

Terpios hoshinota, a new cyanobacteriosponge threatening Pacific reefs*

KLAUS RÜTZLER¹ and KATHERINE MUZIK²

¹ Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

² Muzik, Ink., 580 Tremont Street, Boston, Massachusetts 02118, U.S.A.

SUMMARY: The new species *Terpios hoshinota* (Suberitidae, Hadromerida) is described from coral reefs in the western Central Pacific. It is recognized by its extensive grayish to blackish encrustations on coral, distinctive lobed tylostyle spicules, and association with abundant, large, unicellular cyanobacteria of the *Aphanocaps raspaigella* type. The sponge aggressively competes for space by killing and overgrowing live coral and is responsible for the demise of large reef areas, particularly in pollution-stressed zones near shore. The intercellular zooecyanellae make up half or more of the sponge tissue. Their morphology, as determined by electron microscope observations, is identical to that of symbionts described from two species of an unrelated sponge genus from the Caribbean, *Dictyonella*.

Key Words: Coral Reef, Porifera, competition, symbiosis, cyanobacteria, Pacific.

INTRODUCTION

For the past two decades or more, coral reefs have been increasingly plagued by various pests and other destructive agents. Some of the difficulties they are experiencing are due to natural shifts in population structure that have only recently gained widespread attention because of the greater abundance of scientific divers, but man-induced causes have also had an adverse effect.

The most devastating coral predator in the Pacific is the asteroid echinoderm *Acanthaster planci* (L.). The effect of its population explosions went unnoticed until the late 1960s (for a review, see ENDEAN, 1973), although outbreaks had been observed almost a decade earlier (Rützler, unpublished, at Tany Kely,

Madagascar, 1959). The population density of the starfish varies greatly throughout the Pacific, but recently alarming increases have been recorded in some areas (CHOAT *et al.*, 1988; GOMEZ, 1988), particularly in the Ryukyu Islands and elsewhere along the Pacific coast of Japan (YAMAGUCHI, 1987).

Sponges have repeatedly been portrayed as important space competitors (RÜTZLER, 1970, 1971; GLYNN, 1973; VICENTE, 1978, 1990; SUCHANEK *et al.*, 1983), but they were not considered a threat to entire reefs until BRYAN (1973) reported unprecedented spreading of an encrusting *Terpios* species on the coral reefs of Guam. This phenomenon was further studied by PLUCER-ROSARIO (1987), who listed the distribution of the sponge throughout the Northern Mariana and Western Caroline Islands, the Philippines, Taiwan, and even American Samoa. In 1985, Muzik (unpublished) confirmed that this sponge occurs on reefs in the Ryukyu Archipelago, first reported by local newspapers as "black disease."

* Received February 10, 1993. Accepted June 2, 1993.

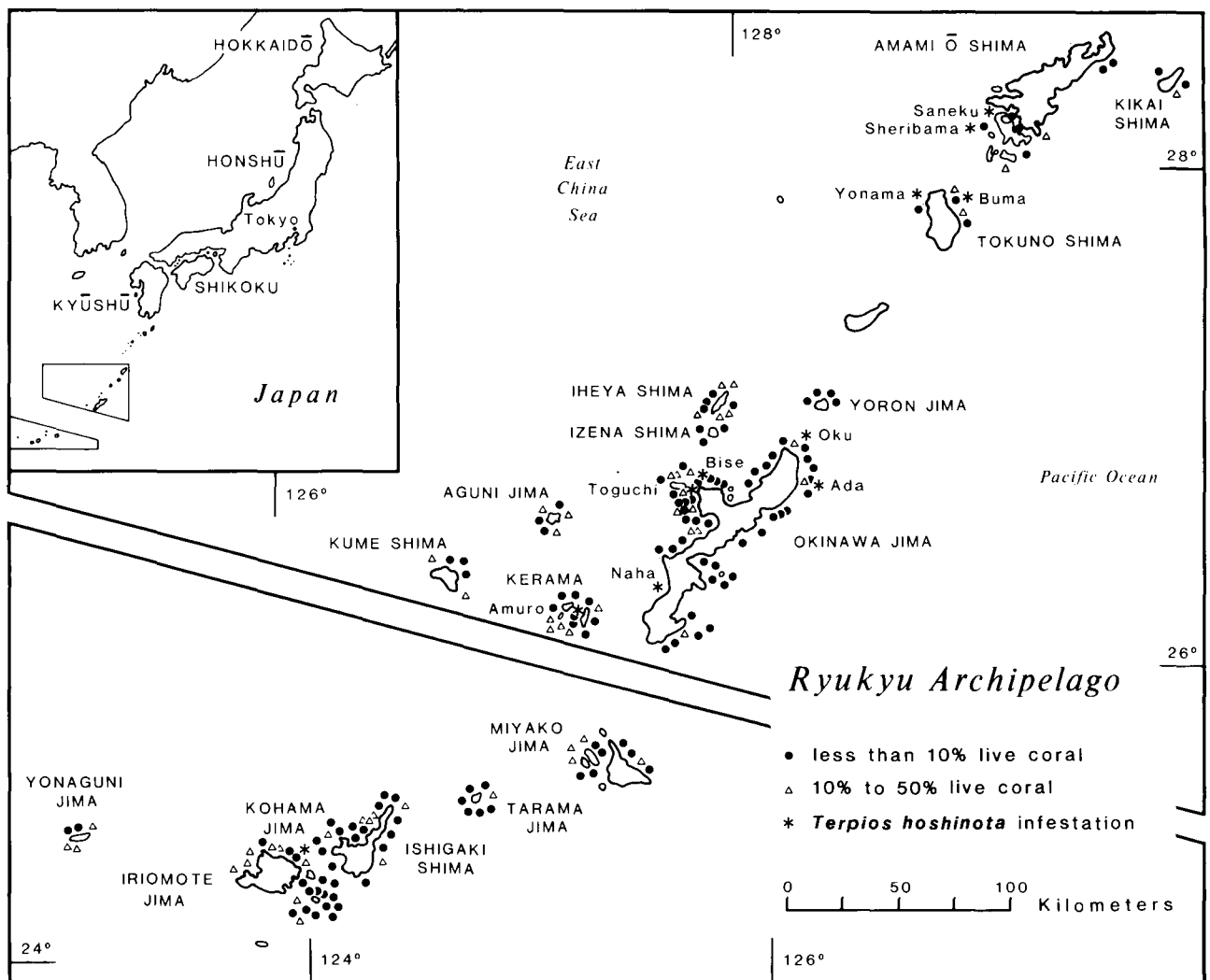


FIG. 1. — Map of 1981-1985 study sites in Japan with location of *Terpios hoshinota* infestations determined in 1984-1985.

Examination of PLUCER-ROSARIO'S (1987) material deposited in the Smithsonian's National Museum of Natural History and of freshly fixed material from Okinawa revealed that the coral competitor *Terpios* sp. is an undescribed species. Microscope preparations also showed an unusually high number of large unicellular cyanobacteria present throughout the sponge in a type of symbiosis similar to that described from *Dictyonella funicularis* and *D. arenosa* from the Caribbean Sea (RÜTZLER, 1981; both as *Ulosa*).

In view of the considerable ecological impact this sponge is known to have on Pacific coral reefs, our objective in this study was to name and describe the species, report on its occurrence and ecology in Japanese waters, and learn more about the nature of its cyanobacterial symbiont.

MATERIAL AND METHODS

Field observations were made in Japan between 1981 and 1985, but the sponge described here was not noted until 1984. Initially, the primary purpose of this work was to inspect the condition of coral reefs in the Ryukyu Archipelago (between 123°E, 24°30'N and 130°E, 28°20'N) that had been heavily infested by starfish (*Acanthaster planci*) and were located in areas of intensive land development for agriculture, industry, and tourism (MUZIK, 1985; Fig. 1). During the survey, more than 300 snorkel and scuba dives were made to a depth of 40 m. In 1986, sponges were photographed in situ and collected by breaking the coral substrate. Specimens for systematic study were fixed and preserved in 80 % ethanol.

The material used for electron microscopy con-

sisted of 1-cm fragments (substrate with sponge crust) fixed in the field in 1.5 % glutaraldehyde buffered in 0.2 M cacodylate with 0.1 M sodium chloride and 0.4 M sucrose (pH 7.2). The samples were shipped to the National Museum of Natural History in the same medium. After about 10 days, postfixation was carried out on 1-2 mm strips of sponge tissue using 2 % osmium tetroxide in the aforementioned buffer. Sections were stained in saturated (5 %) alcoholic uranyl acetate with 0.25 % lead citrate and viewed and photographed through a Jeol 1200 EX electron microscope at 2,000-30,000 × primary magnifications.

Light microscope observations were made on semithin (1-μm) sections stained in methylene blue or Azure A and on thick sections ground and polished to 50-100 μm sections (RÜTZLER, 1978). Spicule size was estimated in 25 randomly selected tylostyles measured at 100 × magnification for overall length; 10 of those were also examined at 1,000 × magnification to determine the maximum diameters of shaft, neck, and head (knob).

RESULTS

Our study of this material led to a review of the Suberitidae and a redefinition of the role that *Terpios* species play in this family (see RÜTZLER and SMITH, 1993).

1. *Terpios hoshinota*, new species

Diagnosis. — Grayish to blackish encrustations on live or dead reef coral in shallow water near shore. With quadrilobate, often subterminal tylostyle heads. Tylostyles, 244.7 μm × 3.0 μm (length × maximum shaft width); head, 5.6 μm wide (mean of means, all type specimens). Symbiotic with large (5.9-μm mean diameter) intercellular zooecyanellae, which form a substantial amount of the cellular tissue in this organism.

Description. — Extremely thin (typically less than 1 mm thick) encrustations (Fig. 2). In life, the sponge is gray, or dark gray to brownish and black. It is often lighter in color when growing on the upper surface of corals, darker on the underside. Small (3-mm) oscula are usually discernible in the field and are at the center of radiating, superficial exhalant networks (structures known as astrorhizae from fossil imprints in calcareous sponge skeletons; Fig. 2c). Pores are located in the meshes of those vein networks. In preserved specimens, oscula are contracted (closed), and pores measure 50-300 μm. Histological sections show a few large pores (350 μm or larger) covered by membranes that are perforated by 10-30 μm openings. The sponge grows by lateral propagation, extending short fine tendrils across crevices to new substrate (Fig. 2b). The sponge thus advances as a sheet over platelike or massive corals and can make bridges between branches of corals in species such as *Acropora*. After sponge encrustation, all polyps die and the remaining coral skeleton becomes weak and easy to collect.

All spicules of this species are tylostyles. They are arranged in criss-cross fashion throughout the choanosome but become organized into radiating bundles near the ectosomal region, where they end in the form of brushes at the surface (Fig. 3). The tylostyles are pin-shaped and are long and slender, only slightly thickened at midshaft, and have weakly pronounced heads. A typically developed head (tyle) consists of four knobs with axes perpendicular to each other and to the shaft. If the head is subterminal, the blunt end of the shaft forms a fifth knob. The majority of heads, however, are strongly reduced and show indications of malformation or erosion (Fig. 4). Measurements are given in Table 1.

In some specimens (e.g., USNM 43143), fine sand is embedded in the ectosome and is possibly responsible for the gray color variants. Choanocyte chambers seem rare or are obscured by the abundance of cyanobacteria; they are oval and measure 20-

TABLE 1. — Spicule (tylostyle) dimensions for *Terpios hoshinota*. Measurements (in μm) are means ± standard errors, with ranges in parentheses.

