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

Suborder Spongillina subord. nov.: Freshwater Sponges

Renata Manconi[1] & Roberto Pronzato[2]

[1] Department of Zoology and Anthropological Biology of the University, via Muroni 25, I-07100, Sassari, Italy. (rmanconi@ssmain.uniss.it)
[2] Department for the Study of the Territory and its Resources of the University, Corso Europa 26, I-16132 Genoa, Italy. (pronzato@hpe35.dipteris.unige.it)

Spongillina subord. nov. (Demospongiae, Haplosclerida) consists of seven families of exclusively freshwater sponges together containing 45 genera: Spongillidae (21 valid genera), Lubomirskiidae (three genera), Malawispongiidae fam. nov. (five genera), Metaniidae (five genera), Metschnikowiidae (monogeneric), Palaeospongillidae (monogeneric), Potamolepidae (six genera), some geographically widespread and others highly endemic. A central body cavity is peculiar to Malawispongiidae. Skeletal network is typically multispicular alveolate-reticulate with scanty spongin in Metaniidae, Potamolepidae and Malawispongiidae, paucispicular irregularly reticulate in Palaeospongillidae, Spongillidae, Metschnikowiidae with a variable amount of spongin, multi- to paucispicular irregularly reticulate with an abundant amount of spongin in Lubomirskiidae. Smooth or variably ornamented megascleres range from oxeas to strongyles in Spongillidae, Lubomirskiidae and Metaniidae, but are exclusively oxeas in Malawispongiidae, Metschnikowiidae, Palaeospongillidae, and exclusively strongyles in Potamolepidae. Microscleres usually present in Spongillidae, Palaeospongillidae and Metaniidae, are rare in Potamolepidae, and absent in Lubomirskiidae, Malawispongiidae and Metschnikowiidae. Microscleres if present are oxeas, strongyles, aster-like, pseudobirotules. Larvae are always parenchymella. Gemmules are typical of Spongillidae, Metaniidae, Palaeospongillidae, rare and strictly adhering to the substratum in Potamolepidae, and absent in Lubomirskiidae, Malawispongiidae and Metschnikowiidae. Gemmular theca is monolayered in Potamolepidae, mono-, bi- or tri-layered in Spongillidae, generally tri-layered in Metaniidae. Gemmules usually armed by gemmuloscleres in Metaniidae, Potamolepidae and Spongillidae, are rarely naked in the latter. Gemmuloscleres are boletiform (tubelliform), parmuliform, pseudobirotules in Metaniidae, and oxeas, strongyles, birotules, pseudobirotules, club-like, botryoidal in Spongillidae. Three more genera *incertae sedis* are included. This work is a relatively critical synthesis of the literature, however, a critical phylogenetic revision of established taxa is still in progress.
Keywords: Porifera; Demospongiae; Haplosclerida; Spongillina subord. nov.; Spongillidae; *Anheteromeyenia; Corvoheteromeyenia; Corvospongilla; Dosilia; Duosclera; Ephydatia; Eunapius; Heteromeyenia; Heterorotula; Nudospongilla; Pachyrotula; Pectispongilla; Racekiela; Radiospongilla; Sanidastra; Saturnospongilla; Spongilla; Stratospongilla; Trochospongilla; Umborotula; Uruguayella;* Lubomirskiidae; *Baikalospongia; Lubomirskia; Swartschewskia*; Malawispongiidae fam. nov.; *Cortispongilla*; *Malawispongia; Ochridaspongia*; *Pachydictyum*; *Spinospongilla;* Metaniidae; *Acalle*; *Corvomeyenia*; *Drulia*; *Houssayella; Metania*; Metschnikowiidae; *Metschnikowia*; Palaeospongillidae; *Palaeospongilla*; Potamolepidae; *Echinospongilla* nom. nov.; *Potamolepis*; *Potamophloios*; *Oncosclera*; *Sterrastrolepis; Uruguaya*; Genera *incertae sedis; Balliviaspongia; Makedia; Ohridospongilla*.

SPONGILLINA SUBORD. NOV.

Definition

Exclusively freshwater sponges, with megascleres consisting of oxeas or strongyles, smooth or spined, forming pauci- to multispicular tracts producing irregular to regular meshes, occasionally with large alveolate cavities (a central body cavity in one family); spongin mostly sparse; microscleres present or absent, including smooth or spined oxeas, aster-like or birotule like spicules. Four families with gemmules (resting bodies containing totipotent cells), which may contain gemmuloscleres of diverse morphology that is often diagnostic. Three families lack gemmules. Where known reproduction is viviparous, with fully ciliated parenchymella larvae.

Diagnosis

Haplosclerida with growth form ranging from encrusting, bulbose, globular, arborescent to massive. Surface smooth, hispid or conulose. Consistency generally not elastic but ranging to notably elastic in some taxa, and also varying from fragile, to firm, to stony hard. Ectosomal skeleton with tangential layer of megascleres, or tufts of spicules arising from apices of primary fibres (most families), or with microscleres in the dermal membrane (Potamolepidae). Choanosomal skeleton with pauci- to multispicular tracts of megascleres forming regular to irregular reticulate meshes, with or without lacunar or alveolate cavities, or occasionally radial ascending paucispicular tracts without anastomoses (Metschnikowiidae). Spongin usually sparse. Megascleres oxeas to strongyles, smooth, spiny or granular, occasionally with larger tuberculate ornamentations, with sharply pointed, rounded or occasionally inflated points. Microscleres may include oxeas or strongyles (smooth or microspined), pseudo-asters or pseudobirotules, but frequently absent. Gemmules, resting bodies containing totipotent cells (thesocytes) are characteristic of spongillines but present in only four freshwater sponge families (Spongillidae, Metaniidae, Palaeospongillidae, Potamolepidae), and absent in three (Malawispongiidae fam. nov., Lubomirskiidae, Metschnikowiidae). If present, gemmules may be dispersed within the choanosome or restricted to the sponge base in contact with the substratum, occurring singly or forming carpets. Gemmule morphology is variable, with or without a foramen (occasionally with several), with or without a gemmular cage connected to the skeletal network or basal plate. Gemmules have a thin or thick gemmular theca formed by one, two or three layers of spongin. The intermediate one is the pneumatic layer

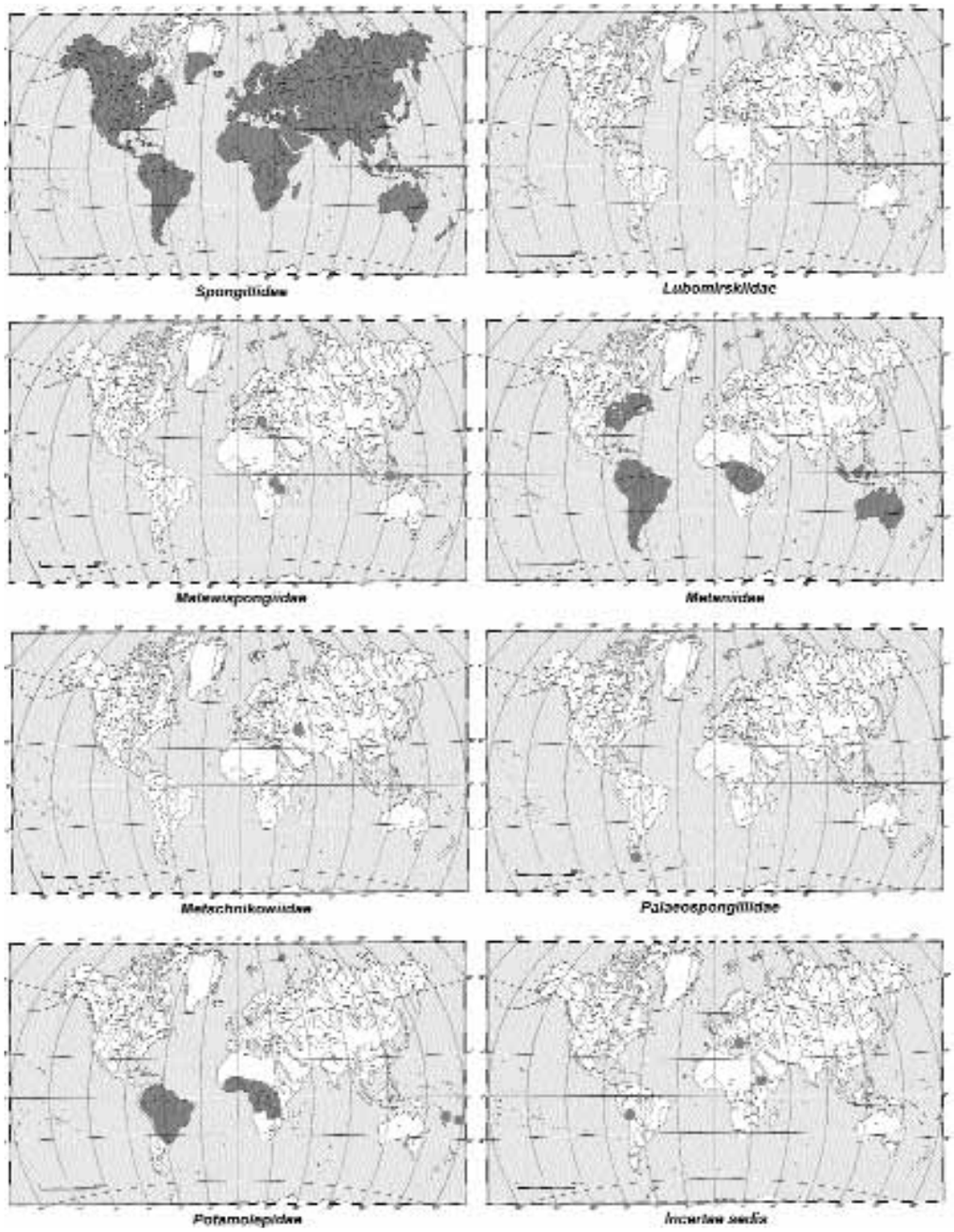

Fig. 1. Geographic distribution of the Spongillina families.

arranged to form chambers, trabecules or fibres. Gemmules can be naked or armed by gemmuloscleres organised radially or tangentially, partially or totally embedded in the surface. Gemmulosclere morphology highly diverse, often diagnostic, including smooth, spiny to granulated oxeas to strongyles, birotules, pseudobirotules, club-like, boletiform (tubelliform), parmuliform or botryoidal. Larvae hollow parenchymella, where known, entirely ciliated, occasionally with larval oxeas. Most freshwater sponges have a poor fossil record (not older than Miocene, Pliocene or Pleistocene) although one (*Palaeospongilla*) is recorded from the Cretaceous.

History, biology and evolution

Although sponges may generally provide good paleontological material, most fossil records of freshwater sponges belong to presently widespread genera, and date back to relatively recent periods of the Miocene, Pliocene and Pleistocene (Rezvoi *et al*., 1971; Harrison & Warner, 1986). It is probable that the colonization of inland waters occurred approximately in the Jurassic Period (210–140 MYA), at the beginning of the disjunction phase between Africa and South America when the southern Atlantic was probably no more than a narrow fjord characterised by shallow brackish

waters subject to strong thermal fluctuations (Pearson, 1978). Among the few fossils known since the Mesozoic Era (Young, 1878; Ott & Volkheimer, 1972), *Palaeospongilla chubutensis* from Patagonia, dated 100 MY, is characterised by a notably evolved gemmular architecture comparable to present taxa of Spongillidae. The phenomenon of cryptobiosis and the modular bauplan of freshwater sponges were very precocious in the evolutionary history of this taxon, and spreading throughout inland waters was favoured by the twofold specialisation of gemmules as resistant bodies and propagules (Simpson & Fell, 1974; Frost *et al*., 1982; Pronzato & Manconi, 1994b, 1995). Growth rhythms range from cyclic, with periodicity timed by climatic seasonal or annual fluctuations, to continuous in perennial forms (Fell & Levasseur, 1991; Manconi & Pronzato, 1991; Fell, 1995).

The colonization strategy by gemmule-producing sponges seems therefore mainly based on morphogenetic processes by totipotent cells to regenerate the vegetative mother sponge as required by the spatial discontinuity of inland waters (Manconi & Pronzato, 1994a), in the wide variety of unpredictable environmental constraints ranging from the long-term dry-up to permafrost or anoxic conditions (Poirrier, 1969; Racek, 1969; Holmquist, 1973; Pronzato *et al*., 1993). Freshwater sponges are dispersed from the water surface to a hundred meters depth, from tropical rainforests, cold and hot deserts, from the Arctic Circle to Patagonia (not yet recorded from Antarctica), and in a wide range of environmental conditions: oceanic islands, subterranean caves, thermal fields in caldera lakes, ancient lakes, springs, ephemeral streams, billabongs, alpine lakes, salt lakes, large rivers, rapids and falls, estuaries, brackish seas, man-made basins from tanks and reservoirs to pools in gardens and fonts in archeological sites.

During the evolutionary radiation of taxa in inland waters, adaptive traits of resistant bodies were subject to processes of remodelling to attain successful performances of passive dispersal, survival and persistence. An extreme morphological plasticity was expressed mainly by the geographically widespread Spongillidae and Metaniidae (Penney & Racek, 1968). In these taxa resistant bodies reached the highest complexity of gemmular architecture, with the theca arranged in two (outer and inner) compact layers of spongin and one (middle) alveolar layer of trabeculated spongin, reinforced by spiny spicules in a variable spatial arrangement. On the other hand, the family Potamolepidae, restricted to ancient large hydrographic basins of the Afrotropical and Neotropical Regions, displayed a limited radiation into few tropical genera characterised by the production of rare gemmules with a simple theca of compact spongin reinforced by non specialised spicules (Brien, 1970a; Volkmer-Ribeiro, 1990). A perennial life style, reproductive modes exclusively sexual, and dispersal by larval stages (Brien & Govaert-Mallebrancke, 1958) characterised Lubomirskiidae, Malawispongiidae and Metschnikowiidae from ancient lakes scattered in the Afrotropical, Neotropical, Palaearctic and Oriental Regions. The simple structure of gemmules in Potamolepidae, and the inability to produce resistant bodies of Malawispongiidae, Lubomirskiidae and Metschnikowiidae could have constrained their dispersal, supporting their restricted geographic range in ancient hydrographic basins (Fig. 1). The biology, the life history and the geographic distribution of these freshwater sponge families stressed the unsolved problem of their taxonomy, systematics and phylogenesis based on the analysis of classical diagnostic traits such as skeletal organisation and spicular morphology. Marshall (1883), Brien (1970a,b), Penney & Racek (1968), Lévi (1973), Bergquist (1978), Hartman (1982), Volkmer-Ribeiro (1990) have debated their mono- or polyphyletic nature in detail.

Scope

The present study provides an exhaustive overview of the taxonomy of freshwater sponges through comparison between original observations and a more modern study of taxa. Our goal was to perform a detailed description, at the genus level, based on holotypes of type species of all existing freshwater sponge families. This very intriguing but difficult and long-term investigation resulted in a relative agreement with the taxonomic status of most genera, although in many cases our analysis highlighted critical decisions of previous authors. Conversely, we refute the validity of the recently described genus *Clypeatula* Peterson & Addis, 2000, considered a possible new species belonging to the genus *Ephydatia*. At a higher level we assign to the new suborder Spongillina all existing families of Malawispongiidae fam. nov. (=[Globulospongillidae] Brien, 1973b), Lubomirskiidae Rezvoi, 1936, Metaniidae Volkmer-Ribeiro, 1986, Metschnikowiidae Czerniavsky, 1880, Palaeospongillidae Volkmer-Ribeiro & Reitner, 1991b, Potamolepidae Brien, 1967, and Spongillidae Gray, 1867a. A phylogenetic analysis is currently in progress.

Methodology

About five hundred specimens were examined to produce the present review, although these are only partly listed in the materials examined, which were obtained from several museum collections throughout the world. This material was tracked down from publications of Gee (1931 *et seq*.), Potts (1888), Penney & Racek (1968), Volkmer-Ribeiro & Traveset (1987). Holotypes, if available, were examined *in primis*, or where not available we examined paratypes, schizotypes and topotypes. Original descriptions and illustrations were repeated only when materials were not available (e.g., *Corvoheteromeyenia*, *Metschnikowia* and *Palaeospongilla*). Our observations were also compared to original descriptions of genera and other literature in order to perform a critical evaluation of morphological traits of each taxon, and we also considered eco-ethological characters to achieve a more defined morpho-functional analysis. A large set of diagnostic macro- and micromorphological characters was also considered: (1) body size, external shape, consistency and colour; (2) architecture and fine organisation of ectosomal and choanosomal skeletons; (3) traits of skeletal megascleres and microscleres; (4) gemmular structure and gemmulosclere morphology. Methods used to examine skeletal and gemmular structure, and spicule geometry using Light (LM) and Scanning Electron Microscopy (SEM) follow Manconi & Pronzato (2000). Fragments of the sponge surface and choanosome were critical-point dried, mounted on stubs and gold sputtered to investigate skeletal architecture. Entire gemmules and cross sections were critical-point dried, mounted and sputtered in the same way. Spicule measurements were performed on several hundreds of megascleres, microscleres, gemmules and gemmuloscleres using light microscopy and digitizer.

Terminology

General terminology of freshwater sponge diagnostic traits follows the *Thesaurus of sponge morphology* (Boury-Esnault & Rützler, 1997). This *Thesaurus*, however, contains a misnomer

regarding the gemmular foramen, erroneously named 'micropyle' (which is a pore in the egg membrane of insects, allowing sperm to enter and fertilise the egg; Oxford Dictionary of Zoology, 1992).

Gemmule. A resistant body and asexual propagule produced by Spongillidae, Metaniidae and Potamolepidae, performing a structural and functional role that includes defence against environmental injuries from mechanical and chemical stress, and favouring the adhesion of these bodies to carriers/vectors. Gemmules may be single, free and scattered in the skeletal network, or restricted to the sponge base in groups, or strictly adherent to the substratum, singly or in carpets.

Gemmular cage. Several freshwater sponge genera produce mono- or multi-gemmular cages of megascleres connected to the skeletal network, or to the basal plate. Cages are generally made by slightly modified skeletal spicules that assume a regular or irregular spatial arrangement around gemmules. Pseudo-cages may be spatially displaced (e.g., *Saturnospongilla*, *Drulia*).

Gemmular theca. Gemmules contain a dense mass of totipotent cells named thesocytes protected by a theca, generally bearing a foramen (an aperture closed by a thin membrane), to favour the migration of cells during hatching. Foramen, absent or primitive, and shaped as an inconspicuous concavity in some genera (e.g., *Potamophloios*), is usually single but gemmules bearing several foramina (up to 6 in *Spongilla lacustris*) are known; foraminal shape ranges from simple to tubular according to the thickness of the theca and it frequently bears a variably-shaped collar. The theca, made of spongin and specialised spicules, displays a highly diversified architecture, ranging from naked gemmule to armed gemmule. Naked gemmules are characterised by a simple layer of laminated compact spongin without spicules (e.g., *Spongilla*, *Nudospongilla*). Armed gemmules range from a monolayered theca of laminated compact spongin with spicules (e.g., *Potamophloios*, *Oncosclera*), to a notably complex and variably arranged tri-layered theca bearing outer, pneumatic, and inner layers with spicules (e.g., most Spongillidae and Metaniidae). The outer layer of compact spongin usually present at the gemmule surface is variably developed and varies from armed with tangential spicules more-or-less embedded, to those pierced by distal apices of radial gemmuloscleres, or to those covering completely or in part the distal gemmulosclere apices. The pneumatic layer, variably structured and thick, is made of spongin arranged to form chambers, trabecules or fibres. Pneumatic layers may appear to be spatially displaced in a few genera (e.g., *Saturnospongilla*, *Eunapius*, *Trochospongilla*). The inner layer of compact spongin sublayered with a variable number of layers is a consistent trait shared by gemmules of Spongillidae, Metaniidae and Potamolepidae.

Gemmuloscleres. Specialised spicules, peculiar to armed gemmules, absent from the naked gemmule of *Spongilla lacustris* and *Nudospongilla coggini*. Gemmuloscleres encompass various morphotypes, ranging from oxeas to strongyles, birotules, pseudobirotules, parmuliform, boletiform-tubelliform to botryoidal forms. The gemmulosclere surface bears ornamentations such as granules, tubercles, spines and microspines, variably associated and spatially arranged. (1) *Birotule*, shared by several genera, bears at the apices of the shaft well-developed plated or curved rotules, sometimes umbonate with shaft slightly projecting beyond the rotule at both ends with blunt rounded processes. (2) *Pseudo-birotule*, shared by few genera (e.g., *Acalle*, *Anheteromeyenia*, *Heteromeyenia*), does not show a developed rotule but a group of curved hooks radiating from the apices of the shaft. (3) *Botryoidal gemmulosclere*, exclusive of the genus *Pectispongilla*, with a curved shaft bearing towards the convex sides of apices a *botryum* (group of concavities) that during development appears as spines in rows joined to each other by siliceous webs. (4) *Parmuliform gemmulosclere*, typical of *Drulia*, with a single rotule supporting a short acute conical stem. (5) *Tubelliform-boletiform gemmulosclere*, typical of *Acalle* and *Metania*, is characterised by a proximal large, irregularly circular, flat rotule with the entire margin supporting a smooth shaft decreasing in thickness toward the distal apex, and shaped as umbonate pseudo-rotule with large hooks bearing microspines at their apices.

KEY TO FAMILIES

Keys to families and genera are primarily constructed for specimens that contain all specific characters, and hence care must be taken when using these for taxa that are 'reduced', or in a non-reproductive 'resting stage'. For example, specimens collected during seasons when gemmules are not produced might be identified as *incertae sedis*, or as one of the genera that do not produce gemmules. When gemmules are present their associated spiculation is often important to the systematics of Spongillina. Among Potamolepidae the genera *Oncosclera* and *Sterrastrolepis* show a trilayered theca, other characters are in agreement with the key; the Spongillidae *Nudospongilla* show a monolayered theca.

(1) Gemmules present 2
Gemmules absent 4

(2) Gemmular theca monolayered. Gemmuloscleres, when present, are short irregular strongyles (tangentially arranged); gemmules are produced in the basal portion (for the few species known to produce them). Skeletal network typically multispicular alveolate-reticulate with scanty spongin; megascleres are almost exclusively strongyles, rarely oxeas; microscleres rarely present ..... **Potamolepidae**
Gemmular theca bi-tri-layered (pneumatic layer generally present) 3

(3) Gemmuloscleres are oxeas, strongyles, birotules, pseudobirotules, botryoidal, club-like (radially and tangentially arranged); skeletal network typically paucispicular irregularly reticulate; smooth or variably ornamented megascleres (oxeas and strongyles); microscleres usually present ..... **Spongillidae**
Gemmuloscleres are tubelliform, parmuliform, pseudobirotules (almost exclusively radially arranged); skeletal network typically multispicular alveolate-reticulate with scanty spongin; smooth or variably ornamented megascleres (oxeas and strongyles); microscleres usually present ..... **Metaniidae**
Gemmuloscleres are spiny oxeas and strongyles (radially arranged); skeletal network typically paucispicular irregularly reticulate megascleres exclusively oxeas; microscleres (oxeas) are present; exclusively fossil ..... **Palaeospongillidae**

(4) Skeletal network typically multispicular alveolate-reticulate, with sparse spongin; megascleres are spiny oxeas and strongyles; microscleres absent (endemic to Lake Baikal) ..... **Lubomirskiidae**

Skeletal network typically paucispicular irregularly reticulate; megascleres exclusively spiny oxeas; microscleres absent (endemic to Caspian Sea) ..... **Metschnikowiidae**
Skeletal network typically multispicular alveolate-reticulate, with sparse spongin; megascleres exclusively spiny or tubercular oxeas; microscleres absent (endemic to ancient lakes) ..... **Malawispongiidae fam. nov.**
Skeletal network variously structured; megascleres are smooth, spiny or tuberculate oxeas; microscleres absent (endemic to ancient lakes ..... **Spongillina *incertae sedis***

FAMILY SPONGILLIDAE GRAY, 1867

Synonymy

Spongillidae Gray, 1867a: 550. Spongillidae Carter, 1881c: 77. Meyeniinae Vejdovsky, 1887–1888: 177. Type genus. *Spongilla* Lamarck, 1816.

Diagnosis

Spongillina with shape ranging from globular to massive, incrusting, lobate, arborescent. Colour in life from whitish to brown or green, from pale to very dark. Surface smooth, hispid, conulose. Consistency ranging from fragile to notably hard. Ectosomal skeleton from spicular brushes at apices of primary fibres to dense tangential spicular network. Choanosomal skeleton reticulate with regular or irregular meshes. Spongin variable but generally scanty. Megascleres are oxeas and strongyles, from smooth to spiny or granulated. Microscleres when present oxeas, strongyles, aster-like, pseudobirotules. Gemmules always present except in very rare perennial specimens. Gemmular cage of megascleres is present in several species. Foramen present except in *Nudospongilla*. Gemmular theca mono-, bi- or tri-layered. Gemmules, generally armed with gemmuloscleres, in some cases naked. Gemmuloscleres, when present, radial or tangential to the surface, partially or totally embedded in the theca. Gemmulosclere shape is often species-specific with a large morphological variation from spiny to granulated or smooth, from oxeas to strongyles, birotules, pseudobirotules, club-like, botryoidal. Larvae, where described, are always parenchymella.

Scope

Spongillidae contains 21 valid genera: *Anheteromeyenia, Corvoheteromeyenia, Corvospongilla, Dosilia, Duosclera, Ephydatia, Eunapius, Heteromeyenia, Heterorotula, Nudospongilla, Pachyrotula, Pectispongilla, Racekiela, Radiospongilla, Sanidastra, Saturnospongilla, Spongilla, Stratospongilla, Trochospongilla, Umborotula, Uruguayella*.

Distribution

Cosmopolitan (Fig. 1).

KEY TO GENERA

(1) Birotules and pseudobirotules present 5
Birotules and pseudobirotules absent 2
(2) Complete absence of microscleres and gemmuloscleres 3
Presence of microscleres and/or gemmuloscleres (not pseudobirotules and/or birotules) 4
(3) Nude gemmule lacking pneumatic layer and gemmuloscleres; microscleres never observed; megascleres are acanthoxeas ..... ***Nudospongilla***
Gemmular theca tri-layered, without gemmuloscleres, covered by a cage of megascleres; microscleres absent; megascleres are spiny oxeas of two size classes ..... ***Duosclera***
(4) Microscleres absent; megascleres are spiny oxeas; gemmuloscleres showing 2–9 spiny axes with rounded or tricuspidate tips embedded radially in the gemmular theca ..... ***Sanidastra***
Microscleres absent; megascleres are spiny oxeas; gemmuloscleres are spiny strongyles radially oriented ..... ***Radiospongilla***
Microscleres absent; megascleres are spiny and smooth oxeas; gemmuloscleres are spiny oxeas of two morphologies: strongyles stout, short and spined, tangentially embedded in the outer layer of gemmular theca; spiny oxeas abruptly pointed, radially arranged in between the inner and outer layer ..... ***Stratospongilla***
Microscleres absent; megascleres are smooth oxeas; gemmuloscleres are oxeas and strongyles, smooth or with spiny tips, tangentially arranged on the gemmular surface ..... ***Eunapius***
Microscleres are spiny oxeas; megascleres are smooth oxeas; gemmuloscleres, when present, are spiny oxeas or strongyles often very curved ..... ***Spongilla***
Microscleres are spiny oxeas; megascleres are spiny oxeas; gemmuloscleres show a typical botryoides shape of the two apices ..... ***Pectispongilla***
(5) Birotules with rotules showing smooth edges, pseudobirotules absent 6
Birotules with rotules showing spiny and indented edges generally associated with pseudobirotules 7
(6) Microscleres absent; megascleres are oxeas very spiny; gemmuloscleres are smooth birotules radially arranged ... ***Trochospongilla***
Microscleres absent; megascleres are microspined short strongyles; gemmuloscleres are smooth birotules radially arranged ..... ***Uruguayella***
Microscleres absent; megascleres are smooth oxeas; gemmuloscleres are smooth birotules radially arranged in the gemmular theca, and spiny oxeas tangentially arranged in the typical thoroidal pneumatic layer (endemic to the River Juruà, Brazil) ..... ***Saturnospongilla***

(7) Birotules and/or pseudobirotules are present, exclusively as microscleres 8
Birotules and/or pseudobirotules are present, exclusively as gemmuloscleres 9
Birotules are gemmuloscleres, pseudobirotules are microscleres 15
(8) Gemmuloscleres are spiny and/or strongyles tangentially arranged on the gemmular theca; megascleres are smoooth microgranulated; microscleres are pseudobirotules with a smooth shaft ..... ***Corvospongilla***
(9) Gemmuloscleres birotules and/or pseudobirotules of a single morphology 11
Gemmuloscleres birotules and/or pseudobirotules belonging to two morphological forms (birotules + pseudobirotules, or birotules + acanthoxeas) 10
(10) Gemmuloscleres are birotules (long shaft) and pseudobirotules (long shaft) radially arranged; microscleres are acanthoxeas; megascleres are acanthoxeas ..... ***Heteromeyenia***
Gemmuloscleres are birotules (short shaft) and pseudobirotules (long and spiny shaft) radially arranged; microscleres are absent; megascleres are spiny oxeas ..... ***Racekiela***
Gemmuloscleres are birotules (variable rotules) and acanthoxeas tangentially arranged; microscleres are absent; megascleres are spiny and smooth oxeas (endemic to New Caledonia) ..... ***Pachyrotula***
(11) Gemmuloscleres are birotules 12
Gemmuloscleres are pseudobirotules (long and spiny shaft); microscleres are absent; megascleres are spiny oxeas ..... ***Anheteromeyenia***
(12) Birotules with a short (usually less than the rotule diameter) shaft 13
Birotules with a long spiny shaft (2–3 times the rotule diameter) 14
(13) Gemmuloscleres are birotules with a short shaft and rotules of identical diameter; microscleres are absent; megascleres are microspined and/or smooth oxeas ..... ***Ephydatia***
Gemmuloscleres are birotules with a short shaft and rotules of different diameter; microscleres are absent; megascleres are microspined and/or smooth oxeas ..... ***Heterorotula***
(14) Gemmuloscleres are birotules with a long spiny shaft; microscleres are absent; megascleres are microspined and rarely smooth oxeas ..... ***Umborotula***
Gemmuloscleres are birotules with a long spiny shaft; microscleres range from acanthoxeas to typical 'euasters' with spiny tips; megascleres are smooth oxeas ..... ***Dosilia***
(15) Gemmuloscleres are birotules with a long spiny shaft; microscleres are pseudobirotules showing a long smooth or spiny shaft; megascleres are smooth oxeas ..... ***Corvoheteromeyenia***

SPONGILLA LAMARCK, 1816

Synonymy

Spongilla Lamarck, 1816: 98. *Euspongilla* Vejdovsky, 1883: 15. Vejdovsky *in* Potts, 1888: 172.

Type species

Spongia lacustris Linnaeus, 1759: 1348 (by subsequent designation; Annandale, 1911b).

Definition

Spongillidae with encrusting, massive, branched to arborescent body shape. Consistency fragile, soft. Ectosomal skeleton consists of spicular brushes. Choanosomal skeleton irregular, from isotropic to anisotropic, pauci- to multispicular. Abundant spongin sheaths. Megascleres smooth to slightly spined oxeas. Microscleres abundant to rare spiny oxeas. Gemmules in dense clusters or scattered. Gemmular cage composed of megascleres sometimes present. Gemmules of two types: naked without gemmuloscleres, and armoured with gemmuloscleres. Gemmular theca from monolayered to tri-layered. Foramen or foramina present. Gemmuloscleres when present spined oxeas or strongyles.

Scope and distribution

In addition to the type species, more than 150 nominal species have been ascribed to this genus, but most of these have been assigned to other genera since. At present, at least seven other valid species of *Spongilla* s.s. have been described: *S. alba* Carter, 1849 (India, SE Asia, Africa, Madagascar, Australia, South America, Turkey); *S. aspinosa* Potts, 1880b (E Canada and USA); *S. inarmata* Annandale, 1918 (Japan); *S. cenota* Penney & Racek, 1968 (Yucatan); *S. wagneri* Potts, 1889 (SE USA, Florida, S Carolina); *S. shikaribensis* Sasaki, 1934 (Japan); *S. stankovici* Arndt, 1938 (Ochrid Lake, Macedonia).

Description of type species

Spongilla lacustris (Linnaeus, 1759) (Figs 2–8).

Material examined. Holotype: LSLH 1295.1, LSLH 1295.2 – lake of Småland, det. Linnaeus. Other material. 'Neotype' (now invalid): RMNH 1053 – Vlaardingse Vaart, The Netherlands, ix.1941. Specimens: MNHN DT2828 – Viene, Limoges. DTRG-FW 558 – Sweden, from ZRS. DTRG-FW 10 – Lago d'Orta, ix.1888. DTRG-FW 33 – Coghinas River, Terme di Casteldoria, Sardinia, 31.v.1985. DTRG-FW 68 – Lake Maggiore, Isole Borromee, 1889. DTRG-FW 73 – Scrivia Stream, Ponte della Ferriera, Ronco Scrivia, 4.ix.1985. DTRG-FW431-FW543 – Ginevra Lake. DTRG-FW123 – Bolle di Magadino, Canton Ticino, 22.iii.1970.

Description. Body shape encrusting, massive, branched to arborescent. Colour whitish, yellow-orange, greenish, emerald green. Consistency fragile, soft. Surface uneven hispid. Oscules not conspicuous, scattered. Dermal membrane aspicular. Ectosomal skeleton occurs as spicular brushes at apices of primary fibres. Choanosomal skeleton irregular from isotropic in encrusting portions, to anisotropic in finger-like projections or branches, pauci- to multispicular primary fibres connected by paucispicular transverse

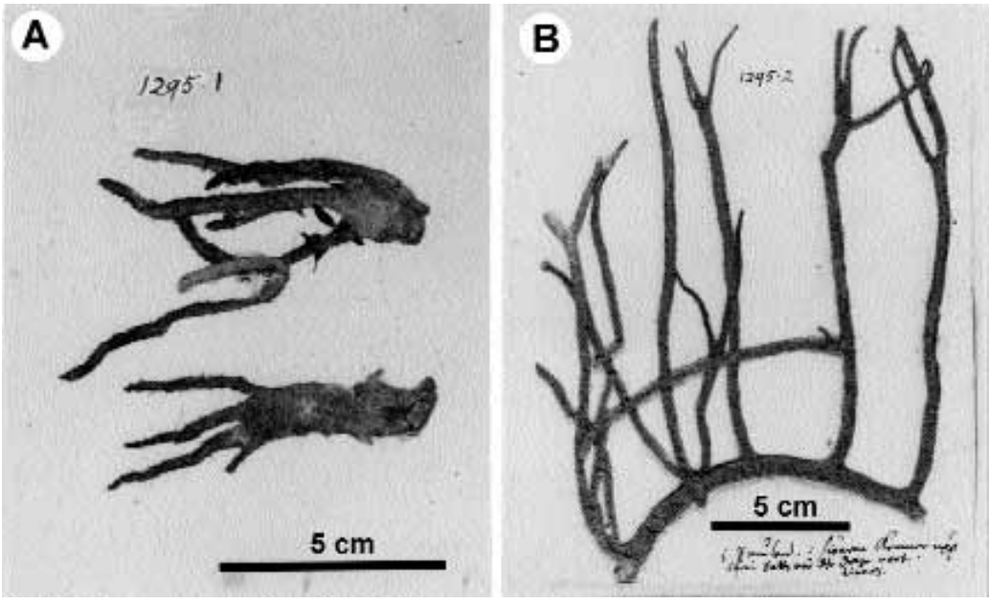

Fig. 2. *Spongilla lacustris*, syntypes (LSLH). A, paralectotype, 1295.1. B, lectotype, 1295.2.

fibres. Abundant spongin sheaths. Megascleres (90–350 × 2–18 μm) smooth fusiform oxeas with tips from gently to sharply pointed, slightly spined if associated to gemmules. Microscleres abundant to rare scattered fusiform oxeas (25–178 × 2–8 μm) with dense spines regularly distributed along the entire length and microspinosity on spines giving them an asterose shape. Gemmules (98–789 μm) from subspherical to oval in dense clusters, or irregularly scattered in the skeletal network. Gemmular cage of megascleres sometimes present in naked gemmules. Gemmules of two types can be found in the same specimen, naked without gemmuloscleres and armoured with gemmuloscleres, tangential to partially embedded in the gemmular theca. Gemmular theca ranging from thick-walled with tri-layers to thin-walled with a monolayer of compact spongin, with a variable number of sublayers (3–7), corresponding to the inner layer of the thick walled gemmule. Outer layer well-developed in some thick-walled gemmules. Foramen slightly elevated without or with a simple collar or plate-like collar, generally single in thick-walled gemmules; multiple foramina (1–6) common in thin-walled gemmules, but also present sometimes in thick-walled gemmules. Gemmuloscleres (21–130 × 1–10 μm), when present, slightly to strongly bent oxeas or strongyles usually with large spines.

Ecology. Standing and running waters, from permafrost area in the Northern Polar Circle, to semi-arid zones in the Mediterranean islands, from brackish waters to alpine lakes or ancient lakes (Lake Baikal). Life cycle hibernating. Distribution: Palaearctic.

Remarks. *Spongia lacustris* was described by Linnaeus (1759: 1348) as "*repens, fragilis, ramis teretibus obtusis*" [creeping, fragile, with cylindrical branches showing swellings at their ends], in the second volume of the *Systema Naturae*, and its type material was previously unknown. "Since a type specimen apparently was never designated, and the original collection most certainly does not exist today", Penney & Racek (1968) subsequently designated a neotype (RMNH 1053), which they further state "... correspond[s] in all details with the description of *Spongilla*

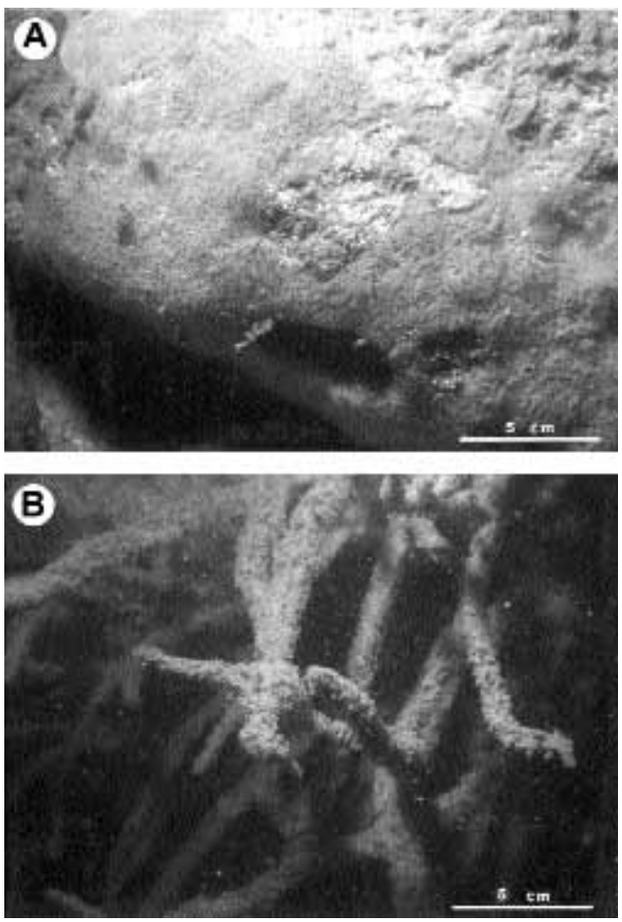

Fig. 3. *Spongilla lacustris* growth forms during an annual life cycle. A, encrusting. B, arborescent.

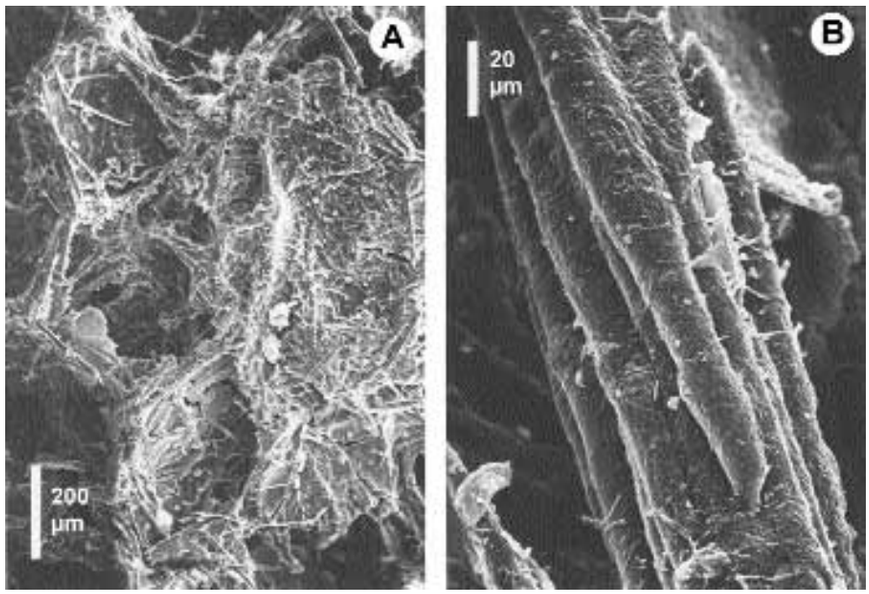

Fig. 4. *Spongilla lacustris*, skeleton (lectotype, LSLH 1295.2). A, ectosomal skeleton. B, a multispicular skeletal tract.

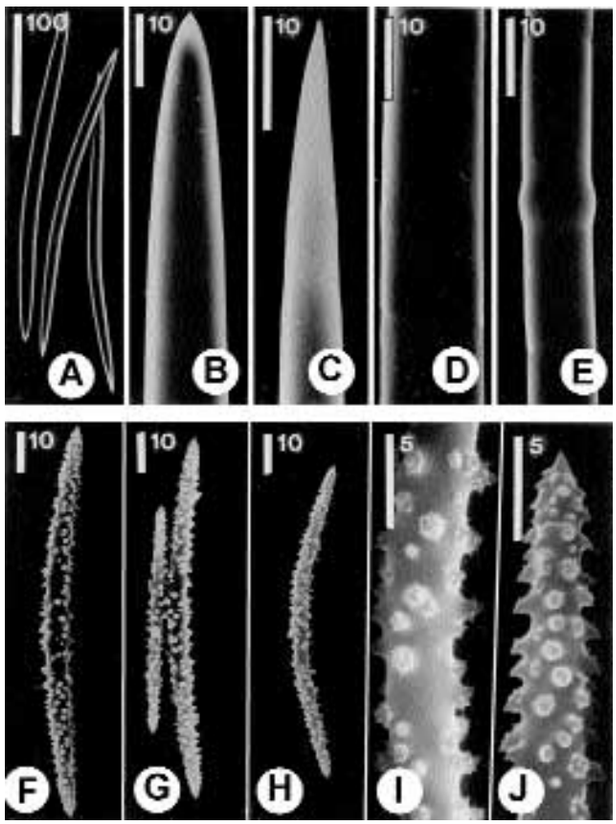

Fig. 5. *Spongilla lacustris*, spicule characteristics (lectotype LSLH 1295.2). Both Linnean specimens lack gemmules. A, megascleres smooth oxeas. B–C, close-up of megasclere tips. D–E, close-up of megasclere shaft. F–H, microscleres. I, close-up of microsclere shaft. J, close-up of microsclere tip. (After Manconi & Pronzato, 2000.)

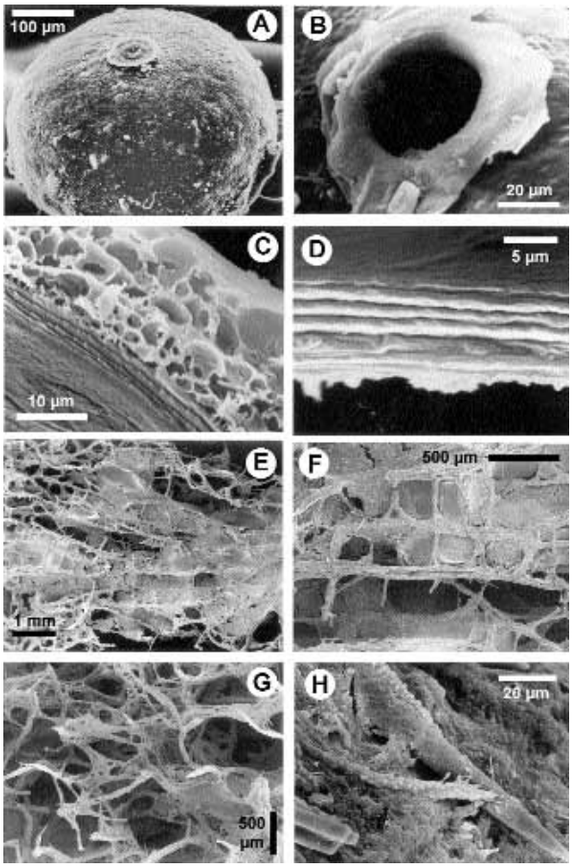

Fig. 6. *Spongilla lacustris*, gemmules, spicules and skeletal architecture (previous 'neotype' RMNH 1035). A, naked gemmule. B, foramen. C, gemmular theca with outer, pneumatic and inner layers. D, gemmular theca without pneumatic layer. E–F, different view of the skeletal network. G, ectosome. H, microscleres irregularly arranged in the sponge mesohyl.

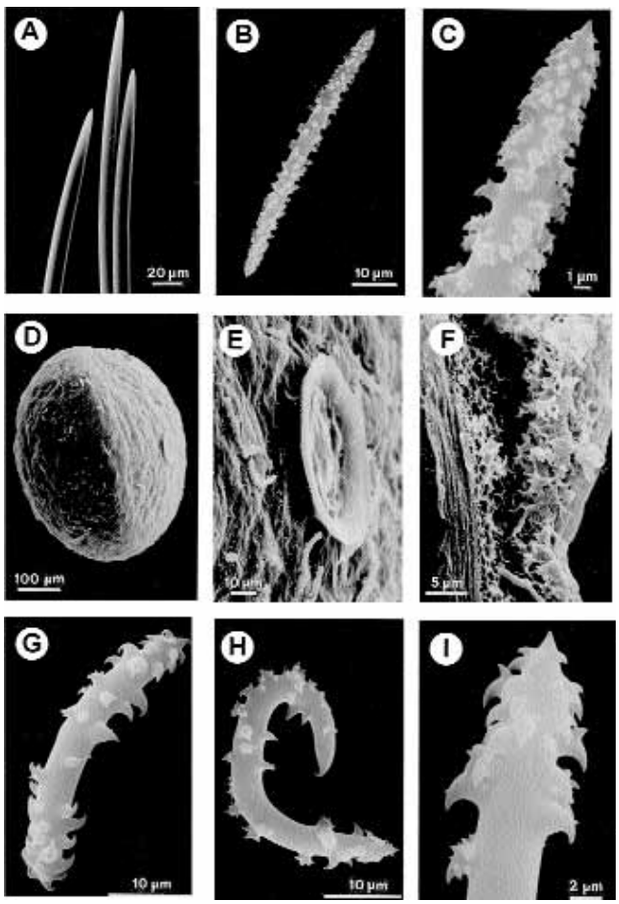

Fig. 7. *Spongilla lacustris*, gemmules and spicules, A–C, G–I, DTRG-FW73 (ex-IZUG); D–F, DTRG-FW123 (ex-IZUG). Specimens belonging to southern populations (Italy) with armed gemmules. A, megascleres. B–C, microscleres. D, armed gemmule. E, foramen. F, trilayered pneumatic layer showing a thick pneumatic layer. G–I, gemmuloscleres.

lacustris Auct. in previous literature", from the collection of the Rijksmuseum van Natuurlijke Historie of Leiden. However, the rediscovery of Linnaeus's original material (Manconi & Pronzato, 2000) invalidates the neotype designation, although the latter specimen seems to be the best 'representative' material of the species, being abundantly full of gemmules and easily accessible for scientific study, as recently shown by Manconi & Desqueyroux-Faúndez (1999).

ANHETEROMEYENIA SCHRÖDER, 1927

Synonymy

Heteromeyenia (Anheteromeyenia) Schröder, 1927: 108. *Anheteromeyenia* de Laubenfels, 1936a: 36.

Type species

Spongilla argyrosperma Potts, 1880b: 357 (by subsequent designation; Penney & Racek, 1968).

Definition

Spongillidae with encrusting growth form. Ectosomal skeleton spicular. Choanosomal skeleton irregular network of megascleres with paucispicular tracts. Sparse spongin. Megascleres acanthoxeas. Microscleres absent. Gemmular theca tri-layered. Gemmuloscleres pseudobirotules radially embedded in the theca.

Scope and distribution

Three other species: *A. pictovensis* (Potts, 1885a) (from E-Canada to New York); *A. biceps* (Lindenschmidt, 1950) (Michigan); *A. ornata* (Bonetto & Ezcurra de Drago, 1970) (S America). Neartic and Neotropical Regions.

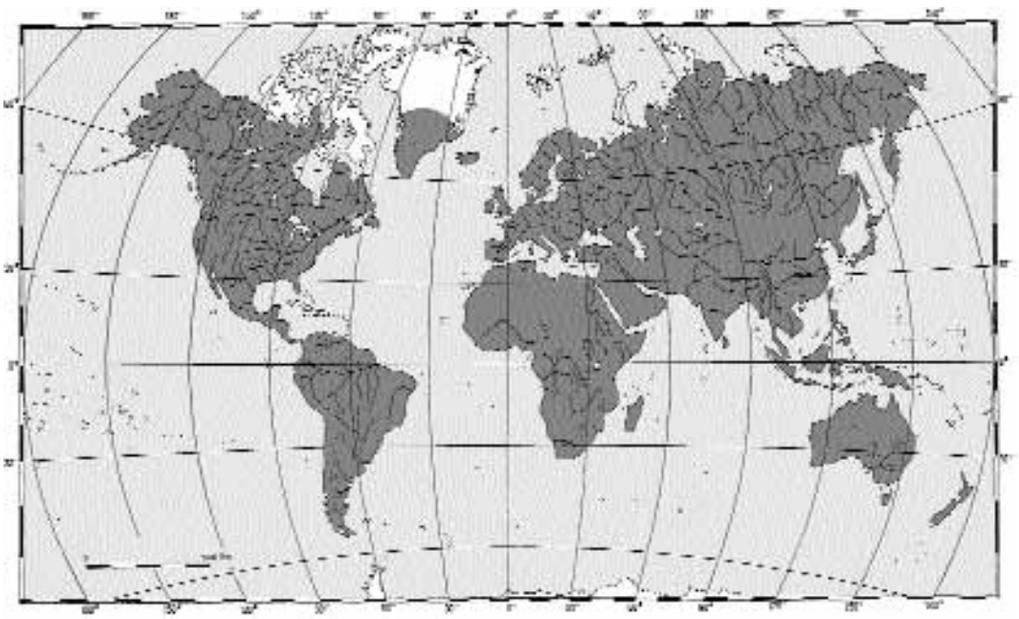

Fig. 8. Geographic distribution of the genus *Spongilla*.

Description of type species

Anheteromeyenia argyrosperma (Potts, 1880b) (Figs 9–12).

Material examined. Lectotype: ANSP PO4538. Paralectotype. ANSP PO4587, box 31-A, Leigh River at Leigh Gap, E. Potts leg. 14.xi.1881. Other material. ROM T1990-015, Lake Temagami, Ko-Ko Bay, 20.viii.1937, leg. J. Oughton, det. N. Gist Gee.

Description. Sponge is thin crust with inconspicuous oscules. Surface hispid due to emerging spicules. Colour grey or green if in symbiosis with zoochlorellae. Dermal membrane spicular. Subdermal cavities not observed. Ectosomal skeleton is a spicular dermal membrane. Choanosomal skeleton irregular network of megascleres with paucispicular tracts. Sparse spongin. Megascleres slightly curved acanthoxeas (250–329 × 10–15 μm) with sparse small spines except at the tips. Smaller megascleres (133 × 7 μm) reported by Volkmer (1996) could be those from the dermal membrane. Microscleres absent. Gemmules subspherical (400–700 μm). Foramen is a short simple tube without collar. Gemmular theca tri-layered. Outer layer thin. Pneumatic layer with irregular chambers. Inner layer multilayered. Gemmuloscleres radially embedded in the theca, emerging from the outer layer according to their different levels of insertion. Gemmuloscleres pseudobirotules with a notably variable length (65–160 μm) with umbonate pseudo-rotules formed by 2–4 hooks, and shafts armed by large spines or more rarely by hooks.

Ecology. Both lentic and lotic habitat in waters of about neutral pH, low-moderate alkalinity, high conductivity, 9–23°C. Distribution: Eastern Nearctic region, from Canada (Quebec, New Brunswick) to Florida.

Remarks. Penney & Racek (1968) and Volkmer-Ribeiro (1996) report two classes of gemmuloscleres, however Ricciardi & Reiswig (1993) and our observations suggested that the insertion of birotules occur at different levels of the gemmular theca.

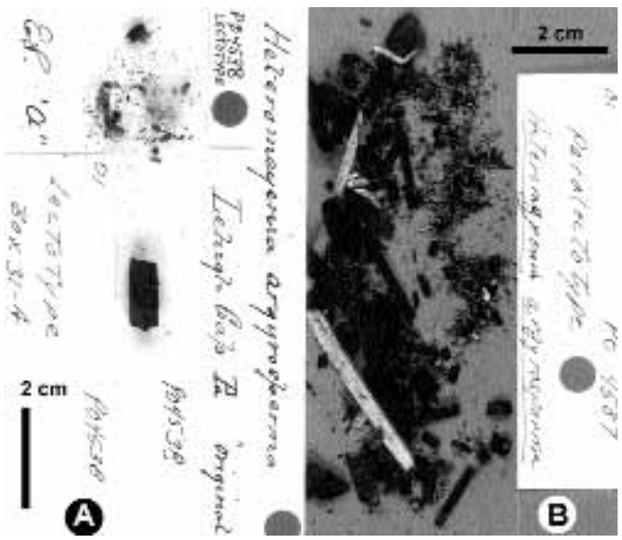

Fig. 9. *Anheteromeyenia argyrosperma*. A. lectotype ANSP PO4538. B, paralectotype ANSP PO4587.

CORVOHETEROMEYENIA EZCURRA DE DRAGO, 1979

Synonymy

Corvomeyenia (part) Bonetto & Ezcurra de Drago, 1966: 129. *Corvoheteromeyenia* Ezcurra de Drago, 1979: 110.

Type species

Corvomeyenia australis Bonetto & Ezcurra de Drago, 1966: 130 (by monotypy).

Diagnosis

Spongillidae with encrusting growth form. Choanosomal skeleton irregularly alveolate. Megascleres curved oxeas generally smooth. Microscleres pseudobirotules. Gemmules adherent to the substratum or free and scattered. Foramen present. Gemmular theca tri-layered with gemmuloscleres radially embedded. Gemmuloscleres birotules.

Scope and distribution

One other species: *C. heterosclera*. Distribution. Neotropical.

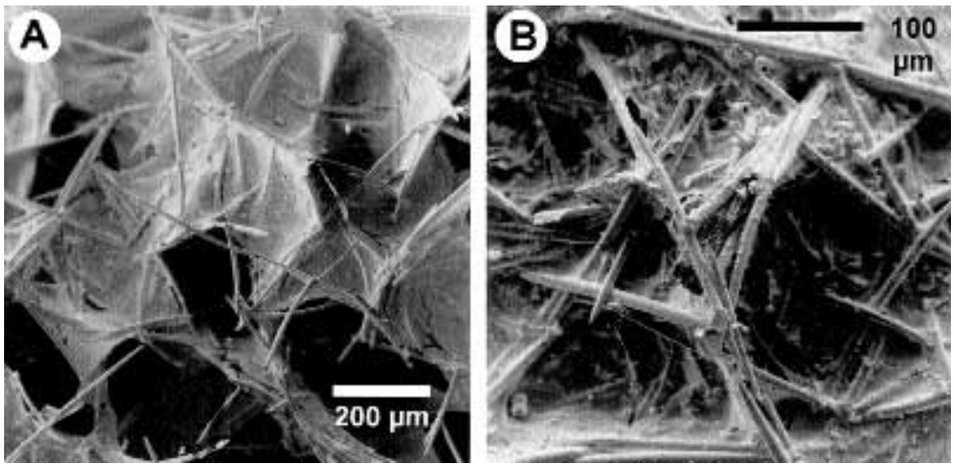

Fig. 10. *Anheteromeyenia argyrosperma*, skeletal network (ROM N° B6, 1990-015). A, sponge surface. B, choanosomal skeleton.

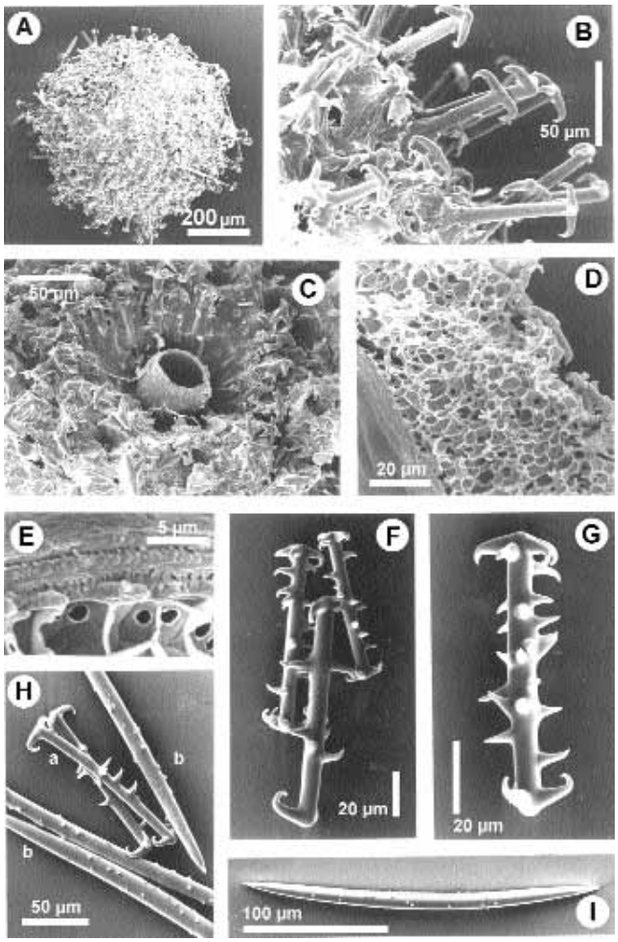

Fig. 11. *Anheteromeyenia argyrosperma*, spicules and gemmules, lectotype ANSP PO4538. A, gemmule. B, gemmular surface. C, foramen. D, cross section of gemmular theca, pneumatic layer with irregular chambers. E, multilayered inner layer. F–G, Ha, gemmuloscleres. Hb, I, spiny oxeas (megascleres).

Description of type species

Corvoheteromeyenia australis (Bonetto & Ezcurra de Drago, 1966) (Figs 13–14).

Material examined. None. Description modified after Bonetto & Ezcurra de Drago (1966). Type material in MABA and INALI not available. Type locality Laguna de Guadalupe (Setubal), at the entrance in the Riacho Santa Fe, Santa Fe, Argentina.

Description. Body shape encrusting. Colour brown-greenish. Hispid surface due to emerging spicules. Oscules inconspicuous. Dermal membrane spicular. Subdermal cavities not observed. Ectosomal skeleton not observed. Choanosomal skeleton is irregularly alveolate (?) with large meshes. Megascleres curved oxeas (300–350 × 13–20 µm) generally smooth, sometimes irregularly microspined. Microscleres pseudobirotules (reported as "isoquelas") very variable in shape and shaft size (20–35 µm up to 90 µm) with slightly curved shaft with pseudo-rotules ranging from small with three curved hooks (2–8 µm) to large without hooks. Gemmules (400–500 µm) flattened yellowish in dry conditions at the basal portion adherent to the substratum or free and scattered in the sponge body. Foramen single and circular. Gemmular theca tri-layered. Outer layer with emerging shafts and distal rotules. Pneumatic layer well developed with gemmuloscleres radially embedded. Inner layer well developed. Gemmuloscleres birotules (43–90 × 17–23 µm) with spined shafts and circular slightly convex rotules with margins from crenulated to indented with teeth long and curved.

Ecology. The holotype was found on a stone wall in the laguna silt bottom in running waters (60 cm/sec). The population of the entire lagoon was notably dense. Distribution. Upper and middle Paranà River, Rio Iguazù, River Uruguay, Guadalupe Lagoon (Argentina).

CORVOSPONGILLA ANNANDALE, 1911

Synonymy

Corvospongilla Annandale, 1911b: 122.

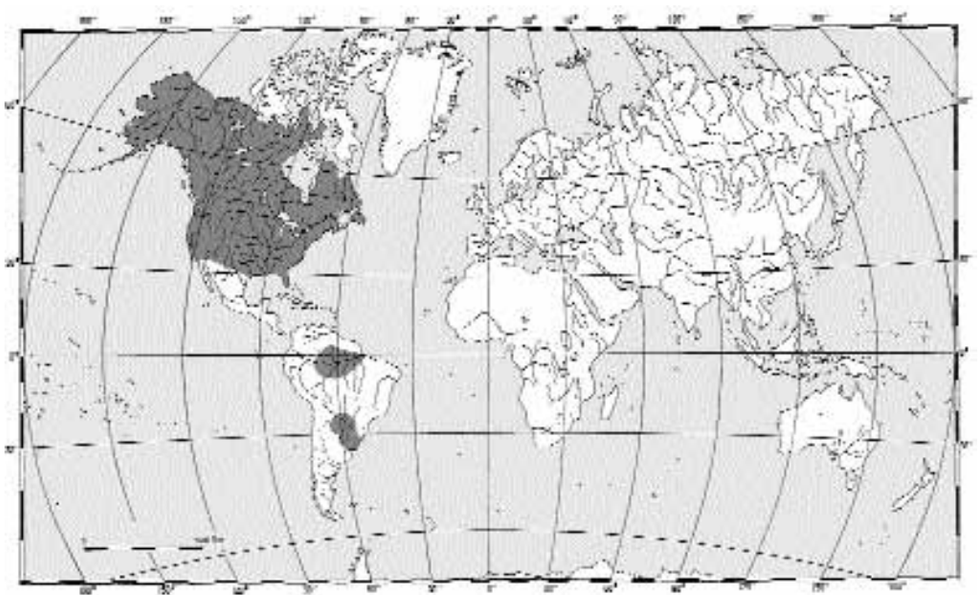

Fig. 12. Geographic distribution of the genus *Anheteromeyenia*.

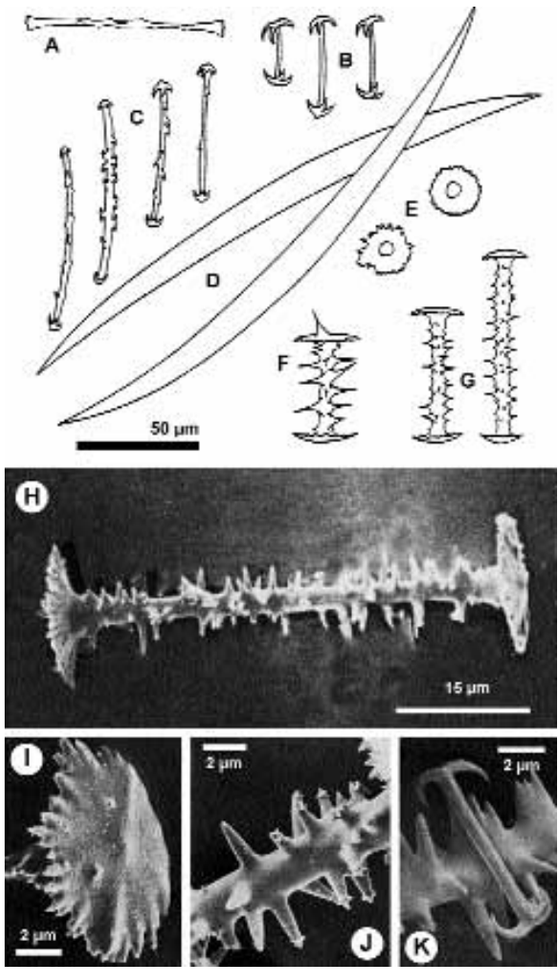

Fig. 13. *Corvoheteromeyenia*, spicules from original papers. A–G, *C. australis*, after Bonetto & Ezcurra de Drago, 1966. H–K, *C. heterosclera*, after Ezcurra de Drago, 1974. A, E–J, gemmuloscleres. B–C, K, microscleres. D, megascleres.

