

Taxonomy of the Caribbean excavating sponge species complex *Cliona caribbaea* – *C. aprica* – *C. langae* (Porifera, Hadromerida, Clionidae)

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ABSTRACT.—In the Caribbean Sea, brown to brown-black sponges that both excavate and encrust calcareous substratum are variably and confusedly reported as *Cliona caribbaea*, *C. aprica* and/or *C. langae* (Family Clionidae, Order Hadromerida). They extend sideward undermining and displacing live coral tissue. To resolve the taxonomy of the species, detailed observations and sampling were carried out in Colombia, Venezuela, Curaçao, Belize, Jamaica and Puerto Rico. Differences in external morphology and color, and subtle, but consistent differences in spicule morphology and size, revealed the existence of three distinct species, *Cliona aprica* Pang, 1973, *Cliona caribbaea* Carter, 1882 (junior synonym *C. langae* Pang, 1973), and *Cliona tenuis* sp. nov. *C. aprica* consists of brown-black, closely spaced papillae that may fuse to form an incomplete thin crust. *C. caribbaea* is amber brown, often fully encrusting, with thicker (up to 2 mm) tissue and conspicuous oscules, often riddled with zoanthids. *C. tenuis* covers the entire substratum with a thin, transparent veneer of brownish tissue; oscules are small and inconspicuous. Spicule morphology and size show geographical variation but remain distinctive for each species within a given locality. Most of the recent substratum monopolization and coral tissue death from species of this complex in many Caribbean fore reefs is attributable to *C. tenuis*.

INTRODUCTION

Among the sponges that are able to excavate tunnels and galleries into carbonate materials, there are some that also encrust, partly or entirely, the surface of the excavated substratum. In the Caribbean Sea, those with a dark brown to brown-black color have been variably reported as *Cliona viridis* (Schmidt 1862), *C. caribbaea* Carter 1882, *C. aprica* Pang 1973a, and/or *C. langae* Pang 1973a (Family Clionidae, Order Hadromerida, Class Demospongiae, cf. Rützler 2002a). These sponges dig a shallow valley in the substratum, which may extend over several square meters. But their tissue penetrates only about 1.5-2 cm below the surface, excavating chambers and galleries which are completely filled with dark yellow tissue. As these sponges encounter live coral tissue, their lateral extension continues on with the aid of excavating pioneering tissue threads, which undermine the polyps skeletal support, resulting in relatively fast (in the order

of cm year⁻¹) and extensive death of coral tissue (Rützler 1975, 2002b; Acker and Risk 1985; Schönberg and Wilkinson 2001; López-Victoria et al. in press). As a result of local population increase of some of the species, the marine scientific community became interested in dark brown clionids. The population change seems to have started around early 1980's, apparently as a result of increased stress and massive mortalities in corals associated to bleaching, disease and high temperature (Cortés et al. 1984; Rützler 2002b). They have since monopolized ample reef space in some localities and as a result additional tissue loss has occurred in colonies of the most common reef-building corals (Williams et al. 1999; Rützler 2002b). These observations prompted us to study these sponges in some areas of the Caribbean Sea and led us to new taxonomical and morphological definitions.

Considerable taxonomic confusion has occurred with the species involved, which promoted the use of the term "complex" to signal suspected genetic heterogeneity. On

the substratum these excavating sponges may appear either as isolated to partially fused fields of papillae, or as a continuous encrusting sheet, thin when the sponge grows actively, and thick when it stops its sideward growth; papillae may also occur at the edges of some encrusting specimens (see López-Victoria et al. in press). Geographical variation in the predominant morphology, and in spicule morphology and size, made it difficult to define species. The studied species were grouped within the larger "*Cliona viridis* complex" that comprises Atlantic, Mediterranean and Indo-Pacific species (Schönberg 2002 and references therein). For the Caribbean, Carter (1882) originally described *Cliona caribbaea* from St. Vincent, Lesser Antilles. Later, Topsent (1900) put it into synonymy with Mediterranean *Cliona viridis* (Schmidt 1862); this decision was followed in other taxonomic studies in the Caribbean (e.g., Hechtel 1965). However, Rützler (1974) re-described *Cliona caribbaea* as a valid Caribbean species. Contemporary to the latter author, Pang (1973a) described two new species, *Cliona aprica* and *C. langae*, but mistakenly described material of a different species under the name *Cliona caribbaea*. From then on, most sponge and coral reef workers used Pang's monograph and identified the brown encrusting reef clionoids as either *C. aprica* or *C. langae* (e.g. Rützler 1975; Humann 1992) and largely ignored *C. caribbaea* (but see Acker and Risk 1985) or followed Pang's mistake (e.g. Hofman and Kielman 1992). Recently, Rützler (2002b) hypothesized that *C. aprica*, *C. caribbaea* and *Cliona langae* represent a single, highly variable species, whose name should be *C. caribbaea*. This idea was proposed in spite that two to three distinct forms had previously been distinguished by other workers (Pang 1973a; Acker and Risk 1985; Zea 2001). In a recent visit to Jamaica as part of this study, three morphotypes were found sympatrically at the fore reef of Discovery Bay; thus, allowed us detailed comparisons. After re-examination of all Caribbean samples collected by the authors and some museum material, the three morphotypes were recognized as good species, subtly, but clearly different. The pur-

pose of this paper is to describe and illustrate these three species of *Cliona*, and provide information on their geographical variability.

MATERIALS AND METHODS

Extensive observations and sampling were carried out in several areas of the south (continental coast of Colombia) and southwestern (San Andrés and Old Providence Archipelago, Colombia) Caribbean Sea. Visits to other areas (Belize, Jamaica, Puerto Rico and Venezuela) yielded further material for comparisons (Fig. 1). Material and observations from Curaçao were provided by M. López-Victoria.

Fragments of sponges encrusting the substratum were obtained with hammer and chisel or a corer, fixed in 96% ethanol or in 10% formalin in seawater buffered with methenamine (20 g l^{-1}), and preserved in 70% ethanol after 2-3 days. Small fragments of sponge tissue with substratum were digested in commercial bleach to obtain clean siliceous spicules suspensions; or they were fully decalcified in 5% nitric acid solution. Spicule suspensions or decalcified tissue were boiled in fuming nitric acid. Permanent spicule slides were prepared for microscopic examination according to Rützler (1974). Spicules of several specimens, from each sampled area, (see Table 1) were measured under a Leitz Wetzlar compound microscope. For megascleres (tylostyles) we measured, at $125\times$, the following: total length, maximum width of shaft, and length and width of the head of 25 spicules per specimen. Total length, width of shaft, largest width of the spire, number of spiral turns, and length of the longest spire (equivalent to largest wavelength, if the spiraster is seen as a projected sinusoidal wave) of 10-15 microscleres (helical spirasters) per specimen, were measured at $1250\times$ with immersion oil.

Internal morphology of sponges was examined microscopically using sections of sponge-substratum fragments that were: cut and trimmed with a low-speed diamond circular saw (IsometTM, Buehler, Chicago); embedded in low viscosity Spurr

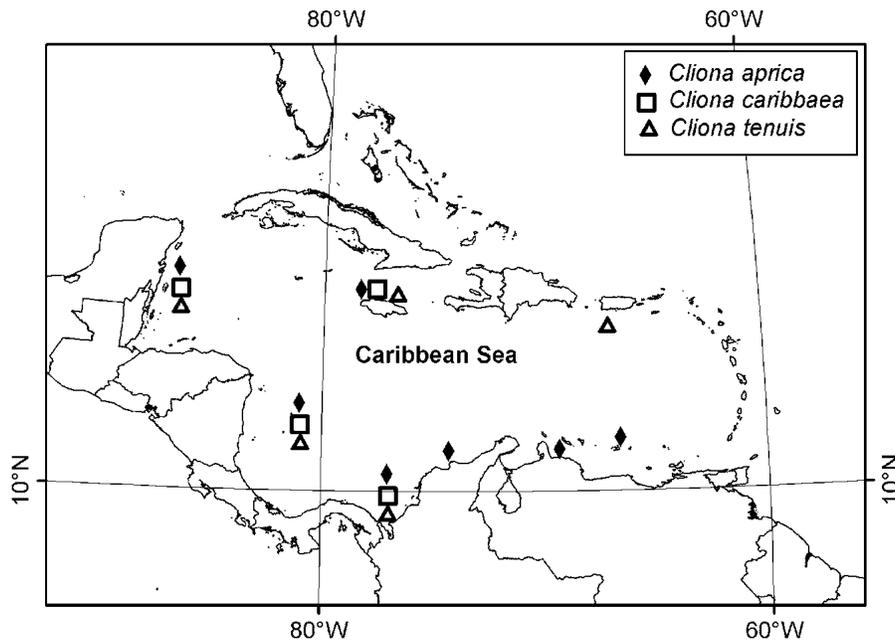


FIG. 1. Map of the Caribbean Sea showing the distribution of the three species in the sampled areas.

resin (ERL 4206, Electron Microscopy Sciences, Fort Washington, Philadelphia); cut and glued onto microscope slides; cut again, ground to ca. 20-50 μm in thickness with a graded series of diamond coated abrasive paper; and polished with commercial aluminum oxide metal polisher, in a petrography grinder/polisher (Minimet 1000, Buehler) (after Rützler 1974; Willenz and Pomponi 1996). Staining was carried out for 5-15 min with basic (or acid) fuchsin and crystal violet, either during the dehydrating process previous to embedding, or directly on the polished sections (the latter on a warm slide plate).

Underwater photographs of sponges were taken with a Nikonos V 35 mm film camera assembled with a SB-105 strobe and close up and macro-ring attachments. Spicules and sections were drawn using a camera lucida. Digital scanning electronic micrographs (SEM) of spicules from some specimens were kindly made by K. Rützler and M. Nestlerode (Smithsonian Institution, Washington, DC).

Unless noted, samples were collected by S. Zea and deposited at the Instituto de Investigaciones Marinas y Costeras –

INVEMAR – Museo Nacional de Historia Natural Marina de Colombia Porifera collection at Santa Marta (INV-POR), and at the Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia at Bogotá [ICN-MHN(Po)]. We also analyzed spicule slides, tissue fragments, digital photographs and/or drawings from Washington National Museum of Natural History (USNM), London British Museum of Natural History (BMNH), Yale Peabody Museum (YPM), and City of Liverpool Museum (LIVCM). Color codes are those of the American Museum of Natural History Naturalist's Color Guide (Smithe 1975) and indicated as NCG. Numbers of studied specimens were: *Cliona aprica*, 54; *C. caribbaea*, 28; *C. tenuis*, 41. Collection number is boldfaced for those specimens whose spicules were measured (Table 1).

RESULTS

Common characteristics of the studied species complex

Excavating. Fields of papillae to completely encrusting. Level of substratum

usually slightly lower than surroundings. Surface brown to brown-black. Oscules small, up to 2.3 mm in diameter (Pl. 1). When thick enough to allow judgment, consistency leathery, velvety to the touch. Sponge penetrates and excavates substratum up to 2 cm beneath surface. Ectosome over excavated troughs a palisade of vertically oriented tylostyle spicule brushes, often separated by incurrent canals; top of shallow substratum rims with paratangentially placed spicules (Fig. 2). Choanosome fleshy, dark yellow, filling entirely corallicular spaces and excavating chambers; sub-superficial color frequently olive green. When growing in flat or cylindrical coral branches, excavating tissue filaments (1-2 mm in diameter) may cross entire expanse of coral skeleton. When growing into live coral tissue, pioneer filaments and chambers undermine below coral polyps over several cm (see also López-Victoria et al. in press). Threads of fusiform contractile cells (*fide* Rützler 1974) common below spicule brushes and lining coral skeleton near top of substratum rims. Choanosomal tissue with loosely arranged tylostyles. Rows of tylostyles occur near and in parallel to walls of excavated troughs, accompanied by connective tissue threads.

Choanosomal canals often lined by spiraster spicules. Superficial tissue packed with intracellular zooxanthellae, 9.2-11.5 μm in diameter, sparser further inside but occur throughout the choanosome, including excavating pioneering filaments. All internal surfaces of substratum with typical concave marks of removed carbonate chips, even on top of rims. **Megascleres:** tylostyles with rounded to slightly elongated heads (Pl. 2; Fig. 3). **Microscleres:** slender, thin spirasters with relatively small spines lined in the convex side. Size of spicules varies with locality, tylostyles generally larger and more robust and spirasters thicker at continental coast of Colombia (see Table 1, Figs. 4-6).

