

## Family Niphatidae Van Soest, 1980

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Niphatidae Van Soest (Demospongiae, Haplosclerida) contains nine valid genera and a number of nominal species with a worldwide distribution. Species live principally in shallow tropical waters, although species of *Amphimedon* and *Pachychalina* are known from Chile, Peru and Magellan regions, and *Gelliodes*, *Microxina* and *Haliclonissa* are also represented in Antarctica. Major taxonomic characters for differentiating genera include: the type of ectosomal skeleton, which is formed by brushes of spicules, sometimes complemented by a fibrous network; morphology of choanosomal fibres, longitudinal, parallel-radially plumose or divergent, often fasciculated or largely ramified; presence of interstitial spicules in some species to form a free network and spicule micrometries, usually larger than in Callyspongiidae, in general, between 100–600 µm length.

**Keywords:** Porifera; Demospongiae; Haplosclerida; Niphatidae; *Amphimedon*; *Cribrochalina*; *Dasychalina*; *Gelliodes*; *Haliclonissa*; *Hemigellius*; *Microxina*; *Niphates*; *Pachychalina*.

### DEFINITION, DIAGNOSIS, SCOPE

#### Synonymy

Niphatidae Van Soest, 1980: 25.

#### Definition

Haplosclerida with three dimensional ectosomal skeleton of multispicular fibres. Choanosomal skeleton of multispicular fibres, cored by oxeas, often strongylote or stylote. Microscleres if present, sigmas or microxeas.

#### Diagnosis

Encrusting, massive, fan-shaped, flabelliform, vase-shaped or branching growth forms, often bearing chimney-like oscular processes. Sponge texture stiff or resilient, to hard and brittle. Surface smooth or rough, partially hispid, tuberculate, ridged, or strongly spiny. Ectosomal skeleton a dense multispicular, tangential (or paratangential) reticulation of brushes of spicules, representing the protruding terminal parts of the choanosomal primary longitudinal fibres, supporting an ectosomal network of rectangular to rounded meshes, made of secondary fibres, characteristic at the surface of some species. This structure sometimes may be absent, weakly developed or obscured by terminal brushes of primary fibres. Interstitial spicules are present in some species and form a free network. Choanosomal skeleton is a dense network of primary multispicular, longitudinal fibres, parallel-radially plumose or divergent, often fasciculated or largely ramified, cored by multispicular bundles of oxeas or strongyles. Primary fibres are transversally connected by short, well developed or irregularly ramified tracts to form confused secondary or connecting fibres. Spongin typically abundant, but may be scarce or just present to unite spicules (e.g., *Microxina*). Megascleres oxeas or strongyles of variable sizes, longer and stronger than in Callyspongiidae (usually between 100–600 µm length and 3–29 µm in diameter). Free spicules often abundant. Microscleres if present, sigmas or microxeas.

### Scope

Twelve nominal genera and possibly more than 100 species are included in this family worldwide. Of the nominal genera nine are considered to be valid genera (taxonomic decision, this work): *Amphimedon*, *Cribrochalina*, *Dasychalina*, *Gelliodes*, *Haliclonissa*, *Microxina*, *Hemigellius*, *Niphates* and *Pachychalina*.

#### History and biology

The family was erected by Van Soest (1980) to include Haplosclerida with an ectosomal paratangential multispicular reticulation of fibres or tracts, and a choanosomal reticulation of multispicular fibres or tracts. Microscleres, if present, include only sigmata or microxeas. Van Soest (1980) remarked this family was specifically created to receive chalinid sponges which had multispicular fibres, and in this work described many Caribbean species of *Amphimedon*, *Niphates* and *Cribrochalina*.

The definition of Niphatidae has evolved from several subsequent reviews of the family. Hartman (1982) based his revision principally on the nature of the ecto- and choanosomal skeleton, the type of mega- and microscleres, and their morphologies. Pulitzer-Finali (1981) included two new species of *Gelliodes* and *Amphimedon* from Australia. Desqueyroux-Faúndez (1984) emphasised the nature of the ectosomal skeleton as the principal taxonomic character, and describing species of *Niphates*, *Amphimedon* and *Gelliodes* from New Caledonia. De Weerd & Van Soest (1986) did not report any Niphatidae from the North Atlantic fauna although mentioning species of *Gelliodes* previously recorded from this region by authors. These authors included Aka de Laubenfels, 1936a in Niphatidae despite similarities with *Siphonodictyon* (both now in Phloeodictyidae). Kelly Borges & Bergquist (1988) reported on species of *Niphates*, *Gelliodes* and *Siphonodictyon* from Papua New Guinea. Wiedenmayer (1989) described only a single species from Bass Strait but provided an analysis of the proportion of spicules to spongin in massive-lobose species of *Gelliodes* with Indo-West Pacific records. Fromont (1993) noted the practical difficulty of using paratangential three dimensional ectosomal structure

as a principal character to define the family, suggesting instead that the strong development of a primary and secondary multispicular skeleton was more useful to differentiate it from Chalinidae, and described species of *Amphimedon*, *Niphates*, *Gelliodes* and *Aka* from the Great Barrier Reef (*Aka* subsequently referred to Phloeodictyidae). Hooper & Wiedenmayer (1994) recognised six valid genera of Niphatidae: *Amphimedon*, *Cribrochalina*, *Gelliodes*, *Microxina*, *Niphates* and *Hoplochalina*, five with Australian records. *Hoplochalina* was included in the family for the first time, whereas previously Van Soest (1980) listed it as a Haplosclerids of uncertain identity. We have examined the type specimen (*H. incrustans*, BMNH 1886.8.27.521), and conclude that it does not belong to Niphatidae. Actually, there is no consensus about valid genera of this family. Van Soest (1980) mentioned seven genera of Niphatidae: *Amphimedon*, *Niphates*, *Siphonodictyon*, *Cribrochalina*, *Hemigellius*, *Haliclonissa*, and probably also *Microxina*, but no representatives of *Gelliodes* and *Siphonodictyon* were found in his West Indies collection. Contradictory opinions about the availability and synonymy of two genera often included in this family: *Aka* de Laubenfels, 1936a and *Siphonodictyon* Bergquist, 1965, are discussed below. In Van Soest's (1980) opinion the identity of some genera remain uncertain. For example, *Gelliodes* is only barely differentiated from *Niphates*, with alleged differences such as the amount of spongin and morphology of interconnecting fibres being difficult to quantify. Notwithstanding the opinion of Wiedenmayer (1977b), who considered characters such as

the structure of the surface and the strong fibres virtually without spongin in *Gelliodes*, Indo-Pacific *Gelliodes* is not congeneric with West-Indian *Niphates*.

#### Distribution

Species are generally found in shallow waters, although Hartman (1982) stated that genera other than *Amphimedon* occur from tropical shallow-waters to depths of 2400m, and Koltun (1964b) recorded species of *Dasychalina* and *Microxina* from 256 and 540m depth. Genera are widely distributed (Van Soest, personal communication): Chile, Peru and Magellan Regions (*Amphimedon*, *Haliclonissa*, *Hemigellius*, *Microxina*, *Niphates* and *Pachychalina*), Antarctica (*Amphimedon*, *Gelliodes*, *Haliclonissa*, *Hemigellius*, *Microxina* and *Niphates*), East South America and Brazilian Regions (*Amphimedon*, *Haliclonissa*, *Niphates*), Caribbean Islands and West Indies (*Amphimedon*, *Gelliodes*, *Niphates*), West Africa (*Amphimedon*, *Gelliodes*, *Hemigellius*, *Niphates*), Mediterranean-Atlantic, West Mediterranean (*Amphimedon*, *Gelliodes*, *Hemigellius*), Boreal West Atlantic (*Hemigellius*, *Pachychalina*), Boreal East Pacific (*Pachychalina*), Japan-China (*Amphimedon*, *Gelliodes*, *Hemigellius*), Red Sea (*Amphimedon*, *Gelliodes*), central Indian Ocean (*Amphimedon*, *Gelliodes*, *Niphates*), Australia (*Amphimedon*, *Cribrochalina*, *Gelliodes*, *Microxina*, *Niphates*), New Zealand (*Gelliodes*).

#### KEY TO GENERA

- (1) Microscleres (sigmas, microxeas, rarely toxas) present ..... 2  
No microscleres ..... 4
- (2) Surface skeleton a paratangential (three-dimensional) network of spongin enclosed paucispicular tracts, surface uneven, maybe conulose, or stiffly spiny but not hispid ..... 3  
Surface skeleton consisting of spicules brushes, surface finely or coarsely hispid, no (para-)tangential spicule tracts, spongin not visible ..... *Hemigellius*
- (3) Surface uneven, microconulose, but not stiffly spiny, choanosomal skeleton regularly anisotropic, microscleres vestigial ..... *Niphates*  
Surface stiffly spiny, choanosomal skeleton with reduced secondary fibres, microscleres numerous ..... *Gelliodes*
- (4) Surface optically smooth, microconulose or bumpy, but not stiffly conulose, spiny or coarsely hispid ..... 5  
Surface stiffly conulose, spiny or coarsely hispid ..... 8
- (5) Ectosomal skeleton a paratangential or three-dimensional network of spicule tracts .....6  
Ectosomal skeleton lacking a network, consisting of the closely set brushed endings of the choanosomal skeleton making a crust-like ectosome ..... *Cribrochalina*
- (6) Spongin absent or invisible, choanosomal skeleton with emphasis on primary tracts, many loose interstitial spicules .... *Pachychalina*  
Spongin clearly present enclosing ectosomal and choanosomal spicule tracts, choanosomal skeleton regularly anisotropic ..... 7
- (7) Surface more or less smooth, but may be uneven or bumpy, ectosomal network tangential ..... *Amphimedon*  
Surface microconulose, ectosomal network paratangential (three-dimensional) ..... *Niphates*
- (8) Surface spiny 'aculeate' (with stiff conules) ..... *Dasychalina*  
Surface coarsely hispid, irregular ..... *Haliclonissa*

#### AMPHIMEDON DUCHASSAING & MICHELOTTI, 1864

##### Synonymy

*Amphimedon* Duchassaing & Michelotti, 1864: 78; de Laubenfels, 1936a: 45. *Hemihaliclona* Burton, 1937: 18, pl. i, fig. 7.

##### Type species

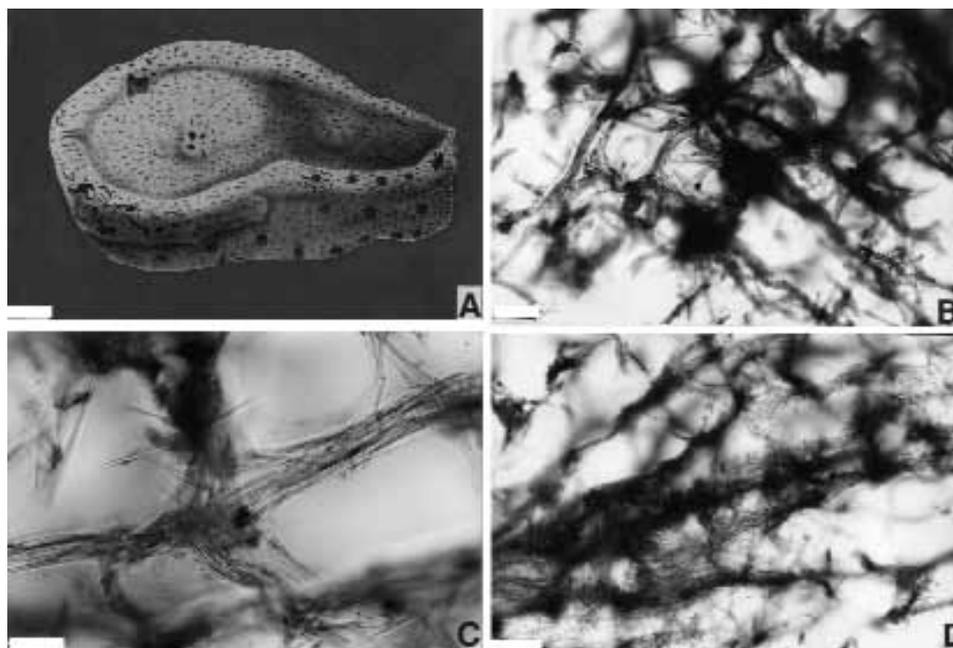
*Amphimedon compressa* Duchassaing & Michelotti, 1864 (by subsequent designation, de Laubenfels, 1936a).

