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

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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 Clionaidae, 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, Curacao, 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 Clionaidae, 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 clionaid s. 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 taxonomic 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 clionaid as either C. aprica or C. langae (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 purpose 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×, 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× 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 (Isomet™, Buehler, Chicago); embedded in low viscosity Spurr
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 Rüttzler 1974; Willenz and Pomponi 1996). Staining was carried out for 5-15 min with basic (or acid) fucsin 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. Rüttzler 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(Fo)]. 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 incumbent canals; top of shallow substratum rims with paratangentially placed spicules (Fig. 2). Choanosome fleshy, dark yellow, filling entirely coral-calicular 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-Victória 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 Clionaidae 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); Diaz 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).


*Non Cliona aprica*; Rützler 1975: 205 (Belize); 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. PI live 4/CICN-MHN(Po) 181; Santa Marta Baai: 5-6 m, INV-POR 623; Blauwbai: 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. caribbea* and *C. tenuis* sp. nov. at each geographic area. Data are min.-max. (mean ± 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.

<table>
<thead>
<tr>
<th>Species/spicule</th>
<th>Area</th>
<th>San Andrés Archipelago*</th>
<th>Jamaica</th>
<th>Puerto Rico</th>
<th>Colombia**</th>
<th>Venezuela</th>
<th>Belize</th>
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<td><strong>Specimens studied</strong></td>
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<td><strong>Tylostyles</strong></td>
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<tr>
<td>Length</td>
<td></td>
<td>232-375 (301 ± 21)</td>
<td>237-394 (324 ± 15)</td>
<td>270-427 (357 ± 9)</td>
<td>204-333 (332 ± 25)</td>
<td>261-399 (332 ± 21)</td>
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<tr>
<td>Shaft width</td>
<td></td>
<td>4.7-14.2 (8.5 ± 0.6)</td>
<td>4.7-10.0 (7.5 ± 1.7)</td>
<td>3.8-19 (12.0 ± 2.5)</td>
<td>3.8-5.7 (5.0 ± 0.5)</td>
<td>4.3-13.3 (8.2 ± 1.3)</td>
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<tr>
<td>Head width</td>
<td></td>
<td>6.6-15.7 (12.3 ± 0.9)</td>
<td>8.1-14.3 (11.8 ± 0.4)</td>
<td>9.0-19.5 (15.5 ± 2.2)</td>
<td>3.8-10.5 (8.6 ± 1.6)</td>
<td>7.6-15.7 (12.0 ± 0.6)</td>
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<tr>
<td>Head length</td>
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<td>7.1-15.7 (11.8 ± 1.0)</td>
<td>8.1-15.2 (10.8 ± 0.8)</td>
<td>10.4-19.0 (16.0 ± 0.4)</td>
<td>8.5-12.8 (10.5 ± 1.0)</td>
<td>8.5-17.6 (12.2 ± 0.9)</td>
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<td>Head length/width</td>
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<td>0.5-1.9 (0.96 ± 0.06)</td>
<td>0.7-1.4 (0.92 ± 0.08)</td>
<td>0.8-1.5 (0.9 ± 0.02)</td>
<td>1.0-2.7 (1.3 ± 0.4)</td>
<td>0.7-1.8 (1.03 ± 0.05)</td>
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<td><strong>Spirasters</strong></td>
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<td>Length</td>
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<td>12.6-34.0 (21.5 ± 2.4)</td>
<td>16.0-33.0 (24.5 ± 1.7)</td>
