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Family Dictyodendrillidae Bergquist, 1980

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Dictyodendrillidae Bergquist (Demospongiae, Dendroceratida) is characterised by having a reticulate skeleton made up of markedly laminate and moderately to strongly pithed fibres of identical construction to those of darwinellid genera. Free fibrous spicules occur in one genus. Four genera are recognised in the family.
Keywords: Porifera; Demospongiae; Dendroceratida; Dictyodendrillidae; *Dictyodendrilla*; *Spongionella*; *Igernella*; *Acanthodendrilla*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Dictyodendrillidae Bergquist, 1980b: 488.

Definition

Dendroceratida in which the skeleton is reticulate with perfectly regular to slightly irregular mesh and fibres which are strongly and coarsely laminate with a pronounced pith region. Fibres cored or uncored. Fibre skeleton is augmented by free fibrous spicules in one genus. Choanocyte chambers are large, oval and eurpylous. The reticulate skeleton, which arises from a basal spongin plate, permits the sponges to attain large size despite the delicate cavernous nature of the soft tissue. Fibre colour contrasts with that of the soft tissue which is uniformly pigmented throughout.

Scope

Four genera are presently included, *Dictyodendrilla, Acanthodendrilla, Spongionella, Igernella*. Distribution is almost cosmopolitan except for polar seas, with species of *Igernella* and *Acanthodendrilla* being tropical while *Dictyodendrilla* occurs in the tropics but is most common in warm temperate regions, *Spongionella* ranges from cool temperate to semi-tropical seas and is recorded from 200 m depth, other genera are predominantly found in shallow waters, 8–20 m depth, but *Acanthodendrilla* occurs down to 100–130 m.

History and biology

The family was established by Bergquist (1980b), recognising the distinctness of a group of species with clear dendroceratid affinities but having reticulate skeletons with fibres of darwinellid morphology. These species had previously been placed in *Megalopastas* Dendy (type species *Megalopastas nigra* Dendy). While *M. nigra* has a reticulate skeleton and eurypylous choanocyte chambers, the fibres are not as coarsely laminated and wide as typical darwinellid fibres, and it is best accommodated in *Spongionella*, which may in future justify sub-family status.

Remarks

As more information has come to light on the structure and chemistry of dictyodendrillid species there has been discussion about the generic composition of the group and its relationships with the Darwinellidae on the one hand, and the dictyoceratid family Dysideidae on the other. No published discussion which has argued for transfer of any dictyodendrillid genus to either the Dysideidae or the Darwinellidae has taken into account the emphasis in the family diagnosis on the presence of a regular reticulate fibre skeleton, with fibres of the type which characterise the order Dendroceratida. Further, free fibrous spicules occur in the order Verongida as well as in both dendroceratid families, as indeed do eurypylous choanocyte chambers. These latter features cannot characterise families within this group of orders. The important familial features are as stated above.

Comment should be made on the genus *Pseudobasta* Topsent (1931), erected to receive *Spongia basta* Lamarck. Bergquist (1980b) pronounced the specimen as unrecognisable except as belonging to the Dictyodendrillidae.

Previous reviews

Bergquist, 1980b; Bergquist, 1995; Kelly-Borges *et al*., 1993; Bergquist, 1996; Uriz & Maldonado, 1996; Maldonado & Uriz, 1999.

KEY TO GENERA

(1) Fibre skeleton includes free spiculose elements ..... ***Igernella***
Spiculose elements absent 2
(2) Fibres cored ..... ***Acanthodendrilla***
Fibres uncored 3
(3) Surface strongly conulose ..... ***Dictyodendrilla***
Surface microconulose ..... ***Spongionella***

