The Burrowing Sponges of Bermuda

KLAUS RUTZLER

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 165

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 mailing lists 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 165

The Burrowing Sponges of Bermuda

Klaus Rützler

SMITHSONIAN INSTITUTION PRESS
City of Washington
1974

ABSTRACT

Rützler, Klaus. The Burrowing Sponges of Bermuda. *Smithsonian Contributions to Zoology,* number 165, 32 pages, 26 figures, 1 table, 1974.—The systematics and distribution of eight species of burrowing sponges found on the Bermuda platform are discussed. These sponges excavate limestone substrata to form burrows in which they live, thus participating in processes of erosion and sedimentation. Seven species belong to *Cliona* (Clionidae): *C. caribbaea* Carter, *C. flavifodina,* new species, *C. paucispina,* new species, *C. vermifera* Hancock, *C. dioryssa* (Laubenfels), new combination, *C. lampa* Laubenfels, and *C. amplicavata,* new species; one species belongs to *Spheciospongia* (Spirastrellidae): *S. othella* Laubenfels. In addition to the three new species, two sponges are new records for Bermuda: *C. caribbaea* (not sensu Verrill, 1907, and Laubenfels, 1950) and *C. vermifera.* Among the *C. lampa* population three phenotypic forms are distinguished: formae *lampa, occulta,* and *flavida.* Appearance of live and preserved specimens, internal structure, spicules, and excavations are described in detail to permit field identification by nonspecialists. Scanning electron photomicrographs are used to clarify the fine structure of microscleres.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year.* SI PRESS NUMBER 4970. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Rützler, Klaus, 1936–
The burrowing sponges of Bermuda.
(Smithsonian contributions to zoology, no. 165)
1. Cliona. 2. Spheciospongia othella. 3. Sponges—Bermuda Islands. I. Title. II. Series: Smithsonian Institution. Smithsonian contributions to zoology, no. 165.
QL1.S54 no. 165 [QL373.D4] 591'.08s [593'.46] 73–12864

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402
Price 80 cents (paper cover)

Contents

The Burrowing Sponges of Bermuda

Klaus Rützler

Introduction

Observant divers are generally impressed by the abundance, diversity, and biomass of sponges in many shallow-water habitats throughout the tropical western Atlantic. Burrowing sponges are the least conspicuous, and their importance in processes of erosion, sediment production, and calcium carbonate dissolution has been greatly underestimated in the past (Goreau and Hartman, 1963; Neumann, 1966; Rützler, in preparation). Most limestone excavating sponges belong to the family Clionidae, but members of Spirastrellidae and Adociidae are also known to burrow (Rützler, 1971; Pang, in press; Rützler and Rieger, 1973). In fact, the concept of the Clionidae as a family, defined by their burrowing habit, requires redefinition as more material and data become available. Generic and familial placement of species should be reconsidered from the standpoint of recognized procedures of sponge systematics, rather than separating burrowing and nonburrowing forms.

The purpose of this paper, however, is not systematic revision, particularly not of higher taxa. Having visited Bermuda during several consecutive years, it became clear to me that manuals describing the local flora and fauna are urgently needed. During its seventy years of existence the Bermuda Biological Station for Research has been a center for investigations in every discipline of nature sciences, including the systematics of local plants and animals. Presently, there is an increasing emphasis on educational activities at the station, most of which, as can be expected at this location, center on marine organisms. Whether studies and research aim at embryology, physiology, and ecology or at calcification, bioerosion, and sedimentation, the organisms are still the key material, and knowledge of their kinds, occurrence, and distribution is of first importance. Some taxa, of course, are better known than others, but most local systematic treatments need to be corrected and updated with new findings. Also, systematic papers, like most technical communications, tend to be written for a small number of specialists and are not readily understood by the less specialized student. Many morphological and anatomical features that are essential for classification are difficult to describe in words, and printing costs have generally curtailed illustrations.

This contribution is an attempt to overcome some of the aforementioned problems and to describe and illustrate a small but significant fauna. I hope that a person untrained in sponge systematics can, by using this report, either identify a given excavating sponge from Bermuda, or determine with reasonable certainty that it had been overlooked during my surveys.

Until recently, no study has ever been devoted entirely to the systematics of burrowing sponges in any one area of the tropical western Atlantic. Pang (in press), describing excavating sponges from Jamaica, increased the number of species known from that island from two to thirteen. Since her paper was still in press during preparation of this manuscript, no discussion of her results is possible in the systematic section.

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

Among the few publications on Bermuda sponges, only two include descriptions of burrowing sponges. Verrill (1907) described *Heterocliona cribaria* (Schmidt). Although this species has to be considered a synonym of *Spheciospongia othella* Laubenfels, Verrill was correct in suspecting it of having a burrowing stage. Verrill (1907) also described the massive stage of what he took to be *Cliona caribbaea* Carter. He failed to find microscleres and, with second thoughts about his identification, proposed the name *Cliona sordida* in a footnote. Ever since, reports of massive *"Cliona caribbaea"* have appeared in the literature (e.g., Laubenfels, 1936, 1950, 1953; Wells et al., 1960). I have not found this massive sponge during my work, and there is no evidence that *Cliona caribbaea* attains a massive (gamma) stage, like *Cliona celata* Grant or *Cliona viridis* (Schmidt) (Topsent, 1900), and it is certainly not conspecific with *Cliona viridis.* It is quite possible that *Cliona sordida,* if a *Cliona* at all, is a valid species. Laubenfels (1950) described massive cake-shaped *"Cliona caribbaea,"* abundant at Daniel's Head, off the west end of Bermuda. He found it nowhere else and speculated that his *Cliona lampa* had taken over its ecological niche since Verrill's paper. This might be a little far fetched but the fact is that during the present study, even after two extensive diving surveys, none of the bright yellow-ocher massive sponges have been found. It is curious, also, that a naturalist like Verrill should have overlooked an abundant and conspicuous sponge like *Cliona lampa.* My own related observations, and recent findings in Florida (A. Antonius, personal communication), indicate that the conspicuous incrusting growth form of this species could be the result of drastic environmental events that occurred after Verrill's time. More work is planned on this subject. In addition to the two species just mentioned, and to *Spheciospongia othella,* Laubenfels (1950) described *Spirastrella diorysa.* He suggested the possibility that this species could be a *Cliona.* Although the excavating habit of this sponge could be confirmed during the present study, the species is transferred to *Cliona* on the basis of the type and structure of its skeleton.

This report adds five burrowing sponges to the list, three new species and two new records for Bermuda, one of which is considered the "true" *Cliona caribbaea* Carter. The illustrations are intended to be comprehensive and representative. Scanning electron photomicrographs aim to clarify details that cannot be resolved by light microscopy, but they are not a substitute for procedures that can be repeated with standard optical laboratory equipment. I advise using the figures like a taxonomic key to narrow down the possibilities of identification, but not to rely on any one or two agreeing features because variability and overlap of characters can mislead even the most experienced. Text and measurements should always be consulted before a final decision is reached.

ACKNOWLEDGMENTS.—Financial support for the project was provided by Smithsonian Research Foundation Fund 427242. I thank Mr. W. R. Brown and Miss M. J. Mann for operating the scanning electron microscope. This is Contribution No. 575, Bermuda Biological Station.

METHODS.—Fieldwork for this study was conducted between October 1969 and January 1973. All specimens were collected by the author, by wading, breath-held or scuba diving, using hammer and chisel. In the laboratory, sponge-infested substrata were broken down and studied under low-power microscope. Small, clean, separate samples of epilithic and endolithic (ecto- and choanosomal) sponge tissue were taken for spicule mounts. Care was taken to avoid contamination by other sponges invading the same substratum fragments.

Quick preparations which assure minimum loss of minute spicules are best made by dissolving tissue fragments, placed on a microscope slide in a drop of commercial bleach (5–10 percent sodium hypochlorite). Small tissue pieces, dehydrated and mounted in a medium like Canada balsam, are also useful for locating small elements of the skeleton. For permanent slides, clean spicules are obtained by boiling tissue in concentrated nitric acid, rinsing in water, and dehydrating in alcohol. For scanning electron microscope viewing, clean spicules were dried on a small circular cover slip and coated with 20 nm of gold. A Cambridge Stereoscan Mark II A was used at × 200 – × 5000, rarely at × 10,000 or × 20,000 primary magnification.

To reveal the structure of burrows, substratum pieces are best cleaned of organic material by soaking overnight in sodium hypochlorite solution. For study of anatomy and histology, two methods have

been used successfully. For both, the material was fixed in buffered 4 percent formalin-seawater (pH 7–7.5), which was replaced by 80 percent ethyl alcohol after not more than 2 weeks. Method 1 involved decalcification in several changes of 5 percent nitric acid, neutralization in 5 percent sodium sulfate solution for 12 hours, and rinsing in running tap water for 6 hours. The tissue was then embedded either in paraffin for standard microtome sectioning, or in 12 percent gelatine for sectioning frozen by a cryostate microtome. Toluidin blue, Mallory's tripple stain, or Ehrlich's hematoxylin-eosin all gave good staining results. For Method 2, fragments of substratum containing the sponge (up to 2 cm^3) were dehydrated in a graded series of alcohol, soaked in three changes of propylene oxide and vacuum embedded in Spurr Low Viscosity Embedding Media (Polysciences, Inc., Warrington, Pennsylvania, U.S.A.). Specimen blocks were glued to microscope slides and wet-ground and polished to 20 μm. The sections were stained in 1 percent aqueous safranin (10–15 minutes) and subsequently in 1 percent aqueous crystal violet (5–10 minutes).

Measurements given in this report are ranges (means in parentheses) for all specimens studied. Means are omitted where less than 5 measurements were made. Spicule sizes are based on 25 measurements per dimension for three representative sponge specimens. The largest diameter was recorded for approximately circular structures, the longest perpendicular axes for oval or irregular features.

In the synonymy, species names and references are restricted to those of the first describer and to subsequent descriptions which, by their quality and relevance, contribute most to the understanding of the species.

The material on which this report is based is deposited in the National Museum of Natural His-

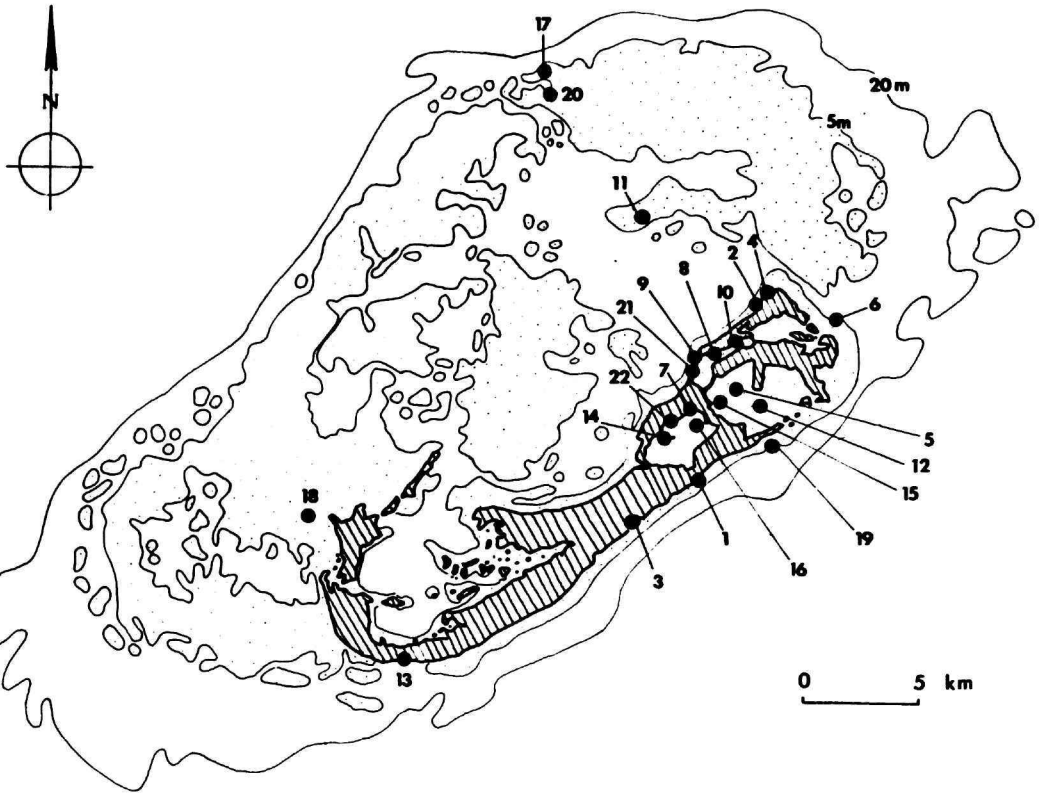

FIGURE 1.—Map of Bermuda showing collecting localities.

tory, Smithsonian Institution. Catalog numbers are those of the old United States National Museum (USNM). Additional reference specimens are deposited at the Bermuda Biological Station.

LIST OF STATIONS (Figure 1, Table 1).—The following is a list of collecting localities that were visited during all surveys (Figure 1). Collecting date and substratum information are given in the material section of each species. Place names are used as shown on the Bermuda Islands Road Map 1966 (Bermuda Department of Tourism and Trade Development) and on chart H.O.27, U.S. Navy Oceanographic Office. Burrowing sponge species found at each station are listed in Table 1.

1. John Smith's Bay. Small reefs, 20 m off shore. 2 m.
2. Tobacco Bay. Rocks and small reef patches. 1–2 m.
3. Devonshire Bay. West flank, rocks halfway to point. Intertidal.
4. Coot Pond. Rocks at entrance. Intertidal to 1 m.
5. Castle Harbour North. Patch reef between Blue Hole and Navy Base Peninsula. 1.5–3 m.
6. The Narrows. Ship channel, east off Town Cut. Patch reef. 4 m.
7. Church Bay, Harrington Sound. Subtidal parts of caves and rocks. Intertidal to 1 m.
8. Ferry Reach, next to Whalebone Bay. Loose rocks; intertidal.
9. Whalebone Bay. East flank and rocks at entrance. Intertidal, tide pools, to 1 m.
10. Ferry Reach. Rocks at "Barnacle" Bay entrance near Biological Station. Intertidal to 1.5 m.
11. Three Hill Shoals. Patch reefs. 3–10 m.
12. Castle Harbour East. Patch reef between Tucker's Town and Navy Base Peninsula. 0.5–2.5 m.
13. Church Bay, South Shore. Boiler Reefs. 0.5–4 m.
14. Harrington Sound. Rock west off Trunk Island. 0.5–1.5 m.
15. Castle Harbor West. Off Walsingham Bay. 0.5–1 m.
16. Harrington Sound. Northeast corner of Hills Island. Small caves. 0.5–1.5 m.

TABLE 1.—*Distribution of burrowing sponge species found at collecting stations in Bermuda*

Stations	*Cliona caribbaea*	*Cliona flavifodina*	*Cliona paucispina*	*Cliona vermifera*	*Cliona diorysa*	*Cliona lampa f. lampa*	*Cliona lampa f. occulta*	*Cliona lampa f. flavida*	*Cliona amplicavata*	*Spheciospongia othella*
1. John Smith's Bay										x
2. Tobacco Bay	x		x		x		x			x
3. Devonshire Bay							x		x	
4. Coot Pond						x	x			
5. Castle Harbour North	x	x	x	x	x	x	x			
6. The Narrows					x					
7. Church Bay, Harrington Sound	x	x		x	x	x	x			
8. Ferry Reach							x			
9. Whalebone Bay	x			x	x	x	x			
10. Ferry Reach	x	x		x	x	x	x	x		x
11. Three Hill Shoals	x	x		x	x		x		x	x
12. Castle Harbour East	x			x		x	x			
13. Church Bay, South Shore		x	x	x	x		x		x	x
14. Harrington Sound		x			x		x			
15. Castle Harbour West				x						x
16. Harrington Sound							x			
17. North Rock	x	x		x	x		x		x	x
18. Daniel's Head	x			x						
19. Battery Bay	x	x		x	x		x			x
20. North Rock South	x		x	x	x		x		x	
21. Ferry Reach Entrance	x	x			x	x	x	x		
22. Harrington Sound					x					x

17. North Rock. Reefs, 3–7 m.
18. Daniel's Head. Patch reefs, 0.5–3 m.
19. Battery Bay. Boiler Reefs. 6–12 m.
20. North Rock South. Patch reef 300 m south of light tower. 5–8 m.
21. Ferry Reach Entrance, North Shore. On and between railway pillars. 3–5 m.
22. Harrington Sound. Cockroach Island, west of Abbot's Cliff. Rocks, 1 m.

TERMINOLOGY.—A minimum of technical terms has been used, most of which can be found in Borojević et al. (1968). Designations for spicule types become clear with a glance at the illustrations. Terms like "head," "neck," and "shaft" for sections of the pin-shaped tylostyles are self-explanatory. The general structure of a clionid sponge has been described and illustrated by Goreau and Hartman (1963). Ectosome is the peripheral region of a sponge lacking choanocyte-chambers; choanosome contains choanocyte-chambers. In most burrowing sponges, the major part of the sponge body is inside the rock and only parts of the ectosome show on the substratum surface. These are called papillae and bear ostia or an osculum (openings of the incurrent and excurrent canals). The perforations on the substratum surface through which they protrude are called papillary perforations, which can be extended by a papillary canal or lead directly into the main burrow. The burrow can have a honey-combed appearance. The units are then called chambers (not to be confused with the choanocyte-chambers of the tissue), which are separated by walls but are in communication through small holes, foramina.

Family CLIONIDAE Gray

Cliona caribbaea Carter

FIGURES 2–4

Cliona caribbaea Carter, 1882:346–347, fig. 26.—Topsent, 1889:49.
Cliona viridis.—Topsent, 1900:84–98 (in part), pl. 3: fig. 3*d*.
Cliona viridis var. *caribbaea*.—Topsent, 1932:563–565, fig. 5.

