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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 (membraniform) 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-

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 nitricacid 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 μ m), 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 ×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 × 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 μm ± 3.16 s.e. for small spicules, 328.0 μm ± 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 *Hymeniacidon 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 *Hymeniacidon 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 700×20 μm in the larger class, 150×7.5 μm 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 ± standard errors, with ranges in parentheses.

| Specimen, location	Total length	×	Max. shaft width	Neck width	Head width	Head length
Terpios fugax						
USNM 31624, Puerto Rico	267.6±11.5 (150-340)	×	3.1±0.1 (2.5-3.5)	2.7±0.1 (2.0-3.0)	5.6±0.2 (5.0-6.5)	4.8±0.2 (4.0-5.5)
USNM 43146, Carrie Bow Cay, Belize	363.2±15.6 (220-460)	×	4.2±0.1 (3.5-5.0)	3.8±0.2 (3.0-4.5)	6.7±0.2 (6.0-8.0)	5.6±0.1 (5.0-6.0)
Terpios manglaris						
USNM 43150, Man-O-War Cay, Belize	305.6± 9.9 (200-450)	×	3.2±0.1 (2.5-3.5)	2.9±0.2 (2.5-3.5)	6.1±0.3 (4.5- 7.5)	3.9±0.2 (3.0-5.0)
USNM 43151, Twin Cays, Belize	249.6± 7.5 (140-300)	×	2.8±0.1 (2.5-3.0)	2.6±0.1 (2.0-3.0)	5.1±0.1 (4.5- 5.5)	3.4±0.2 (2.5-4.5)
USNM 43161, Twin Cays, Belize	330.8±11.5 (210-410)	×	4.2±0.2 (3.5-5.5)	3.9±0.2 (3.5-5.0)	6.7±0.3 (5.0- 7.5)	4.2±0.2 (3.5-5.0)
USNM 43162, Pelican Cays, Belize	376.0±12.5 (240-460)	×	5.7±0.3 (4.0-7.0)	5.3±0.3 (4.0-6.5)	8.8±0.4 (7.0-10.0)	5.5±0.3 (4.0-7.0)
Terpios belindae						
USNM 43147, Tobago	320.0±13.9 (170-390)	×	5.9±0.5 (3.5-7.5)	4.7±0.4 (3.0-6.0)	9.0±0.5 (6.0-11.0)	4.9±0.3 (3.0-6.5)
USNM 43148, Tobago	347.9±14.5 (190-440)	×	5.5±0.3 (4.0-6.5)	4.5±0.3 (3.0-5.5)	8.4±0.6 (5.0-11.0)	4.8±0.3 (3.5-6.0)
USNM 43149, Gulf of Mexico	311.2±15.5 (140-430)	×	7.1±0.6 (3.0-9.0)	5.9±0.5 (2.5-8.0)	10.3±0.5 (7.0-12.5)	6.2±0.4 (3.5-8.0)
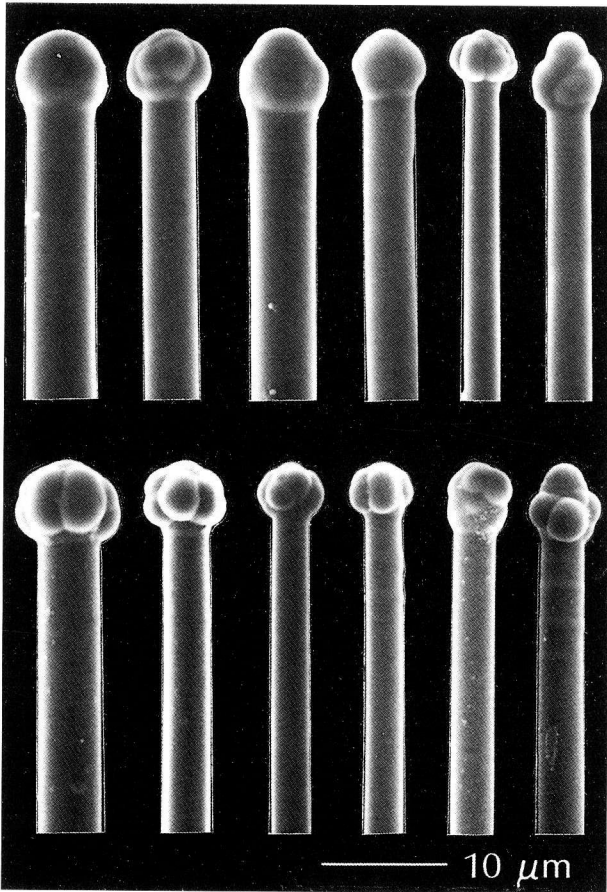
Fig. 1. — *Terpios fugax*, tylostyle heads (SEM) of two specimens: top row, from Puerto Rico (USNM 31624); bottom row, from Belize (USNM 43146).

