

Family Phloeodictyidae Carter, 1882

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Phloeodictyidae Carter (Demospongiae, Haplosclerida), including Akaidae Alander, Oceanapiidae Van Soest, is distinguished from other haplosclerids primarily in having a detachable ectosomal crust, an isotrophic reticulation of single spicules, and a concentric laminated internal structure. Species commonly have fistules and tubes, an adaptation to their common habitat of burrowing or being buried in the substrate. Megascleres are oxeas or strongyles, microscleres, if present, are sigmas and/or toxas. Species are distributed in shallow and deeper tropical waters; *Calyx* and *Pachypellina* have been also recorded from the North Atlantic, Antarctica and subantarctic regions, and *Oceanapia* are known worldwide.

Keywords: Porifera; Demospongiae; Haplosclerida; Phloeodictyidae; *Aka*; *Calyx*; *Oceanapia*; *Pachypellina*; *Tabulocalyx*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Phloeodictyidae Carter, 1882b: 117. Akaidae Alander, 1942: 27. Oceanapiidae Van Soest, 1980: 80.

Definition

Haplosclerida with an ectosomal tangential network of free oxeas or strongyles. Choanosomal network is an isotropic reticulation of free spicules, reinforced or not by an irregular network of fibres or tracts.

Diagnosis (emended from Hooper & Wiedenmayer, 1994: 332)

Encrusting, massive, lobate or more frequently spherical or tubular growth forms, buried in the substrate, with fistules on the surface, occasionally excavating coralline substrates. The ectosomal skeleton is a multilayered irregular tangential reticulation of oxeas or strongyles, forming a distinct usually detachable crust. The choanosomal skeleton is an irregular reticulation of multispicular tracts of diactinal spicules with or without spongin, together with an irregularly dispersed isotropic reticulation of single spicules scattered between these major tracts. Microscleres may include microangulate sigmas and toxas.

Scope

Ten nominal genera have been included in this family (*Aka*, *Biminia*, *Calyx*, *Foliolina*, *Oceanapia*, *Pachypellina*, *Pellina*, *Phloeodictyon*, *Rhizochalina* and *Siphonodictyon*), of which five are recognised in this work: *Aka*, *Calyx*, *Oceanapia*, *Pachypellina* and *Tabulocalyx*.

History and biology

The group Phloeodictyina, was proposed by Carter (1882b) to include 'sponges of variable form, chiefly globular, accompanied by tubular expansions both above and below, or above only, which are closed at the extremities, simple, or branched; ... or vasiform,

with pustular eminences only inside. Structure essentially laminated and concentric; laminae of two distinct kinds, which may alternate with each other in variable plurality, commencing dermally with an apparently homogeneous, fine, isodictyal layer, densely spiculous; followed by a coarse, open spiculo-fibrous reticulated one, whose lamination is parallel to the surface, and contrasts strongly in structure ... with the isodictyal homogeneous one outside; also strongly with the tissue of sponges generally, whose reticulated structure is continuous with the deepest portion, and not laminar like the bark of a tree, as in this instance. Internally hollow or more-or-less filled with a pulpy isodictyal tissue like the outer lamina, i.e. composed of sarcode (=choanosome) densely charged with the spicule of the species. No evident oscula. Pores in the dermal layer. Spicule of one kind only, viz. acerate (=oxea), sometimes accompanied by a biharmate (=sigma) flesh spicule (fibula).

The history of the family is a relative mess. Carter (1882b) based his diagnosis on a species described by two different authors under two different names: Bowerbank (1866), as *Isodictya robusta* and *Desmacidon jeffreysii*, and Norman (1869b) as *Oceanapia jeffreysii*, which he synonymised (*I. robusta* being the most senior name), and assigned to *Oceanapia*. Carter (1882b) also recognised *Rhizochalina* Schmidt, 1870, as a junior subjective synonym of *Oceanapia*, and in the same work (1882b: 120) erected *Phloeodictyon* which he considered different from *Oceanapia*, despite some obvious similarities between both ('at first sight *Phloeodictyon* looks very much as *Isodictya* but, on dissection is found to be similar in structure to *Desmacidon jeffreysii*'). *Phloeodictyon* Carter was considered by de Laubenfels (1936a) to be a junior synonym of *Oceanapia* and *Rhizochalina carotta* Schmidt presumably transferred to *Oceanapia*.

Ridley & Dendy (1887) conserved the taxon Phloeodictyina at subfamily level and assigned species of *Rhizochalina* and *Oceanapia* to it. Dendy (1922b) retained Phloeodictyinae as a subfamily of Haploscleridae, including in it the genera *Phloeodictyon*, *Oceanapia* and *Rhizochalina*. He erected a second subfamily Coelosphaerae for *Coelosphaera*, *Siderodermella* and *Amphiastrella*, to which de Laubenfels (1936a) assigned otherwise typical Phloeodictyidae genera *Oceanapia*, *Rhizochalina* and *Phloeodictyon*, based exclusively on their external form. As a consequence of this mess, it is not surprising that following Bergquist (1965), there has been a great confusion concerning the synonymy of *Oceanapia*, *Rhizochalina* and *Phloeodictyon*, and their alleged relationships to

Coelosphaeridae and Adociidae. Lévi (1973) included most of the genera now considered to belong to Phloeodictyidae in Renieridae, viz., *Pellina*, *Rhizochalina*, *Oceanapia* and *Calyx*.

Based on the premise that the name Phloeodictyidae had not been in regular use Van Soest (1980: 80) established Oceanapiidae, which until recently has been widely accepted by contemporary authors. Unfortunately, however, the name Phloeodictyidae has seniority, irrespective of the synonymies of their respective type species (Hooper & Wiedenmayer, 1994). Van Soest (1980) also included *Pellina* in his new family Oceanapiidae, but this was later modified by de Weerd (1985) and de Weerd & Van Soest (1986), based on the absence of oceanapiid characters in the type species, *Halichondria semitubulosa* Lieberkühn (1859), which conforms to *Halichondria* (see chapter on Halichondriidae). In the same work, de Weerd & Van Soest (1986) proposed a new subgenus, *Rhizochalina* Schmidt, 1870, to include species of *Oceanapia*, like *O. oleracea* the type species of *Rhizochalina*, and three others that differ from typical pulpy *Oceanapia*.

Definitions of taxa belonging to this family are provided by Norman (1869b), Carter (1882b), de Laubenfels (1936a), Bergquist (1965), Fromont (1991, 1993), Rützler (1971), Van Soest (1980)

and Desqueyroux-Faúndez (1987). *Aka* was originally included by authors in Clionidae (=Clionidae) (Hancock, 1849), but Rützler & Stone (1986) recognised in it characters described for *Siphonodictyon* (Phloeodictyidae), and consequently referred *Aka* to this family and as a senior synonym of *Siphonodictyon*. There is still some debate as to the validity of this synonymy, which is discussed further below.

Distribution

Nominal genera have the following recorded distributions (after Van Soest, pers. comm.): Chile-Peru and Magellanic region (*Calyx*, *Oceanapia*, *Pachypellina*), Brasilia (*Calyx*, *Oceanapia*), West Indies (*Aka*, *Calyx*, *Foliolina*, *Oceanapia*, *Rhizochalina*, *Pellina*), Boreal East Atlantic (*Aka*, *Oceanapia*), West Africa (*Aka*, *Calyx*, *Oceanapia*), South Africa (*Oceanapia*), Mediterranean Atlantic (*Aka*, *Calyx*, *Oceanapia*), Central Pacific (*Aka*, *Siphonodictyon*, *Oceanapia*), Japan, China (*Oceanapia*, *Biminia*), Antarctica (*Calyx*, *Vagocia*, *Oceanapia*), New Zealand (*Oceanapia*, *Vagocia*). Species of Phloeodictyidae are absent in Boreal – West Atlantic and Boreal – East Pacific.

KEY TO GENERA

- (1) Burrowing into limestone substrate, secreting a layer of mucus, only the fistules are externally visible *Aka*
Non-burrowing sponges 2
- (2) Variable growth form, with fistules 3
Massive globose or tubulose, without fistules 4
- (3) Hollow body, compact external ectosomal crust, or massive, encrusting from a basal lamina with spreading fistules, oscules only at the end of fistules, or no oscules. Ectosomal skeleton a single tangential layer of spicules or multilayered compact crust. Choanosomal skeleton a network of spicule tracts, abundantly ramified irregular-oval meshes, abundant free oxeas. Microscleres may be present, sigmata and/or toxas *Oceanapia*
Massive to cuplike, coalescent tubes, globose or lamellate, with a short stalk; fistules may be present, oscules in the internal part of the cup. Ectosomal skeleton a compact network, with a surface-membrane, scattered free spicules, and numerous sphaerulous cells. Choanosomal skeleton a network of long, entangled spicule tracts, longitudinal in the interior of the body and tangential to the surface in the peripheral skeleton, with a connecting unispicular reticulation. Spicules oxeas, microscleres if present, toxas *Calyx*
- (4) Massive globose, with a stalk, no fistules, oscules only on the globous body. Ectosomal crust in two separate layers. Choanosomal skeleton a mass of oxeas in confusion and some irregular multispicular tracts *Tabulocalyx*
Massive globose or tubulose. Ectosomal skeleton a single tangential crust, no stalk, no fistules, no oscules. Choanosomal skeleton densely spiculose with large meshes *Pachypellina*

AKA DE LAUBENFELS, 1936

Synonymy

[*Acca*] Johnson, 1899: 461, figs 1–4 (preocc.). *Aka* de Laubenfels, 1936a: 155.

