

A Revision of Axinellidae
(Porifera: Demospongiae)
of the Central West Atlantic Region

BELINDA ALVAREZ,
ROB W.M. VAN SOEST,
and
KLAUS RUTZLER

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*Belinda Alvarez, Rob W.M. van Soest,
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ABSTRACT

Alvarez, Belinda, Rob W.M. van Soest, and Klaus Rützler. A Revision of Axinellidae (Porifera: Demospongiae) of the Central West Atlantic Region. *Smithsonian Contributions to Zoology*, number 598, 47 pages, 23 figures, 18 tables, 1998.—Twenty-one species of the family Axinellidae (sensu Lévi) reside in the central West Atlantic region, from the Carolinas to the southern Caribbean. They are distributed in seven genera, and five are new species: *Axinella pomponiae*, *A. meandroides*, *Pseudaxinella(?) zeai*, *Dragmaxia undata*, and *Auletta tuberosa*. A taxonomic diagnosis of these genera and species indicates that the nominal genera *Teichaxinella* de Laubenfels and *Homaxinella* Topsent previously recorded from the region are invalid and that in the study area their species can be allocated to *Axinella*. *Acanthella* and *Ptilocaulis*, traditionally grouped with the Axinellidae but recently allocated to the families Dictyonellidae and Desmoxyidae of the Order Halichondrida (sensu van Soest et al., 1990), are included in this revision because the scope of the other families has not yet been established. *Ptilocaulis*, at least, is shown to be closely related to *Axinella*.

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A Revision of Axinellidae (Porifera: Demospongiae) of the Central West Atlantic Region

*Belinda Alvarez, Rob W.M. van Soest,
and Klaus Rützler*

Introduction

Like many other families within the Demospongiae, the Axinellidae are the subject of considerable controversy. Lévi (1953) subdivided the Demospongiae into three subclasses and placed the family Axinellidae in the order Axinellida, subclass Tetractinomorpha. Earlier, the family had been considered a member of the order Halichondrina Vosmaer, 1885 (Topsent, 1928; de Laubenfels, 1936). The reassignment was based on the reproductive characteristics (ovipary) of a few species and was supported by skeletal characters (axial condensation) and free amino acid patterns (Bergquist, 1967, 1970; Bergquist and Hartman, 1969; Lévi, 1973; Hartman, 1982).

Subsequently, van Soest (1991) proposed that the use of the order Axinellida be abandoned altogether and that several taxa allocated to the Tetractinomorpha and Ceractinomorpha be grouped into new assemblages. Van Soest et al. (1990) argued that the family had affinities with members of the redefined order Halichondrida and that its skeletal properties were similar to those of the Desmoxyidae, Dictyonellidae, and Halichondriidae; however, the synapomorphies (i.e., unique, derived characters) that define these groups, including the Axinellidae, are not unequivocal (cf. Hooper and Lévi, 1993). Although the homoplastic (i.e., nonhomologous) characters said to define the Axinellidae—namely, the axial condensation of the choano-

somal skeleton and the extra-axial plumoreticulate skeleton—are present in other Porifera, they are not present in all genera herein assigned to the family.

The Axinellidae family is also problematic at the supraspecific level because the morphological characters that define its genera are not discriminatory (Hooper and Bergquist, 1992). Before phylogenetic relationships can be fully understood, the family must be reexamined, its genera must be revised, and the species in each genus must be clearly described. The present study provides the basis for such a revision for the Axinellidae of the central West Atlantic region. Species of the genera *Ptilocaulis* and *Acanthella* are part of the family Axinellidae sensu Lévi, 1973, but are allocated to Desmoxyidae and Dictyonellidae, respectively, by van Soest et al. (1990). They are included herein because the genera in the latter families are still awaiting critical review; the results thus far suggest that at least *Ptilocaulis* is closely related to *Axinella*.

MATERIAL AND METHODS

Most of the material examined in this study is from the continental shelf of the east coast of the United States and Mexico. It was collected by the Mineral Management Service of the U.S. Department of the Interior and is housed at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. A representative set of specimens from this collection is also on deposit at the Zoological Museum of Amsterdam. Both sets of specimens were examined for this study but are not identified separately, except for one representative sample from each locality or depth zone, which is listed (by catalog and station numbers) in the material section for each species. A small number of the specimens studied came from other collections housed at these two museums and from collections at BMNH, MCZ, UMML, and

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YPM (see "Abbreviations," below). The catalog number of the type specimens checked appears in brackets in the synonym lists or in parentheses in the text.

The Axinellidae is one of the best represented families in the study material in terms of the number of species present (several of which were previously undescribed) and the number of specimens. The family shows high intraspecific morphological variation in the study area, also heretofore undescribed.

All specimens were preserved in alcohol. Spicule slides and thick sections were prepared using the methods described by Rützler (1978). At least one specimen from each species and each locality was selected for the spicule measurements. Spicule slides (40 × 22 mm area) were studied using a light microscope. The first 25 spicules of each type were measured (length and width) using an ocular micrometer. The results are presented as ranges of length and width with the average and standard deviation indicated in parentheses. If fewer than 25 spicules of a type were found during the examination of one slide, the number of spicules measured is indicated in brackets. Thick sections, perpendicular to the sponge surface, were photographed and drawn to give both a realistic and slightly idealized, clarified version. The images are oriented with the ectosomal region located at the top or to the right of the page.

The locality and collection data for stations in the Gulf of Mexico are given in the appendix. In the "Material Examined" sections of the text, station numbers for the Gulf of Mexico and collection information for other locations are added in parentheses after the catalog numbers.

ABBREVIATIONS.—The following abbreviations are used throughout the text.

AM	Australian Museum, Sydney
AMNH	American Museum of Natural History, New York
ANU	Australian National University, Canberra
BMNH	Natural History Museum (formerly the British Museum (Natural History)), London
CSA	Continental Shelf Associates, Inc., Jupiter, Florida
DU	Duke University, North Carolina
FCLR	Fundación Científica Los Roques, Venezuela
GMR	Georgia Marine Resources, Brunswick, Georgia
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MMS	Mineral Management Service, Reston, Virginia
MNHN	Muséum National d'Histoire Naturelle, Laboratoire de Biologie des Invertébrés Marins et Malacologie, Topsent collections (LBIM DT), Paris
MT Por	Museo e Istituto di Zoologia Sistemática dell'Università di Torino, Italy; Porifera collection
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
SCMR	South Carolina Marine Resources, Charleston, South Carolina
UMML	University of Miami Marine Laboratory, Miami, Florida
USNM	United States National Museum (collections now in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.)
YPM	Yale Peabody Museum, New Haven
ZMA Por	Zoologisch Museum Amsterdam; Porifera collection

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Results

The specimens studied from the central West Atlantic contain 21 species and seven genera in the family Axinellidae sensu Lévi, 1973. This report provides diagnostic characters of the genera, descriptions of the species with their synonyms, and a key to those species represented in the studied region.

Class DEMOSPONGIAE Sollas, 1885

Family AXINELLIDAE Ridley and Dendy, 1887 (sensu Lévi, 1973)

Axinella Schmidt, 1862

Axinella Schmidt, 1862:60 [type species: *Axinella polypoides* Schmidt, 1862, by subsequent designation (de Laubenfels, 1936:130); BMNH 1867:7:26:81].—Gray, 1867:513.—Ridley and Dendy, 1886:479; 1887:178.—Topsent, 1904:137; 1928:173.—Dendy, 1905:188; 1922:114.—Vosmaer, 1912:308.—de Laubenfels, 1936:130.—Lévi and Vacelet, 1958:233.—Bergquist, 1970:14.—Lévi, 1973:605.—Hooper and Lévi, 1993:1407 [with additional synonyms].

Teichaxinella de Laubenfels, 1936:128 [type species: *Teichaxinella shoemakeri* de Laubenfels, 1936:129; USNM 22450; new synonym].

DIAGNOSIS (emended).—Axinellidae with condensed axial skeleton and plumose or plumoreticulate extra-axial skeleton. Oscules may show star-shaped morphology (i.e., superficial canals leading to opening "imprinted" in the superficial skeleton). Megascleres are styles, or styles and oxeas, or oxeas; when both present, one of them sometimes rare; modifications of megascleres common in several species. Microscleres, if present, are microraphides and raphides, mostly in tightly packed trichodragmata.

Axinella waltonsmithi (de Laubenfels, 1953),
new combination

FIGURE 1; TABLE 1

Homaxinella waltonsmithi de Laubenfels, 1953:533 [holotype, USNM 23407].—Wells and Wells in Wells et al., 1960:222 [USNM 23660].

Phakellia folium.—Pearse and Williams, 1951:136 [listed only; same specimen described by Wells and Wells in Wells et al., 1960:223].—Wells and Wells in Wells et al., 1960:223 [USNM 23664]. [Not *Phakellia folium* Schmidt, 1870:62.]

Thalyseurypon carteri.—Pearse and Williams, 1951:136 [listed only; same specimen described by Wells and Wells in Wells et al., 1960:222, as *Homaxinella waltonsmithi*]. [Not *Clathria carteri* Topsent, 1889.]

(?)*Homaxinella waltonsmithi*.—Storr, 1964:42 [distribution off Florida coast]; 1976:269 [distribution in the Gulf of Mexico].

Axinella waltonsmithi.—Alvarez and Crisp, 1994:119 [cited only].

MATERIAL EXAMINED.—*Nontypes*: North Carolina: USNM 32654 (SE Wilmington, 33°31'30"N, 77°23'42"W, 30 m, coll. DU for MMS), USNM 33593 (SW Cape Lookout, 34°23'42"N, 76°34'00"W, 22 m, coll. DU for MMS, 9 Feb 1981). South Carolina: USNM 33341 (NE Charleston, 32°49'18"N, 78°40'00"W, 33 m, coll. SCMR for MMS), USNM 33544 (off Charleston, 32°29'12"N, 79°42'54"W, 18 m, coll. SCMR for MMS, 15 Apr 1980). Georgia: USNM 42760 (NE Brunswick, 31°23'42"N, 80°53'06"W, 17 m, coll. GMR for MMS, 4 Mar 1981). Gulf of Mexico: USNM 34171 (22), USNM 39681 (21), USNM 39840 (2), USNM 39844 (19), USNM 39845 (7), USNM 42751 (37), USNM 42752 (39), USNM 42754 (40), USNM 42755 (42), USNM 42757 (44), USNM 42758 (44). Representative collection from the same area in ZMA.

SHAPE.—Two basic shapes: flabellate-pedunculate with some digital processes or crenulate margins (large specimens more complex with several folded lettuce-like fronds) (Figure 1a); and bushy with wide branches and crenulate edges rising from peduncle or broad base.

SURFACE.—Smooth to the touch, like chamois, or rougher, as in many bushy-shaped specimens. Vein-like depressions (2–5 mm wide), covered with transparent membranes in some specimens, run lengthwise, generally in one face of frond or branch; pores, 2–3 mm in diameter, located in depressions; some specimens without depressions, completely smooth on both sides. Bushy-shaped specimens pierced with small pores, approximately 0.5 mm in diameter. Epizoid zoanthids common in many specimens.

COLOR.—Reported as bright orange red when alive (de Laubenfels, 1953). Purple, dark brown, light brown, purple brown, or beige in alcohol.

SKELETON (Figure 1b,c).—Axial and extra-axial skeleton with reticulation of primary lines of 5 or more spicules (3–10 µm thick) connected by secondary lines of 1–5 spicules. Both primary and secondary lines cemented and enveloped by spongin. Primary lines run parallel to sponge axis in axial skeleton; lateral condensation of reticulation obvious in column

TABLE 1.—Spicule dimensions for *Axinella waltonsmithi*. Measurements (in µm) are ranges of 25 spicules (or the number indicated in brackets), with means ± standard deviation in parentheses.

Specimen	Styles	Oxeas
South Carolina USNM 33341		
length	220–250 (235.6±10.4)	320–420 (360.0±52.9)[3]
width	10–15 (12±1.9)	7.5–12.5 (10.8±2.9)[3]
Georgia USNM 42760		
length	230–370 (261.2±33.8)	240–380 (287.2±38.9)
width	7.5–12.5 (9.7±1.8)	7.5–12.5 (8.7±1.5)
Gulf of Mexico USNM 34171		
length	260–320 (282.4±15.9)	not detected
width	12.5–22.5 (17.4±2.2)	
USNM 39845		
length	220–280 (250.8±17.1)	290–450 (364.3±55.3)[7]
width	5–15 (10.6±2.9)	7.5–17.5 (12.9±3.4)[7]
USNM 42758		
length	220–290 (242.0±17.3)	250–330 (284.0±31.3)[5]
width	7.5–15 (12.1±2.6)	7.5–15 (12.5±3.1)[5]

of attachment, especially in specimens of flabellate-pedunculate shape. Axial reticulation in bushy-shaped specimens more confused, isotropic with rounded meshes or laterally condensed at central column, but not as much as in specimens of flabellate-pedunculate shape. Primary lines in extra-axial skeleton ascending from axis to surface; generally plumose or “wispy” near margins of fronds of flabellate-pedunculate specimens; ending in projecting spicules at surface, piercing layers of spongin commonly present in some areas of periphery.

SPICULES (Figure 1d, Table 1).—Styles, quite bent near the basal end, always present; oxeas very rare in some specimens.

DISTRIBUTION AND HABITAT.—Widely distributed in the Gulf of Mexico and on east coast of the United States from Georgia to North Carolina. Occurs in patch rock or coral bottom at depths of 13–33 m.

REMARKS.—The specimens examined (approximately 140 lots) varied greatly in shape, skeletal features, and spicule composition. They were compared to the holotype of *Homaxinella waltonsmithi* (USNM 23407) from the Gulf of Mexico and other specimens of *H. waltonsmithi* from North Carolina described by Wells and Wells in Wells et al., 1960 (USNM 23660). The holotype is flabellate-pedunculate, whereas the specimen from North Carolina corresponds to our bushy-shaped material. Oxeas are absent in the holotype, as in many of the specimens studied, but this seems to be a characteristic feature of this species. The species originally was assigned to *Homaxinella* Topsent, 1916 (see the remarks on *Homaxinella* in “Discussion”), by de Laubenfels (1953), but it has all the diagnostic characters of an *Axinella* and is therefore transferred to this genus.

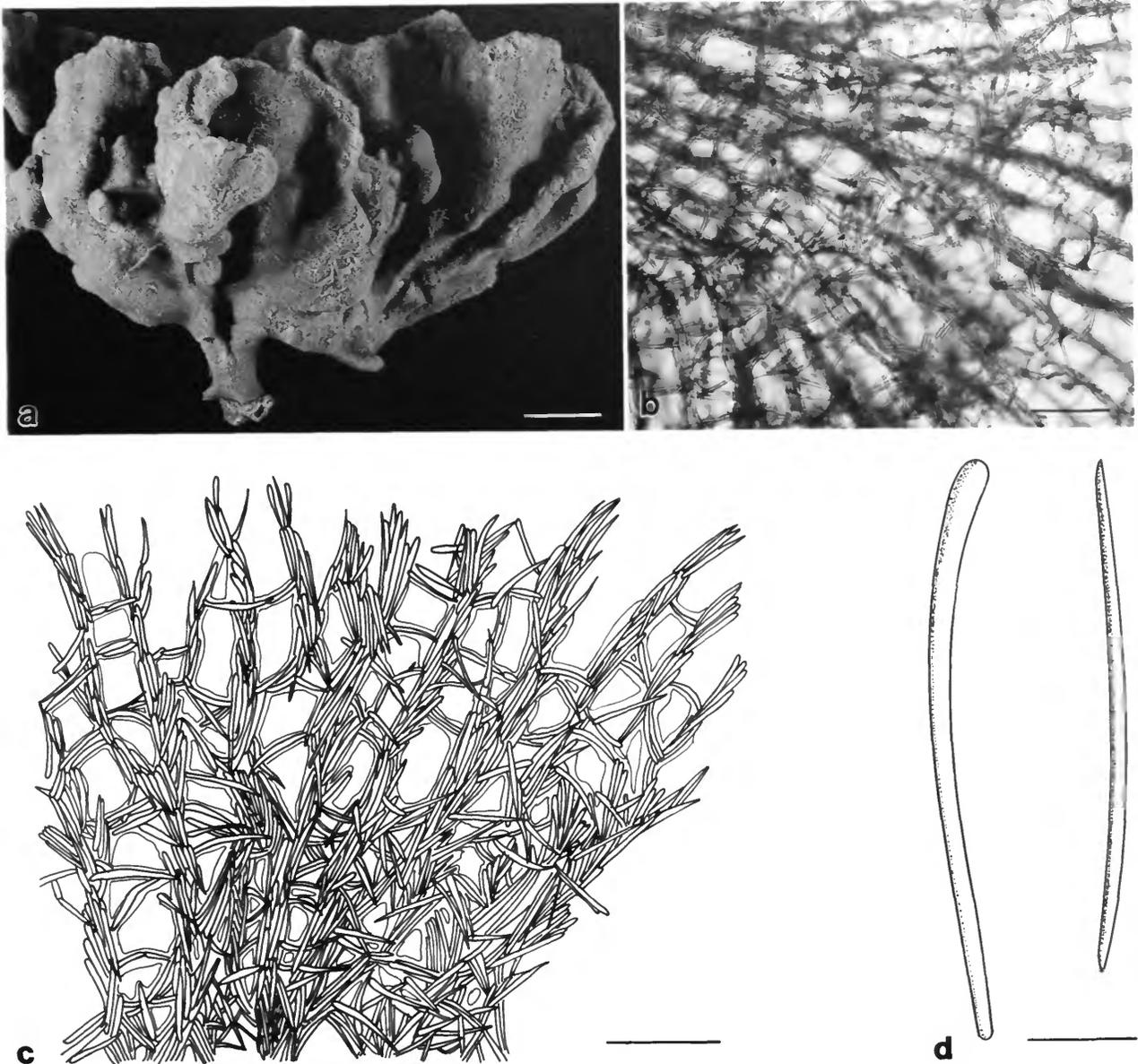


FIGURE 1.—*Axinella waltonsmithi*: a, specimen USNM 39845; b, c, micrograph and diagram, respectively, of the skeleton (USNM 33341); d, spicules (style, oxea; USNM 42757). [Scales: a, 20 mm; b, c, 200 μ m; d, 50 μ m.]

Axinella waltonsmithi is very similar to *A. damicornis* (Esper) Schmidt, 1862, sensu Pansini (1982–1983), from the Mediterranean Sea. Both species show considerable morphological variability in their habits; styles are always present, whereas oxeas are absent in some specimens. Styles in *A. damicornis*, however, are larger (length, 180–1350 μ m; width, 6–18 μ m) and regularly show subterminal swellings.

Axinella pomponiae, new species

FIGURE 2; TABLE 2

Homaxinella rudis.—de Laubenfels, 1953:531 [USNM 23406].—Wells and Wells in Wells et al., 1960:221 [USNM 23620].—Pulitzer-Finali, 1986:103.—[not de Laubenfels, 1950a:87; Rützler, 1986:121 = *Ptilocaulis walpersi* (Duchassaing and Michelotti)]. [Not *Axinella rudis* Verrill, 1907:341.]

TABLE 2.—Spicule dimensions for *Axinella pomponiae*, new species. Measurements (in μm) are ranges of 25 spicules (or the number indicated in brackets), with means \pm standard deviation in parentheses.

Specimen	Styles I	Styles II	Oxeas
Georgia USNM 42769			
length	180–240 (214.0 \pm 17.6)	370–490 (441.0 \pm 35.1)[21]	220–270 (240.0 \pm 21.6)[4]
width	5–10 (8.7 \pm 1.6)	5–7.5 (6.1 \pm 1.3)[21]	5–10 (7.5 \pm 2.0)[4]
Gulf of Mexico USNM 42762			
length	230–300 (265.6 \pm 18.3)	450–690 (567.8 \pm 58.8)	not detected
width	12.5–17.5 (15.3 \pm 1.8)	7.5–15 (11.4 \pm 2.1)	
USNM 42763			
length	250–300 (274.8 \pm 12.6)	450–690 (591.2 \pm 60.7)	340–410 (375.0 \pm 49.5)[2]
width	12.5–17.5 (14.8 \pm 1.8)	5–17.5 (13.5 \pm 3.1)	5–12.5 (13.8 \pm 1.8)[2]
USNM 42765			
length	230–290 (268.8 \pm 16.2)	390–670 (448.1 \pm 72.2)[16]	not detected
width	7.5–12.5 (15.7 \pm 1.4)	2.5–7.5 (9.5 \pm 1.9)[16]	

(?)*Homaxinella rudis*.—Storr, 1964:42 [distribution off Florida coast]; 1976:268 [distribution in the Gulf of Mexico].

Axinella sp.—Alvarez and Crisp, 1994:119.

MATERIAL EXAMINED.—*Holotype*: USNM 42762, Gulf of Mexico (40). *Paratypes*: Off Georgia: USNM 42769 (31°23'42"N, 80°53'06"W, 17 m, coll. GMR for MMS, 4 Mar 1981), USNM 42770 (31°23'36"N, 80°53'00"W, 17 m, coll. GMR for MMS, 4 Mar 1981). Gulf of Mexico: USNM 39680 (19), USNM 42763 and USNM 42764 (37), USNM 42765 (39), USNM 42766 and USNM 42767 (40), USNM 42768 (44). *Nontypes*: Off North Carolina: USNM 32772 (34°24'00"N, 76°35'06"W, 24 m, coll. DU for MMS, 13 Aug 1981). Off South Carolina: USNM 33228 (32°29'18"N, 79°42'36"W, 17 m, coll. SCMR for MMS, 28 Oct 1981). Off Georgia: USNM 33225 (31°41'06"N, 80°20'48"W, 27 m, coll. GMR for MMS, 5 Nov 1981), USNM 42773 (31°23'24"N, 80°53'24"W, 17 m, coll. GMR for MMS, 4 Mar 1981). Florida: USNM 30388 (Looe Key, 24°32'N, 81°24'W, 9–12 m, coll. S. Pomponi, 14 Jan 1984). Gulf of Mexico: USNM 34144 (7), USNM 34145 (16), USNM 34146 (19), USNM 41972 and USNM 42771 (36). Representative specimens from the same area in ZMA.

SHAPE (Figure 2a).—Erect and flexible branches, generally attached on a central column. Total length up to 30 cm. Branches generally tapering and dichotomous at tips, fused to each other at several points, sometimes with massive rings or lumps. Some specimens with incipient surface lobes and processes. Oscules star-shaped and irregularly distributed.

SURFACE.—Finely to coarsely conulose or completely smooth. Conulose specimens vary in length and separation of conules: long conules, up to 2 mm, and 0.5–1 mm apart, and/or shorter conules, sometimes very close to each other, so that surface becomes smooth in some areas of specimen.

COLOR.—Unknown when alive. Purple, dark brown, almost black, light brown, purple brown, pink, or beige in alcohol.

SKELETON (Figure 2b,c).—Axial skeleton vaguely reticulated or halichondroid. Extra-axial skeleton plumoreticulated with primary tracts of 3–8 spicules, 50–150 μm thick, connected by secondary lines of 1–3 spicules, or jointed at some points; sometimes plumose or wispy at tips of branches, ending with projecting spicules. Skeleton of lumps located on branches corresponds with extra-axial skeleton described above.

SPICULES (Figure 2d, Table 2).—Styles of two sizes (I, II); larger ones (II) less frequent; oxeas very rare in most cases.

ETYMOLOGY.—The species is named after Dr. Shirley Pomponi, one of the collectors of this species, in recognition of her contributions to knowledge of the biology of sponges.

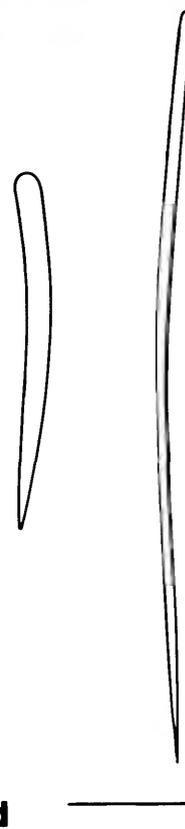
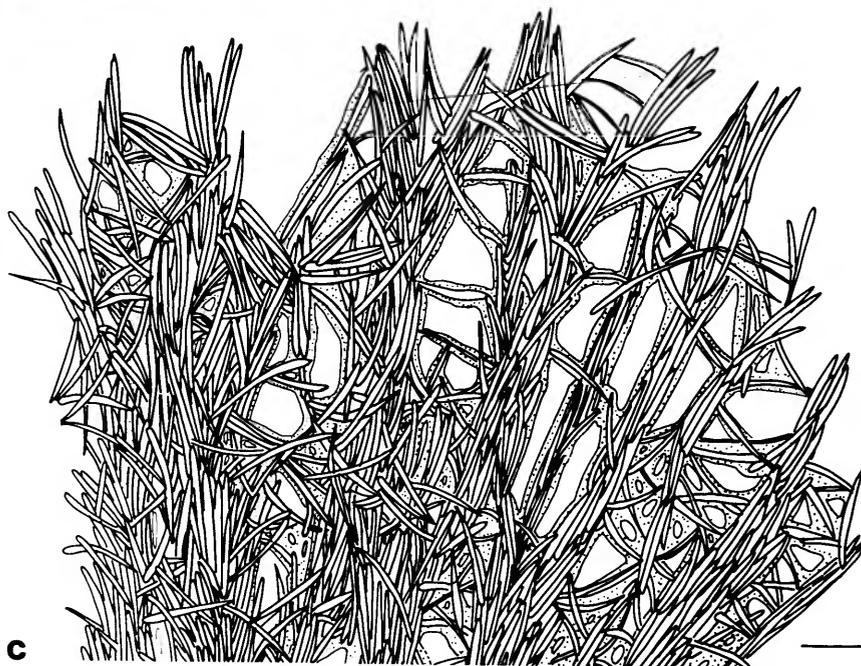
DISTRIBUTION AND HABITAT.—Gulf of Mexico, Looe Key (Florida), and east coast of the United States from Georgia to North Carolina. Occurs in rock patches or coral reef bottom at depths of 13–30.4 m.

REMARKS.—The specimens examined in the NMNH collection represent the variability of the new species. Their surface characteristics vary from coarsely conulose, as in the specimen described by de Laubenfels (1953) (USNM 23406), to smooth, as in the one described by Wells and Wells in Wells et al. (1960) (USNM 23620). These authors, and probably Pulitzer-Finali (1986), too, identified the species as *Homaxinella rudis*, which is a junior synonym of *Ptilocaulis walpersi* (Duchassaing and Michelotti), a species with similar spiculation and morphology (see the description of *P. walpersi*, below). Zea (1987) erroneously assigned the specimens described by de Laubenfels (1953; USNM 23406) to *P. walpersi*.

