

Family Halichondriidae Gray, 1867

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Halichondriidae Gray (Demospongiae, Halichondrida) contains 11 valid genera (of 47 nominal genera) and probably around 180 species. Halichondriidae are widely distributed and live mainly in shallow coastal waters but a few have also been recorded from 500 m depth. The major morphological characters distinguishing this group from related sponges is the thoroughly confused arrangement of the choanosomal megascleres (oxeas, styles and derivatives thereof) usually coupled with a differentiated ectosomal skeleton, consisting of a tangential or concentrated arrangement of spicules mostly smaller sized than those of the choanosome. All spicules are smooth. Except for raphides (trichodragmas) there are no microscleres.

Keywords: Porifera; Demospongiae; Halichondrida; Halichondriidae; *Amorphinopsis*; *Axinyssa*; *Ciocalapata*; *Ciocalypta*; *Epipolasis*; *Halichondria* (*Halichondria*); *Halichondria* (*Eumastia*); *Hymeniacion*; *Laminospongia*; *Spongosorites*; *Topsentia*; *Vosmaeria*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Halichondriidae Gray, 1867a: 518. Halichondridae Vosmaer, 1887: 335. Stylotellinae Lendenfeld, 1888: 185. Ciocalyptidae Hentschel, 1923: 408. Spongosoritidae Topsent, 1928c: 35. 24. Halichondriidae de Laubenfels, 1936a: 133. Hymeniacionidae de Laubenfels, 1936a: 136.

Definition

Halichondrida with a confused arrangement of smooth oxeas and/or styles in the choanosome and usually an organized special ectosomal skeleton consisting of tangentially arranged or densely confusedly arranged crust of oxeas and/or styles of sizes similar to or smaller than those of the choanosome.

Diagnosis

Halichondrida with oxeotes and stylotes, i.e., spicules taking variously the shape of oxeas, strongly oxeas, oxeas with blunt ends, and true styles, occasionally with slightly expanded tyle near one of the endings or more central. Spicules invariably smooth, often elongate fusiform, but also equidiametrical over much of their length, pointed apices normally elongated and gradually narrowing to a sharp point, usually slightly curved, occasionally straight or rarely crooked or doubly angulated. Individual genera and species may be recognizable on possessing either exclusively distinct oxeas or styles, but there is a strong tendency for species and genera to have these extreme shapes intergraded with intermediate forms. Spicules are typically of a wide size range, with not infrequently distinct size categories without a clear overlap; if that is the case, then the smaller sizes are often concentrated at the surface. There is a distinct ectosomal skeletal differentiation with either a tangential crust of intercrossing spicules, which is often easily detached due to underlying subdermal spaces, or a confusedly paratangential or palisade-like arrangement, in which case the surface skeleton is not easily detached and comes off in 'flakes'. The choanosomal skeleton is characterized as confused, with many

of the megascleres seemingly randomly strewn and often with remnants of main spicule tracts and vague interconnecting spicules or tracts. Binding spongin is rare. Choanosomal organic parts show a distinct lack of collagenous matter in many genera. Spicule density may be quite high, and in combination often with large sizes of the megascleres the consistency may become hard and brittle. However, Halichondriidae with smaller spicules are often quite compressible and easily damaged due to lack of skeletal organization. Some genera are 'fleshy' due to relatively high collagen content and low spicule density. Halichondriidae contain 47 nominal genera, 11 of which are considered valid. In one genus *Halichondria*, two valid subgenera are recognized.

Scope

Genera considered valid members of the family: *Amorphinopsis* Carter, 1887, *Axinyssa* Lendenfeld, 1897c, *Ciocalapata* de Laubenfels, 1936a, *Ciocalypta* Bowerbank, 1863, *Epipolasis* de Laubenfels, 1936a, *Halichondria* Fleming, 1828, with subgenera *Halichondria* and *Eumastia*, *Hymeniacion* Bowerbank, 1862, *Laminospongia* Pulitzer-Finali, 1983, *Spongosorites* Topsent, 1896a, *Topsentia* Berg, 1889, *Vosmaeria* Fristedt, 1885.

TAXONOMIC HISTORY AND BIOLOGY

History

This family was established by Gray (1867a) in his overview of sponge taxa known in his time. The type genus *Halichondria* was used in a very general sense by him and his contemporaries, so a wide variety of sponges was included in the family along with the type species *Spongia panicea* Pallas, 1766. Subsequently, the contents of the family were restricted by various authors, often in a widely diverging manner. To date, no consensus has become apparent mainly due to the poorly differentiated characters of the type species of *Halichondria* and its assumed allies. The assignment of genera employed here is again slightly different from the latest revision of the family by Van Soest *et al.*, 1990. Molecular data (Alvarez *et al.*, 2000a; Chombard *et al.*, 1999) indicate we may

expect in future further instability of the family contents. It is beyond the scope of this chapter to enumerate all the genera at one time or another assigned by various authors under this family name, but concepts of the family content used by a few of the major authors are here briefly summarized. Gray, 1867a assigned Halichondriidae (as Halichondriadae) to his subsection Spiculospingiae, order Leiospongia (sponge spicules of one kind only). He defined the family as having a skeleton of 'fusiform' or 'pin-shaped' spicules variously fasciculated together or rarely united by a small quantity of spongin. Genera assigned were subdivided into two groups, one with fusiform or 'needle-like' spicules, perhaps considered as Halichondriidae *sensu stricto*: *Reniera*, *Halichondria*, *Dictyocylindrus*, *Aaptos*, *Halisarca*, *Lieberkuehnia*, *Tedania*, *Oroidea*, *Prianos*, *Schmidtia*, *Crella*, *Sophax*, *Epicles*, *Eurypon*, *Bubaris*, *Ciocalypta*, *Rasalia*, *Adocia*, *Philotia*, and the other with 'pin-shaped' spicules: *Abila*, *Suberites*, *Ficulina*, *Raspalia*, *Raphiophora*, *Spinularia*, *Antho*, and *Pitalia*. The family as a whole is a heterogeneous mixture of Haplosclerida, Poecilosclerida and Hadromerida, but included in the Halichondriidae *s.s.* were *Halichondria* and *Ciocalypta*. Schmidt, 1870 did not employ the genus name *Halichondria*, nor a family Halichondriidae, but he maintained a strict distinction between sponges with oxea- or strongyle-shape (family Renierinae) and those with 'Stecknadeln' (family Suberitidinae). *Halichondria panicea* was considered a member of his genus *Amorphina* and thus *Halichondria* by inference was assigned to Renierinae. In this group he distinguished the following genera: *Reniera*, *Amorphina*, *Pellina*, *Eumastia*, *Foliolina*, *Tedania*, *Schmidtia*, *Plicatella*, and *Auletta*. This is a mixture of modern Halichondrida and Haplosclerida, with *Tedania* as the odd Poecilosclerida. Topsent (1928c) assigned most of the modern Halichondriidae (*Halichondria*, *Ciocalypta*, *Coelocalypta*, *Topsentia*, *Hymeniacion*) to a widely employed family Axinellidae, of which he did not present a formal definition. One notable exception is *Spongosorites*, which is assigned to Hadromerida along with *Aponastra* and *Alloscleria* as a family of its own, Spongosoritidae. In his comments he indicates nevertheless a close, presumably ancestral, relationship with *Topsentia* and *Halichondria*. Of all the older authors, Topsent's classification is probably closest to what is now perceived as a natural classification: close kinship of Axinellidae, Desmoxyidae, Dictyonellidae and Halichondriidae. Topsent also believed this group to stem from hadromerid stock, a notion which may still prove to be of value considering some results of molecular studies. De Laubenfels (1936a: 126–139) employed an order Halichondrina with five families, viz., Axinellidae, Halichondriidae, Semisuberitidae, Hymeniacionidae and Monanthidae. Halichondriidae were defined as having a spiculation of smooth oxeas, a special dermal skeleton and lacking a conspicuously isodictyal reticulation. The family was assumed to contain the genera *Halichondria*, *Apatospongia*, *Ciocalypta*, *Ciocalapata*, *Dactylella* (now considered a genus of Dictyonellidae), *Halichondriella*, *Leucophloeus*, *Trachyopsilla*, and *Trachyopsis*. He assigned *Coelocalypta* as junior synonym to *Apatospongia*, and *Halispongia* and *Spuma* to *Halichondria*. The family Hymeniacionidae de Laubenfels, 1932 was defined by having a fleshy ectosome not profusely echinated by spicules which are usually tangentially placed, with the choanosomal structure plumose to confused and spiculation of oxeas, styles or strongyles, or combinations of these. The family was erected for *Hymeniacion* (with assigned synonyms *Amorphilla* and *Stylohalina*), *Acanthella* (with assigned synonym *Acanthellina*; now considered a genus of Dictyonellidae), *Adreissa* (now considered a junior synonym of

Phakellia), *Batzella* (now considered a valid genus of Chondropsidae), *Collocalypta* (now considered a junior synonym of the Halichondriidae genus *Ciocalypta*), *Densa* (now considered a junior synonym of the haplosclerid genus *Xestospongia*), *Ectyobatzella* (now considered a junior synonym of the Poecilosclerid genus *Monanchora*), *Hoplochalina* (now considered a junior synonym of *Scopalina*), *Oxeostilon*, *Prianos* (now considered a junior synonym of *Haliclona*), *Rhaphidostyla*, *Viles*, *Dictyonella* (now considered a valid genus of Dictyonellidae), and *Hemimycale* (now considered a valid genus of Hymedesmiidae). Lévi (1973: 614) considered Halichondrida to be unrelated to Axinellidae and assigned both to two different subclasses (Axinellidae to Tetractinomorpha, Halichondrida to Ceractinomorpha), on the basis of the possession of brooded larvae in *Halichondria* and *Hymeniacion*. He considered the Halichondrida an artificial group, based on negative characters (absence of microscleres and organization of the skeleton), with two families, Halichondriidae (predominantly with oxeas) and Hymeniacionidae (predominantly with styles). He admits this division was not absolute as Hymeniacionidae might sometimes possess oxeas and Halichondriidae might have styles. Of the genera assigned to his Halichondriidae, *Rhaphisia* is now considered to belong to Haplosclerida. Most of the genera assigned by him to Hymeniacionidae – with the exception of the type genus *Hymeniacion* – are here considered members of the family Dictyonellidae based on the absence of an ectosomal skeleton. Bergquist (1978) and Hartman (1982) essentially followed Lévi's scheme of the two families Halichondriidae and Hymeniacionidae, but only few genera were assigned. Hartman mentions *Rhaphisia* as an example of Halichondriidae but this is now considered a *Haliclona* (see chapter on Chalinidae by de Weerd), and *Ulosa* as an example of Hymeniacionidae, but this is now considered a member of Esperioptidae (see chapter on Mycalidae by Van Soest & Hajdu). Van Soest *et al.* (1990) in a revision of the types of all genera reestablished the close relationship of Halichondriidae and Axinellidae. This scheme was followed substantially by Hooper *et al.* (1997). Conversely, Hooper & Bergquist (1992) and Carballo *et al.* (1996) proposed slight rearrangements of the contents of Halichondriidae and Axinellidae described by Van Soest *et al.* (1990), but these latter proposals are not followed here because they merely represented a reinterpretation of characters of only a few selected genera, and did not explore the consequences of the proposed changes for the overall generic contents of the family. No new data or observations were offered to support the proposals. For the present revision we revisited all the types and additional specimens and could add considerable further material based on visits to the museums of Paris (LSF grant to DE) and London (LSF grant to RVS). This revision supports most of the conclusions of Van Soest *et al.* (1999), but the following changes are proposed: (1) genera with spined microxeas (*Myrmekioderma* and *Didiscus*) are reassigned to Desmoxyidae following e.g., Hooper & Lévi (1993b), Van Soest & Lehnert (1997), (see chapter on Desmoxyidae by Hooper), whereas Van Soest *et al.* (1990), followed by Hooper *et al.* (1997) retained it within Halichondriidae. (2) *Nailondria* de Laubenfels, 1954 is considered a junior synonym of *Amorphinopsis* (instead of a junior synonym of *Hymeniacion*). (3) *Ciocalapata* de Laubenfels, 1936a is revived as a valid genus (previously considered a junior synonym of *Halichondria*). (4) *Collocalypta* Dendy, 1905 is proposed to be a junior synonym of *Ciocalypta* Bowerbank, 1861 (previously considered a valid genus). (5) *Coelocalypta* Topsent, 1927b is proposed to be a junior synonym of *Ciocalypta* Bowerbank, 1861 (previously

considered a junior synonym of *Topsentia*). (6) *Eumastia* Schmidt, 1870 is proposed to be a valid subgenus of *Halichondria* instead of a mere junior synonym. (7) *Pellina* Schmidt, 1870 is proposed to be a junior synonym of *Halichondria* (*Halichondria*). (8) *Laminospongia* Pulitzer-Finali, 1983 is revived as a valid genus (previously considered a junior synonym of *Topsentia*). (9) *Alloscleria* Topsent, 1927b is removed from the family (previously considered a junior synonym of *Topsentia*) and assigned to Desmoxyidae (see Hooper's chapter on Desmoxyidae). (10) *Oxeostilon* Ferrer Hernandez, 1922 is considered a junior synonym of *Spongosorites* (rather than of *Topsentia*). (11) *Oxeosarcodea* de Laubenfels, 1954, previously not considered as a member of Halichondriidae, is included in the synonymy of *Axinyssa*. (12) *Stylinos* Topsent, 1891a, previously not considered as a member of Halichondriidae, is now included in the synonymy of *Hymeniacion*. (13) *Vosmaeria* Fristedt, 1885, previously not considered as a member of Halichondriidae is now included as a valid genus. (14) *Astromimus* Lendenfeld, 1897a, previously not considered as a member of Halichondriidae, is included in the synonymy of *Axinyssa*. (15) *Petromica* Topsent, 1898b (with junior synonym *Monanthus* Kirkpatrick, 1903a) is returned to 'Lithistida' (family Desmanthidae) because of the complement of monocrepid desmas. For this volume the 'Lithistida' are maintained as a polyphyletic higher taxon, awaiting molecular and other characters for assignment to existing orders and families of the Demospongiae. We predict that *Petromica* will eventually be found a valid member of Halichondrida, probably of Halichondriidae.

Arguments for all these proposed changes are given at the appropriate locations below.

Finally, the genus *Cryptax* de Laubenfels, 1954: 214, was erected for type species *Cryptax orygni* de Laubenfels, 1954: 214, fig. 146 (by monotypy) from Majuro Atoll, S Pacific. It was found occupying cavities of up to 4 mm diameter within corals which in turn were covered by a *Spirastrella*. Spiculation was reported to consist exclusively of fusiform tylostyles with rounded endings ('tylostrongyles'), $600\text{--}700 \times 2\text{--}12 \mu\text{m}$. De Laubenfels (1954) was not sure that it was actually boring and assigned it to Suberitidae, but it is also possible it might be a clionaid lacking spiraster microscleres (see chapter on Clionaidae). However, re-examination of the holotype (USNM 22966), consisting of a spicule slide prepared by de Laubenfels, and some coral crumbs from which was peeled bits of the sponge coating them (prepared and examined courtesy of Klaus Rützler), revealed only long oxeas with rounded tips, or with one tip rounded and the other one sharply pointed, or with a few thinner ones both pointed. There was no sign of a tylote modification reported by de Laubenfels (he may have mixed in the *Spirastrella*, but there were no tylostyles in his slide preparation either). The oxeas are $650\text{--}850 \times 5\text{--}12 \mu\text{m}$, agreeing with sizes of 'tylostrongyles' reported by de Laubenfels, with some bent at the center, some off-center, some slightly, some sharply. The peel shows criss-cross orientation parallel to the substrate, indicating possible affinities with the halichondriids, but owing to the discrepancies between the original description and the holotype, the genus *Cryptax* and its type species are declared here *incertae sedis* and unassignable to any known halichondriid.

KEY TO GENERA

- (1) Trichodragmas (hair-like spicules packed in wispy bundles) present *Epipolasis*
 No trichodragmas 2

Taxonomic remarks

The choanosomal (lack of) arrangement of the megascleres in a confused manner constitutes the major synapomorphy for the family, although it is difficult to describe or illustrate this in precise terms or images. There is a lack of visible binding spongin and bundles or tracts of megascleres are not interconnected, and often lack a definite orientation. Vague tracts are found in many halichondrids, especially in the subectosomal region, where they tend to fan out and carry a special tangential skeleton or become part of it. The surface skeletal arrangement is a major discriminating character at the genus level. Some members of the family lack a definite surface skeleton, and the surface is often somewhat conulose due to projecting choanosomal tracts. Such sponges clearly bridge the gap with families Axinellidae and Dictyonellidae, which likewise lack a surface skeleton. Family membership of *Axinyssa* has been contested (e.g., by Hooper & Bergquist, 1992, but later reincluded in the family by Hooper *et al.*, 1997), and it is proposed here to leave it in Halichondriidae based on the confused arrangement of the skeleton of most members of *Axinyssa*. Several Halichondriidae species show a burrowing habit, typically with conical fistules sticking up from the sandy substrate from a massive basis buried underneath the sand. This habit does not agree fully with details of skeletal architecture and spicule shapes and sizes. Moreover, overall similar habits are also found in definitely unrelated orders and families (e.g., Poecilosclerida: Coelosphaeridae, Haplosclerida: Phloeodictyidae). In the classification of the genera of this family such a rather distinctive habit thus will be assumed to have been developed in several genera independently, notably in *Ciocalypta* and *Topsentia*. Only in the case of *Ciocalypta* this habit is part of the discriminating characters for the genus in combination with a particular arrangement of the skeleton and transparency of the fistules. The exclusive occurrence of oxeas is so widespread in the family that it is not a discriminating character for genera; however, the exclusive occurrence of styles of a particular shape (faint tyle near the blunt end) is one of the synapomorphies for the genus *Hymeniacion*. Size categories of a single megascleres or of styles and oxeas combined in the same sponge may constitute additional generic synapomorphies. Secondary metabolites reported from members of this family are abundant and often quite characteristic. Van Soest & Braekman (1999) record isocyanoterpenes (shared with Axinellidae and Dictyonellidae), sulfated sterols and macrolides (both shared with unrelated sponges). Various species of one genus, *Spongosorites*, produce characteristic topsentins.

Biology

Two genera (*Halichondria* and *Hymeniacion*) are viviparous, and their larvae are wholly ciliated. Those of *Halichondria* have a characteristic tuft of long cilia at the posterior pole (Wapstra & Van Soest, 1987). Larvae of other genera so far remain unknown, these may be likely oviparous. Halichondriidae occur in all areas of the world oceans, from the intertidal down to continental slope habitats. Many species are specialists of sedimented habitats.

- (2) Shape a massive base from which rise long conical semitransparent fistules strengthened by an internal spicule axis and extra-axial spicule bundles at right angles to the surface *Ciocalypa*
 Various shapes, may include short fistules or papillae, but no large semitransparent conical fistules 3
- (3) Shape a thin blade, with scattered small oscules *Laminospongia*
 No thin blade 4
- (4) Finely conulose surface, no special surface skeleton, choanosome collagenous, spicule density relatively low *Axinyssa*
 Surface smooth, surface strengthened by special tangential or paratangential skeleton, spongin not visibly present 5
- (5) Spicules exclusively short styles (many with a subterminal swelling) *Hymeniacion*
 Spicules oxeas, or a mixture of oxeas and (sub/tylo-)styles 6
- (6) Surface skeleton easily detachable without taking away part of the choanosome 7
 Surface skeleton only detachable as flakes with part of the choanosome attached 10
- (7) Spicules exclusively oxeas in a wide size range *Halichondria*
 Spicules oxeas and (sub/tylo-)styles 8
- (8) Stylote spicules have a distinct tyle and are in fact (sub-)tylostyles *Vosmaeria*
 True styles, without tyle 9
- (9) Styles only in a small size category (200–400 µm), next to larger oxeas *Amorphinopsis*
 Styles only in a large size category (>800 µm), next to smaller and larger oxeas *Ciocalapata*
- (10) Consistency stony hard, crumbly, surface rough to the touch, choanosome a dense mass of single spicules *Topsentia*
 Consistency dense but compressible, surface smooth, choanosome with tracts of spicules; spicules often angular or doubly bent; most species show aerophobic reaction when collected *Spongosorites*

AMORPHINOPSIS CARTER, 1887

Synonymy

Amorphinopsis Carter, 1887: 77. *Prostylissa* Topsent, 1925b: 208. *Tumata* de Laubenfels, 1936a: 77. *Nailondria* de Laubenfels, 1954: 182.

Type species

Amorphinopsis excavans Carter, 1887: 77 (by monotypy).

Definition

Halichondriidae with ectosomal tangential skeleton of intercrossing megascleres single or in tracts. Spicules differentiated into larger oxeas and derived forms, smaller oxeas and small styles, concentrated at the surface. Choanosomal skeleton confused with high spicular density and little or no spongin.

Diagnosis

Encrusting to massive, occasionally with irregular branches issuing from a massive base. Firm, hard, but fragile sponges. Ectosomal skeleton tangential, with intercrossing larger oxeas and derived forms, often forming intercrossing bundles. Small oxeas and styles concentrated at the surface. Choanosomal skeleton confused, with irregular tracts of large oxeas. Approximately ten species, mostly from the Indian Ocean and West Pacific, but the genus is also recorded from Brazil (Muricy *et al.*, 1991).

Previous reviews

Annandale (1915b), Van Soest *et al.* (1990), Hooper *et al.* (1997).

