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A NEW SPECIES OF *RHABDEREMIA* TOPSENT (PORIFERA: DEMOSPONGIAE) FROM THE GREAT BARRIER REEF

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ABSTRACT

A new species of *Rhabderemia* is described from a fringing coral reef habitat in the Whitsunday Islands Group, Great Barrier Reef, bringing the total number of species known for the genus to 16, although this is only the second record of the genus in Australian waters. The genera *Rhabderemia* Topsent, *Rhabdosigma* Hallmann, and *Nisibaris* de Laubenfels are merged, and the family Rhabderemiidae is defined in the order Poecilosclerida. A key and synonymy of the described species is given, and preliminary phylogenetic and zoogeographic analyses of species are made. Two groups of species are indicated, differentiated by skeletal construction (hymedesmoid-plumose and reticulate skeletons), and there also appears to be two zoogeographically disjunct groups of species separated into the Atlantic and Indo-Pacific systems.

KEYWORDS: Porifera, Demospongiae, Poecilosclerida, Rhabdermiidae, *Rhabderemia*, new species, coral reef, Great Barrier Reef, taxonomy, cladistics, zoogeography.

INTRODUCTION

Recent collections throughout Australian shallow coastal waters by the Australian Institute of Marine Science Bioactivity Unit, Townsville, discovered a species of sponge new to science, inhabiting a fringing coral reef in the Whitsunday Islands, Queensland. This new species is only the second record for the genus *Rhabderemia* Topsent in Australia, and brings the total number of species known for the genus to 16. The species is described and illustrated below, and a key to species is also given. A preliminary investigation on the zoogeography and phylogenetic relationships between species is made, based mostly on descriptions from the literature.

Methods of spicule preparation for light and scanning electron microscopy are described elsewhere (Hooper 1986). A phylogenetic analysis of species was produced using the computer-generated cladistic routine (PAUP; Swofford 1985), which produced minimum length trees under the principle of maximum parsimony, inferring plesiomorphy by outgroup comparisons. A taxonomic key was constructed using ordered binary and multistate characters utilizing the DELTA computer system (Dallwitz and Paine 1986). Abbreviations used in the text and in Appendix 1 are as follows: AIMS, Australian Institute of Marine Science, Townsville; AM, Australian Museum, Sydney; BMNH, British Museum (Natural History), London; CMFRI, Central Marine Fisheries Research Institute, Mandapam Camp, India; ICZN, International Code of Zoological Nomenclature; IM, Indian Museum, Calcutta; MNHN, Muséum National d'Histoire Naturelle, Paris; MOM, Musée Océanographique de Monaco, Monaco; NCI, National Cancer Institute of the United States, Shallow Water Marine Organism Contract, Australian Institute of Marine Science Bioactivity Unit, Townsville; NM, Natal Museum, Pietermaritzburg; NMNZ, National Museum of New Zealand, Wellington; NTM, Northern Territory Museum, Darwin; SM, Musée Zoologique, Strasbourg; SMF, Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt.

SYSTEMATICS

Order Poecilosclerida Topsent
Family Rhabderemiidae Topsent

Rhabderemiidae Topsent, 1928:64, 309.

Diagnosis. Poecilosclerida with monactinal choanosomal rhabdostyles forming hymedesmoid, microcionid-plumose, or plumoreticulate skeletal structures usually with poorly developed spongin fibres. Microscleres include toxiform, sigmoid and microstylote spicules.

Remarks. The definition of Rhabderemiidae given above is from contemporary authors (Lévi 1973; Bergquist 1978; Hartman 1982). The family shows some similarities with the Bubaridae (e.g. *Bubaris* Gray), but it may be most closely related to the Raspailiidae (e.g. *Hemectyonilla* Burton). The rhabderemiids are excluded from the Raspailiidae in having sigmoid, toxiform and microstylote microscleres, whereas most raspailiids lack microscleres, or when present they consist only of raphides. Rhabderemiids also lack any evidence of an extra-axial skeleton, but this feature is not always obvious in many raspailiids either (Hooper, in press). Although typical raspailiids such as *Raspailia* Nardo have well differentiated axial and extra-axial skeletons, others such as *Echinodictyum* Ridley have simply reticulate skeletons, but generally in the Raspailiidae there is always at least some remnants of an extra-axial skeleton. Although some degree of relationship is inferred between these two families, with vague similarities appearing in skeletal architecture and the presence of rhabdostyles in genera of both (e.g. *Rhabderemia* and *Heterectya* Hallmann, respectively), the status of this monogeneric family is uncertain. The spined microscleres discovered in the new species described below are quite unusual, but it is quite likely that they may occur in other species of *Rhabderemia*, and these may eventually be found through extensive SEM studies of other material.

Rhabderemiidae is currently assigned to the polyphyletic order Axinellida, although in the past it has been included with both the Poecilosclerida (e.g. Topsent 1928) and Hadromerida (in the family Spirastrellidae) (de Laubenfels 1936; Bergquist 1968). The family is returned here to the Poecilosclerida on the basis of its monactinal choanosomal megascleres and the diversity and geometry of microscleres.

Genus *Rhabderemia* Topsent

Rhabderemia Topsent, 1890:28; Topsent 1892a:115; Dendy 1905:180; Topsent 1928: 309; de Laubenfels 1936:144; Lévi 1973:606.

Rhabdosigma Hallmann, 1916:520; Hallmann 1917:398; Topsent 1928:312; de Laubenfels 1936:144 [type species *Sigmaxinella mammillata* Whitelegge, 1907:512, by original designation].

Nisibaris de Laubenfels, 1936:144 [type species *Hallmannia spirophora* Burton, 1931: 352, by original designation].

