KLAUS RÜTZLER

Bredin-Archbold-Smithsonian Biological Survey of Dominica: Burrowing Sponges, Genus Siphonodictyon Bergquist, From The Caribbean

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY NUMBER 77

SERIAL PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

The emphasis upon publications as a means of diffusing knowledge was expressed by the first Secretary of the Smithsonian Institution. In his formal plan for the Institution, Joseph Henry articulated a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This keynote of basic research has been adhered to over the years in the issuance of thousands of titles in serial publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Annals of Flight
Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in History and Technology

In these series, the Institution publishes original articles and monographs dealing with the research and collections of its several museums and offices and of professional colleagues at other institutions of learning. These papers report newly acquired facts, synoptic interpretations of data, or original theory in specialized fields. These publications are distributed by subscription to libraries, laboratories, and other interested institutions and specialists throughout the world. Individual copies may be obtained from the Smithsonian Institution Press as long as stocks are available.

S. DILLON RIPLEY
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY

NUMBER 77

Klaus Rützler

Bredin-Archbold-Smithsonian Biological Survey of Dominica: Burrowing Sponges, Genus *Siphonodictyon* Bergquist, From The Caribbean

SMITHSONIAN INSTITUTION PRESS
CITY OF WASHINGTON
1971

ABSTRACT

Rützler, Klaus. Bredin–Archbold–Smithsonian Biological Survey of Dominica: Burrowing Sponges, Genus *Siphonodictyon Bergquist,* from the Caribbean. *Smithsonian Contributions to Zoology,* number 77, 37 pages. 1971.–*Siphonodictyon* (Adociidae, Porifera) was hitherto known only from one species (*Siphonodictyon mucosum* Bergquist) from the Pacific Ocean. In the present paper the species is recorded also from the Indian Ocean. Two new species (*Siphonodictyon cachacrouense,* new species and *Siphonodictyon coralliphagum,* new species) are described from the Caribbean Sea. Based on morphological differences *Siphonodictyon coralliphagum* is divided into four forms (forma *typica,* forma *obruta,* forma *tubulosa* and forma *incrustans).* All species excavate burrows in coral skeletons. Another Caribbean species with sand-burrowing habit *(Siphonochalina siphona* de Laubenfels) is here transferred to *Siphonodictyon.* Based on the new material the definition of the genus is revised. Histological features and ecological data are discussed for all species.

Official publication date is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, Smithsonian Year.

UNITED STATES GOVERNMENT PRINTING OFFICE
WASHINGTON : 1971

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington, D.C. 20402 - Price 50 cents (paper cover)

Klaus Rützler

Bredin-Archbold-Smithsonian Biological Survey of Dominica: Burrowing Sponges, Genus *Siphonodictyon* Bergquist, From The Caribbean

Introduction

Marine sponges which excavate calcium carbonate substrata have been known for well over a century and have since been found within the full horizontal and vertical range of benthic habitats. They are commonly called "boring sponges" and, with more or less justification, are lumped in the family Clionidae (order Clavaxinellida). They burrow in limestone and in all kinds of calcareous algal and invertebrate skeletons. Clionids usually excavate characteristic tunnels and chambers, with only orifice-bearing papillae showing on the substratum surface. Some species can reach a massive epilithic stage (gamma stage) after their original substratum fragment has been completely destroyed.

During several diving descents to Caribbean coral reefs I frequently observed deep-yellow sponge chimneys protruding from living coral heads in depths below 20 m. It was striking to note that these processes were merely vents for larger mucous masses of sponge enclosed deep in the coral skeleton. The regular shape of the excavations and the immaculate white contact areas between substratum and sponge suggested that the sponges were actively excavating in the coral rather than occupying deserted burrows of other organisms. Micro-anatomical preparation of the yellow burrowers revealed that they were congeneric with *Siphonodictyon mucosum* described by Bergquist (1965) from the Pacific Ocean. Further search in the same environment in Jamaica, Dominica, and Barbados and additional study of preserved material collected by colleagues in Jamaica and Puerto Rico produced what are here considered to be four distinct morphological forms of the same new species (*Siphonodictyon coralliphagum*, new species). A second species was discovered in a Dominican coral reef. Specimens of a sand-dwelling species were collected in Bimini and were found to be conspecific with *Siphonochalina siphona* Laubenfels (1949). Based on this new material the species is here transferred to *Siphonodictyon*. Study of burrowing sponges collected during the International Indian Ocean Expedition revealed one specimen of the type species from Indonesia.

Klaus Rützler, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

Methods

After the specimens were photographed under water they were collected, using rock hammer and chisel. Fragments of the substratum were kept for later

identification. Hexamethylenetetramine-buffered 4% formalin-seawater was used as fixative (up to two weeks); subsequently the specimens were transferred into 80% ethyl alcohol. Anatomical preparations consisted of hand sections stained in basic fuchsin and spicule slides produced after separate boiling of ectosomal and choanosomal tissue in concentrated nitric acid. Paraffin and frozen sections were used for histological observations. They were routinely stained with toluidin blue, Mallory's triple stain, and Ehrlich's hematoxylin-eosin.

For each specimen studied 200 spicule measurements were taken by scanning the slides under the microscope and measuring maximum length and width of 100 spicules which entered the field of view and were unbroken and lying flat. Two size categories of oxea were more or less distinct in the choanosome. The thinner and usually shorter oxea are probably younger growth stages but were still measured separately. In case of doubt the shape of the ends was used as a criterion; they are smooth and gradually pointed in the smaller category, and rough, stepped, mucronate, or mammiform in the larger. An additional rapid scan of the slides indicated whether the complete size range had been included in the random measuring technique. The Smithsonian time-share computer was used to evaluate the data.

The terminology here used follows Borojević et al (1968). Abbreviations: USNM: United States National Museum (National Museum of Natural History, Smithsonian Institution, Washington, D.C.); YPM: Peabody Museum of Natural History (Yale University, New Haven, Connecticut); AMNH: American Museum of Natural History (New York, N.Y.).

Acknowledgements

This report is based on work carried out during the Bredin-Archbold-Smithsonian Biological Survey of Dominica. I thank Dr. Horton H. Hobbs, Jr., National Museum of Natural History, for making my participation in the survey possible. Mr. P. Brand and Mr. B. Robinson of Dominica gave valuable help. A large number of Jamaican specimens and microscope slides were made available to me for study through the generosity of Dr. W. D. Hartman, Peabody Museum of Natural History, Yale University. Dr. T. F. Goreau was my kind host in Jamaica and first introduced me to Caribbean deep-water reefs. The laboratory facilities of The Bellairs Research Institute, Barbados were generously made available by acting director Dr. T. H. Carefoot. Drs. E. Kirsteuer, American Museum of Natural History and H. Pulpan, University of Alaska were patient diving companions in Dominica and Barbados. I also acknowledge financial support during the International Indian Ocean Expedition (*Te Vega* cruise A), during my stay at the Lerner Marine Laboratory, Bimini (Office of Naval Research contract NONR 552 [027]) and during laboratory work (Smithsonian Office of Systematics). Dr. J. A. Peters, National Museum of Natural History, introduced me to the use of the Smithsonian time-share computer. Miss M. Dwyer prepared Figure 4. Mrs. C. Sterrer, Bermuda, prepared all other drawings from original photographs and photomicrographs.

Family ADOCIIDAE Laubenfels, 1934

Genus *Siphonodictyon* Bergquist, 1965

Gender: neuter. Type-species: *Siphonodictyon mucosum* Bergquist, 1965

Definition (revised).—Adociidae lacking microscleres. Ectosomal spicule tracts ending in perpendicular brushes supporting surface net. Spongin strongly reduced. Sponginous spicule reinforced membrane sheaths lining exhalant system. Pulpy mucus-secreting choanosome with oogonia cysts and spicules in confusion. Spicules are oxea with mucronate, stepped or rough tips. Smaller size category with gradually pointed tips also present in choanosome (possibly younger growth stages). Habit of burrowing in limestone substrata, only apertures bearing ectosomal structures protruding.

Siphonodictyon mucosum Bergquist, 1965

FIGURES 1, 10*a*; PLATE 1

Siphonodictyon mucosa Bergquist, 1965, pp. 158–161, figures 20*a*, *b*, table 4.

HOLOTYPE.—USMN 23697; Iwayama Bay, Palau Archipelago; 0.9–6 m; 14 August 1955; "Project Coral Fish," col.

MATERIAL.—USNM 24105; *Te Vega* Station 98, Poeloe Melila, Delapan Group (2°15'N, 97°25'E), Indonesia; 0.6 m (low tide); 23 November 1963.

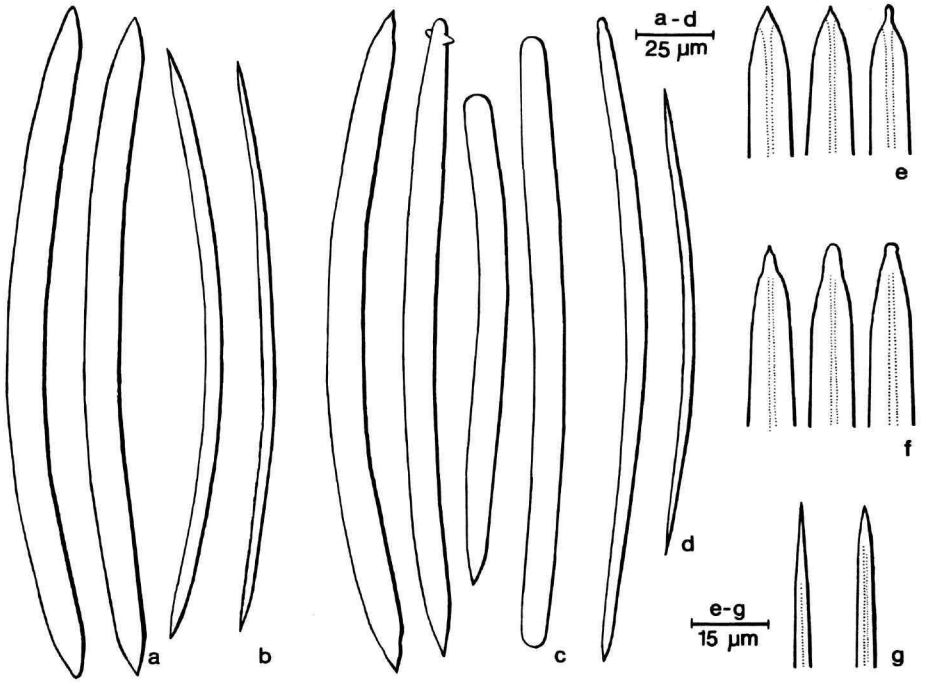


FIGURE 1.—*Siphonodictyon mucosum* Bergquist: large (*a,e*) and small (*b*) oxea of the Indian Ocean specimen; large oxea and derivatives (*c,f*) and small oxea (*d,g*) of the holotype.

DESCRIPTION.—Shape and size: From a substrate area of 150 cm² 26 hollow tubes were protruding. They are 5–10 mm in diameter and attain 88 mm from base to tip. Several of them are bifurcated, two or even three adjoining ones can be fused together sideways in their upper half. Seven of the tubes terminate in oscula, the remaining ones in sieve areas. The choanosome fills a cavity in the coral substrate, approximately 250 cm³ in volume.

Color: The tubes are blackish brown in life, the choanosome greyish tan. The color fades slightly in alcohol.

Consistency: The tubes are stiff and brittle, the choanosome soft, compressible and mucous.

Surface: Microhispid; the bases of the processes are incrusted with various sediment particles.

Apertures: The oscula are restricted to the terminal opening of the tubes. They are circular and measure 3–5.5 mm in diameter. The ostia (23–150 µm) * are distributed over the entire tube surface.

Skeleton: Bundles of stout longitudinal fibers run parallel to the lumina of the ectosomal tubes and radiate toward the surface. They are interconnected by less well defined secondary strands. The primary fibers fan out at the surface where they support a dense tangential reticulation. The main fibers measure 100–375 µm,* the secondaries 100–150 µm, the meshes of the reticulum 100–450 µm. The spiculation of the choanosome is in confusion.

Spicules: Rubust oxea with little developed central canal. Two size categories are distinct in the choanosome. The larger oxea have acute to mucronate, sometimes mammiform tips, the smaller ones are gradually and sharply pointed. Modifications to styles and strongyles are present.

Measurements (of the Indian Ocean specimen): Given in Table 2, and can be compared with the holotype.

REMARKS.—This record extends the range of this species from the Pacific to the Indo-Pacific region.

*Resolution 7 of the Thirteenth General Conference on Weights and Measures, 1968, substitutes for the micron (µ) = 10^{-6} meter the micrometer (µm), the symbol µ being reserved for the prefix micro- in this and other metric uses. See also the recent (1970) "Conversion to the Metric System," by Lord Ritchie-Calder (*Scientific American* 223 (1):17–25).

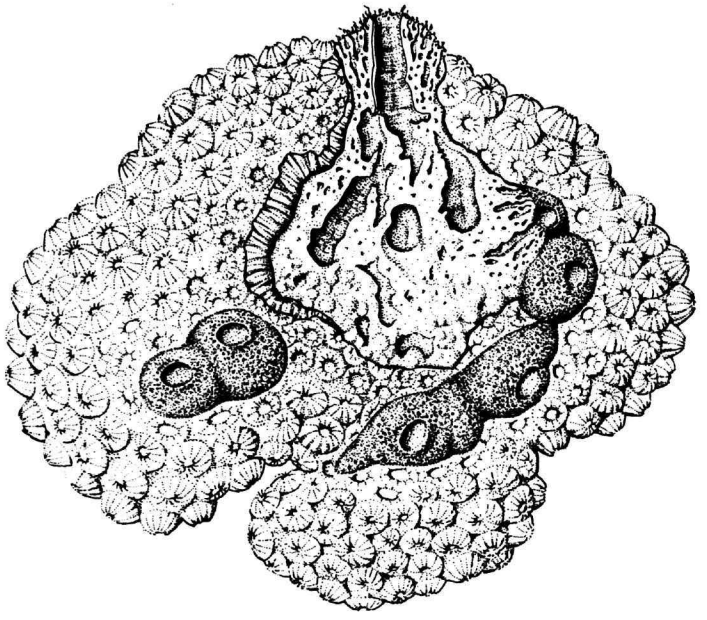


FIGURE 2.—*Montastrea annularis* infested by *Siphonodictyon cachacrouense*, new species. Part of the coral is removed to show the internal structure of the sponge (0.6 ×).