<td>14.9-38.5 (26.0 ± 3.2)</td>
<td>20.0-33.5 (26.2 ± 3.5)</td>
<td>17.0-33.0 (24.6 ± 2.2)</td>
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<tr>
<td>Shaft width</td>
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<td>0.4-1.0 (0.7 ± 0.1)</td>
<td>0.5-1.0 (0.7 ± 0.04)</td>
<td>0.5-1.7 (1.1 ± 0.3)</td>
<td>0.7-1.0 (0.9 ± 0.1)</td>
<td>0.5-1.0 (0.8 ± 0.3)</td>
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<tr>
<td>Spire max. diameter</td>
<td></td>
<td>2.3-7.0 (4.5 ± 0.6)</td>
<td>2.0-5.5 (3.4 ± 0.8)</td>
<td>2.3-8.1 (4.3 ± 0.7)</td>
<td>2.7-5.0 (3.9 ± 0.7)</td>
<td>2.0-5.0 (3.3 ± 0.2)</td>
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<td>Spine height</td>
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<td>0.6-2.0</td>
<td>0.7-2.0</td>
<td>1.0-2.5</td>
<td>1.5-2.0</td>
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<td>Spine branching</td>
<td></td>
<td>Profuse, in bouquets</td>
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<td>Number of turns</td>
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<td>2.6 (3.5 ± 0.5)</td>
<td>2.7 (4.5 ± 0.5)</td>
<td>2.8 (4.3 ± 0.7)</td>
<td>3.7 (4.3 ± 1.3)</td>
<td>2.5 (3.5 ± 0.3)</td>
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<tr>
<td>Length of longest spire</td>
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<td>8.6-21.8 (12.5 ± 1.3)</td>
<td>9-14.5 (11.7 ± 1.4)</td>
<td>8.3-19.2 (11.9 ± 0.5)</td>
<td>10.5-15.0 (12.8 ± 1.8)</td>
<td>9.5-19.0 (12.9 ± 1.5)</td>
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<td><strong>Cliona caribbea</strong></td>
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<td><strong>Tylostyles</strong></td>
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<td>Length</td>
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<td>271-418 (340 ± 26)</td>
<td>275-465 (370 ± 33)</td>
<td>313-418 (379 ± 31)</td>
<td>280-413 (357 ± 26)</td>
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<tr>
<td>Shaft width</td>
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<td>4.7-13.3 (8.4 ± 1.7)</td>
<td>4.7-14.3 (10.2 ± 1.2)</td>
<td>7.3-15.2 (12.0 ± 2.2)</td>
<td>5.2-13.3 (9.0 ± 0.6)</td>
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<tr>
<td>Head width</td>
<td></td>
<td>7.1-15.2 (11.3 ± 1.7)</td>
<td>8.1-15.7 (12.9 ± 0.7)</td>
<td>10.0-18.1 (15.1 ± 1.7)</td>
<td>8.1-16.6 (12.9 ± 0.5)</td>
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<tr>
<td>Head length</td>
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<td>7.1-17.1 (12.1 ± 2.0)</td>
<td>7.1-17.1 (13.9 ± 1.3)</td>
<td>10.5-17.6 (14.3 ± 1.7)</td>
<td>10-17.6 (13.8 ± 0.6)</td>
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<td>Head length/width</td>
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<td>0.5-1.5 (1.02 ± 0.08)</td>
<td>0.8-1.1 (0.9 ± 0.1)</td>
<td>0.8-1.5 (1.08 ± 0.05)</td>
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<td><strong>Spirasters</strong></td>
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<td>Length</td>
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<td>14.9-46.0 (26.7 ± 5.3)</td>
<td>22.0-45.5 (33.7 ± 4.7)</td>
<td>25.5-43.5 (36.3 ± 6.0)</td>
<td>22.0-47.0 (37.3 ± 4.6)</td>
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<tr>
<td>Shaft width</td>
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<td>0.3-1.4 (0.73 ± 0.25)</td>
<td>0.3-1.1 (0.59 ± 0.14)</td>
<td>0.5-1.5 (0.9 ± 0.3)</td>
<td>0.5-1.0 (0.71 ± 0.18)</td>
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<td>1.5-3.5 (2.6 ± 0.3)</td>
<td>1.5-3.3 (2.3 ± 0.5)</td>
<td>1.0-3.0 (2.1 ± 0.2)</td>
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<td>Spine height</td>
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<td>1.0-2.0</td>
<td>0.5-2.0</td>
<td>1.0</td>
<td>1.2-2.0</td>
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<tr>
<td>Spine branching</td>