Type species

Spongilla loricata Weltner, 1895: 138 (by subsequent designation; Annandale, 1911b).

Diagnosis

Spongillidae with encrusting flat to massive, lobate growth form. Consistency extremely hard to delicate. Megascleres vary from smooth to granulated strongyles or rarely oxeas. Microscleres often rare, straight to slightly curved micropseudobirotules with smooth or spined shaft. Gemmules of two types single or grouped, free or fixed at the sponge base, with or without a spicular cage of slender strongyles. Foramen ranging from apical to lateral with a short porus tube. Gemmular theca from tri-layered with a variably developed pneumatic layer to monolayered of compact spongin without pneumatic layer. Gemmuloscleres from elongated slightly curved to oval stout spined strongyles tangentially arranged in the theca.

Scope and distribution

Eleven other species known: *C. burmanica* (Kirkpatrick, 1908b) (Burma, India); *C. bohmii* (Hilgendorf, 1883) (Africa equatorial); *C. caunteri* Annandale, 1911b (India); *C. lapidosa* (Annandale, 1908a) (India); *C. micramphidiscoides* Weltner, 1913 (Congo River); *C. novaeterrae* (Potts, 1886); *C. scabrispiculis* Annandale, 1913a (Tropical Africa, River Nilo); *C. ultima* Annandale, 1910a) (S India); *C. zambesiana* (Kirkpatrick, 1906) (River Zambesi); *C. sekti* Bonetto & Ezcurra de Drago, 1966 (Paranà, Paraguay and Uruguay Rivers, Argentina); *C. volkmeri* (De Rosa-Barbosa, 1988) (Brasil). Distribution. Tropical regions of Africa and Asia (from Burma to Iraq) and S America.

Description of type species

Corvospongilla loricata (Weltner, 1895) (Figs 15–18).

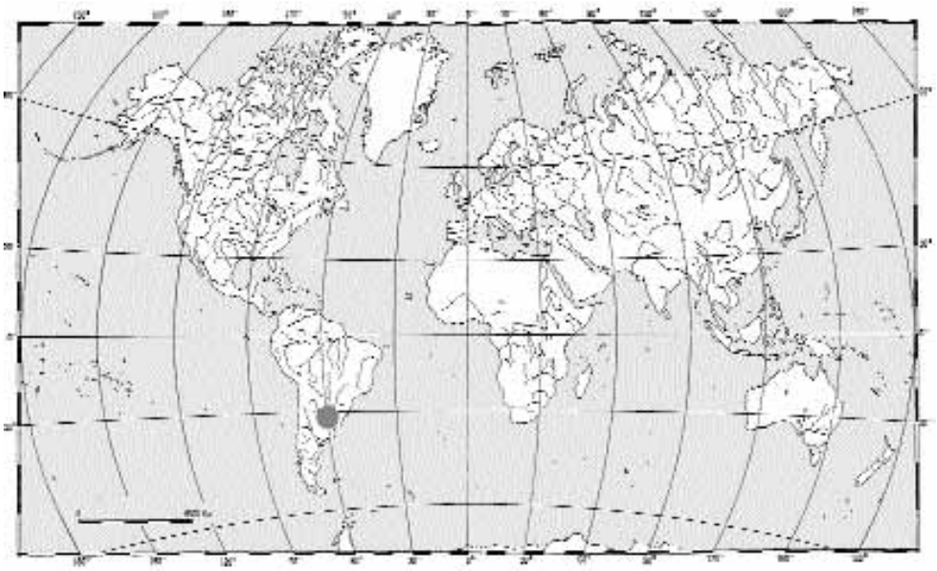

Fig. 14. Geographic distribution of the genus *Corvoheteromeyenia*.

Material examined. Holotype: ZMB2093 – dry gemmules on *Aetheria* shell, Africa. Other material. BMNH 1882.3.22. 1–3 – *C. burmanica*, Burma; *Corvospongilla* sp., River Diyala of R. Tigri Basin, Himmereen Reservoir, Iraq, leg. H.A.A. Saadalla, 1997.

Description. Encrusting flat sponge grossly hispid. Consistency hard. Colour light brown when dry. Surface conulose due to underlying tufts of megascleres in the convergence of fibres toward the surface. Dermal membrane not observed. Ectosomal skeleton dense spicular network. Choanosomal skeleton alveolate from paucispicular to multispicular tracts, more irregular at the sponge base. Basal plate well developed. Megascleres feebly curved smooth stout strongyles (220–226 × 20 μm) with inflated tips in the skeletal network; slender strongyles (125–130 × 7 μm) finely granulated to rarely smooth belong to gemmular cages. Microscleres rare or variably abundant scattered in the choanosome, pseudo-microbirotules (20–40 μm length) with a smooth shaft bearing pseudo-rotules (4–12 μm diam.) with few radial recurved hooks. Gemmules (500–950 μm) of two types, free and fixed at the sponge base, with or without a spicular cage of slender strongyles. Foramen from apical to lateral, with a short tube. Gemmular theca from monolayered with compact spongin without pneumatic layer, to tri-layered with a variably developed pneumatic layer. Gemmuloscleres slightly curved stout spined strongyles (34–75 × 8–14 μm) tangentially embedded in the theca.

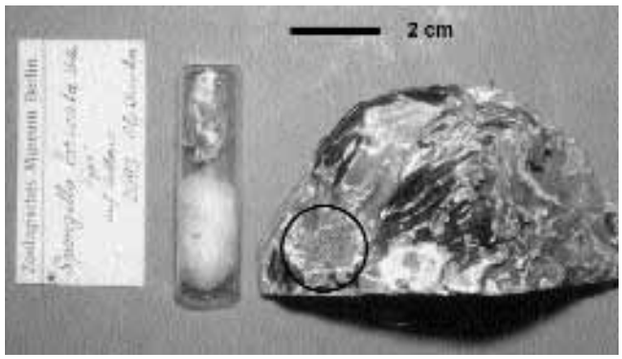

Fig. 15. *Corvospongilla loricata*, holotype ZMB 2093, is a carpet of gemmules (circle) on a shell of *Aetheria*.

Ecology. Undefined, in Africa, growing on shells of *Aetheria* sp.

Remarks. In spite of Penney & Racek (1968) underlining the existence within the genus of two groups characterised by oxeas or strongyles as megascleres, we found a gradient from oxeas to strongyles in the same specimen of *Corvospongilla* sp. from Iraq. As stressed by Brien (1973b) with the proposed subfamily Corvospongillinae, the entire set of diagnostic traits presently studied highlighted a problematic position of this genus between the families Spongillidae and Potamolepidae.

DOSILIA GRAY, 1867

Synonymy

Dosilia Gray, 1867a: 550. *Asteromeyenia* Annandale, 1911a: 593. [*Astromeyenia*] Schröder, 1927: 102 *(lapsus)*. *Astroheteromeyenia* Schröder, 1927: 102.

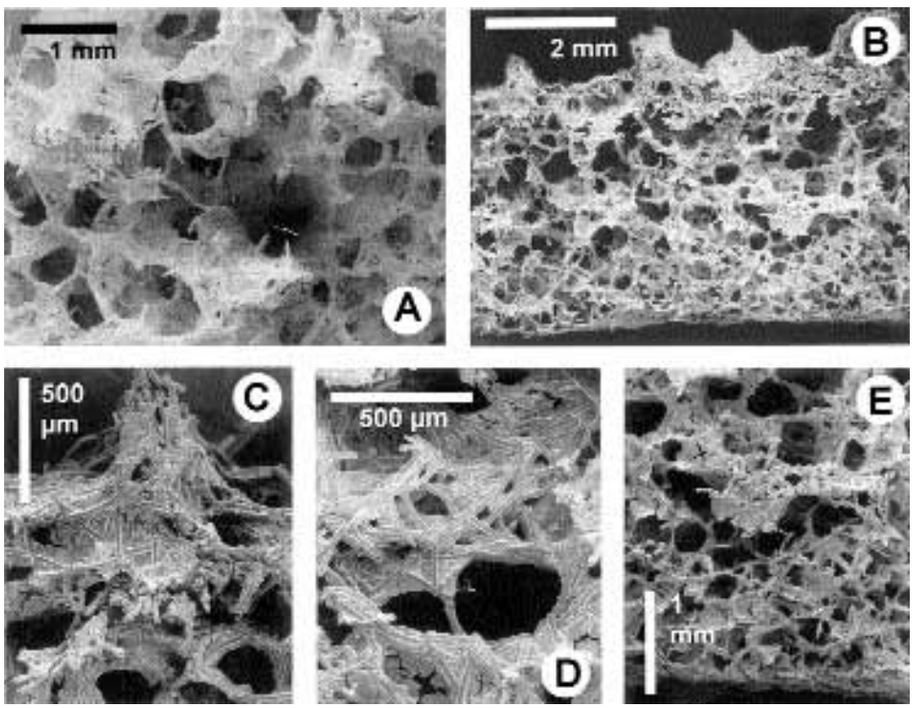

Fig. 16. *Corvospongilla*, skeletal network, fragment of the holotype of *C. burmanica*. BMNH 1882.3.22.1–3 (box 6, dry). A, sponge surface (top view). B, cross section (top = surface with conules; bottom = basal spongin plate). C, lateral view of a conule with peripheral skeleton. D, choanosome. E, choanosomal skeleton at the sponge base (cross section).

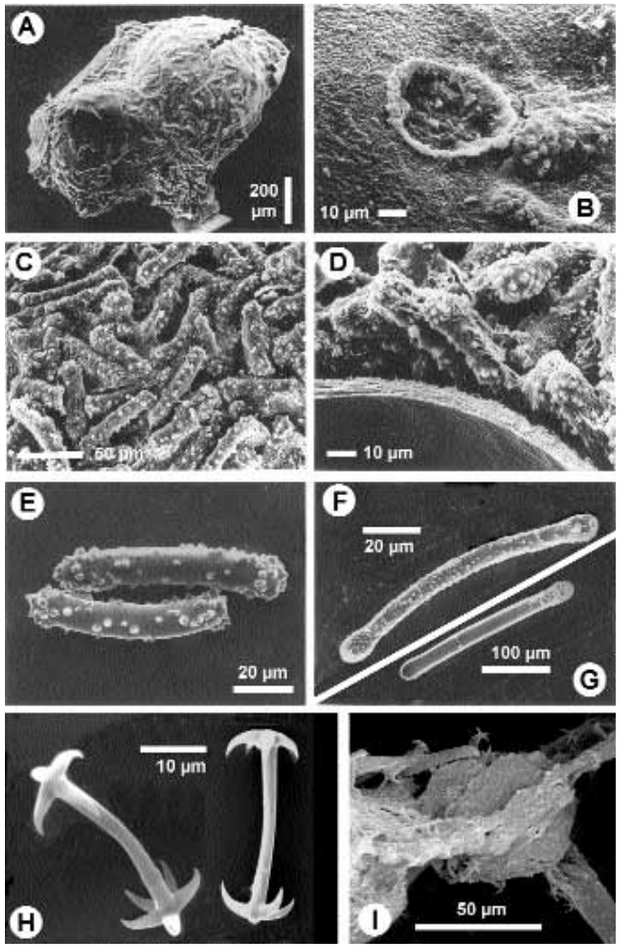

Fig. 17. *Corvospongilla*, spicular and gemmular traits; A–G, *C. loricata*, type specimen, ZMB 2093. H, *C. burmanica*, BMNH 1882.3.22.1–3. I, *Corvospongilla* sp., DTRG-FW574 (ex-IZUG). A, gemmular cage including two fixed gemmules. B, foramen. C, gemmular surface. D, cross section of gemmular theca. E, gemmuloscleres. F–G, megascleres. H, microscleres. I, microscleres in the skeletal network.

Type species

Spongilla plumosa Carter, 1849: 81 (by subsequent designation; de Laubenfels, 1936a).

Diagnosis

Spongillidae with massive lobate growth form. Choanosomal skeleton plumose-reticulated anisotropic. Megascleres smooth oxeas. Microscleres range from acanthoxeas with rays to true 'euasters'. Gemmules scattered. Gemmular theca tri-layered with radially embedded birotules.

Scope and distribution

Three other species: *D. palmeri* (Potts, 1885b) (Central America); *D. brouni* (Kirkpatrick, 1906) (River Nilo E Africa); *D. radiospiculata* (Mills, 1888) (USA, Mexico). Tropical and subtropical areas of S America and Africa.

Description of type species

Dosilia plumosa (Carter, 1849) (Figs 19–22).

Material examined. Holotype: Not examined. Other material. BMNH 1908.2.8.1 – dry, El Obeid, Khartoum, 29.i.1908, Kirkpatrick. BMNH (DTRG-FW421) – Bowerbank collection, dry box 6, 3 specimens.

Description. Sponge shape massive lobate. Consistency moderately soft and very fragile. Colour from greenish to pale brown-yellowish. Surface lobate with hispidation due to spicule tufts at apices of primary fibres. Conspicuous scattered small oscula. Dermal membrane aspiculous. Subdermal cavities not observed. Ectosomal skeleton spicule tufts. Choanosomal skeleton plumose-reticulated, skeleton anisotropic with radial multispicular primary fibres gradually diverging toward the surface and paucispicular secondary tracts. Variable amount of spongin. Microscleres scattered and abundant in the choanosome. Megascleres stout, ranging from straight to slightly curved fusiform smooth oxeas (400–520 × 15–21 µm). Microscleres range from acanthoxeas,

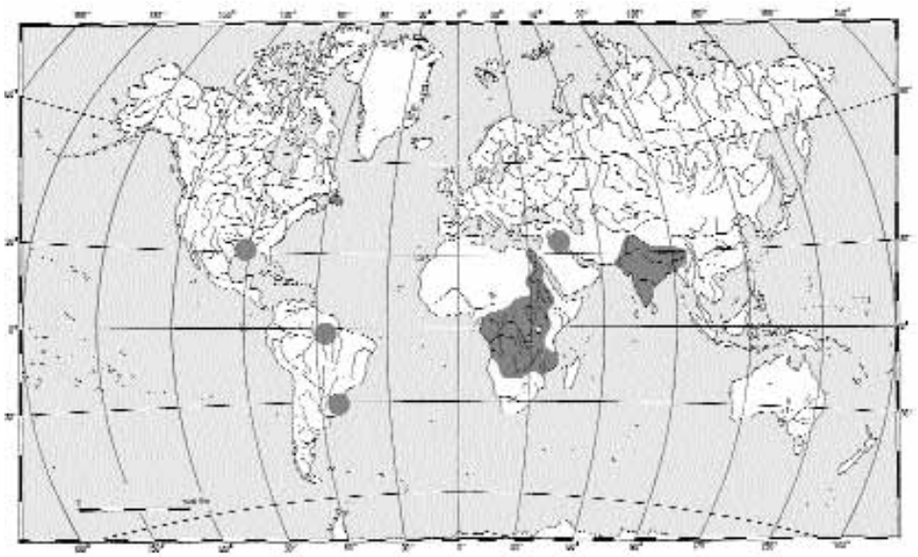

Fig. 18. Geographic distribution of the genus *Corvospongilla*.

to acanthoxeas with few long central rays, to 'euasters' with 8–12 spiny rays projecting from a distinct globular centre. Rays generally smooth with recurved spines at their apex. Size highly variable with rays not exceeding 15–18 μm. Gemmules abundant, scattered within the skeletal network, subspherical to ovoid (500–680 μm). Foramen lateral and tube-like in shape. Gemmular theca trilayered. Outer layer variably developed with emerging free distal rotules. Pneumatic layer well developed of minute regular chambers with radially embedded birotules. Inner layer with 2–3 sub-layers of compact spongin in contact with proximal rotules. Gemmuloscleres birotules, straight cylindrical shaft with large spines. Rotules from flat to slightly umbonate with margins bearing numerous small blunt and recurved teeth (spines) (55–85 × 3–4 μm, diameter of rotules 23–25 μm).

Ecology. Unknown. Distribution. India, Philippines.

Remarks. *Asteromeyenia* Annandale, 1911a: 593 (for type species *Heteromeyenia radiospiculata* Mills, 1888 (by original designation), now *Dosilia radiospiculata*, is thus a junior synonym of *Dosilia* according to Penney & Racek (1968).

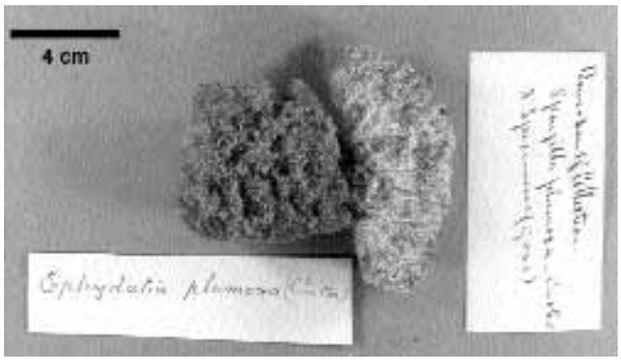

Fig. 19. *Dosilia plumosa*, specimens of Bowerbank's collection BMNH unreg. (box 6, dry).

DUOSCLERA REISWIG & RICCIARDI, 1993

Synonymy

Duosclera Reiswig & Ricciardi, 1993: 275.

Type species

Spongilla mackayi Carter, 1885: 19 (by original designation).

Diagnosis

Spongillidae with encrusting growth form. Choanosomal skeleton moderately developed with fibres of dense spongin. Two classes of megascleres, one in the skeletal framework and the other in the mesohyl, but both also functioning as gemmule spicules. True microscleres absent. Gemmules typically in hemispherical

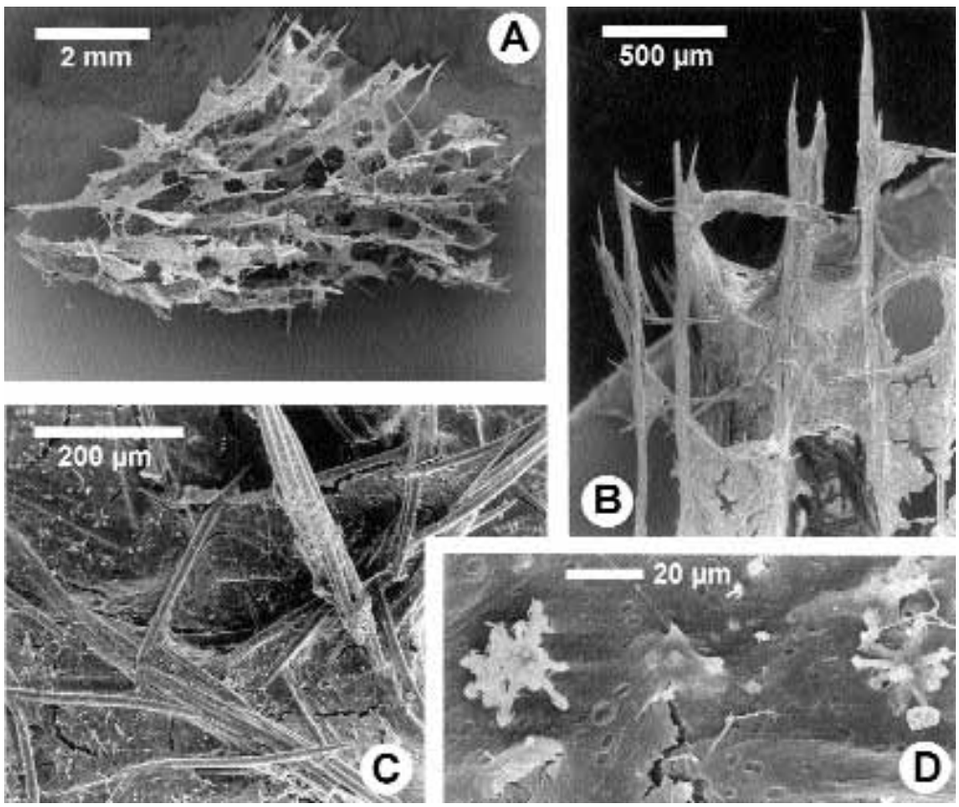

Fig. 20. *Dosilia plumosa*, skeletal network, specimens of Bowerbank's collection, BMNH (box 6, dry). A, a sponge fragment (surface on the right). B, peripheral skeleton (cross section). C, choanosomal spicular arrangement. D, microscleres in the choanosomal matrix.

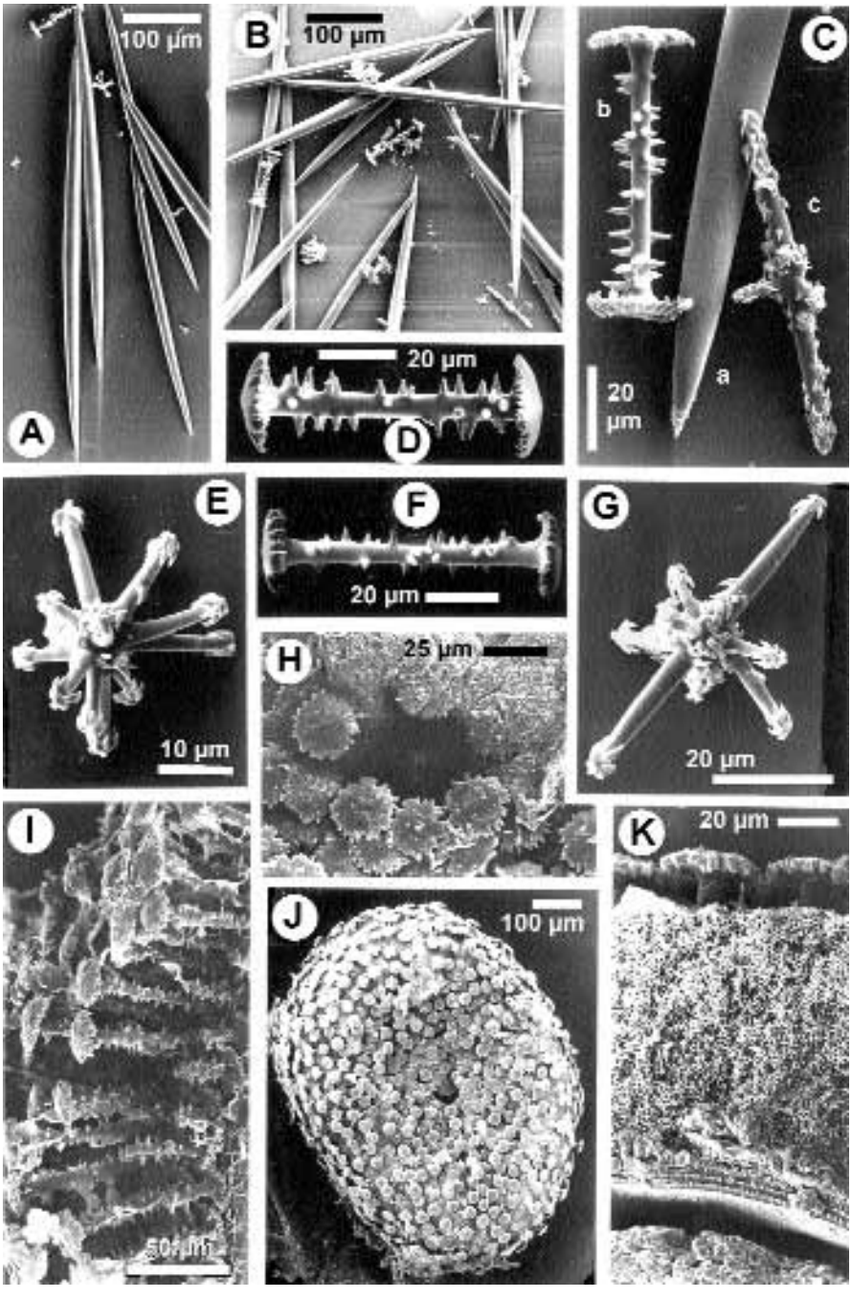

Fig. 21. *Dosilia plumosa*, spicules and gemmules, Bowerbank's collection, BMNH (box 6, dry). A–B, megascleres smooth oxeas, microscleres and gemmuloscleres. Ca, megasclere tip. Cb, D, F, gemmuloscleres. Cc, E, G, microscleres. H, foramen. I, surface of the gemmule. J, gemmule. K, trilayered gemmular theca.

clusters but occasionally occurring as a restricted pavement. Special gemmuloscleres absent.

Scope and distribution

Monotypic, Nearctic (Eastern North America).

Description of type species

Duosclera mackayi (Carter, 1885) (Figs 23–26).

Material examined. Holotype: BMNH 1890.1.9.279–4 – Mackay's lake near Pictou, Nova Scotia, 26.viii.1884.

Description. Encrusting ($2.5 \times 4 \times 1$ cm). Dermal membrane aspicular. Subdermal cavities not observed. Ectosomal skeleton undifferentiated. Choanosomal skeleton with fibre system moderately developed with fibres of dense spongin with 3–10 procurved spicules. Megascleres of two classes: straight slightly curved acanthoxeas with acute spines directed distally (procurved) in the main choanosomal skeleton (251×10.2 µm); and abundant recurved shorter acanthoxeas with long robust spines directed proximally

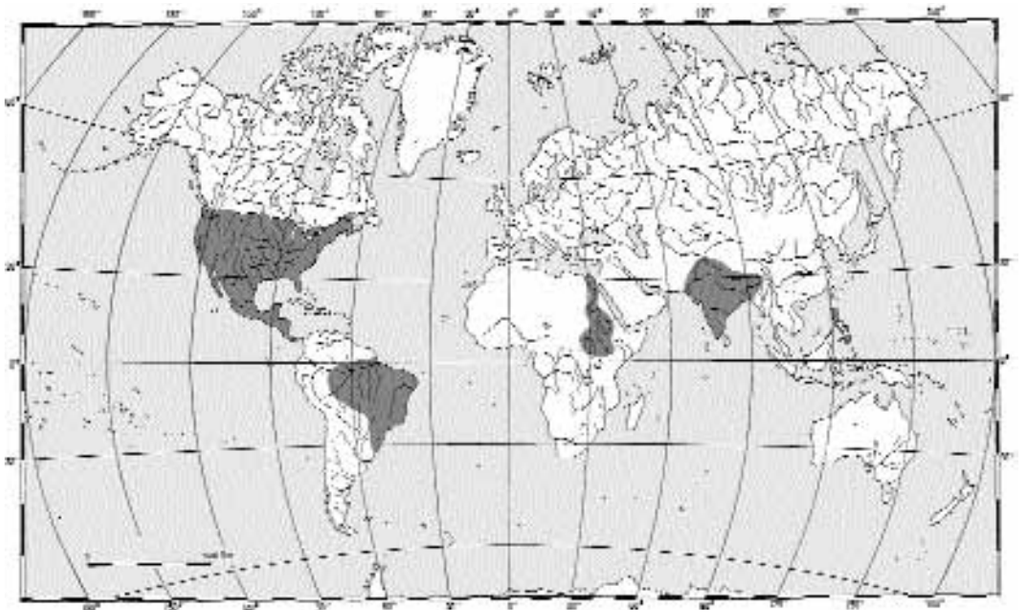

Fig. 22. Geographic distribution of the genus *Dosilia*.

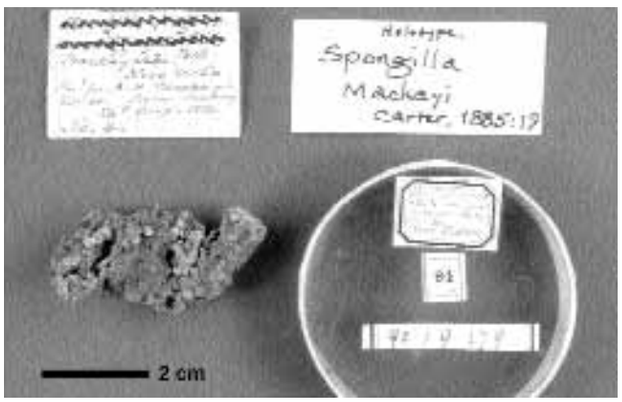

Fig. 23. *Duosclera mackayi*, holotype BMNH 1890.1.9.279, with original labels.

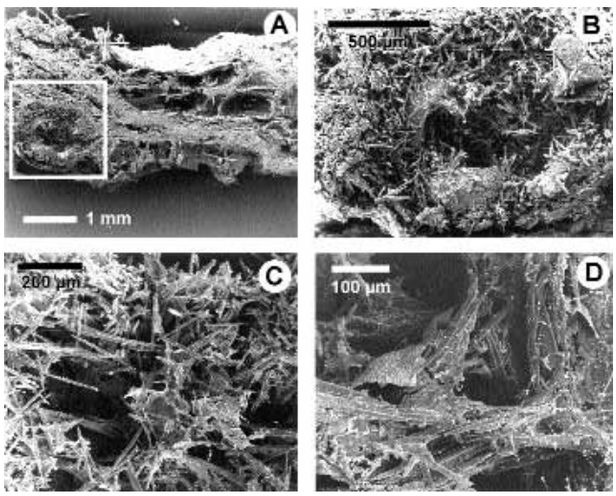

Fig. 24. *Duosclera mackayi*, skeletal network, BMNH 1890.1.9.279. A, cross section of the dry specimen where the poorly evident sponge skeleton is mixed with vegetal fibres. B, detail of A (rectangle) showing a broken gemmule enclosed in the choanosomal skeleton. C–D, sponge surface.

(recurved) scattered in the choanosome, and also functioning as gemmule spicules ($167 \times 10.2\,\mu m$). Microscleres absent. Gemmules typically in hemispherical clusters but occasionally occurring as a restricted pavement. Gemmular cage of megascleres radially oriented within and projecting from the pneumatic layer. Foramina, simple with collar, directed toward the substrate and opening into a restricted cavity. Gemmular theca tri-layered. Outer layer conspicuous with polygonal surface. Pneumatic layer with chambers. Inner layer of multilayered compact spongin. Special gemmuloscleres absent.

Ecology. Restricted to dystrophic lentic waters with a pH range of 4.7–6.2. Symbiotic with green algae, and commonly associated to *Corvomeyenia everetti* and *Trochospongilla pennsylvanica*. In Quebec it was found active and green in November at 4°C, whereas *T. pennsylvanica* under the same conditions was found only as carpets of gemmules (Ricciardi & Reiswig, 1993). Distribution. Newfoundland, Nova Scotia, New Brunswick, Quebec, Massachusetts, New York, Wisconsin, Michigan, New Jersey, Georgia, Florida, Louisiana.

EPHYDATIA LAMOUROUX, 1816

Synonymy

[*Tupha*] Oken, 1814 (unavailable). *Ephydatia* Lamouroux, 1816: 2. *Trachyspongilla* Dybowsky, 1878: 53. *Meyenia* Carter, 1881c: 90. *Pleiomeyenia* Mills, 1884: 147. ?*Clypeatula* Peterson & Addis, 2000: 269.

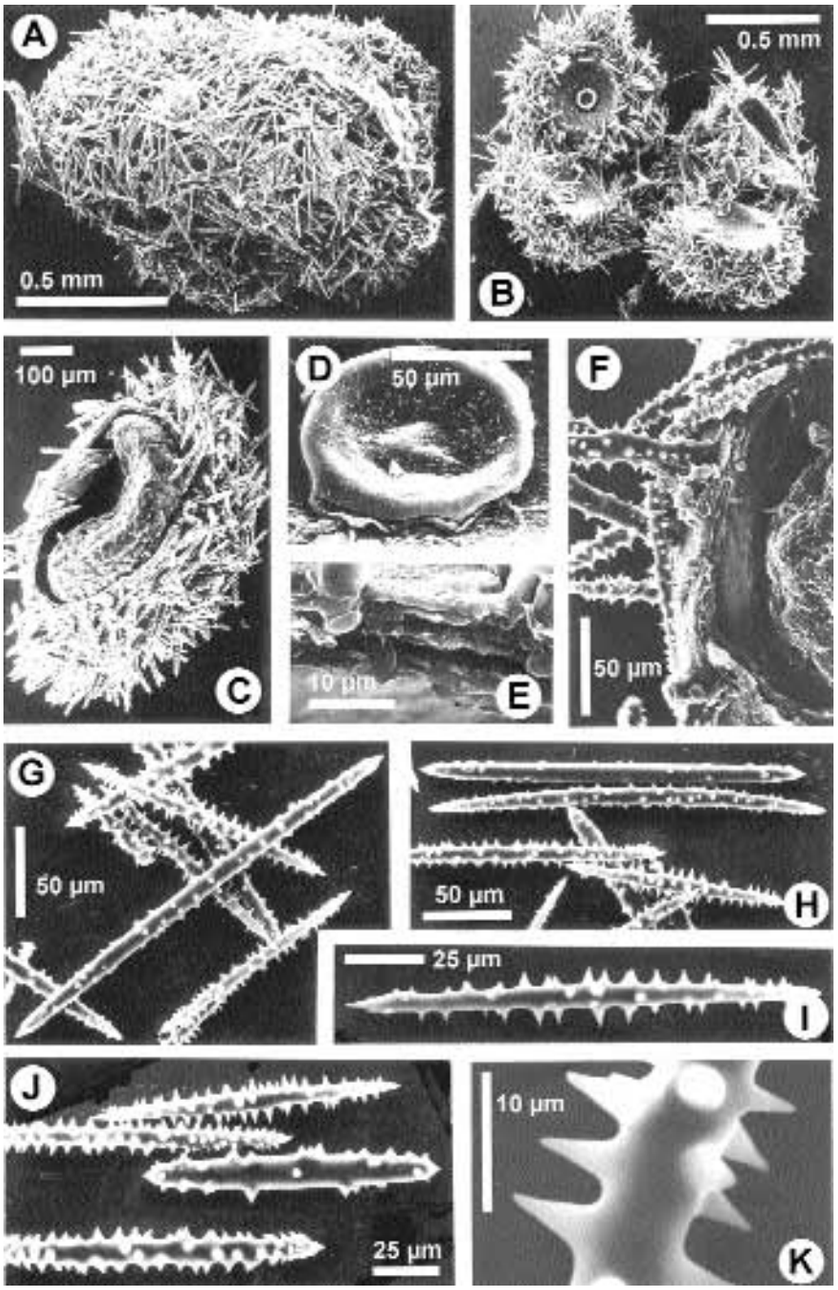

Fig. 25. *Duosclera mackayi*, spicules and gemmules, holotype BMNH 1890.1.9.279. A, gemmular cage including three gemmules. B, some gemmules *in toto*. C, cross section of gemmule. D, foramen. E–F, theca of compact multilayered spongin. G–J, different views of size classes of megascleres. K, spines of megascleres.

Type species

Spongia fluviatilis Linnaeus, 1759: 1348 (by subsequent designation; Annandale, 1911b).

Diagnosis

Spongillidae with encrusting, bulbous, massive growth form. Choanosomal skeleton anisotropic with paucispicular fibres and tracts. Spongin scarce. Megascleres oxeas from smooth to microspined. Microscleres absent. Gemmules scattered. Gemmular theca tri-layered. Gemmuloscleres birotules.

Scope and distribution

Eight other species: *E. meyeni* (Carter, 1849) (India, China); *E. muelleri* (Lieberkuhn, 1855) (N Hemisphere); *E. japonica* (Hilgendorf, 1882) (USA?, Manchuria, Japan); *E. ramsayi* (Haswell, 1882) (Australia, New Zealand, New Guinea?); *E. robusta* (Potts, 1888) (E USA, Mexico, California); *E. facunda* Weltner, 1895

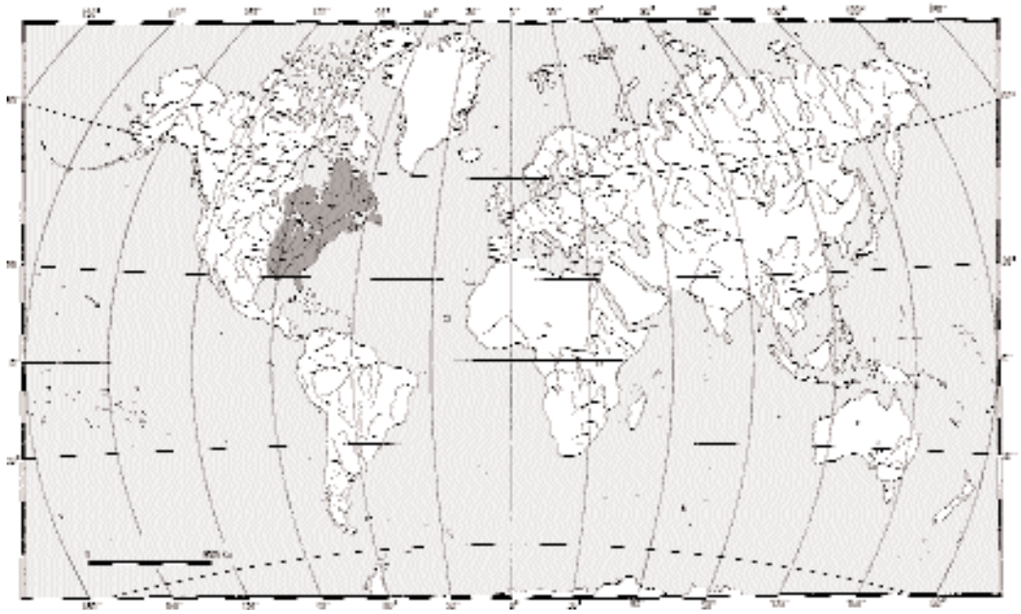

Fig. 26. Geographic distribution of the genus *Duosclera*.

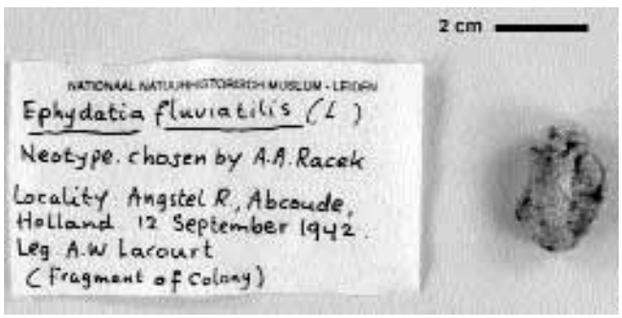

Fig. 27. *Ephydatia fluviatilis* neotype RMNH 1166.

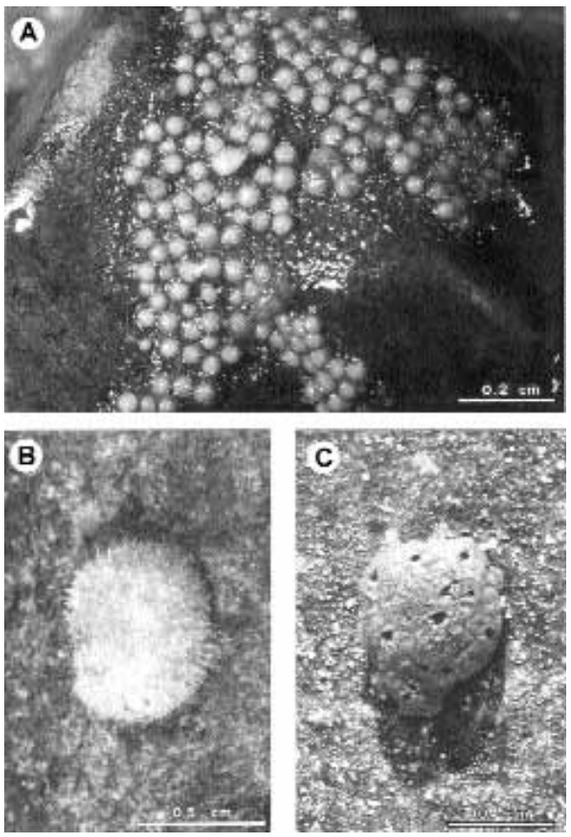

Fig. 28. *Ephydatia fluviatilis*, phases of the life cycle. A, carpet of gemmules on a stone. B, a postlarval stage after settlement. C, a mature colony.

(central and S America); *E. fortis* Weltner, 1895 (Indonesia, Philippines, Japan, Vanuatu); *E. millsii* (Potts, 1888) (Florida).

Description of type species

Ephydatia fluviatilis (Linnaeus, 1759) (Figs 27–31).

Material examined. Neotype: RMNH 1166 (designated by A.A. Racek, cf. Penney & Racek, 1968: 84) – A.W. Lacourt, Angstel River, Abcoude Holland, 12.ix.1942. Other material. DTRG FW31 – Trasimeno Lake 17.iv.1973). DTRG FW33 – Coghinas River, Terme di Casteldoria, 31.v.1985. DTRG FW63 (from MFSN) – Fosse del Patriarca, Roggia di Udine (1868–70). DTRG FW73 – Scrivia Stream, Ponte della Ferriera, Ronco Scrivia (4.9.1985). DTRG FW82 (from MCSN) – Maggiore Lake, Pallanza Basin 29.iii.1970. DTRG FW133 – Tagliavia SS 118 Sicily, 22.iv.1986. DTRG FW257 – Crete Island, between Paraskie and Kastelli, dried river, 30.x.1988. DTRG FW263 – Apulia, Lake Capaciotti, dried 5.xi.1988. DTRG FW295 – Mallorca Island 27.iv.1990. DTRG FW301 – Cernika Lake, Bosnia, 27.vii.1990. MNHN DT2820 – Syria, Barara, 1908. MNHN DT2834 – Algeria, Seurat-Gautier, 1922. MNHN DT2822 – Yerre, Loire River, 2.iv.1896.

Description. Body shapes range from crusts to bulbous or massive, with ridges or rounded lobes. Consistency firm but fragile in life, extremely brittle if dry. Colour from whitish to green or brown. Surface hispid due to emerging spicules. Oscules numerous.

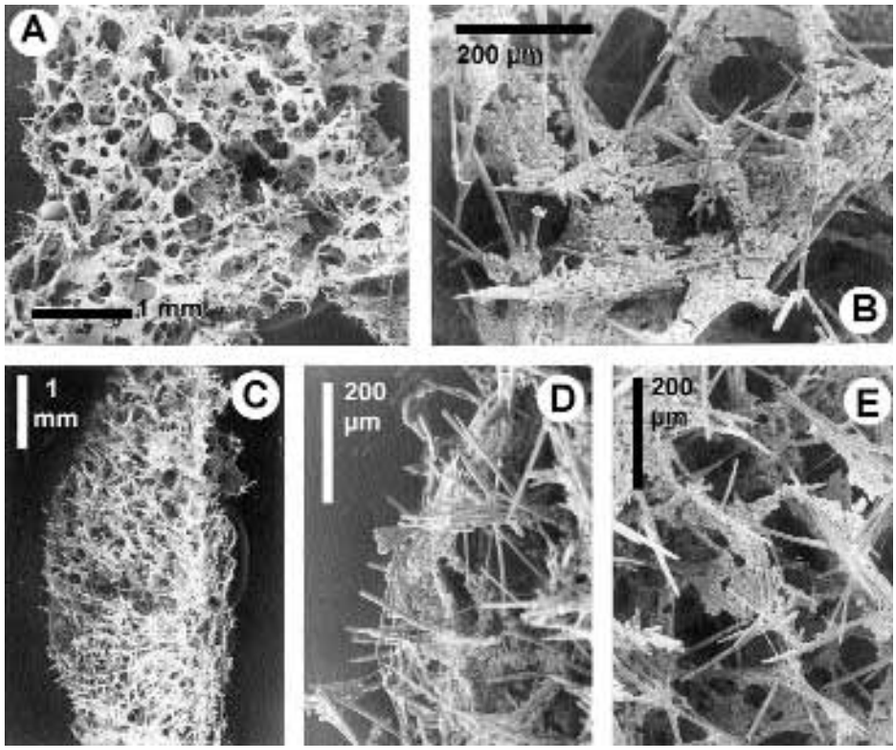

Fig. 29. *Ephydatia fluviatilis*, skeletal network, neotype; RMNH 1166. A–B, sponge surface. C, cross section of a sponge fragment (left = surface). D, superficial hispidation in a cross section (left). E, choanosomal skeleton.

Dermal membrane aspiculous. Ectosomal skeleton not evident. Choanosomal skeleton anisotropic with paucispicular fibres and tracts. Spongin scarce. Megascleres slightly curved or rarely straight oxeas, from smooth to microspined (210–400 × 6–19 µm). Microscleres absent. Gemmules abundant and scattered, subspherical (350–450 µm). Foramen simple without collar. Gemmular theca tri-layered. Outer layer well developed generally covering the distal rotule of gemmuloscleres. Pneumatic layer variably developed with irregular chambers and gemmuloscleres radially embedded in one layer with the proximal rotule in contact with the inner layer. Inner layer of sublayered compact spongin. Gemmuloscleres birotules (26–30 × 18–21 µm) with a smooth or spined shaft, flat rotules of equal diameter, microspined, with incised irregular margins.

Ecology. Running and standing waters from coastal brackish waters to inland salt lakes to alpine lakes. Hibernating, aestivating or perennial life cycle. Sometimes symbiotic with zoochlorellae. Distribution. Cosmopolitan. Widely distributed throughout the N Hemisphere with scattered records from the S Hemisphere. The wide distribution of *E. fluviatilis* suggests the existence of a species-complex.

Remarks. [*Tupha*] Oken, 1814 has been suggested as a synonym of *Ephydatia* Lamouroux, but all of Oken's names have been deemed to be unavailable and therefore the name is unavailable and seniority does not apply (ICZN, 1956: Opinion 417). *Meyenia* Carter, 1881c, with type species *Spongia fluviatilis* L. (by original designation), is an objective junior synonym of *Ephydatia*. *Pleiomeyenia* Mills, 1884, with type species ? *Pleiomeyenia calumeticus* Mills, 1884: 147 (by page priority), is a suspected junior synonym of *Ephydatia* and possible synonym of the species *E. muelleri* (Lieberkühn). Similarly, *Trachyspongilla* Dybowsky, 1878, with type species *Spongia muelleri* Lieberkühn, 1855 (by subsequent designation in de Laubenfels, 1936a: 37), is also a junior synonym of *Ephydatia* by inclusion of *E. muelleri* in this genus.

EUNAPIUS GRAY, 1867

Synonymy

Eunapius Gray, 1867a: 552.

Type species

Spongilla carteri Bowerbank, 1863: 469 (by subsequent designation; Annandale, 1911b).

Diagnosis

Spongillidae with body shape ranging from encrusting to bulbous, from flattish to lobate. Consistency of live sponges from fragile to moderately soft. Anisotropic choanosomal skeleton with pauci- to multispicular fibres and tracts. Medium amount of spongin. Megascleres smooth oxeas. Microscleres absent. Gemmules, single and scattered, subspherical, enveloped in cage of gemmular spicules. Gemmuloscleres smooth or spiny oxeas and strongyles.

Scope and distribution

Thirteen other species: *E. fragilis* (Leidy, 1851) (cosmopolitan); *E. calcuttanus* (Annandale, 1911b) (India); *E. michaelseni* (Annandale, 1914b) (central Africa); *E. crassissimus* (Annandale,

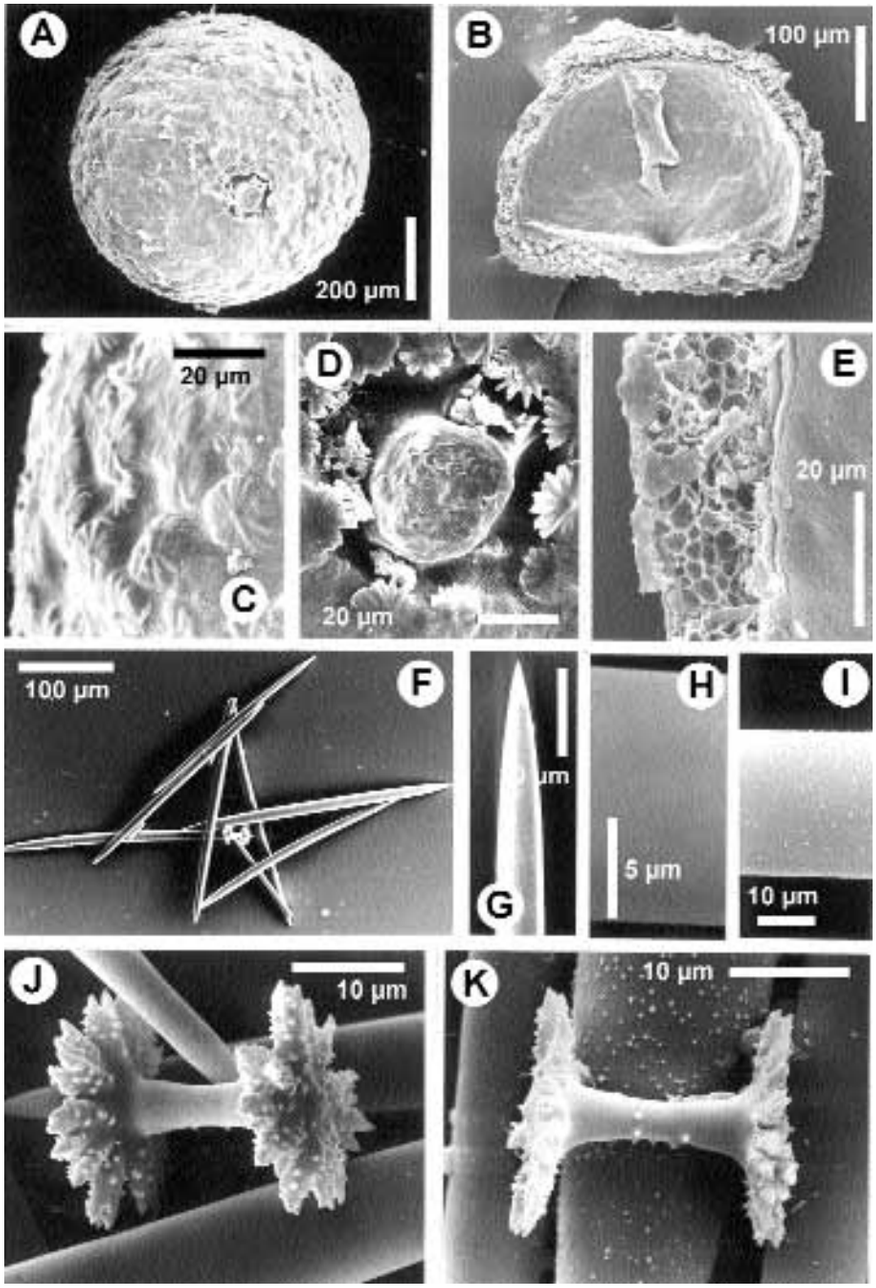

Fig. 30. *Ephydatia fluviatilis*, spicules and gemmules, neotype RMNH 1166. A, gemmule. B, cross section of gemmule. C, gemmular surface. D, foramen. E, trilayered theca (right = multilayered inner layer). F, megascleres and a gemmulosclere. G, oxea tip. H, smooth oxea shaft. I, granules on oxea shaft. J–K, birotule gemmuloscleres with smooth and spiny oxeas.

1907) (India, Australia, tropical SE Asia); *E. igloviformis* (Potts, 1884) (Canada, USA); *E. geminus* (Annandale, 1911b) (India); *E. coniferus* (Annandale, 1916) (China); *E. geei* (Annandale, 1918) (China); *E. tinei* (Gee, 1932) (Philippines); *E. nitens* (Carter, 1881c) (Africa); *E. sinensis* (Annandale, 1910c) (China, Manchuria, Russia, Australia); *E. potamolepis* (Annandale, 1918) (Thailand); *E. ryuensis* (Sasaki, 1970) (Japan). Cosmopolitan.

Description of type species

Eunapius carteri (Bowerbank, 1863) (Figs 32–35).

Material examined. Holotype: Not seen. Other material. ZMB6370–4 (from IM) – India, 8.x.1894. ZMB6365–5 (from IM) – India, 8.x.1894. BMNH 1914.11.24.13 – Trivandrum, India. BMNH 1886.2.9.8 – Mauritius. BMNH 1929.4.13.7 – Canton, China. BMNH 1906.5.31.11 – Lake Victoria, Nyanza, scraped from shell of *Aetheria*. ZMB9544 – Balaton Fured, 19.ix.1938. ZMB2774 – Bombay, 1949.

Description. Body shape ranges from encrusting to bulbous-massive to cone-shaped, from flattish to lobate, or bearing finger-like projections. Colour from yellowish brown to tan to bright green. Consistency of live sponges ranges from fragile to moderately soft to

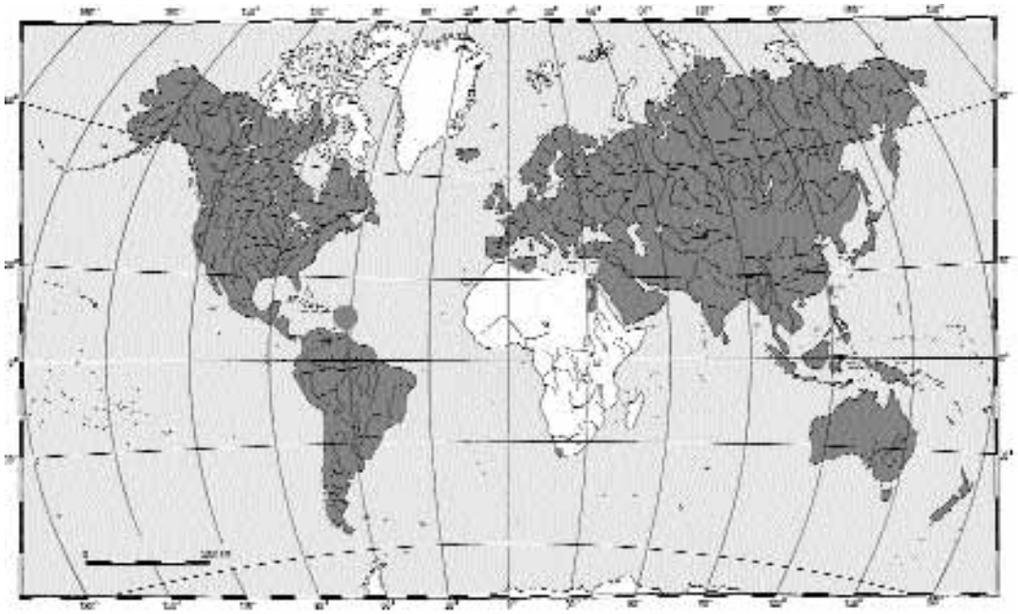

Fig. 31. Geographic distribution of the genus *Ephydatia*.

Fig. 32. *Eunapius carteri*, possible type specimen ZMB 2774.

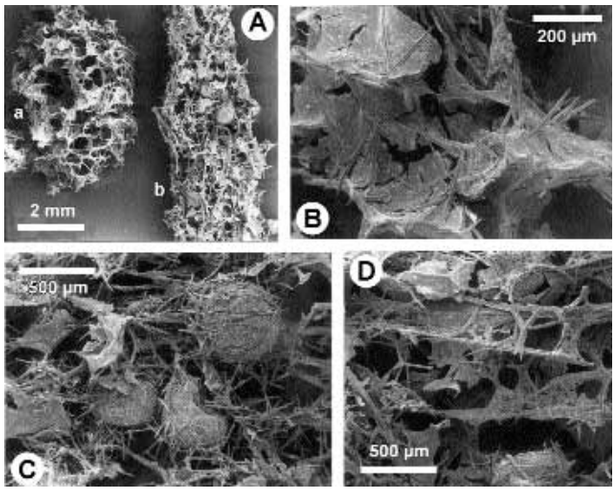

Fig. 33. *Eunapius carteri*, skeletal network, possible type specimen ZMB 2774. Aa, sponge fragment (top view). Ab, sponge cross section (right = surface). B, sponge surface (top view). C–D, choanosomal skeleton with gemmules (detail of Ab).

quite compact. Surface hispid due to tufts of emerging spicules. Dermal membrane thin aspiculous. Oscules from several to single, from very small to large (2 cm) sometimes at the apex of projections. Subdermal cavities not observed. Ectosomal skeleton undifferentiated. Choanosomal skeleton anisotropic with pauci- to multispicular fibres and tracts. Spongin relatively abundant. Megascleres stout fusiform slightly curved smooth oxeas (265–370 × 14–24 µm) with tips from sharply pointed to rounded. Microscleres absent. Gemmules from single to grouped, from scattered to restricted as a carpet at the sponge base. Gemmules subspherical (440–610 µm) enveloped in a cage of gemmuloscleres tangentially or partially embedded in the pneumatic layer. Foramen tubular simple without collar. Gemmular theca bi-layered. Outer layer absent with outlines of pneumatic chambers evident at the gemmular surface. Pneumatic layer thick with regular lines of polygonal chambers. Inner layer sublayered and connected to pneuma by trabecules of compact spongin. Gemmuloscleres smooth oxeas (145–210 × 5–8 µm).

Ecology. In standing waters of ponds, lakes and freshwater tanks on plants, sticks, stones, shells of *Unio* sp., not in running waters. Life cycle characterised by vegetative phase and annual degeneration after sexual and asexual (gemmulation) reproduction. Fast growth rate. Distribution: India, Ceylon, Malaysia, Indonesia, Java, Madura, Burma, Thailand, China, Philippines, Turkestan, Afghanistan, Kurdistan, Iran, E Europe (S Russia, Balaton Lake), Africa?, Mauritius Islands.

HETEROMEYENIA POTTS, 1881

Synonymy

Heteromeyenia Potts, 1881a: 150. [*Carterella*] Potts, 1881b: 176 (preocc.). *Carterius* Petr, 1886: 92. *Oxheteromeyenia* Schröder, 1927: 107. [*Oxyheteromeyenia*] Auct. *(lapsus)*.

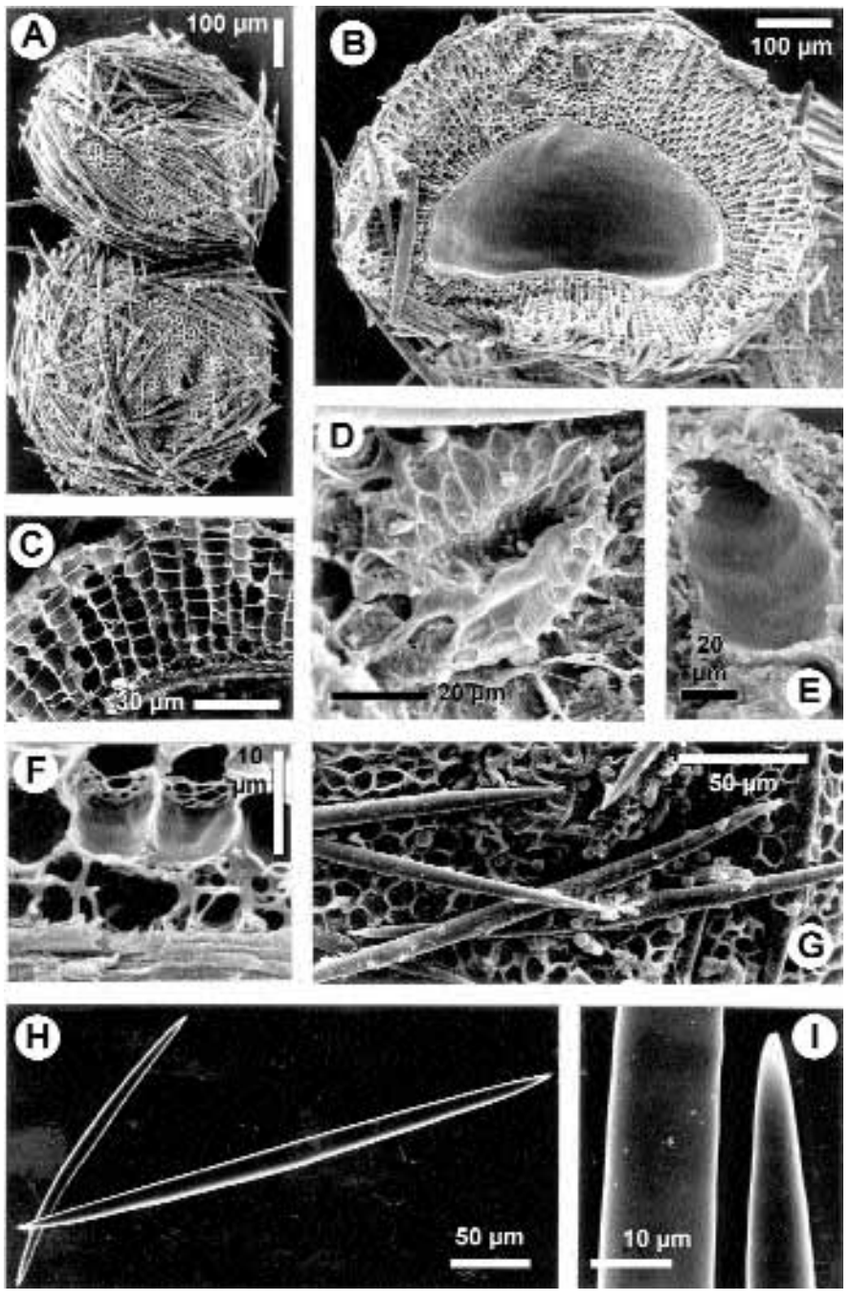

Fig. 34. *Eunapius carteri*, spicules and gemmules; A, C, E, G–I, BMNH 1914.11.24.13. B,D,F, 1886.2.9.8. A, two gemmules. B, gemmular cross section. C, pneumatic layer. D, foramen. E, internal view of the tube-like foramen. F, close-up of the pneumatic layer and sublayered inner layer (bottom) of the theca. G, close-up of the gemmular external surface with gemmuloscleres. H, smooth oxeas. I, tip and shaft of oxeas.

Type species

Spongilla baileyi Bowerbank, 1863: 461 (by subsequent designation; de Laubenfels, 1936a).

Diagnosis

Spongillidae with encrusting growth form. Choanosomal skeleton an irregular network of paucispicular parallel fibres and undefined secondary tracts. Sparse spongin. Megascleres acanthoxeas. Microscleres acanthoxeas. Gemmules scattered in groups. Theca tri-layered with gemmuloscleres radially embedded. Gemmuloscleres birotules of two types: birotules and pseudobirotules.

Scope and distribution

Four other species: *H. stepanowii* (Dybowsky, 1884a) (Europe, Russia, China, Japan, Australia); *H. latitenta* (Potts, 1881b) (NE USA); *H. tentasperma* (Potts, 1880a) (NE USA); *H. tubisperma* (Potts, 1881b) (NE America). Palaearctic, Nearctic and Australian Regions.

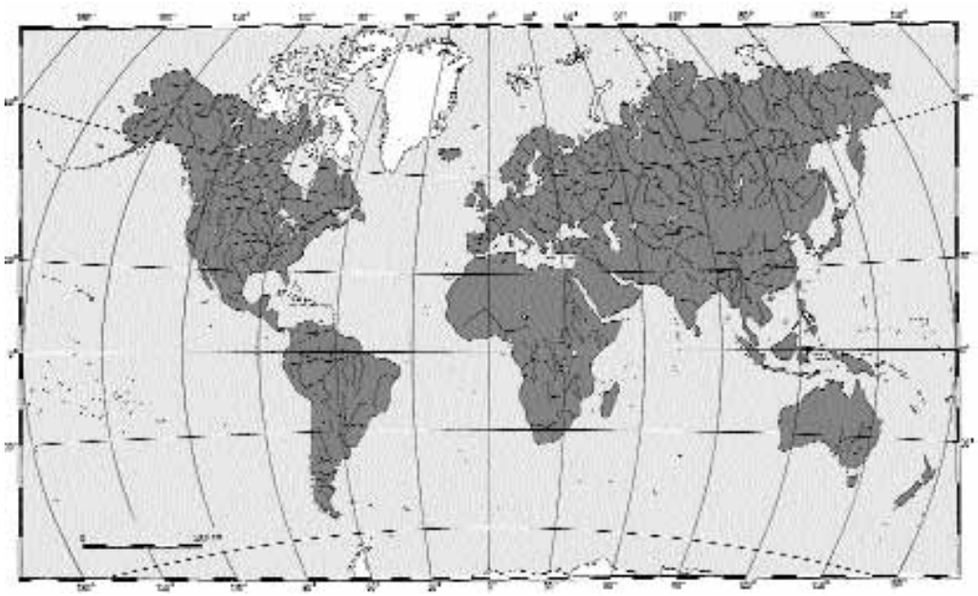

Fig. 35. Geographic distribution of the genus *Eunapius*.