Probably a second Pacific species is *Siphonodictyon aberrans* (Dendy) from Three Kings Islands, New Zealand, transferred to this genus by Bergquist (1965).

Siphonodictyon cachacrouense, new species

FIGURES 2, 3, 10*b*; PLATES 2, 8*a*, *b*, *e*

HOLOTYPE.—USNM 24094 (Figures 2, 3; Plate 2; Table 2). Scotts Head Bay, Dominica, West Indies; 35 m; 19 June 1966 (only specimen).

DIAGNOSIS.—Epilithic sponge portion forming a tough elastic, irregular pillow. Color: dark greyish brown. Surface strongly hispid. Oscula circular, elevated with brush-like collar. Choanosome endolithic, irregularly massive, greyish tan. Oxea, large: 203.9 x 6.9 μm; oxea, small: 181.0 x 3.0 μm (means of 50 measurements each category).

DESCRIPTION.—Shape and size: The exposed ectosomal portion of the sponge forms an irregular pillow extending over an area of 120 cm². There are approximately 25 conical mounds reaching 25 mm in height, each terminating in an osculum. In some places coral fragments are showing between the elevations; these are remnants of the coral substrate. The massive choanosome extends 60 mm into the coral, filling a cavity of approximately 500 cm³.

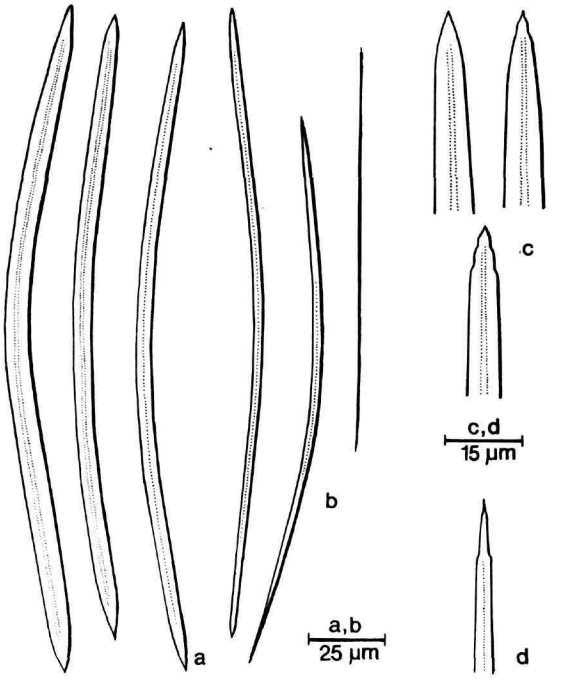


FIGURE 3.—*Siphonodictyon cachacrouense*, new species: large (*a*,*c*) and small (*b*,*d*) oxea of the holotype.

Color: The ectosome and the walls of the aquiferous system are dark greyish brown. The choanosome is light greyish tan with large dirty yellow embryos (June) contrasting from it. In alcohol the color remains the same although it fades slightly.

Consistency: The ectosome is very tough and elastic. In the transition zone to the choanosome it is ligneous due to the spicule-reinforced walls of the aquiferous canals. The choanosome is crumbly soft and compressible, with large amounts of mucus.

Surface: It is smooth to microhispid on the rising sides of the sponge, hispid, like a brush on top. Fiber bristles are slightly higher around the oscula.

Apertures: The elevated circular oscula are 4-8 mm in diameter. Ostia in the side portions of the sponge where they are not obscured by the bristle structure, measure 100–140 μm.

Skeleton: Stout spicule bundles radiate from the choanosome towards the surface. They branch frequently along their way and are interconnected by short secondary tracts. In the last 4–5 mm before the primary fibers reach the top surface of the sponge pillow the connecting secondaries are absent, thus causing the brush-like appearance of the surface. At the side portions of the sponge, however, the primaries are also interconnected near the surface, where they support a tangential fiber reticulation. The primary bundles measure 120–400 μm in diameter, the interconnecting secondary ones 50–150 μm. The meshes of the surface net are 80–200 μm in diameter, its fibers 50–80 μm. In the choanosome spicules are abundant but show no orientation.

Spicules: Bent oxea, quite regular, with thin central canal. The tips are sharply pointed, usually smooth but sometimes rough, seldom stepped. A few modifications to styles or strongyles occur. In the choanosome a second (smaller and thinner) size category is quite distinct.

Measurements: Given in Table 2.

REMARKS.—This species is named after Pointe Cachacrou (Patois for Scotts Head) where it was collected. It is so distinct that it is described as new without hesitation although only one specimen was available for study.

Siphonodictyon coralliphagum, new species

HOLOTYPE.—USNM 24095 (Figure 5; Plates 3 e,f, 4 a-d; Table 2). Discovery Bay, Jamaica; 25 m; 24 March 1966.

DIAGNOSIS.—Epilithic ectosomal portions, if present, are brittle crusts, hollow cones or tubes. They extend over 2 to 600 cm². Color deep yellow, lemon yellow to whitish yellow. Circular oscula on top of elevations, if such are existing. Surface microhispid. Choanosome usually endolithic, ovoid to irregular massive. Color: beige yellow to yellow tan. Oxea, large: 135.9–169.3 x 4.7–6.9 μm; oxea, small: 118.9–159.6 x 2.1–3.2 μm (range of means of all 22 specimens attributed to the species).

Based on morphological and spicule-dimension differences, four forms can be distinguished which might be different ecophenotypes and or growth stages:

Forma *typica:* Ectosomal structures consisting of single conical chimneys or tubes protruding from the substratum. Oxea, large: 142.1–156.3 x 5.0-6.4 μm; oxea, small: 129.0–142.9 x 2.2–2.7 μm (range of means).

Forma *obruta:* No ectosomal structures present. Oxea, large: 135.9–144.0 x 4.9–6.2 μm; oxea, small: 118.9–129.4 x 2.1–2.7 μm (range of means).

Forma *tubulosa:* Clusters of ectosomal tubes, trumpets or finger-shaped hollow processes. Oxea, large: 165.9–169.3 x 6.1–6.9 μm; oxea, small: 144.5–152.2 x 2.2–3.2 μm (range of means).

Forma *incrustans:* Extensive flat ectosomal crusts or pillows. Oxea, large: 150.0–164.9 x 4.7–5.7 μm, oxea, small: 140.5–154.7 x 2.3–2.8 μm (range of means).

Siphonodictyon coralliphagum forma *typica*

FIGURES 4, 5, 9*b, c,* 10*c;* PLATES 3, 4*a-d,* 8*c, d, f,* 9*a-c, e, f*

MATERIAL.—USNM 24095; Discovery Bay, Jamaica; 25 m; 24 March 1966 (holotype of the species). USNM 24096; Scotts Head Bay, Dominica, West Indies; 1.5 m; 4 April 1966. USNM 24097; Scotts Head Bay, Dominica, West Indies; 15 m; 11 July 1969. YPM 6487A; Discovery Bay, Jamaica; 45 m; 19 July 1966; J. Lang, col. YPM 6507; Runaway Bay, Pear Tree Bottom, Jamaica; 30–33 m; 22 July 1966; J. Lang, col. (paratypes of the species).

DESCRIPTION.—Shape and size: Tuberculate chimneys with thick walls are protruding from the live coral substrate. The osculum on top is half to one-third of the chimney diameter. This typical appearance can be modified if no osculum is present; one can find irregular papillae of all sizes, sometimes

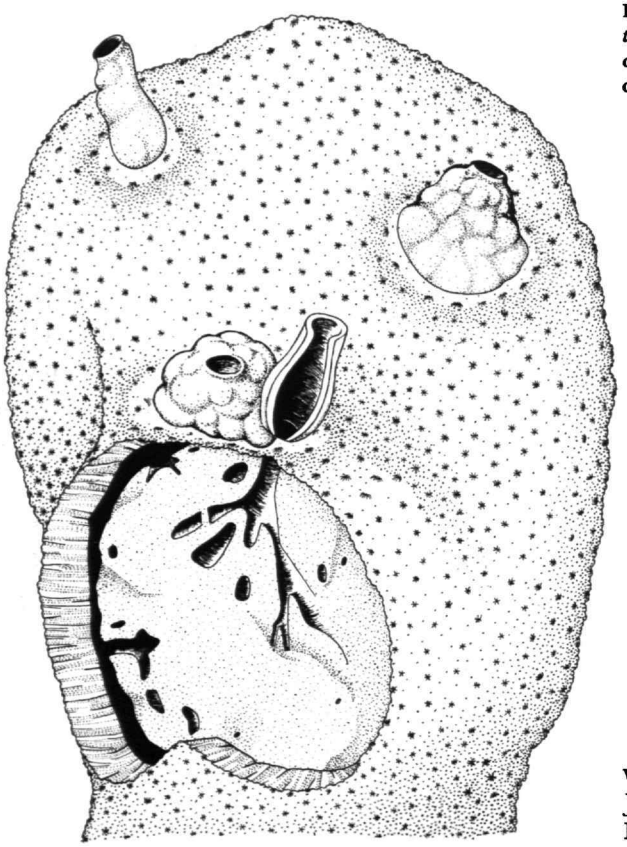


FIGURE 4.—*Stephanocoenia michelinii* infested by *Siphonodictyon coralliphagum*, new species (forma *typica*). Part of the coral is removed and one tubular process is cut open to demonstrate the internal structure of the sponge (0.6 ×).

only a tuberculate pillow. These can also be an outgrowth from the chimney base. Occasional thin-walled tubes are never vase-shaped. On top of some papillae the usually dense network of spicule strands is loosened up in various degree suggesting the break-through of a new osculum. The various epilithic structures are 5–35 mm in diameter, 6–40 mm high. They stand 2–10 cm apart, and 1 to a maximum of 4 were counted for each sponge specimen. The choanosome is endolithic; it may also reach the coral surface or be 20–30 mm removed and connected with the epilithic structures through tunnels of 10–15 mm diameter. The choanosome completely fills the ovoid to irregular cavities in the coral-rock. It has a volume of 20–130 cm^3.

Color: The exposed ectosome is of consistent deep yellow (comparable to egg-yolk) in the live specimens. If left in contact with air for some minutes the color changes to pinkish yellow. The choanosome is yellowish beige; it stains the fingers yellow when handled. Numerous large embryos (April and July) are conspicuous by their bright yellow color. In alcohol the color changes to greyish-tan, light in the ectosome, dark in the choanosome.

Consistency: The ectosome is friable but the chimneys as a whole are quite elastic, due to spicule reinforcement in the walls of the large exhalant canals. The choanosome is soft and mucous and unelastically compressible.

Surface: It is finely porous and microhispid.

Apertures: The oscula are always elevated, i.e., on top of the chimneys or tubes. They are circular, 2–10 mm in diameter. The ostia are distributed over the entire surface and measure 100–250 μm.

Skeleton: A delicate, more or less regular network of polygonal meshes overlays most of the surface parts. The spicule tracts forming the meshes are 2–6 parallel spicules wide. The mesh diameter is 75–125 μm.

The aquiferous canals of the choanosome, as well as the lumina of the oscular chimneys are lined with multiple layers of detachable membranes. These contain loose two-dimensional spicule strands embedded in a spongin matrix. This seems to be the

place of origin for massive longitudinal spicule bundles which start deep in the choanosome and run parallel to the canal lumina to the top surface of the sponge. They are supporters of the exposed sponge processes. They also radiate toward all other parts of the sponge surface, subdivide and are interconnected by secondary tracts to form a solid network. This becomes looser and more delicate the closer it approaches the surface, where it finally supports the tangential surface net.

The primary strands are 100–175 μm across but are frequently fused together to fascicles. The secondary strands measure 40–100 μm, the meshes they form average 120–300 μm. In the choanosome spicules are in confusion.

Spicules: Oxea, usually slightly bent, with more or less distinct central canal. A smaller and thinner size category is distinct in the choanosome. The tips are typically mucronate but many stepped, rounded, mammiform, and tylote modifications are present.

Measurements: Given in table 2.

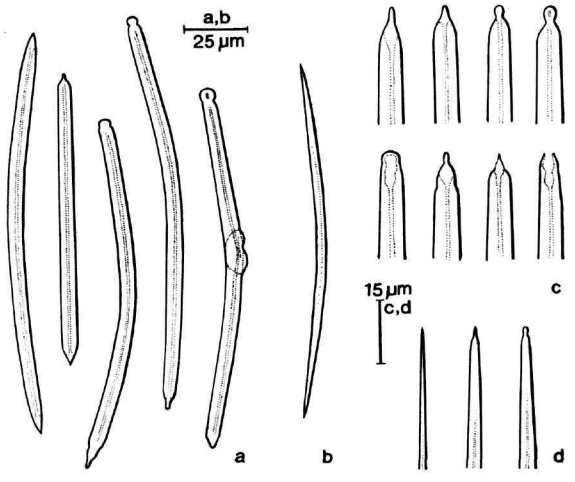


FIGURE 5.—*Siphonodictyon coralliphagum*, new species (forma *typica*); large (*a,c*) and small (*b,d*) oxea (and derivatives) of the holotype.

Siphonodictyon coralliphagum forma *obruta*

FIGURES 6, 9*a*, 10*c*; PLATE 4*e-g*

MATERIAL.—USNM 24098; Southwest of Holetown, Barbados, West Indies; 25 m; 5 July 1969 (specimen representative for the form). USNM 24099; South of Holetown, Barbados, West Indies; 20 m; 7 July 1969. USNM 24100; off Littlegood Harbour, Barbados, West Indies; 23 m; 7 July 1969. YPM 4398; Cayo de Caballo Ahogao, near La Parguera, Puerto Rico; 18 June 1959; W.D. Hartman and J. Rivero, col.