Type species

Aka insidiosa Johnson, 1899 (by subsequent designation; de Laubenfels, 1936a: 155).

Definition (from Johnson, 1899)

Excavating sponges boring calcitic substrata. Spicules only oxeas forming sinuous bands arranged in bundles, producing fistulose tubes.

Diagnosis (from Johnson, 1899 and Thomas, 1968c)

Boring sponges, excavating calcareous substrates (molluscs, coral rocks); externally visible by their fistulose tubes. Skeleton formed only of spicule-bundles in sinuous bands, not in a network, lining walls of fistules. Spicules short, slender, curved oxeas. Without microscleres.

Previous reviews

Thomas, 1968c, 1979; Rützler & Stone, 1986; Fromont, 1993.

Description of type species

Aka insidiosa Johnson, 1899 (not figured).

Synonymy. *Acca insidiosa* Johnson, 1899: 461, figs 1–4.

Material examined. Holotype: lost (Rützler & Smith, pers.comm.)

Description (emended from Johnson, 1899; Thomas, 1968c; Van Soest, unpublished data, pers.comm.). Found on shells of *Ostrea* and *Chama*, lining holes about 1.5 mm in diameter and issuing as short tubes from them. The walls of the tubes are composed of short, small, slender oxeas about 100–200 µm long, 4–11 µm in diameter, grouped to form sinuous bands of spicules arranged in bundles, but not forming a network. The tops of the tubes are covered over with a sieve-like reticulation also formed of spicules in bundles. The spicules are short, cylindrical oxeas, slender, slightly curved. Colour of the sponge when dry, pale brown.

Remarks. De Laubenfels (1936a: 155) replaced Johnson's preoccupied name and nominated its type species *A. insidiosa* Johnson, 1899 (burrowing in molluscs). He also included in the genus *Cliona coralliophaga* Stephens, 1915a (boring coral) and *Cliona labyrinthica* Hancock, 1849 (boring *Tridacna gigas*). Thomas (1968c) included *Aka* in Clionidae, provided a diagnosis of the genus, and described a new species from the Gulf of Manaar, *Aka diagonoxea*, which he considered was related to *Cliona labyrinthica*. Rützler & Stone (1986) studied the microscope slide collections of Hancock (1849, 1867), consisting of excavating sponges from the British coasts and other unspecified localities. From re-examination of spicules of *Cliona labyrinthica* they concluded that *Aka* was a senior subjective synonym of *Siphonodictyon* Bergquist, 1965, but since Johnson's original material of the type species, *A. insidiosa*, is lost, it is impossible to establish the exact differences between *Aka* s.s. and *Siphonodictyon* from a comparative analysis of the skeleton of the type species of both genera. In this work, we follow Van Soest (pers. comm.), to establish the modern concept of *Aka* as revived by Rützler & Stone (1986) and by Van Soest's own studies of his collections. Bergquist (1965) erected *Siphonodictyon*, which she considered closely related to *Phloeodictyon* Carter, 1882b, but differed in the great quantities of mucus produced and by the absence of a bark-like ectosomal region. Bergquist (1965) remarked that she followed Dendy (1922b), taking into consideration morphological details, to include *Siphonodictyon* in Adocidae. By comparison, morphological characters in *Aka* are reduced to only a few remarks in Johnson's description of *Acca insidiosa*. Bergquist (pers.comm.) considers that *Siphonodictyon* is not unequivocally the same as *Aka*.

Van Soest's (pers. comm.) concept of *Aka* includes boring sponges with a skeleton of short oxeas, and papillae with oxeas in a reticulate arrangement. Inside the coral, the skeleton becomes reduced, consisting of a pulpy organic mass. These characters are similar to those of *Siphonodictyon mucosum*, and differences between species of both genera are reduced to the size of papillae. For example, papillae in specimens of *Aka infesta* collected infesting Norwegian deep water corals exhibited small papillae (1 mm or so), whereas in *S. mucosum* they measured about 5 cm. Following Rützler & Stone's (1986) and Hooper & Wiedenmayer's (1994) opinions (the latter based on the former's evidence), in this work we consider that it is likely there is insufficient evidence to date to differentiate *Siphonodictyon* from *Aka*, but we do not make a formal decision about this alleged synonymy, which we leave to future studies, especially on the diverse Indo-west Pacific fauna (see *Siphonodictyon*; Fig. 1A–D; based on USNM 23697, holotype of *Siphonodictyon mucosa* Bergquist, 1965, Palau, Micronesia).

Distribution

Species of *Aka* (as Clionidae) have been described from Great Britain, (Hancock, 1849), Madeira (Johnson, 1899), Coast of Ireland (Stephens, 1915a, as *Cliona coralliophaga*), West-Central Pacific (de Laubenfels, 1954), Gulf of Manaar, and Mozambique Channel (Thomas, 1968c, 1979) and West Indies (Alcolado, 1994). Fossil records of *Aka*, are Middle and Western Europe, and Arizona/Northern Mexico, according to Reitner & Keupp (1991b).

CALYX VOSMAER, 1885

Synonymy

[*Lieberkuhnia*] Balsamo-Crivelli, 1863: 293; Schmidt, 1864: 43; Gray, 1867: 520 (preocc. for *Lieberkuhnia* Claparède & Lachman, 1859, Rhizopoda (Protozoa)). [*Lieberkuhnia*] de Laubenfels, 1936a: 133 (*lapsus* of [*Lieberkuhnia*] Balsamo-Crivelli). *Calyx* Vosmaer, 1885b: 337. *Vagocia* de Laubenfels, 1936a: 133. Taxonomic decision for synonymy: Wiedenmayer, in Hooper & Wiedenmayer (1994).

Type species

Reniera ? calyx Schmidt, 1862: 76 (by monotypy) (= *Calyx nicaeensis* (Risso, 1826: 372), see Topsent, 1925c: 708).

Definition

Phloeodictyidae with massive to cuplike or lamellate, globose growth forms, supported by a short stalk, or stout coalescing tubes growing together. Smooth surface and fibrous choanosome. Ectosomal skeleton a multilayered unispicular network with spongin at nodes. Choanosomal skeleton with entangled longitudinal tracts in the interior and tangential tracts closer to the periphery. Megascleres oxeas, microscleres if present toxas.

Diagnosis

Massive, caliculate (Fig. 2A), short pedunculate, lamellar (Fig. 3A, C, *Calyx arcuarius* as *Vagocia*) or coalescent tubular growth forms, with tubular processes or fistulae may be present. Surface consists of a multilayered, compact ectosomal network, under the surface-membrane (Figs 2B, 3B), with a close-knit unispicular network containing spongin at nodes and scattered free spicules with numerous sphaerulous cells. These cells, brown pigmented or uncoloured, give to the sponge its dark or clear brown colour. Small oscules present in the internal part of the calyx (Fig. 2C), or absent. Choanosomal skeleton composed of long, disorientated, entangled spicular tracts, longitudinal in the interior of the body (Fig. 2D), and tangential to the surface in the periphery (Fig. 2B). Between the fibres there is a connecting unispicular reticulation (Figs 2D, 3D). Spongin in variable amount. Megascleres are oxeas, of two size categories, bent at the center, with conical points. Microscleres toxas (Fig. 3D, in *Calyx arcuarius*).

Previous reviews

Balsamo-Crivelli, 1863: 293 (*Lieberkuhnia calyx*); Carter, 1882b: 116 (*Reniera crateriformis*); Topsent, 1913b: 638

