

## Family Acarnidae Dendy, 1922

**John N.A. Hooper**

Queensland Museum, P.O. Box 3300, South Brisbane, Qld, 4101, Australia. (JohnH@qm.qld.gov.au)

Acarnidae Dendy (Demospongiae, Poecilosclerida, Microcionina) contains 37 nominal genera of which 13 are considered here to be valid, and probably several hundreds of species. Acarnids are distributed worldwide, although several genera are predominant in colder temperate waters, and several have very restricted (apparently endemic) geographic ranges. Major morphological characters diagnostic for the family include massive, burrowing, excavating or encrusting growth forms with fistules, as well as non-fistulose genera with digitate, flabellate, massive or encrusting growth forms; ectosomal skeleton with tangentially arranged tylotes with spined bases; choanosomal skeleton reticulate (in massive) or plumose (in encrusting growth forms), with or without echinating spicules; megascleres include styles; and microscleres are palmate isochelae and toxas, sometimes lost or sometimes with other microscleres such as bipocillae, modified anisochelae, microrhabds and raphides.

**Keywords:** Porifera; Demospongiae; Poecilosclerida; Microcionina; Acarnidae; *Acanthorhabdus*; *Acarnus*; *Acheliderma*; *Cornulella*; *Cornulum*; *Damiria*; *Dolichacantha*; *Iophon*; *Megaciella*; *Paracornulum*; *Tedaniophorbas*; *Wigginsia*; *Zyzzya*.

### DEFINITION, DIAGNOSIS, SCOPE

#### Synonymy

Acarneae Dendy, 1922b. Iophoneae Burton, 1929a. Acarnidae Boury-Esnault, 1973 (Not [Acarniidae] de Laubenfels, 1936a). Cornulidae Lévi & Lévi, 1983b.

#### Definition

Microcionina with apically spined tylotes forming a tangential ectosomal skeleton.

#### Diagnosis

Encrusting, massive, flabellate or digitate growth forms, sometimes burrowing, many genera producing fistules. Ectosomal skeleton composed of tylotes, strongyles or modified tylote spicules bearing microspined bases forming tangential and/or paratangential tracts, often irregular or halichondroid in arrangement. Choanosomal megascleres are styles or modified styles (anisoxeas) forming reticulate structures in massive forms (isodictyal, isotropic, anisotropic or more irregular skeletons) or plumose or hymedesmioid skeletons in encrusting growth forms. Echinating spicules present or absent, consisting of acanthostyles and/or unique cladotylotes. Microscleres include palmate isochelae and toxas of various morphologies (both sometimes lost), with some genera also having other microscleres such as bipocillae, modified anisochelae, microrhabd-like spicules (modified microxeas or microstrongyles) and diamond-shaped microxeas (modified toxas).

#### Scope

Acarnidae contains 37 nominal genera of which only 13 are presently considered to be valid.

#### History and biology

Fistular poecilosclerid genera like *Acheliderma*, *Cornulum*, *Damiria*, *Zyzzya* with tylote ectosomal megascleres have been

traditionally included in the family Coelosphaeridae Topsent. Lévi & Lévi (1983b) subsequently split Coelosphaeridae into two groups for genera with palmate isochelae (Cornulidae Lévi & Lévi) or arcuate isochelae (Coelosphaeridae). Several non-fistular genera had similar skeletal structure and spiculation, such as *Acarnus* and *Iophon*, possessing spined ectosomal tylotes and palmate isochelae, but these were traditionally included in Myxillidae (e.g., Topsent, 1928c; de Laubenfels, 1936a), which predominantly contain taxa with 'tridentate-derived' chelae (arcuate and anchorate) and sigmas, but lack toxas. Hajdu *et al.* (1994a) proposed to merge these two groups of genera by extending the scope of Cornulidae to include both fistulose and non-fistulose genera with similar skeletal arrangements (ectosomal tylotes with spined bases) and spiculation (palmate isochelae, toxas, lack of sigmas).

The correct name for the family is still contentious. Hajdu *et al.* (1994a) noted that the inclusion of *Iophon* in this group necessitated recognition of Burton's (1929a) higher taxon Section Iophoneae, which they elevated to full family status. Iophoneae was initially created only for *Iophon* and *Iophonopsis* within the family Myxillidae. However, the same argument applies with the inclusion of *Acarnus* in this group. Dendy (1922b) had earlier created Section Acarneae for this genus, within the old family Desmacidonidae, subfamily Ectyoninae, which therefore theoretically takes priority over Iophoneae. It could be argued that Hajdu *et al.* (1994a), followed by Van Soest *et al.* (1994a) and Desqueyroux-Faundez & Van Soest (1995) had thus established Iophonidae 'in prevailing usage' (Article 35.5 ICZN; Anon., 1999), in which case 'the older name is not to displace the younger name'. However, these authors overlooked the prior usage of Acarnidae as a family level taxon by Topsent (1928c) and subsequently adopted by several authors (e.g., de Laubenfels, 1932; see discussion in Hooper, 1987), negating the applicability of Article 35.5 of the ICZN.

Under Hajdu *et al.*'s (1994a) concept of this group 36 nominal genera were potentially allocated here. There are several recent reviews outlining the scope and features of this group, including comprehensive revisions of particular genera (Van Soest *et al.*, 1991; Van Soest, Zea & Kielman, 1994; Desqueyroux-Faundez & Van Soest, 1995).

**Differences with similar families**

Acarnidae differs significantly from other Microcionina in possessing apically-spined tylotes or modified strongylote or oxeote ectosomal spicules that typically form a tangential ectosomal skeleton. By comparison the other families (Microcionidae, Raspailiidae, Rhabderemiidae) have monactinal ectosomal spicules which do not generally form a tangential skeleton (although some species of *Clathria* are known to have modified anisostyles with spines on both the base and apex of the spicule

(Hooper, 1996a)). Some of the iophonid genera are clearly similar to the Microcionidae (e.g., *Acarnus*, *Megaciella*) in characters such as the geometry of megascleres and microscleres, whereas others (e.g., *Acanthorhabdus*, *Dolichacantha*) have been modified so extensively that their similarities are barely perceptible.

**Previous reviews**

Berquist & Fromont (1988), Van Soest, Zea & Kielman, 1994; Desqueyroux-Faundez & Van Soest (1995).

**KEY TO GENERA**

- (1) Ectosomal spicules are tylotes, mostly smooth, with apical spines ..... 3  
 Ectosomal spicules modified ..... 2
- (2) Ectosomal tylotes modified to acanthoxeas with apical spines ..... *Acanthorhabdus* (non-fistular)  
 Ectosomal tylotes entirely smooth (secondary loss of spines) ..... *Tedaniophorbas* (non-fistular)
- (3) Choanosomal skeletal structure well-formed ..... 4  
 Choanosomal skeletal structure vestigial, consisting of single tylotes and scattered accessory spicules (acanthoxeas) ..... *Cornulella* (fistular)
- (4) Choanosomal and ectosomal megascleres clearly differentiated in geometry and distribution ..... 6  
 Ectosomal tylotes form both ectosomal and choanosomal skeletal structures ..... 5
- (5) Apically-spined tylotes form both tangential ectosomal and plumo-reticulate choanosomal skeletons (with or without a second category of choanosomal styles) ..... *Cornulum* (fistular)  
 Apically-spined tylotes form both tangential ectosomal tracts and plumose ascending choanosomal tracts (with acanthostyles echinating hymedesmioid basal skeleton) ..... *Paracornulum* (fistular)  
 Apically-spined tylotes are the only megascleres ..... *Damiria* (fistular)
- (6) Choanosomal megascleres consist only of styles, without accessory spicules ..... 8  
 More than one category of choanosomal megascleres, one greatly modified ..... 7
- (7) Accessory spicules consist of verticillately-spined strongyles (or strongyloxeas) ..... *Zyzya* (fistular)  
 Accessory spicules consist of one or more classes of cladotylotes ..... *Acarnus* (non-fistular)  
 Accessory spicules consist of peculiar acanthostrongyles with numerous spined 'cladi' ..... *Dolichacantha* (non-fistular)  
 Accessory spicules consist of 'plocamiform' acanthostrongyles echinating ascending tracts of styles ..... *Wigginsia* (non-fistular)
- (8) With a regular, uni- or pauci-spicular isodictyal choanosomal reticulation of smooth or spined styles, with or without echinating acanthostyles ..... *Iophon* (non-fistular)  
 With confused choanosomal skeleton divided into primary ascending multispicular tracts and secondary interconnecting uni- or bispicular tracts, both cored by basally spined styles, with or without echinating acanthostyles ..... *Megaciella* (non-fistular)  
 Choanosomal skeleton appears predominantly plumose due to the dominance of subectosomal tracts of ectosomal tylotes, whereas the basal choanosomal skeleton is irregularly renieroid-reticulate composed of basally spined styles forming triangular or square meshes; microscleres include elongated diamond-shaped microxeas ..... *Acheliderma* (fistular)

**ACANTHORHABDUS BURTON, 1929****Synonymy**

*Acanthorhabdus* Burton, 1929a: 432.

**Type species**

*Acanthorhabdus fragilis* Burton, 1929a (by monotypy).

**Definition**

Non-fistular Acarnidae with apically-spined ectosomal acanthorhabds, modified choanosomal mucronate anisoxeas and lacking true echinating spicules.

**Diagnosis**

Massive non-fistulose growth form; ectosomal skeleton composed of a loose halichondroid tangential layer of acanthoxeas

(acanthorhabds) with heavy spines and microspined tylote apices; choanosomal skeleton with smooth modified styles (anisoxeas) often provided with a terminal mucron, forming massive multispicular plumose and reticulate columns, with acanthoxeas dispersed between (but not echinating) fibres; microscleres palmate anisochelae with spurs.

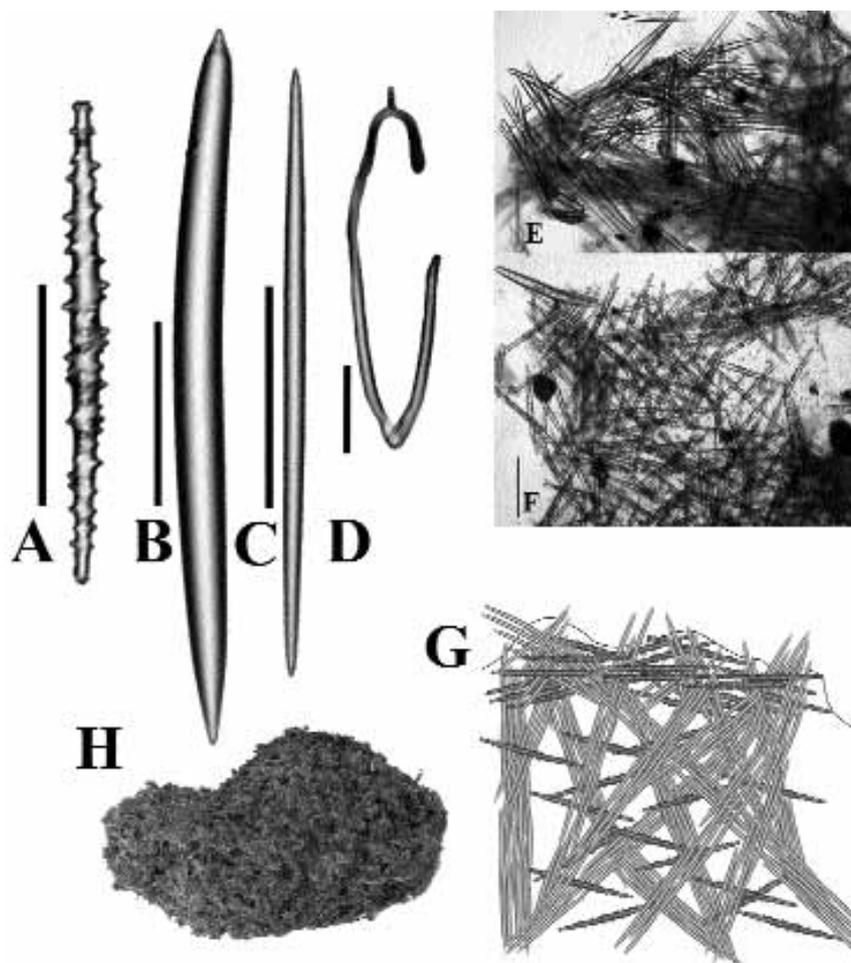
**Description of type species**

*Acanthorhabdus fragilis* Burton, 1929a (Fig. 1).

**Synonymy.** *Acanthorhabdus fragilis* Burton, 1929a: 432, text-fig. 5, pl. 4, fig. 2.

**Material examined.** Holotype: BMNH 1926.10.26.189 – Antarctica.

**Description.** Subspherical, massive growth form; surface minutely conulose; texture friable; oscules raised on small papillae or plush with surface; ectosomal skeleton an irregular surface crust of acanthorhabds lying mostly tangential to surface in an irregular nearly halichondroid criss-cross, but also protruding paratangentally from surface; abundant tracts of anisochelae also scattered



**Fig. 1.** *Acanthorhabdus fragilis* Burton (holotype). A, acanthoxea (acanthorhabd) (scale 300  $\mu\text{m}$ ). B–C, choanosomal anisoxeas (scales 300  $\mu\text{m}$ ). D, spurred palmate anisochelae (scale 25  $\mu\text{m}$ ). E, choanosomal skeleton (scale 1 mm). F, ectosomal skeleton (scale 1 mm). G, idealised reconstruction of skeleton. H, holotype (approximately 25 cm) (H, from Burton, 1929a, pl. 4, fig. 2).

over surface; choanosomal skeleton composed of massive plumose and plumoreticulate columns of smooth anisoxeas with up to 15 spicules per tract, interdispersed with acanthorhabds in nearly halichondroid arrangement and also sometimes interconnecting major anisoxeote spicule tracts; megascleres include fusiform, heavily spined ectosomal acanthoxeas (acanthorhabds) with spines curved towards the middle of spicules and microspined apices (320–365  $\times$  20–35  $\mu\text{m}$ ), smooth choanosomal anisoxeotes often with distinct mucron on the basal end and occasionally a single spine on the point (450–590  $\times$  15–42  $\mu\text{m}$ ); microscleres spurred palmate anisochelae (22–28  $\mu\text{m}$ ).

