

Family Darwinellidae Merejkowsky, 1879

Patricia R. Bergquist & Steve de C. Cook

Department of Anatomy, School of Medicine, University of Auckland, Private Bag 92019, Auckland, New Zealand.
 (pr.bergquist@auckland.ac.nz; cooknz@bigfoot.com)

Darwinellidae Merejkowsky (Demospongiae, Dendroceratida) with strictly dendritic skeletons augmented in one genus by free fibrous spicules. Four genera are included found in all seas.

Keywords: Porifera; Demospongiae; Dendroceratida; Darwinellidae; *Darwinella*; *Aplysilla*; *Dendrilla*; *Chelonaplysilla*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Darwinellidae Merejkowsky, 1879. Aplysillidae Lendenfeld, 1883; Vosmaer, 1883; Dendy, 1905.

Definition

Dendroceratida having a fibrous skeleton which is completely dendritic and, in one genus is supplemented by spongin spicules which are free of the primary skeleton (Fig. 1A). Species are most frequently encrusting but, where massive or erect, their dendritic fibrous skeleton, like that of the encrusting forms, always arises from a flat basal spongin plate. The fibres have a strongly laminated bark surrounding a central, distinct pith region (Fig. 1B).

Scope

Four genera are presently recognised, *Aplysilla*, *Darwinella*, *Chelonaplysilla* and *Dendrilla*. Distribution is cosmopolitan, extending into both polar seas. Depth range is from intertidal to 640 m.

History and biology

Darwinellidae was introduced by Merejkowsky (1879). This publication was overlooked by Lendenfeld and Vosmaer who both, in 1883, established a family Aplysillidae. Lendenfeld's publication was the earlier and hence the name is attributed to him. Vosmaer (1885b) used the name Darwinellidae for the same group. Usage has oscillated back and forth but since Van Soest (1978) Darwinellidae has been consistently in use and there is no doubt that it has precedence. The biology and chemistry of darwinellid sponges to date was summarised by Bergquist (1996).

Taxonomic remarks

Darwinellidae until the present has accommodated two genera which have been the subject of much discussion, none of which was helped by the fact that neither genus was common and both

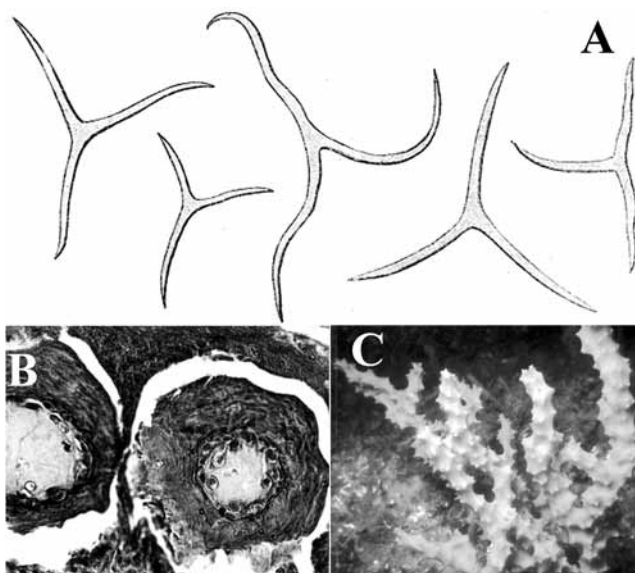


Fig. 1. *Darwinella*. A, *D. intermedia* Topsent, fibrous spicules (after Topsent, 1905b). B, *D. oxeatata* Bergquist, fibre in cross section to show incorporation of cellular material and clearly demarcated bark and pith regions. C, *D. gardineri* Topsent, *in situ*, Leigh, New Zealand, 15 m depth (photo C.N. Battershill).

were fragile encrusters and thus difficult to collect and preserve. Consequently, information on their ultrastructure, reproduction, chemistry and histology has been slow to emerge. These are the genera *Pleraplysilla* Topsent and *Hexadella* Topsent. Both can now be transferred, with the addition of 28s rDNA sequence information: *Hexadella* to the *Verongida* (Ianthellidae) and *Pleraplysilla* to the Dictyoceratida (Dysideidae). These assignments are commented on under the appropriate families.

