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Two new tretodictyids (Hexactinellida: Hexactinosida: Tretodictyidae) from the coasts of North America

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Abstract

Two new species of the hexactinellid family Tretodictyidae, both collected by submersible, have been discovered off the coasts of North America. The Pacific species, *Tretodictyum montereyensis* **n. sp.**, has an unusual skeleton with a fused cortex added over the usual tretodictyid system of ridges and grooves on the dermal surface. The Atlantic species, *Hexactinella carolinensis* **n. sp.**, is unusual among its congeners in having swollen nodes on the dermal skeleton. Diagnoses of both genera have been modified to accommodate the new findings. The fine diactins of both species are found to have shallow brackets and short barbs, confirming their uncinate nature. Addition of these two species raises the number of known North American tretodictyids from one to three.

Key words: taxonomy, hexactinellids, sponges, new species, Porifera, HBOI, MBARI

Introduction

The hexactinellid fauna of North American coasts is still known from the classical works of Schmidt (1870, 1880), Lambe (1893), Schulze (1899), and Wilson (1904). Detailed formal descriptions of one or two new species or range extensions were added by later workers, Wilson and Penney (1930), Tabachnick (1989), Reiswig and Mehl (1994) and Reiswig (1996, 1999, 2001) while informal unsupported additions were suggested in listings in many other reports.

Tretodictyids (family Tretodictyidae) are not important members of the North American hexactinellid fauna. To date only one described tretodictyid is certainly known from the North American coast – *Cyrtaulon sigsbeei* Schmidt, 1880 from the Florida region. Here we describe two new tretodictyids from North America, a species of *Hexactinella* from the Atlantic coast off South Carolina and a species of *Tretodictyum* from the Pacific coast off Monterey Bay, California (Fig. 1).

Material and methods

One specimen of each new species was collected by either manned or remotely operated submersible. They both suffered serious breakage during collection/retrieval but they were not damaged by sediment infiltration

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or spicule wash-out. The California *Tretodictyum* was fixed and stored in ethanol while the Carolina *Hexactinella* was freeze-dried. Spicule preparations were made by digesting tissue fragments from various body regions in hot nitric acid. Cleaned spicules were isolated by either accumulating the spicules on nitrocellulose filters for light microscopy or polycarbonate membrane filters for SEM, or rinsing the spicules by settling/ decantation with water, with final transfer to cover glass on SEM pegs by pipette or forceps. Measurements of slide preparations were made indirectly by a computer-digitizer coupled to light microscopes by drawing tube (camera lucida). Data are presented as mean ± st. dev. (range, number of measurements).

Abbreviations: Scanning electron microscopy (SEM), light microscopy (LM), California Academy of Sciences, Invertebrate Zoology Section (CASIZ), United States National Museum (USNM), Harbor Branch Oceanographic Institute Inc. (HBOI), Monterey Bay Aquarium Research Institute (MBARI).

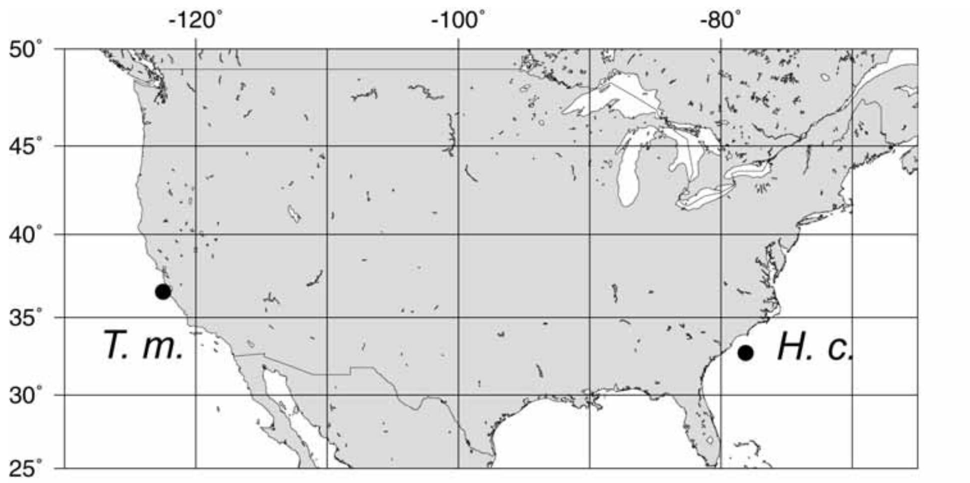

FIGURE 1. Map of collection sites of *Tretodictyum montereyensis* **n. sp.** (T. m.) and *Hexactinella carolinensis* **n. sp.** (H. c.).

Results

Class Hexactinellida Schmidt, 1870

Subclass Hexasterophora Schulze, 1886

Order Hexactinosida Schrammen, 1903

Family Tretodictyidae Schulze,1886

Genus *Tretodictyum* Schulze, 1886

Type species: *Tretodictyum tubulosum* Schulze (by monotypy).

Genus diagnosis: Tretodictyidae with body form of tubular, branching and anastomosing network or stumpy, fused mass of tubules; oscula located terminally or laterally, opening into pit-like or elongate-cylindrical but discontinuous atrial cavities; labyrinthic or cleft-like schizorhyses covered externally by loose dermal spicule lattice, with or without a thin layer of fused cortical strands; dermalia pentactin to pinular subhexactins; scopules strongyloform; oxyhexasters with long principal rays; uncinates lacking or with weakly developed barbs (From Reiswig 2002: 1353, emended).

