Systema Porifera: A Guide to the Classification of Sponges, Edited by John N.A. Hooper and Rob W.M. Van Soest

Family Suberitidae Schmidt, 1870

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Suberitidae Schmidt (Demospongiae, Hadromerida) is characterized by the absence of a cortex and microscleres other than microrhabds or trichodragmas. Spicules are for the most part tylostyles, often in several size categories; in exceptional cases, oxeas or strongyloxeas are the main megascleres. Usually Suberitidae have an ectosomal specialization in the form of a palisade or brushes of spicules making the surface velvety or microhispid in texture (one genus excepted). The interior skeleton tends to be irregular, confusedly reticulate, or condensed, and in general lacks a clear radial arrangement (one genus excepted). There are massive-globular, arborescent-stalked, or thinly encrusting growth forms. Many species and genera live in sedimented environment, often at some depth, either by rooted stalks or by living on the empty shells of gastropods occupied by hermit crabs which carry the sponges around. The family in its present concept includes 26 nominal genera, eleven of which are considered valid. One commonly used genus name, *Laxosuberites*, was found to be untenable, and species assigned to it are for the most part transferred to a revived genus name *Protosuberites*.

Keywords: Porifera; Demospongiae; Hadromerida; Suberitidae; *Aaptos*; *Caulospongia*; *Homaxinella*; *Plicatellopsis*; *Prosuberites*; *Protosuberites*; *Pseudospongosorites*; *Pseudosuberites*; *Rhizaxinella*; *Suberites*; *Terpios*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Suberitidinae Schmidt, 1870: 46. Suberitidae Vosmaer, 1887: 330.

Definition

Hadromerida without cortex and without microscleres other than microrhabds; spicules tylostyles or styles, exceptionally oxeas, arranged in brushes or palisade in the peripheral region.

Diagnosis

Globular, ramose, stipitate, massive or encrusting habit. Megascleres usually tylostyles, occasionally styles, strongyloxeas or centrotylote oxeas; microscleres usually absent, when present confined to microrhabds and trichodragmas. In cross section, megascleres are usually arranged in bouquets at the surface, in more massive species becoming progressively confusedly arranged towards the interior, but overall structure may also be strictly radial or show a strong axial orientation. In one genus the spicules at the surface are arranged tangentially. There is no recognizable cortex. In thinly encrusting species spicule orientation is either parallel or perpendicular to the substratum. Modifications of shape and position of the tylostyle heads are common; they can be lobate, pear-shaped, drop-shaped or subterminal.

Scope

Eleven genera (out of 26 nominal genera) are considered valid: *Aaptos, Caulospongia, Homaxinella, Plicatellopsis, Prosuberites, Protosuberites, Pseudospongosorites, Pseudosuberites, Rhizaxinella, Suberites* and *Terpios*.

History and biology

Taxonomic history. Schmidt (1870) included in his concept of Suberitidae sponges without cortical structures, tylostyles in tracts or in confusion and at the periphery directed outwards. He included next to *Suberites*, the genus *Papillina* (now in Clionaidae), and furthermore a number of genera with cortical structures: *Radiella, Polymastia* in part, *Thecophora, Rinalda* (all four now Polymastiidae), and *Cometella* and *Tethya* (now Tethyidae), thus violating in typical Schmidt manner his own definition. Vosmaer (1887) separated the polymastiid genera from the Suberitidae, and added *Rhizaxinella, Quasillina* (now Polymastiidae), *Poterion* (now Clionaidae) and *Stylocordyla* (now Stylocordylidae). Subsequently, Lendenfeld (1896) united the Polymastiidae and Suberitidae again, but split off Stylocordylidae. Topsent's (1900) revision of the 'Clavulina' of France was the first to define the family in its present outline. He defined Suberitinae as Clavulina without microscleres other than microrhabds and rhaphides, without a cortex, and a skeleton having no strictly radiate arrangement of the spicules. He included *Ficulina* Gray, 1867a, *Laxosuberites* Topsent, 1896a, *Pseudosuberites* Topsent, 1896a, *Prosuberites* Topsent, 1893c, *Rhizaxinella* Keller, 1880a, *Suberites* Nardo, 1833 and *Terpios* Duchassaing & Michelotti, 1864. He assigned *Aaptos* (as *Tuberella*) to Tethyidae. Burton (1930d) more-or-less followed Topsent's classification, adding *Caulospongia* Saville Kent, 1871, *Protosuberites* Swartschewsky, 1905, and erected two additional genera *Laxosuberella* (here considered Clionaidae) and *Terpiosella*. He also included *Tentorium* Vosmaer, 1885a (here considered Polymastiidae) and *Axosuberites* Topsent, 1893a (here considered Microcionidae). Burton (1930d) also indicated that in his view the differences between Polymastiidae and Suberitidae were questionable. Perhaps inspired by this remark, de Laubenfels (1936a: 147) expanded the family to include amongst others Polymastiidae by maintaining a simple definition of "comprising genera having a spiculation of tylostyles as megascleres, and no microscleres at all". This is followed by an unprecedented and partly unexplained plethora of 40 genera, several of which did not even conform to his simple definition. It is beyond the scope of these present brief comments to list and discuss each of his assignments.

Remarkably, de Laubenfels (1936a: 143) assigned *Ficulina* (as *Choanites* Mantell, 1822) to a family Choanitidae, along with spiraster-bearing genera *Spirastrella* and *Speciospongia*. Understandably, his classification found few followers, and subsequent authors (e.g., Lévi, 1973; Bergquist, 1978; Hartman, 1982; Voultsiadou-Koukoura & Van Soest, 1993; Rützler & Smith, 1993) followed basically Topsent's (1900) scheme, with later additions mentioned above. The present concept in its turn deviates from that scheme only on details of inclusion of individual genera. For example, the genus *Poterion* is often included in Suberitidae (e.g., Hooper & Wiedenmayer, 1994: 404), but is here referred to Clionaidae.

Biology. Suberitid sponges include many forms capable of living in sedimented environments, either through the development of stalked or arborescent forms with root systems for attachment, or by encrusting empty gastropod shells with symbiont hermit-crabs, carrying the sponge around. In addition, several genera are thinly encrusting on shells, rocks and corals. Colder, deeper waters are favored by many suberitids, although most genera have representatives in shallow tropical environments. Several species and genera have a means of asexual reproduction by gemmule-type of bodies, formed at the contact area of the substratum, especially in forms living on gastropod shells. These gemmules are not structurally comparable with the elaborate gemmules of freshwater sponges, but may have similar functions.

Chemistry. A chemical marker for at least two genera of the family is the group of compounds dubbed 'aaptamines' (Bergquist *et al*., 1991a; Van Soest & Braekman, 1999).

KEY TO GENERA

(1) Sponge stipitate or arborescent, i.e. having a stem of some length separate from further body parts (ovate bodies, branches, lobes, leaf-like structures) 2
Sponge globular, massive or encrusting; if erect, there is no distinct stem 5
(2) Sponge arborescent, with branches similar to the stem 3
Sponge stipitate with ovate body, or provided with lobes or leaf-like structures 4
(3) Spicules predominantly styles, extra-axial skeleton predominantly with single spicules arranged in brushes at the surface .... ***Homaxinella***
Spicules predominantly tylostyles; extra-axial skeleton with strong spicule bundles fanning out at the surface to form brushes .... ***Plicatellopsis***
(4) Sponges with simple stem and ovate body, which may be pearshaped or otherwise elongated; brushes of smaller spicules over radiate bundles of larger spicules .... ***Rhizaxinella***
Sponges with elaborate shape, either pagoda-like with leafshaped lobes, or flabellate or a system of reticulate branches; tylostyles in a single size category, with peculiarly flattened tyles .... ***Caulospongia***
(5) Sponge globular, massively lobate or digitate, or massively encrusting 6
Sponge thinly encrusting, usually not exceeding a cm in thickness 9
(6) Spicules exclusively tylostyles 7
Spicules include oxeas or strongyloxeas 8
(7) Surface skeleton is a tangential and usually detachable crust carried by subectosomal spicule brushes .... ***Pseudosuberites***
No tangential spicules, surface velvety due to palisade of small tylostyles .... ***Suberites***
(8) Oxeas symmetrical relatively small and sharply pointed; skeletal arrangement more or less confused .... ***Pseudospongosorites***
Strongyloxeas in a large size range, usually accompanied by small styles and/or tylostyles in a low quantity; skeletal arrangement strictly radiate .... ***Aaptos***
(9) Tylostyles single erect on the substrate 10
Tylostyles in bundles or confused 11
(10) Macroscopically hispid, no ectosomal specialization .... ***Prosuberites***
Macroscopically smooth, at the surface tylostyles in brushes .... ***Protosuberites***
(11) Low spicular density, gelatinous consistency, tylostyles predominantly with peculiarly flattened, lobate tyles; size uniformly small .... ***Terpios***
Tylostyles in a dense palisade at the surface and in thicker specimens arranged in parallel bundles; usually a large size range; lobate tyles not common .... ***Protosuberites***

AAPTOS GRAY, 1867

Synonymy

Aaptos Gray, 1867a: 519. *Trachya* Carter, 1870a: 176. *Tuberella* Keller, 1880a: 277. *Tethyophaena* Schmidt, 1880a: 281.

Type species

Ancorina adriatica Gray, 1867a: 519 (by original designation) [=*Aaptos aaptos* (Schmidt, 1864: 33)].

Definition

Suberitidae with radiate skeleton of strongyloxeas in three size categories, the smaller of which form a dense ectosomal palisade. No microscleres.

Diagnosis

Lobate or spherical sponges with a radial skeleton, often consisting of confluent globular or lobate units. Surface smooth or tuberculate-papillate, usually rough to the touch. Some species show a distinct colour change when taken out of the water. In cross

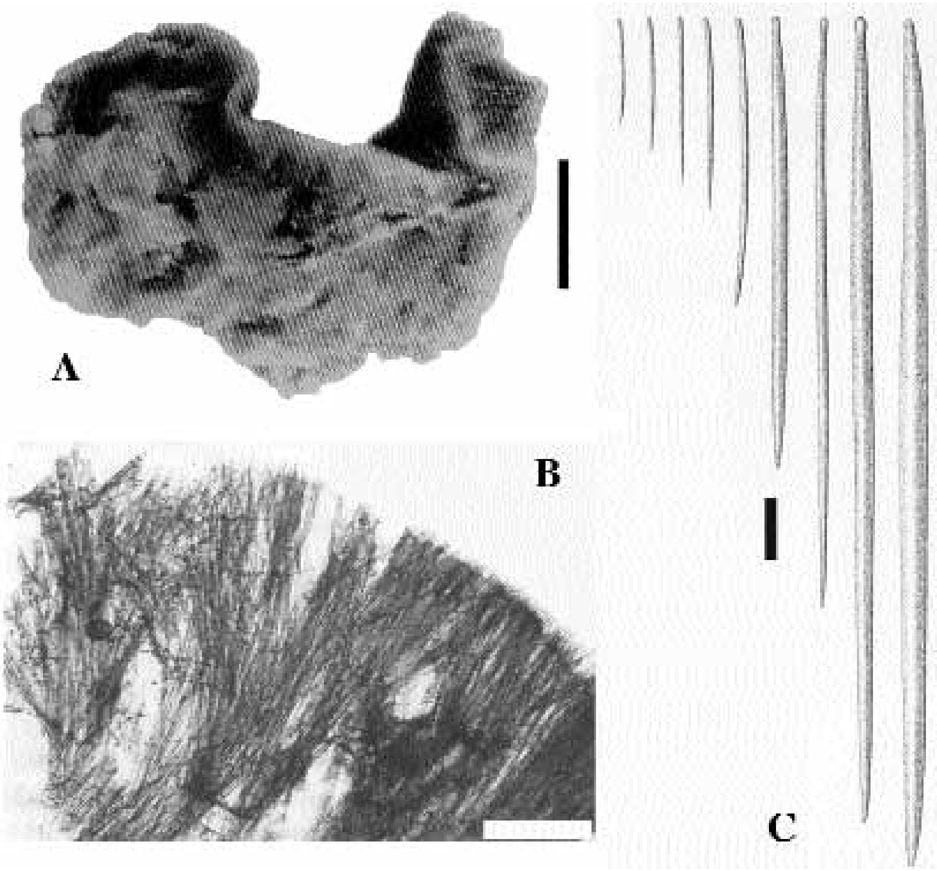

Fig. 1. *Aaptos aaptos* (Schmidt, 1864). A, paralectotype LMJG 15705 from unknown locality (scale 1 cm). B, cross section of peripheral skeleton of lectotype BMNH 1910.1.1.866, Lagoste, Algeria (reproduced from Kelly-Borges & Berquist, 1994: pl. Ia) (scale 1000 μm). C, spicules (reproduced from Lendenfeld, 1896: pl. VII fig. 87) (scale 100 μm).

section, the outer region is often fibrous and may be considered as a cortex which grades into the choanosome. Skeleton strictly radiate, with tracts and single spicules issuing from the centre of the lobe or globular body. At the surface the tracts fan out and form a dense palisade consisting of smaller spicules intermingled between the ends of the larger spicules. Spicules are strongyloxeas, in three overlapping size categories; the intermediate and smaller spicules are occasionally oxeas, styles or tylostyles. The genus is cosmopolitan and currently about 15–20 species have been described, but several more may hide among the widespread records of *Aaptos aaptos*. Several species produce a distinctive compound aaptamine (Van Soest & Braekman, 1999), which appears to be a good marker for the genus.

