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

Family Mycalidae Lundbeck, 1905

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Mycalidae Lundbeck (Demospongiae: Poecilosclerida) is restricted to taxa with the combination of palmate anisochelae and a tangential surface skeleton. It consists of two genera, *Mycale s.l.* and *Phlyctaenopora*, which includes *Barbozia*. The large genus *Mycale* is subdivided in 11 subgenera, viz., *Aegogropila, Anomomycale, Arenochalina, Carmia, Grapelia, Mycale, Naviculina, Oxymycale, Paresperella, Rhaphidotheca* and *Zygomycale*. These subgenera are probably artificial and some 'overlap' in characters, but they may serve to differentiate the 150 or more species assigned to *Mycale*. The genera *Raphioderma*, *Rhaphiodesma, Protoesperia* and *Mycalecarmia* are considered junior synonyms of *Mycale (Mycale)*. The genus *Esperia* and its replacement name *Esperella*, as well as *Pellinula*, are considered junior synonyms of subgenus *Aegogropila*. The genera *Acamas*, *Acamasina*, *Kerasemna* and *Parisociella* are junior synonyms of *Arenochalina*. The genus *Oxycarmia* is considered a junior synonym of *Carmia*. The genus *Pseudoesperia* is considered a junior synonym of *Grapelia*. The genera *Gomphostegia* and *Sceptrospongia* are junior synonyms of *Rhaphidotheca*. Keys to the genera and subgenera are provided.

Keywords: Porifera; Demospongiae; Poecilosclerida; Mycalina; Mycalidae; *Mycale (Aegogropila)*; *Mycale (Anomomycale)*; *Mycale (Arenochalina)*; *Mycale (Carmia)*; *Mycale (Grapelia)*; *Mycale (Mycale)*; *Mycale (Naviculina)*; *Mycale (Oxymycale)*; *Mycale (Paresperella)*; *Mycale (Rhaphidotheca)*; *Mycale (Zygomycale)*; *Phlyctaenopora (Phlyctaenopora)*; *Phlyctaenopora (Barbozia)*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Esperiadae Gray, 1867a: 531. Esperellinae Ridley & Dendy, 1887: 62. Arenochalininae Lendenfeld, 1888. Mycalinae Lundbeck, 1905.

Definition

Mycalina with 'mycalostyles' (styles with slightly constricted neck), occasionally modified to oxeas or strongyles, arranged in a plumose, plumoreticulate or confused manner; microscleres include palmate chelae, sigmas (may be serrated), toxas (may be spined), spined microxeas, and raphides, all of which may be absent; no diancistras or derivates, no commata, no spined micro(subtylo-)styles.

Diagnosis

Encrusting, massive, fan-shaped and branching growth forms. Subectosomal sculpturing, grooves and ridges often found on the surface, within which are usually found the ostia. Skeleton plumose or plumoreticulate, composed of styles or rarely oxeas enclosed in spongin fibres or without visible spongin. Ectosomal tangential skeleton usually present. Ectosomal spicules may differ from the choanosomal ones by smaller size. Megascleres most often subtylostyles (mycalostyles), but (aniso)strongyles, oxeas and exotyles occur occasionally. Microscleres characteristically palmate anisochelae, but also palmate isochelae, sigmas, toxas, spined microxeas and raphides may occur. The family is quite diverse with about two hundred species described occurring in all parts of the world oceans, and possibly many more hundreds awaiting discovery.

Scope

Two genera comprising 13 subgenera out of 25 nominal (sub-) genera are recognized as valid, *Mycale* Gray, 1867a: 533 and *Phlyctaenopora* Topsent, 1904b: 198. The first is subdivided in eleven subgenera, the second in two subgenera.

Remarks

Nomenclatorial remarks. The name Mycalidae and authorship of Lundbeck is to be maintained over the older names Esperiadae, Esperellinae and Arenochalininae because the synonymy of *Esperia, Esperella* and *Arenochalina* with *Mycale* was established before 1961 and Lundbeck's replacement of the family name was likewise made before 1961. Mycalidae has been used hundreds of times in many different publications by many different authors, and thus satisfies the condition of ICZN article 40.2 as 'prevailing usage' (Anon., 1999).

History and biology. Gray (1867a: 531) used the name Esperiadae for a large group of genera covering more-or-less what is now considered the order Poecilosclerida. Ridley & Dendy, 1887: 62 assigned to their Esperellinae all poecilosclerids lacking echinating acanthostyles, thus more-or-less covering what is now understood as the suborder Mycalina. However, they also included *Iophon* (now Microcionina), and *Desmacidon* and *Phelloderma* (now Myxillina). Lendenfeld's 'group' Arenochalininae was assigned to a larger subfamily Chalininae, and he was obviously unaware of the mycalid nature of *Arenochalina*. Lundbeck (1905: 7) erected Mycalinae to replace Esperellinae and included not only Ridley & Dendy's concept, but also most Myxillina; however, he subdivided the group into Mycaleae and Myxilleae, which covered what is now understood as Mycalina and Myxillina. Topsent (1928: 46) returned to Ridley & Dendy's concept, but continued the use of the name Mycalinae. De Laubenfels (1936a: 112) assigned *Mycale*

and its relatives to a family Ophlitaspongiidae, defined as having the fibres echinated by smooth rather than acanthose styles. *Mycale* was defined by him (p. 116) as having 'fibers cored and echinated by smooth monaxons that are frequently subtylostyles'. He assigned a wide range of unrelated genera in Ophlitaspongiidae which are now spread over three suborders. Lévi (1973: 609) was the first to restrict the contents of the family to *Mycale* and its immediate relatives, all sharing the palmate anisochelae. Many authors followed his proposal. Bergquist & Fromont (1988: 17) expanded Lévi's concept with the inclusion of *Esperiopsis*, which is likely to be closely related, but has palmate isochelae. Their proposal was followed by Hajdu & Desqueyroux-Faúndez (1994). They assigned a number of *incertae sedis* genera to the family (e.g., *Ulosa, Phelloderma*), but pointed out that a monophyletic Mycalidae was not established convincingly. If the mycaline families are indeed related as suggested by Hajdu & Desqueyroux-Faúndez (1994), viz., ((Cladorhizidae, Guitarridae) (Desmacellidae (Hamacanthidae, Mycalidae))), Mycalidae *s.l.* (which for them included the family here separated off as Esperiopsidae) could share the possession of chelae, supposedly lost two nodes down the tree, by the ancestor of the Desmacellidae-Hamacanthidae-Mycalidae *s.l.* clade. Another possible synapomorphy, although underlying, is the presence of three categories of chelae. However, these characters do not appear to establish the monophyly very strongly. Further discussions on the phylogenetic relationships of Mycalidae and Esperiopsidae genera and subgenera may be found in Hajdu (1999). The present concept of a restricted Mycalidae may be considered monophyletic based on the shared possession of palmate anisochelae. However, one species of the genus *Amphilectus*, viz., *A. lobata* (Bowerbank, 1866), here assigned to the family Esperiopsidae, also possesses palmate anisochelae. Further character analysis is necessary to arrive at a more robust phylogeny of the families of Mycalina.

Phlyctaenopora, although not usually included in this group, shares anisochelae and a tangential surface crust with *Mycale*, which conforms to the present definition of the family. It differs in having strongyles and oxeas as megascleres instead of the usual mycalostyles. *Barbozia* has similar structure and spiculation, but in addition possesses peculiar spined microxeas. It is here considered a subgenus of *Phlyctaenopora*.

Mycalidae are numerous and common members in all seas and all marine habitats. Reproduction is often seasonal. The larvae have a bare posterior pole and diverse larval spiculation. Gemmule-like resting stages consisting of undifferentiated globular masses of archaeocytes are reported from *Mycale* species from temperate waters.

Previous reviews

Hallmann (1914), Topsent (1924), de Laubenfels (1936a), Van Soest (1984b), Bergquist & Fromont (1988), Hajdu & Desqueyroux-Faundez (1994), Hajdu (1999).

KEY TO GENERA

(1) Only mycalostyles present ..... ***Mycale***
Megascleres oxeas and/or strongyles 2
(2) Megascleres exclusively oxeas ..... ***Mycale (Oxymycale)***
Megascleres oxeas and strongyles ..... ***Phlyctaenopora***

MYCALE GRAY, 1867

Synonymy

[*Esperia*] Nardo, 1833: 522 (preocc.) (not *Esperia* Hübner, 1816: Lepidoptera). [*Acamas*] Duchassaing & Michelotti, 1864: 94 (preocc.) (not *Acamas* Montfort, 1808, Mollusca). *Mycale* Gray, 1867a: 533. *Aegogropila* Gray, 1867a: 533. *Grapelia* Gray, 1867a: 534. *Carmia* Gray, 1867a: 537. *Naviculina* Gray, 1867a: 538. *Esperella* Vosmaer, 1887: 353 (misprinted as [*Esperiella*] on p. 348 (*lapsus*)). *Raphioderma* Bowerbank in Norman, 1869b: 333. *Rhaphidotheca* Saville Kent, 1870a: 219. *Raphiodesma* Bowerbank, 1874b: 235. *Pseudoesperia* Carter, 1886c: 455. *Arenochalina* Lendenfeld, 1887c: 821. *Protoesperia* Czerniavsky, 1879: 248. *Gomphostegia* Topsent, 1896b: 149. *Paresperella* Dendy, 1905: 162. *Anomomycale* Topsent, 1924: 116. *Sceptrospongia* Dendy, 1926: 6. *Oxymycale* Hentschel, 1929: 932. *Zygomycale* Topsent, 1930: 431. *Acamasina* de Laubenfels, 1936a: 117. *Mycalecarmia* de Laubenfels, 1936a: 120. *Parisociella* Burton, 1952: 169. *Oxycarmia* de Laubenfels, 1954: 155. *Kerasemna* Pulitzer-Finali, 1981: 105.

Type species

Hymeniacidon lingua Bowerbank, 1866: 187 (by subsequent designation; Thiele, 1903a: 949).

Definition

Mycalidae with megascleres in a single category of shape. There may be size categories.

Diagnosis

Encrusting, lobate, repent, ramose, branching erect or tubular sponges. Surface irregular or smooth, occasionally grooved. Consistency fibrous, compressible or soft, occasionally firm or hard. Skeleton of discrete bundles of spicules arranged in plumose fashion, with occasional anastomosing, rarely reticulate. Ectosomal skeleton usually a well-developed tangential crust of intercrossing bundles or single megascleres, occasionally absent or consisting of the brushed endings of choanosomal tracts. Spicules usually exclusively mycalostyles, rarely replaced by oxeas; size categories are common. Microscleres palmate anisochelae (exceptionally isochelae), the larger ones frequently in rosettes, sigmas, toxas, raphides; rarely micracanthoxeas which appear to be toxa-derived; size categories common for anisochelae (up to four have been recorded) and sigmas, occasionally also trichodragmas and toxas.

Scope

The genus comprises some two hundred species, subdivided among eleven subgenera, *Mycale (Mycale), Mycale (Aegogropila),*

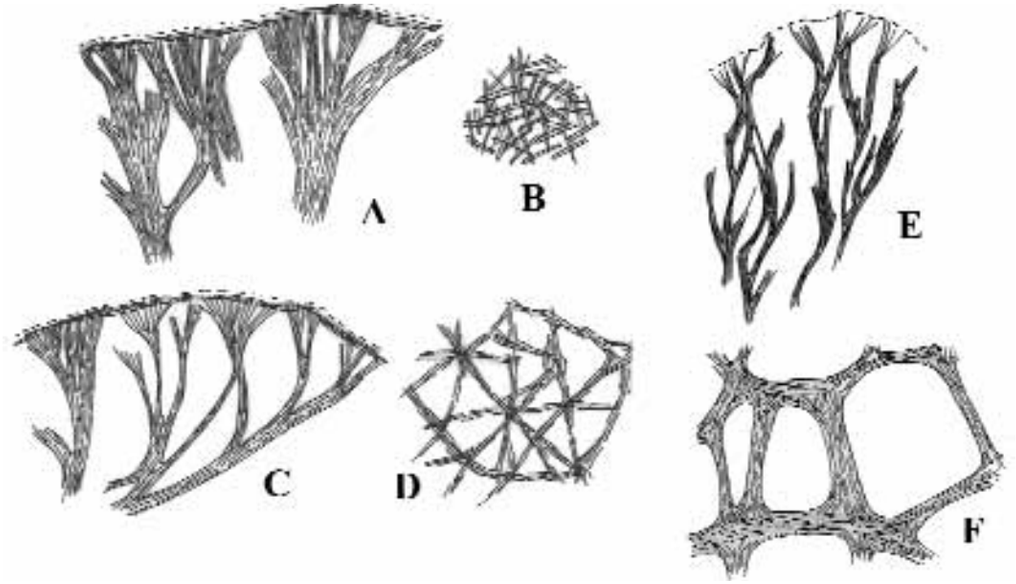

Fig. 1. Skeletal structures of *Mycale* subgenera. A–B, *Mycale (Mycale)*, cross section (A) and tangential section (B) to show ectosomal crust of intercrossing single spicules. C–D, *Mycale (Aegogropila)*, ditto. E, *Mycale (Carmia)*, cross section. F, *Mycale (Arenochalina)*, cross section (all redrawn from Van Soest, 1984b: fig. 1).

Mycale (Anomomycale), Mycale (Arenochalina), Mycale (Carmia), Mycale (Grapelia), Mycale (Naviculina), Mycale (Oxymycale), Mycale (Paresperella), Mycale (Rhaphidotheca), Mycale (Zygomycale). Overall distribution cosmopolitan.

Remarks

The idea that several, relatively homogeneous groups can be recognised within the genus *Mycale* is a concept as old as the genus itself, as Gray (1867a) erected five different genera for sponges sharing a comparable set of spicules (viz. *Mycale, Aegogropila, Grapelia, Carmia* and *Corybas*) and distinguished from each other in minor morphological features only (cf. Hajdu & Desqueyroux-Faúndez, 1994). Hallmann (1914) stressed the need for a division of the large genus, into subgenera *Aegogropila, Paresperella, Grapelia, Arenochalina* and *Mycale*. He was doubtful about *Protoesperia*. Topsent (1924) followed his example and elaborated and extended the subgenera, recognizing *Aegogropila, Anomomycale, Carmia* and *Mycale*. However, he restricted his proposals to species occurring in Western Europe, and thus avoided genera like *Paresperella, Arenochalina* and *Rhaphidotheca*. These proposals found few contemporaneous followers, but they were revived by Van Soest (1984b: 10), who constructed diagrammatic drawings of the major subgeneric skeletal features (here reproduced in Fig. 1A–F). He also added *Acamasina* = *Arenochalina* to the list of subgenera, but assigned *Zygomycale* to the synonymy of *Aegogropila*. Bergquist & Fromont (1988: 7) went further and proposed to raise Topsent's subgenera to genera. Hajdu (1995, 1999) revived some additional (sub)genera, e.g., *Grapelia* and *Naviculina*. Hajdu (1995, 1999) and Carballo & Hajdu (1998) pointed out that characters of several of the (sub-)genera overlapped with other (sub-genera), e.g., *Paresperella* and *Zygomycale* have a typical *Aegogropila* structure (Fig. 1C–D), *Grapelia, Anomomycale* and *Oxymycale* have a typical *Mycale s.s.* structure (Fig. 1A–B). Thus, several of these taxa appear to be paraphyletic or overlapping, as they are based on different features of the skeleton and spicules. It is here decided to keep the species groups possessing a single megasclere type assigned to Mycalidae, all at the level of subgenera of *Mycale* instead of genera. In this way we avoid some of the paraphyly problems, but it is certainly not ideal and must be considered a provisional, convenient system to manage large groups of taxa. When hypotheses of phylogenetic relationships for these taxa, attempted by Carballo & Hajdu (1998) and Hajdu (1999) (amongst others) become more robust, it may turn out to be preferable to have several more genera in Mycalidae (see further comments in the remarks for each subgenus).