##### Definition

Niphatidae with an optically smooth surface, regular tangential ectosomal network with rounded meshes of a single size. Ends of choanosomal longitudinal primary fibres barely protruding. Spongin abundant. Microscleres absent.

##### Diagnosis

Irregularly massive, lamellate, flabelliform, branching growth forms, with numerous oscules linearly distributed on rims or



**Fig. 1.** *Amphimedon* Duchassaing & Michelotti, 1864. A–D, type species *Amphimedon compressa* Duchassaing & Michelotti, 1864. Lectotype ZMA POR 863. A, lectotype (reproduced from Duchassaing & Michelotti, 1864) (scale 1 cm). B, diffuse to radially plumose choanosomal skeleton (scale 50  $\mu\text{m}$ ). C, ascending, longitudinal multispicular primary fibres (scale 50  $\mu\text{m}$ ). D, primary fibres grouped in bundles and irregular interconnections (scale 50  $\mu\text{m}$ ).

scattered on branches. Ectosomal skeleton a tridimensional tangential network of secondary fibres with rounded meshes, covered by a fine membrane. Choanosomal skeleton irregular, diffuse, radially plumose network of primary, ramified multispicular fibres, irregularly connected by secondary multispicular fibres. Abundant spongin. Megascleres oxeas often with modified or strongylote apices. Microscleres absent.

#### Previous reviews

De Laubenfels, 1936a: 213; Burton, 1937: 18; Hartman, 1955: 167; Wiedenmayer, 1977b: 82; Van Soest, 1980: 26; Desqueyroux-Faúndez, 1984: 777; Fromont, 1993: 21.

#### Description of type species

*Amphimedon compressa* Duchassaing & Michelotti, 1864 (Fig. 1).

**Synonymy.** *Amphimedon compressa* Duchassaing & Michelotti, 1864: 78, pl. 17, fig. 2.

**Material examined.** Lectotype ZMA POR. 863 – St. Thomas (designation by Wiedenmayer, 1977b): Not examined. Paralectotype: MT Por. 35 – St. Croix. Schizoparalectotype: BMNH 1928.11.12.42, as *Haliclona* (*Amphimedon*) *compressa*. Other comparative material. Holotype of *Amphimedon cristata* Pulitzer-Finali, 1996: MSNG 48708 – Laing I., PNG. Holotype of *Amphimedon conferta* Pulitzer-Finali, 1996: MSNG 48709 – Laing I., PNG. Holotype of *Amphimedon rudis* Pulitzer-Finali, 1996: MSNG 48711 – Laing I., PNG.

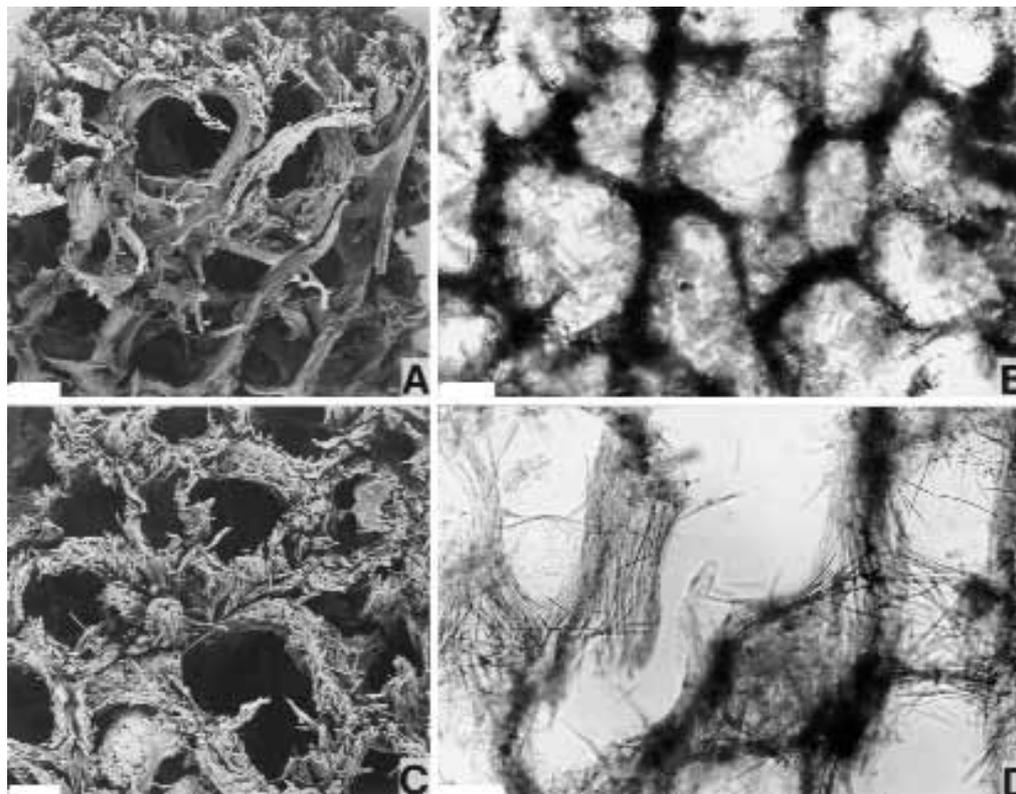
**Description (emended from Van Soest, 1980).** Massive to flabelliform, up to 13 cm high, cylindrical branches 7 cm in diameter, with rows of oscules flush with the surface, 2–8 mm in diameter, scattered over the the upper part of branches or concentrated on side rims. Surface smooth on the flattened parts, tuberculate and ridged on the rims. Colour, bright red, alive, ochre to brown in dry state

(Fig. 1A). Consistency in dry state, hard. Ectosomal tangential network incomplete, irregular, with uniform rounded meshes, 100–200  $\mu\text{m}$ , abundant free spicules, formed by secondary fibres, 20–90  $\mu\text{m}$  in diameter. Choanosomal skeleton a diffuse to radially plumose network (Fig. 1B) with irregular meshes, 90–300  $\mu\text{m}$  in diameter, with ascending, longitudinal multispicular primary fibres, rich in spongin (Fig. 1C), 41–63–120  $\mu\text{m}$  in diameter cored by 15 or more spicules. Primary fibres, grouped in bundles, are quite irregularly interconnected (Fig. 1D), by secondary multispicular fibres, 8–21–33  $\mu\text{m}$  in diameter. Megascleres: oxeas, slightly bent, regular in diameter, with multitelescoped or strongylote apices, 106–140–168  $\mu\text{m}$  length and 3–4.7–5  $\mu\text{m}$  in diameter. Microscleres absent.

**Distribution.** West Indies; east coast of South America; Australia; New Caledonia; Antarctica.

**Remarks.** De Laubenfels (1936a: 45) included *Amphimedon* in his new family Haliclونidae (=Chalinidae) for sponges containing predominantly diactinal spicules distributed more-or-less homogeneously throughout the skeleton, and lacking any ectosomal specialization. He suggested that it differed from *Haliclona* principally by the possession of longitudinal fibres projecting through the surface. Burton (1937) erected *Hemihaliclona*, designating *Amphimedon viridis* as the type species. Wiedenmayer (1977b: 82) considered *Hemihaliclona* as a subjective junior synonym of *Amphimedon*, and assigned it to a subgenus of *Haliclona* based on its possession of a halichondroid-like skeleton with abundant spongin enclosing spicules, and a surface network of hispid fibres partially or well developed. Van Soest (1980) considered that the presence of a special tangential ectosomal reticulation was justification to restore *Amphimedon* to generic rank, and to remove it from Haliclونidae (=Chalinidae) to his new family Niphatidae.

Van Soest (1980) included the poorly known type species of *Pachychalina* Schmidt into synonymy with *Amphimedon*, whereas we suggest that there are significant skeletal differences between their respective type species to recognise both genera as valid.



**Fig. 2.** *Cribrochalina* Schmidt, 1870. A–D, type species *Cribrochalina infundibulum*, lectotype BMNH 1870.5.3.165. A, ectosomal palisade of oxeas and protruding longitudinal primary fibres (scale 200  $\mu\text{m}$ ). B, strong surface crust, transverse section (scale 100  $\mu\text{m}$ ). C, longitudinal section through choanosomal skeleton showing a regular network of multispicular longitudinal primary fibres and elongate mesh with abundant free spicules (scale 50  $\mu\text{m}$ ). D, choanosomal fibres, nearly parallel, with large spongin sheath (scale 50  $\mu\text{m}$ ).

Desqueyroux-Faúndez (1984) followed Van Soest's (1980) concept of *Amphimedon* by introducing a new character (percentage of silica in the skeleton) to define species. These values were found to be very variable (between 8.6–71.0 mg/100 g), but this character now appears to be poorly informative for systematics of this group. Fromont (1993) also included *Pachychalina* into synonymy with *Amphimedon*, and also redefined *Amphimedon* to include the presence of sigma microscleres as a good specific character.

### CRIBROCHALINA SCHMIDT, 1870

#### Synonymy

*Cribrochalina* Schmidt, 1870: 36, pl. 4, fig. 3; 1880: 77. Topsent, 1920a: 6.

#### Type species

*Cribrochalina infundibulum* Schmidt, 1870 (by subsequent designation, de Laubenfels, 1936a: 46).

#### Definition

Niphatidae with ectosomal network masked by a palisade of spicule brushes produced by the ends of primary longitudinal fibres and appearing as a hard, strongly hispid surface crust. Choanosomal skeleton composed of multispicular ascending,

nearly parallel to radiating strong fibres, with a large spongin sheath. Meshes are elongated to rectangular.

#### Diagnosis

Lamellate, folded, fan, vase, or cup-shaped, thin-walled growth forms, attached directly to the substrate, with a basal portion burrowed into the sediment. Oscules generally not distinguishable externally from numerous holes puncturing the surface. Surface optically smooth, with an ectosomal network consisting of a palisade of spicule-brushes covered by a fine membrane (crust). Choanosomal skeleton with strong, ascending longitudinal multispicular primary fibres radially distributed to produce an anisotropical skeleton with regularly elongated meshes. Spongin abundant. Microscleres absent.

#### Distribution

Thirteen nominal species of *Cribrochalina* are known from West Indies and West Central Pacific (Van Soest, pers. comm.).

#### Previous reviews

Topsent, 1920a: 6; de Laubenfels, 1936a: 46; Wiedenmayer, 1977b: 118; Van Soest, 1980: 42.

#### Description of type species

*Cribrochalina infundibulum* Schmidt, 1870 (Fig. 2).

**Synonymy.** *Cribrochalina infundibulum* Schmidt, 1870: 36.

**Material examined.** Lectotype (here designated): BMNH 1870.5.3.165 (fragment) – Antilles. Paralectotypes: MZUS POR 123 (fragment 25, 47) – West Indies (labelled ‘type’ by Schmidt, *vide* Topsent, 1920a). BMNH 1870.5.3.134 – teased fragment. Other comparative material. Holotype of *Spongia bilamellata* Lamarck: MNHN LBIM DT 602 – King I., Bass Strait. Carter’s specimen of *Cavochalina bilamellata*: BMNH 1886.12.15.182 – S coast Australia. *Cribrochalina cretacea* Schmidt, 1870: MCZ 9135 (orig. 6633w) – Florida. MCZ 6090 – ‘Blake Expedition’, stn 200. off Martinique.

**Description.** Lamellate, funnel-shaped, thin-walled. Surface smooth, outer surface irregularly undulated, inner surface concentrically undulated. Under the fine membrane covering the surface (appearing as imperforate), are very small oscules and pores scattered over the surface. The strong surface crust produces a hard consistency, stiff and brittle in the dry state. Colour alive purple to purple-brown. Ectosomal skeleton is a continuous palisade of oxea brushes produced by the diverging surface ends of multispicular longitudinal primary fibres, to form a strong crust (Fig. 2A–B). Choanosomal fibres are nearly parallel, with a large spongin sheath, forming a regular network of multispicular longitudinal fibres, 85–120 µm in diameter, with elongate meshes 300–400 µm in diameter and abundant free spicules (Fig. 2C–D). Diverging terminations of the ascending primary fibres under the surface are prolifically divided to produce an irregular system of subectosomal cavities and peripherally condensed meshes, 120–180 µm in largest diameter. Megasccleres: strongylote oxeas, strongly bent or flexuous. Topsent (1920a) provides the following dimensions, 180–215 × 3.5–5 µm to 250 × 5.5 µm Wiedenmayer (1997: 121) records micrometries as 180–215 × 3.5–5 µm.