DESCRIPTION.—*Ectosome:* The papillae (Figure 2*a*) exhibit basically a greenish color. Specimens can be grayish ocher or dark brown with a green tinge; others are light olive or yellow olive; the majority is of dark olive color. In alcohol, the chlorophyll of the symbiotic algae dissolves and leaves the papillae gray. Dry specimens are grayish ocher. The papillae are circular to oval, and are usually spaced 1–5 mm from each other, but they have a strong tendency to fuse. Their diameters range from 0.5 × 0.5 mm to 4.0 × 3.7 mm (2.4 × 1.9 mm). Fused complex papillae are 3.0 × 1.5 mm–22.0 × 9.0 mm (7.2 × 3.0 mm). Very seldom fusion goes as far as to form continuous incrustations, to the extent of 2–3 cm². The following observations can only be made on undisturbed specimens underwater. The edges of the papillae are raised to about 1 mm above the substratum; their center is depressed. Some of the larger ones bear one or, at most, two oscula with a raised rim (1–2 mm), which is always lighter in color (yellowish) than the papilla. Diameter of the osculum depends on the activity of the animal; it can reach 1.2 mm. Ostia are present on all papillae and can be opened to 0.3 mm. Intracellular symbiotic algae (zooxanthellae) (Figure 2*f*) are packed in rows between the perpendicular spicule strands. They are spherical and measure 8–10 μm in diameter. They decrease in number with distance from the papillary surface. There is also a well-developed connective tissue with numerous fusiform contractile cells, which account for the strong contractibility of the papillae.

Choanosome: Breaking up the substratum exposes sponge tissue of rich yellow ocher color that turns to pale gray in alcohol, but changes little upon drying. The tissue fills the ill-defined, irregularly elongate chambers (Figure 2*b*) except for the major excurrent canals, measuring 0.5–1.0 mm in diameter. The chambers are interconnected by tissue strands of 0.1–1.5 mm. Interstitial spaces in very porous substrata are also infiltrated. Irregular or spindle-shaped cells, 24 × 7 μm–30 × 10 μm, occur in small accumulations. They contain 1 μm basophilic granules (gray cells). Some specimens collected in January contained egg cells and sperm cysts in various stages of development. Choanocyte-chambers measure 30–35 μm.

Excavations: Single papillary perforations (Figure 2*c*) measure 0.5–3.2 mm (1.5 mm). Chambers start at 0.5–2.0 mm under the substratum surface. The chambers (Figure 2*d*) are irregular, ragged, and frequently fused, particularly in porous substrata. They measure approximately 1.9–7.0 mm × 1.3–2.9 mm (4.0 mm × 2.0 mm) if they are well

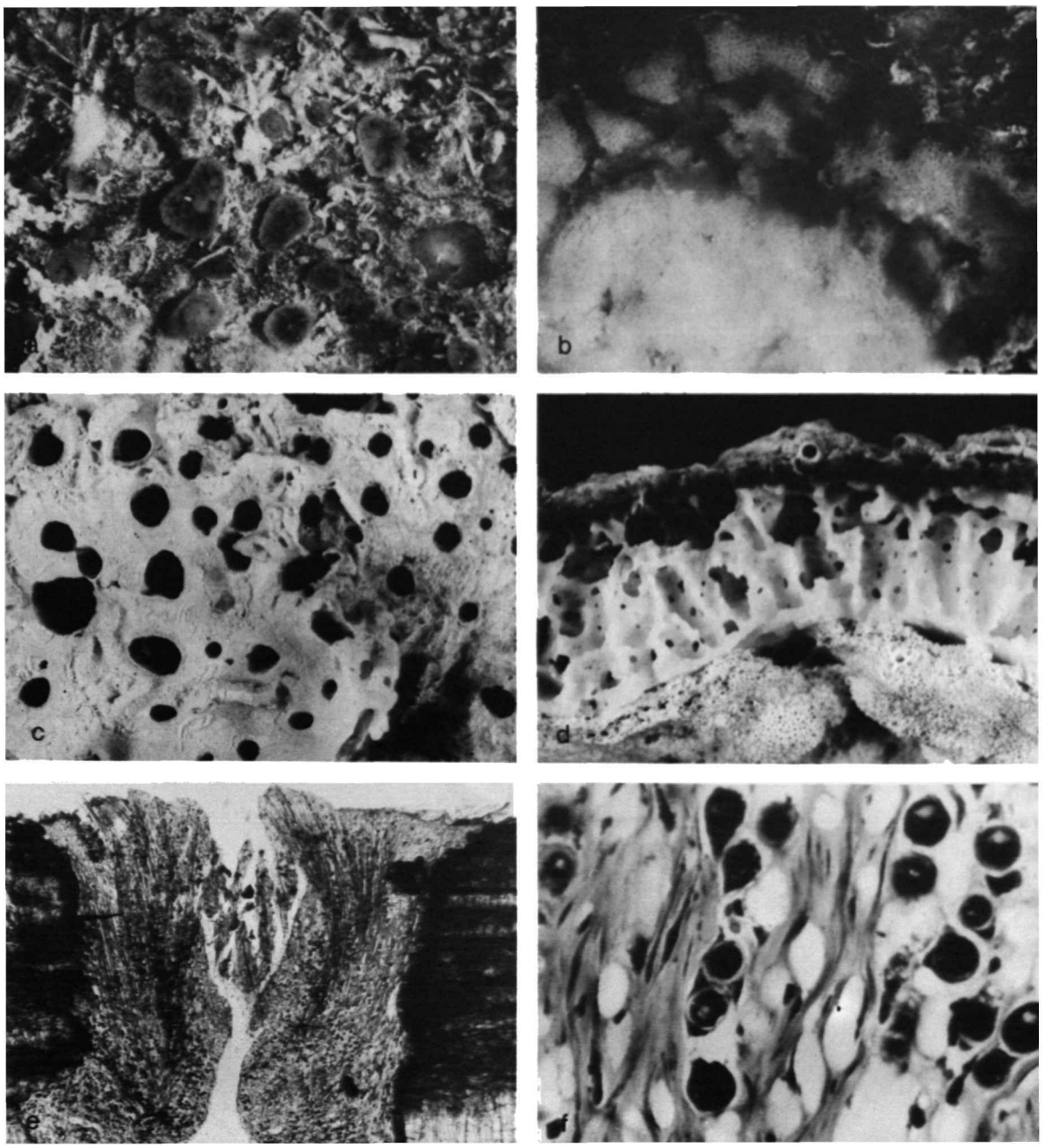

FIGURE 2.—*Cliona caribbaea: a,* papillae of live specimen; *b,* tissue penetrating substratum; 3 papillary canals in left upper corner; *c,* papillary perforations; *d,* chambers inside pelecypod shell; *e,* vertical section through papilla showing excurrent canal, arrangement of tylostyles and distribution of zooxanthellae; *f,* intracellular zooxanthellae enlarged. (Magnification: *a–d,* × 3; *e,* × 50; *f,* × 850.)

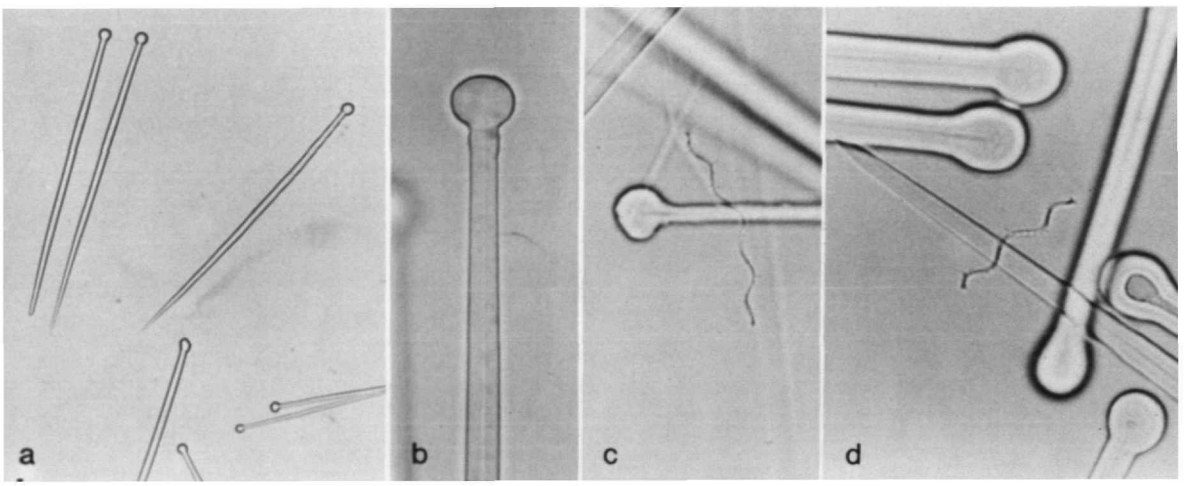

FIGURE 3.—*Cliona caribbaea*, spicules: *a*, tylostyles; *b*, tylostyle head; *c*, *d*, spirasters and tylostyle heads. (Magnification: *a*, × 140; *b–d*, × 850.)

defined. There are 6 to at least 15 foramina per chamber, which are approximately circular and 0.2–1.2 mm (0.5 mm) in diameter. The thickness of the separating walls varies between 0.2 and 1.0 mm. Excavations reach 15 mm into the substratum.

Spicules: Tylostyles occur everywhere, but show orientation perpendicular to the substratum only in the papillae (Figure 2*e*). Spirasters are rare or absent in the papillae, moderately abundant in the choanosome. Tylostyles (Figures 3*a–d*, 4*a*) are straight or slight bent. The point is sharp and gradually tapering from the middle of the spicule. The heads are well set off and usually spheroid. If they are ovoid, the longer axis of the head tends to be perpendicular to the axis of the shaft. Deformations of the heads are common, but rarely are there annular swellings behind them on the shaft. The spirasters (Figures 3*c*, *d*, 4*b*, *c*) are very delicate and easily overlooked. Under the light microscope they appear as finely spined wavy lines, the majority with 4–7 bends. Some are straight or W-shaped.

Spicule dimensions (in μm): Tylostyles, length × width: 204.1–410.0 × 2.6–8.1 (319.0 × 6.0). Neck width: 1.5–7.4 (4.6). Head length × width: 7.4–13.7 × 7.0–14.8 (9.7 × 10.3). Spirasters, length × width (including spines): 9.6–38.4 × 0.8–3.0 (32.8 × 1.8). Spine width: not resolvable by light. Number of spines: 18–50 + (40 +). Number of bends. 3–10 (5.9).

REMARKS.—This species has been greatly misinterpreted in the sponge literature of the tropical western Atlantic. Carter (1882) and Topsent (1900, 1932) accurately illustrated the characteristic spirasters. There are indications in the Bermuda material that *Cliona caribbaea* might adopt an incrusting habit, at least to a certain extent. Bermuda specimens have smaller tylostyles than the holotype from St. Vincent, West Indies. Also the depressed form of the tylostyle heads is more obvious in the Bermuda material. Three specimens studied for comparison from Dominica (West Indies, close to the type-locality) and Galeta Island (Panama) have tylostyles exactly as figured by Carter (1882), with mean tylostyle dimensions, length × width: 399.0 × 9.6 μm (Carter: 396 × 10 μm). Massive (gamma stage) specimens without spirasters, as described by Verrill (1907) and Laubenfels (1950) for Bermuda, and specimens (of various authors) with spirasters bearing prominent spines are almost certainly not conspecific. The latter includes material described by Hechtel (1965) as *Cliona viridis* (Schmidt), and placed in synonymy with *Cliona caribbaea*.

MATERIAL.—USNM 24346; Station 5; 31 December 1969; in dead coral and pelecypod shell. USNM 24347; Station 11; 13 January 1970; in dead parts of coral (*Millepora, Porites*). USNM 24348; Station 21; 15 June 1972, in pelecypod shell. Station 2; 8 May 1971; in dead parts of coral (*Dichocoenia*).

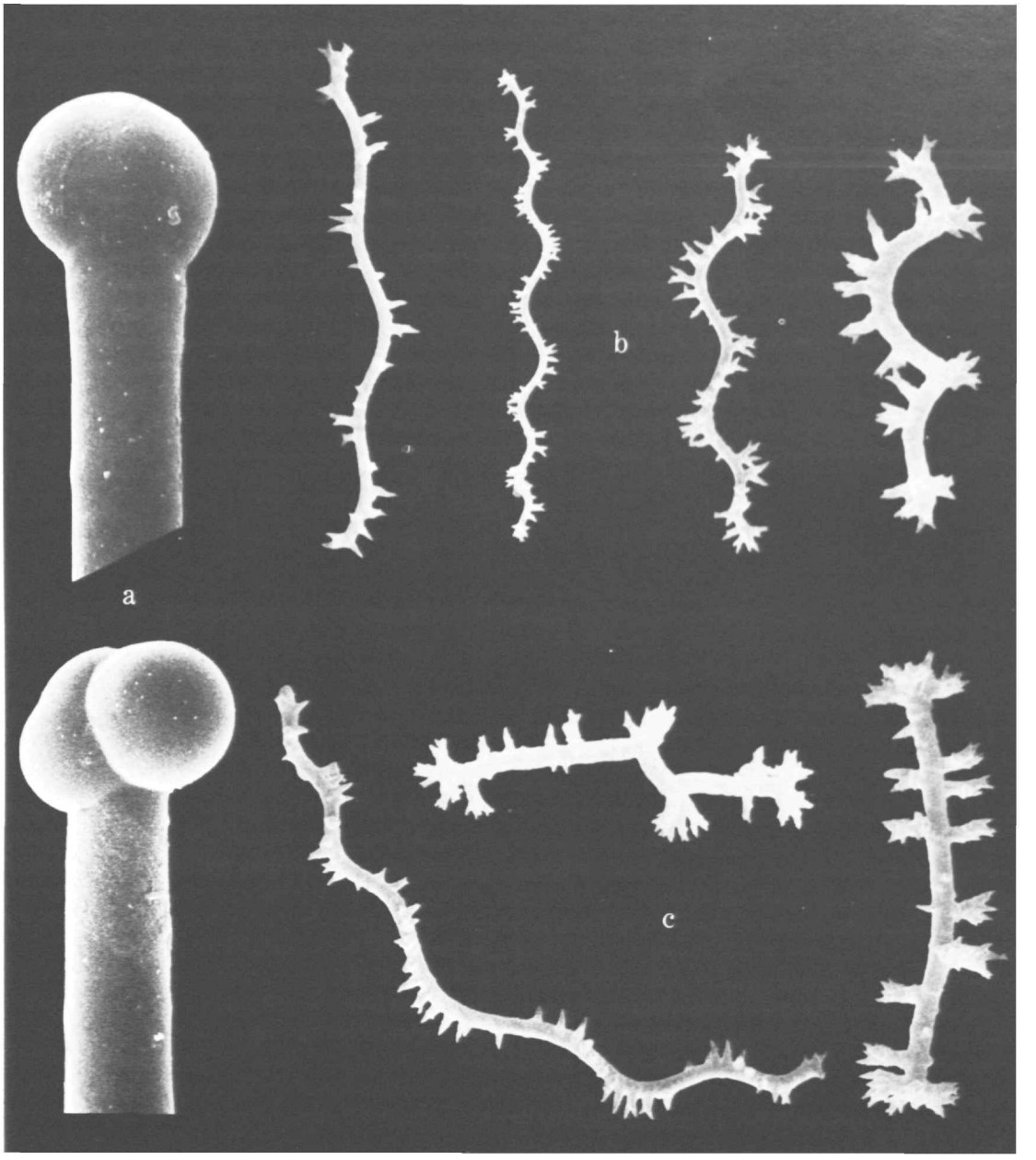

FIGURE 4.—*Cliona caribbaea*, spicules (SEM): *a*, tylostyle heads; *b*, *c*, spirasters and derivatives. (Magnification: *a*, *b*, × 1800; *c*, × 2700.)

Station 5; 31 December 1969; in dead coral. Station 5; 12 January 1970; in dead coral. Station 5; 30 December 1971; in rock. Station 9; 30 April 1971; in coralline incrusted rock. Station 10; 31 May 1972; in rock. Station 12; 27 April 1971; in pelecypod shell, rock, dead parts of coral (*Oculina*). Station 17; 16 May 1971; in dead coral. Station 17; 9 June 1972; in rock. Station 18; 13 May 1971; in dead coral (*Agaricia*). Station 19; 7 June 1972; in dead coral. Station 21; 12 January 1973; in dead pelecypod shell and coral (*Oculina*).

DISTRIBUTION.—With certainty only tropical western Atlantic.

Cliona flavifodina, new species

FIGURES 5–7

DIAGNOSIS.—Papillae yellow-brown, circular, discrete, 2.8 mm (mean diameter). Excavations irregular, tunnel shaped, confluent; filled by yellow, tough tissue. Tylostyles straight, with droplet-shaped or elongate heads, 318.1 × 7.4 μm (mean length × width). Spirasters with thin shaft, average 3–4 bends, 36.9 × 1.6 μm (mean length × width of shaft), and discrete slender spines, 4.5 μm (mean length).

DESCRIPTION.—*Ectosome:* The color of the papillae varies from bright yellow to grayish yellow and chestnut brown. In alcohol and upon drying, it fades to pale gray or grayish brown. The papillae are inconspicuous, level with the surface of the substratum, and well spaced (Figure 5*a*). Not more than ten could ever be observed in any one specimen. Their shape is circular, rarely elongate; their diameters are 1.5 × 1.5 mm–5 × 3 mm (2.8 × 2.2 mm). Papillary fusion is an exception. The surface of the papillae is irregularly porous. Oscula are rare; they open to about 3 mm diameter and have a slightly raised rim. The ectosome contains an abundance of granular cells, ovoid to irregularly elongate, 16 × 16 μm–38 × 8 μm, with granules of 1 μm. A small amount of zooxanthellae was observed in one specimen.

Choanosome: Grayish yellow tissue lines the papillary canals. These open into large, irregular spaces filled with a tough cavernous tissue (Figure 5*b*). The color of the choanosome is bright yellow to deep ocher, occasionally with an orange tinge. In alcohol or when dried, it becomes pale gray. In addition to the granular cells mentioned above, there are numerous cells of a second kind. They are more or less spherical, 18–22 μm in diameter, with a small anucleolate nucleus (like the gray cells), and packed with large spheroid basophilic granules of 1.5–2 μm (Figure 5*f*).

