Family Dictyonellidae Van Soest, Diaz & Pomponi, 1990

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Dictyonellidae Van Soest et al. (Demospongiae, Halichondrida) are sponges with fleshy appearance, lacking a special surface skeleton of spicules. The spicular density is often relatively low and skeletons consist of ill-defined bundles following a dendritic pattern or making an irregular reticulation. Spongin may be important as binding substance. Spicules comprise usually long, often somewhat flexuous styles, occasionally strongyles, oxeas or oxeote derivations, but shorter straight styles are not uncommon. Characteristically, spicule endings are variable and often telescoped. Dictyonellidae are cosmopolitan in occurrence, but are more common in warmer waters. Compared with the original contents, the family has been here extended to include Phakettia, Stylissa and Svenzea, and now comprises ten valid genera (out of 17 nominal genera).

**Keywords:** Porifera; Demospongiae; Halichondrida; Dictyonellidae; Acanthella; Dictyonella; Liosina; Lipastrotethya; Phakettia; Rhaphoxya; Scopalina; Stylissa; Svenzea; Tethyspira.

**DEFINITION, DIAGNOSIS, SCOPE**

**Synonymy**

[Acanthellidae] Carter, 1885d: 364 as Acanthellina (to be suppressed under ICZN Article 23.9.1 as an unused name, not having been used after 1899 and the junior name in frequent use in the last 50 years and longer than 10 years prior to this publication). There is also a genus [Acanthellina] Carter, 1885d which is considered a nomen oblitum (cf. below), which is a further reason not to use Carter’s family name. Dictyonellidae Van Soest, Diaz & Pomponi, 1990: 20.

**Definition**

Halichondrida without ectosomal skeleton, but with dense organic ectosomal layer, giving the sponge a fleshy appearance; choanosomal skeleton is predominantly built of styles, occasionally oxeas or strongyles occur.

**Diagnosis**

Encrusting, massive, lobate, digitate, bushy or columnar-tubular sponges, usually with a conulose surface. Between conules, the surface is shiny-smooth and distinctly fleshy. Ectosomal skeleton is entirely absent. If attempts are made to make a tangential section, the surface comes off in flakes. Choanosomal tracts and individual spicules directed towards the surface, often collected in vague tracts or more definitely in spongin enforced spiculofibre. Irregularly reticulate or confused skeletal arrangements are not uncommon. Spicular density is relatively low compared to other Halichondrida. Spicules predominantly styles, often of considerable length and then flexuous or curved. Occasionally oxeas or strongyles occur. Telescoped endings are common. Ten genera are considered valid of seventeen nominal genera. The family occurs in all three ocean basins, but appears absent from the colder regions.

**Scope**


**TAXONOMIC HISTORY AND BIOLOGY**

The family was only recently erected in an attempt to rearrange the genera assigned to the former orders Axinellida and Halichondrida sensu Lévi, 1973, which was necessary because of the increased awareness that these groups as then understood were clearly polyphyletic (Van Soest et al., 1990; Diaz et al., 1991; Pomponi et al., 1991; Diaz et al., 1993; Alvarez, 1998). Abandonment of a separate order Axinellida and revision of the families Halichondridae and Hymeniacidonidae yielded a proposal for an order Halichondrida sensu lato comprising four families, Axinelliidae, Desmoxyidae, Halichondriidae and a new family Dictyonellidae (Van Soest et al., 1990). Since these families were newly defined, the generic content has been under constant debate and rearrangements have been proposed in the recent literature up to and including this volume. Further challenges of the adopted classification of the order Halichondrida and its families may be expected from the newest DNA sequence results (Chombard et al., 1999; Alvarez et al., 2000a). However, until sponge DNA data have gained sufficient powers of conviction (e.g., multi-gene analyses), we propose to leave the family classification intact. Dictyonellidae are clearly differentiated from Halichondriidae in the absence of a surface skeleton and the presence of some degree of organization of the choanosomal skeleton (lacking in Halichondriidae). From Axinelliidae it is differentiated by the fleshy surface appearance (velvety in Axinelliidae produced by the close-meshed endings...
of the choanosomal skeleton). From Desmoxyidae they are differentiated by the absence of a surface skeleton of (spined) spicules and also the fleshy surface appearance. Compared to Van Soest et al.'s contents of the family, the genera Phaketta, Stylissa, and Svensea have been added in this current revision; [Dactylella] was found to be preoccupied and is replaced by its junior synonym Lipastrotethya.

**KEY TO GENERA**

(1) Surface muddy-sandy with fine grooves making a polygonal surface pattern ......................................................... *Liosina*
   Surface not muddy and grooved ................................................................. 2

(2) Spicules include sinuously bent strongyles or strongyloxeas ................................................................. *Acanthella*
   Spicules may be flexuous but are not bent twice in opposite directions ................................................................. 3

(3) Spicules include oxeeas or oxoeeas ................................................................. *Stylissa*
   Spicules exclusively styles ........................................................................ 5

(4) Skeleton lax, low spicular density, spicule length less than 650 μm ........................................................................... *Rhaphoaxia*
   Skeleton dense, with high spicular density and, spicules over 650 μm ................................................................. *Lipastrotethya*

(5) Next to long thin smooth styles there are (often rare) short spined styles ................................................................. *Phaketta*
   No spined styles ......................................................................................... 6

(6) Encrusting with styles arranged in dendritic fibres originating from a basal spongian plate ........................................... *Scopalina*
   Growth form massive or erect. Styles differently arranged ......................................................................................... 7

(7) Styles arranged in sheets or columns with considerable spongian ................................................................................... 8
   Styles arranged in a reticulation or intercrossing in confusion ....................................................................................... 9

(8) Surface smooth, glistening, bluntly conulose, consistency fairly soft ................................................................. *Dictyonella*
   Surface bristly, consistency hard .................................................................... 10

(9) Reticulation unispicular, regular ................................................................................................. *Svensea*
   Reticulation vague, often somewhat confused ................................................................. *Stylissa*

**ACANTHHELLA SCHMIDT, 1862**

**Synonymy**

*Acanthella* Schmidt, 1862: 65.

