

## Family Raspailiidae Hentschel, 1923

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Raspailiidae Hentschel (Demospongiae, Poecilosclerida), including Euryponidae Topsent, contains 60 nominal genera of which 19 are valid (one *incertae sedis*), with 7 subgenera, and approximately 270 named species worldwide, mainly from shallow waters and a few from abyssal depths. Species have a typically hispid surface, with genera differentiated mainly on the basis of three morphological characters: skeletal architecture ranging from axial compression to reticulate, plumo-reticulate or plumose skeletons; the presence or absence of a specialized ectosomal skeleton (apomorphic for the family, whereby small ectosomal megascleres form bouquets surrounding the longer choanosomal or subectosomal megascleres that penetrate the surface); and geometric modifications to echinating megascleres (with about 15 distinct morphologies recognised). Five new subfamilies are established, based on geometry of echinating megascleres and skeletal structure.

**Keywords:** Porifera; Demospongiae; Microcionina; Raspailiidae; *Amphinomia*; *Aulospongius*; *Axechina*; *Cantabrina*; *Ceratopsion*; *Cyamon*; Cyamoninae subfam. nov.; Echinodictyinae subfam. nov.; *Echinodictyum*; *Ectyoplasia*; *Endectyon*; *Eurypon*; *Hymeraiphia*; *Lithoplocamia*; Plocamioninae subfam. nov.; *Plocamione*; *Raspaciona*; *Raspailia*; Raspailiinae; *Rhabdeurypon*; *Thrinacophora*; Thrinacophorinae subfam. nov.; *Trikentrion*; *Waltherarndtia*.

### DEFINITION, DIAGNOSIS, SCOPE

#### Synonymy

Raspailiidae Hentschel, 1923. Euryponidae Topsent, 1928c.

#### Definition

Microcionina with a special category of smaller ectosomal styles, oxeas or anisoxeas forming discrete bouquets around the protruding larger styles or oxeas.

#### Diagnosis

Encrusting, massive, lobate, fan-shaped or branching growth forms, usually with a very hispid surface. Specialised ectosomal skeleton typically present, consisting of small thin styles, oxeas or anisoxeas forming bouquets around long styles or oxeas that penetrate the surface. Choanosomal skeletal structure is typically reticulate with a compressed axial region and plumo-reticulate extra-axial (peripheral) skeleton, but may range from hymedesmioid and microcionid in encrusting taxa, to plumose, radial or evenly reticulate (non-compressed) skeletons in other taxa. Spongin fibres usually completely enclose coring spicules (choanosomal styles, oxeas or both). Echinating acanthostyles (or modified styles) echinate fibres, standing perpendicular to them. Microscleres are usually absent, although a few genera have raphides in bundles (trichodragmata). Where known, reproduction is oviparous and probably typical for this family.

#### Scope

Sixty generic names have been included in the family at one time or another, but only nineteen of these are valid (Hooper, 1991, and this work), one of which is *incertae sedis*, and with seven subgenera recognised. Hooper (1991) also included *Tethyspira* and *Sigmeuryon* as *incertae sedis* in Raspailiidae whereas these are

referred to Dictyonellidae (Halichondrida) and Microcionidae, respectively (see chapters by Van Soest *et al.*, and Hooper, this volume).

Approximately 270 species have been published worldwide, 56 from Australia alone, with a potential worldwide fauna of about 500 species given that many undescribed species have been discovered and many more probably await discovery, particularly thinly encrusting taxa (Hooper, unpublished collections). For example, *Hymeraiphia* is prevalent on soft sediments of deeper coastal waters in the North Atlantic with few records from elsewhere, so it is possible that there are many similar species throughout the other ocean systems.

#### History and biology

Hentschel's (1923) initial concept of Raspailiidae allowed for the inclusion of species with meniscoid microscleres (chelaes, sigmas), whereas Topsent (1928c) restricted the family to include only species lacking microscleres or having only raphides. The synonymy of Euryponidae and Raspailiidae was proposed by Bergquist (1970: 31), although Lévi (1973: 608) subsequently recognised both as distinct families. Both families have a 'raspailiid' ectosomal skeleton, considered here to be their primary apomorphy, whereas differences in their respective skeletal structures (hymedesmioid versus axially compressed, reticulate skeletons) do not warrant their recognition at the family level. Definitions of the family were progressively developed by Bergquist (1978: 167), Hartman (1982: 647) and Hooper (1991: 1185), and the major characters used to differentiate genera were revised by Hooper (1991) and Hooper *et al.* (1999).

The higher systematics of the Raspailiidae has been debated by several authors (e.g., Ridley & Dendy, 1887; Topsent, 1894c, 1928c; Dendy, 1905; Vosmaer, 1912; Wilson 1921; Bergquist, 1970; Hooper, 1991). It was initially included in Poecilosclerida (Hentschel, 1923; Topsent, 1928c) but subsequently referred to Axinellida on the basis that many taxa had compressed axial skeletons and clearly differentiated radial, plumose or plumo-reticulate

extra-axial skeletons, and where known, species were thought to be oviparous (e.g., Bergquist, 1970, 1978; Hartman, 1982; Wiedenmayer, 1989). Hooper (1991) and Hooper *et al.* (1992) subsequently returned the family to Poecilosclerida based on morphological and biochemical similarities to the Microcionidae (Hooper, 1991), and it now forms one of the four families of Microcionina (Hajdu *et al.*, 1994a). The presence of homologous echinating acanthostyles in both Raspailiidae and Microcionidae is an obvious morphological clue to their common ancestry, but this feature is interpreted as representing the retention of an ancestral character state, and as such the group cannot be defined solely on this basis.

The alternative classification, in which Raspailiidae is assigned to a now more-or-less defunct concept of 'Axinellida', rests solely on supposed homologies in skeletal architecture between representative taxa (i.e., the possession of a differentiated axial and extra-axial skeleton and a compressed axial skeleton – termed here an 'axinellid' skeleton). However, it is obvious from examination of all Raspailiidae genera that the family demonstrates a wide range of architectural types, and many of these structures show only vague or no similarities with 'axinellid' forms at all. In fact the reverse is true: many skeletal types in the family clearly show structural relationships with other poecilosclerids. For example, the raspailiid genus *Aulospongius* is peculiar in having tubular, plumose, skeletal fibre bundles (Hooper, 1991; Hooper *et al.*, 1999), whereas identical fibres are known for the *Clathria* 'parthena' species group of Microcionidae (Hooper, 1996a). Similarly, raspailiids with typical 'axinellid' skeletal structure (e.g., *Raspailia* (*Raspailia*) *vestigifera*) have structural counterparts in the Microcionidae (e.g., *Clathria* (*Axosuberites*) *canaliculata* which has a distinctive compressed axis, plumose-radial extra-axis, in addition to isochelae microscleres). Several other homologies between Raspailiidae and Microcionidae are also apparent. Incorporation of detritus into spicule-bearing fibres is a common trait amongst the Poecilosclerida (e.g., *Clathria* (*Wilsonella*)), and it is also known in several Raspailiidae (e.g., *Raspailia* (*Clathriodendron*), *Echinodictyum arenosum*). Several raspailiids have completely lost their echinating megascleres (e.g., *Raspailia* (*Parasyringella*), *Ceratopsion*, *Thrinacophora*), and this is also a feature of some microcionids (e.g., *Clathria* (*Axosuberites*), *C. (Isociella)*). One raspailiid (*Aulospongiella monticularis*) incorporates echinating acanthostyles secondarily into fibres (Hooper, 1991; Hooper *et al.*, 1999), which is also a feature peculiar to the microcionid *Clathria* 'phorbasiformis' species group (Hooper, 1996a). Some raspailiids lack the specialized ectosomal structure characteristic of the family (e.g., *Raspailia australiensis*), and have instead a continuous crust of spicules also seen in a particular group of Microcionidae (*Clathria* (*Thalysias*)). Thus, morphological comparisons alone suggest that raspailiids are more closely related to Poecilosclerida, such as Microcionidae, than they are to axinellids, such as Hemiasterellidae and Axinellidae, and there is also some biochemical support for this idea (e.g., Hooper *et al.*, 1992).

Revisions of New Zealand, Australian and New Caledonian species were undertaken by Bergquist (1970), Hooper (1991), and Hooper & Lévi (1993), respectively. Several biochemical characteristics of the family have been described by Hooper *et al.* (1992), who noted a disproportionately high level of antibiotic activity against several human pathogens, as compared to other families of sponges sampled.

Species are widely distributed, from shallow-waters, where they are more diverse (Hooper, 1991), to at least 2460 m depth (Hartman, 1982). Shallow water species have been reasonably well

surveyed in the North Atlantic and Mediterranean (e.g., Topsent, 1928c; Vosmaer, 1935; Boury-Esnault & Lopes, 1985), Caribbean (see review in Hooper *et al.*, 1999), southeast Indonesian (Hentschel, 1912), New Zealand (Bergquist, 1970), Australian (Hooper, 1991) and New Caledonian regions (Hooper & Lévi, 1993), although many other publications record one or few species from diverse localities. Deeper-water species have been infrequently recorded by Ridley & Dendy (1887) and Lévi & Lévi (1983b).

#### Differences with similar families

Raspailiidae shares the symplesiomorphy of echinating acanthostyles with other families of Microcionina. Furthermore, some taxa (e.g., *Raspailia s.s.*) show identical construction to some microcionids (e.g., *Axociella s.s.*), and it has been suggested (Hooper, 1991) that a compressed axial skeleton, and differentiated axial and extra-axial skeletons (used to define 'axinellids') has been independently acquired several times throughout the Porifera. This interpretation de-emphasises the primary importance of skeletal structure in sponge systematics. This, together with chemotaxonomic evidence (Hooper *et al.*, 1992) was used to justify the return of Raspailiidae to the Poecilosclerida (Hooper, 1991), although these data require corroboratory support from more contemporary molecular studies.

A generic classification of the Raspailiidae centres around three principal diagnostic features: skeletal architecture, presence or absence of a specialized ectosomal skeleton, and modifications to echinating megascleres (with about 15 distinct morphologies, several apomorphic for various genera). These many examples, comparing microcionid and raspailiid species with similar features, support the hypothesis that these two families are most closely related amongst the Microcionina.

#### Previous reviews

Bergquist (1970), Lévi (1973), Hooper (1991), Hooper *et al.* (1999).

#### PROPOSAL FOR SUBDIVISION OF RASPAILIIDAE

Phylogenetic relationships between genera of Raspailiidae were postulated by Hooper (1991), recognising three major groups (based on skeletal structure) and six subgroups based on differences in spicule geometries forming their choanosomal (axial), subectosomal (extra-axial) and ectosomal skeletons, in addition to echinating spicule morphologies. Synapomorphy for all these groups is the possession of a specialized (raspailiid) ectosomal skeleton, and symplesiomorphy is the possession of echinating acanthostyles: most but not all species have these features, and where absent their obvious affinities to Raspailiidae are indicated by one or more other features shared with other raspailiids.

Five of these six subgroups are elevated here to subfamilies (based predominantly on acanthostyle geometry and skeletal structure), whereas one subgroup is poorly resolved and incorporated in the nominotypical subfamily. Subgroups delineated by Hooper (1991) are as follows.

'Raspailoids', including *Raspailia*, *Ectyoplasia* and *Endectyon*, with a noticeably compressed axial skeleton composed of criss-cross reticulation fibres and/or spicules. Echinating acanthostyles are microcionid-like club-shaped with small granular

or erect spines, ranging to club-shaped with strongly recurved or clavulate spines on the basal and distal ends of spicules, and two subgenera have echinating acanthorhabdostyles. One species has raphides in trichodragmata. This subgroup is elevated to Raspailiinae Hentschel, 1923.

'Axinelloids', including *Ceratopsion*, *Axechina* and *Thrinacophora*, lacking echinating megascleres altogether. Two genera have raphides in trichodragmata. Differentiation between axial and extra-axial skeletons is more prominent. This subgroup is elevated to Thrinacophorinae subfam. nov.

'Triaenoids', including *Trikentrion* and *Cyamon*, having echinating spicules modified to sagittal mono-, di-, tri-, tetra- or pentactinal acanthose megascleres (acanthoplagoitriaenes). These taxa share other common features including the possession of only a slightly compressed axial skeleton composed of plumo-reticulate spicule tracts forming more-or-less rectangular, renieroid meshes, or one that is reduced to a basal spongin layer in encrusting species with erect spicules in hymedesmioid arrangement. One species has raphides in trichodragmata. This subgroup is elevated to Cyamoninae subfam. nov., and to it is added the monotypic *Waltherarndtia* that has presumably lost these triaenes but retains other features common to these taxa

'Hymedesmioid-microcionoids', including *Aulospongos*, *Raspaciona*, *Eurypon*, *Rhabdeurypon* and *Hymeraphia*, have loosely aggregated or plumose skeletal structure, or hymedesmioid structure in encrusting taxa (i.e., megascleres erect on basal spongin), and

lack any marked differentiation between axial and extra-axial skeletons. There are no unique echinating spicule geometries within genera, showing a similar range of geometries as the 'raspailoids'. For example, *Aulospongos* has echinating rhabdostyles similar to *Raspailia* (*Raspaxilla*) and *Endectyon* (*Hemectyon*); *Eurypon* is essentially an encrusting *Raspailia* with hymedesmioid skeletal arrangement (as opposed to a compressed axial reticulate skeleton in the latter), and its echinating acanthostyles are identical to those seen in many *Raspailia*. Several species of *Eurypon* and one of *Aulospongos* have raphides in trichodragmata. These genera, therefore, are justifiably included in the subfamily Raspailiinae.

'Myxilloids', including only *Amphinomia* and *Echinodictyum*, having regularly reticulate choanosomal skeletal structure, with extra-axial skeleton vesigial or virtually absent, and all but one species lack ectosomal specialisation. Echinating megascleres are microcionid-like club-shaped acanthostyles. This subgroup is elevated to Echinodictyinae subfam. nov.

'Plocamoids', includes *Lithoplocamia* and *Plocamione*, having acanthostrongyles or acanthotylostrongyles forming the choanosomal skeleton. This subgroup is elevated to Plocamioninae subfam. nov. *Cantabrina* is excluded from this hierarchy. It is *incertae sedis*, linked to the Raspailiidae only tenuously by its possession of smooth rhabdostyles (which are rare and possibly contaminants), and may not belong in Raspailiidae at all. If it is eventually excluded from Raspailiidae it most closely resembles the Halichondriidae in skeletal structure.

## KEYS TO RASPAILIIDAE

### Key to Subfamilies

- |  |  |
|--|--|
| (1) Echinating megascleres present .....   | 2  |
| Echinating megascleres absent .....  | <b>Thrinacophorinae</b>  |
| Echinating megascleres absent .....  | <b>Raspailiinae (<i>Raspailia</i> (<i>Parasyringella</i>))</b> |
| (2) Echinating megascleres club-shaped or rhabdose .....   | 3  |
| Echinating megascleres modified to sagittal acanthoplagoitriaenes .....  | <b>Cyamoninae</b>  |
| (3) Choanosomal skeleton cored by oxeas or styles .....  | 4  |
| Choanosomal skeleton cored by acanthostrongyles or acanthotylostrongyles ('peg-top' spicules) .....  | <b>Plocamioninae</b>   |
| (4) Choanosomal skeleton with greater or lesser differentiation between axial and extra-axial regions, ectosome with specialised raspailiid skeleton ..... | <b>Raspailiinae</b>  |
| Choanosomal skeleton regularly reticulate, extra-axial skeleton vesigial or virtually absent, and all but one species lack ectosomal specialization .....  | <b>Echinodictyinae</b>   |

### Key to Genera

- |   |   |
|---|---|
| (1) Echinating spicules are microcionid-like, club-shaped, with rounded or sharp points, subtylote bases, and with evenly or unevenly distributed spines .....  | 2   |
| Echinating spicules are club-shaped with clavulate points; axial and extra-axial skeletons are composed of a single category of undifferentiated choanosomal megascleres .....  | <b>Ectyoplasia</b>                        |
| Echinating spicules are acanthose, club-shaped or strongylote, with strongly curved hooks on the base and shaft (cladotylo), and these spicules are usually confined to a particular region within the skeleton ..... | <b>Endectyon</b>                          |
| Echinating spicules are acanthostyles with smooth rhabdose bases, and large recurved spines are distributed over the shaft .....  | <b>Aulospongos</b>                        |
| Echinating spicules are smooth rhabdostyles (rare and possibly contaminants) .....  | <b>Cantabrina (<i>incertae sedis</i>)</b> |
| Echinating spicules are acanthostyles with bulbous tylote bases, with or without spines on the points and other modifications to the distal portion .....   | <b>Hymeraphia</b>                         |
| Echinating spicules are absent, but diactinal acanthorhabds form a compact basal mass throughout the skeleton .....   | <b>Rhabdeurypon</b>                       |
| Echinating spicules are sagittal monact-, diact- or tetractinal (acanthoplagoitriaenes) with only one spined ray .....  | <b>Trikentrion</b>                        |

- Echinating spicules are sagittal tetract- or pentactinal (rarely with fewer rays) (acanthoplagiotriaenes) with all or most rays spined ..... *Cyamom*
- Echinating spicules are absent ..... 3, 8
- (2) Choanosomal skeleton consists of slightly axially compressed reticulation of spongin fibres and/or spicules ..... *Raspailia* ... 3
- Choanosomal skeleton microcionid, basally compressed fibres lying on the substrate, with or without ascending fibre nodes ..... 6
- Choanosomal skeleton reticulate without any trace of axial compression ..... 7
- Choanosomal skeleton consists of loosely aggregated or plumose axial fibres ..... *Raspaciona*
- (3) With echinating acanthostyles ..... 4
- Without echinating acanthostyles ..... *Raspailia (Parasyringella)*
- (4) Choanosomal skeleton consists of an axially compressed reticulation of spongin fibres and/or spicule tracts, with at least some degree of differentiation between axial and extra-axial skeletons ..... 5
- Choanosomal skeleton consists of a reticulation of spongin fibres and/or spicule tracts, without any trace of axial compression, and with reduced differentiation of the axial and extra-axial skeletons ..... *Raspailia (Clathriodendron)*
- (5) Echinating spicules are club-shaped acanthostyles, with subtylote bases and straight shafts ..... *Raspailia (Raspailia)*
- Echinating spicules are acanthose rhabdostyles ..... *Raspailia (Raspaxilla)*
- Echinating spicules have smooth, swollen, tylote bases ..... *Raspailia (Hymeraphiopsis)*
- (6) Spicules in the axial or basal skeleton are acanthostrongyles or acanthotylostrongyles ..... *Plocamione*
- No true choanosomal megascleres occur in the axial skeleton, although large extra-axial spicules and echinating acanthostyles may be embedded in spongin fibres ..... *Eurypon*
- (7) Choanosomal spicules are styles or subtylostyles with spines on both basal and distal ends, forming a renieroid reticulate skeleton ..... *Amphinomia*
- Choanosomal spicules are exclusively oxeas ..... *Echinodictyum*
- Choanosomal spicules are acanthostrongyles or acanthotylostrongyles forming a secondary (sub) isodictyal reticulation ..... *Lithoplocamia*
- (8) Choanosomal skeleton consists of dense axial compression of criss-crossed spicules, without axial fibres ..... *Thrinacophora*
- Choanosomal skeleton with a renieroid reticulate skeleton of multispicular primary fibres interconnected by uni- or paucispicular secondary fibres, forming elongate meshes, slightly more compressed at the axis than in the periphery ..... *Waltherarndtia*
- Choanosomal skeleton consists of axially compressed reticulation of spongin fibres and/or spicule tracts ..... 9
- (9) Spicules in the axial skeleton are sinuous styles or anisoxeas ..... *Ceratopsion*
- Spicules in the axial skeleton include both spined oxeas and smooth anisoxeas ..... *Axechina*

#### SUBFAMILY RASPAILIINIAE NARDO, 1833

##### Definition

Raspailiidae with echinating megasclere geometry ranging from microcionid-like club-shaped acanthostyles with small granular or erect spines, to club-shaped with strongly recurved or clavulate spines on the basal and distal ends of spicules, to acanthose rhabdostyles.

##### Scope

Eight genera and seven subgenera. *Raspailia* (*R. (Raspailia)*), *R. (Clathriodendron)*, *R. (Raspaxilla)*, *R. (Parasyringella)*, *R. (Hymeraphiopsis)*, (*Aulospongius*, *Ectyoplasia*, *Endectyon* (*E. (Endectyon)*, *E. (Hemectyon)*), *Eurypon*, *Hymeraphia*, *Raspaciona* and *Rhabdeurypon*.

#### RASPAILIA NARDO, 1833

##### Synonymy

*Raspelia* Nardo, 1833: 522. *Raspailia* Nardo, 1847a: 3 (*nom. emend.*). See subgenera for full synonymy.

##### Type species

*Raspailia typica* Nardo, 1833 (by monotypy).

##### Definition

Raspailiidae with a more-or-less compressed axial skeleton and a radial, plumose or simply reticulate extra-axial skeleton, with choanosomal spicules consisting of 2–3 or more different size classes (styles and/or oxeas), and echinating acanthostyles microcionid-like or secondarily modified.

##### Diagnosis

Arborescent, lobo-digitate to massive growth form, typically with cylindrical branches and basal holdfast. Surface even or rugose, often optically hispid. Choanosomal skeleton always with fibres and spicules in distinct tracts: axial skeleton typically compressed with widely spaced reticulate fibres cored by styles, but degree of compression varies considerably between species. Extra-axial skeleton typically plumo-reticulate, with extra-axial spicule tracts standing perpendicular to axial skeleton, cored by large styles or oxeas which ascend to and poke through surface in uni- or paucispicular brushes, although this may be reduced to simple plumose structure. Peripheral spicule tracts may be multispicular or reduced to brushes of subectosomal spicules embedded in the subdermal region. Ectosome typically with specialized skeleton of small styles grouped into brushes standing perpendicular to surface, surrounding bases of protruding extra-axial megascleres, but these may be secondarily lost. Fibres usually echinated by acanthostyles or modified forms, sometimes secondarily lost. Structural megascleres styles, oxeas or anisoxeas, typically 3,

sometimes 2, distinct size categories; echinating acanthostyles morphologically similar to microcionid sponges. Microscleres absent.

#### Remarks

The genus *Raspailia* was originally reviewed by Vosmaer (1912, 1935) and subsequently by Hooper (1991), with both revisions based on restricted faunas (European and Australian species, respectively). Vosmaer's (1935) revision must be accepted with caution as he synonymized about 20 nominal species, including Nardo's type species, under *Raspailia hispida* (Montagu), an act which very few authors subsequently accepted. Wilson (1921) made a better attempt in redefining the genus. From an examination of a number of species he arrived at a broad definition for *Raspailia s.l.*, and simultaneously succeeded in conveying the enormous difficulty involved in defining this large and diverse group. There is obviously a high diversity of character states found in the genus, encompassing most characters: growth forms of *Raspailia* range from massive, branching to lobate; skeletal structures vary from compressed axis/radial extra-axial skeleton, to reduced extra-axial, plumo-reticulate extra-axial, reduced plumose extra-axial, or simply reticulate skeletons (nominal genus *Clathriodendron*); structural megascleres may be exclusively stylote, rhabdostyles (nominal genus *Axinectya*), stylote and oxeote together, or exclusively oxeote; ectosomal structure ranges from the 'raspailiid' condition (protruding extra-axial (subectosomal) megascleres surrounded by special ectosomal brushes, to extra-axial megascleres protruding through the surface but without any specialized ectosomal megascleres, or with only special dermal spicules scattered over the surface, or lacking ectosomal specialisation at all (nominal genus *Echinaxia*); and geometry of echinating spicules ranging from cylindrical microcionid-like spicules, acanthose rhabdostyles (nominal genus *Raspaxilla*), or secondarily lost (nominal genera *Raspailopsis*, *Syringella* and *Parasyringella*).

Hooper (1991) used subgeneric taxa to overcome this problem, recognising five subgenera differentiated by the geometry and spination of echinating acanthostyles.

Another nominal genus referred here to *Raspailia* was overlooked by Hooper (1991). *Bethia* de Laubenfels, 1936a: 108 (type species *Dictyocylindrus laciniatus* Carter, 1979b: 296, by original designation), is clearly as raspailiid, and from its description belongs to *Raspailia* (*Raspailia*). The type species, from Mauritius, is described as a hemispherical, long radiated lacinate sponge with extremely hispid surface, a compressible texture, has subradiate plumo-reticulate architecture (reminiscent of Suberitidae according to de Laubenfels, 1936a) with indistinct spongin fibres/spicule tracts becoming more plumose towards the periphery, cored by very long choanosomal subtylostyles (over 4 mm long, about 35 µm wide), protruding through the surface for long distances, small ectosomal oxeas (about 550 µm long and 17 µm wide), and short echinating acanthostyles with well developed slightly swollen base, slightly rounded point, and spines concentrated mainly at extremities (about 95 µm long, 17 µm wide), sparsely echinating fibres. Microscleres are absent.

#### Distribution

There are more than one hundred described species of *Raspailia*, and at least the same number known but which remain

undescribed (Hooper, unpublished data). Species are distributed worldwide, predominantly in shallow waters.

#### SUBGENUS RASPAILIA NARDO, 1833

##### Synonymy

*Raspellia* Nardo, 1833: 522; Burton 1937: 33. *Raspailia* Nardo, 1847a: 3 (*nom. emend.*); Schmidt, 1862: 59; 1866a: 14; Ridley & Dendy, 1887: 188; Hanitsch, 1889: 161; Lendenfeld, 1890b: 401; Topsent, 1894c: 16; Pick, 1905: 19; Hentschel, 1912: 413; Vosmaer, 1912: 313; Wilson, 1921: 54–60; Vosmaer, 1935: 766; Bergquist, 1970: 26; Hooper, 1991: 1195. [*Rasalia*] Gray, 1867a: 522 (*lapsus*). [*Raspalia*] Gray, 1867a: 523 (*lapsus*). [*Abila*] Gray, 1867a: 522 (preocc.) (Not *Abila* Gray, 1867a: 539). *Abilana* Strand, 1928: 33 (replacement name for [*Abila*] Gray; de Laubenfels, 1936a: 102). *Valedictyum* de Laubenfels, 1936a: 102. *Bethia* de Laubenfels, 1936a: 108. Taxonomic decision for synonymy: Hooper (1991), Hooper & Lévi (1993), and this work.

##### Type species

*Raspailia typica* Nardo, 1833 (by monotypy).

##### Definition

*Raspailia* with microcionid-like acanthostyles, myxillid-like acanthostyles or thin vestigial acanthostyles.

##### Diagnosis

Digitate and branching *Raspailia*, usually with a highly hispid surface; choanosomal skeleton composed of distinctive axial and extra-axial components; axial skeleton compressed with reticulate spongin fibres cored by multispicular tracts of principal styles or sometimes oxeas, and echinated by acanthostyles; extra-axial skeleton primarily plumose or radial, with longer principal spicules forming multispicular tracts and interconnected by sparse uni- or paucispicular fibres; extra-axial tracts eventually protruding through the surface, with the larger spicules surrounded by bouquets of ectosomal styles or anisoxeas at the point of their insertion to the surface. Megascleres include styles (and/or or less commonly oxeas or oxeote modifications to styles) of at least 2–3 size classes, varying from robust and long to small, sinuous and vestigial, and echinating acanthostyles that are microcionid-like with a subtylote base, usually a straight shaft, and evenly spined or with an aspinose region proximal to the basal swelling.

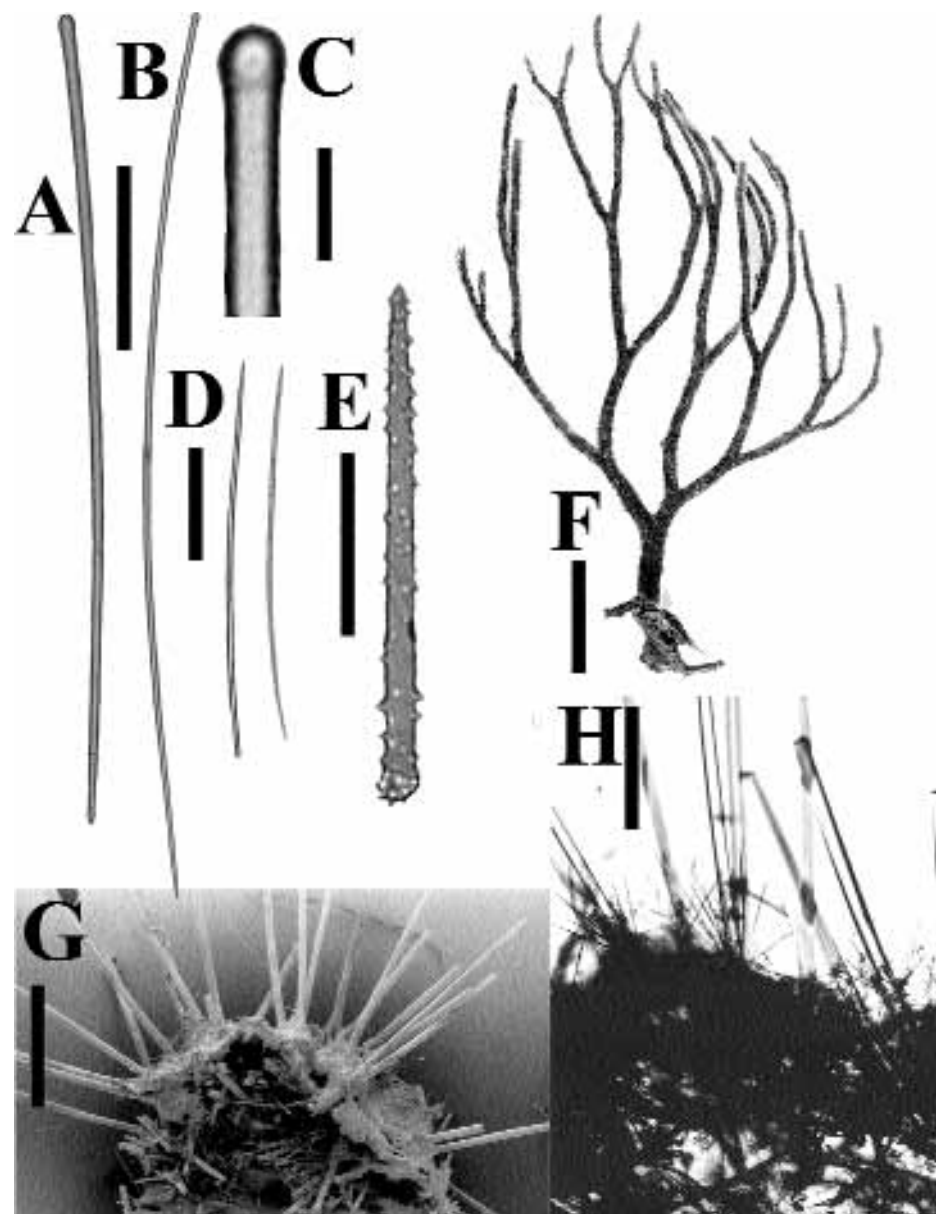
##### Description of type species

*Raspailia typica* Nardo, 1833 (Fig. 1).

