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

Family Microcionidae Carter, 1875

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Microcionidae Carter (Demospongiae, Poecilosclerida), including Clathriidae, Ophlitaspongiidae, contains 77 nominal genera of which only 9 genera and 12 subgenera are considered to be valid (one *incertae sedis*). There are approximately 470 described (valid) species worldwide, living predominantly in shallow waters with a few recorded from deeper seas, and with many other species still collected but remaining undescribed. Microcionids typically have three skeletal regions delineated by the distribution of different structural megascleres: (1) the choanosomal skeleton (with principal monactinal spicules enclosed within spongin fibres and spined monactinal spicules typically echinating fibres; in two groups this is replaced by a basal or axial renieroid skeleton of smooth or acanthose styles or strongyles, with or without echinating spicules); (2) an extra-fibre subectosomal skeleton (with tracts of larger auxillary monactinal spicules ascending to the surface); (3) and a non-tangential ectosomal skeleton (with smaller auxillary styles forming a surface crust perpendicular to the surface). Megascleres are predominantly smooth ectosomal and choanosomal styles, with some diactinal and acanthose modifications. Microscleres are palmate isochelae, only exceptionally modified to superficial arcuate-like or anchorate-like forms (produced by torsion of the shaft and detachment of alae), and toxas with diverse morphologies including microxea-like and raphidiform toxas in few species. Skeletal structures range from 'hymedesmioid' and 'microcionid' in encrusting taxa, to plumo-reticulate and occasionally axially compressed in some species, but usually irregularly reticulate in most taxa. Occasionally spicules are partially or completely replaced by detritus. Two subfamilies are recognised: Ophlitaspongiinae de Laubenfels (with a secondary renieroid spongin fibre and/or spiculose skeleton overlaying a primary reticulate, plumo-reticulate, plumose or hymedesmioid spiculo-spongin skeleton) and Microcioninae Carter (lacking a secondary renieroid reticulate skeleton, having only a reticulate, plumo-reticulate, plumose hymedesmoid, microcionid or axially compressed primary skeleton).

Keywords: Porifera; Demospongiae; Poecilosclerida; Microcionina; Microcionidae; Microcioninae; *Clathria* (*Clathria*); *C.* (*Wilsonella*); *C.* (*Microciona*); *C.* (*Dendrocia*); *C.* (*Axosuberites*); *C.* (*Isociella*); *C.* (*Thalysias*); *Holopsamma*; *Echinochalina* (*Echinochalina*); *E.* (*Protophlitaspongia*); *Pandaros*; Ophlitaspongiinae; *Antho* (*Antho*); *A.* (*Acarnia*); *A.* (*Isopenectya*); *Artemisina*; *Echinoclathria*; *Ophlitaspongia*; *Sigmeurypon* (*incertae sedis*).

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Microcionina Carter, 1875c. Microcionidae Hentschel, 1923. Clathriidae Lendenfeld, 1884. Ophlitaspongiidae de Laubenfels, 1936a.

Definition

Microcionina with terminally spined ectosomal styles, rarely modified to quasidiactinal or diactinal forms; three skeletal regions defined by the presence of different forms of structural styles: (1) choanosomal (axial) skeleton (with spongin fibres enveloping principal styles echinated by acanthose or smooth styles; in two groups this is replaced by a basal or axial renieroid skeleton of smooth or acanthose styles or strongyles, with or without echinating spicules); (2) subectosomal (extra-axial or extra-fibre) skeleton (with individual or tracts of auxiliary styles ascending to the surface); and (3) ectosomal skeleton (with smaller auxiliary styles forming a surface crust tangential, paratangential or perpendicular to the surface). One or more skeletal regions may be lost or modified. Megascleres predominantly smooth styles but may be modified and/or supplemented by quasidiactinal or diactinal forms, or lost completely and replaced with detritus. Microscleres include palmate isochelae and diverse forms of toxas.

Diagnosis

Microcionina with encrusting, lobate, arborescent or flabellate growth forms. Skeleton differentiated into choanosomal (axial), subectosomal (extra-axial) and ectosomal regions. Axial skeleton formed by unispicular or multispicular tracts of choanosomal (principal) megascleres, typically coring spongin fibres or sometimes simply bound together by collagen. Fibres echinated by (acantho-) styles (accessory spicules). Skeletal structures include isodictyal, renieroid, reticulate, plumo-reticulate, plumose or hymedesmioid, but never radial. Subectosomal (extra-axial) skeleton formed by tracts of subectosomal (auxiliary) spicules, usually dispersed outside of fibres, rarely well organised but usually with some degree of difference between axial and extra-axial regions. Ectosomal skeleton ranges from membraneous, or with protruding larger (subectosomal auxiliary) spicules, or with a special category of smaller (ectosomal auxiliary) spicules. Principal megascleres monactinal, predominantly smooth or only partially spined, occasionally vestigial or absent completely, supplemented by another category of acanthose diactinal spicules, or sometimes replaced by detritus. Auxiliary megascleres usually monactinal, rarely quasidiactinal, smooth shaft and basal spines, more slender than choanosomal spicules. Echinating styles or subtylostyles smooth, partially or completely spined. Renieroid skeleton composed of acanthose or occasionally smooth styles or 'dumbell' spicules. Microscleres include toxas of several morphologies (including raphidiform and rarely microxeote toxas), and palmate isochelae.

Some species have modified chelae, arcuate-like or anchorate-like, a result of torsion of the shaft and detachment of alae, but these are exceptional. Larvae viviparous.

Scope

Microcionidae is a highly specious family, containing about 580 described species (of which about 470 are 'valid'), with many other undescribed species already known from various collections worldwide (Hooper, unpublished data). 82 nominal genera have been included in the family at one time or another, of which 77 were recognized as (potentially) residing here (Hooper, 1996a, and more recent additions). Most of these genera were merged into others (e.g., Lévi, 1960b; Simpson, 1968; Van Soest, 1984b; Bergquist & Fromont, 1988; Hooper, 1990b; Hooper & Wiedenmayer, 1994; Hooper, 1996a; Howson & Chambers, 1999), leaving only 9 valid genera and 12 subgenera: *Clathria* (with subgenera *Clathria, Wilsonella, Microciona, Dendrocia, Axosuberites, Isociella, Thalysias*), *Antho* (with subgenera *Antho, Acarnia, Isopenectya*), *Echinoclathria, Holopsamma, Echinochalina* (with subgenera *Echinochalina, Protophlitaspongia*), *Artemisina* and *Ophlitaspongia*, plus *Pandaros* and *Sigmeurypon* as *incertae sedis*. Microcionidae are found in all seas, are sometimes highly diverse and prevalent in shallow coastal waters, comprising up to 16% of species in some regional faunas (Hooper & Lévi, 1993a; Hooper, 1996a). Most species have been recorded from shallow-waters but some range down to 2500 m depth (Hartman, 1982), and it is likely that the family is substantially more diverse than presently known.

History and biology

The disagreement as to which of Microcionidae Carter and Clathriidae Hentschel had priority was settled by Hooper (1996a) based on Article 40 of the International Code of Zoological Nomenclature (Anon., 1999). Hooper (1996a) also provided a comprehensive revision of the family based on extensive re-examination of type material of all nominal type species of genera and over 400 nominal species, primarily from the Indo-west Pacific region.

Several substantial taxonomic publications have appeared for this family, including descriptions of regional faunas, analyses of morphological characters, chemotaxonomy and/or detailed taxonomic revisions (Hallmann, 1920; Lévi, 1960b; Van Soest, 1984b; Bergquist & Fromont, 1988; Hooper, 1990b, 1996a; Hooper & Lévi, 1993a; Hooper *et al*., 1992). These studies have produced several schemes based on the emphasis of certain characters over others, such as patterns of skeletal architecture (Lévi, 1960b), megasclere form and distribution within the skeleton (Hallmann, 1920), ectosomal structure and composition (Van Soest, 1984b), microsclere geometry and diversity (e.g., de Laubenfels, 1936a). More recently all these features, based on a consensus of opinions, were combined into a contemporary classification (Bergquist & Fromont, 1988), with the net result being a proliferation of genera not all of which can be justifiably supported on phylogenetic grounds. This 'consensus' classification is rejected here, although ultimately molecular data may confirm or refute this opinion.

The most recent phylogenetic analysis (Hooper, 1996a) was based primarily on structural features of the skeleton, particularly skeletal architecture and skeletal differentiation. Lesser support was given to megasclere geometry and virtually no support was accorded microsclere modification (cf. Hajdu *et al*., 1994a).

Differences with similar families

Microcionidae is very difficult to define in terms of one or more apomorphies. It differs from other families of Microcionina in lacking certain features: such as apically spined diactinal ectosomal tylotes or tornotes characteristic of Acarnidae; small oxeote or stylote ectosomal spicules forming bouquets, unique to Raspailiidae; or having rhabdostyles and several peculiar microscleres seen in Rhabderemiidae. Similarly, the four families of Microcionina differ from the Myxillina and Mycalina in lacking particular characters, as opposed to possessing unique ones (Myxillina with tridentate-derived chelae; Mycalina with sigmancistra derivatives), yet both these latter suborders may also have palmate chelae in addition to their derived microscleres.

Following a recent comprehensive revision (Hooper, 1996a) Microcionidae is now restricted to genera having predominantly smooth monactinal ectosomal and choanosomal spicules. It excludes certain microcionid-like genera with true tylotes or strongylotes as their ectosomal spicules (e.g., *Acarnus, Megaciella*). These taxa are now included in Acarnidae, as defined by their ectosomal features (Hajdu *et al*., 1994a). However, the definition barely differentiates species with modified or reduced quasidiactinal (styloid) auxiliary megascleres (e.g., several *Echinoclathria, Holopsamma* and *Echinochalina* species), or quasimonactinal (amphistrongylote or tornote-like) auxiliary megascleres (e.g., *Protophlitaspongia*). These modified auxiliary spicules are usually asymmetrical and are interpreted here as convergent upon true diactinal spicules. These anomalous microcionids share certain characteristics of both Microcionidae and Acarnidae, and the importance of these characters at higher levels of systematics must therefore be questioned, or a certain level of homoplasy must be accomodated in the phylogeny of the suborder.

Similarly, the definition given above cannot always clearly distinguish some Microcionidae from some Raspailiidae, but this is a

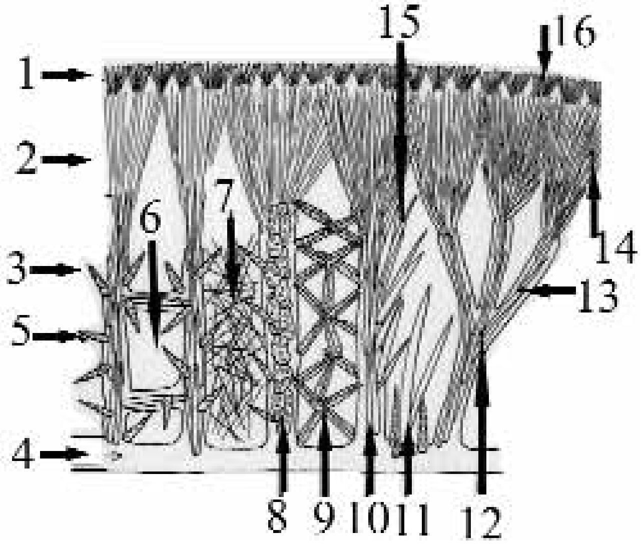

Fig. 1. Idealised microcionid skeletal structure. Key: 1, ectosomal skeleton. 2, subectosomal skeleton. 3, choanosomal skeleton. 4, basal spongin fibre. 5, echinating acanthostyle. 6, reticulate fibre skeleton. 7, isotropic extra-fibre skeleton. 8, detrital entrapping fibre. 9, renieroid reticulate secondary fibre skeleton. 10, microcionid radial fibre skeleton. 11, hymedesmioid spicule skeleton. 12, plumose/dendritic fibre skeleton. 13, coring principal spicules. 14, subectosomal auxuliary spicules. 15, spicate spicule skeleton. 16, ectosomal auxiliary spicules. Modified from Hooper (1996a).

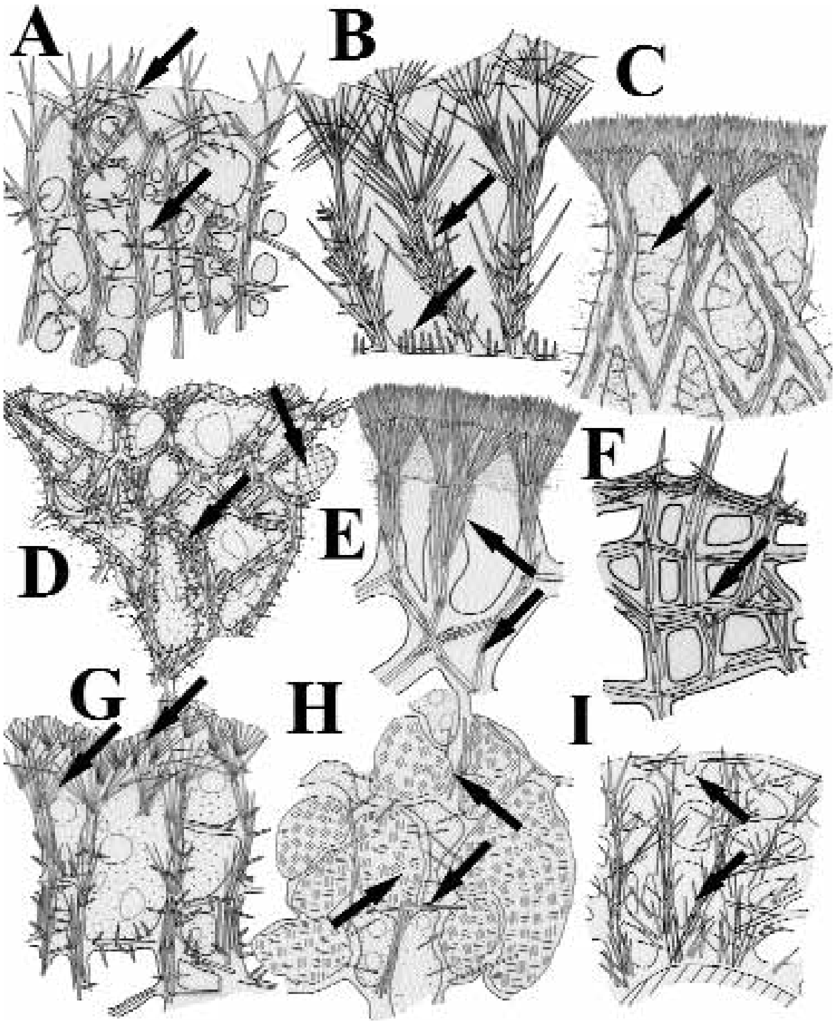

Fig. 2. Range of skeletal structures in Microcionidae. Arrows indicate diagnostic features (as mentioned in the Key to genera and subgenera). A–I, Microcioninae. A, *Clathria* (*Clathria*) (*C.* (*C.*) *lipochela* Burton). B, *Clathria* (*Microciona*) (*C.* (*M.*) *antarctica* (Topsent)). C, *Clathria* (*Dendrocia*) (*C.* (*D.*) *pyramida* Lendenfeld). D, *Clathria* (*Wilsonella*) (*C.* (*W.*) *australiensis* Carter). E, *Clathria* (*Axosuberites*) (*C.* (*A.*) *canaliculatus* (Whitelegge)). F, *Clathria* (*Isociella*) (*C.* (*I.*) *eccentrica* (Burton)). G, *Clathria* (*Thalysias*) (*C.* (*T.*) *rubra* (Lendenfeld)). H, *Holopsamma* (*H. crassa* Carter). I, *Echinochalina* (*Echinochalina*) (*E.* (*E.*) *australiensis* (Ridley)). A–I, modified from Hooper (1996a).

problem of semantics rather than a biological one. In general, most species of Raspailiidae have well-compressed axial skeletons, well-differentiated axial and extra-axial skeletons, and special bouquets of ectosomal spicules surrounding the larger choanosomal spicules protruding through the surface. In contrast, most Microcionidae lack these two former features, or they are only poorly developed and probably convergent, perhaps related to habit (e.g., flexuous whip-like growth forms). Nevertheless, there are examples in both families where the boundaries between taxa blur, such as the microcionid-like *Raspailia* (*Clathriodendron*) *arbuscula* (see Hooper, 1991: figs 19–20), and the raspailiid-like *Clathria* (*Axosuberites*) *canaliculata* (see Hooper, 1996a: figs 118–119). Conversely, the two families are consistently differentiated by this latter ectosomal feature, and possession of chelae microscleres in Microcionidae (absent in Raspailiidae), which appear to be more important characters than skeletal structure.

Hajdu *et al*. (1994a) restricted Microcionina (and hence Microcionidae) to taxa with only palmate isochelae, tacitly excluding several microcionid-like genera specifically created for species with tridentate-derived (arcuate or anchorate) chelae. Theoretically, this is a viable system for the suprafamily classification of Microcionidae, but in practical terms it is not always possible to distinguish between true tridentate-derived chelae and palmate chelae with 'arcuate' or 'anchorate' modifications (i.e., partial torsion of the shaft and partial or complete detachment of alae from the shaft). These few anomalies have yet to be fully resolved.

Previous reviews

De Laubenfels (1936a: 112), Lévi (1960b: 50), Simpson (1968: 102), Van Soest (1984b: 90), Wiedenmayer (1989: 56), Bergquist & Fromont (1988: 106), Hooper & Wiedenmayer (1994: 252), Hooper (1996a: 1).

PROPOSAL FOR A DIVISION OF MICROCIONIDAE

Hooper's (1996a) analysis of Microcionidae showed that there were two fundamental groups of genera within the family, differentiated primarily by their skeletal structure, the complexity

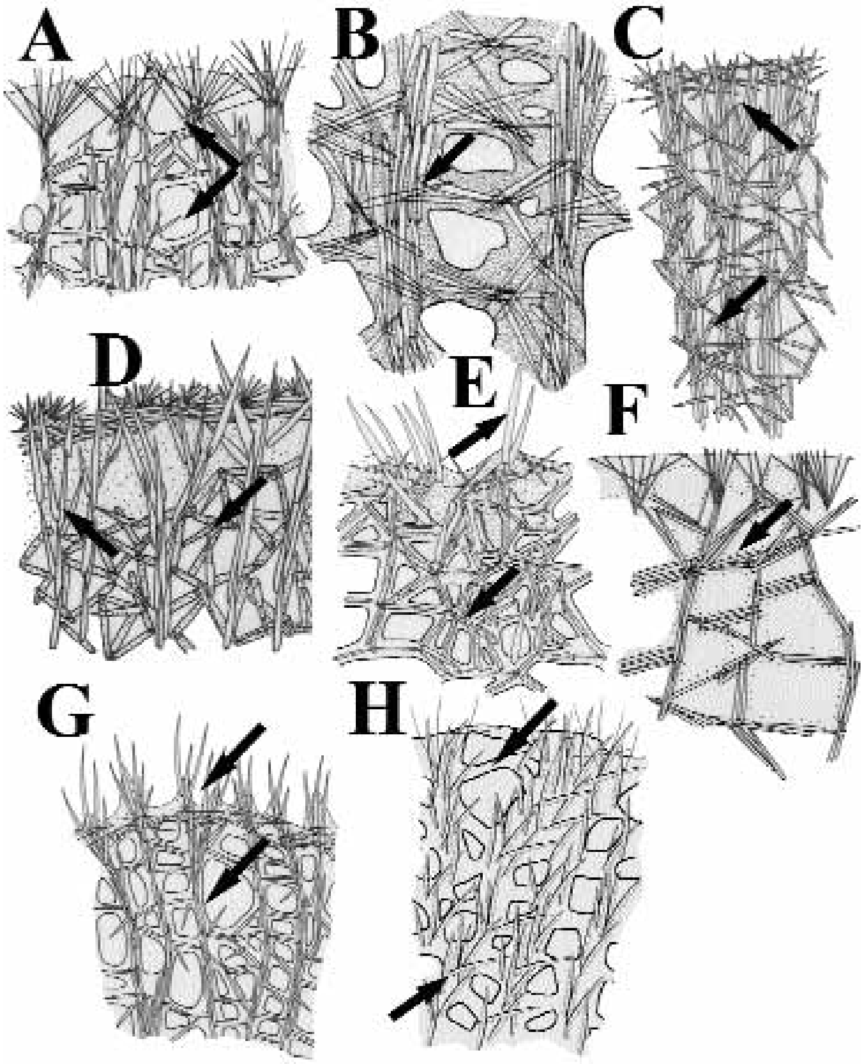

Fig. 3. Range of skeletal structures in Microcionidae (cont.). A–B, Microcioninae. A, *Echinochalina* (*Protophlitaspongia*) (*E.* (*P.*) *tuberosa* Hooper). B, *Pandaros* (*P. acanthifolium* D&M). C–H, Ophlitaspongiinae. C, *Antho* (*Antho*) (*A.* (*A.*) *tuberosa* (Hentschel)). D, *Antho* (*Acarnia*) (*A.* (*A.*) *ridleyi* (Hentschel)). E, *Antho* (*Isopenectya*) (*A.* (*I.*) *chartacea* (Whitelegge)). F, *Artemisina* (*A. jovis* Dendy). G, *Echinoclathria* (*E. parkeri* Hooper). H, *Ophlitaspongia* (*O. papilla* Bowerbank). A, C–G, modified from Hooper (1996a). B, modified from Van Soest (1984b). H, modified from Howson & Chambers (1999).

or differentiation of the skeleton, and the presence or absence, respectively, of a secondary renieroid reticulate skeleton overlaying the primary (reticulate, plumo-reticulate, plumose or hymedesmioid) skeleton. (1) One group, containing *Artemisina, Antho, Echinoclathria* and *Ophlitaspongia*, has suggested myxillid-like features, most possessing a secondary renieroid skeleton overlaying a primary reticulate, plumo-reticulate, plumose or hymedesmioid spiculo-spongin skeleton. (2) The other group, containing *Clathria, Echinochalina, Holopsamma* and *Pandaros*, has suggested raspailiid-like features including similarities to typical raspailiid genera (e.g., *Clathria* (*Axosuberites*) and *Raspailia*) and atypical raspailiid genera (e.g., *Echinochalina* (*Echinochalina*) and *Echinodictyum*, respectively) (Figs 1–3). Within the second group there are also several subgenera of *Clathria* indicated as being possibly polyphyletic (Hooper, 1996a). This second group has only a primary skeletal structure, with reticulate, plumo-reticulate, plumose hymedesmoid, microcionid or axially compressed skeletal architectures. These groups are elevated here to subfamily status: Ophlitaspongiinae and Microcioninae, respectively.

The possibility that designated subgenera should be elevated to full generic status was rejected by Hooper (1996a), on the basis that the characters inferring polyphyly (e.g., partial substitution of coring megascleres by detritus in *Wilsonella*, and loss of principal spicules completely in *Dendrocia*) are homoplasious, representing convergences through functional acquisition or secondary loss of particular features, rather than real apomorphies. Thus, some of these subgeneric taxa may be artificial given the existence of these homoplasies, but the use of this subfamily classification allows us to construct both a working phylogenetic hypothesis as well as the production of a useful, working classification. Of dubious phylogenetic value are the possession of acanthose strongyles in place of acanthose styles in *Antho* and *Plocamia*, presence of detritus within fibres in *Clathria* (*Wilsonella*), and encrusting habit in *Clathria* (*Microciona*). Conversely, other subgenera have a more substantial phylogenetic basis and are more easily justified within the classification presented here (e.g., stylote versus oxeote structural megascleres in *Echinochalina* and *Protophlitaspongia*; presence or absence of ectosomal specialisation in *Thalysias* and *Clathria*).

KEYS TO MICROCIONIDAE

Key to subfamilies

(1) With a single primary skeletal structure: reticulate, plumo-reticulate, plumose hymedesmioid, microcionid or axially compressed (Figs 2A–I, 3A–B) .... **Microcioninae**
With a secondary renieroid spongin fibre and/or spiculose skeleton overlaying a primary reticulate, plumo-reticulate, plumose or hymedesmioid spiculo-spongin skeleton (Fig. 3C–H) .... **Ophlitaspongiinae**

Key to genera and subgenera (Refer to Figs 1–3 for skeletal structures)

(1) Choanosomal skeleton more-or-less undifferentiated, unstructured .... ***Artemisina***
Choanosomal skeleton well structured, ranging from hymedesmioid to reticulate, but lacking any differentiated components 2
Choanosomal skeleton well structured, predominantly reticulate, differentiated into two distinct structural components (e.g., primary renieroid skeleton overlaid by secondary plumose or radial skeletons) 7
(2) Choanosomal fibres cored by one or more category of principal spicules 3
Choanosomal fibres cored by auxiliary spicules partially (or sometimes wholly) replaced by detritus 5
Choanosomal fibres cored by auxiliary spicules identical to those in ectosomal and subectosomal skeletons 6
Choanosomal fibres form a ladder-like isodictyal reticulation, but only primary fibres cored by plumose columns of megascleres and transverse fibres virtually clear .... ***Ophlitaspongia***
Choanosomal fibres or skeletal tracts cored by auxiliary spicules different from those in peripheral skeleton .... ***Pandaros***
(3) Choanosomal skeleton without any marked axial compression or differentiated axial and extra-axial regions 4
Choanosomal skeleton with noticeably compressed axis and well differentiated axial and extra-axial (radial, plumose or plumo-reticulate) regions; lacking echinating megascleres .... ***Clathria (Axosuberites)***
Choanosomal skeleton evenly renieroid reticulate throughout, with well developed spongin fibres cored by smooth principal styles; lacking echinating megascleres .... ***Clathria (Isociella)***
Choanosomal skeleton hymedesmioid or microcionid, with basal layer of spongin lying on substrate without ascending fibre nodes ranging to ascending non-anastomosing columns of spongin fibres; bases of principal styles perpendicular to the substrate or forming plumose tracts in ascending fibres, and with acanthostyles or smooth styles echinating megascleres, differentiated from principal styles coring fibres .... ***Clathria (Microciona)***
(4) With a single category of subectosomal auxiliary spicule forming the ectosomal skeleton, producing tangential, paratangential or plumose tracts; choanosomal skeleton predominantly reticulate or plumo-reticulate .... ***Clathria (Clathria)***
With two categories of auxiliary spicules, smaller ectosomal spicules generally overlaying larger subectosomal spicules forming discrete bundles or continuous palisade on surface .... ***Clathria (Thalysias)***
(5) Echinating acanthostyles differentiated from principal spicules coring fibres .... ***Clathria (Wilsonella)***
Echinating styles or acanthostyles identical to principal styles coring spongin fibres .... ***Holopsamma***
(6) Echinating acanthostyles differentiated from auxillary spicules coring the fibres .... ***Clathria (Dendrocia)***
Fibres cored by a single category of auxillary styles identical to those forming subectosomal and ectosomal skeletons, and echinated by smooth styles derived from principal spicules .... ***Echinochalina (Echinochalina)***
Fibres cored by a single category of auxiliary oxeas or styles different from principal oxeas, anisoxeas or styles that echinate fibres .... ***Echinochalina (Protophlitaspongia)***
(7) Primary skeleton renieroid, cored by axially or basally compressed tracts of acanthostyles; secondary skeleton subisodictyal or plumo-reticulate, cored by smooth principal styles in plumose tracts .... ***Antho (Antho)***
Primary skeleton renieroid, cored by axially or basally compressed tracts of acanthostrongyles; secondary skeleton subisodictyal or plumo-reticulate, cored by smooth principal styles in plumose tracts .... ***Antho (Acarnia)***
Primary skeleton composed of axially compressed spongin fibres cored by renieroid tracts of sparsely spined principal styles intermingled with plumose or plumo-reticulate tracts of smooth principal styles, overlaid by secondary extra-axial plumose skeleton cored by larger smooth principal styles .... ***Antho (Isopenectya)***
Primary renieroid reticulate skeleton cored by smooth principal styles and echinated by identical spicules, with secondary radial extra-axial skeleton on exterior edge of skeleton cored only by larger smooth principal styles .... ***Echinoclathria***

SUBFAMILY MICROCIONINAE CARTER, 1875

Synonymy

Microcionina Carter, 1875c. Microcionidae Hentschel, 1923.