**Type species**

*Acanthella acuta* Schmidt, 1862: 65 (by subsequent designation; Vosmaer, 1912: 312).

**Definition**

Dictyonellidae with choanosomal skeleton of dendritic tracts cored by interwoven sinuously bent strongyles or strongyloxeas and echinated by straight styles, oxeeas or oxoeeas.

**Diagnosis**

Erect, bushy, ramose, lamellate or lobate habit. Surface generally coarsely conulose with protruding choanosomal spicules. Ectosome membranous, glistening in appearance, without specialised skeleton. Consistency cartilaginous-like when alive. Choanosomal skeleton with thick tracts or axes of interwoven strongyles or strongyloxeas, sometimes condensed in the axial region, dendritically branching toward the periphery and ending in conules at surface; reduced to single spicules in some thinly branching forms. Megascleres doubly flexed and sinuously curved strongyles, sometimes strongyloxeas, always coring main spicules tracts; straight styles, oxeeas or oxoeeas in any combination, echinating main tracts; microscleres absent. Distribution. According to Van Soest (1994) the genus has a widespread distribution. A total of 22 species of *Acanthella* are recorded in the literature from the following areas: Central-West Atlantic, Mediterranean Sea, Indian Ocean, Australia, New Zealand, New Caledonia and Japan, (Alvarez 1998).

**Remarks**

*Acanthella* has been referred to Axinellidae by contemporary authors (e.g., Bergquist, 1970; Lévi, 1973; Hooper & Lévi, 1993b; Alvarez et al., 1998; Alvarez et al., 2000a) who adopted vague definitions of the genus with elements such as the presence of an axial skeleton, typical of members of the family Axinellidae. Consequently, *Acanthella* has been confused with other axinellid genera such as *Phakellia*, and contains a heterogenous complex of species. *Acanthella sensu stricto* does not fit in the revised definition of Axinellidae (see chapter on Axinellidae) and therefore it is allocated to Dictyonellidae, as suggested by Van Soest et al. (1990). The habit and skeletal organisation of the type species is quite distinctive, sharing with other dicyonellid genera such as *Dictyonella* and *Scopalina*, the dendritic nature of the choanosomal skeleton, with a central axial column producing dendritically branching spicule tracts and thinning toward the periphery, and the fleshy appearance of the surface.

**Previous reviews**

Vosmaer (1912); de Laubenfels (1936a); Lévi (1973); Van Soest et al. (1990); Hooper & Lévi (1993b).

**Description of type species**

*Acanthella acuta* Schmidt, 1862 (Fig. 1A–E).

**Material examined.** Lectotype: BMNH 1867.7.26.66 – Sebenico, Adriatic. Other material, ZMA POR. 14589 – NW Spain, SYMBIOSPONGE 98/SP/APR12/RG/024, depth 16 m, coll. R. Gomez.

**Description.** Bush-shaped, type specimen approximately 12 cm wide and 13 cm high; on short peduncle; surface conulose; marked with thick spicule tracts and covered with tough and smooth skin-like collagenous membrane. Oscules not seen; colour...
dark orange alive, brown-orange in dry state; consistency firm (cartilage-like when alive) (Fig. 1A–B). Specialised ectosomal skeleton absent; choanosomal skeleton with ascending, thick (up to 500 μm) and dendritic axes of sinuous strongyles plumo-echinated by styles, becoming thinner towards periphery; axial and extra-axial skeleton not differentiated (Fig. 1C). Sinuous strongyles (Fig. 1D), 640–1490 × 5–13 μm; flexuous and straight styles, 970–2150 × 8–15 μm (Fig. 1E). Distribution and ecology. The species is restricted to the Mediterranean, found often between 40–100 m depth, in shallow and dark habitats, on sandy or coralline substrate (Uriz, 1982).

**Type species**

*Dictyonella cactus* Schmidt, 1868: 10 (by subsequent designation; de Laubenfels, 1936a: 139) (=junior synonym of *Acanthella obtusa* Schmidt, 1862: 65).

**Definition**

Dictyonellidae with long styles in anastomosing and diverging bundles progressively thinning out towards the surface.

**Diagnosis**

Thick-lobed bushes or irregular massive sponges with shiny smooth surface covered with blunt ridges and conules. Ectosomal skeleton absent, choanosomal skeleton consisting of anastomosing and diverging spicule bundles arranged lengthwise in the lobes and branches. Spicules long, often curved or flexuous styles. Little spongin. Approximately 15 species spread over the warmer seas of the world.
Remarks

Due to Schmidt’s poor definition and description, this genus was not employed until Topsent (1938a) redescribed the type. Prior to him, Vosmaer (1887, 1935) gave an erroneous interpretation to it and few authors used the name. Of the five specimens of the original Dictyonella collection from Algiers, only the specimen labeled ‘no. 10’ appeared with certainty to conform to Schmidt’s description. The second species of Dictyonella described by Schmidt (1868) along with D. cactus, viz., Dictyonella labyrinthica, is a specimen of Myxilla prouhoi according to Topsent (1938a). In addition to the type specimen mentioned above, there is a microscope slide in MNHN registered as DT. 940 (Desqueyroux-Faúndez & Stone, 1992). A slide in BMNH 1867.3.11.77 labeled ‘Acanthella obtusa 49 Adriatic’ clearly contains spicules of Acanthella acuta. Type material proper of Acanthella obtusa appears to be lost. It is proposed here to assign above mentioned lectotype specimen of Dictyonella as the lectotype of Acanthella obtusa.