Description of type species

Amorphinopsis excavans Carter, 1887 (Fig. 1A–D).

Synonymy. *Amorphinopsis excavans* Carter, 1887: 77, pl. V figs 12–15; Annandale, 1915b: 467, figs 4–5; Hooper *et al.*, 1997: 25, figs 15–16.

Material examined. Holotype (slide): BMNH 1981.10.14.3 – a slide of Carter's type specimen labelled "Mergui Archipelago, fr. Anderson, 28 Dec. 82, don. by Linn. Soc. via Wyn. Wheeler, 1981, '3', '74', sponge surface excavating sp". The holotype (not examined), is apparently located in the Indian Museum, Calcutta IM 6597/7 ZEV (cf. Annandale, 1915b).

Description. This is based on Annandale's (1915b) redescription of a presumed fragment of the type in the Indian Museum Calcutta. The BMNH slide which is – based on the text on the label – quite certainly made from the type is a dissociated spicule mount. Shape of the type specimen is encrusting on a piece of dead coral, size 6 × 3 cm. The surface is smooth but displays some conules in the dry state (Fig. 1C). No visible openings. The dry sponge is firm. Annandale's subsequent specimens were digitate (Fig. 1D). Ectosomal skeleton (Fig. 1A) tangential, consisting of thick intercrossing tracts of larger oxeas, the spaces in between filled with loose oxeas of all sizes as well as small styles. Choanosomal skeleton confused, with thick but vaguely delimited tracts and many loose individual spicules. Megascleres predominantly oxeas in a large size variation and small styles concentrated at the surface (Fig. 1B). Long oxeas, fat, fusiform, curved, 520–700 × 18–20 µm. Shorter oxeas, fusiform, 200–375 × 8–12 µm. Styles (Fig. 1B), thickest in the middle, blunt end tapering 120 × 6 µm. Distribution and ecology. Mergui Archipelago, off the coast of Birma, coral reefs.

Remarks. Carter's description is misleading in its emphasis on a star-shaped surface appearance (very probably caused by desiccation) and 'excavating' habit. Annandale's notes make it clear that the surface is merely slightly conulose due to the ectosome being lifted by thicker choanosomal tracts. The excavating habit is simulated by penetration of portions of the sponge into bore holes made by and subsequently left vacant by clionids. *Amorphinopsis excavans* is not really an excavating sponge and subsequent records of it as such (e.g., Thomas, 1973) must be considered erroneous. New material of the type species was described from NW Australia by Hooper *et al.* (1997).

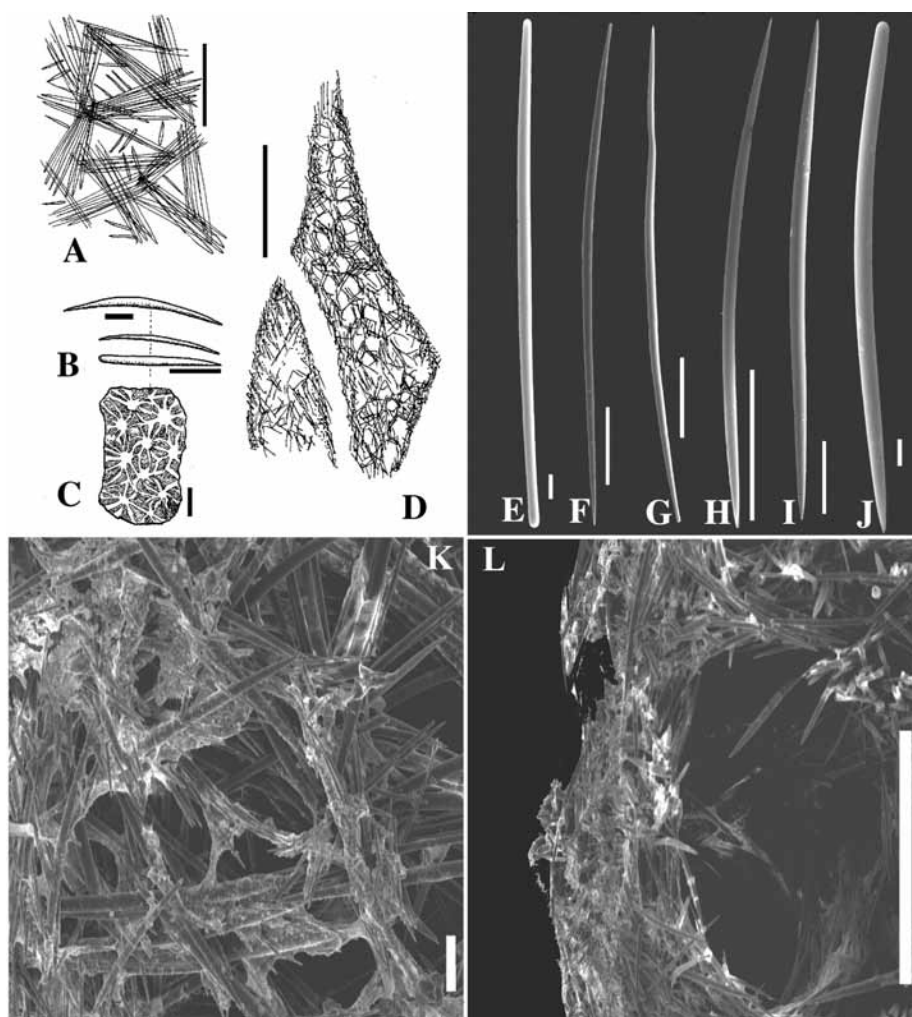


Fig. 1. A–D, *Amorphinopsis excavans* Carter, 1887. A, tangential view of the surface skeleton. B, large megascleres and small styles (scale 100 μm). C, habit of the holotype reproduced from Carter, 1887 (scale 1 mm). D, longitudinal section through a digitiform process reproduced from Annandale, 1915. E–G, *Amorphinopsis maza* (de Laubenfels, 1954 as *Nailondria*) spicules (scales: E–F, 100 μm ; G, 10 μm). H–L, *Amorphinopsis siamensis* (Topsent, 1925b as *Prostylissa*). H–J, spicules (scales: H–I, 100 μm ; J, 10 μm). K, surface view (scale 100 μm). L, view on peripheral skeleton (scale 1000 μm).

The genus *Prostylissa* Topsent (1925b: 208) was erected for *Prostylissa siamensis* Topsent, 1925b: 208, figs 1–2 (by monotypy). The holotype of *Prostylissa siamensis*, MNHN DT. 3453, labeled “Golfe de Siam, A. Krempff leg. 1921”, was reexamined. It consists of a mass of irregular thick anastomosing branches, up to 2 cm in diameter. The surface is smooth but slightly conulose, and it displays a few large openings, presumably oscules. Consistency firm but friable. The ectosomal skeleton (Fig. 1K) is detachable due to some limited subectosomal vestibules (Fig. 1L). It consists of tangentially intercrossing tracts of large oxeas surrounded by small spicules, which are strewn irregularly or appear to ‘echinate’ the tracts. Choanosomal skeleton consisting of thick tracts of large oxeas and many single spicules. Smaller spicules concentrated at the periphery. Large fusiform oxeas (Fig. 1H), $980\text{--}1050 \times 40 \mu\text{m}$. Smaller similar oxeas (Fig. 1I), $300 \times 7\text{--}10 \mu\text{m}$. Small fusiform styles (Fig. 1J), $180\text{--}300 \times 7\text{--}10 \mu\text{m}$. These features make it clear that *Prostylissa* is a synonym of *Amorphinopsis*. *Prostylissa siamensis* was considered an elaborate specimen of the same species *A. excavans* by Van Soest *et al.* (1990) for example, but in view of the clearly larger and thicker size of the large oxea category in combination with the ramose habit, it is likely that

it is a related but separate species, to be named *Amorphinopsis siamensis*.

The genus *Tumata* de Laubenfels, 1936a: 77 was erected for type species *Reniera megarrhaphea* Lendenfeld, 1888: 79 from Port Jackson, East Australia (by original designation). The type series (not examined) is rather confusedly treated by subsequent authors: Whitelegge (1902: 277, 280) redescribed the ‘type’ given as No. 385, presumably from the Australian Museum and from Port Jackson but this is not expressly mentioned and can be only circumstantially deduced. Hallmann (1914: 330, pl. XVII figs 5–6, text-fig. 3) gave a full description with some figures of the type, but failed to mention a specimen number; presumably it was the same specimen referred to as type by Whitelegge, 1902. Hooper & Wiedenmayer (1994: 205) list a series of eight specimens as syntypes, two from AMS and six from BMNH, with slides in AMS of two of the BMNH specimens, and a slide in ZMB from one of the BMNH specimens. However, this series contains specimens from Mauritius and New Zealand, which cannot be part of the type series since these localities were not mentioned in Lendenfeld’s original description. The specimens that are from the type locality, presumably BMNH 1887.4.27.84 (with slide in AMS G3338),

BMNH 1887.4.27.14 (slide AMS G3377), BMNH 1887.4.27.6, AMS G9016 and AMS Z2015, may contain the original type specimen described by Lendenfeld, but this remains undetermined. Both Whitelegge describing the 'type No. 385' and Hallmann noted that their specimen was quite different in shape from what Lendenfeld described. In the absence of a connection between Whitelegge's No. 385 and the type series mentioned by Hooper & Wiedenmayer, it is decided here to indicate AMS G9016 as the lectotype. Reasons are twofold: the first author to redescribe the species referred to a specimen from AMS rather than from BMNH, and the only other AMS specimen is a mere fragment. The descriptions of Whitelegge and Hallmann leave little doubt that *Reniera megarrhaphea* is an *Amorphinopsis*, with an ectosomal skeleton of intercrossing oxeas and small styles and a confused choanosomal skeleton of oxeas. Sizes of oxeas 220–950 × 6–31 μm, of styles 160–250 × 6–9 μm (the original description of Lendenfeld did not mention styles, but only small oxeas of 20 μm (presumably a misprint for 200) × 8 μm. The genus *Tumata* is a junior synonym of *Amorphinopsis*.

The genus *Nailondria* de Laubenfels (1954: 182) was erected (by monotypy) for type species *Nailondria maza* de Laubenfels (1954: 182, fig. 121). The type specimen, USNM 23083, from the West Central Pacific, was reexamined. It is described as an amorphous soft sponge with the consistency of soggy bread, diameter 15 cm, yellow. The surface is smooth, detachable, with conspicuous oscules of 5 mm diameter, 3 cm apart. The ectosomal skeleton is a dense tangential crust of intercrossing single spicules. The choanosome is cavernous, with indistinct spicule tracts 40–100 μm in diameter directed to and carrying the surface crust. Spicules: strongyloxeas (Fig. 1E–F), 460–690 × 10–18 μm, and styles (Fig. 1G), 220–288 × 5–8 μm. Van Soest *et al.* (1990) assigned this species to *Hymeniacion*, because both sizes of spicules could be interpreted as styles. However, the strongyloxeas are definitely oxeote in origin. The soft consistency is unusual, but the other characters match well with *Amorphinopsis*, thus we propose this species to be named *Amorphinopsis maza*.

AXINYSSA LENDENFELD, 1897

Synonymy

Axinyssa Lendenfeld, 1897c: 116. *Astromimus* Lendenfeld, 1897a: 148. *Pseudaxinyssa* Burton, 1931a: 350. *Axinomimus* de Laubenfels, 1936a: 163. *Oxeosarcocoea* de Laubenfels, 1954: 230.

Type species

Axinyssa topsenti Lendenfeld, 1897c: 116 (by monotypy).

Definition

Halichondriidae lacking an ectosomal tangential skeleton. Choanosomal skeleton largely disorganized, but at the periphery the spicules are arranged in bundles at right angles to and protruding slightly beyond the surface causing a fine conulation.

Diagnosis

Massive, lobate or tubular sponges with conulose surface. Ectosomal region lacking a distinct surface skeleton, largely organic, tough, with sparsely scattered spicules and protruding

spicule bundles. Choanosomal skeleton disorganized with spicules strewn in confusion and/or composed of vaguely ascending, widely spaced vertical tracts of large oxeas or strongyloxeas, forming loose bundles. Choanosome with poor or moderate spongin development, but heavy interspicular collagen; spicule density relatively low. Spicules oxeas, strongyloxeas or stylote modifications, usually of only one size class. About 15 species, distributed over the warmer waters of the world oceans.

Previous reviews

Van Soest *et al.* (1990), Hooper & Bergquist (1992), Hooper *et al.* (1997).

Description of type species

Axinyssa topsenti Lendenfeld, 1897c (Fig. 2A–F).

Synonymy. *Axinyssa topsenti* Lendenfeld, 1897c: 116, pl. 10 figs 134–144.

Material examined. Holotype: ZMB 2971 – from Zanzibar. Schizotype: BMNH 1908.9.4.145, including slide 1897.3.25.70.

Description. Lobate mass of tubes, 10 cm in largest expansion. Individual lobes (Fig. 2A) 2 cm high, 3 cm diameter at the base, tapering to 0.5 cm. Lobes tube-like with apical oscules penetrating deep into the interior of the sponge. Surface finely but regularly conulose. Consistency firm. Colour dark green. Ectosomal region (Fig. 2D–E) traversed by protruding choanosomal bundles interconnected more or less tangentially by irregular bundles of 1–2 spicules enclosing large pore-fields. Protruding bundles at the surface consist of small categories of megascleres, whereas the tangential spicules are of a larger category. The subectosomal region contains large open spaces (Fig. 2F) of 300–500 μm diameter separated by bundles of spicules 50–200 μm in diameter. In between are masses of loose direction-less spicules, which may become longitudinally arranged (Fig. 2B) along the inner wall of the oscular cavity. Spicules (Fig. 2C) are large oxeas, 550–740 × 14–18 μm, some with stylote endings and small oxeas located at the conules, 165–250 × 4–5 μm, many with one end rounded but clearly of oxeote origin. Distribution and ecology. Zanzibar, shallow-water.

Remarks. The type species has never been reliably described since its original description (Stephens', 1915b record is dubious, as the description differs substantially from the type), and it appears to be unique in its possession of the tube-shaped habit and distinct size categories of the megascleres. Subsequent use of *Axinyssa* was rare until Burton (1931a: 350) described the genus *Pseudaxinyssa* as distinct from *Axinyssa* in possessing a single size category of megascleres. *Pseudaxinyssa* was erected for type species (original designation) *Axinyssa tethyoides* Kirkpatrick (1903a: 245, fig. 18). The type of this species, BMNH 1902.11.16.25, was redescribed by Van Soest *et al.* (1990) and Hooper & Bergquist (1992). It is a globular black sponge (Fig. 3A) with a papillate surface, which is detachable but organic, and it has a black colour. The skeleton is an irregular dendritic system of bundles and fibres of oxeas (Fig. 3B), 500–1000 μm in diameter, an ectosomal skeleton is lacking entirely. There are many loose spicules. The oxeas are fusiform and thick, oxeas, stylote modifications, 420–700 × 8–34 μm. There is little resemblance to the type specimen of *Axinyssa topsenti*, but like that it appears to be unique in its unusual shape, surface and skeleton. Burton (1931a) described a further species of *Pseudaxinyssa*, *P. tenuispiculata*

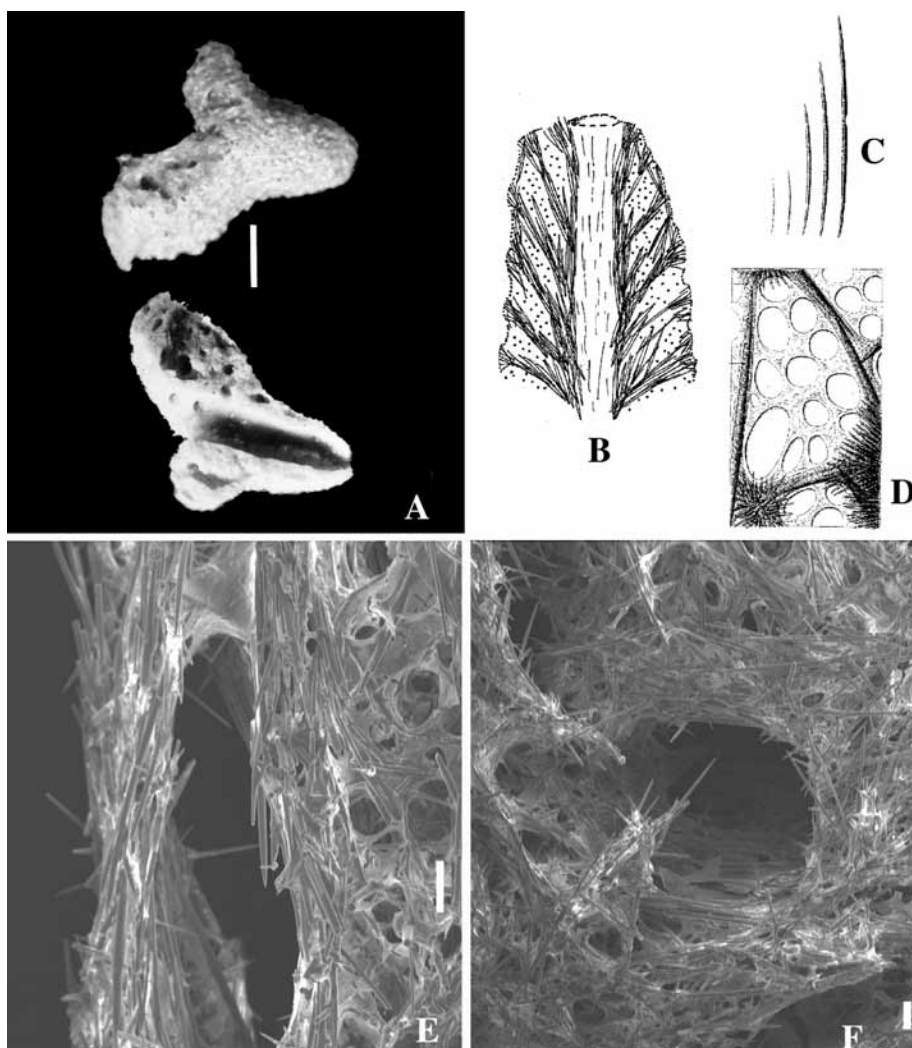


Fig. 2. *Axinyssa topsenti* Lendenfeld 1897. A, BMNH schizotype. B, longitudinal section made from schizotype (size see text). C, spicules. D, surface view (both reproduced from Lendenfeld, 1897: pl. 10 figs 134–144, size see text). E, cross section (scale 100 μm). F, surface view (scale 100 μm).

Burton (1931a). This was reexamined, but the similarity with *A. tethyoides* and *A. topsenti* is low.

The genus *Astromimus* Lendenfeld, 1897a: 148 was erected for type species *Astromimus luteus* Lendenfeld, 1897a: 148, pl. V fig. 44, pl. VII fig. 80, pl. XII figs 217–221, 224, 225 (monotypy) from Lesina, in the Adriatic. The holotype (wet, reexamined) is kept in the Natural History Museum of Vienna and now consists of half the specimen depicted in Lendenfeld's pl. V fig. 44. This is a semiglobular mass of 6 cm diameter and 7 cm height, the live colour quoted as an intense yellow. The surface is smooth to slightly irregular-hispid, somewhat shaggy in appearance, punctate, even seemingly reticulate to the naked eye. Oscules with a raised rim, 4–6 mm diameter. The skeleton is loosely radiate, with vague bundles of oxaeas and single spicules oriented generally towards the surface, where they spread out to form a rather condensed skeleton compared to that of the interior. In cross section of the peripheral skeleton a few paratangentially arranged bundles and loose spicules are apparent, which cause the reticulated aspect of the surface, but there is no easily detachable ectosomal skeleton. Spicules oxaeas, curved, often blunt-ending, in a wide size range, but without clear size categories, 300–1000 \times 8–13 μm . The lack

of a detachable ectosomal skeleton in combination with the surface-oriented vague choanosomal tracts in this species conform to the characters of *Axinyssa* and accordingly it is assigned to the synonymy of that genus. Both names were erected in 1897 (although the title page of 'Die Clavulina' gives 1896, the last page announced that it was in fact printed in 1897). In view of the prevailing usage of *Axinyssa* it is proposed to continue its use and consider *Astromimus* a junior synonym (if necessary under ICZN article 23.9, because *Astromimus* subsequent to its original description was only mentioned in an uncritical species list of Pulitzer-Finali, 1983). *Axinyssa luteus* is very likely a specimen of what is generally known as *Halichondria aurantiaca* (Schmidt, 1864: 38), and accordingly the valid name for it is *Axinyssa aurantiaca* (Schmidt, 1864).

