

REVISION OF *AULOSPONGUS* AND OTHER RASPAILIIDAE WITH RHABDOSTYLES (PORIFERA: DEMOSPONGIAE: POECILOSCLERIDA)

JOHN N.A. HOOPER, HELMUT LEHNERT AND SVEN ZEA

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Aulospongos is revised to contain 10 species (*cerebella* Dickinson, *flabellum* Pulitzer-Finali, *gardineri* (Dendy), *involutum* (Kirkpatrick), *monticularis* (Ridley & Dendy), *novaecaledoniensis* sp. nov., *samariensis* sp. nov., *spinusum* (Topsent), *tubulatus* (Bowerbank) and *villosa* (Thiele)). Other species previously included in *Aulospongos* are referred to *Raspailia* (*Raspaxilla*), most being new combinations. *Raspailia* (*Raspaxilla*) and *Endectyon* (*Hemectyon*) are also reviewed and some re-illustrated, containing 17 and 1 species, respectively. *Aulospongos* is contrasted with these genera, differing in having two homologous size categories of rhabdostyles, apparently of common derivation, coring and echinating fibres; plumose skeletal structure persisting throughout choanosomal and peripheral skeletons composed of ascending compressed fibre-bundles with few or no reticulate elements; lacking any differentiation between axial and extra-axial skeletons. Phylogenetic analysis delineates 2 groups of *Aulospongos* species based primarily on skeletal structure: one group exclusively plumose, the other with rudimentary plumo-reticulate skeletons, with the non-rhabdose raspailiid outgroup predominantly plumo-reticulate or reticulate, with loss of ectosomal specialisation being highly homoplastic and unstable throughout the classification of Raspailiidae. Biogeographic comparisons among rhabdose raspailiids (*Aulospongos* versus *Raspaxilla* and *Hemectyon*) show essential differences in distributions (pan-equatorial versus Pacific rim, respectively). □ *Porifera, Demospongiae, Raspailiidae, Aulospongos, Raspaxilla, Hemectyon, new species, new records, new combinations, taxonomic revision, rhabdostyles.*

John N.A. Hooper, (email: JohnH@qm.qld.gov.au), Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; Helmut Lehnert, Institut & Museum für Geologie und Paläontologie, Goldschmidtstr. 3, 37077 Göttingen, Germany; Sven Zea, Universidad Nacional de Colombia, INVEMAR, Apartado Aereo 10-16, Santa Marta (Magd.), Colombia; 30 November 1998.

Rhabdostyles (structural stylote megascleres with a prominent bend or rhabd at the basal extremity), are found amongst several groups of demosponges. They have been recorded from the order Poecilosclerida, families Raspailiidae (*Aulospongos* Norman, *Raspaxilla* Topsent, *Echinaxia* Hallmann, *Axinectya* Hallmann, *Hemectyon* Topsent), Rhabderemiidae (*Rhabderemia* Topsent), and Desmacellidae (*Biemna* Gray), and order Halichondrida, families Desmoxyidae (*Halicnemis* Bowerbank, *Higginsia* Higgin), and Axinellidae (*Rhabdoploca* Topsent, *Hymenhabdia* Topsent, *Lithobubaris* Vacelet, *Monocrepidium* Topsent, *Perissinella* Topsent), with the implication that they have been derived independently within each group (homoplastic developments).

Amongst Raspailiidae there may be two forms of rhabdostyles. Smaller echinating (usually acanthose) rhabdostyles occur in the three rhabdose genera, and are probably homologous

to typical echinating acanthostyles found throughout Raspailiidae. In *Raspaxilla* (including the synonyms *Echinaxia* Hallmann, *Axinectya* Hallmann) and *Hemectyon* Topsent, as in most raspailiids, fibres are cored by non-rhabdose, smooth styles of distinctly different geometry and origin from the rhabdose echinating spicules. In *Aulospongos* larger, smooth or partially spined choanosomal principal rhabdostyles bear a strikingly resemblance to the smaller rhabdostyles, from which they are probably derived. Nevertheless, despite these apparently straightforward generic differences there are several species currently assigned to *Aulospongos* that do not easily rest there, mostly because they possess characters intermediate to both groups.

The present work revises *Aulospongos*, as a consequence of discovering several characters in the type species (*A. tubulatus*); redescribes and illustrates all known species; describes a new

species from the Caribbean fauna (a new locality record for the genus), and New Caledonia; and reviews and compares all known species of raspailiids with rhabdostyles (*Raspailia* (*Raspaxilla*) and *Endectyon* (*Hemectyon*)).

Aulospongos presently contains 15 species (Hooper, 1991; Pulitzer-Finali, 1993; Desqueyroux-Faundez & van Soest, 1997), including the two new species described in this present work, whereas five of these species are referred here to *Raspailia* (*Raspaxilla*) based on major differences between the two genera in their skeletal structure and geometry of structural megascleres.

Aulospongos, as revised here, contains 10 species and has a disjunct geographic distribution, from the N Atlantic (São Vicente and Cape Verde Islands), SW Indian Ocean (Natal), W and central Indian Ocean (Zanzibar, Kenya, Gulf of Aden, Arabian Gulf, S Arabian coast, Amirante, India, Sri Lanka), NW Pacific (Japan) and SW Pacific Ocean (New Caledonia), E Pacific (Gulf of California), and Caribbean (Colombia and Jamaica). *Raspailia* (*Raspaxilla*) and *Endectyon* (*Hemectyon*) now contain 17 and 1 species, respectively, with wide but very different patterns of distribution than *Aulospongos*.

Australasian and New Caledonian raspailiid faunas (Hooper, 1991; Hooper & Lévi, 1993) are well known compared to most regional faunas, containing 56 and 7 species, respectively. To date there has not been any synthesis of the published Caribbean raspailiid fauna (including the Gulf of Mexico and West Indies), with species records scattered throughout many isolated publications (e.g. see Wiedenmayer, 1977; Zea, 1987). It is therefore appropriate to list the published fauna here, containing 20 raspailiid species for the entire region. These include: Genus *Ceratopsion* Strand (*C. crustosum* Alvarez & van Soest, 1993: 629). Genus *Cyamon* Gray (*C. vickersi* (Bowerbank, 1864: 234) (Dendy, 1922: 109; Arndt, 1927: 149; Pulitzer-Finali, 1986: 199; van Soest & Stentoft, 1988: 115; Hooper, 1991: 1304)). Genus *Ectyoplasia* Topsent (*E. ferox* (Duchaissaing & Michelotti, 1864: 81) (Wiedenmayer, 1977: 158; Pulitzer-Finali, 1986: 105, 199; Zea, 1987: 202; van Soest et al., 1983: 198, 204; Hooper, 1991: 1273)). Genus *Endectyon* Topsent (*E. tenax* (Schmidt, 1870: 62) (Topsent, 1920: 23; Wells et al., 1960: 218; Pulitzer-Finali, 1986: 199; Hooper, 1991: 1284); *E. (Hemectyon) hamatum* (Schmidt, 1870: 62) (Topsent, 1920: 26; Pulitzer-Finali, 1986: 199;

Hooper, 1991: 1285)). Genus *Echinodictyum* Ridley (*E. lugubre* (Duchaissaing & Michelotti, 1864: 89) (de Laubenfels, 1936: 63; Wiedenmayer, 1977: 254; Pulitzer-Finali, 1986: 106, 199; Hooper, 1991: 1349); *E. pennatum* (Duchaissaing & Michelotti, 1864: 88) (de Laubenfels, 1936: 63; Wiedenmayer, 1977: 254; Pulitzer-Finali, 1986: 199; Hooper, 1991: 1349)). Genus *Eurypon* Gray (*E. clavatella* Little, 1963: 49 (Pulitzer-Finali, 1986: 199); *E. cf. clavatum* (Bowerbank, 1866: 143) (sensu Topsent, 1889: 29; Wells et al., 1960: 217; Desqueyroux-Faundez, 1981: 737; Pulitzer-Finali, 1986: 199; Hooper, 1991: 1314); *E. coronula* (Bowerbank, 1874: 246) (Topsent, 1936: 66; Pulitzer-Finali, 1986: 199); *E. laughlini* Diaz et al., 1987: 33; *E. topsenti* (Burton, 1954: 235); *E. toureti* (Topsent, 1894: 30); *E. viride* (Topsent, 1889: 43) (de Laubenfels, 1950: 81; Wiedenmayer, 1977: 160; Pulitzer-Finali, 1986: 199; Hooper, 1991: 1314)). Genus *Plocamione* Topsent (*P. clopetaria* (Schmidt, 1870: 63) (Burton, 1935: 402; Pulitzer-Finali, 1986: 203; van Soest & Stentoft, 1988: 115; Hooper, 1991: 1319). Genus *Raspailia* Nardo (*R. acanthifera* (George & Wilson, 1919: 159); *R. pearsi* (Wells et al., 1960: 218); *R. cf. tenuis* Ridley & Dendy, 1886 (van Soest & Stentoft, 1988: 113). Genus *Thrinacophora* Ridley (*T. spinosa* Wilson, 1902: 400 (Pulitzer-Finali, 1986: 199; Hooper, 1991: 1340); *T. funiformis* Ridley & Dendy, 1886: 484 (1887: 195; Zea, 1987: 198; Hooper, 1991: 1339)).

MATERIALS AND METHODS

Terminology for Raspailiidae follows Hooper (1991). Preparation techniques for light microscopy follows Hooper (1996). Spicule measurements are based on 25 random samples of each spicule category for each species, indicated as range of lengths and widths, or range (and mean) for the new taxa. Spicule and section illustrations were produced using digital light microscopy. Phylogenetic analyses were performed using Paup 3.1.1 (Swofford, 1993), and character changes further explored with MacClade (Maddison & Maddison, 1992). Statistical support for phylogenetic tree branching was undertaken using Bootstrap index (under Paup) and Autodecay (Version 3.0; Eriksson & Wikstrom, 1997). The latter index measures Bremer (Branch) support for the nodes. Bremer (1994) defined branch support as the extra total tree length needed for the specified

branch to be lost in the strict consensus of near-most parsimonious tree. The Autodecay program examines a consensus of all trees of a certain length, increasing by 1 from the most parsimonious tree (MPT) length, and saves the consensus trees until all the nodes in the MPT have disappeared. It then determines the Branch Support by counting the increase in the length before that particular node disappeared. Decay values of <0 indicate that MPT has been constrained and that shorter, unconstrained trees may exist, or that an error has been made with the MPT length. Decay value of 0 indicates there are other MPTs which do not have this branch; and values >1 indicate that all MPTs have this node, with potential level of statistical support for nodes increasing on a scale of 1-10.

Abbreviations: AHF, Alan Hancock Foundation (University of Southern California, Los Angeles); AM, Australian Museum, Sydney; BMNH, The Natural History Museum, London; ICN-MHN, Instituto de Ciencias Naturales – Museo de Historia Natural (Porifera collection) – Universidad Nacional de Colombia, AA 74-95, Santafé de Bogotá DC, Colombia; INV, Instituto de Investigaciones Marinas y Costeras ‘José Benito Vives de Andreis’; INVEMAR, Porifera collection, AA 10-16, Santa Marta, Colombia; MOM, Musée Océanographie Monaco; MNHN, Muséum National d’Histoire Naturelle, Paris; Munsell: Munsell color charts (Munsell, 1977); MSNG, Museum of Natural History of Genoa; MZUS, Musée Zoologique de Strasbourg, France; NCG, Naturalist’s Color Guide (see Smithe, 1975); MONZ, National Museum of New Zealand (Dominion Museum), Wellington; NTM, Northern Territory Museum of Arts and Sciences, Darwin; ORSTOM, Institut Français de Recherche Scientifique pour le Développement en Coopération, Centre de Noumea; QM, Queensland Museum, Brisbane; USC, University of Southern California, Los Angeles; USNM, National Museum of Natural History, Smithsonian Institution, Washington; ZMA, Zoological Museum, University of Amsterdam; ZMB, Zoologisches Museum für Naturkunde an der Humboldt-Universität zu Berlin.

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SYSTEMATICS

Family **Raspailiidae** Hentschel, 1923

KEY TO GENERA WITH RHABDOSTYLES. Those genera with echinating acanthostyles with basal rhabds.

- Both smaller echinating (acanthose) styles and larger choanosomal (smooth or acanthose) principal styles have basal rhabds with more-or-less similar geometry; both categories of rhabdostyles distributed throughout the skeleton, the latter predominantly confined within fibres; axial skeleton slightly more compressed but otherwise virtually undifferentiated from the extra-axial skeleton, both regions dominated by ascending plumose fibre-bundles *Aulospongos*
Choanosomal principal styles geometrically different from echinating rhabdostyles/acanthostyles; choanosomal principal styles entirely smooth, without basal rhabd, often with anisoxeote/strongylote modifications; axial and extra-axial skeletons well differentiated 2
- Echinating rhabdostyles predominant in (although not strictly localised to) peripheral skeleton; axial skeleton compressed and more-or-less reticulate; extra-axial skeleton plumoreticulate cored by choanosomal principal styles and longer subectosomal extra-axial styles, with transverse fibres/tracts interconnecting ascending plumose tracts/fibres all the way to the surface, or reduced to a radial skeleton of single subectosomal extra-axial spicules *Raspailia* (*Raspaxilla*)
Echinating acanthostyles with clavulate spines on apex, bases smooth and sometimes with slight basal rhabd; echinating spicules localised at junction of axial and extra-axial skeletons, outside the axis (in compressed forms with radial extra-axial skeleton) or echinating plumose extra-axial fibres, and often producing spicule brushes at the surface *Endectyon* (*Hemectyon*)

Aulospongos Norman, 1878

Aulospongos Norman, 1878: 267; Dendy, 1889: 89; Dendy, 1922: 61; Burton, 1938: 38; Hooper, 1991: 1307; Hooper & Lévi, 1993: 1294 (not *Aulospongos*; de Laubenfels, 1936: 100). Type species *Haliphysema tubulatus* Bowerbank, 1873: 29 (by original designation).

Heterectya Hallmann, 1917: 393. Type species: *Raspailia* (?) *villosa* Thiele, 1898: 60 (by original designation).

Rhaphidectyon Topsent, 1927: 15. Type species: *Rhaphidectyon spinosum* Topsent, 1927: 15 (by original designation and monotypy; schizotypes MNHN LBIM DT 1139, BMNH 1930.7.1.39).

Aulospongiella Burton, 1956: 141. Type species *Axinella monticularis* Ridley & Dendy, 1886: 481 (by original designation and monotypy).

Hemectyonilla Burton, 1959: 254. Type species: *Stylostichon involutum* Kirkpatrick, 1903: 250 (by original designation and monotypy).

DEFINITION. Raspailiidae with at least two size classes of rhabdostyles of similar geometry, the larger (smooth or partially spined) core spongin fibres, and the smaller (partially spined) echinate fibres although neither are localised to any region of the skeleton; choanosomal skeletal structure is predominantly plumose, with spicules and fibres amalgamated into bulbous tracts ('fibre-bundles'), more-or-less complicated in the axial skeleton, becoming increasingly plumose as they ascend to the periphery, eventually producing a shaggy, compartmentalised or conulose surface; axial and extra-axial skeletons undifferentiated apart from greater amalgamation of fibre-bundles in the axis.

DIAGNOSIS (emended). Growth forms tubular, cup-shaped, lobate, lamellate or erect cylindrical-digitate; individual lobes or branches are composed of large fibre-bundles amalgamated at the core or base of the sponge, diverging and becoming increasingly plumose towards the periphery, eventually producing a compartmentalised surface of discrete lobes or shaggy surface processes. Ectosomal skeleton ranges from: well developed, 'specialised raspailiid' (consisting of long subectosomal extra-axial styles protruding through the surface, surrounded by sparse brushes of ectosomal auxiliary spicules); vestigial (with wispy raphidiform or sinuous ectosomal auxiliary spicules scattered sparsely and indiscriminately over the surface); or absent completely (with only choanosomal principal spicules protruding through the surface, forming discrete surface bundles). Long subectosomal extra-axial spicules produce a hispid surface in some species. Choanosomal skeletal structure predominantly plumose (with very few reticulate connecting fibres, and these mainly towards the axis), with virtually no differentiation between axial and peripheral skeletons. Ascending fibres nearly fully cored by larger choanosomal principal rhabdostyles, forming dense plumose bundles particularly on fibre nodes, and echinated by smaller rhabdostyles, together

producing bulbous spiculo-spongin tracts (termed here 'fibre-bundles'); smaller echinating rhabdostyles more-or-less evenly dispersed throughout the skeleton; interconnecting fibres, if present, are aspicular or paucispicular, and generally confined to the axial region. Megascleres consist of larger choanosomal principal rhabdostyles usually with a relatively slight basal rhabd, entirely smooth or with recurved spines only on apical part of spicules. Smaller echinating rhabdostyles in one or two categories have more pronounced basal rhabd, often prominently subtylote, entirely smooth or with spines only the apex of spicules, or covering most of the spicule except for the base, or rarely completely spined. Subectosomal extra-axial styles or anisoxeas, if present are long and protrude through the surface. Ectosomal auxiliary styles or anisoxeas, if present, are wispy, sinuous or raphidiform, often vestigial. Raphide microscleres are present in only one species.

***Aulospongius tubulatus* (Bowerbank, 1873)**
(Figs 1-2, Table 1)

Haliphysema tubulatus Bowerbank, 1873: 29, pl. 7.

Aulospongius tubulatus; Norman, 1878: 267; Dendy, 1905: 176; Dendy, 1922: 61; Burton & Rao, 1932: 347; Burton, 1938: 32, pl. 3, fig. 24; Burton, 1959: 253; Thomas, 1985: 269, pl. 3, fig. 10; Hooper, 1991: 1307, fig. 66g-k.

Axinella tubulata; Dendy, 1889: 89, pl. 5, fig. 11.

MATERIAL. HOLOTYPE. BMNH1873.7.21.9: Ceylon (Sri Lanka), coll. E.W.H. Holdsworth. **OTHER MATERIAL.** BMNH1931.11.28.18 (fragment MNHNLBIMDCL51): Off Megapatam, Amirante, coll. 'Investigator', 16.vi.1930, 18-22m.

DISTRIBUTION. Amirante, Gulf of Aden, South Arabian Coast, SE coast India and Sri Lanka, W Indian Ocean.

DESCRIPTION. Growth form subspherical, massive, tubular, composed of amalgamated fibre-bundles that extend to the surface and produce a compartmentalised surface of discrete conules. Colour red or pinkish-red alive. Ectosome with vestigial 'raspailiid skeleton' composed of sinuous or raphidiform ectosomal auxiliary styles scattered sparsely and indiscriminately over the surface, and with plumose bundles of both larger and smaller rhabdostyles protruding through the surface mainly at the ends of conules. No subectosomal extra-axial spicules. Adjacent surface conules interconnected by aspicular (membranous) collagen. Choanosomal skeleton exclusively

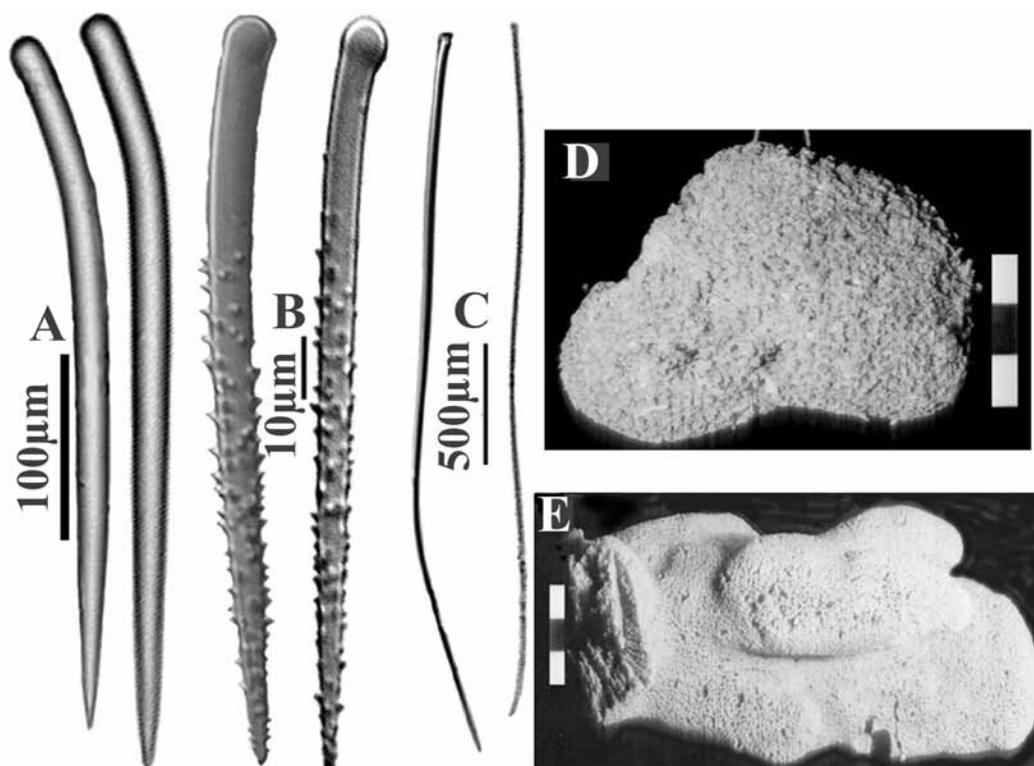


FIG. 1. *Aulospongos tubulatus*. A, Choanosomal principal rhabdostyles. B, Echinating rhabdostyles. C, Ectosomal auxiliary styles. D, Holotype (scale 3cm). E, 'Investigator' specimen (scale 3cm).

plumose with fibre-bundles fused relatively closely towards the base of the sponge and axis of the skeleton, becoming increasingly plumose towards the periphery, and eventually completely discrete/compartimentalised at the surface. Fibre-bundles composed of rhabdostyles, both coring and echinating fibres, forming ascending multispicular columns, branching or unbranched towards their apex, bonded together with light granular collagen. Larger smooth choanosomal principal rhabdostyles extend out from fibres in plumose bundles, particularly near periphery of skeleton. Smaller spined rhabdostyles heavily echinate fibres and fibre nodes. Megascleres consist of larger coring choanosomal principal rhabdostyles with slightly subylote or rounded bases, slight basal rhabd, fusiform points, completely smooth ($304\text{--}462\times 16\text{--}24\mu\text{m}$). Smaller echinating rhabdostyles with entirely smooth, slightly rhabdose, slightly swollen bases, and small spines covering apical half of spicule ($109\text{--}126\times 5\text{--}10\mu\text{m}$). Long, thin, curved, sinuous or raphidiform ectosomal auxiliary styles

($212\text{--}250\times 2\text{--}3\mu\text{m}$). Subectosomal extra-axial spicules absent. Microscleres absent.

REMARKS. Re-examination of the holotype from Sri Lanka and Dendy's (1922) specimen from Amirante found the remnants of a specialised raspailiid ectosomal skeleton present in both, a character overlooked by previous authors, necessitating emendation to the generic diagnosis from that provided by Hooper (1991) and Hooper & Lévi (1993). This omission is not surprising given that the ectosomal skeleton in the type species is sparse and vestigial (consisting of wispy raphidiform anisoxeas scattered more-or-less indiscriminantly within the surface skeleton). Similarly, a more careful re-examination of *Stylostichon involutum* (the holotype of *Hemectyonilla*), also discovered these ectosomal auxiliary spicules to be present (consisting of a few wispy raphidiform oxeote spicules perpendicular to the surface). This confirms the synonymy between *Aulospongos* and *Hemectyonilla*, proposed tenuously by Hooper

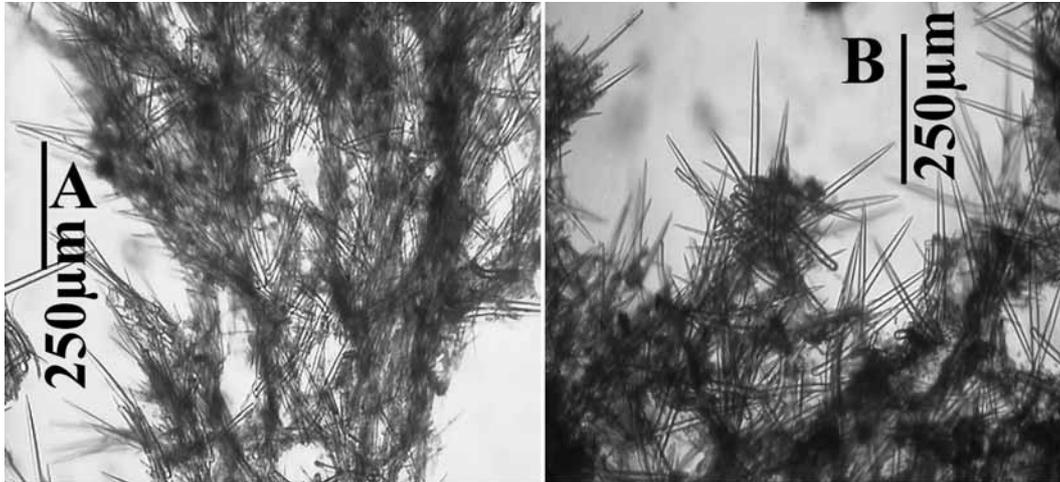


FIG. 2. *Aulospongus tubulatus*. A, Choanosomal skeleton. B, Ectosomal skeleton.

(1991), and also provides more firm evidence in support of the inclusion of *Aulospongus* in Raspailiidae, previously considered to be atypical of the family.

A further consequence of these new findings is that *A. tubulatus* is no longer completely 'typical' of the genus, as defined by Norman (1878) and subsequently understood by other authors. Prior to this study the generic concept centred on the possession of a tubular growth form, only two categories of rhabdose megascleres (the larger coring and the smaller echinating fibres), exclusively plumose fibre-bundles, and lacking ectosomal specialisation and other spicules completely. However, *A. tubulatus* was found to have aspicular fibre connections between ascending plumose fibre-bundles, and ectosomal auxiliary spicules (albeit forming a vestigial ectosomal specialisation), necessitating re-evaluation of the genus and its relationships to *Raspaxilla* in particular. This is discussed further below.

In having vestigial, scattered wispy ectosomal auxiliary spicules which do not necessarily form surface brushes *A. tubulatus* is similar to *A. involutum*, although the latter species also has larger subectosomal extra-axial styles erect on the surface. In having plumose fibre-bundles with few aspicular interconnecting tracts this species is also similar to *A. gardineri* and *A. novae-caledoniensis* sp.nov, although the two groups differ substantially in their spicule geometries. Other comparisons are given in Table 1.

***Aulospongus cerebella* (Dickinson, 1945)**
(Fig. 3, Table 1)

Heterectya cerebella Dickinson, 1945: 22, pl. 34, figs 67-68.

Aulospongus cerebella; Desqueyroux-Faundez & van Soest, 1997: 442.

MATERIAL. HOLOTYPE. AHF no.11 (not seen): Isla Partida, Gulf of California, coll. 'Velero III', 9.iii.1936, 90m depth, sand substrate.

DISTRIBUTION. Known only from the Gulf of California.

DESCRIPTION. Growth form thickly lamellate or massively encrusting. Surface convoluted, meandering over substrate, highly conulose, with conules composed of irregularly fused, erect, fibre-bundles. Colour 'drab' in ethanol. 'Raspailiid ectosomal skeleton' absent although choanosomal principal styles protrude through surface forming conules. Choanosomal skeletal structure plumose, consisting of ascending fibre-bundles eventually forming surface conules, without any reticulate interconnecting tracts. Megascleres include larger, entirely smooth choanosomal principal rhabdostyles coring fibres, with only slight basal rhabd (600×35µm). Rhabdostyles echinating fibres, with smooth rhabdose bases, smooth shafts, and moderately small, granular spines only on the extreme points of spicules (400×30µm). Ectosomal auxiliary and subectosomal extra-axial spicules apparently absent. Microscleres absent (Dickinson, 1945).

TABLE 1. Summary of morphological comparisons between species of *Aulospongius* and type species (indicated by *) of *Raspaxilla* and *Hemectyon*.

Species	Surface features & skeletal fibre-bundles	Skeletal reticulation & axial vs. extra-axial skeleton	Choanosomal principal spicules (spicule size)	Echinating spicules (spicule size)	Specialised ectosomal auxiliary skeleton (spicule size)	Subectosomal extra-axial spicules (spicule size)	Raphides (spicule size)
* <i>A. tubulatus</i>	Discrete surface conules, not hispid; fibre-bundles present	Very slight reticulation with few aspicular fibre connections; undifferentiated axial/extra-axial skeleton	Slightly rhabdose and subtylote, entirely smooth (304-462×16-24µm)	Slightly rhabdose and subtylote, spines on apical third, spines small and slightly recurved (109-126×5-10µm)	Vestigial, sinuous raphidiform styles scattered on surface (212-250×2-3µm)	Absent	Absent
<i>A. cerebella</i>	Surface convoluted, conulose, not hispid; fibre-bundles present	No reticulation; undifferentiated axial/extra-axial skeletons	Slightly rhabdose, entirely smooth (600×35µm)	Strongly rhabdose, spines only on points, spines granular (400×30µm)	Absent, only choanosomal principal styles protrude through surface	Absent	Absent
<i>A. flabellum</i>	Surface with longitudinal ridges and distinct osculiferous and porous faces; fibre-bundles ?	Unknown	Slightly rhabdose, entirely smooth (340-570×16-34µm)	Faintly rhabdose, spines mostly on points, bases and central portion, or more-or-less evenly spined (120-370×11-19µm)	Absent, with only larger choanosomal principal rhabdostyles protruding through surface	Absent	Absent
<i>A. gardineri</i>	Surface smooth, not hispid; fibre-bundles present, plumose and diverging	Slight reticulation with a few aspicular connecting fibres; undifferentiated axial/extra-axial skeletons	Strongly rhabdose, spined on apical third, spines large and recurved (205-385×11-21µm)	(1) Strongly rhabdose, spines on apical half, spines large and recurved (94-136×5-11µm); (2) strongly rhabdose, very slender, entirely smooth, fine point (84-156×1-2µm)	Well developed, brushes of ectosomal auxiliary styles/anisoxeas often surrounding long subectosomal extra-axial styles/anisoxeas (218-442×1-2µm)	Present, subectosomal extra-axial styles protrude through surface singly or in brushes (815-1050×8-22µm)	Absent
<i>A. involutum</i>	Surface shaggy, large conules, not hispid; fibre-bundles present, prominent at surface, ascending in choanosome	No reticulation; undifferentiated axial/extra-axial skeleton	Moderately to strongly rhabdose, spines on apical half, spines large and strongly recurved (224-370×12-22µm)	Strongly rhabdose, spines on apical third, spines small (122-195×5-11µm)	Vestigial, raphidiform oxeas perpendicular to surface but usually not forming brushes (450-640×5-7µm)	Present, single subectosomal extra-axial styles protrude through surface (1010-1390×7-11µm)	Absent
<i>A. monticularis</i>	Surface shaggy, conulose, not hispid; fibre-bundles present, microconionid-like	No reticulation; undifferentiated axial/extra-axial skeleton	Slightly rhabdose and subtylote, entirely smooth (290-518×9-19µm)	Slightly rhabdose and subtylote, evenly spined, spines very small, granular and erect (132-275×2-9µm)	Absent	Present, single subectosomal extra-axial styles protrude through surface (620-960×7-15µm)	Absent
<i>A. novae-caledoniensis</i> sp. nov.	Surface smooth, finely hispid; fibre-bundles present, plumose diverging	Slight reticulation with few aspicular connecting fibres; undifferentiated axial/extra-axial skeletons	Strongly rhabdose, spined only on extreme points, spines large and recurved (275-400×22-24µm)	Mod. Rhabdose, spines on apical half or 2/3, spines large and recurved (115-165×8-10µm)	Vestigial, brushes of ectosomal auxiliary anisoxeas scattered but not surrounding any protruding spicules (455-565×2-5µm)	Absent	Absent
<i>A. samariensis</i> sp. nov.	Surface shaggy, bulbous, hispid; fibre-bundles present, plumose but with a few inter-connecting tracts	Very slight reticulation with sparse aspicular connecting fibres; slightly more compressed in axis than periphery	Slightly rhabdose, spines mostly on base and apex, smooth elsewhere, spines large, recurved, hook-like (218-412×9-18µm)	Slightly rhabdose, evenly spined but fewer spines below basal tye, spines small and recurved (112-232×6-13µm)	Present, loose bundles of ectosomal auxiliary anisoxeas surround subectosomal extra-axial spicules (225-775×2-6µm)	Present, single subectosomal extra-axial styles protrude through surface (920-2750×8-26µm)	Absent

TABLE 1. (Cont.)