The genus Phacantha Vosmaer (1912: 313, pl. 16 figs 1–2) was erected for type species Acanthella obtusa Schmidt, 1862 (original designation). Since this is considered the senior synonym of the type species of Dictyonella, Phacantha becomes an objective synonym.

The genus Perisinella Topsent (1928c: 171) was erected as a subgenus of Stylotella for type species (by monotypy) Stylotella madeirensis Topsent (1928c: 170, pl. II fig. 12, pl. VI fig. 13). This East Atlantic species forms a yellowish mass of digitations on a conical basis, 12 cm high, 11 cm in diameter (Fig. 2G). The skeleton consists of spongin-encased dendritic spicule tracts forming an irregular meshwork. No ectosomal skeleton. Spicules (Fig. 2H) are a mixture of styles, subtylostyles and occasional tylostyles, 400–700 μm.

Carballo et al. (1996) assigned D. madeirensis to the genus Scopalina, based on the abundant spongin, shared with Scopalina lophyropoda (cf. below). However, in view of the thinly encrusting habit and solitary, non-anastomosing fibres of Scopalina this is considered erroneous.

The genus Stylotella Lendenfeld (1888) was used for sponges answering to the present concept of Dictyonella by many authors prior to Topsent’s (1938a) redescription and redefinition of the genus. Stylotella is a junior synonym of Hymeniacidon (Halichondriidae) as it possesses a tangential skeleton and the spicules are small styles (see chapter on Halichondriidae).

Several members of Dictyonella, e.g., D. incisa (Schmidt, 1880a), D. marsilii (Topsent, 1893c), were assigned to the genus Rhaphidostyla Burton (1935b), but the type species R. kitchingi Burton, 1935b is a Hymeniacidon (see chapter on Halichondriidae).

Previous review

Topsent (1938a).
Description of type species

**Dictyonella obtusa** (Schmidt, 1862) (Fig. 2A–F).

**Synonymy.** **Acanthella obtusa** Schmidt, 1862: 65, pl. VI fig. 8. **Dictyonella cactus** Schmidt, 1868: 10. **Phakella plicata** Schmidt, 1889a: 282.

**Material examined.** Lectotype (designated by Topsent, 1938a: 9): MNHN unregistered – labeled ‘No. 10. Exp Algerie’. BMNH slide 1868.3.2.27 – labeled ‘Algiers’ (this contains just a few broken spicules, probably from fairly long styles).

**Description.** Lobate or leafy bushes (Fig. 2A–B) of up to 7 cm high (lectotype is 5 cm high); smaller specimens may be massive-lobate. Colour red alive, pale violet in alcohol. There is a distinct thick organic ‘skin’, stretched over the endings of the choanosomal spicule tracts. This comes off in flakes (Schmidt states ‘Oberhaut lässt sich in Fetzen abziehen’). The choanosomal skeleton consists of bundles of megascleres (Fig. 2C, F) that are generally directed upwards toward the periphery, but they anastomose and diverge along the way in a loose manner. The bundles thin out towards the surface where they may form low conules. Binding spongin is visibly present especially in the interior. Spicules (Fig. 2D–E) long flexuous styles, occasionally with strongylote or telescoped endings, up to 1700 /\mu m long. The choanosomal spicule tracts. This comes off in flakes (Schmidt, 1880a: 282). The muddy appearance and the mud particles form an easily detachable crust of thin-walled shallow grooves. Mud particles enclosed in sponge tissue form a dense surface cover and also penetrate into the interior. Spicules relatively low in density, irregularly arranged into bundles which are bound by variable amount of spongin. Spicules may be both monactinal and diactinal. So far, only two species have been assigned to this genus, both widespread in the Indo-West Pacific.

**Remarks**

The muddy appearance and the mud particles form an easily recognizable feature of this species, and they are also found in the species originally described as *Laxosuberes arenosae* by Vacelet & Vasseur (1971), which however has tylostyles. Nevertheless, this species is reassigned to *Liosina*. The family and class assignment of this genus remains tentative in the absence of any definite synapomorphies with either *Halichondrida* and *Poecilosclerida*. The possession of irregularly arranged oxeotes in a low density and the occurrence of monactinal spicules in a species showing strong overall similarities with the type species both point towards *Halichondrida*, and within that order, to *Dictyonellidae*. Future studies using non-morphological characters need to confirm this.

The genus *Migas* Sollas, 1908 was erected for type species (by monotypy) *Migas porphyrion* Sollas (1908: 395, figs 1–3) from Mozambique. The type material could not be found, but from the description it is clear that it belongs to *Liosina*. With the surface ornamentation and foreign material inclusion, and oxeas of 960 /\mu m, it is very close and probably identical to *Liosina paradoxa*. Thus, *Migas* Sollas is a junior synonym of *Liosina* (see also de Laubenfels, 1936a: 54). De Laubenfels, 1954, however, discovered that *Migas* Sollas, 1908 was preoccupied by Migas Koch, 1873 (Arachnida). He had apparently forgotten that he synonymized *Migas* Sollas with *Liosina* in 1936, and erected the genus *Milene* de Laubenfels, 1954: 116 with *Migas porphyrion* as the type species (by original designation). *Milene*, thus becomes an objective synonym of *Liosina*.