Previous reviews

Kelly-Borges & Bergquist, 1994: 303.

Description of type species

Aaptos aaptos (Schmidt, 1864) (Fig. 1A–C).

Synonymy. *Ancorina aaptos* Schmidt, 1864: 33, pl. IV fig. 11; *Aaptos aaptos*; Vosmaer, 1887: 327; Kelly-Borges & Bergquist, 1994: 304, pl. Ia figs 2a–b; *Suberites aaptos*; Lendenfeld, 1896: 140, pl. VII XII; *Tuberella aaptos*; Topsent, 1900: 285, pl. VIII figs 12, 13. *Aaptos adriatica* Gray, 1867a: 519. *Tuberella tethyoides* Keller, 1880a: 277. *Tethyophaena silifica* Schmidt, 1880a: 281. *Suberites spissus* Topsent, 1892b: xxvii.

Material examined. Lectotype (designation by Kelly-Borges & Bergquist, 1994: 304): BMNH 1910:1:1:866 – Lagoste, Algeria. Paralectotype (designated herein): LMJG 15705 – Schmidt specimen of unknown locality in the Graz Museum (cf. Desqueyroux-Faúndez & Stone, 1992: 7, pl. III fig. 22, here reproduced as Fig. 1A). Other material. ZMA POR. 6164 – Prainha, Madeira, 2 m, coll. R.W.M. van Soest, 3 April 1986.

Description. Massive, lumpy, bluntly lobate (Fig. 1A), typically 3–5 cm in diameter, occasionally larger, fist-size. Surface irregular, hispid, occasionally smooth, seldom elevated in distinct papillae. Oscules up to 3 mm in diameter, few in number, contractile, occasionally elevated. Consistency compact, firm, hard. Colour brown-yellow, occasionally pale yellow or greyish, or blackish brown. Interior yellow. Skeleton architecture (Fig. 1B) is radiate with spicule tracts of 1.5–2 cm length, 10–20 spicules in thickness, radiating from a focal point towards the surface. At the surface these bundles are strengthened and linked by brushes of small styles, making a continuous ectosomal palisade of about 1 mm in thickness, which is however not macroscopically distinct and not fibrous. Inhalant canals traverse the peripheral region in a sinuous way. Below this the choanosomal tracts are separated by subectosomal cavities. Spicules (Fig. 1C) strongyloxeas and styles. The strongyloxeas are characteristically thickest in the middle, thinning out towards the blunt apex, and are divisible in two size categories, 1500–1900 × 12–45 μm and 750–1000 × 10–25 μm. Ectosomal small styles, occasionally subtylostyles: 135–230 × 1–5 μm (data from the holotype, taken from Kelly-Borges & Bergquist, 1994: 306).

Cell biology. The choanosome is rich in spherulous cells. The choanocyte chambers are small, eurypylous, 20–25 μm in diameter. Distribution and ecology. Mediterranean and also occurring off the coasts of NW Spain and Portugal, Azores, Madeira and Canary Islands. Mostly known from deeper water, but occasionally occurring in the shallow sublittoral.

Remarks. Gray (1867a) erected a species of his own (*Aaptos adriatica*) for Schmidt's *Ancorina aaptos* for no apparent reason and without indicating material other than Schmidt's; consequently this is an objective junior synonym. The type species is not well-known. It has been reported from many areas of the world, but it is almost certain that these concern other species of *Aaptos*.

The genus *Trachya* Carter (1870a: 176) was erected for the West Indian species (by monotypy) *Trachya pernucleata* Carter (1870a: 176). It was re-examined by Kelly-Borges & Bergquist (1994: 316) and assigned to *Aaptos*, which is confirmed here.

The genus *Tuberella* Keller, 1880a was erected for type species (by monotypy) *Tuberella tethyoides* Keller, 1880a: 277, pl. XIV figs 7–9). The type material, supposedly in ZMB, was not reexamined, but the species has been discussed by Vosmaer (1887: 327, pl. XXVI fig. 9) and Topsent (1900: 287), making it clear that it is an *Aaptos* species closely similar to and probably conspecific with *A. aaptos*. *Tuberella* is thus a clear synonym of *Aaptos*.

The genus *Tethyophaena* Schmidt, 1880a was erected for type species (by monotypy) *Tethyophaena silifica* Schmidt, 1880a: 281. Although Desqueyroux-Faundez & Stone (1992) do not list any extant type specimens, there is an unnumbered specimen in the Leiden Museum from Naples with label in Schmidt's handwriting ('type'). This is here designated the lectotype. It is an obvious specimen of *Aaptos aaptos* (Schmidt himself likened his new species to *Tuberella tethyoides*).

CAULOSPONGIA KENT, 1871

Synonymy

Caulospongia Kent, 1871: 616. *Plectodendron* Lendenfeld, 1888: 66.

Type species

Caulospongia verticillata Kent, 1871: 616 (by subsequent designation; Hallmann, 1914: 306) (=junior synonym of *Spongia perfoliata* Lamarck, 1814: 439).

Definition

Suberitidae with erect pagoda-like or lobed-lamellated habit and reticulate skeleton of spicule tracts. Surface skeleton with tangential spicules carried by ectosomal brushes. Spicules tylostyles with flattened-lobate tyles.

Diagnosis

Erect sponges with solid stem and either a lobed or interlocking, reticulate branching habit or forming erect fans. Choanosomal skeleton is a plumo-reticulate or reticulate system of spicule tracts; interstitial spicules are frequent. Ectosomal skeleton consists of brushes of spicules covered by a narrow or diffuse layer of spicules parallel to the surface. Spicules relatively small tylostyles with distinct flattened tyles in a single size category. No microscleres. The genus is exclusively Australian in distribution and contains eight species.

Previous review

Fromont, 1998: 67.

Description of type species

Caulospongia perfoliata (Lamarck, 1814) (Fig. 2A–D).

Synonymy. *Spongia perfoliata* Lamarck. 1814: 439; *Caulospongia perfoliata*; Hallmann, 1914: 306, pl. 18 fig. 1. *Caulospongia verticillata* Saville Kent, 1871: 616, pl. XLVIII fig. 1; *Chalina verticillata*; Bowerbank, 1876b: 769, pl. LXXIX.

Material examined. None. Holotype: MNHN DT 3368 – extensively redescribed by Topsent, 1932: 85 and Fromont, 1998: 68. The type of *C. verticillata*, from North Australia, was stated to be in the Liverpool Free Museum and is now considered lost; it is described and figured in Saville Kent, 1871.

Description (from Fromont, 1998: 68). Erect pagoda-like sponge (Fig. 2A, B) with a solid stem and flattened irregular leaf-like lobes which are hollow inside and are sloping upwards towards the apex of the sponge. Length 30–36 cm, with a stem of 5–13 cm, lobes 6–9 cm wide around the stem, 0.3–0.5 cm in thickness. Surface smooth, porous, oscules not apparent. Texture very firm but compressible. Colour cream or yellow-orange. Ectosomal skeleton (Fig. 2C) as defined for the genus with both brushes of spicules and tangentially arranged spicules together forming a detachable surface crust of 90–150 μm in thickness. Choanosomal skeleton (Fig. 2C) is a reticulation of spongin-encased spicule tracts consisting of primary tracts of about 60 μm diameter with a core of five or more spicules and interconnecting thinner tracts of 30 μm diameter and a core of 2–4 spicules. In the stem, spicule tracts may be as thick as 320 μm. Spicules (Fig. 2D) tylostyles with characteristic flattened tyles which frequently are lobate, in a single size category, 118–215 × 2.5–10 μm. Distribution and ecology. SW Australia, on rocks among kelp, 11–30 m.

Remarks. This is a clearly demarcated species and genus through the combination of elaborate shape, reticulate skeleton and flattened tyles of the spicules. The genus *Plectodendron* Lendenfeld, 1888: 66 was erected for *Plectodendron elegans* Lendenfeld, 1888: 66 (by monotypy). Hallmann (1914: 306, pl. 18 fig. 1) assigned the species to *Caulospongia*, and this was followed by Fromont (1998: 78). The lectotype (designated by Fromont, 1998: 79), AM G9186, from Broughton Island, New South Wales, and paralectotypes AM Z5221 and AM Z5271, both from Port Jackson, NSW, were redescribed by Fromont, 1998. Although the gross morphology deviates quite substantially from the type species of *Caulospongia*, the skeletal and spicule characters are the same. Moreover, a further species of *Caulospongia, C. reticulata* Fromont, 1998: 80, bridges the gap between the habits of *C. perfoliata* and *Plectodendron elegans*. The two genera are here confirmed as synonyms.

HOMAXINELLA TOPSENT, 1916

Synonymy

Homaxinella Topsent, 1916: 4. *Pachaxinella* Burton, 1930b: 503.

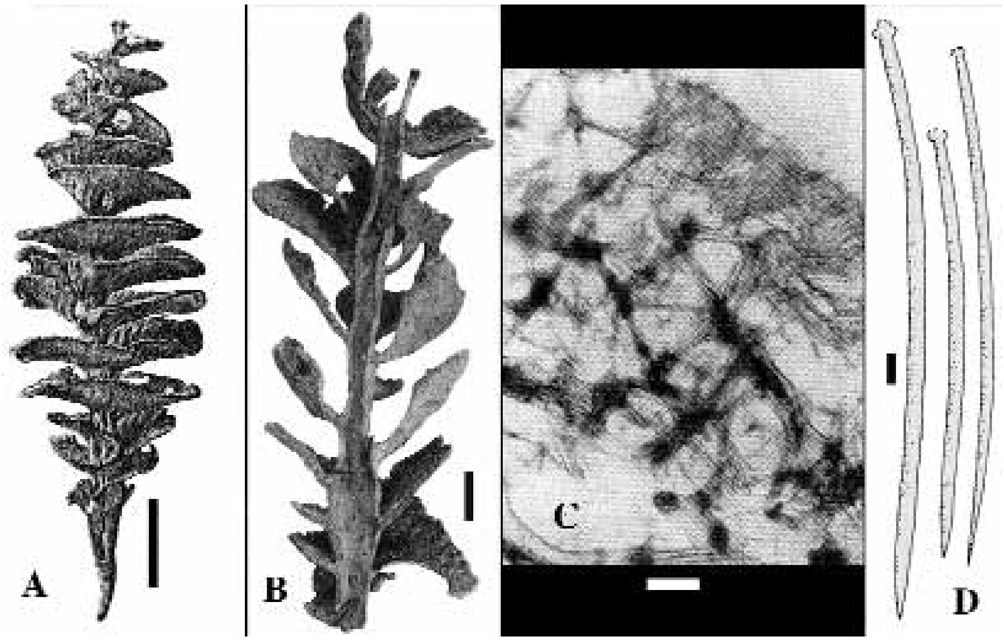

Fig. 2. *Caulospongia perfoliata* (Lamarck, 1814). A, drawing of holotype of *Caulospongia verticillata* Kent, 1871 = jun. syn. of *C. perfoliata*, reproduced from Kent, 1871: pl. XLVIII, fig. 1 (scale 5 cm). B, photo of holotype of *Spongia perfoliata*, MNHN DT 3368 (reproduced from Topsent, 1932: pl. III fig. 4) (scale 1 cm). C, cross section of peripheral skeleton with marked difference between ectosomal and choanosomal arrangement (reproduced from Fromont's 1998: fig. 2c) (scale 100 μm). D, spicules (reproduced from Fromont's 1998: fig. 3a) (scale 10 μm).

Type species

Axinella supratumescens Topsent, 1907: 74 (by original designation), (=generally considered a junior synonym of *Axinella balfourensis* Ridley & Dendy, 1887: 480).

Definition

Suberitidae with ramose habit and axial choanosomal skeleton; extra-axial skeleton of brushes of spicules and spicules in confusion. Megascleres exclusively styles in a large size variation; no microscleres.

Diagnosis

Persistently thinly ramose sponges with pointed branches and a system of roots, stolons or branches creeping over the substrate. Surface optically smooth although may be somewhat furrowed or annular, with small oscules on the branches. Consistency wiry, due to axial skeleton, outer parts soft. Skeleton of the axis a mass of aligned tracts or more commonly confusedly arranged larger megascleres, extra-axial skeleton consisting of brushes of the smaller spicules 'echinating' the axial skeleton. Styles are the only spicules. About 20 described species, recorded from all parts of the three oceans.

Description of type species

Homaxinella balfourensis (Ridley & Dendy, 1887) (Fig. 3A–D).

Synonymy. *Axinella balfourensis* Ridley & Dendy, 1886: 480; Ridley & Dendy, 1887: 179, pl. XXIII fig. 1. *Axinella supratumescens* Topsent, 1907: 74; Topsent, 1908: 32, pl. II fig. 4, pl. III fig. 6, pl. V fig. 2; *Homaxinella supratumescens*; Topsent, 1916: 4.