The morphology and surface characteristics of the new species are very similar to those of Mediterranean *Axinella verrucosa* Esper, 1794, sensu Pansini (1982–1983), but *A. verrucosa* does not grow larger than 10 cm, lacks the smallest category of styles, and has more and larger oxeas.



FIGURE 2.—*Axinella pomponiae*, new species: *a*, holotype (USNM 42762); *b,c*, micrograph (USNM 42773) and diagram (USNM 42764), respectively, of the skeleton; *d*, spicules (two size categories of styles; USNM 42763). [Scales: *a*, 50 mm; *b,c*, 200 μ m; *d*, 100 μ m.]



Axinella polycapella de Laubenfels, 1953

FIGURE 3; TABLE 3

Axinella polycapella de Laubenfels, 1953:530 [holotype, USNM 23405].—Hartman, 1955:177.—Wells and Wells in Wells et al., 1960:221 [USNM 23621].—Little, 1963:51.—Storr, 1964:5, 42; 1976:269 [distribution only].—Alvarez and Crisp, 1994:119 [cited only].

Axinella polypoides.—Schmidt, 1870:60 [BMNH 1939.2.10.29].—[not Schmidt, 1862:62; 1868:9; Donadey, 1990].

Axinella bookhouti Wells and Wells in Wells et al., 1960:219 [holotype, USNM 23659; new synonymy].

Axinella reticulata.—Wells and Wells in Wells et al., 1960:221 [USNM 23625].—[not Ridley and Dendy, 1886:481; 1887:184; Wilson, 1902:400 = *Pseudaxinella reticulata*].

Pseudaxinella wilsoni Wells and Wells in Wells et al., 1960:222 [holotype, USNM 23662; new synonymy].

MATERIAL EXAMINED.—*Nontypes*: Off South Carolina: USNM 42779 (32°49'42"N, 78°39'24"W, 33 m, coll. SCMR for MMS, 27 Feb 1981). Gulf of Mexico: USNM 34170 (22), USNM 39609 (1), USNM 39667 (6), USNM 41971 (42), USNM 42774 (2), USNM 42775 (17), USNM 42776 (36), USNM 42778 (39). Representative specimens from the same area in ZMA.

SHAPE (Figure 3a).—Erect and flexible branches, sometimes whip-like, on a central column of attachment; central column absent in small specimens. Total length up to 50 cm. Branches pointed, rounded, or dichotomous at tips, sometimes jointed. Star-shaped oscules, 2–5 mm in diameter.

SURFACE.—Smooth to velvet. Pierced by small pores less than 1 mm in diameter.

COLOR.—Live specimens reported as orange red or bright red (de Laubenfels, 1953). Purple, tan, dark brown, light brown, or combination of dark and light brown in alcohol.

SKELETON (Figure 3b,c).—Axial skeleton vaguely reticulated to condensed. Extra-axial skeleton plumoreticulated, becoming halichondroid near surface. Primary lines, connected by 1–3 spicules, ending at surface in brushes of spicules.

SPICULES (Figure 3d, Table 3).—Oxeas, usually bent; stronglyloxeas and styles less common in most specimens.

DISTRIBUTION AND HABITAT.—Widely distributed in the Gulf of Mexico, on the Gulf and Atlantic coasts of Florida, and east coast of the United States from South Carolina to North Carolina. Occurs in rock patches or coral reef at depths of 13–44 m.

REMARKS.—*Axinella polycapella* is very similar to Mediterranean *A. polypoides* Schmidt, 1862, in morphology and in the diameter of its branches and central axis. The spicules are also similar in dimension, but the styles of *A. polypoides* are more abundant. Microraphides are present in *A. polypoides* (Donadey et al., 1990) but are absent in *A. polycapella*.

Axinella shoemakeri (de Laubenfels, 1936),
new combination

FIGURE 4; TABLE 4

Teichaxinella shoemakeri de Laubenfels, 1936:129 [holotype, USNM 22450].
Axinella shoemakeri.—Hooper and Bergquist, 1992:105 [cited only].—Alvarez and Crisp, 1994:119 [cited only].

MATERIAL EXAMINED.—*Holotype*: Loggerhead Key, Dry Tortugas, Western Atlantic, 70 m (USNM 22450). *Nontypes*: Off North Carolina: USNM 32723 (33°48'18"N, 76°34'06"W, 100 m, coll. DU for MMS, 14 May 1981). Off South Carolina: USNM 33330 (31°32'06"N, 79°44'06"W, 58 m, coll. SCMR for MMS, 29 Oct 1981). Off Georgia: USNM 33588 (30°26'12"N, 80°12'18"W, 61 m, coll. GMR for MMS, 11 Mar 1980). Gulf of Mexico: USNM 33813 (14), USNM 33816 (24), USNM 33826 (28), USNM 39881 (30), USNM 41600 (4), USNM 41602 (3), USNM 41604 (25). Representative specimens from the same area in ZMA.

SHAPE (Figure 4a).—One to several thin, folded lamellae with undulate, uneven, or rounded margins, sometimes on a short peduncle.

TABLE 3.—Spicule dimensions for *Axinella polycapella*. Measurements (in μm) are ranges of 25 spicules (or the number indicated in brackets), with means \pm standard deviation in parentheses.

Specimen	Styles	Oxeas	Strongyloxeas
South Carolina USNM 42779			
length	180–290 (206.0 \pm 32.7)[10]	190–250 (220.8 \pm 19.3)	not detected
width	7.5–10 (9.0 \pm 1.3)[10]	7.5–12.5 (9.3 \pm 1.4)	
Gulf of Mexico USNM 42774			
length	260–360 (303.3 \pm 33.3)[6]	230–390 (287.6 \pm 40.6)	380–390 (385.0 \pm 7.1)[2]
width	10–20 (16.67 \pm 3.8)[6]	7.5–15 (9.6 \pm 1.9)	17.5–17.5 (17.5 \pm 0)[2]
USNM 42775			
length	220–360 (273.5 \pm 30.5)[23]	260–430 (304.0 \pm 44.0)	240–340 (310.0 \pm 35.1)[7]
width	10–17.5 (13.0 \pm 2.0)[23]	10–22.5 (13.0 \pm 3.1)	15–25 (19.6 \pm 4.4)[7]
USNM 42776			
length	200–260 (224.4 \pm 18.9)	240–340 (266.8 \pm 24.1)	220–310 (248.8 \pm 20.1)
width	15–25 (18.8 \pm 2.6)	15–20 (17.2 \pm 2.1)	12.5–22.5 (18.4 \pm 3.0)

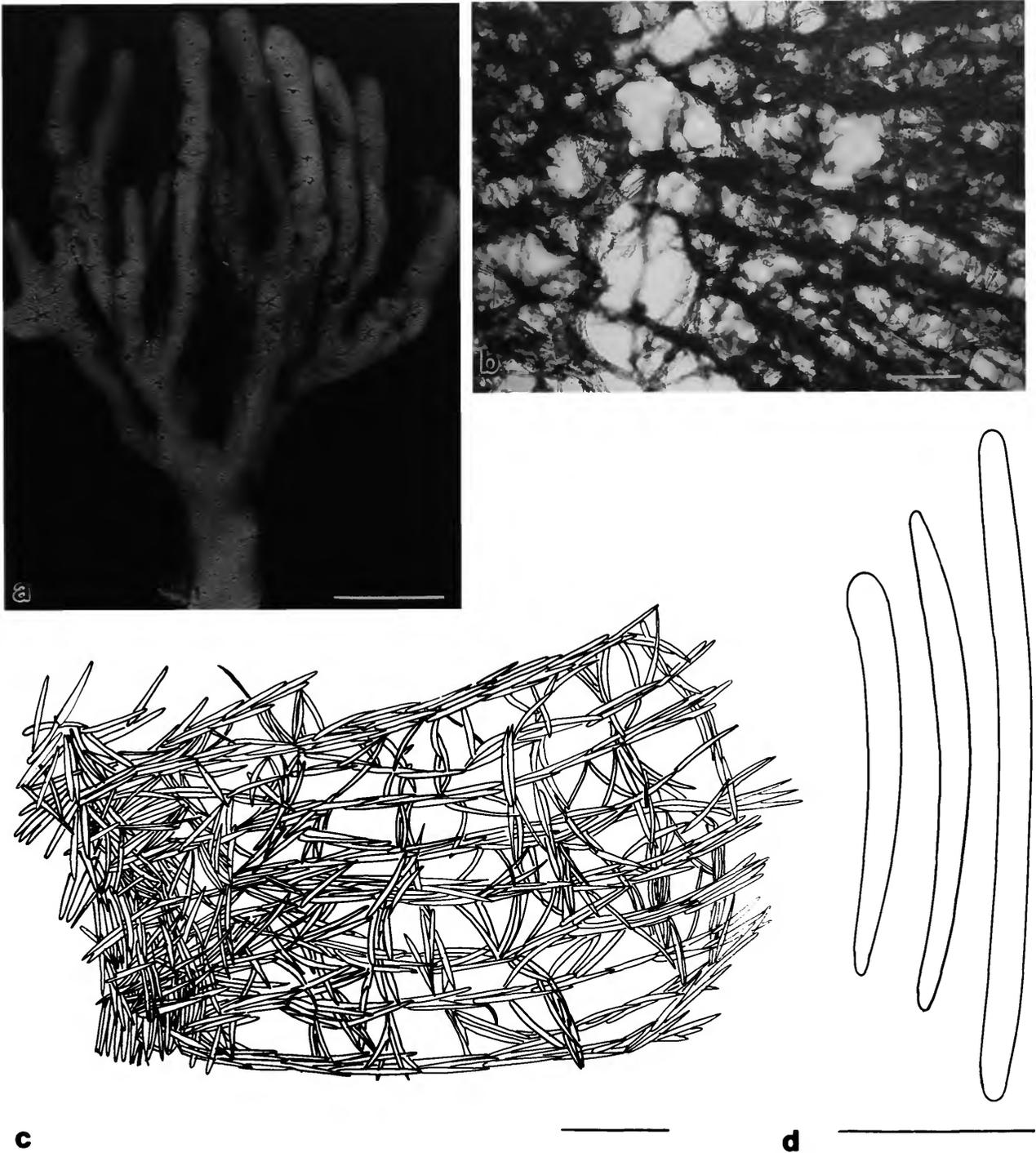


FIGURE 3.—*Axinella polycapella*: a, specimen USNM 42776; b, c, micrograph (USNM 42778) and diagram (USNM 42776), respectively, of the skeleton; d, spicules (style, two types of oxeas; USNM 42776). [Scales: a, 50 mm; b, c, 200 μ m; d, 50 μ m.]

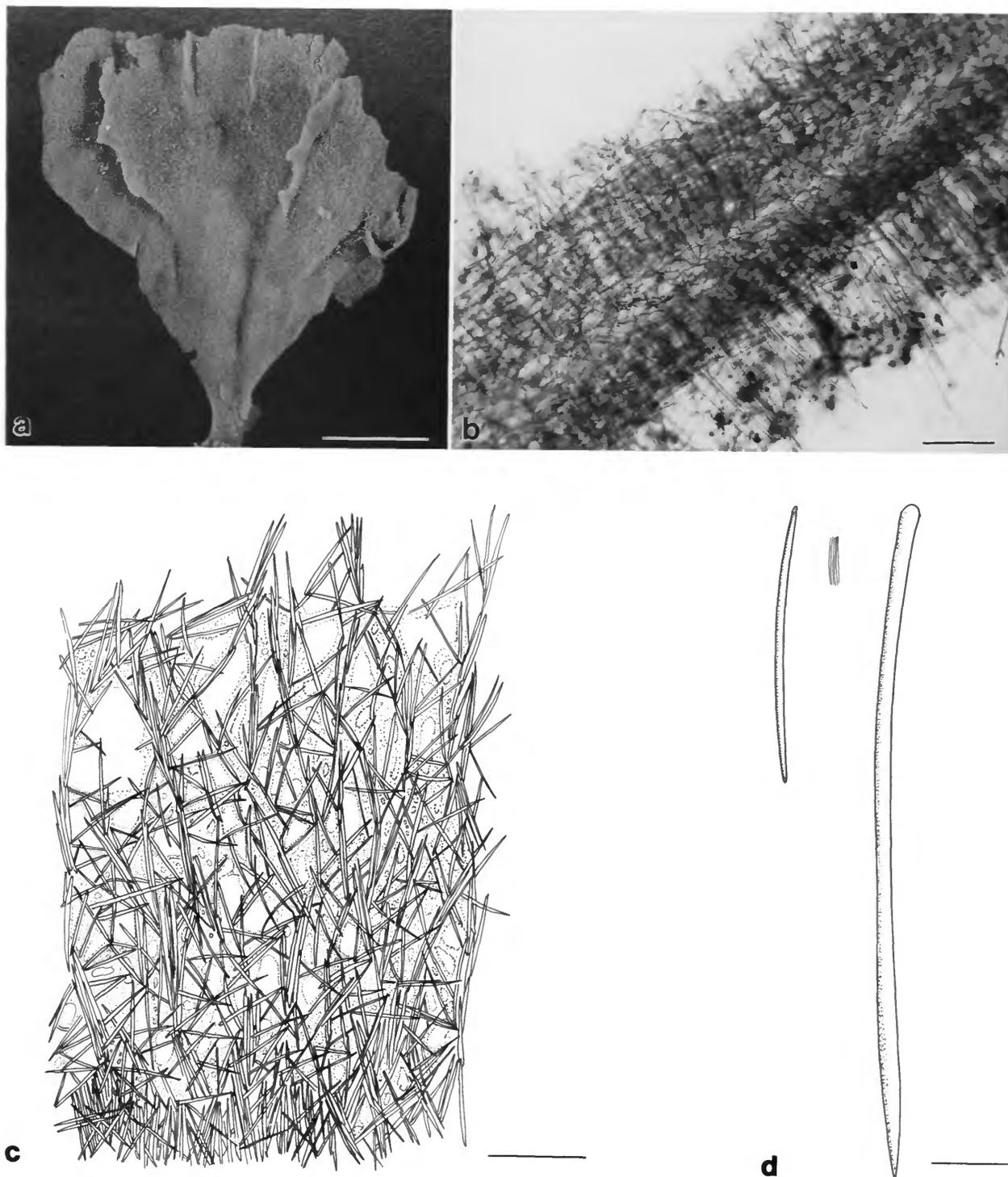


FIGURE 4.—*Axinella shoemakeri*: a, specimen USNM 41600; b, micrograph of the skeleton of the holotype (USNM 22450); c, diagram of the peripheral skeleton (USNM 33588); d, spicules (oxea, trichodragma, style; USNM 41602). [Scales: a, 20 mm; b, c, 200 μ m; d, 100 μ m.]

TABLE 4.—Spicule dimensions for *Axinella shoemakeri*. Measurements (in μm) are ranges of 25 spicules (or the number indicated in brackets), with means \pm standard deviation in parentheses.

Specimen	Styles	Oxeas	Trichodragmata
North Carolina USNM 32723			
length	310–840 (539.6 \pm 153.3)	210–310 (270.0 \pm 27.5)	22.5–32.5 (26.1 \pm 3.5)[7]
width	10–17.5 (14.2 \pm 2.1)	7.5–10 (9.0 \pm 1.3)	5–5 (5.0 \pm 0.0)[7]
South Carolina USNM 33330			
length	270–680 (482.0 \pm 110.5)	260–470 (317.2 \pm 44.3)	not detected
width	10–22.5 (16.4 \pm 3.8)	5–15 (11.0 \pm 2.3)	
Georgia USNM 33588			
length	260–1000 (431.2 \pm 141.6)	200–300 (249.6 \pm 27.3)	22.5–35 (27.3 \pm 3.6)[11]
width	7.5–15 (11.1 \pm 1.9)	5–10 (8.7 \pm 1.5)	5–10 (6.4 \pm 1.7)[11]
Gulf of Mexico USNM 39881			
length	220–1925 (789.0 \pm 527.3)	240–410 (357.6 \pm 44.2)	27.5–32.5 (30.0 \pm 2.5)[5]
width	10–25 (15.8 \pm 4.8)	10–15 (11.9 \pm 1.9)	5–5 (5.0 \pm 0.0)[5]
USNM 41600			
length	190–920 (448.8 \pm 170.0)	210–300 (259.2 \pm 26.4)	not detected
width	7.5–17.5 (12.7 \pm 2.6)	7.5–12.5 (9.5 \pm 1.9)	

SURFACE.—Velvety or smooth, with ridged lines radiating toward margins (see de Laubenfels (1936:128) for more details on shape and surface).

COLOR.—Unknown when alive. Beige or pale drab in alcohol.

SKELETON (Figure 4*b,c*).—Axial skeleton compressed in cross section, with spicules densely packed along folds. Extra-axial skeleton consists of single dermal spicules protruding perpendicularly from the surface and short plumose spicule tracts (30–50 μm thick) connected by single spicules, generally located in distinctive, transparent margin area of folds.

SPICULES (Figure 4*d*, Table 4).—Styles; oxeas sometimes strongly lute; trichodragmas.

DISTRIBUTION AND HABITAT.—Occurs in the Gulf of Mexico, Dry Tortugas, and east coast of the United States from Georgia to North Carolina. Restricted to deep waters between depths of 50 and 100 m.

REMARKS.—*Teichaxinella* de Laubenfels was established for some species of *Axinella* that lack axial condensation because of their external morphology. Like other *Axinella*, however, the type species of this genus, *T. shoemakeri* (USNM 22450; Loggerhead Key, Dry Tortugas, Western Atlantic, 70 m), exhibits axial condensation and an extra-axial skeleton; thus, this generic name should no longer be used. Other characters that de Laubenfels (1936) did not include in his description of this species are the occurrence of styles in the size range of 220–470 μm and the presence of trichodragmata, also present in *Axinella polypoides* from the Mediterranean and *Axinella dissimilis* (Bowerbank, 1866) from the Northeast Atlantic (Donadey et al., 1990).

***Axinella corrugata* (George and Wilson, 1919),
new combination**

FIGURE 5; TABLE 5

Acanthella corrugata George and Wilson, 1919:161.

Oxeostilon burtoni de Laubenfels, 1934:15 [holotype, USNM 22347; new synonymy].—[not Wells and Wells in Wells et al., 1960:227, USNM 23667 = *Halichondria gibbsi* (Wells and Wells in Wells et al., 1960:226)].

Teichaxinella morchella Wiedenmayer, 1977:154 [holotype, USNM 24462; new synonymy].—Alvarez and Diaz, 1985:72.

Teichaxinella burtoni.—Zea, 1987:192.

Axinella corrugata.—Alvarez and Crisp, 1994:119 [cited only].

MATERIAL EXAMINED.—*Nontypes*: Off North Carolina: USNM 32641 (33°48'42"N, 76°35'00"W, 70 m, coll. DU for MMS, 10 Nov 1981). Off South Carolina: USNM 42793 (31°31'36"N, 79°44'48"W, 58 m, coll. SCMR for MMS, 5 Aug 1981), USNM 42794 (32°49'06"N, 78°39'36"W, 33 m, coll. SCMR for MMS, 8 Aug 1981). Off Georgia: USNM 33338 (31°23'36"N, 80°53'12"W, 18 m, coll. GMR for MMS, 15 Nov 1981). Florida, Looe Key: USNM 30392 (West Reef, 9–12 m, coll. S. Pomponi, 14 Jan 1984). Gulf of Mexico: USNM 39852 (6), USNM 39870 (10), USNM 39873 and USNM 39887 (5), USNM 39885(2), USNM 41614 (20), USNM 41974 (42), USNM 42146 (21), USNM 42792 (38). Representative specimens from the same areas in ZMA; in addition, two specimens from Curaçao, off S coast, 34–40 m, ZMA Por 3630, 5708; one specimen from Venezuela, ZMA Por 5337 (Los Roques, 30 m, coll. B. Alvarez and M.C. Diaz, 11 Dec 1983).

SHAPE (Figure 5*a*).—Variable: (1) lamellate-flabelliform, asymmetrical, on small peduncle, 1 cm diameter; (2) small cones or bushes up to 4 cm high, with lamellas folded or

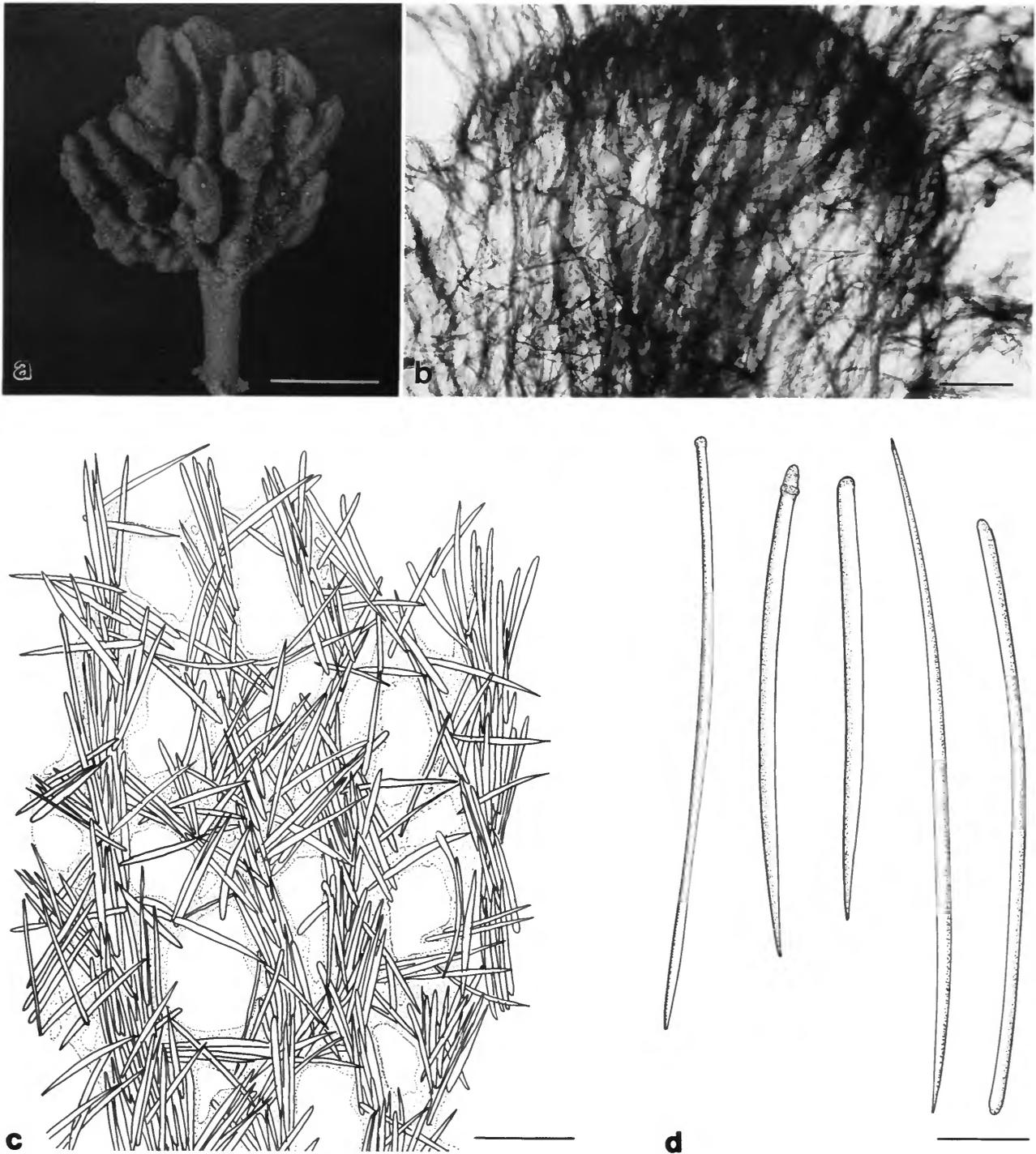


FIGURE 5.—*Axinella corrugata*: a, specimen USNM 41614; b,c, micrograph (USNM 39887) and diagram (USNM 41974), respectively, of the skeleton; d, spicules (three types of styles, two types of oxaeas; USNM 39852). [Scales: a, 20 mm; b,c, 200 μ m; d, 100 μ m.]

TABLE 5.—Spicule dimensions for *Axinella corrugata*. Measurements (in μm) are ranges of 25 spicules, with means \pm standard deviation in parentheses.

Specimen	Subtylostyles, styles, styloids	Oxeas, strongyloxeas, strongyles
South Carolina		
USNM 42793		
length	390–570 (471.6 \pm 51.6)	350–510 (422.8 \pm 45.5)
width	12.5–22.5 (18.0 \pm 3.0)	7.5–22.5 (13.8 \pm 4.0)
USNM 42794		
length	170–420 (262.8 \pm 73.1)	120–280 (202.4 \pm 30.6)
width	5–12.5 (8.4 \pm 1.8)	5–10 (7.1 \pm 1.7)
Florida		
USNM 30392		
length	310–430 (366.8 \pm 27.9)	320–470 (398.4 \pm 42.1)
width	7.5–15 (12.0 \pm 1.9)	7.5–15 (11.3 \pm 2.2)
Gulf of Mexico		
USNM 39852		
length	300–650 (388.8 \pm 100.8)	370–540 (464.8 \pm 39.3)
width	7.5–17.5 (12.5 \pm 2.6)	7.5–20 (13.0 \pm 2.6)
USNM 39873		
length	320–540 (440.4 \pm 63.1)	270–550 (370.8 \pm 63.2)
width	5–22.5 (14.3 \pm 3.9)	7.5–17.5 (11.5 \pm 2.9)

undulating, sometimes anastomosing in triaxial shape; (3) small crested bushes up to 8 cm tall, with long or short peduncle (smooth when long) and clusters of erect branches, generally three-lobed (as in Figure 5a).

SURFACE.—Corrugated, with vertical, horizontal, or jumbled grooves. Branches in bush-shaped specimens with longitudinal, smooth channels running along the inner surfaces, or with small punctuated projections, without striae. Parchment-like dermal skin, lost in most specimens.

COLOR.—Reported as bright orange red (George and Wilson, 1919; Wiedenmayer, 1977; Alvarez and Díaz, 1985) and bright yellow or yellow orange (Zea, 1987) when alive. Chocolate brown or light brown in alcohol.