Fig. 36. *Heteromeyenia baileyi*, lectotype from the collection of E. Potts, ANSP PO4535.

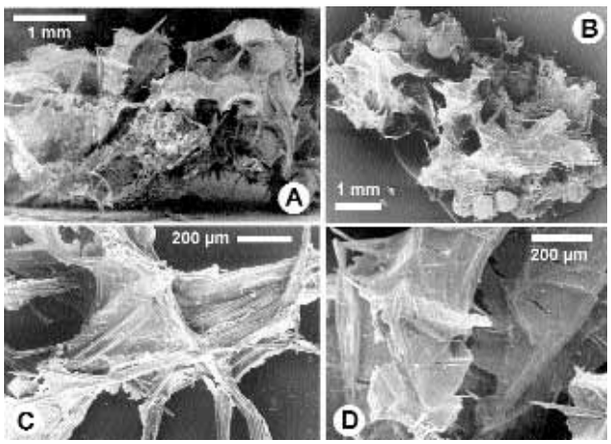

Fig. 37. *Heteromeyenia baileyi*, skeletal network, lectotype ANSP PO4535. A, sponge fragment (side view). B, sponge fragment (top view) with gemmules. C, choanosomal skeleton. D, ectosomal skeleton.

Description of type species

Heteromeyenia baileyi (Bowerbank, 1863) (Figs 36–39).

Material examined. Lectotype: ANSP PO4535 – *Spongilla repens* type a, coll. E. Potts, Leigh Cape, Pennsylvania. BMNH 1890.1.9.216 – Krasetice and Nimency, Boemia, 19.x.1885. ZMB6275 – Munster, 7.vii.1926, det. Arndt, 1927, det. Schröder. ZMB (DTRG-FW538) (*H. baileyi* var. *repens*) – Creba, Kr. Rotemburg, Schlesia, .x.1929, Schröder.

Description. Thinly encrusting sponges. Surface hispid due to spicules emerging through the dermal membrane. Oscules inconspicuous. Consistency of live sponge soft. Colour bright green in life. Dermal membrane spiculose (microscleres). Subdermal cavities not observed. Ectosomal skeleton as spicules in the dermal membrane. Choanosomal skeleton an irregular network of paucispicular parallel fibres and undefined secondary tracts. Sparse spongin. Megascleres (255–315 × 11–10 µm) sharply pointed fusiform oxeas with scattered microspines except at the tips. Microscleres (75–85 × 2–3 µm) sharply pointed oxeas from curved to straight entirely spined with microspines, increasing in length from tips to the central portion, perpendicular and large. Gemmules scattered in groups, subspherical (450–480 µm). Foramen tubular with scarcely developed collar and devoid of cirri. Theca tri-layered with gemmuloscleres radially embedded. Outer layer with emerging shafts and distal rotules of both types of gemmuloscleres. Pneumatic layer well developed with irregular chambers. Inner layer composed of compact sublayered spongin. Gemmuloscleres of two types: pseudobirotules (80–85 × 22 µm), few inserted with their proximal rotules in the outer zone of gemmular theca, cylindrical shaft usually smooth and often irregularly bent, pseudo-rotules bear long recurved hooks with microspinosity at the tips; birotules (50–60 × 22 µm) very numerous with straight shafts bearing few conspicuous conical spines, variably umbonate rotules with incised margins bearing spines.

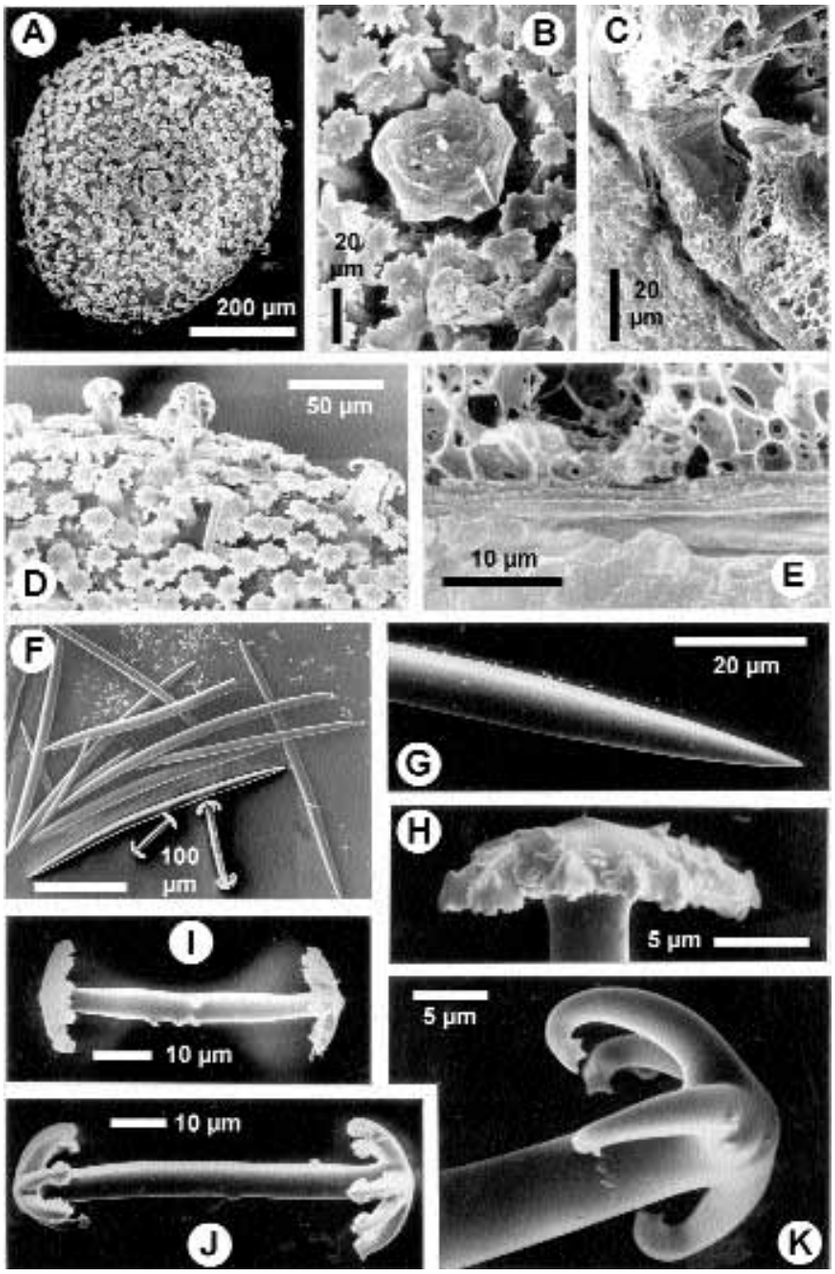

Fig. 38. *Heteromeyenia baileyi*, spicules and gemmules, lectotype ANSP PO 4535. A, gemmule. B, foramen. C, cross section of the foraminal tube. D, gemmular external surface. E, multi-layered inner layer and pneumatic layer of the trilayered theca. F, megascleres oxeas and two types of gemmuloscleres. G, tip of an oxea. H–I, short birotule gemmulosclere. J–K, long pseudo-birotule gemmulosclere.

Ecology. In shallow standing waters on submerged plants, timber and sticks, stems of *Nitella*, leaves of *Potamogeton*. Distribution: N America from Canada to Louisiana, Mexico, Germany ?, Poland ?

Remarks

[*Carterella*] Potts, 1881b, with type species *C. latitenta* Potts, 1881b: 176 (by monotypy) is both preoccupied and a junior synonym of *Heteromeyenia* (Penney & Racek, 1968). Likewise, *Carterius* Petr, 1886, with type species *C. stepanowii* (Dybowsky, 1884a: 507 as *Dosilia*) (by original designation) also belongs to this genus according to Penney & Racek (1968). *Oxheteromeyenia* Schröder, 1927 and a misspelling [*Oxyheteromeyenia*] Auct. probably also belong here.

***HETEROROTULA* PENNEY & RACEK, 1968**

Synonymy

Heterorotula Penney & Racek, 1968: 96.

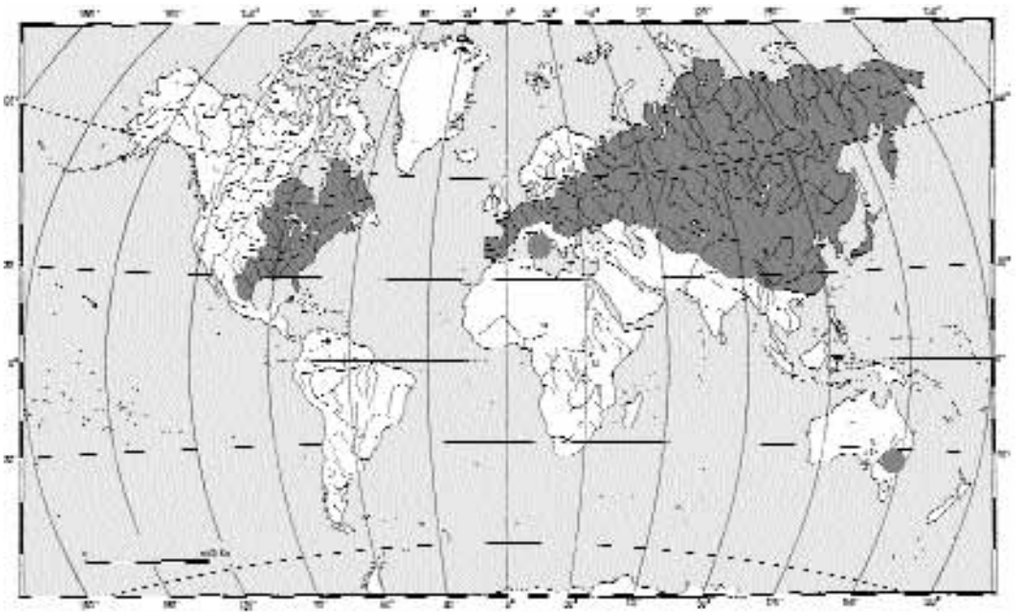

Fig. 39. Geographic distribution of the genus *Heteromeyenia*.

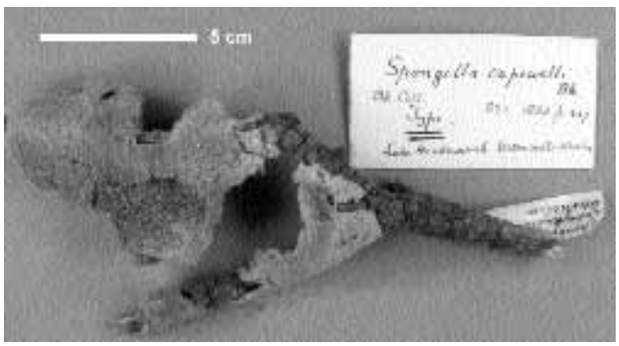

Fig. 40. *Heterorotula capewelli*, type specimen BMNH unregistered.

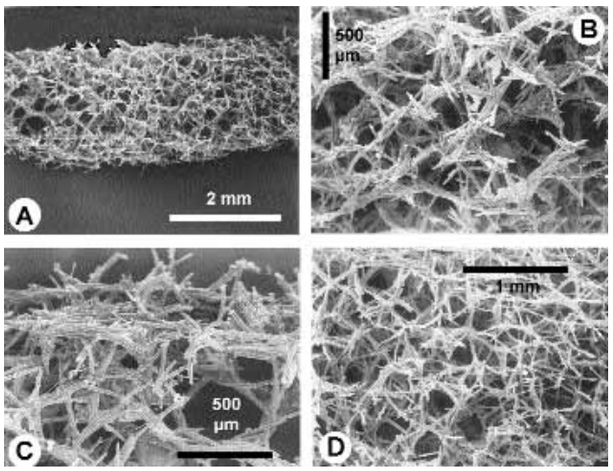

Fig. 41. *Heterorotula capewelli*, skeletal network, type specimen BMNH unregistered. A, cross section (top = sponge surface). B, sponge surface (top view). C, ectosomal skeleton (top). D, choanosomal skeleton.

Type species

Spongilla capewelli Bowerbank, 1863: 447 (by original designation).

Diagnosis

Spongillidae with massive and bulbous growth form and with lobate surface. Choanosomal skeleton irregularly alveolate with paucispicular tracts. Moderate amount of spongin. Megascleres spiny oxeas. Microscleres absent. Gemmules scattered with cages of megascleres. Gemmular theca trilayered with radially embedded gemmuloscleres. Gemmuloscleres birotules.

Scope and distribution

Six other species: *H. nigra* (Lendenfeld, 1887) (E Australia); *H. multidentata* (Weltner, 1895) (E Australia, Tasmania); *H. multiformis* (Weltner, 1910) (W Australia); *H. contraversa* (Racek, 1969) (E Central Australia); *H. kakahuensis* (Traxler, 1896) (New Zealand); *H. fistula* Volkmer & Motta, 1995 (S America). Australian and Neotropical Regions.

Description of type species

Heterorotula capewelli (Bowerbank, 1863) (Figs 40–43).

Material examined. Holotype: BMNH (Bowerbank Coll.) – Lake Hindmarsh, Victoria, SE Australia, 1863.

Description. Sponge massive and bulbous. Colour light tan to brown. Consistency of live sponges moderately hard, firm but brittle. Surface lobate with high and rounded irregular ridges separated from each other by comparatively deep clefts. Oscules few and conspicuous. Dermal membrane well developed separated by the underlying symplasm. Subdermal cavities not observed. Special ectosomal skeleton absent. Choanosomal skeleton irregularly alveolate with paucispicular tracts but also more variably oriented thick fibres joined by slimmer transverse fibres are present in some areas of the sponge body at the level of lobes. Moderate amount of spongin. Megascleres (195–330 × 13–18 µm) stout

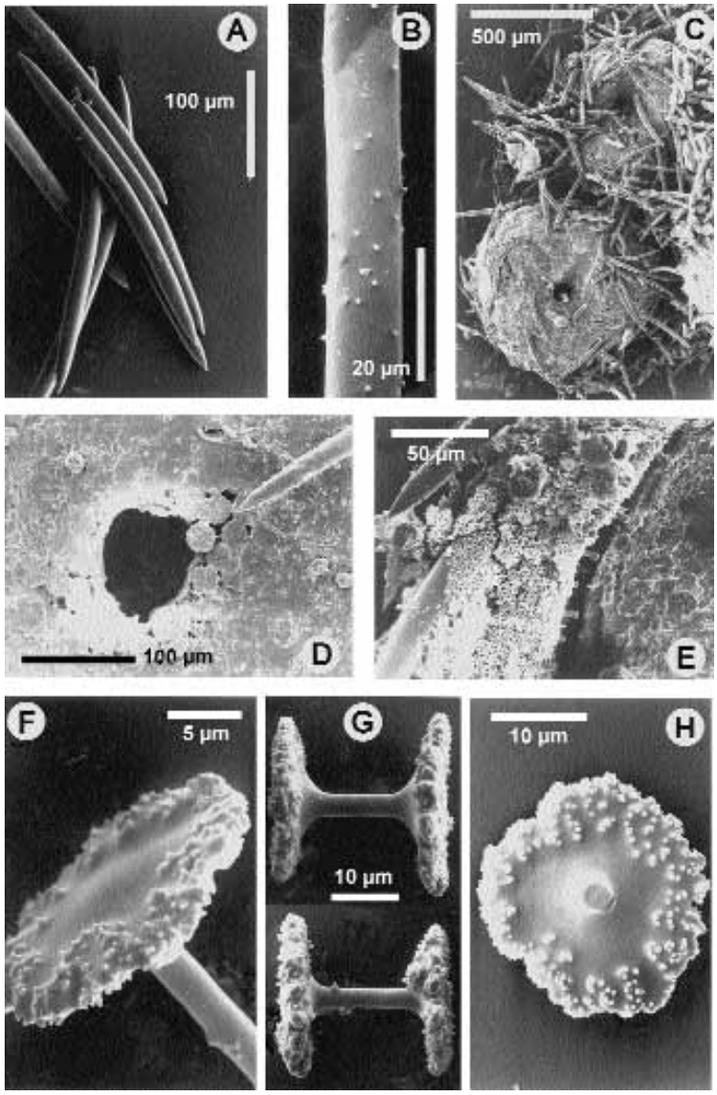

Fig. 42. *Heterorotula capewelli*, spicules and gemmules, type specimen Bowerbank collection BMNH unregistered. A, megascleres oxeas. B, shaft of a spiny oxea. C, gemmules in their cage. D, foramen. E, cross section of gemmular theca. F–H, gemmuloscleres.

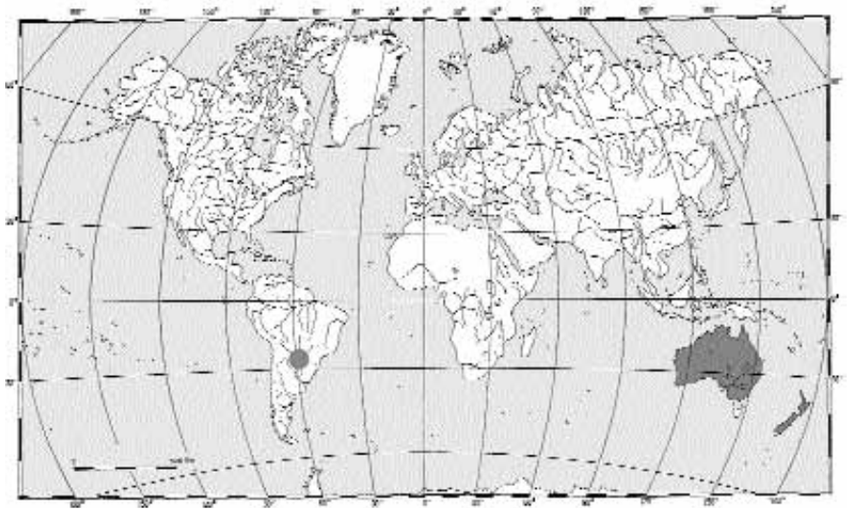

Fig. 43. Geographic distribution of the genus *Heterorotula*.

fusiform oxeas from smooth to microspined. Microscleres absent. Gemmules (510–600 μm) subspherical, scattered in the skeletal network and more abundant and grouped in basal parts. A loose cage of irregularly arranged megascleres envelopes gemmules. Foramen simple or bearing a shallow peripheral collar. Gemmular theca trilayered. Outer layer distinctly corrugated and of pale yellow colour with tangentially arranged megascleres of the cage. Pneumatic layer very thick with radially embedded gemmuloscleres. Inner layer of multilayered compact spongin. Gemmuloscleres in the gemmular theca with proximal rotule firmly inserted in the inner layer and distal rotule generally not reaching the outer layer. Gemmuloscleres birotules (34–52 μm) with a slender smooth shaft bearing sometimes few spines. Rotules flat with small spines and margins irregularly crenulated with rare teeth. Diameter of rotules unequal (24–28 μm; 20–23 μm).

Ecology. Inland slightly brackish athalassic waters of arid regions. Distribution. Central Australia, ranging east of the Great Dividing Range and north to Queensland.

Diagnosis

Spongillidae with encrusting growth form, moderately hard, friable. Dermal membrane supported by spicules. Subdermal cavities notably developed. No well defined central cavity. Choanosomal skeleton variable, never very stout, ranging from reticulate to alveolate with primary fibres quite distinct, transverse fibres not very distinct. Megascleres spined oxeas. Gemmules rare, when present dome-shaped flattened at the base, adherent to basal plate, devoid of foramen, spicules and pneumatic layer.

Scope and distribution

Six other species. *N. yunnanensis* (Annandale, 1910b) (Yunnan, W China); *N. ehraiensis* Lizhen, 1998 (Yunnan, W China); *N. tanganykae* (Evans, 1899) (Lake Tanganyika, Africa); *N. moorei* (Evans, 1899) (Lake Tanganyika, Africa); *N. cunningtoni* (Kirkpatrick, 1906) (Lake Tanganyika, Africa); *N. vasta* (Weltner, 1901) (Celebes [Sulawesi], Indonesia). Oriental and Afrotropical Region.

NUDOSPONGILLA ANNANDALE, 1918

Synonymy

Nudospongilla Annandale, 1918: 62.

Type species

Spongilla coggini Annandale, 1910b (by original designation).

Fig. 44. *Nudospongilla coggini*, paralectotype BMNH 1914.11.24.32 (dry).

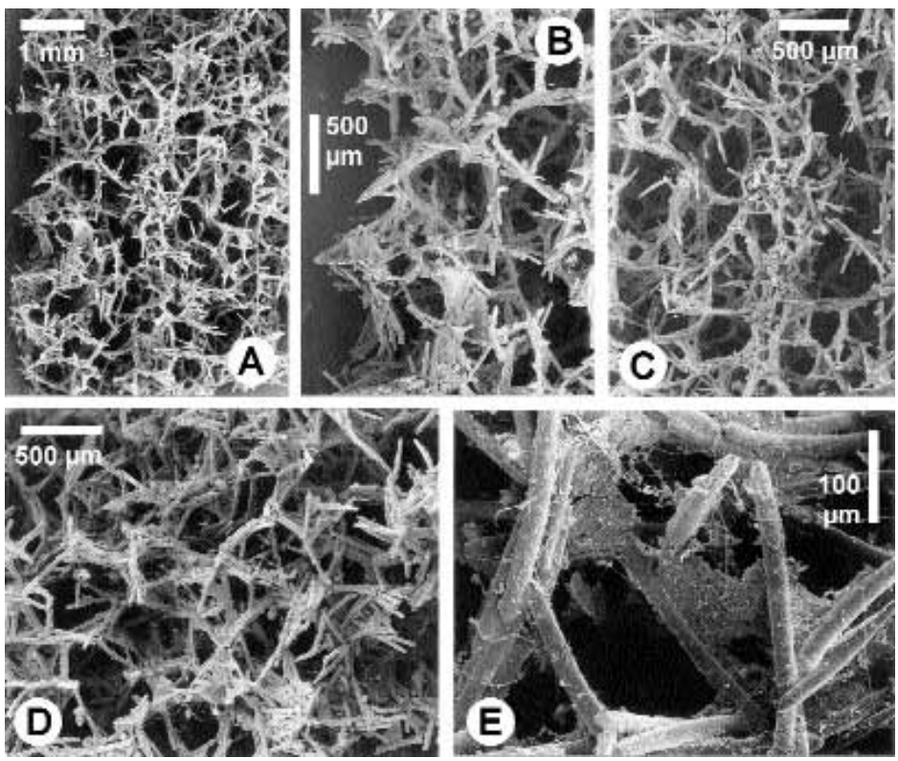

Fig. 45. *Nudospongilla coggini*, skeletal network, paralectotype 1914.11.24.32. A, cross section (left = sponge surface). B, ectosomal skeleton (left). C, choanosomal skeleton. D, sponge surface (top view). E, detail of D.

Description of type species

Nudospongilla coggini (Annandale, 1910b) (Figs 44–47).

Material examined. Paralectotype: BMNH 1914.11.24.32 (ZEV 3809.7) – dry coll., Coggin, Lake Jali-Zu (Hai), Yunnan, W China (without gemmules). Lectotype: IM not available – Lake Erh Hai, Ta-Li Fu, Yunnan, J. Coggin Brown leg.

Description. Encrusting rounded sponge to irregularly massive, occasionally with short flattened branches. Size from 2 × 2 cm to 5 × 4 × 3.8 cm. Living specimens pale grey to brilliant green, light brown when preserved. Consistency moderately hard, fragile. Surface irregular and minutely hispid due to tufts of spicules (3) at the apices of slender fibres (3 spicules thick). Oscules inconspicuous in depressed areas. Dermal membrane closely adherent. Basal spongin plate delicate. Ectosomal skeleton a horizontal network of spicules (according to the original description). Choanosomal skeleton vaguely alveolate-reticulate, paucispicular in the studied syntype (reported in the original descriptions as never very stout), with a close regular network with small meshes, with radiating (vertical) fibres stout and more coherent of distinguishable transverse fibres. The network is more vague at the base of the sponge. Spongin poor. Megascleres (258–283 × 19–28 μm) stout, straight, to feebly curved spined oxeas with spines more dense and larger at the tips. Few smaller and more sharply pointed oxeas are loose within the skeleton. Microscleres absent. Gemmules when present moderate in size (?), naked (without spicules), ovoid and flattened at the base, dome shaped and adherent to the basal plate. Gemmular theca of compact spongin thin and brittle, outer layer in continuity with the basal plate. No foramen, no pneumatic layer, no gemmuloscleres.

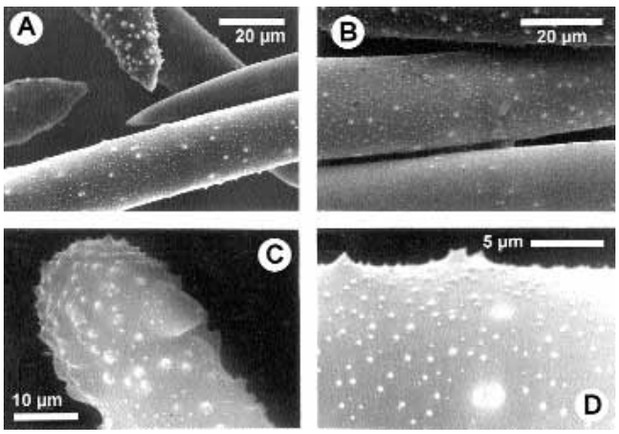

Fig. 46. *Nudospongilla coggini*, skeleton, paralectotype BMNH 1914.11.24.32. A–D, close-up of different characters of tips and shafts of megascleres (spiny oxeas), with two different kinds of spines.

Ecology. In standing waters on the lower surface of stones, sometimes englobing objects such as fragments of sticks, small stones and shells. Often on old shells. Larva parenchymula in October. Distribution. Yunnan Lakes.

Remarks. All species of *Nudospongilla* were initially assigned to *Spongilla*, being spongillid-like with oxeas. To this genus were assigned species with oxeas and no gemmules collected from W China, Sulawesi, Africa and Tiberiade/Kinneret. Racek (1974) relegated *N. aster, N. mappa, N. reversa* of Annandale (1918) as synonyms of *Cortispongilla barroisi*. In spite of this the author declared the genus *Nudospongilla* a *nomen nudum*, which we consider is an invalid action. The gemmular characters of this genus (theca monolayered without gemmuloscleres) is not in agreement with the rules of the family Spongillidae.

PACHYROTULA VOLKMER-RIBEIRO & RÜTZLER, 1997

Synonymy

Pachyrotula Volkmer-Ribeiro & Rützler, 1997: 490.

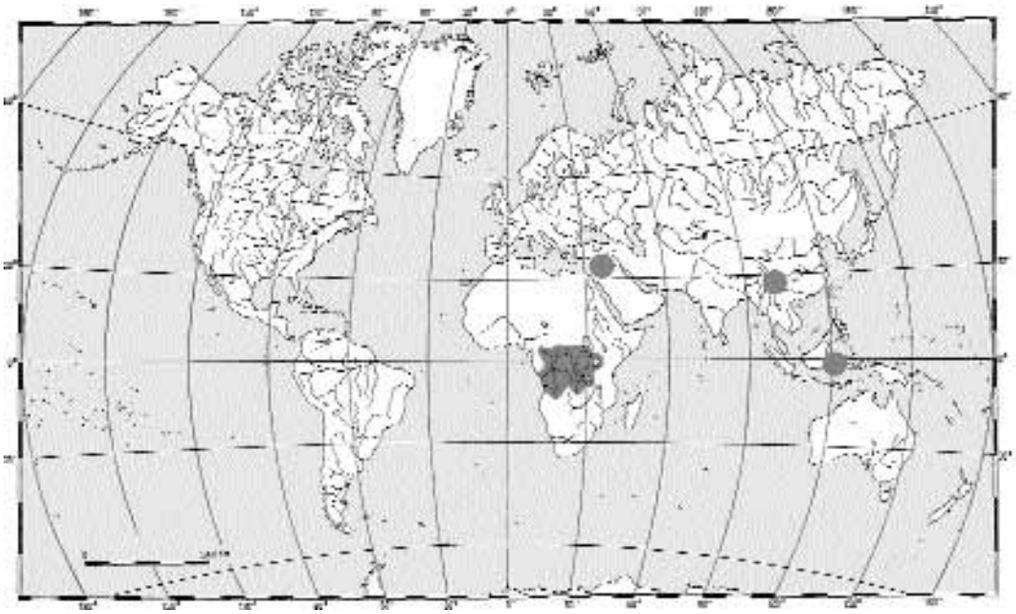

Fig. 47. Geographic distribution of the genus *Nudospongilla*.

Type species

Spongilla (Stratospongilla) raceki Rützler, 1968: 60 (by monotypy).

Diagnosis

Spongillidae with encrusting growth form. Alveolate skeleton with sparse spongin. Megascleres oxeas, ranging from spined to rarely smooth. Microscleres absent. Gemmules at the sponge base in cages of oxea megascleres. Gemmular theca tri-layered. Foramen tube-like. Gemmuloscleres range from birotules with very variable shape to spiny short oxeas.

Scope and distribution

Monotypic, New Caledonia.

Description of type species

Pachyrotula raceki (Rützler, 1968) (Figs 48–51).

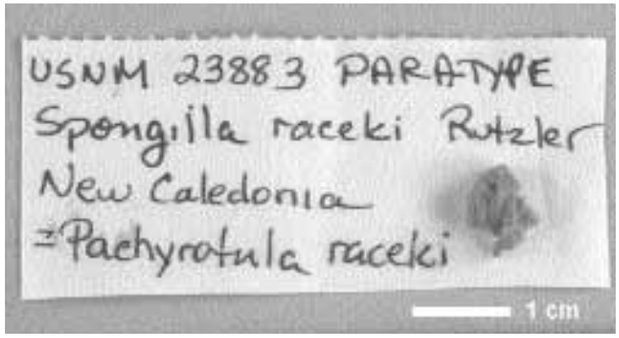

Fig. 48. *Pachyrotula raceki*, paratype USNM 23883.

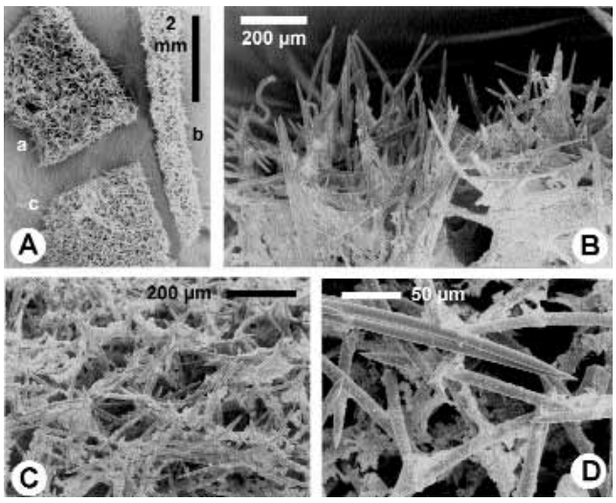

Fig. 49. *Pachyrotula raceki*, skeletal network, paratype USNM 23883. Aa, sponge fragment (top view). Ab, cross section of the sponge fragment (lateral view). Ac, sponge base (top view). B, surface hispidation. C, choanosomal network. D, choanosomal skeleton meshes.

Material examined. Holotype: USNM 238820 – River Le Diahot, New Caledonia, F. Starmuhler, 18.ix.1965. Paratype: USNM 23883 – same details.

Description. Slender, irregular, small soft crusts, ca. 1 mm thick. Colour greyish-ochre in alcohol. Very soft consistency. Oscula and pores inconspicuous. Dermal membrane and subdermal cavities not observed. Hispid body surface due to tufts of spicules. Ectosomal skeleton as tufts of spicules. Choanosomal paucispicular skeleton densely and irregularly alveolate with sparse spongin. Megascleres (160–245 × 7.5–14 µm) straight to curved oxeas ranging from microspined to rarely smooth, tips abruptly pointed. Microscleres absent. Gemmules (350–650 µm)

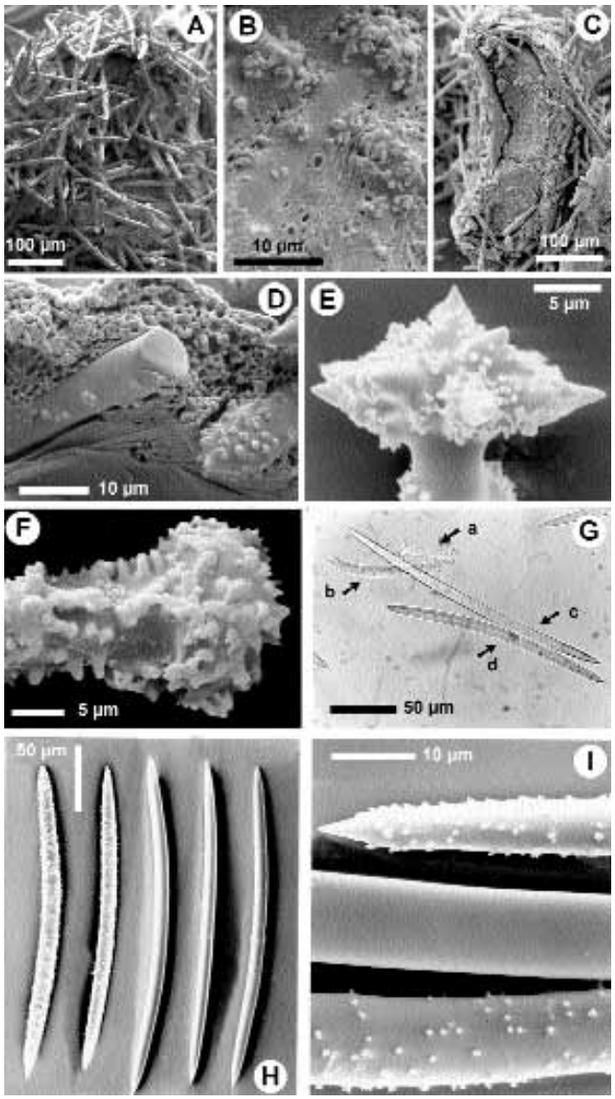

Fig. 50. *Pachyrotula raceki*, spicules and gemmules, A–D, F, holotype USNM 238820. E, G–I, paratype USNM 23883. A, megasclere spicular cage. B, external surface of a gemmule showing the spiny tips of gemmuloscleres (see also F). C, cross section of gemmule and cage. D, trilayered gemmular theca showing a multi-layered inner layer and gemmuloscleres embedded in the pneumatic layer. E, rotule of gemmulosclere. F, modified rotule of a demmulosclere. Ga, microsclere. Gb, gemmulosclere. Gc, megasclere smooth oxea. Gd, megasclere spiny oxea. H, spiny (left) and smooth (right) megascleres. I, tip and shafts of megascleres.

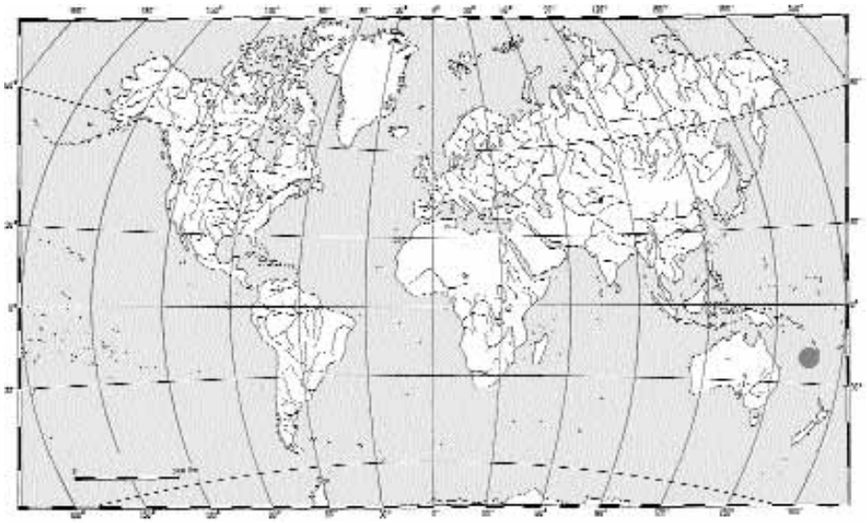

Fig. 51. Geographic distribution of the genus *Pachyrotula*.

subspherical at the base of the sponge, enclosed in a cage of short acanthoxea megascleres, enveloping one or more gemmules (up to 4). Foramen simple as a short tube (45–50 μm). Gemmular theca tri-layered. Outer layer notably thick with emerging distal rotules. Pneumatic layer thin with irregular chambers. Inner layer multilayered. Gemmuloscleres irregularly tangential to radially embedded in the theca. Gemmuloscleres (20–80 μm length) stout birotules notably variable in shape with smooth shafts (5–8 μm thick), rotules or knob-like (9–20 μm in diameter) ends ornamented by tubercules, rosettes or spines; tips sometimes bear grouped spines and appear as oxeas (120 × 8 μm).

Ecology. On the lower surface or concavities of stones, both in running and standing waters with low conductivity (28–56) and pH range 6.6–7.1. Distribution. New Caledonia.

Remarks. Rützler (1968) originally assigned this species to *Spongilla (Stratospongilla)* and considered that it was closely related to *Stratospongilla gilsoni* (Topsent, 1912) from Fiji. Volkmer-Ribeiro & Rützler (1997) subsequently revised the type material and erected this monotypic genus closer to *Heterorotula* Penney & Racek, 1968.

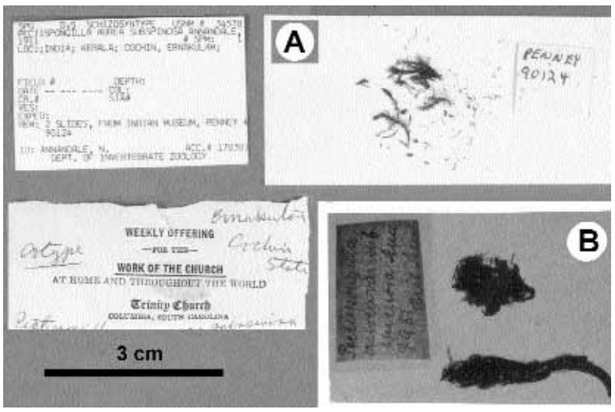

Fig. 52. *Pectispongilla aurea*, two specimens of the variety *subspinosa*. A, schizosyntype from the collection of Penney (90124) with 3 labels (USNM 34578). B, a specimen from the BMNH 1914.11.24.34 and preserved in the ZMB 7981. Both specimens are represented by the same aquatic plant with scanty sponge remains.

PECTISPONGILLA ANNANDALE, 1909

Synonymy

Pectispongilla Annandale, 1909a: 103.

Type species

Pectispongilla aurea Annandale, 1909a: 103 (by original designation).

Diagnosis

Spongillidae forming small cushions. Consistency of live sponges soft. Choanosomal skeleton consisting of feebly coherent spicule fibres. Spongin abundant. Megascleres smooth to spined oxeas. Microscleres microspined oxeas with rhomboid outline. Gemmules scattered in the skeleton. Gemmular theca with three layers. Pneumatic layer of spongin fibres (without chambers). Gemmuloscleres radially embedded, botryoides-like.

Scope and distribution

Three other species: *P. subspinosa* Annandale, 1912 (India, Japan); *P. stellifera* Annandale, 1915b (India); *P. botryoides* Haswell, 1882 (Australia). Tropical India and Australia, ? Japan.

Description of type species

Pectispongilla aurea Annandale, 1909a (Figs 52–55).

Material examined. Holotype: IM not available. Other material. BMNH 1914.11.24.34 – *P. subspinosa*, Ernakulam, Cochin State, India. USNM 34578 – *P. subspinosa*, Ernakulam, Cochin State, India. DTRG FW568 (from NTM) – *Pectispongilla* sp., R. Manconi, Kakadu Park, Northern Territory, Australia.

Description. Body cushion-shaped. Colour deep golden. Consistency of live sponges soft. Oscula few and inconspicuous.

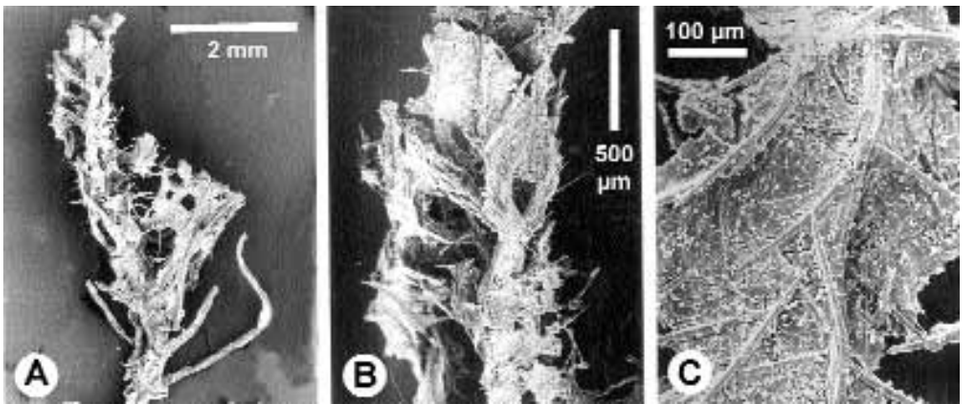

Fig. 53. *Pectispongilla aurea* var. *subspinosa*, skeletal network, schizosyntype USNM 34578. A–C, sponge fragment on an aquatic plant at different magnifications.

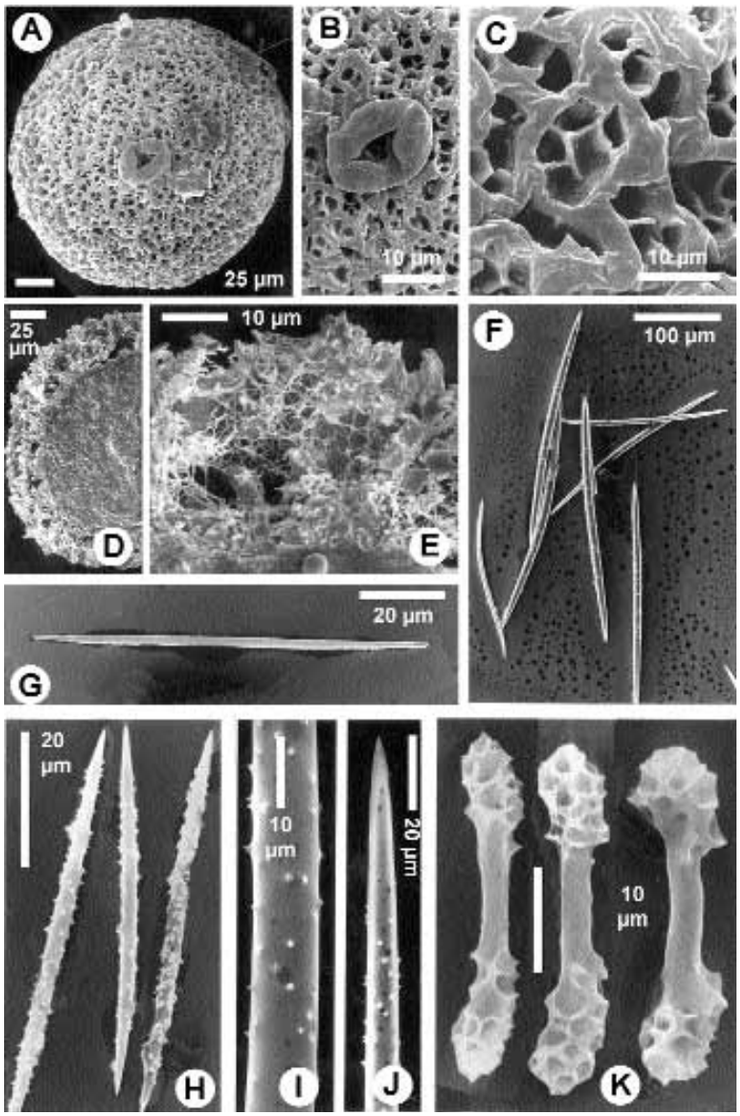

Fig. 54. *Pectispongilla*, spicules and gemmules. A–E, *Pectispongilla* sp. DTRG-FW568 (ex-IZUG). F–K, *P. aurea* variety *subspinosa*, co-type from BMNH 1914.11.24.34. A, gemmule. B, foramen. C, gemmular outer layer surface. D, cross section of gemmule. E, trilayered gemmular theca. F, megascleres oxeas. G, smooth oxea. H, spiny oxeas. I, shaft of a spiny oxea. J, tip of a spiny oxea. K, gemmuloscleres.

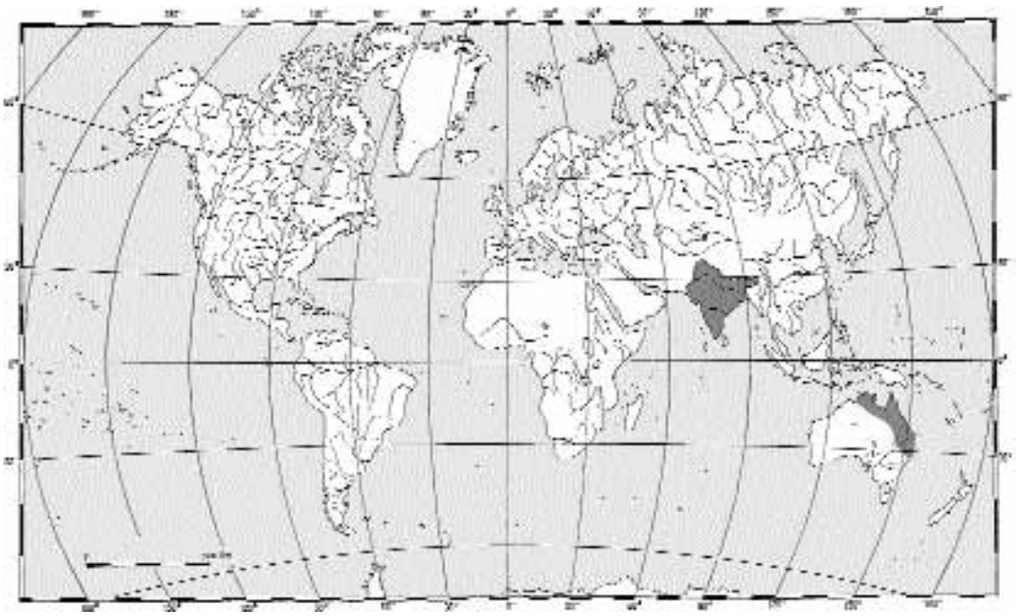

Fig. 55. Geographic distribution of the genus *Pectispongilla*.

Dermal membrane well developed. Surface hispid. Ectosomal skeleton undetected. Choanosomal skeleton consisting of feebly coherent spicule fibres. Spongin abundant. Megascleres (270–320 × 13–16 μm) range from fusiform sharply pointed oxeas from straight to bent, and from smooth to spined. Microscleres (20–50 × 1.5–3.5 μm) reported in the literature as straight and sharply pointed oxeas of rhomboid outline usually microspined. Gemmules (190–220 μm) subspherical, scattered in the skeleton. Foramen tubular. Gemmular theca with three layers. Outer layer surface irregular due to the partial emergence of gemmuloscleres apices. Pneumatic layer well developed as a network of spongin fibres. Gemmuloscleres radially embedded in the theca crossing each other at slanting angles with botryum-like apices variably oriented. Inner layer multilayered. Gemmuloscleres (31–37 × 2.5–4 μm) typical of this genus with smooth distinctly curved shafts characterized, in the apex of convex sides, by the disto-lateral arrangement of spines in rows joined to each other by siliceous webs to form botryoides-like apices in mature gemmuloscleres, with well defined polygonal concavities of the botryum. Apices of young spicules with scarcely developed siliceous webs appear as spines in rows.

Ecology. Unknown for the type species.

Fig. 56. *Racekiela ryderi*, lectotype ANSP PO 4536.

RACEKIELA BASS & VOLKMER-RIBEIRO, 1998

Synonymy

[*Acanthodiscus*] Volkmer-Ribeiro, 1996: 35 [preocc.]. *Racekiela* Bass & Volkmer-Ribeiro, 1998: 125.

Type species

Heteromeyenia ryderi Potts, 1882: 13 (by subsequent designation; Volkmer-Ribeiro, 1996).

Diagnosis

Spongillidae with body shape encrusting to lobate, ramose or massive. Ectosomal skeleton with tangential megascleres on the dermal membrane and irregularly scattered erect megascleres. Choanosomal skeleton consists of irregular paucispicular isotropic network with sparse spongin. Megascleres are acanthoxeas. Microscleres absent. Gemmular theca tri-layered with gemmuloscleres radially embedded. Gemmuloscleres of two types: birotules and pseudobirotules.

Scope and distribution

Only one other species: *R. sheilae* (Volkmer-Ribeiro *et al*., 1988) (S America). Palaeartic, Nearctic and Neotropical.

Description of type species

Racekiela ryderi (Potts, 1882) (Figs 56–59).

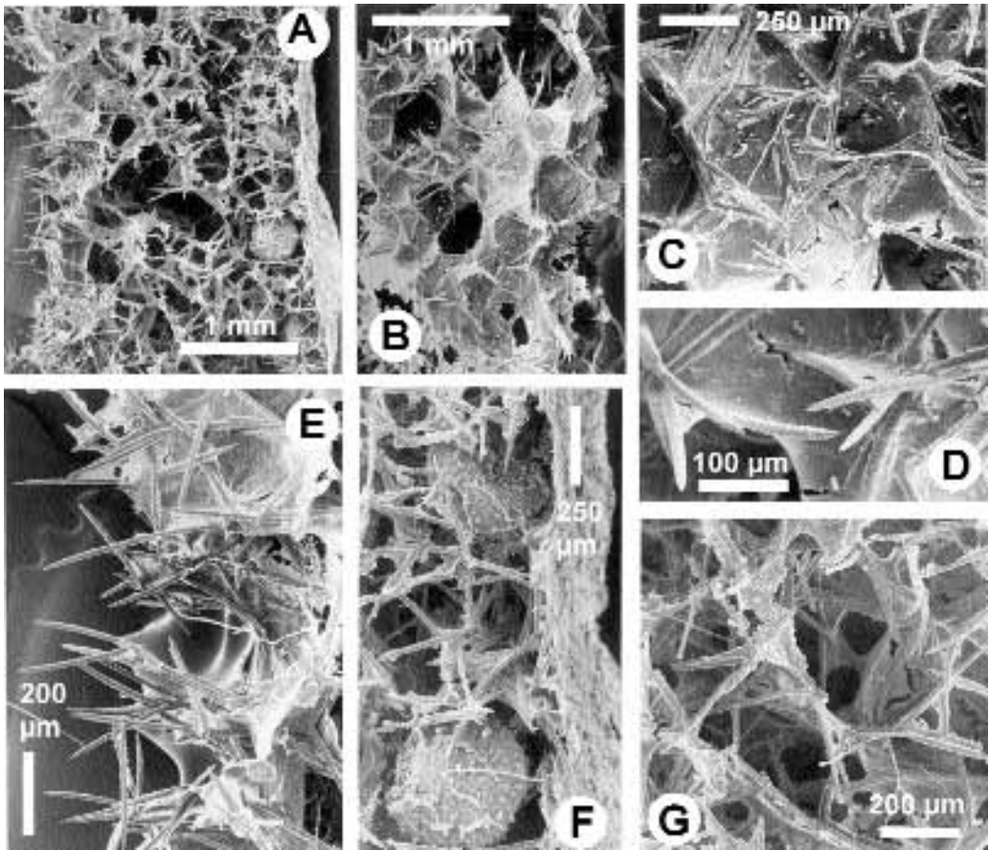

Fig. 57. *Racekiela ryderi*, skeletal network, lectotype ANSP PO4536. A, section through the entire sponge thickness (left = surface; right = spongin basal plate). B–C, sponge surface and ectosomal skeleton (top view) at different magnifications. D–E, surface hispidation (lateral and top view). F, spongin basal plate with gemmules. G, choanosomal skeleton.

Material examined. Lectotype: ANSP PO4536 (Pott's coll.) – Cobb's Creek, Delaware River, USA, E. Potts, 1881. Other material. DTRG FW363 – Norway, Oakland. BMNH 1910.1.1.622.C (from INM) – Ireland. BMNH 1866.12.9.3 – dry box 6, Stream and Loch.

Description. Thinly encrusting to massive ramose or papillate sponges. Colour green, brown or white. Small conspicuous oscules. Dermal membrane spicular (from protruding megascleres). Subdermal cavities not observed. Ectosomal skeleton is composed of irregularly scattered erect megascleres producing a hispid surface and tangential megascleres lying on the dermal membrane. Choanosomal skeleton is an irregularly paucispicular isotropic network with sparse (?) spongin. Megascleres (296–431 × 12–26 µm (holotype); 141–279 × 1–21 µm (other material)) stout to slender, straight to slightly curved, heavily to sparsely spined, abruptly to gradually pointed oxeas; spines range from straight to oriented. Microscleres absent. Gemmules hemispherical (300–800 µm; 300–400 µm), abundant, with no consistent distribution. Foraminal tube inconspicuous, not higher than the shorter gemmuloscleres. Gemmular theca trilayered with radially arranged gemmuloscleres. Outer layer covering the outer rotules of short gemmuloscleres. Pneumatic layer thick, with irregular chambers. Inner layer of sublayered compact spongin (3–4). Gemmuloscleres of two types: with short birotules completely embedded in the theca, whereas long pseudobirotules project distal rotules beyond the outer layer. Number and distribution of pseudobirotules notably variable. Gemmuloscleres of two classes. Pseudobirotules (47–92 × 5–10 µm; 46–64 × 4–8.5 µm) with small umbonate pseudo-rotules (17–23 µm (other material)) bearing irregular hooks variably curved; stout spined shafts, spines irregularly distributed and hook-shaped. Birotules (33–49 × 5–8 µm; 28–41 × 3–5 µm) with usually smooth shafts and large disk-like rotules (25–29 µm; 20–28 µm) bearing serrated margins and irregularly distributed spines or tubercules.

Ecology. Body shape varies significantly according to environmental conditions, encrusting in running waters and massive in lentic conditions. Distribution. Amphiatlantic in the northern hemisphere. From Eastern North America and Canada to W British Islands, Faroes and SW Norway. One record (?) from Central America (Belize).

Remarks. The type species was moved from the genus *Anheteromeyenia* by Volkmer-Ribeiro (1996). However, the proposed generic name [*Acanthodiscus*] was preoccupied and thus *Racekiela* was proposed as a replacement name by Bass & Volkmer-Ribeiro (1998). Moreover in the last paper, the two names *Racekiela* and *Racekiella* are used by the authors. We here propose the first name appeared in the text.

RADIOSPONGILLA PENNEY & RACEK, 1968

Synonymy

Radiospongilla Penney & Racek, 1968: 61.

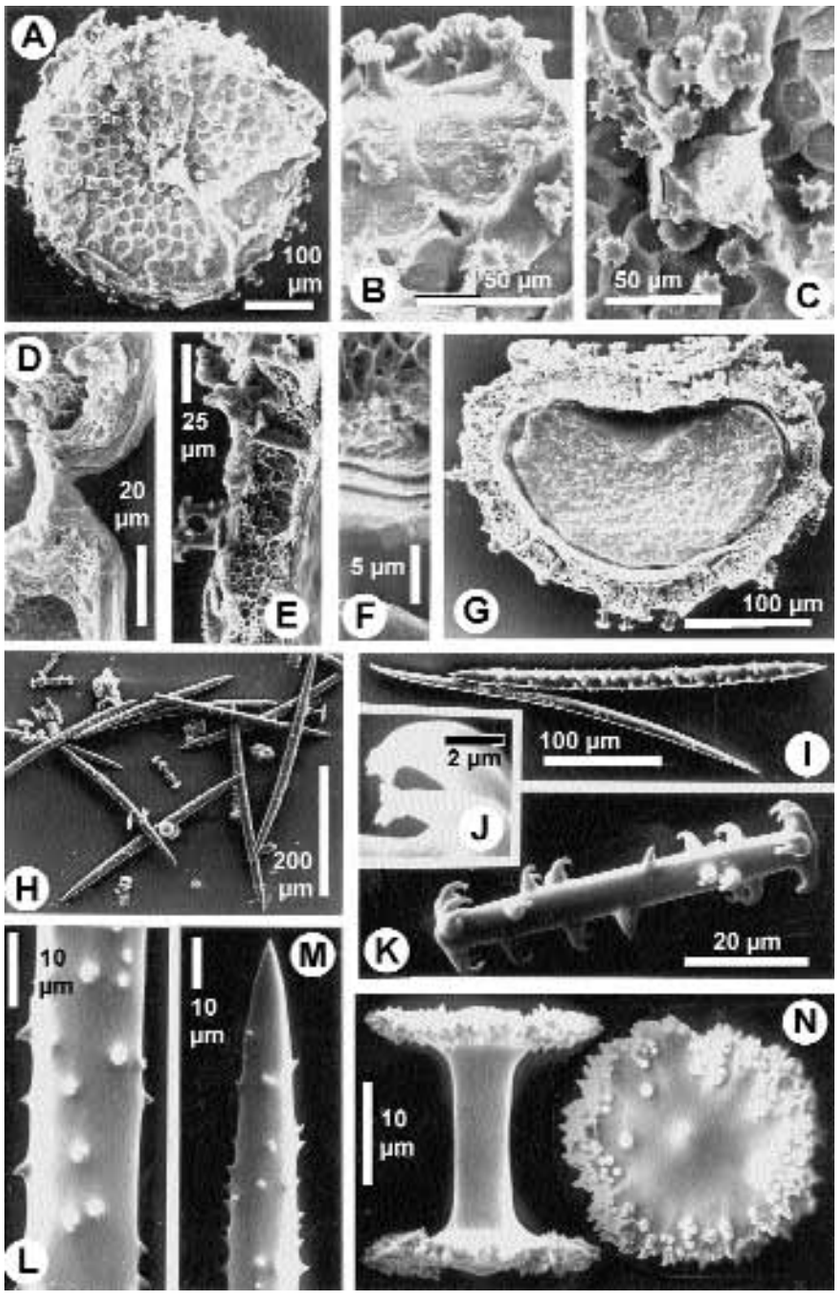

Fig. 58. *Racekiela ryderi*, spicules and gemmules, lectotype ANSP PO4536. A, gemmule *in toto*. B, gemmular surface. C, foramen. D, cross section of foramen. E, trilayered gemmular theca. F, multi-layered inner layer. G, cross section of gemmule. H, spicular complement of spiny oxeas and two types of gemmuloscleres. I, spiny megascleres. J, microspination of pseudo-birotule gemmulosclere. K, pseudo-birotule gemmulosclere. L, megasclere shaft. M, megasclere tip. N, birotule gemmuloscleres.

Type species

Spongilla sceptroides Haswell, 1882: 209 (by original designation; Penney & Racek, 1968).

Diagnosis

Spongillidae with encrusting growth form with occasional delicate cylindrical branches. Choanosomal skeleton paucispicular anisotropic with ill-defined secondary tracts. Megascleres are spined oxeas. Gemmules occur in the basal part of the sponge or are scattered. Gemmular theca tri-layered with gemmuloscleres radially embedded. Gemmuloscleres acanthostrongyles with tips bearing apical spines (oxeas ?).

Scope and distribution

Fourteen other species: *R. amazonensis* Volkmer-Ribeiro & Maciel 1983 (Neotropical region); *R. cantonensis* (Gee, 1929) (China); *R. cerebellata* (Bowerbank, 1863) (tropical and subtropical

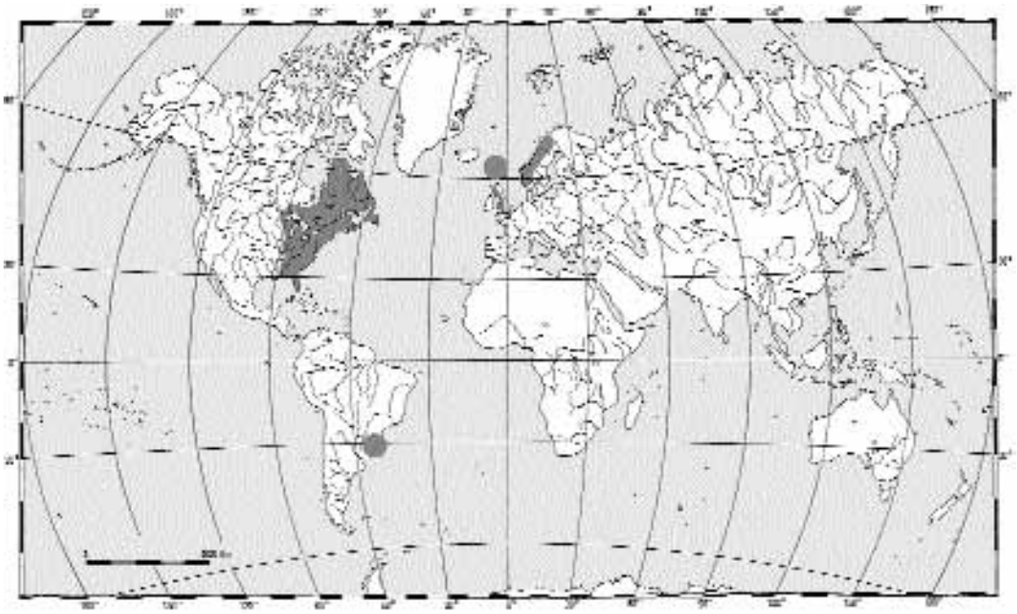

Fig. 59. Geographic distribution of the genus *Racekiela*.

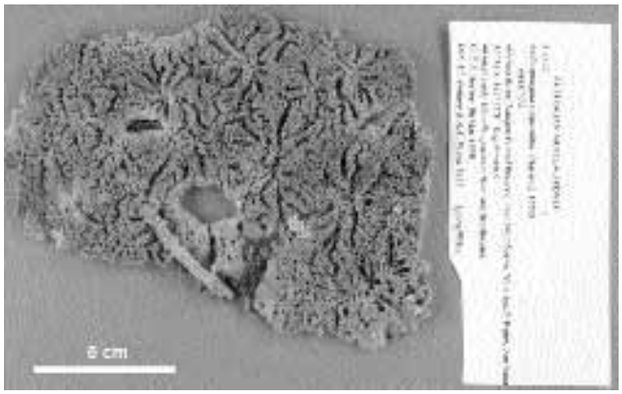

Fig. 60. *Radiospongilla sceptroides*, neotype AMS Z2837.

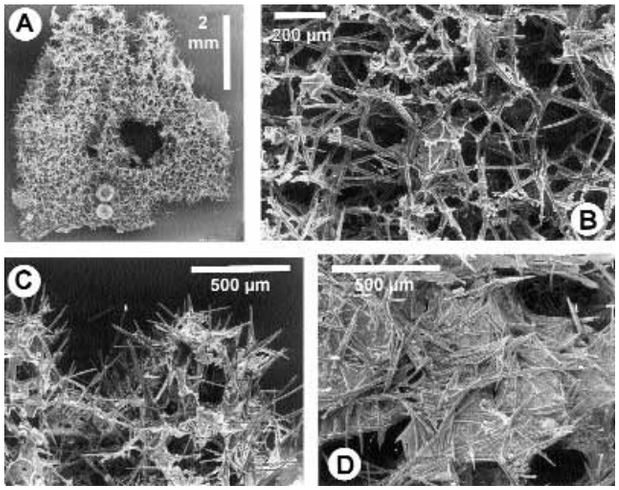

Fig. 61. *Radiospongilla sceptroides*, skeletal network, neotype AMS Z2837. A, cross section (top = surface). B, choanosomal network. C, ectosomal skeleton in irregular surface (lateral view). D, ectosomal skeleton in smooth surface (top view).

