

## Family Coelosphaeridae Dendy, 1922

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Coelosphaeridae Dendy (Demospongiae, Poecilosclerida), originally intended to receive all Poecilosclerida with fistules, parchment-like surface membrane and hollow bladder-like shape, is here rearranged to unite Myxillina possessing arcuate chelae, ectosomal smooth tornotes and if present a reticulate choanosomal skeleton. Fistular shape is considered only significant at the genus level. Genera and species with fistular shape but possessing birotulas palmate chelae and/or toxas previously assigned to Coelosphaeridae are here excluded from the family and reassigned to Iotrochotidae (genus *Amphiasterella*), Microcionina (fistular Acarnidae) and Mycalina (isodictyid genus *Coelocartheria*). In the newly revised family seven genera are considered valid, but several are further subdivided into convenient subgenera.

**Keywords:** Porifera; Demospongiae; Poecilosclerida; Myxillina; Coelosphaeridae; *Chaetodoryx*; *Coelosphaera*; *Forcepia*; *Histodermella*; *Inflatella*; *Lepidosphaera*; *Lissodendoryx*.

### DEFINITION, DIAGNOSIS, SCOPE

#### Synonymy

Coelosphaerae Dendy, 1922b: 95. Coelosphaeridae Hentschel, 1923: 406.

#### Definition

Myxillina with reticulate choanosomal skeleton and arcuate isochelae.

#### Diagnosis

Fistular-hollow, branching, massive or encrusting sponges. Surface smooth in fistular forms. Non-fistular representatives have their surface often irregularly pitted and punctate, but areolated pore-fields are absent. Skeleton reticulate, in fistular forms frequently vestigial. Ectosomal tornotes diactinal (often tylote). Choanosomal megascleres smooth or acanthose styles, occasionally oxeads or strongyles. In fistular forms choanosomal megascleres may be lost. Next to arcuate isochelae, microscleres include sigmas and raphides.

#### Scope

39 nominal genera of which seven are valid: *Chaetodoryx*, *Coelosphaera*, *Forcepia*, *Histodermella*, *Inflatella*, *Lepidosphaera*, *Lissodendoryx*; and in three of which (*Coelosphaera*, *Forcepia* and *Lissodendoryx*) subgeneric units are recognized.

#### History and biology

Originally (Dendy, 1922b; Hentschel, 1923; Topsent, 1928c) this family was restricted to hollow, bladder-like, spherical, club-shaped, tubular, and cushion-shaped growth forms. However, such growth forms are not exclusively occurring in the Myxillina and do not constitute reliable characters for family recognition. Non-fistular sponges with spiculation very similar to those of fistular sponges are indicative of a larger group comprising this family including genera as *Lissodendoryx s.l.* and *Forcepia s.l.* On

the other hand, several genera traditionally assigned to Coelosphaeridae because they possess fistular habit, but otherwise dissimilar in spiculation, are reassigned to disparate families: *Amphiasterella* to Iotrochotidae because of its possession of birotulas, *Coelocartheria* to Isodictyidae because of its possession of palmate chelae in combination with strongyloxeas, genera possessing microspined tylotes in combination with palmate isochelae and/or toxas (*Cornulum s.s.*, see Van Soest *et al.*, 1994) to the Microcionine family Acarnidae. Several of the genera of the newly defined Coelosphaeridae, e.g., *Lissodendoryx* and *Forcepia* have large numbers of species and wide geographic and ecological amplitude. Others are rare deep-water forms (*Histodermella*). Two genera (*Inflatella*, *Lepidosphaera*) are assigned to Coelosphaeridae provisionally, because affinities cannot be determined for their lack of arcuate chelae.

#### Taxonomic remarks

**Skeletal architecture.** Coelosphaeridae are similar to myxillid sponges in the possession of a skeletal architecture of reticulate tracts forming an isodictyal skeleton, with the usual brushes of tornotes assuming a partially tangential position. Skeletal zone II (see chapter on suborder Myxillina) is usually not developed. In the bladder-like fistular forms the choanosomal skeleton is absent or reduced to a few wispy bundles traversing the interior, and the ectosomal skeleton becomes strictly tangential. In one case (*Forcepia* subgenus *Leptolabis*), the choanosomal skeleton is hymedesmioid. Both types of reduced skeletons may be derived from the basic reticulate structure by suppression and reduction, of zone II and III in bladder-shapes, and of zone III in hymedesmioid sponges.

**Echinating acanthostyles.** Like in other families of Poecilosclerida sponges with very similar skeletons and spicules may differ only in the presence or absence of echinating acanthostyles. Although the repetitive occurrence indicates low phylogenetic significance of presence or absence of acanthostyles, it is considered practical to distinguish these variants at the subgenus level in the larger genera (*Lissodendoryx*, *Forcepia*, *Coelosphaera*).

**Previous reviews.** Dendy (1922b), Hentschel (1923), Topsent (1928c), Lévi (1973), Van Soest (1984b), Bergquist & Fromont (1988); Hajdu *et al.* (1994a).

## KEY TO GENERA

- (1) No microscleres, just one type of megascleres ..... *Inflatella*  
 Microscleres (chelae, sigmas, microxeas, trichodragmas, forceps, or écailles) present ..... 2
- (2) Microscleres are peculiarly disc-shaped ('écailles') situated at the surface ..... *Lepidosphaera*  
 No disc-shaped ectosomal spicules ..... 3
- (3) Microscleres include forceps (labis) ..... *Forcepia*  
 No forceps ..... 4
- (4) Spiculation includes entirely spined oxeas ..... 5  
 No entirely spined oxeas ..... 6
- (5) Spined oxeas are oxychaetes (microxeas finely spined all over) ..... *Chaetodoryx*  
 Spined oxeas are megasclere-sized with coarse hook-like spines ..... *Histodermella*
- (6) Sponge hollow, bladder-like with leathery or parchment-like skin; normally with longer or shorter tubular fistules ..... *Coelosphaera*  
 Sponge massive, lobate or branching, but not hollow, bladder-like ..... *Lissodendoryx*

**CHAETODORYX TOPSENT, 1927****Synonymy**

*Chaetodoryx* Topsent, 1927b: 11. *Coelectys* Topsent, 1936: 12.

**Type species**

*Chaetodoryx richardi* Topsent, 1927b: 11 (by monotypy).

**Definition**

Coelosphaeridae with smooth ectosomal tylotes, choanosomal reticulation of styles, echinated by acanthostyles; microscleres include oxychaetes.

**Diagnosis**

Encrusting, massive or fistular-insinuating sponges. Surface smooth or furrowed. Ectosomal skeleton of tylotes or anisotylotes. Choanosomal skeleton reticulate, made up of spined styles, with echinating acanthostyles. Microscleres include arcuate isochelae and rugose oxychaetes.

**Scope**

Two species, both from the Mediterranean–Atlantic area.

**Previous review**

Topsent (1928c).

**Description of type species**

*Chaetodoryx richardi* Topsent, 1927b (Fig. 1A–B).

**Synonymy.** *Chaetodoryx richardi* Topsent, 1927b: 11; Topsent, 1928c: 242, pl. II fig. 8, pl. VIII figs 8–9.

**Material examined.** Holotype (slide): MNHN D.T. 1118 – labeled 'Tedanectyon richardi n.g. n.sp., St. 1203, 1901'.

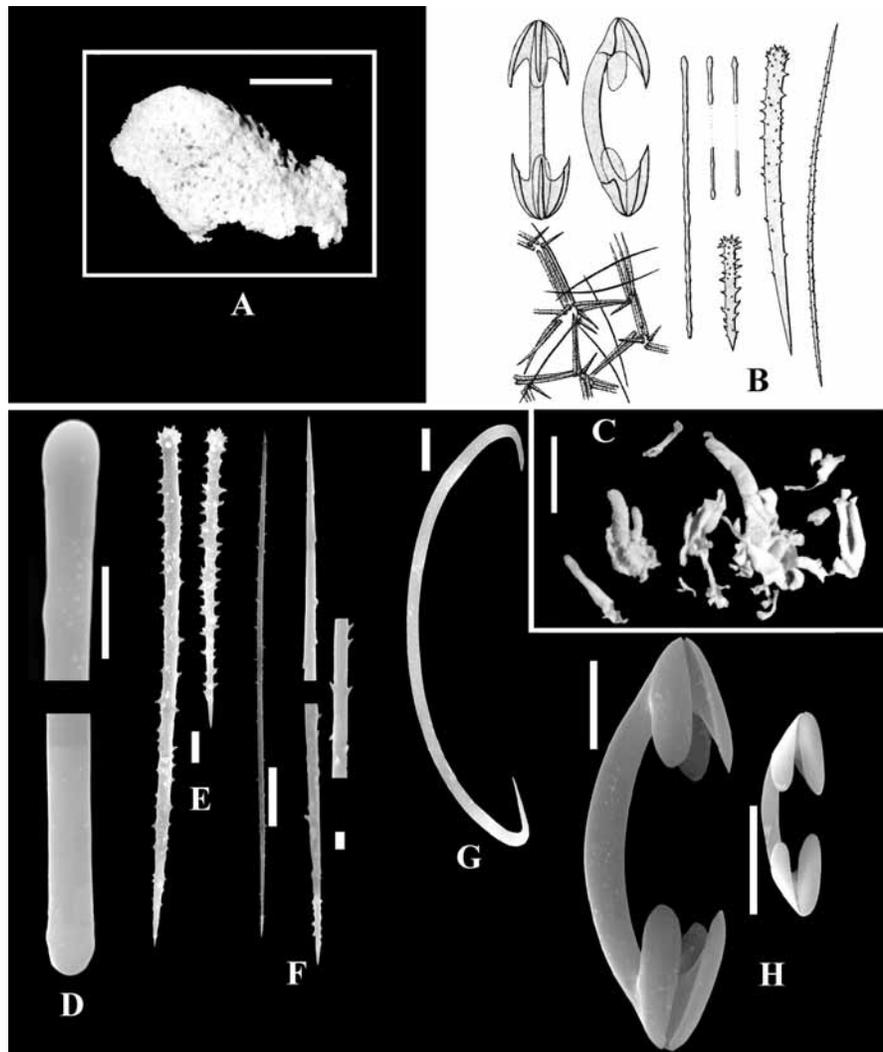
**Description (largely from Topsent, 1928c).** Massively encrusting (Fig. 1A), 2.7 cm long, 0.3 cm high, convex at one side but with a deep furrow on the other; it is attached to a shell. The surface of the convex side bears numerous aquiferous apertures impossible to differentiate into oscules and pores. The consistency is firm.

Colour dark purple in life, white in alcohol. Ectosomal megascleres irregularly arranged in the surface membrane, but erected in bundles around the oscules. Choanosomal skeleton (Fig. 1B) a reticulation of acanthostyles, with smaller echinating acanthostyles at the nodes. Oxychaetes and chelae distributed throughout the interior. Spicules (Fig. 1B), ectosomal anisotylotes, smooth, straight, with elongated but slightly different swollen ends, often polytylote, 155–175 × 3 µm; larger acanthostyles, slightly curved, lightly spined all-over, 175–195 × 10–12 µm; smaller acanthostyles, short and fat, spined all-over, 6–8 µm. Microscleres, arcuate isochelae, curved, relatively elongated, 55–59 µm; long, thin, uniformly spined oxeas (oxychaetes), 225–245 × 2–3 µm. Distribution and ecology. Boavista, Cape Verde Islands, on shells at 91 m.

**Remarks.** Although dissimilar in body shape and surface characters, the type species (by monotypy) of *Coelectys* Topsent, 1936, *C. insinuans* Topsent (1936: 12, figs 2–3) from Monaco (30–60 m) has the same spiculation as *C. richardi*. The holotype, MNHN D.T. 58, was reexamined. It is a fistulose specimen (Fig. 1C) overgrowing a *Hyrtios*. Colour white or pale greenish yellow. Spicules include smooth tylotes with elongate heads (Fig. 1D), 225–400 × 3–5.5 µm, acanthostyles (Fig. 1E), 75–160 × 3 µm; microscleres include arcuate isochelae (Fig. 1H), differentiated into smaller normal isochelae, about 20 µm, and elongate ones with pointed teeth of 40 µm, and finely spined curved microxeas (Fig. 1F), 100–110 × 1 µm. Large thin sigmas (Fig. 1G) were observed in the type specimen, but not recorded by Topsent. The genus *Histodermella* (cf. below) also has spined oxeas, but these are unlike the oxychaetes of *Chaetodoryx*. By their size and position these are considered as choanosomal megascleres. The thin acanthose oxychaetes of *Chaetodoryx* mimic tedaniid onychaetes, but these are stylote, whereas the present microscleres are clearly oxeote.

**COELOSPHAERA THOMSON, 1873****Synonymy**

*Coelosphaera* Thomson, 1873: 484. [*Histoderma*] Carter, 1874a: 220 (preocc.). *Histoderma* Carter, 1886c: 452. [*Sideroderma*] Ridley & Dendy, 1886: 348 (preocc.). *Siderodermella* Dendy, 1922b: 105. *Histodermion* Topsent, 1927b: 9. *Xytopsoocha* de Laubenfels, 1936a: 55. *Naauna* de Laubenfels, 1950a: 78. *Coelosphaericon* Bakus, 1966a: 33.



**Fig. 1.** *Chaetodoryx*. A–B, *C. richardi* Topsent (1927b), habitus of holotype and spicules (scales: A, 1 cm, B, sizes see text) reproduced from Topsent (1928c pl. II fig. 8 and pl. VIII figs 8). C–H, *C. insinuans* Topsent (1936 as *Coelectys*). C, holotype fragments (scale 1 cm). D–H, SEM photos of spicules made from the holotype (scale 10 μm, except F, 1 μm).

**Type species**

*Coelosphaera tubifex* Thomson, 1873: 484 (by monotypy).

**Definition**

Coelosphaeridae with hollow bodies provided with fistules; megascleres tylotes or strongyles, to which echinating acanthostyles may be added; microscleres arcuate isochelae, sigmas and raphides (may be absent).

