

***Mycale (Aegogropila) kolletae* sp. n. from the SE Atlantic,  
with comments on the species of *Mycale* Gray with  
raphidotoxas (Mycalidae, Demospongiae, Porifera)**

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ABSTRACT. A new species of *Mycale* Gray, 1867 bearing raphidotoxas is described from the Namibian coast (SE Atlantic). *Mycale (Aegogropila) kolletae* sp. n. is characterized by having raphidotoxas up to 590 µm long, three distinct categories of anisochelae, two categories of sigmas, very small raphides, and most of all, by toxas serrated in an unusual pattern (on the inner parts of all three bends). *Mycale magnirhaphidifera* Van Soest, 1984 is redescribed from the Brazilian coast, based on a population from the northern São Paulo State coastline. The remaining two species with raphidotoxas, viz. *Mycale raphidotoxa* Hentschel, 1912 and *M. mannarensis* Thomas, 1968 are revised. LÉVI's (1963) record of *Carmia macilenta* (Bowerbank, 1866) for the South African coast was reevaluated and found conspecific with *M. kolletae* sp. n. It has both raphidotoxas as well as toxas with bends which are serrated on their inner surfaces. An identification key for all the *Mycale* with raphidotoxas is given, and a discussion on possible phylogenetic interpretations for the occurrence of raphidotoxas is advanced.

KEY WORDS. Poecilosclerida, Mycalidae, *Mycale*, taxonomy, microscleres, raphidotoxas, subgeneric classification, phylogeny

*Mycale* Gray, 1867 is one of the most diverse sponge genera (DOUMENC & LÉVI 1987; HAJDU 1999), and it is currently one of the most dynamic in discoveries and descriptions of new species (over 15 new species in the last decade), which is suggestive of a considerable adaptative radiation (HAJDU & DESQUEYROUX-FAÚNDEZ 1994; HAJDU *et al.* 1995; CARBALLO & HAJDU 1998; HAJDU & RÜTZLER 1998). *Mycale*'s great diversity is also reflected in the possession of a large variety of architectures, as well as in the number of categories of some of the spicules. Moreover, the micromorphology of the microscleres is also very diversified (HENTSCHEL 1913; DENDY 1921; DOUMENC & LÉVI 1987), and has great taxonomic value (HAJDU 1995; HAJDU & SOEST 1996; CARBALLO & HAJDU 1998). This is evident in the widespread use of scanning electronic microscopy in the description of new species (*e.g.* BUIZER & SOEST 1977; CARBALLO & HAJDU 1998). In spite of a varied set of spicule types and skeletal arrangements, former assays have failed to produce an entirely consistent and much needed classification scheme (*e.g.*

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HAJDU & DESQUEYROUX-FAÚNDEZ 1994; CARBALLO & HAJDU 1998; HAJDU & RÜTZLER 1998; HAJDU 1999). The currently largely accepted scheme is based on the arrangement of the ectosomal skeleton. Proposed by TOPSENT (1924), and amended by later authors (VAN SOEST 1984; BERGQUIST & FROMONT 1988), it was shown to be plastic at the species level (HAJDU & RÜTZLER 1998) as well as incongruent with the distribution of micracantoxeas (CARBALLO & HAJDU 1998).

Another spicule type, with a distribution which is seemingly inconsistent with the ectosomal skeletal arrangement, has been variously termed raphidotoxa (HENTSCHEL 1912) and magnirhaphide (VAN SOEST 1984). These are very long (usually over 200  $\mu\text{m}$ ) and very thin (usually less than 1-2  $\mu\text{m}$ ) microscleres, generally slightly sinuous or gently bent, hence the indecision for calling it a raphid or a toxa. However, we prefer to use the name proposed by HENTSCHEL (1912) because of its precedence over VAN SOEST's (1984), and therefore will be calling these spicules raphidotoxas.

A new species with raphidotoxas, collected off the Namibian coast and a population of *M. magnirhaphidifera* Van Soest, 1984 from the northern São Paulo State coastline (Brazil) are described; and the remaining two species with raphidotoxas, viz. *Mycale raphidotoxa* Hentschel, 1912 and *M. mannarensis* Thomas, 1968 are briefly revised. A discussion on possible phylogenetic interpretations for the possession of raphidotoxas is advanced.

## MATERIAL AND METHODS

Specimens were collected by scuba diving and preserved in 96 % ethanol. The preparation of dissociated spicules, both for light and scanning electron microscopy (SEM), as well as thick sections, followed the techniques described in RÜTZLER (1978). African specimens were studied in a Philips XL 20 SEM under accelerating (AV) voltages between 25 and 30 Kv, working magnifications (M) up to 9013X. Brazilian specimens were studied partly on a Jeol JSM 35-L machine (AV 25 KV, WD 15 mm, M 3600x) of the Institute for Biodiversity and Ecosystem Dynamics (University of Amsterdam); and partly on a Zeiss DSM-940 machine (AV 17-19 KV, WD ca. 8 mm, M up to 10000x) of the Instituto de Biociências (University of São Paulo).