Remarks. The genus diagnosis is emended to combine definition and diagnosis sections given in Reiswig (2002), to correct a typographic error (oscula replaces ostia in the second phrase), and to accommodate the fused cortical strands which occur in the new species.

Tretodictyum montereyensis **n. sp.**
Figs. 2–5, Table 1.

Material examined. Holotype: CASIZ 175317, coll. C. Baxter using MBARI ROV 'Ventana', dive 105, north wall of Monterey Bay Canyon, central California, 36°48'30"N, 122°05'20"W, 92–369 m, 08 Dec. 1989.

Diagnosis. *Tretodictyum* with ridge/groove system covered by a thin fused dermal cortex with thick dictyonal strands oriented in all directions; large rough pentactins and occasional subhexactins serve as both dermalia and atrialia. Microscleres are mainly oxyhexasters, oxyhemihexasters, and oxyhexactins, but rare onychohexactins also occur.

Description. The holotype and only specimen consists of two fragments (Fig. 2), the larger of which was a curved piece 25 mm long, 12 mm wide and 10 mm thick. It was clearly a small fragment from a larger plate or bowl-shaped specimen, calculated as 6.5 cm diameter from projection of the curvature. Both surfaces are smooth and lack prostalia, but appear hirsute when viewed at 50x due to the presence of perpendicularly oriented uncinate bundles. The convex surface, assumed to be dermal, is pierced by small irregular apertures, 90–800 µm diameter while the concave surface, assumed to be atrial, is likewise smooth but pierced by apertures 480–800 µm which are difficult to distinguish from the irregular and variable-sized meshes of the dictyonal network on this surface. Larger inhalant and exhalant canals oriented perpendicular to the outer surfaces are visible through the tissues of both surfaces. The ridge-groove system expected to be present on the basis of spiculation of the specimen, is not visible on either surface. The preserved fragments are white; the texture is stony-hard but the interior is fleshier than that of other dictyonal hexactinellids.

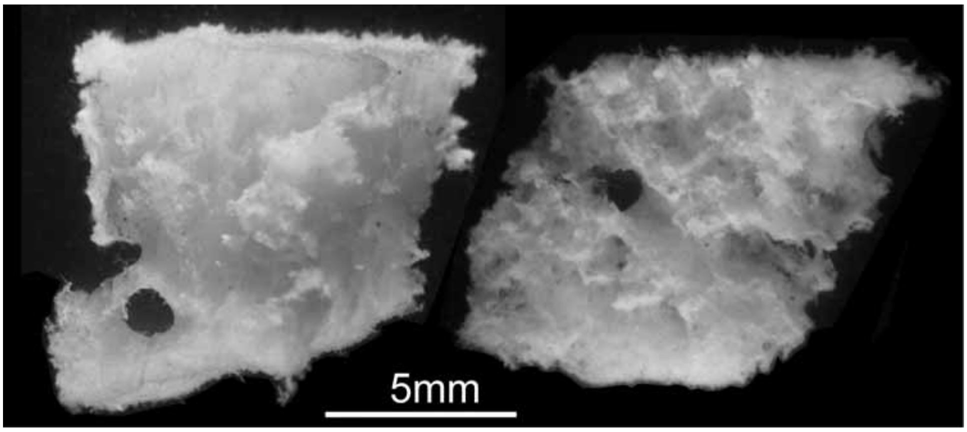

FIGURE 2. Two body fragments of *Tretodictyum montereyensis* **n. sp.** in transverse section, dermal surface upwards, with part of the schizorhysial channel system seen internally.

Dictyonal framework. The dermal framework (Fig. 3A) consists of an irregular network of very thick dictyonal strands running in all directions overlying a likewise irregular network of smaller-meshed, thinner beams, 3–4 dictyonalia in thickness. Some thick surface strands form the boundaries of short channels (Fig. 3A) that lead into a subsurface layer of longitudinal channels (Fig. 3E), which appear to be homologues of the surface groove system common in other tretodictyids. The dermal framework (a cortex) is supported on a series of longitudinal septa (primary framework), which delimit the underlying longitudinal grooves. The septa, homologues of the longitudinal ridges in other tretodictyids, are composed mainly of longitudinal dictyonal strands which curve and spread towards both dermal and atrial surfaces (Fig. 3C); a few very thick longitudinal strands occur here. The framework of the atrial surface (Fig. 3F) is similar to that of the dermal surface, consisting of very thick strands oriented in all directions, and a network of thinner beams under that surface. Both surfaces are thus covered by a very strong framework, which is not primary in origin and thus is secondary and cortical in nature.

The channel system is schizorhysial and can be directly compared to that of other tretodictyids but modified here by addition of a thin dictyonal cortex over the surface ridge-groove system. Channels extending from the bottom of the grooves enter into the lower dense dictyonal network and there join to a labyrinthic system of interconnected large channels. These eventually open through the atrial framework by ill-defined terminal elements of the schizorhysial system.