**Liosina paradoxa** Thiele, 1899 (Fig. 3A–E).

**Synonymy.** *Liosina paradoxa* Thiele, 1899: 17, pl. 2 fig. 5, pl. 4 fig. 4, pl. 5 fig. 9. *Migas porphyrion* Sollas, 1908: 395; *Milene porphyrion* de Laubenfels, 1954: 116.

**Material examined.** Holotype: NMB 22 – Celebes, Sarassin collection. Other material. Many topotypical specimens, including: ZMA POR. 14478, SYMBIOSPONGE 98/SS/APR29/BH/031 – off Langkai Island, SW Sulawesi, 4 m, coll. B.W. Hoeksema.

**Description.** The holotype (Fig. 3A) is an upright mass (which is likely to be part of a tube), topotypical and other specimens are clusters of thick-walled tubes with narrow apical openings. The surface has a characteristic polygonal pattern of grooves and ridges (Fig. 3B). Grooves consist of thin lines connecting small rounded openings. Colour muddy grey or whitish grey, with an orange interior shining through the grooves and openings. Consistency firm, but easily damaged. Ectosomal region a crust of reddish brown, peculiar-looking mud particles enclosed in sponge tissue membranes. The ectosomal mud particles form a dense layer of about 1 mm thickness through which may protrude bundles of spicules or individual spicules (Fig. 3E). No special ectosomal skeleton. The choanosome likewise has a high density of mud particles, partly covering and engulfing irregular bundles of spicules, which are bound by considerable spongin. Bundles vague in outline and of indefinite width. Loose spicules abound, but spiculation has an overall low density. Spicules (Fig. 3C–D) with mostly rounded ends, basically oxeas, but stylostyles forms not infrequent, in a wide size range: 360–900 × 8–20 /\mu m. No microscleres. Distribution and ecology. Indo-West Pacific, widespread, common; shallow-water, on reefs and in lagoons and bays.

**Lipastrotethya de Laubenfels, 1954: 235**

**Type species**


**Definition**

Dictyonellidae with exclusively oxeas or derivates thereof.

**Diagnosis**

Digitate sponges with microhispid, finely grooved surface. Ectosomal skeleton absent. Choanosomal skeleton a bundled mass of oxeas. No microscleres.

**Remarks**

This species sounds close to *Dictyonella* on paper, but in that genus the spicules are invariably styles or monactinal derivatives. Also, spongin is usually abundantly present. On paper it also sounds close to *Axinysa* Lendenfeld, 1897 (family Halichondriidae), but in that genus the spicules are confusedly arranged, lacking a vertical orientation.

The characters of this sponge conform to *Dactylella* Thiele and *Lipastrotethya* would seem a junior synonym. The type species (by monotypy) is *Dactylella hilgendorfi* Thiele, 1898: 56, pl. 4 fig. 8, pl. 5 fig. 25, pl. 8 fig. 41a–b. A fragment of the holotype ZMB 920a from Hokodate, Japan and a further fragment of holotype BMNH 1908.9.24.143 were reexamined. From a shared base arise 4–5 finger-shaped projections (Fig. 4B), about 4 cm long, 1.5 cm diameter. The fingers may have lateral lobes. The ends of the projections are distinctly grooved, and grooves converge into an apical oscule. Surface slightly rugose, microhispid due to projecting spicule bundles. The colour is pale brown in preserved condition. Consistency firm. No ectosomal skeleton. Choanosomal skeleton (Fig. 4D) a mass of bundles of aligned spicules traversing the centre of the projections and diverging outwards. High spicular density, little spongin. Spicules (Fig. 4C) oxeas, straight or slightly curved, 1000–1600 × 20–25 μm. Thiele states they are not infrequently flexuous, but in the fragment examined this is hardly the case. Also the proportion of stylotes is negligible. A second record
of Dactylella is from the Caribbean, D. rhaphoxea de Laubenfels, 1934. It conforms in some detail to D. hilgendorfi, but has a much larger range of spicule sizes, including small ectosomal oxeas. Its identity should be further studied.

This genus [Dactylella] Thiele is preoccupied by [Dactylella] Gray, 1873: 461, which was erected for type species Tethya dactyloidea Carter, 1869a: 15, figs 1–4 from the SE coast of Arabia (by original designation). This is undoubtedly a member of Tetillidae, because Carter described a radiate structure and oxeas and protriaenes as megascleres. No certainty exists about the presence of sigmaspires, because Carter had ‘given away the specimen’ (to Dr Bowerbank, cf. Carter, 1871: 103). In view of the absence of clear porocalyces and apparent lack of a cortical skeleton, this is likely to be a Tetilla. Since the name Dactylella predates Tetilla it needs to be suppressed as an unused name in the sense of ICZN article 23.9. The name has not been used for a tetillid sponge after its original proposal, although subsequently, [Dactylella] was also used by Thiele, 1898 for a sponge in the family Dictyonellidae (now considered preoccupied, and replaced by Lipastrotethya de Laubenfels, 1954). The name Tetilla has been frequently used in the past 50 years by many authors, and thus fulfills the demands for continued usage under ICZN Article 23.9. But, the subsequent use by Thiele of [Dactylella] for a dictyonellid sponge is nevertheless against ICZN rules and it has to be replaced by the present genus name.