The genus *Axinomimus* de Laubenfels (1936a: 163) was erected for type species *Axinella paradoxa* Ridley & Dendy (1886: 482). The type specimen, BMNH 1887.5.2.68, was reexamined. It is a massive lobate sponge (Fig. 3C) of 2.5 cm high and 4 cm diameter. Oscules arranged in small groups on top of the lobes. It has a conulose surface and rubbery-fibrose consistency. The ectosomal region has bundles of spicules protruding beyond the

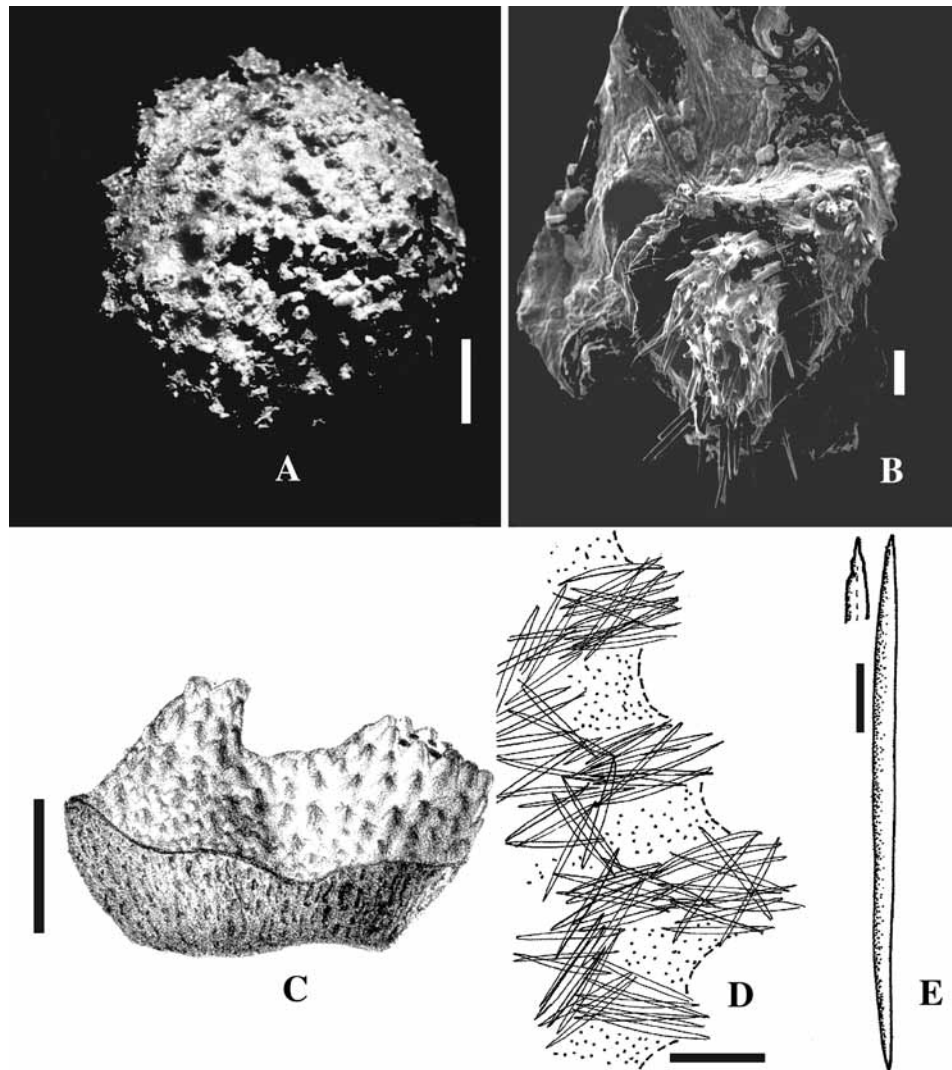


Fig. 3. A–B, *Axinyssa tethyoides* Kirkpatrick (1903a) (= type of *Pseudaxinyssa* Burton 1931a). A, holotype specimen (scale 1 cm). B, SEM image of surface showing bundles of oxeas (scale 100 μ m). C–E, *Axinyssa paradoxa* (Ridley & Dendy, 1886 as *Axinella*) (=type of *Axinomimus* de Laubenfels 1936a). C, holotype (scale 1 cm). D, cross-section, reproduced from Van Soest *et al.* (1990) (scale 500 μ m). E, spicules (scale 100 μ m).

organic skin to form low conules, but it lacks tangential spicules. Between the conules, there are prominent porefields. The choanosomal skeleton (Fig. 3D) consists of large oxeote spicules forming stout fibres running vertically upwards; numerous irregularly scattered spicules between the fibres. Spicules (Fig. 3E) smooth large oxeas, 480–640 \times 14–18 μ m.

It is proposed to distinguish the properties of a genus *Axinyssa* by combining the overlapping characters of the three above described species (*Axinyssa topsenti*, *A. tethyoides* and *A. paradoxa*). They share the absence of a clear ectosomal skeleton (although the type species still has a tangential complement), a conulose surface due to protruding choanosomal spicule tracts, and a fibrous choanosome with low spicular density.

The genus *Oxeosarcodea* de Laubenfels, 1954: 230, which was erected for type (by monotypy) *Oxeosarcodea oinops* de Laubenfels, 1954: 230, fig. 158, from Ebon Atoll, Central Pacific, shares these characters. Slides of the holotype, USNM 22982, were reexamined. This is a red, massive, microconulose sponge, with a confused skeleton of oxeas and stylote/strongylote modifications, 420–660 \times 4–12 μ m. The surface has an incomplete cover

of partly tangential spicules of the same size as those in the interior. *Oxeosarcodea* is considered a junior synonym of *Axinyssa*.

The surface characters of *Axinyssa* are atypical in the family Halichondriidae, but through the presence of a large complement of loose irregularly scattered oxeas in the choanosome the genus *Axinyssa* is more naturally placed in this family than any other family of the order Halichondrida.

CIOCALAPATA DE LAUBENFELS, 1936

Synonymy

Ciocalapata de Laubenfels, 1936a: 134.

Type species

Ciocalypta amorphosa Ridley & Dendy, 1886: 479 (by original designation).

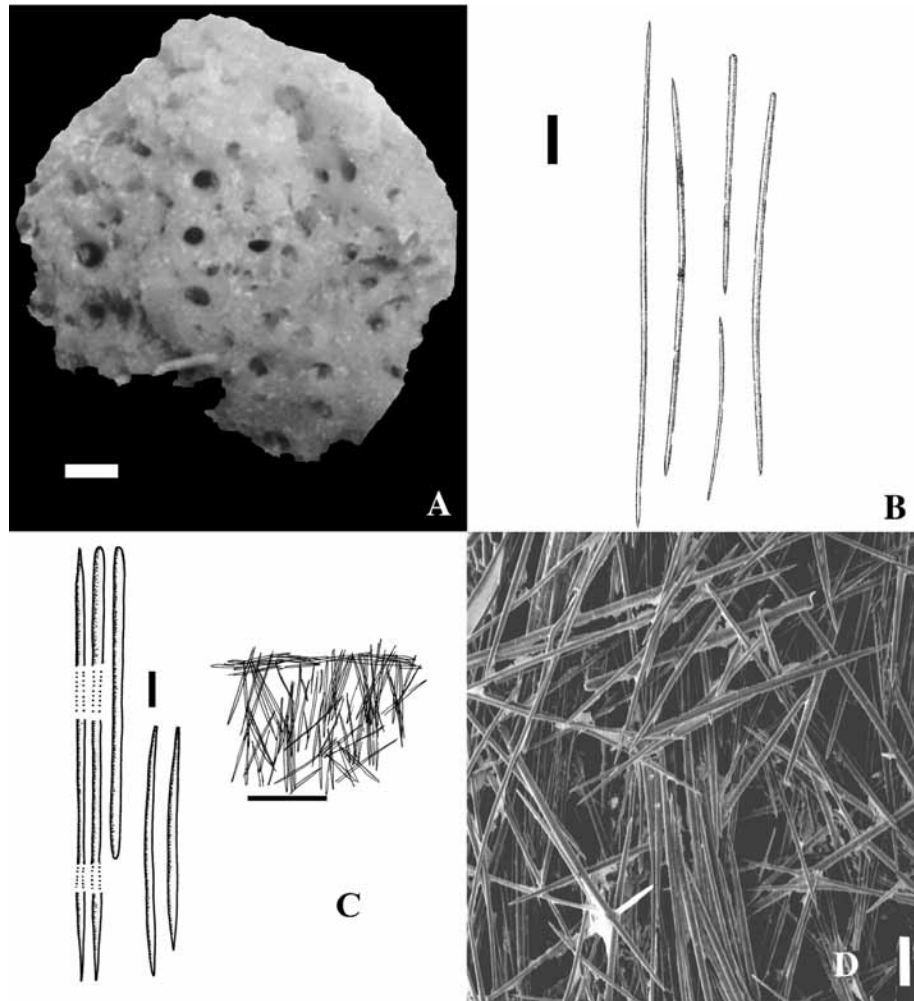


Fig. 4. *Ciocalapata amorphosa* Ridley & Dendy, 1886. A, paralectotype specimen (scale 1 cm). B, spicules (from Ridley & Dendy, 1886, size see text). C, drawing of spicules and cross section of paralectotype (from Van Soest *et al.*, 1990: fig. 73) (scales: spicules, 100 μm ; section, 1 mm). D, SEM image of surface of paralectotype (scale 100 μm).

Definition

Halichondriidae with detachable tangential ectosomal skeleton of intercrossing bundles of spicules and a trabecular choanosomal skeleton of thick spicule tracts. Spicules oxeas (in two size categories in the type species) and a separate category of styles.

Diagnosis

Massive, fragile, soggy sponges, with a thin detachable ectosomal skeleton roofing over a system of large choanosomal holes in the type species. Choanosomal thick spicule tracts forming a trabecular system enclosing the holes. Spicules include both oxeas and genuine styles. A single species from deep water in the SW Atlantic.

Previous review

Van Soest *et al.* (1990, as a junior synonym of *Halichondria*).

Description of type species

Ciocalapata amorphosa (Ridley & Dendy, 1886) (Fig. 4A–D).

Synonymy. *Ciocalypta amorphosa* Ridley & Dendy, 1886: 479; Ridley & Dendy, 1887: 175, pl. XL fig. 9; *Ciocalapata amorphosa*; de Laubenfels, 1936a: 134; *Halichondria amorphosa*; Van Soest *et al.*, 1990: 47, fig. 73.

Material examined. Lectotype: BMNH 1887.5.2.56 – largest of 5–6 fragments, ‘Challenger’ expedition, Stn. 320. Paralectotypes: 4–5 remaining fragments registered under the same number.

Description. Massive, sprawling, riddled with rounded holes (small paralectotype fragment shown in Fig. 4A). Consistency soggy. Surface skeleton (Fig. 4D) where still present, easily detached; elsewhere the surface is rough and tufted. Choanosomal cavities 1–2 mm in diameter. Ectosomal skeleton consisting of intercrossing bundles of megascleres (Fig. 4C), smaller oxeas dominant but larger oxeas and styles also present. Choanosomal spicule bundles of 200–300 μm in diameter form a trabecular system surrounding the holes, but in addition there are many megascleres in confusion. Spicules (Fig. 4B) oxeas in two distinct size categories, 900–1500 \times 18–25 μm and 515–680 \times 8–10 μm , and styles in a single category, 940–1150 \times 30 μm . Strongylote modifications of the styles occur in a low frequency. Distribution and ecology. SW Atlantic, 600 m.

Remarks. The possession of a special category of large true styles is not shared with the type species of *Halichondria* and other related species. *Amorphinopsis* has only small styles and is also otherwise distinct. For that reason we prefer to retain *Ciocalapata* as a valid genus. Van Soest *et al.*'s (1990) suggestion that it may be a member of the genus *Biemna* without microscleres is refuted here, as skeletal architecture is clearly halichondrioid. A second species has been ascribed recently to *Ciocalapata*, viz., *Ciocalapata almae* Carballo *et al.*, 1996. The shape, spicule size, skeletal architecture, and habitat of this species deviate strongly from *C. amorphosa*, so this assignment would stretch the genus characters considerably. The styles described from *C. almae* appear to be modified oxeas rather than true monactinal spicules, and membership of *Halichondria* appears more likely.

CIOCALYPTA BOWERBANK, 1862

Synonymy

Ciocalypta Bowerbank, 1862: 1105. *Leucophloeus* Carter, 1883b: 323. *Collocalypta* Dendy, 1905: 199. *Coelocalypta* Topsent, 1928c: 167. *Pseudohymeniacidon* Carballo, 2001: 258.

Type species

Ciocalypta penicillus Bowerbank, 1864: 179 (by monotypy).

Definition

Halichondrids with finger-shaped fistules possessing a central spicular axis, with strong secondary tracts supporting the ectosome. Spicules styles and/or oxeas, usually in two size categories.

Diagnosis

Basal mass usually buried in the soft sediment with conically tapering erect finger-shaped fistules rising above the sediment. Surface smooth, usually somewhat transparent, without visible oscules. Ectosomal skeleton usually present, but occasionally lacking. If present it is tangential, carried by strong spicule tracts issuing from a thick central spicular axis. Skeleton of basal mass largely confused. About 15 species occurring mostly in temperate and subtropical waters of the Atlantic and the South Pacific.

Description of type species

Ciocalypta penicillus Bowerbank, 1864 (Fig. 5A–D).

Synonymy. *Ciocalypta penicillus* 1864: 179, pl. XXX fig. 360; Bowerbank, 1874b: 33, pl. XIII figs 2–4. *Ciocalypta leei* Bowerbank, 1874b: 295, pl. LXXXVI figs 1–4.

Material examined. Lectotype: BMNH 1877.5.21.1069 (with additional number 1930.7.3.28) – from Hastings, SE England. Paralectotype: BMNH 1830.4.3.29.

Description. Basal cushion of up to 10 cm in diameter buried in sand or gravel, from which project large conical, translucent, ridged, thick walled, non-contractile fistules (Fig. 5B), normally up to about 5–9 cm high, 0.5–0.6 mm in diameter. In the lectotype (Fig. 5A) there are 18 individual fistules, each about 2 cm diameter at the base, 0.5 cm at the apex. Colour white-cream

to cream-yellow to grey. The surface of the fistule has a glassy, translucent appearance, through which vertical spicule fibres can be seen with the unaided eye. Oscules are on top of some of the fistules. Consistency firm. The ectosomal skeleton (Fig. 5C) is a tangential reticulation of intercrossing bundles, thickness 45–110 μm . Spaces in between bundles 100–250 μm with smaller spicules predominant. Subectosomal spaces present. The main skeleton is an irregular, confused reticulation consisting mostly of larger spicules, with a tendency to form ascending fibres. In the fistules there is a central condensation consisting of a column of 3–4 aligned thick tracts (Fig. 5D), together about 800 μm diameter, with radially arranged ascending fibres ending at right angles at the surface and lifting it up in preserved or dried specimens. Distance of these supporting tracts 1500–1600 μm , space between has a low spicular density and carries mostly only single spicules in confusion. The spiculation consists of large and small, slender styles and occasional oxeas. These are incompletely differentiated into two size categories. Long styles, 600–630 \times 12–18 μm . Small styles, 340–390 \times 5–10 μm . Small oxeas, 200–260 \times 5 μm . The spicules frequently have telescoped or distorted extremities, and it is possible that the oxeas are none other than modified styles. Distribution and ecology. European seaboard of Atlantic from Helgoland south to Spain, Portugal Mediterranean, in clear water.

Remarks. By retaining the fistule growth form as an integral feature of the genus definition, we create a possible confusion in the family Halichondriidae, because several halichondrids with fistular growth form appear closely related to non-fistular forms. *Collocalypta digitata* Dendy (1905) (cf. below) is convincingly similar in shape to *Ciocalypta penicillus*, but shares an important feature with *Axinyssa*, i.e., the complete absence of an ectosomal skeleton. These facts cast doubt over the validity of the fistular growth form as a character uniting a monophyletic group of sponges. Emphasis should here be placed on features of the skeleton in addition to the fistular habit: the possession of a central column and extra-axial thick supporting tracts, may serve to differentiate the species of *Ciocalypta* from other fistular halichondrids. Van Soest *et al.* (1990) emphasized possession of styles, thus excluding species like *Coelocalypta porrecta* Topsent, 1928c, *Collocalypta digitata*, *Ciocalypta tyleri* Bowerbank, 1875b and *C. gibbsi* Wells *et al.*, 1960 from *Ciocalypta*. In contrast, we submit here that the possession of exclusively oxeas in an otherwise closely similar species such as found in these mentioned above is insufficient reason to exclude them from *Ciocalypta*, as a minor complement of oxeas is found even in its type species. Topsent (1921) also took the view that oxeas and styles may assume a variable dominance in species of *Ciocalypta*, and it is advocated here to follow this.

The genus *Leucophloeus* Carter (1883b) was erected (by monotypy) for *Leucophloeus massalis* Carter (1883b: 323, pl. XIV fig. 15A–B). The type material cannot be unambiguously identified from well-labelled specimens, but Van Soest *et al.* (1990) report the existence of a specimen labelled *Leucophloeus massalis* in the BMNH 'Bowerbank collection' bearing the numbers 706 and 31, further data and registration lacking, possessing several of the characters described by Carter (1883b). It is a piece of a conical fistule which has a smooth furrowed surface, a thick white surface crust of spicules over a beige coloured interior of spicule tracts forming a central axis and radiating spicule tracts. Spicules (Fig. 7C) are styles in two sizes. It is proposed to adopt this material as the lectotype of *Leucophloeus massalis*. Its properties allow the synonymization of *Leucophloeus* with *Ciocalypta*.

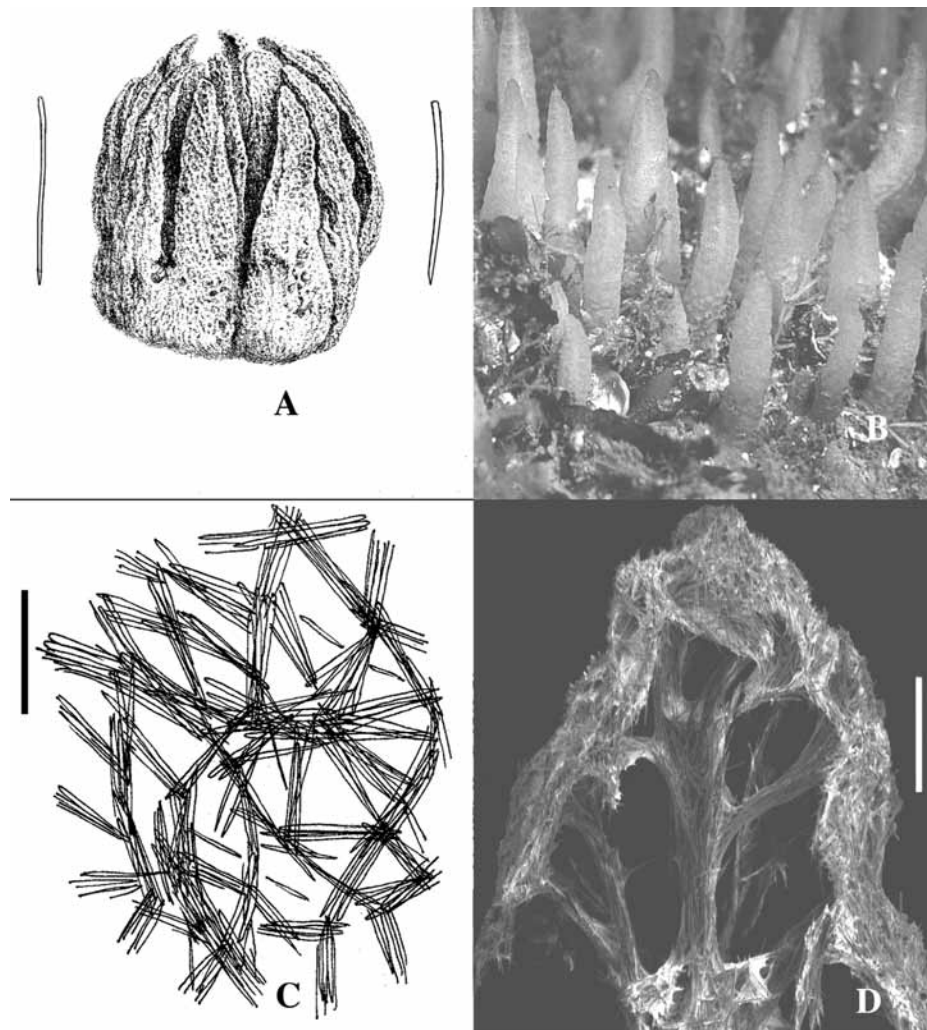


Fig. 5. *Ciocalypta penicillus* Bowerbank, 1864. A, lectotype specimen and spicules (from Bowerbank, 1874b: pl. LXXXVI figs 1–3) (sizes see text). B, specimens photographed *in situ* (photo B. Picton). C, tangential view of surface (from Van Soest *et al.*, 1990: fig. 60) (scale 500 μm). D, SEM image of cross-section (scale 1000 μm).

The genus *Collocalypta* Dendy (1905: 199) was erected (by monotypy) for *Collocalypta digitata* Dendy (1905: 199, pl. VII fig. 6, pl. XIII figs 1–2). The holotype BMNH 1907.2.6.89 was reexamined. It resembles *Ciocalypta* in habitus (Fig. 6A), including the transparent fistules which are furrowed and conulose in preserved condition. The basal mass is flattened, covered with shells and sand, and the fistules are relatively widely apart, up to 5 cm high. No visible oscules. Consistency tough. The skeleton of the basal crust consists of stout, erect, plumose columns of spicule tracts cemented by spongin. The fistules have a central column of aligned spicules, from which diverge thick loose bundles of spicules towards the surface (Fig. 6B, 6D), lifting this up into conules. Oxeas (Fig. 6C), in various shapes, shorter and thicker, slightly curved, irregularly ended 450–630 \times 20–30 μm , and long and slender, slightly curved, 760–930 \times 20–30 μm . A noteworthy difference with *Ciocalypta penicillus* is the absence of an ectosomal tangential skeleton (Fig. 6E), instead of which there is a thick organic skin. This absence was considered to be of generic significance by previous authors (e.g., Van Soest *et al.*, 1990), but in view of the fact there is only a single species with

precisely these features (*Ciocalypta*-like habit without ectosomal skeleton), it is assumed to be autapomorphic. If further species of *Ciocalypta* without ectosomal skeleton are found to exist *Collocalypta* may be raised to subgenus level. Carballo (2000) revived *Collocalypta* as a valid genus in Axinellidae, and associated it with *Hymerhabdia*.

