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RECENT ADVANCES IN ECOLOGY AND SYSTEMATICS OF SPONGES. *M.J. URIZ and K. RÜTZLER (eds.).*

Taxonomy, phylogeny and biogeography of the marine sponge genus *Rhabderemia* Topsent, 1890 (Demospongiae, Poecilosclerida)*

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SUMMARY: The predominantly tropical-subtropical sponge genus *Rhabderemia* Topsent, 1890, is revised following examination of an almost comprehensive series of type and other published specimens. The generic names *Rhabdosigma* Hallmann, 1916, *Hallmannia* Burton, 1931, *Nisibaris* de Laubenfels, 1936, and *Stylospira* de Laubenfels, 1934, are considered junior synonyms of *Rhabderemia*, although the last of these may be a valid (sub-) generic sister group to *Rhabderemia* s.s. A reexamination of the widespread "species" *Rhabderemia "minutula"*/*R. "pusilla"* and *R. "coralloides"* revealed six new species: *R. africana*, *R. antarctica*, *R. burtoni*, *R. gallica*, *R. topsenti*, and *R. uruguaiensis*, most of which were hidden under incorrectly assigned specimens of previously described species. A further new species, *R. destituta*, was found in East-Pacific material conforming to the nominal genus *Stylospira* de Laubenfels. A total of 26 species is now recognized and each of them is diagnosed and discussed. Hypothesized phylogenetic relationships of the members of *Rhabderemia* are proposed on the basis of a morphological character analysis aided by the use of phylogenetic computer programs. Biogeographic observations are made from an areagram based on the *Rhabderemia* phylogeny. Frequent extinction events during the evolution of the genus, since at least the Oligocene, may explain the inferred disjunct sister-group distributions.

Key words: Taxonomy, phylogeny, biogeography, marine sponges, Poecilosclerida, *Rhabderemia*.

INTRODUCTION

Comprehensive revisions of sponge genera, other than those based merely on a study of the literature, are rare for the obvious reason that genera distributions are often quite large and thus make it necessary to study specimens from all parts of the world's oceans. Obtaining the type specimens and other described material is a painstaking process because these are likewise spread throughout the world, in museums and collections. Still, such studies are vital, for they not only shed light on both the genus and its member species, but they also yield hypotheses concerning its evolution and history of diversification (cf. HOOPER, 1987, 1990; HIEMSTRA and VAN SOEST, 1991; VAN SOEST *et al.*, 1991).

The marine sponge genus *Rhabderemia* Topsent, 1890, is a particularly appropriate subject for a revision concerned with marine historical biogeography. It has an unequivocal synapomorphy in that it possesses rhabdostyles with an extra spiral twist at the rounded extremity, the overall distribution of the genus is almost cosmopolitan, and the number of species is relatively limited and thus manageable. Furthermore, perhaps because of the largely cryptic habitat in which most species live, there do not seem to be a large number of descriptions in the older literature, for which material is generally unobtainable.

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In fact, we succeeded in obtaining access to almost all described material, but in those cases where we did not see the original material, there was no problem, because descriptions were unequivocal and clear. All recognized species are diagnosed below and their affinities discussed.

HOOPER (1990) undertook a preliminary analysis of the phylogeny and biogeography of *Rhabderemia*, but this was based mostly on limited available material and relied heavily on literature descriptions. A notable difference between it and the present study is that Hooper maintained the "widespread" species *Rhabderemia minutula/pusilla* and *R. coralloides* as described in the literature. We demonstrate here that a critical study of the various regional forms in most cases yields clear differences indicating separate specific status.

Characters and their likely transformations during the diversification of *Rhabderemia*, since its inception in at least Mesozoic times, are discussed below, and a hypothesis is formed on the likely phylogenetic relationships of the species of the genus. The distributions of the species are compared with the phylogenetic relationships and the distributional history of the genus is discussed.

MATERIAL AND METHODS

The following specimens and microscopic slides were studied (ZMA = Zoölogisch Museum Amsterdam, BMNH = Natural History Museum London, MNHN = Muséum National d'Histoire Naturelle Paris, NTM = Northern Territory Museum Darwin, QM= Queensland Museum, Brisbane, USNM = National Museum of Natural History, Smithsonian Institution, Washington):

Rhabderemia acanthostyla Thomas, 1968: ZMA POR.1926, Indonesia, coll. Siboga Exped.; ZMA POR. 6524, Indonesia, coll. Snellius II Exped.; ZMA POR. 8112, Indonesia, coll. Snellius II Exped.; ZMA POR. 8585, Indonesia, coll. Snellius II Exped.; ZMA POR. 9620, Indonesia, coll. H. Moll; MNHN DCl. 1560, Vietnam, Nha Trang.

Rhabderemia africana n.sp.: Microscopic slides (2) MNHN DT.2054, San Thomé (= São Tomé), West Africa, labeled *R. minutula*.

Rhabderemia antarctica n.sp.: Fragment BMNH 1926: 10: 26: 92, Antarctica, coll. Terra Nova Expedition, labeled *R. coralloides*.

Rhabderemia bistylifera Lévi, 1961: Microscopic slides (2) MNHN DCl. 358, Aldabra, western Indian Ocean.

Rhabderemia burtoni n.sp.: Microscopic slide BMNH # RN CXVI.A, S Indian Ocean, coll. HMS "Sealark," labeled *R. pusilla*.

Rhabderemia coralloides Dendy, 1924: Fragment and microscopic slides BMNH 23: 10: 1: 139, New Zealand, coll. Terra Nova Exped.

Rhabderemia destituta n.sp.: USNM 43065, San Salvador, Islas Galagapos, coll. SEPBOP.

Rhabderemia fascicularis Topsent, 1927: Microscopic slide MNHN DT. 1244, Azores, Campagnes Prince Albert de Monaco.

Rhabderemia forcipula (Lévi and Lévi, 1989): MNHN DCl. 3243, Philippines, coll. Musorstom 2, labeled *Rhabdosigma forcipula*; microscopic slide MNHN DCl. 3387, Philippines, coll. do.

Rhabderemia gallica n.sp.: Microscopic slide MNHN DT. 115, Banyuls, S France, labeled *R. minutula* var.; microscopic slides (2) MNHN DT. 2378, Banyuls, S France, labeled *R. minutula*; microscopic slide MNHN DCl. 874, Roscoff, W France, labeled *R. minutula*; microscopic slide MNHN NBE. 152, Banyuls, Castelloussous, S France, labeled *R. minutula*.

Rhabderemia guernei Topsent, 1890: Microscopic slide MNHN DT. 956, Azores, coll. Hirondelle 1888 Campagne.

Rhabderemia indica Dendy, 1905: Fragment and slides, BMNH 1907: 2: 1: 69, Sri Lanka, Gulf of Manaar (microscopic slide of same specimen: MNHN DCl. 44). Specimen, NTM Z4076, fragment QM G300510, S Gulf of Thailand, coll. J. N. A. Hooper.

Rhabderemia intexta (Carter, 1876): Microscopic slide BMNH 1954: 3: 9: 180, Cape St. Vincent, Portugal, labeled "Deep sea *Microciona intexta.*"

Rhabderemia minutula (Carter, 1876): ZMA POR. 10055, Bonaire; ZMA POR. 10052, 10053, 10054, Curaçao; ZMA POR 10056, Colombia.

Rhabderemia mona (de Laubenfels, 1934): microscopic slide USNM 22324, Puerto Rico (labeled *Stylospira mona*).

Rhabderemia mutans Topsent, 1927: Microscopic slide MNHN DT. 1236, Azores, Campagnes Prince Albert I 1905.

Rhabderemia profunda Boury-Esnault *et al.*, 1993: Microscopic slides (2) MNHN DT. 957, Azores, coll. Princesse Alice 1896, labeled *R. minutula*; microscopic slide MNHN DT. 1339, Azores, coll. Princesse Alice 1912, labeled *R. minutula*.

Rhabderemia sorokinae Hooper, 1990: ZMA POR. 9757, Papua New Guinea; microscopic slide BMNH 1954: 3: 9: 178, "South Sea," 1878, labeled "*Microciona minutula* C. on *Discodermia*, *Stylaster* 10."

TABLE 1. — Spicule categories and sizes (range, mean and standard deviation, in µm) of *Rhabderemia* species.

Spicule category	Rhabdostyles	Microstyles	Small sigmata	Large sigmata	Toxa	Thraustoxea
R. minutula	(I) 81-*111.0 (19.7)*-140 /4-*5.7 (1.5)*-9 (II) 196-*230.9 (88.7)*-352 /4-*5.7 (1.5)*-9	90-*119.8 (19.7)*-135 /1	9-*12.9 (3.3)*-18	—	—	—
R. africana	(I) 60-70 /7 (II) 200-250 /7	(I) 50-*60*-70 /0.5 (II) 85-*98.3 (18.9)*-120 /2	8-12	—	—	—
R. prolifera	(I) 90-99 /4-7-8 (II) 176-209 /4-7-8	82-*112*-147 /1-2	12-13	—	—	—
R. bistylifera	(I) 131-220 /4 (II) 258-305 /5-6	(I) 30-*35.8 (6.8)*-43 /0.2 (II) 110-*127.0 (12.8)*-141 /1	6-*7.7 (1.2)*-10	—	—	—
R. spinosa	(I) 111-*128.3 (19.3)*-156 /6 (II) 310-*393.8 (92.3)*-510 /15	30-*33.0 (2.4)*-36 /0.5	12	—	30—42	—
R. profunda	411-620 /9-14	77-135 /1.5-2.5	9.5-15	—	—	—
R. gallica	54-*102.0 (49.6)*-178 /4-5	55-*70.3 (24.8)*-99 /0.5-1.5	—	17-21	—	—
R. burtoni	(I) 110-*135.0 (17.9)*-155 /4-*5.6 (1.3)*-6 (II) 188-*246.4 (53.4)*-290 /11-*12.0 (1.4)*-14	112-*136.3 (25.0)*-162 /0.5	—	16	—	—
R. acanthostyla	(I) 98 *121.9 (15.9)*-141 /4-*5.0 (1.5)*-7 (II) 183-*232.8 (33.1)*-255 /5-*8.5 (2.7)*-13	20-*29.3 (6.1)*-39 / < 0.5	(I) 6-*6.8 (0.8)*-8 (II) 13-*15.2 (1.9)*-18	—	—	—
R. uruguaiensis	(I) 141-*147.0 (5.2)*-150 /2-*2.7 (0.6)*-3 (II) 166-*231.3 (58.0)*-310 /7-*11.0 (2.9)*-15	43-*49.4 (6.4)*-60 /0.5-*0.9 (0.2)*-1	6-*9.3 (2.5)*-12	—	—	—
R. spirophora	240-*263.0 (26.6)*-286 /6-*8.3 (1.5)*-9	45-*53.3 (6.7)*-61 /0.5-*0.9 (0.5)*-1.6	6-*8.2 (1.6)*-10	—	—	—
R. indicata	211-*238.0 (26.1)*-263 /5-*6.6 (2.1)*-9	42.*46.1 (3.0)*-48 /1-*1.25)0.4)*-2	12-*13.2 (1.3)*-15	—	—	—
R. topsenti	145-*215.9 (45.8)*-315 /2.5-*6.6 (2.3)*-10.5	36-*42.7 (48)*-50 /0.5-*0.95 (0.4)*-1.5	5-*7.7 (1.8)*-10	—	—	—
R. toxigera	(I) 126-137 /5-6 (II) 225-*305.8 (82.3)*-407 /9-*9.4 (1.5)*-11	52-*60.0 (7.2)*-69 /1-*1.25 (0.5)*-2	5-*9.3 (3.8)*-12	—	30-*45.6 (11.6)*-57 /1	—
R. sorokinae	106-*235.1*-283 /3-*14.0*-22	53-*102.0*-141 /0.8-1.5-2	6-*12.2*-15	—	18-*39.4*-72	—
R. antarctica	202-*240.0 (30.7)*-265 /7-*17.6 (9.2)* 24	45-*47.7 (3.1)*-51 /0.5-1	7-*8.3 (0.9)*-9	—	—	—
R. forcipula	230-*307.2 (50.5)*-381 /10-*17.1 (3.4)*-21	150-*162.5 (7.9)*-171 /1-*1.25 (0.4)*-2	12-*14.8 (2.5)*-18	25-*27.0 (2.2)*-30	—	—
R. stellata	200-356 /12-23	36-48 /3-4	10-17	—	—	—
R. fascicularis	122-*231.4 (82.8)*-398 /8-*13.8 (4.1)*-19	—	9-*11.6 (4.2)*-17	—	—	28-*52.0 (16.8)*-30 /1.5-*3.0 (0.8)*-3.5
R. intexta	150-*254.3 (76.7)*-350 /3-*7.6(4.1)-14*	—	*6-10.5 (2.5)*16	25-*35.4 (11.5)*-60	—	—
R. guernei	183-*363.5 (126.2)*-473 /5-*10.3 (5.0)*-15	65-*87.7 (23.5)*-112 /1-*1.7 (0.6)*-2	9-*10.6 (1.5)*-13	—	—	45-*60.0 (11.1)*-75 /2.5 *3.2 (0.8)*-4
R. mutans	190-*237.8 (57.6)*-306 /14-*21.0 (5.8)*28	32-*57.5 (23.4)*-88 /1-*1.3 (0.4)*-2	10-*11.5 (1.7)*-13		35-*49.0 (20.5)*-79 /1-*1.8 (0.5)*-2.5	
R. coralloides	206-*310.6 (68.0)*-394 /13-*24.6 (6.4)*-34	37-*40.4 (3.2)*-45 /1-*1.1 (0.25)*-1.5	6-*9.0 (2.0)*-11	18-*20.3 (2.1)*22	—	32-*32.7 (0.9)*-34 /0.5-*1.5 (0.95)*-2.6
R. mammillata	126-302 /5-8.5	—	9-13	24-42	—	—
R. mona	306-*417.5 (80.7)*-495 /17-*20.2 (2.6)*-24	—	—	—	—	—
R. destituta	305-*343.5 (34.7)*-395.5 /13.5-*23.3 (6.4)*-31	—	—	—	—	—

Rhabderemia spinosa Topsent, 1896: Microscopic slides (2) MNHN DT. 2379, Banyuls, S France.

Rhabderemia spirophora (Burton, 1931): Microscopic slide BMNH 1928: 10: 19: 18, ex Natal Museum 1254, Natal, South Africa, labeled *Hallmannia spirophora;* microscopic slide MNHN DCl. 45, Reef Bay, South Africa.

Rhabderemia topsenti n.sp.: Museum Genova PTR. D5, Middle Italy, labeled *R. minutula*; ZMK and microscopic slide BMNH 1948: 3: 8: 62, Ghana, West Africa, coll. Atlantide Expedition, labeled *R. pusilla*.

Rhabderemia toxigera Topsent, 1892: Microscopic slide MNHN DT.2380, Banyuls, S France.

Rhabderemia uruguaiensis n.sp.: BMNH 1933: 6: 10: 11a, SE of Maldonado, Uruguay, coll. C.A.N.P. "Undine," labeled *R. coralloides*.

Slide preparations for light microscopy and SEM were made according to VAN SOEST *et al.* (1991). Twenty-five specimens of each spicule category present were measured for each species. Measurements quoted usually include the range, the mean, and the standard deviation (in brackets). Measurements for all species are assembled in Table 1.

The following spicule categories are recognized within *Rhabderemia*:

—rhabdostyles (Figs. 27-30), smooth or spined styles, typically with a contort basal twist, less frequently only slightly rhabdose, sometimes in two size categories;

—microstyles (Figs. 31-32), invariably rugose, occasionally in two size categories;

—contorted sigmata (spirosigmata) (Figs. 34-38), unlike true sigmata in other Poecilosclerida they are invariably rugose and strongly twisted and curved, C- and S-shaped; in one species they occur in two size categories;

—thraustosigmata (Figs. 39-40), irregular, rather robust sigmata, often more or less smooth, but may bear spines, usually distinctly larger than the contort sigmata;

—thraustoxea (Figs. 43-44), irregular oxea-shaped microscleres with a twist in the often swollen middle part;

—toxa (Figs. 41-42), usually deeply curved but unreflexed, and unlike true toxa in other Poecilosclerida, they are rugose.

KEY TO THE SPECIES OF *RHABDEREMIA*

The key is an emendation of that given by Hooper, 1990, adapted to the increased number of species. The various character states used to discriminate between the species are illustrated in Figs. 16-44:

1. Microscleres in the form of microstyles or sigmata, or toxa, or thraustoxea present 3
Microscleres absent (subgenus *Stylospira*) 2
2. Color white, rhabdostyles up to 500 by 30 µm .... *R. mona* p. 67
Color orange, rhabdostyles only up to 400 by 20 µm .... *R. destituta* p. 67
3. Microscleres include toxa or toxiform "rhaphides" 4
Microscleres may include sigmata and/or microstyles and/or thraustoxea but never toxa.......... 6
4. Growth form thinly encrusting........... 5
Growth form elaborate, lumpy lobate or ramose .... *R. sorokinae* p. 62
5. Rhabdostyles largely smooth with only occasional spines, toxa distinct .... *R. toxigera* p. 62
Rhabdostyles spined, "toxa" consisting of few toxiform "rhaphides" .... *R. spinosa* p. 54
6. Microscleres include thraustoxea 7
Microscleres may include sigmata and/or microstyles but never thraustoxea 10
7. Microstyles present 8
Microstyles absent .... *R. fascicularis* p. 65
8. Growth form elaborate, lobate-ramose 9
Growth form thinly encrusting . *R. guernei* p. 65
9. Thraustosigmata present; microstyles up to 45 µm .... *R. coralloides* p. 66
No thraustosigmata; microstyles up to 88 µm ... . *R. mutans* p. 66
10. Large (> 20 µm) thraustosigmata present 11
No large thraustosigmata (although smaller ones of 15 µm occur in two species)................ 13
11. Growth form elaborate, ramose 12
Thinly encrusting .... *R. intexta* p. 65
12. Microstyles present...... *R. forcipula* p. 63
Microstyles absent........... *R. mammillata* p. 67
13. Thinly encrusting (less than a few mm in thickness) 14
Massively encrusting (> 1 cm) or lobate..... 20
14. Two distinct size categories of microstyles (long and thick vs. short and thin) 15
A single size category of microstyles........ 16
15. Rhabdostyles with distinct spiral twist .... *R. africana* p. 53
Rhabdostyles barely curved, often almost straight...................... *R. bistylifera* p. 54
16. Rhabdostyles > 400 µm . *R. profunda* p. 55
Rhabdostyles < 400 µm 17
17. Sigmata strongly contort, thin, overall finely rugose 18

Sigmata approaching C-shape, angular, relatively smooth, relatively thick 19

18. Rhabdostyles not larger than 175 μm .... *R. prolifera* p. 54

Rhabdostyles up to 350 μm... *R. minutula* p. 51

19. Rhabdostyles not larger than 180 μm, smooth .... *R. gallica* p. 56

Rhabdostyles up to 290 μm, lightly spined .... *R. burtoni* p. 57

20. Entirely smooth rhabdostyles 21

Lightly or heavily spined rhabdostyles....... 24

21. Microstyles unusually stout, 3-4 μm thick.... .... *R. stellata* p. 64

Microstyles 2 μm or less in thickness 22

22. Contorted sigmata < 10 μm 23

Contorted sigmata > 10 μm ... *R. indica* p. 60

23. Rhabdostyles almost straight, no spiral twist .... *R. spirophora* p. 61

Rhabdostyles with the usual spiral curve .... *R. topsenti* p. 61

24. Two size categories of contorted sigmata (av. 7 and 15 μm) .... *R. acanthostyla* p. 58

A single category of contorted sigmata 25

25. Rhabdostyles thick, up to 24 μm, heavily spined .... *R. antarctica* p. 63

Rhabdostyles only up to 15 μm, less heavily spined, smaller often entirely smooth, abundant pigment granules in superficial parts .... *R. uruguaiensis* p. 57

SYSTEMATIC DESCRIPTIONS

Rhabderemia Topsent, 1890.