Africa, India-Pakistan, Indonesia, Philippines, New Guinea, China, Russia ?, SE Europe [possibly accidental introduction]); *R. cinerea* (Carter, 1849)(Bombay, Himalayas); *R. crateriformis* (Potts, 1882) (USA, Canada, Mexico, West Indies; Suriname, China, Japan, S Asia, Australia); *R. hemephydatia* (Annandale, 1909) (India, New Guinea, E Australia); *R. hispidula* (Racek, 1969) (Australia); *R. indica* (Annandale, 1907) (India, Indonesia, Philippines, New Guinea ?); *R. multispinifera* (Gee, 1933) (E Australia); *R. philippinensis* (Annandale, 1909c) (Philippines to N Australia); *R. sansibarica* (Weltner, 1895) (Zanzibar, N Rhodesia, Belgian Congo); *R. sinoica* (Racek, 1969) (Australia); *R. sendai* (Sasaki, 1936) (Japan); *R. hozawai* (Sasaki, 1936) (Japan). Nearctic, Palearctic, Neotropical, Afrotropical, Australian Oriental Regions.

Description of type species

Radiospongilla sceptroides (Haswell, 1882) (Figs 60–63).

Material examined. Neotype: AMS Z2837 – Merrika River, Nadgee Faunal Reserve near Womboyne (37°15′S, 149°55′E), New South Wales, Australia, on large rock, 0.5 m depth, F. Hersey, 6.iii.1958, det. Penney & Racek, 1968: 66. Other material. BMNH 1886.8.27.665, 13.III.C, Brisbane, Australia. BMNH 1886.8.27.658 – dry box 5, Kakalum River, Australia, Lendenfeld.

Description. Body shape consists of flat crusts or with thin finger-like projections. Consistency of live sponges is firm and elastic. Colour emerald green in life, grey-light brown in dry specimens. Oscules numerous with a system of radiating furrows in lotic habitats. Surface hispid. Dermal membrane well developed. Subdermal cavities not reported. Basal spongin plate not reported. Ectosome not evident. Choanosomal skeleton paucispicular, anisotropic, with ill-defined secondary tracts. Spongin scarce ? Megascleres fusiform slightly curved oxeas

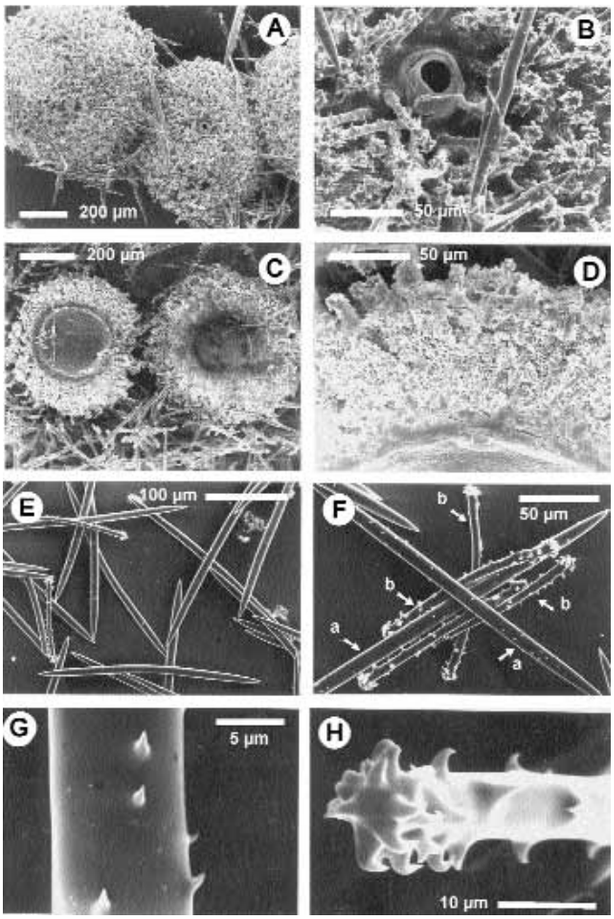

Fig. 62. *Radiospongilla sceptroides*, gemmules and spicules, neotype AMS Z2837. A, gemmules with skeletal megascleres. B, foramen. C, cross section of gemmules with radial gemmuloscleres. D, cross section of the theca with thick pneumatic layer. E, megascleres spiny oxeas and gemmuloscleres. Fa, megascleres. Fb, gemmuloscleres. G, close-up of the megasclere shaft. H, close-up of the gemmulosclere spiny tip.

(240–310 × 8–11 µm) with scattered minute spines except at their tips. Microscleres absent. Gemmules in the basal part of the sponge, subspherical (420–500 µm). Foramen tubular without collar. Gemmular theca tri-layered with gemmuloscleres radially embedded. Outer layer with protruding shafts and distal apices of gemmuloscleres. Pneumatic layer well developed with irregular chambers. Inner layer sublayered. Gemmuloscleres slender acanthostrongyles with tips bearing apical spines (oxeas?). Spines recurved and grouped at the tips to form a scepter-like shape.

Ecology. On wood or rocks. In lentic or lotic waters. Non-alkaline environments with a scattered distribution. Colour in life is due to specific pigments. Distribution: E Australia, New Zealand, New Guinea, New Caledonia.

SANIDASTRA VOLKMER-RIBEIRO & WATANABE, 1983

Synonymy

Sanidastra Volkmer-Ribeiro & Watanabe, 1983: 151.

Type species

Sanidastra yokotonensis Volkmer-Ribeiro & Watanabe, 1983: 151 (by monotypy).

Diagnosis

Spongillidae with encrusting to massive body shape. Choanosomal skeleton irregular with vague pauci- to multispicular tracts. Microscleres absent. Gemmular theca tri-layered. Gemmuloscleres oxeas irregularly radially embedded within the theca.

Scope and distribution

Monotypic. Japan, Sardinia and Corsica.

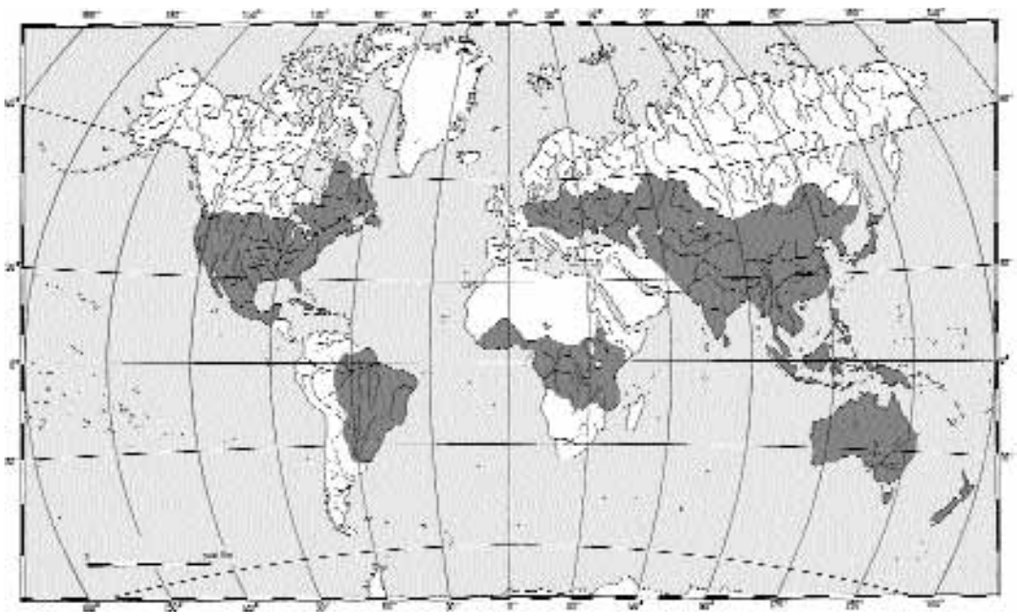

Fig. 63. Geographic distribution of the genus *Radiospongilla*.

Description of type species

Sanidastra yokotonensis Volkmer-Ribeiro & Watanabe, 1983 (Figs 64–67).

Material. Holotype: NSM PO4 – Yokotone-gawa Canal, Nakajima, Azura-mura, Ibaragi, Japan. Other material. DTRG FW156 – Gravona River tributary near Aiaccio, Corsica, 23.iv.1987.

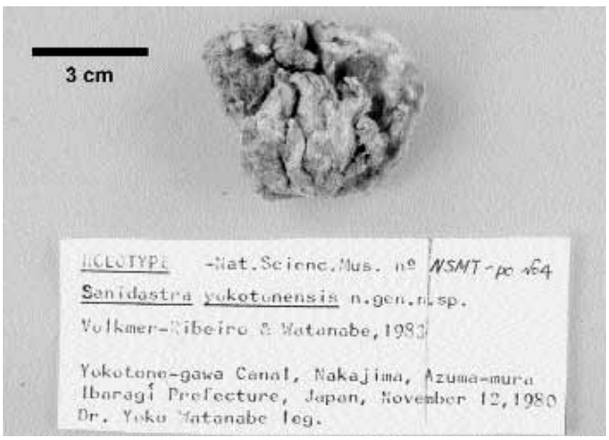

Fig. 64. *Sanidastra yokotonensis*, holotype NSM PO4.

DTRG FW179 – Rio Su Lernu, Sardinia 18.vii.1987. DTRG FW 217 – Gravona River tributary, near Aiaccio, Corsica, 9.viii.1987.

Description. Body shape (5 × 4–5 cm) encrusting with flabellate surface. Colour greenish-yellow to light brown in life. Consistency soft delicate compressible in life. Surface slightly irregular and hispid due to emerging brushes of spicules. Small and scattered oscules. Dermal membrane conspicuous and spicular. Dermal cavities not observed. Ectosomal skeleton as spicules in the dermal membrane. Choanosomal skeleton irregular, vague, pauci- to multispicular tracts, with long axial fibres in flabellate expansions. Megascleres oxeas (190–320 × 8.5–15 μm) ranging from smooth to spiny with microspines notably variable in size and density. Tips, in most cases, sharply pointed, rarely blunt or angulate. Microscleres absent. Gemmules, scattered singly or grouped, subspherical (368–514 μm). Foramen is a short tube (20 μm in diameter), simple without collar. Gemmular theca tri-layered. Outer layer with irregular surface and emerging apices of gemmuloscleres. Pneumatic layer (20–30 μm thick) with irregular chambers. Inner layer multilayered. Gemmuloscleres are irregularly radially embedded within the theca. Gemmuloscleres oxeas (38.5–65.5 × 5.5–9 μm), with 2–9 rays, show tips ranging from rounded to pointed to tricuspidate.

Ecology. In coastal areas of canals and courses in freshwaters from perennial to ephemeral, under stones, associated to *Ephydatia fluviatilis*. Distribution: highly disjunct, from Japan to Mediterranean (Corsica and Sardinia).

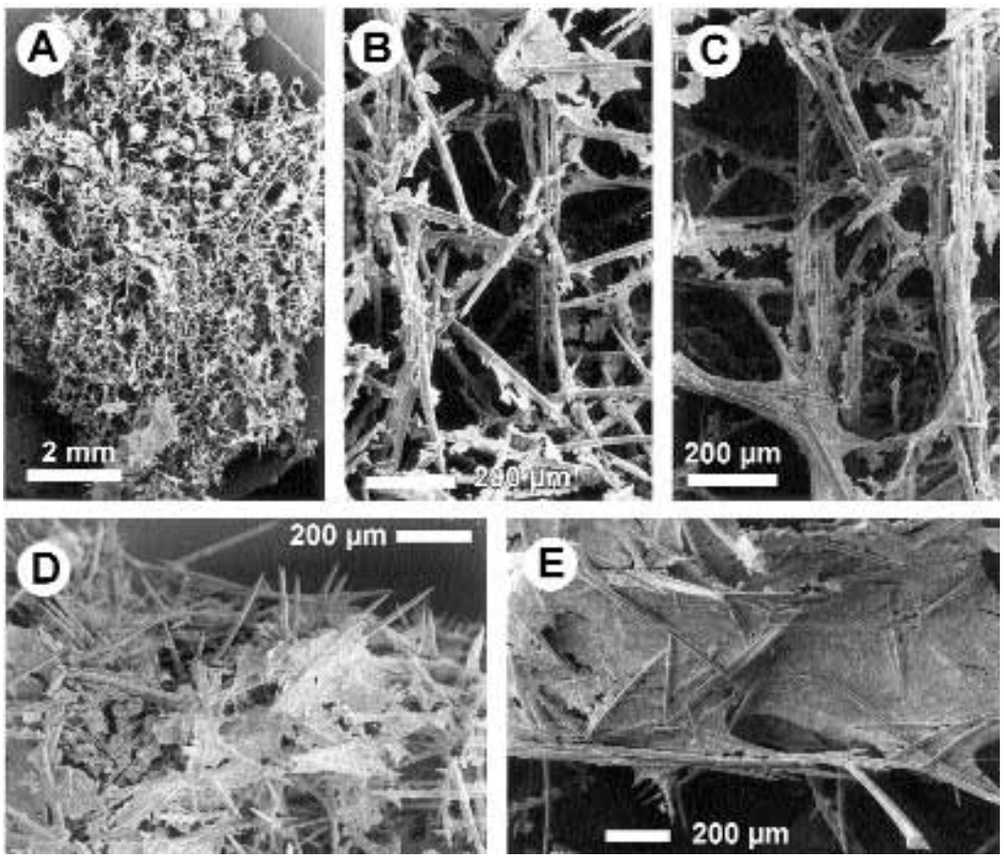

Fig. 65. *Sanidastra yokotonensis*, skeletal network, holotype NSM PO-4. A, cross section through a small digit (sponge surface=all the perimeter). B–C, choanosomal skeleton network. D, ectosomal skeleton of an irregular surface (lateral view). E, ectosomal skeleton of a relatively smooth surface.

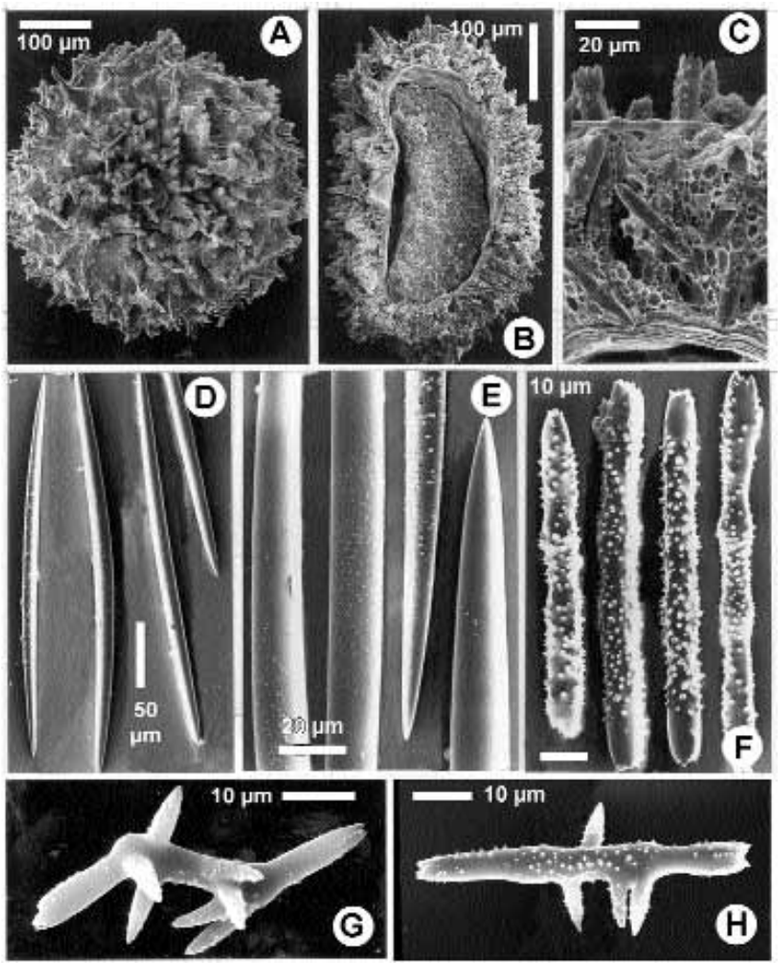

Fig. 66. *Sanidastra yokotonensis*, gemmules and spicules. A–F, holotype NSM PO-4. G–H, DTRG-FW179 (ex-IZUG). A, gemmule with foramen. B, cross section of gemmule with foramen on the left (middle). C, trilayered theca with sublayered inner layer (bottom). D–E, megascleres spiny and smooth oxeas. F–H, gemmuloscleres.

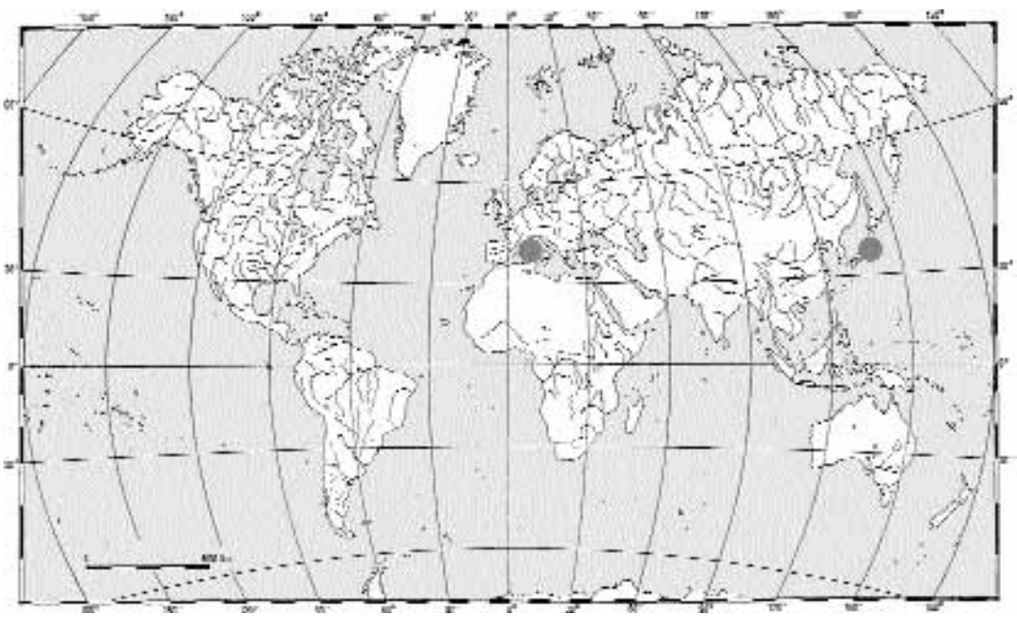

Fig. 67. Geographic distribution of the genus *Sanidastra*.

Remarks. Volkmer-Ribeiro & Watanabe (1983) included *S. yokotonensis* in the family Latrunculiidae, order Poecilosclerida, on the basis of several similarities with hadromerids, such as skeletal subtylostyles and sanidasters as gemmuloscleres. However, re-analysis of skeletal elements showed that spicules were represented only by smooth and spiny oxeas, rarely modified into "freak oxeas with one blunt or angulate tip", and none of them could be defined as substrongyles or tornotes. Regarding gemmuloscleres, a comparison between sanidasters of hadromerids and gemmuloscleres of *S. yokotonensis* indicates that they are clearly not homologous. The typical radial arrangement of gemmuloscleres in the theca of *S. yokotonensis* seems to be allied to the *Radiospongilla* 'group' and fossil Palaeospongillidae Volkmer-Ribeiro & Reitner (1991b).

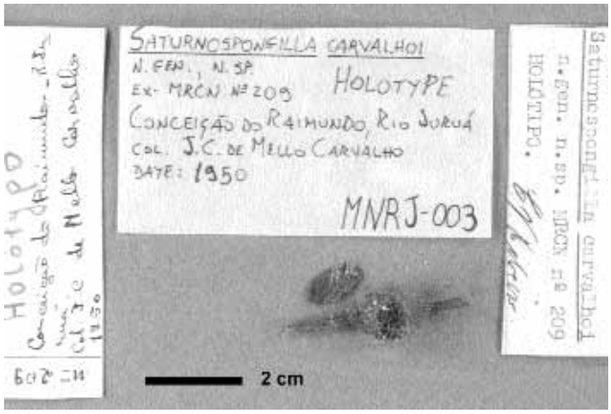

Fig. 68. *Saturnospongilla carvalhoi*, holotype (FZRG) MNRJ-003.

SATURNOSPONGILLA VOLKMER-RIBEIRO, 1976

Synonymy

Saturnospongilla Volkmer-Ribeiro, 1976: 271.

Type species

Saturnospongilla carvalhoi Volkmer-Ribeiro, 1976: 271 (by monotypy).

Diagnosis

Spongillidae with bush-like growth form. Consistency extremely delicate. Ectosomal skeleton occurs as a dense structure on the apex of primary fibres at the surface. Choanosomal skeleton is a loose anisotropic paucispicular reticulation with primary fibres diverging in tufts and becoming more dense towards the sponge surface and with irregular secondary tracts. Spongin very sparse. Megascleres oxeas. Microscleres absent. Gemmules scattered at the sponge base. Saturnian-shaped gemmules with a ring-like pneumatic layer. Pseudo-cage of acanthoxeas exclusively at the ring surface. Gemmular theca of compact spongin. Gemmuloscleres birotules.

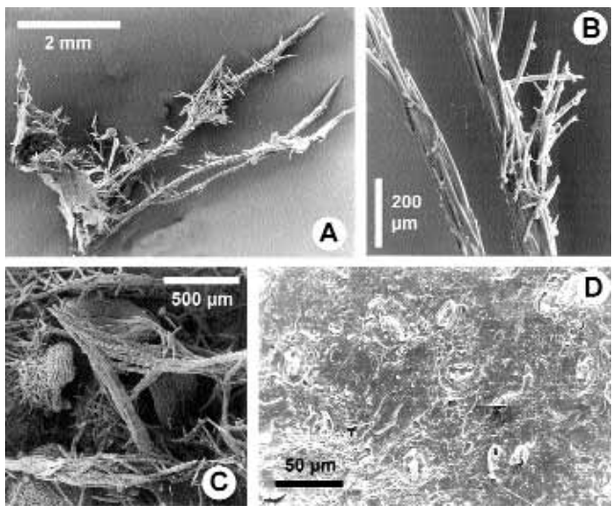

Fig. 69. *Saturnospongilla carvalhoi*, skeletal network, holotype MNRJ-003. A, skeletal fragment with spicular fibres arising from the basal spongin plate. B, multispicular fibres. C, choanosomal skeleton trapping gemmules. D, spongin basal plate.

Scope and distribution

Monotypic. River Juruà.

Description of type species

Saturnospongilla carvalhoi Volkmer-Ribeiro, 1976 (Figs 68–71).

Material examined. Holotype: MNRJ 003 (ex-MRCN 209) – Conceicao do Raimundo, middle Rio Juruà, Brazil, J.C. de Mello Carvalho, 25.vi.1950. Other material. FZRG MRCN107 – Rio Juruà, J.C. de Mello Carvalho.

Description. Body shape bush-like, from hemispherical to spherical (0.2–2.5 cm). Brownish-yellow colour. Consistency extremely delicate, fragile. Oscules inconspicuous. Surface hispid due to emerging tufts of spicules from the conspicuous dermal membrane. Subdermal cavities not observed. Basal spongin plate conspicuous and thin. Ectosomal skeleton is formed by the densely arranged apices of the primary fibres. Choanosomal skeleton is loosely anisotropic, paucispicular, with primary fibres diverging in tufts and becoming more dense towards the sponge surface, and with irregular secondary tracts. Spongin very sparse. Megascleres (215–399.5 × 8.3–25 µm) of the skeleton range from smooth, slender to almost stout, straight to slightly curved abruptly pointed oxeas. Acanthoxeas (123–296 × 6.6–15 µm) of the gemmular pseudo-cage are curved and sharply pointed, with central conical large spines curved and more dense towards the tips. Microscleres absent. Gemmules abundant at the sponge base. Gemmules (541–824.6 µm) with concave-convex profile with foramen bearing a short porus tube at the middle inferior concavity. Gemmules saturnian-shaped with a ring (thoroid) surrounding the central subspherical theca. Tangential acanthoxeas at the ring surface represent a pseudo-cage. The ring is covered by an outer layer chambered spongin, representing a pneumatic layer, shifted from its usual position. Gemmular theca with gemmuloscleres radially embedded in the inner layer of compact sublayered spongin. Gemmuloscleres (10–33 × 3.3–5 µm) stout birotules with smooth shaft. Rotules (13.3–16.6 µm) with recurved circular entire margins and central umbone, proximal rotule flat, distal rotule cup-shaped.

Ecology. This species was reported as dominant in freshwater sponge communities from the middle Rio Juruà, associated with

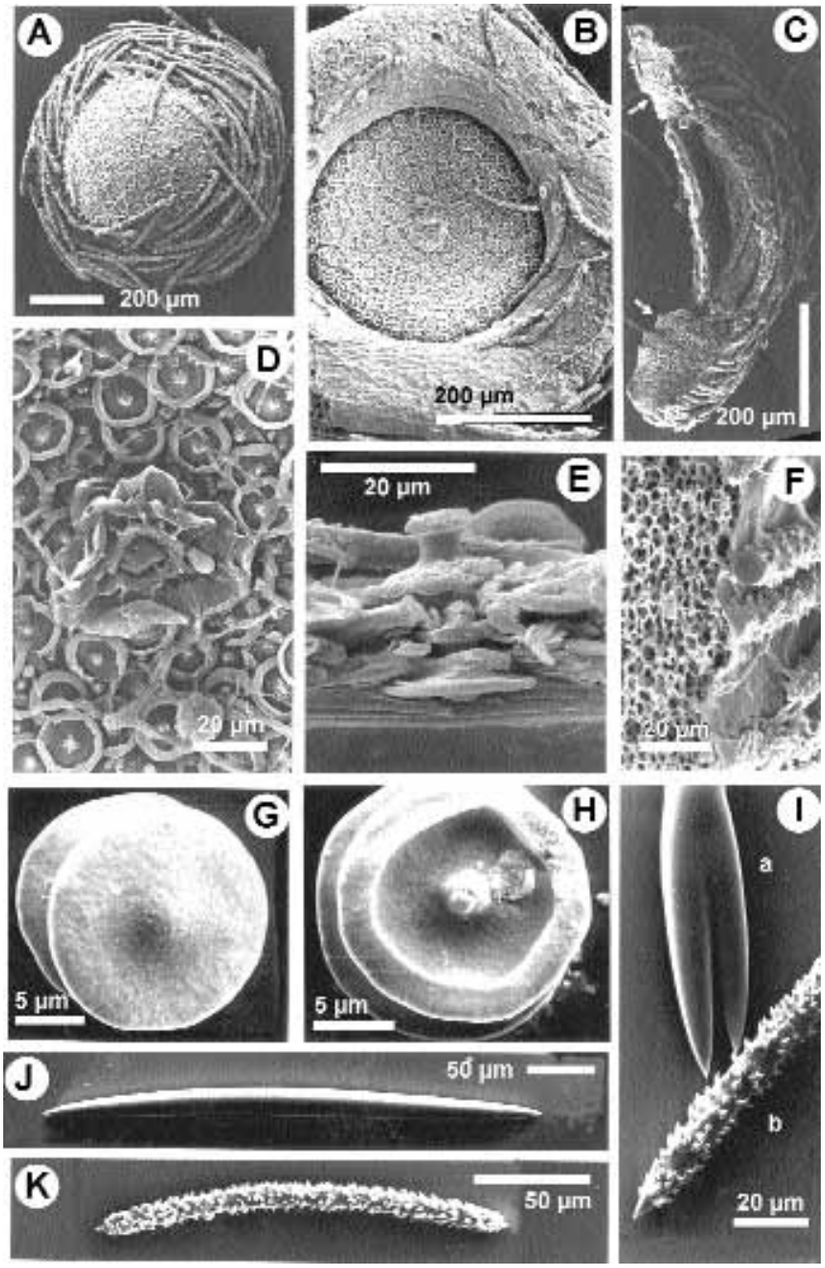

Fig. 70. *Saturnospongilla carvalhoi*, gemmules and spicules, holotype MNRJ-003. A, gemmule from a top view. B, gemmule from a bottom view with foramen in the middle (see also D). C, cross section of gemmule (arrows indicate the thoroidal pneumatic layer). D, foraminal area. E, cross section of the theca lacking outer and pneumatic layer (see C in the middle area not shown by arrows). F, pneumatic layer (left) and surface (right) of the ring with megascleres of the pseudo-cage (see C top and bottom shown by arrows). G–H, gemmulosclere. J, megascleres (smooth oxeas). Ia, monstrous tip of megasclere. Ib, K, spiny oxea of the pseudo-cage around the ring.

Acalle recurvata (Carvalho, 1955; Volkmer-Ribeiro & De Rosa-Barbosa, 1972). Sponges settled on leaves or small branches periodically reached by flooding waters. Body shape varied according to the substrate, ranging from hemispherical on flat surfaces to spherical around tiny branches. Distribution. River Juruà.

Remarks. The peculiar architecture of the gemmules, unique to this genus, seems to be linked to a displacement of the usual gemmular layers during gemmulogenesis. Volkmer-Ribeiro (1976) considers the genus closely related to *Trochospongilla* and particularly to *T. minuta* (Potts, 1881a) and *T. delicata* Bonetto & Ezcurra de Drago, 1967.

STRATOSPONGILLA ANNANDALE, 1909

Synonymy

Spongilla (*Stratospongilla*) Annandale, 1909b: 561. *Stratospongilla* Penney & Racek 1968: 40.

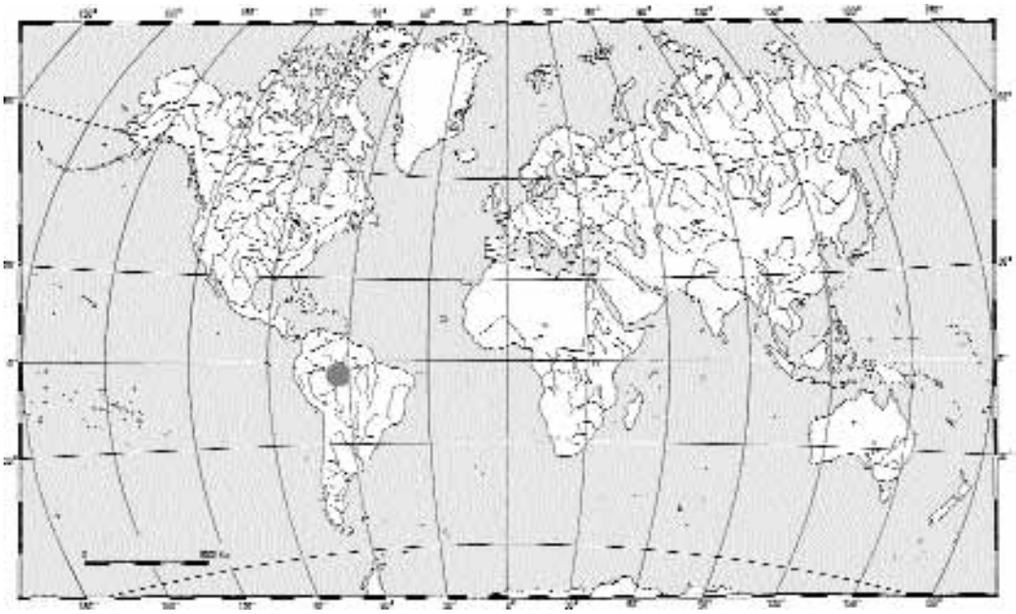

Fig. 71. Geographic distribution of the genus *Saturnospongilla*.

Type species

Spongilla bombayensis Carter, 1882: 369 (by original designation).

Diagnosis

Spongillidae with hard to moderately hard consistency. Choanosomal skeleton vaguely reticulate. Megascleres stout oxeas, smooth or microspined. Microscleres absent. Gemmules strictly adherent to the substratum. Gemmular theca tri-layered. Outer gemmular coat of compact spongin with strongyles tangentially arranged. Pneumatic layer not well defined, appearing as an empty space with thin trabecules of spongin within gemmuloscleres, which consist of spined oxeas radially arranged.

Scope and distribution

Five other species: *S. sumatrana* (Weber, 1890) (Indonesia, India, Africa); *S. indica* (Annandale, 1908a) (Thailand, India, Africa); *S. gravelyi* (Annandale, 1912) (India); *S. clementis* (Annandale, 1909c) (Philippines, China, Japan, tropical W Africa); *S. lanei* (?) Racek, 1969 (Australia); *S. akanensis* (Sasaki, 1970) (Japan). Restricted to the tropical areas of Oriental, Afrotropical and Australian (?) Regions.

Description of type species

Stratospongilla bombayensis (Carter, 1882) (Figs 72–75).

Material examined. Holotype: BMNH 1881.11.29.3 – box 2 dry, small fragment. Other material. BMNH 1882.11.29.3 – Bombay, on a stick associated with *Eunapius carteri* and *Spongilla alba*.

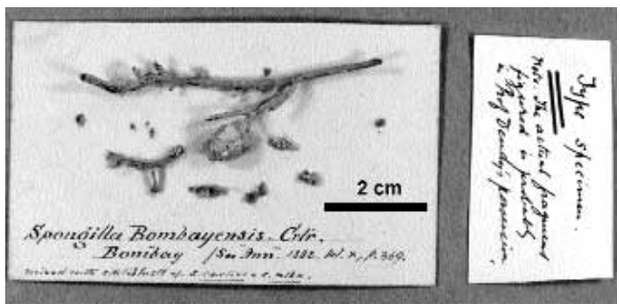

Fig. 72. *Stratospongilla bombayensis*, type specimen BMNH 1882.11.29.3.

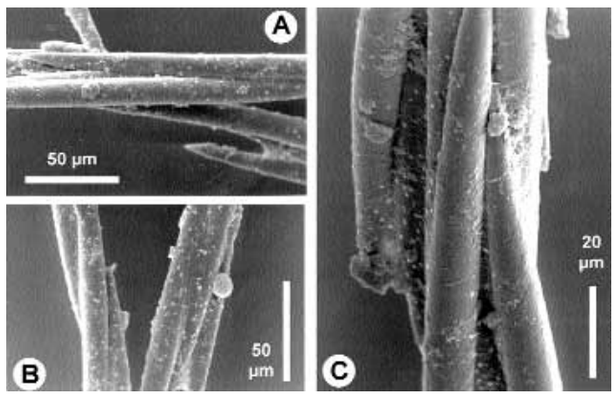

Fig. 73. *Stratospongilla bombayensis*, type specimen BMNH 1882.11. 29.3. A–C, spicular tracts of skeletal remains of the type.

Description. Encrusting with irregular surface. Colour ? Consistency moderately hard but brittle. Oscules inconspicuous. Dermal membrane supported by abundant spicules. Subdermal cavities small. Ectosomal skeleton is a vague reticulation of

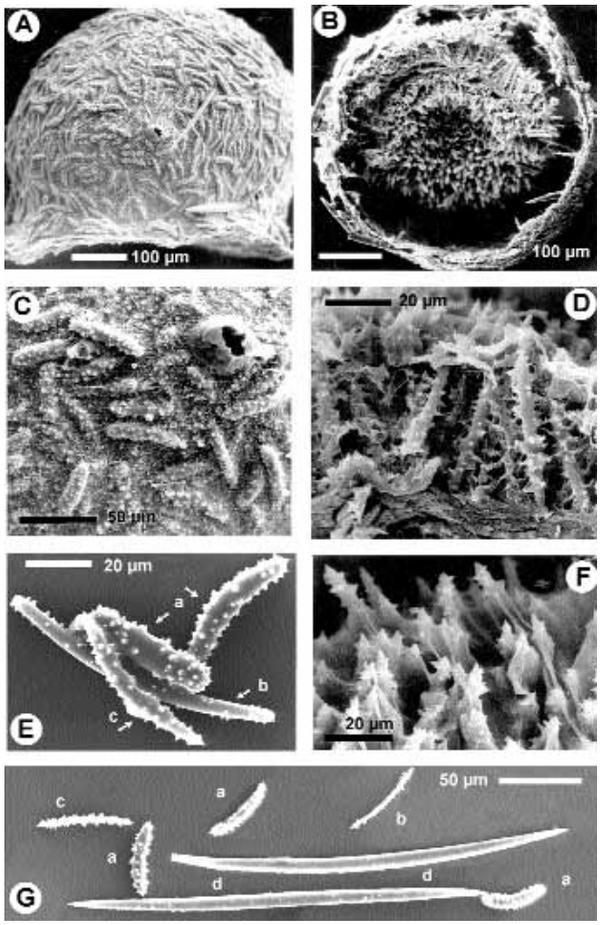

Fig. 74. *Stratospongilla bombayensis*, spicules and gemmules, type specimen BMNH 1882.11.29.3. A, outer gemmular theca with foramen (C). B, cross section of gemmular theca (D). Ea, gemmuloscleres from the outer layer. Eb, Ec, gemmuloscleres of the radial layer. F, surface of the radial gemmular layer. Ga, gemmuloscleres from the outer layer. Gb, Gc, gemmuloscleres of the radial gemmular layer. Gd, megascleres spiny oxeas.

horizontal spicules immediately below the dermal membrane. Choanosomal skeleton with vertical spicular fibres. Very sparse spongin. Megascleres (220–300 × 12–17 µm) slender, ranging from straight to feebly curved oxeas, from finely and irregularly spined to smooth. Microscleres absent. Gemmules singular, variable in size, spherical to ovoid, generally flattened at base, firmly adhered to the basal spongin plate. Foramen (1 or more) tube-like on lateral side. Gemmular theca tri-layered. Outer layer of compact spongin with tangential gemmuloscleres. Pneumatic layer not well defined appearing as an empty space with thin trabecules of spongin between radially arranged oxeote gemmuloscleres. Inner layer multilayered. Gemmuloscleres of two types: strongyles (34–44 × 4.6–8 µm) stout, short and spined, tangentially embedded in the outer layer; oxeas (60–2.5 µm) spined and abruptly pointed, radially arranged between the inner and outer layer.

Ecology. Reported as dense populations adhering to the lower surface of stones. In shallow standing waters subjected to dessication where sponges remain as carpets of gemmules. Gemmules are produced between July and October. Growth notably slow. Distribution: W India (Bombay), South Africa (Natal).

Remarks. Penney & Racek (1968) promoted the subgenus *Stratospongilla* (Annandale, 1909b) to genus status. Microscleres, reported in the vicinity of gemmules in the original description of Carter (1882), and considered up until now to be true microscleres, are demonstrated here to be true gemmuloscleres through SEM, being exclusively present within the gemmular theca having a radial arrangement. *Stratospongilla rousseletii* (Kirkpatrick, 1906) and *S. schubotzi* Weltner, 1913 from South Africa, and *S. gilsoni* (Topsent, 1912) from Fiji were moved to *Oncosclera* by Volkmer-Ribeiro (1970).

TROCHOSPONGILLA VEJDOVSKY, 1883

Synonymy

Trochospongilla Vejdovsky, 1883: 31.

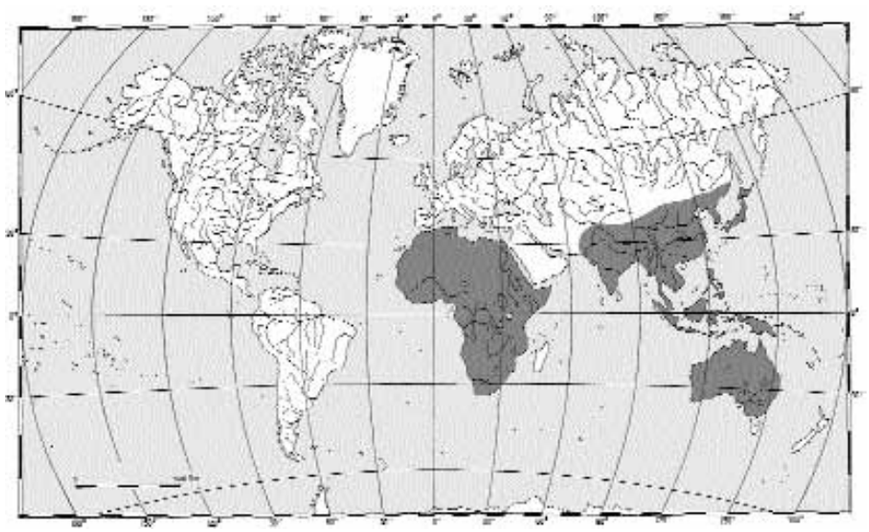

Fig. 75. Geographic distribution of the genus *Stratospongilla*.

Type species

Spongilla erinaceus Lieberkühn, 1856: 496 (by original designation), an unavailable name, replaced by *Trochospongilla horrida* Weltner, 1893: 12.

Diagnosis

Spongillidae with encrusting growth form. Consistency fragile to moderately hard. Ectosomal skeleton with spicules in the dermal membrane. Choanosomal skeleton anisotropic, pauci- or multispicular fibres, more dense at the sponge base. Variable amount of spongin. Megascleres acanthoxeas. Microscleres absent. Gemmules grouped in carpets or singly at the sponge base. Gemmules spherical, enveloped in single or multi-gemmular pneumatic pseudo-cage, armoured by acanthoxea megascleres. Foramen present. Gemmular theca monolayered consisting of compact spongin with radial gemmuloscleres. Gemmuloscleres birotules with a short stout smooth shaft and circular rotules.

Scope and distribution

Eight other species: *T. leidii* (Bowerbank, 1863) (E USA, one locality); *T. paulula* (Bowerbank, 1863) (River Amazon); *T. pennsylvanica* (Potts, 1882) (N America, Ireland ?, Scotland ?); *T. latouchiana* Annandale, 1907 (India, China, SE Australia); *T. philottiana* Annandale, 1907 (tropical Asia: India, S China, Philippines, Africa ?); *T. minuta* (Potts, 1881a) (Argentina, Bolivia, E Brazil); *T. delicata* Bonetto & De Drago, 1967 (Argentina, Brazil); *T. petrophila* Racek, 1969 (E Australia). Palaearctic, Nearctic, Neotropical, Australian and Afrotropical ? Regions.

Description of type species

Trochospongilla horrida (Weltner, 1893) (Figs 76–79).

Material examined. Probable holotype: ZMB5091 – Wellensee Lake, viii.1898, det. Weltner. Other material. ZMB5093 – Spandau Havel, 24.vii.1906, on wood with bivalves. DTRG FW4 – Caorso, Po River, 20.vii.1984, Chiappafreddo. DTRG FW122 – Lago Maggiore, Pallanza, 5.viii.1970, I. De Drago.

Fig. 76. *Trochospongilla horrida*, specimen ZMB 5093. Sponge is encrusting on a woody substratum shared with some small bivalves.

Description. Body shape encrusting. Surface flat, hispid. Consistency fragile to moderately hard. Colour light yellow to dark brown. Dermal membrane spicular. Subdermal cavities undetected. Ectosomal skeleton consists of spicules in the dermal membrane. Choanosomal skeleton anisotropic, pauci- or multispicular fibres and tracts more dense at the sponge base. Variable amount of spongin. Megascleres (170–235 × 11–15 μm) straight to feebly curved fusiform oxeas covered with stout and sharp spines. Microscleres absent. Gemmules in the basal part of the sponge grouped in carpets or singly. Gemmules spherical (475–540 μm) enveloped in a single or multi-gemmular pneumatic pseudo-cage armoured by acanthoxeas. Foramen conical with collar. Gemmular theca monolayered. Outer layer and pneumatic layer absent. Inner layer well developed sublayered with radially embedded gemmuloscleres in one or two layers with overlapping proximal rotules. Gemmuloscleres are birotules with a short stout smooth shaft and circular rotules.

Ecology. Substrata from plants to rocks. Sponges of this genus display a fast growth rate, overgrowing other associated species. Hibernating life cycle. Distribution. Discontinuous in the Northern Hemisphere, in cold-temperate regions.

UMBOROTULA PENNEY & RACEK, 1968

Synonymy

Umborotula Penney & Racek, 1968: 121.

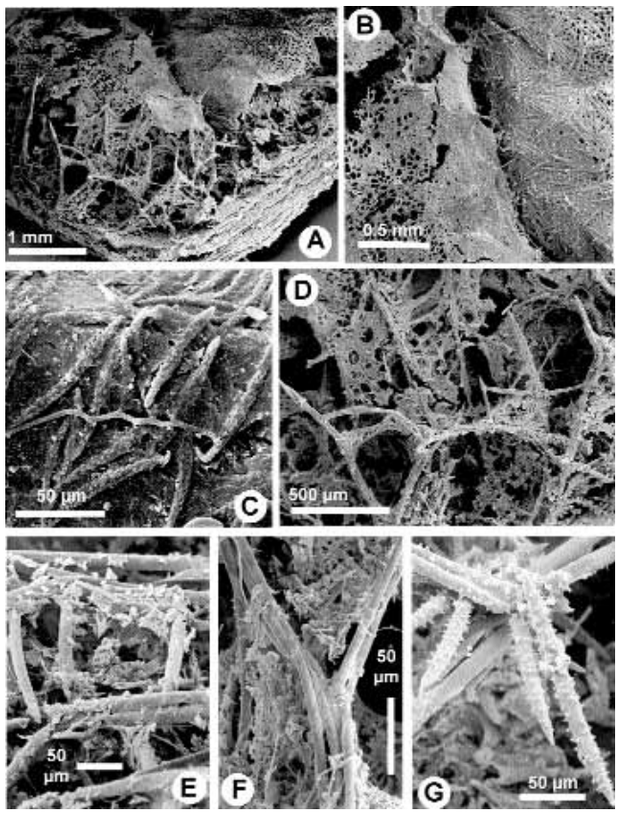

Fig. 77. *Trochospongilla horrida*, skeletal network of ZMB 5093. A, sponge fragment on a woody substrate. B, sponge surface, probably in an area of contact between different specimen. C, surface close-up. D–G, close-up views of the choanosomal skeleton.

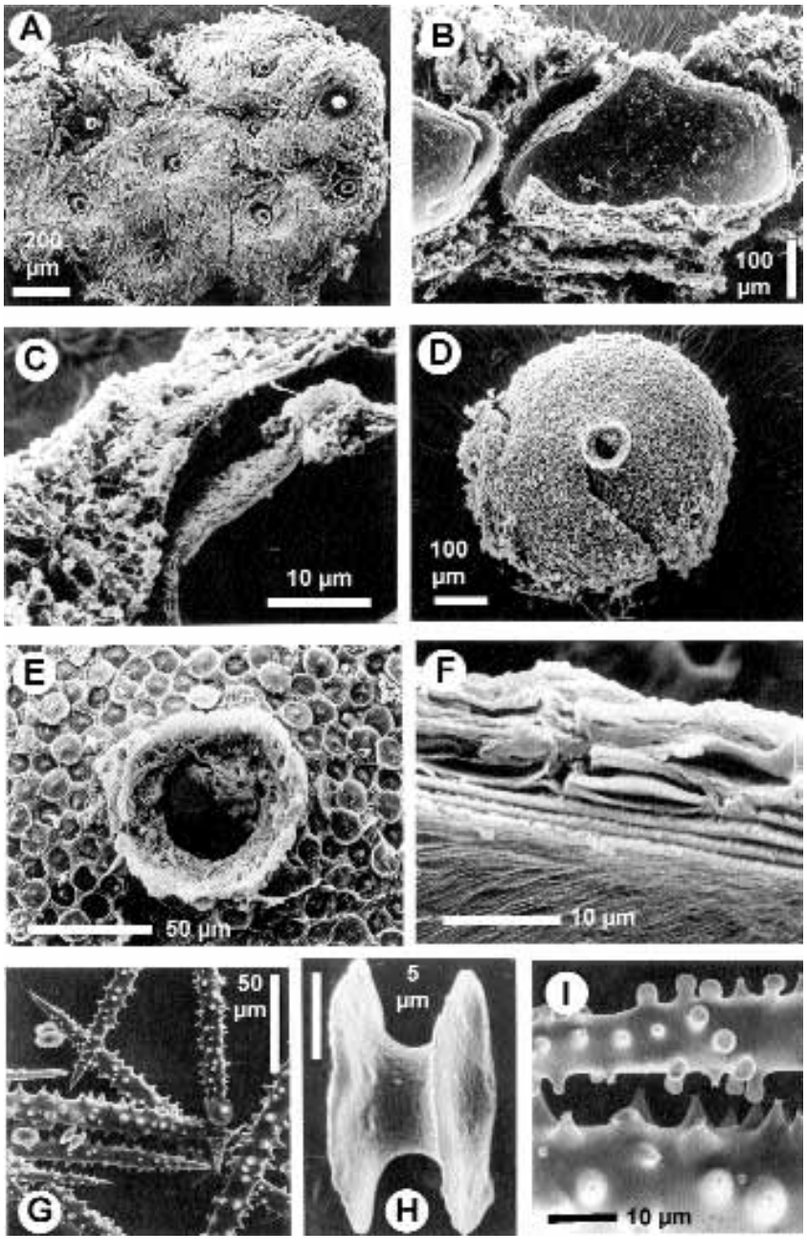

Fig. 78. *Trochospongilla horrida*, gemmules and spicules, specimen ZMB 5091. A, group of gemmules trapped in a common cage. B–C, cross section of gemmule showing that the pneumatic layer is a character of the cage and not of gemmular theca. D, gemmule *in toto*. E, foramen. F, gemmular theca (bottom = sublayered inner layer). G, megascleres (gemmuloscleres are also present). H, gemmulosclere. I, spines of megasclere shaft, rounded terminations are considered as monstrosities.

Type species

Ephydatia bogorensis Weber, 1890: 33 (by original designation).

Diagnosis

Spongillidae with small encrusting growth form. Choanosomal skeleton anisotropic, paucispicular. Megascleres oxeas. Microscleres absent. Gemmuloscleres birotules. Gemmules scattered. Gemmular theca tri-layered. Pneumatic layers of compact spongin trabecules, with no chambers.

Scope and distribution

Monotypic, SE Asia to E Australia.

Description of type species

Umborotula bogorensis (Weber, 1890) (Figs 80–83).

Material examined. Holotype: ZMA – 6 slides, Buitenzorg, 1889, det. M. Weber. Other material. BMNH 1901.10.22.1–2 – *Ephydatia bogorensis* var. *blembingia* Evans, 1901, Blembing, Blembing River, peninsular Thailand, 23.vii.1899.

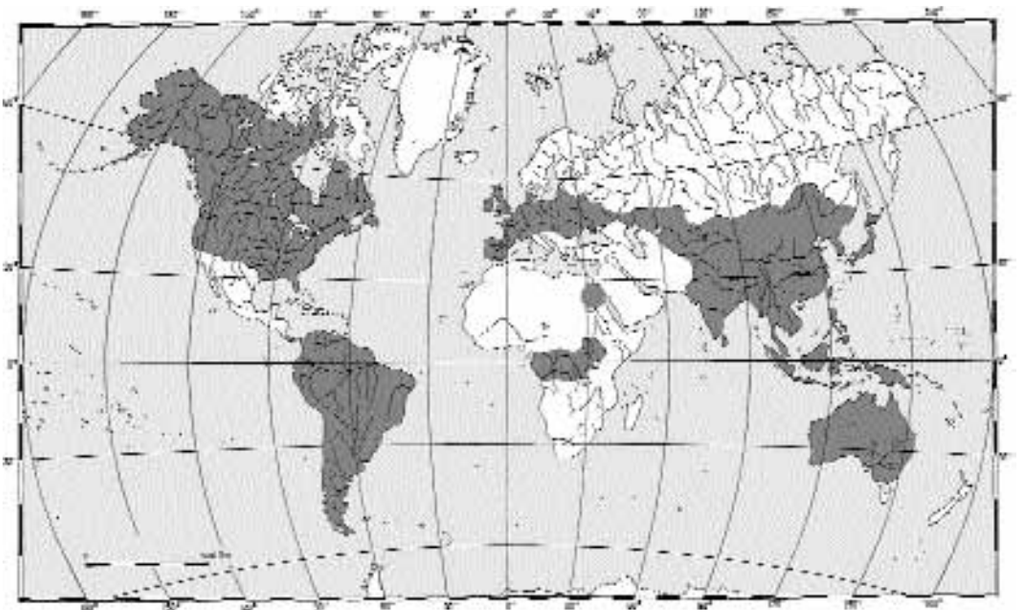

Fig. 79. Geographic distribution of the genus *Trochospongilla*.

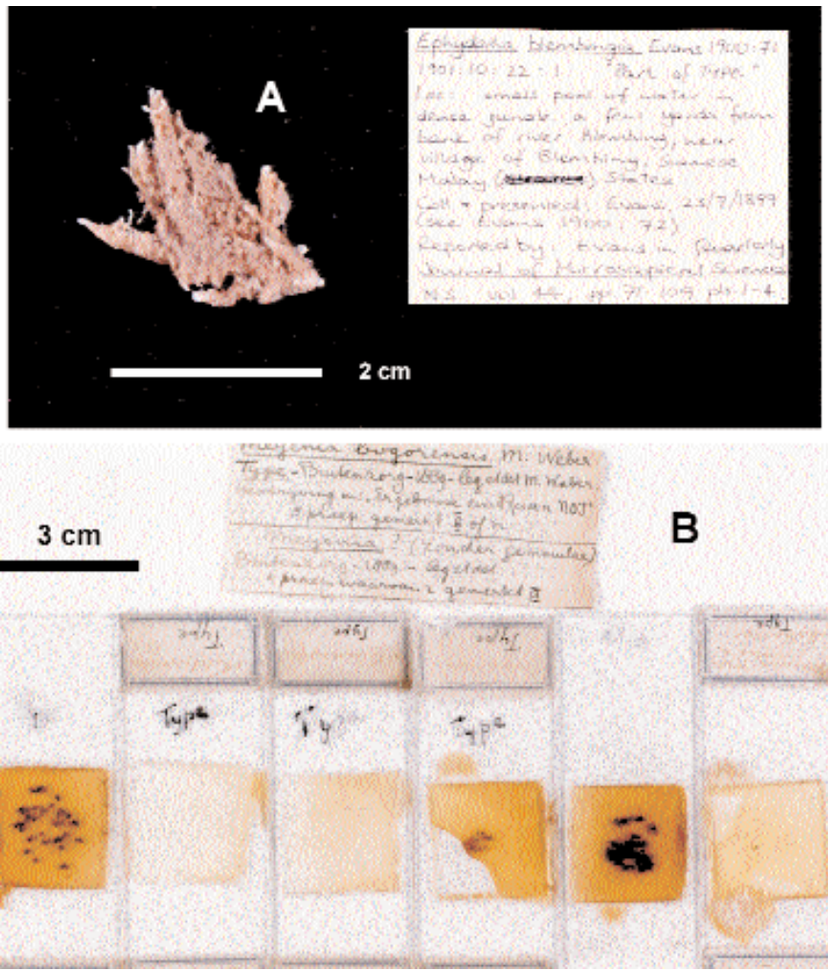

Fig. 80. A, part of the type of *Ephydatia blembingia* = *Umborotula bogorensis*, the Natural History Museum of London; catalogue: 1901:10:22:1. B, six slides are the remains of the type material of *Umborotula bogorensis* preserved in ZMA; catalogue: unregistered.

Description. Shape circular or irregular small crusts (2–3 cm) on aquatic plants. Colour light brown to dark green. Consistency soft, texture loose. Oscules inconspicuous. Surface slightly hispid due to tufts of spicules. Dermal membrane developed. Oscula inconspicuous. Ectosomal skeleton consists of spicules tufts. Choanosomal skeleton paucispicular, anisotropic, large reticulation with slender horizontal fibres branching freely in the sponge and stout transverse irregular fibres, ill-defined. Spongin sparse. Megascleres slender sharply pointed oxeas ranging from microspined to rarely smooth (200–330 × 8–16 μm). Microscleres absent. Gemmules spherical (450–600 μm) not abundant and scattered in the sponge. Foramen tubular without a true collar, in a depression surrounded by a thickening of the gemmular wall. Gemmular theca tri-layered. Outer layer not well developed and distal rotules of gemmuloscleres are evident. Pneumatic layer of

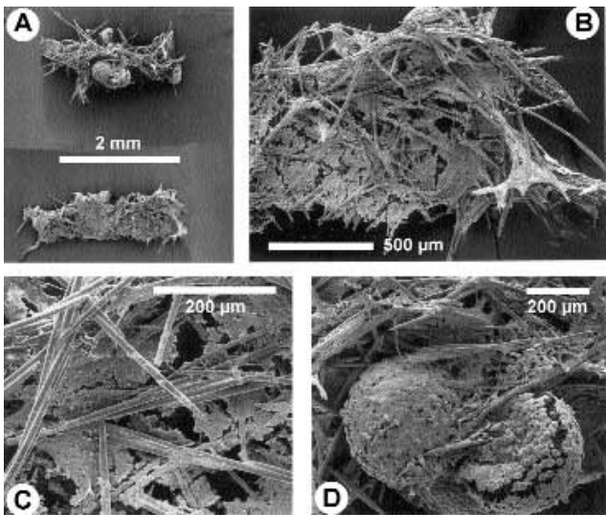

Fig. 81. *Umborotula bogorensis* (pro *Ephydatia blembingia*), skeletal network, BMNH 1901.10.22.1. A, sponge fragments. B–C, skeletal network close-up. D, skeleton with gemmules.

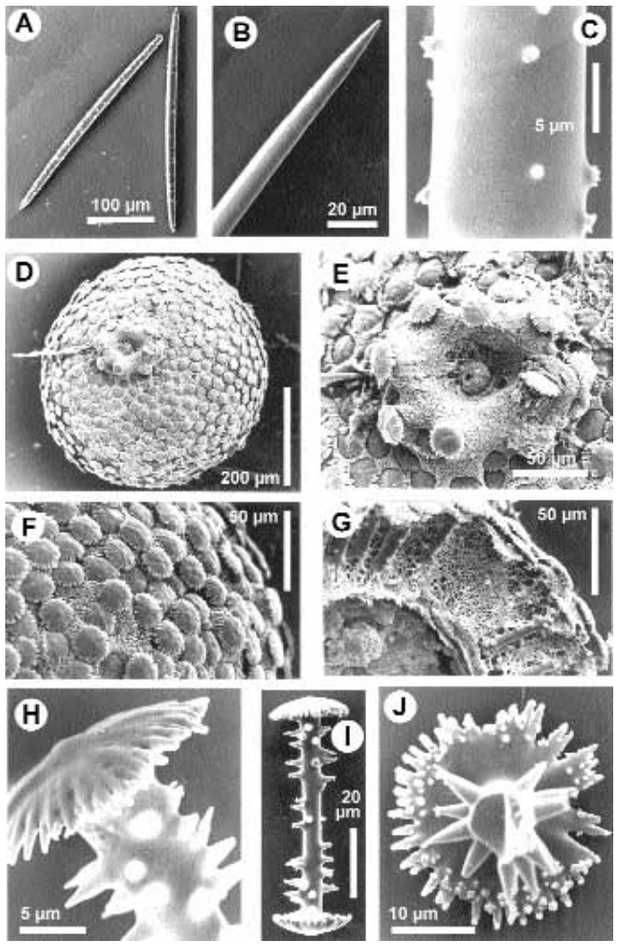

Fig. 82. *Umborotula bogorensis* (pro *Ephydatia blembingia*), gemmules and spicules, BMNH 1901.10.22.1. A, C, spiny megascleres. B, smooth megasclere. D, gemmule. E, foraminal area. F, gemmular outer layer surface with emerging distal rotule of gemmuloscleres. G, trilayered gemmular theca with radial birotules gemmuloscleres. H–J, gemmuloscleres.

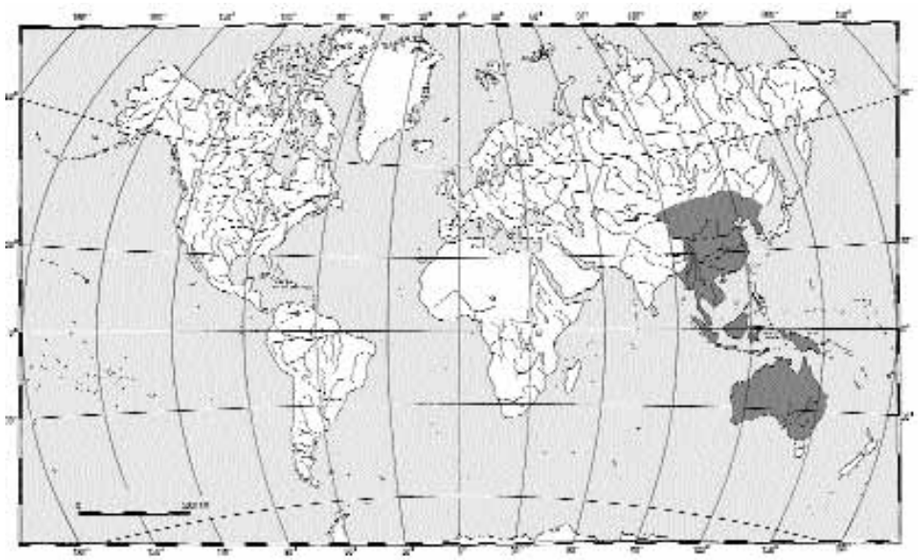

Fig. 83. Geographic distribution of the genus *Umborotula*.

anastomosing trabecules of compact spongin without chambers. Inner layer multilayered. Gemmuloscleres radially embedded in the pneumatic layer, with umbrella-shaped rotules in contact with the inner and outer layer. Gemmuloscleres birotules with spiny shaft (62–82 × 5–8 μm). Rotules (22–27 μm) with distal surface convex and proximal concave, incised margins sometimes with recurved spines.

Ecology. Creeping over branched vegetable supports, or on undersides of floating leaves. Distribution: Malaysia, Java, Makassar, Sulawesi, Thailand, China (Soochow), E Australia.

URUGUAYELLA BONETTO & EZCURRA DE DRAGO, 1969

Synonymy

Uruguayella Bonetto & Ezcurra de Drago, 1969: 356.

Type species

Uruguaya repens Hinde, 1888: 2 (by original designation).

Diagnosis

Spongillidae with encrusting body shape. Choanosomal skeleton alveolate with paucispicular tracts. Megascleres strongyles covered entirely by granules. Microscleres absent. Gemmules single or in small groups strictly adherent to the substratum enclosed in cages of megascleres. Gemmular theca tri-layered. Gemmuloscleres birotules radially arranged.

Scope and distribution

Four other species: *U. macandrewi* (Hinde, 1888) (River Paraguay, River Paranà); *U. pygmea* (Hinde, 1888) (River Paraguay, River Uruguay); *U. amazonica* (Weltner, 1895) (River Amazon); *U. ringueleti* (Bonetto & Ezcurra de Drago, 1969) (upper Paranà River, River Uruguay).

Description of type species

Uruguayella repens (Hinde, 1888) (Figs 84–87).

Material examined. Holotype: BMNH 1881.7.2.1 – dry fragment, River Uruguay, A.R. Mackinnon, vii.1888. Other material. BMNH 1919.10.14.1 – dry on a wood fragment, River Uruguay, South America (no locality specified).

Description. Encrusting body shape. Colour light leadbrown in dry specimens. Consistency rigid and very hard. Surface smooth, even. Oscules inconspicuous. Dermal membrane and subdermal cavities not observed. Ectosomal skeleton is an alveolate meshwork with thick spicular tracts much more closely arranged (130–400 μm) than those of the choanosome. Choanosomal skeleton alveolate with paucispicular tracts. Megascleres (150–240 × 20–30 μm) slightly curved strongyles covered entirely by granules. Microscleres absent. Gemmules single or in small groups (2–5)

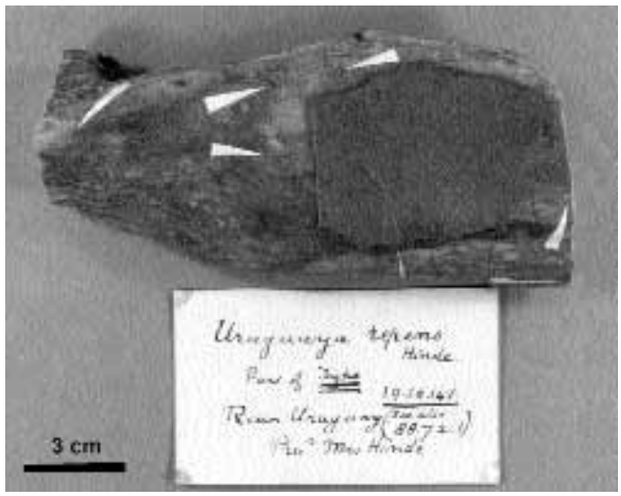

Fig. 84. *Uruguayella repens*, holotype BMNH 1888.7.2.1. Gemmules adherent to the substratum are indicated by arrows.