**Synonymy.** *Raspailia typica* Nardo, 1833: 522; *Raspailia viminalis* Schmidt, 1862: 59.

**Material examined.** Holotype: Unknown. Fragments of Schmidt's specimen MNHN DCL 1237L, BMNH 1867.3.11.8 – Adriatic Sea. Schizotype of *R. viminalis*. MNHN DCL 1238L – Sebenico, Adriatic Sea.

**Description.** Erect, digitate, branching growth form; choanosomal skeleton with differentiated axial and extra-axial



**Fig. 1.** *Raspailia* (*Raspailia*). A–E, *R. (Raspailia) typica* (schizotype BMNH 1867.3.11.8). A–B, choanosomal principal style and subtylostyle (scale 400  $\mu\text{m}$ ). C, base of principal subtylostyle (scale 25  $\mu\text{m}$ ). D, ectosomal style and anisoxea (scale 150  $\mu\text{m}$ ). E, echinating acanthostyle (scale 30  $\mu\text{m}$ ). F–H, *R. (Raspailia) vestigifera* Dendy. F, specimen NTMZ910 (scale 5 cm). G, choanosomal skeleton (scale 500  $\mu\text{m}$ ). H, ectosomal skeleton (scale 300  $\mu\text{m}$ ).

skeletons; compressed axis composed of several, thin, parallel, multispicular tracts running longitudinally through branches separated by relatively wide meshes; extra-axial skeleton more-or-less at right angles to axis, running horizontally through branches, composed of slender, slightly plumose tracts 1–5 principal spicules abreast bound by light collagen, interconnected by unispicular tracts of principal spicules together forming a loose, wide-meshed reticulation; extra-axial tracts ascending to surface and terminating in single principal spicule protruding through surface; spicule tracts echinated by acanthostyles, particularly in axis; specialised ectosomal skeleton consists of small ectosomal styles or oxaeas forming brushes around single protruding principal style at point of insertion in surface; principal styles long slender curved or sometimes sinuous, with subtylostylole or more well-developed tylo-

(1140–1950  $\times$  11–23  $\mu\text{m}$ ), ectosomal styles or anisoxeas slightly curved, tapering to hair-like point at one end (470–595  $\times$  3–9  $\mu\text{m}$ ), echinating acanthostyles with subtylole base and evenly spined (88–112  $\times$  4–7  $\mu\text{m}$ ); microscleres absent.

**Remarks.** See Remarks for the genus. Re-examination of type material confirms the synonymy between *Raspailia* and *Abila* (type species *Raspailia freyerii* Schmidt, 1862: 60, by monotypy) and *Valedictyum* (type species *Raspailia vestigifera* Dendy, 1896, by monotypy).

#### Distribution

Worldwide, shallow seas.

**SUBGENUS RASPAXILLA TOPSENT, 1913****Synonymy**

*Raspaxilla* Topsent, 1913b: 616; Bergquist, 1970: 28–30; Hooper, 1991: 1195, 1245; Hooper *et al.*, 1999: 673. *Echinaxia* Hallmann, 1916b: 543; Hallmann, 1917b: 391; de Laubenfels, 1936a: 102; Bergquist, 1970: 30; Hooper, 1991: 1195; Hooper *et al.*, 1999: 681. *Axinectya* Hallmann, 1917b: 393; Hooper, 1991: 1195; Hooper *et al.*, 1999: 688. Taxonomic decision for synonymy: Hooper (1991), Hooper *et al.* (1999).

**Type species**

*Raspaxilla phakellina* Topsent, 1913b (by monotypy).

**Definition**

*Raspailia* with echinating rhabdostyles geometrically very different from the usually longer choanosomal styles (the latter without any basal rhabd); extra-axial styles forming a radial skeleton perpendicular to the axis; and well differentiated axial and extra-axial skeletons (the former compressed, the latter plumo-reticulate and/or radial).

**Diagnosis**

Digitate, bushy, lobate, lamellate, arborescent, flabellate and vasiform *Raspailia*; with echinating acanthose rhabdostyles; larger choanosomal styles completely smooth, without any basal rhabd, geometrically different from smaller acanthose echinating spicules; axial skeleton well differentiated from extra-axial skeleton; axial skeleton compressed, composed of reticulate tracts cored by choanosomal styles; extra-axial skeleton plumo-reticulate, with plumose ascending tracts interconnected by transverse tracts both cored by choanosomal styles (forming a reticulation), or reduced to radial tracts of single long extra-axial styles embedded in and perpendicular to axis, protruding through the surface; echinating rhabdostyles more abundant in peripheral skeleton.

**Description of type species**

*Raspailia (Raspaxilla) phakellina* Topsent, 1913b (Fig. 2).

**Synonymy.** *Raspaxilla phakellina* Topsent, 1913b: 617; *Raspailia (Raspaxilla) phakellina*; Hooper, 1991: 1196.

**Material examined.** Holotype: MOM (fragment MNHN DT1614) – Antarctica. Other material. BMNH 1928.2.15.781a, 846a – Falkland Islands.

**Description.** Erect, digitate, arborescent, with enlarged basal holdfast attachment and branching in one plane; surface slightly conulose, hispid; ectosomal skeleton with long extra-axial styles protruding through the surface, surrounded at their bases by wispy bundles of ectosomal anisoxeas forming stellate bundles nearly parallel to the surface; axial and extra-axial skeletons well differentiated; choanosomal skeleton with a compressed, strongly reticulate axis composed of multispicular fibres cored by choanosomal styles and echinated sparsely by echinating rhabdostyles; extra-axial skeleton plumo-reticulate, with ascending multispicular fibre bundles cored by choanosomal styles and profusely echinated by rhabdostyles, diverging towards the periphery, interconnected by transverse pauci- or multispicular fibres which

persist all the way to the surface; echinating rhabdostyles predominant in extra-axial skeleton; megascleres include long choanosomal styles, slightly curved centrally or straight, with evenly rounded, smooth, non-rhabdose bases ( $550\text{--}900 \times 10\text{--}16 \mu\text{m}$ ); extra-axial styles long, thick, straight or slightly curved, entirely smooth ( $1100\text{--}1450 \times 12\text{--}18 \mu\text{m}$ ); ectosomal styles wispy, rhabdiform, straight, centrally curved or sinuous ( $450\text{--}650 \times 2\text{--}3 \mu\text{m}$ ); echinating rhabdostyles moderately long, with slightly rhabdose and subtylote bases, entire spicule smooth or small, erect spines on apical two-thirds of spicule only ( $140\text{--}370 \times 8\text{--}18 \mu\text{m}$ ); microscleres absent.

**Remarks.** *Raspailia (Raspaxilla)* differs from typical *Raspailia* in having rhabdose echinating acanthostyles. It differs from other rhabdose raspailiids, notably *Aulospongius*, in having echinating rhabdostyles geometrically very different from the usually longer choanosomal styles (the latter without any basal rhabd); extra-axial styles forming a radial skeleton perpendicular to the axis; and well differentiated axial and extra-axial skeletons (the former compressed, the latter plumo-reticulate and/or radial). Placement of all species, however, is not always straightforward given that some taxa may lose certain characters (e.g., extra-axial skeleton becomes reduced to single long extra-axial spicules embedded in axis and forming a radial skeleton; or the extra-axial spicules are lost completely). There is also a correlation between the localisation of echinating rhabdostyles in the peripheral skeleton and the degree of axial compression. In species with very compressed skeletons the extra-axial skeleton is reduced to single long extra-axial spicules (without reticulate connections) and the echinating rhabdostyles are ‘pushed’ into the ectosomal skeleton where they form brushes or a continuous palisade of rhabdostyles (Hooper *et al.*, 1999). *Echinaxia* (type species *Axinella frondula* Whitelegge, 1907, by original designation) and *Axinectya* (type species *Axinella mariana* Ridley & Dendy, 1886, by original designation) are clearly synonymous with *Raspaxilla*.

**Distribution**

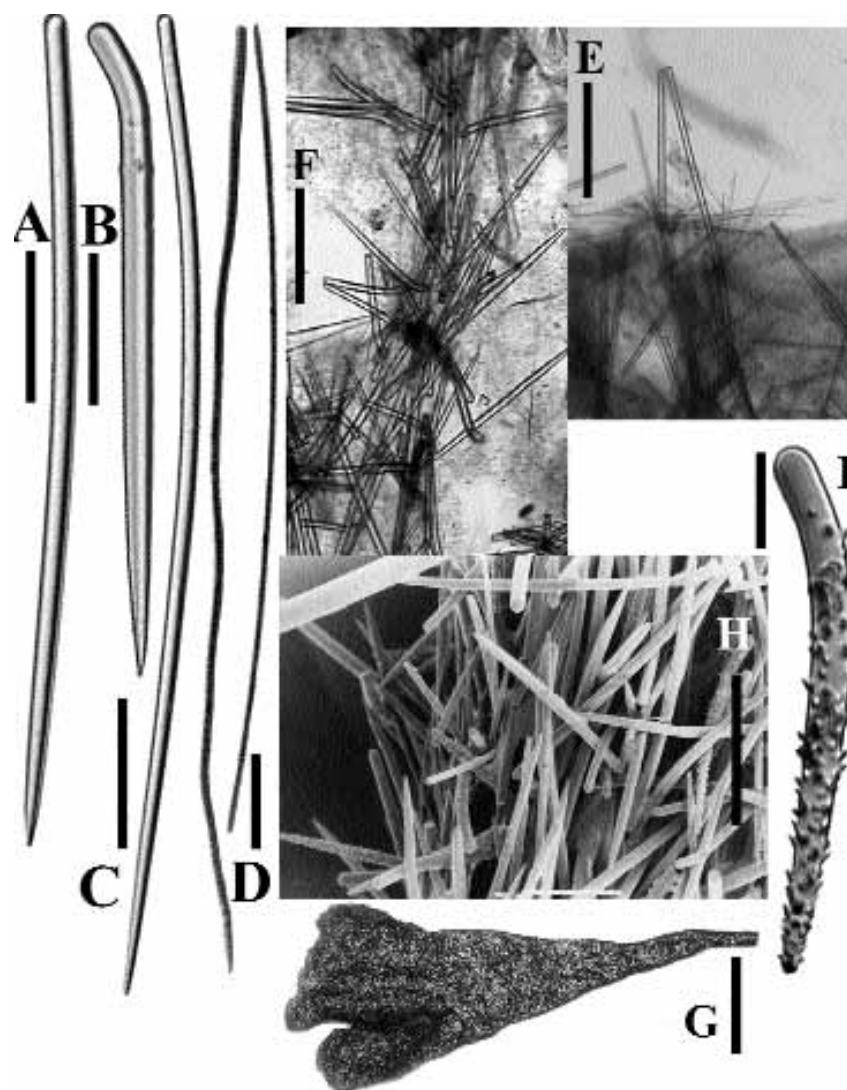
Sixteen species are currently assigned to *Raspailia (Raspaxilla)*, with a wide geographic distribution, ranging from the Indo-west Pacific (north and south New Zealand, northwest Australia, northern Great Barrier Reef, central NSW, New Caledonia, Japan, Micronesia), Caribbean (North Carolina), central east Pacific and the antarctic-subantarctic region (Hooper *et al.*, 1999).

**SUBGENUS CLATHRIODENDRON LENDENFELD, 1888****Synonymy**

*Clathriodendron* Lendenfeld, 1888: 215; Kirk, 1911: 579; Hentschel, 1911: 383; Hallmann, 1912: 295; Topsent, 1894c: 19; de Laubenfels, 1936a: 102; Bergquist, 1970: 30. *Dictyocylindrus* Bowerbank, 1862b: 1108 (in part); Gray, 1867a: 519; Topsent, 1890c: 289; de Laubenfels, 1936a: 102. (Not *Dictyocylindrus*; Carter, 1879b: 297). Taxonomic decision for synonymy: Hooper (1991).

**Type species**

*Clathriodendron arbuscula* Lendenfeld, 1888 (by subsequent designation; Hallmann, 1912: 295).



**Fig. 2.** *Raspailia* (*Raspaxilla*). A–F, *R. (Raspaxilla) phakellina* Topsent (schizotype). A, choanosomal style (scale 100  $\mu\text{m}$ ). B, echinating rhabdostyle (scale 50  $\mu\text{m}$ ). C, extra-axial style (scale 200  $\mu\text{m}$ ). D, ectosomal styles (scale 50  $\mu\text{m}$ ). E, ectosomal skeleton (scale 250  $\mu\text{m}$ ). F, choanosomal fibre bundle (scale 100  $\mu\text{m}$ ). G–I, *R. (Raspaxilla) wardi* Hooper (holotype NTMZ1319). G, holotype (scale 3 cm). H, axial skeleton (scale 40  $\mu\text{m}$ ). I, echinating rhabdostyle (scale 20  $\mu\text{m}$ ).

### Definition

Reduced *Raspailia* lacking any axial compression or any differentiation between axial and extra-axial skeletons, but retaining two or more forms of choanosomal structural megascleres.

### Diagnosis

Digitate, lobate or massive *Raspailia* with microconulose or less commonly hispid surface; choanosomal skeleton exclusively reticulate, with little differentiation between axial and extra-axial regions although peripheral skeleton may still contain the vestiges of radial or plumose tracts; spongin fibres generally well developed, cored by multispicular tracts of principal styles often together with sand grains or other detritus, and echinated by microcionid-like acanthostyles; longer styles may be present in the peripheral skeleton, protruding through the surface, sometimes surrounded by bouquets of ectosomal styles/anisoxeas, but often lacking a specialised ectosomal skeleton; ectosome often highly collagenous and arenaceous.

### Description of type species

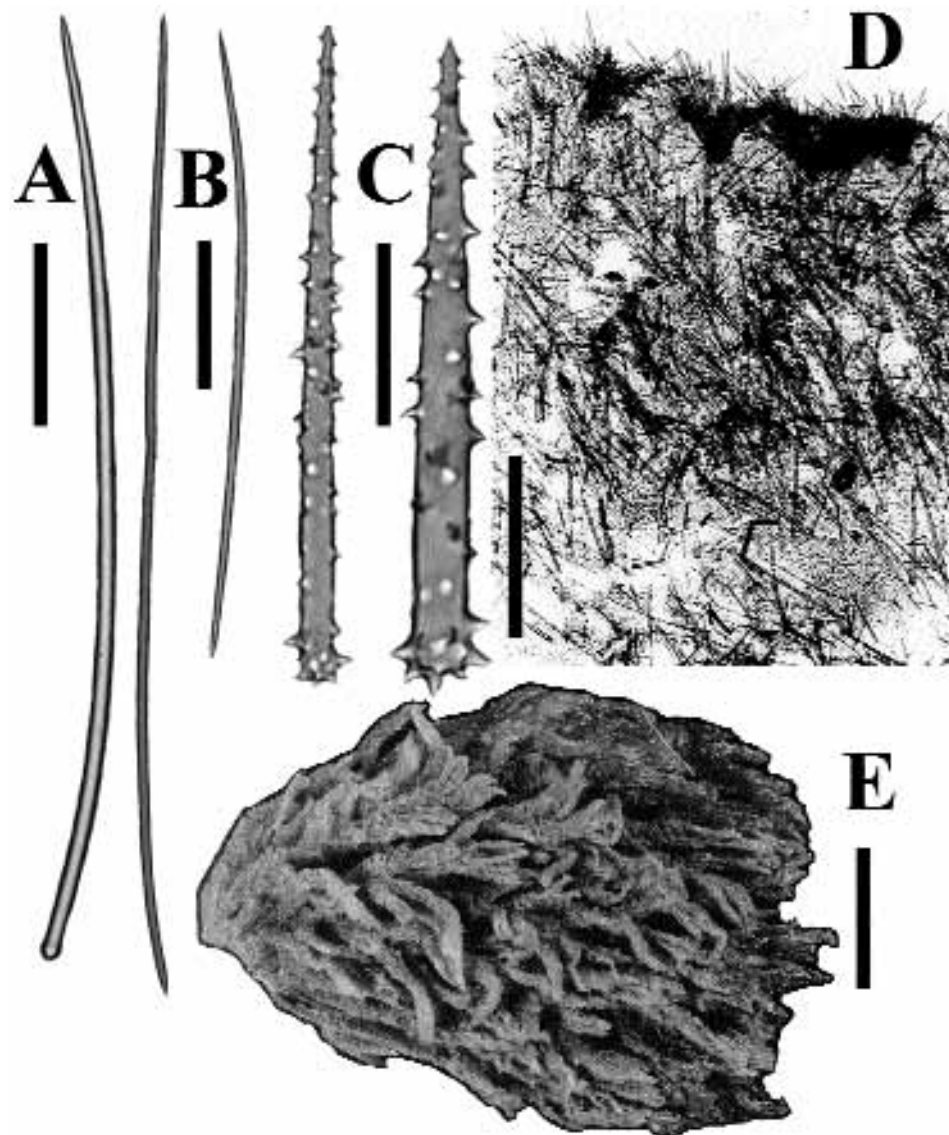
*Raspailia (Clathriodendron) arbuscula* Lendenfeld, 1888 (Fig. 3).

**Synonymy.** *Clathriodendron arbuscula* Lendenfeld, 1888: 215; *Echinonema anchoratum* var. *ramosa* Lendenfeld, in part (as *Echinonema ramosa*); Whitelegge 1901: 81; *Raspailia agminata* Hallmann, 1914b: 438; *Halichondria rubra* var. *digitata* Lendenfeld, 1888: 81; *Clathriodendron nigra* Lendenfeld, 1888: 216 (in part).

**Material examined.** Lectotype: AM G9045 – Port Jackson, NSW. Holotype of *C. nigra* var. *jacksoniana*: BMNH 1887.1.24.64 – Port Jackson, NSW.

**Description.** Shape elongate, laterally flattened, digitate fronds connected to common base; surface prominently hispid, with arenaceous particles embedded in ectosome producing uneven conules dispersed over surface; texture harsh, branches easily flexible, relatively fragile (easily torn); ectosomal skeleton moderately arenaceous; long subectosomal megascleres protrude through surface, sometimes surrounded by sparse brushes of thin ectosomal





**Fig. 3.** *Raspailia* (*Clathriodendron*). A–E, *R. (Clathriodendron) arbuscula* (lectotype AMG9045). A, subectosomal extra-axial style and anisoxea (scale 300  $\mu\text{m}$ ). B, ectosomal auxiliary anisoxea (scale 100  $\mu\text{m}$ ). C, echinating acanthostyles (scale 25  $\mu\text{m}$ ). D, skeleton (scale 500  $\mu\text{m}$ ). E, lectotype (scale 3 cm).

styles or anisoxeas; bases of subectosomal megascleres embedded in axial skeleton, enveloped by heavy fibrous spongin, protruding through surface as single spicules or paucispicular brushes, forming extra-axial skeleton; subectosomal megascleres near centre of axial skeleton smaller than spicules occurring towards periphery; no compression of choanosomal skeleton nor any well differentiated extra-axial skeleton; choanosomal skeleton with very heavy spongin fibres forming irregular reticulation of longitudinal tracts, without special category of choanosomal megascleres, but with aspicular fibres or echinating spicules secondarily incorporated into fibres; skeletal tracts heavily echinated by acanthostyles; principal megascleres absent; subectosomal extra-axial megascleres long, setaceous, straight or slightly curved towards basal end, with rounded stylote, sometimes substylote, less commonly asymmetrical oxeote ends (820–1545  $\times$  11–26  $\mu\text{m}$ ); ectosomal auxiliary styles or anisoxeas relatively small, thin, slightly curved at centre or base, with fusiform points and rounded stylote or fusiform oxeote bases (253–412  $\times$  4–6  $\mu\text{m}$ ); echinating acanthostyles relatively small, substylote, with large granular spination, an

aspinose region near basal region (85–101  $\times$  9–11  $\mu\text{m}$ ); microscleres absent.

**Remarks.** *Clathriodendron* (including junior synonym *Dictyocylindrus*, with type species *Spongia hispida* Montagu, 1814, by original designation) is superficially quite different from *Raspailia* lacking axial condensation, any marked axial and extra-axial skeletal differentiation, and often lacking the specialized ectosomal skeleton typical of other raspailiids. In its aberrant skeletal structure it shows closest similarities to *Echinodictyum*. Some species are also known to incorporate detritus into their skeletons, and in that respect they are homologous to the relationship demonstrated in the Microcionidae between *Clathria s.s.* and *Wilsonella*, the latter used as a ‘convenient’ subgenus for arenaceous species of *Clathria* (Hooper, 1996a). Hallmann (1912), followed by Wiedenmayer (1989), considered that *C. arbuscula* was sufficiently different from *Raspailia* to maintain the two taxa. Conversely, Hentschel (1911), followed by Hooper (1991) suggested that *Clathriodendron* was synonymous with *Raspailia* due to the existence of species that otherwise clearly belonged to

*Raspailia*, but with exclusively or nearly exclusive reticulate choanosomal skeletons and no differences in their echinating acanthostyle geometries.

#### Distribution

Common in Indo-west Pacific region, present in the Caribbean, and possibly worldwide in distribution.

#### SUBGENUS *PARASYRINGELLA* TOPSENT, 1928

#### Synonymy

[*Syringella*] of authors; Ridley, 1884a: 460; Pick, 1905: 18; Topsent, 1892a: 123, 1904b: 138, 1928c: 42; Burton, 1934b: 42; de Laubenfels, 1936a: 121 (Not *Syringella* Schmidt, 1868: 10). *Parasyringella* Topsent, 1928c: 287; de Laubenfels, 1936a: 102. *Raspailopsis* Burton, 1959a. Taxonomic decision for synonymy: Hooper (1991), and this work.

#### Type species

*Raspailia* (*Parasyringella*) *falcifera* Topsent, 1892a (by original designation; schizotype MNHN DT901).

#### Definition

*Raspailia* which have secondarily lost their echinating megascleres.

#### Diagnosis

Unbranched cylindrical, digitate or whip-like *Raspailia* usually with a hispid surface; skeleton divided into distinct axial and extra-axial regions; axial skeleton compressed highly compacted reticulation of fibres and multispicular tracts running mainly longitudinally through branches to produce a flexible skeleton, cored by shorter principal styles; extra-axial skeleton composed of multispicular tracts cored by larger extra-axial styles together forming discrete bundles embedded in the axial skeleton and extending radially to the surface, with single or bundles of extra-axial styles protruding a short way through the surface, and surrounded by bouquets of ectosomal styles; megascleres include at least 2–3 size classes of styles, with the smaller ones sometimes modified to anisoxeas.

#### Description of ‘representative’ species

*Raspailia* (*Parasyringella*) *australiensis* Ridley, 1884a (Fig. 4).

**Synonymy.** *Raspailia* (*Syringella*) *australiensis* Ridley, 1884a: 460.

**Material examined.** Lectotype: BMNH 1882.2.23.253 – Port Darwin, NT.

**Description.** Shape unbranched cylindrical digits, bifurcate, with short holdfast, long slender woody stalks; texture firm, flexible, with woody central stem (=axial skeleton) and fleshy branches (produced by extra-axial region); surface optically even, microscopically rugose and hispid, with minute conules and ridges; ectosomal skeleton with sparse brushes of thin ectosomal styles surrounding multispicular brushes of larger extra-axial styles protruding through the surface; these extra-axial spicule tracts comprise only 20–40% of the

branch diameter, but nevertheless forming thick bundles, arising tangentially or obliquely from axis, and composed of plumose brushes of longer styles or anisoxeas embedded in the axial skeleton and protruding only a relatively short distance through the surface; axial core compressed, comprising 60–80% of branch diameter, composed of discrete, closely set, fasciculated bundles of shorter choanosomal principal styles usually running longitudinally through branches but also at more oblique angles, producing solid but flexible skeleton. Megascleres: both categories of structural megasclere are very similar in their geometry, differing mainly in size and location within skeleton. Shorter choanosomal principal (axial) styles straight or slightly curved, with evenly rounded or tapering fusiform bases and tapering to sharp points ( $232\text{--}365 \times 6\text{--}9 \mu\text{m}$ ); longer subectosomal (extra-axial) styles, thick, relatively straight, with fusiform tapering bases and sharply pointed tips ( $543\text{--}964 \times 9\text{--}25 \mu\text{m}$ ); ectosomal (auxiliary) styles or anisoxeas range from thin wispy flexuous anisoxeas to thicker straight or slightly curved styles ( $145\text{--}237 \times 0.5\text{--}5 \mu\text{m}$ ); echinating megascleres absent; microscleres absent.

**Remarks.** The taxon *Parasyringella* is used here as a convenient subgenus, to delineate a group of *Raspailia* species lacking echinating megascleres, and includes the junior synonym *Raspailopsis* and [*Syringella*] of authors, Ridley (1884a) being the first (not of Schmidt, 1868). Burton (1959a) created *Raspailopsis* (type species *Raspailopsis cervicornis* Burton, 1959a, by original designation; holotype BMNH 1936.3.4.604) for raspailiids that lacked echinating acanthostyles whereas [*Syringella*] (type species *Raspailia syringella* Schmidt, 1868: 10, by monotypy, holotype unknown) was already in use by earlier authors for much the same purpose. In any case, some specimens of the type species of *Raspailopsis*, *R. cervicornis* (BMNH 1936.3.4.521 and BMNH 1936.3.4.522) from the South Arabian coast did have echinating acanthostyles present on the peripheral fibres of the axial skeleton, and in this regard *Raspailopsis* is undoubtedly a synonym of *Raspailia*. Hooper (1991) followed the prior use of the subgeneric name [*Syringella*] for this group, but also noted that Schmidt’s type species, *R. syringella*, did not belong. Consequently, the name ‘*Syringella*’ cannot be used as a valid taxon, with the next available name being *Parasyringella* Topsent. Only a poor microscope slide preparation of *R. falcifera* has been examined from the MNHN collections, so the description of Ridley’s species is provided instead as ‘representative’ of the subgenus.

#### Distribution

Uncommon, Indo-Pacific.

#### SUBGENUS *HYMERAPHIOPSIS* HOOPER, 1991

#### Synonymy

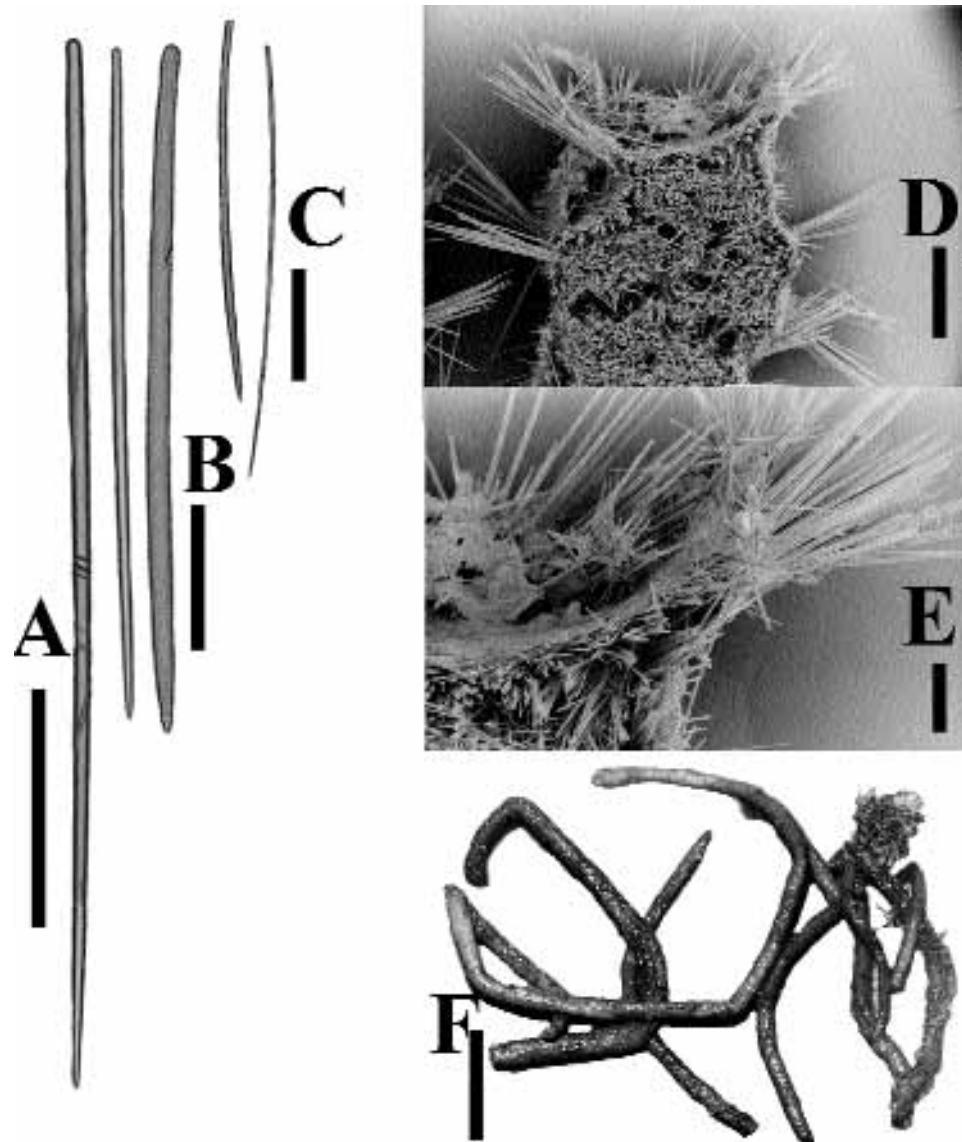
*Hymeraphiopsis* Hooper, 1991: 1270.