**Remarks.** Burton (1929a) initially included this monotypic genus with the mycalid genera (his taxon Mycaleae) based on the possession of anisochelae whereas the presence of acanthorhabds with spined tylote apices is not found in the mycalids but is more consistent for the Acarnidae (Van Soest, Zea & Kielman, 1994; Desqueyroux-Faundez & Van Soest, 1995). This placement is further supported by the shared possession of spurred anisochelae in *Iophon*. However, this genus is very atypical of Acarnidae in the geometry of ectosomal acanthorhabds, which resemble the acanthoxeas of Desmoxyidae more so than poecilosclerid ectosomal spicules, and in the halichondroid reticulate nature of these spicules dispersed within the ectosomal and choanosomal skeletons. Nevertheless, the inclusion of the genus in

Poecilosclerida is without doubt given its possession of chelae microscleres.

#### Distribution

Monotypic, endemic to Antarctica.

#### ACARNUS GRAY, 1867

#### Synonymy

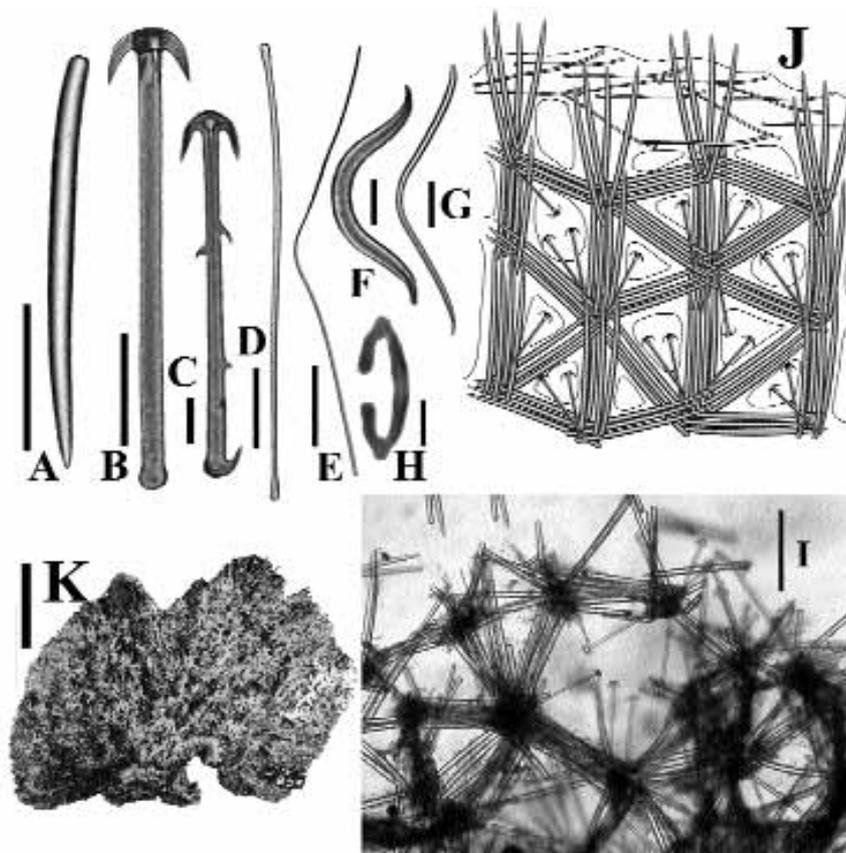
*Acarus* Gray, 1867a. ? *Fonteia* Gray, 1867a. ? *Trefortia* Deszo, 1880. *Microtylotella* Dendy, 1896. *Acanthacarnus* Lévi, 1952. Taxonomic decision for synonymy: Hooper (1987), Van Soest *et al.* (1991).

#### Type species

*Acarus innominatus* Gray, 1867a (by monotypy).

#### Definition

Non-fistular Acarnidae with cladotylote echinating spicules.



**Fig. 2.** A–J, *Acarnus innominatus* Gray (holotype). A, choanosomal style (scale 300  $\mu\text{m}$ ). B–C, larger and smaller echinating cladotylotes (scales 200  $\mu\text{m}$  and 50  $\mu\text{m}$ , respectively). D, ectosomal tylote (scale 200  $\mu\text{m}$ ). E, accolada toxa (scale 200  $\mu\text{m}$ ). F, oxhorn toxa (scale 50  $\mu\text{m}$ ). G, deeply curved toxa (scale 50  $\mu\text{m}$ ). H, palmate isochela (scale 25  $\mu\text{m}$ ). I, peripheral skeleton (scale 1 mm). J, idealised reconstruction of skeleton. K, *Acarnus bergquistae* Van Soest *et al.*, 1991, specimen NTM Z855 (from Hooper, 1987, fig. 40; scale 50  $\mu\text{m}$ ).

### Diagnosis

Non-fistulose, encrusting to massive growth forms; ectosomal tylotes with microspined ends, forming tangential or paratangential tracts (not brushes); choanosomal skeleton isodictyal, isotropic or anisotropic reticulate, occasionally plumo-reticulate or plumose or hymedesmioid in encrusting species; skeletal tracts cored by smooth styles, echinated by 1 or 2 (exceptionally 3) categories of cladotylotes, echinating acanthostyles present or absent; microscleres are palmate isochelae and toxas of several morphologies.

### Description of type species

*Acarnus innominatus* Gray, 1867a (Fig. 2).

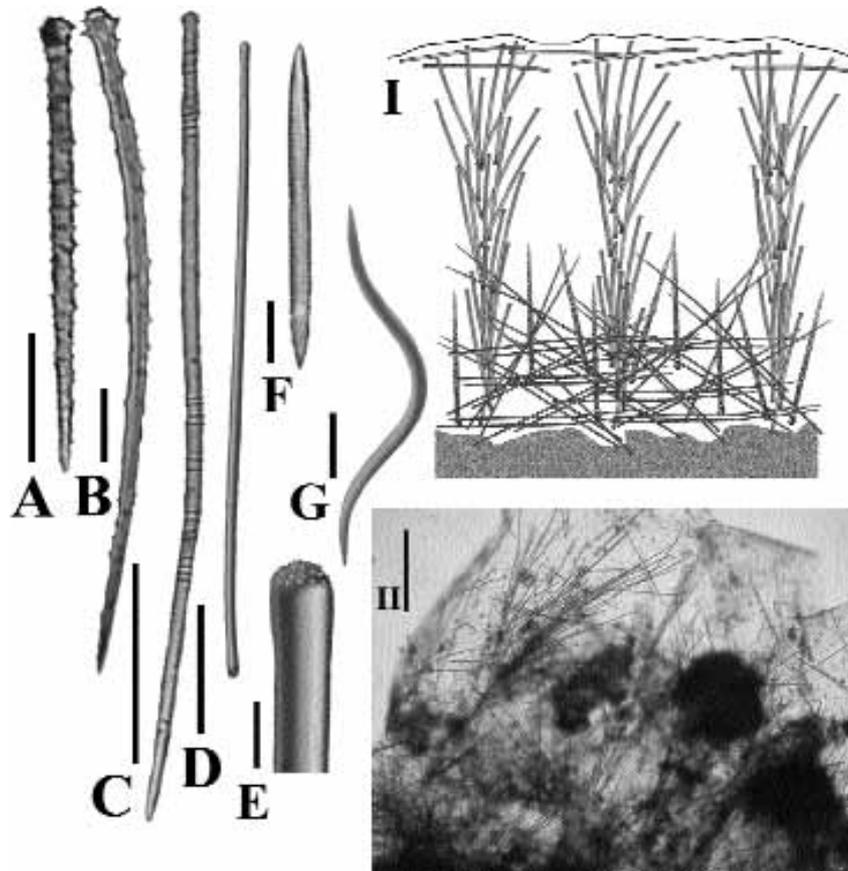
**Synonymy.** *Acarnus innominatus* Gray, 1867a: 544 (based on unnamed spicule drawings of Bowerbank, 1864: pl. 3, figs 73–76, pl. 18, fig. 292). *Acarnus carteri* Ridley, 1884a: 354.

**Material examined.** Holotype (schizotype): BMNH Bowerbank collection 309 – West Indies.

**Description.** Thin or massively encrusting; surface optically smooth; oscules not apparent; texture soft; ectosomal skeleton tangential layer of tylotes; choanosomal skeleton plumose major choanosomal tracts ascending to surface interconnected by renieroid isotropic tracts, both cored by choanosomal styles in 5–15 spicules per tract; renieroid component of skeleton dominates skeletal structure; choanosomal tracts echinated by cladotylotes, particularly at nodes; megascleres ectosomal tylotes with slightly

swollen microspined bases (180–280  $\times$  4  $\mu\text{m}$ ); choanosomal styles robust, smooth, slightly curved at centre (280–460  $\times$  11–22  $\mu\text{m}$ ); echinating cladotylotes in two size classes: larger with entirely smooth shaft, smooth, rounded basal tyle and four apical clads (230–300  $\times$  6–12  $\mu\text{m}$ ); smaller with sparsely spined shaft, smooth, rounded basal tyle and four clads on apical end (80–115  $\times$  2–3  $\mu\text{m}$ ); microscleres with three categories of toxas: oxhorn toxas (50–160  $\times$  2–4  $\mu\text{m}$ ); thin deeply curved toxas (35–150  $\times$  1.5–2  $\mu\text{m}$ ); accolada toxas (220–450  $\times$  0.5–1.5  $\mu\text{m}$ ); palmate isochelae (9–24  $\mu\text{m}$ ).

**Remarks.** *Acarnus* has been revised extensively and many new species described over recent years (Lévi, 1952; Van Soest, 1984b; Hooper, 1987; Van Soest, Hooper & Hiemstra, 1991; Hiemstra & Hooper, 1991; Hooper & Lévi, 1993a; Van Soest, Zea & Kielman, 1994). The generic synonymy is expanded here to now include: *Fonteia* Gray, 1867a (with type species *Fonteia anomala* Gray, 1867a (by monotypy) holotype unknown; *Trefortia* Deszo, 1880 (which is probably a *nomen nudum* as neither the type species nor type material are known (de Laubenfels, 1936a:92)); *Acanthacarnus* Lévi, 1952 (type species *Acanthacarnus souriei* Lévi, 1952 (by monotypy) holotype MNHN LBIMDCL1259); and *Microtylotella* Dendy, 1896 (type species *Microtylotella guentheri* Dendy, 1896 (by monotypy) holotype NMV G2366). The first two genera are included with question given the dubious (or non-existent) status of type material. The latter genus is here included into synonymy based on the discovery of cladotylotes in the holotype. It is nevertheless unusual to the genus in having ectosomal and choanosomal skeletal tracts permeated with sand and with a reduced spicule skeleton.



**Fig. 3.** *Acheliderma lemmiscata* Topsent (holotype). A–B, acanthostyles (scale 50  $\mu\text{m}$  and 20  $\mu\text{m}$ , respectively). C, choanosomal style (scale 100  $\mu\text{m}$ ). D, ectosomal tylote (scale 50  $\mu\text{m}$ ). E, base of tylote (scale 2  $\mu\text{m}$ ). F, diamond-shaped microxea (scale 50  $\mu\text{m}$ ). G, toxa (scale 20  $\mu\text{m}$ ). H, peripheral skeleton (scale 250  $\mu\text{m}$ ). I, idealised reconstruction of skeleton.

### Distribution

Cosmopolitan in temperate and tropical seas, predominantly shallow water.

### ACHELIDERMA TOPSENT, 1892

#### Synonymy

*Acheliderma* Topsent, 1892a. *Astylinifer* Topsent, 1927b. *Fusifera* Dendy, 1896. Taxonomic decision for synonymy: Van Soest *et al.* (1994).

#### Type species

*Acheliderma lemmiscata* Topsent, 1892a (by monotypy).

#### Definition

Fistular Acarnidae with elongated diamond-shaped microxea microscleres.

#### Diagnosis

Fistulose growth forms; ectosomal spicules are tylotes with microspined bases lying tangential to surface (replaced by sand in

one species); choanosomal skeleton an irregular reticulation of microspined styles and echinating acanthostyles; microscleres characteristically elongated diamond-shaped microxeas and toxas; chelae absent.

#### Description of type species

*Acheliderma lemmiscata* Topsent, 1892a (Fig. 3).

**Synonymy.** *Acheliderma lemmiscata* Topsent, 1892a: 24.

**Material examined.** Holotype (schizotypes): MNHN DT170, BMNH 1953.11.9.19 – Banyuls, Mediterranean.

**Description.** Encrusting growth form with small erect fistules up to 10 mm high protruding through substrate; ectosomal skeleton a tangential layer of tylotes with microspined bases overlying a plumose subectosomal skeleton composed of the same spicules extending to the surface from the basal choanosomal skeleton; choanosomal skeletal structure predominantly plumose due to the dominance of the subectosomal tracts of tylotes; basal choanosomal skeleton irregularly renieroid-reticulate composed of choanosomal styles with microspined bases forming tracts of 1–3 spicules and triangular or square meshes; skeletal tracts echinated by acanthostyles; megascleres ectosomal tylotes with microspined bases (250–310  $\times$  3–4  $\mu\text{m}$ ), basally spined choanosomal styles and subtylostyles (420–450  $\times$  4–9  $\mu\text{m}$ ), short acanthostyles evenly spined (80–175  $\times$  3–5  $\mu\text{m}$ ); microscleres wing-shaped toxas (90–130  $\times$  1–2  $\mu\text{m}$ ) and diamond-shaped microxeas (60–70  $\times$  1  $\mu\text{m}$ ); chelae absent.