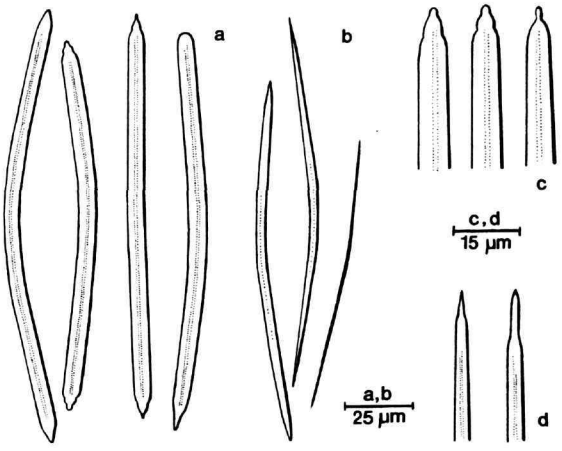


FIGURE 6.—*Siphonodictyon coralliphagum*, new species, forma *obruta*: large (*a,c*) and small (*b,d*) oxea (and derivatives).

DESCRIPTION.—Shape and size: The entire sponge is endolithic. Its choanosome fills cavities in coral rock, 5–10 mm below the coral surface. The cavities are spherical in small specimens (5–10 mm in diameter), ovoid in larger ones (10–20 mm), the larger axis being parallel to the substrate surface. One or two tissue-lined tunnels (0.5–1.8 mm diameter) lead to an opening on the coral rock surface. These tunnels always run at an angle of 20–40 degrees to the perpendicular coral structure, at least in the specimens available.

Color: Uniformly yellowish beige.

Consistency: Soft compressible and slightly mucous.

Surface: No epilithic parts are present.

Apertures: The only apertures detectable are the circular vents of the tunnels mentioned above. They have the same size as the tunnel diameter.

Skeleton: The oxea are abundant but without orientation, like in the choanosome of the typical form. Only near the coral substratum they have a tendency to be placed tangentially.

Spicules: Two size categories of more or less distinctly bent oxeas. Styles occur occasionally. The tips are stepped, mucronate to mammiform.

Measurements: Given in Table 2.

Siphonodictyon coralliphagum forma *tubulosa*

FIGURES 7, 9*e*, 10*c*; PLATES 5*a*, *b*, 6

MATERIAL.—USNM 24101; Scotts Head Bay, Dominica, West Indies; 20 m; 30 May 1966 (specimen representative for the form). USNM 24102; Scotts Head Bay, Dominica, West Indies; 35 m; 18 June 1966. USNM 24103; Scotts Head Bay, Dominica, West Indies, 35 m; 18 June 1966. USNM 24104; Scotts Head Bay, Dominica, West Indies; 15 m; 11 July 1969.

DESCRIPTION.—Shape and size: The epilithic part of single specimens extends over areas of 70–950 cm^2 between live coral heads. It consists of dense clusters of thin-walled tubes (0.8–1.2 mm wall thickness) frequently vase- or funnel-shaped, alternating with hollow finger-shaped processes which can be fused together along their sides, forming humpy pillows. The ectosome between these aquiferous processes (their distance from each other: 5–25 mm) is encrusted with coralline algae which again provide substrate for secondary settlers (algae, sponges, bryozoans, tunicates). The coralline algal crusts can reach up to 5 mm below the oscular rim of the larger tubes (e.g., specimen USNM 24101). The following counts and measurements were taken on the fresh specimens (Table 1):

The choanosome extends horizontally as far as the ectosome. The upper portion lies level with the

TABLE 1.—*Specimen Measurement of* Siphonodictyon coralliphagum *forma* tubulosa.

Specimen Number	Area Measured	Process			
		Type	Number	Diameter	Height
USNM 24101	600 cm^2	open tubes	9	15-25 mm	50-65 mm
		closed fistules, single	43	8-12 mm	6-30 mm
		closed fistules, double and triple	8	12-39 mm	25-30 mm
(not preserved)	300 cm^2	open tubes	26	7-16 mm	10-55 mm
		closed fistules and low papillae (some double or triple)	68	5-15 mm	8-26 mm
USNM 24102	200 cm^2	open tubes, vase-shaped	6	9-20 mm	15-48 mm
		closed fistules, single or double	14	5-10 mm	8-15 mm
		low papillae, all fused together, some also fused with tubes	70 (approx.)	100 mm	6-14 mm
USNM 24103	70 cm^2	open tubes	2	18, 20 mm	20, 25 mm
		papillae, single	4	6-12 mm	6-8 mm
		papillae, fused	-	60 mm	11-15 mm

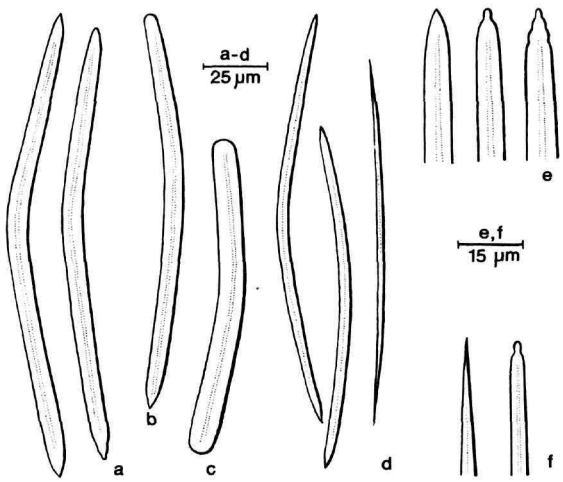


FIGURE 7.—*Siphonodictyon coralliphagum,* new species, forma *tubulosa:* large oxea (*a,e*), style (*b*), strongyle (*c*) and small oxea (*d, f*).

coral substrate, most of which has been dissolved; only some coral fragments are still embedded; the lower portion is endolithic. It attains approximately 2 liters in volume in a large specimen.

Color: The ectosome is a light yolk yellow; one specimen (USNM 24102) was whitish yellow in life. During exposure to air the same color change to pinkish yellow occurs as in the typical form. The color of the choanosome is yellowish beige with bright yellow embryos, as in the typical form. In alcohol the color changes to dark beige or greyish-tan.

Consistency: All ectosomal processes are very fragile. In the transition zone to the choanosome, numerous exhalant canals with spicule-reinforced walls cause a ligneous consistency. The choanosome is soft, compressible, and very mucous.

Surface: The surface, where not covered by coralline algae, is microhispid.

Apertures: The oscula on top of the thin-walled tubes measure 7–19 mm in diameter. The ostia situated on the surface of all processes are 120–280 µm in diameter.

Skeleton: Structure and measurements of the spicule bundles fall in the range of the typical form.

Spicules: Bent oxea with fine central canal. The two size categories of the choanosome are distinct. The tips are rather blunt to mammiform, usually smooth, sometimes rough to stepped. Some styles and strongyles occur.

Siphonodictyon coralliphagum forma *incrustans*

FIGURES 8, 9*d*, 10*c*; PLATES 5*c, d*.

MATERIAL.—YPM 4757; Runaway Bay, Jamaica; 30–33 m; 16 July 1961; D. Fraser, E. Graham, col. (specimen representative for the form). YPM 4816; Runaway Bay, Jamaica; 24 m; 21 July 1961; E. Graham, col. YPM 4831; Runaway Bay, Jamaica; 15–27 m; 21 July 1961; I. Goodbody, R. L. Walker, col. YPM 4930; Runaway Bay, Jamaica; 15 m; 23 July 1961; T. F. Goreau, E. Graham, R. Dalzeel, col. YPM 5346, YPM 5359, YPM 5388, YPM 5395; Runaway Bay, Jamaica; 33–39 m; 21 May 1961; T. F. Goreau, D. Fraser, L. M. Passano, col. YPM 6496, YPM 6896; Discovery Bay, Jamaica; 57 m; 21 July 1966; J. Lang, col.

DESCRIPTION.—Shape and size: Flat crusts, irregular pillows, or flat cones show above substrate level. Oscula, if present are not, or only slightly, elevated. The maximum diameter of these structures varies between 2 and 26 cm, surface area is approximately 3.5 to 350 cm^2. The choanosome is buried in the substrate; its thickness is about one-third the diameter of the whole sponge.

Color: The ectosome varies from deep to lemon yellow, the choanosome is mustard yellow to yellow-tan. Preserved specimens are ochre to dark brown; the preservation alcohol of larger specimens is also stained brown.

Consistency: the ectosome is firm but brittle; the choanosome soft, compressible, and very mucous.

Surface: Microhispid and porous. Oscula are distinct only in larger specimens.

Apertures: The oscula are usually level with the sponge surface, are sometimes slightly elevated, and are surrounded by a slight rim; their shape is typically circular. Occasionally, however, two or more adjoining ones become fused together presenting an oval to irregular outline (very distinct in specimen YPM 6496). The interior of the oscula appears as dark in color as the choanosome (in preserved state). The ostia measure 80–300 µm.

Skeleton: Structure of the skeleton and size of the spicule bundles is not different from the typical form.

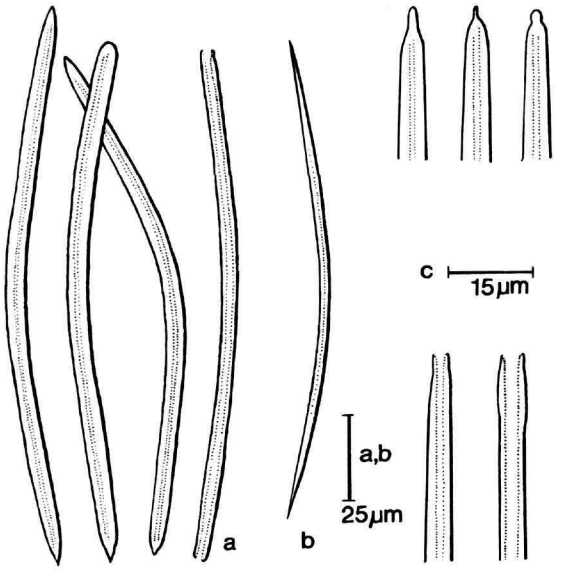


FIGURE 8.—*Siphonodictyon coralliphagum*, new species, forma *incrustans*: large (*a,c*) and small (*b*) oxea (and derivatives).

Spicules: The oxea are usually slightly, sometimes sharply bent. A central canal is distinct only in the ectosomal spicules. Separation into two size categories in the choanosome is only slight since there are many transitional forms. Some styles are present. Tips are blunt, mammiform or mucronate, degenerated where there is a wide central canal developed.

Measurements: Given in table 2.

DISCUSSION.—It can be expected that further and more directed studies in the Caribbean area will shed light on the proper systematic status of the various forms of *Siphonodictyon coralliphagum*. The species is certainly more widely distributed than the available specimens would suggest. According to the author's field notes—which unfortunately, are not documented by specimens—formae *typica* and *obruta* were encountered also around Bimini. Particularly, during earlier collecting forma *obruta* has been frequently discarded because it was considered a secondary settler in clionid burrows and the material was too sparse to be properly recognized. Forma *typica* could on several occasions be clearly identified from amateur under-water photographs taken in Caribbean deep-water reefs. There is no indication, however, that forma *tubulosa* occurs outside of Dominica and that forma *incrustans* has been found outside of Jamaica. Transitional stages between forma *typica* and forma *tubulosa* on the one hand and forma *incrustans* on the other have been observed at Dominica and Jamaica, respectively. No transitional forms between *obruta* and *typica* are evident, although it can be anticipated with little speculation that the latter derives from the former (Figure 9). After plotting means, standard deviation, and double standard error of length and width of the oxea for each species and form (Figure 10) one also arrives at the conclusion that, because of the overlap of the double standard errors, the four forms of *Siphonodictyon coralliphagum* belong to one population (Hubbs and Perlmutter 1942). It might be a coincidence that from the same graph can be read a tendency towards evolution (in a morphological sense) from forma *obruta* via forma *typica* to either forma *tubulosa* or forma *incrustans*.

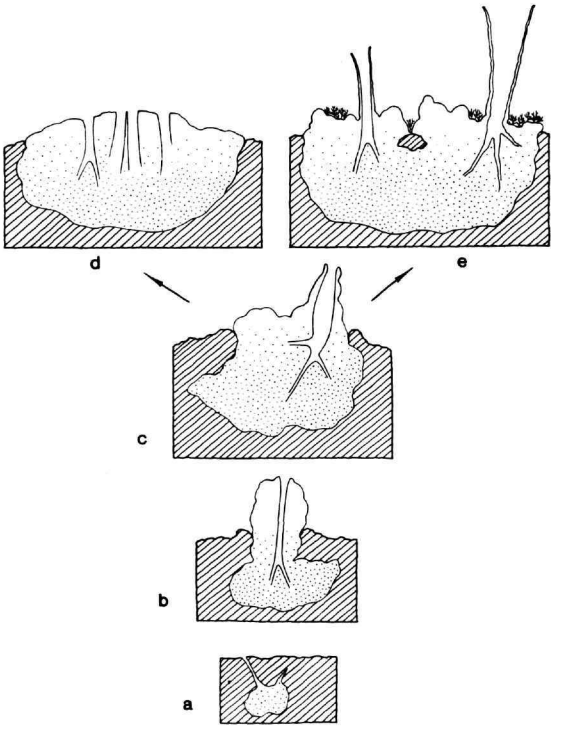


FIGURE 9.—*Siphonodictyon coralliphagum*, new species. Morphological variation of the forms in hypothetical sequence: formae *obruta (a), typica (b), typica (c), incrustans (d), tubulosa (e)*.

