

A NEW GENUS AND SPECIES OF
AULOCALYCIDAE, *LEIOPLEGMA POLYPHYLLON*,
(PORIFERA: HEXACTINELLIDA) FROM THE
BLAKE RIDGE OFF SOUTH CAROLINA, U.S.A.

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ABSTRACT

A new genus and species, *Leioplegma polyphyllon*, of the hexactinellid family Aulocalycidae is described from nearly undamaged fragments collected by submersible from the shipwreck of the S.S. CENTRAL AMERICA. Proposed re-diagnosis of the family stresses as its basic feature the formation of primary dictyonal strands from single hexactin rays and returns this group to Ijima's original concept.

The Hexactinellida or deep-sea glass sponges of the eastern United States coast are poorly known. Although the tropical western Atlantic (Gulf of Mexico, Caribbean Sea, and eastern Florida) contains a relatively rich suite of 36 hexactinellid species (Schmidt, 1880), they were originally so poorly described that most new material from this region can presently only be provisionally identified. The only survey of the hexactinellids along the coast between Florida and Nova Scotia (Schulze, 1899) lists just four identified species (two known from one station each), plus two indeterminate forms, all of which were collected north of Virginia. The only reports of hexactinellids from Georgia to Virginia derive from photographic faunal surveys (Rowe and Menzies, 1969; Rowe, 1971) in which the fairly abundant representatives of this group have been unsatisfactorily identified (e.g., the name *Hyalonema boreale* Lovén reported in these is a junior synonym of a demosponge!). The relative paucity of recent reports on hexactinellids from this region can be attributed to (1) the shortage of oceanographic collections, (2) the scarcity of hard substrate which thus restricts diversity and abundance, and (3) the lack of competent taxonomic specialists for identifying collections.

The recent discovery by the Columbus-America Discovery Group of the 1857 shipwreck of the S.S. CENTRAL AMERICA at a depth of 2,200 m on the Blake Ridge, 320 km ESE of Charleston, South Carolina, and the group's development of the specialized robot submersible NEMO for salvage operations have provided a unique opportunity to examine an "island" of rich hard-bottom community in this previously unexplored area (Herdendorf, 1991). The first report on the surprisingly diverse hexactinellids, a major component of the wreck fauna, documented the large euretid *Chonelasma choanoides* Schulze and Kirkpatrick as a deep water species extending throughout the Atlantic from Antarctica to Greenland (Reiswig and Mehl, 1994). Among many apparently new species of hexactinellids recovered by the group's Blake-Ridge Expedition 1986-1991, we here describe a new genus and species of the family Aulocalycidae.

METHODS

Pieces of the dry holotype were prepared for examination of soft tissue remnants, dictyonal framework, and spicules by light microscopy (LM) and scanning electron microscopy (SEM). Fragments with tissues were hydrated, decalcified with HCl, and dehydrated to absolute alcohol. Portions for SEM were air-dried and mounted on pegs while those for LM were cleared in toluene and whole-mounted in Canada balsam. Paraffin sections, ¼- to 1-mm thick, of pieces with soft tissues in place were prepared for LM by standard embedding and hand slicing. Framework and spicules were prepared

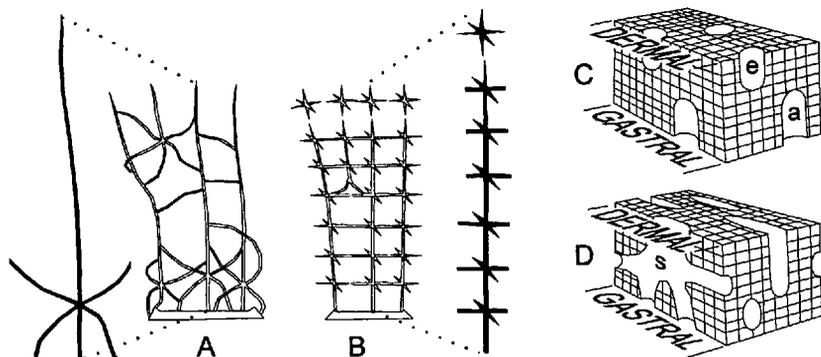


Figure 1. Pertinent skeletal features of Hexactinellida. The basic difference between two skeletal framework types is that primary strands, one extracted from each framework for emphasis, consist of extended single rays of hexactins in the aulocalycids (A) but consist of accreted ranks of aligned hexactins in euretids (B). Typical canals are shown in skeletal wall sections (C and D); canals which extend from the dermal surface and end blindly in the wall (e) are epirhyses (singular: epirhysis), their counterparts extending from the gastral surface (a) are aporhyses (singular: aporhysis), and canals which traverse the entire wall and branch within it (s) are schizorhyses (singular: schizorhysis).

by boiling fragments in HNO_3 , rinsing, drying, and mounting the frame fragments on pegs for SEM while the spicules were either deposited on membrane filters for clearing on slides (Reiswig and Browman, 1987) or rinsed, transferred to slides, dried and mounted directly in balsam. SEM preparations were coated with gold-palladium and viewed with a JEOL-JSM 840A. Spicules and framework structures were measured with a digitizer-microscope connected by camera lucida. Data reported in the text are given as minimum–mean–maximum ($N =$ number of measurements).