**Remarks.** Van Soest *et al.* (1994) suggest that the unusual diamond-shaped microxeas ('raphides fusiformes' of Topsent, 1892a), characteristic of this genus, are derived from toxas, and is most obvious in the transition series of microxeas-toxas seen in *A. planum* Topsent (1928c: 228). In the type species, however, this relationship is less obvious with spicules resembling 'true' microxeas and toxas at each end of the continuum. All three nominal genera (*Acheliderma*, *Astylinifer* (type species *A. planum* Topsent, 1928c (by monotypy) schizotype MNHN DT1288), and *Fusififer* (type species *F. fistulatus* Dendy, 1896 (by monotypy) syntype NMV G2356, schizotype BMNH 1902.10.18.61) have these spicules and have similar growth form, skeletal structure and spiculation and are now considered to be synonyms. Microspined tylole ectosomal spicules support the inclusion of *Acheliderma* in Acarnidae, although in one South Australian species (*A. fistulatus* (Dendy, 1896)) these have been secondarily lost and replaced by sand, and in two other species (*A. planum* and *A. lisannae*) some or all ectosomal spicules are mucronated anisotyloles.

The genus is intermediate between *Paracornulum* and *Cornulum* in having both echinating acanthostyles and structural styles. The type species is somewhat unusual in having an extensive plumose subectosomal region, extending from the irregular renieroid basal skeleton, occupying most of the sponge diameter. This is most evident in the fistular region (section BMNH 1953.11.9.19), whereas in the thinner encrusting section it is not so extensive (section MNHN DT170). In the BMNH material many arcuate and unguiferous arcuate isochelae were also seen, but these are presumably contaminants (possibly artifacts from sectioning), not seen in other material or described in the literature.

#### Distribution

Four valid species are currently recognised (Van Soest *et al.*, 1994). Additional reviews are provided by Topsent (1892a: 24; 1928c: 228–9), Dendy (1896:49) and Desqueyroux-Faudez & Van Soest (1996). Caribbean, Mediterranean, Azores, NE Atlantic and South Australia, shallow water.

#### CORNULELLA DENDY, 1922

##### Synonymy

*Cornulella* Dendy, 1922b: 103.

##### Type species

*Cornulella lundbecki* Dendy, 1922b (by monotypy).

##### Definition

Fistular Acarnidae with vestigial choanosomal skeleton of single tyloles and scattered acanthoxeas.

##### Diagnosis

Thinly encrusting, fistular growth forms; ectosomal skeleton a unispicular network of intercrossing tangential tyloles with spined heads; choanosomal skeleton vestigial, made up of individual tyloles identical to those in the ectosomal skeleton, with accessory acanthoxeas distributed singly among the tyloles; microscleres palmate isochelae and frequently toxas.

#### Description of type species

*Cornulella lundbecki* Dendy, 1922b (Fig. 4).

**Synonymy.** *Cornulella lundbecki* Dendy, 1922b:103.

**Material examined.** Holotype: BMNH 1923.4.1.113 – Seychelles, W Indian Ocean.

**Description.** Delicate thin-walled fistules up to 13 mm high, 3 mm diameter, arising from thinly encrusting base; ectosomal skeleton with unispicular tangential layer of basally spined tyloles forming a criss-cross on the surface with vaguely differentiated ascending and transverse multispicular tracts supporting the fistule wall; choanosomal skeleton vestigial, hymedesmioid in thinner parts of skeleton with individual tyloles and microrhabd-like (acanth)oxeas paratangential to (but not echinating) basal layer of spongin, and tyloles forming multispicular longitudinal tracts supporting fistules and (acanth)oxeas dispersed singly amongst tyloles; no fibres and poor collagen in mesohyl; megascleres tyloles with microspined bases (310–420 × 4–8 μm), small microrhabd-like (acanth)oxeas with a roughened surface and sometimes with a central or sub-central swelling (16–24 × 1–2 μm); microscleres large palmate isochelae with thickened alae (42–58 μm); two sizes of toxas: larger slightly curved at centre with recurved arms (470–640 × 5–8 μm), smaller sharply curved at centre, with recurved arms, rare (110–135 × 2–5 μm).

**Remarks.** *Cornulella* differs from *Paracornulum* in lacking accessory echinating acanthostyles although both genera have microrhabd-like acanthoxeas and lack structural styles in the choanosomal skeleton (Van Soest *et al.*, 1994). Van Soest *et al.* (1994) suggest that these microrhabds are thin, spined oxeas and not true microrhabds, contrary to Dendy's (1922b) interpretation, although they are extremely small and could be validly included as a class of microscleres, particularly in the type species where their ornamentation is poorly developed. The possession of basally spined ectosomal tyloles and palmate isochelae indicates affinities with the Acarnidae. The type species of *Cornulella* has quite different choanosomal skeletal architecture from other Acarnidae, lacking any trace of an organised reticulate skeleton and having instead longitudinal and transverse multispicular tracts typical of fistular growth forms. This skeletal structure is more-or-less typical for the genus, which varies from simply a loose collection of spicules to more organised tracts supporting the choanosome.

Van Soest *et al.* (1994) discuss relationships and provide comparative spicule dimensions for the six recognised species currently included in *Cornulella*. All are similar in habit (thinly encrusting, possibly excavating, fistulose) and are readily differentiated in their toxa morphology and spicule sizes.

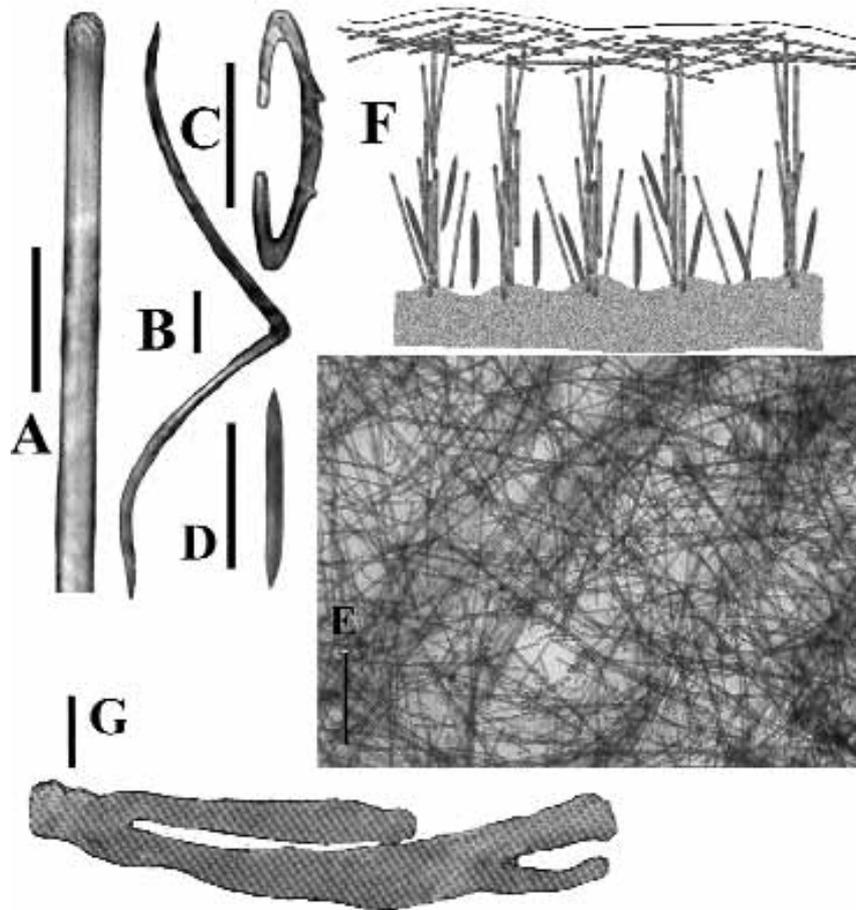
##### Distribution

Western Indian Ocean (Madagascar, Amirante, Seychelles), Caribbean, tropical Western Atlantic.

#### CORNULUM CARTER, 1876

##### Synonymy

*Cornulum* Carter, 1876:309. *Cornulotrocha* Topsent, 1927b:9. *Coelosphaerella* de Laubenfels, 1934. *Melonchela* Koltun, 1955b. *Heterocornulum* Lévi & Lévi, 1983b. Taxonomic decision for synonymy: Van Soest *et al.* (1994: 185) and Hooper (this work).



**Fig. 4.** A–F, *Cornulella lundbecki* Dendy (holotype). A, portion of tylole (scale 20 µm). B, toxa (scale 100 µm). C, palmate isochela (scale 20 µm). D, roughened microrhabd-like (acanth)oxea (scale 20 µm). E, section through peripheral skeleton (scale 1 mm). F, idealised reconstruction of the skeleton. G, *Cornulella tyro* Van Soest *et al.*, 1994 (from their fig. 3; scale 1 mm).

#### Type species

*Cornulum textile* Carter, 1876 (by monotypy).

#### Definition

Fistular Acarnidae with apically-spined tyloles or strongyles forming both tangential ectosomal and plumo-reticulate choanosomal skeletons, sometimes together with choanosomal styles or aniso-strongyles, echinating spicules present in one species only.

#### Diagnosis

Massive or encrusting growth forms, and with erect fistules or pronounced pore areas; ectosomal skeleton consists of a compact crust of spicule layers orientated tangential to the surface, composed of smooth tyloles/strongyles with microspined apices, or reduced to mucronate apices in one species; choanosomal skeleton consists of tracts and scattered tyloles/strongyles as found in the ectosome, with monactinal spicules (styles) bearing microspined bases in some species; echinating acanthostyles present in one species only, erect on a hymedesmioid basal skeleton; microscleres palmate isochelae, toxas, and microstrongyles in one species.

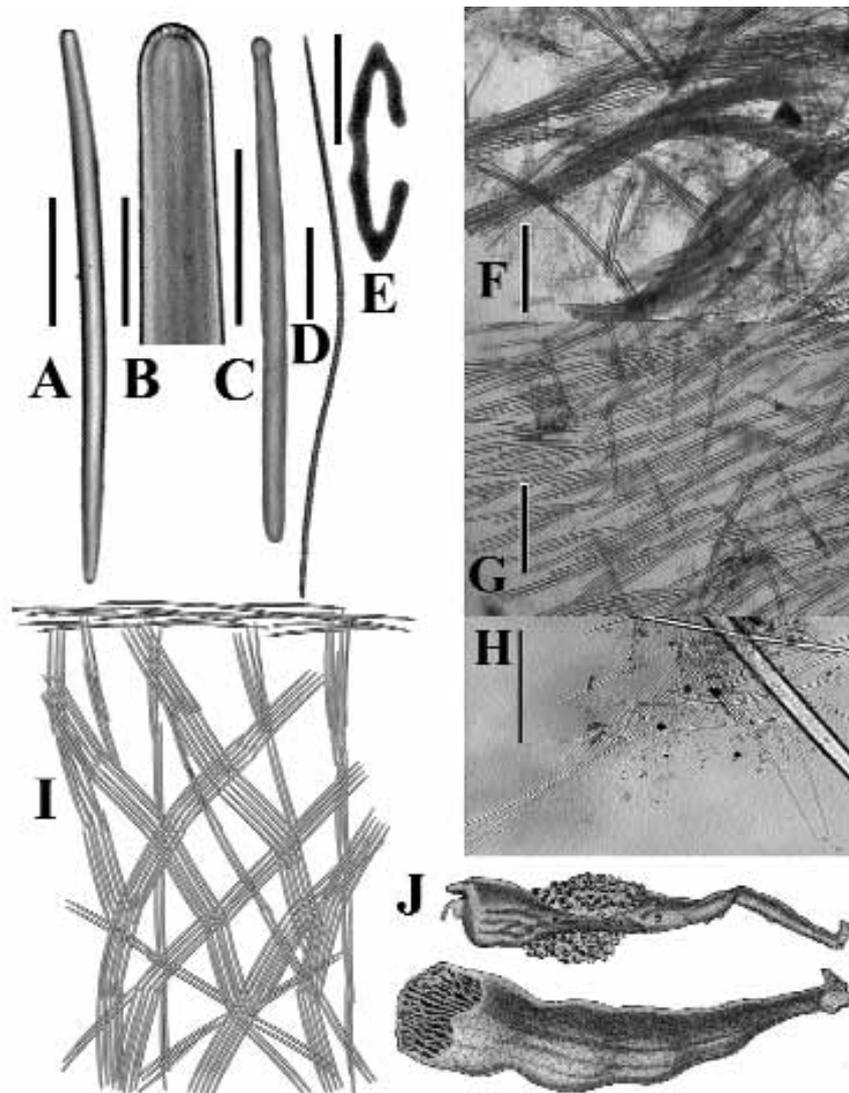
#### Description of type species

*Cornulum textile* Carter, 1876 (Fig. 5).

**Synonymy.** *Cornulum textile* Carter, 1876: 309.

**Material examined.** Holotype: BMNH 1882.7.28.76 (schizotype BMNH 1910.1.1.1363) – NE Atlantic.

**Description.** Growth form lobate-digitate, fistulose; surface optically smooth, concentrically striated; ectosomal skeleton moderately thick tangential layer of tyloles running longitudinally along surface in uni- or bispicular tracts, with occasional transverse unispicular tracts overlaying ectosome; choanosomal skeleton plumo-reticulate with multispicular tracts of both choanosomal styles and ectosomal tyloles forming diverging tract ascending towards surface, cored by 10–15 spicules per tract, interconnected by smaller transverse tracts cored by the same spicules 5–8 spicules per tract, together forming triangular or occasionally square meshes; megascleres include ectosomal tyloles, often asymmetrical, with slightly swollen bases usually microspined, occasionally smooth (290–370 × 8–14 µm); choanosomal styles vary from true styles to aniso-strongyles with asymmetrical slightly swollen, microspined or smooth bases and rounded or pointed tips (390–480 × 15–22 µm); toxas very abundant forming tangled masses in between spicule tracts, usually greatly curved at centre and with slightly reflexed arms, occasionally modified (straight, sinuous) (190–310 × 1–3 µm); small palmate isochelae unmodified,



**Fig. 5.** *Cornulum textile* Carter (holotype). A, choanosomal style (scale 100  $\mu\text{m}$ ). B, base of style (scale 30  $\mu\text{m}$ ). C, ectosomal tylote (scale 100  $\mu\text{m}$ ). D, toxa (scale 100  $\mu\text{m}$ ). E, palmate isochela (scale 5  $\mu\text{m}$ ). F, choanosomal skeleton (scale 1 mm). G, ectosomal skeleton (TS) (scale 1 mm). H, bundles of toxas (scale 50  $\mu\text{m}$ ). I, idealised reconstruction of skeleton. J, specimens of Lundbeck (1910; from his pl. 2, figs 13–14; size 40 mm).

very abundant, often completely lining the choanocyte chambers (11–15  $\mu\text{m}$ ).