<td></td>
<td>Profuse, in bouquets</td>
<td>Sparse, mostly unbranched</td>
<td>Sparse, mostly unbranched</td>
<td>Sparse, mostly unbranched</td>
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<tr>
<td>Number of turns</td>
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<td>1-9 (4.1 ± 1.4)</td>
<td>2.10 (5.6 ± 0.7)</td>
<td>5-10 (7.6 ± 1.6)</td>
<td>8-15 (6.7 ± 1.7)</td>
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<tr>
<td>Length of longest spire</td>
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<td>8.5-26.0 (12.9 ± 3.0)</td>
<td>7.5-21.0 (13.2 ± 2.6)</td>
<td>10-11.5 (10.6 ± 0.6)</td>
<td>8.5-15.5 (12.0 ± 0.8)</td>
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<tr>
<td>Species/spicule</td>
<td>Area</td>
<td>San Andrés Archipelago*</td>
<td>Jamaica</td>
<td>Puerto Rico</td>
<td>Colombia**</td>
<td>Venezuela</td>
<td>Belize</td>
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<tr>
<td><em>Cliona tenuis</em> sp. nov.</td>
<td>Specimens studied</td>
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<td>Tylostyles</td>
<td></td>
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<tr>
<td></td>
<td>Length</td>
<td>199-321 (268 ± 21)</td>
<td>219-299 (258 ± 2)</td>
<td>204-275 (246 ± 3)</td>
<td>219-370 (300 ± 20)</td>
<td>214-380 (308 ± 15)</td>
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<tr>
<td></td>
<td>Shaft width</td>
<td>3.3-9.5 (6.3 ± 1.0)</td>
<td>3.8-8.1 (5.6 ± 0.2)</td>
<td>5.2-12.8 (7.7 ± 0.5)</td>
<td>4.7-14.3 (9.4 ± 1.2)</td>
<td>4.7-12.3 (7.5 ± 0.9)</td>
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<td></td>
<td>Head width</td>
<td>5.7-13.3 (9.7 ± 0.9)</td>
<td>7.1-11.4 (9.2 ± 0.1)</td>
<td>7.6-13.3 (9.8 ± 0.6)</td>
<td>7.1-16.6 (12.4 ± 1.4)</td>
<td>7.6-14.3 (10.9 ± 0.4)</td>
<td></td>
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<tr>
<td></td>
<td>Head length</td>
<td>7.1-13.8 (9.9 ± 0.1)</td>
<td>7.1-10.9 (9.3 ± 0.6)</td>
<td>7.1-14.3 (10.6 ± 1.3)</td>
<td>9.0-18.5 (12.9 ± 1.6)</td>
<td>8.1-14.3 (11.4 ± 0.3)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Head length/width</td>
<td>0.7-1.8 (1.00 ± 0.09)</td>
<td>0.8-1.8 (1.02 ± 0.07)</td>
<td>0.8-1.6 (1.06 ± 0.06)</td>
<td>0.8-1.5 (1.11 ± 0.15)</td>
<td>0.8-1.6 (1.06 ± 0.07)</td>
<td></td>
</tr>
<tr>
<td><em>Spirasters</em></td>
<td>Length</td>
<td>11.0-30.0 (22.7 ± 2.3)</td>
<td>17.0-39.0 (24.3 ± 1.5)</td>
<td>20.5-27.0 (24.4 ± 0.1)</td>
<td>12.0-37.5 (23.8 ± 2.9)</td>
<td>18.5-39.0 (24.8 ± 1.3)</td>
<td></td>
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<tr>
<td></td>
<td>Shaft width</td>
<td>0.5-1.1 (0.7 ± 0.1)</td>
<td>0.5-0.7 (1.0 ± 0.1)</td>
<td>0.5-1.1 (0.7 ± 0.2)</td>
<td>0.3-1.3 (0.9 ± 0.2)</td>
<td>0.40-1.25 (0.70 ± 0.14)</td>
<td></td>
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<tr>
<td></td>
<td>Spire max. diameter</td>
<td>2.3-6.9 (4.1 ± 0.7)</td>
<td>3.0-8.0 (4.8 ± 0.5)</td>
<td>2.0-5.0 (2.8 ± 0.2)</td>
<td>2.0-8.0 (4.2 ± 0.9)</td>
<td>3.0-6.0 (4.3 ± 0.3)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spine height</td>
<td>1.2-2.0</td>
<td>0.7-1.0</td>
<td>0.7-1.5</td>
<td>1.2-1.7</td>
<td>1.0-1.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spine branching</td>
<td>Profuse, in bouquets</td>
<td>Profuse, in bouquets</td>
<td>Profuse, in bouquets</td>
<td>Profuse, in bouquets</td>
<td>Profuse, in bouquets</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Number of turns</td>
<td>1-5 (3.6 ± 0.5)</td>
<td>1-4 (2.7 ± 0.2)</td>
<td>1-6 (4.3 ± 0.4)</td>
<td>1-0.7 (3.7 ± 0.7)</td>
<td>1-5 (2.7 ± 0.3)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Length of longest spire</td>
<td>9.7-20.7 (12.5 ± 0.7)</td>
<td>10.5-25.0 (16.9 ± 2.4)</td>
<td>9.5-14.0 (11.7 ± 1.0)</td>
<td>7.4-43.7 (13.7 ± 1.1)</td>
<td>14.0-25.5 (16.4 ± 2.0)</td>
<td></td>
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</tbody>
</table>