Institution abbreviations used in this paper are The Natural History Museum, London (BMNH), the United States National Museum, Washington (USNM), the Museum of Comparative Zoology, Harvard Univ., Cambridge (MCZ), the Redpath Museum, McGill University, Montreal (RMM), the Muséum National d'Histoire Naturelle, Paris (MNHN), and the Zoological Museum, Amsterdam (ZMA).

SYSTEMATICS

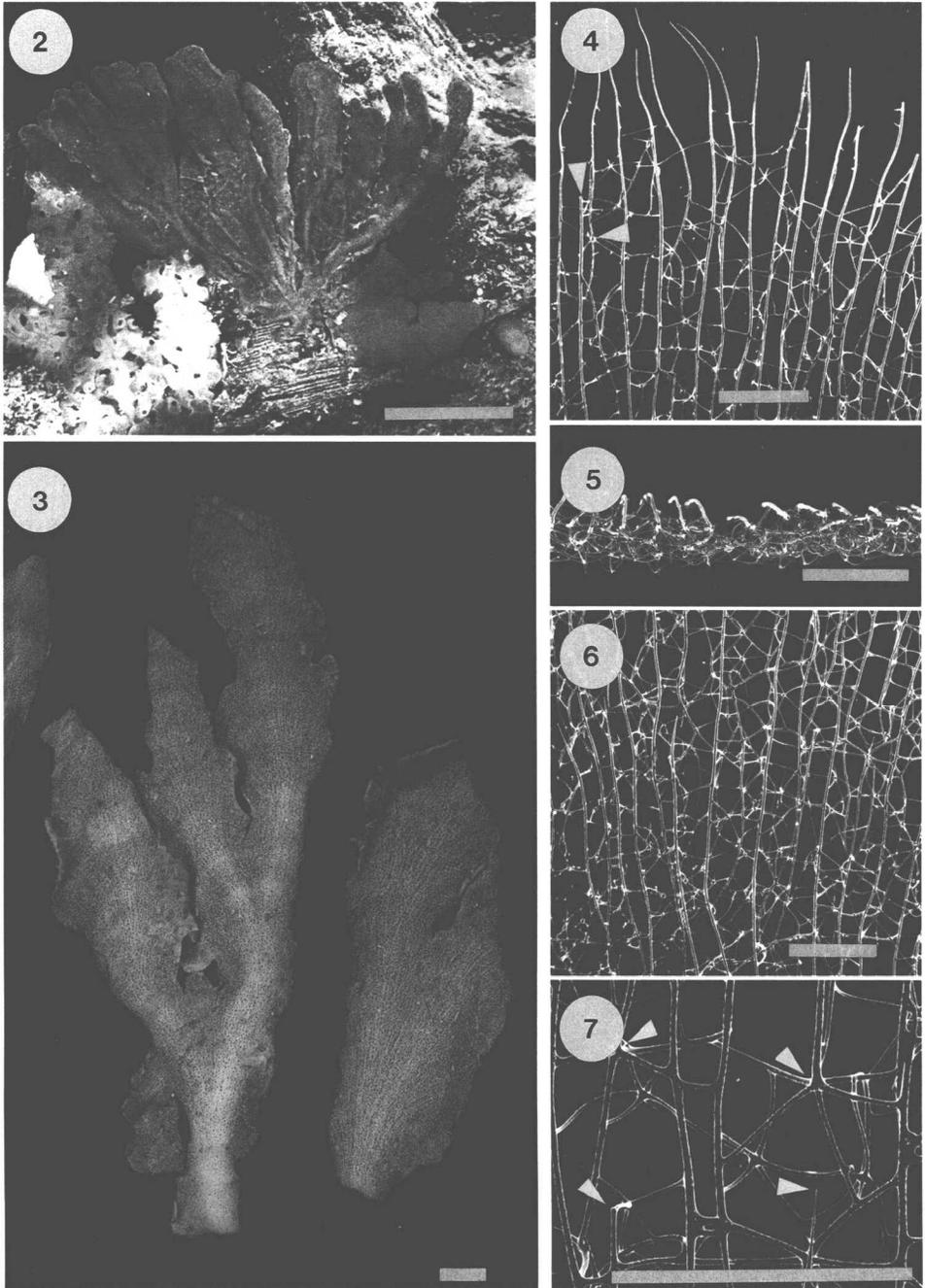
- Class Hexactinellida Schmidt 1870
 Subclass Hexasterophora Schulze, 1886
 Order Hexactinosida Schrammen, 1903
 Suborder Scopularia Schulze, 1885
 Family Aulocalycidae Ijima, 1927

Type Genus.—*Aulocalyx* Schulze, 1886.