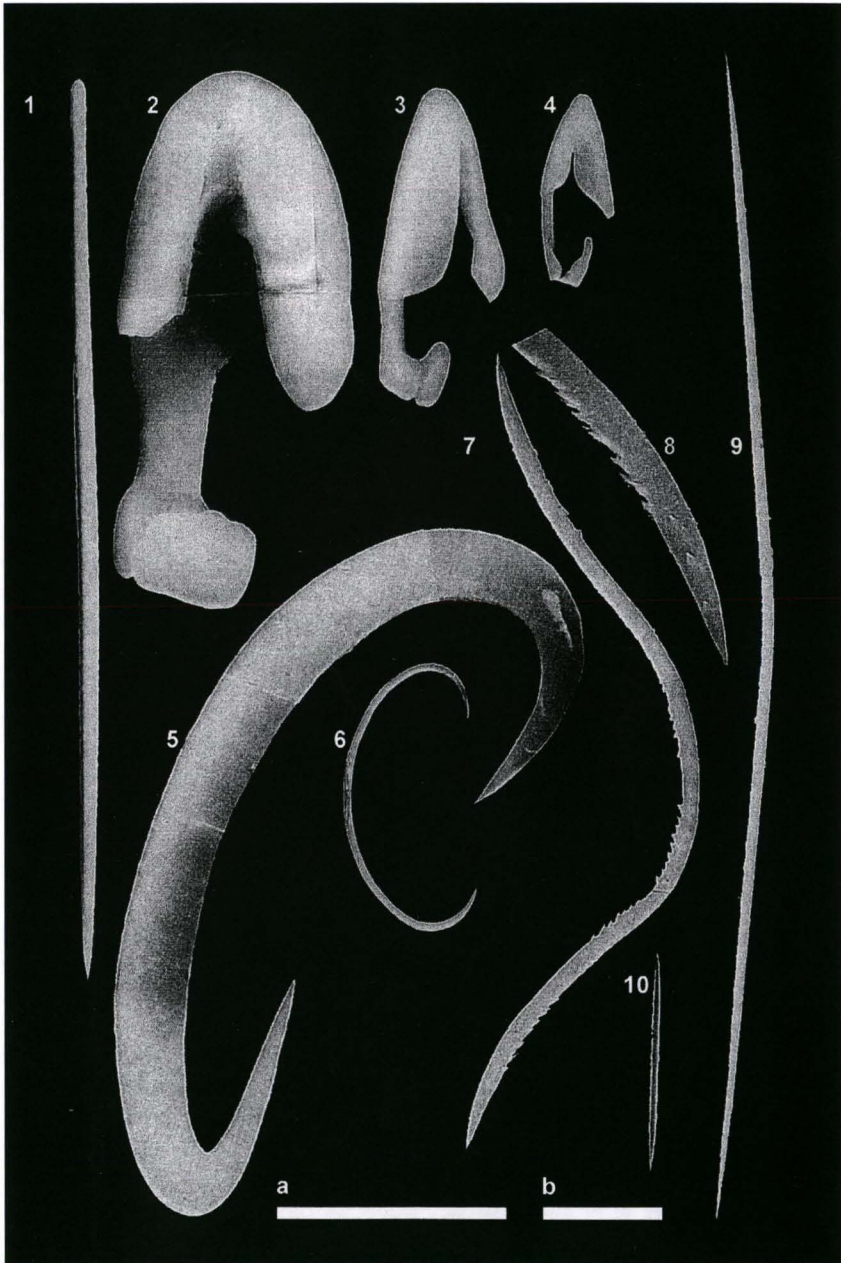
Abbreviations used are LBM (Laboratorio de Biología Marina, Universidad de Sevilla, Spain), MCNM (Museo de Ciencias Naturales de Madrid), MNRJ (Museu Nacional, Universidade do Brasil), SMF (Senckenberg Museum, Frankfurt)

### *Mycale (Aegogropila) kolletae* sp. n.

Figs 1-19, Tab. I

*Carmia macilenta*; Lévi 1963: (non *Hymeniacion* *macilenta* Bowerbank, 1866).

Material studied. Holotype MCNM-1/01/175 (Madrid-Spain), Penguin Island, Namibia, 8-12 m depth, water temperature 10°C, J.L. Carballo *leg.* Paratypes: LBM-28/11/95-1/042 (Sevilla, Spain), Possession Island, 27°00'45 S-15°11'76 W Namibia, 5-7 m depth, water temperature 9°C, J.L. Carballo *leg.* Additional material: LAM 44D, *Carmia macilenta* sensu LÉVI (1963). Comparative material: *Hymeniacion macilenta* Bowerbank, 1866 – Holotype, BMNH 1910.1.1.134-135.



