

# Sponges, genus *Mycale* (Poecilosclerida: Demospongiae: Porifera), from a Caribbean mangrove and comments on subgeneric classification

Eduardo Hajdu and Klaus Rützler

(EH) Institute of Systematics and Population Biology, University of Amsterdam,  
P.O. Box 94766 1090-GT, Amsterdam, The Netherlands;

Present address: Departamento de Invertebrados, Museu Nacional,  
Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, s/n 20940-040, Rio de Janeiro,  
RJ; and Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, SP, Brazil;

(KR) Department of Invertebrate Zoology, National Museum of Natural History,  
Smithsonian Institution, Washington, D.C. 20560, U.S.A.

*Abstract.*—Eight species of *Mycale* Gray (Mycalidae, Poecilosclerida, Demospongiae) are described from marine mangroves on the barrier reef of Belize, Central American Caribbean. Two are new: *Mycale* (*Aegogropila*?) *carmigropila* and *M. (Ae.) citrina*. Other species found are *M. (Ae.) arndti*, *M. (Arenochalina) laxissima*, *M. (Carmia) magnirhaphidifera*, *M. (C.) microsigmatosa*, *M. (Mycale) laevis* and *M. (Paresperella)* sp. A key to the 17 recognized Caribbean species of *Mycale* is provided. Ectosomal skeletal patterns currently used as diagnostic characters for subgenera of *Mycale* may be inadequate for phylogenetic analysis, but reliable alternative congruent traits have not yet been identified to replace these.

More than 150 species of *Mycale* Gray have been described worldwide (Doumenc & Lévi 1987), with representatives in most marine habitats. They are common in both polar and tropical seas, and have been reported from intertidal pools abyssal depths (Hartman 1982). Contemporary monographs have added great numbers of new species (Lévi 1963, van Soest 1984, Bergquist & Fromont 1988, Hajdu & Desqueyroux-Faúndez 1994), indicating that many more undescribed taxa are yet to be found. Our study of the rich marine mangrove ecosystem of Belize (Rützler & Feller 1988, 1996; de Weerd et al. 1991) is no exception and has revealed two new species of *Mycale*. Recent findings of metabolites with pharmacological potential from species of *Mycale* (e.g., Capon & Macleod 1987; Perry et al. 1988, 1990; Fusetani et al. 1989; Corriero et al. 1989; Butler et al. 1991; Northcote et al. 1991; Hori et al. 1993)

have strengthened the need for a better assessment of the genus' biodiversity, for a stable system of classification, and for better descriptions to differentiate between allopatric sibling species.

It has been convincingly argued that descriptions of *Mycale* are often unreliable in respect to noting size categories of microscleres (Hentschel 1913, Doumenc & Lévi 1987). Accordingly, special attention was here paid to this important characteristic. Details of microsclere shape too were long considered to be useful characters because of their low adaptive value (Ridley & Dendy 1887, Dendy 1921, Hajdu et al. 1994a, Hajdu & Desqueyroux-Faúndez 1994). This view is adopted here and supported by our scanning electron micrography.

## Materials and Methods

Sponges were collected by the authors and Kathleen P. Smith during several sur-

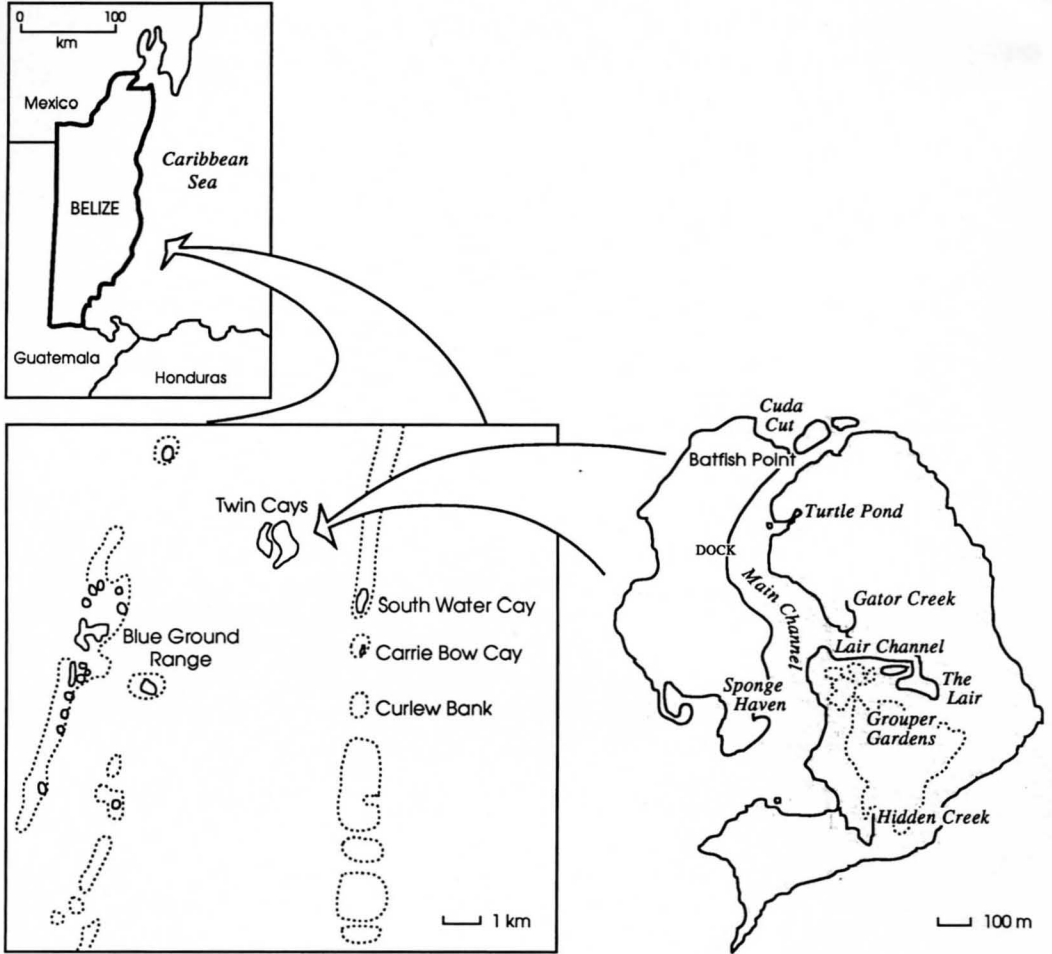


Fig. 1. Map of collecting area on the barrier-reef platform of Belize. Geographical coordinates for principal localities are  $16^{\circ}48.18'N$ ,  $88^{\circ}04.93'W$ , Carrie Bow Cay;  $16^{\circ}49.95'N$ ,  $88^{\circ}06.34'W$ , Twin Cays; and  $16^{\circ}48.55'N$ ,  $88^{\circ}08.89'W$ , Blueground Range.

veys of mangroves in the vicinity of Carrie Bow Cay, Belize ( $16^{\circ}48'N$ ,  $88^{\circ}05'W$ ) (Fig. 1). Specimens are deposited in the sponge collection of the National Museum of Natural History, Washington, subsamples were donated to the Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil. Schizotypes of the two new species were also deposited in The Natural History Museum, London, Queensland Museum, Brisbane, and Zoologisch Museum Amsterdam.

Most anatomical preparations were made according to Rützler (1978) and Hajdu (1994). Additionally, skeletons for study by

scanning electron microscopy (SEM) were prepared in one of the two following ways: Samples in ethanol were washed of debris with several jets of ethanol, air dried in an oven, and mounted on SEM stubs by applying a thin layer of Entellan (Merck); samples from ethanol were washed in warm water (ca. 1 min), immersed in a saturated solution of soda, and heated to  $50\text{--}70^{\circ}C$  (30 min). Then they were again washed in warm water (1 min) and etched in 20%  $HNO_3$  at room temperature. After a few minutes under observation, samples were rinsed with warm-water jets (1 min) and a

few drops of hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) solution added to the last change of water. After 30 min at 50–70°C the samples were rinsed in warm water (1 min), transferred to ethanol (96%, 30 min), air-dried in an oven, and mounted on SEM stubs.

Abbreviations used are: BMNH (The Natural History Museum, London), INV-POR (Invemar-Porifera Collection, Universidad Nacional de Colombia, Santa Marta), MCZ (Museum of Comparative Zoology, Harvard University, Cambridge), MNHN (Muséum National d'Histoire Naturelle, Paris), MNRJ (Museu Nacional, Universidade Federal do Rio de Janeiro), MSNG (Museo Civico di Storia Naturale di Genova), MUT (Museo della Università di Torino), NNM (National Natuurhistorisch Museum, Leiden), QM (Queensland Museum, Brisbane), UFRJPOR (Universidade Federal do Rio de Janeiro, Porifera collection), USNM (National Museum of Natural History, Washington), and ZMA POR (Zoölogisch Museum Amsterdam, Porifera collection).

### Systematic Descriptions

Order Poecilosclerida Topsent, 1928

Suborder Mycalina Hajdu et al., 1994

Family Mycalidae Lundbeck, 1905

Genus *Mycale* Gray, 1867; sensu Hajdu & Desqueyroux-Faúndez 1994

*Diagnosis*.—Mycalidae with skeleton of subtylostyles and palmate anisochelas; additional microscleres may include sigmas, toxas, micracanthoxeas, raphides, unguiferate anisochelas, and palmate isochelas.

Subgenus *Aegogropila* Gray, 1867

*Diagnosis*.—*Mycale* with tangential ectosomal skeleton of reticulate spicule tracts (often easily peeled off), without serrated sigmas. Type species: *Aegogropila varians* Gray, 1867 (= *M. [Ae.] contarenii* [von Martens, 1824, as *Spongia contarenii*.]).

*Remarks*.—Bergquist & Fromont (1988) in quoting *Halichondria aegagropila* John-

ston, 1842 (misspelled as *H. aegogropila*) as a type-species of *Aegogropila* (Thiele 1903) overlooked Gray's (1867) name, *Aegogropila varians*. Because *Ae. varians* was probably a replacement name in order to avoid tautology, although not clearly stated so by Gray (1867), we choose the figured specimen of *H. aegagropila* in Johnston (1842, BMNH 1847.9.7.39) as lectotype of *Ae. varians*. In this way, both species become objective synonyms. This point was made clear by L. B. Holthuis (in lit.).

The plasticity reported here for the presence of ectosomal reticulation in *Mycale* (*Ae.?*) *carmigropila* new species is taken as indication that some representatives of *Carmia* (see below) are more closely related to *Aegogropila* than to other species of *Carmia*, suggesting parphyly of the former subgenus and polyphyly of the latter. Additionally, some *M. (Mycale)* species may have their confused tangential ectosomal skeleton developed so thinly as to make spicules strewn at random appear reticulated to the casual observer (cf. *M. [M.] thielei* Hajdu & Desqueyroux-Faúndez 1994). Species like this have been assigned to *Aegogropila* in the past, for instance *M. (M.) flagelliformis* (Bergquist & Fromont, 1988) which has pore-grooves and a confused ectosomal skeleton. It becomes apparent that the monophyletic status of *Aegogropila* may not hold up in a thorough revision of all species. Such a revision is not yet possible, given that collections are dispersed, many new taxa are still being discovered, and, more importantly, no other congruent characters are yet apparent to replace the existing system.

*Mycale (Aegogropila) arndti* van Soest,  
1984

Figs. 2, 3, 17a; Table 1

*Esperia macilenta*.—Carter 1871:276, pl. 17, fig. 8; not *Hymeniacidon macilenta* Bowerbank, 1866 (= *Mycale (Carmia) macilenta*).

*Mycale macilenta*.—Arndt 1927:143, in

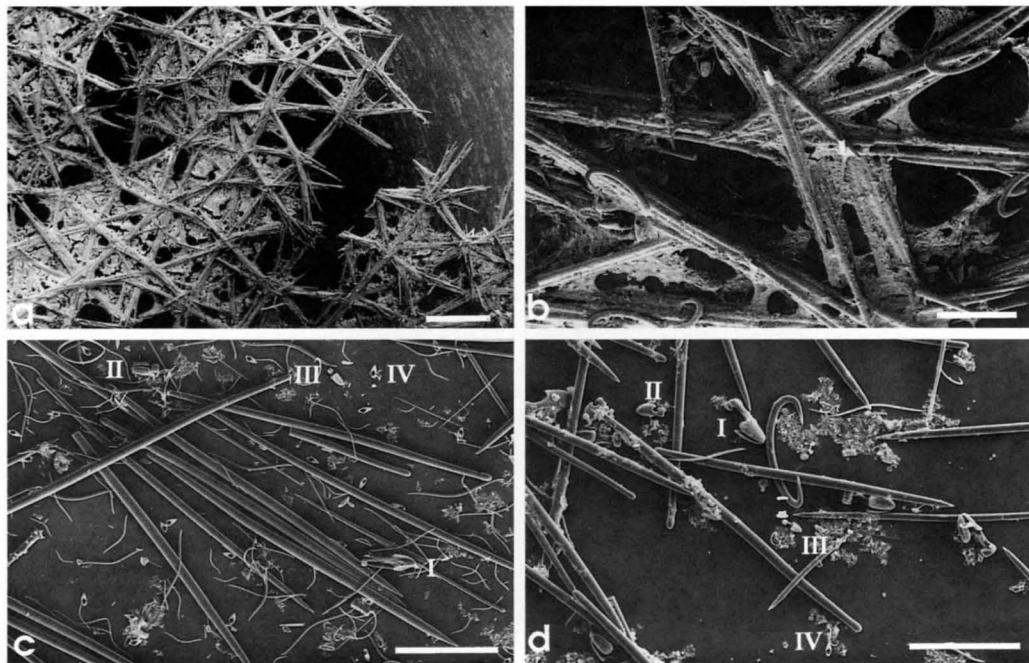


Fig. 2. *Mycale arndti*, skeleton: a, Peeled-off surface showing ectosomal reticulation; scale equals 500  $\mu\text{m}$ ; b, Detail of surface reticulation showing sigmas-I disposed around the bundles of megascleres, and disposition of rosettes (R) in the corners of the meshes; scale equals 100  $\mu\text{m}$ ; c, d, Fusiform subtylostyles and all four categories of anisochelas (I-IV); scale equals 100  $\mu\text{m}$ . (a-c, USNM 39329; d, holotype ZMA POR 3675.)

part (not the figured specimen); not *Hymeniacion macilenta* Bowerbank, 1866 (= *Mycale (Carmia) macilenta*).

*M. (Aegogropila) arndti* van Soest, 1984: 19, pl. II, fig. 1. Zea 1987:140.

**Material studied.**—ZMA POR 3675, holotype, Curaçao; ZMA POR 3842, paratype, Florida. USNM 43032, Belize, Twin Cays, Batfish Point, <1 m, coll. K. Rützler, 27 Apr 1989; USNM 39329 (MNRJ 630), Belize, Blue Ground Range, 1 m, coll. E. Hajdu & K. Smith, 12 Aug 1993; USNM 47871, Blueground Range, on red-mangrove stilt root, <1 m, coll. K. Smith, Nov 1996.

**Diagnosis.**—Bluish, crustose *Aegogropila* with sigmas (three categories) and toxas; four categories of anisochelas, with categories II and IV having exceptionally long frontal alae (alae of head and foot nearly fused), covering the entire shaft in frontal view.

**Description.**—Macroscopic appearance: Grayish blue to gray crust or cushion with oscules often raised like small chimneys; non-slimy when rubbed. Preserved material is composed of seven main fragments, the largest is 55 mm long, 30 mm wide, and up to 4 mm thick. The color in alcohol is drab or pink, varying from light pink to almost violet. The fragments have firm consistency and microhispid surface texture. The ectosome has sand grains embedded in the surface and is easily peeled off. No oscules are apparent.

**Skeleton:** The ectosomal skeleton is a tangential reticulation of 120  $\mu\text{m}$  thick subtylostyle bundles (Fig. 2a), with no apparent cementing spongin. Meshes are mostly triangular and up to 400  $\times$  200  $\mu\text{m}$  in diameter. Microscleres occur in abundance and may be playing the structural role of holding the reticulation intact. Sigmas I (as many as 10 per linear mm) and rosettes

(135  $\mu\text{m}$ , 6 per mm) of anisochelas I can be seen surrounding the megasclere bundles (Fig. 2b). These and other microscleres, occur in great numbers inside the meshes.

The choanosome area appears light brown in transmitted light, with dark-brown blotches of fibrous spongin. The spiculation here is not very dense and no clear pattern is apparent which may be due to the slightly macerated condition of the specimen. Microscleres are scattered throughout this area.

Spicules (Figs. 2c, d, 3; Table 1): Subtylostyles fusiform, gradually tapering to a point, generally slightly bent in upper third and thickest at mid length, with long neck and elliptical head. Anisochelas I stout, with head length 50% of total length, foot in side view at about  $110^\circ$  angle to shaft; frontal alae of foot may bear denticulation on top (Fig. 3e). Anisochelas II similar to anisochelas I but even stouter, with head length 70% of total length, shaft not visible in frontal view, lateral alae of head arcuate. Anisochelas III slender, with head length 70% of total length, shaft slightly bent at the end of the lateral alae of the head. Anisochelas IV very slender, with both frontal alae prolonged into thin, digitiform processes that sometimes cross each other. Sigmas I stout, abruptly bent into very sharp hooks, with almost straight inner faces. Sigmas II slender, with gradual curve and sharp hooks. Sigmas III similar to sigmas II but smaller. Toxas very gently bent (more pronounced in short forms).

*Ecology.*—Associated with mangrove and shallow seagrass bottoms in bays and lagoons.

*Distribution.*—Florida, St. Vincent (Virgin Islands), Curaçao, Colombia, Belize.

*Remarks.*—Only one of this species specimen was found, suggesting that it may be uncommon in the survey area. Details of spicule morphology and presence of four types of anisochelas agree well with the holotype (Figs. 2d, 3b–d).

It should be emphasized that proper assessment of microsclere categories is essen-

tial if a morphological-phylogenetic classification of *Mycale* is to be achieved. In many taxonomic descriptions, one or the other microsclere category is often overlooked or lost to lumping decisions, as in the present species where anisochelas-category III was not recognized by previous authors (van Soest 1984, Zea 1987). Consequently, anisochelas II of *M. arndti* should be described as arcuate because the lateral alae of the head are partly separated from the shaft (Hajdu et al. 1994).

The stout sigmas I are comparable to those of *Esperella simonis* as figured by Ridley & Dendy (1887) and of *M. quadripartita* Boury-Esnault (Hajdu & Desqueyroux-Faúndez 1994), and may be homologous to the diancistras of *Hamacantha* Gray (Hajdu 1994). This similarity is based on the straight inner face and the abrupt tapering of the hooks in this type of sigma and is enhanced by a faintly marked notch at mid-length of some of these spicules (Fig. 3h). Toxas show a remarkable range of size but size-frequency analysis of 100 toxas in the Belizean specimen failed to reveal distinct categories.

