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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I. Michael Heyman
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A Revision of Axinellidae
(Porifera: Demospongiae)
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Belinda Alvarez, Rob W.M. van Soest,
and Klaus Rützler
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
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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 Halichondridae; 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...
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 Museum National d’Histoire Naturelle, Laboratoire de Biologie des Invertébrés Marins et Malacologie, Tôpset collections (LBIM DT), Paris
MT Por Museo e Istituto di Zoologia Sistematica 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

ACKNOWLEDGMENTS

Penny Beherents (AM), Clare Valentine and Shirley Stone (BMNH), Claude Lévi (MNHN), Ardis Johnston (MCZ), Nancy Voss (UMML), Eric A. Lazo (YPM), and William Gladfelter (West Indies Laboratory, St. Croix) kindly provided access to and loans from their collections. Sven Zea (Universidad Nacional de Colombia) supplied the material and photographs used to describe the new species Pseudaxinella(?) zeai. Most of the specimens were obtained from the Mineral Management Service (formerly Bureau of Land Management, U.S. Department of Interior) through Kristian Fauchald, NMNH. Equipment and material were provided by the NMNH and the Division of Botany and Zoology, ANU. Kate Smith (NMNH) helped organize and catalog the material housed in the NMNH and offered constructive comments. Molly K. Ryan (NMNH), Michael Carpenter (NMNH), and Keith Herbert (ANU) assisted with finishing illustrations and photographic work. Eduardo Hajdu (ZMA) provided additional study material. This is contribution number 482 of the Caribbean Coral Reef Ecosystems Program (NMNH).

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


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 I

Homaxinella waltonsmithi de Laubenfels, 1953:533 [holotype, USNM 23407].—Wells and Wells in Wells et al., 1960:222 [USNM 23660].
Phakellia folium.—Pease and Williams, 1951:136 [listed only; same specimen described by Wells and Wells in Wells et al., 1960:222].—Wells and Wells in Wells et al., 1960:223 [USNM 23664].
Thalyseurypon carteri.—Wells and Wells in Wells et al., 1960:222 [USNM 23407].—Wells and Wells in Wells et al., 1960:222, as Homaxinella waltonsmithi. {Not Clathria carteri Topsent, 1899.}

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 (22), 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. Epizoic 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 spongion. Primary lines run parallel to sponge axis in axial skeleton; lateral condensation of reticulation obvious in column 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 spongion commonly present in some areas of periphery.

Spicules (Figure 1d, Table I).—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.

Remark.—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.
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 μm; width, 6-18 μm) and regularly show subterminal swellings.

Axinella pomponiae, new species

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

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Styles I</th>
<th>Styles II</th>
<th>Oxeas</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>length</td>
<td>width</td>
<td></td>
</tr>
<tr>
<td>Georgia</td>
<td>USNM 42769</td>
<td>180-240 (214.0±17.6)</td>
<td>370-490 (441.0±35.1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5-10 (8.7±1.6)</td>
<td>5-7.5 (6.1±1.3)</td>
</tr>
<tr>
<td>Gulf of Mexico</td>
<td>USNM 42762</td>
<td>230-300 (265.6±18.3)</td>
<td>450-690 (567.8±58.8)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.5-17.5 (15.3±1.8)</td>
<td>7.5-15 (11.4±2.1)</td>
</tr>
<tr>
<td>USNM 42763</td>
<td></td>
<td>250-300 (274.8±12.6)</td>
<td>450-690 (591.2±60.7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>12.5-17.5 (14.8±1.8)</td>
<td>5-17.5 (13.5±3.1)</td>
</tr>
<tr>
<td>USNM 42765</td>
<td></td>
<td>230-290 (268.8±16.2)</td>
<td>390-670 (448.1±72.2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>7.5-12.5 (15.7±1.4)</td>
<td>2.5-7.5 (9.5±1.9)</td>
</tr>
</tbody>
</table>

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


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).


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 *Aixinella 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 µm; d, 100 µm.]
**Axinella polycapella de Laubenfels, 1953**

**Figure 3; Table 3**


*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; strongyloxeas 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].