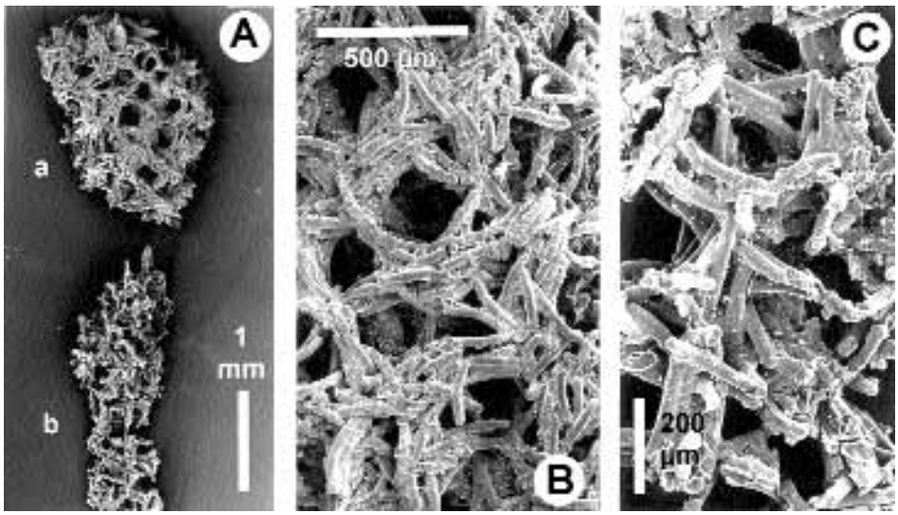

Fig. 85. *Uruguayella repens*, skeletal network, holotype BMNH 1888.7.2.1. Aa, sponge fragment (top view). Ab, a sponge section (left = surface). B, ectosomal skeleton. C, choanosomal skeleton.

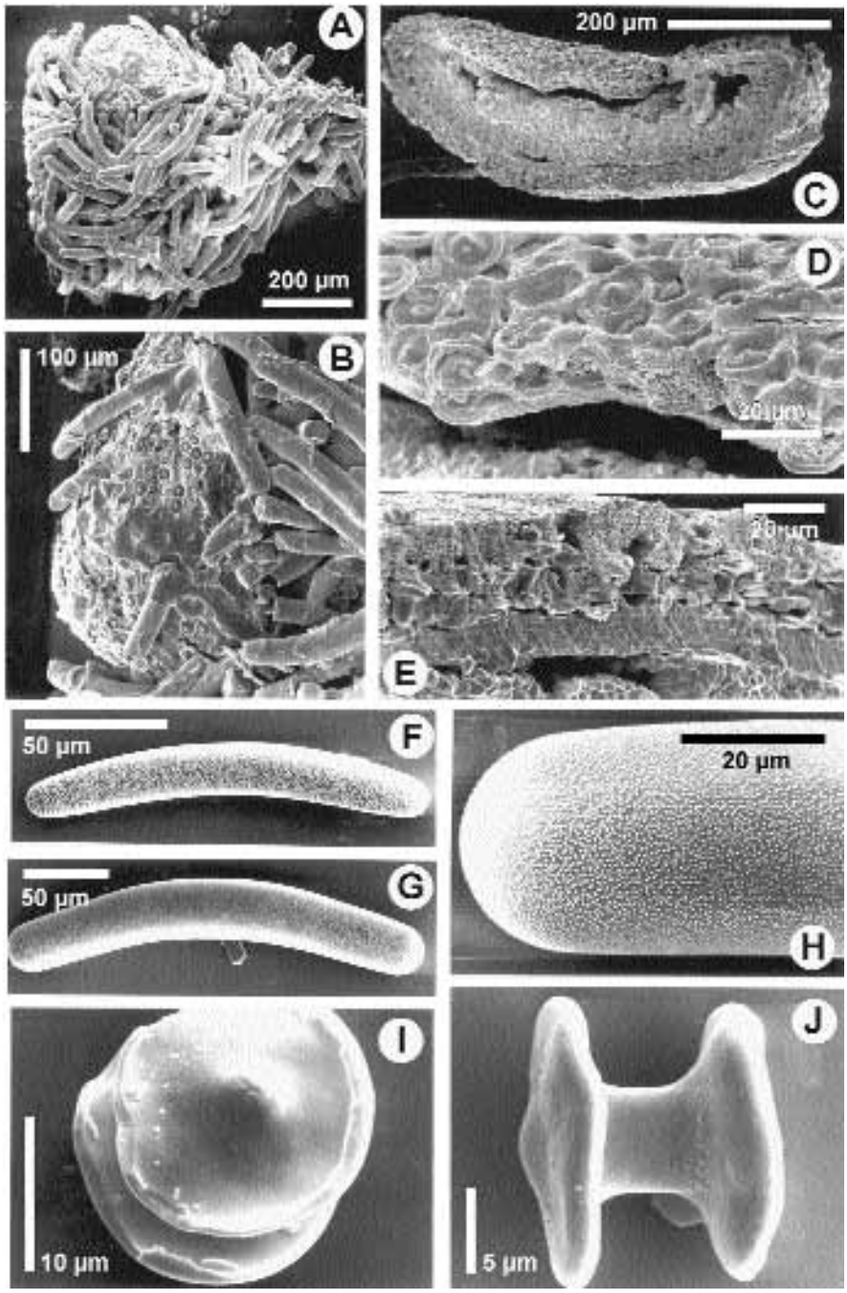

Fig. 86. *Uruguayella repens*, spicules and gemmules, holotype BMNH 1888.7.2.1. A, gemmular cage of megasclere. B, gemmular surface and cage. C, gemmule (cross section). D–E, cross section of gemmular theca with multilayered inner layer and alveolate pneumatic layer. F–H, megascleres. I–J, gemmuloscleres.

strictly adherent to the substratum enclosed by an irregular cage (100–600 µm; mean diameter 500 µm) of finely granulated strongyle megascleres (mean 140–180 µm). Gemmules subspherical (50–200 µm), brownish. Foramen not evident, although in a few gemmules there are one or more slightly raised areas in a lateral position, which may represent apertures. Gemmular theca trilayered with a single radial layer of very regularly and closely arranged birotules. Outer layer smooth covering the distal rotules of gemmuloscleres. Pneumatic layer with chambers and thickness variable in different areas of the same gemmule from thin to thick. Inner layer sublayered with adhering proximal rotules. Birotules very regular in size and shape (16 µm mean length) with smooth stout cylindrical shafts (14–15 × 6 µm). Rotules (16 µm mean) umbonate smooth circular in outline, with both margins invariably incurved in the same direction.

Ecology. On wood debris in running waters. Frequently associated with *Uruguaya corallioides*. Distribution. River Uruguay, upper Paranà River.

Remarks. Other species from South America previously referred to *Trochospongilla* are now assigned to this genus.

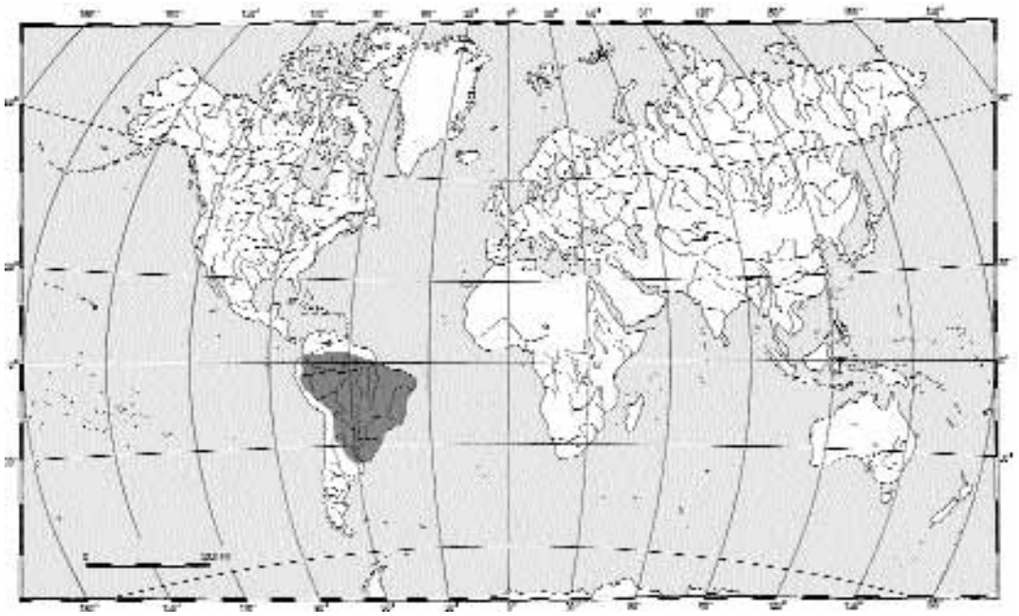

Fig. 87. Geographic distribution of the genus *Uruguayella*.

FAMILY LUBOMIRSKIIDAE REZVOI, 1936

Synonymy

Lubomirskiidae Rezvoi, 1936. Type genus. *Lubomirskia* Dybowsky, 1880.

Diagnosis

Spongillina with body shape ranging from encrusting to cushion-shaped to branched. Subdermal cavities absent. Choanosomal skeleton from pauci- to multispicular, from vague to reticulate. Ectosomal skeleton ranges from spicule tufts, to notably developed, up to a thick cortical layer. Spongin abundant. Megascleres oxeas to strongyles. Microscleres absent. Gemmules absent. Larvae apparently produced parthenogenetically.

Scope

Three genera: *Lubomirskia* Dybowsky, 1880; *Baikalospongia* Annandale, 1914a; *Swartschewskia* Makuschok, 1927a.

Distribution

Hydrographic basin of Lake Baikal, Siberia (Fig. 1).

KEY TO GENERA

(1) Megascleres are typically spiny oxeas; microscleres are absent ..... ***Lubomirskia***
Megascleres are typically spiny stout curved strongyles with spines arranged in rosettes ..... ***Swartschewskia***
Megascleres are typically smooth strongyles with spiny tips, spiny strongyles or/and spiny oxeas may also be present ..... ***Baikalospongia***

LUBOMIRSKIA DYBOWSKY, 1880

Synonymy

Spongia sensu Pallas, 1776 (in part): 710. *Lubomirskia* Dybowsky, 1880: 12.

Type species

Spongia baikalensis Pallas, 1776 (by subsequent designation, Rezvoi *et al*., 1971: 75).

Diagnosis

Lubomirskiidae with body shape ranging from encrusting to cushion-shaped to branched. Consistency elastic, not fragile, from rigid to flabby. Anisotropic regular choanosomal skeleton. Abundant spongin envelopes primary fibres and secondary tracts. Megascleres spined oxeas. Microscleres absent. Gemmules absent.

Scope and distribution

Another two species: *L. abietina* Swartschewsky 1901; *L. fusifera* Soukatschoff, 1895. Hydrographic basin of Lake Baikal, Siberia.

Description of type species

Lubomirskia baikalensis (Pallas, 1776) (Figs 88–92).

Material examined. Type material: not seen. Other material: BMNH 1932.10.3.1 (dry box FW1) – Lake Baikal, coll. R. Kirkpatrick.

Description. Branching shape with an encrusting base (1 cm thick) bearing erect (30–60 cm up to 1 m high) dichotomous branches with rounded apices; diameter of branches is not uniform (1–2 to 3–4 cm thick) and ranges from cylindrical to flattened, fan-shaped (1 cm thick), larger at the apices (up to 5 cm). Colour brilliant green in life, light brown in dry specimens. Consistency elastic, not fragile. Body surface hispid due to emerging spicules. Oscules (3–4 mm diameter) in small pockets, scattered or more rarely in lines on both basal portion and branches, with distances of 1–3 cm from each other. Dermal membrane aspicular. Subdermal cavities absent. Ectosomal skeleton consists of spicule tufts from primary fibres. Choanosomal skeleton regularly anisotropic, multispicular primary fibres and paucispicular secondary tracts; primary fibres diverging in spicule tufts at the surface. Abundant spongin envelopes primary fibres and secondary tracts. Megascleres oxeas, cylindrical to fusiform, uniformly spined with spines of variable size, rarely smooth (145–233 × 9–18 μm, mean 193 × 13 μm). Thin, short, smooth oxeas free in the choanosome are young megascleres. Microscleres absent. Gemmules absent.

Ecology. Common on rocks, boulders and wood along the entire shoreline from 3–4 m to more than 50 m depth. The optimal habitat with flourishing dense populations occurs in the batymetric range of 5–8 m depth (Kozhov, 1931). A peculiar body shape as a long branch with both rounded apices and without encrusting base is displayed by non-sessile specimens living free on soft bottom. This morphology appears to be due to a fragmentation process involving detachment of long branches from sessile specimens, and therefore represents an asexual reproductive mode. A notably diversified benthic 'consortium' of endemic invertebrates and fishes is associated with these sponges.

Remarks. *Lubomirskia baikalensis* was reported by Arndt (1948) in the Behring Sea and around the Kamčatka Peninsula.

Fig. 88. *Lubomirskia baikalensis*, BMNH 1932.10.3.1 (dry box FW1), Lake Baikal, coll. Kirkpatrick.

Fig. 89. *Lubomirskia baikalensis*, specimens in situ in shallow water.

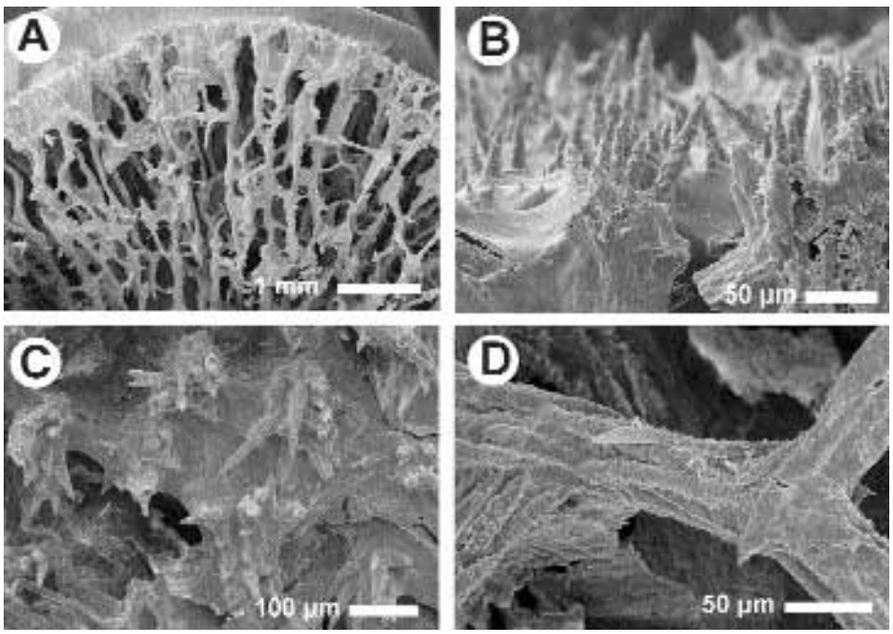

Fig. 90. *Lubomirskia baikalensis*, skeletal network, BMNH 1932.10.3.1. A, cross section of a sponge digitation (top = sponge surface). B, megasclere tips extruding from the sponge surface (lateral view). C, sponge surface (top view). D, multispicular skeleton trait.

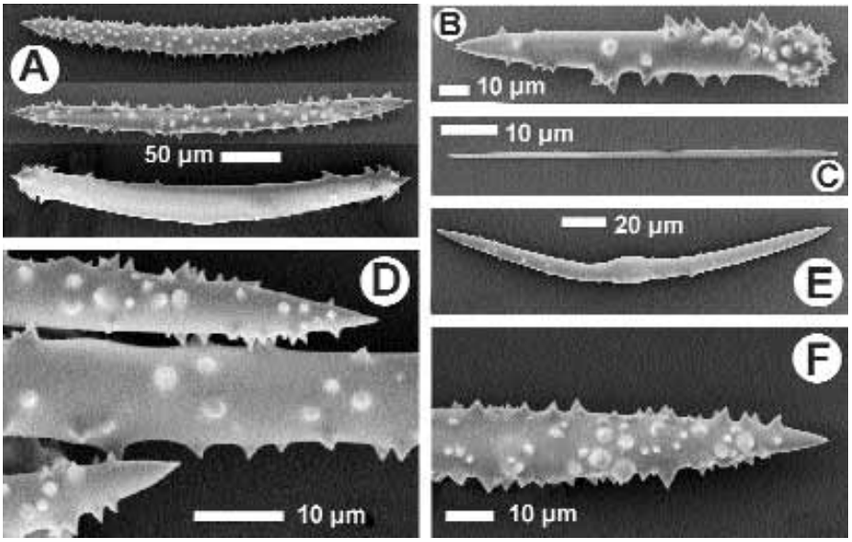

Fig. 91. *Lubomirskia baikalensis*, skeletal spicules, BMNH 1932.10.3.1. A, spiny megascleres. B, C, E, monstrous spicules. D, F, close-up of spicule spination.

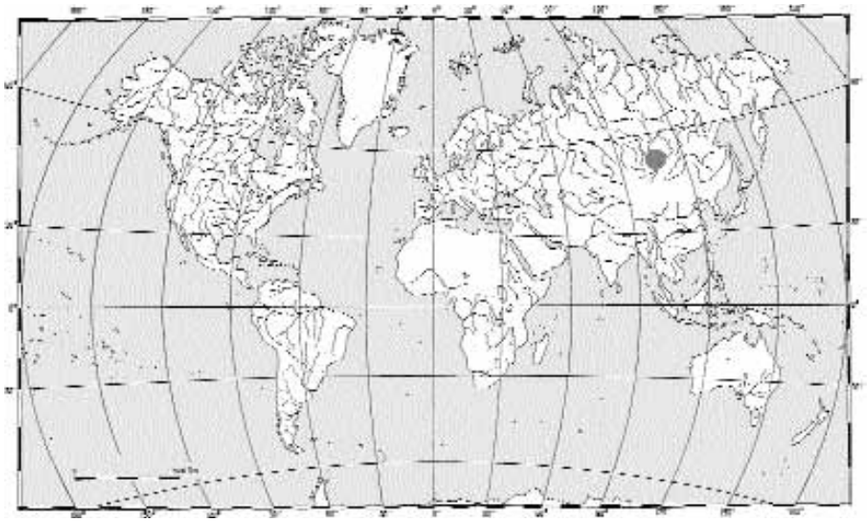

Fig. 92. Geographic distribution of the genus *Lubomirskia*.

BAIKALOSPONGIA ANNANDALE, 1914

Synonymy

Lubomirskia, in part, Dybowsky, 1880: 22. *Baikalospongia* Annandale, 1914a: 144. *Baikalolepis* Makushok, 1927a: 99.

Type species

Lubomirskia bacillifera Dybowsky, 1880: 22 (by subsequent designation, Rezvoi *et al.,* 1971: 75).

Diagnosis

Body shape encrusting to globose, to rarely branched with short anastomosing branches (*B. dzhegatajensis*). Consistency not elastic, fragile, ranging from rigid to soft or flabby. Ectosomal skeleton notably developed as a cortical layer of tangential

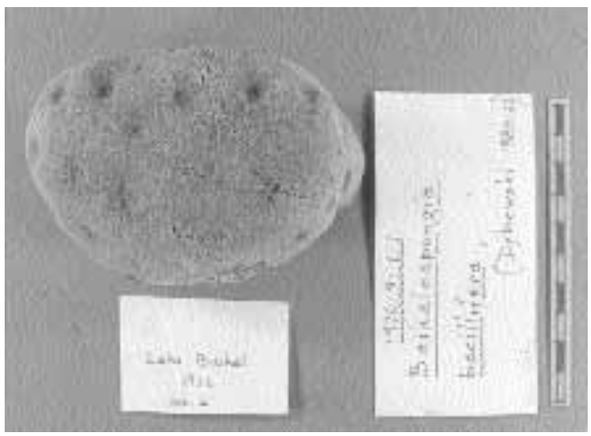

Fig. 93. *Baikalospongia bacillifera*, BMNH 1976.9.1.1, Lake Baikal, SW corner, dredged between Slindyanka and the mouth of River Angara, shallow water, 17.viii.1976, presented by John Massey-Steward (scale = 10 cm).

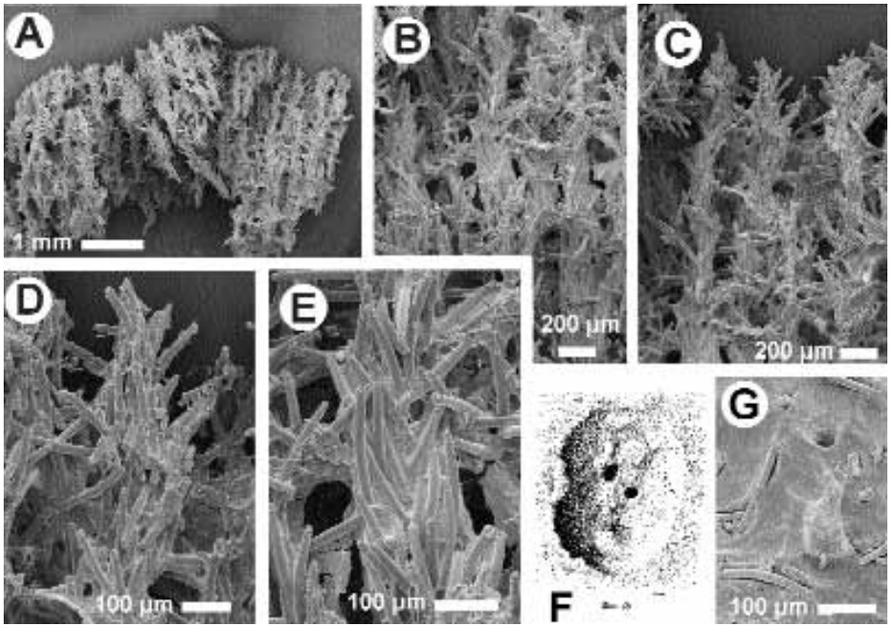

Fig. 94. *Baikalospongia bacillifera*, skeletal network, BMNH 1976.9.1.1. A, cross section throughout the sponge body (top = surface). B, choanosomal skeleton. C, skeleton organisation at the sponge surface. D, more details of C. E, more details of B. F, top view of the sponge external surface, oscular area (modified from Rezvoj, 1936). G, basal membrane.

spicules. Choanosomal skeleton irregularly anisotropic. Megascleres oxeas and strongyles. Spongin variably abundant never forming a continuous layer on fibres and tracts, more developed at nodes of spicules.

Scope and distribution

Another two species: *B. intermedia* Dybowsky, 1880; *B. dzhegatajensis* Rezvoi, 1927 (Djegataj Kul, Urianhajskaja Region). Hydrographic basin of Lake Baikal, Siberia.

Description of type species

Lubomirskia bacillifera Dybowsky, 1880 (Figs 93–96).

Material examined. Specimen: BMNH 1976.9.1.1 – Lake Baikal, SW corner, dredged between Slindyanka and the mouth of River Angara, shallow water, 17.viii.1976, presented by John Massey-Steward.

Description. Body shape encrusting to globose (5–6 cm in diameter). Colour green. Consistency not elastic, fragile, rigid. Oscules in small pockets, in regularly scattered groups. Subdermal cavities absent. Basal spongin plate, according to Rezvoi's (1936) description, is very thick with growth rings evident in sections due to the deposition of spongin in successive layers. Ectosomal skeleton notably developed as a cortical layer produced by irregular spicule tufts at the apices of primaries joined to peripheral secondary tracts in a polygonal network. Choanosomal skeleton variably developed, irregularly anisotropic with spicules irregularly arranged in primary multispicular fibres and secondary paucispicular tracts; primary fibres diverge in spicule tufts at the surface. Spongin variably abundant, but never forming a continuous layer to cover all spicules of fibres, more developed at nodes of spicules. Megascleres strongyles, rarely oxeas ($262 \times 27\,\mu m$), with spines uniformly distributed or more dense at the apices, smooth spicules

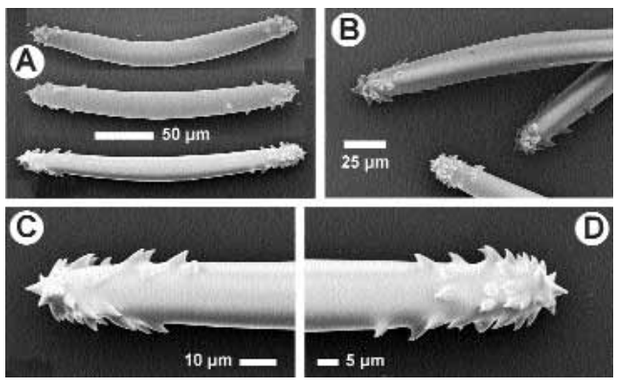

Fig. 95. *Baikalospongia bacillifera*, skeletal network, BMNH 1976.9.1.1. A, megascleres. B–D, different views of the spiny tips of megascleres.

are rare. Microscleres absent. Gemmules absent. Embryos are often abundant, but a free swimming larval stage is unknown.

Ecology. Shallow water from 2–10 m of depth. Some massive specimens with a blue-green brilliant colour have been collected at 533 m depth.

SWARTSCHEWSKIA MAKUSCHOK, 1927

Synonymy

Lubomirskia, in part, Dybowsky, 1880: 13. *Baikalospongia*, in part, Annandale, 1914a: 144. *Lubomirskia papyracea* var. δ Swartschewsky, 1901: 10. *Swartschewskia* Makuschok, 1927a: 79.

Type species. *Lubomirskia papyracea* var. δ Dybowsky, 1880: 13 (by subsequent designation, Swartschewsky, 1901: 10).

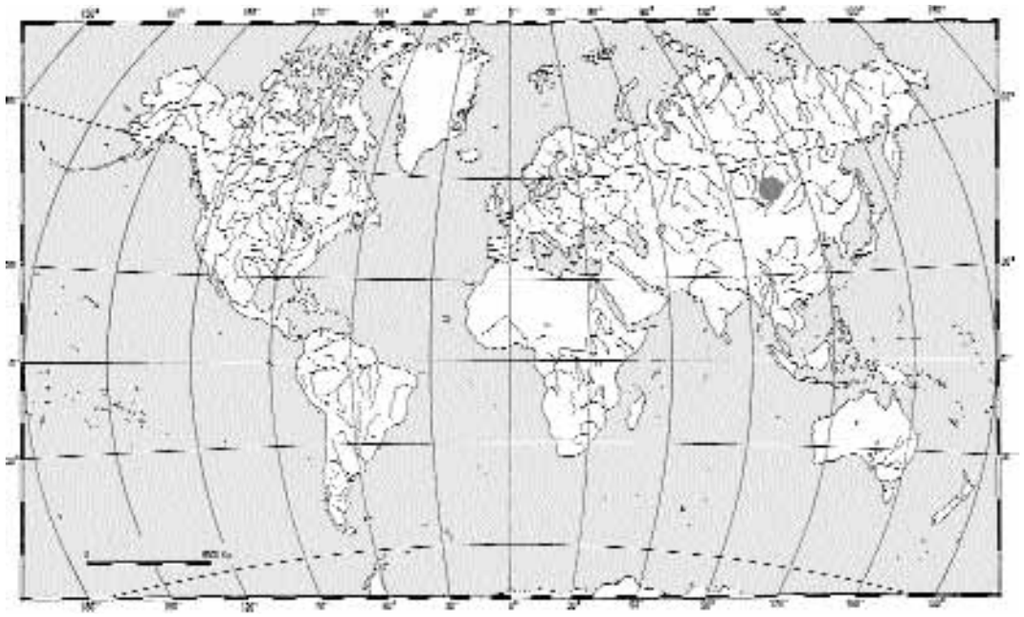

Fig. 96. Geographic distribution of the genus *Baikalospongia*.

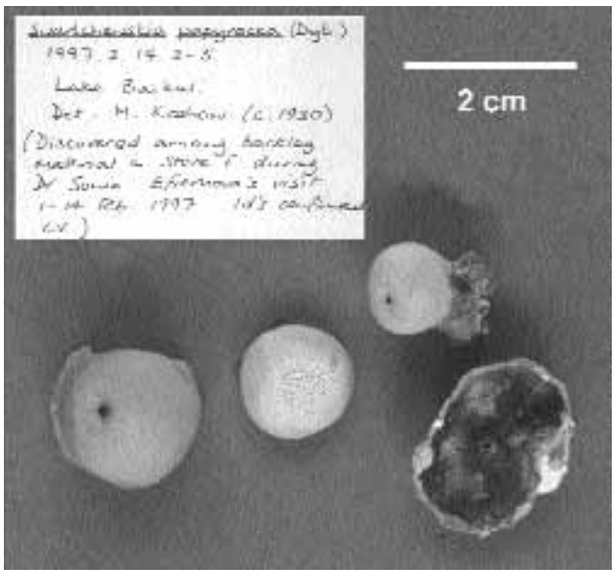

Fig. 97. *Swartschewskia papyracea*, BMNH 1997.2.14.2–5, Lake Baikal, det. M. Kashow (c. 1930), ID confirmed by S. Efremova.

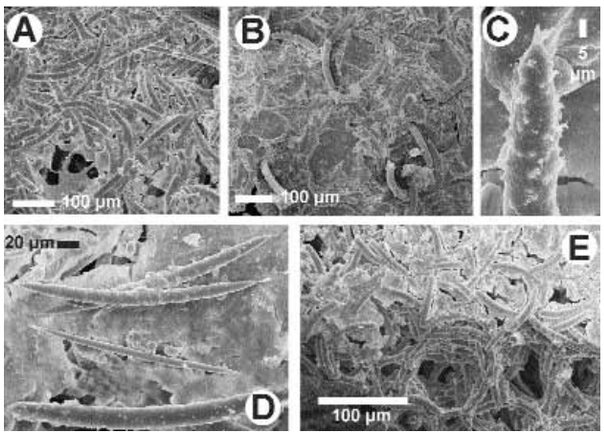

Fig. 98. *Swartschewskia papyracea*, skeletal network, BMNH 1997.2.14.2-5. A–B, top view of sponge external surface. C–D, spiny oxeas lying on the internal sponge body layer. E, internal surface of the sponge.

Diagnosis

Body shape globose to branched. Ectosomal skeleton hard and well developed as a polygonal network of thick tangential spicular fibres. Choanosomal skeleton sparsely developed with scarce spicules irregularly arranged in few weak fibres. Abundant spongin. Megascleres strongyles, from spiny to smooth.

Scope and distribution

Monotypic. Hydrographic basin of Lake Baikal, Siberia.

Description of type species

Swartschewskia papyracea (Dybowsky, 1880) (Figs 97–100).

Material examined. Specimen: BMNH 1997.2.14.2-5 – Lake Baikal, det. M. Kashow (c. 1930) (identification confirmed by S. Efremova).

Description. Body shape globose. Consistency rigid and fragile in the ectosome, soft and flabby in the choanosome. Body surface smooth with an evident alveolar network. Oscules from single at the sponge apex, to rounded in shape occurring in small pockets with a peripheral ring variably developed, to grouped at the apices. Subdermal cavities absent. Ectosomal skeleton a regular thick cortical layer of dense tangentially arranged spicular tracts, shaped as an alveolar network with one inhalant aperture in each mesh. Choanosomal skeleton sparsely developed with vague fibres or scattered spicules; choanosome is therefore soft and flabby.

Megascleres short, bent acanthostrongyles with spines (112–150 × 13–29 μm; mean 103 × 21 μm), grouped in rosettes, more dense at the apices, rarely with smooth surfaces; rare spiny oxeas in the choanosome.

Ecology. This rare species is reported prevalently localised in the area B. Kotov of Lake Baikal, from 2–80 m depth (Kozhov, 1931).

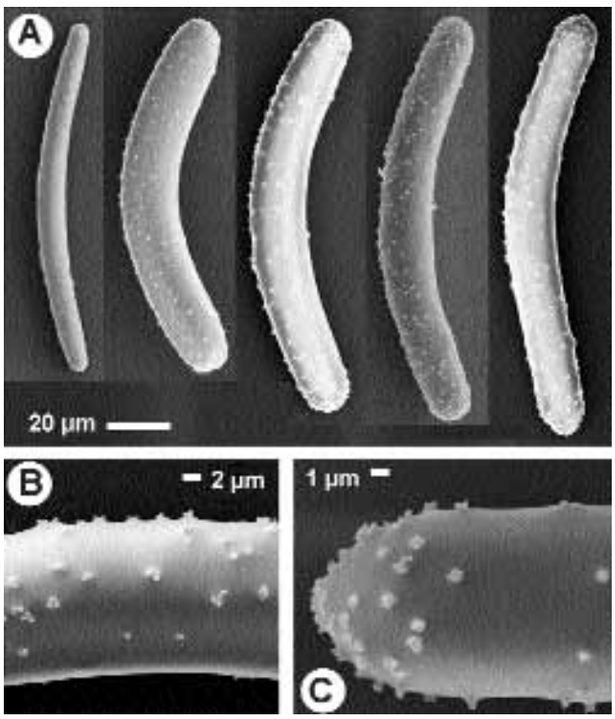

Fig. 99. *Swartschewskia papyracea*, skeletal network, BMNH 1997.2. 14.2-5. A, megascleres. B, spiny shaft of a megasclere. C, spiny tip of a megasclere.

FAMILY MALAWISPONGIIDAE FAM. NOV.

Synonymy

[Globulospongillinae] Brien, 1973b (*nomen nudum*). [Globulospongillidae] Racek, 1974. Type genus. *Malawispongia* Brien, 1972.

Diagnosis

Spongillina with body shape ranging from encrusting in young sponges to globular in well-developed sponges. Consistency firm, not elastic, notably hard, fragile. Central body cavity. Alveolate-reticulate skeleton with multispicular tracts also notably thick. Megascleres spiny or tuberculated oxeas. Microscleres absent. Gemmuloscleres absent. Gemmules absent.

Scope

Five genera: *Malawispongia* Brien, 1972, *Cortispongilla* Annandale, 1918, *Ochridaspongia* Arndt, 1937, *Pachydictyum* Weltner, 1901, *Spinospongilla* Brien, 1974.

Remarks

Brien (1973b) erected the subfamily [Globulospongillinae] within the family Spongillidae, including all genera listed above. Racek (1974) subsequently erected the taxon to family level. However, there is no genus 'Globulospongilla', and therefore the taxon is a *nomen nudum* and requires a new name.

Distribution

Notably disjunct, in ancient lakes: Kinneret (Middle-East), Malawi (African Rift Valley), Ohrida (E-Europe) and Posso (Sulawesi) (Fig. 1).

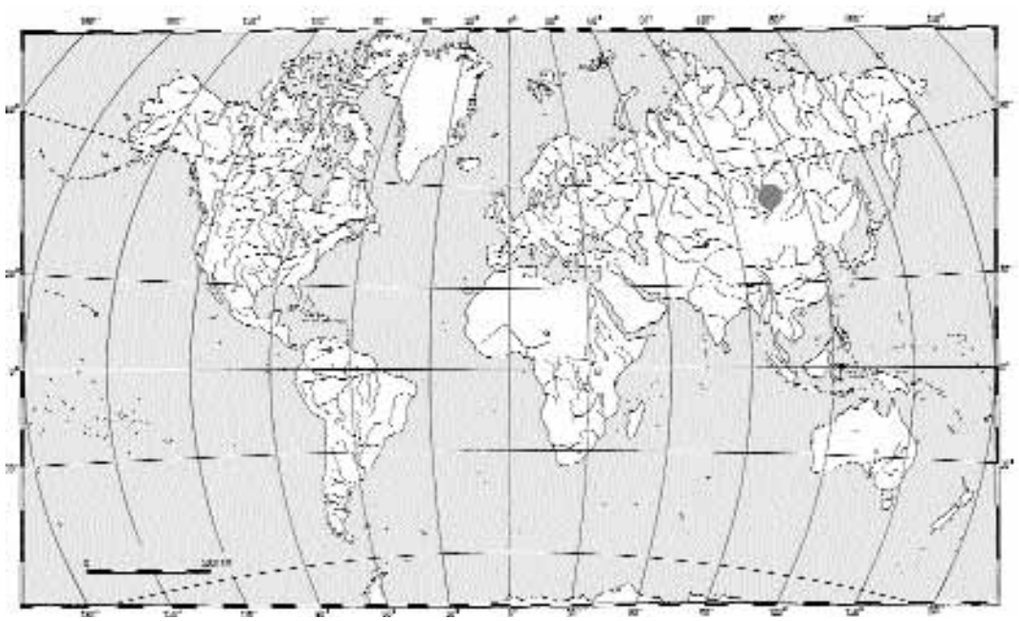

Fig. 100. Geographic distribution of the genus *Swartschewskia*.

KEY TO GENERA

(1) Megascleres are oxeas with scattered evident buttons (rarely one tip is rounded); (endemic to Lake Malawi Niassa) ..... ***Malawispongia***
Megascleres are stout smooth oxeas occasionally with a microspined surface; (endemic to Kinneret Lake and Jordan River). ..... ***Cortispongilla***
Megascleres are oxeas evidencing a very spiny surface (endemic to Ochrid Lake) ..... ***Ochridaspongia***
Megascleres are microgranulated oxeas (endemic to Lake Posso, Sulawesi (Celebes)) ..... ***Pachydictyum***
Megascleres are oxeas with scattered microgranules and big spines (endemic to Tanganyika Lake) ..... ***Spinospongilla***

MALAWISPONGIA BRIEN, 1972

Synonymy

Malawispongia Brien, 1972: 85.

Type species

Malawispongia echinoides Brien, 1972: 82 (by monotypy).

Diagnosis

Malawispongiidae with bush-like body, globular to ovate, and irregular central body cavity. Choanosomal skeleton reticulate. Abundant spongin. Megascleres range from smooth to tuberculated oxeas. Microscleres absent. Gemmules absent.

Scope and distribution

Monotypic. Lake Malawi-Niasa (12°09′S, 34°25′E), Africa.

Description of type species

Malawispongia echinoides Brien, 1972: 82 (Figs 101–104).

Material examined. Paratype: MRAC 001.427 – Monkey Bay, Lake Malawi-Niasa, 22–23 m, D.H. Eccles. 10.vii.1971.

Description. Globular to ovate shape (bush-like body) with 2–4 lobes (size 2 × 5–12 × 8 cm). Colour brown-grey. Consistency hard in dry specimens. A large oscule in each lobe is connected to an irregular central cavity. Young sponges devoid of central cavity show a more irregular lobed body with a single apical oscule devoid of oscular canals. Surface membraneous and hispid. Macro-hispidation due to the apices of vertical fibres. Micro-hispidation produced by spicules tufts from apices of primary tracts on conules. Dermal membrane transparent spicular. Subdermal cavities well developed as open exhalant canals joining to oscules. Ectosomal skeleton consists of tufts of spicules from primary tracts and irregularly arranged tangential megascleres converging to form small conules. Choanosomal skeleton reticulate multispicular with vertical columnar projections connected by an irregular isotropic reticulation to form notably dense central axis of lobes with spicules diverging in tufts toward the apical surfaces. Irregularly scattered tracts connect lobes. Abundant spongin. Megascleres (190–240 × 4–10 μm) oxeas ranging from slender to stout, from straight to slightly curved, from smooth to tuberculated, with acerate to mucronate or blunt tips. Microscleres and gemmules absent. Larva parenchymella spongillid-like. Spermatic cysts never found, parthenogenetic (?).

Ecology. In standing waters at 20–30 m depth. On inner face of bivalves shell (*Apatharia* sp.). Distribution. Malawi Lake.

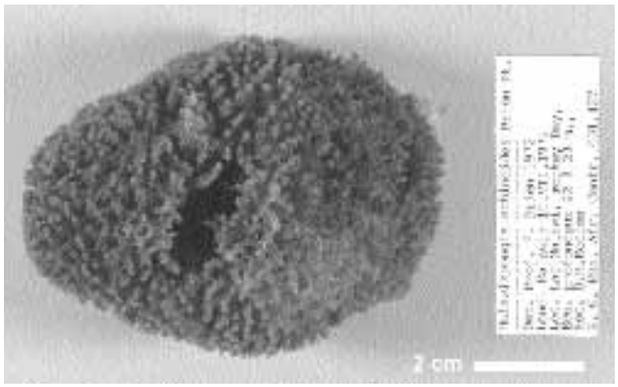

Fig. 101. *Malawispongia echinoides*, paratype, MRAC 1427.

CORTISPONGILLA ANNANDALE, 1918

Synonymy

Cortispongilla Annandale, 1918: 66. *Nudospongilla* (part) Racek, 1974: 146.

Type species

Potamolepis barroisi Topsent, 1892d: 85 (by original designation).

Diagnosis

Malawispongiidae with encrusting to globular-massive body shape. Body central cavity well developed. Reticulate choanosomal skeleton. Megascleres smooth to granulated oxeas. Microscleres absent. Gemmules absent.

Scope and distribution

Monotypic. Lake Kinneret and River Jordan, Syria? Palestine.

Description of type species

Cortispongilla barroisi (Topsent, 1892d) (Figs 105–108).

Material examined. Holotype: MNHN DT3302 – dry, Lac de Tiberiade, Syria, Th. Barrois, v.1890, by dredge. Other material. BMNH 1913.7.31.4C-13.III.C – alcohol, Lake Tiberias, det. N. Annandale. BMNH 1913.7.31.5 – dry, Channel of River Jordan near Semakh, Lake Tiberias, Palestine, det. N. Annandale. BMNH 1910.1.1.480 – Norman Collection, Lake Tiberias. BMNH

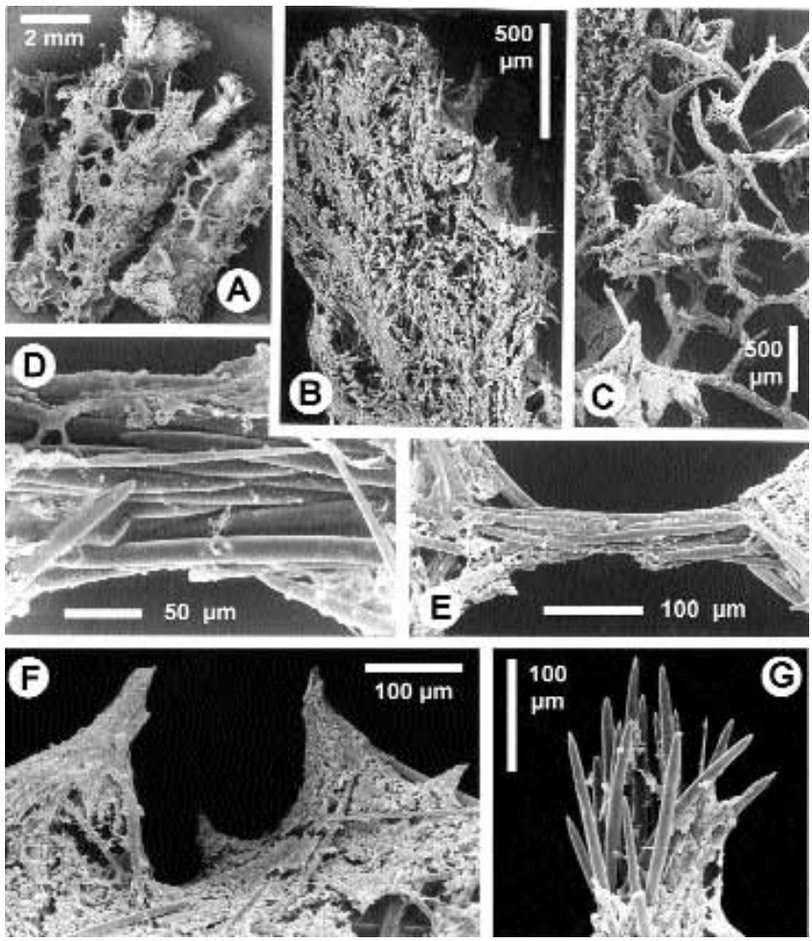

Fig. 102. *Malawispongia echinoides*, skeletal network, paratype MRAC 1427. A, a sponge section (top = surface). B, cross section of a columnar projection (top = surface). C, multispicular connections among columnar projections. D–E, multispicular tracts cemented by spongin. F, conules. G, spicule tuft at the sponge surface.

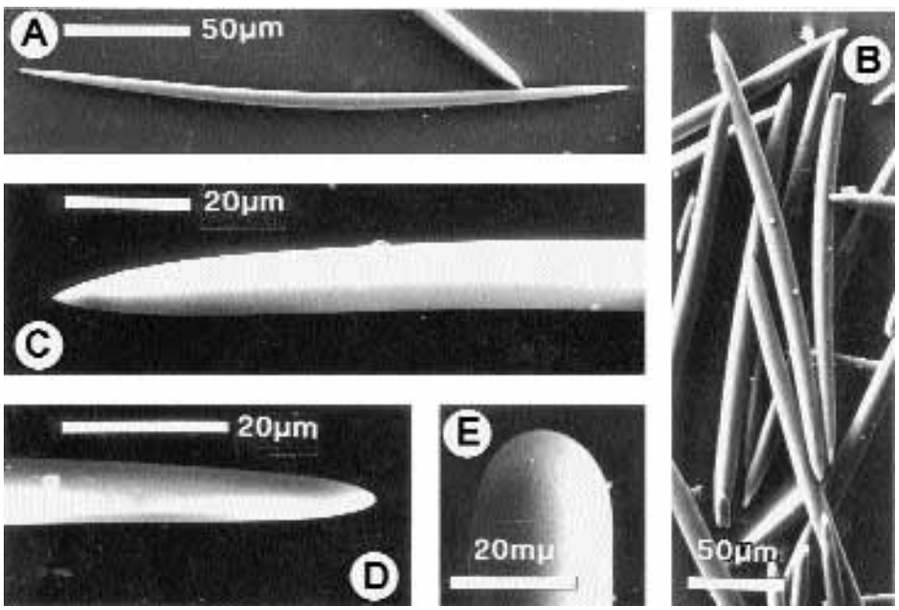

Fig. 103. *Malawispongia echinoides*, spicules, paratype MRAC 1427. A, slim smooth oxea. B, tuberculate oxeas. C–E, tips of skeletal megascleres.

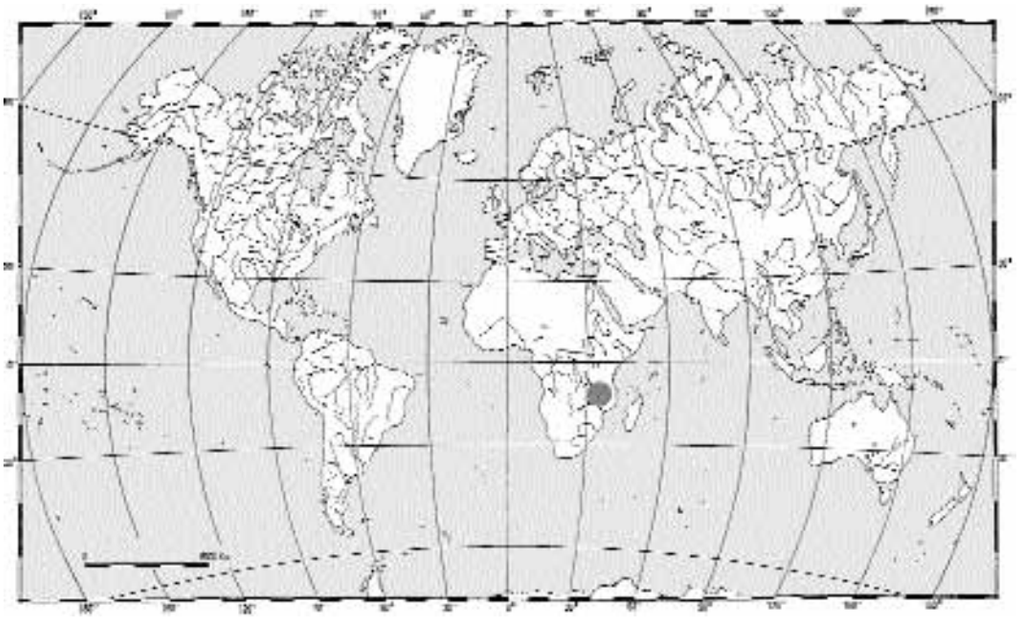

Fig. 104. Geographic distribution of the genus *Malawispongia*.

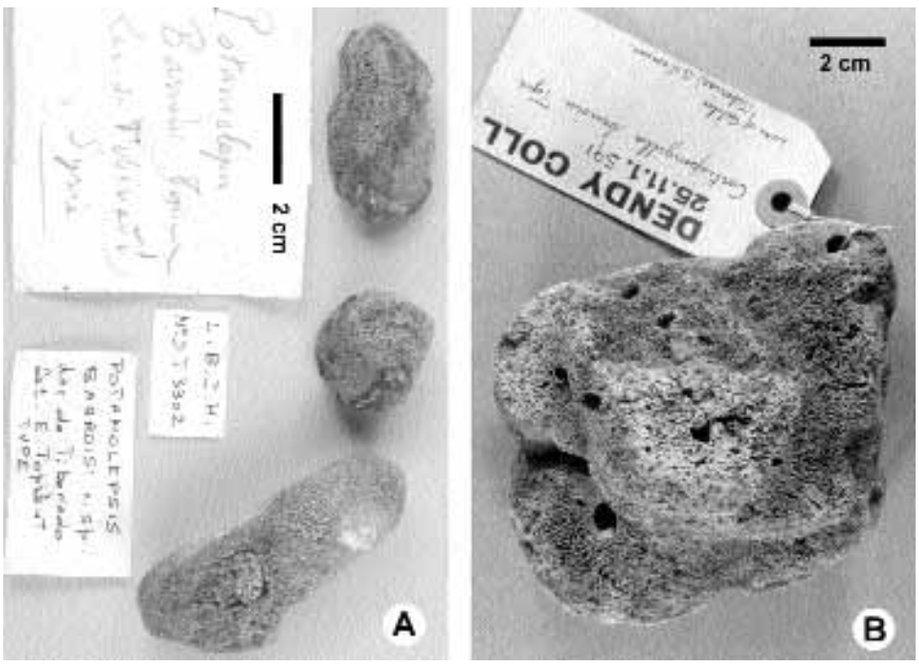

Fig. 105. *Cortispongilla barroisi*, A, type material and original labels MNHN DT3302. B, a specimen from Dendy collection BMNH 25.11.1.591.

1914.11.24.24 (ZEV 5213.7) – Channel of River Jordan, Lake Tiberias, Palestine. BMNH 1925.11.1.591 – Dendy Collection, SW corner of Lake Tiberias.

Description. Sponge encrusting to globular-massive shaped (size $3.5 \times 2.3 \times 2.1$–$8.5 \times 7.5 \times 6$ cm). Compact hard fragile consistency. Colour dull grey to glaucous green. Surface uniformly membraneous, rough but not hispid. Dermal membrane spicular. Some large specimens have large and small pores on the upper and lower surfaces, respectively. Oscule single or 2–3 main oscules with numerous subsidiary oscules with superficial exhalant horizontal radiating canals covered by the dermal membrane. Central body cavity well developed, cylindrical, almost symmetrical, arising from the convergence of canals, leading directly into a large main oscule or oscules. Ectosomal skeleton consists of tangential spicules in the membrane and peripheral thickening of fibres. Choanosomal skeleton alveolate (meshes 500–700 μm),

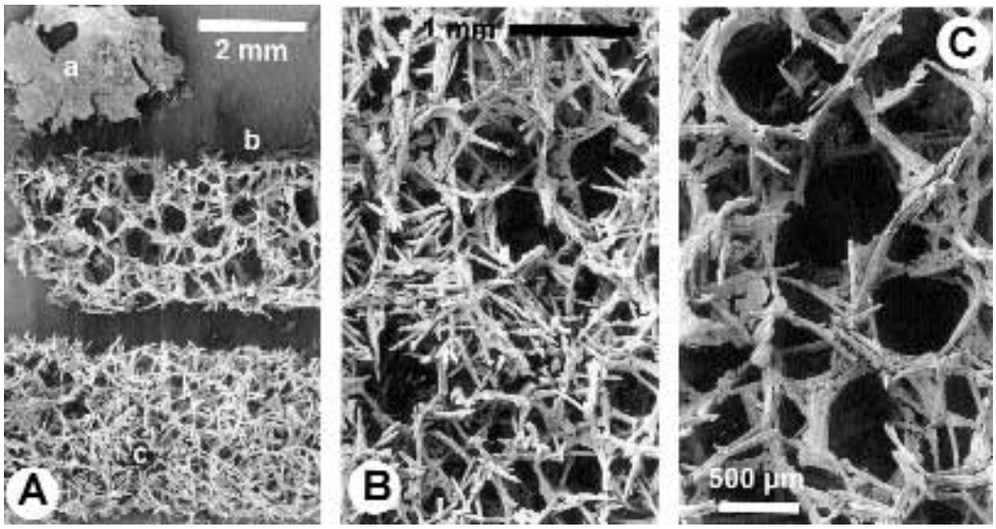

Fig. 106. *Cortispongilla barroisi*, skeletal network, type material MNHN DT 3302. Aa, basal spongin plate. Ab, internal view in cross section. Ac, sponge surface. B, sponge surface. C, choanosomal skeleton.

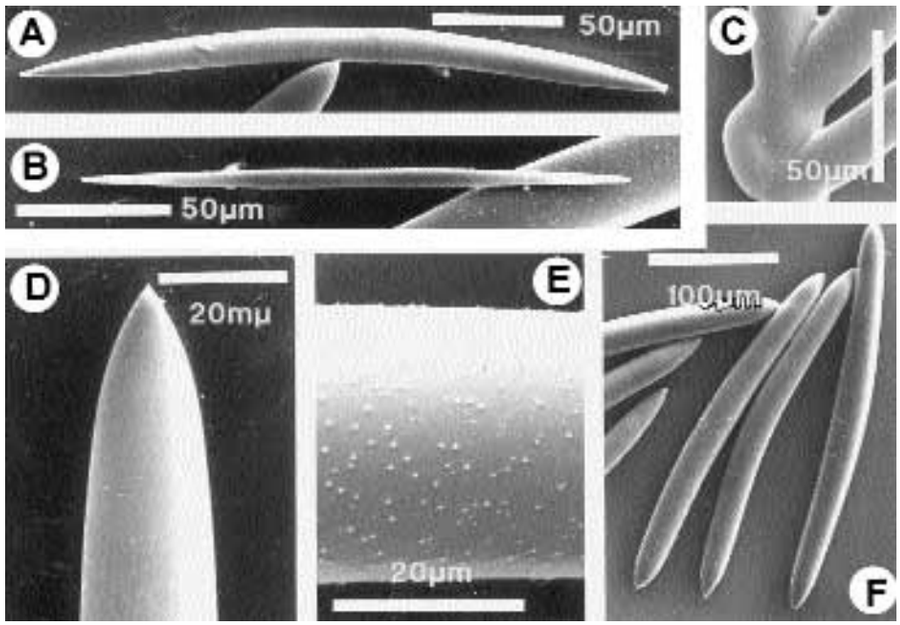

Fig. 107. *Cortispongilla barroisi*, spicular traits. B–E, BMNH 1913.7.31.4C. A, F, BMNH 1914.11.24.24. A, B, F, different oxeas. C, a monster fusion between spicules. D, the most common oxea tip. E, granulated surface of an oxea.

multispicular (6–7) primary tracts and paucispicular secondary tracts more dense and thick toward the surface. Spongin sparse, present exclusively between crossing fibres and in the uneven basal plate at the surface of encrusted pebbles, with scattered oxeas or groups of parallel oxeas. Megascleres stout oxeas (180–370 × 30–33 µm) from straight to slightly curved, from smooth to granulated with evident axial canal and tips abruptly pointed. Slender acerate oxeas are rare. Microscleres absent. Gemmules absent.

Ecology. The original population was reported as being very dense (Annandale, 1918), although it was restricted to a small area (two square miles) of the Jordan canal. Until present records the species was considered to have disappeared. Sponges are from shallow waters subjected to the action of periodical heavy storms, to deep waters of the lake also subjected to considerable currents and on substrate devoid of silt in the Jordan channel that traverses the lake. Sponges settle on the lower surface of stones, on living *Unio* sp., or encrusting on pebbles during growth to become massive specimens. Distribution. Southern Lake Kinneret (Tiberiade), River Jordan, Israel.

Remarks. This species was initially included in the subfamily Potamolepidinae. Topsent (1892d) noted its similarity to *Petrosia* and *Reniera*; Annandale (1918) underlined its similarity to *Lubomirskia papyracea*, *Potamolepis* and *Uruguaya*; and de Laubenfels (1936a) remarked on its notable architectural similarity with *Pachydictyum* Weltner, 1901.

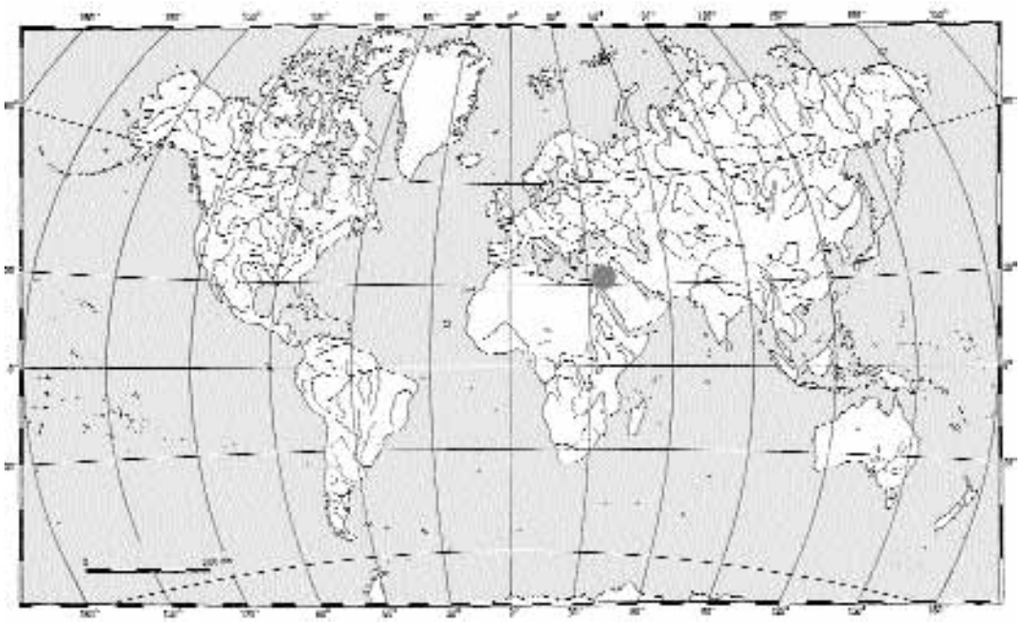

Fig. 108. Geographic distribution of the genus *Cortispongilla*.

Fig. 109. *Ochridaspongia rotunda*, type material and original labels, ZMB POR9337.

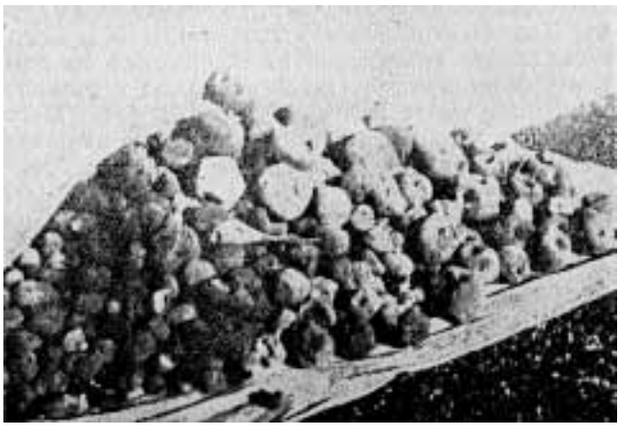

Fig. 110. *Ochridaspongia rotunda*, was very abundant in the Lake Ochrid in the 1950s and many specimens were collected by the nets of professional fishers (figure modified from S. Hadzisce, 1954, *Rec. Trav. Stat. Hidrobiol. Ohrid*, N° 1–6).

OCHRIDASPONGIA ARNDT, 1937

Synonymy

Ochridaspongia Arndt, 1937: 660.

Type species

Ochridaspongia rotunda Arndt, 1937: 660 (by original designation).

Diagnosis

Malawispongiidae with body shape globular to massive. Consistency very resilient, very hard. Single elliptical body cavity and single osculum. Choanosomal skeleton brittle, anisotropic. Ectosomal skeleton hard (up to 2 mm) due to the branching and dense primaries. Megascleres oxeas, smooth to spined. Microscleres absent. Gemmules absent.

Scope and distribution

One other species: *O. interlithonis* Arndt, 1937. Lake Ochrid, Macedonia.

Description of type species

Ochridaspongia rotunda Arndt, 1937 (Figs 109–113).

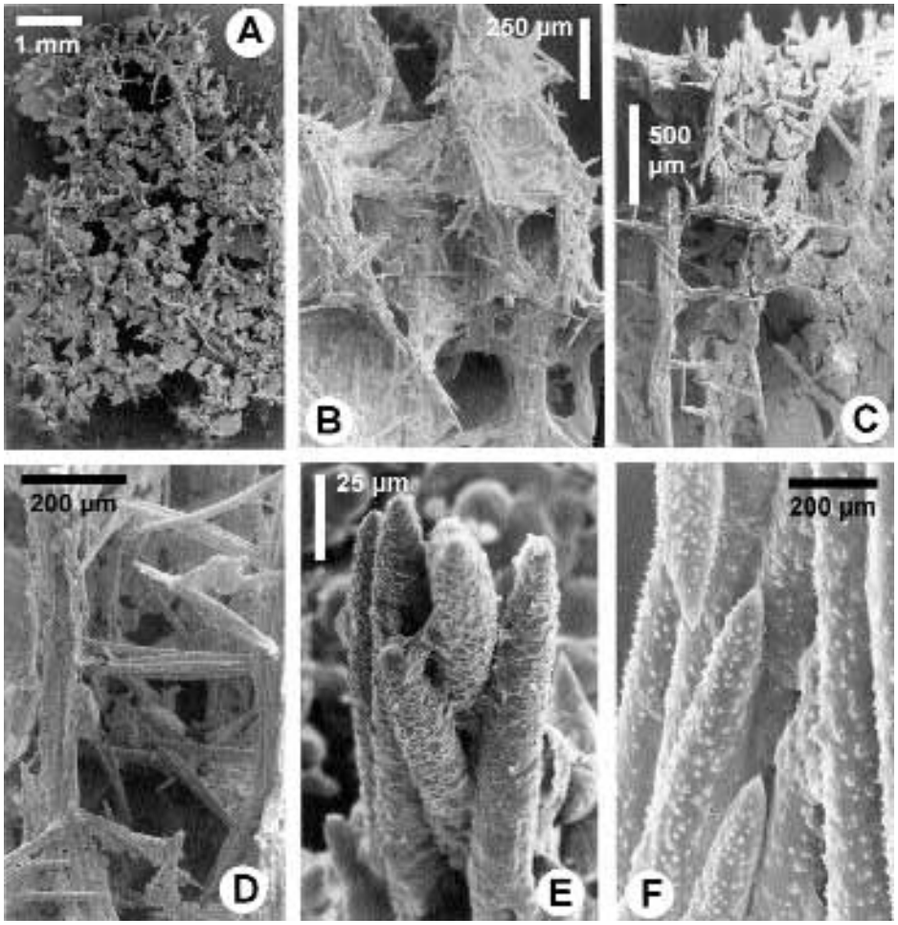

Fig. 111. *Ochridaspongia rotunda*, skeletal network, type material ZMB 9337. A, surface view. B, ectosomal skeleton (top view). C, skeletal arrangement in cross section. D, choanosomal skeleton. E, spicule tuft at the sponge surface. F, multispicular tract.