Species	Surface features & skeletal fibre-bundles	Skeletal reticulation & axial vs. extra-axial skeleton	Choanosomal principal spicules (spicule size)	Echinating spicules (spicule size)	Specialised ectosomal auxiliary skeleton (spicule size)	Subectosomal extra-axial spicules (spicule size)	Raphides (spicule size)
<i>A. spinosum</i>	Surface shaggy, conulose, not hispid; fibre-bundles present but with few inter-connecting tracts	Slight reticulation with only few connecting fibres; undifferentiated axial/extra-axial skeleton	Slight to mod. rhabdlose, entirely smooth (770-1085×28-43µm)	Slight or no basal rhabd, slightly subtylote, evenly spined, spines very large, perpendicular (75-145×7-10µm); strongly rhabdlose, slender, entirely smooth (90-185×5-12µm)	Absent	Absent	Present, singly and in trichodragmata (50µm long)
<i>A. villosa</i>	Surface very shaggy, conulose, not hispid; fibre-bundles present	No reticulation but adjacent echinating rhabdostyles may interconnect; undifferentiated axial/extra-axial skeleton	Strongly rhabdlose, usually completely smooth or with spines on apical half, spines very small, granular (235-370×10-16µm)	Very strongly rhabdlose, spines on apical half or entirely smooth, spines very small and granular (142-165×4-10µm)	Absent	Absent	Absent
* <i>Raspailia</i> (<i>Raspaxilla</i>) <i>phakellina</i>	Surface slightly conulose; fibre-bundles present but confined to peripheral skeleton	Strongly reticulate axis; well differentiated reticulate axis, plumo-reticulate extra-axis, but skeleton dominated by plumose ascending fibres	Non-rhabdlose, entirely smooth (550-900×10-16µm)	Slightly rhabdlose and subtylote, spines on apical two-thirds, spines small and erect (140-370×8-18µm)	Present, brushes of ectosomal auxiliary styles surrounding subectosomal extra-axial styles (450-650×2-3µm)	Present, single subectosomal extra-axial styles protrude through surface (1100-1450×12-18µm)	Absent
* <i>Endectyon</i> (<i>Hemectyon</i>) <i>hamatum</i>	Surface slightly corrugated; fibre-bundles absent	Strongly reticulate axis; compressed axial reticulation, radial extra-axial skeleton	Non-rhabdlose, entirely smooth (270-515×8-18µm)	Mod. rhabdlose, spines only on extremities or apical third at most, spines large and very strongly recurved (120-150×5-10µm)	Vestigial, ectosomal auxiliary styles only found below surface, with rhabdostyles mostly surrounding the protruding choanosomal principal styles (220-275×2-3µm)	Absent	Absent

REMARKS. This species has not been recorded since it was first described, and regrettably the holotype cannot be located in the AHF collections (Prof. G. Bakus, pers.comm.). Dickinson (1945) stated that it was a sister species of *R. inaequalis* Dendy, 1924 (which he also suggested belonged to *Echinaxia* in possessing ectosomal auxiliary oxeas, and which Hooper (1991) subsequently referred to *Raspailia* (*Raspaxilla*)), but this comparison is very superficial: *R. inaequalis* has a distinct, compressed axial and plumo-reticulate extra-axial region, possesses ectosomal specialisation, and has non-rhabdlose choanosomal principal megascleres of distinctly different geometry than rhabdlose echinating megascleres. Although incompletely described *A. cerebella* appears to be most similar to *A. flabellum* and *A. villosa* in having a reduced spiculation consisting only of

choanosomal principal styles and echinating rhabdostyles, lacking any form of ectosomal auxiliary spicules or long subectosomal extra-axial spicules. Unlike both these species the larger choanosomal principal styles in *A. cerebella* do not appear to have a basal rhabd, which has presumably been secondarily modified.

***Aulospongus flabellum* Pulitzer-Finali, 1994**
(Fig. 4, Table 1)

Aulospongus flabellum Pulitzer-Finali, 1994: 308, figs 38-39.

MATERIAL. HOLOTYPE. MSNG 48305 (not seen): North Kenya Banks, off Manda I., Kenya, 02°23'S, 41°04'E, 17.vi.1971, 110-170m depth.

DISTRIBUTION. Kenya, W Indian Ocean.

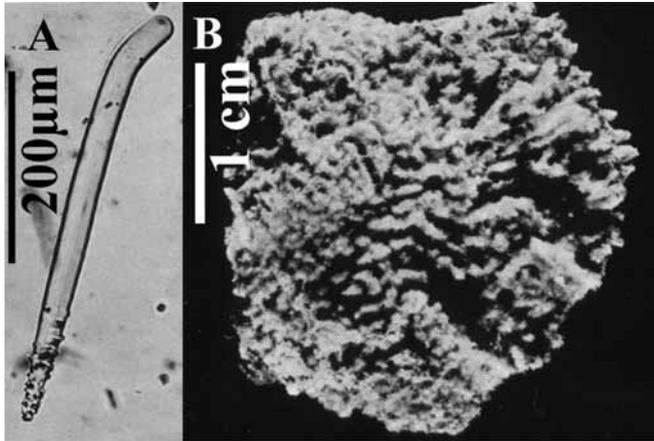


FIG. 3. *Aulospongus cerebella*. A, Holotype. B, Echinating rhabdostyle (figure modified from Dickinson, 1945).

DESCRIPTION. Thinly flabellate, planar, 45-55mm high, up to 4mm thick, with distinct osculiferous and porous surfaces. Osculiferous surface with deep longitudinal ridges running the length of the sponge, with large oscules lying within grooves. Porous surface reticulate. Surface microscopically hispid. Colour unknown. Ectosomal skeleton unknown,

although larger choanosomal principal spicules protrude through surface. Choanosomal skeleton unknown. Megascleres consist of choanosomal principal subtylostyles, completely smooth, with slight basal rhabd and subtylote swelling, straight shaft, fusiform points (340-570×16-34µm). Echinating rhabdostyles with large size range, larger ones subtylote, very slight or faint basal rhabd, straight shaft, with light spination on basal, distal and central portions, more-or-less aspinose between, smaller ones slightly subtylote, faint basal rhabd, straight shaft,

absent. Microscleres absent (Pulitzer-Finali, 1994).

REMARKS. This species is very poorly known only from its original description. Unfortunately type material is not available from the MSNG, and its apparent affinities can only be speculated from Pulitzer-Finali's (1994) incomplete description and illustrations. In the absence of a skeletal description its placement is not certain, although *Aulospongus* may be correct given that both choanosomal principal and echinating styles show various degrees of basal rhabds, indicating possible common origin.

In growth form *A. flabellum* shows an uncanny superficial resemblance to *Echinodictyum mesenterinum* (also known from E Africa; Hooper, 1991), including the possession of differentiated osculiferous and porous surfaces. Assuming that Pulitzer-Finali's (1994) description of the spicule complement is complete for *A. flabellum*, it shows greatest similarities to *A. cerebella* and *A. tubulatus* in spicule diversity, and in particular to the latter species in geometry of the larger, smooth choanosomal principal rhabdostyles (nearly identical size and shape). The two species differ in the diversity and size of smaller echinating rhabdostyles, with *A. flabellum* having two categories and the larger ones nearly twice the size of those in *A. tubulatus* (120-370×11-18µm versus 109-126×5-10µm, respectively).

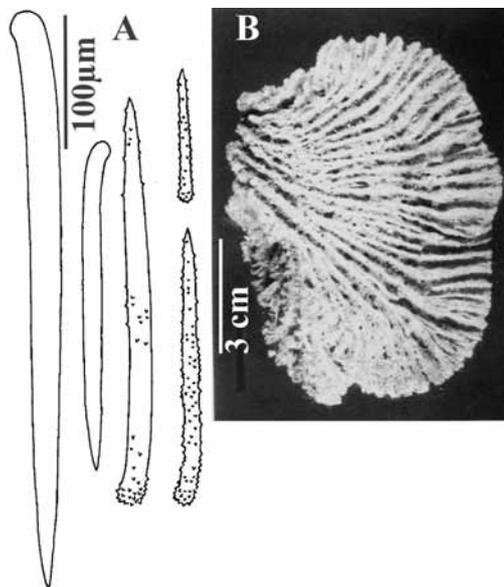


FIG. 4. *Aulospongus flabellum*. A, Choanosomal principal rhabdostyles (left), size range of echinating rhabdostyles (right). B, Holotype (figure modified from Pulitzer-Finali, 1993).

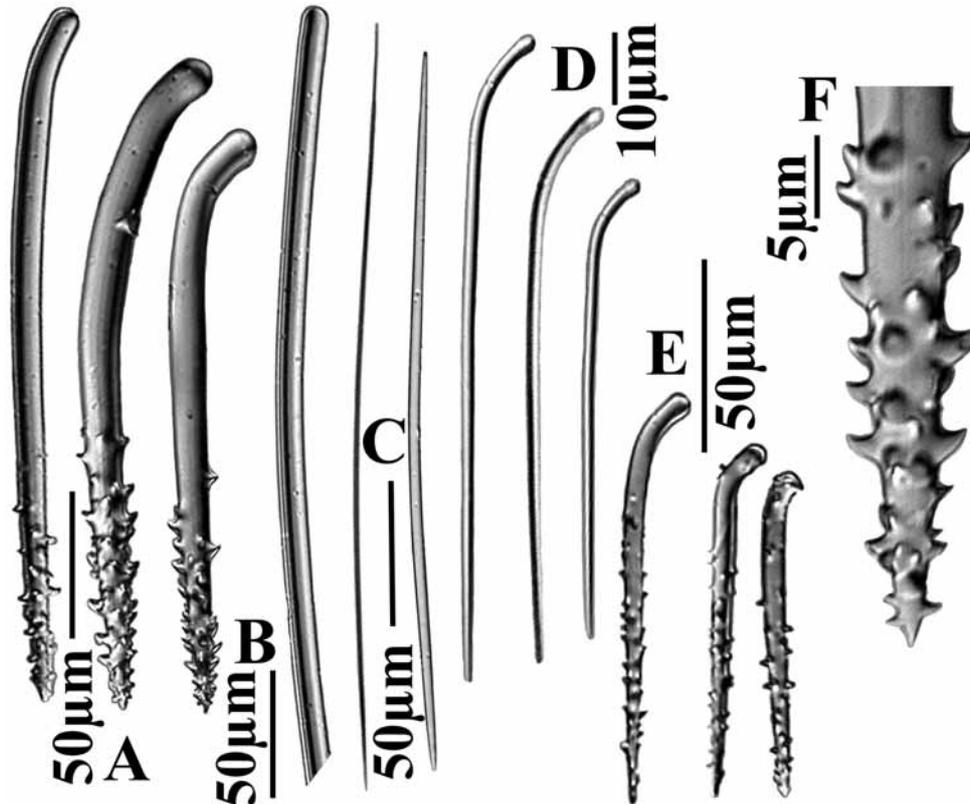


FIG. 5. *Aulospongus gardineri*. A, Choanosomal principal rhabdostyles. B, Subectosomal extra-axial style. C, Ectosomal auxiliary styles/anisoxeas. D, Third category of rhabdostyles. E, Echinating rhabdostyles. F, Apical spination on choanosomal principal rhabdostyle.

Aulospongus gardineri
(Dendy, 1922)
(Figs 5-6, Table 1)

Plumohalichondria gardineri Dendy, 1922: 87, pl. 2, fig. 9, pl. 15, fig. 4a-d; Vacelet & Vasseur, 1971: 83.

Aulospongus gardineri; Hooper, 1991: 1309, fig. 67e-h; van Soest, 1994: 72.

Not *Hemectyonilla gardineri*; Lévi & Lévi, 1983: 950, pl. 2, figs 2,3,5, fig. 14.

MATERIAL. HOLOTYPE. BMNH1921.11.7.74: Amirante, coll. 'Sealark', 18.x.1905, 40-88m depth.

DISTRIBUTION. Amirante, Tulear, Madagascar, Seychelles, Indian Ocean.

DESCRIPTION. Growth form erect lobate, lamellate or bulbous. Surface nearly smooth, granular. Colour dull yellowish-grey in ethanol. 'Raspailiid ectosomal skeleton' moderately well developed, with ectosomal auxiliary styles forming thick surface brushes, although not

always associated with the protruding long subectosomal extra-axial styles, the latter also lying in tracts parallel to fibres and protruding through the surface in radiate tufts. Choanosomal skeleton consists of close-set, thick, plumose fibre-bundles diverging and branching towards the periphery, occasionally interconnected by small aspicular fibres, heavily echinated by both smaller rhabdostyles and smooth rhabdostyles, nearly all pointing outwards. Fibre-bundles only sparsely cored by choanosomal principal rhabdostyles whereas all three size classes of rhabdostyles project nearly at right angles to fibres, together producing much more bulbous fibre-bundles than other species. Megascleres consist of 3 size classes of rhabdostyles: larger choanosomal principal rhabdostyles with prominently curved and subtylote basal rhabd, large recurved spines confined mainly to the apical (pointed) third or half of the spicule, smooth base occasionally with few small spines

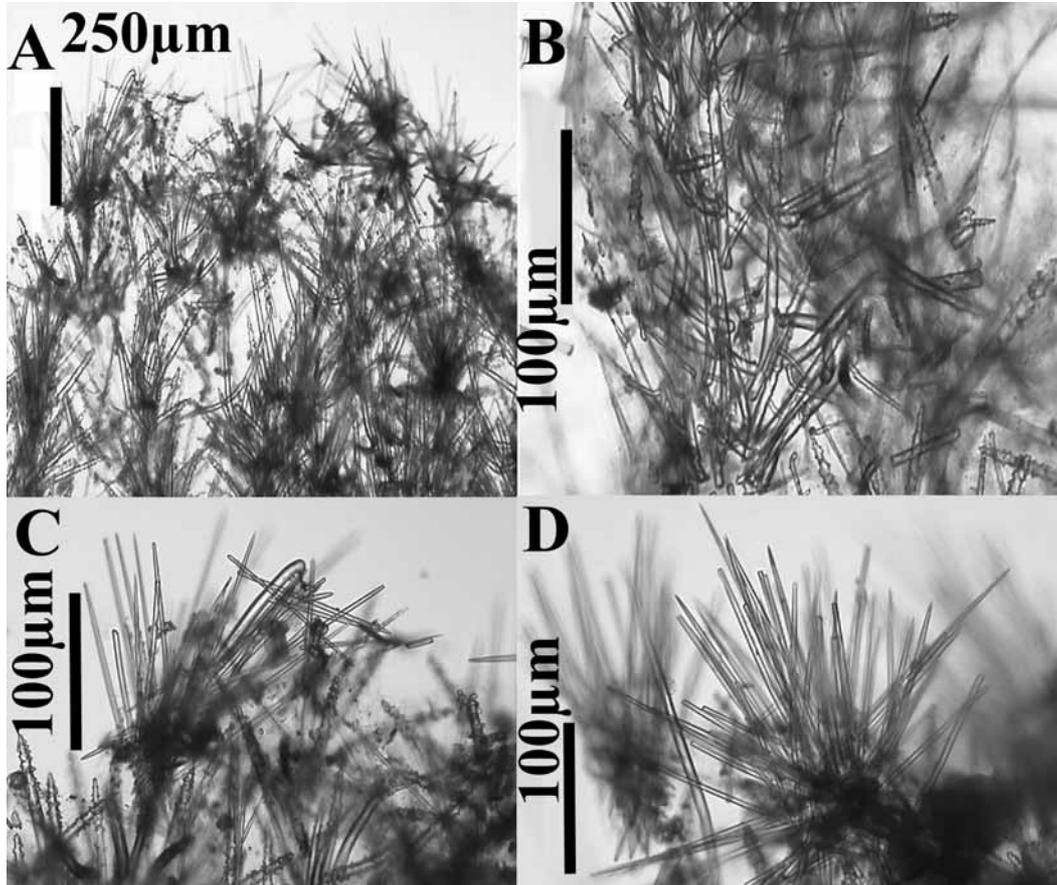


FIG. 6. *Aulospongos gardineri*. A, Peripheral skeleton. B, Choanosomal fibre. C, Ectosomal skeleton. D, Ectosomal auxiliary spicule bundle.

(205-385×11-21µm); smaller echinating rhabdostyles with very strong basal rhabd, base occasionally spined, spines more evenly dispersed or concentrated on apical half, spines relatively large, recurved (94-136×5-11µm); third class of smooth rhabdostyle long, very slender, with strong basal rhabd, subtylote base, completely smooth, tapering to a fine point (84-156×1-2µm). Subectosomal extra-axial styles or anisoxeas long, smooth, slightly curved near base, evenly rounded base (815-1050×8-22µm). Ectosomal auxiliary styles/ anisoxeas straight or slightly curved, usually with one blunt or tornote end, sometimes tapering at both ends (218-442×1-2µm). Microscleres absent.

REMARKS. Lévi & Lévi's (1983) specimen from deeper waters off New Caledonia, described as *A. gardineri*, is not conspecific with

Dendy's (1922) material from Amirante, although the two appear to be related in some of their features. The former material is described below as a new species, *A. novaecaledoniensis* sp. nov. In *A. gardineri* larger subectosomal extra-axial spicules are present and are surrounded by bundles of ectosomal auxiliary styles/anisoxeas (absent in *A. novaecaledoniensis*); there is a unique third category of rhabdostyle (absent in the latter species); spination on rhabdostyles extends at least 25% (or more) along apical end of spicule (confined to extreme apex only in the latter species); spicule dimensions are generally smaller (see Table 1); and there are many more plumose fibre-bundles with rhabdostyles projecting/echinating fibres nearly at right angles (fewer projecting rhabdostyles and echinating at more acute angles in the latter species).

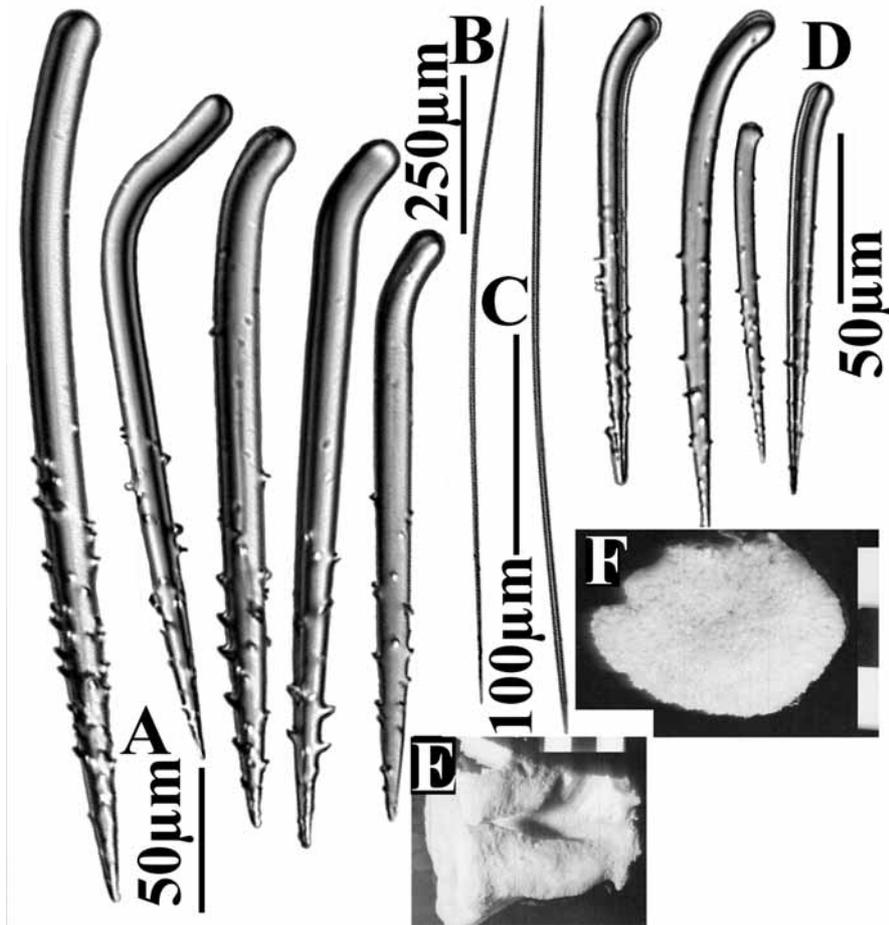


FIG. 7. *Aulospongos involutum*. A, Choanosomal principal rhabdostyles. B, Subectosomal extra-axial anisoxea. C, Ectosomal auxiliary anisoxea. D, Echinating rhabdostyles. E, Holotype (scale 3cm). F, 'John Murray' specimen (scale 3cm).

In rhabdostyle geometry this species is also similar to *A. involutum* (which prompted Burton (1959) to synonymise the two), but they differ in many other respects (fibre characteristics, choanosomal and ectosomal skeletal structure, spicule sizes and spicule diversity (see Table 1)), which Lévi & Lévi (1983) and Hooper (1991) indicated they were distinct species. *Aulospongos gardineri* is unusual in having a macroscopically smooth surface (although microscopically it is hispid from the protruding subectosomal extra-axial styles), and in possessing of a third category of rhabdostyle (similar only to *A. spinosum* in this respect, although the two species differ in virtually all other characters; Table 1).

***Aulospongos involutum* (Kirkpatrick, 1903)**
(Figs 7-8, Table 1)

Stylostichon involutum Kirkpatrick, 1903: 250, pl. 5, fig. 16, pl. 6, fig. 17a-e.
Hemectyonilla involutum; Burton, 1959: 254.
Aulospongos involutum; Pultizer-Finali, 1993: 308-309;
Hooper, 1991: 1307, fig. 66a-f.

MATERIAL. HOLOTYPE. BMNH1902.11.16.33 (fragment MNHN LBIM DCL61): Cone Point, Natal, South Africa, 68m depth. OTHER MATERIAL. BMNH1936.3.4.118: Gulf of Aden, 11°56-57'N, 50°35-39'E, coll. 'John Murray', 12.x.1933, 37m depth.

DISTRIBUTION. Natal, Zanzibar, Kenya, Gulf of Aden, South Arabian coast and Arabian Gulf, Indian Ocean.

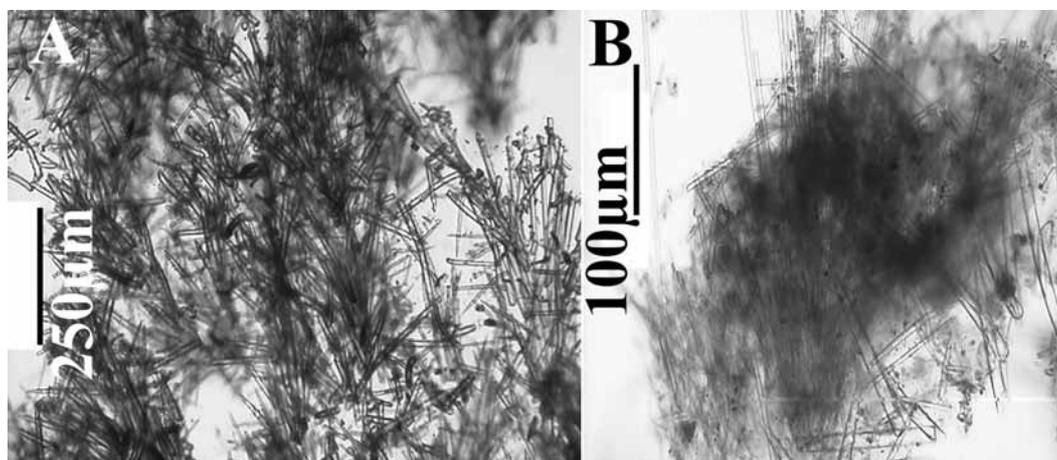


FIG. 8. *Aulospongos involutum*. A, Choanosomal skeleton. B, Ectosomal skeleton.

DESCRIPTION. Growth form plate-like, vasi-form with very thick lamellae. Surface shaggy, conulose. Colour brown in ethanol. 'Raspailiid ectosomal skeleton' reduced, composed of raphidiform ectosomal auxiliary anisoxeas/oxeas perpendicular to the surface, not usually forming brushes, and extremely long, thin subectosomal extra-axial styles or anisoxeas protruding through the surface. Choanosomal skeleton exclusively plumose, lacking any axial compression or obvious differentiation between axial and extra-axial regions, although peripheral skeleton tracts form prominent tufts at the surface, producing relatively large conules. Larger rhabdostyles form plumose tufts along fibre-bundles, which are radial, microcionid-like, plumose, and heavily echinated by smaller rhabdostyles. Megascleres consist of larger choanosomal principal rhabdostyles with moderate to strong basal rhabd, subtylote and completely smooth bases, smooth for most of the distal end of the shaft, with only a few large, strongly recurved spines on the apical third of spicules (224-370×12-22μm). Smaller echinating rhabdostyles with strong basal rhabd, slightly subtylote and completely smooth bases, small spines restricted to apical half of spicules (122-195×5-11μm). Subectosomal extra-axial anisoxeas long, smooth, slightly curved at centre (1010-1390×7-11μm). Ectosomal auxiliary oxeas or anisoxeas are raphidiform, straight or very slightly curved (450-640×5-7μm). Microscleres absent.

REMARKS. Kirkpatrick (1903) described sigma microscleres present in this species, and a few

were seen in spicule preparations made from the holotype, but these are obviously contaminants and were not seen in histological sections. Rhabdostyles of *A. involutum* have a similar geometry to those of *A. gardineri*, although they are not synonyms as suggested by Burton (1959) (Hooper, 1991), with *A. involutum* lacking the third category of rhabdostyle unique to *A. gardineri*, and also lacking aspicular fibres present in *A. gardineri* and *A. tubulatus*. Subsequent records of this species from E Africa by Burton (1959) and Pulitzer-Finali (1993) agree very closely with those of the specimens re-examined here. Pulitzer-Finali (1993) stated that subectosomal extra-axial spicules were styles, but these are clearly anisoxeote.

Aulospongos monticularis
(Ridley & Dendy, 1886)
(Figs 9-10, Table 1)

Axinella monticularis Ridley & Dendy, 1886: 481; 1887: 185, pl. 38, fig. 5.

Aulospongos monticularis; Hallmann, 1917: 373; Hooper, 1991: 1307, fig. 65a-c.

Microcionia monticularis; Burton, 1956: 132.

Aulospongiella monticularis; Burton, 1956: 141.

MATERIAL. HOLOTYPE. BMNH1887.5.2.20: São Vicente Harbour, Cape Verde I., coll. 'Challenger', -vii.1873, 14-40m depth. **PARATYPE.** BMNH-1887.5.2.273: same locality.

DISTRIBUTION. Cape Verde I., N Atlantic, São Vicente, W Africa.

DESCRIPTION. Growth form massive, bulbous-encrusting. Surface shaggy, conulose.

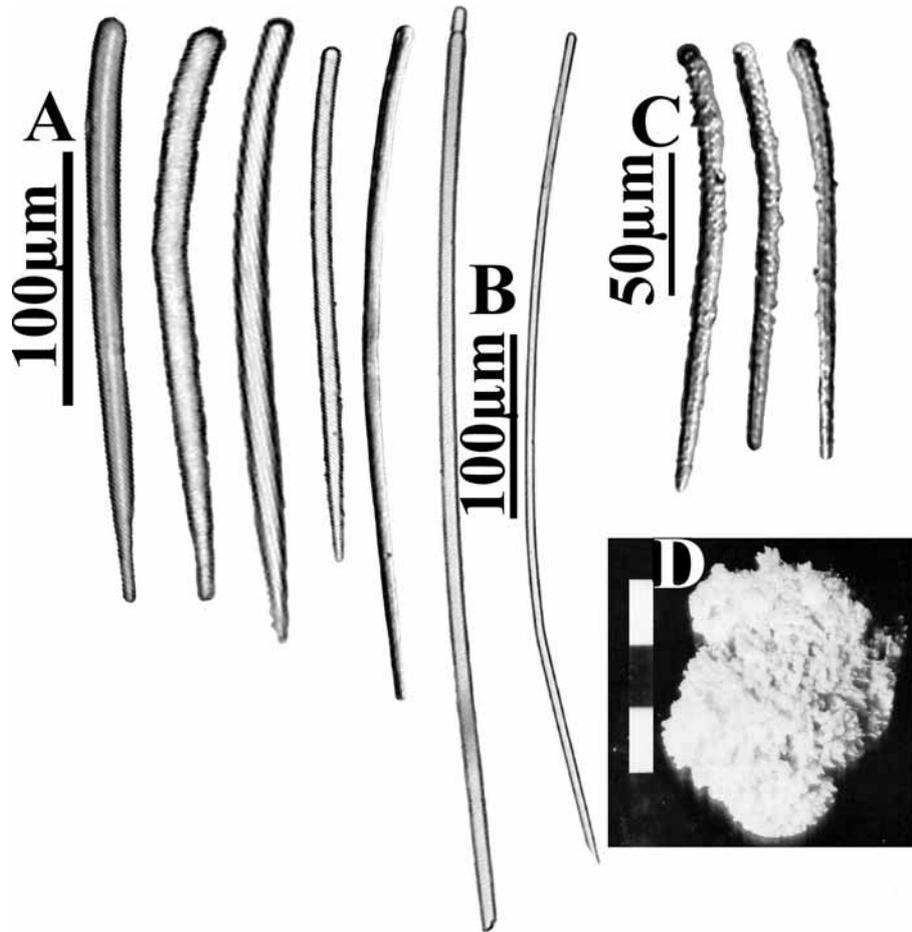


FIG. 9. *Aulospongus monticularis*. A, Choanosomal principal rhabdostyles. B, Basal end of subectosomal extra-axial styles. C, Echinating rhabdostyles. D, Holotype (scale 3cm).