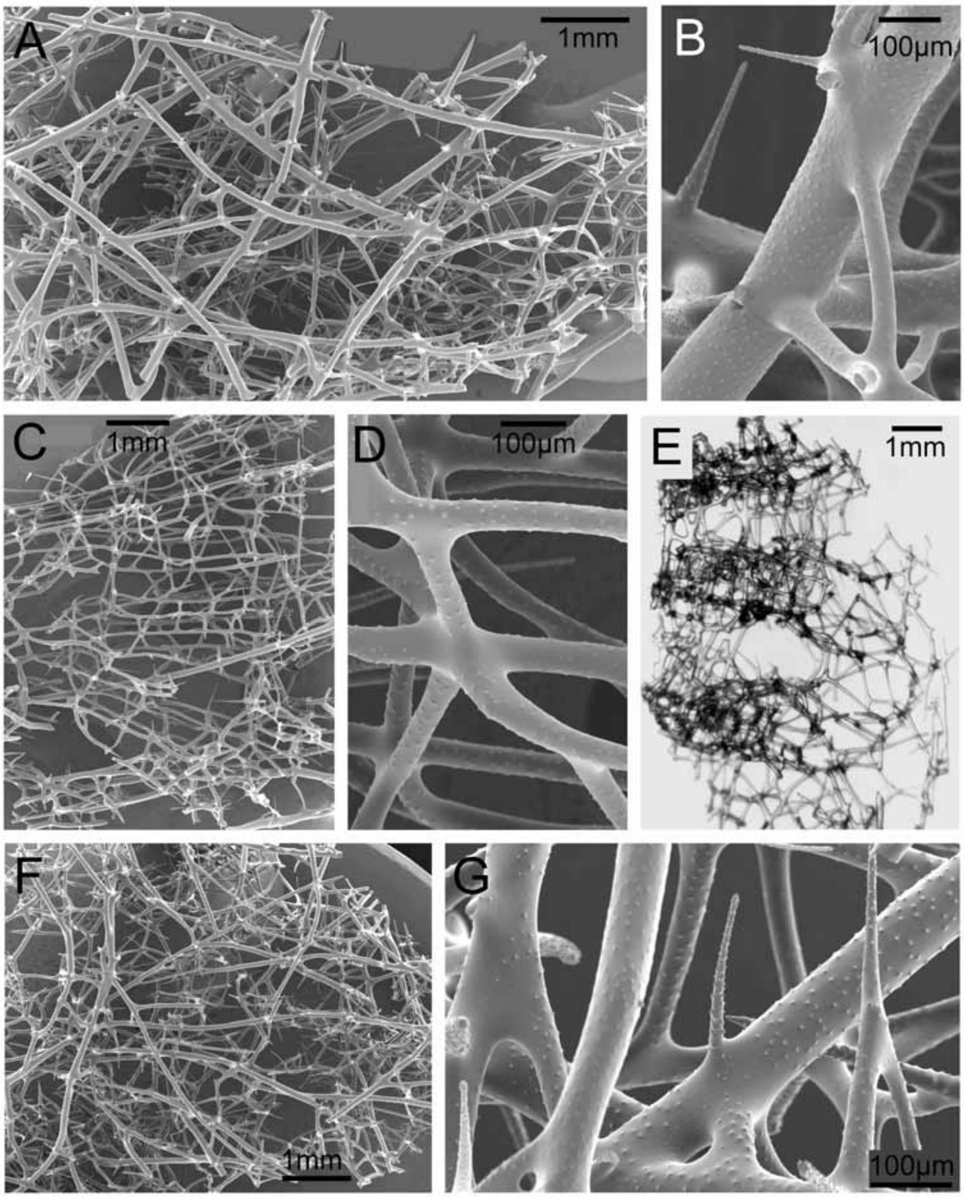

FIGURE 3. Acid-cleaned dictyonal framework of *Tretodictyum montereyensis* **n. sp.** A. dermal surface with entrance apertures to schizorhyses. B. dermal beams and spurs. C. longitudinal section of septum. D. beams and nodes of the internal framework. E. oblique view of ridge/groove system overlain by dermal cortex (dermal surface left). F. atrial surface with indistinct terminations of the schizorhysial channel system. G. beams and spurs of the atrial framework. (A–D, F–G: SEM; E: LM)

The framework meshes are highly variable due to irregular spacing of dictyonal nodes, especially in thick strands (Table 1f). Beams also vary considerably in width as evident in the SEMs (Fig. 3) and measurements (Tab. 1f). Nodes are never swollen and beams are ornamented with small patchily but evenly distributed (within patches) fine spines (Fig. 3B, D, G). Spurs on surface dictyonalia are rough, thin, tapered and sharply pointed.

Spicules. Spicule forms are shown in Figs 4 and 5 and dimensions are given in Table 1. Megascleres are pentactins, occasional subhexactins, strongyloscopules and small uncinates in both dermal and atrial surfaces. Dermalia and atrialia are pentactins and rare subhexactins. They are entirely coarsely rough, and have cylindrical rays that end in abruptly sharp or blunt tips. Irregular step-like reductions in ray diameter are common. The proximal ray may be longer or much shorter than the tangential rays. Scopules occur as a single type as thin (young) and thick (mature) stages; they are entirely rough in SEM but spination can only be resolved on the head with light microscopy. Tines, 3–4 in number, are very slightly splayed and end simply in rounded or indistinct button tips (Fig. 4C). The shaft ends proximally in a sharp tip without inflation or conspicuous increase in spination. Small uncinates occur in bundles oriented vertical to the surface. In light microscopy shallow brackets can be seen with high magnification oil immersion objective, but small barbs (Fig. 5F) can only be seen with SEM.

