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Pachyrotula, a new genus of freshwater sponges from New Caledonia (Porifera: Spongillidae)

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Abstract.—Characteristics found during a review of the type material of *Spongilla (Stratospongilla) raceki* Rützler from New Caledonia point to a new, monotypic genus, *Pachyrotula*. This new genus is closely related to *Heterorotula* Penney & Racek and to *Houssayella* Bonetto & Ezcurra De Drago. *Heterorotula* also occurs in New Caledonia and is represented by the species *H. caledonensis* new species and *H. multidentata* (Weltner). These species, along with *Oncosclera diahoti* (Rützler), new combination, are indicators of a rare and particular freshwater sponge fauna of this island.

For the past three decades, the freshwater sponges of New Caledonia have been known only from the specimens described by Rützler (1968). It recently became clear that this material needed to be reexamined, especially in the light of Penney & Racek's (1968) comprehensive study of all gemmule-producing genera of freshwater sponges and Racek's (1969) extensive work on Australia's freshwater sponges, which provided new insight into the generic and specific relationships of these faunas and revealed their heretofore unsuspected richness. That work and several subsequent studies on the freshwater sponges of South America indicated the need for a taxonomic and systematical updating of the New Caledonia description. As a result of this updating, a new genus is being proposed, with *Spongilla (Stratospongilla) raceki* Rützler as the type species; also, *Ephydatia multidentata* (Weltner) forma *caledonensis* Rützler is elevated to a full species in the genus *Heterorotula* Penney & Racek, and *Spongilla (Stratospongilla) diahoti* Rützler is transferred to the genus *Oncosclera* Volkmer-Ribeiro.

Material and Methods

The material examined consisted of types and paratypes of *Spongilla (Stratospongilla) diahoti, S. (Stratospongilla) raceki,* and *Ephydatia multidentata* f. *caledonensis* (Rützler 1968), all deposited at the National Museum of Natural History, Washington D.C. (USNM); slides of *Houssayella iguazuensis* Bonetto & Ezcurra de Drago, 1966, provided by I. Ezcurra de Drago; and slides of species of the genus *Heterorotula* provided by A. A. Racek; the latter deposited at Museu de Ciencias Naturais (MCN) of Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil.

A minute fragment of *Spongilla (S.) raceki* with gemmules was dissociated after boiling in nitric acid and washed several times in distilled water. When completely dry, the suspended clean spicules were dropped on a stub and coated with gold in preparation for scanning electron microscopic (SEM) observations. Some dry gemmules were hand-sectioned under a stereomicroscope and their halves glued to a stub and also gold-coated for SEM examination. Photomicrographs were obtained with an

MCN JEOL-5200 microscope equipped with a Pentax SF7 35 mm camera.

Systematics

Pachyrotula, new genus

Type species.—*Spongilla (Stratospongilla) raceki* Rützler, 1968. Genus monotypic.

Diagnosis.—Spongillidae with stout, heavily spined birotulate gemmoscleres with knobby rotules progressively reduced from the inside to the outside of the gemmular coat.

Description.—Sponges forming slender, greyish, small, irregular, soft crusts with gemmules loosely distributed near the basal spongin plate. Oscula and pores inconspicuous. The skeleton consists of a dense polygonal network of spicules bound together by scanty spongin. No main fibers are discernible.

Three classes of megascleres. The most abundant are the alpha megascleres, which are finely spined oxea, abruptly and acutely pointed, and with a denser spine arrangement at the extremities. The beta megascleres measure half to two-thirds the length of the alpha megascleres, are curved or even bent oxea or styles, are strongly spined with abruptly and sharply pointed extremities that are enhanced by a distal swelling and a concentration of minute spines turned toward the point. These megascleres are tangentially packed around the gemmules under a loose and haphazard arrangement of the alpha megascleres. The third class consists of very rare, smooth, thin, long oxea with differing mucronated extremities.

Microscleres absent.

Gemmoscleres are dumb-bell-shaped birotules, with knobby rotules ranging from irregularly sculptured, tuberculate, or spiny bulbs to merely knobbed expansions of the shaft (Figs. 1, 2). As the rotules become smaller, the shafts become longer. Sharpened, lanceolated extremities of the shaft may protrude from one or both of the rotules or terminal knobs, thus morphologically grading into beta megascleres. Shafts are spined, some are displaying a few tubercules capped by rosettes of spines.

Gemmules abundant, located at the basal part of the sponge. Inner layer thick; pneumatic layer thin, with small, irregular air spaces and only a few short gemmoscleres radially embedded in it. The longer gemmoscleres form a loose radial arrangement and, together with the derived acanthoxea (beta megascleres), turn more tangential toward the gemmule periphery. The outer rotules and the largest part of the shafts of most gemmoscleres protrude at the gemmular surface. One single foramen in each gemmule.

Pachyrotula raceki (Rützler), new combination

Figs. 1–5, 9

Spongilla (Stratospongilla) raceki.—Rützler, 1968:60, figs. 5–9.

Holotype.—USNM 23882, New Caledonia; Ferdinand Starmühler leg. 18 Sep 1965.

Paratype.—USNM 23883, same location as for holotype.

Type locality.—River Le Diahot, New Caledonia (Fig. 9).

Description.—Soft, grayish, tiny patches 1 mm thick on the lower surface or in concavities of stones. Sponge surface smooth, porous. Oscula inconspicuous. Skeleton a confused arrangement of megascleres with scanty spongin at the crossing points. A tangential packing of the megascleres around the gemmules produces a thickening of the skeleton at the basal portion of the sponge.