**Diagnosis**

Massive, bladder-like, or encrusting, burrowing growth forms with erect fistules; smooth ectosomal tylotes form a compact

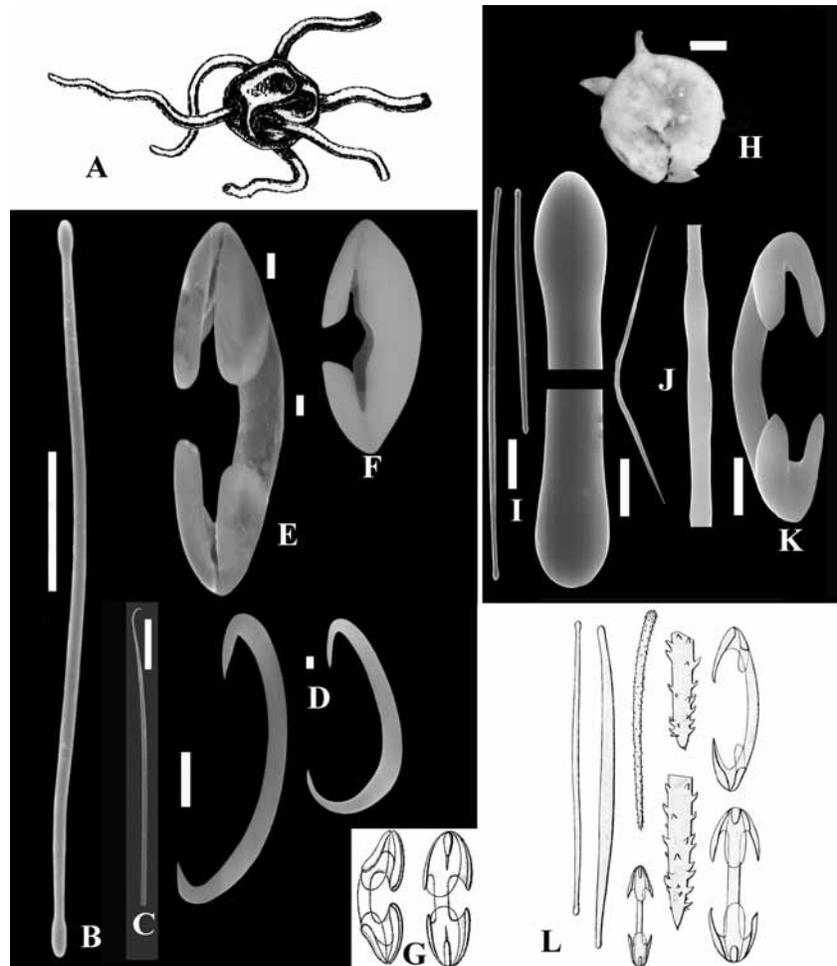
tangential crust; choanosomal skeleton consists of poorly developed tracts and scattered smooth spicules; megascleres are smooth tylotes or strongyles, of one size only, to which acanthostyles may be added; microscleres are arcuate isochelae, sigmas and raphides (often in trichodragmata), some of which may be absent. The genus *Histiodermion* is here included as a subgeneric unit of *Coelosphaera* since it differs only from species of the latter in the possession of echinating acanthostyles. *Coelosphaera s.l.* has a cosmopolitan distribution. About 30–35 species have so far been described.

**Previous reviews**

Van Soest (1984b), Bergquist & Fromont (1988).

**Key to subgenera of *Coelosphaera***

- (1) Spiculation includes acanthostyles ..... *Histiodermion*
- No acanthostyles ..... *Coelosphaera*



**Fig. 2.** *Coelosphaera*. A, *C. (Coelosphaera) tubifex* Thomson (1873), drawing of type specimen reproduced from Thomson (1873). B–F, *C. (Coelosphaera) navicelligera* (Ridley, 1884a as *Sideroderma*), SEM photos of spicules from the holotype (scales: B, 100  $\mu\text{m}$ , C and D left, 10  $\mu\text{m}$ , D right and E–F, 1  $\mu\text{m}$ ). G, *C. (Coelosphaera) peltata* (Topsent, 1904b as *Desmacidon*), type of *Naauna* de Laubenfels (1950a), chelae reproduced from Topsent (1904b) (size 50  $\mu\text{m}$ ). H–K, *C. (Coelosphaera) hatschi* (Bakus, 1966a as *Coelosphaericon*). H, habitus of BMNH paratype (scale 1 cm). I–K, SEM photos of spicules from BMNH paratype (scales: B, 100  $\mu\text{m}$ , C and D left, 10  $\mu\text{m}$ , D right and E–F, 1  $\mu\text{m}$ ). L, *C. (Histoderma) dividuum* (Topsent, 1927b), drawing of spicules reproduced from Topsent (1928c: pl. VIII fig. 1, sizes see text).

### SUBGENUS *COELOSPHAERA* THOMSON, 1873

#### Type species

*Coelosphaera tubifex* Thomson, 1873: 484 (by monotypy).

#### Definition

*Coelosphaera* without echinating acanthostyles.

#### Description of type species

*Coelosphaera (Coelosphaera) tubifex* Thomson, 1873 (Fig. 2A).

**Synonymy.** *Coelosphaera tubifex* Thomson, 1873: 484; ? Carter, 1876: 472. *Histoderma appendiculatum* Carter, 1874a: 220, pl. XIV figs 23–25, pl. XV fig. 39; Carter, 1876: 472; *Coelosphaera appendiculata*; Dendy, 1922b: 102.

**Material examined.** Neotype (proposed herein): BMNH 1882.7.28.27 – labeled '*Histoderma appendiculata* Carter,

Porcupine stat. 24, North Atlantic, one of Carter's syntypes'. Paratype: BMNH 1882: 7:28:38 – North Atlantic, 'Porcupine' stn. 2 (syntype of *Histoderma appendiculata*).

**Description.** Subglobular (Fig. 2A) with several long narrow tubular fistules of different lengths, some of which are open and presumably function as oscules. Inside virtually hollow. Size not recorded. Surface smooth. Consistency tough, parchment-like. Colour light grey. Skeleton a dense tangential crust of intercrossing megalocleres at the surface; choanosome without spicule tracts or fibres, just a pulpy mass of organic material, containing the canal system and loose spicules. Spicules smooth tyloles of  $520 \times 6 \mu\text{m}$ , long smooth tyloles resembling the tyloles but with one end tylole and the other bluntly tylole, up to  $900 \times 14 \mu\text{m}$ ; arcuate isochelae of about  $25\text{--}30 \mu\text{m}$ . Distribution and ecology. North Atlantic and Arctic, deep sea, 200–1500 m depth.

**Remarks.** This species has been ignored in the literature, whereas a very similar species, *C. appendiculata* (Carter, 1874a as *Histoderma*) is recorded several times. It is likely that both are

synonyms. Dendy (1922b) suggested that the type specimens of *Histoderma appendiculatum* (BMNH 1882.7.28.27, 38) from H.M.S. 'Porcupine' Expedition stat. 24, are the same material as that described as *Coelosphaera tubifex* by Thomson, but the proof of that is now wanting. Carter himself (1876) hesitatingly admitted that the two could be synonymous. In the absence of Thomson's material, the type of Carter registered as BMNH 1882.7.28.27 is here proposed as a neotype for Thomson's species. A second North Atlantic species is *C. physa* (Schmidt, 1875 as *Desmacidon*) differing from *C. tubifex* in lacking sigmas and possessing trichodragmas instead. Carter (1886c: 452) realized his name [*Histoderma*] was preoccupied by a fossil annelid, and replaced it by *Histoderma*, with the same type species, and thus it becomes a junior synonym of *Coelosphaera*.

[*Sideroderma*] Ridley & Dendy (1886: 348) was erected (by original designation) for type species *Crella navicelligera* Ridley (1884a: 571). Similar to *Histoderma*, the name [*Sideroderma*] Carter was found to be preoccupied by *Sideroderma* Lendenfeld (1883) for a different sponge now considered a *Polymastia*, and Dendy (1922b: 105) proposed the replacement name *Siderodermella*. The New Guinean sponge *S. navicelligerum* (Fig. 2B–F) is a pulpy mass with long hollow fistules. Megascleres are exclusively tylotes (Fig. 2B), 280–595 × 6–12 μm. Microscleres are two sizes of sigmas (Fig. 2D), 60 μm and 19 μm, raphides (Fig. 2C) in wispy trichodragmas of 450 μm long, arcuate isochelae (Fig. 2E) of about 20 μm and tiny 'navicelliform' thick-shafted chelae (Fig. 2F) of about 10 μm.

The genus *Xytopsoocha* de Laubenfels (1936a: 55) was proposed for the curious North Atlantic deep water species *Gellius macrosigma* Topsent, 1890b: 65 (by original designation, a slide of the type was reexamined, but not illustrated here). This is a thin yellow encrustation with tylotes of 700 × 10 μm as megascleres, and two size categories of sigmas, the largest of which is enormous, 415 × 8 μm, the smaller 30 μm. Trichodragmas of 15–65 μm are present. The giant sigmas can hardly be considered of generic importance. Membership of Coelosphaeridae and synonymy with *Coelosphaera* is tentative, based entirely on the assumption that the chelae have become lost secondarily.

The genus *Naauna* was erected (by original designation) by de Laubenfels (1950a: 78) for type species *Desmacidon peltatus* Topsent (1904b: 204), from deep water (600 m depth) off the Azores. A slide of the type, MNHN DT. 1014, was examined. The type specimen, kept in the Monaco Museum, was apparently damaged when collected. Its skeleton is described as having a fragile skin and pulpy interior. The only megascleres are strongyles of 500–530 × 11–13 μm; microscleres are peculiar palmate-like isochelae (Fig. 2G) of 50 μm here interpreted as arcuate, and trichodragmas of 130 μm.

The genus *Coelosphaericon* Bakus (1966a) was erected for the North Pacific species *C. hatschi* Bakus (1966a: 33). A paratype specimen, BMNH 1965.6.171.1 (Fig. 2H–K) was re-examined. This has the shape (Fig. 2H) and structure of *Coelosphaera*, but in addition to the usual spicule complement of tylotes (Fig. 2I), 525–1010 × 12–22 μm, and arcuate chelae (Fig. 2K), 30–42 μm, it has toxiform microxeas (Fig. 2J). Since proper toxas are not found in any other myxilline sponge it is assumed to be a unique feature of a single species. This is supported by the undulating irregular outline of these spicules (Fig. 2J, at right). In other respects it conforms closely to *Coelosphaera*. If more species with similar spiculation will be found, *Coelosphaericon* may be revived as subgenus of *Coelosphaera*.

## SUBGENUS *HISTODERMION* TOPSENT, 1927

### Type species

*Histodermion dividuum* Topsent, 1927b: 9 (by monotypy).

### Definition

*Coelosphaera* with echinating acanthostyles.

### Description of type species

*Coelosphaera* (*Histodermion*) *dividuum* Topsent, 1927b (Fig. 2L).

**Synonymy.** *Histodermion dividuum* Topsent, 1927b: 9; Topsent, 1928c: 225, pl. VIII fig. 1.

**Material examined.** Holotype: MOM (not seen). Slide of holotype: MNHN D.T. 1170 – labeled 'n.g.n.sp. st. 1420, 1902'.

**Description (largely from Topsent, 1928c).** Encrusting on blackish gorgonian branches, surface smooth, glistening, with cylindrical fistules of several mm high, rarely perforated at the end (presumably oscular). Skin tears off easily. Inside mostly hollow, but some organic material is gathered at the base. Consistency fragile and soft. Colour yellowish or white (alcohol). Ectosomal parchment of tangential tylotes. Thin, scarce, choanosomal tracts of tylotes, 3–4 spicules in diameter, traverse the vast hollow spaces. At the base, single, long acanthostyles are erect on the substrate or are lying loose. Microscleres concentrated at the surface. Spicules (Fig. 2L), tylotes, occasionally strongylote, swollen in the middle part, quite variable in size, 425–740 × 8–15 μm; acanthostyles, entirely spined, long, 450–470 × 13–16 μm, arcuate isochelae, comparatively elongated, with well-developed teeth, quite variable in size but not clearly divisible, 25–50 μm. Distribution and ecology. Azores, deep water, 2460 m depth.

**Remarks.** *Coelosphaera* (*Histodermion*) *cryosi* (Boury-Esnault *et al.*, 1994b) is a closely related species differing in having much smaller acanthostyles and possessing sigmas; the chelae occur in two size categories.

## *FORCEPIA* CARTER, 1874

### Synonymy

*Forcepia* Carter, 1874a: 248. *Forcipina* Vosmaer, 1885a: 26; *Forcepina* Vosmaer, 1887. *Leptolabis* Topsent, 1901b: 353. *Trachyforcepia* Topsent, 1904b: 181. *Clinolabis* Topsent, 1927b. *Wilsa* de Laubenfels, 1930: 27. *Labisophlita* de Laubenfels, 1936a: 120. *Marcusoldia* de Laubenfels, 1936a: 87. *Tedandoryx* de Laubenfels, 1954: 130. *Ectoforcepia* Cabioch, 1968b: 232.

### Type species

*Forcepia colonensis* Carter, 1874a: 248 (by monotypy).

### Definition

Coelosphaeridae with forceps microscleres.

**Diagnosis**

Encrusting to massive growth forms; ectosomal skeleton composed of tangential smooth ectosomal tylotes; choanosomal skeleton composed of choanosomal styles or ectosomal tylotes forming a hymesmioid structure in encrusting species or reticulate architecture in massive forms; microscleres are smooth or spined forceps (labris), arcuate isochelae, sigmas. Occurrence cosmopolitan. About 40 species.

**Previous reviews**

Carter (1874a), Dendy (1895), Van Soest (1984b).