Species descriptions

Order Hadromerida Topsent, 1894
 Family Clionidae D'Orbigny, 1851
 Genus *Cliona* Grant, 1826
Cliona aprica Pang, 1973

Pl. 1 (A, C, E), Pl. 2 (A, D, G, J). Fig. 2 (A), Fig. 3 (A, D, G, J), Figs. 4-6

Cliona aprica Pang 1973a: 42, forma *aprica*, p. 43, figs. 12, 21 (Jamaica, shallow form, 0-5 m, holotype YPM 8772), forma *profunda*, p. 45, fig. 13 (deep form, 12-34 m, paratype YPM 8723) (other paratypes at BMNH and State University of New York at Stony Brooks-University of West Indies); Pang 1973b (Jamaica, ecology); Tunnicliffe 1979: 309 (Jamaica, role in coral fracture); Díaz et al. 1995 (San Andrés, in part, lagoonal and leeward records; windward records are for *Cliona tenuis*); Lehnert and van Soest 1998: 79 (Jamaica, referring to the type material); López-Victoria et al. in press (Colombia, biology).

?*Cliona aprica*; Alcolado, 1976: 6 (Cuba); 1979: 112, table 2; 1989: 6, table 1; 1990: 352; 1999: 121 (Cuba, distribution); MacGeachy 1977: 479 (Barbados, factors controlling erosion); Vacelet 1981: 717 (Guadeloupe, ultrastructure of zooxanthellae); Buznego and Alcolado 1987: 7 (Cuba, erosion in corals).

Non *Cliona aprica*; Rützler 1975: 205 (Belize, bioerosion rates); Pulitzer-Finali 1986: 95 (Puerto Rico); Vicente 1990a: 200 (Puerto Rico, zooxanthellate symbionts); 1990b: 439, fig. 4 (Puerto Rico, overgrowth by other organisms) [**All are** *Cliona tenuis*].

Cliona caribbaea; Hofman and Kielman 1992: 206, fig. 9 (Colombia, in part, only specimen INV-POR 0406; specimens INV-POR 0397 and 0411 are *Cliona flavifodina* Rützler 1974); Rützler 2002b: 64, fig. 4.1 (Belize, in part, only some papillose specimens).

Non *Cliona caribbaea* Carter 1882 (a valid species).

Cliona aprica – *C. langae* – *C. caribbaea* species complex; Valderrama 2001: 31 (morphotype 1, Gulf of Urabá).

Cliona sp. 1; Zea 2001 (SW Caribbean atolls, distribution).

Non *Cliona* sp. 1; Zea 1993: 87 (Santa Marta, distribution, = *Cliona flavifodina* Rützler, 1974).

Studied material.—**Jamaica.** Discovery Bay, Dairy Bull, 8 m: ICN-MHN(Po) 177, INV-POR 609, POR 610; Fore reef: 9-30 m, INV-POR 611, 612, 613, 614. **Curaçao.** (all by M. López-Victoria) Playa Kalki: 4 m, Fig. P1 live 4/CICN-MHN(Po) 181; Santa Marta Baa: 5-6 m, INV-POR 623; Blauwbaai: 10.5 m, INV-POR 624, 625. **Venezuela.** Los Roques Archipelago, Dos Mosquises: 16 m, INV-POR 619. **Continental coast of Colombia.** Santa Marta, Bahía de Nenguange: 1-3 m, ICN-MHN(Po) 179, INV-POR 618, Hofman

TABLE 1. Measurements and spicule characteristics of *Cliona aprica*, *C. caribbaea* and *C. tenuis* sp. nov. at each geographic area. Data are min.-max. (mean \pm 1 standard deviation). Mean and standard deviation calculated from mean sizes of each of *n* specimens measured (which came from 25 tylostyles and 10-15 spirasters). In the case of single specimen samples, means and standard deviations refer to that set of data only. Collection number for those individuals measured is marked in bold in the material studied section for each species.

Species/spicule	Area					
	San Andrés Archipelago*	Jamaica	Puerto Rico	Colombia**	Venezuela	Belize
<i>Cliona aprica</i>						
Specimens studied	9	4		5	1	3
Tylostyles						
Length	232-375 (301 \pm 21)	237-394 (324 \pm 15)		270-427 (357 \pm 9)	204-333 (332 \pm 25)	261-399 (332 \pm 21)
Shaft width	4.7-14.2 (8.5 \pm 0.6)	4.7-10.0 (7.5 \pm 1.7)		3.8-19 (12.0 \pm 2.5)	3.8-5.7 (5.0 \pm 0.5)	4.3-13.3 (8.2 \pm 1.3)
Head width	6.6-15.7 (12.3 \pm 0.9)	8.1-14.3 (11.8 \pm 0.4)		9.0-19.5 (15.5 \pm 2.2)	3.8-10.5 (8.6 \pm 1.6)	7.6-15.7 (12.0 \pm 0.6)
Head length	7.1-15.7 (11.8 \pm 1.0)	8.1-15.2 (10.8 \pm 0.8)		10.4-19.0 (16.0 \pm 0.4)	8.5-12.8 (10.5 \pm 1.0)	8.5-17.6 (12.2 \pm 0.9)
Head length/width	0.5-1.9 (0.96 \pm 0.06)	0.7-1.4 (0.92 \pm 0.08)		0.8-1.5 (0.9 \pm 0.02)	1.0-2.7 (1.3 \pm 0.4)	0.7-1.8 (1.03 \pm 0.05)
Spirasters						
Length	12.6-34.0 (21.5 \pm 2.4)	16.0-33.0 (24.5 \pm 1.7)		14.9-38.5 (26.0 \pm 3.2)	20.0-33.5 (26.1 \pm 3.5)	17.0-33.0 (24.6 \pm 2.2)
Shaft width	0.4-1.0 (0.7 \pm 0.1)	0.5-1.0 (0.7 \pm 0.04)		0.5-1.7 (1.1 \pm 0.3)	0.7-1.0 (0.9 \pm 0.1)	0.5-1.0 (0.8 \pm 0.3)
Spire max. diameter	2.3-7.0 (4.5 \pm 0.6)	2.0-5.5 (3.4 \pm 0.8)		2.3-8.1 (4.3 \pm 0.7)	2.7-5.0 (3.9 \pm 0.7)	2.0-5.0 (3.3 \pm 0.2)
Spine height	0.6-2.0	0.7-2.0		1.0-2.5	1.5-2.0	1.0-2.0
Spine branching	Profuse, in bouquets	Profuse, in bouquets		Profuse, in bouquets	Profuse, in bouquets	Profuse, in bouquets
Number of turns	2-6 (3.5 \pm 0.5)	2-7 (4.5 \pm 0.5)		2-8 (4.3 \pm 0.7)	3-7 (4.3 \pm 1.3)	2-5 (3.5 \pm 0.3)
Length of longest spire	8.6-21.8 (12.5 \pm 1.3)	9-14.5 (11.7 \pm 1.4)		8.3-19.2 (11.9 \pm 0.5)	10.5-15.0 (12. \pm 1.8)	9.5-19.0 (12.9 \pm 1.3)
<i>Cliona caribbaea</i>						
Specimens studied	8	5		1		3
Tylostyles						
Length	271-418 (340 \pm 26)	275-465 (370 \pm 33)		313-418 (379 \pm 31)		280-413 (351 \pm 26)
Shaft width	4.7-13.3 (8.4 \pm 1.7)	4.7-14.3 (10.2 \pm 1.2)		7.1-15.2 (12.0 \pm 2.2)		5.2-13.3 (9.0 \pm 0.6)
Head width	7.1-15.2 (11.3 \pm 1.7)	8.1-15.7 (12.9 \pm 0.7)		10.0-18.1 (15.1 \pm 1.7)		8.1-16.6 (12.9 \pm 0.3)
Head length	7.1-17.1 (12.1 \pm 2.0)	7.1-17.1 (13.0 \pm 1.3)		10.5-17.6 (14.3 \pm 1.7)		10-17.6 (13.8 \pm 0.6)
Head length/width	0.7-1.7 (1.08 \pm 0.17)	0.5-1.5 (1.02 \pm 0.08)		0.8-1.1 (0.9 \pm 0.1)		0.8-1.5 (1.08 \pm 0.05)
Spirasters						
Length	14.9-46.0 (26.7 \pm 5.3)	22.0-45.5 (33.7 \pm 4.7)		25.5-43.5 (36.3 \pm 6.0)		22.0-47.0 (37.3 \pm 4.8)
Shaft width	0.3-1.4 (0.73 \pm 0.25)	0.3-1.1 (0.59 \pm 0.14)		0.5-1.5 (0.9 \pm 0.3)		0.5-1.0 (0.71 \pm 0.18)
Spire max. diameter	2.0-5.0 (2.8 \pm 0.6)	1.5-3.5 (2.6 \pm 0.3)		1.5-3 (2.3 \pm 0.5)		1.0-3.0 (2.1 \pm 0.2)
Spine height	1.0-2.0	0.5-2.0		1.0		1.2-2.0
Spine branching	Profuse, in bouquets	Sparse, mostly unbranched		Sparse, mostly unbranched		Sparse, mostly unbranched
Number of turns	1-9 (4.1 \pm 1.4)	2-10 (5.6 \pm 0.7)		5-10 (7.6 \pm 1.4)		4-9 (6.7 \pm 1.7)
Length of longest spire	8.5-26.0 (12.9 \pm 3.6)	7.5-21.0 (13.2 \pm 2.6)		10-11.5 (10.6 \pm 0.6)		8.5-15.5 (12.0 \pm 0.8)

TABLE 1. Continued.

Species/spicule	Area					
	San Andrés Archipelago*	Jamaica	Puerto Rico	Colombia**	Venezuela	Belize
<i>Cliona tenuis</i> sp. nov.						
Specimens studied	6	2	2	6		3
Tylostyles						
Length	199-321 (268 ± 21)	219-299 (258 ± 2)	204-275 (246 ± 3)	219-370 (300 ± 20)		214-380 (308 ± 15)
Shaft width	3.3-9.5 (6.3 ± 1.0)	3.8-8.1 (5.6 ± 0.2)	5.2-12.8 (7.7 ± 0.5)	4.7-14.3 (9.4 ± 1.2)		4.7-12.3 (7.5 ± 0.9)
Head width	5.7-13.3 (9.7 ± 0.9)	7.1-11.4 (9.2 ± 0.1)	7.6-13.3 (9.8 ± 0.6)	7.1-16.6 (12.4 ± 1.4)		7.6-14.3 (10.9 ± 0.4)
Head length	7.1-13.8 (9.9 ± 0.1)	7.1-10.9 (9.3 ± 0.6)	7.1-14.3 (10.6 ± 1.3)	9.0-18.5 (12.9 ± 1.6)		8.1-14.3 (11.4 ± 0.3)
Head length/width	0.7-1.8 (1.00 ± 0.09)	0.8-1.8 (1.02 ± 0.07)	0.8-1.6 (1.06 ± 0.06)	0.8-1.5 (1.11 ± 0.15)		0.8-1.6 (1.06 ± 0.07)
Spirasters						
Length	11.0-30.0 (22.7 ± 2.3)	17.0-39.0 (24.3 ± 1.5)	20.5-27.0 (24.4 ± 0.1)	12.0-37.5 (23.8 ± 2.9)		18.5-39.0 (24.8 ± 1.3)
Shaft width	0.5-1.1 (0.7 ± 0.1)	0.5-0.7 (1.0 ± 0.1)	0.5-1.1 (0.7 ± 0.2)	0.3-1.3 (0.9 ± 0.2)		0.40-1.25 (0.70 ± 0.14)
Spire max. diameter	2.3-6.9 (4.1 ± 0.7)	3.0-8.0 (4.8 ± 0.5)	2.0-5.0 (2.8 ± 0.2)	2.0-8.0 (4.2 ± 0.9)		3.0-6.0 (4.3 ± 0.3)
Spine height	1.2-2.0	0.7-1.0	0.7-1.5	1.2-1.7		1.0-1.5
Spine branching	Profuse, in bouquets	Profuse, in bouquets	Profuse, in bouquets	Profuse, in bouquets		Profuse, in bouquets
Number of turns	1-5 (3.6 ± 0.5)	1-4 (2.7 ± 0.2)	1-6 (4.3 ± 0.4)	1.0-7.0 (3.7 ± 0.7)		1-5 (2.7 ± 0.3)
Length of longest spire	9.7-20.7 (12.5 ± 0.7)	10.5-25.0 (16.9 ± 2.4)	9.5-14.0 (11.7 ± 1.0)	7.4-43.7 (13.7 ± 1.1)		14.0-25.5 (16.4 ± 2.0)

