Systema Porifera: A Guide to the Classification of Sponges, Edited by John N.A. Hooper and Rob W.M. Van Soest

Family Aulocalycidae Ijima, 1927

Henry M. Reiswig

Natural History Section, Royal British Columbia Museum, 675 Belleville Street, Victoria, British Columbia, Canada V8W 9W2 and Biology Department, University of Victoria, P.O. Box 3020 STN CSC, Victoria, British Columbia, Canada V8W 3N5. (hmreiswig@shaw.ca)

Aulocalycidae Ijima (Hexactinellida, Hexasterophora), and Uncinateridae Reiswig (fam. nov.) make up the recently erected order Aulocalycoida Tabachnick & Reiswig, distinguished by longitudinal strands consisting of extension of individual dictyonal rays and fusion of dictyonalia tip-to-ray. Aulocalycidae is distinguished from Uncinateridae by the uniaxial nature of its longitudinal strands (multiaxial in Uncinateridae), lack of additional dictyonalia along strands (present in Uncinateridae) and abundance of synapticula as stabilizing structures (absent in Uncinateridae). The term for pattern of dictyonal structure of Aulocalycidae is retained as 'aulocalycoid', that for the new pattern of Uncinateridae is 'paraulocalycoid'. Five genera with only six species are presently recognized as members of Aulocalycidae. On the basis of very few documented occurrences the family is world-wide in distribution, but so far unreported from N and E Pacific and S Atlantic regions. Species have been recorded from depths of 204 to 3680 m.

Keywords: Porifera; Hexactinellida; Aulocalycoida; Aulocalycidae; *Aulocalyx*; *Euryplegma*; *Ijimadictyum*; *Leioplegma*; *Rhabdodictyum*.

DEFINITION, DIAGNOSIS & SCOPE

Restricted synonymy

Aulocalycidae Ijima, 1927. Euryplegmatidae de Laubenfels, 1955b.

Definition

Basiphytous Aulocalycoida with connecting framework elements as uniaxial rays of hexactine dictyonalia or anaxial synapticula; primary structural elements usually conspicuous longitudinal strands formed as extended single dictyonal rays; sceptrule absent.

Diagnosis

Body form highly variable from dichotomously branching fan to unbranched tongue-like plate to branching tubes with lateral oscula either as simple wall gaps, sparse or profuse, or extended on tubular projections; channelization absent or as shallow epirhyses and aporhyses, or schizorhyses; dermalia and atrialia always as rough or occasionally smooth pentactins; choanosomal hexactins present in some; microscleres always include discohexasters while rhopalasters, spirodiscohexasters, hemidiscohexasters and discohexactins may occur; rare uncinates may occur as proper or foreign spicules; sceptrules are absent.

Remarks

Schulze (1885) first used the term Euryplegmatidae, but without a described species it was a nomen nudum. Schulze never used the name again; upon first description of *Euryplegma* (1886) he assigned the genus to Tretodictyidae. Euryplegmatidae was used once more by Sollas (1887) after Schulze's descriptions were published, and might be considered a valid formation and hence the senior family name for Ijima's (1927) later grouping, Aulocalycidae, but Sollas was clearly parroting Schulze's 1885 arrangement – he was both behind times and had no intention of erecting a family. Sollas's reiteration is not recognized as a taxonomic action and has neither standing nor priority. Most of the genera now included in the family have a long history of uncertain placement (see remarks of individual genera) due to their deviation from the typical euretoid pattern of framework construction. Ijima (1927) first recognized the distinctive structural pattern in a suite of five genera, but enunciated it crudely and offered no explanatory diagram. The components he offered in his Aulocalycidae diagnosis, here considered important, were: (1) framework rays frequently elongated and curved; (2) framework hexactins oriented without regularity; (3) rays intersecting one another at various angles and fusing at intersections, at lateral appositions or at abutting points; and (4) rays often connected by synapticula. Reid (1963b) defined an aulocalycoid condition of dictyonal framework using, not Ijima's criteria, but his own impressions: "… the meshwork of the dictyonal framework is initially three-dimensional and has dictyonal strands interwoven diagonally in an irregular manner". With this definition, which had nothing to do with Ijima's diagnosis of the family, Reid (1964) removed *Euryplegma*, *Tretopleura* and *Fieldingia* from the family since they did not fit his (not Ijima's) criteria of aulocalycoid construction. As a result of Reid's unfortunate reformation of concept and destruction of Ijima's grouping, Mehl (1992) was understandably confused in dealing with the family. She considered *Rhabdodictyum* to be a lyssacinosan, in spite of complete absence of diactins as framework components, and agreed with Reid that the Aulocalycidae was artificial. She appropriately separated the two existing *Rhabdodictyum* species by erection of a new genus, *Ijimadictyum* for *R. kurense*, a form she incorrectly considered to be euretoid. Reiswig & Tsurumi (1996), in erecting a new genus, *Leioplegma*, reviewed evidence for and against recognition of Ijima's original Aulocalycidae. They found Ijima's characters to be appropriate for his original grouping, and extended the defining criteria to replace Reid's incorrect definition of aulocalycoid. They reformed the

