

Family Crambeidae Lévi, 1963

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Crambeidae Lévi (Demospongiae, Poecilosclerida) is characterized by the possession of anchorate chelae in combination with monactinal ectosomal megascleres in addition to thicker choanosomal styles or tylostyles. Peculiar acanthose microxeas occur in three of the four genera considered valid, whereas two of the four genera are sublithistid, having desmoid spicules. Several species of two genera exhibit unusually large variability of spicule presence and morphology.

Keywords: Porifera; Demospongiae; Poecilosclerida; Myxillina; Crambeidae; *Crambe*; *Discorhabdella*; *Lithochela*; *Monanchora*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

[Crambidae] Lévi, 1963: 16 (preocc.). Crambeidae Maldonado *et al.*, 2001: 1261.

Definition

Myxillina with subtylostyles as ectosomal megascleres and anchorate-unguiferate chelae as microscleres; occasionally also spined microrhabds, sigmoid spicules, and astro- or sphaeroclone desma-like spicules and derivatives thereof are present.

Diagnosis

Encrusting, massive, ramose or tubular growth forms. Ectosomal megascleres consist of smooth subtylostyles, usually arranged in brushes or bundles perpendicular to surface. Choanosomal megascleres are smooth or acanthose styles-tylostyles forming hymedesmioid, plumose or plumoreticulate skeletal structures. Peculiar desma-like spicules, likened to astroclones and sphaeroclones, occur in two genera. Microscleres consist of spatulate or unguiferate anchorate isochelae, occasionally modified to sigma-like reduced forms which in some species cannot be distinguished from true sigmas; finely spined microxeas occur in some species of three genera.

Scope

Ten nominal genera are included, of which four are considered valid: *Crambe*, *Discorhabdella*, *Lithochela* and *Monanchora*.

History and biology

Crambe was originally assigned to the large group of 'Desmacidonidae' by Vosmaer (1880) and retained there by Topsent (1928). De Laubenfels (1936a) assigned the genus to a family Monanthidae based on shared possession of desmas of *Crambe* and e.g., *Monanthus*. The latter genus is here assigned to the family Desmanthidae ('Lithistida'). Lévi (1963) recognized the unique nature of the *Crambe* desmas (they are in fact polyaxonic pseudastrose spicules unlike proper tetracrepid or monocrepid desmas), and accordingly erected a new family Crambidae for it.

Later, Lévi (1973) associated *Crambe* with desma-free genera *Monanchora* and *Echinostylinos*, and assigned these to a large family Esperiopsidae (thus, in fact, returning it to the position given to it by Topsent, 1928). Van Soest (1990) discussed the similarities in chela-shape between *Crambe* and *Monanchora* and Van Soest *et al.* (1996a) added to this the shared chemistry of these genera. The latter authors made the suggestion that *Crambe* and *Monanchora* were likely to be synonyms, but in view of the fact that several species exist with and without the pseudastrose desmoid spicules it is practical to retain both as separate genera. The contents of the family are here extended to include *Discorhabdella* and *Lithochela*, which share important similarities. Maldonado & Uriz (1996) demonstrated the relatedness of *Crambe* and *Discorhabdella*. *Lithochela* is added because of the combination of unguiferate chelae, spined microrhabds and ectosomal styles. Its desmas, though differing in shape and skeletal position, are considered homologous to those of *Crambe*. Crambeidae are encrusting to irregularly ramose or tubular sponges occurring on rocks, corals and mangroves, mostly in shallow water, but some genera occur down to 180 m depth. Reproduction of *Crambe* is viviparous and larvae – exhibiting the usual bare posterior pole – measure $850 \times 450 \mu\text{m}$ (Uriz *et al.*, 1998). Chemistry known from *Crambe* and *Monanchora* includes polycyclic guanidine alkaloids (Berlinck *et al.*, 1990; Van Soest *et al.*, 1996a), which are used in chemical defense (Turon *et al.*, 1996); the compounds are also found to be active in vitro against HIV.

Taxonomic remarks

Synonymy. [Crambidae] Lévi, 1963. This is a junior homonym of Crambidae Latreille, 1810 (Insecta: Lepidoptera). However, the name originally given by Lévi should be emended to Crambeidae, since the stem of *Crambe* is not obviously Cramb- (which is the case for the insect *Crambus*). Thus, the family name should be constructed from stem Crambe- by adding -idae as suffix. In this way, Crambeidae becomes available as an emended family name in Porifera: Poecilosclerida: Myxillina (see Maldonado *et al.*, 2001).

Contents. The contents of this family are here newly assigned. The sponges assembled here share the combination of anchorate chelae with monactinal tornotes. Also the choanosomal megascleres are thick, often knobbed or tuberculate tylostyles or derivations thereof. Echinating acanthostyles are rare, but may be represented in one genus. Several species of three of the four

genera of this family show a remarkable intraspecific variation in spicule presence, size and shape making identification unusually complicated. Diagnostic in such cases are the presence of two morphological megasclere types, relatively long and thin ectosomal spicules (variously subtylostyles, strongyles or anisostrongyles) and relatively short and fat choanosomal spicules (variously tylostyles, styles or strongyles).

Desmoids. Species of two genera, *Crambe* and *Lithochela*, are provided with desmoid spicules. Those of *Crambe* are polyaxone spicules in the form of astro- or sphaeroclones (Uriz & Maldonado, 1995; Maldonado *et al.*, 2001). In several species of *Crambe* these desmas are interlocked to form a basal layer

upon which tylostyles are erected, heads lodged between the desmas (Maldonado & Benito, 1991; Uriz & Maldonado, 1995). The sphaeroclone desmas are similar to those described for the recent 'lithistid' *Vetulina* (Uriz & Maldonado, 1995), but since that genus – along with a series of fossils classed in the family Chastoclonellidae (with no extant representatives; see chapter on fossil lithistids, this volume) – has no spicules other than the desmas, inclusion in the family Crambeidae is postponed until further evidence is provided. *Lithochela* desmas appear to be monocrepid, but some similarity with *Crambe crambe* desmoids is present.

Previous review. Maldonado *et al.* (2001).

KEY TO GENERA

- (1) Megascleres include short, spined, club-shaped pseudastrose tylostyles *Discorhabdella*
No short club-shaped acanthostyles 2
- (2) Spicules include desmas or irregular desmoid polyaxones (the latter may be rare) 3
No desmas or desmoid polyaxones 4
- (3) Desmas are elongate monocrepsids forming a reticulated choanosomal skeleton *Lithochela*
Desmas are small polyaxone or lumpy-lobate spicules concentrated at the base of the sponge *Crambe*
- (4) Live appearance includes white-lined veinal channel patterns *Monanchora*
Live appearance with unlined veinal patterns *Crambe*

CRAMBE VOSMAER, 1880

Synonymy

Crambe Vosmaer, 1880: 135. [*Plicatella*] Schmidt, 1870: 45 (preocc.). *Tetranthella* Lendenfeld, 1894: 101.