*SW Caribbean, but belongs to Colombia

**Continental coast

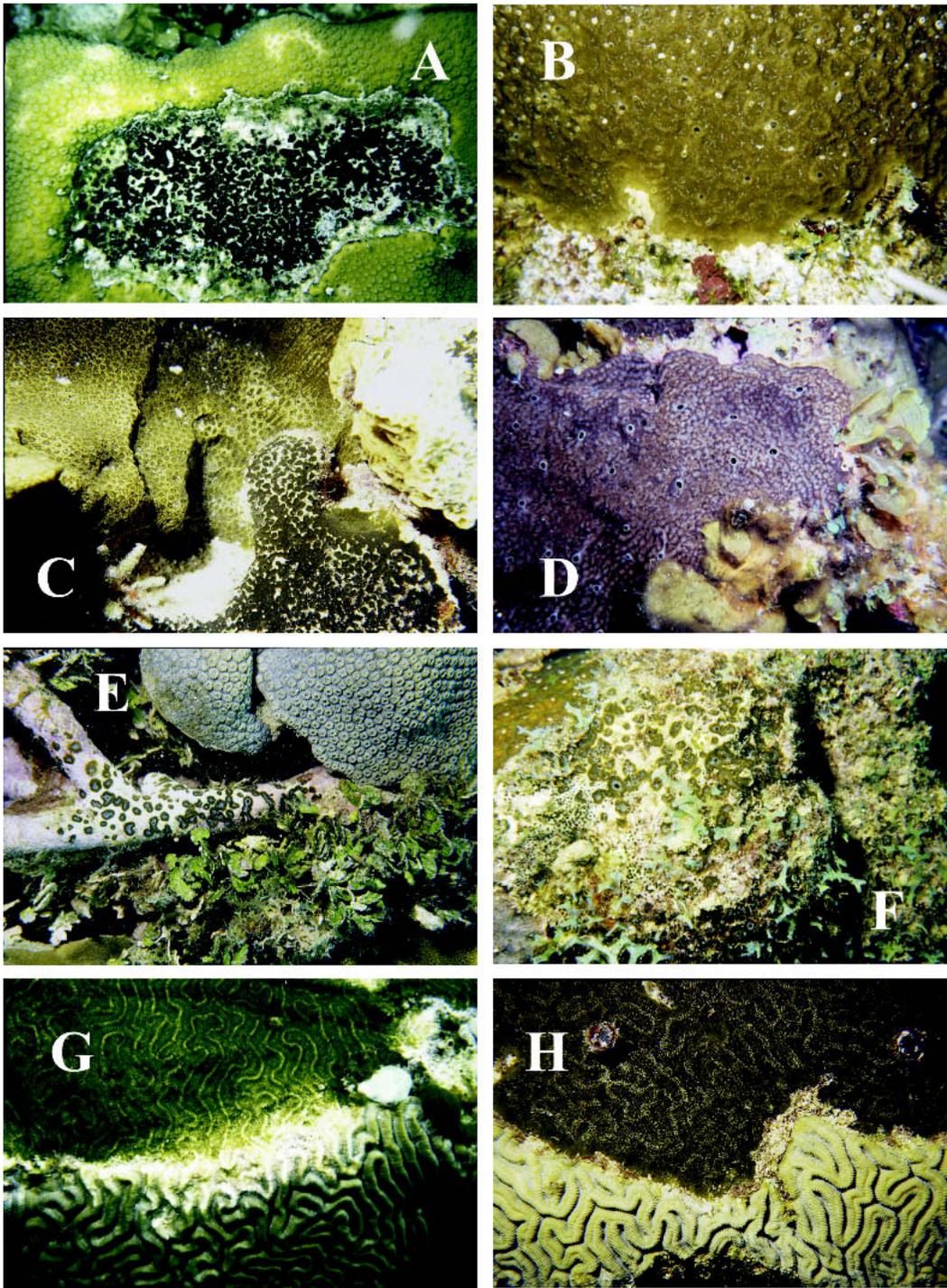


PLATE 1. Underwater close-up photographs of the studied sponges. *Cliona aprica* (A, C-right, E), *C. caribbaea* (B, D, F), *C. tenuis* (C-left, G, H). (A) Quitasueño Bank, on *Montastraea annularis*, lagoon, 3 m. (B) San Andrés Island, leeward terrace, 13 m. (C) Discovery Bay (Jamaica) shallow fore-reef, 4-5 m. (D) Belize, barrier fore reef, 27 m. (E) Islas del Rosario, on a dead coral branch, lagoon, 4 m. (F) Islas del Rosario, 18-21 m. (G) Quitasueño Bank (San Andrés Archipelago, Colombia), fore reef terrace, in coral *Diploria strigosa*, 2 m. (H) Islas del Rosario (continental Colombia), fore reef, in coral *Diploria labyrinthiformis*, 6 m. Width of field approx. 16.4 cm.

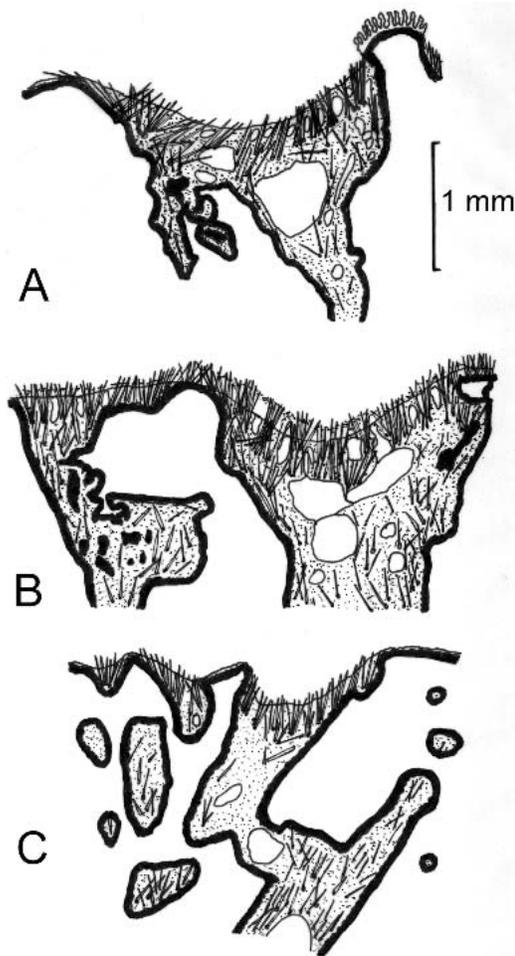


FIG. 2. Camera lucida drawings of sponge-coral substratum sections, ground and polished, of encrusting specimens. (A) *Cliona aprica* on *Siderastrea sideraea*; (B) *C. caribbaea* on *Montastraea cavernosa*; (C) *C. tenuis* sp. nov. on *Diploria strigosa*.

and M. Kielman, 406. Rosario Islands, Pajarales, San Martín: 1-3.6 m, ICN-MHN(Po) 178, M. López-Victoria, INV-POR 630; Isla Grande, Cocoliso, on sea-grasses: 0.5 m, M. López-Victoria, INV-POR 616; Bajo del Medio: 4 m, INV-POR 615. San Bernardo Islands, Múcura: 0.5 m, INV-POR 617. NW Gulf of Urabá, Cabo Pinololo: 6 m, INV-POR 577. **San Andrés and Old Providence Archipelago (Colombia)**. San Andrés Island, Half a Reef: 0.5-5 m, ICN-MHN(Po) 174, INV-POR 594, M. López-Victoria, 596; Wildlife, 4.5-13 m: INV-POR 585, 586, 587, 588, 589, 590, 591, 592, M. López-Victoria,

593, 595, 597, 598, M. López-Victoria, 627, 628; Top Blowing Rocks: 1 m, INV-POR 599; Bajo Bonito: 12 m, M. López-Victoria, INV-POR 626. Courtown (=Bolívar) Cays: 3-8 m, INV-POR 600, ICN-MHN(Po) 175. Old Providence Island, Filo Point: 0.8-2 m, INV-POR 601. Serrana Bank: 1.5-20 m, ICN-MHN(Po) 176, INV-POR 602, 603, 604, 605, 606, 607. Quitasueño Bank: 15 m, INV-POR 608. **Belize**. Carrie Bow Cay area, Carrie Bow Cay: 0.5-21 m, ICN-MHN (Po) 180, INV-POR 620, 622; North of South Water Cay: 0.5, INV-POR 621.

Diagnosis.—Fields of papillae, fused partly to almost completely in a thin (up to 1 mm) encrusting sheet. Size up to about 50 cm in diameter. Dark brown to brown black. Oscules up to 1.9 mm in diameter, sometimes with grayish rim. Tylostyles with rounded heads, 232-427 μm long by 3.8-19.0 μm wide. Spirasters wide turning, 12.6-38.5 μm long, 0.4-1.7 μm thick, with usually 2-4, rarely up to 8 turns; maximum width of spires 2.0-8.0 μm ; spines in branching bouquets, up to 2.5 μm tall.

Morphology.—Groups of inhalant and exhalant papillae, rather small, 0.7-3.7 mm in diameter, dark brown to black (NCG 19-Dusky brown, 20 and 129-Dark grayish brown), on shallow (up to about 1 cm deep) substratum valleys. Papillae usually fuse extensively as sponge grows sideward, covering most of substratum, but leaving scattered uncovered islands of carbonate fouled by algae and other organisms. When growing over and inside coral branches or rubble, papillary fusion is poor; fully relaxed papillae protrude 1-2 mm above substratum. When growing on massive corals or limestone pavement (especially at San Andrés Archipelago and Jamaica), fusion frequently more extensive. Size up to 50 cm to 1 m in the longest diameter. Oscules 0.9-1.9 mm in diameter, inconspicuous or with whitish or grayish collar (NCG 80-Glaucous, 81-Pearl Gray). Only few specimens colonized by light yellow zoanths. Depth of excavation 4-19 mm beneath the surface. Fully excavated areas below papillae or oscules up to 3.3 mm wide and 6.7 mm deep. Elevated rims of substratum not fouled by organisms covered by a thin tissue layer. Solid areas excavated by tunnels

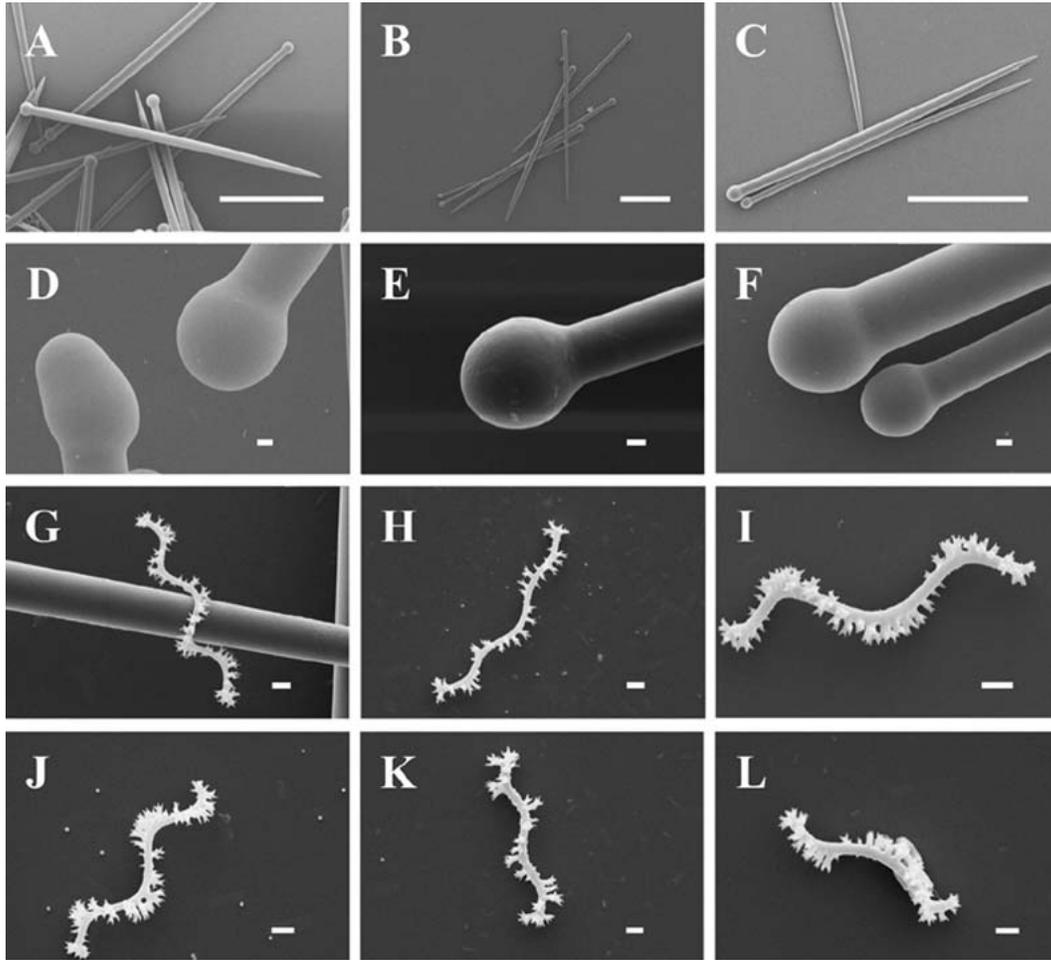


PLATE 2. SEM images of spicules. *Cliona aprica* (A, D, G, J); *C. caribbaea* (B, E, H, K); *C. tenuis* sp. nov. (C, F, I, L). Scale bars for A-C 100 μm ; for D-L, 2 μm .

and circular chambers 67 μm to 3.3 mm in diameter. Tissue traversed by canals 50-760 μm in diameter.