*Mycale (Aegogropila?) carmigropila*,  
new species

Figs. 4, 17b; Table 2

*Type material.*—Holotype, USNM 34560, Twin Cays, Sponge Haven, on roots of *Rhizophora*, 1 m, coll. E. Hajdu & K. Smith, 17 Aug 1993. Paratypes: USNM 42997, Belize, Twin Cays, Batfish Point, on red-mangrove stilt root and peat bank, <1 m, coll. K. Rützler and K. Smith, 5 May 1986; USNM 43048, Belize, Twin Cays, Hidden Creek, on red-mangrove stilt root, <1 m, coll. K. Rützler, 8 May 1987; USNM 43047, Belize, Twin Cays, Hidden Creek, encrusting a cluster of algae, genus *Halimeda*, <1 m, coll. K. Smith, 8 May 1987; USNM 47870, Belize, Twin Cays, Sponge Haven, peat bank with algae, genus *Halimeda*, 1 m, coll. K. Smith, 5 Jul 1990; USNM 34561, Twin Cays, Sponge Haven,

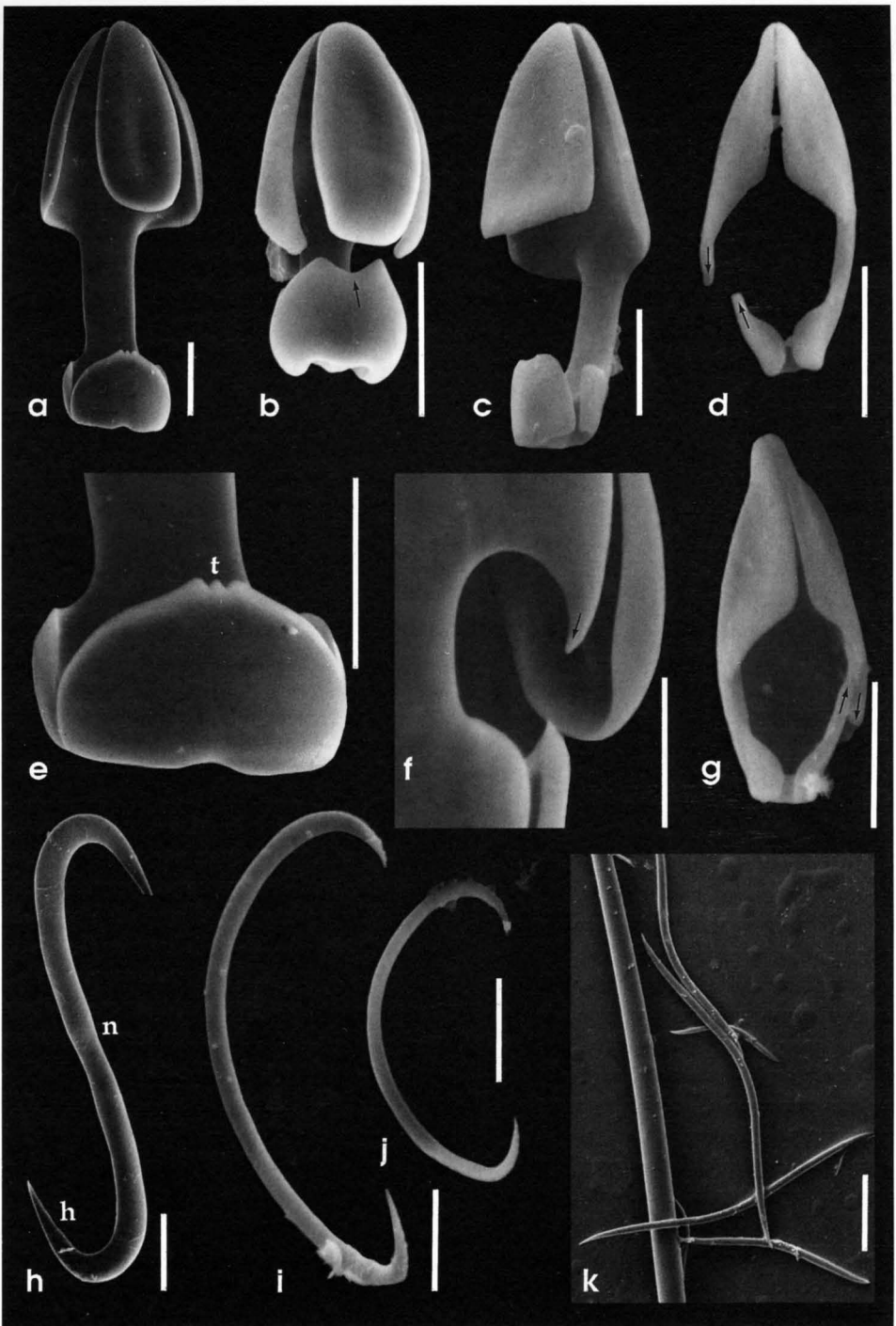


Fig. 3. *Mycale arndti*, spicules: a, Face view of anisochela-I; scale equals  $10\ \mu\text{m}$ ; b, Face view of anisochela-II showing robustness and extremely long frontal ala of head, almost fusing with foot; note deeply concave top portion of frontal ala of the foot (arrow); scale equals  $10\ \mu\text{m}$ ; c, Oblique frontal view of anisochela-III; scale equals  $5\ \mu\text{m}$ ; d, Profile view of anisochela-IV showing thin digitiform prolongations from both frontal alae (arrows) almost fusing; scale equals  $5\ \mu\text{m}$ . e, Detail of foot of anisochela-I in Fig. 3a showing tridentate (t) top

on roots of *Rhizophora*, 1 m, coll. E. Hajdu & K. Smith, 17 Aug 1993; USNM 34587, Twin Cays, Sponge Haven, on roots of *Rhizophora*, 1 m, coll. E. Hajdu & K. Smith, 17 Aug 1993; USNM 38768, Twin Cays, Sponge Haven, on *Halimeda*, 1 m, coll. E. Hajdu & K. Smith, 17 Aug 1993. Schizotypes from holotype, BMNH 1994.3.1.1, QM G313152, MNRJ 631, ZMA POR 10708; fragments of paratypes, MNRJ 632, 633, 634.

**Diagnosis.**—Intensely blue to greenish, encrusting *Mycale* (*Aegogropila*?) with three categories of anisochelas and one type of small (<70  $\mu\text{m}$ ) sigmas.

**Description.**—Macroscopic appearance: Specimens were encrusting ( $\leq 20\text{ cm}^2$ ) on roots of *Rhizophora*, or occurred intermingled with *Halimeda*. In the first case they were cobalt-blue, while in the second they appeared very light green. Other specimens observed alive were blue to violet, turning tan when dying. Subectosomal canals converging on oscules in a star-like pattern are visible in live specimens. The consistency is very soft, slimy, and fragile, the texture rather smooth.

**Skeleton:** The ectosomal skeleton is a polymorphic feature in this species. Two specimens (USNM 34560, 34587) have a tangential reticulation of subtylostyles, single or in 50  $\mu\text{m}$  thick bundles, with large amounts of cementing spongin. Meshes are mostly triangular ( $250 \times 150\ \mu\text{m}$ ). Up to 12 pores ( $40 \times 20$  to  $80 \times 50\ \mu\text{m}$  in diameter) of the aquiferous system can be seen within a single mesh. A few rosettes of anisochelas I ( $\leq 110\ \mu\text{m}$  in diameter), and sigmas I occur scattered among the meshes, frequently around the bundles. The

other two specimens USNM 34561, 38768 lack the specialized tangential ectosomal skeleton, having just a few scattered megascleres, rosettes, and abundant sigmas near the surface.

The choanosomal skeleton is relatively low in spicule density, which accounts for the extreme softness and fragility. Subtylostyles occur scattered in great numbers and also form longitudinal bundles ( $\leq 30\ \mu\text{m}$  wide), frequently meandriform, that end in fan-like brushes ( $\leq 500\ \mu\text{m}$  wide) in the subectosome. These brushes support the tangential ectosomal reticulation, when present, or the rosettes alone; generally, fibers protrude slightly from the surface of the sponge.

**Spicules** (Fig. 3, Table 2): Subtylostyles slender, slightly fusiform, straight or slightly bent in central part, with elliptical head well marked, shaft gradually tapering to a sharp point. Anisochelas I with straight shaft, head 40% of total length; frontal alae forming narrow angle ( $30^\circ$ ) with shaft (profile view), frontal alae of feet lower than lateral alae, general aspect narrow in both frontal and profile views. Anisochelas II shaft markedly bent at head 50% of total length, lateral alae of head longer than frontal alae. Anisochelas III very slender, with shaft gradually curved in profile view, head 40–50% of total length, frontal alae of foot distally extended by angled spurs. Sigmas with markedly bent hooks, gradually sharpening ends.

**Etymology.**—The name *carmigropila* is derived from the juxtaposition of *Carmia* and *Aegogropila*. These are the two subgenera with which specimens of this spe-

---

←  
 portion of frontal ala; scale equals 10  $\mu\text{m}$ ; f, Oblique view from the back of an anisochela-II showing arcuate-like pattern exhibited by the lateral alae of its head, which are elongated (arrow), rather than cut-off from the shaft; scale equals 5  $\mu\text{m}$ ; g, Profile view of cleistochela-like anisochela-IV showing thin digitiform prolongations from both frontal alae intercrossing each other (arrows); scale equals 5  $\mu\text{m}$ ; h, S-shaped, diancistra-like sigma-I showing almost straight inner-face of hooks (h), and rare, notch-like constriction (n) at torsion point; scale equals 20  $\mu\text{m}$ ; i, Sigma-II; scale equals 5  $\mu\text{m}$ ; j, Sigma-III; scale equals 5  $\mu\text{m}$ ; k, Toxas of stable geometry, but variable length; scale equals 20  $\mu\text{m}$ . (a, e–k, USNM 39329; b–d, holotype ZMA POR 3675.)

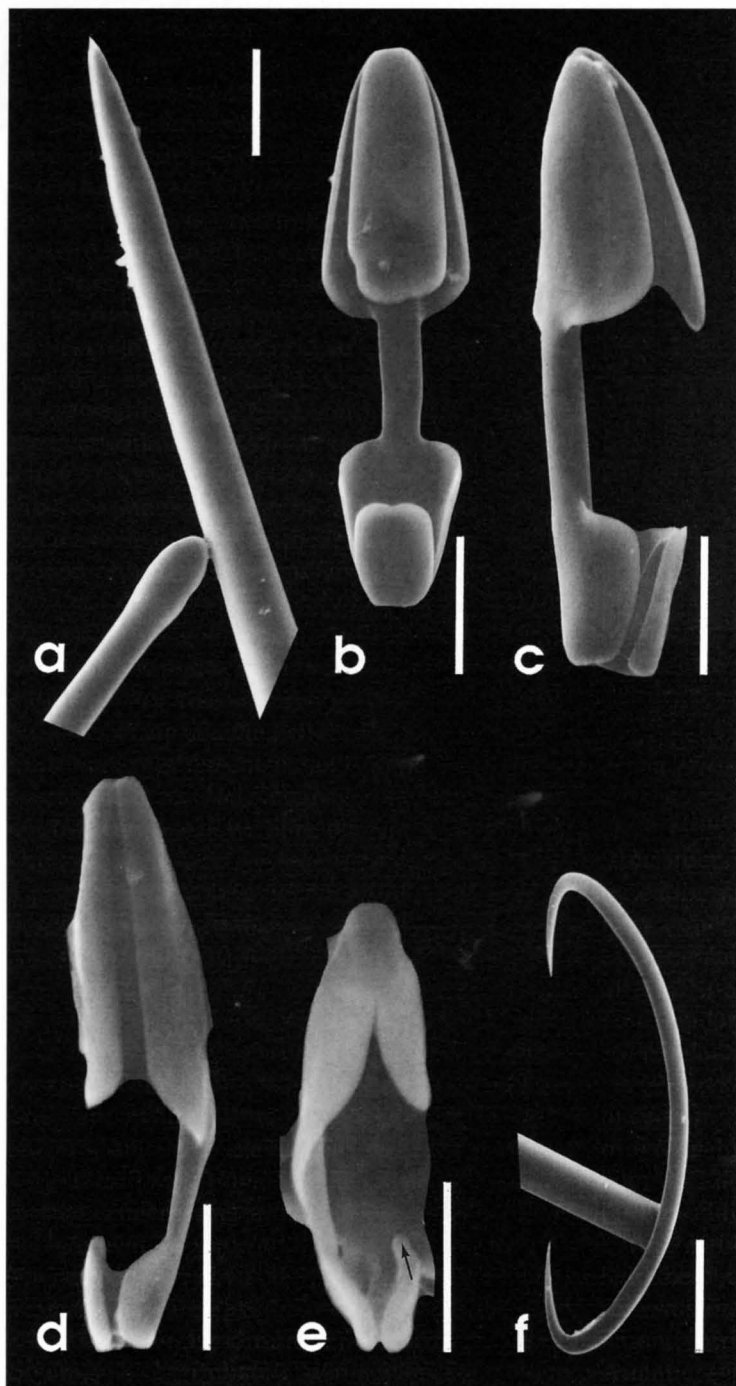


Fig. 4. *Mycale carmigropila*, spicules: a, Terminations of subtylostyles; scale equals 10  $\mu\text{m}$ ; b, Face view of anisochela-I showing narrow aspect; scale equals 10  $\mu\text{m}$ ; c, Profile view of anisochela-I; scale equals 10  $\mu\text{m}$ . d, Profile view of anisochela-II showing narrow aspect, and shaft markedly bent at middle portion; scale equals 5  $\mu\text{m}$ ; e, Profile-view of anisochela-III, note short, and thin digitiform spur on top of frontal ala of foot (arrow); scale equals 5  $\mu\text{m}$ ; f, Sigma; scale equals 20  $\mu\text{m}$ . (a, d-f, *Aegogropila*-like holotype, USNM 34560; b, c, *Carmia*-like paratype, USNM 34561.)



Table 1.—Spicule measurements (in  $\mu\text{m}$ ) for *Mycale arndti* (ranges of length, or length  $\times$  width, with means in italics;  $n = 20$ , unless stated).

Material	Subulostyles	Anisochelas I	Anisochelas II	Anisochelas III	Anisochelas IV	Sigma I	Sigma II	Sigma III	Toxas
Curaçao (holotype ZMA POR 3675 remeasured)	249–278.8–313 $\times$ 8–9.3–10	42–46.7–53	21–24.2–29	19–20.2–23	10–12.0–14	89–99.9–109 $\times$ 6–8	21–29.7–41	13–15.5–17	18–66.3–78
Florida (paratype ZMA POR 3842 remeasured)	297–323.3–355 $\times$ 3–6.2–8	35–45.4–50	22? ( $n = 1$ )	19–21.3–24	11–12.1–13	91–103.2–116 $\times$ 2–5.1–8	31–42.6–62	29–33.7–39	15–17 ( $n = 2$ )
Colombia Zea 1987	297–306.9–332 $\times$ 4–7.1–10	46–49.6–53	not reported	18–20.5–23	18–12.8–15	97–102.9–109 $\times$ 6–7.0–8	14–22.7–38	not reported	14–35.0–85
Belize MNRJ 630	281–309.0–323 $\times$ 8–9.4–12	44–49.1–51	22–26.7–30	19–20.2–22	11–12.0–13	94–99.1–108 $\times$ 6–7	20–27.7–34	13–15 ( $n = 4$ )	13–36.3–83

cies show affinities in ectosomal skeletal patterns.

*Ecology*.—On *Rhizophora* mangrove stilt roots and *Halimeda* algae bordering a large mangrove channel with strong water flow.

*Distribution*.—Belize.

*Remarks*.—Of the four specimens studied, two have *Aegogropila*-like ectosomal skeletons and two lack it, thus resembling *Carmia* (*Arenochalina* species are also without ectosomal skeleton but instead have a stout choanosomal reticulation). Both forms are indistinguishable in the field and have identical spiculation. The assignment to *Aegogropila* is tentative but justified by the view that the ectosomal reticulation is more likely to be lost in a species of *Aegogropila* than acquired spontaneously in one of *Carmia*.

*Mycale* (*Aegogropila*?) *carmigropila* is close to *Mycale* (*Carmia*) *magnirhaphidifera* (see below) except for the possession of one more category of anisochelas, slight differences in the shape of anisochelas and lack of raphides and of a second category of sigmas. Both species may have blue or bluish color in life.

*Mycale* (*Aegogropila*) *citrina*, new species  
Figs. 5, 6, 17c; Table 3

*Mycale americana* van Soest, 1984:22 (in part).—Zea 1987:138.

*Type material*.—Holotype, USNM 38942, Twin Cays, Cuda Cut, 1 m, coll. E. Hajdu & K. Smith, 13 Aug 1993. Paratypes, USNM 43031, Belize, Twin Cays, Cuda Cut near Batfish Point, encrusting a cluster of algae, genus *Halimeda*, <1 m, coll. K. Rützler, 27 Apr 1989; USNM 38956, 38958, 38963, 38967, Twin Cays, Cuda Cut, 1 m, coll. E. Hajdu & K. Smith, 11 Aug 1993; USNM 47872, Belize, Twin Cays, Cuda Cut, peat bank, <1 m, coll. K. Rützler, 10 May 1997; USNM 41443 Belize, Twin Cays, Cuda Cut, peat bank, <1 m, coll. K. Rützler, 10 May 1997. Schizotypes from holotype, BMNH 1994.3.1.2, QM G313153, MNRJ 635, and ZMA POR

Table 2.—Spicule measurements (in  $\mu\text{m}$ ) for *Mycale carnigropila* (ranges of length, or length  $\times$  width, with means in italics;  $n = 20$ ).

Material	Subtylostyles	Anisochelas I	Anisochelas II	Anisochelas III	Sigmas
<b>Holotype</b>					
USNM 34560 (MNRJ 631)	276–311.1–345 $\times$ 5–6.8–9	36–38.6–44	19–19.9–21	13–13.1–14	58–59.7–64
<b>Paratypes</b>					
USNM 34561 (MNRJ 632)	302–322.2–360 $\times$ 4–4.9–7	33–35.5–37	18–19.4–21	10–11.7–13	52–56.8–63
USNM 34587 (MNRJ 633)	281–297.9–323 $\times$ 6–7.2–9	41–42.8–45	19–20.0–23	12–12.7–14	52–58.0–67
USNM 38768 (MNRJ 634)	254–281.4–302 $\times$ 4–5.3–6	35–37.0–40	19–20.1–21	13–13.3–14	51–54.7–58

10709; fragments of paratypes, MNRJ 636–639.

*Diagnosis.*—Lemon-yellow crustose *Aegogropila* with three categories of anisochelas, one type of large sigmas ( $>60 \mu\text{m}$ ), and copious mucus production when handled.

*Description.*—Macroscopic appearance: Thick incrustations (5 mm;  $30 \text{ cm}^2$ ) with protruding oscules encircled by a thin membrane. Extremely soft and fragile, and releasing copious amounts of mucus upon handling. Live-color is lemon yellow to light orange, turning pale yellow in alcohol. Numerous, pronounced subectosomal channels may cover most of the sponge surface and converge toward the oscules. Most specimens contained embryos during August.

*Skeleton* (Fig. 5): The ectosomal skeleton peels off easily and is made of a remarkably pure (no scattered megascleres) tangential reticulation of bundled ( $\leq 85 \mu\text{m}$  thick) subtylostyles (Fig. 5a), mostly forming triangular meshes ( $660 \times 400 \mu\text{m}$ ), with no apparent cementing spongin. Rosettes of anisochelas-I ( $130 \mu\text{m}$  in diameter) occur in places (Fig. 5b, c). Sigmas are very abundant, scattered among the meshes (up to 35 per mesh), and along the strands (30 per mm; Fig. 5d); they seem to play an important structural role in the skeleton.