Specimen, location	Total length	× Maximum shaft width	Neck width	Head width	Head length
Holotype					
USNM 43144, Japan	251.6±4.8 (180-290)	× 3.5±0.1 (3.0-4.0)	2.7±0.1 (2.0-3.0)	6.1±0.2 (5.5-7.0)	5.2±0.2 (4.5-6.0)
Paratypes					
USNM 43143, Japan	244.8±5.3 (170-280)	× 3.2±0.2 (2.5-4.0)	2.5±0.2 (2.0-3.5)	5.7±0.2 (4.5-7.0)	5.3±0.3 (4.0-7.5)
USNM 33316, Guam	234.4±6.5 (160-280)	× 2.6±0.1 (2.0-3.0)	2.1±0.1 (2.0-2.5)	5.6±0.2 (4.5-6.0)	5.4±0.2 (4.5-6.0)
USNM 33317, Guam	247.9±9.8 (200-290)	× 2.7±0.1 (2.0-3.0)	2.1±0.1 (1.5-2.5)	5.0±0.3 (3.5-6.0)	5.2±0.2 (4.5-6.5)

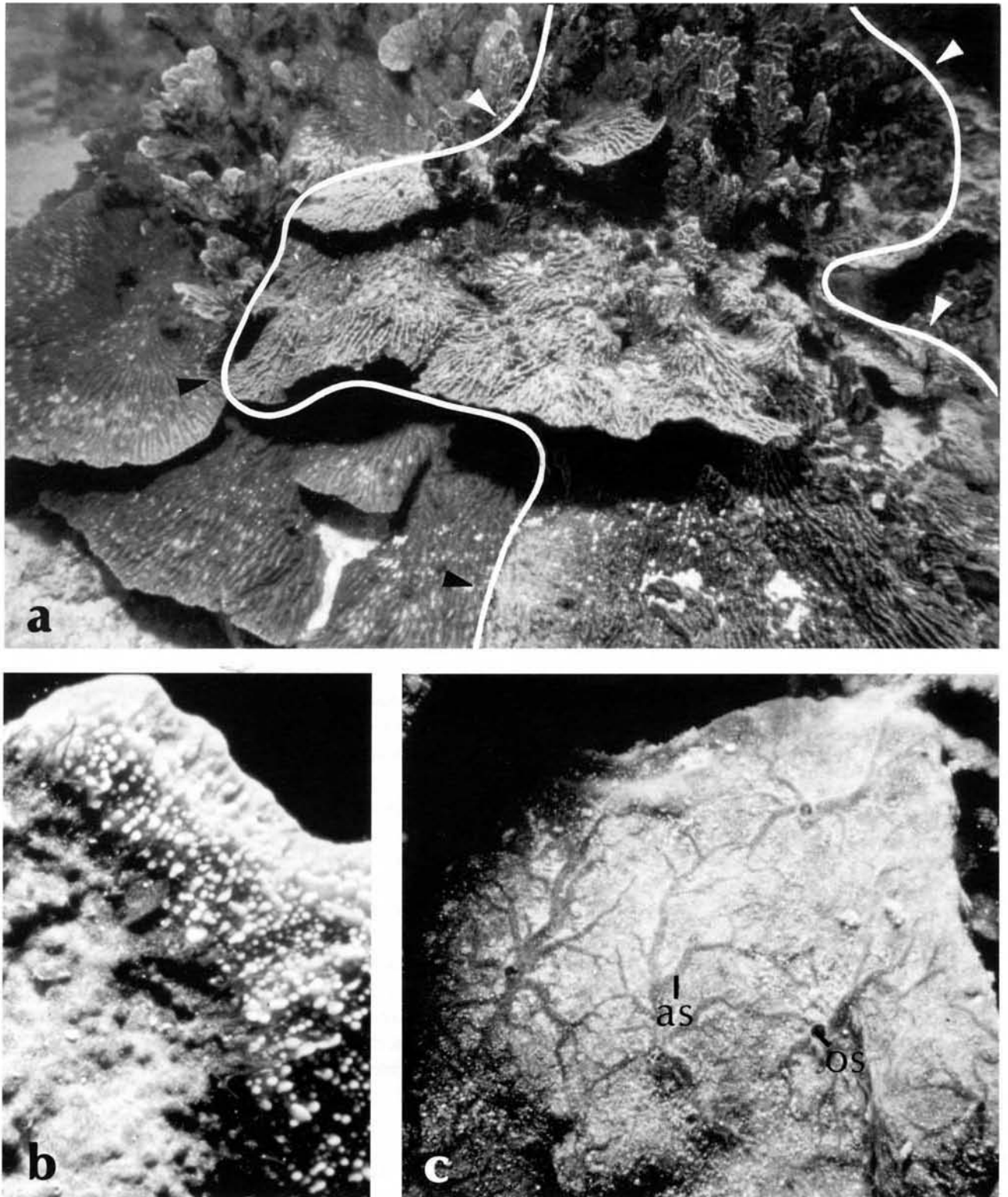


FIG. 2. — *Terpios hoshinota*, views of the sponge *in situ* at Yonama (Tokuno Shima): a, infested reef coral *Merulina ampliata* (Ellis and Solander) still showing coral structure through the thin sponge (arrows delineate sponge-encrusted surface zone; coral outside this zone is alive and healthy); b, transition zone between sponge aggressor (left) and coral victim (*Acropora* sp., right); visible coral is still healthy; c, close-up of sponge crust. (as = astrorhizae, os = osculum; picture width = 1.5 m for a, 40 mm for b, 100 mm for c)

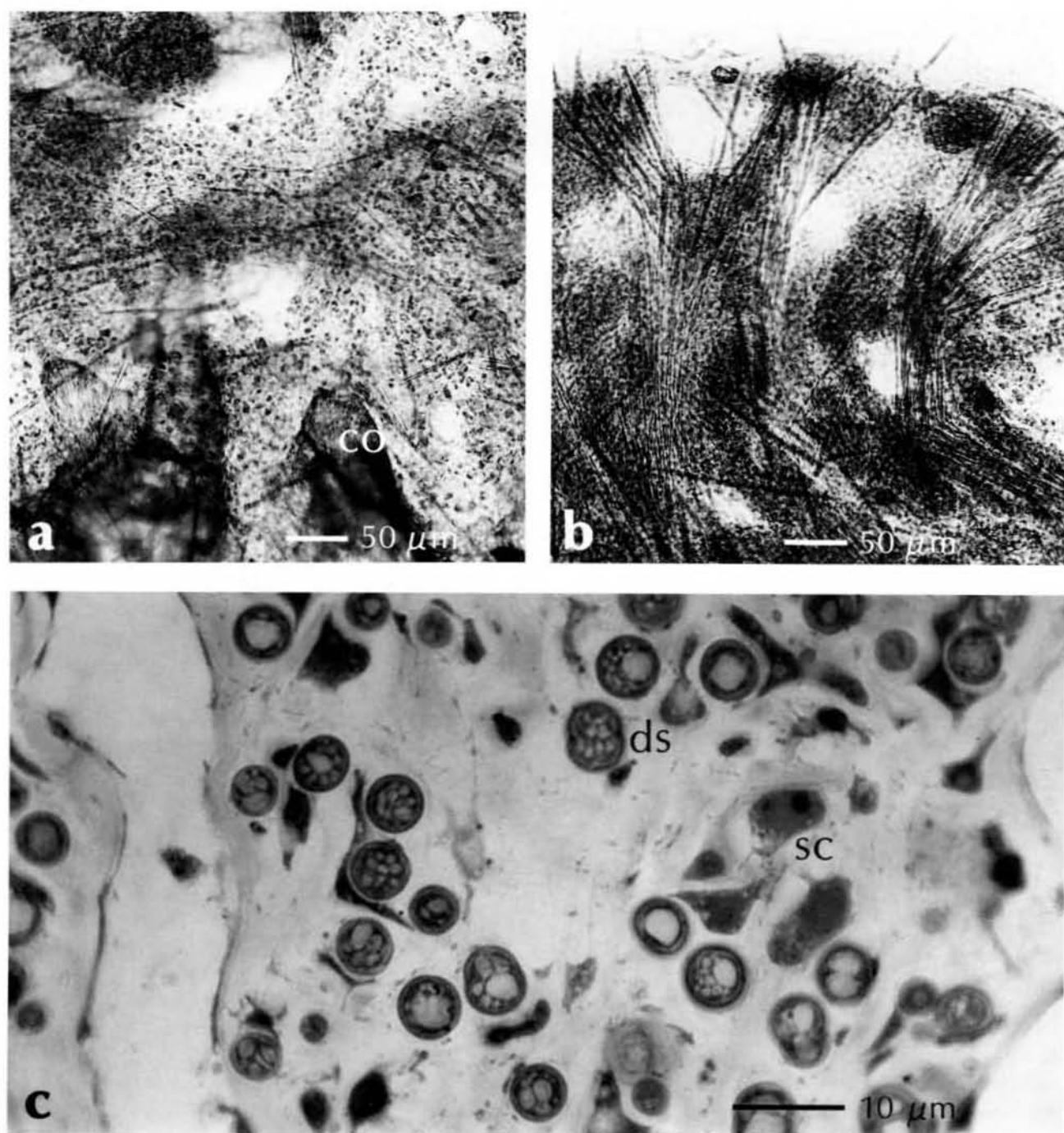


FIG. 3. — *Terpios hoshinota*, light microscopy: a, spicule arrangement in choanosome; b, spicule arrangement in ectosome; c, zoocyanellae in choanosome. (co = coral substrate, ds = dividing stage of zoocyanellae, sc = sponge cells)

36 × 15-20 µm. No reproductive cells were seen in the sections.

Large (6 µm), spherical zoocyanellae occur throughout the tissue, their combined volume approaching or, in places, exceeding that of the sponge cells. In light microscope preparations, the symbionts appear vacuolated, show many dividing stages, and, although closely surrounded by sponge-cell proces-

ses, are never found in intracellular position (Fig. 3c; see detailed description below).

Remarks. — The morphology of *Terpios hoshinota* is similar to that of *T. granulosa* Bergquist, a blue encrusting sponge described from reefs in Hawaii. The principal difference is that *T. hoshinota* is grayish brown, its spicules have characteristically lobed heads, and it has a cyanobacterial symbiont.

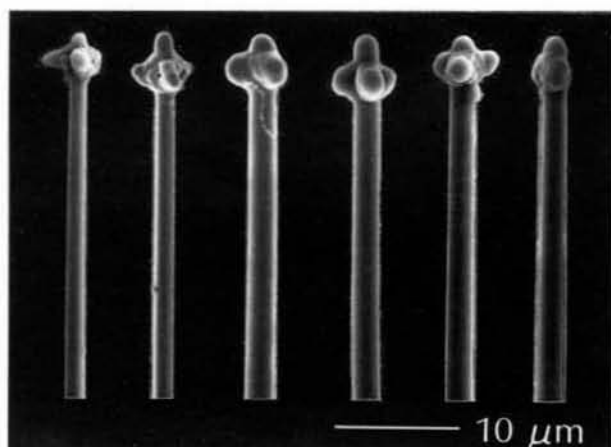


FIG. 4. — *Terpios hoshinota*, scanning electron micrograph of portions of tylostyle head.

Etymology. — Named in memory of our friend and colleague, distinguished sponge systematist Takaharu Hoshino.

Material examined. — The holotype and four paratypes are deposited in the collection of the National Museum of Natural History, Smithsonian Institution (USNM). Holotype: USNM 43144; 23 October 1985; Tokuno Shima, Japan. Paratypes: USNM 43143; 15 October 1985; Tokuno Shima, Japan. USNM 43144; 23 October 1985; Tokuno Shima, Japan. USNM 43145; 6 October 1985; Okinawa, Japan. USNM 33316; 2 October 1984; Cocos Lagoon, Guam. USNM 33317; 2 October 1984; Cocos Lagoon, Guam.

Distribution. — Northwestern Pacific Ocean, from Samoa Islands to Taiwan (PLUCER-ROSARIO, 1987); southern Japan, 2-30 m.

2. The Cyanobacterial Symbiont (Figs. 3c, 5)

Morphology and Relation to Host. — The single cells of the symbiont are perfectly spherical and measure 4.5-7.0 μm (mean: $5.9 \pm 0.2 \mu\text{m}$) in diameter. In histological sections, between 5% and 18% of the cyanobacteria are in different stages of division by binary fission. Cells become elongate, reaching $8 \times 6 \mu\text{m}$ before division. Under the light microscope (stained 1 μm sections), each cell contains clear areas, which may consist of a large central area or, as in most cells, several smaller ones (6-10 or more) (Fig. 3c). The cyanobacteria are extracellular with respect to the sponge-host cells, but some can be seen engulfed by host archeocytes and in different stages of digestion.

Fine structure. — A typical four-layered cell wall, 40-nm thick, lies over the plasmalemma (Fig. 5b, d). There is no indication of a sheath. Undulating photosynthetic membranes run more or less parallel to the cell wall, occupying the outer 15-24% of the cell ra-

dius (Fig. 5a, c). They are characterized by strong vacuolization, with vesicles measuring 15-40 nm in width on average, and ranging from 7 to 120 nm. The nucleoplasm contains large electron-transparent areas; there are 1 to 20 per cross section. They are rounded or angular and the same "vacuoles" already noted under the light microscope. These areas show primarily loosely flocculent material, with a few denser granular inclusions in places. Polyphosphate and polyglucoside granules are the only other noticeable cell inclusions.

3. Ecology and Distribution of *Terpios hoshinota* in the Ryuku Archipelago (Fig. 1)

We first noticed *Terpios hoshinota* at Bise, in northwestern Okinawa Island, in 1984, but it was not widespread and was growing only on dead coral substrate. Massive occurrence and spread of the sponge was first reported to local newspapers on October 14, 1985, by a concerned professional underwater photographer, Yusuke Itagaki, who had found two large areas of "black disease" off Tokuno Shima. Diving routinely on the reefs near shore, he first noted a dramatic increase in the "disease" across what used to be a thriving reef at Yonama, on the west coast of Tokuno Shima. It had spread from one or two coral colonies to numerous species in an area over 100 m long. Suspecting that the problem was due in part to turbidity, which had recently increased at Yonama owing to the construction on and near shore of a large, cement recreation center for tourists, Itagaki also inspected another murky area, Buma, on the east coast of Tokuno Shima. There he found a reef in similar condition: both the living and dead coral were covered by a mysterious dark veneer.

Our own surveys in 1985 confirmed that the "disease" was a sponge infestation and that it had caused extensive reef damage. At Tokuno Shima, this *Terpios* was encrusting and killing (Fig. 2) more than a dozen species of living coral (species of *Porites*, *Montipora*, *Acropora*, *Merulina*, *Goniastrea*, *Lobophyllia*), covering the shells of still-living *Tridacna* sp. and even encrusting a species of fleshy marine alga. Only soft corals (such as species of *Sarcophyton*, and a nephthyid), seemed unaffected—perhaps because of the presence of toxic compounds such as terpenes, widely known to function as chemical defenses in the soft corals (COLL, 1982).

