal structures within the order and derived from the generalized skeleton of typical Microcionina (which is likely the most closely related sister group on account of shared possession of spined auxiliary styles and differentiation of megascleres into ectosomal and choanosomal spicules). The Myxillina skeletal 'bauplan' is assumed to have had at the surface bouquets or palisades of smooth diactinal tornotes (zone I in Fig. 1A), grouped around the peripheral ends of one or a few long smooth styles (possibly with spined heads) (zone II in Fig. 1A). These are erect

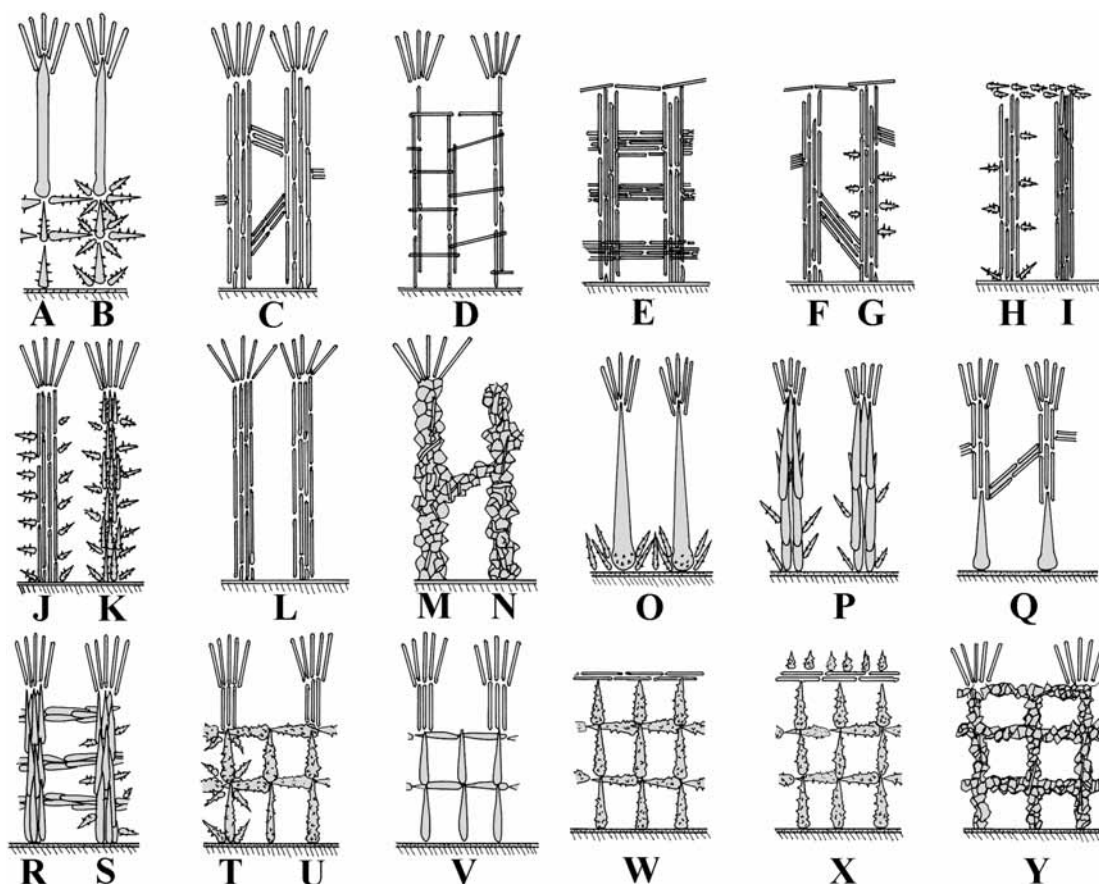


Fig. 2. Schematic drawings of Myxillina skeletal types. A–B, ancestral ‘bauplan’. C–N, skeletal types with suppressed zones II–III. O–Q, with suppressed zones III and deemphasized zone I. R–Y, with emphasized zones III and suppressed zone II.

on the nodes of an isotropic choanosomal skeleton made up of acanthose or smooth styles (zone III in Fig. 1A). The nodes of this reticulation have echinating styles of approximately the same shape and size as those of the meshes. This ancestral skeleton, more-or-less preserved in *Plocamionida*, is fundamentally similar to skeletons found in many Microcionina (e.g., *Clathria*, *Antho*, and *Raspailia*). From this ancestral ‘bauplan’, the following developments led to the skeletal types observed in the various families and genera (summarized in Fig. 2).

