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A reassessment of the phylogeny and biogeography of *Rhabderemia* Topsent, 1890 (Rhabderemiidae, Poecilosclerida, Demospongiae)

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A reassessment of the phylogeny and biogeography of *Rhabderemia* Topsent, 1890 (Rhabderemiidae, Poecilosclerida, Demospongiae). - *Rhabderemia uruguaiensis* van Soest & Hooper, 1993 is redescribed from a depth of 15m at Tempano Fjord (SE Pacific, Chile). Updated phylogenetic hypotheses are offered for *Rhabderemia*, based on two alternative macroevolutionary scenarios - outgroups Desmacellidae and Raspailiidae. The biogeographies implied from these phylogenies are discussed with a focus on those results shared by both phylogenies and a previously published one, as well as on the affinities derived from two recently described new species from the SW Atlantic, *R. besnardi* Oliveira & Hajdu, 2005 and *R. itajai* Oliveira & Hajdu, 2005. Special mention is made of trans-Pacific tracks inferred here and elsewhere in the sponge phylogenetic literature. These span the following four routes: 1) Caribbean - Australia, 2) south-eastern Pacific - Tropical West Pacific, 3) south-eastern Pacific - Easter Island, 4) New Zealand - Boreal Pacific.

Keywords: Porifera - *Rhabderemia* - marine sponges - fjords - taxonomy - phylogeny - biogeography - SE Pacific - *Stylospira* - trans-Pacific tracks.

INTRODUCTION

The SE Pacific bears one of the least studied sponge faunas in the world. Only about 140 species are known from the entire Chilean coast (Desqueyroux & Moyano, 1987), in spite of its 90'000 km of shoreline, stretching approximately 5000 km in a straight line (over 38 degrees of latitude), with an intricate system of islands, fjords and canals unmatched elsewhere on the planet. As part of an international effort to promote further knowledge on Chilean marine sponges, a systematic collecting plan was implemented under the auspices of Belgian, Brazilian, Chilean and Swiss institutions, which permitted visiting 18 localities since 2003 (distributed from 23 to 51°S), including 70 dives for sponge collections. Among the specimens collected several are new records of genera and/or families for the SE Pacific. The results presented here report on a new record for Chile, of *Rhabderemia (R.) uruguaiensis* van Soest & Hooper, 1993 collected at Tempano Fjord.

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In conjunction with two species recently described for the SW Atlantic, *R. besnardi* Oliveira & Hajdu, 2005 and *R. itajai* Oliveira & Hajdu, 2005, this new record povides the basis for reassessing van Soest & Hooper's (1993) proposed phylogeny and biogeography of *Rhabderemia*. An updated identification key is also provided.

MATERIAL AND METHODS

The single specimen studied was collected by scuba and photographed in situ, as part of a collection from Tempano Fjord and vicinity (ca. 48º S, Figure 1) by Günther Försterra and Verena Häusserman, and deposited at Museu Nacional (MNRJ - Brazil) and Muséum d'histoire naturelle, Geneva (MHNG - Switzerland). Any type material derived from the study of these samples will be deposited in Chile (IZUA/UACH - Instituto de Zoologia, Universidad Austral de Chile).

Dissociated spicule slides and thick section mounts were made according to usual procedures (Hooper, 1997), boiling fragments in nitric acid, and secondly both direct cutting of specimen followed by drying under a warm lamp, as well as paraffin immersion. A Digital Scanning Microscope (DSM-940) was used to capture images of spicules at the Invertebrates Department of the Muséum d'histoire naturelle, Geneva.

The cladistic analysis performed here was undertaken with PAUP* vs. 4.0b10 (Swofford, 2002). Characters were treated as unordered or under "Dollo" parsimony, and equally weighted. The use of exact parsimony algorithms was not possible due to the large size of the datamatrix. The minimization of restricted sampling within the archipelago of trees has been achieved through replication (1000x) of heuristic searches, followed by exhaustive branch-swapping on the trees kept in PAUP's memory buffer. Ten thousand heuristic replicates were occasionally also implemented but did not produce more parsimonious results. Further cropping of sets of equally parsimonious trees was sought by subsequently-weighting characters by their RCs, a strategy repeated until size of the set of most parsimonious trees stabilized (usually 2-3 repetitions), followed by filtering for more resolved, equally-parsimonious trees.

Abbreviations used throughout the text are MHNG – Muséum d'histoire naturelle, Geneva (Switzerland), MNRJ – Museu Nacional, Universidade Federal do Rio de Janeiro (Brazil).

RESULTS

Class Demospongiae Sollas, 1885
Order Poecilosclerida Topsent, 1928
Suborder Microcionina Hajdu, van Soest & Hooper, 1994
Family Rhabderemiidae Topsent, 1928

Genus ***Rhabderemia*** Topsent, 1890

DIAGNOSIS: Microcionina with rhabdostyles frequently bearing an extra basal spiral twist, in one or two size categories as the only megascleres. Microscleres, if present, include spirosigmas, micro(sub)(tylo)styles, thraustosigmas, thraustoxeas and toxas. Adapted from Hooper (2002).

REMARKS: The fact that rhabdostyles are neither exclusive of *Rhabderemia*, nor of the Microcionina or the Poecilosclerida, suggests that a reevaluation of the proposed