During subsequent scuba and snorkel surveys in search of *Terpios* off Amami Shima, the large island north of Tokuno Shima (October 21-23, 1985), we found only small amounts of the sponge. In Amami,

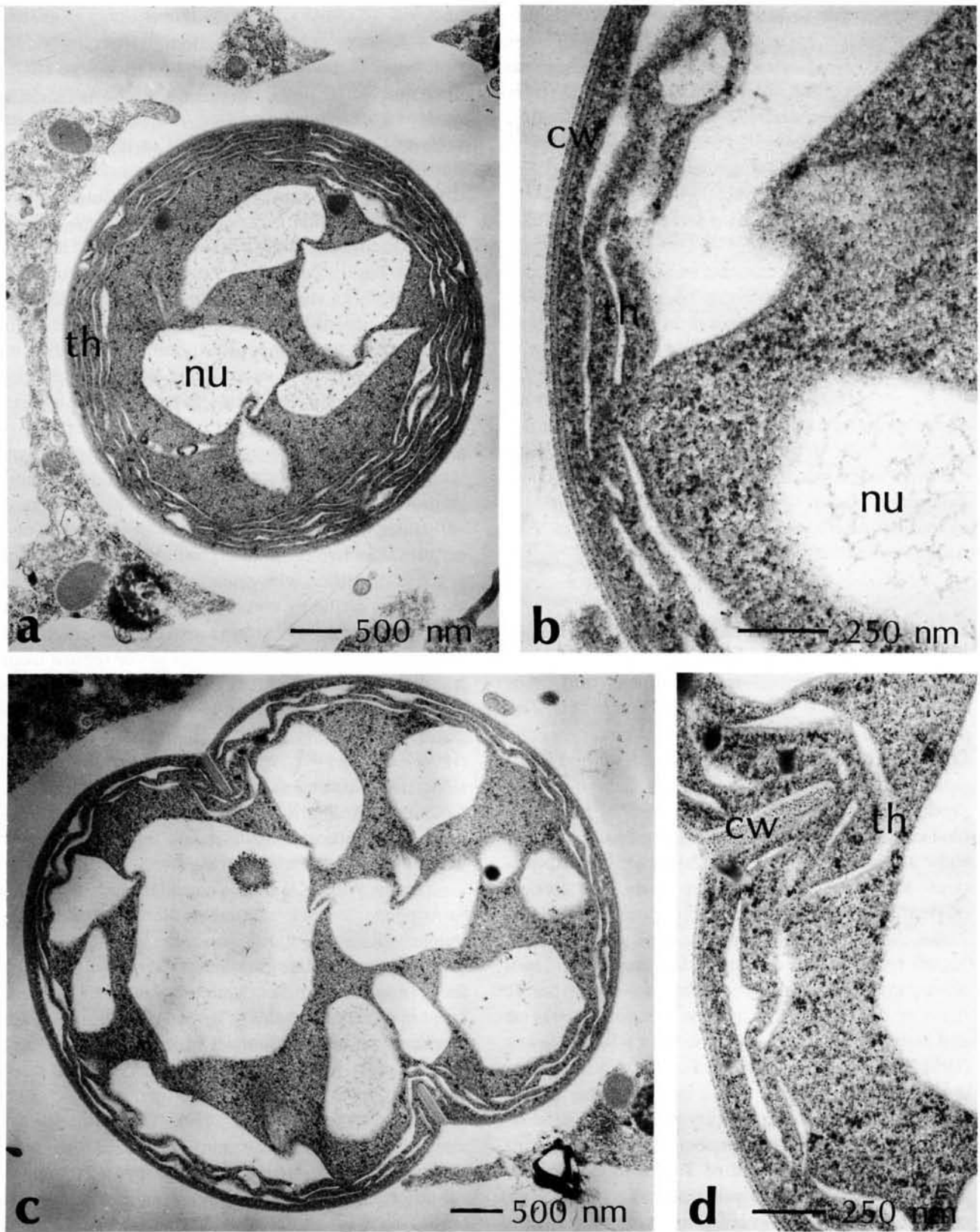


FIG. 5. — *Terpios hoshinota*, transmission electron microscopy of zoocyanelae, *Aphanocapsa raspaigellae*: a, entire bacterial cell next to sponge cell; b, enlarged view of peripheral area; c, dividing stage; d, enlarged view of constricting cell wall and thylakoid in dividing cell. (cw = cell wall, nu = nucleoplasm, th = thylakoid)

the sponge seems to be living only on dead coral substrate in shallow areas of high turbidity (Saneku and Sheribama). No *Terpios* was found in pristine areas with thriving coral reefs near shore (Yoro and Kurosaki), and none on deep (32-40 m) reefs (Tandeshima and Hitotsu Se). November surveys off northwestern Okinawa Island near Toguchi and Bise revealed *Terpios* only on dead coral substrate near shore. Living coral colonies in Toguchi Bay so far remain unaffected. No *Terpios* was found at Naka No Se, an offshore reef with strong currents and heavy wave action several kilometers away from Toguchi (Naka No Se reef had substantial living coral reef cover in August 1985 but soon after became heavily infested with *Acanthaster*).

Recent personal communication with observant divers and photographers in the Ryukyus indicates that *Terpios* is indeed present on near-shore reefs around the Okinawa mainland, on both living and dead coral, and in the Kerama and Yaeyama islands as well. Nowhere yet, however, does it seem to be as widespread as on the Tokuno Shima reefs.

CONCLUSIONS

The unique morphology and ecology of *Terpios hoshinota* makes it easy to separate from other *Terpios* species known from Pacific reef environments. DE LAUBENFELS (1954: 209, fig. 142) described *T. fugax* Duchassaing & Michelotti as forming small patches (the size of a "postage stamp") of rich, dark blue encrustations with tylostyles, the heads of which show some "pentactinal" or "hexactinal" modifications. When we examined both of de Laubenfels's original microscope-slide preparations (USNM 22888, 22951), we found mostly tylostyles with irregularly lumpy heads, and only a few symmetrical modifications with four or five knobs, as is typical for *T. fugax* in the Caribbean, its type location (RÜTZLER and SMITH, 1993). In the same work, DE LAUBENFELS (1954: 210, fig. 143) described *T. aploos* as a massive sponge, ochrous yellow inside and slaty gray at the surface, and as having simple tylostyles with shriveled-looking heads (no knobs) and many styloid modifications. The surface of *T. aploos* is complex lumpy, the interior filled with coarse sand. Another encrusting sponge is *T. granulosa* Bergquist from Hawaii. It forms dark blue, very thin (0.8-1.0 mm) crusts and has tylostyles with terminally flattened heads that show traces of a quadrilobate condition (BERGQUIST, 1967: fig. 5). It also contains filamentous, blue-pigmented (nonphotosynthetic), symbiotic

bacteria (SANTAVY, 1986). These characteristics make *T. granulosa* undistinguishable from the widely distributed *T. fugax* Duchassaing & Michelotti (RÜTZLER and SMITH, 1993).

It is not surprising to find *Terpios hoshinota* on reefs of the Ryukyu Archipelago as it has been reported from many locations in the western Pacific, from American Samoa to Taiwan, including the Philippines and Guam (PLUCER-ROSARIO, 1987). Although the sponge itself was undescribed and its morphology barely known, its ecological characteristics have long been studied in Guam. BRYAN (1973) first described its distribution on the reefs there, its growth rates, and competitive potential, including its ability to overpower live coral. He also suggested that the tissue of victimized corals may provide the sponge with nutrients, which might explain why the sponge is able to expand explosively and infest hundreds of meters of coastline. PLUCER-ROSARIO (1987) has demonstrated, however, that cleaned (air-blasted) coral substrates will support sponge growth at an even faster rate than live coral and concluded that successful space competition with numerous other benthic reef associates, including coral, is primarily due to a fast spreading rate aided by fast asexual propagation and by the ability to bridge coral branches or regrow from fragments. These findings are consistent with those from other successful space competitor among sponges, such as *Cliona lampa* de Laubenfels and *C. caribbaea* Carter (= *C. aprica*; RÜTZLER, 1975), *C. varians* (Duchassaing & Michelotti) (VICENTE, 1978), *Cliona* sp. (similar to *C. varians* but having spirasters instead of anthosigmas; Rützler, unpublished) and *Chondrilla nucula* Schmidt (VICENTE, 1990).

Terpios hoshinota can be considered a "cyanobacteriosponge," which is comparable to a "bacteriosponge" (REISWIG, 1981), meaning species (for instance of Aplousinidae) that harbor large quantities of these (nonphotosynthetic) microorganisms. The symbiont in our sponge belongs to the *Aphanocapsa raspaiellae* type and is identical in its morphology and fine structure to the cyanobacterium described from two Caribbean sponges in the genus *Dictyonella* (= *Ulosa*; RÜTZLER, 1981; 1990). The similarity remained striking even after suboptimal field fixation in the material from Japan. The only apparent structural difference between the organisms is that the Atlantic material shows a very thin sheath (40 nm thick), which is lacking entirely in the Pacific specimens.

Interestingly, most of the successful space competitors mentioned above (except *Cliona lampa*) harbor large quantities of photosynthetic microorga-

nisms. *Chondrilla nucula* is a cyanobacteriosponge like *Terpios hoshinota*, although the symbiont belongs to the small species *Aphanocapsa feldmanni*; *Cliona caribbaea*, *C. varians*, and *Cliona* sp. contain zooxanthellae of two different species (RÜTZLER, 1990). It is likely that the growth potential of these encrusting sponges is considerably enhanced by nutritional benefits derived from the association with photoautotrophs.

ACKNOWLEDGMENTS

We are most grateful to Andrea Blake for sectioning and electron photomicrography and Yusuke Itagaki for the use of some of his underwater photographs. We also thank Pat Condit for preparing the map; Molly K. Ryan and Kathleen P. Smith for assisting with other illustrative work; and Lily Tao for typing.

REFERENCES

- BERGQUIST, P. R. — 1967. Additions to the sponge fauna of the Hawaiian Islands. *Micronesica*, 3: 159-174.
- BRYAN, P. G. — 1973. Growth rate, toxicity and distribution of the encrusting sponge *Terpios* sp. (Hadromerida: Suberitidae) in Guam, Mariana Islands. *Micronesica*, 9: 237-242.
- CHOAT, J. H., D. BARNES, M. A. BOROWITZKA [et al.] (eds.) — 1988. Mini Symposium 2, Crown of Thorns. *Proceedings of the Sixth International Coral Reef Symposium, Townsville, Australia*, 2: 119-188.
- COLL, J. — 1982. Chemical defenses in soft corals (Coelenterata: Octocorallia) of the Great Barrier Reef: a study of comparative toxicities. *Mar. Ecol. Prog. Ser.*, 8: 271-278.
- ENDEAN, R. — 1973. Population explosions of *Acanthaster planci* and associated destruction of hermatypic corals in the Indo-West Pacific region. In: O. A. Jones and R. Endean (eds.), *Biology and Geology of Coral Reefs*, pp. 389-438. Academic Press, New York and London.
- GOMEZ, E.D. — 1988. Status of problems associated with coral reefs in the Pacific Basin. *Coral Reef Newsletter*, 19: 1-10. Pacific Science Association, University of Guam.
- GLYNN, P. — 1973. Aspects of the ecology of coral reefs in the western Atlantic region. In: O. A. Jones and R. Endean (eds.), *Biology and Geology of Coral Reefs*, pp. 271-324. Academic Press, New York and London.
- LAUBENFELS, M. W. DE. — 1954. The sponges of the West-Central Pacific. *Oregon State Monographs, Studies on Zoology*, 7, 306 pp.
- MUZIK, K. — 1985. Dying coral reefs of the Ryukyu Archipelago (Japan). *Proceedings of the Fifth International Coral Reef Congress Tahiti, 1985*, 6: 483-489.
- PLUCER-ROSARIO, G. — 1987. The effect of substratum on the growth of *Terpios*, an encrusting sponge which kills corals. *Coral Reefs*, 5: 197-200.
- REISWIG, H. M. — 1981. Partial carbon and energy budgets of the bacteriosponge *Verongia fistularis* (Porifera: Demospongiae) in Barbados. *Marine Ecology*, 2: 273-293.
- RÜTZLER, K. — 1970. Spatial competition among Porifera: solution by epizoism. *Oecologia*, 5: 85-95.
- 1971. Bredin-Archbold-Smithsonian biological survey of Dominica: burrowing sponges, genus *Siphonodictyon* Bergquist, from the Caribbean. *Smiths. Contrib. Zoology*, 77, 37 pp.
- 1975. The role of burrowing sponges in bioerosion. *Oecologia*, 19: 203-216.
- 1978. Sponges in coral reefs. In: D. R. Stoddart and R. E. Johannes (eds.), *Coral Reefs: Research Methods*, pp. 299-313. Monographs on Oceanographic Methodology 5. Unesco.
- 1981. An unusual bluegreen alga symbiotic with two new species of *Ulosa* (Porifera: Hymenacionidae) from Carrie Bow Cay, Belize. *Marine Ecology*, 2: 35-50.
- 1990. Associations between Caribbean sponges and photosynthetic organisms. In: K. Rützler (ed.), *New Perspectives in Sponge Biology*, pp. 455-466. Smithsonian Institution Press, Washington, D.C.
- RÜTZLER, K. and K. P. SMITH. — 1993. The genus *Terpios* (Suberitidae) and new species in the "lobiceps" complex. *Sci. Mar.* 57(4):108-120.
- SANTAVY, D.L. — 1986. A blue-pigmented bacterium symbiotic with *Terpios granulosa*, a coral reef sponge. *Hawaii Inst. Mar. Biol. Tech. Rep.*, 17: 380-393.
- SUCHANEK, T. H., R. C. CARPENTER, J. D. WITMAN and C. D. HARVELL. — 1983. Sponges as important space competitors in deep Caribbean coral reef communities. In: M. L. Reaka (ed.), *The Ecology of Deep and Shallow Coral Reefs*, pp. 55-60. Symposia Series for Undersea Research, NOAA's Undersea Research Program I(1).
- VICENTE, V. P. — 1978. An Ecological evaluation of the West Indian demosponge *Anthosigmella varians* (Hadromerida: Sphaerostrellidae). *Bull. Mar. Sci.*, 28: 771-777.
- 1990. Overgrowth activity by the encrusting sponge *Chondrilla nucula* on a coral reef in Puerto Rico. In: K. Rützler (ed.), *New Perspectives in Sponge Biology*, pp. 436-442. Smithsonian Institution Press, Washington, D.C.
- YAMAGUCHI, M. — 1987. Occurrences and persistency of *Acanthaster planci* pseudopopulation in relation to the oceanographic conditions along the Pacific coast of Japan. *Galaxea*, 6: 277-288.