**Previous review**

Thiele, 1898 (as [Dactylella]).

**Description of type species**

*Dactylella ana* de Laubenfels, 1954 (Fig. 4A).

**Synonymy.** *Dactylella ana* de Laubenfels, 1954: 235, fig. 162.

**Material examined.** Holotype: USNM 23094 (fragment) – Truk Atoll (Chuuk State), Federated States of Micronesia.

**Description (after de Laubenfels, 1954).** The species is described as an irregularly rounded mass of up to 6 × 8 × 16 cm, golden brown in colour with a slightly greenish, cartilaginous subcutaneous layer. Surface tuberculate. Skeleton consists of ill-defined bundles of oxeas arranged perpendicular to the surface and ending in the surface tubercles. The ectosomal region is described as corticate by de Laubenfels, but this is not a cortex in the usual sense: rather it is an ectosomal layer containing special granular cells and ?calcareous nodules. The spicules (Fig. 4A) are symmetrical oxeas, although some of them are blunt-ending at both sides; they are curved, and occasionally flexuous; in a wide size range, up to 850 × 25 μm. They are clearly not strongyloxeas as de Laubenfels maintained, and the resemblance to *Tethya* megascleres he made is absent. Distribution. Chuuk, Central Pacific, shallow water.

**PHAKETTIA DE LAUBENFELS, 1936**

**Synonymy**

*Phakellia* de Laubenfels, 1936a: 130.

**Type species**

*Phakellia cactoides* Burton, 1928b: 127 (by original designation).

**Definition**

Dictyonellidae with a central region of long styles aggregated in a confused and dense mass, from which they radiate, sometimes in thick bundles, to the periphery and project through the surface.

**Diagnosis**

Erect on broad base or short stems, bushy or with coalescent lobes. Surface bristly. Ectosomal skeleton absent. Choanosomal skeleton with a central region of styles aggregated in a confused and dense mass from which other styles, sometimes in thick bundles radiate to the periphery. Megascleres are only long styles. According to de Laubenfels (1936a) it is widespread, but species assignments need to be verified. The type species is from the Indian Ocean.
Remarks

Several species of *Phakellia* (i.e., *Phakellia beringensis* Hentschel, 1929: 975, *P. bowerbanki* Vosmaer, 1885a: 24, *P. crassa* Carter, 1885d: 363, *P. conulosa* Dendy, 1922b: 116, *P. dalli* Lambe, 1894: 125, *P. fusca* Thiele, 1898: 51, *P. papyracea* Ridley & Dendy 1886: 478, *P. ridleyi* Dendy, 1887: 159; *P. tumida* Dendy, 1897) were referred to *Phakettia* by de Laubenfels (1936a). The assignment of these species to *Phakettia* however, must be revised, as in most cases, they do not fully agree with the definition proposed here. Hooper & Lévi (1993b) included *Phakettia* in synonymy with *Rhaphoxya*, but this is not accepted here, with the two respective type species showing significant differences in their spicule geometry (long styles vs. anisoxeas and styles) and structure (confused central mass with radial periphery vs. halichondrioid with loose wavy anastomosing tracts ascending to the periphery).

Previous reviews

De Laubenfels (1936a); Wiedenmayer (1989).

Description of type species

*Phakettia cactoides* (Burton, 1928b) (Fig. 5A–C).

**Synonymy.** *Phakettia cactoides* Burton, 1928b: 127, pl. I figs 6–8.

**Material examined.** Holotype: BMNH 1926.10.1.38 – wet. Paratype: BMNH 1926.10.1.33 – labeled ‘Co-type, RN. VII (Pars), donated by the Indian Museum’.

**Description.** Bushy, lamellate or lobate on a broad base. The type series apparently consisted of three specimens (Fig. 5A). The holotype (Fig. 5A, left specimen) is 2.5 cm high. Colour in life unknown, beige in alcohol. Surface hispid, due to the projection of single spicules or spicule tracts from the choanosomal skeleton with smooth depressions as channels running longitudinally through the length of the specimen. Consistency hard; fleshy appearance. Ectosomal skeleton absent. Choanosomal skeleton formed by long styles aggregated in a confused and dense mass in the central region of the skeleton (Fig. 5B). From the central skeleton single styles or thick bundles radiate in all directions to the periphery and project through the surface. Megascleles exclusively smooth styles (Fig. 5C), 1850–2800 μm. Distribution and ecology. Bay of Bengal, Indian Ocean, 174 m.

**RHAPHOXYA HALLMANN, 1917**

**Synonymy**


**Type species**

*Rhaphoxya typica* Hallmann, 1917c (by original designation).

**Definition**

Dictyonellidae with anisoxeas and styles, single or in loose wavy and anastomosing bundles, ascending towards the surface and reinforced with spongin.

**Diagnosis**

Massive to thickly flabellate; surface shiny and conulose. Ectosome fleshy without special skeleton. Choanosome cavernous with a lax skeleton of wavy and anastomosing bundles of spicules reinforced with spongin. Spicules are anisoxeas and styles with telescoped ends. Raphides and trichodragmata may be present. Distribution of the genus exclusively Australia. Seven nominal species.

**Remarks**

The genus has been referred to Axinellidae by other authors (e.g., Bergquist, 1970; Wiedenmayer, 1989; Hooper & Lévi, 1993b); however, as Hooper and Lévi (1993b) admitted, the genus is atypical for that family. Based on its close similarity to dictyonellid genera such as *Dictyonella* and *Scopalina*, it is transferred here to the Dictyonellidae. *Raphoxya* shares with other dictyonellids the type of spicules and the presence of bundles of spicules reinforced with spongin or, spongin fibres cored with spicules, single or in loose tracts. The presence of long raphides (or thin oxeas) with rudimentary spination in the type of *Raphoxya* may be peculiar to the type species and not a diagnostic feature to define the genus.