**Taxonomic remarks**

The original material of *Forcepia colonensis* came from ‘an arenaceous deposit in the neighbourhood of Colon or Aspinwall, Panama’ collected by Mr F. Kitton of Norwich. No traces of it have been found in the collections of the Natural History Museum, London, during a search by Ms Clare Valentine. The description of the type was based on characteristic spicules (large forceps) in the fossil sample. In the declared absence of type material, it is desirable to assign a neotype if stability of a species or genus is threatened. In the light of the fact that several rivaling name synonyms (cf. above) are in existence, it is urgent to establish the characters of the type of *Forcepia* (see Article 75 of the ICZN code; Anon., 1999). However, due to the paucity of characters in the original description this is not a straightforward matter. All material labeled as ‘*Forcepia colonensis*’ in the BMNH collection is from the South Australian Bracebridge Wilson collection, described subsequently by Carter (1885a) and Dendy (1896) under this name (Ms Clare Valentine *in litteris*). For obvious geographic reasons alone, it is highly unlikely that this material conforms to the type from Panama. Moreover, the size of the forceps of the South Australian material is less half that of the Caribbean specimen. Consequently this material does not satisfy the qualifying conditions for assigning a neotype. The specimens Dendy classed as *F. colonensis* included Carter’s (1886c) *Suberites biceps* and accordingly it is proposed to use the combination *Forcepia biceps*

(Carter, 1886c) for this South Australian species. This is also in accordance with Wiedenmayer’s (1989) proposals concerning this species. As a neotype needs to be from the same general area to avoid possible confusion with species from other areas, it is necessary to find a neotype among material described from the Caribbean. The Caribbean currently is known to have four species of *Forcepia*: viz., *F. trilabis* (Boury-Esnault, 1973), *F. grandisigmata* Van Soest (1984b), *F. vermicola* Lehnert & Van Soest, 1996 and an unnamed *Forcepia* from the Caribbean (e.g., Colombia and Curaçao; Zea, Van Soest unpublished data). Of these, *F. trilabis sensu* Van Soest (1984b) shows considerable similarity with *F. colonensis* in possessing unusually large forceps (up to 258 µm versus 260 µm of Carter’s description), whereas the other three species have forceps less than 160 µm long. Brazilian *F. trilabis sensu* Boury-Esnault, 1973, shows a minor difference, viz., an extra category of smooth forceps, and possibly concerns a species different from the Caribbean material. It is judged likely that Caribbean *F. trilabis*, and more in particular, the specimen described from deep water off Barbados by Van Soest (1984b) conforms to *F. colonensis*. It is proposed here to adopt that specimen as the neotype of *F. colonensis*. This action also settles the status of the genus *Ectoforcepia* Cabioch (1968b), erected for *Forcepia* species lacking choanosomal styles. Since the neotype does not possess the choanosomal styles (nor were these mentioned in the description of Carter), *F. colonensis* would belong to both *Forcepia* and *Ectoforcepia*, thus making the latter a junior synonym (cf. also below). Previously, sponges possessing forceps microscleres in combination with ectosomal smooth tylotes, were scattered over several families (Myxillidae, Hymedesmiidae and Tedaniidae) because of disparate skeletal structure and variability of forceps shape. However, the myxilline forceps with its rugose or spined surface is a unique spicule type, here interpreted as a synapomorphy for a single genus of sponges. In view of the fact that hymedesmioid structure coincides with the possession of echinating acanthostyles in several species bearing forceps, it is proposed to recognize a separate subgenus *Forcepia (Leptolabis)* for these, differentiated from the nominal subgenus *Forcepia (Forcepia)* which are reticulate. Future subdivisions may be possible on the diverse shapes and sizes of the forceps, but for the time being this is not pursued.

**Key to subgenera of Forcepia**

- (1) Spiculation includes basal acanthostyles in a hymedesmioid arrangement ..... *Leptolabis*  
 No basal acanthostyles; if there are spined styles, then they are the structural megascleres making the choanosomal reticulation ..... *Forcepia*

**SUBGENUS FORCEPIA CARTER, 1874**

**Synonymy**

*Forcepia* Carter, 1874a: 248. *Forcipina* Vosmaer, 1885a: 26 (*Forcepina* Vosmaer, 1887= ? *lapsus*). *Trachyforcepia* Topsent, 1904b: 181. *Wilsa* de Laubenfels, 1930. *Labisophlita* de Laubenfels, 1936a: 120. *Tedandoryx* de Laubenfels, 1954: 130. *Ectoforcepia* Cabioch, 1968b: 232.

**Definition**

*Forcepia* with reticulate skeleton and lacking echinating acanthostyles.

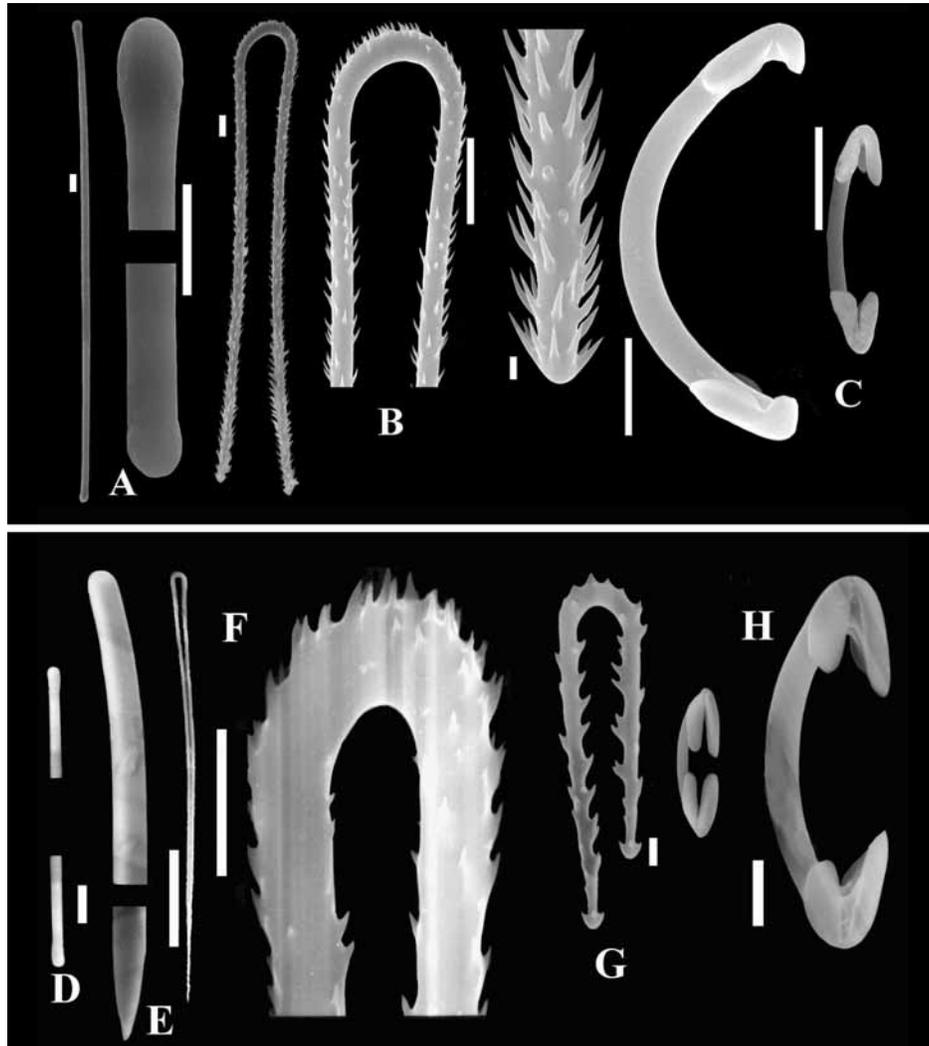
**Description of type species**

*Forcepia colonensis* Carter, 1874a (Fig. 3A–C).

**Synonymy.** *Forcepia colonensis* Carter, 1874a: 248, pl. XV fig. 47. *Forcepia trilabis*; Van Soest, 1984b: 66, pl. VI figs 1–2, text-fig. 24 (not Boury-Esnault, 1973: 280, fig. 32).

**Material examined.** Neotype: ZMA POR. 4564 – Barbados, 0.5 mile off Holetown, 100 m, coll. P. Wagenaar Hummelinck, #1442 (originally described as *F. trilabis*), including four slides.

**Description (from Van Soest, 1984b).** A thin crust on a conglomerate of coral rubble and worm tubes. Size about 1–2 cm<sup>2</sup>. Surface smooth, no apparent oscules. Consistency soft. Colour greyish brown in alcohol. Skeleton. Ectosomal skeleton a crust of intercrossing megascleres; choanosomal skeleton mostly an irregular



**Fig. 3.** *Forcepia*. A–C, *F. (Forcepia) colonensis* Carter (1874a), SEM photos of spicules from the neotype ZMA POR. 4564 (scales: 10  $\mu$ m, except detail of B right, 1  $\mu$ m). D–H, *F. (Forcepia) forcipis* (Bowerbank, 1866), type of *Forcipina* Vosmaer (1885a), SEM photos of spicules of one of Bowerbank's paratypes, BMNH 1882:7:28:30 (scales: 10  $\mu$ m, except E, 100  $\mu$ m).

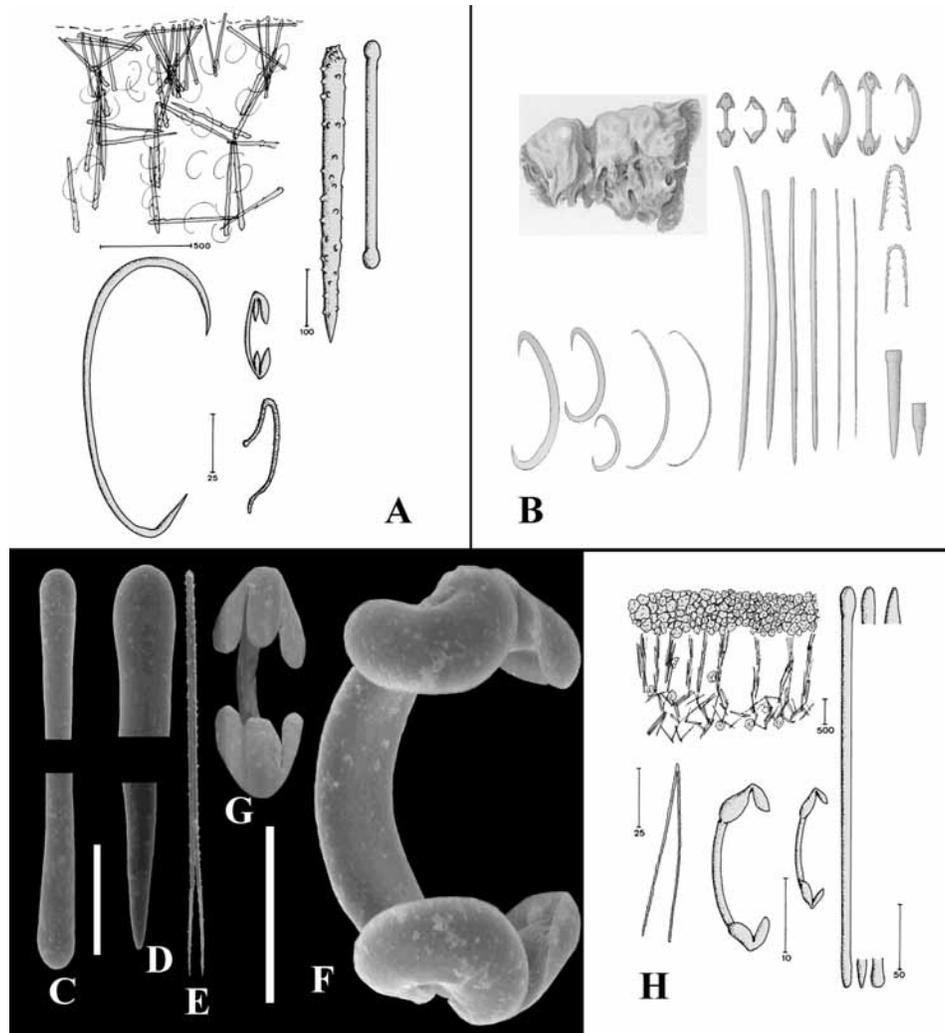
arrangement of single spicules. Spicules. Tyloles (Fig. 3A) smooth, with well-developed tyloles, rather uniform in length, 330–360  $\times$  4–7  $\mu$ m; large arcuate isochelae (Fig. 3C) with reduced alae, 20–38  $\mu$ m; small normal-shaped arcuate isochelae (Fig. 3C), 15–20  $\mu$ m; large forceps (Fig. 3B), spined all over, 200–260  $\times$  3.5–4.5  $\mu$ m (Carter gives 260  $\mu$ m). Distribution and ecology. Panama, Barbados, on coral rubble bottom, at 100 m depth.

**Remarks.** Van Soest recorded also a single smaller acanthose forceps, but subsequent examination of the slides and SEM preparation failed to confirm its presence. Presumably Van Soest (1984b) mistook a broken thin growth stage of the large forceps for it. *Forcepia trilobis* Boury-Esnault (1973: 280) appears quite close to *F. colonensis* in its present interpretation, but differs in having a smooth category of large forceps, as well as a definite smaller category of acanthose forceps. It is likely to be a closely related but separate species.

The genus *Forcipina* Vosmaer (1885a: 26, pl. V figs 60–66), with type *Halichondria forcipis* Bowerbank, 1866: 244 (by original designation), was erected by Vosmaer because he could not accept

Carter's description of *Forcepia* as valid. Later (1887) he expressed doubts (and changed the name into *Forcepina* for no apparent reason; this name is either a *lapsus* or a *nomen nudum*). One of Bowerbank's types, BMNH 1882.7.28.30 from Shetland, was reexamined (Fig. 3D–H). It is a massive sponge with irregular surface. The skeleton is an irregular reticulation of vague tracts (2–6 spicules), forming an anisotropic skeleton. Spicules are smooth tyloles (Fig. 3D), 231–302  $\times$  4–6  $\mu$ m; smooth styles (Fig. 3E), 495–572  $\times$  9–21  $\mu$ m; arcuate chelae (Fig. 3H) in two size categories, 38–65  $\mu$ m and 22–30  $\mu$ m; forcepses (Fig. 3F–G) occur in three categories, all acanthose, 351–432  $\times$  3–4  $\mu$ m, 75–91  $\times$  1  $\mu$ m and 20–33  $\times$  0.5  $\mu$ m, the smaller ones (Fig. 3G) have one longer, curved leg.

The genus *Trachyforcepia* Topsent (1904b: 181) was erected for type species *Forcepia groenlandica* Fristedt, 1887: 453 (by original designation), which has spined choanosomal styles instead of the usual smooth ones. A slide of the holotype was found in the Natural History Museum, London, BMNH 1910.1.1.1322, labeled 'from Herr Fristedt, Grönland, Forcepia groenlandica, Norman coll.' The skeleton at the surface is a tangential crust of tyloles.