The genus *Terpios* (Suberitidae) and new species in the «*Lobiceps*» complex*

KLAUS RÜTZLER and KATHLEEN P. SMITH

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

SUMMARY: The genus *Terpios*, first described from the Atlantic Ocean (West Indies) almost 130 years ago, is redefined on the basis of structural studies of tylostyles and data on procaryotic symbionts. Its relation to similar genera in the family Suberitidae is reviewed by comparing new findings with traditionally used characters, such as body shape, skeleton arrangement, and spicule size. Two new species, *T. manglaris* and *T. belindae*, are described from shallow-water habitats in the Caribbean Sea. They resemble *Suberites lobiceps* Schmidt, a poorly known sponge from Florida that has not been found since its first description in 1870.

Key words: Porifera, bacteria, symbiosis, *Terpios*, new species, Caribbean.

INTRODUCTION

In their pioneering study of Caribbean sponges, DUCHASSAING and MICHELOTTI (1864:97) introduced the genus *Terpios* for thinly encrusting (membrani-form) sponges in which the spicules are arranged haphazardly except for some organization into fan-shaped bundles. They described nine species in four live-color groups. Their diagnosis may have led VOSMAER (1887:359) to place *T. fugax* in this genus and DE LAUBENFELS (1936a:152) to select it as the genotype. *T. fugax* not only conforms to the original definition but is the only encrusting species of the remaining three of the original nine that are still recognizable (VAN SOEST, *et al.*, 1983:204). The other two are *T. aurantiaca*, definitely a massive species, and *T. janiae*, which is a *Dysidea*.

Because of its shape and striking color, *Terpios fugax* is very distinctive, and the genus *Terpios* has remained valid for almost 130 years, although it was not universally adopted. VON LENDENFELD (1897:132), for example, who found the type species in the Adriatic, redescribed it under the name *Suberites fugax*. However, he failed to recognize the taxonomic value of spicule-size classes, as they occur in *Suberites* proper, and of the peculiar shape of *Terpios* tylostyles. The same was true of his colleague TOPSENT (1900:192f), who argued that *Terpios* is distinguished from *Suberites* by encrusting (rather than massive) habit, gelatin-soft consistency, a smooth surface without spicule reinforcement of the ectosome, and regular and loose skeleton structure. TOPSENT (1900:194) pointed out that the tylostyles of *T. fugax* are non-fusiform, as the shaft progressively thins to a sharp point, and their heads are quite variable, from globular with tapered top to depressed, some being tri-

* Received February 10, 1993. Accepted June 2, 1993.

lobed and some having annular swellings in the neck region. These observations were expanded upon by DE LAUBENFELS (1936a:152), who claimed that *Terpios* is "characterized by the quadrilobate form of the heads of spicules that otherwise would be regarded as tylostyles." Subsequently, DE LAUBENFELS (1950:103) was struck by the unique morphology of *Terpios* tylostyles. In particular, he considered the relative size of the head distinct among the suberitids, for it was "nearly double or quite double the diameter of the spicule shaft." He also observed that "in young sponges" the head is distinctly lobate, "with indications that the lateral growth of this head has (primitively) arisen by polyactinal branching. It may represent a pentactinal spicule with four clads in one plane, and a very long rhabd." His interpretation of *Terpios* appears to have been biased by his earlier examinations of encrusting specimens with distinctly lobed heads because the ensuing description and discussion of "*T. fugax*" does not mention these characteristics at all. De Laubenfels was, in fact, describing *T. aurantiaca* DUCHASSAING and Michelotti, not the massive growth form or stage of *T. fugax*, as he presumed.

It is not uncommon for the tylostyles of crustose sponges to have conspicuously lobed heads. This feature is seldom mentioned in the literature because it is usually seen in small, fragmentary, or isolated samples. One exception is SCHMIDT's description and illustration (1870:47; pl. 5, fig. 5) of an unusual sponge crust from Florida, which he named *Suberites lobiceps*. A specimen with similar spicules from the Gulf of Mexico (TOPSENT, 1920:30) was identified (but not described) by SCHMIDT 1880:77, but this species has not been found or discussed since these early reports and remains obscure; DE LAUBENFELS (1950:107) dropped it in synonymy with *T. fugax*.

The question of validity of the genus *Terpios* was reopened recently in a discussion of strongly competitive Pacific reef species of *Terpios* with distinctly lobed tylostyle heads (RÜTZLER and MUZIK, 1993). The question could not be addressed without reviewing *T. fugax*, the genotype, and the status of *Suberites lobiceps* and other closely related species with unusual tylostyle heads, including the two new ones from the Caribbean described in this report.

MATERIAL AND METHODS

Sponges were observed and collected by diving and when possible were studied and photographed

alive and with the help of phase-contrast microscopy. Museum material was fixed in 10 % formalin-seawater and preserved in 80 % ethanol after 24 h. It was deposited in the collection of the National Museum of Natural History, Smithsonian Institution (USNM).

The skeletal structure was examined in sections 100 μm thick that were prepared by grinding and polishing sponge tissue samples embedded with epoxy resin (as described by RÜTZLER, 1978). Spicules were isolated and cleaned by boiling in concentrated nitric acid and washing in demineralized water and absolute alcohol. Measurements are based on 25 tylostyles selected at random. To reveal internal structure and enhance the axial canal, some spicule samples were concentrated by centrifugation in epoxy resin, ground and polished (Carborundum paper and aluminum oxide, to 0.3 μm), and etched by exposure to dilute hydrofluoric acid (6.5 % in distilled water) for 15 sec. Scanning electron micrographs (SEM) were made of spicules and etched sections using a Cambridge Stereoscan 100 microscope at 1,000-3,000 \times magnification.

For transmission electron microscopy (TEM), material was fixed in 3.5% glutaraldehyde in 0.1 M phosphate buffer with the addition 0.45 M sucrose (90 min at 29° C), postfixed in 1 % osmic acid in the same buffer mixture (60 min at 4° C). Sections were stained in saturated (5 %) alcoholic uranyl acetate with 0.25 % lead citrate and viewed and photographed through a Jeol 1200 EX electron microscope (2,000-12,000 \times primary magnification). Light microscope observations of histology and skeleton structure were made on the same material sectioned 1 μm thick, or ground and polished to a thickness of 50 μm , both stained by methylene blue.

RESULTS

1. Superspecific Characterizations

The following diagnoses were compiled from various sources, primarily TOPSENT (1900), DE LAUBENFELS (1936a), and LÉVI (1973), and supplemented by our own observations. Comments on and descriptions of examples for different genera are based primarily on tropical western Atlantic species that are the subject of our ongoing studies. Genera having some unique body plan (such as *Poterion*, *Rhizaxinella*) or accessory spicules (like *Ficulina*, *Protosuberites*) are not relevant to this review and are therefore omitted.

a. Family Suberitidae Schmidt

Diagnosis. — Hadromerida of massive or encrusting habit, without cortex, with a spiculation of tylostyles in typically nonradiating arrangement, generally lacking microscleres. In massive forms, spicule orientation in the choanosome either confused or in tracts ascending from substratum to sponge surface. In thinly encrusting species, spicule orientation either parallel or perpendicular to the substratum. Tylostyle modifications show up in the shape and position of the head, which can be lobate, pear shaped, drop shaped, or subterminal; it can also be inconspicuous or missing in part of the spicule complement (spicules appearing as styles or oxeas). Microscleres are rare but if they occur they are never asteroid or spirasteroid. Genera in the family are distinguished by shape of the adult sponge, by skeleton structure, and by spicule orientation, type, and distribution.

Comments. — R. W. M. van Soest (Amsterdam) has recently suggested (unpublished) that Suberitidae should be placed within the family Polymastiidae Gray, which contains hadromerids with two or more categories of tylostyles and with vents (oscula, pori) located on erect papillae. This move, however, could lead to excessive lumping of sponges with various (even asteroid) microscleres, for example, and to the collapse of a useful (though not perfect) classification.

b. Genus *Suberites* Nardo

Diagnosis. — Massive, compact Suberitidae, with interior skeleton of densely packed tylostyles in confusion, peripheral choanosomal skeleton in closely packed strands, and dense ectosomal phalanx of tylostyles oriented perpendicularly to the sponge surface; ectosomal tylostyles distinctly smaller than choanosomal ones. Type species: *Alcyonium domuncula* Olivi.

Comments. — We examined a specimen from an area close to the type locality in the Adriatic (*Suberites domuncula*, USNM 23956, Rovinj, Croatia) and found that the length of small surface tylostyles averaged 53% of the length of choanosomal tylostyles. Measurements were $175.0 \mu\text{m} \pm 3.16$ s.e. for small spicules, $328.0 \mu\text{m} \pm 10.7$ s.e. for large ones. Tyles are slightly subterminal (drop shaped) but consistently well formed, except for rare annular swelling in the tylostyle neck region.

c. Genus *Pseudosuberites* Topsent

Diagnosis. — Massive Suberitidae structured like

Suberites but with a smooth surface due to ectosomal skeleton of tangential (parallel to sponge surface) tylostyles. Type species: *Hymeniacidon hyalina* Ridley and Dendy.

Comments. — *Pseudosuberites melanos* de Laubenfels is a Caribbean representative of this genus. We examined the holotype from Culebra Island (DE LAUBENFELS, 1934:9; USNM 22360) and a specimen from Dry Tortugas (DE LAUBENFELS 1936a:149; USNM 22431), both of which conform with the diagnosis of the genus.

d. Genus *Prosuberites* Topsent

Diagnosis. — Encrusting Suberitidae with hispid surface, with a phalanx of single, long, tylostyles oriented perpendicularly to the substrate. Type species: *Prosuberites longispina* Topsent.

Comments. — For reasons that were not entirely clear, DE LAUBENFELS (1950:106) expanded this diagnosis to include thicker species, "like those of *Terpios*" but without the proportionally large and "peculiar lobate" tylostyle heads.

Four species have been reported from the western Atlantic: *Prosuberites epiphytum* (Lamarck), *P. microsclerus* de Laubenfels, *P. geracei* van Soest and Sass, and *P. scarlatum* Alcolado. Only two correspond to the generic definition: *P. epiphytum*, redescribed in detail by TOPSENT (1900:179) and *P. geracei*, discussed by VAN SOEST and SASS (1981:336), who also commented on problems with its generic allocation. We examined the holotype of *P. microsclerus* from the Dry Tortugas (USNM 22493), which has a thin crust but has the skeletal structure of *Terpios* and wrinkled, subterminal tylostyle heads; it was transferred to *T. fugax* by DE LAUBENFELS (1950:106). We also examined a schizotype of *P. scarlatum* and could confirm the author's description (ALCOLADO, 1984:13) of a thinly encrusting sponge with spicule tracts (rather than single erect tylostyles). Because most spicules are subtylostyles with elongate heads, including many "shadow" forms (poorly silicified, with widened axial canal), we believe this species is not a suberitid at all but a mycalid with reduced microsclere skeleton; there is not enough material in this sample to determine which of the few evident microscleres may be proper to the species.

e. Genus *Laxosuberites* Topsent

Diagnosis. — Encrusting or massive Suberitidae, with ascending, rarely interconnected strands of tylostyles forming the skeleton, without special ectoso-

mal skeleton. Type species: *Laxosuberites rugosus* Topsent (non *Suberites rugosus* Schmidt).