**Remarks.** *Cribrochalina* Schmidt, 1870 was redescribed by Topsent (1920a) based on two fragments (MZUS 25 and 47, here considered paralectotypes) of *Cribrochalina infundibulum*. Schmidt’s material in ZMUS was also examined but the real status of this material is completely uncertain, with the consequence that the fragment BMNH 1870.5.3.165 was designated as lectotype. This fragment has the exact wording on the label ‘Antillen’, conforming exactly to Schmidt’s (1870) description, whereas the locality of other material is less specific. In our diagnosis here we discuss the properties of this fragment.

Topsent (1920a) remarked that *Cribrochalina* resembled *Pachychalina* in the number of spicules and their arrangement within fibres, with abundant long, fine, bent and sinuous oxeas. But based on our re-examination of the lectotype we conclude that there are important differences between the type material of both genera, which is evidence for recognising them as distinct genera. Fibre structure is similar in both genera, but in *Cribrochalina* fibres are stronger, nearly parallel, with a large spongin sheath and their umbelliform ends and free spicules form a strong surface crust. In *Pachychalina* fibres are vaguely parallel, without visible spongin, and meshes are confused, without properly connecting fibres. A surface crust is not present in *Pachychalina*, but its ectosomal skeleton is three-dimensional, irregular and confused, and it is not recognizable as distinct from the main skeleton.

Topsent (1920a) had a clear concept of *Cribrochalina*, but later (Topsent, 1932a) included *Spongia bilamellata* (typical form) Lamarck in the genus, recognising the same specimen redescribed by Carter (1885; as *Cavochalina bilamellata*, a callyspongiid), and by Lendenfeld (1887c; as *Placochalina pedunculata*). Topsent (1932a) considered *Cavochalina* Carter, 1885 and *Placochalina* Lendenfeld, 1887c as junior objective synonyms of *Cribrochalina*,

and named *Spongia bilamellata* as *Cribrochalina bilamellata* (Lamarck). Re-examination of the Lamarck specimen confirms its suspected affinities with *Cribrochalina* of the West Indies, although in *Cribrochalina* spicule dimensions are larger, the surface is a crust, and fibre structure is more compact – suggesting that *Cavochalina* and *Cribrochalina* are different and probably valid taxa, allocated to two different families: Callyspongiidae and Niphatidae, respectively. Wiedenmayer (1977b: 118) also included *Cavochalina* Carter, 1885 and *Placochalina* Lendenfeld, 1887c in synonymy with *Cribrochalina* (following Topsent, 1932a).

Wiedenmayer (1977b) also associated *Cribrochalina* (in part) with *Petrosia* and *Xestospongia*, as members of the family Nepheliospongiidae, which he revived. In Van Soest’s (1980) opinion the structure of *Cribrochalina* with strong primary fibres, rich in spongin and radially distributed to form a crust, is very different from the isotropical meshes of *Petrosia* and from the skeletal structure of *Xestospongia*. Van Soest (1980: 108, fig. 37) refuted the proposition of Wiedenmayer (1977b) but acknowledged the strong affinity of *Cribrochalina* with *Amphimedon* and *Niphates*, except that *Cribrochalina* had a much finer skeletal mesh and had an ectosomal crust of spicule brushes. In Wiedenmayer’s (1977b) concept *Cribrochalina* also corresponded, in part, to *Pachychalina* (e.g., *Pachychalina aurantiaca* (Lendenfeld) var. *dura* Wilson, 1902, from the Virgin Islands), which is probably a species of *Petrosia* (Van Soest, pers. comm.).

Finally, Wiedenmayer (1977b: 119) considered *Cribrochalina infundibulum* was conspecific with *C. vasculum* (Lamarck). We observed in both species the same types of spicules (slightly longer in *C. vasculum*), with fibres having the same structure (with the mesh of *C. vasculum* irregular and larger in size), and with a subectosomal condensation (less marked than in *C. infundibulum*). Wiedenmayer (1977b) suggested that these differences were intraspecific, despite Topsent’s (1920a) assertion that Lamarck’s specimen was *Calyx vasculum*. Van Soest (pers. comm.) suggested that it was not certain that *Spongia vasculum* was West Indian, irrespective of the alleged similarity between *C. infundibulum* and *C. vasculum*, with the consequence that the argument remains speculative. Wiedenmayer (1977b: 119) noted that two potential syntypes of *Cribrochalina infundibulum* exist in the Museum of Comparative Zoology, Harvard University. Re-examination of this material (courtesy of Ardis B. Johnston, Assistant Curator, Department of Invertebrate of this Museum) indicates that there is no justification to consider this material as representing valid types, with all labelled ‘non type’.

#### DASYCHALINA RIDLEY & DENDY, 1886

##### Synonymy

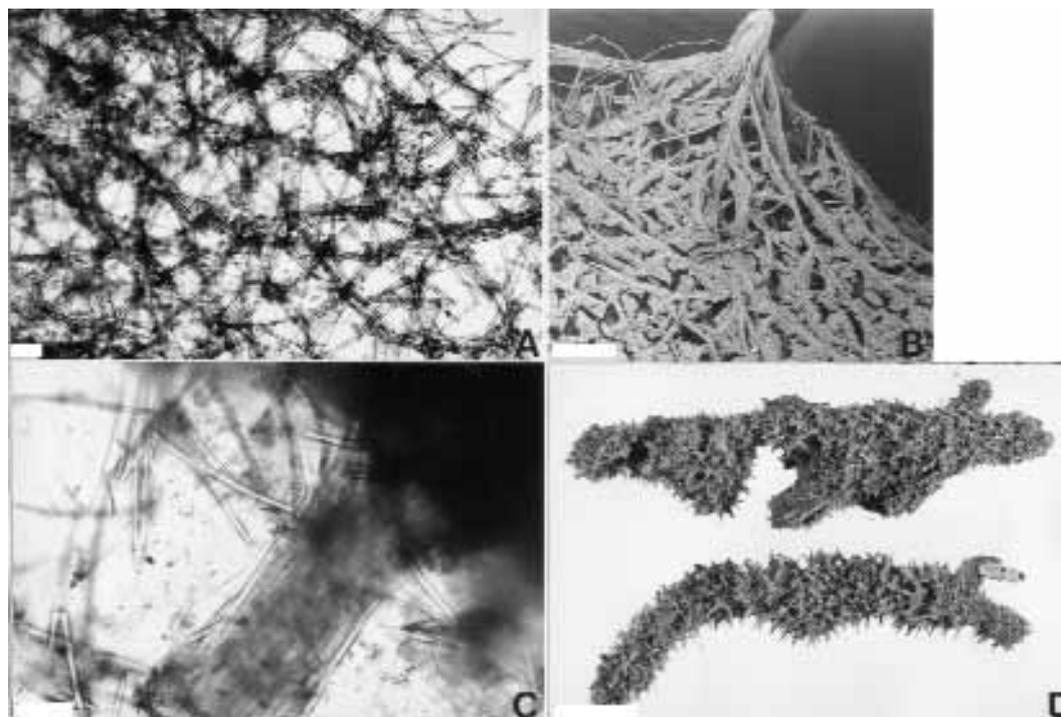
*Dasychalina* Ridley & Dendy, 1886: 329; 1887: 19.

##### Type species

*Dasychalina fragilis* Ridley & Dendy, 1886: 330 (by subsequent designation, Burton, 1932b: 278).

##### Definition

Niphatidae with rugged and spinous or conulose surface. Ectosomal skeleton an irregular network of stout fibres and free



**Fig. 3.** *Dasychalina* Ridley & Dendy, 1886. A–C, type species *Dasychalina fragilis* Ridley & Dendy, 1886, lectotype BMNH 1887.5.2.170. A, ectosomal skeleton, an irregular reticulation of isolated spicules supported by an additional stronger reticulation (scale 50 µm). B, apices of the ectosomal conules (scale 500 µm). C, compact multispicular principal fibres without spongin sheath (scale 500 µm). D, *Gelliodes fibulatus* (Carter) Ridley, 1884a specimen from Torres Strait, BMNH 1882.2.23.202 (scale 1 cm).

spicules, reinforced by a secondary subectosomal reticulation, forming surface conules. Choanosomal skeletal network a compact reticulation of stout fibres and scattered spicules. Spongin not visible.

#### Diagnosis

Massive, irregularly branched, ramose to flabellate growth forms. Surface strongly aculeate, conulose, uneven and striated, with striae radiating from the summit of conules (Ridley & Dendy, 1887: 20). Texture strong, hard and brittle. Oscules large, irregularly scattered on upper side of branches. Ectosomal skeleton, (Fig. 3A) formed by stout, multispicular fibres, and free spicules in a dense irregular network with irregular mesh, under which a subectosomal network of stout fibres is visible. Aculeated conules or spines on the surface (Fig. 3B) are formed by central branches at ends of primary longitudinal fibres. Choanosomal skeleton an irregular network of primary fibres, without clear orientation, strong, abundantly ramified, and with no visible spongin sheath (Fig. 3C).

#### Distribution

Philippines (Ridley & Dendy, 1886); South Georgia, Falkland Islands; South coast of Chile: Calbuco, Magellan Strait; South Georgia; Antarctica (Burton, 1932b, 1934a, 1940; Thiele, 1905; Desqueyroux, 1975, 1976; Koltun, 1964b).

#### Previous reviews

Burton, 1932b: 278; 1934a: 15; [non] de Laubenfels, 1936a: 45; Wiedenmayer, 1977b: 53, 95, 100.

#### Description of type species

*Dasychalina fragilis* Ridley & Dendy, 1886 (Fig. 3).

**Synonymy.** Ridley & Dendy, 1886: 330; 1887: 20, pl. 4, figs 2, 2a.

**Material examined.** Lectotype (here designated): BMNH 1887.5.2.170 – ‘Challenger’ expedition, stn. 208, Philippines. Other comparative material. Holotype of *Dasychalina melior* Ridley & Dendy, 1886: BMNH 1887.5.2.178 – ‘Challenger’ Expedition, stn. 208, Philippines. Holotype of *Dasychalina validissima* (Thiele, 1905): ZMB 2234 – Plate Collection, Calbuco, Chile. Holotype of *Dasychalina magellanica* Thiele, 1905: ZMB 3327 – Plate Collection, Bahia Parke, Cockburn Canal, Punta Arenas, Chile.

**Description (emended from Ridley & Dendy, 1886: 330).** Irregularly ramose, subcylindrical branches about 18 mm in diameter, covered with strong conules or spines (aculeated). Colour in spirit light greyish or brownish yellow. Texture hard and brittle. Surface uneven, delicately striated, with striations radiating from ends of conules. Oscules large, about 4 mm in diameter, almost entirely scattered and restricted to one side of each branch. Ectosomal skeleton (Fig. 3A), an irregular reticulation of isolated spicules supported by an additional stronger reticulation of stouter fibres the ends of which form the apices of the ectosomal conules (Fig. 3B). Choanosomal skeleton an irregular reticulation of very stout, compact multispicular principal fibres, 35–50 µm in diameter, without spongin sheath, spongin present but only cementing spicules (Fig. 3C) in the fibres and in between fibres, with abundantly scattered free spicules. Megascleres: oxeas 350–420–500 µm in long by 15–20 µm in diameter.