**Fig. 4.** *Forcepia*. A, *Forcepia (Forcepia) groenlandica* Fristedt (1887), type of *Trachyforcepia* Topsent (1904b), drawing of skeleton and spicules made from a holotype slide in BMNH. B, *Forcepia (Forcepia) forcipula* Lundbeck (1905 as *Esperiopsis*), type of *Labisophlita*, drawing of shape and spicules reproduced from Lundbeck's pl. I fig. 5 and pl. VIII fig. 5 (for sizes see text). E–G, *Forcepia (Forcepia) lissa* (de Laubenfels, 1954 as *Tedandoryx*), SEM photos of spicules made from the holotype (scale 10  $\mu\text{m}$ ). H, *Forcepia (Forcepia) carteri* Dendy (1896), drawing of skeleton and spicules made from a BMNH type slide.

Choanosomal skeleton (Fig. 4A) an isotropic reticulation of 1–3 spicules per side. No spongin, no echinating acanthostyles. Spicules (Fig. 4A). Ectosomal smooth tylotes, slightly anisotylote but with tyles well-developed, about 400  $\mu\text{m}$ ; choanosomal acanthostyles, lightly spined all over, robust, straight, 500–550  $\mu\text{m}$ ; small arcuate isochelae (Fristedt says they are anchorate, but in the type slide they are clearly arcuate) about 35  $\mu\text{m}$ ; large, somewhat flagelliform sigmas, 100–150  $\mu\text{m}$ ; small finely acanthose forceps, with one leg longer and flagelliform, about 50  $\mu\text{m}$ . Lehnert & Van Soest (1996) employed the name *Trachyforcepia* as a sub-genus for *Forcepia* species with echinating acanthostyles, but these are absent in *F. groenlandica*. For *Forcepia* species with hymedesmioid architecture, like the species described by Lehnert & Van Soest, the subgenus *Leptolabis* is available (cf. below).

The genus *Wilsa* de Laubenfels, 1930: 27 was erected for type species *Wilsa hymena* de Laubenfels, 1930: 27, more extensively described in de Laubenfels (1932: 72, fig. 39). The description of this sponge is ambiguous, with major *Forcepia* features apparently

lacking (no tylotes are mentioned and the chelae are described as palmate). Recently, (Lee, 2002) this species was redescribed from original material and an additional fresh specimen, and assigned to *Forcepia (Forcepia)* on account of its possession of forceps and arcuate chelae.

The genus *Labisophlita* de Laubenfels (1936a: 120) was erected (original designation) for type species *Esperiopsis forcipula* Lundbeck (1905: 17, pl. I fig. 5, pl. VIII fig. 5). The BMNH collection holds a topotypical specimen, BMNH 1910.1.1.644 from Davis Strait, 160–180 m, Norman collection, which was examined. The label suggests this material was sent/donated by Lundbeck. It shows a tangential ectosomal skeleton of smooth styles, up to 680  $\mu\text{m}$  and rare thin smooth tylotornotes up to 470  $\mu\text{m}$ , carried by choanosomal spicule tracts (Fig. 4B). The tylotornotes were not mentioned by Lundbeck and that was enough reason for de Laubenfels (1936a: 120) to erect a new genus. Microscleres include two size categories of arcuate isochelae, about 45 and 10  $\mu\text{m}$  (Lundbeck says the smaller are palmate, but under high

magnification they appear to be arcuate), two size categories of sigmas, 30 and 85  $\mu\text{m}$ , the smaller of which is sharply pointed, and two size categories of small forceps, up to 20  $\mu\text{m}$  (Lundbeck mentions only one).

The genus *Tedandoryx* de Laubenfels, 1954 was erected for type species *Tedandoryx lissa* de Laubenfels (1954: 130). The type specimen, USNM 22906, was re-examined. Its ectosomal skeleton is a tangential crust of tylotes and forcipes, carried by ill-defined bundles of megascleres consisting of a mixture of tylotes and (subtylo-)styles. Single styles are erect at the base of the sponge. Spicules (Fig. 4C–G). Ectosomal tylotes (Fig. 4C), with prominent elongated heads, 243–(265.5)–285  $\times$  2–(3.8)–5  $\mu\text{m}$ ; subtylostyles (Fig. 4D) with elongated swollen heads, 270–(290.6)–303  $\times$  6–7  $\mu\text{m}$ ; chelae in two categories, large thick strongly curved arcuate chelae (Fig. 4F), with only two alae in stead of the usual three, 23–(25.1)–27  $\mu\text{m}$ , and small arcuate chelae (Fig. 4G) of normal form: 10–(10.8)–12  $\mu\text{m}$ ; the forcepses (Fig. 4E) of 120  $\times$  1–1.5  $\mu\text{m}$  are straight and thin, and often broken at the joint. De Laubenfels did not recognize the paired legs of the forcepses and considered them as separate onychaete-like spicules. This explains why he assigned this genus to Tedaniidae close to *Tedania*.

The genus *Ectoforcepia* Cabioch (1968b: 232) was erected for the group of *Forcepia* species without choanosomal styles, apparently having replaced these by the ectosomal tylotes. However, as demonstrated above, the type of *Forcepia* also does not possess the styles, so it conforms to *Ectoforcepia*, making it a junior synonym. Type species was named the South Australian *Forcepia carteri* Dendy (1896: 25). This is a greyish-yellow or ochre-yellow massive, irregular sponge chiefly composed of sand. A slide of the type, BMNH 1902.10.18.286 – RN 607, was examined. The ectosome is a sand crust of up to 1 mm in thickness. The skeleton (Fig. 4H) contains next to sand also a vague reticulation of spicule bundles which become clear plumose tracts of up to 20 spicules in cross section, 50–150  $\mu\text{m}$  in diameter, near the surface. Megascleres (Fig. 4H) are anisotylotes and strongyles of 228–(257.4)–303  $\times$  3–(3.7)–4.5  $\mu\text{m}$ . Microscleres (Fig. 4H) consist of isochelae with reduced alae: 12–(16.6)–22  $\mu\text{m}$  (possibly in two size categories of ca. 12–15 and 18–22  $\mu\text{m}$ ) and thin equal-legged rugose forceps many of which are broken at the sharp angled junction of the the two legs: 63–(79.9)–91  $\mu\text{m}$ .

#### SUBGENUS *LEPTOLABIS* TOPSENT, 1901

##### Synonymy

*Leptolabis* Topsent, 1901b: 353; *Clinolabis* Topsent, 1927b: 14; *Marcusoldia* de Laubenfels, 1936a: 87.

##### Type species

*Dendoryx luciensis* Topsent, 1888: xxxvii (by subsequent designation; Topsent, 1928c: 56).

##### Definition

*Forcepia* with hymedesmioid skeleton, with basal acanthostyles erect on the substrate.

#### Description of type species

*Forcepia (Leptolabis) luciensis* (Topsent, 1888) (Fig. 5A–E).

**Synonymy.** *Dendoryx luciensis* Topsent, 1888: xxxvii. *Leptosia exilis* Topsent, 1892b. xxii. *Leptolabis luciensis*; Topsent, 1901b. 353; Topsent, 1928c. 56

**Material examined.** Holotype (slides): MNHN D.T. 2560, 2561 – Normandy, W France, labeled ‘Luc s Mer, 12-IX-92’. Other material. ZMA POR. 6621: Mauritania Exped. stat. 27-9, off Banc d’Arguin, 16 m depth.

**Description.** Thinly encrusting with upright papillae. Colour yellow. The skeleton shows a rather irregular arrangement of bundles of megascleres with at the base of the sponge single small acanthostyles. Spicules (Fig. 5A–E), tylotes (Fig. 5A), with well-developed heads, 230–310  $\times$  2–5  $\mu\text{m}$ ; acanthostyles (Fig. 5B), 65–100  $\times$  4.5  $\mu\text{m}$ ; no other megascleres; microscleres include two size categories of well-developed arcuate isochelae (Fig. 5E), 12–18 and 33–35  $\mu\text{m}$ , normal small forceps (Fig. 5C) and peculiar small forceps of which one leg may be strongly incurled (Fig. 5D), 5–10  $\mu\text{m}$ . Distribution. W coast of France, S coast of England, Mediterranean, Mauritania, Azores.

**Remarks.** Topsent (1928c) described also sigmas of 35–90  $\mu\text{m}$  in Mediterranean specimens, but these are absent in the type and in the specimens from the Atlantic (see Topsent, 1928c: 185).

The genus *Clinolabis* Topsent, 1927b was erected (by monotypy) for *C. dentifera* Topsent (1927b: 14) from deep water (2460 m) off the Azores (Fig. 5F). A spicule slide of the type was examined, MNHN D.T. 1162, labeled “n.g.n.sp. st. 1420, 1902”, showing a complement of smooth polytylote tylotes, 300–455  $\times$  6–7  $\mu\text{m}$ , heavily spined acanthostyles in two size categories, 320–370  $\times$  20–24  $\mu\text{m}$  and 140–160  $\times$  14–15  $\mu\text{m}$ , unguiferate-arcuate isochelae, 30–46  $\mu\text{m}$ , large sigmas, 95–175  $\mu\text{m}$ , and acanthostyles forceps in two size categories, 65–75 and 23–28  $\mu\text{m}$ . Topsent stressed the fact that the chelae were ‘*isancre*s’ but they never have more than three teeth and show no similarity to anchorate chelae. In all other aspects this species conforms to *Leptolabis*.

The genus *Marcusoldia* de Laubenfels (1936a: 87) was erected (by original designation) for type *Leptolabis tenuissima* Hentschel (1911: 362, fig. 41, here reproduced as Fig. 5G), because it would have palmate isochelae in combination with forceps. Although no material was examined, de Laubenfels was clearly in error. According to Hentschel’s description, it is a thinly encrusting sponge with basal acanthostyles, in at least two size categories, 64–144  $\mu\text{m}$ , ectosomal strongyles-tylotes, 120–168  $\times$  2–3  $\mu\text{m}$ , a single category of arcuate chelae, 12–15  $\mu\text{m}$  (the drawing and the text both confirm the arcuate nature of the chelae), two sizes of sigmas, 27–60  $\mu\text{m}$  and 8  $\mu\text{m}$ , and are small and relatively heavily spined forcepses, 30–38  $\times$  1–2  $\mu\text{m}$ .

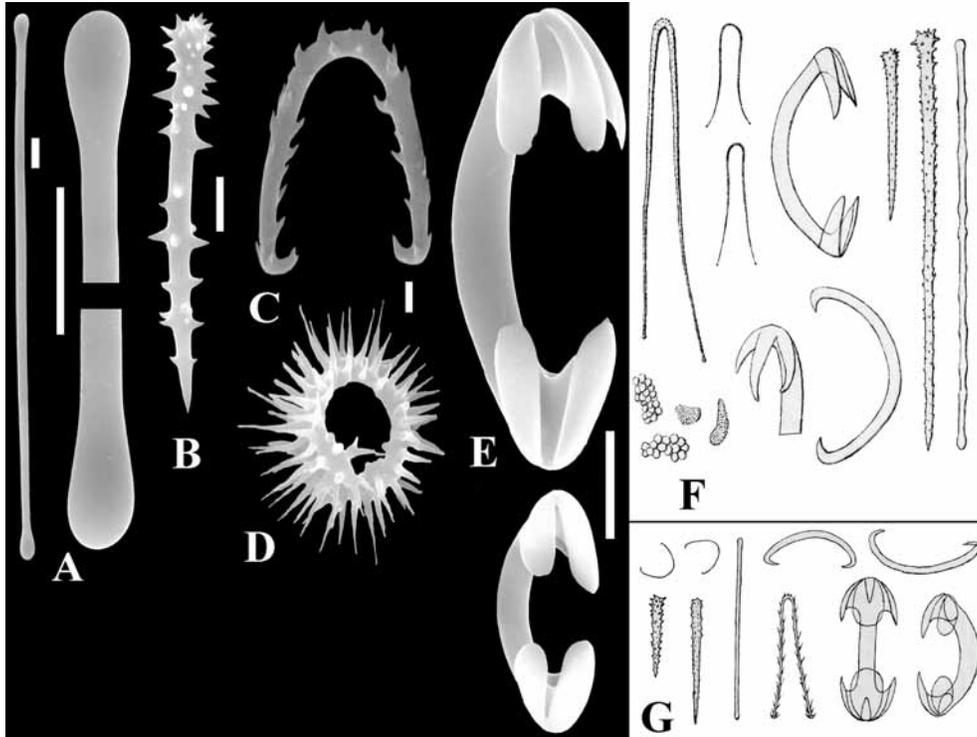
#### *HISTODERMELLA* LUNDBECK, 1910

##### Synonymy

*Histodermella* Lundbeck, 1910: 14. *Hiltonus* de Laubenfels, 1936a.

##### Type species

*Histodermella ingolfi* Lundbeck, 1910: 14 (by subsequent designation; de Laubenfels, 1936a: 72).



**Fig. 5.** *Forcepia (Leptolabis)*. A–E, *Forcepia (Leptolabis) luciensis* (Topsent, 1888 as *Dendoryx*), SEM photos of spicules made from ZMA POR 6621 (from Mauritania) (scales: 10  $\mu\text{m}$ , except C–D, 1  $\mu\text{m}$ ). F, *Forcepia (Leptolabis) dentifera* (Topsent, 1927b as *Clinolabis*), drawing of spicules reproduced from Topsent (1928c, pl. IX fig. 25) (sizes see text). G, *Forcepia (Leptolabis) tenuissima* (Hentschel, 1911), type of *Marcusoldia* de Laubenfels (1936a), drawing of spicules reproduced from Hentschel, 1911: fig. 41 (sizes see text).

### Definition

Coelosphaeridae with heavily spined acanthoxeas as choanosomal megascleres.

### Diagnosis

Spherical base with erect fistules; ectosomal skeleton consists of smooth ectosomal tyloles (or strongyles) forming a thick tangential layer; choanosomal skeleton consists of irregular tracts of scattered tyloles (or strongyles), and acanthoxeas or acanthostrongyles form a layer at right angles to the ectosomal tyloles and are scattered throughout the choanosome; microscleres are arcuate isochelae and sigmas, sometimes also raphides in trichodragmata.