Previous reviews

Van Soest (1984b), Bergquist & Fromont (1988), Hajdu & Desqueyroux-Faúndez (1994), Hajdu (1995), Hajdu & Rützler (1998).

Key to subgenera of *Mycale*

(1) Megascleres exclusively oxeas (Fig. 10B) ..... ***Oxymycale***
Megascleres include exotyles (Figs 12–14), styles with swollen or proliferated ends) piercing the ectosome, next to normal mycalostyles ..... ***Rhaphidotheca***
Megascleres exclusively subtylostyles (mycalostyles) 2
(2) Microscleres include naviculichelae (Figs 8–9: complete or near fusion of both frontal alae, falx markedly expanded along the shaft, lateral alae of the head project backward and upward) ..... ***Naviculina***

Sigmas are serrated (Fig. 11) ..... ***Paresperella***
Microscleres include anomochelae (Fig. 4: palmate anisochelae with a slightly curved shaft on face view; and frontal ala of the foot considerably expanded, approaching or even surpassing the dimensions of the usually larger frontal ala of the head, contorted, sometimes with a serrated upper border) ..... ***Anomomycale***
Microscleres include small isochelae (Fig. 15B) ..... ***Zygomycale***
Microscleres include polydentate unguiferate chelae (Fig. 7); rosettes in two size categories ..... ***Grapelia***
Microscleres consist of normal shaped sigmas and palmate anisochelae; toxas, raphides and micracanthoxeas may be present 3
(3) Ectosomal tangential skeleton present 4
Coherent ectosomal skeleton lacking 5
(4) Ectosomal skeleton consisting of intercrossing bundles of megascleres making triangular or polygonal meshes (Fig. 1D) ..... ***Aegogropila***
Ectosomal skeleton consisting of a felted mass of intercrossing megascleres without clear meshes or bundles (Fig. 1B) ..... ***Mycale***
(5) Choanosomal skeleton consisting of thick spongin enforced spicule tracts arranged in a rectangular reticulation; fibres cored by foreign objects (such as algae or sand); sponges extremely slimy when lifted out of the water (Fig. 1F) ..... ***Arenochalina***
Choanosomal skeleton consisting of wispy plumose bundles of megascleres showing little or no cohesion; sponges usually soft and encrusting (Fig. 1E) ..... ***Carmia***

SUBGENUS *MYCALE* GRAY, 1867

Synonymy

Mycale Gray, 1867a: 533. *Raphioderma* Bowerbank in Norman, 1869b: 333. *Raphiodesma* Bowerbank, 1874b: 235. ? *Protoesperia* Czerniavsky, 1879: 248. *Mycalecarmia* de Laubenfels, 1936a: 120.

Type species

Hymeniacidon lingua Bowerbank, 1864: 48 (by subsequent designation; Thiele, 1903a: 949).

Definition

Mycale with a confused tangential ectosomal skeleton (many with pore-grooves, and/or three categories of anisochelae, and/or basally-spurred anisochelae-III, and/or raphides in two categories).

Description of type species

Mycale (Mycale) lingua (Bowerbank, 1866) (Fig. 2A–C).

Synonymy. *Hymeniacidon lingua* Bowerbank, 1864: 48, pl. VI fig. 147; *Hymeniacidon lingua* Bowerbank, 1866: 187; *Mycale lingua*; Gray, 1867a: 533; *Raphiodesma lingua*; Bowerbank, 1874b: 235, pl. XLVII fig. 8, pl. LXXVII figs 1–6; *Mycale (Mycale) lingua*; Topsent, 1924: 86, fig. 1. *Desmacidon constrictus* Bowerbank, 1866: 350; Bowerbank, 1874b, 181, pl. LXXI figs 3–10. *Raphioderma coacervata* Bowerbank in Norman, 1869b. *Esperia lucifera* Schmidt, 1873: 148. *Esperia placoides* Carter, 1876: 316; *Mycale placoides*; Stephens, 1912: 34. *Esperella vosmaeri* Levinsen, 1887: 20. *Esperella massa*; Arnesen, 1903: 9, pl. I fig. 5, pl. IV fig. 2 (not *massa* Schmidt, 1862).

Material examined: Lectotype (here designated): BMNH 1930.7.3.235 – label in Bowerbank's handwriting reads 'Raphiodesma lingua/Loch Fyne. McNab. Bwk Coll. Vol. 2. p. 187, type of Genus & species 1852'. (Loch Fyne is on the Kintyre peninsula, Argyll, Scotland). Paralectotype: BMNH 1877.5.21.2019 – Shetland; also registered as BMNH 1930.7.3.233, dry; as *Raphiodesma*. Other material. BMNH 1882.7.28.98 – syntype of *Esperia placoides* Carter, 1876, 'Porcupine' Exped., Shetland.

Description (based on Ackers et al., 1992). Encrusting to massive lobose (Fig. 2A–B), to massive fig-shaped. Variously described as being 'roundish', 'resembling the tongue of a sheep', or 'an inverted triangular pyramid'. It is apparent that some specimens tend to grow in an erect, flattened form, with the attached base narrower than the apex. Grows up to 30 cm in height, with variable width and depth. Surface sulcate (Fig. 2A), the furrows forming an irregular reticulation over the surface. Within the furrows, the dermal membrane is smooth, elsewhere it is rather shaggy in appearance. Colour grey, pale buff; in alcohol pale yellow, whitish yellow or gray. Oscules are borne on shallow, transparent cones of height 2–3 mm, and have a diameter of 4–10 mm. The inhalant pores lie along the surface of the furrows, and can only be seen with the aid of a microscope in preserved material but are obvious in living specimens. The sulcate cracks close on collection. Consistency rather tough, very fibrous, but easily compressed. Ectosomal skeleton a mass of tangential spicules. Choanosomal skeleton plumoreticulate, consisting of ascending multispicular fibres of styles, with small amounts of spongin binding the fibres. Towards the surface, some fibres run parallel to the surface, and some become splayed like a brush and penetrate the surface. Megascleres are styles (Fig. 2B–C), usually straight, occasionally slightly curved: 460–1150 × 13–20 μm. Their ends are variable in shape. The head may be that of a typical style, or may tend to be that of a subtylostyle, or may be constricted like a handle ('mycalostyles'). The points may be abrupt or long. Microscleres (Fig. 2B–C) are palmate anisochelae, sigmata and trichodragmas. The anisochelae fall into two distinct size classes, 35 μm and 70 μm, the larger ones being found in rosettes, mainly near the dermal membrane; sigmas, 16–32 μm; trichodragmas, 42–78 × 11–14 μm. Distribution and ecology. Widely distributed over the north Atlantic, from the Azores to Spitzbergen. Also known from the Mediterranean; found at depths between 30 and 2460 m.

Remarks. Gray (1867a: 533) misquotes Bowerbank's type species as *Hymeniacidon lingula*.

The genus *Raphioderma* Bowerbank in Norman, 1869b: 333 was erected for type species (monotypy) *Raphioderma coacervata* Bowerbank in Norman, 1869b. No material of this sponge was examined, but the species and the genus name were ignored by Bowerbank (1874b), and assigned to the synonymy of *Hymeniacidon lingua* in Bowerbank (1882: 162). It is assumed to have been a mistake, later to be replaced by *Raphiodesma lingua* in Bowerbank (1874b: 237). If that is correct, then technically speaking, *Raphioderma* is a senior synonym of *Raphiodesma*.

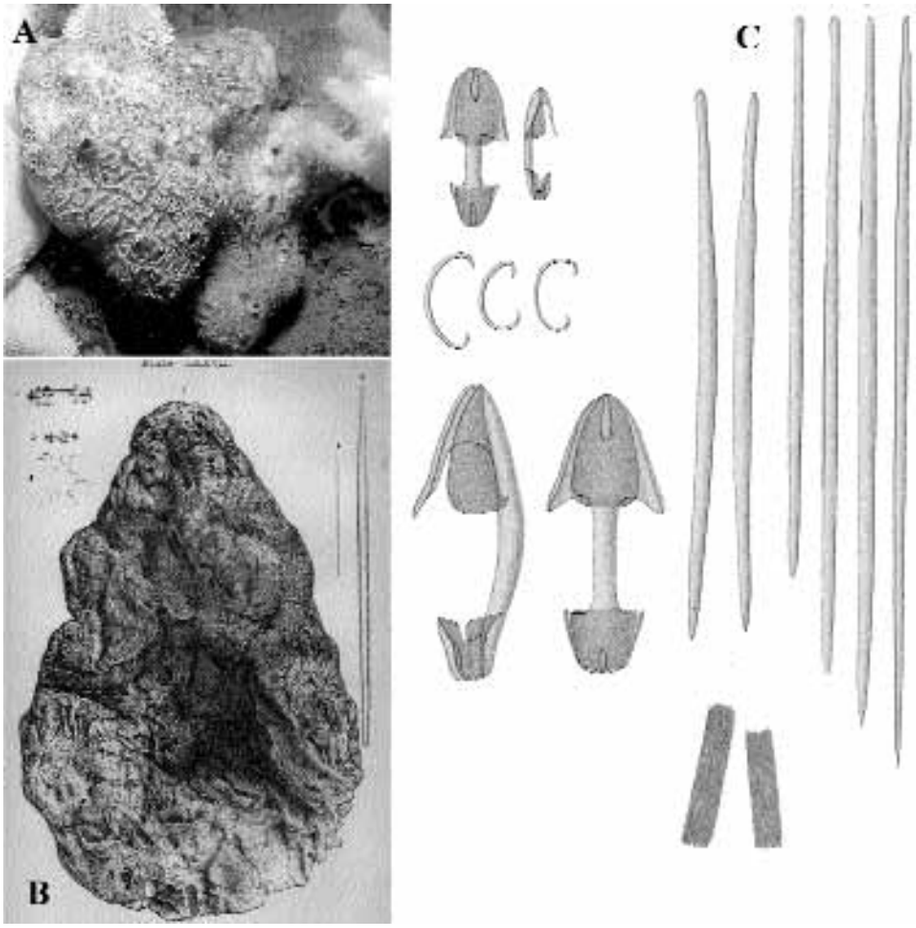

Fig. 2. *Mycale (Mycale) lingua* (Bowerbank, 1864). A, In situ photo from Ireland showing sulcate grooves (photo B. Picton). B, habit and spicules of type specimen, reproduced from Bowerbank, 1874b: pl. LXXVII (size see text). C, spicules reproduced from Lundbeck, 1905: pl. IX fig. 6 (sizes see text).

The genus *Raphiodesma* Bowerbank, 1874b: 235 (earlier also introduced on p. vi) was erected for type species *Hymeniacidion lingua* (subsequent designation by Hallmann, 1914: 399). Since this is also the type species of *Mycale*, the genus *Raphiodesma* is an objective junior synonym of *Mycale (Mycale)*. It is also likely to be a junior synonym of *Raphioderma*, and thus by inference, that genus is also a junior synonym of *Mycale (Mycale)*.

The genus *Protoesperia* Czerniavsky, 1879: 248 was erected for type species (designation herein) *Protoesperia simplex* Czerniavsky, 1879: 249, pl. II fig. 13, pl. III fig. 18, from the Black Sea. The type was stated to be located in the museum of the University of Charkov, Ukrain, but is now presumably lost (Koltun, in litt.). This is a possible synonym of *Mycale (Mycale)*, but the description is ambiguous and the thickly encrusting species has not been rediscovered. The megascleres are said to consist of three categories of subtylostyles ($400 \times 4.5\,\mu m$, $420–480 \times 14\,\mu m$, and $270–500 \times 3–18\,\mu m$, which differ only in the shape of the malformations) and a predominance of oxeas of $135–578 \times 7–16\,\mu m$. The author also recorded the presence of anisochelae. It is here assumed that the oxeas are not proper. This species needs redescription.

The genus *Mycalecarmia* de Laubenfels, 1936a: 120 was erected for type species (by original designation) *Esperella lapidiformis* Ridley & Dendy (1886: 338). Hajdu & Desqueyroux-Faúndez (1994: 574) redescribed the holotype BMNH 1887.5.2.160 and additional material. This is a massive sponge from Southern Argentina, with a skeletal arrangement consisting of thick spicule bundles ending at the surface in dense ectosomal tufts. This is not a typical *Mycale (Mycale)* ectosome, which has tangentially intercrossing spicules, but is sufficiently different from the ectosome of typical *Carmia*, that assignment to *Mycale (Mycale)* is justified. The spicules include a single category of long robust mycalostyles, $500–900 \times 15–20\,\mu m$, three size categories of anisochelae, $75–95\,\mu m$, $45–70\,\mu m$, and $30–45\,\mu m$, and trichodragmas $45–88\,\mu m$; some of the studied specimens also contained sigmas, but these were lacking in the holotype.

De Laubenfels (1936a: 116) restricted *Mycale* to species having anisochelae and sigmas as microscleres, differentiated from other genera like *Carmia* in the lack of toxas. This simplified and artificial restriction found only few followers.

The most recent phylogenetic analysis of the genus *Mycale* by Hajdu (1999) found the confused ectosomal architecture to be synapomorphic for a cluster of species-groups, among which is *Mycale (Mycale)*. Proper classification principles demand unique characters for taxa, and these appear to be lacking for *Mycale (Mycale)*. However, strict application of these principles would have led to the inclusion within *Mycale (Mycale)* of easily recognizable subgenera as *Grapelia* and *Rhaphidoteca*. We prefer to keep them here as provisional separate units without pretending phylogenetic soundness.

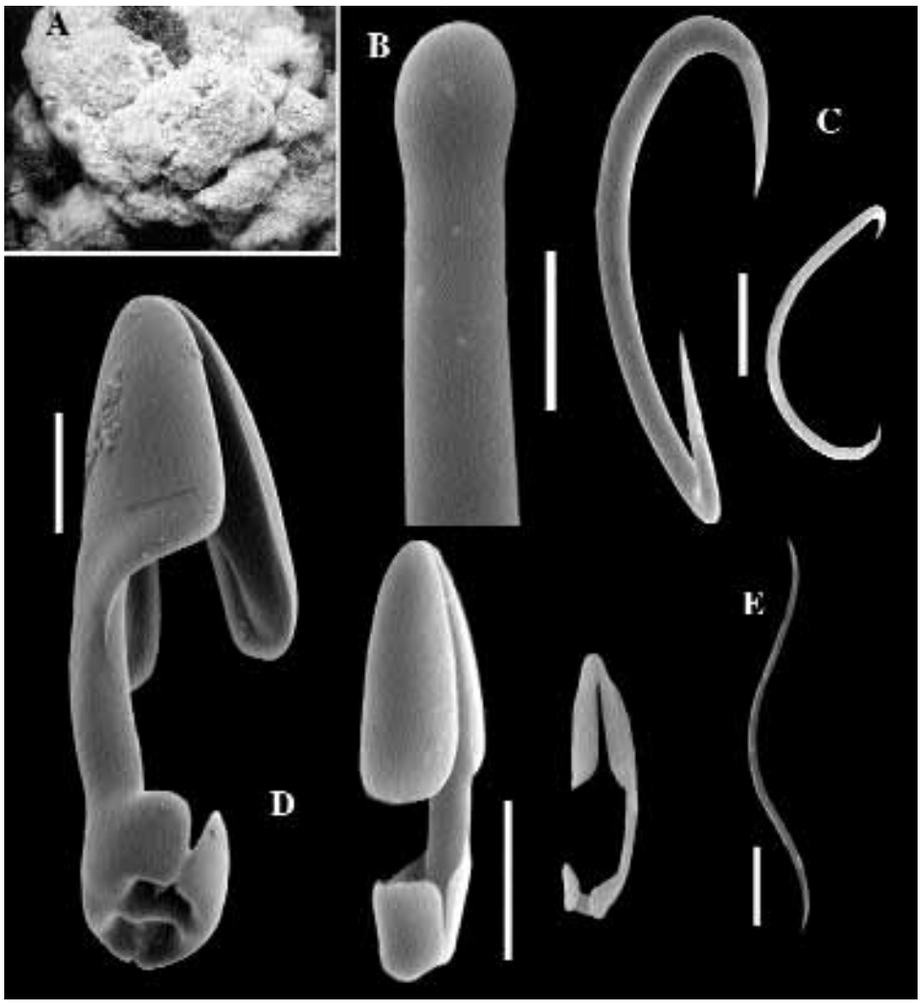

Fig. 3. *Mycale (Aegogropila) contareni* (Martens, 1824). A, In situ photo from Ireland (photo B. Picton). B–E. SEM images of spicules of ZMA POR. 4287 from Sherkin Island, Co. Cork, Ireland (scale bars 10 μm). B, detail of mycalostyle. C, two size categories of sigmas. D, three size categories of anisochelae. E, toxa.