Loss of the basal isotropic reticulation led to hymedesmioid and plumose skeletons depicted in Figure 2C–Q; the variously stronger or suppressed development of tornote bundles gave rise to generic types predominant in the family group Hymedesmiidae (Fig. 2J–K) and Crellidae (Fig. 2F–I). Crellidae emphasized the small acanthose megascleres and built them into unique ectosomal crusts.

Loss of long choanosomal styles led to the proliferation of reticulate skeletons found in Myxillidae and Coelosphaeridae and Tedaniidae (Fig. 2R–Y). Again, the variously stronger or weaker development of ectosomal tornotes may be regarded to account for loss of megasclere diversity observed in all three families.

Loss of both zone II and zone III led to skeletal types found in Desmacididae (Fig. 2D), Ictrochotidae and Crambeidae (Fig. 2E), several fistular Coelosphaeridae (Fig. 2C) and many Chondropsidae (Fig. 2M–N). It is hypothesized that Chondropsidae lost their choanosomal spicules through replacement by foreign material as the skeletal support.

The skeleton of the Dendoricellidae and Phellodermidae (Fig. 2L) may not be easily derived from either the Hymedesmiidae/Crellidae basal type, nor from the Myxillidae/Coelosphaeridae/Tedaniidae type, and we assume it underwent a separate development. In these family there are no echinating spicules and a regularly reticulated skeleton is rare. Instead, skeletons are hymedesmioid or plumose/irregularly plumoreticulate (pointing in the direction of the former line), and chelae are similar to those of the latter line. It is necessary to stress here that skeletal architecture is probably highly adaptive, related to form (habit) and size of sponges. Considerable convergence may have taken place and similar architecture may be found in sponges with very different spiculation. Broadly descriptive terms as ‘isotropic’, ‘plumoreticulate’ or ‘hymedesmioid’ do not appear to have phylogenetic significance at higher level (e.g., families), but may serve to distinguish between related genera and species. Likewise, fistular or bladder-like growth form is considered to be an adaptive character with little significance for higher taxonomic levels, but it may serve to distinguish between related genera and species within a family-level taxon.

Megascleres

Megasclere types may be related to the zones depicted in Figure 1A. Zone I tornotes (cf. Fig. 1B) vary from smooth strongyles, spined or smooth tyloles to subtyloles. Zone II megascleres are normally styles or tyloles with smooth or more

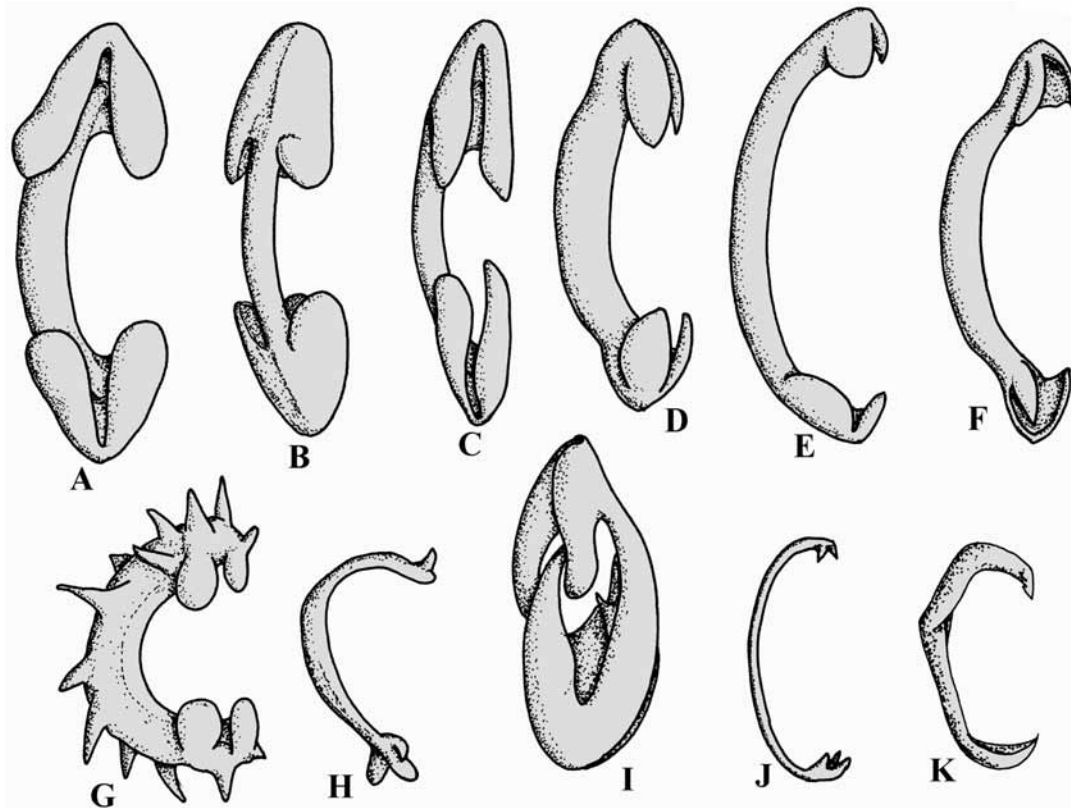


Fig. 3. Arcuate chelae and their derivatives.

