

Axinellida (Porifera : Demospongiae) from the New Caledonia Lagoon

John N. A. Hooper^A and Claude Lévi^B

^A Queensland Museum, P.O. Box 3300, South Brisbane, Qld 4101, Australia.

^B Laboratoire de Biologie des Invertébrés marins et Malacologie,
Muséum national d'Histoire naturelle, 57, rue Cuvier, 75005 Paris, France.

Abstract

Sixteen species of axinellid demosponges, including seven new species and seven new locality records, are described from the shallow-water New Caledonian lagoon and reefs [families Axinellidae (12 species, *Cymbastela*, *Reniochalina*, *Axinella*, *Phakellia*, *Stylissa*, *Ptilocaulis*, *Pseudaxinella*, *Raphoxya*) and Desmoxyidae (4 species, *Myrmekioderma*, *Higginsia*)], bringing the total number of described axinellid species in this region to 25. Brief revisions are provided for several of these genera, based primarily on the Indo-west Pacific fauna, in order to place these New Caledonian species. Non-endemic New Caledonian axinellids belong predominantly to the north-eastern Australian (Solanderian province) and Indo-Malay fauna, usually representing the easternmost extent of these species' distributions in the Indo-west Pacific. Two species, *Axinella carteri* (Dendy) and *Astrosclera willeyana* Lister, were found to be truly widely distributed throughout the Indo-Pacific, typically associated with coral reefs; other previously suspected widely distributed species were generally found to be allopatric, cryptic sibling species related to the tropical Australasian fauna.

Introduction

Prior to the present work, only 11 species belonging to the (polyphyletic) order Axinellida had been described from the New Caledonian region: five in the family Axinellidae (four of which are apparently endemic and one also known from the Indo-Malay archipelago), one in Desmoxyidae (also known in northern New Zealand), one in Trachycladidae (also known from New Zealand and south-eastern and south-western Australia), two in Agelasidae [now considered to be a separate order: Hartman 1982 (one of which is apparently endemic)], and two hypercalcified 'sclerosponges' described by Vacelet (1981) which have also been suggested as having possible affinities with the Agelasida (e.g. Vacelet 1981; van Soest 1984). However, these species represent only a small proportion of the axinellid fauna known to live in this region; furthermore, 6 of these 11 described species are strictly deeper-water taxa, collected from the shelf and slope to the south of New Caledonia. Thus, the shallow-water axinellid sponge fauna is virtually undescribed, although many species have already been collected by ORSTOM.

The present paper describes 16 species of shallow-water sponges in the families Axinellidae and Desmoxyidae living in the lagoon and coral reef habitats surrounding the island. These species represent some of the more visible axinellids in New Caledonian shallow-water habitats, although there are still many more taxa yet to be described from this region (Lévi, unpublished data).

This is the second of a series of papers on the taxonomy of demosponges in the lagoon and outer reefs of New Caledonia (Hooper and Lévi 1993); a third contribution will examine the biogeographical relationships of the New Caledonian Microcionidae, Raspailiidae and Axinellidae (Hooper and Lévi, unpublished data). These papers represent the results of a collaborative investigation amongst several sponge biologists (C. Battershill, P. Bergquist, J. Fromont, J. Hooper, M. Kelly-Borges, C. Lévi, J. Vacelet, C. Wilkinson), to document the major components of this sponge fauna, arising from a series of workshops jointly funded by ORSTOM and DITAC. The eventual aim of this investigation is to produce a comprehensive taxonomic inventory of the islands' shallow-water sponges, and an authoritative lay field guide to this fauna.

Unlike the previous study on Poecilosclerida (Hooper and Lévi 1993) for which there were good contemporary revisions for most of the higher taxa, the axinellids have not been substantially revised, and hence some level of revision was necessary for many of the genera in order to place the New Caledonian species. These revisions, however, are certainly incomplete and relatively cursory due to the unavailability of much of the relevant type material required to undertake this considerable task.

Methods

Methods used to prepare and examine sponges for both light microscopy and scanning electron microscopy follow the procedures described in Hooper (1991). Measurements are based on examination of 25 random samples of each spicule category for each specimen, and are cited as range (and *mean* in parentheses). Abbreviations used in the text are as follows: AIMS, Australian Institute of Marine Science, Townsville; AM, Australian Museum, Sydney; BMNH, The Natural History Museum, London; CMMI, Canterbury Museum, Marine Invertebrate collection, New Zealand; CSIRO, Commonwealth Scientific and Industrial Scientific Organisation, Division of Fisheries, Hobart; DITAC, Commonwealth of Australia Department of Industry, Technology and Commerce, Canberra; ICZN, International Commission for Zoological Nomenclature (Anon. 1985); LFM, Merseyside County Museums, Liverpool (formerly Liverpool Free Museum); MMBS, Mukaishima Marine Biological Station, Faculty of Science, Hiroshima University, Onomichi; MNHN, Muséum National d'Histoire Naturelle, Paris; MHNG, Muséum d'Histoire Naturelle de Genève, Geneva; NCI, U.S. National Cancer Institute shallow-water collection contract (Australian Institute of Marine Science, Townsville; primary collections in AIMS, NTM and QM, duplicates and fragments in USNM); NMNZ, National Museum of Natural History, Wellington; NMV, Museum of Victoria, Melbourne; N.S.W., New South Wales; NTM, Northern Territory Museum of Arts and Sciences, Darwin; ORSTOM, Institut Français de Recherche Scientifique pour le Développement en Coopération, Centre de Nouméa; QFS, Queensland Fisheries Service; Qld, Queensland; QM, Queensland Museum, Brisbane; SM, Strasbourg Museum, France; SMF, Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C.; ZMB, Zoologisches Museum für Naturkunde an der Humboldt-Universität zu Berlin, Berlin; ZMC, Zoologisk Museum, Copenhagen.

Systematics

Order AXINELLIDA Carter

Family AXINELLIDAE Ridley & Dendy

Definition

Axinellid sponges which generally lack microscleres, although several genera (*Dragmaxia*, *Dragmacidon*, *Dragmatella*, *Dragmatyle*, *Raphoxya*, *Raspaiella* and *Tragosis*) may have raphides, occurring singly or grouped into bundles (trichodragmata). Skeleton typically divided into distinct axial and extra-axial components; main skeletal tracts, composed of spongin fibres enclosing megascleres, usually condensed in axis; extra-axial region becoming plumose or plumoreticulate towards surface. However, many exceptions to this pattern shown in this family, and affinities of many species are still contested but poorly understood. Megascleres are monactinal, diactinal, or both, and sinuous spicules (usually strongyles or oxeas) reappear throughout many genera. Axinellidae frequently have branching growth form but funnel-shaped, flabellate, tubular, and massive forms also occur (modified from Wiedenmayer 1989).

Remarks

This family contains a large and heterogeneous assemblage of taxa, with about 50 nominal genera included, and is in urgent need of an extensive, detailed revision; hence, a comprehensive definition of the family is provided here. The heterogeneity of the family has been indicated by several authors (e.g. Bergquist and Hartman 1969; van Soest *et al.* 1990), and Hooper and Bergquist (1992) questioned whether the family was in fact monophyletic. Hooper *et al.* (1992) suggested that the Axinellidae should probably be subdivided further, although they did not propose how this should be done. Many species show a number of similarities with members of the order Halichondrida (skeletal structure, spicule geometry), and indeed a recent revision of that order (van Soest *et al.* 1990) indicated that the Axinellidae should be placed there. However, this hypothesis is premature and uncorroborated by any other evidence, having no greater or lesser support than the existing arrangement. Thus, the higher systematic relationships of the family are still not clear and, for the time being, the family is retained in a polyphyletic order, Axinellida.

Members of this large family occur from polar regions to the tropics, and from tidal habitats to at least 4400 m depth (Hartman 1982). Many species of Axinellidae are known to live in the New Caledonian region (Lévi, unpublished data), but so far only five of these have been published from this region. These are: *Ptilocaulis fusiformis* Lévi, 1967, from the Bay St Vincent (apparently endemic); *Cymbastela cantharella* (Lévi, 1983) from outer reef slopes of New Caledonia (endemic); *Axinella lifouensis* Lévi & Lévi, 1983, from deeper-waters (>350 m) to the south of the island (endemic); *Phakellia columnata* (Burton, 1928) also from deeper-waters (>300 m) (also known from the Andaman Sea); and *Reniochalina plumosa* (Lévi & Lévi, 1983), a new combination here, from deeper-waters (>400 m) (endemic).

Genus *Cymbastela* Hooper & Bergquist

Pseudaxinyssa (in part). — Bergquist and Tizard, 1967: 190; Lévi, 1983: 719.

Cymbastela Hooper & Bergquist, 1992: 103 [type species *Pseudaxinyssa stipitata* Bergquist & Tizard, 1967: 189 (holotype AM Z3101)].

Diagnosis

Typically stalked, cup-shaped, thinly lamellate growth form. Ectosome with or without specialised skeleton of smaller oxeas. Choanosomal skeleton with compressed reticulate axial region, in which major tracts run longitudinally through lamellae, and with gradually ascending, diverging, radial, plumose or plumo-reticulate extra-axial region, in which tracts become plumose and project through surface. Spongin fibres well developed, cored by oxeas, frequently with telescoped points. Predominantly autotrophic, most species containing symbiotic cyanobacteria. Oviparous (from Hooper and Bergquist 1992).

Remarks

This genus was recently erected for atypical species previously referable to *Pseudaxinyssa* Burton, including thinly lamellate, frequently cup-shaped, predominately coral reef species. The genus is known only from Australasia, with seven species described including one endemic to New Caledonia, *C. cantharella*. A second species from this region is described below.

Cymbastela cantharella (Lévi) (Figs 1–2)

Pseudaxinyssa cantharella Lévi, 1983: 719–22, fig. 1, pl. 1.

Cymbastela cantharella. — Hooper and Bergquist, 1992: 119–20, figs 12–14, table 1.

Material Examined

Holotype. MNHN DCL3141: outer reef, SW. coast New Caledonia, 22°20'S., 166°13'E., 40 m depth, coll. ORSTOM.

New Caledonian material. ORSTOM R1261 (fragment QM G300015): stn 198, pinnacle S. of Canyon Central, Chenal des Cinq Milles, 22°30'4"S., 166°45'1"E., 25 m depth, 15.ii.1978, coll. G. Bargibant, SCUBA; ORSTOM R163: stn 116, SW. pointe, Baie de Prony, 22°21'8"S., 166°49'9"E., 40 m depth, 30.vi.1976, coll. P. Laboute, SCUBA.

Comparative material. Refer to Hooper and Bergquist (1992) for additional material from New Caledonia.

Description

Colour. Pale orange-brown alive (Munsell 2·5-7·5 YR 8/10), beige in ethanol.

Shape. Short, erect cup-shaped or vasiform sponges, up to 150 mm high, 170 mm maximum diameter, with relatively thick lamellae, up to 6 mm diameter, usually with convoluted margins, occasionally with secondary cups or lamellae growing inside primary cup, often with buttresses and exterior secondary projections, and with a short, cylindrical, basal stalk, up to 40 mm long, 17 mm diameter.

Surface. Predominantly smooth, with distinct interior (inhalant, osculiferous) and exterior (smooth but uneven, buttressed) faces of lamellae. Oscules small, up to 2 mm diameter, about 2 mm apart, each surrounded by slightly raised membranous lip. Texture firm, flexible, slightly compressible.

Ectosome. Membraneous, with heavy collagen, through which choanosomal oxeas protrude, individually or in paucispicular plumose bundles, arising from ascending radial tracts in peripheral skeleton.

Choanosome. Choanosomal skeleton plumo-reticulate, without axial compression or axial and extra-axial differentiation. Two components of choanosomal skeleton present: longitudinal (radial) spongin fibres run through lamellae, cored by multispicular tracts of oxeas, plumose near periphery; transverse uni- or paucispicular tracts of oxeas interconnecting radial fibres; overall skeleton appears nearly disorganized, almost halichondroid. Mesohyl with heavy collagen.

Megascleres. Oxeas short, slender, slightly curved, symmetrical, occasionally asymmetrical, tapering, fusiform, usually with slightly telescoped points. Length 143-(207.1)-245 μm , width 2.5-(7.6)-12 μm .

Microscleres. Absent.

Distribution

Known only from the New Caledonia region.

Remarks

The description given above is mainly condensed from Hooper and Bergquist's (1992) more comprehensive redescription of the species, as the present study includes only one

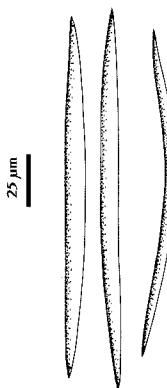


Fig. 1. *Cymbastela cantharella* (Lévi): specimen ORSTOM R1261, structural oxeas.

previously unpublished specimen from the south-west New Caledonia lagoon. This species has also been illustrated in more detail in this earlier work, and present illustrations are provided for comparative purposes.

Cymbastela cantharella differs from other tropical species of the genus by its atypical orange pigmentation in life (most other species are green and mauve), prominent surface sculpturing on the inner (ocular) face of lamellae, having a dense radial-plumose skeleton, with a secondary paucispicular secondary reticulate skeleton, together producing a nearly halichondroid appearance, a radial-plumose ectosomal skeleton, and specific dimensions of its oxeas (refer to Hooper and Bergquist 1992: table 1). The species is most similar to *C. stipitata*, both having thinly flabellate, irregular, buttressed surface processes, and similar geometry of oxea megascleres, but the two species differ markedly in most other features.

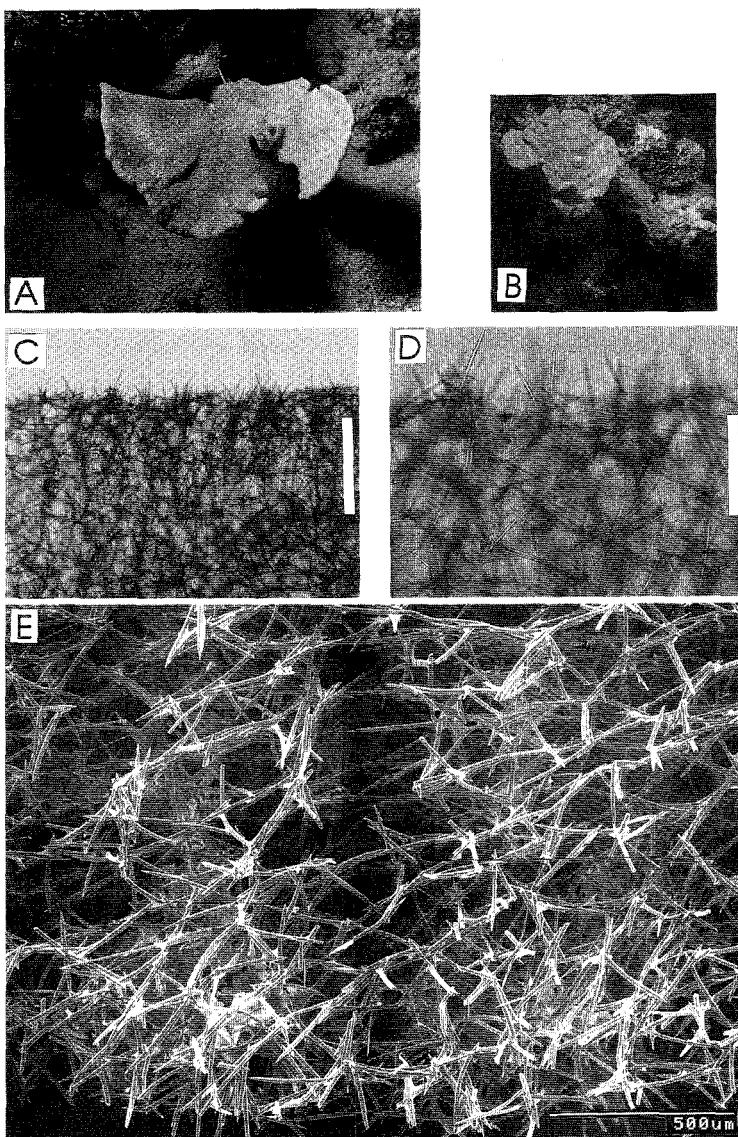


Fig. 2. *Cymbastela cantharella* (Lévi): A, specimen ORSTOM R1261 *in situ* (photo C. Debitus); B, specimen ORSTOM unregistered (stn 163/1) *in situ* (photo P. Laboute); C, skeleton [specimen QM G300015 (ORSTOM R1261)] (scale = 500 μm); D, peripheral skeleton (scale = 200 μm); E, SEM skeletal structure (specimen QM G300004) (scale = 500 μm).

Cymbastela concentrica (Lendenfeld)

(Figs 3-5, Table 1)

Antherochalina concentrica Lendenfeld, 1887: 788, pl. 22, fig. 42.*Cymbastela concentrica*.—Hooper and Bergquist, 1992: 114-19, figs 9-11, table 1.*Material Examined*

Lectotype. AM Z1993: Port Molle (now Airlee Beach), Qld, 20°13'S., 148°49'E., no other details known.

New Caledonian material. QM G301229 (ORSTOM R180): stn 109, Baie des Citrons, Noumea, 22°18'0"S., 166°25'1"E., 10 m depth, 31.v.1976, coll. P. Laboute, SCUBA; QM G301230, G301264, G301266 (ORSTOM R153): stn 180, S. of sand cay, Ilôt l'Areignière, 22°20'0"S., 166°19'1"E., 12 m depth, 4.v.1977, coll. P. Laboute, SCUBA; ORSTOM R363: stn 150, S. of entrance, Baie St Vincent, 22°02'2"S., 165°59'5"E., 18 m depth, 9.ix.1976, coll. P. Laboute, SCUBA; ORSTOM 'cfR363': stn 148, NE. point, Ilôt Mboa, 22°08'3"S., 166°09'3"E., 13 m depth, 9.ix.1976, coll. P. Laboute, SCUBA; ORSTOM 'cfR363': stn 154, channel between Ilôt Puen and Récif, 21°59'0"S., 165°57'1"E., 14 m depth, 15.ix.1976, coll. P. Laboute, SCUBA; QM G301272, G301268, (ORSTOM R180), ORSTOM R181: stn 110, SE. Ilôt Rédika, 22°31'1"S., 166°36'0"E., 15-19 m depth, 3-8.vi.1976, coll. P. Laboute, SCUBA; QM G301330: Croissant-Larégrière, Ilôt Maitre, off Noumea, 22°20'2"S., 166°22'5"E., 20 m depth, 13.x.1992, coll. J. N. A. Hooper, SCUBA.

Comparative material. QM G301233: Davies Reef, Great Barrier Reef, Qld, 18°50'S., 147°39'E., 22 m depth, coll. C. R. Wilkinson, AIMS, 24.iii.1982, SCUBA; QM G301234: same locality, 15 m depth, coll. S. Seddon, 13.ix.1991, SCUBA; AIMS RA42-PS (NTM Z2729): Myrmidon Reef, Great Barrier Reef, Qld, 18°10'S., 147°23'E., 15 m depth, 1.i.1985, coll. C. R. Wilkinson, AIMS, SCUBA; NTM Z3170: Blue Lagoon, Lizard I., Great Barrier Reef, Qld, 14°40'S., 145°28'E., 10-20 m depth, 1.i.1987, coll. A. W. D. Larkum, SCUBA. [Refer to Hooper and Bergquist (1992) for additional material from eastern Australia.]

Description

Colour. Pale beige, olive-brown or reddish brown alive (Munsell 2·5Y 8/6-2·5YR 4/4); chlorophyll pigments present.

Shape. Growth form predominantly vasiform, but varying from more-or-less symmetrical cup-shaped with small basal stalk, to vasiform with symmetrical or asymmetrical lamellae,

Table 1. Comparison in spicule dimensions between known specimens of *Cymbastela concentrica*

All measurements given in micrometres, and expressed as minimum-(*mean*)-maximum range of measurement (comparative data from Hooper and Bergquist 1992). *N*=25 for each specimen

Material (Locality)	Oxeas	
	Length	Width
AM Z1993 (holotype) (Airlee Beach, 20°S.)	172-(239·6)-305	2·5-(9·5)-16
NTM Z3169 (Lizard I., 14°S.)	103-(145·6)-172	2·5-(3·7)-6
QM G301233 (Davies Reef, 18°S.)	138-(165·0)-184	4·0-(5·2)-6·0
QM G301234 (Davies Reef, 18°S.)	92-(118·6)-146	3·5-(5·2)-8·0
ORSTOM R180 (Noumea lagoon, 22°S.)	107-(126·4)-142	3·0-(4·1)-5·0
ORSTOM R153 (Noumea lagoon, 22°S.)	96-(115·2)-132	3·0-(4·9)-6·5
QM G300003 (Moreton I., 26°S.)	67-(86·8)-104	2·5-(3·4)-4·5

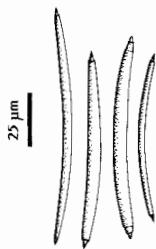


Fig. 3. *Cymbastela concentrica* (Lendenfeld): specimen QM G301229, structural oxeas.

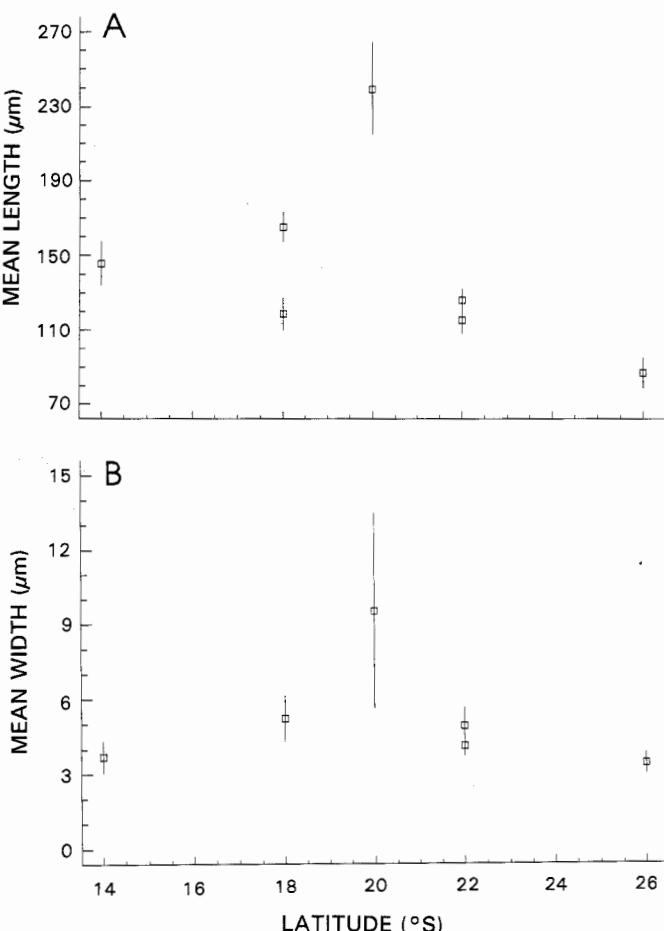


Fig. 4. *Cymbastela concentrica* (Lendenfeld), comparison of spicule dimensions with latitudinal distribution of samples: *A*, mean length; *B*, mean width.

to thickly encrusting plate-like, attached directly to substrate. Size up to 150 mm high, 140 mm maximum width. Lamella thickness variable, ranging from card thin to thick and rubbery, 1·0–3·5 mm thick.

Surface. Typically with convoluted, multiple lamellae inside cups or with digitate projections on exterior surface, but some specimens lack any surface ornamentation. Lamellae smooth, even or irregular. Texture flexible, compressible, velvet-like.

Ectosome. Membraneous without specialised skeleton, but microscopically villose from protruding spicules from peripheral skeleton, usually forming multispicular plumose brushes.

Choanosome. Reticulate to plumo-reticulate mineral and fibre skeleton, with poorly differentiated axial and extra-axial regions. Reticulate skeleton predominant over plumose portion. Fibres in axial region only slightly condensed, forming an open reticulation, cored by uni- or paucispicular tracts of spicules. Extra-axial fibres reticulate, slightly plumose, paucispicular, whereas peripheral skeleton clearly diverges into plumose multispicular spicule bundles. Spongin fibres well developed; collagen abundant in mesohyl.

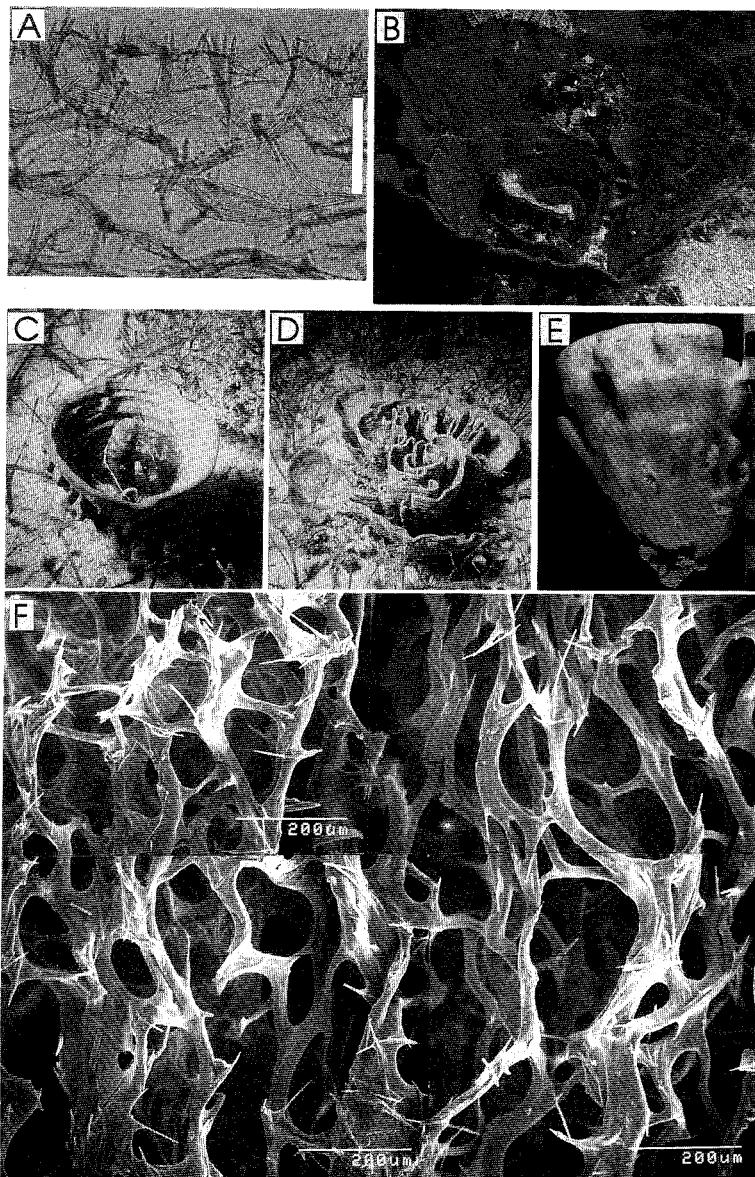


Fig. 5. *Cymbastela concentrica* (Lendenfeld): *A*, peripheral skeleton [specimen QM G301229 (ORSTOM R180)] (scale = 200 μm); *B*, specimen ORSTOM R180 *in situ* (photo P. Laboute); *C*, specimen QM G301230 (ORSTOM R153) *in situ* (photo G. Bargibant); *D*, specimen ORSTOM 'cFR153' *in situ* (photo G. Bargibant); *E*, preserved specimen QM G301229; *F*, SEM skeletal structure (QM G301230) (scale = 200 μm).

Megascleres (refer to Table 1 for dimensions). Oxeas vary considerably in size between specimens, usually slender, fusiform, straight or slightly curved, symmetrical, typically with very faintly telescoped points.

Microscleres. Absent.

Distribution

Northern, central and southern Queensland, and south-west New Caledonia, found in the lagoon, inshore fringing reef or platform coral reef fauna, 10–22 m depth.

Remarks

This is a new locality record for this species in the New Caledonian region. Although *C. concentrica* has recently been comprehensively redescribed and illustrated (Hooper and Bergquist 1992), the description given above is based on a number of previously undescribed specimens from both the Great Barrier Reef and New Caledonia. The present records, together with material described by Hooper and Bergquist (1992), show that the species is widespread throughout all sections of the Great Barrier Reef, and it is possible that the species will eventually be found to inhabit many other islands and reefs throughout the Coral Sea.

This species is remarkable for the heterogeneity in its spicule dimensions, unlike any of the other known species of the genus. Hooper and Bergquist (1992) suggested that this variability may correspond to latitudinal gradients in distribution of the species, although re-examination of spicule dimensions from all known material (Fig. 4) shows no such trend. It is possible that we have two or more sympatric sibling species presently included in *C. concentrica* but present morphometric characters cannot clearly distinguish these morphotypes.

Genus *Reniochalina* Lendenfeld

Reniochalina Lendenfeld, 1888: 82.—Hallmann, 1914b: 346; Wiedenmayer, 1989: 48 [type species *Reniochalina stalagmitis* Lendenfeld, 1888: 82 (lectotype BMNH 1887.4.27.122)].

Axiamon Hallmann, 1914c: 440.—de Laubenfels, 1936: 130 [type species *Axiamon folium* Hallmann, 1914c: 440 ('syntypes' AM G9004, B5478)].

Diagnosis

Arborescent, frondose, rameous or lobate growth forms; typically with tubercular, ridged or closely conulose surface; with plumo-reticulate skeletal structure, mainly in the form of ascending skeletal bundles, and without condensation of axial skeleton or differentiation between axial and extra-axial components; spiculation with interchangeable styles, oxeas and anisoxeas in approximately equal proportions and similar size, without differential distribution within the skeleton (modified from Wiedenmayer 1989).

Remarks

The above diagnosis is for the nominal genus *Axiamon*, since Lendenfeld's diagnosis of *Reniochalina* is grossly inadequate. Furthermore, this genus is best known under its junior synonym of *Axiamon*, and further comment is required on that synonymy. Hallmann (1914b: 346) noted that the primary description of Lendenfeld's *Reniochalina stalagmitis* was erroneous; consequently, *Reniochalina* was considered to be a *genus dubium*. Hallmann (1914c: 440–1) subsequently described a specimen under the name of *Axiamon folium* (from Western Australia), which became the type species of the genus *Axiamon*, whilst at the same time he recognised that it was probably identical to Lendenfeld's *R. stalagmitis* (from the Illawarra region, N.S.W.). De Laubenfels (1936: 47) concurred with Hallmann. However, although Lendenfeld's (1888) definition of *R. stalagmitis* was not entirely accurate, differing significantly from the actual characteristics of the species (Whitelegge 1902: 283), it is still true that Lendenfeld's published name has priority since it is the earliest available for the species (Wiedenmayer 1989): hence, *Axiamon* is an objective synonym of *Reniochalina*.

Prior to the present study, only four nominal species of the genus were known, but of these species only two are valid. Two other species are also referred to the genus in the present study. The genus now contains four valid species, all from the Indo-west Pacific region: *R. condylia*, sp. nov., from the shallow-water New Caledonian fauna (see below) (Figs 7-8); *R. plumosa* (Lévi & Lévi, 1983), comb. nov. (holotype MNHN DCL2972), from the deeper-water New Caledonian fauna (Fig. 6C-D); *R. sectilis* Wiedenmayer, 1989: 49, pl. 4, fig. 1, pl. 23, fig. 1 (holotype NMV F51962), from south-east Australia (not figured here); and the type species *R. stalagmitis* Lendenfeld, 1888, from north-west and north-east Australia (Fig. 6A-B) [with synonyms *R. lamella* Lendenfeld, 1888 (holotype AM B5478 from Western Australia), and *Axinella echidnaea* sensu Ridley (1884; specimen BMNH 1882.2.23.261 from north-west Australia) and Hentschel (1912; specimen SMF1687 from southern Indonesia) not *Spongia echidnaea* Lamarck, 1814 (Wiedenmayer 1989)]. Recent collections from tropical Australasia also discovered another six undescribed species referable to this genus, which will be described elsewhere in the future.

Reniochalina is characterised by its plumo-reticulate skeletal architecture, and in having anisoxeas, sometimes with spinose extremities. The skeletal architecture of *R. stalagmitis* is certainly atypical of Axinellidae, and the existence of such structures makes the task of satisfactorily diagnosing the family a difficult one, but that feature is certainly not unique in the family (e.g. *Phycopsis*). *Reniochalina* should also be compared to *Axinosia* in skeletal construction, and to *Ptilocaulis*, from which it differs mainly in lacking axial skeletal condensation, or differentiation between axial and extra-axial skeletons, and also in lacking telescoped endings on spicules. Wiedenmayer (1989) suggested that the variability in spiculation known to occur in *Reniochalina* (e.g. Hallmann 1914c: 443), and the confused skeletal architecture in some species (e.g. Wiedenmayer 1989), raises doubts about which characters should be treated as most important in the systematics of axinellid genera (spicule geometry or skeletal structure) since these appear to occur in all combinations (cf. *Axinosia* and *Pseudaxinella*, for example). It is clear that an evaluation of those characters in the taxonomy of these genera is central to a revision of Axinellidae, but a satisfactory resolution of these systematics will probably not be possible without additional (non-skeletal) evidence.

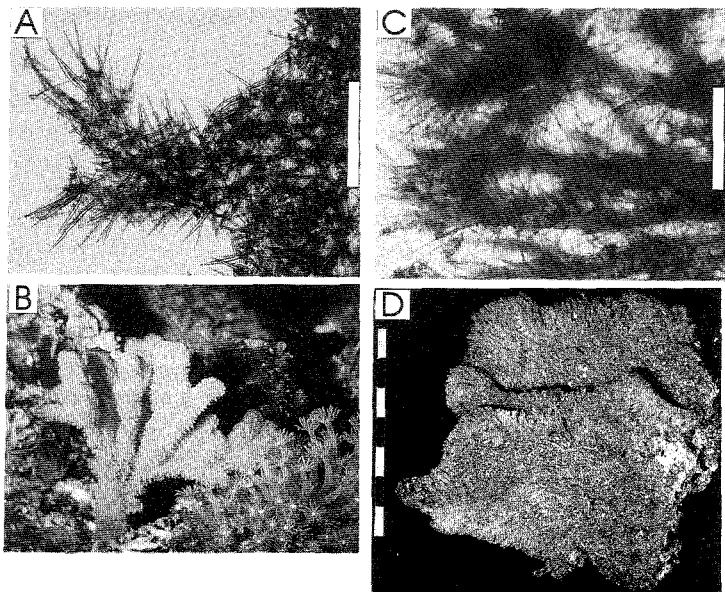


Fig. 6. *Reniochalina* spp.: A, *Reniochalina stalagmitis* Lendenfeld, peripheral skeleton (lectotype BMNH 1887.4.27.122) (scale = 500 μm); B, specimen NTM Z1107 *in situ* (photo J. N. A. Hooper); C, *Phakellia plumosa* Lévi and Lévi, peripheral skeleton (paratype MNHN DCL2974) (scale = 200 μm); D, paratype.

If the evidence cited for *Reniochalina* were to be carried over to other genera, (*viz.* the unstable nature of axial and extra-axial differentiation, and the presence or absence of certain categories of megascleres), then many of the nominal axinellid genera would have to be merged.

Reniochalina condylia, sp. nov.

(Figs 7-8)

Material Examined

Holotype. QM G300020 (ORSTOM R1223); stn 184, SE. of Ilôt Ua, New Caledonia lagoon, 22°42'1"S., 166°49'0"E., 16 m depth, 8.vi.1977, coll. G. Bargibant, SCUBA.

Description

Colour. Pale orange alive (Munsell 7·5YR 8/10), pale grey-brown in ethanol.

Shape. Thickly encrusting plate, 260 mm diameter, 10-35 mm thick, with prominent low, conical-bulbous, digitate projections on upper surface; bulbous digits 14-23 mm high, 10-14 mm maximum diameter, each with a single, large osculum on apex, 3-5 mm diameter.

Surface. Membraneous (where intact in preserved condition), even, porous upper surface, without ornamentation other than large bulbous digits. Subdermal spicule bundles clearly visible below translucent dermal membrane.

Ectosome. Without specialised spiculation; with plumose brushes composed of choanosomal megascleres protruding slightly through surface, up to about 80 µm from surface, but presumably these are confined to within the dermal membrane when intact. Mesohyl in peripheral skeleton with heavier, granular collagen as compared with the deeper choanosomal region.

Choanosome. Skeletal structure plumo-reticulate, without axial compression or differentiation between axial and extra-axial regions. Skeleton divided into ascending, multi-spicular, diverging primary skeletal tracts, up to 150 µm diameter, with well-developed plumose brushes at surface, and transverse, paucispicular, secondary spicule tracts, 20-40 µm diameter, more-or-less interconnecting primary tracts. Skeletal meshes 150-300 µm diameter, with few loose spicules between tracts. Spongin fibres very lightly invested with

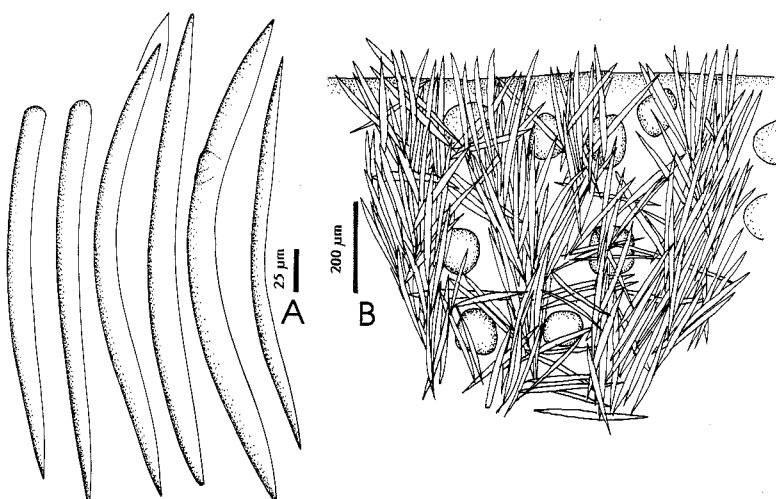


Fig. 7. *Reniochalina condylia*, sp. nov., holotype QM G300020: *A*, oxeas, styles and modifications; *B*, section through peripheral skeleton.

spongin, seen clearly only between major spicule tracts. Choanocyte chambers oval, 80–170 μm diameter. Mesohyl with light collagen.