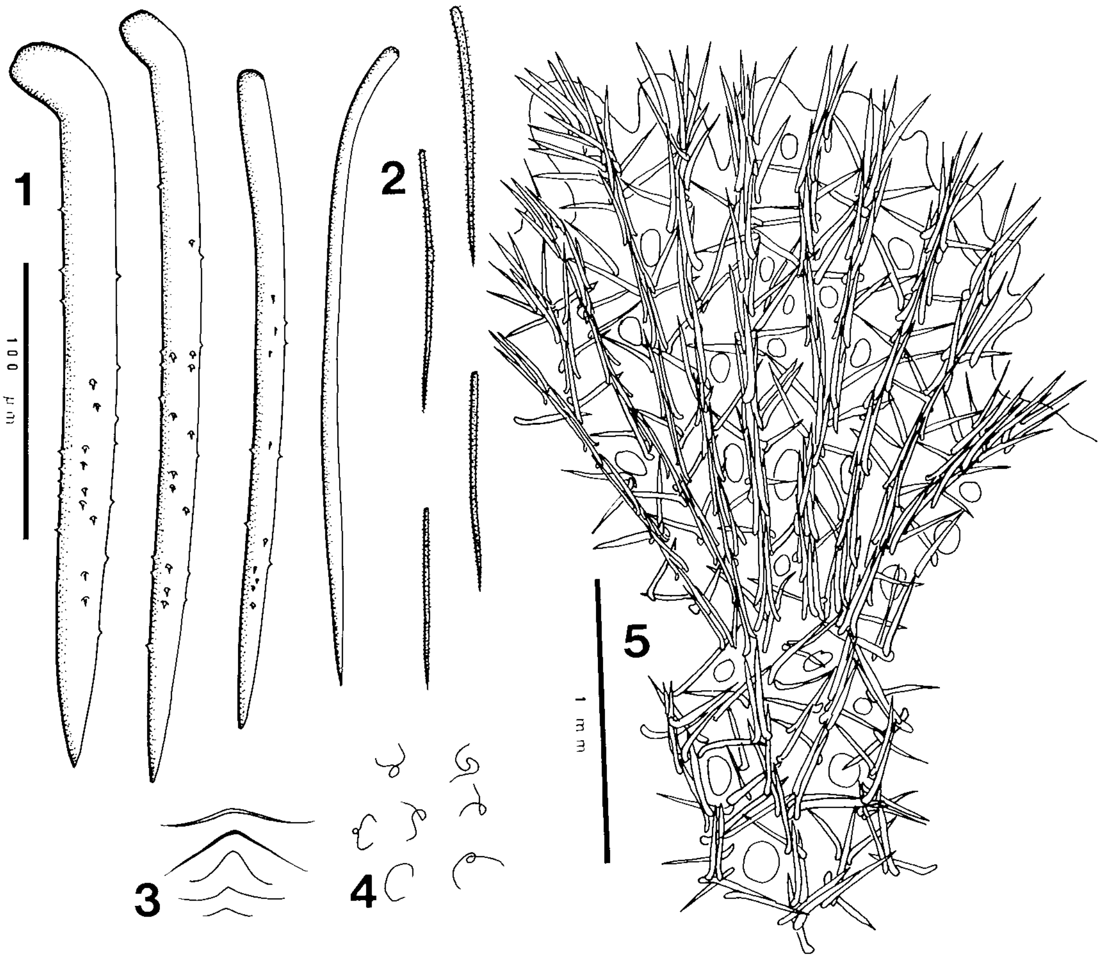
Hallmannia, in part, Burton, 1930:352.

Not *Hallmannia* Burton, 1930:519 [type species *Biemna aruensis* Hentschel, 1912:352, by monotypy].

Type species. *Microciona pusilla* Carter, 1876:239, by subsequent designation (Dendy 1905:180).

Diagnosis. Encrusting, massive or lobate-branching sponges. Choanosomal architecture varies from hymedesmoid, to plumose, to reticulate. Spongin fibres are typically poorly developed and cored by diverging tracts of rhabdostyles. Rhabdostyles may have spined or smooth shafts, or both, and if present spines usually occur at the distal end of spicules. Microscleres include sigmoid spicules (either contort sigmas or true sigmas), microstyles (including both true forms and toxa-like thraustoxeas), and true toxas, all of which may be smooth or microspined.

Remarks. Topsent (1892a) initially created *Rhabderemia* for encrusting species which had smooth (*s.s.*) or microspined rhabdostyles, producing erect-hymedesmoid or plumose-microcionid skeletal columns, and diverse microscleres consisting of contort sigmas, thraustoxeas (spined spicules which are doubly-bent in the middle or centrotylote), smooth or spined microstyles, and toxas. A number of other species were subsequently described with similar characteristics, differing mainly in the size and spination of megascleres, and the presence or absence of particular categories of microscleres. Hallmann (1916) established *Rhabdosigma* for a species which closely resembled *Rhabderemia*, but had an erect growth form, a reticulate spongin skeleton, a plumoreticulate spicule skeleton in



Figs 1-5. *Rhabderemia sorokinae*: **1**, rhabdostyles; **2**, microspined microstyles; **3**, toxas; **4**, contort sigmas with rare non-contort forms; **5**, section through peripheral skeleton.

which rhabdostyles cored spongin fibres in diverging plumose brushes (not echinating fibres as indicated by Hallmann), and with true (not contort) sigmas as the only microscleres. These sigmas appear to be smooth under light microscopy, but like the species described below it is possible that they too are minutely microspined. Until SEM studies of this species are completed the genus is used in the sense of Hallmann (1916).

Topsent (1928) discounted the differences in skeletal structure between *Rhabderemia* and *Rhabdosigma* as unimportant, and he suggested that they were probably merely related to variations in growth form. But he also suggested that the latter genus could be differentiated from *Rhabderemia s.s.* in lacking microstyles, thraustoxeas and toxas. However, this system is not accepted here, as the loss of one or more categories of microscleres can be construed as a simple reduction. Similarly, several species of *Rhabderemia* have since been described with reticulate architecture and with typical microscleres. Thus the only character which can reliably separate the two genera is the possession of contort versus true sigmas.

Burton (1930) established the genus *Hallmannia* for *Biemna aruensis* from the Arafura Sea, but then again (1931:352) he re-designated the type species as *H. spirophora*. De Laubenfels (1936) noted correctly that such an action was invalid under the terms of the (then existing) ICZN, and as such he renamed Burton's (1931) genus *Nisibaris*. *Hallmannia* in the strict sense is a lipochelous *Mycale* (*B.*

aruensis, holotype SMF 958, has subdermal rosettes of microstyles, a fistulose growth form, and longitudinal tracts of subtylostyles), whereas *Hallmannia* in the sense of Burton (1931) (= *Nisibaris*) is a clear synonym of *Rhabderemia*. Burton (1931) also suggested that *H. spirophora* was most closely related to the Trachycladiidae, because both had contort, spined sigmoid-like spicules, but this comparison may be inappropriate. Sigmoid microscleres in *Trachycladus* are vermiform and true sigmaspires, and they appear to be quite different from the contort sigmas of *Rhabderemia*.

The type species designation of *Rhabderemia* is still slightly confused, and requires brief discussion. Topsent (1892a) assigned three species to the genus upon its conception, one of which was described by him as new, but he did not nominate a type species. Dendy (1905) subsequently designated the first-named species of Topsent, *R. pusilla*, as the type of the genus, which thus invalidates de Laubenfels's (1936:144) subsequent designation of *R. guernei*. However, Dendy (1905) also notes that Carter did not originally intend to propose the name *R. pusilla* for this species, but rather he intended to use the name *R. minutula* (Carter 1876:p.239 cf. p.479), and Carter (1880:44) formally emends the species name. This is interpreted as a justified emendation (ICZN Article 19, 33bii), and the type species of *Rhabderemia* is therefore correctly cited as *R. minutula*. Subsequent references to *R. pusilla* (e.g. Hallmann 1917; Dendy 1922; Thomas 1968; van Soest 1984) are erroneous.

Rhabderemia sorokinae sp.nov.
(Figs 1-12, Plate 1a-b, Table 1)

Type material. HOLOTYPE - NTM Z3580: northern end of Deloraine Island, Whitsunday Is, Great Barrier Reef, Qld. 20° 09'S, 149° 04.5'E, 20 m depth, 15 October 1987, coll. S. Sorokin and NCI (NCI Q66C-0811-V).