Type species

Suberites crambe Schmidt, 1862: 66 (by original designation).

Definition

Crambeidae with astroclone or sphaeroclone desmoid spicules, spatulate or unguiferate anchorate isochelae, and spined microxeas (may all be absent). Live appearance shows veinal patterns without white or yellow lining.

Diagnosis

Thin flat crusts or thicker tubercular masses, occasionally more elaborately lobate; surface translucent, slightly hispid, occasionally conulose, detachable, with clear veinal channel pattern in life. Ectosomal skeleton composed of brushes of thin styles-subtylostyles (occasionally strongyles), which may fan out into a tangential layer; choanosomal skeleton composed of desmas forming a semi-rigid basal skeleton (often absent), and stylote spicules forming a plumose skeleton. Megascleres are thicker styles and thinner subtylostyles (may be modified into strongyles); microscleres are pseudastrose desmoid spicules (often absent), spined microxeas (often absent) and anchorate isochelae (occasionally absent or reduced to sigmoid spicules). So far 6–7 species including one fossil have been assigned to this genus (Maldonado & Uriz, 1996).

Previous reviews

Vacelet & Boury-Esnault (1982), Maldonado & Benito (1991), Uriz & Maldonado (1995), Maldonado & Uriz (1996: 371).

Description of type species

Crambe crambe (Schmidt, 1862) (Figs 1, 2A).

Synonymy: *Suberites crambe* Schmidt, 1862: 66, pl. VI fig. 9. *Suberites fruticosus* Schmidt, 1862: 66, pl. VI fig. 10. *Reniera labyrinthica* Schmidt, 1864: 39, pl. IV fig. 9. *Crambe harpago* Vosmaer, 1880: 135. *Crambe crambe*; Rützler, 1965: 32; Maldonado & Uriz, 1996: 372, figs 1F, 2F, 3G. *Stylinos brevicuspis* Topsent, 1892b: xx. *Tetranthella fruticosa*; Lendenfeld, 1894: 101. *Hemimyscale ambigua* Sarà, 1960a: 452, fig. 4. *Hemimyscale brevicuspis*; Sarà & Siribelli, 1960: 44.

Material examined. Lectotype (not examined): LMJG 15265 – Lissa, Adriatic. Paralectotype of *Suberites crambe*: LMJG 15672 – no locality data, Adriatic. Other material. Paralectotype of *Suberites fruticosus*: LMJG 15667 – no locality data, Adriatic.

Description (based on re-examination of the paralectotype specimens of *Suberites crambe* and *Suberites fruticosus*). Thin flat crusts (0.5 cm) or thicker masses (up to 1.5 cm), smooth or with upright tubercles or projections. Surface with distinctly swollen veins in life (Fig. 1F), slightly hispid or conulose. Lateral size may be considerable, up to 0.5 m² (Becerro *et al.*, 1994). Colour orange-red. Skeleton (Fig. 2A), near the surface brushes of ectosomal megascleres fan out and many single spicules occur tangentially. In the choanosome bundles of megascleres (up to 10 or more in cross section) rise up from a basal spongin plate, occasionally single megascleres are in erect position. Binding spongin is variable and bundles may be loose and irregular, 50–130 µm in diameter. At the base peculiar pseudastrose desmas may be present, but these are rare and often absent in specimens. Likewise

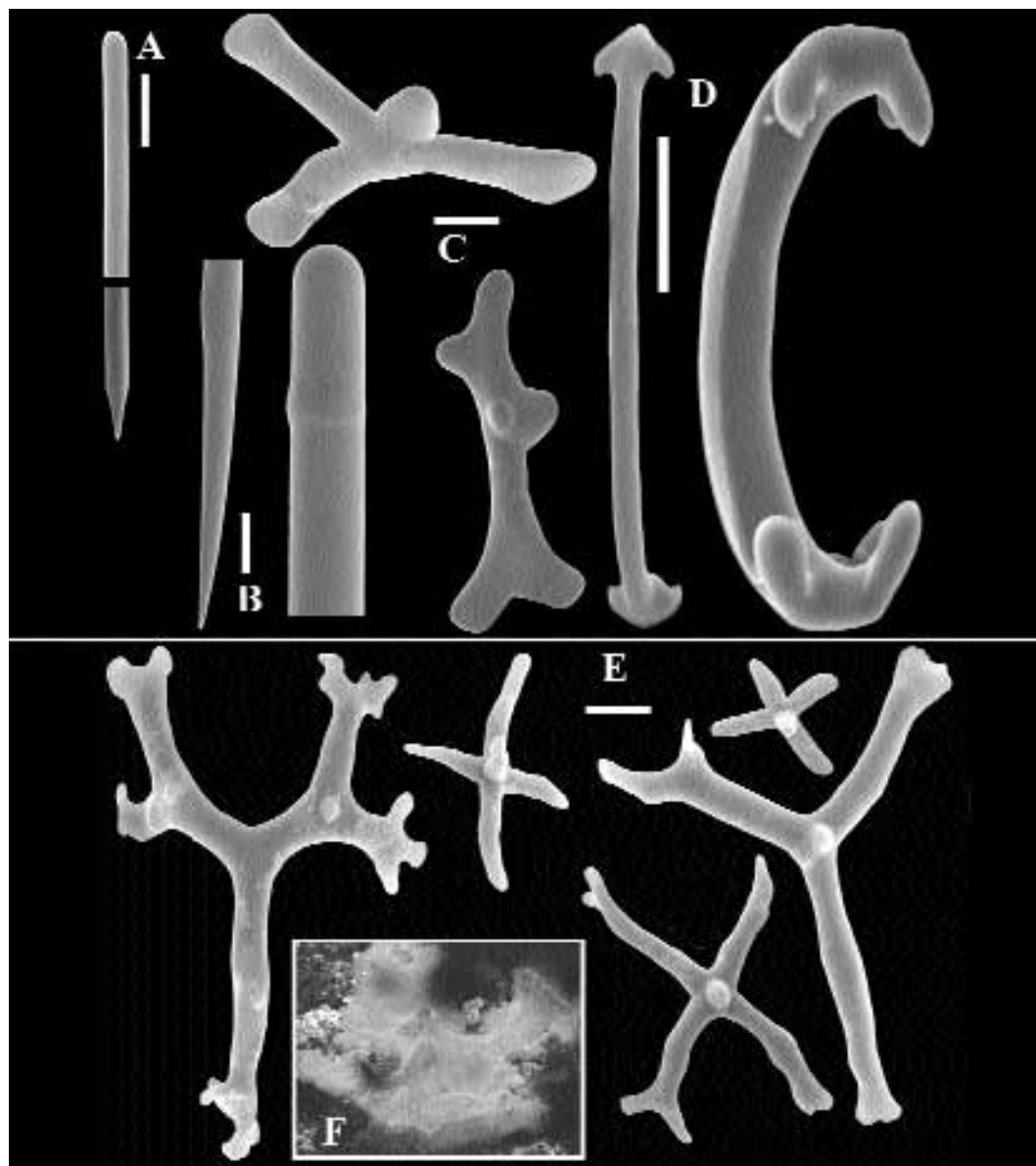


Fig. 1. *Crambe crambe* (Schmidt, 1862 as *Suberites*). A–E, SEM photos of spicules made from paralectotype specimens of *Suberites crambe* (A–D) and *S. fruticosus* (E) (scales 10 μ m). F, specimen photographed in situ (photo B.E. Picton).