### Previous reviews

Lundbeck (1910), Bergquist & Fromont (1988).

### Description of type species

*Histodermella ingolfsi* Lundbeck, 1910 (Fig. 6A–E).

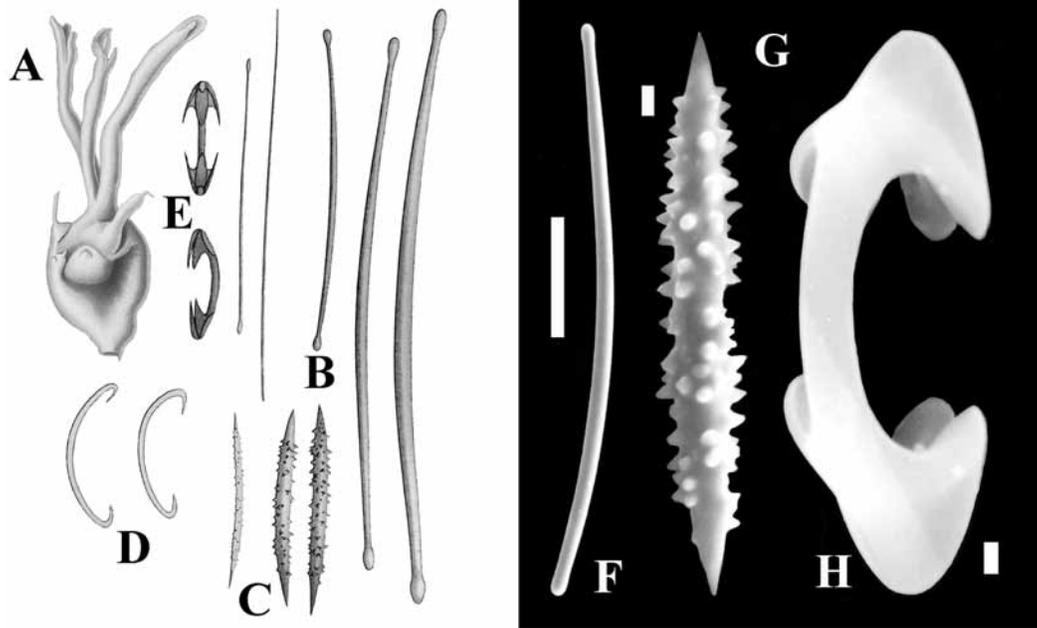
**Synonymy.** *Histodermella ingolfsi* Lundbeck, 1910: 14, pl. II figs 1–4, pl. IV fig. 4.

**Material examined.** Syntypes: Not examined. There are several type specimens, assumed to be in the Copenhagen Museum. Other material. BMNH 1953.11.11.91 – a slide made of the specimen described by Stephens (1920), no. SR 480, from the W coast of Ireland.

**Description (from Lundbeck, 1910).** Hollow, bladder-like main body (Fig. 6A) with long thin fistules, which may be branched. Surface smooth. Oscules at the end of some of the fistules, others are closed and are presumably inhalant. Consistency leathery. Skeleton of the ectosome a feltwork of tangentially placed megascleres, of the choanosome virtually absent, consisting of a few irregular tracts. Spicules, tyloles (Fig. 6B), often somewhat swollen in the middle, 290–650  $\times$  7–17  $\mu\text{m}$ ; heavily spined acanthoxeas (Fig. 6C), 170–210  $\times$  4–14  $\mu\text{m}$ ; sigmas (Fig. 6D) thin, 56–61  $\mu\text{m}$ ; arcuate chelae (Fig. 6E), occasionally somewhat deformed, 21–28  $\mu\text{m}$ . Distribution and ecology. Arctic, deep water, 1438 m depth.

**Remarks.** A second species of *Histodermella* is New Zealand *H. australis* Dendy (1924: 373, pl. XV figs 24–27), redescribed from additional material by Bergquist & Fromont (1988: 49, pl. 19 figs B–F).

De Laubenfels (1936a: 72) erected a genus *Hiltonus* for this species on the alleged presence of acanthostyles instead of acanthoxeas. This was based on the drawing of a blunt-ending acanthoxea next to a normal acanthoxea in Dendy's illustration. The type specimen of *H. australis*, BMNH 1923.10.1.155 was reexamined (Fig. 6F–H). It is closely similar to *H. ingolfsi* in shape and spicules (tyloles 700  $\times$  20  $\mu\text{m}$ , acanthoxeas 170  $\times$  34  $\mu\text{m}$ , arcuate isochelae 18–28  $\mu\text{m}$ , sigmas 30–44  $\mu\text{m}$ ) differing merely in the possession of sigmas and the thicker acanthoxeas (Fig. 6G). Stylole acanthoxeas are rare and obviously the same spicule type. *Histodermella* may be mistaken for the acarnid genera *Zyzya* de Laubenfels (1936a) or *Cornulella* Dendy (1905), if studied superficially, as both have diactinal acanthose auxiliary megascleres in combination with tyloles as principal megascleres. However, the tyloles of the latter two genera are distinctly microspined at both ends, they lack sigmas, and have palmate isochelae.



**Fig. 6.** *Histodermella*. A–E, *Histodermella ingolfi* Lundbeck (1910), drawings of habit (A) and spicules (B–E) reproduced from Lundbeck, 1910 (sizes see text). F–H, *Histodermella australis* Dendy (1924), type of *Hiltonus* de Laubenfels (1936a), SEM photos of spicules from the holotype (scales: F, 100  $\mu\text{m}$ ; G, 10  $\mu\text{m}$ ; H, 1  $\mu\text{m}$ ).

## INFLATELLA SCHMIDT, 1875

### Synonymy

*Inflatella* Schmidt, 1875: 117. *Joyeuxia* Topsent, 1892a: 94.

### Type species

*Inflatella pellicula* Schmidt, 1875: 117 (by monotypy).

### Definition

Coelosphaeridae with fistular shape, lacking choanosomal megascleres and microscleres; the only spicules present are strongylote spicules.

### Diagnosis

Massive, spherical with erect fistules; ectosomal skeleton a compact tangential crust of diactinal spicules; choanosomal skeleton consists of thin tracts of scattered diactinal spicules, the same as on the surface; diactinal megascleres are of a single sort, being smooth ectosomal strongyles or anisotylotes; microscleres absent. Half a dozen species.

### Previous reviews

Lundbeck (1910: 18), Bergquist & Fromont (1988: 51).

### Description of type species

*Inflatella pellicula* Schmidt, 1875 (Fig. 7A–C).

**Synonymy.** *Inflatella pellicula* Schmidt, 1875: 117, pl. I fig. 5; Lundbeck, 1910: 18, pl. II figs 7–9, pl. IV fig. 6. *Reniera*

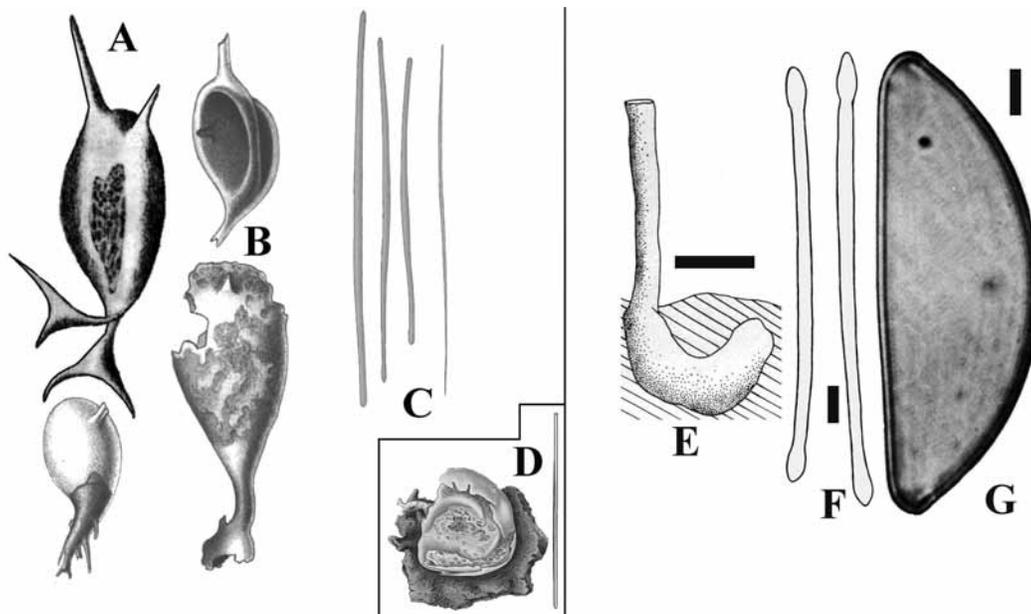
*inflata* Hansen, 1885: 7, pl. I fig. 4. *Joyeuxia viridis*; Topsent, 1904b: 205, pl. III fig. 12 (not: Topsent, 1892a: 94 = *Inflatella viridis*).

**Material examined.** None. Syntypes: 5 specimens, not located. A slide is present in the Berlin Museum (ZMB 6792) according to Desqueyroux-Faúndez & Stone (1992). This is here designated the lectotype.

**Description (mostly derived from Lundbeck, 1910).** Stalked bladders (Fig. 7A–B) with 1–4 short fistules on the smooth upper surface. Size up to 2 cm high, fistules up to 4 mm long. Oscules at the end of a fistule. Interior virtually hollow, skin thin but firm. Consistency leathery. Skeleton of the ectosome is a felted mass of tangential megascleres, intercrossing in all directions. Choanosomal skeleton an irregular system of loose spicule tracts, little spongin. Spicules (Fig. 7C), smooth, strongylote, thickest in the middle, tapering to somewhat unequal endings,  $420 \times 640 \times 10\text{--}28 \mu\text{m}$ . Distribution and ecology. Norway, North Atlantic, deep water below 200 m depth.

**Remarks.** If the strongylote spicules were truly strongyles, this genus should probably be assigned to Chondropsidae. However, in the absence of a choanosomal skeleton and microscleres the assignment of this genus to Coelosphaeridae is based on similarity to *Coelosphaera* and *Histodermella* in habit and megasclere shape, but this assignment is tentative. Vacelet & Vasseur (1971), followed by Desqueyroux-Faúndez (1987) used *Inflatella* as a genus of Phloeodictyidae related to *Oceanapia* but with strongyles instead of oxeas. However, the type of *Inflatella* shows little skeletal resemblance to *Oceanapia* and the spicules are anisostongyles with tapering ends, unlike those of *Oceanapia*.

The genus *Joyeuxia* Topsent, 1892a was erected (by monotypy) for green-coloured *J. viridis* Topsent (1892a: 94, pl. II fig. 8, pl. X fig. 19) from deep water off the Azores. Two slides of one of the type specimens were examined in MNHN, D.T. 64 and 65, labeled 'Camp. Hirondelle, 1888, 100'. The species has a bulbous



**Fig. 7.** A–D, *Inflatella*. A–C, *Inflatella pellicula* Schmidt (1875) (sizes see text). A, Schmidt's figure of the habit. B, various shapes reproduced from Lundbeck (1910, pl. II figs 7–9, pl. IV fig. 6). C, spicules reproduced from Lundbeck (1910). D, *Inflatella viridis* (Topsent, 1892a as *Joyeuxia*), habit and megasclere reproduced from Topsent (1892a, pl. II fig. 8, pl. X fig. 19) (sizes see text). E–G, *Lepidosphaera hindei* Lévi & Lévi (1979). E, habit (scale 1 cm). F, tylotes (scale 100  $\mu\text{m}$ ). G, 'écaille' (scale 10  $\mu\text{m}$ ), all reproduced from Lévi & Lévi (1979, figs 1–5).

form and is largely hollow (Fig. 8D). There is no choanosomal skeleton, only a thick ectosomal consisting of intercrossing strongyles, which are slightly thicker in the middle, size  $765 \times 9 \mu\text{m}$ . The species has also been reported from the Caribbean by Burton (1954). It is a clear *Inflatella*, but definitely a different species (except for Topsent's 1904b record). The major differences with *I. pellicula* are the distinctive colour and the somewhat longer strongyles. The genus name has been used for a number of unrelated sponges (e.g., *Inflatella bartschi* de Laubenfels (1934: 21), *I. dura* Vacelet & Vasseur (1971: 111), *I. perlucida* Desqueyroux-Faúndez (1987: 211), all probably belonging to the phloeodictyid genus *Oceanapia*), and it is likely that only a few species belong to it. These appear to be confined to cold and deep waters in both the North Atlantic (*I. pellicula*, *I. viridis*), the North Pacific (*I. globosa* Burton, 1955, *vide* Koltun, 1959: 105), and the Southern Oceans (*I. belli* Kirkpatrick, 1907a: 203). Dendy, 1924 followed by Bergquist & Fromont (1988: 51) assigned a species with exclusively oxeas to this genus, viz., *Inflatella spherica* Dendy (1924: 373). This is here transferred to Dendoricellidae on account of its similarities in shape, and spicule sizes and form to *Pyloclerum latrunculioides*.

## LEPIDOSPHAERA LÉVI & LÉVI, 1979

### Synonymy

*Lepidosphaera* Lévi & Lévi, 1979: 443.

### Type species

*Lepidosphaera hindei* Lévi & Lévi, 1979: 443 (by monotypy).

### Definition

Coelosphaeridae with ectosomal crust of 'écailles', semicircular disc-shaped spicules; megascleres tylotes only, no microscleres.

### Diagnosis

Basal mass burrowing with erect fistules protruding through substrate; ectosomal skeleton consists of a rigid cortex composed of peripheral layer of platelet-like discs, 'écailles'; choanosomal skeleton pulpy with smooth tylotes dispersed throughout; microscleres absent.

### Description of type species

*Lepidosphaera hindei* Lévi & Lévi, 1979 (Fig. 7E–G).