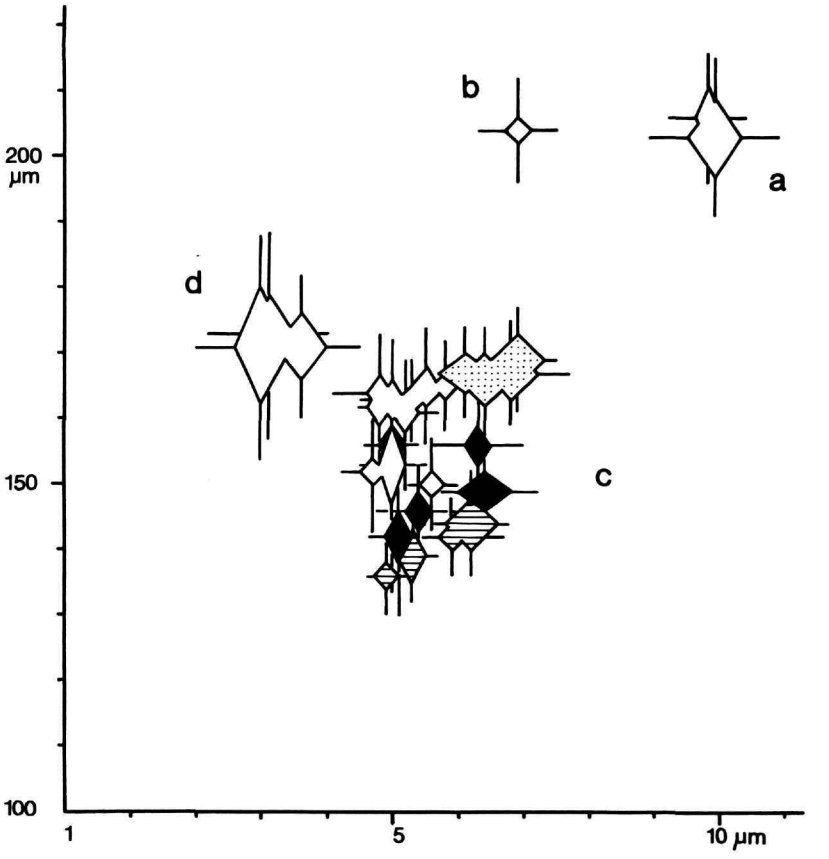


FIGURE 10.—Length versus width plots of spicule measurements for species and forms of *Siphonodictyon*. Means lie in the center of the diamonds; mean plus or minus one standard deviation is represented by bars; the values for mean plus or minus twice the standard error are connected to form the diamonds. *a, Siphonodictyon mucosum* Bergquist; *b, Siphonodictyon cachacrouense*, new species; *c, Siphonodictyon coralliphagum*, new species (hatched=forma *obruta*, black=forma *typica*, white=forma *incrustans*, stippled=forma *tubulosa*); *d, Siphonodictyon siphonum* (Laubenfels).

Siphonodictyon siphonum (Laubenfels), new combination

Siphonochalina siphona Laubenfels, 1949, pp. 11–13.

FIGURES 10*d*, 11; PLATES 7, 9*d*.

HOLOTYPE.—AMNH 468; Bimini, Bahamas; less than 1 m; 1 July 1948.

MATERIAL.—USNM 24106, USNM 24107; East of Turtle-Rocks, Bimini, Bahamas; 1 m; 7 August 1967.

DESCRIPTION.—Shape and size: Clusters of tubes and hollow processes protrude from the sand substratum. They are irregular oval in cross section, 6–18 mm in diameter, and up to 70 mm high (from substrate level). The walls are 1–3 mm thick. Two to seven processes are fused together along their sides. The largest of the collected clusters extended over an area of 20 cm^2, up to 20 were observed per m^2 of sand bottom. Most of the basal mass of the choanosome is buried in the sand, only fragments were recovered.

Color: The exposed parts are chestnut brown, sometimes with a reddish tinge, the choanosome is greyish brown in life. They turn blackish brown in alcohol.

Consistency: The tubes are stiff but elastic, the choanosome is soft, compressible, and mucous.

Surface: Smooth to microhispid, particularly on top of the finger-shaped processes. Numerous wart-like swellings bearing a single pore (ostium?) can be noted.

Apertures: The oscula are more or less circular with irregular brush-like rims. They measure 5–12 mm in diameter. The ostia measure 150–300 μm.

Skeleton: A discontinuous surface reticulation is present. The tracts of spicules embedded in some spongin are 30–150 μm in diameter; they form meshes of 250–600 μm. Below, the ectosomal reticulation consists of radiating primary fibers, brushing

out at the surface; these are connected by secondaries to form rectangular meshes. Fiber diameter, 75–125 μm; mesh diameter, 150–250 x 75–120 μm. In the choanosome the spiculation is in confusion, with the exception of some irregular strands.

Spicules: The slender oxea are usually bent, with a tendency to being flexuous. A second size category is not distinct. In the ectosome they are frequently broken. The tips are rough to acuminate, sometimes modified to styles or strongyles sometimes degenerated.

Measurements (of the present specimens and of the holotype): Given in Table 2.

REMARKS.—As Laubenfels (1949) has pointed out large accumulations of this sponge occur on (and in) shallow-water sand bottoms of Bimini. He also stated that the "basal mass" (actually the whole choanosome) is regularly buried beneath the sand and "its total size was never satisfactorily ascertained." Also in the present collection most of the mucous choanosome was left behind when the specimens were removed from the substratum. Recovered portions showed that fragments of dead coral embedded in the sand were clearly excavated where they interfered with the extending body of the sponge. This proves that the species not only has the morphological and anatomical features of *Siphonodictyon* but also the excavating properties of the genus.

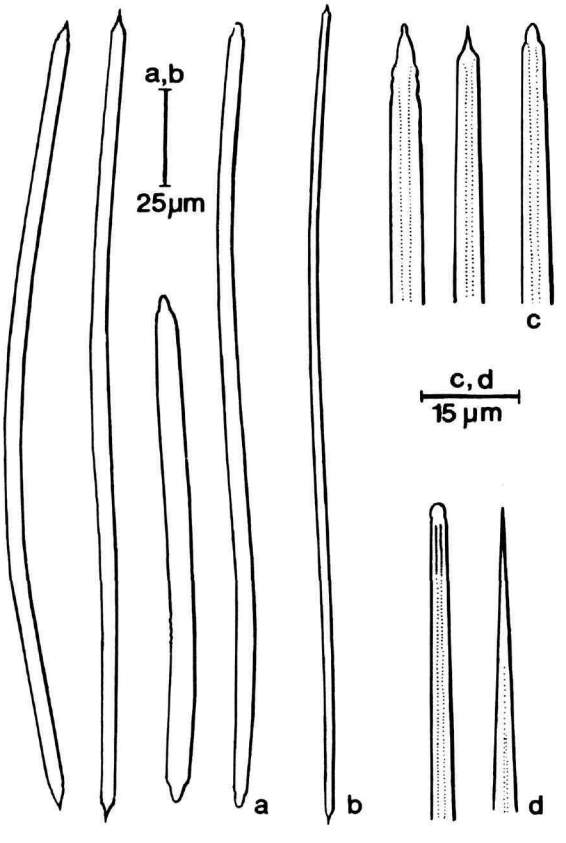


FIGURE 11.—*Siphonodictyon siphonum* (Laubenfels): large (*a,c*) and small (*b,d*) oxea.

Histological Findings

On the level of the presently employed methods the histological picture of the various forms and species is quite similar. Exo- and endopinacoderm are formed in the usual manner by anucleolate cells. The major canals, particularly in the ectosomal region are lined by a multiple layer of thin fibrous membranes (Spongin A? [Gross et al. 1956]) which are stained by aniline blue (Plate 8a).

These membrane sheets vary in thickness from 15–30 μm in the choanosome, to more than 500 μm in the ectosome. In the ectosome they contain spicule strands running crisscross in subsequent layers. Macerated preparations of primary spicule bundles show that they can be connected by such membranes. Thus it appears that the primary spicule fibers originate in membrane sheaths. They run parallel to the exhalant canals until somewhere along their course they radiate towards the sponge surface (see systematic section).

In the extensive lacunar spaces between and attached to the membranes are numerous spindle-shaped nucleolate cells (15–35 μm long, 3–6 μm wide) filled with acidophilic and basophilic grains (Plate 8*b*). There is also another similar cell type which contains finely granular basophilic inclusions and sometimes a larger chromophobic grain. In peel preparations of membranes lining ocular tubes they can be seen in thick strands crowding bundles of spicules.

The ectosomal area of the spicule fiber network shows but little cellular material. Some of the same two cell types as in the membrane section are present as well as circular to oval nucleolate cells with acidophilic granules (6–17 x 5–8 μm. The most abundant cells, however, are anucleolate, 5–12 x 3–6

μm and amphophilic. They secrete a filamentous meshwork of basophilic ground substance. Both, the cells and the filamentous ground substance are particularly dense in an area of regeneration of *Siphonodictyon coralliphagum* forma *typica* (specimen YPM 6507). Part of the choanosome of this specimen had obviously been exposed after perforation of the coral substratum, presumably by scraping fish (Plate 3*d*). Some spicule tracts have also been regenerated in this area, the individual spicules being cemented by fairly large amounts of spongin B (Plate 8*c*). The presence of spongin in *Siphonodictyon* had been overlooked in the original description of the genus (Bergquist 1965). In fact, in normal specimens it occurs only in minute quantities on the ectosomal spicules tracts. However, after careful search its presence could also be confirmed in the holotype of the type species. Apparently, spongin is used only during the first steps of skeleton formation to connect loose spicules and is later reduced or at least not further developed.

Choanocyte chambers occur throughout the choanosome (Plate 8*d*). They are spherical and measure 16–20 μm in diameter. All three nucleolate cell types from the ectosome are also encountered in the choanosome in small numbers. Archeocytes containing 8–12 highly refractile spherules are common, particularly in specimens containing embryos (Plate 8*e*). The spherules occur also free in small aggregations. They measure 2–4 μm and are superficially eosinophilic. Their nature will have to be studied histochemically, but one can assume that they have nutritive function, since they are one of the main constituents of all embryos. Sperm cysts were only rarely found. They are oval, measure approximately 80 x 40 μm, and contain basophilic sperm.

The most conspicuous feature of the choanosome of all specimens are the spherical cell groups which are evenly distributed throughout the choanosome (Plates 8*f*, 9*a*). Each group is surrounded by an epithelium and a fine layer of fibrous basophilic material. These cysts measure 20–70 μm in diameter and contain 5–20 large cells in each cross section. The individual cells measure about 5–15 μm with a turgid nucleolate nucleus of 5–7 μm. Grains of chromatin form a loose net and sometimes filaments. These cell groups must be considered cysts of oogonia. Mature egg cells (Plate 9*b*) attain the size of 20–30 x 8–14 μm, with a nucleus of 7–8 μm and a nucleolus of 2 μm. A single extremely large cell measured 40 x 27 μm; nucleus, 16 μm; nucleolus, 3 μm. They contain acidophilic granules of about 1 μm. Some were fixed in the state of leaving the cyst by means of developed amoeboid processes. Bergquist (1965) suspected the cell groups mentioned as being responsible for mucus production. Unfortunately, attempts to conclusively support or disprove this view were unsuccessful during this study. The mucus (Plate 9*c*) is strongly metachromatic (toluidine blue). Some of the larger eggs cells show some metachromatic inclusions but so do some of the granular cells in the ectosomal membrane layers. Large numbers of what look and stain like isolated collapsed nuclei can be found in mucus accumulations (Plate 9*d*). Individual mucus droplets are also abundant but no cellular material surrounding them was ever evident. It is striking to note that all embryos contain mucus in considerable quantity. This could mean that the egg cells are capable of mucus secretion, since no other means of obtaining mucus were apparent. More work on the histology and histochemistry of this problem is definitely needed.

The embryos are oval and up to 1 mm in length. They are surrounded by a sponginous capsule (Plates 8 *e*, 9 *e*) and an epithelium of roundish or somewhat polygonal cells measuring 14–20 μm, with a 3–4 μm nucleus (Plate 9*f*). They are almost filled with the formerly mentioned highly refractive spherules, some of them in carrier cells and with mucus. Some amoeboidal basophilic cells are present throughout the embryo, nuclei are accumulated toward the periphery.

Ecological Observations and Distribution

With respect to its ecology, available data indicate that *Siphonodictyon* is exclusively an inhabitant of tropical reef environments. Bimini, Bahamas is the northern-most locality where the sponges (*S. coralliphagum* and *S. siphonum*) were found during the present study. Careful search in numerous coral-reef patches off the Bermuda Islands did not reveal a single specimen. Thus, temperature could be considered a limiting factor. In the surface layers of Bermuda it drops down to 15–17° C. in average winters (Laubenfels 1950).

S. coralliphagum is widely distributed throughout the Caribbean. However, it appears to be restricted

TABLE 2.—*Spicule Dimensions in Micrometers (S.D., Standard Deviation; S.E., Standard Error).*

Specimen Number	Oxea Size Category	Length: Range (Mean)	Length: S.D. (S.E.)	Width: Range (Mean)	Width: S.D. (S.E.)
Siphonodictyon mucosum					
USNM 23697	I	171.3-220.0(202.7)	12.0 (2.8)	7.2-12.0(9.9)	1.0 (0.2)
(holotype)	II	142.5-207.5(187.0)	16.0 (3.5)	2.4-8.0(4.2)	1.4 (0.3)
USNM 24105	I	185.6-222.4(205.8)	10.4 (2.3)	8.8-11.2(9.8)	0.6 (0.1)
	II	153.6-198.4(175.1)	13.8 (3.3)	1.6-6.4(4.7)	1.5 (0.4)
Siphonodictyon cachacrouense					
USNM 24094	I	185.0-217.5(203.9)	8.0 (1.2)	6.0-8.0(6.9)	0.6 (0.1)
(holotype)	II	147.5-220.0(181.0)	15.5 (2.2)	1.3-4.8(3.0)	1.1 (0.3)
Siphonodictyon coralliphagum forma typica					
USNM 24095	I	134.4-152.6(145.6)	6.7 (1.5)	3.8-6.5(5.4)	0.7 (0.1)
(holotype)	II	109.0-145.6(129.0)	10.7 (2.4)	1.0-4.0(2.2)	0.6 (0.2)
USNM 24096	I	140.8-164.8(155.6)	6.7 (1.5)	4.8-9.6(6.3)	0.7 (0.1)
	II	124.8-153.6(142.9)	9.4 (2.1)	1.3-3.2(2.3)	0.7 (0.2)
USNM 24097	I	140.0-164.8(148.6)	7.0 (1.5)	5.1-7.9(6.4)	0.8 (0.2)
	II	121.6-150.4(136.5)	7.2 (1.6)	1.6-3.5(2.6)	0.6 (0.1)
YPM 6487A	I	137.6-177.6(156.3)	8.6 (1.3)	4.0-6.1(5.0)	0.4 (0.1)
	II	102.4-160.0(137.1)	17.4 (4.3)	1.3-3.2(2.2)	0.6 (0.2)
YPM 6507	I	112.0-160.0(142.1)	11.7 (2.1)	4.0-6.4(5.1)	0.5 (0.1)
	II	83.2-147.2(129.0)	14.7 (2.9)	1.6-3.5(2.7)	0.7 (0.1)
Siphonodictyon coralliphagum forma obruta					
USNM 24098	I	136.0-152.0(141.9)	5.6 (1.2)	5.3-6.9(5.9)	0.8 (0.2)
	II	113.6-144.0(129.3)	8.2 (1.8)	1.6-2.9(2.1)	0.5 (0.1)
USNM 24099	I	129.6-153.6(139.4)	6.6 (1.8)	3.7-6.4(5.3)	0.4 (0.1)
	II	105.6-139.2(127.4)	8.0 (1.8)	1.6-3.5(2.7)	0.6 (0.2)
USNM 24100	I	126.4-155.2(144.0)	7.7 (1.8)	6.4-7.2(6.2)	0.6 (0.2)
	II	112.0-144.0(129.4)	7.8 (1.8)	1.3-4.0(2.7)	0.8 (0.2)
YPM 4398	I	126.4-153.6(135.9)	5.5 (0.8)	4.0-5.6(4.9)	0.3 (0.1)
	II	107.2-134.4(118.9)	6.9 (1.4)	1.3-3.5(2.3)	0.6 (0.1)
Siphonodictyon coralliphagum forma tubulosa					
USNM 24101	I	156.0-180.8(167.4)	6.6 (1.6)	5.0-7.1(6.1)	0.7 (0.2)
	II	121.6-174.4(152.2)	11.2 (2.6)	1.3-4.0(2.6)	0.8 (0.2)