Spicules.—Tylostyles, usually with round heads, generally slightly vertically compressed (length/width < 1); shafts robust or slender, usually slightly curved. Measurements (Table 1, range of means): length 301-357 μm , shaft width 5.0-12.0 μm , head width 8.6-15.5 μm , head length 10.5-16.0 μm . Heads at San Andrés Archipelago, Jamaica and continental coast of Colombia predominantly compressed to rounded (length/width 0.90-0.96), at Belize rounded to slightly elongated (1.03), at Venezuela quite elongated (1.29) (Fig. 4A). Micro-

scleres: thin spirasters with wide spires, profusely spined; spines branched, forming bouquets; spiraster tips with rather elaborate spine bouquets. Spirasters usually with 2-4 turns, rarely up to 8 turns; the widest spire usually located centrally; lateral spires often smaller and asymmetrical. Measurements (Table 1, range of means): length 21.5-26.1 μm , shaft width 0.7-1.1 μm ; spire maximum diameter 3.3-4.5 μm ; number of turns 3.5-4.5; longest spire length 11.7-12.9 μm . Spine height (total min.-max.) 0.6-2.5 μm .

Distribution.—Jamaica, Curaçao, Venezuela (Los Roques Archipelago and Morrocoy), continental coast of Colombia (Santa

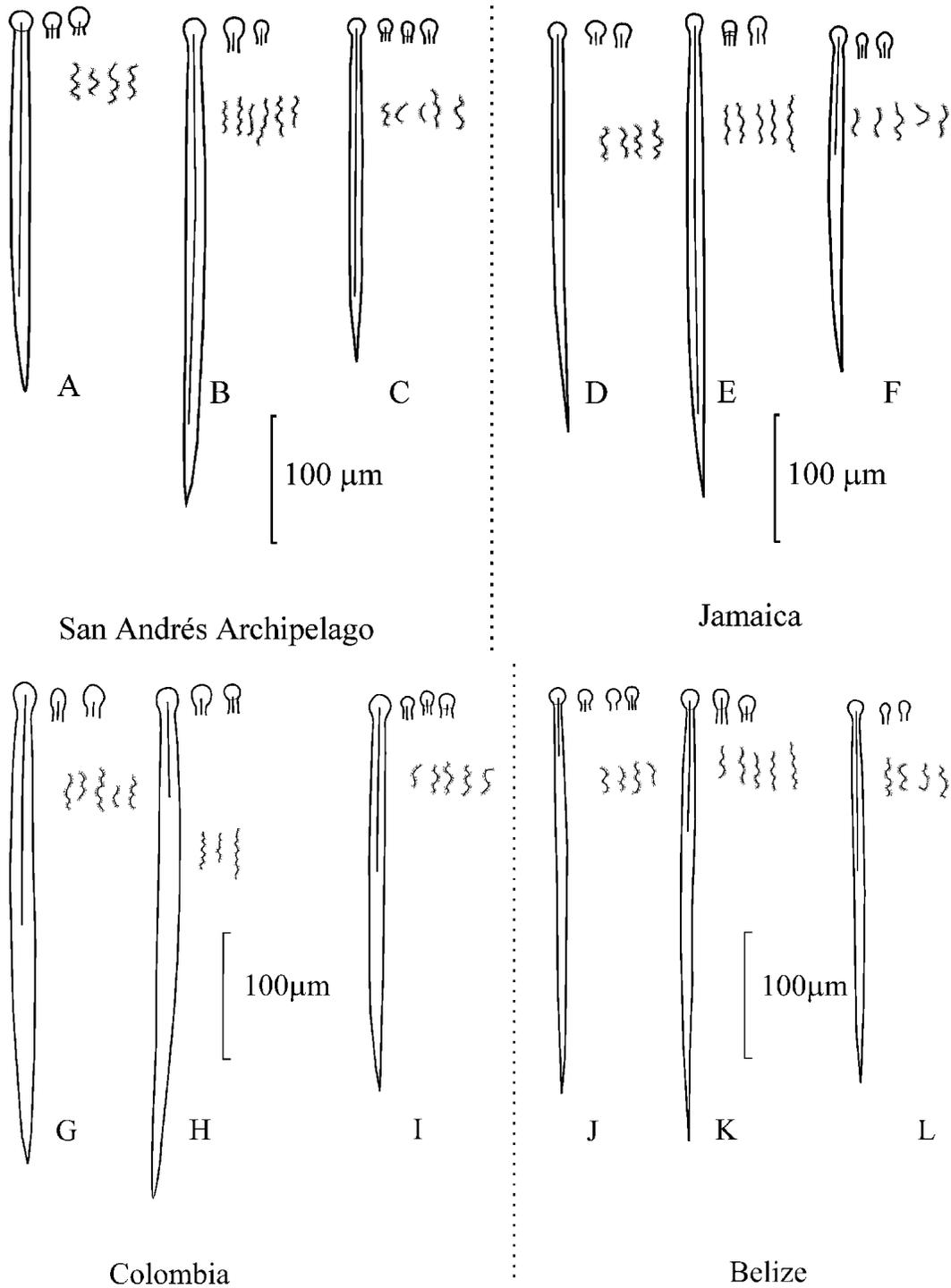


FIG. 3. Comparative view of camera lucida drawings of spicules of the three species at San Andrés Island (A-C), Jamaica (D-E), continental coast of Colombia (G-I) and Belize (J-L). *Cliona aprica* (A, D, G, J); *C. caribbaea* (B, E, H, K); *C. tenuis* sp. nov. (C, F, I, L).

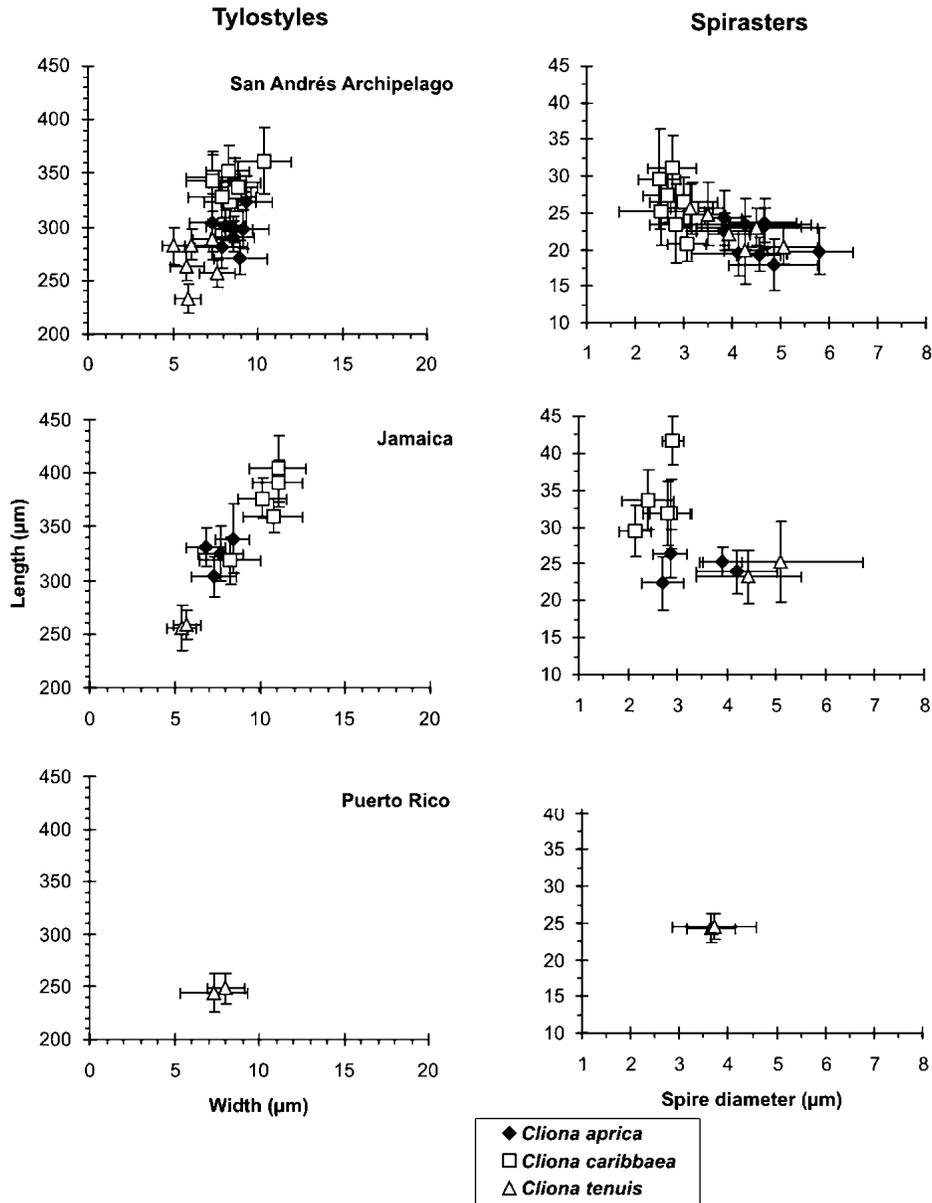


FIG. 4. Size of spicules of the three species at San Andrés Archipelago (SW Caribbean, Colombia), Jamaica and Puerto Rico. Data represent specimen means \pm 1 standard deviation of 25 tylostyles and 10-15 spirasters.

Marta to NW Gulf of Urabá), San Andrés and Old Providence Archipelago (San Andrés, Providencia, Albuquerque Cays, Courtown Cays, Serrana Bank, Roncador Bank, Quitasueño Bank), Belize. Dubious taxonomical and ecological records need confirmation.

Ecology.—Very abundant throughout

most reef and littoral zones of all studied areas, from shallow to deep (30 m) reef bottoms. Found on rubble, bases of corals, on top of dead or live coral, and on limestone pavement. At Islas del Rosario, absent in windward reef zones, but occurs in shallow to mid-depth lagoon and leeward settings (up to ca. 12 m).

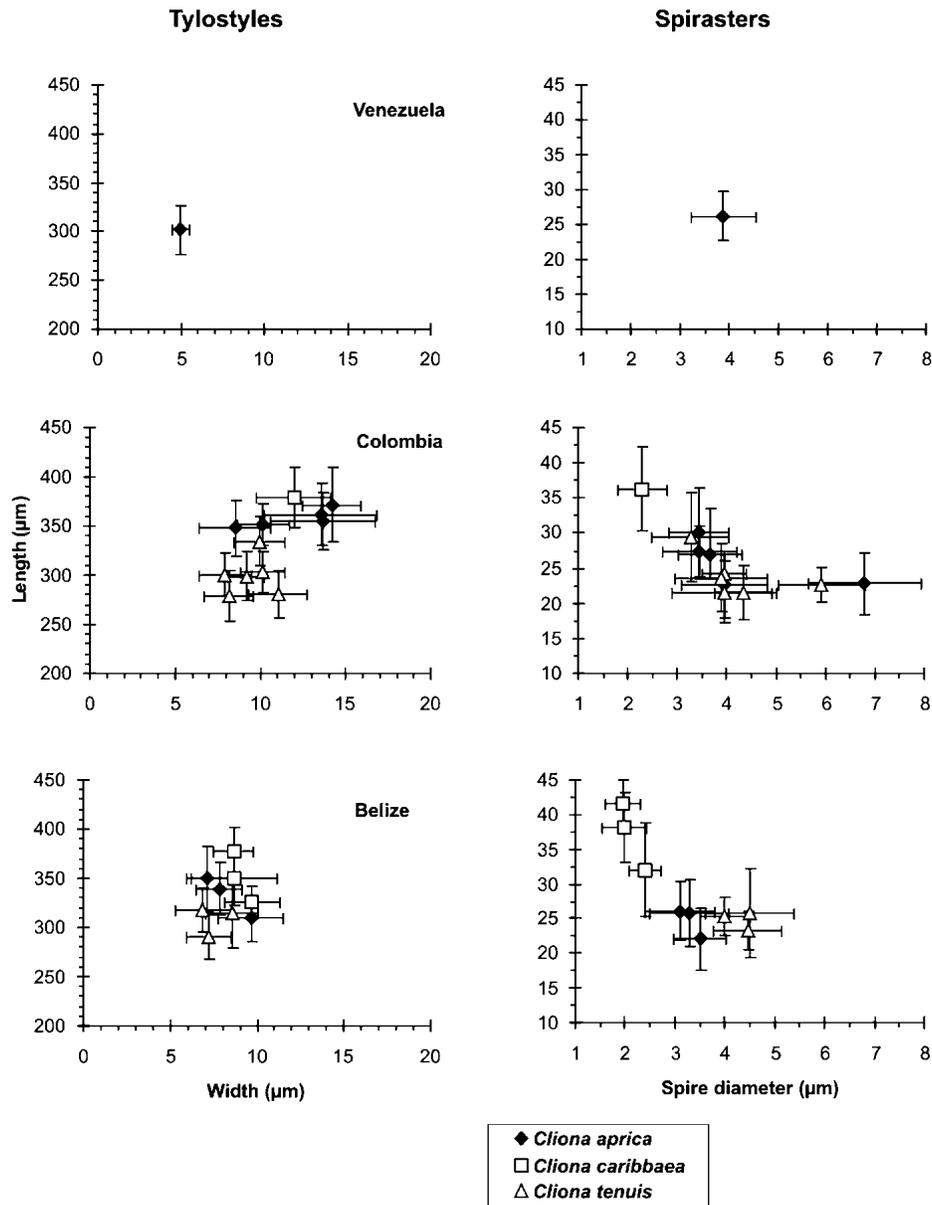


FIG. 5. Size of spicules of the three species at Venezuela, continental coast of Colombia and Belize. Data represent specimen means \pm 1 standard deviation of 25 tylostyles and 10-15 spirasters.