**Synonymy.** *Lepidosphaera hindei* Lévi & Lévi, 1979: 443, figs 1–5.

**Material examined.** None. Holotype: MNHN DCI 2447 – could not be found in 1996 (Claude Lévi, pers.comm.).

**Description (from Lévi & Lévi, 1979).** Fistular sponge, consisting of a basal mass of about  $1 \text{ mm}^3$  fixed on a mass of calcareous debris, issuing a single tube of 3 mm long and 0.35 mm diameter (Fig. 7E). The tube is open at the end. Skeleton. Of the surface, a rigid cortex of semicircular disc-shaped 'écailles', overlapping one another partly, to form a continuous cover. Choanosome pulpy, with dispersed tylotes. Spicules. Ectosomal 'écailles' (Fig. 7G), smooth, ellipsoid, but with one straight and one curved side,  $95\text{--}100 \times 32\text{--}35 \mu\text{m}$ ; tylotes (Fig. 7F), with prominent heads,  $130\text{--}150 \times 5\text{--}6 \mu\text{m}$ . Distribution and ecology. Off New Caledonia, dredged from 200 m offshore from the reefs; no further records.

**Remarks.** The unique 'écailles' are unprecedented in Recent sponges, and their origin and relationships with other spicule types remains a matter of speculation. Regrettably, type material can not

be located anymore, but we rely on Prof. Lévi's vast experience in the assumption that these 'écailles' are truly sponge spicules and not foreign material from some unknown source used by the sponge to enforce its surface. Prof. Lévi pointed out that Hinde & Holmes (1892) recorded very similar fossil spicules (semicircular platelets of  $92 \times 27 \mu\text{m}$ ) from the Oamaru deposits, New Zealand. The membership of the family Coelosphaeridae is determined by elimination, based on the presence of tylotes in combination with fistular shape. No firm evidence for this assignment can be offered without further corroboratory support from re-examination of material.

### **LISSODENDORYX TOPSENT, 1892**

#### **Synonymy**

*Lissodendoryx* Topsent, 1892a: 97. *Paramyxilla* Dendy, 1905: 233. *Ectyodoryx* Lundbeck, 1909: 445. *Anomodoryx* Burton, 1934a: 555. *Damiriella* Burton, 1935c: 404. *Jones* de Laubenfels, 1936a: 79. *Waldoschmittia* de Laubenfels, 1936a: 95. *Zetekispongia* de Laubenfels, 1936b: 446. *Zetekopsis* de Laubenfels, 1936a: 85. *Zottea* de Laubenfels, 1936a: 64. *Damiriana* de Laubenfels, 1950a: 14. *Acanthodoryx* Lévi, 1961b: 516.

#### **Type species**

*Tedania leptoderma* Topsent, 1889: 49 (by original designation) (this is generally considered a junior synonym of *Halichondria isodictyalis* Carter, 1882a).

#### **Definition**

Coelosphaeridae with ectosomal tornotes in the form of tylotes or strongyles; choanosomal smooth or spined styles,

occasionally absent or modified to strongyles or oxeas; arcuate chelae.

#### **Diagnosis**

Massive, lobate, or flabelliform sponges, with irregular or clathrate surface. Ectosomal skeleton with smooth ectosomal tylotes or strongyles forming tangential tracts and surface brushes; choanosomal skeleton composed of smooth or acanthose choanosomal styles, sometimes oxeas or strongyles, forming an isodictyal reticulate architecture of single spicules; echinating spicules may be present; microscleres are arcuate isochelae, sigmas, and raphides in trichodragmata. Cosmopolitan distribution, many species.

#### **Previous review**

Hofman & Van Soest (1995: 78).

#### **Taxonomic remarks**

The present concept of *Lissodendoryx* is widened compared to the latest revision (see Hofman & Van Soest, 1995) with inclusion of species having other tornote morphologies than strictly smooth tylotes, as well as with species lacking sigmas. The widened concept is accompanied by a proposal to recognize five subgenera: *Lissodendoryx* (full spicule complement but no echinating spicules), *Ectyodoryx* (echinating acanthostyles), *Anomodoryx* (single megasclere type consisting of strongyles or tylotes), *Waldoschmittia* (oxeas as choanosomal megascleres) and *Acanthodoryx* (plumose skeleton). It is assumed that the gender of *Lissodendoryx* is female, although no direct evidence for such an assumption is available.

#### **Key to subgenera of *Lissodendoryx***

- |  |                       |
|--|-----------------------|
| (1) Only a single megasclere type .....  | <i>Anomodoryx</i>     |
| At least two megasclere types (differentiated ectosomal and choanosomal megascleres) ..... | 2                     |
| (2) Choanosomal megascleres oxeas .....  | <i>Waldoschmittia</i> |
| Choanosomal megascleres smooth or spined styles .....                                      | 3                     |
| (3) Skeletal architecture plumose with thick tracts of (acantho-) styles .....             | <i>Acanthodoryx</i>   |
| Skeletal architecture reticulate, usually isotropic .....                                  | 4                     |
| (4) Spicules include a second category of smaller acanthostyles .....                      | <i>Ectyodoryx</i>     |
| No second category of smaller acanthostyles .....  | <i>Lissodendoryx</i>  |

### **SUBGENUS LISSODENDORYX TOPSENT, 1892**

#### **Synonymy**

*Lissodendoryx* Topsent, 1892a: 97. ? *Paramyxilla* Dendy, 1905: 233. *Jones* de Laubenfels, 1936a: 79. *Zetekopsis* de Laubenfels, 1936a: 85. *Zottea* de Laubenfels, 1936a: 64.

#### **Type species**

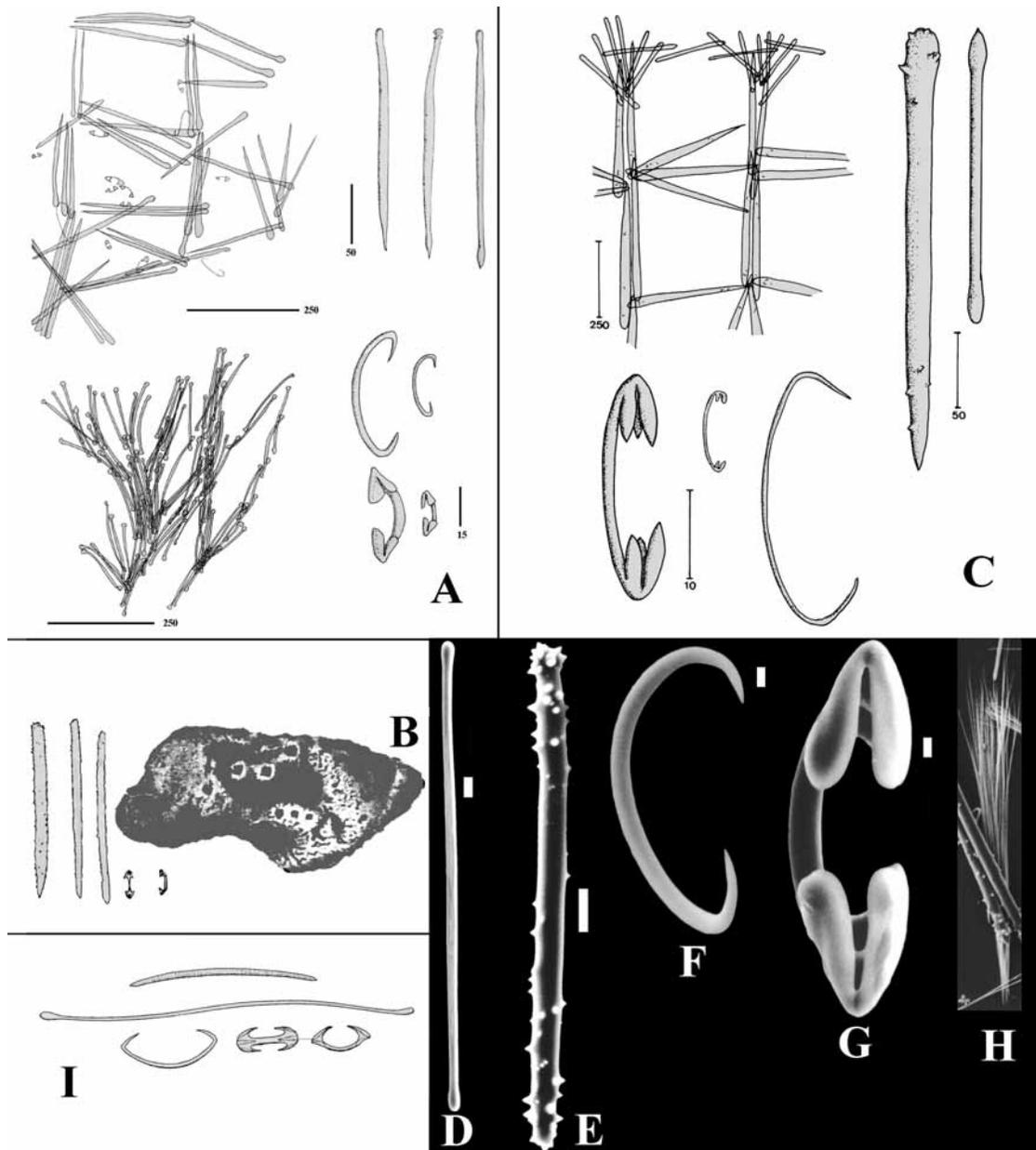
*Tedania leptoderma* Topsent, 1889: 49.

#### **Definition**

*Lissodendoryx* with a full complement of megascleres including ectosomal tylotornotes and choanosomal styles, which may or may not bear spines; no smaller category of echinating acanthostyles microscleres include arcuate isochelae and sigmas, which may be absent. Raphides may be present. Distribution. Circumglobal warm water, occasionally also in temperate and cold water.

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

*Lissodendoryx (Lissodendoryx) isodictyalis* (Carter, 1882a) (Fig. 8A).



**Fig. 8.** *Lissodendoryx* (*Lissodendoryx*). A, *Lissodendoryx* (*Lissodendoryx*) *isodictyalis* (Carter, 1882a as *Halichondria*), drawing of skeleton and spicules reproduced from Van Soest (1984b, fig. 19). B, *Lissodendoryx* (*Lissodendoryx*) *amaknakensis* (Lambe, 1894 as *Myxilla*), type of Jones de Laubenfels (1936a), drawing of shape and spicules reproduced from Lambe (1894, pl. II fig. 10) (sizes see text). C, *Lissodendoryx* (*Lissodendoryx*) *indistincta* (Fristedt, 1887 as *Hastatus*), type of Zetekopsis de Laubenfels (1936a), drawing of skeleton and spicules made from BMNH type slide. D–H, *Lissodendoryx* (*Lissodendoryx*) *grata* (Thiele, 1903a as *Myxilla*), type of Zottea de Laubenfels (1936a), SEM photos of spicules from the SMF holotype, reproduced from Hofman & Van Soest (1995: figs 1–8) (scales: D–E, 10  $\mu$ m, F–G, 1  $\mu$ m). I, *Lissodendoryx* (*Lissodendoryx*) *infrequens* Carter (1881b: 369, as *Halichondria*), type of *Paramyxilla* Dendy (1905), drawing of spicules reproduced from Carter, 1881b: pl. VIII fig. 9 (sizes see text).

**Synonymy.** *Halichondria isodictyalis* Carter, 1882a: 285, pl. XI fig. 2. *Tedania leptoderma* Topsent, 1889: 49; *Lissodendoryx leptoderma*; Topsent, 1892a: 97; *Lissodendoryx isodictyalis*; Topsent, 1897a: 456. *Esperiopsis fragilis* Verrill, 1907: 333, pl. XXXV-C figs 1–3.

**Material examined.** Syntypes (8 specimens, not examined): CLM Sp. 57–58, 62–66, 73 – Puerto Caballo, Nassau, Bahamas (cf. Wiedenmayer, 1977b: 258, table 51). Other material. Specimens of *L. isodictyalis*: ZMA collection (see Van Soest, 1984b). Holotype of *Tedania leptoderma*: MNHN, not examined.

**Description.** Lobate masses, which may attain considerable size, often more than 10 cm in diameter. Surface irregular, ridged, undulating, but smooth inbetween. Oscules may be prominent, on volcano-shaped lobes and deep. Consistency soft, easily torn. Colour light greyish green, occasionally pale yellowish. Skeleton (Fig. 8A) of the ectosome loose or bundled tylotes, not coherent. Choanosomal skeleton reticulate, isotropic, with single styles or paucispicular bundles. Spicules (fig. 8A) tylotes with well-developed heads, occasionally polytylote, heads usually smooth, but occasionally with a few spines, 150–230  $\times$  2–4  $\mu$ m; styles, usually

smooth, but not infrequently with a few spines near the blunt end, occasionally subtylostylote,  $130\text{--}200 \times 2\text{--}6 \mu\text{m}$ ; arcuate isochelae in two distinct size categories,  $19\text{--}34$  and  $8\text{--}16 \mu\text{m}$ ; sigmas in two distinct size categories,  $23\text{--}45$  and  $11\text{--}20 \mu\text{m}$ . Distribution and ecology. West Indies, E coast of North America, also recorded from the E Atlantic and E Pacific; mangroves and sea grass meadows.

**Remarks.** Closely similar species (e.g., *L. similis* Thiele, 1899: 18, and *L. ternatensis* (Thiele, 1903a: 952 as *Hamigera*) are found in a circumtropical belt, and may be considered disjunct populations of a former widespread parent species.

The genus *Jones* de Laubenfels (1936a: 79) was erected (original designation) for type species *Myxilla amaknakensis* Lambe, (1894: 122, pl. II fig. 10, here reproduced as Fig. 8B). This has sparsely spined, blunt-ending tornotes,  $137 \times 8 \mu\text{m}$ , entirely spined styles,  $144 \times 13 \mu\text{m}$ , in a renieroid reticulation; microscleres appear to be arcuate isochelae,  $22 \mu\text{m}$ ; no sigmas. It belongs to a group of *Lissodendoryx* species with spined styles, characteristic of cold water.

The genus *Zetekopsis* de Laubenfels (1936a: 85) was erected (by original designation) for type species *Hastatus indistinctus* Fristedt (1887: 444) on account of alleged spined sigmas. A slide of the holotype was found in the Natural History Museum, London, BMNH 1910.1.1.1424, labeled 'From Herr K. Fristedt, Spitzbergen, År 1872'. The skeleton (Fig. 8C) is an isotropic reticulation of single styles or bundles of 2–3. Ectosomal tylotes are mucronate at one end, normally tylote at the other,  $200 \times 5 \mu\text{m}$ ; styles are lightly spined at both apices but smooth in-between,  $350 \times 14 \mu\text{m}$ . Chelae consist of larger normal arcuate isochelae,  $25 \mu\text{m}$ , and smaller unguiferate isochelae, about  $7 \mu\text{m}$  (considered sigmas by Fristedt). Sigmas are normal shaped and relatively large,  $50 \mu\text{m}$ . No sigmas with 'very long spines' attributed to this species by de Laubenfels were found. The species belongs to the group of cold water *Lissodendoryx* species with spined styles.