Megascleres. Single category of structural megasclere present, varying from oxeas to styles, with various intermediate forms also present. Spicules consist of predominantly slightly curved, slightly asymmetrical oxeas; less frequently styles with evenly rounded bases and slightly curved towards basal end; rarely asymmetrical anisoxeas. Points mostly fusiform, tapering, sharply pointed; occasionally fusiform rounded. Length 208–(259·8)–289 μm , width 10–(12·2)–14 μm .

Microscleres. Absent.

Distribution

Known only from the south-west lagoon of New Caledonia, 16 m depth, on coral rubble substrate.

Remarks

The present species is most similar to *R. stalagmitis* in its skeletal structure (plumose spicule bundles) and spicule geometry (oxeas, styles and anisoxeas), although in *R. stalagmitis* many spicules have spinous extremities, particularly the anisoxeas. *Reniochalina condylia*, sp. nov., is also very similar to two undescribed species of *Reniochalina* from western and north-western Australia (*Reniochalina* provisional species numbers 353, 798), having virtually identical skeletal architecture and spicule geometry, but in both cases these undescribed species have quite different external morphology and surface ornamentation, and there are also differences in the specific dimensions of megascleres (broader and shorter in the two undescribed species). These new species will be contrasted further with other described species in a future revision of *Reniochalina*.

The deeper-water *R. plumosa* from New Caledonia has a plumo-reticulate skeleton composed mostly of ascending discrete skeletal columns, cored by sharply pointed oxeas incompletely separated into two size categories, 112–(284·2)–372 \times 9–(11·0)–15 μm (Fig. 6C).

Etymology

Named for the conical digitate surface projections; Lat. *condylus*, knob, prominence.

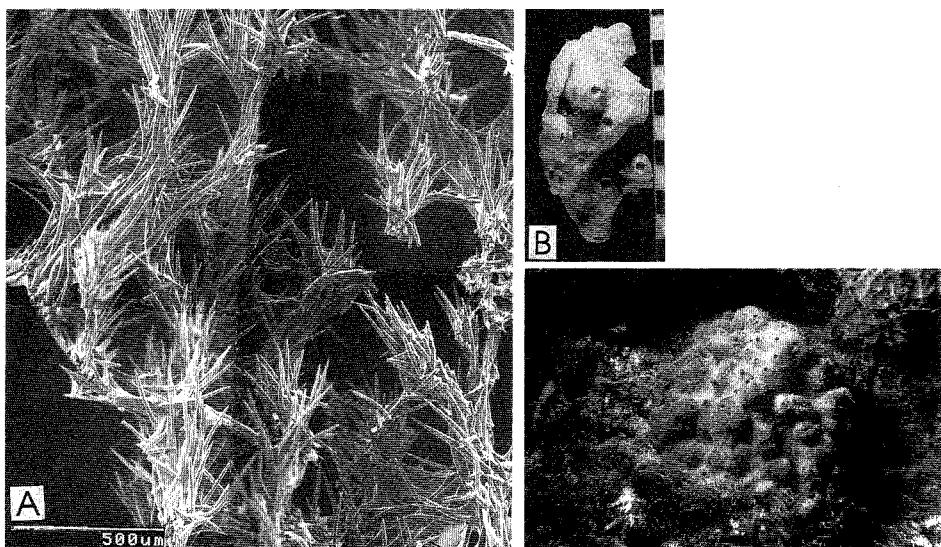


Fig. 8. *Reniochalina condylia*, sp. nov.: A, SEM skeletal structure [holotype QM G300020 (ORSTOM R1223)] (scale = 500 μm); B, holotype; C, holotype *in situ* (photo P. Laboute).

Genus *Axinella* Schmidt

Axinella Schmidt, 1862: 60.—Gray, 1867: 513; Ridley and Dendy, 1887: 178; Dendy, 1905: 193; Dendy, 1922: 114; Vosmaer, 1912: 308, 318; Topsent, 1928: 37–8; Bergquist, 1970: 14; Bergquist, 1978: 167, 192; Lévi, 1973: 605; Pansini, 1983: 79–98 [type species *Axinella polypoides* Schmidt, 1862: 62 (holotype possibly SM, 'schizotypes' MNHN DCL1148L, BMNH 1867.7.26.81) (de Laubenfels 1936)].

Chainissa Lendenfeld, 1887: 771.—Burton, 1927: 502 (type species *Isodictya dissimilis* Bowerbank, 1866) (de Laubenfels 1936).

Astrospongia Gray, 1867: 514 (objective synonym of *Axinella*).

Diagnosis

Variable growth form, ranging from digitate to flabellate; surface typically hispid, conulose; choanosome always with some axial compression of spongin fibres and spicules; with or without differentiated primary and secondary fibre elements; extra-axial skeleton plumose or plumo-reticulate, diverging single or bundles of spicules; ectosome without specialised spiculation, although extra-axial megascleres usually protrude through surface; megascleres oxeas, styles, occasionally strongyles, in various combinations; microscleres may include raphides or microraphides, although these do not appear to be widely distributed within the genus [compiled from Vosmaer (1912) and Donadey *et al.* (1990)].

Remarks

Schmidt (1862) characterised *A. polypoides* in having a peculiar distribution of oscules, for which Gray (1867) erected *Astrospongia*, but Vosmaer (1933, 1935a, 1935b) correctly surmised that the character was unlikely to be of much systematic importance, and in any case he noted that it also occurred in other axinellid genera. Other authors who have dealt with this genus (e.g. Ridley and Dendy 1887; Thiele 1903; Vosmaer 1912, 1935a; Dendy 1922; Babic 1922; Topsent 1934; Vacelet 1961, 1969; Bergquist 1970; Pansini 1983) agree that it is still problematic, with no completely satisfactory or clearly discriminatory diagnosis yet developed. Part of the problem arises from the existence of species with predominantly stylote spiculation (e.g. Dendy 1922), whereas typically the genus has both oxeas and styles of equal size and proportion (e.g. Vosmaer 1935a; Wiedenmayer 1989). Vosmaer (1935a) and Pansini (1983) suggest further that intra-specific variability is known for the type and other nominal *Axinella* species, whereby both oxeas and styles may be modified to anisoxeote or anisostyloform forms, in some cases almost completely. Consequently, the placement of species with a reticulate axially condensed skeleton, and reticulate to plumo-reticulate extra-axial skeleton of oxeas and styles in *Axinella* is relatively easy (e.g. *A. polypoides*; Fig. 10C), whereas species such as *A. spiculifera* (Lamarck), *A. profunda* Ridley and Dendy, and *A. erecta* Carter have greatly modified spiculation, and could be easily placed in genera such as *Phakellia* or *Reniochalina*.

The literature contains records of 39 species from the Australasian region (including New Zealand, New Caledonia, Papua New Guinea and southern Indonesia), that have been referred to *Axinella* at one time or another but, of these, only 18 appear to be correctly placed here. The type material of many of these species has not yet been located, so a specific revision of the Indo-west Pacific fauna in this genus is not yet possible. However, valid species of *Axinella* from this region are presently thought to be: *Phakellia aruensis* Hentschel, 1912 (holotype SMF 953; Fig. 9A–B), from southern Indonesia, north-west Australia around to the Great Barrier Reef (Hentschel 1912; Bergquist *et al.* 1980; Hooper *et al.* 1992); *Axinella australiensis* Bergquist, 1970 (holotype NMNZ Por.18 [not seen]), from New Zealand; *Axinella brondstedi* Bergquist, 1970 (holotype probably ZMC [not seen]), with synonym *Axinella verrucosa sensu* Brondsted, 1923 (preocc.) from New Zealand; *Acanthella carteri* Dendy, 1889, from New Caledonia (Lévi 1979) (Fig. 11–12; see below); *Axinella clathrata* Dendy, 1897a (holotype NMV G2330 [not seen]), from south-east Australia; *Phakellia crassa* Carter, 1885 (holotype BMNH 1886.12.15.129), from south-east Australia (Fig. 9C–D); *Acanthella euctimena* Hentschel, 1912 (holotype SMF 1012; Fig. 9E–F) from southern Indonesia; *Axinella lifouensis* Lévi & Lévi, 1983 (holotype

MNHN DCL2943; Fig. 9G–H), from deeper-waters off New Caledonia; *Axinella globula* Brondsted, 1924 (holotype probably ZMC [not seen]), from New Zealand (Bergquist 1970); *Axinella kirkii* Dendy, 1897a (lectotype NMV G2370 [not seen]), from south-east Australia; *Axinella meloniformis* Carter, 1885 (holotype BMNH 1886.12.15.117; Fig. 9I–J), from south-east Australia (considered atypical of the genus [Vosmaer 1912], but skeletal structure is most similar to *Axinella* of all other genera); *Axinella retepora* (Lendenfeld, 1887) (lectotype BMNH 1886.8.27.417; Fig. 10A–B) from Torres Strait, Qld (not Port Phillip, Vic., as published); *Axinella richardsoni* Bergquist, 1970 (holotype NMNZ Por.19 [not seen]), from New Zealand; *Axinella sinclarii* (Gray) (holotype unknown) from New Zealand (Dendy 1897b; Bergquist 1970); *Axinella torquata* Brondsted, 1923 (holotype probably ZMC

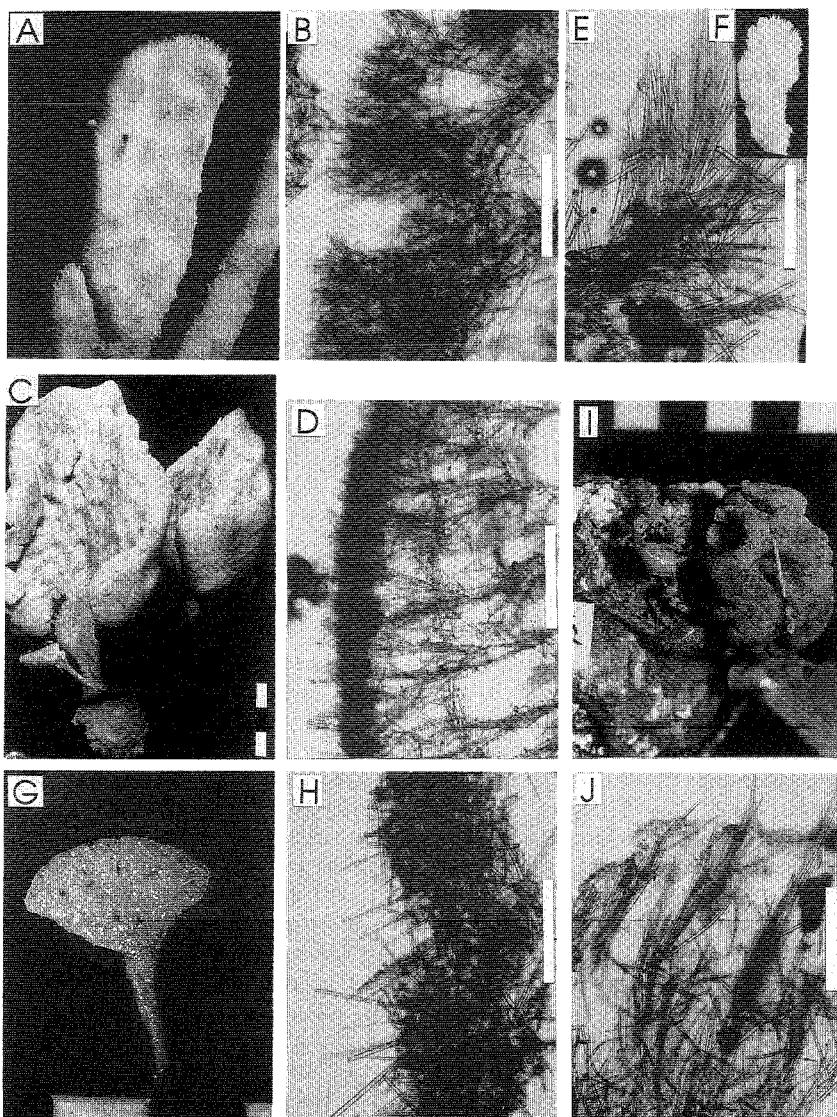


Fig. 9. *Axinella* spp.: *A*, *Phakellia aruensis* Hentschel, *in situ* (specimen NTM Z2156) (photo J. N. A. Hooper); *B*, skeleton (holotype SMF 953) (scale = 500 µm); *C*, *Phakellia crassa* Carter (holotype BMNH 1886.12.15.129); *D*, skeleton (scale = 500 µm); *E*, *Acanthella euctimena* Hentschel (holotype SMF 1012); *F*, skeleton (scale = 500 µm); *G*, *Axinella lifouensis* Lévi and Lévi (holotype MNHN DCL2943); *H*, skeleton (scale = 500 µm); *I*, *Axinella meloniformis* Carter (holotype BMNH 1886.12.15.117); *J*, skeleton (scale = 500 µm).

[not seen]), from New Zealand (Bergquist 1970); *Axinella tricalyciformis* Bergquist, 1970 (holotype CMMI 3/63 [not seen]), with synonym *Axinella lamellata* sensu Bergquist, 1961, from New Zealand; and *Axinella villosa* Carter, 1885 ('syntype' BMNH 1886.12.15.396; Fig. 10D), from south-east Australia (Dendy 1897a). There are another 28 possibly undescribed species collected from tropical Australasia (Hooper, unpublished data), which are also probably most appropriately placed in this genus. These will be described in future revision of the tropical Australasian axinellids.

Other Australasian species described in *Axinella* but better placed elsewhere include: *Axinella aurantiaca* Lendenfeld (1888, 'syntypes' AM G9171, Z468) from south-east Australia belongs with *Bubaris* (Bubaridae) (Whitelegge 1889, 1901; Hallmann 1914a; Burton 1928); *Axinella arborescens* Ridley & Dendy, 1886 (holotype BMNH 1887.5.2.64), from south-east Australia belongs in *Homaxinella* (Whitelegge 1889, 1907; Hallmann 1914c; Vacelet *et al.* 1976); *Axinella atropurpurea* Carter, 1885 (holotype BMNH 1886.12.15.1), from south-east Australia is a species of *Raspailia* (Raspailiidae) (Hooper 1991); *Axinella axifera* Hentschel, 1912 ('syntype' SMF 1666), from southern Indonesia and north-west Australia is a species of *Ceratopsion* (Raspailiidae) (Hooper 1991); *Axinella colvilli* Brondsted, 1924 ('syntypes' probably in ZMC), from New Zealand belongs to *Ciocalypta* (Halichondriidae) (Bergquist 1970); *Axinella chalinoides* et varr. Carter, 1885 (lectotype BMNH 1886.12.15.401), and *Axinella cladoflagellata* Carter, 1886a (holotype BMNH 1886.12.15.407), from south-east Australia, are synonymous and belong to *Echinocladaria* (Microcionidae) (comb. nov., determined from re-examination of the type material); *Axinella* ? *coccinea* Carter, 1886a (holotype BMNH 1886.12.15.8), from south-east Australia is an *Iotrochota* (Desmacididae) (comb. nov.); *Axinella flabellata* Carter, 1885 ('syntypes' BMNH 1886.12.15.471, 143), from south-east Australia belongs to *Sigmaxia* (Desmacellidae) (Hooper 1984); *Axinella frondula* Whitelegge, 1907 (holotype AM G4349), from south-east Australia is a species of *Raspailia* (Hooper 1991); *Axinella hispida* var. *gracilis* Lendenfeld, 1888 (holotype AM G9083), and var. *tenella* Lendenfeld, 1888 (lectotype AM G9074), are species of *Raspailia* (Hooper 1991); *Axinella inflata* Lendenfeld, 1888 (holotype AM G9081), from south-east Australia is virtually unrecognisable (but possibly belonging to Dictyodendrillidae; F. Wiedenmayer,

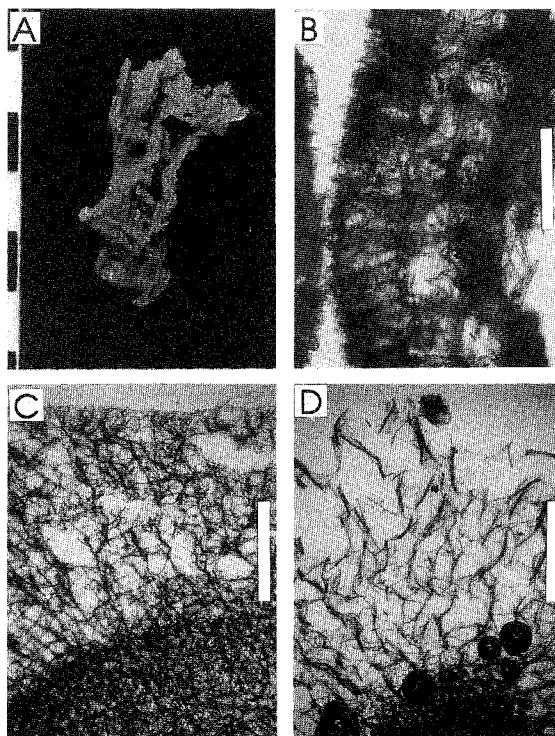


Fig. 10. *Axinella* spp.: A, *Chalinopora retepora* Lendenfeld (lectotype BMNH 1886.8.27.417); B, skeleton (scale = 500 µm); C, *Axinella polypoides* Schmidt, skeleton (specimen BMNH 1925.11.1.1003 from Naples) (scale = 1 mm); D, *Axinella villosa* Carter, skeleton ('syntype' BMNH 1886.12.15.396) (scale = 1 mm).

personal communication); *Axinella labyrinthica* Dendy, 1889 (holotype BMNH 1889.1.21.3), from the Indian Ocean and north-west Australia belongs to *Teichaxinella* (comb. nov.); *Axinella obtusa* Lendenfeld, 1888 (holotype AM G9082, presently missing), from south-east Australia is unrecognisable; *Axinella pilifera* Carter, 1885 (holotype unknown), from south-east Australia is virtually unrecognisable; *Axinella setacea* Carter, 1885 (holotype BMNH 1886.12.15.61) belongs to *Raspailia* and is a synonym of *R. pinnatifida* (Carter) (Hooper 1991); *Axinella solida* Carter, 1885 (lectotype BMNH 1887.7.11.24), from south-east Australia (Dendy 1897a) is a species of *Raphoxya* (comb. nov.; Fig. 32C-D); *Axinella stelliderma* Carter, 1885 (lectotype BMNH 1886.12.15.33), and var. *acerata* Carter, 1885 ('holotype' BMNH 1886.12.15.63), from south-east Australia (Dendy 1897a) are species of *Raspailia* (Hooper 1991); *Axinella symbiotica* Whitelegge, 1907 (holotype AM G4350), from south-east Australia is the type species of *Axinosia* (Hallmann 1914b); *Axinella vermiculata* Whitelegge, 1907 (holotype AM G4360), from south-east Australia belongs in *Teichaxinella* (de Laubenfels 1936); *Axinella virgultosa* var. *massa* Carter, 1886b (holotype BMNH 1889.6.9.4; Fig. 20F-G), from the central Indian Ocean, south-east Asia and north-west Australia, with synonym *Suberites mollis* Kieschnick (1898, 1900), belongs to *Stylissa* (see below). Also, re-examination of material described as '*Axinella echidnaea*' by Ridley (1884) and Hentschel (1912), from north-west Australia and southern Indonesia respectively, shows that they refer to *Reniochalina stalagmitis* (see above).

Axinella carteri (Dendy)

(Figs 11-12, Table 2)

Acanthella carteri Dendy, 1889: 93-4, pl. 4, fig. 6; Dendy, 1905: 193, pl. 8, fig. 6; Dendy, 1922: 119, pl. 5, fig. 5; Vacelet *et al.*, 1976: 43-4, pl. 2, fig. b; van Soest, 1989: 223-4, fig. 14.

Axinella carteri.—Burton, 1959: 258-9; Lévi, 1979: 311.

Acanthella aurantiaca Keller, 1889: 396.—Topsent, 1906: 562; Row, 1911: 356; Dendy, 1922: 119; Vacelet and Vasseur, 1971: 80.

Material Examined

Holotype. BMNH not seen; holotype of *A. aurantiaca*, ZMB 2921.

New Caledonian material. ORSTOM R1056: stn 241, Pointe Nind'Hio, Hienghene, 20°41'0"S., 164°57'2"E., 10 m depth, 6.ix.1978, coll. P. Laboute, SCUBA; ORSTOM R01: stn 153, barrier reef, Ilôt Taenia, Passe de St Vincent, 22°00'1"S., 165°56'1"E., 7 m depth, 14.ix.1976, coll. P. Laboute, SCUBA; ORSTOM 'cfR01': stn 253, barrier reef S. of pass, Yaté, 22°11'2"S., 167°02'1"E., 25 m depth, 26.ix.1979, coll. G. Bargibant, SCUBA; ORSTOM R1429: stn 332, W. entrance Canal Woodin,

Table 2. Comparison in spicule dimensions between published and present records of *Axinella carteri*

All measurements given in micrometres, and expressed as minimum-(mean)-maximum range of measurement. $N=25$ for each specimen

Material/author (Locality)	Length	Styles	Width
Holotype (Dendy 1889)			
(Gulf of Manaar)	400		21
	1200		11
Keller 1889			
(Red Sea)	400-500		6-15
Vacelet <i>et al.</i> 1976			
(Madagascar)	400-520		18-23
Present study			
(Comores) $N=1$	401-(480.5)-546		9-(21.6)-30
(Papua New Guinea) $N=1$	411-(456.4)-552		15-(21.8)-30
(Great Barrier Reef) $N=1$	406-(511.7)-601		6-(16.9)-22
(New Caledonia) $N=4$	415-(513.6)-588		12-(21.1)-28

22°23' 1"S., 166°46' 1"E., 18 m depth, 9.ii.1983, coll. G. Bargibant, SCUBA; NTM Z3883 (ORSTOM R170); stn 136, channel between Ilôt Canard and Ilôt Maitre, 22°19' 2"S., 166°21' 1"E., 12 m depth, 16.iv.1981, coll. J.-L. Menou, SCUBA; NTM Z3890: Ile aux Canards, Noumea lagoon, 22°19' 2"S., 166°26'E., 22 m depth, 26.ix.1990, coll. J. N. A. Hooper, SCUBA; QM G301323: Croissant-Larégrière, Ilôt Maitre, off Noumea, 22°20' 2"S., 166°22' 5"E., 20 m depth, 13.x.1992, coll. J. N. A. Hooper, SCUBA.

Comparative material. Great Barrier Reef, Qld: QM G300291 (fragment NTM Z4027): E. side of Magra I., Cockburn Is., Cape York Region, 11°52' 0"S., 143°17' 0"E., 12·5 m depth, 10.xii.1990, coll. J. N. A. Hooper, USSR RV 'Akademik Oparin', SCUBA, (stn JH-90-051). Papua New Guinea: NCI Q66C-4329-V (fragment QM G300355): Cement Mixer Reef, E. of Christiansen Research Institute, Madang, 6°40' 0"S., 145°49' 0"E., 6 m depth, 3.ix.1990, coll. NCI, SCUBA. Western Indian Ocean: QM G301000: Comoros Is., 12°S., 44°E., 37 m depth, 1991, coll. G. R. Pettit *et al.*, SCUBA (ref. no. M5351).

Description

Colour. Bright orange-brown alive (Munsell 2·5YR 7/8), pale orange-brown in ethanol. Surface slightly darker than interior of sponge.

Shape. Flabellate growth form, 110–400 mm high, with massive, lobate, irregularly planar or globular branching, up to 350 mm wide, and branches consist of relatively thick, flattened planar or buttressed lamellae, 4–11 mm thick, with irregular margins; sponge attached to substrate directly or by small basal stalk, 20–90 mm long, up to 40 mm diameter.

Surface. Fleshy, conulose, rough surface; conules irregular, 3–5 mm high, solitary or joined to form meandering surface ridges; texture rubbery, compressible, easily torn. Small oscules, 2–5 mm diameter, occur predominantly on the margins of lamellae, usually between surface conules.

Ectosome. Membraneous band of heavy collagen, 100–200 μm wide, slightly more darkly pigmented than choanosomal region, with extra-axial spicules protruding only sparsely.

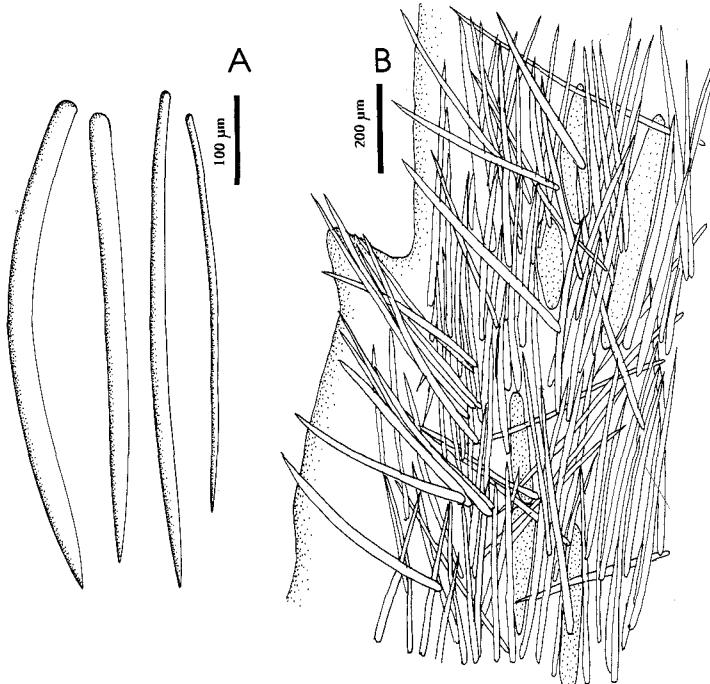


Fig. 11. *Axinella carteri* Dendy, specimen QM G300291: A, structural styles; B, section through peripheral skeleton.

Choanosome. Axial skeleton condensed into several multisicular bundles, 100–250 μm wide, running more-or-less longitudinally through lamellae, fully cored by long slender styles, bound together by very light spongin fibre, and interconnected at irregular angles by vaguely plumose, ascending, paucispicular extra-axial tracts of styles or individual spicules. Fibre reticulation relatively close meshed, with lacunae forming elongate oval chambers, up to $300 \times 70 \mu\text{m}$. Collagen in mesohyl relatively light compared with ectosomal region.

Megascleres (refer to Table 2 for dimensions). Single category of style present, although variable in thickness, occasionally strongylote; styles relatively long, slender or robust, usually slightly curved symmetrically or towards basal end, sharply pointed, fusiform, with evenly rounded base.

Microscleres. Absent.

Distribution

Red Sea (Keller 1889; Row 1911), Arabian Gulf (Burton 1959), western Indian Ocean: Cargados Carajos, Diego Garcia, Amirante, Salomon, Seychelles Is., Comores, Madagascar (Dendy 1922; Vacelet *et al.* 1976; present study), Gulf of Manaar, Sri Lanka (Dendy 1889, 1905), Lesser Sumba region, Indonesia (van Soest 1989), Papua New Guinea and the Great Barrier Reef (present study), and New Caledonia (Lévi 1979; present study). This species is a common component of Indo-Pacific coral reefs, usually found in both the lagoon and

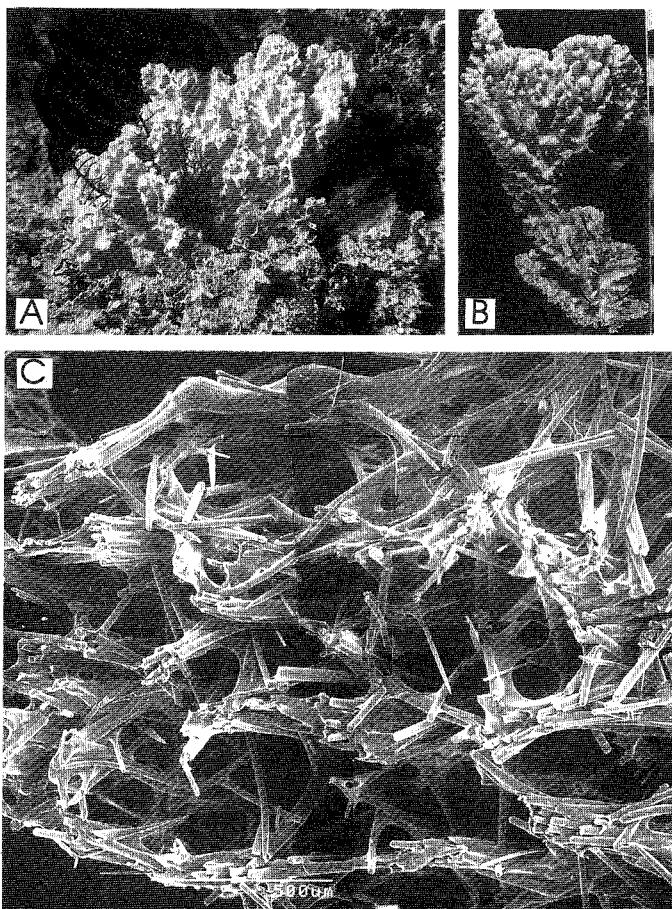


Fig. 12. *Axinella carteri* Dendy: A, specimen ORSTOM R170 *in situ* (photo P. Laboute); B, specimen QM G300291; C, SEM skeleton (scale = 500 μm).

outer reef slope; usually associated with living and dead coral. The species appears to be most common in areas of strong current, attached to coral rubble or rock, in sand and sea grass beds. Known depth range is 6–37 m.

Remarks

None of the material described above had a second category of longer style present, as described in Dendy's (1889) original description (cited as $1200 \times 11 \mu\text{m}$, compared with typical spicules of $400 \times 21 \mu\text{m}$), although Burton (1959) suggests that this longer spicule is present in few of the many known specimens of *A. carteri*. Apart from this feature, the species appears to be fairly homogeneous in skeletal structure, spicule morphology and size across its wide geographic range, although spicule dimensions vary slightly between material (Table 2). The species is readily recognisable in the field by its bright orange-brown coloration, fleshy surface and thick irregular lamellae.

Axinella carteri is difficult to place with absolute confidence in any single genus, given the relatively unclear boundaries between several structurally similar axinellid genera (e.g. *Phakellia*, *Acanthella*, *Axinella*, *Teichaxinella*). Vosmaer's (1912) criteria for differentiation of these taxa are not entirely clear cut, because many more species have been described since that early revision, showing that many intermediate (transformation) states are possible between the skeleton plans he initially proposed. Nevertheless, under his scheme for differentiating such genera, the present species falls closest to *Axinella* in having some axial compression and sparsely diverging, plumose extra-axial spicules.

Genus *Phakellia* Bowerbank

Phakellia Bowerbank, 1864: 186.—Bowerbank, 1866: 122; Schmidt, 1866: 15; Gray, 1867: 516; Ridley and Dendy, 1887: 169; Dendy, 1905: 190; Dendy, 1922: 116; Vosmaer, 1912: 310; Topsent, 1928: 37; de Laubenfels, 1936: 130; Bergquist, 1970: 17 [type species *Spongia ventilabrum* Linnaeus, 1767: 1296, which is a junior synonym of *Phakellia strigosa* (Pallas, 1766) (Vosmaer 1912: 310)]. *Quercyclona* de Laubenfels, 1936: 46 [comb. nov.] (type species *Antherochalina quercifolia* Keller, 1889: 383; holotype ZMB 429).

Diagnosis

Compressed flabellate or cup-like growth forms predominant; surface smooth or microconulose; oscules frequently surrounded by subdermal drainage canals; ectosome membranous without specialised skeleton, often lightly hispid from protruding choanosomal megascleres; choanosomal axial skeleton dense, typically with only interwoven styles, or may include sinuous strongyles and styles, or only strongyles, organised into multispicular ascending and paucispicular transverse tracts, together forming compressed axial reticulation; extra-axial skeleton comparatively sparse, with plumose bundles or single styles or oxeas perpendicular to axis, with or without transverse connecting megascleres; megascleres styles, sinuous strongyles or oxeas; microscleres absent (modified from Vosmaer 1912).

Remarks

Phakellia is similar to, and often confused with, *Acanthella*, differing primarily in having a well-differentiated axial and extra-axial skeleton (Vosmaer 1912; Bergquist 1970). *Quercyclona* de Laubenfels (1936: 46) is an obvious synonym of *Phakellia*, although de Laubenfels initially placed the taxon in Microcionidae. *Pararaphoxya* Burton (1934) may also eventually be merged with *Phakellia*, but is presently maintained separately and distinguished only by the possession of asymmetrical megascleres. However, from examination of nearly 40 species of both *Acanthella* and *Phakellia* from the Indo-Pacific faunas, consisting of both described and undescribed taxa, it is tentatively suggested that the structure of axial and extra-axial skeletons is the only feature that consistently differentiates these genera, lending support to Vosmaer's (1912) original proposal. By comparison, the presence or absence of sinuous axial megascleres seems to be much less stable and appears to occur indiscriminantly in species of both genera, and these features must be used with more caution.

In total, 21 species from the Australasian region (including New Zealand, New Caledonia and southern Indonesia) have been described in, or subsequently referred to, *Phakellia*, but examination of relevant type material suggests that only seven of these are most appropriately placed here. Approximately 20 other, undescribed *Phakellia* species have also been collected from tropical Australia, but these will be described elsewhere at a later date.

Valid Australasian species of *Phakellia* include: *Phakellia carduus* (Lamarck, 1814; holotype MNHN LBIM DT533) from north-west and north-east Australia (Ridley 1884;

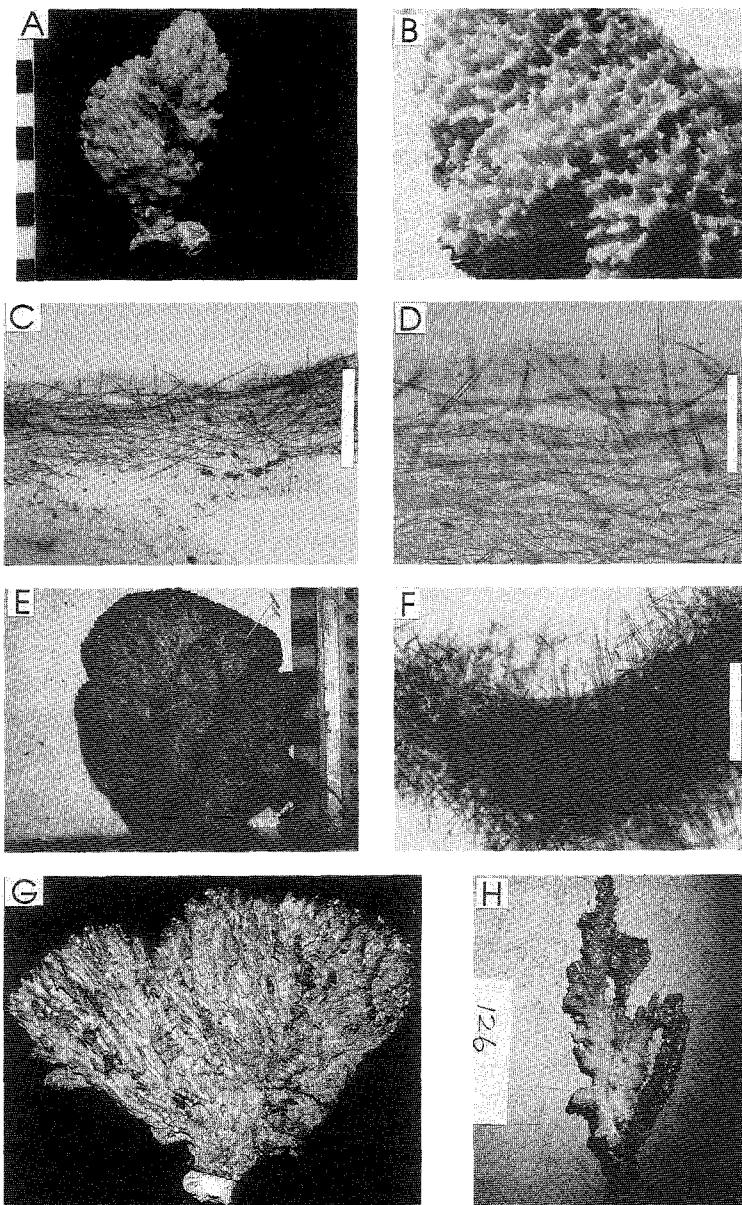


Fig. 13. *Phakellia* spp.: *A*, *Acanthella cavernosa* Dendy (holotype BMNH 1921.11.7.100); *B*, specimen on deck (NTM Z2736); *C*, skeleton (holotype) (scale = 500 µm); *D*, peripheral skeleton (scale = 200 µm); *E*, *Spongia carduus* Lamarck (specimen on deck NTM Z1837); *F*, skeleton (paralectotype MNHN DT3447) (scale = 500 µm); *G*, paralectotype MNHN DT533); *H*, specimen on deck (QM G300431).

Topsent 1930; Bergquist 1970; Hooper, unpublished data) (Fig. 13E–H); *Phakellia cavernosa* (Dendy, 1922; holotype BMNH 1921.11.7.100) [with synonyms *Acanthella stipitata*, in part (variety of Ridley and Dendy, 1887; not *Acanthella stipitata* Carter, 1881; 'holotype' BMNH 1887.5.2.73), and Burton, 1934 (specimen BMNH 1930.8.13.142), and *Acanthella kletchra* Pulitzer-Finali, 1982 (holotype MHNG 46927), from the Indian Ocean, north-west and north-east Australia, and the Great Barrier Reef (Burton 1934; Bergquist 1970; Hooper, unpublished data) (Fig. 13A–D)]; *Phakellia columnata* (Burton, 1928; holotype BMNH [not found]; 'representative specimen' MNHN DCL2934), known from the Andaman Sea and deeper waters off New Caledonia (Lévi and Lévi 1983) (Fig. 14A–B); *Phakellia conulosa* Dendy, 1922 (holotype BMNH [not found]; 'representative specimen' from the Philippines QM G300315), from the Indian Ocean and north-west Australia (Dendy 1922; Hooper, unpublished data) (Fig. 14C–D); *Phakellia dendyi* Bergquist (1970; holotype NMNZ Porif.24) from north-west, north-east and south-east Australia, and New Zealand (Dendy 1897b; Bergquist 1970; Hooper, unpublished data) (Fig. 14E–F); *Phakellia pulcherrima* (Ridley and Dendy, 1886; holotype BMNH 1887.5.2.23) (Figs 14G–H, 15–16) (see below); and *Phakellia stipitata* (Carter, 1881; holotype BMNH [confirmed destroyed]; neotype QM G300874, here designated) from eastern and south-east Australia (see below) (Fig. 17–18).