Rhabderemia Topsent, 1890: 28.
Rhabdosigma Hallmann, 1916: 520.
Hallmannia Burton, 1931: 352.
Stylospira de Laubenfels, 1934: 10.
Nisibaris de Laubenfels, 1936: 144

Definition: Poecilosclerida, of uncertain relationship, characterized by spirally twisted smooth or acanthose rhabdostyles in a plumoreticulate or plumose arrangement, and by microscleres, if present, consisting of rugose microstyles, and/or rugose contorted sigmata ("spirosigmata"), and/or rugose or spined irregular sigmata ("thraustosigmata"), and/or rugose toxa, and/or rugose twisted oxeotes ("thraustoxea").

Remarks: Previous authors, including HOOPER (1990), assigned *Rhabderemia* to a family Rhabderemiidae Topsent, 1928. However, since the only representative of that family is *Rhabderemia*, one might argue that the use of that family name is superfluous. By elimination, the nearest relatives appear to be in the family Raspailiidae (cf. also HOOPER, 1990) (absence of chelae, occasional occurrence of rhabdostyles, which are not spirally twisted in a few raspailiid genera), but HOOPER's (1990) arguments for considering *Rhabderemia* as distinct from most Raspailiid genera are confirmed. The rugose or spined condition of the microscleres, which appears to be uniformly present in all investigated specimens (cf. below), casts doubt on the homology of these spicules with Poecilosclerid equivalents as true sigmata and toxa, which are normally smooth. The rugose microstyles likewise are unlikely to be homologous with acanthostyles of Raspailiidae and other poecilosclerid families. We propose to retain the family Rhabderemiidae for practical purposes, because assignment to other poecilosclerid families would inevitably compromise the definitions of these families.

The species diagnosed below are treated in an order of morphological similarity, beginning with the type species.

Rhabderemia minutula (Carter, 1876)
Figs. 1, 29-30

Microciona minutula Carter, 1876: 479, pl. 16 fig. 51 a-d.
Microciona pusilla Carter, 1876: 239 (lapsus)
Microciona pusilla Carter, 1880: 437.
Microciona pusilla Topsent, 1889: 41, fig. 7.
Rhabderemia pusilla Topsent, 1892a: 116; Hallmann, 1917: 399.
Not: *Rhabderemia minutula sensu* Topsent, 1904, 1928 = *R. profunda* (Boury-Esnault *et al.*, in press).
Nec: *Rhabderemia minutula* var. Topsent, 1904 = *R. gallica* n.sp.
Nec: *Rhabderemia minutula sensu* Topsent, 1918, and Lévi, 1956 = *R. africana* n.sp.
Nec: *Rhabderemia minutula sensu* Boury-Esnault, 1971, Pulitzer-Finali, 1983, and Bibiloni *et al.*, 1990 = *R. topsenti* n.sp.
Nec: *Rhabderemia pusilla sensu* Dendy, 1922 = *R. burtoni* n.sp.
Nec: *Rhabderemia pusilla sensu* Burton, 1956 = *R. topsenti* n.sp.

Material examined: ZMA POR. 10055, Bonaire, Netherlands Antilles, under coral rubble, 5 m, 4-VIII-1987, coll. R. Pennartz and G. J. Roebers, #182; ZMA POR. 10052, 10053, Blauwbaai, Curaçao, Netherlands Antilles, under coral rubble, 35 m, coll. E. Meesters & P. Willemsen, VIII-1989, #B2-A5, B2B6, B12-6; ZMA POR. 10054, Cornelisbaai, Curaçao, 5 m, under coral rubble, coll. E. Meesters & P. Willemsen, VIII-1989, # C28-5; ZMA POR.10056, off Punta Betin, Santa Marta, Colombian Caribbean, encrusting dead corals, 2-I-1991, coll. M. Kielman.

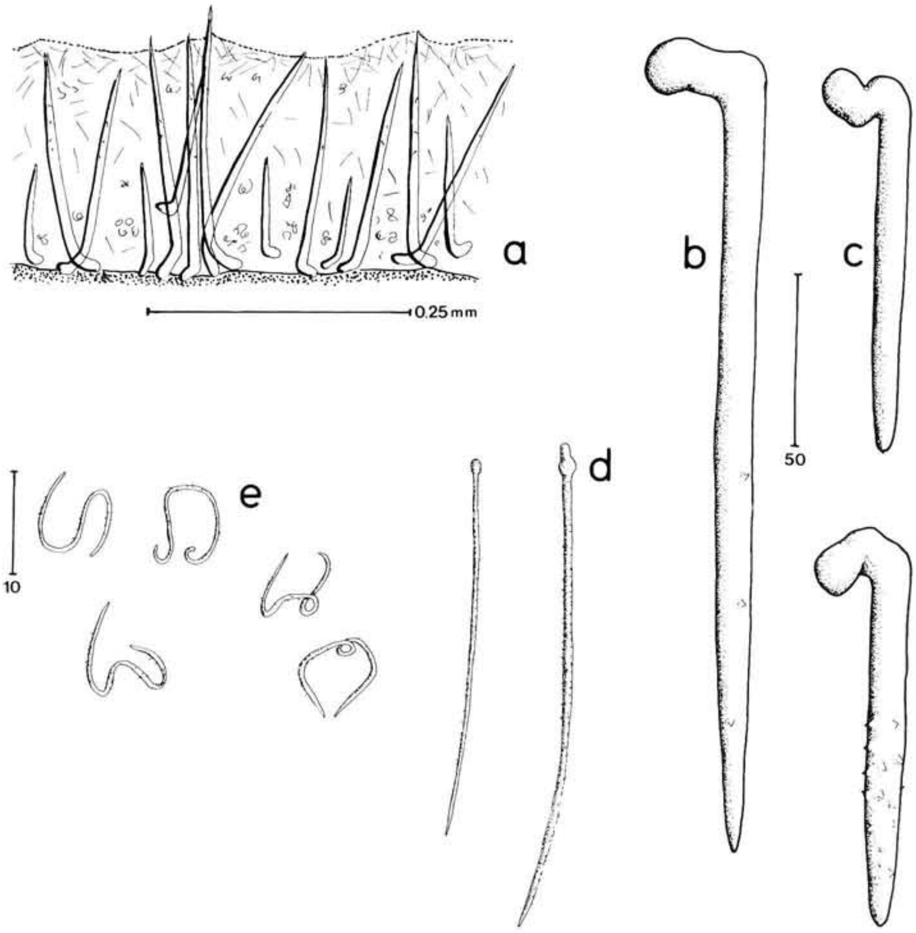

FIG. 1. — *Rhabderemia minutula:* a, cross section of the choanosome showing the single spicule architecture; b, larger category of rhabdostyle with vestigial spines; c, smaller category of rhabdostyles, both smooth and spined; d, microstyles with apical tyle; e, small contorted sigmata.

Diagnosis: Thin, optically smooth encrustations consolidating rubble and insinuating in holes in the substrate. Microscopically hispid. No apparent oscules. Color light brown alive, pale dull brown in alcohol.

Ectosome: Charged with microscleres, at times composed predominantly of microstyles or sigmata.

Choanosome (Fig. 1a) : Megascleres erect on the substrate, singly or in bundles of a few each. Substrate covered by a membrane charged with microstyles.

Spicules: Rhabdostyles (Fig. 1 b-c, 29) occasionally entirely smooth, but more often lightly spined or rugose distally, rhabdose end compact, spirally twisted, distal end often rather blunt or rounded: 81-167.2 (77.7)-352 by 4-5.7 (1.5)-9 µm , usually in two distinct size categories, I: 81-111.0 (19.7)-140 µm and II: 196-230.9 (88.7)-352 µm. Microstyles (Fig. 1d) with slightly tylote swelling subterminally, distinctly rugose: 90-119.8 (19.7)-135 by 1 µm. Contorted small sigmata (Fig. 1e): 9-12.9 (3.3)-18 µm.

Distribution (Fig. 4) and ecology: West Indian region: Yucatan, Bonaire, Curaçao, Colombia, under coral rubble, 5-35 m.

Remarks: The name *R. minutula* is here restricted to shallow-water West Indian representatives of the genus, because it is likely that Carter's original material originated from this area. Although his specimens were from an unknown locality, Carter assumed they were from the tropics. His description and figure of the spicules (rhabdostyles of 150 µm, erect on the substrate, very small contort sigmata, and fine "acuates") matches that of more recent material from that area. The same applies to TOPSENT's (1889) description from the Yucatan area. His emphasis on the smooth condition of the rhabdostyles is understandable in view of the very lightly spined, occasionally entirely smooth, condition found to prevail in this species.

Records of *R. minutula* or *R. pusilla* (this latter name was used first by Carter, but corrected to the former name by himself in 1880) from outside the West Indies are referred to here as other species of *Rhabderemia*. *R. minutula sensu* Topsent, 1904 and 1928 (cf. *R. profunda* Boury-Esnault *et al.*, 1993 below) from deep water off the Azores, has much larger rhabdostyles (> 400 µm), which are entirely smooth, and much thicker microstyles (> 2 µm). *R. minutula* var. *sensu* Topsent, 1904 (cf. *R. gallica* n.sp. below) from Atlantic and Mediterranean shallow waters, differs in possessing smaller, entirely smooth rhabdostyles, but especially in conspicuously less contort thick sigmata (thraustosigmata) of 17-21 µm. *R. minutula sensu* Topsent, 1918, and Lévi, 1956 (cf. *R. africana* n.sp. below), from tropical West African waters, differs only marginally from the West Indian species in color ("grey-green"), in the entirely smooth condition of the rhabdostyles, and in two size categories of microstyles instead of one. Like *R. minutula s.s.*, *R. africana* n.sp. seems to have two size categories of rhabdostyles, and both the spicule sizes and the habit are very similar.

Mediterranean-Atlantic *R. "minutula"* (*sensu* Bibiloni and Gili, 1982, Pulitzer-Finali, 1983, and Bibiloni *et al.*, 1989) and *R. "pusilla"* (*sensu* Vosmaer, 1880, and Burton, 1956) (cf. *R. topsenti* n.sp. below) differ from the West-Indian species in the massive habit, the plumoreticulate skeleton architecture, the entirely smooth condition of the rhabdostyles, and the much smaller microstyles (up to 45 µm). *R. pusilla sensu* Dendy, 1922, from the Indian Ocean (cf. *R. burtoni* n.sp. below) differs in having thraustosigmata, somewhat larger microstyles, and considerably thicker rhabdostyles, but it is otherwise similar.

R. prolifera Annandale, 1915, from the Indian Ocean is a very similar species, occupying boreholes of *Cliona*. The only difference with *R. minutula s.s.* is the rather small size of the rhabdostyles (96-210 µm), which nevertheless occur in two size categories.

Rhabderemia africana n.sp.

Fig. 2

Rhabderemia minutula sensu Topsent, 1918: 541; Lévi, 1956: 393, fig. 2 (not: Carter, 1876).

Holotype, material in MNHN, described by Lévi (1956) from Dakar, Sénégal. Not examined.

Material examined: Microscopic slides MNHN DT. 2054 (2 slides), and MNHN DT. 2055, both from San Thomé (= São Tomé), West Africa (cf. Topsent, 1918), considered schizoparatypes.

Description (based on accounts of Topsent, 1918, and Lévi, 1956): Thinly encrusting and insinuating in limestone holes (often made by boring sponges). Surface smooth, no visible oscules. Color greyish green alive.

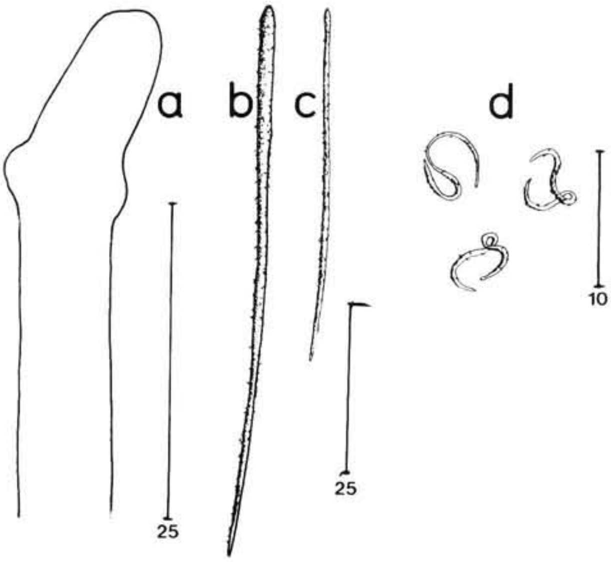

Fig. 2. — *Rhabderemia africana* n.sp.: a, head of rhabdostyle (redrawn from Lévi, 1956); b, larger category of microtyle; c, smaller category of microstyle; d, small contorted sigmata.

Ectosome: A crust of microstyles.

Choanosome: Single rhabdostyles erect on the substrate (Topsent's microscopic slide showed no rhabdostyles).

Spicules: Rhabdostyles (Fig. 2a, redrawn from Lévi, 1956) with barely curved rhabdose ends, with slight subterminal tylote swelling, entirely smooth: 60-250 by 7 µm, quoted as occurring in two size categories by Lévi: I: 60-70 µm and II: 200-250 µm. Microstyles (Fig. 2 b-c) rugose, no obvious apical swelling, in two distinct size categories, especially with respect to thickness I: 50-70 by 0.5 µm and II: 85-98.3 (18.9)-120 by 2 µm. Contorted small sigmata (Fig. 2d): 8-12 µm.

Etymology: The name refers to the exclusive occurrence of this species in Africa.

Distribution (Fig. 4) and ecology: tropical West Africa: São Tomé (Gulf of Guinea), Sénégal, in limestone holes from low tide downward.

Remarks: The new species clearly differs from similar *Rhabderemia* from across the Atlantic (i.e., *R. minutula s.s.*) in that it possesses two size categories of microstyles. Other, more subtle differences are the barely curved rhabdostyles and the absence of a subterminal tylote swelling on the microstyles. Another similar species is the Indian Ocean *R. prolifera*, which also inhabits boreholes. This differs from the present species also by its single microstyle category.

Another West African species of *Rhabderemia* is Mediterranean-Atlantic *R. topsenti* n.sp. (recorded from Ghana as *R. pusilla* by Burton, 1956). It clearly differs from *R. africana* in having a plumoreticulate architecture and small microstyles (45 µm).

Rhabderemia prolifera Annandale, 1915

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

Material examined: none.

Diagnosis (based on Annandale's and Thomas's descriptions): Thinly encrusting corals and shells, and insinuating in *Cliona* boreholes; thickness about 0.75 mm. No visible apertures. Surface hispid. Color not recorded.

Ectosome: Charged with microstyles.

Choanosome: Rhabdostyles erect on the substrate, singly or in bundles.

Spicules: Rhabdostyles entirely smooth, with compact rhabdose end: 90-210 by 4-8 µm in two distinct size categories averaging about 99 (I) and 175 (II) µm. Microstyles rugose, with elongated oval heads: 82-147 by 1-2 µm. Small contort sigmata: 12 µm.

Distribution (Fig. 4) and ecology: western and eastern Indian Ocean: Andaman Islands and Mozambique Channel, on reefs.

Remarks: This species is closest to *R. minutula* and *R. africana* n.sp., sharing with them both the thinly encrusting and insinuating habit as well as similar spicule categories, spicule sizes, and morphologies. It differs from *R. minutula* in the smaller rhabdostyle sizes, especially the larger category, which is smaller than the smallest ones of *R. minutula;* from *R. africana* n.sp. in the lack of a second microstyle category. Other Indian Ocean species are *R. burtoni* n.sp. (= *R. pusilla sensu* Dendy, 1905), *R. indica*, *R. spirophora*, *R. bistylifera*, and *R. acanthostyla*. *R. burtoni* n.sp. and *R. acanthostyla* have heavily spined rhabdostyles, *R. indica* and *R. spirophora* have plumoreticulate skeletons. The differences with *R. bistylifera* are less obvious, but that species has thin shallow-curved rhabdostyles with elongated rhabdose ends as well as a second category of small microstyles.

Rhabderemia bistylifera Lévi, 1961

Rhabderemia bistylifera Lévi, 1961: 15, text-fig. 18.

Material examined: Microscopic slides (2) of the holotype MNHN DCl. 358, Aldabra Atoll, W Indian Ocean, #SY. 11 (cf. Lévi, 1961).

Diagnosis (from Lévi, 1961): Thinly encrusting (holotype was attached on the holdfast of *Acanthella*). Surface showing no visible openings. Color blackish in alcohol.

Ectosome: Not recorded.

Choanosome: Architecture not recorded; rhabdostyles are probably erect on the substrate, to judge by the thinly encrusting habit.

Spicules: Rhabdostyles virtually smooth (only occasionally some vestigial spines were observed), with shallow-curved elongated rhabdose ends: 131-220.0 (66.6)-305 by 3-6 µm, probably in two length categories: 131-220 (I) and 258-305 (II) µm. Microstyles rugose, thin: 30-141 by 0.2-1 µm, in two size categories, I: 30-35.8 (6.8)-43 by 0.2 µm and II: 110-127.0 (12.8)-141 by 1 µm. Small contort sigmata: 6-7.7 (2.1)-10 µm.

Distribution (Fig. 4) and ecology: Known only from the Aldabra reefs.

Remarks: This species is similar to *R. minutula*, *R. africana* n.sp., and *R. prolifera* in the thinly encrusting habit and general spicule morphology. The rhabdostyles are distinct with their shallow-curved rhabdose ends. With *R. africana* n.sp. it shares two distinct microstyle categories. *R. bistylifera* differs from other Indian Ocean species in its habit (*R. acanthostyla* is ramose-lobate, *R. indica* and *R. spirophora* are massive), and skeletal architecture (all three have plumoreticulate skeletons). The color is unusual for the genus and may not be proper, because contact with sponges showing an aerophobic response may be responsible for it.

Rhabderemia spinosa Topsent, 1896

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

Material examined: Microscopic slides (2) of the holotype MNHN DT. 2379, Banyuls, 2-II-1893.

Diagnosis (after Topsent, 1896): Thinly encrusting. Surface hispid, no visible aperture. Color greyish-green in alcohol.

Ectosome: Not recorded.

Choanosome: Single rhabdostyles erect on the substrate.