chelae may be present, rare or absent. Sand and other material are frequently incorporated in the basal parts. Spicules (measurements taken from the paralectotype), styles from the peripheral bundles (Figs 1A, 2A), smooth, straight, faintly constricted underneath the head, occasionally clearly subtylostylote, $316\text{--}(351)\text{--}381 \times 7 \mu\text{m}$ (Rützler, 1965: $225\text{--}320 \times 3.5\text{--}5.5 \mu\text{m}$); styles from the base of the sponge (Figs 1B, 2A), longer and thicker than those of the peripheral bundles, straight, smooth, mostly faintly swollen subterminally, $423\text{--}(489.3)\text{--}539 \times 11\text{--}(14.6)\text{--}17 \mu\text{m}$ (Rützler, 1965: $370\text{--}400 \times 8\text{--}13 \mu\text{m}$); unguiferate anchorate chelae, often with reduced shortened teeth (Figs 1D, 2A), $28\text{--}(38.3)\text{--}43 \mu\text{m}$; astrose desmoid spicules (Figs 1C, E, 2A) with variable number of rays with rounded knobbed ends and of unequal length, cladome $38\text{--}(68.5)\text{--}99$, rays $10\text{--}(35.7)\text{--}47 \times 7\text{--}(10.6)\text{--}14 \mu\text{m}$. Distribution and ecology. Mediterranean, Atlantic coast of Portugal, Canary Islands; encrusting on vertical rocks and ceilings of caves, on shells

and calcareous tubes, and coralline algae; shallow-water down to 367 m depth.

Remarks. The type species *C. crambe* is atypical in the genus for its poorly developed astroclone desmas. Compared to *C. acuata* (Lévi, 1958 as *Folitispa*), *C. talliezi* Vacelet & Boury-Esnault (1982), *C. tuberosa* Maldonado & Benito (1991) and *C. erecta* Pulitzer-Finali (1993), they are reduced in form, asymmetrical and mostly not interlocked. Maldonado & Uriz (1996) mention the occurrence of elaborately shaped sphaeroclones in slides of Topsent from Banyuls, but failed to provide evidence that this material belonged with certainty to *Crambe*. The variability in spicule presence and shape in this species is remarkable and parallels that known for *Monanchora arbuscula* (cf. below). The paralectotype specimen of *S. crambe* here examined has only a few chelae, some of which are reduced (Fig. 2D), and relatively few desmoid spicules (Fig. 2C). The lectotype of *S. fruticosus*,

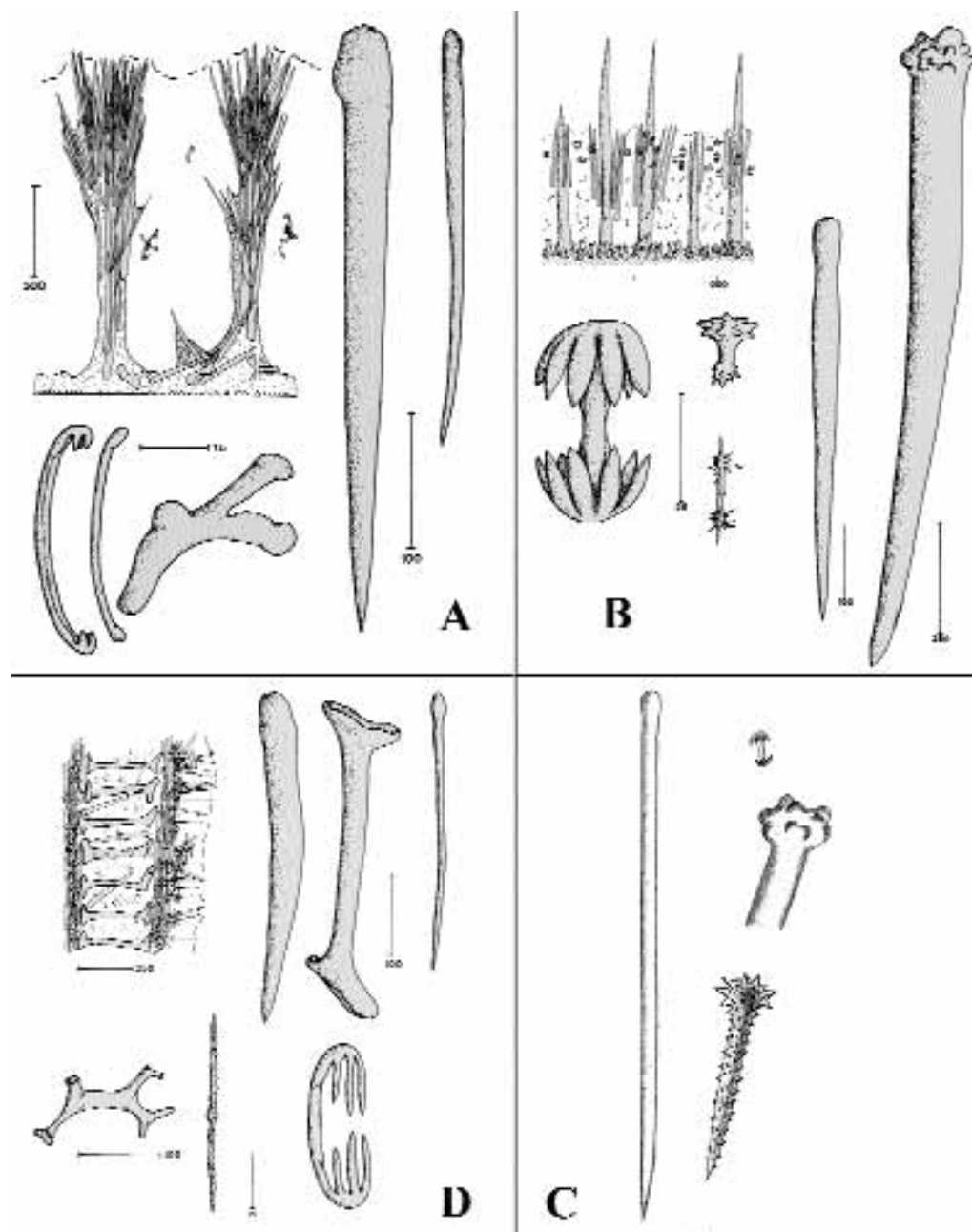


Fig. 2. A, *Crambe crambe* (Schmidt, 1862 as *Suberites*), drawing of skeleton and spicules made from a slide of a paralectotype. B, *Discorhabdella incrustans* Dendy (1924), drawing of skeleton and spicules made from a slide of the holotype. C, *Discorhabdella tuberoscapitata* (Topsent, 1890b as *Hymenaphia*), type of *Cionanchora* de Laubenfels (1936a), drawing of the spicules reproduced from Topsent (1892a: pl. XI fig. 6) (sizes see text). D, *Lithochela conica* Burton (1928), drawing of skeleton and spicules made from a slide of the paralectotype.