Material examined. Holotype of *Axinella balfourensis*: BMNH 1887.5.2.18 – Balfour Bay, Kerguelen, 'Challenger' Collection, 36–108 m. Paralectotype of *Axinella supratumescens*: MNHN 760 – 'Charcot' Expedition 1905, labeled 'type'.

Description. Ramose (Fig. 3A), with branches up to 20 cm long and max. 0.8 cm diameter, at branching points up to 1.5 cm, they may appear somewhat flattened. Branches divide, but seldom anastomose. Stalk is attached to the substrate by a system of roots and/or creeping stolons. Colour various shades of yellow. Surface smooth, microscopically hispid. Skeleton (Fig. 3C, D) divided in an axial and extra-axial region. The extra-axial region is rather soft and consists of somewhat loose brushes of styles (Fig. 3C) with points directed outwards, but many are strewn in confusion. Axial skeleton consisting of a dozen or more unidirectionally or spirally aligned bundles of 80–120 μm diameter separated by less densely spiculated areas. The outer tracts of the central core tend to give off thinner bundles (Fig. 3D) protruding through the surface membrane beyond the extra-axial brushes. At the apices of the branches this structure blurs into a predominantly confused arrangement of spicules. Megascleres (Fig. 3B) exclusively thin styles, mostly faintly subtylostylote (i.e., with an almost imperceptible constriction at some distance from the blunt ending), in a large size range with perhaps a distinguishable smaller and larger category, 100–350 × 1–8 μm (Alvarez, 1998). Distribution and ecology. Subantarctic and Antarctic waters, 35–200 m.

Remarks. The genus was previously assigned to Axinellidae, but the structure of its skeleton, lacking a reticulation and possessing brushes of megascleres at the surface, fits much better in Suberitidae. The structure is in fact quite similar to that of *Rhizaxinella* (cf. below), but that genus has club-shaped habit and tylostyles.

The genus *Pachaxinella* Burton, 1930b: 503 was erected for type species (by original designation) *Halichondria subdola* Bowerbank, 1866: 247. This is a ramose species with axial and extra-axial skeletons and exclusively styles, 220–510 × 3–6 μm. The shape of the sponge (Fig. 4A, B, D) with pointed branches and optically smooth surface is similar to *Homaxinella balfourensis*.

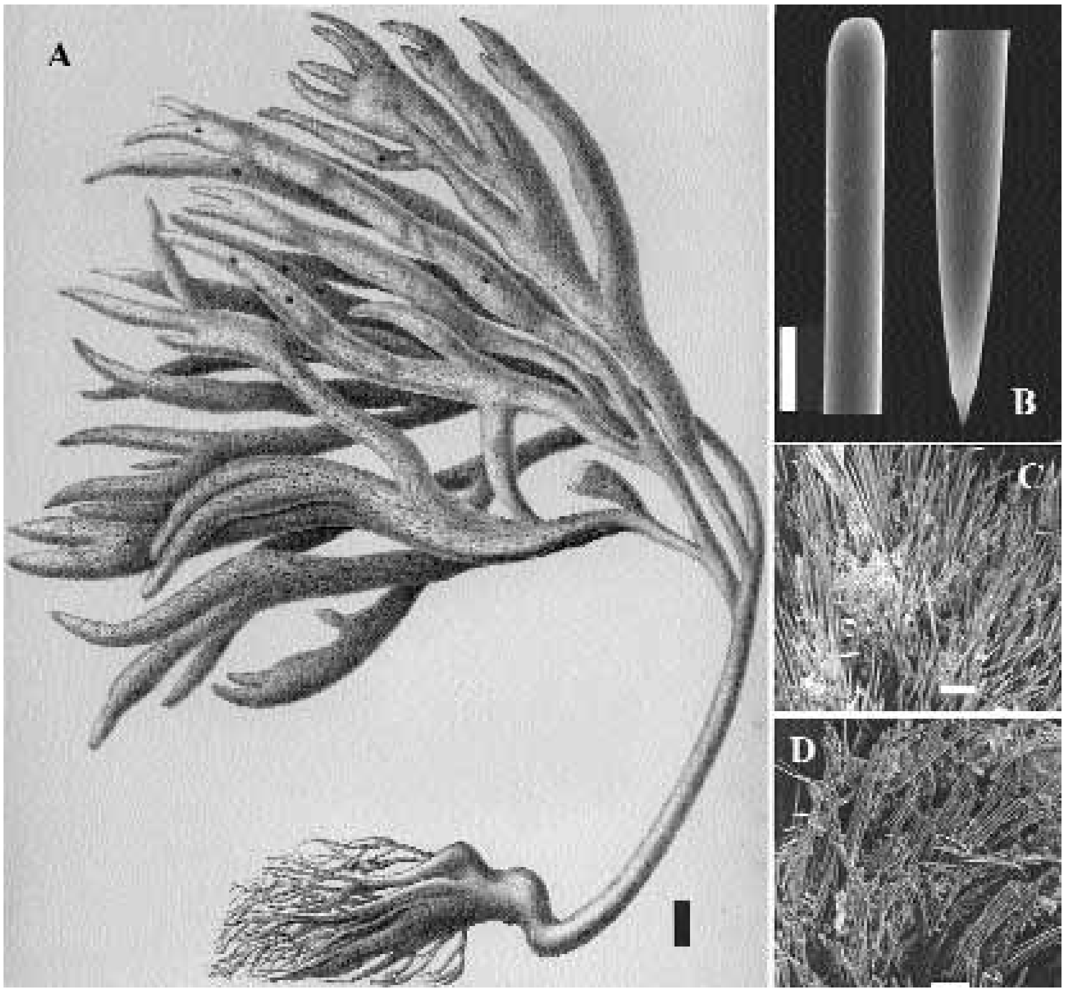

Fig. 3. *Homaxinella balfourensis* (Ridley & Dendy, 1886). A, drawing of habit of lectotype of *Axinella balfourensis*, BMNH 1887.5.2.18 (reproduced from Ridley & Dendy, 1887: pl. XXIII fig. 1) (scale 1 cm). B, SEM images of apices of a representative spicule of ditto (scale 10 µm). C, SEM image of ectosomal spicule brushes of ditto (reproduced from Alvarez, 1996) (scale 100 µm). D, SEM image of cross section of periphery of a branch of ditto (from unpublished Alvarez, 1996) (scale 100 µm).

Burton's reasons for erecting a separate genus are the apparent inversion of spicule density between the axis (rather loosely arranged skeleton) and the peripheral regions with dense mass of spicules in confusion (Fig. 4C). However, these sponges contract notably in preservation, and through this the brushes of smaller styles, present in the fresh condition, are distorted. Bowerbank's holotype, BMNH 1910.1.1.228 (and not BMNH 1929.11.27.1 as Burton: 1930b: 503 stated, Ms Clare Valentine *in litteris*), was re-examined and in many places the extra-axial skeleton is completely gone leaving only a macerated axis, showing the vague spicule bundles characteristic of *Homaxinella*. A recently collected specimen of this species, ZMA POR. 14107, from Roscoff, France (SYMBIOSPONGE 98/FR/SEP11/MK/21), still shows the extra-axial brushes. It is proposed here to consider *Pachaxinella* a junior synonym of *Homaxinella*.

PLICATELLOPSIS BURTON, 1932

Synonymy

Plicatellopsis Burton, 1932b: 332.

Type species

Plicatellopsis arborescens Burton, 1932b: 332 (by original designation).

Definition

Suberitidae with ramose habit and axially condensed skeleton of tylostyles; extra-axial skeleton of bundles of spicules issuing from the central axis to the surface; surface skeleton a dense palisade of smaller tylostyles.

Diagnosis

Thickly branched ramose or irregularly flabellate sponges. Branches with rounded tips, surface microhispid. Surface skeleton consists of the usual brushes of smaller megascleres forming a palisade together with the endings of megasclere bundles of the extra-axial skeleton. The latter originate from the axial skeleton and traverse the extra-axial region towards the surface. Choanosomal skeleton a concentration of aligned or irregularly reticulated

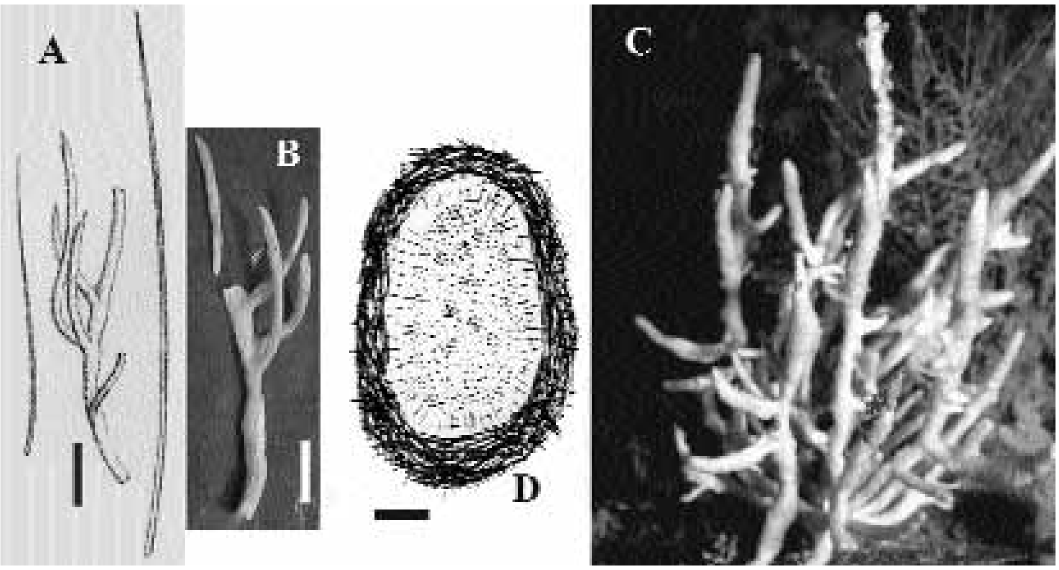

Fig. 4. *Homaxinella subdola* (Bowerbank, 1866), type of *Pachaxinella* (Burton, 1930b), considered jun. syn. of *Homaxinella*. A, habit and spicules (reproduced from Bowerbank, 1874: pl. XLIII fig. 14) (scale 1 cm). B, photo of BMNH holotype (courtesy Ms C. Valentine) (scale 1 cm). C, *in situ* photo of living specimen, St. Mary's, Scilly Isles (courtesy Dr B. Picton). D, drawing of cross section of branch to show axial differentiation of the skeleton (reproduced from Burton, 1930b: fig. 8) (scale 1 mm).

spicule bundles. Megascleres tylostyles (Burton, 1932b: 333 states that the type species has styles – and also figures them as such in text-fig. 37b, cf. fig. 5C – but subsequent examination of the type material revealed only tylostyles, be it with small tyles). The genus is so far only recorded from southern oceans: Falkland Islands, Patagonia, Antarctica, possibly South Australia, approximately 6–7 described species.

Description of type species

Plicatellopsis arborescens Burton, 1932b (Fig. 5A–E).

Synonymy. *Plicatellopsis arborescens* Burton, 1932b: 332, pl. LVI fig. 5, text-figs 36b, 37b.

Material examined. Holotype: BMNH 1928.2.15.388 – Falkland Islands.

Description. Stalked-arborescent (Fig. 5A), more or less dichotomously divided into a three-dimensional bush, 9 cm high, with thick branches of 0.6–1 cm diameter, rounded at the ends. Surface velvety, microhispid, slightly irregular in places, with small rounded depressions on the branches which may represent contracted oscules. Consistency firm, compressible. Colour brown (in alcohol). Ectosomal skeleton (Fig. 5B) a dense palisade of tylostyles which is more or less continuous in preserved specimens. Extra-axial skeleton (Fig. 5B, D) formed by strong, diverging bundles of up to 2.5 mm length, and 200 (at their origin near the axis) to 400 µm wide (at the surface). Axial skeleton a dense mass of aligned spicule bundles, intertwined and anastomosed, 1–2 mm in diameter. Spicules tylostyles (Fig. 5E) with tyle only slightly swollen, in a large size variation, probably divisible in two categories, smaller tylostyles150–320 × 1–8 µm concentrated at the surface, and larger tylostyles, 850–1200 × 10–15 µm (measurements from Alvarez, 1998). Distribution and ecology. Falkland Islands, 130–140 m, on sandy shelly bottom.

Remarks. The genus is very closely related to *Homaxinella* but is distinguished by its possession of tylostyles rather than styles, and also by the more elaborate extra-axial skeleton with its strong bundles. *Rhizaxinella australis* Hentschel, 1909 may be an Australian representative of the genus, which is otherwise known from colder southern ocean waters.

PROSUBERITES TOPSENT, 1893

Synonymy

Prosuberites Topsent, 1893c: xlii.

Type species

Prosuberites longispina Topsent, 1893c: xlii (by monotypy).

