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Family Axinellidae Carter, 1875

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Axinellidae Carter (Demospongiae, Halichondrida) contains 10 valid genera (of 90 nominal genera) and approximately 300 species described so far worldwide. The family has a wide distribution from shallow to deep waters (down to 1800 m depth). Species are generally erect, branching, fan-shaped or tubular, but encrusting and massive forms also occur. Species have no specialised ectosomal skeleton. The choanosomal skeleton is generally differentiated in axial and extra-axial regions with two basic types of skeletal architecture: (1) ascending and anastomosing spicule tracts, spongin fibres cored with spicules or fibrofascicles radiating to the periphery and ending in surface processes; (2) plumose to plumoreticulated. The axial skeleton of some species is either compressed or absent. Megascleres are styles, oxeas (and transitional forms) and sinuous strongyles in any combination. Bubaridae is excluded from synonymy with Axinellidae and reinstated as a valid taxon in Halichondrida.

Keywords: Porifera; Demospongiae; Halichondrida; Axinellidae; *Auletta*; *Axinella*; *Cymbastela*; *Dragmacidon*; *Dragmaxia*; *Pararhaphoxya*; *Phakellia*; *Phycopsis*; *Ptilocaulis*; *Reniochalina*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

[Phakellidae] Gray, 1867a: 503, 518; Gray, 1872a: 447 (*nomen oblitum*, Article 23.9 ICZN (Anon., 1999)). Axinellidae Carter, 1875c; Lendenfeld, 1889a: 903 (in part); de Laubenfels, 1936a: 127 (in part).

Definition

Halichondrida without specialised ectosomal skeleton; with velvety or microhispid surface; with choanosomal skeleton of ascending spiculo-fibres connected irregularly by loose spicules and short tracts, or plumoreticulated with ascending plumose tracts connected by thinner ones or single spicules. Megascleres are oxeas, anisoxeas, styles, sinuous strongyles in any combination. Microscleres are raphides, single or in trichodragmata.

Diagnosis

Encrusting, massive, branching, fan-shaped and tubular; generally red, orange or yellow sponges; surface is usually velvety to hispid due to the projection of choanosomal spicules and without specialised ectosomal skeleton. Choanosomal skeleton is formed by ascending spiculo-fibres that radiate to the periphery, connected irregularly by loose spicules and short tracts, and ending in skeletal projections at the surface, or plumoreticulate with ascending plumose tracts of oxeas and styles connected regularly by paucispicular or multispicular tracts, or reticulated with main spicule tracts of sinuous or vermiform strongyles, or anisoxeas, plumo-echinated by single spicules. In some species the choanosomal skeleton is divided into an axial region, where it often becomes compressed, and an extra-axial region with plumoreticulated skeleton. Megascleres are mainly oxeas, anisoxeas with or without telescoped tips or microspines, straight or sinuous styles, strongyles are always sinuous. Microscleres are raphides, single or in trichodragmata, generally difficult to observe and located near the periphery.

Scope

A literature review revealed a total of 92 nominal genera that have been erected in, or transferred to, the family at one time or another. Of these, only 23 genera belong in the Axinellidae with 10 valid genera (i.e., *Auletta, Axinella, Cymbastela, Dragmacidon, Dragmaxia, Pararhaphoxya, Phakellia, Phycopsis, Ptilocaulis, Reniochalina*) and the rest considered junior synonyms. The total number of species in the family according to Hooper & Lévi (1994) is approximately 300 worldwide, but given the uncertainties in the taxonomy of this family the actual number may differ substantially above or below that figure.

Distribution

According to Van Soest (1994), the Axinellidae has a cosmopolitan distribution without any obvious or distinct centre of diversity. Regional revisions record 15 species for New Caledonia (Hooper & Lévi, 1993b), 11 for New Zealand (Bergquist, 1970), 21 (in 7 genera) from the Central-West Atlantic region (Alvarez *et al*., 1998) and 17 for the NE Atlantic (Van Soest *et al*., 2000). Other estimates are: 57 species described for Australia (Hooper & Wiedenmayer, 1994); 130 species from the Indo-west Pacific region, of which 45% are represented in Australian waters (Hooper & Lévi, 1994); 63 species for the South China Sea (Hooper *et al*., 2000b) and 30 for the Mediterranean (Van Soest, unpublished data).

History and biology

The Axinellidae was initially erected by Carter (1875c: 133, 145) as 'Axinellida' under the order Echinonemata, to include sponges with horny fibres 'echinated with proper spicules projecting from the interior of the fibre'. Carter (1883b: 316) recognised the simplicity of his previous diagnosis and extended the definition of the family as: sponges with an axial and extra-axial skeleton; generally with sinuous oxeas, located in the core of the fibres and echinated by styles of two size categories; with both types of spicules occurring in the axial skeleton. He recognised that the type and location of the spicules could vary among species, but emphasised that the presence of spicules echinating the fibres characterised all species and therefore were diagnostic for the family. He also suggested that *Axinella* Schmidt, 1862 and *Phakellia* Bowerbank, 1862b were typical representatives. Carter (1885d: 348) further expanded the definition of Axinellidae to include one of the most controversial characters in contemporary sponge taxonomy, 'the compression of the axial skeleton'. He also grouped axinellid sponges into several assemblages – branching, stipitate, flabelliform, vasiform and massive shapes – however, he recognised that form was a character with poor informative value.

Ridley & Dendy (1886; 1887) described the family again under the old order Monaxonida. Their definition included sponges having a 'skeleton typically non-reticulate; consisting of ascending axes of fibres from which arise subsidiary fibres radiating to the surface; fibres typically plumose; megascleres chiefly styles to which oxeas and (or) strongyles may be added; microscleres rarely present, never chelas'. The differences between the definitions of Carter and Ridley & Dendy are insignificant. Ridley & Dendy (1886, 1887) did not mention Carter as author of the original description of the Axinellidae and since then, with some exceptions (Wiedenmayer, 1977b; Hooper & Wiedenmayer, 1994), the authority of the family has been incorrectly attributed to these authors instead of Carter (1875c).

The definitions of Carter (1875c, 1883b), Ridley & Dendy (1886, 1887), and the subsequent amendments of Topsent (1894c, 1904b), Dendy (1905; 1916a), Hallmann (1917c), de Laubenfels (1950a), Lévi (1973), Wiedenmayer (1977b); Bergquist (1970; 1978) and Hartman (1982) reflect the lack of diagnostic characters to define the family. Hooper & Wiedenmayer (1994: 69) were the last authors to give a comprehensive definition of the family as follows:

'Encrusting, massive, branching, fan shaped, and tubular; surface usually hispid due to projecting spicules; megascleres are styles, oxeas, strongyles (sometimes sinuous) in all combinations, usually smooth, sometimes tuberculate, spined, flexuous or vermiform; skeleton typically divided into axial and extra-axial components; main skeletal tracts, both spicules and spongin fibres, typically condensed in axial portion of skeleton, with extra-axial plumose or plumoreticulate tracts running to surface; encrusting species having condensed basal skeleton usually with basal flexuous or vermiform strongyles, and perpendicular extra-axial skeleton of styles (straight or rhabdose), or oxeas. Microscleres usually absent, although few genera having raphides or microraphides in groups (trichodragmata) or alone'.

This definition agrees with previous ones and is used in this revision as an initial criterion to select the valid genera of Axinellidae. Hooper & Lévi (1993b) and Hooper & Wiedenmayer (1994) recognised the poor value of the characters included in this definition, the occurrence of many exceptions to the general pattern and the poor understanding of the affinities of many of the included species.

The paucity of reliable diagnostic characters creates a problem at the infra-family level. Many of the nominal genera assigned to the Axinellidae have skeletal structures different to the axinellids in the sense of Hooper & Wiedenmayer (1994). Furthermore, most of these genera are polythetic, in that they cannot be defined by a single set of diagnostic characters. This makes allocation of species problematical, and raises the likelihood that genera contain heterogeneous assemblages of species.

The higher taxonomic position of the family Axinellidae has been very unstable and subjected to different higher taxonomic assignments. Topsent (1894c; 1928c) and de Laubenfels (1936a; 1950a) considered it belonged to the Halichondrina (Vosmaer 1885b), a suborder of the Monaxonida, but later elevated to full order status. Dendy (1916a; 1922b) had a different view, considering it closely related to the family Desmacidonidae (currently in the order Poecilosclerida), and tentatively included it as a subfamily of this group (which he considered to be polyphyletic).

But one of the most remarkable changes influencing the taxonomic position of the Axinellidae was the subdivision of the Demospongiae into the subclasses Ceractinomorpha and Tetractinomorpha by Lévi (1953a). As consequence of this subdivision the Axinellidae was allocated to the former order Axinellida Lévi, 1955, along with other groups allegedly having in common an axially compressed skeleton and an oviparous mode of reproduction. This scheme was criticised by Van Soest *et al*. (1990) and Van Soest (1991) who returned the family to the order Halichondrida in an emended form.

These higher taxonomic changes and the inclusion of other genera with condensed axial skeletons, plumose or plumoreticulate extra-axial skeletons and microscleres by Hallmann (1916a, 1916b, 1917c) and de Laubenfels (1936a) have contributed to the large number of nominal genera (92) included in the family at one time or another.

The phylogenetic relationships of the family Axinellidae in relation to other demosponge families were explored by Van Soest *et al*. (1990) using cladistic and parsimony methods based on morphological characters. In their view, the Axinellidae belongs to a redefined order Halichondrida, and is placed as the sister clade of a group of taxa that includes the families Desmoxyidae, Dictyonellidae and Halichondriidae. The synapomorphy proposed to define the Axinellidae within this order is the presence of an axially condensed and extra-axial plumoreticulate choanosomal skeleton. However, some genera, such as *Dragmacidon* (i.e., *Pseudaxinella* of contemporary authors; see below) and *Ptilocaulis* have (secondarily?) lost the axial skeleton, while others like *Auletta* and *Phakellia* lack a clear axial component, which renders the strict definition untenable. Although axial condensation of the skeleton has been traditionally used to link taxa within the Axinellidae, it is obviously a very weak synapomorphy for the family, as it is also present in other unrelated families such as Raspailiidae (e.g., *Ceratopsion*), Hemiasterellidae (e.g., *Axos*), Desmacidinae (e.g., *Desmacidon*) and some Microcionidae (e.g., *Clathria (Axosuberites)*) Suberitidae (e.g., *Homaxinella, Plicatellopsis, Rhizaxinella*).

The phylogenetic relationships of some members of the family Axinellidae has been studied by Alvarez & Crisp (1994) using a group of axinellid species from the Central-West Atlantic, and more recently by Alvarez *et al*. (2000a). In the latter study, a group of 27 species of Axinellidae and related families (Dictyonellidae, Halichondriidae and Agelasidae) were selected with the aim of testing the monophyly of Axinellidae and to investigate their phylogenetic relationships using morphological and molecular data. The results of this work based on molecular data and some chemical evidence, showed that the family might not be monophyletic; but the analysis based on morphological data indicated however, that the family is monophyletic. Therefore, at this stage there is not sufficient conclusive evidence to establish the monophyly of the Axinellidae or to clearly define the phylogenetic position of the family in the higher classification.

A great number of novel chemical compounds have been isolated from members of this family (e.g., Rudi *et al*., 1997; Mancini *et al*., 1997; Li *et al*., 1998b; Urban *et al*., 1999) some with bioactive properties (e.g., Newbold *et al*., 1999) and others that function as chemical defence (e.g., Wilson *et al*., 1999). The use of these compounds as chemotaxonomic markers has also been discussed (Van Soest & Braekman, 1999).

Some members of the family Axinellidae are oviparous (Siribelli, 1962), but it is true to say that the reproductive biology of the family remains poorly known, and the importance of this character in defining higher taxa is largely speculative – despite extensive interpretation of these few data as 'rules' for the family and for the nominal order 'Axinellida' in general (e.g., Lévi, 1973; Bergquist, 1978; Hartman, 1982).

Remarks

The definition given above restricts Axinellidae to genera without specialised ectosomal skeleton and velvety or microhispid surface; with choanosomal skeleton predominantly plumose to plumoreticulate, mainly formed by spicule tracts of sinuous strongyles, oxeas, anisoxeas or styles and without microscleres other than raphides and trichodragmata. Some dictyonellid genera (e.g., *Acanthella, Stylissa* and *Rhaphoxya*) have skeletal arrangement similar to some genera of Axinellidae (e.g., *Axinella*) but the surface features in those cases are very characteristic of Dictyonellidae (see chapter in this volume).

The definition of the family is also emended from Hooper & Wiedenmayer (1994) to exclude encrusting forms (i.e., *Bubaris, Bubaropsis, Cerbaris, Hymerhabdia, Lithobubaris, Monocrepidium, Rhabdobaris, Rhabdoploca, Skeizia* and *Uplexoa*). These were included in Axinellidae at one time or another based on the similarities between the axial condensation of the skeleton of Axinellidae and the 'basally condensed' skeleton of encrusting forms such as *Bubaris* (see Bergquist, 1970; Van Soest *et al*., 1990). They are transferred here to Bubaridae *sensu* Topsent, 1928c and Desmanthidae (see respective chapters in this volume).

Previous reviews

Carter, 1883b: 316; Ridley, 1884a: 462; Carter, 1885d: 347; Ridley & Dendy, 1886: 477; Ridley & Dendy, 1887: 166; Topsent, 1894c: 24–25; Dendy, 1897: 231; Wilson, 1902: 399; Topsent, 1904b: 137; Dendy, 1905: 181; Row, 1911: 354; Hentschel, 1912: 113; Dendy, 1916a: 96; Hallmann, 1917c: 673–674; Dendy, 1922b: 111; Wilson, 1925: 444; de Laubenfels, 1936a: 127; de Laubenfels, 1950a: 87; Bergquist, 1970; Lévi, 1973: 605; Wiedenmayer, 1977b: 151–152; Bergquist, 1978: 167; Hartman, 1982; Tanita & Hoshino, 1989: 84; Hooper & Lévi, 1993b: 1396; Hooper & Wiedenmayer, 1994: 69; Alvarez *et al*., 2000a.

KEY TO GENERA

(1) Choanosomal skeleton with ascending and anastomosing tracts radiating to periphery; spicule tracts are coring spongin fibres, and/or fibrofascicles 2
Choanosomal skeleton with spicule tracts of sinuous strongyles plumo-echinated (radiating obliquely and perpendicularly) by styles or oxeas 4
Choanosomal skeleton plumoreticulate 5
Choanosomal skeleton consisting of plumose axes of spicules, dendritically branching and rarely interconnected, with peripheral spicules curving outward. Megascleres are only styles, some bent near the base. Microscleres are long sinuous trichodragmata and single raphides ornamented with fine spines at terminal points .... ***Dragmaxia***
(2) Flat spatula-shaped scopiform processes at surface 3
Long and filamentous processes at surface .... ***Phycopsis***
(3) Megascleres are anisoxeas with or without spined tips .... ***Reniochalina***
Megascleres are styles in two size categories .... ***Ptilocaulis***
(4) Body generally fan-shaped and stalked; with ascending choanosomal tracts of strongyles interconnected and plumo-echinated by single or short tracts of styles. Main tracts often imprinting the surface as 'veins' .... ***Phakellia***
Body generally tube-shaped and stalked; with a layer of sinuous strongyles lining the inner wall of the tube and a reticulation, nearly isotropic of choanosomal tracts of strongyles plumo-echinated by styles. Surface free of skeletal projections but with single spicules .... ***Auletta***
Body generally dichotomously branching and stalked, with a main axial core of interwoven strongyles echinated by single oxeas or short plumose tracts of oxeas .... ***Pararhaphoxya***
(5) With styles and oxeas. Microscleres, if present, are trichodragmata 6
Body generally cup-shaped and stalked; no styles .... ***Cymbastela***
(6) Massive or massive encrusting forms; plumose tracts are generally thick and multispicular .... ***Dragmacidon***
Body branching, arborescent or bushy; plumose tracts are pauci-multispicular, connected at regular intervals by uni-paucispicular secondary tracts .... ***Axinella***

AULETTA SCHMIDT, 1870

Synonymy

Auletta Schmidt, 1870: 45.

Type species

Auletta sycinularia Schmidt, 1870: 45 (by monotypy).

Definition

Axinellidae of tubular habit with a layer of sinuous strongyles lining the inner wall of the tube and a reticulation, nearly isotropic of choanosomal tracts of strongyles plumo-echinated by styles.

Diagnosis

Tubular, erect on peduncle or narrow base. Surface smooth with choanosomal spicules projecting slightly; ectosome without specialised skeleton. Choanosomal skeleton plumoreticulate, with longitudinally strongyle tracts, connected by single styles or plumose tracts of styles; masses of sinuous strongyles reinforcing inner tube wall. Megascleres sinuous strongyles, always coring main spicule tracts and inner tube walls; styles and or oxeas, plumo-echinating and connecting main tracts. Microscleres absent.