Type genus

Clathria Schmidt, 1862.

Definition

Microcionidae lacking a secondary renieroid skeleton, with only a reticulate, plumo-reticulate, plumose hymedesmioid, microcionid or axially compressed primary skeleton.

Scope

Four genera and seven subgenera: *Clathria* (*Clathria* (*Clathria*), *C.* (*Wilsonella*), *C.* (*Microciona*), *C.* (*Dendrocia*), *C.* (*Axosuberites*), *C.* (*Isociella*), *C.* (*Thalysias*)), *Echinochalina, Holopsamma* and *Pandaros*.

CLATHRIA SCHMIDT, 1862

Synonymy

Clathria Schmidt, 1862: 57 (see subgenera for full synonymy).

Type species

Clathria compressa Schmidt, 1862: 58 (by subsequent designation; Schmidt, 1864: 35).

Definition

Microcioninae with auxiliary styles in one or two categories forming various ectosomal structures ranging from membraneous paratangential to a dense erect palisade of brushes; choanosomal skeleton well-structured, hymedesmioid to reticulate, with mostly smooth styles enclosed within spongin fibres and fibres echinated by mostly acanthose smaller styles.

Diagnosis

Thinly encrusting, massive, digitate, lamellate, flabellate, arborescent or occasionally fistulose growth forms. Ectosomal skeleton composed of monactinal auxiliary spicules in one or two categories forming structures ranging from sparse, mostly membraneous (subgenus *Microciona*), sparse, paratangential (subgenus *Clathria*) to a dense erect palisade of brushes on the surface (subgenus *Thalysias*). Choanosomal skeletal tracts usually enclosed within spongin fibres, sometimes simply with nodal spongin; fibres cored by smooth, basally spined or partially spined principal monactinal megascleres, usually geometrically different from auxiliary megascleres, sometimes secondarily lost and cored by single category of auxiliary subtylostyle (subgenus *Dendrocia*), or sometimes replaced partially or fully by detritus in fibres (subgenus *Wilsonella*). Echinating megascleres partially or entirely acanthose, occasionally smooth or vestigial spination, sometimes secondarily lost (subgenera *Axosuberites, Isociella*). Choanosomal structure ranges from hymedesmioid, leptoclathrid to microcionid plumose (subgenus *Microciona*), renieroid (subgenus *Isociella*), plumo-reticulate or reticulate, with (subgenus *Axosuberites*) or without compressed axis and radial extra-axial regions. Microscleres include palmate isochelae and modified forms, and toxas with smooth or spined points, occasionally absent.

Remarks

The above definition is necessarily broad to encompass the seven subgenera included in *Clathria*. These characters span a wide spectrum of states, most of which are interpreted as secondary losses rather than unique apomorphies, and many characters show intermediate states making it virtually impossible to maintain strict generic boundaries recognised by earlier authors.

Distribution

Worldwide, predominantly shallow waters.

SUBGENUS *CLATHRIA* SCHMIDT, 1862

Synonymy

Clathria Schmidt, 1862: 57. [*Clatharia*] Kumar, 1925: 221 (*lapsus*). *Allocia* Hallmann, 1920: 768 (type species *Spanioplon cheliferum* Hentschel, 1911: 362 (by original designation and monotypy), holotype ZMB 4440). *Antherochalina* Lendenfeld, 1887c: 741, 786 (type species *Antherochalina crassa* Lendenfeld, 1887c: 787 (by subsequent designation; Burton, 1934a: 558), holotype BMNH 1886.8.27.450). *Bipocillopsis* Koltun, 1964b: 79 (type species *Bipocillopsis nexus* Koltun, 1964b: 80 (by monotypy) holotype ZIL 10644). *Dictyociona* Topsent, 1913b: 579, 618 (type species *Microciona discreta* Thiele, 1905: 447 (by monotypy), holotype ZMB 3302). *Labacea* de Laubenfels, 1936a: 125 (type species *Clathria juncea sensu* Burton, 1931a: 343 (by original designation), schizotype BMNH 1926.2.19.2 (unconfirmed)). *Ligrota* de Laubenfels, 1936a: 125 (type species *Clathria lobata* Vosmaer, 1880: 151 (by original designation) holotype RMNH 276). *Litaspongia* de Laubenfels, 1954: 162 (type species *Ophlitaspongia arbuscula* Row, 1911: 347 (by original designation) holotype BMNH 1912.2.1.63). *Paresperia* Burton, 1930c: 501 (type species *Paresperia intermedia* Burton, 1930c: 501 (by monotypy) holotype BMNH 1910.1.1.912). *Marleyia* Burton, 1931a: 346 (type species *Marleyia irregularis* Burton, 1931a: 346 (by original designation) holotype NM 1279). *Pitalia* Gray, 1867a: 524 (type species *Reniera frondiculata* Schmidt, 1864: 39 (by monotypy) fragment of holotype BMNH 1910.1.1.542). *Ramoses* de Laubenfels, 1936a: 109 (type species *Clathria pauper* Brondsted, 1927: 3 (by original designation and monotypy) schizotype BMNH 1930.11.5.2). *Thalyseurypon* de Laubenfels, 1936a: 107 (type species *Spongia raphanus* Lamarck, 1814: 444 (by original designation) holotype MNHN DT572). Taxonomic decision for synonymy: Hooper (1996a), and this work.

Type species

Clathria compressa Schmidt, 1862: 58 (by subsequent designation; Schmidt, 1864: 35).

Definition

Clathria with only a single category of auxiliary style forming a sparse paratangential ectosomal skeleton; choanosome without marked difference between axial and extra-axial regions.

Diagnosis

Predominantly massive, lamellate, digitate, flabellate or arborescent growth forms; ectosomal skeleton composed of a single undifferentiated category of auxiliary megasclere; choanosomal skeletal structure plumo-reticulate or reticulate, usually without marked difference between axial and extra-axial regions; spongin fibres cored by completely smooth, basally spined or partially spined principal megascleres, geometrically differentiated from auxiliary megascleres, but sometimes secondarily lost; echinating megascleres entirely or partially acanthose, occasionally smooth, sometimes secondarily lost. Microscleres include palmate isochelae and modified forms, and toxas with smooth or spined points.

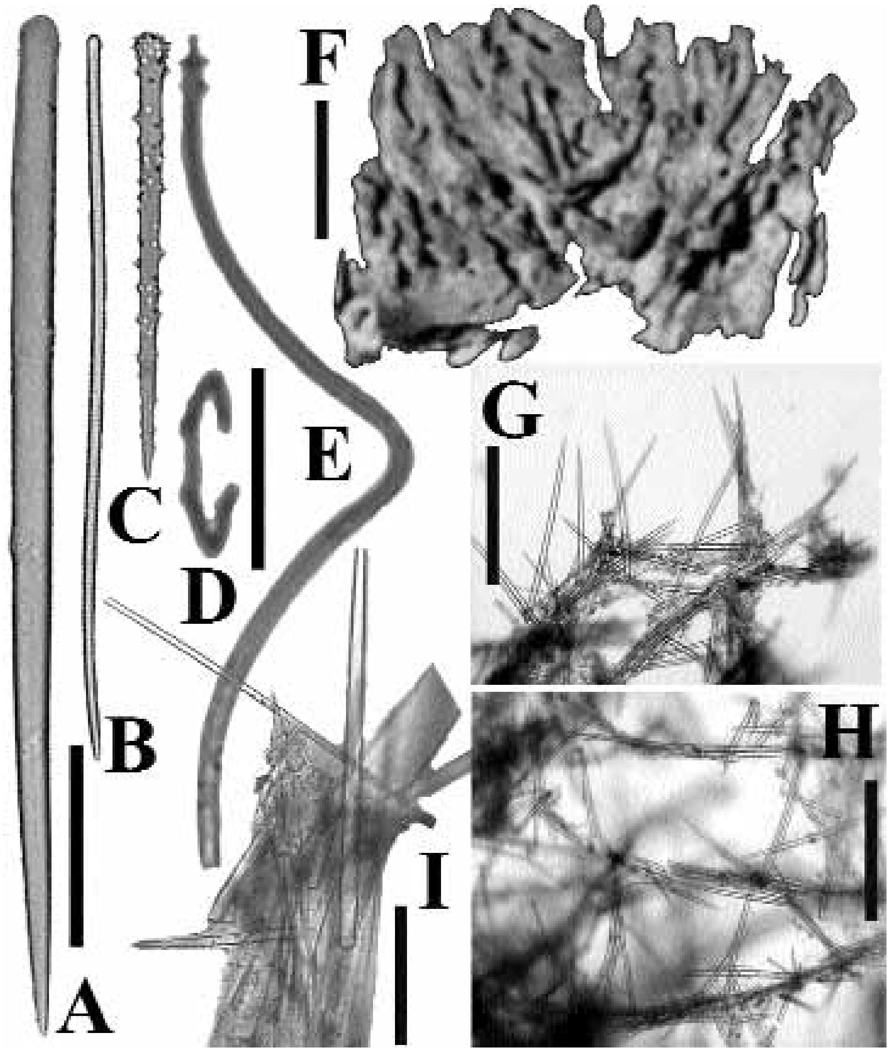

Fig. 4. *Clathria* (*Clathria*). A–I, *C.* (*C.*) *compressa* Schmidt. A, choanosomal principal style. B, subectosomal auxiliary subtylostyle. C, echinating acanthostyle (scale A–C, 50 μm). D, palmate isochelae. E, spined accolada toxa (scale D–E, 10 μm). F, fragment of holotype BMNH 1867.7.2.6.78 (scale 30 mm). G, ectosomal skeleton (scale 150 μm). H, choanosomal skeleton (scale 150 μm). I, fibre structure (scale 50 μm).

Description of type species

Clathria compressa Schmidt, 1862 (Fig. 4).

Synonymy. *Clathria compressa* Schmidt, 1862: 8; *Thalysias compressa;* de Laubenfels, 1936a: 105.

Material examined. Holotype: LMJG 15509 (schizotypes BMNH 1867.7.26.78, BMNH 1910.1.1.2362, 2363) – Adriatic. Refer to Hooper (1996a) for full list of other type material examined.

Description. Erect, arborescent, thinly lamellate, branching growth form. Surface even, not hispid. Choanosomal skeleton regularly reticulate, with well developed spongin fibres forming regular or irregular anastomoses of differentiated primary and secondary spongin fibres. Fibres cored by choanosomal principal subtylostyles in multispicular ascending tracts and uni- or bispicular transverse connecting tracts, and echinated by acanthostyles perpendicular to or at acute angles to spongin fibres. Ectosomal skeleton with tangential layer of subectosomal auxiliary subtylostyles, of a single size category. Megascleres basally spined choanosomal principal subtylostyles (220–345 × 8–14 μm), entirely smooth subectosomal auxiliary subtylostyles (164–235 × 3–6 μm), and echinating acanthostyles with even spination (75–116 × 6–9 μm). Microscleres small palmate isochelae (6–11 μm) and forceps-shaped or accolada toxas with spinose extremities (32–148 × 1.5–4 μm).

Remarks. Of the 160 named species originally described in, or subsequently referred to *Clathria* (*Clathria*), or one of its synonyms listed above, 115 are thought to be valid and most appropriately placed in this subgenus (the others being junior synonyms of established species or referred to other families).

Pitalia Gray is a new synonym included here in *Clathria* (*Clathria*), overlooked by Hooper (1996a). *Paresperia* Burton also belongs to *Clathria*, as originally suspected by Burton (1930c). Van Soest & Stone (1986: 45) suggested it was closer to *Esperiopsis* (? Mycalidae), and was followed by Hooper (1996a: 86) in this determination. Van Soest *et al*. (2000) returned it to *Clathria*, although again with question, and re-examination of type material in this work supports its allocation to Microcionidae rather than to Mycalidae. The species is poorly known only from a single record from Norway, and type material is imperfect (holotype slides BMNH 1910.1.1.912, 2606–7). Re-examination of these slides by Hooper (1996a: 86) failed to adequately fix the affinities of this species. The choanosomal skeleton is loosely reticulate, formed by smaller acanthose styles (principal spicules), bearing an even covering of minute spines (330 × 9 μm), and larger subtylostyles with microspined bases (auxiliary spicules) (510 × 8 μm) also scattered throughout the choanosomal skeleton, although this skeleton is not obviously divisible into primary or secondary tracts as seen in many other *Clathria*. Echinating acanthostyles are absent. Both principal and auxiliary megascleres form a loose tangential ectosomal reticulation, and microscleres consist only of palmate isochelae (24 μm long). Assigning this species accurately to a subgenus is currently impossible given the poor quality of type material. Its lack of echinating acanthostyles indicates possible affinities to *Clathria* (*Isociella*) and *C.* (*Axociella*), but both of these subgenera have distinctive skeletal structure (isodictyal/renieroid reticulate, and axially compressed, extra-axial radial to plumo-reticulate, respectively), and neither has spinose principal spicules. *Isociella* is also exclusively Gondwanan in distribution. *Paresperia* is, by default, left in *Clathria* (*Clathria*), and for the time being is considered a greatly reduced form of this genus (lacking acanthostyles and any definite skeletal structure).

SUBGENUS *WILSONELLA* CARTER, 1885

Synonymy

Wilsonella Carter, 1885d: 366 (Not Hallmann, 1912: 242). *Clathriopsamma* Lendenfeld, 1888: 227 (type species *Clathriopsamma reticulata* Lendenfeld, 1888:227 (by subsequent designation; Hallmann, 1920: 771), lectotype AM G9135). *Aulenella* Burton & Rao, 1932: 345 (type species *Aulenella foraminifera* Burton & Rao, 1932: 345 (by original designation) holotype IM P1167/1). *Psammotoxa* de Laubenfels, 1936a: 99 (type species *Phoriospongia guettardi* Topsent, 1933: 19 (by original designation), lectotype and paralectotype MNHN DT532, 3398, respectively (here designated)). Taxonomic decision for synonymy: Hooper (1996a), and this work.

Type species

Wilsonella australiensis Carter, 1885d: 366 (by monotypy).

Definition

Clathria with sand grains and foreign spicules partially or completely replacing coring spicules inside fibres; coring spicules same or very similar geometry to auxiliary spicules located outside fibres; skeletal architecture reticulate.

Diagnosis

Lobate, clavulate, lamellate or bulbous growth forms; surface arenaceous, and ectosome either lacking any megascleres or with sparsely scattered auxiliary styles; choanosomal skeleton reticulate, cavernous, with fibres cored by sand grains and detritus and varying quantities of principal spicules, and echinated by acanthostyles; principal and auxiliary styles usually poorly differentiated in their geometry; microscleres include palmate isochelae and toxas.

Description of type species

Clathria (*Wilsonella*) *australiensis* (Carter, 1885d) (Figs 2D, 5).

Synonymy. *Wilsonella australiensis* Carter, 1885d: 366; *Clathria australiensis*; Dendy, 1896: 33; *Clathria* (*Wilsonella*) *australiensis*; Hooper, 1996a: 183, figs 83–84. *Clathria australiensis* var. *spinulata* Hentschel, 1911: 374; *Clathriopsamma lobosa* Lendenfeld, 1888: 149; *Thorecta ramsayii* Lendenfeld, 1888: 149; *Sigmatella corticata* var. *elegans* Lendenfeld, 1888: 199 (Not *Clathria australiensis*; Lévi, 1967a: 22. Not *Ophlitaspongia australiensis* Ridley, 1884a: 442. Not *Echinochalina australiensis*; Thiele, 1903a: 961).

Material examined. Lectotype: BMNH 1886.12.15.43 – Port Phillip, Victoria, Australia. Other material. Refer to Hooper (1996a: 183).

Description. Shape lobate, lobate-digitate, club-shaped, thickly lamellate, thickly encrusting-bulbous or rarely fistulose growth forms; large oscules on apical or lateral margins of surface lobes; surface arenaceous; ectosome membraneous, without specialized dermal megascleres; choanosomal skeleton irregularly reticulate, with clearly differentiated primary and secondary spongin fibres, forming a vaguely longitudinal reticulation with cavernous meshes; primary ascending fibres producing ascending lines abundantly cored by detritus, lightly cored by auxiliary styles, heavily echinated by acanthostyles, particularly at fibre nodes; smaller secondary spongin fibres mainly transverse, connecting with primary elements, with no or little detritus, paucispicular tracts of auxiliary styles and lightly echinated by acanthostyles; auxiliary megascleres coring fibres occupy only a small proportion of fibre diameter; megascleres are choanosomal auxiliary styles coring fibres differ from subectosomal auxiliary styles; only in being slightly thicker and lacking characteristic apical microspines of the latter; coring spicules relatively thin, straight, smooth, mostly hastate, with slightly subtylote and occasionally microspined bases (62–152 × 2.5–4 μm); subectosomal auxiliary styles, dispersed between fibres and in dermal skeleton, straight, usually hastate, subtylote bases with microspines on both points and bases (92–152 × 2.5–4 μm); echinating acanthostyles small, evenly spinose or with granular, vestigial spines, slightly subtylote bases, fusiform points (49–68 × 2–4.5 μm); microscleres are palmate isochelae relatively large, unmodified (11–18 μm); toxas oxhorn, uncommon, rare in some specimens, often forming trichodragmata, usually with wide, angular, central curves and slightly reflexed points (35–89 × 0.5–1 μm).

Remarks. This group of arenaceous microcionids has already become well known under the name of *Clathriopsamma* (e.g., Hooper, 1990b; Hooper & Lévi, 1993a), whereas Hooper (1996a) noted that the inclusion of *C.* (*Wilsonella*) *australiensis* in this group unfortunately means that the senior name *Wilsonella* (1885) must take precedence over *Clathriopsamma* (1888).

Unlike *Clathria* (*Dendrocia*), in which there is only a single category of coring and extra-fibre megasclere, most *Clathria* (*Wilsonella*) have more than one form of auxiliary style, one coring the fibres (choanosomal megascleres) and one outside of fibres (subectosomal megascleres). In some cases (e.g., *C.* (*W.*) *australiensis, C.* (*W.*) *ensiae*), these spicules are only slightly different in their geometry, although showing clear differences in their spination; in others (e.g., *C.* (*W.*) *reticulata, C.* (*W.*) *mixta*) these spicules are quite different; whereas in one (*C.* (*W.*) *abrolhosensis*) there is no apparent difference, and this is interpreted as a convergence or subsequent loss of a spicule category. *Clathria* (*Dendrocia*) and *Clathria* (*Wilsonella*) can also be distinguished by their skeletal architecture – being predominantly plumose in the former and reticulate in the latter.

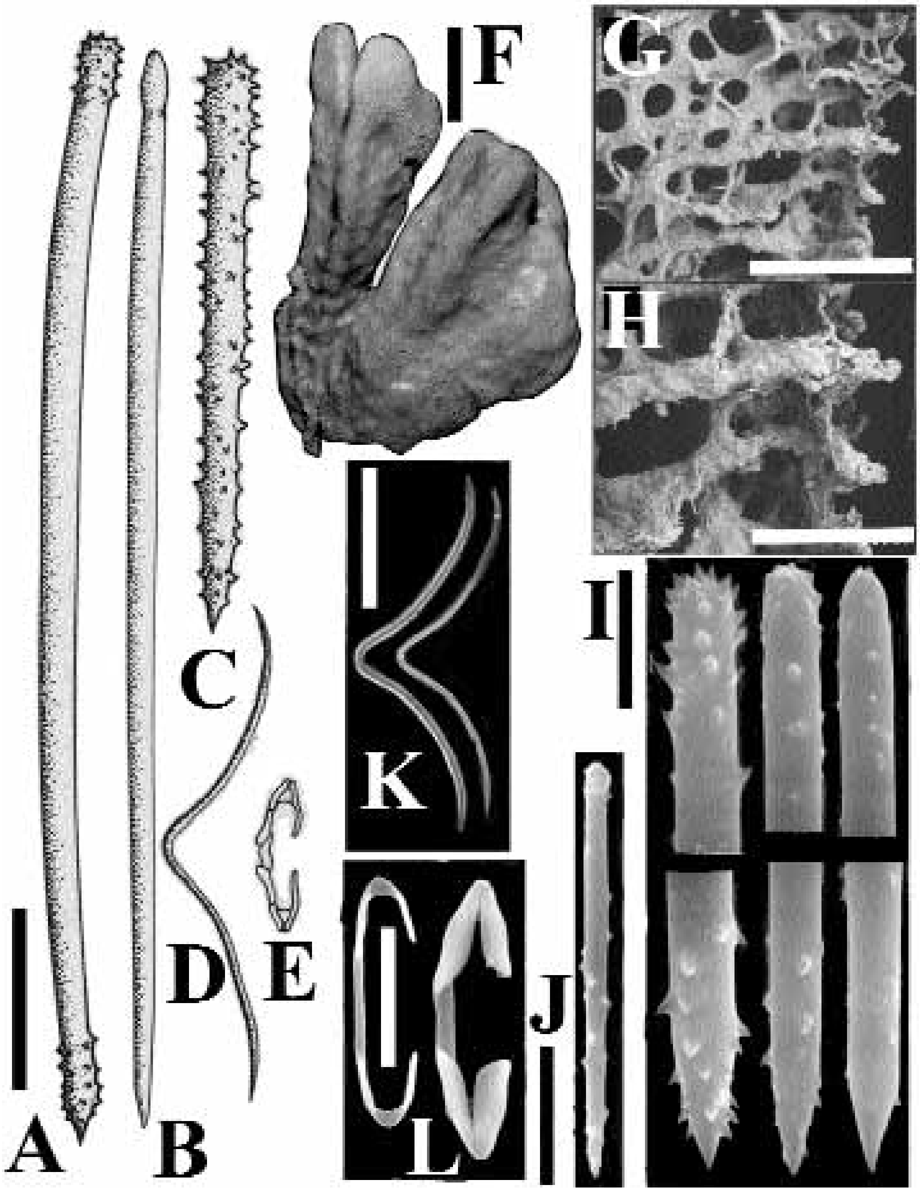

Fig. 5. *Clathria (Wilsonella)*. A–L, *C.* (*W.*) *australiensis* (Carter). A, subectosomal auxiliary subtylostyle. B, choanosomal auxiliary subtylostyle. C, echinating acanthostyle. D, Oxhorn toxa. E, palmate isochela (scale A–E, 25 µm). F, holotype BMNH 1886.12.15.43 (scale 30 mm). G, choanosomal skeleton (scale 1 mm). H, peripheral skeleton (scale 500 µm). I, continuum in basal and apical spination on auxiliary subtylostyles (scale 5 µm). J, echinating acanthostyle (scale 20 µm). K, oxhorn toxas (scale 20 µm). L, palmate isochelae (scale 5 µm). A–L, modified from Hooper (1996a).

Psammotoxa de Laubenfels, 1936a is also a synonym of *Clathria* (*Wilsonella*), previously overlooked by Hooper (1996a). Its type species, *Phoriospongia guettardi* Topsent was a new name proposed for two specimens erroneously identified as *Spongia carduus* by Lamarck, 1814. The lectotype re-examined is of massive flabellate growth form, with well developed spongin fibres forming a nearly regular reticulation of primary (ascending) and secondary (connecting) tracts, partially cored by foreign detritus and multispicular tracts of smooth styles, the latter confined mainly to the axis of the fibre, and echinated sparsely by acanthostyles. The ectosomal skeleton was not observed (dry material, from which the surface is abraded). Microscleres consist of two forms of toxas, long and sinuous ones that form dragmata, and smaller wing-shaped forms.

SUBGENUS *MICROCIONA* BOWERBANK, 1862

Synonymy

Microciona Bowerbank, 1862b: 1109. [*Abila*] Gray, 1867a: 539 (preocc.) (Not *Abila* Gray, 1867a: 522) (type species *Microciona laevis* Bowerbank, 1866:124 (by monotypy) holotype BMNH 1877.5.21.1543). [*Aaata*] de Laubenfels, 1930: 27 (preocc.). *Anaata* de Laubenfels, 1932: 89 (replacement name for [*Aaata*] de Laubenfels) (type species *Aaata spongigartina* de Laubenfels, 1930: 27 (by original designation) holotype USNM 21428). *Axocielita* de Laubenfels, 1936a: 118 (type species *Microciona similis* Stephens, 1915b: 441 (by original designation) holotype RSME 1921.143.1447). *Fisherispongia* de Laubenfels, 1936b: 460 (type species *Fisherispongia ferrea* de Laubenfels, 1936b: 460 (by original designation) holotype USNM 22239). *Holorodesmia* Topsent, 1928c (type species *Hymedesmia flaccida* Topsent, 1927b (by monotypy)). *Hymantho* Burton, 1930c: 503 (type species *Hymantho normani* Burton, 1930c: 503 (by original designation) holotype BMNH 1910.1.1.791). *Hymeraphia*, in part, Hentschel, 1912: 377 (not *Hymeraphia* Bowerbank, 1864: 189). *Leptoclathria* Topsent, 1928c: 298 (type species *Leptoclathria haplotoxa* Topsent, 1928c: 298 (by monotypy) holotype MNHN DT1101). *Ophistospongia* Gray, 1867a: 514 (type species *Ophistospongia australis* Gray, 1867a (by monotypy), from Bowerbank, 1864: pl. 17, fig. 288; holotype unknown). *Paratenaciella* Vacelet & Vasseur, 1971: 103 (type species *Paratenaciella microxea* Vacelet & Vasseur, 1971: 103 (by original designation) holotype MNHN DJV27). *Pseudanchinoe* Burton, 1929a: 433 (type species *Stylostichon toxiferum* Topsent, 1913b: 621 (by original designation and monotypy) holotype MNHN DT1612). *Sophax* Gray, 1867a: 521 (type species *Microciona fallax* Bowerbank, 1866: 128 (by monotypy) lectotype BMNH 1910.1.1.71). *Wetmoreus* de Laubenfels, 1936a: 112 (type species *Microciona novaezealandica* Brondsted, 1924b: 463 (by original designation) holotype UZM not found). Taxonomic decision for synonymy: Hooper (1996a), and this work.