Previous reviews

Lendenfeld, 1889a; Topsent, 1905b; Dendy, 1905; de Laubenfels, 1948; Vacelet, 1959; Van Soest, 1978; Bergquist, 1980b; Bergquist, 1996.

KEY TO GENERA

- (1) Fibre skeleton augmented by free fibrous spicules *Darwinella*
 Fibrous spicules absent 2

- (2) Sponge surface supports a structured, sandy reticulation *Chelonaplysilla*
 Sponge surface clear and smooth 3
- (3) Sponge always encrusting *Aplysilla*
 Sponge erect, stalked with prominent conules *Dendrilla*

DARWINELLA MÜLLER, 1865**Synonymy**

Darwinia Schultze, 1865: 7. *Darwinella* Müller, 1865: 344.

Type species

Darwinella aurea Müller, 1865: 344 (by original designation).

Definition

Darwinellidae in which the dendritic fibre skeleton is supplemented by fibrous spicules which can be diactinal, triactinal or polyactinal. There is no sand in the fibres but dispersed cellular elements can occur (Fig. 1B). The sponges are fleshy, encrusting or massive to lobate (Fig. 1C).

Remarks

Ten species have been described in *Darwinella*, eight were discussed by Topsent (1905b), one was added by Bergquist (1961b) and another by Poiner & Taylor (1990).

Previous reviews

Pronzato, 1975, and see remarks for the family.

Description of type species

Darwinella muelleri (Schultze, 1865) (Fig. 1A–C).

Synonymy. *Darwinia mülleri* Schultze, 1865: 7. *Darwinella aurea* Müller, 1865: 344.

Material examined. None.

Description (after Lendenfeld, 1889a; Topsent, 1905b; Pronzato, 1975). A low encrusting sponge up to 15 mm thick with conulose surface, conules 0.4 mm high, spaced 1–1.5 mm apart, oscules approximately 1 mm in diameter, scattered, colour bright orange-gold in original specimen from Brazil, bright yellow in later described specimens mainly from the Mediterranean. Skeleton is dendritic, made up of uncored fibres arising from a basal plate, and up to 4 mm long and 60–160 µm in diameter. Pith with very marked scalloped appearance, bark strongly laminated. Fibrous spicules are present, concentrated for the greater part toward the base of the sponge, they are sometimes free, sometimes attached to fibres by threads of spongin. Spicules are polyactinal with 3–8 rays mainly straight, sharply pointed 0.1–1 mm long. Choanocyte chambers eurypylous 60–90 µm maximum dimension.

Remarks. *Darwinella* is a well characterised genus once adequate skeletal preparations are made and the presence and morphology of the fibrous spicules can be confirmed. In surface morphology, however, and in the range of pigmentation exhibited in the various species, small specimens can easily be confused with *Aplysilla*. The present authors are not familiar from first hand field

experience, coupled with careful histology, with species of *Aplysilla* and *Darwinella* from regions other than New Zealand, Australia and the Central and Eastern Pacific. However, based upon that experience we are of the opinion that *Aplysilla* is rare to absent in those regions and that the common shallow water and intertidal fleshy encrusting darwinellids are, in the main, species of *Darwinella*. Further, in our view, it is unlikely that the Brazil/Mediterranean distribution given above for the type species, *D. muelleri*, can be substantiated upon closer scrutiny, although there is currently no material to hand suitable for such study. The stability of pigmentation in *Darwinella* species is discussed under the genus *Aplysilla*.

Distribution

The type species occurs in Desterro, Brazil, and apparently also in the Mediterranean and the Red Sea. The genus is cosmopolitan, found in cool temperate to tropical seas.

APLYSILLA SCHULZE, 1878**Synonymy**

Aplysilla Schulze, 1878b: 57. *Simplicella* Merejkowsky, 1878: 259.

Type species

Aplysilla rosea (Barrois, 1876: 57) (by subsequent designation, Topsent, 1905b).