**Remarks.** Van Soest *et al.* (1994) suggested that the nominal genera *Coelosphaerella* (without styles) (type species *Cornulum johnsoni* de Laubenfels, 1934 (by original designation) holotype USNM 22364), *Xytopsene* (without styles or toxas), *Heterocornulum* (with microstrongyles), and *Melonchela* (with peculiar anisochelae described as ‘melonchelas’) are all members of *Cornulum* sharing the microspined condition of megascleres (occasionally verging towards entirely smooth), as opposed to the more heavily and extensively basally spined condition of megascleres seen in other acarnids. This synonymy is supported here with the exception of *Xytopsene* which is included in *Damiria*. Reviews of species are found in Carter (1876:309), Lundbeck (1910: 22), Koltun (1955b: 17; 1959: 187), Lévi & Lévi (1983b: 966), Bergquist & Fromont (1988: 53) and Hooper (1996a).

*Melonchela* (redescribed in detail by Hooper, 1996a:85; type species *Melonchela clathrata* Koltun, 1955b (by monotypy) paratype BMNH 1963.7.29.7) is a doubtful inclusion in this

synonymy. It is remarkable in several features: its erect planar reticulate growth form (superficially resembling the microcionid *Clathria coppingeri* and the raspailiid *Echinodictyum cancellatum*); extremely large size range of principal spicules, the largest protruding a long way through fibre bundles, reminiscent of Raspailiidae; the apparent lack of connecting fibres between the ascending plumose spicule tracts; a ridge-like subterminal ornamentation on toxas; and extremely abundant tracts of chelae microscleres throughout the mesohyl. It is described as having peculiar anisochelae (‘melonchelas’) but in fact these are cleistochelae and belong to the palmate group of chelae. The presence of true diactinal ectosomal spicules (tylotes, strongyles and intermediates, varying in the degree of swelling of their bases), palmate chelae and toxas indicate that *Melonchela* has affinities to genera such as *Acarinus* and referred to the Acarnidae as a synonym of *Cornulum*.

*Heterocornulum* (type species *Heterocornulum virguliferum* Lévi & Lévi, 1983b (by original designation) holotype MNHN DCL2925) is burrowing/excavating with fistules; ectosomal skeleton is a dense criss-cross of tylotes or tylostyles with asymmetrical

ends, microspined on both ends, and abundant microstrongyles. The choanosomal skeleton is pulpy, occupying excavations in the substrate, with tylotes the same as on the surface, smooth small choanosomal styles and smooth microstrongyles. Microscleres are thick accolada toxas, and palmate isochelae (Lévi & Lévi, 1983b: 966).

*Cornulotrocha* (type species *Cornulotrocha cheliradians* Topsent, 1927b (by original designation) type material not examined) also clearly belongs to this group, having a fistulose growth form, lacking any differentiation between ectosomal and choanosomal megascleres, which consist of subtylostyles modified to strongyles, often with mucronate apices; these spicules form weakly reticulate unispicular tracts in the choanosomal skeleton, with poor fibres, and an irregular felt (tangential) ectosomal skeleton; echinating acanthostyles are erect on a hymedesmioid basal layer of spongin; microscleres are palmate isochelae in rosettes lying between the choanosomal spicule tracts, and toxas (Topsent, 1928c: 226). The type species *C. cheliradians* Topsent differs only substantially from *Cornulum s.s.* in having stylote to strongylote megascleres with modified mucronate apices, replacing apical spines, and possessing echinating acanthostyles (unlike other species).

#### Distribution

Indo-west Pacific, Caribbean, NE Atlantic.

#### DAMIRIA KELLER, 1891

##### Synonymy

*Damiria* Keller, 1891. *Anisotylacantha* Vacelet, 1969: 200. *Xytopsene* de Laubenfels, 1936a: 54. Taxonomic decision for synonymy: Van Soest *et al.* (1994: 187).

##### Type species

*Damiria simplex* Keller, 1891 (by monotypy).

##### Definition

Fistular Acarnidae with apically microspined tylotes as the only megascleres.

##### Diagnosis

Fistular growth form; ectosomal skeleton with tangential crust of tylotes with microspined apices; choanosomal skeleton irregularly reticulate with tracts of larger tylotes of similar morphology as ectosomal spicules; no other megascleres; microscleres may include toxas.

##### Description of type species

*Damiria simplex* Keller, 1891 (Fig. 6).

**Synonymy.** *Damiria simplex* Keller, 1891: 309. *Damiria simplex* variety *fistulata* Hentschel, 1912.

**Material examined.** Holotype: ZMB310b (schizotype BMNH presently missing) – Red Sea.

**Description.** Encrusting-massive, with robust fistules; surface optically smooth; ectosomal skeleton with tangential crust of

tylotes bearing microspined bases; choanosomal skeleton slightly irregularly halichondroid with loose reticulated multispicular tracts composed of thicker tylotes in bundles of up to 10 spicules per tract, vaguely subsodictyal in arrangement; megascleres are thinner ectosomal tylotes with microspined bases, frequently with asymmetrical bases ( $255\text{--}312 \times 6\text{--}10 \mu\text{m}$ ), and thicker choanosomal tylotes also with microspined bases ( $200\text{--}250 \times 11\text{--}15 \mu\text{m}$ ); microscleres absent.

**Remarks.** Van Soest *et al.* (1994) broadened the definition of *Damiria* to allow for the inclusion of species with toxas (*D. toxifera* Van Soest *et al.*, 1994) although no other species have yet been described with microscleres. *Damiria* is a sister genus of *Zyzya* and *Cornulella* based on similarities in the spination of tylotes although Van Soest *et al.* (1994) concede that it might be a reduced *Cornulella* or *Paracornulum*-like group having secondarily lost their chelae and acanthose oxeas/styles. Six species are currently included: *D. simplex* Keller, 1891, *D. toxifera* Van Soest *et al.*, 1994, *D. leonora* Van Soest *et al.*, 1994, *D. testis* Topsent, 1928c, *D. curvata* (Vacelet, 1969) and *D. fistulatus* (Carter, 1880b), whereas *D. australiensis* Dendy, 1896 was referred to *Lissodendoryx* given that it has smooth tylotes, oxeas and arcuate isochelae.

The type species of *Xytopsene*, *Suberites fistulatus* Carter from the Gulf of Manaar (and allegedly also from SW Australia) (by original designation, holotype lost), is fistulose, globular growth form, cork-like consistency, has a cavernous choanosomal skeleton composed of loose tracts of basally spined tylotes with microspined bases, and has palmate isochelae microscleres. Unfortunately the type specimen is no longer extant in the LFM or BMNH collections (Hooper & Wiedenmayer, 1994: 139), and Carter's (1880b: 53) description and illustration is so brief that it cannot be ascertained whether there are one or two size categories of megascleres. Nevertheless, from the information available the proposed synonymy between *Xytopsene* and *Damiria* is reasonable.

More uncertain is the placement of *Anisotylacantha*. The type species, *A. curvata* Vacelet from the Mediterranean (by original designation, holotype MNHN DJV689), is fistulose, encrusting or massive, with a detachable ectosomal skeleton of tangential tylotes ('acanthotylostrongyles'), with one swollen base prominently microspined and the other completely smooth, strewn loosely on the surface. The choanosomal skeleton is a fragile, cavernous reticulation of poorly developed tracts, without spongin fibres, composed of both tylotes and styles with smooth bases and acanthose shafts (although there is no clear evidence of spicules being restricted to ectosomal or choanosomal regions of the skeleton). Microscleres are absent. Vacelet (1969) initially included the genus in the Myxillidae based on similarities to the genera *Janulum* and *Damiria*, whereas Van Soest *et al.* (1994) suggest that it may be a synonym of *Damiria* although not conforming closely to it or the allied genera *Zyzya*, *Paracornulum* and *Cornulella*.

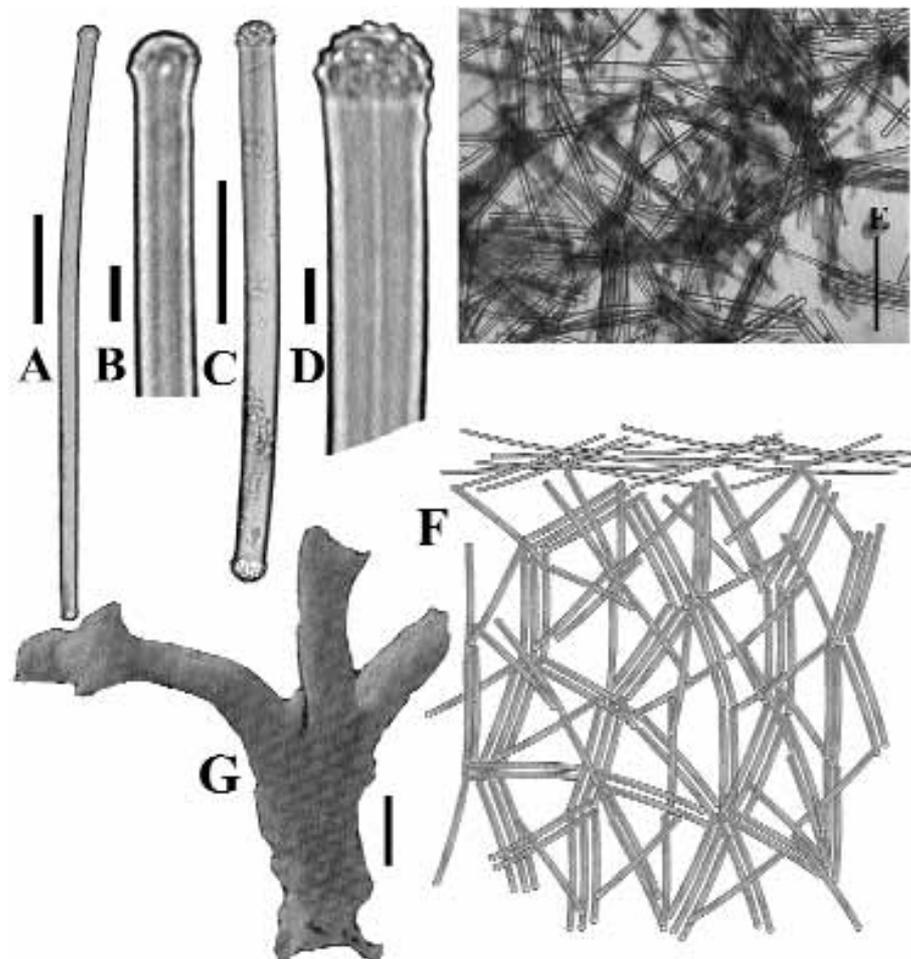
##### Distribution

Indo-Pacific (Madagascar, Red Sea, Amirante, Seychelles, Indonesia), Caribbean, Azores, NE Atlantic.

#### DOLICHACANTHA HENTSCHEL, 1914

##### Synonymy

*Dolichacantha* Hentschel, 1914: 118.



**Fig. 6.** A–F, *Damiria simplex* Keller (holotype). A, ectosomal tylote (scale 50  $\mu\text{m}$ ). B, base of ectosomal tylote (scale 10  $\mu\text{m}$ ). C, choanosomal tylote (scale 50  $\mu\text{m}$ ). D, base of choanosomal tylote (scale 10  $\mu\text{m}$ ). E, peripheral skeleton (scale 100  $\mu\text{m}$ ). F, idealised reconstruction of skeleton. G, *Damiria toxifera* Van Soest *et al.*, 1994 (from their fig. 6; scale 2.5 mm).

#### Type species

*Dolichacantha macrodon* Hentschel, 1914 (by monotypy).

#### Definition

Non-fistulose Acarnidae with long ectosomal acanthostrongyles bearing numerous spined ‘cladi’ along the apical third of shaft.

#### Diagnosis

Encrusting to massive growth forms; ectosomal skeleton with long acanthostrongyles intermingled with tylotornotes arranged in bundles on the surface; choanosomal skeleton hymedesmioid with entirely spined acanthostyles and basally- or vestigially entirely spined subtylostyles embedded in the basal skeleton, standing perpendicular to the substrate, and bundles of tylotornotes and/or acanthostrongyles forming tracts more-or-less ascending through the surface; microscleres include only uncommon palmate isochelae.

#### Description of type species

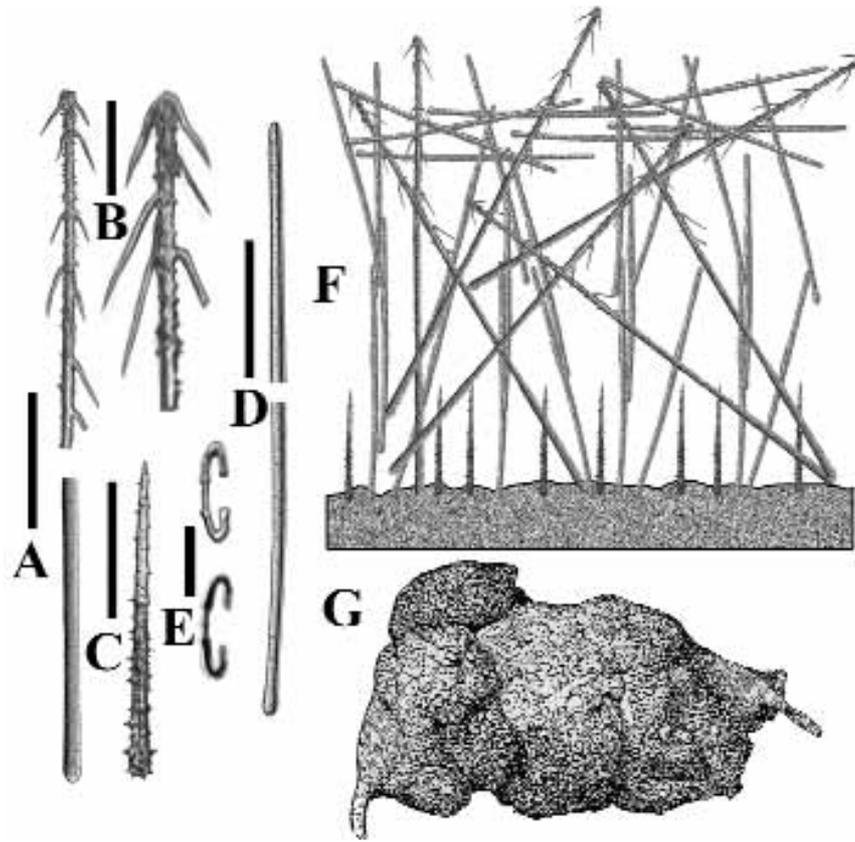
*Dolichacantha macrodon* Hentschel, 1914 (Fig. 7).