Excavation: The size of the circular papillary perforations (Figure 5*c*) corresponds to that of the papillae, although in the macerated specimens measured, it only ranged from 0.5 × 0.5 mm–3.2 × 2.2 mm (1.7 × 1.1 mm); one double perforation was 4.8 × 4.3 mm. The papillary canals are 1.1–7.0 mm (3.1 mm) long, until they widen and reach the choanosomal portion of the sponge. No chambers are developed, at least in the present material. There are large irregular spaces (Figure 5*d*) with tapering tunnels radiating into the substratum to a depth of 20 mm. Horizontal extension of the excavations reaches 25 mm.

Spicules: The papillae are armed with perpendicular typostyles (Figure 5*e*). The choanosome contains tylostyles and large numbers of spirasters. The tylostyles (Figures 6*a–d*) are mostly straight; occasionally they are bent shortly behind the head. The heads are droplet shaped or elongate ovoid; most of them show a central dark spot in transmitted light. Secondary swellings produce characteristic violin-shaped and almost rectangular heads, with an opaque spot close to the neck. The spirasters (Figures 6*b–d*, 7) are uniform in appearance, with a thin shaft and a moderate number of slender but prominent spines. Most of them have four bends, but some are straight with reduced spines (amphiasters).

Spicule dimensions (in μm): Tylostyles, length × width: 178.0–409.4 × 0.7–11.1 (318.1 × 7.4). Neck width: 2.2–10.4 (5.8). Head length × width: 5.9–24.1 × 3.7–17.8 (15.5 × 11.5). Spirasters, length × width (shaft only): 14.4–65.6 × 0.5–3.2 (36.9 × 1.6). Spine length × width (at base): 1.4–7.7 × 0.6–1.9 (4.5 × 1.5). Number of spines: 8–27 (17.4). Number of bends: 1–5 (3.3). Amphiasters, length × width (shaft only): 9.6–38.4 × 0.6–2.5 (22.9 × 2.3). Spine length × width (at base): 1.8–3.2 × 0.5–1.6 (2.7 × 1.1). Number of spines: 5–14 (9.3).

REMARKS.—A number of *Cliona* specimens attributed in the literature to *C. caribbaea* or *C. viridis* could in fact belong to the species described above. This view is particularly supported by

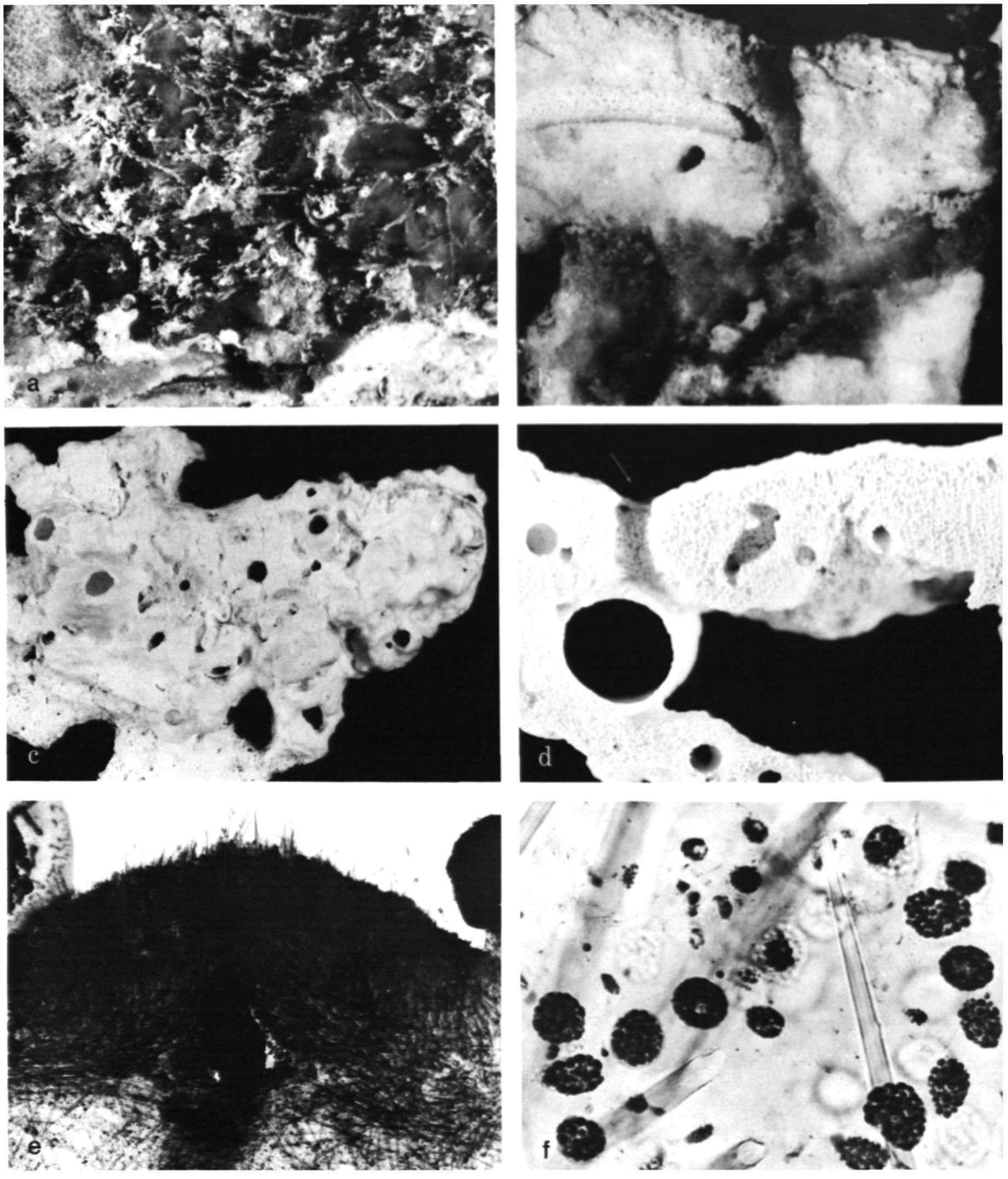

FIGURE 5.—*Cliona flavifodina: a,* 2 papillae (arrows) of live specimen; *b,* papillary canals and tissue inside substratum; *c,* papillary perforations; *d,* papillary canal (arrow) and large burrow (black area, to the right of embedded vermetid tube); *e,* vertical section through papilla; *f,* choanosomal granular cells. (Magnification: *a–d,* × 3; *e,* × 50; *f,* × 520.)

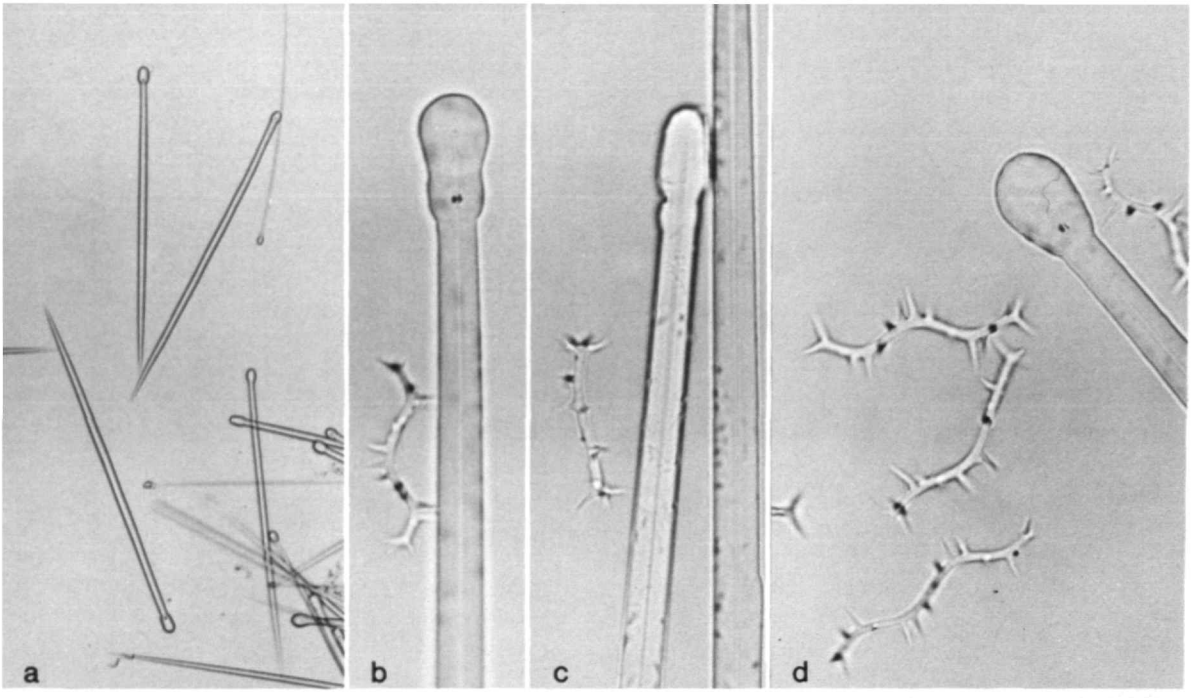

FIGURE 6.—*Cliona flavifodina*, spicules: *a*, tylostyles; *b–d*, spirasters and tylostyle heads. (Magnification: *a*, × 140; *b–d*, × 850.)

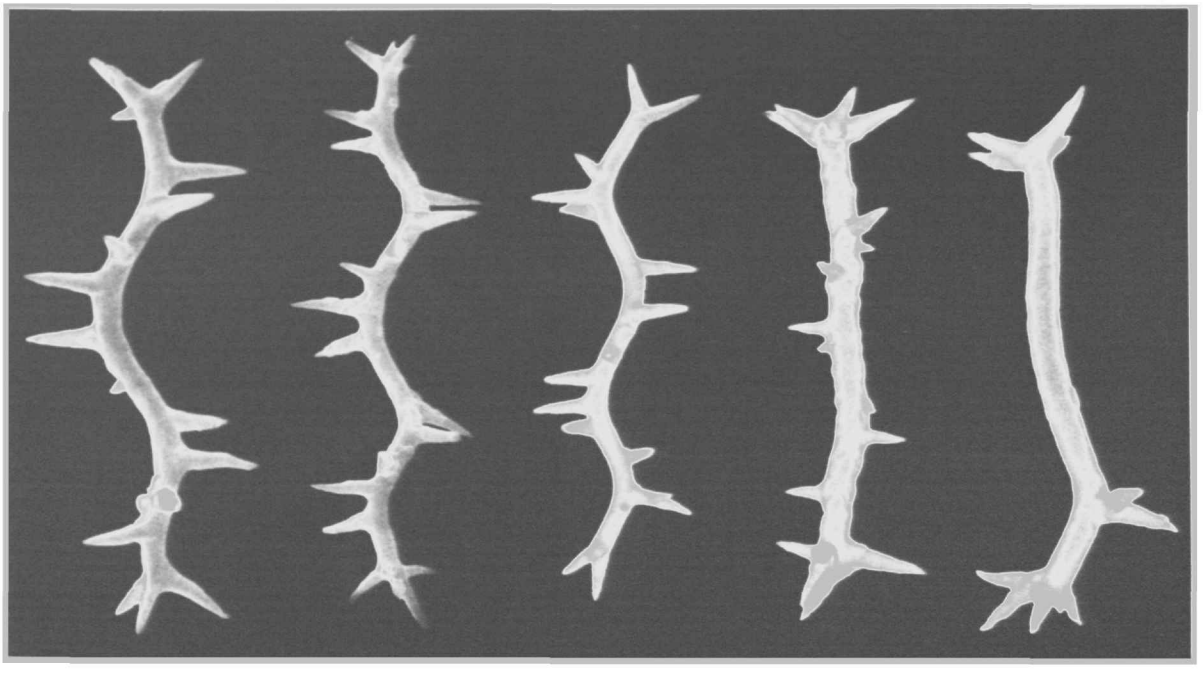

FIGURE 7.—*Cliona flavifodina*, spicules (SEM): spirasters. (Magnification: × 1800.)

Hechtel's (1965) account of two specimens of *C. viridis* from Jamaica. The details of his description of papillae, color, structure, and spicules agree well with my observations on *C. flavifodina*, the only exception being that Hechtel's specimens formed small galleries (1–3 mm in diameter) instead of extensive tunnels. Future studies will certainly reveal the taxonomic significance of this difference.

This species, as judged from its spicules, is related to *C. caribbaea*. It differs by the shape of the tylostyle heads, by size, spination, and number of bends of the spirasters, by the shape of the burrow, and by the lack of zooxanthellae.

The species name (Latin, *flavus*: yellow; Latin, *fodina*: pit, mine) refers to the appearance of the tissue-filled burrow.

MATERIAL.—USNM 24353 (holotype); Station 11; 13 January 1970; in coralline incrusted dead coral. USNM 24354 (paratype); Station 5; 12 January 1970; in dead coral. USNM 24352 (paratype); Station 13; 28 April 1971; in dead coral. Station 5; 12 January 1970; in pelecypod shell. Station 5; 3 January 1972; in rock. Station 7; 6 January 1970; in rock. Station 10; 31 May 1972; in rock. Station 17; 9 June 1972; in dead coral. Station 19; 7 June 1972; in dead coral. Station 21; 21 January 1973; in dead coral.

DISTRIBUTION.—Bermuda.

Cliona paucispina, new species

FIGURES 8–10

DIAGNOSIS.—Brown incrustations, penetrating rock crevices, limited excavating efficiency. Densely arranged, slender, bent tylostyles, with inconspicuous, frequently subterminal heads, 340.7 × 6.2 μm (mean length × width). Spirasters with thin shafts, average 4–5 bends, 28.8 × 1.3 μm (mean length × width of shaft), and low spines, 1.6 μm (mean length). Spiraster spines on shaft characteristically reduced. Abundance of intracellular zooxanthellae.

DESCRIPTION.—This sponge forms irregular, patchy, thin incrustations (Figure 8*a*) on concave surfaces of rock. Judging from the small extent of penetration, it is not a very effective burrower. The erosion pattern on the limestone surface suggests, however, that not only existing crevices are penetrated but that active excavation occurs. The sponge crusts are about 0.5–2.5 mm thick and 3 × 3 mm–10 × 35 mm in horizontal extension. Maximum area coverage observed was 7.5 cm².

Ectosome: The color at the smooth surface of the incrustations is chestnut brown to grayish brown in life, with small yellowish areas around the oscula. The color in alcohol is drab. The oscula are slightly elevated and open to 6 mm in diameter. No observations on open ostia have been made. Zooxanthellae are present in the tissue in large numbers. They are intracellular and measure 10 μm, like in *Cliona caribbaea*. There are also some of the large cells with inclusion described below.

Choanosome: It is light brown to yellowish brown, turning to grayish brown in alcohol. The tissue penetrates and fills small irregular spaces in the substratum (Figure 8*b*). Larger spaces are only lined with tissue. Its horizontal extension does

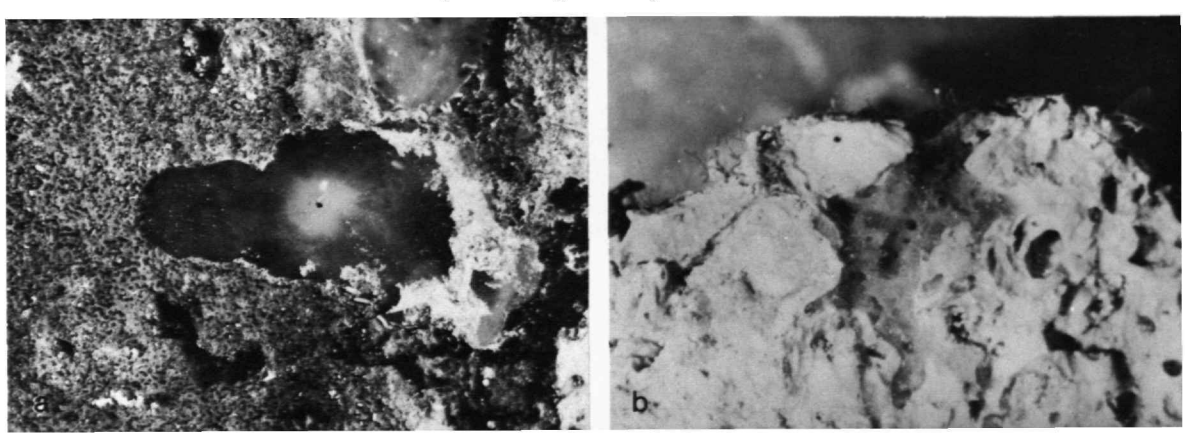

FIGURE 8.—*Cliona paucispina: a*, ectosomal incrustation with osculum partly contracted; *b*, tissue filling burrow. (Magnification: *a*, *b*, × 3.)

not exceed the extension of the incrustations on the surface. Depth of penetration reaches 12 mm at the most. Zooxanthellae are still present here. Large cells, elongate fusiform or irregular in outline, which measure 30 × 10 μm – 40 × 24 μm, are very conspicuous. They are packed with weakly staining spherical inclusions of 1.5–2.4 μm. The nucleus of 3 μm is provided with a nucleolus. Choanocyte-chambers measure 30 μm in diameter.

Excavations: Little can be added to the observations above. The substratum surface below the incrustations is eroded and existing spaces are enlarged. There is no chamber formation, nor distinct tunnels. All observations were made on very porous or poorly cemented substrata which can easily be broken down. Future findings may demonstrate that this sponge can produce more distinctive burrowing patterns in compact substrata.