Definition

Darwinellidae in which the sponge body is always encrusting and the skeleton is composed only of fibres which are clear of detritus and typically unbranched (Fig. 2A). In some species, for example *A. polyraphis* de Laubenfels, branching is frequent.

Remarks

Sixteen species have been described in *Aplysilla*, one, *A. violacea* Lendenfeld, is a species of *Chelonaplysilla*, another, *A. gigantea* Lendenfeld, is a species of *Dictyodendrilla*, with others requiring re-examination before confirming their status.

Previous reviews

Lendenfeld, 1889a; Topsent, 1905b; de Laubenfels, 1948; Vacelet, 1959; Pulitzer-Finali & Pronzato, 1976; Bergquist, 1980b.

Description of type species

Aplysilla rosea (Barrois) (Fig. 2A–B).

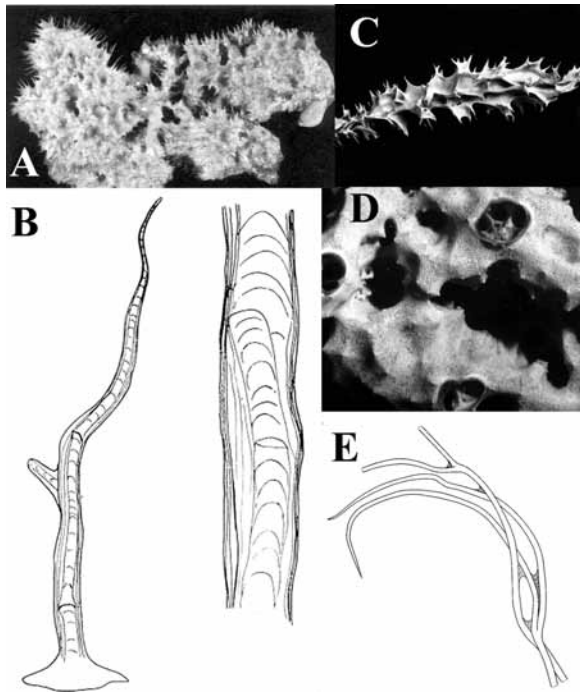


Fig. 2. A, *Aplysilla glacialis* (Merejkowsky), preserved specimen, maximum dimension 5 cm, Pacific Grove California (after Bakus & Abbot, 1980). B, *Aplysilla sulfurea* (Schulze), diagram of fibres (after Vacelet, 1959). C, *Dendrilla rosea* var. *digitata* Lendenfeld, Specimen from South Coast of Australia, J.B. Wilson collection, BMNH 1887.7.11.16; the pronounced conules and slender, erect form of the genus is well depicted. D, *Chelonaplysilla aurea* Bergquist, surface morphology to illustrate the sand reticulated surface diagnostic of the genus. E, *Chelonaplysilla erecta* Tsurumal, diagram to illustrate merging of adjacent fibres (after Tsurumal, 1967).

Synonymy. *Verongia rosea* Barrois, 1876: 57.

Material examined. Holotype: Not seen. Other material. MNHN – Slides from Toppent collection. Authors collections – Roscoff, Plymouth. BMNH, AM, Lendenfeld material.

Description. A thin encrusting sponge 2–3 mm thick, spreading often to cover rocky surfaces in extended plaques, colour pale to bright rose pink. Surface smooth, slightly slimy, clear of epibionts and of sand or foreign materials, with conules 2–3 mm high, spaced approximately 5 mm apart. Skeleton dendritic, made up of fibres 50–300 μm diameter at the base, only slightly narrower apically. Fibres arise from a spreading basal plate and have most of their diameter made up of pith, always with investing stratified bark which is thinner at the summit than at the base (Fig. 2B). Fibres are usually simple but may branch. Choanocyte chambers eupylos, oval, 80 μm in longest dimension. Found in the intertidal and shallow waters to 60 m depth.

Remarks. It is difficult to describe a sponge genus which, superficially at least, has no distinctive features except always being encrusting – a state through which all other dendroceratid genera pass on the way to attaining their final form. *Aplysilla* lacks the fibrous spicules of *Darwinella*, the erect ramifying morphology of *Dendrilla* and the structured, sandy surface of *Chelonaplysilla*. It seems to be characterised by the lack of characters, while still, in terms of histology, fibre structure, surface morphology and chemistry being a typical and distinct dendroceratid genus.