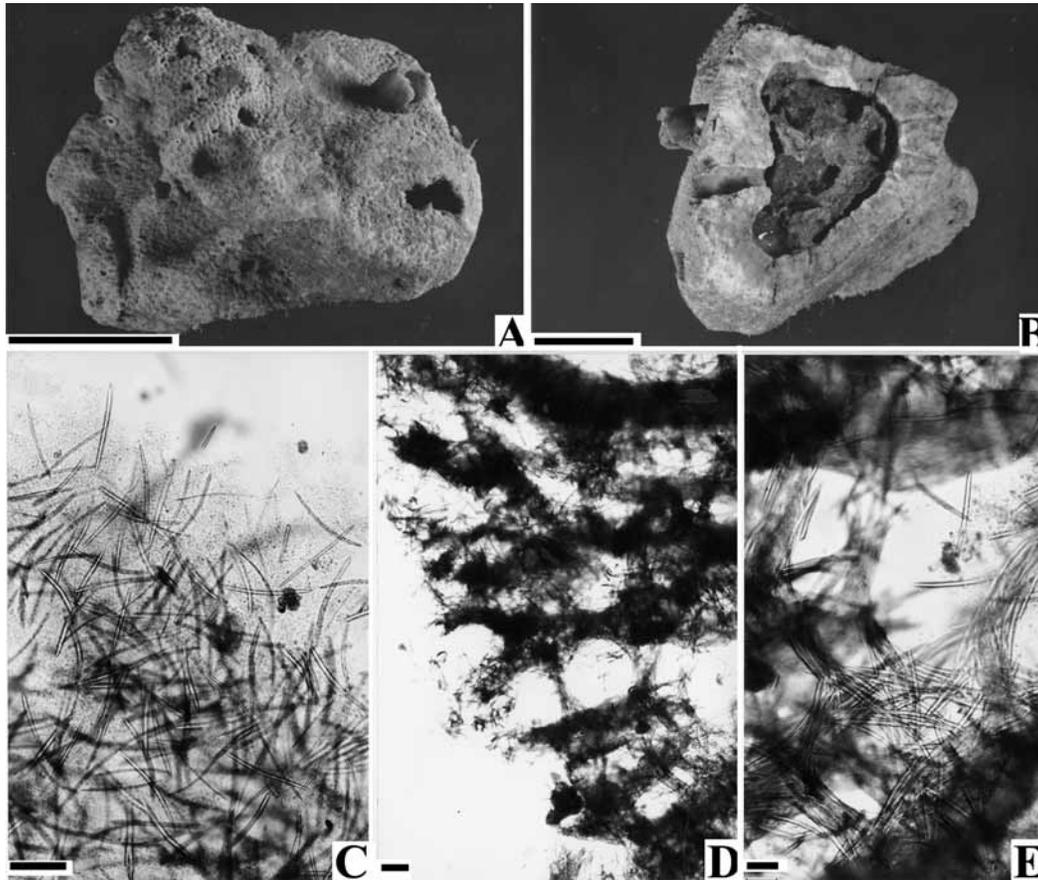


Fig. 1. *Siphonodictyon* Bergquist, 1965. A–E, type species *Siphonodictyon mucosa* Bergquist, 1965, USNM 23697, holotype. A, external basal mass containing the gelatinous body of the sponge (scale 1 cm). B, gelatinous body at the interior of the cavity (at left, part of one of the oscular tubes; scale 1 cm). C, fragment of the ectosomal network of the oscular tube or fistule (scale 50 µm). D–E, view of the choanosomal network and stout primary longitudinal fibres (scale 50 µm).

(*Gellius arcuarius*); 1925c: 708; 1928e: 2, figs 1–5 (*Calyx nicaeensis*); de Laubenfels, 1936a: 133; Wiedenmayer, 1977b: 20, 79, 111, 112, 116, 118, 119, 121, 156; Hooper & Wiedenmayer, 1994: 333.

Description of type species

Calyx nicaeensis (Risso, 1826) (Fig. 2).

Synonymy. *Reniera* ? *calyx* Schmidt, 1862: 76 (= *Spongia nicaeensis* Risso, 1826: 372; see Topsent, 1925c: 708). *Calyx lieberkuhni* Vosmaer, 1885b: 337 (= *Lieberkuhnia calyx* (Nardo) Balsamo-Crivelli, 1863). *Esperia calyx* Nardo, 1863 is a *nomen nudum*. [*Lieberkuhnia*] *calyx* Balsamo-Crivelli is both preoccupied and an unjustified replacement name, so *Reniera* ? *calyx* Schmidt, 1862 became the oldest available name (from secondary source: Wiedenmayer, 1977b: 118).

Material examined. Holotype: BMNH 1867.7.26.71 – *Reniera* ? *calyx* Schmidt, dry, Lesina (specimen of O. Schmidt). Other material. BMNH 1926.3.10.4 – *Reniera calyx* Schmidt, 1862, Sebenico, dry, Norman Collection. BMNH 1866.7.30.3 – *Reniera calyx*, ‘Mer Adriatic’, dry, purchased from Schaufuss. Additional material. *Calyx nicaeensis* Risso: BMNH 1958.12.4.5 – dry, Topsent’s specimen purchased from Professor Tortorese, 1958. Holotype of *Vagocia*, *Gellius arcuarius* Topsent, 1913b: RSME 1921.143.1419 – *Scotia* Bay, Scottish Antarctic Expedition, 1902–1904.

Description. Caliculate or vase-shaped, massive, sponge, 25 cm high, fixed to the substrate by a short peduncle. Texture hard, compact, colour dark brown, greenish. Surface even, rough, or if missing, the compact stout fibres of the body wall are visible at the surface. Oscules not visible in the external part of the body wall, some oscules are visible in the cavity of the body. Choanosomal skeleton: primary multispicular fibres are compact, very variable in diameter, from 10 to more than 100 µm, irregularly distributed, longitudinally, they form a large irregular mesh, in the interior of the mesh there is a unispicular network and a few free spicules are visible. Spicules are oxeas of two size categories (Fig. 3D, *Vagocia*), 99–127–147 µm long by 5–6 µm in diameter and 35–57–80 µm long by 2–3 µm in diameter. Microscleres absent in the type species, present in the type species of *Vagocia*, *Calyx arcuarius* (Topsent).

Remarks. The type species of *Calyx* is, in the opinion of Topsent (1925c), very common in the Mediterranean Sea, where it may grow to a big size. This species is the same as described by Nardo (1833: 522) as *Esperia calix*, and later by Schmidt as *Reniera* ? *calyx*, and finally by Vosmaer (1885b) as the type species of his genus *Calyx*. This sponge was described earlier by Risso (1826: 372) as *Spongia nicaeensis* (see Topsent, 1925c), which is the senior-most available name. Characteristics of this species are: a very variable morphology, stony texture observed in large specimens principally due to the multispicular choanosomal fibres with

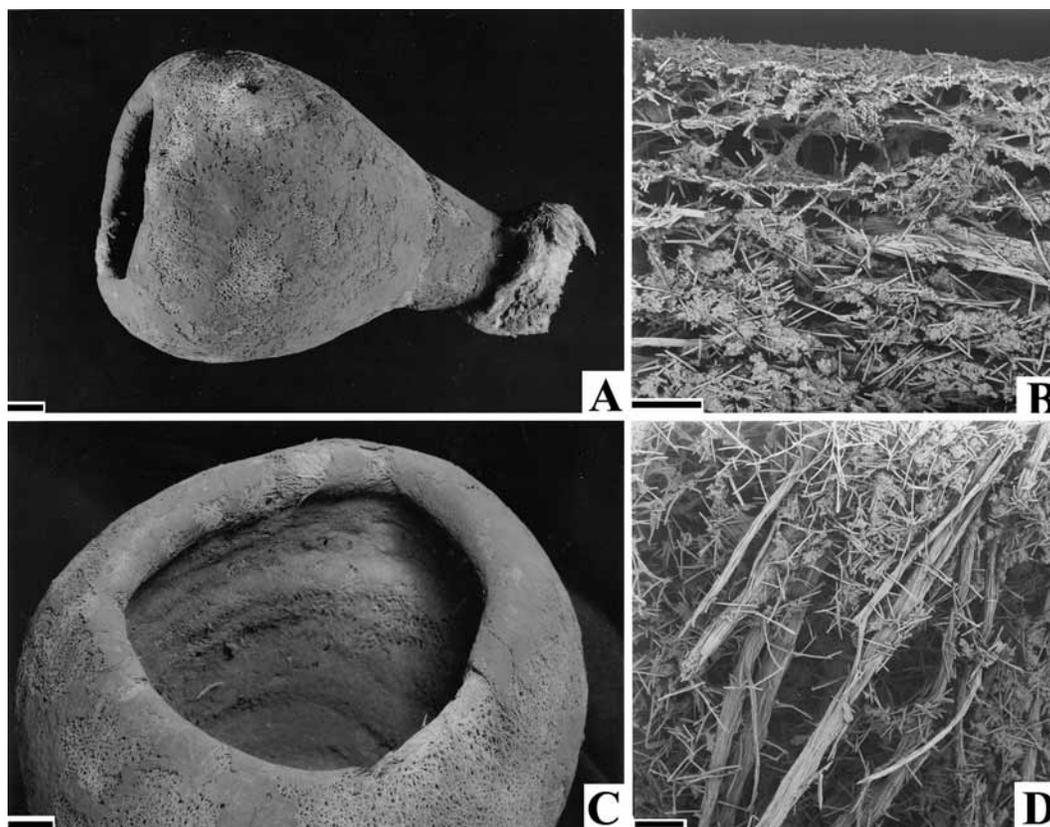


Fig. 2. *Calyx* Vosmaer, 1885b. A–D, type species *Reniera ? calyx* Schmidt, 1862 (= *Calyx nicaeensis* Risso), holotype, BMNH 1867.7.26.71. A, massive, calcified specimen, external view (scale 1 cm). B, longitudinal section through the multilayered, compact ectosomal network or crust, covered by the surface-membrane (scale 200 μ m). Note tangential choanosomal tracts under the surface. C, internal surface of the calyx, small oscules present (scale 1 cm). D, longitudinal section through the choanosomal skeleton, longitudinal tracts and unispicular network (scale 200 μ m).

compact oxeas, distributed longitudinally inside fibres, supported by sparse spongin, and by the multilayered ectosomal skeleton, or strong ectosomal crust. In spite of being easily identified, to date the only complete description of this species is from Topsent (1925c), who illustrated several specimens with different growth forms, found in the Gulf of Naples. One of Topsent's specimens of *Calyx nicaeensis* Risso, BMNH 1958.12.4.5, is illustrated here. *Vagocia* de Laubenfels, 1936a, with type species, *Gellius arcuarius* Topsent, 1913b: 623 (by original designation; Fig. 3), is considered here to be a junior synonym of *Calyx*, following Wiedenmayer (in Hooper & Wiedenmayer, 1994).

Distribution

Calyx is abundant in the world's oceans, including Magellan Province, Brasilia, West and South Africa, Mediterranean Atlantic, Antarctica, Subantarctic, New Zealand and West Indies (Van Soest, 1980, and pers.comm.; Koltun, 1964b; Desqueyroux-Faúndez, 1989).