Definition

Suberitidae with a basal plate of spongin from which rise single tylostyles. No ectosomal specialization, no localized distinct spicule size categories.

Diagnosis

Thinly encrusting sponges with hispid surface. Skeleton consisting of single, long, tylostyles oriented perpendicularly to the substrate, heads embedded in a basal plate of spongin. Spicules tylostyles of variable size, but no distinctly localized size categories. A dozen or more species, distributed over most ocean regions.

Previous reviews

Topsent, 1900: 174; Rützler, 1965: 26; Rützler & Smith, 1993: 383.

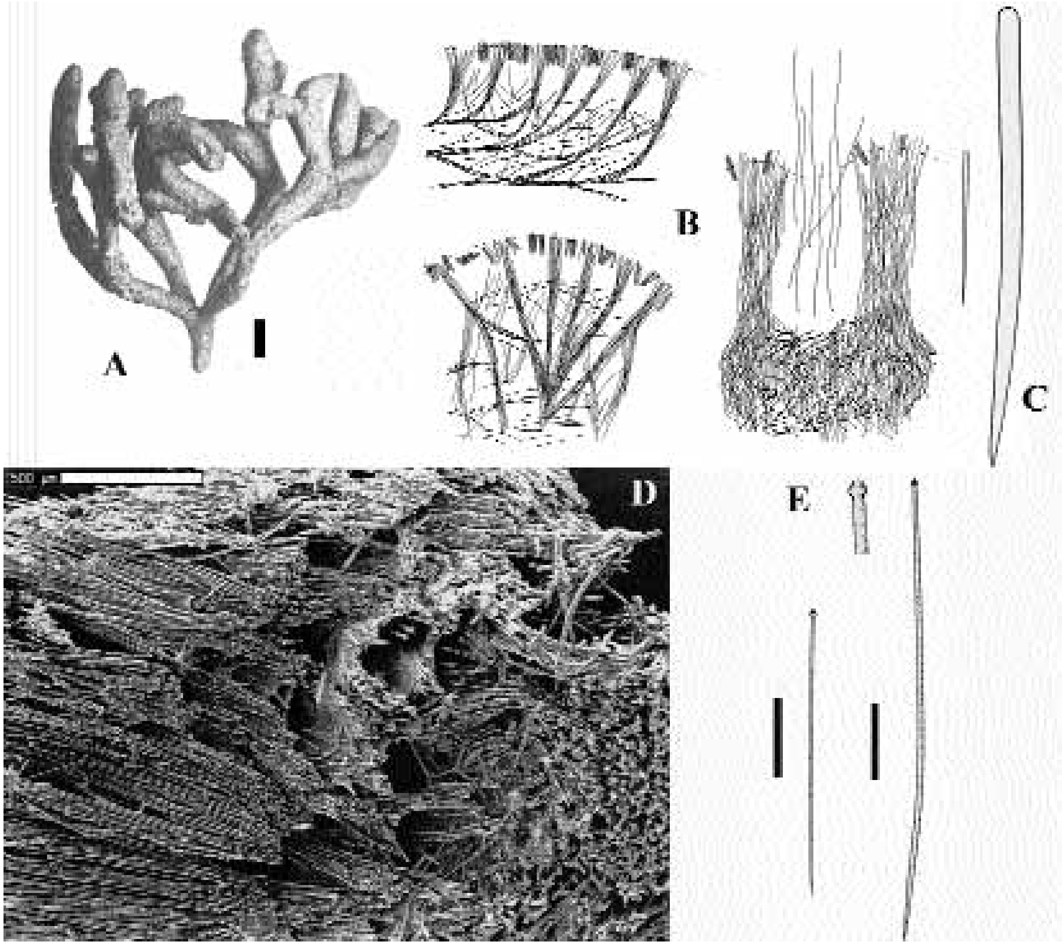

Fig. 5. *Plicatellopsis arborescens* (Burton, 1932b). A, photo of habit of holotype (reproduced from Burton, 1932b: pl. LVI fig. 5) (scale 1 cm). B, drawings of cross sections of various branches of *Plicatellopsis* (reproduced from Burton's text-fig. 36b) (scale see text). C, drawing of spicules of *P. arborescens* reproduced from Burton's 1932b: fig. 37b (subsequent examination of type specimen demonstrated that the styles are in reality all tylostyles) (scale see text). D, SEM image of cross section of a branch of the holotype to show strong axial and extra-axial specialization (reproduced from Alvarez, 1996) (scale 1000 µm). E, drawing of spicule of holotype specialization (reproduced from Alvarez, 1996) (scales: left, 50 µm; right, 100 µm).

Description of type species

Prosuberites longispina Topsent, 1893c (Fig. 6A, B).

Synonymy. *Prosuberites longispina* Topsent, 1893c: xlii; Topsent, 1900: 174, pl. VI fig. 14.

Material examined. Holotype (slide): MNHN DT. 2467 – Banyuls, Western Mediterranean.

Description (based on Topsent, 1900). Thinly encrusting, with strongly hispid surface due to projecting spicules. Lateral size several cm^2. Punctiform oscules. Consistency fleshy, rather soft, rather low spicular density. The skeleton (Fig. 6B) consists of single long spicules standing erect on the substrate with heads attached to it by a spongin layer. Spicules (Fig. 6A). smooth, long tylostyles, all sizes, from $170 \times 4\,\mu m$ up to $2000 \times 17\,\mu m$, with tyle $25\,\mu m$ in diameter. Occasionally, the spicule is polytylote. Smaller tylostyles may occur in groups at the substratum. Distribution and ecology. Western Mediterranean and Adriatic, Canary Islands, Azores. Common in the Banyuls area (Boury-Esnault, 1971a).

Remarks. The distinction of the encrusting suberitid genera remains a difficult problem on account of the possibility that juvenile growth stages of more elaborate adult specimens may be confused with specimens which do not become more elaborate later in their life. *Prosuberites* is here limited to specimens which: (1) have their tylostyles singly embedded with their heads in a basal spongin plate – a feature which is otherwise shared with poecilosclerid genera like *Hymedesmia* and *Clathria (Microciona)*; (2) are strongly hispid due to projection of long tylostyles through the surface membrane; and (3) do not have a surface specialization of brushes of tylostyles or styles. This definition excludes several well-established *Prosuberites* species from the genus, the most prominent being *P. epiphytum*, which is here transferred to *Protosuberites* (cf. below).

PROTOSUBERITES SWARTSCHEWSKY, 1905

Synonymy

Protosuberites Swartschewsky, 1905: 36. *Laxosuberites sensu* Topsent, 1938a: 20 (not Topsent, 1896a: 126). ? [*Gilchristia*] Burton, 1928a: 129 (preocc.) (not Jordan, 1907). *Terpiosella* Burton, 1930d: 675. *Keratylum* de Laubenfels, 1936a: 125.

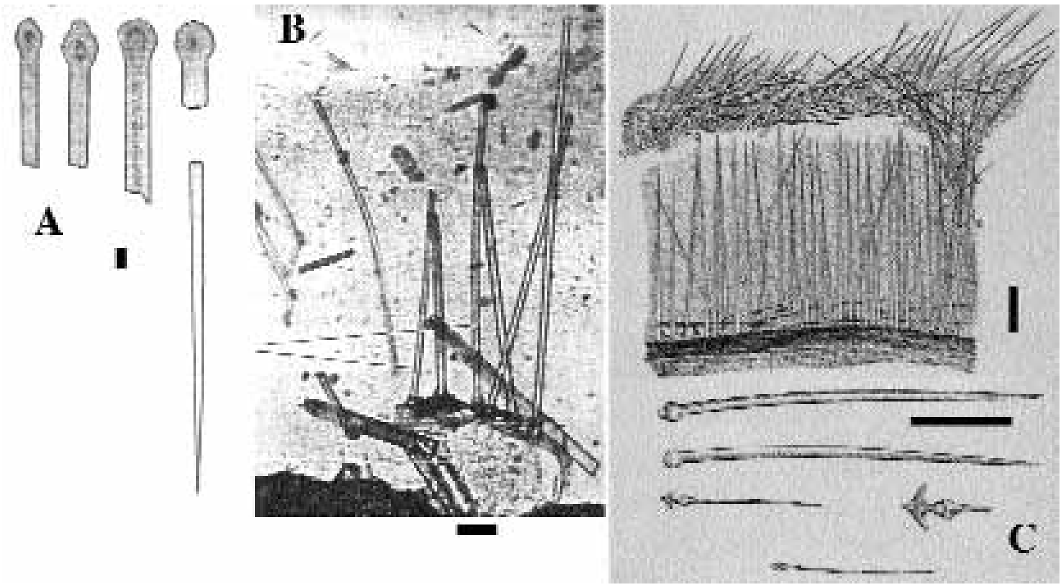

Fig. 6. A, B, *Prosuberites longispina* Topsent, 1893c. A, drawing of spicules (reproduced from Topsent, 1900: pl. VI fig. 14) (scale 10 μm). B, photo of cross section of skeleton (reproduced from Rützler, 1965: fig. 11) (scale 100 μm). C, *Protosuberites prototipus* Swartschewsky, 1905, drawings of cross section of skeleton and tylostyles (reproduced from Swartschewsky, 1905: pl. VI fig. 5) (scale 100 μm).

Type species

Protosuberites prototipus Swartschewsky, 1905: 36 (by monotypy).

Definition

Suberitidae with encrusting habit and a skeleton differentiated in a choanosomal arrangement of single tylostyles or bundles of tylostyles, and ectosomal brushes of tylostyles.

Diagnosis

Thinly to more massively encrusting sponges with a velvety or microhispid surface. Oscular veins often prominently visible. The surface skeleton consists of brushes of tylostyles, which are often somewhat smaller than those of the choanosome. Choanosomal skeleton consists variably of single spicules erect on the substrate or bundles running from the substrate to the surface, usually parallel to each other, without any form of anastomosing. The genus in its present concept includes dozens of species from all parts of the world oceans.

Description of type species

Protosuberites prototipus Swartschewsky, 1905 (Fig. 6C).

Synonymy. *Protosuberites prototipus* Swartschewsky, 1905: 36, pl. VI fig. 5 (in Russian, with a German summary of the species description on p. 52).

Material examined. None. The whereabouts of the type material is not recently confirmed but the material was deposited in the collections of the Academy of St Petersburg and the Zoological Museum of the University of Kharkov.

Description (from Swartschewsky, 1905). Very thin encrustation of a rust-brown color. Ectosomal skeleton (Fig. 6C) a mass of spicules arranged in all directions but probably originally consisting of loosely arranged brushes. Choanosomal skeleton (Fig. 6C) consists of single tylostyles arranged in arranged, heads on the substrate. Spicules (Fig. 6C) tylostyles in a large size range, 162–417 × 5–7 μm. Smaller tylostyles are drawn in the surface brushes and strewn in the interior among the larger erect tylostyles. Distribution and ecology. Black Sea (Liaspi), 60 m.

Remarks This genus name is here revived to take the place of *Laxosuberites sensu* Topsent, 1938a: 20. That genus name can no longer be employed because *Laxosuberites* Topsent, 1896a: 126 is a junior synonym of *Hymeniacidon*. Its type species (by original designation) *Suberites rugosus* Schmidt, 1868, was found to be a specimen of *Hymeniacidon* by Topsent (1938a: 20), and his subsequent attempts to convey the properties of *Laxosuberites* to the Banyuls specimen described as *Laxosuberites rugosus* by Topsent, 1900 (cf. Fig. 7A, B) are inadmissible because a genus cannot have two different type species. Several species traditionally assigned to *Prosuberites*, e.g., *P. epiphytum* (Lamarck, 1814), show skeletal structures intermediate between *Prosuberites longispina* (i.e., single spicules erect on the substrate) and '*Laxosuberites*' spp. (bundles of aligned spicules), even by Topsent's own admission (see Topsent, 1900: 183). Swartschewsky's *Protosuberites prototipus* is likewise somewhat intermediate between *Prosuberites* and '*Laxosuberites*' by combining single spicules erect on the substrate with ectosomal specialization of brushes of spicules. *Protosuberites* is here extended to include thinly encrusting sponges with choanosomal bundles of spicules, as an acknowledgement of the occurrence in a single species of specimens with single spicules erect on the substrate and specimens with bundles of spicules. In Swartschewsky's own words 'The genus described here has properties of the above described genera' – he refers to Topsent's genera *Suberites, Prosuberites, Laxosuberites* and *Pseudosuberites* – 'and this gives me reason to consider it a genus older than the others, and even older perhaps than their ancestors. Hence I propose the name *Protosuberites*' (translation courtesy of Ms T. Das, University of Amsterdam).