Type species

Microciona atrasanguinea Bowerbank, 1862b (by subsequent designation; Bowerbank, 1864: 188).

Definition

Clathria with persistently encrusting growth form, with hymedesmioid skeletal architecture consisting of a basal layer of spongin, typically with ascending, plumose, non-anastomosing spongin fibre nodes, and megascleres embedded and erect on basal layer.

Diagnosis

Thinly or thickly encrusting growth forms; ectosomal skeleton with a single undifferentiated category of auxiliary styles sparsely dispersed on or near surface, lying paratangential or tangential to surface; choanosomal skeleton essentially hymedesmioid, with a basal layer of spongin bearing echinating and principal styles embedded in and perpendicular to it, forming single or plumose ascending columns, and in the latter case having spicule bundles partially enclosed by ascending, plumose, non-anastomosing spongin fibres (fibre nodes); principal styles frequently with prominent basal tyle and/or with basal spination; microscleres palmate isochelae and various toxa morphologies.

Description of type species

Clathria (*Microciona*) *atrasanguinea* (Bowerbank, 1862b) (Fig. 6).

Synonymy. *Microciona atrasanguinea*; Bowerbank, 1862a: 824; *Microciona atrosanguinea*; Gray, 1867a: 535; *Microciona atrasanguineum*; Cuenot, 1903: 4; *Clathria* (*Microciona*) *atrasanguinea*; Van Soest, 1993b: 103; *Amphilectus atrasanguineus*; Vosmaer, 1880: 115; *Plumohalichondria atrasanguinea*; Hanitsch, 1890: 207; *Scopalina atrosanguinea*; Schmidt, 1866b: 149; Schmidt, 1866a: 15; cf. *Microciona prolifera*; Vosmaer, 1935: 604.

Material examined. Holotype: BMNH 1930.7.3.225 – NE Atlantic. Refer to Hooper (1996a) for full list of other type material examined.

Description. Encrusting growth form. Surface hispid, uneven. Choanosomal skeleton hymedesmioid, with spongin fibres reduced to basal layer lying on substrate, bearing erect, non-anastomosing, rarely branching, scattered fibre nodes perpendicular to substrate ('microcionid' fibres), each cored by plumose ascending columns of choanosomal principal subtylostyles, wholly or partly embedded in fibres, with points of spicules usually projecting through ectosome. Echinating acanthostyles also erect on fibre nodes. Subectomal skeleton with tangential layer of subectosomal auxiliary subtylostyles, singly or in bundles on surface. Ectosomal skeleton without specialized spiculation, but choanosomal and subectosomal spicules protude through surface. Megascleres choanosomal principal subtylostyles with smooth or microspined bases (102–385 × 11–22 μm), evenly spined echinating acanthostyles (62–87 × 4–9 μm), and smooth or basally spined subectosomal auxiliary subtylostyles (122–295 × 2–8 μm). Microscleres palmate isochelae (uncommon) (12–17 μm) and oxhorn to wing-shaped toxas (42–110 × 1.5–4 μm).

Remarks. Of 118 named species originally described in, or subsequently referred to *Microciona* or one of its synonyms listed above, 103 appear to be valid taxa (the others being junior synonyms of established species) (Hooper, 1996a). *Microciona* (*s.s.*) differs from *Clathria* (*s.s.*) in having an encrusting growth form, a reduced hymedesmioid skeleton with erect fibre nodes cored by plumose tracts of principal and echinating spicules standing erect on the substrate (= 'microcionid' architecture of Lévi, 1960b), and smooth toxas. The critical difference between these genera, therefore, is the possession of the plumose, non-anastomosing fibre nodes, whereas other encrusting genera in the family have simply hymedesmioid skeletal construction (e.g., *Leptoclathria, Anaata, Hymantho*), a basal renieroid reticulation (e.g., some *Antho, Plocamilla*), or an isodictyal fibre skeleton arising from a hymedesmioid base (*Ophlitaspongia*). By comparison, erect or massive genera of Microcionidae commonly have reticulate or plumo-reticulate skeletons (e.g., *Clathria, Holopsamma*), renieroid or subisodictyal skeletons (e.g., *Isociella, Isopenectya, Pandaros*), or virtually halichondroid skeletal architecture (e.g., *Artemisina*). There are many contemporary authors who maintain this distinction between *Microciona* and erect non-plumose genera, such as *Clathria* at the generic level (e.g., Lévi, 1969; Wiedenmayer, 1977b; Pulitzer-Finali, 1983; Uriz, 1984a,b; Wintermann-Kilian & Kilian, 1984; Boury-Esnault & Lopes, 1985; Bergquist & Fromont, 1988), whereas Van Soest (1984b) and Hooper (1996a) recognise the taxon only at the subgenus level because this particular skeletal architecture is clearly linked to some extent by the ontogeny of the sponge individual (Simpson, 1968), and probably largely a phenotypic response to prevailing ecological conditions. Hooper (1996a) included *Seriatula* Gray (1867a: 515) (type species *Spongia seriata* Grant, 1826c: 116 (by monotypy) holotype BMNH 1847.9.7.14) into synonymy with *Ophlitaspongia* Bowerbank, and hence into synonymy with *Microciona* (following Simpson, 1968), but this was shown to be an incorrect assumption whereby *S. seriata* is identical to *Halichondria panicea* Pallas (Howson & Chambers, 1999). Differences between *Microciona* and other genera are discussed below (see *Ophlitaspongia*).

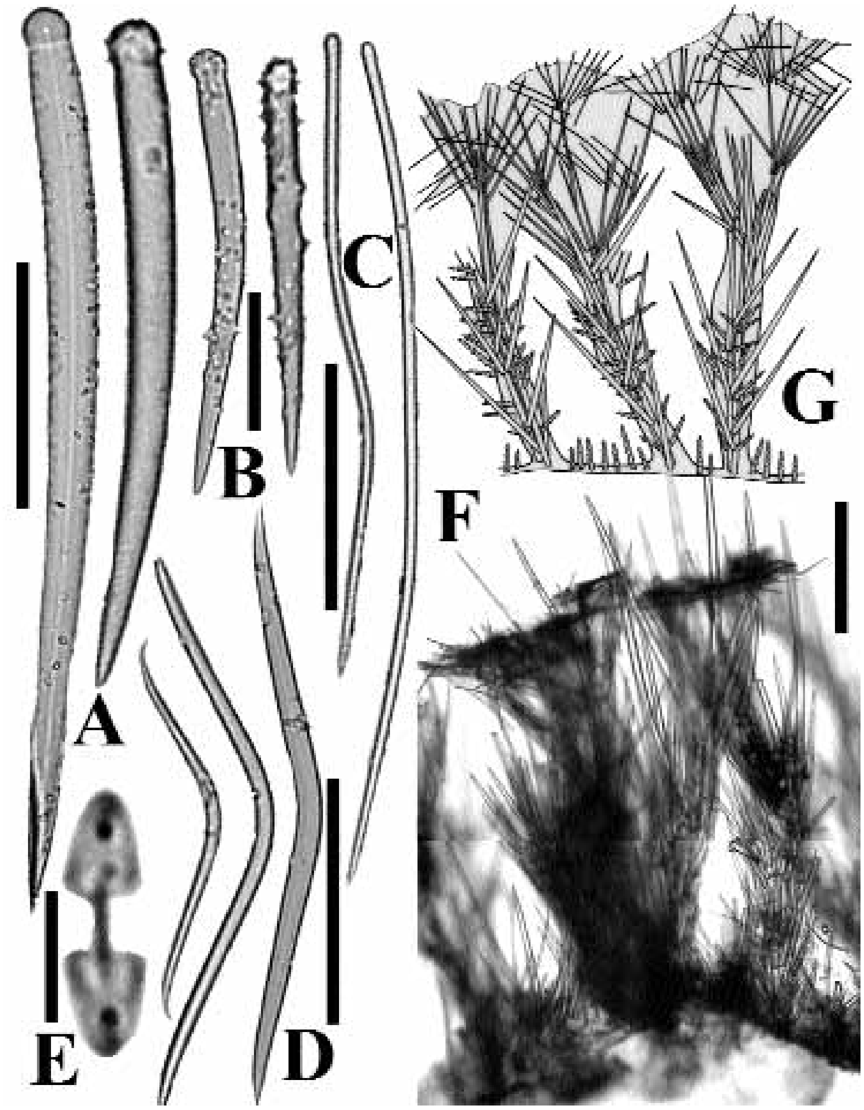

Fig. 6. *Clathria* (*Microciona*). A–G, *C.* (*M.*) *atrasanguinea* (Bowerbank). A, choanosomal principal subtylostyles (scale 100 µm). B, echinating acanthostyles (scale 25 µm). C, subectosomal auxiliary subtylostyles (scale 100 µm). D, oxhorn and wing-shaped toxas (scale 50 µm). E, palmate isochela (scale 5 µm). F, skeletal structure (scale 200 µm). G, reconstruction of skeleton.

SUBGENUS *DENDROCIA* HALLMANN, 1920

Synonymy

Dendrocia Hallmann, 1920: 767. *Paradoryx* Hallmann, 1920: 767 (type species *Clathria dura* Whitelegge, 1901: 83 (by original designation) holotype AM G3046). *Wilsonella* in part; *sensu* Hallmann, 1912: 242 (not Carter, 1885d: 366). Taxonomic decision for synonymy: Hooper (1996a).

Type species

Clathria pyramida Lendenfeld, 1888: 222 (by original designation).

Definition

Clathria with only a single undifferentiated category of structural megasclere (auxiliary styles) forming choanosomal and ectosomal skeletons.

Diagnosis

Massive, lobate, globular, digitate and flabellate growth forms; with a single undifferentiated category of smooth auxiliary spicule (style, subtylostyle or modified style) forming plumose or plumo-reticulate choanosomal tracts, ectosomal brushes and also dispersed between skeletal tracts. Echinating acanthostyles usually heavily spined and distributed evenly over skeletal tracts. Microscleres include isochelae ranging from typical palmate form (straight shaft, lateral alae fused to shaft), modified palmate forms (thickened, curved shaft, partially detached lateral alae) to ‘anchorate-like’ forms (alae detached from shaft, shaft with lateral ridge); toxas if present include oxhorns.

Description of type species

Clathria (*Dendrocia*) *pyramida* Lendenfeld, 1888 (Figs 2C, 7).

Synonymy. *Clathria pyramida* Lendenfeld, 1888: 222; *Wilsonella pyramida*; Hallmann, 1912: 240; *Dendrocia pyramida*; Hallmann, 1920: 767; *Clathria* (*Wilsonella*) *pyramida*; Hooper,

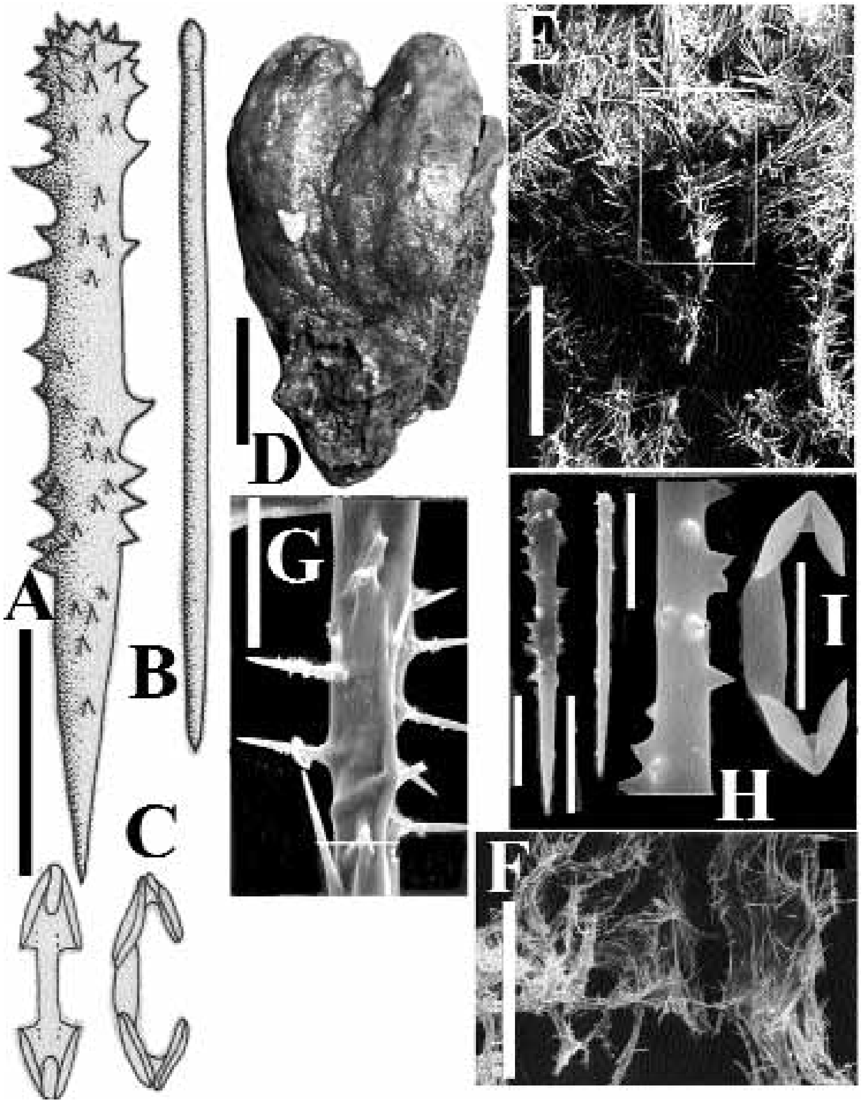

Fig. 7. *Clathria* (*Dendrocia*). A–I, *C.* (*D.*) *pyramida* Lendenfeld. A, echinating acanthostyle. B, subectosomal auxiliary subtylostyle. C, palmate isochelae (scale A–C, 50 μm). D, paralectotype of *C. alata* NMVG2283 (scale 30 mm). E, section through choanosomal skeleton (scale 500 μm). F, peripheral skeleton (scale 1 mm). G, fibre characteristic (scale 100 μm). H, echinating acanthostyles and pattern of spination (scales L–R, 20, 50, 10 μm respectively). I, palmate isochela (scale 10 μm). A–I, modified from Hooper (1996a).

1996a: 242; *Clathria alata* Dendy, 1896: 34; *Wilsonella alata* Hallmann, 1912: 241. *Dendrocia alata* Hallmann, 1920: 767.

Material examined. Lectotype: AMG9047 – Port Jackson, NSW, Australia. Other material. Refer to Hooper (1996a: 242).

Description. Shape massive, lobate, lobo-digitate, irregular growth form with small lobate surface projections; large oscules on apex of lobes, each with slightly raised membraneous lip; smooth, relatively even, bulbous, fleshy surface; ectosome microscopically hispid with dense crust of subectosomal auxiliary styles forming continuous, erect, regular (straight) or irregular (stellate, paratangential), plumose palisade; choanosomal skeleton irregularly plumo-reticulate, with sinuous spongin fibres ascending to surface in meandering tracts; fibres anastomose more frequently at axis than in peripheral skeleton; peripheral fibres and skeletal tracts often diverge becoming plumose in subectosomal region, or form a paratangential layer immediately below erect ectosomal skeleton; fibres cored by multispicular, sinuous tracts of subectosomal auxiliary styles; acanthostyles heavily echinate most fibres; choanosomal principal megascleres absent, or at least undifferentiated from auxiliary spicules; subectosomal auxiliary styles thin, hastate, straight or slightly curved towards basal end, usually with smooth, slightly subtylote bases that taper towards end into a small point (partially mucronate), points hastate (208–321 × 4–8 μm); acanthostyles club-shaped, subtylote, with large spines mostly confined on base and more-or-less aspinose towards point; spines usually robust (87–135 × 8–12 μm); microscleres isochelae large, very abundant, primarily palmate, heavily silicified, usually with thickened and slightly curved shaft, large lateral alae completely fused to shaft resembling 'wings', with front ala free, but sometimes with reduced alae and sigmoid curvature (21–27 μm); toxas absent.

Remarks. Seven species are included in *Clathria* (*Dendrocia*), all of which are endemic to temperate Australian waters, with hypothesised Gondwanan origins.

Dendrocia, like *Wilsonella*, differs from other microcionids in having auxiliary styles both coring fibres and forming the ectosomal skeleton. However, whereas *Wilsonella* has two categories of auxiliary spicules and detritus is incorporated into the skeleton, *Dendrocia* has only one category of structural spicule throughout

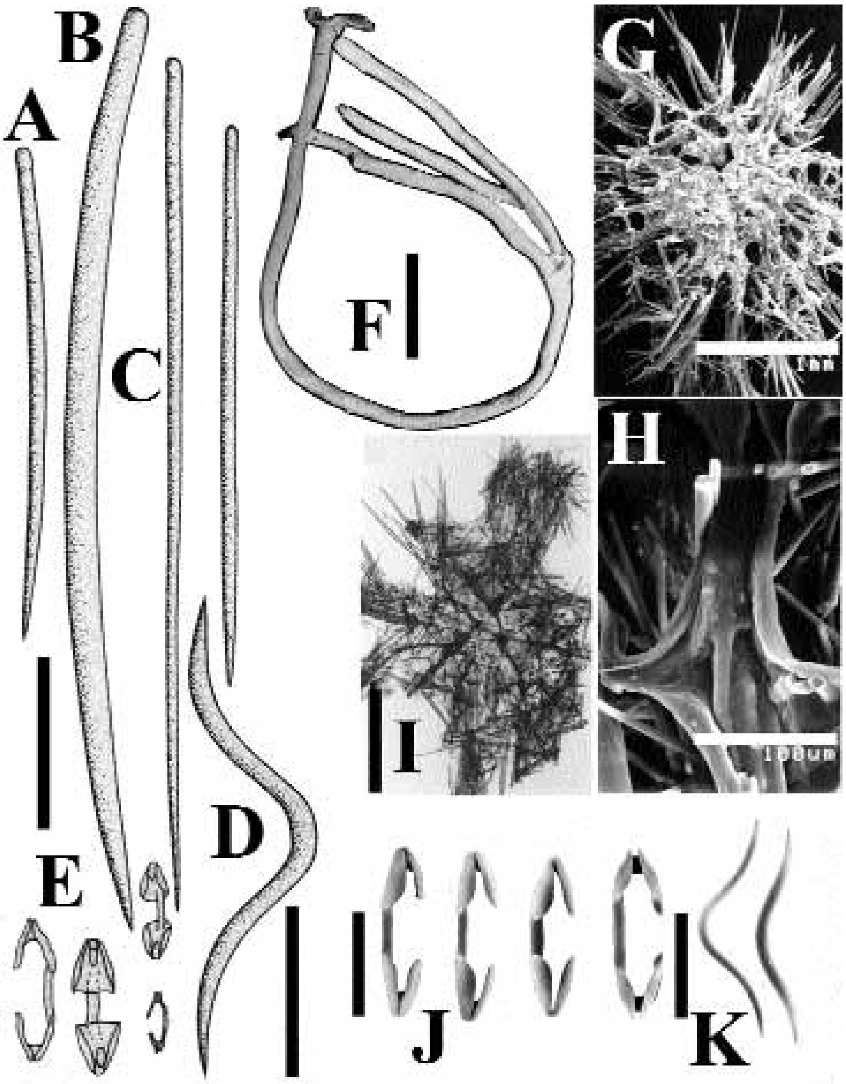

Fig. 8. *Clathria* (*Axosuberites*). A–K, *C.* (*A.*) *cylindrica* (Ridley & Dendy). A, choanosomal principal subtylostyle (coring fibres). B, subectosomal auxiliary style (coring extra-axial skeleton). C, ectosomal auxiliary subtylostyles (scale A–C, 100 μm). D, oxhorn toxa. E, palmate isochelae (scale D–E, 25 μm). F, holotype BMNH 1887.5.2.96 (scale 30 mm). G, choanosomal skeleton (scale 1 mm). H, fibre characteristic (scale 100 μm). I, cross-section through branch (scale 1 mm). J, palmate isochelae (scale 10 μm). K, oxhorn toxas (scale 20 μm). A–K, modified from Hooper (1996a).

the skeleton. *Dendrocia* also has a characteristic dendritic or plumo-reticulate skeletal architecture, whereas *Wilsonella* is invariably reticulate. In having only one geometric form of auxiliary spicule producing the extra-fibre skeleton (i.e., subectosome and ectosomal regions) the genus has closest affinities with *Clathria*, whereas in skeletal structure (with a continuous ectosomal palisade of spicules) the genus resembles the *Thalysias* condition. For this reason *Dendrocia* is enigmatic, and Hooper (1990b) maintained it as a separate taxon, whereas earlier Van Soest (1984b) had indicated that it was probably a synonym of *Clathria*.

SUBGENUS *AXOSUBERITES* TOPSENT, 1893

Synonymy

Axosuberites Topsent, 1893a: 179. *Axociella* Hallmann, 1920: 779 (type species *Esperiopsis cylindrica* Ridley & Dendy, 1886: 340 (by original designation) holotype BMNH 1887.5.2.96). *Tenaciella* Hallmann, 1920: 772 (type species *Esperiopsis canaliculata* Whitelegge, 1906: 471 (by monotypy) lectotype AM G4325). Taxonomic decision for synonymy: Hooper (1996a), and this work.

Type species

Axosuberites fauroti Topsent, 1893a: 179 (by monotypy).

Definition

Clathria with axial skeleton compressed and well differentiated from plumose(-reticulate) extra-axial skeleton; echinating spicules absent; ectosomal skeleton with special category of (smaller) auxiliary style forming surface brushes.

Diagnosis

Digitate, whip-like, arborescent and flabellate growth forms; with well differentiated axial and extra-axial skeletal architecture, reminiscent of Raspailiidae; axial skeleton markedly compressed, reticulate; extra-axial skeleton radial, plumose or plumo-reticulate composed of large subectosomal auxiliary styles-subtylostyles; specialised ectosomal skeleton present composed of smaller auxiliary spicules; echinating megascleres absent although principal spicules may protrude through fibres at acute angles; microscleres absent or may include palmate isochelae and toxas.

Description of type species

Axosuberites fauroti Topsent, 1893a: 179 (by monotypy) (Not figured; refer to Hooper, 1996a: fig. 11c–d).

Synonymy. *Axosuberites fauroti* Topsent, 1893a: 179–181, fig. 3. ? *Rhaphidophlus fauroti*; Van Soest, 1984b: 130. *Clathria* (*Axociella*) *fauroti*; Hooper, 1996a: 247.

Material examined. Holotype: MNHN DT1859 (fragment) – Tadjoura, Gulf of Aden, Arabian Gulf.

Description. Flabellate, flattened digitate growth form. Surface hispid, conulose. Choanosome with compressed reticulate axis and plumose extra-axial skeleton, with only light spongin fibres. Axial fibres produce close-meshed reticulation of multispicular tracts cored by choanosomal principal subtylostyles forming criss-cross reticulation, tracts plumose near periphery. Echinating megascleres absent. Subectosomal extra-axial skeleton well differentiated from axial region, with ascending plumose columns of larger subectosomal auxiliary subtylostyles arising from peripheral choanosomal skeleton. Ectosome with brushes of smaller auxiliary subtylostyles overlaying larger subectosomal spicules. Megascleres entirely smooth choanosomal principal subtylostyles-tylostyles, and two size classes of auxiliary subtylostyles-tylostyles, both with smooth bases. Microscleres absent.

Description of type species of Axociella.

Clathria (*Axociella*) *cylindrica* (Ridley & Dendy, 1886) (Fig. 8).

Synonymy. *Esperiopsis cylindrica* Ridley & Dendy, 1886: 340; *Axociella cylindrica* Hallmann, 1920: 780 (Not *Axociella cylindrica*; Sim & Byeon, 1989: 39); *Clathria cylindrica*; Hooper & Wiedenmayer, 1994: 262. *Clathria* (*Axociella*) *cylindrica*; Hooper, 1996a: 251, figs 120–121. (Not *Rhaphidophlus cylindricus* Kieschnick, 1900: 53).

Material examined. Holotype: BMNH 1887.5.2.96 – off Port Jackson, NSW, Australia. Other material. Refer to Hooper (1996a: 251).

Description. Shape thin, cylindrical digitate, branching, whip-like, with thin, dichotomously branched, cylindrical or slightly flattened, distally tapering branches; firm, flexible, tough consistency; surface even, felt-like, unornamented, prominently hispid; ectosome with sparse, plumose brushes of small ectosomal auxiliary subtylostyles forming discrete, discontinuous bundles on surface, arising from ends of radial skeletal columns, scattered around larger, protruding subectosomal auxiliary styles which project some distance through surface; choanosomal skeletal structure with clearly differentiated axial and extra-axial components, markedly compressed in axis and radial in extra-axis; compressed axial skeleton with longitudinal fibres cored by short choanosomal principal subtylostyles, interconnected by thinner pauci- or aspicular fibres; axial fibres heavily collagenous, and fibre anastomoses very close-meshed forming elongate reticulation; echinating megascleres absent; radial extra-axial skeleton with large auxiliary styles perpendicular to axis, forming pauci- or multispicular radial (non-plumose) tracts associated with very light, ascending spongin fibres but very few transverse uni- or aspicular connecting fibres; megascleres include choanosomal principal subtylostyles coring axial fibres relatively short, slightly curved at centre, with smooth subtylote or sometimes evenly rounded bases and fusiform points (215–395 × 5–15 μm); subectosomal auxiliary styles forming extra-axial bundles much longer and thicker than principal spicules, with smooth rounded or tapering (hastate) bases, and fusiform points (424–725 × 15–29 μm); ectosomal auxiliary subtylostyles straight, variable length, with smooth rounded or slightly subtylote bases and fusiform points (208–575 × 6–10 μm); microscleres palmate isochelae unmodified, differentiated into two size classes, with long lateral alae entirely fused to shaft and completely fused front ala (6–13, 19–25 μm); toxas oxhorn, thick, with wide central curvature and slightly reflexed points (45–130 × 2.5–6 μm).

Remarks. The inclusion of *Axosuberites* into synonymy with *Axociella* (Van Soest, 1984b; Hooper, 1996a) unfortunately requires that the former name takes precedence, based on seniority, a fact overlooked by Hooper (1996a). The type species of both nominal genera are redescribed here whereas the latter is better known from the recent literature.

The existence of microcionids with compressed axial skeletons and differentiated axial and extra-axial skeletons supports the proposal for a closer relationship between Microcionidae and Raspailiidae, as proposed by Hooper (1990b, 1991), and formalised further by Hajdu *et al*. (1994a) in the subordinal classification of Poecilosclerida as suborder Microcionina. In particular, *Axociella* is most reminiscent of *Raspailia* (*Syringella*) and *Ectyoplasia*. Crucial characters differentiating the *Axosuberites* group from typical Raspailiidae are the possession of chelae and absence any true echinating spicules in the former, versus possession of a specialized ectosomal skeleton (composed of small styles or oxeas in brushes surrounding larger protruding spicules) in the latter (see Hooper, 1991, 1996a). Despite contrary arguments by Van Soest (1984b), *Axosuberites* is considered here to be sufficiently different from *Thalysias* in its skeletal construction to be differentiated at the supraspecific level (although not for the reason that it lacks echinating acanthostyles, as suggested by Simpson, 1968).