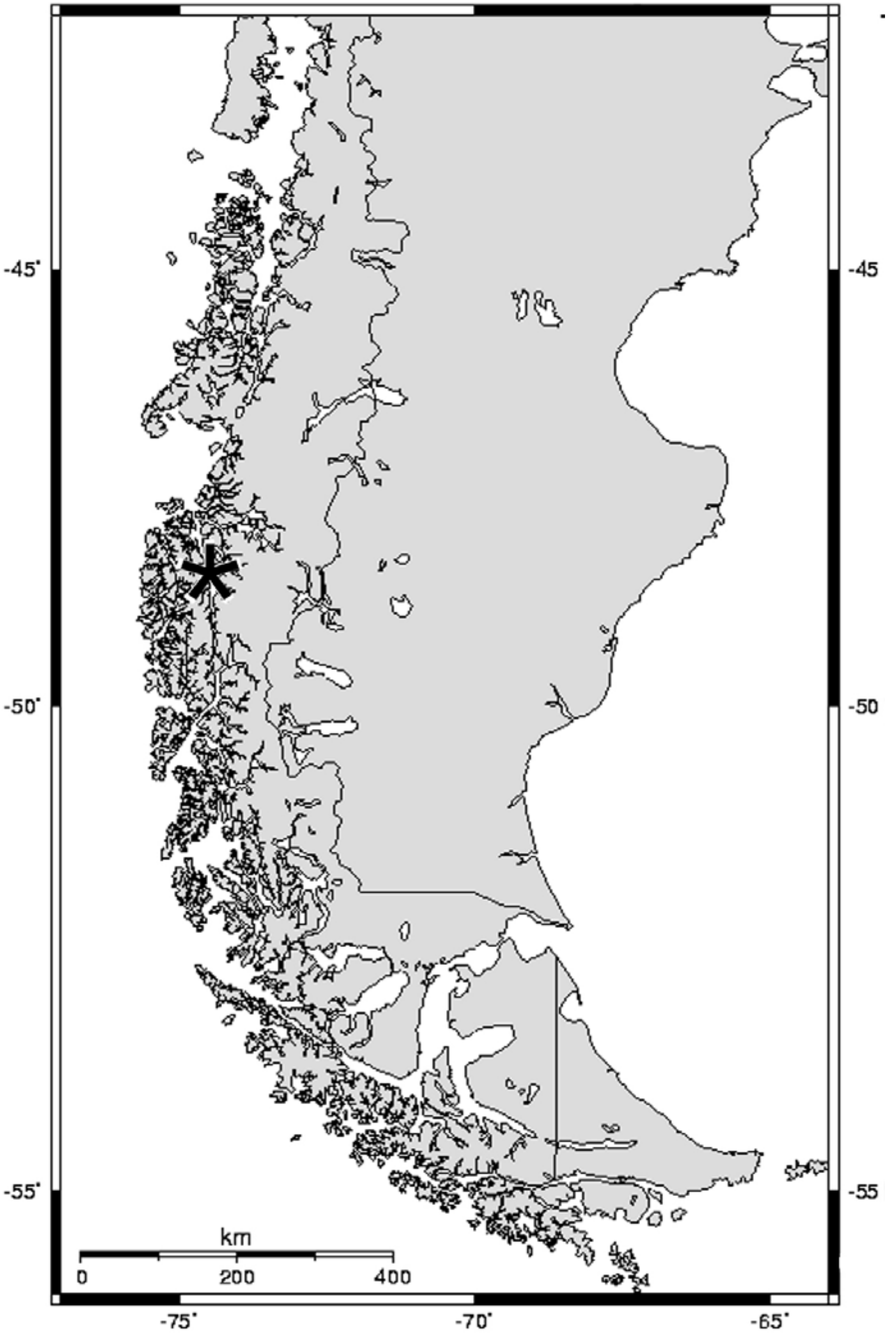

FIG. 1
Map of southern South America pointing the collecting station for *Rhabderemia uruguaiensis* van Soest & Hooper, 1993, at Fjord Tempano (Chile).

synonymy of *Stylospira* de Laubenfels, 1934 (sensu van Soest & Stentoft, 1988) is necessary. It is worthwhile noting that some *Rhabderemia* show a clear terminal twist, which is not found in raspailiids such as *Aulospongus* Norman, 1878 and *Raspailia (Raspaxilla)* (Topsent, 1913), nor in *Dragmaxia* Hallmann, 1916 (Halichondrida). For the present, van Soest & Hooper's (1993) suggestion of keeping *Stylospira* at subgeneric level, with the necessary consequence of assigning all *Rhabderemia* with microscleres to subgenus *Rhabderemia*, appears more appropriate and, accordingly, both are diagnosed below. The decision to keep both at subgeneric level considers that *Stylospira* spp. emerged as monophyletic on the phylogenetic analyses undertaken by van Soest & Hooper (1993) and here, as shown below. But, on the other hand, *Rhabderemia* s.s. may be monophyletic or paraphyletic according to the chosen outgroup, which claims for additional evidence prior to erecting both to full generic status.

Subgenus *Rhabderemia* Topsent, 1890:

Rhabderemia with rhabdostyles in one or two size categories as the only megascleres. These can be smooth or heavily spined. Microscleres always include spirosigmas and/or micro(sub)(tylo)styles. Additional microsclere categories may be present, viz. thraustosigmas, thraustoxeas and toxas. Type species: *Microciona pusilla* Carter, 1876 (by subsequent designation - Dendy, 1905: 180) (junior synonym of *Microciona minutula* Carter, 1876 - van Soest & Hooper, 1993: 323)

Subgenus *Stylospira* de Laubenfels, 1934:

Rhabderemia with a single category of entirely smooth rhabdostyles. No microscleres. Type species: *Stylospira mona* de Laubenfels, 1934: 10.

Rhabderemia (Rhabderemia) uruguaiensis van Soest & Hooper, 1993 Figs 2, 3A-I

MATERIAL STUDIED: MNRJ 9213: Tempano Fjord (48°41'30,3"S – 74°08'9,9"W, Chilean Patagonia), 15m depth, coll. G. Försterra & V. Häusserman, 25/iii/2005. A fragment is deposited under MHNG INVE37425.

REDESCRIPTION

A single specimen has been collected. It was relatively large (over 10x10 cm), a moderately thick cushion (ca. 5 mm), and of beige color, when alive (Fig. 2). Its surface was irregular, with flat roundish projections and a system of dermal grooves which does not appear to converge to oscula. The only fragment available for study is a 3-4 mm thick crust, 34 by 27 mm in area, which kept its original color slightly after preservation. It is soft and fragile, easily torn, and bears a velvety surface, in which no openings of the aquiferous system are visible.

Skeleton. Ectosomal skeletal architecture unspecialized, made up of paucispicular brushes of rhabdostyles (3-8 spicules) slightly piercing the surface (up to 115 μm). Choanosomal skeletal architecture plumose to plumo-reticulate, with rhabdostyles disposed in ascending bundles echinated by the same megascleres, and terminating in the ectosomal brushes. Rhabdostyles also occur strewn at random. Microscleres abound everywhere. Very dark pigment granules (10-30 μm across) can be seen in large numbers in a moderately aggregated distribution.

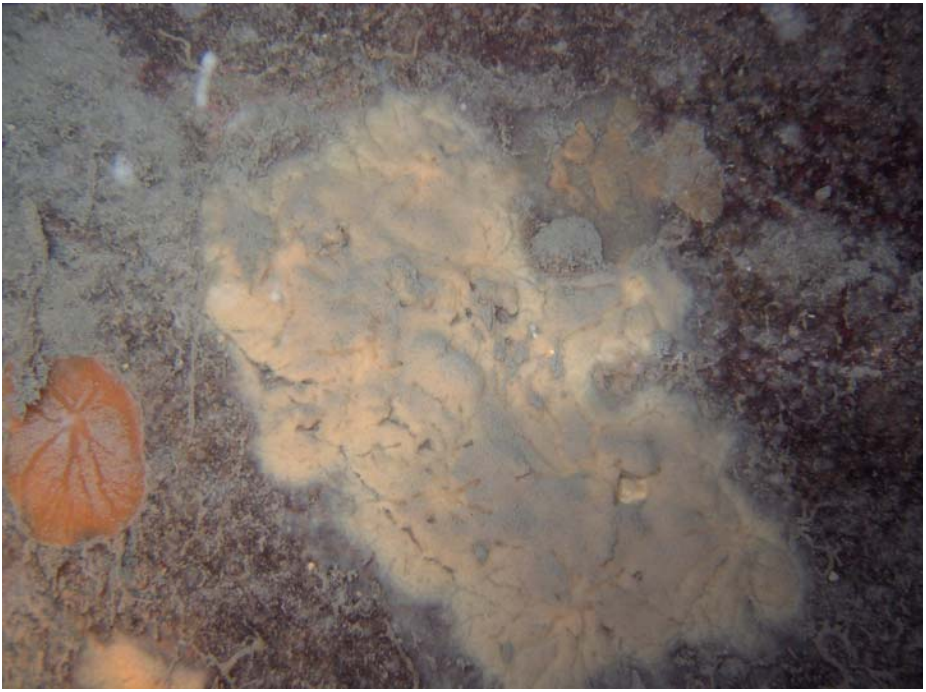

FIG. 2

Rhabderemia uruguaiensis van Soest & Hooper, 1993. Studied specimen photographed *in situ*. Photo by G. Försterra.