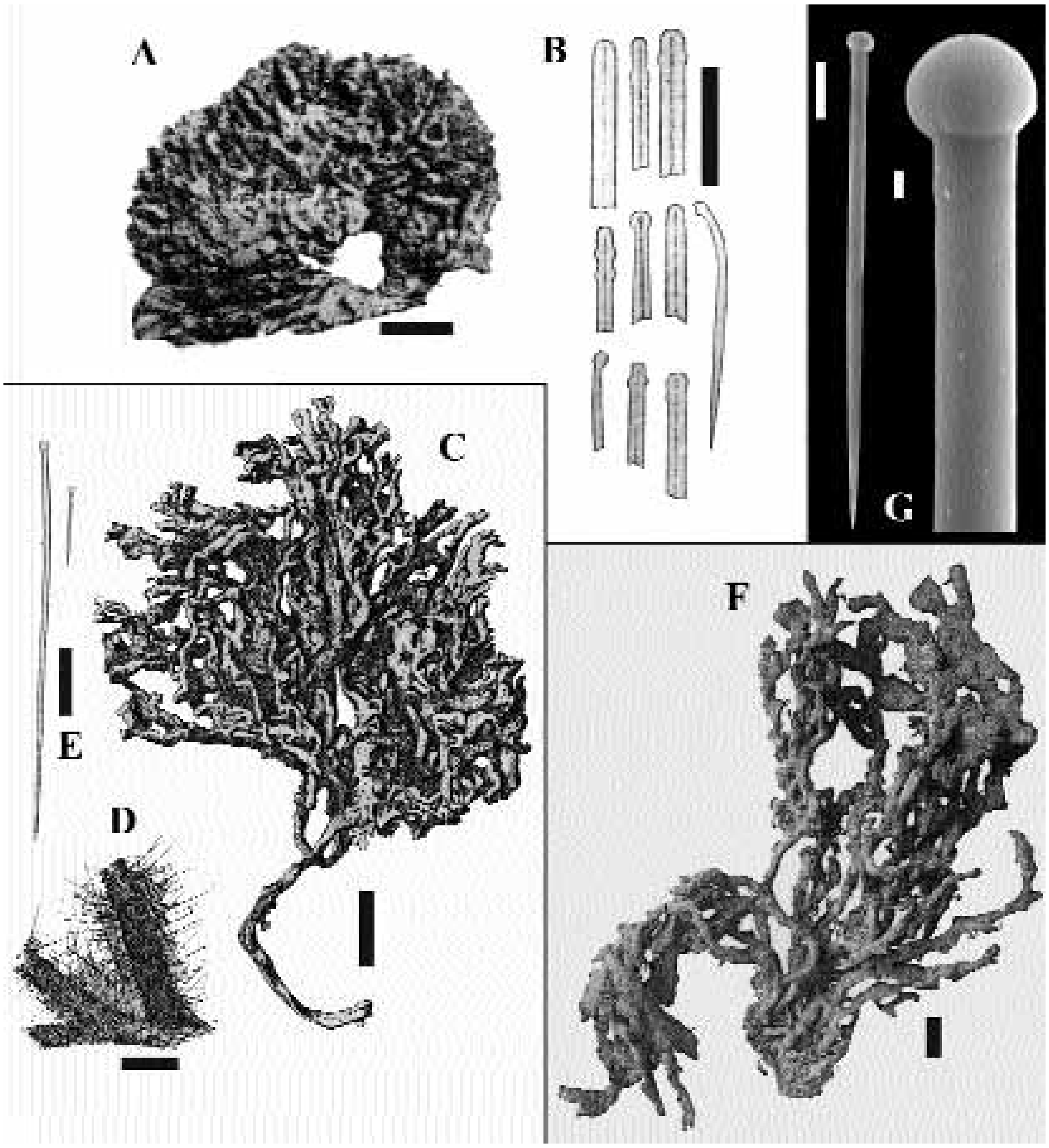

Fig. 7. *Protosuberites* spp. A, B, *Protosuberites rugosus* (Topsent, 1938a). A, habit of Banyuls specimen (scale 1 cm). B, spicules from ditto (scale 100 µm) (both reproduced from Topsent, 1900: pl. V). C–F, *Protosuberites epiphytum* (Lamarck, 1814). C, drawing of habit of *Ophlitaspongia fucoides* Bowerbank, 1876b (jun. syn. of *P. epiphytum*) (scale 5 cm). D, drawing of skeleton of ditto (scale 500 µm). E, spicules of ditto (scale 100 µm) (all reproduced from Bowerbank, 1876b: pl. LXXX). G, SEM image of spicule and detail made from the holotype of *Alcyonium epiphytum* (scale: left, 10 µm; right, 1 µm). F, habit of Lamarck's type specimen (reproduced from Topsent, 1933: pl. III fig. 2) (scale 1 cm).

The genus [*Gilchristia*] Burton, 1928a: 129 was erected for type species (by original designation) *Bubaris reptans* Kirkpatrick (1903b: 248, pl. V fig. 14, pl. VI fig. 15a–c). The name is preoccupied by *Gilchristia* Jordan, 1907 (Pisces, Proc. U.S. Nat. Mus. 32: 236). Burton (1928a: 129) gave no definition other than stating that Kirkpatrick's species is not a *Bubaris* and that the new genus was *incertae sedis* in Suberitidae. The description of Kirkpatrick is peculiar: it concerns an epizoic sponge on *Halichondria pachastrelloides*, apparently forming a meandering crust, leaving free polygonal 'islands' of surface of *Halichondria*. The crust had a skeleton of erect bundles of large fusiform styles (which are here interpreted as tylostyles), up to 530 × 15 µm in size, and ectosomal brushes of small tylostyles, size given as 16 × 6 µm, which cannot be other than a misprint, assumed to be 160 × 6 µm. The properties of this sponge, if interpreted correctly, conform to *Protosuberites*. Kirkpatrick (1903b) also described a basal tangential layer of the fusiform styles, but this is interpreted as a protection against the host sponge, a common enough phenomenon in epizoic sponges.

The genus *Terpiosella* Burton, 1930d: 675 was erected for type species (by original designation) *Ophlitaspongia fucoides* Bowerbank (1876b: 771, pl. LXXX) from Shark Bay, Western Australia. This is a hispid, encrusting sponge on an alga (Fig. 7C–E), with spicules erect on the substrate and some aligning the algal thallus strands (Fig. 7D); in places the skeleton is confused. Spicules (Fig. 7E) are tylostyles of 100–400 µm in length. Burton (1930d) emphasized the symbiosis with the alga as a generic character, and also assigned *Terpios symbiotica* Hentschel, 1909 to *Terpiosella*. The epiphytic habit is not considered a generic feature, as many unrelated sponges exhibit such behaviour. The structure of *O. fucoides* conforms to the definition of *Protosuberites* and thus *Terpiosella* is a junior synonym of this genus. Topsent (1933: 35) in his redescription of what he called *Prosuberites epiphytum* (Lamarck, 1814 as

Alcyonium, type specimen MNHN DT3421) pointed out the similarities with this species, including the extensive overgrowing of algae (cf. Fig. 7F), and suggested they were synonyms. *Prosuberites epiphytum* is considered a cosmopolitan species with characteristic spicules (Fig. 7G); it is reported especially from Europe (e.g., Mediterranean: Topsent, 1900: 178; Netherlands: Van Soest, 1977a: 266), but there are strong indications that the type originated from Australia (collected by Péron and Lesueur). The conspecificity of *Ophlitaspongia fucoides* and *Alcyonium epiphytum* is here accepted and thus its ultimate designation is *Protosuberites epiphytum*.

The genus *Keratylum* de Laubenfels, 1936a: 125 was erected for type species (by original designation) *Suberites capillitium* Topsent (1892a: 130, pl. II fig. 10, pl. IX figs 19-10). The species is an encrustation on brachiopod shells collected at greater depths in the North Atlantic; its skeleton consists of bundles of large tylostyles, up to 1000 × 27 μm, ending in brushes of small tylostyles as small as 250 × 7 μm. These characters conform to *Protosuberites* in the present concept and thus *Keratylum* is a junior synonym.

PSEUDOSPONGOSORITES MCCORMACK & KELLY, 2002

Synonymy

Pseudospongosorites: McCormack & Kelly, 2002: 1019.

Type species

Spongosorites suberitoides Diaz *et al*., 1993: 299 (by original designation).

Definition

Suberitidae with exclusively small oxeas as spicules, arranged in brushes at the surface and confusedly in the interior.

Diagnosis

Sponge massive, irregular in outline, initially encrusting gastropod shells and developing a symbiosis with hermit crabs. Surface smooth, velvety. Skeleton of the surface the usual brushes of megascleres. Choanosomal skeleton predominantly confused with a vague reticulation of spicule tracts. Spicules exclusively small oxeas, in two overlapping size categories. The genus is monotypical, recorded from shallow water in the Central West Atlantic.

Previous reviews

Diaz *et al*. (1993); Sandford & Kelly-Borges (1997).

Description of type species

Pseudospongosorites suberitoides (Diaz *et al*., 1993) (Fig. 8A–D).

Synonymy. *Xestospongia halichondrioides sensu* Wells *et al*., 1960: 210 (not *Petrosia halichondrioides* Wilson, 1902). *Spongosorites suberitoides* Diaz *et al*., 1993: 299, figs 28, 34; Sandford & Kelly-Borges, 1997: 317, figs 1–5; *Pseudospongosorites suberitoides*; McCormack & Kelly, 2002: 1019.

Material examined. Holotype: USNM 32441 – North Carolina, 32 m. Paratype: ZMA POR. 5762 – Margarita Island, Venezuela, 56 m.

Description. 'Mobile' sponge living as a rule as a massive encrustation on empty gastropod shell of the genera *Cantharus* or *Epitonium*, inhabited by a pagurid hermit crab. Shape (Fig. 8A) irregularly spherical to ovoid, with lobose outgrowths in larger specimens, typically 2–5 cm. Usually a single oscule with raised rims, about 3 mm in diameter. Surface smooth, velvety. Consistency firm. Colour greyish green, tan or orange, sometimes mottled. Ectosomal skeleton (Fig. 8B, C) arranged as dense erect tufts. Below this there is an area with many subdermal spaces (Fig. 8C) and generally less dense skeleton. Further into the choanosome, the skeleton consists of irregular tracts of spicules making a confused reticulation with many loose spicules. At the contact with the gastropod shell, the skeleton is a dense confused layer of spicules, and in many specimen this region also contains round flattened spongin encased 'gemmules' of 150–500 μm in diameter. Spicules (Fig. 8D) exclusively smooth sharp pointed oxeas, occasionally centrotylote and bent, occasionally stylote or strongylote, probably divisible in two overlapping size categories, 176–295 × 2–12 μm and 125–185 × 2–10 μm. Distribution and ecology. Common in the Gulf of Mexico and the Atlantic coasts of Florida and North and South Carolina; also recorded from Venezuela, shoreline down to 60 m.

Remarks. Some discussion about the phylogenetic affinities has been going on in the recent literature. Although the similarities in habit and ecology with *Suberites domuncula* are compelling, the exclusive occurrence of oxeas as spicules in this species was considered prohibitive for inclusion in Suberitidae until recently. Initially, this species was assigned to Wilson's (1902) *Petrosia halichondrioides* by Wells *et al*., 1960; however, Wilson's species was discovered to be a *Plakortis* and unrelated to the hermit crab sponge. Diaz *et al*. (1993) noted the similarity with *Suberites domuncula* but considered it to be a convergent association and assigned the species to the halichondrid genus *Spongosorites*. Sandford & Kelly-Borges (1997) described the association in more detail, expressed their dissatisfaction with the assignment to *Spongosorites*, but felt there was not enough evidence to approach the species to Suberitidae. Subsequently, McCormack & Kelly (2002) produced molecular evidence for close relationship of *Suberites* and *S. suberitoides*, and proceded to assign it to a new genus in the family Suberitidae. This is here accepted.

PSEUDOSUBERITES TOPSENT, 1896

Synonymy

Pseudosuberites Topsent, 1896a: 127.

Type species

Hymeniacidon hyalina Ridley & Dendy, 1887: 168 (by subsequent designation; Burton, 1930d: 674).

Definition

Suberitidae with tangential ectosomal skeleton of tylostyles over a confused choanosomal skeleton of tylostyle bundles and individual spicules. Tylostyles variable in length but no localized size category.