LMJG 15105, has abundant desmoids (Fig. 2E). Fossil spicules described from the Oligocene of New Zealand (Hinde & Holmes, 1892) may belong to this species (described as *Crambe oamaruensis*). Many other specimens lack both microscleres and desmoids, and moreover have their spicules modified into strongyles. It is suspected that some of the specimens and species assigned to genera *Batzella* and *Hemimyscale* are in reality specimens of *Crambe* or *Monanchora* (cf. below).

The synonymy of *Reniera labyrinthica* Schmidt, 1864, type of [*Plicatella*] Schmidt, 1870: 45 (by subsequent designation, de Laubenfels, 1936a), with *Crambe crambe* likewise is based on

reduced spiculation. Recent specimens in the ZMA collection, e.g., ZMA POR. 10966, combine a shape reminiscent of Schmidt's drawing of *R. labyrinthica* in combination with a spiculation of exclusively thin strongyles. It is tentatively assumed that Schmidt's material and ZMA POR. 10966 are *Crambe crambe*. The genus name [*Plicatella*] Schmidt is preoccupied by the mollusc genus *Plicatella* Swainson, 1840.

The genus *Tetranthella* Lendenfeld, 1894: 101 was erected for type species *Suberites fruticosus* Schmidt, 1862: 66 (by original designation). As demonstrated above this is a clear synonym of *Crambe crambe*, and thus *Tetranthella* is a junior synonym of *Crambe*.

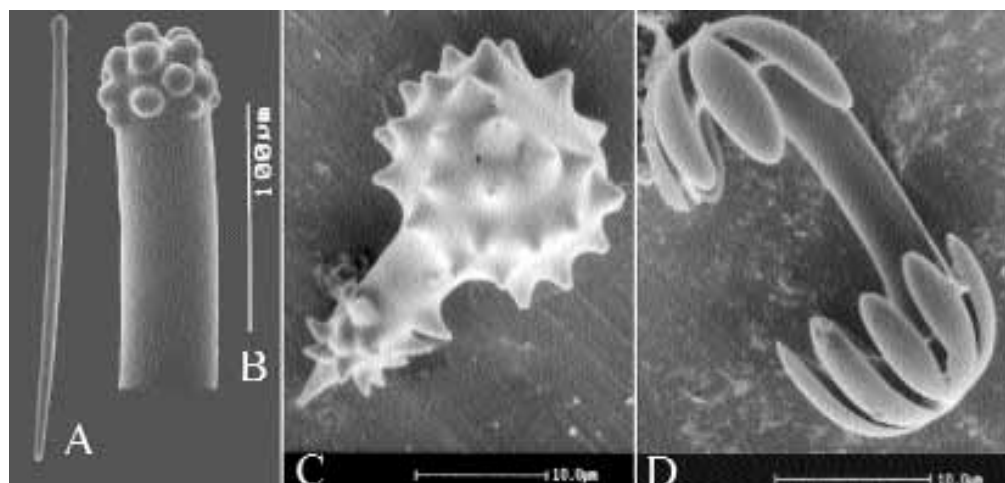


Fig. 3. *Discorhabdella incrustans* Dendy, 1924, SEM images of spicules of type. A, ectosomal subtylostyle. B, choanosomal tylostyle with warty head. C, mace-shaped pseudastrose tylostyle. D, polydentate isochela (photos M. Maldonado).

DISCORHABDELLA DENDY, 1924

Synonymy

Discorhabdella Dendy, 1924: 376. *Cionanchora* de Laubenfels, 1936a: 108.

Type species

Discorhabdella incrustans Dendy, 1924: 376 (by monotypy).

Definition

Crambeidae with hymedesmioid skeleton of choanosomal styles with swollen lumpy bases and tuberculate club-shaped pseudoastrose tylostyles.

Diagnosis

Smooth ectosomal subtylostyles, long choanosomal styles with swollen lumpy bases and tuberculate club-shaped pseudoastrose or heavily spined tylostyles forming erect hymedesmioid skeleton; microscleres anchorate unguiferous isochelae and may include spined microxeas with two lumpy swellings or sigma-like spicules. Four species from all over the world.

Previous reviews

Dendy (1924), Boury-Esnault *et al.* (1992a), Maldonado & Uriz (1996), Maldonado *et al.* (2001).

Description of type species

Discorhabdella incrustans Dendy, 1924 (Figs 2B, 3A–D).

Synonymy. *Discorhabdella incrustans* Dendy, 1924: 376, pl. XV figs 34–38; Boury-Esnault *et al.*, 1992a: 5; Uriz & Maldonado, 1995: 3, figs 1e, 2d, 5a–b, 6b–c; Maldonado & Uriz, 1996: 373, figs 6E, 7D, 8C, 9C, 10F–G.

Material examined. Holotype (slides): BMNH 1923. 10.1.157 – ‘Terra Nova’ Expedition, RN.XLVII-3, Three Kings Island, New Zealand, 180 m depth.

Description. Thinly encrusting, approx. 1.5 mm thick, with spined surface. Skeletal architecture hymedesmioid (Fig. 2B). Main styles huge, singly erect on the substrate, with lumpy heads, but otherwise smooth; distance between them ca. 100–150 μm. Base of huge styles surrounded by masses of pseudoastrose tylostyles echinating the substrate. Smooth subtylostyles are arranged in bundles with heads downwards around the shaft of the main styles. Microscleres zoned, chelae at the periphery, spined microrhabds deeper in the sponge. Spicules (Figs 2B, 3). Ectosomal subtylostyles (Fig. 3A), smooth, with clearly swollen heads, 357–(496.8)–592 × 10–(12.6)–15 μm; choanosomal (tylo-) styles (Fig. 3B) with irregular swollen lumpy heads, mostly broken in the slides, so length is tentative, 900–1700 × 28–(43.1)–61 μm; club-shaped (‘mace’-shaped) pseudoastrose spicules (Fig. 3C), with a swollen crown covered with spines, a short smooth middle part and a swollen and spined end, length 36–(45.4)–53 μm and width of the crown 32–(37.3)–43 μm; anchorate-unguiferate isochelae (Fig. 3D) with up to 7 long well-developed alae, occasionally with reduced alae, 33–(44.0)–51 μm; spined microxeas (Fig. 2B) with two swollen and spined lumps at a short distance from either end, 26–(31.4)–34 μm. Distribution and ecology. Off Three Kings Islands, N New Zealand, dredged from 180 m depth.