When defining species of *Aplysilla* there are only four macroscopic characters to utilise: colour, conulation pattern, degree of

branching of the fibres, and pigmentation of the fibres. There are two viewpoints as to the utility of colour as a specific character in this group of species, with most recent authors who have dealt with Mediterranean species believing it to be variable, particularly within the range of rose-red and yellow specimens. Bergquist (1980b, 1991, 1996) argued that colour is stable within these species. This assertion rests upon work on *Darwinella*, where red and yellow pigmentation, identical to that seen in *Aplysilla*, characterises species. In the case of *Darwinella* there are skeletal differences to help confirm species discrimination. Extensive field work on *Darwinella* and other Dendroceratida in New Zealand and Australia, where morphology was studied in tandem with secondary metabolite chemistry, Bergquist *et al.* (1990b) demonstrated consistent differences in diterpene complement between red and yellow pigmented species, *D. gardineri* Toppent and *D. oxeata* Bergquist, respectively. The same situation pertains to *Aplysilla*, where Bobzin & Faulkner (1989, 1992) studied the chemistry of *A. polyraphis* and *A. glacialis*, finding specific differences in diterpene content. The issue of colour consistency is important in the case of *Aplysilla* with regard to determining the specific name of the type species, whether *A. rosea* (Barrois) or *A. sulfurea* (Schulze). The position adopted here is that colour is consistent and that *A. rosea* is the correct name for the type species. Careful study of Mediterranean species combining morphology and chemistry would be helpful. A further point relates to the different oxidation behaviour of the pigment in the red-pink species where they change to reddish brown in alcohol, and the yellow species where a colour reaction very comparable to that seen in Verongida is followed, on death or damage changing to dark purple in alcohol. This difference was noted by Toppent (1905b), Pulitzer-Finali & Pronzato (1976) and Bergquist (1996) and it indicates that there are chemically distinct pigments in the red and yellow specimens.

Distribution

Cosmopolitan, according to the present literature, with a wide depth range extending from the intertidal to 640 m depth. The disjunct latitudinal and depth distributions given for some species, for example by Lendenfeld (1889a) for *A. rosea*, are likely to be erroneous. No adequate type material has survived to permit checking the existing records.

DENDRILLA LENDENFELD, 1883

Synonymy

Dendrilla Lendenfeld, 1883: 271.

Type species

Dendrilla rosea Lendenfeld, 1883: 271 (by subsequent designation, Toppent, 1905b).

Definition

Darwinellidae of large, flexible, erect, branching or complex-lamellate growth forms (Fig. 2C) in which the fibres branch repeatedly but do not anastomose. Fibres contain no foreign coring material.

Previous reviews

Lendenfeld, 1889a; Topsent, 1905b; Dendy, 1905; Burton, 1934a; de Laubenfels, 1948; Vacelet, 1958; Bergquist, 1980b; Bergquist, 1996.

Description of type species

Dendrilla rosea Lendenfeld (Fig. 2C).

Synonymy. *Dendrilla rosea* Lendenfeld, 1883: 271. Refer to Bergquist, 1996: 19 for extensive synonymy.

Material examined. Holotype: BMNH (fragments of holotype); AM (Lendenfeld collections). Other material. Authors collections from New Zealand and Australia (refer to Bergquist, 1996).

Description. A large erect sponge with lobose-digitate to slender, branching and digitate habit, up to 30 cm high, extending from a narrow attachment base. Surface smooth between pronounced conules 1–5 mm high spaced 3–8 mm apart, surface has a lacy appearance conferred by dispersed pores, oscules scattered, 1–4 mm apart. Colour bright rose-pink throughout, red-brown in alcohol. Skeleton strictly dendritic, fibres arise from a basal spongin plate, are 1.2–1.6 mm in diameter narrowing rapidly to 300 µm, a thickness retained until narrowing abruptly to a point near the surface. Short lateral branches support surface conules. Fibres are strongly stratified with pith making up 80% of the diameter at the tip, 10 percent at the base. Soft tissue structure is complex, ectosome densely collagenous, up to 140 µm deep set off from the choanosome by a system of sub-dermal exhalant canals. An almost tissue-like concentration of myocytes traverses the canal region to link ectosome and choanosome (Bergquist, 1996: pl. 3a). Choanosome densely cellular, choanocyte chambers oval, eurypylous, average 56 µm in longest dimension.