TABLE 1. Spicule and framework dimensions of *Tretodictyum montereyensis* **n. sp.** CASIZ 175317, from Monterey Bay, California, USA (dimensions in µm).

parameter	mean	st. dev.	range	number
a. Surface pentactin and subhexactin				
tangential ray length	328	48	198–440	100
tangential ray width	30.3	6.9	15.1–50.1	100
proximal ray length	711	70	103–1540	77
proximal ray width	32.8	7.7	16.3–52.0	100
distal ray length	53.4	12.5	24.4–85.7	100
b. Scopule total length	575	95	342–801	50
tine length	77.1	10.8	45.8–94.9	50
shaft width	10.2	2.8	5.1–15.1	50
c. Uncinate length	452	68	206–586	50
width	2.8	0.5	1.6–4.0	50
d. Oxyhexaster diameter	80.5	7.6	65.8–97.6	50
primary ray length	14.8	3.2	8.3–20.8	50
secondary ray length	26.2	3.3	19.9–34.0	50
e. Oxyhexactin diameter	80.9	8.8	57.4–101.3	50
f. Framework beam length	699	377	169–1610	62
Dermal beam width	83	24	34–138	67
Internal septa beam width	50	12	36–98	55

Microscleres consist almost exclusively of oxy-tipped forms (hexasters, hemihexasters, hexactins) but onychohexactins rarely occur – only one was found in SEM preparation (Fig. 5D). Oxy-tipped forms have 1–3 terminals, which are sparsely and finely spined (seen only in SEM) and end in slightly curved tips. The onychohexactin is more coarsely spined than oxy-tipped spicules and its ray tips bear a few recurved claws (Fig. 5D) or stellate buttons from which the claws may have been broken. In both oxy- and onychohexactin forms, the point of demarcation of primary and secondary rays is often marked by an irregular bend.

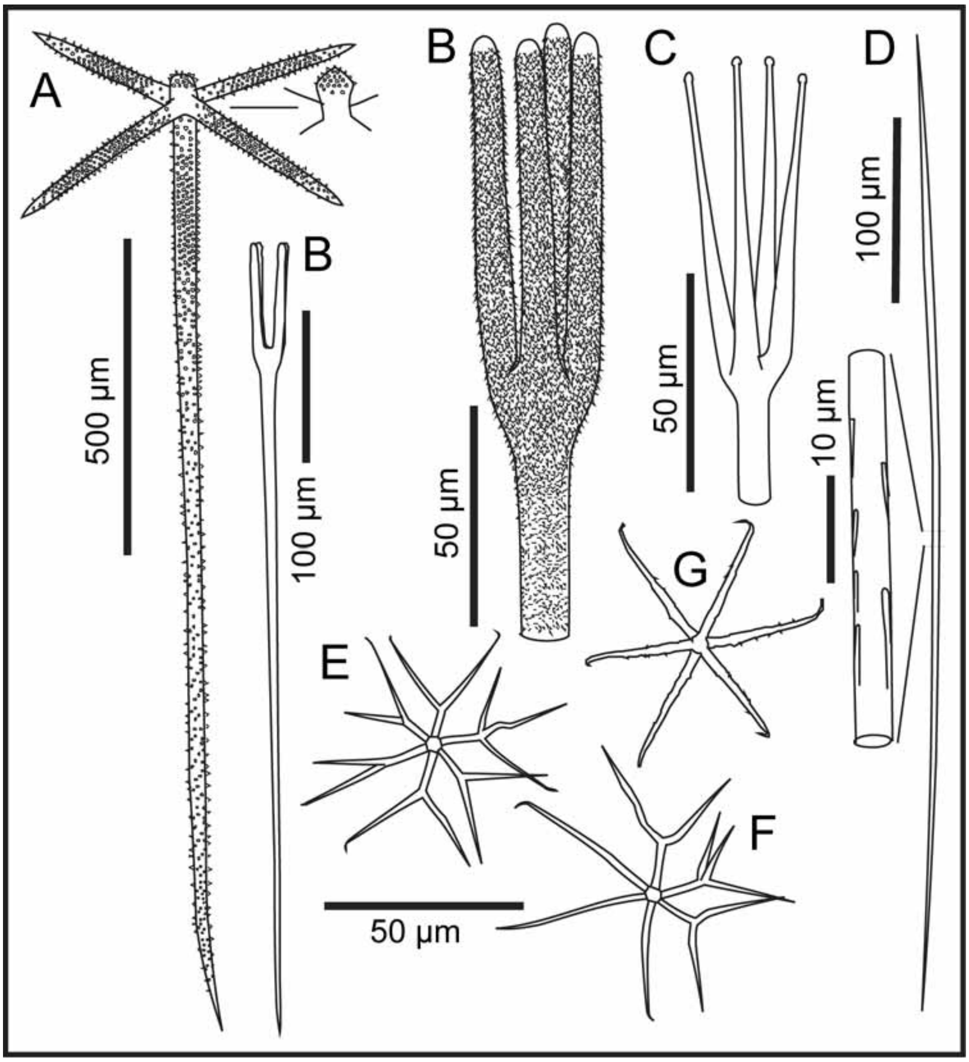

FIGURE 4. Spicules of *Tretodictyum montereyensis* **n. sp.** A. surface pentactin. B, C. narrow and thick stages of scopule. D. uncinate with magnified central section. E. oxyhexaster. F. oxyhemihexaster. G. oxyhexactin.

Etymology. The species name, *montereyensis*, refers to the location of collection, Monterey Bay, California.

Remarks. This species has been briefly described as *Tretodictyum* sp. in Lee *et al.* (2007). Two characters of the framework of this specimen are atypical for members of *Tretodictyum* – the oblique-running, thickened strands in dermal and atrial surfaces and the submersion/overgrowth of the dermal ridge-groove system. Had loose spicules not been available, it would not have been recognizable as a tretodictyid.