Remarks. Boury-Esnault *et al.* (1992a) retained this genus in the family Hymedesmiidae. Maldonado & Uriz (1996) pointed out the similarities between *Discorhabdella* and *Crambe*, but did not assign either genus to a definite family. Similarity with the spicule complement of *Crambe* (shared morphologies of chelae, spined microxeas and pseudoastrose spicules) is so great that the mere sharing of hymedesmioid skeletal architecture with *Hymedesmia* is insufficient to follow Boury-Esnault *et al.* (1992a). *Discorhabdella incrustans* falls naturally to the family Crambeidae on account of ectosomal subtylostyles, tylostylote choanosomal spicules and anchorate chelae. The pseudoastrose styles have been interpreted as homologous to echinating acanthostyles of Hymedesmiidae and other Myxillina families by Boury-Esnault *et al.* (1992a). However, they share similarities to pseudoastrose desma-like spicules in *Crambe* and they have peculiar morphology with spines confined to both swollen ends. Maldonado & Uriz (1996) demonstrated the spines are unlike those of normal acanthostyles in having an axial canal (thus are ‘polyaxial’). It is possible that these spicules derive ultimately from choanosomal

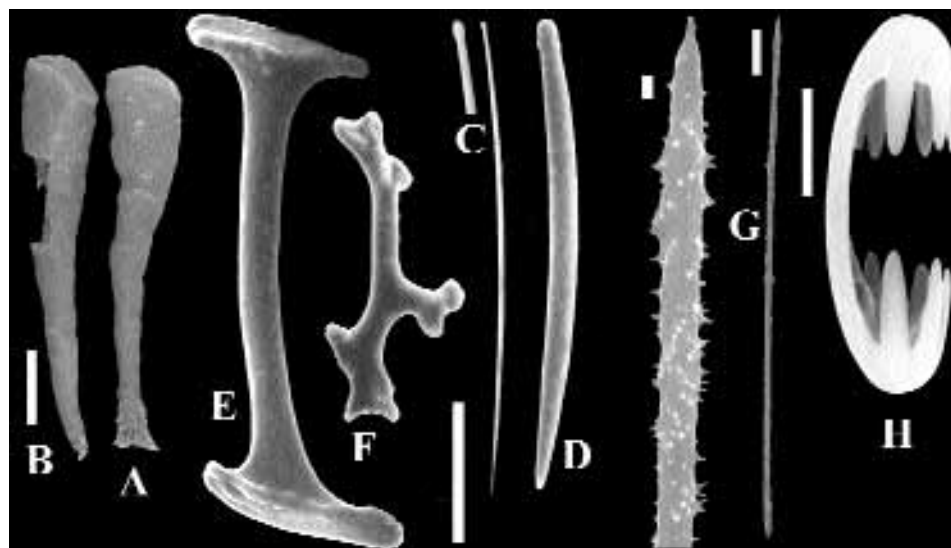


Fig. 4. *Lithochela conica* Burton (1929b). A–B, photos of habit of BMNH lectotype (A) and paralectotype (B) (scale 1 cm). C–H, SEM photos of spicules of lectotype (scales: 10 μ m, except G left, 1 μ m).

tylostyles. Fossil spicules described from the Oligocene of New Zealand (Hinde & Holmes, 1892) may belong to this species.

The type species of the genus *Cionanchora* de Laubenfels, 1936a: 108, *Hymenaphia tuberosocapitata* Topsent, 1890b: 68 (by original designation; full description and illustration in Topsent, 1892a: 113, pl. XI fig. 6, here reproduced as Fig. 2C) is a clear *Discorhabdella*. A microscopic slide of the holotype, which is lodged in MOM, was examined in the Paris Museum, MNHN D.T. 938, labeled 'Camp. Hirondelle 1888, No. 65, 159', as well as a slide of a topotypical specimen MNHN D.T. 939, labeled 'PA 60 1895' (recorded in Topsent, 1904b), both from deep water, 550–736 m, off the Azores. The skeletal architecture of *H. tuberosocapitata* is hymedesmioid with single large tylostyles, about 650 μ m long with tuberoso heads, about 28 μ m in diameter, erect on the substrate, surrounded by small tuberoso acanthotylostyles of about 130 μ m long (interpreted here as homologous to the pseudastrose spicules of *D. incrustans*). Ectosomal subtylostyles are robust, with elliptical heads and short points, length averaging 330 μ m. Anchorate isochelae with prominent fimbriae, 4–5 teeth, averaging 25 μ m. No spined microxeas. For SEM images and light micrographs of this species see Maldonado & Uriz (1996) and Hooper (1996a), the latter author erroneously referring the taxon to Microcionidae as a synonym of *Clathria* (*Microcionia*).

Further species were described by Boury-Esnault *et al.* (1992a) and Maldonado *et al.* (2001). *Discorhabdella hindei* Boury-Esnault *et al.* (1992a) from 600 m in the Mediterranean; is similar to *D. incrustans* but possesses sigma-like microscleres in addition to the usual unguiferate anchorate chelae; like *D. tuberosocapitata*, it lacks spined microxeas. The variability in presence of spined microrhabds and sigma-like microscleres in this genus parallels that found in the genus *Monanchora* (cf. Van Soest *et al.*, 1996a).

LITHOCHELA BURTON, 1929

Synonymy

Lithochela Burton, 1929b: 9.

Type species

Lithochela conica Burton, 1929b: 9 (by monotypy).

Definition

Crambeidae with desmas forming the main skeleton, and possessing robust ectosomal subtylostyles and unguiferate chelae.

Diagnosis

Thin-walled, stalked hollow tubes with desma-reticulation forming the support of the tube wall. Ectosomal brushes of robust styles. Scattered isochelae with long thin teeth. Spined microxeas present. Only a single species known so far.

Description of type species

Lithochela conica Burton, 1929b (Figs 2D, 4A–H).

Synonymy. *Lithochela conica* Burton, 1929b: 9, pl. I figs 9–10, pl. II figs 11–19.

Material examined. Lectotype (designation herein): BMNH 1926.4.14.103. Paralectotype: BMNH 1926.9.3.79 (3 slides RN 169 and RN 204).