#### Type species

*Raspailia irregularis* Hentschel, 1914 (by original designation).

#### Definition

*Raspailia* having acanthostyles with smooth and very swollen tylote bases.



**Fig. 4.** *Raspailia* (*Parasyringella*). A–E, *R. (Parasyringella) australiensis* (lectotype BMNH1882.2.23.253). A, subectosomal (extra-axial) style (scale 200  $\mu\text{m}$ ). B, choanosomal principal (axial) styles (scale 60  $\mu\text{m}$ ). C, ectosomal (auxiliary) style/anisoxea (scale 50  $\mu\text{m}$ ). D, choanosomal skeletal structure (scale 500  $\mu\text{m}$ ). E, ectosomal and extra-axial skeleton (scale 100  $\mu\text{m}$ ). F, specimen (QM GL850) (scale 3 cm).

### Diagnosis

Monotypic. Refer to type species description below.

### Description of type species

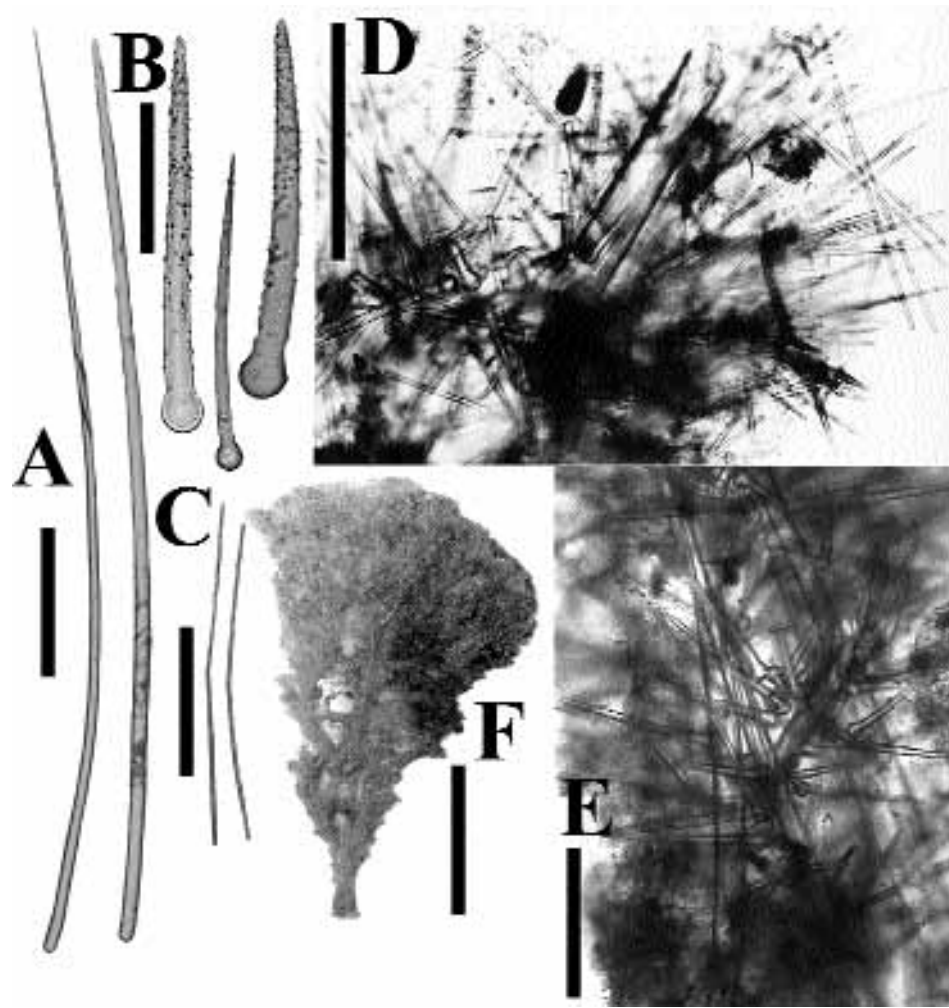
*Raspailia* (*Hymeraphiopsis*) *irregularis* Hentschel, 1914 (Fig. 5).

**Synonymy.** *Raspailia irregularis* Hentschel, 1914: 121; *Eurypon miniaceum*; Burton, 1932b:325; (Not *Eurypon miniaceum* Thiele, 1905: 446).

**Material examined.** Holotype: ZMH (not seen). Specimen of Burton (1932b): BMNH1928.2.15.244 – South Georgia, S Atlantic.

**Description.** Shape small, bushy, branching, with multiple points of attachment, several basal holdfasts and short stalks, and flattened, irregularly bifurcate and bushy branches; surface of

branches aculeate, irregularly conulose and prominently hispid; texture compressible, flexible; ectosomal skeleton with paucispicular brushes of ectosomal styles or anisoxeas, dispersed over surface and intermingled with erect brushes of acanthostyles just below ectosome; brushes not associated with protruding subectosomal extra-axial spicules; subectosomal extra-axial megascleres embedded in axial skeleton, protruding up to 2 mm from surface, dominating skeletal architecture so much that axial skeleton resembles a cluster of spicules surrounding bases of subectosomal megascleres; choanosomal axial skeleton a series of compressed axial clusters of echinating megascleres, without fibres or any specialized choanosomal megascleres, united by granular spongin and forming plumose brushes; echinating spicule brushes near periphery directed outwards, and points of acanthostyles protrude up to but not through ectosome; bases of subectosomal extra-axial spicules embedded in core of axial skeleton; principal megascleres absent; subectosomal extra-axial spicules very long and thick



**Fig. 5.** *Raspailia* (*Hymeraphiopsis*). A–F, *R. (Hymeraphiopsis) irregularis* (specimen BMNH 1928.2.15.244). A, subectosomal styles (scale 450  $\mu$ m). B, echinating acanthotylostyles (scale 100  $\mu$ m). C, ectosomal style and anisoxea (scale 250  $\mu$ m). D, section through peripheral skeleton (scale 250  $\mu$ m). E, choanosomal skeleton (scale 250  $\mu$ m). F, specimen (scale 3 cm).

styles, curved near basal end, with enlarged but not necessarily tylote bases, tapering to sharp points (1969–3016  $\times$  35–54  $\mu$ m); ectosomal auxiliary megascleres relatively long thin styles or anisoxeas, sometimes straight but mostly with prominent curvature at centre, with rounded tapering hastate bases, sometimes oxete, tapering to sharp points (435–712  $\times$  2–11  $\mu$ m); echinating acanthostyles straight, thin or thick, with grossly enlarged tylote base, evenly cylindrical shaft and sharply pointed at apex, with vestigial spination on shaft or sometimes confined to points (181–301  $\times$  12–24  $\mu$ m); microscleres absent.

**Remarks.** *Hymeraphiopsis* is currently monotypic, known only from several records of the Antarctic type species including a comprehensive redescription of type and new material by Hooper (1991). It differs from other subgenera of *Raspailia* essentially in its possession of acanthostyles with swollen bulbous tyloes and spines confined mainly to the apical points of spicules. The type species also differs from typical *Raspailia* in having echinating acanthotylostyles clustered around the bases of the long extra-axial styles, deep within the choanosomal skeleton, and with ectosomal styles/anisoxeas scattered mainly near the peripheral skeleton, below the surface, and rarely forming bouquets around these protruding spicules.

#### Distribution

Monotypic, Antarctica.

#### AULOSPONGUS NORMAN, 1878

#### Synonymy

*Aulospongiella* Norman, 1878: 267; Dendy, 1889: 89; Dendy, 1922b: 61; Burton, 1937: 38; Hooper, 1991: 1307; Hooper & Lévi, 1993: 1294; Hooper *et al.*, 1999: 651 (Not *Aulospongiella*; de Laubenfels, 1936a: 100). *Aulospongiella* Burton, 1956: 141. *Heterectya* Hallmann, 1917b: 393. *Rhaphidectyon* Topsent, 1927b: 15. *Hemectyonilla* Burton, 1959a: 254. *Trachostylea* Topsent, 1928c: 166. Taxonomic decision for synonymy: Hooper (1991), Hooper *et al.* (1999), this work.

#### Type species

*Haliphysema tubulatus* Bowerbank, 1873c (by original designation).

### Definition

Raspailiidae with at least two size classes of rhabdostyles of similar geometry, the larger (smooth or partially spined) core spongin fibres, and the smaller (partially spined) echinate fibres although neither are localised to any region of the skeleton; choanosomal skeletal structure is predominantly plumose, with spicules and fibres amalgamated into bulbous tracts ('fibre-bundles'), more-or-less compacted in the axial skeleton, becoming increasingly plumose as they ascend to the periphery, eventually producing a shaggy, compartmentalised or conulose surface; axial and extra-axial skeletons undifferentiated apart from greater amalgamation of fibre-bundles in the axis.

### Diagnosis

Growth forms tubular, cup-shaped, lobate, lamellate or erect cylindrical-digitate; individual lobes or branches are composed of large fibre-bundles amalgamated at the core or base of the sponge, diverging and becoming increasingly plumose towards the periphery, eventually producing a compartmentalised surface of discrete lobes or shaggy surface processes. Ectosomal skeleton ranges from: well developed, 'specialised raspailiid' (consisting of long subectosomal extra-axial styles protruding through the surface, surrounded by sparse brushes of ectosomal auxiliary spicules); vestigial (with wispy raphidiform or sinuous ectosomal auxiliary spicules scattered sparsely and indiscriminately over the surface); or absent completely (with only choanosomal principal spicules protruding through the surface, forming discrete surface bundles). Long subectosomal extra-axial spicules produce a hispid surface in some species. Choanosomal skeletal structure predominantly plumose (with very few reticulate connecting fibres, and these mainly towards the axis), with virtually no differentiation between axial and peripheral skeletons. Ascending fibres nearly fully cored by larger choanosomal principal rhabdostyles, forming dense plumose bundles particularly on fibre nodes, and echinated by smaller rhabdostyles, together producing bulbous spiculo-spongin tracts (termed here 'fibre-bundles'); smaller echinating rhabdostyles more-or-less evenly dispersed throughout the skeleton; interconnecting fibres, if present, are aspicular or paucispicular, and generally confined to the axial region. Megascleres consist of larger choanosomal principal rhabdostyles usually with a relatively slight basal rhabd, entirely smooth or with recurved spines only on apical part of spicules. Smaller echinating rhabdostyles in one or two categories have more pronounced basal rhabd, often prominently subtylote, entirely smooth or with spines only at the apex of spicules, or covering most of the spicule except for the base, or rarely completely spined. Subectosomal extra-axial styles or anisoxeas, if present are long and protrude through the surface. Ectosomal auxiliary styles or anisoxeas, if present are wispy, sinuous or raphidiform, often vestigial. Raphide microscleres are present in only one species.

### Description of type species

*Aulospongius tubulatus* (Bowerbank, 1873c) (Fig. 6).

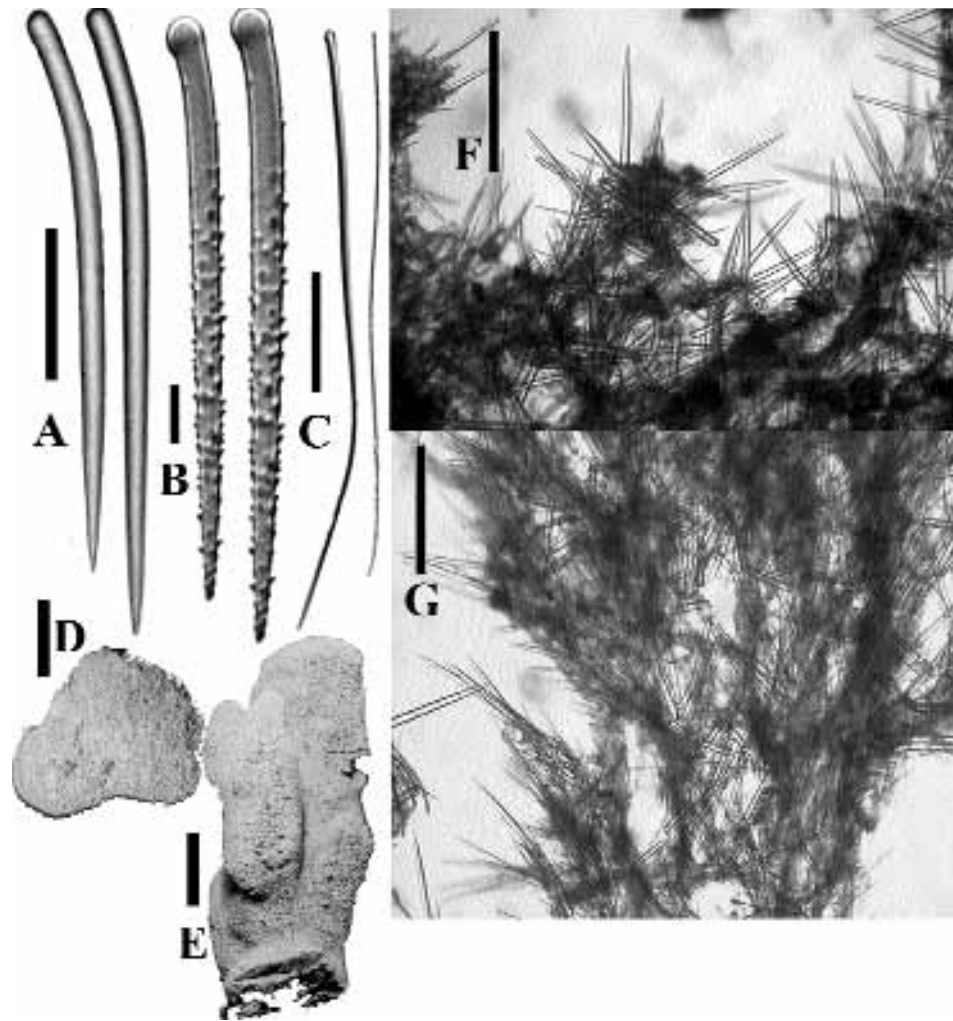
**Synonymy.** *Haliphysema tubulatus* Bowerbank, 1873c: 29; *Aulospongius tubulatus*; Norman, 1878: 267; *Axinella tubulata*; Dendy, 1889: 89.

**Material examined.** Holotype: BMNH 1873.7.21.9 – Ceylon (Sri Lanka).

**Description.** Growth form subspherical, massive, tubular, composed of amalgamated fibre-bundles that extend to the surface and produce a compartmentalised surface of discrete conules; ectosome with vestigial 'raspailiid skeleton' composed of sinuous or raphidiform ectosomal auxiliary styles scattered sparsely and indiscriminately over the surface, and with plumose bundles of both larger and smaller rhabdostyles protruding through the surface mainly at the ends of conules; no subectosomal extra-axial spicules; adjacent surface conules interconnected by aspicular (membranous) collagen; choanosomal skeleton exclusively plumose with fibre-bundles fused relatively closely towards the base of the sponge and axis of the skeleton, becoming increasingly plumose towards the periphery, and eventually completely discrete/ compartmentalised at the surface; fibre-bundles composed of rhabdostyles, both coring and echinating fibres, forming ascending multispicular columns, branching or unbranched towards their apex, bonded together with light granular collagen; larger smooth choanosomal principal rhabdostyles extend out from fibres in plumose bundles, particularly near periphery of skeleton; smaller spined rhabdostyles heavily echinate fibres and fibre nodes; megascleres consist of larger coring choanosomal principal rhabdostyles with slightly subtylote or rounded bases, slight basal rhabd, fusiform points, completely smooth ( $304\text{--}462 \times 16\text{--}24 \mu\text{m}$ ); smaller echinating rhabdostyles with entirely smooth, slightly rhabdose, slightly swollen bases, and small spines covering apical half of spicule ( $109\text{--}126 \times 5\text{--}10 \mu\text{m}$ ); long, thin, curved, sinuous or raphidiform ectosomal auxiliary styles ( $212\text{--}250 \times 2\text{--}3 \mu\text{m}$ ); subectosomal extra-axial spicules absent. Microscleres absent.

**Remarks.** Re-examination of type material by Hooper *et al.* (1999) confirmed the synonymy proposed above between *Aulospongius* and *Aulospongiella* (type species *Axinella monticularis* Ridley & Dendy, 1886, by original designation and monotypy; holotype BMNH 1887.5.2.20), *Heterectya* (type species *Raspailia* (?) *villosa* Thiele, 1898, by original designation; holotype ZMB 2204), *Rhaphidectyon* (type species *Rhaphidectyon spinosum* Topsent, 1927b, by original designation and monotypy; schizotypes MNHN DT 1139, BMNH 1930.7.1.39) and *Hemectyonilla* (type species *Stylostichon involutum* Kirkpatrick, 1903b, by original designation and monotypy; holotype BMNH 1902.11.16.33). *Trachostylea* Topsent (type species *T. semota* Topsent, 1928c, by monotypy, holotype not seen, possibly MOM) should also be referred here (Van Soest, pers.comm.). It has two size classes of acanthose styles, the smaller more rhabdose and subtylote than the larger, the larger only slightly curved near the base. Topsent (1928c) described the skeleton as a relatively lax unispicular reticulate network, not very regular, without distinct tracts and lacking apparent spongin, and the larger spicules only slightly projecting through as a surface hispidation. The species remains poorly known only from its original description and its precise assignment requires corroboration from re-examination of type material.

Rhabdostyles have traditionally been accorded primary diagnostic significance for *Aulospongius* yet these also occur in two other raspailiid genera (*Raspailia* (*Raspaxilla*) including synonyms *Echinaxia* and *Axinetia*, and *Endectyon* (*Hemectyon*)), and ostensibly also in *Cantabrina* (included here as *incertae sedis* in Raspailiidae). They are also found in other Poecilosclerida (*Rhabderemia*, Rhabderemiidae; *Biemna*, Desmacellidae), and the Halichondrida families Desmoxiidae (*Halicnemis* Bowerbank, *Higginsia* Higgin), and Bubaridae (*Rhabdoploca* Topsent,



**Fig. 6.** *Aulospongus*. A–G, *A. tubulatus* (Bowerbank) (holotype). A, choanosomal principal rhabdostyles (scale 100  $\mu\text{m}$ ). B, echinating rhabdostyles (scale 10  $\mu\text{m}$ ). C, ectosomal auxiliary styles (scale 50  $\mu\text{m}$ ). D, holotype (scale 3 cm). E, Dendy (1922b) 'Investigator' specimen (scale 3 cm). F, ectosomal skeleton (scale 250  $\mu\text{m}$ ). G, choanosomal skeleton (scale 250  $\mu\text{m}$ ).

*Hymerhabdia* Topsent, and *Monocrepidium* Topsent), with the implication that they have been derived independently within each group (homoplastic developments). Amongst the rhabdose raspailiid genera, however, *Aulospongus* differs in having two size categories of rhabdostyles (the larger, smooth or partially spined rhabdostyles coring fibres, and the smaller, usually spined rhabdostyles echinating fibres); a plumose skeletal structure composed of ascending compressed fibre-bundles (with few or no reticulate elements, and in cases where reticulate interconnecting fibres are present these are usually aspicular and disappear completely in the peripheral skeleton); lacking any differentiation between axial and extra-axial regions of the skeleton (although plumose fibres are slightly more compressed in the axis than in the periphery). In *Aulospongus*, unlike other rhabdose raspailiid genera, the larger choanosomal principal rhabdostyles bear a striking resemblance to, and are probably commonly derived from, the smaller echinating rhabdostyles. These smaller rhabdostyles are found in all three rhabdose raspailiid genera, and are probably homologous and derived from typical raspailiid echinating acanthostyles. In contrast *Raspaxilla* and *Hemectyon*, as in most raspailiids, have fibres cored by non-rhabdose, smooth styles of distinctly different geometry and origin from the rhabdose echinating spicules.

Hooper *et al.* (1999) found the remnants of a specialised raspailiid ectosomal skeleton to be present in both the type species of *Aulospongus* (*A. tubulatus*) and *Hemectyonilla* (*Stylostichon involutum*), a character overlooked by previous authors. This discovery (a) confirmed the synonymy between *Aulospongus* and *Hemectyonilla*, proposed tentatively by Hooper (1991), (b) provided more firm evidence in support of the inclusion of *Aulospongus* in the Raspailiidae, previously considered to be relatively atypical of the family, and (c) illustrated that ectosomal specialisation is easily lost within a raspailiid taxon, ranging from well developed, typical 'raspailiid condition' (e.g., *A. gardineri* (Dendy)), vestigial with few sinuous ectosomal spicules (e.g., the type species), to absent completely (e.g., *A. monticularis* (Ridley & Dendy)).

A detailed discussion of the genus in relation to other rhabdose raspailiids, and a phylogenetic and biogeographic analysis of species is provided by Hooper *et al.* (1999).

#### Distribution

*Aulospongus* contains 11 species and has a disjunct geographic distribution, from the N Atlantic (São Vicente and Cape Verde Islands), SW Indian Ocean (Natal), W and central Indian

Ocean (Zanzibar, Kenya, Gulf of Aden, Arabian Gulf, S Arabian coast, Amirante, India, Sri Lanka), NW Pacific (Japan) and SW Pacific Ocean (New Caledonia), E Pacific (Gulf of California), and Caribbean (Colombia and Jamaica). Biogeographic analysis showed it to have a pan-equatorial, predominantly tropical-subtropical distribution, with rare incursions into cooler temperate waters, in contrast to the other rhabdose raspailiids which are either centred on the Pacific rim, distributed in tropical, temperate and antiboreal waters, extending into the Antarctic (*Raspaxilla*) or known only from the Caribbean (*Hemectyon*).

### **ECTYOPLASIA TOPSENT, 1930**

#### **Synonymy**

*Ectyoplasia* Topsent, 1930: 23–4; de Laubenfels, 1936a: 102; Wiedenmayer, 1977b: 158.

#### **Type species**

*Spongia tabula* Lamarck, 1814 (by original designation).

#### **Definition**

Raspailiidae with a single category of undifferentiated choanosomal styles, and club-shaped acanthostyles bearing large clavulate spines on the apex and a smooth bulbous base.

#### **Diagnosis**

Flabellate, flattened arborescent or tubular growth form, with even or slightly corrugated hispid surface. Choanosomal skeleton slightly compressed axial reticulation of spongin fibres cored by styles or anisoxeas, echinated by clavulate acanthostyles; subectosomal extra-axial skeleton of radially arranged plumose ascending tracts, composed of undifferentiated choanosomal styles protruding through ectosome, interconnected by uni- or paucispicular transverse spicule tracts producing regular reticulation; ectosomal region with a specialized skeleton of small styles or anisoxeas typically forming brushes around choanosomal styles at surface, but sometimes lying tangential to surface. Structural megascleres styles or rhabdostyles of two sizes, sometimes with anisoxeote or strongylole modifications; echinating spicules always acanthostyles with clavulate points; microscleres absent.

#### **Description of type species**

*Ectyoplasia tabula* (Lamarck, 1814) (Fig. 7).

**Synonymy.** *Spongia tabula* Lamarck, 1814: 374. *Ectyoplasia tabula*; Topsent, 1930: 23.

**Material examined.** Holotype: MNHN DT553 – East of Cape Leeuwin, Western Australia.

**Description.** Flattened bifurcate digitate, stalked, with more-or-less regular lateral surface ridges, sandpaper-like stiff texture; ectosomal skeleton discrete bundles of ectosomal auxiliary styles or anisoxeas ( $244\text{--}331 \times 4\text{--}7 \mu\text{m}$ ) surrounding bases of protruding choanosomal styles extending from extra-axial skeleton; extra-axial skeleton more-or-less radial non-plumose bundles of choanosomal axial spicules, in uni- or paucispicular tracts, extending from axis and protruding through surface for only short

distance; choanosomal and subectosomal megascleres undifferentiated; choanosomal skeleton with distinct, irregularly reticulate axis, radial non-reticulate extra-axis, and plumose ectosomal spicule brushes; well developed spongin fibres cored by paucispicular tracts of choanosomal styles ( $438\text{--}843 \times 17\text{--}29 \mu\text{m}$ ) becoming plumose towards periphery; fibres moderately heavily echinated by clavulate acanthostyles ( $111\text{--}146 \times 6\text{--}11 \mu\text{m}$ ); sub ectosomal megascleres completely undifferentiated from choanosomal spicules.

**Remarks.** The type species of *Ectyoplasia* shows classical raspailiid ectosomal specialization, with brushes of ectosomal auxiliary spicules surrounding the bases of protruding spicules. By comparison, *E. frondosa* (Lendenfeld) and *E. ferox* (Duchassaing & Michelotti) have an atrophied ectosomal skeleton containing only sparsely dispersed tangential ectosomal spicules. Topsent (1930) suggested that the genus differed from *Raspailia* (*s.s.*) in having less compressed skeletal architecture, clavulate tips on acanthostyles, and 'exceptional differentiation' of the exhalant pores (oscula) along the lateral margins of branches. The latter feature has little systematic importance at the generic level, and in any case it does not occur in either *E. frondosa* or *E. vannus* Hooper. Similarly, supposed differences in skeletal architecture between the two genera are not upheld upon comparison with other species (e.g., compare *Raspailia phakellopsis* Hooper, 1991 with *E. frondosa*, and *R. darwinensis* Hooper, 1991 with *E. ferox*). Thus in Topsent's (1930) conception of *Ectyoplasia* this leaves only acanthostyle morphology, or modifications to acanthostyles, as a primary distinguishing feature although Hooper (1991) also noted that *Ectyoplasia* has well differentiated axial and extra-axial skeletons like *Raspailia s.s.* but in which spicules forming both structures are identical; i.e., the genus lacks specialized subectosomal megascleres.

#### **Distribution**

Four species are described from tropical and subtropical Australia, Indonesia, Micronesia (Hooper, 1991; Hooper *et al.*, 1999), and Caribbean (e.g., Wiedenmayer, 1977b).

### **ENDECTYON TOPSENT, 1920**

#### **Synonymy**

*Endectyon* Topsent, 1920a: 25 (see subgenera for full synonymy).

#### **Type species**

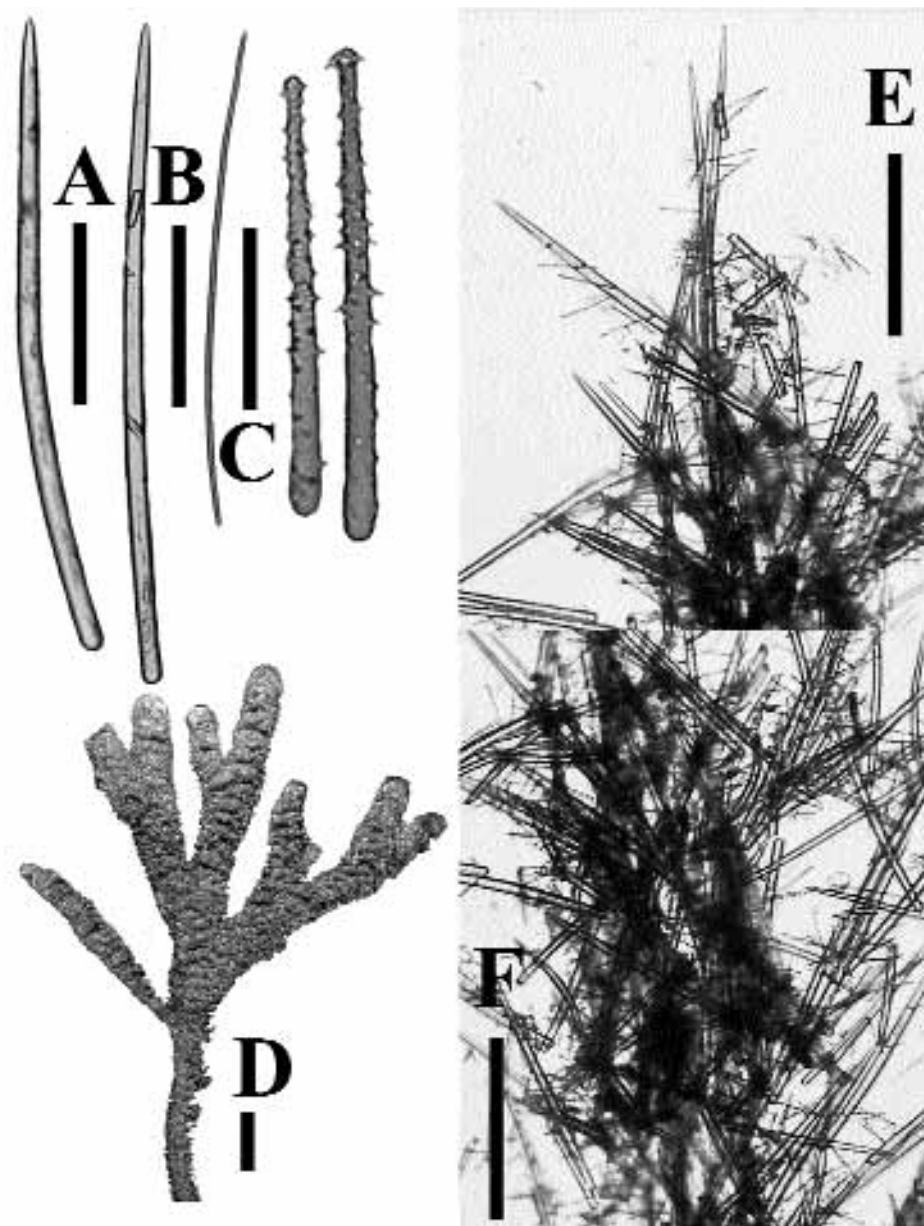
*Phakellia tenax* Schmidt, 1870 (by original designation).