[Acanthellina] Carter, 1885d was erected for type species (by monotypy) *Acanthellina rugolinatea* Carter, 1885d: 365 (Fig. 6D–F) from South Australia. The genus was considered a junior synonym of *Acanthella* by de Laubenfels (1936a). Bergquist
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(1970: 18), however, considered its type species to belong in *Rhaphoxya*. The genus was later declared a *nomen oblitum* under the 50 year rule of the ICZN by Wiedenmayer (1989: 50) (also in Hooper & Lévi, 1993b: 1441; Hooper & Wiedenmayer, 1994: 82), and we propose here to follow this course (ICZN article 23.9.1; Anon., 1999). The skeleton (Fig. 6E) and other features are in agreement with the definition of *Rhaphoxya* as employed here. The genus includes seven species (i.e., *Rhaphoxya cactiformis* Carter, 1885a: 114, *R. felina* Wiedenmayer, 1989: 52, *Rhaphoxya pallida* Dendy, 1897: 257, *R. rugolineata* Carter, 1885d: 365 (junior synonym of *R. cactiformis* according to Bergquist (1970) and Wiedenmayer (1989)), *R. solida* Carter, 1885d: 362 and *R. typica*.

**Previous reviews**

Hallmann (1917c); de Laubenfels (1936a); Bergquist (1970); Wiedenmayer (1989); Hooper & Lévi (1993b).

**Description of type species**

*Rhaphoxya typica* Hallmann, 1917c (Fig. 6A–C).

**Synonymy.** *Rhaphozya typica* Hallmann, 1917c: 643. fig. 1, pl. 29 fig. 3, pl. 38 figs 8–9, pl. 39 fig. 5, pl. 42 figs 1–2.

**Material examined.** Holotype: AM Z1595 – wet, Port Phillip, Victoria, Australia.

**Description.** Massive; holotype fragmented into nine pieces, 2–10 cm of maximum diameter (Fig. 6A); surface with shallow (3.5 cm deep) and narrow (4.5 cm wide) grooves and scattered conuli-papillae 1 mm high. Ectosome membranous, detachable, reticulated with circular-ovoid meshes, 100–200 μm in diameter; colour brown in alcohol; consistency firm. Ectosomal skeleton absent. Choanosomal skeleton halichondrioid (Fig. 6B) with single spicules, in bundles or in vague tracts ascending towards surface or irregularly positioned, enveloped by sheaths or slightly developed fibres of spongine. Megascleres (Fig. 6C) are flexuous anisoxeas with telescoped ends of different shapes, and less frequent styles; length 320–620 μm, width 5 μm. Also raphides, single or in trichodragmata (Fig. 6C, right), smooth or microspined, some with crenulate ridges and small tubercles. Distribution and ecology. Eastern and southern Australian waters (Hooper & Wiedenmayer, 1994).

**SCOPALINA SCHMIDT, 1862**

Synonym

**Type species**

*Scopalina lophyropoda* Schmidt, 1862: 79 (by monotypy).

**Definition**

Encrusting Dictyonellidae with conulose surface caused by prominent dendritic spongin fibres cored by long styles. Basal spongin plate. Consistency soft.

**Diagnosis**


**Remarks**

*Scopalina lophyropoda* is a characteristic species and similar forms are common in all three ocean basins. In the Mediterranean-Atlantic area, at least three species appear to exist: *S. lophyropoda*, *S. azurea* Bibiloni, 1993 and an unnamed species from Canary Islands (Cruz, 1986, pers. comm.). Carballo et al. (1996) erroneously assigned *Dictyonella madeirensis* to *Scopalina* (see above). The common West Indian *Scopalina ruetzleri* (Wiedenmayer, 1977b) was originally assigned to *Ulosa* de Laubenfels, 1936a, but that mycalid genus has a reticulate skeleton quite unlike *Scopalina*. The grainy appearance of the choanosome is characteristic of at least *S. lophyropoda*, *S. ruetzleri*, and the Indo-Pacific *S. australiensis* (Pulitzer-Finali, 1981), and thus may be diagnostic.

The genus *Hoplochalina* Lendenfeld, 1887c: 822 was erected for type species *H. incrustans* Lendenfeld, 1887c: 823 (subsequent designation by Van Soest, 1980: 118; confirmed by Hooper & Wiedenmayer, 1994). The type species designation is based on the fact that it is the first species mentioned by Lendenfeld, but it is admittedly rather unfortunate, as the genus definition given by Lendenfeld and the other species described by him (*H. dendrilla*, *H. tenella*, and *H. renieroides*) are unlike *H. incrustans*. De Laubenfels (1936a: 138) clearly adopted a different view of *Hoplochalina*, emphasizing the possession of oxeas, rather than styles. However, de Laubenfels did not make a type species designation, so his remarks are invalid. The type of *Hoplochalina incrustans* was described as a conulose rosy-red crust, 4 mm in height, with conules of 1.5 mm high. A slide of the type of *H. incrustans* BMNH 1886.8.27.521 from Port Jackson was re-examined and found to conform closely to *Scopalina*, including dendritic spongin fibres of approximately 200 μm diameter, containing tracts of long styles, 600 × 10 μm, and the grainy appearance of the choanosome. It may be close, and even conspecific with *Dictyonella australiensis* Pulitzer-Finali, 1981.