Spicules. Megascleres, rhabdostyles (Fig. 3A-D) in a single size category, mostly smooth, but a few vestigial spines are visible on the apical third under high magnifications (Fig. 3D); rhabd mostly bent close to the base, but bending at varied distances from the center is also seen; base styloid, smooth, more frequently bearing a single regular twist, but many variations in twisting occur amongst spicules examined; 74 – *240.5* – 336 μm long and 9.6 – *12* – 16 μm thick. Microscleres, microsubtylostyles (Fig. 3E-H), acanthose/rugose, gently bent in their basal third; 26-*39.7*-51μm long; spirosigmas (Fig. 3I), acanthose, considerably contorted, frequently with a conspicuous bend on both extremities, 5-*7.9*-10 μm long.

DISTRIBUTION AND ECOLOGY

The species was formerly known only from moderately deep waters off the SE Brazilian and Uruguayan coasts on the SW Atlantic (van Soest & Hooper 1993, Oliveira & Hajdu 2005). Its distribution is now extended to the shallow waters of the Temperate SE Pacific (Tempano Fjord, Chilean Patagonia). The species is most probably widespread in the whole Magellanic area, but given its apparent rarity, a confirmation of this supposition may still be years ahead. In support of our claim the similar Magellanic - SE Brazil distribution of *Hymenancora tenuissima* (Thiele, 1905) and *Raspailia (Raspaxilla) phakellina* (Topsent, 1913) (sensu Hajdu *et al.*, 2004) can

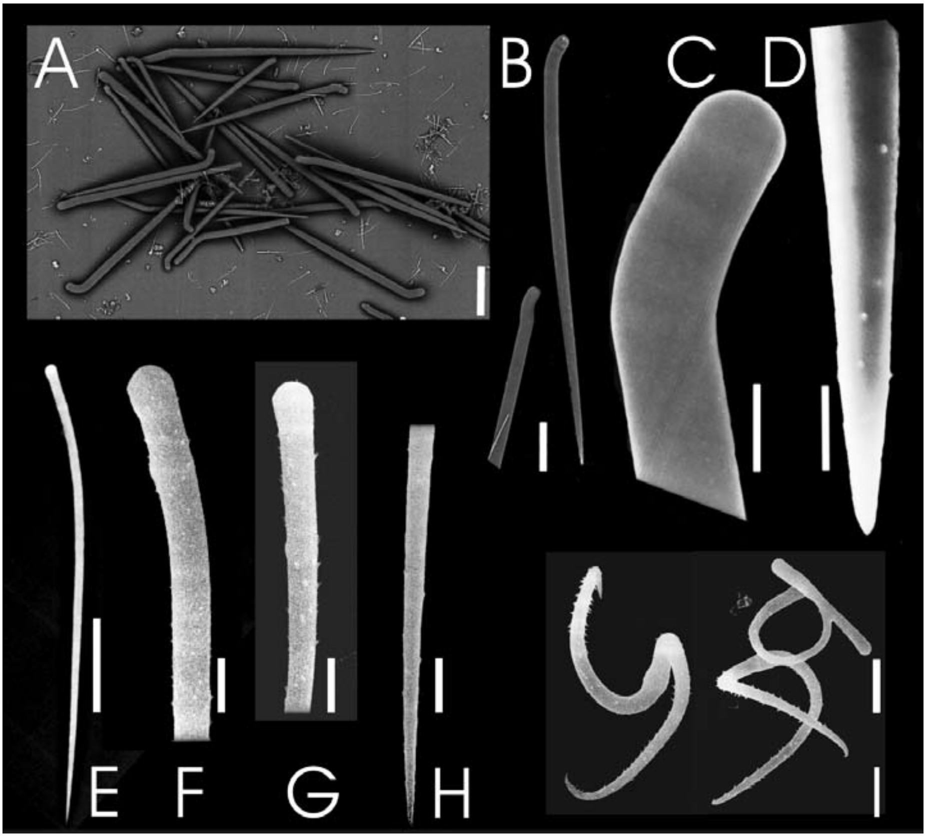

FIG. 3

Rhabderemia uruguaiensis van Soest & Hooper, 1993. Scanning electron micrographs of spicules. (A) Dissociated spicules with an overview of rhabdostyles and microstyles. (B-D) Rhabdostyles. (B) Whole spicule. (C) Detail of smooth rhabdose end (base). (D) Detail of slightly spined end (apex). (E-H) Microstyles. (E) Whole spicule. (F-G) Detail of slightly spined stylote end (base). (H) Detail of sharp, slightly spined end (apex). (I) Slightly centrotylote spirosigmata more heavily spined towards both ends. Scales: A, 100 μm; B, 50 μm; C-E, 10 μm; F-I, 2 μm.

be pointed out. Additional support stems from the historical link implied by the sister-species relationship found by Hajdu (1995) for *Mycale beatrizae* Hajdu & Desqueyroux-Faúndez, 1994 (SE Brazil) and *M. doellojuradoi* Burton, 1940 (NE Argentina and SW Chile).

REMARKS

The Chilean specimen matches perfectly the descriptions provided by van Soest & Hooper (1993) and Oliveira & Hajdu (2005). Noteworthy is the observation of dark microscopical pigment granules, which were not mentioned by Oliveira & Hajdu (2005), but were considered very distinctive by van Soest & Hooper (1993). A minor point of distinction appears to be the presence of microsubtylostyles in the Chilean specimen, as opposed to the microstyles found in Atlantic specimens.

IDENTIFICATION KEY FOR *RHABDEREMIA (RHABDEREMIA)* (expanded from van Soest & Hooper, 1993)

1a Microscleres include toxas or toxiform “raphides” 2
1b Microscleres are never toxas 4
2a Growth form encrusting 3
2b Growth form elaborate, lumpy lobate or ramose . . . . . *R. (R.) sorokinae*
3a Rhabdostyles largely smooth with only occasional spines, toxas are typical . . . . . *R. (R.) toxigera*
3b Rhabdostyles are acanthose, toxas are only a few toxiform “raphides” . . . . . *R. (R.) spinosa*
4a Microscleres include thraustoxeas 5
4b Microscleres are never thraustoxeas 8
5a Microstyles present 6
5b Microstyles absent . . . . . *R. (R.) fascicularis*
6a Growth form elaborate, lobate-ramose 7
6b Growth form thinly encrusting . . . . . *R. (R.) guernei*
7a Thraustosigmas present, microstyles up to 45 μm only . . . . *R. (R.) coralloides*
7b Thraustosigmas absent, microstyles up to 88 μm . . . . . *R. (R.) mutans*
8a Large (>20 μm) thraustosigmas present 9
8b No large thraustosigmas (smaller ones, up to 15 μm occur in two species) 11
9a Growth form elaborate, ramose 10
9b Growth form thinly encrusting . . . . . *R. (R.) intexta*
10a Microstyles present . . . . . *R. (R.) forcipula*
10b Microstyles absent . . . . . *R. (R.) mammillata*
11a Microstyles can be 100 μm long or more, growth form always encrusting . . 12
11b Microstyles always smaller than 70 μm long, growth form encrusting or elaborate 19
12a Microstyles in two size categories, spirosigmas always smaller than 12 μm 13
12b Microstyles in a single size category, spirosigmas are frequently larger than 12 μm 15
13a Rhabdostyles in two size categories seldom reaching 300 μm in length, microstyles always smaller than 150 μm long 14
13b Rhabdostyles in a single, albeit variable, size category reaching 400 μm in length, microstyles may be larger than 150 μm long . . . . . . *R. (R.) besnardi*
14a Rhabdostyles with a distinct spiral twist, frequently smaller than 100 μm long . . . . . *R. (R.) africana*
14b Rhabdostyles barely curved, often almost straight, never smaller than 100 μm long . . . . . *R. (R.) bistylifera*
15a Rhabdostyles always smaller than 400 μm long, smooth or acanthose 16
15b Rhabdostyles can be larger than 400 μm long, always smooth . . . . . *R. (R.) profunda*
16a Spirosigmas strongly contort, thin, finely rugose overall 17