Spicules: Rhabdostyles lightly spined, in two distinct size categories of which the larger is almost entirely smooth: I: 111-128.3 (19.5)-156 by 6 µm, II: 310-393.8 (92.3)-510 by 15 µm. Microstyles with tylote rounded end or centrotylote: 30-33.0 (2.4)-36 by 0.5 µm. Small contorted sigmata: 12 µm.? Toxa: among the numerous fine microstyles a number of similar spicules were observed with pointed apices at both ends, often slightly centrotylote and with a shallow curve. Presumably these spicules are homologous to the better developed toxa of *R. toxigera* and *R. sorokinae*.

Distribution (Fig. 4) and ecology: Mediterranean, on *Arca* mussel.

Remarks: The relationships of this species are ambiguous. It shares the thinly encrusting habit, single-spicules architecture and two rhabdostyle size categories with the above-described species. The largest category of rhabdostyles and the small size of the microstyles is reminiscent of species related to *R. coralloides*, from which it differs, however, in the absence of thraustoxea/thraustosigmata.

Rhabderemia profunda Boury-Esnault *et al.*, in press
Fig. 3

Rhabderemia minutula sensu TOPSENT, 1904: 152, pl. I fig. 10, pl. XIII fig. 13; TOPSENT, 1928: 309 (not: *R. minutula sensu* CARTER, 1896).

Rhabderemia profunda Boury-Esnault *et al.*, in press.

Material examined: Microscopic slides (2) MNHN DT. 957, S of the Azores, 34°N 31°W, depth 1360 m, coll. "Princesse Alice ," 1896 cruise, stat. 703, #181 (specimen itself is lodged in the Monaco Museum, cf. TOPSENT, 1904); microscopic slide MNHN DT. 1339, off Flores, Azores, 38°N 30°W, depth 1331 m, coll. "Princesse Alice" 1912 cruise, stat. 3293 (cf. Topsent, 1928).

Description (after TOPSENT, 1896, and BOURY-ESNAULT *et al.*, in press): Thinly encrusting on dead hexactinellids and octocorals, up to 10 by 4 cm in lateral expansion, and a few mm in thickness. Surface smooth, no apparent oscules. Consistency "not very soft". Color green-black alive, yellow-brown in alcohol.

Ectosome: Crust of microstyles.

Choanosome: Single spicules, occasionally in bundles, erect on the substrate.

Spicules: Rhabdostyles (Fig. 3a) with a relatively shallow curve, with rhabdose ends that are barely spirally twisted, sometimes entirely straight, smooth: (Topsent's material): 411-451.9 (27.2)-500 by 9-11.0 (1.1)-12 µm, (Boury-Esnault *et al.*'s material).: 520-564-620 by 10.5-12.0-14 µm. Microstyles (Fig. 3b) rugose, with a wide, often slightly swollen, rounded end, relatively thick: (Topsent): 108-117.9 (11.1)-135 by 1.5-2.1(0.4)-2.5 µm (Boury-Esnault *et al.*): 77-86-98 by 2 µm. Small contorted sigmata (Fig. 3c) : (Topsent): 13-13.7 (1.5)-15 µm (Boury-Esnault *et al.*): 9.5-10.6-12 µm.

Distribution (Fig. 4) and ecology: Azores and Alboran Sea, western Mediterranean, deep water.

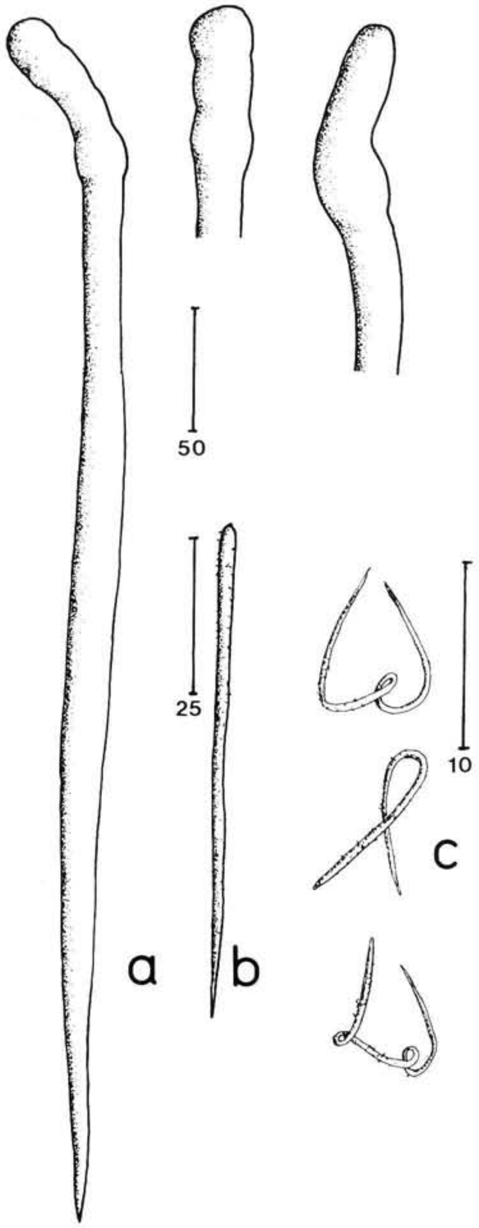

FIG. 3. — *Rhabderemia profunda*: a, rhabdostyles with variable rhabdose ends; b, microstyle; c, small contorted sigmata.

Remarks: The species differs substantially from *R. minutula s.s.* in the size and morphology of the megascleres, and the thickness of the microstyles. It stands out among other *Rhabderemia* species by its green-black color, which is perhaps also found in *R. bistylifera* and *R. africana*, although in these the color is only known in alcohol. A further characteristic is the large megasclere size. In this it approaches *R. spinosa*, which has, however, spined rhabdostyles, including a separate smaller category.

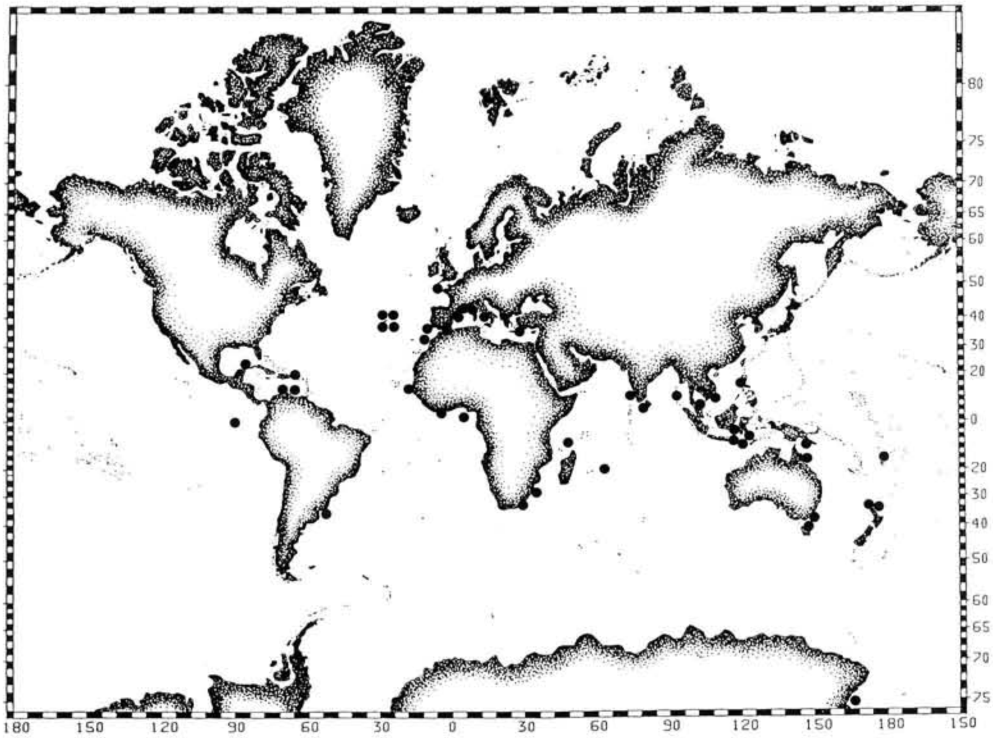

FIG. 4. — Distributions of *Rabderemia minutula* (1), *R. africana* n.sp. (2), *R. prolifera* (3), *R. bistylifera* (4), *R. spinosa* (5), and *R. profunda* (6).

Rhabderemia gallica n.sp.
Fig. 5

Rhabderemia minutula var. TOPSENT, 1904: 153.
Rhabderemia minutula sensu Lévi in BOROJEVIC *et al*., 1968: 13; BOURY-ESNAULT, 1971: 306 (not CARTER, 1876)

Material examined: Microscopic slide of the holotype MNHN DT. 115, Banyuls, Mediterranean coast of France, # 103 (holotype specimen, from "Ile Grosse," cf. Topsent, 1904, presumably in the collections of MNHN); microscopic slide of the paratype MNHN DCl.874, Roscoff, N of Ile de Batz, Atlantic coast of France, 60 m, in a hole of a calcareous nodule (paratype presumably in collections of the Station Biologique at Roscoff, listed in BOROJEVIC *et al.*, 1968); microscopic slide MNHN NBE. 152, Banyuls, Castelloussous, S France, coll. N. Boury-Esnault, 7-VI-1967, labeled as *R. minutula* (not considered type material because of low spicule content of the slide) (cf. BOURY-ESNAULT, 1971).

Description (partly after TOPSENT, 1904): Encrusting (no further macroscopic details recorded).
Ectosome: Not recorded.
Choanosome: Single megascleres erect on the substrate.
Spicules: Rhabdostyles (Fig. 5 a-b) entirely smooth, with compact tightly coiled rhabdose end, unusually short in the Banyuls specimen, larger in the Roscoff specimen; sometimes rhabdostyles are deformed into right-angled spicules: 57-102.0 (49.6)-178 by 4-5 µm.
Microstyles (Fig. 5c), rugose, thin, often with small subterminal tyle: 55-70.3 (24.8)-99 by 0.5-1.5 µm.

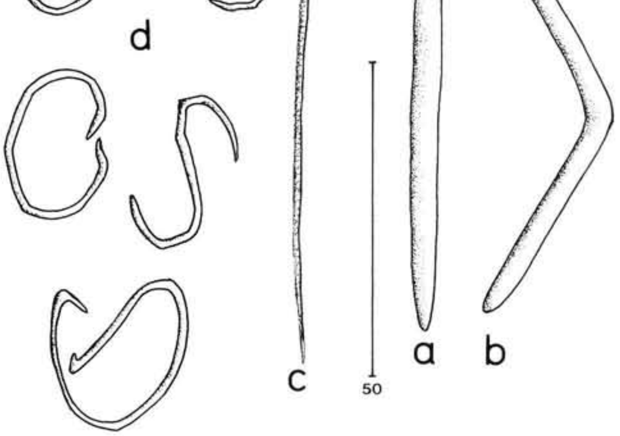

FIG. 5. — *Rhabderemia gallica* n.sp.: a, normal rhabdostyle; b, boomerangshaped malformed rhabdostyle; c, microstyle; d, small thraustosigmata.

Thraustosigmata (Fig. 5d), small, irregularly curved: 17-21 µm.
Etymology: The name refers to the exclusive occurrence of this species in France.

Distribution (Fig. 9) and ecology: Mediterranean-Lusitanian, so far known only from French waters, at intermediate depths.

Remarks: The new species differs from *R. minutula s.s.* in that it possesses thraustosigmata and relatively small megascleres. It shares these characters with the Indian Ocean species *R. burtoni* n.sp. (= *R. pusilla sensu* DENDY, 1922), from which it differs in the entirely smooth condition of the rhabdostyles and the shorter microstyles (up to 135 µm in *R. burtoni* n.sp.). From the sympatric *R. topsenti* n.sp. (= *R. minutula sensu* PULITZER-FINALI, 1983, for example) the new species differs in having thraustosigmata, which are also considerably larger than the small contorted sigmata of *R. topsenti* n.sp., and those in the larger microstyles.

Rhabderemia burtoni n.sp.
Fig. 6

Rhabderemia pusilla DENDY, 1922: 85 (not CARTER, 1876).

Material examined: Microscopic slide of the holotype, BMNH RN CXVI.A, Salomon Island, Chagos Archipelago, Indian Ocean, 05°S 72.5°E, 108-216 m, coll. "Sealark" Exped. (holotype in the BMNH, cf. DENDY, 1922).

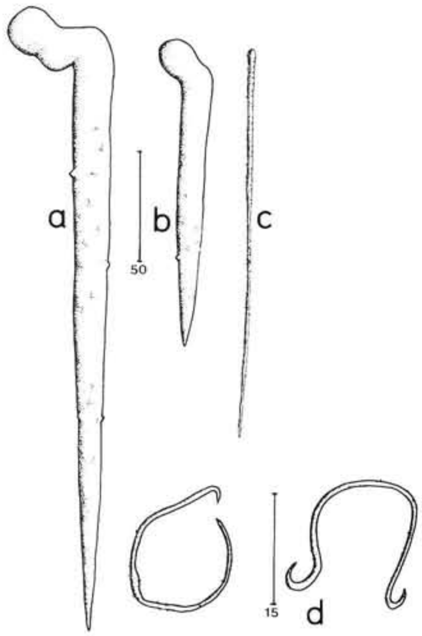

FIG. 6. — *Rhabderemia burtoni* n.sp.: a, larger category of rhabdostyle; b, smaller category of rhabdostyle; c, microstyle; d, small thraustosigmata.

Description (partly after DENDY, 1922): A small fragment containing the characteristic spicules, attached to a specimen of *Spongosorites salomonensis*.

Ectosome: Not recorded.

Choanosome: Short bundles of rhabdostyles perpendicular to the surface.

Spicules: Rhabdostyles (Fig. 6 a-b) with widely curved apices, shaft lightly spined, in two size categories: I: 110-135.0 (17.9)-155 by 4-5.6 (1.3)-6 µm, and II: 188-246.4 (53.4)-290 by 11-12.0 (1.4)-14 µm. Microstyles (Fig. 6c) rugose, long and thin: 112-136.3 (25.0)-162 by 0.5 µm. Thraustosigmata (Fig. 6d), small, irregularly curved: 16 µm.

Etymology: The new species is named in honor of Dr. Maurice Burton, in recognition of his impressive contributions to sponge systematics.

Distribution (Fig. 9) : W Indian Ocean, deeper waters.

Remarks: The new species differs from *R.minutula s.s.* in the thicker rhabdostyle I category and the possession of thraustosigmata. It shares the latter spicules with *R. gallica* n.sp., from which it differs in possessing two sizes of rhabdostyles and longer and thinner microstyles.

Other Indian Ocean species are *R. prolifera*, which has smooth rhabdostyles, a thicker rhabdostyle I category, and thicker microstyles and lacks thaustosigmas; *R. bistylifera*, which differs in all these characters as well as in having two size categories of microstyles; *R. acanthostyla*, which has plumoreticulate architecture, much smaller microstyles, and two sizes of small contort sigmata (not thraustosigmata); *R. spirophora*, which has only a single megasclere category and no thraustosigmata; and *R. indica*, which also has a single megasclere category, much smaller microstyles, a plumoreticulate architecture and no thraustosigmata.

Rhabderemia uruguaiensis n.sp.
Fig. 7

Rhabderemia coralloides sensu BURTON, 1940: 116 (not DENDY, 1924).

Material examined: Holotype, Buenos Aires Museum 15953, schizoholotype BMNH 1933: 6: 10: 11a, SE of Maldonado, Uruguay, 35°08'S 52°35'W, coll. C.A.N.P. "Undine," VII-1925.

Description: Probably lobate (only a fragment was available for study), with an irregular, somewhat villous surface, possibly due to the damaged ectosomal membrane.

Ectosome: Membrane charged with the usual micros cleres, and containing regularly spaced concentrations of pigment granules (averaging 38 µm in diameter).

Choanosome (Fig. 7a): Skeleton architecture plumoreticulate, with main bundles 3-5 spicules in cross section, and single connecting spicules, irregularly protruding from the main bundles.

Spicules: Rhabdostyles (Fig. 7b), often with blunt apices, normally spined but the smaller category often entirely smooth, in two size categories: I: 141-147.0 (5.2)-150 by 2-2.7 (0.6)-3 µm, and II: 166-231.3 (58.0)-310 by 7-11.0 (2.9)-15 µm. Microstyles (Fig. 7c) rugose: 43-49.4 (6.4)-60 by 0.5-0.9 (0.2)-1 µm. Small contorted sigmata (Fig. 7d): 6-9.3 (2.5)-12 µm.

Etymology: The name refers to the type locality off the coast of Uruguay.

Distribution (Fig. 9): Off the coast of Uruguay

Remarks: The new species differs clearly from *R. coralloides* from New Zealand in the much smaller size of the rhabdostyles, and in the absence of thraustoxea and thraustosigmata. It shares overall spiculation and pigment granule concentrations in the surface with *R. acanthostyla,* but the two differ in that two size categories of contorted sigmata are present in the latter. In many respects, *R. uruguaiensis* is similar to *R. antarctica* n.sp. (cf. below), but it differs clearly from that species in having two size categories of rhabdostyles, which are also much less heavily spined.

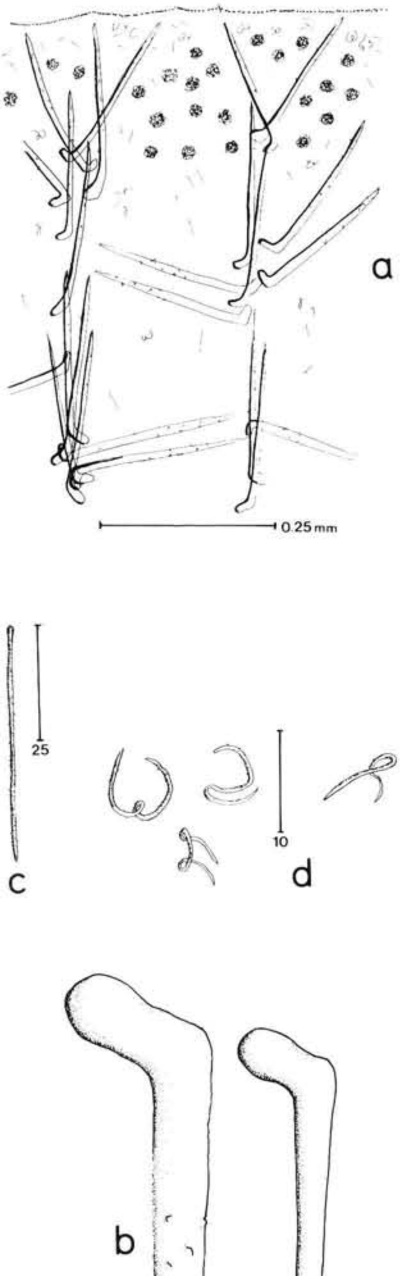

FIG. 7. — *Rhabderemia uruguaiensis* n.sp.: a, perpendicular section of the choanosomal skeleton to show plumoreticulate architecture (note concentration of pigment granules in the peripheral region); b, two size categories of rhabdostyles; c, microstyle; d, small contorted sigmata.

Rhabderemia acanthostyla Thomas, 1968

Figs. 8, 16-19, 34, 37.

Rhabderemia acanthostyla THOMAS, 1968: 247, pl. 2 figs. 4-5.