**Synonymy.** *Dolichacantha macrodon* Hentschel, 1914: 118.

**Material examined.** Holotype: ZMH S2337 – Gauss-Station, Antarctica.

**Description.** Encrusting to massive growth encrusting forms up to 2 mm thick; ectosomal skeleton with peculiar long acanthostrongyles (with spined bases) and tylotornotes (with smooth bases) arranged in bundles on the surface; choanosomal skeleton hymedesmioid with a basal skeleton with embedded small acanthostyles and larger partially spined choanosomal subtylostyles standing perpendicular to the substrate; bundles of tylotornotes and acanthostrongyles form tracts more-or-less ascending through the surface, making the sponge very hispid; megascleres include very long smooth ectosomal tylotornotes with one tylote end and an asymmetrical non-tylote end, both without apparent basal spination ( $776\text{--}1472 \times 9\text{--}12 \mu\text{m}$ ), peculiar acanthostrongyles with numerous spined ‘cladi’ on the apical third of the spicule and granular basal spination on the swollen base ( $1200\text{--}1456 \times 10\text{--}11 \mu\text{m}$ ), entirely spined echinating acanthostyles ( $176\text{--}360 \times 9\text{--}12 \mu\text{m}$ ), larger subtylostyles with vestigial spination on shaft or with spines restricted to the base ( $1120\text{--}1680 \times 20\text{--}23 \mu\text{m}$ ), and palmate isochelae ( $15\text{--}23 \mu\text{m}$ ) (spicule dimensions taken from both type material and Hentschel, 1914).

**Remarks.** Re-examination of a slide preparation of the holotype (kindly loaned by Mr Peter Stiewe, Zoologisches Institut und Zoologisches Museum, Hamburg, with a slide prepared by



**Fig. 7.** A–F, *Dolichacantha macrodon* Hentschel (holotype). A, cladote and basal ends of acanthostrongyle (scale 200  $\mu$ m). B, enlarged cladote end of acanthostrongyle (scale 50  $\mu$ m). C, echinating acanthostyle (scale 100  $\mu$ m). D, apical and basal ends of ectosomal tylotornote (scale 100  $\mu$ m). E, palmate isochelae (scale 10  $\mu$ m). F, idealised reconstruction of skeleton. G, *Dolichacantha shikotani* Koltun, 1970 (from his pl. 3, fig. 4; specimen about 50 mm long).

Rob Van Soest) showed that sigmas present in the tissue tease were loosely scattered between megascleres, whereas isochelae were firmly embedded within collagen throughout the mesohyl. Whereas the former were abundant and the latter were relatively scarce, a fact also recorded by Hentschel (1914), it was decided that sigmas were contaminants whereas isochelae were native to the sponge. This conclusion is supported by Koltun's (1970: 205) description of a second species, *D. shikotani* Koltun from the NW Pacific, in which palmate isochelae were also reported but no sigmas.

The skeletal structure of the type species is difficult to determine precisely, as the surviving portion of the holotype is extremely small and consists of little more than a tease of tissue containing bundles of spicules and some collagen. Hentschel's (1914) description states that the architecture is hymedesmioid, with acanthostyles (i.e., both smaller echinating acanthostyles and larger subtylostyles, which are interpreted here to represent principal choanosomal styles) embedded in basal spongin and standing perpendicular to the substrate. He also states that the ectosomal skeleton has bundles of both tylotornotes and acanthostrongyles lying on the surface, and also projecting a long way through it, and the acanthostyles are said to be mixed in with the tylotornotes.

The peculiar inventory of spicules in this genus make its family assignment difficult. Tylotornotes may perhaps be interpreted as related to microspined tyloles, and the 'cladi' on the acanthostrongyles may indicate *Acarus*-affinities. Alternatively, the hooked acanthostrongyles may also be modified exotyles, in which case they may have little phylogenetic significance (given that they occur in one form or another in Hadromerida and Mycalidae,

and they may be derived from the common ectosomal tyloles/strongyles. For the present the genus is included in Acarnidae given its possession of ectosomal tylotornotes and palmate isochelae. This assignment is supported by the presence of basally-spined subectosomal styles and echinating acanthostyles forming a perpendicular hymedesmioid choanosomal skeleton (with the latter two spicule types common to both Acarnidae and Microcionidae, as well as Hymedesmiidae). The alternative system, that it is a member of Hymedesmiidae, is rejected given the possession of palmate chelae and tangential tornotes in both known species of *Dolichacantha*. Although this current assignment is equivocal given that tylotornotes in *D. macrodon* lack apical spination, a characteristic of Acarnidae, tornotes in Koltun's (1970) species *D. shikotani* do bear basal spines and it may be these have been secondarily lost in the type species.

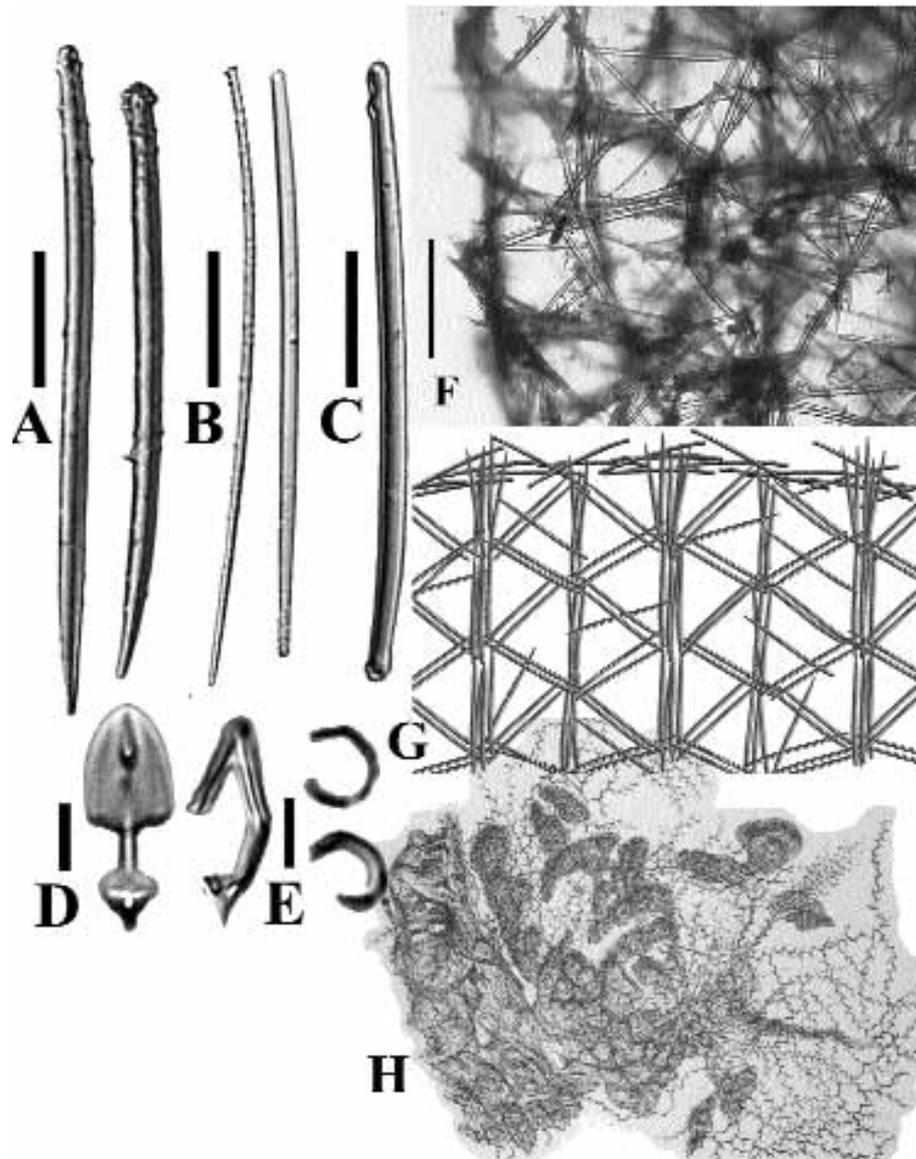
#### Distribution

Cold water; Antarctica and vicinity of Kurile Islands, NW Pacific.

#### IOPHON GRAY, 1867

#### Synonymy

*Iophon* Gray, 1867a: 534. [*Alebion*] Gray, 1867a: 534 (preoccupied). *Menyllus* Gray, 1867a: 533. *Ingallia* Gray, 1867a: 537.



**Fig. 8.** *Iophon scandens* (Bowerbank) (holotype). A, choanosomal styles (scale 50  $\mu\text{m}$ ). B, juvenile choanosomal styles (scale 50  $\mu\text{m}$ ). C, ectosomal tylote (scale 50  $\mu\text{m}$ ). D, spurred palmate anisochelae (scale 10  $\mu\text{m}$ ). E, bipocillae (scale 10  $\mu\text{m}$ ). F, peripheral skeleton (100  $\mu\text{m}$ ). G, idealised reconstruction of skeleton. H, holotype (from Bowerbank, 1874, pl. XLV, fig. 14; size about 9 cm).

*Pocillon* Topsent, 1893c. *Iophonopsis* Dendy, 1924. *Burtonella* de Laubenfels, 1928. *Iophonota* de Laubenfels, 1936a. *Hymedesanisochele* Bakus, 1966b. Taxonomic decision for synonymy: de Laubenfels (1936a: 85), Van Soest *et al.* (1994: 185), Desqueyroux-Faundez & Van Soest (1996: 7), Hooper (this work).

#### Type species

*Halichondria scandens* Bowerbank, 1866 (by original designation; reinstated by Ridley & Dendy, 1886).

#### Definition

Non-fistular Acarnidae with a regular, uni- or pauci-spicular isodictyal choanosomal reticulation of smooth or spined styles, with or without echinating acanthostyles.

#### Diagnosis

Non-fistulose, massive, branching or encrusting growth forms; ectosomal skeleton composed of tylotes with microspined bases, lying tangential to surface, intercrossing and in erect brushes; choanosomal skeleton an isodictyal rounded, triangular or square-meshed reticulation of smooth or spined choanosomal styles, arranged singly or in 2–3 per row, with (s.l.) or without (s.s.) echinating acanthostyles; microscleres inequidended bipocilla and palmate anisochelae with spurs, toxas absent.

#### Description of type species

*Iophon scandens* (Bowerbank, 1866) (Fig. 8).

**Synonymy.** *Halichondria scandens* Bowerbank, 1866: 259; 1874: pl. XLV. *Iophon scandens*; Dendy, 1924: 347.

**Material examined.** Holotype (schizotypes): BMNH 1910.1.1.2255, 2256, 2257, 2258 – Shetland.

**Description.** Growth form ranges from encrusting to cushion-shaped, often epizootic; surface optically smooth; oscules small, scattered; ectosome with irregularly scattered tangential and paratangential bundles of tylotes and many chelae also scattered on surface; choanosomal skeleton with fairly regular isodictyal reticulation of choanosomal styles, arranged 2–3 per row, forming relatively wide, mostly triangular or square meshes, occasionally rounded, and ascending spicule tracts slightly thicker than transverse connecting tracts producing a slightly plumo-reticulate appearance; echinating acanthostyles absent; mesohyl moderately light with numerous chelae and juvenile (wispy) styles scattered between skeletal meshes; megascleres ectosomal tylotes with faint to prominent microspination ( $145\text{--}210 \times 3\text{--}9 \mu\text{m}$ ), choanosomal styles with small spines on the basal end, or sometimes over the entire spicule or completely smooth ( $195\text{--}250 \times 8\text{--}13 \mu\text{m}$ ); microscleres are rare inequidended bipocilla with saucer-shaped alae ( $7\text{--}15 \mu\text{m}$  long) and abundant palmate anisochelae with spurs ( $15\text{--}32 \mu\text{m}$  long); toxas absent.

**Remarks.** Van Soest *et al.* (1994) and Desqueyroux-Faundez & Van Soest (1996) provide a detailed discussion of the genus and its synonymy. *Iophon* lacks toxas, common to many species of this family, but shares palmate anisochelae (cleisto-chelae) with *Melonchela* (= *Cornulum*) and *Acanthorhabdus*. Mycalidae also share this latter character but this is interpreted as a convergence by Van Soest *et al.* (1994). In skeletal structure *Iophon* resembles, and has been traditionally assigned to Myxillidae, but in the revised sense of Hajdu *et al.* (1994a) the latter group is restricted to taxa with anchorate chelae and sigmata. This decision de-emphasises the primary importance of the ‘classic myxillid’ isotropic skeletal reticulation but this certainly occurs in distantly related taxa (e.g., *Antho* of Microcionidae, *Lissodendoryx* of Myxillidae, *Ectyoplasia* and *Amphinomia* of Raspailiidae).