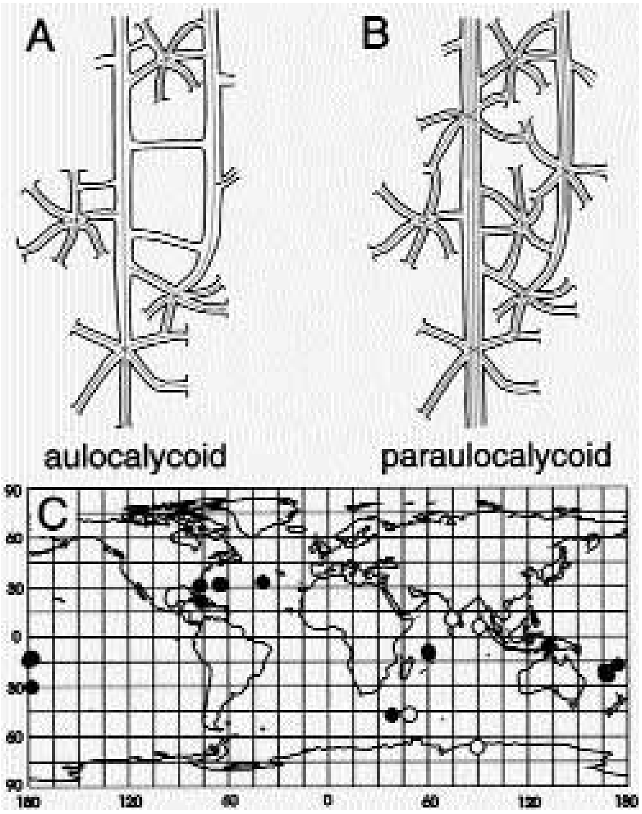

Fig. 1. Aulocalycidae. A–B, aulocalycoid pattern of dictyonal structure in Aulocalycidae (left), with all components uniaxial or anaxial (synapticula), and paraulocalycoid pattern (new) of Uncinateridae (right), with longitudinal strands multiaxial and all connecting beams uniaxial (synapticula absent); growth margin towards top. C, distribution of Aulocalycidea – verified species as filled circles; speciments surely aulocalycids but undeterminable to genus as empty circles.