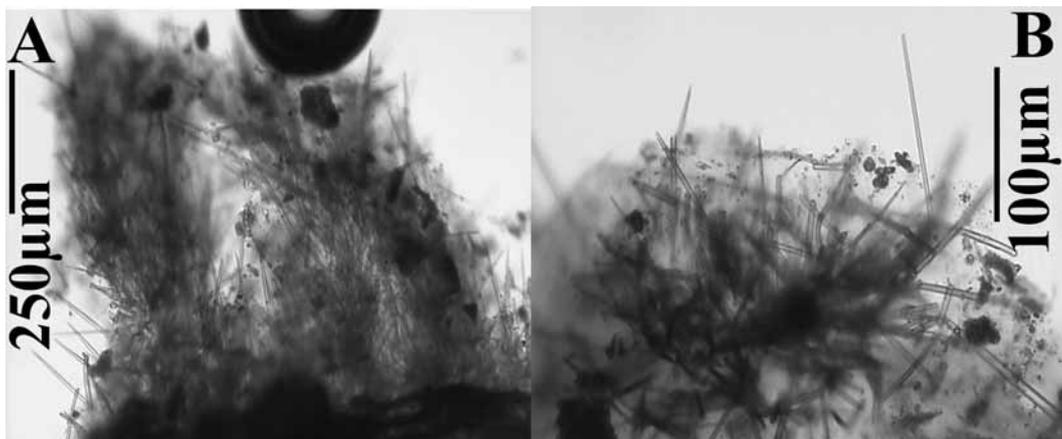


FIG. 10. *Aulospongus monticularis*. A, Microcionid-like choanosomal skeleton arising from basal detritus. B, Peripheral skeleton.

Colour yellowish-grey in ethanol. 'Raspailiid ectosomal skeleton' absent, although larger subectosomal extra-axial styles occasionally protrude through surface. Choanosomal skeleton microcionid-like, composed of large, non-anastomosing, plumose fibre-bundles, without any trace of axial compression or differentiation between axial and extra-axial regions. Ascending fibre-bundles arise from detritus-encrusted basal skeleton, and foreign particles also incorporated into choanosomal skeleton. Ascending fibre-bundles cored and echinated by both categories of rhabdostyles, although larger rhabdostyles comprise most of the coring spicules, as well as protruding through fibres in plumose bundles. Megascleres consist of larger choanosomal principal rhabdostyles with only slight basal rhabd, completely smooth, rounded or slightly subtylote bases (290-518×9-19µm). Smaller echinating rhabdostyles more-or-less evenly spined, microcionid-like, slightly curved at centre, with very small, granular, erect spines, only slight basal rhabd and slight to moderate subtylote basal swelling (132-275×2-9µm). Subectosomal extra-axial styles slightly curved near basal end, with slightly subtylote bases and very long tapering points (620-960×7-15µm). Ectosomal auxiliary spicules absent. Microscleres absent.

REMARKS. This species is similar to *A. involutum* in having long subectosomal extra-axial spicules protruding through the surface, which are not surrounded by ectosomal auxiliary spicules, as typical for most raspailiids. It differs from *A. involutum* in lacking rhabdiform ectosomal auxiliary spicules completely, as well as in other important characters such as the geometry, small size and vestigial spination of rhabdostyles (Table 1). It should also be compared to *A. villosa* and *A. cerebella* which also lack any ectosomal specialisation, differing from *A. villosa* in having completely smooth larger rhabdostyles (generally longer than those of *A. villosa*), microcionid-like, evenly spined smaller rhabdostyles (partially spined in *A. villosa*), and a bulbous growth form (bushy growth form in *A. villosa*) (see Table 2). Rhabdostyle morphology differs substantially between *A. monticularis* and *A. cerebella*: larger rhabdostyles are of similar size, but those in the latter species have only a slight basal rhabd; smaller rhabdostyles are evenly spined in both species but about half the size in *A. monticularis*.

***Aulospongia novaecaledoniensis* sp. nov.**
(Figs 11-12, Table 1)

Hemectyonilla gardineri; Lévi & Lévi, 1983: 950, pl. 2, figs 2,3,5, fig. 14.

ETYMOLOGY. For the type locality.

MATERIAL. HOLOTYPE. MNHN LBIM DCL2941: Havannah, New Caledonia, 22°17'S, 167°14'E, coll. 'Vauban' (stn.DP36), 24.v.1978, 425-430m depth. PARATYPE. MNHN LBIM DCL2940: same locality, 22°19'S, 167°11'E, 300-315m depth.

DISTRIBUTION. New Caledonia.

DESCRIPTION. Growth form massive, tubular. Surface finely hispid, generally smooth apart from several large surface conules, each surmounted by a terminal oscule. Colour in ethanol brownish ocre with slight pinkish tinge. 'Raspailiid ectosomal skeleton' moderately well developed, with ectosomal auxiliary styles forming thick surface brushes, although not associated with any subectosomal extra-axial spicules (the latter absent completely from this species). Choanosomal skeleton essentially plumose, consisting of close-set, thick, ascending fibre-bundles, diverging and branching towards the periphery. Ascending fibres moderately heavily cored by larger rhabdostyles, forming mainly axial bundles within fibres and only slightly plumose tracts of single rhabdostyles protruding through fibres, with their points ascending towards the surface. Smaller rhabdostyles concentrated mainly at the base of main ascending fibres. Ascending fibres interconnected by few, aspicular, transverse fibres sparsely echinated by smaller rhabdostyles. Megascleres consist of larger choanosomal principal rhabdostyles with variably developed smooth basal rhabds, ranging from nearly straight to prominently rhabdose, with basal rhabd occupying between 15-40% of spicule length, shaft smooth except for a few (4-12) large recurved spines located only on the extreme apical (pointed) end of the spicule (275-415×19-26µm). Smaller echinating rhabdostyles with only moderate basal rhabd (sometimes slight), base usually subtylote, smooth or occasionally with a few spines, shaft with spines concentrated on apical half (not merely confined to extreme point of spicule as for larger rhabdostyles), spines relatively large, recurved (122-195×7-13µm). Subectosomal extra-axial megascleres absent. Ectosomal auxiliary anisoxeas (occasionally styles) large, slightly curved at the centre, usually with one blunt or tornote end, sometimes tapering

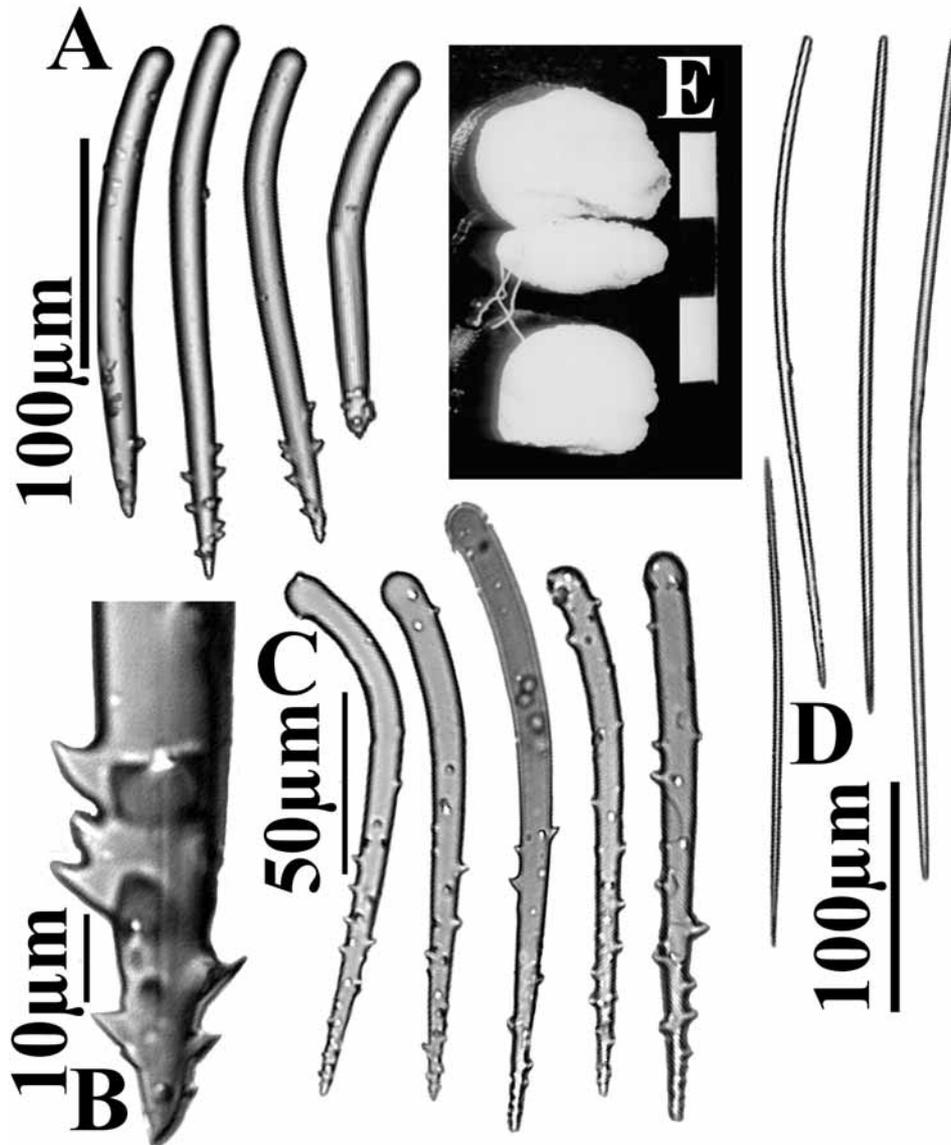


FIG. 11. *Aulospongia novaecaledoniensis* sp. nov. A, Choanosomal principal rhabdostyles. B, Apical spines on choanosomal principal rhabdostyle. C, Echinating rhabdostyles. D, Ectosomal auxiliary anisoxeas. E, Holotype and fragment (scale 3cm).

at both ends, rarely symmetrical sharply pointed ($445\text{--}585 \times 3\text{--}6\mu\text{m}$). Microscleres absent.

REMARKS. Lévi & Lévi (1983) initially referred their material from New Caledonia to Dendy's (1922) species *A. gardineri* (from Amirante, Indian Ocean), based on inferred similarities in their respective growth forms,

pattern of spination and geometry of both smaller and larger rhabdostyles. However, *A. novaecaledoniensis* sp. nov. lacks the third category of rhabdostyle unique to *A. gardineri*; lacks larger subectosomal extra-axial styles/anisoxeas completely; spines on the larger rhabdostyles are much more sparse and confined only to the extreme apex (point) of spicules; and spicule

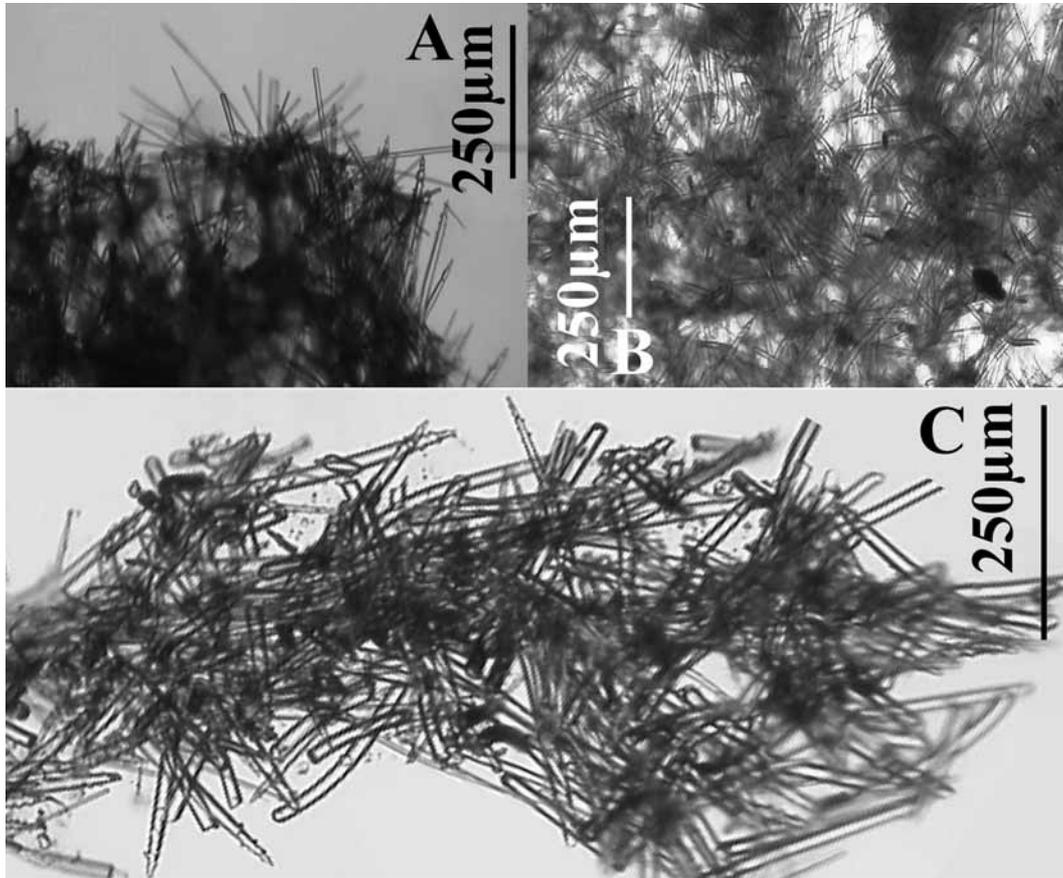


FIG. 12. *Aulospongia novaecaledoniensis* sp. nov. A, Peripheral skeleton. B, Choanosomal skeleton. C, Choanosomal fibre bundle.

dimensions are substantially larger than those of *A. gardineri* (Table 1). More subjectively, this species also has much more compact fibre-bundles than does *A. gardineri*, the former having rhabdostyles mainly confined to the axis of fibres and only slightly projecting through the fibres as single spicules, pointing towards the surface, whereas the latter species has plumose bundles of rhabdostyles projecting nearly at right angles to fibres, forming prominently plumose tracts. Nevertheless, the two species are related by these features.

***Aulospongia samariensis* sp. nov.**
(Figs 13-16, 36A-B, Tables 1-2)

Raspailia (Raspaxilla) sp.; Silvestri, Zea & Duque, 1994: 21.

ETYMOLOGY. Named for the holotype locality of Santa Marta.

MATERIAL. HOLOTYPE. ICN-MHM(Po)0171: Nenguange Bay, 'Piedra Ahogada', Magdalena Department, Colombia, Caribbean Sea, 11°25'N, 75° 10'W, 26m depth, 27-vi-1983, coll. Sven Zea (PEB-013), SCUBA, Second Botanic Expedition, on coral rubble, reef base. PARATYPES. QMG304501: Bahía de Nenguange, Santa Marta, Colombia, Caribbean Sea, 26m depth, 27.vi.1983, coll. S. Zea, SCUBA, coral rubble. QMG313310, G313311: Dairy Bull, Discovery Bay, Jamaica (Caribbean Sea), 18°28'N, 77° 24'W, coll. H. Lehnert, SCUBA using trimix (see Lehnert & van Soest, 1996), 90m depth (ref. no. J96/41, 28.vi.96). INV-POR-0455: 'Punta de Betín', Santa Marta Bay, Magdalena Department, Colombia, Caribbean Sea, 12m depth, 10.ix.1982, coll. S. Zea (PSM229), SCUBA, on dead sides of coral head, patch reef. INV-POR-0456: same locality, 6m depth, 15.xi.1982, metamorphic rock, rocky shore (PSM239).

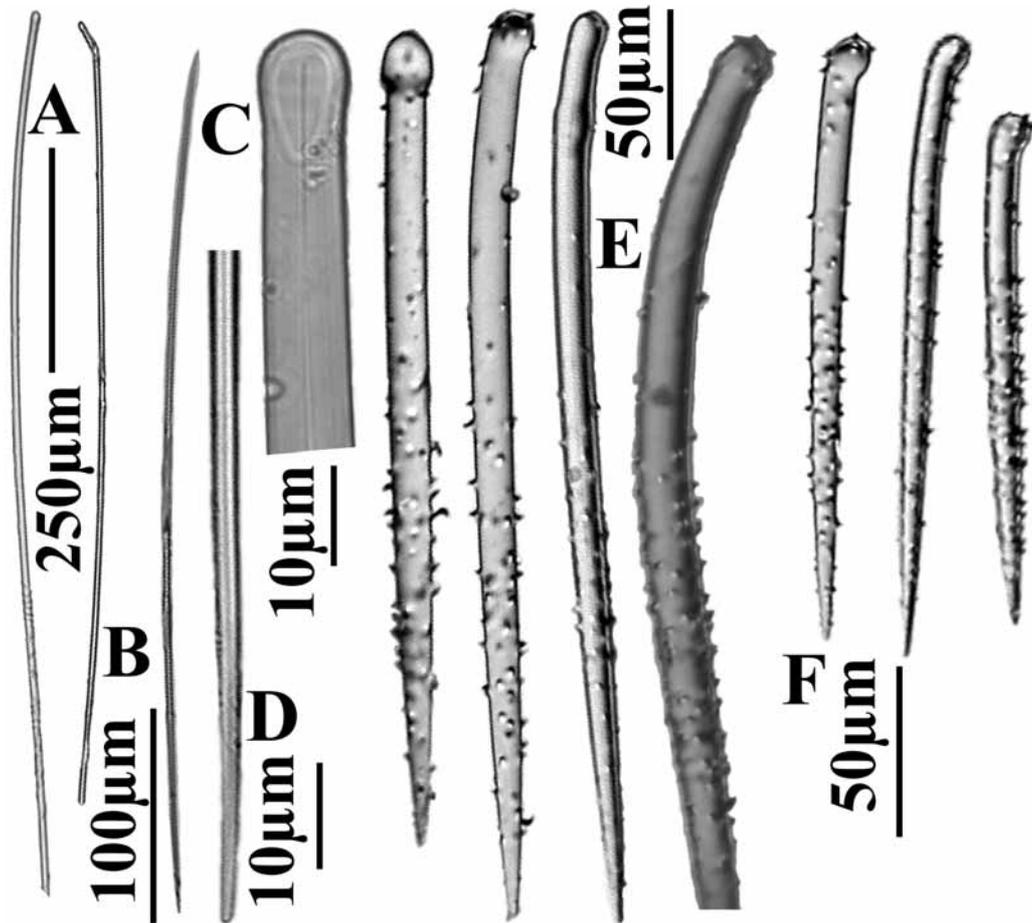


FIG. 13. *Aulospongus samariensis* sp. nov. (W Caribbean population, paratype QMG304501) A, Subectosomal extra-axial styles/subtylostyles. B, Ectosomal auxiliary anisoxea. C, Base of subectosomal extra-axial subtylostyle. D, Apex of subectosomal extra-axial style. E, Choanosomal principal rhabdostyles. F, Echinating rhabdostyles.

DISTRIBUTION. Santa Marta region, W Caribbean, Jamaica, E Caribbean

DESCRIPTION. *Growth form.* Erect, stalked, vaguely cylindrical, club-shaped, slightly bushy, 5-12cm high, 0.5-2.5cm diameter, with several small irregular bulbous lobate branches up to 0.7-3cm diameter, partially fused and becoming more swollen at their tips. Protruding fibre-bundles from underlying skeleton producing a shaggy appearance at the surface, superficially resembling *Pandaros acanthifolium* (Duchassaing & Michelotti, 1864) (Microcionidae). Fibre-bundles at the centre of the sponge are dense, narrow, winding and branching, with the longitudinal axis produced by fusion of fibres

clearly dominant. Numerous short thin branches located towards periphery which subdivide repeatedly.

Surface. Shaggy, slightly bulbous, prominent hispid ridges running longitudinally, subparallel along branches, with individual ridges composed of smaller lamellae or tuberculate conules; valleys between ridges thickly collagenous, smooth, with ectosome stretched between ridges and towards apex of branches forming a shiny surface in life, or with deep valleys when ectosome collapses out of water.

Colour. Brownish yellow (Munsell 5YR 6/6) to dark brown alive (NCG 23 (raw amber), 36 (amber) to 219 (sepia)). Apical branch tips with

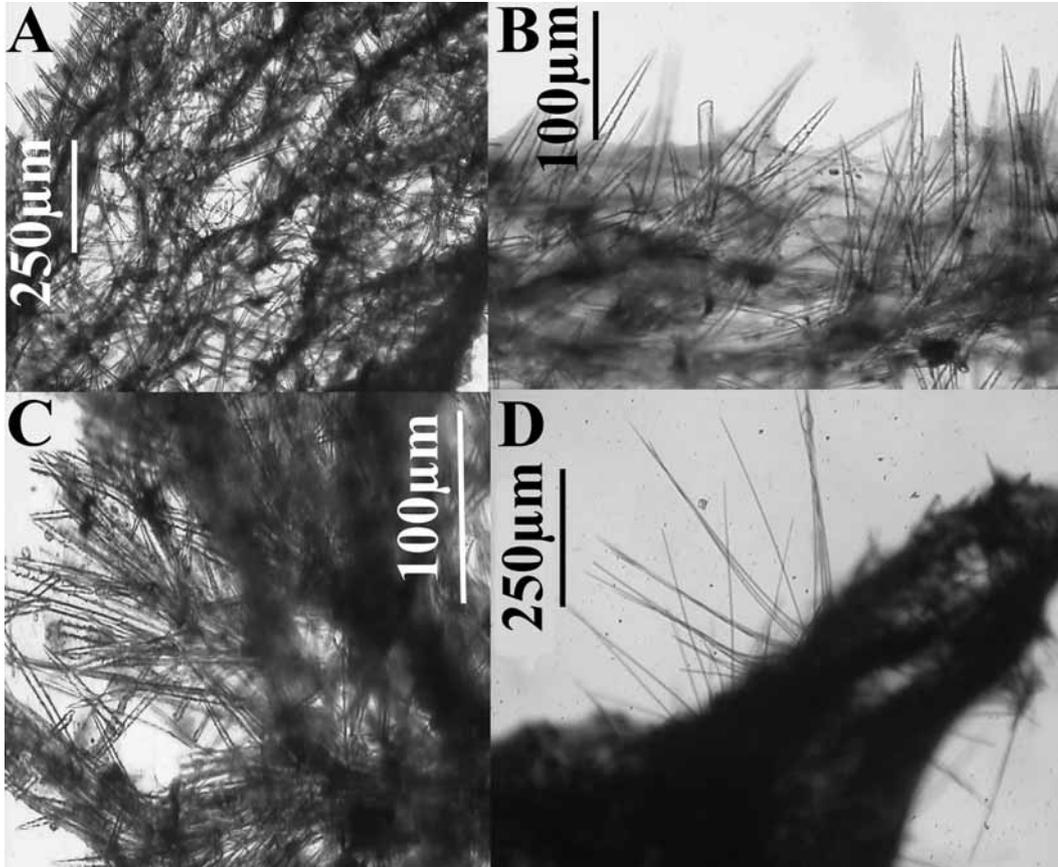


FIG. 14. *Aulospongos samariensis* sp. nov. (W Caribbean population, paratype QMG304501) A, Choanosomal skeleton. B, Peripheral skeleton. C, Peripheral fibre-bundles. D, Ectosomal skeleton.

mustard yellow tinge (NCG 24 (buff)). Preserved specimens evenly brown.

Oscules. Small, <0.5-2mm diameter, interdispersed in cavities on produced by folding of surface ridges, collapsing out of water.

Texture. Firm, compressible, with stiff, flexible, elastic branches.

Ectosomal skeleton. Ectosome with thick, organic, heavily collagenous matrix up to 200µm thick. 'Raspailiid ectosomal skeleton' present consisting of clusters of loose ectosomal auxiliary anisoxeas, forming bouquets on the surface conules, surrounding the usually single, long subectosomal extra-axial styles at the point they protrude through the surface. Occasional plumose bundles of larger choanosomal principal rhabdostyles also protrude through the surface (on conules), and individual rhabdostyles form

an evenly spaced palisade in between surface conules.

Choanosomal skeleton. Skeletal structure predominantly plumose, only very faintly more compressed, slightly reticulate, in axis than in periphery. Axial skeletal reticulation composed of fibre-bundles more-or-less amalgamated into large tracts, sparsely interconnected by collagen and/or aspicular or paucispicular 'secondary fibres'. Fibres in peripheral skeleton with very few reticulate elements, disappearing closer to the surface, with ascending fibre-bundles diverging and forming discrete conules at the surface. Primary reticulate fibres and ascending fibres fully cored by larger rhabdostyles, protruding through fibres at obtuse angles, and heavily echinated by both smaller and larger rhabdostyles forming heavy plumose tracts, producing clumps of spicules particularly at fibre

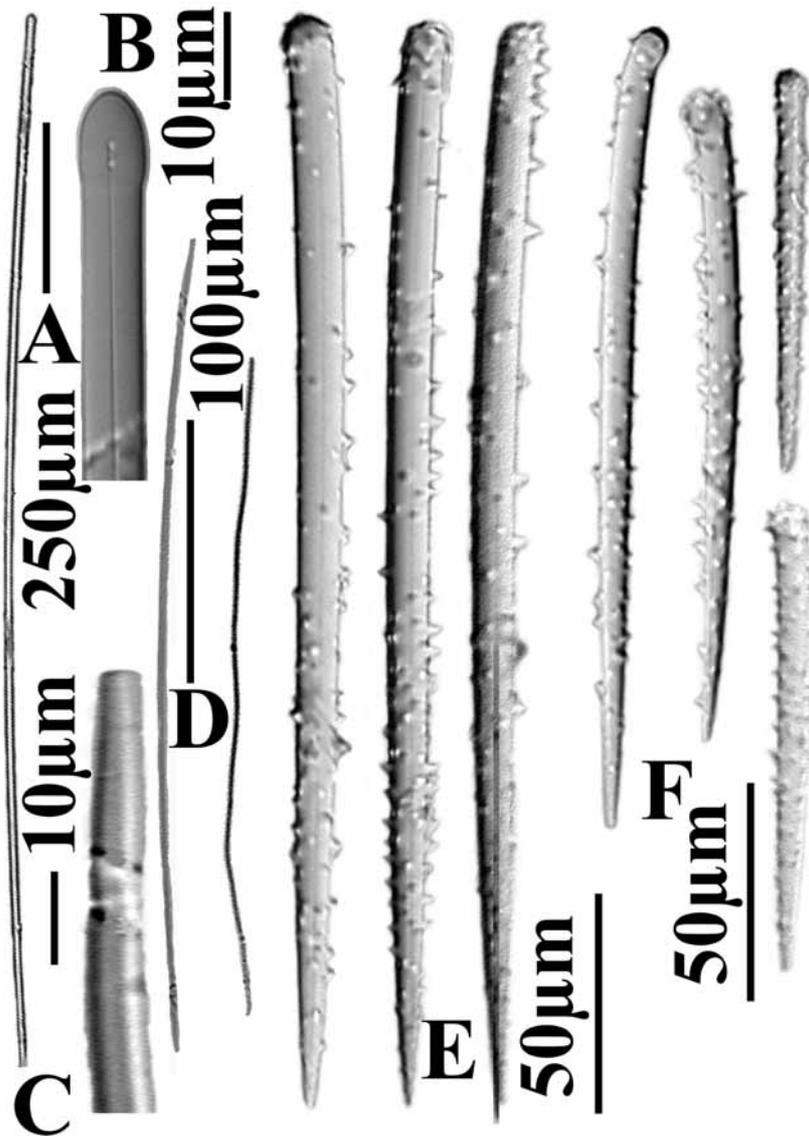


FIG. 15. *Aulospongos samariensis* sp. nov. (E Caribbean population, paratype QMG313310) A, Subectosomal extra-axial subtylostyle. B, Base of subectosomal extra-axial subtylostyle. C, Base of ectosomal auxiliary anisoxea. D, Ectosomal auxiliary anisoxeas. E, Choanosomal principal rhabdostyles. F, Echinating rhabdostyles.

nodes, with larger rhabdostyles dominating tracts and smaller ones interspersed between them. Choanosomal principal rhabdostyles appear larger in the periphery than in axial regions of the skeleton. Long subectosomal extra-axial subtylostyles have their bases embedded in spongin fibres, forming sparse radial tracts

protruding a long way through the surface. Collagen between the fibres is light, generally aspicular, although multispicular tracts of subectosomal extra-axial styles run along the longitudinal axis of branches towards the surface, more-or-less parallel to (and external of) spongin fibres. Meshes between fibre are

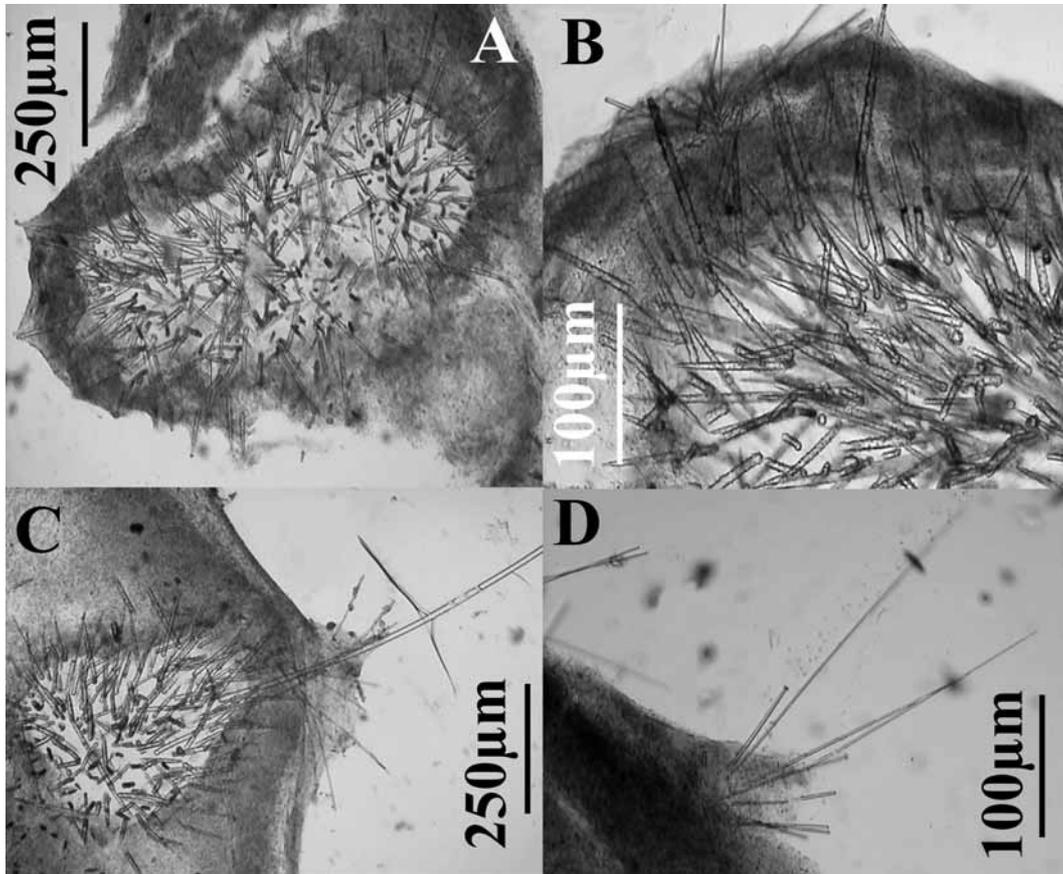


FIG. 16. *Aulospongia samariensis* sp. nov. (E Caribbean population, paratype QMG313310) A, Choanosomal skeleton. B, Peripheral skeleton. C, Subectosomal extra-axial spicule and ectosomal skeleton. D, Ectosomal skeletal bundle.

relatively small, close-set, 150-250µm diameter, generally smaller in the axis than periphery of the skeleton.