Re-examination of relevant type material of both *Iophon scandens* (re-described above) and *I. hyndmani* (Bowerbank, 1858) (schizotypes BMNH Bowerbank collection 147, 935) showed that they are not conspecific as suggested by Desqueyroux-Faundez & Van Soest (1996). The two species differ quite substantially in the geometry, size and spination of their megascleres, possession of echinating acanthostyles in the latter, relative abundance of bipocillae chela in the latter (scarce in the former), and differences in their gross morphologies. *Iophon scandens* has also been misinterpreted by Dendy (1924) and subsequent authors as having echinating acanthostyles, whereas type material clearly shows that it does not. On this basis it falls into Dendy’s (1924) concept of *Iophonopsis* (type species *Halichondria nigricans* Bowerbank, 1866 (by original designation) holotype not examined), created specifically for ‘*Iophon*-like’ species lacking echinating acanthostyles. This makes *Iophonopsis* redundant given that the type species of both nominal genera, *Iophon* and *Iophonopsis*, both lack echinating megascleres. In any case, the generic distinction based on the absence or presence of echinating spicules is not considered of great phylogenetic value at the generic level of classification, with precedent seen in other genera of Poecilosclerida (e.g., *Acarus* versus *Acanthacarus* (Van Soest *et al.*, 1991), *Clathria* versus *Isociella* and *Axociella* (Hooper, 1996a)). *Pocillon* (type species *Isodictya implicita* Bowerbank (by original designation) junior synonym of *Halichondria hyndmani* Bowerbank (Dendy, 1924: 347), holotype not examined) is an objective synonym of *Iophonopsis* through synonymy of their respective type species

(Dendy, 1924), and consequently it also falls into synonymy with *Iophon*.

*Hymedesanisochela* (type species *H. rayae* Bakus, 1966b (by original designation) holotype not examined) differs from *Iophon* s.s. only in having an encrusting habit and two size classes of (acantho)styles forming hymedesmioid skeletal structure, stylote modifications to tylotes, and lacking bipocillae, whereas in other respects it is typical of the genus. Neither of these characters provides any reasonable synapomorphy for Bakus’s genus and hence it is synonymised here. Other nominal genera included into synonymy with *Iophon* are: [*Alebion*] Gray (preoccupied, with type species *A. proximum* Ridley, 1881 (by subsequent designation; Ridley, 1881 (Vosmaer, 1882)); *Menyllus* Gray (type species *Halichondria ingalli* Bowerbank, 1866 (by original designation)), *Ingallia* Gray (type species *I. cupulifera* Gray, 1867a (by monotypy)), *Burtonella* de Laubenfels (type species *B. melanokhemia* de Laubenfels, 1936a (by original designation)) and *Iophonota* de Laubenfels (type species *Iophon aceratus* Hentschel, 1914 (by original designation)). Although none of the holotypes of the type species have been seen by the author this synonymy has been verified by Bakus (1966b: 479), Bergquist & Fromont (1988: 90), Van Soest *et al.* (1994), and Desqueyroux-Faundez & Van Soest (1996).

#### Distribution

Cold and temperate waters of most oceans and seas, not yet known from the shallow tropics.

#### MEGACIELLA HALLMANN, 1920

#### Synonymy

*Megaciella* Hallmann, 1920. *Myxichela* de Laubenfels, 1936a. Taxonomic decision for synonymy: Van Soest *et al.* (1994: 187).

#### Type species

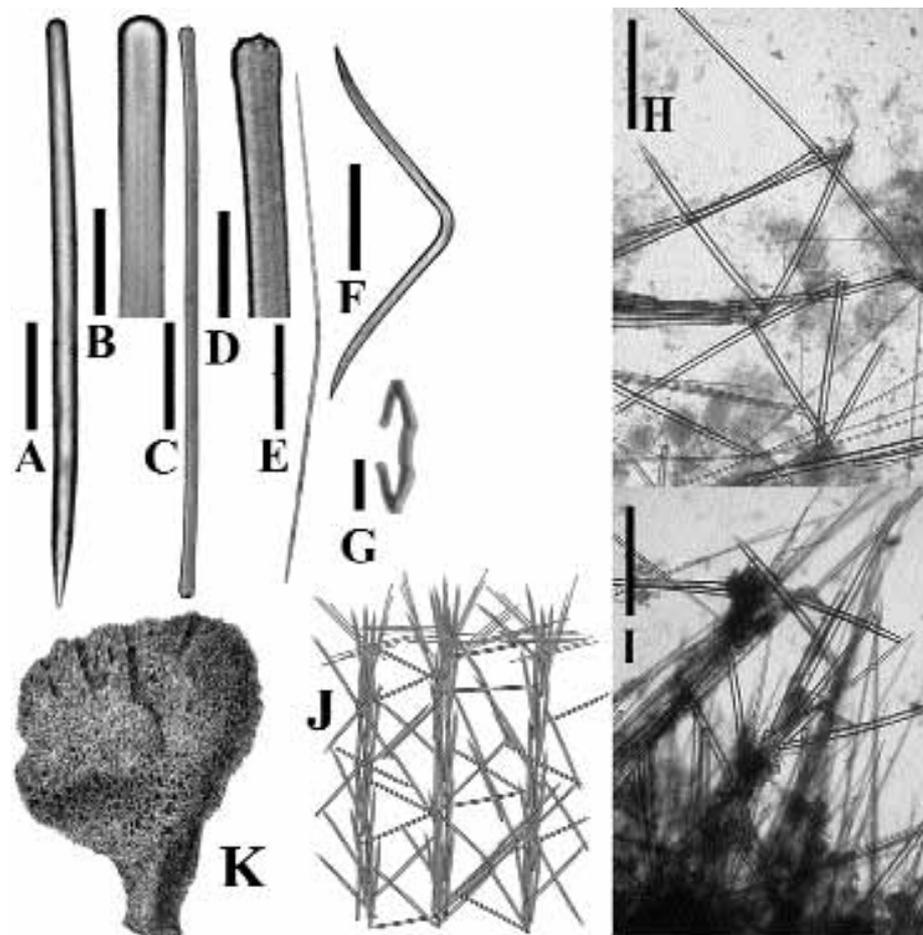
*Amphilectus pilosus* Ridley and Dendy, 1886 (by original designation).

#### Definition

Non-fistular Acarnidae with confused choanosomal skeleton divided into primary ascending multispicular tracts and secondary interconnecting uni- or bispicular tracts cored by basally spined styles, with or without echinating acanthostyles.

#### Diagnosis

Non-fistulose, branching, lobate, flabellate or encrusting growth forms; ectosomal skeleton composed of tangential or paratangential layer of ectosomal tylotes with microspined bases, often sinuous or curved; choanosomal skeleton reticulate or confused (hymedesmioid in encrusting species), with ascending multi- and paucispicular tracts of smooth choanosomal styles with spined bases, interconnected by secondary uni- or bispicular tracts bound together with collagen producing irregular wide meshes; echinating acanthostyles present or absent; microscleres are palmate isochelae and two morphologies of toxas.



**Fig. 9.** *Megaciella pilosus* (Ridley and Dendy) (lectotype). A, choanosomal style (scale 100  $\mu\text{m}$ ). B, base of choanosomal style (scale 50  $\mu\text{m}$ ). C, ectosomal tylote (scale 50  $\mu\text{m}$ ). D, base of ectosomal tylote (scale 20  $\mu\text{m}$ ). E, accolada toxa (scale 250  $\mu\text{m}$ ). F, wing-shaped toxa (scale 50  $\mu\text{m}$ ). G, palmate isochela (scale 2  $\mu\text{m}$ ). H, ectosomal skeleton (scale 200  $\mu\text{m}$ ). I, peripheral choanosomal skeleton (scale 200  $\mu\text{m}$ ). J, idealised reconstruction of skeleton. K, lectotype (from Ridley & Dendy, 1887: pl. XXV, fig. 3; length about 8 cm).

#### Description of type species

*Megaciella pilosus* (Ridley and Dendy, 1886) (Fig. 9).

**Synonymy.** *Amphilectus pilosus* Ridley and Dendy, 1886: 350; *Megaciella pilosus*; Hallmann, 1920: 772.

**Material examined.** Lectotype: BMNH 1887.5.2.125 – Marion Is, Kerguelen.

**Description.** Lobate flabellate growth form; surface shaggy, ridged, hispid; ectosomal skeleton with tangential or paratangential layer of tylotes, often in bundles; subectosomal skeleton radial or plumose, with erect choanosomal principal styles protruding from peripheral fibres through surface; choanosomal skeleton reticulate, with ascending multi- or paucispicular tracts of choanosomal principal styles, interconnected by secondary uni- or bispicular tracts within light spongin, producing irregular wide meshes; echinating spicules absent; megascleres are ectosomal tylotes, often curved or sinuous, with slightly swollen, microspined bases ( $230\text{--}295 \times 3\text{--}5 \mu\text{m}$ ), very large smooth choanosomal principal styles ( $565\text{--}1215 \times 5\text{--}8 \mu\text{m}$ ); microscleres minute palmate isochelae ( $4\text{--}6 \mu\text{m}$ ), two sizes of toxas, very large accolada toxas ( $490\text{--}1200 \times 2\text{--}4 \mu\text{m}$ ) and wing-shaped toxas ( $70\text{--}195 \times 1\text{--}3 \mu\text{m}$ ).

**Remarks.** Ridley & Dendy (1886, 1887) mistakenly considered the very large accolada toxas to be 'long thin centrally curved oxeas' in the type species *Amphilectus pilosus*, and moreover, they

are not associated with the ectosomal skeleton but scattered throughout the mesohyl. Conversely, 'bundles of oxeas' described by Ridley & Dendy (1887) are actually bundles of ectosomal tylotes.

Hallmann (1920) tacitly included *Megaciella* within the Microcionidae, with closest affinities to *Artemisina* (e.g., lax skeletal construction and supposedly comparable spiculation), differing in lacking ornamentation on toxas. However, both genera have quite different ectosomal skeletons (basally spined diactinal tylotes in *Megaciella*, monactinal ectosomal skeleton in *Artemisina*), and consequently Van Soest (1984b) referred it to Myxillidae, whereas Van Soest *et al.* (1994) are not completely certain it belongs to Acarnidae or Microcionidae (with the independent acquisition of tylotes assumed in the former case). However, the type species does appear to have true tylotes with microspined bases, which under the revised scheme of Hajdu *et al.* (1994a) *Megaciella* is more appropriately included in Acarnidae. In fact, the possession of palmate isochelae and toxas being the only real synapomorphy between *Megaciella* and the Microcionidae (i.e., Microcionina). Another Iophonid, *Acarnus*, is also similar in this respect.

The type species of *Megaciella* lacks echinating acanthostyles, whereas Van Soest *et al.* (1994) and Desqueyroux-Faundez & Van Soest (1996) remark that 'similar species with acanthostyles exist', but mention only one: *Myxichela microtoxa* de Laubenfels, 1935.

Van Soest *et al.* (1994) include *Myxichela* de Laubenfels in synonymy with *Megaciella*. The type species *Lissodendoryx tawiensis* Wilson (by original designation, holotype USNM21272) has a lamellate growth form, an ectosomal skeleton composed of erect brushes of spined choanosomal styles protruding through the surface, and a tangential or paratangential layer of ectosomal tylostrongyles (or subtylotes or subtylostyles). The choanosomal skeleton is a multispicular reticulation of differentiated primary ascending and smaller connecting fibres composed of poor spongin, found mainly at nodes of spicule tracts, cored by spinous styles, and tracts becoming plumose in the periphery; microscleres are toxas and palmate isochelae. Further references: Ridley & Dendy (1886: 350); Hallmann (1920: 772); Desqueyroux-Faundez & Van Soest (1996); Hooper (1996a: 84).

#### Distribution

Disjunct, relatively deeper water species-Kerguelen, Sulu Sea (Indonesia), California.

#### PARACORNULUM HALLMANN, 1920

##### Synonymy

*Paracornulum* Hallmann, 1920: 772. [*Cornulacantha*] Lévi & Lévi, 1983b: 966; Desqueyroux-Faundez & Van Soest, 1996: 26 (*nomen nudum*). Taxonomic decision for synonymy: Lévi & Lévi (1983b: 966), Desqueyroux-Faundez & Van Soest (1996: 26).

##### Type species

*Cornulum dubium* Hentschel, 1912 (by original designation).

##### Definition

Fistular Acarnidae with acanthostyles echinating the hymedesmioid basal skeleton overlain by apically-spined tylotes forming both plumose ascending choanosomal tracts and tangential ectosomal tracts.

##### Diagnosis

Encrusting-fistular growth form, with ectosomal skeleton composed of intercrossing halichondroid tracts of larger tylotes with granular or microspined apices, and choanosomal skeleton composed of similar but slightly smaller spicules forming radial or plumose tracts arising from a hymedesmioid layer of basal spongin echinated by acanthostyles perpendicular to the substrate; microscleres are palmate isochelae and toxas.

##### Description of type species

*Paracornulum dubium* (Hentschel, 1912) (Fig. 10).

**Synonymy.** *Cornulum dubium* Hentschel, 1912: 346. *Paracornulum dubium*; Hallmann, 1920: 772.

**Material examined.** Holotype: SMF964 (schizotype BMNH 1930.8.13.83a) – Aru I., Indonesia.

**Description.** Encrusting to fistular growth form. Surface smooth, even. Choanosomal skeleton hymedesmioid, with spongin fibres lying on substrate, bases of acanthostyles embedded and

standing perpendicular to surface. Subectosomal skeleton radial or plumose, with tracts of smaller tylotes ascending to surface, and acanthostyles also scattered throughout mesohyl. Ectosome with tangential tracts of larger tylotes forming a nearly halichondroid reticulate criss-cross on the surface. Megascleres are tylotes with granular-microspined bases, of 2 size categories: mainly ectosomal (380–440 × 4–11 μm) and mainly choanosomal (200–265 × 4–8 μm), and acanthostyles (with some oxete or strongylote modifications) (85–150 × 3–5 μm). Microscleres palmate isochelae (12–17 μm) and oxhorn toxas, slightly curved or straight (30–79 × 1.5–3.5 μm).