**Remarks.** Ridley & Dendy (1886: 329) described *Dasychalina fragilis* as 'solid, coarsely spined on surface; skeleton-fibres stout, spicules polyserial; amount of spongin variable, never very great', further indicating that the solid, coarsely spined surface was the main character differentiating it from *Pachychalina*. However, Ridley & Dendy (1887: 19) realised that the type species of *Pachychalina* (*P. rustica* Schmidt, 1868), may have a spinous ('struppig') surface, and consequently, if both *Dasychalina* and *Pachychalina* had a spinose surface they should be included in a single genus. Thus, *Dasychalina* became a junior subjective synonym of *Pachychalina*, although several authors subsequently continued to use the name *Dasychalina* (e.g., Burton, 1934a: 15, *Dasychalina validissima* (Thiele, 1905)). Burton (1932b: 278) was the first author to comment significantly on the genus, with the type species (designated by him as *Dasychalina fragilis*) exhibiting a different skeletal structure from his concept of *Pachychalina*, although he admitted that *Pachychalina* was unknown to him. Burton's (1932b) definition of *Dasychalina* was confined to sponges like *Adocia* and *Callyspongia* (= *Pachychalina* of authors), defined as 'haplosclerids with ectosomal skeleton irregular multispicular reticulation with primary and secondary mesh'. Wiedenmayer (1977b: 100) included *Dasychalina* into synonymy with *Spinosella* (pro *Cladochalina*), considering that Burton's (1932b) concept of *Dasychalina* corresponded to sponges like *Spinosella* with little or no spongin, and with oxeas packed in tracts (e.g., *Callyspongia (Cladochalina) ridleyi* Burton, 1934a). Van Soest (1980: 106) rejected Ridley & Dendy's (1886) and Wiedenmayer's (1977b) concepts of *Dasychalina* and *Pachychalina*, considering the genus to be a subjective junior synonym of *Niphates*. As we see, however, *Dasychalina* has been compared with genera containing a very different type of skeleton (i.e., *C. (Cladochalina)*, *Pachychalina* and *Niphates*), in spite of the presence of a different type of surface (aculeate) and the large size of its spicules (more than 400 µm). Skeletal differences between these genera, confirmed from study of their respective type species, are important and thus we consider here that these three genera are different and valid. *Pachychalina* has a very irregular surface, abundantly perforated by aquiferous openings, no aculeations, no clear ectosomal tangential network; there is no dermal membrane, fibres are multispicular, of irregular diameter and without a visible spongin sheath. *Niphates* exhibits a conulose to spiny surface with numerous oscules; its irregularly distributed fibres are pauci- to multispicular, but spongin is always dominant. *Callyspongia (Cladochalina)*, in spite of the aculeated surface similar to that of *Dasychalina*, exhibits an ectosomal network with three mesh sizes, all smaller than those of *Dasychalina*, and possession of fasciculated primary fibres. In addition, in all three genera spicules are much smaller than in *Dasychalina*, which appears to be an important character to differentiate species of *Dasychalina* from sponges with an aculeated surface and containing small spicules, resembling *Dasychalina* (which Van Soest (*in litteris*) suggests are common in Indonesia and neighbouring areas, but in reality are species of *Callyspongia (Cladochalina)*).

#### GELLIODES RIDLEY, 1884

##### Synonymy

*Gelliodes* Ridley, 1884a: 426.

##### Type species

*Gelliodes fibulata* Ridley, 1884a (by subsequent designation; Hooper (1986: 187), this is generally considered a junior synonym of *Axos fibulata* Carter, 1881) (by monotypy).

##### Definition

Niphatidae in which the tangential ectosomal layer of fibres with an irregular mesh is interrupted by protruding ends of choanosomal longitudinal fibres. Choanosomal skeletal network is composed of compact multispicular longitudinal fibres.

##### Diagnosis

Thickly incrusting to massive, tubular growth form, intricately branching, long cylindrical stems irregularly ramified and anastomosing at points of contact (single branches attain a length of about 100 mm), rampant or erect, arising from a common basal portion. Oscules usually numerous, unevenly scattered over the surface and often conspicuous. Surface uneven, membranous, strongly aculeated at intervals of about 2–5 mm, sustained by strong, slender, sharp ramified spines, 2–3 mm long (Fig. 3D) surface may be also ridged or tuberculate or smooth, and finely hispid or velvety. Texture very hard. Ectosomal skeleton is a tangential network of secondary fibres, free oxeas and abundant sigmas (Fig. 4A), often interrupted by the ends of the strong primary longitudinal fibres protruding from the choanosomal skeleton to form the spines. Choanosomal skeleton composed of primary longitudinal-radial multispicular and ramified primary fibres, distinct and very compact (Fig. 4B). Primary fibres (Fig. 4C) form rectangular to rounded meshes, subdivided irregularly by secondary fibres, and mesh containing abundant free spicules. Megascleres (Fig. 4D) consist of robust oxeas with sharp apices. Microscleres are abundant sigmas.

##### Distribution

Indian Ocean, West Pacific Ocean, Torres Strait, Northern Territory and Western and N coast of Australia, SE coast of Australia (Port Jackson), Amboina, Indo-Malayan region, New Guinea and New Caledonia (Carter, 1881; Lendenfeld, 1887c; Topsent, 1897a; Thiele, 1903; Dendy, 1905; Van Soest, 1980; Hooper, 1986; Desqueyroux-Faúndez, 1984).

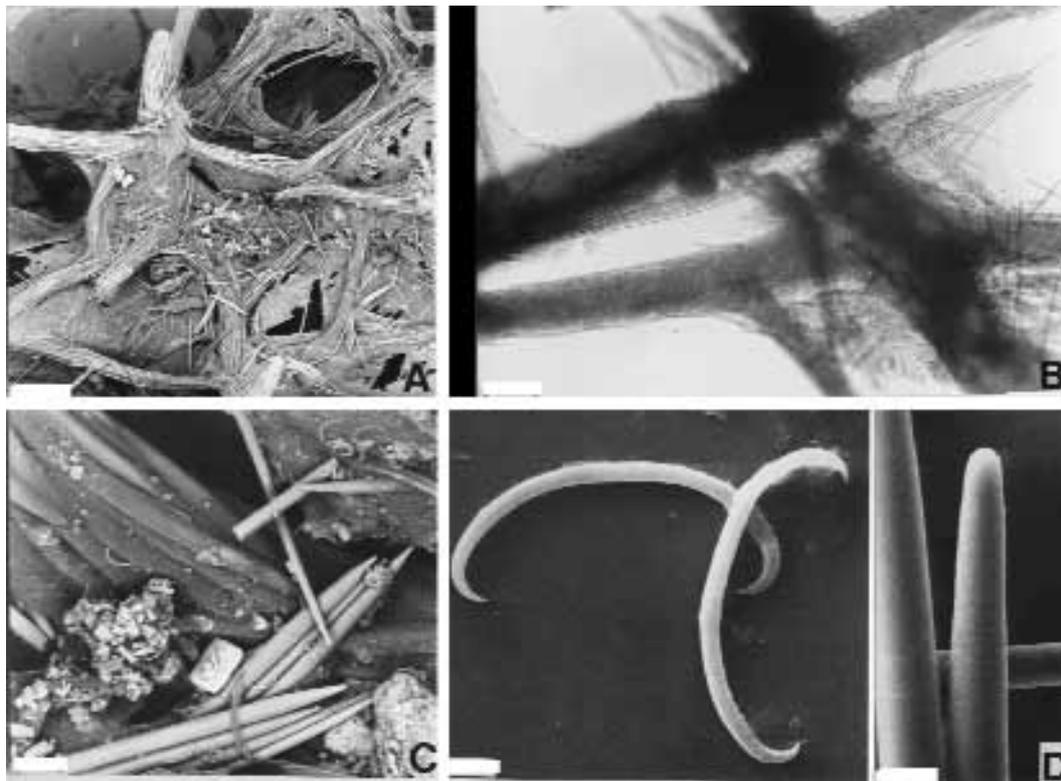
##### Previous reviews

Carter, 1881, 383, pl. 18, fig. 4; 1882: 288; Ridley, 1884a: 427, pl. 39, fig. 1, pl. 41, fig. bb-bbíf; Ridley & Dendy, 1887: 47, pl. 12, fig. 2; Topsent, 1897a: 470; 1932a: 114; Hentschel, 1912: 393; Burton, 1934a: 549; Wiedenmayer, 1977b: 95; 1989: 117; Van Soest, 1980: 106; Desqueyroux-Faúndez, 1981: 744, figs 56, 117; 1984: 780, figs 6, 51, 52, 58–61; Hooper, 1986: 184, figs 11, 12, pl. 1, fig. E; Hooper & Wiedenmayer, 1994: 318.

##### Description of type species

*Gelliodes fibulatus* Ridley, 1884 (Fig. 4).

**Synonymy.** ?*Axos fibulata* Carter, 1881: 383, pl. 18, fig. 4. *Gelliodes fibulata* Ridley, 1884a: 427, pl. 39, fig. 1, pl. 41, figs bb-bbíf.



**Fig. 4.** *Gelliodes* Ridley, 1884a. A–D, *Gelliodes fibulata* Ridley, 1884a, lectotype, BMNH 1882.2.23.226. A, ectosomal skeleton a tangential network of secondary fibres, free oxeas and abundant sigmas (scale 200  $\mu\text{m}$ ). B, choanosomal skeleton with irregularly connected primary fibres and scarce spongin binding spicules (scale 50  $\mu\text{m}$ ). C, choanosomal spicules, robust oxeas with sharp apices (scale 20  $\mu\text{m}$ ). D, sigma microscleres (scale 2  $\mu\text{m}$ ) and oxea megascleres (scale 5  $\mu\text{m}$ ).

**Material examined.** Lectotype (here designated): BMNH 1882.2.23.226 – Prince of Wales channel, Torres Straits, 7–9 fath., bottom sand, coll. Dr Coppinger, 9/1881. Other material. BMNH 1882.2.23.193 – Thursday Island, Torres Straits. BMNH 1882.2.23.202 (dry), 202a (slide) – Prince of Wales channel, Torres Straits. BMNH 1882.2.23.240 (spirit), 240 (slide) – Torres Straits, bottom mud, 10/1881. BMNH 1882.2.23.547, 548, 549 – Thursday Island, Torres Straits, 3–5 fath., bottom mud and sand.

**Description.** Long, cylindrical, repent branches issued at different levels, from a common base, branches anastomosing at points of contact. Surface covered by a transparent membrane, over which protrude the ends of long primary fibres, as long and short spines, making the surface extremely spinous and aculeated at intervals of about 2–5 mm. Longer spines, 2–3 mm long, are ramified to form secondary spines. Choanosomal skeleton cavernous, formed by abundant primary multispicular longitudinal fibres, the spines issue from the ends of primary fibres. Intermediate surface between the spines is cavernous and covered by a transparent membrane. Colour in life grey to pale blue. Ectosomal skeleton is a tangential reticulation of multispicular fibres and triangular to rectangular meshes. Choanosomal skeleton is cavernous, formed by abundant primary longitudinal, multispicular fibres ascending, radiating, strong, 180–450–647  $\mu\text{m}$  in diameter, abundantly ramified to form anastomosing secondary connecting fibres, 82–191–295  $\mu\text{m}$  in diameter as irregular branches of primary fibres. Choanosomal mesh rectangular, 451–670–902  $\mu\text{m}$  in diameter, with abundant free oxeas and a few sigmas. Aquiferous spaces are visible, especially on the surface, sigmas are abundant in this

region but are rare in the choanosomal region. Megascleres: oxeas straight to slightly curved, hastate, 135–182–250  $\mu\text{m}$  long by 3–6–16  $\mu\text{m}$  in diameter. Microscleres: sigmas, c-shaped, slightly centrangulate, 10–12–16  $\mu\text{m}$  long.

**Remarks.** The holotype of *Axos fibulata* Carter, 1881 was confirmed as lost (Burton, 1934a) precluding a definite conclusion that it is a senior synonym of *Gelliodes fibulatus* Ridley, 1884. Hooper (1986) revised the genus *Axos* Gray, 1867 from old and recent material collected from Northern Territory and Western Australia and compared this with *Gelliodes fibulatus* Ridley, 1884a. Hooper confirmed that this species was distinct and clearly differentiated from other species of *Axos* (Hooper, 1986: 187). *Gelliodes fibulatus* has been accurately and frequently described by contemporary authors as it is very easily recognisable by its distinctive arborescent growth form, its strongly spiny surface (with its outer surface ‘beset with pointed eminences’) and its spiculation (Ridley, 1884a: 426), whereas other species subsequently assigned to *Gelliodes* are not consistently spiny, including *G. carnosa* Dendy, 1889, *G. incrustans* Dendy, 1905 and *G. fragilis* Desqueyroux-Faúndez, 1984 which exhibit a smooth surface. Hooper (1986) remarked on the possession of ‘choanosomal fibres are heavily invested by spongin’ in the type species, whereas Wiedenmayer (1989) noted the highly variable proportion of spongin in the skeleton, the presence of secondary fibres that may be largely reduced, the fibrous skeleton that may be isodictyal, and that the surface in some species (other than the type species) may be almost smooth. Variations between species were confirmed by an analysis of the silica content of New Caledonian specimens

(Desqueyroux-Faúndez, 1984), ranging from 8.6% (in *G. incrustans*, with a smooth surface) to 71.0% (in *G. fibulatus*), confirming an apparent level of heterogeneity amongst taxa. Authors have commented on the resemblance between some nominal species of *Gelliodes* and *Niphates*, possibly representing misidentifications of either or both taxa given the emphasis on the presence of sigmas in both genera – regular in *Gelliodes* or irregularly in *Niphates*. Wiedenmayer (1977b) remarked that characters such as the structure of the surface and the strong fibres, the latter virtually without spongin, confirm that Indo-Pacific *Gelliodes* are not congeneric with West-Indian *Niphates*. Both genera are also different in the distribution and structure of their fibres, where in *Gelliodes* fibres are compact, sharply delimited, distinct, multispicular and with scarce, or no visible, spongin. In contrast, in *Niphates* the fibres are pauci- to multispicular, abundantly ramified to form fascicles, spongin is dominant, and always visible.