16b Spirosigmas approaching C-shape, angular, relatively smooth, relatively thick 18
17a Rhabdostyles mostly smaller than 200 μm long, spirosigmas 12-13 μm long . . . . *R. (R.) prolifera*
17b Rhabdostyles up to 350 μm long, spirosigmata 9-18 μm long . *R. (R.) minutula*
18a Rhabdostyles smaller than 180 μm long, smooth . . . . *R. (R.) gallica*
18b Rhabdostyles up to 290 μm long, acanthose . . . . *R. (R.) burtoni*
19a Rhabdostlyes frequently or always larger than 400 μm long, always acanthose 20
19b Rhabdostlyes nearly always smaller than 350 μm long, smooth or acanthose 21
20a Spirosigmas in a single size category always smaller than 10 μm long, thickly encrusting growth form . . . . *R. (R.) itajai*
20b Spirosigmas in two size categories up to 18 μm long, growth form erect . . . . *R. (R.) acanthostyla*
21a Rhabdostyles entirely smooth 22
21b Rhabdostyles lightly or heavily spined 23
22a Rhabdostyles up to 24 μm thick, heavily spined, dark microscopical pigment granules not recorded . . . . *R. (R.) antarctica*
22b Rhabdostyles up to 15 μm thick only, larger ones less heavily spined, smaller ones often entirely smooth, may bear abundant dark microscopical pigment granules . . . . *R. (R.) uruguaiensis*
23a Microstyles less than 2 μm thick 24
23b Microstyles 3-4 μm thick . . . . *R. (R.) stellata*
24a Spirosigmas always smaller than 10 μm long 25
24b Spirosigmas 12-15 μm long . . . . *R. (R.) indica*
25a Rhabdostyles almost straight, no spiral twist, growth form massive or thickly encrusting . . . . *R. (R.) spirophora*
25b Rhabdostyles spirally twisted, growth form massive . . . . *R. (R.) topsenti*

PHYLOGENETIC ANALYSIS

Table 1 shows the datamatrix used here to assess the phylogenetic relationships within *Rhabderemia*. It has been adapted from that developed by van Soest & Hooper (1993), to include the two recently described species, viz. *R. besnardi* and *R. itajai*, and a further outgroup, viz. the Desmacellidae (Mycalina, Poecilosclerida). The possible close relationship between Rhabderemiidae and Desmacellidae was suggested as an alternative phylogenetic hypothesis by van Soest & Hooper (1993), based in comparisons between the rugose microstyles of *Rhabderemia* and the commata of some *Biemna*. Characters and character states are listed as footnote on Table 1.

Notes on the character matrix

A few changes in the character coding adopted by van Soest & Hooper (1993) were implemented as follows:

- Megascleres (character 7) has been recoded into a, styles; b, one category of rhabdostyles; c, two categories of rhabdostyles. Character 9 of van Soest & Hooper (1993) - length of megascleres has been considered non-independent to

TABLE 1: Taxon-character matrix for the cladistic analysis of *Rhabderemia*. Characters and character-states were adapted from those selected and discussed by van Soest & Hooper (1993). Changes implemented on their datamatrix are discussed in the text.

Character Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
R. (R.) acanthostyla	a	a	b	b	a	a	b	b	a	b	c	a	a	a	a	b
R. (R.) africana	b	b	b	b	b	b	c	b	a	d	b	a	a	a	a	a
R. (R.) antarctica	a	a	a	?	a	a	b	c	b	b	b	a	a	a	a	a
R. (R.) besnardi	b	a	a	?	a	a	b	b	ab	d	b	a	a	a	a	a
R. (R.) bistylifera	b	a	b	b	?	?	c	a	a	d	b	a	a	a	a	a
R. (R.) burtoni	b	a	?	?	b	b	b	b	a	b	?	a	b	a	a	a
R. (R.) coralloides	a	a	a	a	a	a	b	c	b	b	b	a	b	a	b	a
R. (S.) destituta	a	a	a	a	a	c	b	a	b	a	a	a	a	a	a	a
R. (R.) fascicularis	b	a	a	?	a	a	b	c	b	a	b	a	a	a	b	a
R. (R.) forcipula	a	a	a	a	a	a	b	b	b	b	b	b	a	a	a	a
R. (R.) gallica	b	a	?	?	b	b	b	a	a	c	?	a	b	a	a	a
R. (R.) guernei	b	a	?	?	a	a	b	b	a	b	b	a	a	a	b	a
R. (R.) indica	a	a	b	b	a	a	b	a	a	b	b	a	a	a	a	a
R. (R.) intexta	b	a	?	a	a	a	b	b	a	a	b	b	a	a	a	a
R. (R.) itajaí	ab	a	a	b	a	a	c	b	b	b	b	a	a	a	a	a
R. (R.) mammillata	a	a	a	a	a	a	b	b	a	a	b	b	a	a	a	a
R. (R.) minutula	b	b	b	b	b	b	b	b	a	c	b	a	a	a	a	a
R. (S.) mona	a	a	a	?	a	c	b	a	b	a	a	a	a	a	a	a
R. (R.) mutans	a	a	a	a	a	a	b	c	b	c	b	a	a	a	b	a
R. (R.) profunda	b	a	?	?	?	?	b	b	a	b	b	a	a	a	a	a
R. (R.) prolifera	b	b	b	b	b	b	b	b	a	c	b	a	a	a	a	a
R. (R.) sorokinae	a	a	b	a	a	a	b	b	a	b	b	a	a	b	a	a
R. (R.) spinosa	b	a	b	b	b	b	b	b	a	b	b	a	a	b	a	a
R. (R.) spirophora	a	a	b	b	a	a	b	a	a	b	b	a	a	a	a	a
R. (R.) stellata	a	a	a	a	a	a	b	a	b	b	b	a	a	a	a	a
R. (R.) topsenti	a	a	b	a	a	a	b	b	a	b	b	a	a	a	a	a
R. (R.) toxigera	b	a	b	?	?	?	b	b	a	b	b	a	a	b	a	a
R. (R.) uruguaiensis	ab	a	a	?	a	a	b	b	a	b	b	a	a	a	a	b
Desmacellidae	a	a	ab	ab	a	a	ab	a	?	ab	a	a	a	b	a	?
Raspailiidae	a	a	a	a	a	a	ab	a	?	a	a	a	a	a	a	?