SUBGENUS *ISOCIELLA* HALLMANN, 1920

Synonymy

Isociella Hallmann, 1920: 784.

Type species

Phakellia flabellata, in part (*sensu* Ridley & Dendy, 1886: 478) (by monotypy) (Not *P. flabellata* Carter, 1885d: 363). Synonymous with *Phakellia jacksoniana* (Dendy, 1897: 236) (holotype BMNH 1887.5.2.9), both junior synonyms of *Clathria macropora*, in part, Lendenfeld, 1888: 221 (holotype AMZ466). Taxonomic decision for synonymy: Hooper (1996a).

Definition

Clathria with evenly renieroid reticulate choanosomal skeleton, with spongin fibres cored by entirely smooth principal styles; echinating megascleres absent.

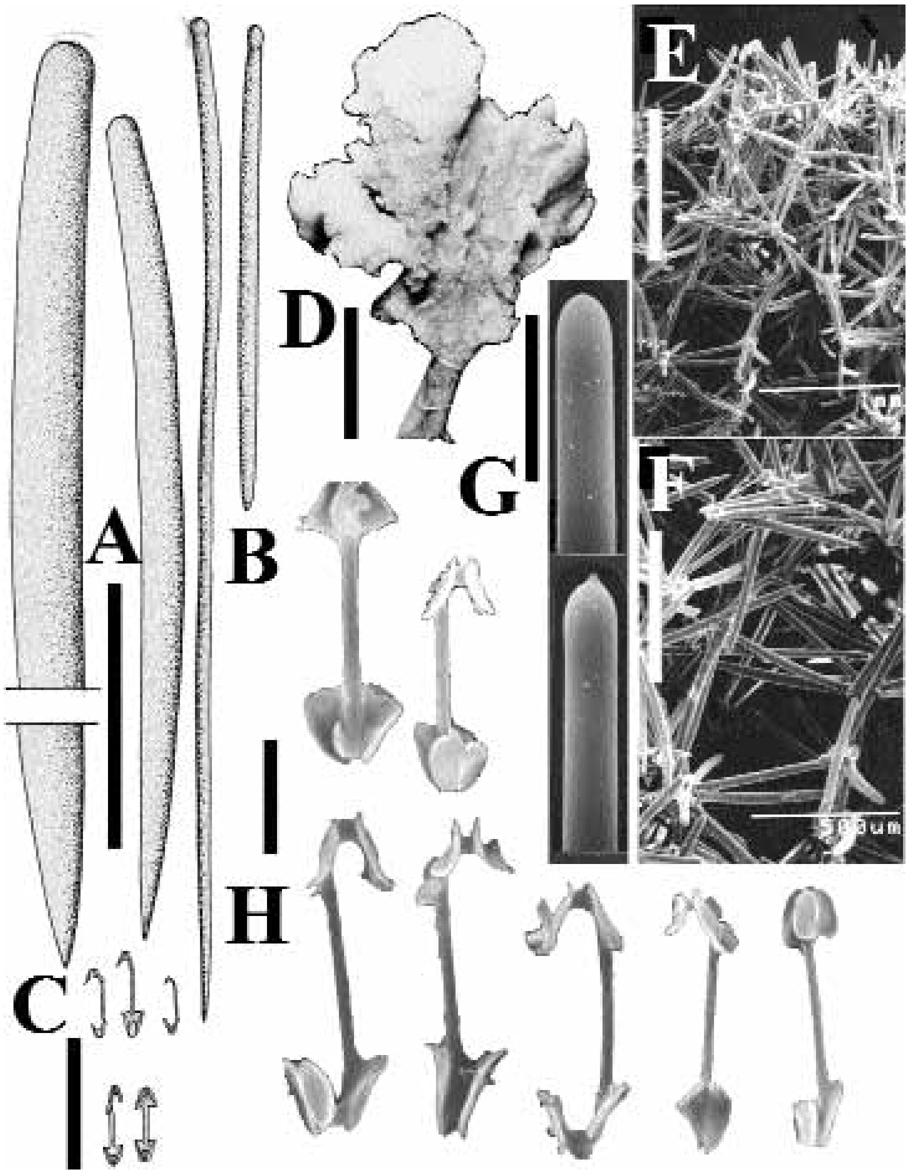

Fig. 9. *Clathria* (*Isociella*). A–H, *C.* (*I.*) *macropora* Lendenfeld. A, choanosomal principal styles. B, subectosomal auxiliary subtylostyles (scale A–B, 100 μm). C, modified palmate isochelae (scale 25 μm). D, paralectotype of *Phakellia jacksoniana* BMNH 1887.5.2.8 (scale 30 mm). E, choanosomal skeleton (scale 1 mm). F, semi-renieroid fibres (scale 500 μm). G, bases of subectosomal auxiliary styles (scale 10 μm). H, modified palmate isochelae (scale 5 μm). A–H, modified from Hooper (1996a).

Diagnosis

Massive, bulbous, lobate, digitate and flabellate growth forms; skeletal structure with relatively homogeneous renieroid or subrenieroid, wide-meshed reticulation; main skeleton with primary plumose ascending, multispicular tracts cored by smooth choanosomal styles, interconnected by secondary, uni- or paucispicular tracts cored by same spicules, and choanosomal spicules sometimes diverging and forming plumose brushes at surface; echinating megascleres absent; ectosomal skeleton with single category of auxiliary spicule, tangential, paratangential. Microscleres palmate-derived isochelae and toxas.

Description of type species

Clathria (*Isociella*) *macropora* Lendenfeld, 1888 (Fig. 9).

Synonymy. *Phakellia flabellata* Ridley & Dendy, 1886: 478 (Not *Phakellia flabellata* Carter, 1885d: 363); *Clathria macropora*, in part, Lendenfeld, 1888: 221. *Clathria* (*Isociella*) *macropora*; Hooper, 1996a: 271. (Not *Plectispa macropora* Lendenfeld, 1888: 226. Not *Clathria macropora* Whitelegge, 1901: 91. Not *Wilsonella macropora*; Hallmann, 1912: 203. Not *Plumohalichondria australis* Whitelegge, 1901: 90); *Isociella flabellata* Hallmann, 1920: 784; *Phakellia jacksoniana* Dendy, 1897: 236; *Isociella jacksoniana*; Bergquist & Tizard, 1967: 187.

Material examined. Holotype: AM Z466 – Port Stephens, NSW, Australia. Other material. Refer to Hooper (1996a: 271).

Description. Shape irregularly flabellate-digitate or flabellate, planar, with short cylindrical stalk, one or more thinly lobate, bifurcated branches, with rounded, digitate, uneven or shaggy margins; oscules small, in special areas (sieve-plates) scattered over surface of branches, with series of stellate subdermal drainage canals surrounding each osculum; branches with separate inhalant and exhalant faces, one porous, rugose, with irregular longitudinal ridges, microconules or irregular striations, other smooth, membraneous; ectosome membraneous, hispid, with points of choanosomal principal styles protruding through surface, individually or in multispicular plumose bundles; surface skeleton with relatively sparse tangential, paratangential or sometimes plumose erect skeleton of small subectosomal auxiliary styles projecting between principal spicules, sometimes surrounding (in proximity of) principal spicules reminiscent of Raspailiidae; choanosomal skeleton with very slightly compressed axis and plumose sub-isodictyal extra-axis; axial region with moderately heavy spongin fibres, forming tight irregularly reticulate meshes cored by paucispicular tracts of choanosomal principal styles; axis (corresponding to central lamellae and basal stalk) has few ascending, primary tracts, forming multispicular, halichondroid structures, producing few multispicular, dendritic tracts running from basal stalk to periphery; extra-axial skeleton with plumose spicule tracts bound by collagen (without fibre component), ascending to surface, cored by uni-, pauci- or less frequently multispicular tracts of choanosomal principal styles; primary ascending extra-axial spicule tracts perpendicular to axis, interconnected by more-or-less transversely orientated, smaller secondary uni- or paucispicular tracts producing the predominantly subisodictyal structure; peripheral spicule tracts more plumose than deeper choanosomal tracts; meshes produced by spicule-fibre anastomoses in extra-axial region rectangular or triangular in shape; echinating acanthostyles absent; megascleres choanosomal principal styles long or short, thick, slightly curved at centre, less often straight, with rounded or slightly tapering, smooth bases, varying from fusiform to hastate points (369–552 × 21–35 μm); subectosomal auxiliary styles variable in length, thin, straight or very slightly curved, with basal terminations varying from evenly rounded, tapering hastate, quasi-diactinal mucronate or slightly subtylote, and with hastate points (191–424 × 4– 9μm); microscleres palmate isochelae with highly modified, relatively small alae bearing wing-shaped fluted processes; lateral alae entirely fused to shaft; front ala complete or bifurcated with medial tooth; chelae frequently twisted or occasionally anisochelate (8–16 μm); toxas absent.

Remarks. Four species of *Isociella* are known for the Australian fauna, three from the tropical coasts of WA, NT and Qld, and one temperate species from NSW. The type species is also known from SE Indonesia, and only one other species is known from the New Zealand fauna. *Isociella* has a slightly compressed axial skeleton partially offset from a diverging, plumose, subisodictyal reticulate extra-axial skeleton, showing vague structural similarities to *Ceratopsion* and *Raspailia* (*Syringella*) (family Raspailiidae). This skeletal structure could also justify its inclusion in the subgenus *Axosuberites*, but it is considered here that the subisodictyal reticulation dominates the skeleton and is more characteristic of *Isociella* than *Axosuberites*, whereas in the latter subgenus the axial compression and differentiation between axis and extra-axis are predominant features.

SUBGENUS *THALYSIAS* DUCHASSAING & MICHELOTTI, 1864

Synonymy

Thalysias Duchassaing & Michelotti, 1864: 82. *Rhaphidophlus* Ehlers, 1870: 19 (type species *Spongia cratitia* Esper, 1797: 195 (by original designation; Ehlers, 1870: 18) schizotypes ZMB 4577). *Tenacia* Schmidt, 1870: 56 (type species *Tenacia clathrata* Schmidt, 1870: 56 (by monotypy) (schizotype BMNH 1870.5.3.156); junior synonym of *Spongia virgultosa* Lamarck, 1814: 444 (fragments of holotype MNHN DNBE1344, 1338)). [*Echinonema*] Carter, 1875c: 194 (*nomen nudum*); Carter, 1881b: 378 (type species *Echinonema typicum* Carter, 1881b: 377 (by typonymy) (lectotype BMNH 1877.5.21.149); junior synonym of *Spongia cactiformis* Lamarck, 1814: 440 (lectotype MNHN DT580)). *Thalassodendron* Lendenfeld, 1888: 222 (type species *Thalassodendron typica* Lendenfeld, 1888: 223 (by indication) (holotype unknown)). *Stylotellopsis* Thiele, 1905: 456 (type species *Stylotellopsis amabilis* Thiele, 1905: 456 (by monotypy) holotype ZMB 3309). *Colloclathria* Dendy, 1922b: 74 (type species *Colloclathria ramosa* Dendy, 1922b: 74 (by monotypy) holotype BMNH 1921.11.7.64). *Damoseni* de Laubenfels, 1936a: 110 (type species *Hymeraphia michaelseni* Hentschel, 1911: 351 (by original designation) fragment of holotype SMF969T). Taxonomic decision for synonymy: Hooper (1996a).

Type species

Spongia virgultosa Lamarck, 1814 (by subsequent designation; de Laubenfels, 1936a: 104) (holotype MNHN missing, schizotype BMNH 1954.2.20.67); junior synonym of *Spongia juniperina* Lamarck, 1814 (lectotype MNHN DT570) (de Laubenfels, 1936a: 104).

Definition

Clathria with two categories of auxiliary styles forming a specialized ectosomal skeleton, the smaller usually forming discrete bundles or a continuous palisade perpendicular to the surface; echinating megascleres present.

Diagnosis

Thickly encrusting, massive, globular, digitate, flabellate and arborescent growth forms; with specialized ectosomal skeleton of differentiated size classes of auxiliary (subtylo)styles, with smaller ectosomal spicules usually overlaying larger subectosomal ones forming erect brushes in a continuous palisade, or discrete bundles, paratangential or rarely tangential to surface. Choanosomal skeleton without any marked differentiation between axial and extra-axial regions. Echinating acanthostyles usually present. Microscleres are palmate isochelae and diverse forms of toxas.

Description of type species

Clathria (*Thalysias*) *juniperina* (Lamarck, 1814) (Fig. 10).

Synonymy. *Spongia juniperina* Lamarck, 1814: 444; *Clathria juniperina*; Hooper & Wiedenmayer, 1994: 270. *Clathria* (*Thalysias*) *juniperina*; Hooper, 1996a: 346, figs 176–177 (Not *Pandaros juniperina*; Duchassaing & Michelotti, 1864: 90. Not *Thalysias juniperina* de Laubenfels, 1936a: 105); *Rhaphidophlus clathratus* Hallmann, 1912: 209 (Not *Tenacia clathrata* Schmidt, 1870: 56).

Material examined. Lectotype: MNHN DT570 – SW coast of Australia. Other material. Refer to Hooper (1996a: 346).

Description. Shape ranges from thickly encrusting to frondose, lamellate, clathrous, with or without free or anastomosing

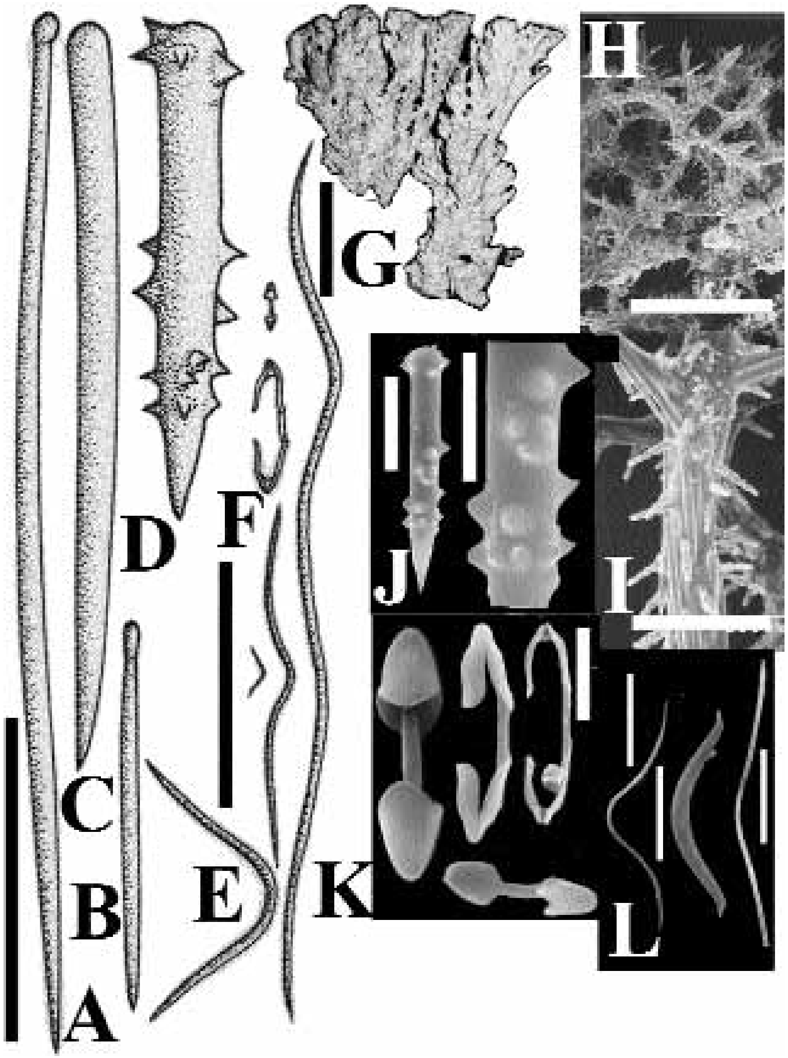

Fig. 10. *Clathria* (*Thalysias*). A–F, I–L, *C. (T.) juniperina* (Lamarck). G–H, *C.* (*T.*) *reinwardti* Vosmaer. A, larger subectosomal auxiliary style. B, smaller ectosomal auxiliary style. C, choanosomal principal style. D, echinating acanthostyle (scale A–D, 100 μm). E, sinuous, accolada and u-shaped toxas. F, palmate isochelae (scale E–F, 25 μm). G, paralectotype MNHN DT3354. H, choansomal skeleton (scale 1 mm). I, echinated fibre (scale 200 μm). J, echinating acanthostyle (scales L–R, 20 and 10 μm). K, palmate isochelae (scale 5 μm). L, toxas (scales L–R, 10, 2 and 20 μm). A–L, modified from Hooper (1996a).

branches; surface relatively smooth, even, with white subdermal canals in encrusting forms, or irregularly microconulose or clathrous in more massive forms; ectosomal skeleton crust-like, easily detachable, relatively thin but dense palisade of erect or paratangential brushes supported by paratangential tracts of larger subectosomal auxiliary megascleres immediately below surface; peripheral fibres immediately subectosomal with vaguely ascending multispicular subectosomal tracts arising to surface; choanosomal skeleton irregularly reticulate, with very heavy spongin fibres forming oval meshes; fibres usually with paucispicular core of subectosomal auxiliary styles occupying only a small proportion of fibre diameter, and fewer choanosomal principal styles which are entirely enclosed in, or project from fibres; in some cases fibres completely uncored, whereas others contain abundant, disorganized auxiliary megascleres; fibres typically heavily echinated, some enveloping echinating megascleres entirely, some fibres without echinating megascleres; megascleres choanosomal principal styles straight or slightly curved near basal end, with smooth, rounded or very slightly subtylote bases (170–280 × 9–12 μm); subectosomal auxiliary subtylostyles straight or curved, sometimes with multiple curves (sinuous), with smooth subtylote bases (169–310 × 4–6.5 μm); ectosomal auxiliary subtylostyles with prominent subtylote, smooth bases (93–110 × 2–4.5 μm); acanthostyles small, stubby, with rounded or only slightly subtylote bases, with few spines and extensive aspinose regions on necks and points; spines large, bulbous, erect (45–65 × 5–8 μm); microscleres palmate isochelae unmodified, incompletely differentiated into two size classes; lateral alae entirely fused to shaft, approximately same length as front ala and completely detached from front ala (6–9, 12–16.5 μm); toxas very variable in length, mostly thin, ranging from accolada forms with large central curvature and slightly reflexed points, large curvature and simply u-shaped, to asymmetrical sinuous forms (55–180 × 0.8–1.5 μm).

Remarks. Of 137 named species described in, or referred to *Thalysias* or one of its synonyms, 93 are thought to be valid. Hooper (1996a) notes that the taxon *Clathria juniperina* as presently understood (e.g., Van Soest, 1984b) is probably composite, incorporating two or more sibling species, with disjunct populations from the Caribbean (e.g., Hartman, 1955; Simpson, 1968; Wiedenmayer, 1977b; Van Soest, 1984b), and Indian Ocean

(Lamarck, 1814, 1816) (i.e., of *Spongia juniperina*). The accepted interpretation is that the nominotypical population from the Indo-west Pacific be known as *C.* (*T.*) *juniperina* whereas the West Indies population accept the most senior available name for several Caribbean species presently included in synonymy with *Spongia virgultosa.*

The primary and only consistent morphological feature that distinguishes *Thalysias* from other *Clathria*-like taxa is the presence of a specialized ectosomal skeleton, consisting of two differentiated categories of auxiliary subtylostyles which form brushes on the surface (either as discrete brushes (*s.s.*) or a continuous palisade). It differs from *Axociella* in having echinating acanthostyles.

ECHINOCHALINA THIELE, 1903

Synonymy

Echinochalina Thiele, 1903a: 961 (see subgenera for full synonymy).

Type species

Ophlitaspongia australiensis Ridley, 1884a: 442 (by subsequent designation; Hallmann, 1912: 288).

Definition

Microcioninae with monactinal, quasi-monactinal or thin diactinal auxiliary megascleres both coring spongin fibres and forming extra-fibre and ectosomal tracts, and principal spicules (styles or oxeas) echinating fibres.

Diagnosis

Thickly encrusting, massive, lobate, bulbous, clavulate, clathrous, honeycomb-reticulate, tubulo-digitate, digitate and arborescent growth forms; with monactinal, quasi-monactinal or thin diactinal auxiliary megascleres tangential or erect on ectosome; choanosomal skeleton irregularly reticulate; fibres cored by tracts of auxiliary megascleres, identical to those in ectosomal skeleton, and echinated by principal megascleres varying from true monactinal, quasi-diactinal to true diactinal forms, smooth or acanthose; microscleres may include palmate isochelae and toxas.

Remarks

The genus contains two groups of species: one (*Echinochalina* (*Echinochalina*)) with true monoactinal spicules, showing superficial affinities with *Holopsamma* (having honeycomb reticulate growth forms) and the Raspailiidae (fibre characteristics), and the other with quasi-diactinal or secondarily modified true diactinal megascleres (*Echinochalina* (*Protophlitaspongia*)) superficially resembling Niphatidae (Haplosclerida). Both groups are linked by the common possession of auxiliary megascleres coring fibres and principal megascleres echinating fibres.

Distribution

Twenty six species have been included in *Echinochalina* at one time or another, of which only twenty are valid (with the remainder being either junior synonyms or more appropriately included in other genera), of which all live in the Indo-west Pacific.

SUBGENUS *ECHINOCHALINA* THIELE, 1903

Synonymy

Echinochalina Thiele, 1903a: 961. *Tablis* de Laubenfels, 1936a: 76 (type species *Echinochalina anomala* Hallmann, 1912: 292 (by original designation) holotype AM G10548). *Echinoclathria sensu* Uriz, 1988: 89 (Not *Echinoclathria* Carter, 1885d). Taxonomic decision for synonymy: Hooper (1996a).

Type species

Ophlitaspongia australiensis Ridley, 1884a: 442 (by subsequent designation; Hallmann, 1912: 288).

Definition

Echinochalina with smooth monactinal, quasi-monactinal or secondarily derived true diactinal auxiliary megascleres coring fibres, and smooth or spined monactinal principal spicules echinating fibres.

Diagnosis

Thickly enrusting, massive, lobate, bulbous, clavulate, branching, clathrous, honeycomb-reticulate, and digitate growth forms; ectosomal skeleton, interstitial skeleton and spongin fibres cored by smooth auxiliary megascleres (subtylostyles, tornostyles or quasi-stongyles); fibres echinated by smooth or spined principal styles; ectosomal skeleton with single or tracts of auxiliary megascleres tangential or paratangential to the surface; choanosomal architecture reticulate with differentiated multispicular primary and paucispicular secondary tracts composed of auxiliary megascleres; microscleres if present palmate isochelae or toxas.

Description of type species

Echinochalina (*Echinochalina*) *australiensis* (Ridley, 1884a) (Figs 2I, 11).

Synonymy. *Ophlitaspongia australiensis* Ridley, 1884a: 442. *Echinochalina australiensis*; Thiele, 1903a: 961. *Echinochalina* (*Echinochalina*) *australiensis*; Hooper, 1996a: 518, figs 278–279.

Material examined. Holotype: BMNH 1881.10.21.299 – Port Molle (Airlee), Qld, Australia. Other material. Refer to Hooper (1996a: 518).

Description. Shape massive, branching, clathrous, honeycomb-reticulate growth form, fibre-branches flattened, with cavernous, angular meshes; oscules small situated between adjacent fibre bundles; conulose surface produced by anastomosing fibre bundles ('lacunae'), interconnected by translucent ectosomal membrane stretched between adjacent conules; ectosome membraneous, with thinner choanosomal, undulating fibres lying immediately below ectosome cored by paucispicular tracts of auxiliary megascleres, and with irregular layer of auxiliary megascleres scattered tangential to surface; choanosomal skeleton vaguely

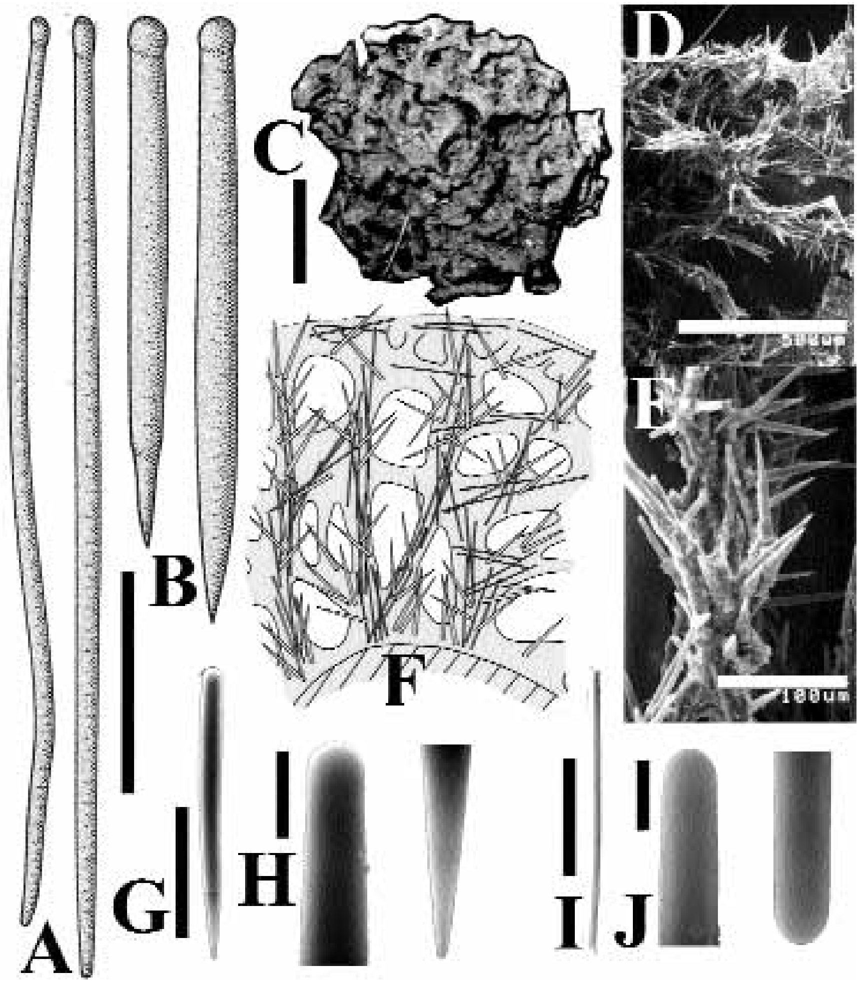

Fig. 11. *Echinochalina* (*Echinochalina*). A–J, *E. (E.) australiensis* (Ridley). A, auxiliary subtylostyles/tornostyles (interstitial and coring fibres). B, principal subtylostyles (echinating fibres) (scale A–B, 50 μm). C, holotype BMNH 1881.10.21.299 (scale 30 mm). D, choanosomal skeleton (scale 500 μm). E, fibre characteristics (scale 100 μm). F, skeletal reconstruction. G, principal subtylostyle (scale 50 μm). H, principal spicule terminations (scale 10 μm). I, auxiliary tornostyle (scale 100 μm). J, auxiliary spicule terminations (5 μm).

regularly reticulate composed of primary, distinctly ascending, multispicular fibres interconnected at irregular intervals by numerous transverse, paucispicular, secondary fibres; fibre anastomoses form rounded or elongate, narrow meshes; fibres cored by auxiliary megascleres, sparsely echinated by principal subtylostyles; megascleres principal subtylostyles (echinating fibres) straight, smooth, tapering, rounded or slightly subtylote bases, fusiform or slightly telescoped points (83–131 × 6–9.5 μm); auxiliary megascleres (coring fibres and interstitial) straight, thin, subtylostyles, tornostyles or quasi-strongyles, with smooth, rounded, or very slightly subtylote bases, tapering-rounded points (147–192 × 1.5–4.5 μm); microscleres absent.