Alpha megascleres are microspined, straight to more often slightly curved oxea with abruptly pointed, spined extremities. Oxea vary noticeably in length. Spines at tips turned outward. These megascleres form the skeleton mesh and also occur in a loose and confused manner around each gemmule.

Beta megascleres are short, slightly to

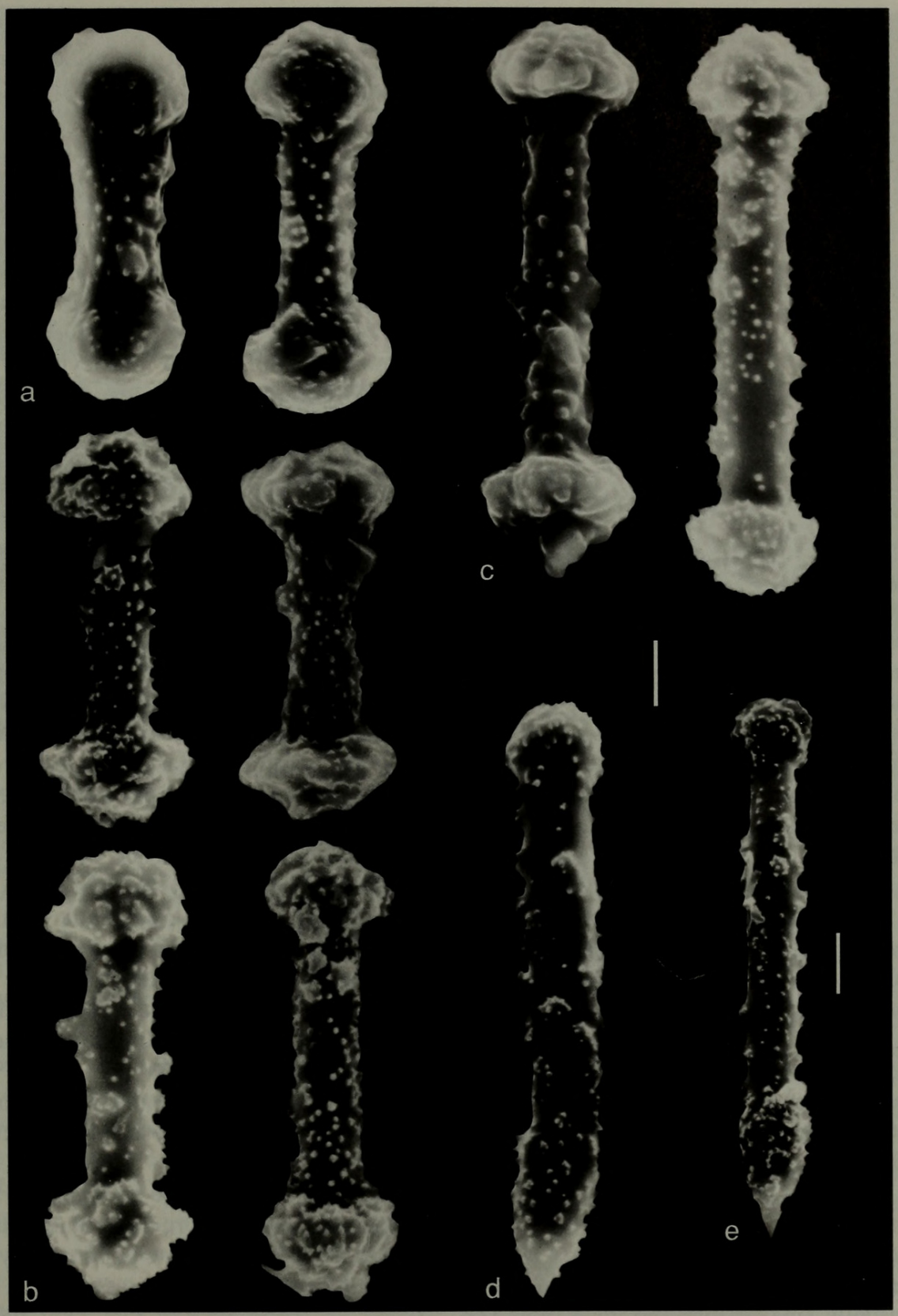

Fig. 1. Gemmoscleres of *Pachyrotula raceki* (Rützler) (SEM). a, Immature or poorly developed spicules; b, Average development; c, Largest class of gemmoscleres exhibiting differentiated rotular reduction; d, Further differentiation; e, Same as d, reduced scale. Scales = 10 μm.

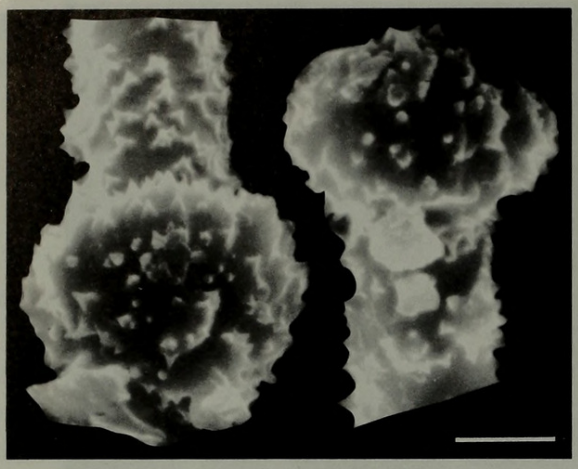

Fig. 2. Enlarged rotules of *Pachyrotula raceki* (Rützler) gemmosclere in Fig. 1b (lower right); note different size of the rotules (SEM). Scale = 5 μm.

strongly curved or even bent, strongly spined oxea or styles with very abruptly pointed extremities. Usually marked by a subterminal swelling or bulb with a heavier covering of spines turned to the spicule extremities. Some beta megascleres are embedded in the gemmular wall together with the gemmoscleres, but for the most part are tangentially packed around the gemmules.