Spicules: A series of vertical tylostyles at the surface is also present in this species, although this structure can be obscured in contracted specimens. The spicules are densely packed throughout the tissue; a small number of spirasters is interspersed among the tylostyles. Some tylostyles are organized in rows which branch and brush out toward the surface. The tylostyles (Figures 9*a*,*b*,*e*, 10*a*) are long and slender. They are usually bent in the upper third or fourth of their length, behind the head. The heads are not well set off, narrow, and elongate. Most of them are mucronate or subterminal; many are reduced. The spirasters (Figures 9*a*–*e*, 10*b*) are delicate, with slender shafts and small spines. The number of spines is frequently reduced on the shaft, but small spines are always

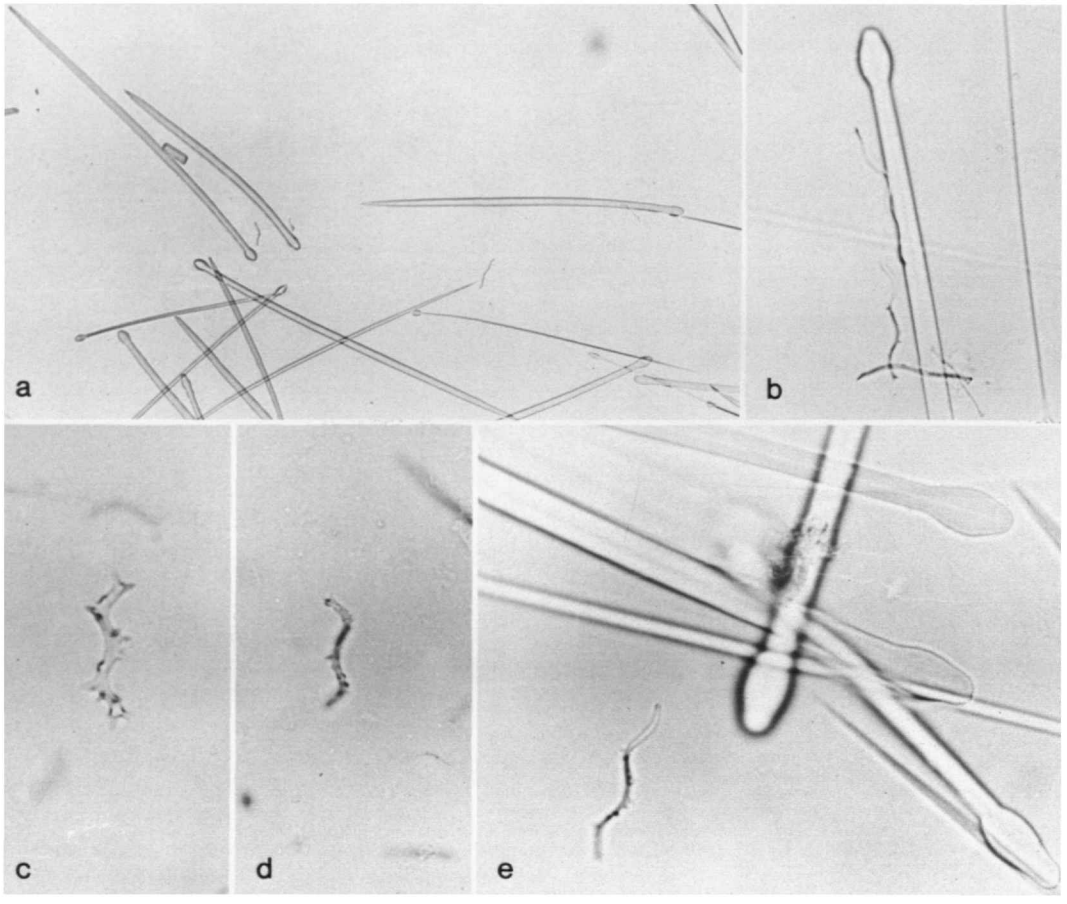

FIGURE 9.—*Cliona paucispina*, spicules: *a*, tylostyles and spirasters; *b*, *e*, spirasters and tylostyle heads; *c*, *d*, spirasters. (Magnification: *a*, × 140; *b*, *e*, × 520; *c*, *d*, × 850.)

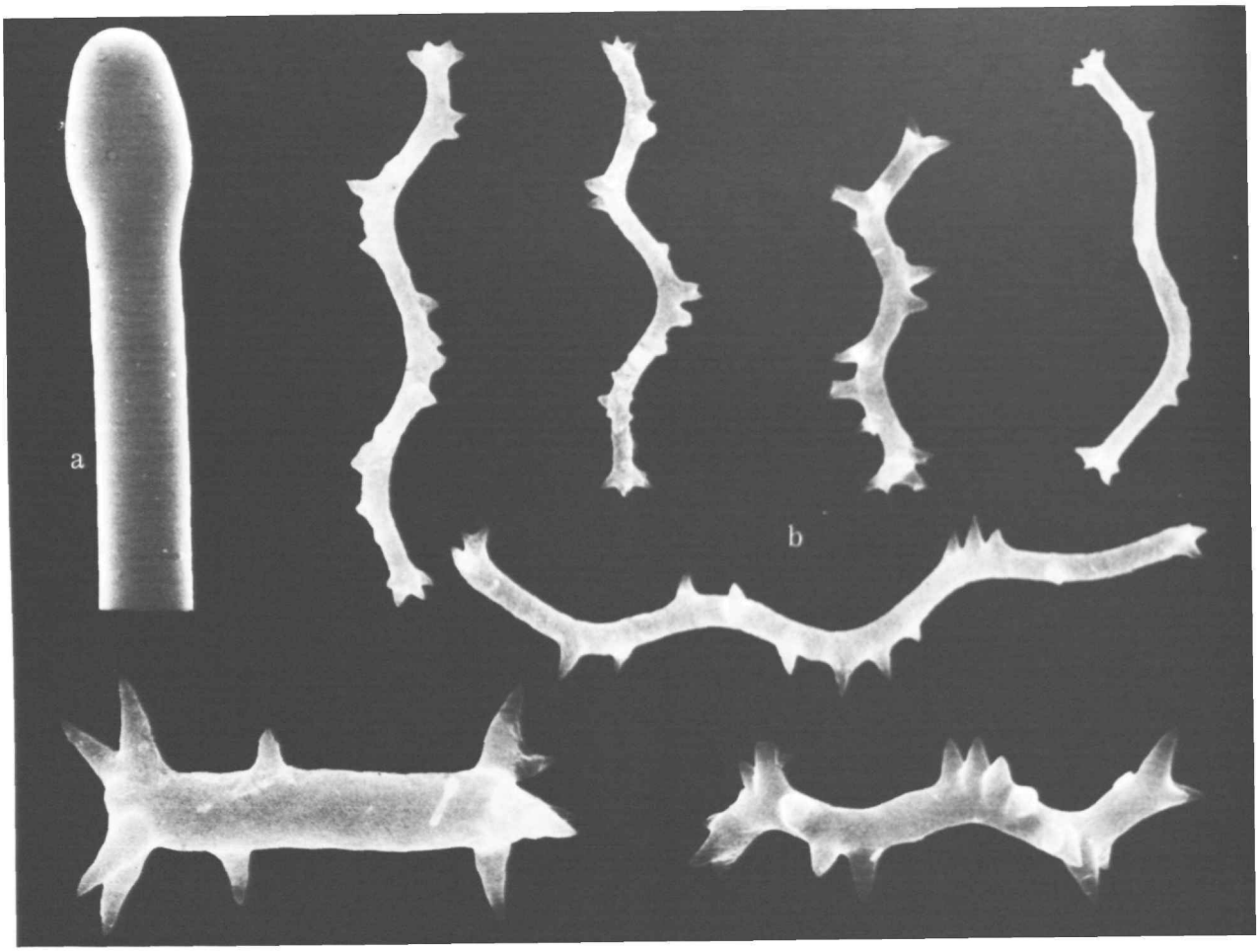

FIGURE 10.—*Cliona paucispina*, spicules (SEM): *a*, tylostyle head; *b*, spirasters and derivatives. (Magnification: *a*, × 1800; *b*, × 2700.)

present at the ends of the spicule. Some shafts are straight or irregularly bent, and W-shaped forms are not uncommon.

Spicule dimensions (in μm): Tylostyles, length × width: 124.6–471.7 × 3.0–8.9 (340.7 × 6.2). Neck width: 2.2–7.4 (5.5). Head length × width: 5.2–22.2 × 4.1–12.6 (12.8 × 8.9). Spirasters, length × width (shaft only): 12.8–43.2 × 0.8–3.0 (28.8 × 1.3). Spine length × width (at base): 0.5–3.2 × 0.5–1.9 (1.6 × 0.8). Number of spines: 6–25 (14.9). Number of bends: 0–7 (4.4)

REMARKS.—In spite of the similarity of spicule complements between this and the two preceding species, there is little likelihood of confusion. *Cliona paucispina* is well characterized by the incrusting, predominately epilithic habit, by the dense arrangement of tylostyles, and by the reduced spination of the spirasters.

The species name is derived from Latin *paucus:* few, little, and *spina:* thorn.

MATERIAL.—USNM 24349 (holotype); Station 5; 12 January 1970; in dead coral. USNM 24350 (paratype); Station 13; 28 April 1971; in dead coral. USNM 24351 (paratype); Station 5; 30 December 1971; in dead coral. Station 2; 28 October 1969; in rock.

DISTRIBUTION.—Bermuda.

Cliona vermifera Hancock

FIGURES 11–13

Cliona vermifera Hancock, 1867:239–240, pl. 8: fig. 2.—Topsent, 1889:35.—Hechtel, 1965:60–61.

DESCRIPTION.—*Ectosome:* The papillae (Figures 11*a, b*) are usually of vivid orange-red color, light ocher in alcohol, or dry. In a few specimens they are dark brownish orange. Their shape is circular or oval, sometimes rather irregular. They are about

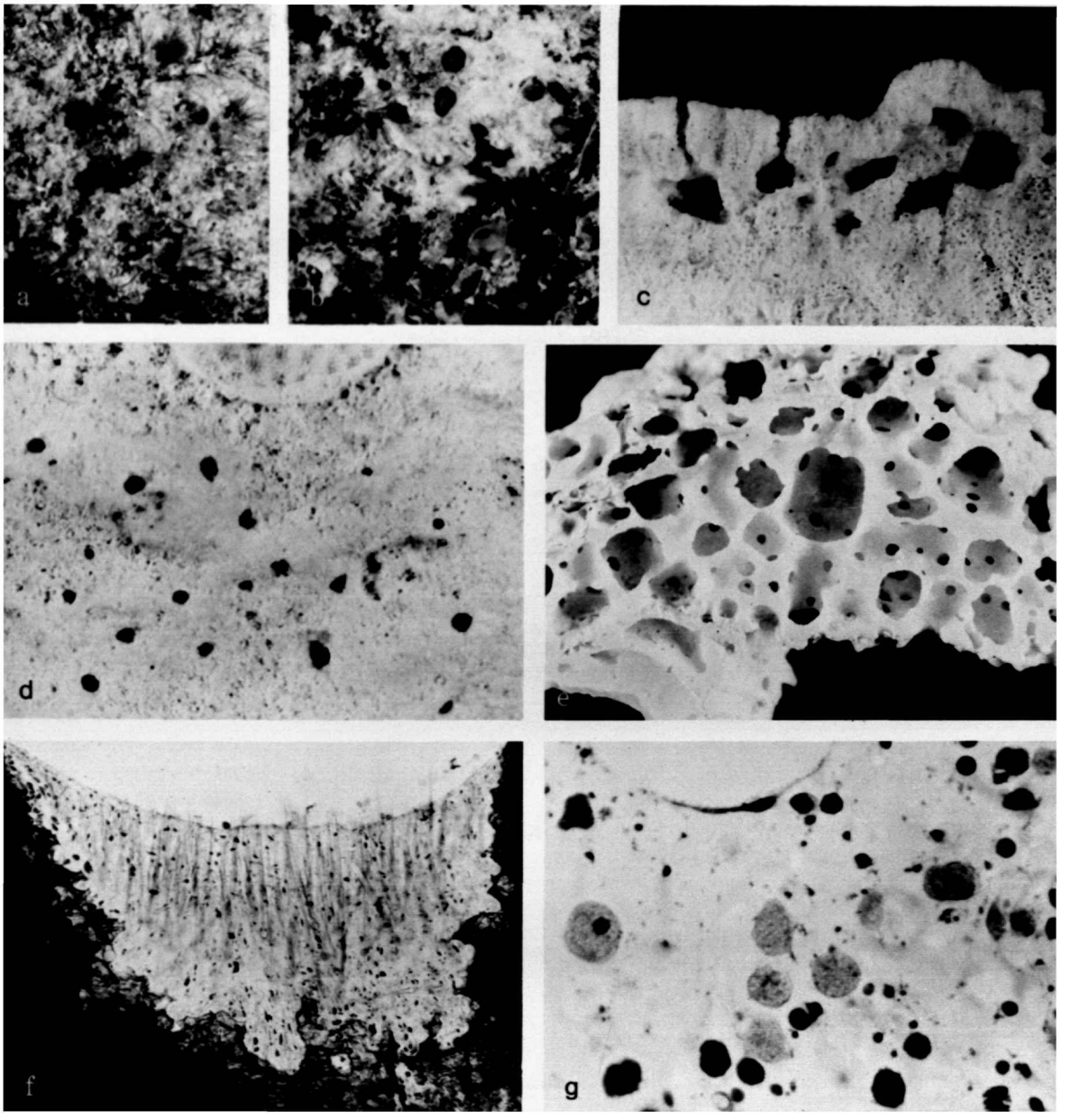

FIGURE 11.—*Cliona vermifera: a, b,* expanded and contracted papillae of live specimen; *c,* papillary canals and burrows in coral rock; *d,* papillary perforations; *e,* chambers with large foramina in pelecypod shell; *f,* vertical section through papilla; *g,* choanosomal a-granular cells. (Magnification: *a–e,* × 3; *f,* × 140; *g,* × 850.)

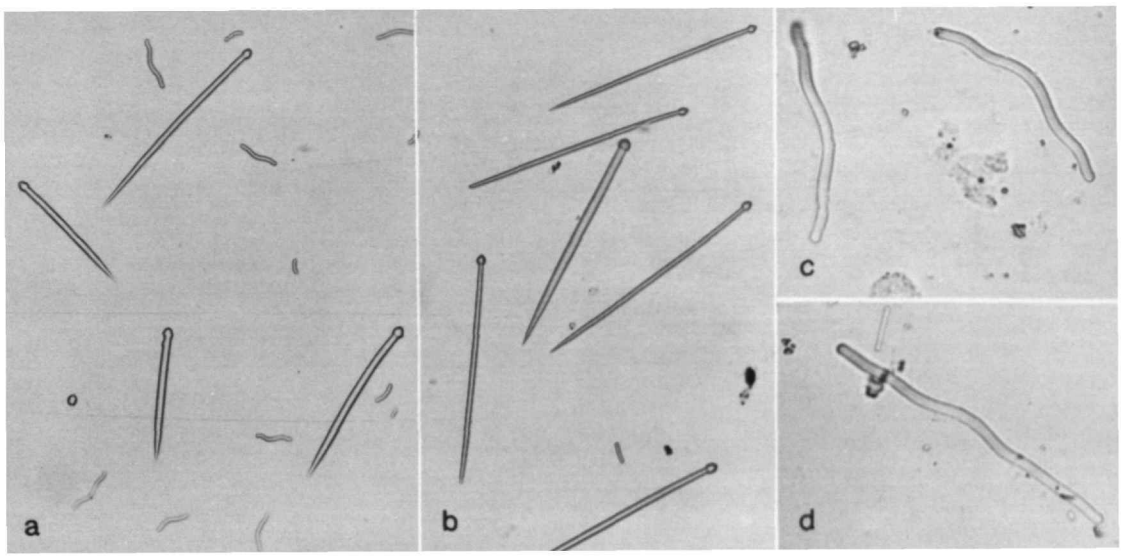

FIGURE 12.—*Cliona vermifera*, spicules: *a*, tylostyles and microscleres; *b*, tylostyles; *c*, *d*, microscleres (smooth spirasters). (Magnification: *a*, *b*, × 140; *c*, *d*, × 520.)

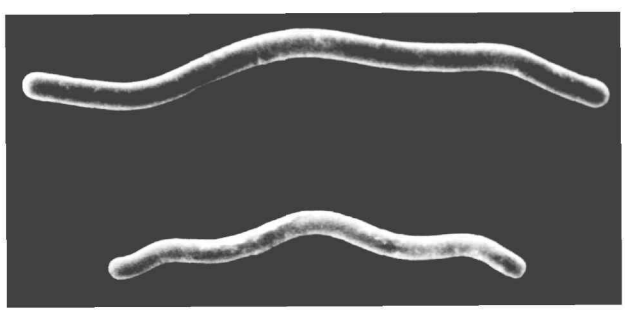

FIGURE 13.—*Cliona vermifera*, spicules (SEM): Microscleres (smooth spirasters). (Magnification: × 1300.)

2 mm apart, with little tendency to fuse and measure 0.3 × 0.3 mm–1.5 × 2.5 mm, 1–1.5 mm for the majority. Oscula are under 1 mm in size, with a raised yellow-orange rim. Ostia can expand to 0.3 mm; their average size, however, is under 50 μm.

Choanosome: The large chambers are almost filled with fleshy, deep red, pale orange, or bright orange tissue that fades to light brown in alcohol or when dried. The same weakly staining, spheroid, a-granular cell type described for *Cliona amplicavata* is present here in large numbers (Figure 11*g*). They are particularly accumulated near the substratum walls of the chambers, in the diaphragm filling the chamber foramina, and also in strands leading through the choanosome. Choanocyte-chambers measure 28 μm. Large spaces devoid of cellular material can be noted in the center of the gallery chambers and to both sides of the foramina.

Excavations: The papillary perforations (Figure 11*d*) are very small and can easily be confused with those of *Cliona lampa* forma *occulta:* 0.3–1.8 mm (1.0 mm). However, there are well-developed papillary canals, 1.3–3.5 mm (2.0 m) long, and large chambers. The chambers (Figures 11*c,e*) are basically ovoid, the longer axis parallel to the substratum surface and with somewhat angular walls. Their size (length × width × height) is 2.7 × 2.7 × 1.0 mm–7.7 × 4.8 × 2.0 mm (4.8 × 3.5 × 1.4 mm). They are separated by walls of 0.3–1.9 mm. The walls are perforated by at least six large foramina, 0.3–1.1 mm (0.6 mm) in diameter. The galleries extend 20 mm into the substratum.