Remarks

The organisation of the skeleton of *Auletta* is comparable to that of *Phakellia* and *Pararhaphoxya*. In *Phakellia* the primary skeleton is reticulated, with axes of sinuous strongyles plumo-echinated by styles, single or in bundles connected by secondary spicule tracts, generally styles; in *Pararhaphoxya* styles have been replaced by oxeas. The three genera have distinctive habit and surface features.

Auletta has been referred previously to Cornacuspongidae: Halichondrina: Halichondridae (Vosmaer, 1885b), Monaxonida: Halichondrina: Axinellidae (Topsent, 1894c; 1904b: 137; de Laubenfels, 1936a), Axinellida: Axinellidae (Lévi, 1973) and Halichondrida: Axinellidae (Van Soest *et al*., 1990: 18; Alvarez *et al*., 1998).

Distribution

A total of 17 species of *Auletta* are recorded in the literature from Central-West Atlantic, East Atlantic, Indian Ocean, NE Australia, Central-West Pacific and Japan.

Previous reviews

Topsent (1894c: 25); Dendy (1889: 93); Topsent (1904b: 137, 143); Dendy (1905: 194); (Dendy 1916a: 119); Dendy (1922b: 121); Burton (1931c: 142); de Laubenfels (1936a: 129); de Laubenfels (1954: 170); Lévi & Vacelet (1958: 233); Lévi (1973: 605); Van Soest & Stentoft (1988: 105); Alvarez *et al*. (1998: 32).

Description of type species

Auletta sycinularia Schmidt, 1870 (Figs 1–2).

Synonymy. *Auletta sycinularia* Schmidt, 1870: 45; Ridley & Dendy, 1887: 187; Topsent, 1904b: 143; Van Soest & Stentoft, 1988: 105; Alvarez *et al*., 1998: 38.

Material examined. Lectotype (here designated): BMNH 1939.2.10.36 – Alligator Reef, Florida, 210 m. (based on data published by Desqueyroux-Faúndez & Stone, 1992: 25).

Description. Cluster of 6 tubes, 1–3 cm long approximately; on thin stalk approximately 1 cm long; surface hispid; oscules apical, with sphincters; pores, 60–80 mm in diameter, within atrial cavity of tubes; colour unknown when alive, beige in alcohol; consistency fragile and soft (Fig. 1A). Specialised ectosomal skeleton absent; choanosomal skeleton with thick and longitudinal strongyle tracts, 50–180 μm, plumo-echinated or connected at right angles by single or plumose tracts of two size categories of styles. Inner tube wall reinforced by masses of sinuous strongyles (Figs 1B–D, 2A). Sinuous strongyles and strongyloxeas, length 300–770 μm (465.8 ± 133.8), width 13–25 μm (18.4 ± 3.1) (n = 24); styles of two size categories: (a) length 450–950 μm (657.9 ± 136.6), width 10–20 μm (15.7 ± 3.2) (n = 13), (b) length 140–280 μm (206.25 ± 57.6), width 8–10 μm (9.5 ± 1) (n = 4) (Fig. 2B). Additional size category of styles found in specimens from Gulf of Mexico (Alvarez *et al*., 1998).

Remarks. This species seems to be variable in its shape, with some specimens having the tubes fused, resulting in a flabelliform shape (Alvarez *et al*., 1998). *Auletta sycinularia* is similar to *A. sessilis* Topsent, 1904b, a species recorded from the Azores but with a slightly different habit in which the tubes are fused to a broad base. *Auletta tuberosa* Alvarez *et al*., 1998, recorded from the Gulf of Mexico, differs from *A. sycinularia* in shape, surface features and in having oxeas, in addition to styles and strongyles.

Habitat and distribution. This species has been found in the Gulf of Mexico, Florida and Barbados at depths of 70–200 m; substrate unknown.

AXINELLA SCHMIDT, 1862

Synonymy

Axinella Schmidt, 1862: 60. *Axidragma* Hallmann, 1917c: 637 (new synonym). *Axinosia* Hallmann, 1914: 349 (new synonym). *Chalinissa* Lendenfeld, 1887c: 771. *Pseudaxinella* Schmidt, 1875: 120. (new synonym; Not *Pseudaxinella* Schmidt *sensu* de Laubenfels, 1936a: 131; Bergquist, 1970: 20; Lévi, 1973; Wiedenmayer, 1977b: 152, 155; Wiedenmayer, 1989: 47; Hooper & Lévi, 1993b: 1436; Alvarez *et al*., 1998 = *Dragmacidon*, see below). *Querciclona* de Laubenfels, 1936a: 46. (new synonym). *Teichaxinella* de Laubenfels, 1936a: 128 *Tragosia* Gray, 1867a: 513. [*Astrospongia*] Gray, 1867a: 514 (objective synonym).

Type species

Axinella polypoides, Schmidt, 1862: 60 (by subsequent designation; de Laubenfels, 1936a).

Definition

Axinellidae with choanosomal skeleton differentiated in axial (compressed or vaguely reticulated) and extra-axial (plumoreticulated) region. Megascleres are styles and oxeas. Microscleres, if present, are microraphides and trichodragmata.

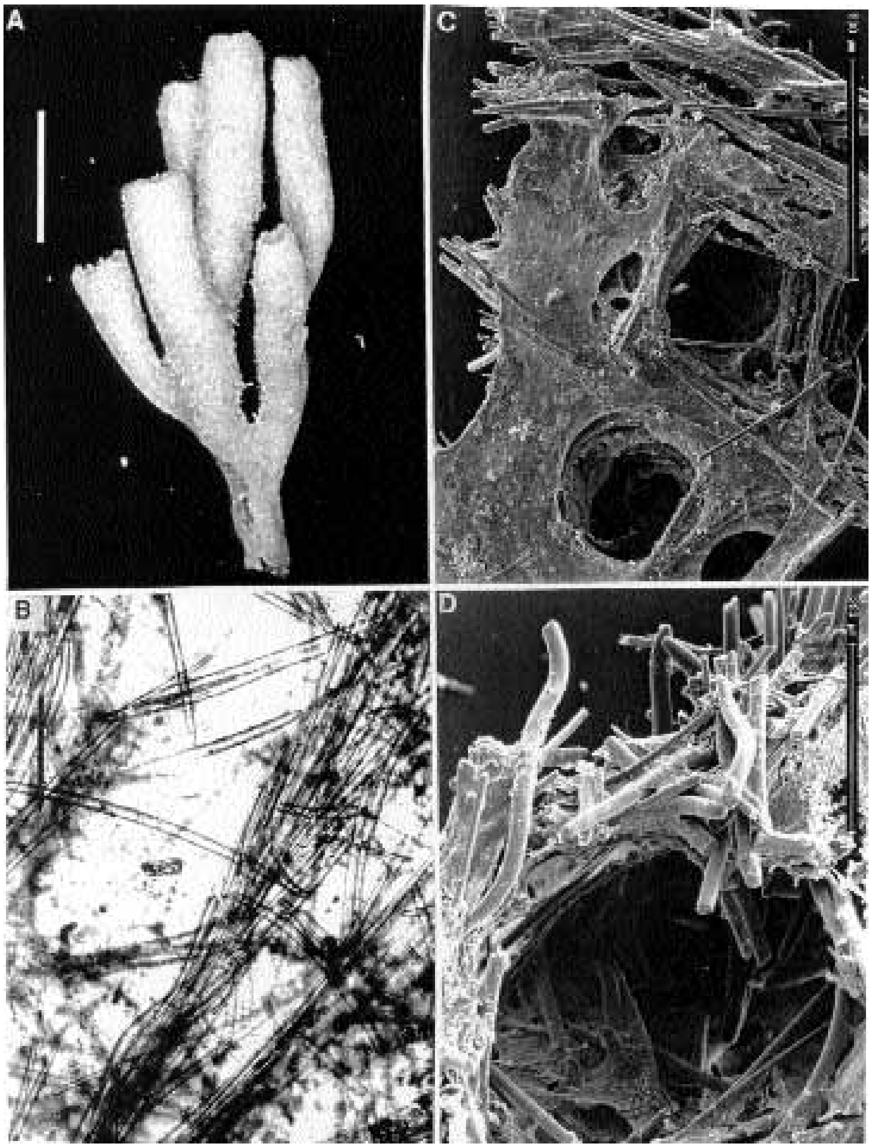

Fig. 1. *Auletta sycinularia* Schmidt. A, lectotype, BMNH 1939.2.10.36. B, longitudinal section through the skeleton. C, SEM of a longitudinal skeletal section. D, SEM of a transverse section through the skeleton (scales A, 1 cm; B, 200 μm).

Diagnosis

Ramose, bushy or lamellate habit. Surface generally smooth with choanosomal spicules projecting slightly; oscules, when visible, with stellate morphology (i.e., superficial canals leading to opening 'imprinted' in superficial skeleton); ectosome without specialised skeleton. Choanosomal skeleton differentiated in axial and extra-axial regions; axial skeleton compressed or vaguely reticulated; extra-axial skeleton plumose or plumoreticulate. Megascleres styles, or styles and oxeas, or oxeas; when both present, one type may be rare; modifications of megascleres common in several species. Microscleres, if present, microraphides and raphides, mostly in tightly packed trichodragmata.

Remarks

Axinella is difficult to define due to the great morphological plasticity exhibited by species. The type species has features generally recognised as typical for the genus (i.e., branching habit, skeleton axially condensed and extra-axial skeleton with a reticulation of plumose tracts, styles and oxeas). However, many other species presently included in *Axinella* lack some of these features; additionally, some of the characters can be variable at the intraspecific level (see Pansini, 1982–1983; Alvarez *et al*., 1998). The genus currently includes a heterogeneous assemblage of species, some of which might be better allocated to *Acanthella* or *Phakellia* based on the revised diagnoses provided in this work. A revision of the nominal species of *Axinella, Phakellia* and *Acanthella* is recommended here, probably best undertaken on a regional basis due the large number of species currently assigned to each of these genera.

Axidragma (type species *Axinella padina* Topsent, 1896a: 431) is considered here to be a junior synonym of *Axinella*, as suggested by Cabioch (1968b). It was erected in the Axinellidae by Hallmann (1917c) to include *Axinella padina*, a species considered to be a junior synonym of *Axinella flustra* by Topsent (1904b). According to Topsent (1904b), *A. padina* differs from *A. flustra*

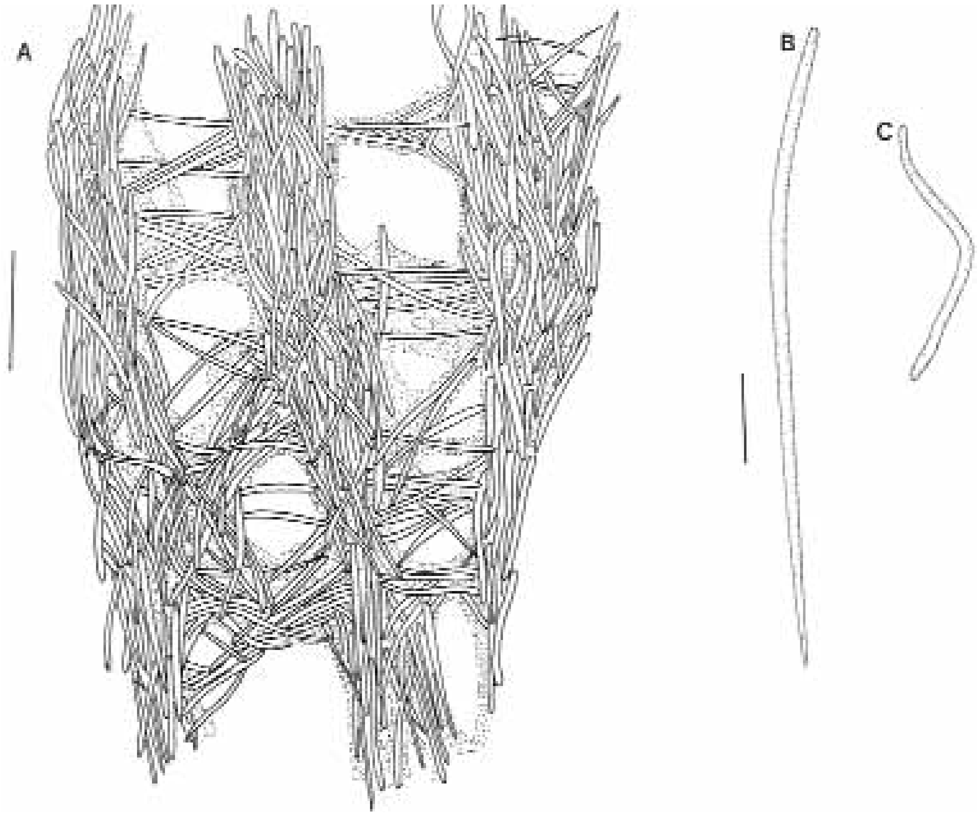

Fig. 2. *Auletta sycinularia* Schmidt, BMNH 1939.2.10.36. A, diagram of the skeleton. B, style. C, sinuous strongyle (scales A, 200 µm; B–C, 100 µm).

only in the thickness of the oxeas which seem to be smaller in *A. padina*, a feature that could vary at intraspecific level. *Axidragma* in the sense of Hallmann shared the presence of trichodragamata with *Dragmaxia* Hallmann and *Dragmacidon* Hallmann, but is different in terms of skeletal architecture. Neither the type material of *Axinella padina* or *A. flustra* could be located but, according to the descriptions given by Topsent (1892a: 122; 1904b: 139; 1928c: 177) and Cabioch (1968b), and based on the examination of a specimen of *A. flustra* from Banyuls (see below) and the published descriptions, the species can be confidently placed in its original genus. Dendy (1922a) and de Laubenfels (1936a:132) regarded *Axidragma* as a junior synonym of *Tragosia*, but this genus is considered also a synonym of *Axinella* in this work.

Axinosia (type species *Axinella symbiotica* Whitelegge, 1907: 508) was erected in the Axinellidae by Hallmann (1914: 269) to include a group of species that he considered congeneric (i.e., *Axinella symbiotica, Stylotella irregularis* Kirkpatrick, 1900a, *Phakellia multiformis* Whitelegge, 1907: 508 and *A. arborescens* Ridley & Dendy, 1886). It was related to *Teichaxinella* by Wiedenmayer (1989: 48–49) and to *Reniochalina* and *Ptilocaulis* by Hooper & Lévi (1993b: 1404). The genus is considered here a junior synonym of *Axinella* based on the re-examination of the type material of *A. symbiotica*, which agrees with the definition of *Axinella* given above. Other species reported under *Axinosia* are: *A. incrustans* Burton, 1930e: 333 from the South Pacific and *A. xutha* Laubenfels, 1954: 175 from the Central-West Pacific. The identity of these species, and those transferred to *Axinosia* by Hallmann (1914) needs to be confirmed as they might belong to genera other than *Axinella*.

Chalinissa (type species *Isodictya dissimilis* Bowerbank, 1866: 318) was erected in the Homorrhaphidae: Chalininae (Lendenfeld, 1889a) and agrees with *Axinella* (Burton, 1927: 502). Other species described under *Chalinissa* (i.e., *C. communis* Lendenfeld, 1887c: 772; *C. communis var. flabellum* Lendenfeld, 1887c: 772; *C. elegans* Lendenfeld, 1887c: 773; *C. elongata* Lendenfeld, 1887c: 774; *C. macropora* Lendenfeld, 1887c: 772; *C. ramosa* Lendenfeld, 1887c: 774; *C. rigida* Lendenfeld, 1887c: 773; *C. serpens* Lendenfeld, 1887c: 773; *C. tenuifibris* Lendenfeld, 1887c: 773) are currently allocated to *Callyspongia serpentina* (Lamarck) (Hooper & Wiedenmayer 1994).

Pseudaxinella (type species *Pseudaxinella sulcata* Schmidt, 1875: 120 by monotypy) is included here as a junior synonym of *Axinella* based on recent examination of its type material (ZMUC DEM-241, lectotype, here designated; ZMUC DEM-242; ZMUC DEM-243, ZMUC DEM-244, paralectotypes, Fig. 5A, wet, SW vorn Bukenfjord, 106 fathoms). The genus was erected by Schmidt (1875) for *Pseudaxinella sulcata*, from the North Sea to allocate those *Axinella*-like species without a clear compression of the axial skeleton, some of which were included in *Dictyocylindrus* and *Isodictya* by Bowerbank (1866) but are currently allocated to *Axinella*, e.g., *A. dissimilis* (Bowerbank, 1866: 318) and *A. infundibuliformis* (Linnaeus, 1791: 1296). Since de Laubenfels (1936a) however, the genus has been reserved for species of massive, subspherical, cushion-shaped, unbranched or lobate growth form, with a skeleton typically plumoreticulate and without axial compression or differentiation between axial and extra-axial regions. Although the concept of *Pseudaxinella* by contemporary authors (Bergquist, 1970: 20; Lévi, 1973; Wiedenmayer, 1977b:

152, 155; Wiedenmayer,1989: 47; Hooper & Lévi, 1993b: 1436; Alvarez *et al*., 1998) has been unequivocal, it does not match either the description of Schmidt, or the redescription of Thiele (1903b: 378), or the observations made from the lectotype of *Pseudaxinella sulcata* which agrees with *Axinella*. Species assigned to *Pseudaxinella* in the past are better placed under *Dragmacidon* Hallmann, 1917c (see below).