OCEANAPIA NORMAN, 1869

Synonymy

Oceanapia Norman, 1869b: 334. *Phloeodictyon* Carter, 1882b: 122. *Rhizochalina* Schmidt, 1870: 35. *Biminia*

Wiedenmayer, 1977b: 124. *Foliolina* Schmidt, 1870: 42, pl. 4, fig. 4. (Taxonomic decision for synonymy, Van Soest, 1980: 91; concerning *Foliolina* Schmidt, 1870: *Zea*, 1987: 136 and Werding & Sanchez, 1991: 204).

Type species

Isodictya robusta Bowerbank, 1866: 334 (by monotypy).

Definition (from de Weerd, 1985)

Phloeodictyidae with a compact external ectosomal crust composed of tangential oxeas, often surrounding a hollow body and numerous ubiquitous fistulae. Megascleres oxeas. Microscleres, if present, sigmata or toxas.

Diagnosis

Massive, globular, lamellate growth forms, with long tubular processes or fistules, opened or closed at their ends. Ectosomal skeleton a tangential multilayered compact crust of tangential spicules. Fistule walls supported by an irregular, network of tracts, with irregular mesh and abundant spongin. Between the tracts, a fine unispicular, subisodictyal network is visible and minute sigmata may be present. Choanosomal skeleton (Fig. 4D, F) of the basal part is formed by an irregular network of strong spicule tracts, parallel to the surface, abundantly ramified to form irregular to oval meshes, with abundant free oxeas and less numerous sigmata. Spongin in variable quantities.

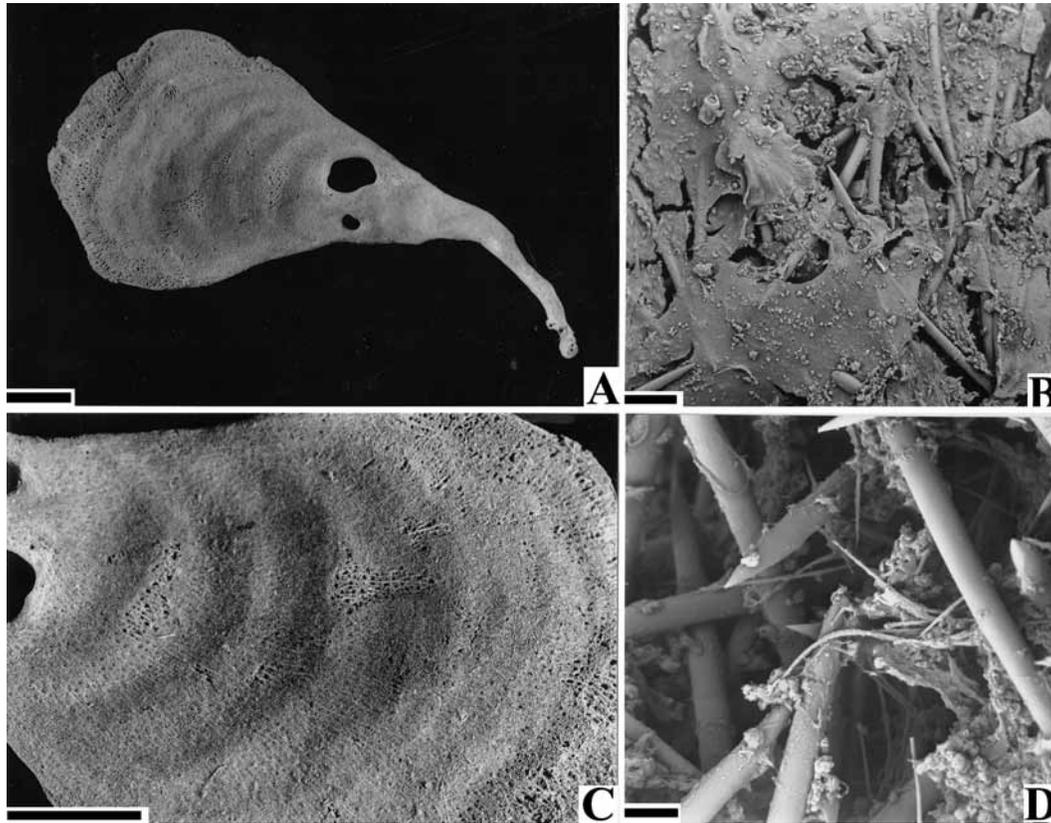


Fig. 3. *Calyx* Vosmaer, 1885b. A–D, *Vagocia* de Laubenfels, 1936a (type species *Gellius arcuarius* Topsent, 1913b, holotype RSME 1921.143.1419). A, external view of the short pedunculate lamellar specimen (scale 1 cm). B, tangential view of the surface membrane over the spicules of the ectosomal network (scale 50 µm). C, terminal part of the lamellae (scale 1 cm). D, confused connecting unispicular reticulation of the choanosomal skeleton, view of the oxeas and fine, largely open, toxas (scale 20 µm).

Previous reviews

Carter, 1882b; Topsent, 1920a: 2 (*Rhizochalina*); Dendy, 1922b; Ridley & Dendy, 1887: 32, 36; Bergquist, 1965: 160; Van Soest, 1980: 85; de Weerd, 1985: 74; Desqueyroux-Faúndez, 1987: 200.

Description of type species

Isodictya robusta Bowerbank, 1866: 334 (Fig. 4).

Synonymy. *Isodictya robusta* Bowerbank, 1866: 304. *Desmacidon jeffreysii* Bowerbank, 1866: 347; 1874: 157, pl. 62, figs 1–5; 1882: 170; Carter, 1882b: 117; *Oceanapia jeffreysii*; Norman, 1869b: 334; *Esperia jeffreysii*; Schmidt, 1870: 77. Not *Oceanapia robusta* Ridley & Dendy, 1887 (= *O. fistulosa*, see Van Soest, 1980: 86).

Material examined. Holotype: BMNH 1877.5.21.2040 – dry, and 5 slides, Norman collection, Shetland. Other material. *Desmacidon jeffreysii*: BMNH 1877.5.21.2041 – dry, Norman collection, Shetland, 1868 (specimen illustrated by Bowerbank, 1874, pl. 62). BMNH 1877.5.21.807 – dry, and 2 slides. Specimen with two labels: BMNH 1883.1.2.5.7 – dry, “*Desmacidon jeffreysii* and *O. robusta*”. BMNH 1910.1.1.372 – dry, “*Isodictya robusta* and *Desmacidon jeffreysii*”, small box contains 5 small lamellate fragments about 0.5 cm. BMNH 1883.1.2.5.7 – dry, Norman Collection, presented by H.J. Carter Esq. BMNH 1900.4.4.36–40 – dry, Shetland, Norman Collection. BMNH 1930.7.3.414–418 – dry,

Shetland, 1867, Norman Collection, correlated with 5 slides in the collection. BMNH 1910.1.1.372–374 – dry, Shetland, 1867, Haaf Gruney, Off Unst Island, Norman collection. *Rhizochalina oleracea*: BMNH 1870.5.3.142 – dry and 1 slide, Antillen, purchased from O. Schmidt.

Description. Globular, regularly bulbous to irregularly rounded or turnip-shaped, massive sponge, 5–6 cm in diameter, surrounded by a strong, compact, hard and breakable (in dry state) external crust (Fig. 4A–C, E). Characteristically one to numerous long cloacal branched or unbranched tubular appendages or fistulae, 0.5–3 cm long, opened or closed at their ends. Appendages issued from the upper part of the sponge are internally branched to form a strong choanosomal reticulation of cylindrical branching tubes. The basal part of the sponge exhibits long, stout compact to partly hollow roots (Fig. 4C), also considered fistular appendages by Norman (1869b), terminating in single strong fibres. These appendages are used as basal attachments to the substratum. Surface smooth, even, slightly hispid, from ends of surface spicules. Consistency of the sponge body and the fistulae is crumbly, consistency of the roots is resilient. The interior of the body in the fresh sponge, contains a pulpy, gelatinous, uncoloured mass, which become hard, yellow to brown in the dry sponge. Oscules are small, 2–3 mm in diameter, and numerous in the internal part of the body wall. Ectosomal skeleton is a compact, multi-layered, tangential, unispicular, unordered network of packed oxeas, supported by the subectosomal multispicular tracts (Fig. 4D, F). The spaces between the tracts are subdivided by thinner