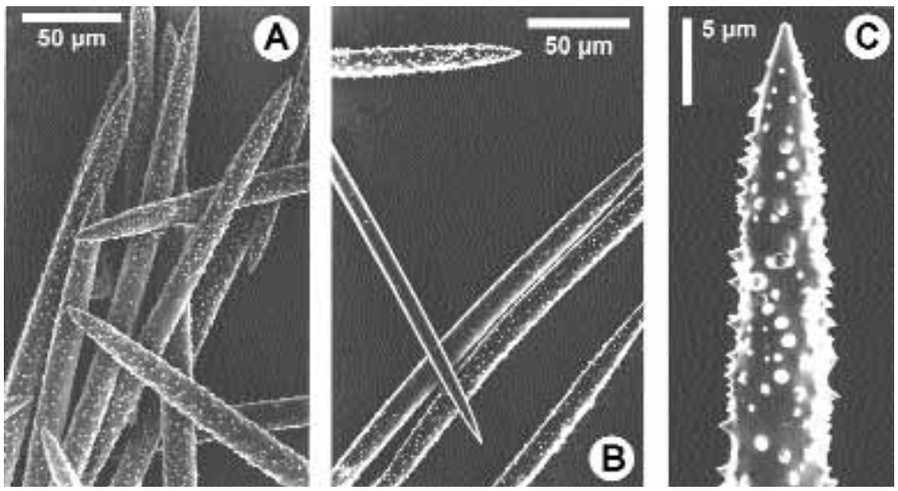

Fig. 112. *Ochridaspongia rotunda*, spiculation, type material ZMB 9337. A, spiny oxeas. B, variations in spine densities. C, spicule tip.

Material examined. Holotype: ZMB POR9337 – Lake Ochrid (41°03′N, 20°43′E), by dredge, 50 m depth, R. Kenk, 12.ix.1935. Paratypes: NZMW not seen.

Description. Body shape ranges from globular to massive, with column-, cone- or top-like shape (7.5 × 4.5–13 × 7.5 cm). Colour yellowish-brownish, both in life or dry. Consistency very resistent, very hard and brittle in dry specimens. Surface velvet-like or rough due to the emerging spicule tufts of primary tracts. Dermal membrane supported by few very thin, straight or slightly curved smooth oxeas. Subdermal cavities present on the upper and

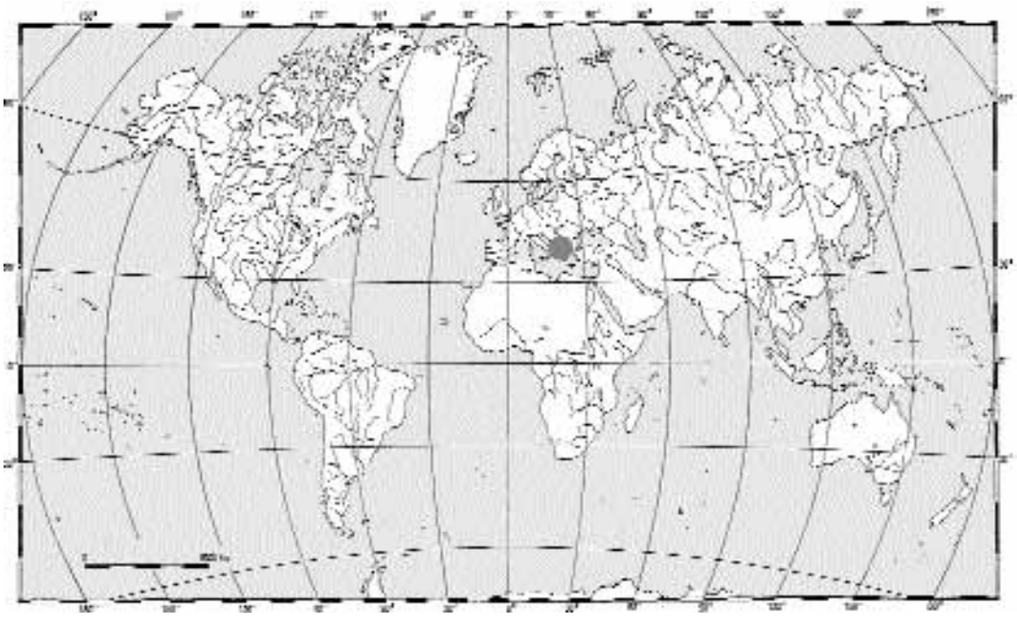

Fig. 113. Geographic distribution of the genus *Ochridaspongia*.

lateral body sides. Oscules (1–2) in the middle of the upper side large (8–18 mm in diameter) circular due to the fusion of several oscules (10–100) into a single elliptical body cavity. Basal spongin plate well developed in specimens living on pebbles. Skeletal architecture with radial primaries originating from the base up to the sponge surface. Ectosomal skeleton hard (up to 2 mm) as tangential oxeas and dense branching of primaries (70 μm thick). Choanosomal skeleton anisotropic with ascending multispicular primary tracts gradually becoming more thin and diverging in tufts toward the surface and uni- to paucispicular (3–5) irregular secondary tracts. Spongin very sparse. Megascleres oxeas (175–367/5–23 μm), ranging from slender to stout, from straight to slightly curved, from smooth to spined mainly towards the ends; acerate tips. Spherical swellings occur in some oxeas. Oxeas of fibre tufts (235–279 × 13 μm), ectosomal oxeas (175–220 × 3 μm), choanosomal oxeas (264–322 × 13–19 μm). Microscleres absent. Gemmules absent. Larvae egg-shaped 100–200 μm in diameter (width anterior 290 μm, posterior 150 μm), bearing very thin smooth oxeas.

Ecology. Eastern shore of the lake, 30–70 m depth, on muddy bottoms or covered by bivalve shells or small pebbles, also in strong currents. Sponges englobe pebbles or shells in the basal area. *Ochridaspongia interlithonis* lives near the shore 1.5–2 m between plants (*Vallisneria*, *Miriophyllum*), on wooden pillars and pebbles with *Dreissena*. Distribution. Lake Ochrid.

Remarks. The single preoscular cavity can be considered homologous to the central cavity of *C. barroisi* and *P. globosum.* The local trivial name of this species is 'shetsherparé' or 'shekerparé', a Turkish word that means sweet cake.

PACHYDICTYUM WELTNER, 1901

Synonymy

Pachydictyum Weltner, 1901: 188.

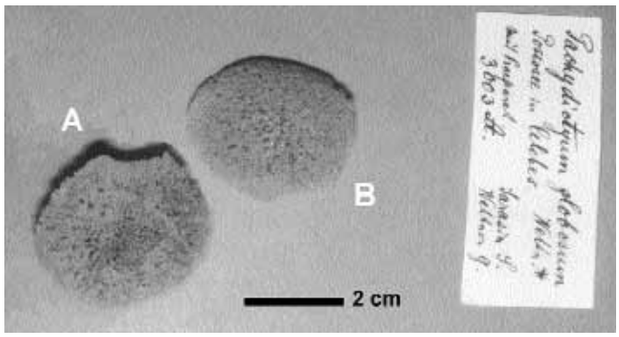

Fig. 114. *Pachydictyum globosum*, type material and original labels ZMB 3003. The single half-specimen is shown from the internal (A) and external (B) surfaces.

Type species

Pachydictyum globosum Weltner, 1901: 188 (by monotypy).

Diagnosis

Malawispongiidae with globular body. Consistency hard and brittle. Body cavity elliptical open directly through the single osculum. Choanosomal skeleton reticulate with notably thick primary fibres. Sparse spongin. Megascleres oxeas, styles, tylostyles, ranging from smooth to granular. Microscleres absent. Gemmules absent.

Scope and distribution

Monotypic. Lake Posso (01°55′S, 120°37′E) Sulawesi (Celebes).

Description of type species

Pachydictyum globosum Weltner, 1901 (Figs 114–117).

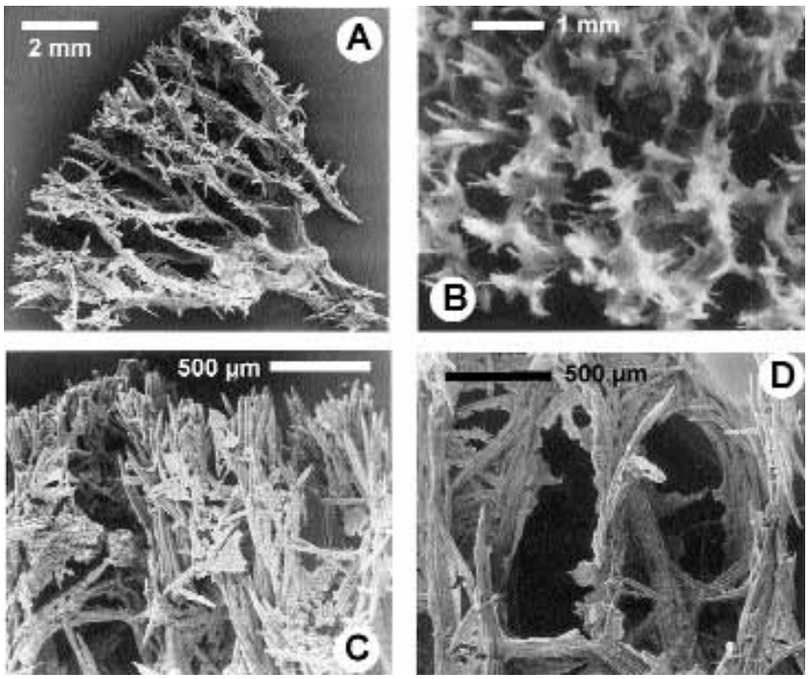

Fig. 115. *Pachydictyum globosum*, skeletal network, type material ZMB 3003. A, cross section from the sponge surface (left) throughout the choanosome (right). B, sponge surface (top view). C, ectosomal skeleton. D, choanosomal skeleton.

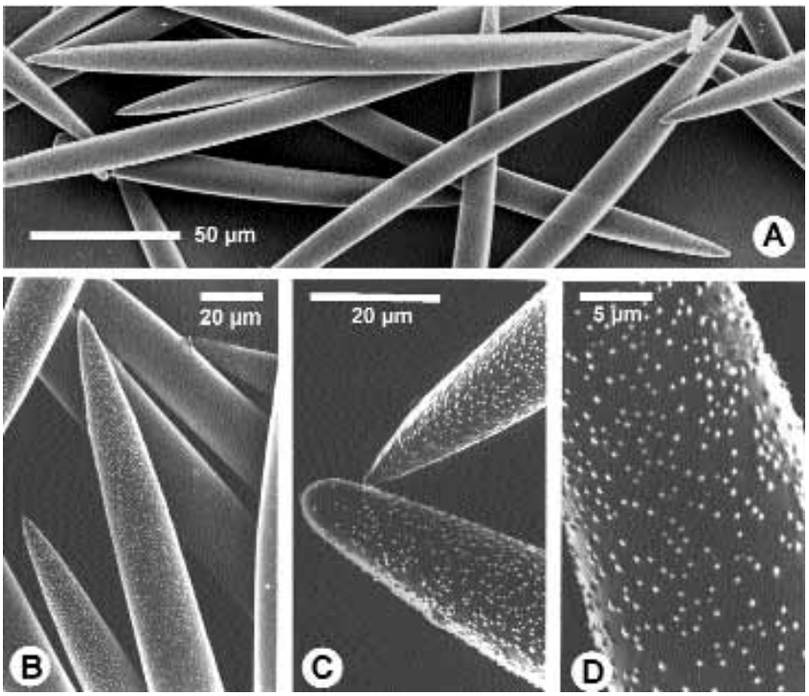

Fig. 116. *Pachydictyum globosum*, spicules, type material ZMB 3003. A, megascleres oxeas. B, spiny and smooth oxeas. C, megasclere tips. D, granules at the megasclere surface.

Material examined. Holotype: ZMB 3003A-SE36, ZMB 3003B-SE36 – Lake Posso, Sulawesi (Celebes), P. & F. Sarasin, ii.1895.

Description. Body shape spherical, oval to club-shaped (size 3.1–3.3 × 2–2.5 cm). Colour bright light green in life, turned to grey or light brown in alcohol. Consistency hard and brittle. Rough surface with protruding ends of primary tracts. Single osculum connected through a broad barrel-shaped canal with the irregular central cavity within the sponge body. Thickness of body wall ranges from 3.5–10 mm related to the size of inner cavity. Basal spongin plate not

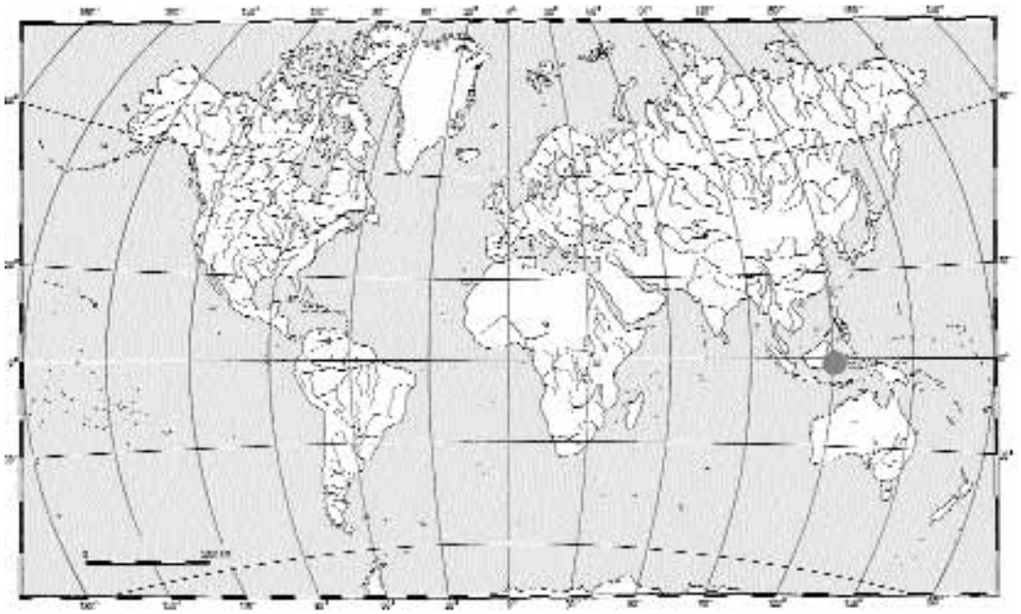

Fig. 117. Geographic distribution of the genus *Pachydictyum*.

observed. Dermal membrane not observed. Subdermal cavities evident. Ectosomal skeleton with spicule tufts at the apices of primary tracts. Choanosomal skeleton irregularly anisotropic, reticulate in some areas with primary tracts multispicular (6–8 to 35–40) diverging in tufts toward both apical and basal (central cavity) surfaces, irregular secondary tracts pauci- (1–2) to multispicular (6–10). Sparse spongin as thin layers around spicules and tracts, with abundant foreign material. Choanocyte chambers range from 20–24 μm. Megascleres of various types: stout smooth, straight to slightly curved, gradually tapering sharp-pointed oxeas with evident axial canal and very variable in size (slender 374 × 25 μm, stout 340–410 × 24–32 μm; mean 360 × 25 μm). Few spicules uniformly thick with rounded tips (320–28 μm). Few smooth styles and tylostyles are also present with common silica spherules. Malformed tips are frequent occurring as bulb-like tips. Microscleres absent. Gemmules absent. Larvae abundant and scattered in two specimens, on three described females with numerous cleavage stages and eggs. Oval larvae (750 × 520 μm) bearing small slender smooth oxeas (230–6 μm) in their posterior ends.

Ecology. Shallow waters at the eastern shore of Lake Posso. Sponges settled on shells of *Melania kuli* Sarasin, *M. centaurus* Sarasin and *Miratesta celebensis* var. *robusta* Sarasin, with the large osculum directed away from the underside of the living snails. Shells surfaces showed signs of corrosion in areas of contact with the sponge. Distribution. Found only in Sulawesi, Indonesia.

SPINOSPONGILLA BRIEN, 1974

Synonymy

Spinospongilla Brien, 1974: 589.

Type species

Spinospongilla polli Brien, 1974: 589 (by monotypy).

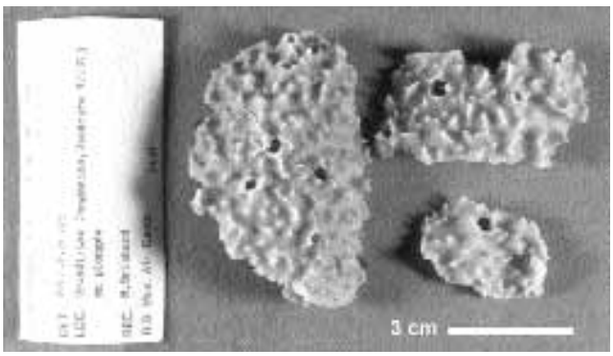

Fig. 118. *Spinospongilla polli*, holotype MRAC 1431.

Definition

Malawispongiidae with encrusting body shape, surface with irregularly scattered oscules. Consistency hard. Ectosomal skeleton shaped as conules and irregular uni- or bispicular meshes tangential to the surface. Alveolate isotropic multispicular choanosomal skeleton with rare scattered smaller oxeas. Scarce spongin. Megascleres oxeas ranging from slender to stout, from straight to slightly curved, from smooth to spined and granulated; tips range from acerate to blunt. Microscleres and gemmules absent.

Scope and distribution

Monotypic. Lake Tanganyika (06°24′N, 29°38′E) Zaire, Afrotropical Region.

Description of type species

Spinospongilla polli Brien, 1974 (Figs 118–121).

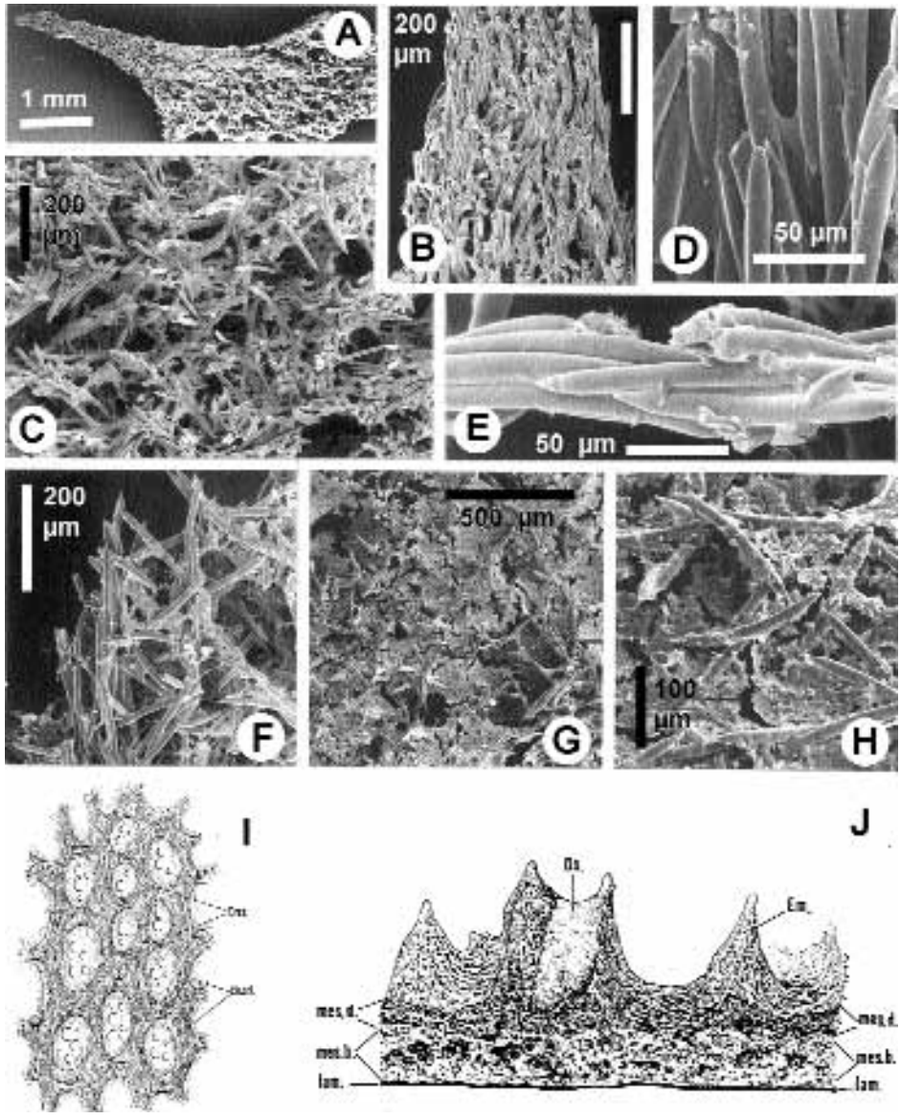

Fig. 119. *Spinospongilla polli*, skeletal network, holotype MRAC 1431. A, cross section of a conule. B, detail of A at the conule base. C, choanosomal skeleton. D, multispicular axis of a conule. E, choanosomal tract. F, surface hispidation (lateral view). G, sponge surface (top view). H, detail of G (top view). I, aquiferous openings (modified from Brien, 1974). J, scheme of surface and a cross section (modified from Brien, 1974).

Material examined. Holotype: MRAC 1431, Lake Tanganyika, Usumbura, Zaire, v.1973, leg. M. Brichard, by diving.

Description. Body shape encrusting 2–5 mm thick. Colour buff, green (surface), white-grey (inner part). Consistency hard. Surface conulose; conules 3–4 mm height. Oscules (2–4 mm) irregularly scattered sometimes crater-like. Dermal membrane spicular. Basal plate well developed, brown. Ectosomal skeleton irregular network of uni- or bispicular meshes tangential to the surface. Choanosomal skeleton alveolate isotropic multispicular with rare scattered smaller oxeas (128 × 2.3 µm) in the original description; at the base of conules fibres converge in vertical thicker tracts. Sparse spongin. Megascleres oxeas (160–208 × 11–12 µm) ranging from slender to stout, from straight to slightly curved, from smooth to spined and granulated; tips range from acerate to blunt. Microscleres absent. Gemmules absent. Larva spongillid-like parenchymula (Brien, 1974: 602). Spermatic cysts never found, parthenogenetic (?).

Ecology. Unknown.

FAMILY METANIIDAE VOLKMER-RIBEIRO, 1986

Synonymy

Metaniidae Volkmer-Ribeiro, 1986: 493. Type genus. *Metania* Gray, 1867a.

Definition

Spongillina with body shape encrusting, massive, bulbose, globular. Surface smooth, hispid to conulose. Consistency from

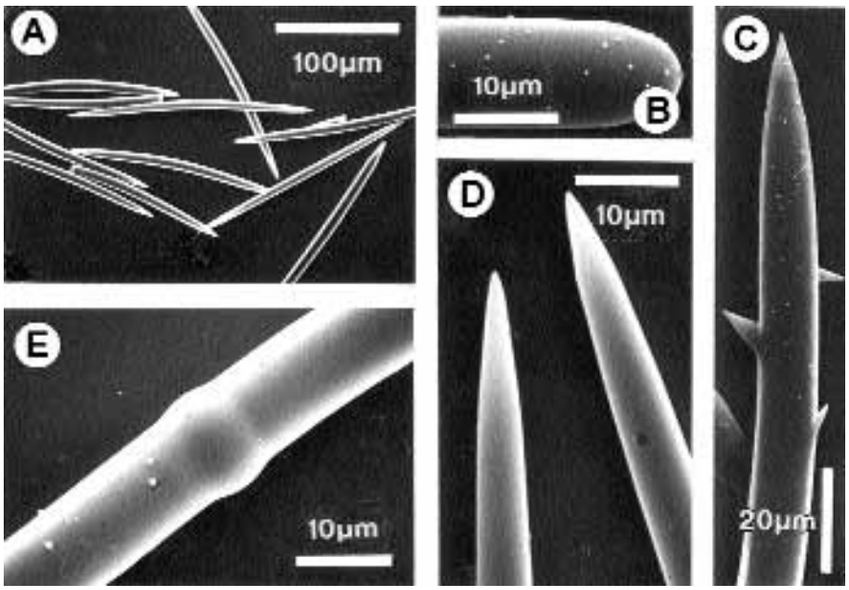

Fig. 120. *Spinospongilla polli*, spicules, holotype MRAC 1431. A, megascleres oxeas. B–D, close-up of megasclere tips with different granulation and spination. E, monstrosity of a megasclere shaft.

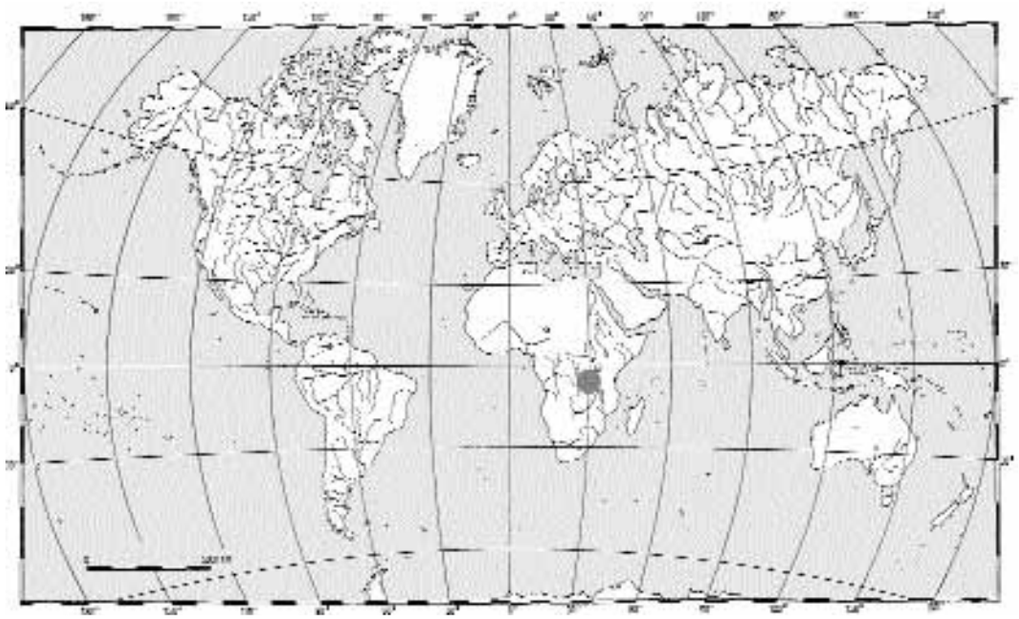

Fig. 121. Geographic distribution of the genus *Spinospongilla*.

fragile to very hard. Ectosomal skeleton consists of tangential spicules in the dermal membrane or spicule tufts from emerging fibres. Choanosomal skeleton alveolate-reticulate irregular. Megascleres are oxeas to strongyles, from smooth to spiny. Microscleres, when present, are acanthostrongyles, acanthoxeas, asters, pseudobirotules. Gemmules subspherical to oval, with or without cage. Foramen present. Gemmular theca usually trilayered with radially arranged gemmuloscleres. Gemmuloscleres boletiform (tubelliform), parmuliform, pseudobirotules.

Scope

Five genera: *Metania*, *Acalle*, *Drulia*, *Houssayella*, *Corvomeyenia*.

Distribution

Nearctic, Neotropical, Afrotropical, Oriental and Australian Regions (Fig. 1).

KEY TO GENERA

(1) Parmuliform spicules (gemmuloscleres) are present; squat and smooth oxeas as megascleres; microscleres are acanthoxeas ..... ***Drulia***
Absence of parmuliform spicules (gemmuloscleres) 2
(2) Tubelliform spicules (gemmuloscleres) are present 3
Absence of tubelliform spicules as gemmuloscleres 4
(3) Gemmuloscleres show a single tubelliform morphology, radially arranged with the larger rotule embedded in the inner layer of the gemmular theca; microscleres are strongyles from smooth to spiny; megascleres are oxeas and strongyles, smooth and spiny ..... ***Metania***
Gemmuloscleres of two different morphs: rare tubelliform, arranged radially on the gemmular theca around the foramen; and pseudobirotules radially arranged inside the gemmular theca; microscleres are absent; megascleres are few smooth oxeas and abundant smooth or microspined strongyles ..... ***Acalle***
(4) Gemmuloscleres are pseudobirotules with a long slim smooth shaft radially arranged; megascleres are long fusiform oxeas showing rare spines or tubercles; microscleres are pseudobirotules with a short smooth shaft ..... ***Corvomeyenia***
Gemmuloscleres are birotules with a short shaft embedded radially inside the gemmular theca; megascleres are acanthostrongyles associated with spiny and smooth oxeas; microscleres are acanthostrongyles and acanthoxeas and exclusive 'aster-like' spicules showing many rays ..... ***Houssayella***

METANIA GRAY, 1867

Synonymy

Metania Gray, 1867a: 551. *Tubella* Carter, 1881c: 96.

Type species

Spongilla reticulata Bowerbank, 1863: 455 (by subsequent designation; Penney & Racek, 1968: 147).

Diagnosis

Metaniidae with body shape bulbous to massive. Consistency hard and brittle. Choanosomal skeleton alveolate with multispicular

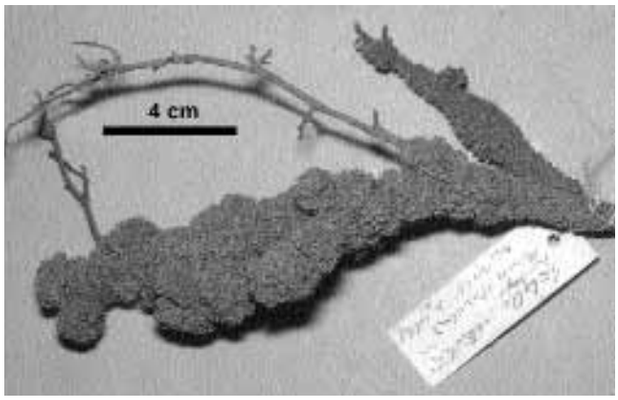

Fig. 122. *Metania reticulata*, specimen ZMB 3735.

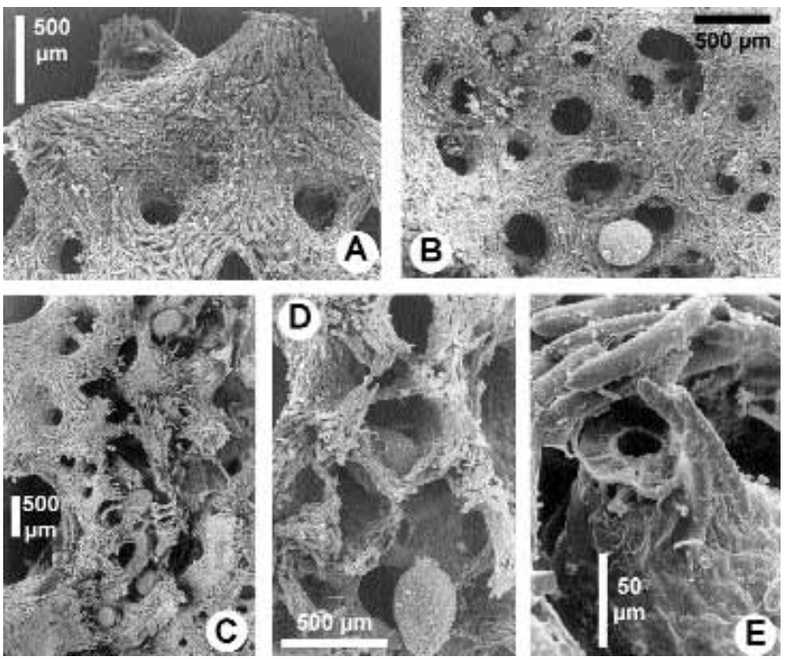

Fig. 123. *Metania reticulata*, skeletal network, specimen ZMB 3735. A, surface with conules and ectosomal tangential skeleton. B, openings of the aquiferous system at the sponge surface. C, ovoidal gemmules within the skeletal meshwork (cross section, left = surface). D, choanosomal skeleton with two gemmules. E, gemmule with an evident foramen.

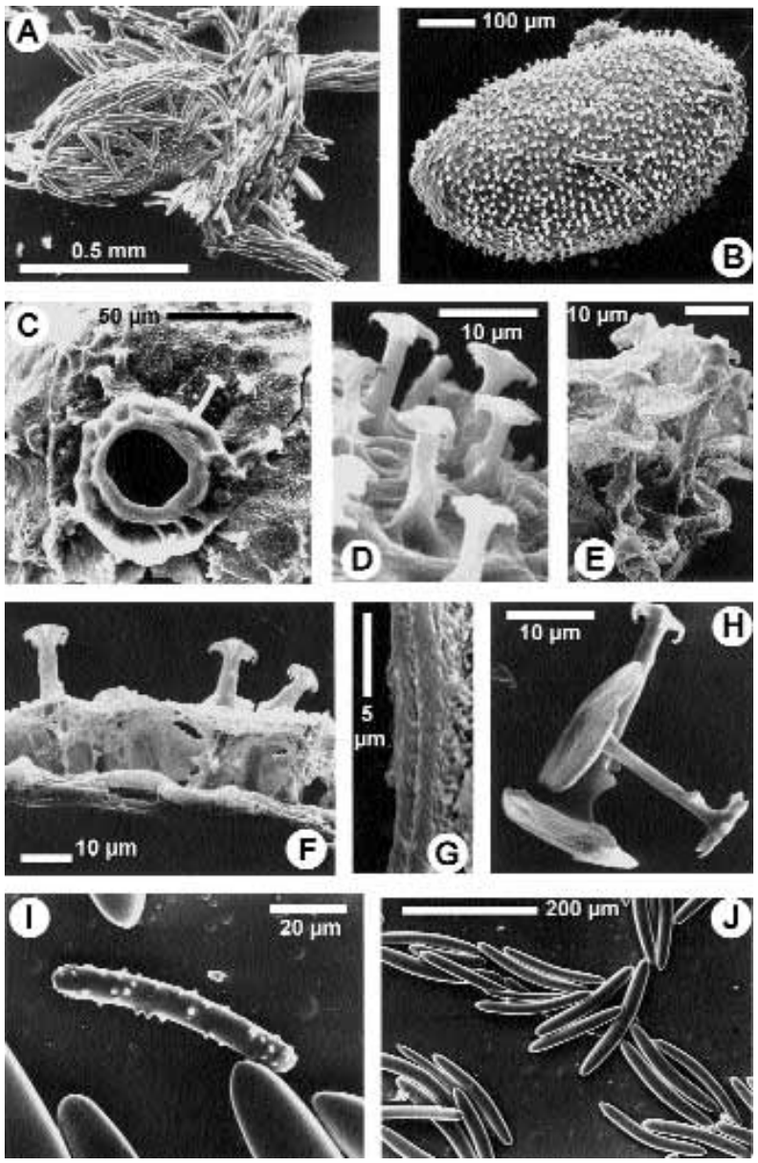

Fig. 124. *Metania reticulata*, spicules and gemmules, A, E, Bowerbank collection BMNH BK 1435. B–D, F–J, specimen ZMB 3735. A, gemmular cage. B, gemmule. C, foramen. D, gemmular outer surface. E, gemmuloscleres embedded in the gemmular theca. F, trilayered theca. G, multilayered inner layer. H, parmuliform gemmuloscleres. I, microsclere. J, megascleres.

tracts. Spongin sparse. Megascleres oxeas to strongyles. Microscleres acanthostrongyles (acanthoxeas?) to pseudobirotules variably bent. Gemmules ovoid, scattered or rarely at the sponge base, enclosed in a variably developed cage of spiny megascleres ranging from oxeas to strongyles. Theca with three layers and gemmuloscleres radially embedded. Pneumatic layer as trabecules (fibres) of spongin. Gemmuloscleres boletiform.

Scope and distribution

Fifteen other species: *M. vesparia* (von Martens, 1868) (Borneo, Indonesia, Central Africa); *M. spinata* (Carter, 1881c) (Amazon Basin); *M. vesparioides* (Annandale, 1908b) (Burma); *M. subtilis* Volkmer-Ribeiro, 1979 (South America, Amazonian Basin); *M. fittkaui* Volkmer-Ribeiro, 1979 (South America, Amazonian Basin); *M. ovogemata* Stanisic, 1979 (Australia); *M. brieni* Burton, 1938 (Congo Basin); *M. innominata* Burton, 1938 (SE Africa); *M. rhodesiana* Burton, 1938 (SE Africa); *M. vanryni* Brien, 1968b (Congo Basin); *M. godeauxi* Brien, 1968b (Central Africa); *M. schoutedeni* Burton, 1938 (Congo Basin); *M. kiliani* Volkmer-Ribeiro & Costa, 1992 (Neotropical Region); *M. pottsi* (Weltner, 1895) (Congo Basin, Congo, Angola); *M. melloleitaoi* (Machado, 1945) (Central Brazil). Distribution. Tropical rain-forests of Neotropical, Afrotropical, Oriental and Australian Regions.

Description of type species

Metania reticulata (Bowerbank, 1863) (Figs 122–125).

Material examined. Holotype: ? BMNH BK1435 – Dark Ygapos in virgin forest, margins of Amazon, Villa Nova,

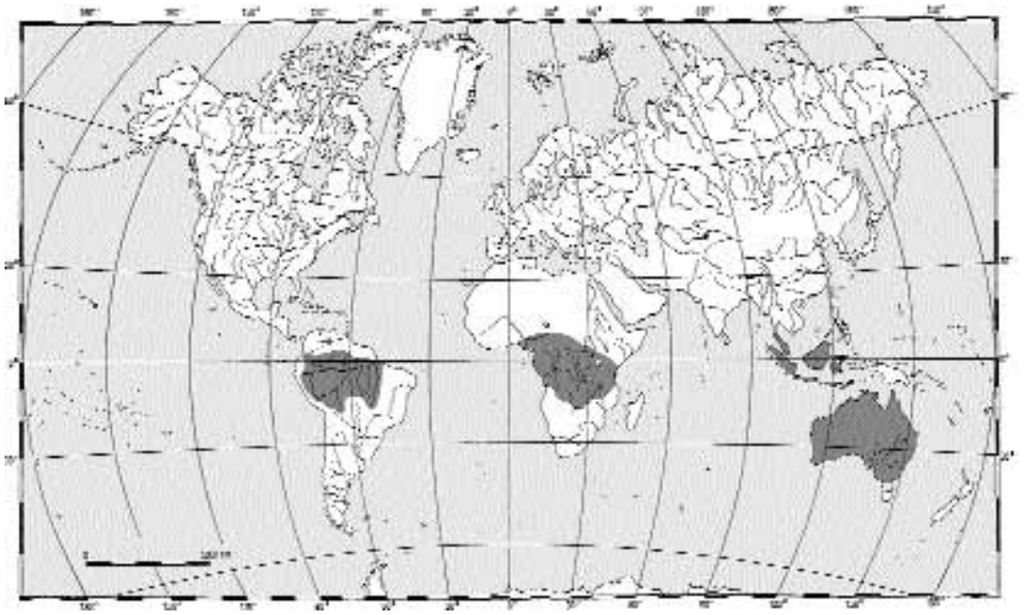

Fig. 125. Geographic distribution of the genus *Metania*.

20.xi.1854, coll. H. Bates, Bowerbank Collection. Other material. ZMB3735 – Rio Negro, Manaus, coll. Retzloff.

Description (most measurements from Volkmer-Ribeiro, 1986). Body shape bulbous to massive, often honey-comb shaped. Colour from dark grey to dark brown in dry specimens. Consistency hard and brittle. Surface reticulate and irregularly conulose due to the arrangement of fibres in superficial tracts. Oscules conspicuous and grouped within conules. Dermal membrane supported by conules. Subdermal cavities not observed. Ectosomal skeleton with spicules grouped in conules. Choanosomal skeleton alveolate with multispicular tracts with meshes increasing from the base to surface. Spongin sparse. Megascleres cylindrical (106–245 × 11–36 μm) from stout smooth oxeas to strongyles. Microscleres acanthostrongyles (acanthoxeas ?) (43–103 × 3–10 μm) with large lanceolate spines at the center and granules at the extremities. Gemmules, scattered in the skeletal network or rarely at the sponge base, enclosed in a variably developed cage of spiny megascleres ranging from oxeas to strongyles. Gemmular shape ovoidal (391–588 μm). Foramen with a well-developed tube-shaped collar of variable length, distinctly projected above the gemmular surface, ornamented by gemmuloscleres at the basis and with an undulated border. Theca with three layers. Outer layer well developed. Pneumatic layer trabeculated by spongin fibres. Inner layer of compact multilayered spongin. Gemmuloscleres radially embedded in the theca in one layer with boletiform rotule in the inner layer and the knoblike pseudo-rotule emerging from the outer layer. Gemmuloscleres boletiform (22–38 × 2–6 μm total length; 16–20 μm diameter rotule). Shafts with variable length of spines (2–4 μm). Proximal rotule large, stout, polygonal, with curved, undulated margins. Distal pseudo-rotule knob-like (7 μm) or aster-like shaped, with a few recurved, scattered spines or hooks, or approaching to a true rotule with marginal curved spines.

Ecology. On overhanging branches of seasonally submerged trees in periodically flooded habitats. Distribution. Brazilian and Venezuelan Amazonia, in the tropical rain forest realm.

Remarks. The systematics and biogeography of the genus was comprehensively studied by Volkmer-Ribeiro (1979, 1984, 1986), Volkmer-Ribeiro & Costa (1993), da Silva & Volkmer-Ribeiro (1998).

The type species of *Tubella* Carter, 1881c, *Spongilla paulata* Bowerbank, 1863: 453 (by subsequent designation, de Laubenfels, 1936a: 37), is possibly a misspelling by Gray (1867a) for *Spongilla paulula* Bowerbank, 1863: 453. If the type species designation is correct, then *Tubella* might become a senior synonym of *Trochospongilla*, because *S. paulula* is assigned to *Trochospongilla* Vejdovsky, 1883 and not to *Metania* Gray, 1867a, while at the same time *Tubella* is declared a junior synonym of *Metania* by Penney & Racek (1968). This proposed synonymy by Penney & Racek is maintained here in view of the confusion over the type species and its subsequent designation.

ACALLE GRAY, 1867

Synonymy

Acalle Gray, 1867a: 551.

Type species

Spongilla recurvata Bowerbank, 1863: 456 (by original designation).

Diagnosis

Metaniidae with encrusting growth form. Consistency of dry sponge fragile. Ectosomal skeleton with a notably dense network of strongyles. Choanosomal skeleton alveolate with paucispicular (strongyles) tracts. Sparse spongin. Megascleres strongyles to large oxeas. Microscleres absent. Gemmules subspherical at the base

of the sponge. Gemmular theca tri-layered. Gemmuloscleres of two types: pseudobirotules and tubelliform.

Scope and distribution

Monotypic. Neotropical Region.

Description of type species

Acalle recurvata (Bowerbank, 1863) (Figs 126–129).

Material examined. Holotype: BMNH 1931.4.23.3 – fragment, dry box 6, River Amazon, Villa Nova, coll. H. Bates, 20.xi.1854.

Description. Sponge consists of thin crusts. Colour light brown in dry specimens. Consistency of dry sponge fragile, crumbling. Surface even, smooth. Oscules numerous scattered inconspicuous simple and of variable size. Dermal membrane thin. Ectosomal skeleton is a notably dense network of strongyles. Choanosomal skeleton alveolate with paucispicular tracts. Sparse spongin. Megascleres stout smooth or microspined abundant strongyles (120–170 × 14–18 μm) and few smooth oxeas (350 × 20 μm) of unknown distribution. Microscleres absent. Gemmules subspherical (350–420 μm) in one stratum at the base of the sponge, with the foramen of the greater part of them directed downwards. Foramen is a short tubule with collar surrounded by distal pseudorotules of tubelliform gemmuloscleres. Gemmular theca trilayered. Well-developed outer layer with emerging gemmuloscleres pseudobirotules. Thick pneumatic layer of small chambers with boletiform (tubelliform) gemmuloscleres radially embedded with large rotules placed at the inner layer. Inner layer with 3–4 sublayers of compact spongin. Gemmuloscleres of two types: pseudobirotules (18–35 × 5–7 μm) with cylindrical shaft and hooks of umbonate pseudo-rotules stout and notably recurved bearing microspines at their apices; and tubelliform gemmuloscleres (30–33 × 1–5 μm) with the proximal large irregularly circular flat rotule (15–16 μm) with entire margin supporting a smooth shaft decreasing in thickness toward the distal end shaped as umbonate knob-like rotule with few teeth.

Ecology. In rivers on small stems of trees periodically submerged. Associated with *Metania reticulata* and *Saturnospongilla carvalhoi.* In dark Ygapos (dark brown waters) in virgin forest, margins of Amazon. Distribution. South America Amazon River, Beni River (Bolivia).

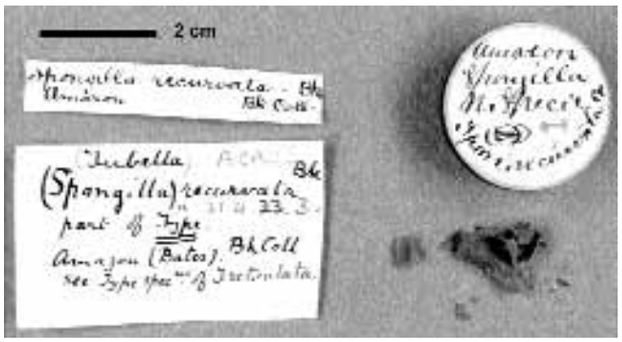

Fig. 126. *Acalle recurvata*, type material and original labels BMNH 1931.4.23.2.

CORVOMEYENIA WELTNER, 1913

Synonymy

Corvomeyenia Weltner, 1913: 480. *Parameyenia* Jewell, 1952: 455.

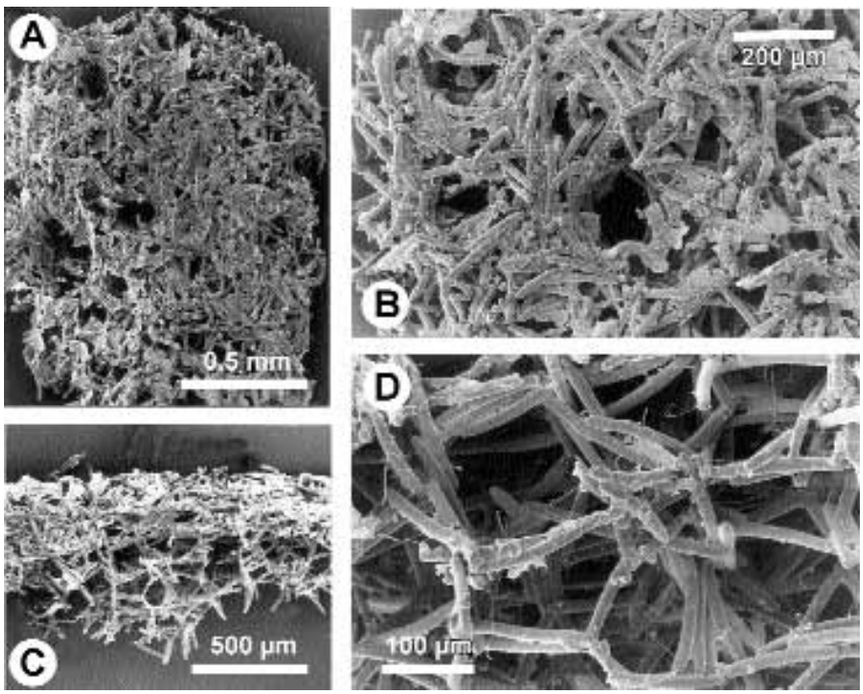

Fig. 127. *Acalle recurvata*, skeletal network, type material BMNH 1931.4.23.2. A–B, sponge surface (top views). C, cross section (top=surface). D, choanosomal skeleton.

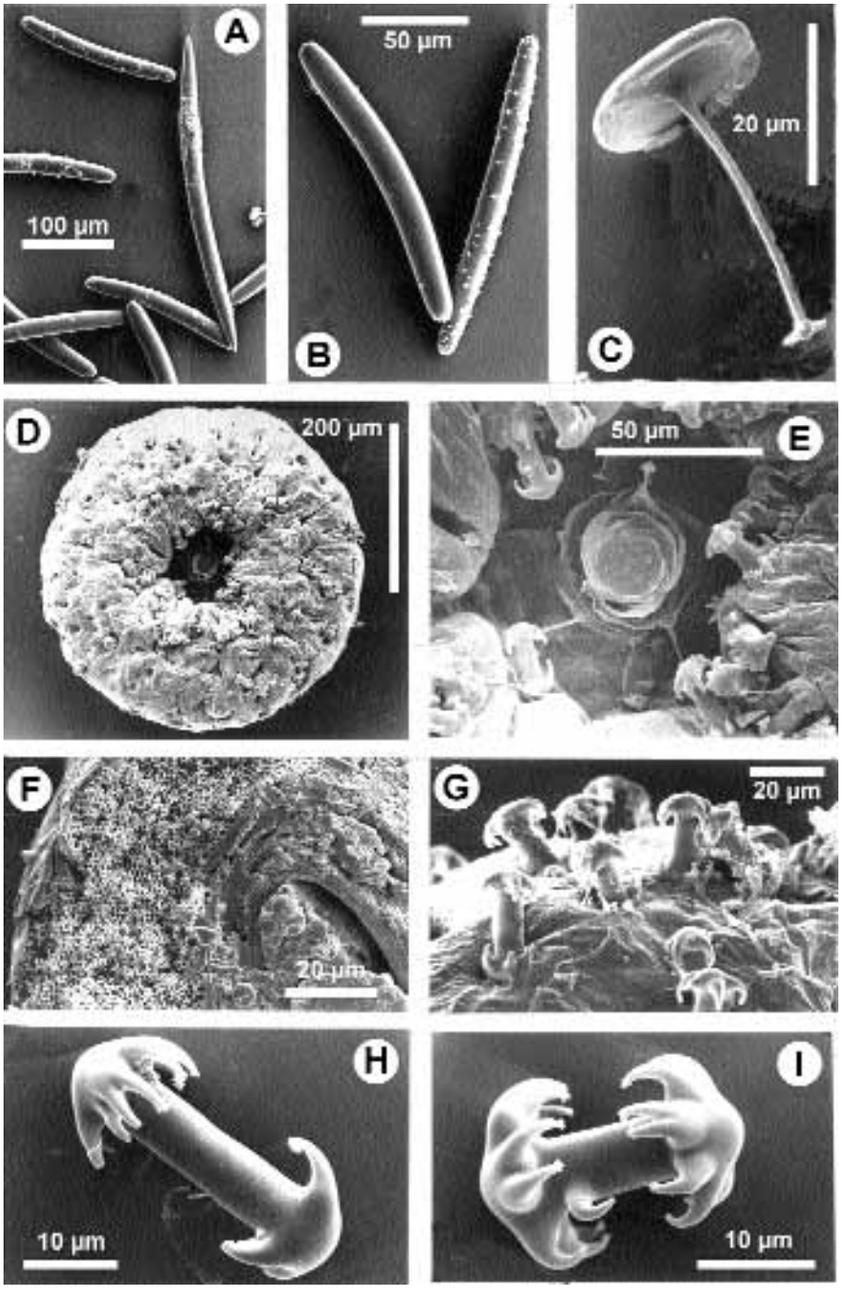

Fig. 128. *Acalle recurvata*, spicular and gemmular traits, type material BMNH 1931.4.23.2. A–B, megascleres. C, tubelliform gemmulosclere. D, gemmule. E, foramen. F, three layered gemmular theca. G, outer layer at the gemmular surface. H–I, gemmuloscleres.

Type species

Meyenia everetti Mills, 1884: 146 (by original designation).

Diagnosis

Metaniidae with encrusting growth form. Anisotropic slightly reticulated choanosomal skeleton with multispicular primary fibres and irregular secondary paucispicular tracts. Sparse spongin. Megascleres oxeas range from smooth to rarely spined or tuberculate. Microscleres pseudobirotules. Gemmules subspherical, single or grouped enclosed in cages of megascleres. Gemmular theca tri-layered. Gemmuloscleres pseudobirotules.

Scope and distribution

One other species. *C. carolinensis* Harrison, 1971 (South Carolina), NE USA (Massachusetts), S Canada (Nova Scotia, Quebec, Newfoundland).

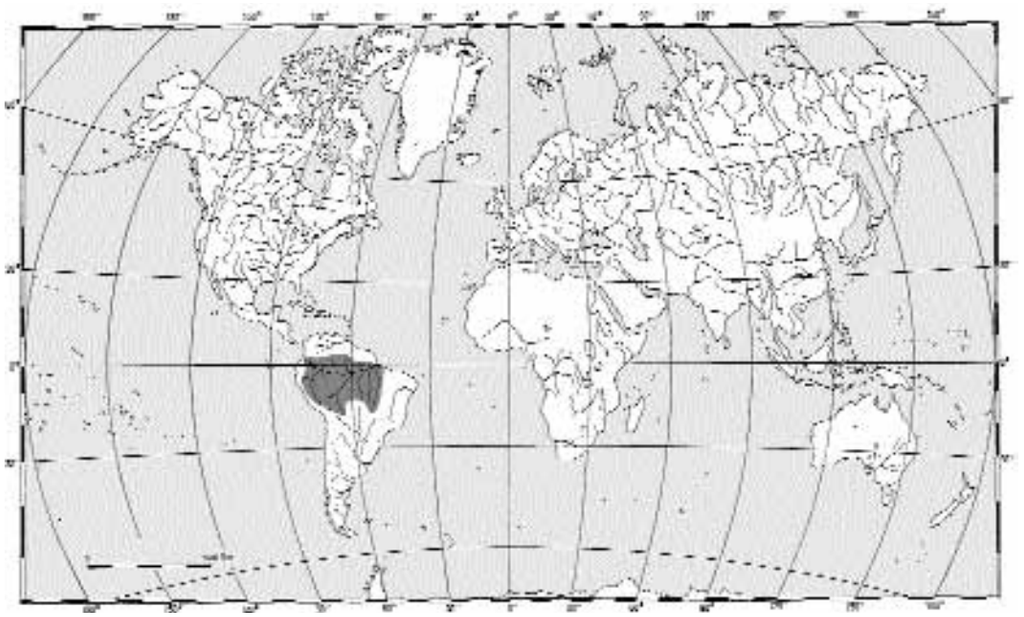

Fig. 129. Geographic distribution of the genus *Acalle*.

Fig. 130. *Corvomeyenia everetti*, topotype and original labels ANSP PO4594.

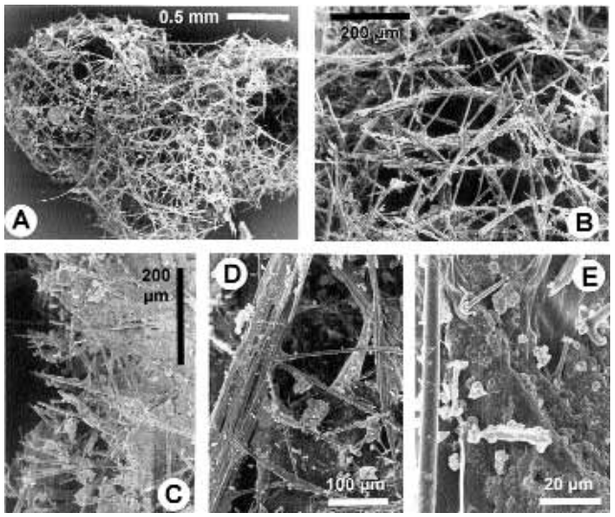

Fig. 131. *Corvomeyenia everetti*, skeletal network, topotype ANSP PO4594. A–B, gemmular cages. C, surface hispidation in cross section. D, choanosomal skeleton. E, microscleres in the choanosomal matrix.

Description of type species

Corvomeyenia everetti (Mills, 1884) (Figs 130–133).

Material examined. Topotype: ANSP PO4594, box 50–Gilder Pond, Mt. Everett, Massachusetts, A. Berklin, 23.ii.1986.

Description. Body shape consists of small thin crusts often with slender finger-like projections (2 mm). Consistency very soft and fragile. Colour emerald green to brown in life. Surface hispid due to spicule tufts. Oscules not conspicuous. Dermal membrane spicular, closely adherent. Subdermal cavities absent. Ectosomal skeleton with scattered single spicules. Choanosomal skeleton anisotropic, slightly reticulate, with multispicular primary fibres and irregular secondary paucispicular tracts. Sparse spongin. Megascleres slender feebly curved fusiform oxeas (143–285 × 3.5–14 µm) ranging from smooth to sparsely spined or tuberculate, with tips gradually or more abruptly pointed. Microscleres (16–26 × 1–3.5 µm) pseudobirotules, with straight to bent slender smooth shafts and pseudo-rotules dome-shaped (3–7 µm) ornamented with 5–8 recurved hooks. Gemmules subspherical (480–530 µm) single or grouped, each enclosed in a loose cage of megascleres (710–902 µm). Shape of foramen not evident. Gemmular theca tri-layered. Outer layer with emerging distal pseudo-rotules of gemmuloscleres. Pneumatic layer, not recorded in the present material, with minute and regular chambers. Inner layer multilayered (up to 40 µm). Gemmuloscleres radially arranged in a single series adhering to the inner layer with proximal rotules. Gemmuloscleres pseudobirotules with straight slender smooth shafts (42–72 × 3–5 µm), pseudo-rotules (16–19 µm) with up to 10 recurved hooks.

Ecology. Moderately acidic (pH 5–6.6) lentic waters, in transparent water, low in calcium (0.4 mg/l) (Jewell, 1935;

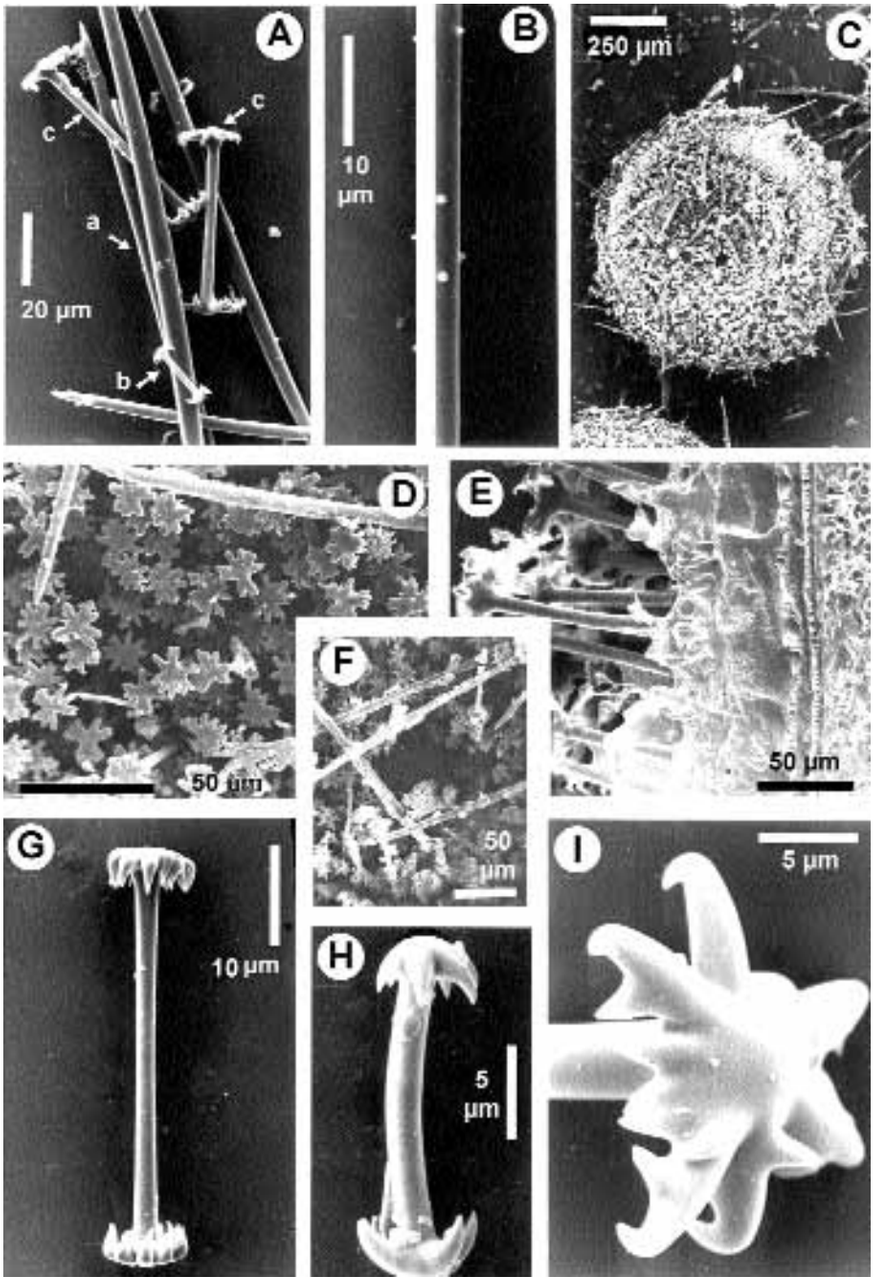

Fig. 132. *Corvomeyenia everetti*, spicular and gemmular characters, topotype ANSP PO4594. Aa, megasclere. Ab, microsclere. Ac, gemmulosclere. B, oxea with scattered spines. C, gemmule with remains of spicular cage. D, gemmule surface. E, cross section of gemmular theca. F, foramen area. G, gemmulosclere. H, microsclere. I, pseudorotule of a gemmulosclere.

Harrison, 1974). Very abundant in shallow water on submerged bushes, water-weeds, grass and wood debris. In symbiosis with green algae. Often associated with *Eunapius mackayi* and *Trochospongilla pennsylvanica*. Distribution. NE USA, S Canada.

Remarks. *Parameyenia* Jewell, 1952, with type species *Spongilla discoides* Penney, 1933 (by original designation), was considered to be a junior synonym of *Heteromeyenia ryderi* (Potts, 1882) (see Penney & Racek, 1968: 125), and therefore an objective junior synonym of *Racekiela*. However, Penney & Racek (1968) also declared *Parameyenia* a *nomen nudum*, and also a junior synonym of *Corvomeyenia*. This confusing situation arose because the original material of the type species *S. discoides* consisted of spicules of both *Corvomeyenia everetti* and *Anheteromeyenia ryderi*. Thus, *S. discoides* appears to be a 'chimaera' and consequently the genus *Parameyenia* is based on faulty characters (but not a *nomen nudum* as supposed by Penney & Racek). According to ICZN Article 17.1 the name is available, but needs to be fixed. Penney & Racek (1968) say *S. discoides* is a synonym of *A. ryderi* (and thus a synonym of *Racekiela*), but it is equally a synonym of *C. everetti* since material of that species is also present in the type material, and consequently we propose here this latter course of action, with *Parameyenia* a synonym of *Corvomeyenia* Weltner,

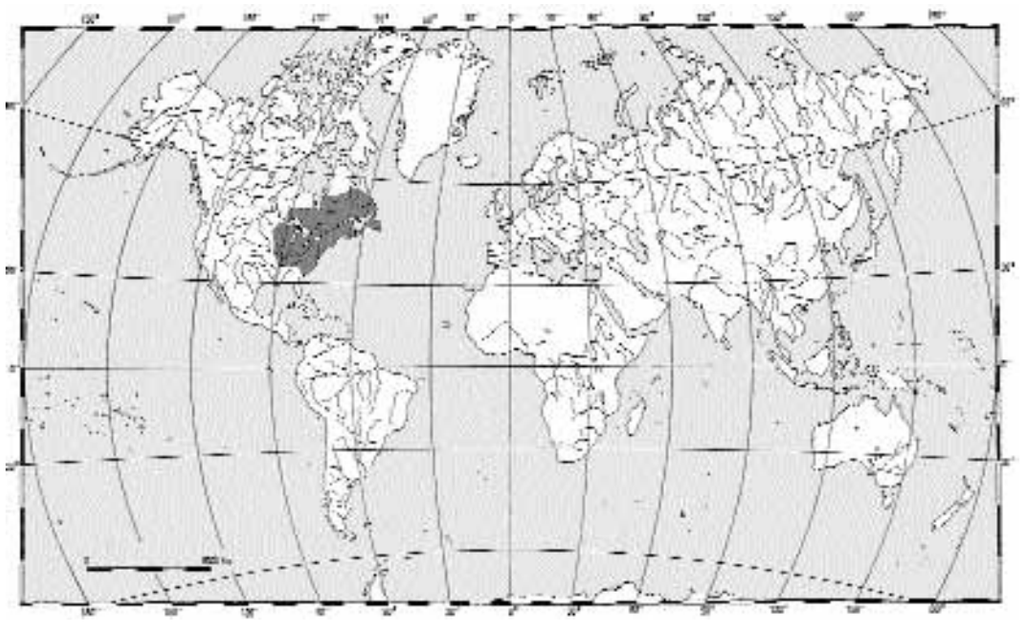

Fig. 133. Geographic distribution of the genus *Corvomeyenia*.