Other Australasian species described in *Phakellia* but better placed elsewhere include: *Phakellia aruensis* Hentschel, 1912 (holotype SMF 953), from southern Indonesia is assigned to *Axinella*; *Phakellia brassicata* Carter, 1885 (holotype BMNH 1886.12.15.75), from south-east and north-east Australia belongs to *Cribrochalina* (Niphatidae, order Haplosclerida); *Phakellia crassa* Carter, 1885 (holotype BMNH 1886.12.15.129), from south-east Australia (Fig. 9C–D) is an *Axinella*; *Phakellia flabellata* Carter, 1885 (holotype BMNH 1886.12.15.471), and *Phakellia villosa* Carter, 1886a (lectotype BMNH 1886.12.15.78), both from south-east Australia, are both synonyms of *Teichaxinella flabellata* (Carter, 1885); *Phakellia inflexa* Pulitzer-Finali, 1982 (holotype MHNG 46931 [not seen by the authors]), from the southern Great Barrier Reef is an *Acanthella*; *Phakellia jacksoniana* Dendy, 1897a (lectotype BMNH 1887.5.2.9), is a synonym of *Clathria (Isociella) jacksoniana* (Dendy) (Microcionidae, order Poecilosclerida); *Phakellia multiformis* Whitelegge, 1907 ('syntype' AM G4358), from south-east Australia belongs to *Axinosa*; *Phakellia papyracea* Carter, 1886a (lectotype BMNH 1886.12.15.231), from south-east Australia is a synonym of *Echinocladaria leporina* (Lamarck, 1814) (Microcionidae, order Poecilosclerida); *Phakellia plumosa* Lévi & Lévi, 1983 (holotype MNHN DCL2972), from deeper waters off New Caledonia belongs in *Reniochalina* (Fig. 6C–D); *Phakellia ramosa* Carter, 1883 (holotype BMNH 1884.4.14.2), from south-east Australia belongs to *Sigmaxinella* (Desmacellidae, order Poecilosclerida); *Phakellia tumida* Dendy, 1897a (holotype NMV G2464), from south-east Australia belongs to *Pseudaxinella*; and *Phakellia ventilabrum australiensis* Carter, 1886a (holotype BMNH 1886.12.15.422), from south-east Australia is a synonym of *Clathria (Thalysias) cactiformis* (Lamarck, 1814) (Microcionidae, order Poecilosclerida).

Phakellia pulcherrima (Ridley & Dendy), comb. nov.

(Figs 14G–H, 15–16, Table 3)

Acanthella sp.—Ridley, 1884: 463.

Acanthella pulcherrima Ridley & Dendy, 1886: 218, 479.—Ridley and Dendy, 1887: 177, pl. 32, fig. 3.

Not *Acanthella pulcherrima*.—Capon and MacLeod, 1988: 979–83.

Acanthella pulcherrima calyx Dendy, 1922: 120, pl. 5, fig. 6.

Material Examined

Holotype. BMNH 1921.11.7.100 (fragment MNHN DCL209L): Prince of Wales Channel, Torres Strait, 14 m depth, HMS 'Challenger'.

New Caledonian material. QM G300019 (ORSTOM R1321): stn 102, mid-channel, Canal Woodin, 22°23' 1"S., 166°48' 1"E., 28.iv.1976, 33 m depth, coll. P. Laboute, SCUBA; ORSTOM R1052: stn 136, channel between Ilôt Canard and Ilôt Maitre, 22°19' 2"S., 166°21' 1"E., 20 m depth, 16.iv.1981, coll. P. Laboute, SCUBA.

Description

Colour. Pale orange-brown or brown alive (Munsell 5YR 7/10), pale beige in ethanol.

Shape. Small club-shaped sponge (75–120 mm long, 58–75 mm maximum breadth), with short cylindrical stalk (12–22 mm long, 7–10 mm wide), enlarged basal holdfast, and several very thin, leaf-like, flattened branches (10–30 mm maximum width, 4–8 mm thick), with even margins.

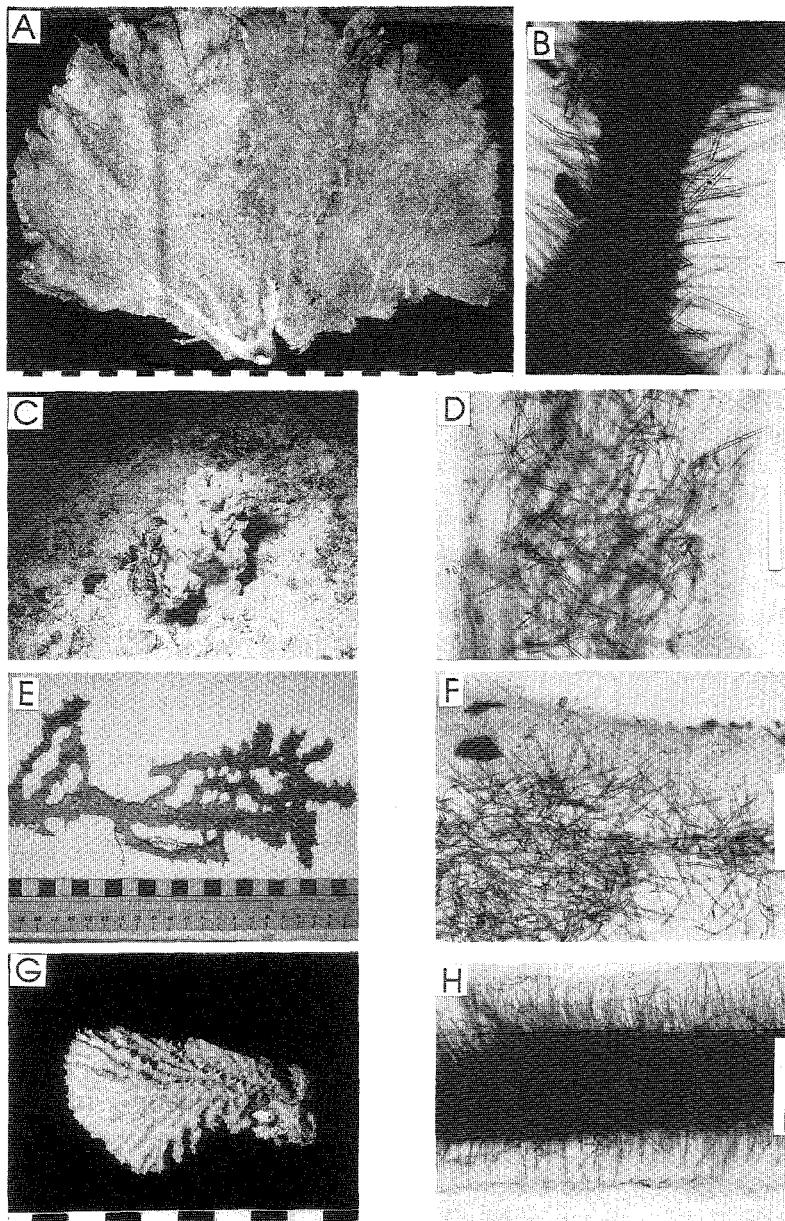


Fig. 14. *Phakellia* spp.: *A*, *Bubaris columnata* Burton (specimen from New Caledonia MNHN DCL2934); *B*, skeleton (scale = 500 µm); *C*, *Phakellia conulosa* Dendy, *in situ* (specimen from the Philippines, QM G300315) (photo J. N. A. Hooper); *D*, skeleton (scale = 200 µm); *E*, *Phakellia dendyi* Bergquist (specimen on deck NTM Z1318); *F*, skeleton (scale = 500 µm); *G*, *Acanthella pulcherrima* Ridley and Dendy (holotype BMNH 1887.5.2.23); *H*, skeleton (scale = 500 µm).

Table 3. Comparison in spicule dimensions between published and present records of *Phakellia pulcherrima*

All measurements given in micrometres, and expressed as minimum-(mean)-maximum range of measurement. $N=25$ for each specimen

Material/author (Locality)		Extra-axial styles	Axial strongyles
Holotype (BMNH 1887.5.2.23)	L	294-(331·2)-392	360-(577·1)-940
Dendy (1922) (Cargados Carajos)	W	$\times 6$ -(11·0)-15	$\times 2$ -(5·2)-9
	L	'Larger'	Up to 1300
Present material (New Caledonia)	W		$\times 8$ ·6
	L	253-(360·3)-413	449-(488·4)-552
	W	$\times 2$ -(5·4)-9	$\times 2$ -(4·2)-6

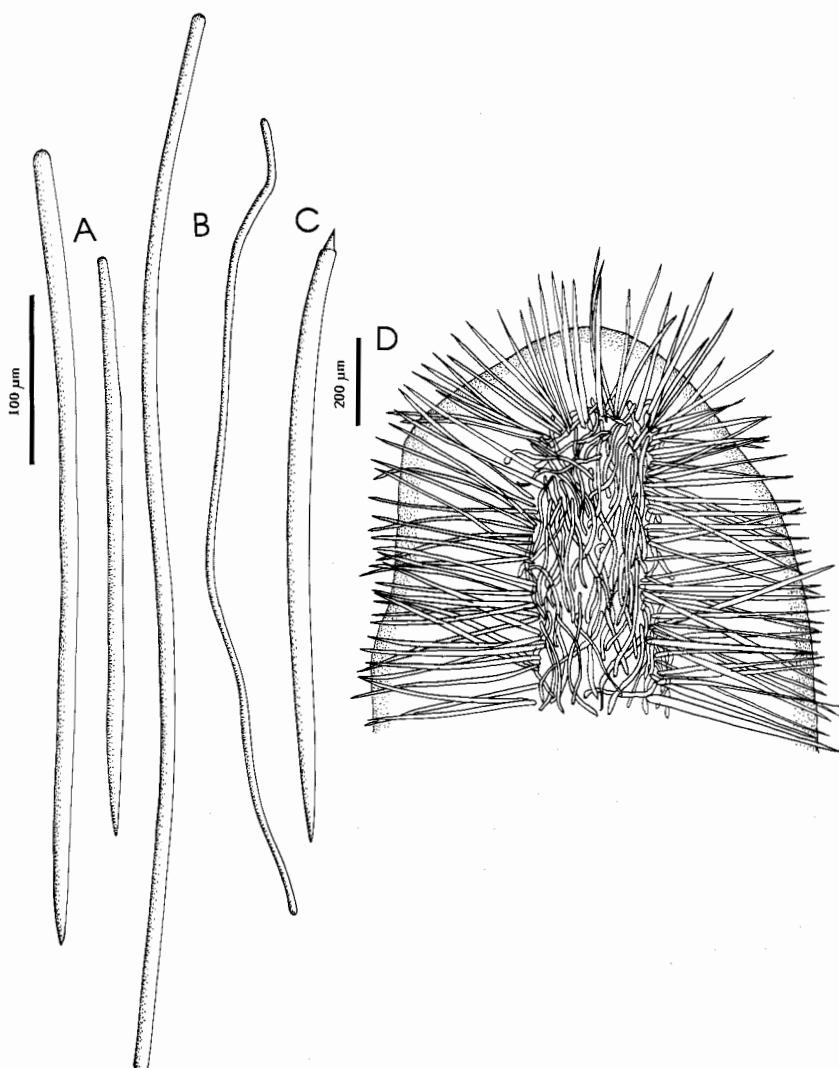


Fig. 15. *Phakellia pulcherrima* (Ridley and Dendy), specimen QM G300019: A, extra-axial styles; B, axial strongyles; C, anisoxeas frequent in holotype BMNH 1887.5.2.23; D, section through peripheral skeleton of specimen QM G300019.

Surface. Evenly conulose; conules rounded or pointed, more-or-less arranged in ridges, up to 5 mm high, running longitudinally along branches, with ridges producing an almost striated pattern. Oscules and pores not seen in preserved material. Texture firm, flexible.

Ectosome. Membraneous, fleshy, without specialised spicules; points of extra-axial styles protrude 100–250 µm from surface conules, whereas between conules ectosome is merely fleshy, with more darkly pigmented granular collagen than in choanosomal region.

Choanosome. Skeleton divided into distinct axial and extra-axial regions. Axis tightly compressed, occupying only about 30% of branch diameter, running longitudinally through branches, cored by closely reticulate sinuous strongyles, more-or-less interlocked and criss-crossed within axis. Extra-axial skeleton consists of radial tracts of individual, or loosely plumose bundles of styles, embedded in and standing perpendicular to the axis. Axial spicules bound by moderately heavy, close-set spongin fibres, up to 30 µm diameter, with fibre reticulation producing elongate meshes, 20–70 µm diameter. Extra-axial spicules free within mesohyl, not associated with spongin fibres except where embedded into axis. No choanocyte chambers observed in peripheral skeleton.

Megascleres (refer to Table 3 for dimensions). Extra-axial styles relatively thick, straight or slightly curved near basal end, with tapering fusiform points and with evenly rounded or slightly constricted bases. Axial strongyles usually sinuous, occasionally completely straight or vermiciform, relatively thick, with evenly rounded bases.

Microscleres. Absent.

Distribution

New Caledonian lagoon, Cape York, Torres Strait, Great Barrier Reef, Cargados Carajos, Indian Ocean; 5–54 m depth; coral rubble.

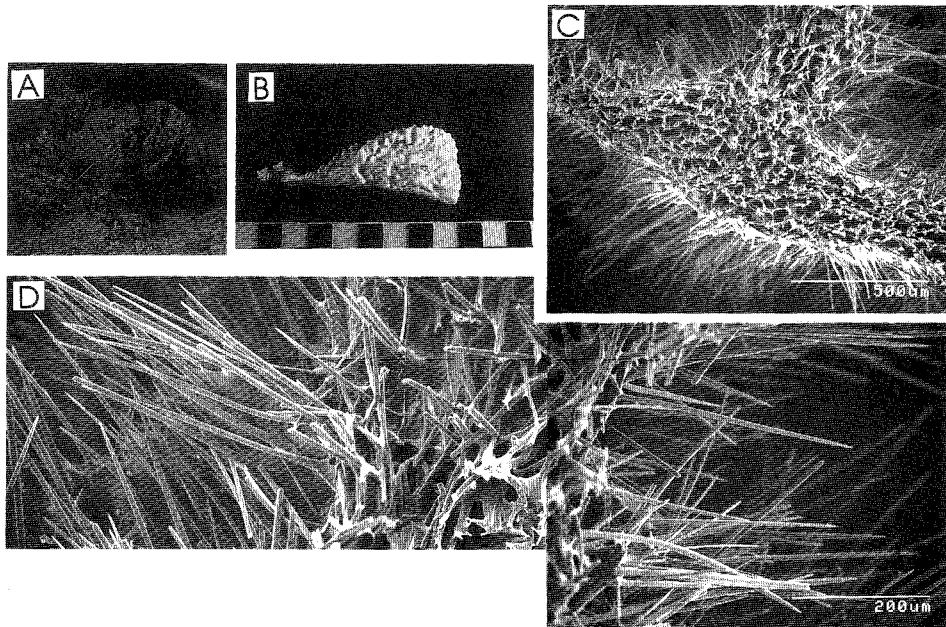


Fig. 16. *Phakellia pulcherrima* (Ridley and Dendy): *A*, specimen *in situ* (ORSTOM R1052) (photo P. Laboute); *B*, specimen QM G300019; *C*, SEM skeleton (magnified 80 \times); *D*, SEM transverse section (magnified 94 \times).

Remarks

The New Caledonian population of *P. pulcherrima* is a new locality record for the species, and is the first validated record (i.e. confirmed by voucher specimen) since Dendy (1922) rediscovered the species from the western Indian Ocean. A major difference between the New Caledonian specimen and the two previously known records of the species is that many of the extra-axial styles have modified oxeote bases in the older specimens, whereas in the New Caledonian specimen these spicules are invariably styloid. Spicule dimensions also vary slightly, particularly in the maximum lengths of strongyles (Table 3), but considering that these spicules break up easily during histological preparation it is possible that they may actually be larger in New Caledonian material than described here. In other details (growth form, surface sculpturing, skeletal structure), all known specimens are similar and undoubtedly conspecific.

This species is contrasted with other Australasian *Phakellia* in Figs 13–14.

Phakellia stipitata (Carter)

(Figs 17–18)

Acanthella stipitata Carter, 1881: 380, pl. 18, fig. 8.

Not *Acanthella stipitata*. — Ridley and Dendy, 1887: 178; Burton, 1934: 565.

Material Examined

Neotype. QM G300874: Peel I., Lazarette Gutter, Moreton Bay, Qld, 27°28·9'S., 153°21·4'E., 8 m depth, 14.iv.1992, coll. J. N. A. Hooper and S. D. Cook, SCUBA.

New Caledonian material. QM G 300280 (fragment NTM Z3888): Ille aux Canards, Noumea lagoon, 22°19·0'S., 166°26·0'E., 22 m depth, 26.ix.1990, coll. J. N. A. Hooper and J. Vacelet, SCUBA, sand, rubble, sea grass beds; ORSTOM R1429 (fragment NTM Z3875): stn 332, W. entrance Canal Woodin, 22°23·1'S., 166°46·1'E., 18 m depth, 9.ii.1983, coll. J.-L. Menou, SCUBA.

Comparative material. QM G301235: same locality as neotype.

Description

Colour. Bright orange-brown alive (Munsell 5YR 7/10), orange-yellow in ethanol.

Shape. Flabellate sponge, 90–130 mm long, 70–110 mm wide, 40–90 mm thick, with one or more fans aligned face-to-face, composed of irregularly fused and reticulated branches, with excavated wide meshes between reticulations, producing thick, nearly bulbous branching; small basal stalk, up to 30 mm long, 15–20 mm diameter (often detached from specimen), with a broad basal holdfast.

Surface. Clathrous, excavated surface, with well-developed, regularly spaced conules, 10–20 mm apart, 5–20 mm high; conules have rounded tips, usually joined together by low ridges, surrounding large excavations through the sponge (4–15 mm diameter) (i.e. producing the surface meshes); remainder of membranous surface with 'goose-flesh' appearance, and covered with small ostia (<1 mm diameter). Large oscules on margins of fans, 15–25 mm diameter, slightly raised above surface, and slightly more darkly pigmented than rest of surface. Texture firm, rubbery, difficult to tear, usually requires cutting off substrate.

Ectosome. Membranous, heavily collagenous, darkly pigmented, without special spicules and only points of extra-axial styles barely protruding through surface (these usually only on ends of surface conules).

Choanosome. Skeleton clearly differentiated into axial and extra-axial regions. Axis moderately compressed, with short, heavy, reticulated spongin fibres, 20–45 µm diameter, producing oval or elongate meshes, 60–110 µm diameter; fibres only partially cored by styles in uni- or multispicular tracts. Extra-axial skeleton not well formed (as in some other species of *Phakellia*), consisting of radially arranged styles, as individuals or multispicular brushes, standing perpendicular or at acute angles to axis, ascending to and usually

protruding through ectosome. Styles in axial and extra-axial skeletons do not appear to be differentiated. Choanocyte chambers small, elongate, up to 40 μm diameter.

Megascleres. Axial and extra-axial megascleres are exclusively styles, long, slender, straight or slightly curved, with abrupt points, sharp or slightly stepped tips, and with evenly rounded or occasionally oxeote bases. Length (neotype): 172-(345.5)-494 μm ; (New Caledonian material): 301-(412.7)-545 μm . Width (neotype): 3-(7.7)-12 μm ; (New Caledonian material): 3-(8.1)-15 μm .

Microscleres. Absent.

Distribution

Gulf of Manaar (original record), south-east Queensland, and New Caledonia; associated with living and dead coral, coral reef lagoon.

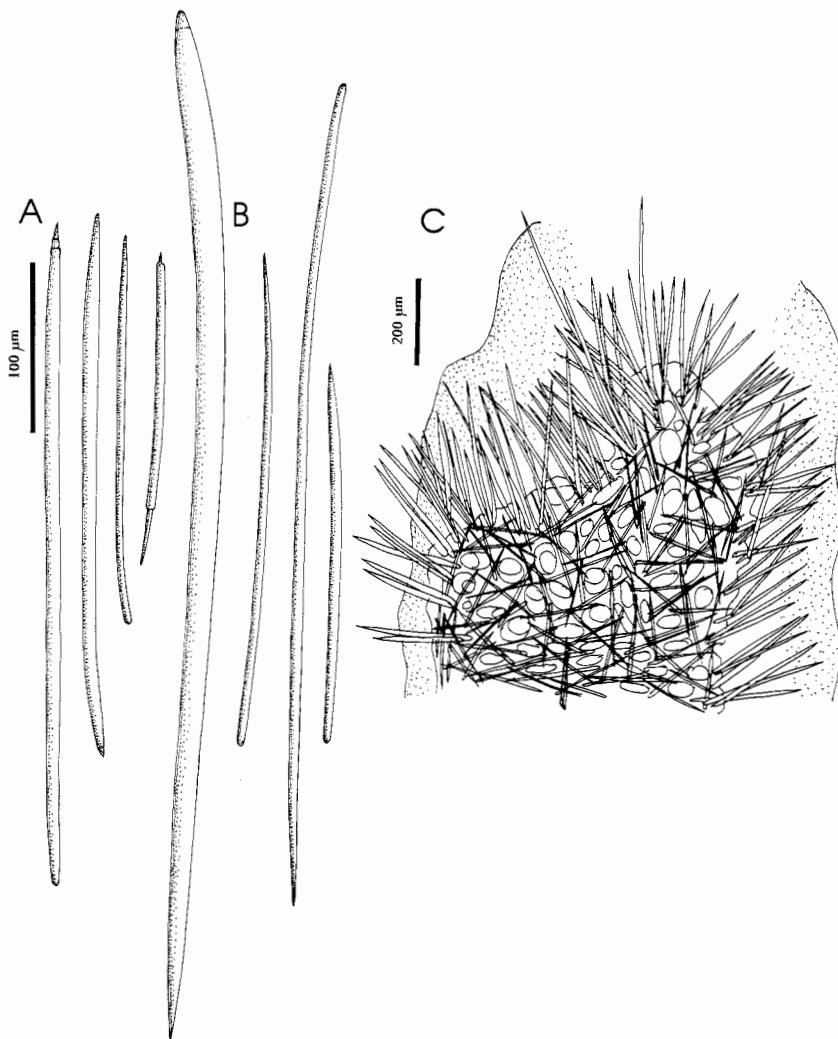


Fig. 17. *Phakellia stipitata* (Carter): A, neotype QM G300874, structural styles and anisoxeas; B, specimen QM G300280 from New Caledonia, styles and anisoxeas; C, section through peripheral skeleton of neotype.

Remarks

There is no extant type material of this species in the BMNH or LFM (S. Stone, BMNH, personal communication, and personal observation), nor has the species been recorded since it was first described. Records cited by Ridley and Dendy (1887) and Burton (1934) refer to *Phakellia cavernosa* (Dendy, 1922), and this is confirmed by the presence of sinuous strongyles in their material (BMNH 1887.5.2.73 and BMNH 1930.8.13.142, respectively). However, some distinctive features of the species are obvious from Carter's (1881) original description, notably the characteristic clathrous, excavated gross morphology, and spicule morphology (particularly spicule size, geometry and presence of abrupt points). These agree closely with the present material from Moreton Bay and the Noumea lagoon. New Caledonian specimens have marginally larger styles than does the neotype from Moreton Bay, but this difference is relatively trivial, and the species are similar in all other features.

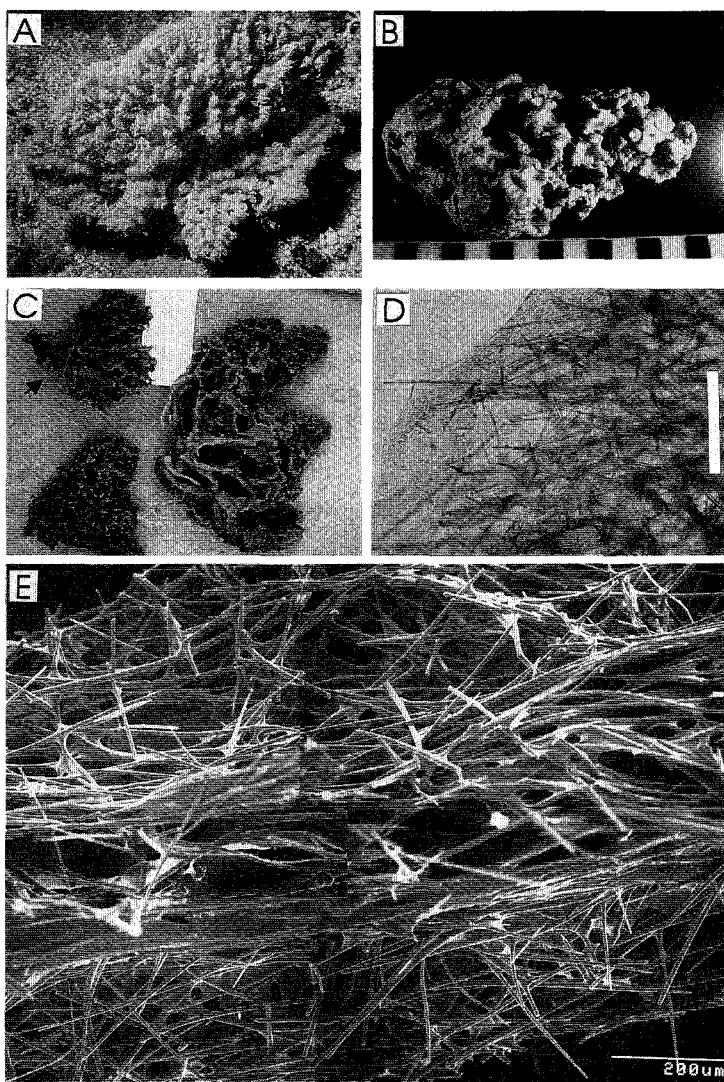


Fig. 18. *Phakellia stipitata* (Carter): *A*, specimen *in situ* (ORSTOM R1429) (photo J.-L. Menou); *B*, preserved specimen (QM G300280); *C*, three specimens on deck (neotype QM G300874 top left, indicated by arrow; other specimens QM G301235); *D*, peripheral skeleton (neotype QM G300874) (scale = 200 μm); *E*, SEM transverse section (specimen QM G300280) (scale = 200 μm).

Genus *Stylissa* Hallmann

Stylissa Hallmann, 1914b: 349 [type species *Stylorella flabelliformis* Hentschel, 1912: 355, holotype SMF 1587].

Dragmaxia Hallmann, 1916a: 543.—Hallmann, 1916b: 674; de Laubenfels 1936: 130 [type species *Spongisorites variabilis* Whitelegge, 1907: 513, holotype AM (presently missing)].

Diagnosis

Fan, cup-shaped or massive foliose growth forms; surface shaggy, often with small papillae or grooved ridges; ectosome fleshy, without specialised spiculation, but with brushes of peripheral choanosomal styles protruding through surface; choanosomal skeleton disorganized plumo-reticulate, with a slightly condensed axis and slight differentiation between axial and extra-axial skeletons; fibres cored by parallel tracts of styles, of 1 or 2 sizes, more-or-less ascending, and diverging towards the periphery; peripheral styles often slightly larger than those in axis. Microscleres absent or present (raphides, trichodragmata) (modified from Hallmann 1914b).

Remarks

Whitelegge (1907) characterised *Spongisorites variabilis* partly by the presence of raphides in the dermal layer, and Hallmann (1916a) erected *Dragmaxia* to emphasise this feature, which he generally considered to be diagnostically important throughout his taxonomy. Hallmann also noted that these raphides occurred throughout the mesohyl, not necessarily confined to the ectosomal region, as supposed by Whitelegge (1907). In addition, Hallmann (1916a) noted that although both *Dragmaxia* and *Stylissa* have comparable architecture and only styles for megascleres, those of the former were differentiated into two size categories, with some evidence of spicule localisation (the larger apparently found closer to the periphery). However, in other *Stylissa* spicule size may extend over a large size range, and often the peripheral spicules are marginally larger than those in the axial skeleton. Whitelegge's holotype of *S. variabilis* is missing from AM collections, and these features cannot be accurately verified, but the species is perfectly recognisable from Hallmann's (1916a: 544) redescription, which includes comprehensive illustrations. It is concluded from this available evidence that *Dragmaxia* differs in no substantial respect from *Stylissa* and the two are here merged, as was suggested by de Laubenfels (1936).

Stylissa presently contains only three valid species, all from the Indo-west Pacific region: the type species *S. flabelliformis* (Hentschel, 1912), previously known only from the Arafura Sea but now known from the Indo-west Pacific region in general (Fig. 19–20); *S. variabilis* (Whitelegge, 1907), known only from the Crookhaven River, N.S.W. (Hallmann 1916a) (holotype AM, missing); and another widely distributed species, *S. massa* (Carter, 1886b) [for *Axinella virgultosa* var. *massa* Carter (holotype BMNH 1889.6.9.4; Fig. 20F–G) (Burton 1959), with synonyms *Suberites mollis* Kieschnick, 1898, and *Stylorella conulosa* Topsent, 1897 (lectotype MHNG C-12/45, paralectotype MNHN LBIM DT1775, here designated)], extending from the south Arabian coast (Burton 1959), the Mergui Archipelago, Andaman Sea (Carter 1886b), Torres Strait, Qld (Kieschnick, 1898, 1900), Ambon, Moluccas (Topsent 1897; Desqueyroux-Faundez 1981), Ternate, Moluccas (Kieschnick 1898, 1900), Java Sea (Lindgren 1897, 1898), and Christmas Island, western Indian Ocean (Kirkpatrick 1900).

Stylissa flabelliformis (Hentschel)

(Figs 19–20, Table 4)

Stylorella flabelliformis Hentschel, 1912: 355–6, pl. 19, fig. 26.

Stylissa flabelliformis.—Hallmann, 1914b: 349.

Teixachinella labyrinthica.—Hooper et al., 1992: 265.

Material Examined

Holotype. SMF 1587 (schizotype MNHN DCL2314): Meriri, Aru I., Arafura Sea, 6°S., 134°50'E., 6–10 m depth.

New Caledonian material. QM G300017 (ORSTOM R1257): stn 166, N. pass Toëmo, Port de Goro, 22°20'·0"S., 167°01'·0"E., 18 m depth, 28.x.1976, coll. A. Intés, SCUBA; QM G300689 (fragment NTM Z3874): Baie des Citrons, Noumea lagoon, 22°18'S., 166°25"E., 3 m depth, 25.ix.1990, coll. J. N. A. Hooper, snorkel; ORSTOM R565: stn 113, L'epave du 'Bonhomme', Grand Récif Mbère, 22°21'·0"S., 166°14'·0"E., 25 m depth, 21.vi.1976, coll. P. Laboute, SCUBA.

Comparative material. **Seychelles Is:** QM G300068: E. of Curieuse I., 4°15'S., 55°47"E., depth and date of collection unknown, coll. Pettit, G. R. et al., SCUBA (ref. no. M5281). **Japan:** QM G301236: Yonaguni I., E. of Taiwan, 24°29'N., 123°00"E., 30 m depth, 1992, coll. T. Higa (ref. K-1). **Sahul Shelf, W.A.:** QM G300183 (fragment NTM Z2817): West I. passage, outer reef, Ashmore Reef, 12°15'S., 122°55"E., 16·5 m depth, 28.vii.1986, coll. C. Johnston, SCUBA; NTM Z2797, 2798: West I. passage, outer reef edge, Ashmore Reef, 12°14'·3"S., 123°56'·0"E., 15·5 m depth, 27.vii.1986, coll. A. M. Mussig, SCUBA; QM G301081, G301082: Cartier I., outer reef slope, N. side reef, 12°31'·4"S., 123°33'·3"E., 14 m depth, 06.v.1992, coll. J. N. A. Hooper, SCUBA. **Northwest Shelf, W.A.:** NTM Z3374: 2 nm from shore, N. of Barrow I., 20°38'·8"S., 115°28'·8"E., 22 m depth, 26.viii.1988, coll. D. Low Choy, SCUBA; NTM Z664: NW. of Yampi Sound, 15°27'·04"S., 121°49'·00"E., 76 m depth, 29.iv.1982, coll. CSIRO R.V. 'Sprightly', dredge; QM G300108 (fragment NTM Z1220), NTM Z1236: N. of Bedout I., W. of Port Hedland, 19°28'·05"S., 118°55'·30"E., 40 m depth, 26.iv.1983, coll. J. N. A. Hooper, R.V. 'Soela', SO2/83, stn B9, trawl; NTM Z1471: W. of Port Hedland, 19°56"S., 117°57"E., 40 m depth, 05.xii.1985, coll. Ward, T., trawl; NTM Z1807, Z1829: W. of Port Hedland, 19°26'·09"S., 118°54'·02"E., 50 m depth, 30.viii.1983, coll. Ward, T. R.V. 'Soela', trawl; NTM Z684: N. of Port Hedland, 19°16"S., 118°50"E., 70 m depth, 4.v.1982, coll. CSIRO R.V. 'Sprightly', dredge; NTM Z2321: NW. of Lacepede Is, 16°31"S., 121°28"E., 38-40 m depth, 17.iv.1985, coll. Russell, B. C., pair trawl; NTM Z731: N. of Adele I., Collier Bay, 15°58'·03"S., 122°39'·07"E., 59 m depth, 21.iv.1982, coll. CSIRO R.V. 'Sprightly', dredge; NTM Z2351: NW. of Lacepede Is, 16°34"S., 121°27"E., 40-46 m depth, 17.iv.1985, coll. B. C. Russell, pair trawl; NTM Z3021: N. of Amphinome Shoals, 19°19'·7"S., 119°08'·8"E., 50 m depth, 19.vii.1987, coll. J. N. A. Hooper, USSR RV 'Akademik Oparin', trawl. **Arafura Sea, N.T.:** NTM Z607: Cootamundra Shoals, N. of Melville I., 10°49'·07"S., 129°12'·09"E., 31 m depth, 6.v.1982, coll. B. Thom, R. Lockyer, SCUBA; NTM Z616: same locality, 10°50'·22"S., 129°13'·17"E., 22 m depth, 10.v.1982, coll. R. Lockyer, SCUBA; NTM Z3081: Parry Shoals, 11°11'·41"S., 129°43'·01"E., 18 m depth, 13.viii.1987, coll. A. M. Mussig, SCUBA.

Description

Colour. Live coloration dark orange-brown (Munsell 5YR 7-6/10), with a paler membranous ectosome, and brighter orange interior (5YR 7/12); red-brown on deck; produces an orange exudate upon collection.

Shape. Growth form generally thickly flabellate, 120-450 mm long, 70-180 mm wide, with flabellate-digitate branches growing in more than 1 plane, with 140 mm maximum span, with even or uneven digitate margins on branches, up to 30 mm thick, attached to substrate by small thickly cylindrical basal stalk, 20-75 mm long, 11-45 mm diameter.

Surface. Characteristically rough, striated, conulose, shaggy surface, with either longitudinal striations in larger specimens, or irregularly conulose, sculptured surface in younger material. Surface soft, fleshy in life, contracting in preserved material to produce harsh texture. Oscules visible on apex of surface ridges and margins of branches, up to 14 mm diameter, with a large membranous lip surrounding each exhalant pore. Fleshy parts of surface porous, with evenly dispersed ostia, predominantly between conules and ridges.

Ectosome. Fleshy, darkly pigmented, heavily collagenous ectosome, with points of styles from peripheral skeleton protruding up to 200 µm from the surface. In vicinity of surface conules peripheral (subectosomal) skeleton extends directly into subdermal region, whereas in fleshy area between conules there are only few spicules present.