*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) Quitasuño 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 aprox. 16.4 cm.
and M. Kielman, Rosario Islands, Pa-
jarales, 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 Me-
dio: 4 m, INV-POR 615. San Bernardo Is-
lands, 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 Is-
land, 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 ex-
halant 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 re-
laxed papillae protrude 1-2 mm above sub-
stratum. 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 speci-
mens colonized by light yellow zoanthids.

**Depth of excavation** 4-19 mm beneath the
surface. Fully excavated areas below papil-
lae 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 tis-
sue layer. Solid areas excavated by tunnels

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**FIG. 2.** Camera lucida drawings of sponge-coral
substratum sections, ground and polished, of encrust-
ing specimens. (A) Cliona aprica on Siderastrea sidera;
(B) C. caribbaea on Montastraea cavernosa; (C) C. tenuis
sp. nov. on Diploria strigosa.
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). Microscleres: 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, Curacão, 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).
Marta to NW Gulf of Uraba), San Andrés and Old Providence Archipelago (San Andrés, Providencia, Albuquerque Cays, Courtown Cays, Serrana Bank, Roncador Bank, Quilasueto 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. 4. Size of spicules of the three species at San Andrés Archipelago (SW Caribbean, Colombia), Jamaica and Puerto Rico. Data represent specimen means ± 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 zoanthids; 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.
extensively fused as to be almost fully en-crusting. 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 tylo-styles, and slender, narrow and wavy spi-rasters.
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 smaller (Figs. 3-6). At Belize, there remains the possibility that what we are calling C. tenuis is a papillated C. aprica. In this area, C. tenuis often develops papillae secondarily wherever the sponge surface has been smothered 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 papillary 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. sorvidia); de Laubenfels 1936a: 155 (Dry Tortugas, as C. caribbaea); 1936b: 461 (Panama, as C. caribbaea); 1950: 108 (Bermuda, as C. caribbaea); 1953a: 540 (eastern Gulf of Mexico, as C. caribbaea); 1953b: 22 (eastern North America, as C. caribbaea) [all these are of uncertain identity, fide 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, fide 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 BMNH 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-
ibean, 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].

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

*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. **Belize.** Carrie Bow Cay, 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). BMHN 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 Kelman 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 interscalar 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. Pal-
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 Belize 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 more 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, zoanthellate-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 epiizoism; 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 sp._; 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).


**Non Anthosigrella 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; Bocatona 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 (=Bolivar) 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-Septia), and lighter shades of brown to cream in thinner portions (23-Raw umber, 24-Cream, 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 either ragged or continuous; Belizean specimens occasionally with papillae at some edges. Sponge penetrates and excavates substratum 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, Alberquerque 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, litoral 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 Cliona 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 Cliona aprica). From its external morphology, it may be confused with fully encrusting Cliona 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 μm × 4.7-6.2 μm, 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 Cliona 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 in-crustans described and illustrated by Lehnhert (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 clionaid

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 pa-
pillated --------------- Cliona caribbaea
1- Spirasters shorter, up to 39 µm, and
many widely turning; spire diam-
eter 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 en-
richment of silica from river runoff (see Zea
1987). But the overall differences, of the
three species, in spicule size and morphol-
yogy are generally maintained indepen-
dently of the locality: tylostyles are stouter
and longer in Cliona caribbaea, intermediate
in C. aprica and smaller in C. tenuis; spi-
rasters 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. ca-
ribbaea tylostyle heads are usually elon-
gated, but at Bermuda they are blunt
(Rützler 1974); spirasters of C. caribbaea
usually have more turns than the other spe-
cies, except at San Andrés (Table 1, Fig. 8).
The predominant external morphology (pa-
pillated, encrusting) of the studied species
also varies geographically. For example,
Cliona caribbaea is mostly papillated in Ber-
muda 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 differ-
ences-, but are different elsewhere in the
Southern Caribbean.

The geographical distribution and the lo-
cal co-occurrence (sympatric vs. allopatric)
of brown clionaids are also puzzling, and
until all dubious records are clarified and
areas re-visited, the picture is far from com-
plete. 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 Co-
lombia, and it is absent from Puerto Rico.
In the Lesser Antilles, from Guadeloupe to St.
Vincent, the only species known is C. carib-
baea, and it is papillated (see Rützler 1974).
Hence, the apparent presence of only pa-
pillated forms of this complex from Guade-
loupe to Santa Marta, including Barbados
(F. Parra pers. obs.) may indicate the occur-
rence 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 spe-
cies. 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 com-
plex presented here is incomplete and that
there may be more un-described cryptic
species or local predominant phenotypes
are genetically fixed. A molecular sys-
tematic analysis is needed to clarify these
issues, but a careful comparison of co-
occurring specimens is necessary to recog-
nize the similarities and differences be-
tween the species in a given geographical
locality.

We have not included Cliona varians (Du-
chassaing and Michelotti) in this “com-
plex” of Caribbean clionaids, as it was de-
scribed 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