The choanosome is crowded with dark-brown granules (about  $40 \mu\text{m}$  in diameter), presumably of mangrove peat, which hamper observation of the skeletal architecture. The underlying pattern seems to be densely spicular, with crisscrossing megasclere bundles ( $150 \mu\text{m}$  thick) and abundant microscleres.

*Spicules* (Fig. 6, Table 3): Subtylostyles straight, slender and slightly fusiform, with poorly marked elliptic head. Anisochelas I with straight shaft, head 50% of total length. Anisochelas-II with shaft bent at head, head 50–60% of total length; frontal alae of foot with short, digitiform processes on top (Fig. 6c). Anisochelas-III very slender, with shaft gradually curved (profile

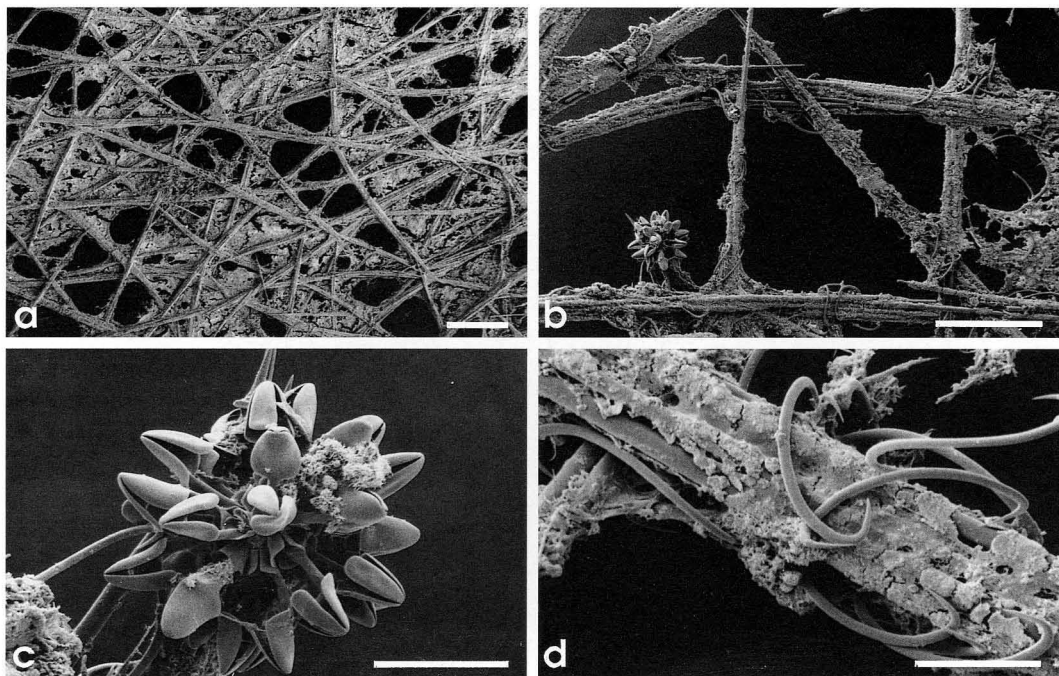


Fig. 5. *Mycale citrina*, skeleton: a, Peeled-off surface showing ectosomal reticulation; scale equals 500  $\mu\text{m}$ ; b, Detail of surface reticulation showing sigmas disposed abundantly around the bundles of megascleres, and rosette of anisochelas-I; scale equals 200  $\mu\text{m}$ ; c, Detail of rosette of anisochelas-I shown on below left corner of Fig. 5b; scale equals 50  $\mu\text{m}$ ; d, Detail of bundle of megascleres showing abundance of sigmas around it; scale equals 50  $\mu\text{m}$ . (a–d, paratype USNM 38963.)

view) head 40% of total length, foot with very small alae, the frontal one ending on top in a thin digitiform process (Fig. 6d). Sigmas slender, markedly bent on hooks.

**Etymology.**—The name *citrina* is derived from citrus, for the lemon-yellow color of the live sponge.

**Ecology.**—Specimens were found under the roofs of mangrove overhangs, or, less commonly, on peat banks where they were protected from direct sunlight by neighboring bushy algae (e.g., species of *Halimeda*, *Caulerpa*, *Jania*).

**Distribution.**—Belize.

**Remarks.**—This species is close to *Mycale americana* van Soest (Fig. 7), but differs by the possession of a third category of anisochelas, larger megascleres and sigmas, and lemon-yellow color. *M. americana* was originally described as red (van Soest 1984), but orange-yellow and olive-yellow specimens have also been reported (Zea

1987). Reexamination of Zea's material revealed the occurrence of an intermediate-size category of anisochelas, overlooked by the author. This feature and the larger dimensions of spicules in the Colombian material make us confident in assigning the Colombian specimens to *M. citrina*.

Only one specimen quoted by van Soest (1984) in the type-series of *Mycale americana* was not collected in a mangrove (ZMA POR 3889, on *Halimeda*). Unfortunately the live color of the specimen was not registered but comparison with the holotype (Table 3) revealed three categories of anisochelas, instead of two as originally quoted, thicker megascleres, and slightly larger sigmas. We suggest to assign this specimen to *M. citrina*.

Subgenus *Arenochalina* Lendenfeld, 1887

**Diagnosis.**—*Mycale* without ectosomal skeleton, with choanosomal skeleton of

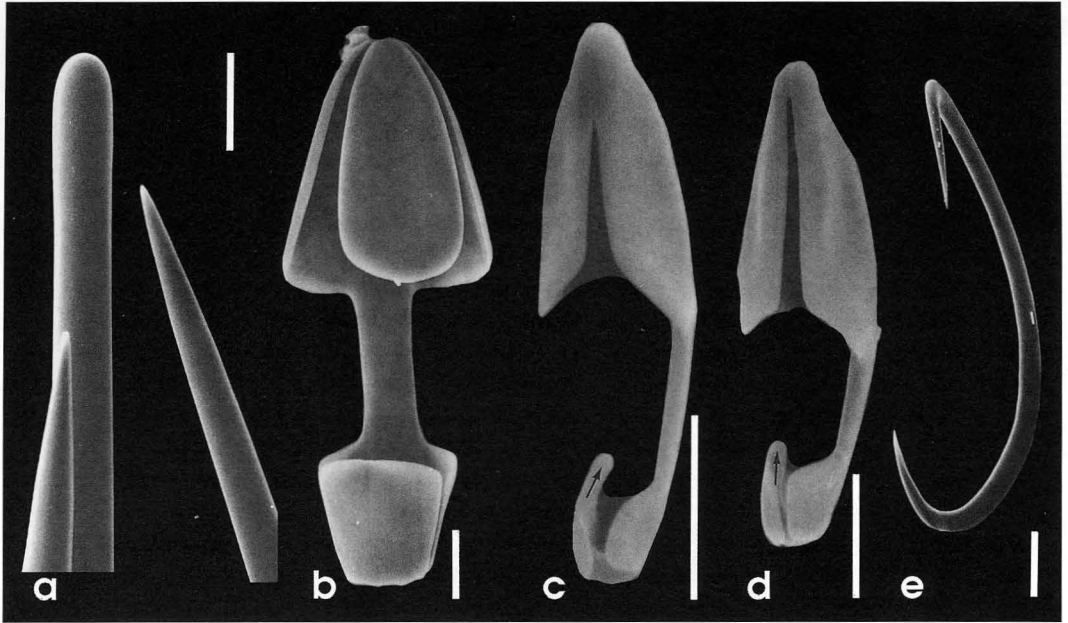


Fig. 6. *Mycale citrina*, spicules: a, Terminations of subtylostyles; scale equals 10  $\mu$ m; b, Face view of anisochela-I; scale equals 5  $\mu$ m; c, Profile view of anisochela-II, note short and thin digitiform spur on top of frontal ala of foot (arrow); scale equals 5  $\mu$ m; d, Profile view of anisochela-III, note thin digitiform prolongation on top of poorly developed frontal ala of foot (arrow); scale equals 5  $\mu$ m; e, Slender sigma; scale equals 10  $\mu$ m. (a–e, holotype USNM 38942.)

stout fibers forming a coarse rectangular reticulation, and with simple spicule complement. Species of this subgenus are known to exude large amounts of mucus upon handling. Type species: *Arenochalina mirabilis* von Lendenfeld, 1887 (= *M. mirabilis*, sensu Wiedenmayer 1989).

*Remarks.*—The status of *Arenochalina* is uncertain. The diagnosis is in essence that provided by van Soest (1984) for *Acamasina* de Laubenfels, 1936a. Wiedenmayer's (1989) addition with respect to the frequent coring of fibers by foreign debris is not upheld here as this seems to be noteworthy for Australian species only. Shared traits among populations from both sides of the Atlantic, the Indo-west Pacific and southern Australia, seem to be the choanosomal, coarse, rectangular reticulation of spiculo-fibers, the low diversity of categories in the spicule complement, and the production of abundant mucus. Nonetheless, the derived condition of these characters is far from be-

ing established, as suggested by similar occurrences here and there in *Mycale* assigned to other subgenera.

*Mycale (Arenochalina) laxissima*  
(Duchassaing & Michelotti, 1864)

Figs. 8, 9, 17d; Tables 4, 5

*Acamas laxissima* Duchassaing & Michelotti, 1864:95, pl. XXII, fig. 3.

*Esperella nuda* Ridley & Dendy, 1886:339; 1887:70, pl. XV, figs. 5, 11, 14; pl. XVI, fig. 1.

*Hircinia cartilaginea*.—Hyatt 1877:549 (not *Spongia cartilaginea* Esper, 1798).

*Hircinia cartilaginea* (Esper) var. *horrida* Hyatt, 1877:549; pl. 17, fig. 29.

*Hircinia purpurea* Whitfield, 1901:49, pl. 4 (not *H. purpurea* Hyatt, 1877:550).

*Mycale angulosa*.—De Laubenfels 1936a: 116, fig. 2, pl. 15, 1.—? Lévi 1959:129; fig. 19; pl. 6 fig. 5; López & Green 1984:

Table 3.—Spicule measurements (in  $\mu\text{m}$ ) for *Mycale citrina* and *Mycale americana* (ranges of length, or length  $\times$  width, with means in italics;  $n = 20$ , unless stated).

Material	Subtylostyles	Anisochelas I	Anisochelas II	Anisochelas III	Sigmas
<i>Mycale citrina</i>					
Holotype					
USNM 38942 (MNRJ 635)	339–382.4–456 $\times$ 8–8.6–9	32–45.5–48	19–21.6–24	13–13.1–14	70–74.9–79
Paratypes					
USNM 38963 (MNRJ 636)	376–418.4–461 $\times$ 8–9.1–10	41–45.5–54	20–21.4–24	12–12.6–14	69–77.7–88
USNM 38956 (MNRJ 637)	350–427.4–477 $\times$ 7–8.6–11	44–49.4–52	19–23.2–26	12–12.9–14	75–80.4–88
USNM 38958 (MNRJ 638)	408–422.9–456 $\times$ 8–9.2–11	43–49.7–54	21–23.0–25	12–13.2–15	72–78.3–86
USNM 38967 (MNRJ 639)	366–399.1–424 $\times$ 7–8.1–10	45–49.2–54	18–21.0–23	12–12.7–14	76–78.7–85
<i>M. americana</i> (Zea 1987)					
INV-POR 0241 (remeasured)	309–341.1–371 $\times$ 3–7.1–9.5	35–40.4–47	not reported	10–11.6–13	60–66.9–70
INV-POR 0241 (remeasured)	318–328.9–366 $\times$ 5–6.9–9	33–38.4–41	21 ( $n = 1$ )	10–13	63–68.4–74 $\times$ 3–4
INV-POR 0276 (remeasured)	276–311.1–350 $\times$ 2–4.5–7	33–36.0–40	16–19 ( $n = 5$ )	11–13	58–64.9–72 $\times$ 2–4
<i>M. americana</i> (van Soest 1984)					
INV-POR 0276 (remeasured)	190–265.6–338 $\times$ 5–7.2–10	30–36.9–40	10–13.9–22	not reported	23–47.6–63
Holotype					
(ZMA POR 4074, remeasured)	196–242.9–260 $\times$ 5–6.8–8	34–36.9–40	not found	12–13.3–14	32–47.0–52
Paratype					
(ZMA POR 3889, remeasured)	276–309.5–329 $\times$ 7–9.0–11	34–37.6–42	18–20.6–22	11–12.4–14	54–61.4–67

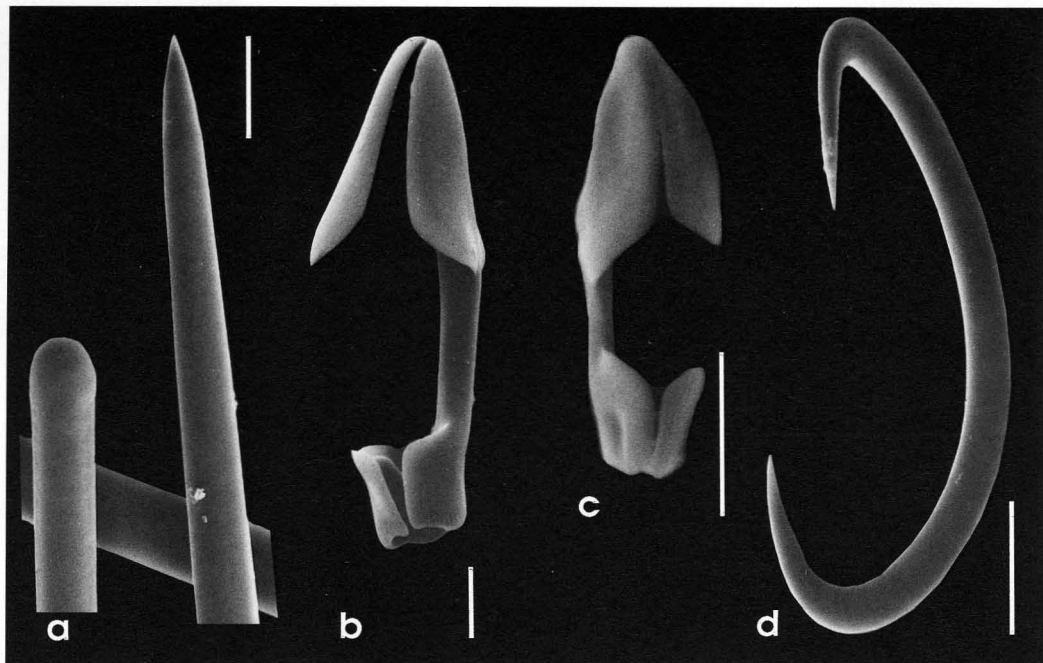


Fig. 7. Scipicules of *Mycale americana*, for comparison with *Mycale citrina* (Fig. 6): a, Terminations of subtylostyles; scale equals 10  $\mu\text{m}$ ; b, Profile view of anisochela-I; scale equals 5  $\mu\text{m}$ ; c, Profile view of anisochela-III, note absence of digitiform process on top of well developed frontal ala of foot (compare with Fig. 6c); scale equals 5  $\mu\text{m}$ ; d, Stout sigma; scale equals 10  $\mu\text{m}$ . (a-d, holotype ZMA POR 4074.)

79 (not *Pandaros angulosa* Duchassaing & Michelotti, 1864:89; pl. IX fig. 4).

*Mycale* sp.—Reiswig 1973.

*Thorecta horridus*.—Wiedenmayer 1977: 70, pl. 8, figs. 2–4; pl. 9, fig. 1.

*Acamasina laxissima*.—Wiedenmayer 1977:146–147, 255.

*Mycale laxissima*.—van Soest 1981:12.—van Soest et al. 1983:200.—Pulitzer-Finali 1986:119.—Rützler 1990:455.—Vacelet 1990:25.

?*Mycale imperfecta*.—Winterman-Kilian & Kilian 1984:133.

*Mycale (Acamasina) laxissima*.—Van Soest 1984:29; pl. III, 1; fig. 9.—Zea 1987:143, 255.

*Mycale mucifluens* Pulitzer-Finali, 1986: 121.

*Mycale nuda*.—Mello-Leitão et al. 1961: 12.—Hechtel 1976:254.—van Soest 1984:31.—Hajdu & Boury-Esnault 1991: 504.

*Mycale jamaicensis* Pulitzer-Finali, 1986: 125.

*Mycale whitfieldi* Pulitzer-Finali, 1986:127.

*Mycale hyatti* Pulitzer-Finali, 1986:129.

*Material studied*.—MUT POR 34, holotype, St. Thomas, Virgin Islands. MSNG, no register number; Jamaica, Port Royal, on submerged ruins, 5–10 m, 27 Mar 1964 (*M. laxissima* sensu Pulitzer-Finali, 1986; number PR. 40); MSNG 47695, Jamaica, Port Royal cays, 10–25 m, 22 Mar 1964 (*M. mucifluens* Pulitzer-Finali, 1986; holotype); MSNG 47697, Jamaica, Duncans, fore-reef slope, 35 m, 30 Mar 1964 (*M. jamaicensis* Pulitzer-Finali, 1986; holotype); ZMA POR 5192, Jamaica, Runaway Bay, 33.5 m, 14 Aug 1969, coll. and det. H.M. Reiswig (*Mycale* sp.). MCZ 7008/cat. 440, Florida, Key West; *Hircinia cartilaginea* sensu Hyatt, 1877 (*M. hyatti* Pulitzer-Finali, 1986; holotype); MCZ 7071/cat. 441, Florida,

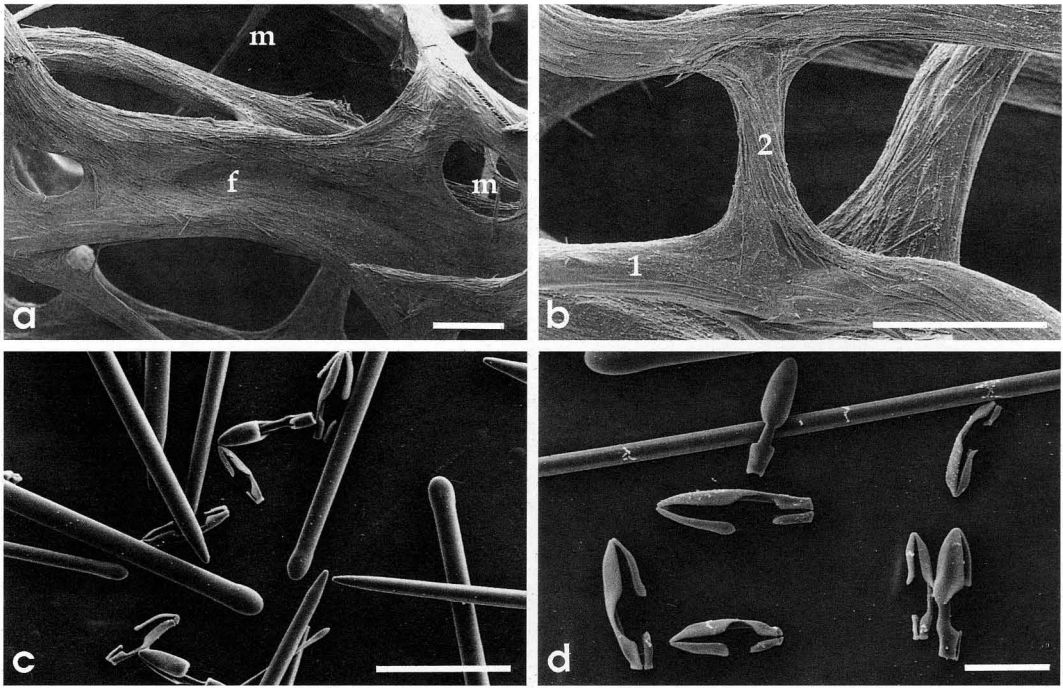


Fig. 8. *Mycale laxissima*, skeleton: a, Detail of skeleton showing fused fibers (f), and meshes of widely variable dimensions (m); scale equals 500  $\mu\text{m}$ ; b, Detail of skeleton showing primary (1) and secondary (2) interconnecting fibers; scale equals 50  $\mu\text{m}$ ; c, Stout megascleres with blunt apex, and anisochelas, young megasclere is seen below center; scale equals 50  $\mu\text{m}$ ; d, Anisochelas of variable geometry; scale equals 20  $\mu\text{m}$ .