Megascleres. Larger choanosomal principal rhabdostyles long, thick; shaft is nearly straight; bases slightly rhabdose; bases also lightly subtylote to prominently tylote, with tyles terminal or subterminal; spination on spicules varies between E & W Caribbean populations (the former with more-or-less even spination although generally heavier at distal and apical ends than at centre, spines relatively large, recurved, hook-like; the latter with bases lightly spined or occasionally completely smooth, with small recurved spines concentrated on apical end of spicule, aspinose below basal swelling); points are tapering, fusiform (218-(322.2)-412×9-(13.2)-18µm). Smaller echinating

rhabdostyles short, relatively thick; shaft straight or slightly curved at centre; basal rhabd slight or occasionally completely straight; points fusiform tapering; bases range from slightly subtylote to well developed tylote; spines more evenly dispersed over whole spicule (as compared to the larger size class), sometimes less spinose below basal swelling than elsewhere, sometimes completely smooth below basal swelling; spines small, recurved (112-(181.2)-232×6-(9.3)-13µm). Several intermediate-sized rhabdostyles present, linking larger and smaller classes. Subectosomal extra-axial styles very long, thin; shaft straight or slightly curved near basal end, occasionally flexuous; base smooth, rounded or slightly subtylote; points tapering to long fusiform (920-(1814.5)-2750×8-(18.3)-26µm). Ectosomal auxiliary anisoxeas moderately long,

TABLE 2. Comparison between spicule dimensions of eastern (Jamaican) and western (Colombian) populations of *A. samariensis* sp. nov.

Spicule	E Caribbean	W Caribbean
Choanosomal principal rhabdostyles	(218-(261.6)-355×10-(13.2)-18µm)	(310-(377.5)-412×9-(13.1)-16µm)
Echinating rhabdostyles	(112-(187.3)-210×6-(7.5)-11µm)	(145-(201.3)-232×8-(10.4)-13µm)
Subectosomal extra-axial styles	(920-(1144.6)->2500×8-(15.5)-25µm)	(1325-(2247.6)-2750×16-(19.7)-26µm)
Ectosomal auxiliary anisoxeas	(225-(584.4)-775×2.5-(4.2)-5.5µm)	(340-(515.3)-612×3-(4.1)-5.5µm)

thin; shaft slightly curved at centre, occasionally flexuous, sinuous or raphidiform; ends are asymmetrical with long tapering points and tapering rounded hastate base (225-(508.5)-775×2.5-(4.1)-5.5µm)

Microscleres. Absent.

ECOLOGY. *Aulospongia samariensis* has not been recorded from any other locality in the Colombian Caribbean. One of us (SZ) has extensively investigated rocky-reef complex areas down to a depth of 40m from the border of Panamá to Santa Marta in the continental coast of Colombia, and in the islands, atolls and banks of the San Andrés and Providencia Archipelago (San Andrés island, Old Providence island, Court-town Cays, Albuquerque Cays, Serrana Bank, Roncador Bank, Quitasueño Bank), SW Caribbean. The fact that this species has been found elsewhere only in deep, insular drop-offs (i.e. Jamaica), suggests it may be a deep water species, that comes up to shallower reefs (above 18m depth) at Santa Marta, where there is a seasonal upwelling of the colder water mass (called 'Subtropical Underwater', 19-25°C, usually localized between 100-200m depth in the Caribbean; Bula-Meyer, 1985). There are unpublished examples of other sponges (and many published records of algae), that follow this pattern, but this is the first published record of this phenomenon for sponges.

REMARKS. Initially the E (Jamaican) and W (Colombian) Caribbean populations were thought to be distinct species, showing some consistent differences in growth form (more elongate versus more bushy), ectosomal auxiliary spicule geometry (anisoxeas with fusiform points versus those with hastate points), ectosomal specialisation (ectosomal auxiliary spicule brushes concentrated mainly around surface conules versus evenly hispid surface), and skeletal structure (axial skeleton more compressed versus more reticulate, respectively). Spicule dimensions also varied slightly between the two populations (Table 2). However, upon further consideration these differences are

less obvious than their similarities, particularly in spicule geometry, and the two populations are considered to be conspecific.

This species belongs to *Aulospongia* in having characteristic fused fibre-bundles forming a denser core in the axial part of the skeleton, and a predominantly plumose structure towards the periphery; lacking any prominent differentiation between axial and extra-axial skeletons apart from the amalgamation of these fibres towards the centre of the skeleton, and having fibres which are cored and echinated by heavy bundles of rhabdostyles, in two size classes.

Aulospongia samariensis differs from the 'typical tubular' *Aulospongia* in its growth form (cylindrical club-shaped), rhabdostyle morphology (more-or-less even spination on both size classes of spicules, slightly less spined in the basal end, and with only a slight basal rhabd), possession of very long subectosomal extra-axial spicules protruding through the surface (in this regard similar only to *A. involutum* (Kirkpatrick)), and possession of a more-or-less well developed, specialised raspailiid ectosomal skeleton. Ectosomal skeletons are well developed in only two species of *Aulospongia* (*A. gardineri* and the present species), consisting of plumose brushes of ectosomal auxiliary styles/anisoxeas surrounding longer subectosomal extra-axial styles/anisoxeas. By comparison, vestigial ectosomal skeletons are present in three species (*A. involutum*, *A. novaecaledoniensis* sp. nov., *A. tubulatus*), consisting of ectosomal auxiliary styles/anisoxeas scattered on or below the surface, but not forming brushes and not necessarily associated with protruding subectosomal extra-axial styles/anisoxeas. Ectosomal auxiliary spicules and a specialised 'raspailiid' ectosomal structure are absent in four species (*A. cerebella*, *A. monticularis*, *A. spinosum*, and *A. villosa*), presumably a derived condition.

This species is similar to *A. gardineri* in ectosomal skeletal structure, *A. involutum* in possession of long subectosomal extra-axial spicules, and to both these species plus *A. novaecaledoniensis* in having both categories of

rhabdostyles partially spined. In other details, however, it differs substantially from all other species, particularly in spicule geometries (Table 1) and dimensions (Table 2).

To some extent this species also resembles *Raspailia acanthifera* (George & Wilson, 1919: 159) from North Carolina, particularly in its growth form (lobate, with lamellate branches), some aspects of skeletal architecture (longitudinal multispicular fibres at the core of the skeleton with only few interconnecting paucispicular transverse fibres; peripheral fibres becoming more radial with fewer interconnecting tracts towards the surface; peripheral fibres fully cored by styles which eventually project through surface in bundles forming surface conules), and ectosomal characteristics (projecting long subectosomal extra-axial styles forming loose bundles at the surface). Conversely, spicule morphology and spicule distribution within the skeleton differ substantially between the two species. In *R. acanthifera* there are five categories of megascleres, each substantially different from those of *A. samariensis* sp. nov., and skeletal structure of *R. acanthifera* is also markedly axially compressed, indicating the latter species should be assigned to *Raspailia* (*Raspaxilla*) (see below), whereas this species is more appropriately referred to *Aulospongia*.

Colombian populations of *A. samariensis* were found to contain both slight antimicrobial against *Staphylococcus aureus* (for ethanol and chloroform extracts) (Silvestri, Zea & Duque, 1994), and strong antitumor activity (Zea, unpublished data), further supporting the relatively high incidence of 'biological activity' reported amongst species of Raspailiidae (Hooper et al., 1992).

Aulospongia spinosum (Topsent, 1927)
(Fig. 17, Table 1)

Rhaphidectyon spinosum Topsent, 1927: 15; 1928: 288, pl. 2, fig. 5, pl. 9, fig. 28, pl. 10, figs 2-3; Lévi, 1960: 752, fig. 7.

Aulospongia spinosum; Hooper, 1991: 1307, fig. 65g-i; Maldonado, 1992: 1149-1150, fig. 9e-j.

MATERIAL. HOLOTYPE. MOM (schizotypes MNHN LBIM DT1139, BMNH1930.7.1.39): Cape Verde Is, near São Vicente I., 16 48'N, 25 06'W, coll. 'Princesse-Alice', 29.vii.1901, 219m depth.

DISTRIBUTION. São Vicente I., North Atlantic, Alboran I., Mediterranean.

DESCRIPTION. Growth form bulbous, erect. Surface shaggy, conulose. Colour dark grey in ethanol. 'Raspailiid ectosomal skeleton' absent, with only larger smooth rhabdostyles protruding through the surface forming shaggy surface processes. Choanosomal skeleton distinctly plumose in both axial and extra-axial regions, composed of very stout, widely separated ascending fibre-bundles with very few interconnecting tracts. Fibres cored by larger (smooth) styles and rhabdostyles (virtually inseparable in their morphology), forming radial tracts in the axis of the skeleton but becoming progressively thicker towards the periphery, ending in discrete plumose bundles at the surface. Largest rhabdostyles/styles appear to be located in the peripheral skeleton. Megascleres include long, thick, choanosomal principal styles and rhabdostyles, completely smooth, with very slight to moderate basal rhabd, the largest occasionally nearly straight at the base (770-1085×28-43µm). Two sizes of smaller rhabdostyles present: long, slender ones, completely smooth, with well curved basal rhabd, predominantly found in choanosomal and peripheral fibres, protruding from fibres at slightly acute angles (90-185×5-12µm), and true echinating acanthostyles with only slight or no basal rhabd, relatively evenly spined, *Eurypon*-like, with swollen subtylote bases bearing very large perpendicular spines (75-145×7-10µm). Subectosomal extra-axial and ectosomal auxiliary spicules absent. Microscleres are raphides occurring singly or in trichodragmata (40-50µm long).

REMARKS. The second category of (smooth) echinating rhabdostyles was overlooked by previous authors, and appears to be quite different from the acanthose echinating acanthostyles. In this regard it is similar to *A. gardineri*, although differing in most other characters (e.g. spicule morphology and spination, spicule sizes, growth form, lack of specialised ectosomal skeleton and possession of raphides in *A. spinosum*).

This species is also highly derived, reduced in most of its morphological characters, and differs from other known *Aulospongia* in having raphide microscleres dispersed throughout the skeleton. Although several other species of *Aulospongia* have been described at some time or another with raphide microscleres, re-examination of relevant type and other material has confirmed that in all cases these were

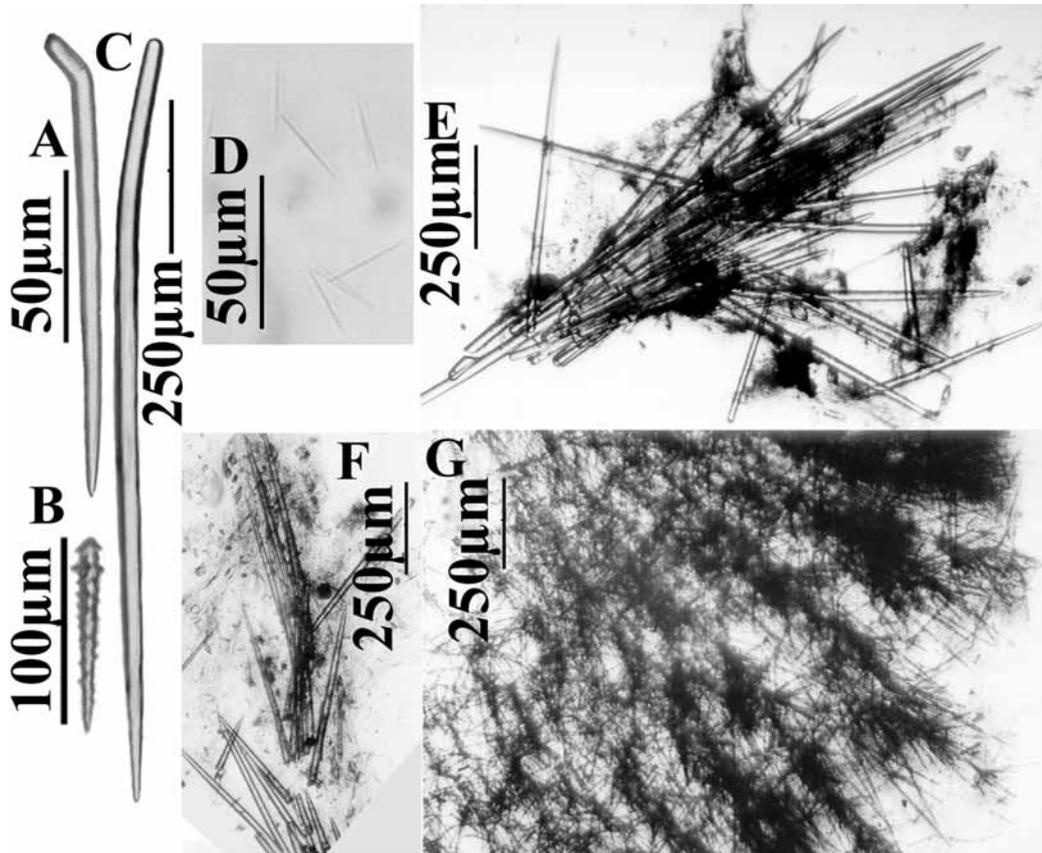


FIG. 17. *Aulospongus spinosum*. A, Third category of rhabdostyle. B, Echinating style/rhabdostyle. C, Choanosomal principal rhabdostyle. D, Raphides. E, Ectosomal auxiliary spicule bundle. F, Choanosomal fibre bundle. G, Choanosomal skeleton.

vestigial (raphidiform) ectosomal auxiliary spicules, whereas in *A. spinosum* these appear to be genuine raphides/ trichodragmata. Nevertheless, Maldonado (1992) notes that raphides appear to be associated with, and possibly reinforce, the pinacoderm. If this correct, it is possible that these raphides may be extremely vestigial ectosomal auxiliary megascleres rather than typical microscleres. Unfortunately no well-fixed material is available to undertake more comprehensive histological analysis to explore this possibility, and for the moment these spicules are assumed to be microscleres.

***Aulospongus villosa* (Thiele, 1898)**
(Figs 18-19, Table 1)

Raspailia (?) *villosa* Thiele, 1898: 60, pl. 4, fig. 10, pl. 8, fig. 48; Koltun, 1970: 270, fig. 32, pl. 8, fig. 4; Hoshino, 1987: 19; Tanita & Hoshino, 1990: 102; Sim, 1990: 317.

Heterectya villosa; Hallmann, 1917: 393; [? doubtful record of Burton, 1959: 45].

Aulospongus villosa; Hooper, 1991: 1307, fig. 65d-f.

MATERIAL. HOLOTYPE. ZMB2204: Hakodate, Japan, coll. Hilgendorf.

DISTRIBUTION. Japan (Hakodate, Sagami Bay), Korea (Japan Sea & Jeju I.) and Russia (Iturup I., Kurile Is, Sea of Ochotsk). Burton's (1959) record from Iceland is dubious. He did not provide a description of the specimen, no voucher material was cited, and it is therefore ignored here.

DESCRIPTION. Growth form massive, sub-spherical, bushy. Surface prominently shaggy, conulose. Colour light brown in ethanol. 'Raspailiid ectosomal skeleton' absent, with only tufts of choanosomal principal rhabdostyles protruding. Choanosomal skeleton exclusively

plumose, composed of relatively thick, compressed fibre-bundles in which the larger rhabdostyles are confined completely within ascending fibres. Smaller rhabdostyles exclusively echinate fibres, standing nearly perpendicular to them, often touching those on adjacent, opposing fibres, together producing the superficial impression of a lattice-like, reticulate skeleton. No notable compression of the axial skeleton, and no specialised subectosomal extra-axial megascleres present. Megascleres consist of larger choanosomal principal rhabdostyles with moderate to strongly developed basal rhabd, usually completely smooth or with small granular spines scattered over the apical half (235-370×10-16µm). Smaller echinating rhabdostyles vary from completely smooth to partially spined on the apical half, usually with a very strong basal rhabd but occasionally straight, spines very small, granular (142-165×4-10µm). Subectosomal extra-axial and ectosomal auxiliary spicules absent. Microscleres absent.

REMARKS. This is a very reduced species of *Aulospongia*, similar to *A. cerebella*, *A. flabellum* and *A. spinosum*, lacking any ectosomal auxiliary or subectosomal extra-axial spicules, and having only two categories of rhabdostyles. Rhabdostyles in *A. villosa* resemble to some extent those of *A. involutum*, *A. gardineri* and *A. novaecaledoniensis* sp.nov, in geometry and approximate size, but whereas those of *A. villosa* are often completely smooth or have small granular spines the other three species have very large, recurved spines covering only the apex of rhabdostyles.

REVIEW OF OTHER RASPAILIIDAE WITH Rhabdostyles

Raspailia Nardo, 1833

Subgenus *Raspaxilla* Topsent, 1913

Raspaxilla Topsent, 1913: 616; Bergquist, 1970: 28; Hooper, 1991: 1195, 1245. Type species: *Raspaxilla phakellina* Topsent, 1913: 617, by monotypy.
Echinaxia Hallmann, 1916a: 543; 1917: 391; de Laubenfels, 1936: 102; Bergquist, 1970: 30; Hooper, 1991: 1195. Type species: *Axinella frondula* Whitelegge, 1907: 509, by original designation.
Axinetia Hallmann, 1917: 393; Hooper, 1991: 1195. Type species: *Axinella mariana* Ridley & Dendy, 1886: 480, by original designation.

DEFINITION. *Raspailia* with echinating acanthose rhabdostyles. Larger choanosomal principal styles completely smooth, without any

basal rhabd, geometrically distinct from smaller acanthose echinating rhabdostyles. Axial skeleton well differentiated from extra-axial skeleton: axial skeletal compressed, composed of reticulate tracts cored by choanosomal principal styles; extra-axial skeleton plumo-reticulate, with plumose ascending tracts interconnected by transverse tracts both cored by choanosomal principal styles (forming a reticulation), or reduced to radial tracts of single long subectosomal extra-axial styles embedded in and perpendicular to axis, protruding through the surface. Echinating rhabdostyles generally more abundant in peripheral skeleton than in axis.

REMARKS. Seventeen species are currently assigned to *Raspailia* (*Raspaxilla*), including species transferred here from *Endectyon*, *Hemectyon* and *Aulospongia*. *Raspaxilla* has a wide geographic distribution, ranging from the Indo-west Pacific (N and S New Zealand, NW Australia, N Great Barrier Reef, central NSW, New Caledonia, Japan, Micronesia), E coast of the United States of America (North Carolina), central E Pacific and the antarctic-subantarctic region (Fig. 35). Apart from the Southern (sub-antarctic) Ocean, *Raspaxilla* has not yet been recorded in either the Atlantic or the E or central Indian Oceans, and is assumed (from present data) to be a Pacific rim species (Fig. 35). It is possible that the specimen described by Pulitzer-Finali (1994) as '*Endectyon hamatum*' from Kenya belongs to *Raspaxilla*, but this species is barely recognisable from his description and for the moment is *incertae sedis*.

Essentially *Raspailia* (*Raspaxilla*) differs from *Aulospongia* in having echinating rhabdostyles geometrically very different from the usually longer choanosomal principal styles (the latter without any basal rhabd); the subectosomal extra-axial styles form a radial skeleton perpendicular to the axis; and axial and extra-axial skeletons are well differentiated (the former compressed, the latter plumoreticulate and/or radial). Placement of all species, however, is not always straightforward given that some taxa may lose certain characters (e.g. extra-axial skeleton becomes reduced to single long subectosomal extra-axial spicules embedded in the axis and forming a radial skeleton; or the subectosomal extra-axial spicules are lost completely). There is also a correlation between the localisation of echinating rhabdostyles in the peripheral skeleton and the degree of axial compression. In species with very compressed

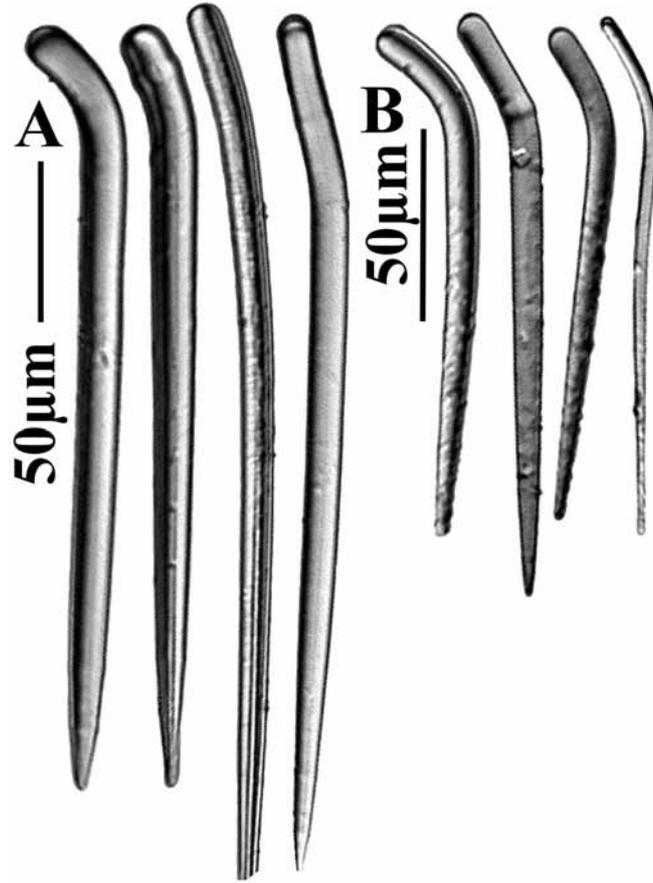


FIG. 18. *Aulospongus villosa*. A, Choanosomal principal rhabdostyles. B, Echinating rhabdostyles.

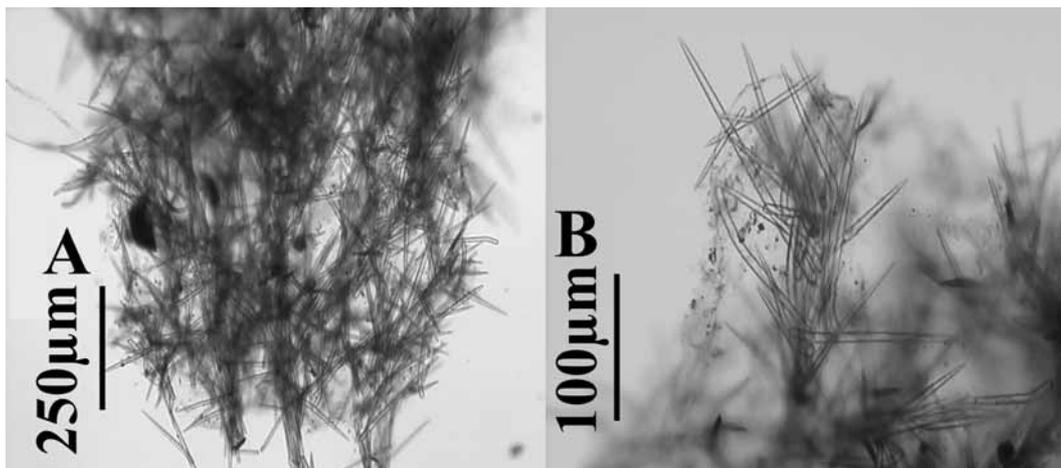


FIG. 19. *Aulospongus villosa*. A, Choanosomal skeleton. B, Peripheral skeleton.

skeletons the extra-axial skeleton is reduced to single long subectosomal extra-axial spicules (without reticulate connections) and the echinating rhabdostyles are literally 'pushed' into the ectosomal skeleton where they form brushes or produce a continuous palisade.

Raspailia (Raspaxilla) phakellina
(Topsent, 1913)
(Fig. 20, Table 1)

Raspaxilla phakellina Topsent, 1913: 617, pl. 1, fig. 4, pl. 6, fig. 15; Burton, 1932: 326; Boury-Esnault & van Beveren, 1982: 51, pl. 7, fig. 26, fig. 12.

Raspailia (Raspaxilla) phakellina; Hooper, 1991: 1196, fig. 7k-l.

MATERIAL. HOLOTYPE. MOM (fragment MNHN LBIM DT1614): Burwood Bank, Antarctica, 54°25'S, 57°32'E, 112m depth. 1.xii.1903. OTHER MATERIAL. BMNH1928.2.15.781a, 846a: Falkland Islands, Argentina, RRS 'Discovery', 75-82m depth.

DISTRIBUTION. Antarctic - subantarctic region (Antarctica, Falkland Is, Kerguelen Is).

DESCRIPTION. Erect, digitate, arborescent, with enlarged basal holdfast attachment and branching in one plane. Surface slightly conulose, hispid. Colour whitish cream to yellowish in ethanol. 'Raspailiid ectosomal skeleton' present but not well developed, consisting of long subectosomal extra-axial styles protruding through the surface, surrounded at their bases by wispy bundles of ectosomal auxiliary anisoxeas forming stellate bundles nearly parallel to the surface. Choanosomal skeleton with well differentiated axial and extra-axial regions. Axial skeleton compressed, strongly reticulate, composed of multispicular fibres cored by choanosomal principal styles and echinated sparsely by echinating rhabdostyles. Extra-axial skeleton plumo-reticulate, with ascending multispicular fibres cored by choanosomal principal styles and profusely echinated by rhabdostyles, diverging towards the periphery, interconnected by transverse pauci- or multispicular fibres which persist all the way to the surface. Echinating rhabdostyles predominant in extra-axial skeleton. Megascleres include long choanosomal principal styles, slightly curved centrally or straight, with evenly rounded, smooth, non-rhabdose bases (550-900×10-16µm). Echinating rhabdostyles moderately long, with slightly rhabdose and subtylote bases, completely smooth or with small, erect spines confined to apical two-thirds of spicule (140-370×8-18µm). Subectosomal extra-axial

styles long, thick, straight or slightly curved, entirely smooth (1100-1450×12-18µm). Ectosomal auxiliary styles wispy, raphidiform, straight, centrally curved or sinuous (450-650×2-3µm). Micscleres absent.

REMARKS. Comparisons between the holotype (Antarctica) and Kerguelen specimens, with the 'Discovery' material described by Burton (1932) show some differences: notably the complete lack of spines on rhabdostyles in the latter specimen (whereas some rhabdostyles have apical spines in the former specimens), and the persistence of the plumo-reticulate extra-axial skeleton for most of the sponge diameter, with only a relatively small, confused, slightly compressed axial component (as compared to a relatively larger central axial skeleton in the holotype and Kerguelen specimen). Nevertheless, there is no doubt that all three specimens belong to the same species. *Raspailia (Raspaxilla) phakellina* differs substantially from other *Raspailia* species only in having basal rhabds on echinating acanthostyles, and having its extra-axial skeleton dominated by ascending fibres reminiscent of *Aulospongus*, but in which transverse connecting fibres persist all the way to the surface and produce a plumo-reticulate skeletal structure (rather than a purely plumose skeleton characteristic of *Aulospongus*).

Raspailia (Raspaxilla) acanthifera
George & Wilson, 1919

Raspailia acanthifera George & Wilson, 1919: 159, pl. 62, fig. 34, pl. 63, fig. 38-39, pl. 66, fig. 59.

MATERIAL. HOLOTYPE. USNM (not seen): Fort Macon beach, Beaufort, North Carolina.

DISTRIBUTION. E coast of USA (North Carolina).

DESCRIPTION. Growth form stalked, lobate, with lamellate branches. Surface with hispid ridges but smooth between ridges. Colour grey-brown with tinge of yellow in ethanol. 'Raspailiid ectosomal skeleton' well developed with projecting long subectosomal extra-axial styles surrounded by ectosomal auxiliary anisoxeas forming loose bundles at the surface. Skeletal architecture with well differentiated axial and extra-axial components. Axial skeleton compressed, with mainly thicker longitudinal fibres fully cored with spicules, loosely interconnected by few transverse paucispicular fibres, together producing a loose, open reticulation. Extra-axial skeleton radial, with

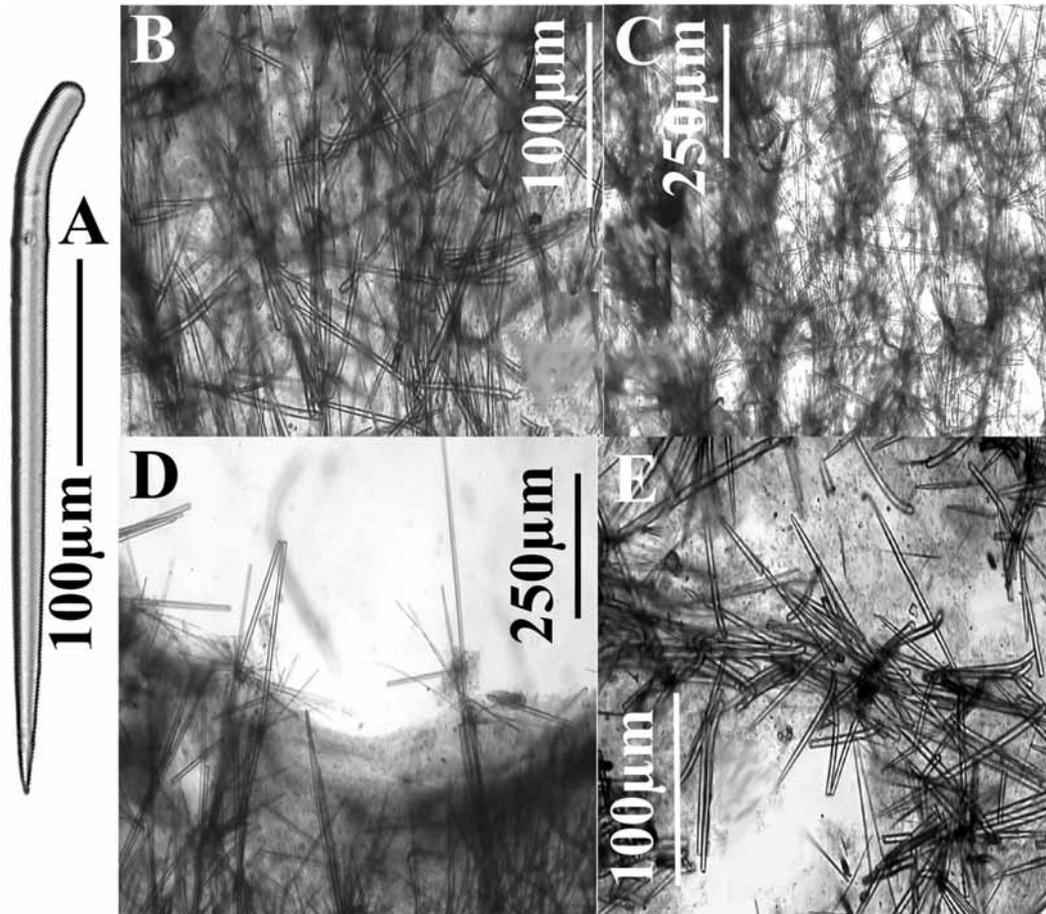


FIG. 20. *Raspailia (Raspaxilla) phakellina*. A, Echinating rhabdostyle. B, Reticulate axial skeleton. C, Plumo-reticulate extra-axial skeleton. D, Ectosomal skeleton. E, Reticulate axial fibres.

fewer interconnecting tracts towards the periphery, but persisting all the way to the surface, and with tracts fully cored by styles. Fibres more bulbous near the surface than in the axial region, and subectosomal extra-axial styles embedded in peripheral fibres project through surface in bundles forming surface conules. Echinating rhabdostyles predominant in the peripheral skeleton, participating in 'raspailiid ectosomal spicule brushes', as well as echinating radial (connecting) fibres near the surface. Five categories of megascleres present. (1) Short, curved, entirely smooth choanosomal principal styles ($160-260 \times 7-12 \mu\text{m}$), coring most fibres and producing the spicule bundles at the surface. (2) Straight, thick styles ($160-240 \times 12-20 \mu\text{m}$) intermingled with the shorter styles in both the peripheral and deeper parts of the skeleton,

presumably modifications to choanosomal principal spicules. (3) Echinating acanthose rhabdostyles ($80-120 \times 6 \mu\text{m}$), with strongly recurved spines over most of the spicule although spines are characteristically absent from the slightly subtylote base, and the base slightly rhabdose. (4) Long, slender subectosomal extra-axial styles ($400-600 \times 6-7 \mu\text{m}$), protruding through the surface. (5) Slender, raphidiform, ectosomal auxiliary anisoxeas ($200 \times 1 \mu\text{m}$) dispersed mainly within the ectosomal skeleton, singly or in loose bundles (described as raphides). Microscleres absent (George & Wilson, 1919).