Material Examined.—*Aulocalyx irregularis* Schulze, 1886, Holotype and Genotype, BMNH 1887.10.20.73, CHALLENGER Station 145A; *Aulocalyx serialis* Dendy, 1916, Holotype, BMNH 1920.12.9.61, SEALARK; *Euryplegma auriculare* Schulze, 1886, Holotype and Genotype, BMNH 1887.10.20.75, CHALLENGER Station 170A; *Rhabdodictyum delicatum* Schmidt, 1880, MCZ 291 BLAKE Station 131; *Leioplegma polyphyllon* n. g., n. sp. (details below).

Diagnosis.—Scopularia with primary dictyonal (skeletal framework) strands consisting of elongate individual rays of hexactins. Rays of all hexactins of the dictyonal skeleton, primary and secondary, do not connect to centra or to terminal ray tips of other hexactins to form serial hexactin structures (Fig. 1A, B). Canalization varies from superficial epirhyses and aporhyses to complex schizorhyses (Fig. 1C, D). Uncinate and scopule usually absent (modified from Ijima, 1927).

Remarks.—In his original formation of the family, Ijima (1927) stressed the irregularity of connection between hexactins of the skeletal frame and included five genera, *Aulocalyx* Schulze, *Rhabdodictyum* Schmidt, *Euryplegma* Schulze, *Tre-*



Figures 2-7. Holotype specimen and skeletal framework of *Leioplegma polyphyllon* n. sp., all with dermal surface towards the viewer, or, in 5, toward the top of page. 2. The holotype in-situ on a timber of the S.S. CENTRAL AMERICA printed from a computer-edited digitized scan of a color slide ©-Columbus-America Discovery Group, Columbus, Ohio, with permission. 3. Two of the main fragments showing thin lamellate structure with axial condensation and branching pattern. 4. Cleaned skeletal frame at the growing margin dominated by primary strands and their stabilization by cross synapticula and sparse hexactine bridging; arrowheads show a termination point of a primary strand by breakage and its replacement from hexactin lying just proximal and gastral to it. 5. Cross section of the skeletal

troleura Ijima and *Fieldingia* Kent. He was unaware of the continuation of apparently superficial canals through the entire framework of *Euryplegma*, thus he included lack of intradictyonal canalization in his diagnosis. Reid (1957) restudied the holotype of *Euryplegma auriculare* and discovered it had schizorhysis canalization. On the basis of this and his claim to have discovered previously undetected uncinates here, he transferred the species to the Tretodictyidae. He neither examined the shared similarities between *E. auriculare* and the other aulocalycids nor considered the more modest action of modifying Ijima's diagnosis of the Aulocalycidae to retain *Euryplegma* in its original location. In our re-examination of the type specimen of *Euryplegma* we find both uncinates and scopules common in its spicule preparations. However, sectioned material shows these to be of extrinsic origin, most likely from *Chonelasma lamella* and *C. hamatum* collected in the same haul. We agree with Schulze's original conclusion that *E. auriculare* has neither uncinates nor scopules as proper spicules. With our dismissal of Reid's claim of uncinates in *Euryplegma*, and our verification that its type specimen shares aulocalycid primary strands, dermal and gastral pentacts, and discohexasters with *Aulocalyx*, rhopalasters being a discohexaster variant, and, where these are known, with *Rhabdodictyum*, we firmly reject Reid's move of *Euryplegma* and retain it within the Aulocalycidae.

In developing his valuable concept of primary dictyonal strand formation as a major taxonomic character for Hexactinosa systematics, Reid (1958) failed to comprehend the basic difference between the strands of the aulocalycids (which are single hexactin rays) and those of the other hexactinosans (which are aligned rays of serially connected hexactins). In strict application of his definition (Reid, 1958: xxv), aulocalycids would lack dictyonal strands. Reid (1963, 1964) also claimed that *Tretopleura* and *Fieldingia* exhibited an irregular "euretoid" framework, his type 4, and moved these to the Tretodictyidae. Reid gave no basis for the claim that these frameworks were "euretoid", and it is clear that he did not review type material of either genus. With earlier removal of *Euryplegma*, this left only *Aulocalyx* and *Rhabdodictyum* within the Aulocalycidae, the diagnosis of which he modified to stress the interweaving of single or multiple strands of the primary framework, a feature shared by these two genera, but entirely outside Ijima's original concept. Although we have also been unable to re-examine type material of these two genera, we nonetheless reject Reid's move of these on the basis that he had inadequate appreciation of the aulocalycid framework structure and that he provided no support for his "euretoid" framework claim. Although *Tretopleura* and *Fieldingia* do not appear to be closely related to the other three (now four) genera of aulocalycids on the basis of published descriptions, we retain Ijima's placement until type material can be examined in light of more recent views on structural patterns.