Figs 1-10. SEM micrographies of spicules of *Mycale kolletae* sp. n. (Holotype). (1) Mycalostyle; (2) Anisochela-I; (3) Anisochela-II; (4) Anisochela-III; (5) Sigma-I; (6) Sigma-II; (7) serrated toxa; (8) detail of serrated toxa, raphide; (9) raphidotoxa; (10) raphide. Scales: a = 100µm (1, 9), b = 10µm (2-7, 10) and 5µm (8).



Diagnosis. *Mycale* (*Aegogropila*) with raphidotoxas, anisochelae-I, -II, -III, two morphologically distinct size classes of sigmas, characteristically bow-shaped toxas serrated on all three bends, and very small raphides.

Description. Encrusting to cushion-shaped up to 1-1.9 cm thick, extent of spread approximately  $11 \times 7 \text{ cm}^2$ . The consistency is soft and slightly compressible. The surface is irregular. Oscules of approximately 1-2 mm in diameter. We did not observe subectosomal canals, but subectosomal spaces are conspicuous. Ectosome supported by specialized skeleton. Colour in life light yellow. Growing on rocks and between *Laminaria* sp. roots.

Skeleton: The ectosomal skeleton varies from tangential loose spicules to a confused network detachable only in parts. The choanosomal skeleton is made of wavy, ascending tracts of mycalostyles, branching towards the ectosome from the base of the sponge. The tracts of mycalostyles have a reticulated/plumoreticulated architecture. In the flesh between the tracts the microscleres are strewn at random without any special arrangement. Anisochelae in rosettes were not observed.

Spicules (Figs 1-10, 11-19, Tab. I): Megascleres are usually straight mycalostyles with hardly perceptible tyle, generally slightly bent at mid length. Microscleres: anisochelae I are stout, with head length almost 60% of total length, frontal alae of foot with a slight central prominence on top. Anisochelae II of a different morphology than the previous one, with head length almost 70% of total length, with nearly straight shaft. Anisochelae III slender, lateral alae of the head commonly fused with frontal one, frontal alae of foot with short, digitiform processes on top. Typically, the frontal alae of the head are longer than the lateral alae. Sigmas I, robust, C-shaped contorted, abruptly bent into hooks with sharp endings. Sigmas II very slender (stout in LAM 44D), C-shaped contorted. Raphidotoxas thin and large, gently curved. Toxas bow-shaped, serrated on the inner parts of all three bends. Raphides straight, sharply pointed, fusiform (microxea-like), seen singly or in very small bundles.

Distribution and ecology. South Africa (LÉVI 1963), Namibia. On rocks, between *Laminaria* sp. roots, etc.

Etymology. The name is after Miss Kollet Glober, of Sea Fisheries Research of the Ministry of Fisheries and Marine Resources of the Republic of Namibia for her help during the sampling.

Remarks. *Mycale kolletae* sp. n. differs from the other known species with raphidotoxas by the possession of three categories of anisochelae and two categories of sigmas. Moreover, to our knowledge, this is the first report of serrated toxas for the genus. Terminally microspined toxas are relatively common in the Microcionidae (Microcionina, Poecilosclerida; e.g. HOOPER 1996), but these are morphologically distinct and most likely not homologous. This is a unique occurrence which widens the already large morphospace exhibited by species of *Mycale* (HAJDU 1995). *Mycale kolletae* sp. n. possesses an ectosomal skeletal arrangement which is not the typical neat reticulation of megasclere bundles of *Aegogropila*, rather, it has a major component of single spicules, where paucispicular tracts are only seldom seen. We consider nevertheless that the reticulated pattern is visible, if not clearly so, and assign *M. kolletae* sp. n. to the subgenus *Aegogropila*. The pattern observed in *Mycale* (*Mycale*) is much more spicule dense than that observed here.

LÉVI's (1963) record of *Carmia macilenta* (Bowerbank, 1866; = *M. macilenta*) has been reexamined (Figs 11-19) and found conspecific to *M. kolletae* sp. n. The holotype of *M. macilenta* has been reexamined too, and found to be distinct from the new species described here in several aspects. It has 1) megascleres which are much thinner; 2) anisochelae-I much skinnier; 3) toxas which can be much larger, and which are never acanthose; and 4) absence of any raphides.