Comments. — When TOPSENT (1896:126) established the genus *Laxosuberites*, he had *Suberites rugosus* Schmidt in mind as the type species. Years later, however, during a revision of Schmidt's species from Algeria, TOPSENT (1938:20) discovered that Schmidt's sponge was in fact *Hymeniacion sanguinea* (Johnston), belonging to the order Halichondrida, and named the sponge that he had described in detail from Banyuls, France (TOPSENT, 1900:185), *Laxosuberites rugosus* Topsent.

For comparison, we examined material from the western Atlantic (Florida), identified and described by DE LAUBENFELS (1936a:148) as *Laxosuberites caerulea* (Carter). Specimen USNM 22488 appears as a thick, intensively blue (in alcohol) cushion, with cavernous endosome and dense ectosome, and with a spiculation of styles. It agrees with *Hymeniacion caerulea* Pulitzer-Finali, not with *Terpios caerulea* Carter (which is a synonym of *Terpios fugax*), with which it only shares the type of symbiont, a blue-pigmented bacterium (see below). Specimen USNM 23357 is tan rather than blue and has the structure and spiculation of *Terpios* (= *Suberites*) *aurantiaca*.

We also studied the type material of *Laxosuberites zeteki* DE LAUBENFELS (1936b:450), which was later transferred to the genus *Terpios* by the same author (DE LAUBENFELS 1950:106). The holotype, USNM 22212 from the Pacific coast of Panama (Balboa), has the structure and spicules of a *Suberites*, with ectosomal brushes of a second, smaller category of tylostyles. Spicules are all robust and well formed, with tyles slightly subterminal and thus pointed (drop shaped) at the base. The tylostyles average $700 \times 20 \mu\text{m}$ in the larger class, $150 \times 7.5 \mu\text{m}$ in the smaller

one. The paratype, USNM 22227 from the Atlantic coast of Panama (Fort Randolph), is not conspecific but a massive stage of *Cliona* (with zooxanthellae as symbionts, close to *C. varians* [Duchassaing and Michelotti]), but with long-spined spirasters rather than anthosigmas).

It appears that none of the western Atlantic suberitids assigned to *Laxosuberites* qualify for this genus.

f. Genus *Terpios* Duchassaing and Michelotti

Diagnosis. — Thinly encrusting Suberitidae, with tylostyles arranged in strands traversing the choanosome and protruding brushlike through the ectosome; loose tylostyles in confusion between strands; spicules in one size class or with large size range, smallest sizes predominantly in surface brushes; tylostyles with irregularly shaped head-wrinkled, lumpy, constricted, flattened, or lobed-due to swelling or branching of axial filament; commonly associated with symbiotic bacteria or cyanobacteria. Type species: *Terpios fugax* Duchassaing and Michelotti.

Comments. — The above diagnosis is supported by the examination of several specimens of the type species, *Terpios fugax*, from the Caribbean and Mediterranean seas and of the two new species, *T. manglaris* and *T. belindae*, to be described below. In contrast, other material studied belongs to *T.* (= *Suberites*) *aurantiaca* (discussed below) and to *Laxosuberites zeteki* (see comments under *Laxosuberites* above).

2. The Status of Caribbean Species of *Terpios*

a. *Terpios fugax* Duchassaing and Michelotti (Figs. 1, 9; Table 1)

TABLE 1. — Spicule (tylostyle) dimensions for selected species of Caribbean *Terpios*. Measurements (in μm) are means \pm standard errors, with ranges in parentheses.

Specimen, location	Total length	\times Max. shaft width	Neck width	Head width	Head length
<i>Terpios fugax</i>					
USNM 31624, Puerto Rico	267.6 \pm 11.5 (150-340)	\times 3.1 \pm 0.1 (2.5-3.5)	2.7 \pm 0.1 (2.0-3.0)	5.6 \pm 0.2 (5.0-6.5)	4.8 \pm 0.2 (4.0-5.5)
USNM 43146, Carrie Bow Cay, Belize	363.2 \pm 15.6 (220-460)	\times 4.2 \pm 0.1 (3.5-5.0)	3.8 \pm 0.2 (3.0-4.5)	6.7 \pm 0.2 (6.0-8.0)	5.6 \pm 0.1 (5.0-6.0)
<i>Terpios manglaris</i>					
USNM 43150, Man-O-War Cay, Belize	305.6 \pm 9.9 (200-450)	\times 3.2 \pm 0.1 (2.5-3.5)	2.9 \pm 0.2 (2.5-3.5)	6.1 \pm 0.3 (4.5- 7.5)	3.9 \pm 0.2 (3.0-5.0)
USNM 43151, Twin Cays, Belize	249.6 \pm 7.5 (140-300)	\times 2.8 \pm 0.1 (2.5-3.0)	2.6 \pm 0.1 (2.0-3.0)	5.1 \pm 0.1 (4.5- 5.5)	3.4 \pm 0.2 (2.5-4.5)
USNM 43161, Twin Cays, Belize	330.8 \pm 11.5 (210-410)	\times 4.2 \pm 0.2 (3.5-5.5)	3.9 \pm 0.2 (3.5-5.0)	6.7 \pm 0.3 (5.0- 7.5)	4.2 \pm 0.2 (3.5-5.0)
USNM 43162, Pelican Cays, Belize	376.0 \pm 12.5 (240-460)	\times 5.7 \pm 0.3 (4.0-7.0)	5.3 \pm 0.3 (4.0-6.5)	8.8 \pm 0.4 (7.0-10.0)	5.5 \pm 0.3 (4.0-7.0)
<i>Terpios belindae</i>					
USNM 43147, Tobago	320.0 \pm 13.9 (170-390)	\times 5.9 \pm 0.5 (3.5-7.5)	4.7 \pm 0.4 (3.0-6.0)	9.0 \pm 0.5 (6.0-11.0)	4.9 \pm 0.3 (3.0-6.5)
USNM 43148, Tobago	347.9 \pm 14.5 (190-440)	\times 5.5 \pm 0.3 (4.0-6.5)	4.5 \pm 0.3 (3.0-5.5)	8.4 \pm 0.6 (5.0-11.0)	4.8 \pm 0.3 (3.5-6.0)
USNM 43149, Gulf of Mexico	311.2 \pm 15.5 (140-430)	\times 7.1 \pm 0.6 (3.0-9.0)	5.9 \pm 0.5 (2.5-8.0)	10.3 \pm 0.5 (7.0-12.5)	6.2 \pm 0.4 (3.5-8.0)

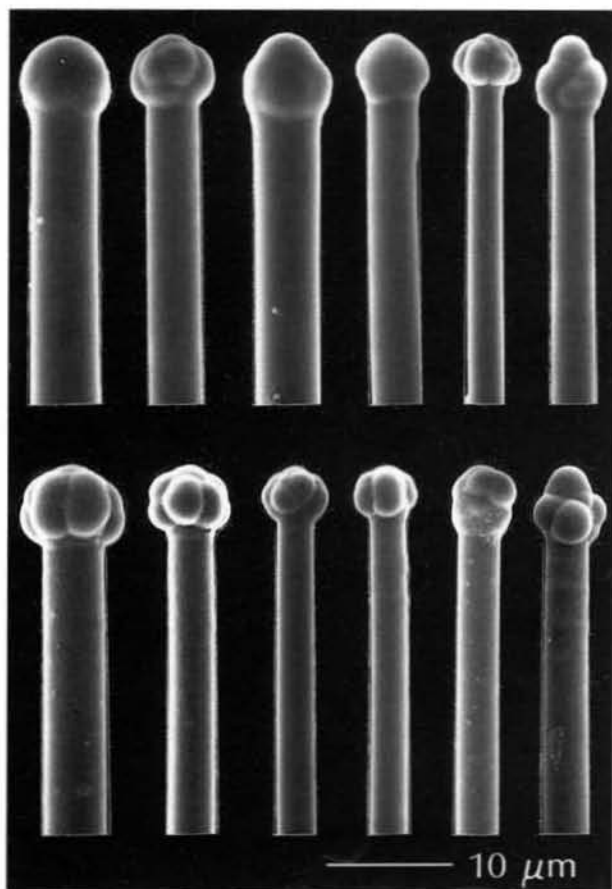


FIG. 1. — *Terpios fugax*, tylostyle heads (SEM) of two specimens: top row, from Puerto Rico (USNM 31624); bottom row, from Belize (USNM 43146).

Diagnosis. — Small, ultramarine to copper-green crusts on shaded parts of shallow reef coral. With simple, rarely branched spicule fibers radiating from substrate to surface. With one size class tylostyles averaging $315 \times 3.7 \mu\text{m}$ (length \times shaft diameter); with depressed (terminally flattened) tylostyle heads, $3.3 \times 5.3 \mu\text{m}$ (width \times length), gently lobed (4-10 or more projections per tyle) due to branching of the axial filament. With filamentous, blue-pigmented bacteria (to be described below) as symbionts responsible for the conspicuous color.

Comments. — CARTER (1882:355) described *Terpios caerulea* from the south of England as being "charged with innumerable short parasitic oscillarian filaments" that he named *Hypheothrix caerulea*. This sponge was correctly synonymized with *T. fugax* (VON LENDENFELD, 1887:132). However, the detailed discussion by DE LAUBENFELS (1950:103) of *T. fugax* from Bermuda actually applies to *T. aurantiaca* (see comments below, under *Suberites*).

Material Examined. — Lectotype in the Natural History Museum, London (BMNH 1928:11.12.11, spicule slide), from St. Thomas, Virgin Islands. USNM 31624; collected 11 April 1967; base of coral *Porites porites* (Pallas), 0-1 m; Laurel Cay reef, Puerto Rico. USNM 43146; collected 31 January 1986; underside of coral rubble, 0.5 m; reef flat, Carrie Bow Cay, Belize. USNM 32068; collected 1961; on rock, 1 m; Rovinj, Croatia.

b. *Terpios lobiceps* (Schmidt)

Comments. — This species, first described by SCHMIDT (1870:47) as *Suberites lobiceps* and transferred to *Terpios* (and synonymized with *T. fugax*) by DE LAUBENFELS (1950:107) is considered unrecognizable (see further comments under *T. belindae* below).

c. *Terpios manglaris*, new species (Figs. 2-4; Table 1)

Diagnosis. — Cobalt blue encrustation on mangrove roots. With quadrilobate tylostyle heads. Tylostyles, $315.5 \times 4.0 \mu\text{m}$ (length \times maximum shaft width); head, $6.7 \mu\text{m}$ wide (mean of means, all type specimens). Symbiotic with filamentous, multicellular, blue-pigmented bacteria.

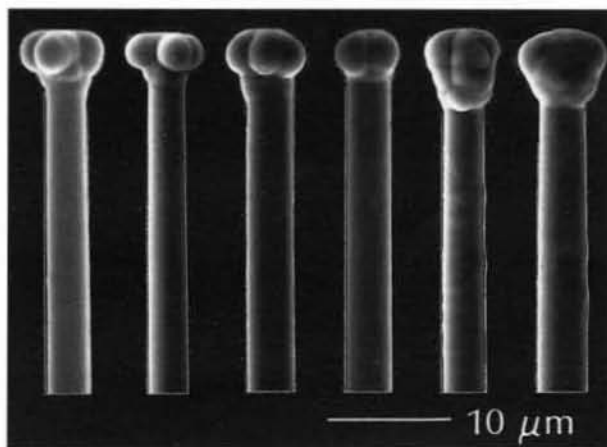


FIG. 2. — *Terpios manglaris*, tylostyle heads (SEM) of holotype (USNM 43150).

Description of the Sponge. — The holotype is an encrustation, less than 1 mm thick, that covered an area of about $7 \times 6 \text{ cm}$ around a red mangrove stilt root. In life, the color was cobalt blue, fading to green in some areas of the crust. There are superficial exhalant canal nets (astrorhizae) with 1 mm (in preserved state) oscula in the center of each; pores are 80-250 μm in diameter.