TABLE 2.—(Continued)

Specimen Number	Oxea Size Category	Length: Range (Mean)	Length: S.D. (S.E.)	Width: Range (Mean)	Width: S.D. (S.E.)
Siphonodictyon coralliphagum forma tubulosa -- Continued					
USNM 24102	I	156.0-182.4(169.3)	7.8 (2.2)	5.7-7.6(6.9)	0.6 (0.2)
	II	121.6-161.6(148.2)	10.4 (2.4)	1.6-4.2(3.2)	0.8 (0.2)
USNM 24103	I	149.6-180.0(165.9)	8.0 (2.0)	5.1-7.6(6.4)	0.7 (0.2)
	II	116.8-168.0(151.2)	11.5 (2.7)	1.6-3.7(3.0)	0.6 (0.1)
USNM 24104	I	154.4-179.2(167.0)	7.5 (2.0)	5.2-8.1(6.8)	0.9 (0.2)
	II	120.0-161.6(144.5)	12.3 (2.7)	1.6-3.5(2.2)	0.6 (0.2)
Siphonodictyon coralliphagum forma incrustans					
YPM 4757	I	108.8-161.6(151.8)	8.5 (1.2)	3.2-6.4(4.7)	0.5 (0.1)
	II	118.4-156.8(140.5)	8.8 (1.8)	1.3-3.5(2.6)	0.7 (0.1)
YPM 4816	I	67.0-184.0(153.2)	19.1 (3.2)	4.0-6.4(5.0)	0.5 (0.1)
	II	123.2-160.0(143.8)	10.5 (3.3)	1.6-3.7(2.8)	0.8 (0.2)
YPM 4831	I	123.2-179.2(163.6)	9.4 (1.3)	3.5-6.7(4.8)	0.7 (0.1)
	II	123.2-166.4(149.7)	10.8 (2.8)	1.3-4.5(2.6)	0.9 (0.2)
YPM 4930	I	139.2-160.0(150.0)	6.6 (1.0)	4.8-6.4(5.6)	0.4 (0.1)
YPM 5346	I	136.0-176.0(163.4)	8.7 (1.4)	4.0-6.1(5.0)	0.5 (0.1)
	II	153.6-168.0(159.6)	3.7 (1.0)	2.1-3.2(2.8)	0.4 (0.1)
YPM 5359	I	137.6-177.6(162.3)	8.6 (1.4)	4.0-5.6(4.8)	0.3 (0.1)
	II	136.0-169.6(154.7)	10.2 (2.6)	1.3-3.5(2.3)	0.6 (0.2)
YPM 5388	I	148.8-174.4(163.0)	5.8 (1.1)	4.8-6.4(5.3)	0.5 (0.1)
YPM 5395	I	147.2-174.4(160.6)	7.8 (1.7)	3.7-6.1(5.2)	0.5 (0.1)
YPM 6496	I	148.8-177.6(164.5)	6.6 (1.1)	4.8-6.4(5.7)	0.6 (0.1)
	II	118.4-163.2(150.2)	12.4 (3.2)	1.3-6.1(2.8)	1.2 (0.3)
YPM 6896	I	147.2-185.6(164.9)	8.9 (1.6)	4.8-6.7(5.5)	0.5 (0.1)
	II	128.0-161.6(147.1)	12.1 (2.8)	1.3-3.7(2.3)	0.8 (0.2)
Siphonodictyon siphonum					
AMNH 468 (holotype)	I	121.6-206.4(170.9)	17.2 (4.3)	1.6-6.4(3.0)	1.0 (0.2)
USNM 24106	I	152.5-192.5(170.8)	11.1 (2.7)	2.4-4.8(3.6)	0.9 (0.2)
USNM 24107	I	152.0-188.8(172.8)	16.0 (2.8)	2.4-5.6(3.1)	0.9 (0.2)

to the lower buttress zone, forereef, and forereef slope of fringing barrier-type reefs as they were described by Goreau (1959) and Goreau and Hartman (1963) from the Jamaican north coast. These habitats are between 10 and 70 m, and are below the direct influence of wave action. Steady but moderate water currents together with the steep bottom gradient prevent accumulation of sediment masses, unless they are trapped in the current shadow of the reef framework. The shallowest record for *S. coralliphagum* (forma *typica*) is 1.5 m in Scotts Head Bay, Dominica. There, geomorphic features and reef zonation are very similar to the Jamaican north coast; but the semicircular bay at the southernmost tip of Dominica is unusually well protected, there is no *Acropora palmata* (Lamarck) zone, and the buttress zone starts at a depth of only 1 m. The nearby deepwater and the massive water exchange caused by currents generated in the Martinique Channel on the other side of the Scotts Head peninsula prevent the bay from becoming a stagnant water body of lagoon character.

In the Bay, *Porites astreoides* (Lamarck) and *Diploria strigosa* (Dana) heads of an estimated 1- 3-liter volume, containing small specimens of the sponge, were lying loosely on the bottom. This situation must change considerably when a hurricane enters its usually leeward opening. As reported by natives of Cachacrou (Scotts Head Village) this occurred "a few years" before collecting time (1966). A perfect sandy beach surrounding the bay had then been washed out, leaving the present gravel shoreline. This may account for the absence of larger specimens of *Siphonodictyon* in shallow water, even in this protected habitat.

The depth range of the *S. coralliphagum* complex, based on the available data, is 1.5–57 m and the resulting mean depth is 29 m. The epilithic ectosomal sponge parts are fully exposed to the ambient light conditions, with exception of one specimen (YPM 5388) which was reported to be found under a shelving coral overhang. The oscular tubes and chimneys have a tendency to be oriented vertically, even if the substratum inclination is as much as 50-80 degrees. The light intensity on the substratum surfaces at noontime varied between 32% and 4% of the value just below the water surface (cadmium sulfide light-meter reading). The only specimen of *S. cachacrouense* was found within the same depth range (35 m) as *S. coralliphagum* and occurred under similar conditions and in the close neighborhood of formae *typica* and *tubulosa*.

Although, from the morphological appearance (Figure 9) it seems quite feasible that forma *tubulosa* derives from *typica* (in Dominica), no convincing transitional stages have been found. The same is true for formae *incrustans* and *typica* (in Jamaica). Still, it is likely that the encrusting as well as the tubular sponge are late stages, comparable to the beta and gamma stages of some clionid sponges. The question remains why the shape of the grown specimens is so strikingly different in the two locations. It is known that encrusting sponges can develop oscular tubes in stagnant water to prevent the expelled waste water from re-entering through the pores (Schäfer 1956). Such extreme conditions however are certainly not applicable here. Until more material from other localities is available it seems safe to assume that the differences have a genetic rather than an environmental basis.

The Indo-Pacific *S. mucosum* and the Caribbean *S. siphonum* have very similar ecological requirements. Both occur in large groups on and in shallow (about 1 m) sand-bottoms in flat bays, in lagoons and in similarly wave-protected environments. They are unaffected by high sedimentation rates and live fully exposed to solar radiation. They are accordingly rather darkly pigmented. S. *mucosum* still excavates burrows in dead coral, although these might be more or less buried in the sand. *S. siphonum* penetrates usually coarse sand but there is evidence on buried coral fragments that the potentiality of attacking limestone is present also in this species.

This leads us to the interesting burrowing habit of *Siphonodictyon*. The excavating technique of this genus as compared with that of clionid sponges will be discussed in a forthcoming communication (Rützler, in preparation). Mention should be made, however, that in contrast to clionid sponges *Siphonodictyon coralliphagum* as well as *S. cacharouense* attack living corals and harm the polyps *Cliona* infests, as a rule, the non-living basal parts of corals and only harms the living colony if the attachment is weakened and the coral breaks loose (Goreau and Hartman 1963). It could be a coincidence that the massive growing *S. cachacrouense* and *S. coralliphagum* forma *tubulosa* (no such information is available on forma *incrustans*) are usually closely surrounded by living coral tissue. The sponges could

still have settled on a dead coral part and eventually, during growth, have reached and oppressed the polyp regions. Forma *typica,* however, has been observed alive in various growth stages and there is little doubt that in most cases settlement took place amongst the living coral polyps. Sponge chimneys protrude so regularly from otherwise perfectly healthy coral heads that it is unlikely that a dead spot (e.g., a barnacle burrow) had been found each time by the larva. The coral shows an early but obviously unsuccessful reaction to the intruder: a circular bulge is formed around the epilithic portion of the sponge (Plate 3e,f). The polyps located on this swelling have eventually died off. This could be due to small quantities of mucus which are expelled through the osculum and run down to the sponge base; and since, as had been mentioned before, even the embryos of *Siphonodictyon* are provided with large amounts of mucus, it seems probable that the mucus protects the larva during settlement on the living coral surface and possibly promotes the killing of the polyps. Experimental evidence, however, will be needed to support these assumptions. It is evident in all coral burrowing species and forms that, once the sponge is established in the substratum, additional vents are formed by excavating from inside towards the surface (Plates 3b, 4g), where a new ectosomal structure is formed.

Forma *obruta* has been observed filling small cavities below living coral tissue but the openings of the vents were never localized. The preserved material on hand was exclusively collected from dead coral rubble.

The following living coral species were found infested: *Stephanocoenia michelinii* (Milne-Edwards and Haime) by *Siphonodictyon corallipha-gum* formae *typica* and *tubulosa; Siderastrea siderea* (Ellis and Solander) by *S.c.* forma *tubulosa; Porites astreoides* (Lamarck) and *Diploria strigosa* (Dana) by *S.c.* forma *typica;* and *Montastrea annularis* (Ellis and Solander) by *S.c.* forma *typica* and *S. cachacrouense.*

No quantitative data are presently available on the extent and frequency of infestation but the breaking up of coral heads reveals many large cavities, now filled with fine sediments, which can be attributed to former *Siphonodictyon* burrowing. Indeed, samples of these sediments still contain spicules of the sponge. The formation of some "microatolls" (i.e., coral heads with a dead center portion occupied by secondary settlers) can also be explained by the initial burrowing activity of *Siphonodictyon.*

Literature Cited

Bergquist, P. R.
1965. The Sponges of Micronesia, Part I: The Palao Archipelago. *Pacific Science,* 9:123–204.

Borojević, R., W. G. Fry, W. C. Jones, C. Lévi, R. Rasmont, M. Sarà, and J. Vacelet
1968. Mise au point actuelle de la terminologie des éponges (A Reassessment of the Terminology for Sponges). *Bulletin du Muséum National d'Histoire Naturelle,* 39:1224–1235.

Goreau, T. F.
1959. The Ecology of Jamaican Coral Reefs. I. Species Composition and Zonation. *Ecology,* 40:67–90.

Goreau, T. F., and W. D. Hartman
1963. Boring Sponges as Controlling Factors in the Formation and Maintenance of Coral Reefs. In *Mechanisms of Hard Tissue Destruction,* R. F. Sognnaes, editor. American Association for the Advancement of Science, Publication 75, pages 25–54.

Gross, J., Z. Sokal, and M. Rougvie
1965. Structural and Chemical Studies on the Connective Tissue of Marine Sponges. *Journal of Histochemistry and Cytochemistry,* 4:227–246.

Hubbs, C. L., and A. Perlmutter
1942. Biometric Comparison of Several Samples, with Particular Reference to Racial Investigations. *The American Naturalist,* 75:582–592.