The genus *Coelocalypta* Topsent (1928c) with type species (by monotypy) *Coelocalypta porrecta* Topsent (1928c: 167, pl. II fig. 6, pl. VI fig. 4) is now considered a member of *Ciocalypta*, not of *Topsentia* as Van Soest *et al.* (1990) proposed. Most of the features (Fig. 7A–B) of this subtropical East Atlantic species conform to *Ciocalypta*, including a central column and supporting spicule tracts in the fistules and an ectosomal skeleton. The tangential tracts in the ectosome are absent, instead of which there are single tangential spicules overlying a dense crust of paratangential brushes of oxeas. Nevertheless, the ectosomal skeleton is detachable like in *Ciocalypta penicillus* because of the presence of a regular system of subectosomal vestibules, between the supporting tracts. Carballo (2001) revived *Coelocalypta* as a valid genus.

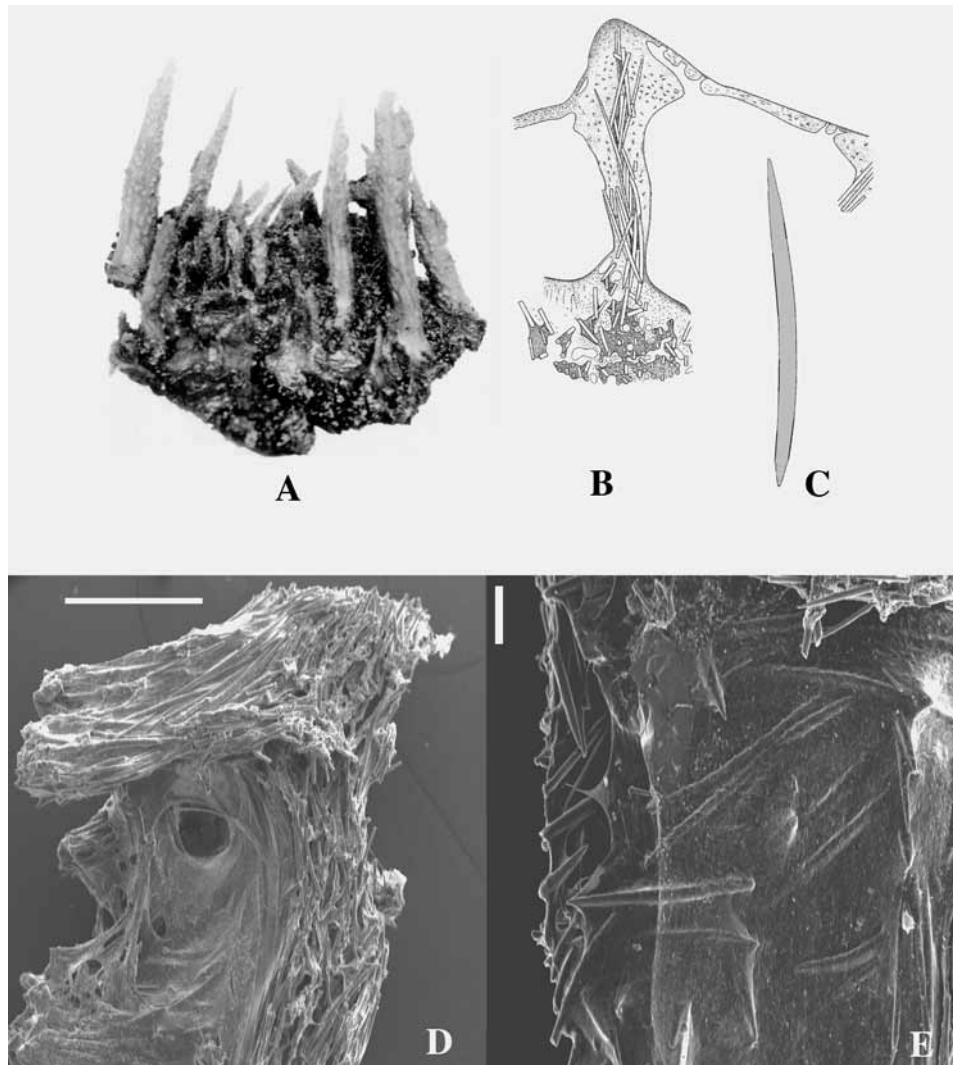


Fig. 6. *Ciocalypta digitata* Dendy (1905, as *Collocalypta*). A, type specimen. B, cross-section. C, oxea (all reproduced from Dendy, 1905: pl. VI fig. 6 & pl. XIII figs 1–2 (sizes see text)). D, SEM image of cross-section made from the type (scale 500 μ m). E, surface view of same (scale 100 μ m).

The genus *Pseudohymeniacidon* Carballo, 2001: 258 was erected for type species *Coelocalypta aderma* Lévi & Vacelet, 1958: 236, fig. 18 from the Azores (original designation). The definition given by Carballo is rather enigmatic, but it is evident from the characters of the type species, that it is intended for *Ciocalypta*- or *Collocalypta*-like fistule-bearing sponges with oxeas as megascleres and lacking a tangential ectosomal skeleton. Previously, Carballo (2000) assigned *Collocalypta* to Axinellidae and associated it with *Hymerhabdia*. We have problems understanding the arguments and classification proposed by Carballo (2000, 2001) for a group of sponges that all seem closely related to us. In his proposals, these must apparently be assigned to four genera of two families (*Ciocalypta*, *Collocalypta*, *Coelocalypta* and *Pseudohymeniacidon*, families Halichondriidae and Axinellidae). We admit that it is possible to rearrange genera of Halichondrida and redistribute them among families, because characters are not clear-cut. However, we claim to have studied this group of difficult sponges in its entirety arriving at the present ‘state-of-the-art’ classification. We propose to consider the above mentioned genera synonymous with *Ciocalypta* s.l. until independent support is obtained for generic and familial distinctness of these forms.

EPIPOLASIS DE LAUBENFELS, 1936

Synonymy

Epipolasis de Laubenfels, 1936a: 162.

Type species

Spongosorites suluensis Wilson, 1925: 331 (by original designation).

Definition

Halichondriidae with trichodragmas. Ectosomal skeleton consisting of an ectosomal crust of intercrossing spicules; choanosomal skeleton a confused mass of single spicules.

Diagnosis

Massive-amorphous to flabellate, with parchment-like ectosomal tangential skeleton, without a collagenous choanosome and

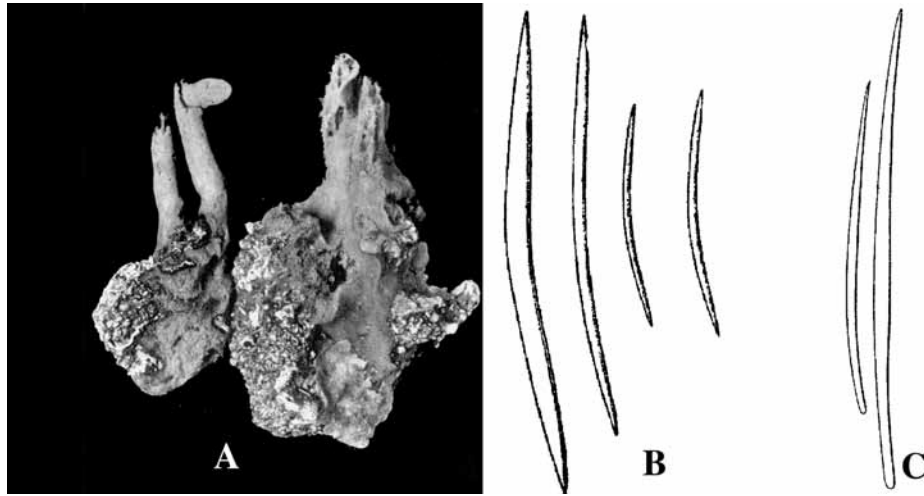


Fig. 7. *Ciocalypta porrecta* (Topsent 1928c as *Coelocalypta*). A, type specimen reproduced from Topsent, 1928c: pl. II fig. 6 (size see text). B, spicules reproduced from Topsent 1928c: pl. VI fig. 4 (size see text). C, *Ciocalypta massalis* Carter (1883b as *Leucophloeus*), spicules reproduced from Carter 1883b: pl. XIV fig. 15 (size see text).

without any spongin, resulting in an utterly confused arrangement of spicules. The spicules include large numbers of trichodragmas (raphides) which may be flexuous or sinuous in appearance. Two species, both from tropical waters.

Previous review

Van Soest *et al.* (1990).

Description of type species

Epipolasis suluensis (Wilson, 1925) (Fig. 8A–D).

Synonymy. *Spongisorites suluensis* Wilson, 1925: 331, pl. 38 fig. 8, pl. 48 fig. 3; *Epipolasis suluensis*; de Laubenfels, 1936a: 162; Van Soest *et al.*, 1990: 41, figs 56, 65.

Material examined. Lectotype and paralectotype: USNM 21297 – Philippines.

Description. Shape lamellate (Fig. 8A). The lectotype is the larger of both original specimens, measuring 8×5.5 cm with a thickness of 6 mm. One side is the poral side without any visible openings, the other is the oscular side, with abundant 2 mm diameter oscules scattered at distances of 3 mm of each other. The surface of both sides is smooth. The ectosomal skeleton at the oscular side is a tangential, parchment-like crust of tightly intercrossing spicules, about $100 \mu\text{m}$ in thickness, that of the poral side (Fig. 8B) consists of close-set brushes of spicules forming a peripheral layer of about $400 \mu\text{m}$ in thickness. The choanosomal skeleton is largely an irregular mass of single spicules with a few vague tracts, spongin very scarce. Spicules (Fig. 8C) oxeas in a large size range, in several size categories, in the ectosomal region they measure $140\text{--}450 \times 7\text{--}16 \mu\text{m}$, in the choanosome the range is $140\text{--}1350 \times 17\text{--}32 \mu\text{m}$. Trichodragmas (Fig. 8D) straight or more often curved, flexuous or sinuous, $100\text{--}228 \times 5\text{--}10 \mu\text{m}$. Distribution and ecology: Philippines, Indonesia, reefs.

Remarks. In many of its characters this genus approaches *Topsentia*, but the possession of trichodragmas in the two species of the genus (also in *Epipolasis profunda* Diaz *et al.*, 1993) makes it likely that *Epipolasis* is a valid genus. Trichodragmas are common in other families of Halichondrida (Axinellidae, Desmoxiidae), but within Halichondriidae they are diagnostic.

HALICHONDRIA FLEMING, 1828

Synonymy

Halichondria Fleming, 1828: 520. *Raspaigella* Schmidt, 1868: 25. *Amorphina* Schmidt, 1870: 40. *Eumastia* Schmidt, 1870: 42. *Pellina* Schmidt, 1870: 41. *Spuma* Miklucho-Maclay, 1870: 13. ? *Tedanione* Wilson, 1894: 338. *Menanetia* Topsent, 1896a: 115. *Halichondriella* Burton, 1931b: 137. *Trachyopsilla* Burton, 1931b: 138. *Cioxeamastia* de Laubenfels, 1942: 265.

Type species

Spongia panicea Pallas, 1766: 388 (by original designation).

Definition

Halichondriidae with tangential ectosomal skeleton carried by subectosomal spicule tracts or brushes separated by subdermal spaces. Megascleres exclusively oxeas or derivates in a wide size range.

Diagnosis

Encrusting, massive, occasionally irregularly branching, or digitate sponges with smooth or papillate surface. Oscules often on conical elevations. Surface skeleton well-developed with tangential bundles of spicules and single spicules intercrossing to form a lighter or heavier built surface crust. Subectosomal spaces usually well-developed causing the surface crust to be often rather independent of the main skeleton and easily peeled off. Choanosomal skeleton of rather ill-defined bundles of spicules, which at the surface become oriented perpendicular to the surface crust. They often fan out and carry the surface crust. Many single spicules distributed randomly. Spongin not visibly present. Spicules oxeas with gradually tapering sharp points, in a wide size range, often seemingly divisible into a smaller and a larger category but overlap is extensive. Occasionally style-like modifications occur at a low frequency. About 110 species distributed over all regions and habitats.

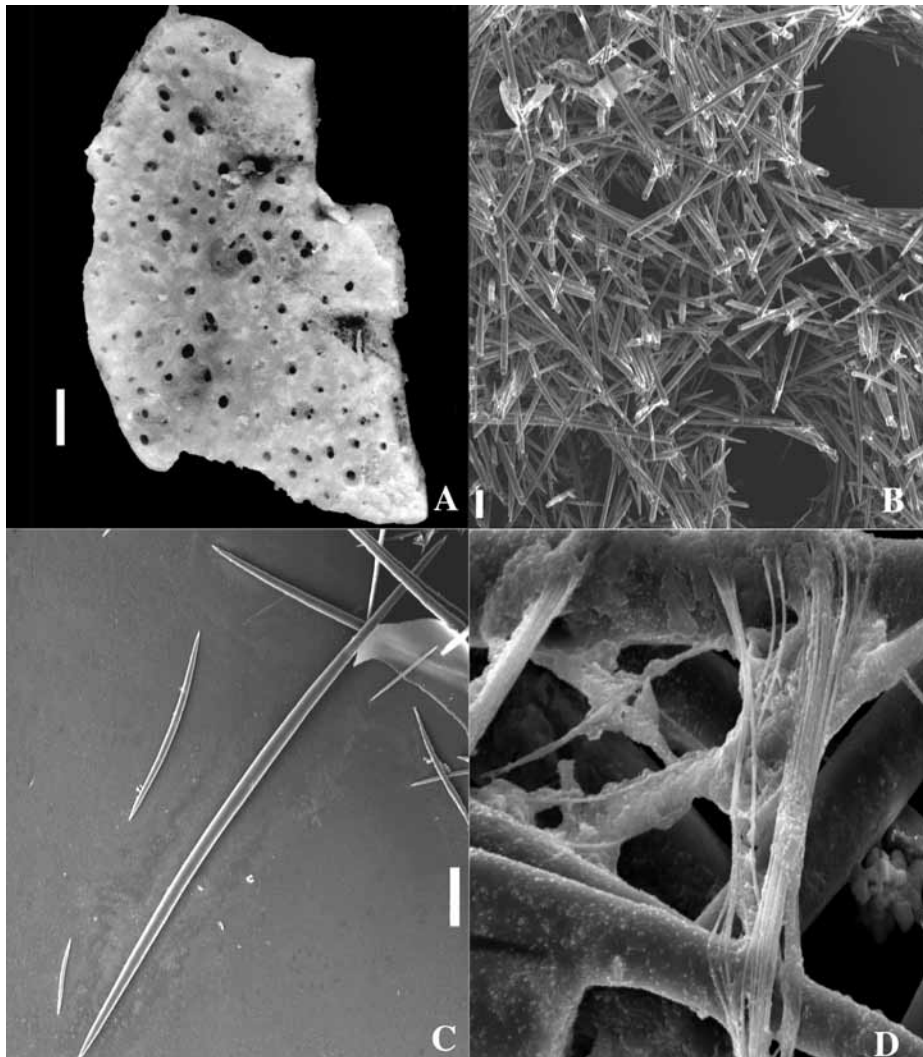


Fig. 8. *Epipolasis suluensis* Wilson, 1925. A, photo of holotype (scale 1 cm). B, SEM image of surface of type (scale 100 μm). C, spicules of type (scale 100 μm). D, trichodragmas of type (scale 10 μm).

Remarks

Several species from high latitudes with *Halichondria*-like skeleton architecture share a surface covered in short papillae. For these several generic names are available, the most senior of which

appears to be *Eumastia* Schmidt (1870). Van Soest *et al.* (1990) simply considered these genera junior synonyms of *Halichondria*, but the shared habitus may indicate common ancestry. For that reason, we propose to employ *Eumastia* as a subgenus within *Halichondria s.l.*

Key to subgenera of *Halichondria*

- (1) Surface densely covered with short conical papillae *Eumastia*
- Surface smooth or digitate, no continuous cover with conical papillae *Halichondria*

SUBGENUS HALICHONDRIA FLEMING, 1828

Synonymy

Halichondria Fleming, 1828: 520. *Halina* de Blainville, 1830: 497 (fide Neave, 1940). *Seriatula* Gray, 1867a: 515. *Raspaigella* Schmidt, 1868: 25. *Amorphina* Schmidt, 1870: 40. *Pellina* Schmidt, 1870: 41. ? *Apatospongia* Marshall, 1892: 16. ? *Tedanione* Wilson,

1894: 338. *Menanetia* Topsent, 1896a: 115. *Halichondriella* Burton, 1931b: 137. *Trachyopsilla* Burton, 1931b: 138.

Type species

Spongia panicea Pallas, 1766: 388 (by original designation).

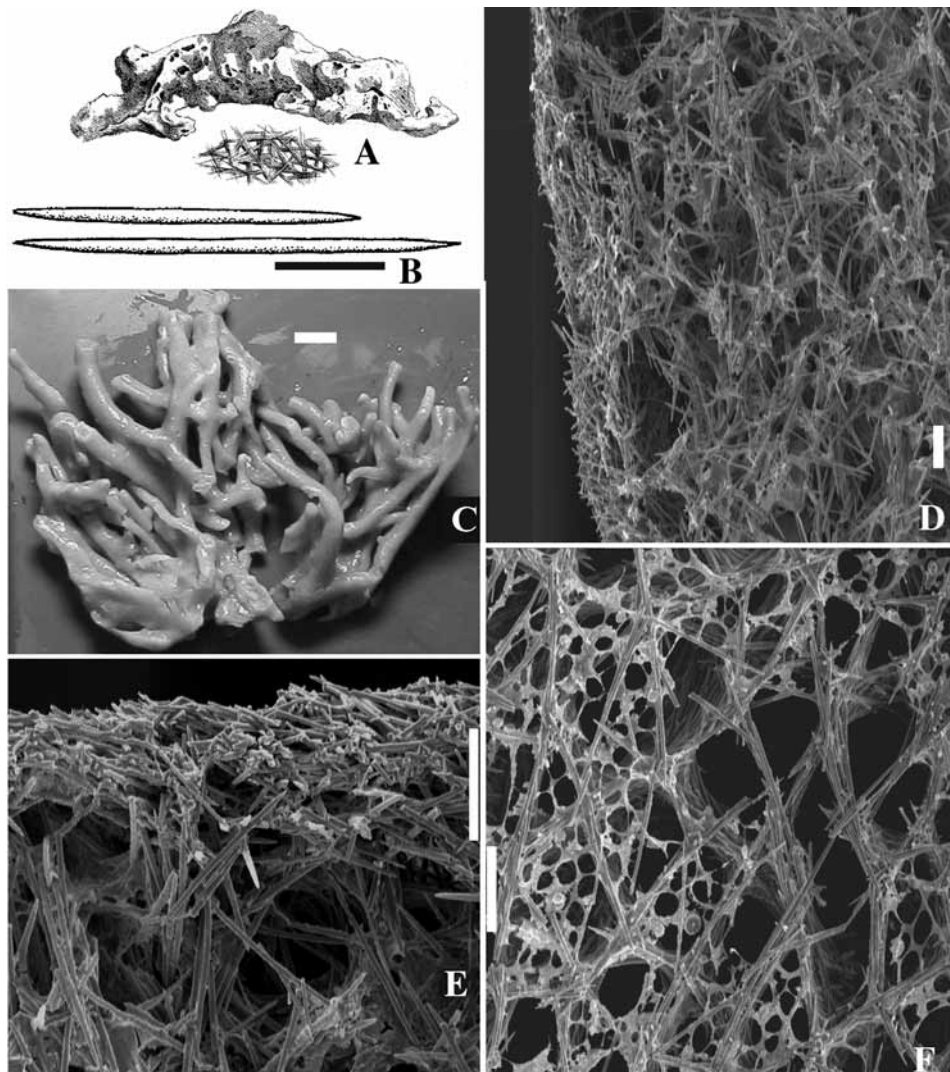


Fig. 9. *Halichondria panicea* Pallas (1766, as *Spongia*). A, original specimen reproduced from Ellis, 1755: plate XVI fig. D. B, spicules reproduced from Van Soest *et al.*, 1990: fig. 69 (scale 100 μm). C, neotype BMNH 1964.6.8.6 (scale 1 cm). D–E, SEM images of cross sections of different ZMA specimens (scale 100 μm). F, tangential ectosomal skeleton in surface view (scale 100 μm).

Definition

Halichondria with smooth or digitate surface.

Description of type species

Halichondria panicea (Pallas 1766) (Fig. 9A–E).

Synonymy (restricted). *Spongia panicea* Pallas, 1766: 388; Linnaeus (in Gmelin), 1791: 3823; *Halichondria panicea*; Fleming, 1828: 520; Johnston, 1842: 114, pls 10–11. *Spongia tomentosa* Linnaeus, 1767: 1299. *Spongia papillaris* Linnaeus (in Gmelin), 1791: 3824; Esper, 1794: pl. Spong. II. *Spongia seriata* Grant, 1826d: 11.