### HALICLONISSA BURTON, 1932

#### Synonymy

*Haliclonissa* Burton, 1932b: 270.

#### Type species

*Haliclonissa verrucosa* Burton, 1932b (by original designation).

#### Definition

Niphatidae with a densely hispid surface composed of isolated brushes of spicules formed at the ends of primary longitudinal fibres. Choanosomal skeleton with primary longitudinal multispicular fibres connected to diffused secondary fibres, to form irregular elongated meshes with numerous free spicules. Spongin scarce.

#### Diagnosis

Stout, tubular growth form with a deep or a shallow atrium and cylindrical branches, irregularly ramified. Sponge fixed directly to the substrate. Oscules conspicuous, connected to the atrium, irregularly scattered over the entire sponge. Surface strongly irregular, spiny, with dense and short spicule projections, produced by the terminal part of primary fibres, with numerous free spicules in between forming an irregular, confused tangential network without a clear mesh. Consistency is soft, easily compressible, friable. Ectosomal skeleton consists of perpendicular spicule brushes protruding from the ends of primary longitudinal multispicular fibres, producing a densely spiny surface. In between brushes of spicules there is an irregular network with abundant free spicules. Choanosomal skeleton composed of pauci- to multispicular primary fibres, longitudinally parallel to oblique, abundantly ramified, anastomosing. Interconnecting diffuse secondary fibres pauci- to multispicular. Irregular mesh with numerous free spicules. Spongin scarce. Megascleres are robust oxeas.

#### Distribution

Antarctica, Palmer Archipelago; Falkland Islands; Atlantic coast of South America. (Burton, 1932b; 1940; Koltun, 1964b).

#### Previous reviews

De Laubenfels, 1936a: 46; Burton, 1940: 100; Koltun, 1964b: 102; Hooper & Wiedenmayer, 1994: 320.

#### Description of type species

*Haliclonissa verrucosa* Burton, 1932b (Fig. 5).

**Synonymy.** *Haliclonissa verrucosa* Burton, 1932b: 270, pl. 51, fig. 3, text-fig. 8.

**Material examined.** Holotype: BMNH 1928.2.15.473 – Palmer Archipelago, stn. 180, 'Discovery' Expedition, 160 m depth.

**Description.** Holotype measures 13–15 cm long and 5 cm in diameter, composed of a stout irregularly cylindrical branch with a few conspicuous oscula connected to a central cavity, 10 mm in diameter, as a shallow, large atrium. Texture soft, friable. Surface densely spined, conulose or verrucose, irregular. Ectosome without a surface membrane, with protruding ends of strong primary longitudinal fibres protruding through the surface at different levels, forming the spines or aculeations, and in between these spines there is an irregular network of abundant free spicules; there is no special surface skeleton. At the surface the primary longitudinal fibres are clearly visible on the outer side of branches, as strong tracts. (Fig. 5A). Choanosomal skeleton (Fig. 5B–C) is an irregular network of diffuse, multispicular, primary longitudinal fibres, with irregular secondary fibres in between, vaguely present or diffuse and forming an irregular mesh, with abundant free spicules. Spongin scarce. Megascleres: oxeas (Fig. 5D) 369–395–422  $\mu\text{m}$  in length and 12–14–16  $\mu\text{m}$  in diameter. A second category of oxeas, 254–290–344  $\mu\text{m}$  in length, 4–8  $\mu\text{m}$  in diameter, was observed although not mentioned by Burton (1932b). Stylote oxeas, 312–377  $\mu\text{m}$  long, 1–15–16  $\mu\text{m}$  in diameter, are also present.

**Remarks.** Burton (1932b) erected *Haliclonissa* for the type species which he considered an intermediate between *Haliclona* and *Microxina*, and cited as a principal diagnostic character its surface, which was verrucose, and the structure of its skeleton composed of diffuse fibres forming an irregular network of isolated spicules. The protruding ends of primary fibres form a special surface skeleton corresponding to the Niphatidae model, although Burton (1932b) defined *Haliclonissa* as lacking a surface skeleton.

### HEMIGELLIUS BURTON, 1932

#### Synonymy

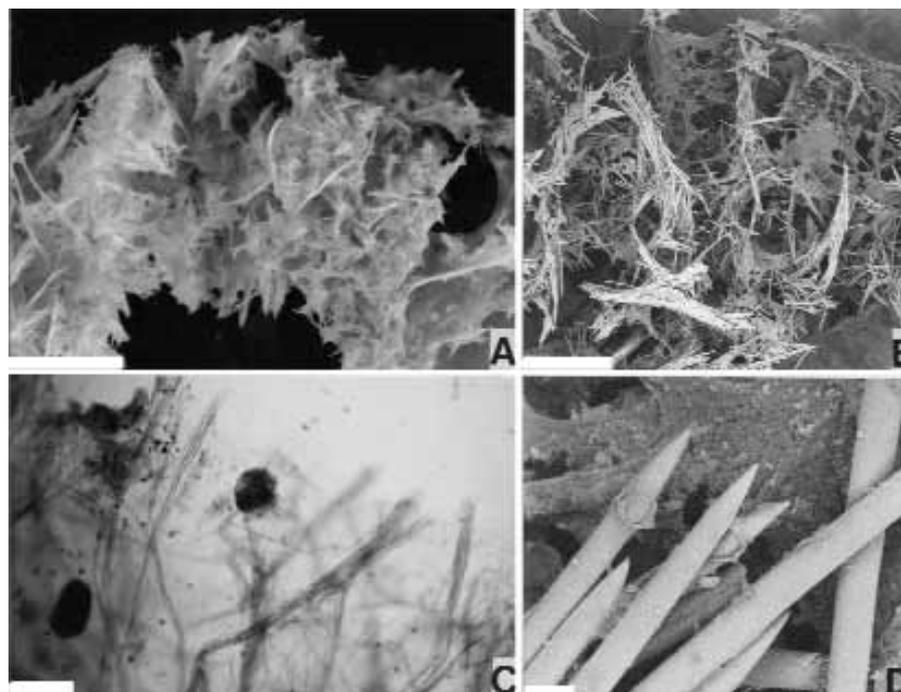
*Hemigellius* Burton, 1932b: 272. ? *Plumocolumetta* de Laubenfels, 1936a: 54. *Calyxadocia* de Laubenfels, 1936a: 70.

#### Type species

*Hemigellius rudis* Burton, 1932b (= *Gellius rudis sensu* Kirkpatrick, 1908c, a synonym of *Gellius fimbriatus* Kirkpatrick, 1908c; not *Gellius rudis* Topsent, 1901a) (by original designation).

#### Definition

Niphatidae with a finely hispid surface produced by the divergent paniculated (*sensu* Kirkpatrick, 1908c) ends of primary



**Fig. 5.** *Haliclonissa* Burton, 1932b. A–D, type species *Haliclonissa verrucosa* Burton, 1932b, holotype BMNH 1928.2.15.473. A, terminal part of tube with longitudinal fibres clearly visible on the outer side of the sponge (scale 1 cm). B, internal view of a longitudinal section of the central cavity (scale 1 mm). C, choanosomal skeleton an irregular network of multispicular primary longitudinal fibres and secondary fibres in between forming irregular meshes with abundant free spicules (scale 50  $\mu$ m). D, oxea megascleres (scale 20  $\mu$ m).

longitudinal fibres arising from the subectosomal region. Choanosomal skeleton is composed of confused multispicular parallel diverging primary fibres, without visible spongin.

#### Diagnosis

Massive to lobate and branching growth forms (Fig. 6A). Oscules large, with raised rims, irregularly distributed. Surface smooth when covered by the surface membrane, finely hispid if the membrane has been rubbed off. Ectosomal skeleton forms a hispid surface by a slight palisade of free spicules issuing from the ends of primary longitudinal fibres. Subectosomal region with numerous (embryonic, *sensu* Kirkpatrick, 1908c) holes formed by uni- to multispicular connecting secondary fibres and by the bifurcated ends of primary longitudinal fibres (Fig. 6B). Choanosomal skeleton composed of primary longitudinal multispicular fibres (Fig. 6C) whose divergent terminal parts in the subectosomal region are divided in a paniculate fashion to strengthen the surface and to form the fine hispidation that characterises the genus. Embryonic holes are well developed (Fig. 6D). Megascleres: Oxeas, slightly bent. Microscleres: sigmas with angulate and curved ends.

#### Distribution

Antarctica: off Winter Quarters, off Coulman Island and Mc Murdo Bay. (Kirkpatrick, 1908c).

#### Previous reviews

Burton, 1932b; Burton, 1938; Vacelet & Arnaud, 1972; Boury Esnault & van Beveren, 1982; Van Soest, 1980; Hooper & Wiedenmayer, 1994.

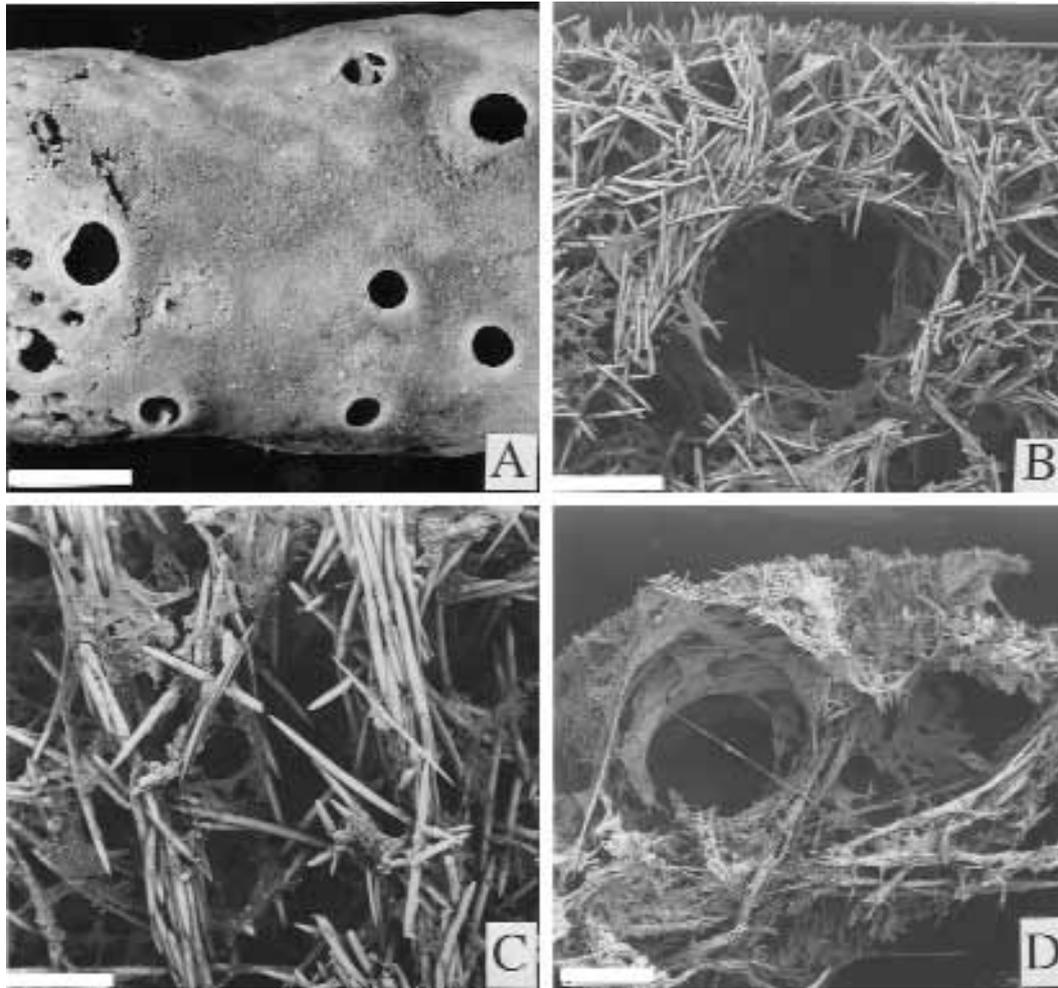
#### Description of type species

*Hemigellius rudis* Burton, 1932b (Fig. 6).