Description. Shaped like a carrot, fistular-tubular, stalked (Fig. 4A–B), up to 5 cm high, 1 cm diameter. Flattened at the apex with a single central papillate oscule, 1 mm in diameter. Inside the central core is hollow, surrounded by a thick wall. Consistency fragile, easily damaged. Colour brownish yellow. Skeleton (Fig. 2D) of the surface a tangential feltwork of styles. Inside a reticulation of styles and larger and smaller desmas form the skeleton of the thick wall. The reticulation is made up of longitudinal tracts of styles connected by single or bundles of elongate desmas. Microscleres extremely abundant along the inner wall. Spicules, styles of the ectosome (Figs 2D, 4C) and the choanosomal tracts (Figs 2D, 4D), curved, sometimes irregular, 360–450 $\times$ 22 μ m; desmas, probably in two categories, the larger ones (Figs 2D, 4E) elongated, rhabd-like

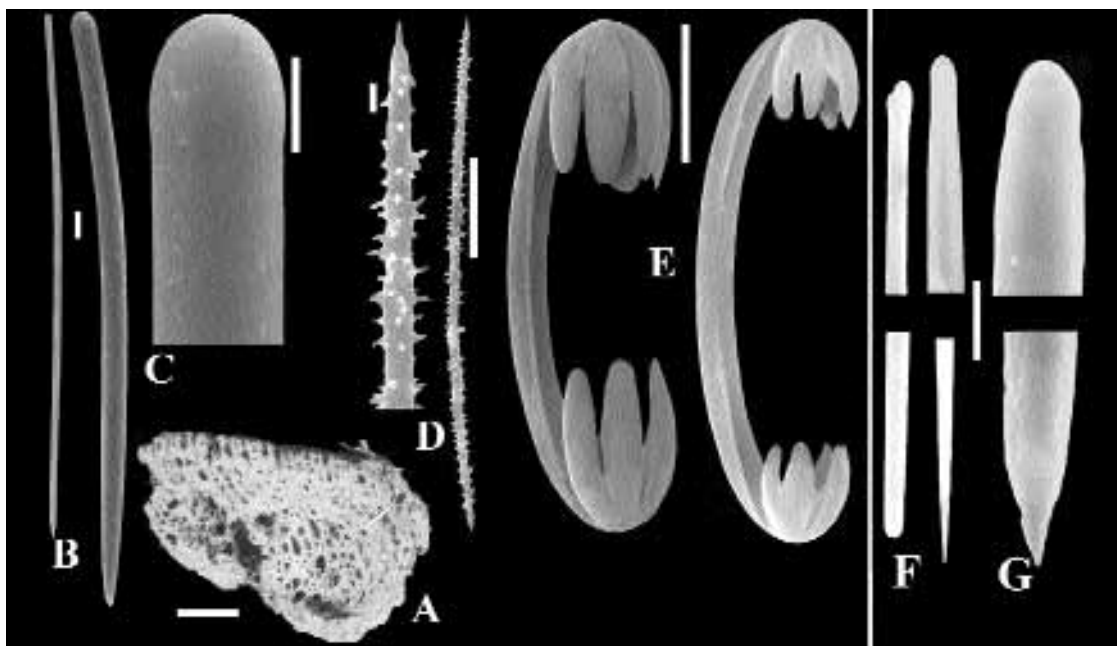


Fig. 5. A–E, *Monanchora clathrata* Carter, 1883c. A, habitus of BMNH holotype (scale 1 cm). B–E, SEM photos of spicules of the holotype (scales: 10 μ m, except D left, 1 μ m). F–G, *Monanchora enigmatica* (Burton & Rao, 1928 as *Ectyobatzella*). F, SEM photos of ectosomal spicules made from the holotype. G, ditto of choanosomal spicule.

with simple flat extensions at the end which connect with the tracts of styles, $270\text{--}360 \times 36 \mu\text{m}$, and the smaller branching and knobbed (Figs 2D, 4F), cladomes $180\text{--}200 \mu\text{m}$, thickness of rhabds $20 \mu\text{m}$; microscleres are unguiferous isochelae (Figs 2D, 4H), $23\text{--}40 \mu\text{m}$, and spined microxeas (Figs 2D, 4G), often with a central 'tyle', $55\text{--}100 \mu\text{m}$ (not reported by Burton). Distribution and ecology. Natal coast, South Africa, collected from green mud bottom at 180 m depth.

Remarks. This is a unique species with no close relatives. The skeletal architecture is highly correlated with the unusual fistular shape of the body. In this aspect *Lithochela* is quite different from *Crambe*. However, some similarities may be present in the sphaeroclone-type desmas of *Crambe* and the smaller desmas of *Lithochela*. There is no differentiation in style types, but the larger desmas may be considered derived from the tylostyles found in the remaining crambeids, because as Burton already demonstrated, they seem to grade into style-like spicules. Also, the spined microxeas, reported for the first time, are similar to those of several *Crambe*, *Monanchora*, and *Discorhabdella* species.

MONANCHORA CARTER, 1883

Synonymy

Monanchora Carter, 1883c: 369. *Amorphoclada* Topsent, 1930. *Ectyobatzella* Burton & Rao, 1932: 332. *Fasubera* de Laubenfels, 1936a: 119. *Folitispa* de Laubenfels, 1936a: 119. [*Okadaia*] de Laubenfels, 1936a: 120 (preocc.). *Neofolitispa* Bergquist, 1965: 172.

Type species

Monanchora clathrata Carter, 1883c: 369 (by monotypy).

Definition

Crambeidae without pseudoastrose spicules or desmas; microscleres spatulate or unguiferate anchorate isochelae (may be absent), reduced sigmoid chelae (may be absent), and spined microxeas (may be absent). In life, the surface has characteristic white- or yellow-lined veinal channel pattern.

Diagnosis

Encrusting to lobate or ramose. Surface smooth or extended into corrugate or spined projections. In life, superficial canals characteristically swollen and with a lighter-coloured lining. Skeletal arrangement is simple: irregular plumose bundles of megascleres, which tend to form loose brushes at the surface without forming a definite ectosomal skeleton. Spongin variably developed but may be considerable. Spicule complement rather variable, both among and within species. Basically, the two size categories of megascleres characteristic for the family are present, but these may be indistinguishable in some species or modified to strongyle-like spicules. Microscleres may include a full complement, then consisting of two categories of anchorate-unguiferate chelae and spined microxeas; frequently one or more of these may be absent or reduced. In extreme cases only reduced and modified megascleres may be found (*Ectyobatzella* form) and then assignment to *Monanchora* remains problematic.

Previous reviews

Van Soest (1984b, 1990), Bergquist & Fromont (1988), Van Soest *et al.* (1996a).

Description of type species

Monanchora clathrata Carter, 1883c (Figs 5A–E, 6A).