Table I. Comparative data for the dimensions of the spicules (in  $\mu\text{m}$ ), ectosomal architecture and geographic distribution of the *Mycale* species with raphidotoxas

	<i>M. raphidotoxa</i>	<i>M. mannarensis</i>	<i>M. magnirhaphidifera</i> <sup>1</sup>	<i>M. magnirhaphidifera</i> <sup>2</sup>	<i>M. kolletae</i> sp. n. <sup>3</sup>
Mycalostyles	304-392 x 5-6	294-315 x 4-8	236-270 x 1.5-3	196-286 x 4.4	250-372 x 9.5-16.5 (250-360 x 6-12)
Anisochelae	I: 39-45 in rosettes II: 17-20	I: 21-42	I: 31-35 in rosettes II: 11-13	I: 31-35 in rosettes II: 11-13	I: 35-43.5 (30-48) II: 20.5-26 (20-28.4) III: 13.5-17 (10-15.9)
Sigmas	63-96	63(75)84 x 1(3.1)4	not found	I: 32(43.6)50 II: 13-21	I: 35-82.5 x 2.2-3 (70-105.5 x 4-7) II: 19-23.5 (14-39)
Toxas	-	-	-	-	45-60 (serrated)
Raphidotoxas	200-300 (in bundles)	376-528	260-310 (in dragmas)	I: 90-241 II: 13-22	380-590
Rhaphides	-	-	-	-	6-11 (5-10)
Ectosomal architecture	<i>Carmia</i>	<i>Aegagropila</i>	<i>Carmia</i>	<i>Carmia</i>	<i>Aegagropila</i>
Distribution	Indian Ocean (Moluccas), over coral, 12 m depth	Indian Ocean on <i>Halimeda</i> sp, 1 m depth	Caribbean (Curaçao), on worm tubes	Caribbean (Belize), on mangroove roots	South east Atlantic, on <i>Laminaria</i> roots, over rocks

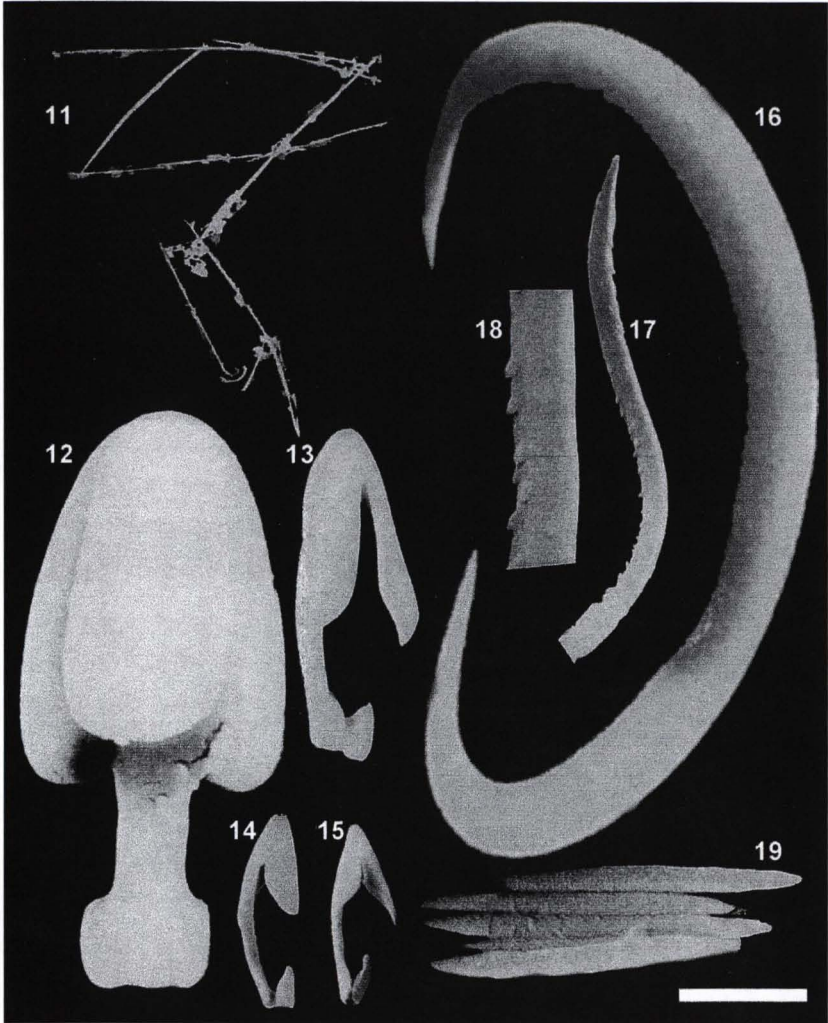
(1) VAN SOEST 1984; (2) HAJDU & RÜTZLER 1998; (3) data for the paratype is shown between brackets.

*Mycale (Aegogropila) mannarensis* Thomas, 1968

Tab. I

Diagnosis. *Mycale (Aegogropila)* with raphidotoxas mostly over 400 $\mu\text{m}$  long, with anisochelae and sigmas not separable into different categories, no toxas.