Long, smooth thin megascleres are very rare but certainly belong to the sponge, as became evident once the series grading from very thin and short ones was perceived in the original preparations. These spicules may be up to four times longer and thinner than the alpha megascleres. However, they are too scarce to determine their locale in the skeleton.

Gemmoscleres stout, strongly spined birotulates of conspicuously large range of lengths. With thick shafts and, terminally, with spool- to knob-like rotules irregularly ornamented by spined lobes, rosettes, or tubercules. The shorter gemmoscleres display larger, more conspicuous rotules, the outer one usually smaller than the inner one. The bulbous endings of the longer gemmoscleres gradually taper, thus changing the spicules into straight or gradually curved oxeas with piercing points enhanced by a slight subterminal swelling of the shaft. Such spicules grade into what are here classed as beta megascleres because they are not embedded in the gemmular wall but are packed around the gemmules (Figs. 1, 2, 3b; and Rützler 1968, figs. 6–8).

Gemmules abundant. They occur from the base to the middle portion of the thin crusts. Because the sponge was in the process of producing gemmules, it is possible to describe the manner in which the gemmular wall is formed. Wherever gemmules are about to be formed, and even prior to the congregation of the thesocytes, a gathering of cells secreting the alpha megascleres takes place, joined shortly thereafter by spicule-forming beta megasclerocytes and gemmosclerocytes. By the time the inner gemmular wall is formed, a large number of the short and longer gemmoscleres are already present and beginning to become inserted at the base of the inner gemmular wall. During the formation of the thin pneumatic coat around the gemmosclere layer, more and more gemmoscleres contribute to this coat. At the same time, the beta and alpha megascleres congregate tightly around the forming gemmule, until only a round mass of alpha megascleres can be perceived. The presence of some gemmoscleres (particularly shorter ones) radially embedded in the pneumatic coat (Fig. 3) indicates that a radial orientation was abandoned for a tangential one. The outer gemmular wall is thin; the foraminal tube is short and does not reach beyond the longer birotulates.

For spicule and gemmule measurements, refer to the original descriptions (Rützler 1968).

Habitat.—The sponge encrusts the lower surface of stones in running and standing waters with extreme low conductivity (28–56) and slightly acidic to neutral pH (6.6–7.1).

Remarks.—Penney & Racek (1968) elevated Annandale's subgenus *Stratospongilla* to a genus, defining its gemmoscleres (p. 40) as "more or less strongly bent amphistrongyles . . . or slightly curved spined amphioxea, or a combination of both" and its

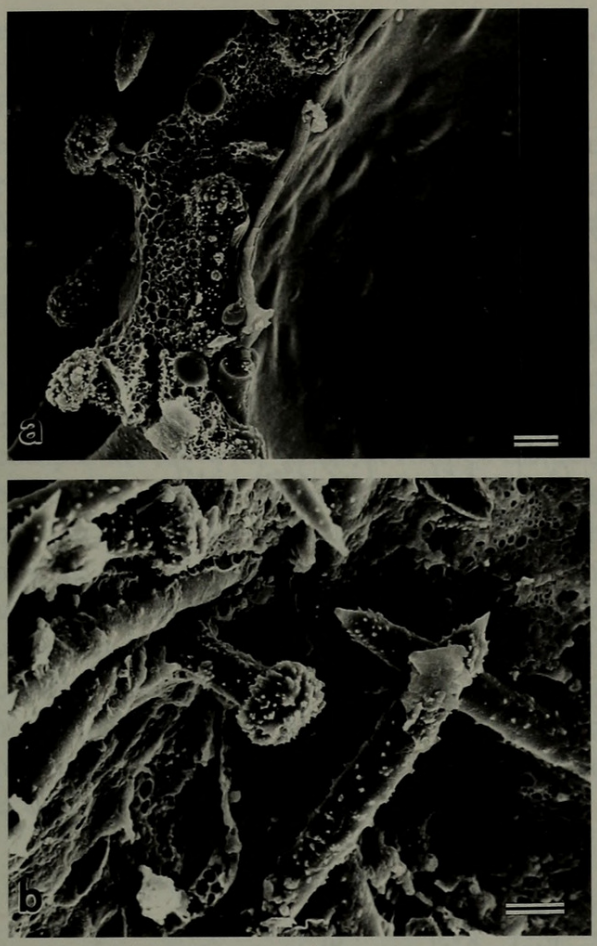

Fig. 3. Gemmular wall in *Pachyrotula raceki* (Rützler) (SEM). a, A cross-section exposes the irregularly smooth surface of the inner coat and the irregular air spaces of the pneumatic coat, with some short birotulates radially embedded and some longer ones tangentially embedded, both kinds projecting beyond the thin outer gemmular coat; b, Gemmular surface, with rotule of one short gemmosclere projecting and several beta megascleres tangentially embedded in the growing pneumatic coat. Scales = 10 μm.