SUBGENUS *AEGOGROPILA* GRAY, 1867

Synonymy

[*Esperia*] Nardo, 1833: 522 (preocc.) (not *Esperia* Hübner, 1816: Lepidoptera). *Aegogropila* Gray, 1867a: 533. *Pellinula* Czerniavsky, 1879: 125. *Esperella* Vosmaer, 1887: 353 (misprinted as *Esperiella* on p. 348).

Type species

Halichondria aegagropila Johnston, 1842: 119 (by subsequent designation; Dendy, 1922b: 55).

Definition

Mycale with surface visibly reticulate to the naked eye; choanosomal skeleton plumose or plumoreticulated made of multispicular tracts of megascleres of one category only; ectosomal skeleton a dense tangential reticulation of megascleres isolated or in tracts, megascleres are subtylostyles (mycalostyles); microscleres are palmate anisochelae in one to four size categories, the larger ones forming rosettes, sigmas, raphides, toxas and eventually micracanthoxeas.

Description of type species

Mycale (Aegogropila) contareni (Martens, 1824) (Fig. 3A–E).

Synonymy. *Spongia contarenii* Von Martens, 1824: 455, 580. *Esperia typica* Nardo, 1833: 522 (*fide* Schmidt, 1862: 54). *Halichondria aegogropila* Johnston, 1842: 119, pl. XI fig. 1; *Mycale aegagropila*; Stephens, 1912: 32. *Esperia foraminosa* Schmidt, 1862: 54, pl. V fig. 3. *Esperia bauriana* Schmidt, 1862: 55. *Esperia modesta* Schmidt, 1862: 57. *Esperia bacillaria* Schmidt, 1864: 34. *Aegogropila varians* Gray, 1867a: 533. *Desmacidon copiosus* Bowerbank in Norman, 1869a: 299. *Mycale microchaela* Ferrer-Hernandez, 1922: 9. *Mycale contareni*; Topsent, 1924: 91, fig. 3.

Material examined. Lectotype of *Halichondria aegagropila*: BMNH 1847.9.7.39. *Esperia contarenii* (*sensu* Schmidt, 1862): LMJG 15364. Syntypes of *Esperia foraminosa* Schmidt, 1862: LMJG 15361, 15372. Syntypes of *Esperia bauriana* Schmidt,

1862: LMJG 15370, 15950, SMF 48? – Bay of Muggia, Adriatic. Other material. ZMA 4187 – Roscoff, France. MNRJ 1081, 1149, 1153, 1157, 1167, 1173, 1175 – Roscoff, France.

Description (from Ackers et al., 1992). The shape varies from sheets or cushions of unequal thickness to massive-lobose (Fig. 3A). The lobes may become elongate and anastomose, leading to a superficially ramose appearance. Specimens can grow to a considerable size, at least 10 cm diameter and thickness. Surface typically covered by small conules, raised up by the skeletal fibres, giving the surface a somewhat reticulate appearance. Oscules few, large when open, found at summits of the lobes or scattered and carried on membraneous fistules on encrusting forms. Colour yellow, yellow green, ochrous yellow; preserved white to light brown. Consistency firm to soft, even, compressible. Smell quite marked, sweetish-pungent. Contraction slight. Skeleton plumoreticulate. The ectosomal skeleton is a tangential, triangular or polygonal reticulation of multispicular fibres. The choanosomal skeleton is an irregular system of anastomosing stout multispicular fibres. Spongin reinforces the skeletal fibres to a varying degree. Megascleres (Fig. 3B) are slightly curved (sub)tylostyles (so-called mycalostyles), thicker towards the pointed end, with a more or less pronounced head, 220–357 × 7–11 μm, varying between individuals. Microscleres include palmate isochelae in three size groups (Fig. 3D), the largest are grouped into rosettes, 31–47 μm; the middle size are solitary and variable in number (and may even be absent), 12–25 μm; the smallest are solitary, often abundant, with one ala characteristically standing out from the shaft giving the spicule a noticeable angular profile, 13–15 μm. Sigmas of two sizes (Fig. 3C) are present, the larger are numerous, robust and somewhat twisted, sizes generally in the range 40–65 μm; the smaller (if present) are thinly scattered and very slender and consequently sometimes hard to find, 16–22 μm. Toxas (Fig. 3E) are either single and scattered or, nearly always, in small bundles forming toxodragmata; they are small and fine, with a widely extended central flexion; they are always present but sometimes rare and difficult to detect; size 20–70 μm. Sexual reproduction in summer. Asexual reproduction also in summer by budding, buds located at summits of the conules. Distribution and ecology. British Isles, Atlantic coast of France and Spain, Mediterranean, Azores; littoral to 37 m, growing on stones, shells, algae, sessile coelenterates and scallop shells, boulders, cobbles, at sheltered sites with moderate tidal streams.

Remarks. Hajdu & Rützler (1998) argued for acceptance of Gray's (1867a) *Aegogropila varians* as type species of *Aegogropila*. However, Dendy (1922b: 55) indicates *Halichondria aegagropila* Johnston, 1842 as the type of *Aegogropila*. Both *A. varians* and *H. aegogropila* were mentioned by Gray, 1867a, and moreover no description of *A. varians* Gray, 1867a was offered, so there is ample reason to accept Dendy's designation as valid. This decision was again confirmed by Van Soest (1984b: 12) and Bergquist & Fromont (1988: 21). Hajdu & Rützler (1998) hypothesized about the reasons for Gray to propose *A. varians* (it is likely that Gray intended the name *A. varians* to replace *A. aegogropila* in order to avoid a tautologous name), but this is not certain from re-examined specimens or slides.

The genus *Pellinula* Czerniavsky, 1879: 125 (1880: 60) was erected for type species (here designated) *Pellinula schmidtii* Czerniavsky, 1879: 126, pl. I (=pl. V) figs 9–10 (1880: 62, pl. I (=pl. V) figs 9–10), from the northern shores of the Black Sea at a depth of 10–15 m. This designation foregoes the choice of *P. cribrosa* Czerniavsky, 1879: 125, pl. I (=pl. V) fig. 8 (1880: 60, pl. I (=pl. V) fig. 8), which has page priority, because a question mark was added to the name by Czerniavsky, possibly indicating he considered this species to be a dubious *Pellinula*. The description of *P. schmidtii* in Latin is not very informative, but from the recorded spicules, it seems a clear *Mycale s.l.*, as styles of up to 220 μm, sigmas of 7–9 μm and chelae of 10–32 μm are described. If the description is understood well, there also was an *Aegogropila*-type of ectosomal skeleton. *Pellinula* is here tentatively assigned to *Mycale (Aegogropila)* as a junior synonym. Its type material is presumably lost (Koltun, in litt.).

Vosmaer (1887: 353) erected *Esperella* for type species (by monotypy) *Spongia contareni* Martens, 1824 (to replace the preoccupied *Esperia*), which he also indicated as senior synonym of *Esperia typica* Nardo, 1833. He ignored the fact that Gray (1867a) already had created a number of genera covering the characters of *Esperia*, among which *Mycale* and *Aegogropila*. He even mentioned Gray's *Aegogropila* and Bowerbank's *Raphiodesma* as synonyms of *Esperella*. By sharing the same type species *Aegogropila* and *Esperella* are objective synonyms.

De Laubenfels (1936a: 122) declared *Aegogropila* a synonym of *Carmia* without explanation.

Aegogropila is not diagnosable on the basis of known morphological characters, yet. Traditionally recognized on the basis of its reticulated ectosomal skeleton, *Aegogropila* was discovered to be paraphyletic by the recognition of more exclusive assemblages also bearing this character, such as *Naviculina*, *Paresperella* and *Zygomycale*, which bear good synapomorphies each. Thus, like *Mycale (Mycale)* the present subgenus is one of convenience, with little phylogenetic basis.

The studied specimens mentioned above assigned to *Mycale contareni* presented some variation in the abundance of microscleres, which is considered here to be of minor importance, especially as artefacts from preparation cannot be completely ruled out. Nevertheless, there has also been detected some variation in the shape of the anisochelae-III. Both specimens of *Esperia foraminosa* (syntypes) possess anisochelae-III which are more straight-shafted, and with more obtuse head and foot, approaching closer an isochela condition. As intermediary forms were not seen, it appears to us that the suggested synonymy between *Esperia foraminosa* and *Mycale contarenii* (*sensu* Topsent, 1924) needs to be checked further.

SUBGENUS *ANOMOMYCALE* TOPSENT, 1924

Synonymy

Anomomycale Topsent, 1924: 116.

Type species

Desmacidon titubans Schmidt, 1870: 55 (by monotypy).

Definition

Mycale with anomochelae (palmate anisochelae with a slightly curved shaft on face view; and frontal ala of the foot considerably expanded, approaching or even surpassing the dimensions of the usually larger frontal ala of the head, contorted, sometimes with a serrated upper border).

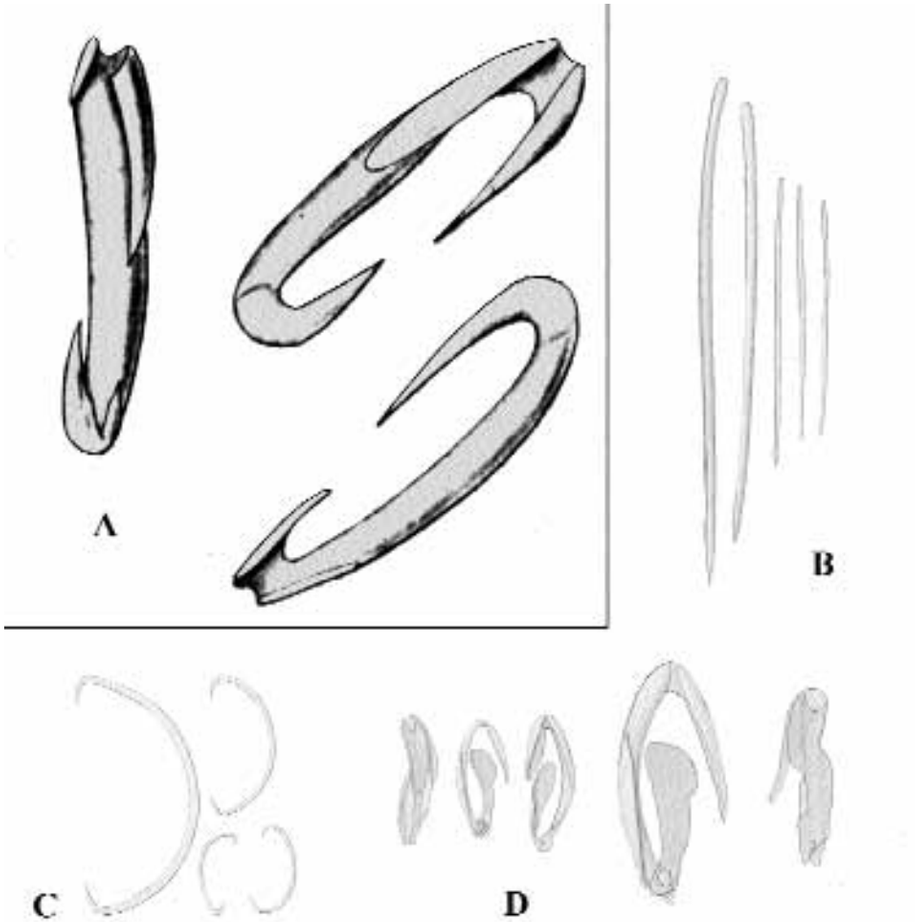

Fig. 4. *Mycale (Anomomycale) titubans* (Schmidt, 1870). A, drawing of anomochelae reproduced from Schmidt, 1870: pl. V fig. 18 (sizes see text). B–D, drawings of spicules reproduced from Lundbeck, 1905: pl. X fig. 3 (sizes see text). B, subtylostyles. C, sigmas. D, anomochelae.

Description of type species

Mycale (Anomomycale) titubans Schmidt, 1870 (Fig. 4A–D).

Synonymy. *Desmacidon titubans* Schmidt, 1870: 55, pl. V fig. 18; *Mycale titubans*; Lundbeck, 1905: 41, pl. X fig. 3; *Mycale (Anomomycale) titubans*; Topsent, 1924: 116, fig. 16.

Material examined. Lectotype (here designated): BMNH 1870.5.3.41 – slide made by Schmidt, labeled 'Florida 176 fms, nr. 79'. Lectotype designation is made for this material since no further material of the type species is known to exist (Desqueyroux-Faúndez & Stone, 1992: 41).

Description (based on Schmidt, 1870). Shapeless mass. Skeleton consisting of an irregular system of firm spicule tracts built from large thick megascleres making an axial structure from which issue at oblique angles thinner tracts made up of smaller megascleres. The megascleres are mycalostyles in two size classes. Microscleres anomochelae (Fig. 4A) of about 30 μm long and sigmas in a large size range, divisible into two sizes, larger ones up to 250 μm and smaller of ca. 30 μm (Schmidt says 3 μm, but that is clearly a misprint), the latter occurring in sigmodragmata. North Atlantic material described by Lundbeck (1905: 41) has mycalostyles (Fig. 4B) in two size categories, 590–900 μm and 320–400 μm long. Microscleres anomochelae (Fig. 4A, D) 24–52 μm long, and sigmas (Fig. 4C), 50–140 μm long. It is uncertain whether this material belongs to the same species as Schmidt's. This is a deep-water species recorded from the Atlantic as well as from the Southern Oceans.

Remarks. We examined further material belonging to this subgenus from Antarctica (USNM 43481, 43482, 43483, Antarctic), identified as *Anomomycale* sp. by V.M. Koltun. These Antarctic specimens have sigmas often 400 μm long. Likewise, material recorded by Boury-Esnault & Van Beveren, 1982 from Kerguelen has overall larger dimensions than the Atlantic material.

SUBGENUS *ARENOCHALINA* LENDENFELD, 1887

Synonymy

[*Acamas*] Duchassaing & Michelotti, 1864: 94 (preocc.) (not *Acamas* Montfort, 1808, Mollusca). *Arenochalina* Lendenfeld, 1887c: 821. *Acamasina* de Laubenfels, 1936a: 117. *Parisociella* Burton, 1952: 169. *Kerasemna* Pulitzer-Finali, 1981: 105.