Characters and their states. 1: habit – a, elaborate; b, encrusting. 2: substrate - a, epibenthic; b, insinuating, occupying holes in the substrate. 3: consistency – a, firm; b, soft. 4: oscules – a, in stellate pattern; b, other. 5: ectosome – a, bouquet of rhabdostyles; b, single rhabdostyles. 6: choanosome – a, plumoreticulate; b, other. 7: megascleres – a, styles; b, single category of rhabdostyles; c, two categories of rhabdostyles. 8: spination of megascleres – a, smooth; b, slightly acanthose; c, heavily spined. 9: width of megascleres – a, up to 20 μm; b, up to between 20-30 μm. 10: microstyles – a, absent; b, present in one category, styloid base; c, present in one category, base slightly subtylostylote; d, present in two categories. 11: spirosigmata – a, absent; b, present. 12: large thraustosigmata – a, absent; b, present. 13: small thraustosigmata – a, absent; b, present. 14: toxas – a, absent; b, present. 15: thraustoxeas – a, absent; b, present. 16: pigment granules – a, absent; b, present.

character 7, as it actually referred to the number of categories of rhabdostyles. It has accordingly been merged here.

- *R. bistylifera* was assigned character-state 7.c here as it has two categories of rhabdostyles. In the datamatrix provided by van Soest & Hooper (l.c.), the species was coded as if possessing the plesiomorphic trait, viz. styles. This was probably a typographic error.

- *R. uruguaiensis* has been coded character-state 7.b, as we interpret the species to possess a single category of rhabdostyles (see also Oliveira & Hajdu 2005), instead of two as originally described by van Soest & Hooper (l.c.).
- Raspailiidae has been coded ambiguously for character 7 (possession of rhabdostyles) as it is yet uncertain whether the rhabdostyles present in some raspailiids are homologous or not to those in *Rhabderemia*.
- Spination of megascleres (character 8) has been recoded into a, smooth; b, slightly acanthose; c, heavily spined.
- Width of megascleres (character 9, = char. 10 of van Soest & Hooper, l.c.) has been recoded into a, up to 20 μm; b, up to between 20-30 μm. We refrained from aprioristically adding character state c for a possible reversal in character states, as suggested by van Soest & Hooper (l.c.) for *R. intexta* and *R. mammillata.*
- Microstyles (character 10) has been recoded into a, absent; b, present in one category, styloid base; c, present in one category, subtylostylote base; d, present in two categories. It results from merging van Soest & Hooper's (l.c.) characters 11, 12, 13 and 14, which we considered non-independent.
- *R. acanthostyla*, *R. gallica* and *R. mutans* were coded character-state 10.c instead of 10.b as they were described, and/or clearly illustrated to possess slightly-swollen basal terminations on their microstyles, but nevertheless, coded by van Soest & Hooper (l.c.) as if their microstyles had non-elaborate bases.
- *R. fascicularis*, *R. intexta* and *R. mammillata* were coded character-state 10.a, as we preferred not to consider aprioristically the absence of microstyles in these species as a subsequent loss.
- Outgroups were coded unknown for character 16 (presence of pigment granules).

For a comprehensive discussion on character coding for the species of *Rhabderemia* and the outgroup Raspailiidae refer to van Soest & Hooper (1993).

Character analysis

If all the characters are treated as unordered under default parsimony, the size of the set of most parsimonious trees explodes, tree-buffer limit (ca. 60'000 trees) is quickly reached, preventing any more parsimonious trees being obtained. Van Soest & Hooper (1993) applied "Dollo" parsimony to megasclere length and thickness only. We have opted for coding characters 11 to 16 under "Dollo" parsimony. These are all simple "present" vs. "absent" characters, for which no biological functionality is yet known or hypothesised, which renders it much more likely that frequent parallel losses occurred, rather than the opposite, viz. parallel gains.

Two different analyses were performed, each with one of the outgroups. The analysis with Raspailiidae as the outgroup yielded on the first run 50821 trees, but only 164 after the first subsequent weighting of characters by their Rescaled Consistency Indices, 20 after the second, and 4 after the third subsequent weighting cycle, when the set of most parsimonious trees stabilized. If filtered for more resolution (polytomous trees discarded when more resolved ones exist), only two trees remained, differing by the allocation of *R. besnardi* and *R. itajai*, which can either be sister species, sisters of the clade ((*intexta*, *mammillata*) *forcipula*); or form an unresolved trichotomy with this

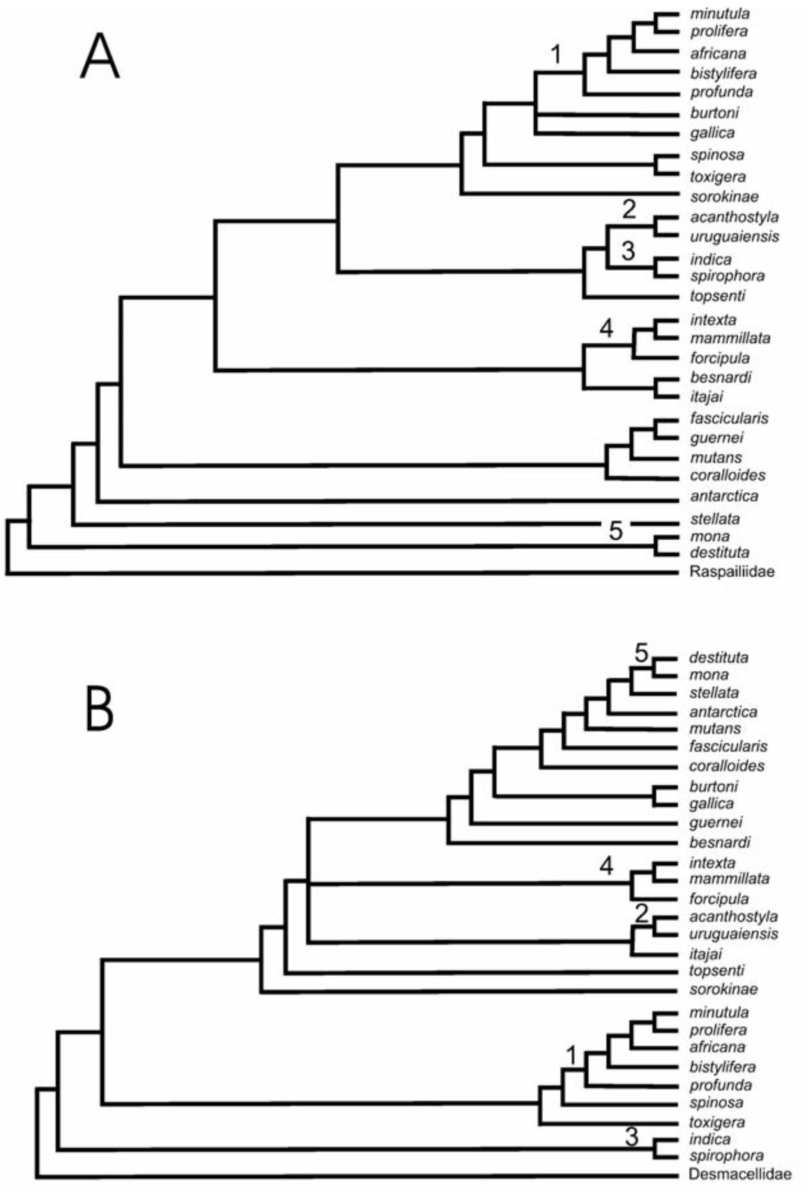

FIG. 4

Hypothetical phylogenetic relationships of the known species of *Rhabderemia*. (A) Polarized against the Raspailiidae. (B) Polarized against the Desmacellidae. Congruent clades on both are numbered 1-5 on the respective nodes. Refer to text for details on how these cladograms were obtained.

clade, and a further clade comprising 20 species. Figure 4a illustrates the first of these two alternatives, which coincides with the Nelson Consensus (sensu Page, 1989; = maximum clique, majority rule consensus with other compatible groupings of PAUP) for the four trees obtained when the set of equally parsimonious trees stabilized (CI = 0.6873, HI = 0.3127 and RI = 0.9596), and which is our preferred working hypothesis based on Raspailiidae as the outgroup.