diagnosis of the family which has recently been accepted by Tabachnick & Reiswig (2000) as defining features of the new order Aulocalycoida. In review of the poorly understood genera *Uncinatera*, *Ijimadictyon* and *Tretopleura* for this work, a new pattern has been recognized within the aulocalycoid group, necessitating slight reorganization of defining criteria. The order Aulocalycoida remains defined by: (1) dictyonal strands formed by prolongation of dictyonal rays; (2) connecting dictyonal rays extend from originating centra to fuse onto other dictyonal rays at any angle, and do not connect to other centra; and (3) all non-strand dictyonal rays are uniaxial since they never align in parallel with other rays. Members of the order may have epirhyses, aporhyses or schizorhyses or no channelization. Within the order, the family Aulocalycidae is here restricted to forms with longitudinal strands consisting entirely of single dictyonal rays, thus bearing single axial filaments from initiation at centra to free-ending tips. The strands are positionally stabilized by synapticula and rays of secondary dictyonalia fused laterally to them. The new family, Uncinateridae, differs in that longitudinal strands are constructed by addition of dictyonal centra directly onto the lateral surfaces of existing strands, and such appended dictyonalia are aligned with one axis to the strand – a pattern of dictyonal structure designated paraulocalycoid. The strands thus become polyaxial with axial filaments extensively overlapping, usually containing three filaments at any point. The role and fusions of secondary dictyonalia remain the same, but synapticula are reduced or absent in the new family. This reformulation negates all elements of Reid's aulocalycoid condition – the framework is not necessarily initially three-dimensional as shown in two dimensional edge of *Leioplegma* – the dictyonal strands are not interwoven diagonally in most genera. The family may represent early stages of development of a fully dictyonal framework as seen in euretoid forms. Initial dictyonal strands, without stabilization of secondary dictyonalia, may have developed from basidictyonal plates known in several lyssacine groups. Structural stabilization may have first occurred by synapticula alone, as in lyssacines, with secondary dictyonalia added progressively as incorporation of basidictyonalia expanded upwards onto the poorly stabilized strands. Eventually, through dictyonal beam alignments seen in strands of Uncinateridae, side-by-side fusion of dictyonalia may have expanded, culminating in the sturdy euretoid construction characteristic of most hexactinosans. It is enticing to consider that the 'irregular' method of secondary dictyonalia addition in the Aulocalycoida may be retained in secondary layers of many euretoid hexactinosans. Much detailed work remains to verify or reject that phylogenetically interesting supposition. The family Aulocalycidae, as formulated here, contains six species in five genera. With exception of *Fieldingia*, here considered Hexactinosida *incertae sedis*, and transfer of *Tretopleura* to Uncinateridae, the rest of Ijima's original genera and additions since then are retained in Aulocalycidae. The family is distributed world-wide, but has not been reported from N and W Pacific and S Atlantic regions. It ranges from 204 to 3680 m in depth.

Scope

Five valid genera: *Aulocalyx* Schulze, 1886. *Euryplegma* Schulze, 1886. *Ijimadictyum* Mehl, 1992. *Leioplegma* Reiswig & Tsurumi, 1996. *Rhabdodictyum* Schmidt, 1880b.

KEY TO GENERA

(1) Body of branching tubes or cup with short lateral tubes 2
Body fan- or tongue-shape without tubular elements 4
(2) With rhopalasters as distinctive microscleres .... ***Aulocalyx***
Without rhopalasters 3
(3) Parietal gaps large and closely spaced; wall lace-like .... ***Rhabdodictyum***
Parietal gaps small, sparse; wall thin and mostly imperforate .... ***Ijimadictyum***
(4) Longitudinal strands in a single plane, frame unchannelized .... ***Leioplegma***
Longitudinal strands in three-dimensional array, with schizorhyses .... ***Euryplegma***

AULOCALYX SCHULZE, 1886

Restricted synonymy

Aulocalyx Schulze, 1886: 56.

Type species

Aulocalyx irregularis Schulze, 1886: 56 (by monotypy).

Definition

Aulocalycidae with thin-wall cup or sac body bearing accessory oscula on short body wall tubes or ridges; with distinctive rhopalasters as large microscleres.

Diagnosis

Body attached to hard substrate by small basal disc with stony-hard skeleton; skeletal frame progressively softer and more flexible towards fragile distal end; framework unchannelized; dermalia and atrialia as rough pentactins; microscleres include rhopalasters, discohexasters, and sometimes oxyhexactins; uncinates and sceptrules are absent.