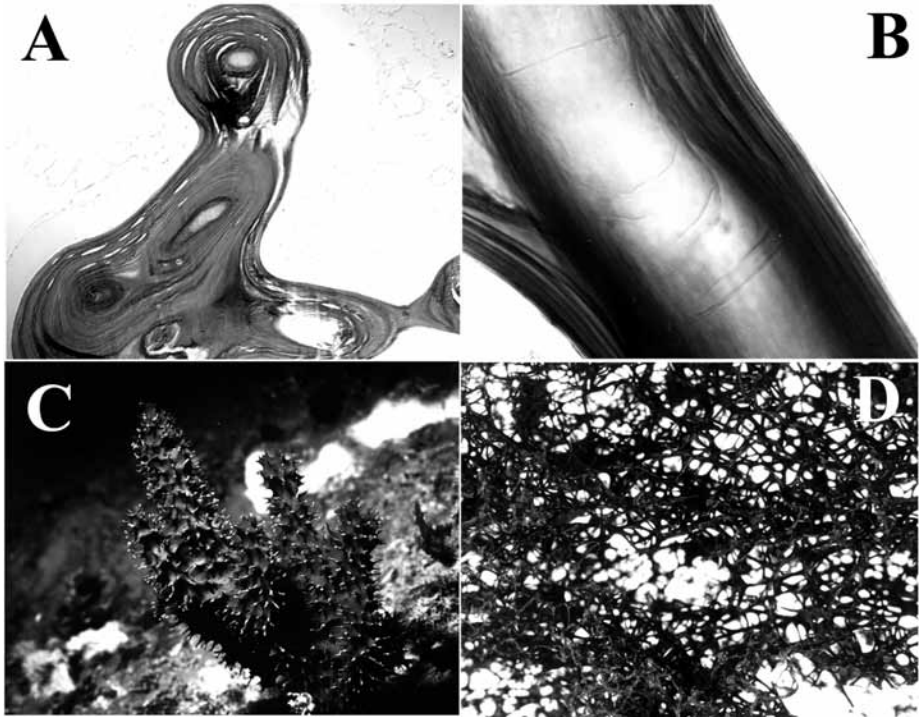

Fig. 1. A–C, *Dictyodendrilla dendyi* Bergquist. A, cross section of fibre. B, longitudinal view of fibre. C, specimen *in situ*, 10 m depth, Poor Knights Is (Photo K. Grange). D, *D. cavernosa* Lendenfeld, holotype, BMNH 1881.10.21.248, dry skeleton.

DICTYODENDRILLA BERGQUIST, 1980

Synonymy

Dictyodendrilla Bergquist, 1980b: 488.

Type species

Dendrilla cavernosa Lendenfeld, 1886b: 557 (by original designation).

Definition

Dictyodendrillidae in which the reticulate fibrous skeleton forms regular rectangular meshes and is composed of pithed, laminated fibres which are free of any coring material (Fig. 1A–B). The tissue construction is delicate and cavernous, and the soft tissue is frequently pale, contrasting with the dark fibres. The sponges when mature are lobate, stalked, vasiform or spreading with digitate projections (Fig. 1C).

Previous review

As for family.

Description of type species

Dictyodendrilla cavernosa (Lendenfeld) (Fig. 1D).

Synonymy. *Dendrilla cavernosa* Lendenfeld, 1886b: 557.

Material examined. Holotype: BMNH 1886.7.8.7 (dry).

Description. Erect sponge extending from a compact attachment base to form variably shaped tubular extensions which are up to 40 cm high with walls 3–5 mm thick. The surface is strongly conulose with conuli irregularly dispersed and up to 4 mm high. Oscules are scattered apically and pores are dispersed over apical and lateral surfaces. The sponge is bright yellow in life, greenish brown in alcohol. Skeleton is reticulate (Fig. 1D) with regular meshes 1.5 mm wide, individual fibres are 2–3 mm thick, darkly pigmented with pith making up more than half the diameter. Choanosome is strongly collagenous, endosome only lightly collagen reinforced, choanocyte chambers 80–100 μm in longest dimension.

Remarks. Lendenfeld (1886b) made several references to the large vestibular space enclosed within the thin walls of *Dictyodendrilla cavernosa*, the dry holotype yields little information on this structure, however a specimen recently collected from Port Jackson, Sydney, Australia and awaiting registration in the AM shows the vestibule to be present but only of modest size. A structure such as this can be expected to vary from one specimen to another. Seven species were originally assigned to *Dictyodendrilla* (Bergquist, 1980b), and two others added more recently, *D. tenella* Lendenfeld and *D. dendyi* Bergquist.