1913, which avoids the problem of seniority of the names *Parameyenia* Jewell, 1952 over *Racekiela* Bass & Volkmer-Ribeiro, 1998.

DRULIA GRAY, 1867

Synonymy

Drulia Gray, 1867a: 552. *Parmula* Carter, 1881c: 99.

Type species

Spongilla browni Bowerbank, 1863: 457 (N.B. De Laubenfels, 1936a cites Bowerbank, 1858: 315) (by subsequent designation; de Laubenfels, 1936a: 36).

Diagnosis

Metaniidae with body shape ranging from encrusting to massive, from nodular to globular around stems. Consistency of dry sponges very rigid, hard. Anisotropic choanosomal skeleton with open large reticulation of diverging multispicular primary fibres and irregularly scattered multispicular secondary tracts. Very sparse spongin. Megascleres smooth oxeas. Gemmules scattered towards the sponge surface, subspherical, enclosed in irregular cages of megascleres. Gemmular theca of compact spongin. Pneumatic layer atypical as large spaces between few trabecules of spongin displaced distally to the outer layer. Gemmuloscleres parmuliform regularly embedded in the inner layer of compact spongin, in a very variable number of layers.

Scope and distribution

Six other species: *D. geayi* (Gravier, 1899) (River Orinoco, Venezuela); *D. cristata* (Weltner, 1895) (Amazon River, Tapajos); *D. batesii* (Bowerbank, 1863) (River Amazon, Rio del Plata Argentina); *D. conifera* Bonetto & Ezcurra de Drago, 1973 (Rio Orenoco, Venezuela); *D. stenosclera* Volkmer-Ribeiro & Mothes de Moraes, 1981 (Rio Negro, tributary of the Amazon); *D. uruguayensis* Bonetto & Ezcurra de Drago, 1969 (Uruguay River, Paranà River, Suriname). Tropical and subtropical South America.

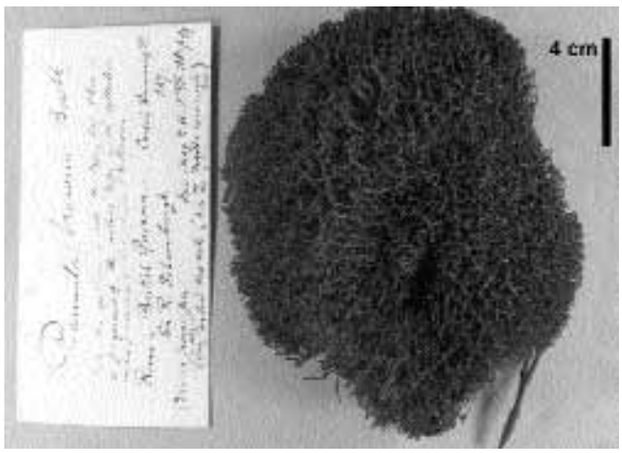

Fig. 134. *Drulia browni*, BMNH 1931.4.23.8, specimen in the same box of the type. "This specimen is not the type, but there is a fragment of the actual type in the collection presented to Bowerbank by R. Brown" (from the original label).

Description of type species

Drulia browni (Bowerbank, 1863) (Figs 134–137).

Material examined. Holotype: not seen. Other material. BMNH 1931.4.23.8 – dry box 6, Carter's running N° 527, River in British Guyana, R. Shomburgk. DTRG FW551 – Brasil, C. Volkmer-Ribeiro.

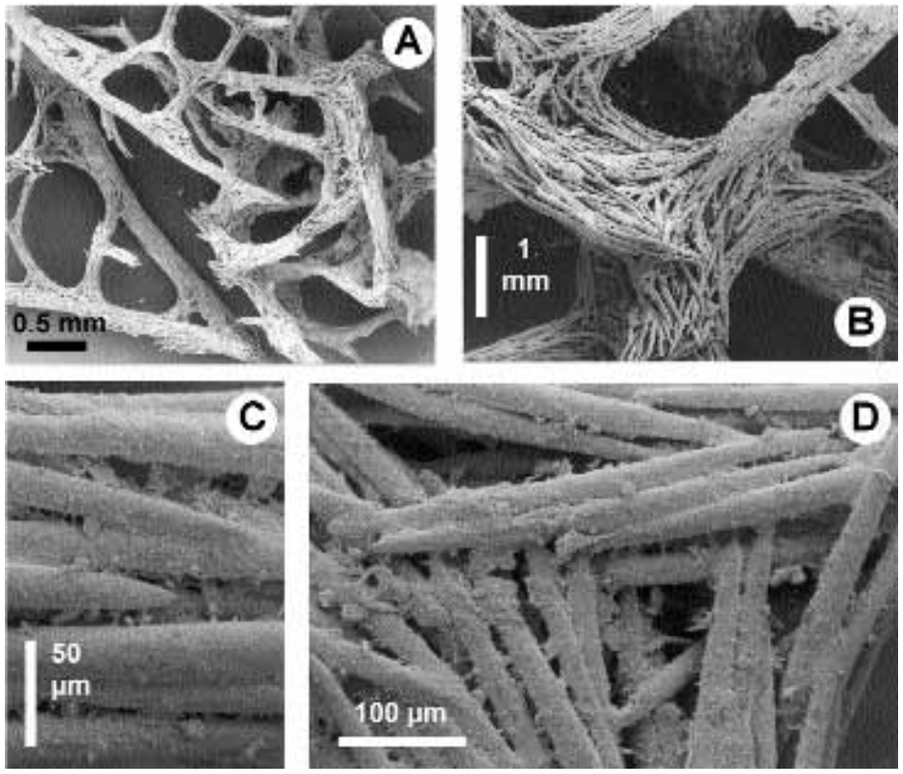

Fig. 135. *Drulia browni*, skeletal network, specimen BMNH 1931.4.23.8. A–B, choanosomal skeleton. C, multispicular tract. D, spicular arrangement at the junction of primary and secondary tracts.

Description. Body shape from encrusting to massive, from nodular to globular around stems. Bush-like grossly hispid surface due to apices of choanosomal fibres on conules. Colour from light green to grey, dark-brown to black in dry specimens. Consistency of dry sponges very rigid, hard, often brittle. Dermal membrane present in some areas. Subdermal cavities not observed. Oscules conspicuous. Ectosomal skeleton with apices of primaries forming conules. Choanosomal skeleton anisotropic with open very large (0.5–2 mm) reticulation of stout very firm multispicular ascending and diverging primary fibres and irregularly scattered multispicular secondary tracts. Very sparse spongin. Basal spongin plate adherent to substratum with an open network of flattened fibres. Megascleres smooth stout bent oxeas (300–550 × 16–43 µm). Small oxeas stout (128–290 × 22–28 µm) slightly curved acerate are involved in the gemmular cage structure. Microscleres rare within the skeletal network, slender and fusiform acanthoxeas (34–99 × 2–10 µm) with scattered spines bearing microspines. Gemmules (580–700 µm) subspherical, scattered towards the sponge surface and enclosed, singly or coupled, in a dense variably developed irregular cage of one or more layers of megascleres. The cage is connected to the gemmular surface by stout large spongin trabecules (fibres). Foramen as a short tube with collar. Gemmular theca bi-layered of compact spongin with outer layer notably developed and inner layer with adhering proximal rotules of gemmuloscleres. Pneumatic layer structure atypical with large spaces between few trabecules of spongin shifted distally to the outer layer. Gemmuloscleres parmuliform (25–28 µm), regularly embedded in the layer of compact spongin, in a very variable number of layers (1–4), with overlapping margins of rotules. The single circular proximal rotule (20–36 µm), with lower surface concave, supports a distal short acute conical stem oriented toward the outer layer.

Ecology. Sponges settle on periodically submerged (3–5 months) branches of trees and rocks. Distribution. Rio Amazon, Rio Negro (Brazil), Rio Beni.

Remarks. *Parmula* Carter, 1881c, with type species *Spongilla batesii* Bowerbank, 1858: 315 (by subsequent designation, de Laubenfels, 1936a: 37), is a synonym of *Drulia* on account of the inclusion of this species in this genus (present work).

HOUSSAYELLA BONETTO & EZCURRA DE DRAGO, 1966

Synonymy

Houssayella Bonetto & Ezcurra de Drago, 1966: 129.

Type species

Houssayella iguazuensis Bonetto & Ezcurra de Drago, 1966: 129 (by monotypy).

Diagnosis

Metaniidae with encrusting body shape with irregular surface. Skeletal network characterised by sparse megascleres

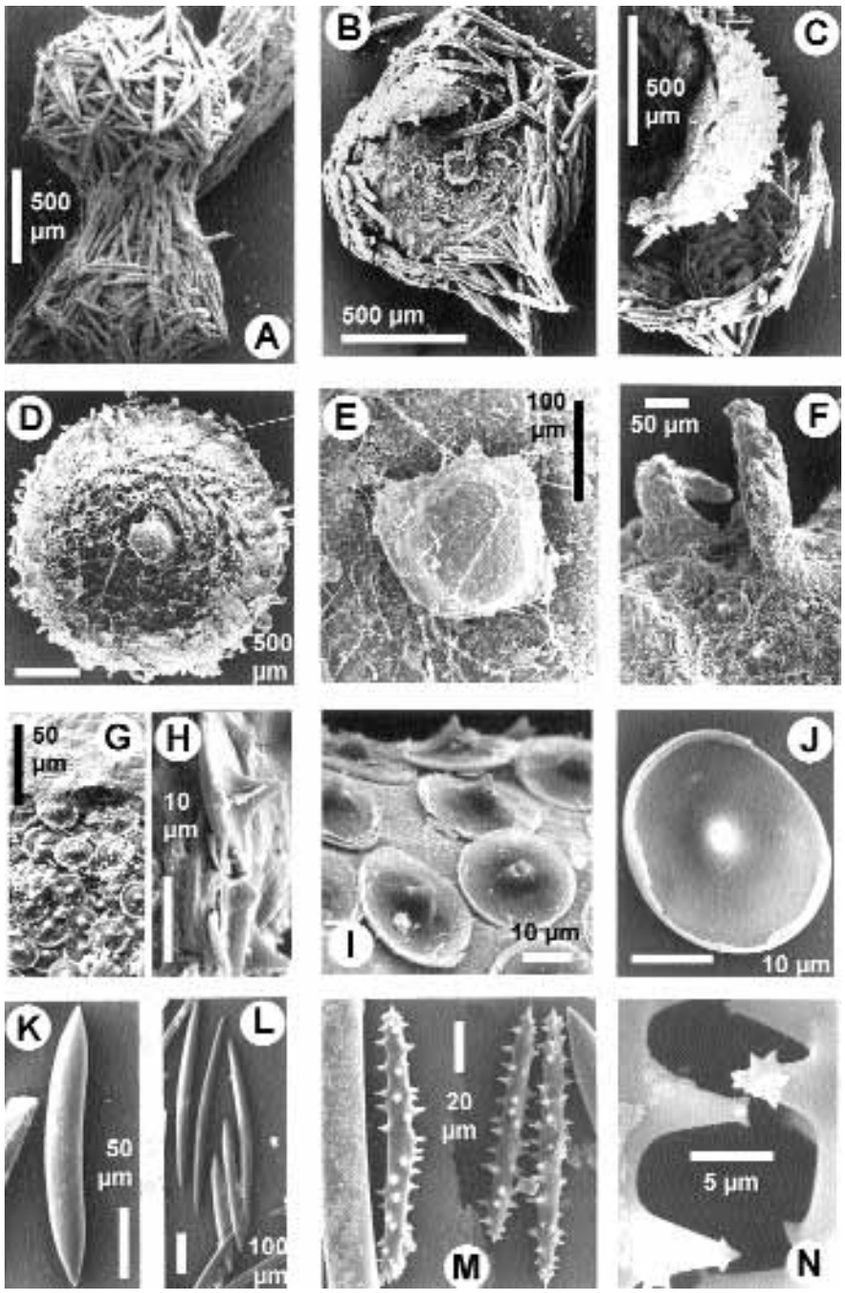

Fig. 136. *Drulia browni*, spicules and gemmules, specimen BMNH 1931.4.23.8. A, cage including two gemmules. B–C, gemmules partly free from cage. D, gemmule. E, foramen. F, spongin projections on outer gemmular layer. G–I, parmuliform gemmuloscleres adhering to the inner layer of the theca. J, gemmulosclere. K–L, megascleres. M, microscleres. N, spines of microscleres.

and abundant microscleres, with dense choanosome paucispicular fibres sometimes arranged perpendicularly. Megascleres range from oxeas in the skeleton to strongyles in the gemmular cage. Microscleres range from acanthostrongyles to oxeas and acanthoxeas with long perpendicular or slanting spines to aster-like shaped spicules. Gemmules in a single layer strictly adhering to the substrate, enclosed in a multigemmular cage of variably shaped acanthostrongyles. Foramen tube-shaped. Gemmuloscleres birotulates with an extremely variable shape radially arranged in a single layer.

Scope and distribution

Monotypic, Neotropical.

Description of type species

Houssayella iguazuensis Bonetto & Ezcurra de Drago, 1966 (Figs 138–140).

Material examined. Type material. INALI and MABA – not available, Salto San Martin, Iguazù falls, Paranà River,

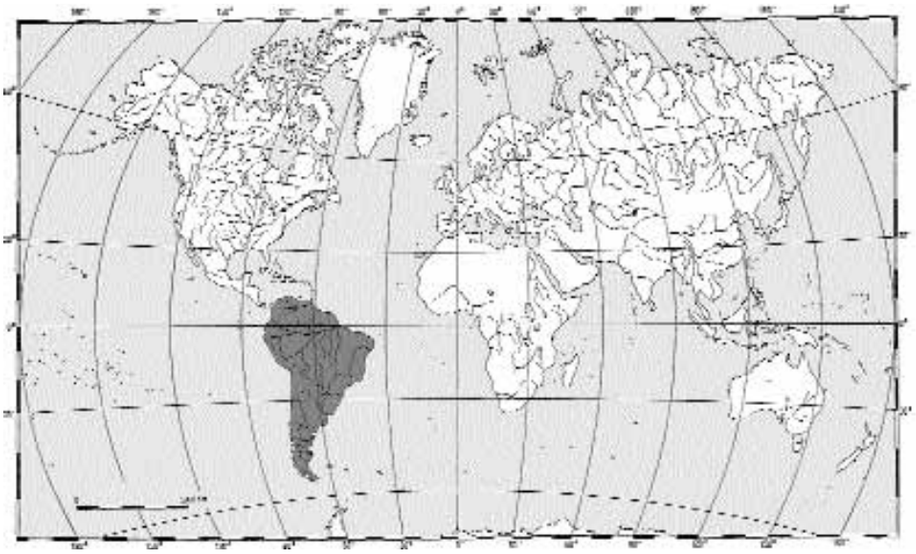

Fig. 137. Geographic distribution of the genus *Drulia*.

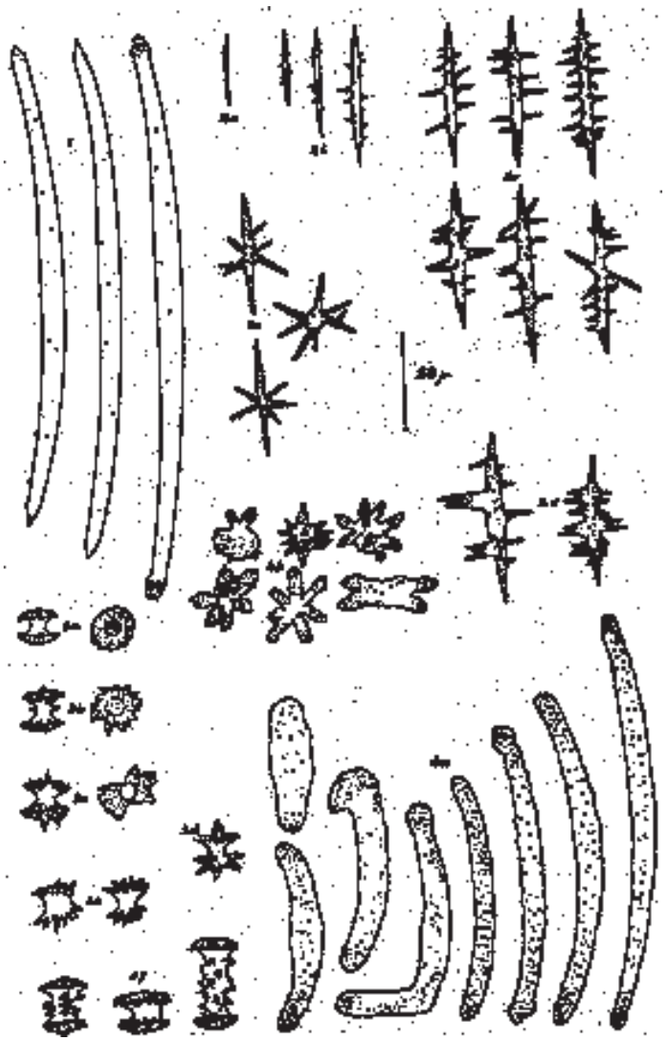

Fig. 138. *Houssayella iguazuensis*, original plate showing the spiculation of the type specimen (modified from Bonetto & Ezcurra de Drago, 1966).

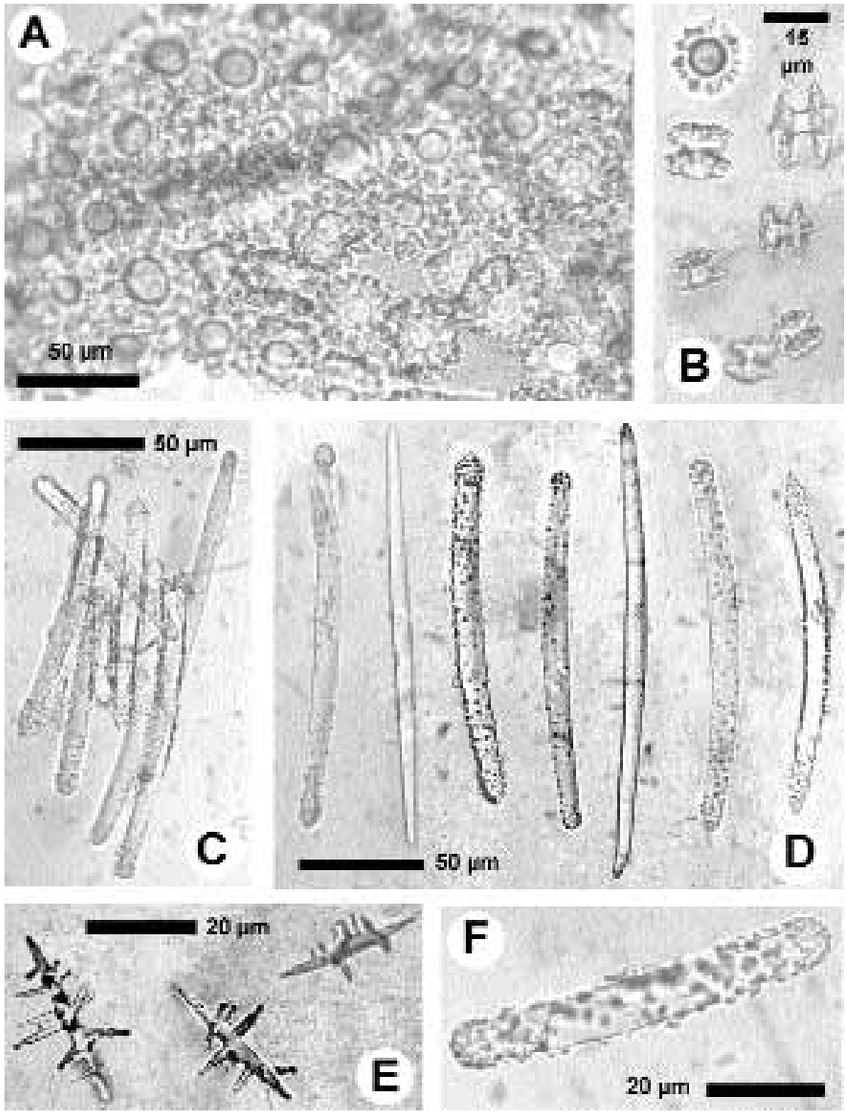

Fig. 139. *Houssayella iguazuensis*, spicular and gemmular characters, (FZRG) MCN 123. A, gemmuloscleres arrangement on the gemmule surface. B, gemmuloscleres. C–D, megascleres. E, microscleres. F, acanthostrongyle of the gemmular cage.

Province of Misiones, Argentina, A.A. Bonetto & I.D. Ezcurra de Drago. Other material. FZRG MCN123 – Rio Itù, 4.vi.1982, det. C. Volkmer-Ribeiro. DTRG FW594 – Rio Itù, 28.iv.1970, det. C. Volkmer-Ribeiro.

Description. Encrusting sponges with irregular shape up to 1.5 cm diameter. Irregular surface from emerging fibres. Dry sponges whitish. Oscules not conspicuous. Dermal membrane not observed. Subdermal cavities not observed. Ectosomal skeleton not evident. Choanosomal skeleton dense with paucispicular fibres sometimes arranged perpendicularly up to the sponge surface. Abundant microscleres irregularly tangentially arranged in a dense network. Megascleres (210–265 × 7–12 µm) from oxeas in the skeleton to strongyles in the gemmular cage from densely spined to smooth particularly at the apices. Microscleres (20–50 µm) range from thin strongyles with spines particularly dense at the tips, to oxeas and acanthoxeas, with long perpendicular or slanting spines ornamented by micro-spines, to an aster-like shaped spicules with up to 7 rays. Gemmules (600–950 µm) of pale yellow colour, grouped in a single layer at the sponge base strictly adhering to the substrate. Gemmules enclosed in a multi-gemmular (2–40) brown-yellowish cage of acanthostrongyles associated to spined spherules of silica with spines of variable length up to aster-like shaped spicules. Acanthostrongyles (100–210 × 12–18 µm) of the cage are curved with inflated tips and a highly variable shape, size and distribution of spines. Gemmular theca not observed. Foramen tube-shaped (30 µm) emerging from the gemmular cage. Outer layer not observed. Inner layer not observed. Gemmuloscleres stout microspined birotulates (17–45 µm total length, 8–15 µm shaft length), radially arranged in a single layer with an extremely variable shape. Microspined rotules (17–23 µm) irregularly indented.

Ecology. Rocky bottoms in rapids on lower side of rocks. Distribution. Argentina, River Paranà; Middle River,

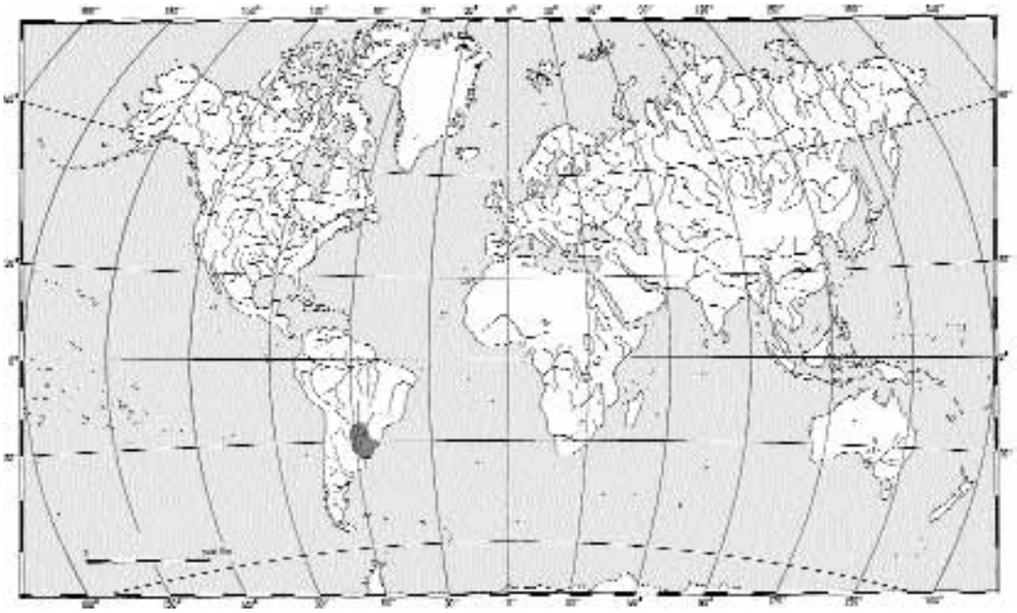

Fig. 140. Geographic distribution of the genus *Houssayella*.

Uruguay; S Brazil, lower River Uruguay; Brazil, Rio Grande do Sul, Itù River.

Remarks. Volkmer-Ribeiro & Rützler (1997) considered *Houssayella* to be closely related to *Pachyrotula* and *Heterorotula*.

FAMILY METSCHNIKOWIIDAE CZERNIAVSKY, 1880

Synonymy

Metschnikowiidae Czerniavsky, 1880. Type genus. *Metschnikowia* Grimm, 1876.

Definition

Spongillina with encrusting to globular body shape. Consistency solid. Ectosomal skeleton occurring at apex of ascending paucispicular tracts. Choanosomal skeleton is a paucispicular reticulation of triangular meshes with radial ascending paucispicular tracts without anastomoses. Sparse spongin. Megascleres range from smooth to tuberculate or densely spined oxeas with acerate tips. Microscleres absent. Gemmules absent. Larvae free, oval, ciliated.

Scope and distribution

Monotypic. Caspian Sea (Fig. 1).

METSCHNIKOWIA GRIMM, 1876

Synonymy

Metschnikowia Grimm, 1876: 3.

Type species

Metschnikowia tuberculata Grimm, 1876: 3 (by original designation).

Diagnosis

Metschnikowiidae with encrusting to globular body shape. Consistency solid. Ectosomal skeleton as apices of ascending paucispicular tracts. Choanosomal skeleton is a paucispicular reticulation of triangular meshes with radial ascending paucispicular tracts without anastomoses. Sparse spongin. Megascleres tuberculate spiny oxeas. Microscleres absent. Gemmules absent. Larvae free, oval, ciliated.

Scope and distribution

Monotypic. Caspian Sea.

Description of type species

Metschnikowia tuberculata Grimm, 1876 (Figs 141–142).

Synonymy. *Metschnikowia intermedia* Grimm, 1876. *Reniera flava* Grimm, 1876. *Amorphina caspia* Grimm, 1877.

Material examined. Type material: not available – Karabughas, E Caspian Sea (40°32′N, 2°33′E).

Description (from Dybowsky, 1880, Czerniavsky, 1880 and Koltun, 1962a). Body shape variable, from a thick crust (15 mm) to globular (5 cm diameter). Consistency solid. Colour from whitish to red. Surface with radiating exhalant canals. Scattered oscules. Subdermal cavities as exhalant canal. Ectosomal skeleton with apices of ascending paucispicular tracts protruding. Choanosomal skeleton a dense isotropic paucispicular (1–3) reticulation of triangular meshes with ascending paucispicular tracts radially arranged, without anastomoses. Sparse spongin. Megascleres stout acanthoxeas (96–186 × 6–15 μm), ranging from straight to slightly

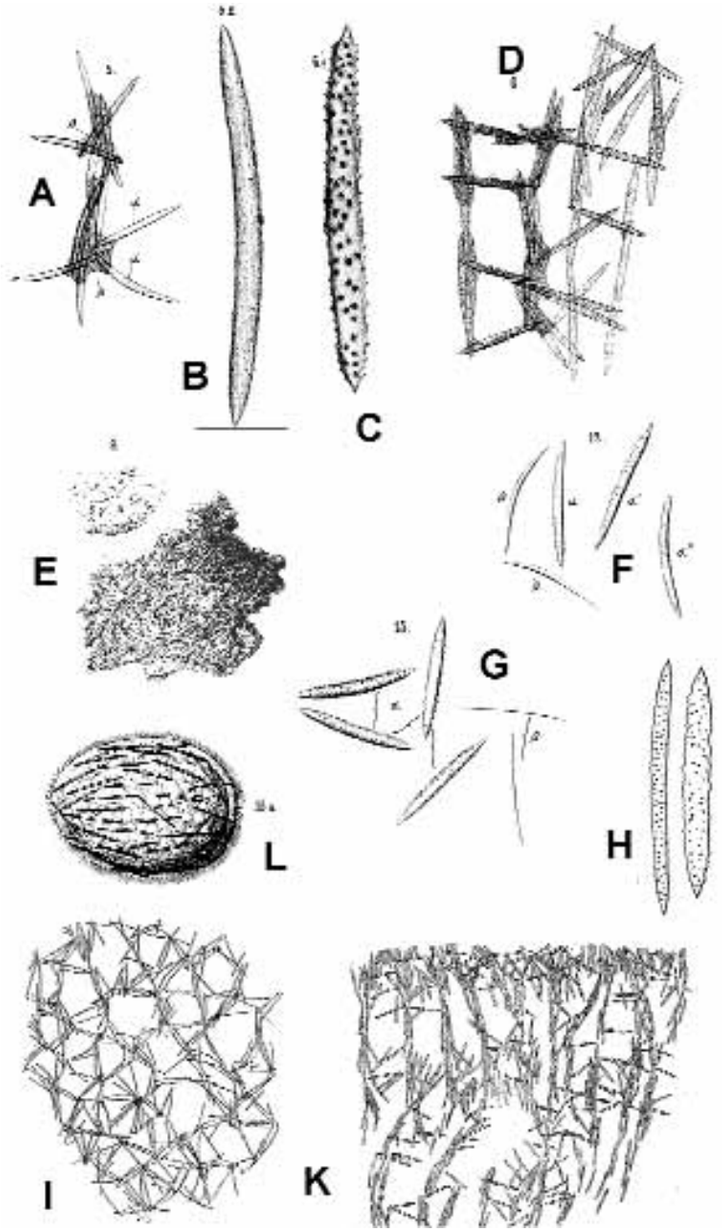

Fig. 141. *Metschnikowia intermedia*, spicules and skeleton organization, as represented in the literature. A, D, I, K, skeletal network. B, C, F, G, H, spiny oxeas. E, drawing of a fresh specimen. L, larva. (A–G, modified from Dybowsky, 1880; H, I, K, L, modified from Koltun, 1962a.)

curved, with dense acute to rounded tubercules for the entire length, and tips abruptly pointed. Axial canal extremely thin, open at the extremities. Microscleres absent. Gemmules absent. Larvae free, ciliated, oval (270 × 210 μm) with several tuberculate oxeas (45 μm length), ranging from straight to slightly curved.

Ecology. Common and abundant large specimens in brackish waters with salinity 10–18‰, 40 m depth. On stones or shells. Distribution. Caspian Sea, Karabughas, Baku.

Remarks. *Metschnikowia* was assigned to the subfamily Renierinae by Lundbeck (1902), and considered closely related to *Baikalospongia* and *Reniera* by Annandale (1914a). The sponge fauna of the Black and Caspian Seas were considered in constant contact by Czerniavsky (1880).

† FAMILY PALAEOSPONGILLIDAE VOLKMER-RIBEIRO & REITNER, 1991

Synonymy

Palaeospongillidae Volkmer-Ribeiro & Reitner, 1991b. Type genus. *Palaeospongilla* Ott & Volkheimer, 1972.

Definition

Spongillina consisting of a single genus of fossil sponges known from the Cretaceous (100-65 MYA), and sharing similarities

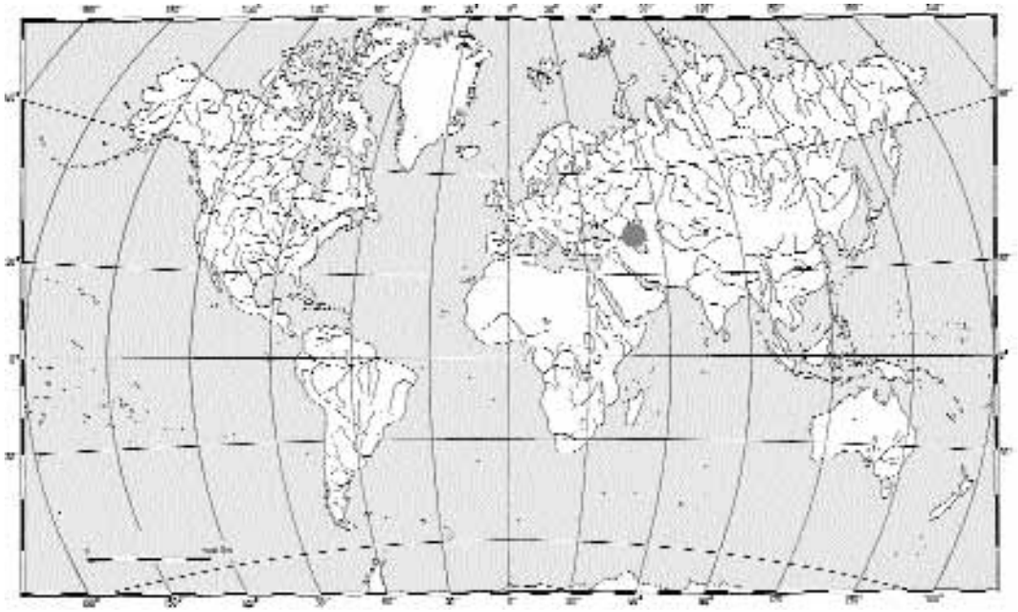

Fig. 142. Geographic distribution of the genus *Metschnikovia*.

in their skeletal, spicular and gemmular traits with modern freshwater sponges. Encrusting body shape. Reticulate skeleton. Abundant spongin. Megascleres smooth and spiny oxeas. Microscleres smooth and spiny oxeas. Gemmules range from naked, with spicular cage, to armoured by gemmuloscleres, with a pneumatic layer variably developed. Foramen well developed. Gemmuloscleres acanthoxeas to acanthostrongyles.

Scope and distribution

Monogeneric. Chubut Valley, Patagonia (Fig. 1).

† *PALAEOSPONGILLA* OTT & VOLKHEIMER, 1972

Synonymy

Palaeospongilla Ott & Volkheimer, 1972: 53.

Type species

Palaeospongilla chubutensis Ott & Volkheimer 1972: 53 (by original designation).

Diagnosis

Palaeospongillidae consisting of an encrusting fossil freshwater sponge from the Patagonian lower Cretaceous. Choanosomal skeleton anisotropic multispicular of smooth to spiny oxeas with abundant spongin. Microscleres acanthoxeas. Gemmules scattered in groups or singly. Two gemmular morphs naked without gemmuloscleres, and armoured by acanthostrongyles to acanthoxeas. Gemmular theca bi- or tri-layered. Gemmular cage of megascleres present.

Scope and distribution

Monotypic. Distribution. Chubut Valley, Patagonia.

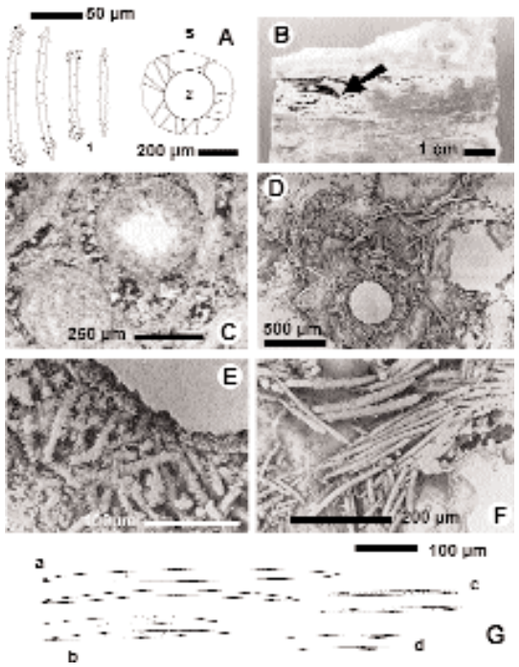

Fig. 143. *Palaeospongilla chubutensis*, spicules, skeleton architecture and gemmules, paratype MABA 24748. A1, gemmuloscleres. A2, gemmule. B, the fossil specimen (arrow) trapped in a sedimentary rock. C, gemmules in formation. D, gemmules and spicular texture of the sponge skeleton. E, gemmular theca. F, multispicular main fibre. Ga, Gb, megascleres. Gc, Gd, microscleres. (A, G, modified from Racek & Harrison, 1975; B–F, modified from Volkmer-Ribeiro & Reitner, 1991b).

Description of type species

Palaeospongilla chubutensis Ott & Volkheimer, 1972 (Figs 143–144).

Material examined. Holotype: Not seen – data based on the original description (Ott & Volkheimer, 1972), and redescriptions (Racek & Harrison, 1975; Volkmer-Ribeiro & Reitner, 1991b).

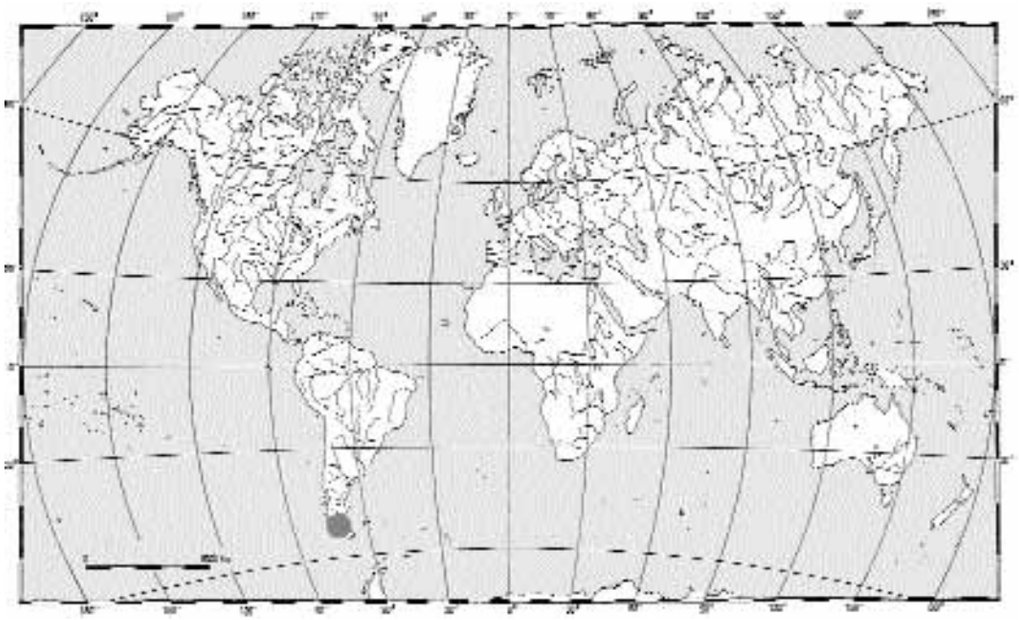

Fig. 144. Geographic distribution of the genus *Palaeospongilla*.

Description. (measurements from Racek & Harrison (1975) and Volkmer-Ribeiro & Reitner (1991b), respectively). Body shape encrusting (2–6 mm thick) with lobose contour. Surface reported as smooth although not well-discernable due to a calcareous algal covering. Ectosomal skeleton undetected. Choanosomal skeleton anisotropic with a regular meshwork and with multispicular (up to 40) vertical and horizontal fibres to form a reticulum of square meshes (1000 μm). Abundant spongin. Megascleres straight to feebly curved oxeas, ranging from stout (230–260 × 15–18 μm; 420–540 × 10–22 μm) cylindrical abruptly pointed and smooth, rarely bearing 1–2 spines, to abundant slender fusiform sharply pointed oxeas finely spined except at their tips (210–260 × 7–10 μm; 180–308 × 4–14 μm). Stout oxeas form the main skeleton of central and basal sponge body whereas slender oxeas are more frequent in peripheral skeletal fibres. Microscleres more abundant above the layer of gemmules, from straight to feebly curved abruptly pointed oxeas, from incipiently to conspicuously spined (179–190 × 3–4 μm) to smooth (77–147 × 3–5 μm; 100–110 × 9–10 μm). Gemmuloscleres (77–168 × 3.5–6 μm; 70–80 × 8 μm) slightly curved slender acanthostrongyles to acanthoxeas according to the position of spines at the tips. Spines, scattered along the entire surface, are more grouped and recurved at the tips, often with a single spine as prolongation of the axis. Gemmules subspherical (483–644 μm; 490–570 μm) diffuse in the skeleton single or grouped. Two types of gemmules: armoured and naked. Naked gemmules without gemmuloscleres, enveloped in a cage of spined megascleres, bi-layered gemmular theca with thin pneumatic layer and conspicuous inner layer, foramen simple without a porus tube. Armoured gemmules with gemmuloscleres variably arranged in one layer crossing each other at various angles; thick tri-layered theca, outer layer ill defined, well developed inner (20 μm) and pneumatic (100 μm) layers, nipple-like foramen.

Ecology. Cretaceous lacustrine sediments of the Chubut Valley. The palaeohabitat was a lake subjected to long periods of drought. Sponge settled around stems of aquatic plants (gymnosperm) and plants remains were seasonally submerged. The sponge surface was covered by a calcareous layer of algae (Cyanophyceae). Distribution: Rio Chubut Valley, 16 km NNW of Cerro Condor (type locality), Chubut Province, Argentina.

Remarks. *Palaeospongilla chubutensis* from the Lower Cretaceous, together the finding of spicular remains in freshwater deposits of the Upper Jura (Young, 1878), represents the oldest confirmed origin of spongillid-like freshwater sponges from fossil evidence. In spite of "the careful examination of the skeletal arrangement of *P. chubutensis* … demonstrated beyond doubt that the spicular components of the fossil belong to a single species" (Racek & Harrison, 1975), from this material a second species was subsequently described, *Spongilla patagonica* Volkmer-Ribeiro & Reitner, 1991b, based on the presence of a second gemmular type. The production of two gemmular morphs, however, is also known from two genera of Spongillidae (*Spongilla* and *Corvospongilla*), both characterised by naked and armoured gemmules, with or without pneumatic layer, and hence the recognition of a second species may be erroneous.

FAMILY POTAMOLEPIDAE BRIEN, 1967

Synonymy

Potamolepidae Brien, 1967. Potamophloiinae Brien, 1969. Type genus. *Potamolepis* Marshall, 1883.

Definition

Spongillina with body shapes ranging from encrusting, massive to arborescent with irregular lobes, ridges or branches. Consistency ranges from rigid to stony hard. Surface smooth

or conulated. Ectosomal skeleton, if present, with microscleres in the dermal membrane. Choanosomal skeleton alveolate-reticulate, notably dense at the surface and more loose and irregular at the sponge base. Very sparse spongin. Megascleres strongyles, varying from smooth to granular or spiny with inflated ends. Microscleres, if present, are slender oxeas in the ectosome. Gemmules located at the sponge base or strictly adhering to the substratum. Gemmular theca monolayered of compact spongin with tangentially more-or-less embedded gemmuloscleres. Gemmuloscleres short or ovular strongyles. Larvae paranchymella, entirely ciliated, with smooth oxeas.

Scope and distribution

Six genera: *Potamolepis*, *Echinospongilla* nom. nov., *Potamophloios, Oncosclera, Sterrastrolepis, Uruguaya*. Distribution. Tropical areas of Afrotropical, Neotropical and Australian (New Caledonia, Fiji) Regions (Fig. 1).

KEY TO GENERA

(1) Gemmules are present, gemmuloscleres are short irregular strongyles 2
Gemmules are absent 3

(2) Microscleres are very spiny ornamented oxeas with tubercles or spines arranged in rosettes; megascleres are stout, slightly curved, ranging from smooth to uniformly granulated strongyles with inflated tips; gemmules are present; gemmuloscleres ovoid or variably spherical with an irregular surface apart from a unilateral smooth area; gemmuloscleres are tangentially embedded in the gemmular theca ..... ***Sterrastrolepis***
Microscleres are absent 4

(3) Megascleres are only smooth strongyles; microscleres, gemmules and gemmuloscleres are absent ..... ***Echinospongilla nom. nov.***
Megascleres are smooth strongyles and smooth oxeas; microscleres, gemmules and gemmuloscleres are absent ..... ***Potamolepis***

(4) Megascleres are strongyles 5
Megascleres are smooth, stout, slightly bent oxeas rarely bearing tubercles or granules with acerate tips; microscleres are absent; gemmules are present; gemmuloscleres are highly variable from true strongyles to irregular ovoid strongyles, from smooth to curved with short spines and tubercles particularly dense at the spicular apices, tangentially arranged ..... ***Oncosclera***

(5) Megascleres are smooth slightly bent strongyles with inflated ends; microscleres are absent; gemmules are present; gemmuloscleres are from elongate to ovular smooth strongyles tangentially embedded in the gemmular theca ..... ***Potamophloios***
Megascleres are granulated strongyles associated with a stout smooth oxeas (present only in the gemmular cage); microscleres are absent; gemmules are present; gemmuloscleres are smooth curved strongyles (beam-like) tangentially arranged ..... ***Uruguaya***

POTAMOLEPIS MARSHALL, 1883

Synonymy

Potamolepis Marshall, 1883: 405.

Type species

Potamolepis leubnitziae Marshall, 1883 (here designated).

Diagnosis

Potamolepidae with body shape encrusting and notably hard. Dense alveolate choanosomal skeleton of conspicuous paucispicular tracts. Sparse spongin. Megascleres stout skeletal strongyles to oxeas in the dermal membrane. Gemmules absent.

Scope and distribution

Six other species: *P. chartaria* Marshall, 1883 (Isangila Congo basin, Lake Niger-Mali, Lake Tanganyika); *P. pechuelii* Marshall, 1883 (Matadi-Matemba Congo basin, Lake Tanganyika); *P. weltneri* Moore, 1903 (Lake Tanganyika, N Rhodesia (Zimbabwe)); *P. marshalli* Burton, 1938 (Matadi Congo basin); *P. micropora* Burton, 1938 (Matadi-Congo basin); *P. thysi* Brien, 1968 (Lake Kumba, Lake Barombi, Cameroun); *P. belingana* Levi, 1965 (Cameroun, River Ivindo Gabon). Distribution. Afrotropical Region.

Description of type species

Potamolepis leubnitziae Marshall, 1883 (Figs 145–148).

Material examined. Holotype: Not seen. Other material. BMNH 1938.2.3.9 – Barrage de Mateba, Congo River, coll. Schouteden.

Fig. 145. *Potamolepis leubnitziae*, specimen BMNH 1938.2.3.9.

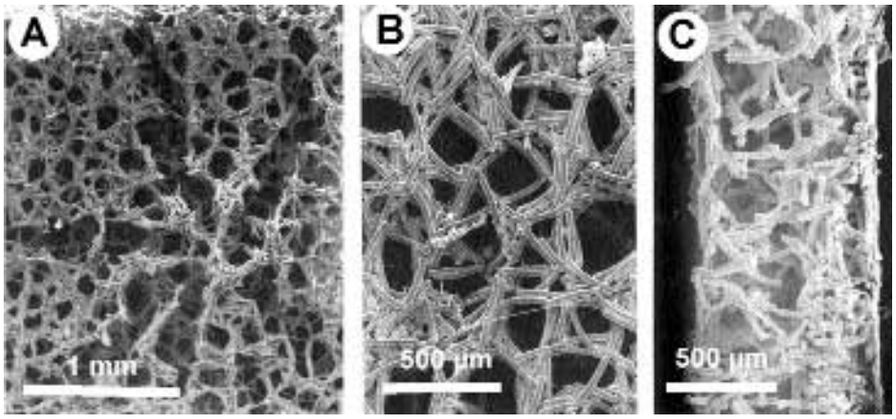

Fig. 146. *Potamolepis leubnitziae*, skeletal network of a specimen, BMNH 1938.2.3.9. A, sponge surface in the oscular area. B, ectosomal network. C, cross section with smooth sponge surface (left) and basal spongin plate (right).

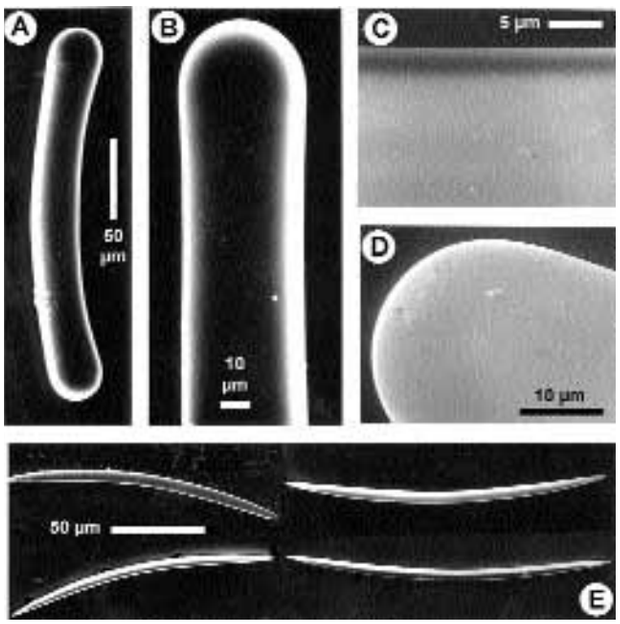

Fig. 147. *Potamolepis leubnitziae*, spicules, specimen BMNH 1938.2.3.9. A–D, different views of smooth strongyles. E, oxeas.

Description. Encrusting body shape (1–1.5 mm thick). Colour yellowish-whitish to ash-grey to light brown or brown in dry specimens. Consistency hard and brittle. Surface finely porous with scattered conules (0.25–0.40 mm high) sometimes arranged in rows. Oscules conspicuous (0.5–1 mm in diameter) from ovate to pentagonal shape, with finely notched margins at the apex of each conule. Dermal membrane spicular. Subdermal cavities developed as star-shaped canals, starting from each oscular cavity, horizontally running with dichotomous branches often connecting with neighbouring oscula. Inhalant apertures ca. 0.1 mm diameter. Basal spongin plate well developed. Ectosomal skeleton with thin tangential spicules in the dermal membrane. Choanosomal skeleton with a dense alveolate paucispicular network (mesh 300 µm) with conspicuous tracts. Sparse spongin. Megascleres smooth stout strongyles with inflated ends (200–237 × 31.2–48.8 µm, mean 214.3 × 40 µm). Smooth oxeas (162.7–214 × 4.6–9.2 µm, mean 184 × 6 µm) tangentially arranged in the dermal membrane. Microscleres absent. Gemmules absent.

Ecology. In Congo River on dry flat surfaces of clay-slate rocks of the inundated level from June to September, submerged at a depth of 2–3 m during summer (high-water season) when running waters reach a notable flow (1 mile/hour). *Potamolepis leubnitziae* was associated with *P. chartaria* and *P. pechuelii* to cover the substratum in large patches (up to 1 m^2) with single specimens not larger than 20–30 cm in diameter. Sponges did not colonize the neighbouring diabase-rocks. Often associated with *Chama*-like bivalves. Distribution. Congo-Zaire Basin, Lake Moero, River Niger (Mali), Lake Tanganiyka.

Remarks. Some species initially assigned to *Potamolepis* were subsequently transferred to *Potamophloios* by Brien (1970b) based on the possession of gemmules.

ECHINOSPONGILLA NOM. NOV.

Synonymy

[*Echinospongia*] Brien, 1974: 605 (preocc.).

Type species

Echinospongia brichardi Brien, 1974: 605 (here designated).

Diagnosis

Potamolepidae encrusting and notably hard with regular conulose surface. Choanosomal skeleton extremely compact without a clear reticulation, multispicular fibres converge to form conules. Sparse spongin. Megascleres smooth strongyles and slender oxeas. Microscleres absent. Gemmules absent. Larvae parenchymella.

Scope and distribution

Monotypic genus. Lake Tanganyika.

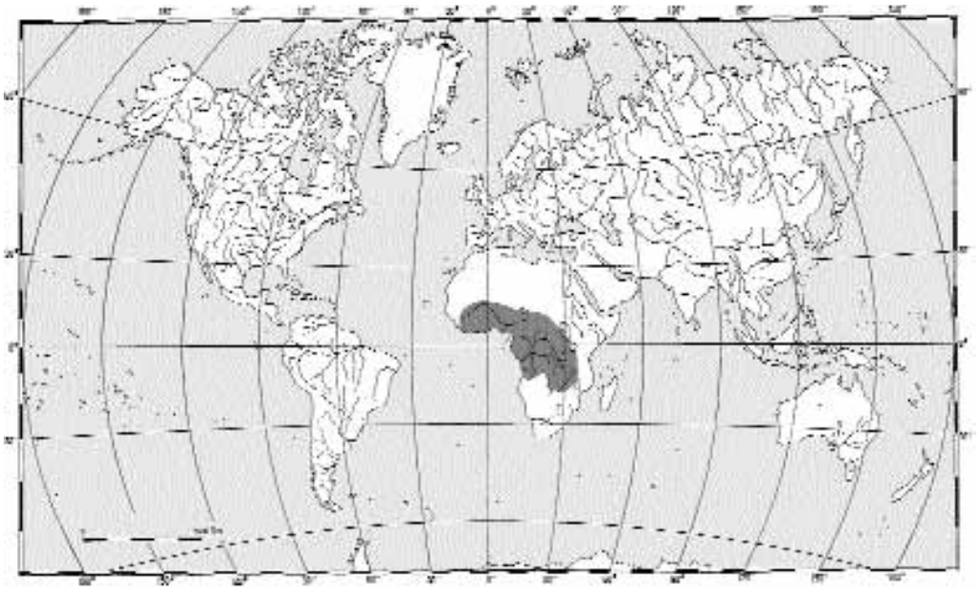

Fig. 148. Geographic distribution of the genus *Potamolepis*.

Fig. 149. *Echinospongilla brichardi*, holotype and original label, MRAC 1430.

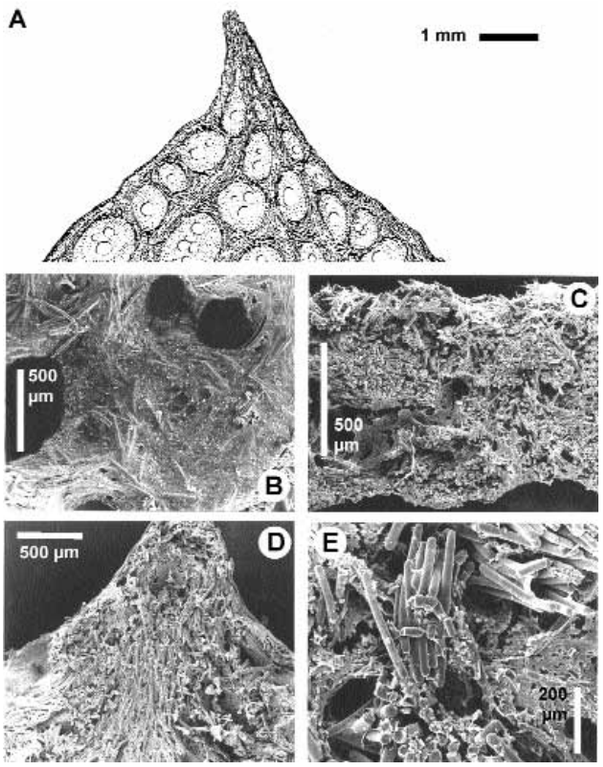

Fig. 150. *Echinospongilla brichardi*, skeletal network, holotype MRAC 1430. A, skeletal arrangement in a conule (modified from Brien, 1974). B, sponge surface showing the ectosomal skeleton and openings of the aquiferous system. C, section across the sponge body (top = sponge surface). D, skeletal arrangement in a conule with a central spicular axis (cross section). E, choanosomal multispicular tracts (cross section).

Description of type species

Echinospongilla brichardi (Brien, 1974) (Figs 149–152).

Material examined. Holotype: MRAC 1430 (IZUGFW489) – fragment (2 × 1 cm), leg. M. Brichard, v.1973, Urundi, Lake Tanganyika, Usumbura,

Description. Encrusting body shape, very thin (2 mm). Colour light brown. Consistency hard. Surface conulose, with regularly scattered short acute conules (2–4 mm high). Oscules (1 mm) few and scattered at the base of conules. Inhalant openings well evident and grouped in pore-sieves lined by skeletal meshes on surface conules. Dermal membrane well-developed. Ectosomal skeleton on apices of conules. Choanosomal skeleton extremely compact more loose at the sponge base, without a clearly evident reticulation but with ascending multispicular fibres emerging at the sponge surface as conules. Sparse spongin. Basal spongin plate well-developed and brown. Megascleres smooth stout (175–230 × 9–22 µm) and slender (175–200 × 4.5–6.5 µm) strongyles with sometimes inflated distal ends. Slender oxeas (175–195 µm) are also reported in the original description. Microscleres absent. Gemmules absent. The specimen was in sexual reproductive phase with several oocytes, embryos and larvae within the basal portion of the sponge. Spermatic cysts were never found. (Parthenogenetic?). Larvae (350–380 × 320 µm) parenchymella with slender smooth oxeas and a small anterior cavity.

Ecology. On rocks. Sexual reproduction in May.

Remarks. [*Echinospongia*] Brien, 1974 is preoccupied by *Echinospongia* Gray, 1867a (type species *E. australis* Gray, 1870a), a junior synonym of *Axos* (Hadromerida, Hemiasterellidae), and requires a new name.

POTAMOPHLOIOS BRIEN, 1970

Synonymy

Potamophloios Brien, 1970b: 25.

Type species

Potamolepis stendelli Jaffe, 1916 (here designated).

Diagnosis

Potamolepidae with large body size (50 × 15 cm) ranging from encrusting to massive and lobate. Colour from grey to dark grey. Consistency hard. Surface irregular with conules. Ectosomal skeleton with tangential small oxeas. Choanosomal skeleton dense alveolate with a more open network in the basal portion. Megascleres stout smooth strongyles with inflated ends but also more slender strongyles are present. Microscleres oxeas as dermal spicules. Gemmules single or grouped, from subspherical to oval or hemispherical when strictly adhered to the substratum. Foramen primitive with a simple inconspicuous concavity. Theca monolayered of compact spongin Gemmuloscleres smooth to spined, elongated to oval strongyles.

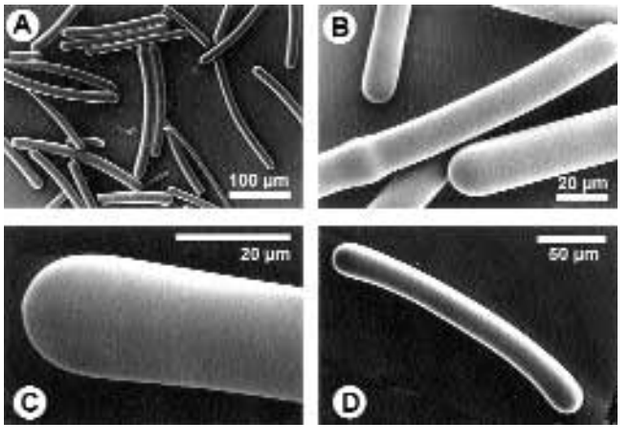

Fig. 151. *Echinospongilla brichardi*, spiculation, holotype MRAC 1430. A–B, D, megascleres. C, smooth surface of a strongyle.

Scope and distribution

Four other species: *Potamophloios songoloensis* Brien, 1970b (Zaire, Zambia); *P. hispida* Brien, 1970b (Zaire, Zambia); *P. gilberti* Brien, 1970b (Congo Basin); *P. symoensi* Brien, 1970b (Congo Basin). Distribution. Tropical Afrotropical Region.

Description of type species

Potamophloios stendelli (Jaffe, 1916) (Figs 153–157).

Material examined. Holotype: MRAC 410-411 – Kasenga Lake Luapula, on shell fragments, mission Stappers, 25.vii. 1911, 0–10 m depth, by dredge. Other material. MRAC 1324 – Lukonzolwa Lake Moero, iii.1966, J. Symoens, det. Brien 1969.

Description. Encrusting body shape. Colour from light grey to dark grey. Irregular surface due to the presence of conules. Consistency hard but very fragile, particularly at the sponge base that generally remains adherent to substrata. Oscules few and scattered at the basis of conules. Exhalant star-shaped canals convergent toward the osculum at the sponge surface. Dermal membrane reinforced by spicules. Basal plate with irregularly scattered strongyles. Ectosomal skeleton with tangential smooth oxeas.

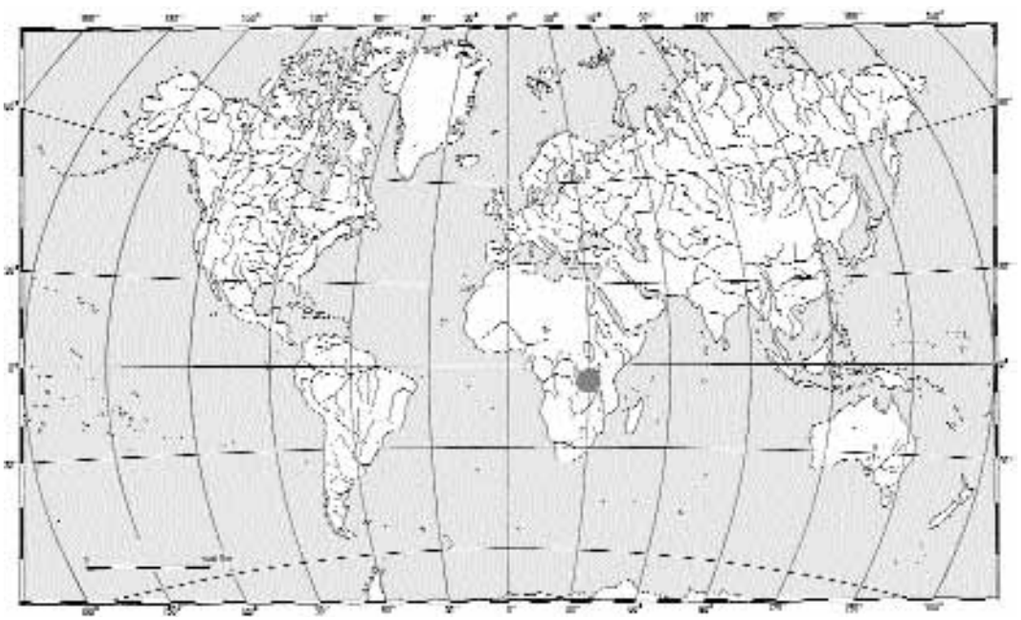

Fig. 152. Geographic distribution of the genus *Echinospongilla*.

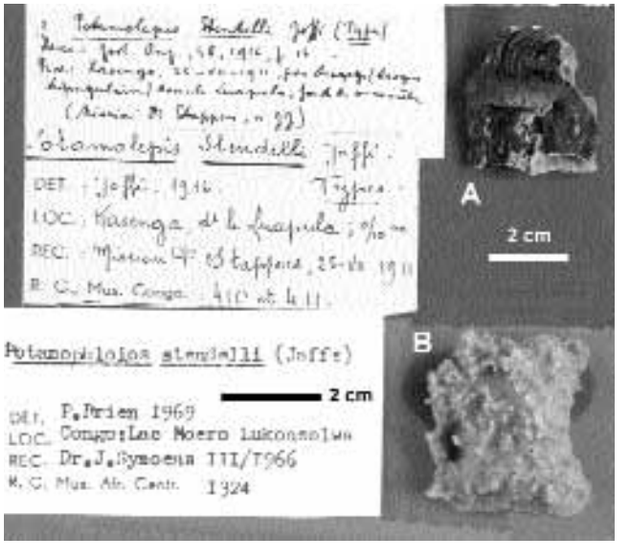

Fig. 153. *Potamophloios stendelli*. A, type specimen MRAC 410-411, without gemmules. B, another specimen with gemmules MRAC 1324.