Remarks. Refer to *Protophlitaspongia*.

SUBGENUS *PROTOPHLITASPONGIA* BURTON, 1934

Synonymy

Protophlitaspongia Burton, 1934a: 562 (Not *Protophlitaspongia*; de Laubenfels, 1954: 96; Pulitzer-Finali, 1986: 138). *Echinochalina* (*Protophlitaspongia*); Hooper 1996a: 543.

Type species

Siphonochalina bispiculata Dendy, 1895: 246 (by original designation).

Definition

Echinochalina with diactinal or quasi-monactinal auxiliary megascleres coring fibres, and diactinal or quasi-monactinal principal spicules echinating fibres.

Diagnosis

Thickly encrusting, massive, lobate, bulbous-digitate, digitate and arborescent growth forms; ectosomal skeleton, interstitial skeleton and spongin fibres cored by auxiliary diactinal or quasi-monactinal spicules; fibres echinated by principal diactinal or quasi-monactinal spicules; ectosomal skeleton with erect plumose brushes of auxillary spicules arising from peripheral spongin fibres; choanosomal skeleton reticulate to sub-isodictyal with differentiated primary multispicular and secondary paucispicular tracts of auxiliary megascleres; microscleres if present palmate isochelae or toxas.

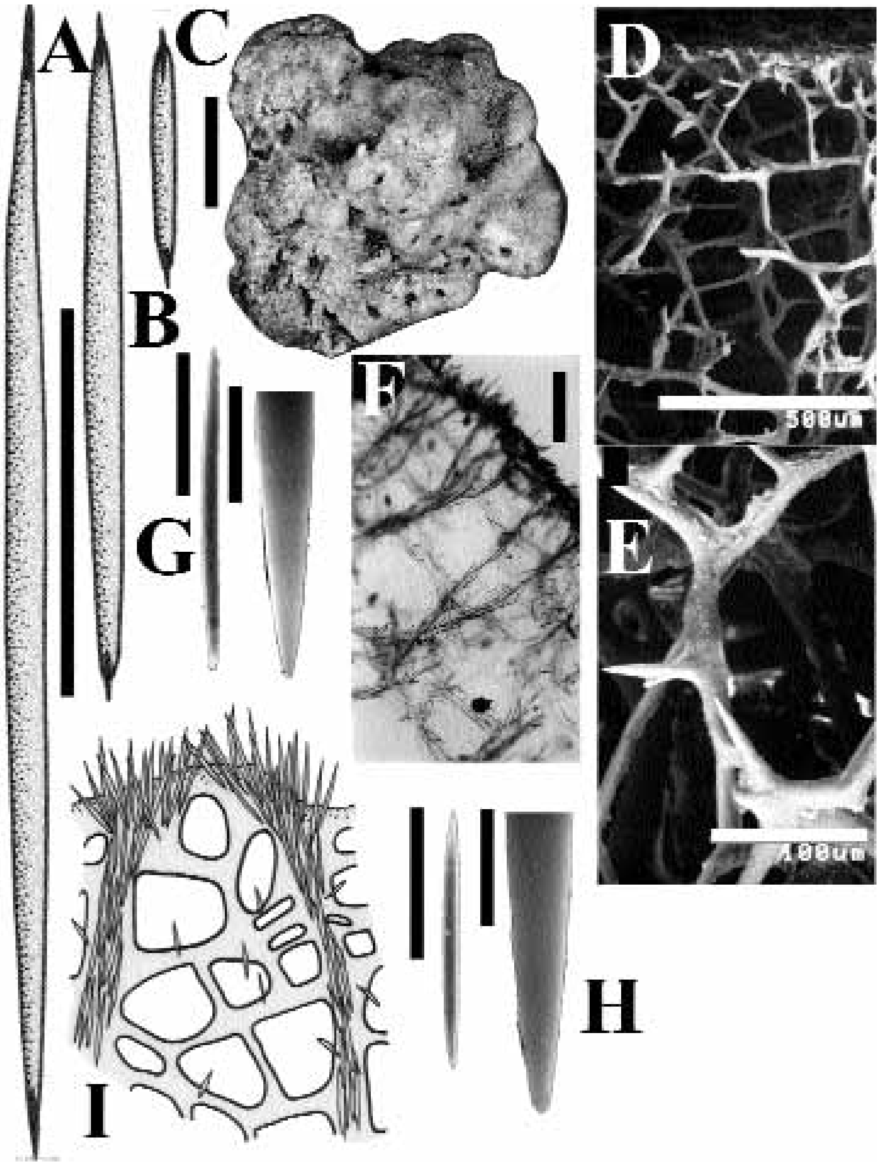

Fig. 12. *Echinochalina* (*Protophlitaspongia*). A, *E.* (*E.*) *bispiculata* (Dendy). A, auxiliary oxeas (interstitial and coring fibres). B, principal oxea (echinating fibres) (scale A–B, 100 μm). C, lectotype NMV G2319 (scale 30 mm). D, choanosomal skeleton (scale 500 μm). E, fibre characters (100 μm). F, spiculo-spongin fibre characteristics (scale 100 μm). G, auxiliary oxea and termination (scales 50, 10 μm). H, principal oxea and terminations (scales L–R, 50, 10 μm). I, skeletal reconstruction.

Description of type species

Echinochalina (*Protophlitaspongia*) *bispiculata* (Dendy, 1895) (Figs 3A, 12).

Synonymy. *Siphonochalina bispiculata* Dendy,1895: 246; *Diplodermia bispiculata*; Hallmann 1912: 255; *Protophlitaspongia bispiculata*; Burton, 1934a: 562; *Echinochalina bispiculata*; Hooper & Lévi, 1993a: 1279. *Echinochalina* (*Protophlitaspongia*) *bispiculata*; Hooper, 1996a: 543, figs 296–297.

Material examined. Lectotype: NMV G2319 – Port Phillip Heads, Vic., Australia. Other material. Refer; to Hooper (1996a: 543).

Description. Shape massive, subspherical, irregularly lobate, with short bulbous surface lobes, or subcylindrical, flattened digitate sponge; oscules small, scattered over surface, particularly on apex of surface lobes; surface optically even, minutely reticulate; ectosome microscopically hispid with scattered plumose brushes of long, thin auxiliary oxeas, arising from the points of peripheral fibres and paratangential to surface; choanosomal fibres immediately below surface although spicule tracts more plumose in peripheral skeleton than at core; choanosomal skeleton regularly reticulate to subisodictyal, with well developed fibres divided into primary, ascending, multispicular fibres forming distinctly plumose tracts within core of fibre, interconnected at more-or-less regular intervals by slightly thinner secondary, transverse, uni-, pauci- or aspicular fibres; fibres cored by long, thin auxiliary oxeas and echinated by short, stout principal oxeas; fibre anastomoses form cavernous ovoid meshes; principal megascleres echinating fibres straight, short, thick, invariably smooth, hastate oxeas, with abruptly pointed or telescoped ends (31–45 × 2–5.5 μm); auxiliary megascleres coring fibres long, thin, straight, hastate or rarely fusiform oxeas (105–266 × 2–5 μm); microscleres absent.

Remarks. In species of *Protophlitaspongia* structural megascleres (coring and echinating fibres) are diactinal and do not appear to be modified from monactinal forms, unlike all other microcionids. Consequently, the inclusion of this taxon in the Microcionidae is equivocal but supported by the possession of more-or-less plumose ascending, primary spicule tracts, true echinating megascleres, isochelae and toxa microscleres in several species, and the possession of true monactinal ectosomal spicules in several species. The coring and echinating megascleres are equated here with auxiliary and principal spicules, respectively, of typical *Echinochalina*. Dendy (1896) originally included the type species in the Haplosclerida, but remarked on its unique spicule arrangement, particularly the ectosomal structure and fibre echination. Burton (1934a) subsequently assigned the type species to Microcionidae, for similar reasons as those outlined above, whereas de Laubenfels (1936a) referred it to the Desmacididae because, he suggested, the hastate diactinal megascleres closely resembled those of *Guitarra* and *Liosina*, although it lacked poecilosclerid microscleres. Nevertheless, *E.* (*P.*) *bispiculata* is included with *Echinochalina* since it has a paratangential ectosomal skeleton composed of auxiliary megascleres, reticulate spongin fibres and echinating principal spicules, whereas other species described by de Laubenfels (1936a) (*P. aga, P. ada* and *P. antillana*) were referred to the Desmacididae and Haplosclerida (Hooper, 1996a).

HOLOPSAMMA CARTER, 1885

Synonymy

[*Halme*] Lendenfeld, 1886a: 285 (preocc.) (Not *Halme* Pascoe, 1869). (type species *Holopsamma laminaefavosa* Carter, 1885b: 212 (by subsequent designation; de Laubenfels, 1936a: 17) holotype BMNH 1886.12.15.312). *Holopsamma* Carter, 1885b: 211. *Plectispa* Lendenfeld, 1888: 225 (type species *Plectispa macropora*, in part, Lendenfeld, 1888: 226 (by subsequent designation; Hallmann, 1912: 204) holotype AM G9159). *Aulena*; in part, Lendenfeld, 1888: 228 (Not Lendenfeld, 1886a: 309). Taxonomic decision for synonymy: Hooper (1996a).

Type species

Holopsamma crassa Carter, 1885b: 211 (by subsequent designation, de Laubenfels, 1936a: 98) (lectotype BMNH 1886.12.15.313; Hooper & Wiedenmayer, 1994), a senior synonym of *Halme globosa* Lendenfeld, 1886a: 303 (lectotype BMNH 1886.8.27.71) (cf. Wiedenmayer, 1989: 63).

Definition

Microcioninae of 'honeycomb reticulate' growth form with coring and echinating spicules identical in geometry, or coring spicules replaced partially or completely by detritus.

Diagnosis

'Honeycombed reticulate' growth form consisting of tightly anastomosing flattened fibre-branches (lacunae); choanosomal skeleton simply reticulate, without any axial compression or differentiation between axial and extra-axial skeletons; principal spicules core and echinate fibres, those inside fibres sometimes partially or completely replaced by detritus although those echinating fibres usually always present. Microscleres palmate isochelae and rarely toxas.

Description of type species

Holopsamma crassa Carter, 1885b (Figs 2H, 13).

Synonymy. *Holopsamma crassa* Carter, 1885b: 211; *Aulena crassa* Lendenfeld, 1889a: 101; *Echinoclathria crassa*; Hallmann, 1912: 287 (Not *Antherochalina crassa* Lendenfeld, 1887c: 787); *Halme micropora* Lendenfeld, 1886a: 303; *Halme globosa* Lendenfeld, 1886a: 303; *Echinoclathria globosa*; Wiedenmayer, 1989: 63.

Material examined. Lectotype: BMNH 1886.12.15.313 – Port Phillip, Vic., Australia. Other material. Refer to Hooper (1996a: 487).

Description. Shape massive, subcylindrical, or lobate-digitate honey-combed reticulate sponge, large oscules slightly recessed within reticulate meshes, surrounded by thin membraneous lip in life; surface reticulate, lacunose, consisting of irregularly meandering ridges forming large meshes producing characteristic honey-comb growth form, in life covered by moderately thin, translucent dermal membrane stretched between adjacent ridges; ectosome heavily arenaceous, with a thick sandy external cortex covered by a fine membraneous ectosomal skeleton usually containing a tangential layer of auxiliary spicules, in tracts or scattered singly across surface, but easily detached; subectosomal region undifferentiated from choanosome, fibres immediately subectosomal; choanosomal skeleton irregularly reticulate, with heavy, relatively homogeneous, lamellated spongin fibres fully cored by sand grains, with or without a core of choanosomal principal styles; fibres usually always echinated by principal styles but sometimes echinating spicules reduced in heavily arenaceous specimens; choanosomal principal styles coring and echinating fibres short, thin, straight, with rounded or tapering smooth bases, fusiform, sharply pointed (53–81 × 1.2–6 μm); subectosomal auxiliary spicules long, slender, strongylote styles, straight or slightly curved or sinuous, with slightly subtylote bases, evenly rounded or bifid points (188–261 × 1.5–6 μm); microscleres palmate isochelae small, straight shaft, long, thick lateral alae fully fused to shaft, nearly completely detached from front ala, front ala shorter than lateral alae (8–15 μm); toxas absent.

Remarks. The genera *Holopsamma* and *Echinoclathria*, as defined here, have been confused throughout the literature and several names (*Echinoclathria, Ophlitaspongia, Plectispa, Halme*) have been used interchangeably for all species. However, *Holopsamma* differs substantially from *Echinoclathria* in having a distinctive 'honeycombed reticulate' growth form, homogeneous fibre reticulation, a single size class of choanosomal spicule found both inside fibres and echinating fibres (lacking the larger, extra-axial styles found in the peripheral skeleton of most *Echinoclathria*). When respective type species are compared it is surprising why these genera have ever been confused at all.

Distribution. Twenty four named species have been referred to this genus at one time or another, of which only ten are well established, all of which are endemic to the Gondwanan fauna.

PANDAROS DUCHASSAING & MICHELOTTI, 1864

Synonymy

Pandaros Duchassaing & Michelotti, 1864: 88.

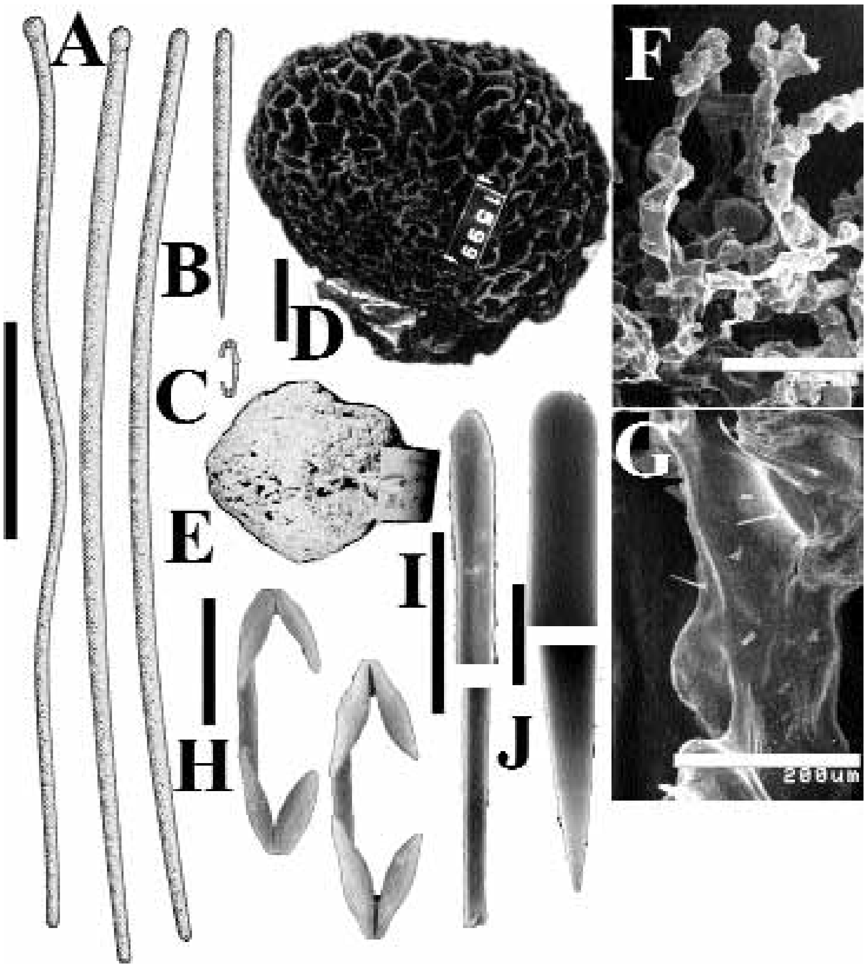

Fig. 13. *Holopsamma*. A–J, *H. crassa* Carter. A, subectosomal auxiliary subtylostyles/strongyles. B, principal style (coring and echinating fibres). C, palmate isochela (scale A–C, 50 μm). D, specimen SAM TS4085. E, lectotype BMNH 1886.12.15.313 (scale D–E, 30 mm). F, choanosomal skeleton (scale 1 mm). G, fibre characteristics (scale 200 μm). H, palmate isochelae (scale 5 μm). I, base and bifid point of auxiliary spicule (scale 5 μm). J, base and point of principal spicule (scale 10 μm).

Type species

Pandaros acanthifolium Duchassaing & Michelotti, 1864: 90 (by subsequent designation; de Laubenfels, 1936a: 123).

Definition

Microcioninae with flattened spongin fibres cored by smooth slightly rhabdose auxiliary styles and echinated by rare acanthose and smooth styles.

Diagnosis

Bushy arborescent growth form; with well developed choanosomal skeletal reticulation of spongin fibres woven into flattened anastomosing branches, or forming continuous sheets without any regular architecture; fibres cored by auxiliary styles, subtylostyles to tylostyles, predominantly smooth, distributed within fibres in criss-cross fashion; fibres echinated by rare acanthostyles, rarely smooth styles; few anisotornotes, verging on oxeas, scattered throughout mesohyl; sparsely dispersed tangential subectosomal auxiliary spicules dispersed throughout peripheral skeleton; microscleres absent.

Description of type species

Pandaros acanthifolium Duchassaing & Michelotti, 1864 (Figs 3B, 14).

Synonymy. *Pandaros acanthifolium* Duchassaing & Michelotti, 1864: 90; *Pandaros arbusculum*, in part, Duchassaing & Michelotti, 1864: 88; *Thalyseurypon conulosa* Hechtel, 1965: 44.

Material examined. Lectotype: TM POR57 (fragments USNM31020, MNHN DNBE1309, BMNH 1928.11.12.15a,16a) – St. Thomas, Virgin Is., Caribbean.

Description. Bushy arborescent growth form. Surface highly conulose, with flattened or lobate lamellae. Choanosomal skeleton reticulate, with well developed flattened spongin fibres (trabeculae) cored by choanosomal principal subtylostyles lying in all directions within fibres (from isodictyal reticulate to echinating) and with sparse acanthostyles echinating or also incorporated into fibres. Subectosomal skeleton radial, reduced to single long subectosomal auxiliary subtylostyles protruding through surface and also scattered throughout mesohyl. Ectosome without special spicules. Megascleres smooth choanosomal principal subtylostyles–tylostyles, often with slightly rhabdose bases and terminal or subterminal basal swellings, and often polytylote or irregular terminations, with large size range (84–435 × 3–11 μm), long

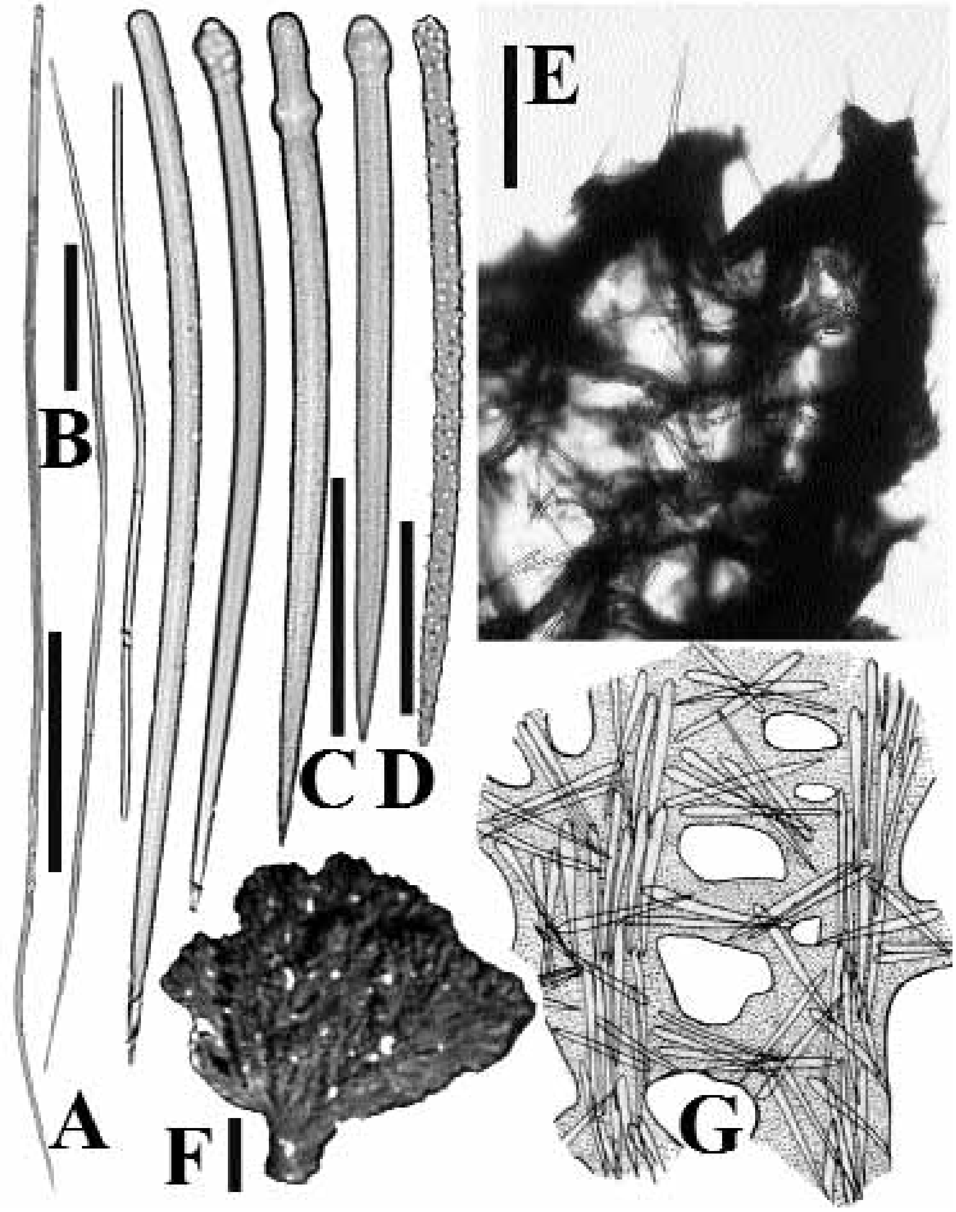

Fig. 14. *Pandaros*. A–G, *P. acanthifolium* Duch. & Mich. A, subectosomal auxiliary subtylostyle (scale 100 μm). B, sinuous raphidiform anisotornotes (scale 50 μm). C, principal subtylostyles (scale 100 μm). D, 'echinating' acanthostyle (scale 50 μm). E, section through peripheral skeleton (scale 500 μm). F, part of lectotype BMNH 1928.11.12.15a (scale 30 mm). G, skeletal reconstruction (after Van Soest, 1984b).

curved or straight subectosomal auxiliary subtylostyles (340–665 × 5–13 μm), lightly acanthose or rarely smooth styles 'echinating' fibres (160–195 × 5–8 μm), and long curved or sinuous, raphidiform spicules verging on anisotornotes (303–455 × 2–4 μm). Microscleres absent.

Remarks. The above diagnosis is compiled from re-examination of type and recent material of *Pandaros acanthifolium* (schizotype MNHN DNBE1309, specimen BMNH 1884.7.11.2) and the redescription of live populations by Van Soest (1984b). The important features of this species and genus *Pandaros* are: (1) the prominently flattened fibres cored by smooth slightly rhabdose principal subtylostyles-tylostyles (more reminiscent of Rhabderemiidae than Microcionidae); (2) the sparse, lightly spined styles which more closely resemble a second category of principal spicules than they do echinating (accessory) spicules typical of other Microcionidae; furthermore, these spicules are only rarely seen echinating fibres, but more commonly they are incorporated into them together with the principal megascleres; (3) the long subectosomal auxiliary subtylostyles that protrude through the surface (more similar to a reduced Raspailiidae, such as *Echinodictyum* or *Ceratopsion*, than to typical Microcionidae); and (4) the possession of long raphidiform, sinuous or curved spicules (classed as 'microscleres' with question by Van Soest, 1984b) that have irregular terminations – sometimes stylote and sometimes strongylote – which he calls anisotornotes.

Pandaros is a borderline taxon that could be legitimately included in either Raspailiidae or Microcionidae. In fact Van Soest (1984b) noted that only the presence of rare echinating acanthostyles in *P. acanthifolium* gives any cause to link it to the Microcionidae at all. He speculated that it might be necessary to erect a separate family for the species, or even remove it from the Poecilosclerida altogether, as it also shows affinities with axinellid genera such as *Ptilocaulis*. There are no microscleres to give any further clues as to its affinities. *Pandaros* is maintained as a separate genus and included in Microcionidae on a tentative basis until further evidence is forthcoming. Of the twelve species previously referred to *Pandaros*, only the type species clearly belongs here. *Raspailia kasumiensis* Tanita (MMBS SIS-052), which Hoshino (1981a) referred to *Thalyseurypon*, should also be allocated to *Pandaros* in its skeletal architecture and spiculation (as suggested earlier by Hooper, 1990b).

Wiedenmayer (1977b) merged *Thalyseurypon* with *Pandaros*, because he considered that the type species of the former (viz., *Spongia raphanus* Lamarck) had architecture closely comparable to *P. acanthifolium* (Hechtel, 1965), but this is not upheld here. The only features these genera have in common is in lacking microscleres. Wiedenmayer (1977b) also speculated that the genus had a close relationship with *Echinoclathria* (=*Holopsamma* as defined here), based on alleged similarities in skeletal architecture, and he suggested that the two genera probably intergrade in habit and spiculation, but these suggested affinities were not noted from re-examination of relevant specimens.

Distribution

Known only from the Caribbean.

SUBFAMILY OPHLITASPONGIINAE DE LAUBENFELS, 1936

Synonymy

Ophlitaspongiidae de Laubenfels, 1936a.

Definition

Microcionidae with a secondary renieroid spiculo-spongin skeleton (see Fig. 1, symbol 9) overlaying a primary reticulate, plumo-reticulate, plumose or hymedesmioid skeletal architecture.