**Remarks.** *Paracornulum* does not appear to be as closely related to microcionids as inferred by Hallmann (1920), showing similarities mainly in the possession of echinating acanthostyles, hymedesmioid basal spongin fibres and palmate isochelae and toxas. Van Soest *et al.* (1994) referred other species previously assigned to *Paracornulum* to *Cornulella*, *Cornulum* and *Zyzyza*, including those included there by Hallmann (1920) and Bergquist & Fromont (1988). Another species assigned to *Paracornulum* at one time or another (*Cliona purpurea* Hancock) remains poorly known and currently uncertain in its placement. Based on its ectosomal characteristics and megasclere spiculation *Paracornulum* was referred to Cornulidae Lévi & Lévi (1983b: 966), whereas under the scheme of Hajdu *et al.* (1994) it belongs to Acarnidae, similar to the fistular genera *Cornulum* Carter, *Iophon* Gray and *Zyzyza* de Laubenfels. Unlike these genera *Paracornulum* has true acanthostyles echinating the basal skeleton, similar to *Acheliderma*.

Lévi & Lévi (1983b) and Desqueyroux-Faundez & Van Soest (1996) mention a genus name '*Cornulacantha* Lévi' as being a synonym of *Paracornulum*, but the name was not found in the literature or *Zoological Record*. Lévi (pers.comm.) stated that he intended to create the name for the South African species, *Paracornulum coherens* Lévi, 1963, but during final editing of his (1963) manuscript he chose instead to use Hallmann's genus *Paracornulum*. Van Soest *et al.* (1994: 184) retained *P. coherens* in *Paracornulum* only on a tentative basis (given that its robust, smooth acanthostyles and ectosomal strongyles are notably different from those of the type species), perhaps justifying the recognition of a separate genus, however '*Cornulacantha*' remains a *nomina nudum*.

##### Distribution

Aru I., Indonesia, and South Africa.

#### TEDANIOPHORBAS DE LAUBENFELS, 1936

##### Synonymy

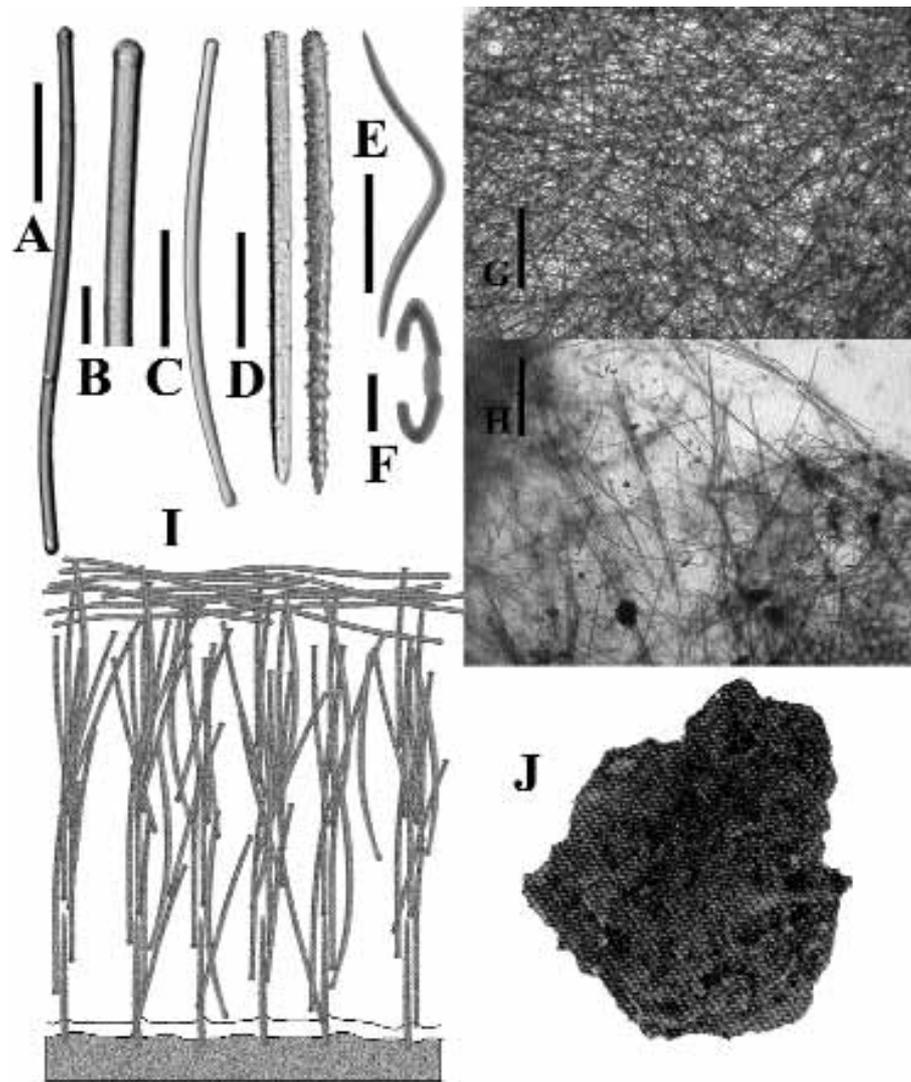
*Tedaniophorbas* de Laubenfels, 1936a.

##### Type species

*Amphilectus ceratosus* Ridley & Dendy, 1886 (by original designation).

##### Definition

Non-fistular Acarnidae with well-developed reticulate spongin fibre skeleton but lacking any coring or echinating



**Fig. 10.** A–I, *Paracornulum dubium* (Hentschel) (holotype). A, ectosomal tylote (scale 50  $\mu\text{m}$ ). B, base of ectosomal tylote (scale 10  $\mu\text{m}$ ). C, choanosomal tylote (scale 50  $\mu\text{m}$ ). D, echinating acanthostyles (scale 25  $\mu\text{m}$ ). E, oxborn toxa (scale 20  $\mu\text{m}$ ). F, palmate isochela (scale 5  $\mu\text{m}$ ). G, ectosomal skeleton (scale 250  $\mu\text{m}$ ). H, peripheral skeleton (scale 250  $\mu\text{m}$ ). I, idealised reconstruction of skeleton. J, *Paracornulum coherens* Lévi, 1963 (from his pl. 4G; about 5 cm diameter).

spicules, having instead apically-smooth ectosomal tylotes scattered between fibres and forming a tangential ectosomal skeleton.

#### Diagnosis

Massive, lobate growth form; ectosomal skeleton detachable, composed of scattered smooth tylotes, singly or in bundles, forming a tangential skeleton; choanosomal skeleton well developed, reticulate, composed of horny spongin fibres lacking coring or echinating spicules, but with ectosomal tylotes scattered between fibres and aggregated into loose wispy tracts near the periphery; microscleres are palmate isochelae; toxas absent.

#### Description of type species

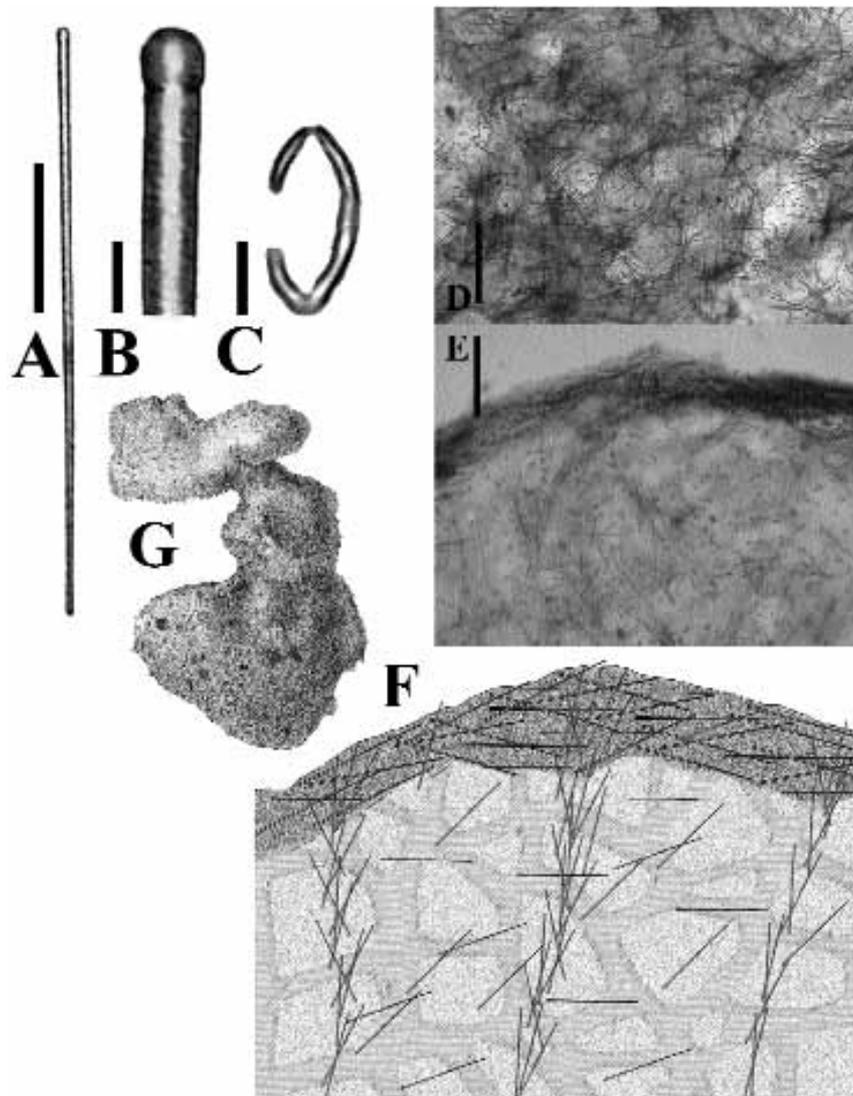
*Tedaniophorbas ceratosus* (Ridley & Dendy, 1886) (Fig. 11).

**Synonymy.** *Amphilectus ceratosus* Ridley & Dendy, 1886: 350. *Tedaniophorbas ceratosus*; de Laubenfels, 1936a: 95.

**Material examined.** Holotype: BMNH 1887.1.24.7 – Port Jackson, NSW, Australia.

**Description.** Massive, lobate growth form, spongy, elastic texture, surface uneven, microconulose; ectosome with distinct, darker, detachable cortex, with a crust of isochelae and irregularly scattered ectosomal tylotes, in bundles or individually; choanosomal skeleton more-or-less evenly reticulate, well developed horny spongin fibres with large, even meshes; fibres completely aspicular although ectosomal tylotes scattered between fibres, individually or forming plumose tracts particularly near the periphery, and abundant chelae throughout the skeleton; ectosomal tylotes with prominently swollen, smooth bases (175–235  $\times$  3–7  $\mu\text{m}$ ); palmate isochelae large, heavily silicified, with prominently thickened lateral alae (18–25  $\mu\text{m}$ ).

**Remarks.** *Tedaniophorbas* is currently a monotypic, orphan genus, which Van Soest *et al.* (1994) suggested might belong to Coelosphaeridae but also closely resembled the Acarnidae. It was also suspected from their respective published descriptions that *Tedaniophorbas* might be a reduced *Megaciella*, however, subsequent comparisons of their respective type species showed



**Fig. 11.** *Tedaniophorbis ceratosus* (Ridley & Dendy) (holotype). A, tylote (scale 50  $\mu\text{m}$ ). B, base of tylote (scale 10  $\mu\text{m}$ ). C, palmate isochelae (scale 10  $\mu\text{m}$ ). D, ectosomal skeleton (scale 250  $\mu\text{m}$ ). E, peripheral skeleton (scale 250  $\mu\text{m}$ ). F, idealised reconstruction of skeleton. G, holotype (from Ridley & Dendy, 1887: pl. XXV, fig. 2; diameter about 3 cm).

marked contrasts in skeletal architecture (horny reticulate, aspicular versus reticulate, heavily spiculose with massive spicules but poor fibre development), composition of choanosomal skeletons (completely aspicular versus completely spicular), ornamentation of ectosomal tylotes (smooth heads versus spined), toxa morphology (absent versus two forms, respectively). The type species differs from other acarnids in lacking spined bases on ectosomal tylotes, and it is assumed that these spines have become secondarily lost.

#### Distribution

Known only from Port Jackson, NSW (Australia).

#### WIGGINSIA DE LAUBENFELS, 1953

#### Synonymy

*Wigginsia* de Laubenfels, 1953: 7.

#### Type species

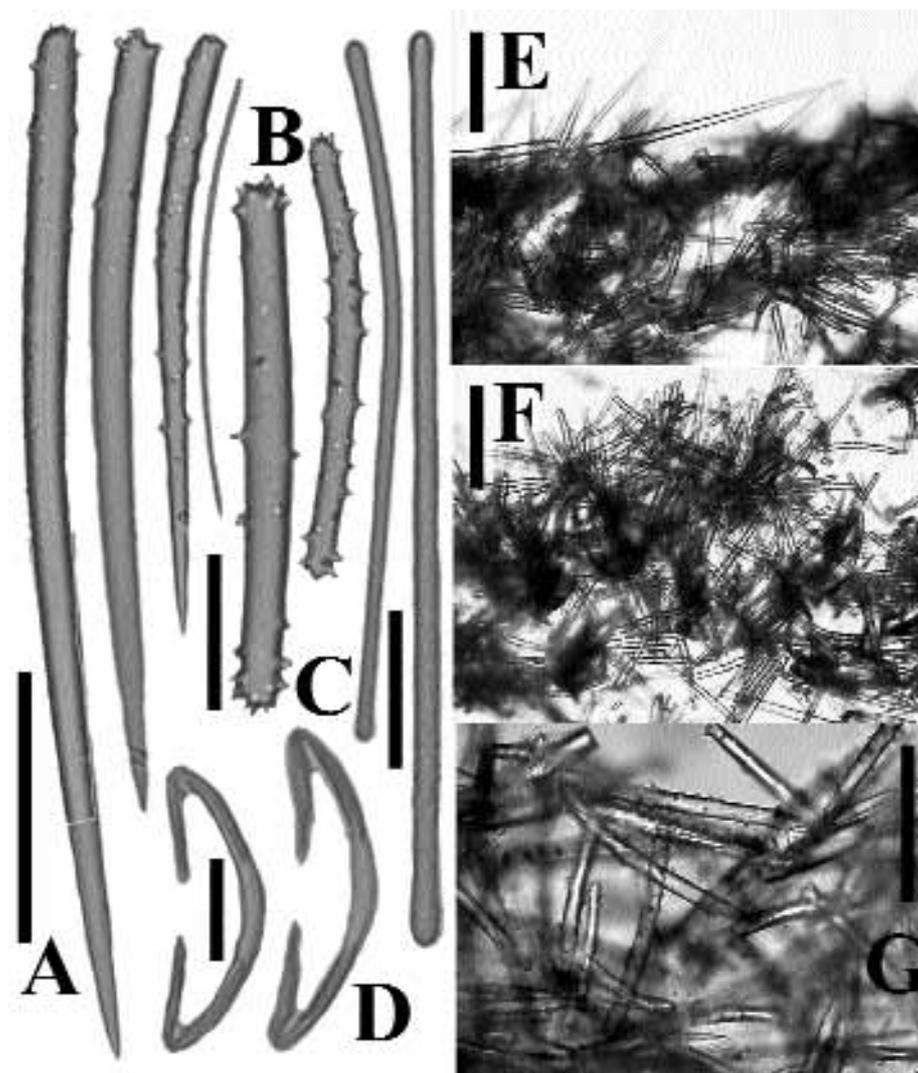
*Wigginsia wigginsii* de Laubenfels, 1953 (by original designation).