Brief description (adapted from THOMAS 1968: 255). Encrusting sponge (maximum thickness of 2mm), rather fleshy and slimy to touch. The colour in life is black. Surface smooth and slimy. Ectosome not detachable, with a well developed reticulation of bundles of mycalostyles, and between them, tracts of raphidotoxas can appear arranged in long and continuous bands. Main skeleton consists of ill-defined fibers arranged at a slanting angle to the surface. Mycalostyles with straight shaft, and head prominent in some. Anisochelae in rosettes, not separable into different categories. Sigmas, flat or contorted. Raphidotoxas slender and straight, middle portion widest.



Figs 11-19. SEM micrographies of the spicules of *Mycale kolletae* sp. n. (Paratype, = *Carmia macilenta* sensu LÉVI 1963). (11) Raphidotoxas; (12) Anisochela-I; (13) Anisochela-II; (14) Anisochela-III (oblique view); (15) Anisochela-III (side view); (16) Sigma-I; (17) serrated toxa (in part); (18) detail of serrated toxa; (19) raphides in a bundle. Scales: a = 200 $\mu$ m (11), 10 $\mu$ m (12-17), 5 $\mu$ m (18), 3 $\mu$ m (19).

Distribution and ecology. So far known from its type locality only, viz. Hare Island (Gulf of Mannar, India). Common on *Halimeda* sp. (calcareous algae) beds, at 1 m depth.

Remarks. It has not been possible to obtain the type of *M. (A.) mannarensis* on loan, but the raphidotoxas with a mean length around 400 $\mu$ m together with the absence of toxas, as recorded by THOMAS (1968), make this species clearly recognizable from other *Mycale* with raphidotoxas.



*Mycale (Carmia) magnirhaphidifera* Van Soest, 1984

Figs 20-29, Tabs 1-2

Refer to HAJDU & RÜTZLER (1998) for a synonymy list.

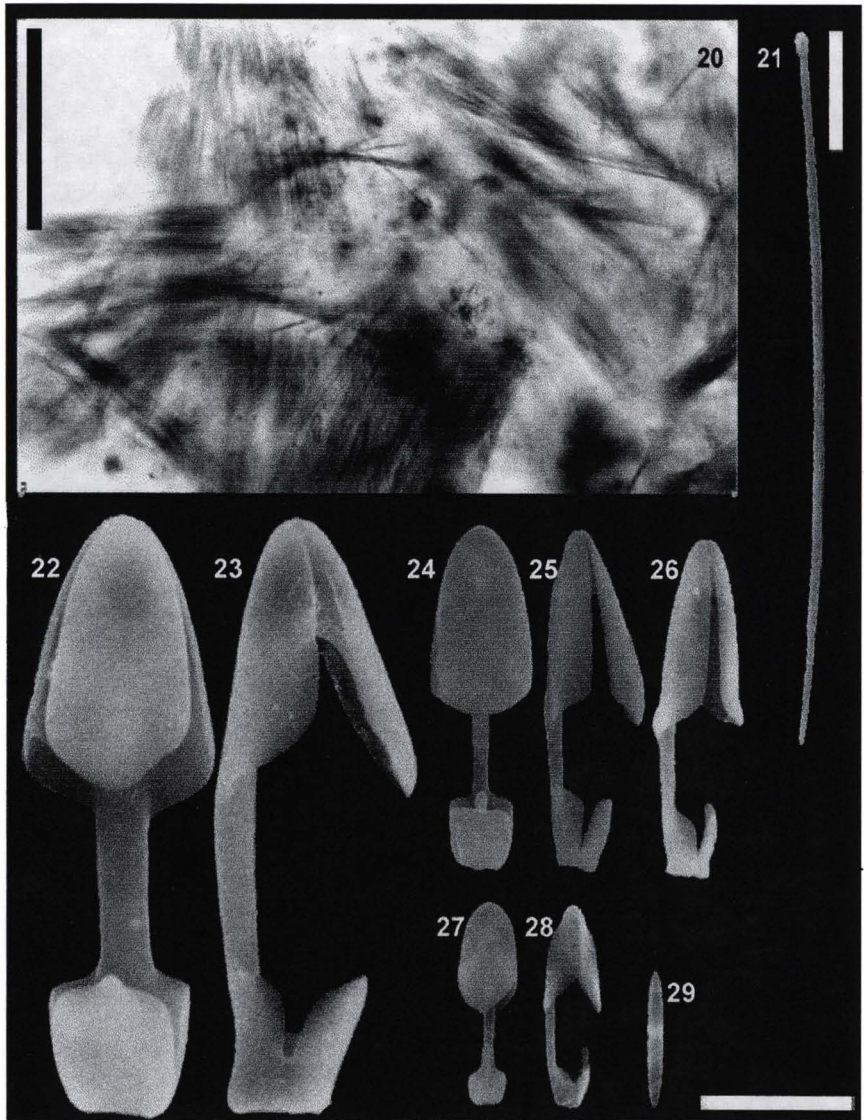
Material studied. BRAZIL, *São Paulo*, Ilha de São Sebastião, Ilhabela: MNRJ-157, Ponta do Frade (23°54.972'S, 45°27.547'W), 24 m depth, E. Hajdu *leg.*, 16.I.1996; MNRJ-196, 197 and 227, small inlet between Ponta da Sela and Ponta da Figueira (23°53.127'S, 45°27.526'W), 12m depth, E. Hajdu *leg.*, 16.I.1996; MNRJ-345, submerged islet (stone slab) on the west of Ilha da Serraria (23°48.758'S, 45°13.812'W), 5-21 m depth, E. Hajdu & G. Muricy *leg.*, 25.I.1996; MNRJ 530, Ponta do Frade (23°54.972'S, 45°27.547'W), 5-8m depth, E. Hajdu *leg.*, 21.VI.1997; MNRJ 532, small inlet between Veloso and São Pedro localities (23°52.863'S, 45°26.930'W), 5-8m depth, E. Hajdu *leg.*, 20.VI.1997; MNRJ 562, Ilhota da Prainha (23°51.146'S, 45°24.997'W), 4 m depth, E. Hajdu *leg.*, 16.VI.1997; MNRJ 591, Portinho (23°50.582'S, 45°24.427'W), 3m depth, E. Hajdu *leg.*, 19.VI.1997; MNRJ-777 and 780, submerged islet (stone slab) on the west of Ilha da Serraria (23°48.758'S, 45°13.812'W), 20 m depth, E. Hajdu *leg.*, 11.I.1996; MNRJ 1330, Praia Preta (23°49.247'S, 45°24.435'W), 1-2 m depth, E. Hajdu, E. Costa & R. Fernandes *leg.*, 22.XII.1997; MNRJ 1334, Saco do Sombrio (23°53.850'S, 45°14.900'W, southern Castelhanos Bay), 2-3 m depth, E. Hajdu *leg.*, 03.XII.1997; MNRJ 1653, northern Ilha das Cabras (23°49.715'S, 45°23.569'W), 3.5 m depth, E. Hajdu *leg.*, 16.IV.1998; MNRJ 1998, western Ilha de Búzios (23°48.290'S, 45°09.448'W), 10 m depth, E. Hajdu & M.C. Guerrazzi *leg.*, 07.II.1999.