#### **Definition**

Raspailiidae with clavulate modifications to acanthostyle geometry, and acanthostyles confined to a particular region outside of the skeletal axis.

#### **Diagnosis**

Prominently hispid, conulose surface, and typically arborescent growth forms. Skeleton always with marked axial and extra-axial



**Fig. 7.** *Ectyoplasia*. A–F, *E. tabula* (holotype). A, choanosomal styles (scale 200  $\mu\text{m}$ ). B, ectosomal auxiliary style (scale 100  $\mu\text{m}$ ). C, clavulate acanthostyles (scale 50  $\mu\text{m}$ ). D, specimen NTM Z2677 (scale 3 cm). E, ectosomal skeleton (scale 150  $\mu\text{m}$ ). F, choanosomal skeleton (scale 150  $\mu\text{m}$ ).

differentiation of skeleton; axial skeleton with well developed spongin fibres forming compressed reticulation, cored by stout choanosomal styles; extra-axial subectosomal skeleton radial or plumose, with multi- or paucispicular tracts of long subectosomal styles (subgenus *Endectyon*) or choanosomal styles (subgenus *Hemectyon*), sometimes connected by unispicular tracts forming hexagonal meshes, usually protruding through surface. Ectosomal skeleton varies from typical raspailiid condition, with thin ectosomal styles grouped in brushes around protruding subectosomal styles (subgenus *Endectyon*), to surface brushes composed of subectosomal styles only (nominal genus *Basiectyon*), to brushes of acanthostyles surrounding choanosomal styles (subgenus *Hemectyon*). Erect brushes of echinating acanthostyles located on outer margin of axial skeleton, surrounding boundary between

extra-axial and axial regions, or forming plumose brushes along length of extra-axial tracts, or localized exclusively to base of sponge (nominal genus *Basiectyon*). Structural megascleres smooth styles of 2–3 size categories; echinating megascleres modified acanthostyles and/or acanthostrongyles with peculiar strongly curved (clavulate) hooks on shaft, base, and/or apex. Microscleres absent.

#### Remarks

*Endectyon* differs from typical raspailiids (e.g., *Raspailia*) in having clavulate modifications to acanthostyle geometry. Moreover, unlike species of *Raspailia* in which echinating spicules are relatively evenly dispersed throughout the skeleton, *Endectyon*



has these confined to a particular region of the skeleton (i.e., outside the axis). Some species of *Endectyon* show reduced characteristics from the typical condition. The affinities of these species are not completely obvious, but the most reasonable interpretation is that they are forms of *Endectyon* (Hooper, 1991). Hooper *et al.* (1999) proposed the recognition of two subgenera.

Species of *Endectyon* (*Endectyon*) (including *Basiectyon*, type species *Basiectyon pilosus* Vacelet, 1961a, by monotypy; lectotype SMEM 1705(1), schizotype MNHN DNBE 718L) have acanthostyles with recurved (clavulate) hooks on both ends and lack any basal rhabd, and with a specialised ectosomal skeleton. *Endectyon* (*Hemectyon*) has a more openly reticulate axial skeletal, lacking differentiated subectosomal megascleres in the extra-axial skeleton, lacking a specialized ectosomal skeleton, and the bases of acanthostyles are predominantly smooth, subtylote, and some are slightly rhabdlose. *Basiectyon* also has a loosely reticulate axial skeleton, lacks ectosomal specialization, and its acanthostyles are localized at the base of the sponge, and based on acanthostyle morphology it appears to be most closely related to *Endectyon* (*Endectyon*).

Based on acanthostyle geometry, acanthostyle distribution, and axial and extra-axial skeletal structure all three genera share features which argue for their inclusion into a single taxon (see Topsent 1920a).

#### Distribution

Twelve species have been described from the Mediterranean (Schmidt, 1870; Vacelet, 1961a), North Atlantic (Schmidt, 1870; Topsent, 1892c; Burton, 1930c; Cabioch, 1968a), Indian Ocean (Ridley & Dendy, 1886; Dendy, 1887; Thomas, 1976), and tropical Australian seas (Lamarck, 1814; Hooper, 1991) (Hooper *et al.*, 1999).

#### SUBGENUS ENDECTYON TOPSENT, 1920

##### Synonymy

*Endectyon* Topsent, 1920a: 25; Burton, 1937: 34; Cabioch, 1968b: 224; Thomas, 1976: 169; Hooper, 1991: 1284. *Basiectyon* Vacelet, 1961a: 37. Taxonomic decision for synonymy: Hooper (1991), Hooper *et al.* (1999).

##### Type species

*Phakellia tenax* Schmidt, 1870 (by original designation).

##### Definition

*Endectyon* with recurved (clavulate) hooks on both ends and lacking any basal rhabd on echinating megascleres, and lacking a special ectosomal skeleton composed of ectosomal styles/anisoxeas grouped around long extra-axial styles.

##### Diagnosis

Arborescent growth form; with a compressed axial skeleton cored by stout choanosomal principal styles, and plumose extra-axial skeleton cored by long subectosomal auxiliary styles producing a hispid surface, surrounded by bundles of ectosomal auxiliary styles at the surface. Echinating acanthostyles are confined to

outside the axial skeleton, and have recurved (clavulate) hooks on both ends but lack any basal rhabd.

##### Description of type species

*Endectyon tenax* (Schmidt, 1870) (Fig. 8).

**Synonymy.** *Phakellia tenax* Schmidt, 1870: 62. *Endectyon tenax*; Topsent, 1920a: 23. *Endectyon* (*Endectyon*) *tenax*; Hooper *et al.*, 1999: 695.

**Material examined.** Holotype: LMJG unregistered, schizotypes MNHN DCL2163, 1194, BMNH 1870.5.3.170 – Florida.

**Description.** Erect, arborescent growth form; choanosomal skeleton with compressed axial skeleton composed of stout choanosomal styles (330–400 × 15–22 μm) enclosed in well developed spongin fibres; extra-axial skeleton plumose, composed of long subectosomal styles (1000–1300 × 20–22 μm) with little or no spongin, protruding a long way and hispidating surface, also with irregular reticulate spicule skeleton composed of choanosomal styles extending up to surface; protruding auxiliary spicules surrounded by bundles of ectosomal styles (220–230 × 2–3 μm) on surface; echinating acanthostyles with clavulate spines on both ends and partially on shaft (122–133 × 15–18 μm), implanted at diverse angles, usually in heavy concentrations, only in extra-axial tracts, producing a unispicular network between tracts in deeper parts of subectosome, standing erect on ectosome closer to surface.

**Remarks.** See remarks for subgenus *Endectyon* (*Hemectyon*).

##### Distribution

Caribbean, Mediterranean, North Atlantic, Indo-Pacific (Hooper, 1991; Hooper *et al.*, 1999).

#### SUBGENUS HEMECTYON TOPSENT, 1920

##### Synonymy

*Hemectyon* Topsent, 1920a: 27; Hooper, 1991: 1284; Hooper *et al.*, 1999: 695.

##### Type species

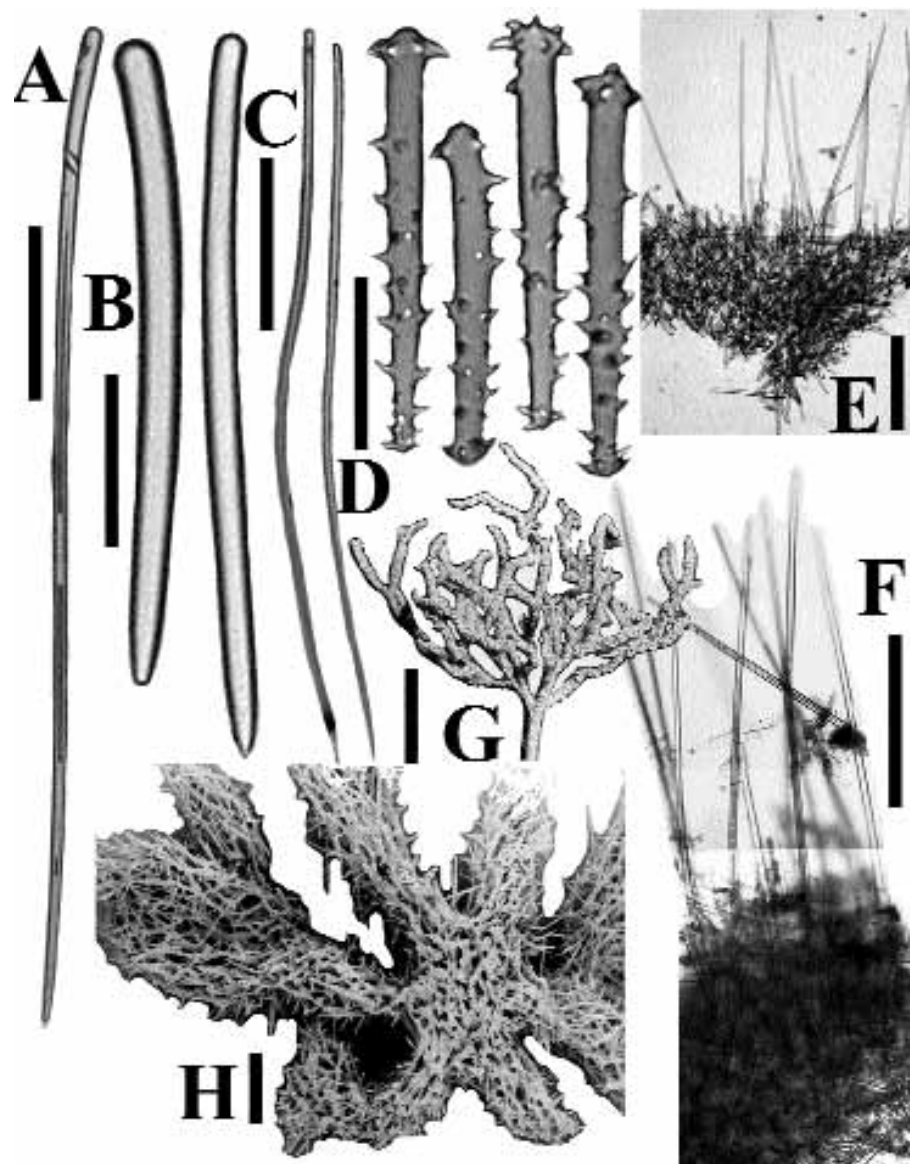
*Raspailia* (?) *hamata* Schmidt, 1870 (by original designation).

##### Definition

*Endectyon* with subtylote echinating rhabdostyles bearing clavulate spines only on apex, grouped around protruding choanosomal styles in the ectosomal skeleton.

##### Diagnosis

Arborescent growth form; echinating acanthostyles bearing clavulate spines only on apex of spicule (not on base), and base is smooth and sometimes slightly rhabdlose; echinating spicules localised outside the axial skeleton, usually at the junction of axial and extra-axial skeletons, and/or forming plumose brushes along extra-axial skeleton, and often also produce spicule brushes at the surface; axial skeleton compressed reticulate; extra-axial skeleton plumose(-reticulate) cored by choanosomal styles.



**Fig. 8.** *Endectyon* (*Endectyon*). A–F, *E. (Endectyon) tenax* (fragment of holotype BMNH 1870.5.3.170). A, subectosomal style (scale 200  $\mu\text{m}$ ). B, choanosomal styles (scale 100  $\mu\text{m}$ ). C, ectosomal styles (scale 50  $\mu\text{m}$ ). D, acanthostrongyles (scale 50  $\mu\text{m}$ ). E, choanosomal skeleton (scale 300  $\mu\text{m}$ ). F, peripheral skeleton (scale 300  $\mu\text{m}$ ). G–H, *E. (Endectyon) elyakovi* Hooper, 1991 (paratype NTMZ2738). G, paratype (scale 3 cm). H, skeletal structure (scale 500  $\mu\text{m}$ ).

#### Description of type species

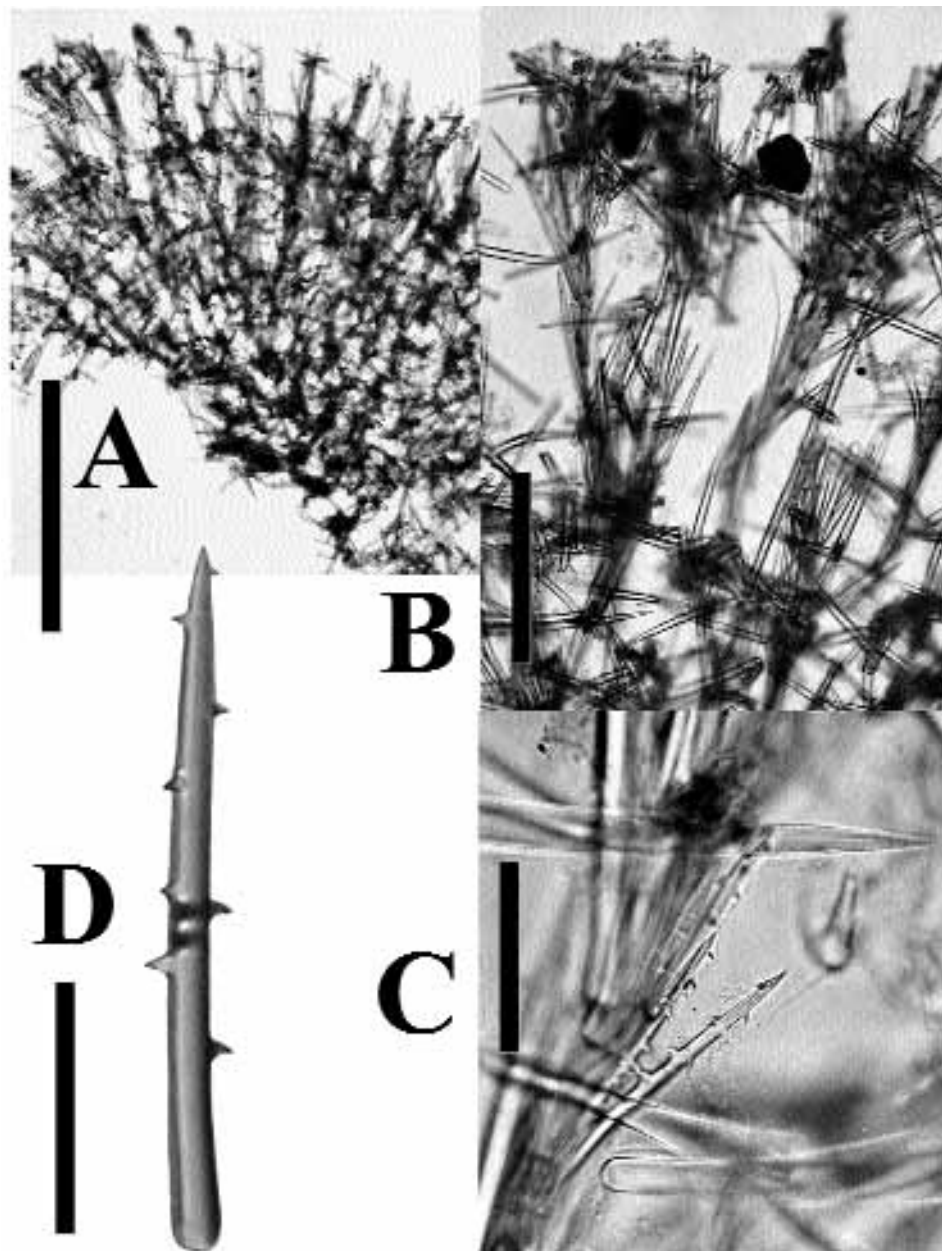
*Endectyon* (*Hemectyon*) *hamata* Schmidt, 1870 (Fig. 9).

**Synonymy.** *Raspailia* (?) *hamata* Schmidt, 1870: 62; *Hemectyon hamatum*; Topsent, 1920a: 26; *Endectyon hamata*; Hooper, 1991: 1284; *Endectyon* (*Hemectyon*) *hamata*; Hooper *et al.*, 1999: 695.

**Material examined.** Holotype: MZUS P0151 (not seen), fragment MNHN DT2161 – ‘West Indies’.

**Description.** Growth form arborescent, cylindrical branches. Surface slightly corrugated. Colour pale brown in dry state. Specialised ‘raspailiid ectosomal skeleton’ absent, with only protruding bundles of a few choanosomal principal styles surrounded at their base by multispicular plumose bundles of rhabdostyles, although vestigial ectosomal auxiliary styles are scattered within the choanosomal skeleton. Axial and extra-axial skeleton moderately

well differentiated. Axial skeleton strongly reticulate, compressed, with heavy fibres cored by small choanosomal principal styles in multispicular tracts mostly running longitudinally through branches, and with few echinating rhabdostyles. Extra-axial skeleton radial-reticulate, without fibre-bundles, with ascending paucispicular tracts interconnected by unispicular transverse tracts of choanosomal principal styles. Echinating rhabdostyles predominantly on exterior surface of primary (ascending) extra-axial fibres, with greatest numbers concentrated at the surface in brushes. Megascleres consist of choanosomal principal styles slightly curved centrally, without basal rhabd, entirely smooth (270–615  $\times$  8–18  $\mu\text{m}$ ). Echinating rhabdostyles with very slight basal rhabd, smooth slightly swollen base, and large clavulate spines only on apical extremity or apical 1/3rd of spicule at most (120–150  $\times$  5–10  $\mu\text{m}$ ). Subectosomal extra-axial styles absent. Ectosomal styles vestigial and scattered within the choanosome (220–275  $\times$  1–2  $\mu\text{m}$ ). Microscleres absent.



**Fig. 9.** *Endectyon* (*Hemectyon*). A–D, *E. (Hemectyon) hamata* (fragment of holotype MNHNLBIMDT2161). A, choanosomal skeleton (scale 1 mm). B, peripheral skeleton (scale 200 µm), C, echinating rhabdostyles in fibres (scale 50 µm). D, echinating rhabdostyle (scale 50 µm).

**Remarks.** *Hemectyon* was merged into synonymy with *Endectyon* by Hooper (1991), on the basis that the two differed in only a few characters: *Endectyon* (*s.s.*) with a special ectosomal skeleton composed of ectosomal styles/anisoxeas grouped around long extra-axial styles, whereas *Hemectyon* lacked both true ectosomal and extra-axial spicules (having instead acanthostyles grouped around protruding choanosomal styles), and the latter also had more openly reticulate axial skeleton than *Endectyon* (*s.s.*). More importantly though, in *Hemectyon* the bases of acanthostyles are predominantly smooth, subtulate, and some are slightly rhabdose, whereas those of *Endectyon* have recurved (clavulate) hooks on both ends and lack any basal rhabd. On this basis Hooper *et al.* (1999) used *Hemectyon* as a convenient subgenus within *Endectyon*, both having in common clavulate spines on acanthostyles, the latter

localised outside the axial skeleton (usually at the junctions of axial and extra-axial skeletons).

Comparisons between other raspailiids with rhabdose acanthostyles (*Aulospongia* and *Raspailia* (*Raspaxilla*)) are slightly misleading. Echinating acanthostyles in *Endectyon* (*Hemectyon*) are not truly rhabdose, like the other two genera, with the slight basal curvature often overemphasised by the basal swelling on these spicules. Nevertheless, rhabdostyles in these three genera may be potentially confused. The subgenus contains only the type species, although arguably *E. fruticosa* (Dendy), *E. fruticosa aruensis* (Hentschel), and *E. xerampelina* (Lamarck) could also be included given that some (but not all) of their echinating acanthostyles have smooth, swollen, slightly rhabdose bases with clavulate spines mainly on the apex of the spicule. They are not included, however, because other spicules

also have clavulate spines on their bases and more closely resemble those of *Endectyon* species (see Hooper, 1991).

#### Distribution

Caribbean.

#### *EURYPON* GRAY, 1867

#### Synonymy

*Eurypon* Gray, 1867a: 521; de Laubenfels, 1936a: 107; Bergquist, 1970: 31. *Epicles* Gray, 1867a: 521; de Laubenfels, 1936a: 110; Bergquist, 1970: 31. *Dragmatyle* Topsent, 1904b: 195. *Acantheurypon* Topsent, 1927b: 15; Topsent, 1928c: 291. *Tricheurypon* Topsent, 1928c: 295; de Laubenfels, 1950a: 80; Wiedenmayer, 1977b: 159. *Protoraspailia* Burton & Rao, 1932: 342. *Leptochelastra* de Laubenfels, 1936a: 111. *Quixilla* de Laubenfels, 1936a: 88. *Proraspailia* Lévi, 1958: 27. Taxonomic decision for synonymy: Hooper (1991), and this work.

#### Type species

*Hymeraphia clavata* Bowerbank, 1866 (by monotypy).

#### Definition

Typically encrusting Raspailiidae with microcionid skeletal structure in which fibre nodes ascend from the basal layer of spongin.

#### Diagnosis

Encrusting, massive or digitate growth forms. Surface hispid, even, granular or conulose. Encrusting species have a microcionid choanosomal skeletal structure with a basally compressed layer of spongin fibres lying on the substrate producing small spongin-fibre nodes echinated by acanthostyles, and radially disposed extra-axial skeleton composed of subectosomal styles standing perpendicular to and embedded in basal fibres. Massive species have slightly axially compressed plumose tracts of extra-axial styles, often forming fan-like bundles, and tracts lightly echinated by acanthostyles. Extra-axial styles may be partially or entirely spined (*Acantheurypon*). Ectosomal specialization present (*s.s.*) or absent; if present ectosomal skeleton consists of fine monactinal (or diactinal) spicule brushes surrounding single protruding extra-axial styles. Structural megascleres consist of 1–2 categories of styles or subtylostyles (rarely modified to oxeas); echinating acanthostyles microcionid-like, typically long and with subtylote bases. Several species (*Tricheurypon*, *Dragmatyle* = *Eurypon*) have raphides in trichodragmata.

#### Description of type species

*Eurypon clavata* (Bowerbank, 1866) (Fig. 10).

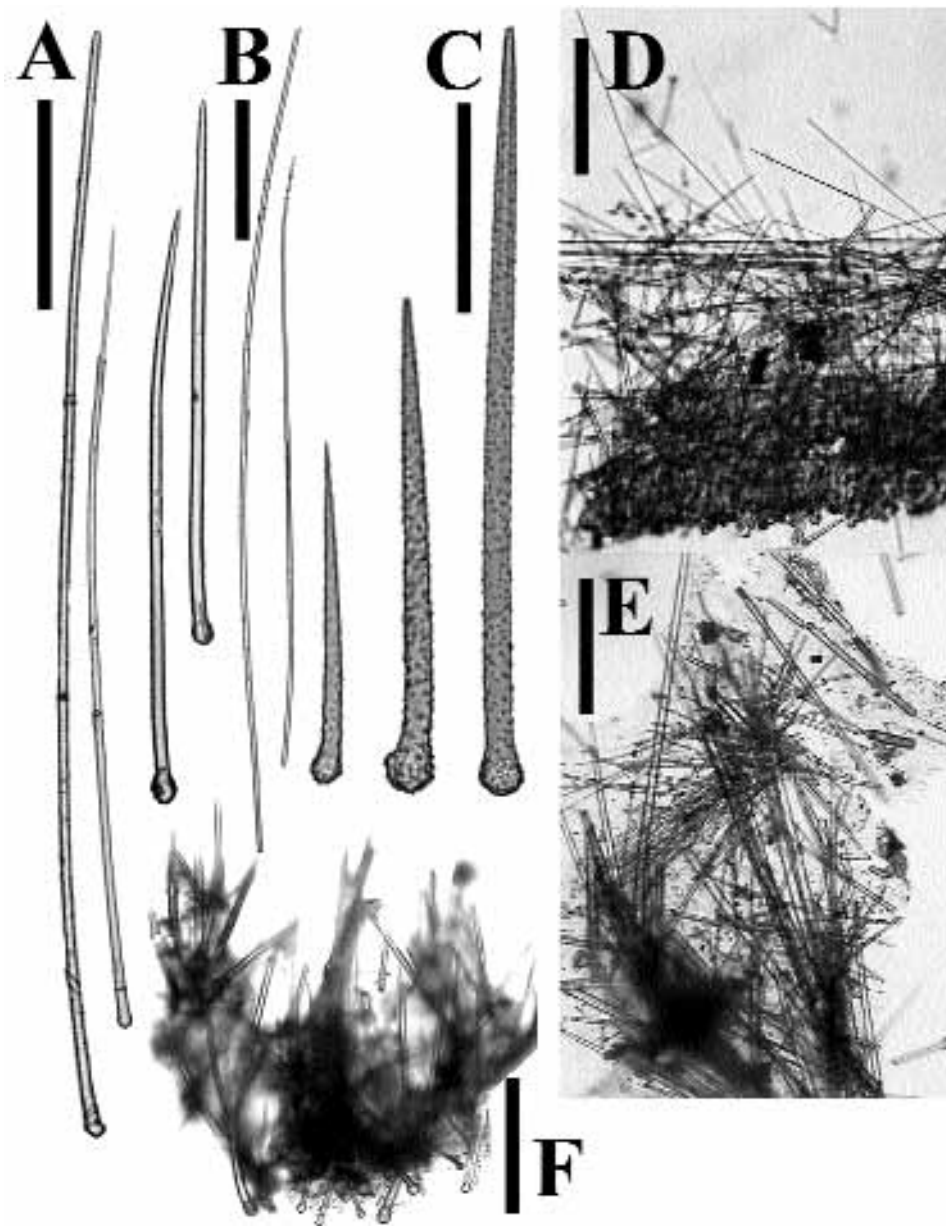
**Synonymy.** *Hymeraphia clavata* Bowerbank, 1866: 143. *Eurypon clavatum*; Vacelet, 1969: 186. *Eurypon clavata*; Hooper, 1991: 1313.

**Material examined.** Holotype: BMNH 1877.5.21.1556 (including 2 unregistered BMNH slides made from type, and MNHN DT942) – Shetland Is. Other material. BMNH 1953.11.11.118.

**Description.** Encrusting growth form; choanosomal skeleton with microcionid structure consisting of a basal layer of spongin on the substrate giving rise to individual fibre nodes, each node cored by thick bundles of long, completely smooth subectosomal (sub)tylostyles (685–2310 × 11–28 μm) forming plumose columns that penetrate and extend a long way through the surface, and echinated by thick bundles of acanthostyles (64–472 × 5–19 μm); acanthostyles most abundant on basal layer of spongin; acanthostyles completely spined, with bulbous tylote bases, and showing a large size range; ectosomal skeleton with ectosomal styles (418–695 × 3–5 μm) forming plumose bouquets surrounding the base of where subectosomal (sub)tylostyles pierce the surface, and also lying paratangential to surface. Microscleres absent.

**Remarks.** The use of the name *Eurypon* over *Epicles* (type species *Hymeraphia radiata* Bowerbank, 1866, by monotypy), was discussed by Hooper (1991), where the latter has page-line priority over the former. Similarly, Hooper (1991) broadened the definition of *Eurypon* to include species with spined as well as smooth choanosomal megascleres (to accommodate species of *Acantheurypon* (type species *Hymeraphia pilosella* Topsent, 1904b, by original designation), with or without raphidiform microscleres to allow the inclusion of species referred to *Tricheurypon* (type species *Hymeraphia viridis* Topsent, 1889, by monotypy) and *Protoraspailia* (type species *Proraspailia polyplumosa* Lévi, 1958, by monotypy), and with the addition of long raphidiform oxeote spicules scattered throughout the mesohyl (*Protoraspailia*, with type species *Protoraspailia cactoides* Burton & Rao, 1932: 343, by original designation). To this list should be added three other nominal genera, overlooked by the Hooper (1991) revision. *Dragmatyle* (type species *Dragmatyle lictor* Topsent, 1904b, by original designation), is very similar to *Tricheurypon*, and is included in synonymy here following the suggestion of Hallmann (1917c). *Dragmatyle* has raphides in trichodragmata, ectosomal oxeas (described as tornotes but usually sharply pointed and flexuous) forming tangential and paratangential tracts (but not a specialised raspailiid skeleton), and also lacks echinating acanthostyles – thus representing a greatly reduced *Eurypon*. *Leptochelastra* de Laubenfels, 1936a (type species *Hymeraphia toureti* Topsent, 1894a: 30, by original designation; slide of holotype MNHN DT1840, from the Banc de Campêche, viewed by R.W.M. Van Soest, pers. comm.). It has tylostyles with grossly swollen heads, typical of *Eurypon*, in combination with short spined acanthostyles and bundles of thin oxeas gathered around the heads of the large tylostyles. Microscleres were not observed. Topsent's (1894a) description mentions dubious chelae and asters, but these are indeed foreign as he suspected. *Quixilla* de Laubenfels, 1936a: 88 (type species *Hymeraphia lacazei* Topsent, 1891a: 541, by original designation, type material not examined), is also clearly a synonym of *Eurypon*. The type species, from Roscoff, is thinly encrusting, with a highly hispid surface. Skeletal structure is hymedesmioid, consisting of long subtylostyles (up to 2 mm long, 20 μm wide), with their bases embedded in basal spongin and points protruding a long way through the surface, club-shaped echinating acanthostyles with heavy spines distributed all over the spicule (75–80 μm long, 10 μm wide), forming a dense erect palisade on the basal spongin, and ectosomal oxeas (230 μm long, 7 μm wide), forming a specialized raspailiid skeleton consisting of bundles surrounding the protruding long subtylostyles. No microscleres.