Remarks.—Slide preparations made by us from a decalcified fragment of the holotype (YPM 8723, forma *profunda*)-kindly sent by E. Lazo-Wasem-did not contain any spicules. Therefore, we used our own material from the type locality (Discovery Bay, north coast of Jamaica) as reference to identify the remaining samples.

Cliona aprica seldom grows thick and becomes riddled with epibiotic zoanths; a form that agglutinates rubble occurs in shallow habitats (López-Victoria et al. in press). At the oceanic islands and atolls of the SW Caribbean and in Jamaica, this species is quite distinctive, being dark brown to black, often with papillae

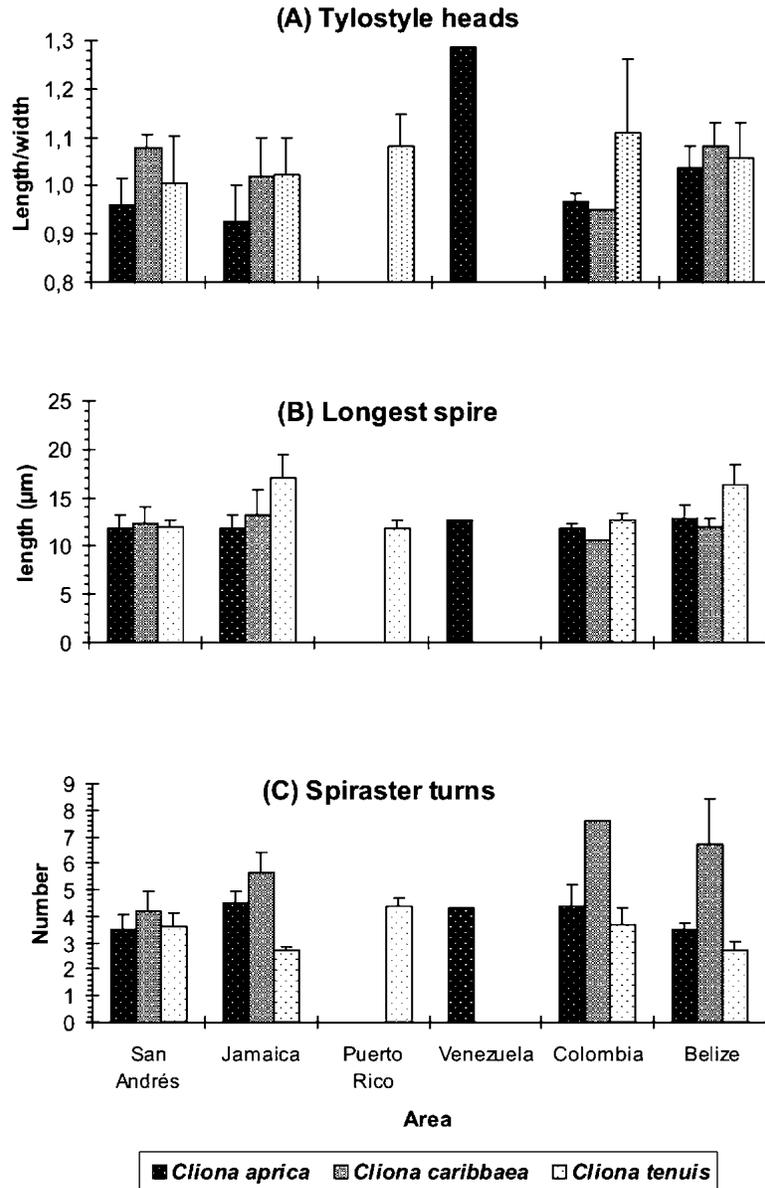


FIG. 6. Comparative view of some spicule characteristics at the areas sampled. Data represent the means \pm 1 standard deviation of the specimen means at each area (for number of specimens measured in each area, see Table 1).

extensively fused as to be almost fully encrusting. Young, papillated specimens of *C. caribbaea* can be distinguished from *C. aprica* by their lighter brown color and the larger papillae with grayish oscules. However, at the coasts of Central and South America, where *Cliona aprica* often also has grayish oscules, and papillated mor-

phology is the norm, specimens may be confused in the field with papillated *C. caribbaea*. In these cases the specimens can be identified with certainty only through analysis of spicules because *C. caribbaea* usually has larger and stouter tylostyles, and slender, narrow and wavy spirasters.

Cliona aprica and *C. tenuis* are easily distinguished by external morphology alone. The former rarely covers the entire substratum when encrusting and the latter is always thinly and fully encrusting. They have very similar wide-turning spirasters, but tylostyles of *C. tenuis* are generally smaller (Figs. 3-6). At Belize, there remains the possibility that what we are calling *C. aprica* is a papillated *C. tenuis*. In this area, *C. tenuis* often develops papillae secondarily wherever the sponge surface has been smothered by sand or bitten by fish. *C. aprica* from Belize is not as dark as in other areas, and is usually found in rubble in shallow bottoms, where the excess sediment and growth of turf algae may prevent papillar fusion. Tylostyles are rather similar in both cases, and although slightly smaller in *C. tenuis*, they largely overlap (Figs. 3-5, Table 1). Spirasters are generally of the same size and shape (Fig. 3, J vs. L), although spires tend to be slightly wider in *C. tenuis* (Fig. 5). These subtle spicule differences were evident only after comparing several sympatric specimens of both species. Transplant experiments carried out at San Andrés (oceanic SW Caribbean) and at Islas del Rosario (continental coast of Colombia) showed that *C. aprica* always grow papillae on new substratum, while *C. tenuis* never did (López-Victoria et al., in press). These results led us to use the name *C. aprica* for those papillated specimens from Belize that did not have the distinctively narrow and wavy spirasters of *C. caribbaea*.

Cliona caribbaea Carter, 1882

Pl. 1 (B, D, F), Pl. 2 (B, E, H, K). Fig. 2 (B), Fig. 3 (B, E, H, K), Figs. 4-6

Cliona caribbaea Carter 1882: 346. fig. 26 (St. Vincent, type at City of Liverpool Museum); Topsent 1889: 49 (Guadeloupe); Rützler 1974: 5, figs. 2-4 (Bermuda, Dominica, Panama); 1975: 214 (Bermuda, biomass, area coverage, density); 1986: 122, fig. 33, color pl. 4.11 (Bermuda); 1990: 460 (Bermuda, zooxanthellate symbionts); 2002a: figs. 5, 6F, 6G, 7C (from Rützler 1974); 2002b: 64, fig. 4.4, 4.5 (Bahamas; Belize; in part, only some of the papillose and thickly encrusting, deep-water specimens); Rose and Risk 1985:

350 (Grand Cayman, in part; combined with *Cliona tenuis* sp. nov.; vs. organic pollution); Acker and Risk 1985: 706, fig. 3 (dark colored form, Grand Cayman, ecology); Schönberg 2000: 168; 2002: 296 (referring to the type material); López-Victoria et al. in press (Colombia, biology).

?*Cliona caribbaea*; Pomponi 1976: 572, fig. 6 (Bahamas, Florida, ultrastructure of burrows); 1977: 485 (Bahamas, Florida, ultrastructure of etching cells); 1979: 317 (Bahamas, Florida, Jamaica, ultrastructure and cytochemistry of etching area); Hudson 1977: 491 (Florida, growth on corals); MacGeachy 1977: 479 (Barbados, factors controlling boring); Risk et al. 1980: 376 (Costa Rica, coral bioeroders); Buznego and Alcolado 1987: 6 (Cuba, boring on corals); Alcolado 1989: table 1 (Cuba, distribution); Schmahl 1990: 379 (Florida, distribution); Rützler et al. 2000: 234 (Belize, lagoon reef mangroves).

Non *Cliona caribbaea*; Verrill 1907: 343, pl. 35d, fig. 4 (Bermuda, proposing a new name, *C. sordida*); de Laubenfels 1936a: 155 (Dry Tortugas, as *C. caribboea*); 1936b: 461 (Panama, as *C. caribboea*); 1950: 108 (Bermuda, as *C. caribboea*); 1953a: 540 (eastern Gulf of Mexico, as *C. caribboea*); 1953b: 22 (eastern North America, as *C. caribboea*) [all these are of uncertain identity, *vide* Hechtel 1965: 60, Pang 1973a:22, and Rützler 1974:7, and from examination of de Laubenfels' Bermudan material deposited at BMNH, 1948.8.6.46]; Wells et al. 1960: 232 (North Carolina); Little 1963:58, fig. 28 (Florida's Gulf of Mexico coast) [the latter two records are *Suberites undulatus* George and Wilson 1916, *vide* W. D. Hartman in Hechtel 1965:60]; Pang 1973a: 22, fig. 5 (Jamaica, = *Cliona flavifodina* Rützler, 1974); Cortés et al. 1984: 228 (Costa Rica, =*Cliona tenuis*); Lehnert and van Soest 1998: 79 (Jamaica, uncertain identity, possibly *C. flavifodina*); Hofman and Kielman 1992: 215, fig. 9 (Colombia; specimen INV-POR 0406 is *Cliona aprica*; specimens INV-POR 0397 and 0411 are *Cliona flavifodina*).

Cliona langae Pang 1973a: 34, fig. 9 (Jamaica, holotype YPM 8716, 7 paratypes at BMHN and State University of New York at Stony Brook-University of the West Indies) [synonymy suggested by Rützler 2002b, and confirmed herein]; Pang 1973b (Jamaica, ecology); Tunnicliffe 1979: 311 (Jamaica, role in coral fracture); Lehnert and van Soest 1998: 79 (referring to the type material).

?*Cliona langae*; Pomponi 1979: 317 (Bahamas, Florida, Jamaica, Ultrastructure and cytochemistry of etching area); Alcolado 1999: 121 (Cuba, distribution).

Non *Cliona langae*; Humann 1992: 56 (Car-

ibbean, material identified by S. Pomponi; the specimen pictured conforms to *Cliona tenuis*].

?*Cliona viridis*; Topsent 1900: 84 (in part, Caribbean material?), pl. 3, fig. 3d [synonymy suggested by Pang 1973a: 22 and Rützler 1974: 5].

?*Cliona viridis* var. *caribbaea*; Topsent 1932: 563, fig. 5 [change of name for Topsent, 1889 material].

Non *Cliona viridis* (Schmidt 1862) (a valid species from the Mediterranean, Croatia); Hechtel 1965:61 (Jamaica, synonymized to *C. caribbaea* by Pang 1973a: 22 which is *Cliona flavifodina*).

Cliona sp. 2; Zea 2001 (SW Caribbean atolls, distribution; in part, lagoon and deep records; shallow windward records are *Cliona tenuis*.)

Studied material.—**Jamaica.** Discovery Bay, Dairy Bull: 8-30 m, ICN-MHN(Po) 185, INV-POR 646, 647, 648, 650; Fore reef: 12-28 m, INV-POR 651, 652, 653, 654. **Continental coast of Colombia.** Rosario Islands, San Martín, Pajarales: 18-21 m, INV-POR 655. **San Andrés and Old Providence Archipelago (Colombia).** San Andrés Island, Wildlife, 9-15 m: ICN-MHN(Po) 182, INV-POR 635, 636, 637, 638. Courtown (=Bolívar) Cays: 6-8 m, INV-POR 639. Old Providence Island, Blue Hole: 15-27 m, ICN-MHN(Po) 183, INV-POR 640. Serrana Bank: 2.5-7 m, ICN-MHN(Po) 184, INV-POR 641, 642, 643, 644. Quitasueño Bank: 12-13 m INV-POR 645, 646. **Belize.** Carrie Bow Cay area, North of South Water Cay: 0.5-27 m, INV-POR 656, 657; Pelican Cays, Cat Cay: 1-2 m, ICN-MHN(Po) 186.

