

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the late 1960s (for a review, see ENDEAN, 1973), although outbreaks had been observed almost a decade earlier (Rützler, unpublished, at Tany Kely,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.

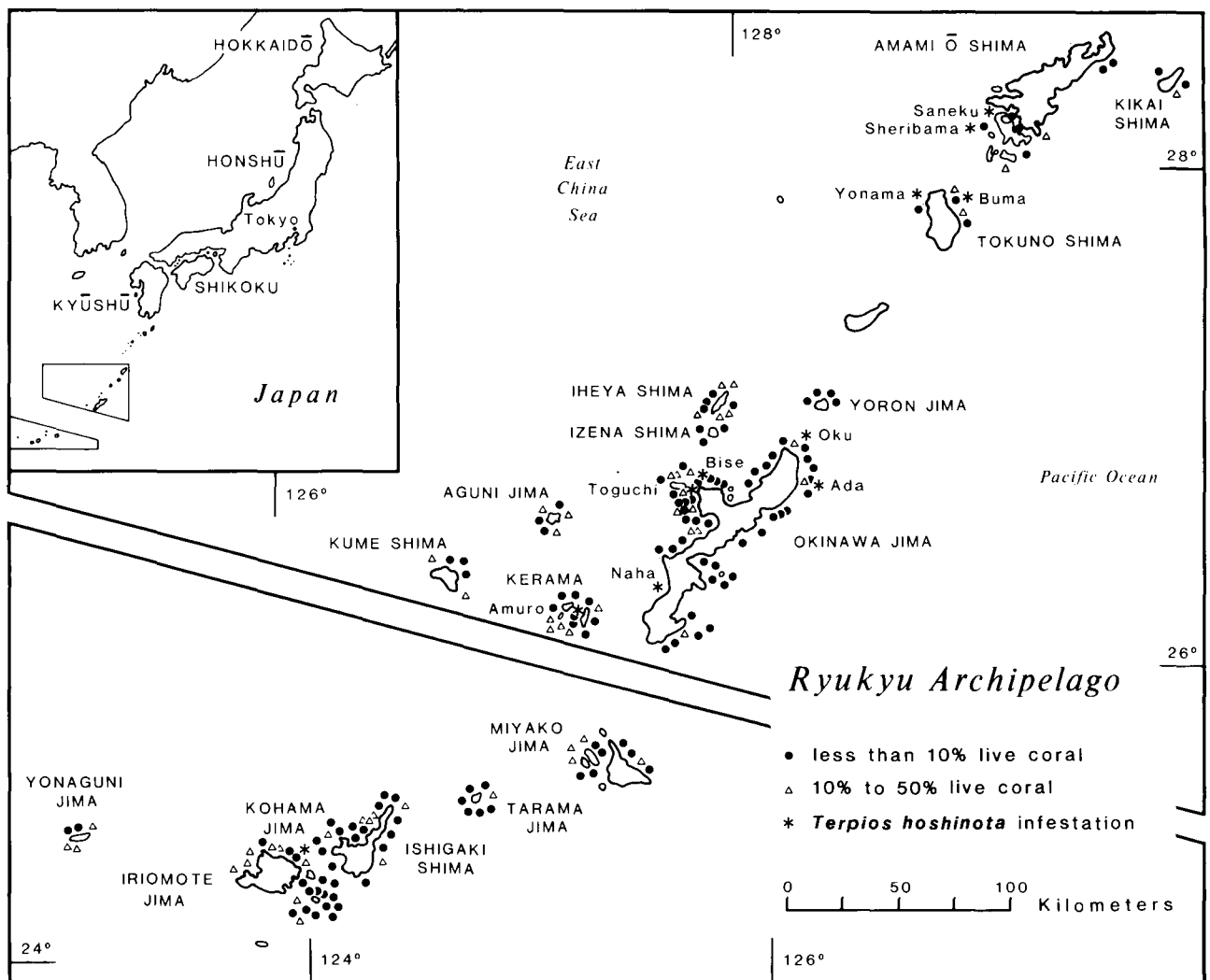


FIG. 1. — Map of 1981-1985 study sites in Japan with location of *Terpios hoshinota* infestations determined in 1984-1985.