Spicules: Tylostyles in the papillae are placed perpendicular to the surface (Figure 11*f*). Elsewhere they are scattered or loosely organized into strands. There appear to be two size classes, one shorter and thicker than the other, but neither has a particular location and there are many transitional forms. The tylostyles (Figures 12 *a,b*) are mostly straight; some are bent in the third behind the head. Frequently, they do not taper toward the point until the last fourth of their length. The heads are spheroid but mostly mucronate, occa-

sionally subterminal. The microscleres (Figures 12 *a,c,d,* 13) occur everywhere in the tissue but they are more abundant in the choanosome. They are smooth spiralled or undulated rods of uniform thickness throughout their length. The ends are rounded. These spicules are commonly called "smooth spirasters."

Spicule dimensions (in μm): Tylostyles, length × width: 133.5–145.0 × 3.0–8.9 (242.4 × 5.7). Neck width: 1.1–7.4 (4.6). Head length × width: 5.6–14.8 × 4.8–13.7 (10.7 × 8.9). Spirasters (smooth), length × width: 16.0–76.8 × 1.0–4.8 (59.3 × 2.8). Number of bends: 0–9 (5.1).

MATERIAL.—USNM 24340; Station 9; 8 January 1970; in rock. USNM 24341; Station 13; 28 April 1971; in rock. USNM 24342; Station 18; 15 May 1971; in dead base of live coral (*Mussa*), dead *Millepora*, pelecypod shell. Station 5; 31 December 1969; in gastropod shell. Station 5; 12 January 1970; in pelecypod shell. Station 7; 6 January 1970; in rock. Station 10; 11 January 1970; in pelecypod shell. Station 10; 31 May 1972; in coralline incrusted rock. Station 11; 13 January 1970; in coralline incrusted coral rubble (*Porites, Millepora*). Station 12, 27 April 1971; in dead coralline incrusted coral. Station 15; 3 May 1971; in rock. Station 17; 9 June 1972. Station 18; 13 May 1971. Station 19; 7 June 1972.

DISTRIBUTION.—Tropical and subtropical Atlantic and Indo-Pacific.

Cliona dioryssa (Laubenfels), new combination

FIGURES 14–16

Spirastrella dioryssa Laubenfels, 1950:98–99, fig. 44.

DESCRIPTION.—*Ectosome:* The ectosomal portions of the sponge which are showing on the substratum surface are of deep orange to yellow-orange color. The color becomes light brown in alcohol and after drying. Some of the smaller isolated structures (1.0 × 1.0 mm–6.0 × 3.5 mm) are approximately circular and resemble typical papillae, bearing oscula or pori. Commonly, however, there are small irregular crusts with ragged outline that have a tendency to fusion (Figure 14 *a, b*). The crusts are about 1 mm high, 8 × 4 mm–16 × 8 mm in diameter. One large single incrustation measured 55 × 30 mm and covered an area of 5 cm^2. Laubenfels (1950) reported specimens that were "still not as much as 10 cm in diameter," with a thickness reaching 3 mm. Oscula are irregularly distributed over the incrustations. They too have ragged edges; they measure 0.5 × 0.5 mm–2.0 × 3.0 mm and can sometimes be provided with a minute membranous collar. Ostia are 0.1 mm in diameter. There are densely accumulated granular cells, irregular or spindle shaped, about 15 μm long, with 1 μm inclusions.

Choanosome: Distinct chambers, as well as crevices in porous substrata, are filled with pale orange tissue that turns pale ocher upon preservation (alcohol or dry). Granular (1 μm granules), spindle, or club-shaped cells (Figure 14*g*), probably the same kind noted above, occur in large numbers. They are larger than those in the ectosome, 24 × 16 × 32 × 13 μm, and it was observed that they show a remarkable resistance to solution in sodium hypochlorite when spicule mounts were prepared. Different stages of developing eggs measure up to 40 μm (May); choanocyte-chambers measure 28 μm.

Excavations: The size of the irregular depressions on the substratum surface (Figure 14*d*) corresponds with that of the tissue incrustations. In macerated rock fragments containing the sponge, they ranged 0.5 × 0.5 mm–8.0 × 5.6 mm (2.3 × 1.9 mm). The larger depressions are 4–6 mm deep and lead directly into the chambers, very much like in the incrusting form of *Cliona lampa*. Only small papillae have a well-defined canal of 0.5–2.4 mm (1.1 mm). The chambers (Figures 14*c,e*) are more or less spherical, but are not well defined because the separating walls are frequently broken down. They measure 1.1–3.2 mm (2.2 mm). The walls are 0.1–1.0 mm (0.3 mm) thick and perforated by at least six foramina per chamber, 0.2–1.2 mm (0.5 mm). Because of many perforations, in addition to natural crevices, the walls are frequently reduced to single bars. Penetration into the substratum attains 25 mm.

Spicules: A palisade of tylostyles is present in the outer ectosome. Just below this, spicules occur in a crisscross fashion (Figure 14*f*). In the choanosome they are sparse and without orientation, some strands excepted. The tylostyles (Figures 15*a–c*) are usually slightly bent. They have a slender, gradually tapering shaft and a relatively large subspherical head, with a tendency to be mucronate. Subterminal and reduced heads or a second swell-

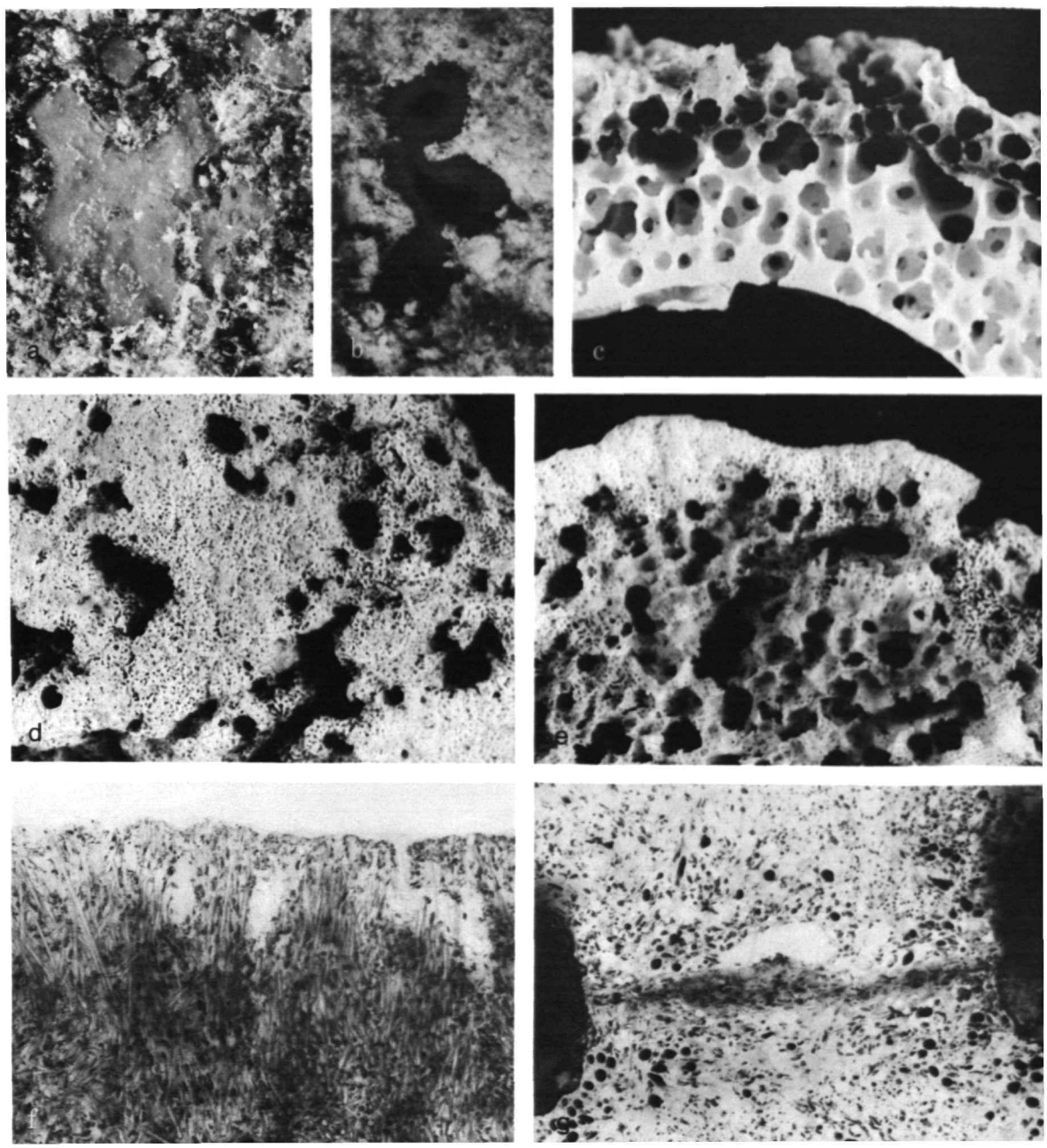

FIGURE 14.—*Cliona dioryssa: a*, incrusting portion of live specimen; *b*, 3 fusing papillae bearing oscula; *c*, chamber arrangement in well-cemented limestone (pelecypod shell); *d*, papillary perforations and *e*, chambers in porous coral rock; *f*, vertical section through sponge crust; *g*, choanosomal granular cells near tissue condensation (diaphragm) between 2 chambers. (Magnification: *a–e*, × 3; *f*, *g*, × 140.)

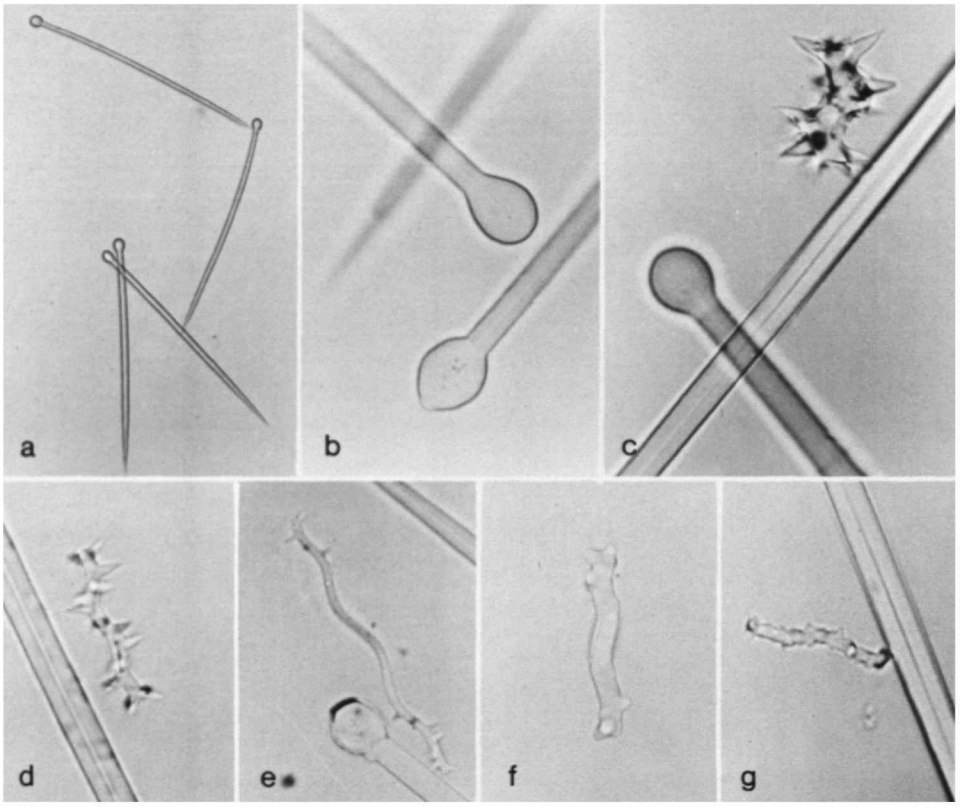

FIGURE 15.—*Cliona dioryssa*, spicules: *a*, tylostyles; *b*, tylostyle heads; *c*, spiraster and tylostyle head; *d–g*, spirasters. (Magnification: *a*, × 140; *b–g*, × 850.)

ing behind the head are infrequent malformations. The spirasters (Figures 15*c–g*, 16) are concentrated in the ectosome without forming a cortex. They are remarkably variable in size and shape and many show a high degree of malformation. Although there are many transitional forms, two types can be recognized. Type I is stout, with a thick shaft densely set with large strong spines, most of which are joined at the base. Type II is more delicate, with a long slender shaft and small spines, which are usually well spaced from each other. Reduction of number or size of spines is very common.

Spicule dimensions (in μm): Tylostyles, length × width: 106.8–391.6 × 3.7–7.4 (244.4 × 5.4). Neck width: 3.3–7.0 (4.4). Head length × width: 3.7–17.8 × 1.9–11.5 (10.0 × 8.3). Spirasters I, length × width (shaft only): 11.2–41.6 × 1.4–4.8 (27.4 × 3.2) Spine length × width (at base): 1.6–6.7 × 1.0–4.0 (4.6 × 2.6). Number of spines: 7–26 (16.0). Number of bends: 0–5 (3.0). Spirasters II, length × width (shaft only): 19.2–43.2 × 0.6–2.2 (33.9 × 1.5). Spine length × width (at base): 0.5–3.8 × 0.5–2.6 (2.3 × 1.3). Number of spines: 7–24 (13.6). Number of bends: 2–6 (4.3).

REMARKS.—Laubenfels (1950) had some doubts about the generic placement of his species. He noted its penetration into the substratum and stated that "if it is truly 'boring,' then it is a *Cliona*, not a *Spirastrella* at all." The burrowing habit of *Cliona dioryssa* is confirmed here. However, it should also be noted that the relatively small number of spirasters and the lack of an ectosomal crust formed by spirasters are untypical for the genus *Spirastrella*.

MATERIAL.—USNM 24343; Station 13; 28 April 1971; in dead coral. USNM 24344; Station 5; 3 January 1973; in dead coral and pelecypod shell.

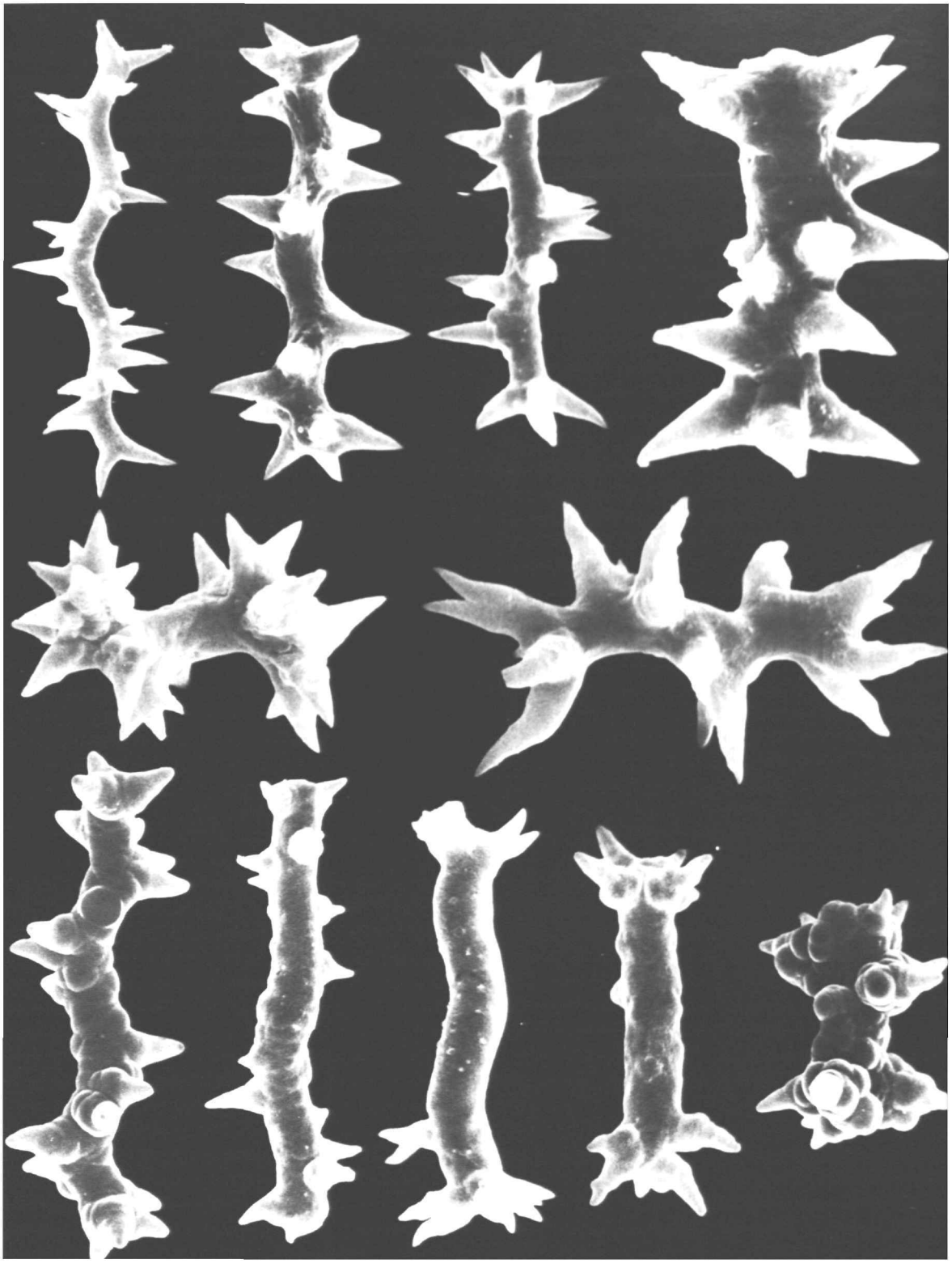

FIGURE 16.—*Cliona diorysa*, spicules (SEM) : Spirasters and derivatives. (Magnification: × 2700.)