SKELETON (Figure 5b,c).—Axial skeleton condensed or with vague reticulation of spicules, enveloped in spongin and arranged in round polygonal meshes 100–150 μm in diameter. Extra-axial spicule bundles, or plumose spicule tracts, connected by single spicule or groups of spicules at branches.

SPICULES (Figure 5d, Table 5).—Styles, subtylostyles, some with mammiform heads, and styloids; strongyloxeas and oxeas with stepped points, bent or double bent.

DISTRIBUTION AND HABITAT.—Found in the Gulf of Mexico, the southern Caribbean along the Venezuelan and Colombian coasts, and off Curaçao, Dominican Republic, the Bahamas, Florida, and east coast of the United States from Georgia to North Carolina. Occurs in rock patches and coral reef bottoms at depths of 17–71.3 m.

REMARKS.—The skeletal features of the specimens examined do not differ significantly from those of the type material of *Acanthella corrugata* George and Wilson (uncataloged thick sections made from the holotype and deposited at the NMNH), *Oxeostilon burtoni* de Laubenfels (USNM 22347), and

Teichaxinella morchella Wiedenmayer (USNM 24462). Although some spicules differed in their external morphology and shape, they were not sufficiently different to indicate a distinct species and are probably related to variations among populations and to environmental influences. Characters of the material examined for these three species appear to concur with typical characters of *Axinella*. The close similarity between the habits of *A. corrugata* and *T. morchella* has already been pointed out by Wiedenmayer (1977), but he considered the skeletal organization of the two species to be different. De Laubenfels (1936:130) suggested that *A. corrugata* should be transferred to *Stylissa* Hallman, 1914; however, the material examined does not correspond to the diagnostic characters of that genus.

Axinella meandroides, new species

FIGURE 6: TABLE 6

MATERIAL EXAMINED.—*Holotype*: Gulf of Mexico: USNM 41612 (20). *Paratypes*: Gulf of Mexico: USNM 42796 (42), USNM 42797 (38), USNM 42798 (39), USNM 42799 (44), ZMA Por 10363 (18). *Nontypes*: Off South Carolina: USNM 33339 (32°29'12"N, 79°42'54"W, 18 m, coll. SCMR for MMS, 16 Jan 1980). Off Georgia: USNM 42800 (31°23'24"N, 80°53'24"W, 17 m, coll. GMR for MMS, 4 Mar 1981).

SHAPE (Figure 6a).—Small coalesced cups with corrugated walls, 9–20 mm in diameter; cups with common vertices or on central, short peduncle.

SURFACE.—Meandrine, corrugated, encrusted with zoanthids.

COLOR.—Unknown when alive. Purple or brown in alcohol.

SKELETON (Figure 6b,c).—Axial skeleton with vague reticulation of longitudinal spongin-enveloped spicule tracts, 50–100 μm thick. Extra-axial anisotropic reticulation of plumose spicule tracts, radial and oblique to surface, connected by 1–5 spicules.

SPICULES (Figure 6d, Table 6).—Styles to subtylostyles in two size categories, often with tylote modifications; thin oxeas and incipient styles; oxeas very rare or absent in most specimens.

DISTRIBUTION AND HABITAT.—Known only from the Gulf of Mexico, Georgia, and South Carolina. Occurs in rock patches or coral reefs at depths of 14–31.5 m.

ETYMOLOGY.—From Meander (Latin *maeander*), a river in Asia Minor noted for its winding course, referring to the winding appearance of the surface.

REMARKS.—The species resembles other species of *Axinella* from the Gulf of Mexico–Atlantic Ocean region in its skeletal architecture, axial and extra-axial differentiation, presence of styles, and scarcity of oxeas. The morphology, spicule dimensions, and geometry of the styles (usually with a tylote modification) differentiate this species from other species of *Axinella* included in this revision.

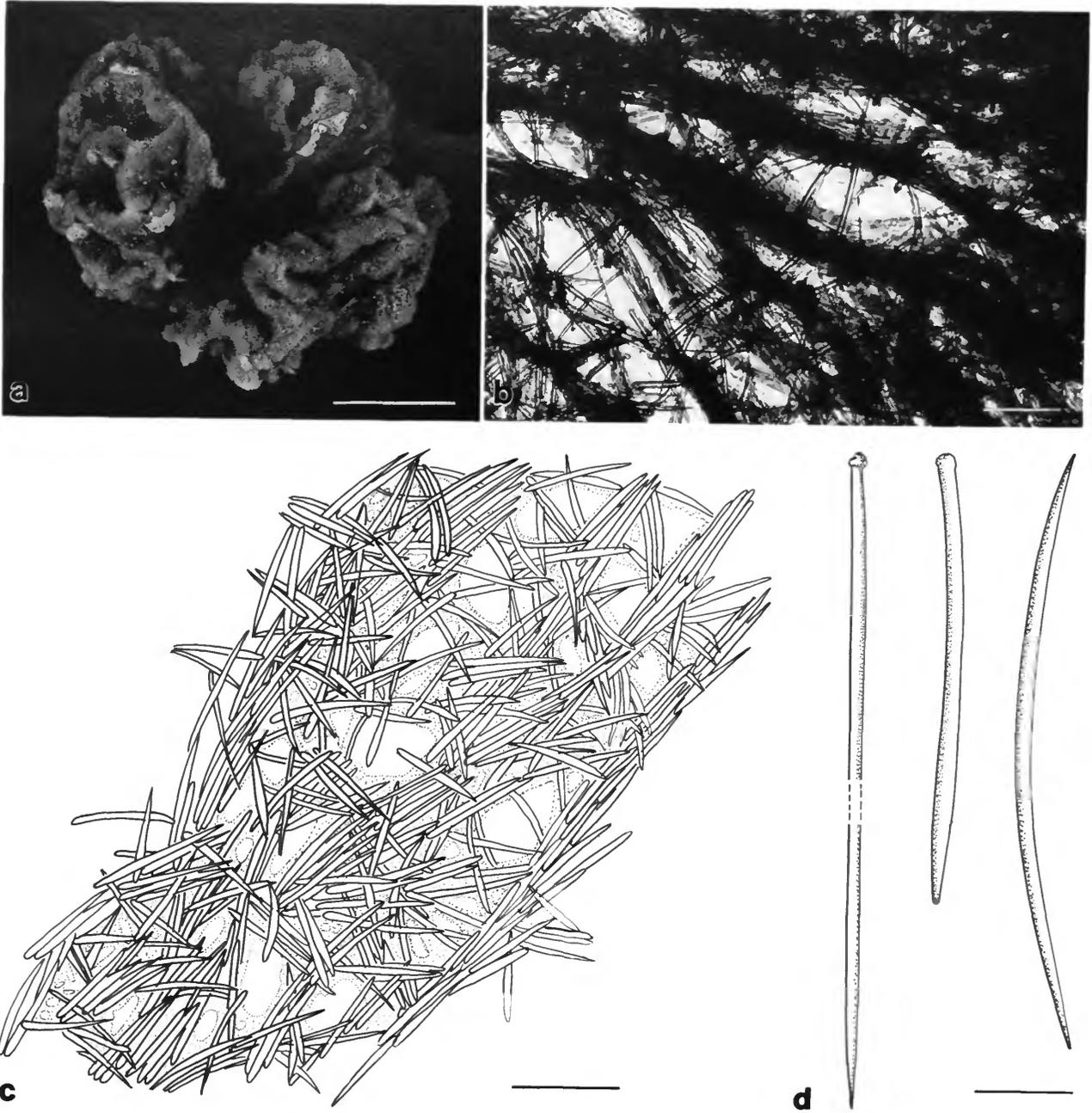


FIGURE 6.—*Axinella meandroides*, new species: *a*, holotype, USNM 41612; *b,c*, micrograph and diagram, respectively, of the skeleton (USNM 42796); *d*, spicules (subtylostyle, style, oxea; USNM 42796). [Scales: *a*, 20 mm; *b,c*, 200 μ m; *d*, 100 μ m.]

TABLE 6.—Spicule dimensions for *Axinella meandroides*, new species. Measurements (in μm) are ranges of 25 spicules (or the number indicated in brackets), with means \pm standard deviation in parentheses.

Specimen	Styles and subtylostyle I	Styles and subtylostyles II	Thin oxeads and styles	Oxeads
South Carolina USNM 33339				
length	680–1025 (896.0 \pm 85.4)	320–440 (397.6 \pm 30.2)	310–410 (361.6 \pm 27.0)	410–520 (477.0 \pm 33.3)[10]
width	7.5–12.5 (10.3 \pm 1.8)	7.5–22.5 (14.4 \pm 3.9)	2.5	2.5–20 (12.8 \pm 5.6)[10]
Georgia USNM 42800				
length	750–1150 (944.4 \pm 104.3)	350–490 (422.8 \pm 37.9)	250–400 (333.3 \pm 40.8)[15]	430–480 (462.5 \pm 20.5)[8]
width	7.5–20 (13.7 \pm 2.9)	10–17.5 (14.9 \pm 2.3)	2.5	5–17.5 (12.5 \pm 4.0)[8]
Gulf of Mexico USNM 41612				
length	1000–1425 (1206.0 \pm 117.8)	410–580 (471.6 \pm 43.8)	310–440 (390.9 \pm 31.2)[23]	not detected
width	5–17.5 (10.7 \pm 3.5)	12.5–22.5 (17.5 \pm 4.1)	2.5	
USNM 42796				
length	1100–1725 (1395.0 \pm 190.7)[20]	330–580 (433.2 \pm 46.3)	300–560 (438.8 \pm 58.4)	not detected
width	10–17.5 (12.0 \pm 1.9)[20]	7.5–22.5 (17.7 \pm 3.1)	2.5	

Axinella sp.

FIGURE 7

MATERIAL EXAMINED.—*Nontypes*: Aruba: ZMA Por 3352 (Bukuti Reef, coll. P. Wagenaar Hummelink, 1930), dry, beach-worm.

SHAPE.—Small dry fragment, 3.5 cm high, with three folds; 0.5 cm thick, with rounded margins and connected at some points.

SURFACE.—Macerate.

COLOR.—Live color unknown. Walnut brown in dry condition.

SKELETON.—Spicule tracts of oxeads and styles organized in anisotropic reticulation, quite halichondroid, with large, rounded to polygonal meshes.

SPICULES (Figure 7).—Oxeads generally bent, 320–420 (369.2 \pm 29.0) μm long and 7.5–15 (12.6 \pm 2.2) μm wide; few styles, 300–1050 (521.3 \pm 263.6)[8] μm long, 7.5–15 (13.4 \pm 2.7)[8] μm wide, mostly broken.

REMARKS.—This specimen resembles *Axinella corrugata* in habit and skeletal organization, but it shows very few styles. It may represent an undescribed species, but this cannot be determined owing to its poor condition.

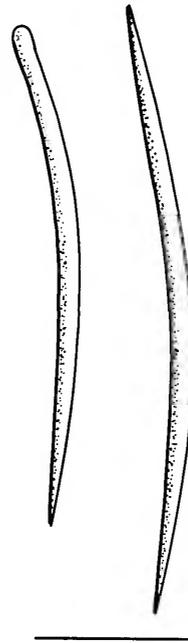


FIGURE 7.—*Axinella* sp.: spicules (style, oxead; ZMA Por 3352). [Scale: 100 μm .]

REMARKS ON THE SPECIES OF *Axinella*

As the preceding discussion makes clear, the classification of *Axinella* species from the central West Atlantic region needs to be amended to include two new species, *Axinella pomponiae* and *A. meandroides*, and also to revise the species previously reported from the region. Only *Axinella polycapella* de Laubenfels was correctly assigned to the genus in earlier classifications. *Axinella waltonsmithi* and *A. shoemakeri* were mistakenly allocated to the genus *Homaxinella* Topsent, 1916, and *Teichaxinella* de Laubenfels, 1936, respectively, but, as

already mentioned, they have all the diagnostic characters of *Axinella*. *Axinella corrugata*, described initially as *Acanthella corrugata*, and its junior synonyms *Oxeostilon burtoni* de Laubenfels and *Teichaxinella morchella* Wiedenmayer also belong to this genus. Other species of *Axinella* cited from the region are synonymized in the present revision (see synonym lists of *A. polycapella*, *Pseudaxinella reticulata*, *Ptilocaulis walpersi*, and *Acanthella mastophora*). Three additional species of *Axinella* previously reported from this region belong to other genera, as confirmed by an examination of the type material: *Axinella nanaspiculata* Hartman (1955:180; ho-

TABLE 7.—Comparison of the central West Atlantic species of *Axinella*.

Species	Shape	Surface	Axial skeleton	Extra-axial skeleton	Spicules (length)
<i>Axinella waltonsmithi</i>	flabellate to bushy	smooth or rough	condensed to vaguely reticulate	plumoreticulate	oxeas (240–450 μm), styles rare (220–370 μm)
<i>Axinella pomponiae</i>	branching	conulose or smooth	vaguely reticulate to confused	plumoreticulate	styles (180–300 μm and 370–690 μm), oxeas rare (220–410 μm)
<i>Axinella polycapella</i>	branching	smooth to velvety	condense to vaguely reticulate	anisotropic reticulation	oxeas (190–430 μm), styles (180–360 μm), strongyloxeas (220–390 μm)
<i>Axinella shoemakeri</i>	thinly lamellate	velvety to smooth	compressed in cross section	dermal spicules and short plumose tracts	styles (190–192.5 μm), oxeas (200–470 μm), trichodragmata (22.5–35 μm)
<i>Axinella corrugata</i>	lamellate to flabelliform bushy	corrugated	condensed to vaguely reticulate	spicule bundles or plumose tracts	subtylostyles to styles to styloids (170–650 μm), oxeas to strongyles to strongyloxeas (120–550 μm)
<i>Axinella meandroides</i>	small, coalescent cups	corrugated	vaguely reticulate	anisotropic reticulation	styles (tylote) and subtylostyles (320–580 and 680–1725 μm), oxeas rare (410–520 μm), thin oxeas and styles (250–560 μm)

lotype, YPM No. 1228) is *Amphimedon compressa* Duchassaing and Michelotti, 1864; *Axinella clava* Schmidt (1870:61; holotype, MCZ 174,8072) is a *Rhizaxinella*; *Axinella rugosa* sensu Schmidt (1870:61; BMNH 1870:5:3:69, from type locality; not *Axinella* (as *Dictyocylindrus*) *rugosa* (Bowerbank, 1866:119)) belongs to the family Raspailiidae, genus *Ceratopsion*.¹

From a comparison of the principal morphological characters of the species of *Axinella* from the central West Atlantic (Table 7), it is clear that individual characters are not sufficient to separate the species, but a combination of characters can be used to do so. As a result, the taxonomy of this group of species is complicated. Additional characters, such as the presence of microscleres (raphides, microraphides, and trichodragmata), the oscules of the star-shaped morphology, and the type and proportions of the megascleres, were therefore included in the definition of *Axinella* to assist in distinguishing it from other genera. An added complication, however, is that these characters may vary intraspecifically (i.e., *A. waltonsmithi*, *A. pomponiae*, *A. polycapella*, *A. corrugata*). The relative number of styles and oxeas, for example, is highly variable within specimens of the same species. Either both styles and oxeas are present, or only styles or only oxeas. When both types of megascleres are present, one of them tends to be rare. Thus, any definition of the genus based on such characters needs to be handled with care.

Transitional forms (i.e., styloids, strongyloxeas) between oxeas and styles also are common among species of *Axinella* in

the central West Atlantic region. These forms also were observed by Pansini (1982–1983) in species of *Axinella* from the Mediterranean Sea.

Pseudaxinella Schmidt, 1875

Pseudaxinella Schmidt, 1875:120 [type species: *Pseudaxinella sulcata*, by monotypy; holotype missing].—Thiele, 1903:378.—de Laubenfels, 1936:131.—Bergquist, 1970:20.—Lévi, 1973:606.—Wiedenmayer, 1977:152, 155; 1989:47.—Hooper and Lévi, 1993:1436.

DIAGNOSIS (expanded).—Unbranched, club-shaped, lobate shrub-like, thickly encrusting or massive Axinellidae, with a more or less smooth surface. Skeletal architecture characterized by parallel and plumose, anastomosing, ascending spicule tracts, without any axial condensation. Spicules are oxeas and/or styles. Microscleres, when present, are trichodragmas.

Pseudaxinella reticulata (Ridley and Dendy, 1886)

FIGURES 8, 9; TABLE 8

Axinella reticulata Ridley and Dendy, 1886:481 [BMNH 1887.5.2.11]; 1887:184.—Wilson, 1902:400.—[not Wells and Wells in Wells et al., 1960:221 = *Axinella polycapella*].

Pseudaxinella rosacea.—de Laubenfels, 1950a:89 [BMNH 1948.8.6.37].—Wells and Wells in Wells et al., 1960:222 [USNM 23661].—[not de Laubenfels, 1949:17 = *Ptilocaulis walpersi* (Duchassaing and Michelotti)]. [Not *Axinella rosacea* Verrill, 1907:341.]

Pseudaxinella sp.—Pearse and Williams, 1951:136 [listed only, same specimen described by Wells and Wells in Wells et al., 1960:222].

Axinella sp.—Storr, 1964:42 [UMML 4:249 and 4:271].

Ectyoplasia ferox explicata Wiedenmayer, 1977:159 [BMNH 1948.8.6.37; new synonymy].

Pseudaxinella lunaecharta Wiedenmayer, 1977:155 [new synonymy].—Alvarez and Diaz, 1985:69.—Pulitzer-Finali, 1986:102.—Zea, 1987:195.—[not Lévi, 1960:750]. [Not *Axinella*(?) *lunaecharta* of Ridley and Dendy, 1886:481 (BMNH 1887.5.2.272); 1887:186; Topsent, 1928:174.]

Pseudaxinella reticulata.—Wiedenmayer, 1977:159 [transfer only].

Pseudaxinella explicata.—Rützler, 1986:121.—Alvarez and Crisp, 1994:119 [cited only].

¹When the type of *Axinella rugosa* Schmidt was examined, the slide matched *Ceratopsion crustosum* Alvarez and Soest, 1993. More material in the BMNH needs to be checked before *C. crustosum* can be declared a junior synonym. There is a small chance that the two specimens that Schmidt described and figured are different species (i.e., one might be *C. crustosum* and the other might correspond to *A. mastophora*).

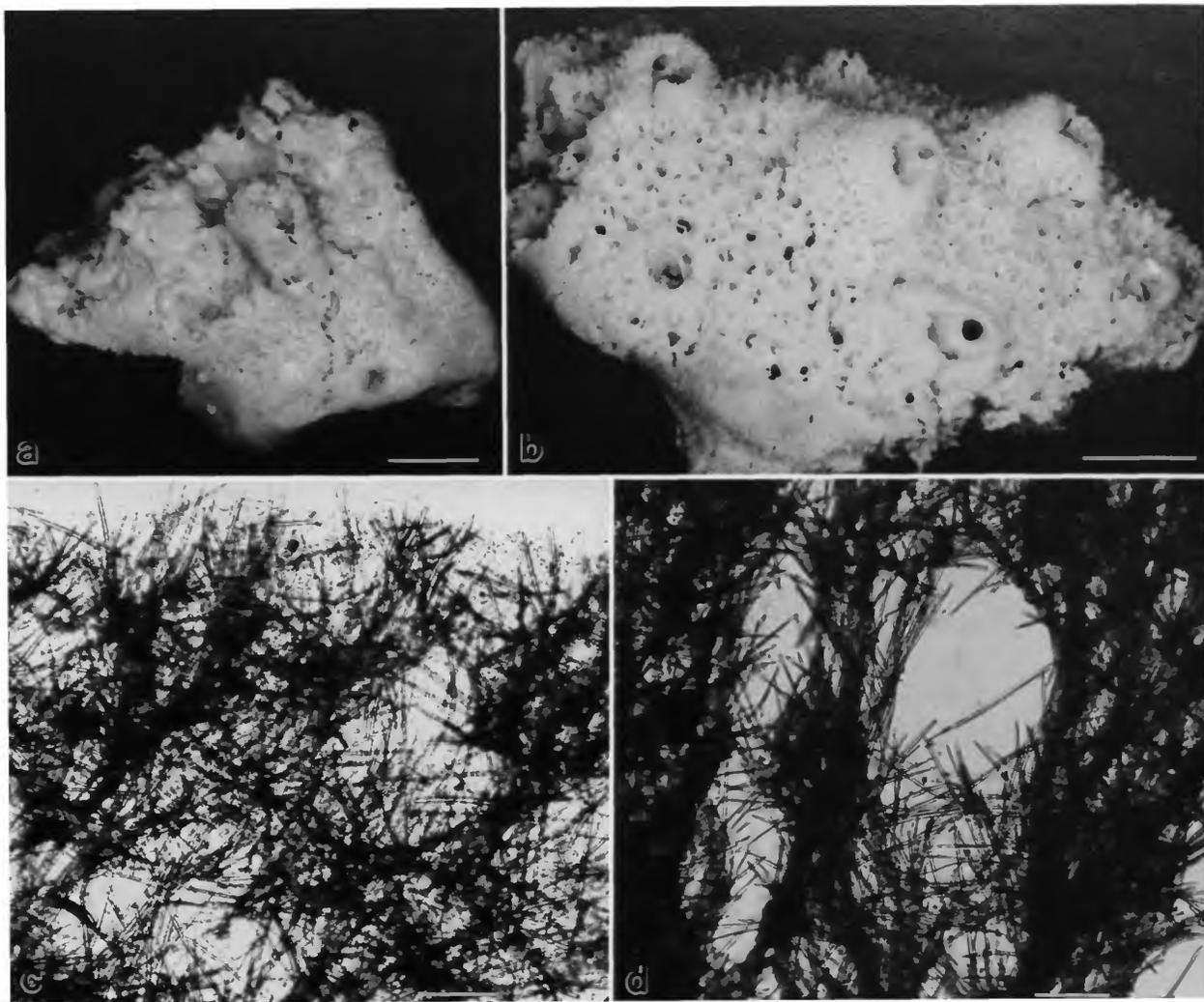


FIGURE 8.—*Pseudaxinella reticulata*: a, holotype, BMNH 87.5.2.11; b, specimen BMNH 1948.8.6.37, neotype of *Pseudaxinella rosacea* (de Laubenfels, 1950a); c, micrograph of the skeleton, holotype, BMNH 87.5.2.11; d, micrograph of the skeleton, specimen BMNH 1948.8.6.37. [Scales: a, b, 10 mm; c, d, 200 μ m.]

MATERIAL EXAMINED.—*Nontypes*: Off North Carolina: USNM 33354 (33°32'12"N, 77°25'06"W, 29 m, coll. DU for MMS, 15 Dec 1980). Off South Carolina: USNM 33349 (32°29'24"N, 79°41'48"W, 19 m, coll. SCMR for MMS, 23 Oct 1985). Off Georgia: USNM 33350 (30°37'00"N, 81°10'36"W, 21 m, coll. GMR for MMS, 26 Jan 1980). Florida: USNM 32876 (Hen and Chicken Reef, off Key Largo, 1–6 m, coll. K. Rützler, 12 May 1973). Bermuda: USNM 32847 (Walsingham Pond, 0.5–2 m, coll. K. Rützler, Aug 1983); ZMA Por 5862 (Walsingham Pond, on mangrove roots, coll. R.W.M. van Soest, 26 Nov 1985). Gulf of Mexico: USNM 34151 (1),

USNM 34154 (8), USNM 34157 (15), USNM 34158 (18), USNM 34159 (21), USNM 34160 (23), USNM 42787 (37), USNM 42788 (39), USNM 42789 (41), USNM 42790 (43). Belize: USNM 32987 (Carrie Bow Cay, M575, deep trench, 24 m, coll. Zingmark et al., 28 Jun 1973). Nicaragua: USNM 31452 (Puerto Cabezas, Miskito Cay, 10–12 m, coll. W. Rainey, 27 Oct 1977). Puerto Rico: USNM 30136 (Punta Higuero, 6–8 m, coll. V. Vicente, 20 Feb 1980). U.S. Virgin Islands: USNM 31552 (Saint John, current hole, 15–20 m, coll. K. Rützler, 4 Apr 1967). Curaçao: ZMA Por 10364 (Seaquarium, coll. P. Hoetjes, 1986). Tobago: USNM 42791 (Bucco Reef, 10 m, on rock patches, coll. R. Hubbard and B. Alvarez,

15 May 1991). Venezuela: ZMA Por 5328 (Los Roques, coral reef, coll. B. Alvarez and M.C. Diaz, 23 Aug 1983). Brazil: ZMA Por 10365 (SE Brazil, coll. E. Hajdu).

SHAPE (Figures 8a,b, 9a).—Massive-amorphous, lobate, flabellate, globular, or mound-shaped.

SURFACE.—Short (0.5 mm high) conules or tubercles, evenly distributed, 0.5–2 mm apart; or tall (1–2 mm high) conules or tubercles, either connected or aligned as meandering ridges, irregularly distributed, 1–3 mm apart, generally in mound-shaped specimens. Oscules conspicuous, circular, with contractile diaphragm, either flush or slightly elevated. Some specimens associated with zoanthids. Some specimens feel slimy.