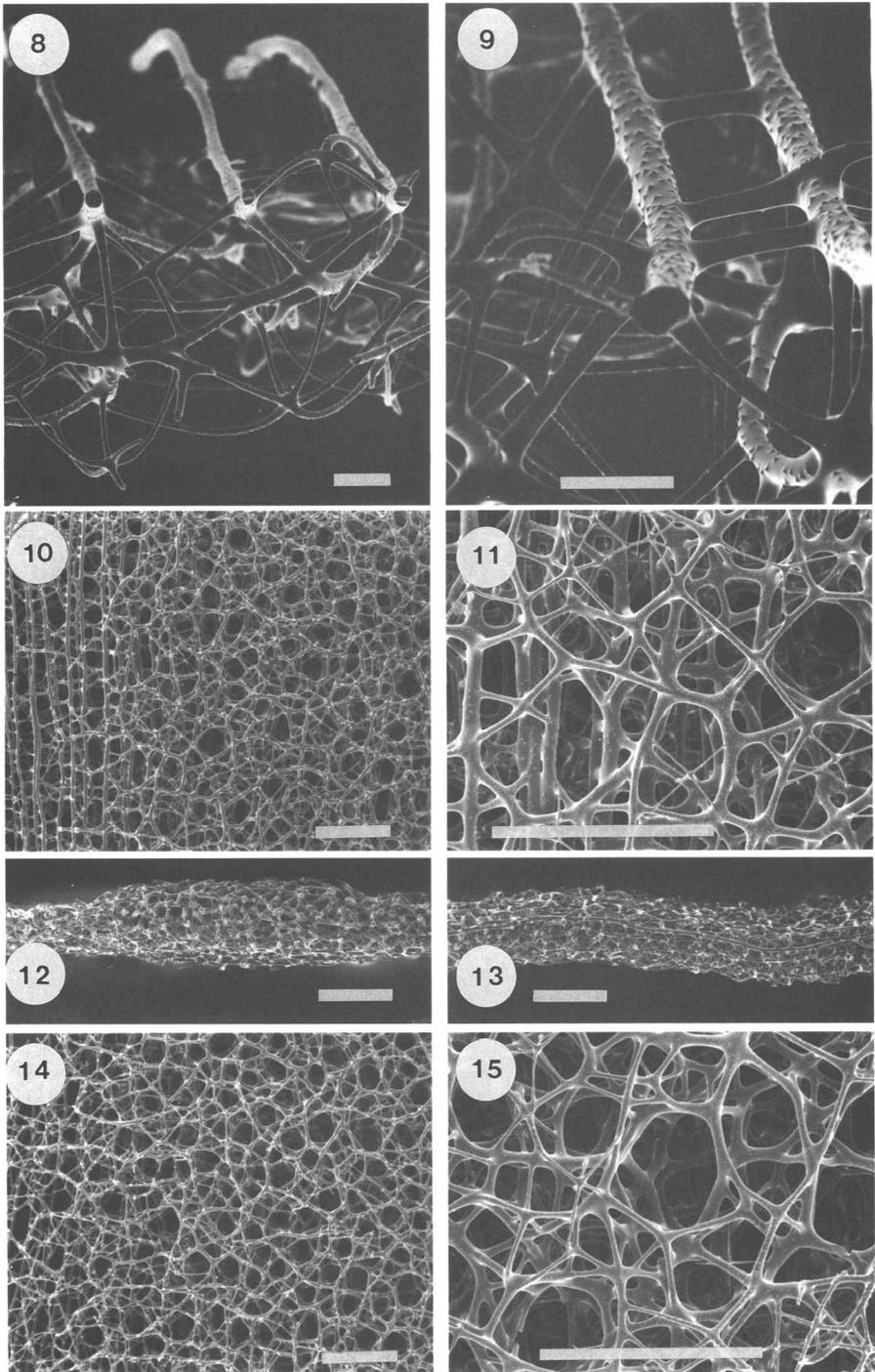
Leioplegma new genus

Type Species.—*Leioplegma polyphyllon* new species

Diagnosis.—Aulocalycid with primary framework composed of longitudinal

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frame about 1 cm from the margin showing slightly undulating primary strands perpendicular to the page and addition of 2–3 layers of irregularly attached hexactins on their gastral side (below). 6. Skeletal frame in facial view 1 cm from the margin (as in 5) with increased density of both synapticula and hexactins. 7. Magnified view of a portion of 6 showing replacement of primary strands after breakage (left arrowheads) and after cessation of growth (central arrowheads). Scale bars are 10 cm in 2, 1 cm in 3, 1 mm in 4–7.