"*Rhabdosigma conulosa*" Lévi MS (name quoted by HOOPER, 1990: 77).

Material examined: ZMA POR. 1926, Indonesia, Saleyer Reef, 06°S 120°E, 0-36 m, coll. "Siboga" Exped., stat.213, 26-X-1900; ZMA POR. 6524, Indonesia, Sumbawa, 08°20.5′S 118°15.7′ E, 0-1 m, coll. R. W. M. van Soest, "Snellius II" Exped. stat.4.120 /10, 23-IX-1984; ZMA POR.8112, Indonesia, Sumbawa, 08°20.5′S 118°15.7′ E, coll. R. W. M. van Soest, "Snellius II" Exped., stat. 4. 120/II/10, 1-4 m, 23-IX-1984; ZMA POR. 8585, Indonesia, Take Bone Rata, Take Karlarang, 4-10 m, coll. R. W. M. van Soest, "Snellius II" Exped., stat. 4. 147 /III/31, 26-IX-1984; ZMA POR. 9620, Indonesia, Sulawesi, Barong Lompo, off Ujung Pandang, 05°S 119°E, 2 m, coll. H. Moll, 18-X-1980; MNHN DCl. 1560, Vietnam, Nha Trang, Tran Ngoc Loi, labeled "*Rhabdosigma conulosa*" by Lévi (MS name).

Diagnosis: The characteristic growth form consists of a few up to a dozen short columnlike branches that anastomose into a loose mass (Figs. 17-18). Individual branches are up to 3.5 cm long and 0.5 cm in diameter. Initial stages of this species manifest them-

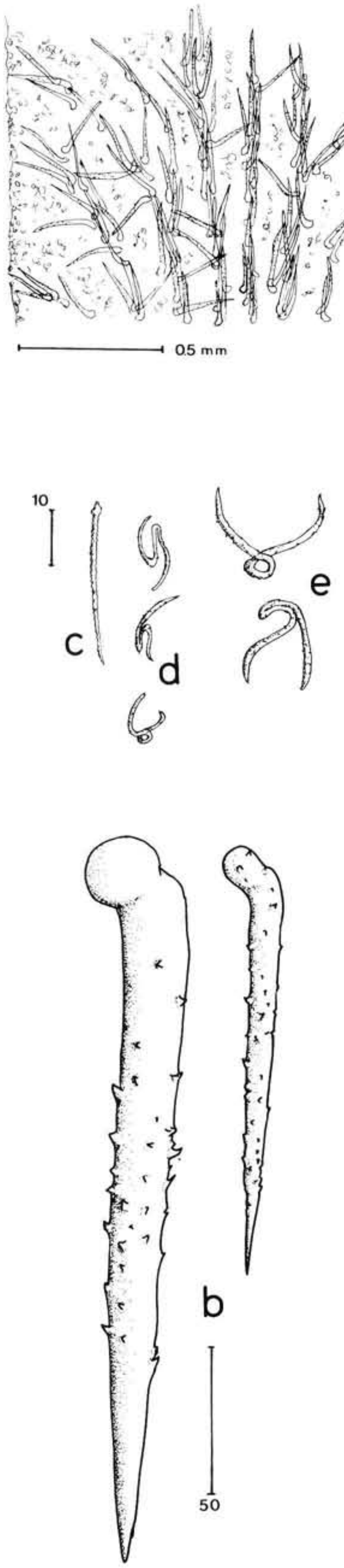

FIG. 8. — *Rhabderemia acanthostyla:* a, perpendicular section through a branch to show the axially plumose skeleton; b, two size categories of rhabdostyles; c, tiny microstyle; d, smaller category of small contorted sigmata; e, larger category of small contorted sigmata.

selves as thick irregular crusts (Fig. 16). Columnlike growth forms are also known (Fig. 19). Surface more or less smooth, but finely granular and easily damaged. No clearly visible oscules. Consistency soft. Color lighter or darker brown alive, pale grey in alcohol.

Ectosome: An organic layer charged with microscleres; concentrations of pigment granules are found in all specimens examined.

Choanosome (Fig. 8a): Skeleton plumose in encrusting forms, plumoreticulate in branches, with main bundles 2-5 spicules in cross section, interconnecting single spicules standing off at more or less right angles to the bundles.

Spicules: Rhabdostyles (Fig. 8b) spined, in two size categories: I: 98-121.9 (15.9)-141 by 4-5.0 (1.5)-7 µm, and II: 183-232.8 (33.1)-255 by 5-8.5 (2.7)-13 µm. Microstyles (Fig. 8c) extremely fine and short: 20-29.3 (6.1)-39 by less than 0.5 µm.

Small contorted sigmata (Fig. 8d-e) in two distinct size categories: I (Fig. 34): 13-15.2 (1.9)-18 µm (these are precisely similar in morphology to the smaller category and definitely not homologous to the thraustosigmata), II (Fig. 37): 6-6.8 (0.8)-8 µm.

Distribution (Fig. 9) and ecology: India, Indonesia, Vietnam, in the open reef habitat at 1-10 m.

Remarks: Although we did not examine Thomas's specimens, the similarities in color (dark brown) and spiculation, including the two sizes of rhabdostyles strongly suggest that it is the same as the Indonesian and the Vietnam specimen. The distinctive character of this species is that it possesses two sizes of small contorted sigmata (not recorded by Thomas, who also overlooked the tiny microstyles), which are not known from other *Rhabderemia*. Also the habit, consisting of anastomosing masses of thin branches, is peculiar. In other respects, the species is similar to *R. uruguaiensis* n.sp.

HOOPER (1990) suggested that New Caledonian *R. forcipula* (LÉVI and LÉVI, 1990) is a junior synonym of the present species, but subsequent examination of *R. forcipula* specimens (cf. below) demonstrated important differences (habit, spicule sizes, possession of thraustosigmata), and there can be no doubt that both are distinct unrelated species.

Rhabderemia indica Dendy, 1905
Fig. 25

Rhabderemia indica DENDY, 1905: 180, pl. 12 fig. 10; HALLMANN, 1917: 399.

Not: *Rhabderemia indica sensu* SARÀ, 1961: 44; nec: SARITAS, 1973: 11 (= *R. topsenti* n.sp.)

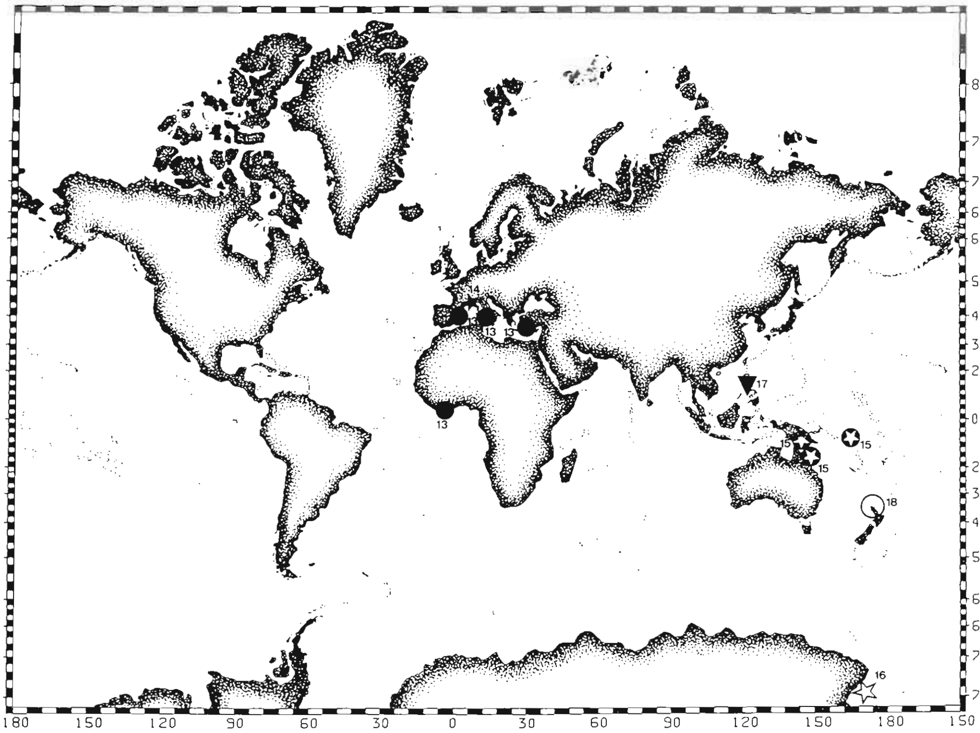

FIG. 9. — Distributions of *Rhabderemia gallica* n.sp. (7). *R. burtoni* n.sp. (8). *R. uruguaiensis* n.sp. (9). *R. acanthostyla* (10). *R. indica* (11). and *R. spirophora* (12).

Material examined: Fragment and microscopic slides of the holotype. BMNH 1907: 2: 1: 69. Gulf of Manaar, Sri Lanka. "Pearl Oyster Fisheries" # N.341 (cf. DENDY. 1905): specimen. NTM Z4076 (fragment QM G300510). Ko Phangan. N of Ko Samui. S Gulf Thailand. 09°47.8′N 99°58.7′E. 15-18 m depth. coll. J. N .A. Hooper. 07-VI-1990.

Diagnosis (after DENDY, 1905): Thickly encrusting to massive, 5 cm in lateral expansion. 7-8 mm thick, enveloping shell fragments. Shape irregular. Surface uneven with small scattered oscules. Consistency spongy but friable. Color dull grey in alcohol.

Ectosome: Translucent membrane charged with microscleres.

Choanosome: Close-meshed irregular (Fig. 25) plumoreticulate skeleton, with multispicular primary tracts and interconnecting tracts. Spongin only at the nodes.

Spicules: Rhabdostyles smooth, although some have vestigial spines (visible in SEM pictures): 211-238.0 (26.1)-263 by 5-6.6 (2.1)-9 µm. Microstyles rugose, short and straight: 42-46.1 (3.0)-48 by 1-1.25 (0.4)-2 µm. Small contorted sigmata: 12-13.2 (1.3)-15 µm.

Distribution (Fig. 9) and ecology: Sri Lanka and Gulf of Thailand, shallow water down to 18 m.

Remarks: *R. spirophora* from the east coast of South Africa is probably the closest relative of this species: it differs in having a large proportion of straight "rhabdo-" styles. Entirely smooth rhabdostyles are shared with Mediterranean *R. topsenti* n.sp. (= *R. minutula sensu* PULITZER-FINALI, 1983, for example). which has been named "*R. indica*" by two authors. not entirely without cause. for the differences between the Mediterranean and the eastern Indian Ocean specimens are subtle. The microstyles of *R. indica* are thicker and the contorted sigmata are larger. The size range of the rhabdostyles of *R. indica* is much narrower (but that may reflect the paucity of material).

Other Indian Ocean species -*R. prolifera*, *R. bistylifera*, *R. burtoni* n.sp., and *R. acanthostyla* -clearly differ in having two size classes of rhabdostyles and a number of other specific characters.

Rhabderemia spirophora (Burton, 1931)

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

Nisibaris spirophora; de LAUBENFELS, 1936: 144. 152.

Rhabderemia spirophora: HOOPER, 1990: 78.

Material examined: Microscopic slide of the holotype BMNH 1928: 10: 19: 18 (holotype in the Museum, # 1254). Natal. South Africa. coll. H. W. Bill Marley. 1919 (cf. BURTON, 1931): microscopic slide of MNHN DCl. 45. Reef Bay. South Africa (containing a majority of *Clathria* spicules but also characteristic spicules belonging to this species).

Diagnosis (after BURTON, 1931): Massive, with hispid surface. A single oscule. Color of beach-worn specimen grey.

Ectosome: Thin membrane, charged with microscleres overlying extensive subdermal grooves.

Choanosome: Skeleton plumoreticulate with multispicular tracts, similar to that of *R. indica*.

Spicules: "Rhabdostyles," of which most are only slightly and evenly curved (instead of abruptly and spirally twisted), entirely smooth: 240-263.0 (26.6)-286 by 6-8.3 (1.5)-9 μm. Microstyles thin, short, rugose: 45-53.3 (6.7)-61 by 0.5-0.9(0.5)-1.6 μm. Small contorted sigmata: 6-8.2 (1.6)-10 μm.

Distribution (Fig. 9): East coast South Africa, no ecological data.

Remarks: A clear difference with *R. indica* (and also *R. topsenti* n.sp.) is the proportion of "unbent" rhabdostyles; in fact, no true rhabdostyle was found. A more subtle difference with *R. indica* is the smaller size of the contorted sigmata (similar to those of *R. topsenti* n.sp.).

East African *R. bistylifera* shares the large proportion of shallowly curved rhabdostyles with *R. spirophora*, but in other aspects the two species differ substantially, so this is assumed to be parallel development in both.

Rhabderemia topsenti n.sp.

Fig. 10.

Desmacodes pusillus; VOSMAER, 1880: 107

Rhabderemia pusilla; BURTON, 1956: 134 (not: CARTER, 1876)

Rhabderemia minutula; BIBILONI and GILI, 1982; PULITZER-FINALI, 1983: 533, fig. 51; BIBILONI *et al.*, 1989: 327, fig. 5a (not: CARTER, 1876; nec: TOPSENT, 1904; nec: BOURY-ESNAULT, 1971)

Rhabderemia indica; SARÀ, 1961: 441, fig. 7; SARITAS, 1973: 11, pl. I fig. 10 (not: DENDY, 1905).

Material examined: Fragment of the holotype, Mus. Genova, # PTR.D5, Tremiti Islands, S Domino, Carla Tonda, Middle Italy, cave, 2-4 m depth, VI-1966 (cf. PULITZER-FINALI, 1983): BMNH 1948: 3: 8: 62, Atlantide Expedition stat. 85, Ghana, West Africa, 05°37′N 00°38′E, 28-40 m, I-1952 labeled *R. pusilla* (cf. BURTON, 1956) (fragment of specimen from Mus. Kopenhagen, in view of geographic separation this has not been assigned paratypic status).

Description: Massive, with lateral outgrowths. Size 4-5.5 cm in diameter and 0.4-1 cm thick. Oscules slightly raised above the surface with subdermal canals leading to it.

Surface granular, irregular. Consistency soft. Color yellow alive, buff or whitish in alcohol.

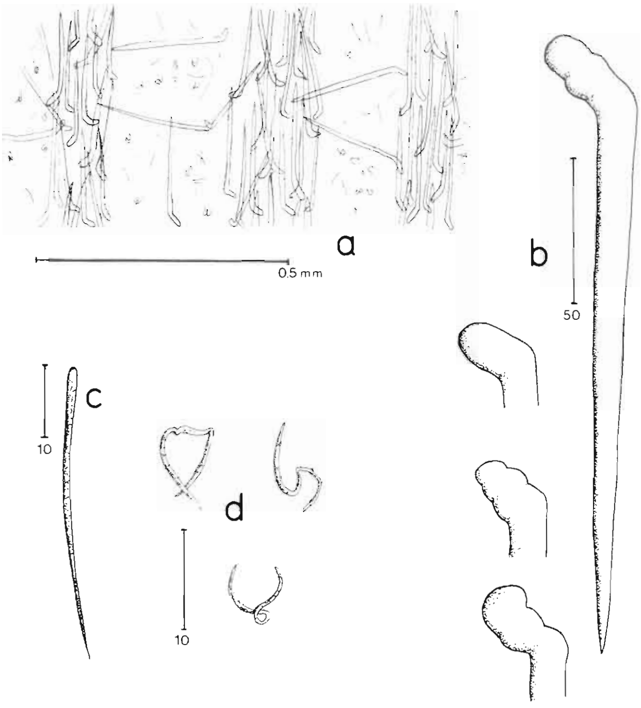

FIG. 10. — *Rhabderemia topsenti* n.sp.: a, perpendicular section of choanosome to show the plumose skeletal arrangement; b, rhabdostyle with variable rhabdose ends; c, microstyle; d, small contorted sigmata.

Ectosome: Thin membrane charged with microscleres.

Choanosome (Fig. 10a): Skeleton loosely plumoreticulate with primary tracts of 3-10 spicules in cross section; little spongin.

Spicules: Rhabdostyles (Fig. 10b) smooth (a few scattered spines were observed only now and then): 145-215.9 (45.8)-315 by 2.5-6.6 (2.3)-10.5 μm. Microstyles (Fig. 10c) thin, short, roughened: 36-42.7 (4.8)-50 by 0.5-0.96 (0.39)-1.5 μm. Small contorted sigmata (Fig. 10d): 5-7.7 (1.8)-10 μm.

Etymology: The new species is named after the late Dr. E. Topsent in recognition of his pioneering studies on *Rhabderemia*.

Distribution (Fig. 12) and ecology: Mediterranean, West Africa, shallow water and marine caves.

Remarks: As explained above, Carter's original *Microciona minutula/pusilla* originated in the tropics, probably the West Indian region. Mediterranean specimens assigned to this species (excepting those recorded by Topsent and Boury-Esnault) differ from the West Indian species in habit (massive instead of thinly encrusting, cf. CARTER, 1876), color (yellow vs. brown), skeletal architecture (plumoreticulate vs. single spicules) and spicule sizes and ornamentation. It is obvious that both are not closely related.

A West African specimen assigned to *R. pusilla* by Burton (1956) also seems to be conspecific with Mediterranean *R. topsenti* n.sp.

The new species is close to *R. indica* and *R. spirophora*, differing from the former in the smooth condition of the rhabdostyles. Other Mediterranean species are *R. spinosa*, which has size classes of spined rhabdostyles erect on the substrate; *R. toxigera*, which has toxa among the microscleres; and *R. gallica* n.sp., which has much smaller rhabdostyles and thraustosigmata rather than small contorted sigmata.

Rhabderemia toxigera Topsent, 1892b

Rhabderemia toxigera Topsent, 1892b: xxv.

Material examined: Microscopic slide of the holotype MNHN DT. 2380, France, Banyuls, Cap l'Abeille, 141.

Diagnosis (after Topsent, 1892b): Thin encrustation with hispid surface. Color not recorded.

Ectosome: Organic membrane charged with microscleres.

Choanosome: Skeleton of short plumose tracts of rhabdostyles.

Spicules: Rhabdostyles smooth or lightly spined, in two size categories, I: 126-137 by 5-6 µm, and II: 225-305.8 (82.3)-407 by 9-9.4 (1.5)-11 µm. Microstyles rugose, thin: 52-60.0 (7.2)-69 by 1-1.25 (0.5)-2 µm. Small contorted sigmata: 5-9.3 (3.8)-12 µm. Toxa, rugose, often centrotylote: 30-45.6 (11.6)-57 by 1 µm.

Distribution (Fig. 12): Known only from the type locality in the western Mediterranean.

Remarks: Rugose toxa are also present in *R. sorokinae*, which is in other aspects rather dissimilar (elaborate habit and plumoreticulate skeleton). Disregarding the toxa, *R. toxigera* is most similar to the sympatric *R. spinosa*, and perhaps the two should not be kept distinct, as some of the microstyles of the latter are toxiform. The alleged sharp distinction between the two in the smooth versus spined condition of their rhabdostyles cannot be upheld here because slightly spined rhabdostyles are not uncommon in the present species.

Sympatric *R. topsenti* n.sp. (= *R. minutula sensu* Pulitzer-Finali, 1983, for example) has much smaller rhabdostyles and no toxa.