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 × 3.7 μm (length x shaft diameter); with depressed (terminally flattened) tylostyle heads, 3.3 × 5.3 μm (width × 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 oscillatorian 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 × 4.0 μm (length × maximum shaft width); head, 6.7 μm wide (mean of means, all type specimens). Symbiotic with filamentous, multicellular, blue-pigmented bacteria.
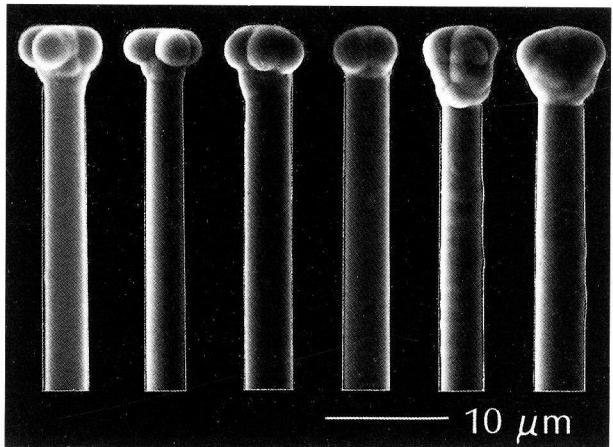

Fig. 2. — *Terpios manglaris*, tylostyle heads (SEM) of holotype (USNM 43150).