Key West; *H. cartilaginea* sensu Hyatt, 1877 (*M. hyatti* Pulitzer-Finali, 1986; paratype); MCZ 7073/cat. 222, Florida, Cape Florida; *H. cartilaginea* var. *horrida* Hyatt, 1877; *M. hyatti* Pulitzer-Finali, 1986; paratype. UFRJPOR 3578, Brazil, Angra dos Reis, Rio de Janeiro State. USNM 41273, Belize, Twin Cays, Cuda Cut near Batfish Point, <1 m, coll. K. Rützler, 4 Jun 1983; USNM 39281 (several lots), Belize, Twin Cays, Cuda Cut, 1 m, coll. E. Hajdu and K. Smith, 11 Aug 1993.

**Diagnosis.**—Dark red, spiny, tubular *Araneochalina* with stout spiculo-fibers enveloped by great amounts of spongin and forming large rectangular meshes. Choanosome cavernous, without noticeable fleshy parts, with only one category of anisochelas and large (>50  $\mu\text{m}$ ) sigmas.

**Description.**—Macroscopic appearance: Specimens are tube shaped, some in clusters up to six, up to 50 cm tall, 15 cm in

diameter, and thin-walled (0.5–2 cm). The color is dark wine red. A large pseudoscule (6 cm diameter) on top of the tubes is encircled by a transparent membrane. The smaller specimens (about 6  $\times$  6  $\times$  6 cm) are globular and already bear an apical pseudoscule. The sponge is tough but elastic, compressible, spiny to the touch, and releases copious amounts of sticky mucus when squeezed. The surface is coarsely conulose from projecting spiculo-fibers.

**Skeleton** (Fig. 8a, b): The surface membrane can be peeled off in places and contains a few scattered spicules and paucispicular strands of subtylostyles. The choanosomal skeleton is made up of a stout, rectangular reticulation of spiculofibers. Meshes formed are generally within the range of 100–150  $\mu\text{m}$  up to 3–4 mm (Fig. 6a). One can distinguish between primary and secondary fibers (50–300  $\mu\text{m}$  thick; Fig. 8b), the latter showing clearer spongin

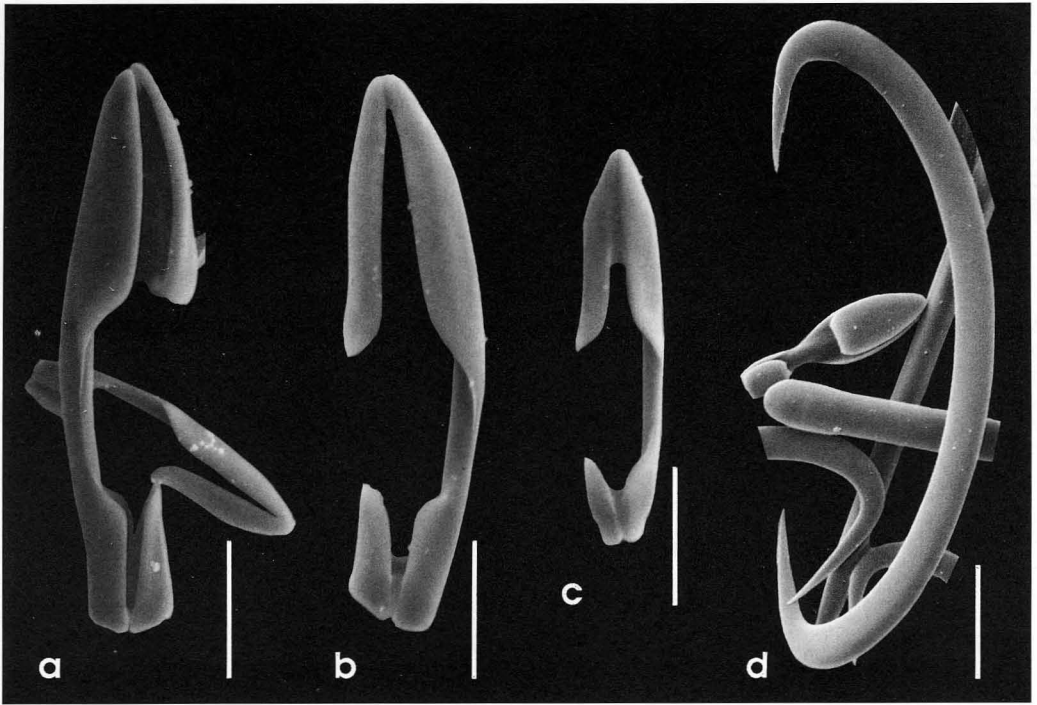


Fig. 9. *Mycale laxissima*, spicules: a, Rare larger, and common smaller anisochelas; scale equals 10  $\mu\text{m}$ ; b, Common anisochela of intermediary size; scale equals 10  $\mu\text{m}$ ; c, Common anisochela of smaller size; scale equals 10  $\mu\text{m}$ ; d, Stout sigmas, and anisochelas of intermediary size; scale equals 20  $\mu\text{m}$ .

in transmitted light. The fibers end as subectosomal, paucispicular tufts. Anisochelas are particularly abundant in a subectosomal layer of spongin where they are spread out without order. Rosettes of anisochelas are seen on the basal plate of spongin in a specimen from Angra dos Reis, Rio de Janeiro State, Brazil; UFRJPOR 3578. Sigmas are very common along the spiculofibers of the choanosome. Isolated megascleres and sig-

mas occur in abundance, strewn at random inside the skeleton meshes.

Spicules (Figs. 8c, d, 9; Table 4): Subtylostyles are straight, variably thick, abruptly tapering to a blunt apex, with ovoid head. Anisochelas are variable in dimensions and geometry, generally appear narrow in profile and face views, have a curved shaft and a head 40–50% of total length. Sigmas are generally stout and

Table 4.—Spicule measurements (in  $\mu\text{m}$ ) for *Mycale laxissima* (fragments of different specimens) from Belize (ranges of lengths, or length  $\times$  width, with means in italics;  $n = 10$ ).

Material	Subtylostyles	Anisochelas	Sigmas
USNM 39281 (MNRJ 640)	270–283.6–302 $\times$ 5–6.5–8	20–23.9–31	83–94.5–106 $\times$ 4–6
MNRJ 641	249–272.4–292 $\times$ 5–6.1–10	22–23.6–29	83–93.3–112 $\times$ 2–3.2–6
MNRJ 642	249–277.2–297 $\times$ 6–6.5–9	18–24.5–30	79–96.1–108 $\times$ 3–5
MNRJ 643	260–279.8–297 $\times$ 3–7.5–9	21–27.2–32	80–96.7–112 $\times$ 4–6
MNRJ 644	249–281.7–307 $\times$ 5–6.9–9	22–27.6–33	87–96.3–105 $\times$ 4–4.8–7
MNRJ 645	244–262.9–286 $\times$ 4–6.6–8	18–24.8–32	90–100.9–114 $\times$ 6
MNRJ 646	265–285.7–302 $\times$ 5–6.3–8	21–25.8–32	83–94.3–110 $\times$ 4–6
USNM 41273	265–285.1–302 $\times$ 5–5.9–7	19–25.6–34	87–97.0–112 $\times$ 4–6



Table 5.—Spicule measurements (in  $\mu\text{m}$ ) for *Mycale laxissima* from Belize compared to other Caribbean locations (ranges of length, or length  $\times$  width, with means in italics;  $n = 20$ , unless stated).

Material	Subtylostyles	Anisochelas	Sigmas	Raphides
Belize (population, $n = 80$ )	244–278.6–307 $\times$ 3–6.5–10	18–25.4–34	79–96.1–114 $\times$ 3–7	not found
Holotype (MUT 34/USNM 31001, remeasured)	224–248.5–272 $\times$ 3–4	14–18.6–21	not found	not found
Holotype (cf. Pulitzer-Finali 1986)	230–260 $\times$ 2.5–3.5	16–20	50–71 (rare)	not reported
van Soest 1984	209–223.2–240 $\times$ 2–3.5	16–20.0–23	70–75.0–81	not reported
Pulitzer-Finali 1986	220–250 $\times$ 3.5–4.5	20–23	69–80 $\times$ 3.5	not reported
remeasured	227–249.9–269 $\times$ 4–4.5–6	21–22.4–23	73–79.5–84 $\times$ 3–4	not found
Zea 1987 (Providencia)	219–276.0–304 $\times$ 4–5.7–6	16–20.1–23	75–83.7–93 $\times$ 2–2.8–4	not reported
Zea 1987 (Santa Marta)	223–254.1–271 $\times$ 2–4.3–6	16–19.7–21	72–78.3–85 $\times$ 2–2.8–4	not reported
Zea 1987 (Cartagena)	242–294.5–323 $\times$ 3–8.1–11	26–30.2–33	109–118.3–128 $\times$ 5–6.2–9	not reported
Zea 1987 (San Bernardo)	213–279.3–313 $\times$ 3–9.0–11	25–29.9–36	109–118.7–133 $\times$ 6–6.7–8	not reported
Ridley & Dendy 1887 (as <i>Esperella nuda</i> )	245 $\times$ 16	25	120	not reported
remeasured	235–259.8–283 $\times$ 5–9.0–13	22–26.1–30	76–100.9–112 $\times$ 4–6	not found
Pulitzer-Finali 1986 (as <i>M. mucifluens</i> )	250–290 $\times$ 3.5–4.5	19–29	77–93 $\times$ 2–3.5	not reported
remeasured	258–278.2–294 $\times$ 3–4.5–6	21–25.1–29	84–88.8–95 $\times$ 2–3.4–4	not found
Pulitzer-Finali 1986 (as <i>M. jamaicensis</i> )	250–280 $\times$ 3–3.5	16–23	65–90 $\times$ 2–2.5	100 (rare)
remeasured	249–266.4–283 $\times$ 3–4.4–6	15–19.5–25	76–80.0–87 $\times$ 2–2.8–3	not found
Pulitzer-Finali 1986 well, I (as <i>M. whitfieldi</i> )	214–270 $\times$ 2.5	18.5–22.5	71–76	not reported
Pulitzer-Finali 1986 (as <i>M. hyatti</i> )	230–300 $\times$ 3–11.5	23–26	75–105 $\times$ 7.5	not reported
remeasured	224–276.8–322 $\times$ 4–6.8–11	23–24.8–29	78–88.8–106 $\times$ 4–4.4–6	not found

abruptly bent into hooks with sharp endings.

*Ecology.*—Moderately common in shaded marine mangrove environments with strong tidal water flow, on protected patch reefs below 5 m, and in fore-reef habitats below 12 m (compare also the detailed analysis of reef populations by Reiswig (1973) in Jamaica (as *Mycale* sp.). The heavy spongin fibers are known to be bored and occupied by filamentous algae (Rützler 1990) and experimental work by one of us (KR) has shown that the coring of siliceous spicules contribute photosynthetically useful light levels inside the dark sponges, comparable to glass-fiber light guides in optical applications (similar observations for other siliceous sponges were reported by Gaino & Sarà 1994, and Cattaneo-Vietti et al. 1996).

*Distribution.*—Florida, Bahamas, Cuba, Jamaica, Puerto Rico, Virgin Islands, Netherlands Antilles, Colombia, Belize, Mexico, Brazil, West Africa.

*Remarks.*—This species was subject of several misinterpretations in the literature. *Esperella nuda* Ridley & Dendy, 1886 from Brazil (holotype BMNH 1887.5.2.171) turns out to be a junior synonym and the originally reported (Ridley & Dendy 1887) exceptional thickness of its megascleres (16  $\mu\text{m}$ ) was found to be only in the range of 5–13  $\mu\text{m}$ . Specimens described by Pulitzer-Finali (1986; as *M. hyatti*) and Zea (1987) possess comparable megascleres (4–11  $\mu\text{m}$  and 2–11  $\mu\text{m}$  thick; Table 5), an isolated characteristic that does not justify separating a species. The species was also confused with *Mycale angulosa* (de Laubenfels 1936a, Lévi 1959), as discussed by van Soest (1984). Another erroneous identification may have been the report of *M. imperfecta* Baer from Colombia (Winterman-Kilian & Kilian 1984). The suggestion of possible amphi-Atlantic distribution of *M. laxissima* (van Soest 1984) raises the question of apomorphies of other distant species, such as *M. setosa* (Keller 1889) and *M. euplectelloides* (Row 1911) from the

Red Sea and Indian Ocean, respectively, because our examinations suggest that there is greater intra- than interspecific variation in this taxonomic complex, for instance, of anisochelas in a single specimen. Clarification of this problem will ultimately depend on study of populations from many localities worldwide and we caution from new descriptions based on poorly preserved or unrepresentative material (e.g., related new taxa in Pulitzer-Finali 1986).

The growth form of *Mycale laxissima* is generally tube or funnel shaped. In Belize, even in shallow water, neither encrusting nor cushion-shaped specimens were seen and early globular stages develop directly into long, thin-walled tubes. This is in contrast to observations in Brazil (between latitudes 8°–24°S; EH) where encrusting forms prevail among shallow-water populations of this species. The consistency of specimens varies, suggesting polymorphism in patterns of skeleton reticulation. Likewise, abundance of microscleres varies among specimens but no attempt was made to quantify differences within and between individuals because these sponges were often large and only fragments have been collected to allow cut specimens to regrow to protect their apparently small population size.

#### Subgenus *Carmia* Gray, 1867

*Diagnosis.*—*Mycale* without ectosomal skeleton, with loose choanosomal skeleton composed mainly of plumose, isolated spiculofibers which are often paucispicular. Type species: *Hymeniacidon macilenta* Bowerbank, 1866 (= *M. [C.] macilenta* sensu Topsent 1924).

*Remarks.*—The absence of an ectosomal skeleton is likely to be a homoplastic occurrence in *Mycale* because it is found in all species of *Carmia* and *Arenochalina*, and possibly also in the subgenus *Mycale*, (for instance, *M. (M.?) lapidiformis* (Ridley & Dendy), Hajdu & Desqueyroux-Faúndez 1994). As such, it is a weak character on

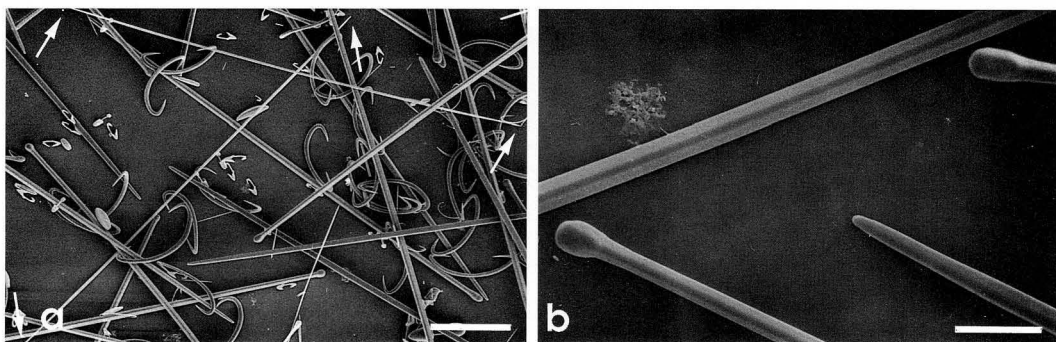


Fig. 10. *Mycale magnirhaphidifera*, spicules: a, Set of spicules showing raphides-I (arrows mark the extremities); scale equals 50  $\mu\text{m}$ . b, Terminations of tylostyles, note blunt apex, and well-marked oval head; scale equals 10  $\mu\text{m}$ . (a, b, USNM 39278.)

which by itself to base a subgeneric diagnosis.

*Mycale (Carmia) magnirhaphidifera*  
van Soest, 1984

Figs. 10, 11, 17e; Table 6

*M. (C.) magnirhaphidifera* van Soest, 1984:  
27; pl II, 7.

*M. cecilia*.—Wells & Wells, in Wells et al.  
1960:212 (not *M. cecilia* de Laubenfels,  
1936b:447).

*Material studied*.—ZMA POR 4885, holotype, Curaçao. USNM 23633, North Carolina, Hatteras Harbor, coll. and det. H. W. & M. J. Wells (as *M. cecilia*), 21 Nov 1959. USNM 42878, Belize, Twin Cays, Lair Channel, on red-mangrove stilt root, <1 m, coll. K. Rützler, 10 May 1985 (dark royal-blue, sigmas rare); USNM 42979, Belize, Twin Cays, Main Channel, on red-mangrove stilt root, <1 m, coll. K. Rützler and K. Smith, 26 Apr 1986 (purplish, with sabellid worm tubes; many sigmas); USNM 42949, Belize, Twin Cays, Main Channel, on red-mangrove stilt root, <1 m, coll. K. Rützler and K. Smith, 26 Apr 1986 (dark wine red, tan below surface; no sigmas); USNM 47874, Belize, Twin Cays, Grouper Gardens entrance, on a strand of rope tied to a plastic pipe protruding from the channel bottom, 1 m, coll. K. Rützler, 1 Feb 1986 (ochre, sigmas rare); USNM 43029, Belize, Twin Cays, Sponge Haven, 1 m,

coll. K. Rützler, 26 Apr 1989 (purplish wine red; sigmas moderately common and clearly in 2 size classes); USNM 43040, Belize, Twin Cays, Hidden Creek, <1 m, coll. K. Rützler, 1 May 1989 (gray, dirty yellow inside and where dying, enveloping sabellid tubes; without sigmas); USNM 43033, Belize, Twin Cays, Hidden Creek, <1 m, coll. K. Rützler, 1 May 1989 (gray; sigmas abundant); USNM 43036, Belize, Twin Cays, Gator Creek, <1 m, coll. K. Rützler, 3 May 1989 (grayish ochre; sigmas very abundant); USNM 43037, Belize, Twin Cays, Gator Creek, <1 m, coll. K. Rützler, 3 May 1989 (grayish ochre, massive; sigmas very abundant; with embryos); USNM 39278, Belize, Twin Cays, Hidden Creek, 1 m, coll. E. Hajdu & K. Smith, 9 Aug 1993 (bluish purple, sigmas common); USNM 39279, Belize, Twin Cays, Cuda Cut, 1 m, coll. E. Hajdu & K. Smith, 11 Aug 1993 (bluish purple, sigmas common; with larvae); USNM 39280, Belize, Twin Cays, Turtle Pond, 1 m, coll. E. Hajdu, 17 Aug 1993 (bluish purple, sigmas common); USNM 41442, Belize, Twin Cays, Cuda Cut, on red-mangrove stilt root, <1 m, coll. K. Rützler, 2 May 1994 (grayish blue, very thin crust; sigmas very rare); USNM 47865, Belize, Twin Cays, Hidden Creek, <1 m, coll. K. Rützler, 29 Mar 1997 (blue, sigmas abundant).