Remarks

In his original formation of the genus, Schulze (1886) had difficulty assigning it to either Dictyonina or Lyssacina because of the completely irregular and distal lightness of the siliceous framework. He eventually chose to include it within the lyssacine Rossellidae. Ijima (1898) aligned *Aulocalyx* with his new *Leucopsacus* but, after finally deciding *Aulocalyx* was more likely a dictyonine, transferred it to the resurrected Dactylocalycidae. Ijima (1927) finally erected the family Aulocalycidae to include *Aulocalyx* as its type and other genera with similarly irregular, non-euretoid skeletal frameworks, later named 'aulocalycoid' by Reid (1963b). The genus consists of two species, *A. irregularis* Schulze and *A. serialis* Dendy. Literature reports of *Aulocalyx* distribution include several errors resulting from the early assumption that any specimen with aulocalycoid framework was *A. irregularis*. Without good spiculation, these specimens (Schulze, 1887: 'Challenger' stns 56, 147; Schulze & Kirkpatrick, 1911: Gauss Station, Antarctica) cannot confidently be assigned to specific genera and must remain Aulocalycidae gen? sp? Thus *A. irregularis* is certainly known from only one location, 'Challenger' station 145a near Marion Is., SE of Cape of Good Hope. The genus is confidently known from only three locations, the preceding and two locations in the Saya de Malha Group, W. Indian Ocean at depths of 567–915 m.

Description of type species

Aulocalyx irregularis Schulze (Fig. 2).

Restricted synonymy. *Aulocalyx irregularis* Schulze, 1886: 56; Schulze, 1887: 174, pl. XL, figs 1–6; Schulze, 1897: 544.

Material examined. Lectotype (here designated): BMNH 1887.10.20.073 (wet specimen) – near Marion Is., SE of Cape of Good Hope. Paralectotypes (here designated): BMNH 1887.10.20.073A (dry fragments) – same location. ZMB 5384 (not examined) – same locality.

Description. Body as a thin-walled (2–3 mm thick), laterally folded cup to 4 cm tall with large terminal stellate osculum; lateral folds bear short tubes with terminal accessory oscula; basally attached to hard substrate by irregular stony-hard basal mass; body rigidity decreases distally to a soft, loose, fragile margin (severely damaged and mostly lost in type series); framework not channelized, very irregular in form, composed of medium-size hexactins (no diactins) connected by direct but haphazard fusion and profuse synapticula; meshes mainly triangular, highly variable in size from few μm to 2 mm; beams smooth, 25–*82*–186 μm thick; nodes simple, not swollen or ornamented; small thickened hexactins fused singly or in groups to framework; dermalia and atrialia as finely-rough pentactins with tangential ray length 191–*281*–384 μm, proximal ray length 313–*450*–560 μm with blunt, eroded tips; microscleres as oxyhexactins, rhopalasters and discohexasters; regular, completely spined oxyhexactins distributed throughout wall 47–*107*–175 μm diameter; large subdermal rhopalasters with very short principal rays each bearing 6 club-shaped terminals completely ornamented with sharp reclined thorns, 300–400 μm diameter; parenchymal discohexasters 50–120 μm in diameter, each principal bearing 5–7 s-shaped terminals ending in toothed discs; uncinates and sceptrules are absent; known only from one location near Marion Is., SE of Cape of Good Hope from 567 m depth.

Remarks. Body form of *A. irregularis* remains poorly known; the original specimens were severely damaged and not effectively illustrated. Size and texture of surface pentactins are also uncertain since Schulze provided no direct measurements and his composite wall section (Schulze, 1887, pl. XL, fig. 3) is likely inaccurate in dimensional details – illustrated pentactins are over 3.5× larger than those measured from lectotype fragments (data in description above). Several location occurrences of the species which are consistently reiterated in literature are unsubstantiated as noted above under genus remarks.

EURYPLEGMA SCHULZE, 1886

Restricted synonymy

Euryplegma Schulze, 1886: 80.

Type species

Euryplegma auriculare Schulze, 1886: 80 (by monotypy).