Rhabderemia sorokinae Hooper, 1990

Figs. 20, 26, 32, 41-42.

Rhabderemia sorokinae Hooper, 1990: 68, pl. I A-B, text-figs. 1-12.

Material examined: Holotype, NTM Z3580 (fragment QM G300624), Deloraine Island, Whitsunday Is, Great Barrier Reef, Qld., 20°09'S 149°04.5'E, 20-m depth, coll. S. Sorokin, 15-X-1987; ZMA POR. 9757, Papua New Guinea, coll. M.C. Diaz, 1991, #91167; microscopic slide BMNH 1954: 3: 9: 178, Carter collection labeled "*Microciona minutula* C. on *Discodermia*, Stylaster 10, South Sea, 1878" (presumably from somewhere in the tropical S Pacific).

Diagnosis: Thickly encrusting clumps to elaborate branching forms (Fig. 20). Size several cm^2. Oscules slightly raised above the surface, with stellate subdermal groove pattern. Surface minutely hispid. Consistency soft, easily damaged. Color yellow-brown alive.

Ectosome: Organic layer carried by spicule brushes. Charged with microscleres.

Choanosome: Skeleton (Fig. 26) plumoreticulate, with main tracts 3-6 spicules in cross section.

Spicules: Rhabdostyles spined, relatively thick: 106-256-283 by 3-14.0-22 µm.

Microstyles (Fig. 32) roughened, large variation in length: 53-102.0 (37.6)-141 by 0.8-1.5-2.0 µm. Small contort sigmata, microspined: 6-12.2 (4.5)-16 µm. Toxa (Figs. 41-42), lightly microspined, sometimes appearing smooth: 18-41.0 (19.8)-72 µm.

Distribution (Fig. 12) and ecology: Great Barrier Reef, Papua New Guinea, S. Pacific, on reefs, down to 20 m.

Remarks: The possession of toxa is shared with *R. toxigera*, but in most other respects the two species differ, so it is not obvious that the toxa are a synapomorphy for the two. The elaborate habit of *R. sorokinae* is shared with *R. coralloides*, *R. acanthostyla*, *R. forcipula*, and *R. mammillata*. Apart from lacking toxa, *R. forcipula* (from nearby New Caledonia) also differs in having thraustosigmata. *R. coralloides* has both thraustosigmata and thraustoxeas, and much shorter microxea. *R. acanthostyla* is dark brown and has two sizes of both rhabdostyles and contorted sigmata. *R. mammillata* has thraustosigmata and lacks microstyles.

Rhabderemia antarctica n.sp.

Figs. 11, 21.

Rhabderemia coralloides; Burton, 1929: 435 (not: Dendy, 1924)

Material examined: Fragment of the holotype (designated herein) BMNH 1926: 10: 26: 92, McMurdo Sound, Antarctica, 77°5'S 164°18'E, 252 m, coll. "Terra Nova"Exped., stat. 339, Agassiz trawl (label still gives the provisional specimen no. Do.8).

Description: Finger-shaped to ramose, length not known (only a fragment, Fig. 21, was available for study), diameter 1.4 cm. Surface villose-irregular, possibly due to damaged ectosomal membrane. No

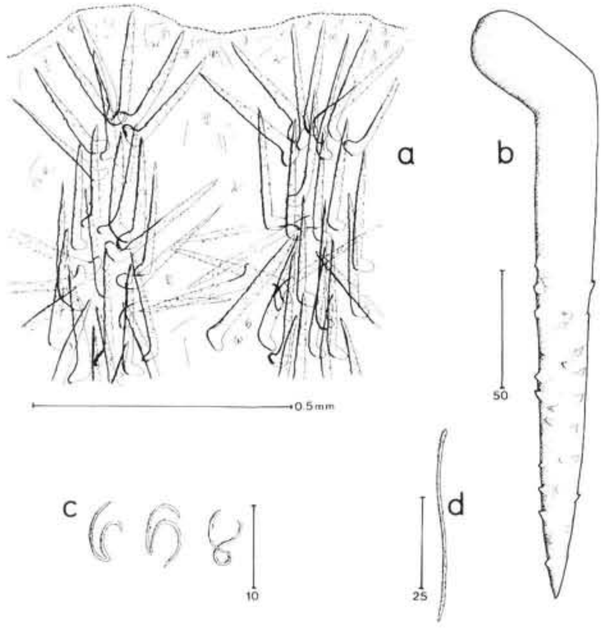

FIG. 11. — *Rhabderemia antarctica* n.sp.: a, perpendicular section of choanosomal skeleton to show plumoreticulate arrangement; b, rhabdostyle; c, small contorted sigmata; d, microstyle.

apparent oscules. Consistency rather tough, but easily damaged. Color beige in alcohol.

Ectosome: A thin membrane charged with microscleres.

Choanosome (Fig. 11a): Plumoreticulate skeleton, with thick, loosely organized tracts of 5-10 spicules in cross section, most of which project from the tracts at some angle. Interconnecting spicules may be singly arranged or in ill-defined bundles. The nodes of the main and the interconnecting tracts frequently appear as radiating masses of spicules.

Spicules: Rhabdostyles (Fig. 11b) thick, heavily spined in the basal half: 202-240.0 (30.7)-265 by 7-17.6 (9.2)-24 µm. Microstyles (Fig. 11d) thin, short, rugose: 45-47.7 (3.1)-51 by 0.5-1 µm. Small contort sigmata (Fig. 11c), rugose: 7-8.3 (0.9)-9 µm.

Etymology: The name refers to the type locality in Antarctica.

Distribution (Fig. 12) and ecology: Known only from the type locality, McMurdo Sound, Antarctica, deep water.

Remarks: Burton's identification of this material as *R. coralloides* is not acceptable, because that species has thraustoxeas and thraustosigmata, as well as much thicker microstyles. Some resemblance with *R. coralloides* is found in the choanosomal plumoreticulate architecture and the heavily spined rhabdostyles. *R. coralloides* seems to be confined to northern New Zealand, as the record from Uruguay (BURTON, 1940) was also assigned to a new species (cf. above). The new species is somewhat similar to *R. uruguaiensis* n.sp. (cf. above), also originally recorded as *R. coralloides*: both share the irregular surface and similar overall spiculation. However, *R. antarctica* has only a single category of rhabdostyle, more heavily spined than those of *R. uruguaiensis*.

Rhabderemia forcipula (Lévi and Lévi, 1989)
Figs. 22-23, 33, 35, 40.

Rhabdosigma forcipula LÉVI and LÉVI, 1989: 75, text-fig. 43, pl. VII fig. 8.

Material examined: Paratype MNHN DCl. 3243, Philippines, off Mindoro, 13°55′N 120°20′E, 85-90 m, coll. MUSORSTOM 2 stat. 8; microscopic slide of MNHN DCl. 3387, Philippines, off Mindoro, 13°51′N 120°50′E, coll. MUSORSTOM 2 stat. 28 (LÉVI and LÉVI, 1989).

Diagnosis (after LÉVI and LÉVI, 1989): Erect, branching, treelike (Figs. 22-23); up to 8 cm high, 4 cm in diameter. Surface granular-hispid. Oscules not clearly apparent. Consistency tough, friable. Color brown-red in alcohol.

Ectosome: A membrane charged with microscleres.

Choanosome: A very dense plumoreticulate skeleton with bundles of 2-4 spicules in cross section interconnected obliquely single spicules; little binding spongin. The branches show a tendency towards axial condensation.

Spicules: Rhabdostyles long, thick, lightly spined, or entirely smooth: 230-307.2 (50.5)-381 by 10-17.1 (3.4)-21 µm. Microstyles long, thin, rugose: 150-162.5 (7.9)-171 by 1-1.25 (0.4)-2 µm. Thraustosigmata (Figs. 33, 40) large, slightly rugose, apices provided with teethlike long spines: 25-27.0 (2.2)-30 µm. Small contorted sigmata (Figs. 33, 35), rugose: 12-14.8 (2.5)-18 µm.

Distribution (Fig. 12) and ecology: Philippines, deeper water.

Remarks: This is a well-defined species with its treelike habit, large spined thraustosigmata, and very long microstyles. New Zealand *R. stellata* is similar in rhabdostyle sizes, but lacks the thraustosigmata, has short, very thick microstyles and is massively encrusting. New Zealand *R. coralloides* differs in possessing thraustoxea and much smaller microstyles. South Australian *R. mammillata* has no microstyles.

HOOPER (1990) suggested that *R. forcipula* is a junior synonym of *R. acanthostyla*, but that is clearly a mistake, as that species differs in several characters (color, habit, spicules sizes, lack of thraustosigmata, presence of two sizes of small contorted sigmata).

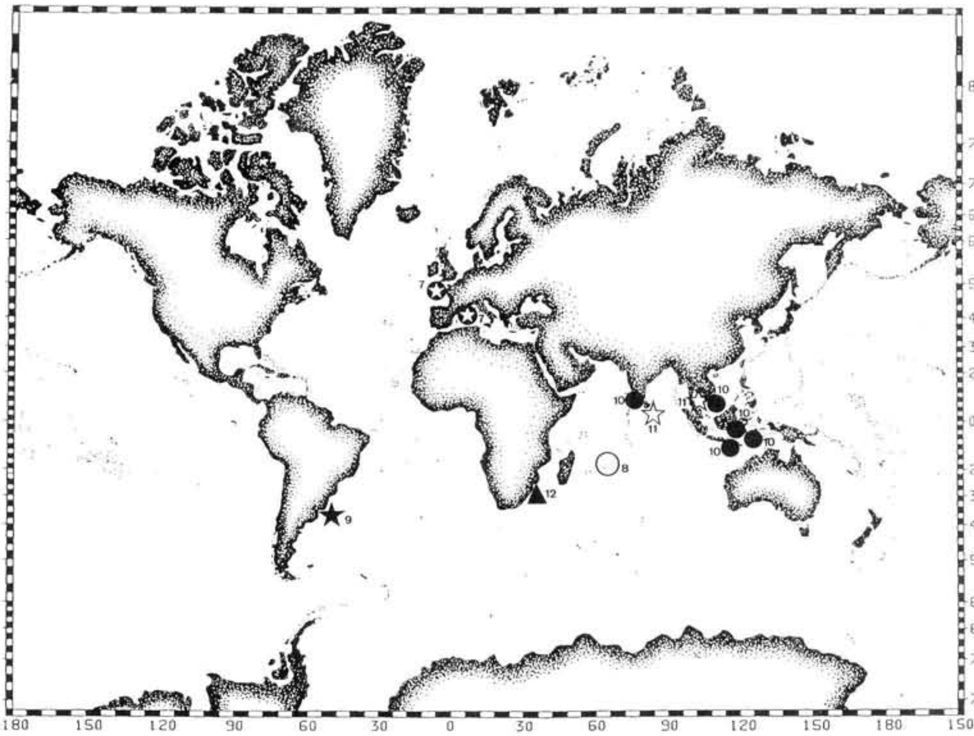

FIG. 12. — Distributions of *Rhabderemia topsenti* n.sp. (130, *R. toxigera* (14), *R. sorokinae* (15), *R. antarctica* n.sp. (16), *R. forcipula* (17), and *R. stellata* (18).

Likewise, Hooper's record of *R. forcipula* from New Caledonia as the type locality is incorrect.

Rhabderemia stellata Bergquist, 1961

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

Material examined: none.

Diagnosis (after BERGQUIST, 1961): Thickly encrusting with stellate subdermal grooves. Surface smooth, punctate. Color in life yellow, in spirit pale brown.
Ectosome: Not recorded.
Choanosome: Skeletal architecture reticulate, mainly unispicular. The plumose aspect is apparently not well-developed.
Spicules: Rhabdostyles entirely smooth, relatively thick: 200-356 by 12-23 µm.
Microstyles conical, short and thick, roughened: 36-48 by 3-4 µm. Small contort sigmata: 10-17 µm.
Distribution (Fig. 12) and ecology: northern New Zealand, under stones at low tide.
Remarks: In some respects, this species is reminiscent of the sympatric *R. coralloides*: the enhanced subdermal grooves, the strongly reticulate architecture, the thick rhabdostyles, and the short conical microstyles. However, important differences are also apparent: *R. stellata* lacks the thraustoxea and the thraustosigmata, and the rhabdostyles are smooth instead of spined. In spiculation, *R. stellata* is probably closest to *R. antarctica*, but this has heavily spined rhabdostyles and much thinner microstyles. The habit of *R. antarctica* is finger-shaped with a shaggy surface.

Rhabderemia fascicularis Topsent, 1927

Rhabderemia fascicularis TOPSENT, 1927: 18; TOPSENT, 1928: 310, pl. 10 fig. 25.

Material examined: Microscopic slide of the holotype MNHN DT. 1244, Azores, west of Flores, depth 1229 m, coll. Campagnes Prince Albert de Monaco, stat. 2210 (cf. TOPSENT, 1928).

Diagnosis (mostly after TOPSENT, 1928): Thick crust on an octocoral. Surface and oscules not recorded. Consistency firm. Color grey.
Ectosome: Charged with thraustoxeas and contort sigmata.
Choanosome: Plumose bundles of rhabdostyles erect on the substrate, diverging toward one another.
Spicules: Rhabdostyles heavily spined, relatively thick: 122-231.4 (82.8)-398 by 8-13.8 (4.1)-19 µm. Mi-

crostyles: absent (a single one was found, but this was an obvious malformed thraustoxea). Thraustoxea, centrotylote in full-grown condition, toxa-like in young growth stages, roughened: 28-52.0 (16.8)-73 by 1.5-3.0 (0.8)-3.5 µm. Small contorted sigmata, roughened: 9-11.6 (4.2)-17 µm. Distribution (Fig. 15) and ecology: Azores, deep water.

Remarks: The distinctive feature of this species is the lack of microstyles, which it shares, however, with *R. intexta*. The two species differ rather widely in other details, such as shape, size, and categories of the sigmata. *R. fascicularis* is close to the sympatric *R. guernei* and *R. mutans*, and in view of this it could be construed that the differences are due to infraspecific variation. However, the differences concerned are of such a nature, that conspecificity is not considered likely (it would also lead to large-scale synonymization among species of the genus *Rhabderemia*). *R. guernei* has almost entirely smooth rhabdostyles and abundant microstyles, while *R. mutans* shares the spined rhabdostyles with *R. fascicularis* but also has abundant microstyles and is fingerlike in growth form.

Rhabderemia guernei Topsent, 1890

Rhabderemia guernei TOPSENT, 1890: 29; TOPSENT, 1892a: 116, pl. XI fig.7; HALLMANN, 1917: 399; TOPSENT, 1928: 312, pl. 10 fig. 24.

Material examined: Microscopic slide of the holotype, MNHN DT. 956 (#105), S of Pico, Azores, depth 736 m, coll. "Hirondelle" 1888 Campagne, stat. 229.

Diagnosis (mostly after TOPSENT, 1892a): Thin crust. Color violet in alcohol. No further details recorded.

Ectosome: Membrane charged with thraustoxea.

Choanosome: Isolated rhabdostyles erect on the substrate.

Spicules: Rhabdostyles almost all smooth, but some have a few spines, relatively long: 183-363.5 (126.2)-473 by 5 –10.3 (5.0)-15 µm. Microstyles thin, roughened: 65-87.7 (23.5)-112 by 1-1.7 (0.57)-2 µm. Thraustoxea thick, roughened, Z-shaped: 45-60.0 (11.1)-75 by 2.5-3.2 (0.8)-4 µm. Small contorted sigmata roughened: 9-10.6 (1.5)-13 µm (Hooper, 1990, table 1, quotes: 18-32 µm, but subsequent study of the slide revealed the range between 9 and 13 µm. There are a few Haplosclerid-type sigmata in it, which Hooper may have mistaken for *Rhabderemia* sigmata).

Distribution (Fig. 15) and ecology: Azores, deep water.

Remarks: *R. guernei* is similar to *R. fascicularis* (see above) and *R. mutans*. The latter differs clearly in habit and also has much shorter and thicker rhabdostyles. The violet color is unusual, but may be due to contamination from other species and in any case is not certainly the live coloration.

Rhabderemia intexta (Carter, 1876)

Microciona intexta CARTER, 1876: 238, pl. XV figs. 43a-c.

Desmacodes intexta; VOSMAER, 1880: 106.

Rhabderemia intexta; TOPSENT, 1892a: 116; TOPSENT, 1904: 152; HALLMANN, 1916: 520; HALLMANN, 1917: 399; HOOPER, 1990: 77.

Rhabdosigma intexta; TOPSENT, 1928: 313, pl. 10 figs. 29-30.

Material examined: Microscopic slide of the holotype BMNH 1954: 3: 9: 180 ("Deep sea *Microciona intexta* No. 19"), encrusting a *Corallistes*, Cape St. Vincent, Portugal, depth 374 fathoms.

Diagnosis (mostly based on TOPSENT, 1928): Thinly encrusting (1 mm thick) on corals and lithistids. Surface smooth, very lightly conulose. No apparent oscules, but subdermal venal pattern present. Color brown (dry condition) or grey-yellow (in alcohol).

Ectosome: Membrane charged with sigmata.

Choanosome: Skeleton spicules arranged in plumose columns.

Spicules: Rhabdostyles relatively long and thin, lightly spined in the lower half (at first sight they appear smooth): 150-254.3 (76.7)-350 by 3-7.6 (4.3)-14 µm. Microstyles: apparently absent. Thraustosigmata roughened, some almost regular sigmata, others crooked or angular: 25-35.4 (11.5)-60 µm. Small contort sigmata roughened: 6-10.5 (2.5)-16 µm.

Distribution (Fig. 15) and ecology: S Portugal, Morocco (HOOPER, 1990, quotes Hebrides, but that is a mistake), deep water (673-2, 165 m).

Remarks: The thraustosigmata in the large size range (25-60) are shared with *R. mammillata*, which also lacks the microstyles. In habit and ecology, both species differ substantially (*R. mammillata* is arborescent and probably from shallow water). As discussed above, *R. fascicularis*, which also lacks the microstyles, is nevertheless dissimilar in other features.

Rhabderemia mutans Topsent, 1927

Rhabderemia mutans TOPSENT, 1927: 17; TOPSENT, 1928: 310, pl. II fig. 2, pl. X fig. 21.

Material examined: Microscopic slide of the holotype, MNHN DT. 1236, W of Flores, Azores, depth 914-650 m, coll. Campagnes Prince Albert I de Monaco 1905, stat. 2214.

Diagnosis (mostly after Topsent, 1928): Cylindrical, 2.5 cm high, diameter 0.7 cm, top rounded (possibly a piece of a larger treelike specimen). Subdermal canal pattern distinct, but no oscules apparent. Consistency firm. Color whitish in alcohol.
Ectosome: Membrane charged with thraustoxea.
Choanosome: Skeleton plumoreticulate.
Spicules: Rhabdostyles short and thick, heavily spined: 190-237.8 (57.6)-306 by 14-21.0 (5.8)-28 µm. Microstyles roughened, often with slight subterminal swelling: 32-57.5 (23.4)-88 by 1-1.3 (0.4)-2 µm. Thraustoxea Z-shaped, roughened, seemingly intermediate between microstyles and thraustosigmata: 35-49.0 (20.5)-79 by 1-1.8 (0.5)-2.5 µm. Small contort sigmata roughened: 10-11.5 (1.7)-13 µm.
Distribution (Fig. 15) and ecology: Azores, deep water.
Remarks: As discussed above, *R. mutans* shares the thraustoxea with two sympatric species, namely, *R. fascicularis* and *R. guernei*. However, the differences in other respects are so great that conspecificity is unlikely. *R. mutans* is most similar to New Zealand *R. coralloides*, but differs in the absence of thraustosigmata and the longer microstyles.