This broad definition of *Eurypon* is consistent with the treatment of the diverse and similar (homologous) features



**Fig. 10.** *Eurypon*. A–F, *E. clavatum*, holotype. A, subectosomal subtylostyles (scale 200  $\mu\text{m}$ ). B, ectosomal styles (scale 100  $\mu\text{m}$ ). C, echinating acanthostyles (scale 100  $\mu\text{m}$ ). D, section through peripheral skeleton (scale 300  $\mu\text{m}$ ). E, ectosomal skeleton (scale 100  $\mu\text{m}$ ). F, microcionid fibre clump (scale 100  $\mu\text{m}$ ).

in Microcionidae, in which genera containing smooth or spined megascleres (e.g., *Clathria* Schmidt, and *Dictyociona* Topsent or *Anaata* de Laubenfels), and with or without microscleres (e.g., *Clathria* and *Abila* Gray) have been merged (van Soest, 1984b; Hooper, 1996a). This comparison with Microcionidae is most appropriate for *Eurypon*, and many species have been removed from Raspailiidae (or Euryponidae) and synonymized with various microcionid genera (e.g., *Eurypon asodes* de Laubenfels, 1930: 27; and *E. microchela* Stephens, 1916: 240 were transferred to *Dictyociona* (de Laubenfels, 1936a); *E. rhopalophora* (Hentschel, 1912: 380), and *E. tenuissima* Stephens, 1916: 240 were transferred to *Microcionia* (Burton, 1959a; Lévi, 1960b)). Those species are now recognized as merely being encrusting *Clathria*-like sponges (Hooper, 1996a). Another aspect which has been used to differentiate the raspailiid-like taxa (*Eurypon*) from microcionid species (*Clathria s.l.*) is acanthostyle morphology (e.g., Berguist,

1970: 32), but given the diversity of those megascleres within obvious microcionids (i.e., chelae-bearing taxa), in some instances this difference must be questioned also. It is possible that *Eurypon* will be eventually divided amongst *Raspailia* (species of *Eurypon* with ectosomal oxeas), *Clathria* (*Clathria*) (without ectosomal megascleres), and *Clathria* (*Thalysias*) (with ectosomal styles or subtylostyles).

Similarly, it could be argued that *Eurypon* and *Hymeraphia* are also potential synonyms, differing only substantially in having microcionid versus hymedesmioid skeletal structure, respectively, and the possession of peculiar spination on acanthostyles in the latter genus. This may be a case for recognising these two taxa as subgenera within a single genus (in which case *Hymeraphia* would have priority), although this action is not formally proposed here without a larger study of the many encrusting raspailiid species and the diversity of their skeletal structures and spicule ornamentation.

*Eurypon* differs from *Raspailia* in having only up to three categories of megascleres (echinating acanthostyles, ectosomal styles/oxeas, and a single category of long spicule which is equated with the long subectosomal extra-axial megascleres found in typical *Raspailia*); basal rather than axial compression of the fibre skeleton, lacking true choanosomal megascleres, and with exclusively plumose architecture (or microcionid fibre structure in thinly encrusting forms). By comparison, typical *Raspailia* have four categories of megascleres. This is, however, a tentative separation based on skeletal architecture (which is not always a reliable diagnostic character).

#### Distribution

Worldwide.

#### HYMERAPHIA BOWERBANK, 1864

#### Synonymy

*Hymeraphia* Bowerbank, 1864: 189 (Not *Hymeraphia*; Hentschel 1912: 377). *Mesapos* Gray, 1867a: 543. Taxonomic decision for synonymy: Hooper (1991).

#### Type species

*Hymeraphia stellifera* Bowerbank, 1864 (by original designation).

#### Definition

Persistently encrusting Raspailiidae with hymedesmioid skeletal structure, echinating acanthostyles having bulbous tylote bases, with or without spines on the points, and often with other modifications to the distal portion of the spicule.

#### Diagnosis

Thinly encrusting growth form. Choanosomal skeleton reduced to basal membrane lying on substrate; bases of echinating acanthostyles and extra-axial styles embedded in basally compressed fibres, in radial or hymedesmioid arrangement, standing perpendicular to substrate, not grouped into brushes or other structures. Choanosomal megascleres absent. Extra-axial styles usually protrude a long way through the ectosome, surrounded by bouquets of ectosomal oxeas or styles at their point of penetration through the surface, or the ectosomal skeleton may be reduced to a tangential layer of oxeas/styles scattered over the surface. Megascleres include longer styles or tylostyles, thinner ectosomal styles/oxeas, and smaller tylostyles with prominently swollen tylote bases echinating the basal layer of spongin (those of type species also have modified stellate-acanthose points and slightly rhabdlose bases). Microscleres absent.

#### Description of type species

*Hymeraphia stellifera* Bowerbank, 1864 (Fig. 11).

**Synonymy.** *Hymeraphia stellifera* Bowerbank, 1864: 189.

**Material examined.** Holotype: BMNH 1877.5.21.460 (fragments BMNH 1910.1.1.87, 2354, 2355, MNHN DT2501) – Shetland, English Channel.

**Description.** Thinly encrusting growth form; choanosomal skeleton hymedesmioid with compressed basal layer of spongin in which the tylote bases of both long subectosomal (sub)tylostyles (295–1875 × 6–19 μm) and echinating acanthostyles (64–147 × 6–12 μm) are embedded, standing erect on the substrate; acanthostyles have slightly rhabdlose, smooth, swollen tubular bases and stellate-spined points; slender straight ectosomal oxeas (220–735 × 2–4 μm) form bouquets around the point of penetration of the longer subectosomal (sub)tylostyles through the surface. Microscleres are absent.

**Remarks.** The type species was redescribed by Ackers *et al.* (1992) from a living population. In their description they mention the presence of a specialised raspailiid ectosomal skeleton of bouquets of oxeas surrounding protruding long styles, whereas in the type specimen (and associated slide preparations) these spicules were uncommon (and hence previously overlooked by Hooper, 1991), and the specialised ectosomal skeleton was not observed in type material preparations.

*Hymeraphia* is unusual amongst Raspailiidae in its hymedesmioid skeletal structure, without any observable fibre nodes or ascending fibre tracts, superficially resembling the microcionid *Leptoclathria* (= *Clathria*) condition. Unlike the latter genus *Hymeraphia* lacks any differentiated choanosomal or subectosomal spicules, has modified acanthostyles, lacks microscleres, and has a specialised raspailiid ectosomal skeleton unique to the family. By comparison, *Hymeraphia sensu* Hentschel (1912) is a microcionid, with chelae, toxas, and ectosomal megascleres that do not form surface bouquets. Other thinly encrusting raspailiids, such as *Eurypon*, have plumose skeletal columns whereas *Hymeraphia* is strictly hymedesmioid. *Mesapos* Gray is an objective synonym (with type species *Hymeraphia stellifera* Bowerbank, 1864, by monotypy).

#### Distribution

Most species records are from the North Atlantic and Antarctica, whereas the genus is probably more widely distributed.

#### RASPACIONA TOPSENT, 1936

#### Synonymy

*Raspaciona* Topsent, 1936: 49; Sarà, 1958: 254; Vacelet, 1961a: 36; Pulitzer-Finali, 1977: 41.

#### Type species

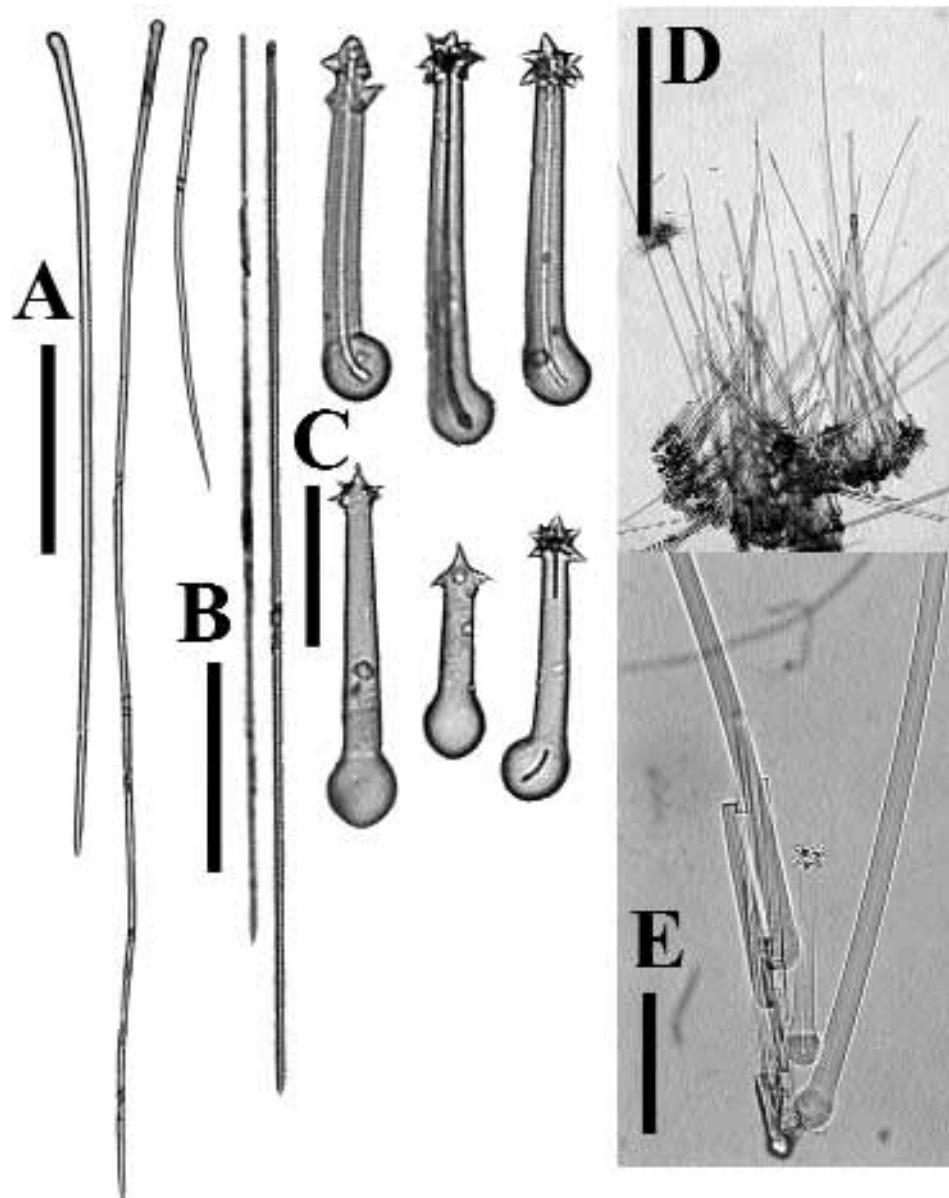
*Halichondria aculeata* Johnston, 1842 (by original designation).

#### Definition

Raspailiidae without axial compression of the skeleton but with loosely aggregated or plumose tracts of a single category of long styles.

#### Diagnosis

Lobo-digitate, or ramose-bushy growth forms; surface hispid and prominently microconulose. Choanosomal skeleton plumose,



**Fig. 11.** *Hymeraphia*. A–E, *H. stellifera*, holotype. A, subectosomal subtylostyles (scale 200  $\mu\text{m}$ ). B, ectosomal oxeas (scale 100  $\mu\text{m}$ ). C, echinating acanthostyles (scale 50  $\mu\text{m}$ ). D, section through peripheral skeleton (scale 500  $\mu\text{m}$ ). E, bundles of erect spicules (scale 50  $\mu\text{m}$ ).

consisting of basally compressed spongin fibres ascending through branches and diverging, but without any special category of choanosomal megasclere. Extra-axial skeleton with weakly developed, ascending, plumose columns of long flexuous subectosomal styles protruding through the ectosome, branching or forming occasional anastomoses, and forming shaggy surface microconules. Ascending extra-axial tracts echinated by acanthostyles, concentrated around the base of the plumose skeletal columns. Spongin predominant in the basal region, at the point of contact between plumose (extra-axial) tracts and compressed (axial) fibres; very little spongin occurs elsewhere in skeleton. Ectosomal skeleton with specialized spiculation of small styles arranged in bouquets around the protruding extra-axial styles. Megascleres include styles or subtylostyles of 2 sizes (ectosomal and subectosomal), and 1–2 size classes of acanthostyles ranging from basally spined to entirely spined. Microscleres absent.

#### Description of type species

*Raspaciona aculeata* (Johnston, 1842) (Fig. 12).

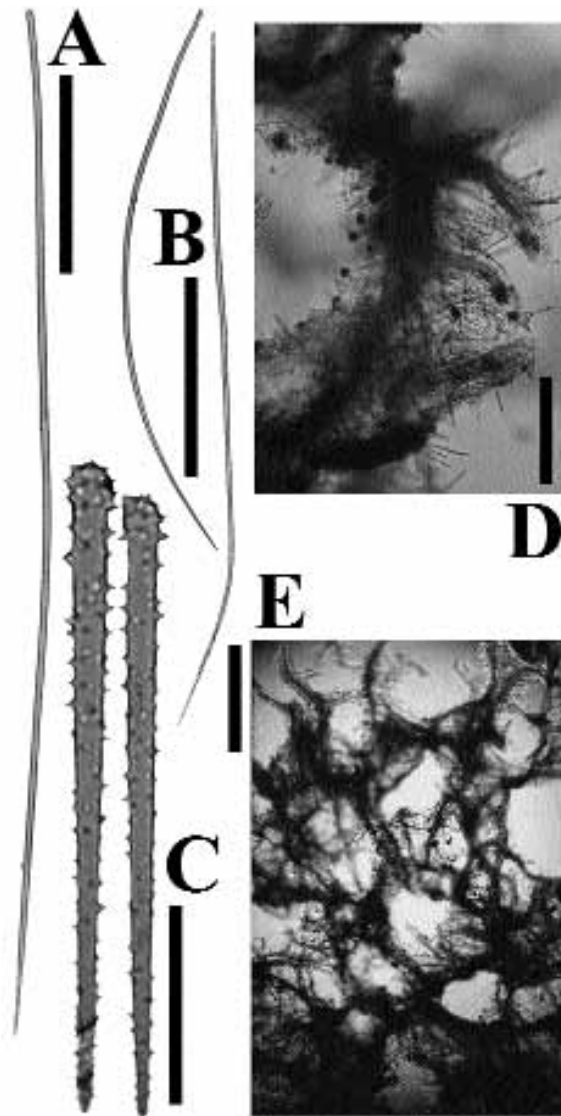
**Synonymy.** *Halichondria aculeata* Johnston, 1842: 131. *Raspaciona aculeata*; Vacelet, 1961a:36.

**Material examined.** Holotype: BMNH 1877.5.21.956, schizotype MNHN DNBE 320L – Mediterranean.

**Description.** Lobo-digitate growth form; choanosomal skeleton microcionid with compressed basal layer of spongin with erect fibre nodes cored by erect plumose columns of long thin and flexuous subectosomal styles (1150–1610  $\times$  9–18  $\mu\text{m}$ ), surrounded at their bases by bundles of small and evenly spined echinating acanthostyles (104–126  $\times$  7–12  $\mu\text{m}$ ); extra-axial plumose columns of long styles protruding through surface, occasionally branching and anastomosing; ectosomal skeleton with sparse bundles of flexuous wispy ectosomal styles (334–638  $\times$  3–6  $\mu\text{m}$ ) surrounding

points of protruding extra-axial styles on the surface. Microscleres absent.

**Remarks.** *Raspaciona* has a spiculation and ectosomal structure typical of Raspailiidae, but a plumose choanosomal and subectosomal architecture reminiscent of several genera of Halichondriidae. Variability in skeletal morphology between specimens of different growth forms has been well illustrated by Topsent (1925c) and Pulitzer-Finali (1977). Those authors showed that megasclere size and ornamentation varied quite considerably, and it has been suggested that Sarà's (1958) *R. robusta* and *R. calva* are merely different morphs of *R. aculeata* (e.g., Vacelet, 1961a). However, the acanthostyles of *R. calva* are illustrated with swollen tylote bases, much the same as those found in *Hymenaphia* species (Sarà, 1958: fig. 21). Although *Raspaciona* lacks any remarkable characters which can distinguish it readily from other genera, it can be differentiated from other species with plumose skeletal architecture (e.g., *Aulospongia*) by its *Raspailia*-like spiculation, and from the typical *Raspailia* condition by its strictly plumose non-reticulate architecture.



**Fig. 12.** *Raspaciona*. A–E, *R. aculeata*, holotype. A, subectosomal style (scale 200  $\mu\text{m}$ ). B, ectosomal styles (scale 200  $\mu\text{m}$ ). C, echinating acanthostyles (scale 30  $\mu\text{m}$ ). D, fibre (scale 200  $\mu\text{m}$ ). E, section through peripheral skeleton (scale 500  $\mu\text{m}$ ).

#### Distribution

Three species, all from the Mediterranean (Johnston, 1842; Sarà, 1958; Vacelet, 1961a; Pulitzer-Finali, 1977).

#### *RHABDEURYPON* VACELET, 1969

#### Synonymy

*Rhabdeurypon* Vacelet, 1969: 188.

#### Type species

*Rhabdeurypon spinosum* Vacelet, 1969 (by original designation).

#### Definition

Raspailiidae lacking echinating spicules but diactinal acanthorhabds are dispersed throughout the skeleton forming a compact mass.

#### Diagnosis

Thinly encrusting growth form. Surface even and hispid. Choanosomal skeleton hymedesmioid with basally compressed spongin lying on substrate. Choanosomal megascleres and true echinating spicules absent, but mesohyl contains acanthorhabds and spined microrhabds scattered throughout basal skeleton, without apparent order. Extra-axial skeleton with long smooth subectosomal subtylostyles embedded in and perpendicular to substrate, protruding through surface. Ectosome with specialized skeleton of oxeas in bouquets surrounding extra-axial styles. Structural megascleres smooth choanosomal styles or subtylostyles of one category, ectosomal auxiliary oxeas, and diactinal acanthorhabds possibly highly modified acanthostyles. Microscleres spined microrhabds.

#### Description of type species

*Rhabdeurypon spinosum* Vacelet, 1969 (Fig. 13).

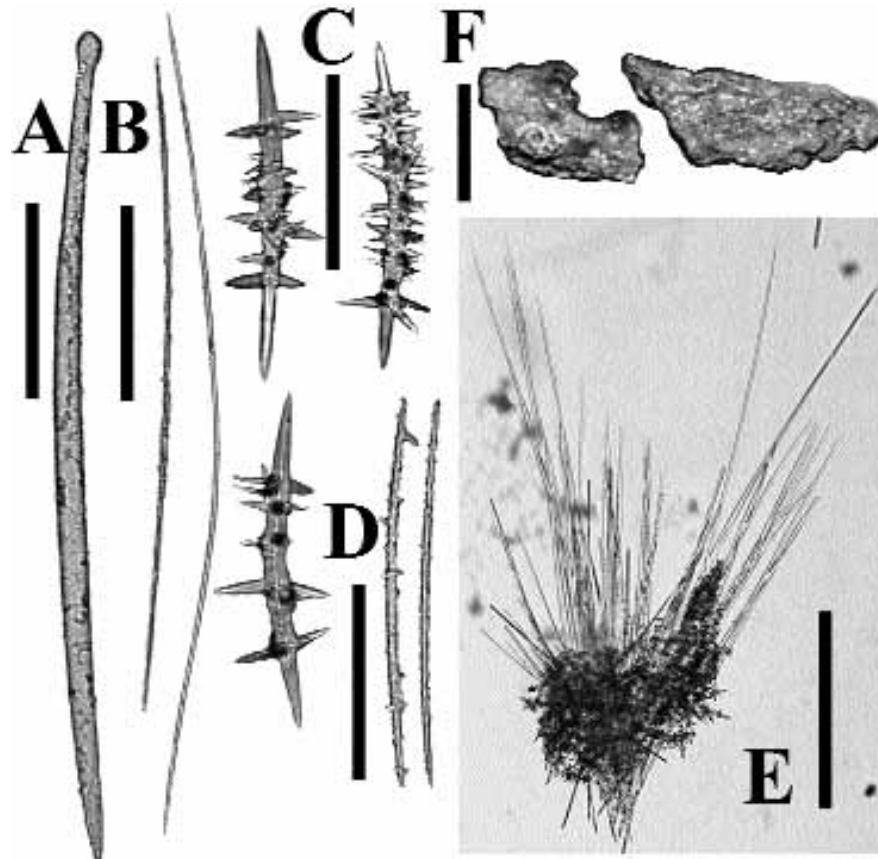
**Synonymy.** *Rhabdeurypon spinosum* Vacelet, 1969: 188.

**Material examined.** Holotype: MNHN DJV4 – Cassidaigne, Mediterranean.

**Description.** Encrusting growth form; choanosomal skeleton hymedesmioid with basal layer of spongin lying on substrate and bases of long subectosomal (sub)tylostyles (1120–3250  $\times$  15–22  $\mu\text{m}$ ) embedded and their points penetrating the surface, surrounded by bouquets of ectosomal oxeas (450–2000  $\times$  2.5–6  $\mu\text{m}$ ) at their point of insertion through the surface; basal skeleton is a compact mass of acanthorhabds (40–110  $\times$  3–8  $\mu\text{m}$ ) orientated in all directions, but not truly echinating. Spined microrhabds (50–60  $\times$  0.5–0.7  $\mu\text{m}$ ) present, scattered throughout the mesohyl, possibly juvenile forms of acanthorhabds.

**Remarks.** The diactinal acanthorhabds of *Rhabdeurypon* are unusual, superficially resembling discorhabds of *Negombo* (Halichondrida, Desmoxyidae), acanthoxeas of *Histodermella* (Poecilosclerida, Coelosphaeridae), and also similar to diactinal forms of acanthose spicules of *Tethyspira* (Halichondrida, Dictyonellidae) and perhaps even *Didiscus* (Halichondrida, Desmoxyidae). If it were not for the possession of a specialized raspailiid skeleton (consisting of bouquets of ectosomal oxeas





**Fig. 13.** *Rhabdeurypon*. A–F, *R. spinosum*, holotype. A, subectosomal subtylostyle (scale 500  $\mu\text{m}$ ). B, ectosomal oxeads (scale 400  $\mu\text{m}$ ). C, acanthorhabds (scale 50  $\mu\text{m}$ ). D, spined microrhabds (scale 30  $\mu\text{m}$ ). E, section through peripheral skeleton (scale 1 mm). F, holotype (scale 2 cm).

surrounding the protruding larger styles) and a plumose extra-axial skeleton (composed of larger (sub)tylostyles) the allocation of *Rhabdeurypon* to any particular genus or family would be very difficult. Vacelet (1969) noted that acanthorhabds are not echinating but merely dispersed throughout the mesohyl – albeit forming a compact basal mass – and therefore perhaps they should not be regarded simply as modified acanthostyles. Hooper (1991) suggested that the microscleres were smooth microxeads whereas more detailed study of the type material confirms that these are spined and possibly represent juvenile forms of acanthorhabds.

#### Distribution

Monotypic, so far known only from the Mediterranean (Vacelet, 1969).

#### SUBFAMILY THRINACOPHORINAE SUBFAM. NOV.

##### Definition

Raspailiidae lacking echinating megascleres, with well differentiated axial and extra-axial skeletons.

##### Scope

Three genera. *Thrinacophora*, *Ceratopsion* and *Axechina*.

#### THRINACOPHORA RIDLEY, 1885

##### Synonymy

*Thrinacophora* Ridley, 1885: 572; Ridley & Dendy, 1886: 483, 1887: 193; Dendy, 1905: 186 (in part); Hallmann, 1917c: 634–7; Hooper, 1991: 1339.

##### Type species

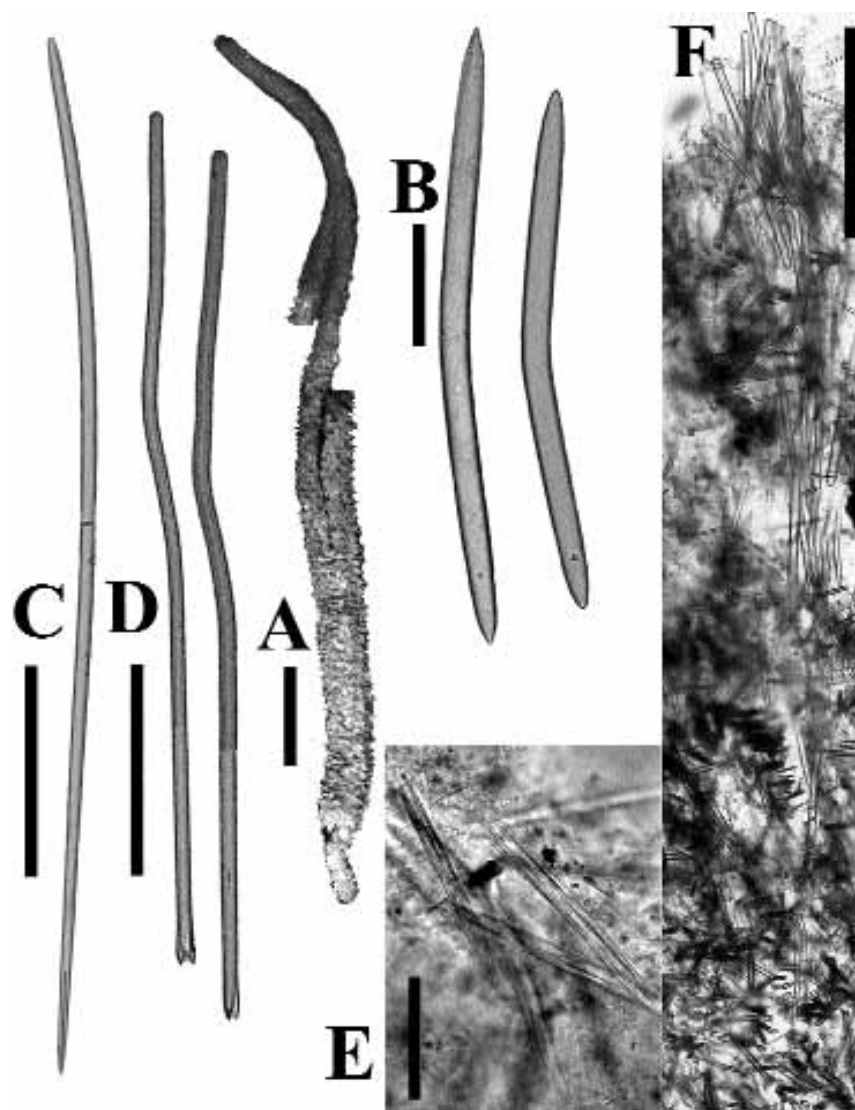
*Thrinacophora funiformis* Ridley & Dendy, 1886 (by monotypy).

##### Definition

Raspailiidae lacking echinating spicules, having a densely compressed axial skeleton, without axial fibres, cored by short oxeads or styles in a criss-crossed reticulation, and a plumose extra-axial skeleton composed of longer styles or anisoxeads. Microsclere are raphides in trichodragmata.

##### Diagnosis

Cylindrical, arborescent or encrusting and massive growth forms. Surface not prominently hispid but evenly conulose. Axial and extra-axial skeletons well differentiated. Choanosomal skeleton markedly axially compressed, with a dense reticulate core occupying



**Fig. 14.** *Thrinacophora*. A–F, *T. funiformis* (holotype). A, holotype (scale 5 cm). B, choanosomal oxeas (scale 50  $\mu\text{m}$ ). C, subectosomal anisoxea (scale 200  $\mu\text{m}$ ). D, ectosomal styles (scale 100  $\mu\text{m}$ ). E, trichodragmata (scale 50  $\mu\text{m}$ ). F, section through peripheral skeleton (scale 1 mm).

a large proportion of branch diameter composed of short, stout oxeas, anisoxeas or occasionally styles. Echinating megascleres absent. Extra-axial skeleton plumose, with uni- or paucispicular tracts radiating towards surface, cored by long, thick subectosomal styles or anisoxeas. Ectosomal skeleton with a special category of styles (sinuous and apically pronged in the type species), forming erect bouquets or paratangential brushes around extra-axial spicules, and also scattered within the mesohyl. Structural megascleres short oxeas and long styles, some with strongylote or oxecote modifications, and ectosomal styles. Microscleres raphides occurring singly or in bundles (trichodragmata).

#### Description of type species

*Thrinacophora funiformis* Ridley & Dendy, 1886 (Fig. 14).

**Synonymy.** *Thrinacophora funiformis* Ridley & Dendy, 1886: 484.

**Material examined.** Holotype: BMNH 1887.5.2.53 – off Bahia, Brazil.

**Description.** Cylindrical digitate, branching growth form; choanosomal skeleton axially compressed with a dense reticulate core composed of short curved choanosomal oxeas ( $220\text{--}345 \times 6\text{--}13 \mu\text{m}$ ) without apparent associated spongin fibres; extra-axial skeleton plumose to radial composed of long paucispicular tracts containing long straight subectosomal styles and anisoxeas ( $722\text{--}1640 \times 16\text{--}24 \mu\text{m}$ ) radiating from the axis and protruding through surface; ectosomal styles, usually sinuous and apically prolonged ( $345\text{--}462 \times 4\text{--}6 \mu\text{m}$ ) form erect or paratangential bouquets around protruding subectosomal tracts; microscleres raphides occurring in trichodragmata ( $85\text{--}110 \times 10\text{--}15 \mu\text{m}$ ).

**Remarks.** Hallmann (1917c) restricted *Thrinacophora* to include only species containing a specialized ectosomal skeleton composed of styles. He redistributed other nominal species (i.e., *Thrinacophora*, *sensu* Dendy, 1905) amongst his new genera *Draxmaxia*, *Draxmacidon* and *Axidragma* (= *Tragosia* Gray) in the Axinellidae. However, these *Thrinacophora* clearly belong to the Raspailiidae as indicated by their special raspailiid ectosomal skeleton.