Type species

Arenochalina mirabilis Lendenfeld, 1887c: 821 (by monotypy).

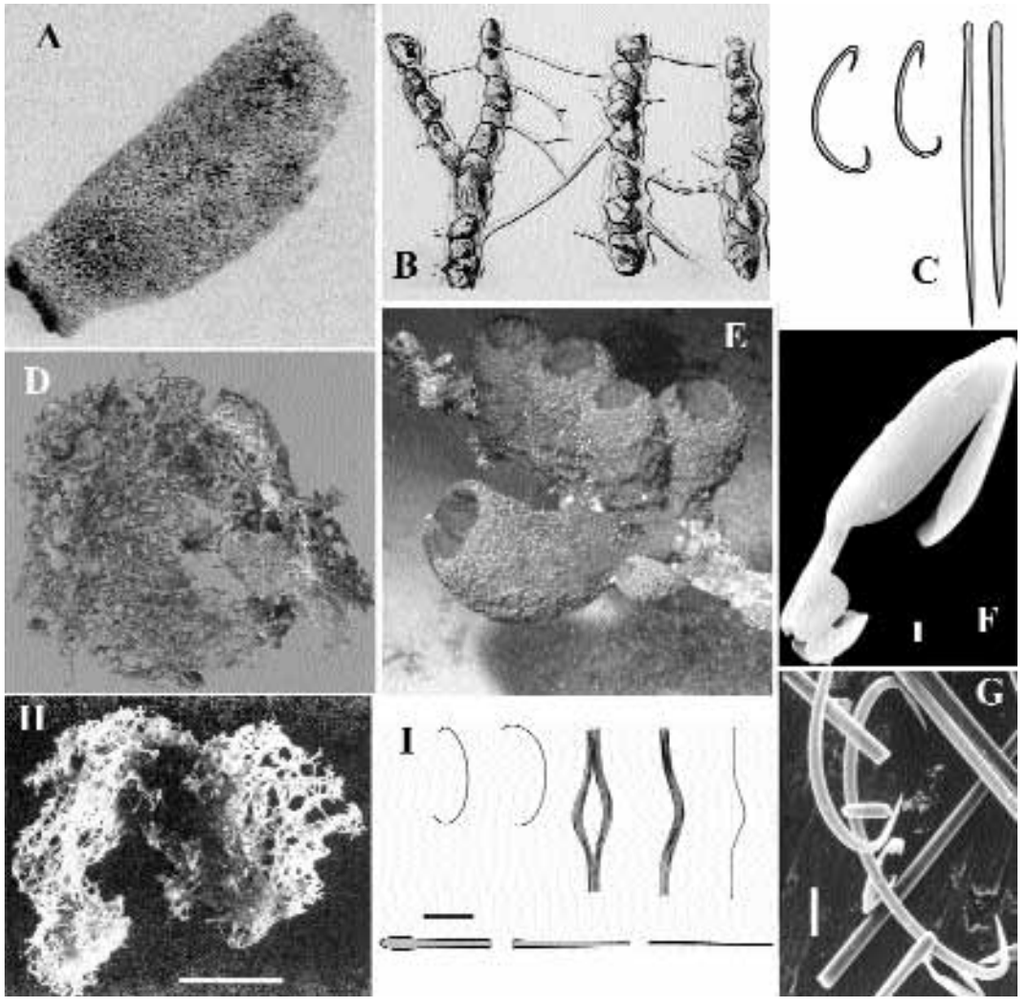

Fig. 5. Subgenus *Mycale (Arenochalina)*. A, photo of holotype of *Arenochalina mirabilis* reproduced from Lendenfeld, 1887c: pl. XXVI fig. 70 (size see text). B, drawing of cross section of skeleton reproduced from Lendenfeld, 1887c: pl. XXVII fig. 28 (size see text). C, drawing of spicules reproduced from Wiedenmayer, 1989: text-fig. 56 (sizes see text). D, holotype of *Acamas laxissima* Duchassaing & Michelotti, 1864 (type of [*Acamas*] and *Acamasina* (photo L.A. van der Laan) (size see text). E, in situ photo of Jamaican specimen of *Mycale (Arenochalina) laxissima* (photo H. Lehnert). F–G, SEM images of spicules of *M (A.) laxissima* (photos H. Lehnert). F, anisochela (scale bar 1 μm). G, sigmas (scale bar 10 μm). H–I. *Kerasemna tenuityla* Pulitzer-Finali, 1981. H. photo of holotype reproduced from Pulitzer-Finali, 1981: fig. 16 (scale bar 1 cm). I, drawing of spicules reproduced from Pulitzer-Finali, 1981: fig. 17 (scale bar 10 μm).

Definition

Mycale with choanosomal skeleton consisting of a stout, mostly quadrangular reticulation of spongin fibres cored by foreign material and/or filamentous algae and few proper megascleres; ectosomal skeleton absent; few scattered choanosomal megascleres and microscleres; megascleres mycalostyles of one category only; microscleres anisochelae of one category only, often absent or rare, and sigmas, occasionally absent or rare.

Previous reviews

Van Soest (1984b as *Mycale (Acamasina)*), Wiedenmayer (1989), Rützler (1990), Hajdu & Rützler (1998).

Description of type species

Mycale (Arenochalina) mirabilis Lendenfeld, 1887c (Fig. 5A–C).

Synonymy. *Arenochalina mirabilis* Lendenfeld, 1887c: 821, pls XXVI fig. 70, XXVII fig. 28; Pulitzer-Finali, 1981: 100, fig. 101; *Mycale (Arenochalina) mirabilis*; Wiedenmayer, 1989: 84, pl. 9 figs 8–10, text-figs 53–56. *Esperella spongiosa* Dendy, 1896: 16. *Mycale fistulata* Hentschel, 1911: 292.

Material examined. Holotype: BMNH 1886.8.27.587 – Torres Straits, North Australia.

Description (adapted from Wiedenmayer, 1989: 84). Variably lobate, massive, contorted, erect or repent, sometimes with pedicel. The holotype (Fig. 5A) is finger-shaped, 10 × 2.5 × 1.5 cm. Oscules conspicuous, apical on lobes, 4–8 mm in diameter in the holotype, other specimens often with much smaller, scattered ones. Surface conulose to bristly, with commonly blunt primary fibre tips piercing dermis. Some specimens with coarser, widely spaced fibres, with longer conules and tapering fibre tips. Other specimens fleshier, with thicker, more continuous dermis, surface then smoother. Softly spongy, very compressible. Much slime upon collecting. Dermis and choanosome mostly yellowish cream to beige in life, with some pink and greenish. Colour recorded as

beige, orange red, cream; in shallow waters off Heron Island (southern Great Barrier Reef) the species is conspicuously blue, with dark-red to purple-coloured fibres in life. Fibrous skeleton mostly regular. In the holotype meshes are rectangular and 400–800 μm wide; in other specimens mesh size may be around 1 mm. Primary fibres (Fig. 5B) usually cored by foreign debris. Meshwork in some specimens lax, less regular, primaries then with few foreign inclusions. Most fibres contain filamentous algae. Thickness of fibres in the holotype averages 50 μm. Megascleres mycalostyles (Fig. 5C), variably thick, mostly slender, in the holotype they measure 155–165 × 4.8–6 μm. These were not noted by Lendenfeld, who quotes oxeas of 20 × 4 μm as megascleres. Other records (Dendy, 1896; Wiedenmayer, 1989) give an overall size range of 155–268 × 1.9–9.5 μm. Microscleres anisochelae and sigmas, but they are very rare in the holotype, only a single palmate anisochela of 35 μm was found. Other descriptions (Dendy, 1896; Wiedenmayer, 1989) give an overall range of anisochelae of 19.6–30 μm. Sigmas (Fig. 5C), 54 μm in the holotype, with recorded range of 24–86 μm. Distribution. North, East and South East Coasts of Australia.

Remarks. Duchassaing & Michelotti, 1864: 95 erected a genus *Acamas* for type species (subsequent designation by de Laubenfels, 1936a: 117) *Acamas laxissima*. The genus name *Acamas* is preoccupied by *Acamas* Montfort, 1808 (Mollusca), which induced de Laubenfels (1936a: 117) to erect a new genus name *Acamasina* with the same species *A. laxissima* as the type. The lectotype (designation by Van Soest *et al*., 1983), Mus. Torino Por. 34 (with fragments deposited in BMNH, MNHN and USNM) was re-examined (Fig. 5D). It is a macerated mass of crooked-laminated fibres, similar to those of *A. mirabilis*, filled usually with algal strands and a core of subtylostyle megascleres. Some sigmas and anisochelae of similar size to *A. mirabilis* are present. Wiedenmayer (1977, as *Thorecta horrida*) described also foreign spicules inside the fibres. The amount and nature of coring with foreign material is here interpreted as species-specific and we follow here Wiedenmayer's (1989) suggestion that *Arenochalina* and *Acamasina* are synonyms. Full-grown specimens of *M. (A.) laxissima* assume the shape of a cluster of tubes (Fig. 5E), but retain the sparing presence of anisochelae (Fig. 5F) and sigmas (Fig. 5G).

The genus *Parisociella* Burton, 1952: 169 was erected for type species *Esperiopsis anomala* Ridley & Dendy, 1886: 341 (see also Ridley & Dendy, 1887: 84) collected near Honolulu and recorded from the Red Sea by Burton (1952), with type BMNH 1887.5.2.165, wet and slides (re-examined here). There are no published illustrations of this species. This is an irregularly ramose, digitate sponge, length 12.5 cm, diameter of the branches 0.6 cm. Colour light or dark grey-yellow, consistency soft, fibrous. The skeleton is a rectangularly meshed system of stout spongin fibres cored by relatively few styles/tylostyles of 250 × 5 μm, vestigial chelae scarce, minute, 10 μm. Ridley & Dendy (1887) call these chelae 'isochelae' whereas Burton (1952) refers to them as palmate anisochelae. They are apparently vestigial and may be difficult to classify as either type. The remaining features are in accordance with characters of *Arenochalina* and it is proposed here to synonymize *Parisociella* with the present subgenus.

The genus *Kerasemna* Pulitzer-Finali, 1981: 105 was erected for type species (by monotypy) *Kerasemna tenuityla* Pulitzer-Finali, 1981: 106, figs 16–17. The type specimen MSNG 46937 was re-examined. This is a clathrate, macerated lobate mass of stout spongin fibres (Fig. 5H) cored by subtylostyles (Fig. 5I) in the same size range as those of *Arenochalina mirabilis*. Microscleres are thin sigmas (Fig. 5I) and, according to Pulitzer-Finali, thin toxas, which were not observed by us. Instead we noticed many juvenile megascleres, which often take a sinuous shape and may have been mistaken for toxas. Pulitzer-Finali (1981) assigned his genus to Desmacellidae because of the lack of anisochelae. However, this is not unusual in species of *Mycale (Arenochalina)* and in view of all other compelling similarities we consider *Kerasemna* a junior synonym of *Arenochalina*.

SUBGENUS *CARMIA* GRAY, 1867

Synonymy

Carmia Gray, 1867a: 537. *Oxycarmia* de Laubenfels, 1954: 155.

Type species

Hymedesmia macilenta Bowerbank, 1866 (by subsequent monotypy).

Definition

Mycale with plumose or plumoreticulated choanosomal skeleton; ectosomal skeleton absent, or only a few scattered megascleres lying tangentially, as well as dispersed microscleres; megascleres are subtylostyles (mycalostyles) in one category only; microscleres are palmate anisochelae in one or more size-categories, the larger of which may form rosettes, as well as a variable complement of sigmas, toxas, raphides and micracanthoxeas.

Previous reviews

Van Soest (1984b), Bergquist & Fromont (1988), Carballo & Hajdu (1998).

Description of type species

Mycale (Carmia) macilenta (Bowerbank, 1866) (Fig. 6A–B).

Synonymy. *Hymeniacidon macilenta* Bowerbank, 1866: 176; *Carmia macilenta*; Gray, 1867a: 537; *Esperella macilenta*; Topsent, 1894: 8; *Mycale macilenta*; Stephens, 1912: 33. *Hymeniacidon floreum* Bowerbank, 1866: 190; Bowerbank, 1874b: pl. XXXIII figs 7–13; *Raphiodesma floreum*; Bowerbank, 1874b: 94. *Raphiodesma fallaciosum* Bowerbank, 1882: 163, pl. XVII figs 7–12. *Esperella hamata* Topsent, 1892b: xxi.

Material examined. Holotype (re-examined in Carballo & Hajdu, 2001): BMNH 1910.1.1.135 – dry, Norman collection. Other material. MNRJ 1013 – La Tortue, Roscoff, France. ZMA 5918 – Sherkin Island, Ireland. ZMA 7218 – Preguiça, São Nicolão, Cape Verde Islands.

Description (after Ackers et al., 1992). Encrusting, sheet or cushion, up to 10 cm across. Surface smooth. Oscules are clearly visible in living sponges, on erect tubes, but are not very numerous. Pores small, scattered over the surface. Alive, the sponge is pale yellow. When preserved it is yellow or brown. Consistency soft. Skeleton plumose; ascending multispicular tracts of subtylostyles (which do not divide or anastomose), ending in loose brushes at the surface, with single megascleres lying scattered in between. Spongin is minimal. There is no specialised ectosomal skeleton. The surface is supported by the widely spaced, terminal brushes of the main skeleton, with a few single megascleres (sometimes these

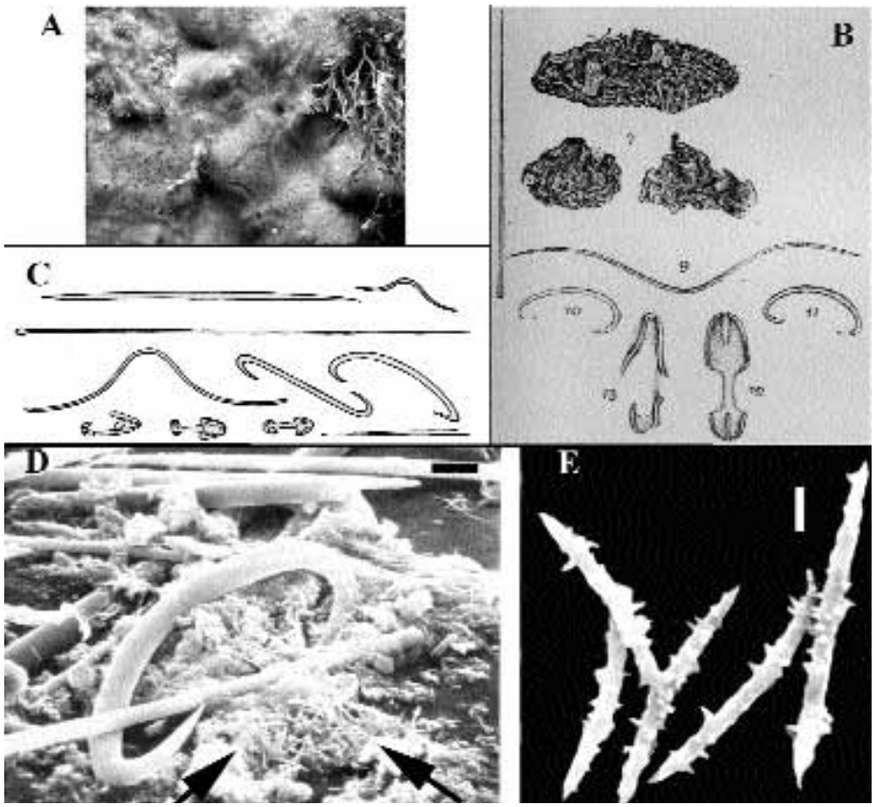

Fig. 6. Subgenus *Carmia*. A–B. *Mycale (Carmia) macilenta*. A, habit of specimen in situ (photo B. Picton). B, type specimens and spicules reproduced from Bowerbank (1874b: pl. XXXIII figs 7–13) (sizes see text). C, spicules of *Oxycarmia confundata* reproduced from de Laubenfels, 1954: fig. 101 (sizes see text). D–E, *Mycale (Carmia) micracanthoxea* Buizer & Van Soest, 1977. D, SEM overview of spicules, showing masses of micracanthoxeas (arrow) (scale bar 10 μm). E, SEM image of micracanthoxeas (scale bar 1 μm).

are absent altogether) scattered in the large interstices. The megascleres are generally straight-shafted, slightly fusiform, subtylostyles, with barely formed elliptical heads, between 200 and 300 μm long. Microscleres include palmate anisochelae of three sizes. The largest are grouped into rosettes in the ectosome, 33–59 μm. The middle size are solitary and scarce, 17–24 μm. Those of the smallest size are very abundant and widely dispersed throughout the body, 11–15 μm. They have a distinctive lower tooth which is very short and curved in towards the shaft. The sigmas fall into two size categories, 65–115 μm and 21–28 μm. Toxas are variable in length, 60–250 μm. Larvae are found between August and mid-October. Distribution and ecology. Common along the Channel coasts of the British Isles and France; Belgium; Atlantic coasts of France, Spain, Mediterranean, North Africa; littoral to 27 m, encrusting mainly on *Pecten* and *Chlamys*.