Distribution

South Eastern Australia, 10–20 m depth.

SPONGIONELLA BOWERBANK, 1862

Synonymy

Spongionella Bowerbank, 1862b. *Velinea* Vosmaer, 1883. *Megalopastas* Dendy, 1905.

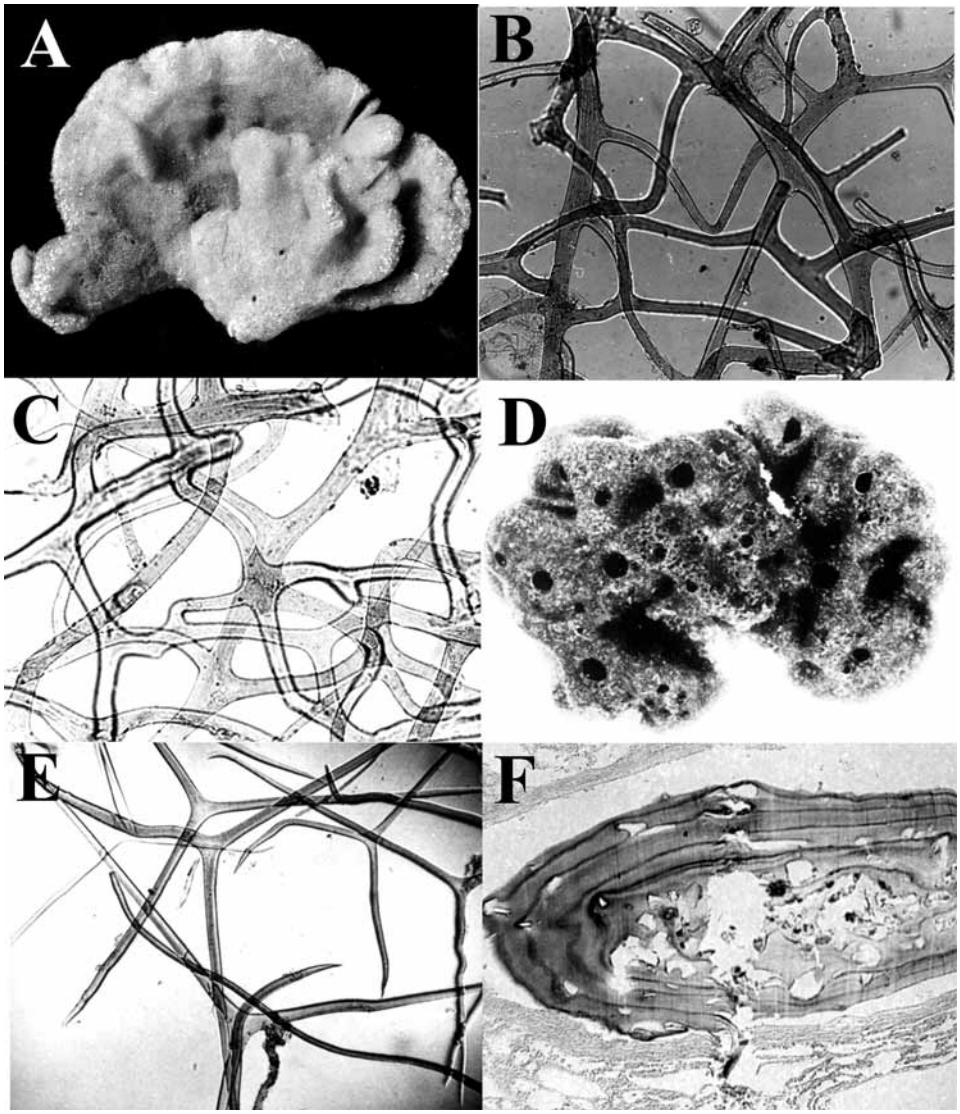

Fig. 2. A–C, *Spongionella pulchella* Sowerby. A, holotype, BMNH 1930.7.3.454, dry skeleton. B–C, light micrographs showing the regular fibrous skeleton. D–E, *Igernella notabilis* (Duch. & Mich.). D, dry skeleton of a large specimen showing oscular rows. E, fibrous spicules. F, *Acanthodendrilla australis* Bergquist, cross section of fibre.