Figures 8–15. Cleaned skeletal framework of *Leioplegma polyphyllon* n. sp., holotype (SEM). 8. Cross section of the peripheral framework showing attachment pattern of gastral and rare dermal secondary hexactins (dermal side up). 9. Magnified view of same showing spination and synapticula joining primary strands. 10. Dermal surface of framework at transition from peripheral (left) to axial (center) regions. 11. Magnified view of secondary meshwork of hexactins and synapticula of the

strands which run parallel to one another in a single plane; each strand originates as a ray of a more basally located hexactin. The strands are interconnected ladder-like by synapticular bridges and irregularly attached hexactins. Lacking scepstrule and uncinata and oxyhexaster.

Eymology.—The generic name is a combination of Greek “leios” = flat and “plegma” = network as descriptive of the one-layered plane of its primary dictyonal strands.

Remarks.—The new genus is most closely related to *Euryplegma* Schulze with which it shares almost identical spiculation and parallel arrangement of longitudinal, nearly straight, primary strands. The major differences between these two are the restriction of the primary strands to a single plane in *Leioplegma* vs. the lateral folding of *Euryplegma* and the simple, poorly differentiated epirhysis and aporhysis in *Leioplegma* vs. schizorhysis in *Euryplegma*.

Leioplegma polyphyllon new species

Figures 2–21

Material Examined.—All specimens: location: Shipwreck of S.S. CENTRAL AMERICA, 31.5°N, 77°W, 2,200 m depth, R/S NEMO from R/V ARCTIC DISCOVERER. Holotype: U.S. National Museum USNM 38774 (25 fragments); Natural History Museum, London BMNH 1994: 8:15:1 (3 fragments); Muséum National d'Histoire Naturelle, Paris MNHN H CL 140 to 142 (3 fragments); Zoological Museum, Amsterdam, ZMA POR 10911 (3 fragments); Redpath Museum, Montreal, RMI-7094 (6 fragments); Coll. R. D. Evans, 21 Sept. 1990, Dive AC. Paratype: USNM 38777, 1 macerated frame fragment; Coll. R. D. Evans, 12 Sept. 1990, Dive HJ. Paratype: USNM 38938, 1 macerated frame fragment; Coll. H. M. Reiswig, 23 Aug. 1991, Dive PUa. Paratype: USNM 38941, 1 macerated frame fragment; Coll. R. D. Evans, 12 Sept. 1990, Dive HJ.

Diagnosis.—Body in the form of an upright, flat fan composed of dichotomously branching shoots emanating from an encrusting basal plate. Spiculation consists of dermal and gastral pentactins, parenchymal intermedial mesohexactins and lophodiscohexasters.

Description.—Size and shape: The holotype, as photographed in-situ before collection, was a flat fan, 37.5 cm wide by 24.1 cm tall (Fig. 2), composed of 5 or 6 main leaf-like branches exhibiting conspicuous axial thickening and emanating from a diffuse basal attachment. The collected material available for description consists of 40 dry fragments exceeding 5 mm in largest dimension and comprising 40.5% of the total 600 cm² surface area of the living specimen. Branching is dichotomous and fusion does not occur between contacting points of adjacent branches. Thickness of the peripheral regions is 0.7–1.0–1.25 mm (N = 5) while that of thickened axial parts is 1.47–1.52–1.57 mm (N = 5). The plumose arrangement of the primary skeletal strands of the dermal surface and the slight longitudinal undulation of the entire branch can easily be seen with the naked eye (Fig. 3). The 3 paratypes, obtained incidentally during general substrate sampling within the shipwreck, are long-dead, macerated fragments, 33–88 mm in length, from axial parts of branches.

DICTYONAL FRAMEWORK. The cleaned framework of the holotype is typically

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dermal surface near the transition. 12. The branch shown in Figure 10 in cross section (dermal side up). 13. Longitudinal section of a branch in the axial region with primary strand enclosed by secondary hexactin coatings on both sides (slightly oblique view, dermal side up). 14. Gastral surface of an axial branch. 15. Magnified view of secondary meshwork of hexactins and synapticular of the axial gastral surface of a branch. Scale bars are 0.1 mm in 8–9; 1 mm in 10–15.