Choanosomal skeleton alveolate with meshes of 300–400 μm, also reported as reticulate in the original description; a more open skeletal arrangement is peculiar at the basal portion where scattered strongyles are tangentially arranged in the basal plate. Megascleres (150–200 μm) stout smooth slightly bent strongyles with inflated ends; rare smooth oxeas and spiny strongyles are also present in the material examined. Microscleres absent in the choanosome. Gemmules single or in groups, with a highly variable shape ranging from subspherical to oval, to lobate, to hemispherical when strictly adhered to the substratum. Foramen primitive as a simple inconspicuous concavity, without tube or collar. Theca monolayered of compact spongin. Outer layer ill-defined. Pneumatic layer absent. Gemmuloscleres embedded in the compact spongin theca together few strongyle megascleres. Gemmuloscleres (20–50 μm) highly variable from elongated to ovular strongyles, from smooth to spined. Spines scattered and short.

Ecology. Unknown. Distribution. Lake Moero, Lake Luapula in the Congo Basin.

Remarks. This species was originally assigned to the genus *Potamolepis* Marshall, 1883 but was subsequently moved to a new

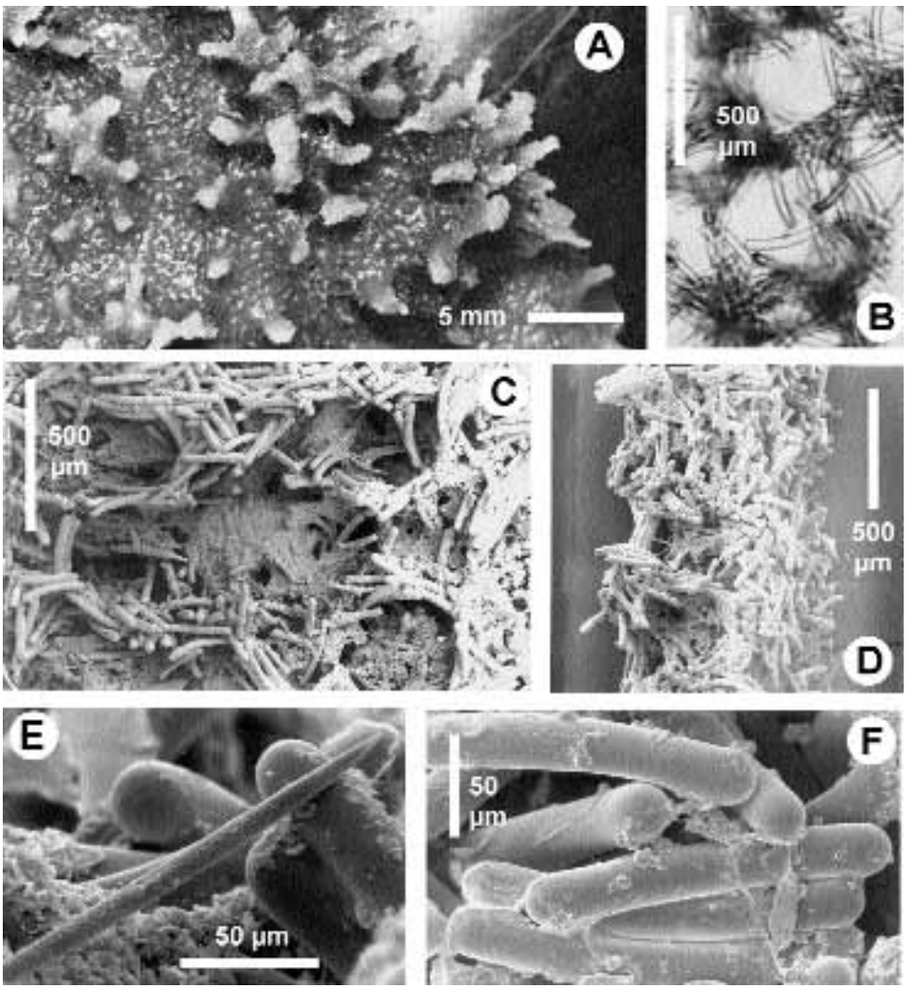

Fig. 154. *Potamophloios stendelli*, skeletal network, specimen MRAC 1324. A, surface hispidation. B, skeletal network. C, sponge surface in smooth areas (top view). D, cross section with smooth sponge surface (left) and basal spongin plate (right). E, ectosomal microsclere. F, choanosomal tract with laminar spongin at the spicule surface. (A–B, modified from Brien, 1967.)

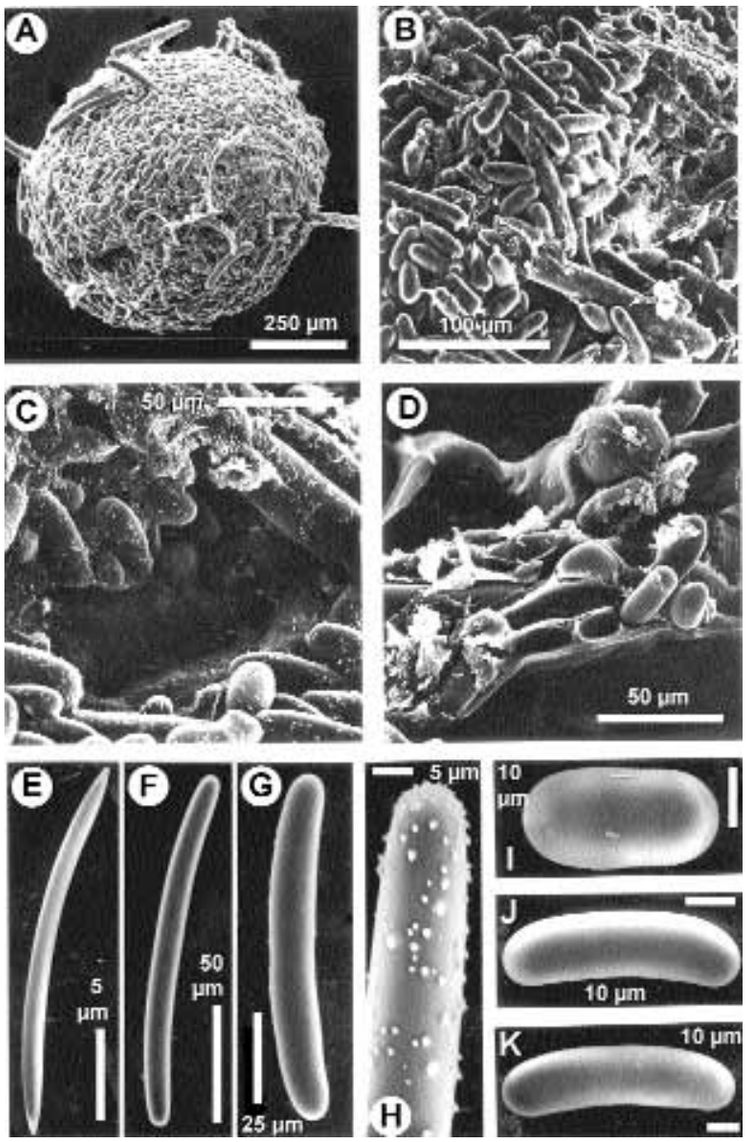

Fig. 155. *Potamophloios stendelli*, spicules and gemmules, specimen MRAC 1324. A, gemmule. B, gemmular surface. C, foraminal area. D, cross section of gemmular theca. E, microsclere. F–G, megascleres. H, close-up of a spiny megasclere. I–K, gemmuloscleres.

genus, *Potamophloios*, by Brien (1970b) based on the presence of gemmules. However, the absence of gemmules from most samples seems more likely to be due to detachment of the sponge base from the entire body during sampling given the notable fragility of the basal skeleton.

ONCOSCLERA VOLKMER, 1970

Synonymy

Oncosclera Volkmer, 1970: 436.

Type species

Spongilla jewelli Volkmer, 1963: 271 (by subsequent designation; Volkmer, 1970).

Diagnosis

Potamolepidae with encrusting body shape and stony hard consistency. Choanosomal skeleton irregularly alveolate with paucispicular tracts. Megascleres stout oxeas. Microscleres absent. Gemmules at the sponge base. Theca trilayered. Gemmuloscleres strongyles.

Scope and distribution

Eleven other species. *O. navicella* (Carter, 1881c) (South America); *O. petricola* (Bonetto & Ezcurra de Drago, 1973) (South America); *O. atrata* (Bonetto & Ezcurra de Drago, 1973) (South America); *O. schuberti* (Bonetto & Ezcurra de Drago, 1973) (South America); *O. spinifera* (Bonetto & Ezcurra de Drago, 1973) (South America); *O. ponsi* (Bonetto & Ezcurra de Drago, 1973) (South America); *O. stolonifera* (Bonetto & Ezcurra de Drago, 1973) (South America); *O. diahoti* (Rützler, 1968)

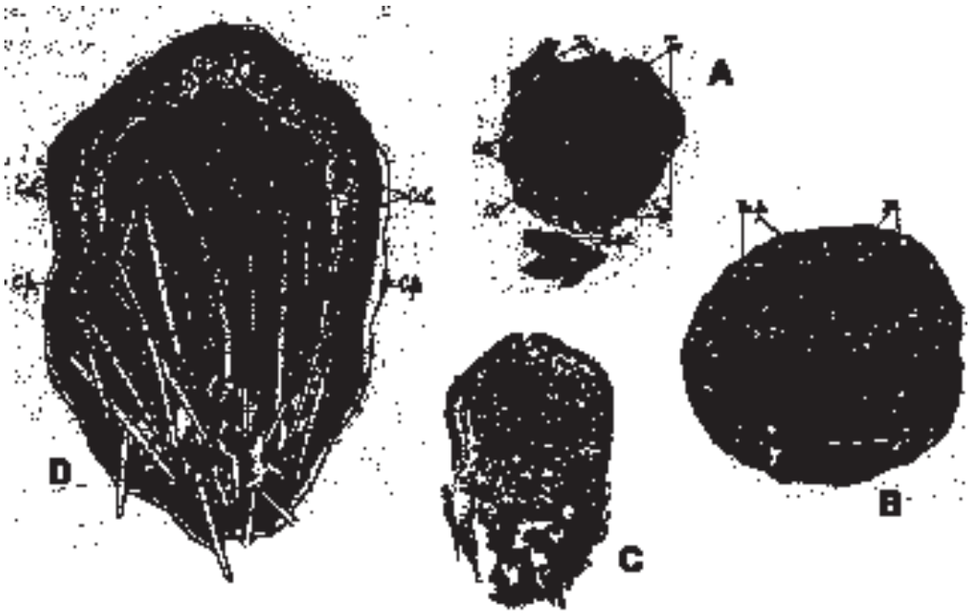

Fig. 156. *Potamophloios stendelli*. A, oocyte. B, stereoblastula. C, parenchymella photo. D, drawing of C (modified from Brien, 1967).

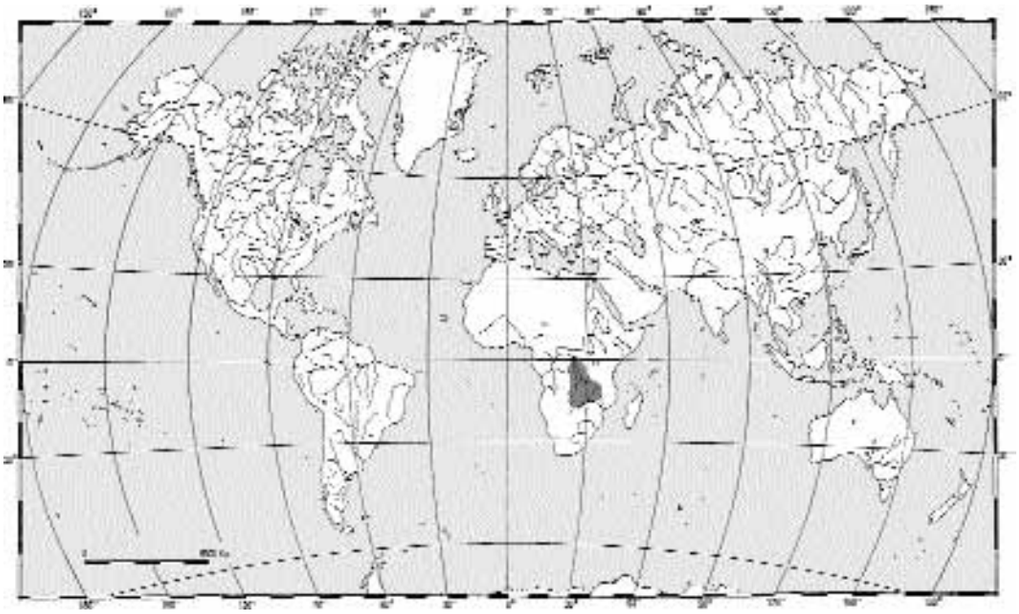

Fig. 157. Geographic distribution of the genus *Potamophloios*.

(New Caledonia), *O. rousseletii* (Kirkpatrick, 1906) (River Zambesi, Africa); *O. schubotzi* Weltner, 1913 (Central Africa); *O. gilsoni* (Topsent, 1912) (Fiji).

Description of type species

Oncosclera jewelli (Volkmer, 1963) (Figs 158–161).

Material examined. Holotype: MNRJ 001 – Rio Thainas, Sao Francisco da Paola, Rio Grande do Sul, 10.ix.1960, det. C. Volkmer-Ribeiro. Other material. BMNH 1978.12.12.12 – Rio Thainas, Sao Francisco da Paola, Rio Grande do Sul, 17.i.1971. FZRG MNC1080, River Teinhesves, 11.i.1983.

Description. Encrusting sponge (0.5 mm thick). Consistency stony hard. Colour green to yellow in life, light brown in dry specimens. Surface irregularly conulose and hispid due to the emerging tufts of spicules. Oscules inconspicuous, sometimes radially arranged on top of conules. Dermal membrane supported by spicule tufts. Subdermal cavities not reported. Ectosomal skeleton with spicules tufts. Choanosomal skeleton irregularly alveolate with paucispicular tracts, more dense and vague at the sponge base. Basal spongin plate well-developed. Megascleres (180–235 × 24 μm, mean 200–24 μm) stout smooth or microspined fusiform oxeas, rarely tuberculate or granular, with acerate tips. Microscleres absent. Gemmules (500–700 μm) yellowish from subspherical to

ovoidal at the sponge base, single or if grouped with a common outer layer. Foramen (1–2) as a simple concavity without tube or collar. Theca with three layers and gemmuloscleres tangentially embedded. Outer layer developed. Pneumatic layer ranges from absent to developed (50 μm), with small chambers. Inner layer of compact spongin well developed and multilayered. Gemmuloscleres (30–106 × 15–30 μm) highly variable from true strongyles to irregularly ovoidal strongyles, from smooth to covered with short spines and tubercules, particularly dense at the spicular apices.

Ecology. On rocky bottoms in large patches, up to 1 m in diameter, or on roots and stems of aquatic bushes along riverbanks. In shaded habitat sponges are yellow, in exposed habitats they are green.

Remarks. The trilayered gemmular theca is typical of Spongillidae and Metaniidae.

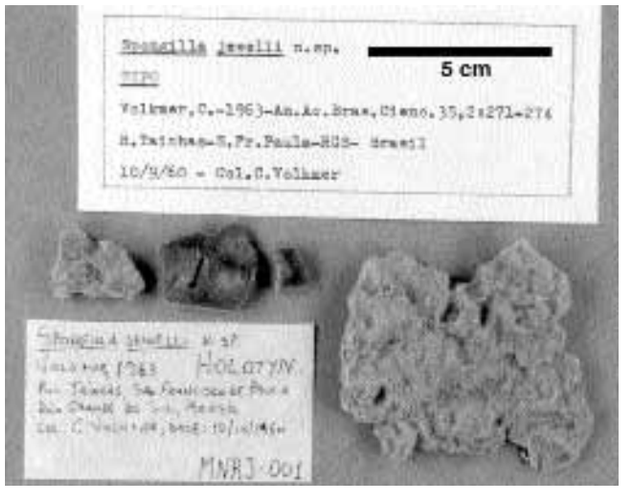

Fig. 158. *Oncosclera jewelli*, holotype and original labels (FZRG) MNRJ-001.

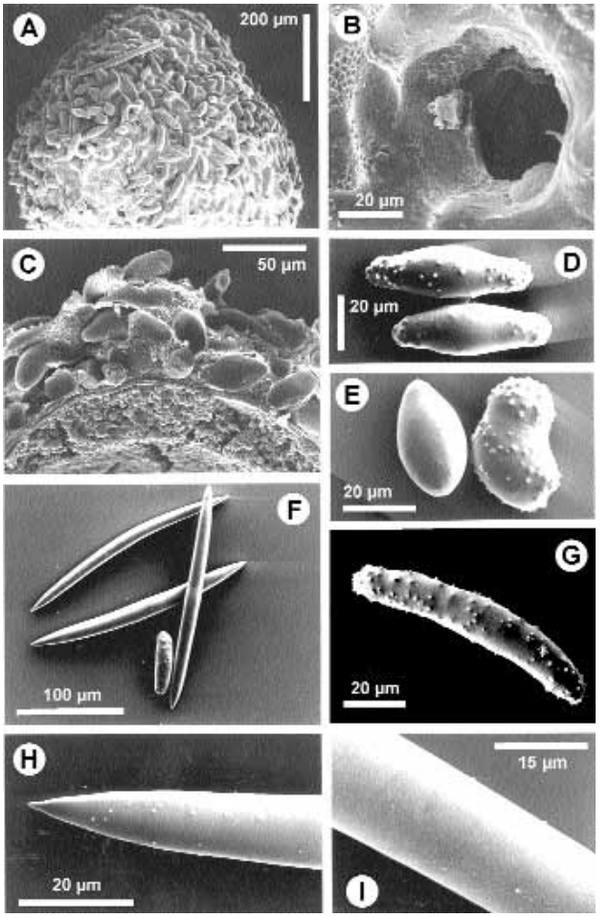

Fig. 160. *Oncosclera jewelli*, spicules and gemmules. A, C–F, H–I, holotype MNRJ-001. B, G, MCN 1080. A, gemmule view. B, foramen. C, trilayered theca. D–E, G, gemmuloscleres. F, megascleres oxeas and gemmulosclere acanthostrongyle. H–I, microspination on oxeas.

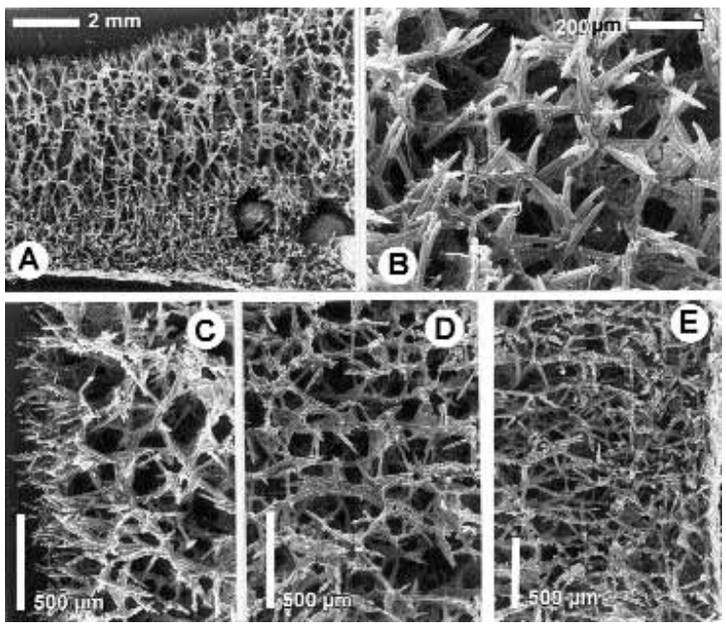

Fig. 159. *Oncosclera jewelli*, skeletal network, holotype MNRJ-001. A, cross section including two basal gemmules (top = sponge surface, bottom = basal spongin plate). B, sponge surface (top view). C, ectosomal skeleton with hispidation (left). D, choanosomal network. E, basal skeleton and spongin plate (right).

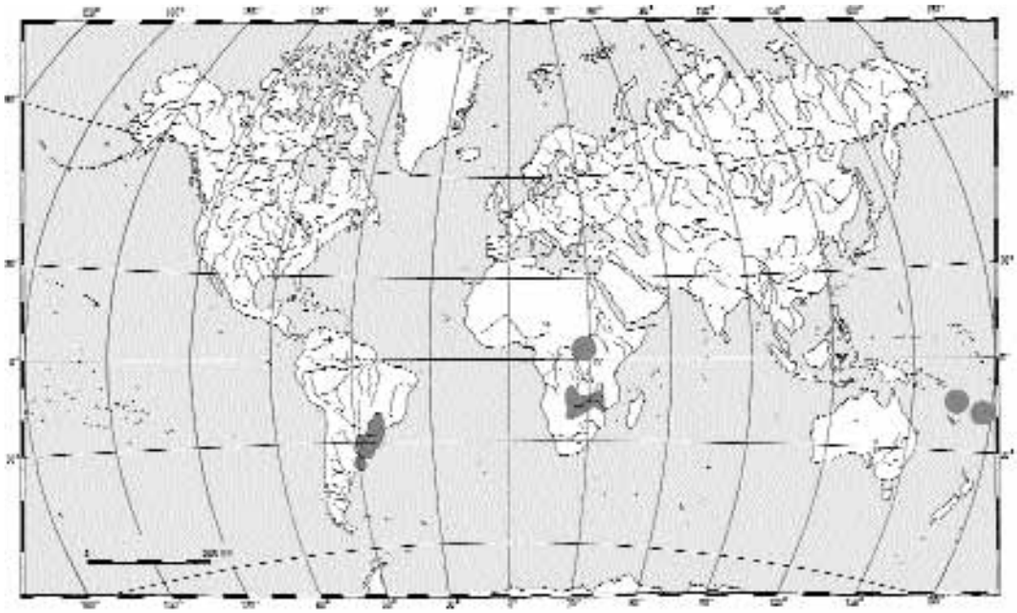

Fig. 161. Geographic distribution of the genus *Oncosclera*.

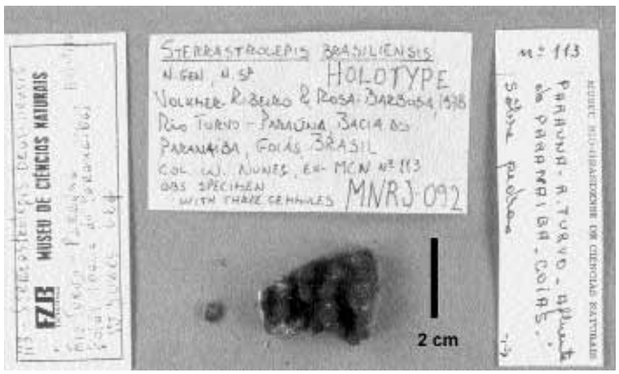

Fig. 162. *Sterrastrolepis brasiliensis*, holotype and original labels (FZRG) MNRJ-092.

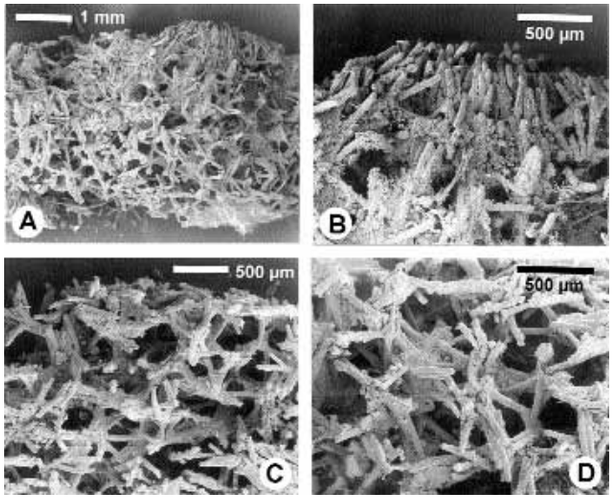

Fig. 163. *Sterrastrolepis brasiliensis*, skeletal network, holotype MNRJ-092. A, sponge cross section (surface at the top). B, tuft of spicules (conule?) at the surface. C, cross section of skeletal meshwork (surface at the top). D, choanosomal skeleton.

STERRASTROLEPIS VOLKMER-RIBEIRO & DE ROSA BARBOSA, 1978

Synonymy

Sterrastrolepis Volkmer-Ribeiro & De Rosa Barbosa, 1978: 103.

Type species

Sterrastrolepis brasiliensis Volkmer-Ribeiro & De Rosa Barbosa, 1978: 103 (by original designation).

Diagnosis

Potamolepidae with body shape encrusting to branching. Consistency stony hard to hard. Choanosomal skeleton alveolate isotropic paucispicular. Sparse spongin. Megascleres stout smooth to granulated strongyles and rare oxeas with blunt tips. Microscleres notably abundant acanthoxeas. Gemmules rare, subspherical. Gemmular cage of strongyles (?). Gemmular theca tri-layered, with several layers of gemmuloscleres. Foramen simple lateral. Pneumatic layer with chambers. Gemmuloscleres ellipsoid or variably subspherical strongyles.

Scope and distribution

Monotypic. Neotropical.

Description of type species

Sterrastrolepis brasiliensis Volkmer-Ribeiro & De Rosa Barbosa, 1978 (Figs 162–165).

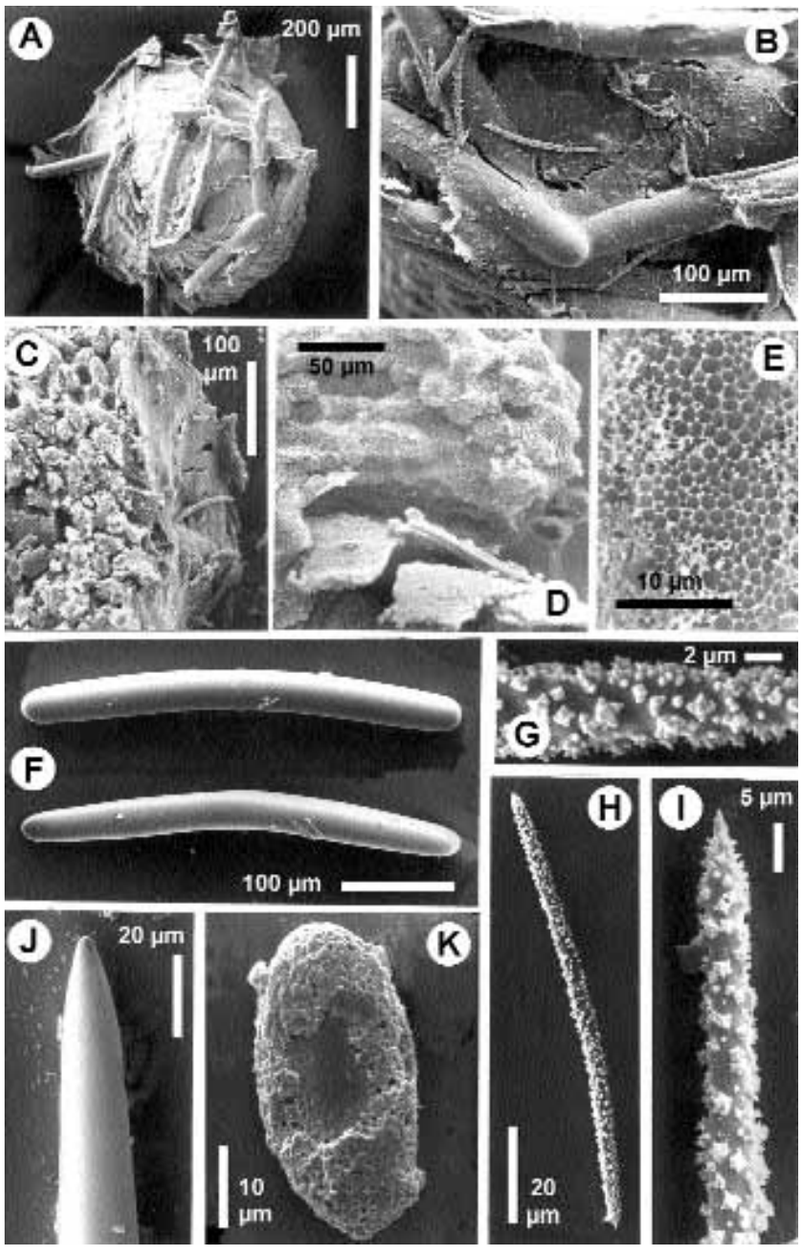

Fig. 164. *Sterrastrolepis brasiliensis*, spicules and gemmules, A–G, J–K, holotype MNRJ-092. H–I, MCN 116. A, gemmule with cage. B, close-up of gemmular surface. C–D, trilayered theca. E, pneumatic layer with chambers. F, J, megascleres. K, gemmulosclere. G–I, microscleres.

Material examined. Holotype: MNRJ 092 (ex-MCN 113) – 3 gemmules, Turvo River, branch of Paranaiba River, Paranà Basin, Goias State, Brazil, W Nunes. Other material. FZRG MCN116 – Brasil.

Description (measurements from Volkmer-Ribeiro & De Rosa Barbosa, 1978). Thickly encrusting (holotype 3 × 2.5 cm × 5 mm) to branching (?) shape, irregularly conulose in encrusting sponges, each conule (1 cm height) raised up by dense tufts of parallel strongyles; short conules became stout conical processes with protruding terminations under optimal growth conditions. Colour grey-greenish to brownish and black. Consistency stony hard to hard. Surface hispid. Dermal membrane spiculous (microscleres). Subdermal cavities not seen. Oscules few at the base of conical processes (some large canals at the sponge base lead to oscules). Ectosomal skeleton with conules, stout conical processes, and tangentially arranged microscleres in the dermal membrane. Choanosomal skeleton alveolate isotropic paucispicular (2–4) with thick and strong axial fibres, with a dense linear packing of strongyles and microscleres from the sponge base extending to the summits of conules. Very little spongin. Megascleres stout, slightly curved from smooth to uniformly granulated strongyles with inflated tips (324–508 × 29–50 µm, mean 415.4 × 40.8 µm). Rare oxeas with blunt tips are also present. Microscleres notably abundant, slender, slightly curved acanthoxeas (reported as tornotes in the original description) entirely ornamented by tubercules or spines with microspines arranged in rosettes (83.2–136.5 × 4.9–6.6 µm,

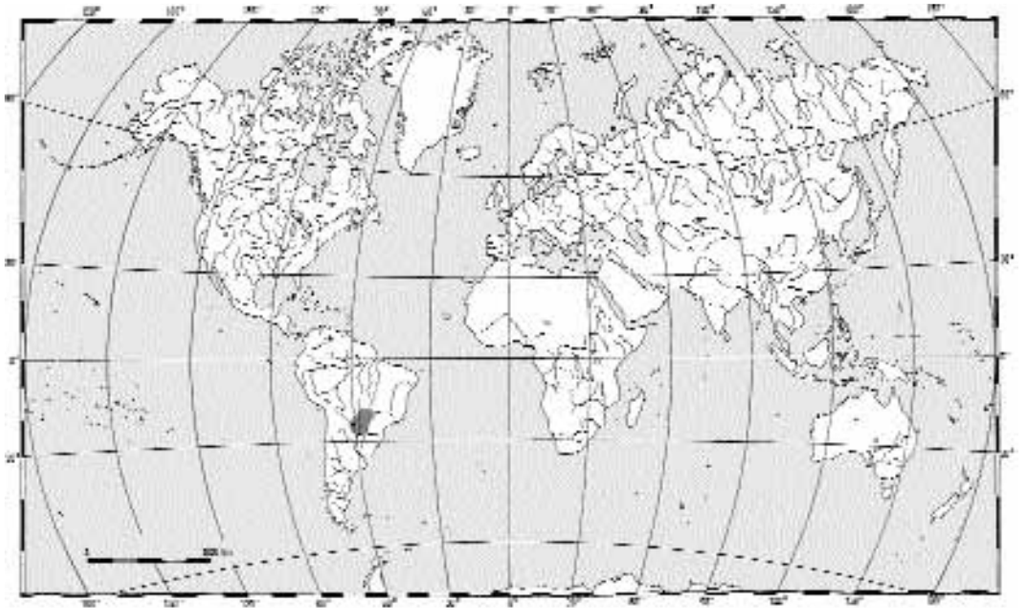

Fig. 165. Geographic distribution of the genus *Sterrastrolepis*.

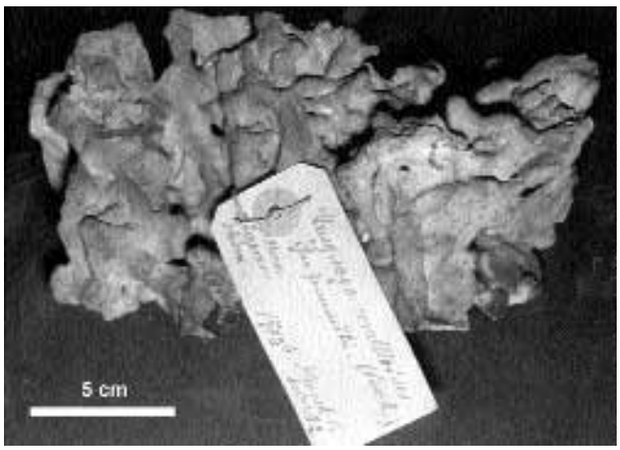

Fig. 166. *Uruguaya corallioides*, specimen, ZMB 1703.

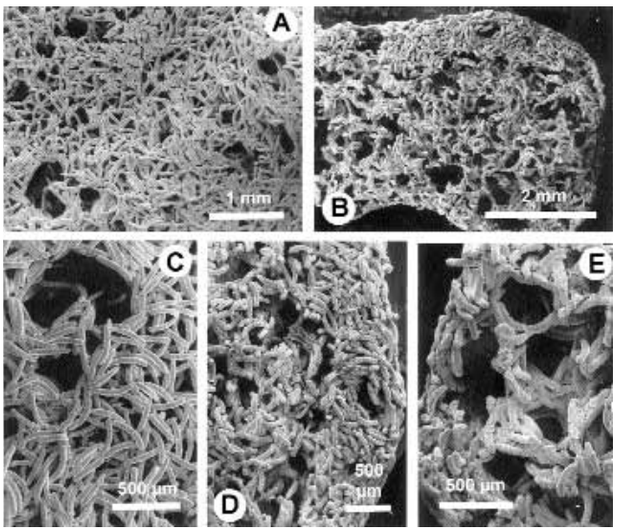

Fig. 167. *Uruguaya corallioides,* skeletal network, specimen MNHN DX325. A, sponge surface with the openings of the aquiferous system (top view). B, cross section of a branch. C, ectosomal skeleton (top view). D, cortical skeleton (lateral view). E, choanosomal skeleton.

mean 109.7 × 6.2 µm). Gemmules rare, subspherical (800–1000 µm), mammillary or dome-shaped, isolated or in groups, strictly adhering to the substratum. Foramen (1–2) lateral, simple, no tube. Gemmular theca tri-layered (in spite of the original description which reported a gemmular wall of compact spongin with no pneumatic layer). Outer layer developed with partially embedded skeletal strongyles suggesting the presence of a gemmular cage. Thick pneumatic layer (110 µm) with minute chambers and several (5–6) layers of closely packed gemmuloscleres. Inner layer multilayered. Gemmuloscleres ellipsoid or variably subspherical strongyles (considered to be sterrasters in the original description), with an irregular surface apart from a unilateral smooth area (33.3–53.2 × 19.9–26.6 µm, mean 42.2 × 22.5 µm).

Ecology. Unknown. Distribution. Turvo River and Itararè River in upper Paranà River Basin, Central-southern Brazil.

Remarks. The trilayered gemmular theca is typical of Spongillidae and Metaniidae.

URUGUAYA CARTER, 1881

Synonymy

Uruguaya Carter, 1881c: 100.

Type species

Spongilla corallioides, Bowerbank, 1863: 460 (by original designation).

Diagnosis

Potamolepidae with body shape ranging from flat crusts to large anastomosing cylindrical compressed branches arising from a flat base. Consistency of both live and dry sponges stony hard. Choanosomal skeleton alveolate with irregular meshes. Sparse spongin. Megascleres range from granulated strongyles to stout smooth oxeas. Microscleres absent. Gemmules generally at the sponge base adhering to the substratum, singly or in clusters, rarely free, enveloped in a cage of smooth oxeas. Gemmule shape ranges from cup-like to hemispherical and spherical. Gemmuloscleres smooth curved strongyles.

Scope and distribution

Monotypic. Tropical South America.

Description of type species

Uruguaya corallioides (Bowerbank, 1863) (Figs 166–169).

Synonymy. *Uruguaya macandrewi* sensu Volkmer-Ribeiro & De Rosa Barbosa, 1979.

Material examined. Holotype: Not seen. Other material. BMNH 1952.6.30.2 – Uruguay River. MNHN DX325 – Orinoco River, 1885, M. Chaffangeon. ZMB1703 – Amazonia, ii.1892, V. Honnef. FZRG MCN 3554 – Rio Uruguay, Usina, Idroeletrica de Ità, Aratiba, 28.ix.1997, C. Volkmer-Ribeiro.

Description. Sponge usually forming anastomosing cylindrical compressed branches (up to 40 cm high) arising from a flat base. Immature sponges often flat crusts irregularly lobed-undulating. Colour from yellow-grey to light ash-grey and dark grey in dry specimens. Consistency of both live and dry sponges is stony hard. Surface smooth and even. Oscules numerous and conspicuous (0.5–1.5 mm diameter), scattered or arranged in a linear series on the compressed edges of branches where they are nearly equidistant. Some oscules have a thick margin or are covered by a membrane with both formations reinforced by skeletal spicules. Oscules circular or elliptical very slightly elevated in areas with few exhalant canals. Dermal membrane thickly translucent and aspicular.

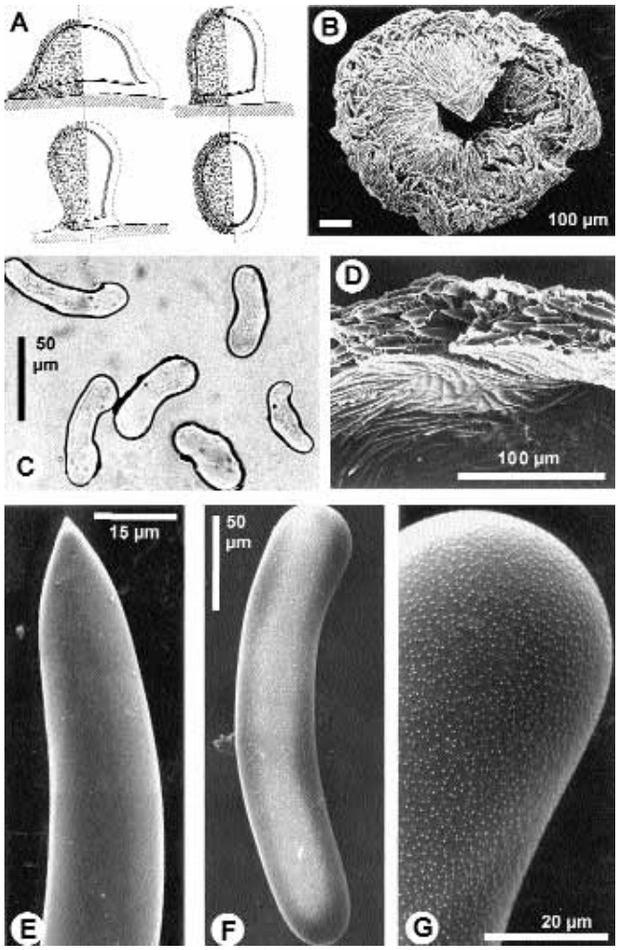

Fig. 168. *Uruguaya corallioides*, spicules and gemmules A, after Bonetto & Ezcurra de Drago, 1969. B, ZMB 1703. C, (FZRG) MCN 3554. D–G, BMNH 1952.6.30.2. A, different gemmular shape (modified from Bonetto & Ezcurra de Drago, 1969). B, gemmular cage of oxeas. C, gemmuloscleres. D, cross section of the cage wall. E, oxea of the gemmular cage. F–G, granulated strongyles of the skeletal network.

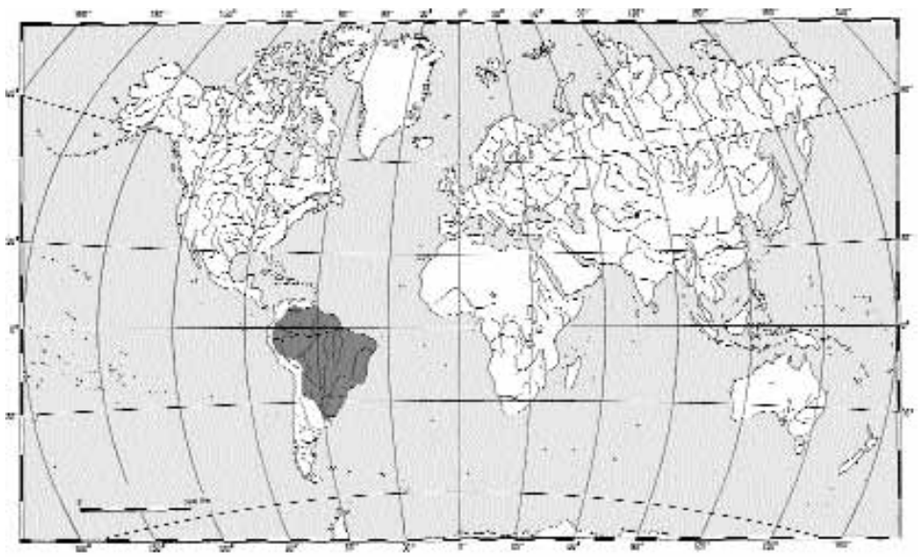

Fig. 169. Geographic distribution of the genus *Uruguaya*.

Basal plate well developed. Ectosomal skeleton not evident except around oscules. Choanosomal skeleton alveolate with irregular meshes, less dense at the apices of branches. Considerable amount of spongin present. Megascleres range from stout curved strongyles (260–320 × 45–60 μm) with granulated surface and a very thin axial canal, to stout smooth oxeas of the gemmular cage (100–127 × 28–30 μm). Microscleres absent. Gemmules not abundant, generally located at the sponge base adhering to the substratum singly or in clusters (2–6), rarely free in the basal choanosome, and enveloped in a cage of smooth oxeas. Gemmule shape ranges from cup-like to hemispherical to spherical (free). Gemmules range from yellowish *in vivo* to whitish-grey when dry. Foramen, if present, located at the top of adherent gemmules as a short tube (70 μm diameter). Gemmular theca very compact. Gemmuloscleres smooth curved strongyles (50–140 × 20–25 μm) tangentially arranged in the layer of compact spongin. Spherules of silica also present.

Ecology. In rapids. Frequently associated with *Uruguayella repens*. Distribution. Tropical and subtropical areas east of the Andes, River Uruguay and River Amazon.

GENERA *INCERTAE SEDIS*

Scope and distribution

Three genera: *Balliviaspongia, Makedia, Ohridospongilla*. Known from Ancient lakes (Fig. 1).

KEY TO GENERA

(1) Megascleres are smooth, spiny or tuberculate (very evidently) oxeas (endemic to Lake Titicaca) ..... ***Balliviaspongia***
Megascleres are oxeas ranging from completely smooth to granulated-tuberculated and/or strongly spined (endemic to Lake Tana) ..... ***Makedia***
Megascleres are oxeas ranging from smooth to more-or-less densely spined with ends sharply tapered (endemic to Lake Ochrid) ..... ***Ohridospongilla***

BALLIVIASPONGIA BOURY-ESNAULT & VOLKMER-RIBEIRO, 1992

Synonymy

Balliviaspongia Boury-Esnault & Volkmer-Ribeiro, 1992: 297.

Type species

Balliviaspongia wirrmanni Boury-Esnault & Volkmer-Ribeiro, 1992: 297 (by original designation).

Diagnosis

Spongillina *incertae sedis*, spongillid-like sponge. Encrusting lobate body shape. Ectosomal skeleton as tangential spicules. Reticulate quite vague irregular choanosomal skeleton. Sparse spongin. Megascleres oxeas from smooth to spined. Microscleres and gemmules absent.

Scope and distribution

Monotypic. Lake Titicaca, Lago Pequeno and South of Lago Grande Copacabana Bay and Sun Island (15°50′S, 69°23′W), Perù-Bolivia.

Description of type species

Balliviaspongia wirrmanni Boury-Esnault & Volkmer-Ribeiro, 1992 (Figs 170–173).

Material examined. Holotype: MNHN DNBE-CVR-1459, leg. D. Wirrmann, 12.v.1986, outlet of Desaguadero, Lake Titicaca, 3 m on algae.

Description. Encrusting lobate body shape. Consistency soft. Colour bright-green to buff light brown. Several oscules irregularly scattered. Surface slightly hispid with protruding oxeas of primary

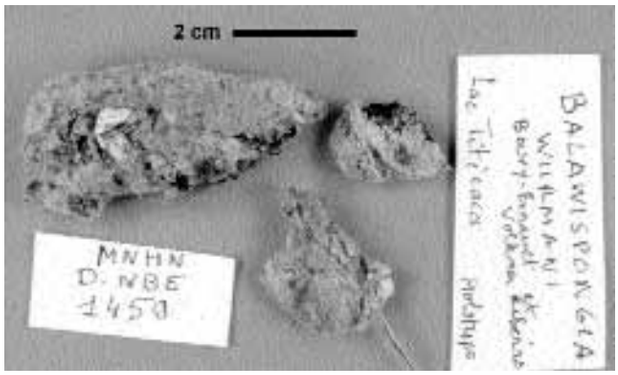

Fig. 170. *Balliviaspongia wirrmanni*, holotype, erroneously labelled in the MNHN DNBE 1459.

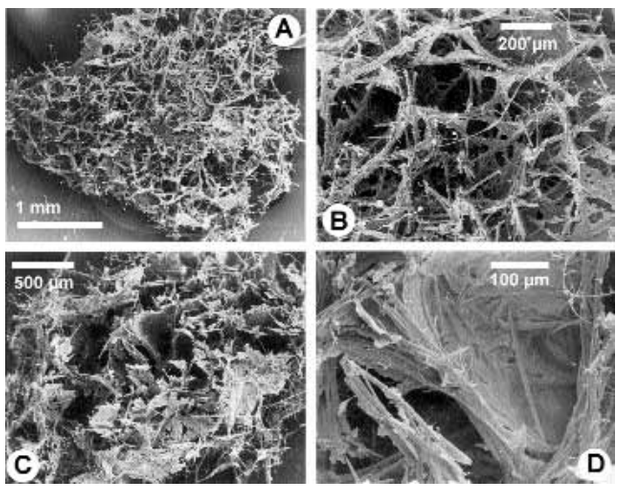

Fig. 171. *Balliviaspongia wirrmanni*, skeletal network, MNHN DNBE 1459. A–B, sponge surface (top view). C–D, choanosomal skeleton.

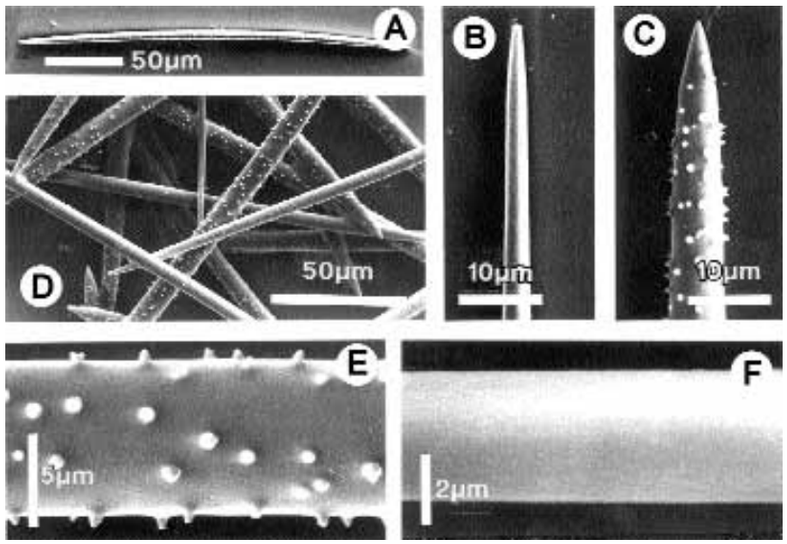

Fig. 172. *Balliviaspongia wirrmanni*, spicules, holotype MNHN DNBE 1459. A, C–E, megascleres spiny oxeas. B, F, megascleres smooth oxeas.

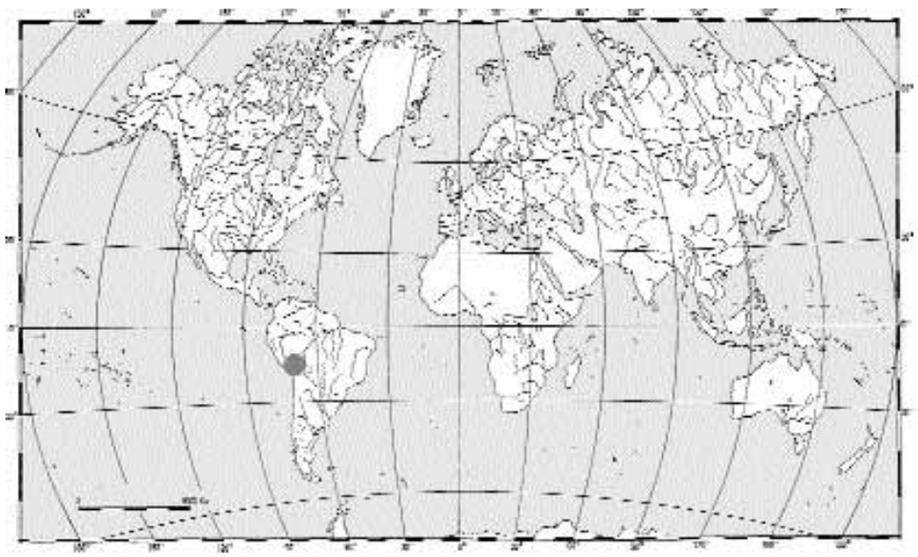

Fig. 173. Geographic distribution of the genus *Balliviaspongia*.

fibres. Dermal membrane supported by uni-bispicular meshes tangential to the surface. Subdermal cavities not observed. Ectosomal skeleton irregular network of uni- bispicular meshes tangential to the surface. Choanosomal skeleton quite vague, irregularly reticulate with multispicular primary tracts (16–53 µm thick) and paucispicular irregular secondary tracts. Sparse spongin. Choanocyte chambers 35–45 µm diameter. Megascleres oxeas ranging from slender to stout, from straight to slightly curved, from smooth to spined (153–450 × 2.6–13 µm, mean 239.9 ± 54.3 µm); acerate tips. Microscleres and gemmules absent. Embryos (235–265 µm diam.) in November.

Ecology. On stones, algae and reeds from 0.1–19 m in standing waters.

MAKEDIA MANCONI, CUBEDDU & PRONZATO, 1999

Synonymy

Makedia Manconi *et al*., 1999: 362.

Type species

Makedia tanensis Manconi *et al*., 1999: 362 (by original designation).

Diagnosis

Spongillina *incertae sedis*; spongillid-like sponge with skeleton shaped as an alveolate isotropic paucispicular network with sparse spongin. No ectosomal differentiation present. Megascleres are oxeas ranging from completely smooth to granulated, tuberculated and/or strongly spined; spines acutely slanting with a globular base, named drop-like spines, with an evident axial canal. Microscleres and gemmules absent.

Scope and distribution

Monotypic. Lake Tana, Ethiopia.

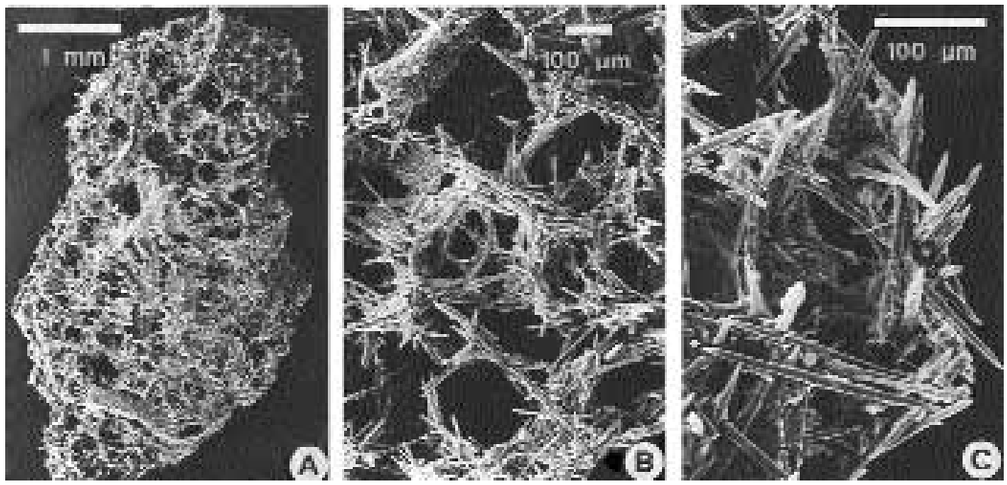

Fig. 174. *Makedia tanensis*, skeletal network, paratype DTRG-FW 250 (ex-IZUG). A, entire specimen. B, alveolate skeleton. C, ectosomal skeleton.

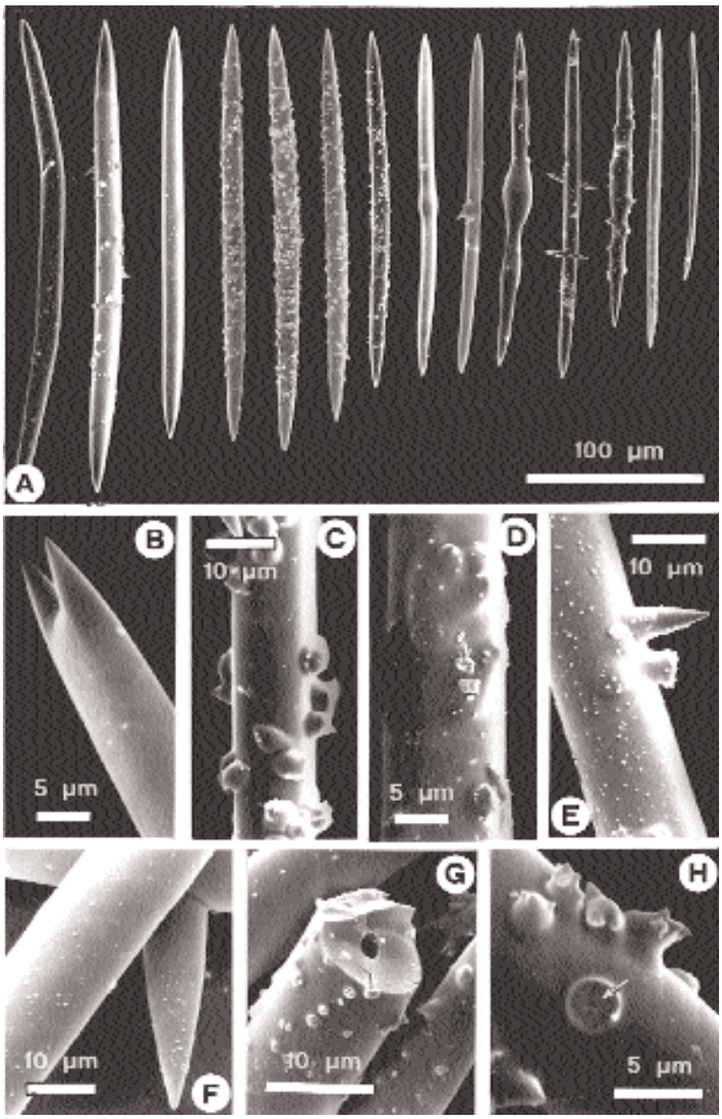

Fig. 175. *Makedia tanensis*, spiculation, paratype DTRG-FW250 (ex-IZUG). A, megascleres oxeas, range of spine dimension and shape. B–F, close-up of megasclere spination. G–H, axial canals.

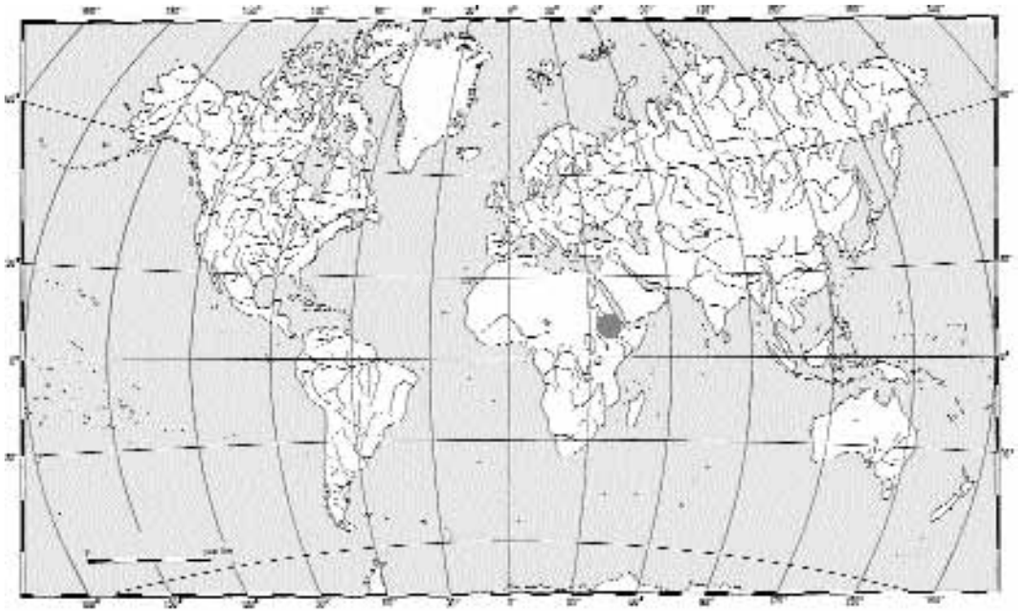

Fig. 176. Geographic distribution of the genus *Makedia*.

Description of type species

Makedia tanensis Manconi *et al*., 1999 (Figs 174–176).

Material examined. Holotype: DTRG FW251 – Bahir Dar, Lake Tana, Ethiopia, R. Manconi & R. Pronzato leg., v.1988. Paratypes: DTRG FW250-FW279-FW280 – same locality.

Description. Whitish encrusting sponges of small size (2 cm in diameter 0.5 cm thick). Consistency soft and fragile. Surface hispid due to emerging spicules. Oscules not conspicuous. Dermal membrane present in some areas. Subdermal cavities not observed. Ectosomal skeleton ill defined. Choanosomal skeleton isotropic alveolate with paucispicular fibres and scanty spongin. Megascleres (151–289 × 5–22 μm, mean 210–233 × 11–13 μm; standard deviation 26–27 × 2.5–3 μm) from slender to stout, straight or slightly curved oxeas, smooth to variably spined with tips from smooth to spiny acerate or rarely atypical. Spicules with wide variety of irregularly scattered sculpturing ranging from granules, granulated tubercules, drop-like granulated spines, to large acute spines. Two or more of these sculptures are associated on the same or in different oxeas. Microscleres and gemmules are absent.

Ecology. In shallow oligotrophic standing waters up to a depth of 20 cm associated to gastropods, bivalves and triclads on the lower or lateral surfaces of littoral volcanic pebbles, cobbles and boulders. Dry sponges on the dried shoreline due to a strong seasonality in water level according to wet and rainy season at an altitude of ca. 1800 m. Water temperature 15.6–20 °C; silica 9–16 mg/l.

OHRIDOSPONGILLA GILBERT & HADZISCE, 1984

Synonymy

Ohridospongilla Gilbert & Hadzisce, 1984.

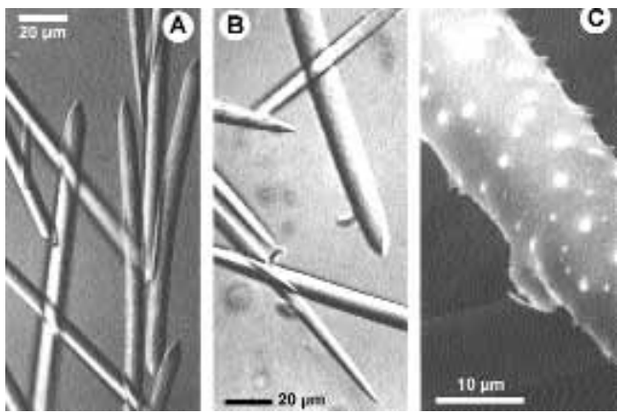

Fig. 177. *Ohridospongilla stankovici*, spicules, as represented in the literature (modified from Gilbert & Hadzisce, 1984). A–B, spiny and smooth oxeas. C, close-up of the spination of a megasclere shaft.

Type species

Ohridospongilla stankovici Gilbert & Hadzisce, 1984: 331 (by original designation).

Diagnosis

Spongillina *incertae sedis*, with encrusting body shape. Consistency quite soft. Ectosomal skeleton unknown. Choanosomal skeleton irregularly reticulate. Megascleres smooth to spiny oxeas. Microscleres absent. Gemmules absent.

Scope and distribution

Monotypic. Lake Ohrid, Macedonia.

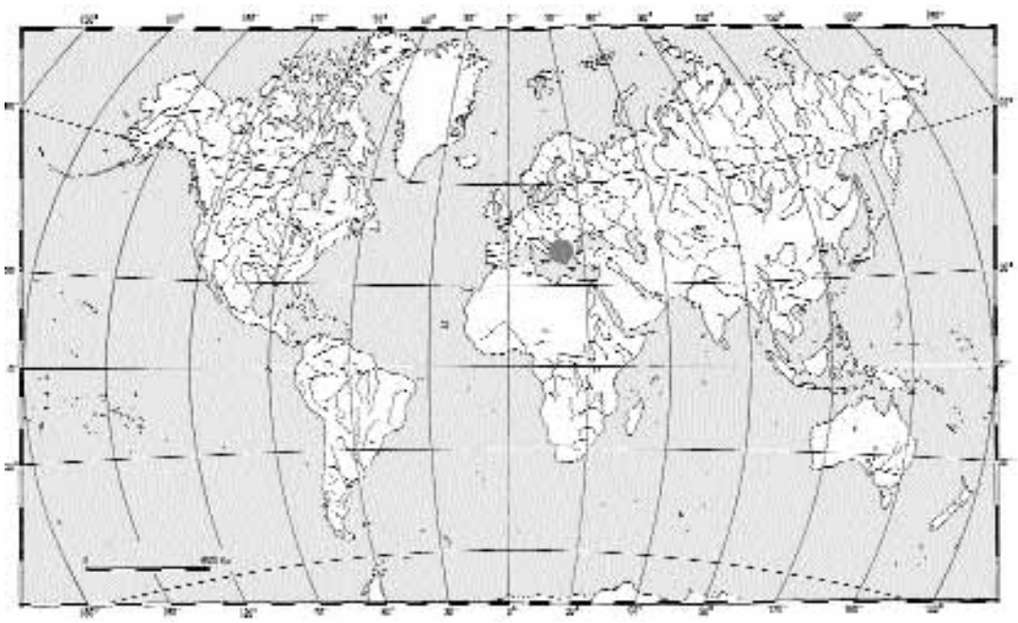

Fig. 178. Geographic distribution of the genus *Ohridospongilla*.

Description of type species

Spongilla stankovici Gilbert & Hadzisce, 1984 (Figs 177–178).

Material examined. Holotype (part of holotype of *Spongilla stankovici* Arndt, 1938): Not available – data from the original description (Arndt, 1938) and Gilbert & Hadzisce (1984).

Description. Body shape encrusting, about 20 mm thick. Colour brown. Consistency soft. Ectosomal skeleton not defined. Choanosomal skeleton irregularly reticulate. Megascleres oxeas from smooth to more-or-less densely spined with ends sharply tapered. Microscleres absent. Gemmules absent.

Ecology. Associated with *Spongilla stankovici* on rocks in superficial waters of the Lake Ochrid (Macedonia). Perennial forms with no signs of degeneration during winter.

Remarks. Originally included in the species *Spongilla stankovici* by Arndt (1938), it was subsequently considered strictly allied to *Ochridaspongia* by Gilbert & Hadzisce (1984).

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