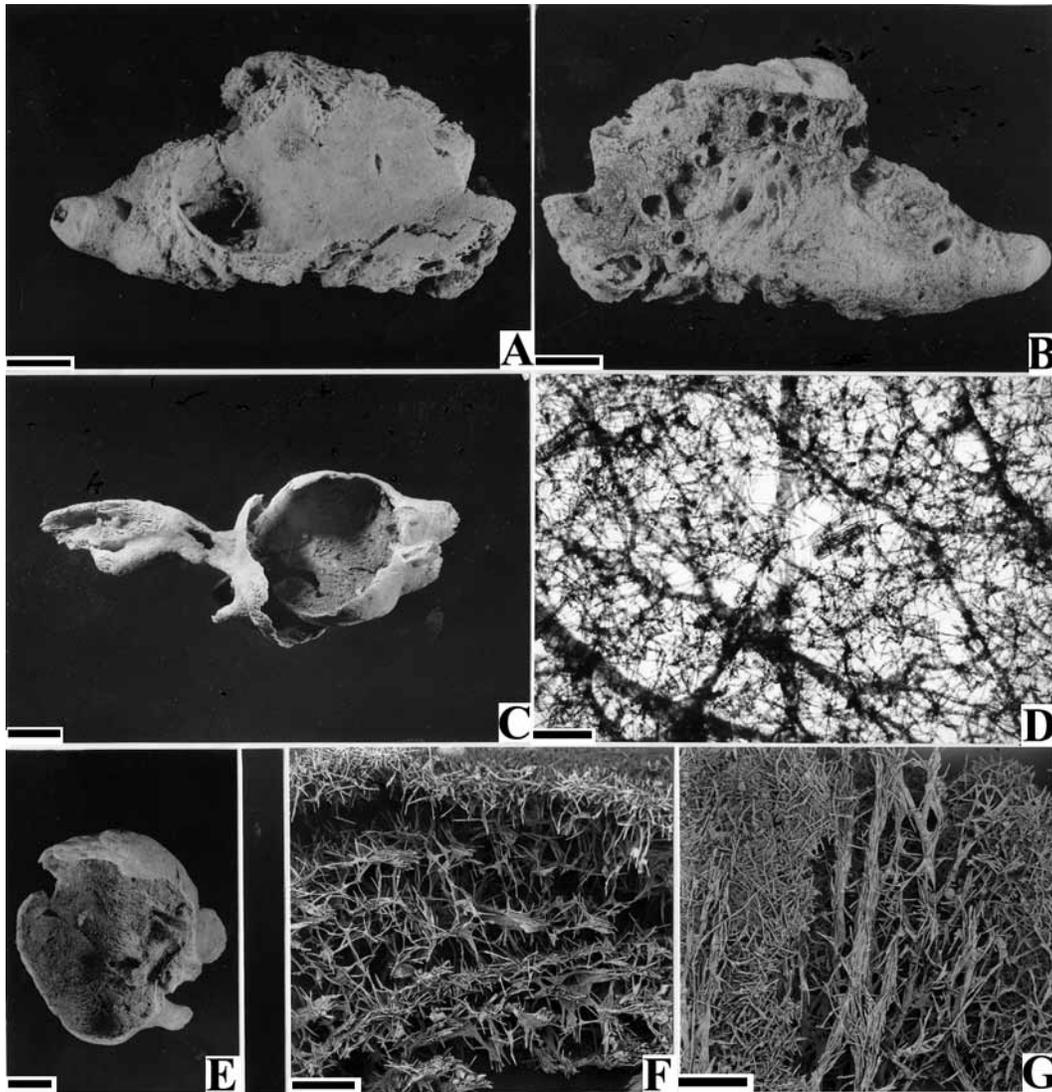


Fig. 4. *Oceanapia* Norman, 1869b. A–B, type species *Isodictya robusta* Bowerbank, 1866, BMNH 1877.5.21.2040, holotype, internal and external view of the body wall (scale 1 cm). C–E, *Desmacidon jeffreysii*, BMNH 1877.5.21.2041, specimen illustrated by Bowerbank (1874, pl. 57). C, E, lateral view of the globular, regularly bulbous to irregularly rounded or turnip-shaped massive specimen, with fistules and long root-like structures (scale 1 cm). D, choanosomal skeleton, longitudinal section (scale 50 μm). F–G, *Desmacidon jeffreysii*, BMNH 1900.4.4.36. F, longitudinal section through the surface (at top) (scale 500 μm). G, long choanosomal multispicular stout fibres and dense unispicular connecting network (scale 500 μm).

paucispicular tracts forming irregular meshes. Choanosomal skeleton is an irregular network of multispicular longitudinal stout tracts, parallel to the surface, forming large, irregularly elongate meshes, sub-divided by a regular isodictyal network of single spicules, with spongin only found at the nodes (Fig. 4G). Megascleres are oxeas, slightly bent, 170–200–260 μm long by 6–8–10 μm in diameter. Microscleres are sigmata, thin, irregularly curved, 10–12–18 μm long.

Distribution. De Weerd (1985) remarked that *Oceanapia robusta* had not been reported from the Mediterranean, nor from the Western part of the Atlantic Ocean, and concluded the species was geographically restricted only to the northern part of the North Eastern Atlantic Ocean, viz. from East of Greenland, Iceland and Norway down to the Azores (37° N).

Remarks. In describing *Oceanapia* Norman (1869b) underlined the problem of Bowerbank's identification of this species.

The first specimen dredged by Norman in 1861, a portion of crust, was identified and described by Bowerbank as *Isodictya robusta* Bowerbank, 1866. A new collection by Norman yielded fragments of the crust and of detached fistulae of a similar specimen. On this occasion Norman remarked that the entire specimen should be very different from Bowerbank's description. From a new collection of the same sponge by Norman in 1864, Bowerbank was convinced that he was dealing with a new species that he named *Desmacidon jeffreysii* Bowerbank, 1866. After subsequent collections, Norman retrieved an entire specimen and he described this remarkable sponge himself as a new genus *Oceanapia*, explaining the different interpretations of its type species. Norman's (1869b) diagnosis of *Oceanapia jeffreysii* Bowerbank (1869: 334), included its synonymy with *Desmacidon jeffreysii* and *Isodictya robusta*. Bowerbank (1866) only gave indications of the sponge's habit, the type of skeleton and the spicules.

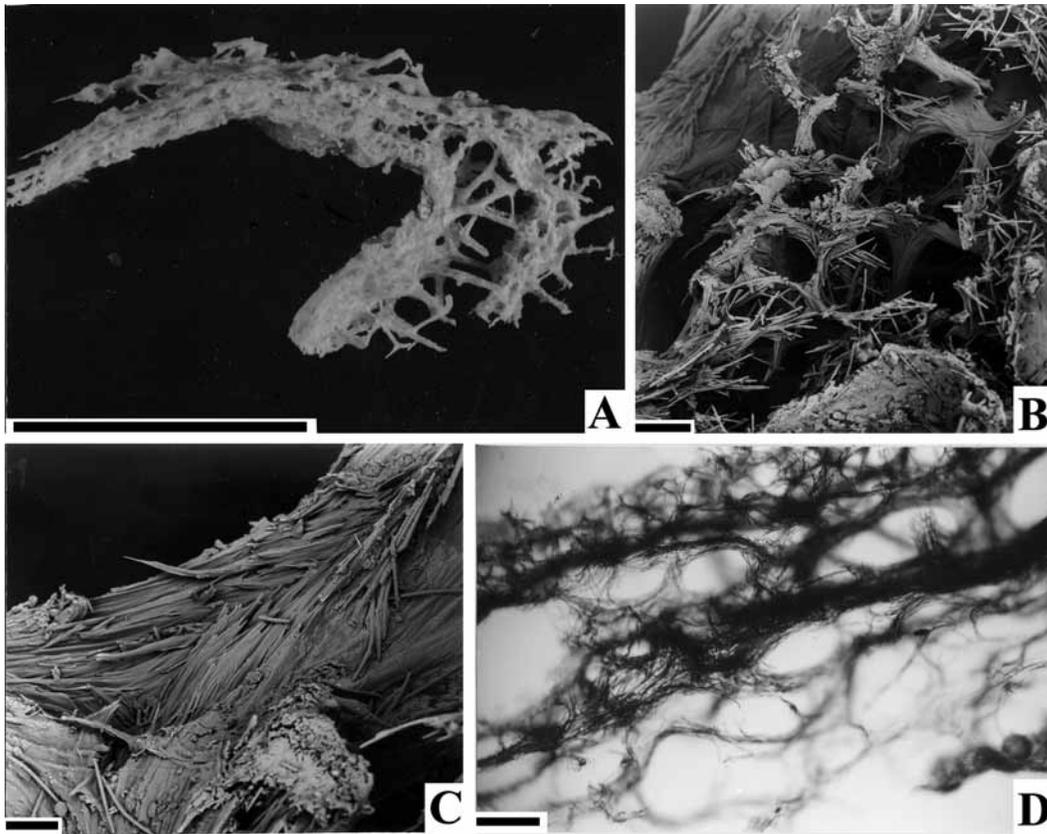


Fig. 5. *Oceanapia* Norman, 1869b. A–D, *Rhizochalina* Schmidt, 1870 (type species *Rhizochalina oleracea* Schmidt, 1870, holotype BMNH 1870.5.3.142, fragment of *Rhizochalina carotta* Schmidt, 1870). A, extant fragment of specimen (scale 1 cm). B, ectosomal network, transverse section of the surface (scale 100 μ m). C, multipisular compact choanosomal tracts with sparse spongin (scale 50 μ m). D, transverse section of choanosomal skeleton, below the surface network (scale 50 μ m).

Van Soest (1980) proposed including *Rhizochalina* Schmidt, 1870 (Fig. 5A–D) (type species *Rhizochalina oleracea* Schmidt, 1870: 35, by subsequent designation (de Laubenfels, 1936a) and *Phloeodictyon* Carter, 1882b (Fig. 6A–C) (type species *Phloeodictyon isodictiformis* Carter, 1882b: 122, by subsequent designation (de Laubenfels, 1936a: 72) in synonymy with *Oceanapia* because their respective type species were very similar in their basic characters. The presence or absence of sigmata was judged to be of little value. Wiedenmayer, in Hooper & Wiedenmayer (1994), also included the genus *Biminia* Wiedenmayer, 1977b into synonymy (Fig. 6D–F) with *Oceanapia*.

Actually, we do not know the exact value of microscleres as generic characters of Phloeodictyidae. Characters such as the presence of an ectosomal crust and the globular habit, which we assume are consistently present in *O. robusta* (e.g., Desqueyroux-Faúndez, 1987), misled Bowerbank (1874: 158, 161), to propose substituting his first description of fragments of Norman's specimens with a new species (*Desmacidon jeffreysii*). In the same way, the presence or absence of a given type of microsclere in species of Phloeodictyidae justified the erection of genera which today are considered by most authors to be junior synonyms of *Oceanapia* (see above).