Scope

Four genera and three subgenera: *Antho* (*Antho* (*Antho*), *A.* (*Acarnia*), *A.* (*Isopenectya*)), *Artemisina*, *Echinoclathria* and *Ophlitaspongia.*

ANTHO GRAY, 1867

Synonymy

Antho Gray, 1867a: 524 (see subgenera for full synonymy).

Type species

Myxilla involvens Schmidt, 1864: 37 (by monotypy).

Definition

Ophlitaspongiinae with choanosomal skeleton modified to a basal or axial renieroid reticulation of acanthose or occasionally smooth styles and/or strongyles, overlaying a plumose(-reticulate) subectosomal skeleton of smooth principal styles, with or without echinating spicules.

Diagnosis

Encrusting, massive, bulbous, lobate, digitate and flabellate growth forms; skeleton with 2 distinct components: (1) primary (basal or axial) renieroid choanosomal skeleton replacing usual microcionid choanosomal skeleton, composed of acanthostyles and/or acanthostrongyles; (2) secondary (extra-axial, subectosomal) skeleton composed of smooth choanosomal styles forming dendritic, plumose, subisodictyal or plumo-reticulate tracts, or simply echinating main spicule tracts; secondary skeleton usually arising from nodes of renieroid skeleton, or ascending upwards from basal spongin fibres, with or without axial compression; spongin fibres relatively poorly developed; additional category of echinating acanthostyles present or absent; ectosomal skeleton tangential, paratangential or plumose tracts of 1 or 2 categories of auxiliary styles; microscleres diverse forms of isochelae and toxas.

Remarks

Under Van Soest & Stone's (1986) system all microcionids having a renieroid basal (or axial) skeleton composed of acanthose megascleres are grouped in a single genus (*Antho s.l.*). This system was supported by Hooper (1996a) with the distinction that three subgenera are recognised within *Antho* based on structure and composition of the renieroid skeleton: the nominotypical subgenus *Antho* (with predominantly (acantho)styles forming the renieroid skeleton, less often acanthostrongyles, without echinating acanthostyles), *Acarnia* (with predominantly (acantho)strongyles forming the renieroid skeleton, less often acanthostyles, and a special category of echinating acanthostyles overlap the main skeleton), and *Isopenectya* (with an axially compressed and extra-axially renieroid reticulate skeleton composed of two forms of choanosomal spicules inside spongin fibres, overlaid by a second extra-axial plumose skeleton). It could be argued that *Isopenectya* (*s.s.*) could also be included in *Echinoclathria*, given the close resemblance in growth form and renieroid skeletal structure with the type species *E. leporina*, but in *Isopenectya* the renieroid skeleton is composed of sparsely spined principal styles (clearly differentiated from the larger smooth styles of the extra-axial skeleton), with differentiated axial (compressed) and extra-axial (renieroid) regions, overlaid by a second extra-axial (plumose) skeleton composed of larger, smooth principal styles. In *Echinoclathria*, as redefined by Hooper (1996a) based on its type species, megascleres of the renieroid skeleton are exclusively smooth, and the larger, smooth principal styles which form a radial skeleton are only found on the surface, embedded in peripheral fibres. Nevertheless, both genera, *Antho* and *Echinoclathria*, differ from other microcionids in having a basically renieroid skeletal construction and it is possible that *Echinoclathria* are highly derived forms of *Antho* (loss of spinated principal spicules, loss of extra-fibre skeleton, loss of spined acanthostyles (geometrically different from principal spicules)).

Distribution

Indo-Pacific, W Indian Ocean, NE and NW Atlantic, Mediterranean.

SUBGENUS *ANTHO* GRAY, 1867

Synonymy

Antho Gray, 1867a: 524. *Anomoclathria* Topsent, 1929a: 26 (Not Topsent, 1932a: 103) (type species *Alcyonium opuntioides* Lamarck, 1815: 164 (by original designation) lectotype MNHN DT654). *Anthoarcuata* Bakus, 1966b: 431 (type species *Anthoarcuata graceae* Bakus, 1966b: 431 (by original designation and monotypy) holotype USNM 36284 (161848)). *Dictyoclathria* Topsent, 1920a: 18 (type species *Clathria morisca* Schmidt, 1868: 9 (by original designation) (schizotype BMNH 1868.3.2.21); junior synonym of *Antho involvens* (Schmidt, 1864) (Lévi, 1960b: 57) schizotype BMNH 1867.3.11.92). [*Dyctioclathria*] Ferrer-Hernandez, 1921: 172 (*lapsus*). *Isociona* Hallmann, 1920: 768 (type species *Lissodendoryx tuberosa* Hentschel, 1911: 326 (by monotypy) holotype ZMB 4417). *Jia* de Laubenfels, 1930: 28 (type species *Jia jia* de Laubenfels, 1930: 28 (by original designation) holotype USNM 21510). *Plocamilla*, in part, Burton, 1935a: 402 (Not *Plocamilla* Topsent, 1928c: 63). ? *Quintoxilla* de Laubenfels, 1950a: 18 (type species *Myxilla arcitenens* Topsent, 1892b: 24, by original designation; no extant type material). *Quizciona* de Laubenfels, 1936a: 111 (type species *Microciona heterospiculata* Brondsted, 1924b: 465 (by original designation) schizotype BMNH 1901.12.26.13). Taxonomic decision for synonymy: Hooper (1996a), and this work.

Type species

Myxilla involvens Schmidt, 1864: 37 (by monotypy).

Definition

Antho with predominantly (acantho)styles forming the renieroid skeleton, less often acanthostrongyles, without echinating acanthostyles.

Diagnosis

Encrusting, lobate and digitate growth forms; with a primary basal renieroid choanosomal skeleton composed of acanthostyles and/or acanthostrongyles; secondary extra-axial (subectosomal) skeleton plumose, plumo-reticulate, or simply composed of choanosomal styles echinating (project from) basal renieroid skeleton; spongin fibres poorly developed; special category of echinating acanthostyles absent; ectosomal skeleton with tangential, paratangential, or plumose tracts of one size of auxiliary styles or subtylostyles; microscleres include diverse forms of isochelae and toxas.

Description of type species

Antho (*Antho*) *involvens* Schmidt, 1864 (Figs 3C, 15).

Synonymy. *Myxilla involvens* Schmidt, 1864; *Hymedesmia involvens*; Schmidt, 1866a: 16; *Antho involvens*; Gray, 1867a: 524; *Desmacodes involvens*; Vosmaer, 1880: 108; *Myxilla banyulensis*, in part; Topsent, 1892b: 23; *Clathria morisca* Schmidt, 1864: 37, 45; *Dictyoclathria morisca*; Topsent, 1920a: 18; *Plocamia inconstans*; Topsent, 1925c: 661; *Holoplocamia inconstans*; de Laubenfels, 1936a: 75. *Antho inconstans*; Ackers, Moss & Picton, 1992: 140; *Isodictya beani* Bowerbank, 1866: 274; *Dictyoclathria beanii*; Arndt, 1935: 81; *Amphilectus beanii*; Vosmaer, 1880: 115; *Clathria beanii*; Ridley, 1881: 485; *Myxilla beanii*; Topsent, 1892b: 23; *Artemisina mediterranea* Babic, 1921: 87; *Microciona virgula* Sarà & Siribelli, 1960: 77; ? *Artemisina paradoxa* Babic, 1921: 87; *Clathria paradoxa*; Burton, 1930c: 528; *Antho paradoxa*; Pulitzer-Finali, 1983: 610. ? *Raspailia incrustans* Swarczewsky, 1906: 52.

Material examined. Holotype: LMJG (fragment BMNH 1867.3.11.92) – Adriatic.

Description. Thinly encrusting growth forms; surface rugose, hispid; choanosomal skeleton renieroid reticulate with acanthostyles-strongyles coring spongin fibres, or simply united at nodes by variable quantities of spongin, producing triangular and rectangular skeletal meshes; junctions of skeletal meshes with principal choanosomal styles echinating fibre nodes, standing erect or at oblique angles, in tufts or singly; true echinating megascleres absent (i.e., undifferentiated from choanosomal principal styles); ectosome contains tangential or paratangential multispicular brushes of subectosomal auxiliary styles protruding through surface; megascleres acanthose principal styles/strongyles of renieroid basal skeleton (124–187 × 2–12 μm), smooth or slightly acanthose principal styles/subtylostyles of the choanosomal skeleton (164–335 × 9–14 μm), and smooth subectosomal auxiliary styles, often with basal spines (175–386 × 4–7 μm); microscleres palmate isochelae (13–20 μm), wing-shaped and accolada toxas (22–175 × 1–4 μm).

Remarks. Twenty two named species have been included in, or referred to, *Antho* (*Antho*), although only twelve of these are currently widely accepted as being valid. The subgenus was recently revised (Hooper, 1996a) and needs no further discussion here apart from some comment on the inclusion of *Quintoxilla* de Laubenfels in the above synonymy, with question. The type species is described as thinly encrusting, having large acanthostyles 330 × 4–5 μm, echinating acanthostyles 190 μm long, and ectosomal smooth tylostyles or tylostrongyles (no sizes given). Microscleres are toxas 90–330 μm long, 'palmate tridentate' chelae 20 μm long, and flexuous raphides which could be young toxas 100 μm long, often forming bundles (toxodragmata). No skeletal structure was described, but Topsent's (1892b) inclusion of the taxon in *Myxilla* was presumably on account of an observed reticulate arrangement of the skeleton, and this, together with megasclere and microsclere geometries, suggests affinities with *Antho*. De Laubenfels' (1936a) assumption that chelae are anchorate is unfounded. Unfortunately there appears to be no surviving type material (or slides) of the type species (Hooper, Van Soest, personal observations of the MNHN collections), so these details and the true allocation of this taxon cannot be verified. It remains *Antho* (*Antho*) *incertae sedis*.

SUBGENUS *ACARNIA* GRAY, 1867

Synonymy

Acarnia Gray, 1867a: 515. *Plocamia* Schmidt, 1870: 62 (type species *Plocamia gymnazusa* Schmidt, 1870: 62 (by subsequent designation; Burton, 1935a: 401 (holotype possibly LMJG, schizotype

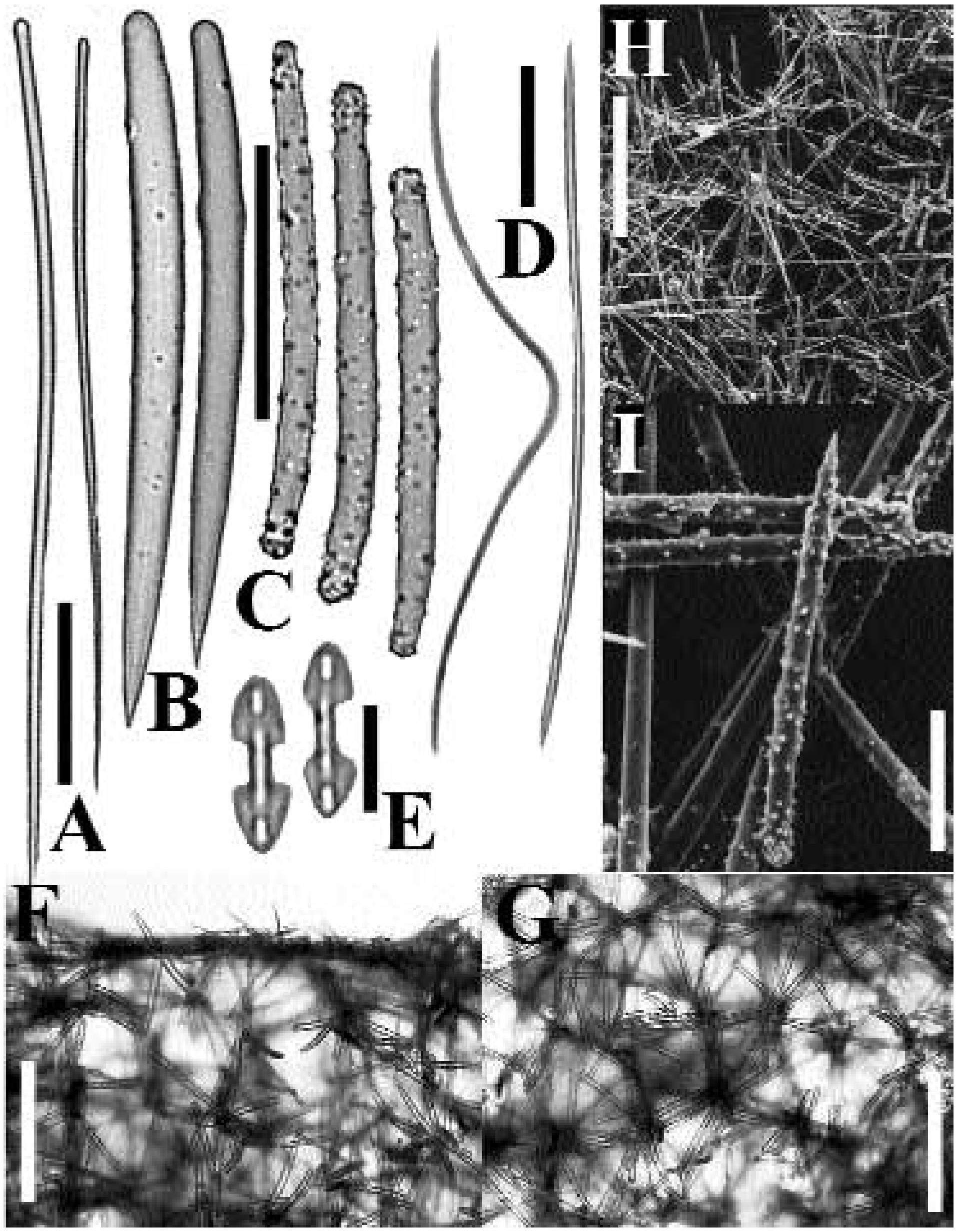

Fig. 15. *Antho* (*Antho*). A–G, *A.* (*A.*) *involvens* (Schmidt). H–I, *A.* (*A.*) *tuberosa* (Hentschel). A, subectosomal auxiliary styles. B, smooth principal styles of the choanosomal skeleton (scale A–B, 50 μm). C, acanthostyles/strongyles of the renieroid basal skeleton (scale 100 μm). D, wind-shaped and accolada toxas (scale 25 μm). E, palmate isochelae (scale 10 μm). F, ectosomal skeleton. G. choanosomal skeleton (scale F–G, 250 μm). H, choanosomal skeletal structure (scale 250 μm). I, renieroid skeleton (scale 50 μm).

MNHN DCL1105L)) (Fig. 17). [*Dirrhopalum*] Ridley, in Ridley & Duncan, 1881: 477 (unjustified replacement name for *Plocamia*). *Plocamiopsis* Topsent, 1904b: 155 (type species *Plocamiopsis signata* Topsent, 1904b: 155 (by monotypy) holotype MNHN DT947). *Heteroclathria* Topsent, 1904c: 93 (type species *Heteroclathria hallezi* Topsent, 1904c: 94 (by original designation and monotypy) schizotype MNHN DT1884). *Lissoplocamia* Brøndsted, 1924b: 470 (type species *Lissoplocamia prima* Brøndsted, 1924b: 470 (by original designation) holotype not seen; specimen MNHN DCL637 ex. South Africa). *Plocamilla* Topsent, 1928c: 63 (Not Burton, 1935a: 402) (type species *Isodictya coriacea* Bowerbank, 1874b: 136 (by original designation; Topsent, 1928c: 63) holotype BMNH 1910.1.1.251). *Anomoclathria*; in part, Topsent, 1932: 103 (Not Topsent, 1929a: 26). *Protoclathria* Burton, 1932b: 320 (type species *Protoclathria simplicissima* Burton, by monotypy, type material not examined). *Holoplocamia* de Laubenfels, 1936a: 75 (type species *Holoplocamia penneyi* de Laubenfels, 1936a: 75 (by original designation) holotype USNM 22460). *Echinoplocamia* Burton, 1959a: 252 (type species *Echinoplocamia arbuscula* Burton, 1959a: 252 (by original designation) holotype BMNH 1936.3.4.413). Taxonomic decision for synonymy: Hooper (1996a), and this work.

Type species

Hymeniacidon cliftoni Bowerbank, 1862a (by monotypy) (junior synonym of *Spongia frondifera* Lamarck, 1814; Hooper, 1996a: 422).

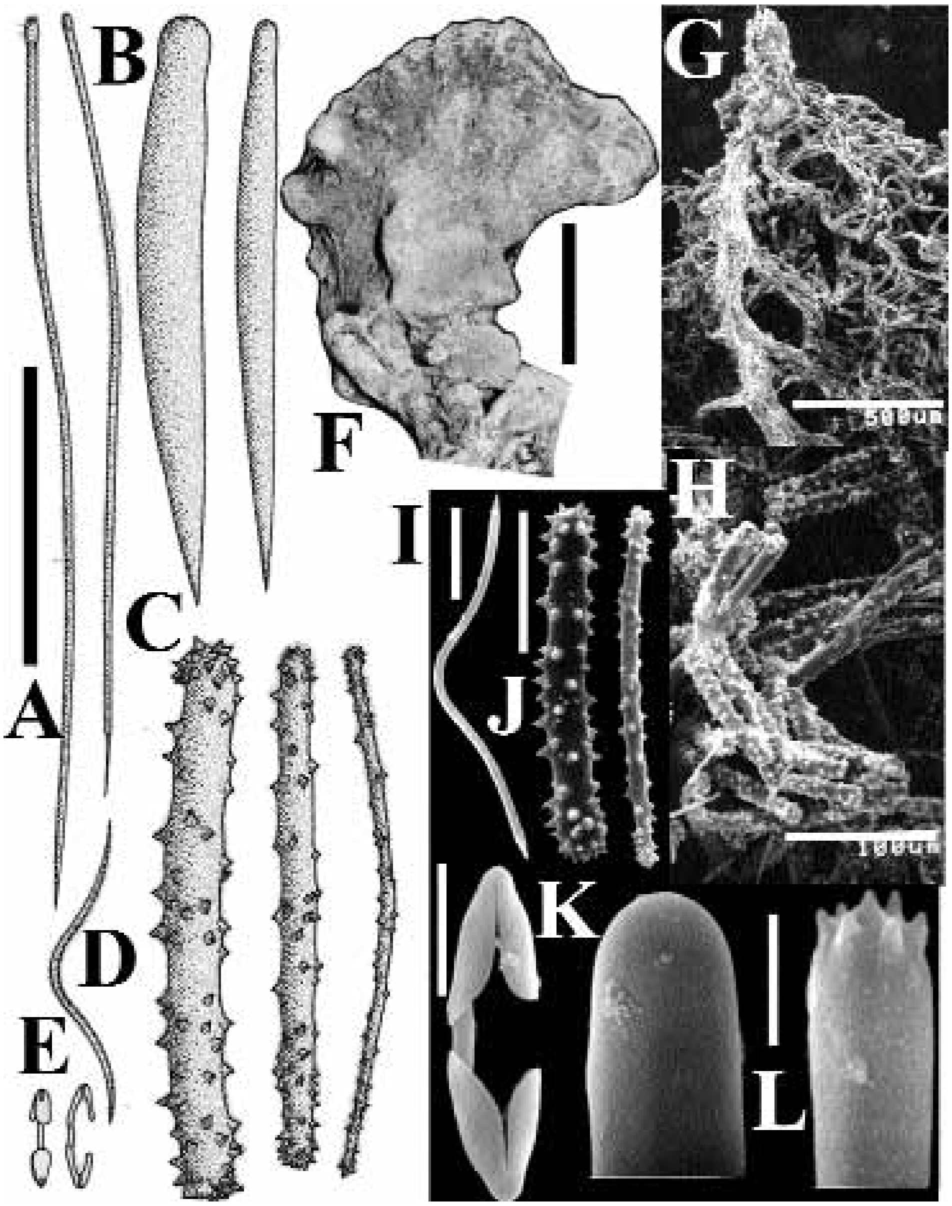

Fig. 16. *Antho* (*Acarnia*). A–L, *A.* (*A.*) *frondifera* (Lamarck). A, subectosomal auxiliary subtylostyles. B, choanosomal principal subtylostyles. C, acanthotylostrongyles of the renieroid skeleton. D, wing-shaped toxa. E, palmate isochelae (scales A–E, 50 μm). F, lectotype MNHN DT565 scale 30 mm. G, choanosomal skeleton (scale 500 μm). H, renieroid skeleton (scale 100 μm). I, toxa (scale 50 μm). J, acanthotylostrongyles (scale 50 μm). K, palmate isochelae (scale 5 μm). L, bases of choanosomal principal style and auxiliary subtylostyle (scale 5 μm).

Definition

Antho with predominantly (acantho)tylostrongyles forming the renieroid skeleton, less often acanthostyles, and a special category of echinating acanthostyles overlap the main skeleton.

Diagnosis

Encrusting, lobate, digitate and flabellate growth forms; with regular basal or axial renieroid skeleton of acanthostrongyles (less frequently acanthostyles or smooth tylostrongyles), with or without spongin fibres. Renieroid tracts may be echinated by acanthostyles at spongin fibre nodes. Basal renieroid skeleton overlays hymedesmioid, leptoclathriid or microcionid main skeleton composed of echinating (acantho-)styles and/or choanosomal styles, standing perpendicular to base or axis, joining with echinating megascleres to produce ascending plumose skeletal tracts. Extra-axial (subectosomal) skeleton plumose, dendritic, or subisodictyal, composed of choanosomal styles, originating from substrate or simply confined to periphery, forming tangential, paratangential or plumose extra-axial tracts. Ectosomal skeleton with or without specialized spiculation (one or two categories of auxiliary styles). Microscleres include diverse forms of isochelae and toxas.

Description of type species

Antho (Acarnia) frondifera (Lamarck, 1814) (Fig. 16).

Synonymy. *Spongia frondifera* Lamarck, 1814: 445; Lamarck, 1816: 374. *Anomoclathria frondifera*; de Laubenfels, 1936a: 108. *Antho frondifera*; Hooper & Wiedenmayer, 1994: 256.

Antho (Plocamia) frondifera; Hooper, 1996a: 422, figs 216–217. *Anomoclathria opuntioides* var. *frondifera* Topsent, 1929a: 26–29, figs 10–14; Topsent, 1932a: 103, pl. 1, figs 6–7. *Hymeniacidon cliftoni* Bowerbank, 1862a: 773, pl. 30, fig. 9; Bowerbank, 1864: 276, figs 70, 291. *Acarnia cliftoni*; Gray, 1867a: 515. (Not *Alcyonium opuntioides* Lamarck, 1815: 164.)

Material examined. Lectotype: MNHN DT565 – ? SW. Australia (Turgot collection). Paralectotype: MNHN DT3356 – same details. Holotype of *H. cliftoni*: BMNH 1877.5.21.608 (fragments BMNH 1877.5.21.616, 1185, 218) – SW Australia.

Description. Lobate, thickly flabellate, digitate fans with uneven, digitate margins and irregular lobate surface. Large oscules scattered evenly over surface and lateral margins of digits, with remnants of stellate drainage canals converging on each oscule. Ectosomal skeleton membraneous, heavily collagenous, with some embedded detritus and sparse tangential and paratangential tracts or single auxiliary subtylostyles scattered near periphery, sometimes forming bundles protruding through ectosome; points of (smooth) choanosomal principal styles from ascending plumose tracts protrude only slightly through collagenous surface membrane; subectosomal skeleton virtually undifferentiated from choanosome, although peripheral choanosomal styles of plumose skeleton slightly more dense, diverging, than tracts in skeletal core. Choanosomal skeleton with two distinct components: (1) ascending plumose and (2) basal/axial renieroid (in some places isodictyal). Plumose skeleton with pauci- or multispicular tracts of smooth choanosomal principal styles ascending to surface, rarely branching or anastomosing; tracts associated with, but not necessarily coring, heavy, dark brown, spongin-coated algal filaments (ostensibly *Ficus*; Topsent, 1932a), which dominate skeleton; filaments up to 250 μm diameter, 300–400 μm apart, branching, diverging from base of sponge through sponge surface. Renieroid skeleton composed of 1 or 2 acanthotylostrongyles abreast forming square or triangular meshes up to 120 μm diameter, even mesh size throughout skeleton, overlaying plumose skeleton; some detritus scattered between renieroid skeletal meshes, usually coated with spongin; mesohyl not intact although some granular collagen containing microscleres scattered between spicule meshes. Megascleres: choanosomal principal styles entirely smooth, short, robust, slightly curved at centre, with rounded or slightly subtylote bases, fusiform points (88–118 × 4–13 μm). Acanthotylostrongyles of the renieroid skeleton thick or thin, rounded or slightly subtylote at both ends, heavily spined particularly at points, spines large, conical or slightly recurved, sharply pointed (85–103 × 3–14 μm). Subectosomal auxiliary subtylostyles long, very slender, curved at centre or sinuous, subtylote usually microspined bases, fusiform or occasionally telescoped points (120–184 × 1–2.5 μm). Microscleres: palmate isochelae large, unmodified, with front and lateral alae approximately same length, lateral alae entirely fused to shaft, front ala detached along lateral margin (15–20 μm long). Toxas wing-shaped, short, moderately thick, with large central curvature and slightly reflexed points (40–116 × 1–2 μm).

Remarks. The inclusion of *Hymeniacidon cliftoni* Bowerbank into synonymy with the type species of *Plocamia* (*Spongia frondifera* Lamarck) unfortunately requires that the subgenus name be emended to *Acarnia*. Previously, Hooper (1996a: 422) suspected that the two species were synonymous but the available type material of *Acarnia* was so poor to be uncertain. Subsequent examination of a better slide preparation confirms this synonymy.

Twenty two nominal species have been referred to this subgenus, all of which are presently recognized as valid species by current authors. However, one of those species (*A.* (*Acarnia*) *erecta*) is very poorly known, and it is also possible that a number of other species will be eventually merged. The nominal genus *Echinoplocamia* was also overlooked by Hooper (1996a) and is included here as a new synonym within the subgenus.