When using Desmacellidae as the outgroup, the first run yielded only 112 trees, subsequently weighted to 12, where the set of equally parsimonious trees stabilized. If filtered for more resolution, only four trees remained, differing by the allocation of *R. profunda*, *R. fascicularis* and *R. mutans*. *R. profunda* is the sister of (((*prolifera*, *minutula*) *africana*) *bistylifera*) on two trees and forms an unresolved trichotomy with *R. besnardi* and a clade composed by another ten species. *R. fascicularis* and *R. mutans* can either be sister-species, sister to (((*destituta*, *mona*) *stellata*) *antarctica*), or *R. mutans* can be the sister to this clade, and *R. fascicularis* sister of them all. Figure 4b illustrates the preferred topology, the Nelson Consensus for the twelve trees obtained when the set of most parsimonious trees stabilized (CI = 0.5319, HI = 0.4681 and RI = 0.9286).

Important congruences are observed on both analyses. The following five clades were observed both with Raspailiidae and Desmacellidae as outgroups: *((((minutula, prolifera) africana) bistylifera) profunda)* – clade 1, *(acanthostyla, uruguaiensis)* – clade 2, *(indica, spirophora)* – clade 3, *((intexta, mammillata) forcipula)* – clade 4 and *(destituta, mona)* – clade 5. Clades 2, 3, 4 and 5 also occurred on van Soest & Hooper's (1993) analysis, and are thus considered likely robust hypotheses about phylogenetic relationships within *Rhabderemia*.

Important incongruences are more abundant though. Among these, the opposite allocation of *Rhabderemia destituta* and *mona* [= *R. (Stylospira)* spp.], *R. antarctica* and *R. stellata* is the most remarkable. Polarized against Raspailiidae these species are at a basal position on the *Rhabderemia* tree. When polarized against the Desmacellidae, they all end up at a very derived position in the cladogram. This is certainly a consequence of assuming the possibility that the microstyles of *Rhabderemia* are homologous to the commas of Desmacellidae (the family has been coded polymorphic for character 10, being thus allowed both to possess and not to possess microstyles), so that the lack of these microscleres in *R. (Stylospira)* spp. would become a derived loss higher in the tree. Such a major shift of clades in the competing postulated histories for *Rhabderemia* makes it clear that a sounder picture on the genus' whereabouts in poecilosclerid classification is needed, before the exercise of inferring its deep historical biogeography can proceed any further than essayed here.

As most of the new information discovered in this present study relates to southern South American *Rhabderemia*, these species, along with clades mentioned above as likely to be robust, form the basis for the following biogeographic analysis.

BIOGEOGRAPHIC DISCUSSION

Clades shared by both phylogenetic reconstructions, and also found by van Soest & Hooper (1993)

Figure 5 shows a world map with superimposed clades 2-5 of the *Rhabderemia* phylogenies in Fig. 4. Clade 2 comprises *R. uruguaiensis* from southern South America, and *R. acanthostyla* from India and the Indonesia area. Clade 3, *R. spirophora*, from southern Africa, and *R. indica*, also from India and the Indonesia area.

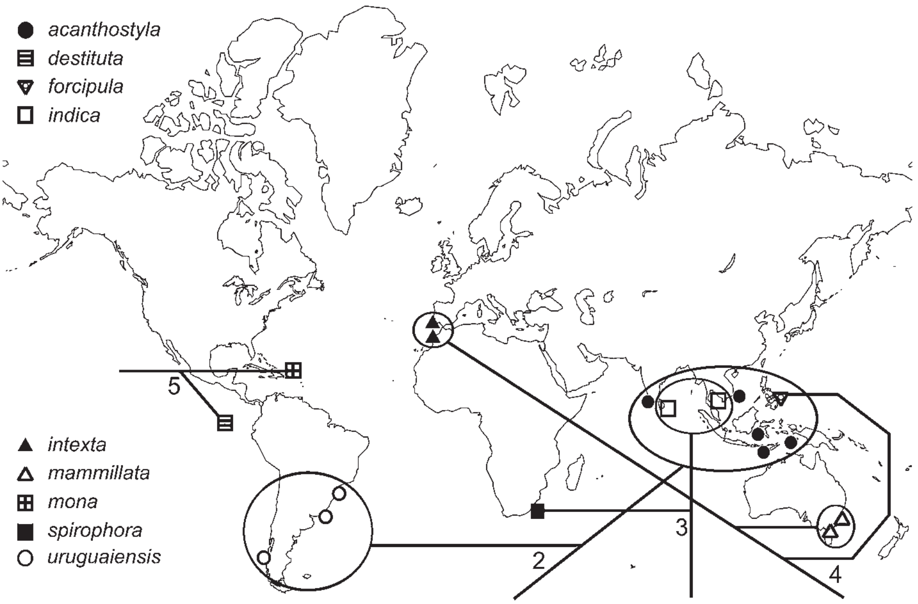

FIG. 5

World map with *Rhabderemia* clades 2-5 (Fig. 4) plotted. These clades were also obtained by van Soest & Hooper (1993). The largest ellipse plotted in the Indonesia area refers only to *R. acanthostyla*. *Rhabderemia indica* and *R. forcipula*, which also appear in the ellipse, belong to clades 3 and 4, respectively.

Clade 4 includes *R. intexta* and *R. mammillata*, respectively from the Lusitanian and south-eastern Australian areas, and their sister species, *R. forcipula*, from the Philippines. Clade 5 comprises both species of subgenus *Stylospira*, *R. (S.) mona* and *R. (S.) destituta*, respectively from the Caribbean and the Galapagos areas.