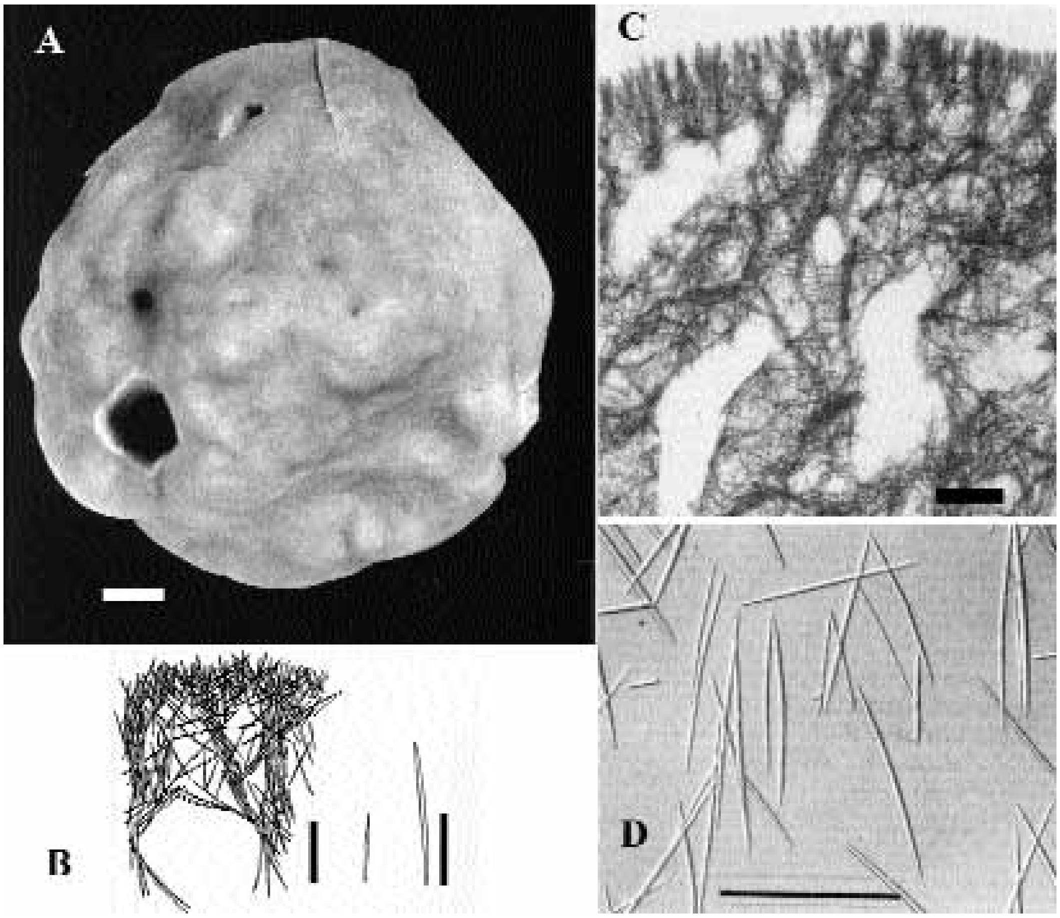

Fig. 8. *Pseudospongosorites suberitoides* (Díaz *et al*., 1993). A, habit of paratype ZMA 5762 (scale 1 cm). B, drawing of skeleton and spicules (reproduced from Díaz *et al*., 1993: fig. 34) (scales: 200 μm, 100 μm). C, photo of peripheral skeleton (reproduced from Sandford & Kelly-Borges, 1997: fig. 3a) (scale 500 μm). D, photo of spicules (reproduced from Sandford & Kelly-Borges, 1997: fig. 2d) (scale 100 μm).

Diagnosis

Massively or thinly encrusting sponges, structured like *Suberites*, but with a smooth surface due to a tangential ectosomal skeleton. Consistency fleshy, due to an irregular arrangement of spicule tracts. Spicules tylostyles in a large size variation but without distinct size categories. Distribution cosmopolitan, with about 20 species described, some of which are reported to have unusually disjunct occurrence.

Previous reviews

Topsent, 1900: 164; Burton, 1930d: 674; Rützler & Smith, 1993: 383.

Description of type species

Pseudosuberites hyalina (Ridley & Dendy, 1887) (Fig. 9A–D).

Synonymy (restricted). *Hymeniacidon ? hyalina* Ridley & Dendy, 1887: 168, pl. XLV fig. 6; *Pseudosuberites hyalina*; Topsent, 1896a: 127; Topsent, 1900: 164; Burton, 1930d: 674.

Material examined. Holotype: BMNH 1887.5.21.41 – as 'Hymeniacidon (?) hyalina' (wet), off SW coast of Patagonia, 'Challenger' coll. (not examined). Other material. Topotypical specimen: ZMA POR. 14929 – Chile, Isla San Ambrosio, 26°20′S 80°0′W, coll. SEPBOP Exped. stat. 17–676B, 160–170 m, 12 July 1966 (donated by USNM-SOSC). European specimen: ZMA POR. 5013 – Norway, Bergen area, Vaagegrund, 100 m, dredged, coll. R.W.M. Van Soest, c.s. 19 July 1982.

Description. The type consists of a few shapeless fragments (Fig. 9B), encrusted by foreign organisms. The Chilean SEPBOP specimens (Fig. 9D) thought to be this species are whitish lobate fragments with indeed some encrusting hydroids. The species is 'hyaline' in appearance due to large subdermal cavities roofed over by the surface skeleton (Fig. 9C). The type is rather soft and spongy, but the recent specimens, both the Chilean and the putative representatives from Norway, are rather firm. Oscules were stated to be large but a question mark was added; in the recent material no oscules are apparent. The ectosomal skeleton is unusual for a suberitid in containing a distinct tangential arrangement of spicules carried by thick bouquets of subdermal spicules spaced rather far apart and leaving large subdermal cavities in between (Fig. 9C). The choanosomal skeleton is largely confused, with few spicule bundles. Tylostyles (Fig. 9A) robust, with prominent globular heads ('pin-shaped'), fusiform; those at the surface and in the subdermal bouquets often smaller, but probably not clearly divisible in two size categories: 220–1200 × 2–25 μm. Distribution and ecology. SE Pacific, and recorded disjunctly from the North Atlantic, in deeper water. Many other records, including tropical localities, are suspect.

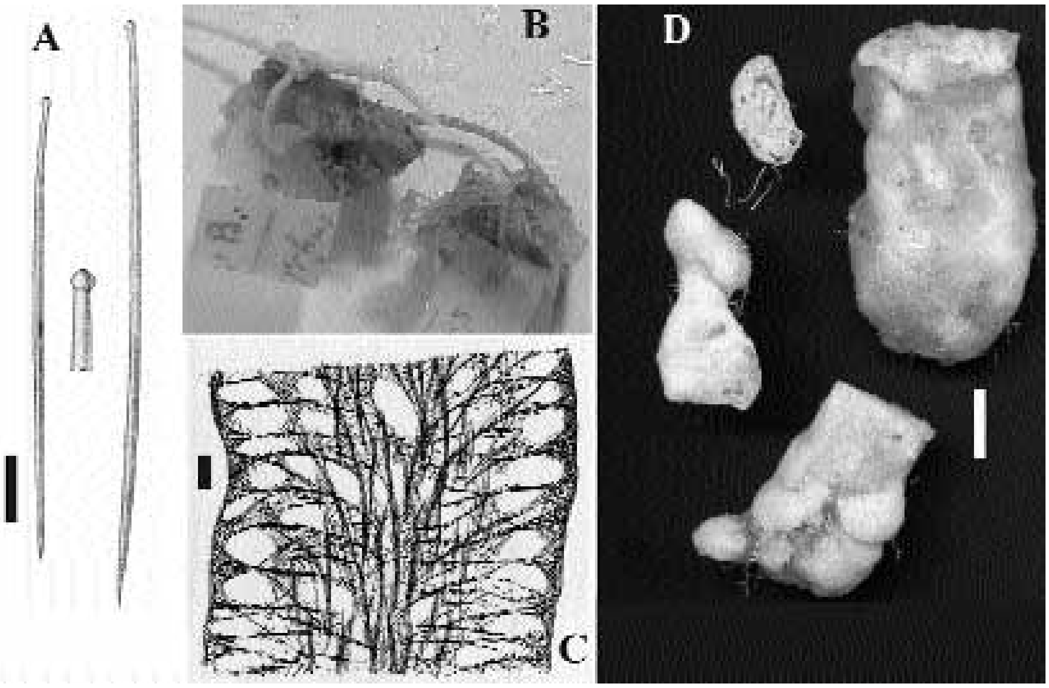

Fig. 9. *Pseudosuberites hyalina* (Ridley & Dendy, 1886). A, drawing of spicules (reproduced from Ridley & Dendy, 1887: pl. XLV fig. 6) (scale 100 μm). B, habit of type material BMNH 1887.5.21.41 (photo courtesy Ms C. Valentine) (scale see text). C, cross section of skeleton (reproduced from Kirkpatrick, 1908c: pl. XXVI fig. 7) (scale 500 μm). D, photo of topotypical fragments, ZMA 14929 (scale 1 cm).

Remarks. The original habitat of this species is not recorded, other than that it came from off SW Patagonia. The type material is meagre and the authors even state that they were at loss about its affinity and had doubts describing it as a new species. It is surprising, that it subsequently was recorded from all over the world. The identity of those records remains in most cases dubious, because of the paucity of data available on the original specimen. *Pseudosuberites hyalina* was recorded from such extremely different habitats as deep water (500–600 m) in the Mediterranean (Topsent, 1900: 171), tropical mudflats in the Suez area (Row, 1911), and the freezing cold water at McMurdo Sound and other Antarctic locations at depths of 300 m or more (Kirkpatrick, 1908c: 21; Burton, 1929a: 445), as well as from the Arctic Ocean between Bear Island and Norway (Topsent, 1913a: 26). It is obvious that not all these records concern the same species. From Topsent's (1896a, 1900) treatment of *Pseudosuberites*, it is clear that he intended the well-established species *P. sulphurea* (Bowerbank, 1866: 208, as *Hymeniacidon*) as the type of the genus. Unfortunately, he mentioned *Hymeniacidon ? hyalina* Ridley & Dendy (1887) as a second species of *Pseudosuberites*, and omitted to state expressly that *P. sulphurea* was the type. Equally unfortunately, Burton (1930d) chose *hyalina* as the 'genotype', thus making the status and affinities of *Pseudosuberites* less clear than it would have been with *P. sulphurea* as the type, because apart from all the dubious records from various localities around the world there have been no further published records from the Chilean Patagonian coast. The nearest subsequent record is from the Falkland Islands (Burton, 1932b), but no further descriptive data were provided. *P. sulphurea* is a yellow-orange encrusting species fairly common along the coasts of Europe and well-established by type and additional material. Burton (1930d: 674) mentioned *Suberanthus* Lendenfeld as a junior synonym of *Pseudosuberites*, giving Lendenfeld's publication as 1897 (1897a). If he would have been right in his assumption that the two are synonyms then *Suberanthus* would have had priority, since the publication date is in fact January 9, 1896. Fortunately, *Suberanthus* is a synonym of *Suberites* (cf. below).

RHIZAXINELLA KELLER, 1880

Synonymy

Rhizaxinella Keller, 1880a: 272.

Type species

Rhizaxinella clavigera Keller, 1880a: 272 (by monotypy) (=junior synonym of *Alcyonium pyrifera* delle Chiaje, 1828: 151).

Definition

Suberitidae with spherical or ovoid body carried on a long thin stalk. Skeleton radially arranged with ectosomal spicule brushes at the surface. Spicules tylostyles, and if present rhaphides arranged in trichodragmas.

Diagnosis

Pedunculate sponges, with spherical, ovoid or cylindrical body carried on a simple or ramified stalk, normally attached to the substrate by a root system; usually an apical oscule. Body with a more-or-less radial skeleton and with brushes of spicules at the surface, skeleton of the stalk a tightly packed mass of aligned megascleres,

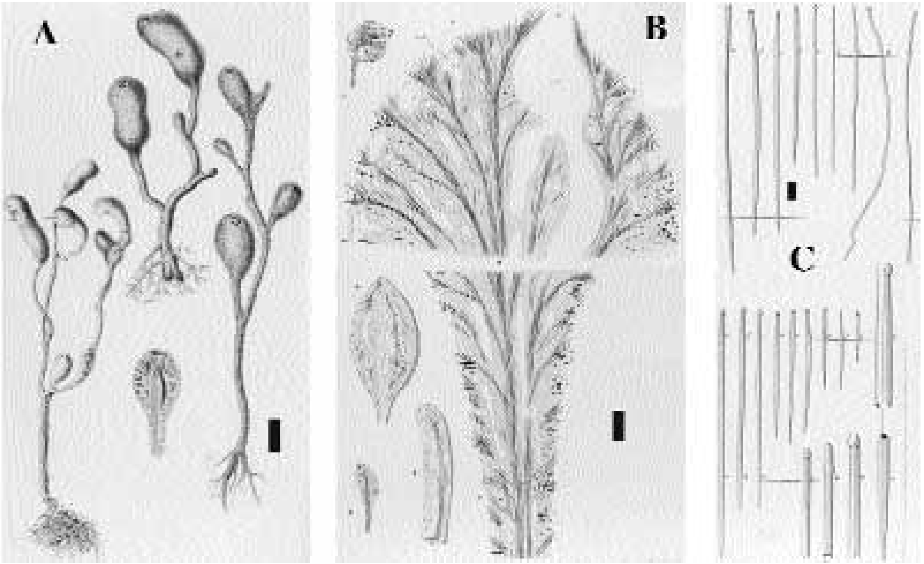

Fig. 10. *Rhizaxinella pyrifera* (Delle Chiaje, 1822). A, drawing of habit (scale 1 cm). B, cross section of main body (scale 1 mm). C, tylostyles (scale 100 μm) (all reproduced from Vosmaer, 1935: pls 38–40).

bound by spongin. Megascleres are tylostyles of different sizes with raphides in trichodragmas. About 20 species have been described from all three ocean basins, usually from deeper or colder waters.

Previous reviews

Keller (1880a), Vosmaer (1887), Topsent (1900), Vosmaer (1935).