The genus *Zottea* de Laubenfels (1936a: 64) was erected (by original designation) for type species *Myxilla grata* Thiele (1903a: 954, fig. 19) on account of its choanosomal spined strongyles (Fig. 8E). The holotype from the Senckenberg Museum, SMF 1783, from Ternate, Indonesia, was re-examined (see also Hoffman & Van Soest, 1995: 83). This is a massive lobate sponge with ectosomal smooth tylotes (Fig. 8D),  $190\text{--}235 \times 2\text{--}6 \mu\text{m}$ , and an isodictyal skeleton of acanthose strongyle-like spicules (in fact they are stylote spicules with a blunt and a more pointed end),  $130\text{--}180 \times 5\text{--}16 \mu\text{m}$ . The microscleres are normal arcuate isochelae (Fig. 8G),  $16\text{--}32 \mu\text{m}$ , sigmas (Fig. 8F),  $12\text{--}26 \mu\text{m}$ , and trichodragmas (Fig. 8H),  $45\text{--}140 \mu\text{m}$ . The species falls within the synonymy of the present subgenus.

The genus *Paramyxilla* Dendy (1905: 233) was erected for type species *Halichondria infrequens* Carter (1881b: 369, pl. VIII fig. 9, here reproduced as Fig. 8I). The type specimen was not found during a recent search in the BMNH, so we cannot be sure of its exact affinities. It possesses spined oxaeas, about  $130 \times 4\text{--}5 \mu\text{m}$ , as choanosomal megascleres; ectosomal spicules are the usual tylotes, about  $260 \times 3 \mu\text{m}$ , and microscleres comprise arcuate isochelae, about  $40 \mu\text{m}$ , and sigmas about  $60 \mu\text{m}$  (sizes calculated from Carter's drawings). On this basis it may be considered close to *Lissodendoryx* (*Lissodendoryx*) *grata*. However, it may also be a member of *Lissodendoryx* (*Waldoschmittia*), of which the type has smooth oxaeas (cf. below). The spined oxaeas are unusual, so far unique, and its importance as a phylogenetic character remains to be studied.

## SUBGENUS ACANTHODORYX LÉVI, 1961

### Synonymy

*Acanthodoryx* Lévi, 1961b: 516.

### Type species

*Acanthodoryx fibrosa* Lévi, 1961b: 516 (by monotypy).

### Definition

*Lissodendoryx* with radiating choanosomal skeleton of thick bundles of acanthostyles, showing little anastomosing, no sigmas.

### Previous review

Lévi (1961b: 516).

### Description of type species

*Acanthodoryx fibrosa* Lévi, 1961b (Fig. 9A–D).

**Synonymy.** *Acanthodoryx fibrosa* Lévi, 1961b: 516, fig. 8.

**Material examined.** Holotype: MNHN DCI. 700 – Zamboanga, Philippines.

**Description.** Massive sponge (Fig. 9A), size about  $2.5 \times 4 \text{ cm}$ , composed of a mass of radiating fibres covered by a thin membrane. Colour white in alcohol, probably red in life. Skeleton plumose, strong choanosomal fibres form a system of radiating tracts, occasionally anastomosing and with divergent spicules, but not echinated. Fibres  $50\text{--}160 \mu\text{m}$  in diameter. The ectosomal skeleton is poorly developed. Spicules (Fig. 9B–D), ectosomal tylotes, elliptical heads slightly inequidended,  $200\text{--}240 \times 3\text{--}4 \mu\text{m}$ ; acanthostyles, lightly spined all over, in a large size variation, up to  $150 \times 170 \times 7 \mu\text{m}$ ; arcuate isochelae in two size categories,  $33\text{--}34$  and  $20\text{--}21 \mu\text{m}$ . Distribution and ecology. Philippines, shallow water coral reefs.

**Remarks.** So far only a single species can be attributed to this subgenus. The structure of the skeleton reminds of the genus *Phorbas* in the family Hymedesmiidae, but the choanosomal tracts in that genus are truly plumose with no anastomosing and they are usually echinated by acanthostyles; the surface characters of *Phorbas* with the areolae are lacking in the present species.

## SUBGENUS ANOMODORYX BURTON, 1934

### Synonymy

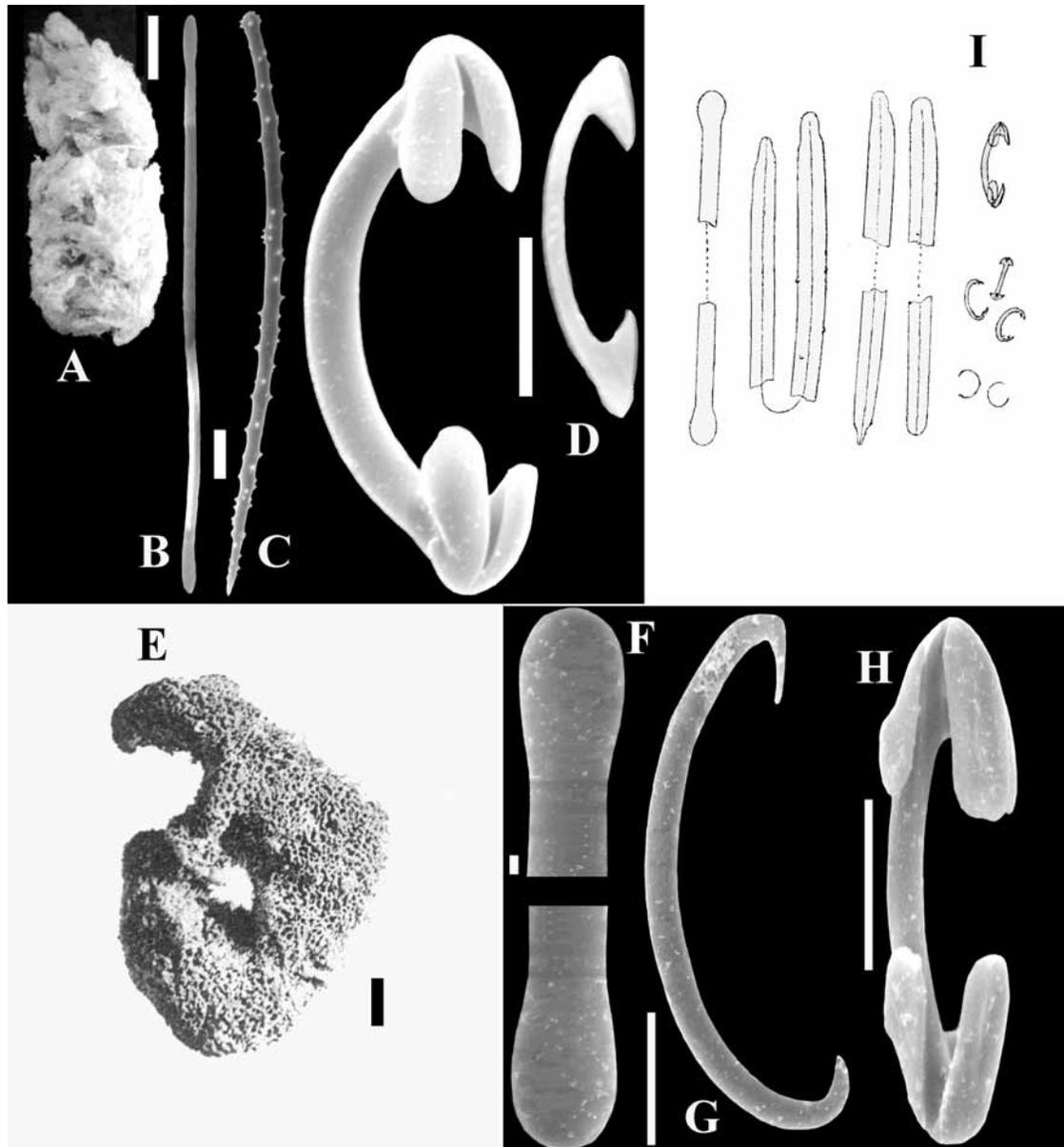
*Anomodoryx* Burton, 1934a: 555. *Damiriella* Burton, 1935a: 404.

### Type species

*Desmacidon dendyi* Whitelegge, 1901: 78 (by original designation).

### Definition

*Lissodendoryx* with a single megasclere type.



**Fig. 9.** A–D, *Lissodendoryx (Acanthodoryx) fibrosa* (Lévi, 1961b). A, habit of holotype (scale 1 cm). B–D, SEM photos of spicules made from the holotype (scale 10  $\mu\text{m}$ ). E–H, *Lissodendoryx (Anomodoryx) dendyi* (Whitelegge, 1901 as *Desmacidon*). E, habit of holotype reproduced from Whitelegge (1901) (scale 1 cm). F–H, SEM photos of spicules from the type (scales: F, 1  $\mu\text{m}$ ; G–H, 10  $\mu\text{m}$ ). I, *Lissodendoryx (Anomodoryx) cavernosa* (Topsent, 1892a as *Damiria*, type of *Damiriella* Burton (1935c), drawing of spicules reproduced from Topsent (1936: fig. 4) (sizes see text).

#### Previous review

Burton (1934a: 554).

#### Description of type species

*Lissodendoryx (Anomodoryx) dendyi* (Whitelegge, 1901) (Fig. 9E–H).

**Synonymy.** *Desmacidon dendyi* Whitelegge, 1901: 78, pl. X fig. 9; *Homoeodictya dendyi*; Hentschel, 1911: 319, fig. 17; *Anomodoryx dendyi*; Burton, 1934a: 555.

**Material examined.** Holotype (fragment): BMNH 1927.6.23.9 – Port Stephens, New South Wales, Australia (from AM G304Z).

**Description.** Massive, clathrate sponge (Fig. 9E). Reticulated, grooved surface, space between ridges 2–3 mm. Oscules scattered, about 5 mm in diameter. Consistency spongy, somewhat brittle. Colour yellowish grey (dry condition). The fragment examined in the Natural History Museum, London, was 1.5  $\times$  1.5  $\times$  1.5 cm, original specimen 15  $\times$  10 cm (Fig. 9E). At the surface individual megascleres are scattered in the dermal membrane; the choanosomal skeleton is an irregular system of wispy fibres of spongin filled with spicules, of about 100  $\mu\text{m}$  in diameter, interconnected irregularly with thinner bundles, 3–4 spicules thick. Meshes 150–200  $\mu\text{m}$ . Spicules. Tylotes (Whitelegge calls them strongyles, but the megascleres have distinct tyles (Fig. 9F) and are truly equiended tylotes), 150–250  $\times$  2.5–9  $\mu\text{m}$ ; arcuate chelae (Fig. 9H) in a variable but continuous size, 18–25  $\mu\text{m}$  (Whitelegge

mentions two sizes, 25 and 18  $\mu\text{m}$ ); sigmas (Fig. 9G), 35–40  $\mu\text{m}$ . Distribution and ecology. Central coast, New South Wales, Australia, shallow water.

**Remarks.** The genus *Damiriella* was erected by Burton, 1935a: 404 for type species *Damiria cavernosa* Topsent (1892b: xxii) (by original designation), from Cap l'Abeille, Banyuls area. Topsent's original description mentions a cavernous, massive, brown soft sponge, with ectosomal smooth tylotes,  $300 \times 6\text{--}10 \mu\text{m}$ , a reticulation of smooth strongyles,  $250 \times 15 \mu\text{m}$ , and isochelae which are not further characterized. Later, Topsent (1936: 19, fig. 4, here reproduced in Fig. 9I) redescribed the species on the basis of new material collected off Monaco. Hoffman & Van Soest (1995) on the basis of this description assumed that ectosomal and choanosomal megascleres were differentiated into tylotes and strongyles. For the present study, a MNHN slide of the later Topsent material was examined labeled "Lissodendoryx cavernosa Monaco, 19.IV.27" registered as D.T. 74. It has plumose bundles of tylote-like tornotes,  $275\text{--}350 \times 7\text{--}9 \mu\text{m}$ , fanning out at the surface to form a tangential skeleton. The tylotes vary in shape to include strongylote and even stylole forms, but they are obviously the same structural type. The choanosomal skeleton is a reticulation of smooth stylotes, rarely provided with a few spines, and not infrequently strongylote or even tylote,  $235\text{--}325 \times 7\text{--}10 \mu\text{m}$ . In fact, the ectosomal and choanosomal spicules are not at all clearly differentiated, and Topsent's (1936) attempt to consider the choanosomal spicules as (acantho-)styles was misleading. The microscleres are relatively elongated larger arcuate chelae 23–30  $\mu\text{m}$  and smaller reduced arcuate chelae 10–13  $\mu\text{m}$ . Pulitzer-Finali (1978: 56) described further material, confirming that the megascleres are mere variations of the same (probably ectosomal) spicule type. Thus, the only difference with *Anomodoryx* is the absence of sigmas, which is considered to be of specific level.

#### SUBGENUS *ECTYODORYX* LUNDBECK, 1909

##### Synonymy

*Ectyodoryx* Lundbeck, 1909: 445.

##### Type species

*Hastatus foliatus* Fristedt, 1887: 443 (by original designation).

##### Definition

*Lissodendoryx* with echinating acanthostyles.

##### Previous reviews

Lundbeck (1909: 445), Hofman & Van Soest (1995: 81).

##### Description of type species

*Lissodendoryx (Ectyodoryx) foliata* (Fristedt, 1887) (Fig. 10A).

**Synonymy.** *Hastatus foliatus* Fristedt, 1887: 443, pl. 25 figs 7–12; *Ectyodoryx foliata*; Lundbeck, 1909: 445.

**Material examined.** ? Holotype (slides): BMNH 1910.1.1.1435, 1435A – labeled "Hastatus foliatus Fristedt,

Grönland, Exp. af Sophia, år 1883, from Herr K. Fristedt, Norman Coll. (with sections), and 'Hastatus foliatus Fristedt, Greenland, from K. Fristedt, Norman Coll.', prepared from slide 10.1.1.1435' (spicule mount).