Clades 2 and 4 were listed as examples of markedly separate sister-relationships and likely consequences of widespread extinction in the history of the genus (van Soest & Hooper, 1993). The extended distribution range of *R. uruguaiensis* observed here though, turned clade 2 into another example of a Trans-Pacific track (e.g. Sluys, 1994). Formerly known only from the south-western Atlantic, the species was discovered here from the south-east Pacific (Chilean fjord area), thus slightly shortening its distance to the known distribution of its sister-species (as above). Previous approaches to demosponge biogeography found additional Trans-Pacific tracks. Hooper & Lévi (1994) found a sister-species relationship for *Ptilocaulis walpersi* (Duchassaing & Michelotti, 1864) and *P. echidnaeus* (Lamarck, 1814), a Caribbean - southern Australia relationship, which could easily date farther back than the closure of the Isthmus of Panama, thus representing another Trans-Pacific track. Hajdu (1995) found precisely the same track for the sister-pair *Mycale unguifera* Hajdu, Zea, Kielman & Peixinho, 1995 and *M. australis* (Gray, 1867). On the other hand, rather distinct routes were observed for the sister-pair *Mycale novaezelandiae* Dendy, 1924 and *M. toporoki* Koltun, 1958, respectively from New Zealand and the Boreal Pacific; as well as for *M. arenaria* Hajdu & Desqueyroux-Faúndez, 1994, *M. thielei* Hajdu & Desqueyroux-Faúndez, 1994 and *M. paschalis* Desqueyroux-Faúndez, 1990, whose clade implied the following biogeographic relationships [(south-western Atlantic, south-eastern Pacific), Easter Island]. The bridging of similarly long distances across the Pacific has been explained by several competing hypotheses, such as Expanding Earth, lost Pacifica continent and allochthonous terranes (Sluys, 1994; McCarthy, 2005), but as pointed out by van Soest & Hooper (1993), the dispersal hypothesis cannot be ruled out. Even though no concrete evidence for Trans-Pacific dispersal of sponges is available to date, a growing body of literature is demonstrating how well the rafting hypothesis fits the known distributions of several poor dispersers (e.g. pumice rafting in particular - Jokiel, 1984; Ó Foighil *et al.,* 1999; Waters & Roy, 2004; Donald *et al.,* 2005), and it is quite conceivable that sponges could rank among these.

Clade 3 shows an Indian Ocean track which, given its distinct positions in the *Rhabderemia* phylogenies obtained (Fig. 4), could be explained through the competing scenarios of vicariance and dispersal. A dispersalist hypothesis appears conceivable when Raspailiidae is used as an outgroup (Fig. 4A), because the separation of *R. indica* and *R. spirophora* appears at a more derived position in the *Rhabderemia* phylogeny, a time when the African and Indian (sub)continents were isolated for tens of millions of years already. This contrasts to van Soest & Hooper's (1993) preferred hypothesis, which albeit construed as Recent, chose a vicariant mode explanation. Which Recent vicariance it might have been was not mentioned, and none is known to us. A vicariant explanation appears more likely though, when Desmacellidae is used as an outgroup, because the position of clade 3 shifts to the basalmost location in *Rhabderemia*'s hypothetical evolutionary tree (Fig. 4B). Van Soest & Hooper (l.c.) argued that *Rhabderemia* was most likely already diverse in early Tertiary times as a consequence of Hinde & Holme's (1892) finding of *Rhabderemia*-like rhabdostyles in Late Eocene - Early Oligocene strata of New Zealand. This hypothesis assumes that widespread Recent dispersal is less likely a scenario. If these premises are indeed true, it is conceivable that clade 3 could represent the early to late Cretaceous break-up and drifting of India from the African continent.

Clade 5 stretches across the Isthmus of Panama. Van Soest & Hooper (1993) took this as sufficient evidence to infer the likelihood of a vicariance explanation for the sister pair *R. destituta* and *R. mona*, linked to the raising of the isthmus. Nevertheless, as pointed out above, the position of this clade shifts to opposite polarities (time frames) within the *Rhabderemia* phylogeny depending on the chosen outgroup. We judge that this classical vicariance explanation cannot fit such possibly distinct inferred timing for this cladogenesis. In fact, the basal position of clade 5 in van Soest & Hooper's (l.c.) cladogram, which matches our result for outgroup Raspailiidae (Fig. 4A), appears to favour more ancient than a Recent vicariance event such as the last closing of the trans-isthmian passage. This Recent vicariance scenario is more likely an explanation when Desmacellidae is used as an outgroup and clade 5 ends up at a very derived position in the *Rhabderemia* tree.

Given the likelihood that *Rhabderemia* diversified earlier than the Tertiary, *R. (Stylospira),* clade 5, must have been around significantly earlier than the nearly concomitant appearance of the recent Galapagos Islands and the raising of the Isthmus of Panama by accretion of the Chortis block (Honduras and Nicaragua) in between

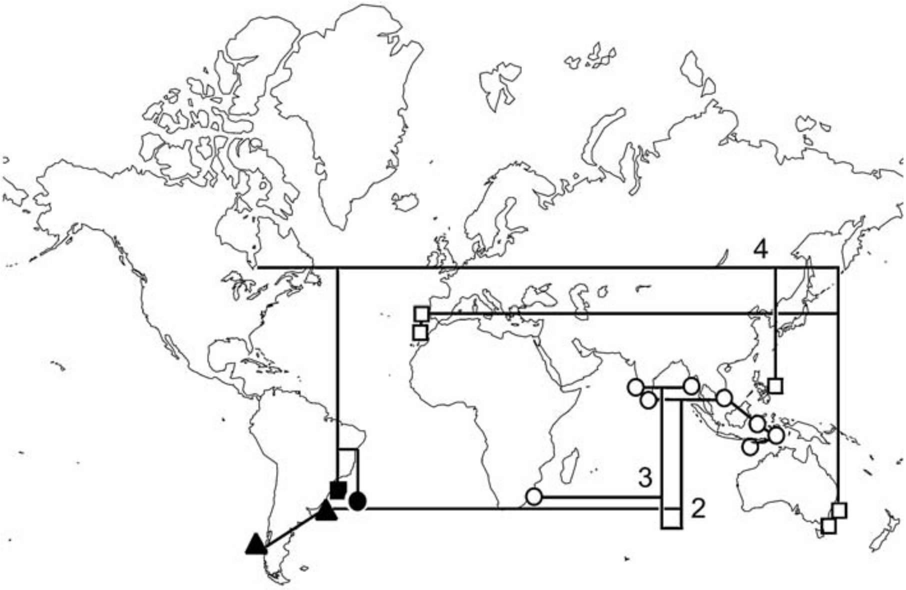

FIG. 6

World map illustrating the biogeographic affinities of *Rhabderemia besnardi* (dark square), *R. itajai* (dark circle) and *R. uruguaiensis* (dark triangles) to additional *Rhabderemia* in clades 2, 3 and 4, implied from the hypothetical phylogeny with Raspailiidae as the outgroup.

northern and southern Central America (Rosen, 1985). A scenario compatible with these events implies that *R. (Stylospira)* existed for a considerably long time, somewhere in the Tropical Eastern Pacific, from where it reached the Galapagos Islands in quite recent times via dispersal, at about the same time the clade became extinct in Tropical Eastern Coastal Pacific. Nevertheless, it is now accepted that a much older history of oceanic islands in the intersection of the Pacific, Nazca and Cocos Plates triple junction exists (Grehan, 2001), which could spread as far back as the 80-90 My of geologic hotspot activity in the area. Accordingly, clade 5 might have been around Galapagos for a rather longer time. In this way, the vicariance accounting for both species in clade 5 could have been related to other phenomena in Tropical Eastern Pacific / Caribbean geohistory, possibly in connection with the complex movements of Caribbean terranes and microplates (Rosen, 1985) and their associated volcanism.