#### Definition

Non-fistulose Acarnidae with 'plocamiform' acanthostrongyles echinating tracts of choanosomal styles forming isodicyal tracts.

#### Diagnosis

Encrusting lamellate non-fistular sponge with tangential ectosomal tylotes bearing faint basal spination, thin, vaguely ascending tracts of smooth or faintly basally spined styles and a secondary skeleton of 'plocamiform' acanthostrongyles forming a tight meshed isodictyal skeleton. Microscleres palmate isochelae only.



**Fig. 12.** *Wigginsia wigginsii* de Laubenfels (holotype). A, choanosomal (acantho-)styles, including juvenile form (scale 100  $\mu\text{m}$ ). B, 'plocamiform' acanthostrongyles (scale 50  $\mu\text{m}$ ). C, ectosomal tylotes (scale 50  $\mu\text{m}$ ). D, palmate isochelae (scale 10  $\mu\text{m}$ ). E, ectosomal skeleton (scale 100  $\mu\text{m}$ ). F, choanosomal skeleton (scale 100  $\mu\text{m}$ ). G, isodictyal skeleton formed by 'plocamiform' acanthostrongyles (scale 100  $\mu\text{m}$ ).

#### Description of type species

*Wigginsia wigginsii* de Laubenfels (Fig. 12).

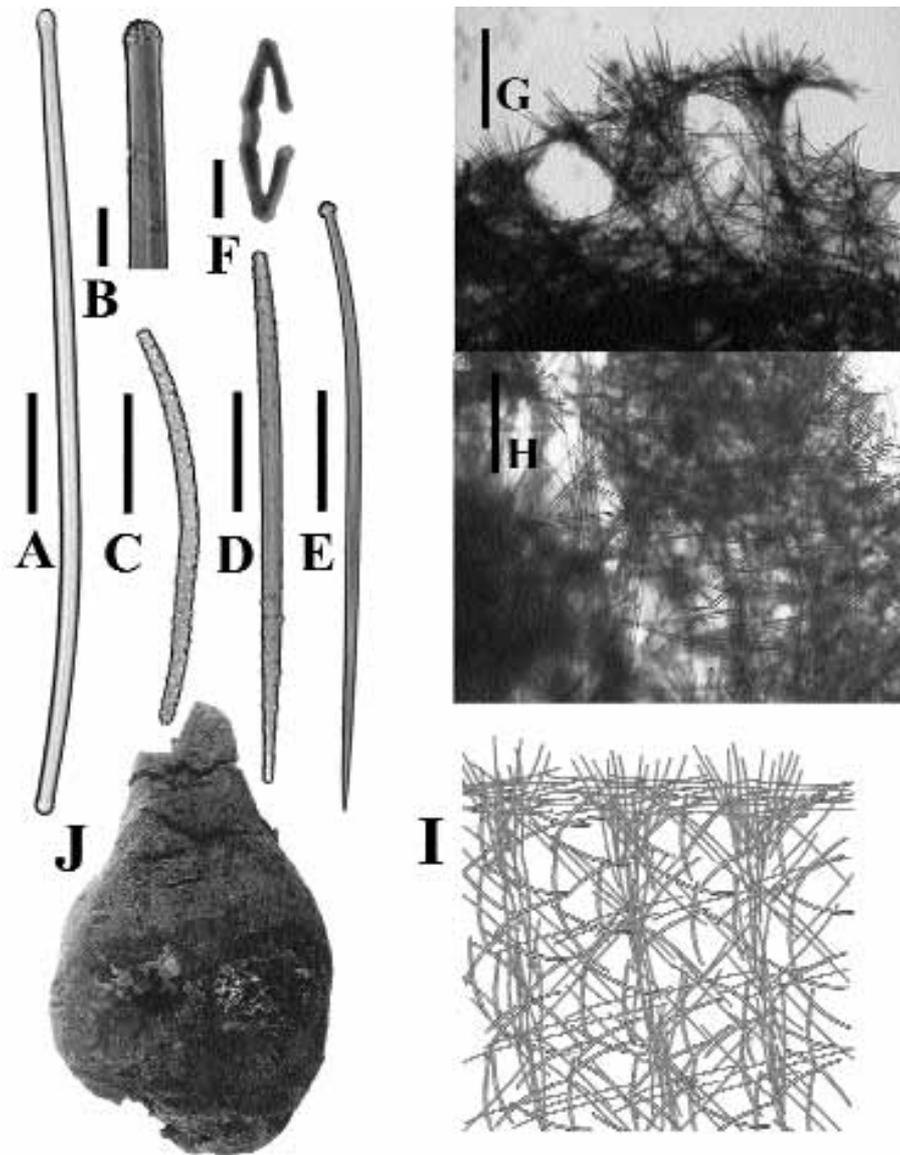
**Synonymy.** *Wigginsia wigginsii* de Laubenfels, 1953: 7–9, fig. 4.

**Material examined.** Holotype: USNM 23222 – 24 km from Point Barrow, Alaska, 153 m depth.

**Description.** Small lamellate growth form encrusting rock, 3 mm high  $\times$  50 mm wide  $\times$  3 mm lamellae thickness, with smaller lamellae abutting larger ones; surface with small elevations 1 mm high each covered with smaller microconules; red alive; oscules not observed; consistency firm, harsh. Ectosomal skeleton dense, with tangential layer of tylotes, 2–3 mm deep, through which protrude long choanosomal (acantho-)styles in bundles erect on the surface, their bases embedded in terminal ascending spongin fibres. Choanosomal skeleton with ascending multispicular tracts of large styles, heavily 'echinated' by 'plocamiform' acanthostrongyles, the latter forming close-set parallel tracts and producing a regular isodictyal reticulation ('log cabin architecture' of de Laubenfels). Megascleres short thick ectosomal tylotes with slightly swollen

tylotes, often asymmetric between ends, and smooth or only very faintly microspined bases (190–245  $\times$  5–9  $\mu\text{m}$ ); choanosomal (acantho-)styles, long curved shaft, tapering and sharply pointed, the larger entirely smooth or with few basal spines, the smaller more heavily spined at the base and distal portion of shaft (175–484  $\times$  11–19  $\mu\text{m}$ ), with raphidiform juvenile styles also common (about 120  $\times$  2  $\mu\text{m}$ ); 'plocamiform' acanthostrongyles with slightly curved shaft, spines dispersed over whole spicule but thicker on basal and central portions of the spicule, with evenly rounded or asymmetrical ends (138–174  $\times$  8–13  $\mu\text{m}$ ). Microscleres palmate isochelae, with shaft contorted and reduced alae to resemble pseudo-arcuate forms (25–36  $\mu\text{m}$ ).

**Remarks.** This monotypic genus is referred to Acarnidae from Myxillidae, to which it was originally assigned, based on the possession of faintly spined bases of ectosomal tylotes, some choanosomal styles also have faintly microspined bases, isochelae are palmate, and it lacks sigmas. It is unique in Acarnidae in having 'plocamiform' acanthostrongyles that form a secondary isodictyal reticulate skeleton, reminiscent of other 'plocamiform' Microcionina such as *Antho* (Microcionidae) and *Plocamione* (Raspaillidae).



**Fig. 13.** *Zyzzya fuliginosa* (Carter) (holotype). A, ectosomal tylote (scale 50  $\mu\text{m}$ ). B, base of tylote (scale 10  $\mu\text{m}$ ). C, acanthostrongyle (scale 50  $\mu\text{m}$ ). D, acanthotylote (scale 50  $\mu\text{m}$ ). E, tylostyle (scale 50  $\mu\text{m}$ ). F, palmate isochela (from QM specimen, scale 5  $\mu\text{m}$ ). G, ectosomal skeleton (scale 250  $\mu\text{m}$ ). H, choanosomal skeleton (scale 250  $\mu\text{m}$ ). I, idealised reconstruction of skeleton. J, specimen NTM Z2891 (from Hooper & Krasochin, 1989: fig. 1; specimen approx. cm).

The species has not been recorded since it was first described from the Arctic, and its skeleton and spicules have not been previously illustrated. Measurements provided by de Laubenfels (1953) for spicules were also in error.

#### Distribution

Known only from the Alaskan Arctic.

#### ZYZZYA DE LAUBENFELS, 1936

#### Synonymy

*Zyzzya* de Laubenfels, 1936a. *Damirina* Burton, 1959a. *Histodermopsis* de Laubenfels, 1936a. Taxonomic decision for synonymy: Van Soest *et al.* (1994: 165).

#### Type species

*Plocamia massalis* Dendy, 1922b (by original designation) (junior synonym of *Suberites fuliginosus* Carter, 1879b; taxonomic decision for synonymy Van Soest *et al.*, 1994).

#### Definition

Fistulose Acarnidae with verticillately-spined strongyles (or strongyloxeas).

#### Diagnosis

Massive, burrowing, fistulose or cryptic encrusting growth form with solid apical fistules or blind papillae; ectosomal skeleton thick detachable crust of tangentially orientated tylotes with microspined bases; choanosomal skeleton with distinctive irregular

or plumose multispicular, widely spaced tracts ascending to the surface cored by the same tylotes, interspersed with a unispicular, irregular isodictyal reticulation of verticillately-spined strongyles (or strongyloxeas); microscleres if present are palmate isochelae and toxas.

#### Description of type species

*Zyzzya fuliginosa* (Carter, 1879b) (Fig. 13).

**Synonymy.** *Suberites fuliginosus* Carter, 1879b: 347. *Zyzzya fuliginosa*; Van Soest *et al.*, 1994: 168. *Plocamia massalis* Dendy, 1922b: 78. *Dendoricella massalis*; Topsent, 1928c: 64. *Lissodendoryx massalis*; Burton, 1935a: 400; Thomas, 1973: 32. *Zyzzya massalis*; de Laubenfels, 1936a: 64. *Damirina verticillata* Burton, 1959a: 240. *Paracornulum atoxa* Vacelet *et al.*, 1976: 59.

**Material examined.** Holotype of *S. fuliginosus*: BMNH 1846.8.5.8 – Torres Strait, far north Queensland. Holotype of *P. massalis*: BMNH 1921.11.7.67 – Mauritius.

**Description.** Excavating, thinly encrusting, fistular, massive to pear-shaped; endolithic parts insubstantial, invasive of the substrate, but without producing distinct galleries or chambers; surface smooth, consistency generally fragile, live colouration brown to black; ectosomal skeleton multilayered crust of intercrossing tangentially arranged tylotes; choanosomal skeleton unispicular isodictyal reticulation of acanthostrongyles plus many ectosomal tylotes interspersed, as well as multispicular tracts traversing basal part; megascleres ectosomal tylotes with well developed, often asymmetrical, microspined bases ( $173\text{--}590 \times 1.5\text{--}20 \mu\text{m}$ ), occasionally modified to stylote spicules; acanthostrongyles verticillately-spined, or simply regularly or irregularly spined, or occasionally smooth on shaft, rarely stylote ( $109\text{--}300 \times 3\text{--}28 \mu\text{m}$ ); microscleres palmate isochelae, but often absent from some specimens (including holotype) ( $14\text{--}22 \mu\text{m}$ ).

**Remarks.** *Damirina* Burton (with type species *D. verticillata* Burton (by original designation, holotype BMNH 1936.3.4.510) is an objective synonym of *Zyzzya* due to synonymy of their respective type species. *Histodermopsis* de Laubenfels is also included here in synonymy with *Zyzzya* based on Lundbeck's (1910) comprehensive description and illustrations of the type species. The holotype of *H. coriacea* Lundbeck from the North Sea (by original designation) has yet to be found (Zool. Mus. Copenhagen – missing) but is described as being elongated, bulbous, fistulose growth form, with a tangential ectosomal skeleton composed of tylotes (and strongylotes) with microspined bases and swelling of variable development, an irregularly reticulate choanosomal skeleton composed of scattered acanthostrongyles and acanthocheas without definite arrangement, no echinating spicules, and no microscleres. De Laubenfels (1936a:72) included other species in *Histodermopsis*, some with arcuate chelae and sigmas, but these were misplaced, and only the type species is here included.

This genus was comprehensively revised by Van Soest *et al.* (1994), including a review of all published Indo-west Pacific populations. From this revision only three species are now recognised: the type species (with several junior synonyms listed above), *Z. papillata* (Thomas, 1968) from India and the Seychelles, *Z. invemar* Van Soest *et al.*, 1994 from Colombia, and tentatively *Z. coriacea* (Lundbeck) from the North Sea (pending re-examination of its holotype). The unique feature of this genus is the possession of verticillately-spined strongyles, but otherwise it conforms quite closely to other Acarnidae in ectosomal and microsclere spiculation.

#### Distribution

Widespread Indo-Pacific, from Zanzibar to Fiji, and Colombian Carribean, one species from sub-Arctic deeper waters.