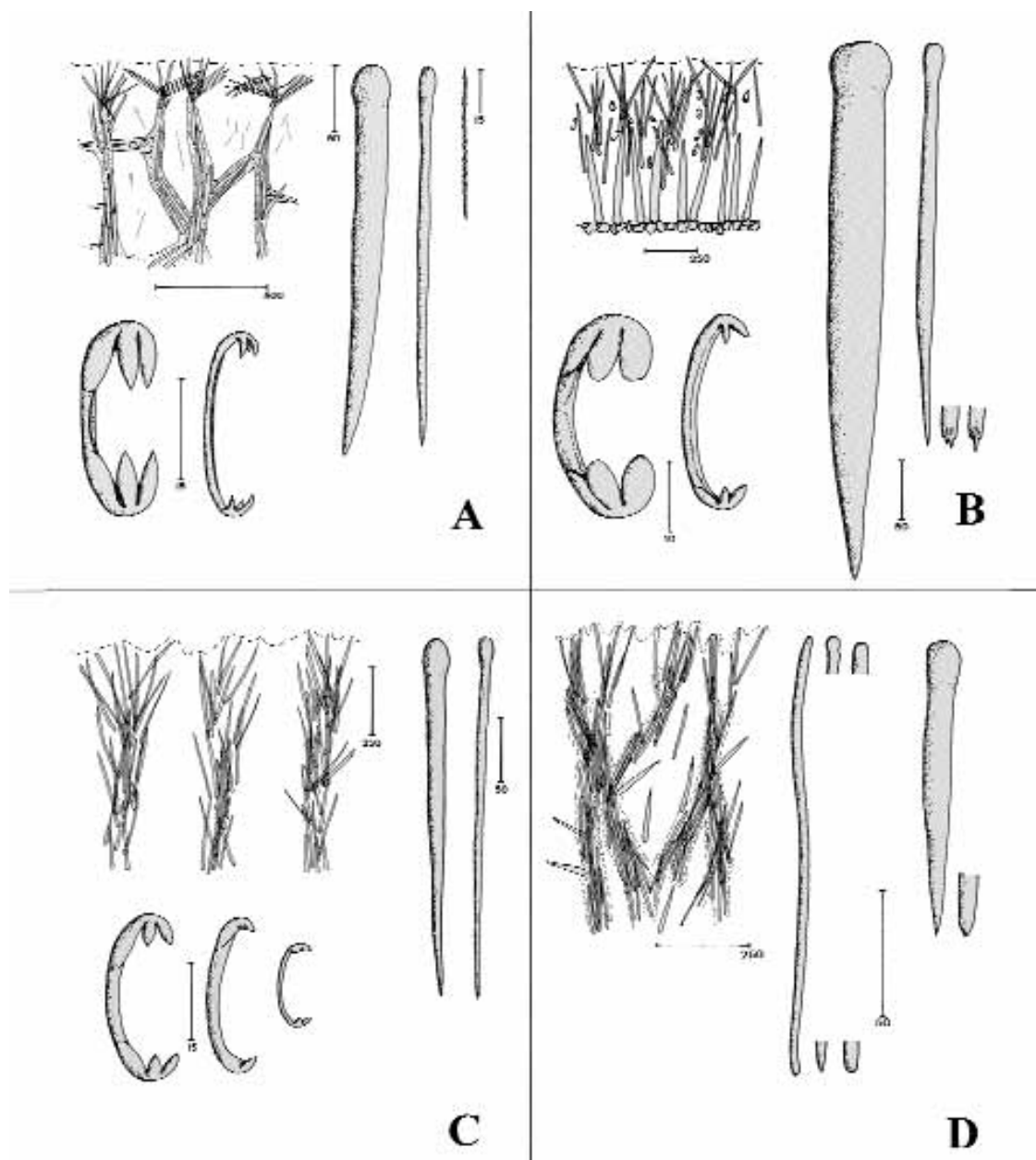


Fig. 6. A, *Monanchora clathrata* Carter (1883c), drawing of skeleton and spicules made from a slide of the type. B, *Monanchora laevissima* (Dendy, 1922b as *Hymedesmia*), type of *Folitispia* de Laubenfels (1936a), drawing of skeleton and spicules made from a slide of the type. C, *Monanchora unguiculata* (Dendy, 1922b as *Amphilectus*), type of [*Okadaia*] de Laubenfels (1936a), drawing of skeleton and spicules made from a slide of the type. D, *Monanchora enigmatica* (Burton & Rao, 1932 as *Ectyobatzella*), drawing of skeleton and spicules made from a slide of the type.

Synonymy. *Monanchora clathrata* Carter, 1883c: 369, pl. XV fig. 10.

Material examined. Holotype: BMNH 1973.12.5.1 – Fre-mantle, Bowerbank collection; two slides of the type with same number.

Description (based on a beach-worn specimen, partly after Carter, 1883c). Massive, clathrous, crumb-of-bread texture (Fig. 5A). Size $6 \times 4 \times 4.5$ cm. Colour ‘tawny’. Skeleton (Fig. 5A), a reticulation of cored spongin fibres and interconnecting spicules. Fibres up to $150 \mu\text{m}$ in diameter, cored by up to 4–5 spicules; interconnecting spicules 1–3. Spicules (Figs 5A–E, 6A), subtylostyles, 248 – (268.6) – 297×4 – (5.2) – $7 \mu\text{m}$; tylostyles, robust, smooth, with faintly developed tyle, 330 – (343.4) – 362×10 – (12.8) – $14 \mu\text{m}$;

anchorate-unguiferate chelae with 3–5 teeth, 26 – (30.8) – $36 \mu\text{m}$, reduced unguiferate chelae with spiky teeth in the same size range; microspined microxeas (Figs 5E, 6A), 36 – $57 \times <0.5 \mu\text{m}$. Distribution. Western Australia.

Remarks. The similarity with *Crambe* is strong, including similar chemistry (e.g., Braekman *et al.*, 1996; cf. also Van Soest *et al.*, 1996a), but the two genera differ in the presence or absence of desma-like spicules. A dozen species have been described. Some species of the genus are notorious for frequently lacking a full complement of spicules. For example, in *Monanchora arbuscula* (Duchassaing & Michelotti, 1864) the following combinations of shape and spiculation have been found: ramose, with conulose surface, with a full complement of megascleres and microscleres,

including spined microxeas; ramose, with conulose surface, with subtylostyles, thicker styles, reduced sigma-like chelae; ramose, with conulose surface, with anisostrogyles and thicker strongyles; thickly encrusting, with conulose surface, with full complement of spicules; thinly encrusting, with smooth surface, with subtylostyles, styles, reduced sigmoid chelae, and anchorate chelae; thinly encrusting with smooth surface, with subtylostyles, styles and reduced sigmoid chelae; and, thinly encrusting with smooth surface with subtylostyles and thicker styles, no microscleres.