Habitat. Found in a crevice on a dead coral head of a fringing coral reef, on the edge of a steep drop-off (Plate 1A).

Description. Shape: Thickly encrusting clump, approximately 22 x 10 cm, composed of lobate-bulbs scattered over the dead coral surface (Plate 1A).

Oscula: Large oscula are raised above the surface of the sponge on conical membraneous pedicels, and these appear to be confined to the upper external surfaces of lobes (Plate 1B). Minute ostia (<0.5 mm diameter) are numerous and evenly distributed over the upper (exposed) surface of lobes, with a few slightly larger examples situated within shallow exhalant drainage canals (Plate 1B).

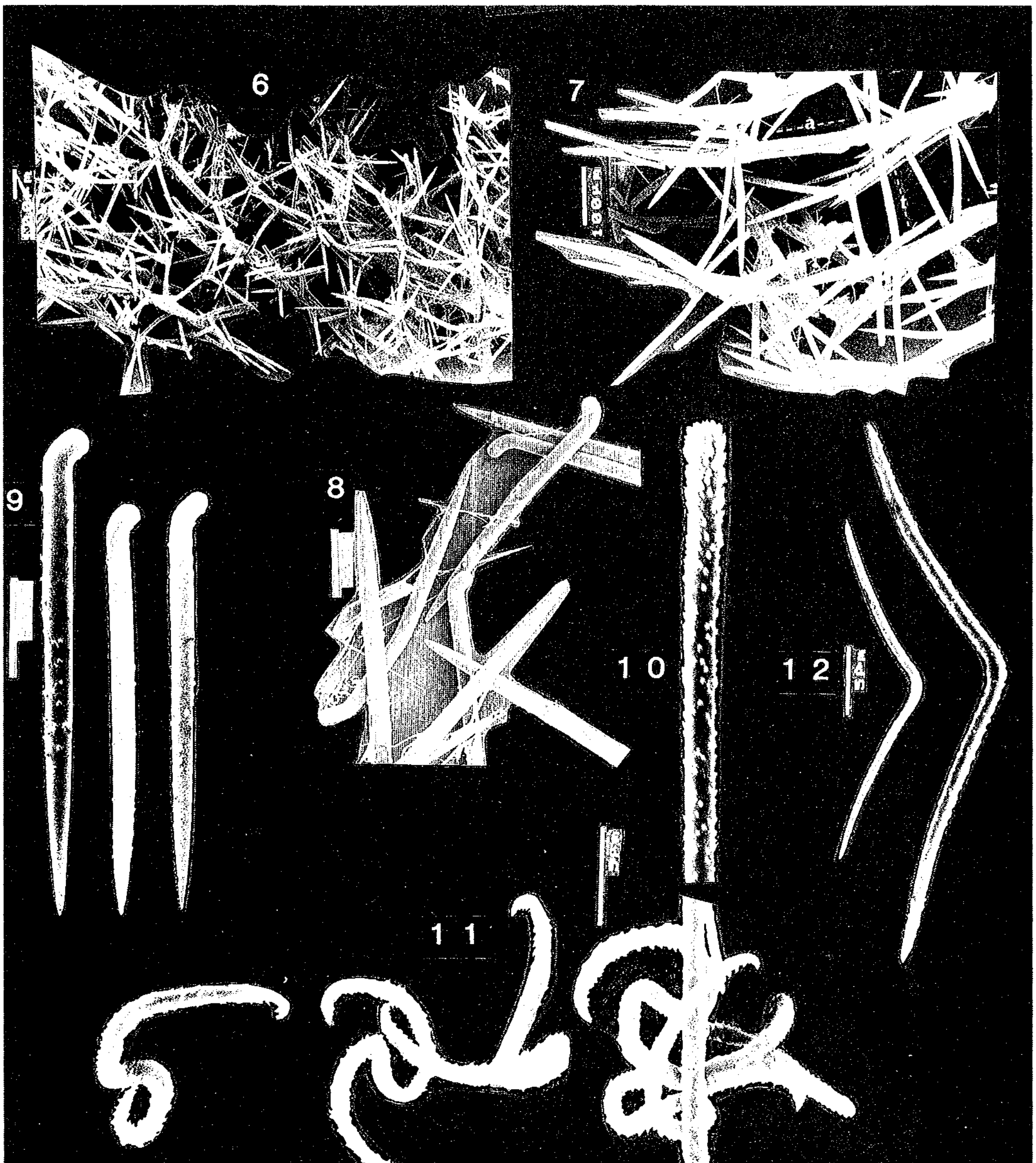
Colour: Live colouration is yellow-brown alive (Munsell 2.5Y 8/6; Plate 1B) and slightly darker in ethanol.

Texture: Sponge consistency is relatively soft, easily compressible and easily torn.

Surface: The surface is macroscopically even *in situ*, but minutely hispid, even shaggy in places in preserved material, produced by the terminal choanosomal spicule brushes. Scattered over lobes are evenly rounded bumps and bulbs, and the sponge appears insubstantial due to the numerous small oscula

Table 1. Comparison between published records of all described species of *Rhabderemia*, showing extreme ranges of spicule dimensions denoted as length x width (where known). All measurements are given in micrometres. Refer to Appendix 1 for sources of information. Key to symbols: e=encrusting, l=lobodigitate, b=lobate-bulbous, * denotes that measurements were taken from the material examined (otherwise they were taken from the literature).

SPECIES	CHARACTER					
	Growth form	Rhabdostyles	Microstyles	Thraustoxeas	Toxas	Sigmas
R. acanthostyla	e	I:84-258 x2-4 II:109-315 x6-12	absent	absent	absent	12-25
*R.bistylifera**	e	120-317 x2-5.5	I:30-40x0.2 x0.5-1 II:110-130 x0.5-1.5	absent	absent	5-12 x1-1.5
R.coralloides	l	340 x34	40 x2	32 x2.6	absent	8
*R.fascicularis**	e	122-358 x8-17	absent	28-73 x1.5-3.5	absent	9-17 x1-2
*R.guernei**	e	183-473 x5-15	65-112 x1-2	45-75 x2.5-4	absent	18-32 x1-2
R.indica	e	230-315 x3.5-10.5	42-49 x0.7-2	absent	absent	6.3-12
*R.intexta**	e	150-350 x9-14	absent x0.5-1	absent	absent	I:6-16 II:28-60 x1-2
*R.mammillata**	l	126-302 x5-8.5	absent	absent	absent	I:9-13 x1-2 II:24-42 x1.5-4
*R.minutula**	e	I:45-75 x4-6 II:170-480 x10-17	I:30-55 x0.5-1 II:88-177 x1-3	absent	absent	8-16.4 x0.5-1.5
*R.mutans**	l	190-306 x14-28	32-88 x1-2	37-79 x1-2	absent	10-13 x1-2
R.prolifera	e	90-210 x4-8.2	82-147 x1-2	absent	absent	12-12.3
*R.sorokinae**	b	178-283 x3-22	53-96 x0.8-2	absent	18-72 x0.4-1.2	6-15 x0.5-1.2
*R.spinosa**	e	134-327 x4-15	20-35 x0.5-1.5	27-39 x1.5-4	absent	6-13 x0.5-1
*R. spirophora**	b	215-288 x5-9	32-51 x1-2	absent	absent	3-8 x0.5-1
R.stellata	e	200-356 x12-23	36-48 x3-4.3	absent	absent	10.6-17
*R.toxigera**	e	225-407 x7-11	53-63 x1-2	absent	37-57 x1-2.5	5-11 x0.5-2