Material examined. Neotype (here designated): BMNH 1964.6.8.6 – Burnham-on-Crouch, Essex (Fig. 9B). Other material. Numerous freshly collected specimens incorporated in ZMA.

Description. Quite variable in shape, related to exposure to water movement. Specimens growing in intertidal localities exposed to the full oceanic surf may be entirely smooth with barely visible oscular chimneys. More intermediate environments show

the typical volcano-shaped chimneys up to 4 or 5 cm high. Oscules are relatively large, conspicuous, 2–4 mm in diameter. Sponge body may be up to 25 cm thick and 60 cm across, but much smaller specimens are the rule. In localities with strong currents specimens may grow out to form longer oscular chimneys closely adhering and verging toward palmate forms. In deeper or stagnant waters, with absence of wave surge, specimens may form masses of anastomosing branches, with oscular chimneys here and there on the branches. Consistency is firm, compressible, easily torn. Colour basically light orange-yellow or pale yellowish green. However, intertidal specimens exposed to the light may be dark greyish green, presumably due to microsymbionts. Ectosomal skeleton (Fig. 9D–E) tangential (as is usual for the genus), with spicules arranged disorderly or in tight bundles of 10–30 μm in diameter, leaving very little open space (usually only up to 100 μm in diameter) for ostia. Specimens in exposed localities have thicker and more organized ectosomal skeletons. Thickness of the ectosomal spicule crust (Fig. 9C) 200–300 μm . Choanosomal skeleton (Fig. 9C) largely confused, but near the surface some organization into tracts of ca. 50 μm diameter is observed in many specimens.

These tracts carry the ectosomal reticulation, leaving characteristic subectosomal spaces of up to 100 μm diameter between them. There is very little visible spongin. Spicules (Fig. 9B) oxeas only; size in specimens from Western Europe: 124–482 \times 2–15 μm . Average sizes are: 300 \times 7 μm (Holland), 280 \times 8 μm (France), 360 \times 9 μm (Ireland). Several authors report a subtle but statistically significant difference in spicule lengths between ectosomal (shorter) and choanosomal (longer) spicules, but no definite size categories can be distinguished due to large overlap. Distribution and ecology. Northern Atlantic, both along the European coasts and those of America; from intertidal down to more than 500 m.

Remarks. *Proposal for neotype designation.* Pallas (1766) did not describe specimens in his hands, but instead erected new species for pictures and descriptions of pre-Linnean authors. In the case of *Spongia panicea* Pallas, 1766: 388 he refers to drawings of Ellis, (1755), and Seba (1758), and also to a description of Ray (1724). The specimens depicted in Seba (pl. 96 fig. 4, and pl. 99 fig. 3) are atypical, probably beachworn specimens, from England and North America (no further indication), whereas Ellis pictured an obvious living specimen (his plate XVI fig. D, here reproduced as Fig. 9A) freshly collected off the shore, somewhere in England, probably off the mouth of the Thames. This location is based on Ellis' (p. 30) remarks on a *Tubularia* depicted in the same plate growing apparently in close contact with the sponge (of which no locality is mentioned by Ellis). An obvious choice of the lectotype would have been Ellis' specimen, but this material is no longer extant. *Halichondria panicea* has been recorded from all over the world, at all depths. To ascertain stability in this group of sponges with rather vague and variable characters, a neotype needs to be established. We propose to adopt the specimen BMNH 1964.6.8.6 (Fig. 9C) from Burnham-on-Crouch, Essex, about 20 kms from mouth of Thames. Labelled "28.9.1963, off Power Station, tacking from bank to bank, Stn. 2, Otter trawl, 12–30 ft. Rich yellow-brown in colour. Quite prolific & found with a number of Polycladi. Coll. Miss S.M. Stone & Mr. J.F. Castle" (courtesy Ms Clare Valentine) as the neotype of *Spongia panicea*. A photo of the neotype is given in Fig. 9B.

Biology and variability. This is a viviparous species; larvae have been observed by many authors (e.g., Topsent, 1911; Hartman, 1958b; Wapstra & Van Soest, 1987 (SEM photos)). They are orange-yellow, oval to oblong, ciliated uniformly, but with a posterior tuft of longer cilia; size up to 600 \times 18 μm . Conflicting observations have been made about the sexual cycle of this species. Sponges in Holland were found to be hermaphroditic (Wapstra & Van Soest, 1987), those in the Baltic gonochoric (Witte & Barthel, 1994). Reproductive periods are April to September, with larvae being released from June to September. Sometimes parasitized by the alga *Tribonema endozooticum* (Wille) (Borojevic *et al.*, 1968c). This species occurs in the intertidal region as well as in the sublittoral down to more than 500 m. In the intertidal region it occurs on upper, lateral and undersides of boulders and holdfasts of brown algae. It is the commonest intertidal sponge of the Eastern Atlantic. In the sublittoral it is likewise common, especially in northern areas, e.g., the coasts of the North Sea. Vethaak *et al.* (1982) established that its tolerance towards siltation is lower than its sympatric sister species *H. bowerbanki* Burton, 1930c, preferring somewhat more exposed habitats. However, the ecological range is broad and overlaps considerably with that of *H. bowerbanki*. Ecophysiological aspects such as substrate specificity, growth, biomass, production and energy budget were studied by Barthel (1986; 1988; 1991). Production of faecal pellets was measured by Wolfrath & Barthel

(1989). Riisgard *et al.* (1993) measured the rate of suspension feeding of this species and determined its energy costs at different temperatures. Forester (1979) studied the association between this species and scallops (*Chlamys varia*). The scallops allow breadcrumb sponges to overgrow their shells in order to escape predation by starfishes; the sponge receives increased nutrient supply from the inhalant current created by the bivalve. Other associated fauna include endosymbiont nematodes (Bongers, 1983), annelids, crustaceans, pycnogonids, echinoderms and fish (Frith, 1976). Distribution is the entire Northern Atlantic, both along the European coasts and those of America. High arctic occurrence has not been established with certainty, but the species is certainly found in northern Norway, Iceland and northern Canada. Similar sponges occur in the North Pacific and their conspecificity with Atlantic populations is likely. Southward, the species reaches New England and the Mediterranean, although it is uncommon in the Mediterranean itself. Records from the southern ocean (e.g., New Zealand) are doubtful. A separate species *H. reticulata* (Bowerbank, 1866) (with junior synonym *H. topsenti* de Laubenfels, 1936a: 133) has been distinguished for species from exposed habitats showing thick ectosomal intercrossing tracts and strongly developed surface crust. *Halichondria topsenti* is not considered valid for intergrading of specimens with lesser and stronger developed surface skeletons are observed when a larger series of specimens from various localities is studied (Van Soest *et al.*, 1999).

Synonymy of *Halichondria* (*Halichondria*). The genus *Halina* De Blainville, 1830: 497 is apparently a junior synonym of *Halichondria*, intended to replace Fleming's name without justification and for the same type species. A later genus [*Halina*] Bowerbank, 1858 was employed for type species *Halina bucklandi* Bowerbank, 1858, which was renamed *Dercitus* by Gray, 1867a (see Maldonado's chapter on Pachastrellidae).

The genus *Seriata* Gray, 1867a: 515 was erected for type species *Spongia seriata* Grant, 1826d: 11. A neotype for this species was designated by Hooper, 1966a: 62 as BMNH 1847.9.7.14, Johnston's specimen of *Halichondria seriata*. However, Howson & Chambers (1999: 612) discovered that slides of the Grant collection are still extant in the University College of London. Among these are several slides numbered UCLZ B73, all individually wrapped in paper, and on one of the paper wraps it is written "Spongia seriata Gr variety of *S. papillaris*" (quote from Howson & Chambers). This slide is here designated the lectotype of *Spongia seriata* Grant, 1826d. The identity of this material was established as *Halichondria panicea* (Howson & Chambers, 1999: 612) and accordingly, *Seriata* becomes a junior synonym of *Halichondria*.

The genus *Raspigella* Schmidt (1868: 25) was erected for type species (by monotypy) *Raspigella brunnea* Schmidt, 1868: 25. The lectotype LMJG 15330 (designation herein) from Trieste, the paralectotype LMJG 15524 from an unknown locality, and a slide BMNH 68.3.2.29, probably of one of the type specimens, were examined. This sponge forms a mass of irregularly anastomosing limp branches of 11–16 cm length and 5 mm diameter (Fig. 10A). Consistency in the dry condition: fragile, easily broken. Surface crust easily removable (Fig. 10B). Ectosomal skeleton (Fig. 10C) of irregular thin short bundles of oxeas, 2–3 spicules in cross section, with a high concentration of smaller spicules. Choanosomal tracts wispy, following mostly the length of the branches, many single spicules distributed randomly. Oxeas in a wide size range, seemingly in two categories, 150–600 \times 3–10 μm (Fig. 10D). These characters conform to *Halichondria* and accordingly *Raspigella* is considered a junior synonym.

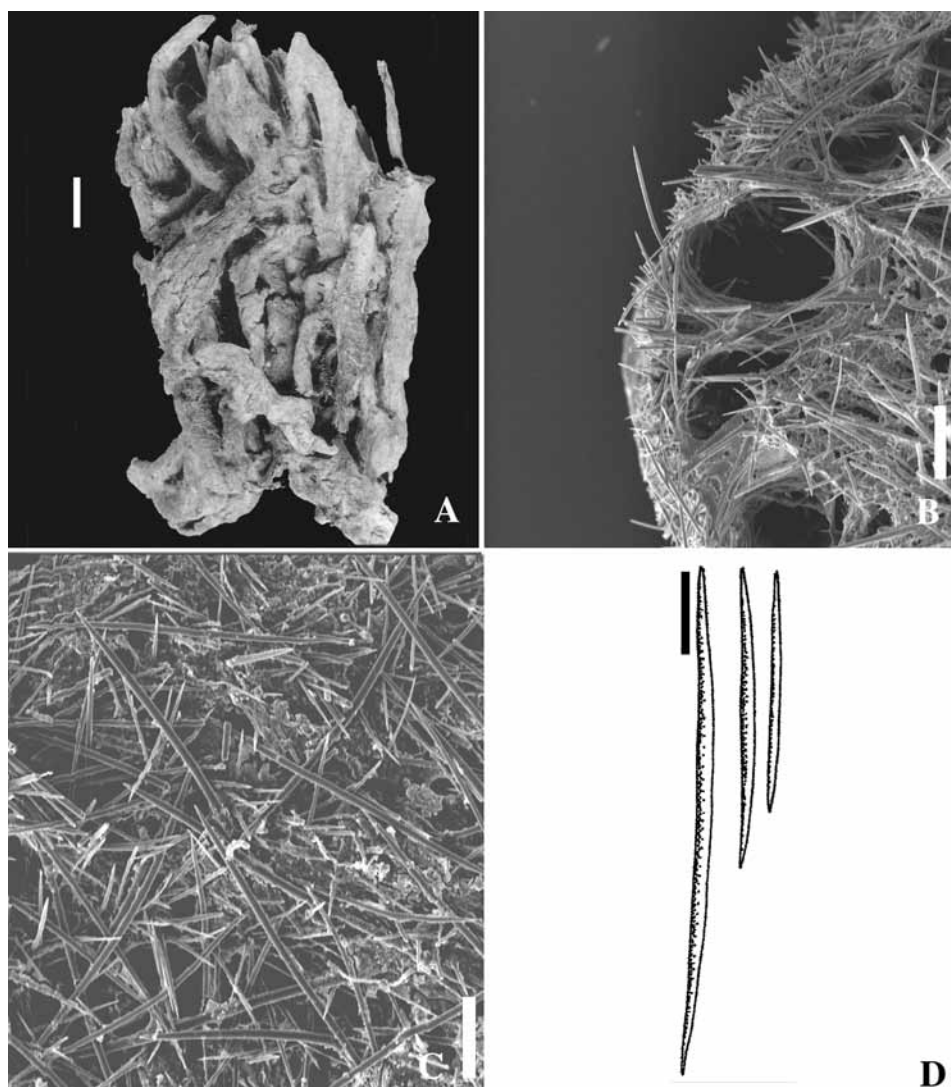


Fig. 10. *Halichondria brunnea* Schmidt (1868, as *Raspaiigella*). A, photo of LMJG lectotype (scale 1 cm). B, SEM image of cross section (scale 100 μm). C, ditto of surface (scale 100 μm). D, spicules drawn from slide of type (scale 100 μm).

The genus *Amorphina* Schmidt, 1870: 40 was erected for *Reniera grossa* Schmidt, 1864, *Halichondria panicea sensu* Bowerbank (1866), *Reniera compacta* Schmidt, 1864 and *Reniera aurantiaca* Schmidt, 1864. Several authors (Topsent, 1925b; Burton, 1934a; de Laubenfels, 1936a) assumed *Reniera grossa* to be the type of *Amorphina*. The type specimens of *R. grossa*, LMJG 15329 from Lesina and LMJG 15189, from unknown locality were examined. Since LMJG 15329 (figured in Desqueyroux-Faúndez & Stone, 1992: fig. 186) is the only specimen with the type locality on its label, it is here proposed as the lectotype, and the remaining series of specimens in LMJG are thus paralectotypes. Several other specimens are in existence with Schmidt's labels (Strassbourg, Berlin), but their type status is doubtful. Both reexamined specimens are members of what is now considered *Haliclona s.l.*, probably of De Weerd's *Haliclona (Rhizoniera)* (De Weerd, pers. comm.), with *Haliclona*-type oxeas of about $160 \times 5 \mu\text{m}$. The skeletons are irregularly reticulate, and in places somewhat confused, hence Schmidt's association of this species with *Halichondria panicea*. The status of *Reniera grossa* as type of the genus *Amorphina* is, however, a matter of discussion. Hooper & Wiedenmayer (1994) indicate Higgin (1877) as the first revisor

who made a subsequent designation of *Reniera grossa* as type, but this designation could not be found in Higgin's paper. Topsent (1925b) suggested that Schmidt himself indicated *Reniera grossa* as the type of *Amorphina*, but this is strictly speaking not true: Schmidt only started his list of assigned species with *R. grossa*, but did not indicate it as type. Burton (1934a) reluctantly accepted that *Reniera grossa* is the type based on Topsent's suggestion, although he emphasized that Schmidt intended the genus to be for sponges like *Halichondria panicea*. This is certainly obvious from Schmidt's definition and some of the species formally described by him as *Amorphina*, e.g., *A. genitrix* Schmidt, 1870 which is a *Spongisorites* (cf. below). Since no formal (correct) type species designation, (i.e., a species expressly stated to be the type) appears to have been made (Hooper & Wiedenmayer's erroneous reference cannot be counted as such), it is proposed to select *Halichondria panicea sensu* Bowerbank, 1866 – which conforms to the neotype of *Spongia panicea* Pallas, 1766 selected above – as the type species, which makes *Amorphina* an objective synonym of *Halichondria* Fleming.

The genus *Pellina* Schmidt, 1870: 41 was erected for type species (by original designation) *Reniera semitubulosa* Schmidt,

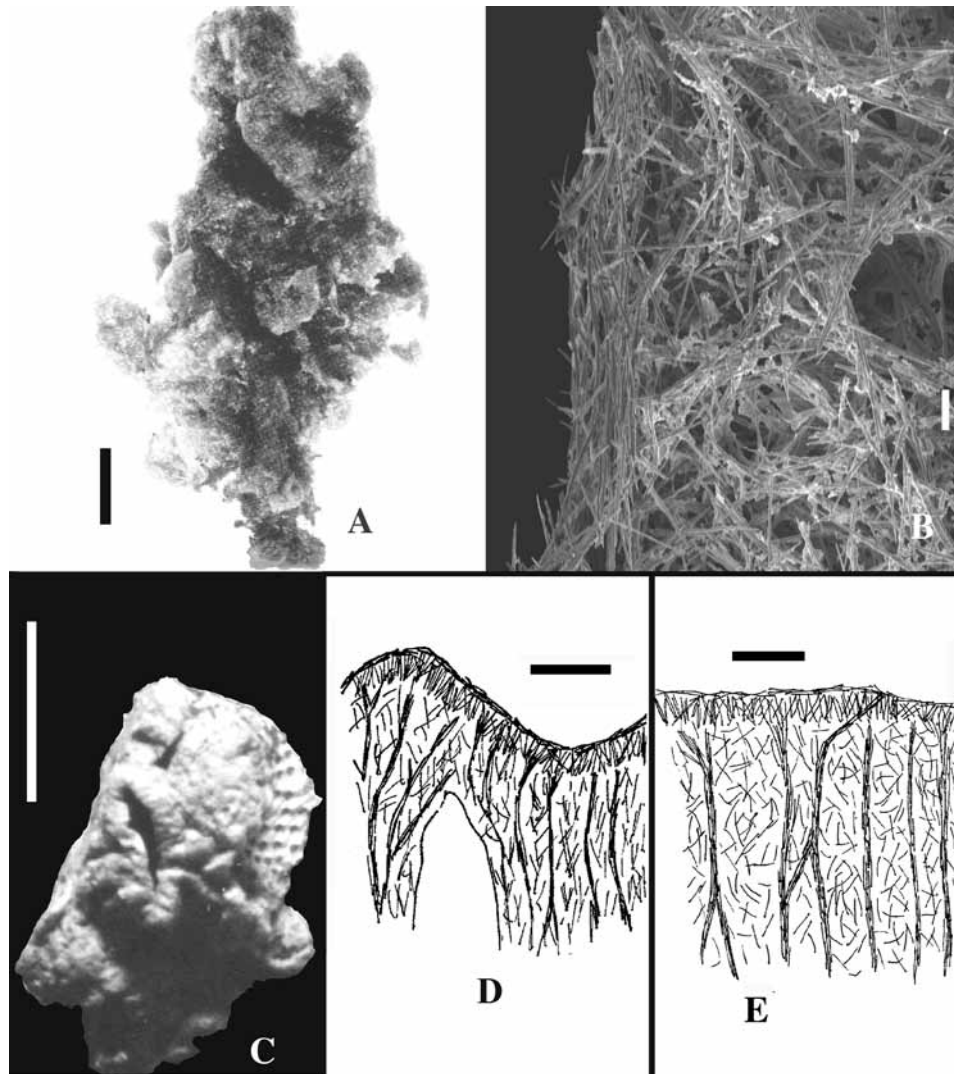


Fig. 11. A–B, *Halichondria semitubulosa* (Schmidt 1862 as *Reniera*) (=type of *Pellina* Schmidt, 1870). A, photo of type specimen (reproduced from Desqueyroux-Faúndez & Stone, 1992) (scale 1 cm). B, SEM image of cross section made from the lectotype (scale 100 μm). C–D, *Halichondria minchini* (Topsent, 1896a as *Menanetia*) (=junior synonym of *H. panicea*). C, photo of MNHN type specimen (scale 1 cm). D, cross-section made from a slide of the type (scale 1 mm). E, *Halichondria corticata* (Burton 1931b as *Halichondriella*) (=junior synonym of *H. panicea*), cross-section reproduced from Burton (1931b: fig. 2) (scale 1 mm).

1862, which may or may not be a junior synonym of *Spongia semitubulosa* Lamarck (1813: 455; 1816: 380). Since the Lamarck material is no longer extant, it is impossible to ascertain what the exact properties of this species are. However, Schmidt's material of *Reniera semitubulosa* is extant in LMJG, and the properties of these specimens objectively determine the nature of *Pellina* (see also De Weerd, 1986: 114). The type material of *Reniera semitubulosa* consists of 7 samples (cf. Desqueyroux-Faúndez & Stone, 1992: 17), but only one bears a label with the type locality ('Venedig'), LMJG 15320, figured in Desqueyroux-Faúndez & Stone, 1992: fig. 203 (here reproduced as Fig. 11A). It is here chosen as the lectotype, while the other specimens all from unknown localities (LMJG 15616, 15617, 15990, 15614, 15615 and 15991) are assigned paralectotype status. The lectotype and paralectotype LMJG 15991 were reexamined. This species forms an irregular mass of lobes, surface smooth, consistency firm. The ectosomal skeleton is detachable and consists of a fairly light tangential skeleton, mostly of single spicules, with very few tracts, surrounding rounded porefields. Subectosomally there is a system of fairly large

rounded holes of 250 μm diameter, separated by thin tracts of spicules. The choanosomal skeleton (Fig. 11B) is a largely confused mass of single spicules, very few tracts. Spicules oxeas, in a large size range but undifferentiated categories, smaller spicules concentrated at the surface, 250–400 \times 3–8 μm . These characters conform to *Halichondria* and it is possible that the species *semitubulosa* is identical to *brunnea* described above. The genus *Pellina* has been employed as a Haplosclerida genus by many authors, but this is obviously erroneous.

The genus *Apatospongia* Marshall, 1892: 16 was apparently erected for type species *Apatospongia fallax* Marshall, 1892: 16 (monotypy). We have been unable to find the paper, as the volume it is supposed to be published in does not seem to contain it. De Laubenfels (1936a: 134) assigned it to the synonymy of *Halichondria*, and we maintain this on his authority.

The genus *Menanetia* Topsent (1896a: 115) was erected (by monotypy) for type species *Menanetia minchini* Topsent (1896a: 115). A type specimen MNHN DT. 2099 from Roscoff, including a slide was examined. It is massively encrusting (Fig. 11C), with

smooth surface, large oscules, firm consistency. The ectosomal skeleton is made up of heavily spiculated bundles of 50–70 µm diameter intercrossing to form a tight reticulation with triangular to rounded meshes of 50–120 µm diameter. The thickness of the ectosomal-subectosomal region is 300–400 µm. In the choanosome (Fig. 11D) there are wavy bundles of spicules, 30–40 µm in diameter following an erratic course with frequent anastomoses. In between, many single spicules lie in confusion. Oxeas relatively small, seemingly divisible in two sizes but with considerable overlap, 100–280 µm. This is a specimen similar to *Halichondria reticulata* (cf. above), which is considered the exposed form of *H. panicea*. Accordingly, *Menanetia* is considered a junior synonym of *Halichondria*.