**Synonymy.** *Gellius rudis sensu* Kirkpatrick, 1908c: 45, pl. 17, figs 1, 1a, pl. 24, fig. 1a. *Gellius fimbriatus* Kirkpatrick, 1908c: 46, pl. 17, figs 2, 2a, 24, fig. 2a–b. Not *Gellius rudis* Topsent, 1901a. *Hemigellius rudis* Burton, 1932b: 272.

**Material examined.** Specimen of *Gellius rudis sensu* Kirkpatrick, 1908c: BMNH 1908.2.5.197A–B – Mc Murdo Bay, Winter Quarters, Antarctic Expedition. Holotype of *G. fimbriatus* Kirkpatrick, 1908c: BMNH 1908.2.5.192C – Winter Quarters, off Hut Point, 12–20 fms. Other material. Lectotype of *Hemigellius rudis* Burton, 1932b: BMNH 1928.2.15.128, stn. 39 (RN CIX.I.197–235), 25.03.1926, 'Discovery'. BMNH 1928.2.15.95 – same locality data.

**Description (emended from Kirkpatrick, 1908c).** Massively lobate or thick subcylindrical unbranched or branched fragments of sponges. The largest fragments are  $18 \times 5 \times 2.5$  cm and  $14 \times 5 \times 2.5$  cm. Several fragments exhibit oscules 7 mm in diameter, with circular raised rims. The surface, where the ectosome exists, is quite smooth (Fig. 6A), and where the ectosome has been rubbed off is finely hispid. Ectosomal skeleton is a finely hispid network formed by the terminal ends of primary fibres (Fig. 6B). Choanosomal skeleton (Fig. 6C) is formed by multispicular longitudinal, irregular, confused, discontinuous fibres or tracts, without visible spongin and curved outwards; some of them with more than 10 spicules, 1118–3160  $\mu$ m in diameter. Primary fibres are subsequently divided in paniculated branches (Fig. 6D), and each terminal branch is 80–171–380  $\mu$ m in diameter, ending below the ectosomal membrane, and producing an ectosomal palisade formed by the central oxeas of each end of the branches. This network is visible as the support for the ectosomal membrane.



**Fig. 6.** *Hemigellius* Burton, 1932b. A–C, type species, *Gellius rudis sensu* Kirkpatrick, 1908c. A, specimen BMNH 1908.2.5.197B (scale 1 cm). B, longitudinal view of ectosomal hispid surface and subectosomal rounded cavity (scale 500  $\mu$ m). C, choanosomal skeleton of primary longitudinal multispicular fibres with robust oxoas (scale 200  $\mu$ m). D, *Hemigellius rudis*, Burton's lectotype BMNH 1928.2.15.128. Longitudinal section of subectosomal region, with embryonic holes, multispicular primary fibres without visible spongin (scale 1 mm).

Immediately under the surface network there are several subectosomal rounded cavities, 600–1556–2000  $\mu$ m in diameter, formed by paniculated curved branches of principal fibres (Fig. 6D), which finally expand to form the ectosomal network. These cavities are defined by Kirkpatrick (1908c) as embryo-containing cavities (although in our studies of specimens these cavities were empty).

**Remarks.** Burton (1932b) erected *Hemigellius*, and designated *Gellius rudis* Topsent, 1901a as the type species. However, Burton misinterpreted Topsent's (1901a) description of *Gellius rudis* (1929a) and thus *Hemigellius* is based on Kirkpatrick's (1908c) specimens of *Gellius rudis*, which Burton named *Hemigellius*, and which are certainly different from Topsent's specimen (= *Haliclona* (*Gellius*); see Vacelet & Arnaud, 1972: 20). Burton (1932b) remarked that the original description of Topsent (1901a) gave little information regarding the structure of the skeleton, but the surface was said to be finely hispid, and in Burton's opinion specimens of *Gellius rudis* Topsent described by Kirkpatrick (1908c) allegedly resembled the holotype of Topsent closely enough to justify his diagnosis of *Hemigellius* (i.e., based on Kirkpatrick's specimens of *G. rudis*). Vacelet & Arnaud (1972: 20) remarked on the differences exhibited between *G. rudis* Topsent, collected by the 'Belgica' Expedition, 1897–99, from

Antarctica (70°23'S, 82°47'W), and *G. rudis* collected by Kirkpatrick (1908c), from Mc Murdo Bay, especially concerning the subectosomal ends of primary longitudinal fibres in both: paniculated in *G. rudis* Topsent collected by Kirkpatrick, and non paniculated in the type of *G. rudis* Topsent, 1901a. At the same time Vacelet & Arnaud (1972) remarked that *G. fimbriatus* and *G. rudis sensu* Kirkpatrick, 1907a were subjective synonyms. The character 'paniculated ends' of primary fibres in Kirkpatrick material, in their opinion, justified the erection of the new genus *Hemigellius* by Burton (1932b). Burton (1932b: 272) considered his genus *Hemigellius* to be closely allied to *Haliclona*, but later (Burton, 1938: 7), observing the variation in the skeletal arrangement of *H. pachyderma*, he considered it was doubtful whether the species was distinct from the type species of his genus, and indeed if the genus *Hemigellius* itself was distinct from *Haliclona*. These arguments are rejected here and *Hemigellius* clearly belongs to Niphatidae as presently interpreted.

Van Soest and de Weerd (in litteris) remarked on the genus *Plumocolumetta* de Laubenfels, 1936a: 54 (type species *Gellius bidens* Topsent, 1901a: 2 from Antarctica, by original designation). For a full description see Topsent (1901d: 14, pl. II fig. 8, pl. III fig. 7). The holotype (not examined) is in IRSNB no. POR032,

cf. Willenz, 1994: 8). A subsequently collected specimen from MNHN (Jean Charcot Expedition 1905, No. 47) was examined and this was found to conform to Topsent's original description. It is a hollow cylindrical species with a finely hispid, punctate surface. The choanosomal skeleton consists of very loose longitudinal spicule tracts and many single spicules arranged in confusion. At the surface there is a more-or-less tangential crust of disorderly arranged spicules carried by the endings of the choanosomal spicule tracts, which also protrude beyond the surface for slight distance. The megascleres are robust curved oxeas,  $660\text{--}700 \times 17\text{--}20 \mu\text{m}$ . Microscleres are sigmas with unique bifid apices, curved outwards and downwards, rather resembling a snake's tongue. Its oxeas and surface skeleton are quite different from sponges of *Haliclona* (*Gellius*), and in combination with the peculiar sigmas, this induced de Laubenfels (1936a) to erect a separate genus for this species. However, apart from the uniquely ornamented sigmas, this sponge conforms to *Hemigellius*. Until further species with such sigmas are found, we prefer to consider *Gellius bidens* a member of this genus and accordingly *Plumocolumetta* is a subjective junior synonym of *Hemigellius* (taxonomic decision this work).

*Calyxadocia* de Laubenfels, 1936a was considered to be a junior synonym of *Microxina* by Wiedenmayer (in Hooper & Wiedenmayer, 1994), but its allocation there is debatable. The type species, *Gellius calyx* Ridley & Dendy, 1887 (by original designation), has an external morphology close to that of *Calyx* (a thin walled hollow body), but the surface skeleton is closer to that of *Haliclona* (a loose, single layer of oxeas). Ridley & Dendy (1887) describe it as having 'loose main bundles of spicules running in a direction vertical to the surface of the sponge. At the surface these spicula project freely, giving it a characteristic hirsute appearance'. The main skeleton resembles *Gellius* (a loose reticulation and some loose bands of big oxeas, connected by free spicules, projecting freely in a hispid surface), and microscleres are abundant sigmas. Burton (1959), describing a specimen from Iceland as *Haliclona calyx* (Ridley & Dendy, 1887), said that it coincided exactly with the holotype of *Gellius calyx*, except that it lacked sigmas. An alternative view, that *Calyxadocia* may belong to the subgenus *Gellius* of genus *Haliclona*, is rejected because in the skeleton is more confused, subhalichondroid, and on this basis de Weerd (pers. comm.) suggests that it is closer to *Hemigellius*. The large oxeas of *Gellius calyx* is also another clue as to its affinities with Niphatidae, where these huge oxeas are never found in Chalinidae. *Calyxadocia* is considered a synonym of *Hemigellius* (taxonomic decision this work).

### MICROXINA TOPSENT, 1916

#### Synonymy

*Microxina* Topsent, 1916: 170; 1917: 72. ? *Sigmaxinysa* Kirkpatrick, 1907a: 272.

#### Type species

*Microxina charcoti* Topsent, 1916 (by monotypy).

#### Definition

Niphatidae with strongly spined surface formed by the terminal tufts of primary fibres, with a tangential layer of free oxeas between the spines, and microxeas are present.

#### Diagnosis

Tubular and branched, to globular with cylindrical branching growth forms. Tubes or branches are issued from a common base, have thin walls, and the sponge has a deep central exhalant cavity. Several scattered oscules, terminal if singular. Surface is uneven, membranous and strongly spined. Ectosomal skeleton forms a tangential irregular network of oxeas between the spines, and appears obscured by them. Choanosomal skeleton exhibits longitudinal, compact, multispicular, fasciculate and anastomosing primary fibres, issuing from the base of the sponge. Between the fibres, large, irregular meshes occur with abundant free spicules. No visible spongin. Microscleres microxeas.

#### Previous reviews

Topsent, 1916, 1917; Hooper & Wiedenmayer, 1994.

#### Description of type species

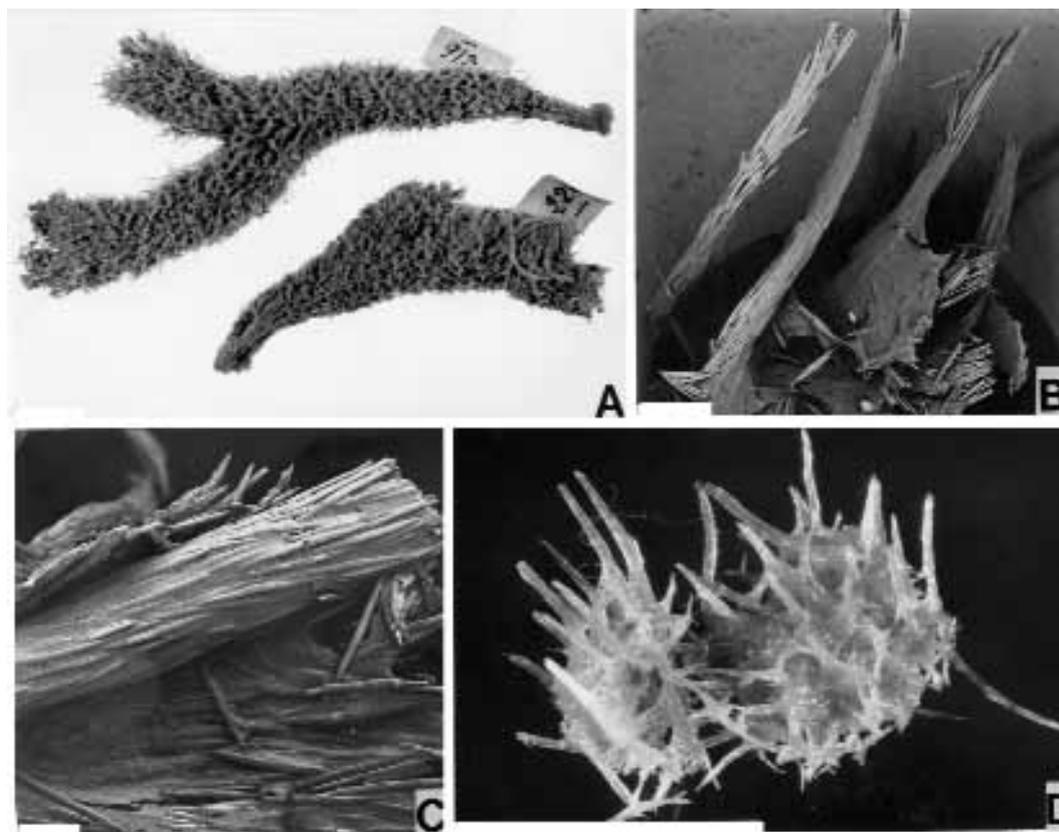
*Microxina charcoti* Topsent, 1916 (Fig. 7).