Figs 6-12. Scanning electron micrographs of the skeleton of *Rhabderemia sorokinae*: 6, plumo-reticulate skeletal structure; 7, plumose ascending multispicular tracts (a), and transverse unispicular tracts (t), forming isodictyal meshes; 8, groups of rhabdostyles, microstyles, toxas and sigmas; 9, rhabdostyles; 10, spined microstyles; 11, spined sigmas; 12, sparsely spined toxa.

scattered over the surface. Most bulbous lobes are excavated by one or more shallow drainage canals. Membraneous pedicels on which oscula are raised, seen in live material (Plate 1b), collapse upon preservation.

Ectosome: The ectosomal skeleton is membraneous, without any specialized spiculation, but a prominent feature of this region is the protruding spicule brushes from the primary choanosomal tracts (Fig. 6). These tracts of rhabdostyles diverge near the surface, becoming increasingly plumose, and spicule brushes may extend for up to 400 µm from the surface. Spicule brushes of the peripheral skeleton are loosely bound together with heavy granular type B spongin. This ectosomal spongin contains numerous irregularly scattered microstyles, but these also occur in equally heavy concentrations elsewhere in the skeleton.

Choanosome: The choanosomal skeleton is plumo-reticulate. There is no trace of axial compression of the skeleton, but in the centre of each lobate bulb the spicule tracts form regular or irregularly reticulate, triangular or square isodictyal meshes, up to 180 µm in diameter, bounded on all sides by uni-, pauci- or multispicular tracts of rhabdostyles (Fig. 7). Spongin fibres are poorly invested in type A spongin, but spicule tracts also have heavy deposits of spongin B surrounding them, and these deposits are particularly heavy in the axis of the skeleton. In the extra-axial region of the choanosomal skeleton, towards the periphery, spicule tracts become clearly separated into primary ascending multispicular tracts, with 3-6 spicules in each row, and secondary transverse unispicular components, one or two spicules in length. Transverse spicules and spicule tracts diverge from the ascending fibres at angles of 30-90°, and these could be interpreted as echinating spicules (e.g. Hallmann 1917). However, most of these transverse secondary spicule tracts in the extra-axial skeleton interconnect with the adjacent primary ascending fibres, producing a vaguely isodictyal reticulation, whereas at the periphery they are clearly plumose, so the term "echinating" may be misleading. Choanocyte chambers are oval, 150-260 µm in diameter. The mesohyl matrix is very heavily invested with dark brown type B spongin, which contains numerous microscleres.

Megascleres: Choanosomal rhabdostyles are relatively robust, thick, with rhabdose bases bent at between 35-70° from the shaft, evenly rounded, unspined, and never contort; occasionally styles are seen without rhabdose bases, but these are rare. The apex varies from fusiform sharply pointed in smaller spicules to hastate-pointed in larger examples, and the shaft usually contains a sparse scattering of small spines in the distal two-thirds of the spicule (Fig. 9): 178-(235.1)-283 x 3-(14.0)-22 µm.

Microscleres: Microstyles are relatively long, thin, sometimes straight but usually with a flexuous bend near the middle, with a slightly subtylote base, tapering to sharp raphidiform points. Microstyles have prominent microspination over their shafts and rounded bases, like other members of the genus, but these spines appear only as a slight roughening of the surface under light microscopy, whereas higher magnification clearly shows individual spines (Fig. 10): 53-(82.4)-96 x 0.8-(1.5) 2.0 µm.

Toxas are sparsely microspined (Fig. 12), small, thin, ranging from v-shaped to forms with a gentle central curvature and reflexed arms: 18-(39.4)-72 x 0.4-(0.9)-1.2 µm.

Sigmas are small, thin, contort, usually with a central curl, but occasionally they are regularly c-shaped. Sigmas are shown to be smooth under light microscopy, but higher magnification reveals prominent microspination, as for microstyles and toxas (Fig. 11): 6-(12.2)-15 x 0.5-(0.8)-1.2 µm.

Etymology. This species is named in honour of Shirley Sorokin, marine biologist with the NCI shallow-water collection project, Australian Institute of Marine Science Bioactivity Unit, who was the original collector of the species, and in encouragement to continue working on Porifera.

Remarks. The discovery of this species from the Great Barrier Reef is only the second record for the genus in Australian waters. The new species also shows some affinities with the other Australian representative, *R. mammillata*. These apparent affinities are based on the presence of similar skeletal architecture, similar geometry and size of rhabdostyles. Growth form is also similar, with *R. mammillata* being an erect lobodigitate sponge with a short stalk, whereas *R. sorokinae* has a lobate-bulbous shape, but microscleres are quite different. *Rhabderemia mammillata* has two size categories of and normally formed c- and s-shaped sigmas, whereas those of *R. sorokinae* are microspined, predominantly contort with very few normally-formed ones, and the new species also has microspined microstyles and toxas. The only other species with true toxa microscleres is *R. toxigera* from the Mediterranean, but that species is encrusting, the toxas and microstyles appear to be smooth (under light microscopy at least), and it has entirely smooth and much larger rhabdostyles (Table 1). The presence of microspined sigmas and toxas in *R. sorokinae* are new characters for the genus *Rhabderemia*. However, these features are not over-emphasized here since it is probable that other studies in electron microscopy may discover their occurrence in other species.

In growth form, skeletal structure and some aspects of spiculation *R. sorokinae* also shows close affinities with *R. coralloides*. The latter species consists of irregular, subcylindrical lobate digits, and it too has a membraneous skin-like dermis which covers a prominently sculptured surface excavated by subdermal drainage canals. Choanosomal skeletal architecture is a compact isodictyal reticulation of fibres and spicules, with differentiated primary ascending and transverse secondary lines. In these features the two species are closely related, but they may be differentiated by their respective spicule dimensions (Table 1), and in the presence of toxas in *R. sorokinae* and thraustoxeas in *R. coralloides*. A key to the described forms of the genus is given below.

Key to the species of *Rhabderemia*.