REMARKS. Skeletal structure of *R. acanthifera* is characteristically axially compressed, with well differentiated axial and extra-axial skeletons, well developed ectosomal skeleton,

and geometrically different echinating rhabdostyles and choanosomal principal styles, indicating that it is most appropriately assigned to *Raspailia* (*Raspaxilla*) and not to *Aulospongius*.

Raspailia* (*Raspaxilla*) *clathrioides
(Lévi, 1967)
(Figs 21, 36C)

Aulospongius clathrioides Lévi, 1967: 21, text-fig. 5, pl. 2, fig. c; Hooper, 1991: 1311, fig. 67a-d; Hooper & Lévi, 1993: 1295, figs 40-41; Hooper & Battershill, 1998: 136.

MATERIAL. HOLOTYPE. MNHN LBIM DCL823: Canala, Melasceu, New Caledonia, coll. 'Singer-Polignac', 4.i.1962, 22°30'S, 166°45'E, 35m depth. OTHER MATERIAL. New Caledonia (refer to Hooper & Lévi, 1993).

DISTRIBUTION. Known only from the SW New Caledonian lagoon.

DESCRIPTION. Growth form stalked, arborescent, bushy, cylindrical-branching. Surface shaggy, prominently conulose. Colour yellow-orange alive. 'Raspailiid ectosomal skeleton' either completely absent or with very few vestigial ectosomal auxiliary styles/anisoxeas, forming vestigial brushes surrounding protruding choanosomal principal styles or scattered below the surface. Subectosomal extra-axial spicules absent. Surface dominated by swollen fibres and plumose brushes of smooth styles both producing surface conules. Choanosomal skeleton predominantly plumose or plumo-reticulate, with a slightly compressed reticulate axial core dominated by well developed spongin fibres, with the spicule skeleton proportionally reduced. Axial fibres are vestigially cored by choanosomal principal styles. Extra-axial fibres are prominently plumose and heavily multispicular, with fewer paucispicular interconnecting fibres persisting in the peripheral skeleton and to the surface. Echinating rhabdostyles are slightly more abundant in the peripheral skeleton than in the axis. Megascleres include choanosomal principal styles, smooth, slightly curved or occasionally sinuous, sometimes modified to anisoxeas, only occasionally with a very faint basal curvature (145-454×3-7µm). Echinating rhabdostyles, microcionid-like, long, slender, straight or slightly curved towards the basal end, with a relatively well developed basal swelling, straight base or only slight basal rhabd, evenly spined except for smooth base, spines small, granular

(58-82×1.5-4µm). Subectosomal extra-axial spicules absent. Ectosomal auxiliary styles and anisoxeas present or absent, always very rare, raphidiform, straight or sinuous (97-134×0.8-1.5µm). Microscleres absent.

REMARKS. This species is a borderline case between *Aulospongius* and *Raspaxilla*, and is referred here to *Raspailia* (*Raspaxilla*) given that the ascending fibre system has transverse connecting fibres extending all the way from the axis to the surface (producing a plumo-reticulate rather than a strictly plumose skeleton as is typical for *Aulospongius*); the axial and extra-axial skeletons are slightly differentiated (reticulate versus plumo-reticulate), with the axis showing slight compression; the larger choanosomal principal styles are entirely smooth, and they have no, or at most only very faint, basal curvature (i.e. only a few might be termed vaguely rhabdose), and furthermore, anisoxeote modifications of choanosomal principal spicules are relatively common, indicating that choanosomal principal and echinating spicules are morphologically quite distinct; and the smaller echinating rhabdostyles also have only slight basal rhabd, more in common with species of *Raspaxilla* than with *Aulospongius*.

This is a sister species of *R. (Raspaxilla) reticulata* (N Great Barrier Reef) and *R. (R.) topsenti* (N New Zealand), having a similar arborescent growth form, echinating rhabdostyles with swollen, smooth, straight- or relatively poorly rhabdose-bases (at least compared to most species of *Raspaxilla* and *Aulospongius*); the reticulate axial region is slightly compressed; and the extra-axial skeleton is plumo-reticulate in which the ascending plumose fibres dominate but the reticulate fibre connections persist all the way to the surface. The three species differ in their spicule compositions (presence of a specialised ectosomal skeleton in *R. (R.) reticulata*, including possession of long subectosomal extra-axial styles; vestigial ectosomal auxiliary styles/anisoxeas in *R. (R.) topsenti*), spicule sizes (compare with the respective descriptions below), morphology of choanosomal principal styles (particularly *R. (R.) topsenti*), and greater dominance of the reticulate versus plumose components of the skeleton in both the other species.

Re-examination of the material described as *Aulospongius clathrioides* by Hooper & Lévi (1993) also found that one specimen out of four

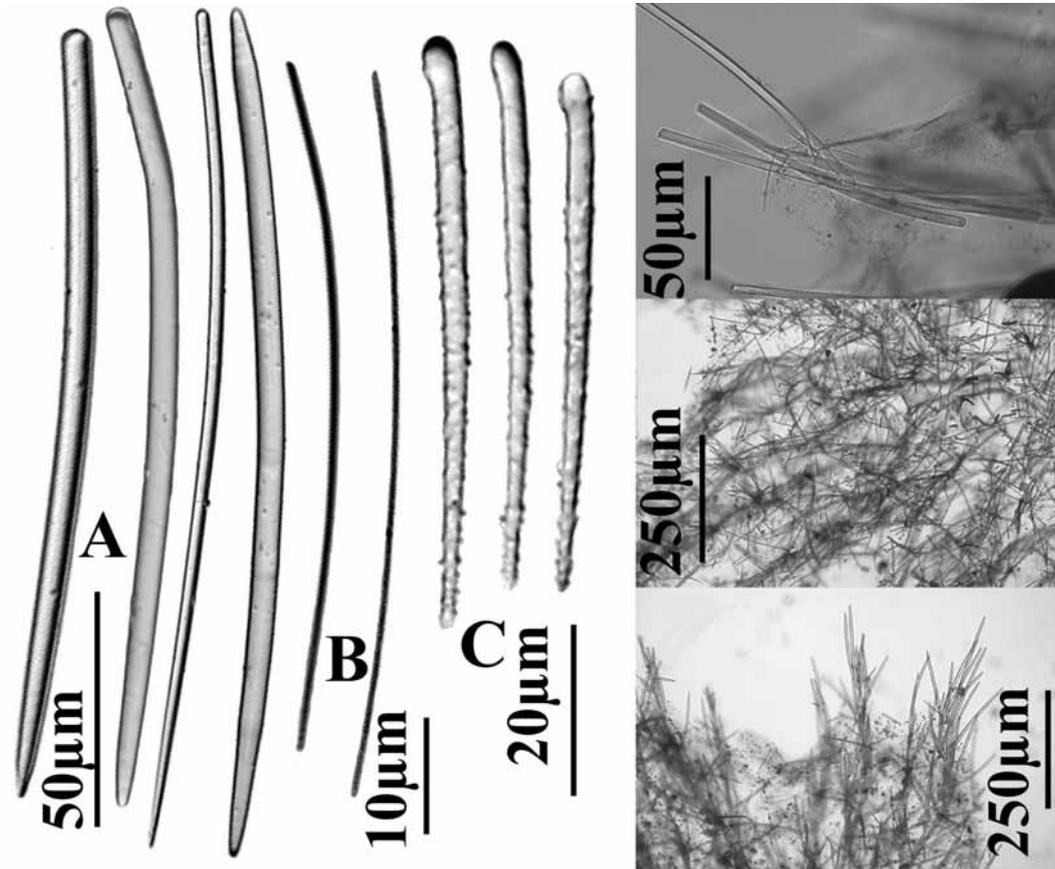


FIG. 21. *Raspailia (Raspaxilla) clathrioides*. A, Choanosomal principal styles/anisoxeas. B, Ectosomal auxiliary anisoxeas. C, Echinating rhabdostyles. D, Ectosomal skeleton. E, Reticulate axial skeleton. F, Plumo-reticulate extra-axial skeleton.

contained very few vestigial ectosomal auxiliary styles/anisoxeas scattered below the surface, or occasionally forming sparse brushes surrounding choanosomal principal styles in the peripheral skeleton. These are obviously the remnants of a specialised 'raspailiid ectosomal skeleton', but this feature is so vestigial and rare in the 5 described specimens of *R. (R.) clathrioides* (i.e. absent in the holotype), that it can hardly be constituted as a character 'typical' for the species. These vestigial ectosomal auxiliary spicules are also present in *R. (R.) topsenti*, and both species lack any subectosomal extra-axial spicules, whereas the ectosomal skeleton of *R. (R.) reticulata* is consistently well developed and 'typical' of Raspailiidae. Nevertheless, it is conceivable that all three species are geographic variants of a single species, with these observed

differences being ones indicating isolated, intraspecific population variability rather than interspecific differences. Genetic comparisons are required to verify this supposition.

Raspailia (Raspaxilla) compressa
Bergquist, 1970
(Fig. 22)

Raspailia compressa Bergquist, 1970: 29-30, text-fig. 3a, pls 7b, 11a; Hooper, 1991: 1245, figs 32-33.

MATERIAL. HOLOTYPE. MONZ POR 30: NE. of North Cape, New Zealand, 173° 04'E, 34° 28'S, 54 m depth. OTHER MATERIAL. NTM Z1748: W of Port Hedland, Northwest Shelf, WA, 19° 05.1'S, 118° 47.7'E, 84m depth, coll. 'Soela'.

DISTRIBUTION. North Cape, New Zealand; Northwest Shelf, Western Australia.

DESCRIPTION. Growth form arborescent, stalked, digitate, with bifurcating, cylindrical or slightly flattened branches. Colour bright yellow in life. Surface hispid, otherwise even. 'Raspailiid ectosomal skeleton' present composed of plumose brushes of ectosomal auxiliary anisoxeas surrounding bases of subectosomal extra-axial styles (the latter protruding through the surface), and also with bundles of rhabdostyles intermingled with spicule brushes on the surface, both perched on ends of the peripheral extra-axial skeletal tracts. Axial and extra-axial skeletons well differentiated. Axial skeleton heavily compressed, consisting of a close-meshed reticulation of multispicular fibres cored by choanosomal principal styles mostly orientated along longitudinal axis of branches, interconnected by pauci- or multispicular transverse skeletal tracts. Extra-axial skeleton plumo-reticulate with multispicular ascending tracts interconnected by paucispicular transverse tracts. Ascending tracts in peripheral skeleton with long subectosomal extra-axial styles embedded and extending a long way through surface. Echinating rhabdostyles concentrated on fibres at the junction of axial and extra-axial skeletons, usually in thick bundles. Megascleres include choanosomal principal styles slightly curved towards basal end, with rounded non-tylote bases, without any basal rhabd (240-449×6-25µm). Echinating rhabdostyles with basal rhabd varying from prominent to slightly bulbous, nearly straight, and with smooth base and small granular spines on apical third of spicule (93-360×4-9µm). Long subectosomal extra-axial styles relatively thick, slightly curved near base or straight, with rounded or slightly subtylote bases (887-1400×16-24µm). Ectosomal auxiliary anisoxeas nearly rhabdiform, flexuous, sometimes straight or slightly curved at centre, occasionally stylote (234-360×2-4µm). Microsclere absent.

REMARKS. Bergquist (1970) suggested that this species had close affinities to *Aulospongia* based on rhabdostyle geometry, but skeletal structure (compressed axis, reticulate extra-axis), lack of any basal rhabds on choanosomal principal styles, and lack of plumose fibre-bundles indicate that it belongs to *Raspaxilla*. This species shows some similarities to *R. (Raspaxilla) clathrioides* and *R. (Raspaxilla) reticulata* (compare descriptions above and below). As mentioned by Hooper (1991), there is some doubt about the conspecificity of the New Zealand and Western Australian populations,

given that they appear to differ only in the lengths of echinating acanthostyles (half as long in the Western Australian population), and slightly in their live colouration. No other observed features were able to differentiate the two populations based on existing material.

Raspailia (Raspaxilla) flaccida
Bergquist, 1970

Raspailia flaccida Bergquist, 1970: 27: pls 6b, 10b, 18c.
Raspailia (Raspaxilla) flaccida; Hooper, 1991: 1199.

MATERIAL. HOLOTYPE. MONZ POR29 (not seen): Menzies Bay, Christchurch, New Zealand

DISTRIBUTION. Known only from S New Zealand.

DESCRIPTION. Growth form digitate, irregularly branching, thickly cylindrical digits. Surface conulose, hispid. Colour bright orange in life. 'Raspailiid ectosomal skeleton' vestigial, consisting of rhabdiform styles/anisoxeas lying in poorly defined groups at the surface. Axial and extra-axial skeletons well differentiated. Axial skeleton plumo-reticulate, with fibres cored by choanosomal principal styles/oxeas. Extra-axial skeleton with ascending fibres, more slender than axial fibres, cored by paucispicular tracts of mainly choanosomal principal styles (fewer oxeas), branching towards the surface, interconnected by sparse unispicular tracts. Echinating rhabdostyles predominant in extra-axial skeleton. Megascleres consist only of choanosomal principal styles/oxeas of a single size category but with very variable terminations, also varying in curvature from straight to contorted, and points often mucronate (314-790×9-14µm). Echinating rhabdostyles with smooth, slight basal rhabd, small granular spines covering apical 2/3 of spicule, occasionally modified to acanthoxeas with central bend (121-145×5-7µm). No special category of subectosomal extra-axial spicules. Ectosomal auxiliary styles/anisoxeas vestigial, rhabdiform, slightly curved or toxiform (up to 340×1.5µm). Microscleres absent (Bergquist, 1970).

REMARKS. This species is unlike all other described *Raspaxilla*, being substantially reduced in many of its characters, notably: vestigial ectosomal specialisation, lacking any subectosomal extra-axial spicules, reduced reticulate connections between ascending extra-axial tracts, and many geometric modifications to megascleres. Nevertheless, the possession of axial and extra-axial

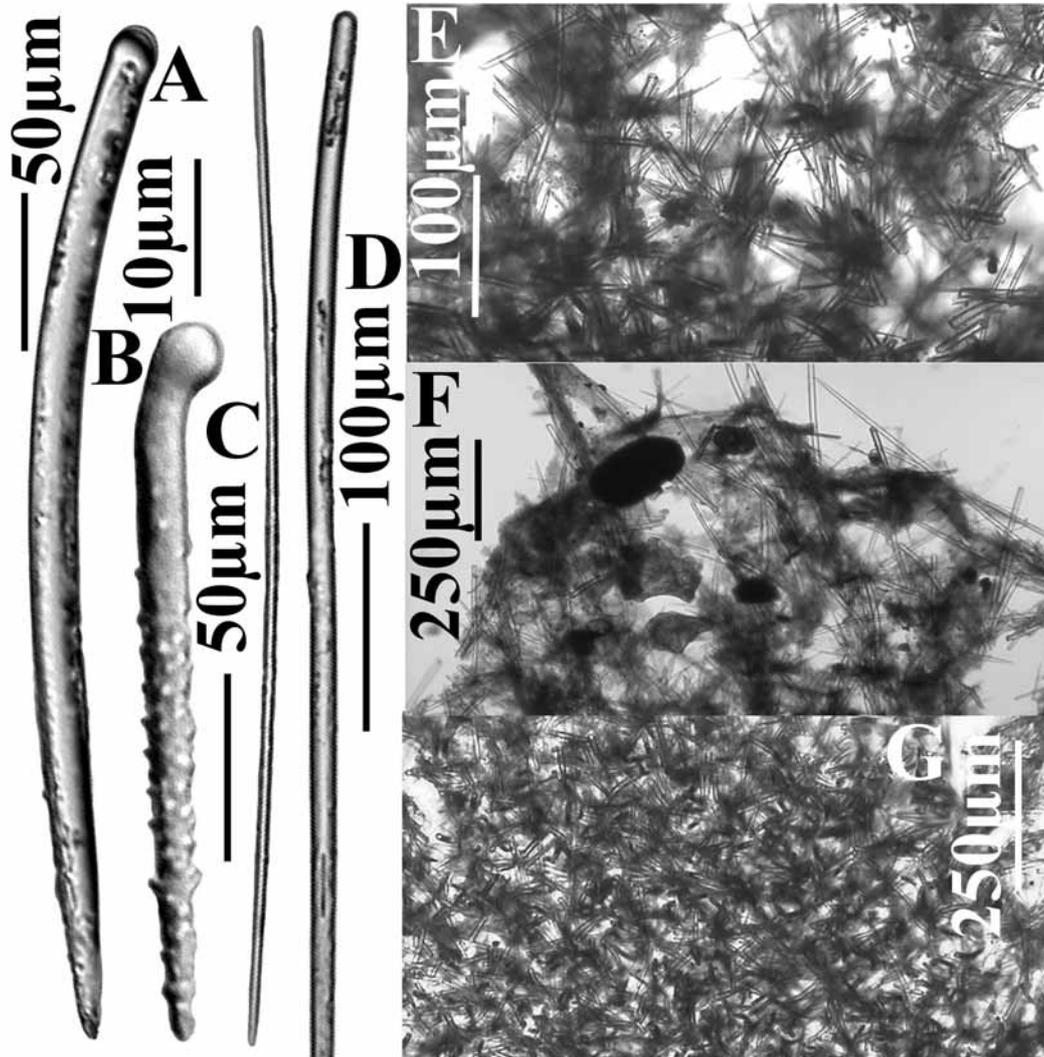


FIG. 22. *Raspailia* (*Raspaxilla*) *compressa*. A, Choanosomal principal subtylostyle. B, Echinating rhabdostyle. C, Ectosomal auxiliary anisoxea. D, Basal end of subectosomal extra-axial style. E, Plumo-reticulate fibres in extra-axial skeleton. F, Ectosomal skeleton and detritus incorporated into skeleton. G, Reticulate axial skeleton.

differentiation, axial compression, non-rhabdose choanosomal principal megascleres together with echinating rhabdostyles indicate that it is most appropriately included in *Raspaxilla*.

***Raspailia* (*Raspaxilla*) *folium* Thiele, 1898**

Raspailia folium Thiele, 1898: 60, pl. 3, fig. 7, pl. 8, fig. 47a-c; Hoshino, 1976: 6, pl. 1, figs 6-7; Hoshino, 1981: 215-216, fig. 7; Hoshino, 1987: 18; Tanita & Hoshino, 1990: 99, pl. 10, fig. 8, text-fig. 61; Sim, 1990: 317. *Echinaxia folium*; Hallmann, 1917: 392. *Raspailia* (*Raspaxilla*) *folium*; Hooper, 1991: 1199.

MATERIAL. HOLOTYPE. ZMB (not seen): Enoshima, Japan.

DISTRIBUTION. Japan (Enoshima, Sagami Bay, Ariake Sea) and Korea (Sea of Japan, Jeju I., South Sea).

DESCRIPTION. Growth form stalked, flabellate, vasiform, with thin lamellae. Surface rough, minutely hispid. Colour pinkish-brown alive. 'Raspailiid ectosomal skeleton' nearly vestigial, with raphide-like anisoxeas tangential to surface in sparse bundles or lying singly on

surface. Axial and extra-axial skeletons well differentiated. Axial skeleton reticulate, with fibres cored by small choanosomal principal styles. Extra-axial skeleton radial, with long tracts of choanosomal principal styles heavily echinated by rhabdostyles, and larger subectosomal extra-axial styles embedded in peripheral fibres and projecting a long way through the surface. Megascleres consist of entirely smooth, slender choanosomal principal styles, straight, slightly centrally curved or sinuous, evenly rounded or anisoxeote bases, without any basal rhabd ($240\text{--}(292)\text{--}325 \times 5\text{--}(6.7)\text{--}11\mu\text{m}$). Echinating rhabdostyles relatively large, thick, with basal rhabd varying from slightly curved to basal curvature nearly at right angles to the shaft, with smooth base and small spines restricted to the apical extremity or the apical 1/3 of spicule ($141\text{--}(264)\text{--}500 \times 8\text{--}(12.5)\text{--}25\mu\text{m}$). Subectosomal extra-axial styles thick, long, slightly curved near basal end, evenly rounded base and hastate point (up to $1120\text{--}(1236)\text{--}2000 \times 16\text{--}(25)\text{--}36\mu\text{m}$). Ectosomal auxiliary spicules raphidiform oxeotes or anisoxeas (asymmetrical ends), usually bent or sinuous ($270\text{--}320 \times 1.5\text{--}3\mu\text{m}$). Microscleres absent (Thiele, 1898; Hoshino, 1981; Sim, 1990).

REMARKS. A search for the holotype, undertaken by the author and Dr D. Kühlmann at the ZMB in 1988, was unsuccessful. This species is only barely recognisable from Thiele's (1898) original description, in which specific details of its skeletal structure were missing. However, Thiele's illustrations of its spicules were adequate to indicate that it was most appropriately included in *Raspaxilla*. Recent recollections of the species from Japan and Korea provided additional skeletal details to confirm this placement.

Raspailia (Raspaxilla) frondula
(Whitelegge, 1907)
(Fig. 23)

Axinella frondula Whitelegge, 1907: 509-510, pl. 46, fig. 32.

Echinaxia frondula; Hallmann 1916a: 543; Hallmann 1917: 394-398, text-fig. 1, pl. 21, figs 3-4, pl. 22, figs 1-2.

Raspailia frondula; Bergquist 1970: 30.

Raspailia (Raspaxilla) frondula; Hooper, 1991: 1248, fig. 34

MATERIAL. HOLOTYPE. AM G4349: Shoalhaven Bight, S coast of NSW, $34^{\circ} 51'S$, $150^{\circ} 45'E$, 60 m depth, coll. 'Thetis'.

DISTRIBUTION. Shallow coastal waters of S NSW, Australia.

DESCRIPTION. Stalked branching flabellate growth form. Surface with fine, close-set microconules. Colour light brownish-grey in ethanol. 'Raspailiid ectosomal skeleton' absent, although long subectosomal extra-axial styles form plumose brushes around terminal portions of ascending peripheral fibres, protruding through the surface and producing distinctive surface conules. Axial and extra-axial skeletons moderately well-differentiated. Axial skeletal slightly compressed, with the axial core composed of very light spongin fibres, forming an irregular subrenieroid reticulation cored by pauci- or multispicular longitudinal tracts and interconnected by uni- or paucispicular transverse tracts of choanosomal principal styles. Extra-axial skeleton composed of prominently radial, non-plumose bundles of choanosomal principal styles arising perpendicular to axis, without interconnecting reticulate tracts. Echinating acanthostyles slightly more abundant in peripheral skeleton than in axis. Megascleres include choanosomal principal styles, short, thin, slightly curved at centre or towards basal end, occasionally oxeote or strongylote, with rounded non-tylote bases, without basal rhabd, and with slightly hastate points ($87\text{--}165 \times 3\text{--}8\mu\text{m}$). Echinating rhabdostyles short, thin, with smooth, slightly swollen, rhabdose bases and distal (pointed) 2/3 of spicule evenly covered with vestigial spines ($72\text{--}133 \times 4\text{--}9\mu\text{m}$). Subectosomal extra-axial styles long, slightly curved towards basal end, with rounded non-tylote bases ($278\text{--}710 \times 4\text{--}16\mu\text{m}$). Ectosomal auxiliary megascleres absent. Microscleres absent.

REMARKS. This species differs from most *Raspaxilla* in having radial, non-plumose tracts of choanosomal principal styles and subectosomal extra-axial styles forming the ascending fibres in the peripheral skeleton, and lacking any reticulate connections between adjacent radial tracts; lacking the special ectosomal auxiliary spicules characteristic of raspailiids; having a wide-meshed reticulation in the axial skeleton (less compressed than most species of *Raspaxilla*); and having choanosomal principal styles (coring axial fibres) of similar size to echinating rhabdostyles, differing only in their thickness, hastate points and entirely smooth surface. Hallmann (1917) suggested that choanosomal principal (coring) and echinating spicules in *R. frondula* may have a common origin, as indicated by their similar size, similar to those found in species of *Aulospongia*. However, the respective geometries of these

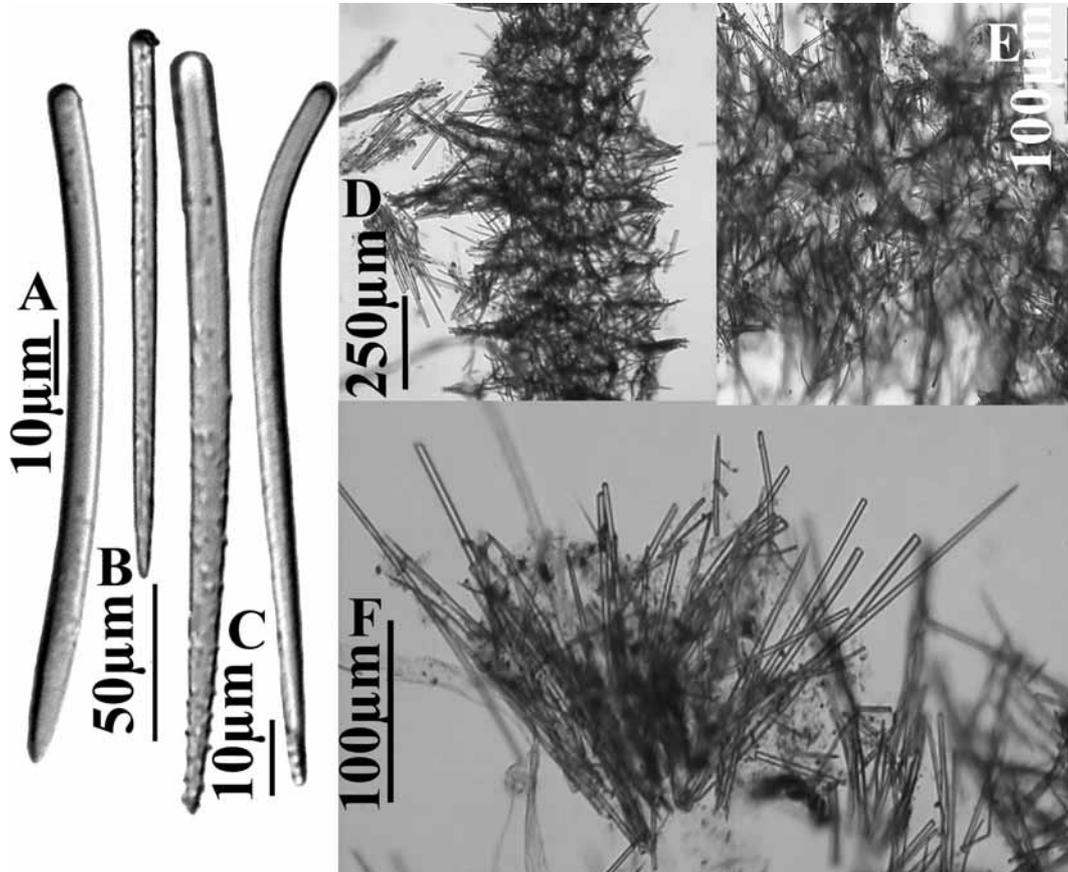


FIG. 23. *Raspailia (Raspaxilla) frondula*. A, Choanosomal principal style. B, Subectosomal extra-axial style. C, Echinating rhabdostyles. D, Skeletal cross-section through branch. E, Reticulate axial skeleton. F, Ectosomal spicule bundle composed of subectosomal extra-axial styles.

spicules appear to be different and this proposed relationship is not supported: coring styles are nearly hastate-pointed with curvature closer to the centre (including occasional oxete/strongylote forms), whereas echinating rhabdostyles are tapering fusiform-pointed, with slightly swollen bases and slight to moderate basal rhabds.

Raspailia (Raspaxilla) galapagensis
(Desqueyroux-Faundez & van Soest, 1997)
(Fig. 24)

Aulospongia galapagensis Desqueyroux-Faundez & van Soest, 1997: 441, figs 165-168.

MATERIAL. HOLOTYPE. USNM43173 (fragment ZMA POR11241): Albemarle I., Galapagos Is, 00°37'S, 90°51'W, coll. 'Anton Bruun', 1966, 78m depth.

DISTRIBUTION. Known only from the Galapagos Is.

DESCRIPTION. Growth form branching. Surface highly hispid. Colour beige in ethanol. 'Raspailiid ectosomal skeleton' present consisting of a central long subectosomal extra-axial style surrounded by small ectosomal auxiliary styles/anisoxeas in large bundles at the surface. Axial and extra-axial skeletons well differentiated. Axial skeleton consists of a well compressed, close-meshed reticulation of long choanosomal principal styles running mainly longitudinally through branches, with fewer transverse interconnecting fibres, with compression so strong that reticulate fibres are often masked. Extra-axial skeleton reduced to single long subectosomal extra-axial styles embedded

in, and perpendicular to, axis. Echinating rhabdostyles localised at the junction of axial and extra-axial skeletons, outside and perpendicular to the axis, extending up to and occasionally through the surface, usually occurring singly. Megascleres consist of entirely smooth choanosomal principal styles, oxeas, stongyles or stronglostyles, without any obvious basal rhabd, slightly curved centrally or with curvature closer to the basal end (400-1700×20-45µm). Echinating rhabdostyles with slight to moderate basal rhabd (very occasionally completely smooth), bases mostly smooth and slightly subtylote, with moderately large recurved spines confined to the apex, occasionally also spined on the base (170-320×15-30µm). Subectosomal extra-axial styles very long, slightly curved near base, also with stronglostylote modifications (1300-1700×20-45µm). Ectosomal auxiliary styles/anisoxeas relatively large, thick, straight, very slightly curved at centre or exceptionally sinuous, usually asymmetrical with one blunt end, sometimes symmetrical, oxeote (450-550×8-15µm). Microscleres absent.

REMARKS. This species is referred here to *Raspailia* (*Raspaxilla*) on the basis that its choanosomal principal styles are morphologically very different from echinating rhabdostyles, lacking any traces of basal rhabds, and moreover they are frequently modified to strongylote or oxeote forms; there are no fibre-bundles characteristic of *Aulospongia*, instead the axial and extra-axial skeletons are well differentiated, with the axis compressed and extra-axis reduced to radial single spicules; and echinating rhabdostyles form a dense perpendicular layer at the surface, outside the axial skeleton.