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)

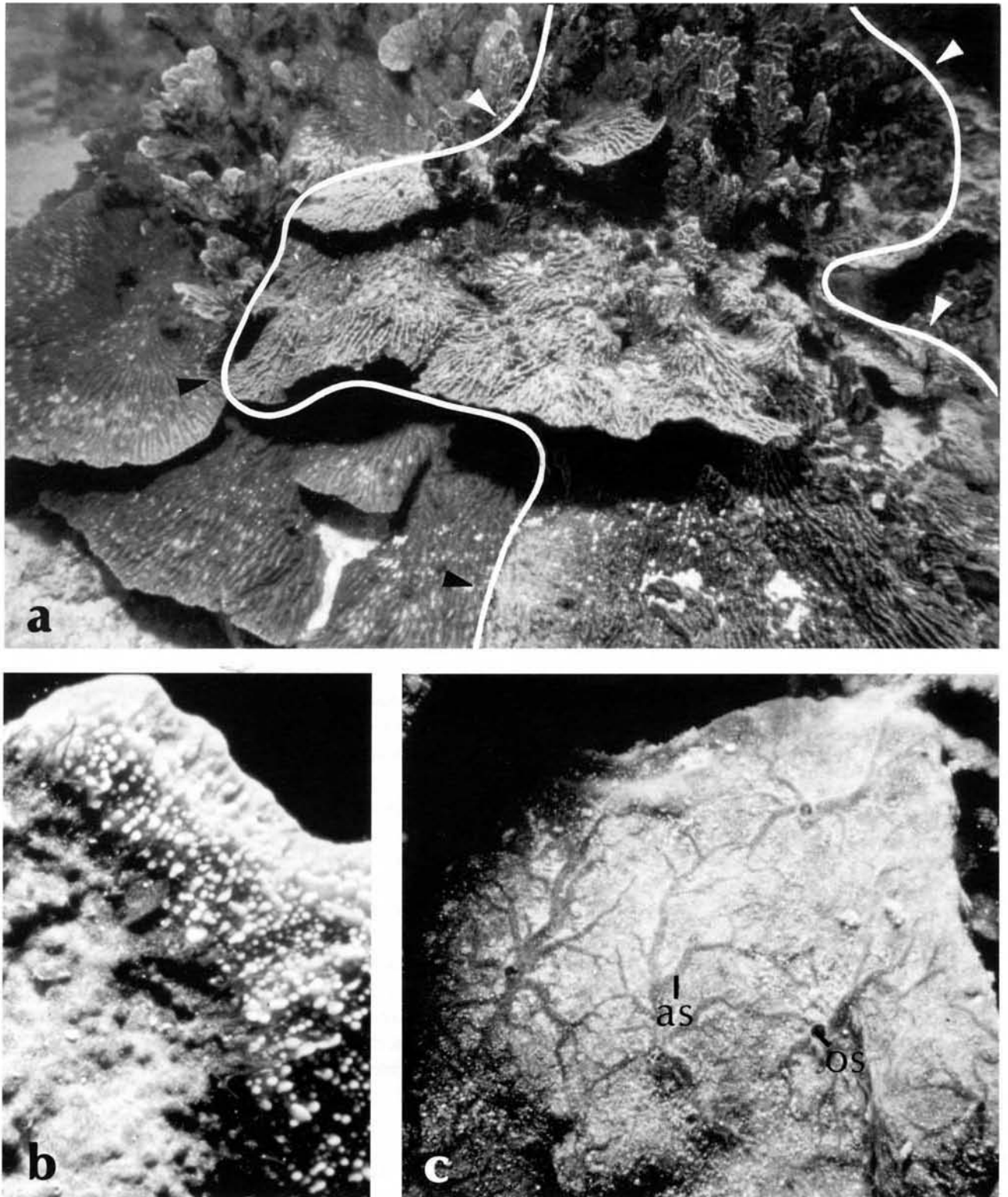


FIG. 2. — *Terpios hoshinota*, views of the sponge *in situ* at Yonama (Tokuno Shima): a, infested reef coral *Merulina ampliata* (Ellis and Solander) still showing coral structure through the thin sponge (arrows delineate sponge-encrusted surface zone; coral outside this zone is alive and healthy); 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)