**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 ± standard deviation in parentheses.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Styles</th>
<th>Oxeas</th>
<th>Strongyloxeas</th>
</tr>
</thead>
<tbody>
<tr>
<td>South Carolina</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>USNM 42779</td>
<td>180-290 (206.0±32.7)[10]</td>
<td>190-250 (220.8±19.3)</td>
<td>not detected</td>
</tr>
<tr>
<td>length</td>
<td>7.5-10 (9.0±1.3)[10]</td>
<td>7.5-12.5 (9.3±1.4)</td>
<td></td>
</tr>
<tr>
<td>width</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gulf of Mexico</td>
<td>260-360 (303.3±33.3)[6]</td>
<td>230-390 (287.6±40.6)</td>
<td>380-390 (385.0±7.1)[2]</td>
</tr>
<tr>
<td>USNM 42774</td>
<td>10-20 (16.67±3.8)[6]</td>
<td>7.5-15 (9.6±1.9)</td>
<td>17.5-17.5 (17.5±0)[2]</td>
</tr>
<tr>
<td>length</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>width</td>
<td>260-360 (273.5±35.0)[23]</td>
<td>260-430 (304.0±54.0)</td>
<td>240-340 (310.0±35.1)[7]</td>
</tr>
<tr>
<td>USNM 42775</td>
<td>10-17.5 (13.0±2.0)[23]</td>
<td>10-22.5 (13.0±3.1)</td>
<td>15-25 (19.6±4.4)[7]</td>
</tr>
<tr>
<td>length</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>width</td>
<td>200-260 (224.4±18.9)</td>
<td>240-340 (266.8±24.1)</td>
<td>220-310 (248.8±20.1)</td>
</tr>
<tr>
<td>USNM 42776</td>
<td>15-25 (18.8±2.6)</td>
<td>15-20 (17.2±2.1)</td>
<td>12.5-22.5 (18.4±3.0)</td>
</tr>
</tbody>
</table>
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 μm; d, 50 μm.]
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 μm; d, 100 μm.]
TABLE 4.—Spicule dimensions for *Axinella shoemakeri*. Measurements (in µm) are ranges of 25 spicules (or the number indicated in brackets), with means ± standard deviation in parentheses.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Styles</th>
<th>Oxeas</th>
<th>Trichodragmata</th>
</tr>
</thead>
<tbody>
<tr>
<td>North Carolina</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>USNM 32723 length</td>
<td>310-840 (539.6±133.3)</td>
<td>210-310 (270.0±27.5)</td>
<td>22.5-32.5 (26.1±3.5)[7]</td>
</tr>
<tr>
<td>USNM 32723 width</td>
<td>10-17.5 (14.2±2.1)</td>
<td>7.5-10 (9.0±1.3)</td>
<td>5-5 (5.0±0.0)[7]</td>
</tr>
<tr>
<td>South Carolina</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>USNM 33330 length</td>
<td>270-680 (482.0±110.5)</td>
<td>260-470 (317.2±44.3)</td>
<td>not detected</td>
</tr>
<tr>
<td>USNM 33330 width</td>
<td>10-22.5 (16.4±3.8)</td>
<td>5-15 (11.0±2.3)</td>
<td></td>
</tr>
<tr>
<td>Georgia</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>USNM 33588 length</td>
<td>260-1000 (431.2±141.6)</td>
<td>200-300 (249.6±27.3)</td>
<td>22.5-35 (27.3±3.6)[11]</td>
</tr>
<tr>
<td>USNM 33588 width</td>
<td>7.5-15 (11.1±1.9)</td>
<td>5-10 (8.7±1.5)</td>
<td>5-10 (6.4±1.7)[11]</td>
</tr>
<tr>
<td>Gulf of Mexico</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>USNM 39881 length</td>
<td>220-1925 (789.0±257.3)</td>
<td>240-410 (357.6±44.2)</td>
<td>27.5-32.5 (30.0±2.0)[5]</td>
</tr>
<tr>
<td>USNM 39881 width</td>
<td>10-25 (15.8±4.8)</td>
<td>10-15 (11.9±1.9)</td>
<td>5-5 (5.0±0.0)[5]</td>
</tr>
<tr>
<td>USNM 41600 length</td>
<td>190-920 (448.8±170.0)</td>
<td>210-300 (259.2±26.4)</td>
<td>not detected</td>
</tr>
<tr>
<td>USNM 41600 width</td>
<td>7.5-17.5 (12.7±2.6)</td>
<td>7.5-12.5 (9.5±1.9)</td>
<td></td>
</tr>
</tbody>
</table>

**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 4b,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 4d, Table 4).—Styles; oxeas sometimes strongylote; 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 polyoides* 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)].