USNM 24345; Station 10; 31 May 1972; in rock. Station 5; 31 December 1969; in dead coral. Station 5; 12 January 1970; in rock. Station 5; 12 January 1970; in dead coral. Station 5; 3 January 1972; in rock. Station 5; 30 December 1971; in rock. Station 6; 1 January 1970; in dead coral. Station 7; 6 January 1970; in dead coral. Station 9; 6 January 1970; in dead coral. Station 10; 11 January 1970; in rock. Station 10; 31 May 1972; in rock. Station 11; 13 January 1970; in rock, dead coral, pelecypod shell. Station 13; 28 April 1971; in dead coral. Station 14; 2 May 1971; in rock, pelecypod shell. Station 16; 6 May 1971; in rock. Station 17; 6 May 1971; in coralline incrusted rock. Station 17; 9 June 1972. Station 19; 7 June 1972; in rock. Station 20; 9 June 1972; in dead *Millepora*. Station 21; 12 January 1973. Station 22; 26 June 1972; in rock.

DISTRIBUTION.—Bermuda.

Cliona lampa Laubenfels

FIGURES 17–20

Cliona lampa Laubenfels, 1950:110–112, fig. 49.

DESCRIPTION.—*Ectosome:* This sponge has three distinct morphological forms. Forma *lampa* (Figure 17*a*) is the one described by the original author. It is also the most conspicuous variety. The ectosome encrusts the substratum with a continuous very fine layer of vermilion, occasionally rusty red tissue. It turns faintly gray in alcohol, light brown in the dry state. The extension of the incrustations ranges from 2 cm² to approximately 1.5 m² per specimen. Oscula are scattered over the surface, usually circular, 2–4 mm in diameter, with a raised rim. Ostia measure about 0.8 mm. Forma *occulta* (Figure 17*b*) is easily overlooked because only very small circular papillae penetrate the rock surface to the exterior. Their color is basically the same as in forma *lampa,* perhaps less vivid. They are densely spaced, about 25 per cm², but fusion is extremely rare. Diameter of the papillae is 0.2–1.5 mm, mostly 0.8 mm. The larger ones bear circular oscula of 1–3 mm. The papillae are level with the substratum surface; only expanded oscula protrude. Forma *flavida* has the identical appearance as forma *lampa,* except that the incrustations have sulfur yellow color. Only two yellow specimens have been found, one covering about 120 cm², the other about 300 cm². The histology and cytology of this species have been discussed in detail by Rützler and Rieger (1973). An extensive contractile tissue, reaching 0.8 mm below the sponge surface, is present in forma *lampa.*

Choanosome: The tissue completely fills small galleries which are always developed if the sponge burrows in compact substrata. In very porous substrata, as many of the invaded corals are, galleries are ill-defined and existing spaces are permeated. Color of the choanosome is dull rusty red, orange, or yellow-orange in formae *lampa* and *occulta,* grayish ocher in forma *flavida.* It fades to become almost colorless after preservation. Specimens collected in January and June contained numbers of orange gemmules in the choanosome. They measure 0.7–0.9 mm, with a noncellular envelope 10 μm thick Between the enveloping membrane and the reserve material filling most of the gemmule, there is a thin layer of loosely spaced spindle-shaped cells (Figure 18*b*).

Excavations: The substratum surface that was previously covered by the incrusting forms (*lampa* and *flavida*) of this sponge is obviously eroded (Figure 17*c*), but only to a certain degree, without destroying major structural features. It looks porous, like pumice stone, the pores leading directly into the chambers. At the location of the oscula there are ragged depressions, 1.6–3.2 mm (2.4 mm), about as deep as wide. They lead directly into the chambers. The sponge can infiltrate porous substrata where chambers are obscure (Figure 17*f*). In compact substrata the small chambers are spheroid, 0.5–2.0 mm (1.2 mm) (Figure 17*e*). The walls of the chamber are 0.1–0.5 mm thick, and pierced by numerous (at least four to nine) foramina of 0.2–0.6 mm (0.3 mm). The substratum can be penetrated to a depth of 80 mm. Form *occulta* has small papillary perforations, 0.3–1.8 mm (0.8 mm) (Figure 17*d*). There is no distinct papillary canal; the chambers start 0.1–0.6 mm under the surface. The chambers are like in the other forms, 1.0–2.0 mm (1.4 mm), perhaps somewhat more spaced, i.e., with thicker walls: 0.2–0.8 mm. A maximum of 12 mm penetration into the substratum was observed.

Spicules: In the ectosome, just below the surface, there is a layer of spiny microrhabds without orientation and a series of perpendicular tylostyles which partly penetrate the surface with their tips

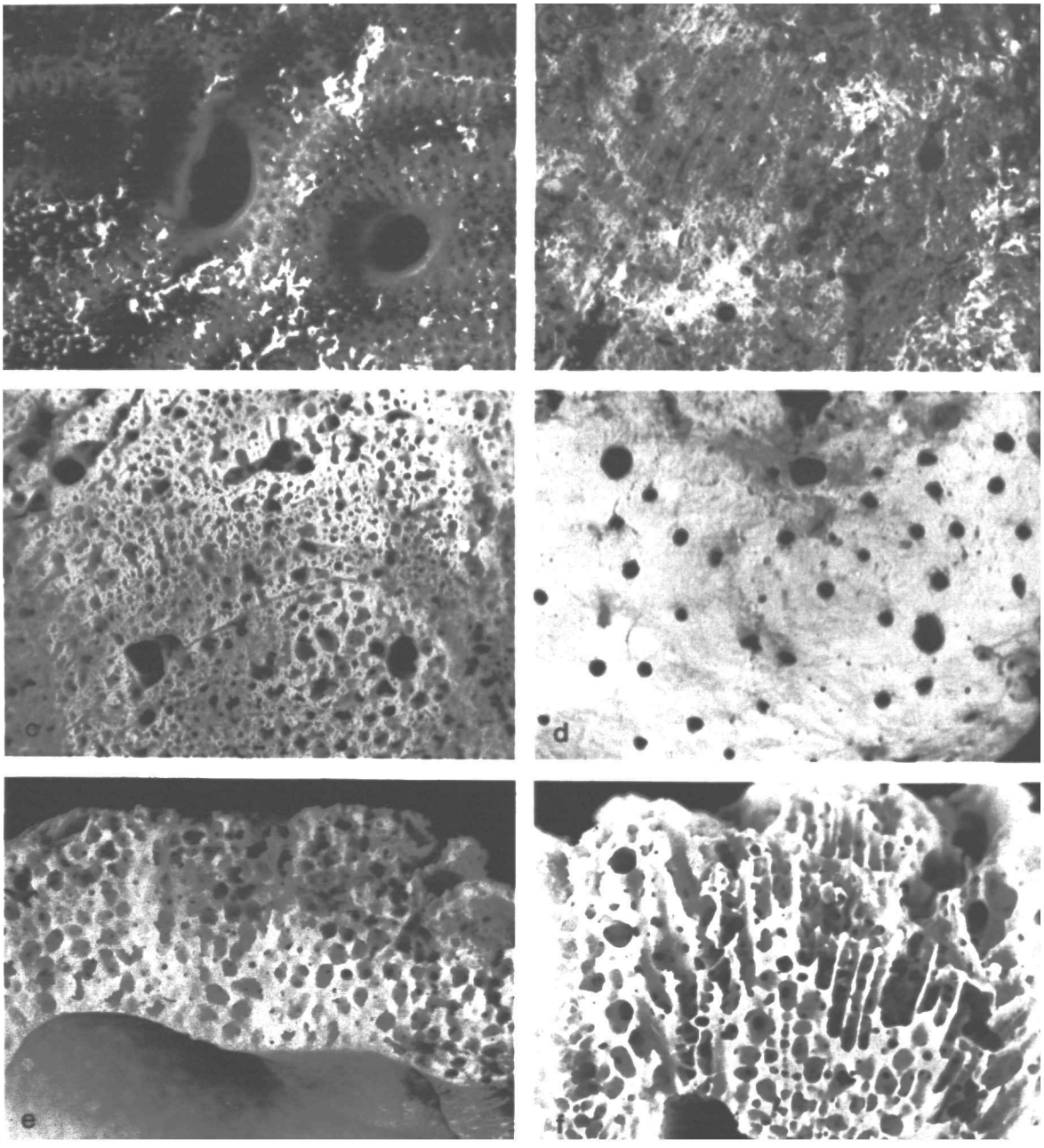

FIGURE 17.—*Cliona lampa: a*, forma *lampa* incrusting the coral *Diploria*, 2 oscula are showing; *b*, papillae of live forma *occulta; c*, eroded surface of pelecypod *(Chama)* shell burrowed by forma *lampa*. Larger holes indicate former position of oscula; *d*, papillary perforations produced by forma *occulta; e*, chamber arrangement in compact (pelecypod shell) and, *f*, in porous substratum (coral). (Magnification: *a–f*, × 3.)

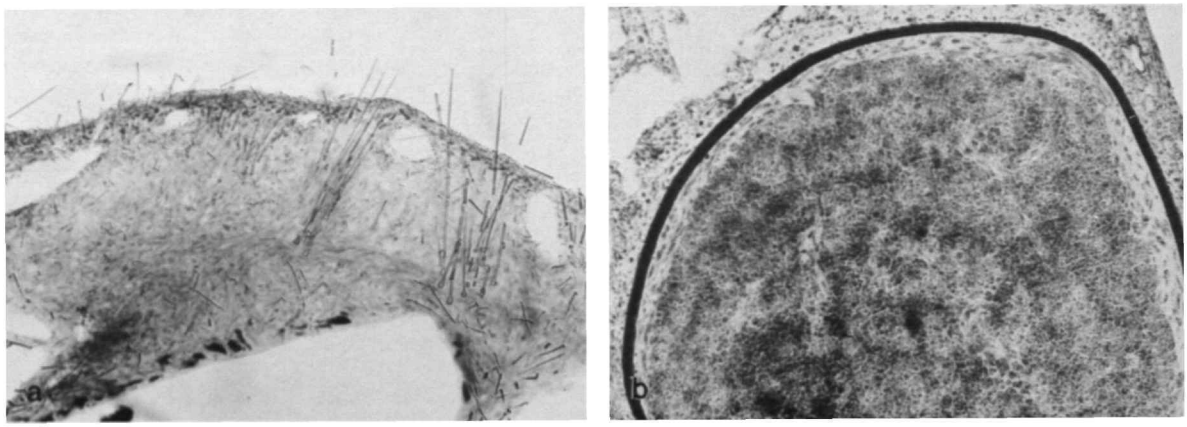

FIGURE 18.—*Cliona lampa: a*, vertical section through incrusting tissue of forma *lampa; b*, section through gemmula. (Magnification: *a, b*, × 140.)

(Figure 18*a*). Below, there is a zone of tylostyles, oxea, and microrhabds without orientation, but rather parallel than perpendicular to the surface. All three spicule types occur also in the choanosome but there they are quite rare. Some of the tylostyles are organized into strands. The tylostyles (Figure 19*a*) are straight and gradually tapering to a sharp point. Their heads are spherical or ovoid; the longer axis is always in the direction of the shaft. The oxea (Figures 19*b, c*, 20*a, b, f*) are bent in the center and provided with minute spines over the entire surface. At high magnification (scanning electron microscope), it can be seen that the spines resemble hooks or double hooks. Central swellings are very rare. The microrhabds (Figures 19*c*, 20*c–f*) are mostly straight and densely covered by robust single or furcated spines.

Spicule dimensions (in μm): Forma *lampa*. Tylostyles, length × width: 118.4–259.0 × 0.8–3.8 (196.7 × 2.8). Neck width: 0.8–3.2 (2.1). Head length × width: 3.2–7.8 × 2.4–7.4 (5.6 × 4.3). Oxea, length × width: 59.2–115.2 × 1.0–2.9 (85.7 × 1.8). Microrhabds, length × width: 4.0–25.6 × 0.8–3.8 (13.5 × 1.6).

Forma *occulta*. Tylostyles, length × width: 142.0–320.4 × 1.1–5.8 (245.6 × 3.7). Neck width: 1.0–3.7 (2.9). Head length × width: 4.0–8.0 × 1.9–8.0 (7.1 × 6.0). Oxea, length × width: 51.2–94.4 × 0.8–5.6 (75.6 × 2.8). Microrhabds, length × width: 6.4–21.6 × 1.3–4.8 (12.9 × 2.3).

Forma *flavida*. Tylostyles, length × width: 107.3–222.0 × 0.7–4.1 (183.8 × 2.8). Neck width: 0.5–3.7 (2.2). Head length × width: 3.7–7.4 × 3.0–6.7 (5.5 × 4.4). Oxea, length × width: 57.6 × 92.8 × 1.4–2.1 (73.2 × 1.7). Microrhabds, length × width: 4.8–16.0 × 0.6–2.6 (12.4 × 1.8).

REMARKS.—Laubenfels (1950), in justifying the naming of *Cliona lampa*, listed a number of characteristics to distinguish his new species from *C. vastifica* Hancock. The present findings will weaken his argument considerably if it can be maintained that the three forms of *C. lampa* in Bermuda are merely different phenotypes of the same species: yellow and "rusty" red (rather than vermilion) color varieties are represented by formae *flavida* and *occulta* (occasionally also *lampa*). Distinct burrows (chambers), circular in cross-section (rather than permeation), are produced by all forms and are particularly discernible in densely structured substrata. Forma *occulta* has small, circular papillae exactly like *C. vastifica*. A "slight spicular difference," that spiny microrhabds of *C. vastifica* are "distinctly angulated, whereas those of *lampa* are straight," was also pointed out by Laubenfels (1950, 1953). The shape of this spicule type, however, has been shown to vary considerably in *C. vastifica*, even within a single specimen (Topsent, 1891), straight microrhabds being a common type. *C. corallinoides* Hancock, characterized by flexuous microrhabds, is considered a mere variation of *C. vastifica* (Topsent, 1891, 1900, 1932; Volz, 1939). The formation of gemmules in *C. lampa*, not reported by previous authors, is also characteristic of *C. vastifica* (Topsent, 1932).

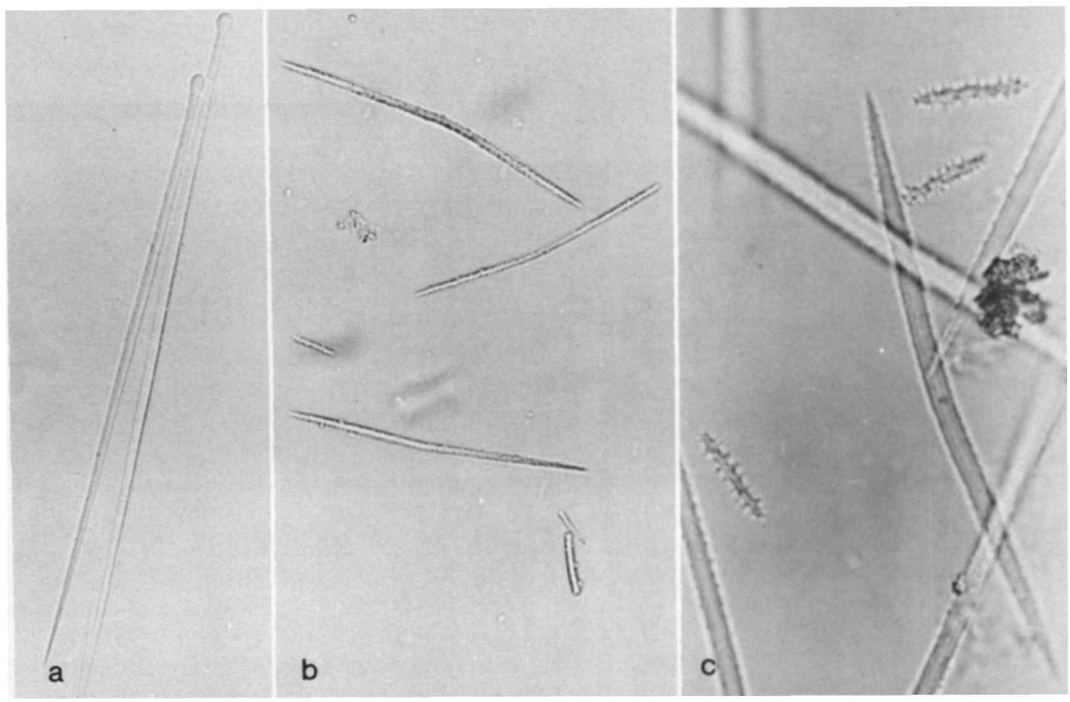

FIGURE 19.—*Cliona lampa*, spicules: *a*, tylostyles; *b*, oxea; *c*, oxea and spiny microrhabds. (Magnification: *a*, *b*, × 520; *c*, × 1400.)

A worldwide revision of the *Cliona vastifica* complex, which is beyond the scope of this paper, will probably clarify also the status of the present species. Only substantial revisionary data should justify the elimination of a well-established name like *C. lampa*.

The names chosen to designate the phenotypic forms of *Cliona lampa* are derived from Latin, *occultus*: hidden, concealed; *flavidus*: yellowish.

MATERIAL.—Forma *lampa:* USNM 24330; Station 4; 30 December 1969; in rock. USNM 24331; Station 7; 6 January 1970; in pelecypod shell *(Chama)*. USNM 24332; Station 5; 12 January 1970; in dead coral *(Diploria)*. Station 4; 30 December 1969; in rock. Station 5; 31 December 1969; in coral, pelecypod shell. Station 5; 30 December 1971; in pelecypod shell. Station 7; 6 January 1970; in pelecypod shell. Station 10; 11 January 1972. Station 12; 27 April 1971; in pelecypod shell. Station 21; 26 June 1972; in pelecypod shell *(Chama)*. Station 21; 12 January 1973.

Forma *occulta:* USNM 24339; Station 4; 26 December 1969; in rock. USNM 24338; Station 9; 8 January 1970; in rock. USNM 24337; Station 5; 3 January 1972; in pelecypod shell. Station 2; 8 May 1971; in rock. Station 3; 26 December 1969; in rock. Station 5; 31 December 1969; in pelecypod shell. Station 5; 12 January 1970; in dead part of live coral *(Porites)*. Station 5; 30 December 1971; Station 7; 6 January 1970; in rock, pelecypod shell. Station 8; 6 January 1970; in rock. Station 10; 11 January 1970; in rock, pelecypod shell. Station 11; 13 January 1970; in pelecypod shell, coral rubble *(Porites)*. Station 12; 27 April 1971; in pelecypod shell. Station 13; 28 April 1971; in dead coral. Station 17; 9 June 1972. Station 19; 7 June 1972; in rock. Station 20; 9 June 1972; in dead coral *(Montastrea)*. Station 21; 15 June 1972.