Diagnosis. Encrusting, deep-purple to brown-grey *Mycale (Carmia)* with anisochelae-I always smaller than 40µm long, and anisochelae-II always smaller than 15µm long, with or without sigmas smaller than 50µm long; and two size classes of raphides, the larger ones, raphidotoxas over 200µm in length, and the smaller ones mostly under 20µm.

Description. The species is always thinly encrusting, less than 2 mm thick. Specimens often cover over 100 cm<sup>2</sup>, and in some cases were observed to spread over 300 cm<sup>2</sup>. They are fragile (very soft), and possess a smooth surface where irregularities are due to the underlying substrate (*e.g.* barnacles, limpets, bivalves, coralline algae). Colour alive is most frequently a deep-purple. Oscula are few, spread over the sponge surface, and often small (< 5 mm in diameter). Subectosomal canals are frequently conspicuous, sometimes marked by a whitish tinge, and converge in a starry pattern to the oscula.

Skeleton. The ectosomal skeleton consists in some specimens, of a dense feltwork of large raphidotoxas (ca. 100 x 400 µm), where rosettes of anisochelae-I (10-15 spicules, ca. 100 µm in diameter) are common too. The choanosomal skeleton is made of sinuous ascending tracts of megascleres, which diverge slightly into brushes when approaching the surface. Anisochelae-II and -III may be very common all over the sponge.

Spicules. (Figs 20-29, Tab. I-II) Megascleres are mycalostyles, smooth, straight or nearly so, slender, with abrupt sharpening of the apex, and well-marked



Figs 20-29. Ectosomal skeleton and SEM micrographies of the spicules of Brazilian *Mycale magnirhaphidifera* Van Soest, 1984. (20) Ectosomal architecture with conspicuous large trichodragmas of raphidotoxas. Rosettes of anisochelae-I are visible near the centre of the image; (21) Mycalostyle; (22) Anisochela-I, face view; (23) Anisochela-I, side view; (24) Anisochelae-II, face view; (25) Anisochela-II, side view; (26) Anisochela-II, side view; (27) Anisochela-III, face view; (28) Anisochela-III, side view; (29) Raphide. Scales = 100 $\mu$ m (20), 50 $\mu$ m (21), 10 $\mu$ m (22-29).



elliptic heads. Microscleres: Anisochelae-I, slender, very slightly curved on profile view, head about 50% of total spicule length, both frontal alae nearly straight, faint digitiform process on top of the frontal alae of the foot. Anisochelae-II, nearly straight on profile view, head about 55% of total spicule length, base of frontal alae of the head may be slightly bent forward, base of lateral alae of the head may be slightly bent backward protruding over the shaft, digitiform process on top of the frontal alae of the foot may be present. Anisochelae-III, slender, slightly curved on profile view, head about 50% of total spicule length, head slightly constricted distally, marked digitiform process on top of the frontal alae of the foot (nearly doubling the length of the foot). Raphidotoxas, very thin, straight, slightly bent or slightly sinuous, sharply pointed. Raphides, short, stout, fusiform (microxea-like), sharply pointed.