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


**SHAPE** (Figure 5a).—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 oxeas; USNM 39852). [Scales: a, 20 mm; b,c, 200 μm; d, 100 μm.]
**Axinella meandroides, new species**

**FIGURE 6; TABLE 6**


**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 subtylostyloids 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 meander), 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 μm; d. 100 μm.]
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 ± standard deviation in parentheses.

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

**Axinella sp.**

**FIGURE 7**

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

**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 oxeas and styles organized in anisotropic reticulation, quite halichondroid, with large, rounded to polygonal meshes.

**SPICULES** (Figure 7).—Oxeas generally bent, 320-420 (369.2 ± 29.0) μm long and 7.5-15 (12.6 ± 2.2) μm wide; few styles, 300-1050 (521.3 ± 263.6)[8] μm long, 7.5-15 (13.4 ± 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.

**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 *Oxeostylon 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-
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 Schmidt (1870:61; saing and Michelotti, 1864; the type and proportions of the megascleres, were sufficient to separate the species, but a combination of individual characters are not 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., stylos, 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 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].


[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].


[Not *Axinella? lunaecharza* of Ridley and Dendy, 1886:481 (BMNH 1887.5.2.272; 1887:186; Topsent, 1928:174).

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

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 μm.]

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

SURFACE.—Short (0.5 mm high) conules or tubercules, evenly distributed, 0.5-2 mm apart; or tall (1-2 mm high) conules or tubercules, 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.
TABLE 8.—Spicule dimensions for *Pseudaxinella reticulata*. Measurements (in \( \mu \text{m} \)) are ranges of 25 spicules (or the number indicated in brackets), with means ± standard deviation in parentheses.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Styles</th>
<th>Oxeas</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>length</td>
<td>length</td>
</tr>
<tr>
<td></td>
<td>width</td>
<td>width</td>
</tr>
<tr>
<td>North Carolina</td>
<td>220-310 (266.0±27.1)</td>
<td>220-330 (268.0±26.1)</td>
</tr>
<tr>
<td>USNM 33334</td>
<td>7.5-15 (10.7±1.7)</td>
<td>7.5-15 (10.0±2.5)</td>
</tr>
<tr>
<td>South Carolina</td>
<td>210-390 (272.2±38.0)</td>
<td>210-340 (282.0±34.9)</td>
</tr>
<tr>
<td>USNM 33349</td>
<td>7.5-17.5 (12.0±3.4)</td>
<td>5-15 (8.3±3.1)</td>
</tr>
<tr>
<td>Bermuda</td>
<td>300-440 (365.6±42.7)</td>
<td>320-490 (373.2±36.3)</td>
</tr>
<tr>
<td>USNM 32847</td>
<td>7.5-12.5 (10.2±1.0)</td>
<td>7.5-12.5 (10.0±1.0)</td>
</tr>
<tr>
<td>Gulf of Mexico</td>
<td>260-400 (342.8±41.6)</td>
<td>310-440 (385.6±34.9)</td>
</tr>
<tr>
<td>USNM 42787</td>
<td>15-22.5 (18.2±2.6)</td>
<td>12.5-20 (16.2±1.8)</td>
</tr>
<tr>
<td>Belize</td>
<td>210-330 (302.4±27.6)</td>
<td>330-400 (362.8±18.1)</td>
</tr>
<tr>
<td>USNM 32987</td>
<td>10-20 (16.0±2.2)</td>
<td>12.5-17.5 (16.0±1.8)</td>
</tr>
<tr>
<td>Nicaragua</td>
<td>240-350 (287.6±29.3)</td>
<td>310-400 (342.4±19.8)</td>
</tr>
<tr>
<td>USNM 31452</td>
<td>7.5-15 (12.1±2.1)</td>
<td>10-15 (12.8±1.5)</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>260-340 (303.2±22.5)</td>
<td>310-410 (354.4±22.2)</td>
</tr>
<tr>
<td>USNM 30136</td>
<td>10-20 (15.3±1.8)</td>
<td>12.5-17.5 (15.2±1.8)</td>
</tr>
<tr>
<td>U.S. Virgin Islands</td>
<td>230-330 (282.8±33.5)</td>
<td>290-370 (331.6±22.1)</td>
</tr>
<tr>
<td>USNM 31552</td>
<td>10-15 (12.5±1.8)</td>
<td>7.5-12.5 (11.3±1.5)</td>
</tr>
<tr>
<td>Tobago</td>
<td>170-320 (260.4±41.8)[24]</td>
<td>230-330 (282.1±22.6)[24]</td>
</tr>
<tr>
<td>USNM 42791</td>
<td>7.5-20 (13.6±3.2)[24]</td>
<td>5-17.5 (11.1±3.2)[24]</td>
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<tr>
<td>Brazil</td>
<td>240-416 (347.1±54.4)</td>
<td>340-470 (395.8±34.8)</td>
</tr>
<tr>
<td>BMNH 87.5.2.11</td>
<td>7.5-21.4 (14.23±3.6)</td>
<td>10-17.3 (12.4±2.0)</td>
</tr>
</tbody>
</table>