Querciclona (type species *Antherochalina quercifolia* Keller, 1889: 338, by original designation) was synonymised with *Phakellia* by Hooper & Lévi (1993b: 1413). Hooper (1996a) redescribed the type material (BMNH 08.9.24.179) and referred it to *Phakellia*; he further suggested that *A. quercifolia* might be a synonym of *Phakellia donnani* (Bowerbank, 1873c as *Isodictya*). The type specimen of *A. quercifolia* was re-examined here and nothing additional needs to be added to the description of Hooper (1996a). However, the material, is considered to be in agreement with *Axinella* and not with *Phakellia*. It is very similar to other species of *Axinella* such as *A. symbiotica* Whitelegge, 1907: 508 from Australia, *A. waltonsmithi* (de Laubenfels, 1953a: 533) from the Central-West Atlantic, and *A. damicornis sensu* Pansini, 1982–1983, from the Mediterranean. The oxeas in these species, including the type species of *Querciclona*, are rare or absent; the choanosomal skeleton is clearly plumoreticulate, with paucispicular primary tracts ending in brushes that protrude through the surface, and connected by uni-paucispicular secondary tracts generally one spicule long. The skeleton is slightly compressed in the axial region.

Teichaxinella (type species *Teichaxinella shoemakeri* de Laubenfels, 1936a: 129, by original designation) was established for some species of *Axinella* that lack axial condensation because of their external morphology (de Laubenfels, 1936a: 128–129; Wiedenmayer, 1977b: 154). Detailed examination of several specimens of the type species, including the holotype (see Alvarez *et al*., 1998) showed that the extra-axial skeleton consists of single spicules and short plumose spicule tracts and therefore should be included in *Axinella*. As in other species of *Axinella*, e.g., *A. polypoides* Schmidt, 1862: 60, *A. dissimilis* (Bowerbank, 1866: 318) and *A. infundibuliformis* (Linnaeus, 1791: 1296), the type species of *Teichaxinella* has also trichodragmata which supports further synonymy with *Axinella*. Other species reported under *Teichaxinella* are: *Phakellia flabellata* Carter, 1885d: 363 and *Axinella vermiculata* Whitelegge, 1907: 511 (Hooper & Wiedenmayer, 1994: 85), *Axinella labyrinthica* Dendy, 1889: 88 (Hooper & Lévi, 1993b: 1410) and *T. morchella* Wiedenmayer, 1977b: 154 (junior synonym of *Axinella corrugata* (George & Wilson, 1919: 161)). The generic placement of these species needs to be re-examined.

Tragosia (type species *Spongia infundibuliformis* Linnaeus, 1791: 1296, by original designation) (Fig. 5B) was revised by Dendy (1922a) and differentiated from *Axinella* based on the presence of trichodragmata. This character is also present in other species of *Axinella* including the type species (i.e., *A. dissimilis, A. flustra, A. polypoides, A. shoemakeri*) and also in other genera of Axinellidae (e.g., *Dragmacidon* Hallmann, 1917c, *Dragmaxia* Hallmann, 1916b) and is considered here of little value to differentiate the genus. Cabioch (1968b) considered *Tragosia* as a subgenus of *Axinella* and included *A. dissimilis* and *A. flustra*. Some species currently assigned to *Tragosia* such as, *T. alba* Descatoire, 1969: 188, *T. fibrosa* Topsent, 1890b: 65, *T. hirondellei* Topsent, 1892a: 120, should be revised as they might not belong in *Axinella.*

Axinella has been referred previously to Halichondriae (Schmidt, 1862), Keratospongia: Chalinidae (Gray, 1867a), Echinonema: Axinellida (Carter, 1885d), Cornucuspongidae: Halichondrina: Halichondridae (Vosmaer, 1885b); Monaxonida: Halichondrina: Axinellidae (Ridley & Dendy, 1886; Topsent, 1894c; 1896a; 1904b; de Laubenfels, 1936a), Sigmatomonaxonida: Axinellidae (Dendy, 1905; Topsent, 1928c); Axinellida: Axinellidae (Bergquist, 1970; Lévi, 1973) and Halichondrida: Axinellidae (Van Soest *et al*., 1990; Alvarez *et al*., 1998).

Distribution

The genus has a widespread distribution (Hooper & Wiedenmayer, 1994; Van Soest, 1994) and approximately 60 valid species (Alvarez, 1998).

Previous reviews

Gray (1867a: 513); Ridley & Dendy (1886: 479; 1887: 178); Topsent (1894c); Lendenfeld (1888: 234); Dendy (1897: 231); Wilson (1902: 400); Topsent (1904b: 137); Dendy (1905: 188); Vosmaer (1912: 308); George & Wilson (1919: 158); Dendy (1922b: 114); Topsent (1928c: 173); Vosmaer (1932–35: 721); de Laubenfels (1936a: 130); Lévi & Vacelet (1958: 233); Vacelet (1969: 177); Lévi (1973: 605); Bergquist (1970: 14); Donadey *et al*. (1990: 259); Hooper & Lévi (1993b: 1407); Alvarez *et al*. (1998).

Description of type species

Axinella polypoides Schmidt, 1862 (Figs 3–4).

Synonymy. *Axinella polypoides* Schmidt, 1862: 60; Gray, 1867a: 514; Schmidt, 1868: 9; (not Schmidt, 1870: 60 = *Axinella polycapella* de Laubenfels, 1953a: 530); Carter, 1884b: 205; Topsent, 1902: 348; Babic, 1922: 238; Topsent, 1928c: 173; Vosmaer, 1932–35: 723; Topsent, 1934a: 34; Sarà, 1960a: 32; Vacelet, 1969: 175; Boury-Esnault, 1971b: 303; Pulitzer-Finali, 1983: 516; Uriz, 1982: 59 (with additional records). *Tragosia polypoides*; Hanitsch, 1894a: 179.

Material examined. Lectotype (here designated): BMNH 1867.7.26.81, dry – Schmidt's specimen from type locality, Adriatic. Paralectotype (here designated): BMNH 1929.10.11.1 and BMNH 1877.5.2.335 (registered twice according to the BMNH records) – fragment of Schmidt's specimen from type locality.

Description. Branching-ramose, 30 cm high; dichotomous branches, 1–2 cm in diameter; surface smooth-velvety when moist; oscules areolate star-shape, 0.5–5 mm diameter approximately, uniformly distributed; colour orange or yellow-orange in life, dark-brown in dry state; consistency firm but flexible (description of external features taken from Uriz, 1982) (Fig. 3A). Specialised ectosomal skeleton absent; choanosomal skeleton differentiated in axial and extra-axial regions; extra-axial skeleton plumoreticulate with primary tracts, plumose, pauci-, pluri- or multi-spicular, 20–100 μm thick, radiating from the axis towards the surface, ending in single spicules or brushes projecting slightly through ectosome, connected at more-or-less regular intervals by secondary tracts of 1–3 spicules, generally no more than one spicule long; axial skeleton condensed to reticulate, present both in central column of specimens and in branches (Figs 3C–D, 4A). Megascleres are styles, length 210–500 μm (345 ± 118.6), width 8–12 μm (9.4 ± 1.3) (n = 10) and oxeas, length 270–420 μm (324 ± 45.3) (n = 10) 5–12 μm (8.7 ± 1.9) (n = 10) (Fig. 4B–C). Microscleres are trichodragmata, up to 30 μm in length, difficult to observe (Fig. 3B).

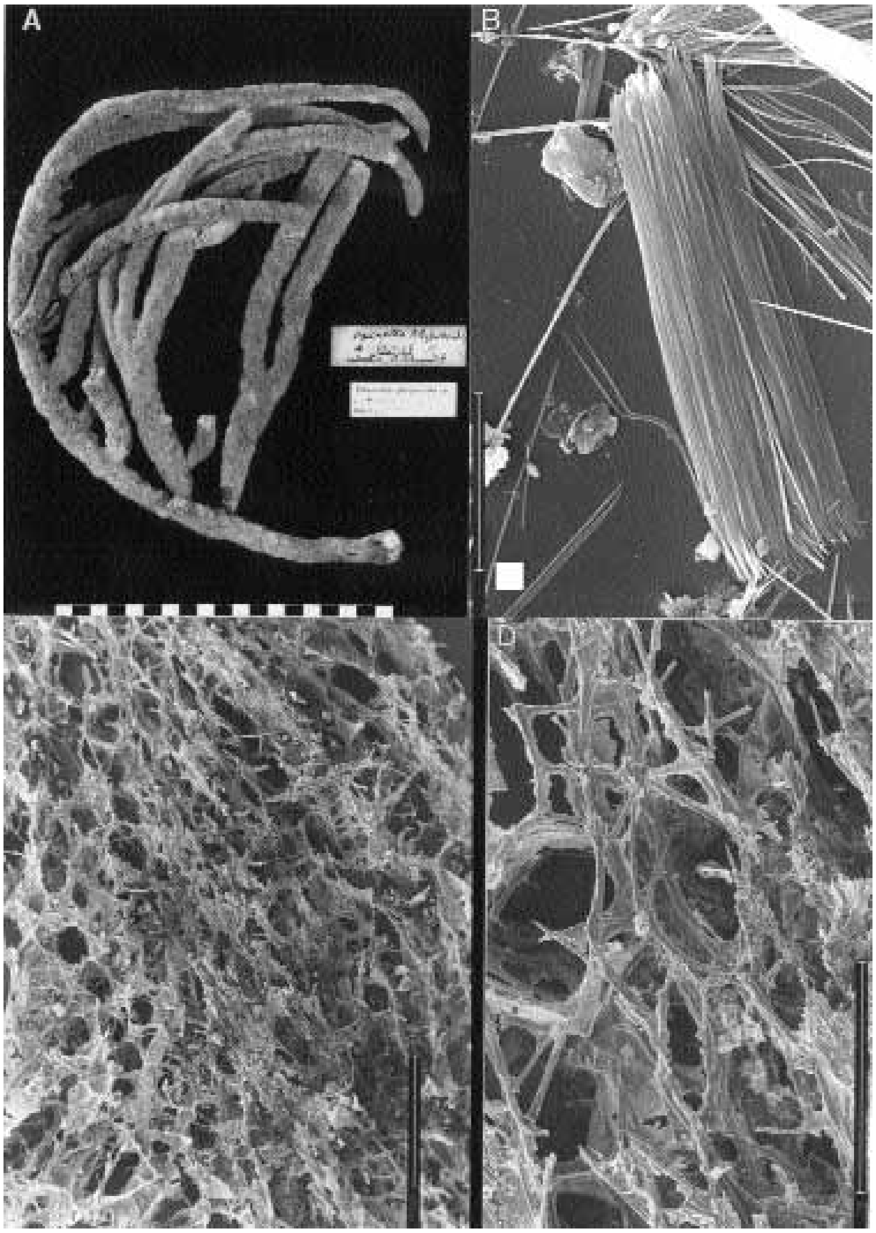

Fig. 3. *Axinella polypoides* Schmidt, 1862. A, lectotype, BMNH 1867.7.26.81. B, trichodragmata. C, SEM of the choanosomal skeleton. D, detail of the choanosomal skeleton (scales A, 10 cm; B, 10 μm; C, 1 mm; D, 500 μm).

Remarks. *Axinella polypoides* is very similar in general morphology, skeletal architecture and spicule dimensions to *A. polycapella* de Laubenfels, 1953a, from the Central-West Atlantic and *A. australiensis* Bergquist, 1970, from New Zealand. In the material examined trichodragmata are not very abundant, difficult to detect and generally located near the surface; they do not appear to be homologous to the microraphides detected by Donadey *et al*. (1990). *Axinella polypoides* shares the presence of trichodragmata with other species of *Axinella*, such as *A. flustra* Topsent, 1892a, A. *dissimilis* (Bowerbank, 1866), *A. infundibuliformis* (Linnaeus, 1791) and *A. shoemakeri* (de Laubenfels, 1936a).

Habitat and distribution. The species is restricted to the Mediterranean and East Atlantic. It is found from shallow water to 367 m depth but is generally abundant at depths of 30–40 m associated to soft or hard substrates, protected vertical walls or shallow and dark habitats (Uriz, 1982).

CYMBASTELA HOOPER & BERGQUIST, 1992

Synonymy

Cymbastela Hooper & Bergquist, 1992: 103.

Type species

Pseudaxinyssa stipitata Bergquist & Tizard, 1967: 189 (by original designation).

Fig. 4. *Axinella polypoides* Schmidt, 1862. A, diagram of the choanosomal skeleton. B, style. C, oxea (scale 50 μm).

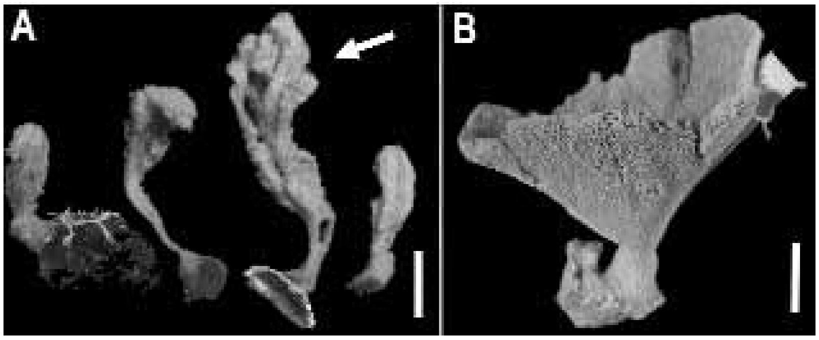

Fig. 5. A, *Axinella sulcata* (Schmidt, 1875), lectotype, ZMUC DEM-241 (indicated with an arrow) and paralectotypes, ZMUC DEM-242-244. B, *Axinella infundibuliformis* (Linneaeus, 1791), BMNH 1930.7.3.370 (scales A, 1 cm; B, 2.5 cm).

Definition

Axinellidae with choanosomal skeleton plumoreticulated and made exclusively of oxeas.

Diagnosis

Cup-shaped, thinly lamellate or lamellate-flattened-encrusting habit. Surface smooth with choanosomal or ectosomal spicules projecting slightly; with or without specialised skeleton of smaller oxeas. Choanosomal skeleton generally differentiated in axial and extra-axial regions; axial skeleton condensed or vaguely reticulated; extra-axial skeleton plumoreticulate with plumose spicule tracts enveloped with thin sheets of spongin or well formed spongin fibres. Megascleres are oxeas often with telescoped points (emended from Hooper & Bergquist, 1992; Van Soest *et al*., 1996b).

Remarks

Cymbastela is considered here to have close affinities with species of *Axinella* having similar growth forms (i.e., flabellate-lamellate) and skeleton as suggested by Hooper & Bergquist (1992). One of its species however, *C. coralliophilla* Hooper & Bergquist, possesses a specialised ectosomal skeleton which is not typical of other Axinellidae. Phylogenetic analysis using partial 28S rDNA sequences also showed that *C. coralliophilla* is not closely related to other *Cymbastela* species, such as *C. stipitata* and *C. vespertina* (Alvarez *et al*., 2000a). Future studies are required to confirm the generic position of *C. coralliophila. Cymbastela hooperi* Van Soest *et al*., 1996b reported from the Great Barrier Reef, is distinguished from other species of *Cymbastela* by its growth form, which is stalkless and flattened on the substratum, yellow coloured with a loose skeletal morphology of vaguely plumose and wavy ascending tracts (Van Soest *et al*., 1996b).

Amphimedon terpenensis Fromont, 1993 is now considered a species of *Cymbastela* based on skeletal and chemical (i.e., presence of di-isocyano-adociane) similarities with *C. hooperi* (Van Soest *et al*., 1996b).

Other species of *Cymbastela* are: *C. cantharella* (Lévi, 1983) (as *Pseudaxinyssa*) (Hooper & Lévi, 1993b: 1397); *C. concentrica* (Lendenfeld, 1887c) (as *Antherochalina*); *C. coralliophila* Hooper & Bergquist, 1992: 120; *C. hooperi* Van Soest *et al*., 1996b: 104; *C. marshae* Hooper & Bergquist, 1992: 127; *C. notiaina* Hooper & Bergquist, 1992: 128; *C. vespertina* Hooper & Bergquist, 1992: 110.

Distribution

The genus has been reported from Australia (Hooper & Bergquist, 1992; Hooper & Wiedenmayer, 1994) and New Caledonia (Hooper & Lévi, 1993b) but is also present in New Zealand (Alvarez, unpublished data).

Description of type species

Cymbastela stipitata (Bergquist & Tizard, 1967) (Figs 6–7).

Synonymy. *Pseudaxinyssa stipitata* Bergquist & Tizard, 1967: 189–191. *Cymbastela stipitata*; Hooper & Bergquist, 1992: 106.