Description of the Sponge. — The holotype is an encrustation, less than 1 mm thick, that covered an area of about 7 × 6 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.
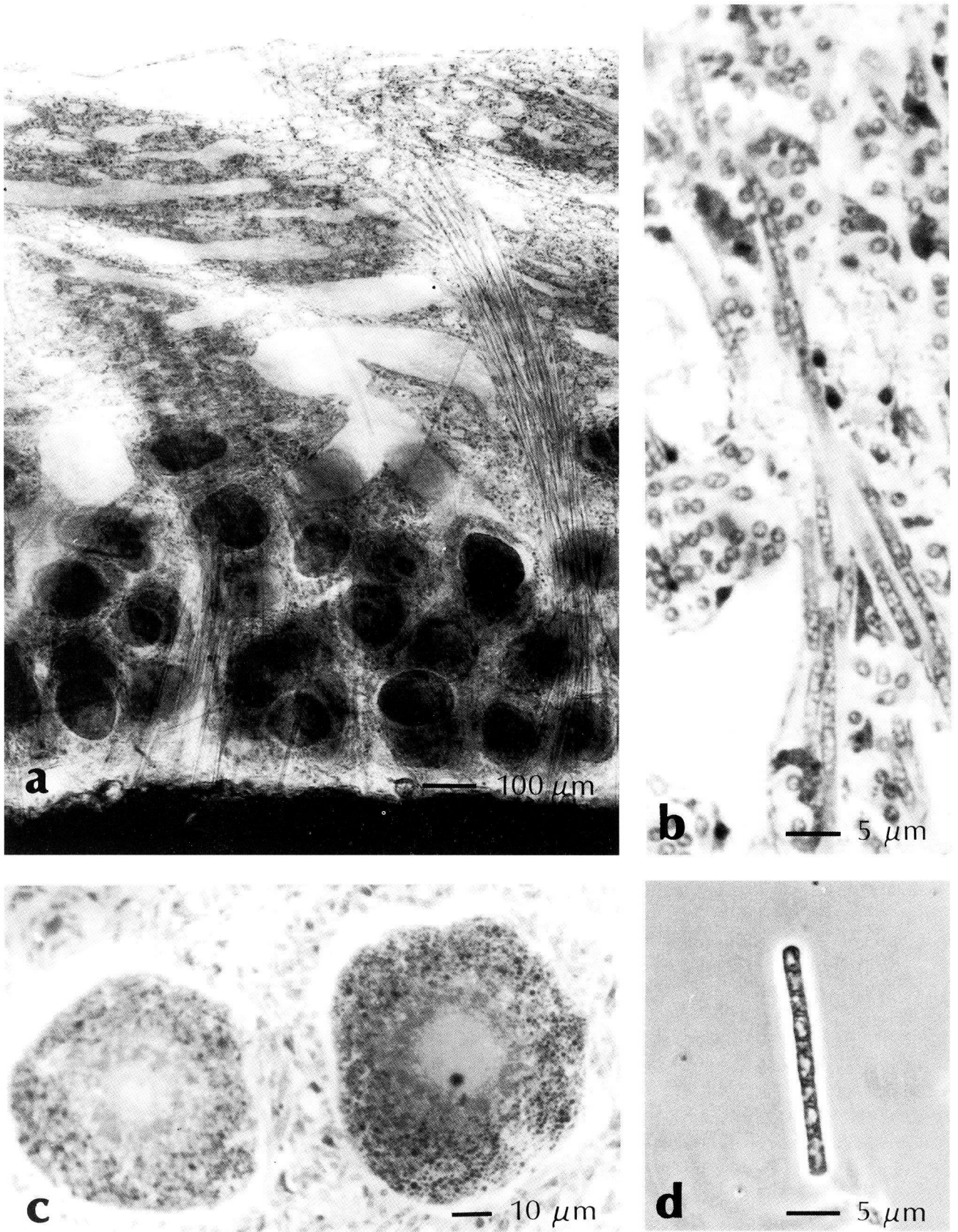
FIG. 3. — *Terpios manglaris*, tissue preparations (light microscopy): a, section showing substrate with cluster of oocytes and spicule strands ascending to surface; b, choanosome filled with filamentous bacteria (in longitudinal and cross sections); c, two oocytes; d, isolated bacterial trichome.
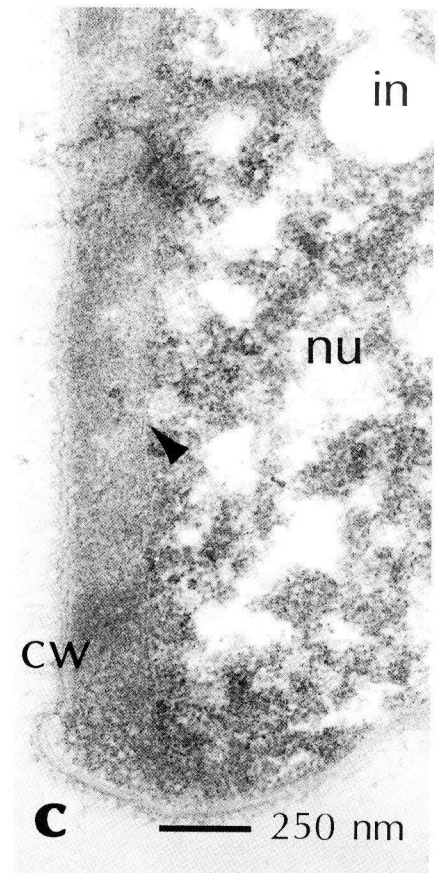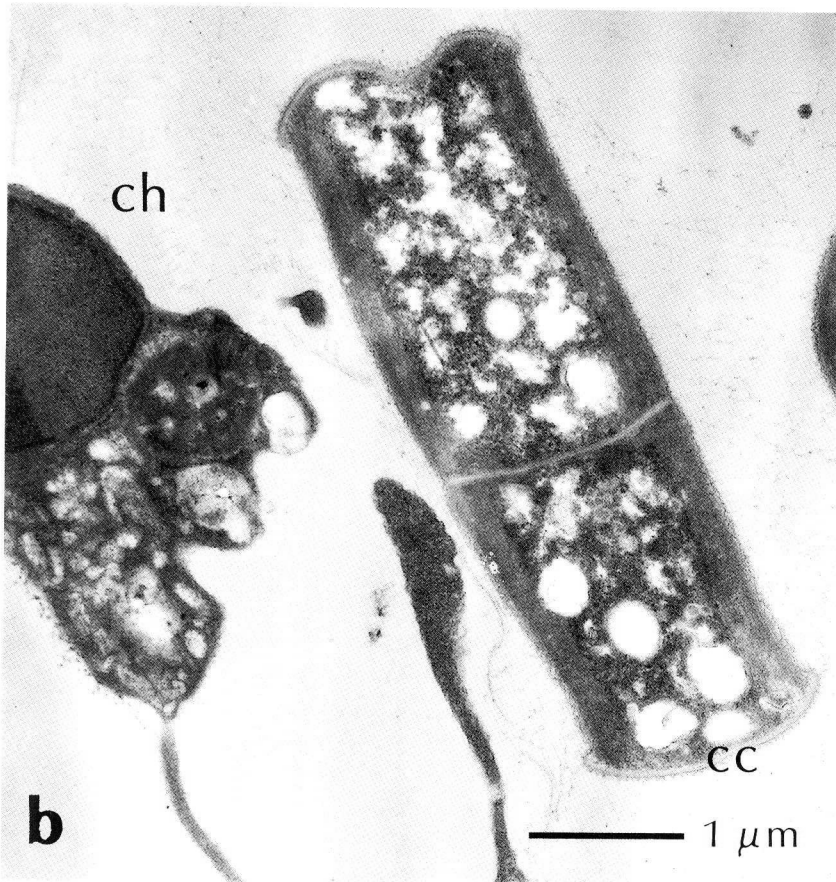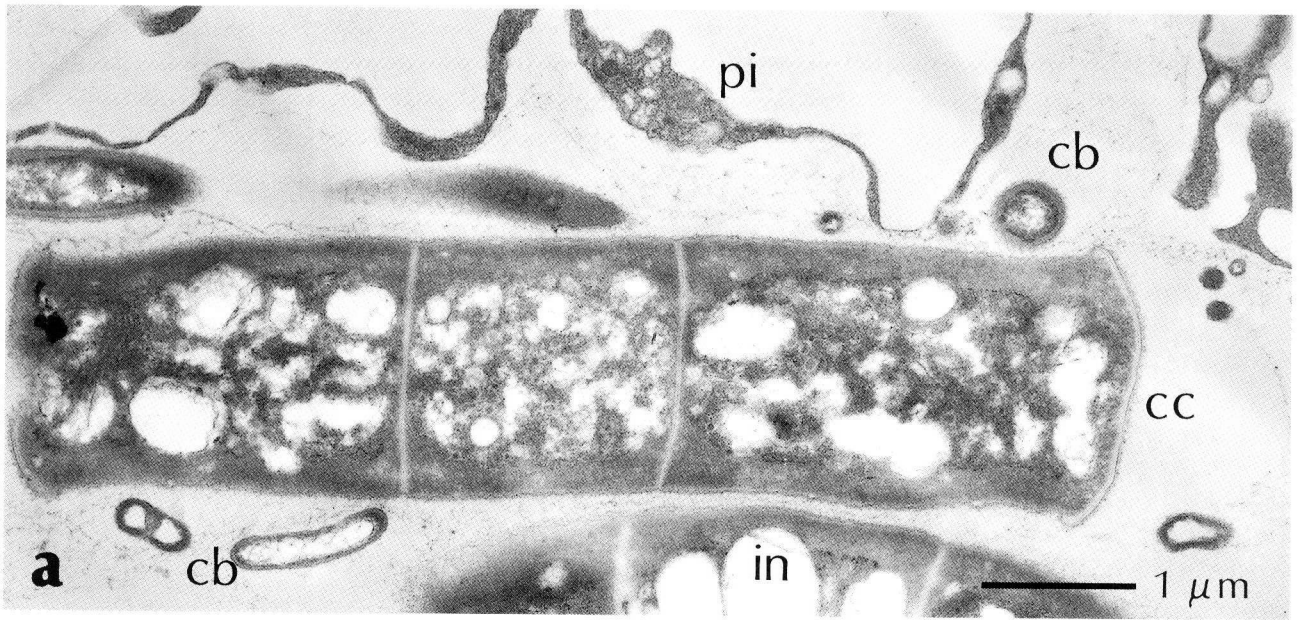