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 \( \mu \text{m} \) thick) perpendicular to the surface, without axial condensation.

SPIECULES (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 Curacao 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 Diaz, 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 \( \mu \text{m} \) long, and oxeas are up to 500 \( \mu \text{m} \) 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].


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 (31°23'24"N, 80°53'00"W, 17 m, coll. GMR for MMS, 4 Mar 1981), USNM 42781 (31°23'36"N, 80°53'00"W, 17 m, coll. GMR for MMS, 4 Mar 1981). South Carolina: USNM 42782 (41°40'30"N, 79°53'30"W, 0-10 m, coll. M.W. de Laubenfels, 28 Jul 1947), referred to *Pseudaxinella rosacea* by Verrill (1907:340) is questionable; it is probably a species of *Pseudaxinella lunaecharta* (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 Diaz, 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 \( \mu \text{m} \) long, and oxeas are up to 500 \( \mu \text{m} \) 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).
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 μm; d, 100 μm.]
TABLE 9.—Spicule dimensions for Pseudaxinella grayi. Measurements (in μm) are ranges of 25 spicules (or the number indicated in brackets), with means ± standard deviation in parentheses.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Styles I</th>
<th>Styles II</th>
<th>Oxeas</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>length</td>
<td>width</td>
<td>length</td>
</tr>
<tr>
<td>Georgia USNM 42786</td>
<td>450-490 (463.3±23.1)</td>
<td>5-7.5 (5.8±1.4)</td>
<td>200-340 (265.2±39.5)</td>
</tr>
<tr>
<td>Gulf of Mexico USNM 42780</td>
<td>670-1200 (991.4±128.2)</td>
<td>5-15 (9.8±2.3)</td>
<td>300-380 (335.8±22.1)</td>
</tr>
</tbody>
</table>

**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].


Calyx podanypa.—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.**—Crumbly, 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.

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

**DISTRIBUTION AND HABITAT.**—Colombia, Tobago (where it 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
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 walperst*).
Ptilocaulis Carter, 1883


**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].


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

(*)Axinella rosacea Verrill, 1907:341.


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


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


**Shape.**—Variable (Figure 12a-d): encrusting, irregularly massive, plate-shaped, fan-shaped, or erect finger-shaped; dichotomously branching or forming branches 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 spongins) 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 Moskito 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 synonyms 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

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**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 \( \mu \text{m} \); c. 100 \( \mu \text{m} \).]
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 marquezi.*

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 marquezi* (Duchassaing and Michelotti, 1864), new combination

**Figure 14:** Table 12

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

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

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


**Shape.**—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 marquezi* Duchassaing and Michelotti, 1864, 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* (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 marquezi* 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. marquezi* 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**


**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. Microscleres, 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.
**Dragmaxia undata, new species**

*Dragmaxia variabilis*.—Wintermann-Kilian and Kilian, 1984:131 [listed only].