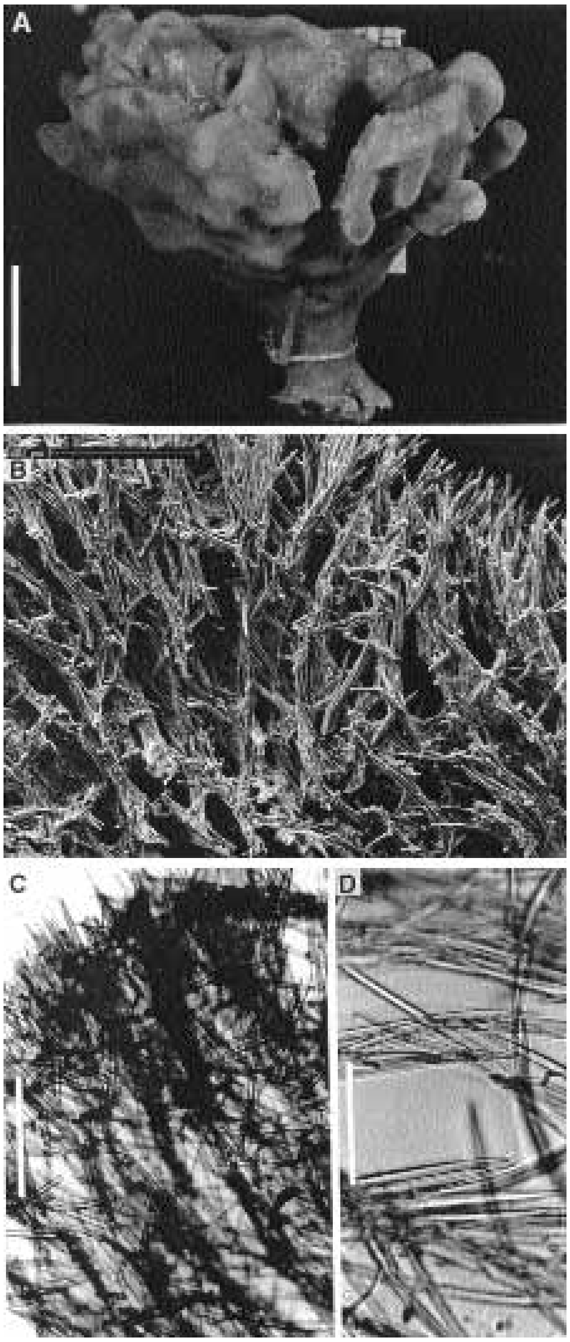

Fig. 6. *Cymbastela stipitata* (Bergquist, 1967). A, holotype, AM Z3101. B, SEM of the skeleton. C, longitudinal section through the periphery. D, detail of spicule tracts (scales A, 2 cm; B, 500 μm; C, 200 μm; D, 100 μm).

Material examined. Holotype: AM Z3101, wet – Dudley Point Reef, Darwin, Northern Territory, coll. E. Pope & J. Boase, 13. x.1965.

Description. Cup-shaped, approximately 8 cm wide and 7 cm tall; on stalk 2 cm in diameter; surface smooth with rounded and digitate projections, microscopically hispid due to projection of spicules; pores 1–1.8 mm in diameter, evenly distributed; colour green-brown; consistency firm but flexible (Fig. 6A). Specialised ectosomal skeleton absent. Choanosomal skeleton plumoreticulate with plumose primary tracts, 50–150 μm thick, ending in brushes at surface; secondary tracts (no more than one spicule long), often paucispicular but some multispicular, with spicules stacked, connecting primary tracts at more or less regular intervals. (Figs 6B–D, 7A). Spicules are oxeas, length 250–320 μm (290 ± 22.0), width 5–20 μm (13.4 ± 3.9) (n = 10) (Fig. 7B–D).

Remarks. *Cymbastela stipitata* has been extensively redescribed and compared to other species of *Cymbastela* by Hooper and Bergquist (1992). Its closest relative is *C. vespertina* Hooper & Bergquist, 1992, another northwestern Australian species, that differs from *C. stipitata* in habitat, colour and in the thickness of the lamella (Hooper & Bergquist, 1992). Phylogenetic analyses based on molecular and morphological data, also point out to the closest relationships between these two species (Alvarez *et al*., 2000a).

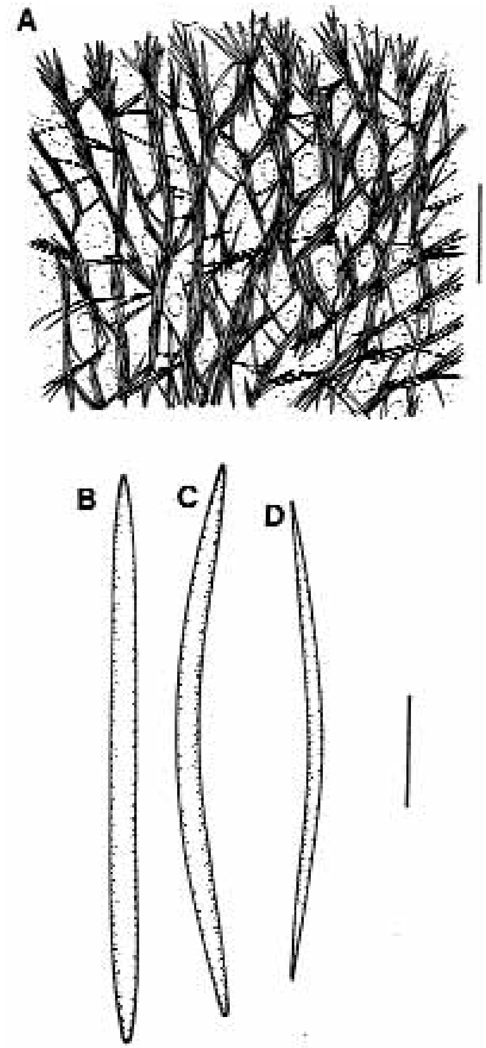

Fig. 7. *Cymbastela stipitata* (Bergquist, 1967). A, diagram of the choanosomal skeleton. B, oxeas (scales A, 200 μm; B–D, 50 μm).

Habitat and distribution. The species is restricted to northern Australia. It is found from shallow waters to 19 m depth; mostly associated to hard substrates and turbid waters (Hooper & Bergquist, 1992).

DRAGMACIDON HALLMANN, 1917

Synonymy

Dragmacidon Hallmann, 1917c: 639. *Pseudaxinella sensu* de Laubenfels, 1936a: 131; Bergquist, 1970: 20; Lévi, 1973; Wiedenmayer, 1977b: 152, 155; Wiedenmayer, 1989: 47; Hooper & Lévi, 1993b: 1436; Alvarez *et al*., 1998; Not *Pseudaxinella* Schmidt, 1875: 120; Thiele, 1903b: 378 (=*Axinella*).

Type species

Thrinacophora agariciformis Dendy, 1905: 186 (by original designation).

Definition

Axinellidae with a plumoreticulate choanosomal skeleton and undifferentiated axial and extra-axial regions. Megascleres are oxeas and styles. Microscleres if present, are trichodragmata.

Diagnosis

Unbranched, club-shaped, lobate, shrub-like, thickly encrusting or massive habit. Surface more or less smooth with short conules or tubercles; oscules circular, flush or slightly elevated, sometimes with superficial canals leading to opening. Ectosome without specialised skeleton. Choanosomal skeleton plumoreticulate with ascending plumose tracts, anastomosing or interconnected by secondary multispicular tracts; not differentiated into axial or extra-axial regions. Megascleres oxeas and/or styles generally in similar proportions and dimensions. Microscleres if present, raphides in tightly packed trichodragmata.

Remarks

Dragmacidon was erected by Hallmann (1917c) to include two species of *Thrinacophora* that lack the special dermal megascleres (i.e., without a typical raspailiid ectosome). The genus was reserved for more or less massive species with skeleton of plumose columns of styles and oxeas, and with raphides, single or in trichodragmata as the only type of microscleres. Other species included in *Dragmacidon* by Hallmann (1917c) were *T. durissima* Dendy, 1905, *Halichondria clathriformis* Lendenfeld, 1888 and *Ciocalypta incrustans* Whitelegge, 1897. Hallmann's diagnosis of *Dragmacidon* corresponds to the concept of *Pseudaxinella* by recent authors (Bergquist, 1970: 20; Lévi, 1973; Wiedenmayer, 1977b: 152, 155; Wiedenmayer, 1989: 47; Hooper & Lévi, 1993b: 1436; Alvarez *et al*., 1998). Given that *Pseudaxinella s.s* is a junior synonym of *Axinella* (see above under remarks of *Axinella*), *Dragmacidon* becomes a suitable genus to locate those species that have been referred to *Pseudaxinella* by most authors. The above diagnosis is based on the type species of *Dragmacidon* and the descriptions of many of those *Pseudaxinella* spp.

The closest genera to *Dragmacidon* are *Axinella* and *Cymbastela*. They all share a plumoreticulate choanosomal skeleton of ascending plumose tracts but *Dragmacidon* differs from them in growth form, surface features and in the absence of an axial skeleton. *Dragmacidon* also shares with *Axinella* the spicule composition (i.e., oxeas, styles and trichodragmata in similar size categories). These three genera are likely to constitute a monophyletic group that could be classified as a subfamily within Axinellidae. Phylogenetic analyses based on morphological characters support this view (Alvarez, 1998).

Distribution

The genus has a widespread distribution according to Van Soest (1994) and contains approximately 17 species, including those assigned to *Pseudaxinella* by previous authors (Alvarez, 1998).

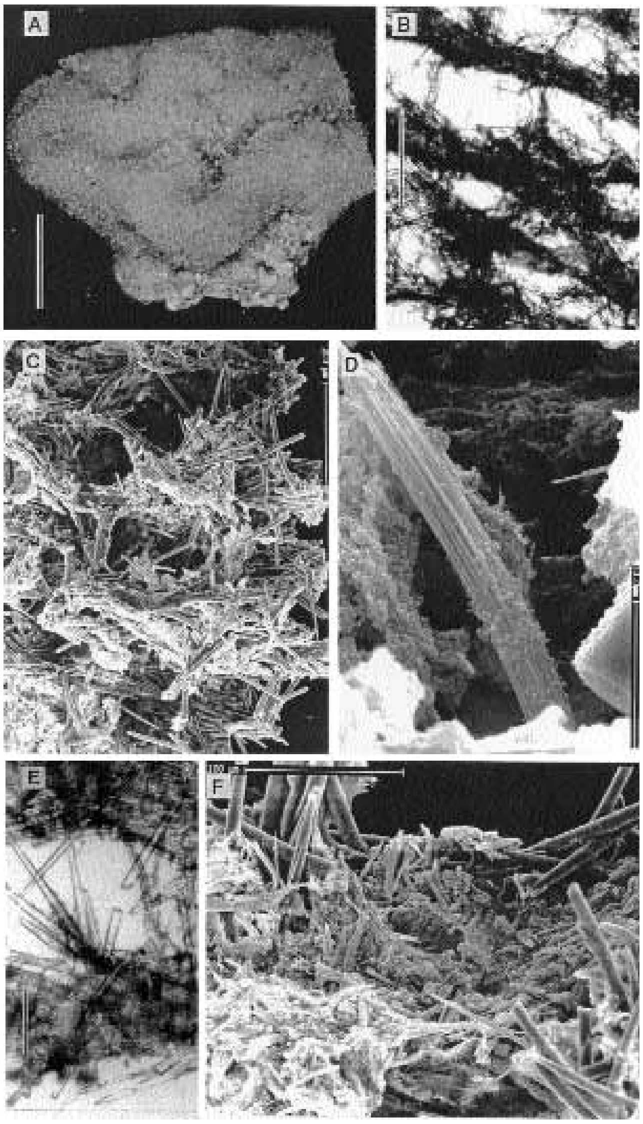

Fig. 8. *Dragmacidon agariciformis* (Dendy). A, holotype, BMNH 1907.2.1.74. B, longitudinal section through the periphery. C, SEM of longitudinal section through skeleton. D, trichodragmata. E, detail of spicule tracts. F, SEM of skeleton and trichodragmata near surface (scales A, 120 mm; B; 300 μm; E, 50 μm).

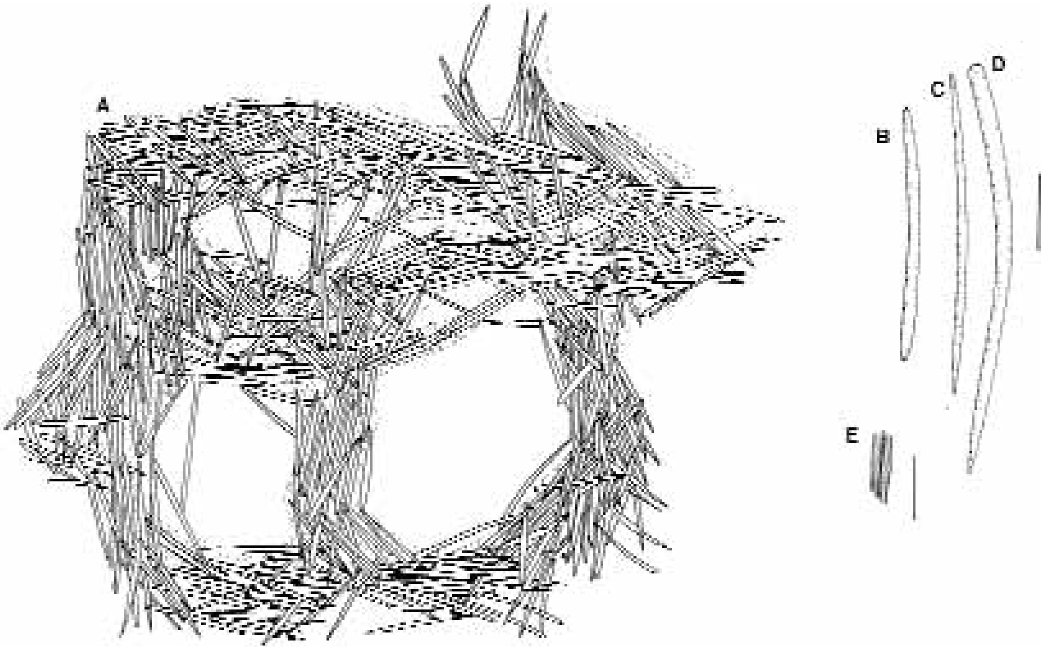

Fig. 9. *Dragmacidon*. A, *Dragmacidon reticulata* (Ridley & Dendy, 1886), diagram of the choanosomal skeleton. B–E, *Dragmacidon agariciformis* (Dendy), spicules (scales B–D, 50 μm; E, 10 μm).

Previous reviews

Topsent (1928c: 37); de Laubenfels, 1936a: 131; Bergquist, 1970: 20; Lévi, 1973; Wiedenmayer, 1977b: 152, 155; Wiedenmayer, 1989: 47; Hooper & Lévi, 1993b: 1436; Alvarez *et al*., 1998.

Description of type species

Dragmacidon agariciformis (Dendy, 1905) (Fig. 8).

Synonymy. *Dragmacidon agariciformis* Hallmann, 1917c: 639; *Axinella agariciformis* Burton, 1959a: 259.

Material examined. Holotype: BMNH 1907.2.1.74 – Ceylon.

Description. Massive, cushion shaped, approximately 4 cm in diameter; on broad base; surface conulose, corrugated with rounded to irregular depressions, covered by a thin transparent membrane; colour yellow-orange in alcohol; consistency firm. (Fig. 8A). Specialised ectosomal skeleton absent; choanosomal skeleton plumoreticulate, with ascending plumose tracts, 60–150 μm loaded with broken spicules and cemented by spongin, connected by uni-multispicular tracts, up to 100 μm, in all directions.(Figs 8B–C, E–F, 9A). Styles in two size categories: (a) length 650–670 μm (656.7 ± 11.6), width 5–8 μm (6 ± 1.7) (n = 3) very rare; (b) length 165–335 μm (212.6 ± 56.4), width 5–10 μm (6.5 ± 2.1) (n = 11). Oxeas, with telescoped tips, length 185–298 μm (224.5 ± 34.9), width 3–10 μm (7.8 ± 2.3) (n = 10). (Fig. 9B–E). Trichodragmata, length 20–70 μm (43.3 ± 25.2), width 6–35 μm (15.7 ± 16.7) (n = 3), perhaps in two categories, generally located below the surface (Figs 8D, F, 9E).

Remarks. *Dragmacidon agariciformis* was referred to *Axinella* by Burton (1959a) without comment and its transfer here to *Dragmacidon* was suggested by Hallmann (1917c). It is very similar to *D. durissima* (Dendy, 1905) from the same locality, differing slightly in habit and in the dimensions of the megascleres. *Dragmacidon durissima* is closely related, both genetically and morphologically to other species of *Dragmacidon* previously referred to *Pseudaxinella*, i.e., *D. australis* from the South Pacific and North coast of Australia (Hooper & Wiedenmayer, 1994; Alvarez *et al*., 2000a) and *D. reticulata* from the Central-West Atlantic (Alvarez *et al*., 1998).

Habitat and distribution. The species is restricted to the Indian Ocean at depths of 38 m (Dendy, 1922b; Burton, 1959a).