Forma *flavida:* USNM 24328; Station 10; 11 January 1972; in rock. USNM 24329; Station 21; 12 January 1973; in live pelecypod *(Chama)*.

DISTRIBUTION.—Tropical western Atlantic.

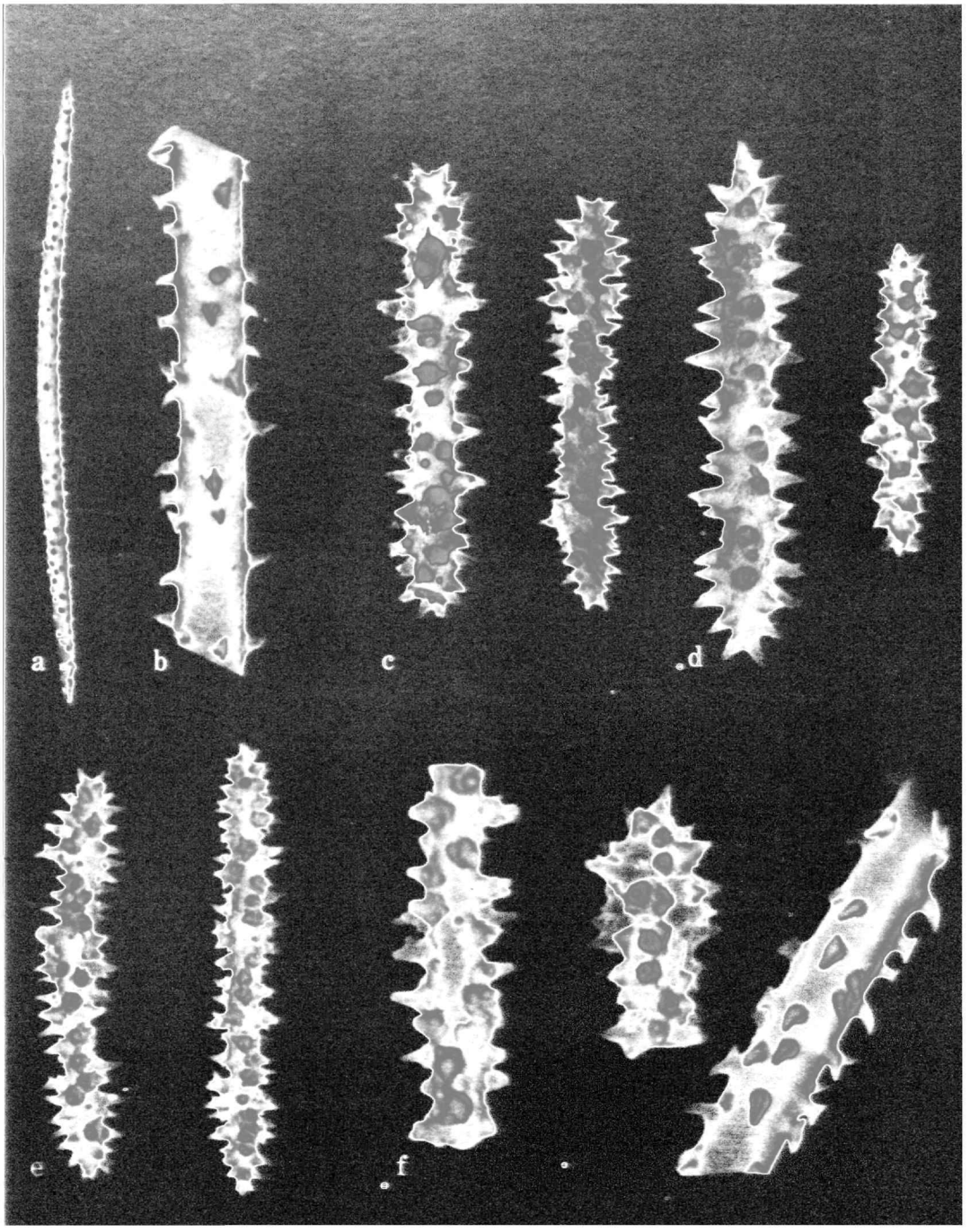

FIGURE 20.—*Cliona lampa*, spicules (SEM): Forma *lampa*: *a*, *b*, oxea with spines; *c*, spiny microrhabds. Forma *occulta*: *d*, spiny microrhabds. Forma *flavida*: *e*, *f*, spiny microrhabds and portion of oxeon. (Magnification: *a*, × 1300; *b–e*, × 4500; *f*, × 9000.)

Cliona amplicavata, new species

FIGURES 21–23

DIAGNOSIS.—Papillae yellow, circular, discrete, 1.4 mm (mean diameter). Excavations typically single, ovoid 10 × 7 mm (mean dimensions); filled by yellow, soft, mucuous tissue. Tylostyles curved, with spherical, mucronate heads, 262.5 × 7.1 μm. Rhaphides, in choanosome only, 129.8 × 0.8 μm (mean length × width).

DESCRIPTION.—*Ectosome:* The papillae of this sponge are easily overlooked, although the single large cavities containing the choanosome are most conspicuous as soon as the substratum is split open. The papillae are bright yolk yellow, circular, and measure 0.8–2.6 mm (1.4 mm) in diameter. Some bearing oscula can attain 3 mm with oscula of 0.5–1.0 mm. They occur in clusters of 2–5, but they always remain separated. In undisturbed specimens they protrude 0.5–1.0 mm from the rock surface. Ostium papillae have the shape of a short cylinder; oscular papillae are cone shaped. The color in alcohol or when dry is dull gray. There are no symbiotic algae. The most conspicuous histological feature is a number of large strongly staining irregular bodies (Figure 21*f*), 35 × 24 μm, that contain calcareous fragments. These are possibly chips freed by the sponge during the burrowing process. A considerable amount of mucoid material is contained in the exhalant canals.

Choanosome: This is yolk yellow like the ectosomal papillae. It is very soft, mucuous, and cavernous and fills the large chambers. In specimens that have been kept outside the water for some time, the tissue collapses and covers the chamber walls only. The irregular bodies mentioned above are also present here in abundance. In addition, there are large, spherical, weakly staining cells without prominent inclusion. They measure 11–14 μm in diameter and contain a small anucleolate nucleus (Figure 21*e*). Another very similar abundant cell type contains basophilic granules of 1 μm (Figure 21*f*). Choanocyte-chambers measure 30–35 μm.

Excavations: One to five papillary perforations (Figure 21*a*) serve each chamber. They are 0.8–2.0 mm (1.3 mm) in diameter and connect with the chamber by cylindrical or sometimes flaring canals, 1.1–4.8 mm (3.2 mm) long. The chambers (Figures 21*c, d*) are frequently single, ovoid, sometimes angular, and width and height are about equal. The larger axis is usually parallel with the substratum surface. The chambers measure 5 × 3 mm–22 × 12 mm (16 × 9 mm). Only few, if any, adjacent chambers are communicating. In that case they are separated by walls of 0.5–0.8 mm thickness. In addition to natural crevices, there are four to more than forty round or oval foramina per chamber, 0.3–1.0 mm wide. Excavations reach 17 mm into the substratum.

Spicules: The tylostyles are usually curved (Figures 22*a, b*, 23*a*). In the papillae they are dense and oriented perpendicular to the surface (Figure 21*b*). This orientation is basically maintained also in the choanosome, but the spicules are much less common and many are placed in disorder. Their heads are well set off, spherical, and typically mucronate; some are distinctly subterminal. A dark axial spot in the center of the head appears in transmitted light In some specimens there is a small percentage of styles. Bundles of fine rhaphides (Figures 22*b*, 23*a–c*) are common in the tissue of the galleries. There are no spirasters or related microscleres.

Spicule dimensions (in μm): Tylostyles, length × width: 190.0–290.0 × 4.5–8.0 (262.5 × 7.1). Neck width: 3.2–6.4 (5.0). Head length × width: 4.8–12.0 × 4.8–10.4 (10.1 × 9.4). Rhaphides, length × width: 117.5–150.0 × 0.8 (129.8 × 0.8).

REMARKS.—This species has the spiculation of *Cliona celata* Grant. It differs from the latter by the development of the papillae, by shape and size of the burrow, by the consistency of the tissue, and by the lack of incrusting and massive stages. No rhaphides have been reported for American populations of *C. celata* (Hartman, 1958).

Cliona amplicavata can be confused with *C. flavifodina* in the field. Its soft, mucuous tissue and the more regular, ovoid chambers serve best for characterization without looking at the spicules. *Siphonodictyon coralliphagum* Rützler, forma *obruta* (Rützler, 1971), another excavating sponge, not yet known from Bermuda, resembles *C. amplicavata* by having a mucuous tissue and a very similar burrow. In fact, from descriptions of the sponge and from a sketch of the burrow (Noel P. James, personal communication), I have previously, in absence of preserved material, erroneously identified this sponge as *Siphonodictyon*. The spiculation (oxea only) in the latter species, however, is very different.

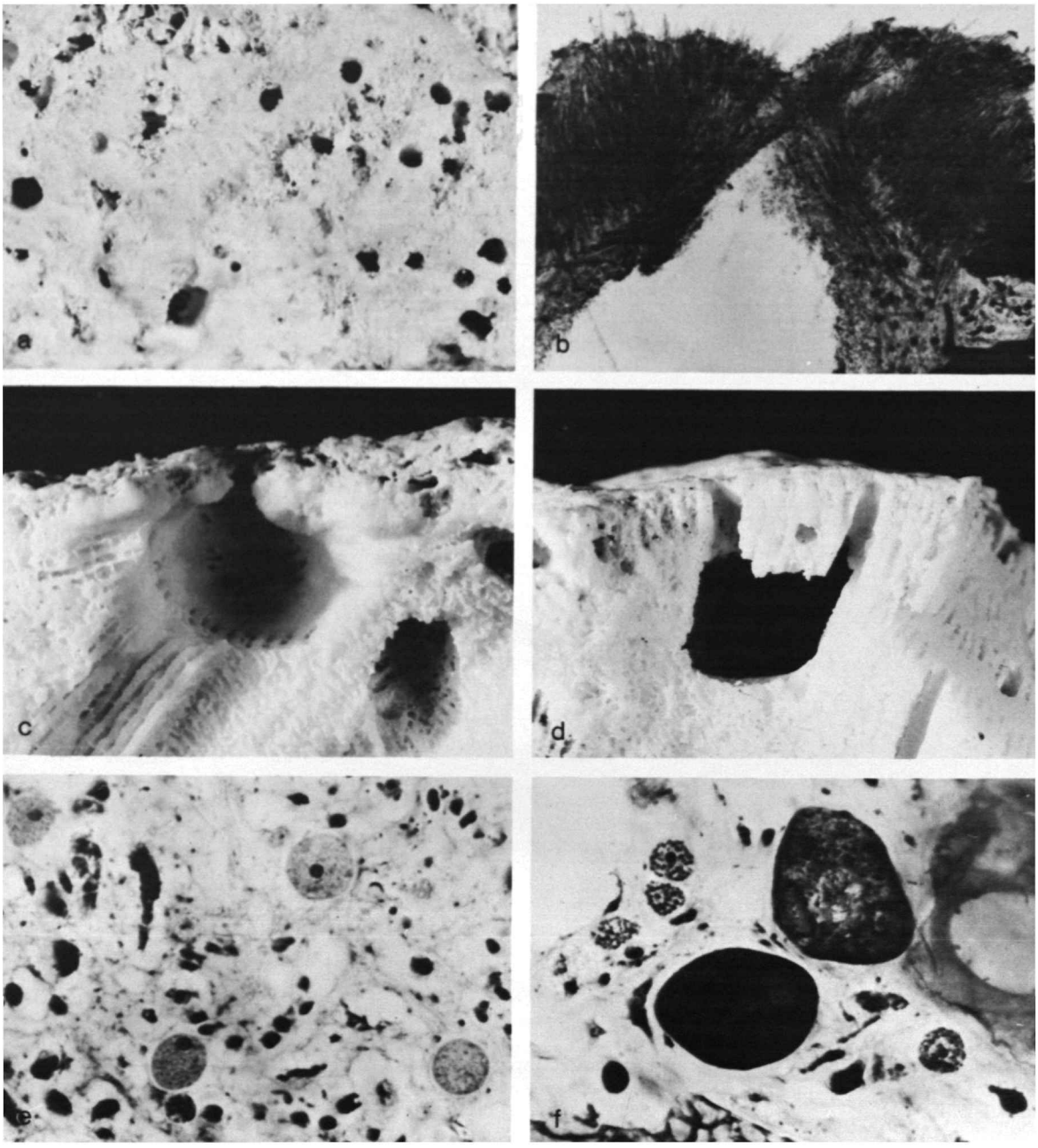

FIGURE 21.—*Cliona amplicavata: a,* papillary perforations; *b,* vertical section through papilla; *c, d,* burrows with 1 and 2 papillary canals; *e,* choanocyte chamber and a-granular cells; *f,* granular cells and irregular bodies containing calcareous fragments. (Magnification: *a,* × 3; *b,* × 50; *c, d,* × 3; *e, f,* × 850.)

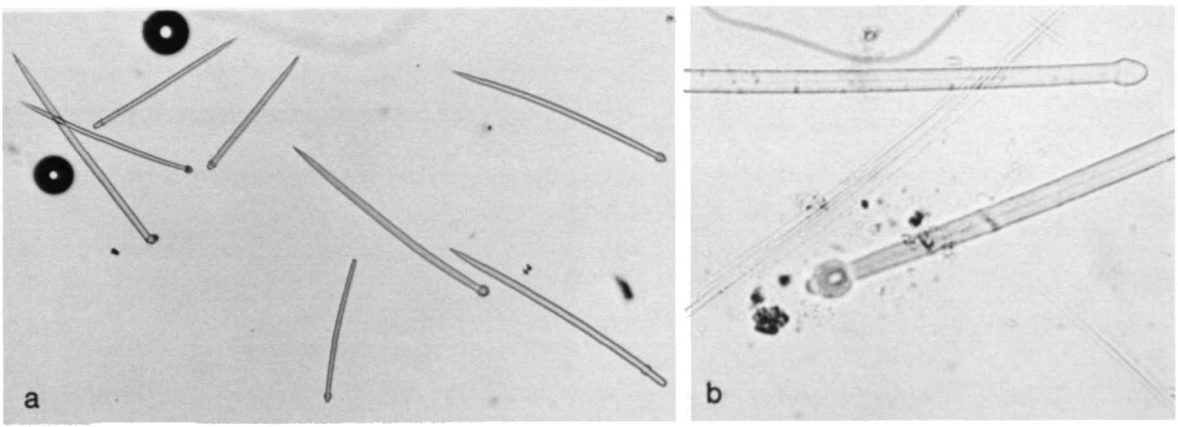

FIGURE 22.—*Cliona amplicavata*, spicules: *a*, tylostyles; *b*, tylostyle heads and rhaphids. (Magnification: *a*, × 140; *b*, × 520.)

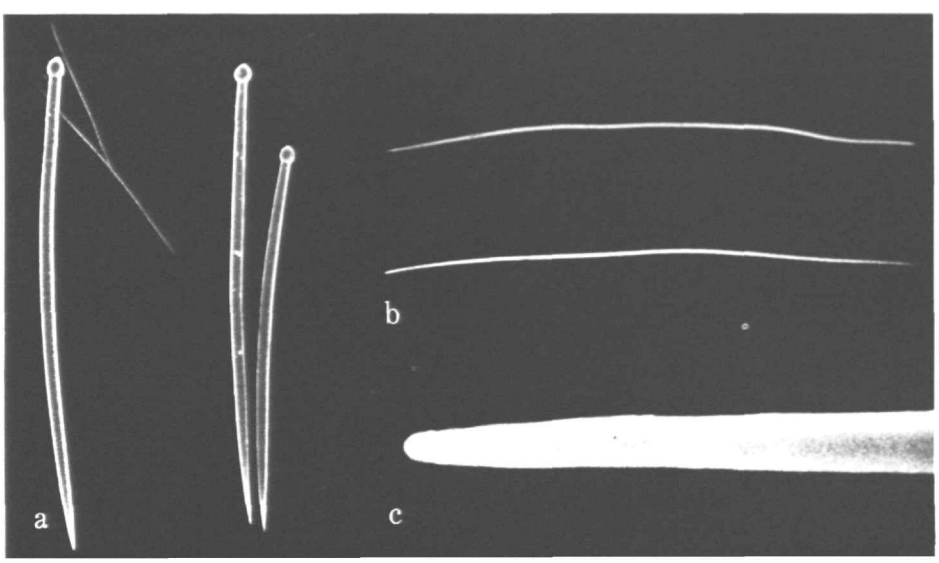

FIGURE 23.—*Cliona amplicavata*, spicules (SEM): *a*, tylostyles and rhaphids; *b*, rhaphids; *c*, magnified end of rhaphid. (Magnification: *a*, × 270; *b*, × 700; *c*, × 18000.)

The species name of *Cliona amplicavata* is derived from Latin *amplus*: large, spacious; *cavatus*: hollowed out, and refers to the characteristic burrow.

MATERIAL.—USNM 24335 (holotype); Station 20; 9 June 1972; in dead portions of coral (*Diploria*). USNM 24333; Station 11; 5 October 1969; in rock. USNM 24334; Station 13; 9 May 1971; in dead coral. USNM 24336; Station 17; 9 June 1972; in dead portion of coral (*Montastrea*). Station 3; 26 December 1969; in dead coral.

Family SPIRASTRELLIDAE Ridley and Dendy

Spheciospongia othella Laubenfels

FIGURES 24–26

Spheciospongia othella Laubenfels, 1950:94–96, fig. 42; pl. 2: fig. 6.

Heterocliona cribaria.—Verrill, 1907:342–343, pl. 35D: figs. 2,3.