[Not *Spongosorites variabilis* Whitelegge, 1907.]

*Dragmaxia sp*.—Koblik and van Soest, 1989:1215.

**Material Examined.**—*Holotype*: Curacao: 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.—Dragmexia 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 trichodragoma, USNM 39451). [Scales: a, 2 mm; b, 200 µm; c, 1 µm; d, 0.2 µm; e, 200 µm; f, 100 µm.]
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 exosome.

CONSISTENCY.—Fragile.

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

SKELETON (Figure 15b,c).—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 (721.1 ± 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 rhaphids 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 Axinella 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 Styliissa will be considered in a forthcoming revision of Axinellida genera.

Phakellia folium Schmidt, 1870

Phakellia Bowerbank, 1862


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 stronyloxeas 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 flabelligeriform 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.
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 μm; d, 100 μm.]
Phakellia connexiva Ridley and Dendy, 1887

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 17a,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 17c,d).—Primary lines of sinuous-vermiculate strongyles and strongyloxeas, echinated by styles, forming stout lines like "veins" (see "Surface").

SPICULES (Figure 17e, 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 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.]

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

<table>
<thead>
<tr>
<th>Specimens</th>
<th>Styles I</th>
<th>Styles II</th>
<th>Strongyles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Florida</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BMNH 70.5.3.76</td>
<td>540-1230 (878.7±235.5)[15]</td>
<td>240-340 (286.3±37.0)[8]</td>
<td>260-920 (575.2±178.4)</td>
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<tr>
<td>length</td>
<td>12.5-22.5 (18.2±2.8)[15]</td>
<td>12.5-20 (13.8±2.7)[8]</td>
<td>7.5-27.5 (18.1±4.1)</td>
</tr>
<tr>
<td>width</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BMNH 70.5.3.77</td>
<td>660-1900 (1094.4±359.3)[18]</td>
<td>350-500 (451.5±35.7)[14]</td>
<td>490-750 (627.6±61.0)</td>
</tr>
<tr>
<td>length</td>
<td>25-45 (32.8±5.5)[18]</td>
<td>12.5-32.5 (20.2±6.4)[14]</td>
<td>20-32.5 (26.5±3.5)</td>
</tr>
<tr>
<td>width</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barbados</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ZMA Por 5414</td>
<td>320-550 (446.0±57.4)</td>
<td>90-170 (130.0±19.6)</td>
<td>300-630 (473.6±83.3)</td>
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<td>7.5-12.5 (8.4±1.4)</td>
<td>2.5-5 (3.4±1.2)</td>
<td>10-17.5 (14.0±2.5)</td>
</tr>
<tr>
<td>width</td>
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<td></td>
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</tr>
<tr>
<td>Grenada</td>
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</tr>
<tr>
<td>USNM 982</td>
<td>330-780 (491.6±100.4)</td>
<td>150-200 (174.4±14.2)</td>
<td>390-910 (589.2±138.0)</td>
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<tr>
<td>length</td>
<td>10-17.5 (12.8±1.8)</td>
<td>7.5-12.5 (8.9±1.5)</td>
<td>10-20 (14.1±3.1)</td>
</tr>
<tr>
<td>width</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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**


**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 \( \mu \text{m} \) thick, echinacted 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**


**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 \( \mu \text{m} \) 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 \( \mu \text{m} \)) are ranges of 25 spicules (or the number indicated in brackets), with means ± standard deviation in parentheses.

<table>
<thead>
<tr>
<th>Specimens</th>
<th>Styles I</th>
<th>Styles II</th>
<th>Styles III</th>
<th>Strongyles</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Florida</strong></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>BMNH 1939.2.10.36</td>
<td>not detected</td>
<td>450–950 (648.2±154.0)[11]</td>
<td>not detected</td>
<td>300–660 (429.5±81.0)[20]</td>
</tr>
<tr>
<td>length</td>
<td></td>
<td>10–20 (14.8±2.9)[10]</td>
<td></td>
<td>13–20 (17.4±2.4)[18]</td>
</tr>
<tr>
<td>width</td>
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<td><strong>Gulf of Mexico</strong></td>
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</tr>
<tr>
<td>USNM 42023</td>
<td>740–1450 (1095±206.4)</td>
<td>360–690 (492.0±84.8)</td>
<td>170–260 (197.2±20.5)</td>
<td>350–770 (550.4±96.5)</td>
</tr>
<tr>
<td>length</td>
<td>5–17.5 (11.9±3.5)</td>
<td>7.5–15 (11.0±2.3)</td>
<td>5–10 (7.9±1.4)</td>
<td>7.5–25 (17.5±4.6)</td>
</tr>
<tr>
<td>width</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
FIGURE 18.—Auletta 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 μm; e, 100 μm.]
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 19d, Table 16).—Oxeas, oxeotes, or strongyloxeas, 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
from *A. scychnaria* 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 *Auletta***