Rhabderemia coralloides Dendy, 1924

Figs. 27-28, 31, 36, 38-39, 43-44.

Rhabderemia coralloides Dendy, 1924: 357, pl. XII fig. 3, pl. XV figs. 1-4; Topsent, 1928: 65; Bergquist, 1968: 19.
Not: *Rhabderemia coralloides sensu* Burton, 1929: 435 (= *R. antarctica* n.sp.)
Nec: *Rhabderemia coralloides sensu* Burton, 1940: 116 (= *R. uruguaiensis* n.sp.)

Material examined: Fragment and microscopic slides of the holotype BMNH 23: 10: 1: 139, 7 miles E of North Cape, New Zealand, 126 m, coll. "Terra Nova" Exped. stat. 96.

Diagnosis (mostly from Dendy, 1924): A mass of irregular subcylindrical branches, each 1.2 cm in diameter; entire mass 12 cm in diameter. Surface granular, marked by stellate grooves (subdermal canals). Consistency firm and compact, friable. Color pale grey-yellow in alcohol.
Ectosome: Membrane containing only microscleres.
Choanosome: Skeleton a compact reticulation of spicule tracts and single spicules, forming quadrangular and triangular meshes.
Spicules: Rhabdostyles (Figs. 27-28) stout, heavily spined in the lower half: 206-310.6 (68.0)-394 by 13-24.6 (6.4)-34 µm. Microstyles roughened, short, and thin: 37-40.4 (3.2)-45 by 1-1.1 (0.25)-1.5 µm. Thraustoxea (Figs. 43-44) roughened, Z-shaped, some resembling toxa: 32-32.7 (0.9)-34 by 0.5-1.5(0.95)-2.6 µm. Thraustosigmata (Fig. 39) small, roughened: 18-20.3 (2.1)-22 µm. Small contorted sigmata (Figs. 36, 38) roughened: 6-9.0 (2.0)-11 µm.
Distribution (Fig. 15) and ecology: northern New Zealand, deeper water.
Remarks: This species is unique to the genus in having a combination of thraustoxea and thraustosigmata. Sympatric *R. stellata* differs widely in habit, spiculation (no thraustoxea or thraustosigmata), and habitat (intertidal). *R. coralloides* is most similar to the Mid-Atlantic deep-water species *R. mutans* (cf. above).

Rhabderemia mammillata (Whitelegge, 1907)

Sigmaxinella mammillata Whitelegge, 1907: 512, pl. 46 fig. 39.
Rhabdosigma mammillata; Hallmann, 1916: 520; Hallmann, 1917: 399, pl. 21 figs. 1-2, text-fig. 2; Shaw, 1927: 427.

Material examined: none.

Diagnosis (mostly after Hallmann, 1917): Lobate fan-shaped, with a short stout stalk, 7 cm high, 6.5 cm wide, and 4 cm thick. Oscules in groups on the summit of the lobes, with star-shaped subdermal grooves leading to them. Surface velvety. Consistency firm, tough, resilient. Color light brown in alcohol.
Ectosome: A thin membrane.
Choanosome: Skeleton plumoreticulate with a more plumose peripheral region and a reticulate somewhat denser axial region. Primary tracts of 3-8 spicules in cross section, connected by single spicules.
Spicules: Rhabdostyles lightly spined or entirely smooth, occasionally with rounded instead of pointed ends: 126-302 by 5-18 µm. Microstyles: absent. Thraustosigmata (?) of a shape reminding of sigmancistras, apparently smooth: 24-42 µm. Small contort sigmata apparently smooth: 9-13.
Distribution (Fig. 15) and ecology: New South Wales and Tasmania, southern Australia, shallow water(?).
Remarks: This is a distinct species in shape and spiculation. The combination of thraustosigmata and small contort sigmata is shared with *R. coralloides* (but that species has microstyles and thraustoxea), *R. forcipula* (but that has microstyles and larger rhabdostyles), and *R. intexta*, which is perhaps closest of all to *R. mammillata* but is thinly encrusting in deep water.

Rhabderemia mona (de Laubenfels, 1934)

Fig. 13

Stylospira mona de LAUBENFELS, 1934: 10.

Rhabderemia mona van SOEST and Stentoft, 1988: 115, table VII.

Material examined: microscopic slide of the holotype USNM 22324, off Puerto Rico, 18°10-15'N 67°42-46'W, 10-II-1933, 432-468 m.

Diagnosis (mostly after de Laubenfels, 1934): Massive, 1.5 by 3 by 3.5 cm, with a central hollow. No oscules visible. Surface smooth. Consistency tough. Color white in alcohol.

Ectosome: A thin membrane without spicules.

Choanosome (Fig. 13a): Reticulate skeleton of single rhabdostyles, occasionally bundles of two or three occur.

Spicules: Rhabdostyles (Fig. 13b) long and thick, entirely smooth, with pronounced axial canal: 306-417.5 (80.7)-495 by 17-20.2 (2.6)-24 µm. Microstyles: absent. Sigmata: absent.

Distribution (Fig. 15) and ecology: Puerto Rico, deep water.

Remarks: This is a dubious *Rhabderemia* because major synapomorphies such as the microspined microstyles and the contort sigmata are lacking. However, the rhabdostyles are similar to those found in the other *Rhabderemia* species, and they are arranged in a loosely reticulate way. DE LAUBENFELS (1934) erected the genus *Stylospira* for this species; in view of the fact that there is apparently a second species (*R. destituta* n.sp., cf. below) lacking both microstyles and contort sigmata, we propose that *Stylospira* be recognized as a subgenus.

Rhabderemia destituta n.sp.

Figs. 14, 24.

Material examined: Holotype, USNM 43065, San Salvador, Islas Galagapos, 00°12'S 090°51'W, depth 34 m. SEPBOP "Anton Bruun" Cruise 16, stat. 794E (fragment in ZMA).

Description: Semiglobular encrustation (Fig. 24) with smooth surface, rough to the touch. Subdermal grooves form a distinct but irregular venal pattern. No apparent oscules. Consistency hard, barely compressible. Color orange-brown in alcohol.

Ectosome: A thin membrane without spicules.

Choanosome (Fig. 14a): Skeleton in parts a single spicule reticulation, in other parts bundles of three or more spicules occur; overall organization rather confused, with little or no binding spongin.

Spicules: Rhabdostyles (Fig. 14b) robust, entirely smooth, with prominent axial canals: 305-343.5 (34.7)-395.5 by 13.5-23.3 (6.4)-31 µm. Microstyles: absent. Sigmata: absent.

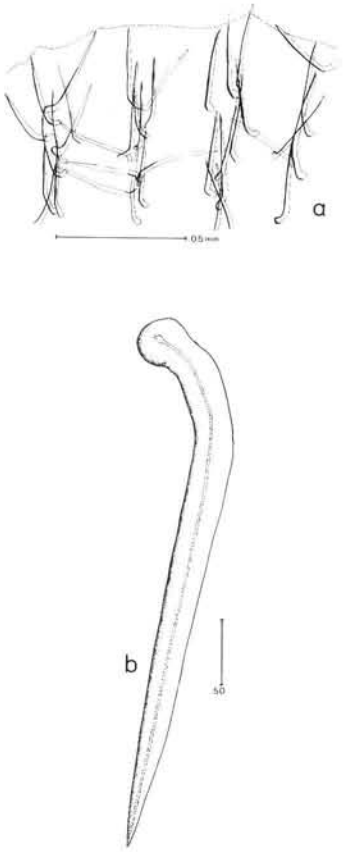

FIG. 13. — *Rhabderemia (Stylospira) mona*: a, perpendicular section of the choanosomal skeleton to show reticulation; b, rhabdostyle.

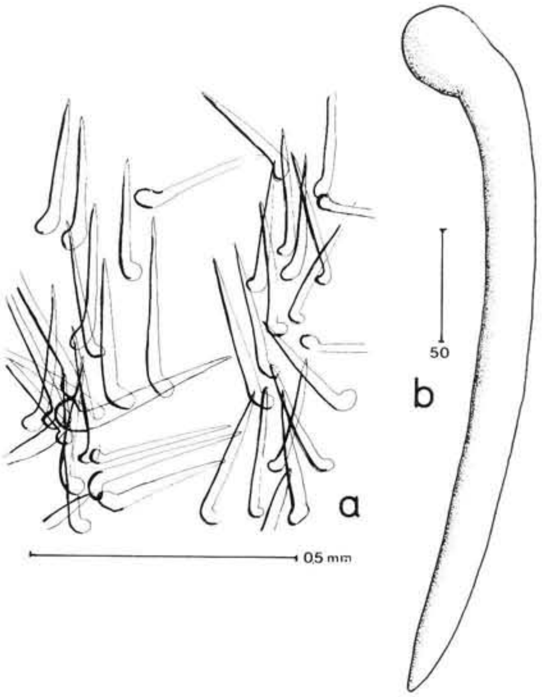

FIG. 14. — *Rhabderemia (Stylospira) destituta* n.sp.: a, perpendicular section of the choanosomal skeleton to show confused reticulation; b, rhabdostyle.

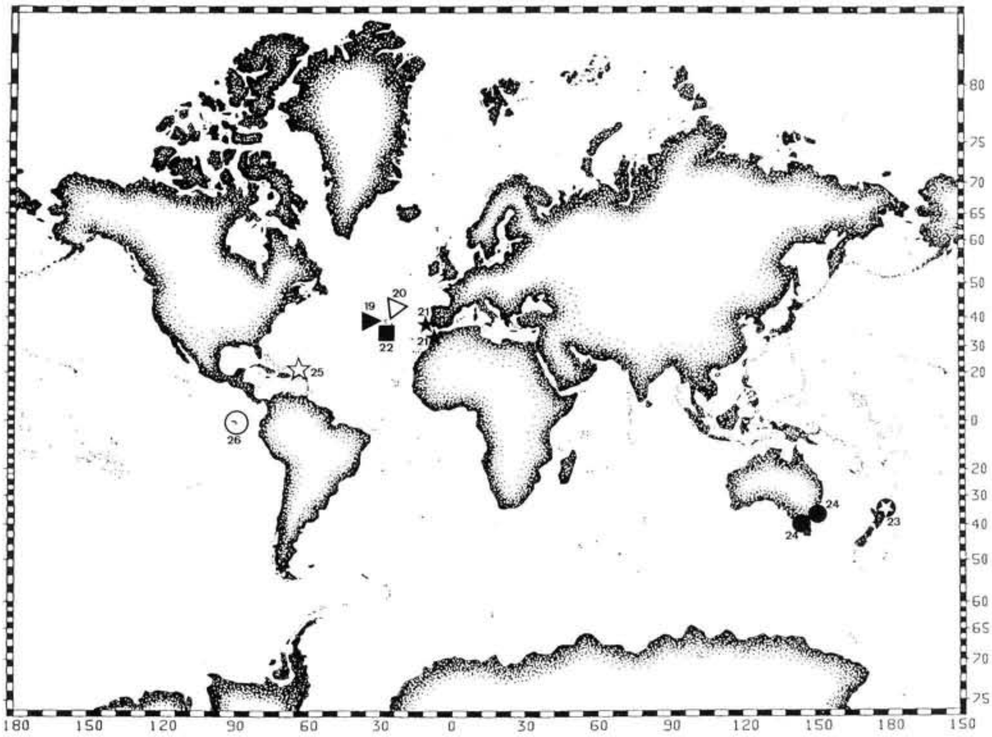

FIG. 15. — Distributions of *Rhabderemia fascicularis* (19), *R. guernei* (20), *R. intexta* (21), *R. mutans* (22), *R. coralloides* (23), *R. mammillata* (24), *R. (Stylospira) mona* (25), and *R. (Stylospira) destituta* (26).

Etymology: The name refers to the destitute spiculation.

Distribution (Fig. 15) and ecology: Known only from the type locality in the Galapagos Islands, shallow water.

Remarks: This is a second species answering to DE LAUBENFELS's (1934) genus *Stylospira*. It is quite probably a sister species of *Rhabderemia* (*Stylospira*) *mona*. Differences are the color (orange vs. white) and the spicule length, which is distinctly greater in *R. mona*. The new species is the only member of *Rhabderemia* known from the eastern Pacific.

PHYLOGENETIC ANALYSIS

HOOPER (1990) conducted a preliminary phylogenetic analysis on the basis of morphological characters using the computer program PAUP (SWOFFORD, 1985). In view of the considerable additions presented above, including *Stylospira* adopted as a likely *Rhabderemia* group, this analysis has been redone. Also, a new character has been introduced in the present study. That is, in contrast to Hooper, we distinguished contorted small sigmata from thraustosigmata, and this made it necessary to renew the discussion of character state transformations in this group. HOOPER (1990) used the Raspailiid genera *Aulospongus* and *Hemectyonilla* as outgroups. Here we expand the outgroup to include the Raspailiidae as a whole, thus avoiding the possibility that character polarization may have been biased by the peculiarities of particular genera within this outgroup.

The procedure adopted below is to examine each character and its states in both the ingroup and the outgroup. Where possible, hypotheses about the transformation of ancestral (outgroup) states into the various ingroup states are put forth with each character. Characters were not weighted, neither aprioristically nor subsequently, on account of the lack of criteria for relative weights of unrelated characters. However, for those characters that seemed clear synapomorphies, the "irreversibility" option of PAUP was chosen. In the case of a few characters, the "Dollo-option" of PAUP (loss of characters [-states] treated as being easier to achieve than new independent character states) was used to account for the absence of these characters or reversal of character states in species thought to be closely related. Ancestral characters (-states) are scored as "a" in the character matrix. In all cases in which the characters

(-states) were unknown, whether through the lack of information (e.g., in species known only from preserved material) or through the absence of the structures concerned (e.g., characters of microscleres that are not present in certain species), this was scored as "?" in the character matrix.

List of Characters and Their Distribution over the Various Species of *Rhabderemia*

Characters are illustrated in Figs 16-44.

1. Habit: Outgroup habits include a range of forms, but elaborate ramose forms are characteristic for many taxa. It is assumed here that massive or branching forms are not a synapomorphy (1a) for *Rhabderemia*, but thinly encrusting (1b) forms may possibly be considered a homoplasic synapomorphy for the groups *R. minutula-R. africana-R. prolifera-R. bistylifera-R. gallica-R. burtoni-R. toxigera-R. spinosa-R. profunda* and for *R. fascicularis-R. guernei* with a homoplasic apomorphy in *R. intexta*.

2. Substrate: In connection with the above, it is likely that within the *R. minutula* group mentioned above, the insinuating habit, occupying holes in the substrate, is probably a further synapomorphy (2b) for the group *R. minutula-R. africana-R. prolifera*, which forces us to assume a loss of this particular character in *R. bistylifera*. State 2a may then be defined as epibenthic.

3. Consistency: Most Raspailiidae are rather firm, often because of axial and other skeletal reinforcements. In fact, such organization is found in some *Rhabderemia*, too. Thus, it is assumed that a firm consistency is ancestral (3a), and that soft *Rhabderemia* (3b) are related (all species excepting *R. mona, R. destituta, R. mammillata, R. coralloides, R. mutans, R. fascicularis, R. antarctica, R. stellata* and *R. forcipula*). For some species, the consistency is unknown. If *Eurypon* and allied encrusting genera were to be included in Raspailiidae, the synapomorphic nature of this character would be compromised and a parallel development would have to be assumed.

4. Oscules: In many *Rhabderemia* species (*R. intexta-R. coralloides-R. stellata-R. forcipula-R. sorokinae-R. topsenti-R. mutans-R. mammillata-R. destituta*), the oscules are surrounded by a superficial stellate groove pattern caused by the canals leading the exhalant currents to them. This pattern is imprinted in the superficial skeleton. Such a pattern is recognized in many Raspailiidae (and also in Axinellidae and many Poecilosclerida). It is assumed here this stellate pattern is ancestral (4a), whereas the absence of it (4b) is a synapomorphy for *R. minutula, R. africana, R. prolifera, R. bistylifera, R. spinosa, R. acanthostyla, R. spirophora*, and *R. indica*. Because the life characteristics of many species are unknown, it is impossible to determine whether this character is present.

5. Ectosome: The ectosome is not reinforced by a special ectosomal skeleton in *Rhabderemia*, in contrast to the characteristic skeleton of many Raspailiidae, which has a single larger style, surrounded by a bouquet of smaller ectosomal spicules. The ectosomal membrane contains a large number of microscleres, but it is carried by the choanosomal skeleton. In many *Rhabderemia*, this support is produced by a bouquet of rhabdostyles, which is the nearest thing to the Raspailiid ectosomal arrangement and thus is considered the plesiomorphic condition (5a). In many thinly encrusting forms (*R. spinosa-R. africana-R. burtoni-R. minutula-R. prolifera-R. gallica*), the ectosomal support consists of single rhabdostyles (5b). In some, the skeletal arrangement is unclear.

6. Choanosome: The choanosomal skeletal arrangement in Raspailiidae is typically plumoreticulate: main tracts of several spicules in cross section are connected by single spicules standing at acute angles. This same arrangement (6a) is found in many *Rhabderemia* species; in others (*R. spinosa-R. africana-R. minutula-R. burtoni-R. prolifera-R. gallica*), the skeleton consists of single spicules (6b) or confused masses of spicules (*R. mona* and *R. destituta*) (6c). In some, the arrangement is unknown.

7. Megascleres: in *Rhabderemia*, these differ from most Raspailiidae styles (7a) in being rhabdostyles (7b). The megascleres in the genus *Hemectyonilla* superficially resemble those of *Rhabderemia*, but so do those of unrelated *Biemna rhabderemioides* Bergquist, 1961, or *Biemna rhabdostyla* Uriz, 1988. Such megascleres are also known in *Halicnemia* (?Desmoxyidae) (unpublished data of R. W. M. van Soest). In all these cases, it is assumed that they represent homoplasic developments that do not point to phylogenetic relationships. This is justified by the observation that most *Rhabderemia rhabdostyles* have a spiral twist in the rhabdose end; where this is obscured, it is assumed to have been present originally. The peculiar rhabdostyles are an autapomorphy for the genus.