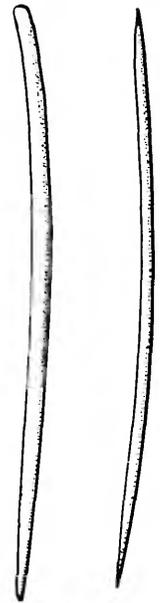
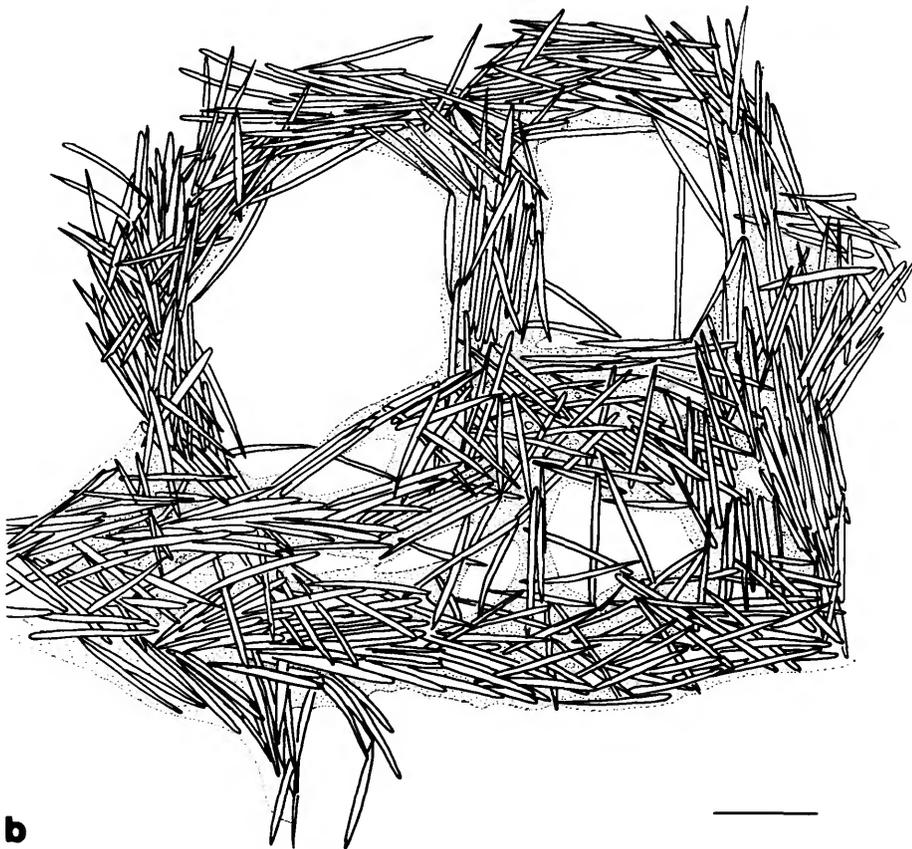
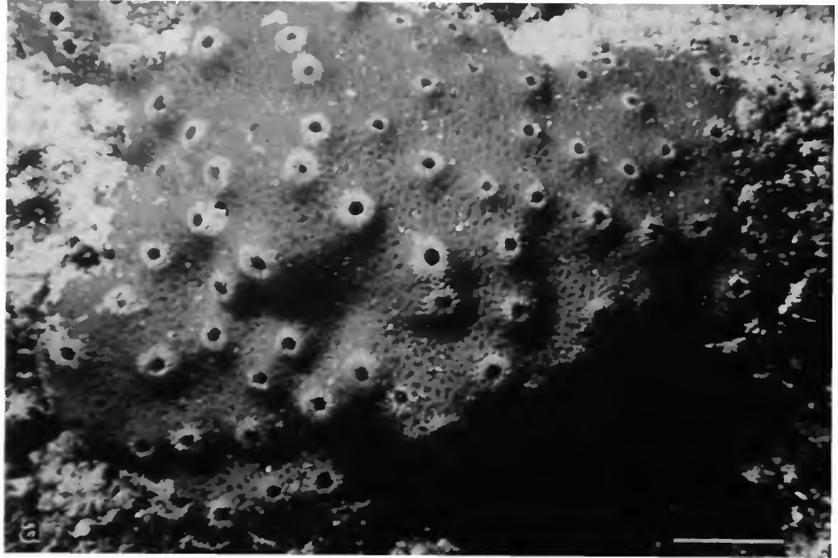


FIGURE 9.—*Pseudaxinella reticulata*: a, specimen photographed in situ at the Archipelago Los Roques, Venezuela (photo, E. Weil); b, diagram of the skeleton (USNM 42787); c, spicules (style, oxea; holotype BMNH 87.5.2.11). [Scales: a, 20 mm; b, 200 μ m; c, 100 μ m.]

TABLE 8.—Spicule dimensions for *Pseudaxinella reticulata*. Measurements (in μm) are ranges of 25 spicules (or the number indicated in brackets), with means \pm standard deviation in parentheses.

Specimen	Styles	Oxeas
North Carolina USNM 33354		
length	220–310 (266.0 \pm 27.1)	220–320 (268.0 \pm 26.1)
width	7.5–15 (10.7 \pm 1.7)	7.5–15 (10.0 \pm 2.5)
South Carolina USNM 33349		
length	210–390 (272.2 \pm 38.0)	210–340 (282.0 \pm 34.9)
width	7.5–17.5 (12.0 \pm 3.4)	5–15 (8.3 \pm 3.1)
Bermuda USNM 32847		
length	300–440 (365.6 \pm 42.7)	320–490 (373.2 \pm 36.3)
width	7.5–12.5 (10.2 \pm 1.0)	7.5–12.5 (10.0 \pm 1.0)
Gulf of Mexico USNM 42787		
length	260–400 (342.8 \pm 41.6)	310–440 (385.6 \pm 34.9)
width	15–22.5 (18.2 \pm 2.6)	12.5–20 (16.2 \pm 1.8)
Belize USNM 32987		
length	210–330 (302.4 \pm 27.6)	330–400 (362.8 \pm 18.1)
width	10–20 (16.0 \pm 2.2)	12.5–17.5 (16.0 \pm 1.8)
Nicaragua USNM 31452		
length	240–350 (287.6 \pm 29.3)	310–400 (342.4 \pm 19.8)
width	7.5–15 (12.1 \pm 2.1)	10–15 (12.8 \pm 1.5)
Puerto Rico USNM 30136		
length	260–340 (303.2 \pm 22.5)	310–410 (354.4 \pm 22.2)
width	10–20 (15.3 \pm 1.8)	12.5–17.5 (15.2 \pm 1.8)
U.S. Virgin Islands USNM 31552		
length	230–330 (282.8 \pm 33.5)	290–370 (331.6 \pm 22.1)
width	10–15 (12.5 \pm 1.8)	7.5–12.5 (11.3 \pm 1.5)
Tobago USNM 42791		
length	170–320 (260.4 \pm 41.8)[24]	230–330 (282.1 \pm 22.6)[24]
width	7.5–20 (13.6 \pm 3.2)[24]	5–17.5 (11.1 \pm 3.2)[24]
Brazil BMNH 87.5.2.11		
length	240–416 (347.1 \pm 54.4)	340–470 (395.84 \pm 34.8)
width	7.5–21.4 (14.236 \pm 3.6)	10–17.5 (12.4 \pm 2.0)

COLOR.—Bright red when alive. Greyish white, brown beige, purple, or combination of these when in alcohol.

SKELETON (Figures 8c,d, 9b).—Reticulation of plumose spicule tracts (60–540 μm thick) perpendicular to the surface, without axial condensation.

SPICULES (Figure 9c, Table 8).—Styles bent in middle or toward round end; fusiform-hastate oxeas bent in middle.

DISTRIBUTION AND HABITAT.—Widely distributed in the Caribbean Sea, including Curaçao and Venezuela, and the Gulf of Mexico and also off Brazil, the Bahamas, Bermuda, and the east coast of the United States from Florida to North Carolina. Occurs in rock patches, on mangrove roots, and on coral reefs at depths of 0.5–70 m.

REMARKS.—When the specimens in this study were compared with the type specimen of *Axinella reticulata* (BMNH 1887.5.2.11, Bahia, Brazil, 14–40 m), they matched previous descriptions of a western Atlantic population referred to as *Pseudaxinella lunaecharta* (see Wiedenmayer, 1977; Alvarez and Díaz, 1985; Zea, 1987). Yet these specimens differed from the West African species *Pseudaxinella lunaecharta* sensu Ridley and Dendy in several characters. For example, trichodragmata, which were found in the type specimen of *Axinella lunaecharta* (BMNH 1887.5.2.272) and in other specimens from the Cape Verde Islands, are absent in the central West Atlantic populations. Megascleres in the West African specimens are slightly larger (styles are 280–430 μm long, and oxeas are up to 500 μm long) and the spicule tracts are far thinner and less plumoreticulate than in the specimens in this study.

Specimen BMNH 1948.8.6.37 (Harrington Sound, Bermuda, coll. M.W. de Laubenfels, 28 Jul 1947), referred to *Pseudaxinella rosacea* by de Laubenfels (1950a) and *Ectyoplasia ferox explicata* by Wiedenmayer (1977), is also conspecific with *Pseudaxinella reticulata* (Ridley and Dendy). De Laubenfels (1953) called the same specimen the neotype of *Axinella rosacea* Verrill, but Wiedenmayer (1977:159) considered this designation invalid. The identity of *Axinella rosacea* described by Verrill (1907:340) is questionable; it is probably a species of *Ptilocaulis* (see “Remarks” for *Ptilocaulis walpersi*, below).

Pseudaxinella grayi (Wells and Wells in Wells et al., 1960)

FIGURE 10; TABLE 9

Teichaxinella grayi Wells and Wells in Wells et al., 1960:223 [USNM 23663].
Pseudaxinella grayi.—Wiedenmayer, 1977:155 [transfer only].—Alvarez and Crisp, 1994:119 [cited only].

MATERIAL EXAMINED.—*Nontypes*: Off Georgia: USNM 42785 (31°23'36"N, 80°53'00"W, 17 m, coll. GMR for MMS, 4 Mar 1981), USNM 42786 (31°23'24"N, 80°53'24"W, 17 m, coll. GMR for MMS, 4 Mar 1981). Gulf of Mexico: USNM 42780 (38), USNM 42781 (39), USNM 42782 (42), USNM 42783 (43), USNM 42784 (44). Representative specimens from the same area in ZMA.

SHAPE (Figure 10a).—Small hemispherical masses up to 10 cm in diameter.

SURFACE.—Rough to touch, coarsely porous. Star-shaped oscules.

COLOR.—Live color unknown. Rosy brown or beige in alcohol.

SKELETON (Figure 10b,c).—Halichondroid confused to plumoreticulate, with radial plumose spicule tracts (40–100 μm thick) connected by 1–3 spicules. Axial condensation absent.

SPICULES (Figure 10d, Table 9).—Styles in one or two size categories; smaller size dominant when both sizes present; smaller styles usually with tylote endings. Oxeas usually rare.

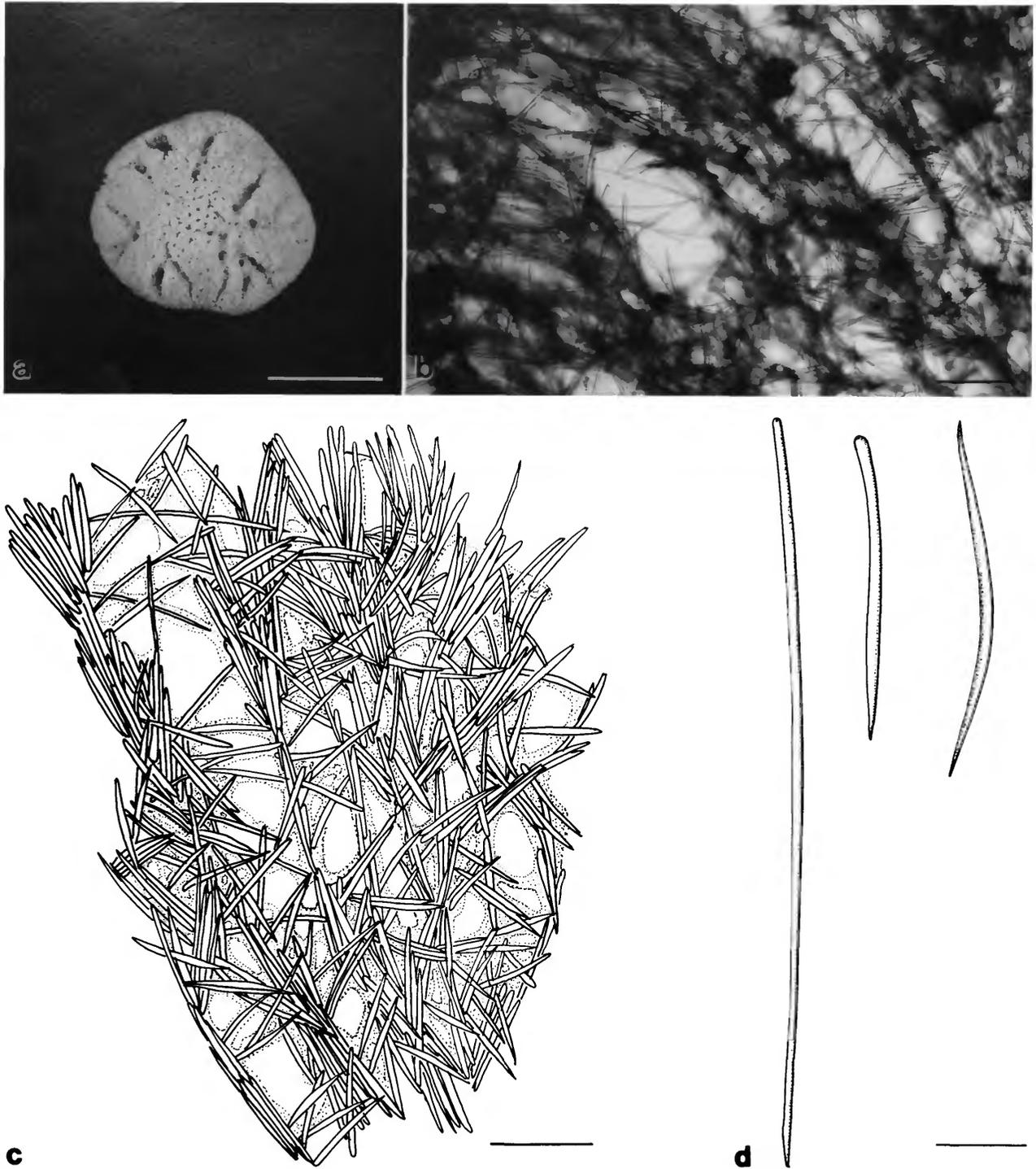


FIGURE 10.—*Pseudaxinella grayi*: a, specimen USNM 42780; b,c, micrograph and diagram, respectively, of the skeleton (USNM 42780); d, spicules (two categories of styles, one oxea; USNM 42780). [Scales: a, 20 mm; b,c, 200 μ m; d, 100 μ m.]

TABLE 9.—Spicule dimensions for *Pseudaxinella grayi*. Measurements (in μm) are ranges of 25 spicules (or the number indicated in brackets), with means \pm standard deviation in parentheses.

Specimen	Styles I	Styles II	Oxeas
Georgia USNM 42786			
length	450–490 (463.3 \pm 23.1)[3]	200–340 (265.2 \pm 39.5)	200–390 (243.6 \pm 42.2)
width	5–7.5 (5.8 \pm 1.4)[3]	7.5–25 (12.6 \pm 3.6)	2.5–12.5 (7.9 \pm 2.5)
Gulf of Mexico USNM 42780			
length	670–1200 (991.4 \pm 128.2)	300–380 (335.8 \pm 22.1)[24]	320–400 (367.5 \pm 34.0)[4]
width	5–15 (9.8 \pm 2.3)	10–25 (19.2 \pm 4.3)[24]	5–15 (12.5 \pm 5.0)[4]

DISTRIBUTION AND HABITAT.—Distributed in the Gulf of Mexico and off Georgia and North Carolina. Occurs in rock patches or coral bottom at depths of 14–17 m.

REMARKS.—The species differs from *Pseudaxinella reticulata* (Ridley and Dendy) in overall shape and size, in having star-shaped oscules, and in having spicule tracts that are thinner and not as echinated. The relative proportion of styles and oxeas varies intraspecifically, as in other species of the family.

Pseudaxinella(?) zeai, new species

FIGURE 11; TABLE 10

Pseudaxinella zeai.—Erhardt and Moosleitner, 1995:52 [prematurely referring to this publication].

Hymeniacidon amphilecta.—Pulitzer-Finali, 1986:117.—[not de Laubenfels, 1936:137].

Pseudaxinella sp.—Alvarez and Crisp, 1994:119.

Calyx podatypa.—Humann, 1992:33.

MATERIAL EXAMINED.—*Holotype*: USNM 39361 (C-POR-087, Colombia, Islas del Rosario, Isla Tesoro, 18 m, coll. S. Zea). *Paratypes*: ZMA Por 8876 (U.S. Virgin Islands, St. Croix, 40 ft (12 m), coll. W.B. Gladfelter, Buck Channel); USNM 42805 (Tob-002, Little Tobago, 60 ft (18 m), coll. B. Alvarez, 11 May 1991). *Nontypes*: USNM 39401 and USNM 39426 (Tob-018 and Tob-021, Angel Reef, 110 ft (33 m), coll. B. Alvarez, 14 May 1991).

SHAPE (Figure 11a).—Spreading, massive, thick, with lobes up to 6 cm high and chimney-like oscules up to 1 cm in diameter.

SURFACE.—Smooth, with small pores, approximately 1 mm in diameter, irregularly distributed, and with dermal reticulation (see "Skeleton," below). Infected with zooanthids.

CONSISTENCY.—Crumby, soft.

COLOR.—In life, surface purple brown, choanosome yellowish. Beige white in alcohol.

SKELETON (Figure 11b,c).—Ectosomal reticulation of spicules obscured by pigment(?) grains, distinguishable with the naked eye. In the choanosome, ascending spicule tracts with 1–3 spicules (generally unispicular), connected by single spicules, also obscured by pigment(?) grains.

SPICULES (Figure 11d, Table 10).—Styles and oxeas.

DISTRIBUTION AND HABITAT.—Colombia, Tobago (where it

TABLE 10.—Spicule dimensions for *Pseudaxinella zeai*, new species. Measurements (in μm) are ranges of 25 spicules, with means \pm standard deviation in parentheses.

Specimen	Styles	Oxeas
St. Croix ZMA Por 8876		
length	190–290 (245.6 \pm 28.9)	240–330 (272.4 \pm 26.2)
width	5–10 (7.2 \pm 1.8)	5–10 (7.3 \pm 1.4)
Colombia C-Por-087		
length	220–290 (270.4 \pm 17.7)	270–330 (301.6 \pm 15.5)
width	7.5–12.5 (11.1 \pm 1.5)	7.5–12.5 (10.4 \pm 1.2)
Tobago USNM 42805		
length	230–300 (263.6 \pm 19.3)	220–320 (272.4 \pm 25.5)
width	7.5–10 (9.5 \pm 1.0)	7.5–12.5 (9.6 \pm 1.2)

is particularly common), and U.S. Virgin Islands (St. Croix). Found in coral reefs at depths of 13–20 m.

ETYMOLOGY.—The species is named after Dr. Sven Zea, who first collected it and recognized it as being new, in recognition of his great contribution to the knowledge of southern Caribbean sponges.

REMARKS.—This species is remarkably similar to species belonging to the Haplosclerida (i.e., *Xestospongia*, *Petrosia*) and is noted for its ectosome, which is obscured by very fine pigment(?) grains. All the specimens studied have this feature. The skeleton, almost a unispicular reticulation of styles, differs significantly from that of other species of *Pseudaxinella* from the region. Nevertheless, we are tentatively placing the new sponge in *Pseudaxinella* based on (1) an absence of axial condensation, (2) the anisotropic skeleton (primary tracts connected by secondary tracts or single spicules), (3) a mixture of styles and oxeas without distinct localization, and (4) a spicule size range roughly similar to that of *P. reticulata*. We will reconsider this issue after performing additional field observations and histological examination, particularly of the reproductive structures.

REMARKS ON THE SPECIES OF *Pseudaxinella*

The species of *Pseudaxinella* described above have distinct morphological characters and skeletal organization. They lack

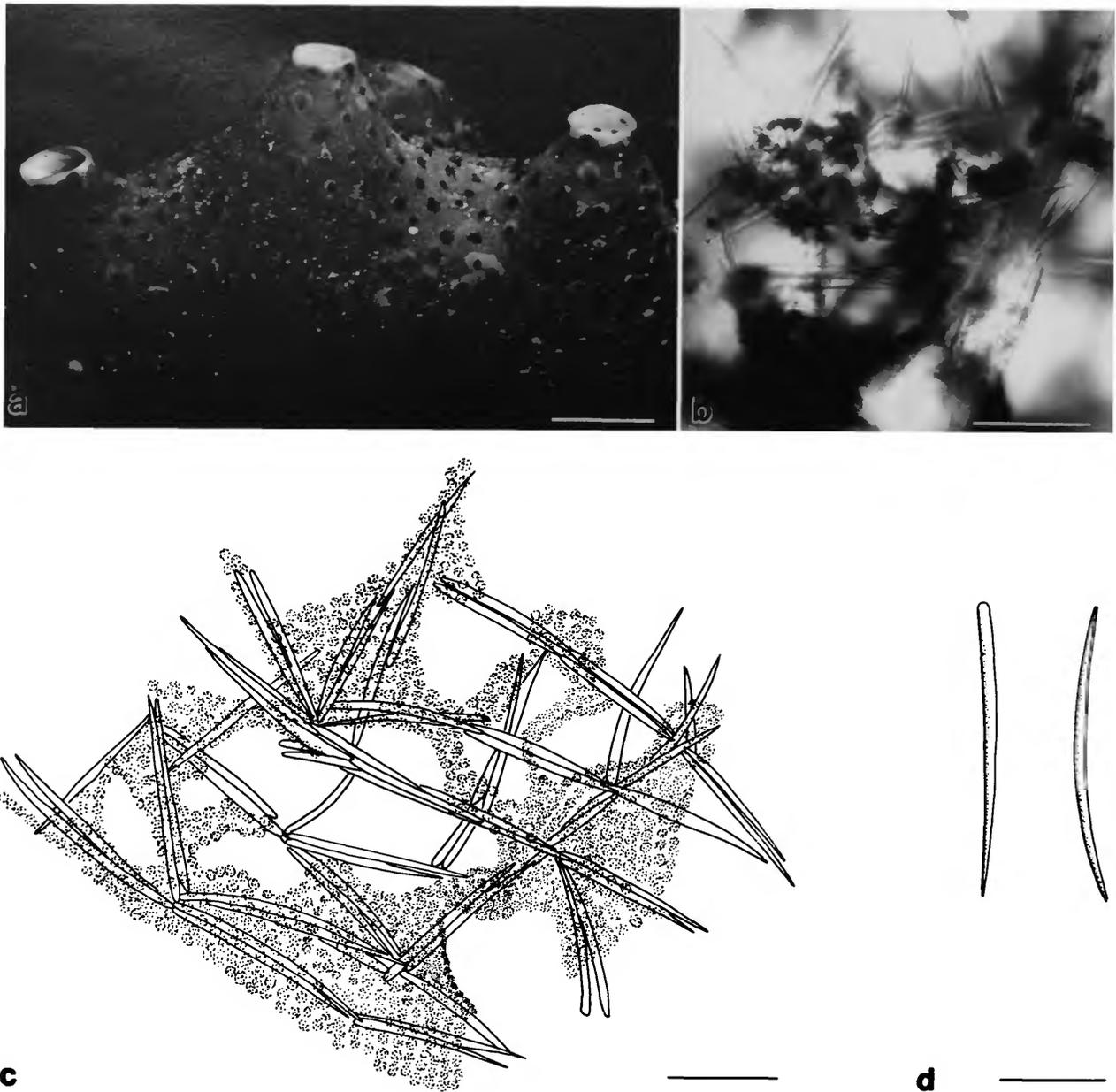


FIGURE 11.—*Pseudaxinella(?) zeai*, new species: *a*, specimen photographed in situ at Santa Marta, Colombia (photo, S. Zea); *b,c*, micrograph and diagram, respectively, of the skeleton (USNM 42805); *d*, spicules (style, oxea; holotype USNM 39361). [Scales: *a*, 20 mm; *b,c*, 200 μ m; *d*, 100 μ m.]

axial condensation, which is the principal characteristic of other genera in the family; instead, the skeleton is formed by plumose and parallel tracts of oxeas and styles. Note, too, that the type species of the genus, *Pseudaxinella sulcata* Schmidt, has never been properly redescribed, although Thiele

(1903:378) made some preliminary attempts to do so.

Other species of *Pseudaxinella* previously recorded from the central West Atlantic region are synonymized in the present revision (see *Axinella polycapella*, *P. reticulata*, and *Ptilocaulis walpersi*).

***Ptilocaulis* Carter, 1883**

Ptilocaulis Carter, 1883:321 [type species: *Ptilocaulis gracilis*, by subsequent designation (de Laubenfels, 1936:127); holotype, BMNH 1845.12.30.1 = *Ptilocaulis walpersi* (Duchassaing and Michelotti, 1864), slide from type, USNM 31025; see below].—Carter, 1884:130.—Topsent, 1928:37, 172.—de Laubenfels, 1936:127.—Lévi, 1973:605.—Wiedenmayer, 1977:152.—Hooper and Lévi, 1993:1426.

DIAGNOSIS (emended).—Axinellidae with separate axial and extra-axial skeleton, but without clear axial condensation, with irregularly plumoreticulate skeleton of styles (generally) bound by spongin, with extra-axial parts in the form of characteristic “scopiform” processes (Carter’s terminology) uniformly distributed, and without “star-shaped” oscules.

***Ptilocaulis walpersi* (Duchassaing and Michelotti, 1864)**

FIGURES 12, 13; TABLE 11

Pandaros walpersii Duchassaing and Michelotti, 1864:90 [USNM 31025; spicule slide, thick section, and color photograph made from the lectotype MT Por 56].

Ptilocaulis gracilis Carter, 1883:321 [holotype, BMNH 1845.12.30.1].—Wiedenmayer, 1977:152.—Zea, 1987:187 [synonymy].

Axinella appressa Verrill, 1907:340 [new synonymy].

(?)*Axinella rosacea* Verrill, 1907:341.

Axinella rudis Verrill, 1907:341.—Zea, 1987:188 [synonymy].

Pseudaxinella rosacea.—de Laubenfels, 1949:17 [AMNH 494].—Wiedenmayer, 1977:152 [synonymy].—Zea, 1987:187 [synonymy].—[not de Laubenfels, 1950a:89; Wells and Wells in Wells et al., 1960:222 = *Pseudaxinella reticulata*].

Homaxinella rudis.—de Laubenfels, 1950a:87 [BMNH 1948.8.6.36, designated neotype of *Axinella rudis* (Figure 12a)].—Rützler, 1986:121.—Zea, 1987:187 [synonymy].—[not de Laubenfels, 1953:531; Wells and Wells in Wells et al., 1960:221 = *Axinella pomponiae*, described above; Pulitzer-Finali, 1986:103].

Axinella ramosa Burton, 1954:229 [holotype, BMNH 1938.6.30.37 (Figure 12b); new synonymy].

Ptilocaulis spiculifer.—Pulitzer-Finali, 1986:103.—[not Wiedenmayer, 1977:153 = *Monanchora arbuscula*. [Not *Spongia spiculifera* Lamarck, 1814:449.]

Ptilocaulis walpersi.—Zea, 1987:187 [with additional synonyms].—Alvarez and Crisp, 1994:119 [cited only].—Hooper, 1994:206 [distribution only].

Ptilocaulis marquezii.—Kobluk and van Soest, 1989:1215. [Not *Ptilocaulis marquezii* (Duchassaing and Michelotti, 1864:40).]