*Diagnosis*.—Bluish-purple to brown-gray, crustose *Carmia* with two types of an-

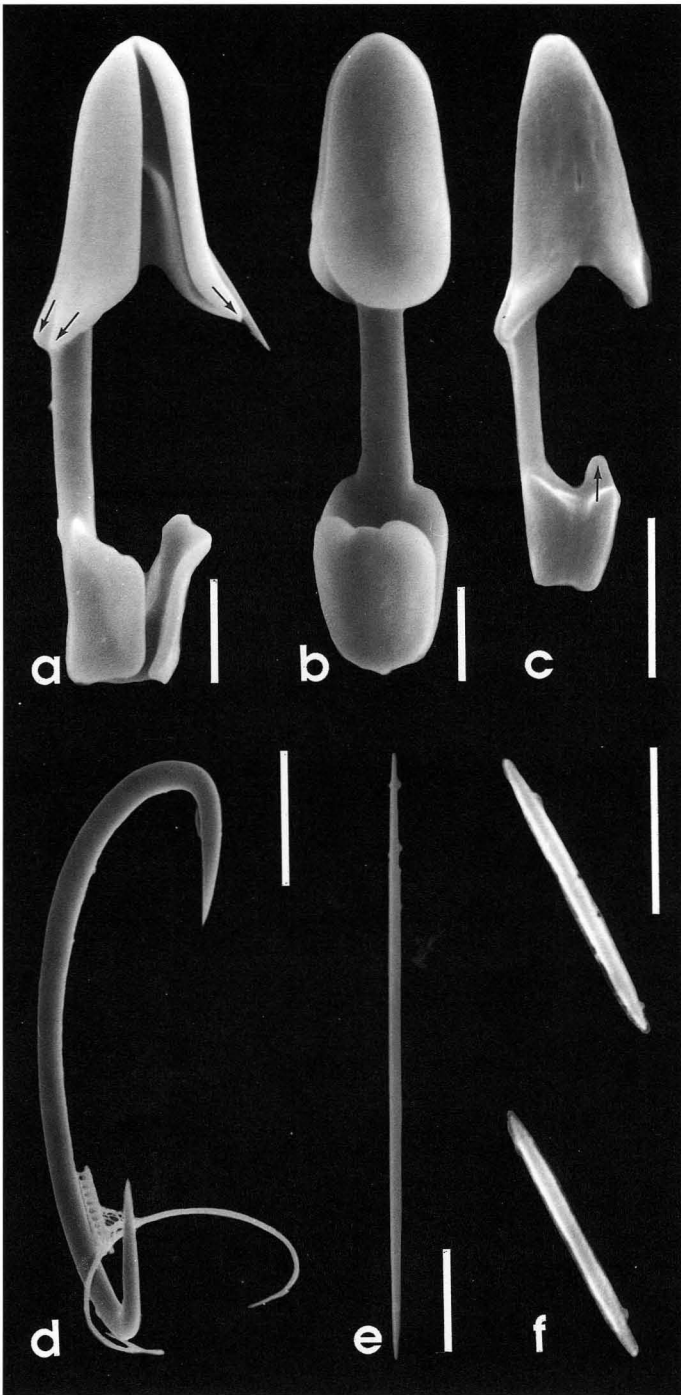


Fig. 11. *Mycale magnirhaphidifera*, spicules: a, Profile view of anisochela-I, note basal portion of lateral and frontal alae of the head diverging from each other (arrows), the lateral ones projecting behind the shaft; scale equals  $5\ \mu\text{m}$ ; b, Face view of narrow anisochela-I, and part of anisochela-II on top; scale equals  $5\ \mu\text{m}$ ; c, Profile view of anisochela-II showing short, thin digitiform spur on top of frontal ala of its foot (arrow); scale equals  $5\ \mu\text{m}$ ; d, Sigmata-I and -II; scale equals  $10\ \mu\text{m}$ . e, Raphides-I; scale equals  $5\ \mu\text{m}$ ; f, Raphides-II; scale equals  $5\ \mu\text{m}$ . (a, b, d, e, USNM 39278; c, f, holotype ZMA POR 4885.)

Table 6.—Spicule measurements (in  $\mu\text{m}$ ) for *Mycale magnirhaphidifera* (ranges of length, or length  $\times$  width, with means in italics;  $n = 20$ , unless stated).

Material	Subtylostyles	Anisochelas I	Anisochelas II	Sigmas I	Sigmas II	Raphides I	Raphides II
Curaçao							
Holotype (ZMA POR 4885)	236–254.2–270 $\times$ 1.5–2.2–3	19–27.6–33	10–12.4–17	not found	not found	260–291.3–310	8–9.4–11
North Carolina							
Wells & Wells 1960 (USNM 23633, as <i>M. cecilia</i> )	250–270 $\times$ 4–6	30–36	14–16	50–58	not reported	not reported	not reported
remeasured	196–231.0–258 $\times$ 4–6	30–30.9–35	13–15.6–18	46–49.1–55	not found	168–204 ( $n = 7$ )	11–20 ( $n = 4$ )
Belize							
USNM 39278 (MNRJ 647)	196–258.2–286 $\times$ 4.4	31–35 ( $n = 4$ )	11–13	32–43.6–50	13–21 ( $n = 3$ )	90–143.4–241	13–17.5–22
MNRJ 648	232–266.6–294 $\times$ 4.4–6.0	21–24.4–35	12–13.4–15	26–31 ( $n = 2$ )	not found	280–304.9–322	15–17.0–19
MNRJ 649	232–278.0–308 $\times$ 3.9–5.0	29–36 ( $n = 5$ )	9–11.3–13	45–47.1–52	not found	112–189.8–249	13–20.9–28
MNRJ 650	258–283.1–308 $\times$ 3.9–5.5	29–31.6–34	10–11.2–13	37–43.7–47	19–23.0–26	120–153.7–260	14–19.3–37
MNRJ 651	232–269.4–283 $\times$ 4.4–5.3	31–32.7–36	11–14.1–16	40–43.1–48	19 ( $n = 1$ )	95–154.3–252	11–14.1–16
MNRJ 652	274–303.0–322 $\times$ 4.4–6.6	33–37 ( $n = 5$ )	11–11.9–18	42–45.0–47	20 ( $n = 1$ )	109–192.6–255	15–18.5–21
USNM 39280 (MNRJ 653)	255–279.2–300 $\times$ 4.2–5.4	31–32.8–36	11–12.0–13	40–43.2–46	not found	129–214.8–286	13–16.4–19
MNRJ 654	238–275.0–294 $\times$ 4.2–6.1	31–31.8–34	12–12.7–13	37–44.9–48	22 ( $n = 1$ )	101–213.1–280	14–19.3–23

isochelas, with or without sigmas, and with two size classes of raphides, the larger ones reaching more than 200  $\mu\text{m}$  in length.

*Description.*—Macroscopic appearance: Encrusting, up to (5 mm thick) very soft and fragile. Subectosomal channels of the aquiferous system converging to oscula ( $\leq 3$  mm diameter) which are raised and surrounded by transparent collars. Color in life is highly variable (see material section above), burgundy to bluish-purple and grayish blue in light-exposed areas, cream to yellowish in shaded zones; drab in dying tissue parts. Most specimens collected (May to August) contained larvae (150–300  $\mu\text{m}$  in diameter) in the choanosome; many were associated with clusters of serpulid polychaete tubes.

*Skeleton:* The ectosome, lacking a special skeleton, consists of a superficial membrane bearing pores (30–50  $\mu\text{m}$  diameter) and is supported by terminal brushes of choanosomal spiculofibers. A few sigmas and single anisochelas are seen between the pores, rosettes of anisochelas I (ca. 70  $\mu\text{m}$  diameter) occur in the subectosomal zone.

The choanosome has a low spicule density, with subtylostyles organized in paucispicular (3 to 10) ascending tracts of 15–30  $\mu\text{m}$  in diameter. The fibers branch seldomly and generally run parallel to each other without anastomosing. Close to the surface they diverge to form brushes. Sigmas are very common throughout the sponge. Raphides too are dispersed, not organized into trichodragmas.

*Spicules* (Figs. 10, 11; Table 6): Subtylostyles straight, slender, blunt, with characteristic irregularly-oval head. Anisochelas I, narrow in face and side views, head about 50% of total length, base of frontal ala of the head curved forward, base of lateral alae of the head curved backward and slightly protruding over the shaft (in side view). Anisochelas II slender, head about 50% of total length, frontal ala of foot extended on top in a short digitiform process. Sigmas I with almost straight inner face, abruptly bent into very sharp hooks. Sigmas

II delicate with sharp points. Raphides I slender, straight, sharply pointed. Raphides II stout, straight, sharply pointed.

*Ecology.*—A common species in the survey area where it prefers shaded substrates. Many specimens were found on the bare tips of new *Rhizophora mangle* prop roots suggesting capacity to quickly colonize newly available substrate (R-strategist). The common association with polychaete worms was also observed by Wells et al. (1960, as *M. cecilia*) and van Soest (1984).

*Distribution.*—North Carolina, Curaçao, Belize.

*Remarks.*—In contrast to the holotype from Curaçao, most Belizean specimens contain abundant sigmas (see material section above). On the other hand, color, shape, and morphology of all spicules other than sigmas agree well, including the second smaller category of raphides that was found in the holotype (Fig. 11f) but was not originally reported (van Soest 1984). Nevertheless, the abundance of sigmas in some specimens is striking (see material section above) and may justify separating the sigma-bearing population as a different species if more supporting data become available.

The material from North Carolina identified by Wells & Wells, in Wells et al. (1960) as *Mycale cecilia* has previously been referred to both *M. microsigmatosa* (Hechtel 1965) and *M. americana* (van Soest 1984). We have analyzed the specimen (USNM 23633) and found it conspecific with *M. (C.) magnirhaphidifera*, also bearing sigmas (Table 6). Wells & Wells, in Wells et al. (1960) described their material as pale yellowish-green or yellowish-tan, similar to the color of *M. (C.) magnirhaphidifera* from shaded habitats.

*Mycale (Carmia) microsigmatosa* Arndt,  
1927

Figs. 12, 13, 17f; Table 7

*Mycale fistulata* var. *microsigmatosa* Arndt,  
1927:144, pl. I, 9.

*Mycale microsigmatosa.*—Burton 1956:

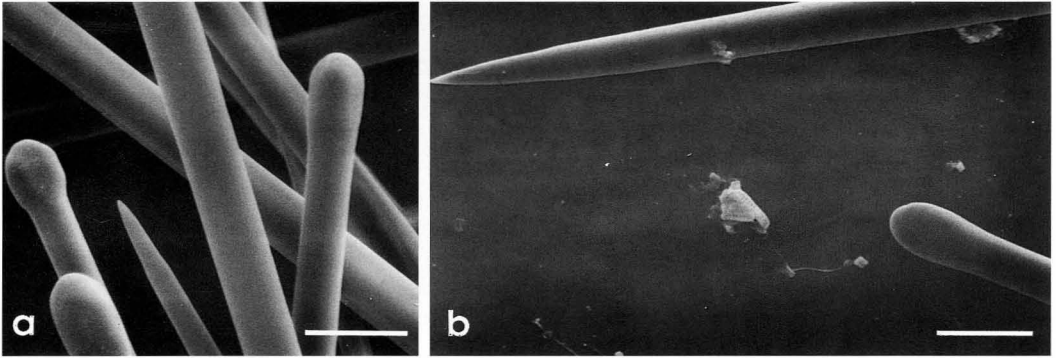


Fig. 12. *Mycale microsigmatosa*, spicules: a, Terminations of subtylostyles showing heads, and gradually sharpening apex; scale equals 10  $\mu\text{m}$ ; b, Terminations of subtylostyles showing head and gradually sharpening apex; scale equals 10  $\mu\text{m}$ . (a, USNM 33580; b, holotype ZMA POR 1593.)

129.—Hechtel 1965:47.—van Soest 1981:12.—Winterman-Kilian & Kilian 1984:132.—Pulitzer-Finali 1986:124.—Rützler 1986:120.

*Mycale (Carmia) microsigmatosa*.—van Soest 1984:24; pl.II, fig. 6.—Zea 1987: 142. Not sensu Green & Gomez 1986: 284 (= *M. cecilia* de Laubenfels).

*Carmia microsigmatosa*.—Hajdu & Boury-Esnault 1991:510.

*Material studied*.—ZMA POR 1593, holotype, Curaçao. USNM 22207, holotype of *M. cecilia*, Panama City, Panama. USNM 33580, Belize, Twin Cays, Turtle Pond entrance, on root of *Rhizophora*, coll. I. Goodbody, 24 Feb 1985; USNM 34625, Belize, Twin Cays, coll. I. Goodbody, Feb 1986; USNM 41258, Belize, Twin Cays, Main Channel south of dock, on mangrove roots, coll. K. Rützler, 12 Jun 1983; USNM 39302 (several lots), Belize, Twin Cays, Cuda Cut, coll. E. Hajdu & K. Smith, 13 Aug 1993; USNM 39326 (several lots), Belize, Twin Cays, Sponge Haven, coll. E. Hajdu & K. Smith, 9 Aug 1993; USNM 47873, Belize, Blueground Range, <1 m, coll. K. Rützler, 6 May 1994. USNM 42951, Belize, Twin Cays, Batfish Point, <1 m, coll. K. Rützler, 19 Apr 1996.

*Diagnosis*.—Orange-dotted to reddish, crustose *Mycale (Carmia)*, with two categories of small (<30  $\mu\text{m}$ ) anisochelas and small (<50  $\mu\text{m}$ ) sigmas.

*Description*.—Macroscopic appearance: Specimens are encrusting or cushion-shaped (5 cm thick), very soft and fragile. Subectosomal channels of the aquiferous system converge to scattered oscula (<5 mm) with transparent, membranous collar. Live color is highly variable but predominantly reddish orange. Even grayish-greenish specimens have recognizable bright orange specks which aid in field recognition of the species. Specimens with larvae were found during August.

*Skeleton*: A thin surface membrane with scattered megascleres and a few paucispicular (3 to 6 spicules wide) bundles can be peeled off and terminal spicule brushes of the ascending choanosomal fibers reach and penetrate the ectosome.

The choanosome is supported by meandering tracts of subtylostyles (50  $\mu\text{m}$  thick) which may be more or less replaced by foreign structures, such as algae and sabellid polychaete tubes. These tracts split up and anastomose near the surface where they fan out in brushes. Scattered megascleres are common throughout and sigmas are seen here and there in large concentrations.

*Spicules* (Figs. 12, 13; Table 7). Subtylostyles slender, mostly straight, with faintly marked oval head, apex sharpening gradually or abruptly. Anisochelas I, head about 60% of total length, shaft gradually curved, basal portion of frontal and lateral alae

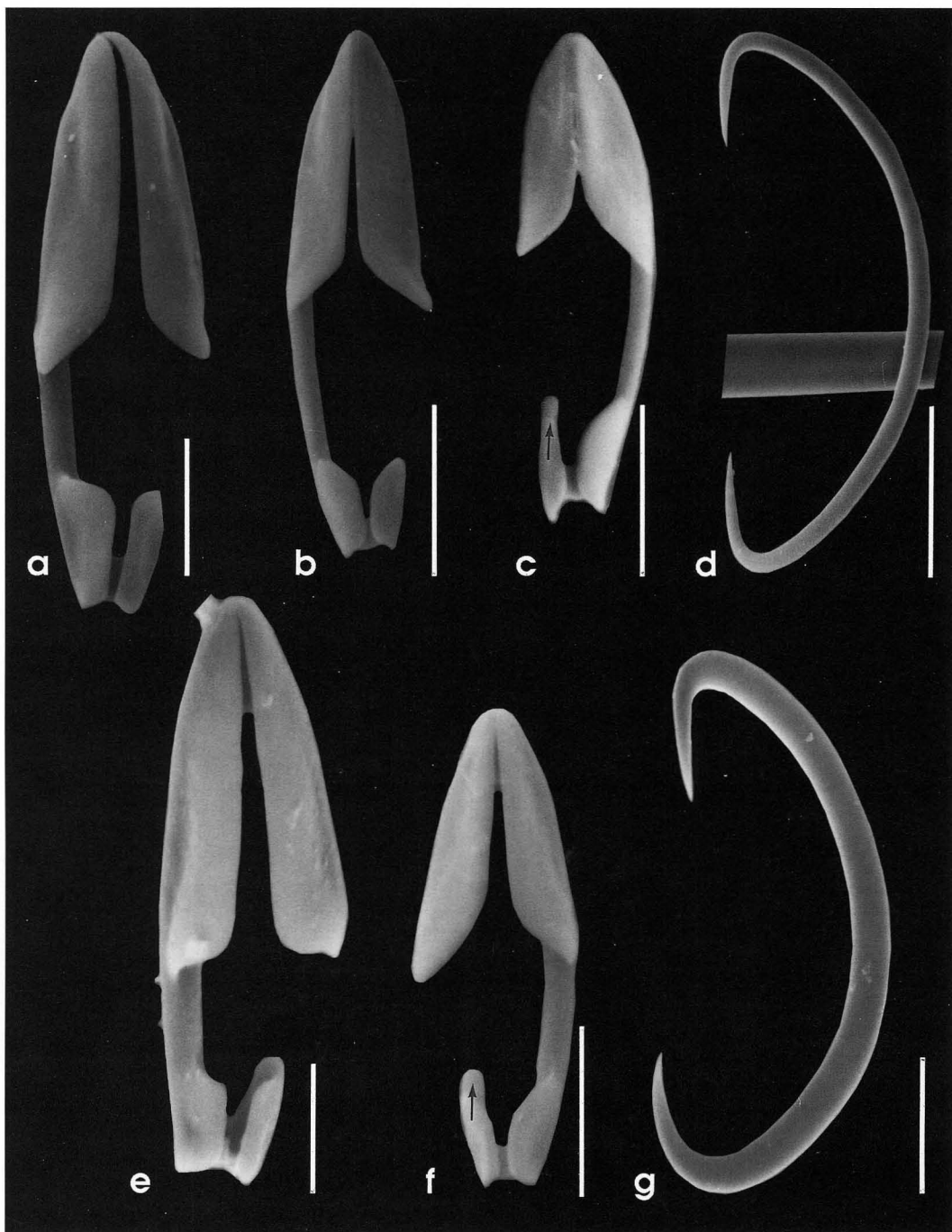


Fig. 13. *Mycale microsigmatosa*, spicules: a, Profile view of anisochela-I; scale equals 5  $\mu\text{m}$ ; b, Profile view of anisochela-II; scale equals 5  $\mu\text{m}$ ; c, Profile view of anisochela-II showing thin digitiform process on top of frontal ala of foot (arrow); scale equals 10  $\mu\text{m}$ ; d, Slender sigma; scale equals 10  $\mu\text{m}$ ; e, Profile view of anisochela-I; scale equals 5  $\mu\text{m}$ ; f, Profile view of anisochela-II showing thin digitiform process on top of frontal ala of foot (arrow); scale equals 5  $\mu\text{m}$ ; g, Stout sigma; scale equals 10  $\mu\text{m}$ . (a, b, d, USNM 33580; c, holotype ZMA POR 1593; e-g, holotype of *M. cecilia*, USNM 22207.)