Distribution and ecology. The species is widespread in the Tropical western Atlantic, with a single dubious report from Subtropical NW Atlantic waters. In the SW Atlantic (São Sebastião Channel and its environs) it is a common species, usually confined to semi-obscure environments. It will occur outside small caves, but on vertical rocky walls. Its known depth range is from ca. 1 to 24 m. A specimen bearing larvae was seen in 16.VI.1998. MNRJ 1334 was associated to a living scallop, and was thus a “mobile sponge”.

Remarks. The presence of sigmas seems to be a variable trait among different populations of this species, which conform on many other details of sponge habitus and spicule morphology. Micrometric data reported here match well with data for Caribbean specimens (VAN SOEST 1984; HAJDU & RÜTZLER 1998; Tab. II).

Table II. Comparative data for the dimensions of the spicules (in  $\mu\text{m}$ ) of selected Brazilian specimens of *Mycale (Carmia) magnirhaphidifera* Van Soest, 1984. Values between brackets are means. Micrometries for the megascleres are shown as length/head width/shaft width.

Specimens	Mycalostyles	Anisochelae	Raphidotoxas	Raphides
MNRJ 196	270(287.5)300 /3.7(5.6)8.8 /2.5(4.6)7.5	I: 35(38.2)42 II: 22(23.0)24 III: 12(14.0)16	243(257.0)310	
MNRJ 197	184(277.9)320 /2(2.5)3 /1(2.1)3	I: 38(39.5)42 II: 20(22.9)25 III: 11(13.6)16	281(322.0)359	
MNRJ 227	243(255.3)272 /1.5(2.5)3 /1.5(2.0)3	I: 34(38.2)46 II: 20(22.8)24 III: 13(14.5)16	272(309.9)340	7.2 (N=1)
MNRJ 345	262(277.9)301 /1.5(2.4)3 /1(2.1)3	I: 31(34.1)36 II: 19(20.8)23 III: 11(12.4)14	180(237.5)280	
MNRJ 777	233(257.5)301 /5(6.3)7.5 /3.8(5.1)7.5	I: 28(31.0)37 II: 19(22.0)24 III: 12(13.3)14	272(304.6)330	
MNRJ 780	224(269.2)310 /5(6.9)8.8 /3.8(5.8)7.5	I: 29(32.4)36 II: 19(21.6)26 III: 11(13.1)16	213(266.7)310	

*Mycale (Carmia) raphidotoxa* Hentschel, 1912

## Tab. I

Material studied. Holotype SMF 1034, Strait of Dobo (stn. 15), Aru Islands, Indonesia, 12.III.1908.

Diagnosis. *Mycale (Carmia)* sp. with raphidotoxas mostly smaller than 400  $\mu\text{m}$ , encrusting, yellowish-brown, with anisochelae-I mostly over 40  $\mu\text{m}$  long, anisochelae-II over 15  $\mu\text{m}$  long, and abundant sigmas over 60  $\mu\text{m}$  long.

Brief description (adapted from HENTSCHEL 1912: 340). Thinly encrusting, 9.5 cm long by 1 mm thick. Surface finely granulated. Live colour same as in fixative, yellowish-brown. Plumose architecture with ascending spicule tracts ca. 40  $\mu\text{m}$  wide and bearing no visible spongin. Ascending tracts diverge in 3 to 7 smaller tracts when approaching the surface. A surface membrane hangs on the terminations of these fibres. Many embryos, ca. 400  $\mu\text{m}$  wide, occur in the choanosome. Megascleeres are mycalostyles, straight, base only slightly inflated, abruptly pointed, 304-392/5-6  $\mu\text{m}$  (length/width). Microscleeres are anisochelae I in rosettes, slightly curved shaft, head nearly 50% the total microsclere length, 39-45  $\mu\text{m}$ . Anisochelae II scattered around, elongated and slender, shaft nearly straight, head 50-66% of the total microsclere length, 17-20  $\mu\text{m}$ . Sigmas (63-96  $\mu\text{m}$  long) and raphidotoxas, mostly in bundles, occur more frequently near the surface. Raphidotoxas often bent at the center, and sometimes in the opposite direction near each end, 200-400  $\mu\text{m}$ .