**Description of type species**

*Scopalina lophyropoda* Schmidt, 1862 (Fig. 7A–E).

**Synonymy.** *Scopalina lophyropoda* Schmidt, 1862: 79, pl. VII fig. 18.

**Material examined.** Lectotype: LMJG 15117 – Sebenico, Adriatic. Other material. Several totopypical specimens including: ZMA POR. 14434 – NW Spain, SYMBIOSPONGE 98/SP/APR12/MK/028, 9 m, coll. M.J. de Kluijver.
Porifera • Demospongiae • Halichondrida • Dictyonellidae

**Description.** Thinly encrusted with characteristic sharp conules. In life the orange to dark red sponges appear fleshy, pumped up, but in preserved or dry condition the sponge collapses to form pale beige, fleshy crusts. Surface layer without spicules, thickly organic with characteristic grainy appearance caused by clusters (20–40 μm in diameter) of pigment granules. Choanosomal skeleton consists of spongin fibres rising up from a basal spongin plate covering the surface. The fibres consist of layered spongin with a central core of 1–4 spicules. Fibre system dendritic, i.e., they are singly rising towards the periphery or are subdividing, but do not anastomose. Length of fibres at least 1 mm, frequently longer when subdividing, lying at distances of 200–500 μm. Spicules styles, flexuous, often curved in the lower half, 950–1200 × 12–15 μm. Distribution and ecology. Mediterranean-Atlantic, possibly extending as far south as the Cape Verde Islands.

**STYLISSA HALLMANN, 1914**

**Synonymy**

*Styliella* Hallmann, 1914: 349.

**Type species**

*Stylorella flabelliformis* Hentschel, 1912: 355 (by original designation).

**Definition**

Dictyonellidae with a skeleton consisting of styles arranged in a confused plumose reticulation, with many single spicules in confusion. Styles in a single size category.

**Diagnosis**

Erect, flabellate, or compressed-lobate sponges with irregularly conulose and/or ridged surface. Conules blunt. Surface smooth between conules often with a slight colour difference between smooth and conulose parts. Colours usually red, orange or yellowish. Skeleton confused, but some plumose reticulation usually recognizable. In the interior and in the stem of erect forms there is axial condensation. Styles curved, usually stout, relatively short and of a single size category. Several species are common in the Indo-West Pacific, one is recorded from the Caribbean.

**Remarks**

Hallmann (1914) erected this genus because *Stylorella flabelliformis* did not agree with his definition of *Stylorella*. The latter genus is now considered a junior synonym of *Hymeniacidon* (family Halichondriidae), as its type species has a tangential ectosomal skeleton. De Laubenfels (1936a: 130) related *Styliella* to *Homaxinella* based only on the presence of styles. *Homaxinella* is now considered a suberitid. *Styliella* was revived by Hooper & Lévi, 1993b for the type species *S. flabelliformis*, *S. massa* (Carter, 1881b, as *Axinella virgulosa massa*, a.k.a. *Hymeniacidon conulosa* topsent, 1897a or *Stylorella aurantium* Kelly-Borges & Bergquist, 1988), and *S. variabilis* (Whitelegge, 1907 as *Spongosorites*). A further prominent species of this genus is *Styliella carteri* (Dendy, 1889), a.k.a. *Acanthella carteri* or *Axiella carteri* (with junior synonym *Acanthella ehrenbergii* Keller, 1889 and *Acanthella aurantica* Keller, 1889). Hooper & Lévi (1993b) assigned to the type species specimens from New Caledonia which appear to belong to *Styliella carteri*. This differs from *S. flabelliformis* in having a stalked thickly lobate to flabellate growth form with strongly papillate-conulose surface. Hooper & Lévi (1993b) proposed that the genus *Styliella* be considered a senior synonym of *Dragmaxia*, but that genus has long sinuous trichodragmata.

**Description of type species**

*Styliella flabelliformis* Hentschel, 1912 (Fig. 8A–F).

**Synonymy.** *Stylorella flabelliformis* Hentschel, 1912: 355, pl. XIX fig. 26; *Styliella flabelliformis*; Hallmann, 1914: 349 (not Hooper & Lévi, 1993b: 1422 = *Styliella carteri*).


**Description.** Thinly flabellate, with side-blades in the larger specimens. The lectotype (Fig. 8A) measures 10 cm high and 5 mm thick. It is probably a fragment of an originally much larger specimen, because Hentschel mentions a specimen of 20 cm high, and recent specimens may be even larger (Fig. 8B). There is no genuine stalk although the sponge narrows towards the base, but distinct thickened ‘ribbed veins’ consisting of thick spicule tracts traverse the body radially from base and subdivide and anastomose peripherally. These ribs often bear conulose projections. In between the ribs, the surface is smooth and bears a few oscules. The edges of the blade are incised and bear projections. Colour dark orange-brown, beige in alcohol. Skeleton consisting of thicker and thinner spicule tracts, bound by spongins, and confusedly plumoreticulate arranged single spicules (Fig. 8C–D). Spicules curved styles (Fig. 8E–F), 450–(478)–550 × 10–(17.7)–25 μm. Distribution and ecology. Occurring in many Eastern Indonesian reefs.

**SVENZEA ALVAREZ ET AL., 2002**

**Type species**

*Pseudaxinella zea* Alvarez et al., 1998: 20 (by original designation).