DRAGMAXIA HALLMANN, 1916

Synonymy

Dragmaxia Hallmann, 1916b: 543.

Type species

Spongosorites variabilis Whitelegge, 1907: 513 (by original designation).

Definition

Axinellidae (?) with styles/rhabdostyles forming plumose axes and pointing outwards in the periphery. Microscleres are long sinuous trichodragmata and raphides. Terminal ends of raphides ornamented with fine spines.

Diagnosis

Lamellate, flabellate, cup-shaped or massive habit; surface marked with small ridges; ectosome without specialised ectosomal skeleton. Choanosomal skeleton composed of ascending and dendritically branched axes of spicules, with peripheral individual spicules curving outward toward surface and rarely interconnected. Megascleres styles only, straight or bent near the base, in widely different sizes. Microscleres long, sinuous trichodragmata and single raphides ornamented by fine spines at terminal points.

Remarks

Dragmaxia was erected by Hallmann (1916b) in Axinellidae to include *Spongosorites variabilis*, a species characterised by a skeleton of plumose axes of styles and by the presence of long raphides (trichites in Hallmann's terminology) that were interpreted by Whitelegge (1907) as microxeas and sinuous trichodragmata. The definition of Hallmann was expanded by Alvarez *et al*. (1998) to include *D. undata* Alvarez *et al*., 1998: 26, a massive encrusting species with the same type of long raphides and trichodragmata, but without clear spicules bundles, as the ones present in the type species. The raphides, in both *D. variabilis* and *D. undata* are ornamented with extremely fine spines in arrow shape, which seems to be a diagnostic feature for the genus (Fig. 11).

Dragmaxia was considered a synonym of *Stylissa* by Hooper & Lévi (1993b) following de Laubenfels (1936a). According to these authors, the differences between the two genera were not substantial to keep them separated; however, after examination of the type material of *Stylissa* it is concluded that the two genera, should be kept separate. The skeleton in *Stylissa* (see chapter on Dictyonellidae) is less organised, nearly halichondrioid as in other Dictyonellidae such as *Dictyonella, Scopalina* and *Rhaphoxya* (transferred to Dictyonellidae in this work). The skeleton of *Dragmaxia* consists of dendritic axes with spicules pointing outward toward the surface.

Dragmaxia is provisionally kept in Axinellidae as it lacks a clear plumose or plumoreticulate skeleton. Further, some of the megascleres are rhabdostyle-like, which resembles a feature present in raspailiid sponges and the raphides with ornamented ends do not seem to be homologous with those present in species of *Axinella* or *Dragmacidon*.

Distribution

The genus is represented only by two species with a disjunct distribution: *Dragmaxia variabilis*, from the East coast of Australia and *D. undata* Alvarez *et al*., 1998 from the Caribbean. *Tuberella ciliata* Wilson, 1925 from the Philippines, was redescribed by de Laubenfels (1935a) under *Dragmaxia*. The descriptions of Wilson (1925) and de Laubenfels (1935a), however, do not agree with the concept of *Dragmaxia* given in this work. That species seems to belong to the genus *Aaptos* (Suberitidae).

Previous reviews

Hallmann (1916b): 543; de Laubenfels, 1936a: 130; Hooper & Lévi, (1993b): 1422. Alvarez *et al*. (1998).

Description of type species

Dragmaxia variabilis (Hallmann, 1916b) (Figs 10–11).

Synonymy. *Spongosorites variabilis* Whitelegge, 1907: 513. *Dragmaxia variabilis*; Hallmann, 1916b: 543. *Stylissa variabilis*; Hooper & Wiedenmayer, 1994: 84.

Material examined. Holotype: AM, missing. Other material. AM G10173 – dry, off Wata Mooli, NSW, Australia, coll. R.V. 'Thetis', stn 41. AM Z5103-Z 5109 – slides, Off Wata Mooli, NSW, Australia.

Description. Flabelliform, approximately 7 cm high and 9 cm wide; on small peduncle; surface marked by a reticulum of spicule tracts; colour brown-orange in dry state. Specialised ectosomal skeleton absent; choanosomal skeleton with ascending plumose tracts, 300–600 μm thick, with spicules or brushes of spicules of same kind, curved outward to surface; generally dendritic but might anastomose or be joined by spicules of adjacent tracts (Fig. 10A–B). Subtylostyles-styles-rhabdostyles, length 354–709 μm (549.4 ± 87.8), width 10–26 μm (16.8 ± 4.2) (n = 25) (Fig. 10D–E), some sinuous; raphides, single and as trichodragmata (Fig. 10F), ornamented with extremely fine spines (Fig. 11), length 60–110 μm (90.8 ± 17.4).

Remarks. Although the holotype of the species is missing, the species can be recognised from the descriptions given by Whitelegge (1907) and Hallmann (1916b) and from the examination of additional specimens collected in the same area and expedition.

Habitat and distribution. The species is known only from the type locality (SE coast, New South Wales, Australia). It is found at depths of 42 m (Hooper & Wiedenmayer, 1994).

PARARHAPHOXYA BURTON, 1934

Synonymy

Pararhaphoxya Burton, 1934a: 565.

Type species

Pararhaphoxya tenuiramosa Burton, 1934a: 565 (by original designation; junior synonym of *Sigmaxinella pulchra* Brøndsted, 1924a).

Definition

Axinellidae with an axial core of interwoven strongyles and extra-axial skeleton made exclusively by oxeas.

Diagnosis

Stalked and branching habit. Surface smooth; oscules, when visible, form stellate patterns on the branches; consistency cartilaginous-like when alive; ectosome membranous without specialised skeleton. Choanosomal skeleton differentiated in axial and extra-axial regions; axial skeleton with thick core of interwoven strongyles dividing dichotomously along the branches; extra-axial skeleton with oxeas, single or in plumose tracts orientated at right angles to the axis. Megascleres sinuous strongyles, always located at the axial skeleton and oxeas. Microscleres absent.

Remarks

Sigmaxinella pulchra was considered conspecific with *Pararhaphoxya tenuiramosa* by Bergquist (1970) based on her examination of the type material. Brøndsted's specimen was

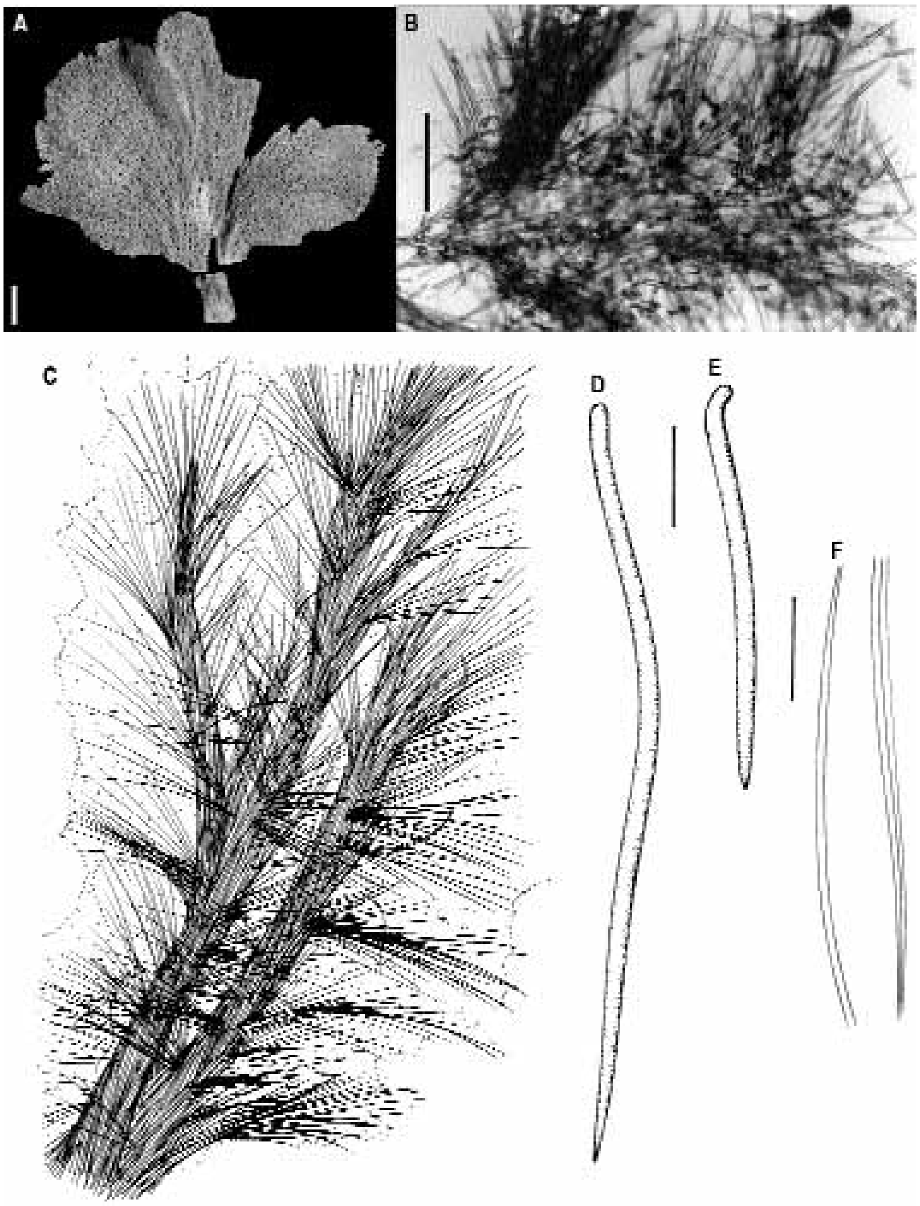

Fig. 10. *Dragmaxia variabilis* (Whitelegge, 1907). A–B, possible syntype, AM G10173. C, diagram of the skeleton. E–D, styles. F, raphides (scales A, 1 cm; B–E, 100 μm; F, 50 μm).

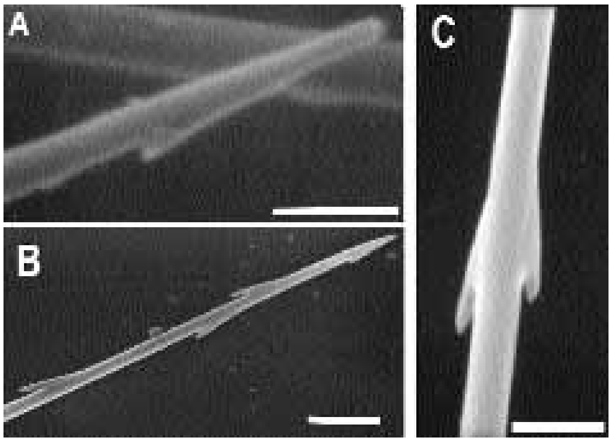

Fig. 11. *Dragmaxia*. SEMs of spiny raphides. A, *Dragmaxia variabilis*, AM G10173. B–C, *Dragmaxia undata*, USNM 39451 (scales 1 μm).

contaminated with spicules from the species *Biemna stylotata* and therefore overlooked by Burton when he erected *Pararhaphoxya*.

Pararhaphoxya is a typical axinellid, well defined by the features of the extra-axial skeleton. It shares features with *Axinella* (i.e., branching habit, surface imprinted by stellate oscules; skeleton differentiated in axial and extra-axial regions, extra-axial skeleton plumoreticulated and oxeas) and *Phakellia* and *Auletta* (i.e., sinuous strongyles in the main axis).

Pararhaphoxya has been previously referred to the Axinellidae (Burton, 1934a), Halichondrina: Axinellidae: Axinellinae (de Laubenfels, 1936a) and Axinellida: Axinellidae (Bergquist, 1970).

Distribution

The genus is restricted to Australia, New Zealand and W Pacific Ocean and currently represented only by the type species. A second species from northern New Zealand (Battershill & Bergquist, 1990: 68) remains to be formally described. Other material from Western Australia examined by one of us (BA) also belongs to this genus.

Previous reviews

De Laubenfels, 1936a: 130; Bergquist, 1970: 16; Hooper & Lévi, 1993b: 1413.

Description of type species

Pararhaphoxya pulchra (Brøndsted, 1924a) (Fig. 12).

Synonymy. *Sigmaxinella pulchra* Brøndsted, 1924a: 151. *Pararhaphoxya pulchra* Bergquist, 1970: 16. *Pararhaphoxya tenuiramosa* Burton, 1934a: 565; de Laubenfels, 1954: 173; Bergquist, 1970: 16.

Material examined. Holotype (of *Pararhaphoxya tenuiramosa*): BMNH 1930.8.13.145 – Great Barrier Reef.

Description. Erect on stalk; branches dichotomous, slender and cylindrical (3–7 mm in diameter), generally with bifid ends; surface hispid; colour orange alive, grey-white in alcohol; consistency cartilaginous (description of external characters completed from Burton, 1934a; Bergquist, 1970) (Fig. 12A). Specialised ectosomal skeleton absent; choanosomal skeleton with axial core of interwoven strongyles, dividing dichotomously along the branches, plumo-echinated by oxeas single, or in bundles (Fig. 12B). Sinuous strongyles, length 950–2050 μm (1314 ± 401), width 5–10 μm (6.1 ± 1.9) (n = 10) some with subterminal knobs; oxeas, length 340–610 μm (492 ± 76.6), width 5–10 μm (7.2 ± 2.0) (n = 10) with telescoped, blunted tips. Occasionally styles (see Bergquist, 1970: 16) (Fig. 12C–D).

Remarks. *Pararhaphoxya pulchra* is so far the only species described for the genus. It is related to an undescribed common northern New Zealand species recorded by Battershill & Bergquist (1990). Both are arborescent species with dichotomous branches. In the latter, however, the extra-axial skeleton is well defined, plumoreticulate and formed exclusively by oxeas.

Habitat and distribution. The species has been recorded from the Great Barrier Reef, New Zealand and western Pacific, at depth range 4–81 m.

PHAKELLIA BOWERBANK, 1862

Synonymy

Phakellia Bowerbank, 1862b: 1108. *Adreissa* Topsent, 1932a: 63 (new synonym).

Type species

Halichondria ventilabrum (sic) (=*Spongia ventilabra* Linnaeus, 1767: 1296) (by original designation).

Definition

Axinellidae of planar habit with multiple axes of sinuous strongyles connected by secondary tracts of single spicules.

Diagnosis

Thin-plated or fan-shaped growth form, generally on peduncle. Surface hispid, with points of large choanosomal styles projecting through ectosome; ectosome without specialised skeleton. Choanosomal skeleton plumoreticulate, with multiple axes differentiated into primary and secondary tracts. Primary tracts, thick, visible as 'veins' or stout lines strengthening fan; formed by sinuous strongyles or strongyloxeas; plumo-echinated by styles and connected by secondary tracts of styles, strongyles or strongyloxeas. Megascleres, sinuous or vermiform strongyles, strongyloxeas, and styles sometimes in several size categories; occasionally oxeas. Microscleres absent.

Remarks

Some authors (Vosmaer, 1912; Bergquist, 1970; Hooper & Lévi, 1993b) employ a broad definition of *Phakellia*, which overlaps with what is considered *Acanthella* by others (Van Soest *et al*., 1990; Alvarez *et al*., 1998). The lack of clear definition and differentiation between the two genera has created confusion and consequently they contain a heterogenous complex of species. We emphasise here the reticulate (*Phakellia*) versus the dendritic (*Acanthella*) peripheral skeletons, and the flabelliform (*Phakellia*) versus the irregularly ramose-bushy form (*Acanthella*) as distinctive characters to define both genera and avoid further confusion over the assignment of species. Regional revisions of species are required to allocate taxa to either *Acanthella* or *Phakellia*.

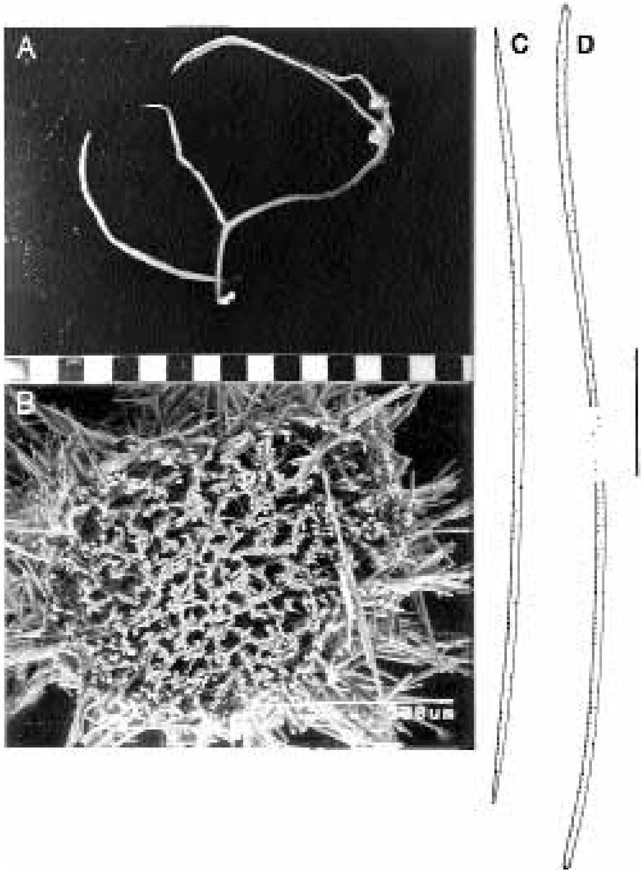

Fig. 12. *Pararhaphoxya tenuiramosa* Burton. A, holotype, BMNH 1930.8.13.145. B, SEM of the choanosomal skeleton. C–D, spicules (scale 100 μm).