FIG. 4. — *Terpios manglaris*, symbiont (TEM): a, 3-cell trichome along a pinacocyte; b, 2-cell trichome next to choanocyte; c, enlarged portion of end cell (arrow points to cytoplasmic membrane). (cb = coccoid bacteria, cc = cell cap of terminal cell, ch = choanocyte, cw = cell wall, in = inclusion, 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 × 59 μm (mean diameters), choanocyte chambers average 20 × 12 μm. 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 μm in length, 1.5 μm 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°39.8'N; 88°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 × 6.2 μm (length × maximum shaft width); head, 9.2 μm 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 × 45 μm, mean diameters) dispersed loosely throughout the tissue (Fig. 6a,c). Choanocyte chambers are small, rarely exceeding 12 × 10 μm. Long, filamentous bacteria, 1 μm 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 μm (overall length) × 2.2 μm (shaft diameter) × 5.0 μm (head width); no other anatomical features of the sponge are available, and
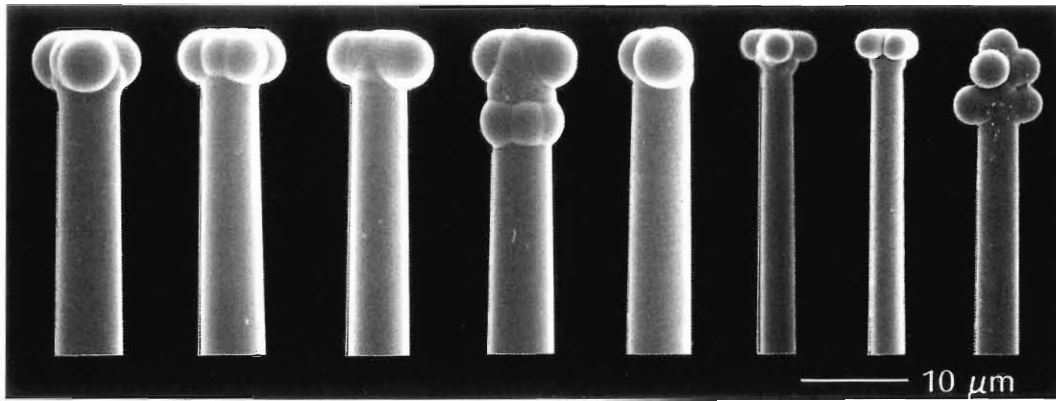
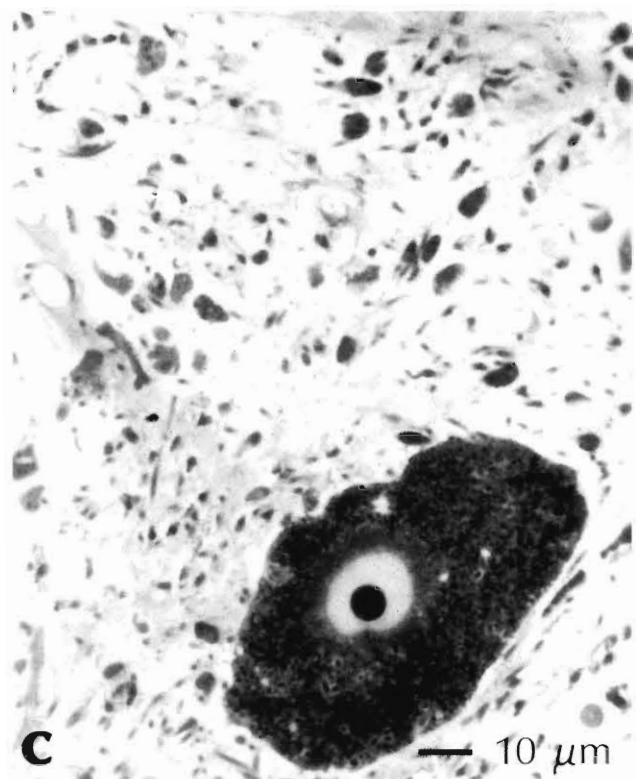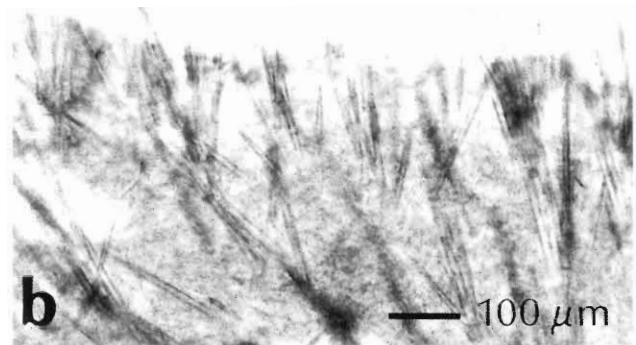Fig. 5. — *Terpios belindae*, tylostyle heads (SEM) of holotype (USNM 43147).