The new form differs from the four known species of *Tretodictyum* in these framework characteristics as well as other features. The species *T. minor* (Dendy & Burton), from the Andaman Islands, has the body form of laterally fused tubes, lacks atrialia, has dermalia much thinner than the new form, scopules with up to 9 tines (only 4 in the California form), and lacks oxyhemihexasters and oxyhexactins. *Tretodictyum pumicosum* Ijima, from Indonesia, has dermalia in the form of hexactins with well-developed distal rays. *Tretodictyum schrammeni* Ijima, also from Indonesia, has a branching body form and beam ornamentation of spines in transverse rows. *Tretodictyum tubulosum* (Schulze), from Japan, also has branched body form and no atrialia. The *Tretodictyum* reported from the NE Atlantic and Mediterranean (Boury-Esnault *et al.* 1994) as *T. tubulosum* is similar to the Japan form, but probably represents an undescribed species.

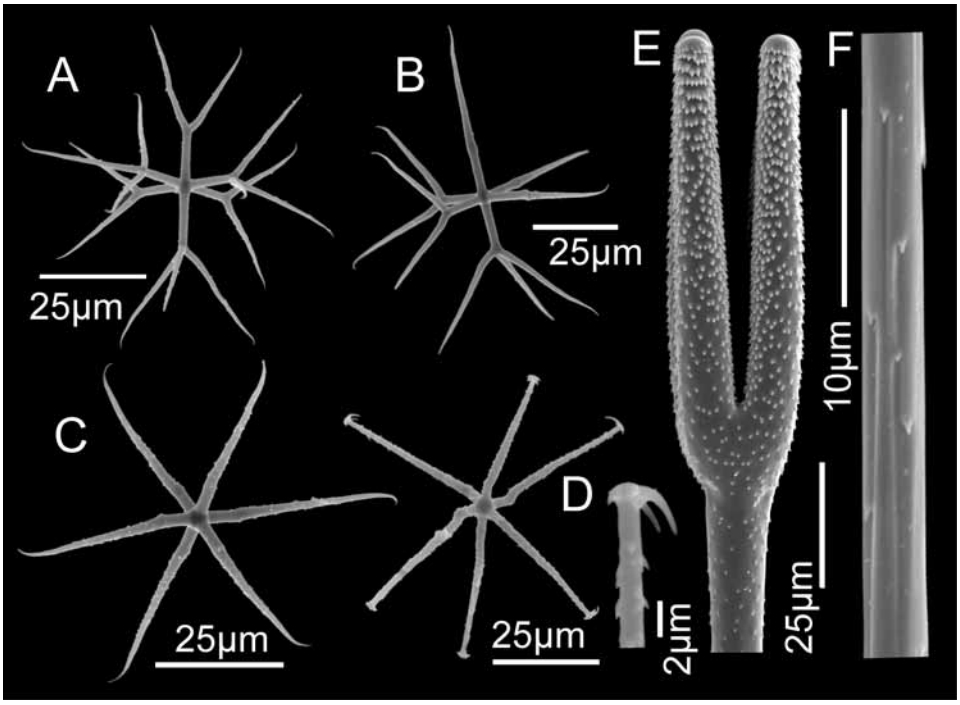

FIGURE 5. SEM micrographs of spicules of *Tretodictyum montereyensis* **n. sp.** A. oxyhexaster. B. oxyhemihexaster. C. oxyhexactin. D. onychohexactin with magnified tip. E. thick scopule head. F. central part of small uncinate showing brackets and very small barbs.

Genus *Hexactinella* Carter

Type species: *Hexactinella ventilabrum* Carter (by monotypy).

Genus diagnosis: Tretodictyidae of variable shape from simple vase or bowl-like to branching tubules; entire external surface including labyrinthic schizorhysial entrances (usually as grooves) covered by a dermal lattice of loose pentactins to subhexactins; discohexasters or variant always present; oxyhexasters present or absent; dictyonal beams ornamented with microtubercles either scattered or in transverse rows; dictyonal nodes usually not swollen but may occur on the dermal frame; scopule usually strongyloform but tylote and oxyote tine tips occur; raphidial uncinates common with or without indications of brackets and barbs (From Reiswig 2002: 1346, emended).

Remarks. The diagnosis is emended to combine definition and diagnosis sections of Reiswig (2002), and to accommodate the swollen dermal nodes in the new species.

***Hexactinella carolinensis* n. sp.**
Figs. 6–9, Table 2.

Material examined. Holotype: USNM 1110009, coll. J. Reed using HBOI manned submersible Johnson-Sea-Link II, Dive 2339, Charleston Lumps, off Charleston, South Carolina, 32°44.068'N, 078°05.955'W, 213 m, 25 May 1992.

Diagnosis. *Hexactinella* with body of branching tubules with microscleres as stellate discohexasters, oxyhexasters and onychohexasters.

Description. The complete body form remains unknown but 8 broken fragments collected (Fig. 6A) are short branching tubules, 6.3-<u>10.6</u>-18.6 mm diameter (n=50). Those fragments that are clearly end branches have terminal oscula leading into atrial tubes 3–4 mm in diameter; tubule walls are 1.5–4.8 mm in thickness. It is possible, but unlikely that atrial tubes are continuous throughout the entire branching body. The outer surface is regularly nodulose due to the coarse schizorhysial skeletal framework (Figs 6B, 7A) consisting of a system of branching and anastomosing ridges outlining irregular surface gaps (grooves) 0.4–1.0–1.7 mm in width (n = 50). When alive, the grooves are covered by a lattice formed by loose pentactine and subhexactine dermalia. The texture is stony hard; the color of the dried fragments is dirty white.