MATERIAL EXAMINED.—*Nontypes*: Bermuda: USNM 31903, USNM 34663 (Shark Hole, Harrington Sound, 0.5–3 m, coll. K. Rützler, 19 Sep 1985). Florida: USNM 42803 (Fort Lauderdale, 20 m, coll. A. Antonius, Jun 1979). Bahamas: USNM 42802 (B-307, Bimini, 1–5 m, coll. K. Rützler, 1 Aug 1967). U.S. Virgin Islands: USNM 31573 (St. Thomas, 1–3 m, coll. K. Rützler, 4 Apr 1967), USNM 32229 (St. John, coll. F. Schmitz, 8 May 1981). Puerto Rico: USNM 32255 (Guayanilla Bay, 15 m, coll. V. Vicente, Jul 1978), ZMA Por 3627 (La Parguera, 20–35 m, coll. J.H. Stock, 3 Mar 1963). Belize: USNM 42804 (79.5.23-B, Carrie Bow Cay, 6 m, coll. K. Rützler, 23 May 1979). Colombia: ZMA Por 10032 (Santa

TABLE 11.—Spicule dimensions for *Ptilocaulis walpersi*. Measurements (in μm) are ranges of 25 spicules, with means \pm standard deviation in parentheses.

Specimen	Styles I	Styles II
Bermuda USNM 34663		
length	260–370 (317.2 \pm 34.3)	630–890 (779.2 \pm 74.2)
width	10–15 (12.4 \pm 2.2)	7.5–12.5 (9.7 \pm 1.5)
Puerto Rico ZMA Por 3627		
length	270–310 (288.4 \pm 11.4)	610–1000 (795.2 \pm 110.0)
width	7.5–15 (12.2 \pm 2.2)	5–12.5 (9.2 \pm 2.0)
St. Thomas USNM 31025		
length	260–340 (295.6 \pm 18.0)	490–860 (715.6 \pm 81.0)
width	10–15 (13.3 \pm 1.9)	5–10 (7.2 \pm 2.2)
Curaçao ZMA Por 10031		
length	310–400 (354.4 \pm 22.7)	730–1075 (868.0 \pm 105.1)
width	5–15 (10.1 \pm 2.1)	5–12.5 (9.1 \pm 2.7)

Marta, 18–27 m, coll. S. Zea, Sep 1987). Curaçao: ZMA Por 10031 (Playa Kalki, 10–20 m, coll. R.W.M. van Soest, 30 Dec 1980).

SHAPE.—Variable (Figure 12a–d): encrusting, irregularly massive, plate-shaped, fan-shaped, or erect finger-shaped; dichotomously branching or forming brushes of 10 or more close-cropped branches.

SURFACE.—Uniformly covered with flattened processes.

COLOR.—Orange red when alive. White beige in alcohol.

SKELETON (Figure 13a,b).—Strongly developed fascicles of primary fibers (spicules and spongin) ending in surface processes, irregularly interconnected by single fibers and short tracts.

SPICULES (Figure 13c, Table 11).—Styles of two sizes; shorter styles more frequent than longer styles, longer styles project from surface brushes.

DISTRIBUTION AND HABITAT.—Widely distributed in the Caribbean, from Florida to Colombia, and around Bermuda. Not found in the Gulf of Mexico or off the east coast of the United States. Occurs on coral reef bottoms at depths of 0.5–35 m.

REMARKS.—The material examined is conspecific with the type specimen of *Ptilocaulis walpersi* (Duchassaing and Michelotti). The specimen described by Duchassaing and Michelotti (1864) corresponds to the bushy shape of this species.

The holotype of *Ptilocaulis gracilis* Carter (BMNH 1845.12.30.1), type species of the genus, also matches the material studied, including the holotype of *P. walpersi*. The holotype of *P. gracilis*, however, lacks the large-size styles, but these may have been lost as a result of the damage to the surface of the specimen.

The specimen of *Pseudaxinella rosacea* sensu de Laubenfels

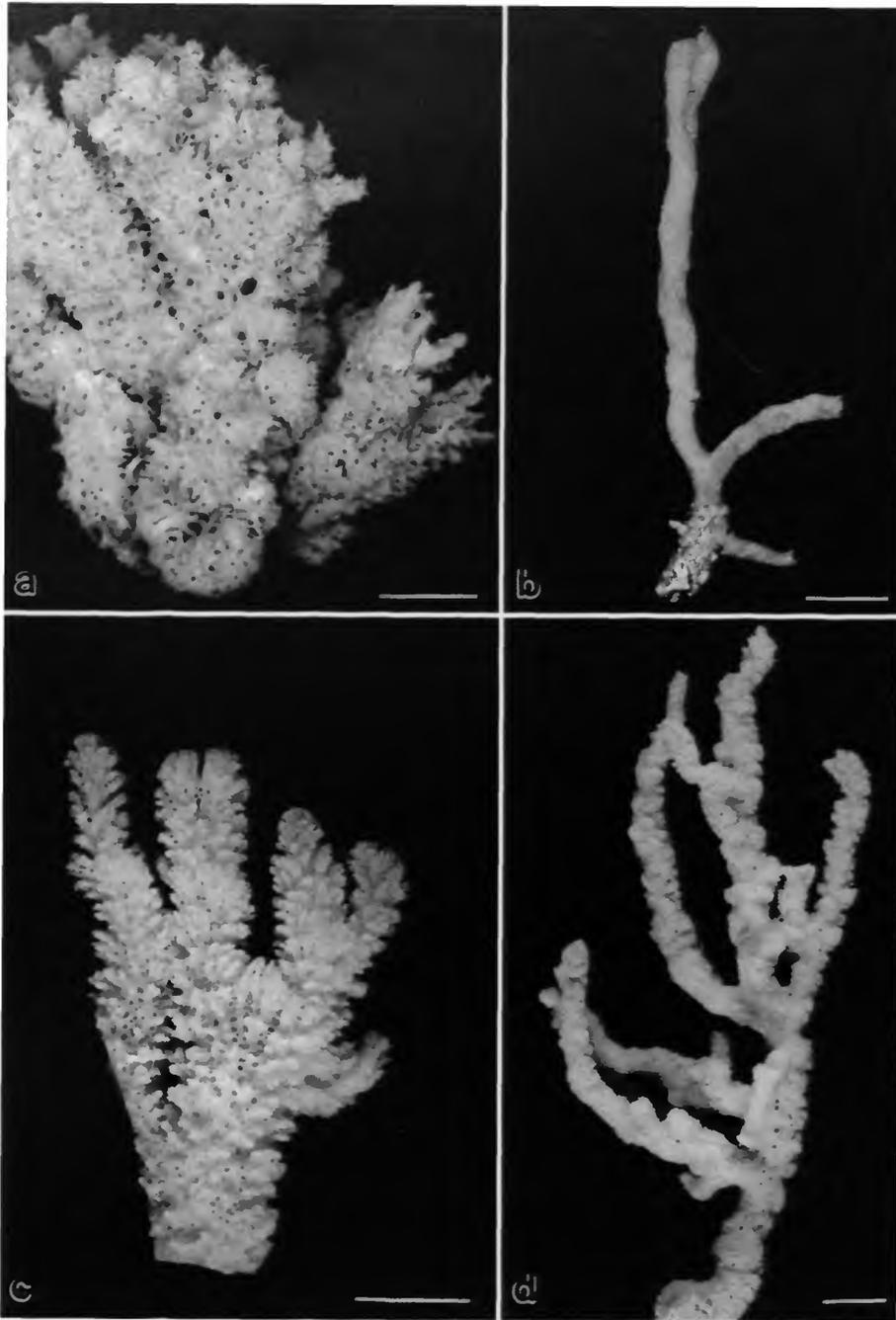


FIGURE 12.—*Ptilocaulis walpersi*: a, specimen BMNH 1948.8.6.36, designated neotype of *Homaxinella rudis* (de Laubenfels, 1950a); b, holotype of *Axinella ramosa* Burton (1954) from Mosquito Bank, Honduras (BMNH 1938.6.30.37); c, specimen USNM 31573 from St. Thomas, U.S. Virgin Islands; d, specimen USNM 34663, Harrington Sound, Bermuda. [Scales: a, b, 10 mm; c, d, 20 mm.]

(1949) (AMNH 494, currently deposited at the NMNH), considered a synonym of *Ptilocaulis gracilis* by Wiedenmayer (1977), is conspecific with *Ptilocaulis walpersi*. The synonymies of *Ptilocaulis walpersi* with *P. gracilis*, *Pseudaxinella rosacea* sensu de Laubenfels, 1949, *Homaxinella rudis* sensu de Laubenfels, 1950a, and *Axinella rudis* Verrill were first

established by Zea (1987), and they are confirmed in the present revision. Consequently, we consider *Pandaros walpersii* Duchassaing and Michelotti to be the type species of *Ptilocaulis*.

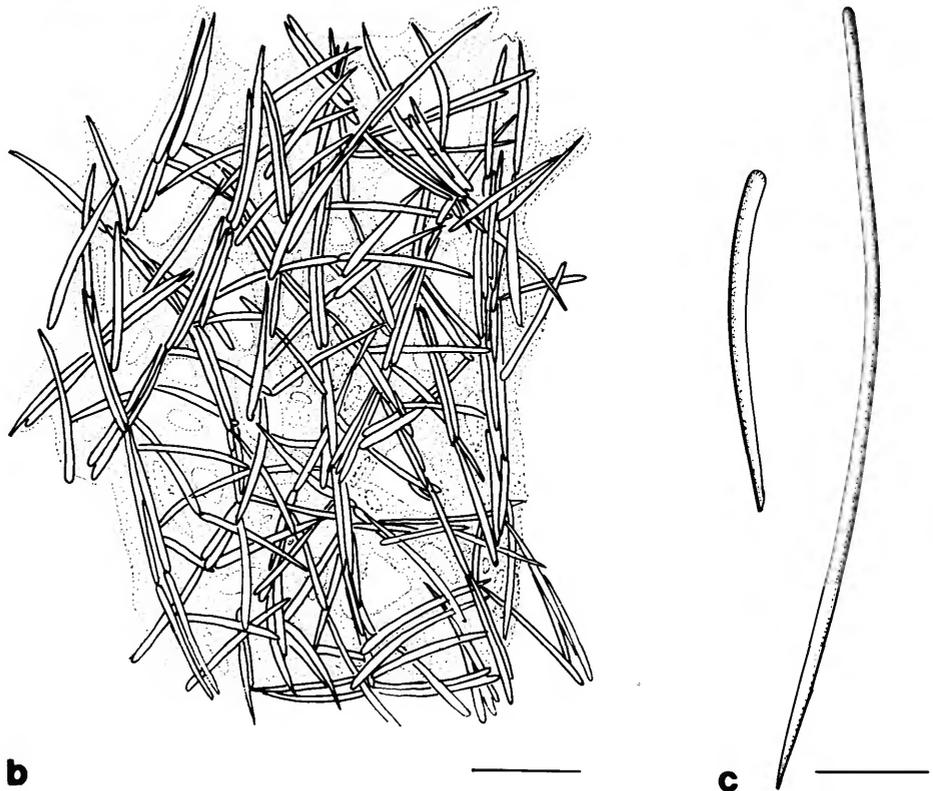
Ptilocaulis spiculifer sensu Pulitzer-Finali (1986) matches the present species, and the two are considered conspecific.

Pulitzer-Finali (1986) confirmed that his material is similar to the type specimen of *Ptilocaulis walpersi*. *Ptilocaulis* aff. *spiculifer* sensu Wiedenmayer (1977) (= Duchassaing and Michelotti's *Pandaros arbuscula*, ZMA Por 1728) is *Monanchora arbuscula* (Duchassaing and Michelotti, 1864).

The external morphology of *Axinella ramosa* Burton differs from the rest of the material studied. Both holotype and paratype are very small ramose specimens, 6 cm and 3 cm long, respectively, with one to three thin branches (5 mm in diameter) and a



FIGURE 13.—*Ptilocaulis walpersi*: a, b, micrograph (USNM 34663) and diagram (USNM 31573), respectively, of the skeleton; c, spicules (two categories of styles; from lectotype MT Por 56). [Scales: a, b, 200 μ m; c, 100 μ m.]



microhispid surface. Skeletal arrangement and spicule composition, however, are in agreement with the rest of the material identified as *Ptilocaulis walpersi*.

The synonymy with *Axinella rosacea* Verrill remains questionable. Verrill (1907) mentioned the presence of oxeas, which are not normally found in the present species. The species described by Verrill might be the same species described herein as *Ptilocaulis marquezii*.

Species similar to Caribbean *Ptilocaulis walpersi* (i.e., *P. spiculifer* (Lamarck, 1813) and *P. trachys* (de Laubenfels, 1954, as *Homaxinella*)) occur in the Indo-Pacific (the Red Sea, the waters around New Caledonia, Australia, and Indonesia, and the central Pacific Ocean). They, too, have a characteristic surface ornamentation, possibly a synapomorphy for the genus.

***Ptilocaulis marquezii* (Duchassaing and Michelotti, 1864),
new combination**

FIGURE 14: TABLE 12

Spongia marquezii Duchassaing and Michelotti, 1864:40 [USNM 31040: spicule slide, thick section, and color photograph made from the lectotype MT Por 86].

Teichaxinella marquezii.—Zea, 1987:191 [with additional synonyms].

Ptilocaulis marquezii.—Alvarez and Crisp, 1994:119 [cited only].—[not de Laubenfels, 1936:127 = *Xestospongia* sp.; (?)de Laubenfels, 1950b:168].

MATERIAL EXAMINED.—*Nontypes*: U.S. Virgin Islands: ZMA Por 8355 (St. Croix, coll. W.B. Gladfelter, 1990). Belize: USNM 31040, USNM 42801 (S-S-9, Carrie Bow Cay, outer reef, 12 m, coll. W. Fenical, 25 Apr 1977).

SHAPE (Figure 14a).—Branching or bushy.

SURFACE.—Small branching processes with bifurcate ends stretching over a dermal skin.

COLOR.—Red orange when alive. Brown beige in alcohol or in dry condition.

SKELETON (Figure 14b,c).—Longitudinal plumose spicule tracts, connected at some points by 1–2 spicules, vaguely condensed in axial parts and diverging to periphery, becoming halichondroid.

SPICULES (Figure 14d, Table 12).—Styles transitional to styloids and oxeas transitional to strongyloxeas.

DISTRIBUTION AND HABITAT.—West Indies (Guadalupe, St. Croix), (?)Bermuda, Belize, and Colombia. Coral reefs at depths of 13–20 m.

REMARKS.—The species, originally described as *Spongia marquezii*, was interpreted to belong to *Ptilocaulis* by de Laubenfels (1936), but the proposed combination was based on a specimen (USNM 22528) that is a *Xestospongia*. Wiedenmayer (1977) related this species to *Teichaxinella*, a genus that should be abandoned (see “Remarks” under *Axinella shoemakeri*). The material studied is conspecific with the sponge described by Duchassaing and Michelotti (1864).

This species is very similar in habitat to *Ptilocaulis walpersi*

TABLE 12.—Spicule dimensions for *Ptilocaulis marquezii*. Measurements (in μm) are ranges of 25 spicules, with means \pm standard deviation in parentheses. 1 = Styles transitional to styloids; 2 = oxeas transitional to strongyloxeas and strongyles.

Specimen	Length	Width
Belize USNM 42801 1 and 2	220–570 (384.4 \pm 81.8)	7.5–22.5 (15.7 \pm 3.3)
St. Thomas USNM 31040 1 and 2	270–560 (366.0 \pm 65.3)	7.5–17.5 (12.7 \pm 2.7)
St. Croix ZMA Por 8355 1	250–570 (385.2 \pm 71.5)	5–15 (8.9 \pm 2.3)
2	190–570 (296.0 \pm 73.8)	5–12.5 (7.1 \pm 2.0)

(see above), but the spiculation is quite different. *Ptilocaulis walpersi* has just two size categories of styles. That feature is constant among all the specimens studied (see Table 11), including the holotype of *P. walpersi*. In contrast, *Ptilocaulis marquezii* has styles transitional to styloids and oxeas transitional to strongyloxeas (see Figure 14d), and size categories for styles cannot be distinguished (see Table 12).

REMARKS ON THE SPECIES OF *Ptilocaulis*

So far, *Ptilocaulis walpersi* and *P. marquezii* are the only valid species of the genus in the central West Atlantic region. Another species belonging to this genus, originally described as *Perissinella fosteri* by Hechtel (1983:73) (type material, YPM 9009 and YPM 8984), occurs off Brazil.

***Dragmaxia* Hallmann, 1916**

Dragmaxia Hallmann, 1916:543 [type species: *Spongosorites variabilis* Whitelegge, 1907:513 (AM G10173; off Wata Mooli, New South Wales, coll. H.M.C.S. *Thetis*, sta 41)].

DIAGNOSIS (emended from Hallmann, 1916).—Axinellidae of lamellar, flabellate, cup-shaped, or massive habit. Skeleton composed of axially condensed plumose spicule tracts with peripheral individual spicules curving outward toward the surface. Megascleres, styles only, often in widely different sizes. Microscleres, long, sinuous trichodragmas and single raphides.

REMARKS.—The definition by Hallmann (1916) is extended to include massively encrusting species that do not very clearly show the axially condensed bundles. The distinctive generic characteristics are the absence of a reticulate (extra-axial) skeletal structure and the presence of a long, sinuously curved trichodragmata. Hooper and Lévi (1993) considered the latter character to be of low weight and believed that *Dragmaxia* should be synonymized with *Stylissa* Hentschel.

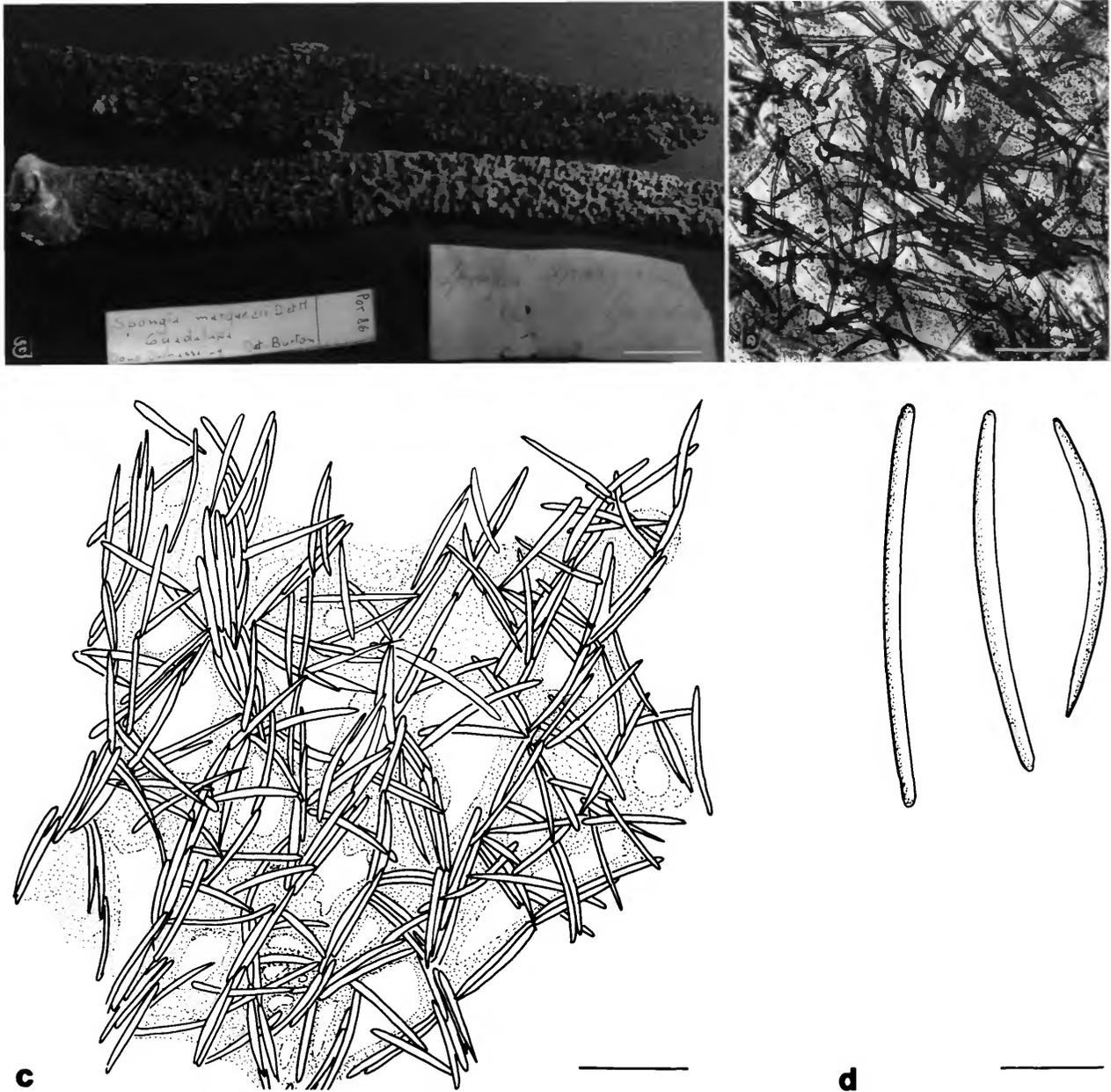


FIGURE 14.—*Pilocaulis marquezii*: a, lectotype of *Spongia marquezii* Duchassaing and Michelotti (MT Por 86); b, c, micrograph and diagram, respectively, of skeleton (USNM 31040); d, spicules (strongyloxeas, styloid; from lectotype MT Por 86). [Scales: a, 20 mm; b, c, 200 μ m; d, 100 μ m.]

***Dragmaxia undata*, new species**

FIGURE 15

Dragmaxia variabilis.—Wintermann-Kilian and Kilian, 1984:131 [listed only].
[Not *Spongosorites variabilis* Whitelegge, 1907.]
Dragmaxia sp.—Kobluk and van Soest, 1989:1215.

MATERIAL EXAMINED.—*Holotype*: Curaçao: ZMA Por 10030 (Buoy 4, 20–25 m, coll. R.W.M. van Soest, Jan 1981).
Paratype: USNM 39451 (same data as holotype). *Non-types*: Colombia: ZMA Por 10366 (Santa Marta area, Ojo de Aguja, 23 m, coll. M. Rozemeijer and W. Dulfer, Jul–Dec

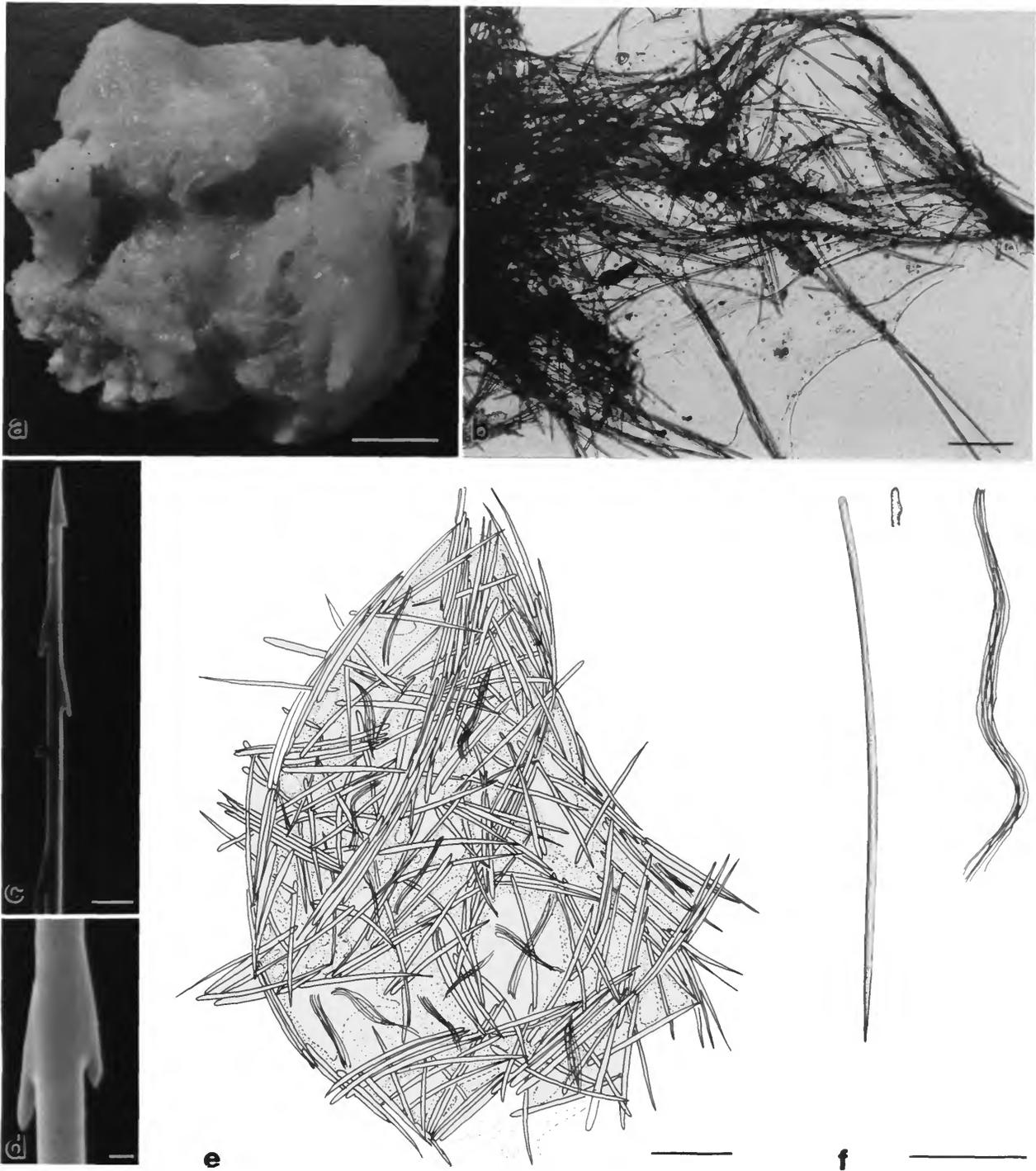


FIGURE 15.—*Dragmaxia undata*, new species: *a*, holotype ZMA Por 10030 (photo, L.A. van der Laaw); *b*, light micrograph (USNM 39451) of the skeleton; *c,d*, scanning electron micrographs of the spiny raphids; *e*, diagram (USNM 39451) of the skeleton; *f*, spicules (style and styloid modification, sinuous trichodragama; USNM 39451). [Scales: *a*, 2 mm; *b*, 200 μ m; *c*, 1 μ m; *d*, 0.2 μ m; *e*, 200 μ m; *f*, 100 μ m.]