**Description (from Fristedt, 1887).** Leaf-shaped. Height up to 3.5 cm, thickness 3 mm. Surface even and smooth. Oscules numerous, small. Consistency fragile, soft. Colour grey in alcohol. Skeleton (Fig. 10A, few ectosomal tornotes scattered near the surface; choanosomal skeleton an irregular isotropical reticulation of bundles of 3–5 acanthostyles echinated by smaller acanthostyles. Spicules (Fig. 10A), ectosomal tornotes, tylote-like with unequal mucronated heads,  $200\text{--}280 \times 4 \mu\text{m}$ ; large structural acanthostyles, up to  $300 \times 20 \mu\text{m}$ ; smaller acanthostyles, entirely but weakly spined, 130–300  $\mu\text{m}$ ; arcuate isochelae, strongly but evenly curved, possibly in two size categories, 25–35  $\mu\text{m}$ ; sigmas small and thin, 20  $\mu\text{m}$ . Distribution and ecology. Norway; North Atlantic, Arctic, also recorded from South Africa; deep water, 70–1948 m depth.

**Remarks.** Lundbeck (1909) proposed to subdivide the genera *Myxilla* and *Lissodendoryx* (which were stated to differ only in possession of anchorate vs. arcuate chelae) further into those with smaller echinating acanthostyles (*Ectyomyxilla* and *Ectyodoryx*) and those without them (*Myxilla* and *Lissodendoryx* s.s.). This artificial distinction is here maintained only at the subgenus level. It should be noted that *Ectyomyxilla* was a *nomen nudum* since no type species was mentioned (cf. chapter on Myxillidae). Lundbeck (1909) reexamined Fristedt's type specimen and ascertained it had the echinating spicules (be it few in number). This is confirmed from the slide material examined. Other sympatric *Lissodendoryx (Ectyodoryx)* species are *Ectyodoryx atlanticus* Stephens (1920: 43) and *E. multiformis* Brøndsted (1932: 10). These differ substantially in shape (thinly encrusting in *E. atlanticus*) and spicule sizes and categories (megascleres twice as long in *E. atlanticus*; several categories of microscleres in *E. multiformis*). Both are to be renamed *Lissodendoryx (Ectyodoryx) atlantica* and *L. (E.) multiformis*.

#### SUBGENUS *WALDOSCHMITTIA* DE LAUBENFELS, 1936

##### Synonymy

? *Paramyxilla* Dendy, 1905: 233. *Waldoschmittia* de Laubenfels, 1936a: 95. *Zetekispongia* de Laubenfels, 1936b: 446. *Damiriana* de Laubenfels, 1950a: 14.

##### Type species

*Crella schmidti* Ridley, 1884a (by original designation).

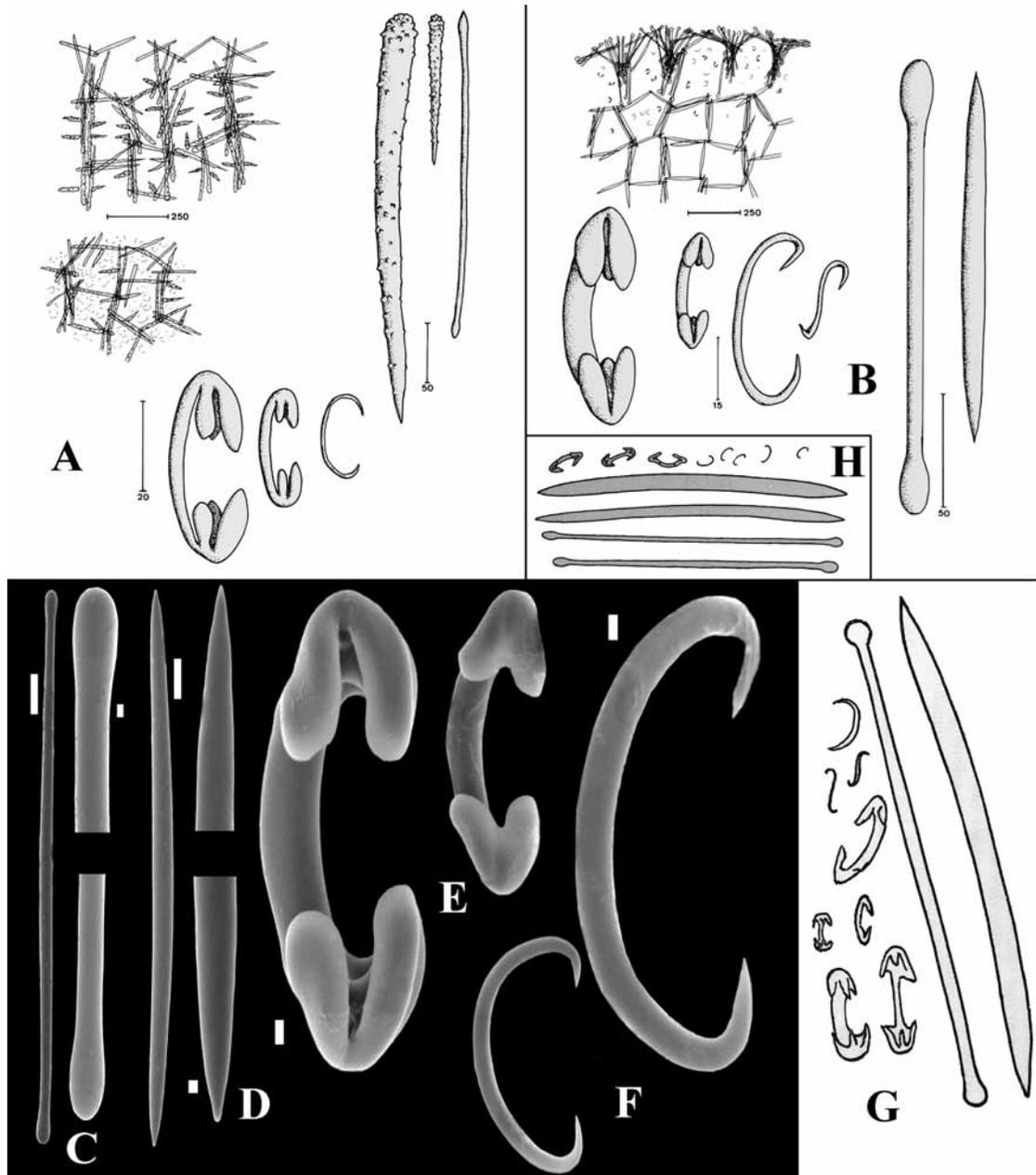
##### Definition

*Lissodendoryx* with oxeas as choanosomal megascleres.

##### Description of type species

*Lissodendoryx (Waldoschmittia) schmidti* (Ridley, 1884a) (Fig. 10B–G).

**Synonymy.** *Crella schmidti* Ridley, 1884a: 432, pl. XLI fig. A; *Damiria schmidti*; Topsent, 1897a: 455. *Damiria australiensis*



**Fig. 10.** A, *Lissodendoryx (Ectyodoryx) foliata* (Fristedt, 1887 as *Hastatus*), drawing of skeleton and spicules made from a BMNH type slide. B–G, *Lissodendoryx (Waldoschmittia) schmidti* (Ridley, 1884a as *Crella*). B, drawing of skeleton and spicules made from the BMNH holotype. C–F, SEM photos of spicules from the BMNH holotype (scales: 1  $\mu\text{m}$ , except A left and B left, 10  $\mu\text{m}$ ). G, drawing of spicules of *Lissodendoryx (Waldoschmittia) zonea* de Laubenfels (1936b as *Zetekispongia*), junior synonym of *L. (W.) schmidti*, reproduced from his fig. 40 (sizes see text). H, drawing of spicules of *Lissodendoryx (Waldoschmittia) hawaiiiana* de Laubenfels (1950a as *Damiriana*), junior synonym of *L. (W.) schmidti*, reproduced from his fig. 7 (sizes see text).

Dendy, 1896: 28; Lindgren, 1898: 25, pl. 17 fig. 10, pl. 19 fig. 15; *Myxilla schmidti*; Thiele, 1903a: 954; *Dendoricella schmidti*; Hentschel, 1911: 328, fig. 22; *Waldoschmittia schmidti*; de Laubenfels, 1936a: 95. *Zetekispongia zonea* de Laubenfels, 1936b: 446, fig. 40. *Damiriana hawaiiiana* de Laubenfels, 1950a: 14, fig. 7; *Damiriana schmidti*; Lévi, 1958: 30, fig. 25. *Lissodendoryx aspera*; Hofman & Van Soest, 1995: 87, figs 19–24 (not *Halichondria aspera* Bowerbank, 1875b: 287).

**Material examined.** Holotype: BMNH 1881.18.23.329 (dry), BMNH 1881.18.23.328 (slides with sections). Other material. Several specimens from Indonesia cited by

Hofman & Van Soest, 1995. Type slide of *Damiria australiensis*: BMNH 1929.1.26.39. Holotype of *Zetekispongia zonea*: USNM 22215 (considered synonymous with the former). Holotype of *Damiriana hawaiiiana*: USNM 22737 (also considered synonymous).

**Description.** Massive, lobate, riddled with channels of 1–4 mm diameter. Surface covered with narrow longitudinal ridges, rough, but smooth in between. Oscules small and few, lying in depressions. Consistency crumbly, colour dirty yellowish white (in alcohol), probably red in life. Skeleton (Fig. 10B). The ectosomal skeleton consists of brushes of tylotes lying at distances of 250  $\mu\text{m}$

enclosing distinct subdermal spaces. The tylotes fan out at the surface to form a tangential skeleton. The sections show an irregular isotropic skeleton of single oxeas or 2–3 per side forming meshes of  $150 \times 250 \mu\text{m}$ . Scattered microscleres occur especially at the surface. Spicules. Ectosomal tylotes (Fig. 10C), entirely smooth, with distinct, elongate heads, slightly flattened at the end:  $210\text{--}(228.9)\text{--}264 \times 4\text{--}(5.3)\text{--}7 \mu\text{m}$ ; oxeas (fig. 10D), smooth, with sharp occasionally mucronate ends:  $183\text{--}(194.5)\text{--}210 \times 6\text{--}(7.4)\text{--}8 \mu\text{m}$ ; arcuate chelae (Fig. 10E) in two size categories, chela I  $29\text{--}(33.3)\text{--}39 \mu\text{m}$ ; chela II  $18\text{--}(20.5)\text{--}24 \mu\text{m}$ ; sigmas (Fig. 10F) in two size categories, sigma I:  $26\text{--}(28.9)\text{--}31 \mu\text{m}$ ; sigma II:  $16\text{--}(18.4)\text{--}21 \mu\text{m}$ . Distribution and ecology. Described originally from Port Jackson, SE Australia, but subsequently recorded from all over the Indo-Pacific. If synonymy is correct, then the species also occurs in Hawaii and along the W coast of Panama; shallow-water.

**Remarks.** This species was considered a junior synonym of *Halichondria aspera* Bowerbank, 1875b from the Straits of Malacca, type of the genus *Xytopsihis* de Laubenfels (1936a) by Hofman & Van Soest (1995: 87). Bowerbank's description is misleading in giving the spicule combination of tylotes, oxeas, styles, two size categories of chelae, sigmas. The type specimen and two microscopic slides are kept in the BMNH London, unregistered. It is an irregularly lobate sponge of  $8 \times 6 \times 3 \text{ cm}$ , with an irregularly pitted surface. At its undersurface there is a smaller cushion-shaped sponge attached, size  $3 \times 2 \times 0.5 \text{ cm}$ , with a smooth surface. The larger sponge is a *Tedania*, probably matching the description of *T. dirhaphis* Hentschel (1912). No chelae or sigmas are found in this specimen. However, the smaller sponge is a *Lissodendoryx*, keying out as *L. ternatensis* (Thiele, 1903a). Since the *Tedania*

makes up the bulk of the material of *Halichondria aspera* and was obviously the material intended for it by Bowerbank, Hofman & van Soest's (1995) use of the species name for *Lissodendoryx* material with oxeas as the structural megascleres is thus incorrect (see also chapter Tedaniidae).

The genus *Zetekispongia* de Laubenfels, 1936b was erected (by monotypy) for the type species *Z. zonea* de Laubenfels (1936b: 446, fig. 40, here reproduced as Fig. 10G). The type specimen USNM 22215 from the Pacific coast of Panama was re-examined. This is a massive sponge with reticulate skeleton of smooth oxeas,  $210\text{--}215 \mu\text{m}$ , with ectosomal tylotes,  $170\text{--}200 \mu\text{m}$ , and arcuate isochelae,  $36$  and  $16\text{--}24 \mu\text{m}$ , and sigmas,  $16\text{--}24 \mu\text{m}$ . This is a junior synonym of *L. (Waldoschmittia) schmidti*.

The genus *Damiriana* de Laubenfels, 1950a was erected (by monotypy) for *D. hawaiiiana* de Laubenfels (1950a: 14, fig. 7, here reproduced in Fig. 10H). The type specimen USNM 22737 was reexamined. This is a massive red sponge, smooth with some digitations; oscules relatively large. Spicules include ectosomal smooth tylotes,  $170 \times 4 \mu\text{m}$ ; smooth oxeas,  $200\text{--}230 \times 8\text{--}9 \mu\text{m}$ ; arcuate isochelae,  $15\text{--}27 \mu\text{m}$ ; sigmas  $13 \mu\text{m}$ . This is also a likely junior synonym of *L. (Waldoschmittia) schmidti*.

The genus *Paramyxilla* Dendy (1905: 233) was erected for type species *Halichondria infrequens* Carter (1881b: 369, pl. VIII fig. 9, here reproduced as Fig. 8I), see description and discussion above under *Lissodendoryx* (*Lissodendoryx*). It possesses spined oxeas as choanosomal megascleres, which spined oxeas are unusual, so far unique. It may be close to either *Lissodendoryx* (*Lissodendoryx*) *grata* (cf. above) or to *Lissodendoryx* (*Waldoschmittia*) *schmidti*.