8. Spination on megascleres: Raspailiid structural megascleres are mostly smooth, some are spined, while the auxiliary megascleres are echinating acanthostyles. Are the rhabdostyles of *Rhabderemia* homologous to the main Raspailiid megascleres or to the auxiliary megascleres? And if the first possibility is correct, has the nearest Raspailiid a spined mega-

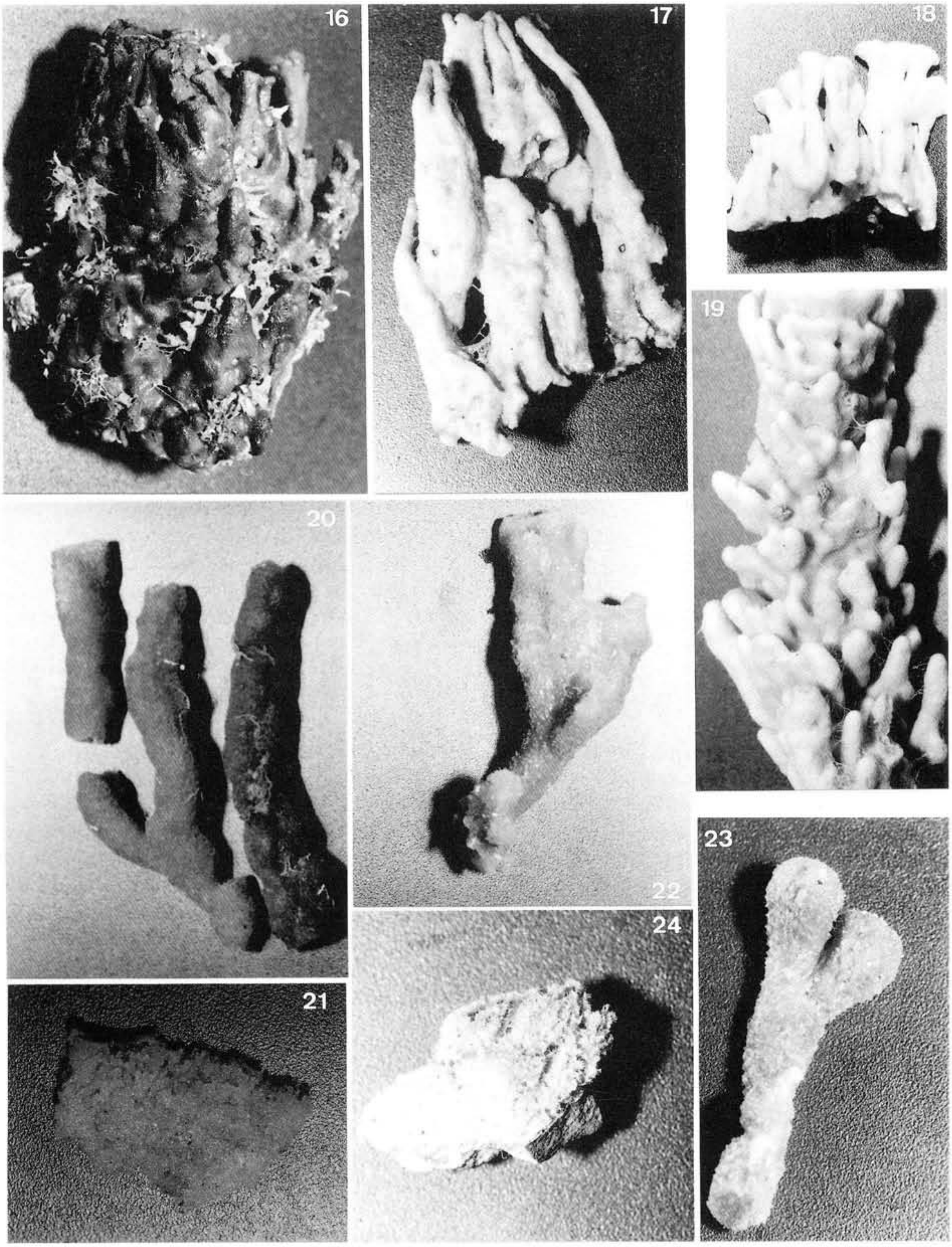

FIG. 16-24. — Growth forms of some *Rhabderemia* species. 16-19. *R. acanthostyla*, various growth forms found in the same species. 16. encrusting specimen from Sumbawa, Indonesia, ZMA POR. 6524. 17. erect specimen from Sulawesi, Indonesia, ZMA POR. 9620. 18. mushroomlike specimen from Saleyer, Indonesia, ZMA POR. 1926. 19. columnlike specimen from Nha Trang, Vietnam, MNHN DCl. 1560. 20 — *R. sorokinae*, fragments of branching specimen from Papua New Guinea, ZMA POR. 9757. 21. *R. antarctica* n.sp., fragment of branch of type specimen, BMNH 1926:10:26:92. 22-23 — *R. forcipula*, fragments of branching paratypes MNHN DCl. 3243. 24 — *R. destituta* n.sp., encrusting holotype, USNM 43065.

sclere? Here it is assumed that the "main megasclere" option is the most likely, in view of the presence of the spined microstyles in most *Rhabderemia*, which are possibly reduced auxiliary megascleres (they are not echinating and hence the homology is obscure). Tentatively, however, some form of spination of the rhabdostyle is considered derived, even though it is sometimes vestigial, while the smooth condition (8a) is considered primitive (it is found in *R. mona* and *R. destituta*). The other (true) *Rhabderemia* species are assumed to have, or to have originally had, some spines (8b) on the rhabdostyles. In this group, however, entirely smooth rhabdostyles are found in *R. africana*, *R. indica*, *R. spirophora*, *R. bistylifera*, *R. prolifera*, *R. stellata*, and *R. gallica*. Possibly, in view of the occurrence of the spined and the smooth condition in different specimens of the same species (e.g., in *R. mammillata* and *R. minutula*), the spined condition has been suppressed in some species that are related to other species with spined rhabdostyles, thus forming independent secondary smooth homoplasies (8c). The group *R. minutula-R. prolifera-R. africana-R. bistylifera-R. gallica-R. burtoni* has two size categories of rhabdostyles (cf. character 9 below), both of which may be smooth (8d), or one or both categories may have reverted back to the spined condition (scored as reversal 8b). A group of *Rhabderemia* species are characterized by heavily spined rhabdostyles, often with big recurved spines; although the distinction "lightly" vs. "heavily" spined is relative and subjective, this group nevertheless seems monophyletic, and this condition is considered a further synapomorphy (8e) for *R. coralloides*, *R. mutans*, *R. fascicularis*, and *R. antarctica*.

9. Length of megascleres: Rhabdostyles in the group vary greatly in size: from 60 to 575 μm long and 2 to 34 μm thick. A large group can be subdivided into larger and smaller rhabdostyles, although the distinction is seldom absolute. Where this subdivision is clear, this has been noted in the species descripions and in some cases has served as a means to distinguish closely similar forms. Presumably the occurrence of more than one category of megascleres is a derived feature (9b), not (widely) observed in the outgroup (9a). It is found in *R. minutula*, *R. africana*, *R. prolifera*, *R. bistylifera*, *R. spinosa*, *R. toxigera*, *R. burtoni*, *R. acanthostyla*, and *R. uruguaiensis*. This character is treated as "Dollo" because of the absence of the derived state in species otherwise closely similar to ones possessing this state.

10. Width of megascleres: With respect to the larger rhabdostyles, it is possible to recognize a group of *Rhabderemia* species with unusually thick shafts of 20-30 μm (10b), namely, *R. coralloides*, *R. mutans*, *R. fascicularis*, *R. stellata*, *R. antarctica*, *R. forcipula*, *R. sorokinae*, *R. mona*, and *R. destituta*. Outgroup condition varies, so this synapomorphy is based entirely on ingroup analysis. Thickness up to 20 μm is considered plesiomorphic (10a). We have to assume a reversed development from over 20 μm to thinner forms again (10c) in the pair *R. intexta-R. mammillata*. Again, the "Dollo" treatment is considered appropriate here because of this reversal of character state.

11. Presence of microstyles: This is considered a synapomorphy (11b) for most *Rhabderemia* species, except *R. mona* and *R. destituta* (11a). The absence of microstyles in *R. fascicularis*, *R. intexta*, and *R. mammillata* is interpreted as a secondary loss (11c) in view of the similarities shared between these species and related species possessing microstyles. The rugose microstyles are possibly homologous to the echinating acanthostyles in Raspailiidae, but then they have evolved to such an extent that their condition is easily accepted as derived. An outside possibility has to be kept in mind: that the microstyles are homologous to *Biemna* commata (family Desmacellidae), which are likewise rugose and often have an apical tyle such as is found in many *Rhabderemia* microstyles. The small, wispy microstyles of *R. acanthostyla*, in particular, make this possibility a serious one. This hypothesis can be questioned, however, on the grounds that microstyles in *Rhabderemia* are on the average tens of times larger than the tiny commata. A further, even more remote possibility is that the microstyles are homologous to the rugose tylostyles of certain *Cladorhiza* and *Chondrocladia* (family Cladorhizidae); however, these are much larger (up to 400 μm) than the *Rhabderemia* microstyles.

12. Length of microstyles: The microstyles occur in a large size range (20-170 by 0.2-4 μm). In view of the absence in the outgroup, it is difficult to determine which size is ancestral. The majority of the species are 40-100 μm long (state 12a), a few have larger ones. Among the latter it is possible to recognize a group of two *Rhabderemia* species sharing a larger and a smaller category of microstyles, and this is considered a synapomorphy (12b) for *R. africana* and *R. bistylifera*.

13. Width of microstyles: The thickness of the microstyles also makes it possible to recognize a group sharing relatively short and thick ones (averaging 50 by >1.5 μm) (13b), namely, *R. stellata*, *R. coralloides*, *R. mutans*, and *R. guernei*. Doubtful cases are *R. profunda*, *R. sorokinae*, *R. forcipula*, and *R. africana*, which have microstyles in the required range of thickness, but these are longer and thus relatively

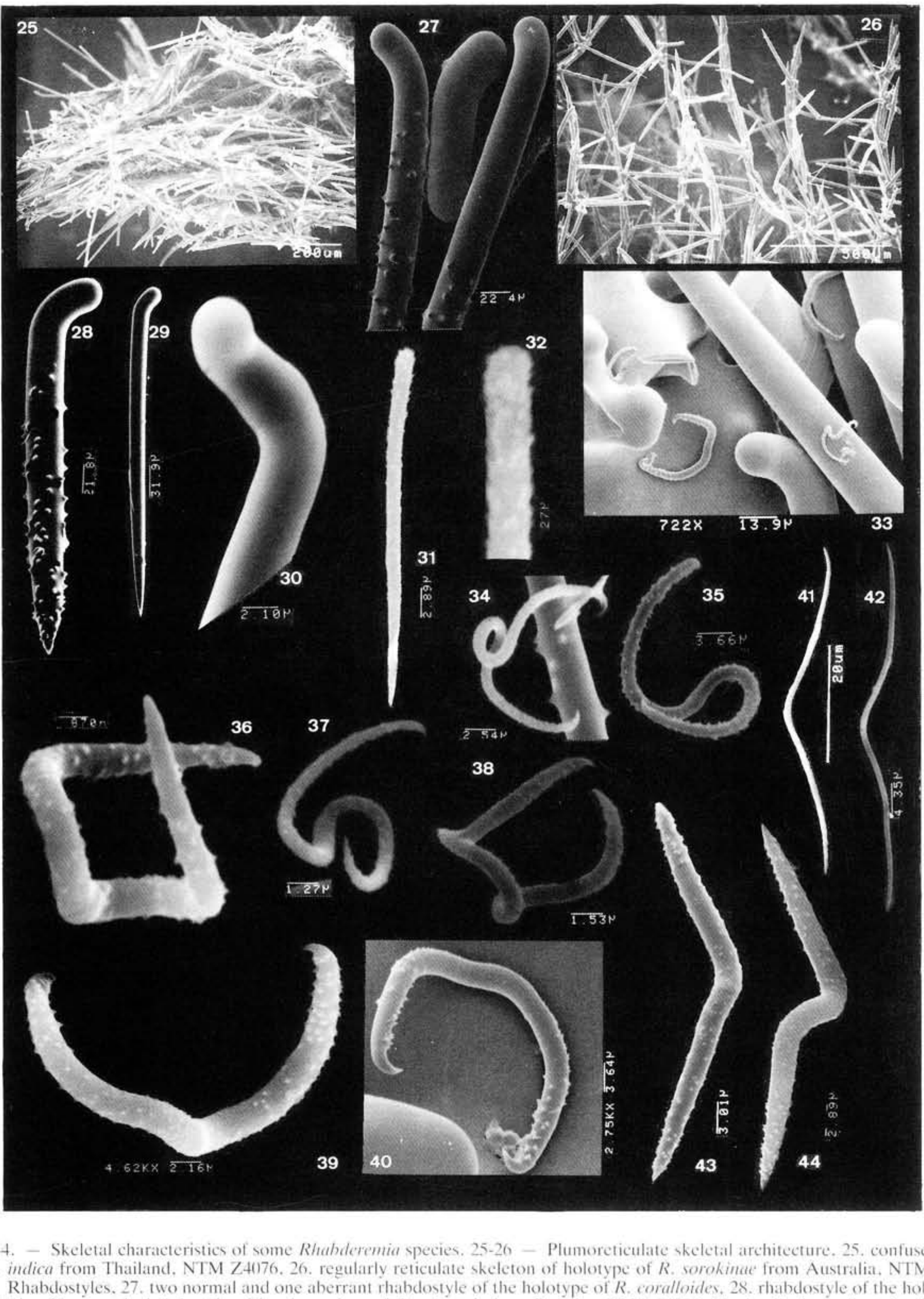

FIG. 25-44. — Skeletal characteristics of some *Rhabderemia* species. 25-26 — Plumoreticulate skeletal architecture. 25. confused skeleton of *R. indica* from Thailand, NTM Z4076. 26. regularly reticulate skeleton of holotype of *R. sorokinae* from Australia, NTM Z3585. 27-30 — Rhabdostyles. 27. two normal and one aberrant rhabdostyle of the holotype of *R. coralloides*, 28. rhabdostyle of the holotype of *R. coralloides*, 29. smooth rhabdostyle with a few spines of *R. minutula* from Bonaire, ZMA 10055, 30. detail of spirally twisted head of rhabdostyle of Bonaire *R. minutula*. 31-32 — Microstyles. 31. Microstyle of holotype of *R. coralloides*, 32. detail of head of microstyle of *R. sorokinae* from Papua New Guinea, ZMA POR. 9757. 33-34 — Sigmoid microscleres, 33. contorted small sigma and thraustosigmata of paratype of *R. forcipula*, MNHN DCL 3243, viewed together to show size difference. 34-38, various forms of contorted small sigmata. 34. *R. acanthostyla*, larger category, from ZMA POR. 1926. 35. *R. forcipula*. 36. *R. coralloides*. 37. *R. acanthostyla* smaller category (note that scale bar is half that of fig. 34), 38. *R. coralloides*; 39-40, thraustosigmata. 39. *R. coralloides*, 40. *R. forcipula*. 41-24. Toxa. 41. from the holotype of *R. sorokinae*, slightly rugose. 42. from Papuan specimen of *R. sorokinae*, almost smooth. 43-44 — thraustoxea, two forms from the holotype of *R. coralloides*.

slim. The thinner microstyles are considered to be plesiomorphic (13a).

14. Ornamentation of microstyles: In two species, *R. minutula* and *R. prolifera*, the microstyles are distinctly swollen near the apex, and this condition is considered evidence of relatedness (14b). Gradually tapering microstyles are considered plesiomorphic (14a).

15. Spirosigmata: The rugose or spined sigmata are here divided in three independent categories, the contorted small sigmata (spirosigmata), which tend to be uniform in size (one exception: *R. acanthostyla*, which has two distinct size categories), and the larger irregular sigmata, here dubbed thraustosigmata (cf. below), of which there seem to be two categories. The presence of contorted small sigmata is considered a synapomorphy (15b) for all *Rhabderemia* except *R. mona*, *R. destituta*, *R. gallica*, and *R. burtoni* (15a), although the possibility of loss in the latter two species cannot be excluded. The homology of these contorted rugose sigmata with smooth regularly shaped sigmata in other Poecilosclerid groups remains to be demonstrated. Raspailiidae do not possesses sigmata, nor other sigmiform microscleres such as chelae or toxa. Even if the spirosigmata are homologous with true sigmata, the condition found in *Rhabderemia* is unique and constitutes an undoubted synapomorphy.

16. Large thraustosigmata: The presence of the larger, true thraustosigmata is likewise considered a synapomorphy (16b) for species possessing them (*R. coralloides*, *R. forcipula*, *R. intexta*, *R. mammillata*), although here the question of homology with true sigmata is even more pressing. In those cases where they have been examined by scanning electron microscope, they were found to possess some spines, less densely distributed than in the spirosigmas, but coupled with their irregular, angular, and crooked shape, their condition is certainly apomorphic. Absence is plesiomorphic (16a).

17. Small thraustosigmata: The thraustosigmata of *R. gallica* and *R. burtoni* are distinctly smaller than those in the other species, and this constitutes a dubious synapomorphy (17b) for the two (absence is plesiomorphic: 17a). Possibly, the thraustosigmata are devoluted contorted sigmata, but in the absence of true contorted sigmata in the two this remains academic.

18. Toxa: The toxa found in three species (in one, the presence is dubious) of *Rhabderemia* are microspined, like the sigmata and the microstyles, and resemble both these spicule categories. Many toxa are

TABLE 2. — Taxon-character matrix for the cladistic analysis of *Rhabderemia*. Characters/-states are explained and discussed in the text.