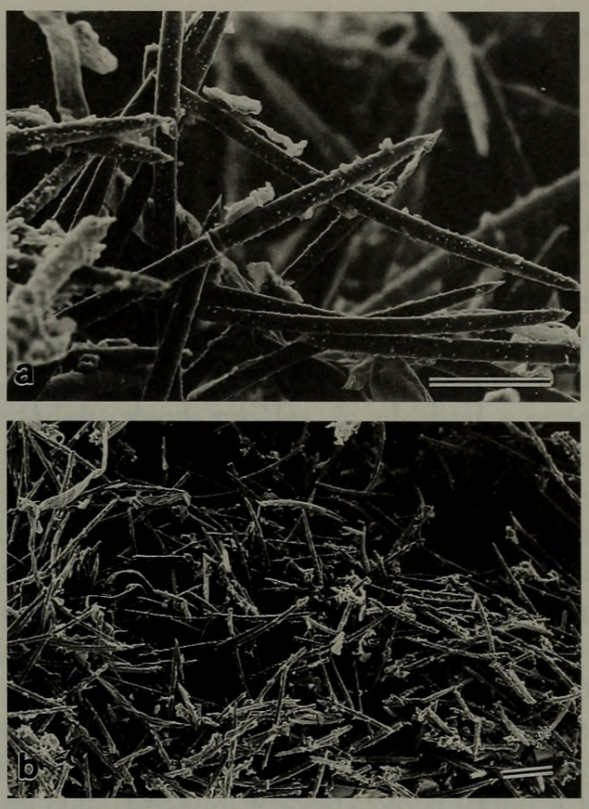

Fig. 4. Skeletal arrangement in *Pachyrotula raceki* (Rützler) (SEM). a, Detail of the loose arrangement of the alpha megascleres cemented by scanty spongin; b, Cross section of the sponge crust showing the loose skeletal arrangement of the megascleres. Scales = 50 μm (a); 100 μm (b).

microscleres as "shorter and slender amphioxea." They suggested, however, that *Stratospongilla* species lacking microscleres might be grouped under a new genus. Volkmer-Ribeiro (1970) followed up on this suggestion by defining the genus *Oncosclera,* with *Oncosclera jewelli* (Volkmer 1963) as the type species. *Oncosclera* species not only lack microscleres but differ markedly from *Stratospongilla* in their gemmular structure. At the time the genus *Oncosclera* was defined, it was assigned several South American species previously described as *Stratospongilla* by Bonetto & Ezcurra de Drago (1966). Also included in the genus were the Oriental and Ethiopian *Stratospongilla* species reported to be lacking microscleres (Penney & Racek 1968).

A reexamination of the spicular set and gemmular coat of *Spongilla (Stratospongilla) raceki* shows its gemmoscleres to be birotulates, modified by a graded reduction in the size of their rotules that depends on their position relative to the inside or outside of the gemmular coat; this morphological series ends in highly variable acanthoxeote or acanthostylote forms. Just as such gemmoscleres cannot be considered strongyles, the gemmular structure of *Pachyrotula* has no parallel in the large mammilate gemmules that are cemented to the substrate in both *Stratospongilla* and *Oncosclera.* Neither of these genera show any trace of radially arranged gemmoscleres that are evident in *Pachyrotula* new genus. Nor are the size, the shape, or the localization of the

Fig. 5. Camera lucida drawings of spicules of *Pachyrotula raceki* (Rützler). a, Alpha megascleres grading to beta megascleres; b, Gemmoscleres. Scale = 50 μm.

acanthoxea or acanthostyles around the gemmules characteristic of microscleres. Rather, they point to a second category of megascleres. The selective process responsible for the production of such megascleres also caused the birotulate spicules in the gemmular wall to depart from a radial pattern. The new genus is closer to genus *Het-*

erorotula Penney & Racek, 1968, which at the time of its discovery was known only from Australia and New Zealand. Only a recent study of some spongillite (ore) deposits from Brazil (Volkmer-Ribeiro & Motta 1995) has brought to light the first neotropical species of the genus. The new genus clearly stands apart from *Heterorotula,* whose diagnostic characteristic consists of gemmoscleres with "slender, usually granulated shafts and terminally with comparatively wide and flat rotules of moderately to greatly varying diameter, the inner invariably larger than the outer" (Penney & Racek 1968:96). Furthermore, the very distribution of *Pachyrotula raceki,* which appears to be the most widely occurring species on New Caledonia (Fig. 9) and is also known for its broad range of habitats, indicates that it cannot be a mere ecomorph of a *Heterorotula* species.

Heterorotula caledonensis, new species
Figs. 6, 9

Ephydatia multidentata (Weltner) f. *caledonensis* Rützler, 1968:63, figs. 13–19.

Holotype.—USNM 23884 (the gemmule slide preparation figured in Rützler, 1968, fig. 15), sta. FNK 36 (in Rützler 1968:58), New Caledonia; Ferdinand Starmühlner leg. 25 Jul 1965.

Paratypes.—USNM 39463 (5 slides), sta. FNK 36 (in Rützler 1968:58) New Caledonia, Ferdinand Starmühlner leg. 25 Jul 1965.

Remarks on the syntypic series.—The description of the new species is based on several fragments from three specimens. The fragments in alcohol and five slides (two of them with entire gemmules) representing the three specimens are deposited in the USNM.