Definition

Semi-involute tongue-shaped body with aulocalycoid framework bearing schizorhyses-like channels; dermalia and atrialia as pentactins; choanosomal hexactins spanning micro- and megasclere size ranges; proper microscleres are mainly perianthic discohexasters.

Diagnosis

Monospecific. See type species description.

Remarks

Placement of this genus during early development of Hexactinellida systematics was very unstable – it did not fit

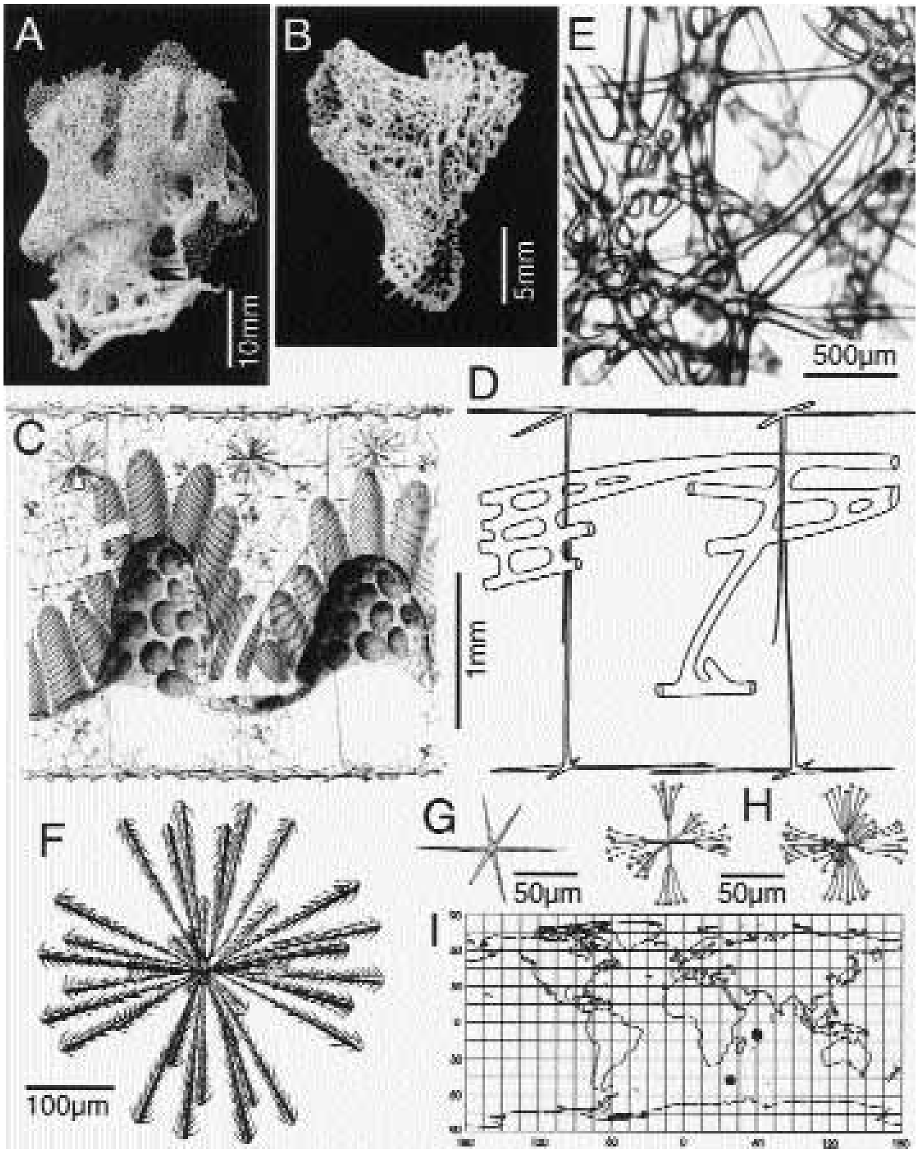

Fig. 2. *Aulocalyx irregularis* and distribution of *Aulocalyx*. A–B, body form of the lectotype (A) and a paralectotype fragment (B). C, composite wall section. D, dictyonal frame and surface megascleres (extracted from C). E, irregularity of dictyonal framework viewed from atrial surface. F, rhopalaster. G, microhexactin. H, two discohexasters differing in primary/secondary length ratios. I, distribution of *Aulocalyx*. (A–D, F–H, from Schulze, 1887, pl. XL.)