It is possible that species with smooth tylostrongyles forming the renieroid skeleton (‘sausage-shaped spicules’ of Ridley, in Ridley & Duncan, 1881) should be separated into a separate taxon (e.g., subgenus *Plocamia*). These spicules superficially appear to be geometrically distinct from (and therefore possibly not homologous with) acanthotylostrongyles in typical *Acarnia* (Fig. 17). These smooth smooth ‘sausage-shaped spicules’ are found in the nominal genera *Plocamia* (including *Dirrhopalum*), *Heteroclathria* and *Lissoplocamia*. However, skeletal structures are identical between both groups without any other obvious corroboratory characters to support their differentiation. Another nominal

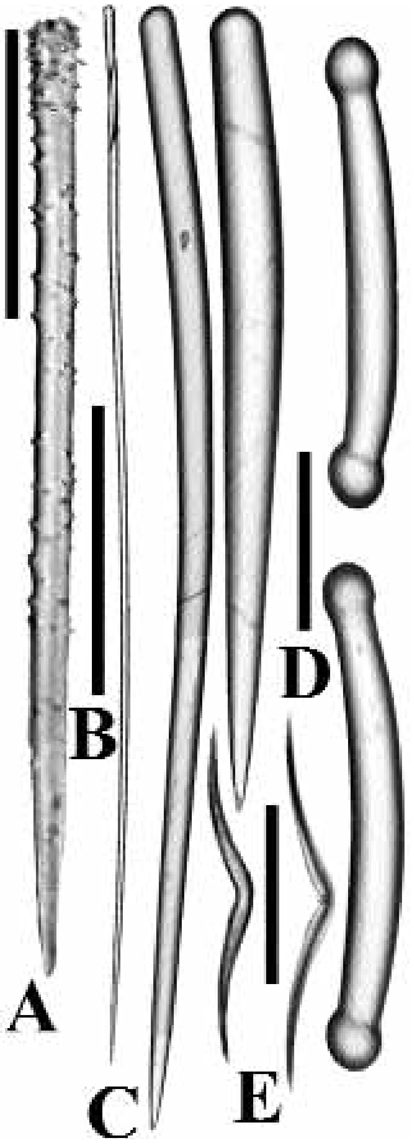

Fig. 17. *Antho* (*Acarnia*), cont. A–E, *A.* (*A.*) *gymnazusa* (Schmidt, 1870) (type species of *Plocamia* Schmidt). A, echinating acanthostyle (scale 50 μm). B, subectosomal auxiliary subtylostyle. C, choanosomal principal styles (scale B–C, 100 μm). D, tylostrongyles (scale 50 μm). E, toxas (scale 10 μm).

genus, *Protoclathria* Burton, 1932b, is also included here as a synonym of *Antho* (*Acarnia*), overlooked by Hooper (1996a). The type species, *P. simplicissima* Burton from Tristan da Cunha, is a massive pyriform sponge with a hispid, even surface. The skeleton is renieroid, composed of dense reticulation of triangular, mostly multispicular meshes cored by a single category of smooth subtylostyle (260 × 15 μm), occasionally with oxeote modification, intermingled with modified acanthostrongyles (180 × 12 μm) coring fibres, apparently not echinating them. No ectosomal spicules were described and microscleres are also apparently absent. It is likely that this species was imperfectly described by Burton (1932b) as no mention was made of a secondary plumose or plumo-reticulate skeleton common to all members of *Antho*.

SUBGENUS *ISOPENECTYA* HALLMANN, 1920

Synonymy

Isopenectya Hallmann, 1920: 789. *Clathriella* Burton, 1935c: 73 (type species *Clathriella primitiva* Burton, 1935c: 73 (by original designation) holotype BMNH 1938.7.4.93). Taxonomic decision for synonymy: Hooper (1996a).

Type species

Clathria (?) *chartacea* Whitelegge, 1907: 497 (by monotypy).

Definition

Antho with an axially compressed and extra-axially renieroid reticulate skeleton composed of two forms of choanosomal spicules inside spongin fibres, overlaid by a second extra-axial plumose skeleton.

Diagnosis

Bulbous, arborescent and flabellate growth forms; with three skeleton components: (1) renieroid reticulation of acanthose styles, (2) overlayed by isodictyal or subisodictyal reticulation of smooth styles coring spongin fibres, (3) surmounted by plumose or radial extra-axial skeleton of larger smooth styles, perpendicular to axis, in peripheral region; skeleton may be slightly compressed at core, spongin fibres only moderately developed; echinating megascleres absent; ectosomal skeleton with single category of auxiliary subtylostyle forming tangential or paratangential tracts; microscleres absent.

Description of type species

Antho (*Isopenectya*) *chartacea* (Whitelegge, 1907) (Figs 3E, 18).

Synonymy. *Clathria* (?) *chartacea* Whitelegge, 1907: 497. *Isopenectya chartacea*; Hallmann, 1920: 789. *Antho chartacea*; Rudman & Avern, 1989: 335. *Antho* (*Isopenectya*) *chartacea*; Hooper, 1996a: 433, figs 221–222. *Antherochalina perforata* Lendenfeld, 1887c: pl.22, fig.44 (Not *Antherochalina perforata* Lendenfeld, 1887c: 788; Lendenfeld, 1888: 89–90).

Material examined. Holotype: AMZ436 – Off Coogee, NSW, Australia. Other material. Refer to Hooper (1996a: 433).

Description. Shape thinly flabellate with long, thickly cylindrical stalk, very thin lamellae, slightly digitate or evenly rounded margins; firm, barely compressible, flexible, slightly spiky; optically smooth, even surface; ectosome prominently hispid, with pauci- or multispicular plumose brushes of larger, smooth choanosomal principal styles protruding through surface, forming a vestigial radial extra-axial skeleton, arising from pauci- or multispicular tracts of (marginally) smaller smooth principal styles in subectosomal region; subectosomal auxiliary subtylostyles tangential, paratangential, or rarely plumose, at base of protruding choanosomal spicule brushes; peripheral skeleton relatively cavernous in comparison to the central choanosomal skeleton, moderately heavily collagenous; choanosomal skeletal structure with 3 distinct components: (1) slightly compressed spongin fibres forming close-meshed anastomoses at core of skeleton, more cavernous towards surface, (2) renieroid skeleton composed of acanthose styles, overlaying other structures, (3) longitudinal, ascending tracts of smooth principal styles, marginally smaller than those protruding through surface, forming subisodictyal tracts at core, more plumose in periphery, and usually (but not invariably) associated with larger spongin fibres; spongin fibres in axial skeleton heavy, producing irregularly oval or elongate meshes, cored by uni- or bispicular tracts of smaller, smooth choanosomal principal styles; fibres closer to surface regularly anastomosing, wide-meshed, forming regularly renieroid (triangular) spicule meshes and oval or elongate fibre meshes, cored by uni- or bispicular tracts of smaller acanthose styles; plumose extra-fibre skeleton composed of uni-, pauci- or multispicular ascending tracts of smooth choanosomal styles standing perpendicular to axis, becoming increasingly plumose, larger, and typically multispicular towards periphery; echinating megascleres absent; megascleres smooth choanosomal principal styles long, thick, slightly curved or straight, with rounded or very slightly subtylote bases, rarely with basal microspination, fusiform points (168–274 × 13–17 μm); acanthose choanosomal styles of renieroid skeleton short, thick, fusiform, slightly curved or straight, with rounded or slightly subtylote bases, lightly microspined bases and points, with fewer spines scattered on shaft, occasionally completely smooth shaft (92–127 × 9–12.5 μm); subectosomal auxiliary subtylostyles short, thin, usually straight, with prominent subtylote, typically microspined bases, hastate points, abrupt points, or sometimes telescoped or bifid points (163–243 × 2–4.5 μm); microscleres absent.

Remarks. Incuding the present work *Isopenectya* contains only four species, three from the SW. Pacific and one from the NW Pacific Ocean. All species lack microscleres but this is interpreted as a secondary loss and consequently not given primary diagnostic importance. Hallmann (1920) created *Isopenectya* for the type species primarily on the basis of having a renieroid skeleton, with two categories of choanosomal styles, without echinating acanthostyles, and without microscleres. The type species has obvious affinities with *Antho*. It differs from other microcionids with myxillid-like renieroid skeletons (viz., *Antho* (*Antho*), *Antho* (*Acarnia*), *Clathria* (*Clathria*) *and Clathria* (*Isociella*)) in having a condensed axis and more-or-less plumose extra-axial skeletons cored by smooth choanosomal (principal) styles, in one or more size categories, together with the usual renieroid structure overlaying the remainder of the skeleton composed of acanthose (or sometimes smooth) styles different from principal spicules.

The subgenus superficially resembles *Echinoclathria leporina*, mainly in the emphasis of the compressed central skeleton and subrenieroid skeletal structure in both species, whereas megascleres

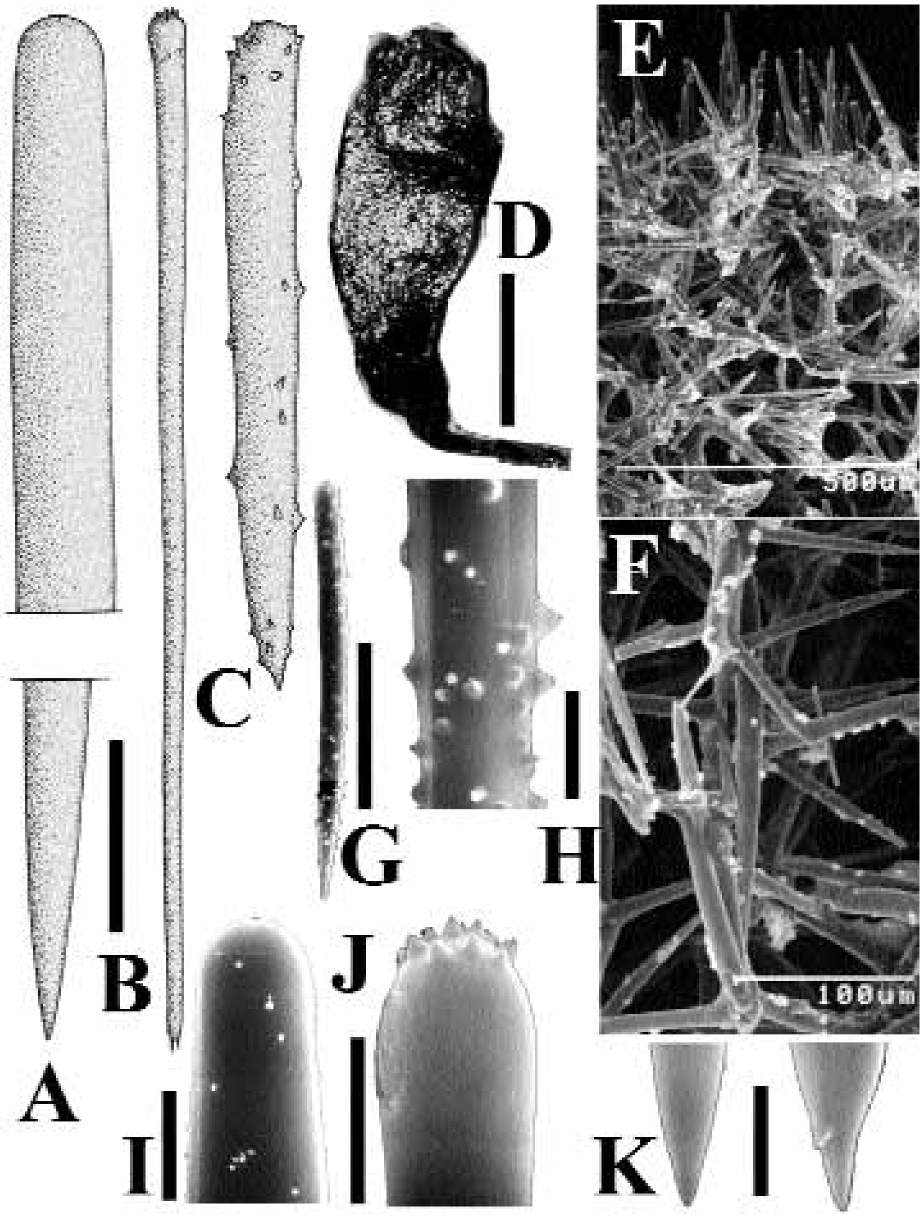

Fig. 18. *Antho* (*Isopenectya*). A–K, *A.* (*I.*) *chartacea* (Whitelegge). A, choanosomal principal style. B, subectosomal auxiliary style. C, acanthostyle of the renieroid skeleton (scale A–C, 25 µm). D, holotype AMZ436 (scale 30 mm). E, choanosomal skeleton (scale 500 µm). F, fibre characteristics (scale 100 µm). G, acanthostyle (scale 50 µm). H, acanthostyle shaft spines (scale 5 µm). I, base of principal style (scale 10 µm). J, base of auxiliary style (scale 5 µm). K, tips of auxiliary styles (scale 5 µm).

forming these skeletons are quite different. Choanosomal megascleres in *A.* (*I.*) *chartacea* are clearly differentiated: small acanthose styles forming the renieroid skeleton (not echinating fibres), small smooth styles forming a secondary radial ascending skeleton, and larger smooth styles forming the peripheral perpendicular skeleton. By comparison, in *E. leporina* there is a smaller size class of smooth principal styles both coring and echinating heavy spongin fibres, forming a renieroid skeletal structure, and a second, larger class of smooth principal styles forming a sparse radial or plumose peripheral skeleton (embedded in peripheral fibres). This latter structure links the two groups. *Antho chartacea* should also be contrasted with the renieroid raspailiid genus *Amphinomia*, which also has acanthose structural spicules (Hooper, 1991).

ECHINOCLATHRIA CARTER, 1885

Synonymy

[*Echinoclathria*] Carter, 1884b: 204 (*nomen nudum*). *Echinoclathria* Carter, 1885d: 355 (Not Uriz, 1988: 89).

Type species

Echinoclathria tenuis Carter, 1885d: 355 (by subsequent designation; Burton, 1934a: 562) (holotype BMNH 1886.12.15.147); junior synonym of *Spongia leporina* Lamarck, 1814: 444 (Topsent, 1932a: 101) (holotype MNHN LBIM DT567).

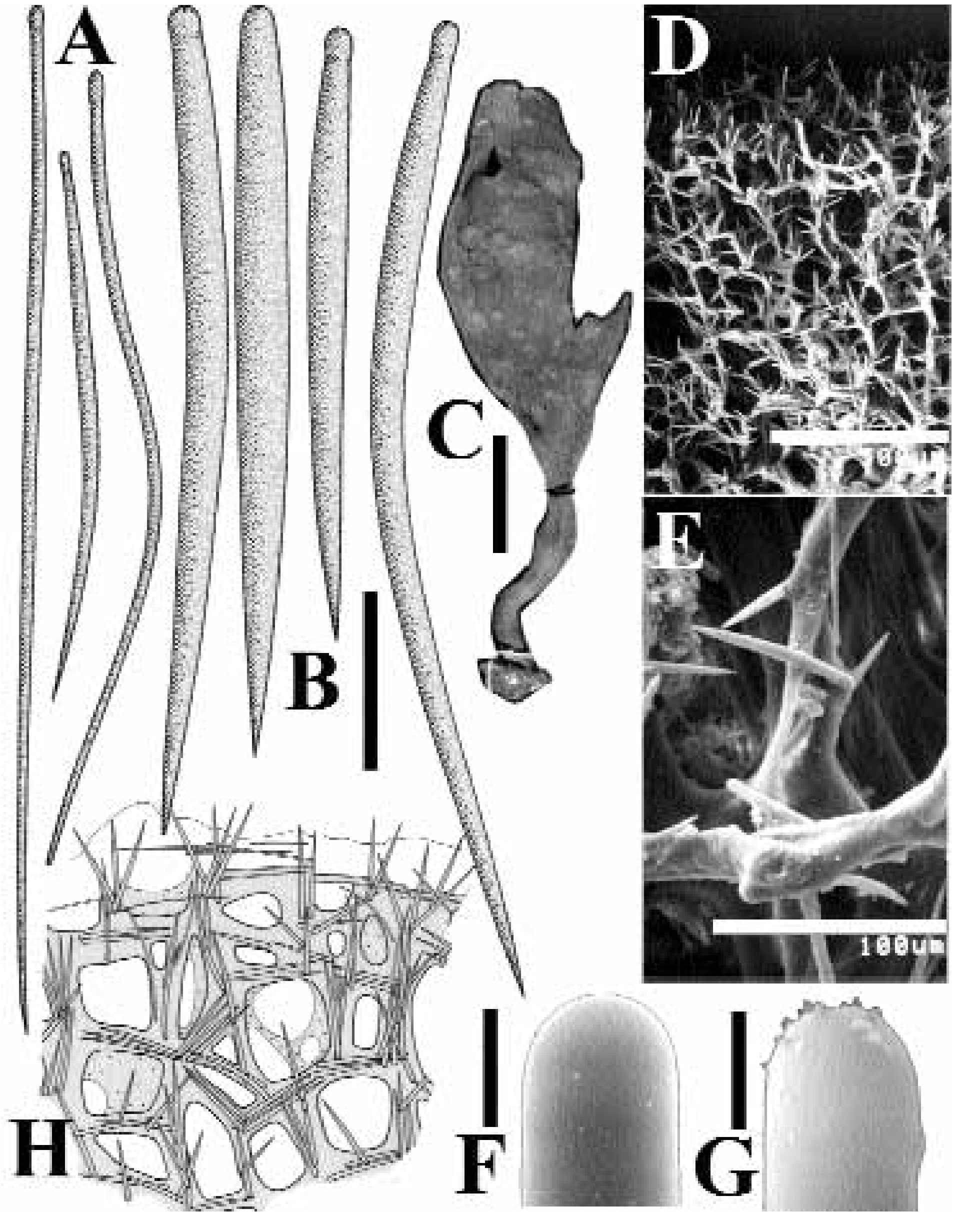

Fig. 19. *Echinoclathria*. A–H, *E. leporina* (Lamarck). A, subectosomal auxiliary subtylostyles. B, principal styles/subtylostyles (coring and echinating fibres) (scale A–B, 25 μm). C, holotype of junior synonym *E. tenuis* (scale 30 mm). D, choanosomal skeleton (scale 500 μm). E, fibre characteristics (scale 100 μm). F, base of larger principal style (protruding through surface) (scale 10 μm). G, base of smaller principal style (in renieroid skeleton; scale 5 μm). H, reconstruction of choanosomal skeleton.

Definition

Ophlitaspongiinae with the choanosomal skeleton consisting of a relatively homogeneous renieroid spongin fibre reticulation cored by smaller, smooth principal spicules and echinated by the same spicules, and a vestigial radial extra-axial skeleton composed of larger principal spicules forming plumose brushes on the external surface.

Diagnosis

Thickly encrusting, bulbous, claviform, bushy, digitate, lamellate, arborescent and flabellate growth forms; with two distinct skeletal components: (1) predominantly renieroid reticulate main skeleton cored by smaller, smooth principal styles, echinated by identical spicules (occasionally absent), typically very well developed spongin fibres sometimes slightly compressed at axis, more openly reticulate towards periphery; and (2) a vestigial radial extra-axial skeleton perched on the external surface, barely extending into choanosome, consisting of larger, smooth principal spicules, with identical geometry to those at core, forming radial or plumose brushes on surface. Ectosomal skeleton with single size class of auxiliary subtylostyle lying paratangentially or embedded perpendicular to surface. Microscleres include toxas and palmate isochelae.

Description of type species

Echinoclathria leporina (Lamarck, 1814) (Fig. 19).

Synonymy. *Spongia leporina* Lamarck, 1814: 444. *Echinoclathria leporina*; Topsent, 1932a: 101. *Ophlitaspongia leporina*; Burton, 1934a: 558. *Echinoclathria tenuis* Carter, 1885d: 355. *Ophlitaspongia tenuis*; Dendy, 1896: 37 (Not *Clathria tenuis* Hentschel, 1911: 377; Parish *et al*., 1991: 56). *Phakellia papyracea* Carter, 1886c: 379. *Antherochalina tenuispina* Lendenfeld, 1887c: 789.

Material examined. Holotype: MNHN DT567 – 'Australian Seas'. Other material. Refer to Hooper (1996a: 462).

Description. Shape persistently very thin, flabellate digits ranging from single elongate planar fans with evenly rounded margins, to bifurcate palmate digits growing in more than one plane, with uneven margins, usually with cylindrical basal stalk; oscules small dispersed over margins of digits; surface even; ectosome microscopically hispid, with larger sizes of principal style/subtylostyle protruding through surface, singly or in brushes, forming vestigial plumose or radial extra-axial skeleton in peripheral region, with a distinct tangential layer of subectosomal auxiliary subtylostyles, in pauci- or multispicular tracts, underlying erect principal spicule brushes; choanosomal skeleton with three components: (1) irregularly isodictyal, slightly compressed axis with single, thickened central core of heavy fibres, vaguely separated into primary, plumose, arborescent, ascending pauci- or multispicular fibres producing radial tracts, and secondary, mostly transverse uni- or paucispicular, regularly renieroid fibres; (2) more open-reticulate renieroid or subrenieroid extra-axial region; and (3) (vestigial) plumose or radial skeleton in peripheral region with spicule tracts increasingly plumose, protruding through fibres, in peripheral skeleton; fibres cored and sparsely echinated by smaller choanosomal principal styles/subtylostyles in choanosomal skeleton (larger in peripheral skeleton); echinating principal spicules located predominantly on primary fibres; fibre anastomoses form rectangular, triangular, or less often oval meshes more compressed in axis than at periphery; megascleres choanosomal principal styles larger in peripheral region than in axis, thick, straight or slightly curved, with smooth, evenly rounded, or slightly tapering subtylote bases, sometimes quasi-oxeote, rarely microspined bases, usually with fusiform points (62–305 × 4–14 μm); subectosomal auxiliary subtylostyles long, thin, straight, slightly curved, or frequently sinuous, with predominantly smooth, occasionally microspined, subtylote bases, hastate points (148–321 × 1.5–4.2 μm); microscleres absent.

Remarks. Sixty nine species names have been referred to or included in *Echinoclathria* (or one of its synonyms) at one time or another, but of these only 29 are appropriately referred here (most of the remainder belonging either to *Holopsamma* or *Clathria*, or are junior synonyms or homonyms of other taxa).

Echinoclathria is similar to *Antho* (*Isopenectya*), as noted above, differing in having only two skeletal components: a relatively homogeneous renieroid choanosomal skeleton composed of smaller, smooth principal spicules; a vestigial radial extra-axial skeleton on the external surface. *Isopenectya* has in addition a renieroid skeleton of acanthose spicules, and the smooth principal styles form longitudinal tracts extending all the way from the axis to the surface and beyond. The difficulty lies in trying to determine affinities of species in either genus with reduced structural characters. For example, *A.* (*I.*) *punicea* Hooper has spined renieroid spicules whereas *E. riddlei* Hooper has smooth renieroid spicules, and both species have a reduced extra-fibre skeleton.

Within *Echinoclathria* most of the variability concerns the development of the extra-fibre skeleton. In some species (e.g., *E. leporina*, *E. confragosa* (Hallmann)) there are obvious size differences between principal styles coring fibres in the choanosome and those protruding through the surface, whereas in others (e.g., *E. nodosa* Carter) there is no obvious size differences between principal styles at the core and those at the periphery, although structurally these are similar to the first condition. In others (e.g., *E. egena* Wiedenmayer, *E. waldoschmitti* de Laubenfels) there is further reduction whereby the extra-fibre skeleton is virtually absent and all spicules are vestigial, poorly silicified. Further discussion of the genus, particularly in relation to its alleged similarities to *Ophlitaspongia* (sensu Howson & Chambers, 1999), are presented below (see *Ophlitaspongia*).

Distribution

Eighteen species are confined to the Indo-west Pacific region, and another eleven have been recorded from the Caribbean, SW Atlantic, Arctic, Mediterranean and W Indian Ocean.

ARTEMISINA VOSMAER, 1885

Synonymy

Artemisina Vosmaer, 1885a: 25. [*Artenisina*] Burton, 1934b: 54 (*lapsus*). *Qasimella* Thomas, 1974: 311 (type species *Qasimella indica* Thomas, 1974: 311 (by original designation) holotype CMFRI T84/1 not seen). Taxonomic decision for synonymy: Hooper (1996a).

Type species

Artemisina suberitoides Vosmaer, 1885a: 25 (by monotypy) (holotype ZMA POR443); junior synonym of *Suberites arciger* Schmidt, 1870: 47 (Burton, 1930c: 528) (schizotype BMNH 1870.5.3.90).

Definition

Ophlitaspongiinae lacking a distinctive choanosomal skeleton or definite spongin fibres, lacking echinating spicules, and having a nearly radial ectosomal skeleton.

Diagnosis

Massive, cushion-shaped, bulbous, clavulate, tubular, digitate and flabellate growth forms; without choanosomal fibres or indefinite fibres, whereas skeletal architecture consists of vaguely ascending longitudinal tracts of spicules bound by abundant collagen, cored by smooth choanosomal principal subtylostyles in a more-or-less confused halichondroid reticulation of vaguely multispicular ascending and scattered transverse megascleres; echinating megascleres absent; subectosomal peripheral skeleton more radially arranged; ectosome membraneous, skin-like, with smooth styles of a single size category protruding through surface, forming paratangential or erect, discrete spicule bundles; microscleres palmate or arcuate isochelae and toxas with smooth or spined points.

Description of type species

Artemisina arcigera (Schmidt, 1870) (Fig. 20).

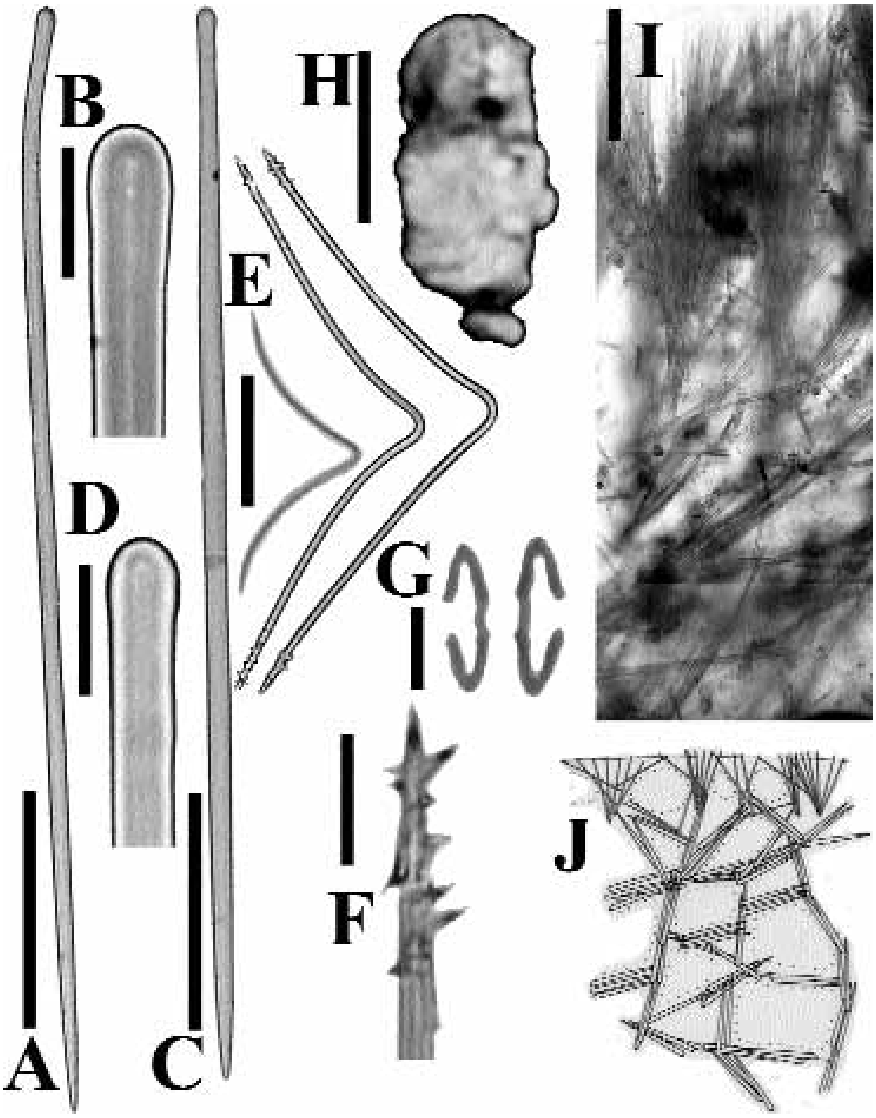

Fig. 20. *Artemisina*. A–I, *A. arcigera*. J, *A. jovis* Dendy. A, choanosomal principal subtylostyle (scale 100 μm). B, base of principal subtylostyle (scale 20 μm). C, subectosomal auxiliary style (scale 50 μm). D, base of auxiliary style (scale 10 μm). E, wing-shaped toxas (scale 50 μm). F, spined tip of toxa (scale 2 μm). G, palmate isochelae (scale 5 μm). H, fragment of holotype BMNH 1870.5.3.90 (scale 30 mm). I, section through peripheral skeleton (scale 250 μm). J, reconstruction of peripheral skeleton.