Dictyonal framework. Dimensions of framework elements are given in Table 2. The skeletal framework is constructed of a primary frame of longitudinal strands (Fig. 7C), which run straight or curve to the dermal surface. Internal meshes are mainly rectangular; beams are sparsely spined and internal nodes are not thickened (Fig. 7D, F). A thin cortex is formed on the dermal (distal) and lateral surfaces of ridges where meshes are irregularly 3–5-sided, beams are sparsely spined and nodes are thickened and bear strong conical spines (Fig. 7B, D). Spurs on dermal and lateral ridge surfaces are long, thin and finely rough (Fig. 7D). The atrial framework surface consists mainly of exposed primary strands, but in places small spiny hexactins are fused to the bounding surface forming a dense mat as a thin cortical layer (Fig. 7E).

TABLE 2. Spicule and framework dimensions of *Hexactinella carolinensis* **n. sp.** USNM 1110009, from off Charleston, S. Carolina, USA (dimensions in µm).

parameter	mean	st. dev.	range	number
a. Dermal hexactin				
tangential ray length	210	51	51–313	50
tangential ray width	11.9	3.2	5.4–22.2	50
proximal ray length	366	143	127–738	50
proximal ray width	11.6	2.9	6.5–17.7	50
distal ray length	25.8	9.3	8.6–45.6	50
distal ray width	16.1	3.8	8.1–25.4	50
b. Scopule total length	475	47	385–600	50
tine length	58.3	8.5	33.1–73.8	50
shaft width	4.9	0.7	2.2–6.5	50
c. Uncinate length	607	134	320–903	50
width	2.9	0.7	1.4–4.3	50
d. Discohexaster diameter	74	12	43–99	50
primary ray length	23.3	4.6	11.2–33.4	50
secondary ray length	13.6	2.2	9.7–19.5	50
e. Oxyhexaster diameter	74	10	61–106	50
primary ray length	18.0	3.8	11.4–27.9	50
secondary ray length	20.0	3.1	15.1–30.2	50
f. Onychohexaster diameter	50.5	8.7	34.3–67.6	30
primary ray length	7.1	1.9	4.3–11.1	30
secondary ray length	18.7	3.5	11.1–24.4	30
g. Framework beam length	207	60	82–412	100
dermal beam width	35.7	6.0	24.8–50.3	24
internal septa beam width	30.8	8.8	20.3–54.8	24

Spicules. Spicule forms are shown in Figs 8 and 9; dimensions are given in Table 2. Megascleres are pentactins, subhexactins, strongyloscopules and small uncinates in both dermal and atrial surfaces. Dermalia and atrialia are pentactins and hexactins with very short distal rays. They are entirely finely rough, and have cylindrical rays that end in abruptly sharp or rounded tips. Irregular step-like reductions in ray diameter are common. The proximal ray may be longer or much shorter than the tangential rays. Scopules occur as a single type; they are entirely rough but often spination can only be resolved on the head with light microscopy. Tines, 3–4 in number, are very slightly splayed and end simply in rounded or indistinct button tips (Fig. 9B). The shaft ends proximally in a sharp tip without inflation or conspicuous increase in spination. Small uncinates occur in bundles oriented vertical to the surface. In light microscopy they appear as structureless sharp-tipped rhaphides, but in SEM their shallow brackets and very short barbs are clear. Many have a small central swelling, but an axial cross is not detectable.

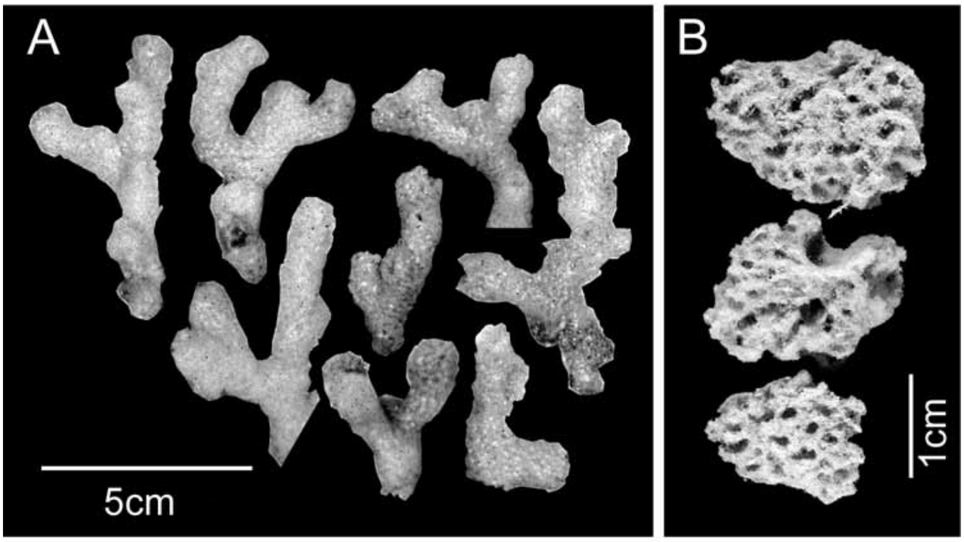

FIGURE 6. *Hexactinella carolinensis* **n. sp.** A. wet body fragments immediately after capture, courtesy of Harbor Branch Oceanographic Institution. B. freeze-dried branch tips.

Microscleres consist of discohexasters, oxyhexasters and onychohexasters. The stellate lophodiscohexasters (Figs. 8E, 9A) are the most abundant microsclere; they are entirely rough, with relatively long primary rays each bearing 6–16 short terminal rays ending in small, marginally-toothed discs. The degree of splay of the terminal tuft is highly variable. Diaster variants of this microsclere type are rare. Oxyhexasters (Figs. 8F, 9D) are the same size as the discohexasters; they are also entirely rough (in SEM) but their primary and terminal rays are almost equal in length. Each primary ray carries 2–3 or rarely 4 terminals ending in sharp, slightly hooked tips. The spherical onychohexasters (Fig. 8G) are rarer, smaller, and thinner than the other microscleres. Each short primary ray bears 2–4 long terminals, ornamented with recurved hooks and tipped with a whorl of 3–5 recurved claws.