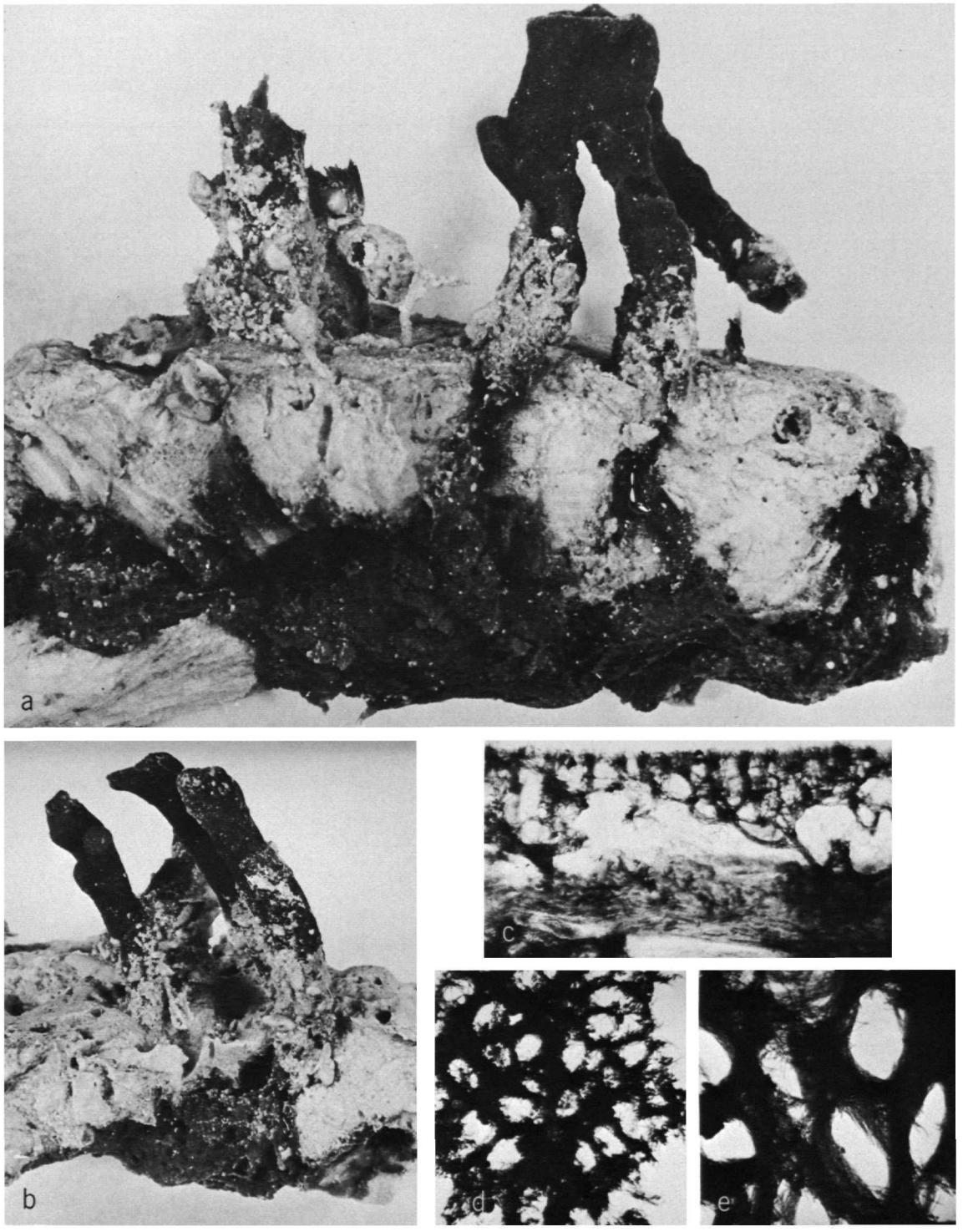
Laubenfels, M. W. de
1934. New Sponges from the Puerto Rican Deep. *Smithsonian Miscellaneous Collections,* 91 (17):1–28.
1949. Sponges of the Western Bahamas. *American Museum Novitates,* number 1431, 25 pages.
1950. An Ecological Discussion of the Sponges of Bermuda. *Transactions of the Zoological Society of London,* 27:155–201.

Schäfer, W.
1956. Der kritische Raum und die kritische Situation in der tierischen Sozietät. Aufsätze und Reden, Senckenberg Naturforschende Gesellschaft, number 9, 38 pages.

PLATES

PLATE 1.—*Siphonodictyon mucosum* Bergquist:

a,b Habitus of the Indian Ocean specimen (*a*:2.6 ×, *b*: 1.8 ×)
c Thick-section perpendicular to the surface of the tubes (36 ×)
d Surface net (36 ×)
e Main fiber tracts (36 ×)


a
b
c
d
e

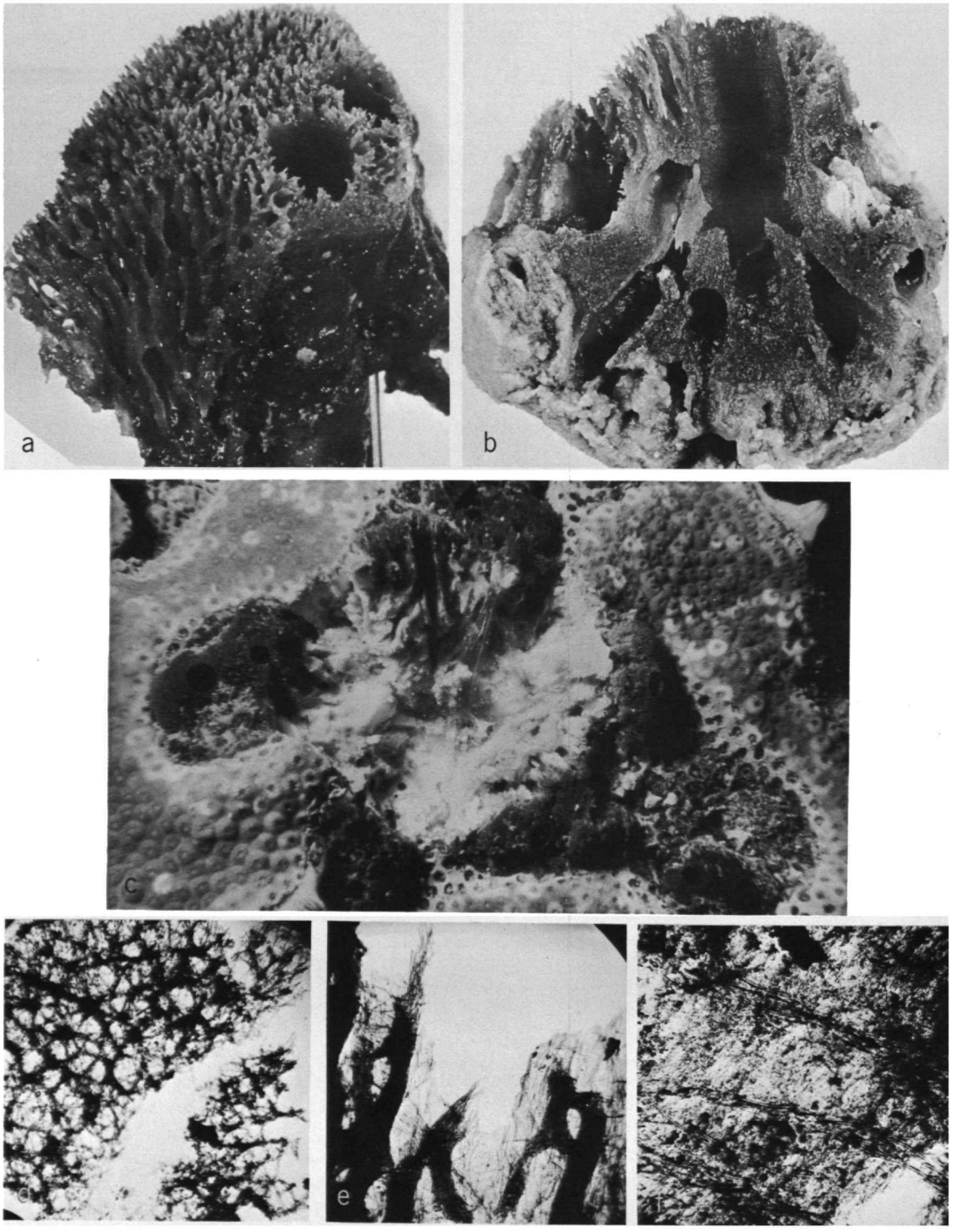

a
b
c
d
e
f

PLATE 2.—*Siphonodictyon cachacrouense,* new species, holotype:

a Habitus of one ectosomal cone with two oscula (3 ×).

b Part of specimen cut through the center of one osculum. Note coral fragments to the right which indicate the level of the substratum (3 ×).

c Underwater view of coral with sponge. Part of the sponge had been removed. Note mucus on the injured specimen and zone of dead coral exactly around it (0.8 ×).

d Surface fiber net (36 ×).

e Primary fibers (36 ×).

f Spicule strands in canal lining membrane (36 ×).

PLATE 3.—*Siphonodictyon coralliphagum*, new species, forma *typica*:

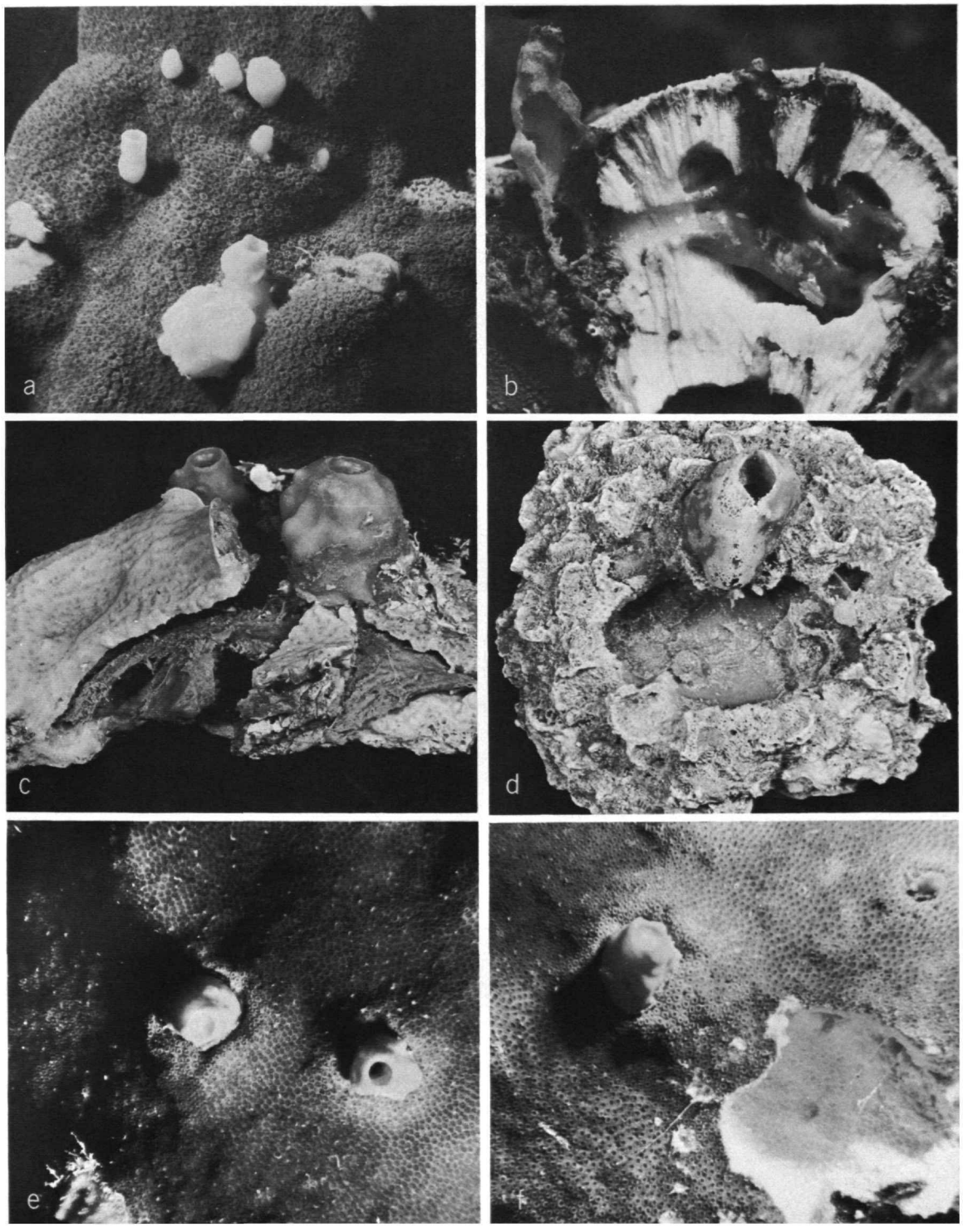
a *Stephanocoenia michelinii* infested by several specimens (Dominica) (0.5 ×).

b Specimen USNM 24097 (paratype, Dominica), coral cut in half (0.5 ×).

c Specimen YPM 6487 A (paratype, Jamaica) (0.8 ×).

d Specimen YPM 6507 (paratype, Jamaica). Note exposed choanosomal portion (0.8 ×).

e,f Underwater view of holotype USNM 24095 (right) before and after it had been removed from the substratum (0.5 ×).