The genus *Halichondriella* Burton (1931b: 137) was erected for type species (by monotypy) *Halichondriella corticata* Burton (1931b: 137, fig. 2). A portion of the holotype BMNH 1931.10.28.25 from the wall of the Tromsøe aquarium (Norway) was examined, as well as a fragment BMNH 1938.8.18.2 subsequently collected and incorporated in the Oslo Museum identified by Arnesen as *H. corticata*. This is a cushion-shaped sponge, without visible oscules, with an undulating mammillate surface. The ectosomal skeleton is detachable with difficulty and consists of randomly strewn single spicules. Thickness of the ectosomal crust ca. 40 µm. The subectosomal lacunae are small, about 50 µm, separated by spicule tracts of 50–60 µm fanning out to carry the ectosomal crust. The choanosomal skeleton (Fig. 11E) is organized in bundles 20–50 µm in diameter with 6–8 oxeas in cross section, oriented perpendicular to the surface. Many loose single spicules. Oxeas relatively thin and short, 160–300 × 1–4 µm. Since this is an aquarium specimen it is to be expected that it would show adaptation of shape and poor silica supply. Other features in combination are in general agreement with *Halichondria* and the fact that *Halichondria panicea* is a dominant sponge in the Tromsøe environment, make it quite likely that this is a rather delicate form of *H. panicea*.

The genus *Trachyopsilla* Burton (1931b: 138) was erected for type species (by monotypy) *Trachyopsilla glaberrima* Burton (1931b: 138, figs 3–4) in the same paper as the *Halichondriella*. A portion of the holotype from the Trondheim fjord (Norway), BMNH 1931.10.28.77) was examined. This is a cushion-shaped sponge (Fig. 12A) without visible oscules. The surface is smooth, consistency friable, soft. The ectosomal skeleton is a loose and thin tangential layer of mostly single spicules intercrossing randomly. The subectosomal skeleton shows subdermal spaces (Fig. 12B) of 200–300 µm separated by brushes of spicules carrying the ectosome. Choanosomal skeleton of ill-defined bundles of ca. 50 µm diameter, with many confusedly arranged single spicules. Oxeas, 240–340 × 4–8 µm. Burton emphasized the brushes or palisades at the surface as peculiar to his new genus, but such structures are also found in many *Halichondria* spp. including *H. panicea*. Again, it is our firm belief that *Trachyopsilla* is a mere extreme form of *H. panicea* and accordingly falls into synonymy of *Halichondria*.

The genus *Tedanione* Wilson (1894) was erected (by monotypy) for *T. foetida* Wilson, 1894: 338, figs 95–113. This genus was misinterpreted by Dendy (1922b) as a tedaniid genus (now known as *Strongylamma*, see chapter on Tedaniidae elsewhere in this volume). The description and figures of Wilson (no original Wilson material has been unearthed so far, it is not in USNM, K. Rützler *in litteris*) allow the conclusion that the only spicules likely to be proper to the sponge are oxeas 350 µm long and “microscleres (oxeas) of varying length”, and also that the larvae are uniformly

ciliated. Tylotes were also mentioned, but only “very few” were observed. The description fits perfectly with sponges of the genus *Halichondria* and not with tedaniids on two important counts: *Halichondria* species often have a smaller and a larger category of oxeas whereas tedaniids have differentiated spicules including onychaetes, and *Halichondria* larvae are typically ciliated all-over, whereas tedaniid larvae have a bare posterior pole. Until Wilson’s material has been traced, it is not possible to draw a firm conclusion about this synonymy.

Van Soest *et al.* (1990) suggested as further synonyms of *Halichondria*: *Ciocalapata*, *Cioxeamastia*, *Eumastia*, *Pylooderma* and *Spuma*. *Eumastia* with junior synonyms *Cioxeamastia* and *Spuma* is proposed as a valid subgenus of *Halichondria*, rather than a junior synonym, because of the possession of a mass of hollow papillae in combination with a *Halichondria* type skeletal arrangement in several distinct species (cf. below). *Ciocalapata* possesses a complement of genuine styles in addition to the *Halichondria*-like skeleton of oxeas, and for that reason is considered valid. *Pylooderma* has been found to conform to the Poecilosclerida family Dendoricellidae (see Van Soest’s chapter on that family) because of compelling similarity of its type species, *P. latrun-culioides* with chela-bearing *P. demonstrans*.

SUBGENUS *EUMASTIA* SCHMIDT, 1870

Synonymy

Eumastia Schmidt, 1870: 42. *Spuma* Miklucho-Maclay, 1870: 13. *Cioxeamastia* de Laubenfels, 1942: 265.

Type species

Eumastia sitiens Schmidt, 1870: 42 (by monotypy).

Definition

Halichondriidae with surface covered by short conical fistules. Ectosomal detachable tangential skeleton, choanosomal confused skeleton. Spicules exclusively oxeas.

Previous review

Van Soest *et al.* (1990, as junior synonym of *Halichondria*).

Description of type species

Eumastia sitiens Schmidt, 1870 (Figs 12C–D, 13A–C).

Synonymy. *Eumastia sitiens* Schmidt, 1870: 42, pl. V fig. 12; *Halichondria sitiens*; Van Soest *et al.*, 1990: 49, fig. 79.

Material examined. Holotype: ZMUC – Egdesminde, W Greenland, 56–100 m, coll. Olrik. Microscope slide: BMNH 1870.5.3.112 – labelled “Grönland 50”. Other material. Specimens: ZMA POR. 1014 and 4707 – Arctic waters.

Description. Semi-globular cushion (Fig. 12D), yellowish inside, with white surface, densely covered with cone-shaped papillae (Fig. 12C–D) which may be branched and may have an oscule. Size up to 15 cm across. Surface smooth, papillae hollow, conical, stubby at the summit, or more tapering if they bear a terminal oscule. Consistency rather firm. Ectosomal skeleton a tangential ‘skin’ of intercrossing bundles of oxeas (Fig. 13B); subdermal

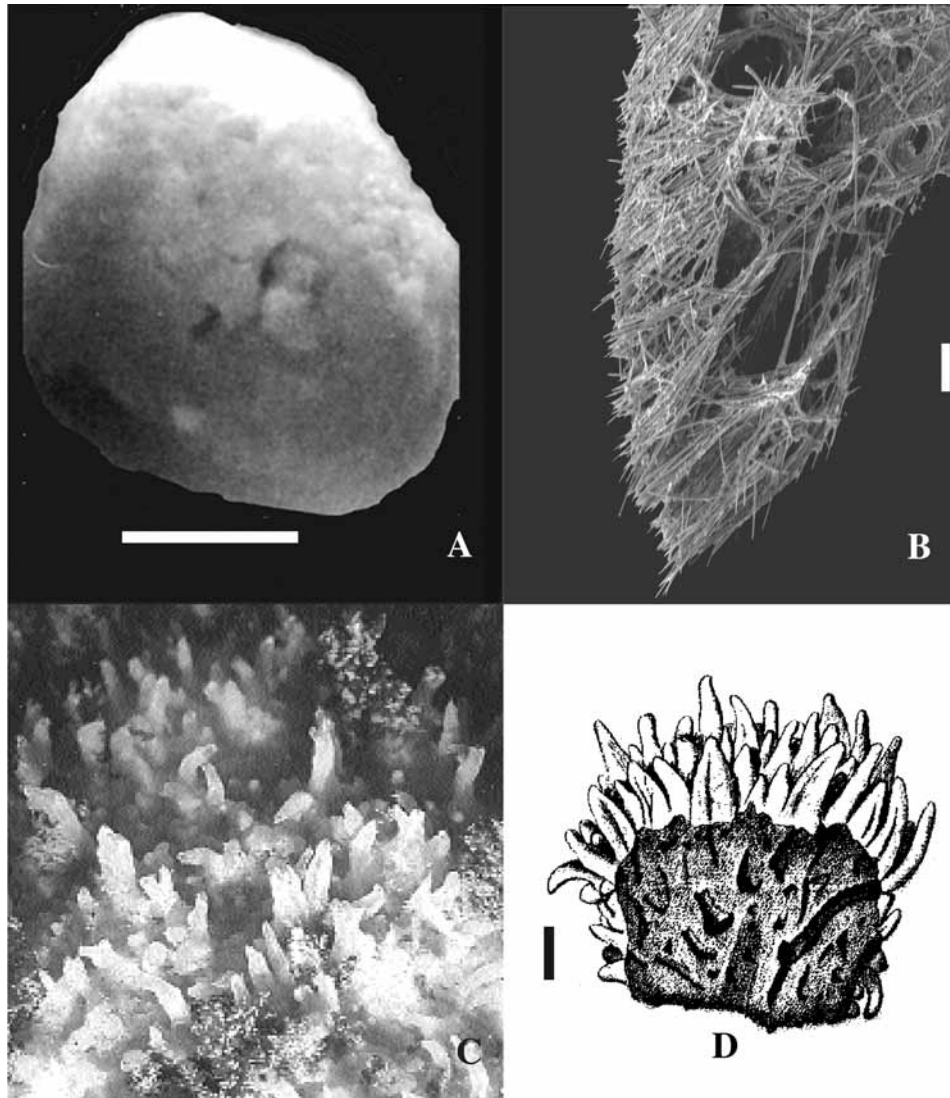


Fig. 12. A–B, *Halichondria glaberrima* (Burton 1931b as *Trachyopsilla*). A, photo of BMNH schizotype (scale 1 cm). B, SEM image of peripheral skeleton of type (scale 100 μm). C–D, *Halichondria (Eumastia) sitiens* (Schmidt, 1870 as *Eumastia*). C, specimen photographed *in situ* (photo B. Picton). D, drawing of type specimen (reproduced from Schmidt, 1870: pl. V fig. 12) (scale 1 cm).

lacunae make the ectosome easily detachable. Choanosomal skeleton of ill-defined spicule tracts and many loose single spicules; spicule tracts may reach a diameter of $\sim 90 \mu\text{m}$. In the papillae longitudinal supporting fibres (Fig. 13A) may be as thick as $1500 \mu\text{m}$. Spicules (Fig. 13C) exclusively oxeas, gradually tapering and sharply pointed, in a single but variable size category: $360\text{--}1020 \times 7\text{--}20 \mu\text{m}$. Distribution and ecology. Boreo-Arctic, down to 100 m.

Remarks. A second species of *Eumastia*, *E. attenuata* Topsent, 1915b, was reported from the Falkland Islands, Southern Atlantic.

The genus *Spuma* Miklucho-Maclay (1870) was erected (by monotypy) for *Spuma borealis* Miklucho-Maclay (1870: 13, pl. II figs 23–30) from the White Sea. No material of this species was examined. The type material is reported lost by Koltun (1959), who had access to the collections of the St. Petersburg Museum. The species is described in four varieties, *papillosa*, *convoluta*, *tuberosa*, and *velamentosa*, which appear to belong to two different species. *Spuma borealis papillosa* is mentioned first and the

drawing of its habit (Fig. 13D), an encrusting cushion covered with long papillae, resembles *Eumastia sitiens*. The var. *convoluta*, *tuberosa* and *velamentosa* are unmistakably *Halichondria panicea*. The paper of Miklucho-Maclay is dated 1869 but in fact has not appeared earlier than 1870, thus simultaneously with *Eumastia* Schmidt, 1870. For reasons of stability *Eumastia* has been chosen as the senior of the two names.

The genus *Cioxeamastia* de Laubenfels (1942) was erected (by monotypy) for *Cioxeamastia polycalypta* de Laubenfels (1942: 265). The holotype USNM 22691 from the northern Hudson Bay, N Canada, was reexamined. It is a subspherical sponge of 3 cm diameter, with surface covered by more than 50 short papillae of 4 mm high and 1–3 mm in diameter. Consistency spongy. Ectosomal tangential skeleton of intercrossing spicules, carried by subectosomal bundles of aligned spicules, up to 15 spicules in cross section. Choanosomal skeleton of single spicules in confusion. Spicules exclusively oxeas, $200\text{--}700 \times 4\text{--}12 \mu\text{m}$. In view of the close similarity to *Eumastia sitiens* this is a likely junior synonym of this apparent circum-arctic species.

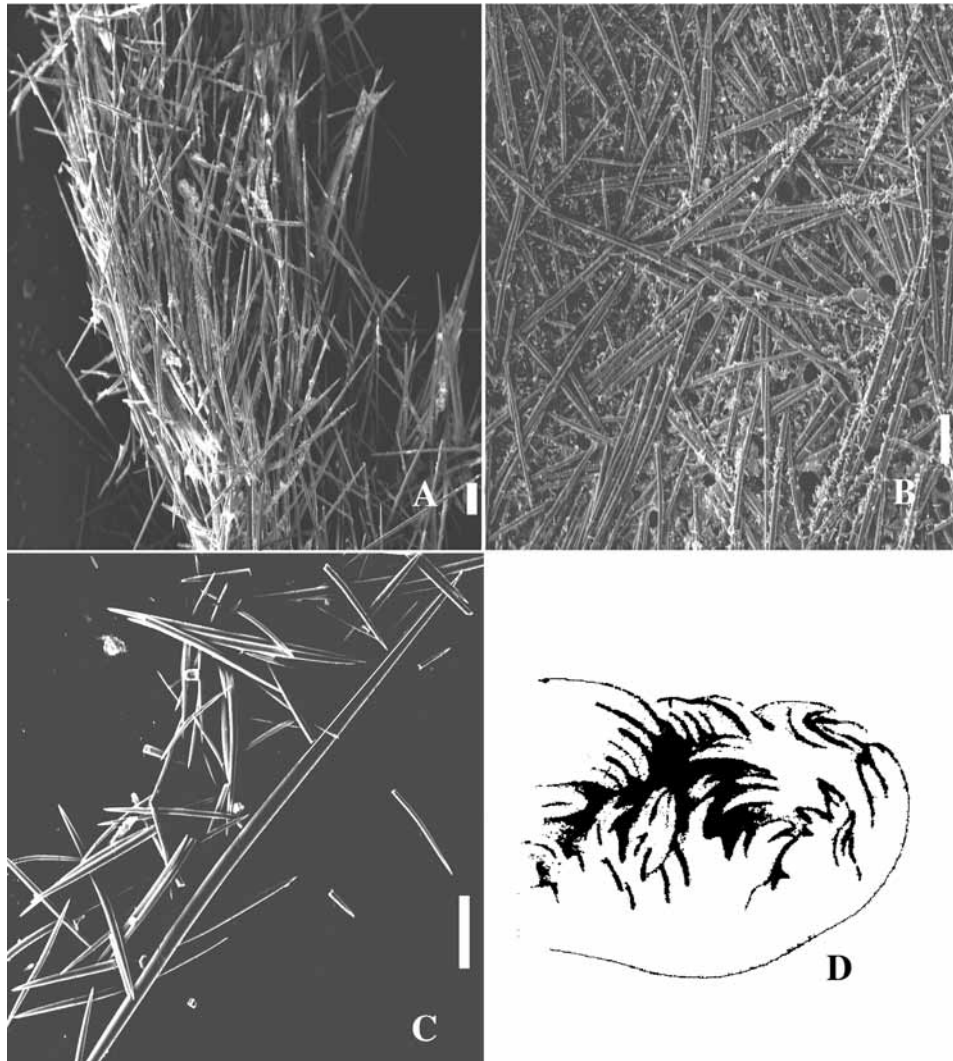


Fig. 13. A–C, *Halichondria (Eumastia) sitiens* (Schmidt, 1870 as *Eumastia*). A, SEM image of fistule skeleton of ZMA specimen (scale 100 μm). B, surface view of same (scale 100 μm). C, spicules of same (scale 100 μm). D, *Halichondria (Eumastia) borealis* (Miklucho-Maclay, 1870 as *Spuma*) (=junior synonym of *H. (E.) sitiens*), drawing of type specimen reproduced from Miklucho-Maclay, 1870 (no size data).

HYMENIACIDON BOWERBANK, 1859

Synonymy

Hymeniacion Bowerbank, 1859: 286. *Stylotella* Lendenfeld, 1888: 185. *Stylinos* Topsent, 1891a: 535. *Amorphilla* Thiele, 1898: 44. *Stylohalina* Kirk, 1909: 539. *Thieleia* Burton, 1932b: 329. *Uritaia* Burton, 1932a: 199. *Rhaphoxiella* Burton, 1934a: 544. *Rhaphidostyla* Burton, 1935b: 651.

Type species

Hymeniacion caruncula Bowerbank, 1859: 286 (by subsequent designation; Bowerbank, 1864: 191) (this is considered a junior synonym of *Spongia perlevis* Montagu, 1818: 86).

Definition

Halichondriidae with encrusting or massively lobate shape and exclusively small styles (>500 μm) for megascleres.

Ectosomal tangential skeleton of intercrossing bundles end single megascleres. Choanosomal skeleton with ascending vague bundles and many loose, confusedly arranged megascleres.

Diagnosis

Encrusting to massive, lobate or occasionally irregularly branching growth forms. Surface irregularly papillate, grooved, corrugated or smooth. Ectosomal skeleton is a thin tangential or paratangential crust, often incomplete, membranous, detachable or coming off in flakes, containing styles or stylotes. Choanosomal skeleton varies from truly confused to disorganized with wispy, slightly plumose ascending spicule tracts of styles or stylotes. Most species have a characteristic fleshy consistency; oxeas have been lost completely and megascleres consist only of styles or stylotes. Several dozens of species, predominantly from temperate and colder waters, but several tropical species have been reliably reported.

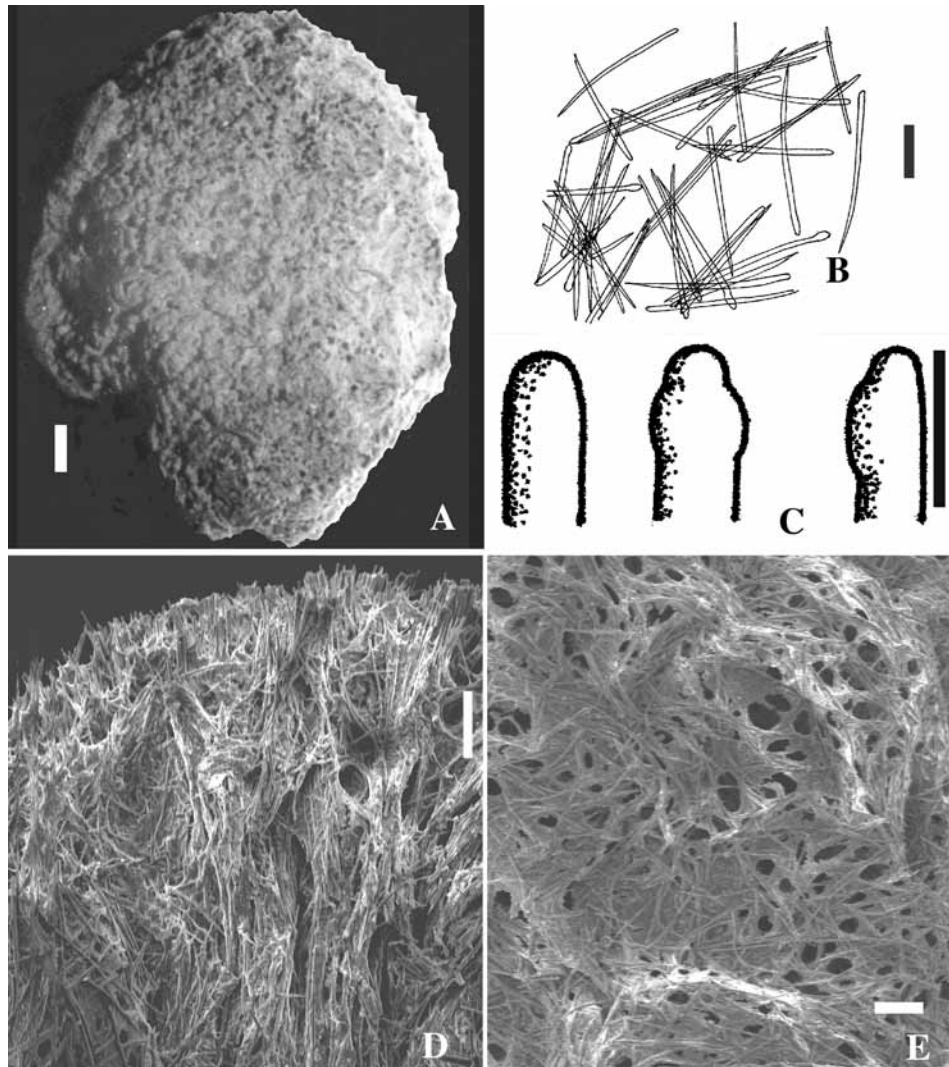


Fig. 14. A–C, *Hymeniacionid perlevis* (Montagu, 1818 as *Spongia*). A, type specimen of *Hymeniacionid caruncuncula* Bowerbank, 1859 (=junior synonym of *H. perlevis*) (scale 1 cm). B, tangential view of ectosomal skeleton reproduced from Van Soest *et al.*, 1990: fig. 87 (scale 100 μm). C, blunt end of apices of styles from ditto (scale 10 μm). D–E, *Hymeniacionid agminata* Ridley, 1884a (=type species of *Stylotella*). D, SEM image of cross section of holotype (scale 100 μm). E, surface view of same (scale 100 μm).