Description of the species

Rhizaxinella pyrifera (delle Chiaje, 1828) (Fig. 10A–C).

Synonymy. *Alcyonium pyriferum* delle Chiaje, 1828: 151; *Rhizaxinella pyrifera*; Vosmaer, 1887: 331; Topsent, 1900: 243. *Rhizaxinella clavigera* Keller, 1880a: 272, pl. XIII figs 1–3.

Material examined. Holotype: Delle Chiaje's material is not located. Type material of Keller may be in ZMB (not seen). Other material. Aegean Sea specimens reported in Voultsiadou-Koukoura & Van Soest, 1993.

Description. Stalked sponges with pyriform or cylindrical main body (Fig. 10A), length of total sponge 3–23 cm, main body 0.5–19 cm. Stalk usually gradually broadening into the main body. Stalk fixed in or to substratum by a fine-threaded root system. Color whitish or greyish. Surface velvety. Usually a single apical oscule. Skeleton (Fig. 10B) axially condensed, in the stalk the surface brushes are immediately perpendicular on the aligned and spongin-enforced axial spicules, but in the main body the axis diverges into thinner secondary axes and finally end at the surface in the brushes. In between numerous trichodragmas are found. On the whole the spicules at the periphery are smaller than those of the axial parts, but no sharp distinction can be made. Spicules (Fig. 10C) tylostyles, 300–2500 × 3–20 μm, possibly divisible in smaller tylostyles 300–1200 μm at the surface, and larger, often flexuous tylostyles 800–2500 μm of the axial bundles. Raphides, usually in trichodragmas, 80–120 μm. Distribution and ecology. Mediterranean, deep water, 70–600 m.

Remarks. This is a clearly demarcated genus. It shows some superficial resemblance to *Stylocordyla* (family Stylocordylidae) but differs in having only tylostyles as megascleres.

SUBERITES NARDO, 1833

Restricted synonymy

Suberites Nardo, 1833: 523. *Ficulina* Gray, 1867a: 523. *Suberanthus* Lendenfeld, 1896: 144. *Suberella* Thiele, 1905: 416. [*Suberella*] Burton, 1929a: 446. *Carnleia* Burton, 1930c: 519; *Laxosuberella* Burton, 1930d: 675.

Type species

Alcyonium domuncula Olivi, 1792: 241 (by original designation).

Definition

Suberitidae with ectosomal skeleton consisting of bouquets of smaller tylostyles carried by subradiate bundles of larger tylostyles; choanosomal skeleton confused or alveolar arrangement of larger tylostyles. If present, microscleres are spined centrotylote microstrongyles.

Diagnosis

Massive, compact, usually with velvety smooth surface, caused by dense ectosomal arrangement tylostyles oriented perpendicularly to the sponge surface, points outward; peripheral choanosomal skeleton consists of closely packed strands of tylostyles distinctly larger than ectosomal ones, with interior skeleton of densely packed tylostyles in confusion. Centrotylote, minutely spined microstrongyles may be present in a few species and if so are concentrated

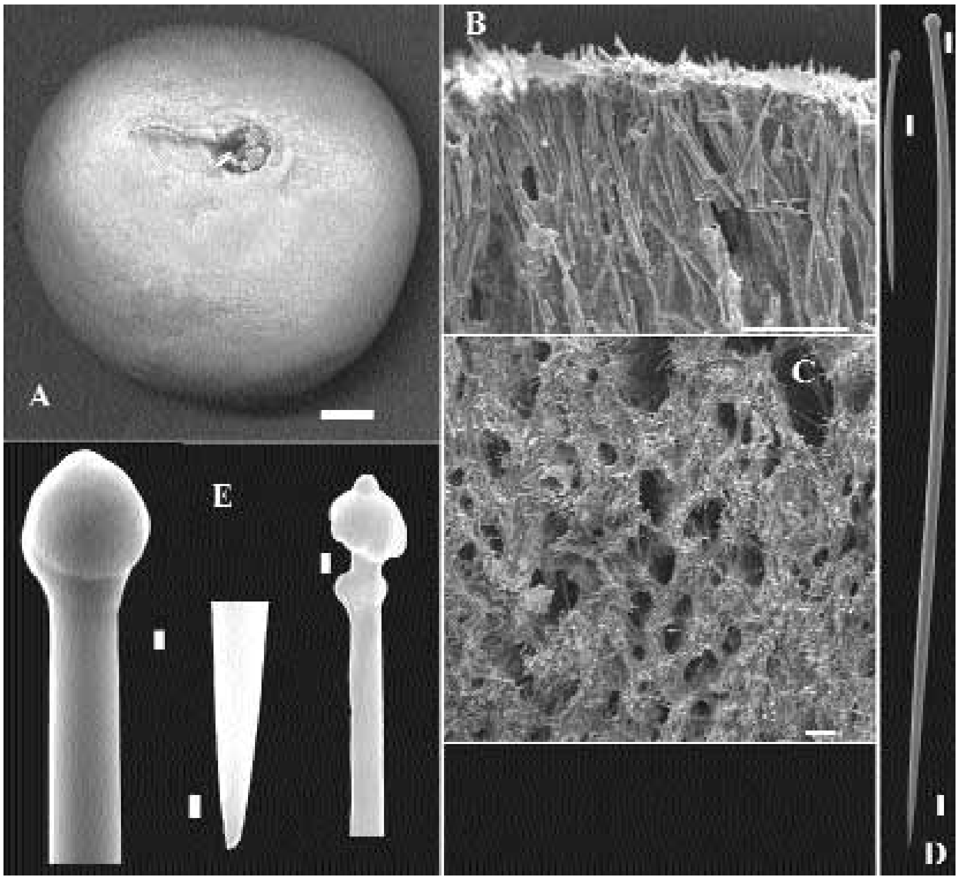

Fig. 11. *Suberites domuncula* (Olivi, 1792). A, habit of neotype ZMA 2237 (scale 1 cm). B, SEM image of cross section of peripheral skeleton (scale 100 μm). C, SEM image of cross section of choanosome (scale 100 μm). D, SEM image of spicules (scale 10 μm). E, SEM images of details of tylostyle heads (scale 1 μm).

at the surface. Approximately 80 species have been described (obvious synonyms and invalid genus assignments omitted). The genus is cosmopolitan in distribution but is most common in cold temperate waters.

Previous reviews

Lendenfeld (1896), Topsent (1900), Vosmaer (1935), Burton (1953), Rützler & Smith (1993).

Description of type species

Suberites domuncula (Olivi, 1792) (Fig. 11A–E).

Restricted synonymy. *Alcyonium domuncula* Olivi, 1792: 241; *Suberites domuncula*; Nardo, 1833: 523; Topsent, 1900: 225, pl. VI figs 1–9; Burton, 1953: 353.

Material. Type material: considered lost. Neotype (designated herein): ZMA POR. 2237 – Triest, no further data. Other material. Numerous ZMA specimens from the Mediterranean-Atlantic.

Description. The neotype (Fig. 11A) has an ellipsoid-oval shape, size 7 × 7 × 6 cm. Surface velvety smooth. Consistency firmly compressible. Two apertures are apparent. One leads to the cavity in which a hermit crab is lodged. In smaller specimens an empty gastropod shell or its remains are still to be found and then the hermit crab that lives in it; however, larger specimens usually have no trace of the shell, and the crab lives inside the sponge. On the opposite side of the hermit crab aperture, in the neotype, there is an oscule 1 cm in diameter. Other specimens may have two oscules, arranged occasionally also nearer to the hermit crab aperture. Many specimens have a layer of asexual rounded bodies on the surface adhering to the mollusc shell or the hermit crab cavity, often referred to as 'gemmules'. The colour of the neotype is not given, but most specimens recorded alive are bright orange, some are mottled with brown, red or blueish spots (so called 'marmorated' form). Skeleton (Fig. 11B, C) perpendicularly arranged in the peripheral 10 mm, becoming progressively confused towards the interior, where the spicules are packed around interior holes and canals. The ectosomal spicules are arranged in bouquets of smaller spicules carried by radiating larger spicules. Spicules tylostyles (Fig. 11D, E) with a slightly subterminal (drop-shaped) but mostly well-formed tyle, except for rare annular swellings in the neck region. Small surface tylostyles, 100–350 × 4–8 μm, larger choanosomal tylostyles 250–480 × 5–8 μm, the length of small surface tylostyles averaging 53% of the length of choanosomal tylostyles. Distribution and ecology. Originally described from the Adriatic, but subsequently widely recorded from all over the world. It is likely that this widespread occurrence is an artefact of low amount of discriminatory morphological characters, and in reality represents a complex of species living in symbiosis with hermit crabs. The depth preference of the species is between 10 and 100 m.

Remarks. *Suberites domuncula* occurs in a uniform orange and a marmorated form. The latter is extremely common along the sandy coasts of West Africa (Van Soest, 1993). So far it is unclear what the cause is of the difference in surface markings; in alcohol the distinction between the colour morphs disappears. The species is reliably recorded from the Mediterranean, and the adjacent Atlantic coasts. Records from boreal Atlantic waters may have been confused with *Suberites suberia* (Montagu, 1818), which has a duller colour and possesses spined microstrongyles, but otherwise is similar in habit and hermit crab symbiosis. This species may also occur in the Aegean Sea (Voultsiadou-Koukoura & Van Soest, 1993: 179, as *Suberites ficus*) and in the Black Sea (Swartchevsky, 1905). *Lithumena* Nardo, 1833 is associated with *Suberites domuncula* by Lieberkühn, 1869: 520, but this was not verified. If this is indeed the case, then *Lithumena* is an objective synonym of *Suberites* because both share the same type species.

The genus *Ficulina* Gray, 1867a: 523 was erected for Suberitidae with spined microstrongyles. Its type species (by monotypy) is *Halichondria ficus* Johnston, 1842. The synonymy of this genus with *Suberites* has been the subject of a long debate among taxonomists (see review by Burton, 1953: 353). With the species *Ficulina ficus* – as with many other *Suberites* species – there are taxonomic as well as nomenclatorial problems: the name *ficus* goes back to Pallas (1766, as *Alcyonium*), but that is generally assumed to have been a compound ascidian. Subsequent uses of the name *ficus* by Linnaeus (1767), Esper (1794) and Lamarck (1814), all as *Alcyonium*, were likewise uncertain. Only when British authors (Johnston, 1842; Bowerbank, 1866) used this name in combination with descriptions of the spicules, the name became more profiled. It is proposed here to retain *Suberites ficus* authored by Johnston, 1842: 144, pl. XV figs 4, 5 as the proper name for the type species of *Ficulina* (as originally stated by Gray, although this may not have been intentional), and BMNH 1847.9.7.51 is here chosen as the lectotype. *Suberites ficus sensu* Johnston, 1842 (Fig. 12A–E), is a big massive lobate, occasionally cylindrical, orange sponge with one or more conspicuous, large oscules. It has a velvety smooth appearance. Growth forms may include specimens enveloping gastropod shells and encrusting scallops. Size variable, 10–40 cm in length. Contraction noticeable: when removed from the water the sponge contracts to about 3/4 of its size when undisturbed underwater. Internally the skeleton is confused, almost halichondroid. Tylostyles (Fig. 12C) divided into two size groups (100–250 μm and 350–500 × 5–10 μm), the larger growing in a wide size range. Microscleres (Fig. 12D) are microrhabds (microspined microstrongyles, usually centrotylote), often rare and needing careful searching of the ectosome, amongst the tips of the palisade spicules (Fig. 12B, arrow). Size 15–50 μm. Considered as cosmopolite this species is very likely a complex of sibling species. It has been demonstrated that among *Suberites ficus* from the Irish Sea three genetically isolated species are present (Solé-Cava & Thorpe, 1986). De Laubenfels (1936a: 143) considered *Choanites* Mantell, 1822: 178 a senior synonym of *Ficulina*, but this has not been further verified. Subsequently, the same author (de Laubenfels, 1955b: E108) considered *Choanites* a genus of Tunicata based on the technicality that the type species was named *Alcyonium ficus sensu* Pallas (probably a tunicate) and not *sensu* Johnston. In view of the fact that *Ficulina* is here considered a junior synonym of *Suberites*, we propose to follow de Laubenfels' technical solution; if not, *Choanites* would have to be suppressed because it threatens the junior name *Suberites*.

The genus *Suberanthus* Lendenfeld, 1896: 144 was erected for type species (by monotypy) *Halichondria flava* Lieberkühn, 1859: 521, pl. XI fig. 5), now generally considered a junior synonym of *Suberites massa* Nardo, 1847a. *Suberanthus* is a case of thorough confusion. The only species described when the genus was erected, was *Suberanthus flavus* (see Lendenfeld, 1896: pl. V figs 45, 46, pl. VII fig. 71, pl. XII figs 215, 216, 222, 223, 226), so this is firmly established as type species. However, Lendenfeld's definition and the synonymy he gave of *S. flavus* implied that he intended the genus to be what is now generally considered as the genus *Pseudosuberites* (cf. below). He defined *Suberanthus* as having a reticulation of tangential megascleres at the surface and included *Hymeniacidon sulphurea* Bowerbank, 1866 in the synonymy of *S. flavus*. Topsent (1900: 236) rejected this synonymy and considered *S. flavus* a form of *Suberites carnosus* Johnston (1842), thereby implying that *Suberanthus* is a junior synonym of *Suberites*.