**Synonymy.** *Microxina charcoti* Topsent, 1916: 170; 1917: 73, pl. 1, fig. 3, pl. 2, fig. 3, pl. 6, fig. 17; [in part] Burton, 1932b: 271, pl. 50, fig. 1 (under *M. benedeni* (Topsent, 1901a)).

**Material examined.** Lectotype (here designated): MNHN LBIM DT 226 – Antarctica, near Terre Alexandre, Baie Marguerite, 200–297 m. Paralectotypes: MNHN LBIM DT 692, 216, 217, 223, 316, 317 (BMNH 1926.10.26.338 slides) – stn 8, Man-O-War Anchorage, Funchal, Madeira. 0–25 m, 'Terra Nova' collection. Other comparative material. Holotype of *Microxina benedeni* (Topsent, 1901a) (Fig. 7D): IRSNB 24 POR MOD II – Antarctica, 70°20'S, 83°23'W, 29.11.1898, 'Belgica' 1897–99, no. 725.

**Description.** Tubular and ramified from a narrow fibrous base (Fig. 7A), with a deep central aquiferous cavity ending in a large oscule of the same diameter. Surface strongly spined by long surface spines up to 10 mm long (Fig. 7B). Ectosomal skeleton is a tangential network of oxeas interrupted by the terminal tufts of longitudinal primary fibres subdivided to form the surface spines (Fig. 7B). Choanosomal skeleton with large and irregular meshes delimited by fasciculate, longitudinal primary multispicular fibres, containing more than 15 spicules, packed compactly (Fig. 7C) and issued from the base of the sponge, 296–426–800  $\mu\text{m}$  in diameter. Primary fibres may be irregularly split to form secondary fibres, 41–90–148  $\mu\text{m}$  in diameter. Meshes contain abundant microscleres and free oxeas. No visible spongin. Megascleres: oxeas 1, strong, slightly curved with acerate points, 459–512–600  $\mu\text{m}$  long  $\times$  20–25–29  $\mu\text{m}$  in diameter; oxeas 2, 262–360–459  $\mu\text{m}$  long  $\times$  4–7–12  $\mu\text{m}$  in diameter. Microscleres: microxeas, 45–73–95  $\mu\text{m}$  long  $\times$  3–4  $\mu\text{m}$  in diameter.

**Remarks.** Topsent (1917) included his new genus *Microxina* in the Gelliinae, and made a comparison between *Microxina* and *Strongylophora*. This genus was included in Gelliinae by Dendy (1905), and Topsent (1917) considered that both genera were close due to the common possession of microxeas, and because of the fibrous character of their skeletons. At the same time he also remarked that both genera should probably be included with the axinellids. Later, in the same work, he gave up this idea because *Strongylophora* was (in his opinion) less fibrous than *Microxina*, and because of the existence of other Gelliinae with a spined surface (e.g., *Gelliodes*). We consider that both genera are sufficiently different in their skeletal structures to be valid. Burton (1932b) considered



**Fig. 7.** *Microxina* Topsent, 1917. A–C, type species *Microxina charcoti* Topsent, 1916. A, tubular branched fragments of lectotype MNHN LBIM DT 226 and 216, with strongly spined surface and spines up 10 mm long (scale 1 cm). B, terminal tufts of longitudinal primary fibres subdivided to form the surface spines (scale 500  $\mu$ m). C, primary longitudinal choanosomal fibres with no visible spongin (scale 200  $\mu$ m). D, *Microxina benedeni* (Topsent, 1901a), holotype IRSNB 24 POR MOD II (scale 1 cm).

that *Gelliodes benedeni* and *Microxina charcoti* were subjective synonyms, due to their external form and spiculation, with the only notable difference being that *G. benedeni* had only sigmas (and additional raphides in var. *fortior*). By comparison, *Microxina* had only microxeas although Burton (1932b) also observed raphides. Wiedenmayer (1989) regarded *Hemigellius* as a subjective synonym of *Microxina*. We also compared both genera and observed significant differences between their respective type species, such as the presence (in *Hemigellius rudis*, *sensu* Kirkpatrick, 1908c) of paniculate primary fibres and subectosomal 'embryonary holes', and differences in the continuous fibres or tracts observed in *Microxina charcoti*. In addition, we found that the structure of the choanosomal skeleton was compact and disorganised in *Hemigellius rudis*, but clearly fibrous in *Microxina charcoti*. The external morphology, consistency and surface skeleton are also different: *Hemigellius* is massively lobate or thickly subcylindrical, whereas *Microxina* is tubular, to massive or globular (e.g., *M. benedeni*; Fig. 7D). *Hemigellius* has a clear surface palisade or a finely hispid surface, whereas in *Microxina* there is a fine membrane between the solid surface spines producing a strongly spiny surface.

#### **NIPHATES DUCHASSAING & MICHELOTTI, 1864**

##### **Synonymy**

*Niphates* Duchassaing & Michelotti, 1864: 93; de Laubenfels, 1936a (as unrecognisable).

##### **Type species**

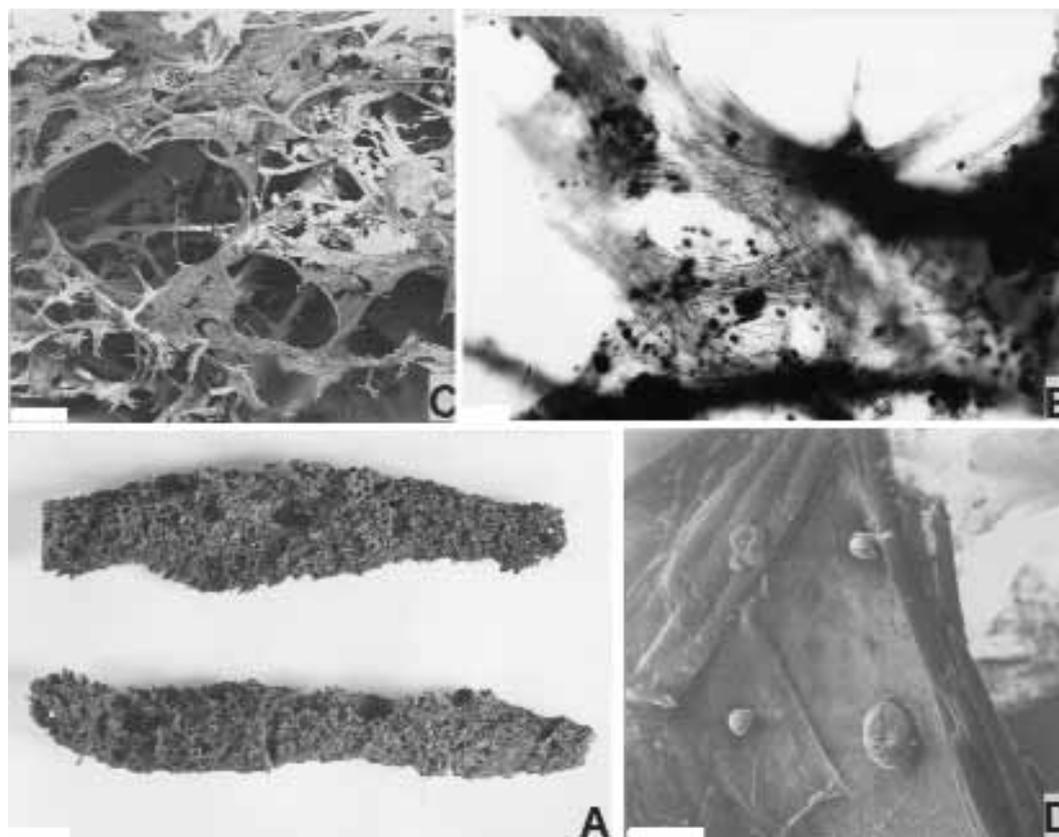
*Niphates erecta* Duchassaing & Michelotti, 1864 (by subsequent designation; Wiedenmayer, 1977b).

##### **Definition**

Niphatidae with a paratangential ectosomal reticulation of fibres or tracts, obscured by the conulose surface produced by the ends of primary longitudinal fibres.

##### **Diagnosis**

Massive-vasiform, funnel-shaped to tubular or ramose growth forms (Fig. 8A). Surface conulose to spiny, irregularly smooth to rough, produced by primary longitudinal fibres ending on surface. Oscules numerous, irregularly distributed, flush with the surface or slightly raised. Consistency spongy to rigid, tough, firm. Ectosomal skeleton is a tangential network of secondary fibres, obscured by protruding tufts of primary fibres. Microscleres are rare sigmas. Choanosomal skeleton an irregularly diverging reticulum of pauci- to multispicular primary longitudinal fibres, abundantly ramified, (Fig. 8B) to form fibrofascicles and irregular branches ascending to the surface. Interconnecting secondary fibres pauci- to multispiculate, well developed to form rounded to irregular meshes. Spongin dominant, abundant and covering the spicules (Fig. 8C). Megascleres oxeads (Fig. 8D). Microscleres sigmata, present or absent.



**Fig. 8.** *Niphates* Duchassaing & Michelotti, 1864. A–D, type species *Niphates erecta* Duchassaing & Michelotti, 1864. A, lectotype (fragments) ZMA POR 1633, MT Por 51, two branches with conulose surface and scattered oscules (scales 1 cm). B, choanosomal skeleton with an irregularly diverging reticulum of pauci- to multispicular primary longitudinal fibres (scale 50  $\mu\text{m}$ ). C, ectosomal skeleton with polygonal meshes and multispicular fibres (scale 200  $\mu\text{m}$ ). D, oxeote to strongylote megascleres and abundant spongin (scale 20  $\mu\text{m}$ ).

### Distribution

Caribbean: Bimini, Florida, St Thomas, Curaçao, Bonaire; Colombia; Barbados, Cuba (as *Gelliodes ramosa*), Tortola, Viecques, Mexico, Jamaica (as *Gelliodes aerolata*). Saba, Puerto Rico. Indo-west Pacific: New Caledonia; Papua New Guinea; Australia (decision for synonymy Van Soest, 1980).

### Previous reviews

Duchassaing & Michelotti, 1864; Wiedenmayer, 1977b: 95; Van Soest, 1980: 35; Desqueyroux-Faúndez, 1984: 50; Fromont, 1993: 17.

### Description of type species

*Niphates erecta* Duchassaing & Michelotti, 1864 (Fig. 8).

**Synonymy.** *Niphates erecta* Duchassaing & Michelotti, 1864: 93 pl. 21. fig 3; Wiedenmayer, 1977b: 96, pl. 20, figs 7, 8, pl. 21, figs 1–4, text-fig. 119; Zea, 1987 (with additional synonyms).

**Material examined.** Lectotype (designation Weidenmayer, 1977b: 96, 271): ZMA POR. 1633 – St. Thomas. Paralectotype MT Por 51 – St. Thomas. Schizoparalectotype: USNM 31018. Other material. ZMA 3305 – Curaçao, W of Piscadera. ZMA 3518 – near Carmabi. ZMA 3642 – outside of Jan Thiel Bay, Curaçao.

**Description (emended from Van Soest, 1980).** Ramose with branches 15 cm long and 1.5–2 cm in diameter. Branches undivided over most of their length. Oscules numerous, 4–7 mm, irregularly scattered over branches. Surface smooth to conulose-spinous. Consistency fragile, spongy, tough. Ectosomal skeleton an irregular to polygonal network of superficial multispicular fibres extending between the protruding ends of primary fibres. This network is covered by protruding and ramified ends of primary longitudinal fibres producing a conulose to spiny surface. Choanosomal skeleton an irregular reticulation with rounded to angular meshes formed by radiating and fasciculate ascending longitudinal, multispicular fibres. Meshes average between 139–435  $\mu\text{m}$  in largest diameter. Primary fibres are 55–100  $\mu\text{m}$  in diameter, cored by 6–20 spicules. At the surface they are 200–500  $\mu\text{m}$  apart. Secondary or interconnecting fibres are 25–45–90  $\mu\text{m}$  in diameter, cored by 4–15 spicules. Primary fibrofascicules 361–515–615  $\mu\text{m}$  in diameter. Megascleres: Oxeas, slightly curved, oxeote and strongylote forms are present, 99–139–154  $\mu\text{m}$  long, 2–5–6  $\mu\text{m}$  in diameter. Microscleres: if present, sigmata, 12–15  $\mu\text{m}$ .