Remarks. The suggested synonymy of *Oxycarmia* de Laubenfels, 1954: 155 (type species (by monotypy) *O. confundata* de Laubenfels, 1954: 155, fig. 101; here reproduced in Fig. 6C), needs to be confirmed by re-examination of the holotype. The genus was founded on the presence of large numbers of oxeas of 685 × 15 μm, apparently arranged perpendicular to the surface and criss-cross in the choanosome. The remaining skeleton is typically that of *Carmia*; it consists of the usual bundles of thin subtylostyles of 225 × 1 μm, palmate anisochelae, 20 μm, two size categories of sigmas, 70 μm and 20 μm, toxas of 130–235 μm and trichodragmas of 60–120 μm long. The oxeas would seem to indicate its closest affinities to *Oxymycale* Hentschel, 1929 (see below), instead, but in that subgenus these replace the mycalostyles. In this case it is thought more likely that the oxeas may be foreign. *Carmia* was given a quite different emphasis by de Laubenfels (1936a: 118), who defined it as an independent genus similar to *Mycale* but differing from it through the possession of toxas.

A remarkable species of *Carmia* is *Mycale (Carmia) micracanthoxea* Buizer & Van Soest, 1977, based on its possession of a special microsclere type, the micracanthoxeas (Fig. 6D–E). These tiny microscleres were subsequently found in a *Mycale* of the Straits of Gibraltar (Carballo & Garcia-Gomez, 1994) assigned to the same species, *M. micracanthoxea*, but also in a NE Pacific species (*M. bamfieldensis* Reiswig & Kaiser, 1989, as *bamfieldense*) and a South American species (*M. escarlatei* Hajdu *et al*., 1995). The latter two species are assignable to subgenus *Aegogropila* on the basis of their reticulate tangential skeleton. Carballo & Hajdu (1998) described another two species with micracanthoxeas, viz. *M. (Aegogropila) lilianae* Carballo & Hajdu, 1998 and *M. (Carmia) urizae* Carballo & Hajdu, 1998.

The observation that at least one species of *Aegogropila* may lack the ectosomal skeleton (cf. Hajdu & Rüetzler, 1998), and that micracanthoxeas are shared by some species of *Carmia*-like sponges and some *Aegogropila*-like sponges, is a strong indication that *Carmia* is most likely polyphyletic. The assemblage is kept for convenience only, and should preferably not be given full generic status (as did Bergquist & Fromont, 1988), until a more comprehensive revision of its species is undertaken.

A further remarkable species of *Carmia* is an unnamed species forming a close symbiotic relationship with the octocoral *Tubipora musica*, reported by Van Soest & Verseveldt, 1987, from Indonesia. The normally semiglobular colonies of *Tubipora* are forced into clusters of tubes with apical vents by the cohabitation with the *Mycale* species.

SUBGENUS *GRAPELIA* GRAY, 1867

Synonymy

Grapelia Gray, 1867a: 534. *Pseudoesperia* Carter, 1886c: 455.

Type species

Grapelia australis Gray, 1867a: 534 (by monotypy).

Definition

Mycale with a confused tangential ectosomal skeleton, and with three categories of anisochelae one or more of which have unguiferate alae or alae reduced to a series of spines.

Remarks

The definition may be extended with the following details: anisochelae-I with a curved shaft in profile view, ratio height of the head/total height of the spicule <25%, alae of the foot projecting downward forming a pore, and rosettes built both by anisochelae-I and -II; mostly with unguiferate anisochelae-I, acanthose anisochelae-II, and basally-spurred anisochelae-III). Hajdu (1995) assigned one species apparently lacking unguiferate or spined chelae to *Grapelia*, but the only available material, a microscopic slide, prevented a clear determination of the fine structure of the alae.

Description of type species

Mycale (Grapelia) australis Gray, 1867a (Fig. 7A–C).

Synonymy. *Hymeniacidon* spec. Bowerbank, 1864: fig. 135. *Grapelia australis* Gray, 1867a: 534. *Esperia parasitica* Carter, 1885a: 108. *Pseudoesperia enigmatica* Carter, 1886c: 455. *Mycale parasitica var. arenosa* Hentschel, 1911: 311.

Material examined. Neotype (designated by Hajdu *et al*., 1995: 9): BMNH 1886.12.15.467 (=holotype of *Pseudoesperia enigmatica* Carter, 1886c). Other material. Dendy's (1896) material of *Esperella enigmatica*: NMV F 65700–65704. Hentschel's (1911) material of *Mycale parasitica var. arenosa*: ZMH 1666. Material of *M. (G.) parasitica var. arenosa* (*sensu* Shaw, 1927): BMNH 1925.11.1.729; ZMA 10712 – Tasmania, coll. M. Carpay.

Description (adapted from Hajdu, 1995). Specimens massive, lobose, or spherical, with or without conical protuberances (up to 5 cm high). Dimensions of the neotype (Fig. 7A) 15 × 15 × 10 cm. Surface mostly reticulated to the naked eye, occasionally wrinkled or conulose, easily removed. Oscula large, up to 7 mm in dry neotype, in a row, or on top of protuberances, sometimes not seen. Consistency elastic, soft to firm, dry specimen is hard. Colour of the specimens from Port Phillip Heads, dull orange-yellow or ochre-yellow (Dendy, 1896). Specimen from Stockyard Point beige to mustard-yellow in life. Ectosomal skeleton often strengthened by inclusion of variable amounts of sand grains, in a tight pack, spread, or in patches. Spicular density varies inversely. Architecture confused; sometimes reticulated, with megascleres not organized in well defined bundles. Projecting terminations of subectosomal brushes often well apparent, along with few tangentially displaced megascleres. Rosettes of anisochelae-I (ca. 100 μm in diameter) uncommon. Rosettes of anisochelae-II (ca. 50 μm in diameter) very rare, not seen in some specimens, to common in ZMA 10712. Apparent absence could be an artefact due to the dry (=contracted) state of the specimens and/or abundance of sand-grains, which renders (uncommon) spicular characters difficult to assess in thick-sections. Anisochelae-III may be common among subtylostyles. Choanosomal skeleton often bearing a remarkable number of sand grains, with megascleres merely filling-in interstices. Sand-cored fibres more than 1 mm wide in the subectosomal area, where they diverge in profusion to support the ectosomal layer. Fibres no more than 400 μm wide, where subtylostyles predominate. Spongin present, more apparent in sand-cored fibres. Overall pattern observed is plumo-reticulated, ascending fibres diverging and anastomosing frequently, spreading into brushes in the subectosomal area. One specimen from Tasmania (ZMA 10712) possesses a much more spicular, much less sandy skeleton, with fibres equally stout. Spongin scarce, which seems compensated by a spread pattern shown by subtylostyles in places where tracts intersect. Megascleres: Subtylostyles, straight, slightly sinuous, gently or markedly curved, slender with elliptic head or stout with oval head, sharp apex (228–382 × 3–12 × 3–15 μm, total length × width of head × width of shaft, 254–(291.5)–313 × 4–(5.4)–7 × 5–(6.1)–7 μm in neotype). Microscleres (Fig. 7C), anisochelae-I, shaft markedly curved on profile view, unguiferate head, lateral alae narrow and sharp, often longer than frontal alae, frontal alae bifid, height of the head 15–20% of total length; palmate foot, top border of frontal ala often wavy, or with a single, variably sharp projection, or small spines (29–61 × 4–12 μm, total height × height of head, 36–(41.2)–50 μm in neotype); anisochelae-II, shaft markedly curved on profile view, variably stout; acanthose head with crown of spines, alae not distinguishable, larger-primary (up to 8–9) and smaller-secondary spines (20–30 or more) often recognizable; palmate foot, height 25–35% of total length, spiny top border of the alae (15–22 μm, 15–(17.6)–20 μm in neotype); anisochelae-III, palmate, shaft gently curved on profile view, height of the head 30–50% of total length, lateral alae longer than frontal one; reduced foot with variably vestigial alae, basal spur-like projection (15–21 μm, 15–(17.0)–19 μm in neotype).

Remarks. *Grapelia* is one of the most easily diagnosed subgenera of *Mycale*. Extensive taxonomic remarks on *Grapelia* are provided by Hajdu (1995) and Hajdu *et al*. (1995). The subgenus has representatives in all tropical and warm-temperate regions of the world oceans.

By choosing the holotype of *Pseudoesperia enigmatica* Carter, 1886c as neotype of *Grapelia australis*, the genus *Pseudoesperia* Carter, 1886c was made an objective synonym of *Grapelia*. A recently described species from the Colombian Caribbean, *Mycale (Grapelia) unguifera* Hajdu *et al*., 1995, although differing greatly in habit (thin slimy crusts) exhibits strikingly similar anisochelae, both in shape and size (Fig. 7D–E). Differences are the slightly larger subtylostyles and the presence of sigmas in *M. (G.) unguifera*. Other species of *Grapelia* likewise are closely similar to the type species in spicular characters.

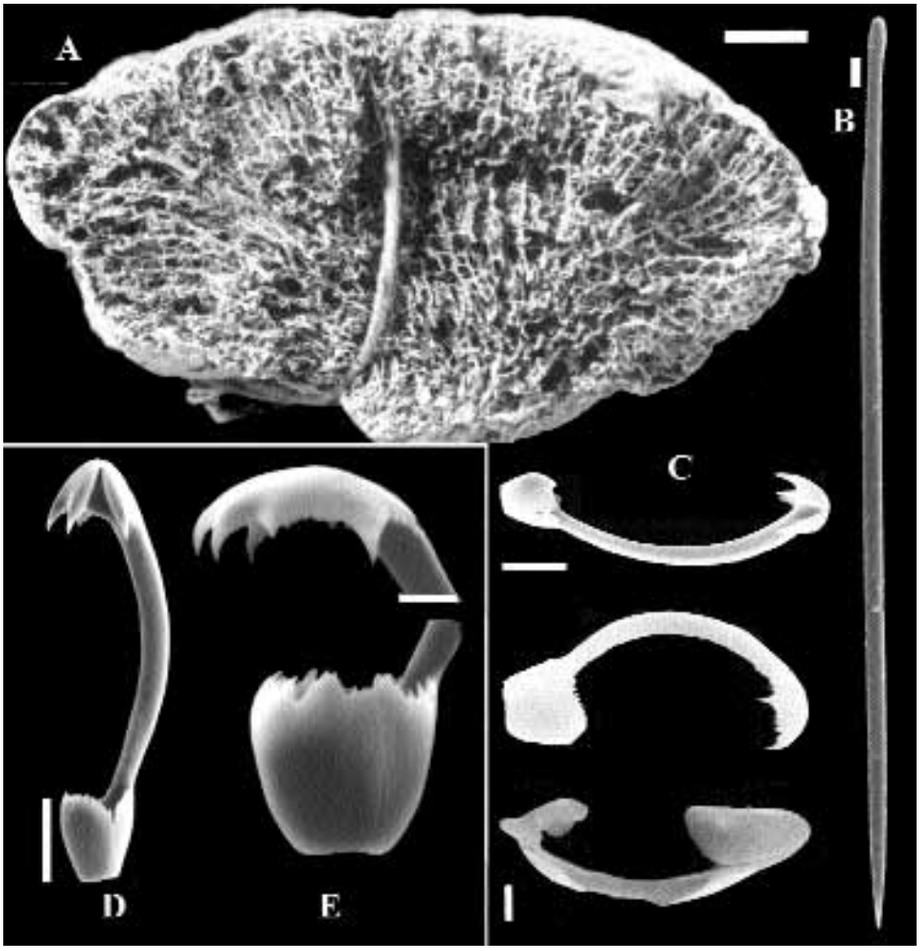

Fig. 7. Subgenus *Grapelia*. A–C, neotype of *Mycale (Grapelia) australis* (Gray, 1867a) =holotype specimen of *Esperia parasitica* Carter, 1885a, reproduced from Hajdu (1995; Figs 6.3, 6.9–12). A, habit photographed from damaged (under-)side to show skeletal structure (scale bar 1 cm). B, subtylostyle (scale bar 10 μm). C, anisochelae I (top, scale bar 10μm), II (middle) and III (bottom) (bottom scale bar 2 μm). D–E, *Mycale (Grapelia) unguifera*, anisochelae I (D, scale bar 10 μm) and II (E) (scale bar 2 μm), reproduced from Hajdu *et al*., 1995; figs 24, 27–28.

SUBGENUS *NAVICULINA* GRAY, 1867

Synonymy

Naviculina Gray, 1867a: 538.

Type species

Naviculina cliftoni Gray, 1867a: 538 (by monotypy).

Definition

Mycale with a reticulated tangential ectosomal skeleton and naviculichelae (complete or near fusion of both frontal alae, falx markedly expanded along the shaft, lateral alae of the head project backward and upward).

Previous review

Hajdu (1999).

Description of type species

Mycale (Naviculina) cliftoni Gray, 1867a (Fig. 8A–C).

Synonymy. *Hymedesmia* spec. Bowerbank, 1864: 252, fig. 152. *Naviculina cliftoni* Gray, 1867a: 538; Hooper & Wiedenmayer, 1994: 293; *Mycale (Naviculina) cliftoni*; Hajdu, 1999: 227, figs 1–2.

Material examined. Holotype: BMNH 1877.5.21.270 – slide, Freemantle, Western Australia.