Other material examined.—Holotype, LIVCM 2177 (SEM images of spicules, drawings and photos of preserved specimen, also published in Schönberg 2002); USNM 24346, 24348 (Bermuda, spicule slides of Rützler 1974 material). BMNH 1948.8.6.46 (Bermuda, mistaken record by de Laubenfels 1950, fragment and spicule slides INV-POR 631); BMNH 1973.8.21.9 (Jamaica, mistaken record of Pang 1973a, collected by H. M. Reiswig, fragment and spicule slides INV-POR 632); INV-POR 0406, 0397. 0411 (Colombia, mistaken records by Hofman and Kielman 1992); Holotype of *Cliona langae* Pang 1973a, YPM 8716 (Jamaica, spicule slides INV-POR 633).

Diagnosis.—Thick encrustations (up to 2 mm), growing over and completely covering substratum. Size up to 1 m in diameter. Amber brown to gray brown. Oscules up to

2.3 mm in diameter, scattered and conspicuous, usually with a creamy rim. Younger individuals may be entirely papillated; fully encrusting specimens occasionally with papillae at growing edge. Tylostyles robust, with rounded to slightly elongated heads, 271-465 μm long by 4.7-14.3 μm wide. Spirasters narrowly turning, 14.9-47.0 μm long, 0.3-1.5 μm thick, with usually more than 5-6, and up to 10 turns (but only 5-6 at San Andrés Archipelago); maximum width of spire 1.5-5.0 μm ; spines up to 2 μm , branched at the San Andrés Archipelago, mostly unbranched elsewhere.

Morphology.—Encrusting; sponge generally completely covering the excavated substratum with rather thick tissue (up to 1-2 mm), amber brown to gray brown (NGC 21-Fuscous, 22-Burnt umber, 23, 223-Raw umber, 37-Drab, 32-Chestnut, 36-Amber), in places with darker grayish tones (19-Dusky brown, 20-Dark grayish brown, 21-Fuscous, 44-Smoke gray). Size may range from few centimeters to about 1 m in diameter. Oscules usually large (0.9-2.3 mm) and conspicuous, frequently with a slightly elevated and lighter-colored collar. Surface smooth, with fields of pores in interoscular areas of some specimens, 0.9-1.5 mm in diameter, visible as lighter-colored meshes within darker tissue. When young or in bases of corals, sponge occasionally papillated, papillae 0.9-3 mm in diameter, often fused in scattered groups or having a central, fully encrusting portion. Fully encrusting specimens in active growth somewhat thinner (<1 mm), often with scattered papillae at growing edges, papillae 0.3-1.8 mm in diameter. Specimens that cannot advance further grow thicker, often invaded by light yellow zoanthids. Sponge penetrates and excavates 0.7-1.3 cm below the surface. Excavated troughs in *Montastraea cavernosa* coral skeleton (the only ones examined in cross section for *Cliona caribbaea*) cylindrical, 580 μm -1.3 mm wide, 2.2-9 mm deep. Young specimens with solid pillars of coral skeleton more or less intact, although pierced by circular excavated chambers 95-332 μm wide; intertabular coral spaces generally rectangular. Coral pillars in older specimens strongly eroded, much thinner and irregular. Pali-

sade of tylostyle brushes covers both excavated troughs and substratum rims; tips of spicules protrude about 1/3 of their length above the pinacoderm, brushes often fouled with debris. Incurrent canals, 19-76 μm wide, common in between spicule brushes, reaching down to subectosomal spaces and canals, 47-114 μm wide, more or less parallel to the surface. Thickness of ectosomal area 28-285 μm in thin actively growing specimens; on non-growing specimens may reach 220-860 μm . Tissue occasionally traversed by circular canals 28-330 μm in diameter.

Spicules.—Tylostyles usually with rounded heads, generally slightly elongated (length/width >1), half above the neck trapezoidal in profile, upper half rounded; shafts robust, usually slightly curved. Measurements (Figs. 4-6, Table 1, range of means): length 340-379 μm , shaft width 8.4-12.0 μm , head width 11.3-15.1 μm , head length 12.1-14.3 μm , head length/width 0.9-1.1 μm . Spirasters long, narrowly turning, sparsely to profusely spined; spines relatively short, branched in bouquets on material from San Andrés Archipelago, but with little branching elsewhere. Most spirasters with many turns usually more than 5-6 and up to 10; spirasters with fewer turns can occur within the same specimen. At San Andrés Archipelago, most spirasters with up to 5 turns. Measurements (Table 1, range of means): length 26.7-37.3 μm , shaft width 0.59-0.9 μm ; spire maximum diameter 2.1-2.8 μm ; number of turns 4.3-7.6; longest spire length 10.6-13.2 μm . Spine full height (min.-max.) 0.5-2.0 μm .

Distribution.—Bermuda, San Salvador (Bahamas), Jamaica, Grand Cayman, Guadeloupe, Dominica, St. Vincent, Continental coast of Colombia (Islas del Rosario), Panama, San Andrés and Old Providence Archipelago (San Andrés, Providencia, Albuquerque Cays, Courtown Cays, Serrana Bank, Roncador Bank, Quitasueño Bank), Belize. Dubious taxonomical and ecological records need confirmation.

Ecology.—At northern Jamaica from about 6 m to reef slope, in deeper waters generally papillated. Not very common at Central and South American coasts; in Be-

lize in shallow rubble (papillated) and on deep slopes (encrusting); in continental coast of Colombia seen only in papillated form on deep, leeward reef slopes. At SW Caribbean oceanic islands and atolls, lagoon and leeward settings from about 3 m to reef slopes (ca. 30 m); in windward settings on deeper reefs; most specimens encrusting. Thick portion of specimen collected at San Andrés on dead *Montastraea annularis* coral head on May 22, 2001, with eggs 114-133 μm in diameter, scattered throughout choanosomal tissue; thin portion of same specimen lacked eggs. Eggs with nucleus and a nucleolus, surrounded by layer of nurse cells.

Remarks.—The identity of the studied material was confirmed by examination of spicule slides from Bermudan specimens described by Rützler (1974), a drawing and SEM photos of the holotype spicules (made and published by Schönberg 2002). Junior synonymy of *Cliona langae* was determined from examination of the species at Jamaica, its type locality, and from the analysis of holotype spicules. Upon examination of the material deposited at BMNH, we confirmed Pang's (1973) mistaken use of the name *C. caribbaea* for *C. flavifodina* Rützler.

To the unaware observer, encrusting specimens of this species can be easily confused with *Cliona tenuis*. They are distinguished by the greater tissue thickness and oscule size in *C. caribbaea*. However, some well developed specimens of *Cliona tenuis* may be as thick as thinner *C. caribbaea*, and some may show oscules with a slightly elevated collar. Transplanted fragments of *C. caribbaea* grew initially papillated in the new substratum, while those of *C. tenuis* never did (López-Victoria et al. in press). Papillated specimens of *C. caribbaea* resemble *C. aprica* in the field, but tend to have larger papillae and a lighter coloration. But some specimens of *C. caribbaea* in Belize had a dark brown surface and slightly larger papillae than co-occurring specimens of *C. aprica*. The more robust and long tylostyles, and the narrower spires of the spirasters clearly distinguish this species from the other two described here. Except at the San Andrés Archipelago, where spirasters are relatively short, all others

specimens have some or most spirasters long and with 6 or more turns. On the encrusting specimens of this species, the ectosome is the only one where the palisade of erect spicule brushes occurs throughout the entire surface.

Cliona tenuis sp. nov.

Pl. 1 (C, G, H), Pl. 2 (C, F, I, L). Fig. 2 (C), Fig. 3 (C, F, I, L), Figs. 4-6

Cliona aprica; Rützler 1975: 205 (Belize, bioerosion rates); Pulitzer-Finali 1986: 95 (Puerto Rico); Vicente 1990a: 200 (Puerto Rico, zooxanthellate symbionts); Vicente 1990b: 439, fig. 4 (Puerto Rico, overgrown by other organisms); Díaz et al. 1995 (San Andrés Island, distribution; in part, p. 56, plate 4; only data from windward settings; in other habitats it really is *C. aprica*).

Non *Cliona aprica* Pang 1973a (a valid species).

Cliona caribbaea; Cortés et al. 1984: 228 (Costa Rica, invasion of dying corals, as *C. caribbaea*); Rose and Risk 1985: 350 (Grand Cayman, in part; probably combined with the real *C. caribbaea*; vs. organic pollution); Acker and Risk 1985: 706, figs. 3, 5, 6 (light colored form, Grand Cayman); Antonius and Ballesteros 1998: 151, figs. 7-8 (Belize, as epizooism; as *C. caribbaea*); Rützler 2002b: 64, figs. 2, 3, 4.2, 4.3, 6 (in part, thinly encrusting specimens).

Non *Cliona caribbaea* Carter 1882 (a valid species).

Cliona langae; Humann 1992: 56 (Caribbean, material identified by S. Pomponi); Williams et al. 1999: 843 (Puerto Rico, on live and dead corals).

Non *Cliona langae* Pang 1973a; 1973b (= *C. caribbaea* Carter 1882).

Cliona aprica – *C. langae* – *C. caribbaea* species complex; Valderrama 2001: 32; Valderrama and Zea in press (morphotype 2, Gulf of Urabá, distribution).

Cliona sp. 2; Zea 2001 (SW Caribbean atolls, distribution; in part, only windward shallow sites; lagoon and deep records are *Cliona caribbaea*).

Cliona sp.; López-Victoria et al. in press (Colombia, biology).

Anthosigmella varians forma *incrustans*; Lehnert 1993: 60, Tab. 22, figs. 22, 33-35, 130-131 (Cozumel).

?*Anthosigmella varians* forma *incrustans*; Lehnert and Fischer 1999: 309 (Jamaica, distribution).

Non *Anthosigmella varians* (Duchassaing and Michelotti 1864) forma *incrustans* Wiedenmayer 1977 [= *Cliona varians*, a valid species].

Type material.—**Holotype**: ICN-MHN(Po) 187, San Andrés Island, Half a Reef, shallow windward fore-reef terrace, 5 m, on dead *Acropora palmata* coral, coll. M. López-Victoria. **Paratypes**: **Jamaica**. Discovery Bay, Dairy Bull: 7-14 m, ICN-MHN(Po) 188, INV-POR 667; Fore reef: 9 m, INV-POR 668. **Puerto Rico**. La Parguera, coastal reefs: E. Weil, INV-POR 691; El Veril: 20 m, ICN-MHN(Po) 192, INV-POR 688, 689, 690. **Continental coast of Colombia**. Rosario Islands, Isla Grande, Canal del Francés: 5-6 m, INV-POR 670, 671; Pajarales, Majayura: 4.5-6 m, ICN-MHN(Po) 189, INV-POR 672, 673, 674, INV-POR 675, 676, 677, 678. San Bernardo Islands, Bajo Minalta: 5-13 m, INV-POR 679, 680, M. López-Victoria, 682; Tintipán: 3 m, ICN-MHN(Po) 190; Bajo Tiosolda: 10 m, M. López-Victoria, INV-POR 681. NW Gulf of Urabá, Cabo Tiburón: 9 m, INV-POR 578, 579; Sapzurro: 5 m, INV-POR 580. **San Andrés and Old Providence Archipelago (Colombia)**. San Andrés Island, Sound Bay: 1.5 m, INV-POR 659; Bocatora Hole: 10 m, INV-POR 660; Half a Reef: 4.5 m, INV-POR 661; East Reef, south: 3 m, INV-POR 662, 663, 664. Courtown (= Bolívar) Cays: 3 m, INV-POR 665. Quitasueño Bank: 1.5 m, INV-POR 666. **Belize**. Carrie Bow Cay area, Carrie Bow Cay: 0.5-7 m, INV-POR 683, 684, 685, 686, 687; North of South Water Cay: 0.5 m, ICN-MHN(Po) 191.

Type locality.—San Andrés Island, SW Caribbean Sea, spur and groove fore reef at Half a Reef, 5 m, 12°32'35" N, 81°40'57" W.

Diagnosis.—Thin, entirely encrusting veneer of rather transparent brown tissue, with yellowish, greenish, reddish or orange tones. Size up to several meters in diameter. Oscules small and inconspicuous, up to 1.4 mm in diameter. Tylostyles rather short, with elongated heads, 199-380 µm long by 3.3-14.3 µm wide. Spirasters wide turning, 11-39 µm by 0.5-1.3 µm, with usually 1-4 turns; maximum width of spires 8 µm; heavily branched spines, up to 2.0 µm tall; a few straight or u-shaped spirasters.