Table 7.—Spicule measurements (in  $\mu\text{m}$ ) for *Mycale microsigmatosa* (ranges of length, or length  $\times$  width, with means in italics;  $n = 20$ , unless stated).

Material	Subtylostyles	Anisochelas I	Anisochelas II	Sigmas
Holotype (ZMA POR 1593, Arndt 1927)	250–294 $\times$ 4.8	8–19	not given	32–38
remeasured	232–260.8–283 $\times$ 4–6	16–18.0–20	13–13.3–14	30–32.4–37
USNM 33580	224–241.9–263 $\times$ 4–6	18–19.3–21	13–14.1–15	30–35.0–42
USNM 34625	213–237.4–252 $\times$ 6–7	18–19.0–20	12–14.0–15	25–33.8–36
USNM 41258	216–241.6–260 $\times$ 3–4	18–18.6–20	13 ( $n = 3$ )	30–38.3–45
USNM 39302 (MNRJ 655)	235–253.8–274 $\times$ 3–5	18–19.5–20	13–14 ( $n = 3$ )	29–33.8–37
MNRJ 656	224–236.9–249 $\times$ 2–4.1–5	17–18.9–21	12–13.5–15	34–35.0–37
MNRJ 657	216–239.7–277 $\times$ 3–4.1–6	17–19.6–21	14–14.3–16	30–33.2–35
MNRJ 658	244–269.6–288 $\times$ 4–4.7–7	19–20.3–24	12–13.8–15	33–36.9–41
MNRJ 659	235–247.0–263 $\times$ 4–6	18–18.7–20	13–13.8–15	32–34.8–39
MNRJ 660	246–267.7–288 $\times$ 4–6	18–20.6–23	14–14.8–15	31–36.6–42
MNRJ 661	238–252.0–273 $\times$ 3–5	18–18.8–20	12–13.4–15	32–35.7–39
MNRJ 662	227–240.5–258 $\times$ 3–4.2–6	17–18.2–20	13–13.4–15	36–37.8–39
MNRJ 663	232–251.7–267 $\times$ 3–4.2–6	17–18.6–20	11–13 ( $n = 2$ )	31–34.4–39
USNM 39326 (MNRJ 664)	243–266.1–288 $\times$ 4–6	18–19.5–21	13–13.8–15	32–37.0–43
MNRJ 665	230–240.2–259 $\times$ 4–5.0–7	18–20.2–21	12–14 ( $n = 6$ )	31–35.9–39
MNRJ 666	224–255.4–274 $\times$ 3–4.5–6	18–20.0–23	13–14.6–16	32–34.7–36
MNRJ 667	221–249.2–269 $\times$ 3–4	18–19.0–20	13–14.1–15	32–35.5–39

slightly divergent. Anisochelas II, head about 50% of total length, shaft gradually curved, with basal portion of frontal and lateral alae of head slightly divergent; in some of these spicules the top of the frontal ala of the foot tapers to a thin digitiform process (Fig. 13f). Sigmas slender, both ends markedly bent into sharp hooks.

*Ecology.*—Common on mangrove prop roots, including new growth tips, and all other light-exposed substrates in shallow lagoon and harbor habitats (R-strategist). The species is also reported as tolerant of oil and domestic wastes (Muricy 1989). Sabellid polychaetes are commonly associated with and overgrown by this sponge.

*Distribution.*—Bermuda, Florida, Bahamas (?), Cuba (?), Jamaica, Puerto Rico, Venezuela, Netherlands Antilles, Colombia, Belize; also from Brazil, West Africa (?), Açores (?), and Eastern Mediterranean (?).

*Remarks.*—Agreement with the holotype (Figs. 12b, 13c) is excellent, including the presence of two categories of anisochelas which has not before been reported for the species. Because anisochelas are rare in this species (van Soest 1984, Hajdu & Boury-Esnault 1991), it is not surprising that occurrence of a second category was previously overlooked.

*Mycale microsigmatosa* is very common in Belizean mangroves, displaying mainly reddish-orange color but also red and translucent gray. Similar color variability was reported by Hechtel (1965, Jamaica), van Soest (1984; Curaçao, Bonaire, Margarita, and Florida), and Zea (1987, Colombia). Hajdu & Boury-Esnault (1991) found Brazilian specimens (collected between latitudes 13° and 24°S) to be exclusively red but subsequent observations (EH) found pale-yellow specimens from Angra dos Reis (Rio de Janeiro state).

Bergquist (1965) and Hechtel (1965), suggested the synonymy of *Mycale microsigmatosa* with *M. cecilia* de Laubenfels. Another opinion by van Soest (1984) favored a close relationship between *M. cecilia* and *M. americana*. The present finding

of two categories of anisochelas in *M. microsigmatosa* rather supports the former view, agreement with *M. cecilia* (holotype, Fig. 13e–g). Furthermore, de Laubenfels (1936b) describes *M. cecilia* as “basically green, abundantly provided with bright red specks”, similar to our own observations on *M. microsigmatosa*. However, we prefer to keep *M. cecilia* as a valid name for eastern Pacific records of the sponge, basing this decision on geographic separation and small differences in spicule dimensions. Therefore we propose to assign the record of *M. (C.) microsigmatosa* from the Pacific coast of Mexico (Green & Gómez 1986) to *M. cecilia*, this sponge has relatively thick subtylostyles (5–9 µm) and anisochelas with a large range of length (12–21 µm), possibly representing two categories. Van Soest (1984) also suggested possible synonymy of *Mycale microsigmatosa* with *M. senegalensis* Lévi, 1952, *M. sanguinea* Tournour, 1969, and *Desmacella meliorata* Wiedenmayer, 1977. To this list we may add *Desmacella janiae* Verrill, 1873, *Biemna microstyla* de Laubenfels, 1950a, and *Prosuberites scarlatum* Alcolado, 1984, but formal decision must await re-examination of all types.

#### Subgenus *Mycale* Gray, 1867

*Diagnosis.*—*Mycale* with ectosomal skeleton of confused tangential megascleres over perpendicular, dendritic choanosomal spicule tracts that end in subectosomal brushes. Type species: *Hymeniacidon lingua* Bowerbank, 1866 (Hajdu & Desqueyroux-Faúndez 1994).

*Remarks.*—A subgenus *Anomomycale* was erected by Topsent (1924) for *Desmacidon titubans* Schmidt (1870). This sponge, however, has most characteristics of the subgenus *Mycale*, including the subectosomal brushes, large megascleres (one size class >700 µm), and possibly tangential subtylostyles in the ectosome (Lundbeck 1905). Only the distinctive shape of its anisochelas separates it. This single fea-

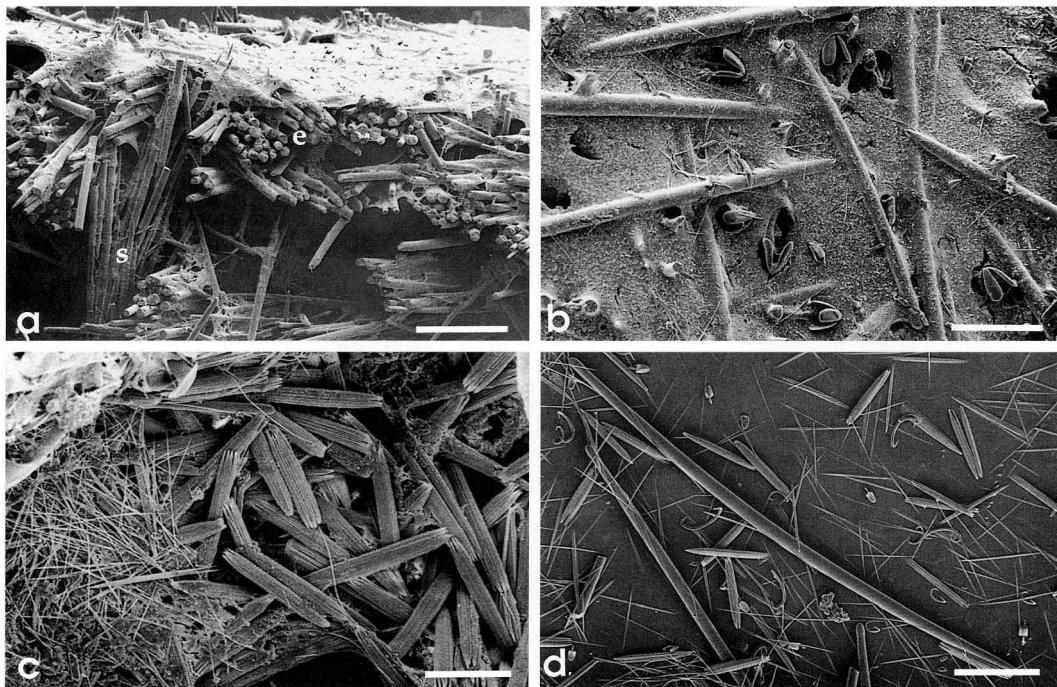


Fig. 14. *Mycale laevis*, skeleton: a, Transverse section showing terminally divergent spicule brushes (s) of ascending choanosomal tracts supporting the tangential ectosomal skeleton (e); scale equals 200  $\mu\text{m}$ ; b, Detail of surface showing tangentially disposed megascleres, and abundance of microscleres; scale equals 100  $\mu\text{m}$ ; c, Detail of subectosomal area showing typical patches of trichodragmas, and also of isolated raphides; scale equals 50  $\mu\text{m}$ ; d, Fusiform, bent subtylostyle, note abundance of trichodragmas; scale equals 100  $\mu\text{m}$ .

ture is insufficient to justify subgeneric separation and it seems appropriate to keep *M. tibubans* in the subgenus *Mycale*.

*Mycale (Mycale) laevis* (Carter, 1882)

Figs. 14, 15, 17g; Table 8

Synonymy, see Hajdu & Desqueyroux-Faúndez (1994); in addition:

*Mycale fusca*.—Mello-Leitão et al. 1961: 12; Hechtel 1976:254; Hajdu & Boury Esnault 1991:504.

*Mycale (Mycale) laevis*.—Lehnert 1993:54.

*Material studied*.—USNM 41267, Belize, Twin Cays, Sponge Haven, <1 m, on mangrove roots, coll. K. Rützler, 13 June 1983; USNM 39328 (3 lots), Belize, Blue Ground Range, 1 m, coll. E. Hajdu & K. Smith, 12 Aug 1993.

*Diagnosis*.—Orange to yellow, encrusting or massive *Mycale* with large (>500

$\mu\text{m}$ ) megascleres and two size classes of anisochelas; with basal, spur-like projections on the smaller anisochelas; also present, two classes of sigmas and raphides in trichodragmas.

*Description*.—Macroscopic appearance: Thick cushions (up to 5 cm) or clusters of 20 or more branches (1–10 cm diameter, up to 50 cm tall) rising from a massive base and often with apical oscula (up to 4 cm diameter). Oscula have fibrous-looking collars made up of tracts of megascleres. Consistency is rough but compressible and the texture rough. Color in life is a bright orange-yellow, but also a few whitish specimens were seen. Specimens with embryos were seen in August.

*Skeleton* (Fig. 14a–c): The ectosome is reinforced by a thin layer of tangentially strewn subtylostyles interspersed with abundant microscleres. A very dense, con-

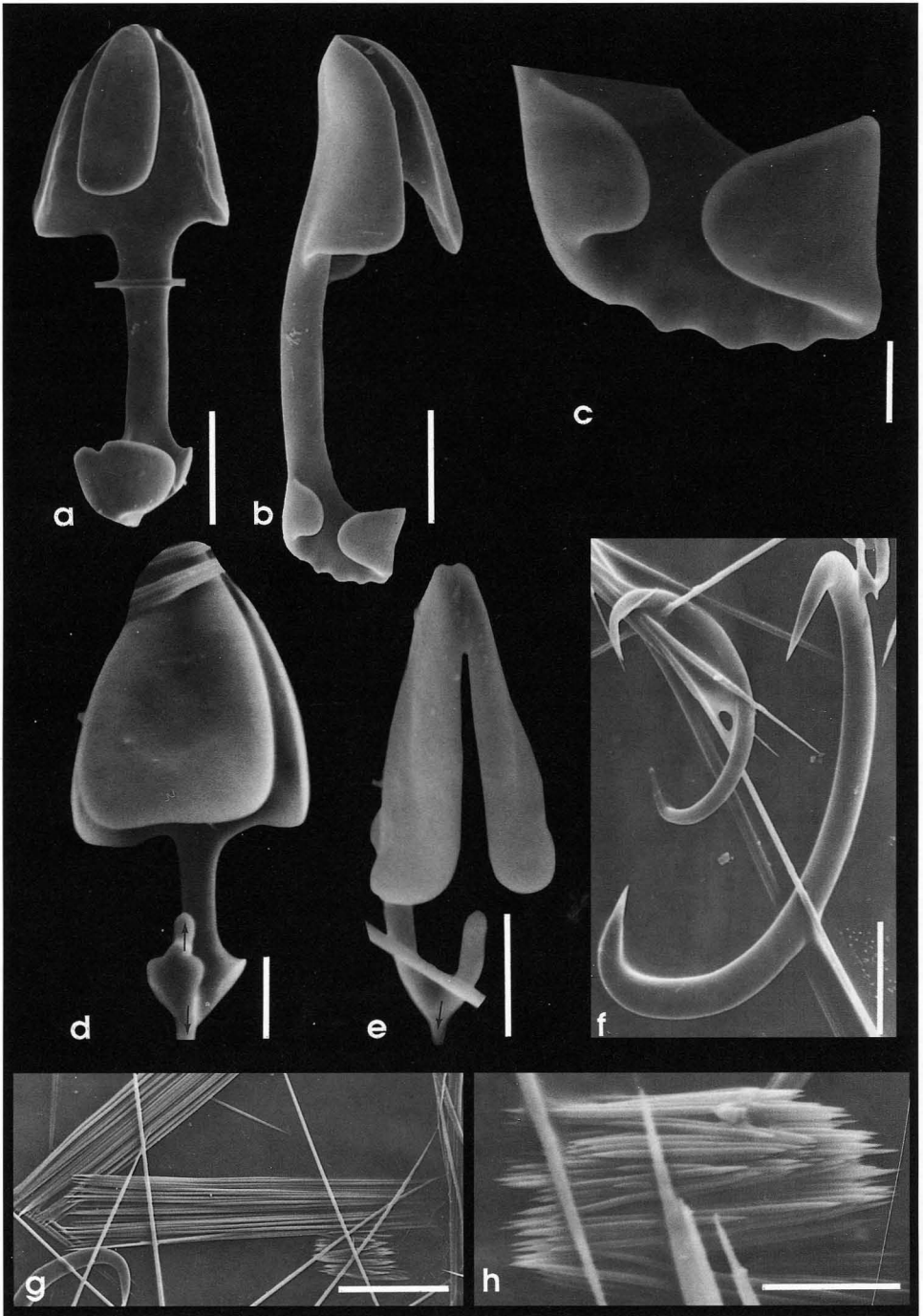


Fig. 15. *Mycale laevis*, scapules: a, Face view of anisochela-I; scale equals 20  $\mu\text{m}$ ; b, Profile view of anisochela-I, note slight s-shape of shaft; scale equals 20  $\mu\text{m}$ ; c, Detail of foot of anisochela-I shown in Fig. 15b, with an undulated basal portion of the falx; scale equals 5  $\mu\text{m}$ ; d, Face view of rare, robust anisochela-III showing thin digitiform prolongation on top of frontal ala of foot (arrow up), and basal spur (arrow down); scale equals 5  $\mu\text{m}$ ; e, Profile view of typical anisochela-III showing basal spur (arrow), note reduced foot without alae; scale equals 5  $\mu\text{m}$ ; f, Sigmata-I and -II; scale equals 10  $\mu\text{m}$ ; g, Trichodragmas-I and -II; scale equals 20  $\mu\text{m}$ ; h, Rare trichodragmas-II; scale equals 5  $\mu\text{m}$ .

Table 8.—Spicule measurements (in  $\mu\text{m}$ ) for *Mycale laevis* (ranges of length, or length  $\times$  width, with means in italics;  $n = 20$ , unless stated).

Material	Subtylostyles	Anisochelas I	Anisochelas II	Sigmas I	Sigmas II	Trichodragmas I	Trichodragmas II
USNM 39238 (MNRJ 668)	429-504.6-551 $\times$ 6-15.9-20	78-83.5-89	18-18.7-21	29-42.0-50 $\times$ 2-3	15-20.2-23	74-77.4-86 $\times$ 8-12	not found
MNRJ 669	509-550.7-610 $\times$ 9-16.0-23	72-81.8-95	19-22.1-33	31-39.5-47 $\times$ 2	18-22 ( $n = 5$ )	72-80.1-87 $\times$ 4-8.5-17	not found
MNRJ 670	525-566.0-588 $\times$ 13-15.8-21	72-80.1-89	17-24.7-33	32-39-49 $\times$ 3	14-16.8-21	72-79.6-90 $\times$ 8-10	11-13.0-15 $\times$ 4-5.9-8
USNM 41267	514-560.7-610 $\times$ 12-14.2-18	73-83.4-91	17-18.8-28	32-43.3-52 $\times$ 3	17-20.1-24	70-78.4-85 $\times$ 5-9.2-15	13-17.6-26 $\times$ 3-4.8-8

fused subectosomal reticulation of multi-spicular subtylostyle tracts (up to 300  $\mu\text{m}$  thick) is oriented mainly parallel to the surface. Spaces between tracts are filled by large amounts of scattered subtylostyles, anisochelas I, and patches of trichodragmas I (by far the most common microscleres, Fig. 14c). Brushes of subtylostyles support the ectosomal network (Fig. 14a), and pierce the surface slightly. Anisochelas I form a few rosettes (160  $\mu\text{m}$ ) but more often occur scattered or surrounding the bundles of megascleres.

The choanosome shows high spicule density and includes criss-crossing subtylostyle tracts with loose subtylostyles and patches of numerous trichodragmas I in between. Digitiform processes of the larger specimens are supported by longitudinal spicule tracts and a secondary, transverse plumo-reticulate skeleton.

Spicules (Figs. 14d, 15; Table 8): Subtylostyles fusiform, mostly bent with faintly marked, oval head and abruptly sharpened, or stronglyloid apex. Anisochelas type I, with shaft slightly s-shaped, head ca. 40% of total length, basal portion of falx on foot undulated (Fig. 15c). Anisochelas type III slender, head 70% of total length, foot often reduced (lacking alae) and with basal spur. Sigmas I stout, with sharply bent hooks. Sigmas II similar to I but more slender. Trichodragmas I; trichodragmas II.