Choanosome. Skeletal structure plumo-reticulate, although it appears disorganised due to proportionally large size of megascleres in relation to spongin fibres, with only slightly differentiated axial and extra-axial regions. Axial skeleton reticulate, with heavy spongin fibres (80-170 µm diameter), forming rectangular meshes (80-170 µm diameter), cored by multispicular tracts of styles. Extra-axial skeleton vaguely plumo-reticulate, with multi-spicular ascending tracts of styles interconnected at irregular intervals by uni- or pauci-

Table 4. Comparison in spicule dimensions between published and present records of *Stylissa flabelliformis* and other members of the genus

All measurements given in micrometres, and expressed as minimum-(mean)-maximum range of measurement. $N=25$ for each specimen

Population	Styles	
	Length	Width
<i>Stylissa flabelliformis</i> (Hentschel)		
Indonesia (holotype)	348-(447.1)-522	9-(16.9)-23
New Caledonia ($N=2$)	339-(433.5)-516	6-(15.8)-22
Seychelles ($N=1$)	343-(423.6)-482	13-(19.7)-27
Japan ($N=1$)	396-(486.5)-582	8-(20.5)-28
North-west Australia ($N=13$)	341-(444.6)-554	7-(17.4)-28
Atypical specimen, Northwest Shelf, W.A. (QM G300108)	272-(333.9)-380	7-(20.1)-32
<i>Stylissa massa</i> (Carter)		
Mergui Archipelago (holotype)	504-(564.4)-648	11-(17.8)-22
<i>Stylissa variabilis</i> (Hallmann)		
Southern New South Wales (Hallmann 1916a)	350-900 1000-1500	33-45 18

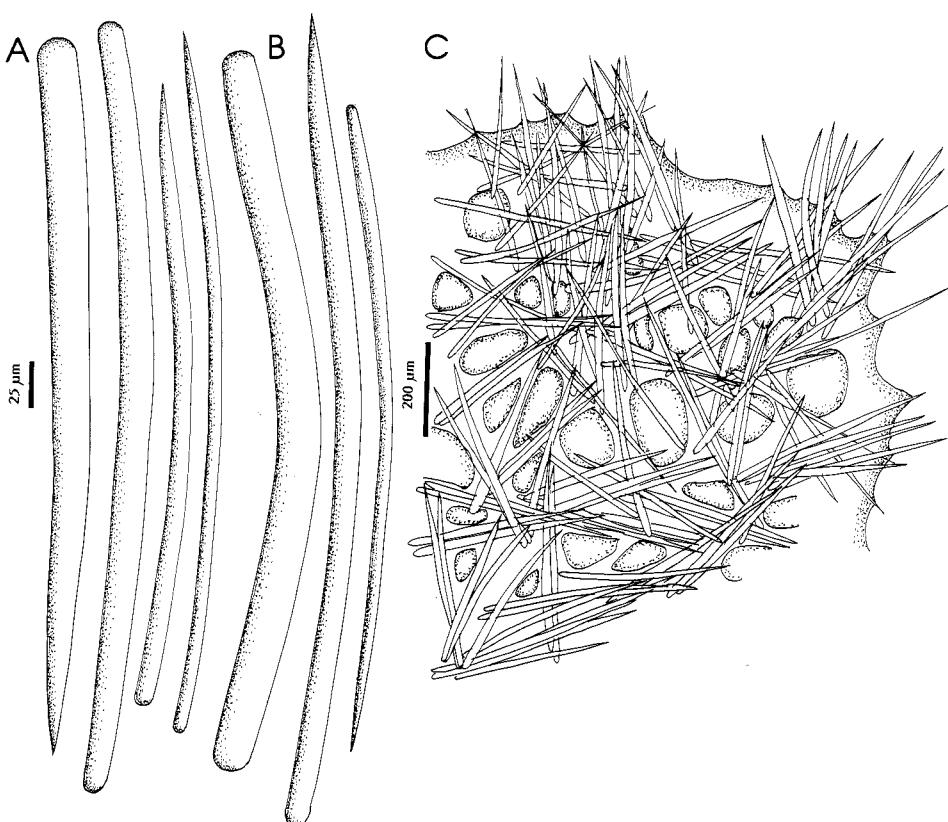


Fig. 19. *Stylissa flabelliformis* (Hentschel): *A*, specimen QM G300017, styles and strongyloite spicules; *B*, schizotype MNHN DCL2314, structural spicules; *C*, section through peripheral skeleton of New Caledonian specimen QM G300017.

spicular transverse tracts. Fibre reticulation in extra-axial region slightly more cavernous than axis, with meshes up to 300 µm diameter. Collagen abundant; choanocyte chambers small, elongate, 70–90 µm diameter.

Megascleres (refer to Table 4 for dimensions). Styles of a single size class, although great variability in thickness; styles predominantly robust, slightly curved near basal end, rarely straight, usually with evenly rounded bases, rarely rhabdose, tapering to fusiform points, and occasionally modified to strongyles.

Microscleres. Absent.

Distribution

Indian Ocean and Indo-west Pacific, known from the Seychelles, south-eastern Indonesia, Arafura Sea, Timor Sea, mid-Western Australia, Japan and New Caledonia. Recorded from

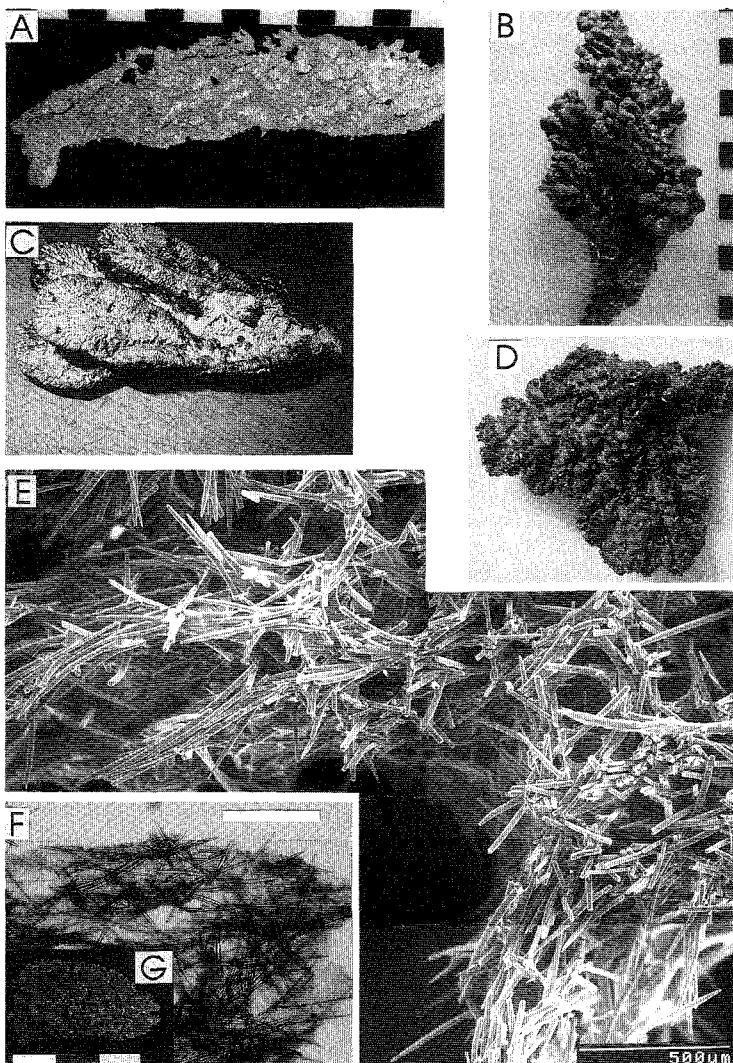


Fig. 20. *Stylissa flabelliformis* (Hentschel): *A*, fragment of (?) paratype SMF1690 (schizotype MNHN DCL2314); *B*, specimen from New Caledonia [ORSTOM R1257 (QM G300017)]; *C*, specimen on deck from NW. Australia (NTM Z1807); *D*, specimen from Ashmore Reef (QM G300183); *E*, SEM skeleton (scale = 500 µm); *F*, *Stylissa massa* (Carter), skeleton of holotype BMNH 1889.6.9.4 (scale = 500 µm); *G*, holotype.

coral reefs, in lagoon, fringing and patch reefs and outer reef slope, sand and coral rubble, 3–76 m depth.

Remarks

The New Caledonian population of *S. flabelliformis* is currently the most easterly known record of the species. The species is probably a prominent member of the Indo-west Pacific fauna, although its known distribution is patchy. Certainly, in the eastern Indian Ocean, from eastern Indonesia to the vicinity of Northwest Cape, Western Australia, the species is relatively abundant in the subtidal to about 50 m depth, whereas its relative abundance outside this zone is unknown. In New Caledonia the species is also moderately common within the lagoon, less abundant on the outer reefs, and from the restricted material examined there were no obvious differences detected between any of the regional populations (see also Table 4). However, one specimen trawled from the Northwest Shelf of Western Australia (QM G300108) was atypical in growth form (being much larger, with even margins on the lobate branches, and having distinct longitudinal surface ridges), and in spicule dimensions (having generally shorter and thicker spicules; Table 4), but these differences are not considered to be significant and in other features it agreed closely with all other known material of this species.

Stylissa flabelliformis is closely related to its sympatric sibling species, *S. massa*, which, from re-examination of the holotype, appears to differ only in growth form (the latter being massive; Fig. 20G), skeletal structure (*S. massa* has an even more disorganised reticulate skeleton than *S. flabelliformis*; Fig. 20F), and larger spicule dimensions (Table 4). These features appear to be consistent in all the descriptions of *S. massa*, and the two species are retained here, but morphologically they are certainly closely related. From Hallmann's (1916a: 544) comprehensive redescription of *S. variabilis*, it appears to be similar in growth form to *S. flabelliformis*, whereas the skeleton is much more organised, plumose (plumo-reticulate, resembling *Teichaxinella* more than *Stylissa*), styles are larger and more-or-less divisible into two size classes, and raphides are also present.

Genus *Ptilocaulis* Carter

Ptilocaulis Carter, 1883: 321.—Carter, 1884: 130; Topsent, 1928: 37, 172; de Laubenfels, 1936: 127; Wiedenmayer, 1977: 152 [type species *Ptilocaulis gracilis* Carter, 1883: 321 (holotype BMNH 1845.12.30.1) (de Laubenfels, 1936) (Fig. 21D)].
Plicatella Schmidt, 1864: 39 [preocc.].—de Laubenfels, 1936: 132 [type species *Reniera labyrinthica* Schmidt, 1864: 39].

Diagnosis

Typically erect, cylindrical, digitate, clavate to bushy, occasionally lamellate growth form; surface conulose or with numerous elongate and overlapping papilliform projections, often dividing at the apex. Choanosomal skeleton plumo-reticulate, with clearly differentiated axial and extra-axial components; axial portion of skeleton condensed, composed of irregularly anastomosing, close-set spongin fibres and spicules; extra-axial skeleton plumo-reticulate or plumose, with heavy fibres cored by ascending multispicular tracts of megascleres, interconnected by paucispicular transverse tracts forming subisodictyal reticulation (s.s.), or without transverse spicule skeleton and simply with meandering, plumose extra-axial spicule tracts; ectosome fleshy, without specialised spiculation, although plumose brushes of spicules may protrude through surface. Megascleres styles, subtylostyles, anisoxeas or strongyles (usually asymmetrical), sometimes including sinuous forms. Microscleres absent (modified from Wiedenmayer 1977).

Remarks

De Laubenfels (1936: 127) suggested that *Ptilocaulis* was characterised by having superficial surface processes, a condensed and plumo-reticulate skeleton rich in spongin, and only styles for megascleres, but these features barely define the taxon and in any case are not completely accurate (i.e. spicules usually include styles, anisoxeas, strongyles, and oxeas,

some or all with telescoped ends). Wiedenmayer (1977: 152) suggested that longer spicules in the extra-axial skeleton, larger than those found in the choanosome, could also be used as a discriminatory character for the genus, but this feature is not present in the type species nor in many other described species. Wiedenmayer's observations were based on two species that he placed in *Ptilocaulis*, one of which was *Spongia spiculifera* Lamarck (1814) from southern Australia, following Topsent (1932), which had clearly differentiated size classes of ectosomal and choanosomal megascleres but was similar in other characters to other members of the genus, but this feature cannot be construed as being typical of *Ptilocaulis*.

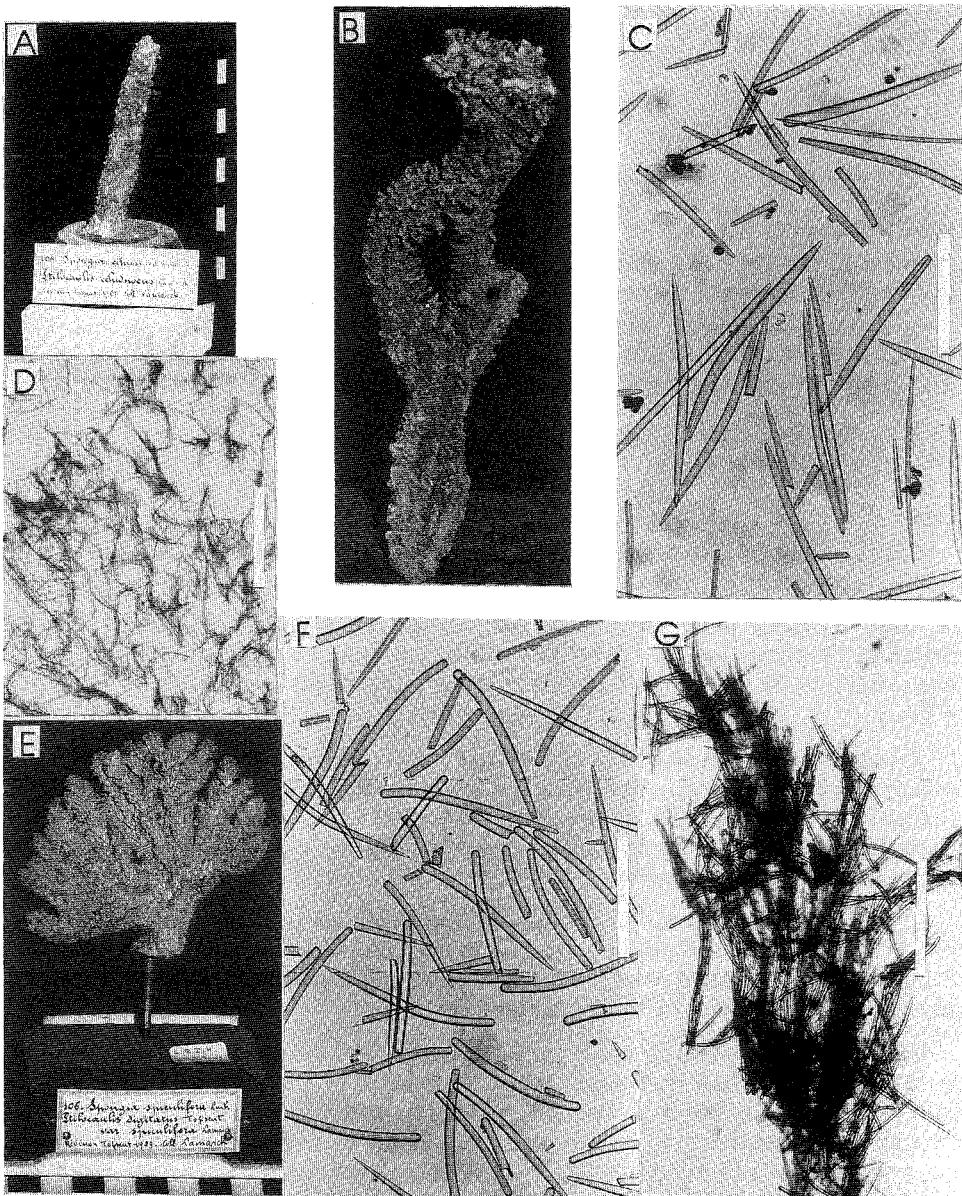


Fig. 21. *Ptilocaulis* spp.: A, *Spongia echidnaea* Lamarck (holotype MNHN DT640); B, specimen (MNHN DT3347); C, Topsent's spicule preparation of holotype (scale = 200 µm); D, *Ptilocaulis gracilis* Carter, skeleton of holotype (BMNH 1845.12.30.1) (scale = 500 µm); E, *Spongia spiculifera* Lamarck (lectotype MNHN DT3345); F, Topsent's spicule preparation of lectotype (scale = 200 µm); G, section of peripheral skeleton (scale = 500 µm).

The presence of anisoxeas and a plumo-reticulate extra-axial skeleton in some species of *Ptilocaulis* is also similar to *Reniochalina*, as noted above.

Prior to the present study only four species of *Ptilocaulis* had been described from the Australasian region (including New Caledonia), although several others are known worldwide (e.g. Wiedenmayer 1977). Australasian species include: *Spongia echidnaea* Lamarck, 1814, probably from southern Australia (holotype MNHN DT640; Fig. 21A-C) (Topsent 1932; not Ridley 1884); *Ptilocaulis fusiformis* Lévi, 1967, from New Caledonia (see below; Figs 22-23); *Ptilocaulis rigidus* Carter, 1883, from southern Australia (?holotype BMNH 1936.5.16.1) (Thiele 1899; Hallmann 1914c; de Laubenfels 1936); and *Spongia spiculifera* Lamarck, 1814, from Bass Strait, Vic. (holotype MNHN DT638; Fig. 21E-G) (Ridley 1884; Dendy 1922; Topsent 1932, 1933; de Laubenfels 1936; Wiedenmayer 1977).

Ptilocaulis fusiformis Lévi

(Figs 22-23, Table 5)

Ptilocaulis fusiformis Lévi, 1967: 21, pl. 1, fig. b, text-fig. 4.

Material Examined

Holotype. MNHN DCL818: Baie St Vincent, Grand Tenia, New Caledonia, 40 m depth, 10.xii. 1962, coll. Mission Singer-Polignac.

New Caledonian material. QM G300719 (ORSTOM R1547): stn 503, Pointe des Pins, Canal Woodin, 22°23'4"S., 166°49'6"E., 25-35 m depth, 11.x.1991, coll. G. Bargibant, SCUBA; QM G301262 (ORSTOM R854): stn 198, pinnacle S. of Canyon Central, Chenal des Cinq Milles, 22°30'4"S., 166°45'1"E., 35 m depth, 15.ii.1978, coll. G. Bargibant, SCUBA; QM G301324, G301327, G301335, G301341: Croissant-Larégrière, Ilôt Maitre, off Noumea, 22°20'2"S., 166°22'5"E., 20 m depth, 13.x. 1992, coll. J. N. A. Hooper, SCUBA.

Description

Colour. Live coloration pale orange, yellow-brown (Munsell 7·5YR 8/10), pale orange-brown in ethanol.

Shape. Digitate or arborescent digitate, 42-110 mm long, with cylindrical bifurcate branches, 23-55 mm long, up to 10 mm diameter, tapering towards ends, and with short basal stalk, 15-19 mm long, 7-10 mm diameter, and broad basal holdfast, 12-21 mm diameter.

Surface. Highly conulose, with more-or-less evenly distributed conules, up to 5 mm high, usually forming meandering ridges running longitudinally along branches. Conules interconnected by fleshy surface membrane, pierced by small ostia (visible only between conules), about 500 µm diameter. Oscules small, 1·5-2 mm diameter, rarely observed, near apex of branches. Texture firm, flexible.

Ectosome. Fleshy, mostly membranous surface, with sparse plumose brushes of longer, usually sinuous megascleres barely protruding through ectosome, restricted to tips of conules. Ectosomal membrane highly collagenous, more darkly pigmented than choanosomal mesohyl, and with small quantities of detritus embedded.

Choanosome. Skeletal structure plumo-reticulate, with clearly differentiated axial and extra-axial regions. Axial skeleton compressed, composed of a heavy spongin fibre skeleton with individual fibres no more than 150 µm long, up to 50 µm diameter, forming a close-set reticulation producing with oval meshes, 30-90 µm diameter, and cored by plumose, paucispicular tracts of mostly shorter anisoxeas and fewer sinuous strongyles. Extra-axial skeleton corresponds with distribution of surface conules. Extra-axial fibres plumo-reticulate, noticeably more cavernous than in axis, with individual fibres extending for up to 300 µm, 25-35 µm diameter, producing elongate meshes, and extra-axial fibre system runs predominantly laterally through branch cross-section. Fibres cored by multispicular plumose tracts of both sinuous strongyles and anisoxeas ascending towards surface. Extra-axial skeletal columns are separated by large cavernous areas (canals, up to 650 µm diameter),

covered by an external collagenous layer (up to 550 µm wide, extending for 750–1250 µm between surface conules.

Megascleres (refer to Table 5 for dimensions). Two length-classes of megascleres distinguished here, although these clearly intergrade in size and morphology. Longer megascleres are thin, curved or sinuous strongyles, predominantly in extra-axial region of choanosome and at surface, although also coring axial fibres, with asymmetrical (styloid), or symmetrical rounded ends.

Shorter megascleres are slightly curved, thin anisoxeas, found predominantly in the axial skeleton, although also dispersed in peripheral skeleton, usually with symmetrical rounded or pointed, usually telescoped ends ('oxeas'), or less often with asymmetrical ends (hastate points and evenly rounded bases; 'styles').

Microscleres. Absent.

Distribution

Known only from the coral reefs of the New Caledonian lagoon, 25–40 m depth.

Remarks

Although two size classes of megascleres (longer sinuous strongyles and shorter curved anisoxeas) are differentiated in the above description, these intergrade to some extent and intermediate 'oxeas' and 'anisoxeas' could fit into either category. There was no observed regional localisation of these two categories of spicules to any particular region of the

Table 5. Comparison in spicule dimensions between species of *Ptilocaulis*

All measurements given in micrometres, and expressed as minimum–(mean)–maximum range of measurement. $N=25$ for each specimen

Species (material)	Megascleres	
	Length	Width
<i>Ptilocaulis echidnaeus</i> (Lamarck) (holotype MNHN DT640)	493–(647·8)–816	18–(22·4)–29
Styles anisoxeas, oxeas		
<i>Ptilocaulis epakros</i> , sp. nov. (holotype QM G300016)	424–(448·2)–448	1·5–(1·8)–2
Vestigial strongyles		
	134–(268·4)–328	2·5–(3·4)–5
Styles, styloids		
<i>Ptilocaulis fusiformis</i> Lévi (holotype MNHN DCL818) (QM G300719)	414–(664·0)–900	2·5–(3·5)–6
	516–(649·3)–743	2–(2·7)–3·5
Sinuous strongyles		
	224–(267·5)–350	6–(8·2)–11
	196–(269·9)–339	2·5–(3·7)–6
Styles, anisoxeas, oxeas with telescoped ends		
	183–(290·6)–562	5–(6·2)–8
Styles, sinuous styles		
	140–(190·1)–243	1·5–(2·4)–4
<i>Ptilocaulis gracilis</i> (Carter) (holotype BMNH 1845.12.30.1)		
<i>Ptilocaulis papillatus</i> , sp. nov. (holotype QM G300748)	Vestigial styles, styloid, rarely strongyloid	
	252–(364·0)–481	13–(17·6)–21
<i>Ptilocaulis rigidus</i> Carter (?holotype BMNH 1936.5.16.1)	Styles, oxeas, anisoxeas	
	242–(291·6)–334	11–(16·4)–20
<i>Ptilocaulis spiculifera</i> (Lamarck) (holotype MNHN DT638)	Short robust curved styles	
	492–(599·6)–704	11–(12·2)–14
	Long slender, curved styles	

skeleton, and thus we cannot confirm Wiedenmayer's (1977) 'typical' diagnosis of these characters for the genus. Similarly, unlike most other species of *Ptilocaulis*, it is difficult to classify the spicules in *P. fusiformis* as either styles, oxeas or strongyles, due to the great range in spicule terminations (abrupt points, telescoped endings, evenly rounded bases, tapering points). Lévi (1967) suggested that the spicules in the holotype were mostly styles, but re-examination of this material confirmed that a diversity of spicule terminations is characteristic of the species, although 'true styles' also occur in low numbers.

In its spiculation, the present species is most similar to *Rhaphoxya* (e.g. *R. typica* Hallmann, 1916b: 645, text-fig. 17), and thus the species is virtually intermediate between *Ptilocaulis* and *Rhaphoxya*. However, its characteristic growth form, surface sculpturing (papillae), well-differentiated axial and extra-axial skeletal structure (including a compressed axial skeleton) indicate that *P. fusiformis* is most appropriately placed in *Ptilocaulis*. The species is contrasted further with other Australasian *Ptilocaulis* below, and in Table 5.

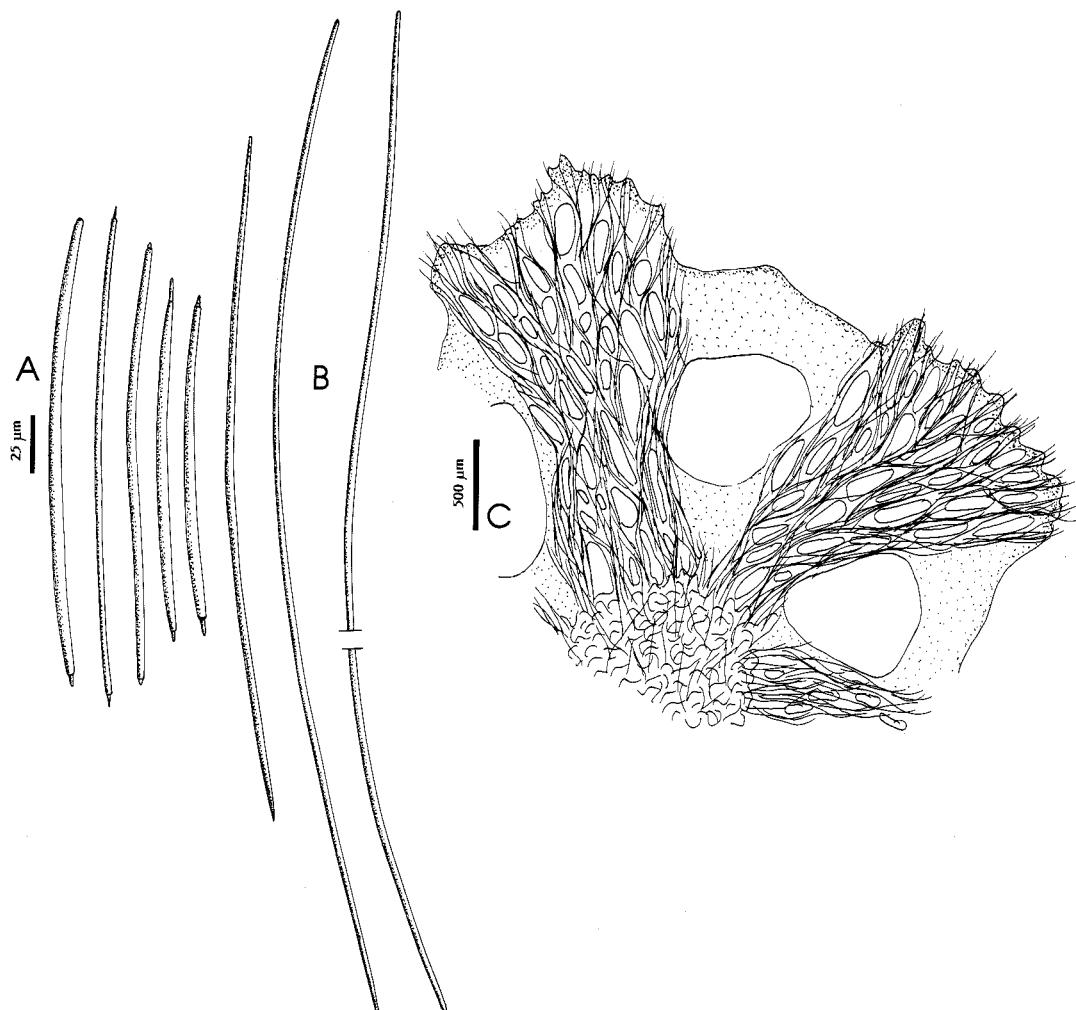


Fig. 22. *Ptilocaulis fusiformis* Lévi, specimen QM G300719: A, shorter predominantly axial anisoxeas; B, longer predominantly extra-axial strongyles; C, section through peripheral skeleton.

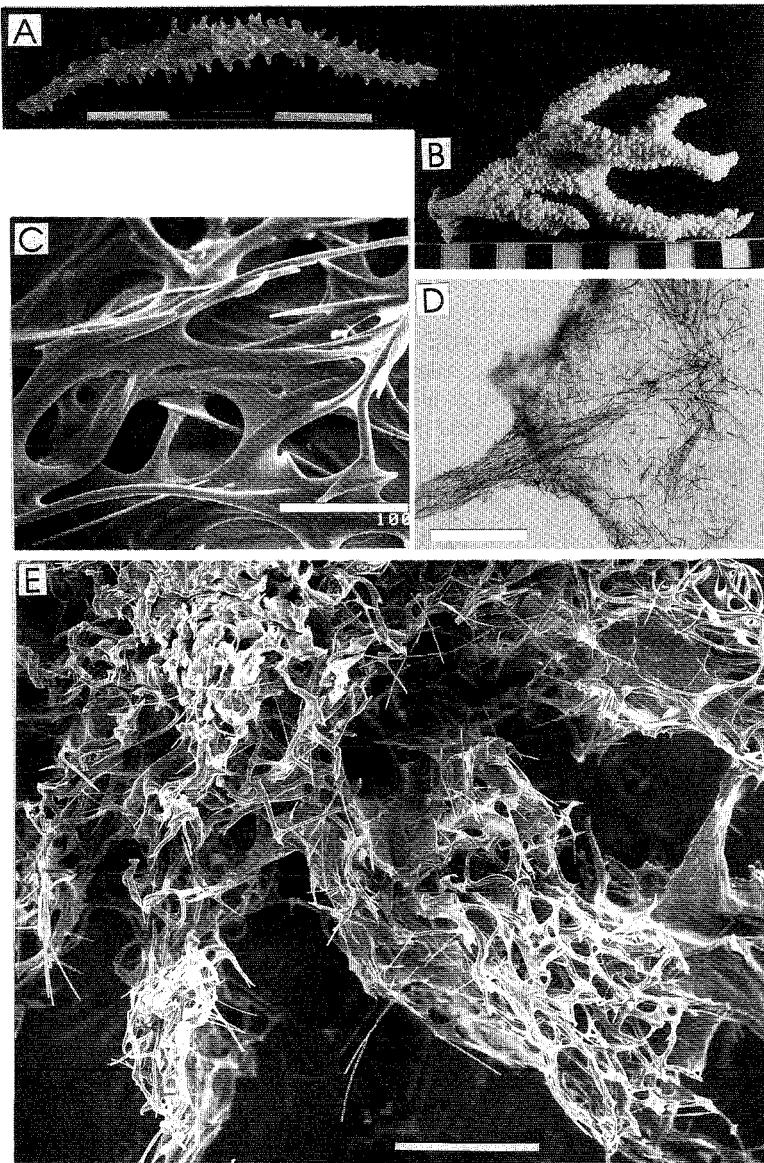


Fig. 23. *Ptilocaulis fusiformis* Lévi: *A*, holotype (MNHN DCL818); *B*, specimen [QM G300719 (ORSTOM R1547)]; *C*, SEM axial fibres (magnified 400 \times); *D*, skeleton of holotype (scale = 500 μm); *E*, SEM skeleton (QM G300719) (magnified 40 \times).

Ptilocaulis epakros, sp. nov.

(Figs 24–25, Table 5)

Material Examined

Holotype. QM G300016 (ORSTOM R1232): stn 247, Baie Kouo, Canal Woodin, New Caledonia lagoon, 22°23'5"S., 166°49'2"E., 40 m depth, 29.xi.1978, coll. P. Laboute, SCUBA.

Description

Colour. Live coloration pale yellow-brown (Munsell 2·5YR 8/8), beige in ethanol.

Shape. Arborescent, bifurcate branching, 200 mm long, 70 mm maximum lateral branch span, with thin, cylindrical branches, 27–60 mm long, 5–17 mm wide including papillae, tapering towards pointed branch tips, with long, unornamented stalk, 75 mm long, 4 mm diameter, and expanded basal attachment, 13 mm diameter.

Surface. Heavily ornamented, papillose surface, with long, close-set, sharply pointed, soft papillae, 2–4 mm long, 0.5–1 mm diameter, up to 2 mm apart; tips of papillae bifurcate and/or hispid; bases of adjacent papillae interconnected by membranous ridges running longitudinally along branches, slightly elevated above surface of sponge. Oscules not observed; minute ostia, about 200 μm diameter, scattered between papillae.

Ectosome. Fleshy, membranous ectosome, without specialised spicules, with sparse detritus embedded in and on surface, with heavy collagenous, aspicular matrix, 150–200 μm wide, lying between papillae (=surface ridges) and on sides of papillae; apex of each papilla has plumose brushes of choanosomal styles, in small multispicular bundles, protruding for short distances, up to 200 μm from surface.

Choanosome. Skeleton structure plumo-reticulate, with clearly differentiated axial and extra-axial regions, and a compressed axial skeleton. Compressed region of skeleton occupies only about half (2–3 mm) of branch diameter (3–5 mm), composed of heavy, bulbous spongin fibres, with individual fibres only about 100 μm long, 50–70 μm diameter, together

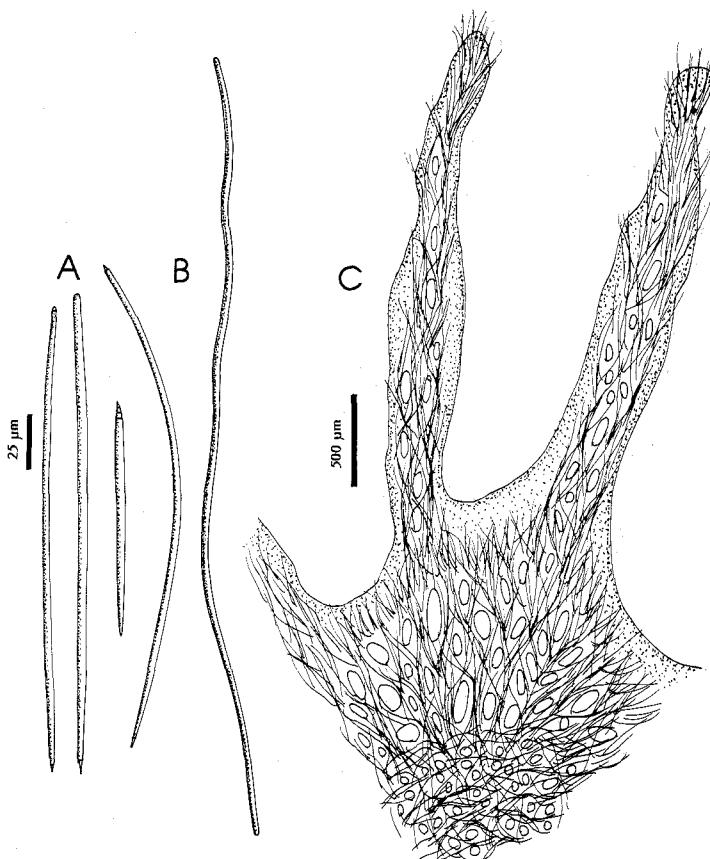


Fig. 24. *Ptilocaulis epakros*, sp. nov., holotype QM G300016: *A*, styles and styloids, comprising the majority of spicules; *B*, sinuous strongyle, relatively rare; *C*, section through peripheral skeleton.

forming a close-set reticulation and producing small oval meshes, 50–90 μm diameter; axial fibres cored by uni-, pauci- or multisicular tracts of thin megascleres, occupying only a small proportion of fibre diameter. Abundant, lightly pigmented collagen in mesohyl of axial skeleton. Extra-axial skeleton extensive, including area immediately surrounding axis of branches (1–2 mm diameter) as well as elongated, slender skeletal columns (= papillae; up to 4 mm long). Extra-axial skeleton composed of primary and secondary fibre systems, differentiated mainly by presence or absence of coring spicules; both fibre systems composed of heavy spongin fibres, with individual fibres up to 300 μm long, 40–60 μm diameter, producing a relatively wide, elongate mesh reticulation, 110–170 μm mesh diameter; ascending extra-axial fibres cored by multisicular, plumose columns of choanosomal styles, with spicule tracts becoming heavier towards peripheral skeleton [eventually terminating in plumose brushes which may or may not protrude through surface (tips of papillae, versus between papillae respectively)]. Many (but not all) transverse, connecting fibres in extra-axial skeleton uni- or aspicular, with long exceedingly slender strongyles (although these were invariably broken *in situ*, and consequently were not observed in spicule preparations). Collagen abundant and slightly more darkly pigmented in extra-axial region; choanocyte chambers not observed.

Megascleres (refer to Table 5 for dimensions). Two categories of spicules present, clearly differentiated in morphology but not obviously localised to any particular region of skeleton. Few transverse, connecting fibres contain a single, long, thin, sinuous strongyle, but these spicules are rare.

Majority of spicules are styles or styloids, short or long, slender, straight or slightly curved asymmetrically, with evenly rounded or tapering mucronate bases, and hastate, fusiform or telescoped points.

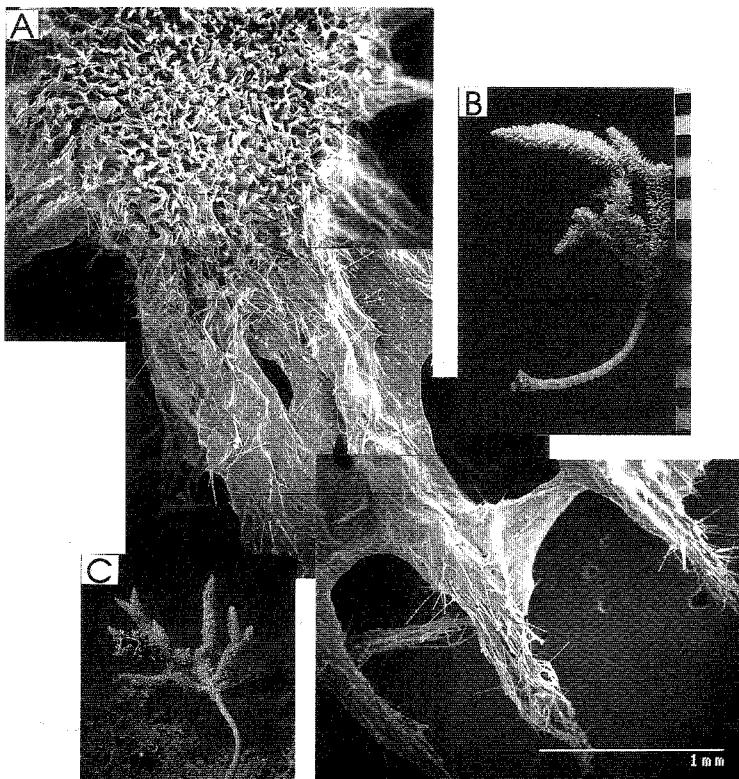


Fig. 25. *Ptilocaulis epakros*, sp. nov.: A, SEM skeletal structure (scale = 1 mm); B, holotype [QM G300016 (ORSTOM R1232)]; C, holotype *in situ* (photo P. Laboute).

Microscleres. Absent.

Distribution

Known only from the New Caledonian lagoon, inter-reef region, 40 m depth.

Remarks

This species is obviously a closely related, sibling species of *Ptilocaulis fusiformis*. In its external morphology, including shape and size of surface papillae, it is easily differentiated from *P. fusiformis*, whereas there are only subtle differences in the geometry and size of megascleres (Table 5), and in the structure of the skeleton between the two species (Figs 22, 23 cf. Figs 24, 25). In fact, all three sympatric sibling species, *P. fusiformis*, *P. epakros* and *P. papillosus*, are most visibly differentiated only by these features. It is conceivable that all three nominal species are members of a single, extremely polymorphic species, but gross external morphology and more subtle skeletal differences do not presently support this hypothesis, and the three taxa are retained here. Only molecular evidence will support or refute this hypothesis.