developing patterns of either dictyonine or lyssacine skeletal organization. Schulze (1885) first assigned the new genus *Euryplegma* to Euryplegmatidae, both names in that work being *nomina nuda* since the species had not yet been described. In the first valid description, Schulze (1886) assigned the genus to a dictyonine group, Tretodictyidae, then quickly moved it (Schulze, 1887) to a lyssacine group, Rossellidae. Sollas (1887) meanwhile retained Euryplegmatidae, thereby making it an available family name. Ijima (1898) noting the absence of diactine megascleres, maintained a lyssacine assignment for the genus but moved it to the subfamily Leucopsacinae of Rossellidae where diactins are absent. Since no other leucopsacid (or rossellid) had a frame of fused hexactins such as that in *Euryplegma*, Ijima (1903) finally retraced steps and assigned the genus to the dictyonine Dactylocalycidae. This was maintained until realization of the distinctive aulocalycoid framework stimulated Ijima (1927) to erect the family Aulocalycidae, and assigned *Euryplegma* to that new grouping. It has remained there with few disturbances – de Laubenfels' (1955b) formation of Euryplegmatidae as a 'new' family group, Reid's (1957a) transfer to Tretodictyidae because of channelization pattern (schizorhyses) and erroneously attributed proper uncinates, and Mehl's (1992) erroneous interpretation of the *Euryplegma* framework as being diactinal, prompting her to suggest an *incertae sedis* lyssacine assignment.

Description of type species

Euryplegma auriculare Schulze (Fig. 3).

Restricted synonymy. *Euryplegma auriculare* Schulze, 1886: 80; Schulze, 1887: 176, pl. CII, figs 1–6.

Material examined. Lectotype: BMNH 1887.10.20.075 (wet) – near Raoul Islands, NE of New Zealand. Paralectotype: BMNH 1887.10.20.075A (dry) – same locality (Lectotype designation by Reid (1957a: 907), Tabachnick & Reiswig (2000: 42)).