frequently spined heads. Zone III megascleres are short, often entirely spined styles, occasionally strongyles. Zone I tornotes are normally easily recognized, but zone II and III megascleres may intergrade and become indistinguishable. Zone I megasclere types appear to be unrelated to the skeletal architecture, nor to the Zone II and III megascleres. There also appears to be considerable intra-specific and supra-specific variation of tornote morphology and ornamentation. Zones II and III spicules show only limited intra-specific and supra-specific variation and have an overall less diverse morphology and ornamentation. Where they are present, they appear to be unrelated to skeletal architecture.

Microscleres

Microscleres provide a most informative set of characters by their diversity and intricate and complicated micromorphology. Within Myxillina chelae may be derived from a basic arcuate type and are variously modified from this arcuate type (Fig. 3) or, by addition of alae, from an anchorate type (Fig. 4). Because of the complicated morphology, the chelae are considered to reflect phylogenetic relationships at both the family and the genus levels. Further microscleres encountered (Fig. 5) are less informative of phylogenetic relationships, with the exception of onychaetes (Fig. 5J), which are a synapomorphy for Tedaniidae, and forcipes (Fig. 5C–D), which are a synapomorphy of a genus *Forcepia s.l.*

Echinating acanthostyles

Presence or absence of echinating acanthostyles occurs in many otherwise not-closely related families and genera (including

those of the suborder Microcionina), and thus is considered to be a 'switch-on/switch-off' character. Their significance as phylogenetic markers at the supraspecific level is dubious but in view of the often great numbers of species in the various families and genera of Myxillina it may be convenient to have a taxonomic rank to unite similar sponges differing only in the lack or possession of these spicule types. It is proposed to retain these groupings at the sub-genus level, similar to solutions proposed for the Microcionina genera. Similar pragmatic solutions are suggested for presence or absence of other spicule types, such as chelae or sigmas.

Sand incorporation

It is a relatively common phenomenon for Myxillina to incorporate sand grains and other detritus, partly or wholly replacing native megascleres. Nevertheless, this is not exclusive to Myxillina, as it is also commonly observed in Microcionina, and outside the Poecilosclerida, such as in the haplosclerid family Callyspongiidae, and many dictyoceratids such as Thorectidae. It is striking to note that by far the highest proportion of poecilosclerid species with sand skeletons occur in South Australia (Wiedenmayer, 1989). The ecological and evolutionary implications for this are still a major sponge conundrum. Sand skeletons cannot be used to unite genera into families within Myxillina without violating otherwise highly informative microsclere and megasclere distribution patterns. Consequently, there is no clear indication to assign sand sponges to taxa above the genus level, and even at the genus level this feature is a doubtful synapomorphy. The family Chondropsidae contains the majority of the sand genera, but arenaceous species and genera also occur in most of the other families (Crellidae excepted).