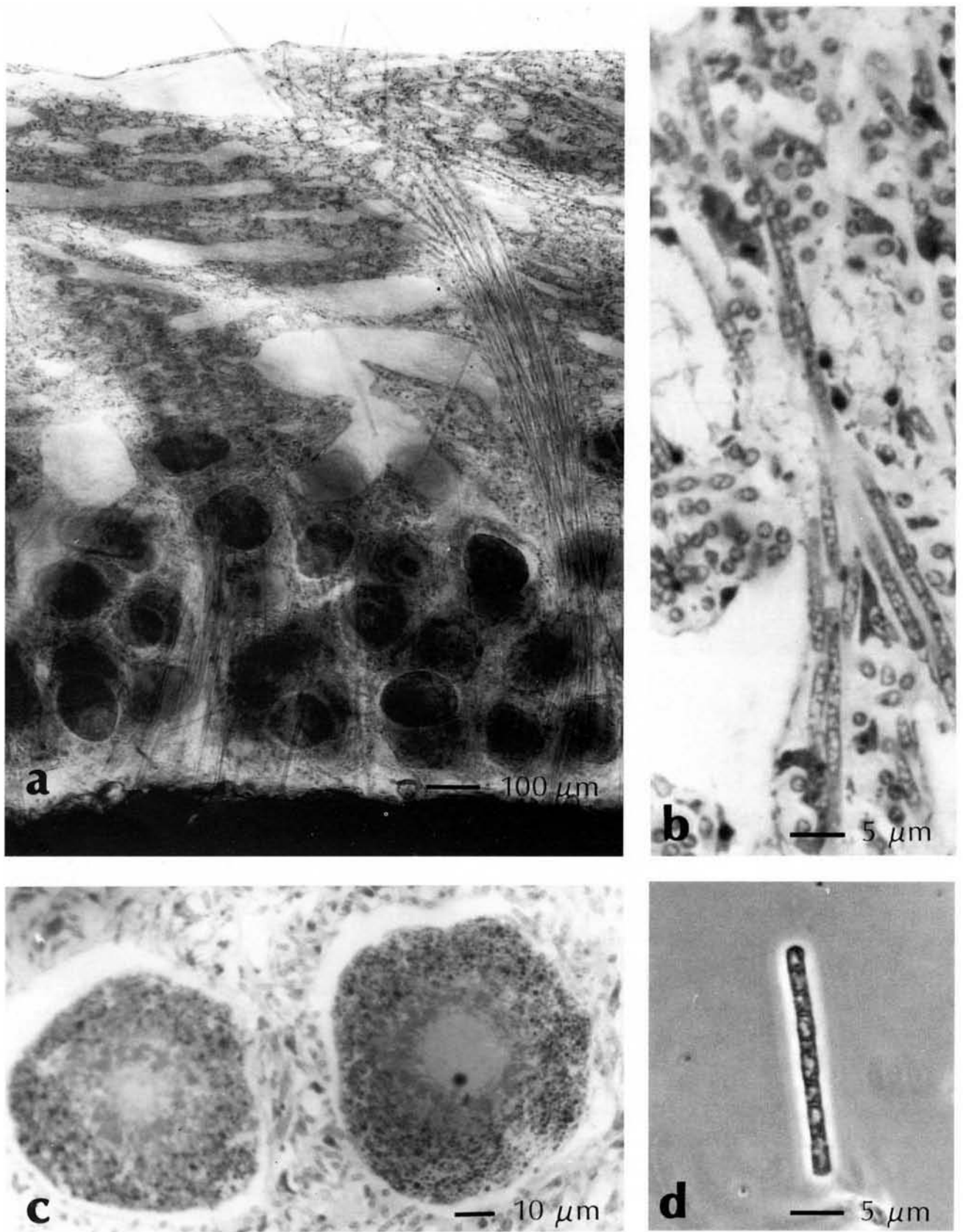


FIG. 3. — *Terpios manglaris*, tissue preparations (light microscopy): a, section showing substrate with cluster of oocytes and spicule strands ascending to surface; b, choanosome filled with filamentous bacteria (in longitudinal and cross sections); c, two oocytes; d, isolated bacterial trichome.

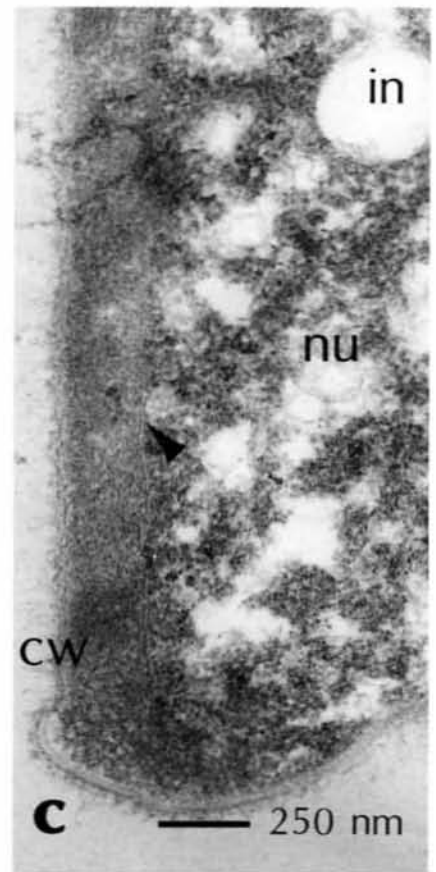
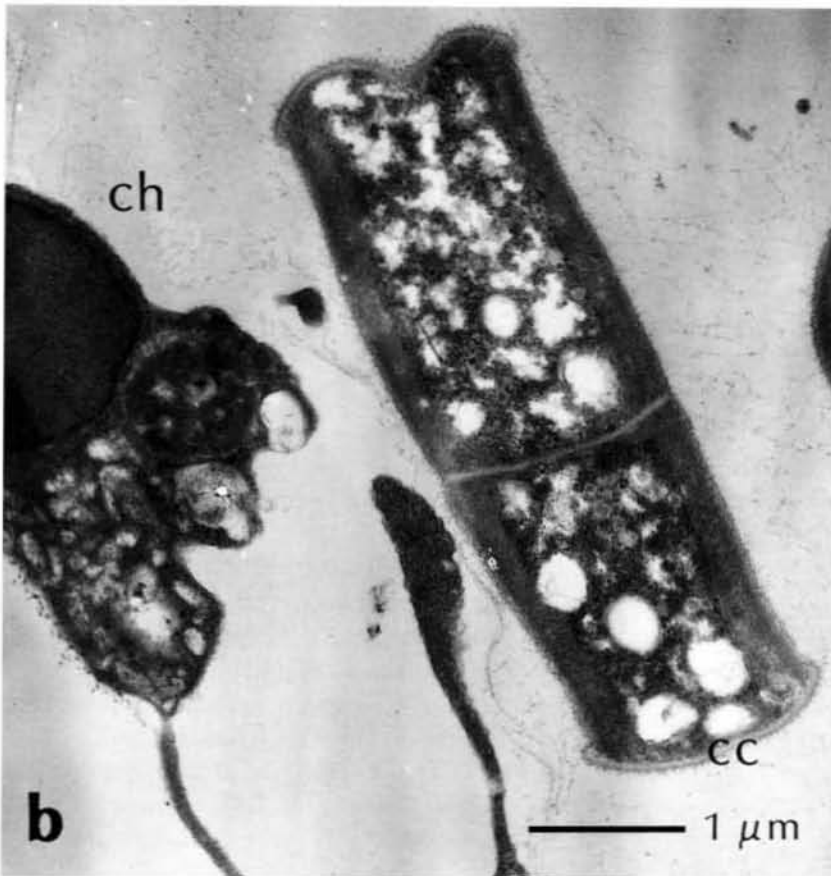
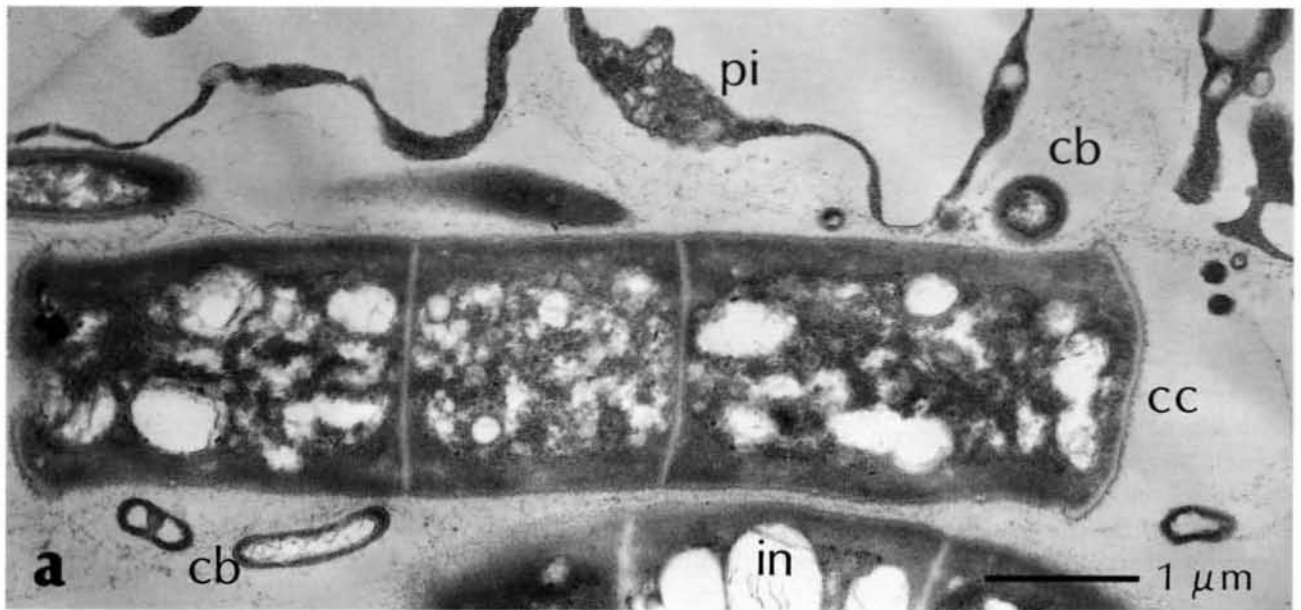


FIG. 4. — *Terpios manglaris*, symbiont (TEM): a, 3-cell trichome along a pinacocyte; b, 2-cell trichome next to choanocyte; c, enlarged portion of end cell (arrow points to cytoplasmic membrane). (cb = coccoid bacteria, cc = cell cap of terminal cell, ch = choanocyte, cw = cell wall, in = inclusion, nu = nucleoplasm, pi = pinacocyte).

Spicules are pin-shaped, straight, only slightly thinner in the neck region; dimensions are given in Table 1; they are arranged as specified in the generic diagnosis (Fig. 3a). Heads are flattened at the top, never subterminal; most display four distinct bulbous projections or lobes (Fig. 2). Malformations include extra lobes and annular swellings at the neck.

Tissue sections show numerous oocytes densely clustered at the base of the sponge body (Fig. 3a,c). The large, ovoid, nucleolate egg cells measure $73 \times 59 \mu\text{m}$ (mean diameters), choanocyte chambers average $20 \times 12 \mu\text{m}$. The entire tissue is charged with filamentous bacteria (Fig. 3b,d).

Description of the Symbiont. — The extracellular bacterial symbionts are responsible for the cobalt blue color of the sponge. The water-soluble pigment (stable in ethanol) is not restricted to the bacteria but is also incorporated into sponge cells, as demonstrated by the oocytes, which are of the same blue but free of microorganisms. Bacterial filaments are difficult to isolate without breaking. A typical trichome of 10 cells measures about $20 \mu\text{m}$ in length, $1.5 \mu\text{m}$ in diameter. Two to 15-cell trichomes were observed. The bacteria are Gram negative and show refractile blue inclusions and squared-off end cells under phase contrast illumination (Fig. 3d).

Electron micrographs (Fig. 4) depict structural details of the symbionts, particularly the peculiar end-cell caps, the areas of inclusions, and the structure of the cell wall.

Comments. — This species resembles *Terpios fugax*, particularly because it harbors the same kind of bacterial symbiont that lends it the same conspicuous color. It can be easily distinguished by the distinctively lobate tylostyle heads. It also differs in its habitat (mangrove lagoons) and has a thicker and more expansive growth pattern.

Etymology. — Named for the sponge's habitat, roots of red mangrove, *Rhizophora mangle* L.

Material Examined. — Holotype: USNM 43150; collected 16 May 1988; from mangrove root, 0.5-m depth; Man of War Cay, Belize. Paratypes: USNM 43151 (spicule slide only); collected 4 May 1987; from acrylic settling plate between two mangrove roots, 1-m depth; Twin Cays, Belize. USNM 43161; collected 9 August, 1993; from mangrove root, 0.5-m depth; Sponge Haven, Twin Cays, Belize. USNM 43162; collected 18 August, 1993; from mangrove root, 0.5-m depth; unnamed cay, part of Pelican Cays complex, $16^{\circ}39.8'N$; $88^{\circ}11.5'W$, Belize.

Distribution. — Shallow lagoons with mangroves, Central American Caribbean (Belize).

d. *Terpios belindae*, new species (Figs. 5, 6, 9; Table 1)

Diagnosis. — Red encrustations on reef substrates.

With quadrilobate or multilobed, robust tylostyle heads. Tylostyles, $326.4 \times 6.2 \mu\text{m}$ (length \times maximum shaft width); head, $9.2 \mu\text{m}$ wide (mean of means, all type specimens).

Description. — The holotype and one paratype formed bright red, thin crusts on dead shell substrate (habitat not known for the Gulf of Mexico paratype). There are no observations on the living sponge other than color. It forms fleshy encrustations, 1-2 mm thick; horizontal growth was limited by the size of the shell substrate to circa 20 cm. Superficial exhalant canals (astrorhizae) are present but obscured (collapsed) and openings contracted in preserved material.

Spicule dimensions are summarized in Table 1. Tylostyles occur in a considerable size range; the smaller ones are located in the surface brushes formed by the ends of the spicule fibers (Fig. 6b). Tylostyles are robust, with strongly lobed tyles; four protrusions are the rule, but 2-5 lobes are common; there are also many malformations, including lobed annular swellings of the tylostyle neck.