Adreissa (type species *Spongia labellum* Lamarck, 1814, Lamarck'species No. 56, two specimens, MNHN LBIM DT607 and DT3385; locality, Madagascar [?]) is considered here to be a synonym of *Phakellia*. The species is a typical *Phakellia* in growth form and surface features, with vein-like tracts enforcing the fan, and with two size categories of styles. It differs from other species in that strongyles are reduced to very thin and sinuous styles-strongyles.

Phakellia has been previously referred to Silicea (Bowerbank, 1862b: 1095), Coralliospongia: Phakelliadae (Gray, 1867a), Echinonema: Axinellida (Carter, 1885d), Axinellidae: Axinellinae (Lendenfeld, 1889a), Monaxonida: Halichondrina: Axinellidae (Ridley & Dendy, 1886; Topsent, 1894c; Topsent, 1896a; Topsent, 1904b; Topsent, 1928c) and Halichondrida: Axinellidae (Van Soest *et al*., 1990; Alvarez *et al*., 1998).

Distribution

According to Van Soest (1994), the genus has an Arctic-Boreal distribution and is restricted to deep and/or colder waters. On the other hand Hooper & Wiedenmayer (1994) reported a wider distribution for the genus, which includes the amphi-Atlantic, Mediterranean Sea, Red Sea, Indian Ocean, Indo-Malayan region, Japan and New Zealand. Species of *Phakellia* are also present in the Central-West Atlantic (Alvarez *et al*., 1998). Differences in the patterns of distribution are a consequence of the different interpretations of this genus by various authors and the fact that many species allocated to *Phakellia* probably belong to other genera. The genus contains approximately 34 valid species (Alvarez, 1998).

Previous reviews

Bowerbank, 1864: 186; Bowerbank, 1866: 122; Gray, 1867a: 516; Schmidt, 1880b: 81; Ridley & Dendy, 1886: 478; Ridley & Dendy, 1887: 169; Dendy, 1897: 235; Thiele, 1898: 51; Topsent, 1894c; Wilson, 1902: 399; Topsent, 1904b: 137; Dendy, 1905: 190; Vosmaer, 1912: 310; Ferrer-Hernández, 1914b: 26; Dendy, 1922b: 116; de Laubenfels, 1936a: 130; Lévi, 1973: 605; Bergquist, 1970: 17; Hooper & Lévi, 1993b: 1413.

Description of type species

Phakellia ventilabra (Linnaeus, 1767) (Figs 13–14).

Synonymy. *Spongia ventilabra* Linnaeus, 1767: 1296. *Halichondria ventilabrum* (sic); Johnston, 1842: 107. *Phakellia ventilabrum* (sic); Bowerbank, 1866: 122; Carter, 1876: 240; Fristedt, 1885: 47; Vosmaer, 1885a: 23; Ridley & Dendy, 1887: 170; Topsent, 1891a: 529; Vosmaer, 1912: 316; Dendy 1922b: 118; Topsent, 1928c: 174; Cabioch, 1968b: 221; Vacelet, 1969: 178; Ackers *et al*., 1992: 85; Boury-Esnault *et al*., 1994b: 89.

Material examined. Neotype (proposed): BMNH 10.1.1.2687, dry – near Lervig, Norway. Other material. Nine specimens, BMNH 77.5.21.141, wet – Haff Banks, Shetland, coll. Humphreys, 1852.

Description of neotype (Fig. 13A). Flabellate specimen, dry, approximately 10–23 cm high by 10–20 cm wide; on short peduncle, approximately 1 cm in diameter; surface hispid, marked by reticule of spicule tracts, some ascending ones thick (5–7 mm) like veins. Specialised ectosomal skeleton absent; choanosomal skeleton reticulated, with primary tracts of sinuous strongyles, 300–600 μm thick, plumo-echinated by styles or connected by secondary unispicular or paucispicular tracts of styles, and sometimes strongyles, 60–200 μm thick (Figs 13C, 14A). Spicules are sinuous strongyles, length 630–1060 μm (897 ± 155.1), width 13–18 μm (14.1 ± 1.7) (n = 10) and styles, length 360–710 μm (505 ± 93.8), width 10–15 μm (11.7 ± 1.9) (n = 10), some flexuous and generally bent near the head (Fig. 14B–D).

Description of species. Flabelliform or cup-shaped to flabelliform; on small peduncle; surface marked by a reticulation of 'vein-like' lines; oscules pores uniformly distributed on one or both sides of the lamella; colour grey or pale-yellow-green; grey- beige in alcohol; consistency firm, elastic (external features taken from Bowerbank 1866; Ackers *et al*., 1992) (Fig. 13A–B). Specialised ectosomal skeleton absent; choanosomal skeleton consists of an ascending reticulation of thick primary tracts (up to 7 mm), marking surface, densely packed with sinuous strongyles, plumo-echinated by styles single or in bundles and connected by lines or secondary tracts of sinuous strongyles or styles; axial skeleton compressed and only distinguishable at peduncle (Figs 13D, 14A). Sinuous strongyles, length 460–1060 μm (758 ± 189.1) (n = 20); width 10–18 μm (13.4 ± 2.3) (n = 20); styles, length 340–710 μm (458 ± 91.0) (n = 20); width 8–15 μm (11.2 ± 1.8) (n = 20).

Remarks. The description of *Spongia ventilabra* of Linnaeus refers to an illustration given by Seba (1758: 184, tab. 95 fig. 8) and also to *Spongia strigosa* Pallas, 1766: 397. The description of Pallas' species also mentions Seba's illustration. Vosmaer (1912: 311), following Esper (1794), suggested on this basis that both species were synonyms and that the type of *Phakellia* should be called *Phakellia strigosa* (Pallas). However, no author except Bergquist (1970) who merely listed the name *P. strigosa* has followed this synonym.

An application to suppress the name of *Spongia strigosa* Pallas, 1766 has been submitted to the International Commission on Zoological Nomenclature (Alvarez & Willan, in press). This application (Case number 3216) seeks also to preserve the spelling of Linneaus' species as *ventilabrum* as this is the name in prevailing use, and to designate the specimen BMNH 10.1.1.2687 as the neotype of the species, given that there is good evidence that the original specimen of *Spongia ventilabra* is no longer extant.

Habitat and distribution. The species is distributed in the Arctic, North and East Atlantic and Mediterranean. It is found at depths of 10–1863 m on sheltered locations and rock ridges (Ackers *et al*., 1992; Boury-Esnault *et al*., 1994b).

PHYCOPSIS CARTER, 1883

Synonymy

Phycopsis Carter, 1883b: 319. *Ketosus* de Laubenfels, 1936a: 130 (new synonym).

Type species

Phycopsis hirsuta Carter, 1883b: 319 (by subsequent designation; Thiele, 1899: 11).

Definition

Axinellidae with ascending multispicular tracts, radiating from central axis and ending in long and filamentous surface processes.

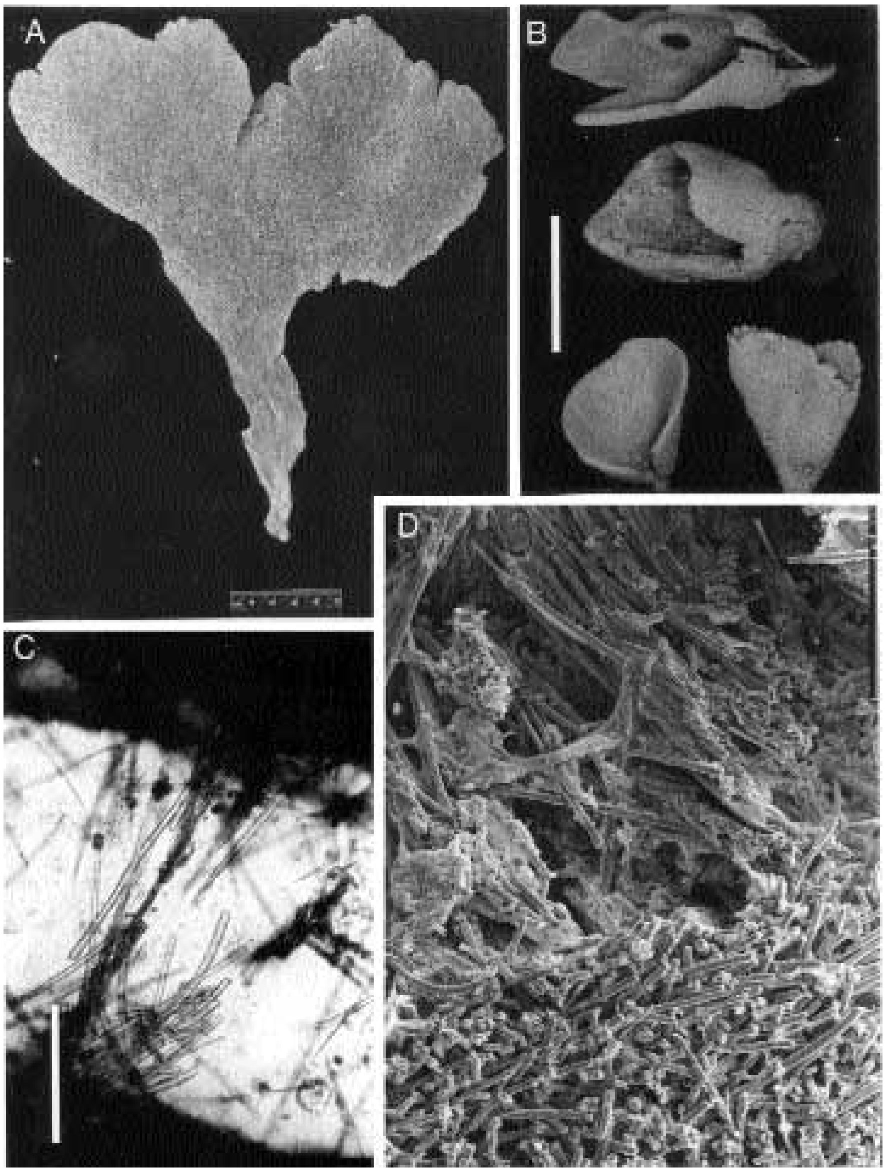

Fig. 13. *Phakellia ventilabra* (Linneaus). A, neotype, BMNH 10.1.1. 2687. B, 4 of 9 specimens from the Shetlands, BMNH 77.5.21.141. C, BMNH 10.1.1.2687, section through the choanosomal skeleton at the periphery. D, BMNH 77.5.21.141, SEM of the choanosomal skeleton (scales B, 3 cm; C, 400 μm; D, 200 μm).

Diagnosis

Branching-bushy-stipitate and stalked growth form. Surface villous with long processes as filaments; ectosome without specialised skeleton. Choanosomal skeleton differentiated into axial and extra-axial regions. Axial skeleton compressed and vaguely reticulated with close-set of spongin fibres and spicules. Extra-axial skeleton with thick spongin fibres cored by ascending multispicular tracts, radiating from central axis and ending in surface processes. Megascleres strongyles, oxeas-anisoxeas and styles (including sinuous forms), not localised in any particular area of the skeleton. Microscleres absent.

Remarks

Phycopsis is related to *Reniochalina* and *Ptilocaulis*. The three genera have similar spicule composition (with only *Reniochalina* having oxeas-anisoxeas with spined tips) and a skeleton of ascending spicule tracts sheathed by spongin, that end as surface processes (distinct for each of the genera).

Ketosus is a monotypic genus erected by de Laubenfels (1936a) for *Dictyocylindrus setosus* Bowerbank, 1873b: 325, with a brief diagnosis that overlaps significantly with several genera of Axinellidae (i.e., *Acanthella, Phakellia, Pararhaphoxya*). The features of the type species *Phycopsis setosa* (Bowerbank, 1873b) (new combination and lectotype designated here, BMNH 1877.5.21.1310, slide, ‘Bowerbank collection, Bere Regis, Devonshire (?)’) as well as the original description given by Bowerbank (1873b), agrees with the diagnosis of *Phycopsis* as presently understood. *Phycopsis setosa* has surface projections in the shape of ‘setae’, considered here homologous with the long filamentous processes present in other species the genus. It also shares with other species the skeletal organisation (Fig. 15E) and the type of spicules (strongyles, oxeas-anisoxeas and styles; Fig. 16D–E). It, however, differs in growth form, which is fan-shaped instead branching or arborescent as seen in other *Phycopsis* spp.

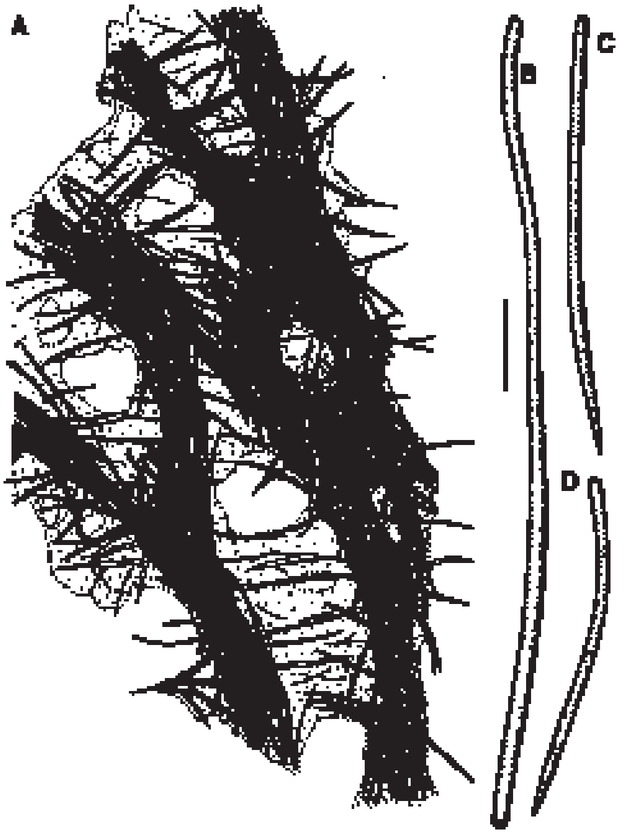

Fig. 14. *Phakellia ventilabra* (Linneaus), BMNH 10.1.1.2687. A, diagram of the skeleton. B, strongyle. C–D, styles (scale 100 μm).

The type locality of *P. setosa* is ambiguous, given the possibility that the locality originally assigned by the collector is erroneous (Bowerbank, 1873b). Indeed a species like this one has not been recorded yet from the well-known fauna of the NE Atlantic and therefore this record is definitely not reliable to expand the distribution of *Phycopsis* which, is currently limited to southern latitudes.

Both *Phycopsis hirsuta* and *P. setosa* closely resemble species of *Ptilocaulis* reported from New Caledonia, viz., *P. fusiformis* Lévi, 1967a, *P. epakros* Hooper & Lévi, 1993b and *P. papillatus* Hooper & Lévi, 1993b. *Phycopsis* might be a more appropriate genus for the New Caledonian species; they all share with *Phycopsis hirsuta* the long surface projections of the choanosomal skeleton and have similar spicule composition and habit. Close phylogenetic relationships among these species were also shown by Hooper & Lévi (1994). Other species of *Phycopsis* are: *P. fruticulosa* Carter, 1883b: 320 and *P. hispidula* (Ridley, 1884a), and *P. terpnis* de Laubenfels, 1954: 176. *Axinyssa aculeata* Wilson, 1925 from Hawaii was referred to *Phycopsis* by de Laubenfels (1936a: 131; 1951: 263) and Tanita & Hoshino (1989: 89), but the species is currently assigned to its original genus (Van Soest *et al*., 1990; Hooper & Bergquist, 1992).

Phycopsis has been previously referred to Echinonemata: Axinellida (Carter, 1883b; Carter, 1884a,b, 1885d), Halichondrina: Axinellidae (Topsent, 1904b; Topsent, 1928c) and Raspailiidae (Van Soest *et al*., 1990).

Distribution

Tasmania, South Australia, Indo-Malaysia, W Pacific (Hooper & Wiedenmayer, 1994), New Caledonia.

Previous reviews

Carter, 1883b: 319; Carter, 1884a: 130; Thiele, 1899: 11; Topsent, 1904b: 137; Vosmaer, 1932–35: 721, 722; de Laubenfels, 1936a: 131; Tanita & Hoshino, 1989: 88.

Description of type species

Phycopsis hirsuta Carter, 1883b (Figs 15–16).

Synonymy. *Phycopsis hirsuta* Carter, 1883b: 319; Hooper & Wiedenmayer, 1994: 79.