Type locality.—Sta FNK 36 (in Rützler 1968:58), near La Foa, southwest New Caledonia (Fig. 9).

Diagnosis.—*Heterorotula* species with stout megascleres and stout, highly variable spined to granulated gemmoscleres that make up a series, running from quite long acanthoxea with bulbous, strongly spined extremities to more typical birotules, to quite short, irregularly shaped "aster-like" spicules. The series of regular, birotulate *Heterorotula* gemmoscleres tends to form freak rotules and displays granulated to almost smooth shafts.

Description.—Rützler's (1968:65) detailed description of *Ephydatia multidentata* f. *caledonensis* holds for *Heterorotula caledonensis* new species. In addition, a series of very short "aster-like" gemmoscleres not referred to originally may be seen in Rützler's, 1968, fig. 16 alongside the gemmoscleres in the pneumatic coat. Such birotulate-derived gemmoscleres are abundant in the original slides examined.

Remarks.—*Ephydatia multidentata* Weltner 1895 was one of the species that Penney & Racek (1968) transferred to their new genus *Heterorotula.* Racek (1969) found it to be one of the most common freshwater sponge species in eastern Australia and reported considerable variation in its spicular components. On New Caledonia, *H. multidentata* (Weltner 1895) occurs almost sympatrically with *H. caledonensis* new species (sta. FNK 36 and 44, both described in Rützler, 1968) and in quite similar water-quality and substrate conditions. The great variations in the gemmoscleres of *H. caledonensis* new species could not be found in specimens of *H. multidentata* from either eastern Australia or New Caledonia and are now considered to be of such magnitude that they denote a new species.

Oncosclera diahoti (Rützler),
new combination
Fig. 9

Spongilla (Stratospongilla) diahoti Rützler, 1968:59, figs. 2–4.

Holotype.—USNM 23881 (5 fragments), New Caledonia, Ferdinand Starmühlner leg. 16 Sept 1965.

Type locality.—River Le Diahot near Quénia, sta. FNK 105, North New Caledonia (Fig. 9).