Description (from Hajdu, 1999: 227). One single thick-section preparation remains. It contains a perfectly preserved fragment of the specimen's surface peel, from which it is possible to gather the whole series of spicules in *Mycale*. This peel contains an ectosomal skeleton characterized by a neat reticulation (Fig. 8A) of megasclere bundles (2–6 spicules across) or single megascleres, forming meshes which are mostly triangular (from 40×70 to 240×350 μm across), and inside which pores are clearly visible (60 μm across). Naviculichelae abound inside the meshes (Fig. 8B), especially around the bundles of megascleres. Megascleres mycalostyles, smooth, mostly straight, slightly

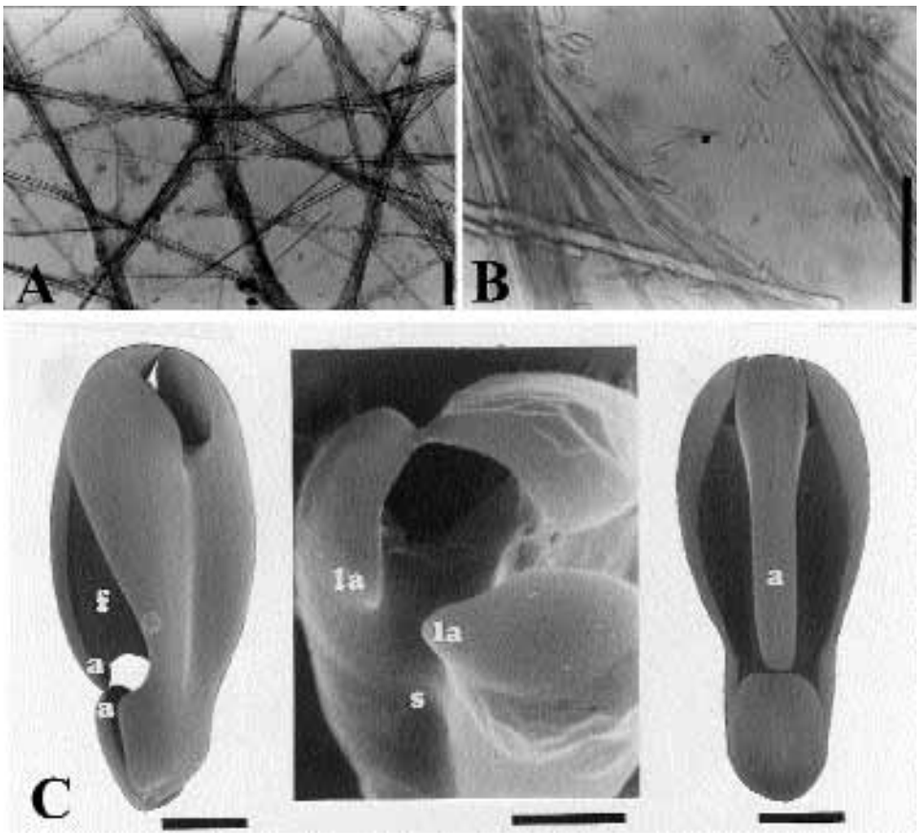

Fig. 8. *Mycale (Naviculina) cliftoni* (Gray, 1867a). A, tangential view of surface skeleton (scale bar 100 μm). B, detail to show spicule bundles and naviculichelae (scale bar 100 μm). C, naviculichelae photographed from various angles and details (scale bars 5 μm) (all reproduced from Hajdu, 1999: figs 1–2).

fusiform, with elliptic or oval heads, and points which taper more-or-less gradually, 330–(357.4)–388 (N = 20) × 4.8–8.4 (head, N = 10) × 6–9.6 μm (shaft, N = 10). Microscleres naviculichelae (Fig. 8C), head 60–70% the total spicule length, with narrowing or complete regression of the frontal alae of the head, which may touch the one of the foot, lateral alae of the head projecting backward and slightly upward, downward expansion of the upper falx along the shaft, 12–(17.3)–21.6 (N = 100). Sigma (proper ?), slender, smooth, sharp endings, 14.4 μm (N = 1).

Remarks. *Naviculina* is diagnosed in accordance with recent assessment of its characters (see Hajdu, 1999). Hooper & Wiedenmayer (1994: 293) employed *Naviculina* as a separate genus in Mycalidae and apparently emphasized different aspects of *Naviculina*. They made *Arenochalina* a junior synonym, but made no statements to support this. We fail to detect similarities or shared features between *Naviculina cliftoni* and *Arenochalina mirabilis* Lendenfeld, 1888 (see above). Hajdu (1999) proposed to assign all *Mycale* species with so-called 'cleistochelae' (in which the frontal alae touch and the shaft expands towards them), probably about half a dozen in total, to *Naviculina*, since these all share a reticulated ectosomal skeleton. Examples are *Mycale diversisigmata* Van Soest, 1984b (Fig. 9A–C) and *Mycale cleistochela flagellifera* Vacelet & Vasseur, 1971 (Fig. 9D–F). By this feature *Naviculina* belongs to the *Aegogropila*-like *Mycale*, but differs from that subgenus in having the peculiar chelae. The type species *M. (N.) cliftoni* lacks normal chelae, but *M. diversisigmata* and *M. cleistochela flagellifera* possess them, as well as a varied complement of sigmas (Fig. 9A–F). In order to avoid confusion with the isochelae of *Clathria cleistochela* Topsent, 1925, Hajdu (1999) proposed to name naviculichelae, the so-called 'cleistochelae' of *Mycale*.

SUBGENUS *OXYMYCALE* HENTSCHEL, 1929

Synonymy

Oxymycale Hentschel, 1929: 932.

Type species

Esperia intermedia Schmidt, 1874: 433 (by monotypy).

Definition

Mycale with exclusively oxeas as megascleres.

Previous review

Hentschel (1929).

Description of type species

Mycale (Oxymycale) intermedia (Schmidt, 1874) (Fig. 10A–B).

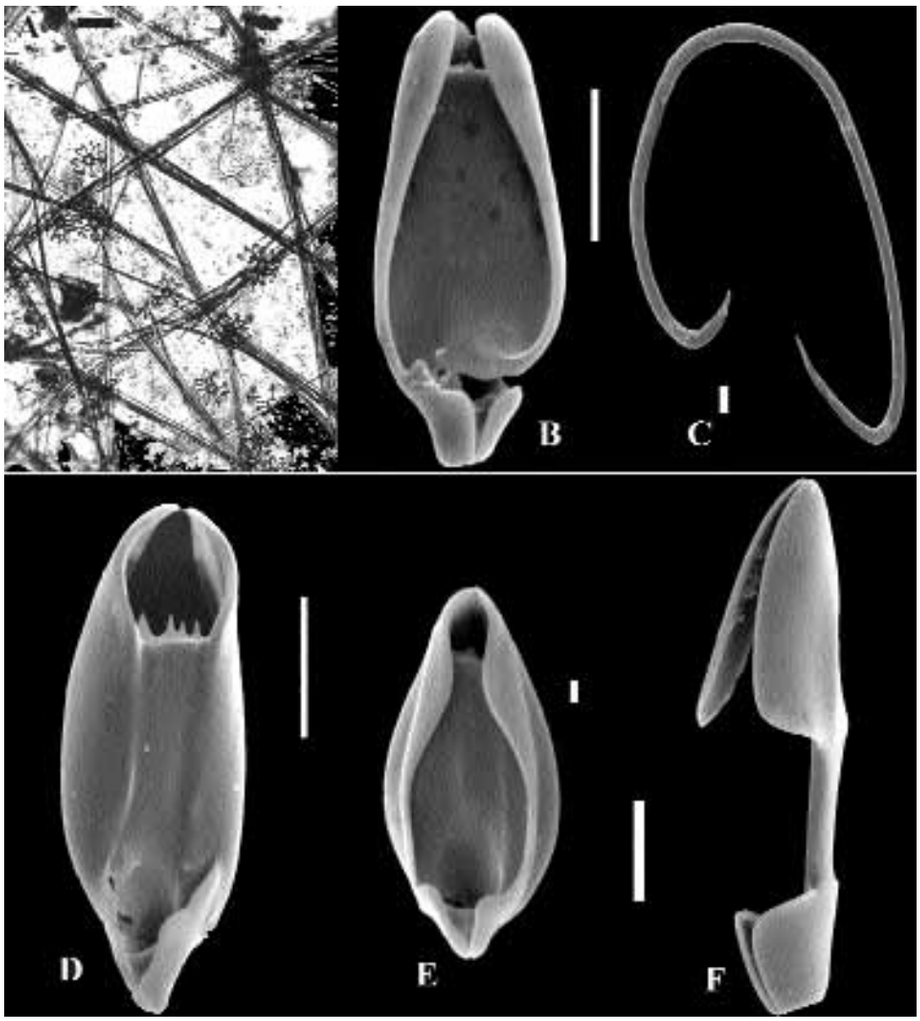

Fig. 9. *Mycale* with naviculichelae, assigned to *Naviculina*. A–C, *Mycale diversisigmata* Van Soest, 1984b from Curaçao, ZMA 4783. A, tangential view of reticulate ectosomal skeleton (scale bar 100 μm). B, SEM image of naviculichela (scale bar 10 μm). C, flagellated sigma (scale bar 10 μm). D–F, *Mycale cleistochela flagellifera* Vacelet & Vasseur, 1971, SEM images of spicules of ZMA 4597 from Indonesia. D, naviculichelate anisochela II (scale bar 10 μm). E, naviculichelate anisochela III (scale bar 1 μm). F, normal anisochela I (scale bar 10 μm).

Synonymy. *Esperia intermedia* Schmidt, 1874: 433, fig. 10; *Mycale intermedia*; Thiele, 1903b: 381, fig. 12; *Oxymycale intermedia*; Hentschel, 1929: 932. *Oxymycale wagini* Koltun, 1952: 127.

Material examined. None. Type material has not been recovered so far. Thiele (1903b) described a slide made by Weltner, which could be in ZMB.

Description (adapted from Thiele, 1903b: 381 and Koltun, 1959: 71). The type apparently was an insignificant fragment. Koltun describes the species as cushion-shaped, 'lumpy', up to 5 cm in height, often in the form of an elongated oval encrustation on the branches of hydroids, polychaete tubes, algae etc. There is apparently an ectosomal skeleton, but no details are recorded. The skeleton consists of weakly developed bundles of megascleres which are not cemented together. Megascleres curved, sharply pointed oxeas (Fig. 10B) of 300–550 × 10–16 μm. Microscleres anisochelae I (Fig. 10A–B), 50–74 μm, and II (Fig. 10B), 8–27 μm. No further microscleres are recorded. Distribution and ecology. E coast of Greenland (type locality), no depth known; subsequent specimens have been reported from the Barents Sea, Laptev Sea and the sea NW of Greenland; depth 17–325 m.

Remarks. Other species may be used to complete the diagnosis of this subgenus. We examined material of *Mycale (Oxymycale) acerata* Kirkpatrick, 1907a (BMNH 1933.6.10.128, South Georgia; MNRJ 1212, Chilean Antarctic Territory; MNRJ 1254, off Elephant Island, Antarctica). Some of the North Pacific species described by Sim *et al*. (1988) also appear to be true members of this subgenus. *Oxymycale* comprises massive or lobate sponges with skeleton of spicule bundles, which may be coarsely reticulate. Surface skeleton usually developed consisting of intercrossing spicule bundles. Megascleres exclusively sharp-pointed oxeas. Microscleres the usual complement of several size categories of anisochelae, sigmas may be present but are lacking in the type species. A couple of species from cold water mostly.

SUBGENUS *PARESPERELLA* DENDY, 1905

Synonymy

Paresperella Dendy, 1905: 162.

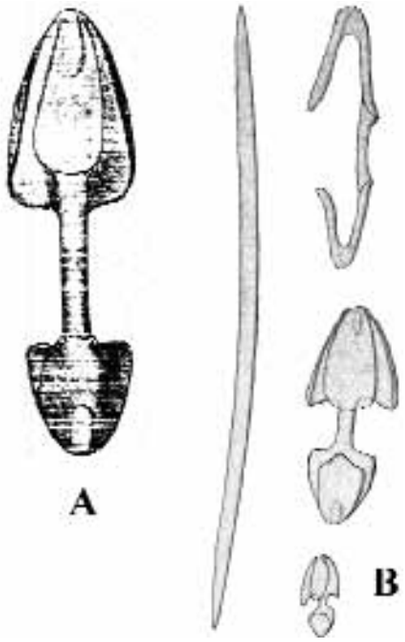

Fig. 10. *Mycale (Oxymycale) intermedia* (Schmidt, 1874). A, drawing of anisochela I reproduced from Schmidt, 1874: fig. 10 (size see text). B, spicules of the type reproduced from Thiele's (1903b: fig. 12) redescription (sizes see text).

Type species

Esperia serratohamata Carter, 1880b: 49 (by original designation).

Definition

Mycale with choanosomal skeleton plumose or plumoreticulated, made of multispicular tracts of megascleres; ectosomal skeleton often a tangential reticulation of megascleres; megascleres subtylostyles (mycalostyles) often of one size category only; microscleres are palmate anisochelae of one or more categories, the larger ones may form rosettes, serrated sigmas, and occasionally toxas.

Previous reviews

Dendy (1905), Hajdu & Rützler (1998).

Description of type species

Mycale (Paresperella) serratohamata (Carter, 1880b) (Fig. 11A).

Synonymy. *Esperia serratohamata* Carter, 1880b: 49, pl. V fig. 20; *Paresperella serratohamata*; Dendy, 1905: 162, pl. XI fig. 2.

Material examined. Type material: not in BMNH (Ms C. Valentine, pers. comm.). Other material. ZMA 1739 – *Paresperella* spec., Indonesia, Siboga Exped. stat. 318, 06°36′S 114°55′E, depth 88 m.

Description (from Carter, 1880b). The type apparently was a minute encrustation, 0.4 cm in horizontal expansion, on a calcareous alga. There was enough material to make a slide and still keep a dry piece (which was probably destroyed during the bombing of the Liverpool Free Museum). Spicules (Fig. 11A) consisting of fusiform subtylostyles, 175 × 6 μm; microscleres large robust serrated sigmas, 100 μm (thickness 6 μm), palmate anisochelae, occurring singly or in rosettes, 17 μm, toxas arranged in toxodragmas (not shown in Fig. 11A), 50 μm. Distribution and ecology. Gulf of Manaar, off Galle, Sri Lanka. If Dendy's subsequent record is correct, then it is a deep water species.

Remarks. Dendy's (1905) subsequent record of *Paresperella serratohamata* likewise was a minute specimen encrusting calcareous algae, so it may well be the usual shape of this species. Dendy (1905: 163) recorded a second species from Sri Lanka with a more elaborate shape allowing description of details of the skeletal structure. The ectosomal skeleton consists of tangential spicule tracts making a wide-meshed reticulation. The choanosomal skeleton consists of multispicular columns and many loose single spicules. These skeletal details match the ZMA Indonesia specimen studied here (Fig. 11B–F), so it is likely that all members of this subgenus have an *Aegogropila*-type of ectosomal skeleton. The ZMA specimen studied here, which bears an unpublished name given by M. Burton, is peculiar in having the pointed ends of many megascleres formed into an exotyle-like crown of spines or lobes (Fig. 11D), quite similar to those described for the subgenus *Sceptrospongia* (see below). Another comparable occurrence is the bifid termination in the megascleres of *M. (Paresperella) bidentata* (Dendy, 1905).

SUBGENUS *RHAPHIDOTECA* SAVILLE KENT, 1870

Synonymy

Rhaphidotheca Saville Kent, 1870a: 219. *Gomphostegia* Topsent, 1896b: 149. *Sceptrospongia* Dendy, 1926: 7.

Type species

Rhaphidotheca marshallhalli Saville Kent, 1870a: 219 (by monotypy).

Definition

Mycale with ectosomal skeleton pierced by club-shaped exotyles. Next to these there are the usual mycalostyles, anisochelae, sigmas and raphides.

Previous reviews

Thiele (1903b), Hajdu (1995).

Description of type species

Mycale (Rhaphidotheca) marshallhalli (Saville Kent, 1870a) (Fig. 12A–E).