Clades found for Rhabderemia besnardi and R. itajai

Two species were included here for the first time in the postulated phylogeny of *Rhabderemia*, viz. *R. besnardi* and *R. itajai*, both known only from their type localities, in the SW Atlantic. Curiously, their postulated affinities in the phylogenetic trees (illustrated in figures 4A and 4B) are rather different. Figure 4a shows both as sister species, this sister pair being sister of the clade *((intexta, mammillata), forcipula)*. Figure 6 is a graphical representation of the clades including *R. besnardi, R. itajai* and *R. uruguaiensis*, with outgroup Raspailiidae. The implied local vicariance in the south-western Atlantic area accounting for the sister pair *R. besnardi* and *R. itajai* is not obvious to us, possibly related to range expansions / retractions associated to varying sea levels following glacial / interglacial periods. No obvious biogeographic barrier occurs in the area, neither is known to us to have occurred. Both species were found only 200 km apart, on the outer platform or upper slope, seemingly occurring on the same water mass (Central South Atlantic Water). Nevertheless, *R. besnardi* was collected from the shallower limit of this water mass, thus suggesting a possible preference for Tropical waters. A possibly similar scenario for speciation in the south-western Atlantic has been proposed by Muricy *et al.* (2001) to explain the sister pair *Petromica ciocalyptoides* (Zea & van Soest, 1986) and *P. citrina* Muricy *et al.*, 2001 (Desmanthidae, "Lithistida"). Ecophysiological barriers could exist, explaining *P. ciocalyptoides*' apparent preference for warmer Tropical Brazilian Current waters, as found north of Rio de Janeiro State, and *P. citrina's* for slightly colder Brazilian Current waters, intermittently mixed to upwelling Central South Atlantic Waters to the south of Rio de Janeiro. This kind of reticulate evolutionary scenario was developed from inferred historical changes to connectivity derived from changing current regimes, and the opening and closing of passages, on glacial vs. inter-glacial periods (e.g. Veron, 1996).

The next cladogenetic event of concern here (CE 4) is the one responsible for the separation of *R. besnardi* plus *R. itajai* from clade 4 in figure 6. A likely vicariant explanation is not obvious, partly as a consequence of the markedly discontinuous distributions observed in the latter clade (van Soest & Hooper, 1993; and above). At least five earlier cladogenetic events are postulated for *Rhabderemia* in fig. 4A, which contribute to render an association of CE 4 with the Atlantic Deep Sea Barrier vicariance an unlikely reconstruction of the evolutionary history of these species, as this would push the genus' history too far back. The kinematics of the South Atlantic opening is still controversial (Eagles, 2007), but if CE 4 is postulated to match the onset of this biogeographic barrier, *Rhabderemia* must have been around and quite diverse in Cretaceous times already (at least six clades). At this time, a warm, narrow and shallow South Atlantic was there, and as such, the clade comprising clade 4 + *R. besnardi* and *R. itajai* would have had an open avenue for the colonization of the south-eastern Atlantic and the entire western Indian Ocean. No apparent reason, other than widespread extinction, can reasonably account for present days failure to recover descendants of CE 4 on these areas, if the time frame constructed here is correct. But, the present day moderately deep-water occurrence of both south-western Atlantic species in question, 153-380 m depth, suggests a possible preference for sub-tropical/temperate waters of their ancestors too. When did such conditions develop in the South Atlantic? A more recent jump dispersal may be the best hypothesis in the moment to account for CE 4.

Figure 7 illustrates the cladogenetic events associated with *R. besnardi* and *R. itajai*'s history in the tree shown in Figure 4B, with Desmacellidae as the outgroup. The trans-pacific track spanned by *R. uruguaiensis* and *R. acanthostyla* (clade 2) has been discussed above. Differently from what has been discussed in the above paragraph, *R. itajai* has a sister species relationship to this clade (instead of to *R. besnardi* as in Fig. 4a), which is suggestive of an unusual east-west polarity for the above quoted track. As the whole clade pertains to a trichotomy, it is difficult to pursue any further discussion on deeper historical events leading to the colonization of the south-western Atlantic.

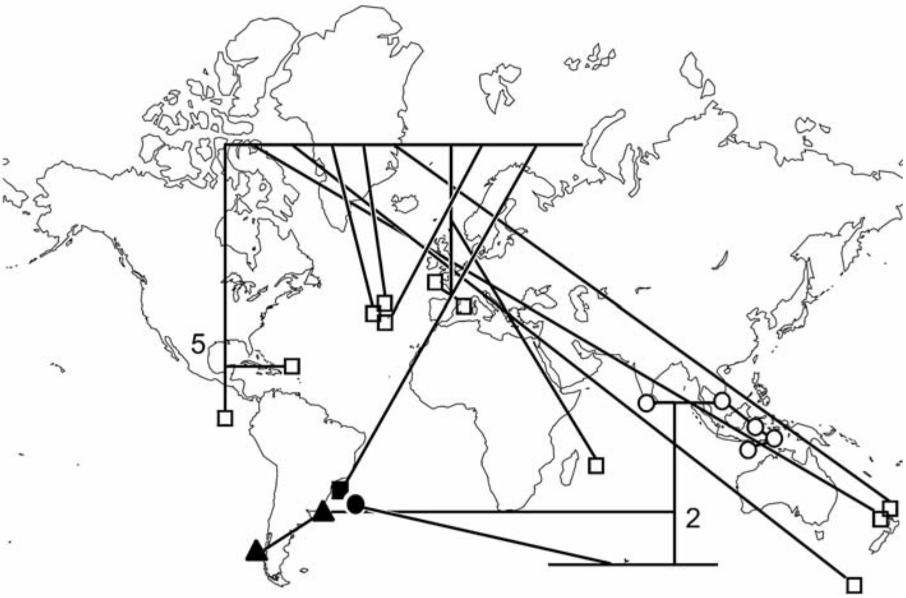

FIG. 7

World map illustrating the biogeographic affinities of *Rhabderemia besnardi* (dark square), *R. itajai* (dark circle) and *R. uruguaiensis* (dark triangles) to additional *Rhabderemia* in clades 2, 3, 4 and 5,implied from the hypothetical phylogeny with Desmacellidae as the outgroup.

Rhabderemia besnardi, on the other hand, is sister to another ten species in the genus, with important North Atlantic (five species) and south-western Pacific (two species) components. The occurrence of *R. burtoni* in the western Indian Ocean, and of its sister species *R. gallica* extending its known distribution in the western Mediterranean, makes a Tethyan relict hypothesis more conceivable for the entire ten species clade. The cladogenetic event splitting these two species has been equated by van Soest & Hooper (1993) to a likely consequence of the Miocene collision of the African and Asian continents, severing the Tethyan gateway. What is perhaps unusual for a Tethyan clade is a south-western Atlantic sister species, which in this case has to be seen as a Gondwanan relict, as its ancestors must have reached the south-western Atlantic from the south. The alternative scenario of this entire clade reaching the south-western Atlantic through the Equatorial Atlantic implies accepting an early connection between the northern and southern sectors of this ocean, which appears likely in recent reconstructions (e.g. Silveira & Stutzmann, 2002; Eagles, 2007), but also of possible widespread extinction of shallower species in the western margin of the South Atlantic, as well as every likely founder *Rhabderemia* species on its eastern margin.

A last point for consideration regards the highly derived position of clade 5 in Figure 4B. Opposing what has just been suggested for clade 2, the polarity of clade 5 is most likely a west-east one, as inferred from the present days distribution of its two next sister species. First, *R. stellata*, which is known from northern New Zealand.

Second, *R. antarctica*, known from the Antarctic region. These two species suggest a range extension towards the Tropical Eastern Pacific first, followed by invasion of the Caribbean area.

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