In its arborescent growth form, with thinly cylindrical bifurcate branches and long, unornamented stalk, and its long, tapering, sharply pointed surface conules, *P. epakros* shows remarkable superficial resemblance to *Thrinacophora funiformis* Ridley & Dendy (1887: pl. 24, fig. 1) (Raspailiidae), although obviously in spiculation and skeletal architecture the two species are otherwise quite different.

Etymology

Named for the long, attenuated, sharply pointed surface papillae, from *epakros* (Gk), pointed at the end.

Ptilocaulis papillatus, sp. nov.

(Figs 26–27, Table 5)

Material Examined

Holotype. QM G300748 (ORSTOM R564): stn 113, L'epave du 'Bonhomme', Grand Récif Mbère, 22°21·0'S., 166°14·0'E., 25 m depth, 21.vi.1976, coll. P. Laboute, SCUBA.

Description

Colour. Live coloration unknown, white in ethanol.

Shape. Elongate, cylindrical digitate, 120 mm long, 14 mm wide at widest point, 4 mm wide at end of branch, single branching and bifurcate tips at end of branches, with short (unornamented) stalk, 17 mm long, 5 mm diameter, and enlarged basal attachment, 16 mm diameter.

Surface. Prominently sculptured surface composed of large discrete papillae, each papilla formed by extra-axial skeletal columns, up to 6 mm long, 2·5 mm diameter, standing perpendicular to axial core, dispersed approximately 1·5–3 mm apart, enlarged, flattened and bifurcate at apex, usually interconnected by translucent dermal membrane, but cavernous below membrane.

Ectosome. Translucent dermal membrane, collagenous, aspiculose except at ends of extra-axial skeletal columns (papillae) where tufts of megascleres protrude slightly through surface.

Choanosome. Skeletal structure plumo-reticulate, with very well differentiated axial and extra-axial skeletons, and heavily compressed axial skeleton. Spongin fibres dominate both sections of skeleton; in axial region fibres heavy, close-set, up to 150 µm long, 50 µm diameter, bulbous, meandering, producing oval, elongate or irregular meshes, 30–140 µm diameter, with heavy collagenous mesohyl; in extra-axial skeleton fibres less heavily compacted, with individual fibres up to 250 µm long, 30 µm diameter, producing elongated

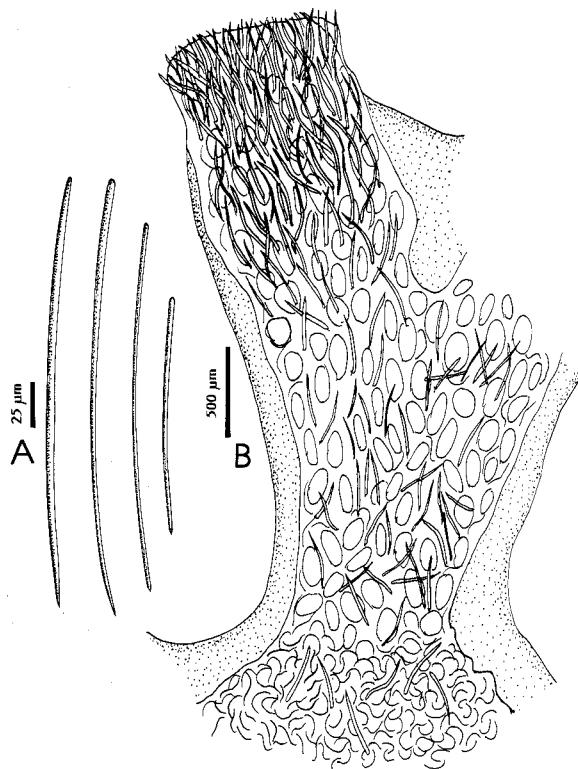


Fig. 26. *Ptilocaulis papillatus*, sp. nov., holotype QM G300748: *A*, vestigial styles, styloids and strongylote spicules; *B*, section through peripheral skeleton.

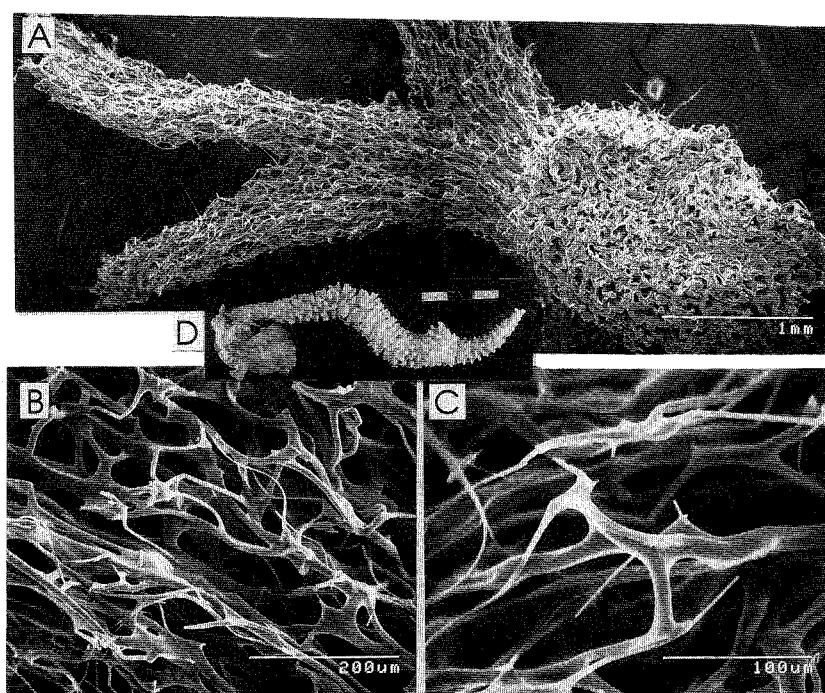


Fig. 27. *Ptilocaulis papillatus*, sp. nov.: *A*, holotype (QM G300748), SEM skeletal structure (scale = 1 mm); *B*, SEM axial fibres (scale = 200 μ m); *C*, SEM fibre structure (scale = 100 μ m); *D*, holotype.

meshes up to 170 µm diameter, more-or-less directed towards surface, and fibres become thinner and more widely spaced near ectosome. Spicule skeleton nearly vestigial, with very few megascleres in axial region, but becoming increasingly abundant towards surface; extra-axial spicule skeleton plumose, ending with plumose bundles of megascleres protruding slightly through surface, at apex of skeletal columns (papillae). Area between skeletal columns usually cavernous, without collagen, fibres or mineral skeleton, measuring up to 2 mm between adjacent columns. Collagen in extra-axial skeletal columns abundant but lightly pigmented; choanocyte chambers small, oval, 20–40 µm diameter.

Megascleres (refer to Table 5 for dimensions). Most spicules vestigial, with blackened axial canals, exclusively styles or styloids, rarely strongylote, usually slightly curved, sometimes sinuous, with evenly rounded or tapering bases and hastate points, not telescoped.

Microscleres. Absent.

Distribution

Known only from the New Caledonian lagoon, in the inter-reef region on sand/rubble substrate.

Remarks

This species is most similar to the sympatric *P. fusiformis* in its skeletal structure, growth form and spiculation, except that all these characters are greatly exaggerated in *P. papillatus*. Surface papillae are exceptionally large and bifurcate, and rejoin with adjacent papillae at their apex by a translucent dermal membrane; spongin fibre compression is relatively greater in both axial and extra-axial regions; spicules are virtually vestigial in most of the skeleton, except towards the surface where they become exclusively plumose; and spicules are exclusively styloid, without any apparent differentiation in size (Table 5). These features clearly differentiate this species from *P. fusiformis*, whereas differences between *P. fusiformis* and *P. epakros* are more subtle.

Etymology

Named for the unusual surface sculpturing, from *papillatus* (Lat.), bud-like, papillose.

Genus *Pseudaxinella* Schmidt

Pseudaxinella Schmidt, 1875: 120.—Thiele, 1903: 378; Bergquist, 1970: 20; Lévi, 1973: 606; Wiedenmayer, 1977: 155 [type species *Pseudaxinella sulcata* Schmidt, 1875: 120].

Diagnosis

Usually massive, subspherical, cushion-shaped, unbranched or lobate growth forms, with finely conulose or tuberculate, corrugated surface. Skeleton typically plumo-reticulate, without axial compression or differentiation between axial and extra-axial regions; skeletal tracts consist of oxeas and styles, often in crowded, ascending tracts. Ectosome fleshy, and megascleres in this region may be thinner than choanosomal spicules, but not definitely so. Megascleres typically include only (anis-)oxeas and styles in equal proportions, but some species also have long flexuous styles or strongyles confined to the surface. Microscleres absent (modified from Wiedenmayer 1989).

Remarks

The presence, absence or modification of megascleres to long flexuous diacts (strongyles) probably has questionable diagnostic value in the Axinellidae. Vacelet (1969) and Pansini (1983) have shown that the traditional distinction between *Axinella* and *Phakellia* (cf. Vosmaer 1912), based on external form and the presence of flexuous diactines in the axial skeleton, is not reliable. Consequently, the importance of those spicules in diagnosing *Pseudaxinella* may also be of doubtful systematic value (Wiedenmayer 1989). Nevertheless, in the absence of a reliable, comprehensive revision of the Axinellidae, incorporating all taxa that have sinuous strongylote modifications, it is not possible to evaluate whether or not

those megascleres occur consistently or at what level they have systematic value. Consequently, definitions of *Pseudaxinella* provided by Ridley and Dendy (1887), Vosmaer (1912, 1935a), Babic (1922) and Topsent (1934) must be treated with circumspection.

Pseudaxinella was originally erected for species 'like *Axinella*' (i.e. in spiculation), but lacking axial compression (de Laubenfels 1950); but Wiedenmayer (1989) noted that some species [e.g. *P. convexa* (Hoshino, 1981), *P. decipiens* Wiedenmayer, 1989] have nearly confused skeletons, atypical of the genus, although agreeing in all other respects. Thus, in Wiedenmayer's (1989) opinion, skeletal organisation may be a poor diagnostic character for these groups, whereas features such as the absence of a special axial skeleton and external morphology (massive subspherical in *Pseudaxinella*, thinly flabellate in *Axinosa/Teichaxinella*) might be more reliable diagnostic features. However, rightly or wrongly, the present scheme of classification for the Axinellidae differentiates all constituent genera at least partly on the basis of their skeletal construction, and without revising this current basis for the classification, which is unrealistic in the present work, we propose to retain this character [i.e. the non-compressed, plumose (plumo-reticulate) spicule skeleton] for now. The genus is discussed further at length by Wiedenmayer (1989: 48).

Prior to the present work, only three species had been recorded from the Indo-west Pacific: *Pseudaxinella australis* Bergquist, 1970, from northern New Zealand (holotype NMNZ Por.26 [not seen]), also recorded recently from northern Australia (Hooper, unpublished; Fig. 30, Table 6); *Pseudaxinella decipiens* Wiedenmayer, 1989, from Bass Strait, Vic. (holotype NMV F51961 [not seen]); and *Phakellia tumida* Dendy, 1897a, from Port Phillip, Vic. (holotype NMV G2464 [not seen]) (Vosmaer 1912). A fourth species is also known from the neighbouring province, Ariake Sea, Japan: *Axinella convexa* Hoshino, 1981 (holotype MMBS AR-1-11 [not seen]).

Pseudaxinella debitusae, sp. nov.

(Figs 28–29, Table 6)

Material Examined

Holotype. QM G300725 (ORSTOM 'cfR806'): stn 124, Ilôt Maitre, 22°20'1"S., 166°25'1"E., 25 m depth, 1.x.1991, coll. G. Bargibant, SCUBA.

Paratypes. QM G300722 (ORSTOM 'cfR806'): stn 181, Ilôt Maitre, 22°20'0"S., 166°25'0"E., 10 m depth, 1.x.1991, coll. J.-L. Menou, SCUBA; NTM Z3887, QM G300695: Baie des Citrons, off Noumea, 22°20'S., 166°27"E., 3 m depth, 25.ix.1990, coll. J. N. A. Hooper, snorkel, stn JH-90-019.

Other New Caledonian material. QM G301263 (ORSTOM R1227), ORSTOM 'cfR1221': stn 261, SW. Ilôt Nda, Lagon Sud, 21°52'5"S., 166°51'2"E., 33 m depth, 4.xi.1979, coll. P. Laboute, ORSTOM, SCUBA; QM G301319, G301328, G301332: Croissant-Larégrière, Ilôt Maitre, off Noumea, 22°20'2"S., 166°22'5"E., 20 m depth, 13.x.1992, coll. J. N. A. Hooper, SCUBA.

Description

Colour. Orange to orange-yellow alive (Munsell 10R 6/10-2·5YR 7/8), beige or light brown in ethanol.

Shape. Massive, irregularly or regularly subspherical, cushion shaped, 55–80 mm diameter, 32–40 mm maximum height above substrate, loosely attached to large pieces of detritus (e.g. dead coral, pelecypod valve), or occasionally rolling free on the substrate (i.e. 'tumbleweed' effect).

Surface. Evenly microconulose, goose-flesh appearance, covered by small conules, 1–2 mm diameter, less than 0·5 mm high, scattered over entire surface, interconnected by semi-translucent dermal membrane. Oscules scattered over 'upper' surface, large in life (5–10 mm diameter), contracted in ethanol (1–2 mm diameter), located in slight depressions on surface and surrounded by slightly raised membranous lip. Texture soft, compressible, relatively easy to tear.

Ectosome. Membraneous, fleshy surface, with tips of choanosomal spicules protruding for short distances, up to 150 µm, from surface in sparse plumose brushes. Heavy, more darkly pigmented collagen clearly marks peripheral region, whereas in choanosomal mesohyl

collagen is only lightly pigmented. Oval choanocyte chambers in peripheral skeleton, 70–190 µm diameter, also clearly outlined by more darkly pigmented, granular spongin.

Choanosome. Skeleton plumo-reticulate, without axial compression or any noticeable difference between axial and extra-axial regions. Spongin fibre skeleton reticulate, with predominantly ascending primary fibres, up to 70 µm diameter, interconnected by shorter, thinner secondary fibres, 40–60 µm diameter, together producing oval meshes 70–140 µm diameter. Spicule skeleton plumo-reticulate, with clearly differentiated primary, ascending, multispicular tracts, cored by spicules in plumose bundles, interconnected by secondary, uni- or paucispicular, more-or-less transverse spicule tracts, and spicule reticulation producing a vaguely subrenieroid reticulate skeleton, although the plumose component is emphasised over the reticulate component. Mesohyl moderately light, lightly pigmented.

Megascleres (refer to Table 6 for dimensions). Spicules predominantly oxeas, with rare styles and strongyloxeas also present; all spicules relatively long, slender, usually asymmetrically curved (but not rhabdose), sometimes straight, mostly sharply pointed, fusiform, although telescoped and bifurcate points also observed.

Microscleres. Absent.

Table 6. Comparison in spicule dimensions between similar species of *Pseudaxinella*

All measurements given in micrometres, and expressed as minimum-(mean)-maximum range of measurement. $N=25$ for each specimen

Species (Locality) (material)	Megascleres Length	Megascleres Width
<i>Pseudaxinella australis</i> Bergquist (New Zealand) (holotype; Bergquist 1970: 20)	203–(402)–560 Styles, slightly rhabdose bases 320–(367)–406 Thinner ectosomal styles 217–(260)–339 Centrally curved oxeas 172–(274·0)–312 Styles, slightly rhabdose bases 252–(289·2)–315 Centrally curved oxeas	9–(15·0)–22 3–(4·0)–6 8–(9·6)–10 10–(13·2)–16 8–(11·8)–15
(Great Barrier Reef) (QM G300295, G301089, G300880; Hooper, unpublished)		
<i>Pseudaxinella debitusae</i> , sp. nov. (New Caledonia) (holotype) (paratypes)	243–(358·5)–503 223–(369·9)–483 Predominantly asymmetrical oxeas, rare styles or strongyloxeas	4–(9·6)–15 2–(7·8)–12
<i>Pseudaxinella convexa</i> (Hoshino, 1981: 207)	550–(760)–920 Oxeas, occasionally styles 330–950 Sinuous oxeas, strongyloxeas	10–(18)–26
<i>Pseudaxinella decipiens</i> Wiedenmayer (1989: 48) (holotype)	278–(350)–483 Oxeas, styles, strongyloxeas, anisoxeas 542–770 Sinuous strongyles	4–(7·8)–11
<i>Pseudaxinella rosacea</i> (Verill) (de Laubenfels, 1950)	235–400 Styles 300–320 Oxeas	8–11 8
<i>Pseudaxinella tumida</i> (Dendy, 1897a: 237)	About 180 Styles only	About 6

Distribution

Known only from the New Caledonian lagoon, subtidal fringing coral reefs, coral rubble substrate, 3–33 m depth.

Remarks

This species is closely related to *Pseudaxinella australis* Bergquist, to which it was initially assigned. However, a detailed comparison between the New Caledonian material described above, the New Zealand holotype of *P. australis* (Bergquist 1970: 20), and another three specimens of *P. australis* from northern Australia (QM G300880, Moreton Bay, Qld; G300295, Snake Reef, northern Great Barrier Reef, Qld; G301089, Cartier I., Sahul Shelf, W.A.; Fig. 30, Table 6), showed quite a number of differences.

The New Caledonian material was pale orange in life, and this colour is probably truly representative of the population as it was observed in all three specimens from the lagoon. In contrast, both New Zealand and Great Barrier Reef material was consistently bright red in life, and all known material was observed to exude clear mucus, whereas this trait was not observed in New Caledonian specimens. *Pseudaxinella debitusae* has a plumo-reticulate skeleton, with adjacent plumose, ascending skeletal columns interconnected by a paucispicular subrenieroid skeleton, whereas in *P. australis* the ascending, plumose spicule tracts are more or less discrete with few interconnections (cf. Figs 28B, 29D–E and 30B). In New Caledonian specimens, the plumose spicule brushes protruding through the ectosome were not noticeably thinner than those in the choanosome, unlike the holotype of *P. australis* (although these ‘ectosomal spicules’ were not observed in Great Barrier Reef material

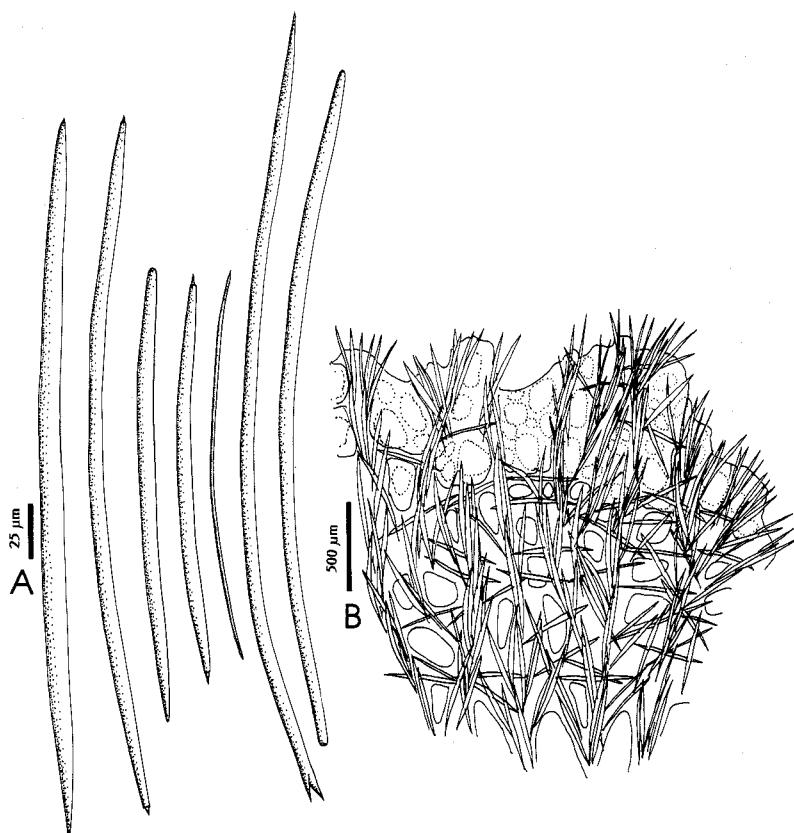


Fig. 28. *Pseudaxinella debitusae*, sp. nov., paratype QM G300722: *A*, oxeas, styles and strongyloxea structural spicules; *B*, section through peripheral skeleton.

either). Similarly, there was no apparent localisation of different spicule morphologies in *P. debitusae* (either oxeas, or the rarer styles or strongyloxeas) to any particular region of the skeleton, whereas the plumose spicule columns of *P. australis* are usually made up of a central core of oxeas surrounded by plumose brushes of styles (the styles verging on echinating). Bergquist (1970) also noted that, in the holotype, oxeas become more abundant towards the peripheral skeleton, but this was not confirmed in northern Australian material of *P. australis*. Most megascleres observed in *P. debitusae* were strictly oxeote, with far fewer 'abnormal terminations' (styloid, strongyloid) than seen in *P. australis*, in which

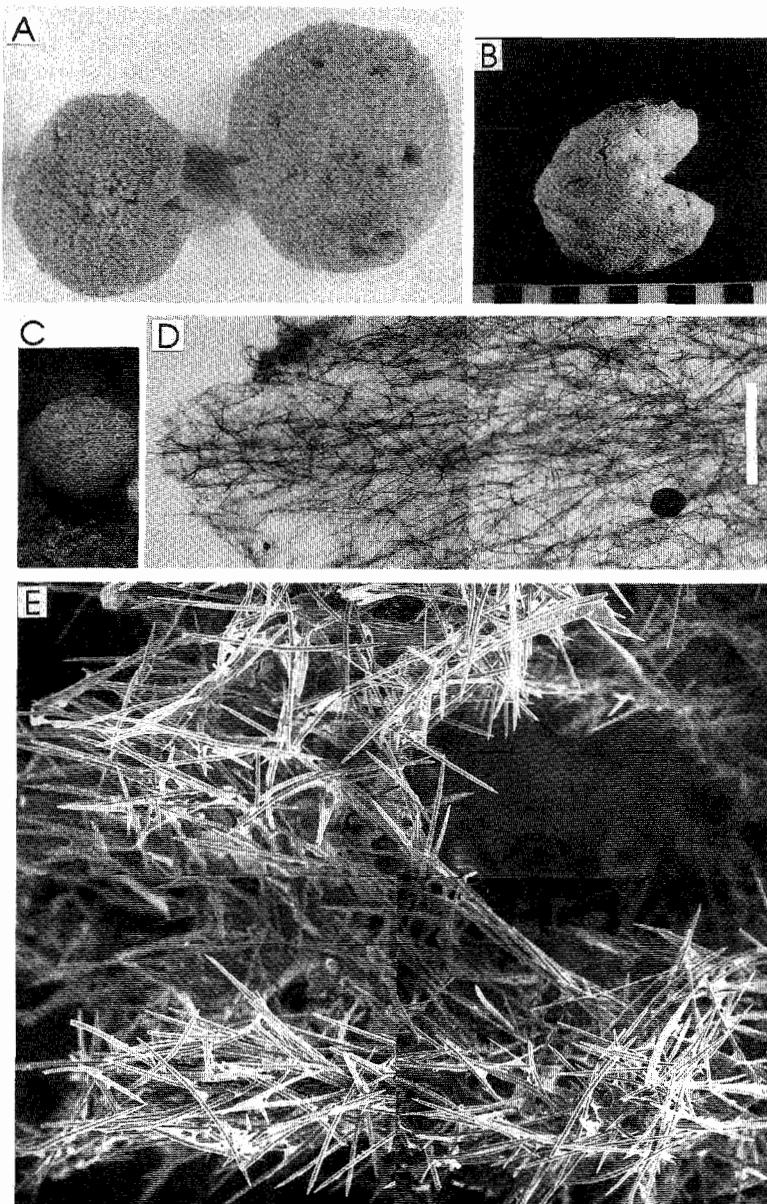


Fig. 29. *Pseudaxinella debitusae*, sp. nov.: *A*, paratypes (NTM Z3887, QM G300695); *B*, paratype (QM G300722); *C*, specimen *in situ* (ORSTOM R1227) (photo P. Laboute); *D*, peripheral skeleton (QM G300722) (scale = 500 µm); *E*, SEM skeleton (magnified 50×).

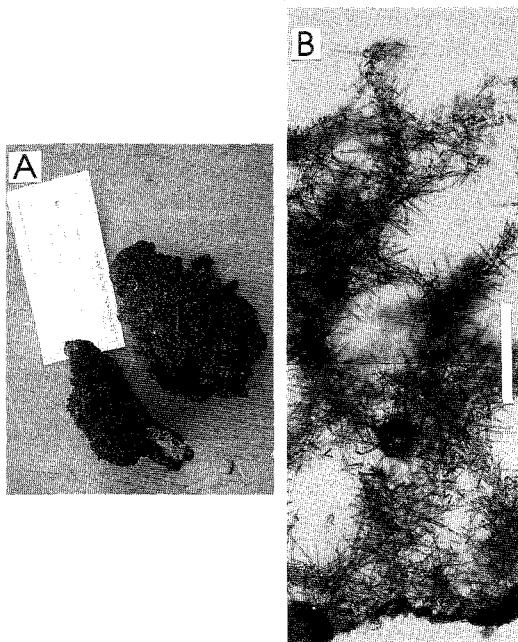


Fig. 30. *Pseudaxinella australis* Bergquist: *A*, specimens from northern Australia on deck (QM G300880); *B*, skeletal structure of specimen QM G300295 (scale = 500 μm).

oxes and styles occur in about equal proportions. Bergquist (1970) also notes that the texture of the holotype was firm, compressible and brittle, which was similar for the northern Australian material of *P. australis*, whereas *P. debitusae* is distinctly soft and compressible, easily torn, probably reflecting the relatively higher spongin fibre content of New Caledonian sponge.

Bergquist (1970) contrasts *P. australis* further with a similar species from Bermuda, *P. rosacea*, and other *Pseudaxinella* described from the Indo-west Pacific are also compared in Table 6. It is our opinion that these subtle and more gross differences between the New Caledonian species and other species of *Pseudaxinella* justify the creation of a new taxon for this population, although we recognise that the allopatric populations of northern New Zealand, south-east Queensland, Great Barrier Reef, and the Sahul Shelf are closely allied species of this New Caledonian form.

Etymology

Named for Dr Cécile Debitus, ORSTOM Noumea, in appreciation for facilitating our access to the vast ORSTOM collections, and for her role in the organisation of the collaborative workshops, leading to the publication of the present series of papers on the New Caledonian sponge fauna.

Genus *Rhaphoxya* Hallmann

Rhaphoxya Hallmann, 1916b: 641.—de Laubenfels, 1936: 136; Bergquist, 1970: 18 [type species *Rhaphoxya typica* Hallmann, 1916b: 643 (holotype AM Z1595)].
[Acanthellina] Carter, 1885: 365 [*nomen oblitum*; ICBN 50 year rule].—de Laubenfels, 1936: 139; Bergquist, 1970: 18 [type species *Acanthellina rugolineata* Carter, 1885: 139, holotype BMNH 1886.12.15.94].

Diagnosis

Massive growth form; surface with papilliform conules. Skeleton not axially condensed, without axial and extra-axial differentiation, consisting of loose, irregularly reticulate, often meandering tracts of spongin fibres and spicules; spicule tracts may (s.s.) or may not protrude through ectosome. Ectosome fleshy, lacking any specialised spiculation. Spicules often sinuous or curved, slender, monactinal and/or diactinal (styles, oxeas and strongyles,

of one size category, differing only in the character of their extremities). Microscleres raphides, occurring singly or in bundles (trichodragmata) (modified from Hallmann 1916b).

Remarks

Under van Soest *et al.*'s (1990) scheme for the distribution of axinellid genera into four families, based on skeletal architecture (i.e. Axinellidae with axially compressed and extra-axially plumoreticulate skeletons; Desmoxyidae with reticulate skeletons; Dictyonellidae with dendritic skeletons; and Halichondriidae with 'halichondroid' disorganized skeletons), *Rhaphoxya* would fall under Dictyonellidae, together with other genera with atypical, non-compressed, meandering skeletal structure, such as *Acanthella*. Although we do not currently subscribe to this division of Axinellidae and sister-groups, it does illustrate the problem in classifying axinellids, especially in relying mostly (or exclusively) on skeletal structure.

Rhaphoxya does not fit easily with other axinellid genera that have typical skeletal structure (compressed reticulate axial skeleton and plumoreticulate extra-axial skeleton), but it also shows many similarities to *Ptilocaulis*, as noted above, which does have a typical

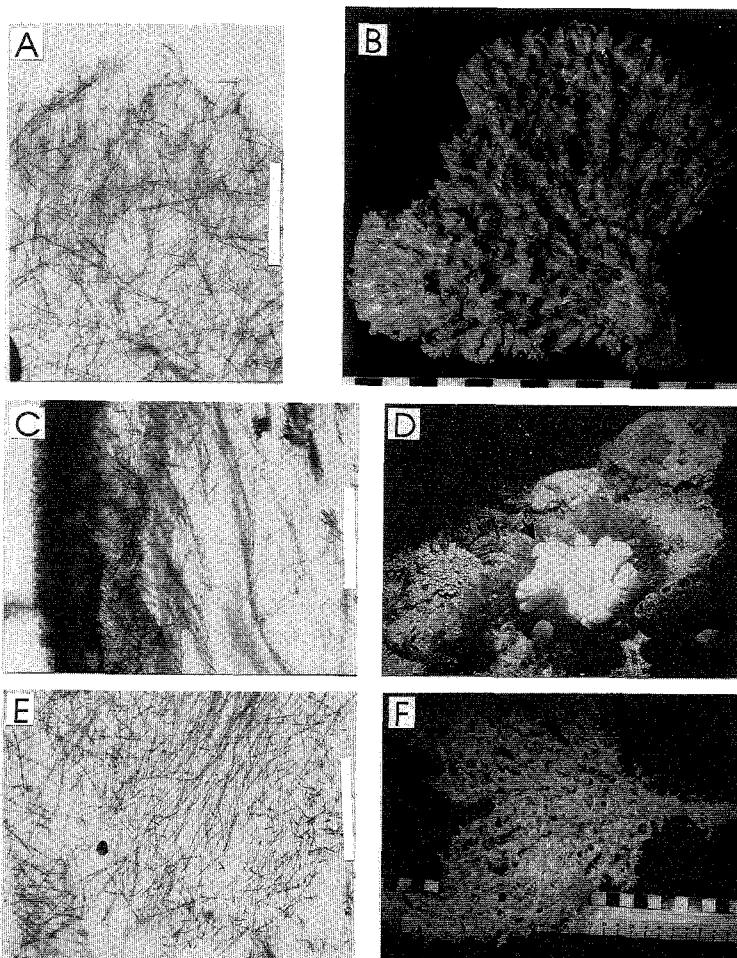


Fig. 31. *Rhaphoxya* spp.: *A*, *Acanthella cactiformis* Carter, skeleton of lectotype (BMNH 1886.12.15.81) (scale = 500 µm); *B*, lectotype; *C*, *Rhaphoxya felina* Wiedenmayer, peripheral skeleton of specimen (NCI Q66C-3339-U) (photo NCI); *D*, specimen; *E*, *Rhaphoxya pallida* Dendy, choanosomal skeleton of specimen (QM G300469) (scale = 500 µm); *F*, specimen from northern Queensland.

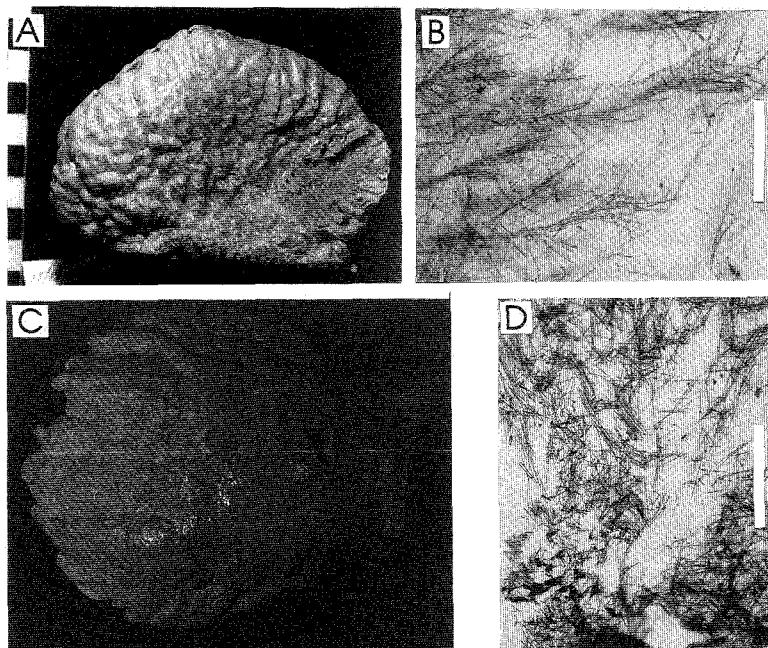


Fig. 32. *Rhaphoxya* spp.: *A*, *Acanthella rugolineata* Carter (holotype BMNH 1886.12.15.24); *B*, peripheral skeleton (scale = 500 μm); *C*, *Axinella solida* Carter (holotype BMNH 1887.7.11.24); *D*, peripheral skeleton (scale = 500 μm).

axinellid skeleton. These similarities are especially seen by comparing spiculation of *Ptilocaulis fusiformis*, *P. papillatus* and *P. epakros* with *Rhaphoxya systremma*, sp. nov. (Figs 22, 24, 26 and 33).

Bergquist (1970) suggested that *Rhaphoxya* was also close to *Desmoxyidae* (Desmoxyidae) in spiculation and architecture, but differed in having a more lax, less halichondroid skeleton, and in lacking centrangulate spined microscleres. In fact, Bergquist (1970) previously included *Rhaphoxya* with the Desmoxyidae, whereas Wiedenmayer (1989) referred it to the Axinellidae, illustrating its closer relationships with other axinellids such as *Axinyssa*.

Prior to the present study, six species were assigned to the genus, all recorded from Australasian waters: *Acanthella cactiformis* Carter, 1885, from Port Phillip Heads, Vic. (lectotype BMNH 1886.12.15.81; Fig. 31A-B) (Carter 1885; Dendy 1897a; Burton 1934; Bergquist 1970; Wiedenmayer 1989); *Rhaphoxya felina* Wiedenmayer, 1989, from Bass Strait, Vic. (holotype NMV F51964 [not seen]; specimen NCI Q66C-3339-U; Fig. 31C-D); *Raphisia pallida* Dendy, 1897a: 257, from Bass Strait, Vic., and far north Queensland (holotype NMV G2377 [not seen]; specimen QM G300469; Fig. 31E-F) (Hallmann (1916b: 646); *Acanthella rugolineata* Carter, 1885: 365, from Port Phillip Heads, Vic. (holotype BMNH 1886.12.15.24; Fig. 32A-B); *Axinella solida* Carter, 1885, from south-east Australia (lectotype BMNH 1887.7.11.24; Fig. 32C-D) (Dendy 1897a); and *Rhaphoxya typica* Hallmann, 1916b: 643, also from Port Phillip Bay, Vic., and Tasmania (holotype AM Z1595 [not seen]) (Guiler 1950: 9).

Rhaphoxya systremma, sp. nov.

(Figs 33-34, Table 7)

Material Examined

Holotype. QM G300013 (ORSTOM R1221): stn 261, SW. Ilot Nda, Lagon Sud, 21°52'5"S., 166°51'2"E., 33 m depth, 4.xii.1979, coll. P. Laboute, ORSTOM, SCUBA.

Paratype. QM G300442 (fragment NTM Z1500): Euston Reef, NE. of Cairns, Great Barrier Reef, Qld, 16°43'0"S., 146°13'8"E., 42·5 m depth, 26.i.1981, coll. QFS, dredge (stn B6, Cairns ground truth survey).

Description

Colour. Pale or dark orange-brown alive (Munsell 7·5 YR 7/10-5/6), beige (holotype) to dark brown (paratype) in ethanol.

Shape. Spherical or subspherical, globular growth form, 32–75 mm high, 28–60 mm diameter, consisting of aggregated, globular lamellae ('lacunae' of earlier authors), producing a conglomerated, honeycombed, *Echinocladaria*-like reticulation with numerous, oval, cell-like cavities and large canals excavating entire sponge. Sponges are only loosely attached to pieces of coral rubble or shell fragments, or occasionally rolling free on substrate ('tumbleweed' sponges).

Surface. Membraneous, gelatinous, irregularly convoluted surface, with prominent, rounded papillae, up to 3 mm high, 2 mm diameter, most abundant on apical surface of sponge; largest papillae near apex ('upper surface') surround 1 or more oscules, 2–4 mm diameter, although oscules also occur in other places on the 'upper surface', such as in ridges between surface papillae. Texture soft, compressible, difficult to tear.

Ectosome. Fleshy, heavily collagenous, darkly pigmented ectosomal region, without spongin fibres or spicules, but with a thick collagen layer (up to 80–300 µm thick) between surface and beginning of choanosomal spongin fibre skeleton; this collagenous layer is thicker in between the surface ridges and papillae than on top of these structures; sparse

Table 7. Comparison in spicule dimensions between *Raphoxya* species

All measurements given in micrometres, and expressed as range of measurement

Species (locality) [source of information]	Megascleres Length	Megascleres Width	Raphides
<i>Raphoxya cactiformis</i> (Carter) (Port Phillip Bay) [lectotype BMNH 1886.12.15.81]	167–432	4–12	Absent
	Predominantly oxeas with telescoped ends, some styles		
<i>Raphoxya felina</i> Wiedenmayer (Bass Strait) [specimen NCI Q66C-3339-U]	192–415	5–12	110–245
	Exclusively oxeas		
<i>Raphoxya pallida</i> (Dendy) (Port Phillip Head and Bass Strait) [specimen QM G300469]	211–430	4–9	110–370
	Predominantly oxeas with telescoped ends, some anisoxeas and stronglyxeas		
<i>Raphoxya rugolineata</i> (Carter) (Port Phillip Bay) [holotype BMNH 1886.12.15.24]	305–514	7–12	Absent
	Predominantly oxeas with telescoped ends, some styles		
<i>Raphoxya solida</i> (Carter) (Port Phillip Head and Bass Strait) [lectotype BMNH 1887.7.11.24]	232–388	4–8	65–146
	Predominantly styles with hastate or telescoped points, some oxeas and anisoxeas		
<i>Raphoxya systemma</i> , sp. nov. (New Caledonia and northern Great Barrier Reef) [holotype QM G300013] [paratype QM G300442]	248–(304·6)–369 201–(299·8)–382	2–(2·8)–4 2–(3·7)–5	Absent Absent
	Predominantly vestigial, sinuous stronglyles, rarer oxeas with telescoped ends		
<i>Raphoxya typica</i> Hallmann (Port Phillip Bay and Bass Strait) [Hallmann 1916b: 646]	100–700	2–9	55–400
	Predominantly oxeas with telescoped ends, fewer styles or stronglyles		

plumose brushes of choanosomal spicules may also protrude through surface, up to 100 μm , especially on tips of papillae, otherwise entire ectosomal skeleton is collagenous. Sparse deposits of detritus also dispersed over surface and incorporated into ectosomal collagenous layer, but this is not a prominent feature of the skeleton.