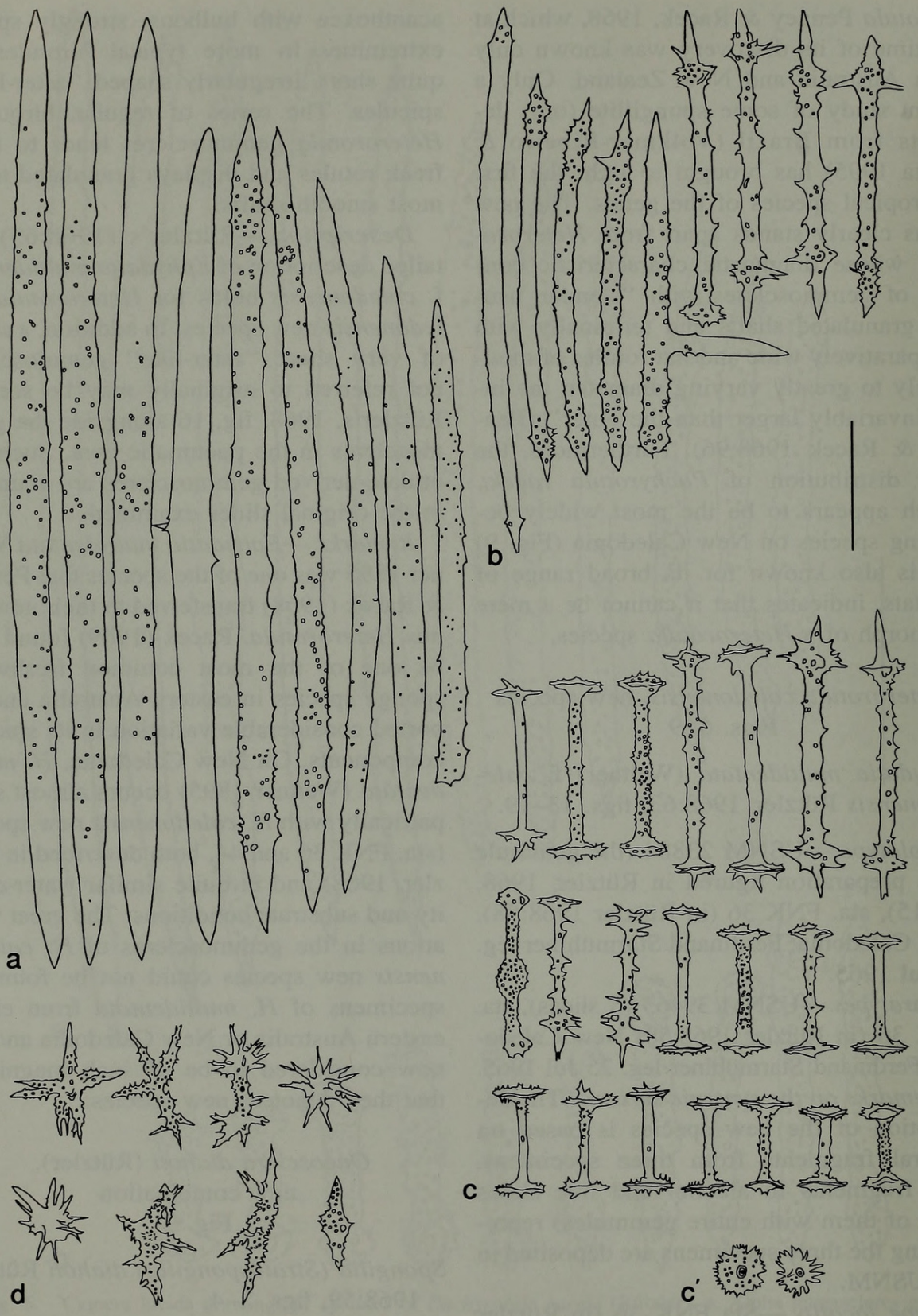

Fig. 6. Camera lucida drawings of spicules of *Heterorotula caledonensis*, new species. a, Megascleres; b, acanthoxeote gemmoscleres; c, birotulate gemmoscleres (c', head-on view of rotules); d, "aster-like" gemmoscleres. Scale = 50 μm.

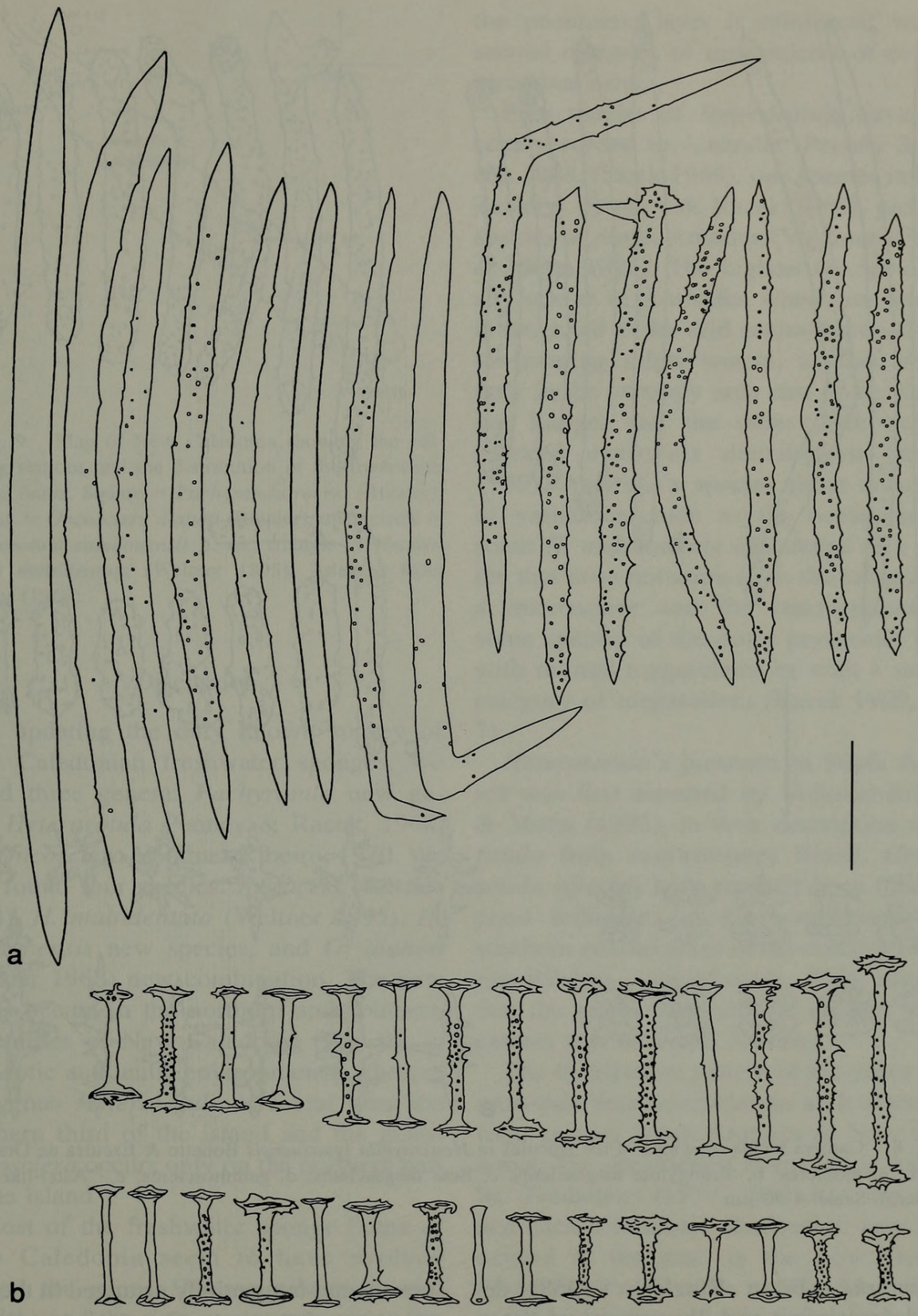

Fig. 7. Camera lucida drawings of the spicules from several specimens of *Heterorotula multidentata* (Weltner) from Australia. a, Megascleres, b, Gemmoscleres. Scale = 50 μm.