*Thrinacophora* is most similar to *Ceratopsion*, both possessing a specialized ectosomal skeleton, large extra-axial megascleres and a more-or-less radial arrangement of the extra-axial skeleton which protrudes a long way through the surface, well developed axial and extra-axial differentiation, and lacking echinating megascleres. *Thrinacophora* has a dense axial reticulation of short, stout choanosomal spicules, usually oxeas but occasionally anisoxeas or rarely styles, and this axial region lacks any evidence of spongin fibres. The criss-cross of axial spicules, which occupies most of the diameter of branches, differentiates *Thrinacophora* from *Raspailia* (*Parasyringella*). Earlier authors (e.g., Ridley & Dendy, 1887; Hallmann, 1916b) considered that the possession of raphides was an important generic diagnostic character, and placed secondary emphasis on ectosomal specialization (used here to define the Raspailiidae), megasclere geometry and skeletal architecture. In *Thrinacophora*, at least, it is unlikely that the possession of raphides can define the genus (as supposed by Ridley & Dendy, 1887: 193), and more recently this was confirmed by the description of a species of *Ceratopsion* bearing raphides (Alvarez & Van Soest, 1993).

#### Distribution

Four species are known so far, from Brazil (Ridley & Dendy, 1886, 1887), Puerto Rico (Wilson, 1902), Philippines (Ridley & Dendy, 1887), Arafura Sea and Moluccas, Indonesia (Kieschnick, 1896; Hentschel, 1912) and Northwest Australia (Hooper, 1991).

#### CERATOPSION STRAND, 1928

##### Synonymy and type species

[*Ceratopsis*] Thiele, 1898: 57 (preocc.); Hallmann 1916b: 541. *Ceratopsion* Strand, 1928: 33; de Laubenfels 1936a: 132; Bergquist 1970: 18; Hooper, 1991: 1327; Alvarez & Van Soest, 1993: 629; Hooper & Lévi, 1993: 1287. *Ommatosa* de Laubenfels, 1936a: 132.

##### Type species

*Ceratopsis expansa* Thiele, 1898 (by original designation).

##### Definition

Raspailiidae lacking echinating spicules, having an axially compressed choanosomal skeleton with reticulate fibres cored by sinuous styles or anisoxeas and a well differentiated radial extra-axial skeleton cored by longer megascleres.

##### Diagnosis

Erect, lamellate or arborescent growth forms. Surface granular and hispid. Axial and extra-axial skeletons well differentiated. Choanosomal skeleton a compressed axial reticulation of spongin fibres, deficient in collagen, cored by sinuous or straight styles, anisoxeas or strongyles. Echinating megascleres absent. Extra-axial skeleton of radially arranged subectosomal styles, anisoxeas or strongyles, including sinuous and/or straight forms, embedded in and perpendicular to axial core, projecting through surface. Specialized ectosomal skeleton present (s.s.) or absent, and where present consisting of oxeas or styles forming structures ranging

from a continuous palisade on the surface to discrete bouquets of spicules grouped around the projecting extra-axial megascleres where they penetrate the surface. Structural megascleres include at least two categories of styles, anisoxeas or strongyles (one often sinuous), oxeas or anisoxeas, and thin ectosomal oxeas or styles. Microscleres usually absent or may include raphides in trichodragmata.

##### Description of type species

*Ceratopsion expansa* (Thiele, 1898) (Fig. 15).

**Synonymy.** *Ceratopsis expansa* Thiele, 1898: 57. *Ceratopsion expansa*; Hooper, 1991: 1327.

**Material examined.** Holotype (fragment): MNHN DCL981L – Sagami Bay, Japan. Comparative material. Holotype of *Ceratopsion dichotoma* (Whitelegge): AM G4353 (see Hooper, 1991).

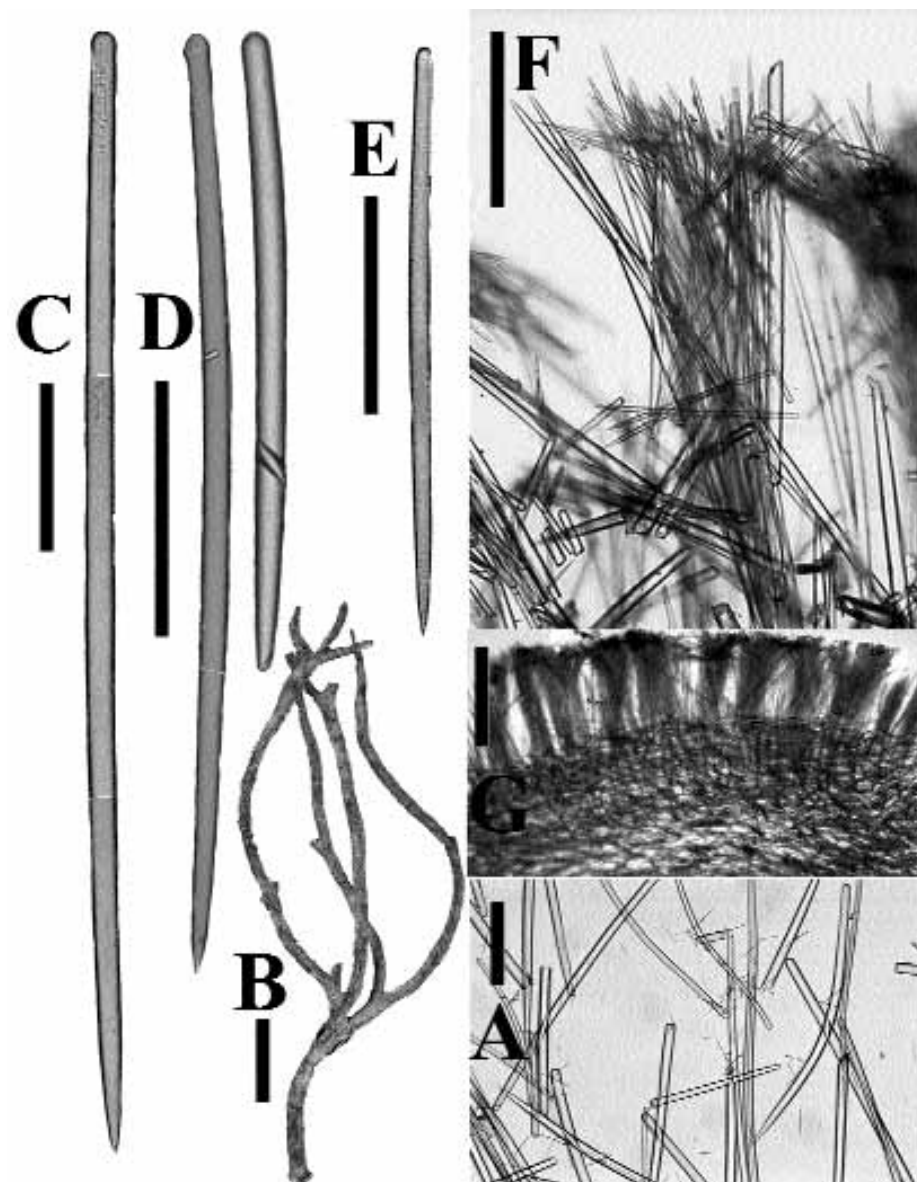
**Description.** Erect, palmate-flabellate, digitate growth form; choanosomal skeleton a compressed axial reticulation of fibres cored by robust choanosomal oxeas ( $230\text{--}270 \times 4\text{--}11 \mu\text{m}$ ) forming longitudinal tracts through branches, with a well differentiated radial extra-axial skeleton composed of curved subectosomal styles ( $750\text{--}1200 \times 20\text{--}30 \mu\text{m}$ ) embedded in and perpendicular to axis and protruding through surface; ectosomal skeleton composed of small ectosomal oxeas ( $80\text{--}110 \times 2\text{--}3 \mu\text{m}$ ) forming a nearly continuous palisade on surface mainly clustered around the projecting bundles of subectosomal styles. Microscleres absent.

**Remarks.** *Ceratopsion* includes species which have either monactinal or diactinal axial megascleres and extra-axial megascleres (Hooper, 1991). Hallmann (1916b) used *Ceratopsion* as a catch-all for various 'Axinellidae with microxeas' (excluding sigma-bearing and desmoxyid genera). However, Bergquist (1970) showed that these 'microxeas' were in fact ectosomal megascleres, raphidiform in some species, and on this basis the genus was referred to Raspailiidae (Hooper, 1991).

*Ceratopsion* lacks echinating megascleres, but has other features found in most raspailiids. On paper the genus is difficult to distinguish from *Raspailia* (*Parasyringella*), but the presence of sinuous axial styles or anisoxeas in some species, and the possession of distinctly radial extra-axial skeleton of styles, anisoxeas or strongyles may serve to differentiate these two genera. The genus was previously defined as lacking raphides whereas Alvarez & Van Soest (1993) described a species from the Florida Keys with trichodragmata, and they remark further on the affinities between *Thrinacophora* and *Ceratopsion*.

Only two species of *Ceratopsion* have a 'classic' ectosomal skeleton consisting of bouquets of ectosomal styles or oxeas surrounding the projecting extra-axial megascleres (*C. cuneiformis* Bergquist, *C. montebelloensis* Hooper), whereas all other species have a more dense palisade of ectosomal brushes erect on the surface. *Ceratopsion clavata*, *C. microxephora* and *C. minor* form a group possessing sinuous strongyles in the axial skeleton, reminiscent of the Bubaridae. *Axinella aurantiaca* Lendenfeld, 1888, should also be transferred to *Ceratopsion*.

*Ommatosa* de Laubenfels was previously considered a junior synonym of *Bubaris* by Carballo (2000: 585), as also suggested by Hooper & Lévi (1993) for Bubaridae, whereas re-examination of the holotype of the type species, *Axinella rugosa* (Schmidt, 1870: 61), by Belinda Alvarez (pers. comm.) confirmed that it belongs to *Ceratopsion*, and furthermore the type species was the senior synonym of *C. crustosum* Alvarez & Van Soest, 1993.



**Fig. 15.** *Ceratopsion*. A, *C. expansa* (fragment of holotype). A, spicules (scale 500  $\mu\text{m}$ ). B–G, *C. dichotoma* (holotype). B, holotype (scale 3 cm). C, subectosomal style (scale 100  $\mu\text{m}$ ). D, choanosomal styles (scale 100  $\mu\text{m}$ ). E, ectosomal style (scale 100  $\mu\text{m}$ ). F, ectosomal skeleton (scale 200  $\mu\text{m}$ ). G, section through peripheral skeleton (scale 500  $\mu\text{m}$ ).

#### Distribution

Eleven species are known, from Florida (Schmidt, 1870; de Laubenfels, 1936a; Alvarez & Van Soest, 1993), Mediterranean (Pulitzer-Finali, 1983: 520), Japan (Thiele, 1898), New Zealand (Bergquist, 1970: 18), north, east and west coasts of Australia (Whitelegge, 1907; Hooper, 1991), New Caledonia (Hooper & Lévi, 1993), South Africa (Kirkpatrick, 1903b: 242), and Indonesia (Hentschel, 1912).

#### AXECHINA HENTSCHEL, 1912

#### Synonymy

*Axechina* Hentschel, 1912: 417; de Laubenfels, 1936a:102; Hooper, 1991: 1344.

#### Type species

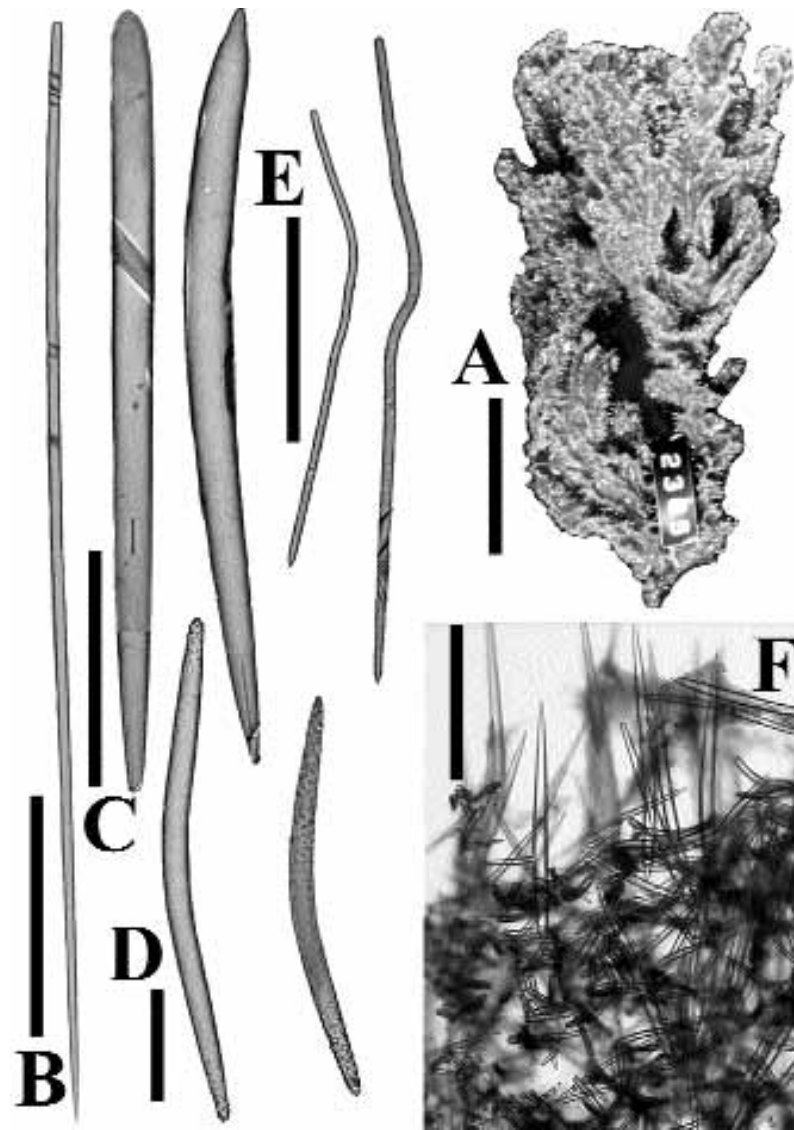
*Axechina raspailioides* Hentschel, 1912 (by original designation).

#### Definition

Raspailiidae lacking echinating acanthostyles, having an axially compressed choanosomal skeleton divided into two components: a central tightly reticulate region cored by oxeas with spined points, and a peripheral radial region formed by smooth anisoxeas projecting outwards.

#### Diagnosis

Bushy flabellate growth form. Surface rugose, conulose, and hispid. Choanosomal skeleton with two components: compressed,



**Fig. 16.** *Axechina*. A–F, *A. raspailioides*. A, specimen NTM Z2385 (scale 3 cm). B–F, holotype. B, subectosomal style (scale 500  $\mu\text{m}$ ). C, choanosomal anisoxeas (scale 100  $\mu\text{m}$ ). D, choanosomal spined oxeas (scale 50  $\mu\text{m}$ ). E, ectosomal styles (scale 300  $\mu\text{m}$ ). F, peripheral skeletal structure (scale 150  $\mu\text{m}$ ).

tightly reticulate axis cored by oxeas with spined points; radial peripheral region formed by columns of smooth anisoxeote spicules projecting outwards from axis. Echinating megascleres absent. Extra-axial skeleton radial, with tracts of long, thick, subectosomal styles embedded in the outer (radial) portion of the axis, ascending to surface and projecting through it. Ectosomal skeleton composed of peculiarly curved or sinuous toxiform styles with spined terminations, grouped around a central extra-axial style in a bouquet. Structural megascleres include oxeas with spined terminations, smooth anisoxeas, large styles or anisoxeas with rounded bases, and dermal flexuous toxiform styles with spined terminations. Microscleres absent.

#### Description of type species

*Axechina raspailioides* Hentschel, 1912 (Fig. 16).

**Synonymy.** *Axechina raspailioides* Hentschel, 1912: 417.

**Material examined.** Holotype: SMF991 (schizotype MNHN DCL2261) – Arafura Sea.

**Description.** Bushy arborescent, stalked, cylindrical branches, prominently conulose or clathrous; surface prominently hispid; choanosomal skeleton with well differentiated axial and extra-axial regions; axial skeleton with two components: a compressed axial formed by tightly reticulate tracts of choanosomal oxeas with spined points ( $195\text{--}264 \times 8\text{--}16 \mu\text{m}$ ) forming a dense central criss-cross running longitudinally through branches, and a plumose or radial region at the periphery of the axial skeleton formed by columns of smooth anisoxeote spicules ( $305\text{--}425 \times 16\text{--}24 \mu\text{m}$ ) embedded in the axis and directed outwards singly or in paucispicular bundles, often also penetrating the surface; extra-axial skeleton radial, with long subectosomal styles ( $1044\text{--}2760 \times 15\text{--}20 \mu\text{m}$ ) embedded in the radial portion of the axial skeleton, projecting a long way through the surface; ectosomal skeleton with bouquets of sinuous ectosomal styles ( $231\text{--}305 \times 2\text{--}6 \mu\text{m}$ ) surrounding the longer extra-axial styles; echinating spicules absent; microscleres absent.

**Remarks.** The type and only species of *Axechina* has a typical raspailiid ectosome formed by bouquets of special styles, clearly

indicating its affinities with this family although previously the genus was included in Axinellidae (Hentschel, 1912). In fact the axial skeletal architecture and possession of megascleres with spined terminations is reminiscent of *Reniochalina* (Axinellidae) but this comparison is superficial and they have little else in common. *Axechina* could possibly be reasonably included with *Ceratopsion* on the basis of its spiculation, or *Thrinacophora* in having at least part of its axial skeleton consisting of a dense criss-cross reticulation of spicules without obvious fibres, but it fits into neither genus easily. The genus is retained on a tentative basis, differentiated from others by the presence of the following features: an axial reticulate core, a radial (or plumose) region at the periphery of the axis, a radial extra-axial skeleton, and a plumose ectosomal skeleton, the absence of choanosomal fibres or definite axial spicule tracts (cf. *Thrinacophora*), the presence of basal and apical spination on both choanosomal and ectosomal megascleres, and the absence of echinating megascleres.

#### Distribution

Monotypic, endemic to southeast Indonesia and northwest Australia.

#### SUBFAMILY CYAMONINAE SUBFAM. NOV.

#### Definition

Raspailiidae with echinating spicules modified to sagittal acanthoplagiotriaenes, with one species having trichodragmata.

#### Scope

Three genera. *Cyamon Trikentron* and *Waltherarndtia*.

#### CYAMON GRAY, 1867

#### Synonymy

*Cyamon* Gray, 1867a: 546; Dendy, 1922b: 107; de Laubenfels, 1936a: 80; Lévi, 1973: 609; Sim & Bakus, 1986: 17.

#### Type species

*Dictyocylindrus vickersii* Bowerbank, 1866 (by monotypy).

#### Definition

Raspailiidae with acanthostyles modified to sagittal triactinal or tetractinal acanthoplagiotriaenes with all rays spined.

#### Diagnosis

Encrusting to massive growth form. Surface hispid and usually conulose. Choanosomal skeleton basally compressed layer of spongin fibres lying on substrate, with microcionid-like plumose spongin-fibre nodes ascending to surface. Basal fibres cored by pauci- or multispicular plumose tracts of choanosomal styles, with

no or few anastomoses. Extra-axial skeleton with few very long thin extra-axial styles, embedded in choanosomal fibre nodes and protruding through surface. Extra-axial spicules also scattered throughout mesohyl. Fibres very heavily echinated by sagittal triacts, tetracts, or forms even further modified, producing almost rigid interlocking secondary skeleton. Ectosomal specialization absent. Structural megascleres styles or subtylostyles of 2–3 sizes; thinner may have few spines and subtylote swellings on distal and basal ends, respectively; echinating spicules sagittal tetracts or pentactinal megascleres (acanthoplagiotriaenes), less commonly diacts or triacts, with all (*s.s.*) or at least more than one acanthose ray. Microscleres absent.

#### Description of type species

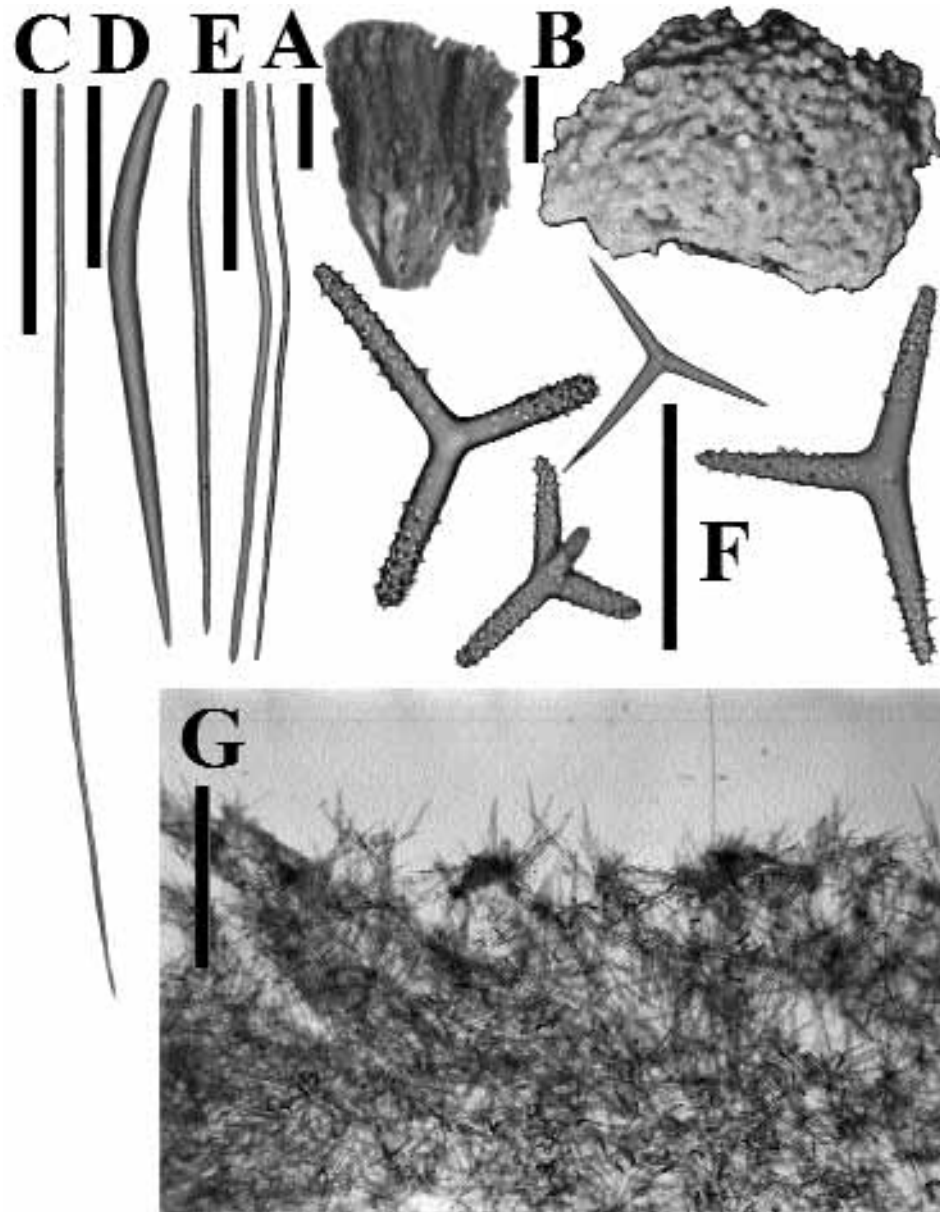
*Cyamon vickersii* (Bowerbank, 1866) (Fig. 17).

**Synonymy.** *Dictyocylindrus vickersii* Bowerbank, 1866: 267. *Cyamon vickersii*; Dendy, 1922b: 108.

**Material examined.** Holotype: BMNH 1877.5.21.1887 – West Indies.

**Description.** Lamellate, columnar, cushion-shaped or massive-encrusting growth forms; choanosomal skeleton microcionid with compressed basal layer of spongin with individual fibre nodes erect on basal spongin, cored by smaller stout choanosomal styles (564–745 × 19–30 μm) in columns of 2–4 spicules, also projecting from fibres in plumose tufts; extra-axial skeleton with diverging plumose columns of both choanosomal styles and longer thin subectosomal styles (935–1368 × 9–14 μm) embedded in microcionid fibres and protruding through surface; peripheral fibres echinated by sagittal triactinal, tetractinal and pentactinal acanthoplagiotriaenes with all rays bearing spines (98–132 × 10–16 μm), and including juvenile forms (superficially resembling orthotriaenes of the Astrophorida) bearing vestigial spination on all rays (62–125 × 3–8 μm); acanthoplagiotriaenes form an almost interlocking secondary skeleton within the choanosome; ectosomal skeleton without specialised brushes typical of most raspailiids but with ectosomal auxiliary styles (212–415 × 2–6 μm) scattered between skeletal columns and forming bundles within choanosomal and subectosomal regions. Microscleres absent.

**Remarks.** Bowerbank's (1866) original description of *C. vickersii* is inadequate and barely characterises the genus, whereas Carter's (1879b: 292) redescription of the type specimen is much more detailed and useful. The BMNH holotype is dry but still in good condition, and from that material (and accompanying slide preparations) it is confirmed that skeletal structure consists of plumose columns of choanosomal and subectosomal styles, there is no special ectosomal skeleton but a thinner (third, ectosomal) category of styles is present within the choanosomal skeleton, and there is also an almost interlocking secondary skeleton composed of sagittal acanthoplagiotriaenes. This structure is quite different from *Trikentron*, but it is probably one related to *Cyamon*'s growth form. Nevertheless, there are also significant differences in the geometry and spination of sagittal acanthoplagiotriaenes between the two genera: *Trikentron* has monact-, diact-, triact- or rarely tetractinal sagittal spicules, with only one spined ray; *Cyamon* (*s.s.*) has rarely triactinal, mostly tetractinal and sometimes pentactinal sagittal spicules, and all rays are spined, at least at their apex. Dendy (1922b: 108) and de Laubenfels (1936a: 80) also redescribed additional material of *C. vickersii* from Amirante



**Fig. 17.** *Cyamon*. A–G, *C. vickersii*. A, holotype (scale 3 cm). B, specimen BMNH 1931.1.1.19 (scale 5 cm). C, subectosomal style (scale 250  $\mu\text{m}$ ). D, choanosomal styles (scale 200  $\mu\text{m}$ ). E, ectosomal styles (scale 100  $\mu\text{m}$ ). F, acanthoplagiotriaenes including juvenile form (scale 100  $\mu\text{m}$ ). G, section through peripheral skeleton (scale 500  $\mu\text{m}$ ).

(BMNH 1931.1.1.19; Fig. 17B) and the West Indies, respectively, although de Laubenfels (1936a) questioned the conspecificity of Dendy's material. Nevertheless, from those accounts it appears that *Cyamon* differs from *Triken-trion* in several significant respects and is maintained here as a separate genus.

#### Distribution

Seven species of *Cyamon* are presently known: West Indies (Bowerbank, 1866; de Laubenfels, 1936a), southern California (de Laubenfels, 1930; Dickinson, 1945; Sim & Bakus, 1986), Gulf of Manaar, Indian Ocean (Carter, 1880b), and Indonesia (Hentschel, 1912; Hooper, 1991).

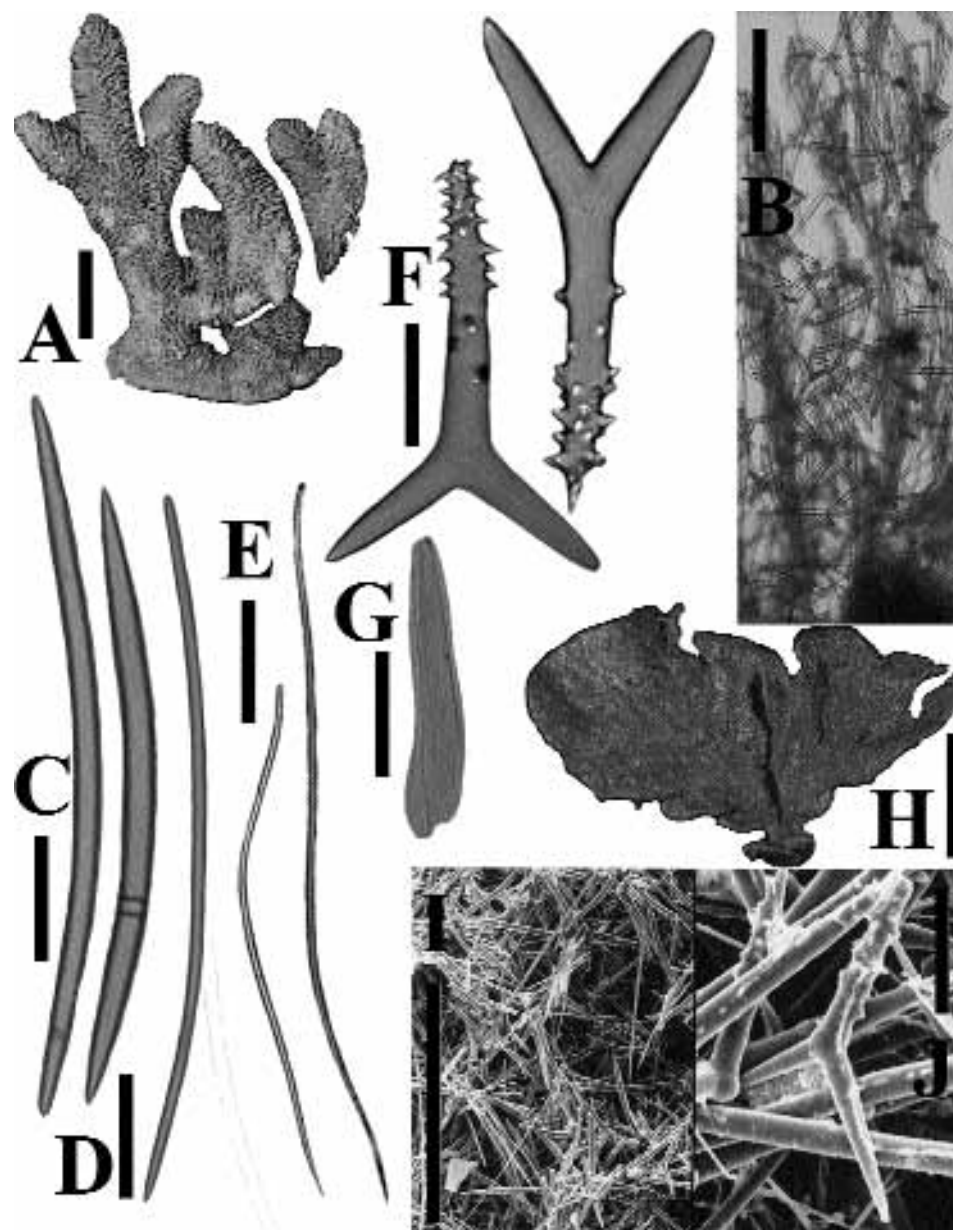
#### TRIKENTRION EHLERS, 1870

##### Synonymy

*Triken-trion* Ehlers, 1870: 6, 31; Carter, 1879b: 291; Hentschel, 1912: 373; Topsent, 1928c: 58; de Laubenfels, 1936a: 80; Lévi, 1973: 609. [*Tricentrium*] Ridley, 1879 (in *Zoological Record* 16: 5) (*lapsus*). *Plectronella* Sollas, 1879b: 17; de Laubenfels, 1936a: 81. Taxonomic decision for synonymy: Hooper (1991).