The genus *Ectyobatzella* Burton & Rao, 1932 was erected for Indian Ocean *Ectyobatzella enigmatica* Burton & Rao (1932: 332) (by monotypy), a lobate sponge with irregularly conulose to digitate surface. A microscopic slide of the holotype from the Indian Museum is kept in the Natural History Museum, London, BMNH 1934.11.24.100. This contains a cross section (cf. Fig. 6D) showing a plumose-dendritic skeleton of bundles of thin strongyles enclosed partly in spongin (increasing towards the base of the sponge). The bundles fan out towards the surface without forming a special ectosomal skeleton. Thicker and shorter styles are scattered singly in the interior and echinate the bundles of strongyles. Spicules, strongyles (Figs 5F, 6D), straight, occasionally styles (Figs 5F, 6D) or with irregular ends, $162\text{--}(177.2)\text{--}189 \times 1.5\text{--}(2.6)\text{--}3.5 \mu\text{m}$; (tylo-)styles (Figs 5G, 6D), smooth, with constricted 'neck', $114\text{--}(128.9)\text{--}144 \times 4\text{--}(5.6)\text{--}7 \mu\text{m}$; no microscleres. This species is assigned to *Monanchora* on the basis of the variability observed in Caribbean *Monanchora arbuscula*, in which the morphology of the megascleres and the presence of the microscleres shows extremes from fully characteristic – including subtylostyles, tylostyles, anchorate chelae, reduced sigmatose chelae and spined microrhabds – to largely reduced with thin strongyles as the only spicules (see Van Soest *et al.*, 1996a).

The genus *Folitisa* de Laubenfels (1936a: 119) was erected for Indian Ocean *Hymedesmia laevisissima* Dendy (1922b: 81) (by original designation). Slides of the type were re-examined BMNH 1931.1.7.69a ('Sealark', RN CXXV.6). This is a thinly encrusting sponge with a transparent membrane showing irregular clusters of pores. The choanosomal skeleton is hymedesmioid (Fig. 6B) with single large styles erect on the substrate (head down) and bundles of subtylostyles carrying the ectosome. Spicules are ectosomal subtylostyles with pointed or telescoped ends, which are occasionally rugose or grooved, $240\text{--}(307.7)\text{--}364 \times 4\text{--}(5.1)\text{--}7 \mu\text{m}$, robust choanosomal tylostyles, $288\text{--}(473.5)\text{--}615 \times 15\text{--}(21.4)\text{--}27 \mu\text{m}$; microscleres are spatulate anchorate chelae and reduced chelae of similar length, not interpreted as a separate category: $26\text{--}(29.1)\text{--}31 \mu\text{m}$. It is a clear *Monanchora* lacking spined microrhabds; the hymedesmioid architecture is not sufficient grounds for retaining the genus as separate from *Monanchora*. Hooper (1996a: 45) erroneously included this nominal genus into synonymy with *Clathria* (*Microciona*).

The genus [*Okadaia*] de Laubenfels (1936a: 120) was erected for type species *Amphilectus unguiculatus* Dendy (1922b: 58) (by original designation). Examined material comprised two microscopic slides, BMNH 1921.11.7.47a, Indian Ocean, "'Sealark' sponges, #RN CXIII.10". This thinly encrusting species shows the typical simple plumose skeleton of bundles of subtylostyles (Fig. 6C), length 1–2 mm, thickness ca. 15 spicules in cross section ($50\text{--}250 \mu\text{m}$), at distances of 200–350 μm . No ectosomal specialization. Megascleres not distinguishable into two distinct categories, subtylostyles with variable sharp or blunt ends grading into each other, $284\text{--}(316.4)\text{--}350 \times 3\text{--}(4)\text{--}10 \mu\text{m}$. Microscleres reduced unguiferate chelae in two size categories which are morphologically

similar, $29\text{--}(31.3)\text{--}34 \mu\text{m}$ and $15\text{--}(18.4)\text{--}22 \mu\text{m}$. Further species assigned to [*Okadaia*] by de Laubenfels were *Esperiopsis viridis* Kieschnick (1898: 59), *E. rigida* Lambe (1892: 60), *E. vancouveri* Lambe (1892: 68), and *E. quatsinoensis* Lambe (1892: 69). [*Okadaia*] de Laubenfels was found to be preoccupied by *Okadaia* Baba (1930), and de Laubenfels (1949a: 15) replaced it by *Neoesperiopsis*; however, in the same publication he named as the type of *Neoesperiopsis*, *N. deichmannae*, a species unrelated to *Amphilectus unguiculatus* and from descriptions and studies of the type material by Hartman (1958: 45) a probable synonym of *Isodictya palmata* (suborder Mycalina, family Isodictyidae).

The genus *Neofolitisa* Bergquist (1965: 172), with type species the Philippine sponge *Monanchora dianchora* de Laubenfels (1935a) (by original designation), was erected as a 'new name' for the preoccupied *Okadaia* (cf. above), but since the two do not have the same type species, *Neofolitisa* effectively became a new genus, not merely a new name. Bergquist was reluctant to assign *A. unguiculatus* to *Neofolitisa* without having studied its type specimen. She distinguished *Neofolitisa* from *Monanchora* and *Folitisa* by the lack of differentiation in megascleres and the possession of two categories of chelae instead of one. In view of the above mentioned variability in spicule presence and form *Neofolitisa* is regarded as a synonym. The whereabouts of the type specimen of *M. dianchora* is unknown, it is not in USNM (Ms K. Smith, pers. comm.); it is a light orange-red, thickly encrusting, lamellate mass, surface irregular. Ectosomal spicules arranged tangentially, choanosomal spicules in confusion. Megascleres 'tylostyles', differentiated only in size, in the ectosomal region they measure approx. $283 \times 4 \mu\text{m}$, in the choanosome $270\text{--}370 \times 5\text{--}9 \mu\text{m}$; microscleres anchorate unguiferate chelae of $33 \mu\text{m}$ and reduced unguiferate chelae with three minute teeth of $20 \mu\text{m}$. *Folitisa pingens* de Laubenfels (1954: 159) is a junior synonym of this species.

The genus *Fasubera* de Laubenfels, 1936a: 119 was erected for type species *Hymedesmia lipochela* Dendy, 1922b: 82, pl. 6 fig. 3, pl. 15 fig. 2 (by original designation), from Cargados Carajos in the Western Indian Ocean. Slides of the holotype (BMNH 1931.11.7.70) were reexamined. This is an irregularly lobate ('cauliflower') sponge, with few small oscules. The skeleton consists of lax spicule bundles and a lot of coarse sand. Dendy's contention that the sand is organized as part of the skeleton cannot be confirmed, but individual spicule tracts arise from these concentrations of sand and they are 'echinated' by the spicules. At the surface the spicule bundles fan out and form characteristic bouquets. Megascleres subtylostyles $280\text{--}396 \times 2\text{--}7 \mu\text{m}$, thick (tylo-)styles with swollen heads, $306\text{--}430 \times 12\text{--}18 \mu\text{m}$, and microscleres (not described by Dendy) thin spined microxeas, up to $30\text{--}42 \times 0.5 \mu\text{m}$. Despite the lack of chelae, this species appears to be a clear *Monanchora*, based on the characteristic spiculation, including the spined microxeas. Accordingly, *Fasubera* is assigned to *Monanchora* as a junior synonym. Amorphoclada Topsent, 1930 was erected (designation herein) for type species *Chondrocladia alaskensis* Lambe, 1894: 119, together with a second species *C. pulchra* Lambe, 1894. This is a junior synonym of *Monanchora*.

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