The species is distinctive in the very large size and robust nature of its spicules. Desqueyroux-Faundez & van Soest (1997) suggested that *R. (R.) galapagensis* was most similar to, and possibly conspecific with, *R. (R.) hyle*, with apparent notable differences being a branching growth form (versus frondose, vasiform), a prominently hispid surface (versus smooth), much larger ectosomal auxiliary styles/anisoxeas, and long subectosomal extra-axial styles perpendicular to the axis (supposedly absent in *R. (R.) hyle*). However, re-examination of respective holotypes found that *R. (R.) hyle* has substantially smaller choanosomal principal styles than *R. (R.) galapagensis*; long subectosomal extra-axial styles are definitely present in *R. (R.) hyle* with only a few erect on the surface (the remainder

confined within the mesohyl); ectosomal auxiliary styles/anisoxeas do not form characteristic raspailiid surface brushes in *R. (R.) hyle* but are scattered within the peripheral skeleton, entirely within the mesohyl; the surface in *R. (R.) hyle* is conulose and shaggy; and rhabdostyles have a substantially different morphology between the two species (see Figs 24-25).

***Raspailia* (*Raspaxilla*) *hirsuta* Thiele, 1898**

Raspailia hirsuta Thiele, 1898: 59, pl. 3, fig. 9, pl. 8, fig. 46a-d; Tanita, 1961: 344, fig. 4, pl. 3, fig. 10; Tanita, 1970: 102, pl. 2, fig. 8; Hoshino, 1971: 24; Hoshino, 1975: 32, pl. 4, figs 8-9; Hoshino, 1981: 216-218, fig. 8; Hoshino, 1987: 18; Sim & Kim, 1988: 28; Tanita & Hoshino, 1990: 100, text-fig. 62; Sim, 1990: 317.
Echinaxia hirsuta; Hallmann, 1917: 392.
Raspailia (*Raspaxilla*) *hirsuta* [sic.]; Hooper, 1991: 1199.

MATERIAL. HOLOTYPE. ZMB (not seen): Sagami Bay, Japan.

DISTRIBUTION. Japan (Sagami Bay, Kii Channel, Seto Inland Sea) and Korea (Chejudo, South Sea coast, Jeju I.).

DESCRIPTION. Growth form erect, irregularly digitate, foliose lamellae, branches flattened and irregularly bulbous. Surface minutely conulose and hispid. Colour orange or pinkish-brown alive. 'Raspailiid ectosomal skeleton' present but rudimentary, composed of vestigial raphide-like anisoxeas, and larger subectosomal extra-axial styles protruding through surface. Axial and extra-axial skeletons moderately well differentiated. Axial skeleton composed of a network of heavy fibres cored by smaller choanosomal principal styles, abundantly echinated by rhabdostyles. Extra-axial skeleton composed of fibres cored by longer subectosomal extra-axial styles extending radially from the axis all the way to the periphery and projecting through the surface. Megascleres include choanosomal principal styles, slender, slightly curved at centre or towards base, entirely smooth, without basal rhabd (405-(787)-1015×9-(18)-40µm). Echinating rhabdostyles relatively long, thick, base smooth with moderate to well developed basal rhabd, small granular spines on apical half or 2/3 of spicule (210-(282)-390×8-(12)-14µm). Subectosomal extra-axial styles rare, long, thick, straight or slightly curved towards base, occasionally strongylote (250-(495)-800×3-(4.6)-8µm). Ectosomal auxiliary oxeas or anisoxeas, raphidiform, slightly sinuous, tapering from the middle to each end, with asymmetrical points (140-(252)-400×

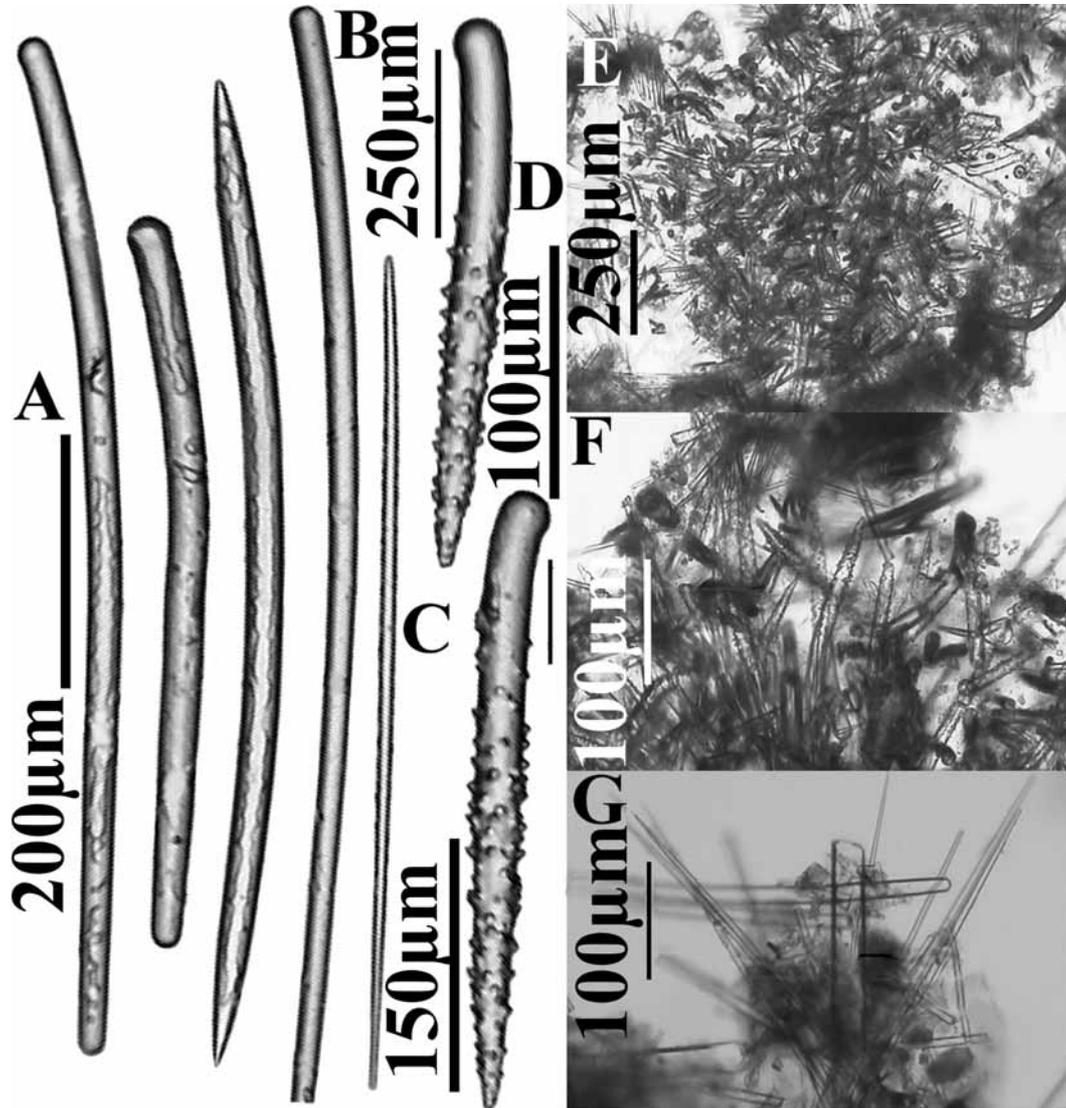


FIG. 24. *Raspailia (Raspaxilla) galapagensis*. A, Choanosomal principal strongylostyles and oxea. B, Basal end of subectosomal extra-axial style. C, Ectosomal auxiliary anisoxea. D, Echinating rhabdostyles. E, Compressed reticulate axial skeleton. F, Rhabdostyles in extra-axial skeleton. G, Ectosomal skeleton.

1-(2)-3µm). Microscleres absent (Thiele, 1898; Tanita, 1961; Hoshino, 1981; Sim, 1990: 317).

REMARKS. Thiele's (1898) original description of *R. (R.) hirsuta* was incomplete, providing only cursory information on ectosomal and choanosomal skeletal structure or spicule localisation, and the type material is currently missing (not located in the ZMB during a search

by the author and Dr D. Kühmann in 1988). Fortunately, newer material described from Japanese and Korean waters provides more precise details on external, skeletal and spicule morphologies, and the above description was compiled from this literature.

Raspailia (Raspaxilla) hyle
(de Laubenfels, 1930)
(Fig. 25)

Hemectyon hyle de Laubenfels, 1930: 28; 1932: 107, fig. 64; Dickinson, 1945: 21, pl. 31, figs 61-62, pl. 32, figs 63-64; Bakus & Green, 1987: 79; Green & Bakus, 1994: 37-39, fig. 20.

Aulospongia hyle; Desqueyroux-Faundez & van Soest, 1997: 442.

MATERIAL. HOLOTYPE. USNM21418 (fragment BMNH1929.9.30.4): Point Fermin, San Pedro, California, coll. USC, 16.ii.1924, 30-150m depth.

DISTRIBUTION. Queen Charlotte Is, British Columbia, Canada to Tanner Bank, California coast, Gulf of California, Mexico.

DESCRIPTION. Growth form frondose, vasiform. Surface smooth. Colour pale drab in ethanol. 'Raspailiid ectosomal skeleton' vestigial, with ectosomal auxiliary styles/anisoxeas scattered on or below the surface, usually in bundles parallel to the surface, not forming brushes and not associated with protruding erect subectosomal extra-axial styles. Axial and extra-axial skeletons well differentiated. Axial skeleton more-or-less a loose-meshed reticulation of multispicular fibres cored by smooth choanosomal principal styles enclosed within light spongin fibres forming a nearly halichondroid criss-cross reticulation. Extra-axial skeleton consists of erect subectosomal extra-axial styles perpendicular to axis, protruding through the surface, and also lying parallel to the surface within the mesohyl, with a dense layer of erect rhabdostyles embedded and perpendicular to the axial skeleton, not protruding through the surface. Megascleres consist of slender, entirely smooth choanosomal principal styles, sometimes modified to strongyles, with curvature varying from slight to greatly curved, curvature central or slightly basal, without any basal rhabd (322-585×12-190µm). Echinating rhabdostyles with slight to moderate basal rhabd, sometimes completely straight, base slightly subtylote, entirely smooth on basal half with large, erect, slightly recurved spines sparsely scattered on apical (pointed) half of spicule (155-364×9-22µm). Subectosomal extra-axial styles long, slender, straight or slightly curved near basal end, occasionally strongylote (715-1650×9-16µm). Ectosomal auxiliary styles, or less commonly anisoxeas, raphidiform, curved in basal third or sinuous (165-385×0.8-1.5µm). Microscleres absent.

REMARKS. The species has been discussed above in comparison with *R. (R.) galapagensis*. De Laubenfels (1930, 1932) and Dickinson (1945) recorded raphides in their material but

these are vestigial ectosomal auxiliary styles/anisoxeas. Several other inconsistencies between the type material and original descriptions have been corrected in the redescription above.

De Laubenfels (1932) originally included this species in *Hemectyon* on the basis of its allegedly strong similarities with the type species, *Hemectyon hamatum* (Schmidt, 1870): viz. possession of rhabdostyles with strongly recurved spines more-or-less restricted to the apex of spicules; localisation of echinating rhabdostyles to the peripheral skeleton; and 'unusual' axial core of styles enclosed in spongin (although this is now widely known to occur throughout the Raspailiidae). However, the resemblance between these two species is minimal: they are neither closely related nor does this species belong in *Endectyon* (*Hemectyon*). Desqueyroux-Faundez & van Soest (1997) subsequently referred *H. hyle* to *Aulospongia* based on its similarities with *R. (R.) galapagensis* (although these similarities are also only very slight; see remarks for *R. (R.) galapagensis*), whereas it is suggested here that both these species are more appropriately included in *Raspailia* (*Raspaxilla*).

Raspailia (Raspaxilla) hymani
(Dickinson, 1945)
(Fig. 26)

Hemectyon hymani Dickinson, 1945: 21, pl. 33, figs 65-66; Green & Bakus, 1994: 39-40, fig. 21.

Aulospongia hymani; Desqueyroux-Faundez & van Soest, 1997: 442.

MATERIAL. HOLOTYPE. AHF no.10 (not seen): San Jaime Banks, Cabo San Lucas, Mexico, 22°50'N, 110°15'W, coll. 'Veleró III', 3.iii.1937, 150m depth.

DISTRIBUTION. California to Cape San Lucas, Gulf of California, Mexico.

DESCRIPTION. Growth form flabellate, reticulate branching. Surface slightly hispid. Colour light drab, almost white, in ethanol. 'Raspailiid ectosomal skeleton' vestigial, with raphidiform ectosomal auxiliary styles/anisoxeas forming sparse brushes or scattered below the surface, but not necessarily surrounding the protruding spicules. Axial and extra-axial skeletons well differentiated. Axial skeleton composed of a highly compressed solid core of choanosomal principal styles aligned longitudinally through branches. Extra-axial skeleton plumo-reticulate composed of tracts of choanosomal principal styles embedded in axis and protruding at right angles through the surface, echinated on their outer edge by

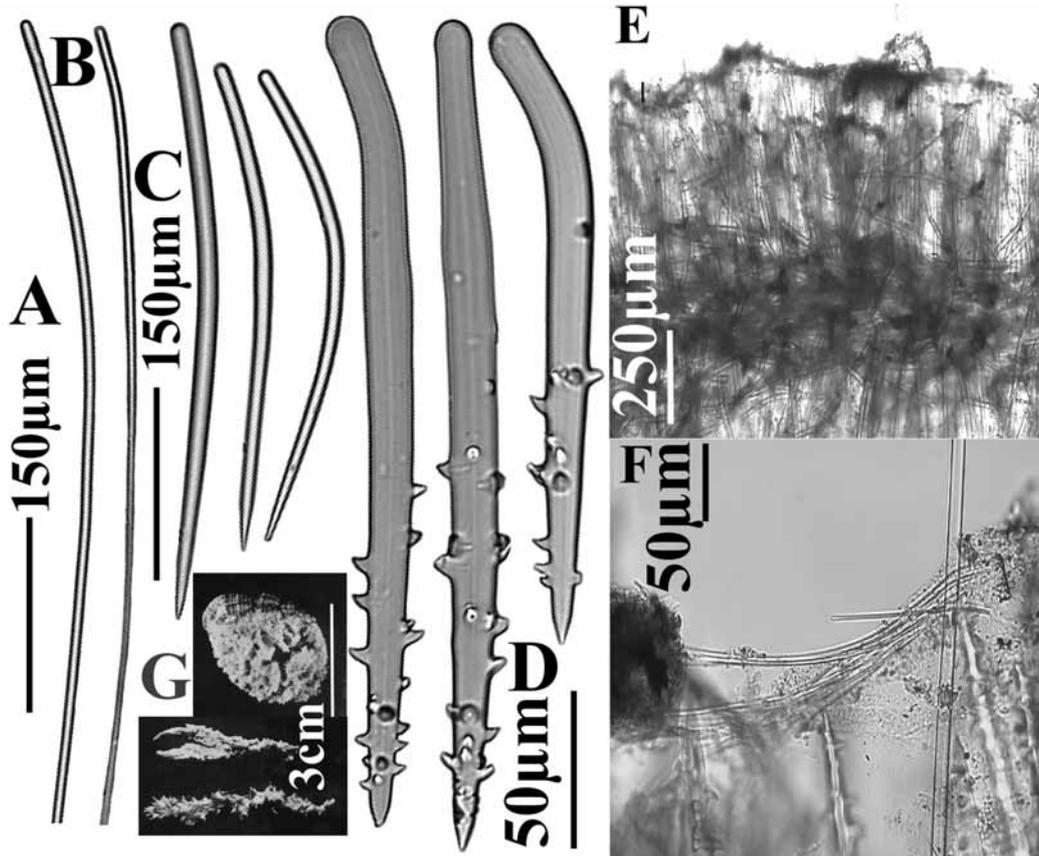


FIG. 25. *Raspailia (Raspaxilla) hyle*. A, Basal portion of subectosomal extra-axial style. B, Basal portion of ectosomal auxiliary style. C, Choanosomal principal styles. D, Echinating rhabdostyles. E, Axial and extra-axial skeletons. F, Ectosomal skeleton. G, Specimens AHF (modified from Dickinson, 1945).

rhabdostyles. Echinating rhabdostyles predominant in peripheral skeleton. Megascleres consist of long, smooth choanosomal principal styles, straight or slightly curved, entirely smooth, without any basal rhabd ($650\text{--}1700 \times 12\text{--}36\mu\text{m}$). Echinating rhabdostyles with basal rhabd varying from slight to well curved, bases entirely smooth, with large recurved spines only on the apical half of spicule, sometimes modified to acanthotylostyles ($130\text{--}300 \times 6\text{--}30\mu\text{m}$). Subectosomal extra-axial spicules absent. Ectosomal auxiliary styles/anisoxeas raphidiform (dimensions unknown). Microscleres absent (Dickinson, 1945; Green & Bakus, 1994).

REMARKS. This species has been recorded only twice, and regrettably the holotype cannot be located in the AHF collections (Prof. G. Bakus, pers.comm.). From its published descriptions the

species has a distinctive reticulate-branching, flabellate growth form resembling *Echinodictyum cancellatum* (Lamarck) (Raspailiidae) and *Clathria coppingeri* (Ridley) (Microcionidae). It is assigned here to *Raspailia (Raspaxilla)* in having coring and echinating spicules of different morphology; echinating rhabdostyles localised outside the axis, perched on the junction of the axial and extra-axial skeletons; having well differentiated axial and extra-axial skeletons; and lacking the characteristic fibre-bundles found in *Aulospongius*. The E Pacific species *R. (R.) hymani*, *R. (R.) hyle* and *R. (R.) galapagensis* are similar in many of their characteristics and probably represent allopatric sibling species, analogous to the relationship between the sister species *R. (R.) clathrioides*, *R. (R.) reticulata* and *R. (R.) topsenti* from the SW. Pacific.

Green & Bakus (1994) briefly describe two other unnamed species under *Hemectyon*, both similar to *R. hymeni* but differing in several features. The status of these species is still uncertain, but it is possible that they are variable populations of *R. hymeni*.

Raspailia (Raspaxilla) inaequalis

Dendy, 1924

Raspailia inaequalis Dendy, 1924: 355, pl. 12, fig. 1, pl. 14, figs 17-19; Bergquist, 1970: 28, fig. 2.

Raspailia (Raspaxilla) inaequalis; Hooper, 1991: 1199.

MATERIAL. HOLOTYPE: BMNH1923.10.1.138 (not seen), North Cape, New Zealand, 140m depth, coll. 'Terra Nova'.

DISTRIBUTION. Known only from N New Zealand.

DESCRIPTION. Growth form digitate, stalked, thinly cylindrical, bifurcate branches. Surface granular, velvety, finely hispid. Colour greyish in ethanol. 'Raspailiid ectosomal skeleton' absent, although bundles of longer subectosomal extra-axial styles protrude slightly through the surface. Axial and extra-axial skeletons well differentiated. Axial skeleton compressed with dense reticulation of thick fibres cored by choanosomal principal styles, appearing almost disorganised halichondroid, with fibres only lightly echinated by rhabdostyles in axis. Extra-axial skeleton plumoreticulate, dominated by ascending, plumose, multispicular columns of choanosomal principal styles, columns embedded in and perpendicular to axis, interconnected by pauci- or unispicular transverse fibres extending all the way to the surface, ending in bundles of larger subectosomal extra-axial styles embedded in peripheral fibres. Ascending fibres in peripheral skeleton echinated by rhabdostyles, singly or in plumose bundles. Megascleres consist of slender choanosomal principal styles, centrally curved, entirely smooth, with evenly rounded base ($220 \times 5 \mu\text{m}$). Echinating rhabdostyles with moderate basal rhabd, smooth base, and small granular spines on apical 2/3 of spicule ($130 \times 8 \mu\text{m}$). Subectosomal extra-axial styles thick, relatively short, centrally curved, with evenly rounded base and hastate point ($370-480 \times 14-17 \mu\text{m}$). Special category of ectosomal auxiliary spicules absent. Microscleres absent (Dendy, 1924; Bergquist, 1970).

REMARKS. The species clearly belongs to *Raspaxilla* in its skeletal structure (well differentiated axial and extra-axial skeletons, compressed axis, plumoreticulate extra-axis) and

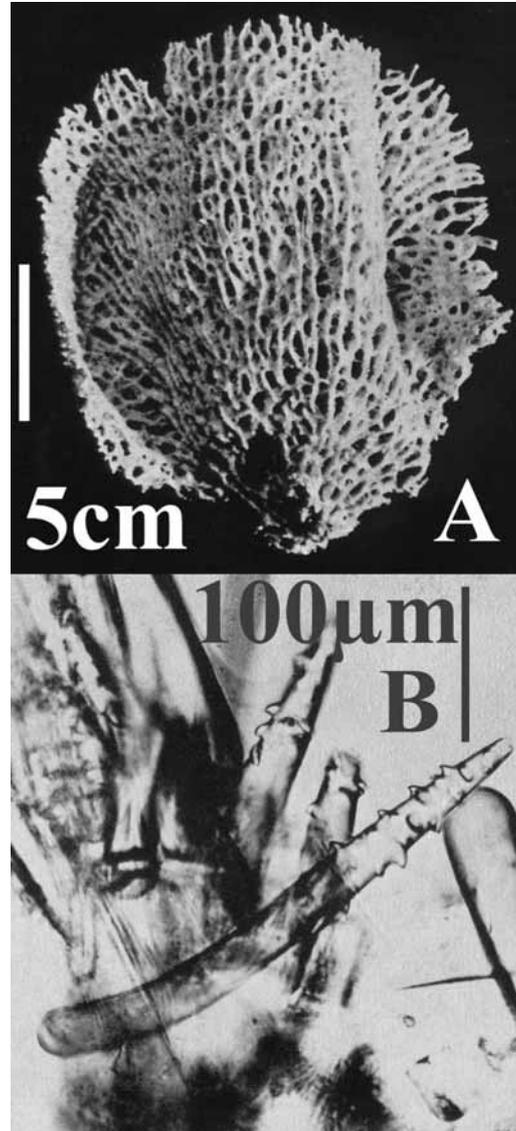


FIG. 26. *Raspailia (Raspaxilla) hymeni*. A, Holotype. B, Echinating rhabdostyles (figure modified from Dickinson, 1945).

spicule morphology (non-rhabdose choanosomal principal styles), although it lacks specialised ectosomal auxiliary spicules and there is little differentiation between choanosomal principal and subectosomal extra-axial styles. In some respects it is similar to *R. (R.) wardi* from Western Australia in spicule morphology and ectosomal features, whereas the two species differ

substantially in their growth form, surface features, density and location of echinating spicules, and spicule sizes.

Raspailia (Raspaxilla) mariana
(Ridley & Dendy, 1886)
(Fig. 27)

Axinella mariana Ridley & Dendy, 1886: 480; 1887: 180, pl. 34, fig. 1, pl. 40, fig. 2; Koltun, 1964: 83, pl. 13, figs 7-10.

Axinectya mariana; Hallmann, 1917: 393.

Raspailia (Raspaxilla) mariana; Hooper, 1991: 1196, fig. 7d-f.

MATERIAL. HOLOTYPE. BMNH1887.5.2.28: Marion I., Prince Edward Islands, subantarctic, 100-150m depth, coll. 'Challenger'.

DISTRIBUTION. Known only from the subantarctic islands.

DESCRIPTION. Arborescent, bifurcate branching, flattened branches. Surface prominently hispid. Colour greyish-yellow in ethanol. 'Raspailiid ectosomal skeleton' absent, although extremely long subectosomal extra-axial styles protrude through the surface, singly or in bundles, surrounded by plumose brushes of rhabdostyles at their point of insertion through the surface. Axial and extra-axial skeletons well differentiated. Axial skeleton greatly compressed, heavy fibres, without any coring spicules but with the bases of long subectosomal extra-axial styles embedded. Extra-axial skeleton radial, with long subectosomal extra-axial styles radiating from the axis to the surface, surrounded along most of their length (within the sponge body) by echinating rhabdostyles in plumose bundles. Megascleres consist only of two forms. Principal spicules absent. Echinating rhabdostyles moderately thick, with smooth non-tylote base, basal rhabd varying from slight to well developed (strongly curved), and either completely smooth point or with small granular spines covering apical 2/3 of spicule (185-370×8-18µm). Subectosomal extra-axial styles long, thick or slender, slightly curved near the basal end, slightly subtylote, completely smooth (1550-2400×12-29µm). Ectosomal auxiliary megascleres absent. Microscleres absent.

REMARKS. This species is unusual amongst *Raspaxilla* in lacking principal spicules completely, having only long subectosomal extra-axial styles radially oriented and embedded within axial fibres (i.e. no reticulate connecting tracts), and plumose bundles of echinating rhabdostyles throughout the axial and extra-axial

skeletons. The absence of principal spicules makes it difficult to determine whether it belongs to *Aulospongos* (principal spicules with basal rhabds) or *Raspaxilla* (without basal rhabds), whereas the possession of a compressed axis and absence of fibre-bundles suggests it belongs to the latter genus. The species is a highly reduced *Raspaxilla* (also lacking specialised ectosomal auxiliary spicules).

Raspailia (Raspaxilla) pearsei
(Wells, Wells & Gray, 1960)

Hemectyon pearsei Wells, Wells & Gray, 1960: 218, figs 14,26.

MATERIAL. HOLOTYPE. USNM 23651 (not seen): off Beaufort, North Carolina, 5m depth.

DISTRIBUTION. Known only from E coast USA.

DESCRIPTION. Small ellipsoidal mass composed of many compressed vertically elongated lamellae, 30mm long, 20mm high, encrusting rock. Texture stiff. Surface with many upright ridges 1-1.5mm apart, hispid particularly on ridges, with glabrous ectosomal membrane stretched between adjacent ridges. Colour unknown. Oscules up to 0.6mm diameter scattered over ectosomal membrane. Ectosomal specialisation unknown. Choanosomal skeleton composed of a axial reticulation of vertical and radial spongin fibres cored by choanosomal principal subtylostyles and echinated by rhabdostyles, with radial fibres and choanosomal principal spicules forming plumose bundles at the surface. Megascleres include choanosomal principal subtylostyles, entirely smooth, slightly curved at centre, with prominent tylote base and lacking any basal rhabd (190-340×10-14µm). Echinating rhabdostyles with prominent basal rhabd, entirely spined or with smooth base (85-115×3-7µm). Subectosomal extra-axial spicules not recorded. Ectosomal auxiliary spicules not recorded. Microscleres absent (Wells, Wells & Gray, 1960).

REMARKS. The type material of this species has not been re-examined, and it is only known so far from its original description. The true nature of its ectosomal and choanosomal skeletal structures is still uncertain, and it is possible that ectosomal auxiliary spicules and/or subectosomal extra-axial spicules were overlooked by Wells et al. (1960), or that it is indeed a very reduced species in its spicule complement. From its description it appears to conform best to

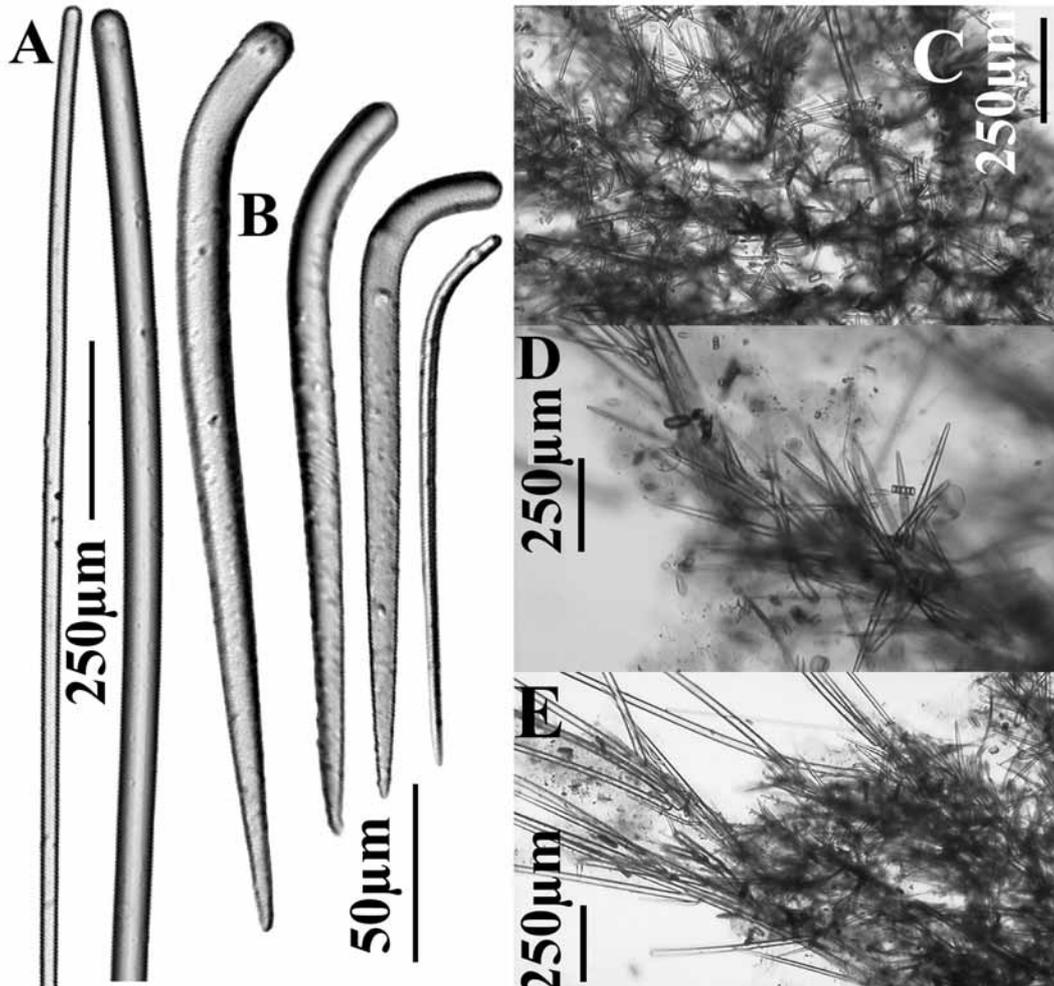


FIG. 27. *Raspailia (Raspaxilla) mariana*. A, Basal portion of subectosomal extra-axial styles. B, Echinating rhabdostyles. C, Reticulate axial skeleton. D, Peripheral fibre. E, Ectosomal skeleton.

Raspailia (Raspaxilla) (i.e. choanosomal principal styles are morphologically very different from echinating rhabdostyles, entirely smooth and lacking any traces of basal rhabds; there are no fibre-bundles characteristic of *Aulospongia*; and skeletal structure apparently varies between axial and extra-axial regions). Wells et al. (1960) noted that *R. pearsei* resembles *R. hyle* to some extent, differing in the respective sizes of echinating rhabdostyles, but these affinities require confirmation from the type material.

Raspailia (Raspaxilla) reticulata

Hooper, 1991
(Figs 28-29, 36D)

Raspailia (Raspaxilla) reticulata Hooper, 1991: 1250, figs 35-36.

MATERIAL. HOLOTYPE. QMGL1982: Green I., Cairns Section, Great Barrier Reef, 16°46'S, 145°58'E. OTHER MATERIAL. QMG307874, QMG313312: Wooded Islet, Low Isles, Cairns Section, GBR, 16°23.7'S, 145°34.3'E, 24m depth, 18.i.1997, coll. 'Gwendolyn May'.

DISTRIBUTION. Known only from the N Great Barrier Reef.