##### Type species

*Spongia muricata* (Pallas, 1766) Esper, 1794 (by monotypy).



**Fig. 18.** *Trikentron*. A–G, *T. muricata*. A, specimen BMNH 1872.10.19.1 (scale 3 cm). B–G, schizotype ZMB7160. B, section through peripheral skeleton (scale 300  $\mu\text{m}$ ). C, choanosomal oxeads (scale 50  $\mu\text{m}$ ). D, subectosomal style (scale 100  $\mu\text{m}$ ). E, ectosomal styles (scale 50  $\mu\text{m}$ ). F, acanthoplagiotriaenes (scale 50  $\mu\text{m}$ ). G, trichodragmata (scale 20  $\mu\text{m}$ ). H–J, *T. flabelliforme* Carter. H, specimen (NTM Z2383) (scale 5 cm). I, section through choanosomal skeleton (scale 500  $\mu\text{m}$ ). J, acanthoplagiotriaenes in situ (scale 100  $\mu\text{m}$ ).

### Definition

Raspailiidae with acanthostyles modified to sagittal monactinal, diactinal or tetractinal acanthoplagiotriaenes with only one spined ray.

### Diagnosis

Arborescent, digitate and flabellate growth forms. Surface usually hispid, and even or rough and microconulose. Choanosomal skeleton with poorly developed wide meshed reticulation,

with only slightly compressed axial fibres running longitudinally through axial core. Fibres cored by pauci- or multispicular tracts of oxeads. Axial and extra-axial skeletons not markedly differentiated; extra-axial skeleton consists of ascending multi- or paucispicular primary fibres cored by choanosomal oxeads, interconnected by uni- or paucispicular secondary fibres, together producing a more-or-less regular reticulation. Single or brushes of subectosomal styles embedded at ends of ascending primary fibres, poking through peripheral skeleton. Peripheral fibres moderately heavily echinated by sagittal triacts. Ectosome with specialized skeleton of ectosomal styles in brushes surrounding bases of extra-axial styles.



Megascleres styles of two sizes, choanosomal oxeas, echinating megascleres sagittal triacts (or acanthoplagiotriaenes) with only one spined ray. Microscleres may include raphides, occurring singly or in bundles (= trichodragmata).

#### Description of type species

*Trikenrion muricata* (Pallas, 1766) (Fig. 18).

**Synonymy.** *Spongia muricata* (Pallas, 1766) Esper, 1794: 185. *Trikenrion muricata*; Carter, 1879b: 293.

**Material examined.** Holotype: Unknown, schizotype ZMB7160 – West Africa.

**Description.** Arborescent, digitate growth form; choanosomal skeleton with wide meshed reticulation, with little or no axial compression, composed of relatively close-meshed paucispicular tracts cored by choanosomal oxeas ( $235\text{--}320 \times 8\text{--}18 \mu\text{m}$ ); extra-axial skeleton plumoreticulate with ascending primary multispicular tracts interconnected by transverse tracts of choanosomal oxeas; sparse subectosomal styles ( $555\text{--}964 \times 6\text{--}15 \mu\text{m}$ ) embedded at ends of primary ascending spicule tracts protruding a short distance through the surface, surrounded by sparse brushes of ectosomal anisoxeas, occasionally styles ( $195\text{--}315 \times 2\text{--}4 \mu\text{m}$ ) forming bouquets around protruding subectosomal styles; peripheral fibres echinated by nearly symmetrical sagittal diacts with only the longest ray spined at its apex ( $132\text{--}165 \times 12\text{--}18 \mu\text{m}$ ); microscleres are raphides in trichodragmata ( $65\text{--}85 \times 10\text{--}15 \mu\text{m}$ ).

**Remarks.** *Trikenrion* is similar to *Cyamon* in having highly modified echinating spicules called sagittal triacts (or acanthoplagiotriaenes), usually triradiate or further modified to quadriradiate and other forms. On this basis alone these genera could be eventually synonymised but they differ in other significant details: *Trikenrion* has only one spined ray on echinating spicules, it has diactinal choanosomal spicules, a non-plumose skeleton, and a specialized raspailiid ectosomal skeleton. For those reasons they are maintained separately here (see also remarks for *Cyamon*).

*Plectronella* (type species *Plectronella papillosa* Sollas, 1879b, by monotypy) was merged with *Trikenrion* in 1879 (by Ridley in the *Zoological Record* for that year), and again by de Laubenfels (1936a), when it was found that its type species was synonymous with *T. muricata* from West Africa.

#### Distribution

Four species are presently known: West Africa (Esper, 1874; Ehlers, 1870; Carter, 1879b), Gulf of California (Dickinson, 1945), tropical Australia and Indonesia (Carter, 1882b; Hallmann, 1914b; Hooper, 1991).

#### WALTHERARNDTIA DE LAUBENFELS, 1936

##### Synonymy

*Waltherarndtia* de Laubenfels, 1936a: 131.

##### Type species

*Hymeniacion caliculatum* Kirkpatrick, 1903b: 241 (by original designation).

##### Definition

Cyamoninae which have lost sagittal triaenes but retain a renieroid reticulate skeleton slightly compressed in the axial region and more open with elongate meshes in the periphery.

##### Diagnosis

Raspailiidae, monotypic, flabellate, stalked, with regularly spaced depressed oscules scattered over an optically smooth surface; specialized ectosomal skeleton present consisting of bundles of microxeas with spined tips surrounding protruding choanosomal styles; choanosomal skeleton renieroid reticulate with differentiated primary multispicular tracts interconnected by uni- or paucispicular tracts of styles forming regular meshes, slightly compressed in the axis and more elongate and regular in the periphery forming longitudinal serial meshes, with choanosomal styles protruding at the surface. Megascleres consist of styles in two size classes, the smaller with spined bases, and ectosomal microxeas with spined tips. Echinating sagittal spicules absent.

##### Description of type species

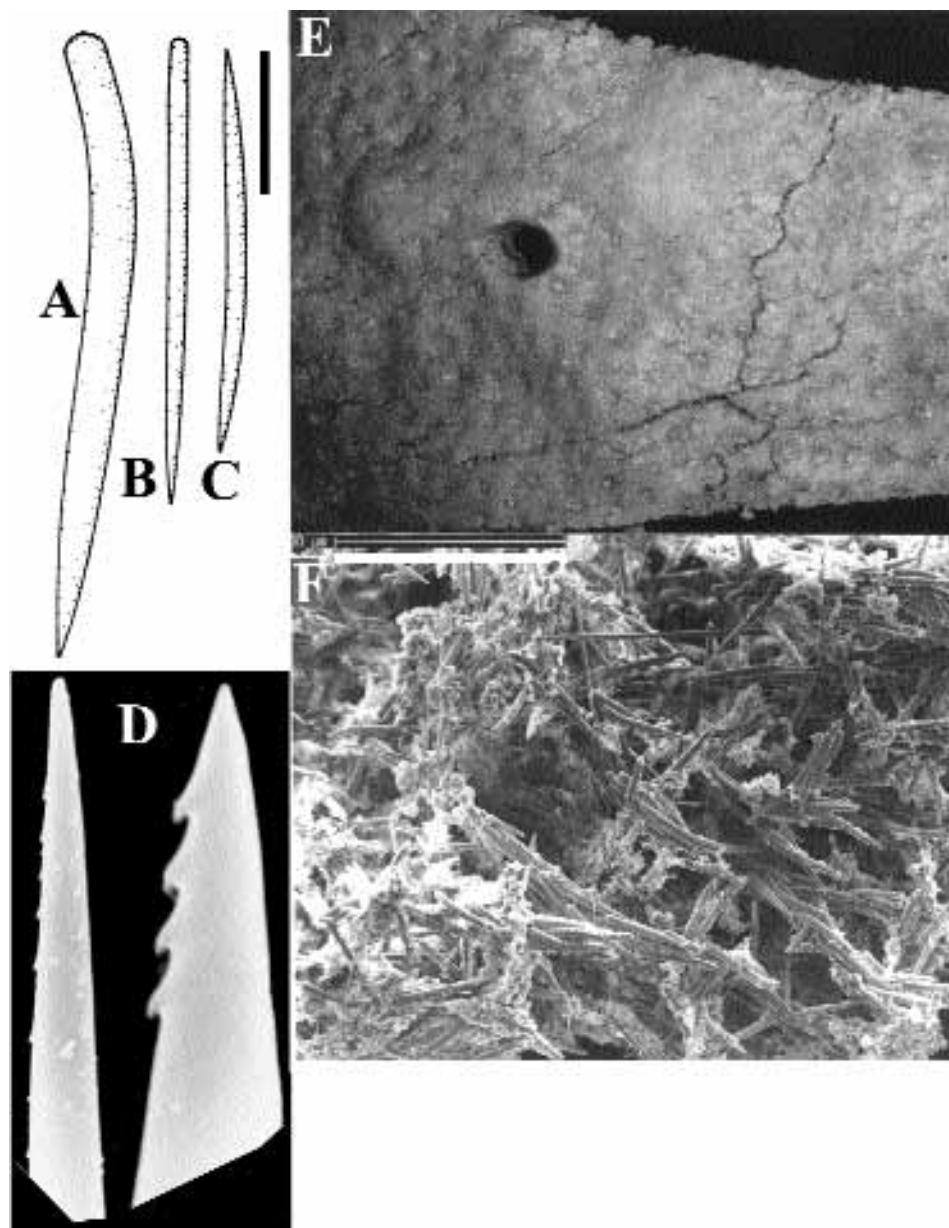
*Waltherarndtia caliculatum* (Kirkpatrick) (Fig. 19).

**Synonymy.** *Hymeniacion caliculatum* Kirkpatrick, 1903b: 241–242, pl. 5, fig. 8, pl. 6, fig. 12. *Hymeniacion caliculatum* var. *osculatum* Kirkpatrick, 1903b: 242, pl. 6, fig. 13.

**Material examined.** Holotype: BMNH 1902.11.16.20 (slide) – South Africa, E London, 170 m, Gilchrist collection. Other material. Holotype of *H. caliculatum* var. *osculatum*: BMNH 1902.11.16.21 – South Africa, E London coast, 170 m, Gilchrist collection.

**Description (partly from Kirkpatrick, 1903b and re-examination of type material).** Flabellate, with a thick flat lamella, 0.7–1.5 cm thick, originally 19 cm high, 17 cm wide, on a broad stalk. Surface optically smooth but rough to touch due to projecting tufts of spicules, with a subsurface lace-like reticulation visible below the dermal membrane. Oscules small 2 mm in diameter on one face of the lamella, in oscular depressions. Colour brick red alive, orange brown in alcohol. Ectosomal skeleton with microxeas in brushes surrounding the protruding choanosomal megascleres or lying paratangential to the ectosome. Choanosomal skeleton renieroid reticulate with multispicular primary tracts ( $50\text{--}100 \mu\text{m}$  diameter) connected by uni- to paucispicular secondary ones, at relatively regular intervals, forming rectangular meshes approximately  $200 \times 50 \mu\text{m}$  in dimension. Meshes arranged serially and longitudinally in a central lamella, more compressed near the axis of lamella than at the surface where they become elongated with respect to the surface. Megascleres larger styles thick and slightly curved, with rounded bases,  $210\text{--}(233.8)\text{--}290 \mu\text{m}$  long,  $5\text{--}(15.9)\text{--}20 \mu\text{m}$  wide; smaller styles with 1–3 microspines on the base,  $115\text{--}(141.3)\text{--}225 \mu\text{m}$  long,  $5\text{--}(5.3)\text{--}8 \mu\text{m}$  wide; microxeas with a row of 3 or more (up to 8) spines near their tips,  $40\text{--}(63.8)\text{--}75 \mu\text{m}$  long,  $<1 \mu\text{m}$  wide.

**Remarks.** The genus is monotypic and originally assigned to Axinellidae by de Laubenfels (1936a). However, both the spicule complement and the organisation of the skeleton do not agree with the concept of Axinellidae adopted in this work (see chapter by Alvarez de Glasby), and the possession of a specialized ‘raspailiid’ ectosomal skeleton indicates closer affinities with Raspailiidae, but its inclusion in this family remains a tentative



**Fig. 19.** *Waltherarndtia* de Laubenfels. A–F, holotype *Hymeniacion calciculatum* var. *osculatum* Kirkpatrick, BMNH 1902.11.16.21. A–C, spicules (scale 50 µm). D, SEM of tips of microxeas. E, holotype. F, SEM of choanosomal skeleton (scale 100 µm).

hypothesis. Kirkpatrick (1903b: 242) noted that the choanosomal skeleton was transitional between renierioid and axinellid architecture, showing both a slight axial compression at the core of the lamella and regular reticulate meshes near the surface. While its affinities to Raspailiidae are obvious from the possession of a specialized ‘raspailiid’ ectosomal skeleton, its relationships within Raspailiidae remain speculative. It is tentatively assigned to the Cyamoninae based on the possession of styles with spines at their base which occur in other Raspailiidae, and that the ectosomal skeleton composed of microxeas bearing basal spines is reminiscent of *Trikentrion flabelliformis* (Alvarez de Glasby and Van Soest, pers. comm.; who have both personally examined the type material), in addition to the renierioid and slightly compressed choanosomal skeletal architecture reminiscent of other Cyamoninae. In this placement it is hypothesized that the genus has lost its sagittal spicules.

#### Distribution

Known only from the East London coast, South Africa.

#### SUBFAMILY PLOCAMIONINAE SUBFAM. NOV.

#### Definition

Raspailiidae with acanthostrongyles or acanthotylostrongyles (‘peg-top’ spicules) forming choanosomal skeletal tracts.

#### Scope

Two genera. *Plocamione* and *Lithoplocamia*.

**PLOCAMIONE TOPSENT, 1927****Synonymy**

*Plocamione* Topsent, 1927b: 16; 1928c: 63. *Raspeloplocamia* Burton, 1935a: 402. *Axoplocamia* Burton, 1935a: 402; Bergquist & Fromont, 1988: 122. Taxonomic decision for synonymy: Hooper (1991), and this work.

**Type species**

*Plocamione dirrhopalina* Topsent, 1927b (by monotypy).

**Definition**

Raspailiidae with an axially or basally compressed microcionid skeleton of which the axial skeleton is formed by acanthostrongyles or acanthotylostrongyles.

**Diagnosis**

Encrusting or digitate growth forms. Surface even and hispid. Choanosome basally or axially compressed reticulation of choanosomal acanthostrongyles, forming thick longitudinal core; echinating acanthostyles embedded in core, standing perpendicular to axis. Extra-axial skeleton radial or plumose columns of long subectosomal styles. Ectosomal skeleton with or without specialized skeleton of ectosomal styles or anisoxeas forming brushes around extra-axial spicules. Structural megascleres include two categories of styles or subtylostyles; echinating spicules evenly spined acanthostyles with subtylote bases, sometimes entirely smooth, partially acanthose, or with smooth, spined or tuberculate bases. Choanosomal axial or basal acanthostrongyles or acanthotylostrongyles, straight or slightly curved, distinctly acanthose, merely tuberculate, or rarely entirely smooth (= 'peg-top' spicules of Ridley in Ridley & Duncan, 1881). Microscleres absent.

**Description of type species**

*Plocamione dirrhopalina* Topsent, 1927b (Fig. 20).

**Synonymy.** *Plocamione dirrhopalina* Topsent, 1927b: 16.

**Material examined.** Holotype: MOM (not seen), schizotype MNHN DT1245 – Azores. Comparative material. *P. clopetaria* (Schmidt, 1870): fragments of holotype MNHN DCL1106L, BMNH 1870.5.3.78. *P. ornata* (Dendy, 1924): holotype BMNH 1923.10.1.126. *P. pachysclera* (Lévi & Lévi, 1983b): holotype MNHN DCL2448.

**Description.** Encrusting growth form; choanosomal skeleton hymedesmioid with basal layer of spongin on substrate cored by longitudinal tracts of choanosomal acanthostrongyles (70–95 × 7–10 μm) forming thick basal crust or loosely reticulate basal skeleton, with bases of echinating acanthostyles (175–280 × 11–14 μm) and long subectosomal styles (800–3500 × 18–35 μm) embedded in spicule reticulation and standing perpendicular to substrate; ectosomal skeleton with bouquets of ectosomal styles (455–700 × 3.5–5 μm) surrounding protruding subectosomal spicules.

**Remarks.** There is a large number of species and genera of 'plocamiform' sponges which have a basal or axial skeleton of acanthose diactinal megascleres, but most of those taxa are relatively poorly known. Most are obvious members of the

order Poecilosclerida related to the Myxillidae, Crellidae or Microcionidae (*Plocamia* Schmidt, 1870, [*Dirrhopalum*] Ridley in Ridley & Duncan, 1881, *Lissoplocamia* Bronsted, 1924b, *Heteroclathria* Topsent, 1904c, *Plocamiopsis* Topsent, 1928c, *Echinoplocamia* Burton, 1959a, *Plocamionida* Topsent, 1927b, *Plocamissa* Burton, 1935a, *Plocamiancora* Topsent, 1927b, *Damiria* Keller, 1891, *Damiriella* Burton, 1935a, and *Damiriopsis* Burton, 1928a). Two of these belong to the Raspailiidae: *Plocamione* (including *Raspeloplocamia*, with type species *Plocamia clopetaria* Schmidt, 1870, by original designation; and *Axoplocamia* with type species *Bubaris ornata* Dendy, 1924, by original designation), and *Lithoplocamia* (see below). Both have modified acanthostyle 'peg top spicules' but differ essentially in their skeletal structure and disposition of these spicules.

Five of the six known species are typical of Raspailiidae in having a specialized raspailiid ectosomal skeleton and curved or vermiform 'sausage shaped' spicules (acanthostrongyles) which are characteristic of 'plocamiform' sponges (*sensu* Burton, 1935a). Specialised ectosomal bouquets and 'sausage shaped' spicules are absent in *P. pachysclera* (Lévi & Lévi), but that species has other features that suggest a close relationship with the group. Several other species have also been included in this genus or one of its synonyms by authors at one time or another but these have been demonstrated to have affinities with Microcionidae (Hooper, 1991, 1996a). This includes *Plocamia gymnazusa* Schmidt, the type species of *Plocamia* Schmidt (not *Plocamia* Lamouroux) and [*Dirrhopalum*] Ridley in Ridley & Duncan, 1881, which Hooper (1996a) showed was a microcionid related to *Antho*.

**Distribution**

Six species are known from the North Atlantic (Duncan in Ridley & Duncan, 1881; Topsent, 1927b) and southwest Pacific (Dendy, 1924; Lévi & Lévi, 1983b).

**LITHOPLOCAMIA DENDY, 1922****Synonymy**

*Lithoplocamia* Dendy, 1922b: 79. ? *Janulum* de Laubenfels, 1936a: 79. *Monectyon* Lévi & Vacelet, 1958: 236. Taxonomic decision for synonymy: Hooper (1991), and this work.

**Type species**

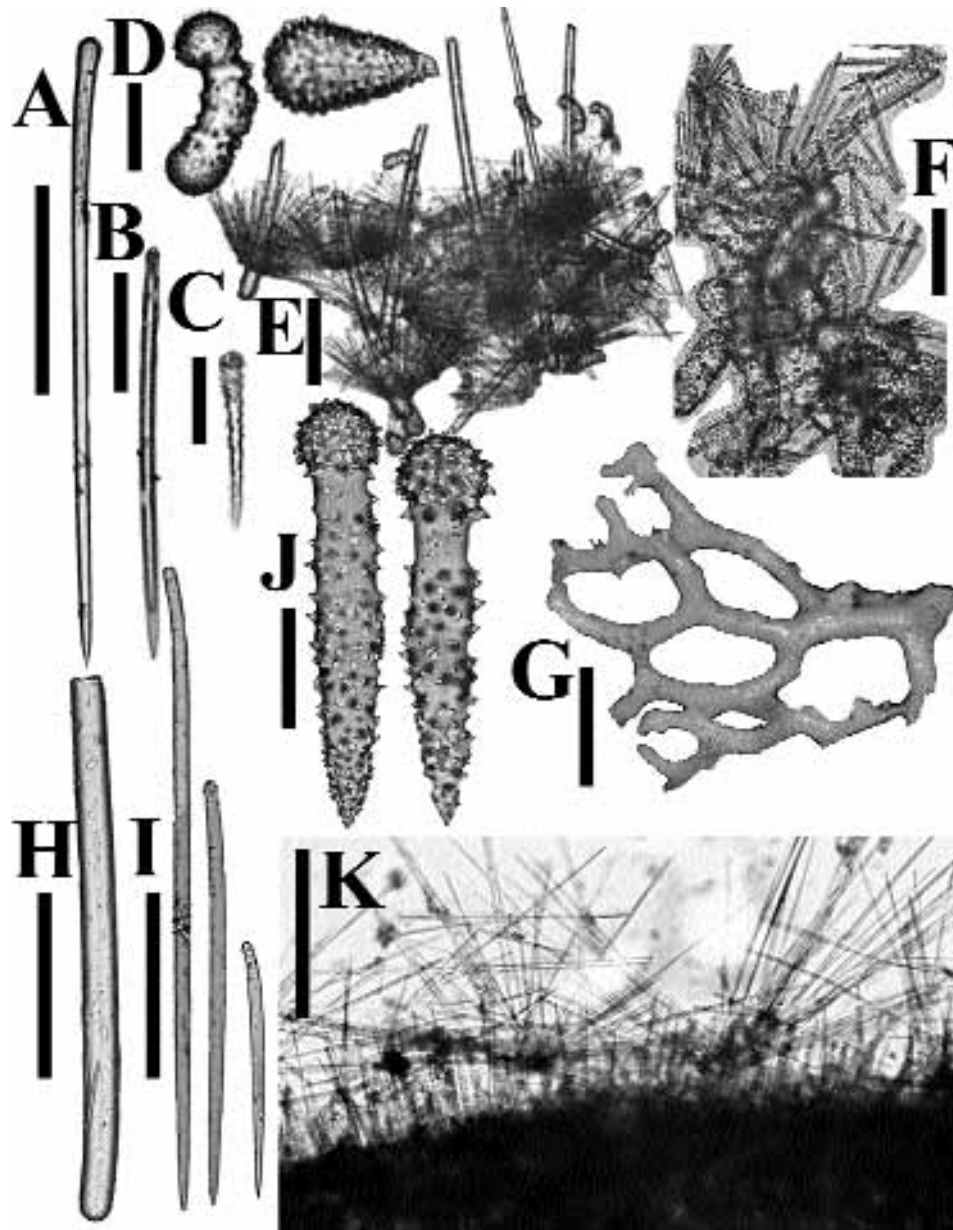
*Lithoplocamia lithistoides* Dendy, 1922b (by monotypy).

**Definition**

Raspailiidae with a secondary basal reticulate skeleton lacking any trace of axial compression, formed by (sub)isodictyal tracts of acanthostrongyles or acanthotylostrongyles.

**Diagnosis**

Massive or semi-encrusting growth forms. Surface often sculptured by drainage canals. Choanosomal skeleton lacks axial compression, consisting of a dense regular isodictyal (*s.s.*) or irregular subsodictyal secondary reticulation of acanthostrongyles. Primary skeleton consists of radial or plumose tracts of styles



**Fig. 20.** *Plocamione*. A–F, *P. dirrhopalina* (holotype). A, subectosomal style (scale 500  $\mu\text{m}$ ). B, ectosomal style (scale 200  $\mu\text{m}$ ). C, echinating acanthostyle (scale 100  $\mu\text{m}$ ). D, choanosomal acanthostrongyles (scale 50  $\mu\text{m}$ ). E, section through peripheral skeleton (scale 500  $\mu\text{m}$ ). F, choanosomal spicule bundle (scale 300  $\mu\text{m}$ ). G–J, *P. pachysclera* (holotype). G, holotype (scale 2 cm). H, basal end of large extra-axial style (scale 50  $\mu\text{m}$ ). I, choanosomal styles (scale 100  $\mu\text{m}$ ). J, acanthostyles (scale 50  $\mu\text{m}$ ). K, *P. ornata* (holotype), section through peripheral skeleton (scale 200  $\mu\text{m}$ ).

ascending to the surface and protruding slightly through it, only visible near the surface and usually obscured by the dense secondary isodictyal reticulation. Ectosome with specialized skeleton of long, slender oxeas forming sparse bouquets at the ends of primary skeletal tracts. Structural megascleres are smooth styles or subtylostyles, ectosomal oxeas, diactinal or pseudodiactinal acanthostrongyles, with or without (*s.s.*) echinating acanthostyles. Microscleres absent.

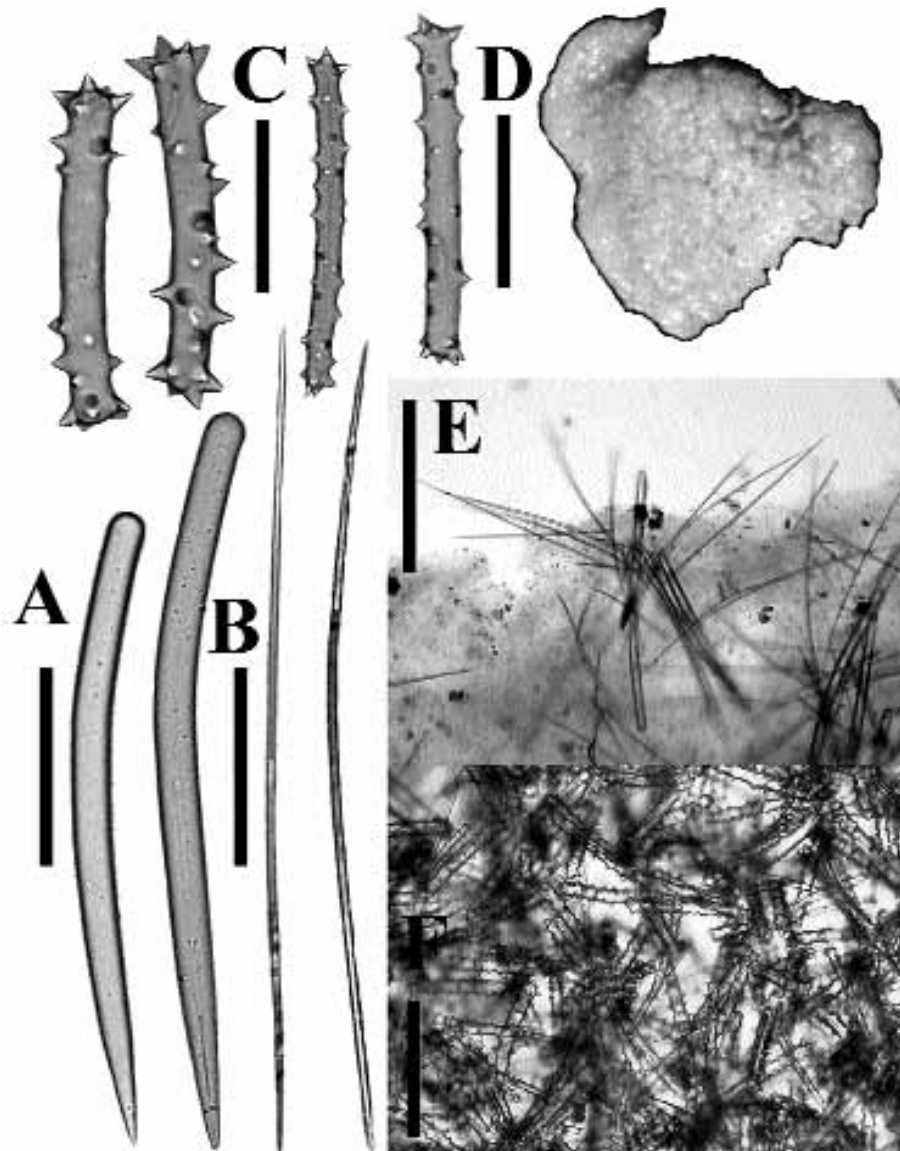
#### Description of type species

*Lithoplocamia lithistoides* Dendy, 1922b (Fig. 21).

**Synonymy.** *Lithoplocamia lithistoides* Dendy, 1922b: 79.

**Material examined.** Holotype: BMNH 1921.11.7.68 – Mauritius.

**Description.** Massive growth form; choanosomal skeleton composed of a subisodictyal (secondary) reticulation of acanthostrongyles ( $122\text{--}226 \times 12\text{--}24 \mu\text{m}$ ) occupying majority of choanosome, with radial or plumose tracts of choanosomal styles ( $252\text{--}427 \times 9\text{--}14 \mu\text{m}$ ) running towards surface; no axial compression or differentiation between axial and extra-axial regions; no true echinating spicules present; ectosomal skeleton present consisting of bouquets of long thin rhabdiform oxeas ( $322\text{--}435 \times 3\text{--}5 \mu\text{m}$ ) surrounding the protruding choanosomal spicules. Subectosomal spicules and microscleres absent.