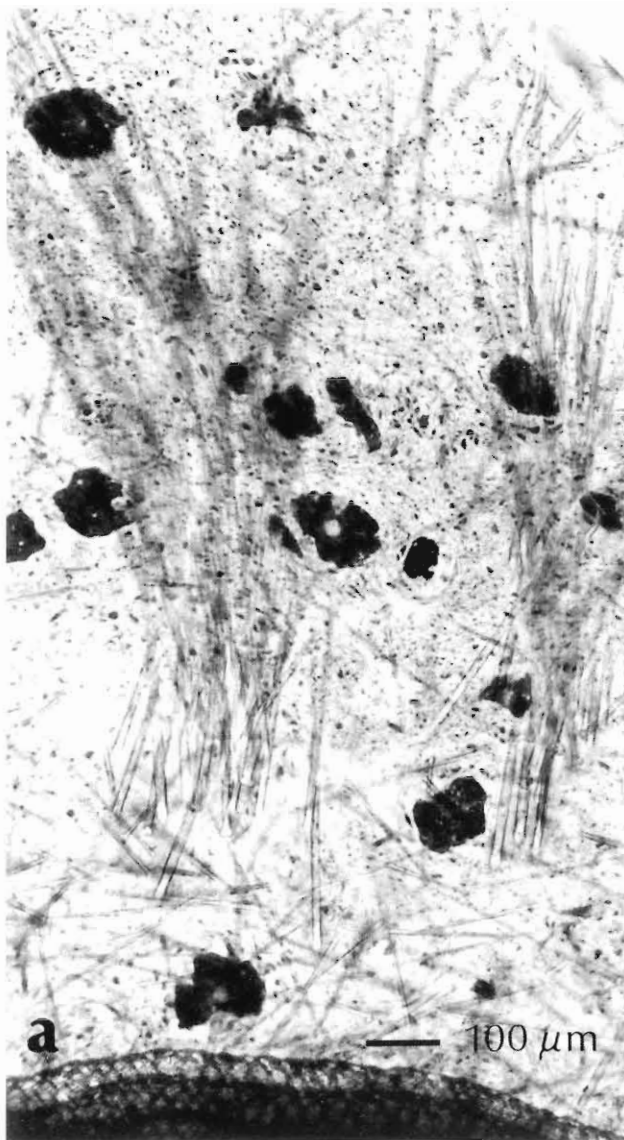

Fig. 6. — *Terpios belindae*, tissue preparations (light microscopy): a. section showing substrate with ascending spicule strands and loosely dispersed oocytes; b. ectosomal region showing spicule brushes topping choanosomal strands; c. enlarged oocyte and a few choanocyte chambers and bacterial filaments.

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 sepatate 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-FAÚNDEZ 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, schizolectotype) 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
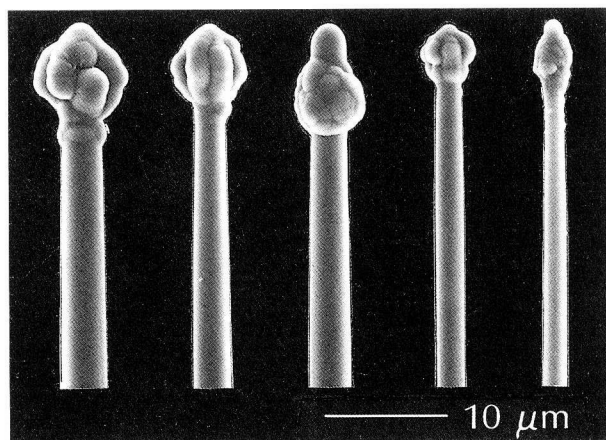

FIG. 7. — *Terpios (=Suberites) aurantiaca*, tylostyle heads (SEM), specimen from Mangrove Lake, Bermuda (USNM 43154).