**Definition.** Dictyonellidae with a neat uni- paucispicular reticulation of styles.

**Diagnosis**

Massive, cake shaped or more thinly encrusting. Surface optically smooth, slightly microhispid. Soft consistency. No ectosomal skeleton. Choanosomal skeleton uni- paucispicular reticulation,
with some spongin at the nodes. Characteristic grainy soft parts (similar to Scopalina). Spicules short styles and less frequent oxeas. Reproduction viviparous, larvae huge, up to 5 mm or more, oval, entirely ciliated. Three species from the tropical Atlantic and Indo-Pacific.

**Remarks**

The type species was tentatively assigned to the genus *Pseudaxinella* (now Draggmacidon, see chapter on Axinellidae) by the original authors (Alvarez *et al.*, 1998), but it was already noted...
that it did not fit into *Pseudaxinella* because of the thin spicular tracts and soft consistency. With the discovery of two other species with similar properties as *P. zeai* sufficient evidence was assembled for the erection of a new genus *Svenzea*, named after the original discoverer of the type specimen, Prof. Sven Zea. The reassignment of the genus from Axinellidae to Dictyonellidae is made largely on the circumstantial evidence presented by the characteristic mass of granular cells found in all three species and shared with *Scopalina* species. In most other respects, including its peculiar haplosclerid-type skeleton, *Svenzea* is not typical of the family Dictyonellidae.

**Description of type species**

*Svenzea zeai* (Alvarez et al., 1998) (Fig. 9A–D).


**Material examined.** Holotype: USNM 39361 – Islas del Rosario, Colombia. Paratypes: ZMA 8876 – U.S. Virgin Islands. USNM 42805 – Little Tobago, Trinidad & Tobago. Other material. ZMA POR. 14359 – Curaçao, SYMBIOSPONGE 98/CU/MAY23/ RG/017, 33.4 m, coll. R. Gomez.

**Description.** Spreading thick masses with lobes (Fig. 9A), up to 6 cm thick and indefinite lateral expansion. Oscules chimney-like, 1 cm in diameter. Surface smooth, punctate. Consistency crumbly, soft. Colour brown with yellow interior. Skeleton (Fig. 9B) a reticulation of spicule tracts of 1–3 spicules interconnected by single spicules. In the peripheral parts of the sponge, extending deep into the choanosome, there is a mass of dark granular cells, obscuring the spicules and the skeleton. This is similar to the condition observed in *Scopalina*. Spicules (Fig. 9C–D): short styles, occasionally with oxeote endings, 190–330×5–12.5 µm less frequent oxeas with similar range. Distribution and ecology. Colombia, Bahamas, Belize, Jamaica, Curaçao, deeper parts of the reefs.
TETHYSPIRA TOPSEN, 1890

Synonymy


Type species

Tethea spinosa Bowerbank, 1874b: 279 (by original designation).

Definition

Dictyonellidae with auxiliary spined styles in addition to long choanosomal styles.

Diagnosis

Massive cushion-shaped sponges with slippery conulose appearance. No ectosomal skeleton. Choanosomal skeleton consisting of bundles of long styles and single styles; at the base there are short long-spined (tylo-)styles. A single species from the Eastern Atlantic.

Remarks

The record of Rhaphidostyla incisa by Van Soest & Weinberg (1980) from Sherkin Island, Ireland, was found on re-examination to be Tethyspira spinosa (Van Soest, 1987). This genus so far remains only known from a single, rather enigmatic species. Topsent (1900) assigned it to his family Mesapidae in the order Clavulida (=Hadromerida), interpreting the spined spicules as microrhabds. Hooper (1991) assigned it to Raspailiidae as incertae sedis on the basis of resemblance of the spined styles to those of Endectyon, for example. However, with regard to general appearance and structure of the skeleton, T. spinosa fits better in Dictyonellidae. The peculiar spined styles are here interpreted as an apomorphy and are not homologous to echinating megascleres common to the poecilosclerids.

The genus Lissomyxilla Hanitsch, 1894a is an objective junior synonym of Tethyspira as it shares the same type species (by original designation).

Previous review

Topsent, 1900: 257.

Description of type species

Tethyspira spinosa (Bowerbank, 1874b) (Fig. 10A–E).

Synonymy. Tethea spinosa Bowerbank, 1874b: 279, pl. LXXXIII figs 17–22; Tethyspira spinosa; Topsent, 1890a: 195; Topsent, 1900: 257, pl. VII fig. 7; Lissomyxilla spinosa; Hanitsch, 1894a: 194. Rhaphidostyla incisa sensu Van Soest & Weinberg, 1980: 3, fig. 4 (not Schmidt, 1880a).


Description. Low cushion (Fig. 10A–B) with tall sides and rugose upper surface. Larger specimens may become massive-globose, to ca 15 cm across, and are often angular with ridges and crests. Surface slippery, conulose. Oscules translucent chimneys (Fig. 10B). Consistency firm, slightly compressible, elastic. Greyish-white or orangish. Choanosomal skeleton consists of parallel bundles of long megascleres cemented to some extent by spongins (Fig. 10C). Some spicules penetrate the surface. There is a scattered basal layer of small acanthostyles. These are easily missed as the basal layer of massive sponges is not always collected or sectioned, and also the acanthostyles may be scarce or absent. The main structural megascleres are straight or somewhat curved styles or subtylostyles (Fig. 10A, E); up to 1–2 mm × 3–12 µm. Long-spined microtylostyles (Fig. 10A, D); ca. 70–120 × 4–6 µm. Distribution and ecology. British Isles, Brittany; on wave exposed rocks, from 6 m to at least ca. 60 m.