Choanosome. Skeleton plumose, slightly plumo-reticulate, without axial compression or differentiation between axial and extra-axial skeletons; skeleton is dominated mainly by diverging, meandering, sinuous spongin fibres and spicule tracts; spongin fibre system composed of ascending, primary fibres, with individual fibres up to 350 μm long, 50–70 μm diameter, cored by multisporous tracts of choanosomal megascleres, and interconnected by shorter, transverse, secondary fibres, up to 120 μm long, 20–40 μm wide, usually aspicular or sometimes paucispicular; generally the reticulate, connecting, secondary spicule tracts are greatly reduced in proportion to the primary, plumose, ascending skeleton. Fibre reticulation produces elongate, often cavernous meshes, 70–230 μm long, up to 80 μm wide, becoming more cavernous in periphery than in axis, with some scattered, sinuous spicules outside fibres; choanosomal mesohyl with abundant but only lightly pigmented collagen, with only few, small choanocyte chambers seen, up to 30 μm diameter.

Megascleres (refer to Table 7 for dimensions). Single category of choanosomal spicule present, relatively homogeneous in size, although terminations of spicules vary from symmetrical, evenly rounded and hastate tapering rounded ends (strongyles), to sharply pointed, telescoped ends (oxeas). Majority of spicules strongly elongate, sinuous, very slender.

Microscleres. Absent.

Distribution

New Caledonian lagoon and northern Great Barrier Reef, coral reef rubble and inter-reef region, 30–43 m depth.

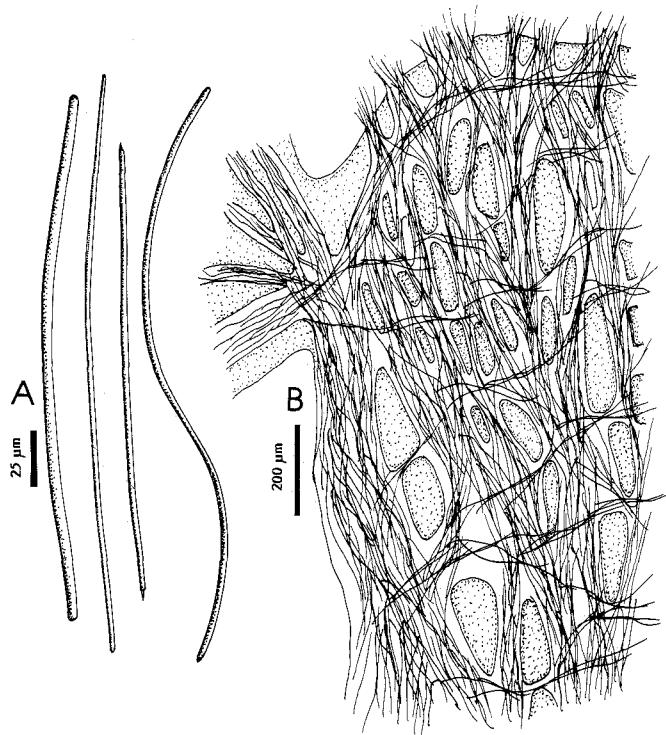


Fig. 33. *Rhaphoxya systrema*, sp. nov., holotype QM G300013: A, strongyles and oxea structural spicules; B, section through peripheral skeleton.

Remarks

This is the first record of the genus outside southern Australian waters. *Rhaphoxya systemma* differs from most other species of the genus in lacking raphide microscleres (four of the six described species have raphides), having exceedingly thin megascleres with predominantly strongylote endings (most other species have predominantly or exclusively styles or oxeas with telescoped ends; Table 7), and having a sinuous, virtually non-reticulate skeleton (similar to *R. typica*).

According to their published descriptions, all six previously described species of *Rhaphoxya* are morphologically very similar and difficult to clearly distinguish on the basis of their published gross characteristics, including growth form, surface features, skeletal architecture and spiculation. However, examination of type material and other representatives of these species shows a number of distinctive, cryptic characters which support their differentiation (Figs 31–34). *Rhaphoxya felina* has a distinctive, perpendicular ectosomal skeleton, a more confused plumo-reticulate choanosomal skeleton, and megascleres are exclusively oxeas; *R. cactiformis* has a more confused plumo-reticulate skeleton, heavy collagenous mesohyl, spicules are predominantly oxeas with telescoped ends, and raphides are absent; *R. rugolineata* has a virtually plumose, diverging spicule skeleton in which the outer layer of spicules on spicule tracts are inserted at acute angles (i.e. nearly echinating), spicules are predominantly oxeas with telescoped ends, and raphides are absent; *R. solida* has a skeleton similar to that of *R. felina*, with a perpendicular ectosomal skeleton and compact, confused, plumo-reticulate skeletal tracts, and spicules are predominantly

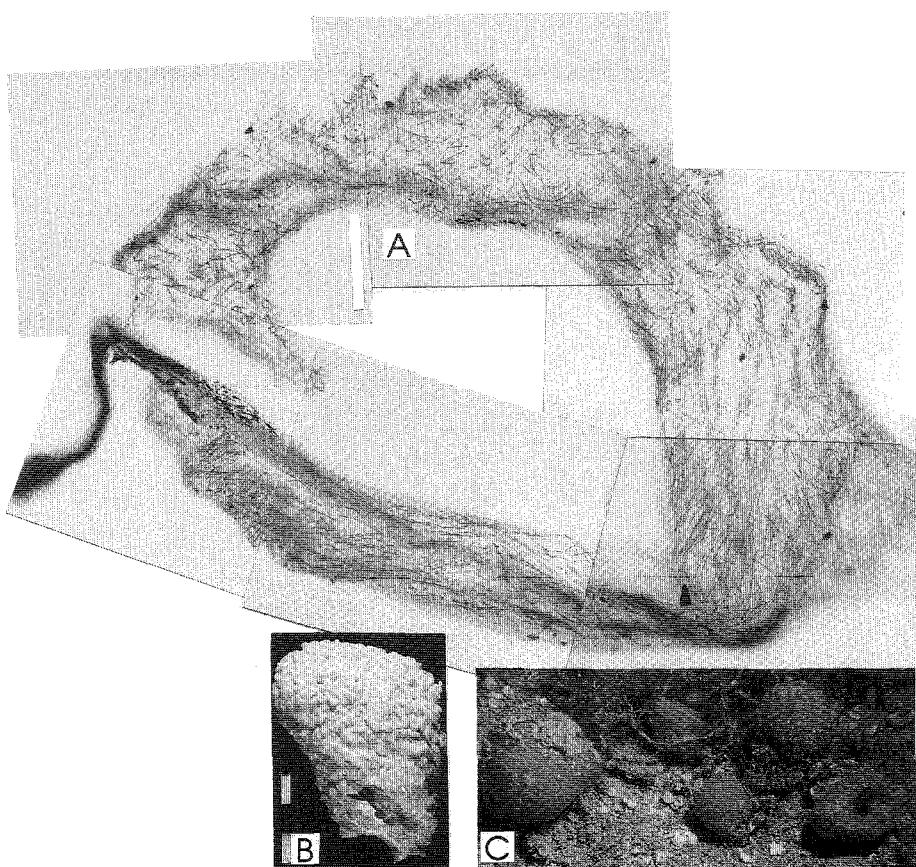


Fig. 34. *Rhaphoxya systemma*, sp. nov.: *A*, cross-section through surface papilla (holotype QM G300013) (scale = 500 μm); *B*, holotype; *C*, specimen *in situ* (ORSTOM R1221) (photo P. Laboute).

asymmetrically curved styles with hastate or telescoped points, with less frequent anisoxeas and oxeas; *R. pallida* has a meandering plumo-reticulate skeleton similar to that of the present species, with plumose (plumo-reticulate) spicule tracts and a heavy collagenous mesohyl, but spicule tracts are not sinuous and spicules are predominantly oxeas with telescoped ends; *R. typica* also has a meandering, plumo-reticulate skeleton, similar to that of *R. systemma*, and its growth form is similar in being massive, subspherical, with papillae on the upper surface, but spicules are substantially larger and consist predominantly of oxeas with telescoped ends, with only few strongyles or styloid modifications (which are predominant in the present species), and raphide microscleres are also abundant. A comparison of spicule dimensions between these species is given in Table 7. Altogether, the present species appears to be most closely related to, and clearly a sibling species of, the southern Australian *R. typica*.

Etymology

The species name refers to the subspherical conglomeration of lacunae, forming a honey-combed mass, from the Greek *systemma*, relating to anything aggregated, consolidated, or twisted together into a round object.

Family DESMOXYIDAE Hallmann

Definition

Axinellid sponges with 'microscleres' in the form of smooth or spined microxeas, often centrangulate or strongly bent centrally, sometimes also with raphides, occurring singly or in bundles (trichodragmata), or acanthose cladotoxa and birotules in one genus. Megascleres monactinal, diactinal or both. Skeleton consisting of widely spaced reticulate bundles of multispicular fibres, with little spongin, with poorly developed or no axial compression, and relatively poorly differentiated extra-axial skeleton (disorganised-plumose). Growth forms encrusting, massive or ramosae [compiled from Hartman (1982) and Wiedenmayer (1989)].

Remarks

The presence of smooth or spined oxeas is characteristic of, and apomorphic for, desmoxytid genera. These spicules are traditionally classed as microscleres (e.g. Hallmann 1916b, Wiedenmayer 1977), although in comparison to many other taxa they are generally much too large to be considered as such (e.g. *Myrmekioderma*). Wiedenmayer (1977) suggested that the Desmoxyidae had affinities with the Hemiasterellidae (e.g. *Laonaenia* Hallmann), and the Hadromerida (e.g. *Paratimea* Hallmann). However, Topsent (1928) had previously included these genera in the Hemiasterellidae, but he was not followed by subsequent workers. Although some similarities can be drawn between some taxa of both families, the hemiasterellids are restricted to forms with asterose microscleres, whereas the desmoxyids included forms with microxeote spicules. On that basis, several genera currently assigned to Bubaridae (e.g. *Rhabdoploca*, *Bubaropsis*) also have inferred affinities with the Desmoxyidae, having acanthose or smooth oxeote megascleres.

This family was established by Hallmann (1916b: 673; with synonym *Higginsiinae* de Laubenfels, 1936: 132), initially for five genera, of which only four were correctly assigned (*Desmoxyta*, *Higginsia*, *Holoxea* and *Halicnemia*). Numerous other genera were subsequently added or associated with the family, although affinities between them were not always completely clear. Of these, the following genera are excluded from the family: *Negombo* Dendy (type species *N. tenuistellata* Dendy) and *Diacarnus* Burton (type species *Axos spinipoculum* Carter) are probably best assigned to the Latrunculiidae [both suggested as possible synonyms according to Hooper (1986), but this has not been firmly established]; *Allantella* Hallmann (type species *Trachytedania arborea* Keller) is probably a hadromerid; *Laonaenia* Hallmann (type species *Hymeraphia verticillata* Bowerbank), and *Paratimea* Hallmann (type species *Bubaris constellata* Topsent) are aster-bearing taxa, both belonging to *Halicnemia* Bowerbank according to Topsent (1928), but are probably hemiasterellids or hadromerids (e.g. Hooper 1986). *Ommatosa* (*sensu* de Laubenfels 1936; type and only

species *Axinella rugosa* Schmidt) is either a desmoxyid or a bubarid; its placement is problematic, but it probably has closest affinities with *Bubaris*.

Eight genera are considered to be valid and presently included in Desmoxyidae (*Acanthocladia* Bergquist, *Halicnemia* Bowerbank, *Heteroxya* Topsent, *Higginsia* Higgin, *Holoxea* Topsent, *Microxistyla* Topsent, *Myrmekioderma* Ehlers and *Parahigginsia* Dendy) but, as van Soest *et al.* (1990) suggest, there is a pressing need for a complete revision of the family and a re-evaluation of its constituent genera.

Only one species of Desmoxyidae has been recorded previously for the New Caledonian region, *Parahigginsia phakellioides* Dendy, 1924, also known from northern New Zealand.

Genus *Myrmekioderma* Ehlers

Myrmekioderma Ehlers, 1870: 28. — Bergquist, 1965: 177 [type species *Alcyonium granulatum* Esper, 1830: 71].

Acanthoxifera Dendy, 1905: 156. — Dendy, 1922: 129; Bergquist, 1965: 177 [type species *A. ceylonensis* Dendy, 1905: 157].

Anacanthaea Row, 1911: 329. — van Soest *et al.*, 1990: 31 [type species *A. nivea* Row, 1911: 329]. *Callistes* Schmidt, 1868: 16. — van Soest *et al.*, 1990: 31 [type species *C. lacazii* Schmidt, 1868: 16]. *Neoprosypa* de Laubenfels, 1954: 189 [type species *N. atina* de Laubenfels, 1954: 190].

Diagnosis

Growth form massive or encrusting; surface hispid, with characteristic canals and grooves forming polygonal tuberculate plates. Choanosome condensed, with confused mass of acanthoxeas and oxeas, strongyles or less frequently styles, forming irregular, ascending, multispicular tracts bound together with sparse collagen. Extra-axial skeleton dense paratangential layer of acanthoxeas, with larger choanosomal styles protruding. Ectosomal skeleton without specialised spiculation, subectosomal acanthoxeas protrude, forming closely adjacent brushes perpendicular to surface. Megascleres long, smooth oxeas, strongyles, or more rarely styles, often sinuous, and centrally flexed or straight acanthoxeas. Microscleres raphides, occurring singly or in bundles (trichodragmata) (modified from Bergquist 1965).

Remarks

Bergquist (1965) meticulously redescribed the type species from type and recent material, and showed conclusively that the type species of both *Acanthoxifera* and *Neoprosypa* were junior synonyms of *M. granulata*, despite their apparent differences according to their published descriptions. Bergquist (1965) also noted that *M. granulata* had a wide geographical distribution with a corresponding high degree of skeletal variability, particularly in the presence, absence and size of certain spicule categories. The genus is similar to *Anacanthaea* and *Heteroxya*, and also apparently related to *Higginsia*.

Van Soest *et al.* (1990) revised the higher systematics of *Myrmekioderma*, placing it in a redefined order Halichondrida and family Halichondriidae, and suggested that it was most closely associated with a genus-group also containing *Didiscus* (based on a synapomorphy of one or more categories of trichodragmata, the larger sinuously curved). They suggested that within this group, the smaller oxea 'microscleres' varied from an acanthose to a completely smooth condition, and thus had a dubious systematic value. In contrast, *Higginsia* was retained in Desmoxyidae by van Soest *et al.* (1990), implying a more distant relationship with *Myrmekioderma* than previously recognised, but this opinion was not supported by a chemotaxonomic study (Hooper *et al.* 1992). Consequently, *Myrmekioderma* and *Higginsia* are retained here in the same family.

Van Soest *et al.* (1990) included six species in the genus, of which only two live in the Indo-west Pacific: *M. dendyi* (Burton, 1959) from the south Arabian coast and Indonesia, *M. granulata* widespread throughout the Indo-west Pacific (Figs 35–36), *M. rea* de Laubenfels, 1934, from the vicinity of Puerto Rico, *M. spelea* (Pulitzer-Finali, 1983) from the Mediterranean, *M. styx* de Laubenfels, 1953, from the Gulf of Mexico, and *M. tulearensis* (Vacelet *et al.*, 1976) from south-west Madagascar.

Myrmekioderma granulata (Esper)

(Figs 35–36)

Alcyonium granulatum Esper, 1830: 71, pl. 24.*Myrmekioderma granulata*. — Ehlers, 1870: 28; Burton, 1938: 39, pl. 7, fig. 42; de Laubenfels, 1954: 121, fig. 75; Lévi, 1961: 14, fig. 17; Bergquist, 1965: 177, fig. 27a, b; van Soest *et al.*, 1990: 29, fig. 28; Hooper *et al.*, 1992: 265.*Acanthoxifer ceylonensis* Dendy, 1905: 157, pl. 9, fig. 5. — Dendy, 1922: 129.*Myrmekioderma tylota* de Laubenfels, 1954: 119, fig. 74.*Neoprosopya atina* de Laubenfels, 1954: 190, fig. 127.*Acanthoxifer fourmanoiri* Lévi, 1956: 5.**Material Examined**

New Caledonian region material. QM G300022 (ORSTOM R1347): stn 427, Caye de l'Observatoire, Chesterfield Is, 21°24·6'S., 158°50·3'E., 28 m depth, 26.vii.1984, coll. G. Bargibant, SCUBA.

Comparative material. **Darwin region, N.T.**: NTM Z196: Dudley Pt, East Pt, 12°25'S., 130°49·01'E., 0–0·5 m depth, 13.ix.1981, coll. J. N. A. Hooper, by hand; NTM Z2053: same locality, 12°25·0'S., 130°48·4'E., 6–10 m depth, 10.v.1984, SCUBA, coll. J. N. A. Hooper; NTM Z214: Lee Pt, 12°19·02'S., 130°53·01'E., 0 m depth, 14.xi.1981, coll. J. N. A. Hooper, by hand; NTM Z430: same locality, 13.xii.1981. **Arafura Sea, N.T.**: NCI Q66C-0540-A (fragment NTM Z3097): Parry Shoals, 11°11·41'S., 129°43·01'E., 18 m depth, 14.viii.1987, coll. A.-M. Mussig and NCI, SCUBA. **Cobourg Peninsula, N.T.**: NTM Z2508: NW. Table Head, Port Essington, 11°13·5'S., 132°10·5'E., 3–5 m depth, 14.ix.1985, SCUBA, coll. J. N. A. Hooper; NTM Z3249: SW. Table Head, Port Essington, 11°13·5'S., 132°10·5'E., 2–5 m depth, 11.ix.1986, coll. J. N. A. Hooper and C. Johnson, C., SCUBA. **Wessel Islands, N.T.**: NCI Q66C-4769-Y (fragment QM G300741): Bay N. side of Cumberland Strait, 11°28·0'S., 131°29·0'E., 20 m, 14.xi.1990, coll. J. N. A. Hooper and NCI, SCUBA. **Northwest Shelf, W.A.**: NTM Z3423: 150 m W. of Enderby I., Dampier Archipelago, Dampier, 20°35·8'S., 116°28·0'E., 14 m depth, 31.viii.1988, coll. Low Choy, D. and NCI, SCUBA; NCI Q66C-1447-O (fragment NTM Z3332): S. reef 500 m from Direction I. Natl Pk, 21°33·1'S., 115°07·1'E., 6 m, 24.viii.1988, coll. Low Choy, D. and NCI, SCUBA. **Sahul Shelf, W.A.**: QM G301141: Hibernia Reef, entrance to lagoon, NE. side reef, 11°57·8'S., 123°22·3'E., 23 m depth, 10.v.1992, coll. J. N. A. Hooper, SCUBA; QM G301104: Cartier I., outer reef slope, N. side of reef, Australia, 12°31·4'S., 123°33·3'E., 22 m depth, 7.v.1992, coll. J. N. A. Hooper, SCUBA.

Description

Colour. Light orange-brown to bright orange exterior alive (Munsell 7·5YR 7/10-5YR 6/10), often with silt covered 'dusty' surface, orange-brown exterior and beige interior in ethanol.

Shape. Massive, subcylindrical, vaguely elongate, rounded, bulbous growth form, partially burrowing soft sediments or excavating hard sediments, up to 350 mm long, 200 mm wide, 160 mm thick (although on the Sahul Shelf specimens several metres in diameter were observed).

Surface. Pineapple-like, convoluted, crustose surface, with large conules or rounded or polygonal plates, 18–35 mm diameter, slightly raised above surface and separated by shallow but distinct grooves; apex of sponge with irregularly meandering or discrete series of relatively deep, excavated channels (sieve-plates or porocalyces), up to 60 mm deep, containing large oscules (up to 50 mm diameter) especially near apex of sponge, each oscule with a raised membranous lip. Exterior surface invariably silt covered, interior soft, mango-like. Texture harsh, firm, spiculose.

Ectosome. Distinct, thick, detachable, paratangential crust of smaller (ectosomal) oxeas, 400–850 µm wide, with innermost layer nearly horizontal and outermost layer nearly perpendicular to the surface, together forming a continuous palisade of spicules. Ectosomal crust supported by long, pillar-like tracts of large oxeas, usually widely spaced (450–780 µm long, 750–900 µm apart), producing an excavated subdermal region containing large cavities, about 650 µm diameter, with sparse collagen, collagenous fibrils, bundles of raphides and sparsely scattered smaller oxeas.

Choanosome. Cavernous, reticulate skeletal structure, with differentiated primary and secondary spongin fibres and spicule tracts; primary, ascending, multispicular fibres (70–250 µm diameter) more-or-less regularly spaced, 300–650 µm apart, interconnected by secondary, transverse or oblique, pauci-, uni- or aspicular fibres (30–80 µm diameter). Fibres lightly or heavily invested with spongin, depending on their thickness, and cored only by larger (choanosomal) oxeas. Fibre meshes evenly rectangular, triangular or irregularly oval, 90–260 µm diameter, containing abundant collagen, collagenous fibrils, many scattered smaller oxeas, and bundles of raphides. Choanocyte chambers small, oval, 40–70 µm.

Megascleres. Two categories of megascleres of similar morphology, clearly distinguished only by size and distribution in skeleton; both entirely smooth, relatively large, straight or slightly curved at centre, rarely asymmetrical, tapering to sharp fusiform points. Smaller (ectosomal) oxeas: length 319–(535·3)–708, width 4–(9·2)–12. Larger (choanosomal) oxeas: length 644–(688·1)–782, width 13–(17·3)–22.

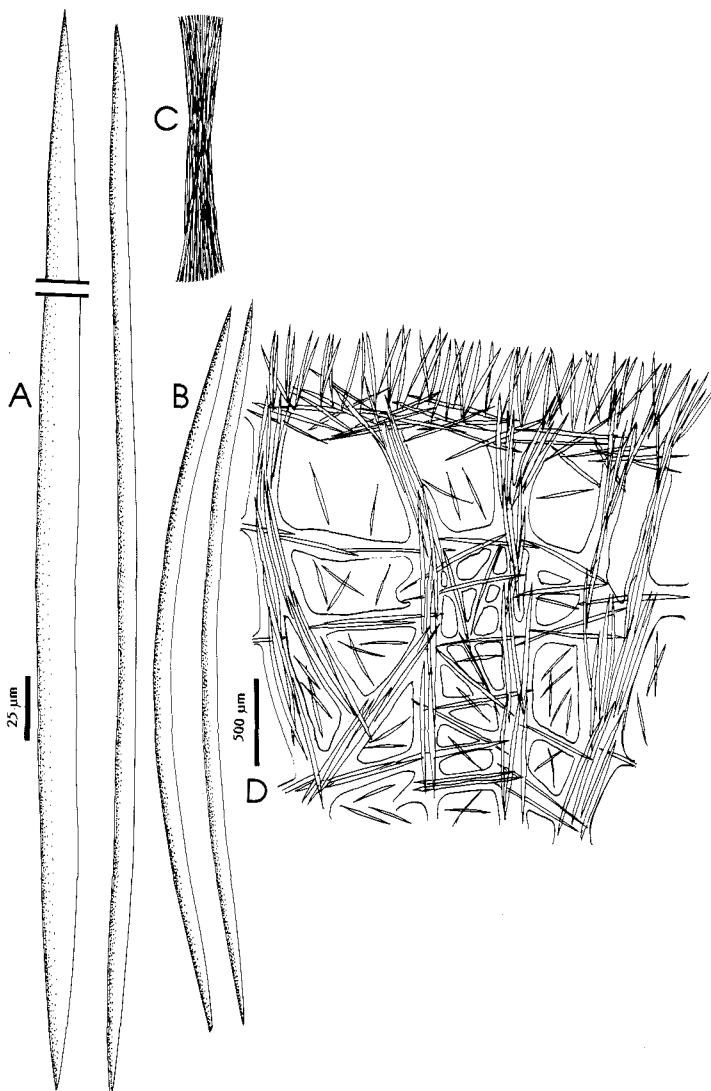


Fig. 35. *Myrmekioderma granulata* (Esper), specimen QM G300022: A, larger (choanosomal) oxeas; B, smaller (ectosomal) oxeas; C, bundles of raphides (trichodragmata); D, section through cavernous peripheral skeleton.

Microscleres. Raphides rarely seen individually, but more commonly occurring as bundles of hair-like raphides (trichodragmata). Dimensions of bundles up to $140 \times 15 \mu\text{m}$.

Distribution

Widely distributed throughout the Indo-west Pacific: Madagascar, Aldabra (Lévi 1956, 1961), Seychelles (Dendy 1922; Hooper, unpublished data); Gulf of Manaar (Dendy 1905; Burton 1938); Indonesia (Esper 1830; Ehlers 1870; van Soest *et al.* 1990); north-west Australia (Hooper, unpublished data); central western Pacific: Ponape, Truk, Ebon Atoll (de Laubenfels 1954), Palau, Ifaluk (Bergquist 1965); Chesterfield Islands and New Caledonia (present study). Common habitats range from heavily sedimented fringing coral platforms and coral pools, in sand, silt, beach rock and dead coral rubble substrates, to pristine coral reef slopes, often in spurs and grooves; sublittoral depths to approximately 20 m.

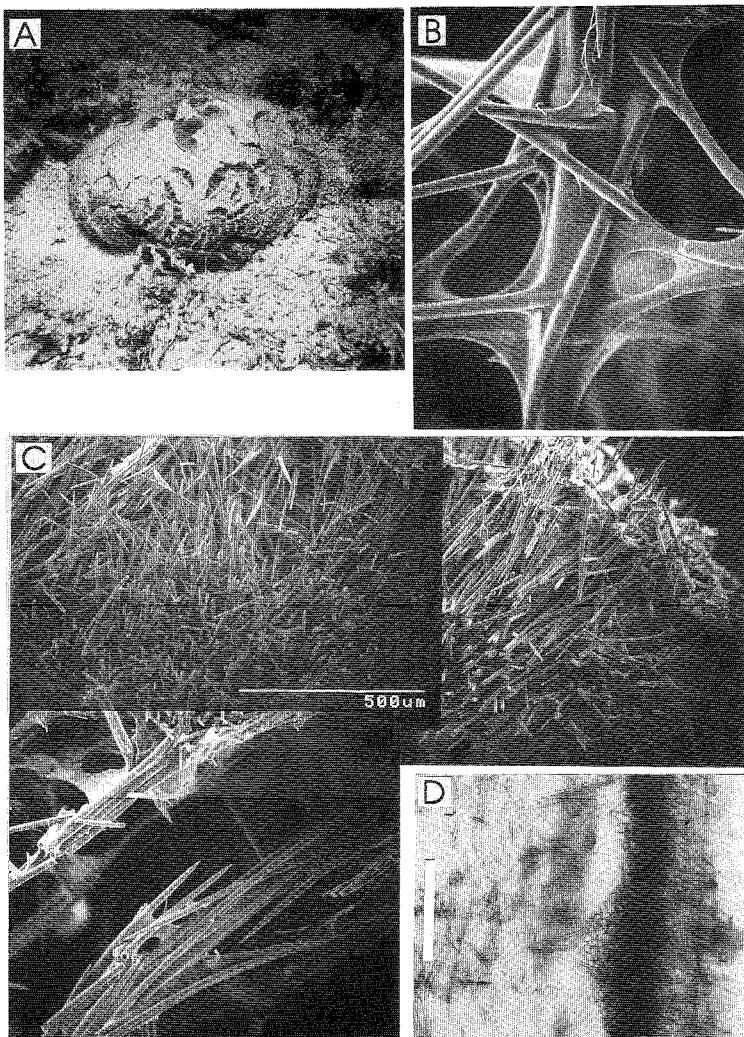


Fig. 36. *Myrmekioderma granulata* (Esper): *A*, specimen *in situ* (ORSTOM R1347) (photo J.-L. Menou); *B*, SEM fibre junction (specimen QM G300022) (magnified 100 \times); *C*, SEM skeletal structure (magnified 100 \times); *D*, peripheral skeleton (scale = 500 μm).

Remarks

There is no doubt that *M. granulata*, and probably all of its sibling species, fits poorly with the present concept of the axinellids, and possibly the hypothesised relationship with the halichondrids, as proposed by van Soest *et al.* (1990), may be more appropriate. However, this relationship between the desmoxyids, axinellids and halichondrids is still very poorly understood, and indeed none of these taxa have yet been revised or well investigated. The conservative choice of leaving *Myrmekioderma* in Desmoxyidae is presently the best alternative and also supported by chemotaxonomic data (Hooper *et al.* 1992).

The New Caledonian specimen (described above) differs from typical morphotypes of the species in lacking any spination on the smaller (ectosomal) oxeas, and in lacking any modification to the oxea morphology; in lacking acanthose oxeas the species is not clearly a desmoxyid. However, in most other comparative material examined (listed above), the smaller oxeas are clearly acanthose (and also sometimes modified to strongyles, anisoxeas or styles). Bergquist (1965) provides a comprehensive comparison in spicule dimensions between all nominal species and regional populations of *M. granulata*, and a detailed discussion of the species' morphometric variability and relationships.

Genus *Higginsia* Higgin

Higginsia Higgin, 1877: 291.—Hallmann, 1916b: 655; Dendy, 1922: 126; Topsent, 1928: 39; de Laubenfels, 1936: 132; Burton, 1959: 255; Wiedenmayer, 1977: 156 [type species *Higginsia coraloides* Higgin, 1877: 291 (Hallmann 1916b: 656), possible junior synonym of *Spongia strigilata* Lamarck, 1814: 450].

Dendropsis Ridley & Dendy, 1886: 483.—Ridley and Dendy, 1887: 191; Hallmann, 1916b: 693; de Laubenfels, 1936: 132; Lévi, 1973: 606 [type species *Dendropsis bidentifera* Ridley and Dendy, 1886: 483].

Desmoxya Hallmann, 1916b: 649.—de Laubenfels, 1936: 132; van Soest *et al.*, 1990: 18 [type species *Higginsia lunata* Carter, 1885: 358].

Diagnosis

Growth forms erect, lamellate, massive, vasiform or lobate; surface conulose, papillose, often silt covered or membranous. Skeletal structure ranges from halichondroid with a partially compressed, reticulate axis, and an irregularly plumo-reticulate extra-axial region (*Higginsia*), a compressed axis and a radial, non-plumose extra-axial region (*Dendropsis*), to a lax plumose or plumo-reticulate axial and extra-axial region, without axial compression or regional differentiation of the skeleton (*Desmoxya*); spongin fibres usually poorly developed although heavy collagen forms mesohyl, usually with numerous megascleres and microscleres scattered between main skeletal tracts; all skeletal tracts cored by monactinal and/or diactinal megascleres. Ectosome without specialised spiculation, but with extra-axial spicule tracts (1 or 2 categories of megascleres) protruding through surface. Megascleres oxeas, strongyles and/or styles of 1–3 sizes. Microscleres include spined, centrangulate curved or straight microxeas, and sometimes also raphides occurring singly or in bundles (trichodragmata) (modified from Wiedenmayer 1977).

Remarks

The nominal genera *Higginsia*, *Dendropsis* and *Desmoxya* differ essentially in skeletal construction (reticulate or plumo-reticulate; with a compressed axis and radial extra-axis; and plumose-halichondroid, with meandering, occasionally reticulate skeletal tracts respectively). Most species lack definite axial compression of the skeleton (except *Dendropsis bidentifera*), having instead a halichondroid, vaguely reticulate axis, and in most species there is often some differentiation of axial and extra-axial skeletons (except *Desmoxya lunata*), suggesting some sort of affinity with the concept of Axinellida. All three nominal genera share the apomorphy of spined microxeas, but we are not completely convinced that the major differences in their skeletal structures can be ignored, particularly in the case of *Dendropsis* which has a nearly 'classical axinellid' architecture, in recognising these taxa merely as synonyms of *Higginsia* (e.g. Hallmann 1916b; van Soest *et al.* 1990).

It is possible that resurrection of *Desmoxya* is required to accommodate *Higginsia*-like species that lack any evidence of axial compression (as seen in both *H. lunata* and *H. anfractuosa*, sp. nov.), having instead a simply halichondroid, meandering *Rhaphoxya*-like reticulation of choanosomal tracts. These species also differ from *Higginsia sensu stricto* only in having one size category of megascleres, having raphides in addition to spined microxeas, as well as the more lax skeletal architecture. However, intermediate forms of architecture between *Higginsia* and *Desmoxya* are present in some species of *Higginsia* (e.g. *H. massalis*), and this condition is interpreted here as being merely a reduced form of the skeleton that is typical for *Higginsia* (van Soest *et al.* 1990).