Synonymy. *Rhaphidotheca marshallhalli* Saville Kent, 1870a: 219, pl. XV figs 1–7. *Esperia rhopalophora* Schmidt, 1875: 118, pl. I fig. 12; *Rhaphidotheca rhopalophora*; Thiele, 1903b: 383, fig. 14. *Rhaphidotheca affinis*; Carter, 1879c: 496.

Material examined. Holotype (not examined): BMNH 1882.4.27.5 – 1 slide labelled 'from type', from Saville Kent's type specimen. Presented by Dr J. Millar FRS. Cambridge House, Bethnal Green'. Other material. ZMA 5017, 5018 – from Bergen area, Norway, depth 100–600 m.

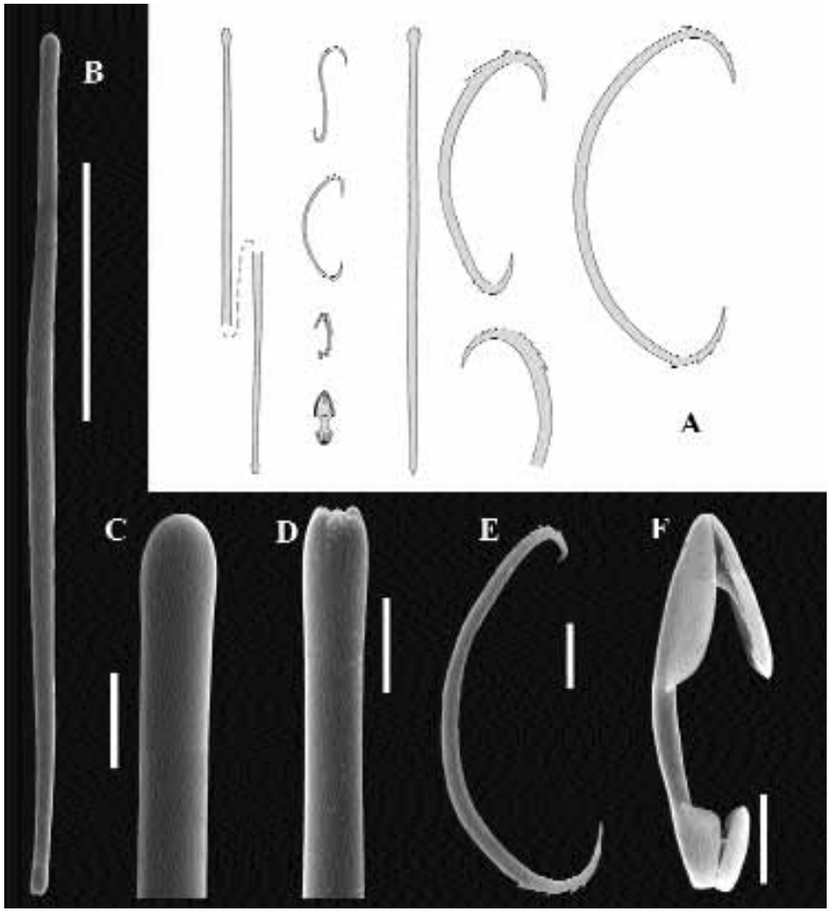

Fig. 11. Subgenus *Paresperella*. A. *Mycale (Paresperella) serratohamata* Carter, 1882a, drawing of spicules of the holotype reproduced from Dendy, 1922b: pl. XI fig. 2 (sizes see text). B–F, SEM images of spicules of Indonesian specimen of *Paresperella*, ZMA 1739. B–C, subtylostyle (scale bars: B, 100 μm; C, 10 μm). D, detail of crown of lobes of 'pointed' end of subtylostyles (scale bar 10 μm). E, serrated sigma (scale bar 10 μm). F. anisochela II (scale bar 10 μm).

Description (after Saville Kent, 1870a and Thiele, 1903b). Cushions or thick encrustations, 1–3 cm wide, 1 cm high. Surface hispid ('bristling') due to projecting exotyles. Colour beige. Consistency soft and fragile. Skeleton of strongly developed plumose spicule tracts, up to 150 μm in thickness, spreading out near the surface to carry a mass of tangential megascleres. Beyond that surface skeleton, individual exotyles protrude some distance. Megascleres styles (Fig. 12B), slightly constricted near the base ('mycalostyles'), fusiform shaft (hence they were termed 'acerate' by Saville Kent), 500–1000 × 16 μm; exotyles (Fig. 12A–D) with a large but variably shaped and sized elongated tyle the head of which is rugose (Fig. 12D), protruding beyond the surface of the sponge tyles outward, 800–1400 × 15–25 μm, tyles 35–55 μm. Microscleres palmate anisochelae (Fig. 12B, F) in two size categories, 75–90 μm (arranged in rosettes), and 25–40 μm; sigmas (Fig. 12B, not recorded by Saville Kent), 13–20 μm; trichodragmas (Fig. 12B, mistaken for 'acerates' by Saville Kent), 60–80 μm. Distribution and ecology. Off Spain and Portugal, W coast of Ireland, between Scotland and the Faroes, Norway; on rocks and dead corals in deep water, from 75 m downwards (type from 900 m).

Remarks. Several North Atlantic deep water species belonging to this subgenus have been described, due to the fact that the original descriptions were incomplete; these (cf. above synonymy) are here considered a single species.

The genus *Gomphostegia* Topsent, 1896b was erected for type species (by monotypy) *Gomphostegia loricata* Topsent, 1896b: 149, fig. 2, from 845 m near the Azores. A schizotype of the MOM holotype was studied (BMNH 1930.7.1.18). This species is very similar to *R. marshallhalli*, but the exotyles have a flattened, almost cup-shaped tyle (Fig. 13), which is not found in *marshallhalli*, although Hajdu (1995: 103) reports variability in this feature. In any case, the similarities are sufficiently great to consider *Gomphostegia* a clear junior synonym; this was already acknowledged by Topsent (1904b: 202, pl. XIV fig. 15) himself.

The genus *Sceptrospongia* Dendy, 1926: 6 (see also Burton, 1928a: 121) was erected for type species (by monotypy) *Sceptrospongia coronata* Dendy, 1926: 6, pl. I figs 1–8 (see Burton, 1928a: 121, text-figs 4–5, here reproduced in Fig. 14). The type material of the 'Investigator' collection from the Arabian Gulf and Andaman Sea is in the Indian Museum Calcutta, IM P308 and 309. These are subspherical sponges with an ectosomal skeleton of tangential intercrossing mycalostyles of 360 × 13 μm (Fig. 14A). Single exotyles (called 'stephanotyles' by the author), of similar size as the mycalostyles, are erected at right angles, in a regular loose palisade, heads embedded in the ectosomal skeleton and swollen ends

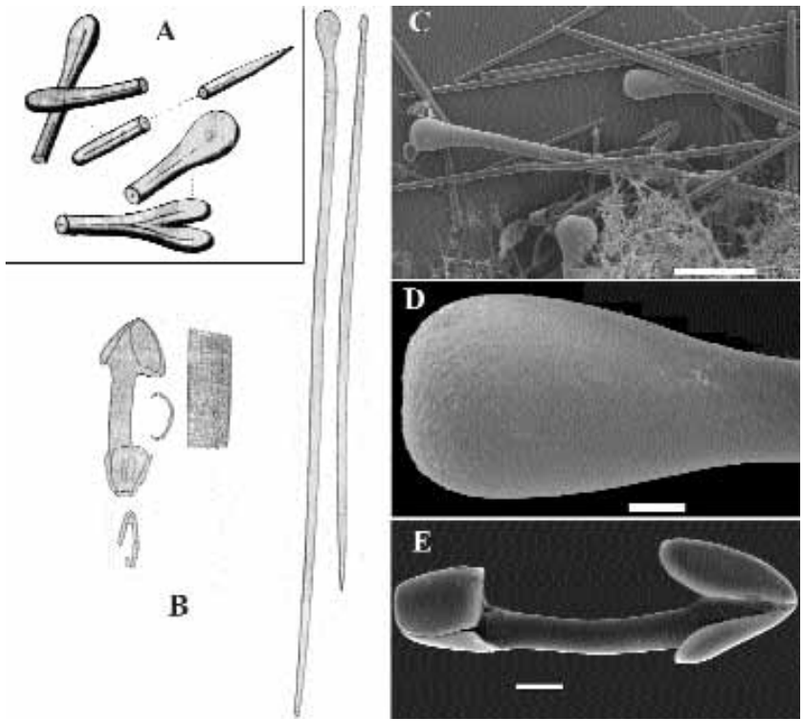

Fig. 12. *Mycale (Rhaphidotheca) marshallhalli* (Saville Kent, 1870a). A–B, *Esperia rhopalophora* Schmidt (1875) considered a junior synonym. A, drawing of exotyles reproduced from Schmidt, 1875: pl. I fig. 12 (size see text). B, drawing of spicules of *Esperia rhopalophora* reproduced from Thiele's (1903b: fig. 14) redescription of Schmidt's type. C–E, SEM images of spicules of ZMA 5017, from Bergen, Norway. C, overview of spicules (scale bar 100 μm). D, detail of exotyle (scale bar 10 μm). E, anisochela I (scale bar 10 μm).

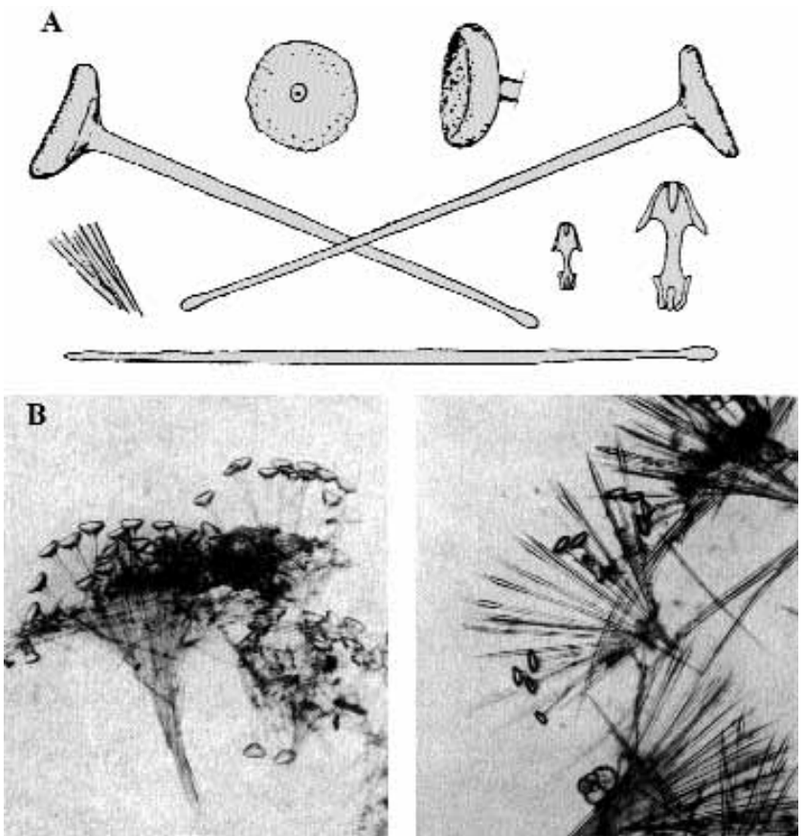

Fig. 13. *Mycale (Rhaphidotheca) loricata* (Topsent, 1896b as *Gomphostegia*). A, drawing of spicules reproduced from Topsent, 1896b: fig. 2 (size see text). B, photos of sections reproduced from Topsent (1928: pl. VII figs 11–12) (size see text).

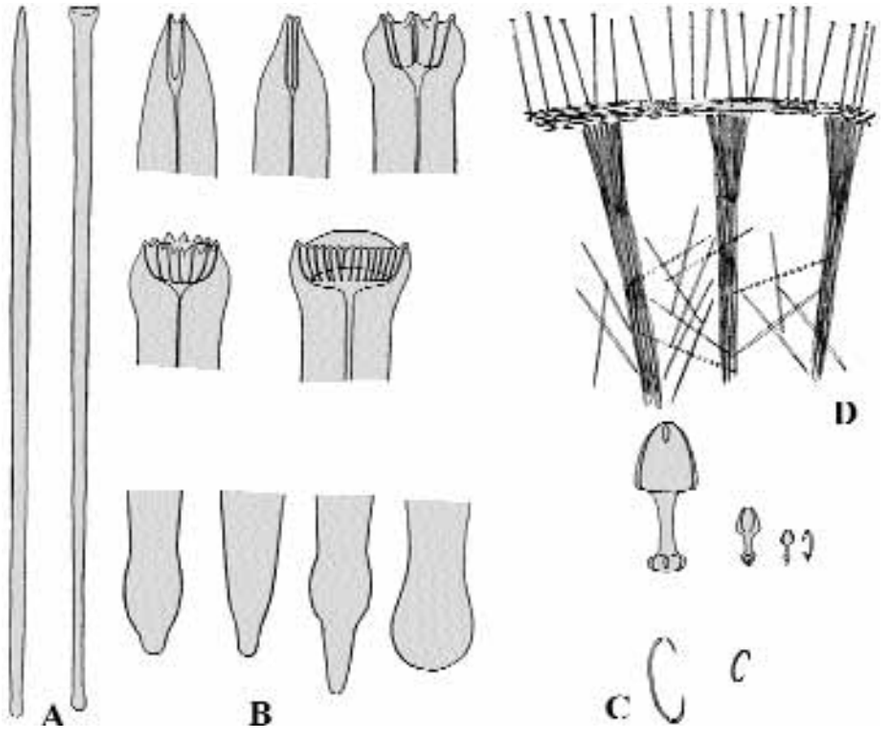

Fig. 14. *Mycale (Rhaphidotheca) coronata* (Dendy, 1926 as *Sceptrospongia*), drawings of spicules reproduced from Burton, 1928a: text-figs 4–5. A–B, megascleres consisting of normal subtylostyles and exotyles with a crown of spines. C, microscleres. D, cross section of peripheral skeleton showing arrangement of the exotyles (sizes see text).

projecting outwards (Fig. 14D). The swollen ends are peculiar in being flattened and crowned with a circle of spines (Fig. 14B), which are the result of proliferation of the axial canal. Microscleres (Fig. 14C) consist of the usual complement of anisochelae, I: 75 μm, II: 27 μm and III: 15 μm, sigmas I: 45 μm, II: 18 μm, and trichodragmata I: 45 × 9 μm, II: 15 × 9 μm. The exotyles of this species are perhaps peculiar, but not fundamentally different from those of *M. (R.) marshallhalli*, and accordingly *Sceptrospongia* is considered a junior synonym. We also found megascleres of similar shape in an unidentified specimen ZMA 1739, from Indonesia, possessing also serrated sigmas (see Fig. 11D). Since these megascleres do not occupy a perpendicular ectosomal position in the Indonesian specimen, they are not functional exotyles, although they are morphologically quite similar. By showing these overlapping characters it is demonstrated that subgenera *Paresperella* and *Rhaphidotheca* are likely to be artificial.

SUBGENUS *ZYGOMYCALE* TOPSENT, 1929

Synonymy

Zygomycale Topsent, 1930: 431.

Type species

Raphiodesma parishi Bowerbank, 1875b: 283 (by original designation).

Definition

Mycale with plumose or plumoreticulated choanosomal skeleton made of multispicular tracts of megascleres of one category only; ectosomal skeleton a dense tangential reticulation of megascleres, singly or in tracts; megascleres mycalostyles; microscleres palmate anisochelae in one or more size categories, the larger ones forming rosettes, small palmate isochelae, sigmas, raphides and toxas, the latter two often in bundles (dragmas).