Remarks. *Dendrilla* is a well characterised genus, but bringing coherence to the species grouped within it has been difficult. The main problem was that Lendenfeld himself had no consistent view of *Dendrilla*, as opposed to *Aplysilla* and *Aplysina*, he also defined the genus as having a dendritic skeleton, but included species with obvious reticulate skeletons. A number of authors contributed to the resolution of this problem, notably Dendy (1905) and Vacelet (1958). Bergquist (1980b) established the genus *Dictyodendrilla* to receive the forms with reticulate skeletons, since an earlier genus, *Megalopastas* Dendy, 1905, proved to be a synonym of *Spongionella*. In the same work species were transferred to *Dictyodendrilla*, *Dendrilla* and *Aplysina* as appropriate. Twenty species have been described within *Dendrilla*, but only seven are valid species within this genus.

Distribution

Dendrilla occurs from Antarctic to tropical seas in the Southern Hemisphere, and in tropical to cool temperate seas in the Northern Hemisphere. It is never a common sponge and appears to favour depths between 15–45 m.

CHELONAPLYSILLA DE LAUBENFELS, 1948**Synonymy**

Chelonaplysilla de Laubenfels, 1948: 167.

Type species

Chelonaplysilla noevus (Carter, 1876: 228) (by original designation).

Definition

Darwinellidae which have a structured and separable cortex reinforced by a delicate reticulum of sand grains (Fig. 2D), supported by collagen tracts. Fibre structure is like that of *Aplysilla*, but in species that become erect, lamellate and branching, the supporting skeleton becomes branched.

Previous reviews

De Laubenfels, 1948; Vacelet, 1959; Bergquist, 1980b; Bergquist, 1996.

Description of type species

Chelonaplysilla noevus (Carter).

Synonymy. *Aplysilla arenosa* Topsent, 1925c: 717.

Material examined. Holotype: Not seen. Other material. Slides from Mediterranean specimens, coll. J. Vacelet.

Description. Sponge is a bright purple–violet crust, less than 2 mm thick, with surface elevated into sharply pointed conules by evenly spaced fibres. The surface is covered by a structured reticulation of sand grains which confers a coarse roughened appearance. The meshes of the reticulum are regular, 200–300 µm in diameter. Within the boundaries of the meshwork the thin dermal membrane is pierced by pores, 15–40 µm in diameter. The skeleton is dendritic made up of short tapering, strongly pigmented fibres which arise from a basal spongin plate. Fibres are uncored, up to 3 mm long, unbranched, 70–80 µm thick basally, 20 µm near the surface. Pith 35 µm in diameter.

Remarks. *Chelonaplysilla* is an easily recognisable genus with the structured sandy surface reticulum reinforcing the otherwise soft, delicate tissue (Fig. 2D). De Laubenfels (1948) recognised the distinctness of the surface structure and established *Chelonaplysilla* for *Aplysilla arenosa* Topsent, which he designated type species, and *C. psammophila* Topsent. Vacelet (1959) demonstrated that *C. arenosa* was a junior synonym of *Aplysina noevus* Carter, and this has been accepted by subsequent authors. There have been suggestions that larger species of the genus, for example lamellate specimens of *C. violacea* (Lendenfeld) and *C. erecta* Tsurumal, develop a reticulate skeleton. This is not the case. Adjacent or converging fibres can merge and diverge frequently, leaving a fine fibrous plate at points of convergence. The figure given by Tsurumal (1967) (Fig. 2E) makes the distinction clear. Lendenfeld (1889a) noted the same fibre structure occurring in *Dendrilla*.

Distribution

Cosmopolitan in tropical to cool temperate seas, extremely common as a fouling organism on ascidians.