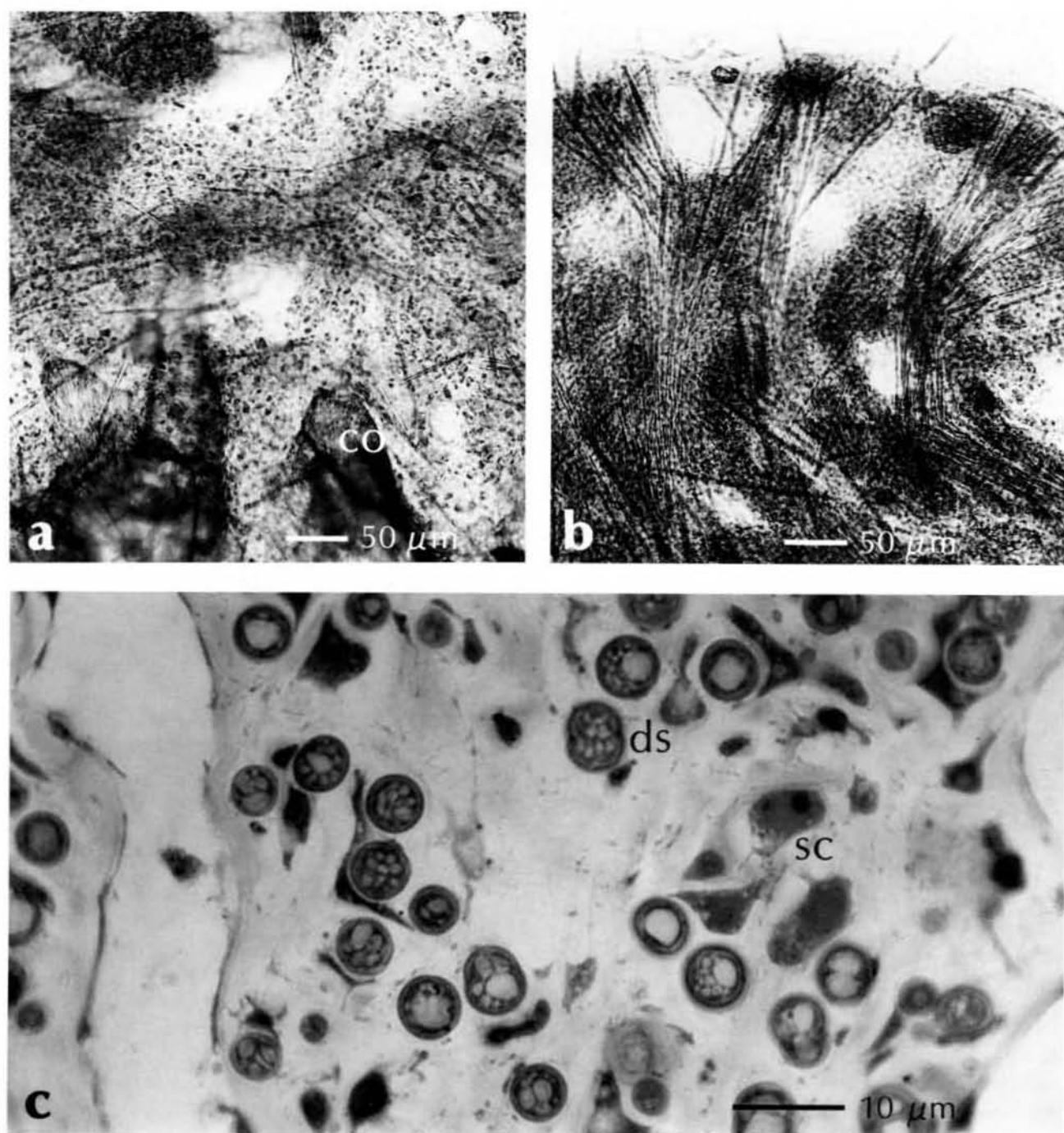


FIG. 3. — *Terpios hoshinota*, light microscopy: a, spicule arrangement in choanosome; b, spicule arrangement in ectosome; c, zoocyanellae in choanosome. (co = coral substrate, ds = dividing stage of zoocyanellae, sc = sponge cells)

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.

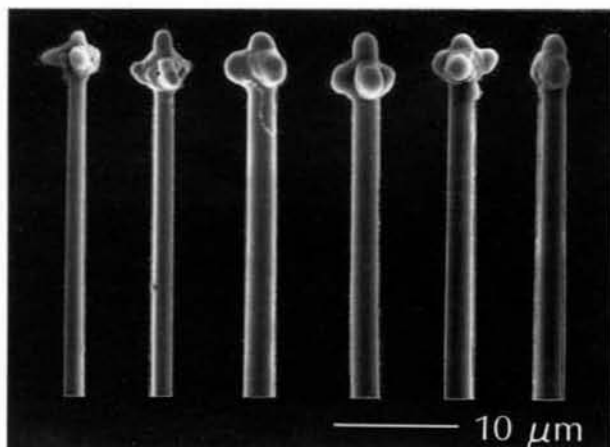


FIG. 4. — *Terpios hoshinota*, scanning electron micrograph of portions of tylostyle head.