The species of *Auletta* 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**


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*


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

**Table 16.** Spicule dimensions for *Auletta tuberosa*, new species. Measurements (in µm) are ranges of 25 spicules, with means ± standard deviation in parentheses.

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

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

<table>
<thead>
<tr>
<th>Specimens</th>
<th>Styles I</th>
<th>Styles II</th>
<th>Strongyles to Strongyloxeas</th>
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</thead>
<tbody>
<tr>
<td>North Carolina</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>USNM 33343</td>
<td>570–870 (735.6±95.5)</td>
<td>330–540 (452.0±63.4)</td>
<td>470–870 (686.4±100.6)</td>
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<tr>
<td>length</td>
<td>10–22.5 (14.8±3.3)</td>
<td>7.5–20 (15.7±2.8)</td>
<td>7.5–17.5 (12.2±2.8)</td>
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<td>width</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gulf of Mexico</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>USNM 42175</td>
<td>620–1150 (810.4±147.9)</td>
<td>300–490 (389.5±54.6)</td>
<td>200–910 (628.0±164.6)</td>
</tr>
<tr>
<td>length</td>
<td>15–37.5 (27.6±5.5)</td>
<td>10–30 (22.0±4.0)</td>
<td>15–35 (26.1±6.2)</td>
</tr>
<tr>
<td>width</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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**


**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. Diaz 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 strongyles.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Styles</th>
<th>Strongyles</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length</td>
<td>Width</td>
</tr>
<tr>
<td>North Carolina</td>
<td></td>
<td></td>
</tr>
<tr>
<td>USNM 33340</td>
<td>520–1200</td>
<td>330–1175</td>
</tr>
<tr>
<td></td>
<td>(816.2±184.6)</td>
<td>(642.0±276.4)</td>
</tr>
<tr>
<td></td>
<td>10–15 (11.7±2.0)</td>
<td>7.5–17.5 (11.9±2.8)</td>
</tr>
<tr>
<td>Gulf of Mexico</td>
<td></td>
<td></td>
</tr>
<tr>
<td>USNM 42164</td>
<td>420–990</td>
<td>300–930</td>
</tr>
<tr>
<td></td>
<td>(656.0±156.7)</td>
<td>(575.2±193.3)</td>
</tr>
<tr>
<td></td>
<td>5–10 (8.0±1.6)</td>
<td>7.5–17.5 (12.3±3.1)</td>
</tr>
<tr>
<td>USNM 42171</td>
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</tr>
<tr>
<td></td>
<td>(1031.0±102.8)</td>
<td>(715.2±250.8)</td>
</tr>
<tr>
<td></td>
<td>12.5–25 (18.8±2.6)</td>
<td>17.5–32.5 (25.5±4.0)</td>
</tr>
<tr>
<td>Los Roques (Venezuela)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FCLR 217</td>
<td>630–1050</td>
<td>260–670</td>
</tr>
<tr>
<td></td>
<td>(830.6±110.9)</td>
<td>(436.8±113.9)</td>
</tr>
<tr>
<td></td>
<td>5–15 (9.7±2.0)</td>
<td>7.5–25 (11.5±3.6)</td>
</tr>
<tr>
<td>Tobago</td>
<td></td>
<td></td>
</tr>
<tr>
<td>USNM 42806</td>
<td>440–890</td>
<td>350–900</td>
</tr>
<tr>
<td></td>
<td>(699.2±116.0)</td>
<td>(568.0±153.4)</td>
</tr>
<tr>
<td></td>
<td>5–10 (8.0±1.9)</td>
<td>5–17.5 (12.1±3.0)</td>
</tr>
</tbody>
</table>
styles, some bent at apex. Several specimens with foreign sigmas (70–100 μm 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...
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 23a).—Cone-shaped with long flagellar apex.