Synonymy. *Suberites arciger* Schmidt, 1870: 47; *Artemisina suberitoides* Vosmaer, 1885a: 25; *Artemisina arcigera*; Lundbeck, 1905: 110; *Artemisina arcigera*; Burton, 1959b: 42.

Material examined. Holotype: ZMUC (not seen) (fragment BMNH 1870.5.3.90) – Arctic.

Description. Massive, subspherical growth form. Surface skin-like, microscopically hispid, with few raised oscules; texture distinctly stringy. Choanosomal fibres indefinite or absent, overall architecture plumo-reticulate, nearly halichondroid in places, composed of multispicular ascending and paucispicular transverse tracts of choanosomal principal styles, bound together with collagen. Echinating megascleres absent. Ectosomal skeleton plumose, composed of single category of subectosomal auxiliary styles forming discontinuous palisade of discrete brushes. Megascleres smooth choanosomal principal subtylostyles (416–624 × 9–12 μm) and smooth fusiform subectosomal auxiliary styles or subtylostyles (275–390 × 8–16 μm). Microscleres palmate isochelae (8–14 μm), and wing-shaped toxas with spinous extremities (55–280 × 2–4 μm).

Remarks. Defining *Artemisina* in phylogenetic terms is most difficult. The taxon has no real distinctive features, although it differs from other Microcionidae in lacking a distinctive choanosomal skeleton or definite spongin fibres (also found in the nominal genus *Qasimella* Thomas which Hooper, 1996a synonymised with *Artemisina*), lacking echinating spicules, and having a nearly radial ectosomal skeleton reminiscent of some *Ceratopsion* (Raspailiidae; Hooper, 1991). These characteristics, two of which might be interpreted as reductions or secondary losses and the third as a convergence, are the only definable morphological apomorphies. Moreover, ectosomal structure varies between several species, ranging from the typical condition composed of erect brushes (e.g., *A. arcigera*) to a tangential layer of spicules in criss-cross fashion (e.g., *A. melana* Van Soest). This variability is equivalent to the *Mycale* subgenera *Carmia* and

Aegagropila, respectively (e.g., Topsent, 1924). At least one species lacks a specialized ectosomal skeleton completely (e.g., *A. transiens* Topsent).

Some species of *Artemisina* have honeycombed reticulate growth forms, approaching the characteristic *Holopsamma* morphology, but there is no consistency or pattern of gross morphologies amongst *Artemisina*, and in any case it is unlikely that the genus can be defined on that basis. De Laubenfels (1936a) and Ristau (1978b) suggested that *Artemisina* could be characterized by the absence of echinating acanthostyles and by the presence of spinous extremities on toxas. Neither character has much systematic value at the generic level. In the present interpretation echinating acanthostyles represent the retention of an ancestral character, in which case their presence or absence does not constitute a valid reason to define a phylogenetic grouping, and in any event they occur and disappear throughout numerous microcionid and raspailiid taxa. Similarly, toxas with spinous extremities are also known to occur in many Microcionidae, including the type species *Clathria compressa* Schmidt (and other species *Microciona spinarchus* Carter & Hope, *M. coccinea* Bergquist, *M. rubens* Bergquist, *Eurypon acanthotoxa* Stephens, *M. spinatoxa* Hoshino, *Stylostichon toxiferum* Topsent, *Labacea juncea* Burton, *Plocamia ridleyi* Hentschel, and *Ophlitaspongia thielei* Burton). They also occur in genera which have an ectosomal structure consistent with the Myxillidae (e.g., *Melonchela clathrata* Koltun), and consequently it is not parsimonious to base a definition of *Artemisina* on this feature. Similarly, several other species of *Artemisina* have smooth toxas (e.g., *A. melana*), and one (*A. archegona* Ristau) has oxeote toxas similar to *Paratenaciella microxea* Vacelet and Vasseur.

Thus, in the broad sense *Artemisina* contains a heterogenous assemblage of species, which prompted Burton (1930c) to divide the group into three sections based on the number of megasclere categories present. The simplest forms have only one category of spicule (choanosomal principal megascleres; e.g., *A. transiens* Topsent); the typical form has two categories of megascleres (larger choanosomal principal styles and smaller subectosomal auxiliary styles; e.g., *A. arcigera*); and the third form has an incompletely differentiated series of three megasclere types (two choanosomal spicules and one subectosomal spicule; *A. plumosa* Hentschel). In all these forms species are only really united in their lax choanosomal skeletal structure.

Distribution

Predominant in colder waters including Antarctica, Arctic, Greenland, Iceland, New Zealand, NE and SW Atlantic, NW, NE and SW Pacific, but also recorded from Mediterranean, Caribbean, central Indian Ocean and SW Pacific.

OPHLITASPONGIA BOWERBANK, 1866

Synonymy

Ophlitaspongia Bowerbank, 1866: 14, 378. (Not *Ophlitaspongia* of most authors).

Type species

Ophlitaspongia papilla Bowerbank, 1866: 378 (by original designation).

Definition

Ophlitaspongiinae with isodictyal reticulate spongin fibre skeleton arising from a hymedesmioid basal fibre skeleton; mineral skeleton is predominantly or exclusively plumose, with no or very few spicules coring transverse fibres; echinating megascleres absent although principal subtylostyles protrude through fibres in plumose arrangement; and megascleres are exclusively smooth subtylostyles.

Diagnosis

Encrusting growth form; with an isodictyal reticulate, ladder-like, spongin fibre skeleton composed of parallel ascending fibres with regular cross-connecting fibres arising from a hymedesmioid basal layer of spongin fibre. Mineral skeleton exclusively plumose, with only ascending fibres cored by plumose columns of entirely smooth principal subtylostyles, with very few or no spicules coring the transverse connecting fibres. Tracts of principal subtylostyles protrude through ascending fibres, diverging towards the surface. True echinating spicules absent but principal styles project from fibres as echinating spicules and/or in spicate arrangement. Microscleres include toxas and palmate isochelae (the latter absent in the type species).

Description of type species

Ophlitaspongia papilla Bowerbank, 1866 (Figs 3H, 21).

Synonymy. *Ophlitaspongia papilla* Bowerbank, 1866: 14; ? *Clathria papilla*; Schmidt, 1870: 77; *Echinoclathria papilla*; Hanitsch, 1894a; *Ophistospongia papilla*; Gray, 1867a: 515.

Material examined. Holotype: BMNH 1910.1.1.395 – Vazon Bay, Guernsey.

Description (partly from Howson & Chambers, 1999, and re-examination of type material). Thinly encrusting, with firm elastic texture, smooth and finely hispid surface with regularly arranged oscules flush with surface, lacking subdermal drainage canals. Ectosomal skeleton consists of sparse paratangential bundles of auxiliary subtylostyles usually at the ends of ascending choanosomal tracts, and also scattered tangential to the surface together with toxas. Choanosomal skeleton consists of parallel columns of well developed spongin fibres arising from a hymedesmioid basal fibre skeleton, with ascending fibres regularly interconnected by transverse ones, forming a ladder-like isodictyal reticulation. Ascending fibres cored by plumose tracts of choanosomal principal subtylostyles whereas transverse fibres are rarely cored. True echinating megascleres absent. Choanosomal spicule tracts protrude through the ectosome in sparse bundles, and in some places they can be said to be ‘echinating’ whereas in others merely ‘spicate’ (i.e., protruding from fibres in plumose fashion). Mesohyl is highly collagenous and contains scattered auxiliary subtylostyles and toxas. Megascleres consist choanosomal principal subtylostyles, completely smooth, often curved, widest at the centre and tapering towards both terminations, with a well developed subtylote swelling and constricted ‘neck’ (64–143 × 5–13 μm). Subectosomal auxiliary subtylostyles short, thin, straight, entirely smooth, with well developed subtylote basal swelling (71–167 × 2–3 μm). Microscleres consist of oxhorn to wing-shaped toxas in a single but wide-ranging size class (64–127 × 2–4 μm); chelae absent.

Remarks. The history of *Ophlitaspongia* is complex and tortuous, based largely on misidentifications, misdiagnoses and

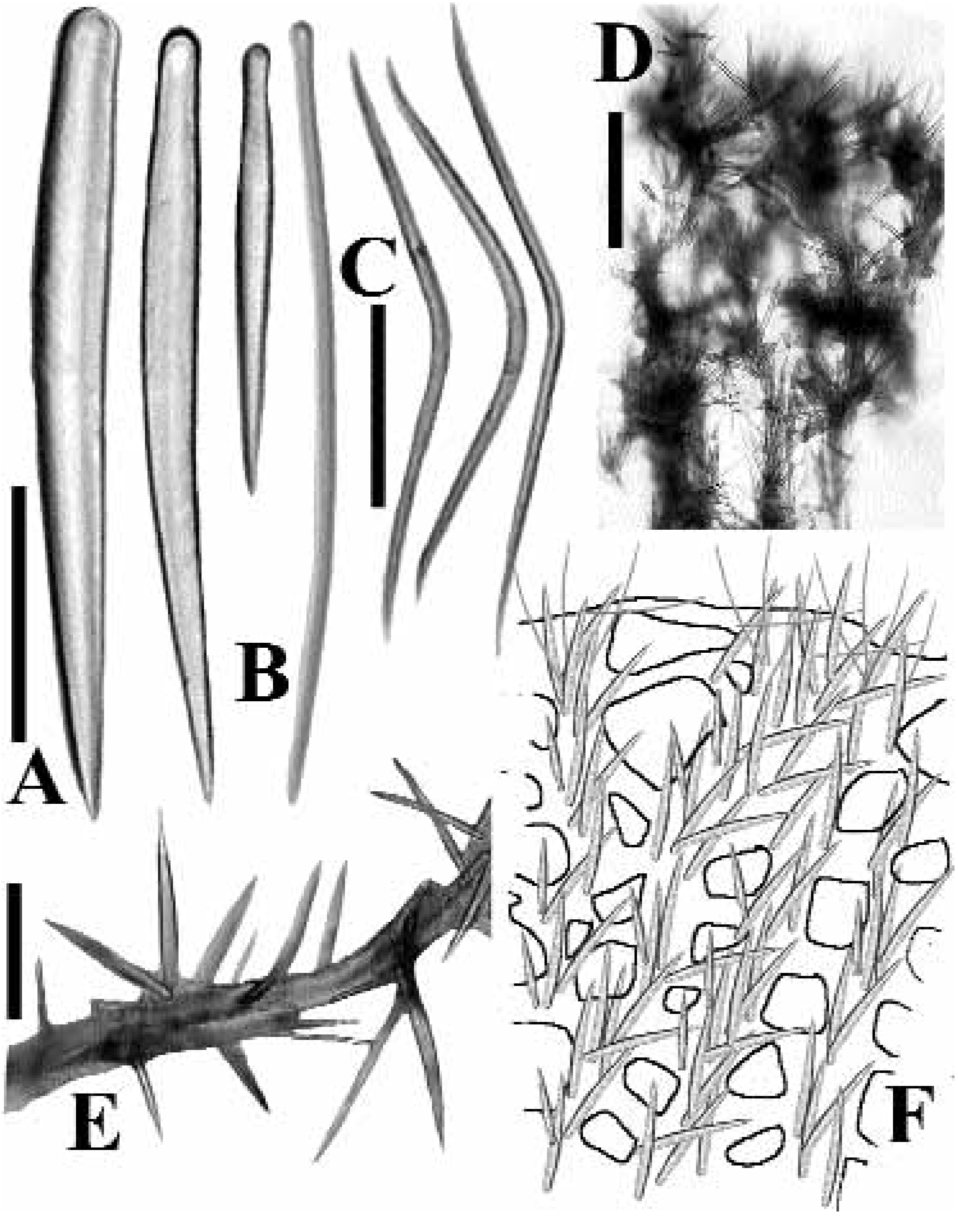

Fig. 21. *Ophlitaspongia*. A–F, *O. papilla* Bowerbank. A, choanosomal principal subtylostyles. B, subectosomal auxiliary subtylostyle (scale A–B, 50 μm). C, oxhorn and wing-shaped toxas (scale 50 μm). D, section through peripheral skeleton (scale 200 μm). E, fibre characteristic (scale 100 μm). F, skeletal reconstruction.

incorrect assumptions concerning type material. The genus was erected by Bowerbank (1866) with *O. papilla* nominated as the type species (with holotype BMNH 1910.1.1.395). Simpson (1968) subsequently proposed that *O. papilla* was a synonym of *O. seriata* (Grant, 1826c; with alleged holotype being BMNH 1847.9.7.14; but see below), which therefore became the senior name for the type species, and which was also reportedly cytologically identical to *Microciona atrasanguinea* Bowerbank, 1862b (the type species of *Microciona* Bowerbank, 1863; holotype BMNH 1930.7.3.225). Thus, under this interpretation, adopted by many contemporary authors (including Hooper, 1996a), *Microciona* became the senior-most available name for a group of largely encrusting taxa characterised in having smooth echinating megascleres and hymedesmioid or microcionid skeletal architecture. However, the genus was recently resurrected by Howson & Chambers (1999) without any full or appropriate discussion of the significance or implications of its important morphological characters within the Microcionidae, and consequently a detailed resumé of these justifications is provided here.

Howson & Chambers (1999) discovered that the concept of "*O. seriata*" of authors was based on a false premise. They rediscovered Grant's original slide preparation of *Spongia seriata* (UCLZ B73; '*Spongia seriata* Gr "variety of *S. papillaris* ?" ') which they found was identical to *Halichondria panicea* Pallas (i.e., Grant's, 1826c diagnosis of *S. seriata* was incorrect). They negated the long-held assumption that Johnson's (1842) material (BMNH 1847.9.7.14) was the holotype of *S. seriata* (e.g., Simpson, 1968; see Hooper, 1996a: 62); and that Johnston (1842) had in his possession material of a new species (BMNH 1847.9.7.14), which he misidentified as Grant's taxon. Johnson's (1842) material is identical to Bowerbank's (1866) material of *O. papilla* (BMNH 1910.1.1.395), and therefore, *O. papilla* Bowerbank becomes the next available species name for the concept of "*O. seriata*" *sensu* Johnston and authors, and the type species of *Ophlitaspongia*.

Similarly, comparisons between the holotype of *Microciona atrasanguinea* (BMNH 1930.7.3.225) and *Ophlitaspongia papilla* show that Simpson (1968) was incorrect in merging the two taxa, and in his conclusion that *Ophlitaspongia* was a synonym of *Microciona*. The two species are not at all closely related in their skeletal details, virtually having only their encrusting growth forms in common. Not only was spicule morphology very incongruent, but also skeletal structure, the number and distribution of spicule categories present, and spicule sizes differed significantly between the two species. This finding therefore raises questions concerning the systematic value of Simpson's (1968) unique cytological data used at the supraspecific level given its flawed taxonomic basis.

Differences between *Ophlitaspongia* and *Microciona* are clear from their respective type material, and these descriptions (see above) form the bases of the respective diagnoses. *Ophlitaspongia* has a very prominent spongin skeleton that forms an isodictyal reticulation, ranging from a hymedesmioid basal fibre skeleton to near the surface, whereas the mineral skeleton is exclusively plumose, principal spicules coring only ascending fibres and no or only very few spicules coring the transverse fibres; there are no true echinating spicules (although principal subtylostyles protrude through fibres in plumose arrangement); and megascleres are exclusively smooth subtylostyles. By comparison, *Microciona* has a plumose, ascending (i.e., non-reticulate) spongin fibre skeleton with fibre nodes arising from a hymedesmioid spongin base ('microcionid' architecture), and adjacent fibre nodes do not form a reticulation (i.e., they are exclusively plumose). The spicule skeleton consists of choanosomal principal subtylostyles (larger, smooth or basally spined styles) forming ascending plumose tracts usually perched on the ends of spongin fibre nodes, well differentiated from smaller echinating (acantho-) styles which are dispersed over the basal layer of spongin and ascending fibre nodes, individually or in bundles. Both genera have smooth wing-shape toxas, and smooth auxilliary subtylostyles forming an extra-fibre and/or dermal skeleton.

At present *Ophlitaspongia* is restricted to two species in the NE Atlantic (Howson & Chambers, 1999). Although other authors have reported alleged populations of *O. papilla* (or *O. seriata sensu* Johnson) from New Zealand (Bergquist *et al*., 1968, 1969, 1973) and South Africa (Lévi, 1963), it is highly unlikely these are conspecific with the NE Atlantic species given the reported differences between the highly disjunct populations. However, this assumption is difficult to test given that no voucher material has been located (NMNZ, AMS or MNHN). The NZ species was never formally described, although Bergquist & Sinclair (1968) stated that 'there is … no doubt that this sponge is conspecific with *O. seriata* Bowerbank from Britain'. However, from the brief description provided by Hogg (1967) it appears that the NZ species is not related to *O. papilla*, but closer to *Microciona aceratoobtusa* (i.e., having smaller smooth echinating spicules clearly differentiated from the larger principal spicules in fibres; the mineral skeleton is plumose as is the fibre skeleton, with plumose bulbous fibre nodes but no reticulations between fibres). It is clear that Hogg (1967) did not re-examine any type material, and this New Zealand population is more appropriately referred to *Microciona*. Levi's (1963) material of '*O. seriata*' from South Africa probably also represents a separate species of *Microciona*, with differentiated coring and echinating subtylostyles (albiet both smooth), although the skeleton reportedly consists of a reticulate network of horny fibres (reminiscent of *Ophlitaspongia s.s.*). Lévi states that the South African and North Atlantic populations are 'in all points identical', but this has yet to be corroborated through re-examination of relevant type material (although it is highly probable that Lévi's voucher material does not exist).

Many other records of *Ophlitaspongia* species in the literature can also be referred to *Echinoclathria*. A comparison between the emended definition of *Echinoclathria* (Hooper, 1996a, differing from previous concepts of the genus; e.g., Hallmann, 1911, 1912), *Clathria* and *Microciona* (as revised by Hooper, 1996a), and *Ophlitaspongia* (as revised by Howson & Chambers, 1999, and summarised here) shows each to have substantially different fibre structure, skeletal structure and distribution of spicule types within fibres. There is no doubt that each serves its purpose to group like-taxa, but it is still equivocal at what level they diverge (genus or subgenus). *Echinoclathria* has two distinct skeletal components: (1) an evenly renieroid reticulate skeleton, including a slightly compressed axis, with all axial fibres cored by smaller principal choanosomal styles and echinated by the same principal choanosomal styles; (2) the extra-axial or peripheral skeleton is radial, vestigial, with the largest principal spicules perched on the outer radial fibres and projecting through the surface individually or in bundles; in addition to this there are also auxiliary styles or subtylostyles tangential or erect on the surface. By comparison, *Ophlitaspongia* has a homogeneous isodictyal reticulate fibre skeleton in both the basal and peripheral regions, with a compressed layer of spongin fibres lying on the substrate and regularly reticulate spongin fibres arising from this base, producing a regular isodictyal fibre network divided into ascending primary and secondary transverse elements. Mostly only the primary ascending fibres are cored by principal choanosomal spicules producing a strictly plumose mineral skeleton; there is no differentiated radial skeletal component in the periphery (as in *Echinoclathria*); there are no true echinating spicules (as in *Echinoclathria*); and whereas the fibre skeleton is reticulate the mineral skeleton is plumose.

In resurrecting *Ophlitaspongia*, and recognising these differences between it and *Echinoclathria*, it could be argued that some of the species described by Hooper (1996a) may be conceivably included in it. However, these arguments are rejected as follows. (1) *Echinoclathria egena* Wiedenmayer, 1989 lacks true echinating spicules, and its skeletal strucutre is dendro-reticulate. However, although spicules coring the transverse connecting fibres are reduced, as compared to those in ascending fibres at least, many reticulate tracts are definitely present such that overall mineral skeletal structure remains reneiroid reticulate (certainly not plumose as in *Ophlitaspongia*). Moreover, ascending tracts of spicules are confined entirely to within the axes of fibres, not diverging, protruding through fibres or as plumose columns as in *Ophlitaspongia*. This species should, therefore, be left in *Echinoclathria* and the alleged similarities between it and NE Atlantic *Ophlitaspongia* species should be attributed to (i.e., hypothesised as) a secondary loss of connecting transverse spicule tracts, with the consequent reduction in renieroid structure, and secondary loss of echinating spicules. (2) *Echinoclathria subhispida* Carter, 1885d also has few transverse connecting spicule tracts, producing a nearly radial mineral skeleton. But true echinating spicules are present; spongin fibres are well compressed in the axial skeleton and clearly diverging in the peripheral region (not homogeneously isodictyal renieroid as in *Ophlitaspongia*); spicules are confined to straight tracts in the axes of fibres and not diverging-plumose as in *Ophlitaspongia*. This species should also be retained in *Echinoclathria*, with the assumption that transverse spicule tracts have again been secondarily lost. (3) Some of the N Atlantic and Mediterranean species included in *Echinoclathria* by Hooper (1996a: 480) are speculative, such as *E. beringensis* (Hentschel, 1929), *E. hjorti* Arnesen, 1920, *E. translata* (Pulitzer-Finali, 1977), but these do not clearly fit into the revised concept of *Ophlitaspongia* either (Howson & Chambers, 1999), and their precise assignment requires re-evaluation. Earlier interpretations of *Echinoclathria*, conceived (and grossly misinterpreted) mainly by Hallmann (1912) are invalid, as unfortunately was Wiedenmayer's (1989) assessment of the genus. *Echinoclathria* as redefined by Hooper (1996a) includes only those species agreeing with the type species, *E. leporina*, with most others redistributed to *Holopsamma, Echinochalina* or *Clathria* (*Wilsonella*). In my opinion none of the *Echinoclathria* described by Hooper (1996a) should be transferred or returned to *Ophlitaspongia* (with the possible exception of these three N Atlantic and Mediterranean species).

Wiedenmayer (1989: 59) provided a succinct discussion of *Ophlitaspongia* (*sensu stricto*), *Ophlitaspongia* (of authors) and *Echinoclathria*. He noted that Simpson (1968) merged *Ophlitaspongia* in *Microciona* based on re-examination of 'topotypes' of the type species *O. papilla.* Wiedenmayer (1989) upheld Simpson's decision (for no apparent reason, apart from the fact that Simpson had apparently already done the ground-work of re-examining specimens collected from the vicinity of the type locality, and therefore there was no further reason to question his conclusions). Wiedenmayer was followed by several other authors, including Hooper (1996a), correctly noting that most species of *Ophlitaspongia* were more closely related to species of *Echinoclathria* or *Echinochalina* (i.e., renieroid reticulation, echinating spicules, etc., as defined above), whereas the type species *O. papilla* was clearly different. Of contemporary authors Levi (1960b) and Van Soest (1984b) provided virtually monospecific definitions for *Ophlitaspongia*, which in retrospect they were correct and it is this concept which is maintained here (i.e., isodictyal reticulate fibre skeleton, plumose mineral skeleton, homogeneous coring spicules, no echinating spicules) and not one which includes *Microciona* or *Echinoclathria* as potential synonyms.

Distribution

Restricted to the NE Atlantic.

SIGMEURYPON TOPSENT, 1928 (*INCERTAE SEDIS*)

Synonymy

Sigmeurypon Topsent, 1928c: 59.

Type species

Microciona fascispiculiferum Carter, 1880b (by original designation).

Definition

? Microcionidae with hymedesmioid spongin fibres cored by erect long styles and acanthostyles, with a tangential ectosomal skeleton composed of oxeas (? anisoxeas) and scattered raphides (? raphidiform toxas) and sigmas (? chelae).

Diagnosis

Thinly encrusting growth form. Surface even and hispid. Choanosomal skeleton basally compressed uncored spongin fibres lying on the substrate and a thin mesohyl containing raphides and sigmas. Subectosomal skeleton with long smooth styles embedded in basal spongin, standing perpendicular to substrate and protruding through ectosome. Echinating acanthostyles present and erect on substrate, interspersed with choanosomal megascleres. Ectosomal skeleton with protruding styles from choanosome and bundles of raphides lying tangential to surface. Structural megascleres styles and acanthostyles. Microscleres raphides occurring singly or in bundles (trichodragmata).

Description of type species

Sigmeurypon fascispiculiferum (Carter, 1880b) (not illustrated)

Synonymy. *Microciona fascispiculiferum* Carter, 1880b: 44. *Sigmeurypon fascispiculiferum*; Hooper, 1991: 1394.

Material examined. None. Holotype: LFM (destroyed).

Description (from Carter, 1880b). Thinly encrusting plate-like growth form. Surface even and hispid. Ectosomal skeleton with bundles of raphides (trichodragmata) (280 µm long) lying tangential to the substrate and also forming erect brushes. Choanosomal skeleton basally compressed hymedesmioid fibres with rhabdose bases of long styles (980 × 25 µm) and echinating acanthostyles (70 µm long) erect on the substrate, with the former projecting a long way through the surface; microscleres raphides and (?) sigmas (8 µm chord length) dispersed throughout mesohyl. Structural megascleres subectosomal styles, ectosomal oxeas and acanthostyles. Microscleres ? sigmas and raphides occurring singly or in bundles (trichodragmata).

Remarks. There is no surviving material of *M. fascispiculiferum*. The holotype was destroyed in the LFM during World War II (Ms Shirley Stone, pers. comm.), and no spicule preparations were discovered in the BMNH. Therefore, the type species of *Sigmeurypon* is only known from Carter's (1880b) brief original description. It is possible that raphides recorded by him are raphidiform toxas, which are known to occur in several microcionids (e.g., Hooper *et al*., 2000). Furthermore, it is also possible that 'sigmas' recorded by Carter (1880b) in this species are actually examples of sigmoid isochelae. These possibilities prompted de Laubenfels (1936a: 110) to refer this species to his genus *Damoseni* in the family Microcionidae, but it is not possible to confirm or refute those ideas without checking type material. If these assumptions are correct then it is probable that it is no more than a thinly encrusting *Clathria* (*Microciona*). However, the species and genus are *incertae sedis* with no resolution possible without new material.

Distribution

Monotypic, from Sri Lanka.