1(0) Thraustoxea microscleres are present 2
Thraustoxea microscleres are absent 5

2(1) Microstyle microscleres are roughened (onychaete-like) or microspined 3
Microstyle microscleres are entirely smooth 4
Microstyle microscleres are absent .... *R. fascicularis* Topsent

3(2) Skeletal architecture is irregularly plumoreticulate, without fibres .... *R. mutans* Topsent
Skeletal architecture is a compact isodictyal reticulation .... *R. coralloides* Dendy

4(2) Rhabdostyle megascleres are spined in the distal half .... *R. spinosa* Topsent
Rhabdostyle megascleres are entirely smooth .... *R. guernei* Topsent

5(1) True toxa microscleres are present 6
True toxa microscleres are absent 7

6(5) Rhabdostyle megascleres are spined in the distal half .... *R. sorokinae* sp.nov.
Rhabdostyle megascleres are entirely smooth .... *R. toxigera* Topsent

7(5) Sigmoid microscleres consist of true sigmas 8
Sigmoid microscleres are contort sigmas 9

8(7) Skeletal architecture is plumose microcionid .... *R. intexta* (Carter)
Skeletal architecture is plumoreticulate, with well developed fibres .... *R. mammillata* (Whitelegge)

9(7) Microstyle microscleres are roughened (onychaete-like) or microspined 10
Microstyle microscleres consist of both microspined and smooth varieties .... *R. minutula* (Carter)
Microstyle microscleres are entirely smooth 11
Microstyle microscleres are absent .... *R. acanthostyla* Thomas

10(9) Skeletal architecture is erect hymedesmoid .... *R. bistylifera* Lévi
Skeletal architecture is plumose microcionid, with unispicular connecting tracts .... *R. stellata* Bergquist
Skeletal architecture is irregularly plumoreticulate, without fibres .... *R. indica* Dendy

11(9) Skeletal architecture is erect hymedesmoid .... *R. prolifera* Annandale
Skeletal architecture is a compact isodictyal reticulation .... *R. spirophora* (Burton)

DISCUSSION

The 16 species currently known for the genus *Rhabderemia* are not well differentiated by their morphological characters, with species showing minor differences in the diversity, geometry, and the presence or absence of spination on their microscleres. Other characters such as megasclere spination, growth form and skeletal architecture may also be useful in determining relationships between species, and these are investigated using cladistics techniques below. This analysis relies heavily on descriptions from the literature, since most of the type material seen (listed in Appendix 1) consisted only of microscopic slide preparations of spicules, and consequently it must be considered to be somewhat preliminary. It is possible that some of the species recognized today may be only extreme forms of the more variable species, and these may be eventually merged.

Skeleton: Species of *Rhabderemia* are either encrusting or lobate-digitate, including bulbous forms; the encrusting growth form is considered here to be the plesiomorphic con-

Table 2. Characters used to investigate phylogenetic relationships between species of *Rhabderemia*. Criteria for judging apomorphy are discussed in the text.

	PLESIOMORPHIC STATE		APOMORPHIC STATE
1A	Skeletal architecture is erect hymedesmoid.	1C	Plumose with unispicular connecting tracts.
1B	Plumose microcionid.	1D	Irregularly plumoreticulate, without fibres.
1E	Plumoreticulate, with well developed fibres.	1F	Compact isodictyal reticulation.
2A	Choanosomal megascleres are isolated rhabdostyles erect on the substrate	2D	Multispicular ascending plumose columns interconnected by unispicular tracts of rhabdostyles.
2B	Isolated and diverging plumose bundles of rhabdostyles.	2E	Paucispicular isodictyal reticulation of rhabdostyles
2C	Multispicular ascending plumose columns of rhabdostyles.		
3A	Ectosomal skeleton is simply membraneous.	3B	Dermal crust of microstyles.
4A	Growth form is encrusting.	4B	Lobodigitate.
5A	Rhabdostyle megascleres are spined in the distal half.	5B	Both smooth and spined forms.
		5C	Entirely smooth.
6A	Microstyle microscleres are microspined.	6B	Consist of both microspined and smooth forms.
6C	Entirely smooth.	6D	Absent.
7A	Thraustoxea microscleres are present.	7B	Absent.
8A	True toxa microscleres are present.	8B	Absent.
9A	Sigmoid microscleres consist of true sigmas.	9B	Contort sigmas.

dition (see Hooper 1987). To a greater or lesser extent skeletal architecture is related to growth form, whereby thinly encrusting species only have erect-hymedesmoid or plumose-microcionid choanosomal skeletons, whereas lobodigitate species are usually reticulate or plumoreticulate. The latter feature is apomorphic. The distribution of megascleres within fibres is linked to choanosomal skeletal architecture, ranging from the plesiomorphic condition which consists of isolated rhabdostyles embedded in basal spongin and erect on the substrate (i.e. a hymedesmoid skeleton) or with multispicular plumose columns of rhabdostyles (i.e. a microcionid skeleton), to plumoreticulate multispicular tracts or regularly formed paucispicular isodictyal tracts of rhabdostyles. There are no specialized ectosomal megascleres in this genus, but in two species microstyles are aggregated on the surface producing a dermal skeleton. This is considered to be a derived character, whereas plesiomorphy is simply a membraneous ectosome (although in these cases spicules derived from the primary ascending tracts may protrude through the surface).

Spicules: In all species the only megascleres are rhabdostyles, which is an apomorphy for the genus. These spicules vary between species in being either smooth (the derived condition), or with both smooth and spined forms, or with spines occurring on all spicules, usually dispersed over the distal portions of spicules (plesiomorphy). This determination is consistent with the conclusions of van Soest (1984), Hooper (1987) and Hieemstra and Hooper (1990). Microscleres are of four kinds. Microstyles range from microspined (onychaete-like) to entirely smooth forms, and the latter condition is considered here to be apomorphic. One species has examples of both, and in several species these spicules are absent entirely, which is interpreted as a secondary loss, and both conditions are derived. Thraustoxeas, which are thought to be derived forms of microstyles (Topsent 1928:311), occur in about half the number of species, and these are usually spined and contort with double central bends or centrotylote. Similarly, true toxas are present in two species, and these have straight or slightly reflexed arms and slight central curvature. Species which possess thraustoxeas do