Histological sections show large oocytes ($74 \times 45 \mu\text{m}$, mean diameters) dispersed loosely throughout the tissue (Fig. 6a,c). Choanocyte chambers are small, rarely exceeding $12 \times 10 \mu\text{m}$. Long, filamentous bacteria, $1 \mu\text{m}$ thick, are abundant but fixation of this material was not adequate to study them.

Comments. — This species differs from its nearest relative, *Terpios manglaris*, by its red color, larger and more robust spicules, strongly bulbous tyles, lack of blue-pigmented bacterial symbionts, and reef-like habitat. SCHMIDT (1880:77) listed the Gulf of Mexico material as *Suberites lobiceps* Sdt. but did not describe it. Much later, TOPSENT (1920:30) provided a description of the Strasbourg Museum specimen under the same name but noted that tylostyle heads did not have the terminal lobe noted and figured in the original description of the species (SCHMIDT, 1870:47, pl. V, fig. 5) based on the type from a depth of 12 fathoms (21.9 m) off Salt Key, Florida (now Cay Sal, Bahamas). Fortunately, we were able to examine the only extant type material (cf. DESQUEYROUX-FAÚNDEZ and STONE, 1992:72), a slide in the Natural History Museum, London (BMNH 1870:5.3.96). We found most spicules on the slide preparation to belong to *Tedania ignis* (Duchassaing and Michelotti), but there are at least 10 characteristic tylostyles, closely resembling SCHMIDT's (1870) depiction, but less perfect in shape. The mean dimensions for the 10 spicules were $224.3 \mu\text{m}$ (overall length) \times $2.2 \mu\text{m}$ (shaft diameter) \times $5.0 \mu\text{m}$ (head width); no other anatomical features of the sponge are available, and

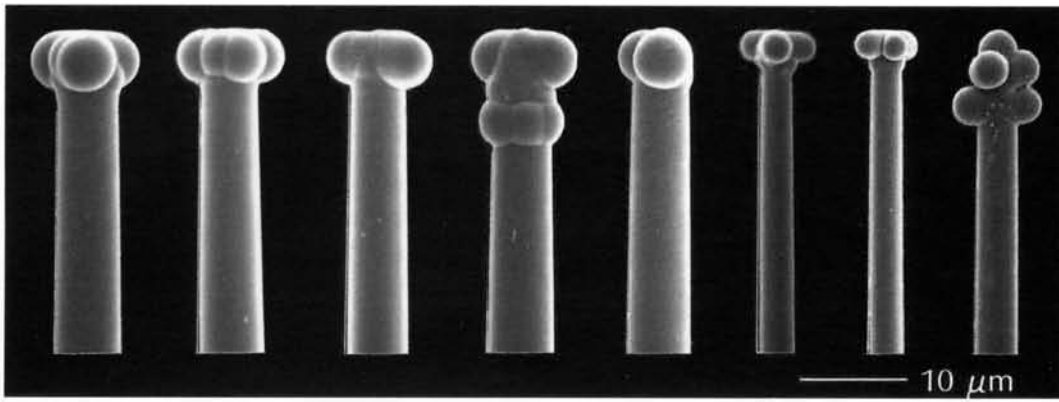


FIG. 5. — *Terpios belindae*, tylostyle heads (SEM) of holotype (USNM 43147).

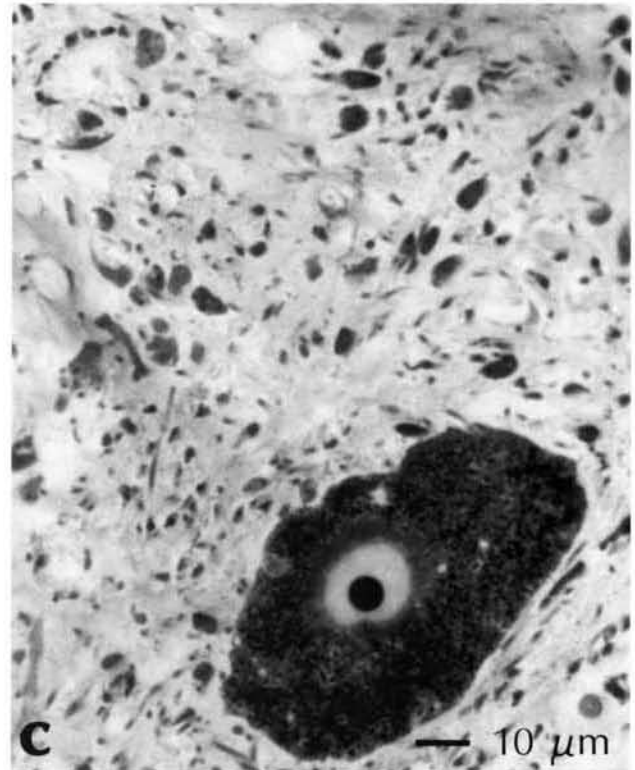
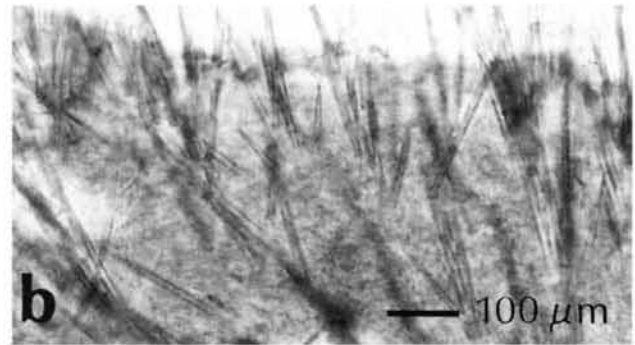
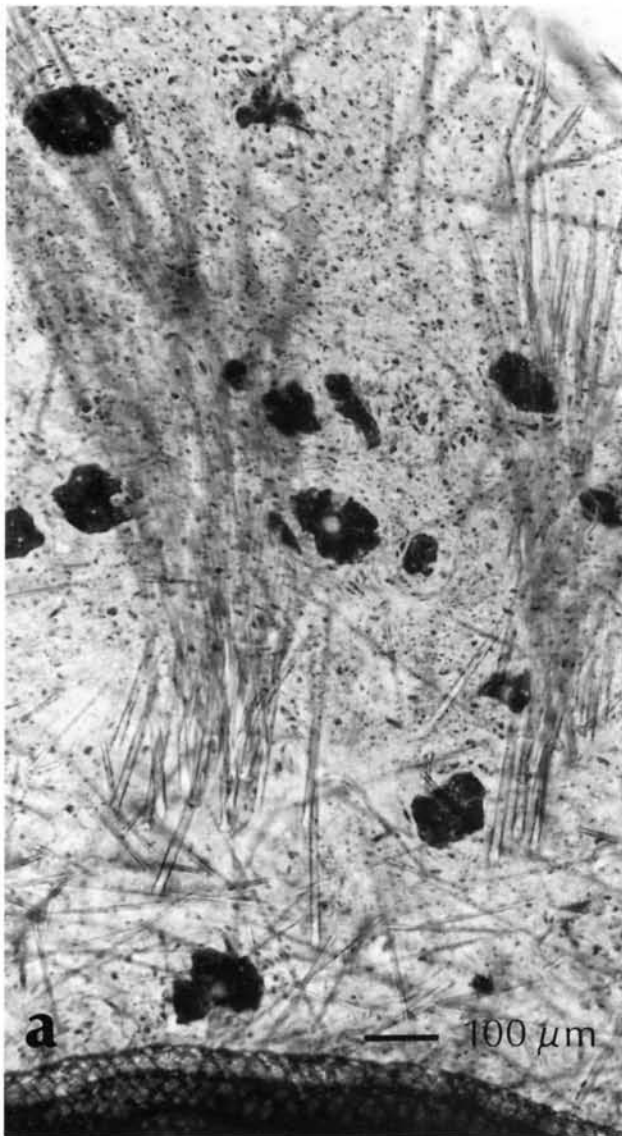


FIG. 6. — *Terpios belindae*, tissue preparations (light microscopy): a, section showing substrate with ascending spicule strands and loosely dispersed oocytes; b, ectosomal region showing spicule brushes topping choanosomal strands; c, enlarged oocyte and a few choanocyte chambers and bacterial filaments.

we consider it unrecognizable. The closest match of tylostyle form and dimensions is, ironically, that of the new Pacific coral-killing *Terpios* described elsewhere in this volume (RÜTZLER and MUZIK, 1993); we are not suggesting a close relationship.

Etymology. — Named for the collector, Belinda Alvarez Glasby.

Material Examined. — Holotype: USNM 43147; 16 May 1991; on dead bivalve shell, 3-24 m; Man of War Bay, North Point, Tobago. Paratypes: USNM 43148; same data as holotype, on separate bivalve shell. USNM 43149; fragment of specimen PO 150 in the collection of MZUS (Musée Zoologique de l'Université Strasbourg), labeled "*Suberites lobiceps* O. Schmidt," Gulf of Mexico, Agassiz, 1879 (cf. DESQUEYROUX-FAUNDEZ and STONE, 1992:72).

Distribution. — Eastern Caribbean (Tobago), Gulf of Mexico.

e. Suberites aurantiaca (Duchassaing and Michelotti), new combination (Figs. 7-9)

Comments. — Study of type and other specimens from a number of locations shows that this sponge has the massive shape and dense skeleton structure, with perpendicular ectosomal brushes of a small class of tylostyles, of typical *Suberites*. Tylostyles in some specimens have wrinkled (not lobed) heads (Fig. 7), presumably because of habitat conditions in mangrove swamps.

Detailed descriptions of this species were provided by DE LAUBENFELS (1950:103, as *Terpios fugax*); HECHTEL (1965:59, as *T. zeteki*); PULITZER-FINALI (1986:88, as *T. zeteki*); and RÜTZLER (1986:124, as *T. aurantiaca*).

Laxosuberites zeteki, generally known as *Terpios zeteki*, is morphologically identical to *Suberites aurantiaca*, except that the tylostyles of the holotype are very well formed, without wrinkled or otherwise deformed heads, a condition possibly due to favorable silica conditions in its habitat on the Pacific coast of Panama (DE LAUBENFELS, 1936b) (Fig. 8). We agree with KOBLUK and VAN SOEST (1989:1213) that this is a junior synonym of *S. aurantiaca* (see also comments for *Laxosuberites*).

Material Examined. — *Terpios aurantiaca* from St. Thomas, Virgin Islands (USNM 31045, schizolecotype) and other specimens of this species from mangroves in St. Thomas, Virgin Islands (USNM 31572), La Paguera, Puerto Rico (USNM 43153), Bermuda (USNM 43154), Tobago (USNM 43155), and Twin Cays, Belize (USNM 42873, 43156, 43157), and from the Gulf of Mexico coast of Florida (USNM 43158). *Laxosuberites zeteki* from Balboa, Pacific coast of Panama (USNM 22212, holotype).

3. Observations on Tyle Structure

A tylostyle is a pin-shaped spicule typically consisting of a rounded (spherical, ovoid) head (tyle) at

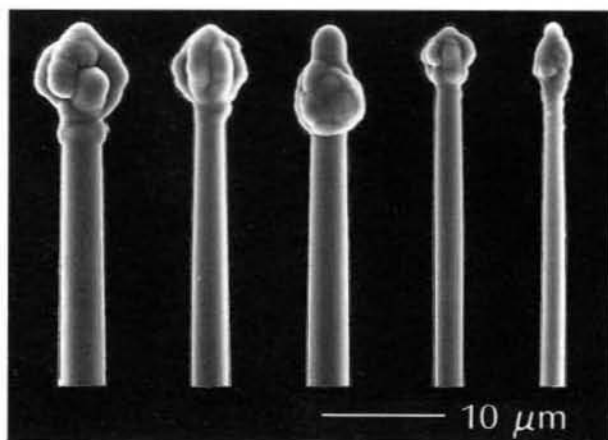


FIG. 7. — *Terpios* (= *Suberites*) *aurantiaca*, tylostyle heads (SEM), specimen from Mangrove Lake, Bermuda (USNM 43154).

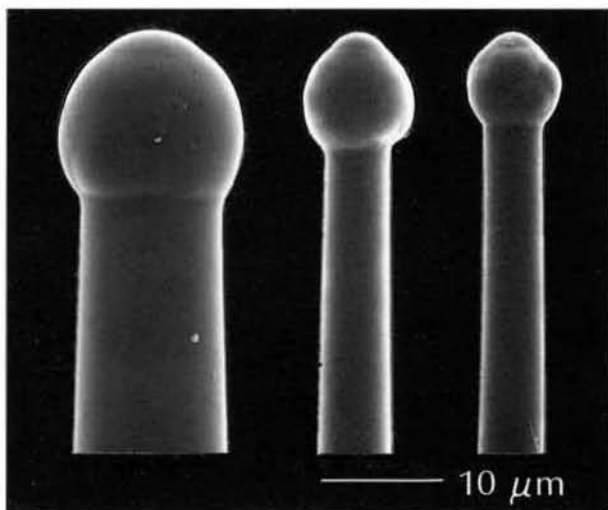


FIG. 8. — *Laxosuberites zeteki* (= *Suberites aurantiaca*), tylostyle heads (SEM), specimen from Pacific end of Panama Canal, Panama (USNM 22212, holotype).

the base and a shaft tapering gradually to a sharp point. Visible under the light microscope, there is an extremely fine canal following the axis of rotation and leading from just inside the point to the center of the tyle. This axial canal encloses an organic filament — a genetically determined structure — that is instrumental in silica deposition during the formation of the spicule.