DESCRIPTION.—This species has a different appearance from the preceding clionids since, except in very early stages, large parts of the sponge grow on the surface of the rock. The epilithic portions of the sponge consist of convex membranes, hollow pillows, hollow tubercular humps (Figure 24*a*), or smooth conical chimneys that cover or protrude from vertical tunnels in the substratum rock. Their diameters range from 3 × 3 mm–30 × 20 mm; their height attains 1–30 mm. Only one really large and still obviously burrowing specimen was found during the present survey. It was irregular massive, 20 × 12 cm in horizontal dimensions, 5 cm in height.

Ectosome: This is represented by a deep black or dark grayish brown outer layer, grayish black in alcohol, dark gray when dry. The surface is smooth; only near the base it is covered by adherent sediment particles. The oscula are 1–7 mm in diameter (15 mm maximum in the large specimen). They have a raised collar, sometimes lighter in color, and are strongly contractile. Ostia are scattered over the surface and are less than 100 μm wide. A third kind of opening of undetermined function is also abundant. These circular openings, also noted by Laubenfels (1950), stand in groups, are not contractible, have no collars, and measure 0.5–4 mm in diameter. A cross-section through the wall of an epilithic chimney shows a dense outer zone, about 100 μm thick, of spheroid or elongate cells (10 × 10 μm–25 × 3 μm), containing minute black pigment grains (Figure 24*f*). These pigment cells occur scattered throughout the tissue but, except for the outer layer, they are only condensed where they form loose branching strands. They are very rare in the innermost 100–150 μm zone, bordering the atrium. There they are taken over by contractile cells. Granular cells, 16 × 16 μm–30 × 10 μm, containing small (1 μm) or larger (2 μm) granules are abundant.

Choanosome: This is grayish to greenish ocher and becomes dark gray in alcohol or when dry. The fleshy tissue fills natural crevices and small (new) tunnels; it thickly covers the walls of large (old) tunnels (Figure 24 *c*). The central lumen (exhalant canal) is circular in cross section and measures 7–12 mm in diameter. Also the choanosome contains thin branching strands (50–80 μm wide) of pigment cells. Choanocyte-chambers measure 25–30 μm.

Excavations: There are essentially two size classes of perforations produced at the substratum surface (Figure 24 *b*). From the larger ones the epilithic portions of the sponge protrude. There can be one to several such structures, connected by a common endolithic portion, which protrude from holes 4–30 mm and more in diameter. In advanced stages, the epilithic parts of a specimen can be united to form a large massive sponge that is still rooted in the substratum. The second, smaller communicative perforations are probably secondarily produced by outgrowth of the endolithic sponge mass. They measure 0.1–3.2 mm (2.4 mm) in diameter, with a connecting canal of 1–3 mm in length. The large openings lead directly into flaring tunnels, which branch and continue in horizontal and vertical direction under the rock surface (Figure 24*d*). The tunnels are circular or eliptical in cross section, ragged in outline, and reach diameters of at least 22 × 10 mm. They are difficult to pursue throughout their length. Tunnels can extend at least 100 mm into the substratum.

Spicules: Tylostyles in the ectosome run in strands parallel to the surface. Frequently these strands branch and bend toward the surface, where the spicules protrude in tufts (Figure 24*e*). Additional perpendicular tylostyles occur between the tufts. Spirasters are rare and scattered. Tylostyles in the choanosome are mostly scattered; some occur in strands. The shaft of the robust tylostyles (Figure 25*a, c*) is quite uniform in thickness through most of its length. The shaft is bent a short distance behind the head. It does not taper toward the point until approximately the last fourth of its length. The heads are small, spheroid, or elongate. Malformations are common. The spirasters (Figures 25*b, c*, 26) are small and ornate with clusters of spines, particularly at both ends.

Spicule dimensions (in μm): Tylostyles, length × width: 115.7–373.8 × 1.5–8.9 (279.6 × 6.3).

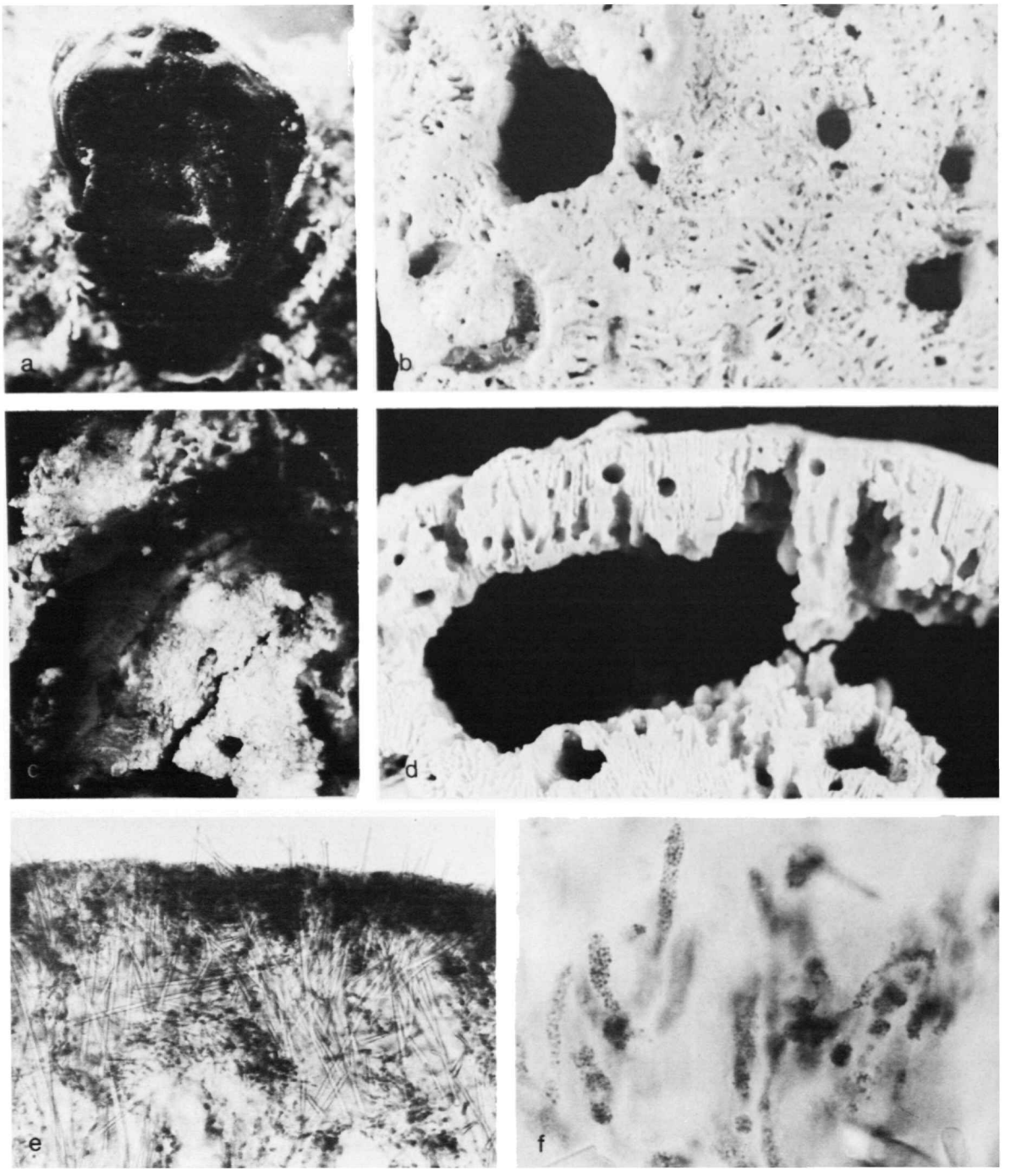

FIGURE 24.—*Spheciospongia othella: a,* pillow-shaped specimen protruding from substratum; *b,* 2 size classes of perforations on substratum surface; *c,* tissue-covered tunnel inside rock; *d,* cross section through 2 large tunnels, running below surface of coral rock; *e,* vertical section through ectosome; *f,* pigment cells. (Magnification: *a, b, d,* × 3; *c,* × 1; *e,* × 140; *f,* × 850.)

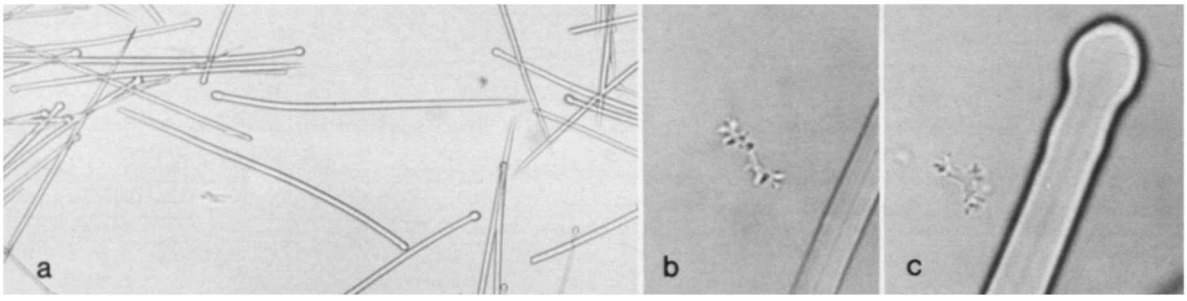

FIGURE 25.—*Spheciospongia othella*, spicules: *a*, tylostyles; *b*, spiraster; *c*, spiraster and tylostyle head. (Magnification: *a*, × 140; *b*, *c*, × 1400.)

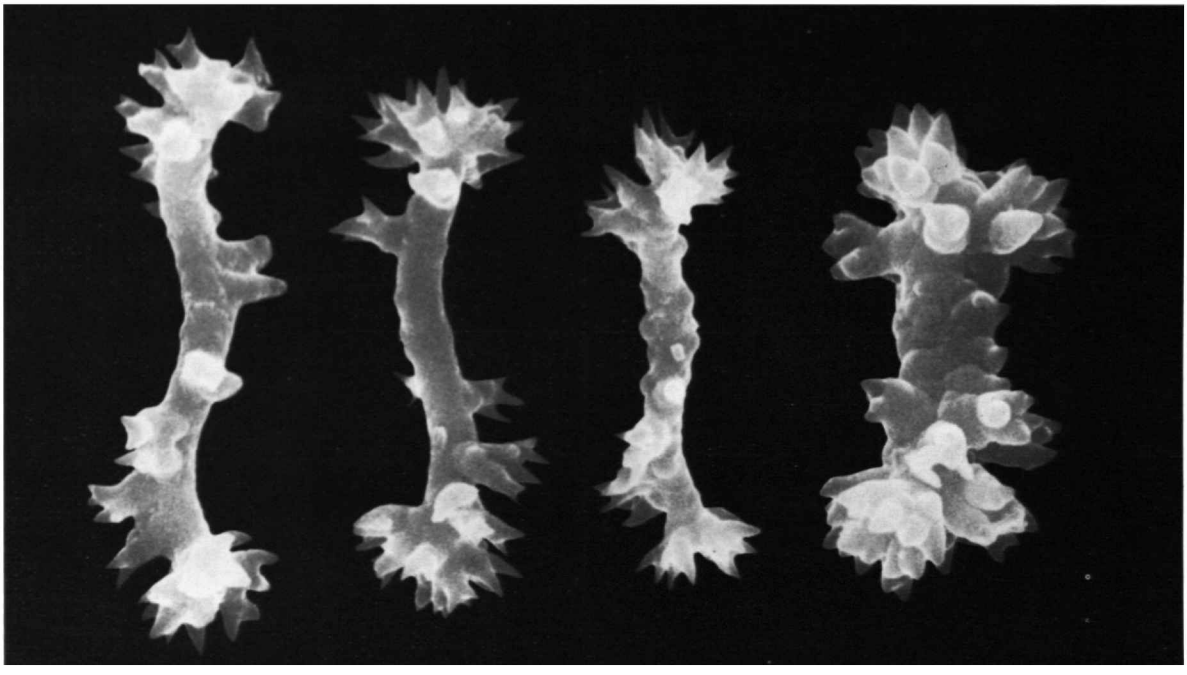

FIGURE 26.—*Spheciospongia othella*, spicules (SEM): Spirasters. (Magnification: × 4500.)

Neck width: 1.5–8.1 (5.6). Head length × width: 3.7–14.8 × 3.7–11.5 (9.5 × 7.6). Spirasters, length × width (shaft only): 8.0–25.6 × 0.8–3.2 (14.0 × 1.4). Spine clusters, maximum width: 2.8–5.6 (4.0). Number of spines: 40–80+ (50+). Number of bends: 1–5 (2.1).

REMARKS.—The preceding description is based on specimens which were in an active burrowing state. Large massive specimens, infrequently collected during the present survey, are described by the original author (Laubenfels, 1950). It is not established if and when, during the life cycle of the species, the burrowing capacity stops.

MATERIAL.—USNM 24355; Station 2; 28 October 1969; in dead coral. USNM 24356; Station 10; 11 January 1970; in rock. USNM 24357; Station 13; 9 May 1971; in dead coral. Station 1; 26 October 1969; in dead coral. Station 10; 31 May 1972; in rock. Station 11; 13 January 1970. Station 15; 3 May 1971; in rock. Station 17; 9 June 1972; in dead coral. Station 19; 7 June 1972; in dead coral. Station 22; 26 June 1972; in rock.

DISTRIBUTION.—Bermuda.

Literature Cited

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.

Carter, H. J.

1882. Some Sponges from the West Indies and Acapulco in the Liverpool Free Museum Described, with General and Classificatory Remarks. *Annals and Magazine of Natural History,* 9(5):266–301. 346–368, 2 plates.

Goreau, T. F., and W. D. Hartman

1963. Boring Sponges as Controlling Factors in the Formation and Maintenance of Coral Reefs. *In* R. F. Sognnaes, editor, Mechanisms of Hard Tissue Destruction. *American Association for the Advancement of Science Publication,* 75:25–54, 16 figures.

Hancock, A.

1867. Note on the Excavating Sponges; with Descriptions of Four New Species. *Annals and Magazine of Natural History,* 9(3) :229–242, 2 plates.

Hartman, W. D.

1958. Natural History of the Marine Sponges of Southern New England. *Peabody Museum of Natural History, Yale University Bulletin,* 12: 155 pages, 46 figures, 12 plates.

Hechtel, G. J.

1965. A Systematic Study of the Demospongiae of Port Royal, Jamaica. *Peabody Museum of Natural History, Yale University Bulletin,* 20: 94 pages, 15 figures, 8 plates.

Laubenfels, M. W. de

1936. A Comparison of the Shallow-Water Sponges Near the Pacific End of the Panama Canal with Those at the Caribbean End. *Proceedings of the United States National Museum,* 83:441–466, 6 figures.

1950. The Porifera of the Bermuda Archipelago. *Transactions of the Zoological Society of London,* 27: 154 pages, 65 figures, 2 plates.

1953. Sponges from the Gulf of Mexico. *Bulletin of Marine Science of the Gulf and Caribbean,* 2:511–557, 17 figures.

Neumann, A. C.

1966. Observations on Coastal Erosion in Bermuda and Measurements of the Boring Rate of the Sponge, *Cliona lampa. Limnology and Oceanography,* 11:92–108, 11 figures.

Pang, R. K.

In press. The Systematics of Some Jamaican Excavating Sponges. *Postilla.*

Rützler, K.

1971. Bredin-Archbold-Smithsonian Biological Survey of Dominica: Burrowing Sponges, Genus *Siphonodictyon* Bergquist, from the Caribbean. *Smithsonian Contributions to Zoology,* 77: 37 pages, 11 figures, 9 plates.

In preparation. Participation of Burrowing Sponges in Erosion and Sediment Production on the Bermuda Platform.

Rützler, K., and G. Rieger

1973. Sponge Burrowing: Fine Structure of *Cliona lampa* Penetrating Calcareous Substrata. *Marine Biology,* 21:144–162, 11 figures.

Topsent, E.

1889. Quelques spongiaires du Banc de Campêche et de la Pointe-A-Pitre. *Mémoires de la Société Zoologique de France,* 2:30–52, 12 figures.

1891. Deuxième contribution a l'étude des Clionides. *Archives de Zoologie Expérimentale et Générale,* 9 (2) : 555–592, 1 plate.

1900. Étude monographique des spongiaires de France, III: Monaxonida (Hadromerina). *Archives de Zoologie Expérimentale et Générale,* 8(3):331 pages, 8 plates.

1932. Notes sur des Clionides. *Archives de Zoologie Expérimentale et Générale,* 74:549–579, 11 figures.

Verrill, A. E.

1907. Porifera of the Bermuda Islands. *Transactions of the Connecticut Academy of Arts and Sciences,* 12: 330–347, 2 plates.

Volz, P.

1939. Die Bohrschwämme (Clioniden) der Adria. *Thalassia,* 3: 64 pages, 16 figures, 5 plates.

Wells, H. W., M. J. Wells, and I. E. Gray

1960. Marine Sponges of North Carolina. *Journal of the Elisha Mitchell Scientific Society,* 76:200–245, 63 figures.

☆ U.S. GOVERNMENT PRINTING OFFICE: 1974—546-357/4

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 will 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 consecutively all pages, including title page, abstract, text, literature cited, legends, and tables. The minimum length is 30 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 an entry, use a period-dash (.—) to separate each reference. Enclose with square brackets any annotation in, or at the end of, the entry. For *references within the text,* use the author-date system: "(Jones, 1910)" and "Jones (1910)." If the reference is expanded, abbreviate the data: "Jones (1910:122, pl. 20: 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) 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 components should be indicated by lowercase italic letters on the illustration, in the legend, and in text references: "Figure 9*b*." If illustrations (usually tone photographs) are printed separately from the text as full pages on a different stock of paper, they will be termed *Plates,* and individual components should be lettered (Plate 9*b*) but may be numbered (Plate 9: figure 2). Never combine the numbering system of text illustrations with that of plate illustrations. Submit all legends on pages separate from the text and not attached to the artwork. An instruction booklet 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 50 free copies; order forms for quantities above this amount with instructions for payment will be supplied when page proof is forwarded.