**Fig. 21.** *Lithoplocamia*. A–F, *L. lithistoides* (holotype). A, choanosomal styles (scale 100  $\mu$ m). B, ectosomal oxeas (scale 100  $\mu$ m). C, acanthostrongyles (scale 100  $\mu$ m). D, holotype (scale 2 cm). E, ectosomal skeleton (scale 200  $\mu$ m). F, choanosomal subsisodictyal reticulation (scale 200  $\mu$ m).

**Remarks.** The diagnosis of this genus has been emended above from Hooper (1991) due to the discovery of some additional features overlooked in the type material. The genus shows some superficial similarities to *Antho* (Microcionidae) and *Damiria* (Acanthidae), and Dendy (1922b) suggested that the type species was most closely related to *Plocamia massalis* (Microcionidae). However, *Lithoplocamia* is clearly a raspailiid given the presence of a specialised raspailiid skeleton, and similarities with poecilosclerid ‘plocamiiform’ sponges are based on their common possession of a secondary isodictyal skeleton of acanthose spicules. Dendy (1922b) and Lévi & Lévi (1983b) remark on the close resemblance in the basal skeletal construction between this genus and ‘Lithistida’ with monocrepidial desmas (e.g., *Lithobubaris* Vacelet = *Sulcastrella* Schmidt). Intermediate forms also exist (e.g., *Cerberis* Topsent; family Bubaridae). Dendy speculates further that monocrepidial desmas may have developed from the

curved acanthostyles characteristic of *Lithoplocamia* (and other ‘plocamiid’ sponges), but if any relationship exists between these two forms of megascleres it is probably more likely that the reverse is true. Lévi & Lévi (1983b) also compare *Lithoplocamia* with *Endectyon*, the former having a massive and non-branching growth form and a compact isodictyal or subsisodictyal reticulation of acanthostrongyles, whereas *Endectyon* has acanthose spicules echinating plumose columns of choanosomal axial styles. In this regard *Lithoplocamia* must also be compared with the renieroid reticulate raspailiid genus *Amphinomia* Hooper.

The nominal genus *Monectyon* (type species *Monectyon atlanticus* Lévi & Vacelet, 1958, by monotypy) was described as having a skeleton composed only of acanthostrongyles, without other megascleres present at all, but Lévi & Lévi (1983b) suggest that additional material of *M. atlanticus* may eventually show that the species does possess true ectosomal auxiliary and

subectosomal extra-axial spicules, and consequently Hooper (1991) synonymised *Lithoplocamia* and *Monectyon*.

*Janulum* de Laubenfels, 1936a: 79 (type species *Isodictya spinispiculum* Carter, 1876: 310, by original designation), also appears to belong to this genus. The type species, from 'Cape St. Vincent', is described as laminiform, thickly encrusting, with porous, even surface and friable consistency. Fibre skeleton forms areolate wide-meshed isodictyal reticulation, with fibres cored by regular lines of acanthostrongyles arranged end-to-end (plocamiform arrangement). Acanthostrongyles are peculiar in that they are bent at each end, in the same direction, and heavily spined at the middle of the spicule but not at the ends. It is possible that there are other types of spicules present, overlooked by Carter (1876), but the type specimen, if it still exists, has not been located and re-examined. This species seems close to the plocamiform group of raspailiids, in particular *Lithoplocamia*, to which it is assigned with question (pending rediscovery of the type material).

#### Distribution

Known only from Mauritius and Seychelles (Dendy, 1922b), New Caledonia (Lévi & Lévi, 1983b), and eastern Atlantic (Lévi & Vacelet, 1958), all relatively deep water species.

### SUBFAMILY ECHINODICTYINAE SUBFAM. NOV.

#### Definition

Raspailiidae with regularly reticulate choanosomal skeletal structure, extra-axial skeleton vestigial or virtually absent, and all but one species lacks ectosomal specialisation. Echinating megascleres are microcionid-like club-shaped acanthostyles.

#### Scope

Two genera. *Echinodictyum* and *Amphinomia*.

### ECHINODICTYUM RIDLEY, 1881

#### Synonymy

*Echinodictyum* Ridley, in Ridley & Duncan, 1881: 493; Ridley, 1884a: 454; Ridley & Dendy, 1887: 164; Topsent, 1894c: 19; Dendy, 1896: 44, 1905: 175, 1916a: 129; Thiele, 1899: 15; Kieschnick, 1900: 570; Hentschel, 1911: 385, 1912: 369; Hallmann, 1912: 171–5; Burton, 1931a: 348; Burton & Rao, 1932: 347; Lévi, 1965: 19, 1969: 966; Hooper, 1991: 1347. *Kalykenteron* Lendenfeld, 1888: 216; Hallmann, 1912: 171. *Kieplitela* de Laubenfels, 1954: 116. Taxonomic decision for synonymy: Hooper (1991).

#### Type species

*Spongia bilamellata*, var.  $\beta$ , Lamarck, 1816 (in part) (by original designation), junior synonym of *Spongia mesenterina* Lamarck, 1814 (Topsent, 1932a: 101).

#### Definition

Raspailiidae with an exclusively reticulate choanosomal skeleton, without any trace of axial compression, cored exclusively by smooth oxeas, and vestigial radial extra-axial and ectosomal skeletons.

#### Diagnosis

Erect, vasiform, flabellate, ramose or massive growth forms. Surface typically rugose, with ridges, conules and other processes. Texture characteristically harsh, brittle and flexible, reflecting high ratio of silica to spongin in skeleton. Axial and extra-axial skeletons virtually undifferentiated. Choanosomal skeleton not compressed, irregularly reticulate. Spongin fibres usually massive, fully cored by oxeas, and echinated by acanthostyles. Extra-axial skeleton vestigial, consisting of individual subectosomal styles embedded in peripheral fibres, and projecting through ectosome or merely dispersed between fibres. Ectosomal skeleton usually membranous, sometimes skin-like, typically without specialized spiculation (except in one species). Ectosomal region contains heavy deposits of type B spongin, frequently with dense deposits of pigment granules. Structural megascleres are oxeas of 1–2 sizes, together with acanthostyles, long or short subectosomal styles, and short slender ectosomal styles in one species. Microscleres absent.

#### Description of type species

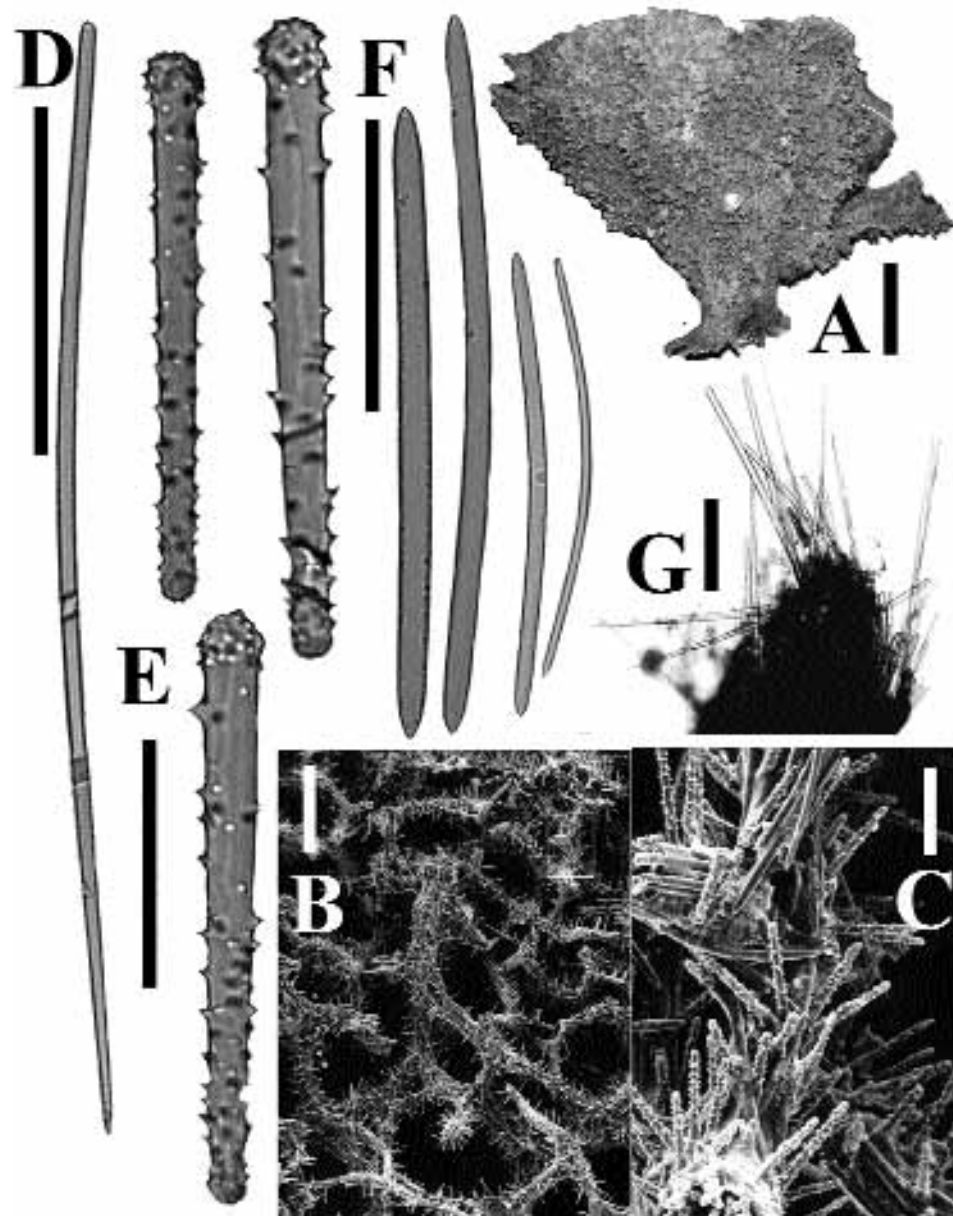
*Echinodictyum mesenterinum* (Lamarck, 1814) (Fig. 22).

**Synonymy.** *Spongia mesenterina* Lamarck, 1814: 444. *Echinodictyum mesenterinum*; Carter, 1882b: 114. *Spongia bilamellata* Lamarck, 1816: 436 (in part, var.  $\beta$ ). *Echinodictyum bilamellatum*; Ridley, in Ridley & Duncan, 1881: 493. *Kalykenteron elegans* Lendenfeld, 1888: 216. *Echinodictyum elegans*; Hallmann, 1912: 171. *Kalykenteron silex* Lendenfeld, 1888: 217. *Echinodictyum topsenti* de Laubenfels, 1936a: 63. *Thalassodendron typica*; Whitelegge, 1901: 86 (in part) (Not *Thalassodendron typica* Lendenfeld, 1888: 233). *Echinonema vasplicata* Carter, 1882b: 114.

**Material examined.** Lectotype: MNHN DT568 – 'Australian Seas'. Comparative material. Refer to extensive list in Hooper (1991).

**Description.** Erect, vasiform or cup-shaped, on short stalk; harsh texture, only slightly compressible or flexible, difficult to tear; exterior surface conulose, prominently fibrous, greatly undulating, interior surface more compressed; ectosome membranous, without specialized spiculation, with tympanic skin-like membrane stretched between adjoining surface conules and subectosomal styles ( $112\text{--}318 \times 4\text{--}7 \mu\text{m}$ ) piercing surface skeleton mainly on conules; choanosomal skeleton irregularly reticulate, without axial compression or any axial and extra-axial differentiation, meshes cavernous, ovoid; spongin fibres heavy, multispicular, cored by choanosomal oxeas ( $112\text{--}276 \times 3\text{--}15 \mu\text{m}$ ); echinating acanthostyles ( $71\text{--}105 \times 6\text{--}11 \mu\text{m}$ ) with prominent swollen, spined bulb at apex, evenly dispersed over fibres.

**Remarks.** *Echinodictyum*, including synonyms *Kalykenteron* (type species *K. elegans* Lendenfeld, 1888, by subsequent designation; Hooper, 1991), and *Kieplitela* (type species *K. antrodes* de Laubenfels, 1954, by monotypy), is atypical of Raspailiidae. Its affinities with the family lie mainly in the presence of echinating acanthostyles and subectosomal styles, which appear to be remnants of an extra-axial skeleton. This weak



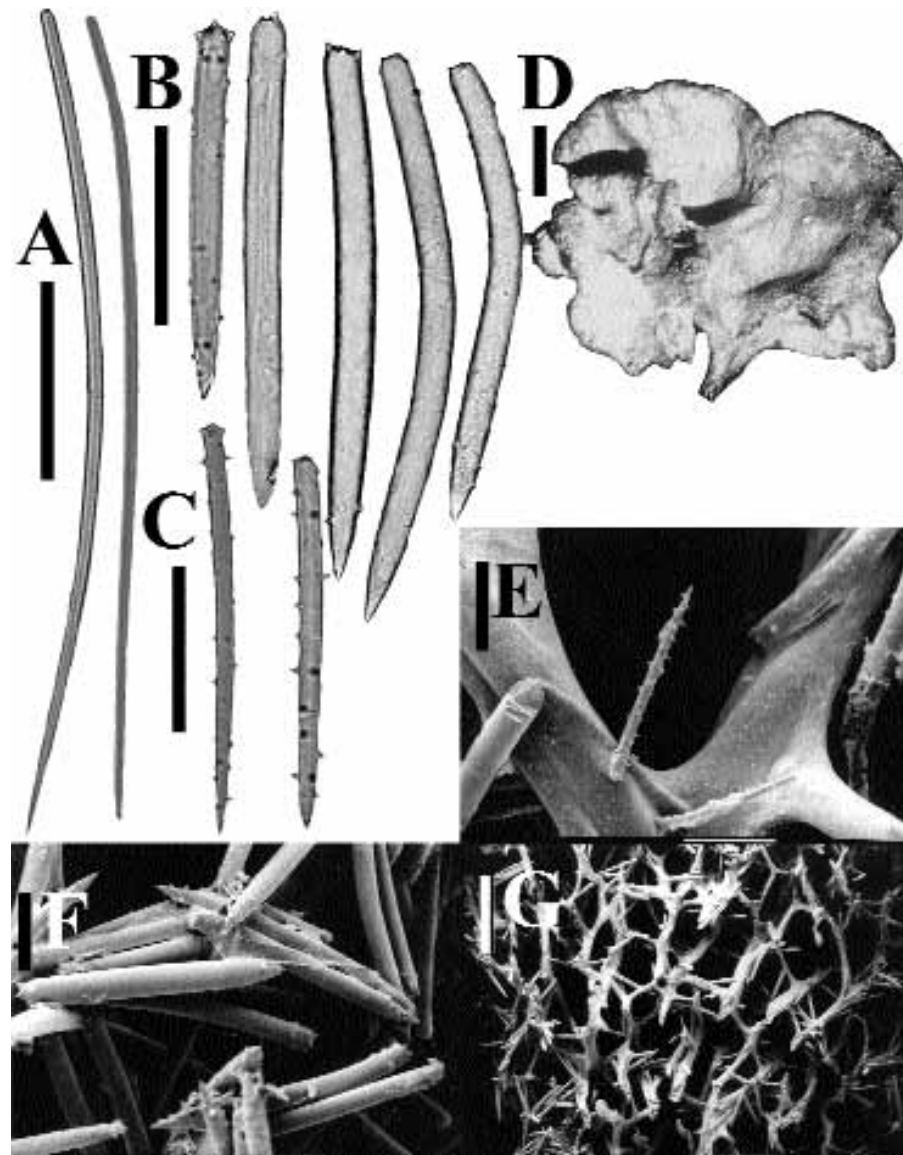
**Fig. 22.** *Echinodictyum*. A–F, *E. mesenterinum*. A, specimen NTM Z1171 (scale 5 cm). B–C, specimen NTM Z2645. B, SEM section through choanosomal skeleton (scale 500  $\mu\text{m}$ ). C, SEM section of echinated fibre (scale 200  $\mu\text{m}$ ). D–F, holotype. D, subectosomal style (scale 100  $\mu\text{m}$ ). E, echanting acanthostyles (scale 50  $\mu\text{m}$ ). F, choanosomal oxeas (scale 100  $\mu\text{m}$ ). G, *E. nidulus* (specimen NTM Z2882), ectosomal specialisation (scale 100  $\mu\text{m}$ ).

evidence, however, was strengthened by the discovery of a special raspailiid ectosomal skeleton in one species (*E. nidulus*) (Hooper, 1991). *Echinodictyum* is most similar to the nominal raspailiid genus *Clathriodendron*, the type species of which also has a predominantly reticulate skeleton, lacks any specialized ectosomal skeleton, and in which the fibres are echinated by microcionid-like acanthostyles (i.e., with evenly distributed recurved spines, and with or without an aspinose ‘neck’). *Echinodictyum* is exclusively reticulate, with only vestigial development of the extra-axial skeleton (occurring as individual extra-axial styles), and choanosomal megascleres are always short, stout oxeas. By comparison, *Clathriodendron* has more obvious affinities with *Raspailia*, with at least some differentiation of the axial and extra-axial skeleton and with choanosomal styles or modified styles coring well developed spongin fibres. The comparison should also be made

between *Echinodictyum* and the microcionid genus *Echinochalina* Thiele. *Echinochalina* is reticulate, with minimal spongin, with either oxeas, quasi-monactinal or quasi-diactinal megascleres coring fibres, and it has smooth (*s.s.*) echanting styles (Hooper, 1996a), whereas *Echinodictyum* invariably has acanthostyles.

#### Distribution

Thirty six species are known so far from the Indo-west Pacific region, and probably at least double this number worldwide. Species have been described from circum-Australia (see Hooper, 1991), central Indian Ocean (Carter, 1886d; Dendy, 1905; Thomas, 1968b), western Indian Ocean (Carter, 1879b), South Africa (Burton, 1931a), Arabian Gulf (Ridley, 1881), Indo-Malay



**Fig. 23.** *Amphinomia*. A–G, *A. sulphurea* (holotype). A, extra-axial styles (scale 50  $\mu\text{m}$ ). B, choanosomal styles (scale 100  $\mu\text{m}$ ). C, echinating acanthostyles (scale 50  $\mu\text{m}$ ). D, holotype (scale 3 cm). E, echinated fibre (scale 50  $\mu\text{m}$ ). F, choanosomal renieroid reticulation (scale 50  $\mu\text{m}$ ). G, choanosomal skeleton (scale 500  $\mu\text{m}$ ).

archipelago (Thiele, 1889; Brøndsted, 1929), central west Atlantic (Hechtel, 1983), North Atlantic (Lévi, 1969), west Africa (Topsent, 1906a), Red Sea (Keller, 1889; Topsent, 1892b; Lévi, 1965), Mediterranean (Topsent, 1892b), and West Indies (Duchassaing & Michelotti, 1864).

#### **AMPHINOMIA HOOPER, 1991**

##### **Synonymy**

*Amphinomia* Hooper, 1991: 1321.

##### **Type species**

*Amphinomia sulphurea* Hooper, 1991 (by original designation).

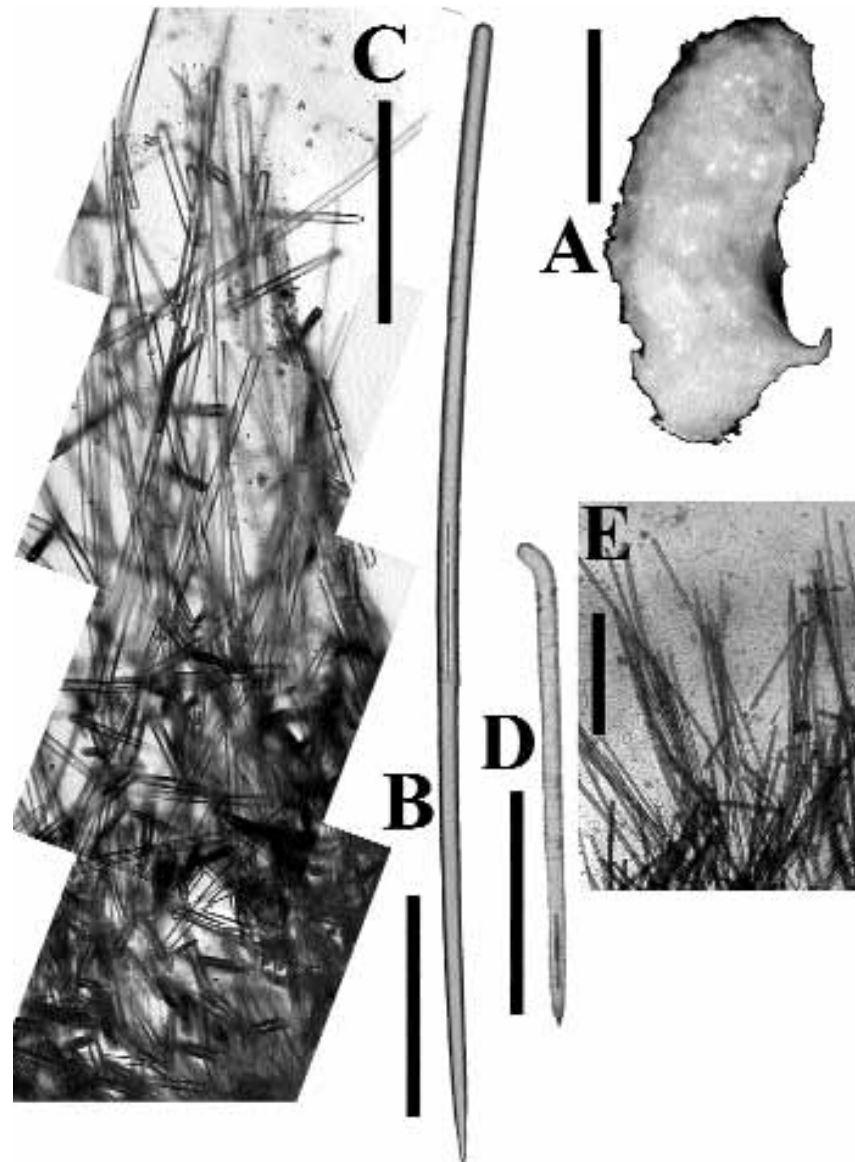
##### **Definition**

Raspailiidae having a renieroid reticulate choanosomal skeleton, lacking any axial compression, cored by choanosomal styles with spines on both basal and distal ends.

##### **Diagnosis**

Massive flabellate-lobate growth form. Surface fleshy, uneven and not hispid. Choanosomal skeletal architecture regularly renieroid-reticulate, without any axial compression or marked differentiation between axial and extra-axial skeletal tracts. Spicules and fibres form ascending multispicular tracts, interconnected by uni- or paucispicular transverse tracts, and fibres are lightly echinated by acanthostyles. Extra-axial skeleton vestigial, with subchoanosomal styles scattered throughout the skeleton especially near the periphery. Ectosomal skeleton thickly membranous, without





**Fig. 24.** *Cantabrina*. A–E, *C. erecta*. A, paratype (scale 1 cm). B, style (scale 200  $\mu\text{m}$ ). C, section through peripheral skeleton (scale 300  $\mu\text{m}$ ). D–E, MNHN fragment of paratype. D, rhabdostyle (scale 100  $\mu\text{m}$ ). E, section through peripheral skeleton (scale 400  $\mu\text{m}$ ).

specialized spiculation. Megascleres include smooth subectosomal styles, choanosomal styles with large spines on both basal and distal ends, and evenly spined echinating acanthostyles. Microscleres absent.

#### Description of type species

*Amphinomia sulphurea* Hooper, 1991 (Fig. 23).

**Synonymy.** *Amphinomia sulphurea* Hooper, 1991: 1322.

**Material examined.** Holotype: NTMZ1787 – Amphinome Shoals, Northwest Shelf, Western Australia.

**Description.** Massive, thickly lobate-lamellate growth form, with flabellate lobes, and rounded or slightly undulating margins; large oscules on edges of lobes; surface thickly glabrous, fleshy, prominently crinkled and uneven, produced by irregular, interconnected low ridges, depressions and microconules; ectosomal skeleton membranous, heavily collagenous, with few choanosomal styles protruding; choanosomal skeleton regularly

renieroid reticulate, with ascending multispicular tracts interconnected by transverse uni- or paucispicular tracts near centre of skeleton but more obviously renieroid near periphery, with triangular, hexagonal or square meshes; light spongin fibres cored by choanosomal styles with spined points and bases ( $152\text{--}274 \times 18\text{--}26 \mu\text{m}$ ), some uncored; echinating acanthostyles dispersed over fibres ( $102\text{--}138 \times 4\text{--}11 \mu\text{m}$ ); subectosomal extra-axial styles scattered between fibres throughout skeleton ( $178\text{--}248 \times 4\text{--}12 \mu\text{m}$ ); microscleres absent.

**Remarks.** *Amphinomia* differs from other raspailiids in its regularly renieroid reticulate skeleton, without any trace of axial compression, cored by choanosomal styles bearing both basal and distal spination. These megascleres are unusual but not unique amongst Porifera. Hooper (1991) documents several other species with similar spicules, many from the older literature (e.g., Bowerbank, 1864), although none of them are raspailiids. *Amphinomia sulphurea* is superficially similar to the massive suberitids (Hadromerida) in growth form and texture; it also shows superficial

similarities in skeletal construction to members of the order Agelasida, Poecilosclerida families Microcionidae (such as *Antho (Isopenectya)*), Acarnidae (*Acarnus*) and Myxillidae (*Myxilla*). Based on its affinities with *Lithoplocamia*, and in possessing the remnants of an extra-axial skeleton and echinating acanthostyles, the genus was referred to Raspailiidae although it has potential affinities to the Microcionidae and Acarnidae. It differs from *Lithoplocamia* by the different geometries of their basal choanosomal spicules (monactinal versus diactinal, respectively), and the latter having a secondary (sub)isodictyal reticulate skeleton composed of spined acanthostyles, an extra-axial plumose or radial skeleton of smooth choanosomal styles, lacking echinating acanthostyles and having a specialised raspailiid ectosomal skeleton.

*Acanthostylotella* Burton & Rao, 1932 (type species *Stylotella cornuta* Topsent, 1897a: 464, from Ambon, Indonesia and the Maldives) is described as having a skeleton composed of uni- to paucispicular tracts of styles, smooth or with terminal rudimentary spines, forming an irregular anisodictyal reticulation with weak spongin fibres. The subsequent descriptions of Topsent (1897a), Burton & Rao (1932) and Desqueyroux-Faundez (1981) are still very inconclusive as to its true identity, with the possibility that it belongs amongst the Raspailiidae, and with terminal spination on choanosomal styles (perhaps superficially) reminiscent of *Amphinomia*. However, no true echinating acanthostyles or extra-axial styles were reported and its allocation remains *incertae sedis* until original material is re-examined.

#### Distribution

Monotypic, endemic to northwest Australia.

#### **CANTABRINA FERRER-HERNANDEZ, 1914** (*INCERTAE SEDIS*)

#### Synonymy

*Cantabrina* Ferrer-Hernandez, 1914a: 453; Ferrer-Hernandez, 1914b: 22; Hooper, 1991: 1394.

#### Type species

*Cantabrina erecta* Ferrer-Hernandez, 1914 (by monotypy).

#### Definition

Raspailiidae with rare echinating rhabdostyles completely smooth, a halichondroid reticulate choanosomal skeleton becoming plumose near the periphery.

#### Diagnosis

Erect lobate growth form. Conulose and hispid surface. Choanosomal skeleton halichondroid in the axis composed of a disorganized criss-cross of long thick styles. No fibres present. Subectosomal extra-axial skeleton increasingly plumose towards the periphery, with long thick styles protruding through surface only at the tips of conules. Echinating megascleres rare. Ectosomal skeleton with long thin styles, sinuous or straight, in sparse bundles associated with plumose tracts near the surface. Structural megascleres are long styles of two categories and rare smooth echinating styles with slightly rhabdose bases. Microscleres absent.

#### Description of type species

*Cantabrina erecta* Ferrer-Hernandez, 1914 (Fig. 24).

**Synonymy.** *Cantabrina erecta* Ferrer-Hernandez, 1914a: 453.

**Material examined.** Paratype. BMNH 1930.1.21.9, schizotype MNHN LBIM DCL174L-Spain.

**Description.** Erect lobate bulbous growth form. Surface conulose and hispid. Ectosomal skeleton membranous, with paucispicular bundles of thinner (? ectosomal) styles (long thin, straight or sinuous; 640–920 × 4–6 μm) clustered around the plumose choanosomal tracts in the peripheral skeleton, although these do not appear to penetrate the surface; subectosomal skeleton plumose, with multispicular ascending tracts of thicker (? choanosomal) styles (very long, thick, with evenly rounded base; 950–1475 × 12–22 μm) diverging towards and penetrating the surface only on the tips of conules; choanosomal skeleton halichondroid reticulate, with disorganized criss-cross of thicker (? choanosomal) styles. No fibres present. Mesohyl only lightly invested with spongin towards the axis becoming more dense near the periphery. Echinating styles entirely smooth with slightly rhabdose base (220 × 6 μm), very rare or possibly contaminants. Structural megascleres consist of two categories of long styles, the larger often with telescoped points and rounded bases, and smooth echinating styles with slightly rhabdose bases. Microscleres absent.

**Remarks.** The affinities of this monotypic genus are still uncertain. Echinating megascleres supposedly native to this species (Ferrer-Hernandez, 1914a,b) are extremely rare in the paratype (including several BMNH slide preparations) a spicule slide also made from this material in MNHN. It is possible that these rhabdostyles are contaminants in which case it may belong to Halichondriidae given its classic halichondrid skeletal structure.

#### Distribution

Monotypic, Spain.