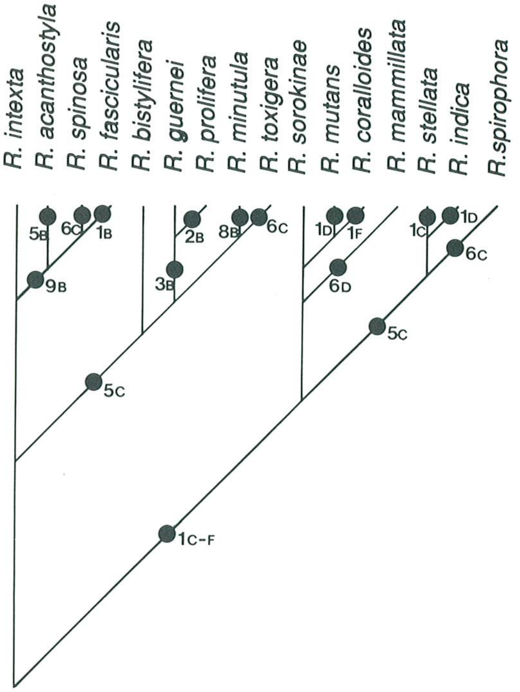
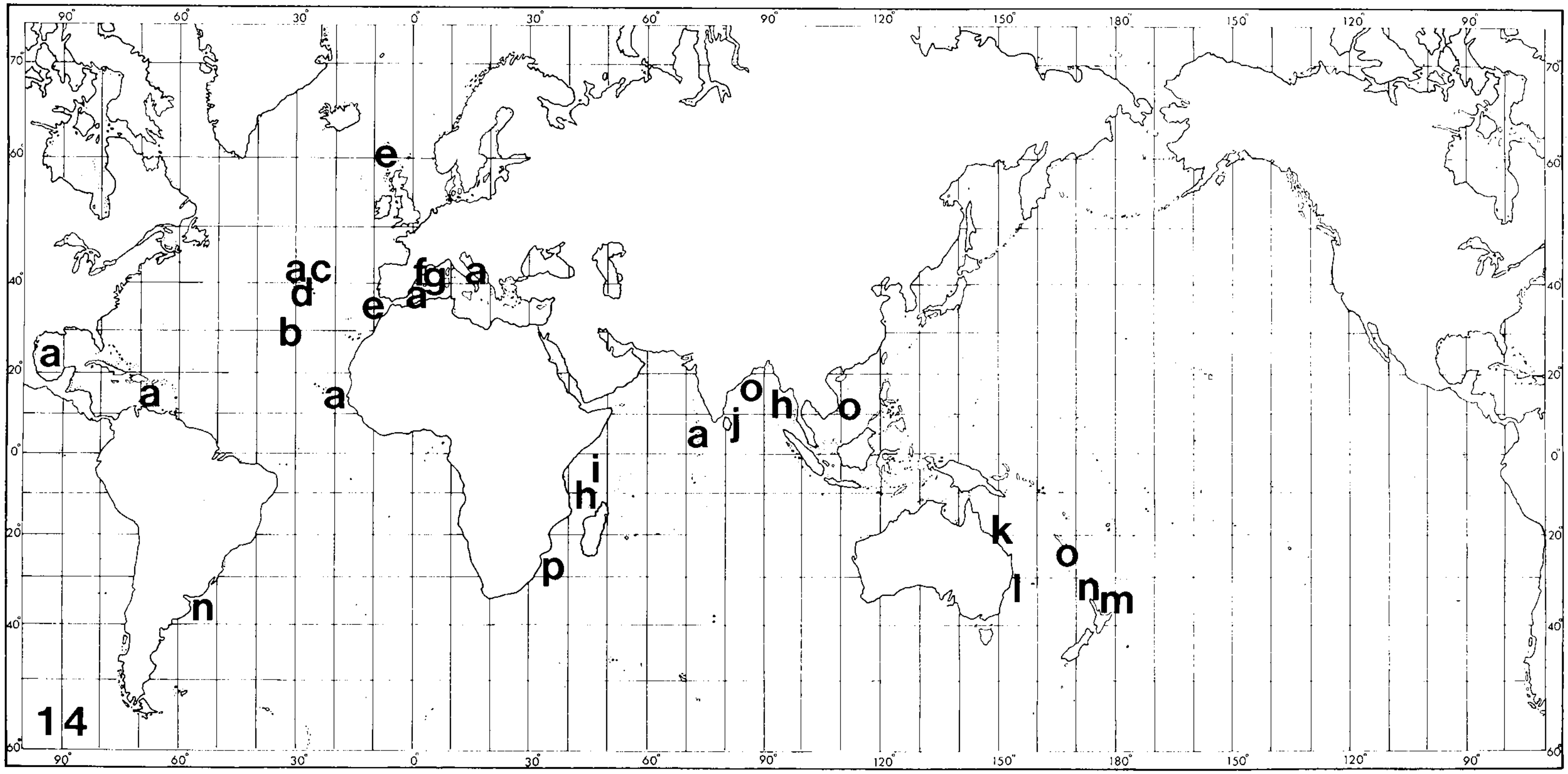


Fig. 13. Cladogram of the hypothesized relationships between species of *Rhabderemia*, with indication of two species groups. Each number and letter on the cladogram corresponds to a character and character state, respectively, summarized in Table 2, and represents an evolutionary change from a relatively plesiomorphic to a relatively apomorphic state (consensus information = 0.528).

Fig. 14. Distribution of nominal *Rhabderemia* species. Conspecificity is assumed from the literature. Refer to Appendix 1 for sources of information. Key to species: **a,** *R. minutula* (Carter); **b,** *R. guernei* Topsent; **c,** *R. fascicularis* Topsent; **d,** *R. mutans* Topsent; **e,** *R. intexta* (Carter); **f,** *R. toxigera* Topsent; **g,** *R. spinosa* Topsent; **h,** *R. prolifera* Annandale; **i,** *R. bistylifera* Lévi; **j,** *R. indica* Dendy; **k,** *R. sorokinae* sp.nov.; **l,** *R. mammillata* (Whitelegge); **m,** *R. stellata* Bergquist; **n,** *R. coralloides* Dendy; **o,** *R. acanthostyla* Thomas; **p,** *R. spirophora* (Burton).



not have toxas, and the converse is also true. All species of *Rhabderemia* have some sort of sigmoid microscleres, and these are apomorphic for the genus in general. But sigmas vary from normal forms with c- and s-shapes, which are possessed by only two members of the group and interpreted here as the plesiomorphic condition, to derived contort forms, sometimes referred to as sigmaspires by authors (e.g. Lévi 1961). In this genus the contort sigmas appear to be derived from normal forms, and the application of the term sigmaspire, coined by Sollas for spiraster-derived microscleres, may be inappropriate. Thus, the differentiation of these two groups of species into two genera, *Rhabdosigma* and *Rhabderemia*, with either normal or contort sigmas, respectively, is artificial and not recognized here. This interpretation is supported by the distribution of other characters amongst the species (hymedesmoid-plumose versus reticulate skeleton types, spination of rhabdostyles), and the occurrence of both contort and (rare) normal sigmas in *R. sorokinae*. The presence of the newly discovered characters of spines on sigmas and toxas in *R. sorokinae* is not included in these analyses, since electron microscopic examination of all species is required to verify the presence or absence of this feature amongst other species.

Postulated relationships between species of *Rhabderemia* were investigated using a numerical computer method for inferring phylogenies (PAUP, Swofford 1985). This analysis utilizes the Wagner method, taking the preferred phylogenetic tree as the most parsimonious one, i.e. the one with the fewest number of evolutionary steps. Data used in this analysis were derived from a binary and an unordered multistate character set, and the criteria for judging apomorphy are discussed above and summarized in Table 2. Outgroups chosen were from the family Raspailiidae, and these included species from the genera *Aulospongus* (*A. tubulatus* (Bowerbank)) and *Hemectyonilla* (*H. involutum* (Kirkpatrick)). A consensus tree, produced from 28 minimum length trees, is depicted in Figure 13. Levels of homoplasy within this classification are quite high, as indicated by the number of characters which reoccur throughout the tree. The construction of a phylogeny for this group is quite difficult because the most unusual features in most species are the diversity and geometry of microscleres, but these appear amongst species in all combinations, and they are rarely concordant with the distribution of other features. Nevertheless, this cladogram does represent a phylogeny in which there are fewest convergences, and Figure 13 suggests that the genus can be subdivided into two major groups, with emphasis placed on the characters of choanosomal architecture and spination on rhabdostyles.