Etymology. The species name, *carolinensis*, refers to the location of collection, off S. Carolina, USA.

Remarks. The specimen was originally used for biochemical analysis (identified as "*Farrea* (?) sp.") in Thiel *et al.* (2002), and in the forthcoming first molecular phylogenetic study of Hexactinellida by Dohrmann *et al.* (in press).

Within the genus *Hexactinella*, spiculation of three Indonesian forms, *H. rugosa* Ijima, *H. spongiosa* Ijima and *H. vermiculosa* Ijima, remain unknown. Their geographic location and body form exclude them from receiving the Carolina specimen. Stellate discohexasters are known to occur in only three *Hexactinella* species, *H. grimaldi* Topsent, *H. lata* (Schulze), and *H. lingua* Ijima. Of these, the only one occurring in the Atlantic region, *H. grimaldi*, as redescribed by Ijima (1927), differs from the Carolina specimen in its plate-like body form, probably when entire consisting of a large cup or bowl. It also has oxy-tipped microscleres, but as oxyhexactins instead of oxyhexasters. The Pacific *H. lata* differs from the Carolina specimen in its massive rather than branching body shape and possession of discohexactins and spherical discohexasters instead of stellate ones. The Indonesian form, *H. lingua*, differs from the Carolina specimen in its large plate body form (known only as fragments), and its complete lack of oxy-tipped microscleres. The S. Carolina specimen clearly represents a member of a new species of *Hexactinella*.

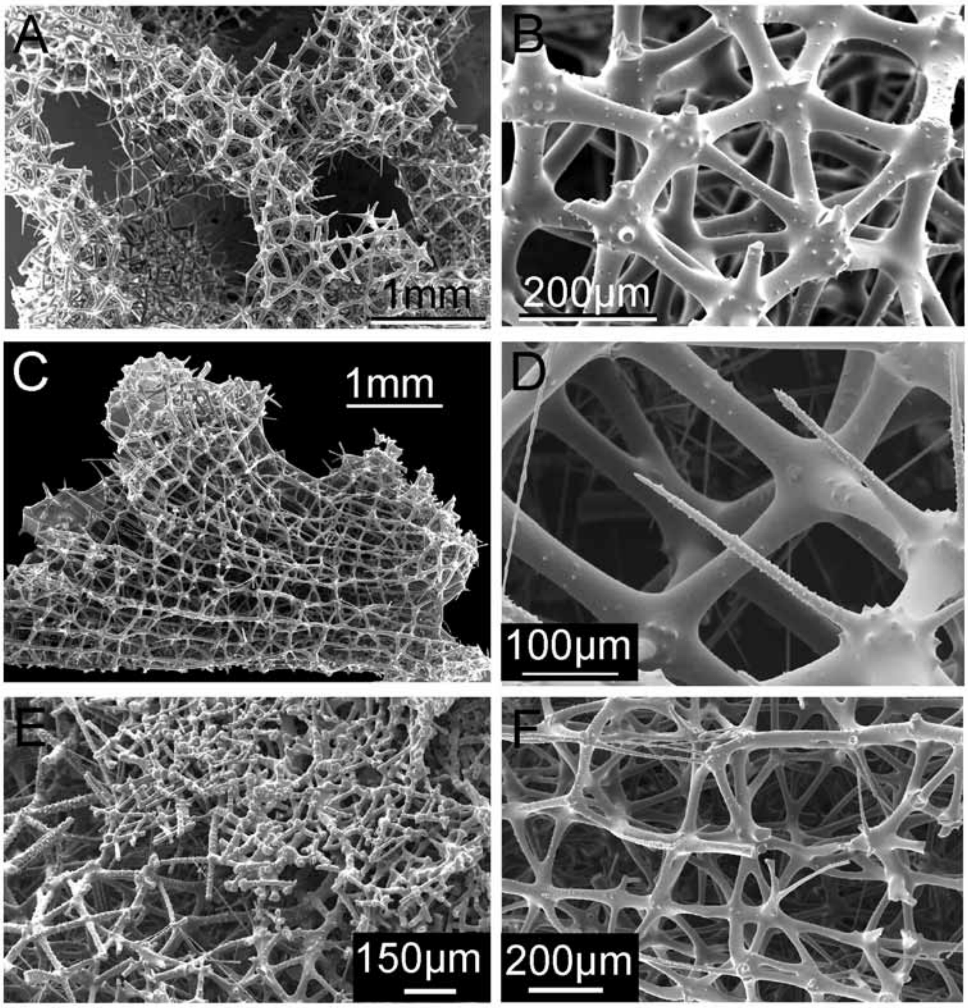

FIGURE 7. Dictyonal framework of *Hexactinella carolinensis* **n. sp.** (all SEM). A. dermal surface with ridge/groove system. B. swollen nodes of the dermal surface. C. longitudinal section through septum showing longitudinal strands, dermal side up. D. beams, nodes and spurs of the outer sides of septum. E. deposition of small spined spicules on the atrial wall. F. magnified view of longitudinal septal section C showing internal beams, nodes, spurs.