**Remarks.** The precise species content of this genus, and indeed the family, remains uncertain. For example, many species presently included in *Pachychalina* have been referred to *Amphimedon*, with some originally described as *Pachychalina* of authors more closely related to *Callyspongia*, e.g., *Pachychalina fibrosa* Ridley & Dendy, 1887. Similarly, some *Amphimedon* and *Niphates* may be better referred to *Pachychalina*, although

precisely which ones requires a more thorough revision. The presence or absence of sigma microscleres in *Niphates* is considered an unreliable generic character (see Van Soest, 1980; Fromont, 1993).

### **PACHYCHALINA SCHMIDT, 1868**

#### **Synonymy**

*Pachychalina* Schmidt, 1868: 8; Ridley & Dendy, 1887: 19.

#### **Type species**

*Pachychalina rustica* Schmidt, 1868: 8 (by monotypy).

#### **Definition**

Niphatidae with a paratangential ectosomal reticulation of fibres or tracts obscured by the irregularly, conulose to spiny surface, pierced by abundant aquiferous orifices.

#### **Diagnosis**

Columnar, clavate, subcylindrical growth forms (Fig. 9A), having a well-developed aquiferous system with large canals rendering the texture highly compressible. Numerous small rounded aquiferous openings not clearly differentiated into oscules or pores. Some of these openings are lengthened and divided by a fine wall with irregular edges, especially at the high part of the sponge where pores are very close to one another. At this location the surface has a very irregular character due to the numerous aquiferous orifices and because the surface lacks a membrane. Ectosomal skeleton (Fig. 9B) appears to be undifferentiated from the choanosomal skeleton, and is extremely irregular because of the numerous aquiferous orifices at the surface. No ectosomal membrane is present. Ectosomal skeleton with rounded meshes and free spicules, three-dimensional, irregular and confused, between the ends of primary fibres and aquiferous canals. Choanosomal skeleton is confused, ascending, slightly parallel multispicular primary fibres of irregular diameter, with compact spicules and no visible spongin binding them. Primary fibres are obliquely branched to form secondary lines, with decreasing diameter towards the high part of the sponge (Fig. 9C). The choanosomal skeleton is highly lacunar due to the aquiferous canals, with lacunae as large as the narrow spongin walls between them. Spongin not visible. Megascleres: oxeads, irregularly bent, with short apices and regular diameter (Fig. 9D). Microscleres: absent.

#### **Distribution**

Mediterranean; Australia (many recorded as *Cribrochalina* and *Amphimedon*, in Hooper & Wiedenmayer, 1994). Chile-Peru and Magellan region; West Indies, Bahamas, St Thomas, Guadeloupe, New Providence, (as *Amphimedon* [part]), Boreal East Pacific, Red Sea, Indian Ocean, Tasmania. (Van Soest, personal communication, in part.)

#### **Previous reviews**

Topsent, 1901b: 357; 1938a: 6; 1938b: 31; Burton, 1929a: 505.

#### **Description of type species**

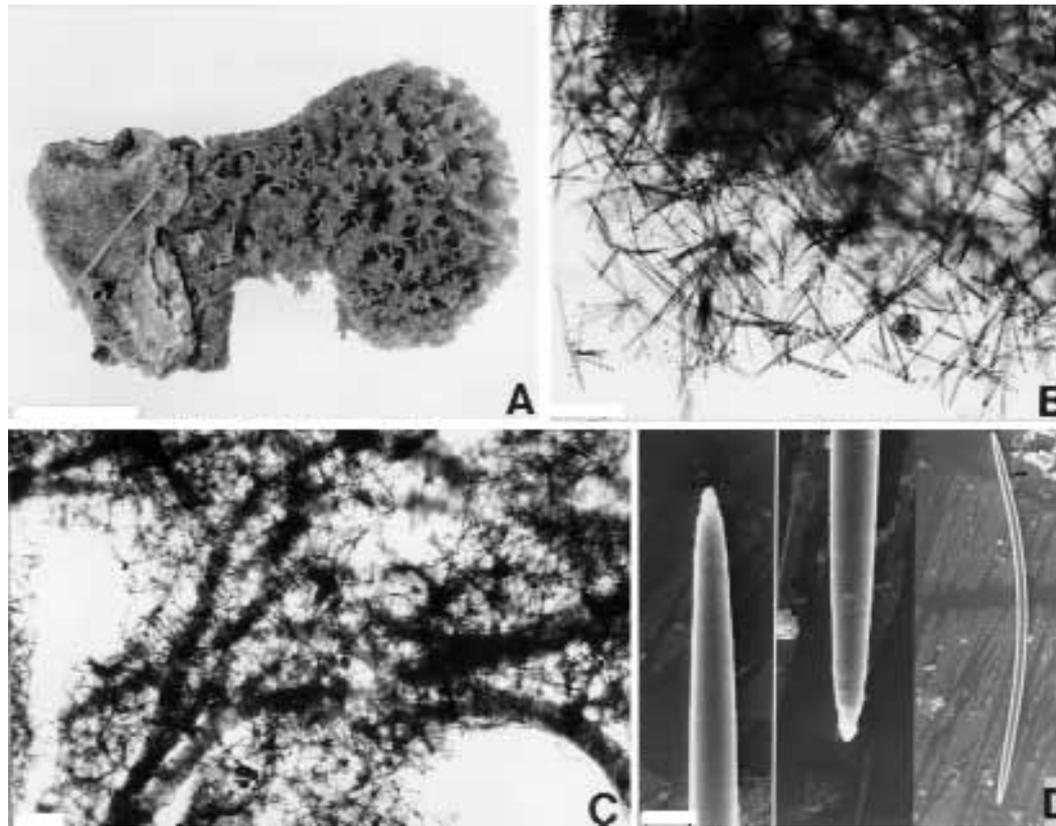
*Pachychalina rustica* Schmidt, 1868 (Fig. 9).

**Synonymy.** *Pachychalina rustica* Schmidt, 1868: 8, pl. 2, fig. 6; Topsent, 1901b: 357, pl. 13, fig. 4; 1938a: 6; 1938b: 31.

**Material examined.** Lectotype (here designated): MNHN LBIM DT47 – La Calle, Algeria, Expedition Lacaze-Duthier. Paralectotype: MNHN LBIM DT25.

**Description.** Lobate, claviform, compact branches, growing on a fragment of mollusc shell or on a calcareous pebble, small, 2–3 cm high, 1–2 cm wide. Surface with numerous orifices, conulose or strongly spiny in appearance (Fig. 9A). Without surface membrane. Consistency elastic, compressible, due to its strongly developed aquiferous system with large irregular canals, limited by spongin plates. Ectosomal skeleton not clearly visible; in the type material it contains free spicules and fragments of fine tracts, producing a tridimensional network (Fig. 9B). Choanosomal skeleton irregular and confused, formed by strong multispicular fibres without preferential orientation in the skeleton, large and repeatedly longitudinally divided, ultimately forming isolated and finer ramifications (Fig. 9C). All fibres are multispicular, with more than 15 spicules, no visible spongin sheath. Diameter of primary fibres 100–272–440  $\mu\text{m}$ , secondary fibres are not connecting fibres but free within the choanosomal skeleton, 40–60–80  $\mu\text{m}$ , tertiary fibres paucispicular, free in the terminal parts of secondary tracts, 20–30  $\mu\text{m}$  diameter. The interfibre spaces contain few free spicules. Megascleres: from type material, 138–171–195  $\mu\text{m}$  long, 3–5–6  $\mu\text{m}$  wide. Topsent (1938b), 190–240  $\times$  4–7  $\mu\text{m}$ , with most 215–225  $\times$  5–6  $\mu\text{m}$  (see Table 1).

**Remarks.** Lendenfeld (1887c: 775) provided an emended diagnosis of *Pachychalina* and described ten new species from Australia, none of which has been re-examined. Dendy (1905) included *Pachychalina* in the subfamily Chalininae, but recognised that genera included in this group (viz., *Pachychalina*, *Chalina*, *Ceraochalina* and *Siphonochalina*), were impossible to define sharply. Some of these species are actually *Calyspongia*, such as *Pachychalina* (pro *Calyspongia*) *spinilamella* Dendy, 1889. Burton (1929a) considered *Pachychalina incertae sedis* as he was uncertain as to what ‘Schmidt intended it to include’. The type specimen, in Burton’s (1928) opinion, was ‘for the moment, apparently irretrievably lost, and not available for re-examination’. Nevertheless, Topsent (1901b) found in MNHN collections, two small specimens, which are probably the specimens we have studied in this work, but he did not describe them providing only an illustration (Topsent, 1901b: pl. 13, fig. 4) and spicule dimensions (which are similar to those observed in the type material re-examined). Wiedenmayer (1977b) included with doubt *Pachychalina* in synonymy with *Niphates*. He remarked that the surface of *Pachychalina*, illustrated by Topsent (1901b), was very similar to that of West Indian *Niphates* but without a developed surface reticulum. *Pachychalina*, was subsequently included as a subjective junior synonym of *Amphimedon* by Van Soest (1980: 34) and followed by Hooper & Wiedenmayer (1994). Van Soest (1980) supported his decision by the fact that *Pachychalina* has probably been compromised in the older literature, and consequently a doubtful taxon although a well-established genus in the sense of the ICZN. The knowledge of the real taxonomic features of *Pachychalina sensu stricto*, from re-examination of the type material, reveals several distinctive features and indicates that the genus is valid within Niphatidae. Future work is required to determine the species and geographic scope of the genus, requiring re-examination of all nominal species assigned to the various niphatid genera.



**Fig. 9.** *Pachychalina* Schmidt, 1868. A–D, type species *Pachychalina rustica* Schmidt, 1868. A, lectotype MNHN LBIM DT 747 (scale 1 cm). B, ectosomal skeleton extremely irregular undifferentiated from choanosome (scale 50  $\mu\text{m}$ ). C, choanosomal skeleton with an irregular network of confused ascending, slightly parallel multispicular primary fibres obliquely branched to form secondary lines (scale 50  $\mu\text{m}$ ). D, oxeas (scale 5  $\mu\text{m}$ ).

*Pachychalina* differs from *Amphimedon*, *Gelliodes* and *Niphates* as follows.

It differs from *Amphimedon* as it lacks a clear ectosomal tangential network or membranous ectosomal skeleton. In *Amphimedon* there is a regular tangential skeleton of secondary fibres with regular rounded meshes, overlying the choanosomal canals and covered by a fine membranous organic layer. In addition, the choanosomal skeletal reticulation of *Pachychalina* is peculiar in having an almost tertiary structure, with thick primary tracts, thinner irregular very thin interconnecting tracts, and with loose spicules in between. By comparison, in *Amphimedon* the choanosomal skeleton has a regular system of main and secondary fibres which do not differ much in diameter. In *Pachychalina* the whole skeleton is rather confused, with the choanosomal skeleton irregular, diffuse, and occurring as a radially plumose network of primary, ramified, multispicular fibres, irregularly connected by no proper secondary multispicular fibres and no visible spongin.

The skeletons of *Pachychalina* and *Gelliodes* have both similarities and differences, with the former having an emphasis on the main fibres, producing a coarse skeleton with secondary tracts thinner and ill-defined and with loose spicules, and lacking sigmas which are present in *Gelliodes* (Fig. 9C). In addition,

*Pachychalina* possesses a three-dimensional surface skeleton largely undifferentiated from the main skeleton, and with no surface membranous organic layer distinguishable from the subdermal portion. In *Gelliodes* there is a light organic surface layer and the ectosomal skeleton is a tangential system of multispicular fibres through which the protruding ends of primary fibres are clearly observed.

*Niphates* is also similar to *Pachychalina* but has a more regular skeleton with secondary fibres well-developed to form a regular rectangular reticulation. Their surface skeletons are also similar, being three-dimensional and not well-separated from the choanosomal skeleton in *Pachychalina*, compared to *Niphates* which has a surface that is conulose to spiny, and irregularly smooth to rough produced by primary longitudinal fibres ending at the surface, and well differentiated from the choanosomal skeleton. Consistency in both genera is also different. *Niphates* is spongy to rigid, tough, firm, whereas *Pachychalina* has an extremely compressible texture. Choanosomal skeletons in *Pachychalina* and *Niphates* differ where the former has a skeleton containing irregular fibres, without a visible spongin sheath, and highly lacunar, and *Niphates* has pauci- to multispicular fasciculated primary and interconnecting fibres, which are well-developed and spongin is dominant, abundant, and covers the spicules.