Foliolina Schmidt, 1870 (type species *Foliolina peltata* Schmidt, 1870: 42, pl. 4, fig. 4, by monotypy; see Fig. 7) is another genus often associated with *Oceanapia*. Van Soest (pers.comm.) considers that this genus is very similar to *Oceanapia* due to its turnip-shaped main body, which is also buried in the sand, and held up by a 'root system'

(compare with Fig. 6A–D). The method by which water is ingested into these *Oceanapia* species is peculiar. The fistules are inhalant and the exhalant openings are buried in the sand (Fig. 6A, B). We studied the type species and remarked that *Foliolina*'s skeleton is of the same type as that of *Oceanapia* (cf. Figs 4F, G and 6C, D), with an ectosomal hispid layer of compact spicules, with choanosomal stout multipisular tracts having only sparse spongin, and thinner paucispicular tracts forming an irregular mesh. *Foliolina peltata* is also different in its peculiar external morphology, having fistules with disc-like or platform-like extensions along their length. These characters and the absence of sigmas in *Foliolina* are certainly considered significant at the species-level, whereas close similarities in their respective skeletal structures suggest to us that *Foliolina* is a junior synonym of *Oceanapia*, as was proposed earlier by Zea (1987: 136) and reiterated by Werding & Sanchez (1991), based on their studies of two species of Phloeodictyidae (*Rhizochalina oleracea* and *Foliolina peltata*, from Uraba and Cartagena, and Santa Marta, Colombia, respectively). From these comparisons, which included living populations of both species, *Foliolina* was relegated into synonymy with *Oceanapia*.

Rhizochalina (Fig. 5A–D) and *Phloeodictyon* (Fig. 7A–C) differ from *Oceanapia* only by their lack of sigmas. *Biminia* (Fig. 6D–F) Wiedenmayer, 1977b (type species *Oceanapia toxophila* Dendy, 1922b: 45, pl. 8, fig. 2, by original designation) on the other hand has both sigmas and toxas (Fig. 7D, F), but also exhibiting the same type of skeleton as *Oceanapia*, and consequently Wiedenmayer in Hooper & Wiedenmayer (1994) considered *Biminia* also a junior synonym of *Oceanapia*.

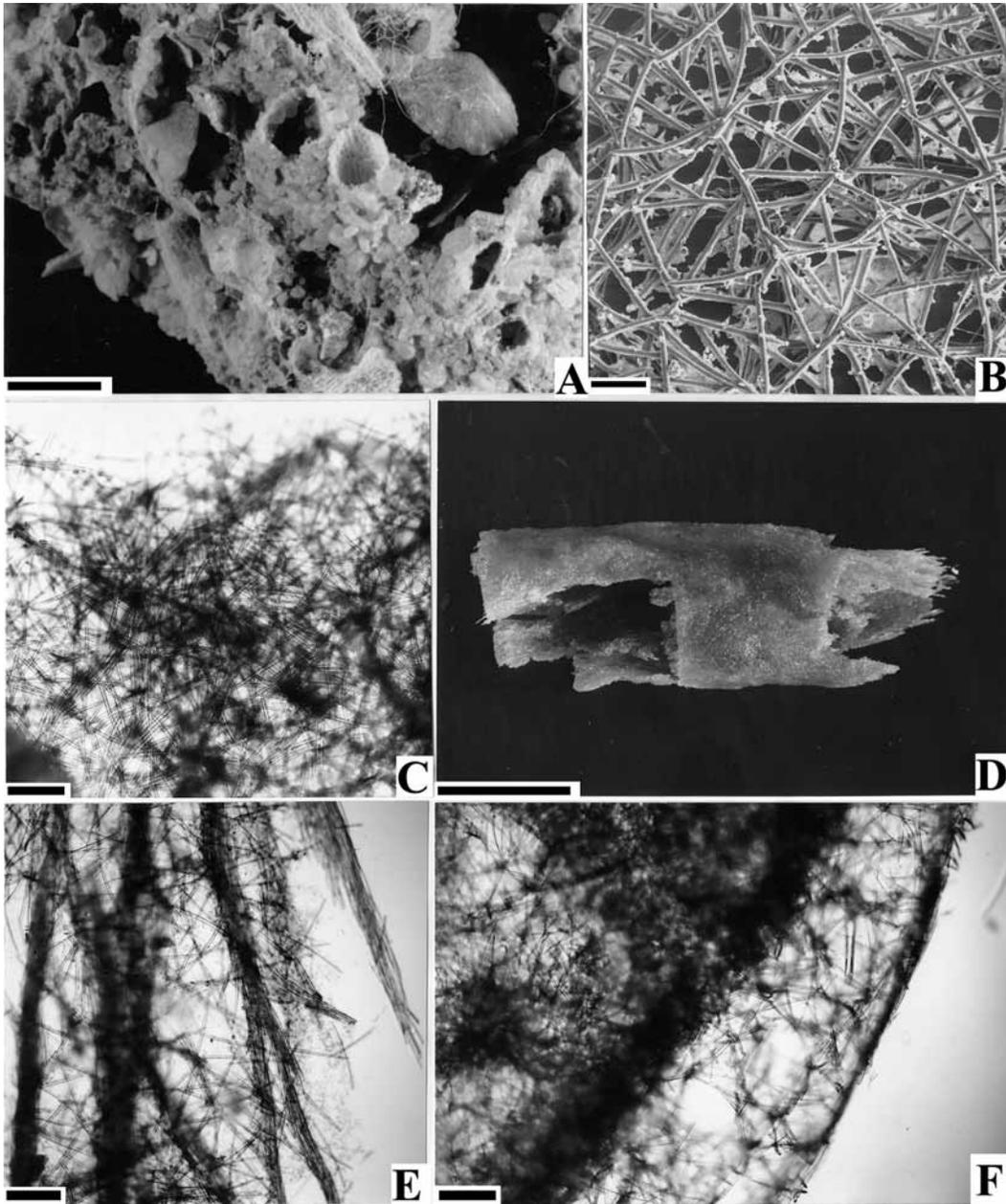


Fig. 6. *Oceanapia* Norman, 1869b. A–C, *Phloeodictyon* Carter, 1882b (type species *Phloeodictyon isodictyiformis* Carter, 1882b, holotype BMNH 1872.5.4.1). A, external view of the massive specimen, erect cylindrical appendages and the basal lamina. B, tangential view of the ectosomal unispicular network with spongin only at the nodes. C, fistule-wall, unispicular confused dense irregular network. D–F, *Bimina* Wiedenmayer, 1977b (type species *Oceanapia toxophila* Dendy, 1922b, holotype BMNH 1921.11.7.37). D, holotype. E, longitudinal section of the fistulae, with long, multispicular tracts and connecting unispicular network. F, longitudinal section through the body wall of the tube, ectosomal skeleton at right.

Distribution

Worldwide.

Type species

Petrosia fistulata Kirkpatrick, 1907a (by original designation).

PACHYPELLINA BURTON, 1934

Synonymy

Pachypellina Burton, 1934b: 18; de Laubenfels, 1936a: 70; Van Soest, 1980: 91.

Definition (from Van Soest, 1980)

Oceanapiidae with a thick ectosomal crust of tangential spicules and a densely spiculous choanosome which is riddled with holes. Megascleres are oxeas, no microscleres, no fistules.

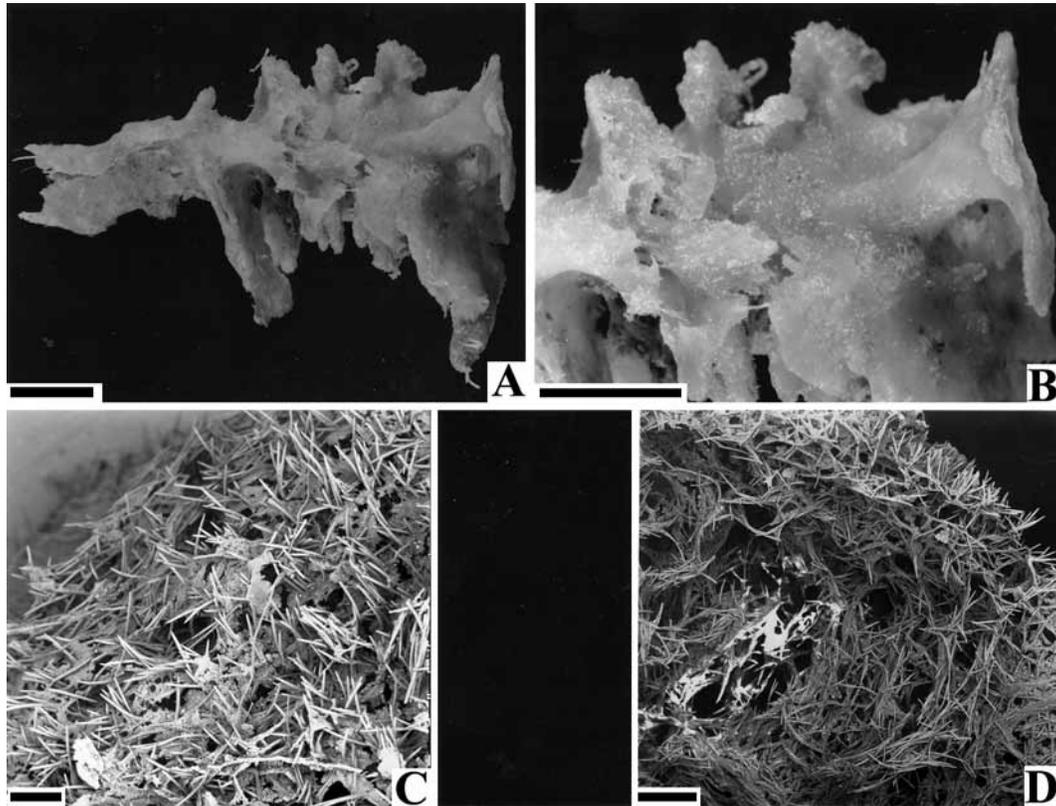


Fig. 7. *Oceanapia* Norman, 1869b. A–D, *Foliolina* Schmidt, 1870 (type species *Foliolina peltata* Schmidt, 1870, specimen BMNH 1948.3.8.37–39, Atlantic Expedition). A, view of specimen (scale 0.6 cm). B, enlarged view of the same specimen, basal part. C–D, BMNH 1870.5.3.105, slide of Schmidt, Florida. C, tangential view of the hispid surface. D, longitudinal view of the choanosomal skeleton, through the surface, illustrating identical structure to *Oceanapia*.