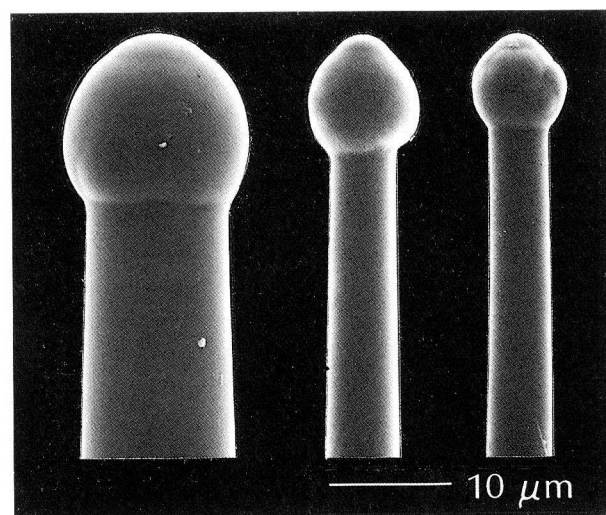

FIG. 8. — *Laxosuberites zeteki (=Suberites aurantiaca)*, tylostyle heads (SEM), specimen from Pacific end of Panama Canal, Panama (USNM 22212, holotype).

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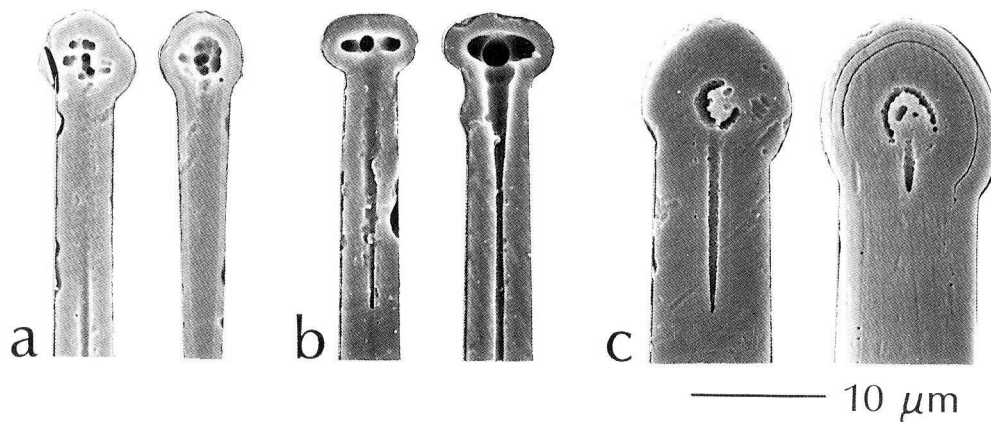
FIG. 9. — Tylostyle heads (tyles) of *Terpios* compared with *Suberites* (cut and etched, SEM): a, *T. fugax*, Belize (USNM 43146); b, *T. belindae*, Tobago (USNM 43147, holotype); c, *Laxosuberites zeteki* (=*Suberites aurantiaca*) from Pacific end of Panama Canal, Panama (USNM 22212, holotype).

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 microsclere 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 | | Procaryote symbionts |
		Choanosome	Ectosome	Size classes	Tyle shape	
Suberites	massive	confused in center tracts in periphery	phalanx of smaller tylostyles perpendicular	2	normal	no
Pseudosuberites	massive	confused in center tracts in periphery	tangential	1	normal	no
Prosuberites	encrusting	single tylostyles erect on substrate	no separate skeleton	1 (very long)	normal	no
Laxosuberites	massive	ascending tracts with single spicules confused	no separate skeleton	1 (very long)	tyle often reduced	no
Terpios	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 *Hymeniacidon 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

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