The genus *Suberella* Thiele, 1905: 416 was erected as a subgenus of *Suberites* for type species (by original designation) *Suberites heros* Schmidt, 1870: 46 from the West Indies. The description of Schmidt is somewhat ambiguous, mentioning both tylostyles and oxeas. A specimen in ZMUC labeled "type, ?Vestindien" is here designated as lectotype (cf. Fig. 12F). It conforms in all respects to *Suberites domuncula*, including the usual hole of a hermit crab and exclusively tylostyles in two size categories. The original locality of this specimen is dubious because so far no recent records of such sponges are reported from the West Indian region, but in any case *Suberella* Thiele is a clear junior synonym of *Suberites*.

The genus [*Suberella*] Burton, 1929a: 446 was erected for type species (by original designation) *Suberites topsenti* Burton (1929a: 446, pl. IV fig. 5). The holotype is BMNH 1926.10.26.186 from McMurdo Sound, Antarctica. However, belatedly, Burton (1930d) discovered that *Suberella* was preoccupied and erected the genus *Laxosuberella* Burton (1930d: 675) with the same type species as a replacement. The genus was intended for sponges intermediate between *Pseudosuberites* and *Suberites*, showing a confused choanosome and organised 'cortical layer' of spicules, which are arranged with the apices pointing outwards. The name *Suberella topsenti* was intended to replace *Suberites montiniger sensu* Topsent, 1915b: 39, a globular-massive species with papillae at the surface resembling those of *Cliona* or *Polymastia*. Spicules are tylostyles in a single but variable size, no tangential or cortical structures are present. (The original *Suberites montiniger* Carter, 1880d: 256, described from the Arctic, was considered a different species by Burton (1929a), but later authors (e.g., Koltun, 1964b) disagreed and reverted to *Suberites montiniger* again). It is here acknowledged that *Suberites montiniger* Carter is probably different from *Suberites montiniger sensu* Topsent (1915b), but the characters on which to distinguish a separate genus *Laxosuberella* appear to be insufficiently different from *Suberites* species, and accordingly *Laxosuberella* is considered a junior synonym.

The genus *Carnleia* Burton, 1930c: 519 was erected for type species *Biemna rhaphidiophora* Brøndsted, 1923: 136, fig. 17 from New Zealand (original designation). The type material (in ZMUC, not examined) is described as a series of lumpy, club-shaped sponges, attached to shells, of which the biggest is 4.5 cm in diameter. Surface smooth. Skeleton of the surface a partly perpendicular arrangement of megascleres, becoming less densely arranged and more confused towards the interior. Megascleres are two size categories of tylostyles, 275–460 × 5 μm and 143–208 × 5–6 μm, apparently not localized in the skeleton. Microscleres reported as sigmas, probably in two size categories, 10–65 μm, but they are quoted to be infrequent, probably foreign (Bergquist, 1970: 26) and microxeas 46–52 × 1.5–2.5 μm (likewise foreign according to

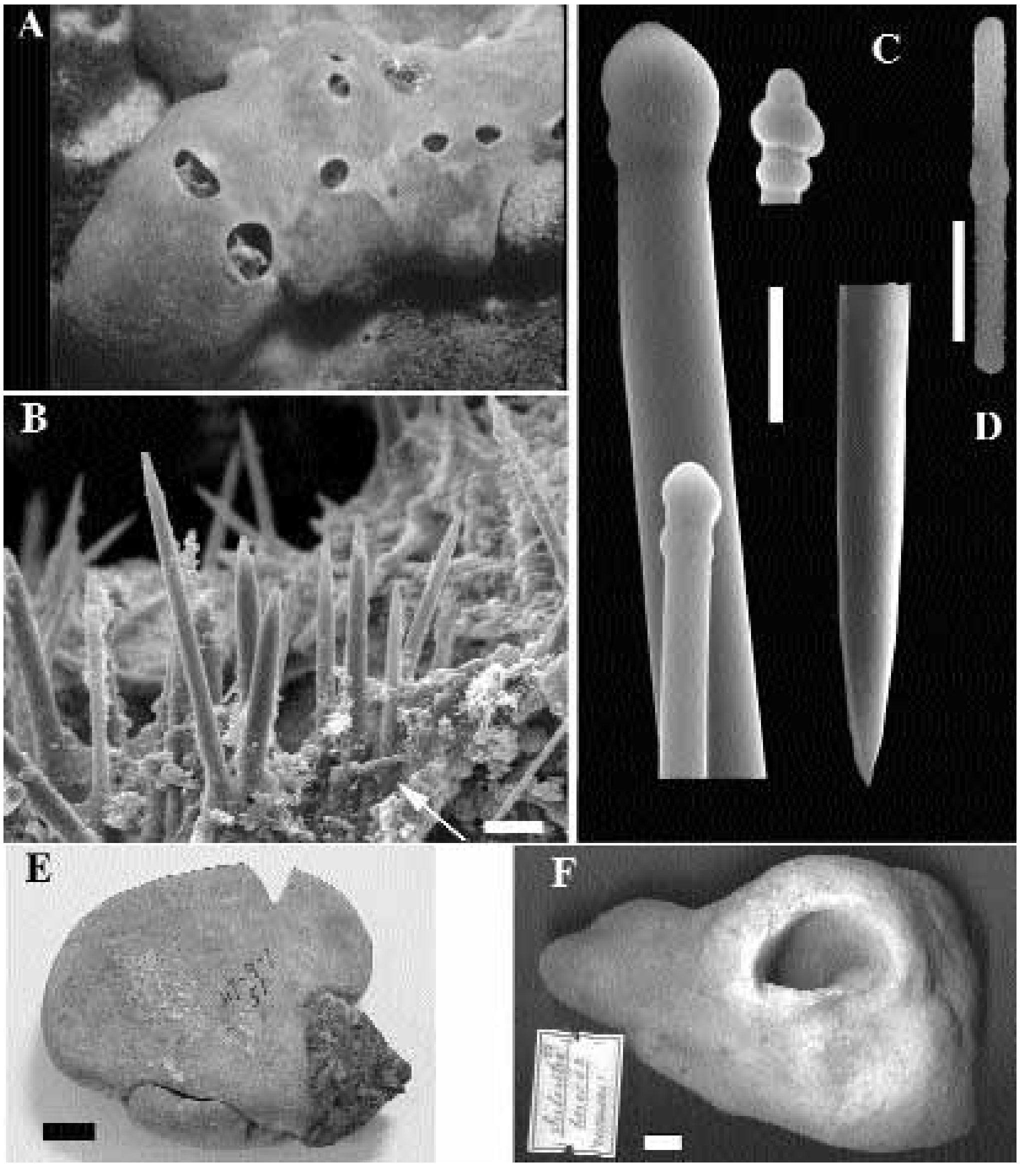

Fig. 12. *Suberites* spp. A–E, *Suberites ficus sensu* Johnston, 1842. A, habit *in situ* (photo B. Picton). B, SEM view of surface showing palisade of spicules and (arrow) microrhabd (scale 100 μm). C, SEM images of tylostyles (scale 10 μm). D, SEM image of spined microrhabd (scale10 μm). E, photo of lectotype of *Halichondria ficus* Johnston, 1842, BMNH 1847.9.7.51 (scale 1 cm). F, ZMUC lectotype of *Suberites heros* Schmidt, 1870, type of the genus *Suberella* Thiele, 1905, considered jun. syn. of *S. domuncula* (scale 1 cm).

Bergquist, l.c.). Both Bergquist (1970) and Hooper (1984: 34) proposed to synonymize *Carnleia* with *Suberites*, and this is followed here.

TERPIOS DUCHASSAING & MICHELOTTI, 1864

Synonymy

Terpios Duchassaing & Michelotti, 1864: 102.

Type species

Terpios fugax Duchassaing & Michelotti, 1864: 102 (by subsequent designation; Topsent, 1900: 192).

Definition

Suberitidae with encrusting habit and with a single category of tylostyles with flattened lobate tyles.

Diagnosis

Thinly encrusting sponges with optically smooth surface, but microscopically hispid due to projecting spicules. Consistency gelatinous, soft. No special ectosomal skeleton other than brush-like endings of the weakly developed choanosomal spicule strands. Choanosome with relatively low spicular density and many loose spicules in confusion. Bacterial symbionts of common occurrence and often causing blue-pigmented or other bright coloration. Spicules thin relatively short tylostyles in a single size category and

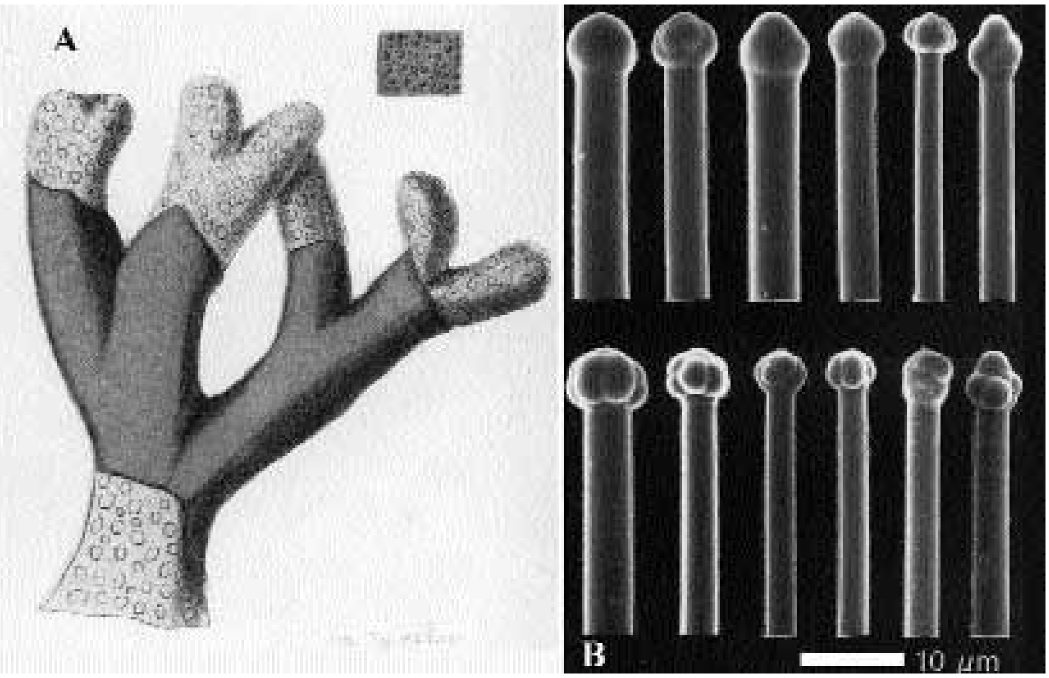

Fig. 13. *Terpios fugax* Duchassaing & Michelotti, 1864. A, water color image of type (reproduced from Duchassaing & Michelotti, 1864: pl. XXIV fig. 6) (size see text). B, SEM images of tylostyles (scale 10 µm).

possessing characteristic flattened-lobate or lumpy, wrinkled tyles. Distributed over all three oceans with a predominance in warm or warm-temperate waters. About 10–15 species have been described.

Previous review

Rützler & Smith (1993).

Description of type species

Terpios fugax Duchassaing & Michelotti, 1864 (Fig. 13A, B).

Synonymy. *Terpios fugax* Duchassaing & Michelotti, 1864: 102, pl. XXIV figs 6, 7.

Material examined. Lectotype (designated by Van Soest *et al*., 1983: 201): BMNH 1928.11.12.11 – spicule slide from St Thomas, West Indies. Other material. ZMA POR. 5155 – Curaçao, reef, 15 m, coll. G. van Moorsel. ZMA POR. 8355 – St Croix, Virgin Islands, coll. B. Gladfelter.

Description (mostly from Rützler & Smith, 1993). Thin crusts (Fig. 13A) on and under dead and overhanging corals, colour dark green or blue. Surface smooth, consistency soft, easily damaged. Skeleton feebly developed, with thin strands of tylostyles running from substrate to surface, with single spicules scattered in between. Spicules (Fig. 13B) tylostyles in a single size category, 150–460 × 2.5–5 µm, with peculiarly lobate, semiglobular or flattened tyles. The tyles contain a branched axial canal. Symbiotic bacteria blue-pigmented, filamentous (multicellular). Distribution and ecology. Originally described from the West Indies, in shallow reefs. Subsequently recorded from many different parts of world, including Europe.

Remarks. The European representatives of *T. fugax* show some discrepancies in spicule size (cf. Voultsiadou-Koukoura & Van Soest, 1993: 178) and probably belong to a species separate from the West Indian population. They may conveniently be called *Terpios gelatinosa* (Bowerbank, 1866: 222, as *Hymeniacidon*). The genus is well-established by the combination of the lobate tylostyle heads (which appear similar to those of *Caulospongia*), encrusting habit and low spicular density.