**SURFACE.**—Hispid.

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

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

**SPICULES** (Figure 23d).—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 μm.]
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 vaceleti* 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

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

3(2). Plumose spicule tracts bound by spongin. Surface with branching or “scopiform” processes .......................... 4

4(3). Spicules are styles in two size categories .......................... *Ptilocaulis walpersi*

5(3). Extra-axial skeleton not plumoreticulate, formed by dermal spicules, spicule bundles, plumose tracts, or combination of these .......................... 6

6(5). Habit is thinly lamellate; surface velvety smooth; trichodragmata present (they may be hard to find) .......................... *Axinella shoemakeri*

7(3). Habit is branching-arborescent (tree-like) .......................... 8

8(7). Surface smooth and velvety, pierced by small pores (<1 mm). Spicules in one size category .......................... *Axinella polycapella*

9(7). Habit is coalescent small cups; surface corrugated; styles in two size categories (320–580 μm and 750–1725 μm long), often with tylole modifications .......................... *Axinella meandroides*

10(2). Skeleton formed by plumose and long bundles of styles. Spicules are styles, often with tylole swelling and characteristic long and wavy trichodragmata (100–220 μm long) .......................... *Dragmacia 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**

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). 12

12(11). 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

14(13). Tubes with prominent tubercules. **Auletta tuberosa**

14(13). Tubes smooth, without projections. **Auletta sycinularia**

15(13). Cone-shaped with long flagellar apex. **Acanthella flagelliformis**

16(15). Flabellate, with skeletal tracts strengthening the fan, sometimes imprinting the surface as “veins.” Hard and brittle. **Phakellia folium**

17(16). Styles differentiated into two size categories. Spicule tracts do not clearly imprint the surface as “veins”. **Phakellia connexiva**

18(16). Skeletal spicule tracts are thick and vaguely anastomosing. Surface conulose, reticulate, or corrugated; consistency is soft and fragile. **Acanthella cubensis**

19(15). Surface smooth and shiny, marked with longitudinal grooves; consistency is cartilaginous. **Acanthella vaceleti**

Discussion

Nine genera (*Axinella*, *Teichaxinella*, *Homaxinella*, *Pseudaxinella*, *Ptilocaulis*, *Dragmaxia*, *Phakellia*, *Auletta*, and *Acanthella*) of the approximately 50 nominal genera (Hooper and Levi, 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 waltonsmithii* belongs to *Axinella* and *Teichaxinella de Laubenfels* is a synonym of *Axinella*. Two additional genera, *Ceratopsis* and *Thrinacophora*, traditionally included in the family Axinellidae but now thought to belong to Raspailiidae, order Poeclisoclerida (Hooper, 1991), are also represented in the region (Alvarez and van Soest, 1993).

*Bubaris Gray*, 1867, a genus included in the family Bubaridae sensu Levi, 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 Sienstra, 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 microsclere 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 biogenic 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

<table>
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<th>Longitude</th>
<th>Locality</th>
<th>Depth (m)</th>
<th>Date</th>
</tr>
</thead>
<tbody>
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<td>26°45'46&quot;N</td>
<td>82°43'07&quot;W</td>
<td>off Fort Myers</td>
<td>24.0</td>
<td>2 Feb 1982</td>
</tr>
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<td>1/III-03</td>
<td>26°45'52&quot;N</td>
<td>83°21'26&quot;W</td>
<td>off Fort Myers</td>
<td>50.2</td>
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<td>off Fort Myers</td>
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</tr>
<tr>
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<td>83°21'26&quot;W</td>
<td>off Fort Myers</td>
<td>50.2</td>
<td>1 Feb 1982</td>
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**Locality**
- off Fort Myers
- off Naples
- off Cape Sable
- off Florida Keys
- off Sanibel Island
- off Marco Island
- off Cape Sable
- off Cape Sable
- off Fort Myers
- off Naples
- off Naples
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Zea, S.
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