DESCRIPTION. Erect, arborescent, stalked, cylindrical branches, bulbous nodes. Surface finely conulose, fleshy, hispid, slightly shaggy. Colour yellow-orange (Munsell 2.5Y 8/10) alive. Oscules very small (<1mm diameter), slightly raised above the surface with membranous lip when alive, with small surface drainage canals radiating towards oscules. Texture stiff (basal stalk), flexible (branches), fleshy when alive. Ectosome hispid, moderately collagenous, with darkly pigmented collagen layer up to 200µm thick. Specialised 'raspailiid ectosomal skeleton' present, consisting of long thin subectosomal extra-axial styles and stout choanosomal principal styles protruding through surface in small bundles of 2-5 spicules, or singly, surrounded at their bases by ectosomal auxiliary anisoxeas, which form large bundles in plumose, radial or clumped-sinuuous tracts. Projecting ectosomal and subectosomal spicules extend up to 500µm from the surface, producing irregularly spaced, long, slender conules. Collagenous component of conules extends 100-350µm from the surface. Axial and extra-axial skeletons only slightly differentiated. Axial skeleton predominantly reticulate, only slightly compressed, with relatively tight meshes formed by well developed spongin fibres (35-70µm diameter), bulbous at fibre nodes (up to 90µm diameter), forming elongate-oval meshes (150-320µm long, 90-140µm wide), with abundant granular collagen within mesohyl; fibre size relatively homogeneous throughout axial skeleton, although ascending fibres are cored by paucispicular tracts of 2-3 choanosomal principal styles and transverse fibres are aspicular or unispicular. Extra-axial skeleton plumo-reticulate, with skeletal tracts diverging as they ascend, becoming more plumose, with progressively fewer interconnecting tracts towards the peripheral skeleton, although interconnections between adjacent fibres persist all the way to the surface. Peripheral skeleton with pauci- or multispicular ascending fibres, cored by 2-5 choanosomal principal styles per tract; transverse connecting fibres are aspicular or unispicular. Coring styles in peripheral skeleton are generally larger than those in axial fibres. Echinating rhabdostyles more-or-less evenly scattered throughout the skeleton, perhaps slightly more dense at fibre nodes, protruding perpendicularly from fibres. Megascleres consist of larger choanosomal principal styles, entirely smooth, slightly curved at centre, with straight base or occasionally with a slight basal rhabd, bases

evenly rounded, occasionally modified to strongly rounded forms (165-(344.1)-402×8-(10.6)-13µm). Smaller echinating rhabdostyles club-shaped, with prominent smooth subtylote base, with or without well-developed basal rhabd, spines granular, evenly dispersed but restricted to apical two-thirds of spicule (58-(80.3)-97×3-(6.6)-9µm). Subectosomal extra-axial styles very long, slender, entirely smooth, with variable shape ranging from slightly curved near basal end, straight, with several asymmetrical curves, sinuous or raphidiform (455-(726.7)-1025×2-(6.4)-10µm). Ectosomal auxiliary anisoxeas raphidiform, slightly curved near basal end, asymmetrical ends with points tapering, fusiform and bases tapering, hastate, rounded, completely smooth (255-(325.3)-445×1.5-(2.2)-3µm). Microscleres absent.

REMARKS. This species was known previously only from a single dead, trawled sample, with living populations recently discovered on the Low Isles providing additional characters for the species (hence redescribed in detail above; compare spicule measurements with those of Hooper, 1991: 1252). This species is a sister-species to (and potentially a synonym of), *R. (R.) clathrioides* (New Caledonia) and *R. (R.) topsenti* (N New Zealand), with observed differences significant certainly at the population level, but equivocally at the species level (refer to remarks under *R. (R.) clathrioides*).

***Raspailia (Raspaxilla) topsenti* Dendy, 1924**
(Fig. 30)

Raspailia topsenti Dendy, 1924: 354, pl. 12, fig. 4, pl. 14, figs 14-16; de Laubenfels, 1936: 102; Bergquist, 1970: 28, fig. 3b, pls 6c-d, 7a, 10d, 18d, 19d.

Raspailia (Raspaxilla) topsenti; Hooper, 1991: 1199.

MATERIAL. HOLOTYPE. BMNH1923.10.1.135: North Cape, New Zealand, 140m depth, coll. 'Terra Nova'.

DISTRIBUTION. Known only from N New Zealand.

DESCRIPTION. Arborescent, stalked, dichotomously branching, cylindrical branches. Surface granular, minutely hispid. Colour deep dull-orange alive. 'Raspailiid ectosomal skeleton' vestigial, with sparse, wispy ectosomal auxiliary styles/anisoxeas scattered on or below surface, singly or in sparse brushes. Axial and extra-axial skeletons moderately well differentiated. Axial skeleton compressed, close-meshed reticulation of heavy fibres cored by choanosomal principal styles, with few echinating spicules. Extra-axial skeleton

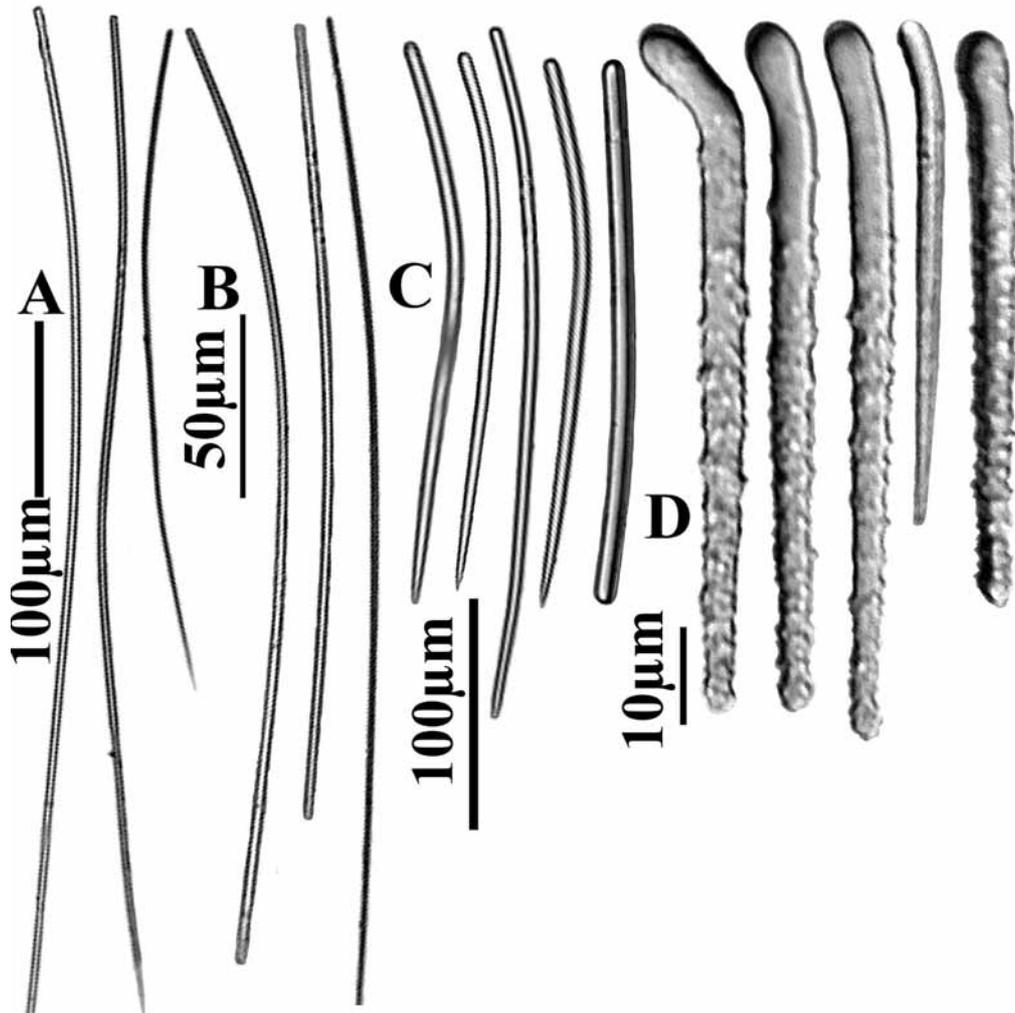


FIG. 28. *Raspailia (Raspaxilla) reticulata*. A, Subectosomal extra-axial styles. B, Ectosomal auxiliary anisoxeas. C, Choanosomal principal styles. D, Echinating rhabdostyles.

plumo-reticulate, with pauci- or multispicular tracts of choanosomal principal styles ascending to the surface (often protruding through fibres), interconnected by uni- or paucispicular tracts, abundantly echinated by rhabdostyles particularly close to surface. Megascleres include short, thick choanosomal principal styles, slightly curved at centre or towards base, sometimes straight, with evenly rounded smooth base, occasionally oxete, with abrupt hastate points ($265-474 \times 12-21 \mu\text{m}$). Echinating rhabdostyles short, thick, with swollen, smooth, bulbous bases, basal rhabds ranging from slightly curved to prominently curved, with small

granular spines on apical 3/4ths of spicule ($68-125 \times 7-10 \mu\text{m}$). No specialised subectosomal extra-axial spicules present. Ectosomal auxiliary styles or anisoxeas very thin, nearly raphidiform, straight, slightly curved or sometimes sinuous ($185-245 \times 1-2 \mu\text{m}$). Microscleres absent.

REMARKS. This species clearly belongs to *Raspaxilla* in having a compressed reticulate axial skeleton, a plumo-reticulate extra-axial skeleton, choanosomal principal styles lacking basal rhabds and of distinctly different morphology than echinating rhabdostyles, and lacking any sign of plumose fibre-bundles. It is

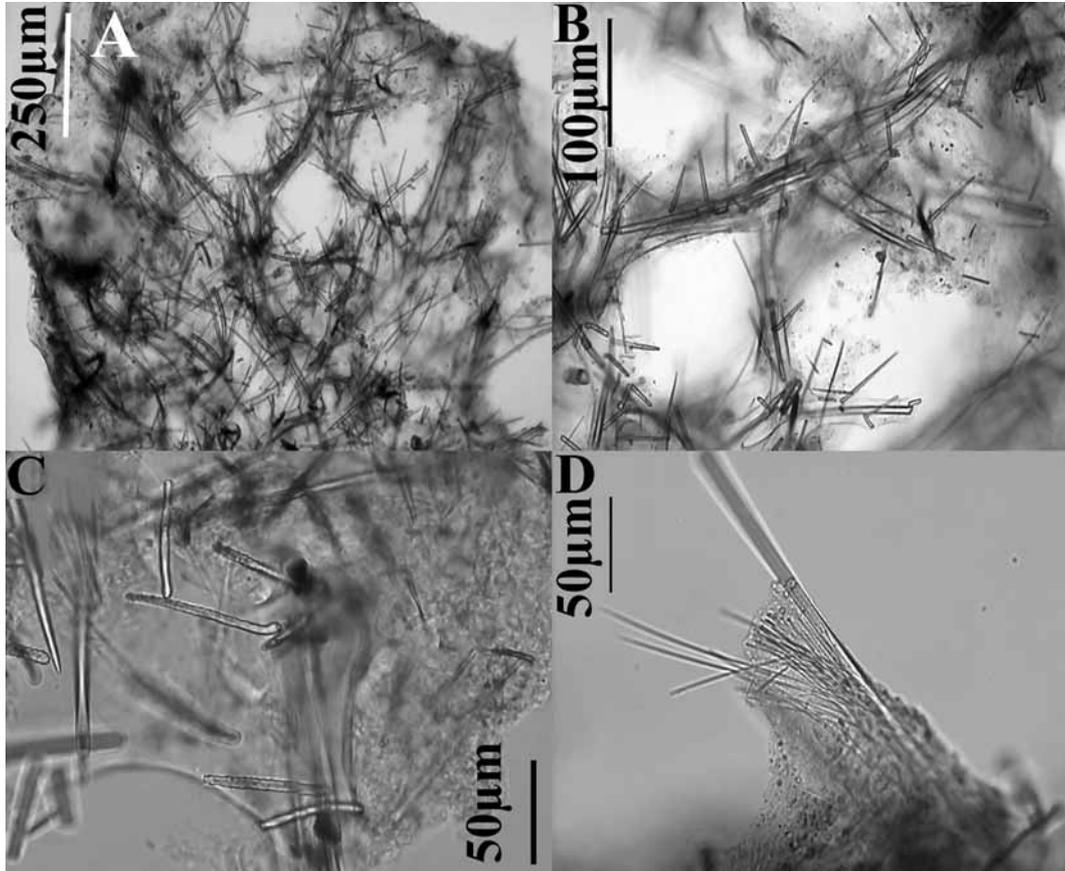


FIG. 29. *Raspailia (Raspaxilla) reticulata*. A, Reticulate choanosomal skeleton. B, Reticulate extra-axial skeleton. C, Choanosomal fibre. D, Ectosomal skeleton.

reduced in its ectosomal features, lacking any specialised subectosomal extra-axial spicules (i.e. undifferentiated from choanosomal principal spicules), and having only a vestigial specialised 'raspailiid ectosomal skeleton'. Based on rhabdostyle morphology (shape and spination) it is altogether most similar to *R. (R.) clathrioides* (New Caledonia) and *R. (R.) reticulata* (N Great Barrier Reef): the three species forming a sibling species group.

***Raspailia (Raspaxilla) wardi* Hooper, 1991**
(Fig. 31)

Raspailia (Raspaxilla.) wardi Hooper, 1991: 1252, figs 37-38.

MATERIAL. HOLOTYPE. NTM Z1319: W of Port Hedland, Northwest Shelf, WA, 19° 03.5'S, 119° 03.6'E, 81 m depth, 28.iv.1983, coll. 'Soela'.

DISTRIBUTION. Known only from the Northwest Shelf, Western Australia.

DESCRIPTION. Thin, stalked, elongate, flabellate growth form. Surface smooth, microscopically very hispid. Colour bright red-orange alive. 'Raspailiid ectosomal skeleton' absent, although subectosomal extra-axial styles protrude a long way through the surface surrounded by bundles of echinating rhabdostyles standing perpendicular to the axial skeleton, forming tightly plumose brushes and producing a continuous subdermal palisade. Axial and extra-axial skeletal architecture markedly differentiated. Axial skeleton moderately compressed, composed of close-meshed, regularly renieroid reticulate fibres cored by uni- or paucispicular tracts of choanosomal principal styles. Extra-axial skeleton radial, with long subectosomal

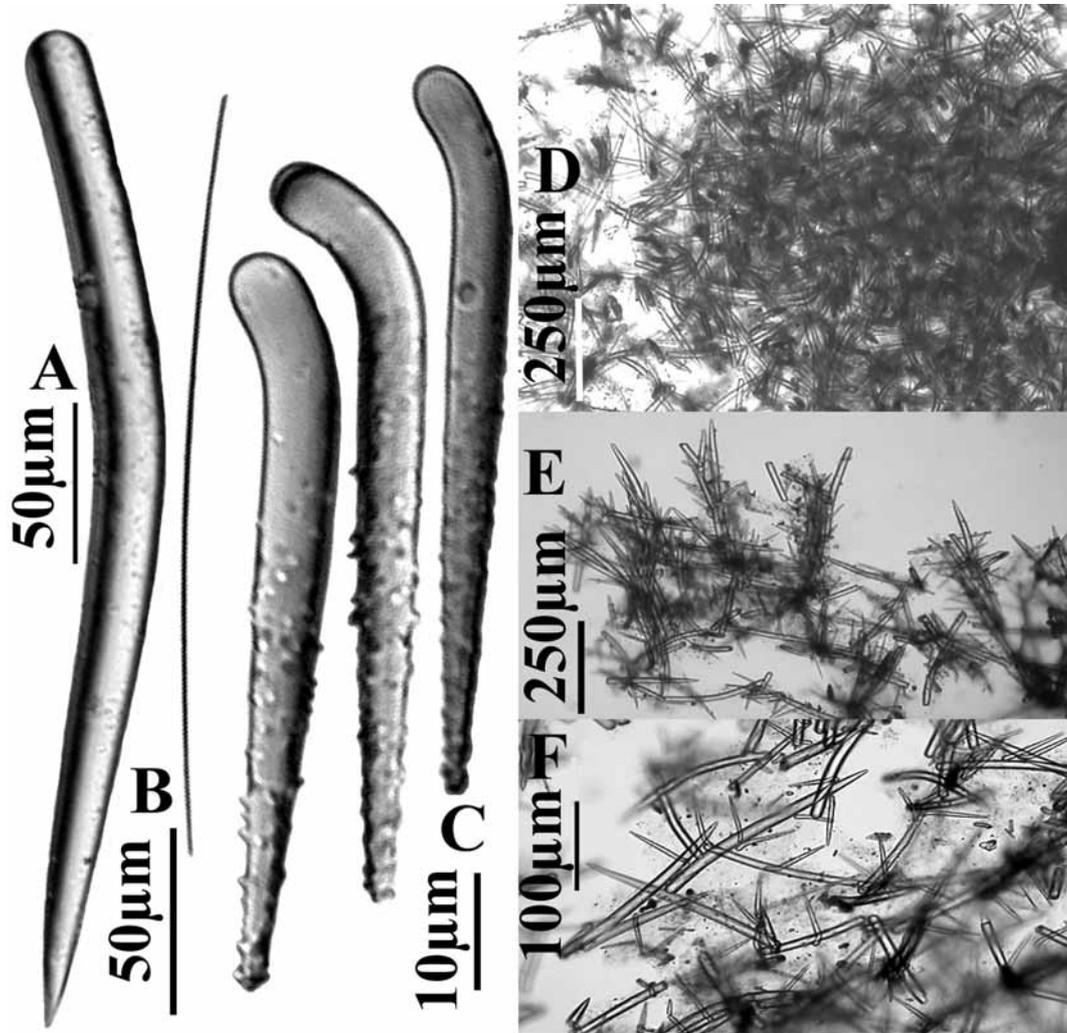


FIG. 30. *Raspailia (Raspaxilla) topsenti*. A, Choanosomal principal style. B, Ectosomal auxiliary anisoxea. C, Echinating rhabdostyles. D, Reticulate axial skeleton. E, Ectosomal skeleton. F, Extra-axial fibres.

extra-axial styles embedded in peripheral fibres and protruding through the surface. Echinating rhabdostyles absent from axial skeleton, occurring only as a palisade on the outer edge of the axis. Megascleres include choanosomal principal styles, rarely anisoxeas, entirely smooth, most slightly curved centrally towards basal end, with rounded non-tylote bases or very occasionally with slight basal rhabd (147-222×5-9µm). Echinating rhabdostyles thick, with basal rhabds ranging from slight to moderately curved, with a few basal spines but more heavily spined on apical part of spicule, spines small, recurved

(112-165×8-12µm). Subectosomal extra-axial styles long, thick, slightly curved towards basal end or occasionally straight, with almost hastate points and rounded non-tylote bases (515-1122×7-16µm). Specialised ectosomal auxiliary spicules absent. Microscleres absent.

REMARKS. This species differs from most other *Raspaxilla* in its extremely thin flabellate growth form, renieroid reticulate axial skeleton, and possession of a continuous palisade of rhabdostyles on the ectosome, forming plumose brushes, but which are otherwise absent from the

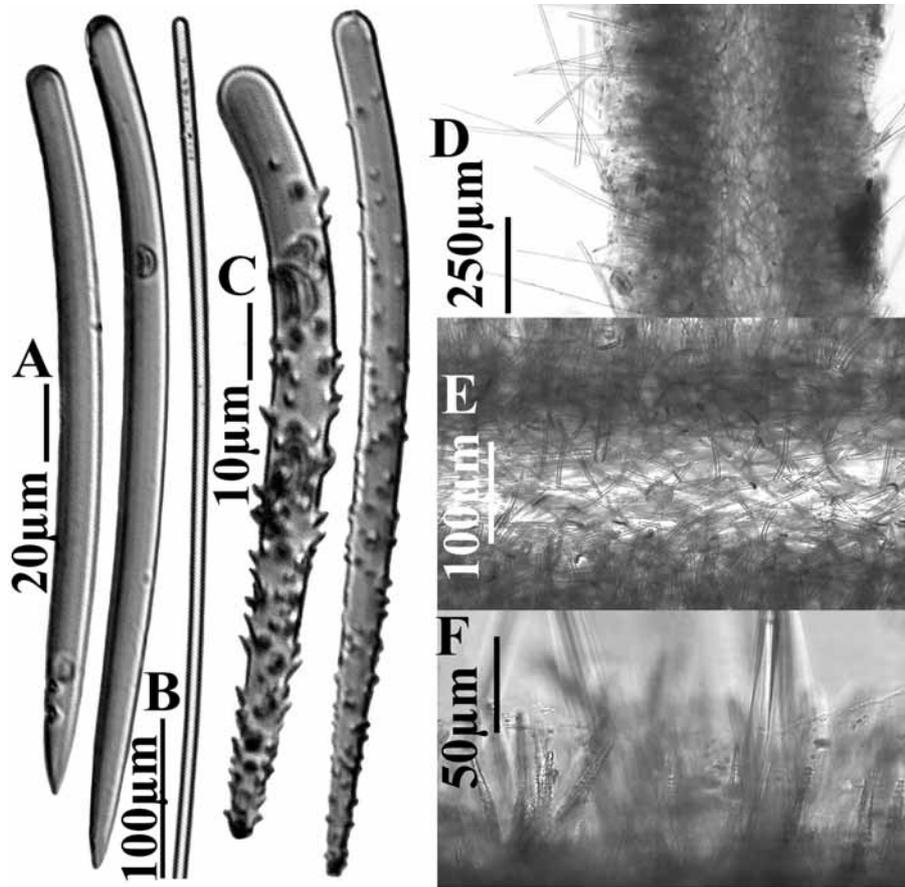


FIG. 31. *Raspailia (Raspaxilla) wardi*. A, Choanosomal principal styles. B, Basal portion of subectosomal extra-axial style. C, Echinating rhabdostyles. D, Skeletal cross-section through branch. E, Axial and extra-axial skeletons. F, Rhabdostyles in extra-axial skeleton.

axial skeleton. In this latter feature this species could arguably be included in *Endectyon* (*Hemectyon*) (see below), although in this case the localisation of rhabdostyles mainly on the surface is probably a function of the thin flabellate growth form, whereby the choanosomal skeleton is compacted and essentially the rhabdostyles are 'pushed' into the peripheral region. It is not included in *Endectyon* (*Hemectyon*) given the geometry and spination of rhabdostyles. It is included in *Raspailia (Raspaxilla)* as a reduced species, lacking specialised ectosomal auxiliary megascleres. In spicule morphology and spicule diversity it shows a closer relationship to *R. (R.) inaequalis* than to any other species.

Endectyon Topsent, 1920
Subgenus **Hemectyon** Topsent, 1920

Hemectyon Topsent, 1920: 27; Hooper, 1991: 1284. Type species *Raspailia (?) hamatum* Schmidt, 1870: 62, by original designation.

DEFINITION. *Endectyon* with echinating acanthostyles bearing clavulate spines only on apex of spicule, with smooth bases sometimes having a slight basal rhabd. Echinating spicules localised outside the axial skeleton, usually at the junction of axial and extra-axial skeletons, and/or forming plumose brushes along extra-axial skeleton, and often also producing spicule brushes at the surface. Axial skeleton compressed, reticulate. Extra-axial skeleton plumose or plumoreticulate cored by choanosomal principal styles.

REMARKS. *Hemectyon* was merged into synonymy with *Endectyon* by Hooper (1991), on the basis that the two differed in few characters. *Endectyon* (s.s.) has a specialised 'raspailiid ectosomal skeleton' composed of small ectosomal auxiliary styles/anisoxeas grouped around long subectosomal extra-axial styles. By comparison, *Hemectyon* lacks either of the special categories of ectosomal auxiliary or subectosomal extra-axial styles, and its ectosomal skeleton consists instead of acanthostyles grouped around protruding choanosomal principal styles. *Hemectyon* also has a more openly reticulate axial skeleton than does *Endectyon* (s.s.). More importantly though, in *Hemectyon* the bases of acanthostyles are predominantly smooth, subtylote, and some are slightly rhabdose, whereas those of *Endectyon* have recurved (clavulate) hooks on both ends and lack any basal rhabd. On this basis *Hemectyon* may be treated as a convenient subgenus within *Endectyon*, both having in common clavulate spines on acanthostyles, but in the latter genus these are localised outside the axial skeleton (usually at the junctions of axial and extra-axial skeletons).

Comparisons between *Endectyon* (*Hemectyon*) and *Aulospongus* and *Raspailia* (*Raspaxilla*) are slightly misleading. Echinating acanthostyles in *Endectyon* (*Hemectyon*) are not truly rhabdose, like the other two genera, with the slight basal curvature often overemphasised by the presence of a pronounced basal swelling on these spicules. Nevertheless, rhabdostyles in these three genera may be potentially confused. The subgenus contains only the type species, although arguably *E. fruticosa* (Dendy), *E. fruticosa aruensis* (Hentschel), and *E. xerampelina* (Lamarck) could also be included given that some (but not all) of their echinating acanthostyles have smooth, swollen, slightly rhabdose bases with clavulate spines mainly on the apex of the spicule. They are not included, however, because other spicules also have clavulate spines on their bases and more closely resemble those of *Endectyon* species (see Hooper, 1991).

Endectyon* (*Hemectyon*) *hamatum

Schmidt, 1870
(Fig. 32, Table 1)

Raspailia ? *hamata* Schmidt, 1870: 62; Desqueyroux-Faundez & Stone, 1992: 56.
Hemectyon hamatum; Topsent, 1920: 26, fig. 4a
Endectyon hamata; Hooper, 1991: 1284, fig. 53d-f (not Pulitzer-Finali, 1993: 307).

MATERIAL. HOLOTYPE. MZUS P0151 (fragment MNHN LBIM DT2161): 'West Indies'.

DISTRIBUTION. Caribbean.

DESCRIPTION. Growth form arborescent, cylindrical branches. Surface slightly corrugated. Colour pale brown in dry state. Specialised 'raspailiid ectosomal skeleton' absent, with only protruding bundles of a few choanosomal principal styles surrounded at their base by multispicular plumose bundles of rhabdostyles, although vestigial ectosomal auxiliary styles are scattered within the choanosomal skeleton. Axial and extra-axial skeleton moderately well differentiated. Axial skeleton strongly reticulate, compressed, with heavy fibres cored by small choanosomal principal styles in multispicular tracts mostly running longitudinally through branches, and with few echinating rhabdostyles. Extra-axial skeleton radial-reticulate, without fibre-bundles, with ascending paucispicular tracts interconnected by unispicular transverse tracts of choanosomal principal styles. Echinating rhabdostyles predominantly on exterior surface of primary (ascending) extra-axial fibres, with greatest numbers concentrated at the surface in brushes. Megascleres consist of choanosomal principal styles slightly curved centrally, without basal rhabd, entirely smooth (270-615×8-18µm). Echinating rhabdostyles with very slight basal rhabd, smooth slightly swollen base, and large clavulate spines only on apical extremity or apical 1/3 of spicule at most (120-150×5-10µm). Subectosomal extra-axial styles absent. Ectosomal auxiliary styles vestigial and scattered within the choanosome (220-275×1-2µm). Microscleres absent.

REMARKS. This species is still known only from a surviving fragment of Schmidt's (1870) holotype, redescribed by Topsent (1920) and reillustrated by Hooper (1991). Although some features of the species are unknown, we do have sufficient details of skeletal structure, spicule morphology and spicule dimensions to clearly distinguish this species from all other raspailiids with rhabdostyle-like echinating spicules. It is particularly characteristic in its rhabdostyle morphology, which more closely resembles those of *Raspaxilla* species than of *Endectyon* species (cf. Hooper, 1991: 1284). Recently Pulitzer-Finali (1994) briefly described a specimen collected from the Kenya region which he assigned to *E. hamatum* (Schmidt). Unfortunately no illustrations were provided (and material from the Genova Museum is not

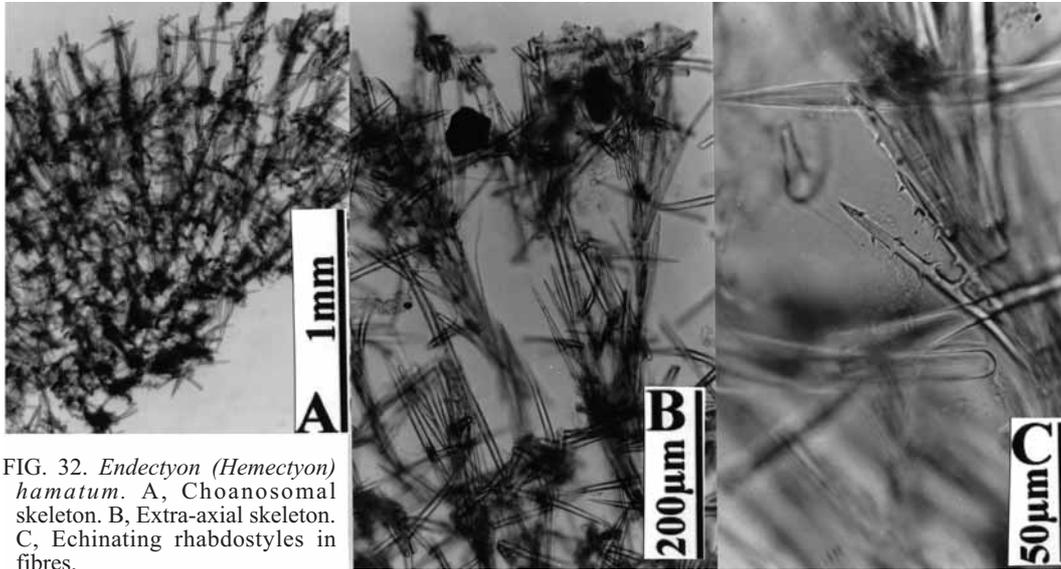


FIG. 32. *Endectyon (Hemectyon) hamatum*. A, Choanosomal skeleton. B, Extra-axial skeleton. C, Echinating rhabdostyles in fibres.

presently accessible for loan). However, it is clear when comparing both descriptions that the E African population is not conspecific with the Caribbean species (i.e. it has long subectosomal extra-axial styles lacking in *E. hamatum*, and several notable differences in spicule dimensions). It is likely that Pulitzer-Finali's (1994) species is new, but its generic placement remains uncertain.

DISCUSSION

Aulospongos differs from other Raspailiidae in having two size categories of rhabdostyles (the larger, smooth or partially spined rhabdostyles coring fibres, and the smaller, usually spined rhabdostyles echinating fibres); a plumose skeletal structure composed of ascending compressed fibre-bundles (with few or no reticulate elements, and in cases where reticulate interconnecting fibres are present these are usually aspicular and disappear completely in the peripheral skeleton); lacking any differentiation between axial and extra-axial regions of the skeleton (although plumose fibres are slightly more compressed in the axis than in the periphery). Although traditional definitions of the genus are based on possession of a 'peculiar tubular' growth form, exclusively plumose (i.e. non-reticulate) skeletal fibre-bundles, absence of any ectosomal specialisation, and distinctive rhabdose spicules, many species (including the type species *A. tubulatus*), show variations on

this supposedly 'typical' theme, such that the previously sharp generic boundary blurs somewhat with other raspailiids which have rhabdose echinating acanthostyles (viz. *Raspailia (Raspaxilla)*, and to a lesser extent *Endectyon (Hemectyon)*). Detailed comparisons between these genera are discussed below, and the range of characters and character states are listed in Table 3.