Because morphology of the axial canal — which is much easier to make visible than the filament — can be assumed to reflect shape and branching of the axial filament, we used a simple method for examining the canal by scanning electron microscopy in order to reconstruct the possible development of differ-

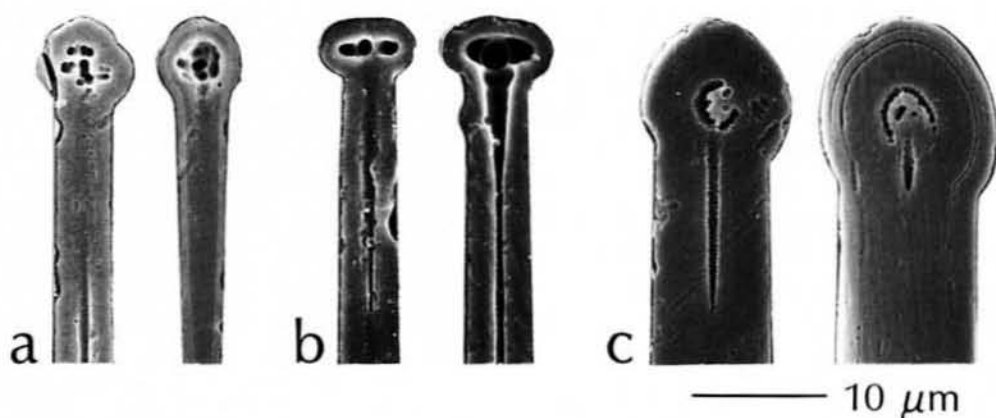


FIG. 9. — Tylostyle heads (tyles) of *Terpios* compared with *Suberites* (cut and etched, SEM): a, *T. fugax*, Belize (USNM 43146); b, *T. belindae*, Tobago (USNM 43147, holotype); c, *Laxosuberites zeteki* (= *Suberites aurantiaca*) from Pacific end of Panama Canal, Panama (USNM 22212, holotype).

ent types of mature tyles. To avoid shattering of the silica by knife cutting, we ground and polished epoxy-resin embedded spicules. When we viewed the preparation after gold coating, we were unable to clearly discern the axial canal until we enhanced it by briefly etching the polished surface in dilute hydrofluoric acid, a method successfully used before in a study of microscle structure (RÜTZLER and MACINTYRE, 1978).

Results of some of these experiments are shown in Fig. 9. The tyle of *Terpios fugax* is penetrated by several radiating canals (Fig. 9a), each representing a branch of axial filament responsible for a bulge on the head surface (compare Fig. 1). The tyle of *T. belindae* displays canals crossing at roughly right angles (Fig. 9b), reflecting the symmetry of major lobes

(Fig. 5). In contrast, the nonlobed tyle of *Suberites aurantiaca* (Fig. 8) indicates no branching of the axial filament, only a possible thickening, as indicated by the simple cavity at the end of the canal (Fig. 9c).

CONCLUSIONS

The genera of Suberitidae considered here are quite well separated if one accepts body shape and spicule characteristics as distinguishing features (Table 2). As much as they have been criticized, both characters have traditionally been used, and they are still valid in separating suberitid genera other than those discussed here (note the cup shape of *Poterion*, for instance). Transitional forms will always come to

TABLE 2. — Summary of generic characteristics in Suberitidae discussed in this review.

	Body shape	Skeleton orientation		Tylostyle		Procarvate symbionts
		Choanosome	Ectosome	Size classes	Tyle shape	
<i>Suberites</i>	massive	confused in center tracts in periphery	phalanx of smaller tylostyles perpendicular	2	normal	no
<i>Pseudosuberites</i>	massive	confused in center tracts in periphery	tangential	1	normal	no
<i>Prosuberites</i>	encrusting	single tylostyles erect on substrate	no separate skeleton	1 (very long)	normal	no
<i>Laxosuberites</i>	massive	ascending tracts with single spicules confused	no separate skeleton	1 (very long)	tyle often reduced	no
<i>Terpios</i>	encrusting	ascending tracts with single spicules confused	no separate skeleton	1 or 2	lobed	yes

light as the volume of material (species) available for study increases. In our interpretation, *Terpios* should represent encrusting forms —thinly spreading to almost indefinite dimensions— as convincingly demonstrated by the complementary treatment of a Pacific coral competitor (RÜTZLER and MUZIK, 1993). *Prosuberites* is another example in which crustose growth can be accepted as a generic character because it is dictated by the unique arrangement of a spicule phalanx, one tylostyle high.

Since conclusions about skeletal structure are greatly affected by preparatory methods and individual interpretation, it is of utmost importance to use standardized techniques, especially to cut sections to uniform thickness and not have structures distorted or obscured. Spicules should also be prepared in a way that will be suitable for random selection of different slopes and statistical treatment of measurements.

A great deal more attention needs to be given to the unusual tyle shape and structure of species of *Terpios*. Transmission electron microscopy of developmental stages would be particularly useful, although there seems to be no strong evidence to indicate the presence of pentactinal and hexactinal symmetries, as they exist in Hexactinellida, as suggested by some authors (DE LAUBENFELS, 1954:209). Over the past three decades, several light and electron microscope studies elucidated demosponge siliceous spicule secretion (see review in SIMPSON, 1984). Only a few of these have dealt with megascleres, and not a single report has considered the formation of tyles. It is widely believed that siliceous spicules are produced by intracellular processes in sclerocytes, which have an organic thread (axial filament) roughly hexagonal in cross section and 0.3 μm thick onto which silica is deposited. Some surface complexities, such as spines, are known to be generated by branching of the axial filament. Similar processes seem to affect the head structure of *Terpios* tylostyles. At the same time, it has been shown that bulbous swellings on megascleres of certain experimentally grown freshwater sponges are the result of the bulging of the silicalemma-a membrane instrumental in transporting silicic acid (SIMPSON, 1984). The question is, are regular tyles formed in this way, or does a special structure, a knob for instance, of the axial filament generate such a tyle, as indicated by the cavity in sectioned *Suberites* tylostyles (Fig. 9c)?

An important role is clearly played by procaryotic symbionts, which are not a solid taxonomic character but an intriguing feature common to the species assigned to *Terpios*. The species *T. fugax*, *T. granulosa*

Bergquist (a Pacific sponge but probably a junior synonym of *T. fugax*), and *T. manglaris* (but also *Hymeniacion caerulea*) share a blue-pigmented, multicellular, filamentous bacterium, as already mentioned and described in more detail by SANTAVY (1986). A new *Terpios* from the Pacific, on the other hand, harbors a cyanobacterial symbiont (RÜTZLER and MUZIK, 1993). Bacterial filaments are also present in *T. belindae* but suitably fixed material has yet to be studied to evaluate their nature and importance.

ACKNOWLEDGMENTS

We thank Andrea Blake for help with electron microscopy and Molly K. Ryan for assistance with the illustrations. Joseph Devidts, Musée Zoologique de l'Université Strasbourg, and Mary Spencer Jones, the Natural History Museum, London, kindly loaned us material for study. We are also grateful to Shirley Stone, also of the Natural History Museum (now retired), who examined the lectotype of *Terpios fugax*. This is contribution number 382 of the Caribbean Coral Reef Ecosystems program of the National Museum of Natural History, Washington, D.C., which is supported in part by the EXXON Corporation.

REFERENCES

- ALCOLADO, P. M. — 1984. Nuevas especies de esponjas encontradas en Cuba. *Poeyana*, 271, 22 pp.
- CARTER, H. J. — 1882. Some sponge from the West Indies and Acapulco in the Liverpool Free Museum described, with general and classificatory remarks. *Ann. Mag. Nat. Hist.*, 9(5):265-367.
- DESQUEYROUX-FAUNDEZ, R. and S. M. STONE. — 1992. *O. Schmidt Sponge Catalogue. An Illustrated Guide to the Graz Museum Collection, with Notes on Additional Material*. Muséum d'Histoire Naturelle, Geneva. 190 pp.
- DUCHASSAING DE FONBRESSIN, P. and G. MICHELOTTI. — 1864. Spongiaires de la Mer caraïbe. *Natuurk. Verh. Mij. Haarlem*, 21, 1124 pp.
- HECHTEL, G. J. — 1965. A systematic study of the Demospongiae of Port Royal, Jamaica. *Peabody Mus. Nat. Hist. Bull.*, 20, 104 pp.
- KOBLUK, D. R. and R. W. M. VAN SOEST. — 1989. Cavity-dwelling sponges in a southern Caribbean coral reef and their paleontological implications. *Bull. Mar. Sci.*, 44:1207-1235.
- LAUBENFELS, M. W. DE. — 1934. New sponges from the Puerto Rico deep. *Smith. Misc. Coll.*, 91(17), 28 pp.
- 1936a. A discussion of the sponge fauna of the Dry Tortugas in particular, and the West Indies in general, with material for a revision of the families and orders of the Porifera. *Carnegie Inst. of Washington*, 467 (*Papers from Tortugas Lab.*, 30), 225 pp.
- 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.
- 1950. The Porifera of the Bermuda Archipelago. *Trans. Zool. Soc. London*, 27, 154 pp.
- 1954. The sponges of the West-Central Pacific. *Oregon State Monographs, Studies on Zoology*, 7, 306 pp.

- LENDENFELD, R. VON. — 1897. Die Clavulina der Adria. *Nova Acta Acad. Leop. Carol.*, 69, 251 pp.
- LEVI, C. — 1973. Systématique de la classe des Demospongiaria (Démospogies). In: P.P. Grassé (ed.), *Traité de Zoologie*, (3), *Spongiaires*, pp. 577-631. Masson & Co, Paris.
- PULITZER-FINALI, G. — 1986. A collection of West Indian Demospongiae (Porifera). In appendix, a list of the Demospongiae hitherto recorded from the West Indies. *Ann. Mus. Civ. Stor. Nat. Genova*, 86:65-216.
- RÜTZLER, K. — 1978. Sponges in coral reefs. In: D.R. Stoddart and R.E. Johannes (eds.), *Coral reefs: research methods*, pp. 299-313. Monographs on oceanographic methodology 5. Unesco.
- 1986. Phylum Porifera (Sponges). In: W. Sterrer (ed.), *Marine Fauna and Flora of Bermuda*, pp. 111-128. John Wiley & Sons, New York.
- RÜTZLER, K. and I. G. MACINTYRE. — 1978. Siliceous sponge spicules in coral reef sediments. *Marine Biology*, 49:147-159.
- RÜTZLER, K. R. and K. MUZIK. — 1993 *Terpios hoshinota*, a new cyanobacteriosponge threatening Pacific reefs. *Sci. Mar.* 57 (4):121-129.
- SANTAVY, D. L. — 1986. A blue-pigmented bacterium symbiotic with *Terpios granulosa*, a coral reef sponge. *Hawaii Inst. Mar. Biol. Tech. Rep.*, 17:380-393.
- SCHMIDT, O. — 1870. *Grundzüge einer Spongien-Fauna des Atlantische Gebietes*. Wilhelm Engelmann, Leipzig, 88 pp.
- 1880. *Die Spongien des Meerbusen von Mexico (part 2). Reports on the dredging, under the supervision of Al. Agassiz, in the Gulf of Mexico*. Gustav Fischer, Jena, 90 pp.
- SIMPSON, T. L. — 1984. *The Cell Biology of Sponges*. Springer-Verlag, New York, 662 pp.
- SOEST, R. W. M. and D. B. SASS. — 1981. Marine sponges from an island cave on San Salvador Island, Bahamas. *Bijdr. Dierk.*, 51:332-344.
- SOEST, R. W. M., S. M. STONE, N. BOURY-ESNAULT and K. RÜTZLER. — 1983. Catalogue of the Duchassaing & Michelotti (1864) collections of West Indian sponges (Porifera). *Bull. Zool. Mus. Univ. Amsterdam*, 9(21):189-205.
- TOPSENT, E. — 1896. Matériaux pour servir à l'étude de la faune de spongiaires de France. *Mém. Soc. Zool. de France*, 9:113-133.
- 1900. Spongiaires de France. III. Monaxonida (Hadromerina). *Arch. Zool. Exp. Gén.*, series 3, 8, 328 pp.
- 1920. Spongiaires de Musée Zoologique de Strasbourg. Monaxonides. *Bull. Inst. Océanogr. Monaco*, 381, 36 pp.
- 1938. Contribution nouvelle à la connaissance des Éponges des côtes d'Algérie. Les espèces nouvelles d'O. Schmidt, 1868. *Bull. Inst. Océanogr. Monaco*, 758:1-32.
- VOSMAER, G. G. J. — 1887. Porifera. In: H. G. Bronn (ed.), *Die Klassen und Ordnungen des Tierreichs*, 2. C.F. Winter, Leipzig, 496 pp.