Character Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Raspailiidae	a	a	a	a	a	a	a	a	a	?	a	?	?	?	a	a	a	a	a	a
minutula	b	b	b	b	b	b	b	b	b	a	b	a	a	b	b	a	a	a	a	a
africana	b	b	b	b	b	b	b	b	b	a	b	b	?	a	b	a	a	a	a	a
prolifera	b	b	b	b	b	b	b	b	b	a	b	a	a	b	b	a	a	a	a	a
bistylifera	b	a	b	b	?	?	a	d	b	a	b	b	a	a	b	a	a	a	a	a
gallica	b	a	?	?	b	b	b	d	a	a	b	a	a	a	?	a	b	a	a	a
burtoni	b	a	?	?	b	b	b	b	b	a	b	a	a	a	?	a	b	a	a	a
spinosa	b	a	b	b	b	b	b	b	b	a	b	a	a	a	b	a	a	b	a	a
toxigera	b	a	b	?	?	?	b	b	b	a	b	a	a	a	b	a	a	b	a	a
profunda	b	a	?	?	?	?	b	b	a	a	b	a	?	a	b	a	a	a	a	a
acanthostyla	a	a	b	b	a	a	b	b	b	a	b	a	a	a	b	a	a	a	a	b
uruguaiensis	a	a	?	?	a	a	b	b	b	a	b	a	a	a	b	a	a	a	a	b
spirophora	a	a	b	b	a	a	b	a	a	a	b	a	a	a	b	a	a	a	a	a
indica	a	a	b	b	a	a	b	c	a	a	b	a	a	a	b	a	a	a	a	a
topsenti	a	a	b	a	a	a	b	b	a	a	b	a	a	a	b	a	a	a	a	a
sorokinae	a	a	b	a	a	a	b	b	a	a	b	a	?	a	b	a	a	b	a	a
antarctica	a	a	a	?	a	a	b	c	a	b	b	a	a	a	b	a	a	a	a	a
stellata	a	a	a	a	a	a	b	c	a	b	b	a	b	a	b	a	a	a	a	a
forcipula	a	a	a	a	a	a	b	b	a	b	b	a	?	a	b	b	a	a	a	a
fascicularis	b	a	a	?	a	a	b	c	a	b	c	?	?	?	b	a	a	a	b	a
intexta	b	a	?	a	a	a	b	b	a	c	c	?	?	?	b	b	a	a	a	a
guernei	b	a	?	?	a	a	b	b	a	c	b	a	b	a	b	a	a	a	b	a
mutans	a	a	a	a	a	a	b	c	a	b	b	a	b	a	b	a	a	a	b	a
coralloides	a	a	a	a	a	a	b	c	a	b	b	a	b	a	b	a	b	a	b	a
mammillata	a	a	a	a	a	a	b	b	a	c	c	?	?	?	b	b	a	a	a	a
mona	a	a	a	?	a	c	b	a	a	b	a	?	?	?	a	a	a	a	a	a
destituta	a	a	a	a	a	c	b	a	a	b	a	?	?	?	a	a	a	a	a	a

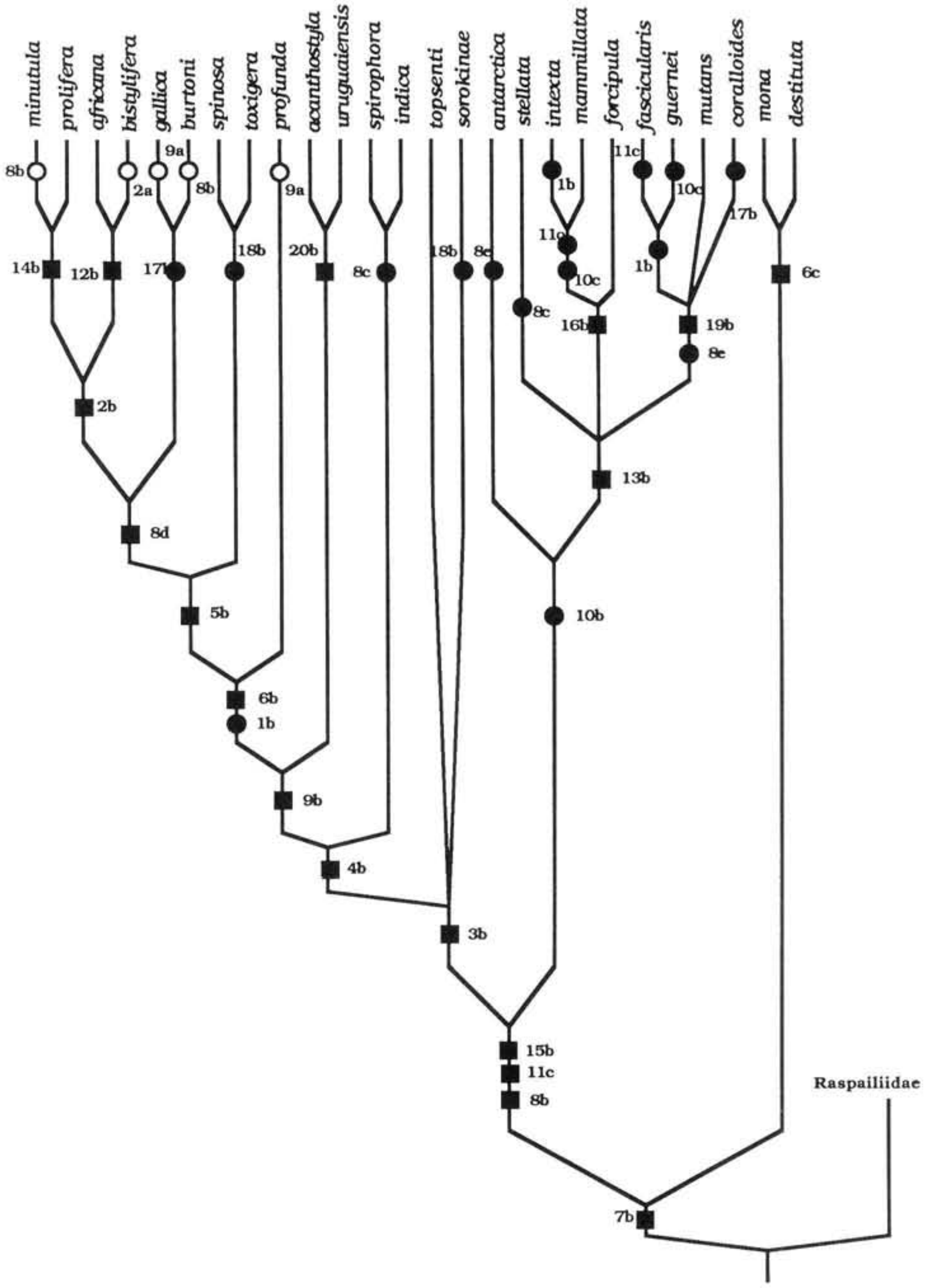

FIG. 45. — Phylogenetic relationships of recognized members of the genus *Rhabderemia* based on cladistic analysis of the character matrix of Table 2. Numbers refer to characters and character states listed in Table 2 and discussed in the text. Black squares represent synapomorphies, black dots are homoplasic (syn)apomorphies, and open circles are reversed character states.

irregular or asymmetrical, and therefore the presence is considered apomorphous (18b) for the three species concerned: *R. toxigera*, *R. spinosa*, and *R. sorokinae*. Because of conflicting character distributions for only two of these (*R. toxigera* and *R. spinosa*), they can be considered a synapomorphy, with a homoplasic autapomorphy in *R. sorokinae*. Again, it is possible that some species have secondarily lost their toxa, in which case they could be considered an underlying synapomorphy for a larger group, including the three species mentioned. In this analysis, however, absence is treated as plesiomorphic (18a).

19. Thraustoxea: The possession of thraustoxea is a unique feature of (some) *Rhabderemia*. They resemble the thraustosigmata to some extent, particularly in *R. coralloides*, but also the microstyles, par-

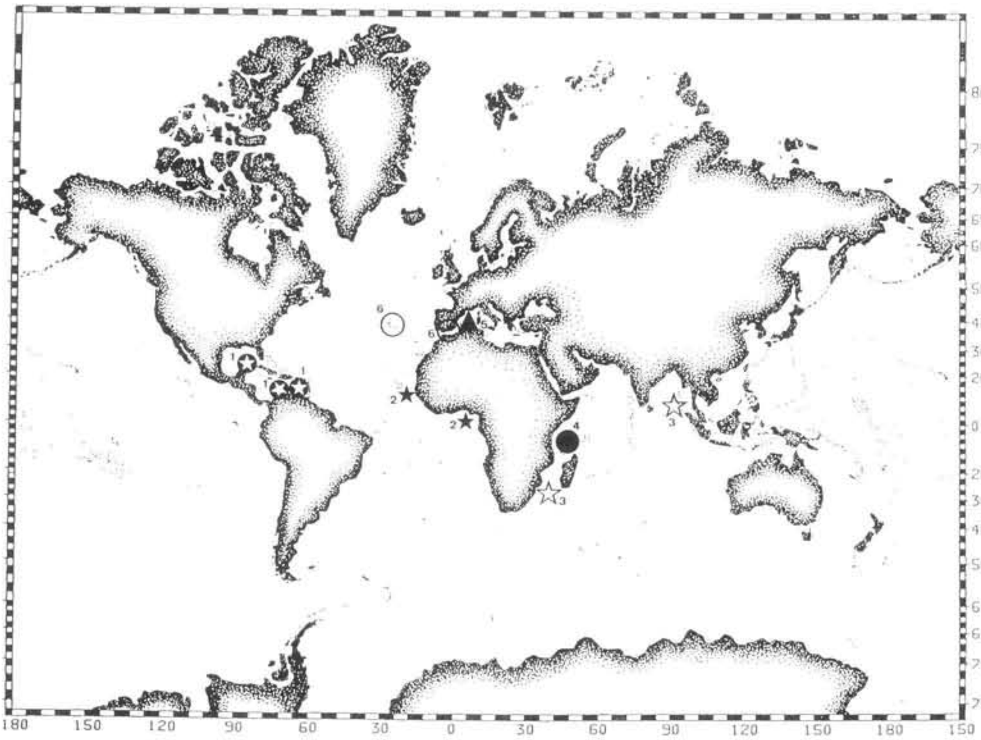

FIG. 46. — The geographic distribution of *Rhabderemia* based on the combined records of all recognized species.

ticularly in *R. mutans*. Possibly they are not all homologous, but this will be difficult to prove, so we decided to consider them all alike here. They are found (19b) in *R. coralloides*, *R. mutans*, *R. guernei*, and *R. fascicularis*. Absence is plesiomorphic (19a).

20. Pigment granules: Two species were found to share a particular concentration of pigment granules in the subectosomal region, and this is considered a synapomorphy (20b) for the two: *R. acanthostyla* and *R. uruguaiensis*. Absence is plesiomorphic.

The character states are scored against the species in the matrix of Table 2. Character analysis using PAUP 3.0 (MacIntosh version) yielded over 100 equally parsimonious trees of 40 steps each (unweighted, characters 1, 6, 8, 12, 17 were treated unordered; characters 9 and 10 were treated as "Dollo"; characters 2, 3, 4, 5, 7, 11, 13, 14, 15, 16, 17, 18, 19, and 20 were treated as irreversible). Consensus trees (strict, semistrict, Adams, and 50% majority) all yielded polytomies to such an extent that trees were rendered of limited value as a hypothesis of the evolutionary development within *Rhabderemia*. Subsequent assignment of potential synapomorphies to groups within the polytomies (using MACCLADE option) yielded a 40-steps tree with only two trichotomies, and with a Consistency Index of 0.65. This tree (Fig. 45) is considered the best estimate of the phylogenetic relationships within *Rhabderemia*.

The tree differs considerably from HOOPER's (1990) earlier attempt, but in view of the large number of newly recognized taxa included here and the more extensive observations of type material and ultrastructure of the microscleres, it is not useful to make a close comparison between the two trees.

BIOGEOGRAPHY

The distribution of the genus as a whole (Fig. 46) shows it to be widespread but relatively rare (of the 26 species recognized, 13 are known only from single records). The genus is remarkable for occurring in tropical shallow waters, Antarctic waters, and the deeper-slope waters. Perhaps for that reason, it is slightly more diverse than the marine sponge genus *Acarnus* (21 species), which shows the same geographic distribution, except that it does not occur in Antarctica (VAN SOEST *et al.*, 1991).

Rhabdostyles of a type found in *Rhabderemia* are known at least from the Oligocene (HINDE and HOLMES, 1891) onward. The geographic position of these remains (New Zealand), in combination with

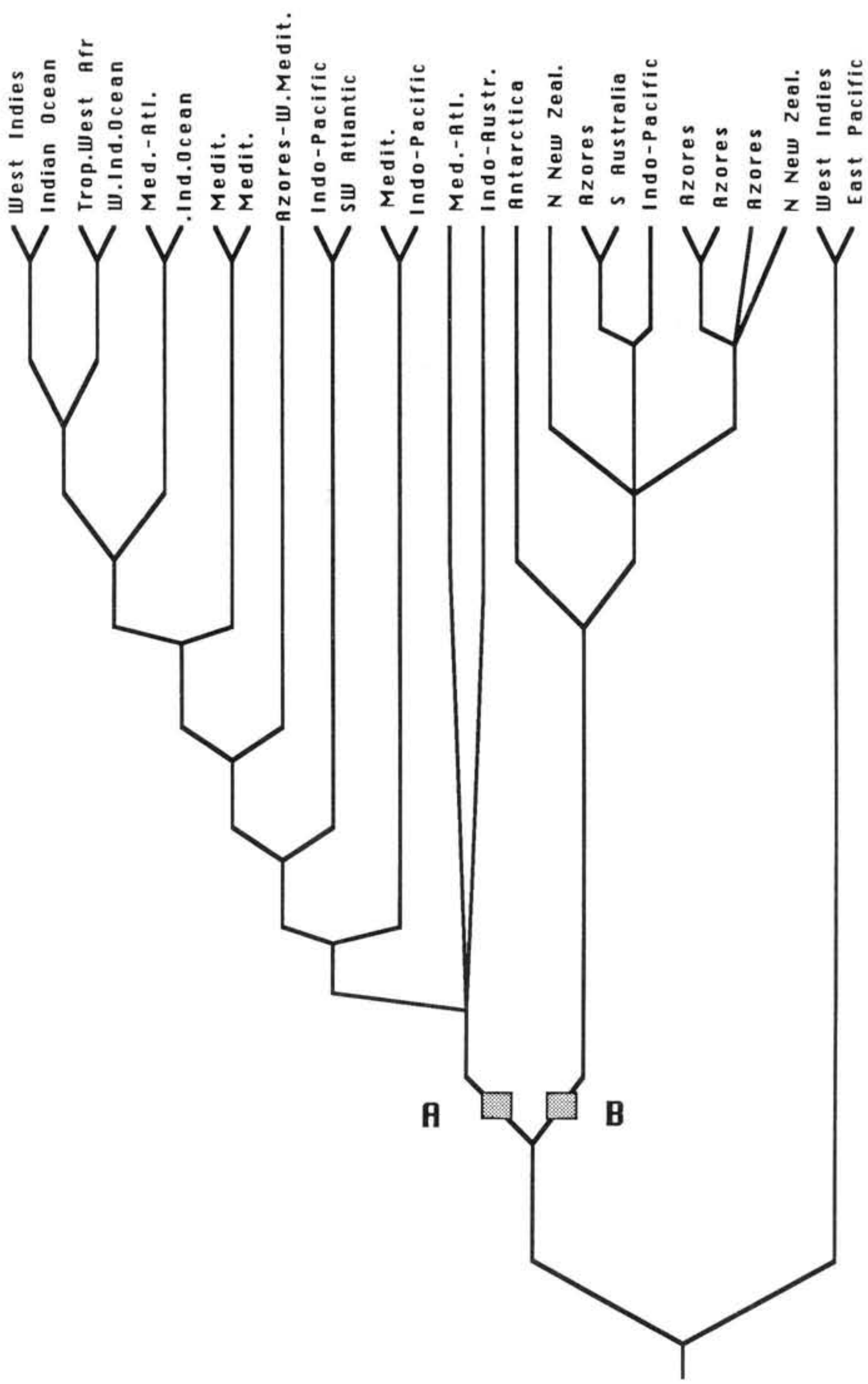

FIG. 47. — Areagram of the genus *Rhabderemia* made by inducing the distributions of the species into the cladogram of Fig. 45.

the recent distribution, strongly suggest that the genus was already widespread in the Early Tertiary.

In accordance with recent advances made in biogeographic methodology (HUMPHRIES and PARENTI, 1986; LADIGES *et al.*, 1991), the distributions (see Figs. 4, 8, 12, and 15) were introduced in the cladogram of Fig. 45 to arrive at a taxon-areacladogram (or areagram) (Fig. 47). This may be regarded as representing the subsequent geographic events that gave rise to the present diversity of *Rhabderemia* species from a past ancestor. Unfortunately, in the absence of a general areacladogram of marine areas, it is not possible to objectively separate the potential recent dispersal of individual species over large distances from passive geographic speciation or past extinctions. Thus, detailed hypotheses of evolutionary scenarios that have given rise to present-day diversity cannot be built on solid ground. Some trends, however, may be observed in the areacladogram of Fig. 47.

A rather distinct division was found between warm-subtropical areas and cold-water southern areas. At the diverging point A in Fig. 47, predominantly shallow-water distributions in tropical/subtropical areas are gathered, which when mapped form a circumtropical belt (West Indies-tropical West Africa-Mediterranean-western Indian Ocean-central Indian Ocean and Indo-West Pacific). The distribution of *R. uruguaiensis* in the southwestern Atlantic is adjacent to tropical waters and may also be considered part of this circumtropical warm-water belt. One distribution —namely, that of *R. profunda*— does not seem to fit in this belt. At diverging point B in Fig. 47, predominantly cold-water/deep-water distributions are gathered, which when mapped show concentrations in the mid-North Atlantic (Azores) and the South Pacific (Australia-New Zealand-Antarctica). The distribution of *R. forcipula* does not seem to fit in this group.

Possibly, as in *Acarnus* (see VAN SOEST *et al.*, 1991), this result again points to both a previous Tethyan distribution of marine shallow-water organisms, and a Gondwanan distribution of organisms more adapted to cold water, which in this case seems to include also deeper waters. Inexplicable results at present are the Azorean-southern Ocean relationships, represented by the group of *Rhabderemia* species with thraustoxeas, thraustosigmata, and heavily spined rhabdostyles. Particularly difficult to explain in accordance with the ruling paradigm of geographic speciation is the sympatric cluster of related species in deep water around the Azores (*R. mutans*, *R. guernei*, *R. fascicularis*, and *R. intexta*). It will be very difficult to devise scenarios for vicariant events resulting in this particular pattern of distribution and phylogenetic relatedness.

In view of several other strongly disjunct sister-relationships (West Indian *R. minutula*-Indian Ocean *R. prolifera*, Indian Ocean *R. acanthostyla*-Southwest Atlantic *R. uruguaiensis*, Azorean R. *intexta*-South Australian *R. mammillata* and Azorean *R. mutans*- and New Zealand *R. coralloides*), it seems likely that widespread extinctions have taken place in the history of the genus. Such disjunctions are also observed in *Acarnus*.

Other observed disjunctions are fairly easily explained by historical events: *R. mona* and *R. destituta* are separated by the Isthmus of Panama, which was an open passage as recently as 3 million years ago. Both are hypothesized to have differentiated after the closure of the isthmus. During the Miocene, an open connection between the Atlantic Ocean, Mediterranean, and the Indian Ocean was present, allowing a continuous distribution of the ancestors of *R. africana* and *R. bistylifera*, as well as *R. gallica* and *R. burtoni*. The meeting of the continents of Africa and Europe presumably severed these connections and allowed different species to evolve. *R. spirophora* and *R. indica* have adjacent distributions, which can easily be explained as the result of a relatively recent vicariant event involving the relative positions of Africa and South Asia.

DISCUSSION

It is tempting to try to combine the present results with those obtained with *Didiscus* (cf. HIEMSTRA and VAN SOEST, 1990) and *Acarnus* (cf. VAN SOEST *et al.*, 1991), to arrive at a general sponge areacladogram (for which methods are available: BPA [WILEY, 1988], CAFCA [ZANDEE and ROOS, 1987], and COMPONENT [PAGE, 1990]). However, there are still not enough data to expect a successful attempt in the marine shallow waters (compared, for example, with the attempts in terrestrial areas by CRISCI *et al.*, 1991, and OOSTERBROEK and ARNTZEN, 1992); furthermore, the results for marine areas are either uninformative or confusing. Several other marine areacladograms are available (DE WEERDT, 1987: Chalinid sponges; HOEKSEMA, 1989: mushroom corals; BLUM, 1989: Chaetodontid fishes; HOWES, 1990: Muraenolepid fishes; REID, 1990: Littorinid gastropods; MØLLER ANDERSEN, 1990: water striders), but often these concern either only northern marine areas (REID, 1990; GUIRY and GARBARY, 1990) or even more restricted areas (DE WEERDT, 1987; MØLLER ANDERSEN, 1991), and thus cannot be easily combined with the present circumtropical and southern areas. More areacladograms are currently being constructed, and these studies will no doubt eventually lead someone to attempt to arrive at a general areacladogram of marine areas of endemism.

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