a
b
c
d
e
f

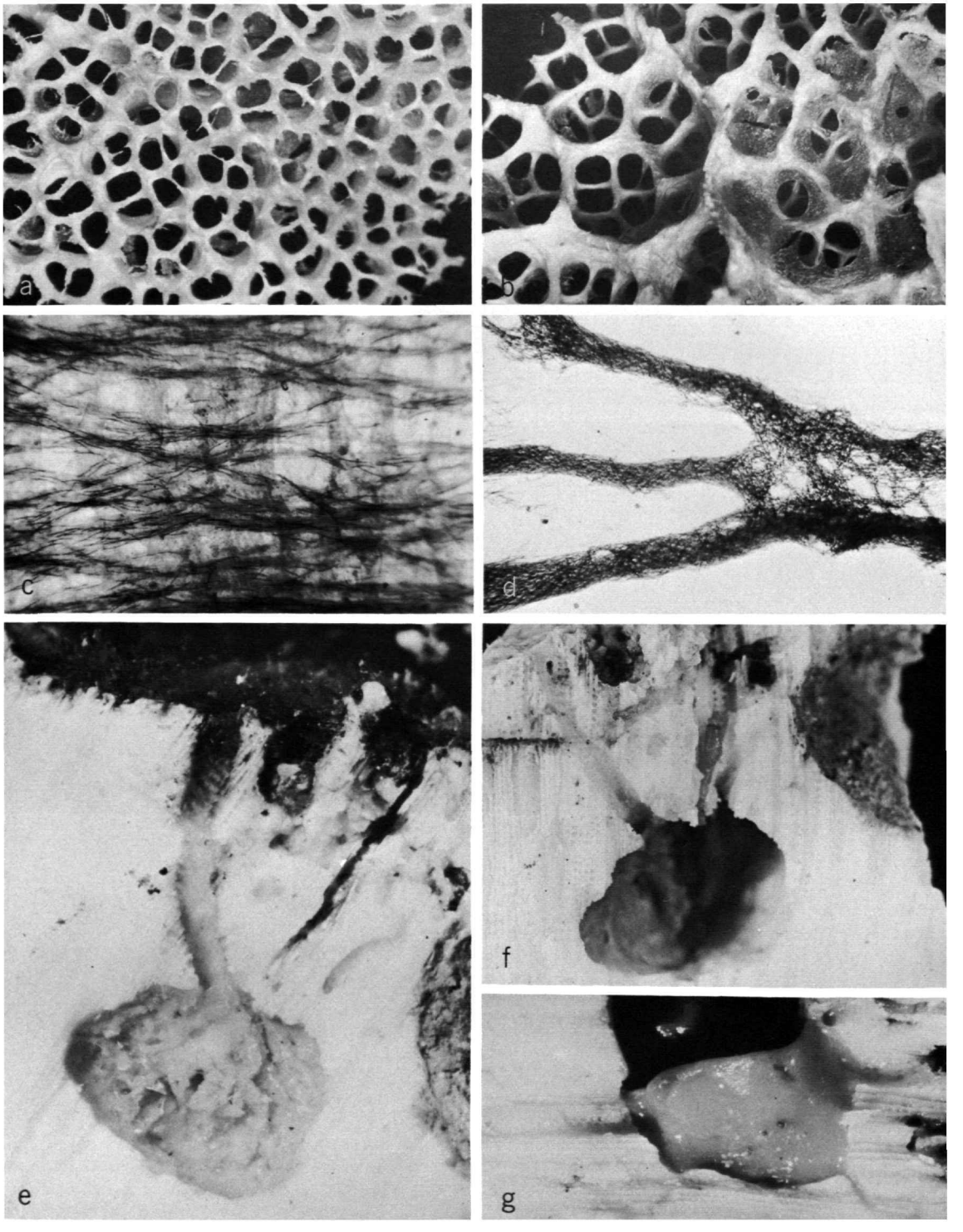

a
b
c
d
e
f
g

PLATE 4.—*Siphonodictyon coralliphagum*, new species, forma *typica*:

a,b Surface fiber net as viewed from above (*a*) and below (*b*). The supporting main fibers are apparent (16 ×).

c Spicule strands in canal lining membrane (36 ×).

d Primary fibers (36 ×).

Forma *obruta*:

e-g Habitus of the sponges in their burrows (2 ×).

PLATE 5.—*Siphonodictyon coralliphagum*, new species, forma *tubulosa*:

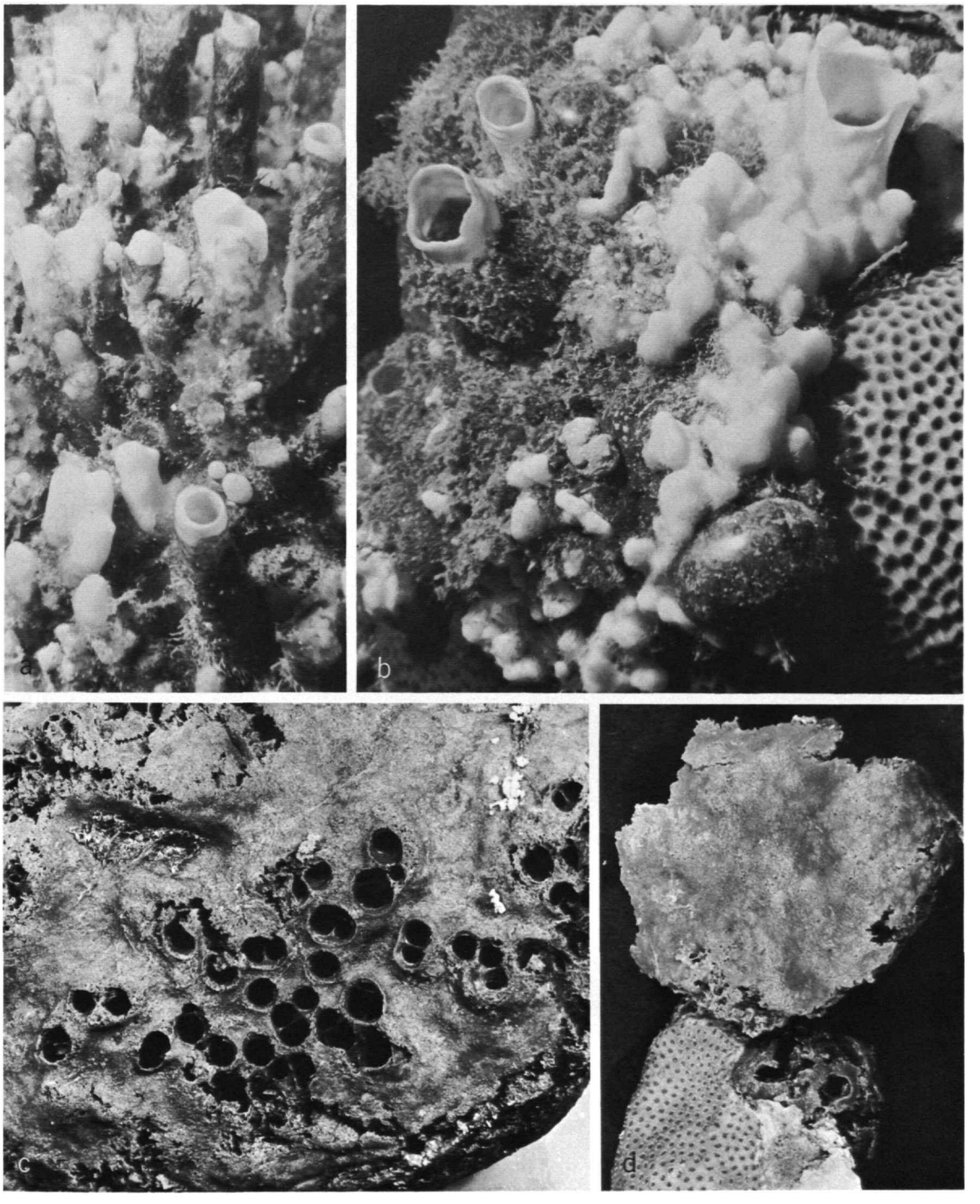
a Habitus, specimen USNM 24101 (Dominica) (0.8 ×).

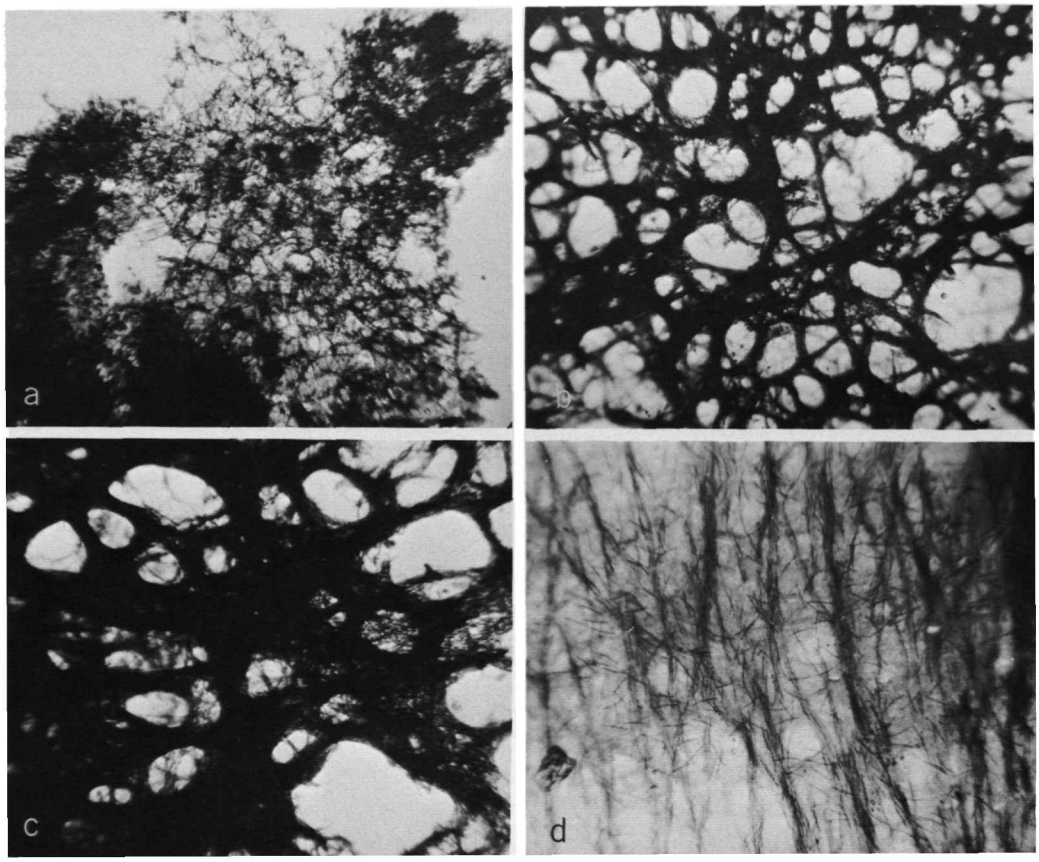
b Habitus, specimen USNM 24102 (Dominica) (0.8 ×).

Forma *incrustans*:

c Habitus, specimen YPM 6496 (Jamaica) (0.9 ×).

d Habitus, specimen YPM 4831 (Jamaica) (0.8 ×).


a
b
c
d


a
b
c
d

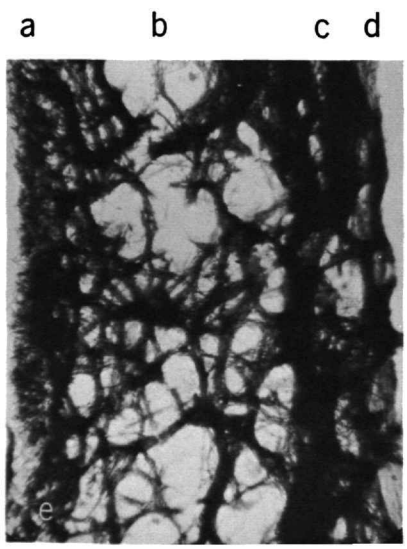

a
b
c d
e

PLATE 6.—*Siphonodictyon coralliphagum,* new species, forma *tubulosa,* thick-sections parallel to the surface of one tube (36 ×):

a Surface net

b Fiber net below surface

c Primary fibers near tube lumen

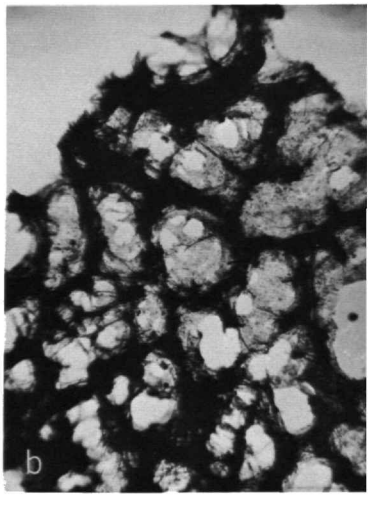
d Spicule strands in membrane lining tube lumen

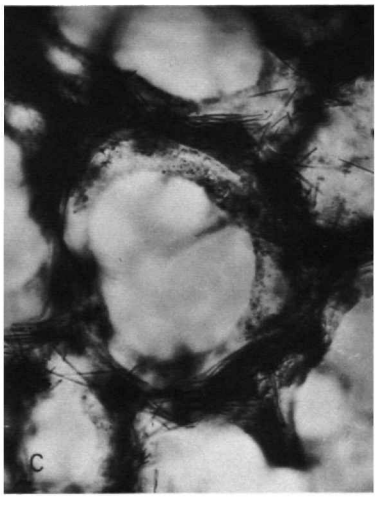
e Thick-section perpendicular through the wall of one tube (surface left, lumen right). The letters indicate from which area the tangential sections above were taken.

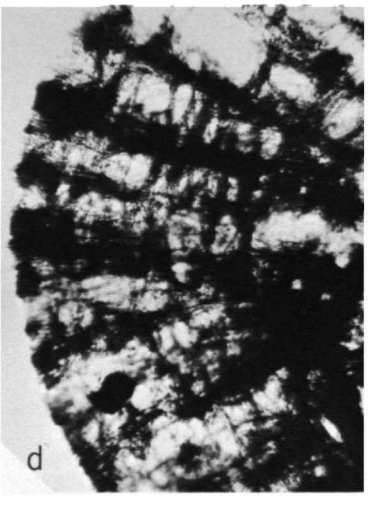
PLATE 7.—*Siphonodictyon siphonum* (Laubenfels):

a Underwater view of several tubes protruding from the sand (Bimini) (0.8 ×).
b,c Surface fiber net (*b*: 36 ×, *c*: 90 ×).
d Perpendicular thick-section through the wall of one tube (36 ×).