1986). Curaçao: ZMA Por 10367 (Buoy 2, 25 m, coll. R.W.M. van Soest, 2 Jan 1981).

SHAPE (Figure 15a).—Massively to thinly encrusting, 1–10 mm thick, with irregular thin projections, sometimes dichotomously branched, up to 2 cm long, 0.5–3 mm in diameter.

SURFACE.—Hispid, irregular, covered by an organic ectosome.

CONSISTENCY.—Fragile.

COLOR.—Bright red when alive. Whitish in alcohol.

SKELETON (Figure 15b,e).—Plumose bundles of styles, longer of which project beyond surface; projections with a semblance of axially arranged spicules; individual spicules curve outward to surface. Trichodragmata abundantly strewn among megascleres.

SPICULES (Figure 15c,d,f).—Styles, often with tylote swelling, in a large size range, 420–1050 μm long (721.12 ± 130.5) by 4–21 (9.6 ± 3.5) μm wide, but not readily divisible into categories; microscleres, characteristic, long, wavy trichodragmata, 100–220 μm long, made of raphids ornamented by fine spines that align away from the terminal points.

ETYMOLOGY.—The name refers to the wavy form of the trichodragmata.

DISTRIBUTION AND HABITAT.—Curaçao, Bonaire, and Colombia, in cryptic reef habitats encrusting coral rocks.

REMARKS.—The generic assignment is considered reliable even though the growth form and skeletal architecture are not the same as in the type species. The absence of reticulation, the condensed spicule bundles or “funes” (Hallman’s terminology), the long flexuous trichodragmata, and the often tylote swelling of the styles are all in agreement with *D. variabilis*. Because of some of these features, *Dragmaxia* is not a typical Axinellidae and perhaps is more closely related to *Acanthella* and *Dictyonella*. The possible synonymy of *Dragmaxia* and *Stylissa* will be considered in a forthcoming revision of Axinellid genera.

Phakellia Bowerbank, 1862

Phakellia Bowerbank, 1862:1108 [type species: *Spongia ventilabra* (Linnaeus, 1767:1296) by original designation; holotype missing at present].—Gray, 1867:516.—Ridley and Dendy, 1886:478; 1887:169.—Thiele, 1898:51.—Topsent, 1904:137.—Dendy, 1905:190; 1922:116.—Vosmaer, 1912:310.—de Laubenfels, 1936:130.—Bergquist, 1970:17.—Lévi, 1973:605.—Hooper and Lévi, 1993:1413 [with additional synonyms].

DIAGNOSIS (emended).—Thin-plated, fan-shaped Axinellidae; fans strengthened by presence of multiple axes in the form of thick spicule tracts visible as “veins” or stout lines. Skeletal architecture consists of reticulation of primary tracts of sinuous strongyles or strongyloxeas and secondary tracts of straight styles.

REMARKS.—Hooper and Lévi (1993) employed an unusually broad definition of *Phakellia*, which overlapped what traditionally has been considered *Acanthella* (see below). This

study, which is based on an examination of several species of *Phakellia* and *Acanthella*, indicates that the two genera can be separated on the basis of overall shape and skeletal form. Members of *Phakellia* are flabelliform and have an axial and extra-axial skeleton and a reticulate peripheral skeleton. Members of *Acanthella* have an irregular ramose-bushy shape, lack an axial and extra-axial skeleton, and have a dendritic peripheral skeleton.

Phakellia folium Schmidt, 1870

FIGURE 16; TABLE 13

Phakellia folium Schmidt, 1870:62 [BMNH 1870.5.3.77, according to Dequeyroux-Faúndez and Stone (1992:55)].—van Soest and Stentoft, 1988:103.—Alvarez and Crisp, 1994:119 [cited only].—[not Pearse and Williams, 1951:136; Wells and Wells in Wells et al., 1960:223 = *Axinella waltonsmithi* (de Laubenfels, 1953)].

Phakellia ventilabrum.—Schmidt, 1870:61 [USNM 982 and BMNH 1870.5.3.76, according to Dequeyroux-Faúndez and Stone (1992:55)]. [Not *Spongia ventilabra* Linnaeus, 1767:1296; *Halichondria ventilabrum*.—Johnston, 1842:107; *Phakellia ventilabrum* sensu Bowerbank, 1864:186; Ridley and Dendy, 1887:170 = *Spongia strigosa* Pallas, 1766 (fide Vosmaer 1912:311; Bergquist, 1970:18).]

(?)*Phakellia* sp.—Schmidt, 1880:81.

MATERIAL EXAMINED.—*Nontypes*: Barbados: ZMA Por 5414 (off Paynes Bay, 162 m, 22 Jun 1978). Grenada: USNM 982 (Str. Blake, 166 m).

SHAPE (Figure 16a).—Fan- or funnel-shaped thin plate on short peduncle with basal disc.

SURFACE.—Smooth to slightly hispid.

CONSISTENCY.—Firm or fragile.

COLOR.—Whitish grey when alive. Beige in alcohol.

SKELETON (Figure 16b,c).—Regular isodictyal reticulation of primary lines of sinuous strongyles, 100–150 μm thick, directed outward from stalk, connected by secondary lines of sinuous strongyles, and/or styles, 50–100 μm thick, with brushes of short styles “echinating” tracts at contact points.

SPICULES (Figure 16d, Table 13).—Sinuous strongyles and two sizes categories of styles.

DISTRIBUTION AND HABITAT.—Florida, Barbados, Grenada, St. Vincent, between 162 and 600 m (van Soest and Stentoft, 1988).

REMARKS.—The description of this species is based on the only two specimens available. One of these, USNM 982, is a small, thin, fan-shaped plate, 4 cm wide and 6 cm long, on a short peduncle, identified by O. Schmidt as *Phakellia ventilabrum*. The other specimen, also described by van Soest and Stentoft (1988), is funnel-shaped with a short stalk and basal disc. Schmidt (1870) referred to two other funnel-shaped specimens from Barbados and St. Vincent as *P. ventilabrum* but did not describe them.

The specimen of *Phakellia folium* described by Wells and Wells in Wells et al. (1960) and cited by Pearse and Williams (1951) is *Axinella waltonsmithi* (see above).

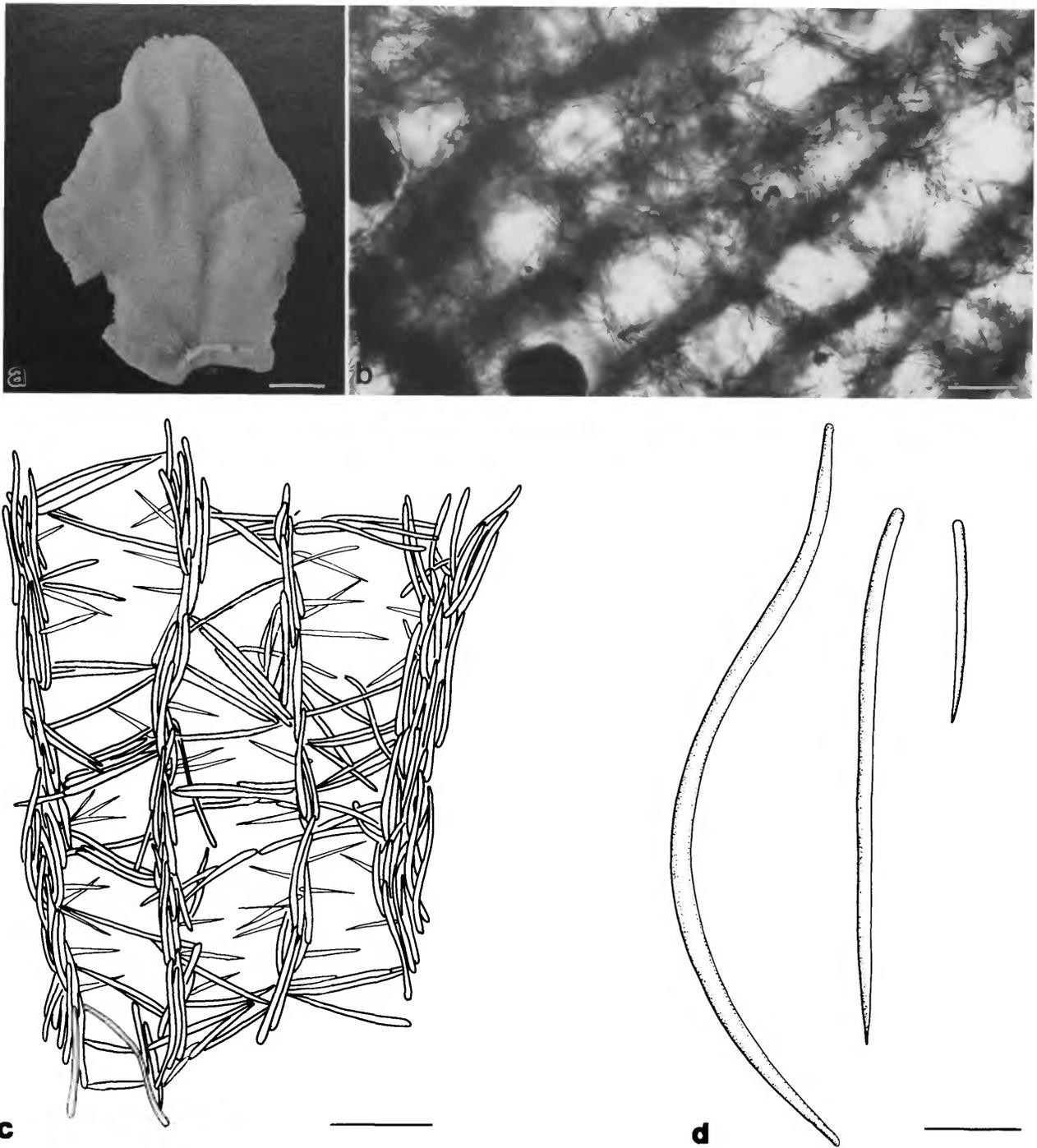


FIGURE 16.—*Phakellia folium*: a, specimen USNM 982, from Grenada; b,c, micrograph and diagram, respectively, of the skeleton (USNM 982); d, spicules (sinuous strongyle, two categories of styles; USNM 982). [Scales: a, 10 mm; b,c, 200 μ m; d, 100 μ m.]

TABLE 13.—Spicule dimensions for *Phakellia folium*. Measurements (in μm) are ranges of 25 spicules (or the number indicated in brackets), with means \pm standard deviation in parentheses.

Specimens	Styles I	Styles II	Strongyles
Florida			
BMNH 70.5.3.76			
length	540–1230 (878.7 \pm 235.5)[15]	240–340 (286.3 \pm 37.0)[8]	260–920 (575.2 \pm 178.4)
width	12.5–22.5 (18.2 \pm 2.8)[15]	12.5–20 (13.8 \pm 2.7)[8]	7.5–27.5 (18.1 \pm 4.1)
BMNH 70.5.3.77			
length	660–1900 (1094.4 \pm 359.2)[18]	350–500 (451.5 \pm 35.7)[14]	490–750 (627.6 \pm 61.0)
width	25–45 (32.8 \pm 5.5)[18]	12.5–32.5 (20.2 \pm 6.4)[14]	20–32.5 (26.5 \pm 3.5)
Barbados			
ZMA Por 5414			
length	320–550 (446.0 \pm 57.4)	90–170 (130.0 \pm 19.6)	300–630 (473.6 \pm 83.3)
width	7.5–12.5 (8.4 \pm 1.4)	2.5–5 (3.4 \pm 1.2)	10–17.5 (14.0 \pm 2.5)
Grenada			
USNM 982			
length	330–780 (491.6 \pm 100.4)	150–200 (174.4 \pm 14.2)	390–910 (589.2 \pm 138.0)
width	10–17.5 (12.8 \pm 1.8)	7.5–12.5 (8.9 \pm 1.5)	10–20 (14.1 \pm 3.1)

***Phakellia connexiva* Ridley and Dendy, 1887**

FIGURE 17; TABLE 14

Phakellia ventilabrum var. *connexiva* Ridley and Dendy, 1887:170 [holotype, BMNH 87.5.2.2]. [Not *Spongia ventilabra* Linnaeus, 1767:1296; *Halichondria ventilabrum*.—Johnston, 1842:107; *Phakellia ventilabrum* Bowerbank, 1864:186 = *Spongia strigosa* Pallas, 1766 (fide Vosmaer, 1912:311; Bergquist, 1970:18).]

Phakellia connexiva.—Alvarez and Crisp, 1994:119 [cited only].

MATERIAL EXAMINED.—*Nontypes*: Virgin Islands: USNM 22375 (18°45'40"N, 64°48'W, 540 m, coll. Johnston-Smithsonian Deep-Sea expedition, 4 Mar 1933).

SHAPE (Figure 17*a,b*).—Fan-shaped, quite concave, up to 20 cm long and 10 cm wide with 1 cm diameter stalk.

SURFACE.—Hispid, with longitudinal, stout, vein-like lines, 1–3 mm in diameter, anastomosed or ramified; with membranous skin pierced by small pores, 20–40 μm diameter, on one side of fan, and bigger pores, 320–460 μm diameter, on opposite surface.

COLOR.—Unknown when alive. Brownish yellow or whitish in alcohol.

CONSISTENCY.—Hard to brittle.

SKELETON (Figure 17*c,d*).—Primary lines of sinuous-vermiculate strongyles and strongyloxeas, echinated by styles, forming stout lines like “veins” (see “Surface”).

SPICULES (Figure 17*e*, Table 14).—Sinuous-vermicular strongyles and strongyloxeas, and styles.

DISTRIBUTION AND HABITAT.—Brazil, Virgin Islands. Occurs below depths of 200 m.

REMARKS.—This species differs from the type species of *Phakellia ventilabrum*, described initially from the British seas (Johnston, 1842; Bowerbank, 1862, 1864) and recorded from other cold waters of the Northern seas and Falkland Islands. It has a different shape, is larger and more robust, and has stronger venation than the type species. Also, the spicules of

TABLE 14.—Spicule dimensions for *Phakellia connexiva*. Measurements (in μm) are ranges of 25 spicules, with means \pm standard deviation in parentheses.

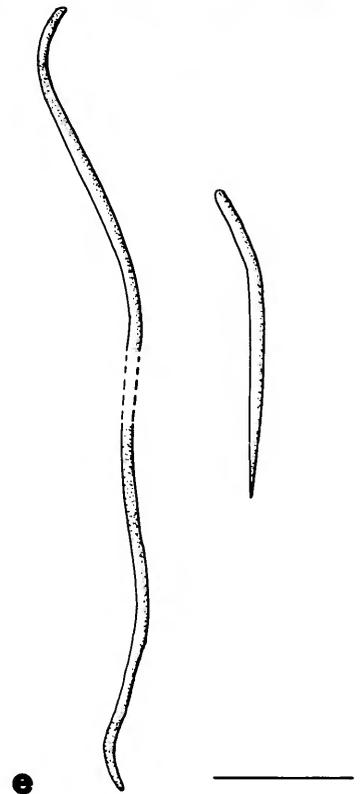
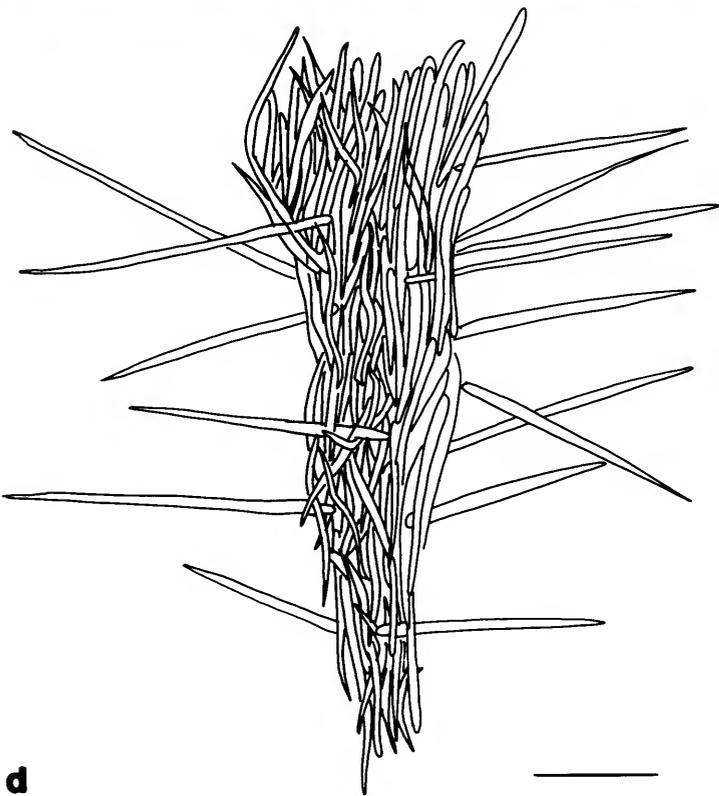
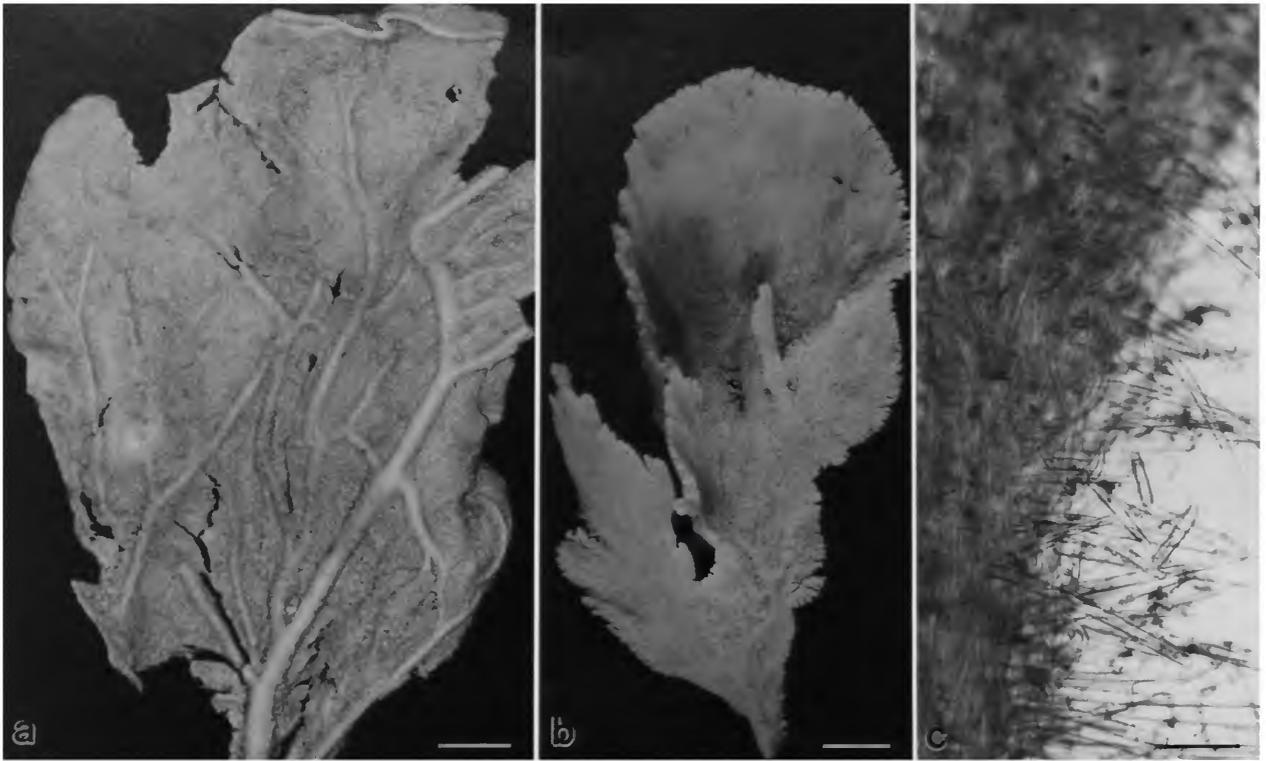
Specimens	Styles	Vermicular strongyles to strongyloxeas
U.S. Virgin Islands		
USNM 22375		
length	330–890 (500 \pm 120.8)	280–1175 (743.8 \pm 213.6)
width	22.5–42.5 (29.5 \pm 4.6)	17.5–47.5 (31.2 \pm 7.6)
Brazil		
BMNH 87.5.2.2		
length	232–1000 (490.9 \pm 139.0)	470–2050 (1308.9 \pm 472.5)
width	7.5–30 (19.8 \pm 5.2)	15–35 (25.3 \pm 5.4)

European specimens are much thinner, not exceeding 10–12 μm thick. Schmidt's (1870, 1880) records of *Phakellia ventilabrum* for Florida, Barbados, and St. Vincent correspond to *P. folium*.

REMARKS ON THE SPECIES OF *Phakellia*

The two species of *Phakellia* described herein are quite distinctive. They differ in surface, spicule size, and skeleton, which is more reticulated in *P. folium* than in *P. connexiva*. There is no clear difference between the axial and extra-axial skeleton, although the mass of interwoven spicules, restricted to the stalk, could be interpreted as the axial skeleton, and the system of spicule tracts that strengthen the fan could be the extra-axial skeleton.

FIGURE 17 (opposite).—*Phakellia connexiva*: *a*, holotype, BMNH 87.5.2.2; *b*, specimen USNM 22375 from the Virgin Islands; *c,d*, micrograph and diagram, respectively, of the skeleton (USNM 22375); *e*, spicules (sinuous strongyle, style; BMNH 87.5.2.2). [Scales: *a,b*, 20 mm; *c–e*, 200 μm .]



No other valid species of *Phakellia* has been recorded for the area. The material described as *Phakellia lobata* by Wilson (1902:399) (USNM 7684) belongs to the family Suberitidae. *Phakellia tenax* Schmidt, 1870, was redescribed and transferred to the genus *Endectyon* by Topsent (1920).

Auletta Schmidt, 1870

Auletta Schmidt 1870:45 [type species: *Auletta sycinularia* Schmidt, 1870, by monotypy (BMNH 1939.2.10.36, from type locality (Florida; Figure 18a))].—Topsent, 1904:137, 143.—Dendy, 1905:194; 1916:119; 1922:121.—Burton, 1931:142.—de Laubenfels, 1936:129; 1954:170.—Lévi and Vacelet, 1958:233.—Lévi, 1973:605.

DIAGNOSIS (emended).—Axinellidae with tube-shaped habit or with a cluster of tubes; inner tube wall reinforced by masses of sinuous strongyles (comparable to the axial condensation of *Axinella* and *Phakellia*); peripheral walls consist of extra-axial reticulation of styles.

Auletta sycinularia Schmidt, 1870

FIGURE 18; TABLE 15

Auletta sycinularia Schmidt, 1870:45.—van Soest and Stentoft, 1988:105 [with additional synonyms].—Alvarez and Crisp, 1994: 119 [cited only].

MATERIAL EXAMINED.—*Nontypes*: Florida: BMNH 1939.2.10.36 (type locality, O. Schmidt identified). Gulf of Mexico: USNM 34289 (29), USNM 34290 (31), USNM 34335 (32), USNM 42023 (35), USNM 42129 (23), USNM 42134 (33), USNM 42135 (34).

SHAPE (Figure 18a,b).—Clusters of one to several tubes on thin stalk approximately 2–3 cm long, with apical oscules up to 1 cm in diameter. Tubes sometimes bifurcate or fused in lower parts.

SURFACE.—Smooth; microhispid to pilose in some specimens.

COLOR.—Unknown when alive. Beige in alcohol; some specimens with purple tinges.

CONSISTENCY.—Fragile and soft.

SKELETON (Figure 18c,d).—Axis of strongyles echinated occasionally by styles at peduncle. Walls of tubes consist of

thick, longitudinal strongyle tracts, 50–180 μm thick, echinated at right angles by plumose tracts of styles that may be connected by single or secondary lines of spicules.

SPICULES (Figure 18e, Table 15).—Sinuous strongyles and strongyloxeas, and styles of two or three size categories.

DISTRIBUTION AND HABITAT.—Gulf of Mexico, Florida, Barbados, Azores. Specimens from Gulf of Mexico occur at depths of 70–159 m; elsewhere, down to 200 m.

REMARKS.—The specimen from Barbados described by van Soest and Stentoft (1988) differs in habit from the specimens studied herein and from the specimen described by Schmidt (1870) and Topsent (1904). The tubes of the specimen from Barbados are fused, resulting in a flabelliform shape. This could represent a different growth shape, as van Soest and Stentoft (1988) have suggested. The habit of *Auletta sessilis*, described by Topsent (1904) and considered by van Soest and Stentoft (1988) to be synonymous with the present species, is intermediate in shape between the specimens studied herein and the specimen from Barbados.

Auletta tuberosa, new species

FIGURE 19; TABLE 16

Auletta sp.—Alvarez and Crisp, 1994:119.

MATERIAL EXAMINED.—*Holotype*: Gulf of Mexico: USNM 34281 (21). *Paratype*: Gulf of Mexico: USNM 34283 (26). *Nontypes*: Gulf of Mexico: USNM 34333 (14), USNM 42281 (26). Two ZMA specimens from the same area.

SHAPE (Figure 19a).—Clusters of tubes with short and narrow peduncle, anastomosed and generally crooked with apical or lateral oscules; oscules up to 3 cm in diameter, covered by membranes.

SURFACE.—Smooth with prominent tubercles in most cases.

CONSISTENCY.—Resilient.

COLOR.—Unknown when alive. Beige in alcohol.

SKELETON (Figure 19b,c).—Plumose tracts, 50–100 μm thick, connected by single or secondary lines of spicules or forming a reticulum of rounded meshes; ending in brushes of spicules.

TABLE 15.—Spicule dimensions for *Auletta sycinularia*. Measurements (in μm) are ranges of 25 spicules (or the number indicated in brackets), with means \pm standard deviation in parentheses.