Distribution and ecology. The only published record of the species was from its type locality in the Arafura Sea (Dobo Strait, Aru, Indonesia), at 12 m depth, on coral rocks.

Remarks. The holotype of *M. (C.) raphidotoxa* has been reexamined and data as provided by HENTSCHEL (1912) in the original description, found to be correct. The species is clearly set apart from other *Mycale* with raphidotoxas by its *Carmia* type of ectosomal skeletal arrangement, and common and conspicuous sigmas always larger than 60  $\mu\text{m}$ .

Identification key for the species of *Mycale* with raphidotoxas

1. Ectosomal skeleton reticulated (*Aegogopila* type) ..... 2
- . No ectosomal skeletal specialization (*Carmia* type) ..... 3
2. Toxas present (serrated) ..... *M. (A.) kolletae* sp. n.
- . Toxas absent ..... *M. (A.) mannarensis*
3. Sigmas always larger than 60  $\mu\text{m}$  ..... *M. (C.) raphidotoxa*
- . Sigmas, when present, mostly smaller than 50  $\mu\text{m}$  ... *M. (C.) magnirhaphidifera*

## DISCUSSION

Species of *Mycale* with raphidotoxas, like those species possessing micracontoxeas (CARBALLO & HAJDU 1998), also exhibit more than one type of ectosomal architecture. Given the current classification, those sponges are to be spread over more than one subgenus, viz. *Aegogopila* and *Carmia*. The alterna-

tive interpretation for the apparently very restricted occurrence of micracantoxeas, i.e. that they might have been frequently overlooked due to their minute dimensions, is not plausible in regard to raphidotoxas as these are very conspicuous. The remaining possible interpretations focus on the phylogeny of the characters, which may have had either a single or multiple origins. Two possible evolutionary scenarios can be thought of given a single origin of large raphides within *Mycale*. 1) Species may form a monophyletic group, and their spreading over two distinct subgenera may be entirely artificial; or 2) raphidotoxas may have had an earlier origin with many subsequent losses and reappearances (a switch-on, switch-off model), in which case the splitting of extant species with these microscleres in distinct subgenera need not be artificial. Origin of the character might have been prior to the subgenera in question. Another two possible interpretations can be envisaged given the character's multiple origin. 3) Raphidotoxas may have had a single independent origin within each subgenus, in which case species of *Aegogropila* bearing the character would most likely constitute a cluster of closely allied species, the same applying to the species of *Carmia* with raphidotoxas. Two monophyletic clusters of species would exist then. 4) Raphidotoxas may have had several independent origins instead, in which case no *Mycale* species with these microscleres need be closely allied to any other species with similar spicules, as these are only analogous.

Multiple origin scenarios could be further split into those followed by losses and those where no losses occurred, which only points to how inconclusive this line of reasoning can eventually be.

A quick scrutiny of the character's distribution over a more inclusive universe favours interpretation 2 (the switch-on, switch-off model). It is based on the observation that the raphidotoxas co-occur with the very small, fusiform, microxea-like raphides in *Mycale kolletae* sp. n. and *M. magniraphidifera*, the two better known species considered here. The possibility cannot be discarded that such fusiform raphides may be found in the other two species upon closer scrutiny. These smaller raphides were reported recently from *Mycale (Mycale) laevis* (Carter, 1882), where they occur in dense bundles (trichodragmata; HAJDU & RÜTZLER 1998). Nevertheless, other species bearing more closely on the issue of the phylogenetic significance of the raphidotoxas, viz. belonging to subgenera *Aegogropila*, *Carmia* or *Naviculina*, have been described recently based on SEM analysis, but no comparable small fusiform raphides were found (e.g. BUIZER & SOEST 1977; REISWIG & KAISER 1989; CARBALLO & GARCIA-GOMES 1994; CARBALLO & HAJDU 1998; HAJDU & RÜTZLER 1998; HAJDU 1999). It is possible then that a single switch-on event gave rise to the small fusiform, microxea-like raphides considered here, which is congruent with the distribution of the raphidotoxas, but not with the ectosomal architecture, and, perhaps neither with the shape of the anisochelae-I which varies considerably in stoutness.

Raphides of varied lengths are also widespread outside *Mycale*, both within and outside the Mycalina. Their intermittent occurrence at these levels corroborates the "switch-on, switch-off" mechanism of character expression advocated above (THROCKMORTON 1965; SLUYS 1989; HAJDU *et al.* 1994). These



characters can be interpreted as synapomorphies at more exclusive levels of universality, and as "underlying synapomorphies" at more inclusive ones. For a criticism of the concept of "underlying synapomorphies" see FARRIS & PLATNICK (1989), NELSON (1994) and HAJDU (1995).

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