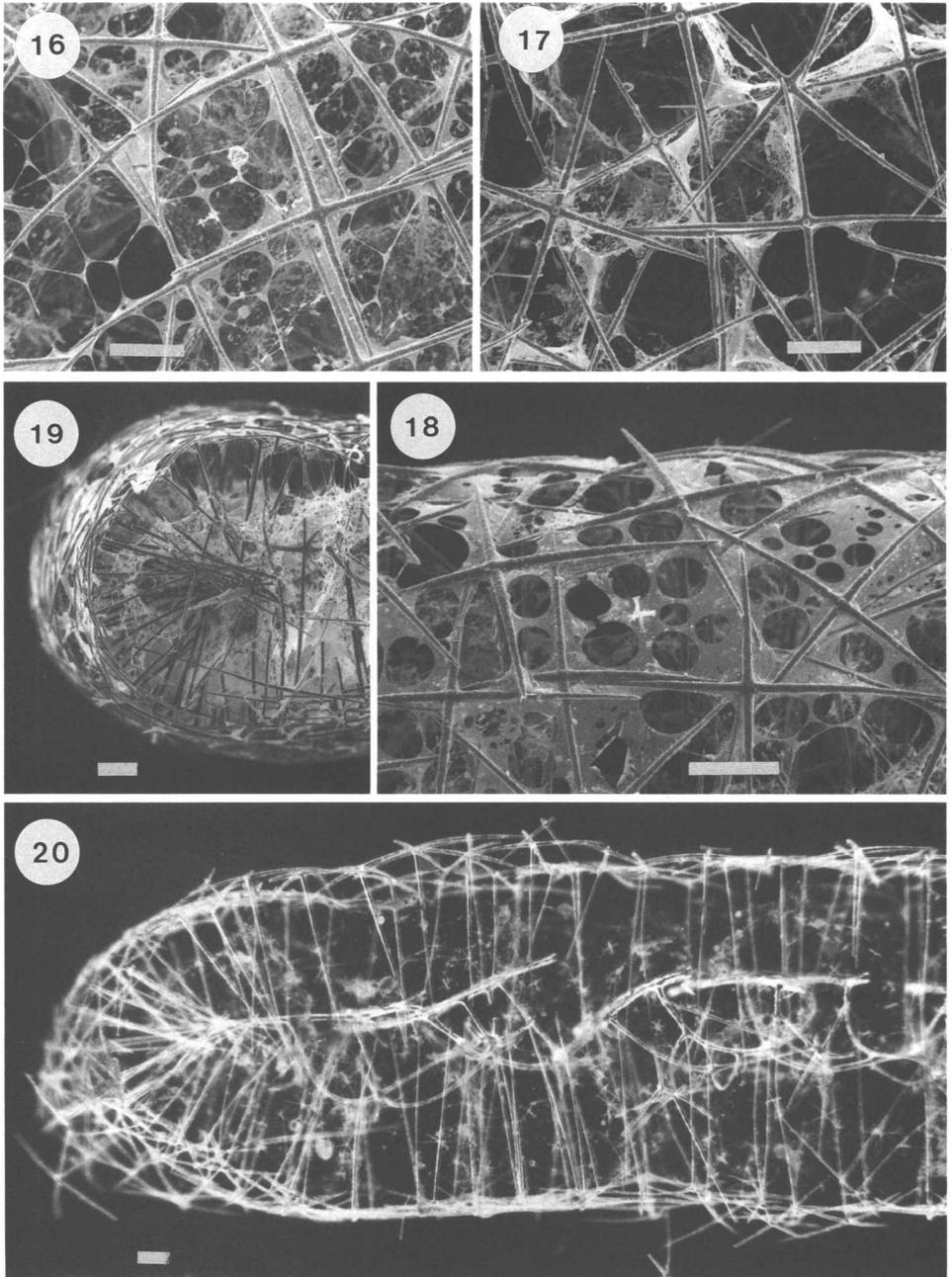
aulocalycid (Fig. 1A). A primary system of longitudinal strands is arrayed in a single plane; each strand is an extension of a individual ray of a hexactin. Support for the longitudinal strands is provided by transverse synaptacula and hexactins mainly attached to the gastral side of the primary strands with all rays fused to any other fixed part of the framework (longitudinal strands, synaptacula, other hexactins) without regularity and without formation of spurs as free ray tips (Figs. 4 to 7). The increase in numbers of hexactins and thickness of beams in central areas of both gastral and dermal surfaces results in visually prominent axial condensation.