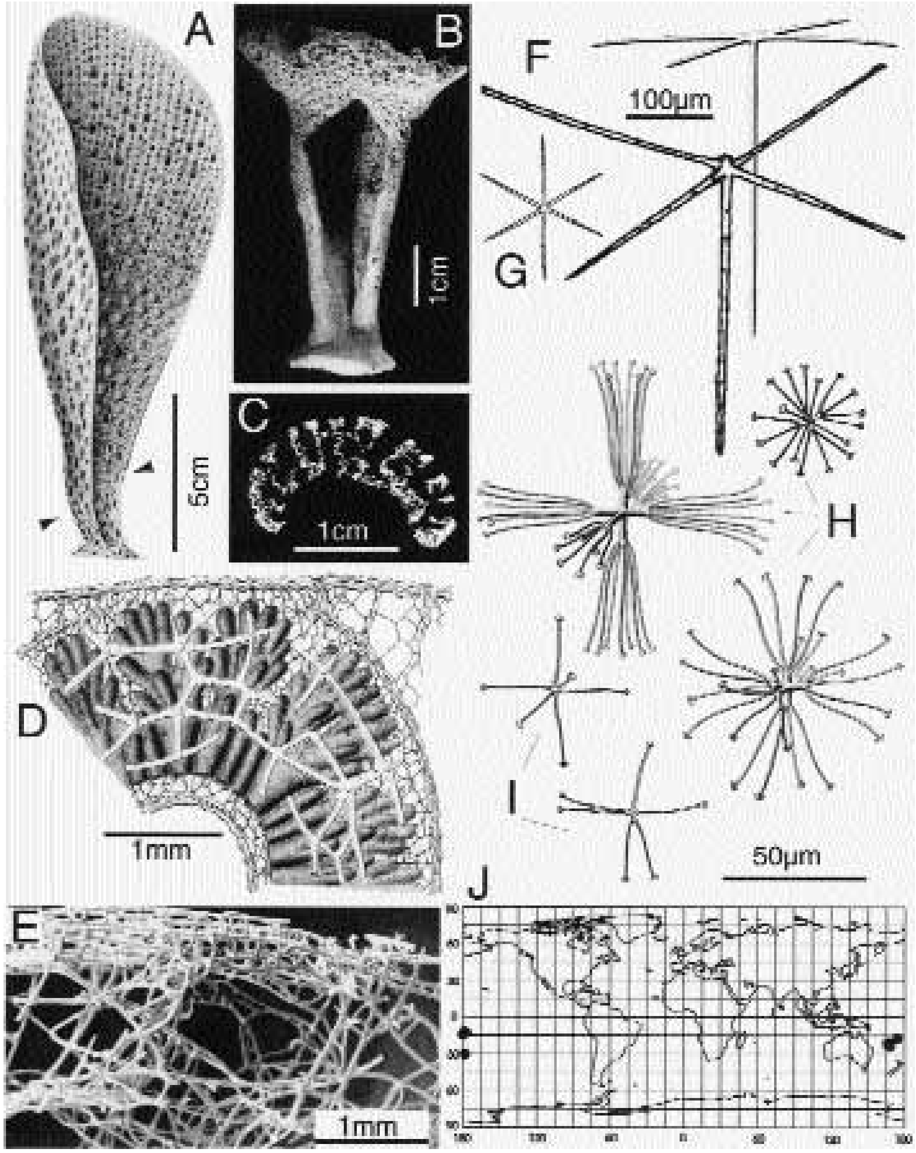

Fig. 3. *Euryplegma auriculare*. A, lectotype BMNH specimen. B, specimen from New Caledonia, MNHN HCL 369 with lateral margin fusion. C, transverse section showing interconnection of channel system (non-type specimen). D, transverse section of lectotype distal wall with tissues. E, scanning electron micrograph of lectotype aulocalycoid framework with channels. F, two surface pentactins. G, small example of oxyhexactin. H, three regular discohexasters showing range of form. I, two discohexaster variants, discohexactin and hemidiscohexaster. J, distribution of *Euryplegma*. (A, D, F (part), H (part) from Schulze, 1887, pl. CII; B, C, F (part), H (part), I, from Tabachnick & Reiswig, 2000; E, from Mehl, 1992, pl. 16.)

Description. Semi-involute tongue-shaped body to 17 cm long by 7 cm wide, 3–9 mm wall thickness; some specimens with fusion of lateral margins to enclose lower slit and provide base for distal extension as a complete funnel; smooth external dermal surface bearing irregularly distributed oval apertures 2–4 mm diameter; concave atrial inner surface distally bearing 2 mm wide grooves and ridges oriented longitudinally, with 1–3 mm diameter irregularly round apertures in series along grooves; proximal internal surface with added transverse ridges 4–5 mm broad inflated irregularly to 3–4 mm diameter cushions or bumps upon which open small apertures; entire wall permeated by interconnected network of 1–2 mm wide channels with main development as continuous longitudinal components, opening on both surfaces by mentioned apertures – a schizorhysis-like system; all surfaces of body and internal channels lined by pentactin-supported lattice membrane, also spanning some, perhaps all, surface apertures; framework very delicate, flexible distally, gradually increasing in density to a stony hard basal attachment; dictyonal frame constructed exclusively of hexactins connected by direct fusion of rays and extensive synapticula forming ladder-like junctions between rays running in parallel; main strands longitudinal extensions of thickened single hexactin rays forming longitudinal septa-like lamellae in walls between schizorhysis-like channels; strands connected by local hexactins with short and often curved rays joined by ray–ray fusion at various angles and synapticula; beams 30–110 µm thick, usually covered by short conical spines but some patches smooth; outer spurs entirely rough or smooth except at tip; small hexactins not appended to main framework; dermalia and atrialia as pentactins with tangential rays 80–448 µm long, proximal rays 68–669 µm long, ray thickness 7–34 µm, rays smooth or sparsely spined and densely spined at tips; choanosomal oxyhexactins of same texture of 23–400 µm ray length, ranging across micro- to megasclere sizes; discohexasters of perianthic (stellate) or spherical form 40–180 μm diameter with short 6–8 μm-long primary rays bearing 3–10 s-shaped or straight terminals ending in toothed discs; reduced discohexasters as hemidiscohexasters and discohexactins are rare in lectotype but may predominate in some specimens; neither uncinates nor sceptrules are proper; known only from depths of 540–3680 m in a restricted SW Pacific region: off Raoul Islands NE of New Zealand, New Caledonia, Loyalty Islands, Fiji, Wallis and Futuna Islands.