The first group is predominantly encrusting and has skeletal structure ranging from hymedesmoid to plumose-microcionid. It is united only by these plesiomorphic features, and includes 9 species: *R. intexta*, *R. acanthostyla*, *R. spinosa*, *R. fascicularis*, *R. bistylifera*, *R. guernei*, *R. prolifera*, *R. minutula* and *R. toxigera*. The second group of *Rhabderemia* is predominantly lobodigitate in growth form, with a reticulate skeletal architecture. It contains seven species: *R. sorokinae*, *R. mutans*, *R. coralloides*, *R. mammillata*, *R. stellata*, *R. indica* and *R. spirophora*. Both groups of species may be further split into subgroups based on the presence or absence of spination on rhabdostyles.

Although relying heavily on the literature to assume conspecificity, a plot of species' distributions (Fig. 14) shows that with the exception of two anomalies there are two zoogeographical groups: one in the Atlantic system and the other in the Indo-Pacific. The Atlantic fauna (Caribbean, North Atlantic, Mediterranean) consists of seven species: (a) *R. minutula*, (b) *R. guernei*, (c) *R. fascicularis*, (d) *R. mutans*, (e) *R. intexta*, (f) *R. toxigera*, and (g) *R. spinosa*. Most of these species are known from only one or two isolated records, and most of these were described by Topsent (1892 *et seq.*), whereas *R. minutula* is relatively widely distributed, extending from the Gulf of Mexico into the Mediterranean, with a single (and possibly aberrant) record from the central Indian Ocean (Salomon, Chagos Archipelago; Dendy 1922). Confirmation of the distribution of this species into the Indian Ocean requires corroboration from a comparison between Dendy's (1922) specimen in the BMNH and the holotype (BMNH 1902.11.16.32), which may reveal hitherto undetected cryptic differences. The Indo-Pacific fauna consists of nine species: (h) *R. prolifera* from both sides of the Indian Ocean, (i) *R. bistylifera*, (j) *R. indica*, (k) *R. sorokinae*, (l) *R. mammillata*, (m) *R. stellata*, (n) *R. coralloides*, (o) *R. acanthostyla*, and (p) *R.*

spirophora. Most of these species are known only from single records, but the New Zealand species *R. coralloides* is also apparently present in the South Atlantic, off the coast of Uruguay (Burton 1940). This record may be anomolous, or it is possible that this species is austral (antiboreal) in distribution. Similarly, an examination of unpublished material collected by Claude Lévi and housed in the MNHN Paris (see Appendix 1) also extends the known distribution of *R. acanthostyla* considerably. The species was originally recorded from Galaxea Reef in the Gulf of Manaar, whereas MNHN specimens are reportedly from Vietnam and New Caledonia.

There is no correlation between the two species groups determined from phylogenetic relationships, shown in Figure 13, and the two groups indicated by their zoogeographic distributions in Figure 14. The former groups of species appear to be distributed between the Atlantic and Indo-Pacific systems.

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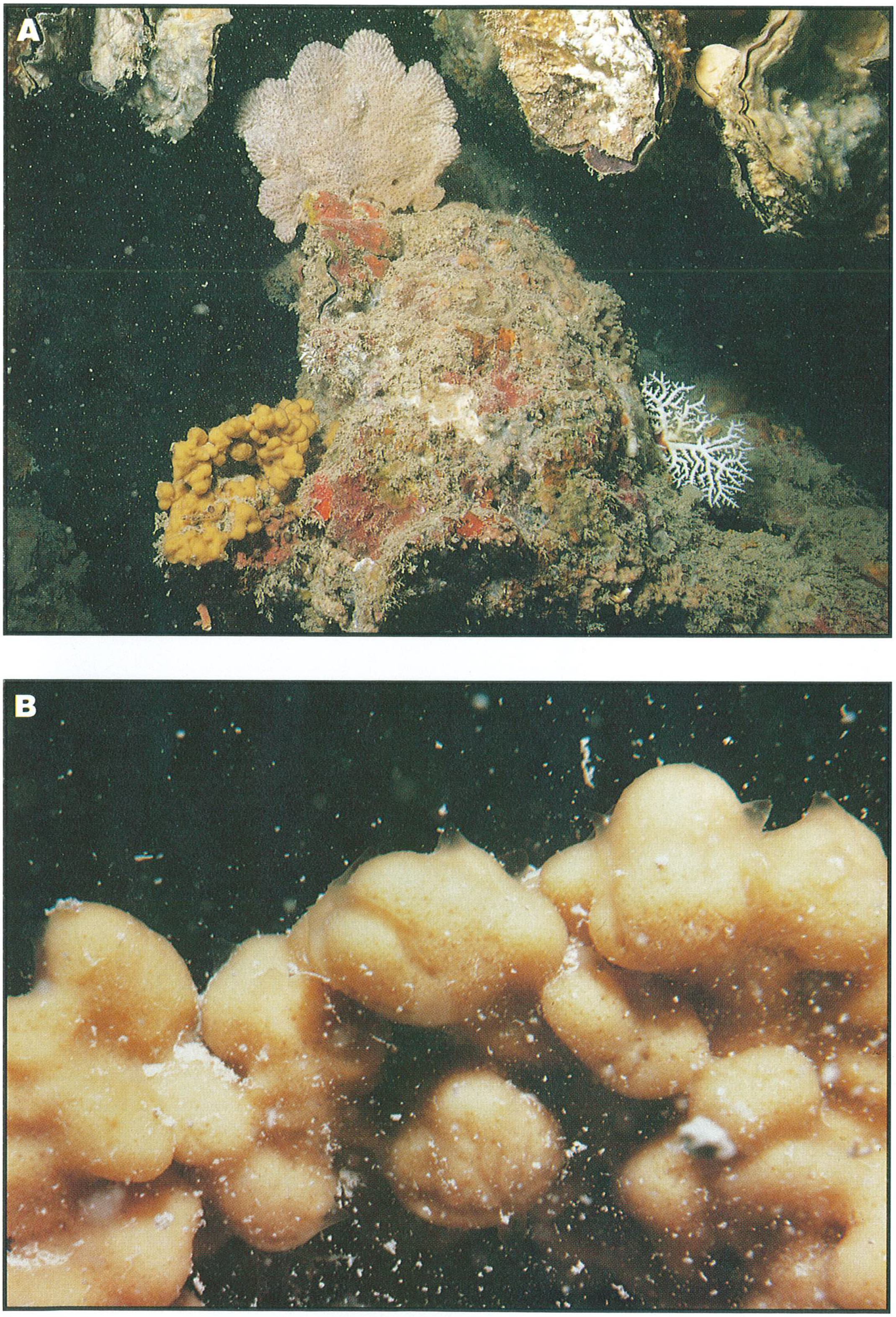

Plate I. *Rhabderemia sorokinae* sp.nov.: **A,** holotype *in situ*, Whitsunday Islands, Great Barrier Reef, 20 m depth; **B,** close-up of the same, showing individual lobate bulbs with evenly dispersed small ostia, surface drainage canals, and larger oscula surmounted on conical membraneous pedicels at the apex of lobes. Photos NCI.