Hallmann (1916b: 655–9) provides a comprehensive review of the genus and many of the species it contained at that time, but many more species have since been included in the

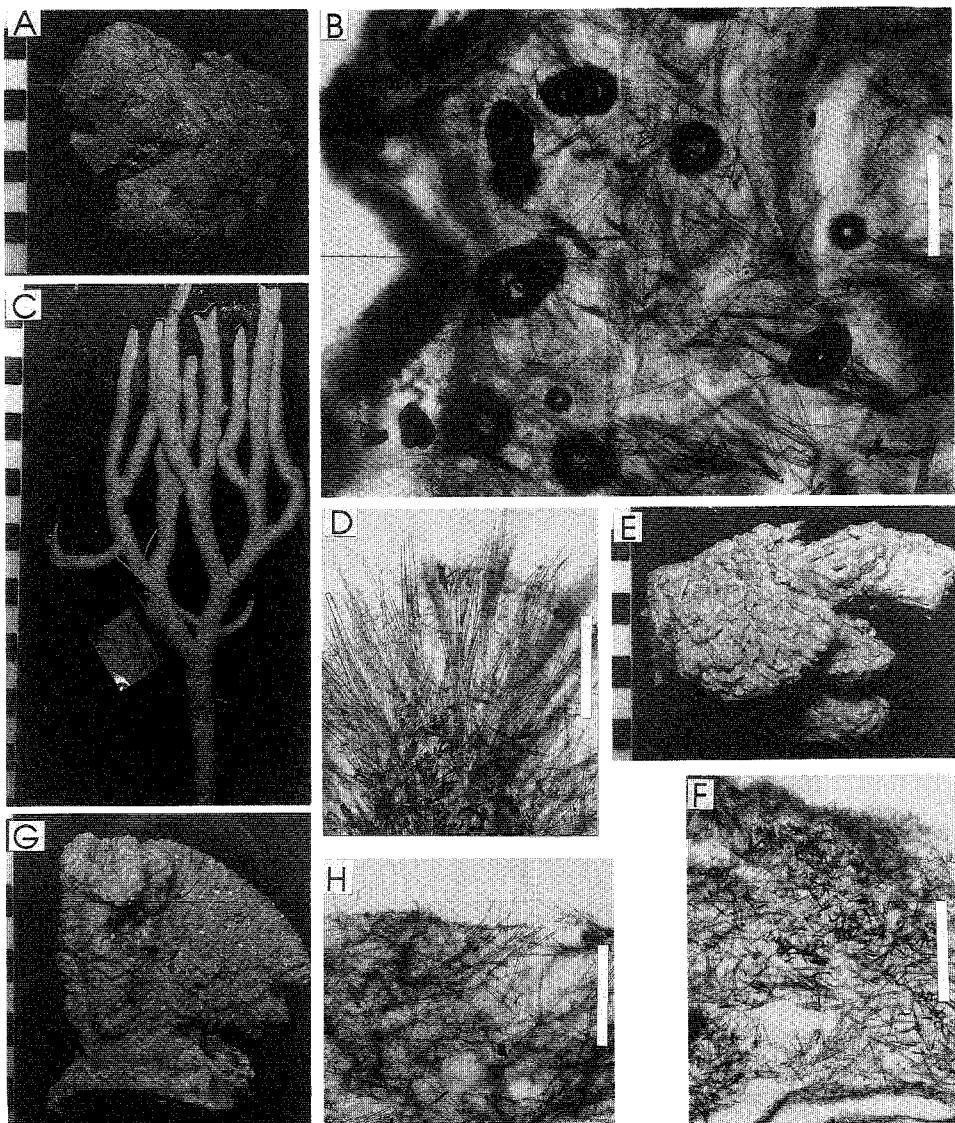


Fig. 37. *Higginsia* spp.: A, *Higginsia lunata* Carter (holotype BMNH 1886.12.15.138); B, peripheral skeleton from BMNH slide (scale = 500 µm); C, *Dendropsis bidentifera* Ridley and Dendy (holotype BMNH 1887.5.2.59); D, skeleton (scale = 500 µm); E, *Higginsia coralloides* var. *massalis* Carter (holotype of variety, BMNH 1886.12.15.122); F, skeleton (scale = 500 µm); G, *Higginsia coralloides* (*sensu* Carter 1885) ('representative specimen' BMNH 1886.12.15.79); H, skeleton (scale = 500 µm).

genus, and all are in need of detailed revision. Few type specimens have yet been located and seen, so it is not possible to undertake a review of these species at the present time. Species thought to be valid are: *H. bidentifera* (Ridley & Dendy) from the Cape of Good Hope, South Africa (holotype BMNH 1887.5.2.59; Fig. 37C-D); *H. coralloides* Higgin from the Caribbean (holotype BMNH [not seen]), with varieties *H. c. liberiensis* Higgin, 1877, and *H. c. arcuata* Higgin, 1877 [possible synonym of *H. strigilata* (Lamarck); Wiedenmayer 1977]; *H. higginsi* Dendy, 1922, from the western Indian Ocean (Okhamandal, Diego Garcia, Providence, Egmont Reef, and south Arabian coast; Dendy 1922; Burton 1959) (holotype BMNH [not seen]); *H. lunata* Carter from Port Phillip Heads (Dendy 1897a; Hallmann 1916b) (holotype BMNH 1886.12.15.138, schizotype MNHN LBIM DCL283; Fig. 37A-B); *H. massalis* Carter, 1885, from Port Phillip Heads, Vic., and Ambon, Indonesia (Dendy 1897a; Topsent 1897; Hallmann 1916b) (holotype BMNH 1886.12.15.122; Fig. 37E-F), with

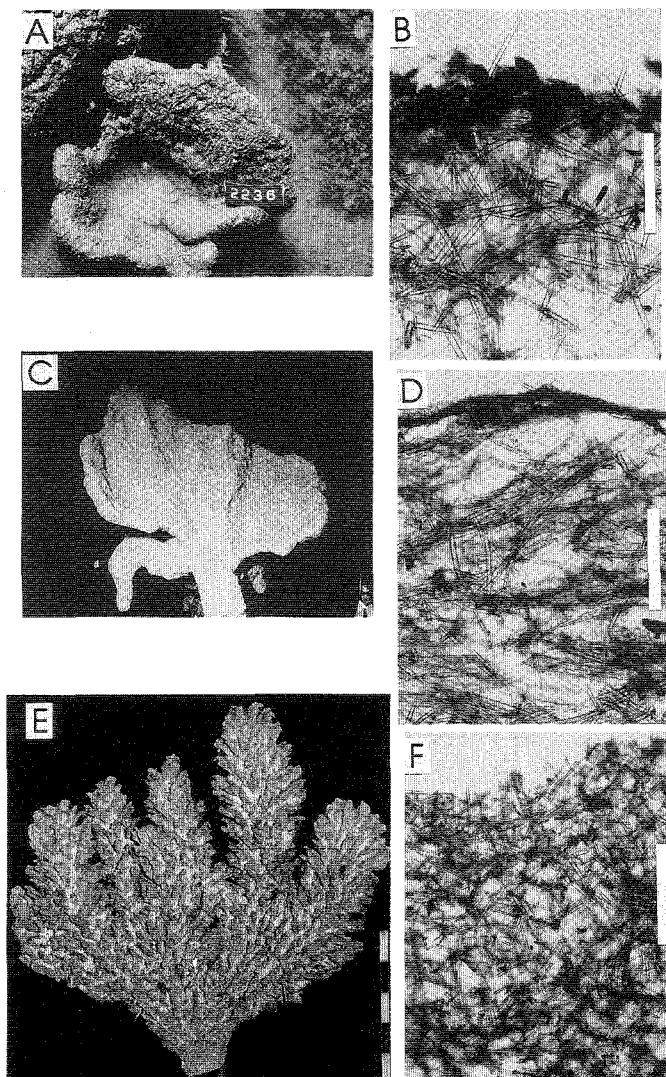


Fig. 38. *Higginsia* spp.: A, *Higginsia mixta* Hentschel ('representative specimen' NTM Z2236); B, skeleton (scale = 500 µm); C, *Higginsia scabra* Whitelegge (specimen on deck NCI Q66C-0523-J) (photo NCI); D, skeleton of specimen NTM Z2801 (scale = 500 µm); E, *Spongia strigilata* Lamarck (holotype MNHN DT637); F, skeleton (scale = 500 µm).

synonym '*H. coralloides*' of Carter (1885) from Port Phillip Heads ('representative specimen' BMNH 1886.12.15.79; Fig. 37G-H), and '*H. strigilata*' of Desqueyroux-Faundez (1981); *H. mixta* Hentschel, 1912, from southern Indonesia (holotype SMF 968 [not seen]) and Palau (Bergquist 1965), also known from north-west and north-east Australia (Hooper, unpublished data; 'representative specimen' NTM Z2236; Fig. 38A-B); *H. natalensis* Carter, 1885, from the Cape of Good Hope, South Africa (holotype BMNH [not seen]); *H. papillosa* Thiele, 1905, from Calbuco, Chile (holotype probably ZMB [not seen]); *H. petrosioides* Dendy, 1922, from the Seychelles and Indonesia (holotype BMNH [not seen]); *H. pumila* (Keller, 1889) from the Red Sea (holotype ZMB 442 [not seen]); *H. robusta* Burton, 1959, from the Gulf of Aden (holotype BMNH 1936.3.4.342 [not seen]); *H. scabra* Whitelegge, 1907, from Port Jackson, N.S.W. (Hallmann 1916b), and north-west and north-east Australia (Hooper, unpublished data) (holotype AM Z480; 'representative specimen' NCI Q66C-0523-J; Fig. 38C-D); *H. strigilata* (Lamarck) from an uncertain locality (Turgot collection), possibly originating from the West Indies (holotype MNHN DT637; Fig. 38E-F) (Topsent 1932; Wiedenmayer 1977); and *H. thielei* Topsent, 1904, from the Azores (holotype possibly Monaco).

Of these species, only five have been recorded from the Indo-west Pacific: *H. lunata*, *H. massalis*, *H. mixta*, *H. petrosioides* and *H. scabra*.

Higginsia anfractuosa, sp. nov.

(Figs 39-40, Table 8)

Material Examined

Holotype. QM G300723 (ORSTOM 'cfR806'): stn 181, E. reef flat, Ilôt Maitre, New Caledonia lagoon, 22°20'·1"S., 166°25'·0"E., 1·5 m depth, 2.vi.1977, coll. G. Bargibant, by hand.

Description

Colour. Pale orange alive (Munsell 7·5YR 8/8), olive-brown in ethanol.

Shape. Erect, globular, cylindrical digit, tapering towards base and apex, 62 mm long, 24 mm diameter at base, 32 mm widest diameter, attached directly to substrate (with embedded detritus in basal end), without stalk or other processes.

Surface. Evenly distributed, rounded *Cliona*-like papillae, up to 2·5 mm diameter, only raised slightly above surface, each with a terminal apical oscule (now closed), 1·0-1·5 mm

Table 8. Comparison in spicule dimensions between *Higginsia anfractuosa*, sp. nov., and *H. lunata*
All measurements given in micrometres, and expressed as minimum-(mean)-maximum range of measurement. $N=25$ for each specimen

Spicules	Species		
	<i>H. anfractuosa</i> , sp. nov. (holotype QM G300723)		<i>H. lunata</i> Carter (holotype BMNH1886.12.15.138)
Megascleres	L	238-(298·2)-318	498-(698·0)-862
	W	2·5-(3·3)-4·5 (Vestigial, predominantly strongyles)	8-(11·9)-15 (Robust, predominantly styles, fewer strongyles)
Microscles	L	106-(129·3)-173	30-(38·1)-48
	W	2·5-(2·9)-3·5 (Straight, evenly spined)	2·0-(2·8)-4·0 (Curved, terminally spined)
Raphides I	L	176-(252·9)-286	448-(540·8)-620
	W	1·5-(2·1)-2·5	0·5-(1·3)-2·0
Raphides II	L	91-(99·8)-112	60-(132·3)-210
	W	0·5-(1·1)-2·0	0·5-(1·3)-2

diameter. Surface with distinct (non-detachable) dermis, more darkly pigmented than choanosomal region, and has overall goose-flesh appearance. Texture rubbery, compressible.

Ectosome. Heavy collagenous ectosomal layer, 100–250 μm wide, darkly pigmented, containing scattered megascleres and microscleres, predominantly paratangential to the surface. Around oscules spicules ordered into diverging rays, presumably supporting surface papillae and providing support for oscule contractile mechanism (Fig. 40C).

Choanosome. Skeleton plumose-halichondroid, with predominantly ascending skeletal tracts, meandering and rejoining throughout skeleton; fibre meshes irregular, elliptical-oval, more cavernous in interior than peripheral skeleton; no axial compression and no differentiation between axial and extra-axial skeletons; spongin fibres only lightly invested with spongin, 30–90 μm diameter, with poorly differentiated primary and secondary elements; fibres fully cored with megascleres, dispersed in plumose-diverging tracts. Mesohyl contains heavy collagen and abundant loose megascleres and microscleres. Choanocyte chambers 20–85 μm diameter.

Megascleres (refer to Table 8 for dimensions). Vestigial megascleres, predominantly strongyles, occasionally styloid or strongyloxeas, straight, slender, with symmetrical, rounded ends, or slightly tapering hastate points.

Microscleres (refer to Table 8 for dimensions). Acanthoxeas long, slender usually straight, occasionally asymmetrical, evenly spined, granular spination, with tapering, sharply pointed ends.

Two size categories of raphides present, both straight, thin, tapering to sharp fusiform points, the larger category nearly the same length as megascleres, differentiated only by

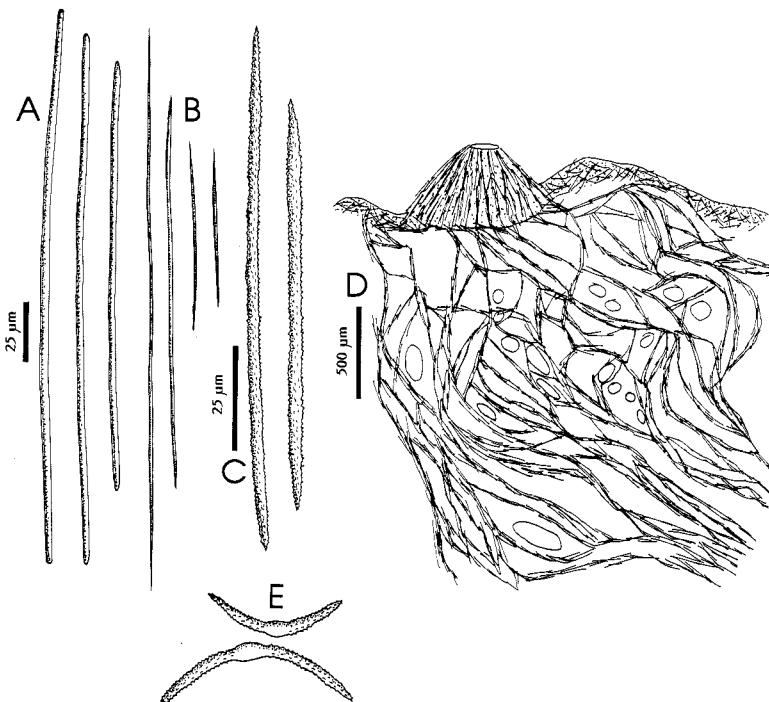


Fig. 39. *A–D*, *Higginsia anfractuosa*, sp. nov., holotype QM G300723: *A*, vestigial strongyles, strongyloxeas and styloids; *B*, two sizes of raphide microscleres; *C*, acanthoxeas; *D*, section through peripheral skeleton. *E*, *Higginsia lunata* Carter, holotype BMNH 1886.12.15.138, curved acanthoxeas.

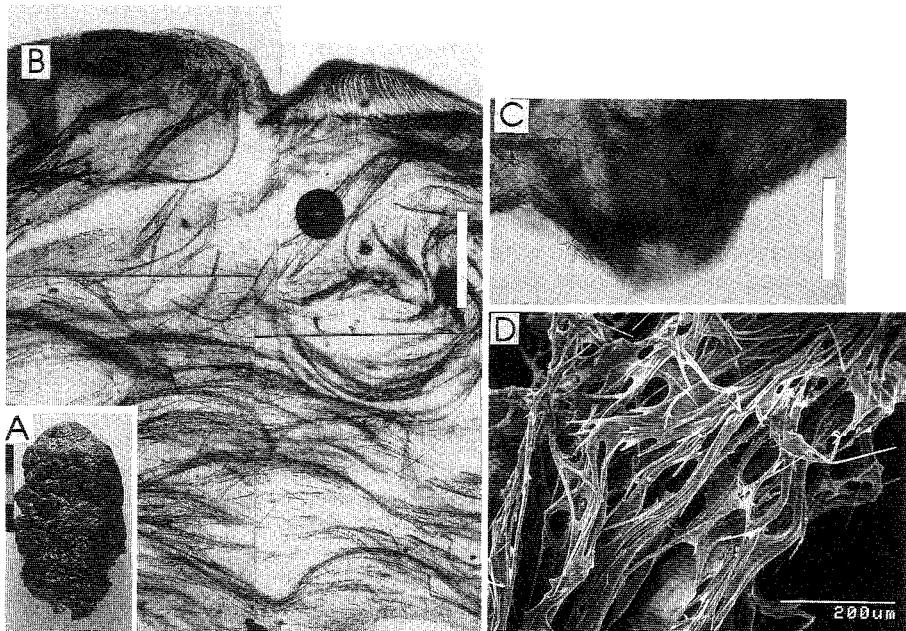


Fig. 40. *Higginsia anfractuosa*, sp. nov.: *A*, holotype (QM G300723); *B*, peripheral skeleton (scale = 500 μm); *C*, oscule and supporting spicules radiating around oscule (scale = 200 μm); *D*, SEM fibre characteristics (scale = 200 μm).

their terminations and relative thickness. Raphides dispersed individually in skeleton, no trichodragmata observed.

Distribution

Known only from the type locality, coral rubble.

Remarks

This species is a closely related, sibling species of *Higginsia lunata* Carter (Carter 1885; Dendy 1897a) from Port Phillip, Vic., meticulously redescribed by Hallmann (1916b: 650). The two species differ substantially only in the size of megascleres and microscleres (Table 8), and geometry of acanthoxeas (curved, terminally spined, slightly centrangleate in *H. lunata*; straight, evenly spined, not swollen at centre in the present species; Fig. 40*C*, *E*). Growth form, papillose surface features and skeletal structure are comparable between the two species, and both are atypical of all other *Higginsia* in having a lax, plumose-halichondroid, meandering skeleton. Nevertheless, these differences between the New Caledonian and Port Phillip populations are greater than normally attributed to interspecific variability, substantially more than cryptic differences, and the New Caledonian population is considered to represent a separate species.

Etymology

Named for the winding, meandering skeletal columns; from *anfractuosus* (L.), very winding, sinuous.

Higginsia tanekeia, sp. nov.

(Figs 41–42, Table 9)

Material Examined

Holotype. QM G300024 (ORSTOM R1298): stn 305, N. Ile Paaba, New Caledonia lagoon, 19°55'3"S., 161°37'3"E., 27 m depth, 24.vi.1981, coll. G. Bargibant, SCUBA.

Description

Colour. Pale orange alive (Munsell 7·5YR 7/10), beige in ethanol.

Shape. Massive, irregularly bulbous, subspherical, subcylindrical sponge, 210 mm long, 80 mm wide, 55 mm thick, without stalk or other processes, loosely attached directly to substrate, with embedded detritus on 'ventral surface', or unattached and rolling free on substrate ('tumbleweed' sponge).

Surface. Slightly bulbous surface, with low, rounded ridges, distinct skin-like, detachable dermis and irregularly dispersed microconules, up to 2 mm diameter, conical or elongate and irregular in shape, not raised more than 2 mm from surface, interconnected by shallow canals and grooves. Surface smooth, not hispid. Texture soft, compressible, relatively fragile, easily torn. Internal consistency porous, cavernous, *Echinocladaria*-like. Oscules not observed.

Ectosome. Collagenous detachable dermis, 100–350 µm wide, containing darkly pigmented collagen, sparsely dispersed thinner ectosomal oxeas forming paratangential tracts, interdispersed with crust of acanthoxeas mostly erect on surface, mostly confined to peripheral skeleton. Choanosomal megascleres not protruding beyond surface. Subdermal region cavernous, directly below skin-like collagenous layer, with sparse tracts of choanosomal megascleres supporting dermal layer.

Choanosome. Skeleton halichondroid-reticulate, with vaguely ascending spongin fibres and skeletal tracts forming wide-meshed reticulation. Spongin fibres light, more-or-less

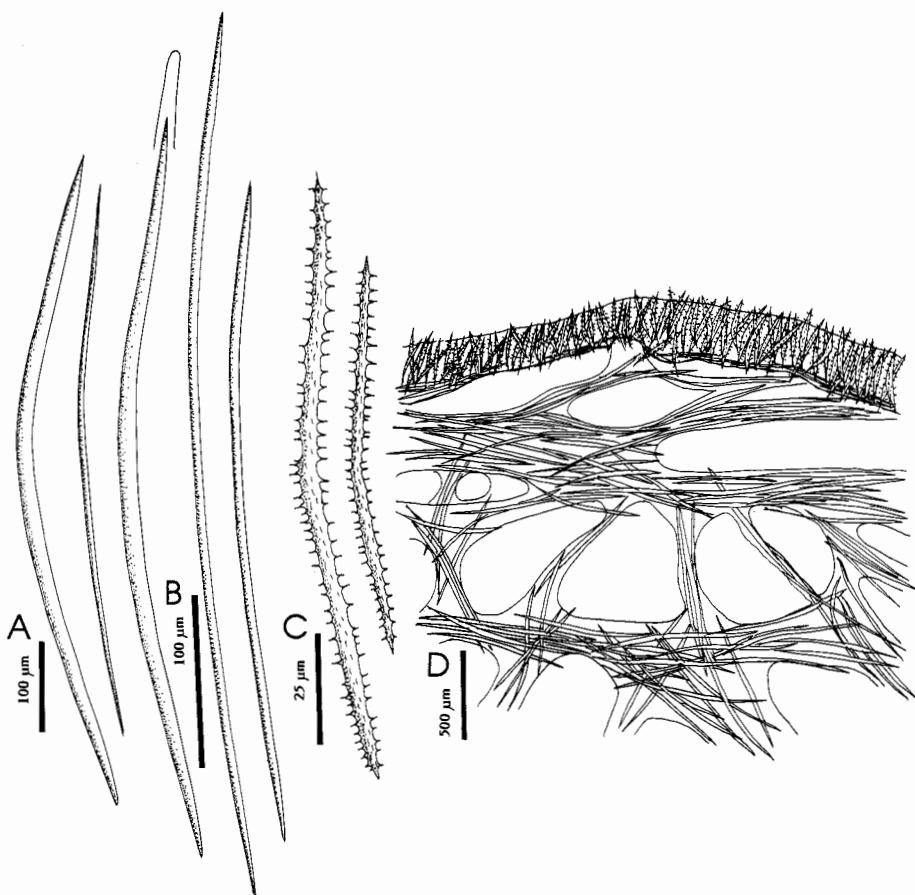


Fig. 41. *Higginsia tanekeia*, sp. nov., holotype QM G300024: A, choanosomal oxeas and styloids; B, ectosomal oxeas; C, acanthoxeas; D, section through peripheral skeleton.

divided into primary, ascending, multispicular fibres, 60–160 μm diameter, and shorter, interconnecting, predominantly transverse, uni- or paucispicular, secondary fibres, 30–75 μm diameter; fibre reticulation forming cavernous, oval or elongate meshes, 350–1200 μm diameter, wider in peripheral skeleton than in deeper regions of choanosome; all fibres cored by larger oxeas, forming irregular, slightly confused, sometimes meandering tracts, with spicules usually occupying most of fibre diameter; numerous larger choanosomal and

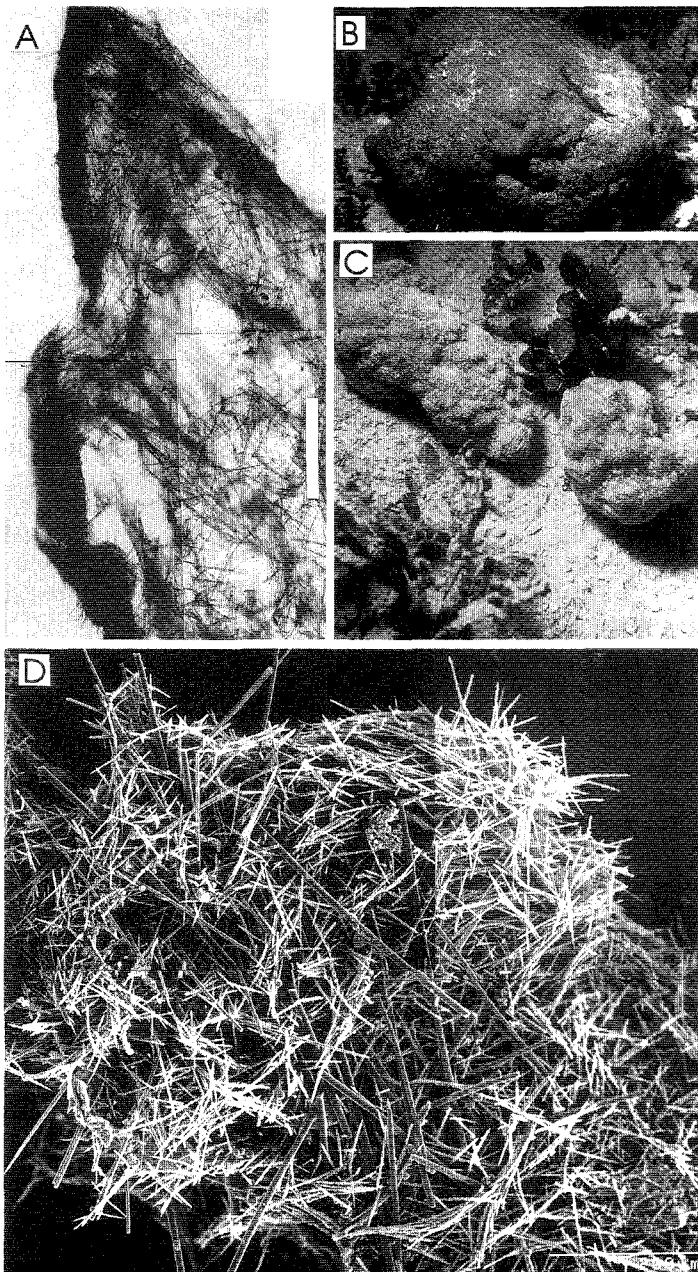


Fig. 42. *Higginsia tanekeae*, sp. nov.: *A*, holotype [QM G300024], peripheral skeleton (scale = 500 μm); *B*, specimen *in situ* (ORSTOM 'cfR1298') (photo P. Laboute); *C*, holotype *in situ* (ORSTOM R1298, on right) (photo P. Laboute); *D*, SEM skeletal structure (scale = 200 μm).

smaller ectosomal oxeas also dispersed between fibre skeleton, but few acanthoxeas seen in choanosome. Fibre meshes contain abundant collagen, more lightly pigmented than in peripheral skeleton, and small oval or elliptical choanocyte chambers, 25–70 µm diameter in peripheral region.

Megascleres (refer to Table 9 for dimensions). Choanosomal megascleres predominantly oxeas, rarely styloid, usually long, slender, symmetrically curved, with fusiform, sharply pointed ends.

Ectosomal oxeas with same morphology, slightly shorter and substantially thinner.

Microscleres (refer to Table 9 for dimensions). Acanthoxeas variable in length, mostly relatively long, slender, usually with slight, angular, central curvature, occasionally straight or with acute bend, sharply pointed tips, with evenly dispersed, large spines.

Distribution

Known only from the New Caledonia lagoon, in *Halimeda* beds in the inter-reef region, 27 m depth.

Remarks

The relationship of *Higginsia tanekeia* to other members of the genus is uncertain. It is not obviously closely related to any other species in the combination of its morphological characters (skeletal structure, spicule size or spicule geometry), although individually most of these features can be found in at least one other species of the genus. In fact, the only apomorphic character in *H. tanekeia* appears to be the possession of unusually large, perpendicular spines on acanthoxeas; a plesiomorphic feature is the lack of long, extra-axial styles which are present in most other species. *Higginsia tanekeia* shows some similarities, in some of its features, with several other species, but these can be differentiated as follows: *H. scabra* has long slender extra-axial styles, lacks smaller, slender ectosomal oxeas, and has an axinellid skeleton with distinctive plumo-reticulate, diverging architecture, and differentiated axial and extra-axial regions (depicted by Hallmann 1916b: pl. 41, figs 1–3); *H. massalis* has a similar skeletal architecture and has similarities in the geometry of some of its spicules, but it has shorter, more robust choanosomal oxeas (often asymmetrical and with telescoped points), long extra-axial styles, and shorter acanthoxeas; *H. mixta* has much thicker choanosomal oxeas (some styloid, some with telescoped points), also with long, slender extra-axial styles, longer ectosomal oxeas, and has an axinellid skeletal structure; *H. robusta* has much thicker choanosomal spicules (varying from styles to oxeas), long, slender extra-axial styles are present, acanthoxeas substantially shorter, and it too has an axinellid skeleton; *H. pumila* is poorly known but, from Keller's (1891) description, it differs in having choanosomal spicules consisting of thick styles, and the extra-axial spicules are long, slender styles. Spicule dimensions of these species are compared in Table 9.

Etymology

Named for the long, slender, sharp spines on acanthoxea microscleres; *tanekeis* (Gk), long-pointed.

Higginsia massalis Carter

(Figs 43–44, Table 9)

Higginsia coralloides.—Carter, 1885: 357.

Not *Higginsia coralloides* Higgin, 1877: 291, pl. 14, figs 1–5.

Higginsia coralloides Higgin var. *massalis* Carter, 1885: 357.—Dendy, 1896: 243; Hallmann, 1916b: 656, 659–65, pl. 29, fig. 6, pl. 38, figs 6–7, pl. 39, figs 1–2, pl. 40, figs 1–4.

Material Examined

Holotype. BMNH 1886.12.15.122: Port Phillip Heads, Vic., coll. J. B. Wilson.

New Caledonian material. QM G300023 (ORSTOM R1222): stn 124, Ilôt Maitre, 22°20' 1"S., 166°25' 1"E., 20 m depth, 15.vii.1976, coll. P. Laboute, SCUBA; ORSTOM unregistered: Fosse aux

Canards, 22°19'2"S., 166°26"E., 20–25 m depth, date of collection unknown, coll. P. Laboute, SCUBA; QM G301321: Croissant-Larégrière, Ilôt Maitre, off Noumea, 22°20'2"S., 166°22'5"E., 20 m depth, 13.x.1992, coll. J. N. A. Hooper, SCUBA.

Comparative material. BMNH 1886.12.15.79: Port Phillip Head, Vic., 22 m depth, coll. J. B. Wilson.

Description

Colour. Pale orange alive (Munsell 5YR 8/6), grey-brown in ethanol.

Shape. Massive, elongate, irregularly subspherical, 73 mm long, 46 mm diameter, without stalk or other processes, attached directly but loosely to the substrate with embedded detritus in 'ventral surface', or rolling freely on the substrate ('tumbleweed' sponge).

Table 9. Comparison in spicule dimensions between *Higginsia tanekeia*, sp. nov., and related species

All measurements given in micrometres, and expressed as range of measurement

Species (locality; source of data)	Spicule			
	Choanosomal megascleres	Extra-axial megascleres	Ectosomal megascleres	Acanthoxea microscleres
<i>Higginsia tanekeia</i> , sp. nov. (New Caledonia; holotype QM G300024)				
L	628–(824·3)–993	Absent	392–(512·9)–622	71–(111·6)–143
W	4–(10·2)–14 (Slender oxeas, rarely styloid)		3–(4·7)–7 (Oxeas)	1·5–(2·9)–4·5
<i>H. mixta</i> (Hentschel) (Aru I.; Hentschel 1912)				
L	624–744	2240	775–1175	88–152
W	28–31 (Robust oxeas)	20–31 (Long styles)	4–5 (Oxeas)	3–5
<i>H. mixta</i> (Hentschel) (Palau; Bergquist 1965)				
L	1025–1150	1900–3125	650–912	62–200
W	16–21	14–18	5–7	2–5
<i>H. mixta</i> (Hentschel) (NW. Australia; unpublished data, NTM collection)				
L	570–(871·3)–1250	850–(1260·0)–2015	Absent	70–(108·3)–175
W	25–(38·6)–50	4–(9·8)–16		3–(6·1)–10
<i>H. scabra</i> (Port Jackson, N.S.W.; Hallmann 1912)				
L	550–770	950–1100	Absent	60–130
W	8–35 (Robust oxeas)	15–25 (Long styles)		Up to 5
<i>H. scabra</i> Whitelegge (NW. Australia; unpublished data, NTM collection)				
L	550–(608·3)–675	222–(327·3)–417	Absent	72–(110·0)–154
W	18–(33·4)–42	5–(7·3)–11		1–(4·1)–6
<i>H. massalis</i> Carter (Port Phillip, Vic.; holotype BMNH 1886.12.15.122)				
L	535–(599·8)–706	492–(1129·8)–1750	321–(568·4)–704	72–(97·8)–124
W	10–(13·4)–17 (Robust oxeas, less often styloid)	5–(9·0)–14 (Long styles, rarely strongyles or oxeas)	2–(6·4)–11 (Oxeas, occasion- ally bidentate)	2–(3·7)–5
<i>H. massalis</i> Carter (Port Phillip, Vic.; specimen BMNH 1886.12.15.79)				
L	464–(610·1)–692	412–(867·0)–1221	265–(468·8)–669	71–(84·7)–96
W	8–(12·8)–16	7–(10·6)–15	4–(6·4)–9	2·5–(3·8)–5
<i>H. massalis</i> Carter (Port Phillip, Vic.; Hallmann 1916b)				
L	560–700	Up to 900	200–400	40–130
W	14–18	9	4–5	4–5
<i>H. massalis</i> Carter (New Caledonia; specimen QM G300023)				
L	841–(898·8)–936	632–(1484·3)–2121	512–(716·8)–843	74–(96·4)–137
W	12–(14·6)–18 (Robust oxeas, never styloid)	6–(8·2)–10 (Long styles, never oxeas)	2–(5·1)–8 (Oxeas)	2–(3·1)–4·5

Surface. Uneven, irregular, lumpy surface, with a distinct skin-like, detachable dermis, covered with evenly dispersed, irregularly shaped microconules, up to 3 mm diameter, raised no more than 2 mm from surface, forming meandering, crenellated ridges and valleys. Oscules, 3–6 mm diameter, slightly raised above surface, with membranous lip; smaller ostia, less than 1 mm diameter, situated between ridges. Texture soft, compressible, easily torn; internal consistency compact, only slightly cavernous, spiculose, friable, with low spongin fibre component.

Ectosome. Minutely hispid surface produced by sparsely dispersed, long extra-axial styles, protruding through a highly collagenous, darkly pigmented dermal layer, 70–220 μm wide. Ectosomal layer contains sparse, paratangential tracts of smaller, thinner oxeas and a thick, paratangential crust of acanthoxeas; acanthoxeas mainly confined to dermal skeleton. Subdermal region slightly cavernous, with elongate canals, 350–900 μm diameter.

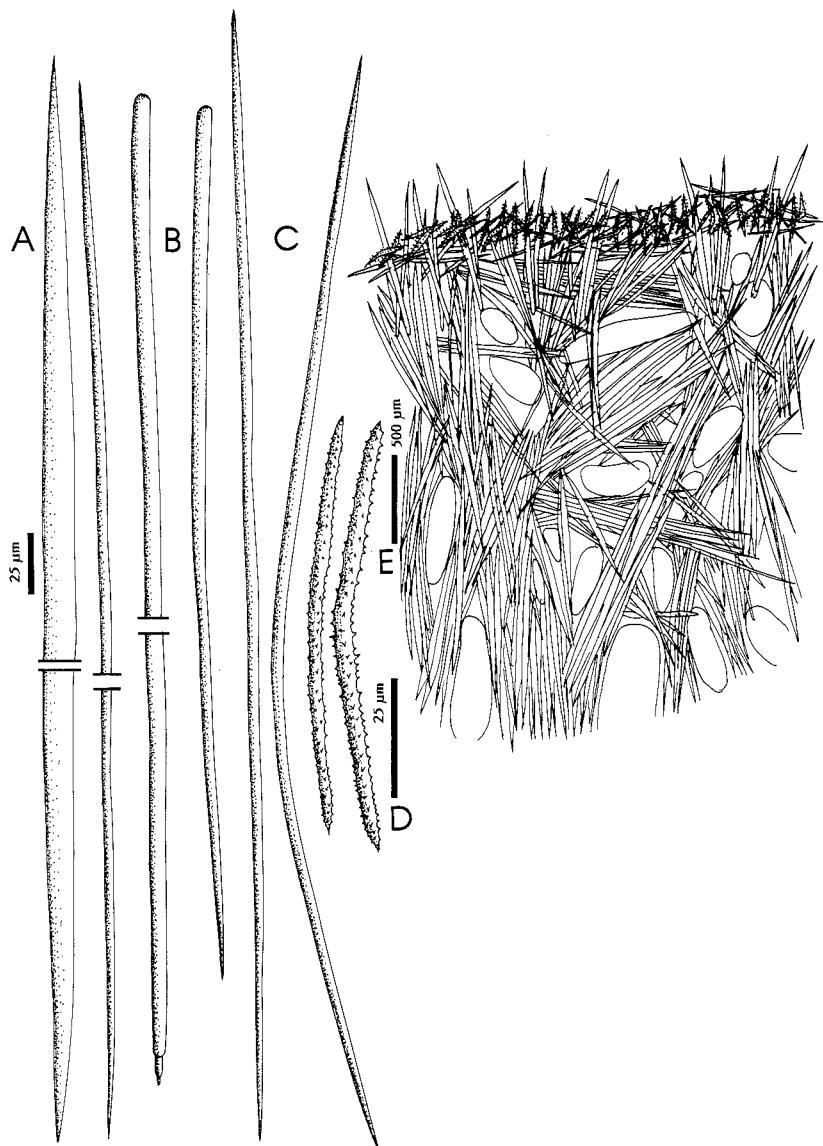


Fig. 43. *Higginsia massalis* Carter, specimen QM G300023: A, choanosomal oxeas; B, extra-axial styles; C, 'ectosomal' oxeas; D, acanthoxeas; E, section through peripheral skeleton.

Choanosome. Skeleton plumo-reticulate, verging on disorganised-halichondroid, without well developed axial compression of skeleton, with only poorly differentiated axial and extra-axial regions, with extra-axial spicule tracts slightly more plumose than more reticulate choanosomal spicule tracts, and containing long extra-axial styles in peripheral region, usually perpendicular to surface; skeleton consists of differentiated primary, more-or-less ascending, multisporic tracts, 70–110 μm diameter, interconnected by shorter, uni- or paucispicular, secondary, mostly transverse tracts, 20–70 μm diameter, cored exclusively by long choanosomal oxeas, with some thinner 'ectosomal' oxeas interdispersed; fibre reticulation produces elongate meshes, 110–300 μm diameter, but often partially obscured by choanosomal spicules dispersed between major skeletal tracts; spongin fibre system poorly developed, spicules appear to be cemented together primarily by granular collagen; meshes contain abundant collagen, with numerous choanosomal oxeas, only few acanthoxea microscleres, and very small quantities of detritus (arenaceous); choanocyte chambers small, oval to elongate, 25–45 μm diameter.

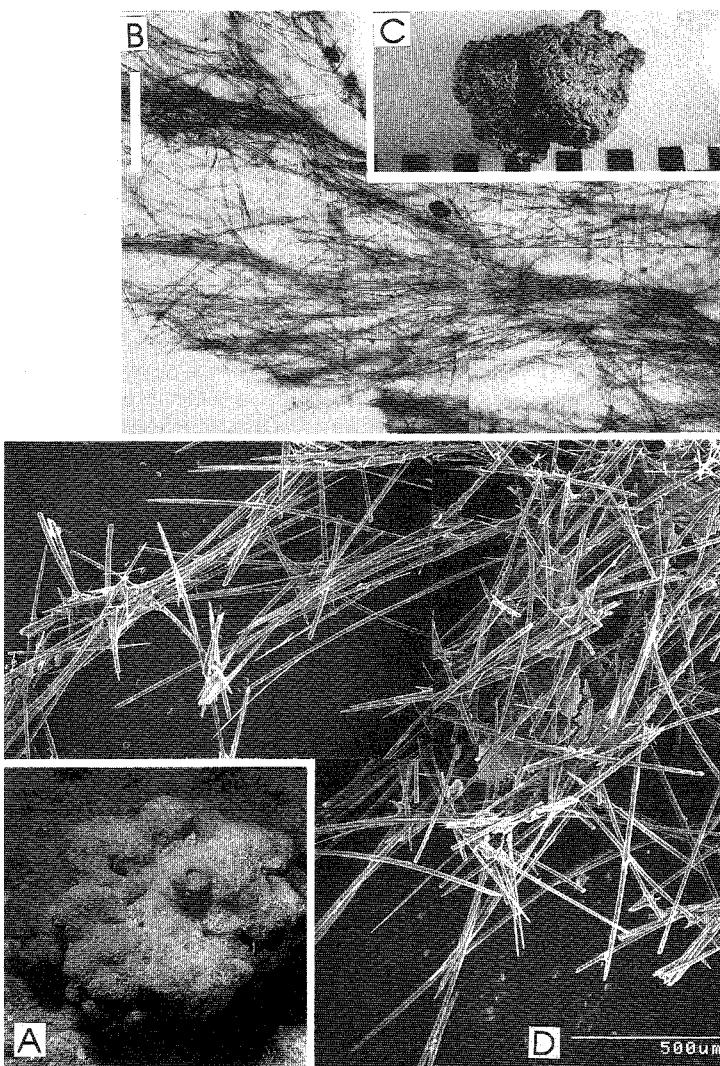


Fig. 44. *Higginsia massalis* Carter: *A*, specimen *in situ* [ORSTOM R1222 (specimen QM G300023)] (photo P. Laboute); *B*, peripheral skeleton (scale = 500 μm); *C*, same specimen preserved; *D*, SEM peripheral skeleton (scale = 500 μm).

Megascleres (refer to Table 9 for dimensions). Choanosomal megascleres exclusively oxeas, robust, relatively long, straight or slightly curved at centre, usually symmetrical, with fusiform, tapering, sharp, rarely telescoped points.

Extra-axial styles variable in length, usually very long, slender, slightly curved, sometimes straight or sinuous, with evenly rounded bases, tapering to sharp or slightly telescoped points.

'Ectosomal' oxeas very long, slender, usually slightly curved, sometimes greatly curved or sinuous, sharply pointed; these spicules not confined exclusively to ectosomal region, but also found in smaller quantities in choanosomal skeletal tracts.