At the growing edge, the tips of the longitudinal strands extend as free rays (but within the enclosing tissue envelop) beyond the first few stabilizing synaptacula and gastral hexactins which occur about 1 mm behind the edge (Fig. 4). Primary strands here are 18–22–26 μm diameter ($N = 15$) with center-to-center spacing of 150–200–275 μm ($N = 15$). A few mm behind the free margin, the hexactins added to the gastral side of the undulating plane of the primary strands form a secondary network several layers in thickness (Figs. 5, 8) and synaptacula density also increases (Figs. 6, 9). Addition of new primary strands, required to maintain constant spacing of strands in the expanding plane and to replace broken or naturally terminating strands, occurs almost exclusively by failure of one ray of a newly added hexactin to fuse to the existing frame elements; these unattached rays then undergo continuous elongation (Figs. 4, 7). Of twenty new strand initiations inspected, only one appeared to originate by bifurcation of an existing strand. In this single case, division of the axial thread could not be verified microscopically. New strands extend distally approximately equidistant from, and in the plane of, neighboring primary strands of more basal origin. These strands are conspicuous relative to other frame components in their parallel arrangement, their greater thickness and heavier spination (Figs. 8, 9).

In the axial regions of the main branches a rather abrupt transition occurs on the dermal side of the frame from the uncovered primary strands of the peripheral regions (Figs. 10, 12 left side) to coverage of these by a dense, 300 μm -thick layer of secondary hexactins (Figs. 10, 12 center). This secondary layer consists of hexactins added exactly like those on the gastral surface (without relationship to one another), forming a network with irregular polygonal meshes with a few poorly defined larger vertical channels or poorly delineated epirhyses (Figs. 10, 11). On the gastral side, the coating of secondary hexactins shows no abrupt change from the peripheral regions, but gradually thickens to about 500 μm (Figs. 12, 14). The arrangement of hexactins, meshes, and larger spaces, or poorly delineated aporhyses, is almost indistinguishable from the central axis of the dermal side (Figs. 14, 15). In the branch axis, both secondary layers conform to the longitudinal undulations established during extension of the primary strand layer (Fig. 13).

The primary strands of the axial regions are thicker, 50–63–80 μm ($N = 15$), and more closely spaced, 100–125–140 μm ($N = 15$) center-to-center, than in peripheral regions. They also exhibit more laterally undulating courses, resulting in frequent contact and fusion with adjacent strands. Although new primary strands originate continuously within the peripheral framework, they are also added occasionally in axial regions. The possibility that a few strands may continue from the original set of juvenile hexactins to the distal tips of the mature branches is supported by the length of 35 mm recorded for an incomplete portion of a single strand.

TISSUE SUPPORT. While the aulocalycoid framework provides general support for the entire sponge, local support of tissues and surface membranes is provided



Figures 16–20. Intact tissues and skeleton of *Leioplegma polyphyllon* n. sp., holotype (SEM and LM). 16. Dermal surface showing dermal membrane with ostia supported by pentactins. 17. Gastral surface with open gaps between supporting pentactins. 18. Dermal view of the growth margin showing dermal membrane, ostia and supporting pentactins extending around the edge. 19. Growth margin of a branch with pentactins supporting the encompassing dermal membrane (dermal side up). 20. Slightly oblique cross section of the peripheral region and growth margin of a branch (LM). All scale bars are 0.1 mm.

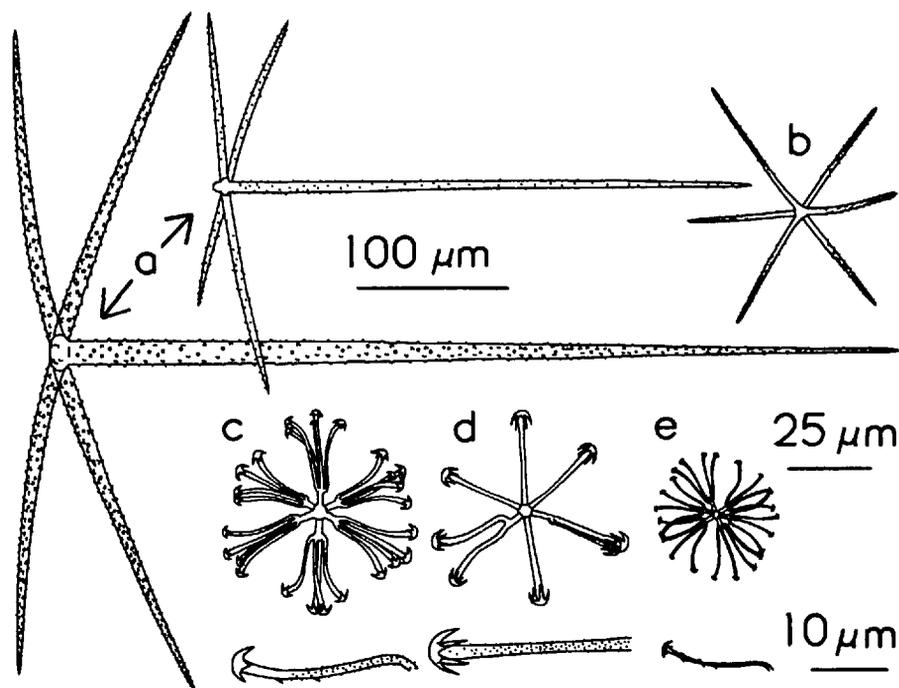


Figure 21. Spicules of *Leioplegma polyphyllon* n. sp., holotype; a, two pentactins; b, mesohexactin; c, most common lophodiscohexaster with terminal ray magnified; d, robust hemilophodiscohexaster with terminal ray magnified; e, delicate lophodiscohexaster variant with greater angle of secondary tuft, terminal ray magnified.