Previous reviews

Van Soest *et al.* (1990); Hooper *et al.* (1997).

Description of type species

Hymeniacionid perlevis (Montagu, 1818) (Fig. 14A–C).

Synonymy (restricted). *Spongia perlevis* Montagu, 1818: 86; *Hymeniacionid perlevis*; Burton, 1957: 31; *Hymeniacionid perlevis*; Van Soest, 1977a: 270, fig. 5, pl. 3D. *Spongia aurea* Montagu, 1818: 87. *Spongia sanguinea* Grant, 1826d: 203, pl. 2 fig. 9. *Hymeniacionid caruncula* Bowerbank, 1859: 286; Bowerbank, 1864: 191, pl. XXXV fig. 372; Bowerbank, 1866: 179; Bowerbank, 1874b: pl. XXXII fig. 1. *Isodictya uniformis* Bowerbank, 1866: 329; Bowerbank, 1874b: 139, pl. LV figs 8–10.

Material examined. Lectotype of *Hymeniacionid caruncula*: BMNH 1930.7.3.1290 (including spicule slide) – Tenby, Wales.

Description. A rounded thickly encrusting mass $5 \times 4.5 \times 1.5$ cm, orange-brown in dry condition, bearing some resemblance to Bowerbank's (1874b) drawing (Fig. 14A). Surface

covered with irregularly shaped short papillae and small digitations. Consistency fragile, crumbly. Fresh specimens of this species (Ackers *et al.*, 1992; Van Soest *et al.*, 1999) are orange to blood-red and have a fleshy consistency. The ectosomal skeleton (Fig. 14B) is a dense crust, with spicules and spicule bundles or brushes in paratangential (at some angle to the surface), rather than strictly tangential arrangement. The choanosomal skeleton is less dense, with wispy bundles following a wavy course to the surface, and many single spicules in confusion. Spicules exclusively styles, slightly curved, often with a faint tylote swelling subterminally (Fig. 14C), $152\text{--}475 \times 3\text{--}12$ μm . Distribution and ecology. NE Atlantic, from Norway (as *Hymeniacionid fallax*) and the British Isles along most European coasts, penetrating the Mediterranean and reaching south and west to Macaronesian islands, intertidal to shallow subtidal, on rocks, *Laminaria* holdfasts, and also buried in the sand (then developing relatively long papillae). This is one of the most common species of Europe.

Remarks. The gender of *Hymeniacionid* remains contentious. It is true that most names ending in the Greek suffix '-on' are of neuter gender, but the combination 'Hymeniacionid' is not

a known noun in the Greek language, so there is room for doubt. It is also customary to derive the gender of a genus name from the use by its author, and it is clear from Bowerbank's use of the genus name that he considered *Hymeniacion* to be female (e.g., *H. caruncula*, *H. aurea*, *H. mammeata*, *H. perlevis*, *H. sanguinea*). We propose here to settle this matter by establishing the gender as female. Although the type specimen(s) of *Spongia perlevis* Montagu (1818) are not with certainty identified in the collections of BMNH, there are two unregistered slides labelled "*Hymeniacion perlevis* Montagu (*Halichondria* Montagu) from type 'Devon'" which may represent Montagu's material. The slides conform closely to *Hymeniacion caruncula*. The affinities of *Hymeniacion* are controversial. The genus was made the type of a family Hymeniacionidae de Laubenfels, 1936a (see above), which was subsequently used by many authors for genera with exclusively styles as megascleres and a dendritic or confused architecture. Genera with such characters are now distributed over various families (Dictyonellidae and Axinellidae), whereas *Hymeniacion* because of its possession of a (para-) tangential surface crust is assigned to Halichondriidae, as a genus with exclusively truly monactinal megascleres (styles of the other genera are suspected diactinal modifications).

The genus *Stylotella* Lendenfeld (1888) was erected for type species *Stylotella digitata* Lendenfeld (1888: 185) (by subsequent designation; Hallmann, 1914: 349) from N Australia. A portion of the type specimen is kept in the collections of BMNH under an unpublished name '*Truncatella micropora*'. We agree with Hallmann (1914), that this is an obvious junior synonym of *Hymeniacion agminata* Ridley (1884a: 466, pl. XLI fig. E, pl. LIII fig. f), of which the type specimen, BMNH 1881.10.21.347, was reexamined. This is a mass of erect, limp cylindrical branches and digitations tapering to a thin apex. The surface is smooth, small inconspicuous oscules are scattered in low numbers over the branches. The ectosomal skeleton is a tangential crust of intercrossing spicule tracts (Fig. 14E), very much like that found in *Halichondria*, overlying a more open choanosomal skeleton with few tracts and many loose confusedly arranged megascleres (Fig. 14D). Spicules slightly curved styles, $182\text{--}271 \times 4\text{--}8 \mu\text{m}$. These characters approach *Hymeniacion* to such an extent that we propose to consider *Stylotella* a junior synonym. The genus name has been used for a variety of sponges different from the type in lacking a surface skeleton, e.g., *Stylotella aurantium* Kelly & Bergquist (1988). This and similar sponges assigned to *Stylotella* are better placed in the Dictyonellidae genus *Stylissa*, which has a rather confused choanosomal skeleton of thick styles, but lacks any surface skeleton. In fact, the species '*Stylotella* *aurantium*' conforms closely to *Stylissa massa* (Carter, 1887, as *Axinella virgultosa massa*). Wiedenmayer (1989) employed a subfamily Stylotellinae for poecilosclerid sponges lacking microscleres, possessing thin styles or strongyles as megascleres, and having their skeletal tracts frequently partly or wholly replaced by sand columns. Such sponges are now united in the family Chondropsidae (see Van Soest's revision of that family elsewhere in this volume), but the genus *Stylotella* by virtue of the properties of its type species is excluded from this family, and assigned here to Halichondriidae.

The genus *Stylinos* Topsent, 1891a: 535 was erected for type species *Isodictya uniformis* Bowerbank, 1866: 329 (by subsequent designation; Hooper & Wiedenmayer, 1994: 295). A microscopical slide containing cross sections of the type specimen labelled "*Isodictya uniformis* Bk... from Type, BMNH 1877.5.21.751",

bearing the number "Bk.751" and with engraved number "R2698" was reexamined. The skeleton is confused with vague spicule bundles without visible spongin running to the surface following a wavy course. Many interstitial spicules in confusion. At the surface there is a crust of tangential and paratangential spicules intercrossing at all angles. The spicules are smooth styles, $220\text{--}310 \times 3\text{--}6 \mu\text{m}$, matching those of *Hymeniacion perlevis* as do the other features. All of these observations match the description by Bowerbank. *Stylinos* is an obvious synonym of *Hymeniacion* by virtue of the perhaps unfortunate type species designation by Hooper & Wiedenmayer. Topsent, in subsequent publications (Topsent, 1892a; 1892b) made clear that he intended this genus to be a poecilosclerid, as he erected *Stylinos jullieni* in 1892a: 137 as type of *Stylinos*. This species is very probably a member what is now to be called *Ulosa* de Laubenfels, 1936a, and consequently Hooper & Wiedenmayer attempted to sink *Ulosa* into synonymy of *Stylinos*. However, since *S. jullieni* was not among the species mentioned in Topsent's 1891a publication, it cannot be the type of *Stylinos*. Hooper & Wiedenmayer (1994) were apparently unaware of the true nature of *Isodictya uniformis* when they designated this the type of *Stylinos*.

The genus *Amorphilla* Thiele (1898: 44) was erected for type species (by original designation) *Hymeniacion sanguinea* Grant (1826d: 203, pl. 2 fig. 9). No type material could be found in BMNH. It is described as encrusting on the surface of rocks, 6.5 cm diameter, more than 1.5 cm thick. Surface flat, but with small, round elevations and depressions, colour deep red, numerous small oscules. Slimy when torn. Spicules depicted as styles, curved, equally thick throughout, but no size given. The described characters conform to those of *Hymeniacion perlevis* and we consider *H. sanguinea* a junior synonym of it, thus making *Amorphilla* an objective junior synonym of *Hymeniacion*.

The genus *Stylohalina* Kirk, 1909 was erected for type species (by monotypy) *Stylohalina conica* Kirk (1909: 539, pl. 25) from New Zealand. The type material is probably lost (Barraclough Fell, 1950), but the description is clear enough to be able to establish that this is an obvious junior synonym of *Hymeniacion*. The type is described as a flattened, conical mass, with a single large oscule at its apex. The surface has minute elevations, small, round or oval pores, it is glossy and of dense texture. The ectosomal skeleton is quite thin, and minutely conulose through projecting spicules, but they are parallel to the surface. Choanosomal skeleton consists of irregularly scattered spicules, in low density, sometimes arranged in small irregular bundles. Spicules styles, with slight swelling at stylote end, slightly curved, average $360 \times 10 \mu\text{m}$.

The genus *Thieleia* Burton (1932b: 329) was erected for type species (by original designation) *Hymeniacion rubiginosa* Thiele (1905: 421, fig. 44), from the SE Pacific. A paralectotype BMNH 1908.9.24.133 was reexamined. The species is a flat crust (Fig. 15A) with undulating but optically smooth surface, yellowish in alcohol. The ectosomal skeleton is paratangential (Fig. 15B), consisting of brushes diverging at all angles, no tangential spicules are apparent. The choanosomal skeleton consists of thin bundles running parallel to the surface, in between which there is a confused mass of single megascleres. Spicules styles, $325 \times 7 \mu\text{m}$. This species conforms to *Hymeniacion* but for its lack of tangential spicules. Since so far only one such species has been described, we propose to consider *Thieleia* a junior synonym.

The genus *Uritaia* Burton, 1932a was erected for type species (by monotypy) *Uritaia halichondrioides* Burton (1932a: 199, pl. 7 figs 3–4, text-fig. 4). The type is not in BMNH, but may still be

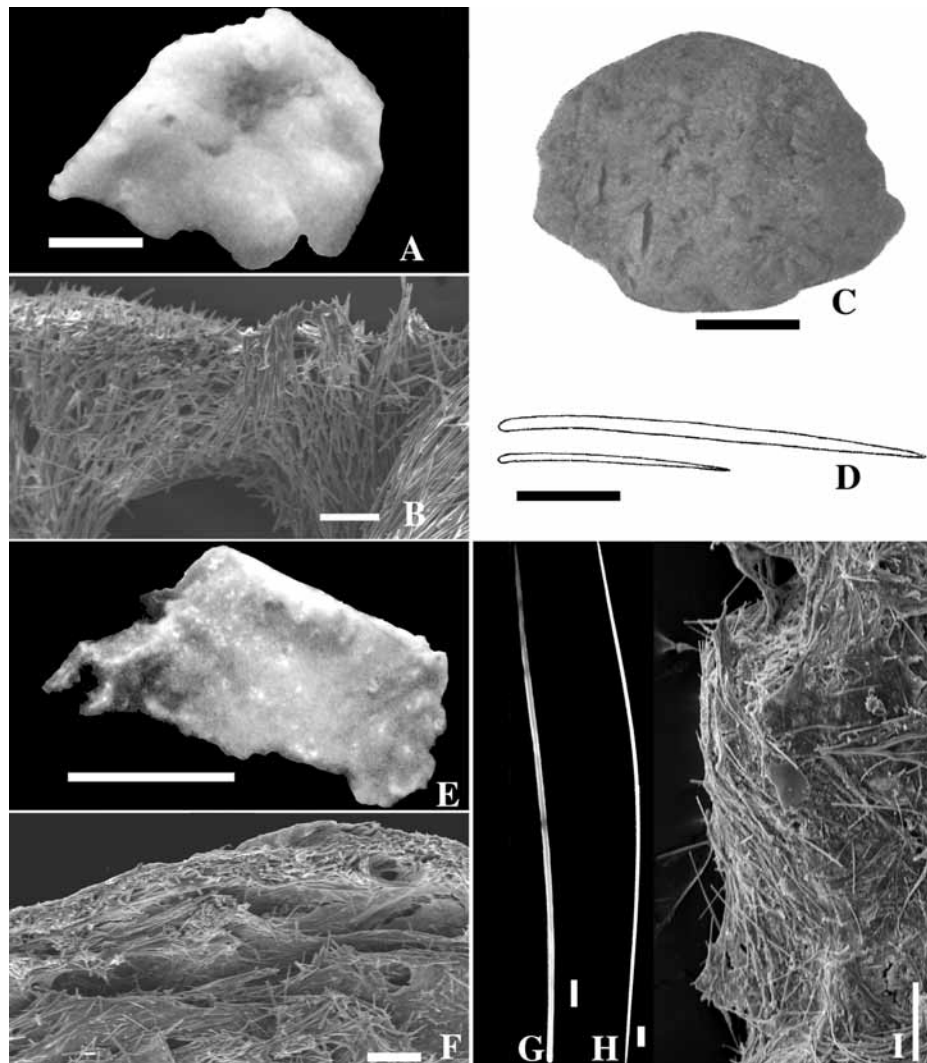


Fig. 15. A–B, *Hymeniacion rubiginosa* (Thiele, 1905) (=type of *Thieleia* Burton, 1932a). A, BMNH paralectotype specimen (scale 1 cm). B, SEM image of ectosomal skeleton of paralectotype (scale 100 μm). C–D, *Hymeniacion halichondrioides* (Burton, 1932 as *Uritia*). C, type specimen reproduced from Burton, 1932: pl. 7 fig. 3 (scale 1 cm). D, spicules from Burton, 1932, text fig. 4 (scale 100 μm). E–F, *Hymeniacion corticata* (Thiele, 1905 as *Batzella*) (=type of *Rhaphoxiella* Burton, 1934a). E, photo of BMNH schizotype (scale 1 cm). F, SEM image of cross section of schizotype (scale 250 μm). G–I, *Hymeniacion kitchingi* (Burton, 1935b as *Rhaphidostyla*). G–H, spicules of holotype (scale 10 μm). I, SEM image of cross-section of holotype (scale 100 μm).

extant in the Tohoku Imperial University, Japan. It is described and figured as an irregularly massive sponge (Fig. 15C). The surface bears irregular ridges or tubercles; few, small, inconspicuous oscules level with the surface. The ectosomal skeleton is described and figured as a close-set palisade of brushes of spicules with single spicules arranged tangentially. The choanosomal skeleton is loose and irregular, with many spicules in confusion. Spicules styles in two size categories (Fig. 15D), the smaller concentrated at the surface, $420 \times 14 \mu\text{m}$ and $260 \times 7 \mu\text{m}$. The only character in which it differs from *Hymeniacion* proper is the possession of two distinct size categories of styles rather than a single overlapping size range. In view of the fact that the sizes of both category fall within the size range of the styles of the type species of *Hymeniacion* (cf. above), we propose to consider this a junior synonym.

The genus *Rhaphoxiella* Burton (1934a: 544) was erected for type species (by original designation) *Batzella corticata* Thiele (1905: 438, fig. 58) from Juan Fernandez Island in the SE Pacific. A type fragment (2×1 cm) and slide, BMNH 08.9.24.151, were

reexamined. This is a rather distinct species forming a flat thick crust (Fig. 15E) with smooth but somewhat irregular surface. It has a thick, dense ectosomal crust consisting of a mass of intercrossing single spicules (Fig. 15F), overlying a choanosome with large open spaces and low spicular density. Spicules include all forms between strongyles and oxeas, up to $430 \times 7 \mu\text{m}$ in size. Burton erected this genus because of the possession of strongyles in combination with styles. For the time being it is proposed to class this ill-known species in the genus *Hymeniacion*, but should other similar species be found, then the genus may be revived.

The genus *Rhaphidostyla* Burton (1935b: 651) was erected for type species (by original designation) *Rhaphidostyla kitchingi* Burton (1935b: 652) from Scotland. The holotype BMNH 1934.9.26.79 and four paratypes 1934.9.26.80–83 were reexamined. The holotype is an irregularly massive sponge of $2 \times 3 \times 2$ cm, with glabrous, uneven surface, yellow/yellow-green in colour. Fresh specimens (Ackers *et al.*, 1992; Van Soest *et al.*, 1999) are pinkish yellow and may have long limp digitations. Oscules rather

conspicuous with raised rim. The consistency is soft, compressible. The ectosomal skeleton is light, with spicule cover rather patchy. The choanosomal skeleton (Fig. 15I) is distinct in consisting of a confused mass of wispy bundles, each 20–30 µm in diameter and following an erratic course, to end eventually at the surface where the spicules fan out to form bundles of more or less tangential ectosomal megascleres. Spicules slender styles (Fig. 15G–H), relatively few with telescopic ends, thin, rather uniformly 220–230 × 2–6 µm. Burton emphasized the telescopic ends of the spicules and included for that reason several species with dendritic spicules tracts and very much longer styles in *Rhaphidostyla*. These other species are obvious members of *Dictyonella* (family Dictyonellidae). The type of *Rhaphidostyla* conforms to *Hymeniacidon*, but differs from *H. perlevis* in colour, smaller and thinner spicules, and wispy tracts.

Van Soest *et al.* (1990) suggested that *Nailondria* de Laubenfels (1954) was a junior synonym of *Hymeniacidon*, but subsequent study of the type material, revealed that it conforms to *Amorphinopsis* (cf. above).

LAMINOSPONGIA PULITZER-FINALI, 1983

Synonymy

Laminospongia Pulitzer-Finali, 1983: 546.

Type species

Laminospongia subtilis Pulitzer-Finali, 1983: 546 (by monotypy).

Definition

Halichondriidae (?) without special ectosomal skeleton, with confused choanosomal skeleton; megascleres variable in size and shape.

Diagnosis

Laminar shape, with evenly distributed small oscules at one of the sides. Skeleton of confusedly arranged single spicules, no visible spongin. Spicules oxeas and styles in a large size range. A single species which is not certainly a member of this family and is considered valid only because it does not conform clearly to any described genus.

Description of type species

Laminospongia subtilis Pulitzer-Finali, 1983 (Fig. 16A–D).

Synonymy. *Laminospongia subtilis* Pulitzer-Finali, 1983: 546, fig. 50; *Topsentia subtilis*; Van Soest *et al.*, 1990: 39, fig. 50.

Material examined. Holotype: MCSNG 47175 – Calvi, Italy.

Description. The holotype now consists of several fragments of a single laminar specimen of 120 cm² in lateral expansion and max 3 mm thick (Fig. 16A). The surfaces are both optically smooth but differ in the occurrence of numerous scattered small oscules, 0.2–0.3 mm in diameter. The ectosome is not detachable. Consistency firm, lamella breaks, when bent. The skeleton lacks an ectosomal cover or other specialization (Fig. 16C), the choanosome is halichondrioid, with single spicules in confusion

(Fig. 16B). Spicules (Fig. 16D) oxeas to styles, not separable in categories, among which a few strongyles with unequal ends, 350–1300 × 9–19 µm. Distribution and ecology: Italian Mediterranean, 137 m.

Remarks. Van Soest *et al.* (1990) assigned this species to *Topsentia*, but there is little evidence to support that assignment. The lack of a clearly detachable surface crust as well as a large size range in spicules are shared with *Topsentia*, but there the agreement ends. *Laminospongia subtilis* has the bladed form and indiscriminate occurrence of styles and oxeas of some Axinellidae genera (*Axinella*, *Cymbastela*, *Phakellia*), but these have a well-organized reticulate choanosomal skeleton entirely lacking in *Laminospongia*. It is proposed here to leave this distinctive species as a valid genus of Halichondriidae until further evidence for its systematic position has been obtained.

SPONGOSORITES TOPSENT, 1896

Synonymy

Spongisorites Topsent, 1896a: 117. *Aponastra* Topsent, 1927b: 5. *Oxeostilon* Ferrer Hernandez, 1922: 9.

Type species

Spongisorites placenta Topsent, 1896a: 117 (by monotypy).

Definition

Halichondriidae with smooth surface caused by dense ectosomal crust of smaller megascleres; choanosomal skeleton a densely confused mass of smaller and larger megascleres traversed by directionless vaguely delimited multispicular tracts. Megascleres oxeas in several size categories.

Diagnosis

Massive-amorphous to subspherical. Surface optically smooth. Oscules inconspicuous. Ectosomal skeleton a thick flaky crust of paratangentially arranged, relatively thin and small spicules; choanosomal skeleton with spicules strewn in confusion, occasionally grouped in spongin-enforced tracts, directed mainly parallel or oblique to the surface. Many species with aerophobic pigments causing a discolouration to dark or black tinges after collection. Megascleres are oxeas of various sizes, sometimes with their points modified to strongyles or styloids, often centrangulate. Approximately ten species distributed in deeper waters of all oceans.

Recent reviews

Van Soest *et al.* (1990), Pomponi *et al.* (1991), Hooper *et al.* (1997).

Description of type species

Spongisorites placenta Topsent (1896a) (Fig. 17A–B).

Synonymy. *Spongisorites placenta* Topsent, 1896a: 117.

Material examined. Holotype: MNHN DT. 2409 – Concarneau, W France.