Morphology.—Sponge encrusts entire valley of excavated substratum with a thin, smooth tissue veneer through which the underlying substratum structure is visible. Valley up to 1-2 cm deep, can reach several

meters in diameter, rounded when small, irregular, amoeba-like in outline when large. Color depends on tissue thickness, density of substratum, and illumination, appearing greenish-brown, yellowish-brown, reddish-brown, orange-brown or dark chocolate brown. Sponges from Puerto Rico, continental Colombia and Belize generally maroon to dark brown. Tissue color of samples brought to daylight were various shades of brown to grayish brown in the thicker portions (19-Dusky brown, 20-Dark grayish brown, 21-Fuscous, 22-Burnt umber, 31-Maroon, 119-Sepia), and lighter shades of brown to cream in thinner portions (23-Raw umber, 26-Clay color, 54-Cream). Edges of sponges either ragged or continuous; Belizean specimens occasionally with papillae at some edges, which appear to be secondarily developed wherever sponge surface smothered by sand or bitten by fish. Oscules small (0.4-1.4 mm in diameter), inconspicuous, without contrastingly colored collar, except in some specimens at Belize with slightly elevated, transparent conical collars. Surface occasionally colonized by light yellowish zoanths, although only seen in some deep-water specimens (ca. 20 m). Sponge penetrates and excavates substratum only upper 0.6-2.0 cm. Excavated troughs rather narrow, up to 800 μm wide, with coral septae more or less intact (Fig. 2C). Elevated rims of substratum covered by a thin tissue layer. Denser substratum areas with irregular excavated chambers and tunnels, 140 μm -1 mm wide. Incurrent canals, 23-57 μm wide, occur in between some ectosomal spicule brushes and open below into subectosomal spaces. Choanosomal tissue rather dense, with few and small canals, 28-465 μm wide.

Spicules.—(Fig. 4C, F, I, L; 5C, F, I, L) Tylostyles, many with elongated heads (length/width >1), half portion above neck trapezoidal in profile, upper half rounded; shafts rather short, robust or thin, slightly curved; when robust, neck is wide. Measurements (Figs. 4-6, Table 1, range of means): length 246-308 μm , shaft width 5.6-9.4 μm , head width 9.2-12.4 μm , head length 9.3-12.9 μm , head length/width 1.0-1.1 μm . Spirasters, relatively short, with

widely turning spires, profusely spined, spines relatively short, branched in bouquets; ends of spirasters with elaborate spination. Spirasters usually with 1-4 turns although some with up to 7 turns; widest spire usually located at center, other spires often smaller and asymmetrical. Almost straight spirasters common, a few u-shaped. Measurements (Table 1, range of means): length 22.7-24.8 μm , shaft width 0.7-1.0 μm ; Spire maximum diameter 2.8-4.3 μm ; number of turns 2.7-4.3; longest spire length 11.7-16.9 μm . Spine total height (min.-max.) 0.7-2.0 μm . Size of spicules varies with locality (Table 1, Figs. 6, 7), with tylostyles generally larger and more robust and spirasters thicker at continental coast of Colombia.

Distribution.—Bahamas, Florida, Puerto Rico, Jamaica, Grand Cayman, Dominican Republic, Continental coast of Colombia (Islas del Rosario to Gulf of Urabá), Panamá, Nicaragua-Roatán, San Andrés and Old Providence Archipelago (San Andrés, Providencia, Albuquerque Cays, Courtown Cays, Serrana Bank, Roncador Bank, Quitasueño Bank), Belize, Cozumel. Localities in italics given above are from observations by the junior author.

Ecology.—*Cliona tenuis* is abundant in shallow (2-3 m) to mid depth (15-20 m), wave-exposed environments, including fore- and back-reef settings, littoral limestone cliffs and terraces. It is dominant in branches and pavement of dead and collapsed *Acropora palmata* reef zone in many localities throughout the Caribbean and abundant in deep windward terraces of SW Puerto Rico (ca. 20 m). Widespread in windward fore-reef terraces of SW Caribbean islands, atolls and banks, but absent at similar sites in Serrana Bank (San Andrés Archipelago, Colombia) and Los Roques Archipelago (Venezuela).

Etymology.—From Latin *tenuis*, meaning thin; referring to the thinness of the tissue through which the structure of excavated substratum can be seen.

Remarks.—Of the three species described here, *Cliona tenuis* has re-colonized freed substratum after the massive die-off of acroporid corals from disease and bleaching in the early 80's (Cortés et al. 1984; Acker

and Risk 1985; Antonius and Ballesteros 1998; Williams et al. 1999; Rützler 2002b). It is different from *C. aprica* by the external morphology and color. The spirasters are rather similar: widely turning spires and profusely spined; the tylostyles are smaller, but only slightly at Belize (see remarks for *C. aprica*). From its external morphology, it may be confused with fully encrusting *C. caribbaea*; however, when they are compared side by side the differences are clear. The problem was and remains that these two species seldom co-exist in the same habitat. The two species are separated by studying their spicules: *C. caribbaea* possess rather large and stout tylostyles, and the spirasters are narrowly turning, usually longer and possess more turns. In contrast to the other two species, *C. tenuis* transplanted fragments always grow fully encrusting, although the edges may be ragged and with bits of tissue unconnected to the main body.

The only other clionaid of similar color and habit to *Cliona caribbaea* and *C. tenuis* is *C. orientalis* Thiele (1900), which is a common and widespread species of the Great Barrier Reef, Australia (Schönberg 2000; Schönberg and Wilkinson 2001). We observed *C. orientalis* at Heron Island in the Great Barrier Reef, and the similarities are obvious. Schönberg (2000) described tylostyles similar in size and shape, but spirasters are more narrowly turning. Examination of a specimen fragment from Heron Island (INV-POR 658) showed similar tylostyles size (252-299 $\mu\text{m} \times 4.7\text{-}6.2 \mu\text{m}$, length by width), but smoothly elongated, drop-shaped, and irregular heads; spirasters are on average longer (29-35 μm), with narrower spires (3-4 μm) sparse spination. *C. orientalis* spirasters mostly have 3-6 turns while in *C. tenuis* there are many with 1-3 turns. Also, *C. orientalis* tissue penetrates more deeply and uniformly into the substratum: up to 1.9 cm in our specimen from a *Porites* head and up to 3 cm in those cited by Schönberg (2000). Tissue fills up the skeletal coral pores, and sparse chambers were up to 1 mm in diameter. *C. orientalis* falls outside of *C. tenuis* spiculation variation.

Pang (1973a, 1973b) did not notice or find

Cliona tenuis at Jamaica while we frequently encountered it in 2002 in shallow littoral terraces and in the Elkhorn coral rubble zone in fore reef settings. From her descriptions of *C. aprica* and *C. langae*, and analysis of type material, it is clear that the new species was not mistakenly included within neither of them. Perhaps the species was uncommon or absent in the late 60's when Pang did her work, and when the Elkhorn coral was healthy and dominant.

The above remarks may support one of our hypotheses, viz., that *Cliona tenuis* is an introduced species whose source may be *C. orientalis*. *Pione lampa* (de Laubenfels, 1950), is a bright vermilion red, thinly encrusting clionaid, which seems to have been introduced to Bermuda from the Indo-Pacific sometime before the 1950's (Rützler 2002b). *C. tenuis* has been at the San Andrés Island fore-reef terrace at least since 1970. If *C. orientalis* was introduced to the Caribbean, this occurred before 1970 and from an original population with a spicule complement somewhat different to that from the GBR. Perhaps the apparent absence of *C. tenuis* from east of Puerto Rico, throughout the Lesser Antillean arc, to Santa Marta in South America may be related to barriers of dispersion after its introduction. More detailed studies of specimens of *C. tenuis* collected in the Caribbean earlier than 1970, and a molecular systematic analysis would help to solve this problem.

The specimens of *Cliona varians* forma *incrustans* described and illustrated by Lehnert (1993 as *Anthosigmella*) from Cozumel, seem to belong to *Cliona tenuis*. Some of the specimens photographed look thick and riddled with zoanthids, typical of old *C. caribbaea*; their tylostyles size (190-290 μm long, 3-10 μm wide) and shape (Lehnert's Figs. 130 and 131), closely conform to *C. tenuis*. The sponge pictured on Fig. 22 is more like *C. varians*.

Key to species of brown, encrusting Caribbean clionoids

- 1- Spirasters long, some surpassing 40 μm , and narrowly turning; maximum spire diameter 3.5 μm ; within a single specimen there are al-

- ways some spirasters with many turns, 6 or more; encrusting or papillated ----- *Cliona caribbaea*
- 1- Spirasters shorter, up to 39 μm , and many widely turning; spire diameter reaches 5 μm or more ----- 2
- 2- Papillated; if encrusting, seldom covers the entire substratum; brown black ----- *Cliona aprica*
- 2- Fully encrusting, not papillated, various shades of brown, but not black ----- *Cliona tenuis*

GENERAL DISCUSSION AND CONCLUSIONS

From subtle but consistent differences in external and spicule morphology, size and observations from transplant experiments, we conclude that there are three distinct species of brown to brown-black encrusting and excavating sponges in the Caribbean. In the three species, the greater spicule size occurs in southern Colombia, as in many other sponges; possibly related to local enrichment of silica from river runoff (see Zea 1987). But the overall differences, of the three species, in spicule size and morphology are generally maintained independently of the locality: tylostyles are stouter and longer in *Cliona caribbaea*, intermediate in *C. aprica* and smaller in *C. tenuis*; spirasters tend to be longer, have many turns and the spire is generally narrower in *C. caribbaea* (Table 1, Figs. 4-7). Nevertheless, some spicule characteristics, within each species, vary with geographical location: *C. aprica* tylostyle heads are blunt (head length/width <1), in comparison with the other two species, at San Andrés, Jamaica and the continental coast of Colombia, but are greatly elongated at Venezuela; *C. caribbaea* tylostyle heads are usually elongated, but at Bermuda they are blunt (Rützler 1974); spirasters of *C. caribbaea* usually have more turns than the other species, except at San Andrés (Table 1, Fig. 8). The predominant external morphology (papillated, encrusting) of the studied species also varies geographically. For example, *Cliona caribbaea* is mostly papillated in Bermuda and the Central and South American coasts, while predominantly encrusting

elsewhere. Papillated forms of *C. aprica* and encrusting *C. tenuis* are similar in color and spiculation in Belize -although comparison of neighboring specimens show differences-, but are different elsewhere in the Southern Caribbean.

The geographical distribution and the local co-occurrence (sympatric vs. allopatric) of brown clionoids are also puzzling, and until all dubious records are clarified and areas re-visited, the picture is far from complete. Of the three species studied, *Cliona aprica* is apparently the only that occurs in southeastern Caribbean, from Los Roques in Venezuela, through The Netherlands Antilles, to Santa Marta in continental Colombia, and it is absent from Puerto Rico. In the Lesser Antilles, from Guadeloupe to St. Vincent, the only species known is *C. caribbaea*, and it is papillated (see Rützler 1974). Hence, the apparent presence of only papillated forms of this complex from Guadeloupe to Santa Marta, including Barbados (F. Parra pers. obs.) may indicate the occurrence of a single species. If they are what we named *C. aprica*, this species will fall into the synonymy of *C. caribbaea*, and *C. langae* will recover its status of valid species. Given these taxonomical implications, further observations and sampling in the Lesser Antilles is needed.

The examples given above may imply that the taxonomical resolution of the complex presented here is incomplete and that there may be more un-described cryptic species or local predominant phenotypes are genetically fixed. A molecular systematic analysis is needed to clarify these issues, but a careful comparison of co-occurring specimens is necessary to recognize the similarities and differences between the species in a given geographical locality.

We have not included *Cliona varians* (Duchassaing and Michelotti) in this "complex" of Caribbean clionoids, as it was described before and it is distinguished by its: thicker (up to 1-2 cm) external tissue, light amber color, tylostyle shape, and the u-shaped spirasters (see also Schönberg 2002). In contrast to the group of species studied here (see López-Victoria et al. in press), *C. varians* seem to overgrow the

substratum before excavating it (Vicente 1978) and it does not use pioneering tissue threads to undermine coral polyps (S. Zea and M. López-Victoria, unpublished observations).