Material examined. Holotype: BMNH 84.4.14.1, dry – Australia, 'D6 KK1, Deditam Dickie, Presd. by H.J. Carter'.

Description. Branching, 20 cm high and 15 cm wide on broad stalk, 0.5 cm in diameter; branches cylindrical, generally dichotomously divided, rigid, tapering towards ends, some anastomosing; surface with thin and long processes 1–2 mm long; colour brown in dry condition; consistency hard (Fig. 15A). Specialised ectosomal skeleton absent. Choanosomal skeleton differentiated in axial and extra-axial regions. Axial skeleton condensed with close-set spongin fibres and spicules forming a vague reticulation; extra-axial skeleton with light spongin fibres 60–100 μm, cored by spicule tracts, radiating from central axis and ending in surface processes. Single spicules dispersed among spongin fibres or arranged in a halichondrioid-like skeleton. Spicules are not localised in any particular area of the skeleton (Figs 15B–E, 16A). Oxeas-anisoxeas, length 310–410 μm (366 ± 34.7), width 5–12 μm (9.9 ± 2.3) (n = 10), fusiform or telescoped, straight, slightly bent or slightly sinuous; strongyles, length 300–690 μm (502 ± 136.45), width 5–13 μm (8.8 ± 2.1) (n = 10), sinuous or straight; styles-styloids, length 310–410 μm (355 ± 34.7), width 5–12 μm (9.1 ± 2.1) (n = 10) (Fig. 16B–E).

Remarks. The species has not been recorded since its original description. The type material is well preserved and corresponds partially with the description given by Carter (1883b) in which only one type of spicules (i.e., oxeas-anisoxeas) was reported. The strongyles and the styles found in the type material were not mentioned in the original description of Carter. According to Carter (1883b), the species resembles *Phycopsis fruticulosa* recorded from Tasmania, differing only in the length of the surface processes and the diameter of the axis. No strongyles or styles were reported for this species either. *Phycopsis hispidula* (Ridley, 1884a), another species from the north coast of Australia, was originally described under the genus *Protoschmidtia* Czerniavsky, 1879 (=*Haliclona*) and referred to *Phycopsis* by Hooper & Wiedenmayer (1994). The identity of this species needs confirmation as its original description disagrees with the diagnosis of *Phycopsis* given here.

Habitat and distribution. Only known from its type locality (South Australia).

PTILOCAULIS CARTER, 1883

Synonymy

Ptilocaulis Carter, 1883b: 321.

Type species

Ptilocaulis gracilis Carter, 1883b: 321 (by subsequent designation; de Laubenfels 1936a: 127) (junior synonym of *Pandaros walpersi* Duchassaing & Michelotti, 1864).

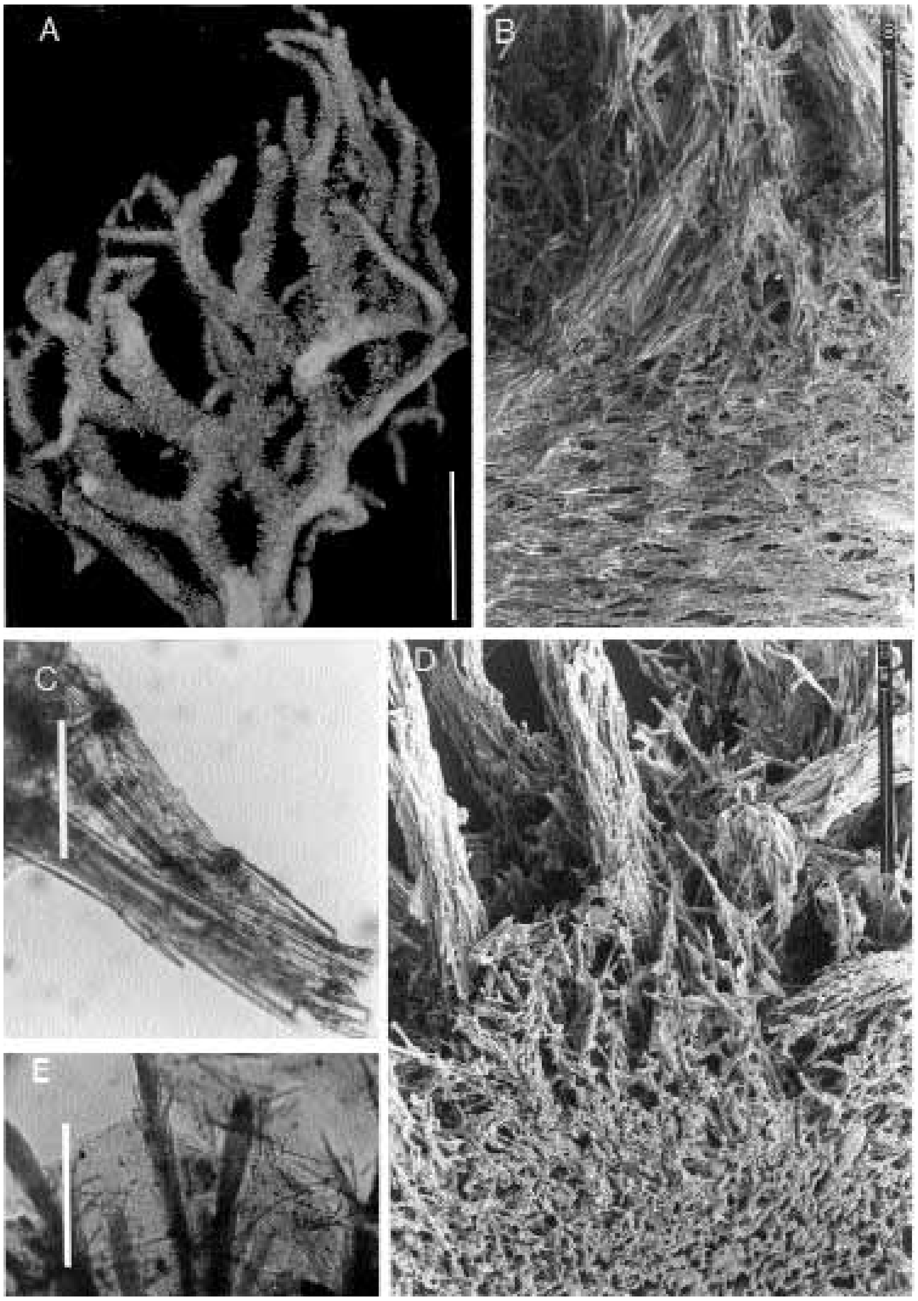

Fig. 15. *Phycopsis*. A–D, *Phycopsis hirsuta* Carter. A, holotype BMNH 84.4.14.1. B, SEM of a longitudinal section through the skeleton. C, detail of skeletal projection at surface. D, SEM of a transverse section through the skeleton. E, *Phycopsis setosa* (Bowerbank), longitudinal section through the lectotype BMNH 1877.5.21.1310 (scales A, 2.5 cm; B, 500 μm; C, 30 μm; D, 500 μm; E, 600 μm).

Definition

Axinellidae with axial skeleton vaguely reticulated and extra-axial skeleton formed by ascending fibrofascicles cored with styles and ending in surface processes.

Diagnosis

Clavate, branching, bushy or lamellate growth form. Surface covered by scopiform (i.e., flattened and spatula-shaped (Carter, 1833)) processes; ectosome without specialised skeleton. Choanosomal skeleton differentiated in axial and extra-axial regions; axial skeleton vaguely reticulated; extra-axial skeleton irregularly reticulated with ascending fibrofascicles cored with styles and ending in surface processes. Megascleres are styles generally in two size categories; occasionally oxeas or anisoxeas. Microscleres absent.

Remarks

The flattened surface processes, also referred to as 'scopiform' (Carter, 1883b), 'surface tufts' (Ridley, 1884a), papilliform

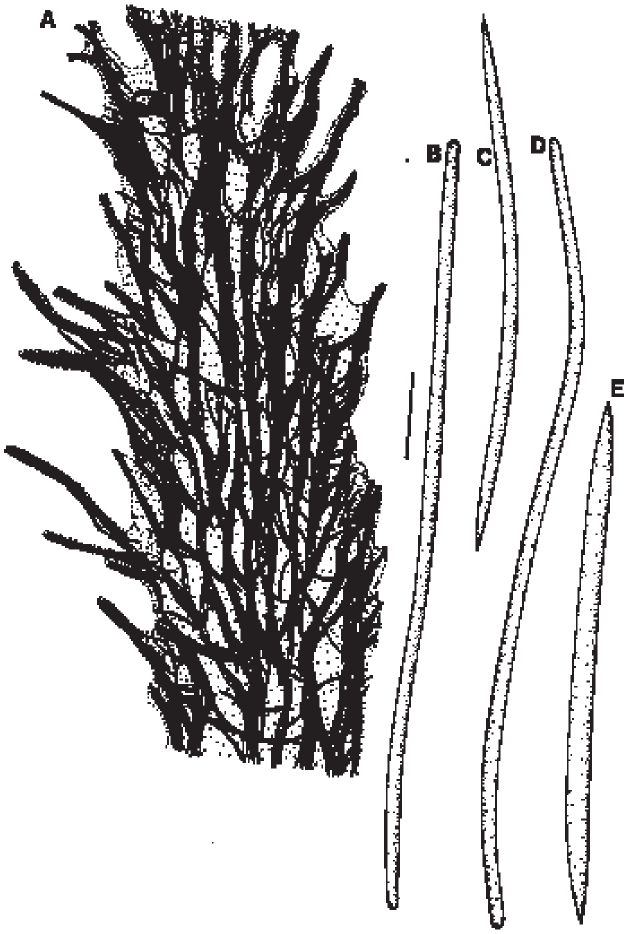

Fig. 16. *Phycopsis*. A–C, *Phycopsis hirsuta* Carter, holotype BMNH 84.4.14.1. A, diagram of the skeleton. B, strongyle. C, oxea. D–E, *Phycopsis setosa* (Bowerbank), lectotype BMNH 1877.5.21.1310. D, strongyle. E, oxea (scale 100 μm).

projections (Hooper & Lévi, 1993b) are distinctive for species of *Ptilocaulis* but cannot be used as a diagnostic character to define the taxon. The genus was included in the Desmoxyidae by Van Soest *et al*. (1990) based on the similarities in surface characteristics with other species of Desmoxyidae, such as *Higginsia*. Alvarez *et al*. (1998) showed that similar surface processes were present in some species of *Axinella* and on this bases the genus was transferred to its original family. Similar surface processes are found also in *Phycopsis* and *Reniochalina*.

The organisation of the choanosomal skeleton, although differentiated in axial and extra-axial regions, differs slightly from other axinellid genera. The extra-axial skeleton of *Ptilocaulis*, instead of plumo-reticulated (e.g., *Axinella, Cymbastela, Dragmacidon*) is formed by fibres that merge or intricately interconnect (fibrofascicles) in an irregular reticulation. Similar architecture is also seen in *Phycopsis* and *Reniochalina*.

The similarities and close phylogenetic relationships among species of *Ptilocaulis* and *Reniochalina* has been well established by Hooper & Lévi (1993b; 1994) and Alvarez *et al*. (2000a).

The genus has been previously referred to Echinonemata: Axinellida (Carter, 1884a,b; 1885d), Halichondrina: Axinellidae (Topsent, 1904b; 1928c), Halichondrida: Desmoxyidae (Van Soest *et al*., 1990); Axinellida: Axinellidae (Hooper & Lévi, 1993b) and Halichondrida: Axinellidae (Alvarez *et al*., 1998).

Distribution

The genus has relatively well-recognised species with disjunct distributions (Hooper & Lévi, 1994). These are: *Ptilocaulis rigidus* Carter, 1883b: 322 from Australia, *P. marquezi* (Duchassaing & Michelotti, 1864: 40 and *P. walpersi* (Duchassaing & Michelotti, 1864) from the central West Atlantic (Alvarez *et al*., 1998); *P. digitatus* Topsent, 1928c: 172 from the central North Atlantic; *P. spiculifera* (Lamarck, 1813–1814: 449) from the Indo West Pacific (Ridley, 1884a: 617; Dendy, 1922b: 115; Burton, 1959a: 266; Pulitzer-Finali, 1993: 289); *P. epakros* Hooper & Lévi, 1993b; *P. fusiformis* Lévi, 1967a and *P. papillatus* Hooper & Lévi, 1993b from New Caledonia (Hooper & Lévi, 1993b). As mentioned above, the species of *Ptilocaulis* reported from New Caledonia by Hooper & Lévi (1993b) have affinities with *Phycopsis* and are probably better placed in this genus. *Ptilocaulis echidnaeus* (Lamarck, 1813) (*fide* Topsent, 1932a: 108) is recorded for the coast of Africa (?) by Lamarck (1813), and thus the type locality of this species remains ambiguous.

Previous reviews

Carter, 1884a: 130; Topsent, 1928c: 37, 172; de Laubenfels, 1936a: 127; Lévi, 1973: 605; Wiedenmayer, 1977b: 152; Hooper & Lévi, 1993b: 1426; Alvarez *et al*., 1998: 22.

Description of type species

Ptilocaulis walpersi (Duchassaing & Michelloti, 1864) (Figs 17–18).

Synonymy. *Pandaros walpersi* Duchassaing & Michelloti, 1864: 90. *Ptilocaulis gracilis* Carter, 1883b: 321. *Ptilocaulis walpersi*; Zea 1987; Alvarez *et al*. 1998 (with additional synonyms).

Material examined. Lectotype: MT Por. 56 (USNM 31025 slide) – St. Thomas, Virgin Islands, Caribbean. Holotype of *Ptilocaulis gracilis*: BMNH 1845.12.30.1, dry – Caribbean.

Description. Encrusting, irregularly massive, plate-shaped, fan-shaped, or erect finger-shaped; dichotomously branching (as in the lectotype of *Ptilocaulis gracilis*) or forming brushes of 10 or more closely-cropped branches. Surface uniformly covered with scopiform flattened processes, 2 mm long and approximately 5–10 mm apart and minute pores, less than 1 mm in diameter; colour orange-red when alive; white-beige in alcohol; brown in dry state (Fig. 17A–B). Specialised ectosomal skeleton absent; choanosomal skeleton with developed fascicles of ascending and anastomosing primary fibres (styles and spongin), radiating to the periphery and ending in flattened surface processes. Main fibres interconnected irregularly by single fibres, some unevenly core with single spicules, and/or short and thin paucispicular tracts (Figs 17C–D, 18A). Styles of two sizes: (1) length, 260–340 μm (295.6 ± 18.0), width 15−10 μm (13.3 ± 1.9) (n = 25); (2) length, 860−490 μm (715.6 ± 81.0), width 10−5 μm (7.2 ± 2.2) (n = 25); longest projecting from scopiform processes and less frequent than shorter ones of the choanosomal skeleton (Fig. 18B–C).

Remarks. The species is common in the Caribbean and due to its variable growth form has often been confused with other axinellids (see list of synonyms and extended remarks in Alvarez *et al*., 1998). *Ptilocaulis walpersi* is similar to *P. marquezi* in its growth form, skeletal organisation and distribution, but differs in spiculation. *Ptilocaulis marquezi* has styles transitional to styloids, in only one size category, and oxeas transitional to strongyloxeas.

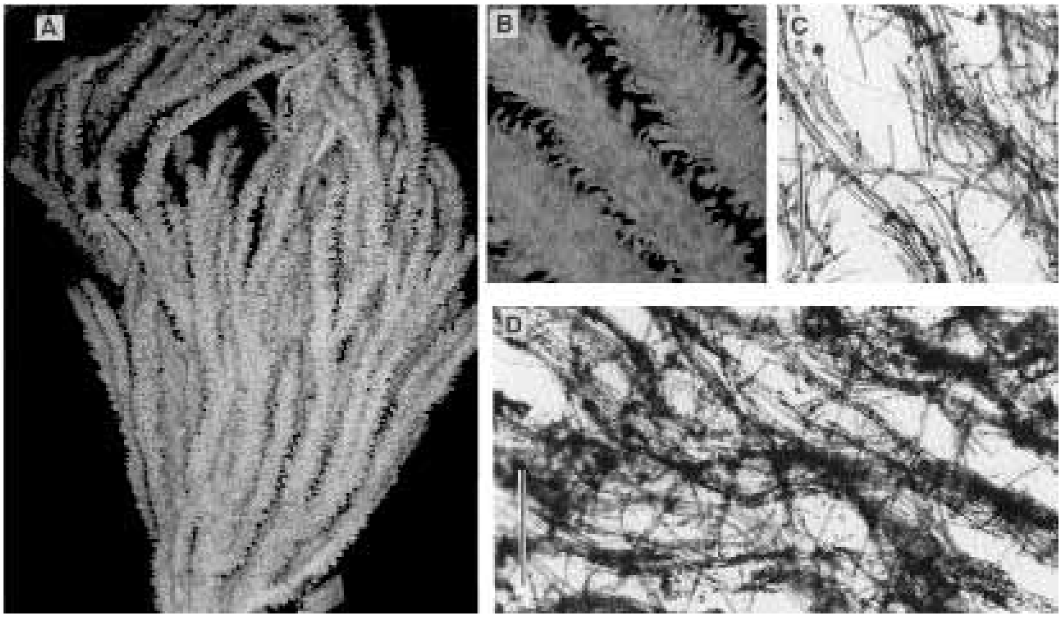

Fig. 17. *Ptilocaulis gracilis* Carter. A, holotype BMNH 1845.12.30.1, dry. B, detail of scopiform processes. C, detail of spiculo-fibres. D, longitudinal section through the choanosomal skeleton (scales A, 5 cm; C, 50 μm; D, 300 μm).