Specimens	Styles I	Styles II	Styles III	Strongyles
Florida BMNH 1939.2.10.36	not detected	450–950 (648.2 \pm 154.0)[11] 10–20 (14.8 \pm 2.9)[10]	not detected	300–660 (429.5 \pm 81.0)[20] 13–20 (17.4 \pm 2.4)[18]
Gulf of Mexico USNM 42023	740–1450 (1095 \pm 206.4) 5–17.5 (11.9 \pm 3.5)	360–690 (492.0 \pm 84.8) 7.5–15 (11.0 \pm 2.3)	170–260 (197.2 \pm 20.5) 5–10 (7.9 \pm 1.4)	350–770 (550.4 \pm 96.5) 7.5–25 (17.5 \pm 4.6)

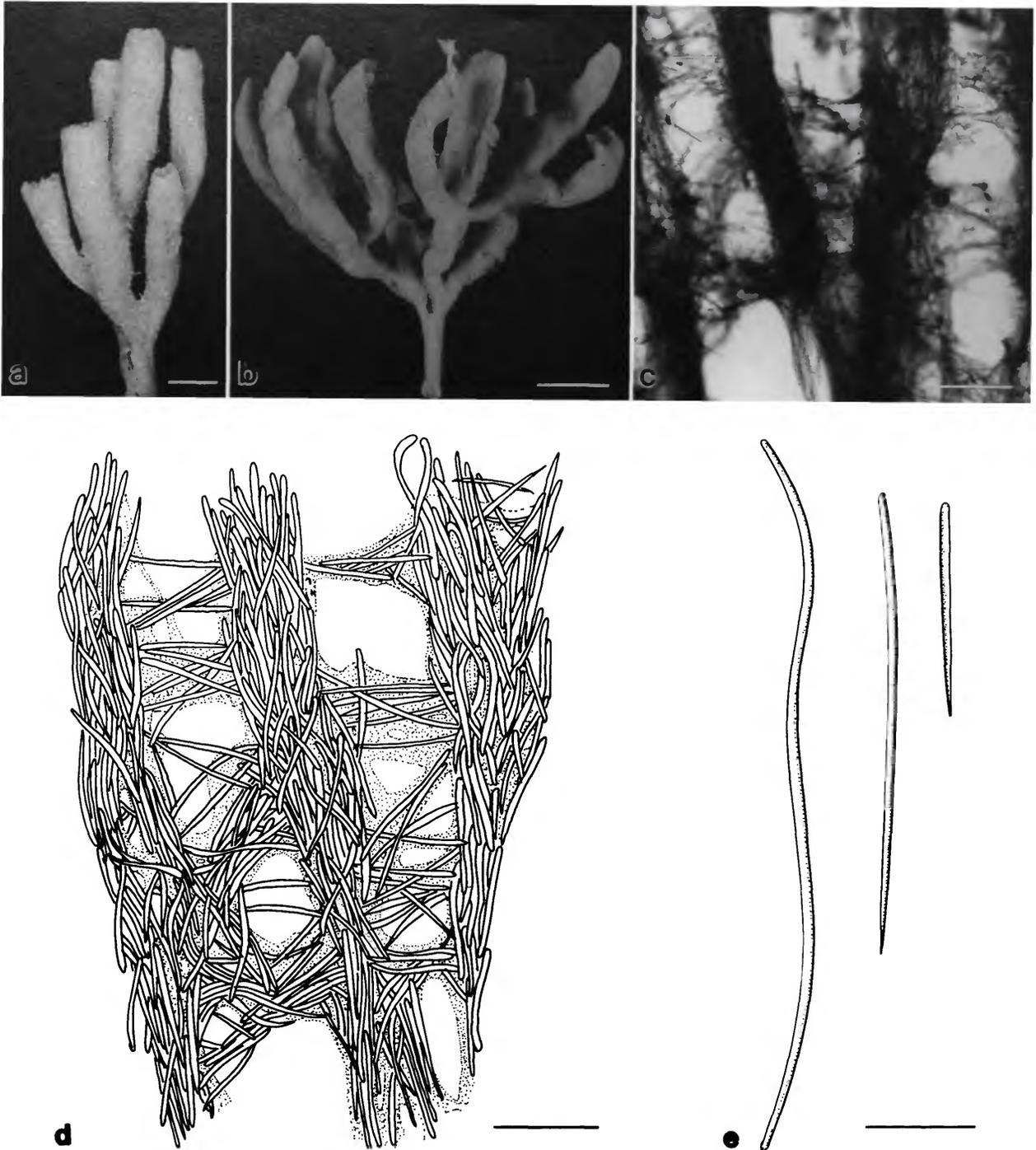


FIGURE 18.—*Auleta sycinularia*: *a*, specimen BMNH 1939.2.10.36 from the type locality (Florida) identified by O. Schmidt; *b*, specimen USNM 34335 from the Gulf of Mexico; *c,d*, micrograph and diagram, respectively, of the skeleton (USNM 42129); *e*, spicules (sinuous strongyle, two size categories of styles; USNM 42129). [Scales: *a*, 5 mm; *b*, 20 mm; *c,d*, 200 μ m; *e*, 100 μ m.]

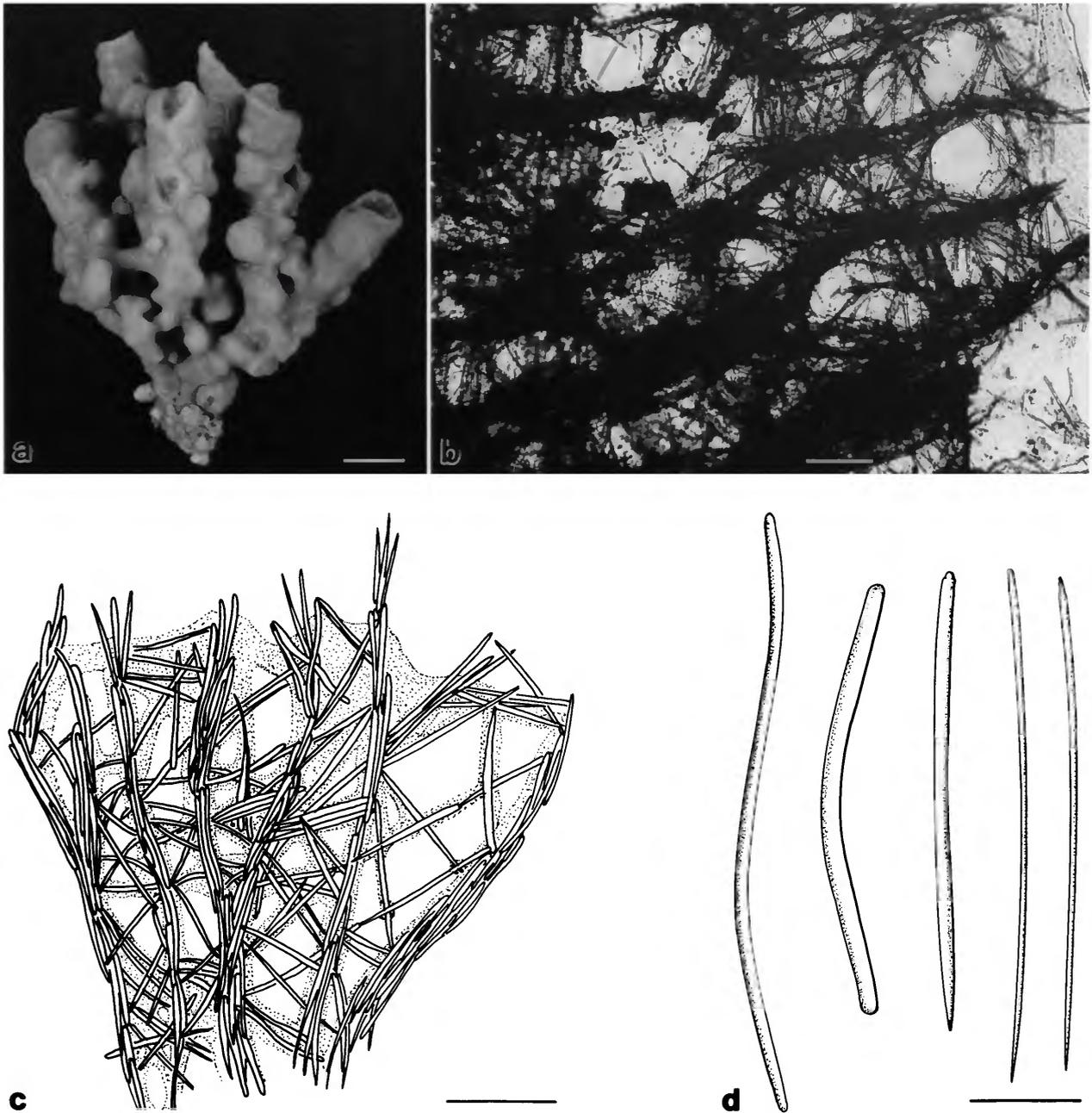


FIGURE 19.—*Auletta tuberosa*, new species: *a*, holotype, USNM 34281; *b,c*, micrograph and diagram, respectively, of the skeleton; *d*, spicules (two sinuous strongyles, one style, two oxeas). [Scales: *a*, 20 mm; *b,c*, 200 µm; *d*, 100 µm.]

SPICULES (Figure 19*d*, Table 16).—Oxeas, oxeotes, or stronglyxeas, sinuous to wavy; strongyles and styles.

ETYMOLOGY.—From the Latin *tuberosus*, meaning full of lumps or protuberances; referring to the surface.

REMARKS.—The new species is typical of the genus in terms of habit and spiculation. The architecture is atypical because it lacks a clear axial component. The new species is the second record of *Auletta* in the central West Atlantic region. It differs

TABLE 16.—Spicule dimensions for *Auleta tuberosa*, new species. Measurements (in μm) are ranges of 25 spicules, with means \pm standard deviation in parentheses.

Specimens	Styles	Oxeas and modifications	Strongyles
Gulf of Mexico USNM 34281			
length	270–430 (381.2 \pm 34.3)	310–470 (399.6 \pm 41.3)	320–580 (438.4 \pm 55.0)
width	7.5–12.5 (9.1 \pm 1.4)	2.5–10 (7.0 \pm 2.2)	7.5–15 (11.3 \pm 2.5)
USNM 42281			
length	280–470 (358.0 \pm 44.2)	340–530 (430.0 \pm 49.7)	350–640 (462.0 \pm 77.8)
width	2.5–10 (7.0 \pm 2.2)	5–10 (8.2 \pm 1.4)	7.5–15 (9.9 \pm 2.6)

from *A. sycinularia* in the shape and surface of its tubes; the presence of oxeotes, oxeas, and strongyloxeas; and its more reticulate skeleton.

REMARKS ON THE SPECIES OF *Auleta*

The species of *Auleta* described above are typical of the genus in terms of external morphology and spiculation. In both species, the axial component of the skeleton is not clearly defined, and the skeletal organization resembles that of *Phakellia*. The two genera also have similar profiles of free amino acids (Bergquist and Hartman, 1969), which might be additional evidence of a close relationship.

Acanthella Schmidt, 1862

Acanthella Schmidt, 1862:64 [type species: *Acanthella acuta* Schmidt, 1862, by subsequent designation (Vosmaer, 1912:312); BMNH 1867.7.26.66, dry, from type locality].—Gray, 1867:512.—Ridley and Dendy, 1886:479; 1887:176.—Topsent, 1896:127; 1904:137.—Thiele, 1898:53.—Dendy, 1905:193; 1922:119.—Vosmaer, 1912:312, 319; 1932–1935:760.—de Laubenfels, 1936:138.—Lévi, 1973:605.—van Soest et al., 1990:20.—Hooper and Lévi, 1993:1413.

DIAGNOSIS.—Axinellidae(?) with thick dendritic axes of sinuous strongyles echinated by styles; generally bushy, ramose, or lobate with hard or cartilaginous consistency.

REMARKS.—Hooper and Lévi (1993) followed a considerably different definition of *Acanthella* based on the alleged absence of an extra-axial skeleton in this genus. This study

emphasises the dendritic nature of the skeleton, a central axial column that sends out dendritically branching and thinning spicule tracts toward the periphery. In thinly branching forms, these peripheral tracts may be reduced to single spicules.

Acanthella mastophora (Schmidt, 1870), new combination

FIGURE 20; TABLE 17

Axinella mastophora Schmidt, 1870:61 [holotype, MCZ 92(8073)].
Bubaris rugosa.—van Soest and Stentoft, 1988:109.

MATERIAL EXAMINED.—*Nontypes*: North Carolina: USNM 33343 (33°48'18"N, 76°34'06"W, 100 m, coll. DU for MMS, 14 May 1981). Gulf of Mexico: USNM 33924 (28), USNM 41578 (12), USNM 42174 (30), USNM 42175 (32), USNM 42176 (35), USNM 42177 (35). Barbados: ZMA Por 5361–63, 5407 (153–212 m).

SHAPE (Figure 20*a, b*).—Bushy, with short or long peduncle and sometimes with branching processes oriented approximately radially from base; or massive, with small lobes.

SURFACE.—Tuberculate with small and rounded swellings; microhispid. Grooves covered by parchment-like membrane.

CONSISTENCY.—Hard, cartilaginous.

COLOR.—Pale ocher yellow to honey yellow when alive. Beige, grey, or pink in alcohol.

SKELETON (Figure 20*c, d*).—Dendritic, thick tracts or axes (400–600 μm thick) of crooked strongyloxeas and strongyles, echinated by styles.

TABLE 17.—Spicule dimensions for *Acanthella mastophora*. Measurements (in μm) are ranges of 25 spicules (or the number indicated in brackets), with means \pm standard deviation in parentheses.

Specimens	Styles I	Styles II	Strongyles to Strongyloxeas
North Carolina USNM 33343			
length	570–870 (735.6 \pm 95.5)	330–540 (452.0 \pm 63.4)	470–870 (686.4 \pm 100.6)
width	10–22.5 (14.8 \pm 3.3)	7.5–20 (15.7 \pm 2.8)	7.5–17.5 (12.2 \pm 2.8)
Gulf of Mexico USNM 42175			
length	620–1150 (810.4 \pm 147.9)	300–490 (389.5 \pm 54.6)[22]	200–910 (628.0 \pm 164.6)
width	15–37.5 (27.6 \pm 5.5)	10–30 (22.0 \pm 4.0)[22]	15–35 (26.1 \pm 6.2)

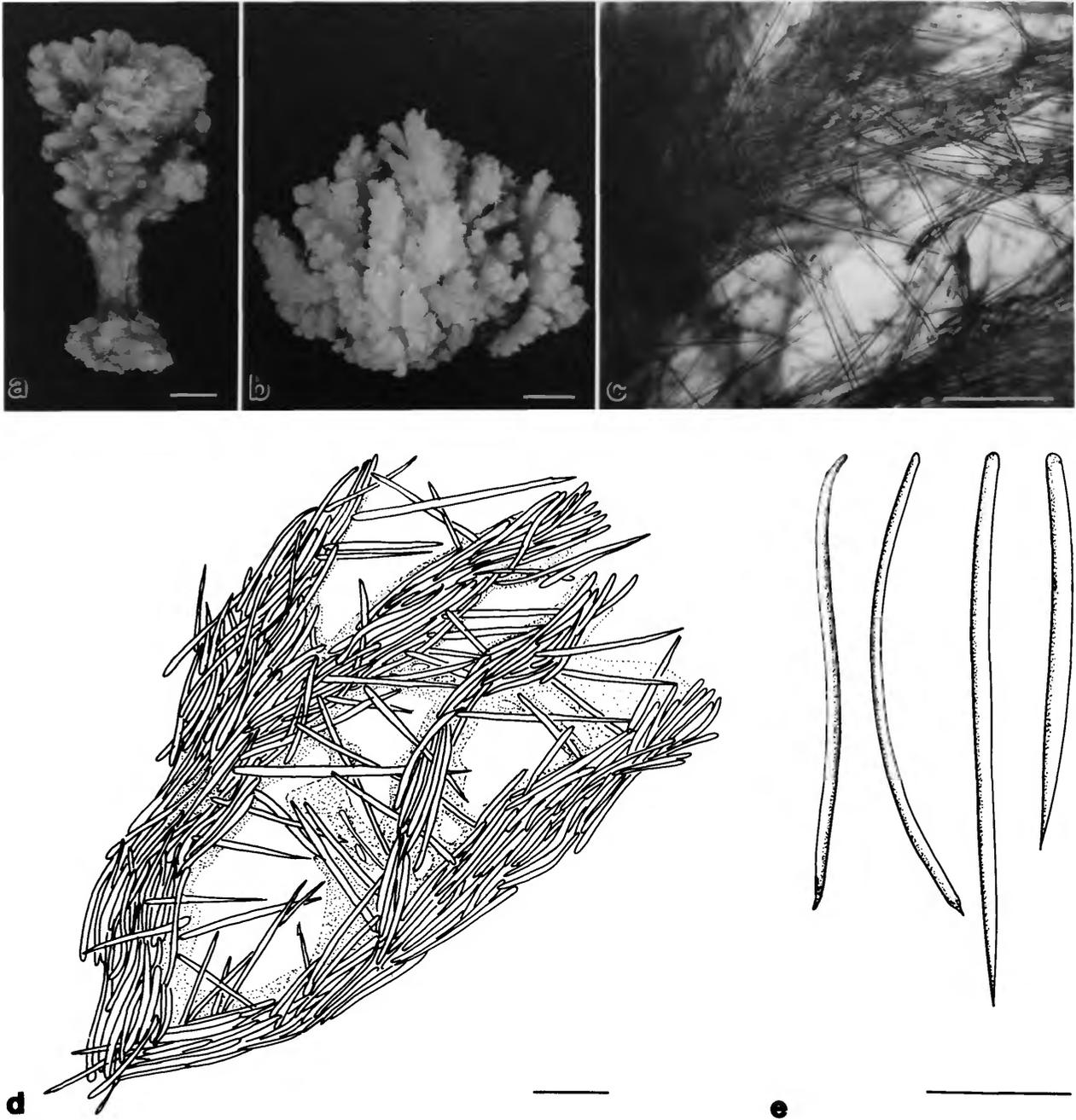


FIGURE 20.—*Acanthella mastophora*: a, specimen USNM 41587 from the Gulf of Mexico; b, specimen USNM 42177 from the Gulf of Mexico; c,d, micrograph and diagram, respectively, of the skeleton (USNM 42176); e, spicules (sinuous strongyloxea, two sizes of styles; USNM 42177). [Scales: a,b, 10 mm; c-e, 200 μ m.]

SPICULES (Figure 20e, Table 17).—Strongyloxeas and strongyles generally sinuous and crooked; styles of two sizes, sometimes modified to subtylostyles; oxeas may be present.

DISTRIBUTION AND HABITAT.—North Carolina, Florida, Gulf of Mexico, Barbados. On hard bottoms at depth of 77–534 m.

REMARKS.—The species was assigned to *Acanthella* because of its architecture and spiculation. The material studied is conspecific with *Axinella mastophora* Schmidt, 1870, and *Bubaris rugosa* sensu van Soest and Stentoft (1988).

***Acanthella vaceleti* van Soest and Stentoft, 1988**

FIGURE 21

Acanthella vaceleti van Soest and Stentoft, 1988:107 [holotype, ZMA Por 5418].—Alvarez and Crisp, 1994:119 [cited only].

MATERIAL EXAMINED.—*Nontypes*: Gulf of Mexico: USNM 38652, USNM 42165 (28). Barbados: ZMA Por 5418 (off Paynes Bay, 108 m, 8 May 1979).

SHAPE (Figure 21a).—Small lobes or branches, tapering at one end, coalesced at base and anastomosing at some points. Oscules on top of branches or lobes.

SURFACE.—Smooth and shiny, thick skin-like ectosome marked with longitudinal grooves.

CONSISTENCY.—Quite compressible.

COLOR.—Yellow orange when alive. Tan in alcohol.

SKELETON (Figure 21b,c).—Dendritic axes of strongyles echinated with styles, sometimes in bundles; sometimes halichondroid, confused.

SPICULES (Figure 21d).—Sinuous strongyles, 410–980 (643.6 ± 125.4) μm long, 5–12.5 (9.6 ± 1.9) μm wide; styles 420–1475 (743.8 ± 242.8) μm long, 10–17.5 (11.3 ± 1.9) μm wide.

DISTRIBUTION AND HABITAT.—Barbados and Gulf of Mexico. On hard bottoms at depths of 76–108 m.

REMARKS.—Our material from the Gulf of Mexico agrees well with the type material from Barbados; however, the Gulf

of Mexico material differs from the Barbados material in having less robust styles and in lacking a wide axial lumen. Some minor differences in the spicule dimensions also were found.

***Acanthella cubensis* (Alcolado, 1984), new combination**

FIGURE 22; TABLE 18

Bubaris cubensis Alcolado, 1984:10 [holotype, USNM 39227].

MATERIAL EXAMINED.—*Nontypes*: North Carolina: USNM 33340 (33°48'12"N, 76°34'24"W, 116 m, coll. DU for MMS); ZMA specimens from the same area. Gulf of Mexico: USNM 34332 (9), USNM 34340 (27), USNM 42139 (11), USNM 42142 (13), USNM 42148 (25), USNM 42164 (28), USNM 42171 (30). Colombia: ZMA Por 10370 (Santa Marta area, Bahia Granate, 15 m, coll. R.W.M. van Soest, 14 Nov 1986). Venezuela: FCLR 217 and 218 (Los Roques, 46 m, coll. M.C. Díaz and B. Alvarez). Tobago: USNM 42806 (TOB-066, Charlotteville Bay, 29 m, coll. B. Alvarez).

SHAPE (Figure 22a,b).—Massive, with or without lobes. Oscules, when visible, 4–7 mm.

SURFACE.—Conulose, reticulate or corrugated, with parchment-like membrane stretched on ridges or conule tips. Subdermal canals, up to 2 cm wide.

CONSISTENCY.—Soft and fragile.

COLOR.—Orange red when alive. Beige, yellow in alcohol.

SKELETON (Figure 22c,d).—Plumose spicule tracts, 100–300 μm thick, connected by sheets of spongin with spicules, and/or by thick spicule tracts forming a vague reticulation of rounded meshes. Skeleton quite halichondroid near surface.

SPICULES (Figure 22e, Table 18).—Sinuous strongyles and

TABLE 18.—Spicule dimensions for *Acanthella cubensis*. Measurements (in μm) are ranges of 25 spicules, with means ± standard deviation in parentheses.

Specimen	Styles	Strongyles
North Carolina USNM 33340		
length	520–1200 (816.2±184.6)	330–1175 (642.0±276.4)
width	10–15 (11.7±2.0)	7.5–17.5 (11.9±2.8)
Gulf of Mexico USNM 42164		
length	420–990 (656.0±156.7)	300–930 (575.2±193.3)
width	5–10 (8.0±1.6)	7.5–17.5 (12.3±3.1)
USNM 42171		
length	900–1300 (1031.0±102.8)	460–1400 (715.2±250.8)
width	12.5–25 (18.8±2.6)	17.5–32.5 (25.5±4.0)
Los Roques (Venezuela) FCLR 217		
length	630–1050 (830.6±110.9)	260–670 (436.8±113.9)
width	5–15 (9.7±2.0)	7.5–25 (11.5±3.6)
Tobago USNM 42806		
length	440–890 (699.2±116.0)	350–900 (568.0±153.4)
width	5–10 (8.0±1.9)	5–17.5 (12.1±3.0)

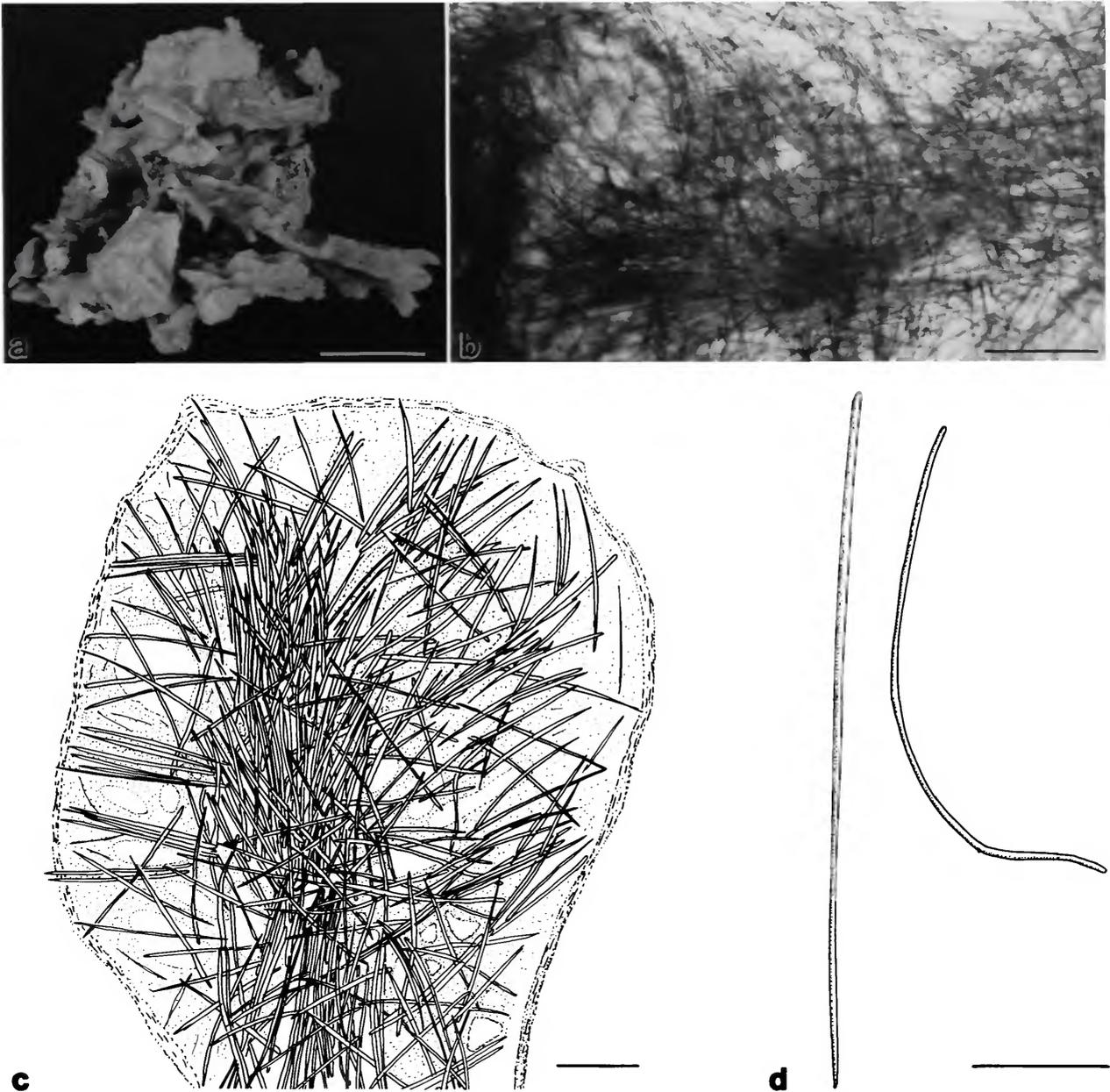


FIGURE 21.—*Acanthella vaceleti*: a, specimen USNM 38652; b,c, micrograph and diagram, respectively, of the skeleton (USNM 42165); d, spicules (style, sinuous strongyle; USNM 42165). [Scales: a, 20 mm; b–d, 200 μ m.]

styles, some bent at apex. Several specimens with foreign sigmas (70–100 μ m long).