*Ecology.*—This is a well known reefal species (Goreau & Hartman 1966) and is widely distributed in the shallow parts (16-25 m) of the fore-reed of Carrie Bow Cay (see Rützler & Macintyre 1982 for the bionomy of the reef). In the mangroves, *Mycale laevis* is restricted to areas with good exposure to the open, near-reef lagoon (it is common at Blue Ground Range and Cat Cay Lagoon, but very rare at Twin Cays). There, however, the sponges attached to red mangrove roots can grow to record size. Specimens laying unattached on the bottom (presumably fallen from the roots) and intergrown with turtle grass survive well and appear healthy.

*Distribution.*—Cuba, Jamaica, Dominican Republic, Puerto Rico, Venezuela, Colombia, Belize, Mexico; also Brazil.

*Remarks.*—A few details should be added to former descriptions of the species. Notably, we recognize two categories of sigmas (smaller one can be rare) rather than a large size range of one, and two categories of trichodragmas in some of the specimens (again, the smaller being rare see Hajdu & Desqueyroux-Faúndez 1994, tab. 1, and references therein). No taxonomic importance is given to these characters here.

*Esperia massa* Schmidt, 1862 sensu Schmidt 1870:58 and *Mycale massa* (Schmidt, 1862) sensu Winterman-Kilian 1984:133, are likely to be synonyms of *Mycale laevis* because the latter species was originally described from the Mediterranean Sea and a West-Indian distribution is highly unlikely despite the similarities in skeleton morphology.

#### Subgenus *Paresperella* Dendy, 1905

*Diagnosis.*—*Mycale* with an ectosomal skeleton of reticulated tangential megascleres and with serrated sigmas among the microscleres. Type species: *Esperia serratohamata* Carter, 1880.

*Remarks.*—Van Soest (1984), based on the very peculiar characteristics of serrated sigmas, considers *Paresperella* a monophyletic group. Nevertheless, in the absence of another congruent diagnostic character, *Paresperella* may fall to *Aegogropila* (see comments on *Anomomycale*, above, under subgenus *Mycale*). However, until further study of species in *Paresperella* and other closely related subgenera (*Aegogropila*, *Carmia*), it is convenient to maintain this subgenus for the 20 or so species already described with serrated sigmas.

*Mycale (Paresperella)* species indet.

Fig. 16

*Material studied.*—Spicules found contaminating sample of *Mycale citrina*,

USNM 38967, Belize, Twin Cays, Cuda Cut, 1 m, coll. E. Hajdu & K. Smith 13 Aug 1993.

*Spicules.*—Sigmas (Fig. 16), slender, o- or s-shaped, shaft subcylindrical (flattened in cross section), with ca. 10 spines each along the outer bends of the hooks; spines single or double and directed toward spicule center.

*Remarks.*—These distinctive spicules are the only material found, thus making species diagnosis impossible. The sigmas came in abundance from a very small specimen or fragment (used up in making the preparation) inadvertently collected as part of a specimen of *M. citrina*.

Comparison with the only *Paresperella* species described from the western Atlantic, *Mycale (P.) spinosigma* (Boury-Esnault 1973; MNHN D NBE 968), indicates that the latter is most likely contaminated with *Paresperella* spicules. The anisochelas reported by Boury-Esnault (1973) were not found in a preparation of the type specimen and sigmas were very rare. The ZMA collection has a very small macerated specimen (ZMA 5389) from inside Curaçao (Barbara Beach, 1–3 m) which, from the appearance of serrated sigmas may be conspecific with the Belizean material. The Curaçao specimen has slender subtylostyles (270–323  $\mu\text{m}$  long), one category of anisochelas (24–30  $\mu\text{m}$  long), and the serrated sigmas (78–98  $\mu\text{m}$  long). One toxa (34  $\mu\text{m}$  long) was also seen but may be foreign. We refrain from making an identification until more material is available.

#### Discussion

Some names associated with Caribbean *Mycale* are still in need of a reappraisal. Winterman-Kilian & Kilian (1984) listed *M. cleistochela flagellifer* Vacelet & Vas-seur, 1971 (a species from Madagascar) in Colombia, with sigmas twice the size of the original report. We have not examined the Colombian material but assume that it is conspecific with *M. (Ae.) diversisigmata*

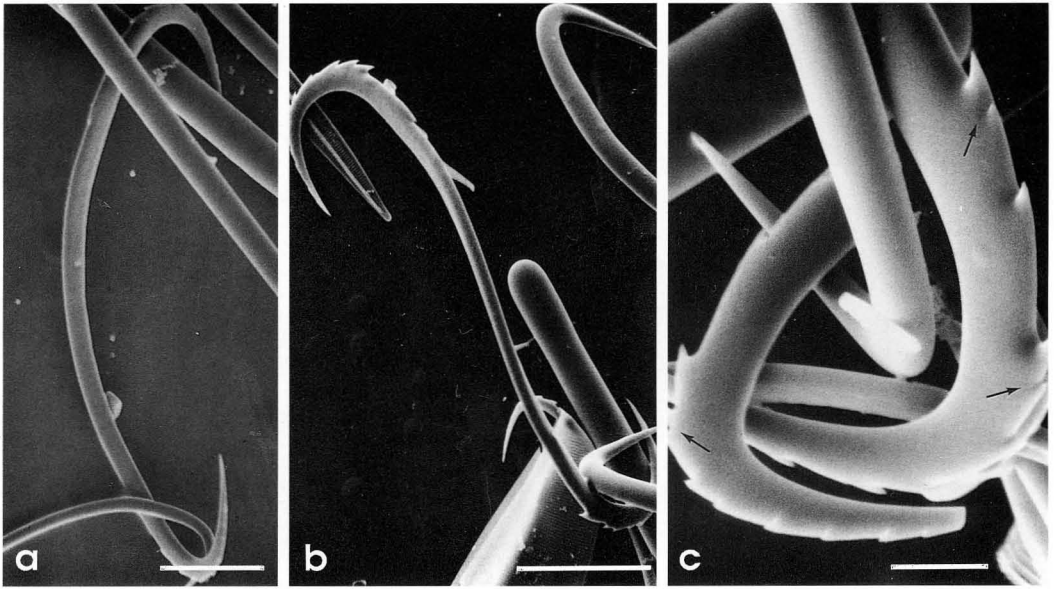


Fig. 16. *Mycale (Paresperella)* sp., characteristic sigmas (other spicules belong to *M. citrina*): a, Serrated sigma; scale equals 20  $\mu\text{m}$ ; b, Serrated sigma showing non-cylindrical shaft, note narrower middle portion when compared to wider hooks; scale equals 20  $\mu\text{m}$ ; c, Detail showing spines on hooks of serrated sigmas, note heterogeneous distribution with the occurrence of twins (arrows); scale equals 5  $\mu\text{m}$ .

van Soest, 1984 (from Curaçao), which contains flagelliform sigmas (150–200  $\mu\text{m}$ ), as well as semi-closed anisochelas. Similarity of the latter species with *M. cleistochela flagellifer* was suspected by van Soest (1984) who must have been unaware of the morphology of true cleistochelas which was only recently revealed by scanning electron microscopy (Pulitzer-Finali 1996:fig. 15; for *M. (Ae.) peculiaris*).

Schmidt (1870) cited five species from Florida under genera *Esperia* Nardo, 1833 and *Desmacidon* Bowerbank, 1864, that were referred to *Mycale* by subsequent authors. The specimen originally named *Esperia renieroides* Schmidt (1870) was referred to *Oxymycale* by van Soest (1984) and to *Mycale* by Pulitzer-Finali (1986). Neither author had examined Schmidt's preparation (BMNH 1870.5.3.31) which reveals an isotropic reticulation of small oxaeas, part of a haplosclerid sponge, and a single rosette of anisochelas of the type that is indicative of *M. immitis* (Schmidt 1870). The specimen identified as *Esperia massa*

Schmidt, 1862 (sensu Schmidt 1870) is considered dubious by Topsent (1924), and unrecognizable by van Soest (1984). Winterman-Kilian & Kilian (1984) report *M. massa* from Colombia. However, data indicate that these specimens are conspecific with *M. laevis* which has indeed very similar spiculation.

As argued above, *Desmacidon tibubans* described by Schmidt (1870) is best identified as *Mycale (M.) tibubans*, although the conspecificity of populations from Florida (Schmidt 1870), the northeastern-Atlantic (Lundbeck 1905, Topsent 1924) and the Antarctic (Boury-Esnault & Van Beveren 1982) is certainly unlikely and needs to be confirmed. *Esperia diaphana* Schmidt (1870; material examined: dissociated spicules mount made by Schmidt, BMNH 1870.5.3.32) and *Esperia immitis* Schmidt (1870; material examined: dissociated spicules mount made by Schmidt, BMNH 1870.5.3.30, MCZ No. 42; label could be in Schmidt's handwriting but depth of 274 m differs from that of 230 m in the original

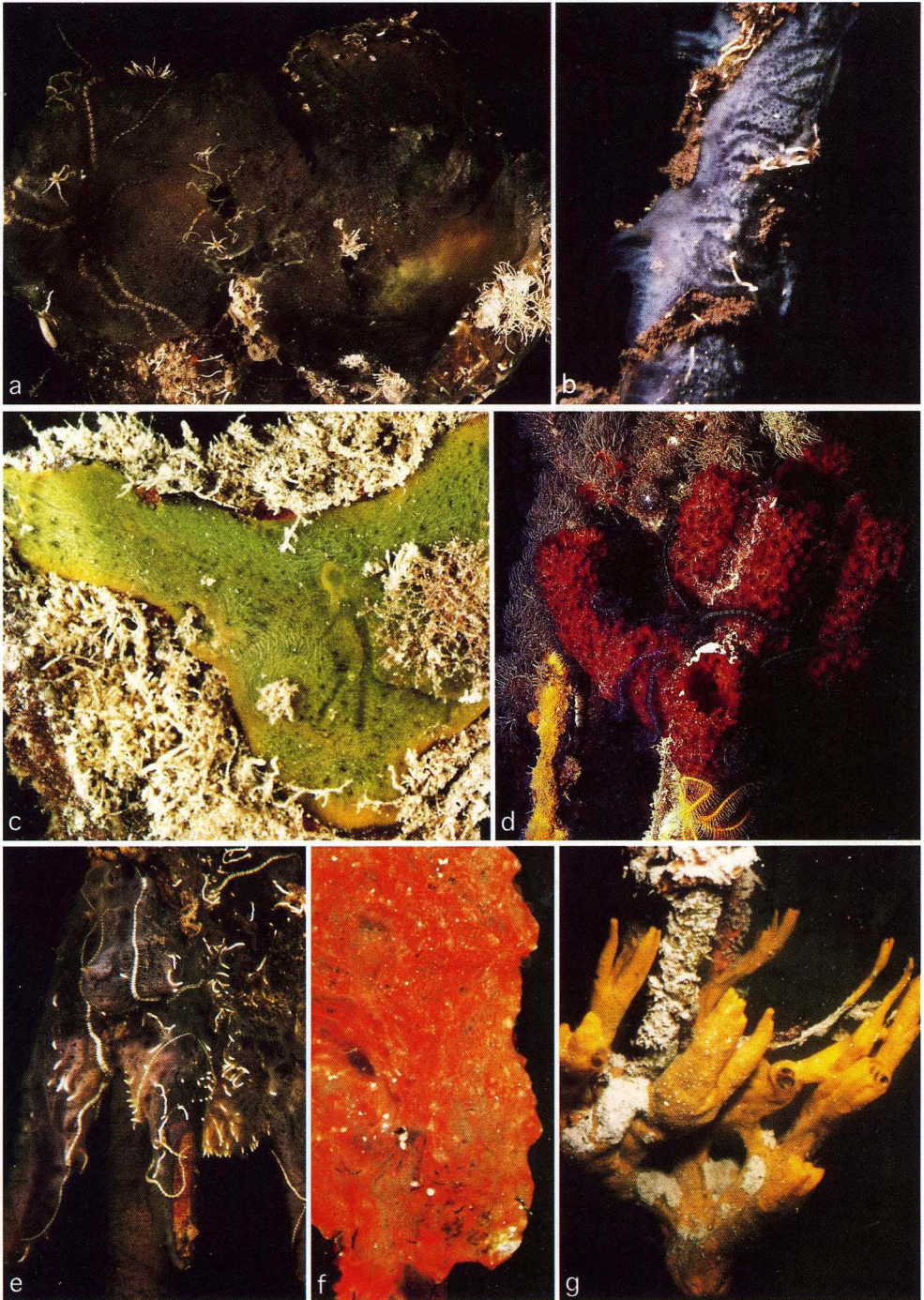


Fig. 17. Underwater photographs of live *Mycale* specimens representing seven of the eight species found at Twin Cays: a, *M. arndti*, grayish-colored specimen,  $\times 1.0$ ; b, *M. carmigropila* new species, on red-mangrove stilt root,  $\times 0.9$ ; c, *M. citrina* new species, on mangrove peat,  $\times 1.3$ ; d, *M. laxissima*, on red-mangrove stilt roots,  $\times 0.3$ ; e, *M. magnirhaphidifera*, overgrowing serpulid polychaete tubes on red-mangrove stilt roots,  $\times 0.5$ ; f, *M. microsigmatosa*,  $\times 1.0$ ; g, *M. laevis* on red-mangrove stilt root,  $\times 0.3$ .



account) are regarded as good species of *Mycale* (*Mycale*). *Esperia diaphana* has two categories of megascleres (721–827  $\mu\text{m}$  and 509–604  $\mu\text{m}$ ), three categories of anisochelas (148–170  $\mu\text{m}$ , 31–40  $\mu\text{m}$ , 19–25  $\mu\text{m}$ ), one category of sigmas (16–23  $\mu\text{m}$ ), and one category of trichodragmas (41–70  $\mu\text{m}$ ), and seems close to *M. (M.) grandis* Gray, 1867 (Indo-west Pacific), and *M. (M.) anisochela* Lévi, 1963 (south and southwestern Africa). Abundant material from the Gulf of Mexico, agreeing with *M. (M.) diaphana* is in the USNM collection. *M. (M.) immitis* has two categories of megascleres (996–1198  $\mu\text{m}$  and 466–530  $\mu\text{m}$ ), three categories of anisochelas (90–105  $\mu\text{m}$ , 29–33  $\mu\text{m}$ , 20–25  $\mu\text{m}$ ), one category of sigmas (35–45  $\mu\text{m}$ ), and two categories of trichodragmas (90–108  $\mu\text{m}$ , 18–33  $\mu\text{m}$ ).

Van Soest (1984) considers Little's (1963) *Mycale macilenta* from the Gulf of Mexico to be a likely new species in the subgenus *Aegogropila*. In the account below we will treat it as *Mycale* (*Ae.*) species.

The following key to 17 recognized species of *Mycale* of the Caribbean should be used in conjunction with the relevant literature (most recent reliable or available reference).

<i>Mycale</i> ( <i>Aegropila</i> )	van Soest 1984
<i>americana</i> van Soest	
<i>M. (Ae.) angulosa</i>	van Soest 1984
(Duch. & Mich.)	
<i>M. (Ae.) arndti</i> van	van Soest 1984
Soest	
<i>M. (Ae.) carmigropila</i>	this paper
new species	
<i>M. (Ae.) citrina</i>	this paper
new species	
<i>M. (Ae.) diversigmata</i>	van Soest 1984
van Soest	
<i>M. (Ae.) escarlatai</i> Haj-	Hajdu et al. 1995
du et al.	
<i>M. (Ae.)</i> species indet.	Little 1963 (as <i>M. macilenta</i> )
<i>M. (Arenochalina) lax-</i>	this paper
<i>issima</i> (Duch. &	
Mich.)	
<i>M. (Carmia) magnirha-</i>	van Soest 1984
<i>phidifera</i> van Soest	

<i>M. (C.) microsigmatosa</i>	this paper
Arndt	
<i>M. (Grapelia) ungui-</i>	Hajdu et al. 1995
<i>fera</i> Hajdu et al.	
<i>M. (Mycale) diaphana</i>	Schmidt 1970 (as
(Schmidt)	<i>Esperia</i> ); this pa-
	per (discussion)
<i>M. (M.) immitis</i>	Schmidt 1970 (as
(Schmidt)	<i>Esperia</i> ); this pa-
	per (discussion)
<i>M. (M.) laevis</i> (Carter)	this paper
<i>M. (M.) titubans</i>	Schmidt, 1870 (as
(Schmidt)	<i>Desmacidon</i> ); this
	paper (comment,
	subgenus <i>Mycale</i> )
<i>M. (Paresperella)</i> spe-	this paper
cies indet.	

Key to the species of Caribbean *Mycale*

1. Megascleres near 500  $\mu\text{m}$  common . . . 2  
    Megascleres always <500  $\mu\text{m}$  . . . . . 5
2. Two categories of megascleres . . . . . 3  
    One category of megascleres, trichodragmas often abundant . . . . .  
    . . . . . *Mycale (M.) laevis*
3. Three categories of anisochelas, anisochelas I >60  $\mu\text{m}$  . . . . . 4  
    One category of anisochelas <60  $\mu\text{m}$ , twisted . . . . . *M. (M.) titubans*
4. Anisochelas I  $\leq$ 150  $\mu\text{m}$  common . . . . .  
    . . . . . *M. (M.) diaphana*  
    Anisochelas I <110  $\mu\text{m}$ , with shaft markedly curved in profile view . . . . .  
    . . . . . *M. (M.) immitis*
5. Serrated sigmas present . . . . .  
    . . . . . *M. (Paresperella)* species indet.  
    Serrated sigmas absent . . . . . 6
6. Three or more categories of anisochelas 7  
    One or two categories of anisochelas . . . 12
7. Sigmas present . . . . . 8  
    Sigmas absent, two categories of toxas . . . . .  
    . . . . . *M. (Aegropila)* species indet.
8. Two or more categories of sigmas . . . 9  
    One category of sigmas . . . . . 10
9. Two categories of sigmas, anisochelas II very narrow ("duck's-bill") . . . . .  
    . . . . . *M. (Ae.) escarlatai*  
    Two categories of flagelliform sigmas, three of normal ones . . . . .  
    . . . . . *M. (Ae.) diversisigmata*  
    Three categories of sigmas, four categories of anisochelas . . . *M. (Ae.) arndti*
10. Anisochelas only palmate . . . . . 11

- Anisochelas I and II unguiferate, anisochelas III palmate with spur . . . . .  
 . . . . . *M. (Grapelia.) unguifera*
11. Sigmas  $\geq 70$   $\mu\text{m}$  common, live sponge lemon-yellow . . . . . *M. (Ae.) citrina*  
 Sigmas  $< 70$   $\mu\text{m}$ , live sponge blue . . . . .  
 . . . . . *M. (Ae.) carmigropila*
12. Raphides common . . . . . 13  
 Raphides absent or very uncommon (possibly contaminants) . . . . . 14
13. Two categories of raphides, raphides I  $> 100$   $\mu\text{m}$ , isochelas absent . . . . .  
 . . . . . *M. (Carmia) magniraphidifera*  
 One category of raphides  $< 50$   $\mu\text{m}$ , isochelas present . . . . . *M. (Ae.) angulosa*
14. With tangential ectosomal reticulation . . . . . *M. (Ae.) americana*  
 Without tangential ectosomal skeleton 15
15. Sigmas common,  $> 50$   $\mu\text{m}$ , coarse choanosomal spongin fibers, massive sponges . . . . *M. (Arenochalina) laxissima*  
 Sigmas  $< 40$   $\mu\text{m}$ , delicate choanosomal skeleton strands, encrusting sponges . . . . .  
 . . . . . *M. (C.) microsigmatosa*

### Acknowledgments

We are indebted to F. R. Schram and R. W. M. van Soest (Amsterdam) for critical review of early drafts of the manuscript. L. B. Holthuis (NNM) clarified doubts concerning the type species of *Aegogropila*. A. B. Johnston (MCZ), C. Lévi (MNHN), V. Rainieri (MSNG), S. Stone and C. Valentine (BMNH), and S. Zea (INV) are thanked for the loan of specimens. C. Valentine is specially thanked for her efforts on behalf of Johnston's *Halichondria aegagropila*. K. Smith (National Museum of Natural History, Washington, D.C.) assisted in field work in Belize and in laboratory preparations; she is credited for finding a new species, *Mycale (Aegogropila?) carmigropila*. We thank M. K. Ryan (National Museum of Natural History, Washington, D.C.) for preparing Fig. 1 and helping with other illustration chores, and C. C. Hansen (also from the Museum) for taking and printing the photograph in Fig. 17d. F. Hiemstra (Amsterdam) is thanked for advice on SEM preparation. EH was support-

ed by fellowships and grants from CNPq and FAPESP, Brazil. His field work in Belize was made possible by a short-term visitor grant from the Smithsonian Office of Fellowships and Grants and by a fellowship from the Smithsonian's Caribbean Coral Reef Ecosystems program (CCRE; partly supported by a grant from the EXXON Corporation), National Museum of Natural History. This is CCRE contribution number 531.