Type species

Spongionella pulchella (Sowerby, 1862: 508) (by monotypy).

Definition

Dictyodendrillidae in which the skeleton is a compact reticulum of uncored primary and secondary fibres in which concentric lamination and a pith component are always apparent, though variable in relative proportion between pith and bark. The skeletal arrangement is regular, and almost perfectly rectangular in the type species. The surface is microconulose due to primary fibres extending into fine, tapered projections at the periphery.

Remarks

The discovery of additional living material of the type species confirms the presence of a microconulose surface in this species, not obvious from the dry holotype. Twelve species have been described in *Spongionella*, one belongs to *Lendenfeldia*, one to *Phyllospongia*, two to *Spongia*, one is assignable only to the Dictyodendrillidae and five, *pulchella, gracilis, nigra, pulvillus*, and *foliascens* are valid species. No comment can be made on the records from Nha Trang and Norway. The distribution for the genus, based on published records, is from the North Sea and English Channel to the Mediterranean, West Atlantic to the Indian Ocean.

Previous reviews

Lendenfeld, 1889a; de Laubenfels, 1948; Vacelet, 1959; Bergquist, 1980b; Kelly-Borges *et al*., 1993.

Description of type species

Spongionella pulchella (Sowerby) (Fig. 2A–C).

Synonymy. *Spongionella pulchella* (Sowerby, 1862: 508)

Material examined. Holotype: BMNH 1930.7.3.454 (dry). Other material. Spirit preserved specimens from Mediterranean

(J Vacelet, personal collection), English Channel (B. Picton, personal collection).

Description. Lamellate to cushion shaped, up to 9 cm high, 6 cm wide, lamellae are 0.8 cm thick; the texture is soft, flexible and elastic; colour in life is gray to brownish or yellow, pale golden in dry state (Fig. 2A). Surface is very regular with fine, terete, low conules each marking the termination of an ascending primary fibre. The skeleton is composed of an extremely regular meshwork of primary and secondary fibres, all are uncored and stratified with a marked central pith region, there is little distinction in dimension between primary and secondary elements, all 30–40 μm in diameter (Fig. 2B–C). Choanocyte chambers are eurypylous, 80 μm in longest dimension.

Remarks. Much of the hesitation evident in literature pertaining to the systematic position of *Spongionella* can be attributed to the long period over which assessments had to be based only on the dry skeleton of the holotype, recollections of well preserved specimens have been recent. Small Mediterranean specimens reported in 1959 could not confidently be referred to the type species. There is still no chemistry known for the type species, only for *S. gracilis* and this argues for dendroceratid affinity. It is the case that *Spongionella* species, with their fine, uncored fibres show less similarity with the fibres of Darwinellidae than do other dictyodendrillids, this assignment could in future, be revisited and subfamily status for the group may be justified. There is insufficient evidence at present to support such action.

Distribution

North Sea, English Channel, Mediterranean.

IGERNELLA TOPSENT, 1905

Synonymy

[*Euryades*] Duchassaing & Michellotti, 1864: 106 (preocc. by *Euryades* Felder, 1864, Lepidoptera) (type species *Euryades notabilis* Duchassaing & Michelotti, 1864) (declared unrecognisable by de Laubenfels, 1936: 30). *Igernella* Topsent, 1905b.

Type species

Igernella notabilis (Duchassaing & Michelotti, 1864: 106) (by original designation).

Definition

Dictyodendrillidae in which the fibrous skeleton is irregular, reticulate, and in some species reduced in relation to the bulk of the soft tissue. In some specimens/species fibres are concentrated superficially. Fibres are laminated and pithed, the latter can be obscured by detritus. Fibre skeleton augmented by diactinal and triactinal fibrous spicules comparable in morphology, but not in collagen type, to those of *Darwinella*.

Previous reviews

De Laubenfels, 1948; Van Soest, 1978; Bergquist, 1996; Uriz & Maldonado, 1996.