Microscleres (refer to Table 9 for dimensions). Acanthoxeas relatively long, slender, with slight angular curvature at centre, tapering to sharp points, evenly covered with small spines; spines possibly larger at centre of spicule than on ends of spicule.

Distribution

Southern Australia and New Caledonia lagoon, inter-reef region on sand and coral rubble substrate, 10–22 m depth.

Remarks

There are several differences between the New Caledonian specimen of *H. massalis*, described above, and the holotype from southern Australia. Apart from minor differences in spicule sizes (Table 9), the points of choanosomal oxeas are often telescoped in the holotype, whereas they are rarely so in the present material, being more commonly sharply pointed; ectosomal oxeas in the holotype often have slightly rounded or bidentate terminations, whereas those in the New Caledonian specimen appear to be exclusively sharply pointed; extra-axial styles in the present material are always styloid, whereas those in the holotype are occasionally oxeote; and skeletal architecture is a little more disorganised in the New Caledonian specimen, whereas it is more regularly plumo-reticulate in the holotype. According to Hallmann (1916b: 659), the skeletons of several non-typical specimens from the Port Phillip region are composed of a series of thin lamellae, separated at the periphery but united further towards the choanosome, producing a shaggy peripheral skeletal structure (or 'skeleton-sponge' of Hallmann 1916b). This latter feature was not obvious in the New Caledonian specimen, nor was it apparent in the holotype.

These apparently minor differences may eventually prove to be indicative of two cryptic sibling species, possibly justifying the erection of a new taxon for the New Caledonian population. However, examination of a second specimen from Port Phillip Heads, originally assigned to the West Indies species *H. coralloides* by Carter (1885), showed it to be virtually intermediate in most of these characters, making it nearly impossible to clearly delineate the populations into separate species (without other, non-morphological characters to support such a proposal).

Hallmann's (1916b) measurements of spicules in his material differ slightly from those observed in both the holotype and Carter's (1885) specimen, especially the size of ectosomal spicules, and the corrected measurements for this material are presented in Table 9. Species related to *H. massalis* have already been discussed above and are also compared in Table 9.

Discussion

An earlier study of five families of poeciloscleridan sponges from the New Caledonian region (Hooper and Lévi 1993) listed 28 species, 18 of which were apparently endemic to this fauna. Although it was noted that there was a greater proportion of indigenous poecilosclerid sponge species (71%) living exclusively in deeper-waters of the shelf and slope of New Caledonia, agreeing with the preliminary biogeographic model suggested by Lévi (1979), the level of endemism for the shallow-water poecilosclerid fauna in the lagoon and outer reefs was also found to be significantly higher (62%) than previously predicted by Lévi. The present study described or redescribed 16 axinellid species from the shallow-waters in the lagoon and outer reefs surrounding New Caledonia, bringing the total number of

known axinellid species in this region to 25, of which 7 are new species and 7 are new locality records.

The non-endemic, shallow-water axinellid fauna appears to be most closely related to the north-east Australian (Solanderian) and Indo-Malay fauna, usually representing the eastern-most extent of their known distributions in the Indo-west Pacific. The shallow-water fauna also includes two authenticated 'widely distributed' species: *Axinella carteri* (Dendy) (distributed throughout coral reefs of the western and eastern Indian Ocean, the Indo-west Pacific and the western Pacific rim), and *Astrosclera willeyana* Lister [found in the western Indian Ocean (Réunion, Madagascar and Mozambique; Vacelet and Vasseur 1965, 1971; Vacelet 1967; Vacelet *et al.* 1976), eastern Indian Ocean (Christmas I.; Kirkpatrick 1910; Ashmore, Cartier and Hibernia Reefs, Sahul Shelf; Hooper 1992; southern Indonesia; van Soest 1990), central western Pacific Ocean (Guam; Hartman in Vacelet 1967), south-western Pacific Ocean (Great Barrier Reef; Ayling 1982; Loyalty and Tuvalu Is; Lister 1900; New Caledonia; Vacelet 1981), and central southern Pacific (French Polynesia; Vacelet 1977)], whereas other previously suspected 'widely distributed' species were generally found to be separate, closely related, cryptic sibling species. By comparison, the previous study on the poecilosclerid fauna indicated that its affinities lay mainly with both the northern and southern Australian shallow-water fauna, with surprisingly fewer similarities with the northern New Zealand fauna, plus a relatively higher endemic element (Hooper and Lévi 1993). Similar to the Poecilosclerida, however, many of the new axinellids described here were recognisable as sister-species of known, mainly tropical Australasian axinellids. These observed cryptic differences between many of the New Caledonian and Australasian sister-species are considered to be real, representing specific fixed differences in the genotype, rather than phenotypic variability of single, widely distributed species. This point of view contrasts with earlier studies in the western Pacific region (e.g. Burton 1934), and generally has empirical support (biochemical, genetic and detailed morphometric analyses of both sympatric and allopatric species; exhaustive comparison of relevant voucher material cited in these earlier studies, with less reliance on the published literature; Hooper *et al.* 1990, 1992; van Soest *et al.* 1991; van Soest and Hooper 1993).

Of the four families and 25 species of axinellids known to live in the vicinity of New Caledonia, 12 have not been recorded elsewhere (48% endemism). Most of this endemism can be accounted for by the deeper water fauna (three of five species), compared with only nine of the 20 species being shallow-water species. The proportion of endemic species for all four axinellid families is significantly lower than equivalent figures obtained for five families of Poecilosclerida (71% deeper-water, 63% shallow-water; Hooper and Lévi 1993), or for the entire described sponge fauna in this region (72% deeper-water, and 40% shallow-water). However, considering only the family Axinellidae so far collected and described for the region, the proportion of endemic species is high for both the shallow- and deeper-water species. Further comments on the biogeographic affinities of the New Caledonian Axinellidae will be discussed in a separate contribution.

A summary of the New Caledonian axinellid fauna is presented below [S, predominantly or exclusively shallow-water species (0–100 m depth); D, predominantly or exclusively deeper-water species (100–500 m depth); species marked with an asterisk are thought to be endemic to the region].

Axinellidae (15 species have been described for this region, nine of which are apparently endemic):

- Cymbastela cantharella* (Lévi, 1983) [S]*
- C. concentrica* (Lendenfeld, 1887) [S]
- Reniochalina plumosa* (Lévi & Lévi, 1983) [D]*
- R. condylia*, sp. nov. [S]*
- Axinella lifouensis* Lévi & Lévi, 1983 [D]*
- A. carteri* (Dendy, 1889) [S]
- Phakellia columnata* (Burton, 1928) [D]
- P. pulcherrima* (Ridley & Dendy, 1886) [S]
- P. stipitata* (Carter, 1881) [S]

- Styliissa flabelliformis* (Hentschel, 1912) [S]
Ptilocaulis fusiformis Lévi, 1967 [S]*
P. epakros, sp. nov. [S]*
P. papillatus, sp. nov. [S]*
Pseudaxinella debitusae, sp. nov. [S]*
Rhaphoxya systremma, sp. nov. [S]*

Desmoxiyidae (five species known for the region, only two of which are possibly endemic):

- Myrmekioderma granulata* (Esper, 1830) [S]
Higginsia anfractuosa, sp. nov. [S]*
H. tanekeia, sp. nov. [S]
Higginsia massalis Carter, 1885 [S]
Parahigginsia phakellioides Dendy, 1924 [D]

Trachycladidae (one species known for the region, also recorded from south-eastern and south-western Australia):

- Trachycladus digitatus* Lendenfeld, 1887 [S]

Agelasidae [now in the order Agelasida; two species known for the region, one apparently endemic, and two hypercalcified 'sclerosponges' are also included here (following van Soest 1984 and others)]:

- Agelas mauritiana* (Carter, 1883) [S]
A. novaecaledoniae Lévi & Lévi, 1983 [D]*
Astrosclera willeyana Lister, 1900 [S]
Stromatospongia micronesica Hartman and Goreau, 1976 [S]

Acknowledgements

We are extremely grateful to Dr Cécile Debitus, ORSTOM, Noumea, for assisting with the acquisition of specimens and *in situ* photographs of live material, which have greatly facilitated the preparation of this publication. We also gratefully acknowledge funding provided by both ORSTOM Noumea and DITAC Canberra, which enabled the authors to participate in a series of workshops at ORSTOM Noumea on the taxonomy of New Caledonian shallow-water sponges. This publication is one of several recent contributions on the shallow-water fauna of the Noumea lagoon, as a prelude to the publication of a forthcoming popular book on the subject, and we acknowledge the assistance and interaction of our colleagues Chris Battershill, Patricia Bergquist, Jane Fromont, Michelle Kelly-Borges, Jean Vacelet and Clive Wilkinson. For collection of specimens and photographs we thank Pierre Laboute, Georges Bargibant, Jean-Louis Menou, and other members of ORSTOM Noumea for the hospitality, helpful assistance and cooperation during this project.

References

- Anon. (1985). 'International Code of Zoological Nomenclature.' 3rd edn. pp. 1-338. (International Trust for Zoological Nomenclature, H. Charlesworth and Co.: Huddersfield.)
- Ayling, A. (1982). A redescription of *Astrosclera willeyana* Lister, 1900 (Ceratoporellida, Demospongiae), a new record from the Great Barrier Reef. *Memoirs of the National Museum of Victoria* **43**, 99-103.
- Babic, K. (1922). Monactinellida und Tetractinellida des Adriatischen Meeres. *Zoologische Jahrbücher Jena Abteilung für Systematik, Okologie und Geographie der Tiere* **46**, 217-302, pls 8-9.
- Bergquist, P. R. (1961). Demospongiae (Porifera) of the Chatham Islands and Chatham Rise, collected by the Chatham Islands 1954 Expedition. *New Zealand Department of Scientific and Industrial Research Bulletin 139. Biological Results of the Chatham Islands 1954 Expedition* **5**, 169-206.
- Bergquist, P. R. (1965). The sponges of Micronesia, Part 1. The Palau Archipelago. *Pacific Science* **19**(2), 123-204.

- Bergquist, P. R. (1970). The marine fauna of New Zealand: Porifera, Demospongiae, Part 2. (Axinellida and Halichondrida). *New Zealand Department of Scientific and Industrial Research Bulletin. New Zealand Oceanographic Institute Memoir* **197**, 1–85, pls 1–20.
- Bergquist, P. R. (1978). 'Sponges.' pp. 1–268. (Hutchinson: London.)
- Bergquist, P. R., and Hartman, L. D. (1969). Free amino acid patterns and the classification of the Demospongiae. *Marine Biology* **3**(3), 247–68.
- Bergquist, P. R., and Tizard, C. A. (1967). Australian intertidal sponges from the Darwin area. *Micronesica* **3**, 175–202, pls 1–6.
- Bergquist, P. R., Hofheinz, W., and Oesterhelt, G. (1980). Sterol composition and the classification of the Demospongiae. *Biochemical Systematics and Ecology* **8**, 423–35.
- Bowerbank, J. S. (1864). 'A Monograph of the British Spongiidae.' Vol. 1, pp. 1–290, pls 1–37. (Ray Society: London.)
- Bowerbank, J. S. (1866). 'A Monograph of the British Spongiidae.' Vol. 2, pp. 1–388. (Ray Society: London.)
- Brondsted, H. V. (1923). Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. 15. Sponges from the Auckland and Campbell Islands. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening* **75**, 117–67.
- Brondsted, H. V. (1924). Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. 23. Sponges from New Zealand. Part 1. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening* **77**, 435–83.
- Burton, M. (1927). A revision of the genera and species contained in Lendenfeld's 'Die Chalineen des australischen Gebietes'. *Annals and Magazine of Natural History* (9) **20**, 289–98, 502–12.
- Burton, M. (1928). Report on some deep-sea sponges from the Indian Museum collected by the R.I.M.S. "Investigator". Part II. Tetraxonida (concluded) and Euceratosa. *Records of the Indian Museum* **30**(1), 109–38, pls 1–2.
- Burton, M. (1934). Sponges. In 'Scientific Reports of the Great Barrier Reef Expedition 1928–29'. Vol. 4(14), pp. 513–621, pls 1–2. [British Museum (Natural History): London.]
- Burton, M. (1938). Supplement to the littoral fauna of Krusadai Island in the Gulf of Manaar. Porifera. *Bulletin of the Madras Government Museum (n.s.), Natural History Section* **1**(2), 1–58, pls 1–9.
- Burton, M. (1959). Sponges. In 'Scientific Reports of the John Murray Expedition 1933–34'. Vol. 10(5), pp. 151–281. [British Museum (Natural History): London.]
- Capon, R. J., and MacLeod, J. K. (1988). New isothiocyanate sesquiterpenes from the Australian marine sponge *Acanthella pulcherrima*. *Australian Journal of Chemistry* **41**, 979–83.
- Carter, H. J. (1881). Supplementary report on specimens dredged up from the Gulf of Manaar, together with others from the sea in the vicinity of the Basse Rocks and from Bass's Straits respectively, presented to the Liverpool Free Museum by Capt. H. Cawne Warren. *Annals and Magazine of Natural History* (5) **7**, 361–85, pl. 18.
- Carter, H. J. (1883). Contributions to our knowledge of the Spongida. *Annals and Magazine of Natural History* (5) **12**, 308–29, pls 11–14.
- Carter, H. J. (1884). Catalogue of marine sponges, collected by Mr. Jos. Willcox, on the west coast of Florida. *Proceedings of the Academy of Philadelphia* (1884), 202–9.
- Carter, H. J. (1885). Descriptions of sponges from the neighbourhood of Port Phillip Heads, South Australia. *Annals and Magazine of Natural History* (5) **15**, 107–17, 196–222, 301–21, pl. 4. **16**, 277–94, 347–68.
- Carter, H. J. (1886a). Descriptions of sponges from the neighbourhood of Port Phillip Heads, South Australia, continued. *Annals and Magazine of Natural History* (5) **17**, 40–53, 112–27, 431–41, 502–16. **18**, 34–55, 126–49.
- Carter, H. J. (1886b). Report on the marine sponges, chiefly from King Island, in the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr. John Anderson, F.R.S., Superintendent of the Museum. *Journal of the Linnean Society of London, Zoology* **21**, 61–84, pls 5–7.
- de Laubenfels (see Laubenfels, M.W. de).
- Dendy, A. (1889). Report on a second collection of sponges from the Gulf of Manaar. *Annals and Magazine of Natural History* (6) **3**, 73–99, pls 3–5.
- Dendy, A. (1896). Catalogue of non-calcareous sponges collected by J. Bracebridge Wilson, Esq., M.A., in the neighbourhood of Port Phillip Heads. Part 2. *Proceedings of the Royal Society of Victoria* **2**(8), 14–51.
- Dendy, A. (1897a). Catalogue of non-calcareous sponges collected by J. Bracebridge Wilson, Esq., M.A., in the neighbourhood of Port Phillip Heads. Part 3. *Proceedings of the Royal Society of Victoria* **2**(9), 230–59.

- Dendy, A. (1897b). On the sponges described in Dieffenbach's "New Zealand". *Transactions of the Philosophical Institute of Canterbury* **30**(13), 316–20, pls 33–4.
- Dendy, A. (1905). Report on the sponges collected by Professor Herdman, at Ceylon, in 1902. In 'Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar'. (Ed. W. A. Herdman.) Vol. 3(18), pp. 57–246, pls 1–16. (Royal Society: London.)
- Dendy, A. (1922). Report on the Sigmatotetraxonida collected by H.M.S. "Sealark" in the Indian Ocean. In 'Reports of the Percy Sladen Trust Expedition to the Indian Ocean in 1905, Volume 7'. *Transactions of the Linnean Society of London, Zoology* **18**, 1–164, pls 1–18.
- Dendy, A. (1924). Porifera. Part I. Non-Antarctic sponges. In 'British Antarctic (*Terra Nova*) Expedition, 1910. Natural History Report, Zoology'. Vol. 6(3), pp. 269–392, pls 1–15 [British Museum (Natural History): London].
- Desqueyroux-Faundez, R. (1981). Révision de la collection d'éponges d'Amboine (Moluques, Indonésie) constituée par Bedot et Pictet et conservée au Muséum d'histoire naturelle de Genève. *Revue Suisse de Zoologie* **88**(3), 723–64.
- Donadey, C., Paris, J., and Vacelet, J. (1990). Occurrence and ultrastructure of micrорaphides in *Axinella polypoides*. In 'New Perspectives in Sponge Biology'. (Ed. K. Ruetzler.) Third International Conference on the Biology of Sponges, convened by Klaus Ruetzler and Willard D. Hartman, Woods Hole, USA, November 17–23 1985. (Smithsonian Institution Press: Washington, D.C.)
- Ehlers, F. (1870). 'Die Esper'schen Spongien.' *Zoologischen Sammlung der König. Universität Erlangen. Progra mm zum Eintritt in der Senat der Königlichen Friedrich-Alexanders-Universität in Erlangen*: 36 pp.
- Esper, E. J. C. (1830). 'Die Pflanzenthiere in Abilungen nach der Natur mit Fabbenerleuchtet nebst Beschreibungen.' (Dritter Theil: Nürnberg.) pp. 1–230, pls 1–25.
- Gray, J. E. (1867). Notes on the arrangement of sponges, with description of some new genera. *Proceedings of the Zoological Society of London* (1867), 492–558, pls 27–8.
- Guiler, E. R. (1950). Notes on Tasmanian marine sponges. *Records of the Queen Victoria Museum, Launceston* **3**(2), 5–14.
- Hallmann, E. F. (1914a). A revision of the monaxonid species described as new in Lendenfeld's "Catalogue of the Sponges in the Australian Museum". Part 1. *Proceedings of the Linnean Society of New South Wales* **29**, 263–315, pls 15–24.
- Hallmann, E. F. (1914b). A revision of the monaxonid species described as new in Lendenfeld's "Catalogue of the Sponges in the Australian Museum". Part 2. *Proceedings of the Linnean Society of New South Wales* **29**, 327–76, pls 15–24.
- Hallmann, E. F. (1914c). A revision of the monaxonid species described as new in Lendenfeld's "Catalogue of the Sponges in the Australian Museum". Part 3. *Proceedings of the Linnean Society of New South Wales* **29**, 398–446, pls 15–24.
- Hallmann, E. F. (1916a). A revision of the genera with microscleres included, or provisionally included, in the Family Axinellidae, with descriptions of some Australian species. Part ii (Porifera). *Proceedings of the Linnean Society of New South Wales* **41**(3), 495–552, pls 29–38.
- Hallmann, E. F. (1916b). A revision of the genera with microscleres included, or provisionally included, in the Family Axinellidae, with descriptions of some Australian species. Part iii (Porifera). *Proceedings of the Linnean Society of New South Wales* **41**(4), 634–75, pls 29, 33, 38–44.
- Hartman, W. D. (1982). Porifera. In 'Synopsis and Classification of Living Organisms'. (Ed. S. P. Parker.) Vol. 1, pp. 640–66. (McGraw-Hill: New York.)
- Hartman, W. D., and Goreau, T. F. (1976). A new Ceratoporellid sponge (Porifera:Sclerospongiae) from the Pacific. In 'Aspects of Sponge Biology'. (Eds F. W. Harrison and R. R. Cowden.) pp. 329–47. (Academic Press: New York.)
- Hentschel, E. (1912). Kiesel- und Hornschwämme der Aru und Kei-Inseln. *Abhandlungen Senckenbergiana naturforschende Gesellschaft* (1912), 295–448.
- Higgin, T. H. (1877). Description of some sponges obtained during a cruise of the steam-yacht "Argo" in the Caribbean and neighbouring seas. *Annals and Magazine of Natural History* (4) **19**, 291–9, pl. 14.
- Hooper, J. N. A. (1984). *Sigmaxinella soelae* and *Desmacella ithystela*. Two new desmacellid sponges (Porifera, Axinellida, Desmacellidae) from the Northwest Shelf of Western Australia, with a revision of the family Desmacellidae. *Monograph Series, Northern Territory Museum of Arts and Sciences* **2**, 1–58.
- Hooper, J. N. A. (1986). Revision of the marine sponge genus *Axos* Gray (Demospongiae:Axinellida) from northwest Australia. *The Beagle, Occasional Papers of the Northern Territory Museum of Arts and Sciences* **3**(1), 167–89, pl. 1.
- Hooper, J. N. A. (1991). Revision of the Family Raspailiidae (Porifera: Demospongiae), with description of Australian species. *Invertebrate Taxonomy* **5**(6), 1179–415.

- Hooper, J. N. A. (1992). Sponges. In 'Survey of the Marine Resources of Cartier Island and Hibernia Reefs, Timor Sea'. (Eds J. R. Hanley and B. C. Russell.) pp. 25–34. Northern Territory Museum of Arts and Sciences Technical Report No. 2.
- Hooper, J. N. A., and Bergquist, P. R. (1992). *Cymbastela*, a new genus of lamellate coral reef sponges. *Memoirs of the Queensland Museum* 32(1), 99–137.
- Hooper, J. N. A., and Lévi, C. (1993). Poecilosclerida (Porifera:Demospongiae) from the New Caledonia Lagoon. *Invertebrate Taxonomy* 7, 1221–302.
- Hooper, J. N. A., Capon, R. J., Keenan, C. P., and Parry, D. L. (1990). Biochemical and morphometric differentiation of two sympatric sibling species of *Clathria* (Porifera:Demospongiae) from northern Australia. *Invertebrate Taxonomy* 4(1), 123–48.
- Hooper, J. N. A., Capon, R. J., Keenan, C. P., Parry, D. L., and Smit, N. (1992). Chemotaxonomy of marine sponges: families Microcionidae, Raspailiidae, and Axinellidae, and their relationships with other families in the orders Poecilosclerida and Axinellida (Porifera:Demospongiae). *Invertebrate Taxonomy* 6(2), 261–301.
- Hoshino, T. (1981). Shallow-water demosponges of western Japan, I. *Journal of Science of the Hiroshima University Series B, Division 1 (Zoology)* 29(1–2), 47–205, pls 1–7; 207–89, pls 1–11.
- Keller, C. (1889). Die Spongienfauna des rothen Meeres. I. Hälfte. *Zeitschrift fur Wissenschaftliche Zoologie* 48, 311–406, pls 20–5.
- Keller, C. (1891). Die Spongienfauna des rothen Meeres II. Hälfte. *Zeitschrift fur Wissenschaftliche Zoologie* 52, 294–368, pls 16–20.
- Kieschnick, O. (1898). 'Die Kiesel Schwämme von Amboina.' pp. 1–66. (Inaugural Dissertation: Jena.)
- Kieschnick, O. (1900). Kiesel Schwämme von Amboina. Zoologische Forschungoreisen in Australien und den Malayischen Archipel ... ausgeführt in den Jahren 1891–1893. 5/5. *Denkschriften Medizinisch Naturwissenschaftliche Gesellschaft, Jena* 8, 545–82, pls 44–5.
- Kirkpatrick, R. (1900). On the sponges of Christmas Island. *Proceedings of the Zoological Society of London (1900)*, 127–41, pls 12–13.
- Kirkpatrick, R. (1910). On the affinities of *Astrosclera willeyana* Lister. *Annals and Magazine of Natural History* (8) 5, 380–3.
- Lamarck, J. B. P. de Monet (1814). Sur les polypiers empâtés. *Annales du Muséum d'Histoire naturelle, Paris* 20, 294–312, 370–86, 432–58.
- Laubenfels, M. W. de (1934). New sponges from the Puerto Rican Deep. *Smithsonian Miscellaneous Collections* 91(17), 1–28.
- Laubenfels, M. W. de (1936). A discussion of the sponge fauna of the Dry Tortugas in particular, and the West Indies in general, with material for a revision of the families and orders of the Porifera. Carnegie Institute of Washington Publication Number 467. *Papers of the Tortugas Laboratory* 30, 1–225, pls 1–22.
- Laubenfels, M. W. de (1950). The Porifera of the Bermuda Archipelago. *Transactions of the Zoological Society of London* 27, 1–154, pls 1–2.
- Laubenfels, M. W. de (1953). Sponges from the Gulf of Mexico. *Bulletin of Marine Science of the Gulf and Caribbean* 2(3), 511–57.
- Laubenfels, M. W. de (1954). The sponges of the West-Central Pacific. *Oregon State Monographs, Zoology* 7, 1–306, pls 1–12.
- Lendenfeld, R. von (1887). Die Chalineen des australischen Gebietes. *Zoologische Jahrbücher, Jena* 2, 723–828, pls 18–27.
- Lendenfeld, R. von (1888). 'Descriptive Catalogue of the Sponges in the Australian Museum, Sydney.' pp. 1–260, pls 1–12. (Taylor and Francis: London.)
- Lévi, C. (1956). Spongiaires des côtes de Madagascar. *Mémoires de l'Institut Scientifique de Madagascar (A)* 10, 1–23.
- Lévi, C. (1961). Résultats scientifique des campagnes de la "Calypso" Fascicule V. XIV. Campagne 1954 dans l'Océan Indien. 2. Les spongiaires de l'île Aldabra. Campagne Océanographique de la "Calypso" (May–Juin 1954). *Annales de l'Institut Océanographique, Monaco* 39, 1–31, pls 1–2.
- Lévi, C. (1967). Démosponges récoltées en Nouvelle-Calédonie par la Mission Singer-Polignac. Expédition Française sur les récifs coralliens de la Nouvelle-Calédonie. *Éditions de la Foundation Singer-Polignac* 2, 13–26, pls 1–3.
- Lévi, C. (1973). Systématique de la classe des Demospongaria (Démosponges). In 'Traité de Zoologie. Anatomie, Systématique, Biologie. III. Spongiaires'. (Sér. ed. P.-P. Grassé.) pp. 577–631. (Masson et Cie: Paris.)
- Lévi, C. (1979). The demospónge fauna from the New Caledonian area. In 'Proceedings of the International Symposium on Marine Biogeography and Evolution in the Southern Hemisphere'. New Zealand Oceanographic Institute Special Volume 1979, pp. 307–15.

- Lévi, C. (1983). *Pseudaxinyssa cantharella* n.sp., Démospunge Axinellidae du lagon de Nouméa (Nouvelle-Calédonie). *Bulletin du Muséum National d'Histoire Naturelle* (4) 5(A, no. 3), 719–22.
- Lévi, C., and Lévi, P. (1983). Démospanges bathyales récoltées par le N/O "Vauban" au sud de la Nouvelle-Calédonie. *Bulletin du Muséum National d'Histoire Naturelle* (4) 5(A, no. 4), 931–97, pls 1–8.
- Lindgren, N. G. (1897). Beitrag zur Kenntniss der Spongiensfauna des Malaiischen Archipels und der Chinesischen Meere. *Zoologischer Anzeiger* 20, 480–7.
- Lindgren, N. G. (1898). Beitrag zur Kenntniss der Spongiensfauna des Malayischen Archipels und der chinesischen Meere. *Zoologischer Jahrbücher, Jena* 11, 283–378, pls 17–20.
- Linnaeus, C. (1767). 'Systema Naturae Editio duodecima reformata.' Holmiae 1(2).
- Lister, J. J. (1900). *Astrosclera willeyana* the type of a new family of sponges. *Willey's Zoological Results* 4, 459–82.
- Pallas, P. S. (1766). 'Elenchus Zoophytorum sistens Generum Adumbrationes Generaliores et Specierum Cognitarum succinctas Descriptiones cum Selectis Auctorum Synonymis Hagae.' Comitum, apud Petrum van Cleef. pp. 1–451.
- Pansini, M. (1983). Notes on some Mediterranean *Axinella* with description of two species. *Bulletino dei Musei e degli Istituti Biologici dell'Università di Genova* 50–51, 79–98.
- Pulitzer-Finali, G. (1982). Some new or little-known sponges from the Great Barrier Reef of Australia. *Bulletino dei Musei e degli Istituti Biologici dell'Università di Genova* 48–49(1980–1981), 87–141.
- Pulitzer-Finali, G. (1983). A collection of Mediterranean Demospongiae (Porifera) with, in appendix, a list of the Demospongiae hitherto recorded from the Mediterranean Sea. *Annali del Museo Civico di Storia Naturale di Genova* 84, 445–621.
- Ridley, S. O. (1884). Spongiida. In 'Report on the Zoological Collections made in the Indo-Pacific Ocean during the Voyage of H.M.S. 'Alert' 1881–2.' pp. 366–482, 582–630, pls 39–43, 53–4. [British Museum (Natural History): London.]
- Ridley, S. O., and Dendy, A. (1886). Preliminary report on the Monaxonida collected by the H.M.S. *Challenger*. *Annals and Magazine of Natural History* (5) 18, 325–51, 470–93.
- Ridley, S. O., and Dendy, A. (1887). Report on the Monaxonida collected by H.M.S. *Challenger* during the years 1873–76. In 'Report on the Scientific Results of the Voyage of H.M.S. *Challenger* during the Years 1873–76'. Vol. 20, pp. 1–275, pls 1–51. (Her Majesty's Stationery Office: London, Edinburgh, Dublin.)
- Row, R. W. H. (1911). Reports on the marine biology of the Sudanese Red Sea, from collections made by Cyril Crossland, M.A., B.Sc., F.Z.S. XIX. Report on the sponges collected by Mr. Cyril Crossland in 1904–5. Part II. Non-Calcarea. *Journal of the Linnean Society, Zoology* 31(208), 287–400, pls 35–41.
- Schmidt, E. O. (1862). 'Die Spongiens des Adriatischen Meeres.' pp. 1–88, pls 1–6. (Wilhelm Engelmann: Leipzig.)
- Schmidt, E. O. (1864). 'Supplement der Spongiens des Adriatischen Meeres. Enthaltend die Histologie und Systematische Ergänzungen.' pp. 1–48, pls 1–4. (Wilhelm Engelmann: Leipzig.)
- Schmidt, E. O. (1866). 'Zweites Supplement der Spongiens des Adriatischen Meeres. Enthaltend die Vergleichung der Adriatischen und Britischen Spongiengattungen.' pp. 1–24, pl. 1. (Wilhelm Engelmann: Leipzig.)
- Schmidt, E. O. (1868). 'Die Spongiens der Küst von Algier. Mit Nachträgen zu den Spongiens des Adriatischen Meeres. (Drittes Supplement).' pp. 1–44, pls 1–5. (Wilhelm Engelmann: Leipzig.)
- Schmidt, E. O. (1875). Spongiens. In 'Die Expedition zur physikalisch-chemischen und biologischen Untersuchung der Nordsee im Sommer 1872. V. Zoologische Ergebnisse der Nordseefahrt'. Jahresbericht Comm. Wissenschaft Unterabteilung Deutsch. Meere 2–3, 115–20, pl. 1.
- Soest, R. W. M. van (1984). Deficient *Merlia normani* Kirkpatrick, 1908, from the Curaçao reefs, with a discussion on the phylogenetic interpretation of sclerosponges. *Bijdragen tot de Dierkunde* 54(2), 211–19.
- Soest, R. W. M. van (1989). The Indonesian sponge fauna: a status report. *Netherlands Journal of Sea Research* 23(2), 223–30.
- Soest, R. W. M. van (1990). Shallow-water reef sponges of Eastern Indonesia. In 'New Perspectives in Sponge Biology'. (Ed. K. Ruetzler.) pp. 344–8. (Smithsonian Institution Press: Washington.)
- Soest, R. W. M. van, and Hooper, J. N. A. (1993). Taxonomy, phylogeny and biogeography of the marine sponge genus *Rhabdereumia* (Porifera: Poecilosclerida). *Scientia Marina* (in press).
- Soest, R. W. M. van, Diaz, M. C., and Pomponi, S. A. (1990). Phylogenetic classification of the halichondrids (Porifera, Demospongiae). *Beaufortia* 40(2), 15–62.
- Soest, R. W. M. van, Hooper, J. N. A., and Hiemstra, F. (1991). Taxonomy, phylogeny and biogeography of the marine sponge genus *Acarinus* (Porifera: Poecilosclerida). *Beaufortia* 42(3), 49–88.

- Thiele, J. (1899). Studien über pazifische Spongiens. II. Heft. *Zoologica* 24, 1–33, pls 1–5.
- Thiele, J. (1903). Beschreibung einiger unzureichend bekannten monaxonen Spongiens. *Archiv für Naturgeschichte* 69(1), 375–98, pl. 21.
- Thiele, J. (1905). Die Kiesel- und Hornschwamme der Sammlung Plate. *Zoologische Jahrbücher, Jena Supplement* 6 [Fauna chilensis (3)], 407–96, pls 27–33.
- Topsent, E. (1897). Spongaires de la Baie d'Amboine. Voyage de MM. M. Bedot et C. Pictet dans l'Archipel Malais. *Revue Suisse de Zoologie* 4, 421–87.
- Topsent, E. (1904). Spongaires des Açores. *Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert Ier Prince Souverain de Monaco* 25, 1–280, pls 1–18.
- Topsent, E. (1906). Éponges recueillies par M. Ch. Gravier dans la Mer Rouge. *Bulletin du Muséum National d'Histoire Naturelle* (1906), 557–70.
- Topsent, E. (1928). Spongaires de l'Atlantique et de la Méditerranée provenant des croisières du Prince Albert Ier de Monaco. *Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert Ier Prince Souverain de Monaco* 74, 1–376, pls 1–11.
- Topsent, E. (1930). Éponges de Lamarck conservées au Muséum de Paris. *Archives du Muséum National d'Histoire Naturelle* (6) 5, 1–56, pls 1–4.
- Topsent, E. (1932). Éponges de Lamarck conservées au Muséum de Paris. Deuxième partie (I). *Archives du Muséum National d'Histoire Naturelle* (6) 8, 61–124, pls 1–6.
- Topsent, E. (1933). Éponges de Lamarck conservées au Muséum de Paris. Fin (I). *Archives du Muséum National d'Histoire Naturelle* (6) 10, 1–60, pls 1–3.
- Topsent, E. (1934). Etude d'Éponges littorales du Golfe de Gabès. *Bulletin de la Station Aquiculture et Pêche Castiglione* (1932), 71–102.
- Vacelet, J. (1961). Spongaires (demosponges) de la région de Bonifacio (Corse). *Recueil des Travaux de la Station Marine d'Endoume* 36(22), 21–45.
- Vacelet, J. (1967). Quelques éponges Pharétronides et "silico-calcaires" des grottes sous-marines obscures. *Recueil des Travaux de la Station Marine d'Endoume* 58(42), 121–32.
- Vacelet, J. (1969). Éponges de la roche du large et de l'étage bathyal de Méditerranée. *Mémoires du Muséum National d'Histoire Naturelle* (A, Zoologie) 59(2–3), 145–219, pls 1–4.
- Vacelet, J. (1977). Éponges Pharétronides actuelles et Sclérosponges de Polynésie Française, de Madagascar et de La Réunion. *Bulletin du Muséum National d'Histoire Naturelle* 3, (no. 444; zoologie) (307), 345–64, pls 1–2.
- Vacelet, J. (1981). Éponges hypercalcifiées ("Pharétronides", "Sclérosponges") des cavités sea récifs coralliens de Nouvelle-Calédonie. *Bulletin du Muséum National d'Histoire Naturelle* (4) 3 (A, 2), 313–51.
- Vacelet, J., and Vasseur, P. (1965). Spongaires de grottes et surplombs des récifs de Tuléar (Madagascar). *Recueil des Travaux de la Station Marine d'Endoume, Supplement* 4, 71–123.
- Vacelet, J., and Vasseur, P. (1971). Éponges des récifs coralliens de Tuléar (Madagascar). *Tethys, Supplément* 1, 51–126, pls 1–4.
- Vacelet, J., Vasseur, P., and Lévi, C. (1976). Spongaires de la pente externe des récifs coralliens de Tuléar (sud-Ouest de Madagascar). *Mémoires du Muséum National d'Histoire Naturelle* (A, Zoologie) 49, 1–116, pls 1–10.
- van Soest (see Soest, R. W. M. van).
- Vosmaer, G. C. J. (1912). On the distinction between the genera *Axinella*, *Phakellia*, *Acanthella* a.o. *Zoologische Jahrbücher, Jena Supplement* 15, 307–22, pls 15–16.
- Vosmaer, G. C. J. (1933). 'The Sponges of the Bay of Naples. Porifera Incalcaria with Analyses of Genera and Studies in the Variations of Species.' Vol. 1, pp. 1–456. (Martinus Nijhoff: The Hague.)
- Vosmaer, G. C. J. (1935a). 'The Sponges of the Bay of Naples. Porifera Incalcaria with Analyses of Genera and Studies in the Variations of Species.' Vol. 2, pp. 457–828. (Martinus Nijhoff: The Hague.)
- Vosmaer, G. C. J. (1935b). 'The Sponges of the Bay of Naples. Porifera Incalcaria with Analyses of Genera and Studies in the Variations of Species.' Vol. 3, pp. 829–48, pls 1–71. (Martinus Nijhoff: The Hague.)
- Whitelegge, T. (1889). List of the marine and freshwater invertebrate fauna of Port Jackson and the neighbourhood. *Journal of the Royal Society of New South Wales* 23(2), 163–323.
- Whitelegge, T. (1901). Report on sponges from the coastal beaches of New South Wales. *Records of the Australian Museum* 4(2), 1–70 [55–118], pls 10–15.
- Whitelegge, T. (1902). Notes on Lendenfeld's Types described in the Catalogue of Sponges in the Australian Museum. *Records of the Australian Museum* 4(7), 274–88.

- Whitelegge, T. (1907). Sponges. Part I.—Addenda. Part 2. Monaxonida continued. In 'Scientific Results of the Trawling Expedition of H.M.C.S. "Thetis" Off the Coast of New South Wales in February and March, 1898'. *Memoirs of the Australian Museum* 4(10), 487–515, pls 45–6.
- Wiedenmayer, F. (1977). 'Shallow-Water Sponges of the Western Bahamas.' Vol. 28, pp. 1–287, pls 1–42. (*Experimentia Supplementa*. Birkhäuser: Basel.)
- Wiedenmayer, F. (1989). Demospongiae (Porifera) from northern Bass Strait, southern Australia. *Memoirs of the Museum of Victoria* 50(1), 1–242, pls 1–38.

Manuscript received 2 December 1992; accepted 14 April 1993