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LITERATURE CITED

- Acker, K. L., and M. Risk. 1985. Substrate destruction and sediment production by the boring sponge *Cliona caribbaea* on Grand Cayman Island. *J. Sedim. Petrol.* 55:705-711.
- Antonius, A., and E. Ballesteros. 1998. Epizoism: a new threat to coral health in Caribbean reefs. *Rev. Biol. Trop.* 46:145-156.
- Alcolado, P. M. 1976. Lista de nuevos registros de poríferos para Cuba. *Acad. Cienc. Cuba, Inst. Oceanol. Ser. Oceanología* 36:1-11.
- Alcolado, P. M. 1979. Estructura ecológica de la comunidad de esponjas de un perfil costero de Cuba. *Cien. Biol.* 3:105-127.
- Alcolado, P. M. 1989. Estructura ecológica de las comunidades de esponjas del arrecife de Rincón de Ganabo, Cuba. *Rep. Invest. Inst. Oceanol.* 10:1-16.
- Alcolado, P. M. 1990. General features of Cuban sponge communities. In *New perspectives in sponge biology*, ed. K. Rützler, 351-357. Washington, DC: Smithsonian Institution Press.
- Alcolado, P. M. 1999. Comunidades de esponjas de los arrecifes del archipiélago Sabana-Camagüey, Cuba. *Bol. Invest. Mar. Cost.* 28:95-124.
- Buznego, M., and P. M. Alcolado. 1987. Frecuencias de ataques de esponjas perforadoras sobre algunos corales escleractíneos y otros sustratos marinos en Cuba. *Rep. Invest. Inst. Oceanol.* 59:1-18.
- Cortés, J., M. Murillo, H. M. Guzmán, and J. Acuña. 1984. Pérdida de zooxantelas y muerte de corales y otros organismos arrecifales en el Caribe y Pacífico de Costa Rica. *Rev. Biol. Trop.* 32:227-231.
- Díaz, J. M., J. Garzón-Ferreira, and S. Zea. 1995. *Los Arrecifes coralinos de la isla de San Andrés, Colombia: estado actual y perspectivas para su conservación*. Bogotá: Acad. Colomb. Cienc. Exact. Fis. Nat., Colección Jorge Alvarez Lleras 7.
- Duchassaing de Fombressin, P., and G. Michelotti. 1864. Spongiaires de la Mer Caraïbe. *Natuurk. Verh. Mij. Haarlem* 21:1-124.
- Carter, H. J. 1882. Some sponges from the West Indies and Acapulco in the Liverpool Free Museum described, with general and classificatory remarks. *Ann. Mag. Nat. Hist.* 9:266-301, 346-368, pl. 11-12.
- George, W. C., and H. V. Wilson. 1919. Sponges of Beaufort (N.C.) Harbor and vicinity. *Bull. U.S. Bur. Fish.* 36:133-179.
- Hechtel, G. J. 1965. A systematic study of the Demospongiae of Port Royal, Jamaica. *Bull. Peabody Mus. Nat. Hist.* 20:1-103.
- Hofman, C. C., and M. Kielman. 1992. The excavating sponges of the Santa Marta area, Colombia, with description of a new species. *Bijd. Dierk.* 61:205-217.
- Hudson, J. H. 1977. Long-term bioerosion rates on a Florida reef: a new method. *Proc. 3rd Int. Coral Reef Sym., Miami* 2, Geology, 491-497.
- Humann, P. 1992. *Reef creature identification. Florida, Caribbean, Bahamas*. Jacksonville: New World Publications, Inc.
- Laubenfels, M. W. de. 1936a. A discussion of the sponge fauna of Dry Tortugas in particular, and the West Indies in general, with material for a revision of the families and orders of the Porifera. *Carnegie Inst. Washington Publ.* 467:1-225.

- Laubenfels, M. W. de. 1936b. A comparison of the shallow water sponges near the Pacific end of the Panama Canal with those at the Caribbean end. *Proc. U.S. Nat. Mus.* 83:441-466.
- Laubenfels, M. W. de. 1950. The Porifera of the Bermuda Archipelago. *Trans. Zool. Soc. Lond.* 27:1-201.
- Laubenfels, M. W. de. 1953a. Sponges of the Gulf of Mexico. *Bull. Mar. Sci. Gulf Caribb.* 2:511-557.
- Laubenfels, M. W. de. 1953b. *A guide to the sponges of Eastern North America*. Miami, Florida: Univ. of Miami, Special Publ.
- Lehnert, H. 1993. Die Schwämme von Cozumel (Mexiko). Bestandsaufnahme, kritischer Vergleich taxonomischer Merkmale und Beschreibung einer neuen Art. *Acta Biol. Benrodis* 5:35-127.
- Lehnert, H., and H. Fischer. 1999. Distribution patterns of sponges and corals down to 107 m off North Jamaica. *Mem. Qld. Mus.* 44:307-316.
- Lehnert, H., and R. W. M. van Soest. 1998. Shallow water sponges of Jamaica. *Beaufortia* 48:71-103.
- Little, Jr., F. J. 1963. The sponge fauna of St. George's Sound, Apalachee Bay, and Panama City regions of the Florida Gulf Coast. *Tulane Stud. Zool.* 11:31-71.
- López-Victoria, M., S. Zea, and E. Weil. In press. New aspects on the biology of the encrusting excavating sponges *Cliona aprica*, *Cliona caribbaea* and *Cliona* sp. *Boll. Mus. Ist. Biol. Univ. Genova*.
- MacGeachy, J. K. 1977. Factors controlling sponge boring in Barbados reef corals. *Proc. 3rd Int. Coral Reef Sym., Miami* 2, Geology, 477-483.
- Pang, R. K. 1973a. The systematics of some Jamaican excavating sponges (Porifera). *Postilla* 161:1-75.
- Pang, R. K. 1973b. The ecology of some Jamaican excavating sponges. *Bull. Mar. Sci.* 23:227-243.
- Pomponi, S. A. 1976. An ultrastructural study of boring sponge cells and excavated substrata. *Scanning Electron Microscopy* 8:569-576.
- Pomponi, S. A. 1977. Etching cells of boring sponges: an ultrastructural analysis. *Proc. 3rd Int. Coral Reef Sym., Miami* 2, Geology, 485-490.
- Pomponi, S. A. 1979. Ultrastructure and cytochemistry of the etching area of boring sponges. *Coll. Int. C.N.R.S.* 291:317-232.
- Pulitzer-Finali, G. 1986. A collection of West Indian Demospongiae (Porifera). In Appendix, a list for the Demospongiae hitherto recorded from the West Indies. *Estratto dagli Annali del Museo Civico di Storia Naturale di Genova* 86:65-216.
- Rose, C. S., and M. J. Risk. 1985. Increase in *Cliona delitrix* infestation of *Montastrea cavernosa* heads on an organically polluted portion of the Grand Cayman. *P.S.Z.N.I: Mar. Ecol.* 6:345-363.
- Risk, M. J., M. M. Murillo, and J. Cortés. 1980. Observaciones biológicas preliminares sobre el arrecife coralino en el Parque Nacional de Cahuita, Costa Rica. *Rev. Biol. Trop.* 28:361-382.
- Rützler, K. 1974. The burrowing sponges of Bermuda. *Smithson. Contrib. Zool.* 165:1-32.
- Rützler, K. 1975. The role of burrowing sponges in bioerosion. *Oecologia (Berl.)* 19:203-216.
- Rützler, K. 1986. Phylum Porifera (Sponges). In *Marine fauna and flora of Bermuda*, ed. W. Sterrer, 111-128. New York: John Wiley & Sons, Inc.
- Rützler, K. 1990. Associations between Caribbean sponges and photosynthetic organisms. In *New perspectives in sponge biology*, ed. K. Rützler, 455-466. Washington, DC: Smithsonian Institution Press.
- Rützler, K. 2002a. Family Clionidae D'Orbigny, 1851. In *Systema Porifera: a guide to the classification of sponges*, ed. J. N. A. Hooper and R. W. M. van Soest, 173-185. New York: Kluwer Academic/Plenum Publishers.
- Rützler, K. 2002b. Impact of crustose clionid sponges on Caribbean reef corals. *Acta Geol. Hisp.* 37:61-72.
- Rützler, K., M. C. Díaz, R. W. M. van Soest, S. Zea, K. P. Smith, B. Alvarez, and J. Wulff. 2000. Diversity of sponge fauna in mangrove ponds, Pelican Cays, Belize. *Atoll Res. Bull.* 476:229-248.
- Schmahl, G. P. 1990. Community structure and ecology of sponges associated with four southern Florida coral reefs. In *New perspectives in sponge biology*, ed. K. Rützler, 376-383. Washington, DC: Smithsonian Institution Press.
- Schmidt, E. O. 1862. *Die Spongien des adriatischen Meeres*. Leipzig: Wilhelm Eglemann.
- Schönberg, C. H. L. 2000. Bioeroding sponges common to the Central Australian Great Barrier Reef: Descriptions of three new species, two new records, and additions to two previously described species. *Senckenbergiana marit.* 30:161-221.
- Schönberg, C. H. L. 2002. Sponges of the 'Cliona viridis complex'—a key for species identification. *Proc. 9th Int. Coral Reef Sym., Bali* 1:295-300.
- Schönberg, C. H. L., and C. R. Wilkinson. 2001. Induced colonization of corals by a clionid bioeroding sponge. *Coral Reefs* 20:69-76.
- Smithe, F. B. 1975. *Naturalist's color guide. Part. I. Color guide*. New York: The American Museum of Natural History.
- Thiele, J. 1900. Keselschwämme von Ternate 1 Abh. *Senckenb. naturforsch. Ges.* 25:19-80.
- Topsent, E. 1889. Quelques spongiaires du Banc de Campêche et de la Pointe-a-Pitre. *Mém. Soc. Zool. France* 2:30-52.
- Topsent, E. 1900. Étude monographique des spongiaires de France, III: Monaxonida (Hadromerina). *Arch. Zool. Exp. Gen.* 9:555-592.
- Topsent, E. 1932. Notes sur des Clionides. *Arch. Zool. Exp. Gen.* 74:549-579.
- Tunnicliffe, V. 1979. The role of boring sponges in coral fracture. *Coll. Int. C.N.R.S.* 291:309-315.
- Vacelet, J. 1981. Algal-sponge symbioses in the coral reefs of New Caledonia: a morphological study. *Proc. 4th Int. Coral Reef Sym., Manila* 2:713-719.
- Valderrama, D. F. 2001. *Taxonomía y distribución de esponjas arrecifales (Porifera) del noroccidente del Golfo de Urabá, Caribe colombiano*. B.Sc. Thesis. Santa Marta: Univ. Jorge Tadeo Lozano.
- Valderrama, D. F., and S. Zea. In press. Esquemas de distribución de esponjas arrecifales (Porifera) del

- noroccidente del Golfo de Urabá, Caribe sur, Colombia. *Bol. Inst. Invest. Mar. Cost.* 32.
- Verrill, A. E. 1907. The Bermuda Islands. Part IV. Geology and Paleontology, and part V. An account of the coral reefs. *Trans. Conn. Acad. Arts. Sci.* 12:45-348 [Porifera: 330-334, figs. 176-181, pl. 35C, D].
- Vicente, V. P. 1978. An ecological evaluation of the West Indian demosponge *Anthosigmella varians* (Hadromerida: Spirastrellidae). *Bull. Mar. Sci.* 28: 771-779.
- Vicente, V. P. 1990a. Response of sponges with autotrophic endosymbionts during the coral-bleaching episode in Puerto Rico. *Coral Reefs* 8:199-202.
- Vicente, V. P. 1990b. Overgrowth activity by the encrusting sponge *Chondrilla nucula* on a coral reef in Puerto Rico. In *New perspectives in sponge biology*, ed. K. Rützler, 436-442. Washington, DC: Smithsonian Institution Press.
- Wells, H. W., M. J. Wells, and I. E. Gray. 1960. Marine sponges of North Carolina. *J. Elisha Mitchell Sci. Soc.* 76:200-245.
- Wiedenmayer, F. 1977. *Shallow-water sponges of the western Bahamas*. Basel and Stuttgart: Birkhauser Verlag.
- Williams E. H., P. J. Bartels, and L. Bunkley-Williams. 1999. Predicted disappearance of coral-reef ramps: a direct result of major ecological disturbances. *Global Change Biology* 5:839-845.
- Willenz, P., and S. A. Pomponi. 1996. A new deep sea coralline sponge from Turks and Caicos Islands: *Willardia caicosensis* gen. et. sp. nov. (Demospongiae: Hadromerida). *Bull. Inst. R. Sci. Nat. Belgique, Biol.* 66 suppl.:205-218.
- Zea, S. 1987. *Esponjas del Caribe colombiano*. Bogotá: Editorial Catálogo Científico.
- Zea, S. 1993. Cover of sponges and other sessile organisms in rocky and coral reef habitats of Santa Marta, Colombian Caribbean Sea. *Caribb. J. Sci.* 29: 75-88.
- Zea, S. 2001. Patterns of sponge (Porifera, Demospongiae) distribution in remote, oceanic reef complexes of the southwestern Caribbean. *Rev. Acad. Colomb. Cienc.* 25:579-592.