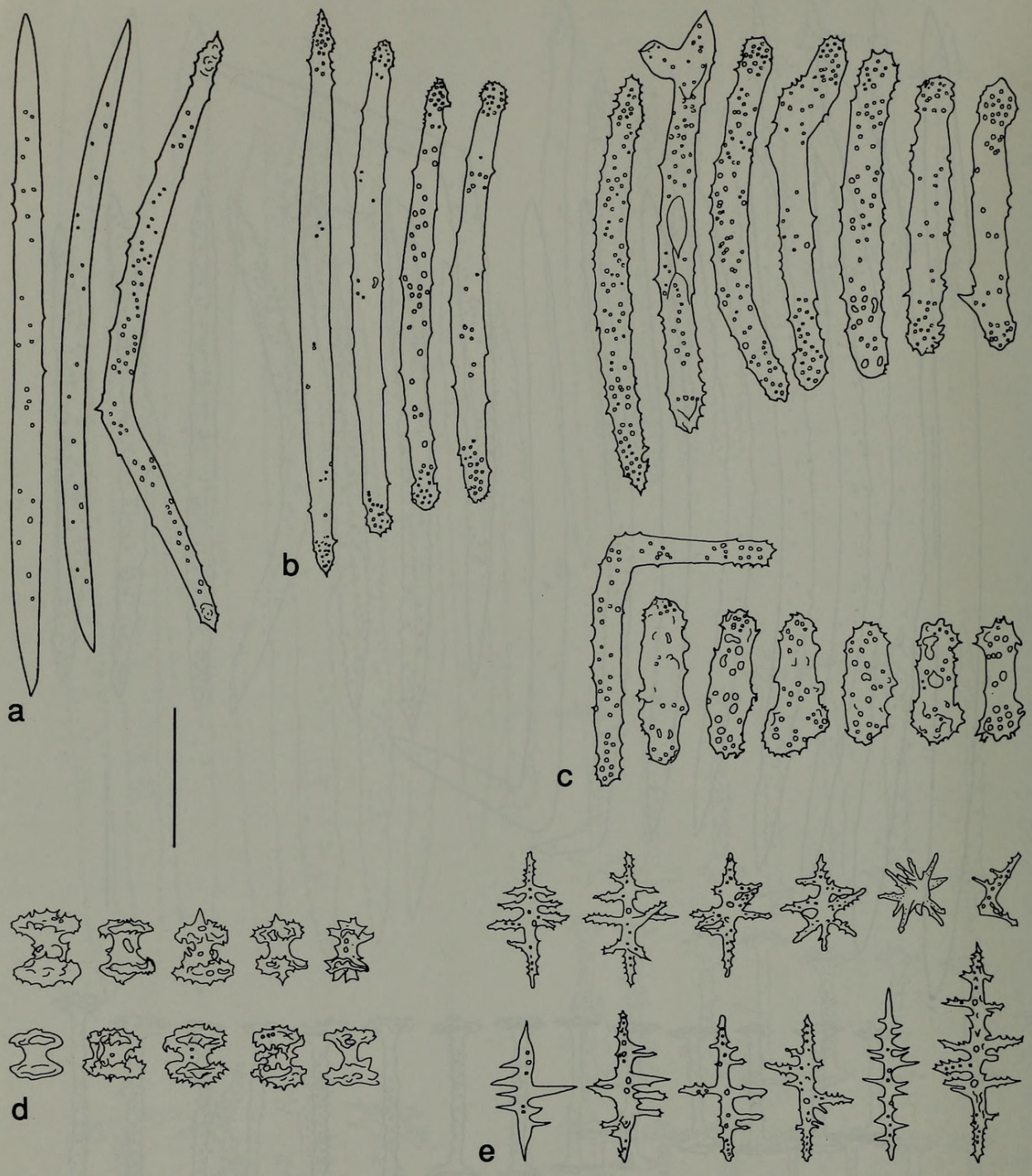

Fig. 8. Camera lucida drawings of the spicules in *Houssayella iguazuensis* Bonetto & Ezcurra de Drago. a, Tornote megascleres; b, Strongylote megascleres. c, Beta megascleres; d, gemmoscleres; e, "Aster-like" microscleres. Scale = 50 μm.

Remarks.—From Rützler's (1968) detailed description and illustrations of *Spongilla (S.) diahoti,* particularly of the gemmular structures, it appears the species belongs to the genus *Oncosclera* Volkmer-Ribeiro, 1970, which by definition contains *Stratospongilla*-like species that lack microscleres and have their gemmoscleres loosely and tangentially arranged in the outer gemmular coat. *Oncosclera diahoti* stands very close to *O. navicella* from South America, which also has small oxea with a middle thickening as gemmoscleres. However, the gemmoscleres of *O. navicella* all have a strong middle curvature that makes them look like small boomerangs.

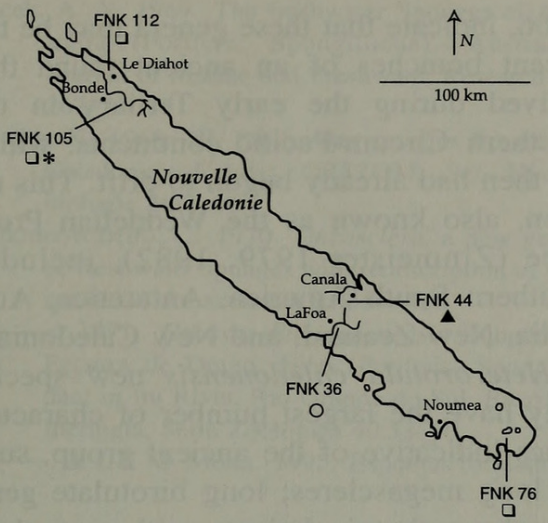

Fig. 9. Map of New Caledonia showing the collecting stations and the distribution of the freshwater sponge fauna. Square = *Pachyrotula raceki* (Rützler); asterisk = *Oncosclera diahoti* (Rützler); open circle = *Heterorotula caledonensis* n. sp.; triangle = *Heterorotula multidentata* (Weltner 1895). Adapted from Rützler (1968).