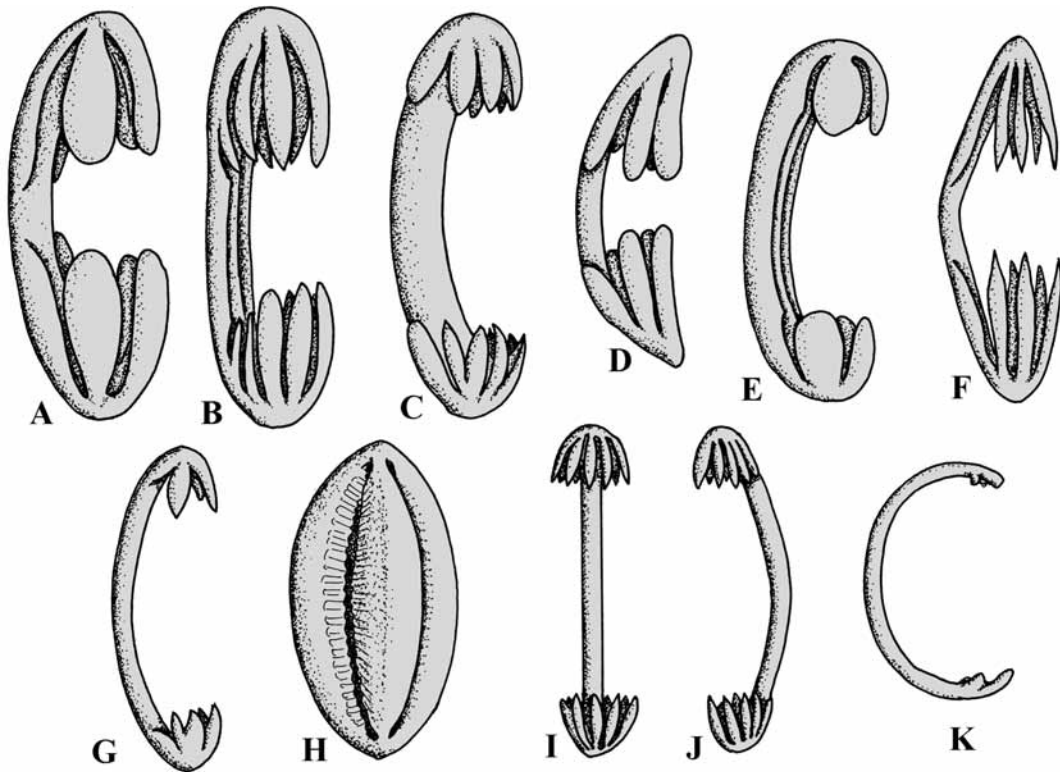


Fig. 4. Anchorate chelae and their derivatives.

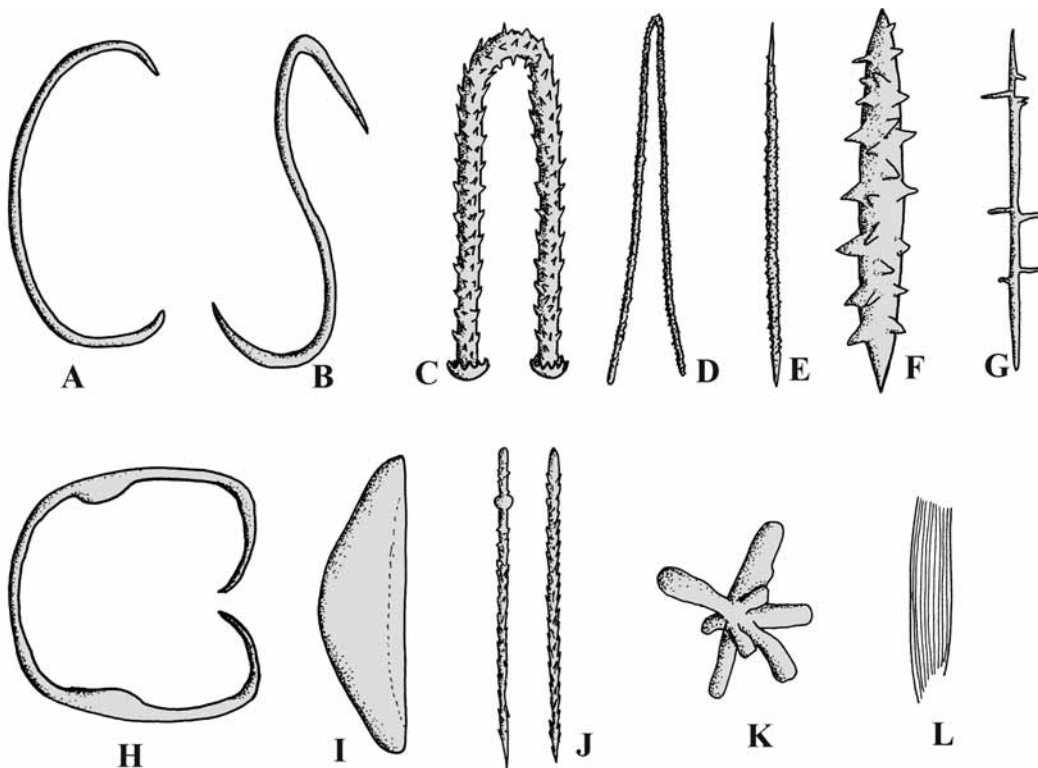


Fig. 5. Microscleres (other than chelae) occurring in various Myxillina groups.