by radiating systems of unfused, large, pentactine spicules. The dermal membrane is supported by a slightly irregular, quadrate latticework formed by the tangential rays of the pentacts (Fig. 16). Ostia which range from 10–100 μm in the rehydrated and redried specimen may not reflect dimensions of those openings in the living state. The gastral surface, also supported by tangential rays of large pentacts, is less regularly quadrate and lacks a differentiated membrane over most of its surface (Fig. 17). Large gaps between the pentactin rays are widely open to the exhalant channels of the choanosome and the exhalant apertures of flagellated chambers located in the subgastral space. At the growing margin, the dermal membrane, with ostia, is supported around the hemispherical (in section) rim by a radiating palisade of closely-spaced pentactins (Figs. 18, 19, 20). Occasional pentacts project above the surface plane near the growth margin but these are not sufficiently common to form a veil. Proximal rays of the supporting pentactins project into the region of the central aulocalycoid framework but do not make direct contact with those elements (Fig. 20). This arrangement combines structural support provided by the central framework with a flexible system of loose pentacts capable of extension and retraction of tissues on both sides of the framework.

SPICULES. The relatively simple loose spiculation consists of three types: pentactins, hexactins, and discohexasters (Fig. 21 and Table 1). The microtuberculate pentactins are highly variable in size, but differ significantly in length of rays on the two sides of the framework, the dermal pentactins have longer tangential rays but shorter parenchymal rays than those of the gastral surface (*t*-test, $P < 0.01$). The medium-size, microspined hexactins (mesohexactins) are distributed through-

Table 1. Spicule dimensions of the *Leioplegma polyphyllon* holotype in μm except where noted; SD = standard deviation; N = number of measurements

Spicule type	Length \pm SD	Range	N	Width \pm SD	Range	N
Pentactin, dermal						
tangential ray	235 \pm 40	99–300	100	11.6 \pm 1.7	8.0–15.8	100
parenchymal ray	512 \pm 80	316–731	100	11.6 \pm 2.3	5.9–18.4	100
Pentactin, gastral						
tangential ray	214 \pm 29	156–284	100	10.7 \pm 1.9	5.8–15.9	100
parenchymal ray	597 \pm 56	461–741	100	11.4 \pm 1.5	8.3–15.2	100
Hexactin, ray	77 \pm 16	41–138	100	2.9 \pm 0.5	1.5–4.7	100
Discohexaster						
radius	25.0 \pm 4.3	9.9–37.5	502	—	—	—
primary ray	5.8 \pm 1.1	3.3–8.5	100	—	—	—
secondary angle*	46 \pm 12	18–89	250	—	—	—

* Angle in degrees of secondary tuft profile from branch point to widest tips.

out the gastral choanosome but on the dermal side are limited to a band about 200 μm wide adjacent to the framework. Their distribution coincides with sites of hexactin addition to the framework, providing strong circumstantial evidence that this spicule class provides components for framework expansion. The discohexasters, generally distributed throughout the body wall, are highly variable in size and in form, the most common being the relatively robust lophodiscohexaster (Fig. 21c). Although hexactinoid, hemihexasterous (Fig. 21d) and more delicate lophoid forms with greater splay of the secondary tuft (Fig. 21e) occur in moderate numbers; they are not separable as distinct spicule classes from the more common lophoid type by size-frequency analysis of spicule radius or angle of the secondary tuft.

Etymology.—The species name is derived from Greek “polyphyllon” = leafy (neuter: “polyphyllon”) as a reflection of its body form.

Remarks.—The holotype has been previously figured by Noonan (1992: 40). This species is considered to be most closely related to *Euryplegma auriculare* for reasons reviewed under generic remarks. *Leioplegma polyphyllon* is very similar in body form to the Pacific eurentid *Bathyxiphus subtilis* Schulze, 1899. In benthic video or photographic surveys it might easily be confused with branching variants, *Bathyxiphus* sp. (Schulze and Kirkpatrick, 1911) reported from the Atlantic basin near Antarctica. The basic differences between these convergent, flattened, branching forms in dictyonal framework structure is obvious when inspected with even a low power hand lens—*L. polyphyllon* exhibiting the distinctive aulocalycid structure (Fig. 1A) and *Bathyxiphus* exhibiting the more common eurentid structure (Fig. 1B).

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