ANALYSIS OF CHARACTERS. *Growth form.* The characteristic 'tubular' growth form seen in the type and several other species of *Aulospongos* (whereby large fibres are fused together into bundles to form a massive tubular construction), is supposedly 'typical' of the genus and is certainly unusual amongst Raspailiidae. This feature, however, is not universal amongst all *Aulospongos*, with a great variety of growth forms amongst species. Growth forms range from: arborescent, with cylindrical branches seen in many raspailiids including *Raspailia*, *Raspaxilla*, *Hemectyon* and *Thrinacophora*; cylindrical club-shaped with bulbous surface processes seen in *A. samariensis* sp. nov.; massive, subspherical, bushy in *A. villosa*; 'typical' *Aulospongos* form of subspherical, massive, tubular in *A. tubulatus*; plate-like, vasiform in *A. flabellum* and *A. involutum*; bulbous-lobate, thickly lamellate in *A. cerebella*, *A. gardineri* and *A. novaecaledoniensis* sp. nov.; and bulbous encrusting in *A. monticularis* and *A. spinosum* (Table 3).

Determination of whether particular growth forms are derived or ancestral is relatively subjective and equivocal in any character analysis (e.g. Hooper, 1991), but there is already some precedence for such interpretations amongst several groups of demosponges: Axinellidae (Alvarez & Crisp, 1994), Rhabderemiidae (van Soest & Hooper, 1993), *Acarinus* (van Soest et al., 1991), Microcionidae (Hooper, 1996), Mycalidae (Hajdu, in press). Based on outgroup analyses these studies hypothesise that the more massive, erect growth forms are less derived than thinly encrusting ones, the latter frequently indicative of successful adaptation and survival in ephemeral habits, such as the intertidal zone and interstitial habitats. Amongst Raspailiidae 'typical' growth forms are erect, digitate, branching sponges, with far fewer encrusting or bulbous species, and this interpretation is consistent for *Aulospongius*, which is interpreted here as being a highly derived raspailiid. However, this interpretation must be taken with caution because it is likely that species independently colonise these ephemeral habitats, and more unlikely that they have evolved there.

Plumose fibre-bundles. Species of *Aulospongius* are characterised in having their fibres and spicule tracts amalgamated into bundles, termed here 'fibre-bundles', composed of bulbous spongin fibres cored and echinated by rhabdostyles in plumose tracts, forming individual plumose ascending (usually non-reticulate) branches, and terminating as surface lobes and/or processes. This feature is apparently unrelated to overall growth form and also appears to be unique within Raspailiidae. These fibre-bundles are superficially reminiscent of the spiculo-spongin tracts seen in *Pseudaxinella* (Axinellidae) (see Hooper & Lévi, 1993) and *Clathria* (*Microcionia*) (Microcionidae) (see Hooper, 1996), although fibre structure and localisation of spicules associated with these fibres are substantially different in both these genera, and there is no inferred relationship between them and *Aulospongius*. Similarly, in *R.* (*Raspaxilla*) *phakellina*, and some other species assigned to *Raspaxilla*, ascending fibres are plumose and dominate the extra-axial skeleton, with (e.g. *R.* (*R.*) *reticulata*) or without (e.g. *R.* (*R.*) *compressa*), interconnecting fibres extending all the way to the peripheral skeleton. However, in these species fibres are generally not bulbous, nor do spicules form dense plumose tracts around the bulbs, amalgamated at the core but diverging

towards the periphery, as in *Aulospongius*. Instead, fibres in *Raspaxilla* arise from a well developed, compressed reticulate axis, connecting fibres are paucispicular, and skeletal structure can best be described as plumo-reticulate. 'Fibre-bundles' are also absent from *Endectyon*.

Choanosomal skeletal structure. In *Aulospongius* there is no appreciable difference between the axial or basal region and the peripheral (extra-axial) regions of the skeleton, although there is often a greater degree of amalgamation (or fusion) of the system of plumose fibre-bundles at the core of the skeleton (or base of the sponge), than in the peripheral skeleton (where fibres simply diverge further apart). Reticulate fibres are present in the axial skeletons of several species (*A. tubulatus*, *A. gardineri*, *A. spinosum*, *A. novaecaledoniensis* sp. nov., *A. samariensis* sp. nov.), in which there are few aspicular or rarely paucispicular (transverse) fibres interconnecting adjacent (ascending) plumose fibre-bundles, but these do not persist into the peripheral region and cannot be classed as 'reticulate' skeletons.

By comparison, *Raspailia* (*Raspaxilla*) and *Endectyon* (*Hemectyon*) have well differentiated axial and extra-axial skeletons; well developed, compressed, reticulate axial skeletons; and plumoreticulate or radial extra-axial skeletons (similar to most other raspailiids). In these genera extra-axial skeletal structure consists of plumose ascending multispicular fibres interconnected by uni- or paucispicular transverse fibres that persist all the way to the surface. In some of these species where axial compression is extreme, or where the diameter of the skeleton is narrow (e.g. thin branches), extra-axial tracts are reduced to single radial subectosomal extra-axial styles embedded in and perpendicular to the axis, protruding through the surface, with echinating rhabdostyles appearing to be 'pushed' to the outer edge of the skeleton.

In choanosomal skeletal structure species of *Aulospongius* fall into two groups, with two other character states seen in the Raspailiidae outgroups (*Raspailia* (*Raspailia*), *Raspailia* (*Raspaxilla*), *Endectyon* (*Hemectyon*), *Thrinacophora*). Skeletal structures include: species with compressed axial and radial extra-axial skeletons (the latter composed of subectosomal extra-axial styles embedded in and perpendicular to the axial skeleton), seen in many raspailiids including *Endectyon* (*Hemectyon*) and *Thrinacophora* (this is probably a reduced,

TABLE 3. List of characters and character states used to judge apomorphy in the construction of the cladogram of relationships between species of *Aulospongia* based on outgroup comparisons with members of the family Raspailiidae.

<p>1. Growth form: 1(1), arborescent, cylindrical branches; 1(2), cylindrical club-shaped with bulbous surface processes; 1(3), massive, subspherical, bushy; 1(4), subspherical, massive, tubular, erect digitate cup-shaped; 1(5), plate-like, vasiform; 1(6), bulbous-lobate; 1(7), bulbous encrusting. 2. Fibre-bundles: 2(1), absent; 2(2), present. 3. Axial skeleton: 3(1), compressed, solid; 3(2), compressed, more open-reticulate; 3(3), slightly compressed, predominantly plumose, few reticulate connections; 3(4), exclusively plumose, slightly compressed, no fibre reticulation. 4. Extra-axial skeleton: 4(1), radial, with longer extra-axial auxiliary styles/ anisoxeas embedded in and perpendicular to axis, with or without unispicular reticulate connections; 4(2), reticulate or slightly plumoreticulate, reticulate connections persistent throughout; 4(3), plumose, few aspicular or unispicular reticulate connections disappearing in periphery; 4(4), exclusively plumose, without reticulate connections. 5. Location of protruding extra-axial styles/ anisoxeas: 5(1), absent; 5(2), embedded in ascending peripheral fibres and protruding through surface, singly or in bundles. 6. Interconnecting reticulate fibres: 6(1), well developed, persistent throughout skeleton; 6(2), well developed in axis, poorly developed in extra-axial skeleton; 6(3), vestigial, with aspicular or unispicular interconnecting fibres diminishing along ascending fibres and absent from periphery; 6(4), absent completely. 7. Location of (smaller) echinating styles or rhabdostyles: 7(1), evenly dispersed throughout skeleton; 7(2), restricted to axis, absent from periphery; 7(3), reduced in axis, concentrated mainly in peripheral skeleton embedded in primary ascending fibres, protruding through surface; 7(4), localised to outer surface of peripheral fibres, echinating surface and/or forming brushes around protruding extra-axial auxiliary spicules; 7(5), absent (presumed secondary loss). 8. Specialised 'raspailiid ectosomal skeleton': 8(1), well developed, composed of brushes of ectosomal auxiliary styles/ anisoxeas surrounding the longer protruding subectosomal extra-axial styles; 8(2), vestigial, composed of sparse ectosomal auxiliary styles/ anisoxeas scattered on or below the surface, not forming bundles, with or without the longer protruding subectosomal extra-axial styles; 8(3), vestigial, with only protruding long subectosomal extra-axial styles but no ectosomal auxiliary styles; 8(4), absent, lacking any ectosomal or extra-axial auxiliary spicules. 9. Basal rhabds on styles: 9(1), absent (never present); 9(2), present only on echinating styles/ acanthostyles; 9(3), present on both echinating and principal styles/ acanthostyles, 9(4), absent (secondarily modified). 10. Spination on rhabdostyles: 10(1), rhabdostyle spicules absent completely; 10(2), smaller echinating acanthostyles spined or partially spined, and at least partially rhabdostyle, whereas larger choanosomal principal styles entirely smooth and non-rhabdostyle; 10(3), larger choanosomal principal rhabdostyles entirely smooth, echinating rhabdostyles spined or partially spined, basal rhabd moderate or slightly developed on both sorts of spicule; 10(4) both echinating and choanosomal principal rhabdostyles at least partially spined, basal rhabd strongly developed on both. 11. Number of categories of (smaller) echinating rhabdostyles: 11(1), none; 11(2), one; 11(3), two. 12. Raphide microscleres: 12(1), present; 12(2), absent.</p>

derived character related to the degree of axial compression and loss of a more extensive extra-axial skeleton); species with a compressed reticulate axis, and a reticulate or plumo-reticulate extra-axis in which interconnecting fibres persist throughout the entire peripheral skeleton, also seen in many raspailiids including *Raspailia* (*Raspaxilla*) and *R. (Raspailia)*; species with few aspicular or occasionally paucispicular fibres interconnecting the ascending plumose fibre-bundles, with reticulate connecting fibres diminishing and disappearing towards the periphery, seen in *A. gardineri*, *A. spinosum*,

A. tubulatus, *A. novaecaledoniensis* sp. nov. and *A. samariensis* sp. nov.; species with exclusively plumose fibre-bundles arising from a slightly compressed base, with fibres diverging towards the periphery, without any reticulate connections, seen in *A. cerebella*, *A. involutum*, *A. monticularis* and *A. villosa*. These skeletal structures are subdivided into several characters, based on the subdivision of the skeleton into axial, extra-axial and peripheral skeletons, and the presence, absence and nature of reticulate skeletal tracts (Table 3).

In *Aulospongia* there appears to be a correlation between possession of massive, encrusting or tubular growth forms and absence of any notable axial compression, versus possession of lamellate or branching, flexible growth forms with a compressed axial skeleton. Presumably this is an ecological response to a flexible growth form (and consequently of debatable phylogenetic significance). In all these species the ascending plumose fibre-bundles dominate the skeleton and this is a major feature of *Aulospongia*.

Ectosomal specialisation. *Aulospongia* was originally described without a specialised 'raspailiid ectosomal skeleton' (i.e. with brushes of ectosomal auxiliary styles/anisoxeas surrounding the longer protruding subectosomal extra-axial styles), and lacking any ectosomal auxiliary and subectosomal extra-axial spicules. These characters were also overlooked in the recent review of Raspailiidae (Hooper, 1991). More detailed re-examination of type material, however, confirms there is a gradual transition-series amongst species in 'raspailiid ectosomal structure', falling into four groups: 1) well developed (seen in *A. gardineri* and *A. samariensis* sp. nov.); 2) vestigial, with sparse ectosomal auxiliary styles/anisoxeas scattered on or below the surface, not forming bundles, with or without the longer protruding subectosomal extra-axial styles (in *A. novaecaledoniensis* sp. nov., *A. involutum* and *A. tubulatus*); 3) vestigial, with only protruding long subectosomal extra-axial styles but no ectosomal auxiliary styles (seen in *A. monticularis*); 4) and absent completely, without any ectosomal or extra-axial auxiliary spicules (in *A. cerebella*, *A. flabellum*, *A. spinosum* and *A. villosa*) (Table 3).

The possession of a well developed ectosomal skeleton is interpreted here as a primitive condition and the retention of an ancestral (family) characteristic, but probably more importantly, it also appears to be an unstable character even within genus-groups. For example, *Raspailia* (*Raspailia*) *wilkinsoni* Hooper lacks specialised ectosomal spicules, with only choanosomal and extra-axial spicules protruding (corresponding to group 3 above); *R. (R.) echinata* Whitelegge has long protruding extra-axial styles with very few vestigial ectosomal styles embedded on the surface but not forming characteristic raspailiid surface brushes (group 2); whereas most raspailiids, such as *R. (R.) vestigifera* Dendy and *R. phakellina* Topsent, have well developed 'raspailiid ectosomal skeletons' (group 1 above). *Endectyon* (*Hemectyon*) has vestigial ectosomal

auxiliary spicules scattered within the choanosome (but not forming surface brushes) (group 2 above), whereas its senior generic synonym *Endectyon* retains the specialised 'raspailiid ectosomal skeleton' (group 1 above) (Hooper, 1991).

Under this interpretation, *Aulospongia* group 1 species, with well developed 'raspailiid ectosomal skeletons', are more primitive (ancestral) than others; vestigial ectosomal skeletons (groups 2-3) are more derived, representing a gradual secondary loss of this character; and group 4 species that have completely lost any ectosomal skeletal specialisation are most derived. A similar interpretation was taken for the raspailiid genus *Echinodictyum* by Hooper (1991), in which only one of thirteen Australian species possessed a 'typical raspailiid ectosomal skeleton', the others likely to have secondarily lost these spicules completely.

Rhabdosome spicules. The most significant character shared by *Aulospongia*, *Raspaxilla* and to a lesser degree *Hemectyon* is the possession of echinating rhabdostyles. The existence of this character in other demosponge families suggests they are homoplastic developments, whereas within the group *Aulospongia* - *Raspaxilla* the smaller echinating rhabdostyles are clearly homologous derivatives of typical echinating acanthostyles, and for *Aulospongia* the possession of these spicules is synplesiomorphic. Conversely, the larger choanosomal principal rhabdostyles found only in *Aulospongia* are unique and synapomorphic.

Generally, the coring and echinating rhabdostyles of *Aulospongia* are much more similar in their morphology, including the possession of spines on the larger choanosomal principal spicules, whereas in *Raspailia* (*Raspaxilla*), *Endectyon* (*Hemectyon*) and other raspailiids coring spicules are non-rhabdosome, entirely smooth, with distinctly different geometry than echinating spicules. In *Aulospongia* there are two groups of species with different patterns of spination on rhabdostyles: one group with larger choanosomal principal rhabdostyles entirely smooth, echinating rhabdostyles spined or partially spined, basal rhabd moderate or slightly developed on both sorts of spicules (seen in *A. cerebella*, *A. flabellum*, *A. monticularis*, *A. spinosum*, *A. tubulatus*); and the other group with both echinating and choanosomal principal rhabdostyles at least partially spined, basal rhabd strongly developed on both (in *A. gardineri*, *A. involutum*, *A. novaecaledoniensis* sp. nov.; *A.*

TABLE 4. Taxon-character matrix for *Aulospongos* and outgroups *Raspailia* (*Raspaxilla*), *Raspailia* (*Raspailia*), *Endectyon* (*Hemectyon*) and *Thrinacophora* (*=type species). See Table 3 for explanation of characters and their states. Consistency index (C.I.) and Rescaled Retention Index (R.C.) is indicated for each character obtained from parsimony analysis (Swofford, 1993).

Species	Character											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>A. cerebella</i>	6	2	4	4	1	4	1	4	3	3	2	2
<i>A. flabellum</i>	5	?	?	?	1	?	?	4	3	3	2	2
<i>A. gardineri</i>	6	2	3	3	2	3	1	1	3	4	3	2
<i>A. involutum</i>	5	2	4	4	2	4	1	2	3	4	2	2
<i>A. monticularis</i>	7	2	4	4	2	4	1	3	3	3	2	2
<i>A.novaecaledoniensis</i>	6	2	3	3	1	3	2	2	3	4	2	2
<i>A. samariensis</i>	2	2	3	3	2	3	1	1	3	4	2	2
<i>A. spinosum</i>	7	2	3	4	1	3	1	4	3	3	3	1
<i>A. tubulatus*</i>	4	2	4	4	1	4	1	2	3	3	2	2
<i>A. villosa</i>	3	2	4	4	1	4	1	4	3	4	2	2
<i>R. (R.) phakellina*</i>	1	1	2	2	2	2	3	1	2	2	2	2
<i>R. (R.) typica*</i>	1	1	2	2	2	1	1	1	1	1	1	2
<i>E. (H.) hamatum*</i>	1	1	1	1	1	2	4	2	2	2	2	2
<i>T. funiformis*</i>	1	1	1	1	2	2	5	1	1	1	1	1
C.I.	0.86	1.00	0.75	0.75	0.33	1.00	1.00	0.60	1.00	0.60	0.67	0.50
R.C.	0.64	1.00	0.66	0.67	0.22	1.00	0	0.40	1.0	0.40	0.33	0

villosa, *A. samariensis* sp. nov.). Most species of *Aulospongos* have only one category of smaller echinating rhabdostyles, whereas two species have a second category which is slender, entirely smooth, and differentiated from the spined echinating rhabdostyles (*A. gardineri* and *A. spinosum*) (Table 3).

Microscleres. Raphide microscleres occur in several raspailiid genera (singly or in trichodragmata): *Aulospongos*, *Thrinacophora*, *Trikenrion* and *Eurypon* (with synonyms *Tricheurypon* and *Protoraspailla*), and *Rhadbeurypon*. Thus, the presence of raphides in one species of *Aulospongos* (*A. spinosum*), is interpreted here to represent the retention of an ancestral family character (following Hooper, 1991), with the corollary that loss of raphides is a secondarily derived character given that it is more parsimonious that these spicules are independently lost than independently acquired.

PHYLOGENETIC ANALYSIS. Table 4 shows the distribution of characters and character-states amongst species of *Aulospongos* and the raspailiid outgroups. Several outgroups were chosen representing a range of affinities with *Aulospongos*, their characters described from the type species of each taxon as follows: *Raspailia* (*Raspaxilla*) (type species *Raspaxilla phakellina*

Topsent, holotype fragment MNHN LBIM DT1614); *R. (Raspailia)* (type species *R. typica* Nardo, holotype lost, Schmidt's 'representative specimen' from the Adriatic BMNH 1867.3.11.8), *Endectyon* (*Hemectyon*) (type species *Raspailia ? hamata* Schmidt, holotype fragment MNHN LBIM DT2161); and *Thrinacophora* (type species *T. funiformis* Ridley & Dendy, holotype BMNH 1887.5.2.53).

Phylogenetic analysis found good statistical support for the differentiation of *Aulospongos* from both closely related (*Raspaxilla*, *Raspailia*) and more distantly related raspailiid outgroups (*Endectyon*, *Thrinacophora*) (Bootstrap/Decay indices = 93/3; Fig. 33). Principal differentiating characters for *Aulospongos* consist of the synapomorphies: possession of plumose fibre-bundles (character 2); both principal and echinating styles with rhabdose bases, and patterns of spination on rhabdostyles (characters 9-10); and a synplesiomorphy of echinating rhabdostyles more-or-less evenly distributed throughout the skeleton, not confined to the peripheral skeleton (character 7) (Fig. 33; length = 43; number of minimum length trees = 36; consistency index = 0.744; retention index = 0.796; rescaled retention index = 0.593). Characters 5 (location of protruding extra-axial spicules), 7 (location of echinating styles/ rhabdostyles), 11 (number of

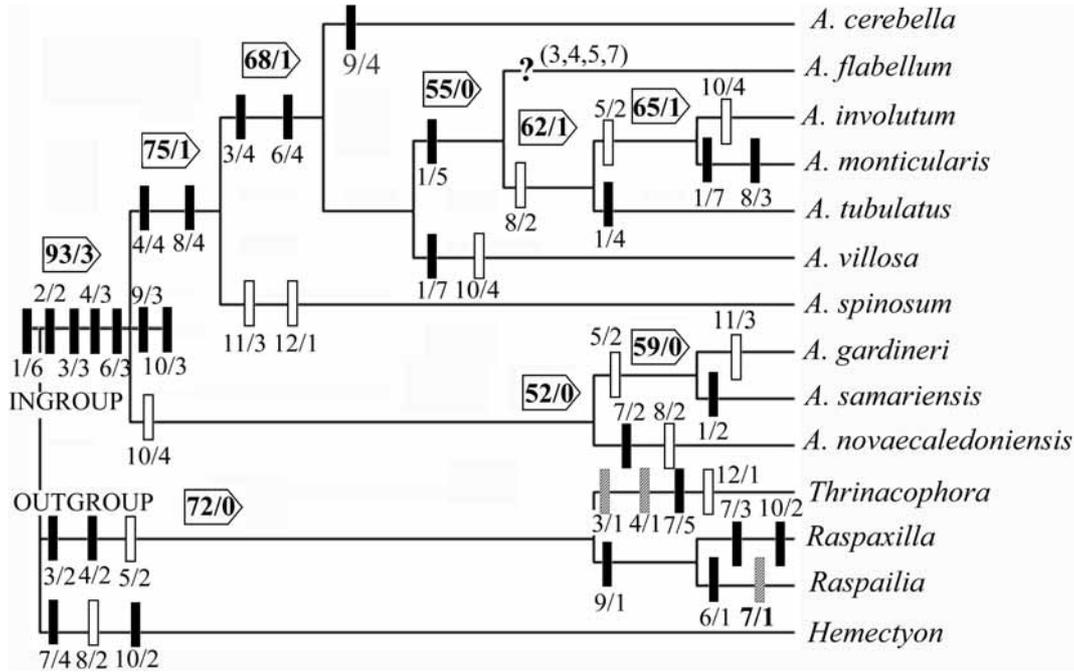


FIG. 33. Phylogenetic analysis of *Aulospongus* using parsimony (Paup 3.1.1), indicating the most parsimonious tree (of 36 possible minimum length trees), with characters 3, 4 and 6 ordered (Table 4). Character state changes, under accelerated transformation (ACCTRAN), are indicated as character/state; solid bars = synapomorphies; open bars = parallelisms; stippled bars = reversals. Statistical support for branching, indicated inside the arrows at branch nodes, as bootstrap/decay values.

categories of echinating rhabdostyles) and 12 (possession of raphides) were the least informative, with rescaled retention index ranging from 0-0.33 (Table 4).

The high numbers of homoplastic character states and relatively low bootstrap/decay indices supporting branching suggest that the phylogeny of the genus is not fully resolved by this analysis. However, within *Aulospongus* two groups of species are clearly indicated (Fig. 33), differentiated mainly by their choanosomal skeletal structures (ordered characters 3,4,6), with moderate level of statistical support (Bootstrap/Decay = 75/1). Group 1 species (*A. cerebella*, *A. involutum*, *A. monticularis*, *A. tubulatus*, *A. villosa*, and *A. spinosum*) have a plumose axial skeleton composed of compressed, 'fused' fibre-bundles, axial and extra-axial skeletons with exclusively plumose structure, lacking any interconnecting reticulate tracts in the peripheral skeleton. *Aulospongus flabellum* is tentatively included in this group, despite the unknown status of these characters (i.e. not described by

Pulitzer-Finali, 1994), based on inferred closer similarities with other Group 1 species than with Group 2 species in growth form and pattern of spination on rhabdostyles. Group 2 species (*A. gardineri*, *A. samariensis*, *A. novaecaledoniensis*) have vestigial reticulate fibres remaining in the extra-axial skeleton, although these diminish as they ascend towards the periphery and disappear altogether in the outer skeleton. By comparison, the raspailiid outgroups have reticulate fibres persistent throughout the axial and extra-axial skeletons.

All Group 2 species have spines on both larger (choanosomal) and smaller (echinating) rhabdostyles (character 10/4) (*A. gardineri*, *A. samariensis*, *A. novaecaledoniensis*), but this feature is also present in two Group 1 species (*A. villosa*, *A. involutum*), whereas all other Group 2 species have completely smooth choanosomal principal rhabdostyles (character 10/3: *A. cerebella*, *A. flabellum*, *A. monticularis*, *A. tubulatus*, *A. spinosum*). This is interpreted as a homoplastic development, given that none of the

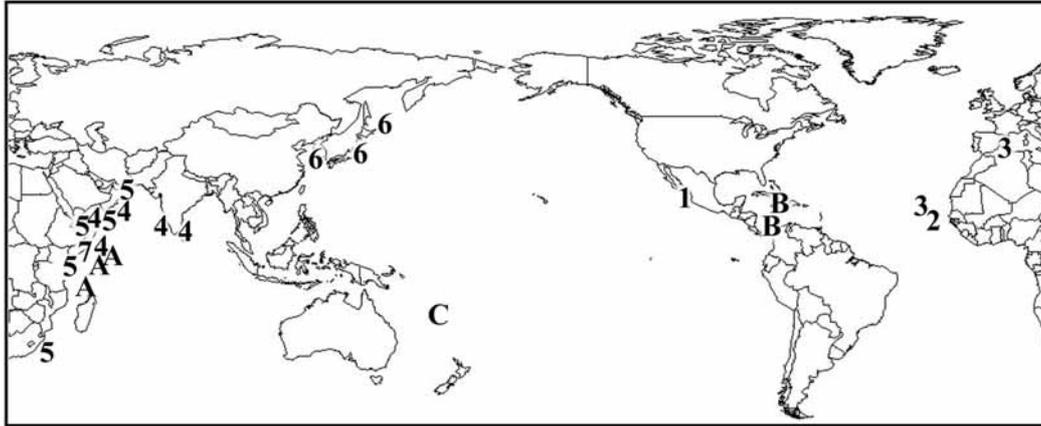


FIG. 34. Geographic distribution of *Aulospongos* species. Group 1 species (1, *A. cerebella*, 2, *A. monticularis*, 3, *A. spinosum*, 4, *A. tubulatus*, 5, *A. involutum*, 6, *A. villosa*, 7, *A. flabellum*); group 2 species (A, *A. gardineri*, B, *A. samariensis* sp. nov., C, *A. novaecaledoniensis* sp. nov.).

outgroup taxa have spined principal choanosomal spicules. However, it is also possible that character 10/4 is synplesiomorphic for *Aulospongos*, with the more derived state (10/3) occurring through secondary loss of spines on principal rhabdostyles.

The possession, loss and modification of a 'raspailiid ectosomal skeleton' (character 8) is also clearly homoplastic within *Aulospongos*. This supports the view of Hooper (1991) that the independent secondary loss (derivation) of ectosomal specialisation occurs in virtually all

raspailiid genera, even though it is supposedly a major synapomorphy for Raspailiidae. In *Aulospongos* several species retain (the ancestral) specialised condition (*A. gardineri*, *A. samariensis*), others have no specialised ectosomal skeleton at all (*A. cerebella*, *A. flabellum*, *A. spinosum*, *A. villosa*), and others have conditions intermediate to these, with partial loss of spicule types and/or ectosomal skeletal structures (*A. involutum*, *A. monticularis*, *A. novaecaledoniensis*, *A. tubulatus*). Thus, ectosomal skeletal structure is the most easily

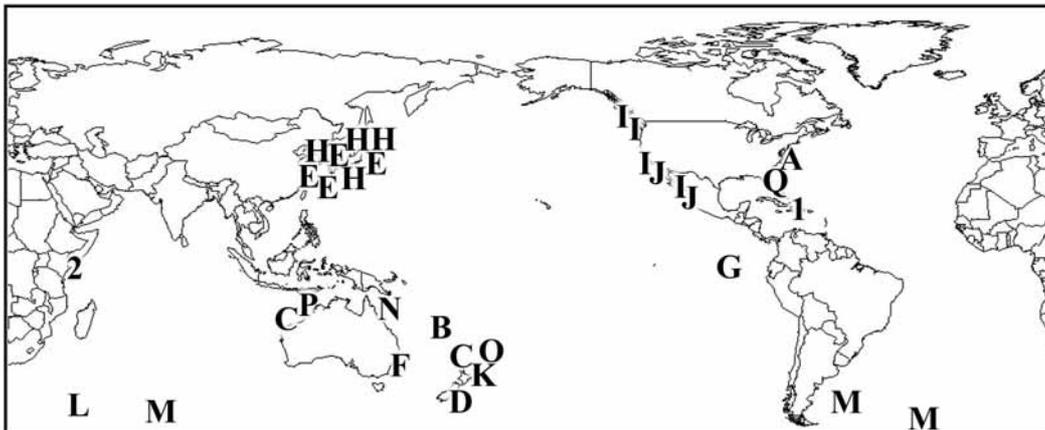


FIG. 35. Geographic distribution of *Raspailia* (*Raspaxilla*) and *Endectyon* (*Hemectyon*) species. A, *R.(R.) acanthifera*, B, *R.(R.) clathrioides*, C, *R.(R.) compressa*, D, *R.(R.) flaccida*, E, *R.(R.) folium*, F, *R.(R.) frondula*, G, *R.(R.) galapagensis*, H, *R.(R.) hirsuta*, I, *R.(R.) hyle*, J, *R.(R.) hymani*, K, *R.(R.) inaequalis*, L, *R.(R.) mariana*, M, *R.(R.) phakellina*, N, *R.(R.) reticulata*, O, *R.(R.) topsenti*, P, *R.(R.) wardi*, 1, *E.(H.) hamatum*, 2, 'E. hamatum' sensu Pulitzer-Finali (1993)).



FIG. 36. A, *Aulospongus samariensis* sp. nov. (W Caribbean population), Santa Marta, Colombia (photo S. Zea). B, *Aulospongus samariensis* sp. nov. (E Caribbean population), Discovery Bay, Jamaica (photo H. Lehnert). C, *Raspaxilla (Raspaxilla) clathrioides* (Lévi), SW Noumea Lagoon, New Caledonia (photo G. Bargibant). D, *Raspaxilla (Raspaxilla) reticulata* Hooper, Low Isles, Great Barrier Reef (photo J. Hooper).

modified (or lost) feature within the genus (and family), and consequently the least valuable diagnostic character amongst *Aulospongus*.

BIOGEOGRAPHY. The distribution of *Aulospongus* (Fig. 34) is pan-equatorial, predominantly tropical – subtropical, with rare incursions into cooler temperate waters. The central E Atlantic region contains two species, both from Group 1 (*A. monticularis*, *A. spinosum*, the latter with incursion into the Mediterranean Sea); the central American (E Pacific) – Caribbean (W Atlantic) region contains two species, with representatives from both Groups 1 and 2 (*A. cerebella*, *A. samariensis*, respectively); the W Pacific region contains only two species from both Groups 1 and 2 (*A. villosa*, *A. novaecaledoniensis*, respectively); and the W Indian Ocean region contains four species, also with representatives from both groups 1 and 2 (*A. tubulatus*, *A. involutum*, *A. flabellum* and *A. gardineri*, respectively). To date no species have been recorded for the Indo-Malay archipelago,

Australasia or the Pacific islands apart from a deeper water record from New Caledonia.

Distribution of *Raspaxilla* is different to that of *Aulospongus* (Fig. 35). *Raspaxilla* species are virtually centred on the Pacific rim, distributed in tropical, temperate and antiboreal waters, extending into the subantarctic islands and Antarctica peninsula. To date there are no records of *Raspaxilla* species from either the Atlantic or Indian Oceans. Similarly, *Hemectyon* is so far known only from the type species in the Caribbean. The species and genus allocation of Pulitzer-Finali's (1994) specimen from the W Indian Ocean (Fig. 32, number 2), is presently unknown, but clearly not conspecific to *E. (H.) hamatum*.

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