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,

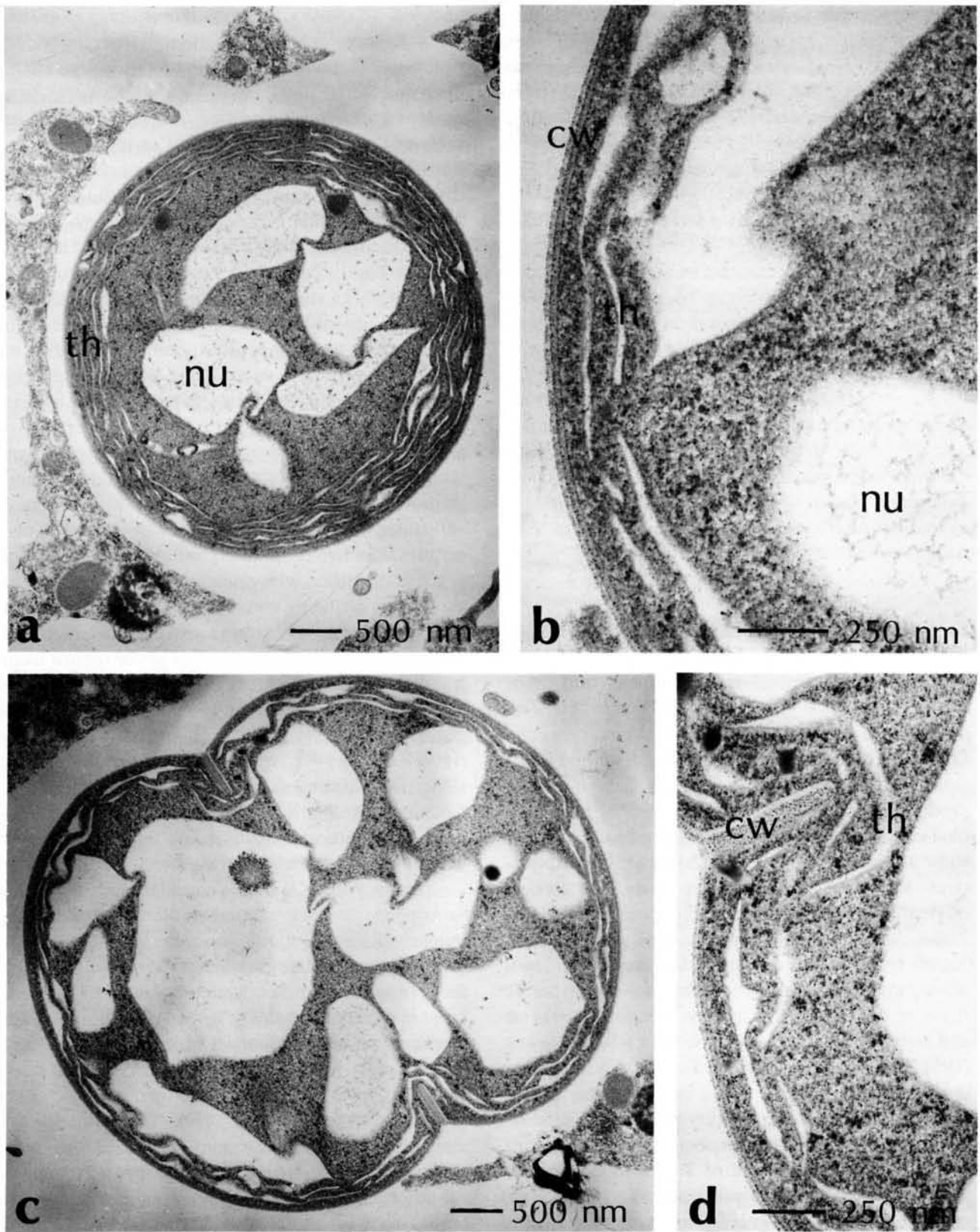


FIG. 5. — *Terpios hoshinota*, transmission electron microscopy of zoocyanelae, *Aphanocapsa raspaigellae*: a, entire bacterial cell next to sponge cell; b, enlarged view of peripheral area; c, dividing stage; d, enlarged view of constricting cell wall and thylakoid in dividing cell. (cw = cell wall,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