a


b


c


d

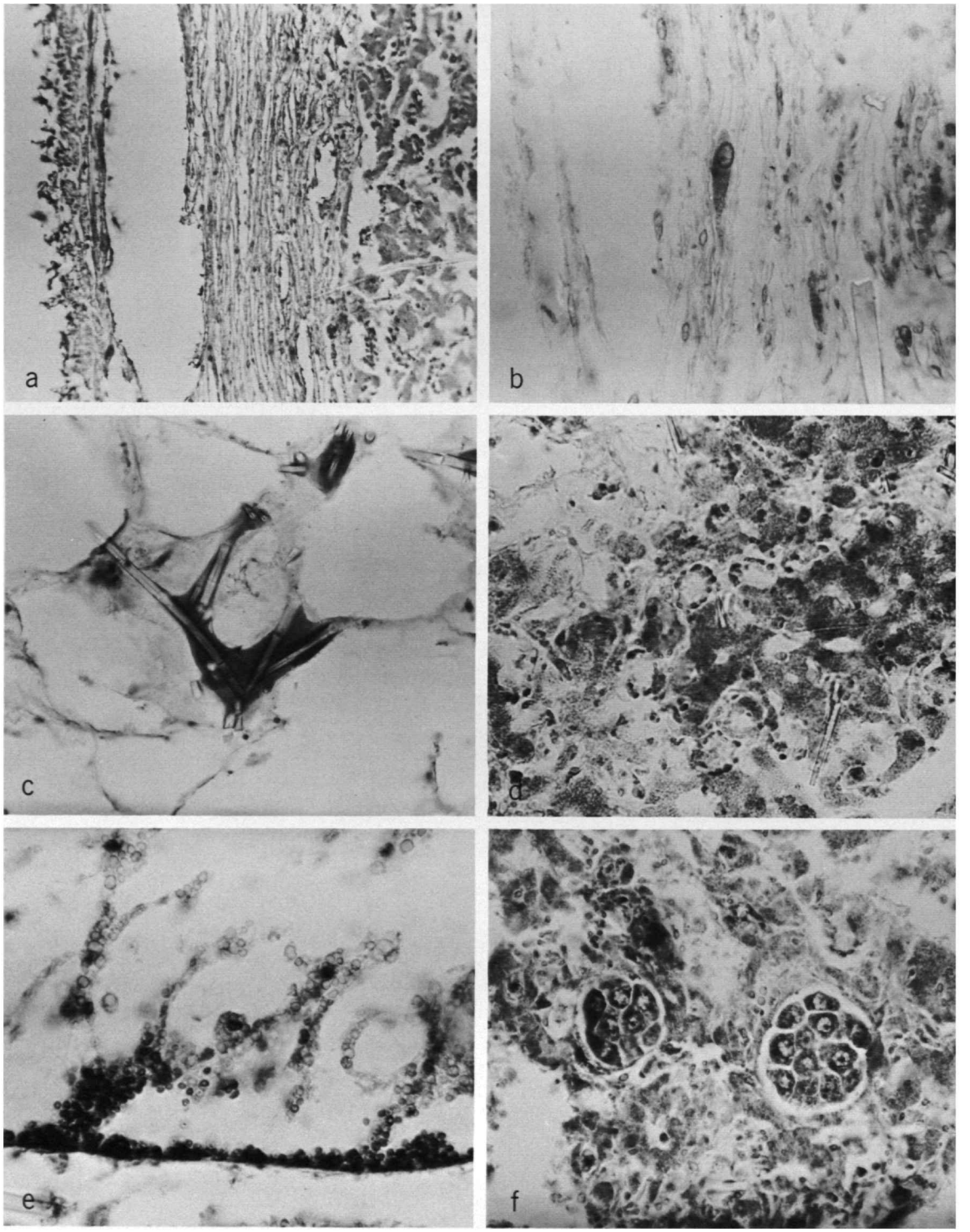

a
b
c
d
e
f

PLATE 8.—*Siphonodictyon,* histology:

a *S. cachacrouense*: canal with membrane lining. The choanosome proper shows at the right. H & E (90 ×).

b *S. cachacrouense:* granular nucleolate spindle cell in membrane sheath. Mallory (900 ×).

c *S. coralliphagum*: spicules connected by spongin. Mallory (450 ×).

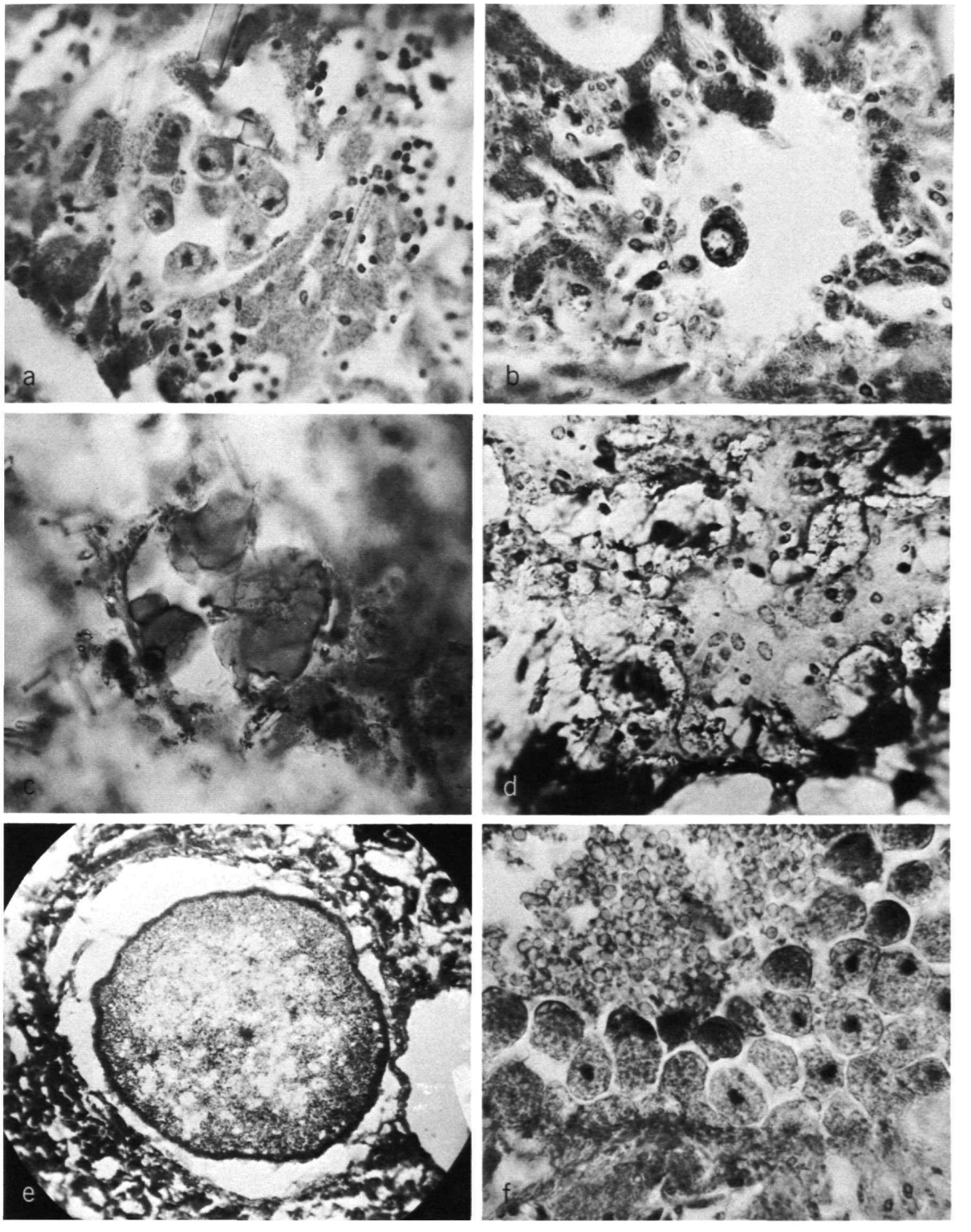
d *S. coralliphagum*: choanocyte chambers. Mallory (450 ×).

e *S. cachacrouense*: archeocyte containing highly refractile spherules and free spherules inside an embryo. A section of the embryonic capsule can be noted. Mallory (900 ×).

f *S. coralliphagum:* two cysts of oogonia. Mallory (450 ×).

PLATE 9.—*Siphonodictyon*, histology:

a *S. coralliphagum*: cyst of oogonia. H & E (900 ×).
b *S. coralliphagum*: mature egg cell. Mallory (900 ×).
c *S. coralliphagum*: mucus droplets. Toluidin (900 ×).
d *S. siphonum*: mucus containing isolated nuclei. Mallory (900 ×).
e *S. coralliphagum*: embryo. H & E (90 ×).
f *S. coralliphagum*: embryo epithelium and spherules. Mallory (900 ×).



☆ U. S. GOVERNMENT PRINTING OFFICE : 1971 O - 397-767

Publication in Smithsonian Contributions to Zoology

Manuscripts for serial publications are accepted by the Smithsonian Institution Press subject to substantive review, only through departments of the various Smithsonian museums. Non-Smithsonian authors should address inquiries to the appropriate department. If submission is invited, the following format requirements of the Press should govern the preparation of copy.

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1½″ top and left margins, submitted in ribbon copy with a carbon or duplicate, and accompanied by the original artwork. Duplicate copies of all material, including illustrations, should be retained by the author. There may be several paragraphs to a page, but each page should begin with a new paragraph. Number all pages consecutively, including title page, abstract, text, literature cited, legends, and tables. A manuscript should consist of at least thirty pages, including typescript and illustrations.

The *title* should be complete and clear for easy indexing by abstracting services. Taxonomic titles will carry a final line indicating the higher categories to which the taxon is referable: "(Hymenoptera: Sphecidae)." Include an *abstract* as an introductory part of the text. Identify the *author* on the first page of text with an unnumbered footnote that includes his professional mailing address. A *table of contents* is optional. An *index,* if required, may be supplied by the author when he returns page proof.

Two *headings* are used: (1) text heads (boldface in print) for major sections and chapters and (2) paragraph sideheads (caps and small caps in print) for subdivisions. Further headings may be worked out with the editor.

In *taxonomic keys,* number only the first item of each couplet; if there is only one couplet, omit the number. For easy reference, number also the taxa and their corresponding headings throughout the text; do not incorporate page references in the key.

In *synonymy,* use the short form (taxon, author, date, page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within a taxon, use a period-dash (.—) to separate each entry. Enclose with square brackets any annotation in or at the end of the taxon. For *synonymy* and *references within the text,* use the author-date system: "(Jones 1910)." Use the colon system for page references: "(Jones 1910:122)," and abbreviate further data: "(Jones 1910:122, fig. 3, pl. 5: fig. 1)."

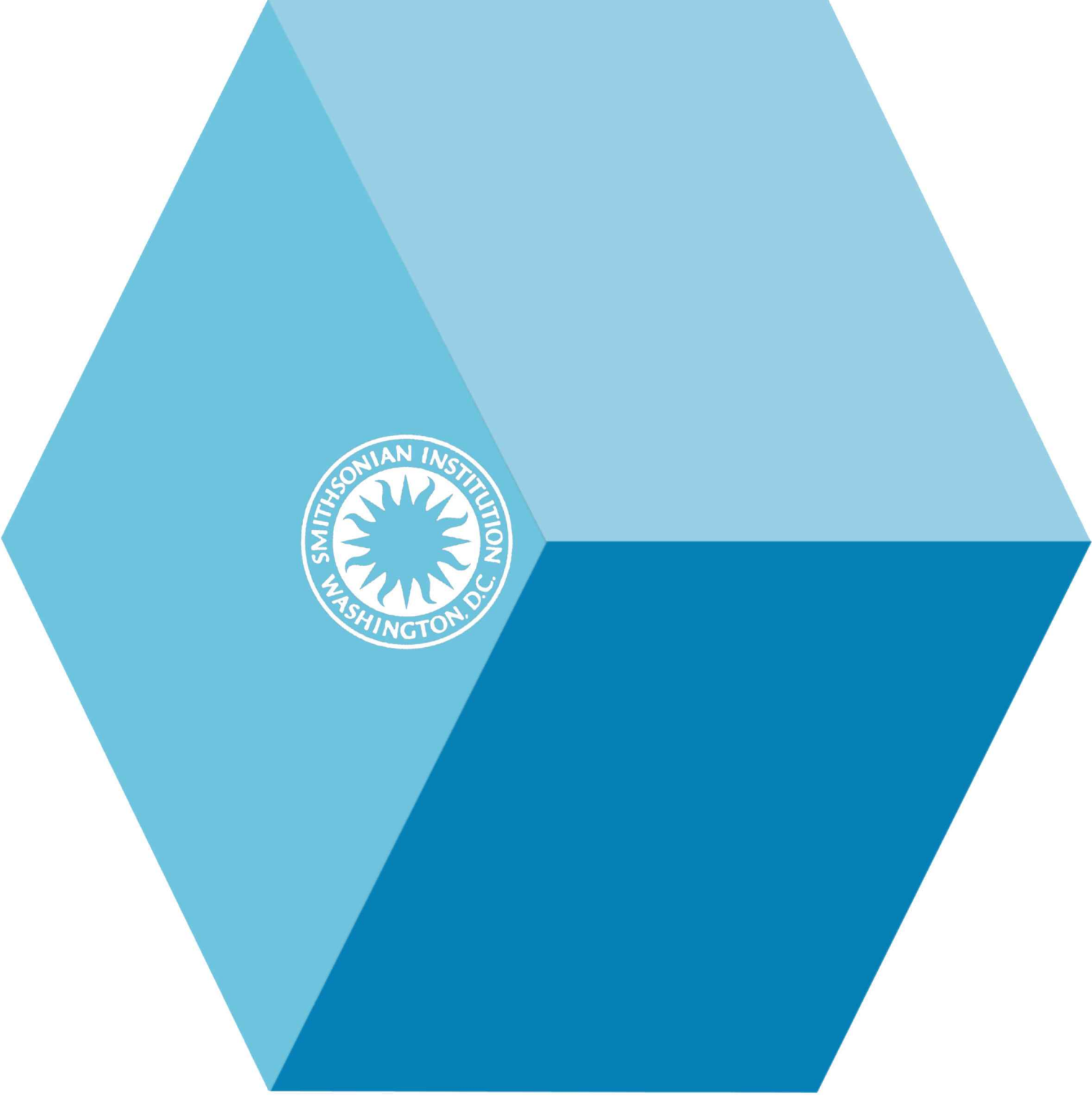
Simple *tabulations* in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal *tables* must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

Use the *metric system* instead of (or in addition to) the English system.

Illustrations (line drawings, maps, photographs, shaded drawings) usually can be intermixed throughout the printed text. They will be termed *Figures* and should be numbered consecutively; however, if a group of figures is treated as a single figure, the individual components should be indicated by lowercase italic letters on the illustration, in the legend, and in text references: "Figure 9*b*." Submit all legends on pages separate from the text and not attached to the artwork. An instruction sheet for the preparation of illustrations is available from the Press on request.

In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." (For capitalization of titles in foreign languages, follow the national practice of each language.) Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume number and page citations: "10(2):5–9." Spell out such words as "figures," "plates," pages."

For *free copies* of his own paper, a Smithsonian author should indicate his requirements on "Form 36" (submitted to the Press with the manuscript). A non-Smithsonian author will receive fifty free copies; order forms for quantities above this amount, with instructions for payment, will be supplied when page proof is forwarded.


SMITHSONIAN INSTITUTION
WASHINGTON, D.C.