MYXILLINA FAMILY-LEVEL CHARACTERISTICS

Eleven families are tentatively recognized in Myxillina, but they still need further corroboration. Most Myxillina have arcuate chelae, but three families (Myxillidae, Desmacididae and Crambeidae) have exclusively anchorate chelae. Such restriction has resulted in the – possibly artificial – separation of genera previously united within a single family Myxillidae (e.g., *Lissodendoryx* and *Myxilla*). So far only a single exception to this chela-type distribution has been observed: the genus *Crellomima*, which is a typical representative of Crellidae in most respects, but has (polydentate) anchorate chelae. This casts some doubt on the validity of using the anchorate condition of the chelae as a synapomorphy for genera and families (as was also noted by Hooper (1996a) for a few Microcionidae).

Biotulas are considered to be homologous for all genera that possess them, and they are probably derived from anchorate chelae; genera bearing them are consequently assigned to a single family Iotrochotidae, a sister family to the Myxillidae and Desmacididae.

Crambeidae is exceptional in having subtylostyle-like ectosomal megascleres; they are included in Myxillina on the basis of their anchorate chelae.

Fistular or bladder-like growth forms are considered to be an adaptive, non-phylogenetic character and consequently Coelosphaeridae *sensu* Topsent (1928c) is united with non-fistular genera with reticulate skeletons into Coelosphaeridae *s.l.*

Anchinoidae Topsent (1928c: 284) is here merged with Hymedesmiidae as a consequence of discussions in the literature:

hymedesmioid growth form and architecture is thought to grade into anchinoid architecture; spiculation is largely similar in all members of these two nominal families. In support of this hypothesis is the existence of a similar continuum from microcionid to anchinoid-like architecture in some Microcionidae (e.g., *Clathria* (*Thalysias*) *phorbasiformis* Hooper, 1996a), suggesting that these skeletal structures pertain to grades of construction rather than phylogenetic clades.

Crellidae is closely related, sharing the areolate porefields with many Hymedesmiidae, but having the tangential crust of acanthose megascleres as a clearly distinctive trait.

Chondropsidae remain problematic because of their reduced nature; they are united in having a single megasclere category in the form of thin smooth strongyles or styles.

Dendoricellidae has been revived based on the combination of arcuate chelae as microscleres (often with sigmas) and oxeas (tornote derivatives) as the only megascleres present; architecture is plumose.

Desmacididae has been restricted to encompass sponges with a similar spicule complement to that of Dendoricellidae but in these chelae are anchorate and skeletal architecture is reticulate.

A new family Phellodermidae is proposed to accommodate species possessing arcuate chelae and exclusively styles for megascleres.

Tedaniidae is exceptional in lacking microscleres other than onychaetes, and lacking auxiliary acanthostyles; its assignment to Myxillina is based on similarities in tornote shape.

KEY TO FAMILIES

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| (1) Microscleres exclusively onychaetes (very thin spined or rugose unequal-ended spicules) (Fig. 5J) | Tedaniidae |
| Microscleres include biotulas (double-umbrella microscleres) (Fig. 4I) | Iotrochotidae |
| No onychaetes or biotulas | 2 |
| (2) Megascleres exclusively of one type, either oxeas, styles or strongyles | 3 |
| Megascleres of diverse types (may include oxeas in combination with other types) or entirely absent | 5 |
| (3) Megascleres oxeas only | 4 |
| Megascleres thin strongyles only (occasionally thin styles only); chelae arcuate or absent (Fig. 3) | Chondropsidae |
| Megascleres robust styles only; chelae arcuate or derivatives thereof (Fig. 3) | Phellodermidae |
| (4) Skeleton reticulate, microscleres anchorate chelae (Fig. 4) | Desmacididae |
| Skeleton plumose or irregular, microscleres arcuate chelae (Fig. 3) | Dendoricellidae |
| (5) Megascleres consisting of peripheral thinner subtylostyles and choanosomal thicker styles; chelae exclusively anchorate (Fig. 4A, B, E, G) | Crambeidae* |
| Megascleres a combination of diactinal and monactinal spicules, or entirely absent | 6 |
| (6) Ectosomal skeleton consisting of vertical brushes of megascleres fanning out and becoming tangential or megascleres entirely absent | 7 |
| Ectosomal skeleton a crust of entirely spined oxeas or styles | Crellidae |
| (7) Chelae anchorate or polydentate (Fig. 4) | Myxillidae |
| Chelae arcuate or absent (Fig. 3) | 8 |
| (8) Choanosomal skeleton plumose or hymedesmioid; ectosome with areolated porefields | Hymedesmiidae |
| Choanosomal skeleton reticulate or absent (in fistular forms); no areolated pore fields | Coelosphaeridae |
| Choanosomal skeleton a reticulation of sand grains, neither megascleres nor microscleres | Chondropsidae |

*Several species in this family show considerable infraspecific variability in spicule presence and shape. Individuals showing reduced and modified spiculation may key out in other families.