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APPENDIX 1

Synonymy of described *Rhabderemia* species, including the known distribution of each and repository of the holotype (where known. Those specimens marked with an asterisk denote material seen by the author). Although 16 species are presently recognized, it is possible that some of these may eventually be merged into other taxa.

1. ***Rhabderemia acanthostyla* Thomas**
   Rhabderemia acanthostyla Thomas, 1968: 247-248, pl. 2, figs 4-5.
   "*Rhabdosigma forcipula*" MS name ["paratype" MNHN LBIM DCL3243*].
   "*Rhabdosigma conulosa*" MS name [attributed to Lévi 1961, but apparently unpublished; specimen MNHN LBIM DCL1560*].
   Distribution: Galaxea Reef, Gulf of Manaar (Thomas 1968); New Caledonia region (MUSORSTOM stn. 2) (Lévi, unpublished data); Nha Trang, Vietnam (Lévi, unpublished data).
   Holotype: CMFRI 131.
2. ***Rhabderemia bistylifera* Lévi**
   Rhabderemia bistylifera Lévi, 1961:15, text-fig. 18.
   Distribution: Aldabra, W.Indian Ocean.
   Holotype: MNHN DCL358*.
3. ***Rhabderemia coralloides* Dendy**
   Rhabderemia coralloides Dendy, 1924: 357, pl. 12, fig. 3, pl. 15, figs 1-4; Topsent 1928:65; Burton 1940:116; Bergquist 1968:19.
   Distribution: North Cape, New Zealand and Maldonado, Uruguay.
   Holotype: BMNH number unknown.
4. ***Rhabderemia fascicularis* Topsent**
   Rhabderemia fascicularis Topsent, 1927: 18; Topsent 1928:310, pl. 10, fig. 25.
   Distribution: Azores, North Atlantic.
   Holotype: ? MOM; slide MNHN DT1244*.
5. ***Rhabderemia guernei* Topsent**
   Rhabderemia guernei Topsent, 1890:29; Topsent 1892a:116, pl. 11, fig. 7; Hallmann 1917:399; Topsent 1928:312, pl. 10, fig. 24.
   Distribution: North Atlantic.
   Holotype: ? SM; slide MNHN DT956*.
6. ***Rhabderemia indica* Dendy**
   Rhabderemia indica Dendy, 1905:180, pl. 12, fig. 10; Topsent 1928:310.
   Distribution: Ceylon, Indian Ocean.
   Holotype: BMNH number unknown.
7. ***Rhabderemia intexta* (Carter)**
   Microciona intexta Carter, 1876:238, pl. 15, fig. 43a-c; Vosmaer 1935:607.
   Rhabderemia intexta - Topsent 1892a:116; Topsent 1904:152; Hallmann 1916:520; Hallmann 1917:399.
   Rhabdosigma intexta - Topsent 1928:313, pl. 10, figs 29-30.
   Distribution: Hebrides and Morocco, North Atlantic.
   Holotype: BMNH 1890.4.10.12*.
8. ***Rhabderemia mammillata* (Whitelegge)**
   Sigmaxinella mammillata Whitelegge, 1907:512.
   Rhabdosigma mammillata - Hallmann 1916:520; Hallmann 1917:399, pl. 21, figs 1-2, text-fig. 2; Shaw 1927:427.
   Distribution: Norah Head, New South Wales, and Maria I., Tasmania, Australia.
   Holotype: AM G4356*.
9. ***Rhabderemia minutula* (Carter)**
   Microciona minutula Carter, 1876:479, pl.

16 [emend.]; Carter 1880:44; Vosmaer 1935:608.

Rhabderemia minutula - Topsent 1904: 152-153, pl. 1, fig. 10, pl. 13, fig. 13; Lévi 1956:393, fig. 2; Boury-Esnault 1971:306; Biblioni and Gili 1982:231; Pulitzer-Finali 1983:533, text-fig. 51.

Microciona pusilla Carter, 1876:239, pl. 16, figs 51a-d; Carter 1880:437; Topsent 1889:41, text-fig. 7.

Rhabderemia pusilla - Topsent 1892a:116; Hallmann 1917:399; Dendy 1922:85; van Soest 1984:108.

Rhabderemia indica - in part, Sarà 1961: 44, text-fig. 8; Pulitzer-Finali 1983:534.

Distribution: Gulf of Mexico and Antilles, Caribbean, Azores and Dakar, North Atlantic, Mallorca and Adriatic Sea, Mediterranean, and Chagos Archipelago, Indian Ocean.

Holotype: BMNH 1902.11.16.32*.

10. ***Rhabderemia mutans* Topsent**

Rhabderemia mutans Topsent, 1927:17; Topsent 1928:310, pl. 2, fig. 2, pl. 10, fig. 21.

Distribution: Azores, North Atlantic.

Holotype: ? MOM; slide MNHN DT1236*.

11. ***Rhabderemia prolifera* Annandale**

Rhabderemia prolifera Annandale, 1915:464, pl. 34, fig. 3, text-fig. 3; Hallmann 1917:399; Thomas 1979:26, pl. 1, fig. 19

Distribution: Andaman Islands, E. Indian Ocean, and Mozambique Channel, W. Indian Ocean.

Holotype: IM 6420/7 ZEV.

12. ***Rhabderemia sorokinae* sp.nov.**

13. ***Rhabderemia spinosa* Topsent**

Rhabderemia spinosa Topsent, 1896:121; Hallmann 1917:399; Topsent 1928:310, pl. 10, fig. 22.

Distribution: Banyuls, Mediterranean.

Holotype: ? MOM; slide MNHN DT2379*.

14. ***Rhabderemia spirophora* (Burton)**

Hallmannia spirophora Burton, 1931:352, pl. 23, fig. 12, text-fig. 8.

Nisibaris spirophora - de Laubenfels 1936: 144, 152.

Distribution: Natal, South Africa.

Holotype: NM 1254; slide BMNH 1928.10.19.18*.

15. ***Rhabderemia stellata* Bergquist**

Rhabderemia stellata Bergquist, 1961:41, fig. 13a-c; Bergquist 1968:19, pl. 1c, fig. 11h, text-fig. 3

Distribution: Bay of Plenty, New Zealand.

Holotype: NMNZ unnumbered.

16. ***Rhabderemia toxigera* Topsent**

Rhabderemia toxigera Topsent, 1892b:25; Hallmann 1917:399; Topsent 1928:310, pl. 10, fig. 23.

Distribution: Banyuls, Mediterranean.

Holotype: ? SM; slide MNHN DT2380*.