Description of type species

Igernella notabilis (Duchassaing & Michelotti) (Fig. 2D–E).

Synonymy. *Euryades notabilis* Duchassaing & Michellotti, 1864: 106. *Igernella joyeuxi* Topsent, 1905b.

Material examined. Lectotype: ZMA POR1044 – St. Thomas (fragment BMNH 1928.11.12.38). Other material. Authors collection – Discovery Bay, Jamaica.

Description. Sponge a cushion-like basal mass from which clusters of tubes up to 6 cm high by 4 cm wide arise. Oscules apical on tubes which tend to align in rows in larger specimens (Fig. 2D). Surface is conulose, texture compressible, rough to the touch, fragile. Colour in life deep rose pink to red. Skeleton an irregular fibrous reticulum arising from a basal spongin plate, primary fibres are cored, concentrically laminated and pithed, the latter largely obscured by detritus. Secondary fibres largely clear. Primary fibres 100–350 μm diameter, secondaries 15–100 μm, mesh size very variable. Triactinal and diactinal fibrous spicules occur throughout the sponge, diactines 1210–1600 μm long, 20–22 μm wide, triactine rays 500–900 μm long, 17–25 μm wide (Fig. 2E).

Remarks. The genus *Igernella* was established by Topsent (1905b) within his family Pleraplysillidae, to accommodate a specimen from the Gulf of Mexico previously described as *Darwinella joyeuxi*. Van Soest (1978) synonymised this species with *I. notabilis* (Duchassaing & Michellotti). As in the case of *Spongionella, Igernella* has been a problem to assign between the Darwinellidae and the Dictyodendrillidae. The presence of elaborate spongin spicules in both *Darwinella* and *Igernella* has been held to indicate homology, however the structures differ in the type of collagen of which they are composed, indicative of distinct developmental pathways being utilised in their formation (Garrone, 1978). Secondary metabolite chemistry is insufficiently known for species of dictyodendrillid genera to permit clear resolution of the assignment but the presence of spongiane diterpenes in *Igernella* favours relationship with the Dictyodendrillidae. Thus far no sequence analysis has been done.

Distribution

Carribean, Gulf of Mexico, Brazil and Indian Ocean. It is probable, given this distribution, that further species remain to be discovered.

ACANTHODENDRILLA BERGQUIST, 1995

Synonymy

Acanthodendrilla Bergquist, 1995: 33.

Type species

Acanthodendrilla australis Bergquist, 1995: 33 (by monotypy).

Definition

Dictyodendrillidae in which the reticulate fibrous skeleton has an irregular mesh arrangement with all elements cored with detritus. Reticulation is more pronounced superficially, and ascending, primary fibres project markedly above the sponge surface. The strongly cored fibres and irregular reticulum distinguish the genus from

Dictyodendrilla and *Spongionella*, and the absence of free fibrous spicules distinguishes it from *Igernella*.

Previous reviews

Bergquist, 1995; Uriz & Maldonado, 2000.

Description of type species

Acanthodendrilla australis Bergquist (Fig. 2F).

Synonymy. *Acanthodendrilla australis* Bergquist, 1995: 33.

Material examined. Holotype: QMG304698 – Ilot Canard, New Caledonia.

Description. Sponge a thick fan arising from broad attachment base, 11 cm high, 13 cm wide, 4.5 cm thick, oscules confined to the broad upper surface, large, 0.2–1 cm diameter. Colour in life unknown, deep cream to amber in ethanol, texture soft, compressible but fibres confer rigidity to the texture. Surface ornamented by irregularly disposed conules 2–4 mm high from which primary fibres protrude. Skeleton with irregular mesh, thick coarse laminated fibres 250–2000 μm diameter and cored (Fig. 2F). Central pith region evident. Ectosome 200–400 μm deep with collagenous superficial region 30–50 μm deep. Choanosome cavernous, mesohyl reduced in extent, choanocyte chambers oval, eurypylous, 60–120 μm in longest dimension.

Remarks. The addition of a second species with a dendroreticulate, cored fibre skeleton expands the concept of the genus slightly but the predominant pattern remains reticulate.

Distribution

New Caledonia, Mediterranean.