Remarks

This subgenus is based on the possession of small palmate isochelae in addition to the usual anisochelae. Most recent authors considered these to be plesiomorphic and in view of the fact that other features are shared with *Aegogropila* synonymized it with that subgenus. Nevertheless, there are at least two species with small isochelae and thus it is convenient to distinguish these from *Aegogropila* proper.

Description of type species

Mycale (Zygomycale) parishi (Bowerbank, 1875b) (Fig. 15A–D).

Synonymy. *Raphiodesma parishi* Bowerbank, 1875b: 283; *Amphilectus parishi*; Vosmaer, 1880: 119; *Esperella parishi*; Ridley & Dendy, 1887: 65; *Zygomycale parishi*; Topsent, 1930: 431.

Material examined. Holotype (not examined): BMNH 1877.5.21.2113 (dry) and 4 slides 1877.5.21.1358 – labeled 'from type. Str. of Malacca' (Ms C. Valentine, pers. comm.). Bowerbank (1875b) noted there were 6 specimens in the original collection made by Commander Parish. Other material. ZMA 1606–1609 – all from Indonesia, Siboga collection. ZMA 9590 – Pulau Hantu, Singapore, coll. H. Moll.

Description (based on Bowerbank, 1875b). Thinly encrusting, up to 8 × 4.5 × 0.3 cm in the original type series; mostly

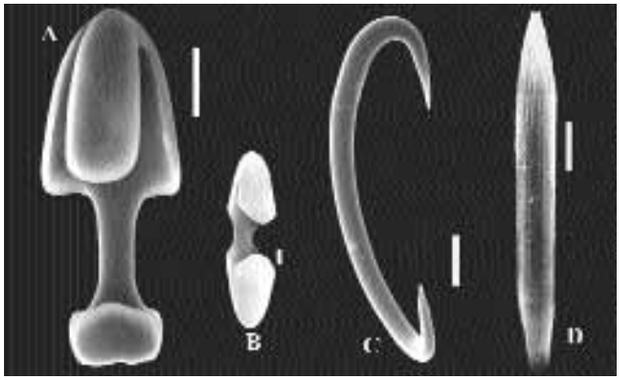

Fig. 15. *Mycale (Zygomycale) parishi* (Bowerbank, 1875b), SEM images of spicules made from ZMA 1606 from Indonesia. A, anisochela I (scale bar 10 μm). B, isochela (scale bar 1 μm). C, sigma I (scale bar 10 μm). D, trichodragma (scale bar 10 μm).

similar thin encrustations in reliably identified subsequent specimens. Colour grey-brown alive, cream-white in the dried state. Surface optically smooth, microscopically hispid due to projecting choanosomal spicule tracts. Consistency firm. Ectosomal skeleton consists of intercrossing tracts of megascleres. Choanosomal skeleton an irregular system of anastomosing spicule tracts, with little spongin. Megascleres subtylostyles (mycalostyles) up to 350 × 10 μm; microscleres anisochelae I (Fig. 15A), arranged in rosettes, 55 μm, anisochelae III, 17 μm, palmate isochelae (Fig. 15B), 12 μm, sigmas I (Fig. 15C), 82 μm, sigmas II, 17 μm, and toxas, 82 μm. Apparently there were also raphides in trichodragmas (Fig. 15D), 30–160 μm, in the type (subsequent observation by Ridley, 1884: 436), and in many subsequently recorded specimens. Distribution and ecology. Indo-West Pacific, widespread, also reported from the East Pacific; shallow-water.

Remarks. The species has also been reported from the West Indies and Brazil (e.g., de Laubenfels, 1956 and Hechtel, 1965), but this concerns *Mycale (Zygomycale) angulosa* (Duchassaing & Michelotti, 1864 as *Pandaros*), a blueish ramose sponge, clearly different from *M. (Z.) parishi* (see e.g., Van Soest, 1984b: 16).

PHLYCTAENOPORA TOPSENT, 1904

Synonymy

Phlyctaenopora Topsent, 1904b: 199. *Barbozia* Dendy, 1922b: 131.

Type species

Phlyctaenopora bitorquis Topsent, 1904b: 199 (by monotypy).

Definition

Mycalidae with a megasclere complement of oxeas and strongyles in combination with a microsclere complement which may include peculiar amphiaster-like spined microxeas and anisochelae, to which sigmas may be added.

Diagnosis

Massive, smooth or with erect fistules; confused compact choanosomal skeleton of smooth oxeas and scattered bundles of isolated strongyles; ectosomal skeleton a crust of smooth strongyles; microscleres include palmate anisochelae which may be basally spurred, sigmas and spiny rhabds, the latter two of which may be absent.

Scope

The genus is divided in two subgenera, *Phlyctaenopora (Phlyctaenopora)* and *Phlyctaenopora (Barbozia)*, both with two species from Atlantic and Pacific localities. The subgenera differ in the presence or absence of spined microxeas (dubbed 'oxydiscorhabds' by various authors).

Previous reviews

Lévi & Lévi (1983b), Van Soest & Stentoft (1988).

Key to subgenera of *Phlyctaenopora*

(1) Spined microxeas present ..... ***Barbozia***
Spined microxeas absent ..... ***Phlyctaenopora***

SUBGENUS *PHLYCTAENOPORA* TOPSENT, 1904

Synonymy

Phlyctaenopora Topsent, 1904b: 199.

Type species

Phlyctaenopora bitorquis Topsent, 1904b: 199 (by monotypy).

Definition

Phlyctaenopora lacking spined microxeas.

Description of type species

Phlyctaenopora (Phlyctaenopora) bitorquis Topsent, 1904b (Fig. 16A–B).

Synonymy. *Phlyctaenopora bitorquis* Topsent, 1904b: 199, pl. V fig. 24, pl. XIV fig. 18.

Material examined. Holotype: MOM (not seen) – 599 m off the Azores. Fragment examined: MNHN DT 1022 – microscopic slide made from the holotype.

Description (from Topsent, 1904b). Convex crust (Fig. 16A), torn at the underside (forcibly removed from the substratum), 4 × 5 × 0.6 cm. Cream-coloured. Surface shiny-smooth, bearing numerous unequal papillae of about 5 mm high. One large elevated oscule, with exhalant canals leading up to it. Ectosomal

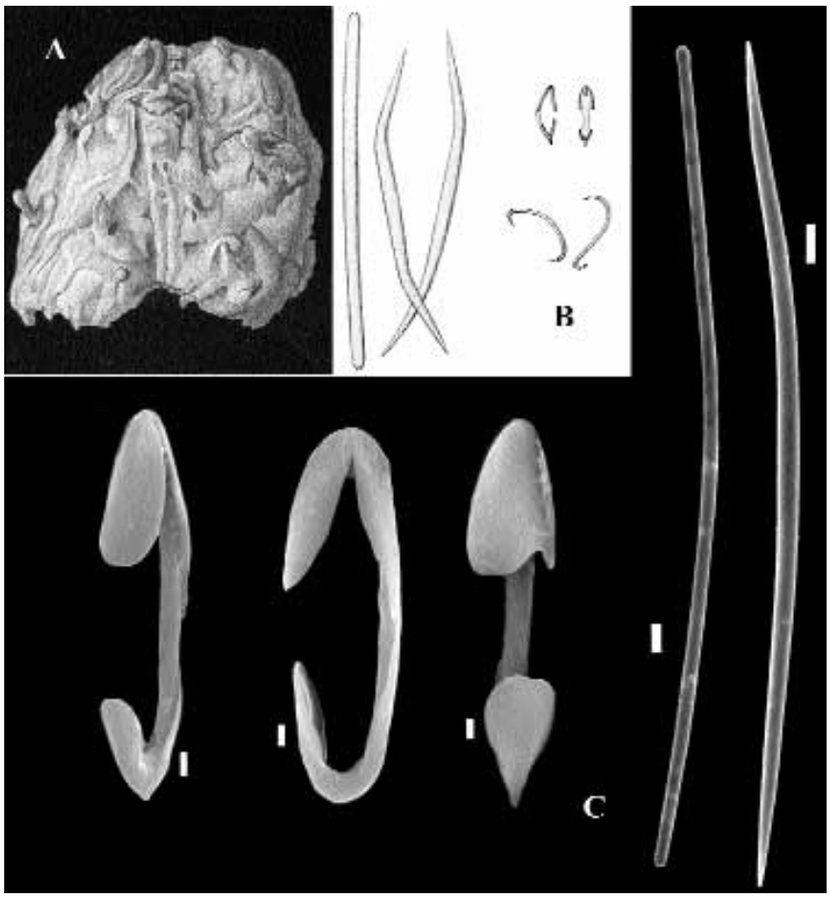

Fig. 16. Subgenus *Phlyctaenopora (Phlyctaenopora)*. A–B, *Phlyctaenopora (Phlyctaenopora) bitorquis* Topsent, 1904b. A, habit of holotype reproduced from Topsent, 1904b: pl. V fig. 24 (size see text). B, spicules of holotype reproduced from Topsent, 1904b: pl. XIV fig. 18 (sizes see text). C, *Phlyctaenopoa (Phlyctaenopora) halichondrioides* Van Soest & Stentoft, 1988, SEM images of spicules of holotype (scale bars: anisochelae, 1 μm; megascleres, 10 μm).

crust firm, 250–300 μm in thicknes, made up of a tightly massed tangential spicule skeleton. Most ectosomal spicules are oxeas. Choanosomal skeleton largely confused, with strongyles tending to form ill-defined tracts, whereas oxeas are intercrossing at all angles. In the walls of the papillae the strongyles are arranged parallel to the axis of the papilla. Megascleres (Fig. 16B) oxeas, angularly curved twice, 300 × 10–12 μm; strongyles slightly curved, slightly thinner at the rounded ends, 360 × 12 μm. Microscleres (Fig. 16B) anisochelae, usually spurred, 20–27 μm; sigmas, abundant, 38 μm. Distribution and ecology. Azores, deep water.

Remarks. The habit and ectosomal reinforcement indicate that the sponge probably lives buried in the sediment with the papillae and oscules raised above it. A second species of this subgenus, *P. (P.) halichondrioides* was described by Van Soest & Stentoft (1988: 119, fig. 59), from Barbados. It differs from *P. (P.) bitorquis* in lacking sigmas and having smaller sized oxeas (Fig. 16C).

SUBGENUS *BARBOZIA* DENDY, 1922

Synonymy

Barbozia Dendy, 1922b: 132.

Type species

Barbozia primitiva Dendy, 1922b: 132 (by subsequent designation herein).

Definition

Phlyctaenopora with spined microxeas.

Description of type species

Barbozia primitiva Dendy, 1922b (Fig. 17A).

Synonymy. *Barbozia primitiva* Dendy, 1922b: 132, pl. VIII fig. 9, pl. 18 fig. 1.

Material examined. None. Holotype (not examined): BMNH 1921.11.7.111 – wet & slide, 'Sealark' Expedition, Indian Ocean RN.LXXXII.1.

Description (from Dendy, 1922b). Hemispherical sponge of 7.5 cm diameter and a height of 4.5 cm, with truncated fistules of 4 mm on the upper surface. Oscules likewise conically elevated. The ectosomal skeleton is a thick crust (up to 350 μm in thickness) of mostly tangentially arranged megascleres. This is carried by the peripheral columns of spicules of the choanosomal skeleton, which consists of an irregular system of very thick spicule tracts.

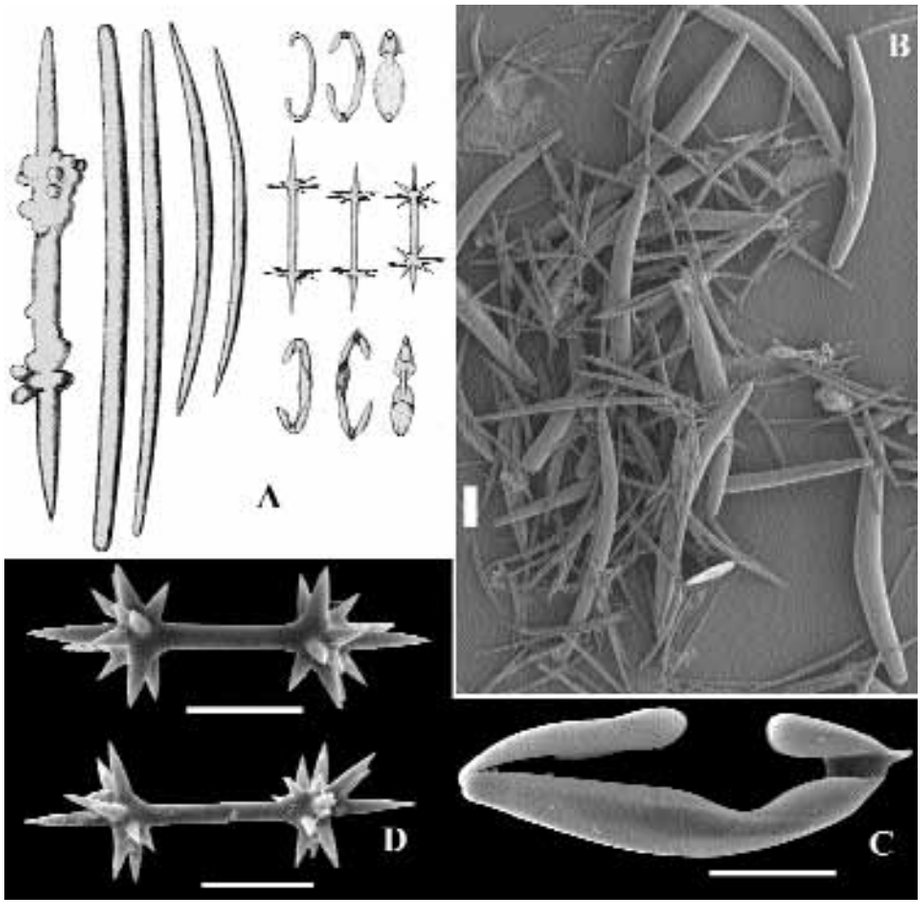

Fig. 17. Subgenus *Phlyctaenopora (Barbozia)*. A, *Phlyctaenopora (Barbozia) primitiva* (Dendy, 1922b), drawing of spicules reproduced from Dendy's pl. 18 fig. 1 (sizes see text). B–D, *Phlyctaenopora (Barbozia) bocagei* Lévi & Lévi (1983b), SEM images of spicules of the type. B, SEM overview of megascleres (scale bar 100 μm). C, chela (scale bar 10 μm), D, amphiaster-like microxeas (scale bar 10 μm).

Megascleres (Fig. 17A), strongyles, slightly curved, 350 × 13 μm, oxeas, often biangulate, some with proliferations along the shaft, 266 × 10 μm. Microscleres (Fig. 17A), palmate anisochelae, spurred, numerous, 20 μm; amphiaster-like microxeas, 36–57 μm. Distribution and ecology. Amirante Islands, W Indian Ocean, dredged at a depth of 40–153 m.

Remarks. Lévi & Lévi (1983b: 955) described *Phlyctaenopora bocagei* from New Caledonia (here illustrated in Fig. 17B–D), differing from *P. (Barbozia) primitiva* in the lack of true strongyles, instead of which there are blunt-ended styles, and in possessing two size categories of oxeas (Fig. 17B), the larger of which is 1050 × 80 μm. Subsequently, Lévi (1993: 58) reported the same species again from New Caledonia, with one of the specimens possessing 'serpentiform' oxeas. Lévi (1993) suggested that *Phlyctaenopora* and *Barbozia* are synonyms, which is here partially confirmed by recognizing both at the subgenus level.

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