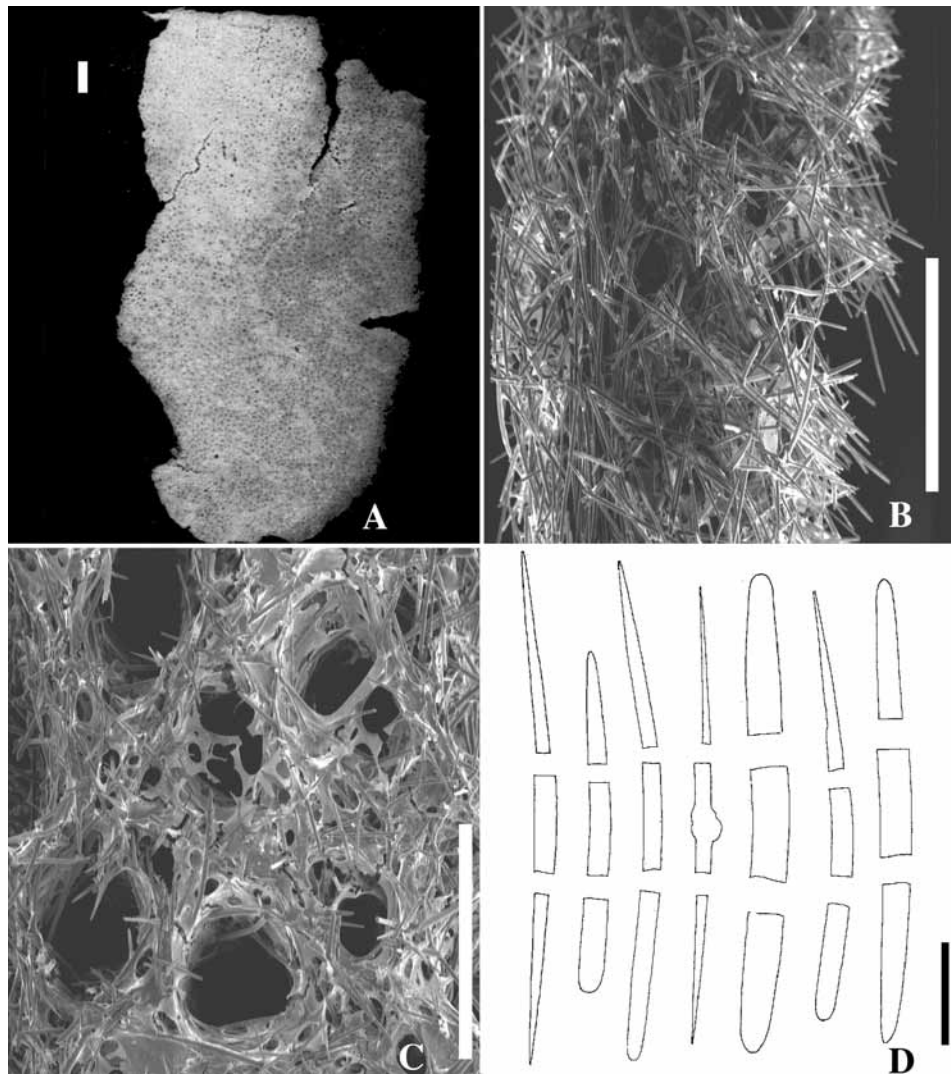


Fig. 16. A–D, *Laminospongia subtilis* Pulitzer-Finali 1983. A, type specimen reproduced from Pulitzer-Finali, 1983: fig. 59 (scale 1 cm). B, SEM image of cross section of fragment of the holotype (scale 1 mm). C, surface view of ditto (scale 1 mm). D, spicules reproduced from Pulitzer-Finali 1983: fig. 59b (scale 50 μm).

Description. Shape a flat massive, thick crust. The holotype in MNHN consists of two small, globular, fragments (Fig. 17A). Surface smooth, no visible apertures. Consistency firm but friable. The ectosomal skeleton is a dense mass of smaller spicules, arranged in all directions (Fig. 17B). It is detachable only as a thicker flake. Choanosome cavernous, but densely spiculated between the cavities, tracts vaguely delimited and not oriented towards the surface. Spicules, smooth oxeas double curve, sharply pointed at the endings, large size range and probably at least two size categories, in ectosome a shorter category of approximately $70 \times 5 \mu\text{m}$, in the choanosome a relatively long and thin category $300\text{--}360 \times 6 \mu\text{m}$ predominates. Distribution and ecology. W coast of France, probably also along most other coasts of Europe, dredged from deeper waters.

Remarks. The type was presumed to be lost by Van Soest *et al.* (1990), but a subsequent visit to MNHN revealed that it still exists. Van Soest *et al.* (1999) synonymized *Spongosorites placenta* with *Amorphina genitrix* Schmidt, 1870. We reexamined some of Schmidt's type specimens from the Copenhagen Museum. It is definitely a *Spongosorites*, but it has the larger spicule sizes

clearly in excess (up to $600 \mu\text{m}$) of those of the type specimen of *S. placenta*, which may indicate specific distinctness.

The genus *Aponastra* Topsent (1927b: 5) was erected (by monotypy) for type species *Aponastra dendyi* Topsent (1927b: 5, see also Topsent, 1928c: 159, pl. III fig. 24, pl. V fig. 12) from 91 m off the Cape Verde Islands. A slide of the type, MNHN DT. 2865 from stat. 1203, was reexamined. This sponge (Fig. 17C) has an irregular massive base from which rises a short branch of black colour with smooth surface. The ectosomal skeleton consists of a layer of tangential smaller spicules, deposited on an inner layer of tangential larger spicules. The interior is cavernous. The choanosomal skeleton consists of single, irregularly arranged spicules. Spicules (Fig. 17D) oxeas, the smaller of which are termed 'microrhabds' by Topsent, because of their position and frequent possession of centrotyle swelling. We believe there are at least two categories, $500 \times 16\text{--}20 \mu\text{m}$ and $45\text{--}145 \times 2\text{--}7 \mu\text{m}$, but common intermediate sizes constitute probably a third category. The shape and arrangement of the spicules conforms to *Spongosorites* and accordingly we propose to consider *Aponastra* a junior synonym.

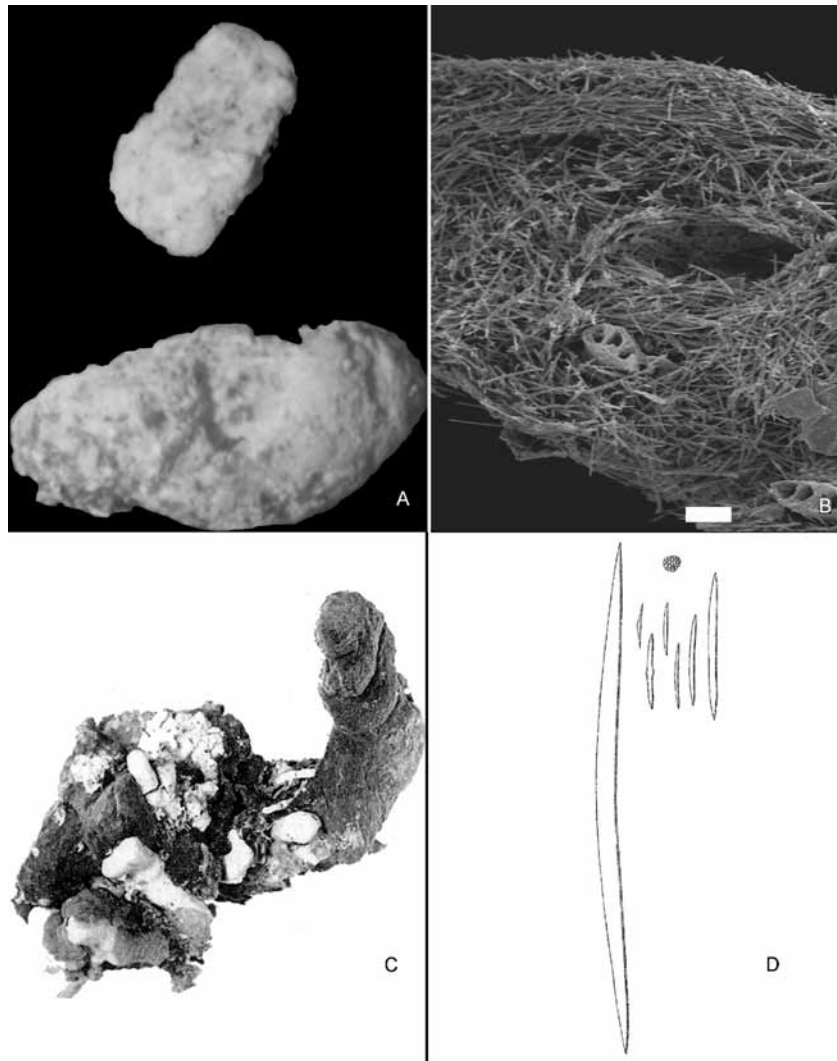


Fig. 17. A–B. *Spongosorites placenta* Topsent, 1896. A, holotype specimen. B, peripheral skeleton of holotype (scale 100 μm). C–D *Spongosorites dendyi* (Topsent, 1927 as *Aponastra*). C type specimen. D, spicules (both from Topsent, 1928).

The genus *Oxeostilon* Ferrer Hernandez (1922: 9) was erected (by monotypy) for *Oxeostilon annandalei* Ferrer Hernandez (1922: 9, figs 8–9). No material could be traced. It is described as a thick mass with undulating shiny surface. The skeleton is confused with some thicker tracts developed. Spicules are oxeas and strongly modified, often curved abruptly, in a large size range of 320–800 μm , possibly in size categories. Van Soest *et al.*, 1990 proposed to consider this genus a junior synonym of *Topsentia* on the grounds that the large spicule size conformed to *Topsentia* rather than to *Spongosorites*. This decision is reversed here, as spicule sizes overlap with those of *Spongosorites* and also the surface characters of *S. annandalei* are more reminiscent of that genus. The species remains ill-known.

TOPSENTIA BERG, 1899

Synonymy

[*Anisoxya*] Topsent, 1898b: 234 (preocc. by *Anisoxya* Mulsant, 1856, Coleoptera). *Topsentia* Berg, 1899: 77. *Trachyopsis* Dendy, 1905: 147. *Viles* de Laubenfels, 1934: 13.

Type species

Anisoxya glabra Topsent, 1898b: 234 (by original designation).

Definition

Halichondriidae with an ectosomal skeleton consisting of a crust-like partly tangential or paratangential arrangement of spicules grading into the densely confused choanosomal skeleton. Ectosome detachable only in flakes due to lack of subdermal cavities, but choanosome cavernous. Spicules oxeas or modifications, in a large size range, including smaller spicules concentrated at the surface.

Diagnosis

Massive, lobate, or wall-shaped sponges, with brittle and rough texture; bright colours typically absent; ectosomal skeleton composed of crust of compact, smaller ectosomal oxeas lying tangentially or paratangentially producing a microhispid surface (but optically smooth); choanosomal skeleton with very little collagen,

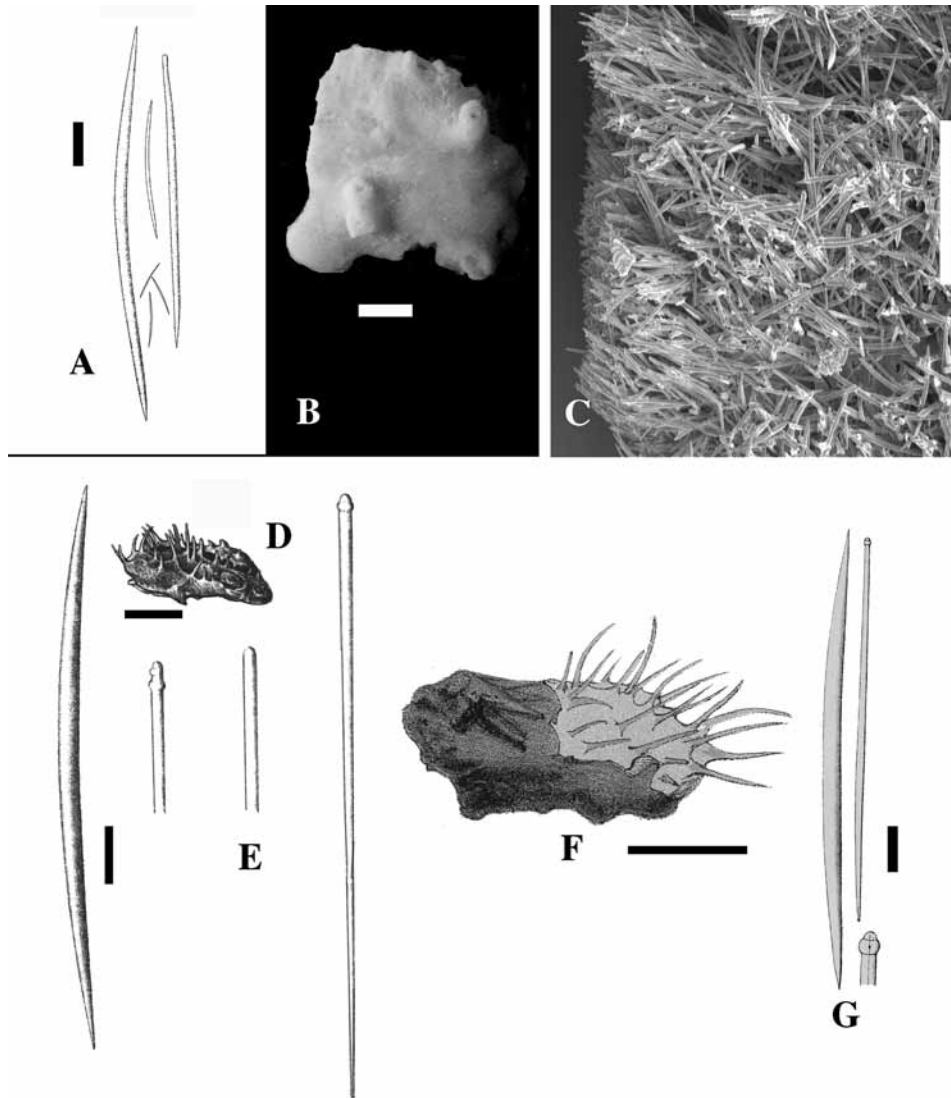


Fig. 18. A–C, Genus *Topsentia*. A, *Topsentia glabra* (Topsent, 1898b as *Anisoxya*), spicules reproduced from Topsent, 1904b: pl. XIII fig. 4 (scale 100 μm). B–C, *Topsentia halichondrioides* (Dendy, 1905 as *Trachyopsis*). B, photo of BMNH holotype (scale 1 cm). C, SEM image of cross section of holotype (scale 1 mm). D–G, *Vosmaeria crustacea* Fristedt, 1885. D, drawing of habit, reproduced from Fristedt, 1885, pl. II fig. 5 (scale 1 cm). E, drawing of spicules from ditto (scale 100 μm). F, watercolour of Vosmaer's (1885a) *Inflatella* spec. considered a synonym of *V. crustacea*, reproduced from his pl. II fig. 5 (scale 1 cm). G, spicules from ditto (scale 100 μm).

no spongin-cemented fibres, resulting in an utterly confused, directionless arrangement of spicules packed around canals and cavities; megascleres are oxeas of a wide size range, usually in 2–3 size classes; twisted, bent or doubly-bent spicules sometimes present; no raphide microscleres. A dozen species recorded from all three oceans, mostly at lower latitudes.

Previous reviews

Van Soest *et al.* (1990), Hooper *et al.* (1997).

Description of type species

Topsentia glabra (Topsent, 1898b) (Fig. 18A).

Synonymy. *Anisoxya glabra* Topsent, 1898b: 234; *Topsentia glabra*; Berg, 1899: 77; Topsent, 1904b: 131, pl. XIII fig. 4.

Material examined. Lectotype: MOM (not seen). Slide: MNHN DT. 1169 – Prince de Monaco Expedition, stn. 589, Azores.

Description. Massive flat yellowish crust; thickness 2–5 cm. Surface smooth, but rough to the touch, no visible oscules. Consistency fragile, due to cavernous interior. Ectosome easily detachable, but comes off in flakes. The ectosomal skeleton consists of an abundance of larger oxeas tangential to the surface, with spaces in between these filled by irregularly arranged small oxeas intercrossing at all angles. Choanosome cavernous, skeleton a solid halichondrioid mass of spicules. No spongin, no fibres or tracts. Spicules (Fig. 18A) oxeas, occasionally stylote modifications, in three size categories, large oxeas, smooth, fusiform sharply pointed, curved in the middle, $500\text{--}1000 \times 13\text{--}30 \mu\text{m}$; intermediate oxeas, smooth, fusiform, sharply pointed, slightly curved, $200\text{--}350 \times 5\text{--}7 \mu\text{m}$; small oxeas, fusiform, sharply pointed, slightly curved, concentrated at the surface, $50\text{--}120 \times 1\text{--}4 \mu\text{m}$. Distribution and ecology. Azores, deep water.

Remarks. The discriminating characters of this genus concern the brittle consistency based on a high spicule density in the absence of tracts and spongin, and the occurrence of a large size range of fusiform oxeas, the largest of which are 600 µm long or more.

The genus *Trachyopsis* Dendy (1905: 147) was erected (by monotypy) for type species *Trachyopsis halichondrioides* Dendy, 1905: 147, pl. X fig. 10. The holotype BMNH 1907.2.1.44 was reexamined. This is a massive sponge with volcano-shaped oscules (Fig. 18B). Surface rough, consistency hard. Skeleton an extremely dense confused mass of oxeas (Fig. 18C), of which the larger are 600–700 × 30–35 µm; small oxeas rare. Although the spicule size categories are not obvious, the remaining characters of the species conform quite closely to *Topsentia* and accordingly this genus is considered a junior synonym. Most other species assigned to *Trachyopsis* belong to *Axinyssa* rather than to *Topsentia*. Van Soest *et al.* (1990) considered the genus *Alloscleria* Topsent, 1927b to be a junior synonym of *Topsentia*, ignoring the description of spined oxeas among the megascleres. Reexamination of a type slide in MNHN revealed that these are indeed present in the slide, and for that reason we reassign this genus to the family Desmoxyidae (see chapter on Desmoxyidae by Hooper in this volume).

The genus *Viles* de Laubenfels, 1934: 13 was erected for type species *Viles ophiraphidites* de Laubenfels, 1934: 13 from Puerto Rico (monotypy). The holotype USNM 22334 was reexamined. This is greyish pink, massive sponge, 4 cm in diameter, 2 cm high. The skeleton is confused, and at the surface there is some notable strengthening in the ectosomal region, with a concentration of smaller megascleres. Megascleres oxeas in a large size range, 300–1000 × 10–20 µm. Irregularly curved or twisted forms are not uncommon among the smaller oxeas. Characters of *Viles ophiraphidites* conform to those of *Topsentia* (see also Diaz *et al.*, 1993: the species is widespread in Caribbean reefs), and accordingly the genus is a junior synonym.

VOSMAERIA FRISTEDT, 1885

Synonymy

Vosmaeria Fristedt, 1885: 24.

Type species

Vosmaeria crustacea Fristedt, 1885: 24 (by monotypy).

Definition

Halichondriidae with tylostyles and oxeas as megascleres, and tangential ectosomal skeleton.

Diagnosis

Encrusting sponges; type species with long thin papillae. Surface smooth. Tangential ectosomal skeleton of oxeas carried by bundles of tylostyles. Three species from the cold or temperate Atlantic and Pacific.

Description of type species

Vosmaeria crustacea Fristedt, 1885 (Fig. 18D–G).

Synonymy. *Vosmaeria crustacea* Fristedt, 1885: 24, pl. II fig. 5; Burton, 1930c: 672; Arndt, 1935: 37, fig. 60; Alander, 1942: 76; Koltun, 1966: 91, pl. XXIV figs 5–6, text-fig. 62. *Inflatella* spec. Vosmaer, 1885a: 24, pl. II fig. 5; *Inflatella crustacea*; Levinsen, 1893a: 414. *Inflatella robusta* Swartschevsky, 1906: 320, pl. 14.

Material examined. None. The type material is presumed to be in the Stockholm museum.

Description. Encrusting with numerous thin papillae (Fig. 18D, F), lateral size 10 × 25 mm, papillae 2–7 mm long. Surface smooth, oscules on apex of papillae. Colour white. The ectosomal skeleton is a detachable membrane entirely composed of intercrossing oxeas. The choanosomal skeleton consists of oxeas and tylostyles in confusion. The skeleton on of the papillae is exclusively built by tylostyles. Spicules (Fig. 18D–E, G). Oxeas, smooth, curved, sharply pointed, 520–850 µm (Arndt, 1935) or 440–1100 × 18–38 µm (Koltun, 1966); (sub-)tylostyles, straight, with tyle often subterminal, occasionally true styles, pointed end often blunt or rounded, 850–910 µm (Arndt, 1935) or 600–1000 × 12–22 µm. Distribution and ecology. Scandinavia, Arctic Ocean, 13–311 m.

Remarks. There are two other species assigned to *Vosmaeria*, *V. laevigata* Topsent, 1896a from Roscoff, and *V. reticulosa* Thiele, 1905 from Iquique, Northern Chile. Both are devoid of papillae, but share the combination of a tangential ectosomal skeleton of oxeas and vertical bundles of tylostyles. The genus *Vosmaeria* has been assigned variously to Suberitidae (Fristedt), Polymastiidae (Arndt, Koltun) and Axinellidae (Topsent). However, it fits in Halichondriidae on account of its tangential skeleton of intercrossing oxeas. The papillate habit and combination of diactines and monactines reminds of *Ciocalypta*.