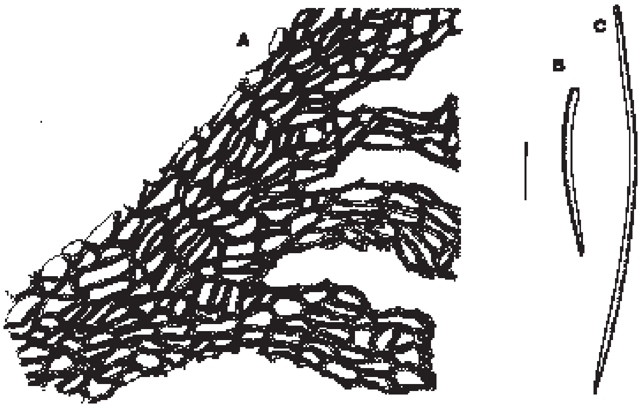

Fig. 18. *Ptilocaulis*. A, diagram of the skeleton of the type species. B–C, styles of USNM 31025 (spicule preparation made from the lectotype MT POR. 56 of *Ptilocaulis walpersi* (Duchassaing & Michelotti)) (scale 100 μm).

Habitat and distribution. Widely distributed in the Caribbean, from Florida to Colombia and off Bermuda. It is found from shallow water to 35 m depth on coral reef bottoms.

RENIOCHALINA LENDENFELD, 1888

Synonymy

Reniochalina Lendenfeld, 1888: 82. *Axiamon* Hallmann, 1914: 440 (objective synonym).

Type species

Reniochalina stalagmitis Lendenfeld, 1888: 82 (by subsequent designation; Hallmann, 1914).

Definition

Axinellidae with extra-axial spongin fibres projecting into surface processes and cored with paucispicular tracts of oxeas, anisoxeas and styles. Oxeas with tips surmounted by microspines.

Diagnosis

Branching or fan-shaped, occasionally lobate, growth form. Surface covered by flattened (spatulate) long processes. Ectosome without specialised skeleton. Choanosomal skeleton differentiated into axial and extra-axial regions, projecting into surface processes. Extra-axial skeleton reticulated with ascending spongin fibres, interconnected at all angles by single spicules or short fibres, or anastomosing and forming oval to round meshes; spongin fibres cored with paucispicular spicular tracts, sometimes plumose; axial skeleton slightly condensed and reticulated as in extra-axial region. Megascleres are oxeas-anisoxeas with tips surmounted by microspines, which are rudimentary or absent; occasionally styles or styloids. Microscleres absent.

Remarks

The morphological and genetic affinities among species of *Ptilocaulis* and *Reniochalina* have been well established (Hooper & Lévi, 1993b, 1994; Alvarez *et al*., 2000a). These genera together with *Phycopsis* have a similar choanosomal skeleton of ascending spiculo-fibres ending in conspicuous processes at the surface. They differ in spicule composition and shape of the surface processes (long and flattened in *Reniochalina*, spatula-shaped in *Ptilocaulis* and filamentous in *Phycopsis*. These three genera are likely to constitute a monophyletic group that could be classified as a subfamily within Axinellidae. Phylogenetic analyses based on morphological characters support this view (Alvarez, 1998).

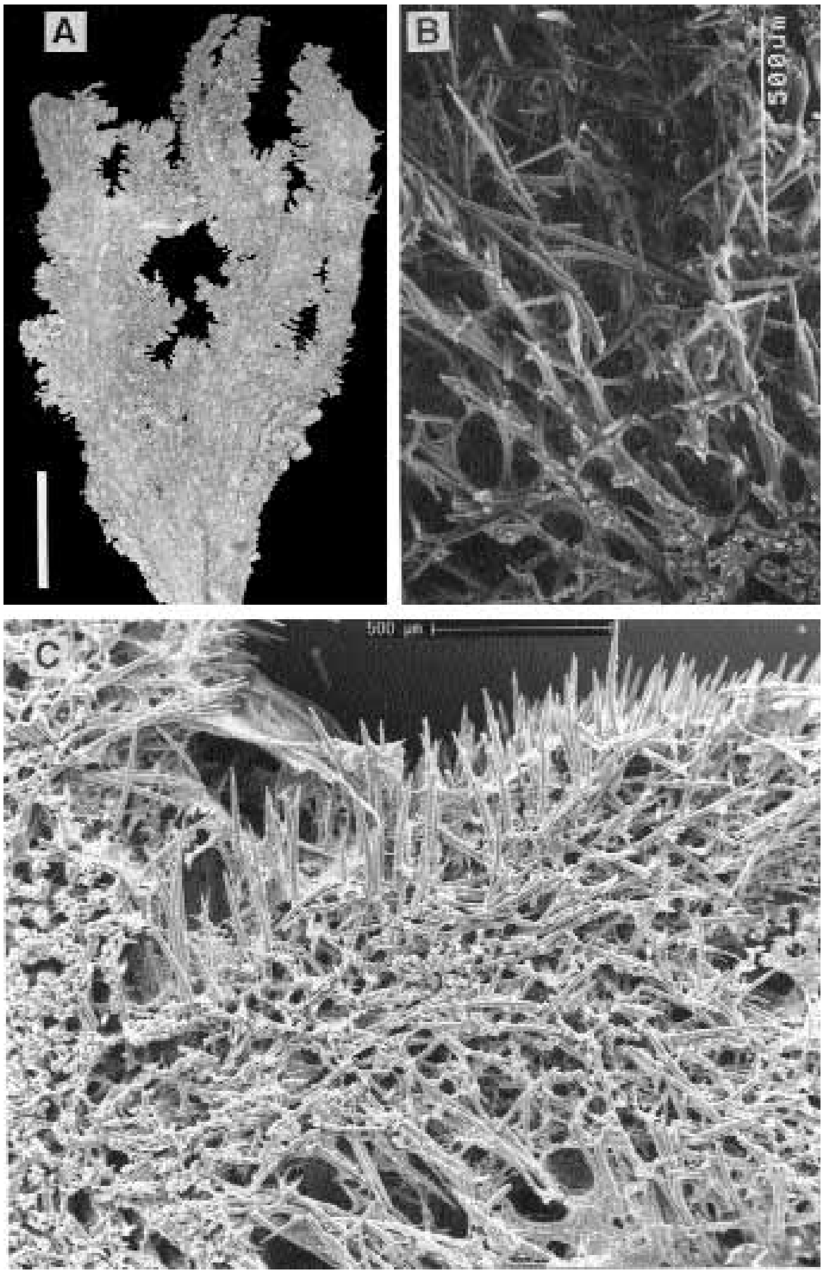

Fig. 19. *Reniochalina stalagmitis* Lendenfeld. A, lectotype BMNH 1887.4.27.122. B–C, SEM of the choanosomal skeleton (scale A, 2 cm).

The synonymy of *Axiamon* with *Reniochalina* was established by Wiedenmayer (1989) and confirmed here by comparison of their respective type specimens (see Hooper & Lévi, 1993b for further comment in this synonymy).

The genus has been previously referred to Halichondrina: Haploscleridae: Renierinae (Topsent, 1894c), Homorrhaphidae: Renierinae (Lendenfeld, 1889a), Haploscleridae (de Laubenfels, 1936a) and Axinellida: Axinellidae (Wiedenmayer, 1989; Hooper & Lévi, 1993b).

Distribution

Reniochalina seems to be restricted to Australia, Indo-west Pacific region (Hooper & Wiedenmayer, 1994; Van Soest, 1994) and New Zealand (Alvarez, unpublished data). It is represented so far by three other species besides the type: *Reniochalina sectilis* Wiedenmayer, 1989: 49, from South Australia, *R. condylia* Hooper & Lévi, 1993b: 1405, and *R. plumosa* (Lévi & Lévi, 1983b: 945) from New Caledonia (Hooper & Lévi, 1993b; 1994). The descriptions of these species, however, do not fully agree with the diagnosis of the genus proposed here and their identities need to be confirmed.

Previous reviews

Whitelegge, 1902: 283; Hallmann, 1914: 346; de Laubenfels, 1936a: 47, 130; Wiedenmayer, 1989: 48; Hooper & Lévi, 1993b: 1403.

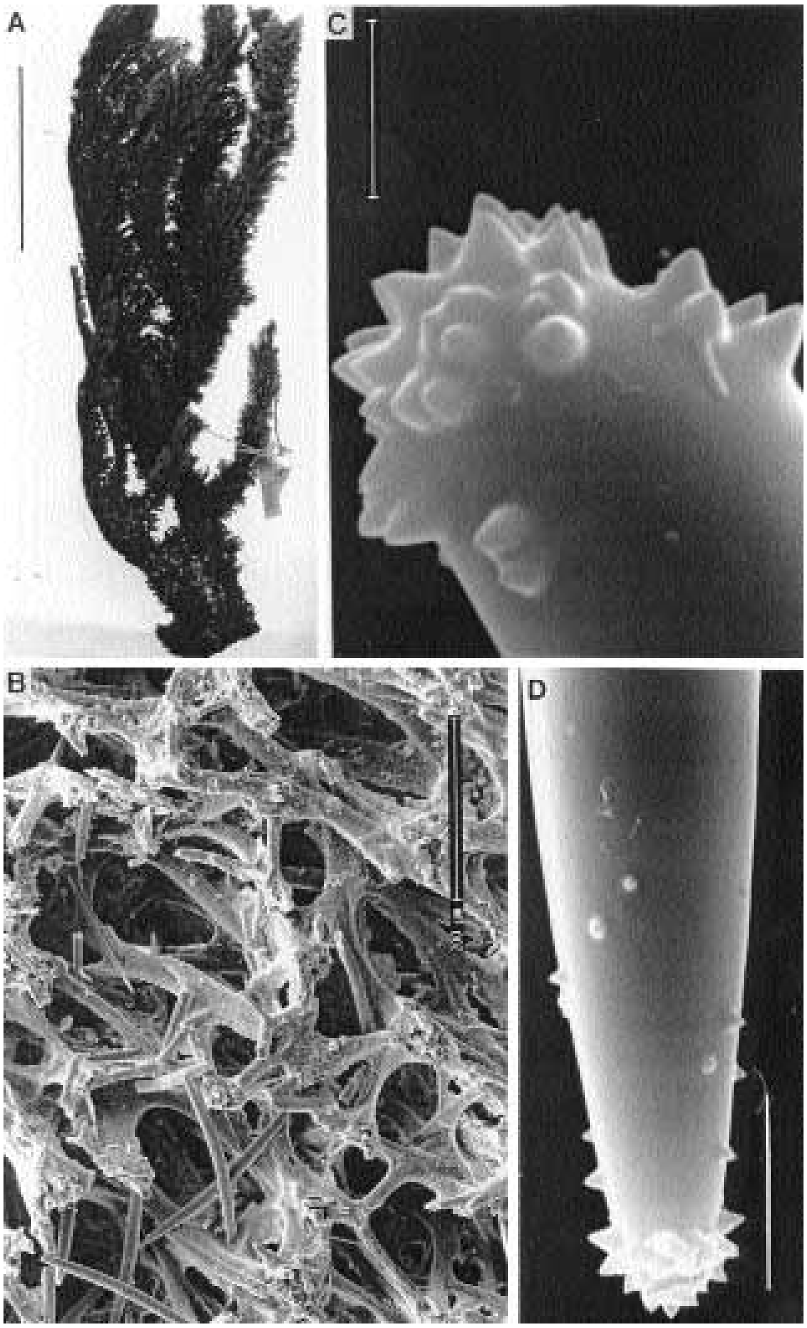

Fig. 20. *Reniochalina stalagmitis* Lendenfeld. A, holotype of *Axiamon folium* Hallmann, AM G9004. B, SEM of the skeleton. C–D, tips of anisoxea (scales A, 10 cm; B, 200 μm; C, 2 μm; D, 5 μm).

Description of type species

Reniochalina stalagmitis Lendenfeld, 1888 (Figs 19–21).

Synonymy. *Reniochalina stalagmitis* Lendenfeld, 1888: 83; Whitelegge, 1902: 283; Hallmann, 1914: 346; Hooper & Wiedenmayer, 1994: 81 (with additional synonyms).

Material examined. Lectotype: BMNH 1887.4.27.122 – Western Australia. Holotype of *Axiamon folium*: AM G9004, wet – Western Australia. 'Syntype' (?): AM B5478, wet – no locality data.

Description. Branching to fan-shape, flat branches, dichotomous or fused; surface with long surface processes and parallel channels, 1 mm apart, 1 mm depth, running longitudinally with projecting spicules; colour orange-red alive, dark brown in alcohol; consistency firm but flexible (Figs 19A, 20A). Specialised ectosomal skeleton absent; choanosomal skeleton differentiated in axial and extra-axial regions. Extra-axial skeleton reticulated with ascending spongin fibres, 50–100 μm interconnected at all angles by single spicules or short fibres, or anastomosing and forming oval to round meshes up to 200 μm in diameter. Spongin fibres slightly developed and cored with paucispicular tracts, sometimes plumose. Axial skeleton slightly condensed and reticulated as in extra-axial region (Figs 19B–C, 20B, 21A). Oxeas or anisoxeas, straight, bent or slightly sinuous; with tips surmounted by microspines, which might be rudimentary or absent; microspines at one end might be half size to those at other end; length 190–315 (240.2 ± 37.6) μm, width 8–15 (11.9 ± 2.8)μm (n = 10) (Figs 20C–D, 21B–D).

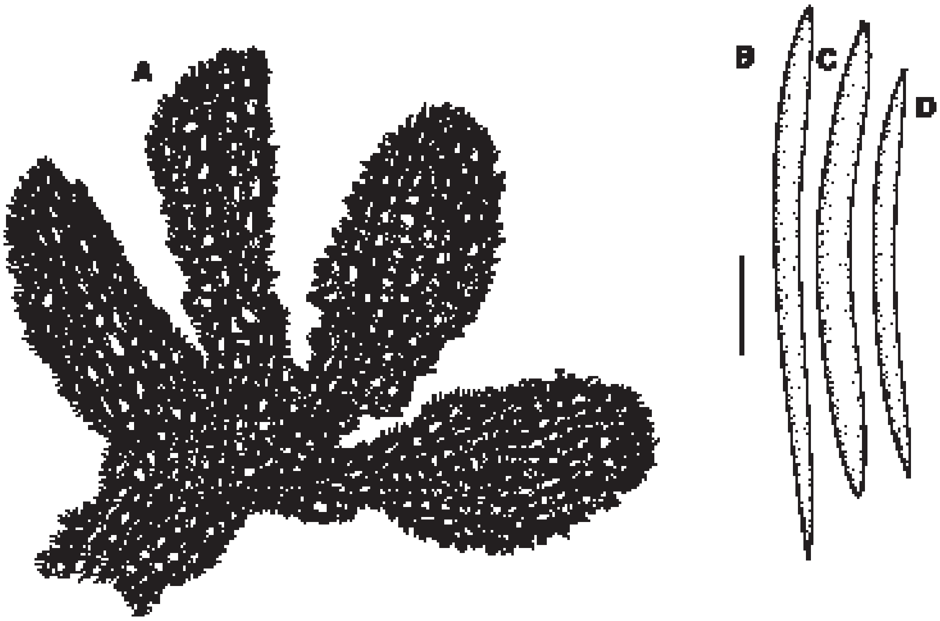

Fig. 21. *Reniochalina stalagmitis* Lendenfeld: A, diagram of the choanosomal skeleton; B–D, different classes of anisoxeas (scale 100 μm).

Remarks. According to Wiedenmayer (1989) the species is similar to *Reniochalina sectilis* but we consider that the latter has affinities with the Raspailiidae (see below). *Reniochalina lamella* Lendenfeld, 1888 was synonymised by Wiedenmayer (1989) with *R. stalagmitis*. The two species seem to differ slightly in habit (see Wiedenmayer, 1989: plate 4.2, and additional remarks therein).

Reniochalina stalagmitis is genetically and morphologically similar to an undescribed species of *Reniochalina* from the Great Barrier Reef, Australia, recorded in Alvarez *et al*. (2000a). This species differs from *R. stalagmitis* in habit, which is branching-erect; with cylindrical branches, semi-buried in the substrate, dichotomously divided near the tips. It differs also in the size of the oxea microspines, which are much smaller and only visible under high magnification (e.g., SEM analysis).

Habitat and distribution. The species seems to be widely distributed throughout Australia: W coast, Western Australia, Great Barrier Reef, Queensland coast, Torres Strait (see Hooper & Wiedenmayer, 1994: 82). It is found in coralline substrate between 10–20 m depth.

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