Diagnosis

Tubular to massive growth forms. Ectosomal skeleton a dense, tangential network of oxeas. External surface smooth but hispid due to the intercrossed ends of the ectosomal oxeas. Choanosomal skeleton is a confused spiculous network with numerous aquiferous canals. Megascleres are oxeas. Microscleres are absent.

Previous reviews

De Laubenfels, 1936a: 70, 1950: 66; Van Soest, 1980: 91, 117; de Weerd & Van Soest, 1986: 44.

Description of type species

Petrosia fistulata Kirkpatrick, 1907a (Fig. 8).

Synonymy. *Petrosia fistulata* Kirkpatrick, 1907a: 290; 1908c: 51; [in part] Burton, 1929a: 420, as *Chalina dancoi* (Topsent); *Pachypellina fistulata*; Burton, 1934b: 18, Fig. 2. Not Burton, 1938: 6 (= *Haliclona dancoi* (Topsent)).

Material examined. Holotype: BMNH 1908.2.5.200 – Winter Quarters, 25–30 ftm. Holotype (slide): BMNH 1933.3.17.172 – 64°20'S 56°38'W, 150 m depth. Paratype: BMNH 1908 2.5.202a, b – McMurdo Bay, 96–120 ftm, Antarctica, 'Discovery' Expedition. Other material. Holotype of *Pachypellina fistulata* Burton, 1934b: USNM 20884 – Graham region, SE Seymour Island, 64°20'S 56°38'W, 150 m depth. Holotype (slide): BMNH 1933.3.17.172.

Description. Three fragments of a tubular sponge, with a finely hispid, smooth internal and external surfaces. Tubes form a thick wall with a terminal oscule, measuring 2–2.5–6 cm high by 3–2.5–2 cm in diameter. A fine ectosomal membrane covers the numerous ostia, 0.5–3 mm in diameter. Oscules are only present in the internal surface of the tube, they are small about 1 mm in diameter. Texture is hard and friable. Spongin is not visible, except at skeletal nodes. Ectosomal skeleton is a multispicular tangential compact network of closely packed oxeas (Fig. 8A, B), without visible spongin, forming a strong, regular crust of spicules of 900–1520 μm large, supported by terminal brushes of choanosomal longitudinal principal tracts. Ends of tracts partly visible at the surface. Choanosomal skeleton is a dense irregular network permeated by numerous aquiferous canals (Fig. 8C), with multispicular longitudinal tracts, 4–8 spicules wide, running perpendicular to the surface, connected by short, irregular paucispicular tracts, 3–4 spicules wide and 1–2 spicules long. Megascleres are only oxeas, slightly bent with blunt ends: 328–388–439 \times 12–16–20 μm , and 238–296–344 \times 4–6–8 μm (Burton's specimens; Fig. 8D); 394–430–463 \times 12–19–25 μm , and 262–343–385 \times 4–6–8 μm (Kirkpatrick's specimens).

Distribution. Antarctica, Subantarctic (Kirkpatrick, 1907a; Burton, 1934b).

Remarks. The type species of *Pachypellina*, *Petrosia fistulata* Kirkpatrick, was originally regarded by Burton (1929a: 420) as an immature form of *Reniera dancoi* Topsent, 1901, and consequently relegated into synonymy with the latter species.

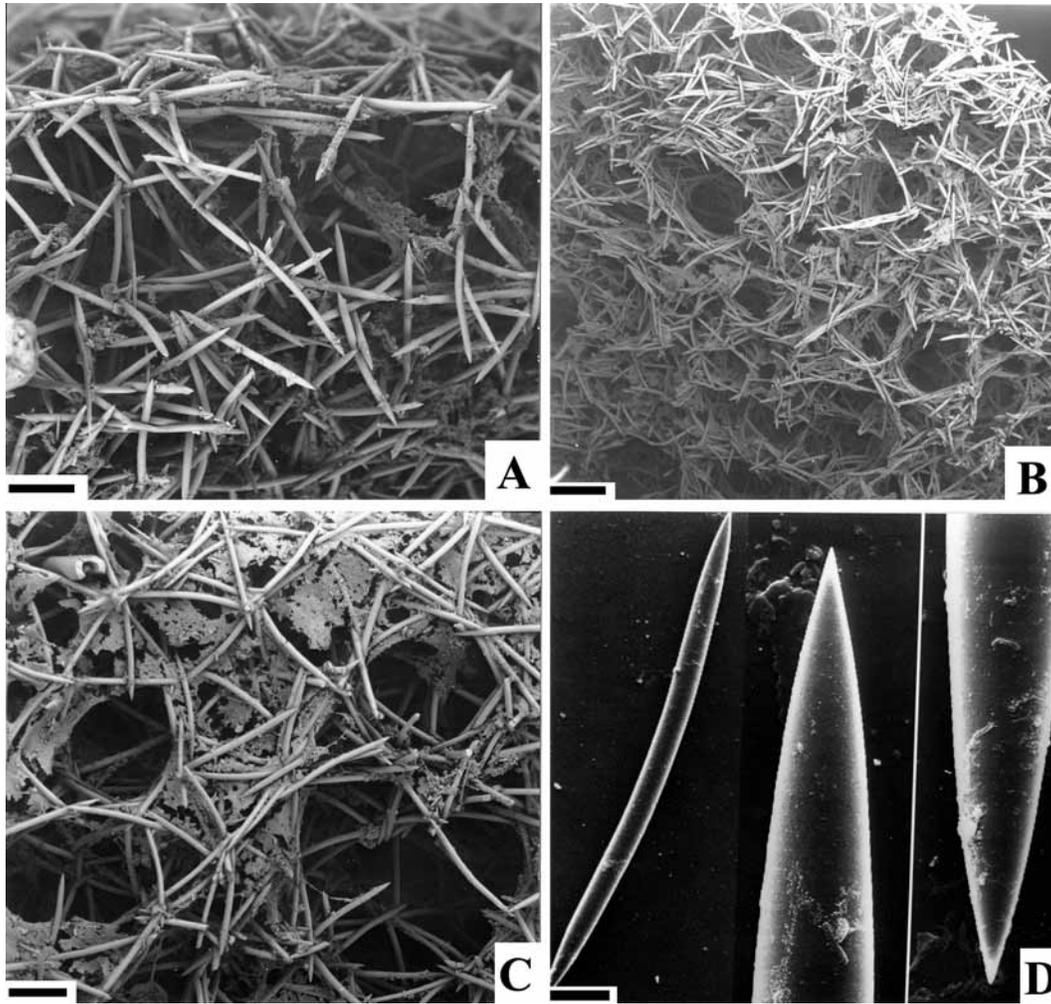


Fig. 8. *Pachypellina* Burton, 1934b. A–B, type species *Petrosia fistulata* Kirkpatrick, 1907a, BMNH 1908.2.5.202, and BMNH 1908.02.1902. A, fragment of specimen, longitudinal view through the surface, ectosomal crust on top and loose choanosomal network below (scale 200 μm). B, the same specimen showing choanosomal network and aquiferous canals (scale 500 μm). C–D, holotype of *Pachypellina fistulata*; Burton, 1934b, RSME 20884. C, ectosomal network of dense tangential layer of oxeas, or ectosomal crust, tangential view (scale 200 μm). D, the same specimen, two types of oxea, slightly bent, with blunt ends (scale 10 μm).

De Laubenfels (1936a: 70) remarked *Pachypellina* was very much like *Adocia* except that its spicules were hastate and its ectosomal much denser and not typical of *Adocia*. Van Soest (1980) characterised *Pachypellina* by its distinctive ectosomal crust and its dense choanosomal skeleton. He also included *Haliclona podatypa* de Laubenfels, 1934, from Puerto Rico, in the genus presumably due to its possession of an ectosomal crust and isotropic choanosomal reticulation bound together with sparse spongin. We think that this inclusion is a mistake because the spicules of *P. podatypa* (158–170.2–180 \times 4.5–5.1–6.5 μm) are much smaller than those of the type species of *Pachypellina*, although in the opinion of Van Soest (1980: Table 2), the Atlantic specimens of *P. podatypa* exhibit a variable morphology. De Weerd & Van Soest (1986) recorded only one species of *Pachypellina* from the North Atlantic Ocean, *Reniera tufa* Ridley & Dendy, 1887, from Cape Verde Is., referred to the genus by Burton (1934b).