DISTRIBUTION AND HABITAT.—Gulf of Mexico; Cuba; Tobago; Los Roques, Venezuela; Santa Marta, Colombia. Coral reefs and hard bottoms at depths of 15–137 m.

REMARKS.—The material examined is conspecific with the

specimen described by Alcolado (1984) as *Bubaris cubensis*. The new combination is proposed because *Bubaris* forms are typically encrusting. The species is assigned to *Acanthella* on the basis of the skeletal architecture and spiculation; however, the consistency is not typical of the genus, and the skeleton lacks a thick central column. The species also shares characters

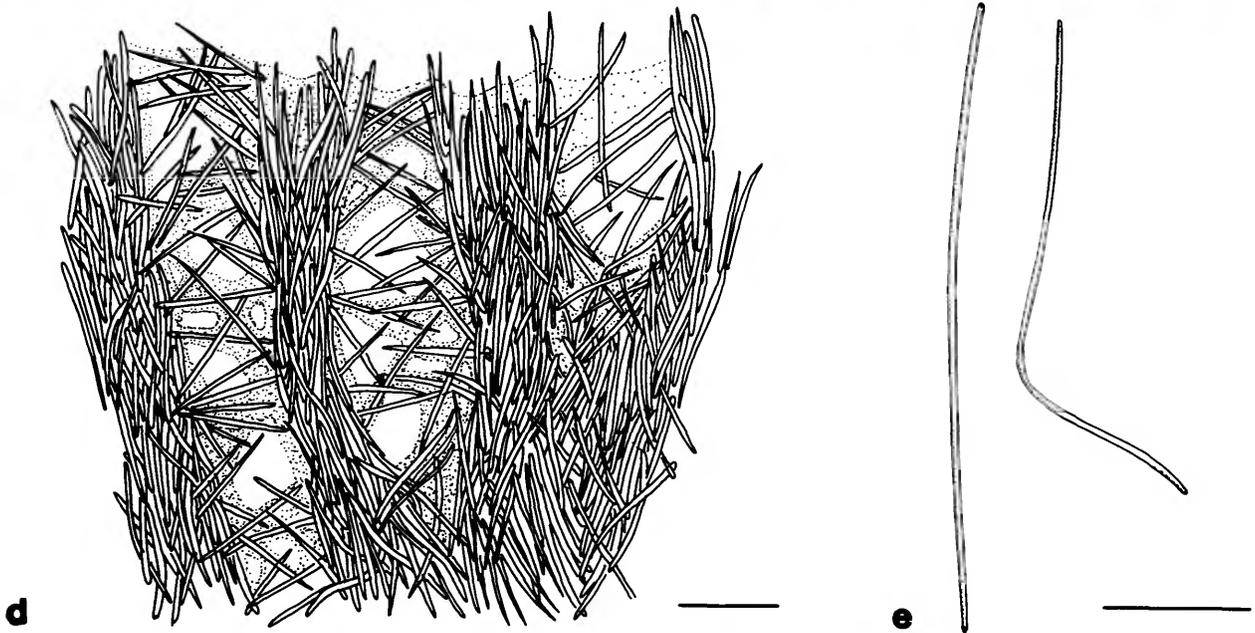
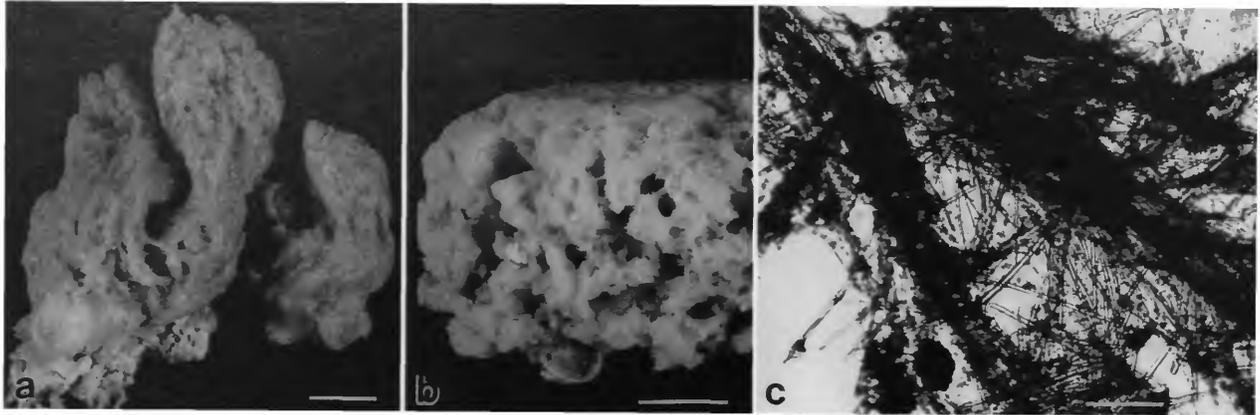


FIGURE 22.—*Acanthella cubensis*: *a*, specimen USNM 42148; *b*, internal structure as seen in part of specimen USNM 34332; *c, d*, micrograph (USNM 42148) and diagram (FCLR 217), respectively, of the skeleton; *e*, spicules (style, sinuous strongyle; USNM 42148). [Scales: *a*, 10 mm; *b*, 20 mm; *c–e*, 200 μ m.]

with *Dictyonella* Schmidt, 1868:10; for example, the consistency is soft and fragile, and the spiculation is not clearly divisible into thicker styles and sinuous strongyles but instead is a mixture of sinuous strongyles and styles.

***Acanthella flagelliformis* (van Soest and Stentoft, 1988),
new combination**

FIGURE 23

Bubaris flagelliformis van Soest and Stentoft, 1988:110 [holotype, ZMA Por 5366].

MATERIAL EXAMINED.—*Nontypes*: Barbados: ZMA Por 5366 (200 m), USNM 39462 (off Paynes Bay, 168 m, coll. N. Stentoft, 1978–1980).

SHAPE (Figure 23*a*).—Cone-shaped with long flagellar apex.

SURFACE.—Hispid.

COLOR.—Unknown when alive; grey white in dry condition.

SKELETON (Figure 23*b, c*).—Axis of sinuous megascleres echinated by styles.

SPICULES (Figure 23*d*).—Strongyles, occasionally oxea,

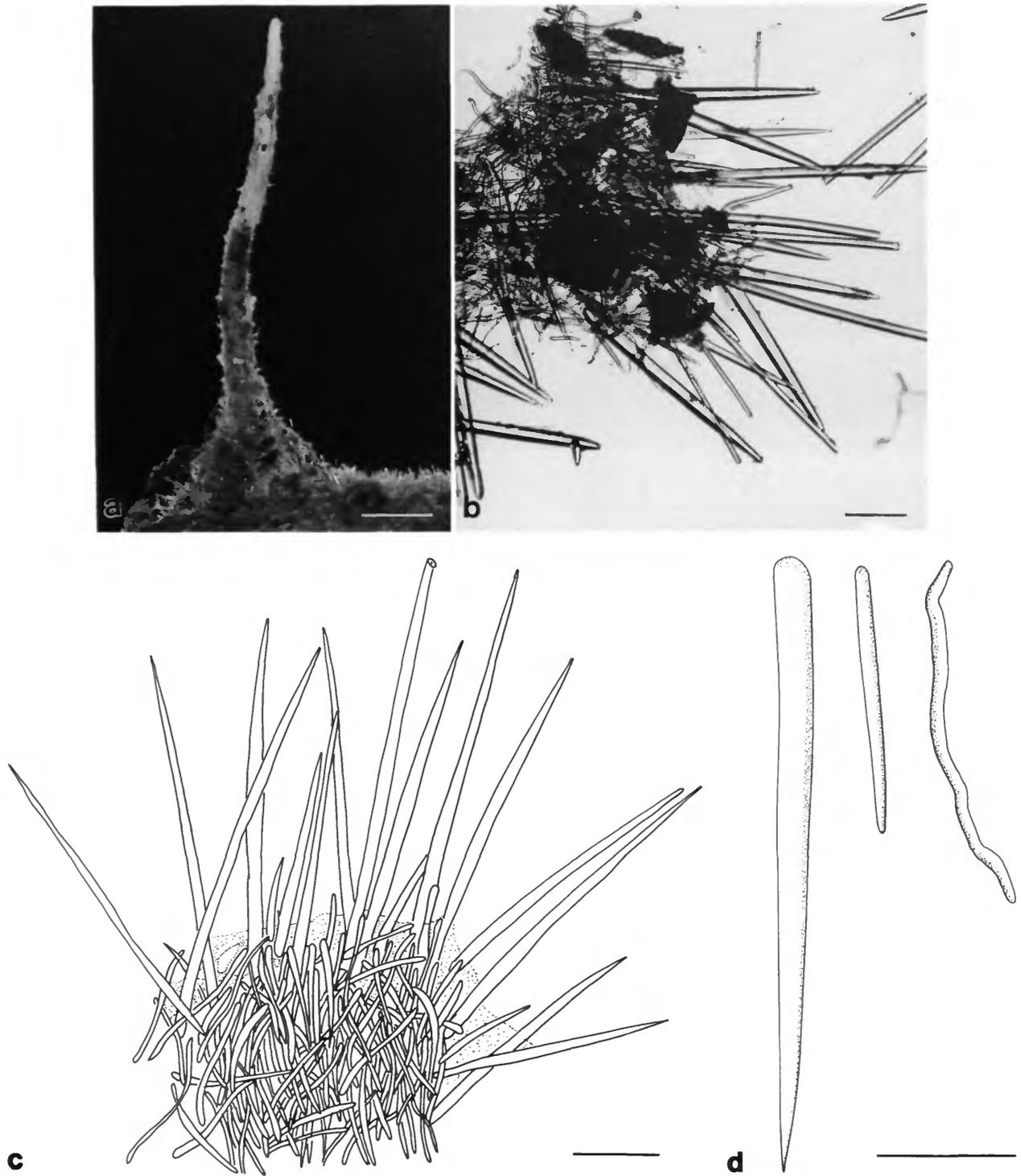


FIGURE 23.—*Acanthella flagelliformis*: *a*, specimen USNM 39462 (photo, K. Herbert); *b,c*, micrograph and diagram, respectively, of the skeleton; *d*, spicules (two size categories of styles, one sinuous strongyle). [Scales: *a*, 2 mm; *b-d*, 200 μ m.]

wavy to sinuous, 175–1400 (561 ± 242.2) μm long and 5–15 (10.4 ± 2.7) μm wide; styles, 510–1950 (828.6 ± 368.2) μm long and 12.5–52.5 (34.8 ± 10.5) μm wide; a smaller category of styles, 200–480 (368.4 ± 96.1) μm long and 12.5–32.5 (21.4 ± 5.7) μm wide. (Van Soest and Stentoft (1988) reported acanthose endings in some of the styles, but these spicules were not proper to the sponge.)

DISTRIBUTION AND HABITAT.—Known only from Barbados.

REMARKS.—This species is hesitatingly assigned to *Acanthella* because its hispid surface and small growth form is very different from the slippery smooth elaborate form of *A. acuta*, the type species of *Acanthella*.

REMARKS ON THE SPECIES OF *Acanthella*

Acanthella vacaleti is the only species of this genus previously identified in the study area. Now three additional species—*A. mastophora*, originally described under *Axinella*, and *A. cubensis* and *A. flagelliformis*, previously allocated to *Bubaris*—are assigned to *Acanthella*. This genus appears to have little connection with other members of the family Axinellidae; according to van Soest et al. (1990), it should be in the Dictyonellidae family, together with *Dictyonella* and *Scopalina*. The generic content of the Axinellidae and Dictyonellidae needs to be revised, however, before the position of *Acanthella* can be more accurately ascertained.

KEY TO THE CENTRAL WEST ATLANTIC SPECIES OF AXINELLIDAE

1. Skeleton formed by thick axes of sinuous megascleres echinated by styles. Spicules are strongyles and styles, both sinuous and straight 13
 Skeleton plumose or plumoreticulate. Spicules are oxeas or styles or modifications of these, never sinuous 2
- 2(1). Skeleton formed by plumose spicule tracts condensed or vaguely condensed in the axial parts of the sponge body, or differentiated in axial and extra-axial regions 3
 Skeleton formed by plumose spicule tracts without any axial condensation 10
- 3(2). Plumose spicule tracts bound by spongin. Surface with branching or “scopiform” processes 4
 Plumose spicule tracts enveloped but not bound with spongin. Surface smooth or conulose 5
- 4(3). Spicules are styles in two size categories *Ptilocaulis walpersi*
 Spicules are styles transitional to styloids and oxeas transitional to strongyloxeas; spicules not differentiated in size categories
 *Ptilocaulis marquezii*
- 5(3). Extra-axial skeleton not plumoreticulate, formed by dermal spicules, spicule bundles, plumose tracts, or combination of these 6
 Extra-axial skeleton plumoreticulate 7
- 6(5). Habit is thinly lamellate; surface velvety smooth; trichodragmata present (they may be hard to find) *Axinella shoemakeri*
 Habit is lamellate-flabelliform or bushy; surface corrugated; subtylostyles, styloids, and strongyloxeas present *Axinella corrugata*
- 7(3). Habit is branching-arborescent (tree-like) 8
 Habit is flabelliform-lamellate or coalescent small cups 9
- 8(7). Surface smooth and velvety, pierced by small pores (<1 mm). Spicules in one size category *Axinella polycapella*
 Surface finely to coarsely conulose or completely smooth. Styles in two size categories (180–300 μm and 370–690 μm long) . . . *Axinella pomponiae*
- 9(7). Habit is coalescent small cups; surface corrugated; styles in two size categories (320–580 μm and 750–1725 μm long), often with tylote modifications *Axinella meandroides*
 Habit is flabellate-bushy; surface smooth and velvety; oxeas generally rare, styles in one size category *Axinella waltonsmithi*
- 10(2). Skeleton formed by plumose and long bundles of styles. Spicules are styles, often with tylote swelling and characteristic long and wavy trichodragmata (100–220 μm long) *Dragmaxia undata*

- Skeleton plumoreticulate with ascending spicule tracts. Spicules are oxeas and styles 11
- 11(10). Skeleton plumoreticulate with ascending thin spicule tracts (<4 spicules per cross section) perpendicular to surface; surface smooth with a dermal reticulation of pigment(?) grains *Pseudaxinella(?) zeai*
Skeleton plumoreticulate with ascending thick spicules tracts (>4 spicules per cross section) perpendicular to surface; surface conulose or coarsely porous 12
- 12(11). Cushion-shaped, generally small specimens, with star-shaped oscules (when visible); surface coarsely porous. Spicules are styles, in two sizes categories with tylostylote modifications, and oxeas (generally rare)
. *Pseudaxinella grayi*
Variously shaped, generally massive-amorphous or mound-shaped; surface conulose. Spicules are oxeas, invariably present, and styles in one size category *Pseudaxinella reticulata*
- 13(1). Tube-shaped 14
Not tube-shaped 15
- 14(13). Tubes with prominent tubercules *Auletta tuberosa*
Tubes smooth, without projections *Auletta scynularia*
- 15(13). Cone-shaped with long flagellar apex. *Acanthella flagelliformis*
Flabellate, bushy, massive, with or without lobes 16
- 16(15). Flabellate, with skeletal tracts strengthening the fan, sometimes imprinting the surface as "veins." Hard and brittle 17
Massive, with or without lobes; surface conulose, reticulate, or corrugated. Soft and fragile, or firmly cartilaginous 18
- 17(16). Styles differentiated into two size categories. Spicule tracts do not clearly imprint the surface as "veins" *Phakellia folium*
Styles not differentiated into size categories. "Veins" strengthening the fan well marked *Phakellia connexiva*
- 18(16). Skeletal spicule tracts are thick and vaguely anastomosing. Surface conulose, reticulate, or corrugated; consistency is soft and fragile
. *Acanthella cubensis*
Skeletal spicule tracts are thick and dendritic. Surface smooth with longitudinal grooves, or tuberculate and microhispid; consistency is cartilaginous to hard 19
- 19(15). Surface smooth and shiny, marked with longitudinal grooves; consistency is cartilaginous *Acanthella vacoleti*
Surface tuberculate and microhispid; consistency is hard to cartilaginous
. *Acanthella mastophora*

Discussion

Nine genera (*Axinella*, *Teichaxinella*, *Homaxinella*, *Pseudaxinella*, *Ptilocaulis*, *Dragmaxia*, *Phakellia*, *Auletta*, and *Acanthella*) of the approximately 50 nominal genera (Hooper and Lévi, 1993) assigned to the Axinellidae are represented in the central West Atlantic region. A careful examination of *Homaxinella* Topsent, 1916, and its type species (*Axinella supra tumescens* Topsent, 1907, lectotype MNHN LBIM DT 1660, and its senior synonym, *Axinella balfourensis* Ridley and Dendy, 1887, holotype, BMNH 1987.5.2.18) indicates that this genus should be transferred to the family Suberitidae Schmidt, 1870. Further conclusions of this study are that the species

Homaxinella waltonsmithi belongs to *Axinella* and *Teichaxinella* de Laubenfels is a synonym of *Axinella*. Two additional genera, *Ceratopsion* and *Thrinacophora*, traditionally included in the family Axinellidae but now thought to belong to Raspailiidae, order Poecilosclerida (Hooper, 1991), are also represented in the region (Alvarez and van Soest, 1993).

Bubaris Gray, 1867, a genus included in the family Bubaridae sensu Lévi, 1973, but considered to be closely related to Axinellidae (van Soest et al., 1990), is represented in the region by *Bubaris ammosclera*, an encrusting species first described from Barbados (Hechtel, 1969:25) and later from Colombia (Zea, 1987:206). Three other species of *Bubaris*

reported from the area are *B. ramosa* (Schmidt, 1870) (which is a synonym of *Axinella mastophora* Schmidt, 1870) and *B. flagelliformis* van Soest and Stentoft, 1988, and *B. cubensis* Alcolado, 1984 (both transferred herein to *Acanthella* (see the descriptions of these species, above)). Another bubarid genus thought to occur in the western Atlantic is *Hymerhabdia* Topsent, 1892, reported off Bonaire (Kobluk and van Soest, 1989). So little material has thus far been collected, however, that a definite assignment must await further findings.

Whether all seven genera described herein belong to the family Axinellidae is still unclear. The surface characteristics of *Ptilocaulis*, for example, might suggest that it should be included in the family Desmoxyidae, along with *Higginsia* (see van Soest et al., 1990). Yet such an allocation seems inappropriate in view of the close morphological similarity between the new *Axinella* species *A. pomponiae* and *Ptilocaulis marquezii* (as discussed above). *Higginsia* is represented in the central West Atlantic by *H. strigilata* Lamarck (= *H. coralloides* Higgin, 1877). *Acanthella*, along with *Dictyonella* and *Scopalina*, was considered a member of the family Dictyonellidae because of the presence of spongin-enforced dendritic choanosomal spicule tracts and a fleshy conulose surface (van Soest et al., 1990). That continues to be a serious possibility, but as mentioned earlier, these newly defined families cannot be used properly until their genera have been revised. Some of this work is already in progress for the Axinellidae.

The phylogenetic relationships of the family and related groups also need to be investigated. The family Axinellidae is now thought to belong to the order Halichondrida (van Soest et al., 1990), and it is defined as having an axially condensed skeleton and an extra-axial plumoreticulated skeleton. Because some genera (e.g., *Pseudaxinella* and *Ptilocaulis*) have (secondarily?) lost the axial skeleton and others (e.g., *Phakellia* and *Auletta*) lack a clear axial component, the definition remains debatable. Although traditionally the axial condensation of the skeleton has been used to link the taxa within the Axinellidae,

it is a very weak synapomorphy for the family, as it is present in other forms outside the group, notably in the Raspailiidae and Hemiasterellidae. This type of skeletal architecture is one of the diagnostic characters of genera such as *Axinella* and the recently described *Cymbastela* Hooper et al., 1992, but by itself it offers little assistance in distinguishing the family from the other groups within Halichondrida. These and other genera of the family can only be diagnosed through additional morphological characters, such as the composition and relative proportion of spicules, habit, surface projections, and enveloping spongin. Although most of these are of little use in delimiting the family, they do shed some light on the phylogeny at the species level, as shown in the preliminary phylogenetic analysis of the species included in this revision (Alvarez and Crisp, 1994).

The definitions of *Axinella* and *Pseudaxinella* were expanded to include species with raphides and trichodragmata. The presence of this type of microsclore in the family is not significant at higher levels of classification because it is also present in many other groups of the Demospongiae; perhaps it is a character that could be used to differentiate species.

According to recent chemotaxonomic studies of various families, including Axinellidae (Braekman et al., 1992; Hooper et al., 1992), biochemical characters (i.e., secondary metabolites, free amino acids, carotenoid pigments, and general proteins) could provide additional information on phylogenetic relationships. For example, most species of Axinellidae tested biochemically have been found to contain isocyanide or proline-2-carboxylic acid derivatives, two types of secondary metabolites that probably have a biogenetic origin (Braekman et al., 1992). The relative concentrations of some free amino acids and carotenoid pigments seem to vary among genus groups within Axinellidae (Hooper et al., 1992). Further information of this kind could help to identify additional synapomorphies to test the monophyletic origin of the Axinellidae.

Appendix

Station Data for the Material Examined from the Gulf of Mexico, Collected by
Continental Shelf Associates, Inc., for MMS

Number	Station	Latitude	Longitude	Locality	Depth (m)	Date
1	1/IV-01	26°45'46"N	82°43'07"W	off Fort Myers	24.0	2 May 1981
2	2/III-01	26°45'46"N	82°43'07"W	off Fort Myers	24.0	2 Feb 1982
3	1/III-03	26°45'52"N	83°21'26"W	off Fort Myers	50.2	29 Oct 1980
4	2/II-03	26°45'52"N	83°21'26"W	off Fort Myers	50.2	18 Jul 1981
5	2/III-03	26°45'52"N	83°21'26"W	off Fort Myers	50.2	1 Feb 1982
6	1/III-07	26°16'49"N	82°44'01"W	off Fort Myers	30.4	6 Nov 1980
7	2/II-07	26°16'49"N	82°44'01"W	off Fort Myers	30.4	19 Jul 1981
8	2/III-07	26°16'49"N	82°44'01"W	off Fort Myers	30.4	3 Feb 1982
9	1/IV-09	26°16'50"N	83°23'49"W	off Fort Myers	55.5	4 May 1981
10	1/III-10	26°16'44"N	83°42'49"W	off Fort Myers	71.3	3 Nov 1980
11	1/IV-10	26°16'44"N	83°42'49"W	off Fort Myers	71.3	30 Apr 1981
12	1/III-11	26°16'43"N	83°46'49"W	off Fort Myers	77.0	4 Nov 1980
13	1/IV-11	26°16'43"N	83°46'49"W	off Fort Myers	77.0	30 Apr 1981
14	2/II-11	26°16'43"N	83°46'49"W	off Fort Myers	77.0	24 Jul 1981
15	1/III-13	25°45'56"N	82°09'21"W	off Naples	19.6	8 Nov 1980
16	2/II-13	25°45'56"N	82°09'21"W	off Naples	19.6	29 Jul 1981
17	1/III-15	25°45'53"N	82°31'37"W	off Naples	31.5	9 Nov 1980
18	1/IV-15	25°45'53"N	82°31'37"W	off Naples	31.5	28 Apr 1981
19	2/II-15	25°45'53"N	82°31'37"W	off Naples	31.5	28 Jul 1981
20	2/III-15	25°45'53"N	82°31'37"W	off Naples	31.5	12 Feb 1982
21	1/III-21	25°17'16"N	82°52'10"W	off Cape Sable	44.2	18 Nov 1980
22	2/III-21	25°17'16"N	82°52'10"W	off Cape Sable	44.2	11 Feb 1982
23	1/III-23	25°16'53"N	83°37'47"W	off Cape Sable	70.0	17 Nov 1980
24	1/IV-23	25°16'53"N	83°37'47"W	off Cape Sable	70.0	26 Apr 1981
25	2/II-23	25°16'53"N	83°37'47"W	off Cape Sable	70.0	1 Aug 1981
26	2/III-23	25°16'53"N	83°37'47"W	off Cape Sable	70.0	08 Feb 1982
27	2/II-29	24°27'31"N	83°41'11"W	Florida Keys	62.5	4 Aug 1981
28	1/III-30	24°47'25"N	83°51'09"W	Florida Keys	76.1	21 Nov 1980
29	2/II-32	26°16'40"N	84°04'05"W	off Naples	137.0	25 Jul 1981
30	2/III-32	26°16'40"N	84°04'05"W	off Naples	137.0	6 Feb 1982
31	2/II-35	25°44'50"N	84°21'02"W	off Naples	159.0	26 Jul 1981
32	2/III-35	25°44'50"N	84°21'02"W	off Naples	159.0	7 Feb 1982
33	2/II-36	25°16'50"N	83°57'21"W	off Cape Sable	127.0	2 Aug 1981
34	2/III-38	25°16'30"N	84°14'46"W	off Cape Sable	159.0	10 Feb 1982
35	2/II-39	24°47'10"N	83°55'22"W	Florida Keys	151.5	3 Aug 1981
36	II-44	26°17'52"N	82°12'37"W	Sanibel Island	13.0	5 Dec 1982
37	III-44	26°17'52"N	82°12'37"W	Sanibel Island	13.0	31 May 1983
38	II-45	26°03'11"N	82°08'27"W	off Naples	17.0	6 Dec 1982
39	III-45	26°03'11"N	82°08'27"W	off Naples	17.0	1 Jun 1983
40	III-47	26°46'01"N	82°06'04"W	Marco Island	19.0	2 Jun 1983
41	II-51	25°17'40"N	81°48'00"W	Cape Sable	16.0	8 Dec 1982
42	III-51	25°17'40"N	81°48'00"W	Cape Sable	16.0	3 Jun 1983
43	II-52	25°17'48"N	81°39'48"W	Cape Sable	14.0	9-11 Dec 1982
44	III-52	25°17'48"N	81°39'48"W	Cape Sable	14.0	3-4 Jun 1983

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