Discussion

In updating the only known survey of New Caledonian freshwater sponges, we found three genera: *Pachyrotula* new genus, *Heterorotula* Penney & Racek, 1968, and *Oncosclera* Volkmer-Ribeiro, 1970. We also found four species: *P. raceki* (Rützler 1968), *H. multidentata* (Weltner 1895), *H. caledonensis* new species, and *O. diahoti* (Rützler 1968) new combination. The new genus occurs in the northern and southern extremities of New Caledonia (Fig. 9), in both lotic and lentic environments, whereas the genus *Heterorotula* is found near the southern third of the island and the genus *Oncosclera* occurs only on the northern part of the island.

Most of the freshwater sponge fauna of New Caledonia seem to have evolved around the genus *Heterorotula* (with two species) and the new monotypic genus *Pachyrotula,* which stands closer to *Heterorotula* than to any other known genus of freshwater sponge on account of its thick, dissimilar-sized rotules of gemmoscleres with scalloped profiles, its lack of microscleres, and the fact that the outer part of the pneumatic layer is reinforced with a second category of megascleres of evident birotulate origin.

Five species of *Heterorotula* have also been recorded in Australia (Penney & Racek 1968, Racek 1969), one species in New Zealand (Penney & Racek 1968), and one species in South America (Volkmer-Ribeiro & Motta 1995). The highest species diversity occurs in Australia, where one species is restricted to the arid central part and thus to standing saline waters, another occurs only in the swampy area east of the Dividing Range, and the other three have a marked east-west distribution (Racek 1969). Australia's species show a number of variations, such as the occurrence in some *H. multidentata* specimens of a spicule that does not seem to fit the category of a microsclere and the reinforcement in some species of the outer pneumatic layer with normal megascleres or with a second category of megascleres (Racek 1969, Fig. 7).

Heterorotula's presence in South America was first reported by Volkmer-Ribeiro & Motta (1995), in their description of *H. fistula* from southwestern Brazil. *Heterorotula* spicules have recently been found in pond sediments in the northeastern and southern coastal areas of the country (Volkmer-Ribeiro, unpublished). This suggests that the genus may also be present in the eastern part of South America.

The distribution pattern of the genus *Heterorotula* thus resembles an arch extending from eastern South America to New Caledonia. The area richest in species is Australia. Zinmeister (1979, 1982) has suggested that such a faunistic distribution may have existed in the past, in the Low Tertiary Weddelian Province, as indicated by a fossil molluscan fauna. At that time, the Antarctic-Australian bloc occupied a central position in a splitting land arch that had isolated the South Circum-Pacific for a considerable period of geological time.

It may be that the genus *Pachyrotula* stands for the eastern branch of an old pa-

rental stock with *Heterorotula* relationship. This suggestion is supported by the similarity in characteristics, the central position of the Antarctic and Australian in the Weddelian Province, and the fact that the highest *Heterorotula* species diversity occurs in Australia. Could a western branch of that group also have evolved in South America? This question brings to mind the monotypic genus *Houssayella* with *H. iguazuensis* Bonetto & Ezcurra de Drago, 1966, described from the lower Parana River rocky bottom in Argentina and later from the lower Uruguay River in southern Brazil (Volkmer-Ribeiro 1971, Fig. 8). In *H. iguazuensis,* the short birotulates with thick shafts are arranged radially in the gemmules. This species is also known for its irregularly sculptured granulated rotules of dissimilar size, and for a series of beta megascleres that form a palissade packing around the gemmules; this series of beta megascleres ends in short, almost birotulate spicules quite similar to the ones found in *P. raceki.* The megascleres in *H. iguazuensis* vary from tylote to strongylote and are spined, with a concentration of spines near both ends. A third category of highly variable strongylote spicules with bulbed ends approaches the shape of beta megascleres of *Heterorotula caledonensis* new species. At the same time, *H. iguazuensis* has aster-like microscleres that closely resemble the aster-like gemmoscleres found in *H. caledonensis* new species.

No fossil or extant freshwater sponges have yet been reported from Antarctica. However, the freshwater sponge genera considered in this discussion may well have evolved from an ancient Weddelian *Heterorotula*-like stock.

Conclusions

The geographical distribution and the characteristics shared by the freshwater sponge genera *Heterorotula* (Penney & Racek 1968), *Pachyrotula* new genus, and *Houssayella* Bonetto & Ezcurra de Drago, 1966, indicate that these genera may be the recent branches of an ancient fauna that thrived during the early Tertiary in the southern Circum-Pacific continents, which by then had already begun to drift. This region, also known as the Weddelian Province (Zinmeister 1979, 1982), included southern South America, Antarctica, Australia, New Zealand, and New Caledonia.

Heterorotula caledonensis new species may have the largest number of characteristics indicative of the ancient group, such as long megascleres; long birotulate gemmoscleres that include transitions to beta megascleres; short gemmoscleres, some of which grade into an "aster-like" spicule situated in the gemmule or outside it; and the regular, spiny to granulated birotulates with thick, unequal and ragged rotules.

Acknowledgments

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This paper is dedicated to the memory of A. A. Racek, eminent freshwater-sponge systematist who died in early 1997.

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