We examined two species of *Pachypellina* to assess relationships for the present study: a slide of the holotype of the type species *Petrosia fistulata* Kirkpatrick, and Burton's material of *Pachypellina*

fistulata. Kirkpatrick's (1907a) material is clearly tubulose, whereas Burton's (1934b) specimen is massive-tubulose, but in both specimens the skeletal structure is identical, and megasclere geometry is the same (bent oxeas, with blunt or tornote ends). This material indicates to us that the connective tracts in the choanosomal skeleton, formed by only few transverse spicules, are very typical and differ from the typical *Petrosia* skeletal structure (Petrosiidae). In addition, its tangential surface skeleton makes *Pachypellina* Burton a well defined genus which we consider to be valid. Undertaking a revision of species from Antarctica originally described under *Reniera* and *Petrosia*, would certainly assist in recognising new species of *Pachypellina*, and also in providing further biological data as to the distribution and morphological characteristics of the type species.

Distribution

Antarctica, Subantarctic (Burton, 1934b; Kirkpatrick, 1907a; Koltun, 1964b).

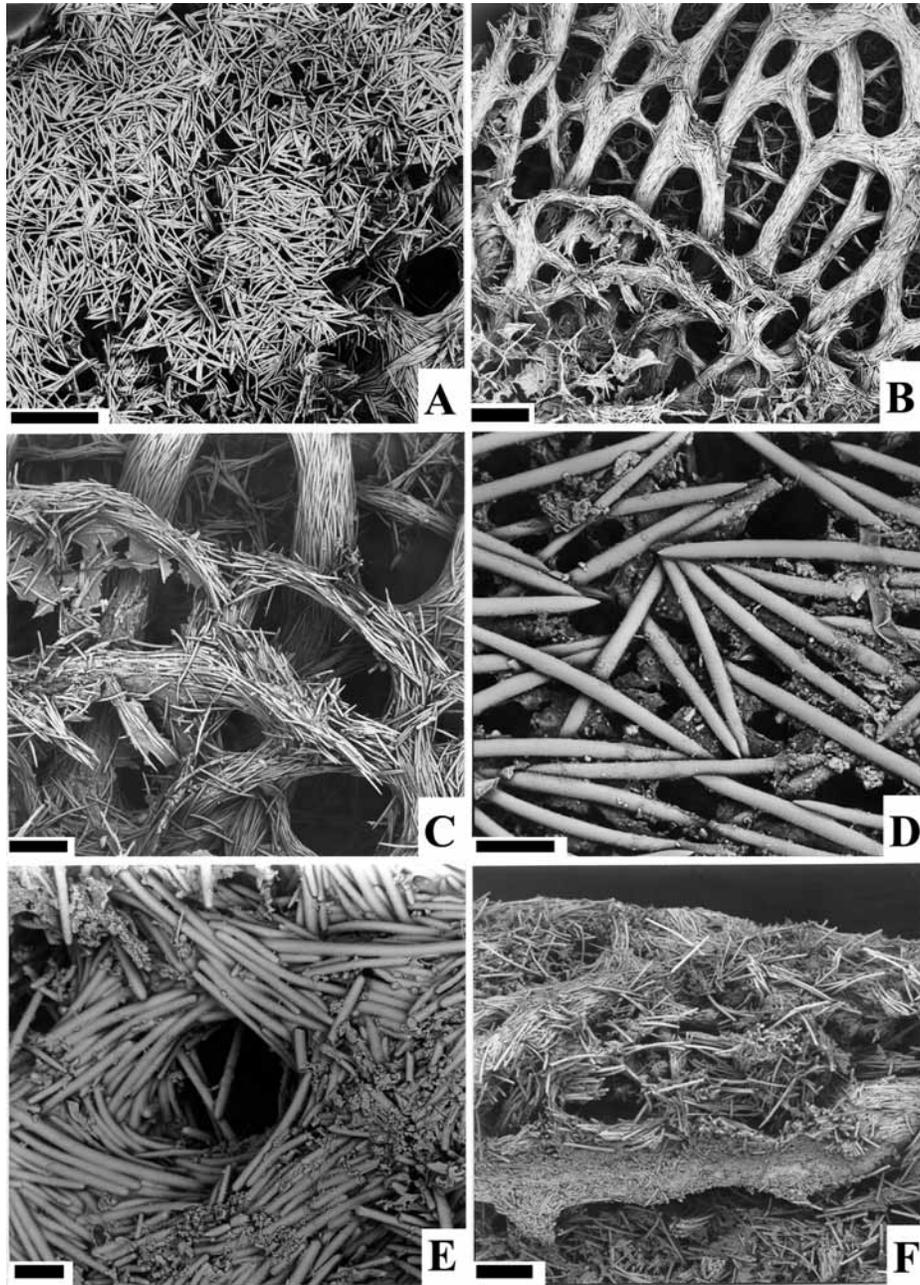


Fig. 9. *Tabulocalyx* Pulitzer-Finali, 1993. A–F, type species *Tabulocalyx pedunculatus* Pulitzer-Finali, 1993, MSNG 48327, holotype. A, ectosomal crust a single tangential layer of free oxeas in confusion, occasionally forming confused tracts (scale 500 μm). B–C, subectosomal two-dimensional network of multispicular fibres with large and smaller mesh, view taken from below the surface (scales B, 500 μm ; C, 200 μm). D, deeper within the interior of the globous body, the mass of oxeas in confusion (scale 50 μm). E, enlarged view, part of the subectosomal network (scale 50 μm). F, longitudinal view of one of the subectosomal networks of multispicular fibres, parallel to the surface (scale bar 200 μm).

TABULOCALYX PULTIZER-FINALI, 1992

Synonymy

Tabulocalyx Pulitzer-Finali, 1992: 322.

Type species

Tabulocalyx pedunculatus Pulitzer-Finali, 1992 (by original designation).

Definition

Phloeodictyidae without fistules. Cortex in two separate layers with an ectosomal network of a single layer of oxeas, supported by subsequent ectosomal layers of multispicular fibres in the subectosome, representing earlier growth stages.

Diagnosis (from Pulitzer-Finali, 1992, 1996)

Irregularly massive, cylindrical-lobate growth forms with a tangential ectosomal crust of free oxeas in confusion (Fig. 9A), forming

occasional thin, vague tracts, supported by a strong two-dimensional network of multispicular fibres (Fig. 9B, C), under which there is a dense mass of oxeas (Fig. 9D), which are cut across by several two-dimensional networks like those mentioned above; each of these two dimensional networks is separate from each other and more-or-less parallel to the surface. All the internal part of the body is occupied by a mass of oxeas in confusion and some irregular multispicular fibres.

Previous reviews

Pulitzer-Finali (1992).

Description of type species

Tabulocalyx pedunculatus Pulitzer-Finali, 1993 (Fig. 9).

Synonymy. *Tabulocalyx pedunculatus* Pulitzer-Finali, 1993: 323, figs 61, 62.

Material examined. Holotype: MSNG 48327 – North Kenya Bank, 02°47.5'S, 41°00'E, 110m depth. Other material. *Tabulocalyx corticatus* (Wilson): MSNG P.60 – Pulitzer-Finali collections, 1986, Laing island, New Guinea, 17.08.1986.

Description. Globose, 5.5 cm in diameter, supported by a long stem, 1.5 cm thick, 6 cm long. Oscules, crateriform, numerous, 3–5 mm in diameter. Ectosomal crust a single tangential layer of free oxeas in confusion, occasionally forming confused tracts, supported by a two dimensional network of multispicular fibres, 82–164–287 µm in diameter with large meshes, 246–443–820 µm,

and smaller meshes, 205–323–533 µm (Fig. 9B, C). Within the interior of the body the mass of oxeas is traversed by two or three networks of multispicular fibres, parallel to the surface, appearing in longitudinal section as different growth stages (Fig. 9F), reminiscent of *Callyspongia (Euplacella)* (Callyspongiidae) and in *Neopetrosia* (Petrosiidae), and presumably independently acquired. Megascleres oxeas, 185–200 × 10.5 – 11.5 µm.

Distribution. Known exclusively from the type locality: East Africa, North Kenya Bank, 110 m depth.

Remarks. Pulitzer-Finali (1992) erected this genus principally due to the characteristic structure of its ectosomal network, and included it in Phloeodictyidae irrespective that it lacked fistules (Pulitzer-Finali, 1996: 128, Fig. 24A–B). This skeletal structure consisting of the double layered ectosomal network appears to us as a pivotal character in its diagnosis, differentiating it from other genera of Phloeodictyidae. Pulitzer-Finali (1996) also included the Petrosiidae species *Strongylophora corticata* Wilson, 1925, in this genus despite the fact that its spicules corresponded to typical *Strongylophora*, and his action was also probably due to the presence of the double layered ectosomal. In our opinion, the spiculation of *S. corticata* is typical of *Strongylophora*, and we maintain here *Strongylophora corticata* Wilson, 1925, as a valid species of *Petrosia (Strongylophora)*. Pulitzer-Finali (1996) also amended the diagnosis of *Tabulocalyx* as follows 'cortex in two separated layers, the subdermal one being a rigid cribriform lamella consisting of a close network of compact spiculo fibres developed in a tangential plane. Former ectosomal lamellae may be found inside the choanosome, marking earlier growth stages'.