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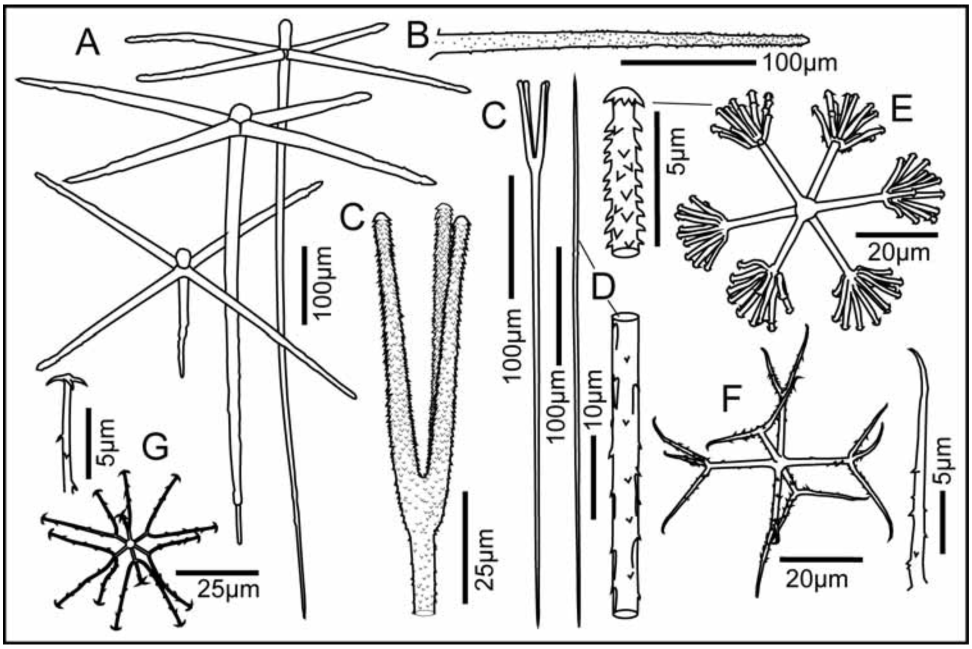

FIGURE 8. Spicules of *Hexactinella carolinensis* **n. sp.** A. various forms of surface pentactins and subhexactins. B. tangential ray of dermal pentactin. C. scopule. D. small uncinate and magnified central part. E. stellate lophodiscohexaster with magnified ray tip. F. oxyhexaster with magnified ray tip. G. onychohexaster with magnified ray tip.

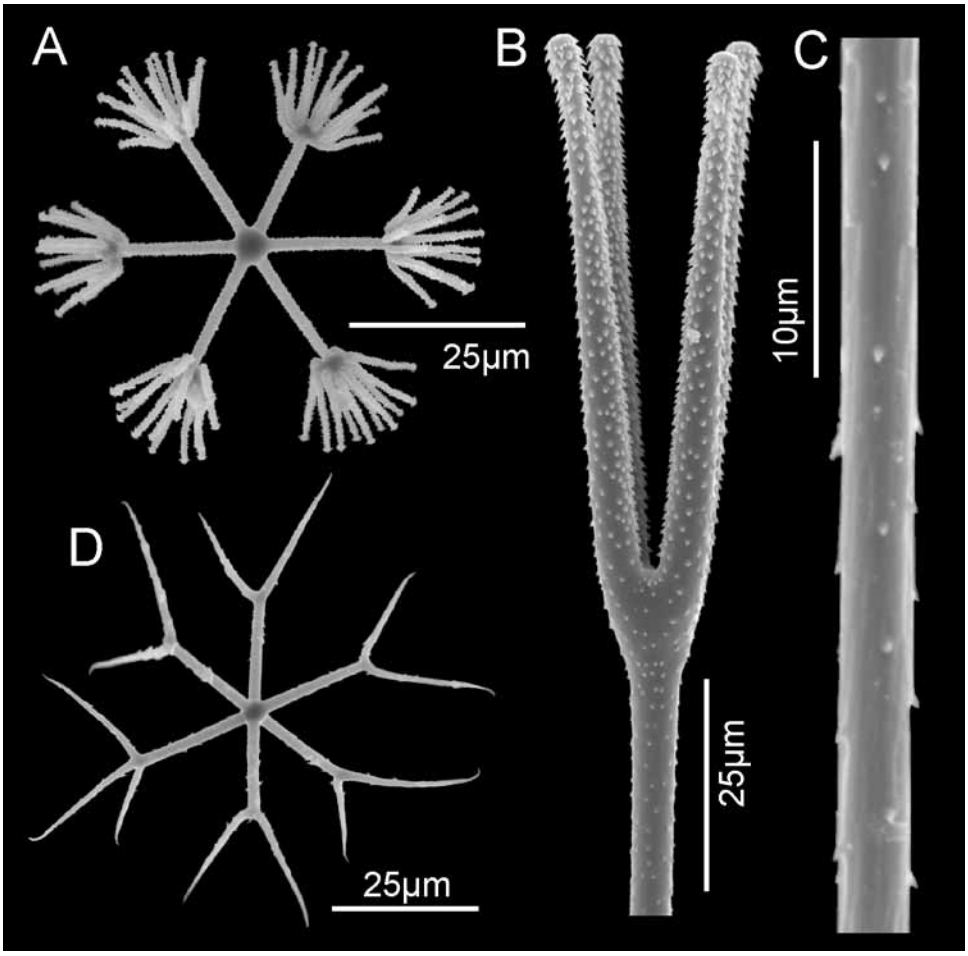

FIGURE 9. SEM micrographs of spicules of *Hexactinella carolinensis* **n. sp.** A. stellate lophodiscohexaster. B. scopule head. C. central part of small uncinate. D. oxyhexaster.

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