### Literature Cited

- Alcolado, P. 1984. Nuevas especies de esponjas encontradas en Cuba.—*Poeyana* 271:1–22.
- Arndt, W. 1927. Kalk- und Kieselschwämme von Curaçao.—*Bijdragen tot de Dierkunde* 25:133–158, pls. I–III.
- Bergquist, P. R. 1965. The sponges of Micronesia, part 1. The Palau Archipelago.—*Pacific Science* 19:123–204.
- , & J. P. Fromont. 1988. The marine fauna of New Zealand: Porifera, Demospongiae. Part 4 (Poecilosclerida).—*New Zealand Oceanographic Institute Memoir* 96:1–197.
- Boury-Esnault, N. 1973. Campagnes de la Calypso au large des côtes atlantiques de l'Amérique du Sud (1961–1962). I. 29. Spongiaires.—*Résultats scientifiques des Campagnes de la Calypso* 10:263–295.
- , & M. van Beveren. 1982. Les Demosponges du plateau continental de Kerguelen-Heard.—*Comité National Français des Recherches Antarctiques (CNFRA)* 52:1–175.
- , & M. T. Lopes. 1985. Les Démosponges littorales de l'archipel des Açores.—*Annales de l'Institut Océanographique, nouvelle série* 61(2):149–225.
- Bowerbank, J. S. 1864. A monograph of the British Spongiadae. Vol. 1:1–290, pls. I–XXXVII. Ray Society, London.
- . 1866. A monograph of the British Spongiadae. Vol. 2:1–388. Ray Society, London.
- Burton, M. 1956. The sponges of West Africa.—*Atlantide Report*. Copenhagen 4:111–147.
- Butler, M. S., R. J. Capon, R. Nadeson, & A. A. Beveridge. 1991. Aromatic Bisabolones from an Australian Marine Sponge, *Arenochalina* sp.—*Journal of Natural Products* 54:619–623.
- Capon, R. J., & J. K. Macleod. 1987. Structural and stereochemical studies on marine norterpene cyclic peroxides; part 2.—*Journal of Natural Products* 50:225–229.
- Carter, H. J. 1871. On two undescribed sponges and two Esperidae from the West Indies; also on

- the nomenclature of the calcisponge *Clathrina*, Gray.—Annals and Magazine of Natural History (4)8:1–28.
- . 1880. Report on specimens dredged up from the Gulf of Manaar and presented to the Liverpool Free Museum by Capt. W. H. Cawne Warren.—Annals and Magazine of Natural History (5)6:35–61.
- . 1882. Some sponges from the West Indies and Acapulco in the Liverpool Free Museum, described with general and classificatory remarks.—Annals and Magazine of Natural History (5)9:266–301, 346–368, pls. XI–XII.
- Cattaneo-Vietti, R., G. Bavastrello, C. Cerrano, M. Sarà, U. Benatti, M. Giovine, & E. Gaino. 1996. Optical fibres in an Antarctic sponge.—Nature 383:397–398.
- Corriero, G., A. Madaio, L. Mayol, V. Picadilli, & D. Sica. 1989. Rotalin A and B, two novel diterpene metabolites from the encrusting Mediterranean sponge *Mycale rotalis*.—Tetrahedron 45: 277–288.
- Dendy, A. 1905. Report on the sponges collected by Prof. Herdman at Ceylon in 1902.—Report to the government of Ceylon on the pearl-oyster fisheries of the Gulf of Manaar 3 (Supplement 18):57–246, pls. I–XVI (Royal Society, London).
- . 1921. The tetraxonid sponge spicule: a study in evolution.—Acta Zoologica V (2):95–152.
- Doumenc, D., & C. Lévi. 1987. Anisochelae analysis and taxonomy of the genus *Mycale* Gray (Demospongiae). Pp. 73–92 in J. Vacelet & N. Boury-Esnault, eds., Taxonomy of Porifera from the northeast Atlantic and Mediterranean Sea. NATO ASI Series, vol. G13. Springer-Verlag, Berlin, 332 pp.
- Duchassaing de Fonbressin, P., & G. Michelotti. 1864. Spongiaires de la mer Caraïbe. Natuurkundige Verhandelingen van de hollandsche Wetenschappen te Haarlem (2)21(III):1–124, pls. I–XXV.
- Esper, E. J. C. 1791–1830. Die Pflanzenthier. Raspe, Nürnberg.
- Fusetani, N., N. Yasumuro, S. Matsunaga, & K. Hashimoto. 1989. Mycalolides A–C, hybrid macrolides of ulupalides and halichondramide, from a sponge of the genus *Mycale*.—Tetrahedron Letters 30:2809–2812.
- Gaino, E., & M. Sarà. 1994. Siliceous spicules of *Tethya seychellensis* (Porifera) support the growth of a green alga: a possible light conducting system.—Marine Ecology Progress Series 108: 147–151.
- Goreau, T. F., & W. D. Hartman. 1966. Sponge: effect on the form of reef corals.—Science 151:343–344.
- Gray, J. E. 1867. Notes on the arrangement of sponges, with the description of some new genera.—Proceedings of the Zoological Society of London 1867:492–558, pls. XXVII–XXVII.
- Green, G., & P. Gómez. 1986. Estudio taxonómico de las esponjas de la Bahía de Mazatlan, Sinaloa, México.—Anales del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México 13(3):273–300.
- Hajdu, E. 1994. A phylogenetic interpretation of hamacanthids (Demospongiae, Porifera) with a re-description of *Hamacantha popana* (de Laubenfels, 1935).—Journal of Zoology 232:61–77.
- , & N. Boury-Esnault. 1991. Marine Porifera of Cabo Frio (Rio de Janeiro, Brazil). The family Mycalidae Lundbeck, 1905, with the description of a new species.—Revista brasileira de Biologia 51(3):503–513.
- , & R. Desqueyroux-Faúndez. 1994. A synopsis of South American *Mycale* (*Mycale*) (Poecilosclerida, Demospongiae), with the description of three new species and a preliminary cladistic analysis of Mycalidae.—Revue suisse de Zoologie 101(3):563–600.
- , R. W. M. van Soest, & J. N. A. Hooper. 1994. Proposal of a phylogenetic subordinal classification of poecilosclerid sponges. Pp. 123–139 in R. W. M. van Soest, Th. M. G. van Kempen & J. C. Braekman, eds., Sponges in time and space. Proceedings of the Fourth International Porifera Congress. Balkema, Rotterdam, 515 pp.
- , S. Zea, M. Kielman, & S. Peixinho. 1995. *Mycale escarlatei* n.sp. and *Mycale unguifera* n.sp. (Mycalidae, Poecilosclerida, Demospongiae) from the tropical western Atlantic.—Beaufortia 45:1–16.
- Hartman, W. T. 1982. Porifera. Pp. 640–666 in S. P. Parker, ed., Synopsis and classification of living organisms (I). MacGraw-Hill, New York, 1166 pp.
- Hechtel, G. J. 1965. A systematic study of the Demospongiae of Port Royal, Jamaica.—Peabody Museum of Natural History Bulletin 20:1–103.
- . 1976. Zoogeography of Brazilian marine Demospongiae. Pp. 237–260 in F. W. Harrison & R. R. Cowden, eds. Aspects of sponge biology. Academic Press, New York, 354 pp.
- Hentschel, E. 1911. Tetraxonida 2. Teil. Pp. 277–393 in W. Michaelsen, & R. Hartmeyer, eds., Die Fauna Südwest-Australiens 3 (10). Gustav Fischer, Jena, 467 pp.
- . 1913. Über einen Fall von Orthogenese bei den Spongien.—Zoologischer Anzeiger 13:255–167.
- Hori, M., S. Saito, Y. Z. Shin, H. Ozaki, N. Fusetani, & H. Karaki. 1993. Mycalolide-B, a novel and specific inhibitor of actomyosin ATPase isolated

- from marine sponge.—Federation of European Biochemical Societies 322(2):151–154.
- Hyatt, A. 1877. A revision of the North American Poriferae; with remarks upon foreign species. Part 2.—Memoirs of the Boston Society of Natural History 2:399–408, pl. 13.
- Johnston, G. 1842. A history of British sponges and lithophytes. W. H. Lizars, Edinburgh, 264 pp, pls. I–XXV.
- Laubenfels, M. W. de. 1934. New sponges from the Puerto Rican deep.—Smithsonian Miscellaneous Collections 91(17):1–28.
- . 1936a. A discussion of the sponge fauna of the Dry Tortugas in particular and the West Indies in general, with material for a revision of the families and orders of the Porifera.—Papers of the Tortugas Laboratory 30:1–225.
- . 1936b. A comparison of the shallow-water sponges near the Pacific end of the Panama Canal with those at the Caribbean end.—Proceedings of the United States National Museum 83(2993):441–466.
- . 1950a. The Porifera of the Bermuda Archipelago.—Transactions of the Zoological Society of London 27:1–154, pls. 1–2.
- . 1950b. The sponges of Kaneohe Bay, Oahu.—Pacific Science 4(1):3–36.
- Lehnert, H. 1993. Die Schwämme von Cozumell (Mexico). Bestandsaufnahme, kritischer Vergleich taxonomischer Merkmale und Beschreibung einer neuen Art.—Acta Biologica Benrodensis 5:35–127.
- Lendenfeld, R. von. 1887. Die Chalineen des australischen Gebietes.—Zoologische Jahrbücher 2: 723–828, pls. 18–27.
- Lévi, C. 1952. Spongiaires de la Côte du Sénégal.—Bulletin de l'Institut français d'Afrique noire 14(1):34–59.
- . 1959. Campagne de la "Calypso": Golfe de Guinée. Spongiaires.—Annales de l'Institut océanographique 37:115–141, pls. 5–6.
- . 1963. Spongiaires d'Afrique de Sud. (1) Poeciloscélérdes.—Transactions of the Royal Society of South Africa 37(1):00–71, pls. I–XI.
- Little, F. J. 1963. The sponge fauna of the St. George's Sound, Apalache Bay, and Panama City regions of the Florida Gulf coast.—Tulane Studies in Zoology 11:1–71.
- López, P. G., & G. Green. 1984. Sistemática de las esponjas marinas de Puerto Morelos, Quintana Roo, Mexico.—Anales del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México 11(1):65–90.
- Lundbeck, W. 1905. Porifera (Part 2). Desmacidonidae (Pars).—Danish Ingolf-Expedition 6(2):1–219, pls. I–XX.
- Mello-Leitão, A., A. F. Pêgo, & W. M. Lopes. 1961. Poríferos assinalados no Brasil.—Avulsos do Centro de Estudos zoológicos da Universidade do Brasil, 10:1–29, addenda, corrigenda.
- Muricy, G. 1989. Sponges as pollution biomonitors at Arraial do Cabo, southeastern Brazil.—Revista brasileira de Biologia 49:347–354.
- Nardo, G. D. 1833. Auszug aus einem neuen System der Spongiarien, wonach bereits die Aufstellung in der Universitäts-Sammlung zu Padua gemacht ist.—Isis (Oken), Jena:519–523.
- Northcote, P. T., J. W. Blunt, & M. H. G. Munro. 1991. Pateamine: a potent cytotoxin from the New Zealand marine sponge, *Mycale* sp.—Tetraedron Letters 32:6411–6414.
- Perry, N. B., J. W. Blunt, M. H. G. Munro, & L. K. Pannell. 1988. Mycalamide A, an antiviral compound from a New Zealand sponge of the genus *Mycale*.—Journal of the American Chemical Society 110:4850–4851.
- . J. W. Blunt, M. H. G. Munro, & A. M. Thompson. 1990. Antiviral and antitumor agents from a New Zealand Sponge, *Mycale* sp. 2. Structures and solution conformations of Mycalamides A and B.—Journal of Organic Chemistry 55:223–227.
- Pulitzer-Finali, G. 1986. A collection of West Indian Demospongiae (Porifera). In appendix a list of Demospongiae hitherto recorded from the West Indies.—Annali del Museo Civico di Storia Naturali "Giacomo Doria" 86:65–216.
- . 1996. Sponges from the Bismark Sea. Bollettino del Museo ed Istituto Biologico dell'Università di Genova: 60–61:101–138.
- Reiswig, H. M. 1973. Population dynamics of three Jamaican Demospongiae.—Bulletin of marine Science 23:191–226.
- Ridley, S. O., & A. Dendy. 1886. Preliminary report on the Monaxonida collected by H.M.S. Challenger.—Annals and Magazine of Natural History, (5)18:325–351, 470–493.
- . 1887. Report on the Monaxonida collected by H.M.S. Challenger during the years 1873–1876.—Report on the scientific Results of the Exploring Voyage of H.M.S. Challenger 1873–76, Zoology 20(59):i–lxviii, 1–275, pls. I–LI.
- Rützler, K. 1978. Sponges in coral reefs. Pp. 299–313 in D. R. Stoddart, & R. E. Johannes, eds., Coral reefs: research methods. Monographs on Oceanographic Methodology 5. Unesco, Paris, 581 pp.
- . 1986. Phylum Porifera (Sponges). Pp. 111–127 in W. Sterrer, ed., Marine fauna and flora of Bermuda. John Wiley & Sons, New York, 742 pp.
- . 1990. Associations between Caribbean sponges and photosynthetic organisms. Pp. 455–466 in K. Rützler, ed., New perspectives in sponge biology. Smithsonian Institution Press, Washington, D.C., 533 pp.

- , & C. Feller. 1988. Mangrove swamp communities.—*Oceanus* 30(4):16–24.
- . 1996. Caribbean mangrove swamps.—*Scientific American*, March 1996:94–99.
- , & I. G. Macintyre. 1982. The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. Pp. 9–45 in K. Rützler & I. G. Macintyre, eds, *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, I: structure and communities*.—*Smithsonian Contributions to the Marine Sciences* 12. Smithsonian Institution Press, Washington, D.C., 539 pp.
- Schmidt, E. O. 1862. Die Spongien des Adriatischen Meeres. Leipzig 1–88, pls. I–VII.
- . 1870. Grundzüge einer Spongien-Fauna des atlantischen Gebietes. Leipzig, 1–88, pls. I–VI.
- Soest, R. W. M. van. 1981. A checklist of the Curaçao Sponges (Porifera Demospongiae) including a pictorial key to the common reef-forms.—*Verslagen en Technische Gegevens, Instituut voor Taxonomische Zoölogie, Universiteit van Amsterdam* 31:1–39.
- . 1984. Marine sponges from Curaçao and other Caribbean localities. Part 3. Poecilosclerida.—*Studies on the Fauna of Curaçao and other Caribbean Islands* 66(199):1–167, pls. I–X.
- . 1987. Biogeographic and taxonomic notes on some eastern Atlantic sponges. Pp. 13–28 in W. C. Jones, ed., *European contributions to the taxonomy of sponges*. Sherkin Island Marine Station, Ireland, 140 pp.
- , S. M. Stone, N. Boury-Esnault, & K. Rützler. 1983. Catalogue of the Duchassaing & Michelotti (1864) collection of West Indian sponges (Porifera).—*Bulletin, Zoologisch Museum Universiteit van Amsterdam* 9(21):189–205.
- Thiele, J. 1903. Kieselschwämme von Ternate. II.—*Abhandlungen herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft* 25:933–968, pl. 28.
- Topsent, E. 1924. Révision des *Mycale* de l'Europe occidentale.—*Annales de l'Institut Océanographique*, Monaco 1(3):77–118.
- Tsurnamal, M. 1969. Four new species of Mediterranean Demospongiae and new data on *Callistes lacazei* Schmidt.—*Cahiers de Biologie marine* 10:343–357.
- Vacelet, J. 1990. Les spongiaires. Pp. 16–33 in C. Bouchon, ed., *La Grande Encyclopédie de la Caraïbe*. Le Monde Marin, Sanoli, Italy, 207 pp.
- , & P. Vasseur. 1971. Éponges des récifs coralliens de Tuléar (Madagascar).—*Téthys*, supplément 1:51–126.
- Verril, A. E. 1873. Report upon the invertebrate animals of Vineyard Sound. United States Fisheries Commission Internal Report on the Condition of the Sea Fisheries on the South Coast of New England. Pp 295–778, pls. 1–38.
- Weerd, W. H. de, K. Rützler, & K. P. Smith. 1991. The Chalinidae (Porifera) of Twin Cays, Belize, and adjacent waters.—*Proceedings of the Biological Society of Washington* 104:189–205.
- Wells, H. W., M. J. Wells, & I. E. Gray. 1960. Marine sponges of North Carolina.—*Journal of the Elisha Mitchell Scientific Society* 76(2):200–245.
- Whitfield, R. P. 1901. Notice of a new sponge from Bermuda and of some other forms from the Bahamas.—*Bulletin of the American Museum of Natural History* xiv:47–50, pls. I–V.
- Wiedenmayer, F. 1977. Shallow-water sponges of the western Bahamas. Birkhäuser Verlag, Basel, 287 pp., 43 pls.
- . 1989. Demospongiae (Porifera) from northern Bass Strait, southern Australia.—*Memoirs of the Museum of Victoria* 50(1):1–242.
- Winterman-Kilian, G., & E. F. Kilian. 1984. Marine sponges of the region of Santa Marta (Colombia). Part II. Homosclerophorida, Choristida, Spirophorida, Hadromerida, Axinellida, Halichondrida, Poecilosclerida.—*Studies on Neotropical Fauna and Environment* 19(3):121–135.
- Zea, S. 1987. Esponjas del Caribe Colombiano. *Catálogo Científico*, Colombia, 286 pp.