Remarks. The channelization of *Euryplegma* was incorrectly understood to consist of epirhyses and aporhyses by Ijima (1927). Reid (1957a) correctly described and interpreted the channel system as schizorhysial, but incorrectly assumed it was identical to that of typical Tretodictyidae. Tabachnick & Reiswig (2000) explored the nature and origin of the *Euryplegma* channels and, on the basis of the free pentactin lining of their surfaces (not present in tretodictyid schizorhyses), and the distinctive aulocalycoid framework of the genus, concluded that the channel system here must be considered an independent development, evolutionarily distinct from, but functionally convergent to that of Tretodictyidae. They also provide a complete list of all known specimens of *E. auriculare* – the BMNH type series and an extensive collection at MNHN.

IJIMADICTYUM MEHL, 1992

Synonymy

Ijimadictyum Mehl, 1992: 75.

Type species

Rhabdodictyum kurense Ijima, 1927: 46 (by monotypy).

Definition

Aulocalycidae of deceptive euretid aspect as irregularly branching and anastomosing tubular stock with terminal oscula and sparse parietal oscula; dictyonal primary framework euretoid-like but construction is aulocalycoid in that all beams are uniaxial and longitudinal strands composed of single dictyonal rays are present, but are supplanted by secondary dictyonalia as main structural components; dermalia and atrialia are pentactins; microscleres include spirodiscohexasters and spherical discohexasters; uncinates, sceptrules and oxyhexasters absent.

Diagnosis

Monospecific. See type species description.

Remarks

In his original description of *Rhabdodictyum kurense*, Ijima (1927) recognized the aulocalycoid nature of its dictyonal frame, but, excepting the uniaxial longitudinal strands, he did not appreciate other basic aspects of construction – all beams uniaxial, beams joined tip to ray, abundant synapticula. Both Reid (1964) and Mehl (1992) were impressed with both the euretid-like body form and the euretoid-like framework. Unlike Ijima, they did not apparently recognize the underlying constructional similarity to that of other aulocalycids. Both proposed at least removal from *Rhabdodictyum*. Mehl's (1992) formation of a new genus, *Ijimadictyum*, for the species, was supported by Tabachnick & Reiswig (2000), and is maintained here, but in both cases, as a member of Aulocalycidae, not as Hexactinosida *incertae sedis* as proposed by Mehl. Although the basic elements of dictyonal construction are the same in both concerned monospecific genera, the dominant main structural components as longitudinal strands in *Rhabdodictyum*, and secondary dictyonalia in *Ijimadictyum* are considered sufficiently different to deserve generic separation. While framework differences are extreme, the two species are virtually identical in loose spiculation.

Description of type species

Ijimadictyum kurense (Ijima) (Fig. 4).

Synonymy. *Rhabdodictyum kurense* Ijima, 1927: 227, pl. XXIV, figs 1–12. *Ijimadictyum kurense* Mehl, 1992: 75, pl. 12, fig. 5.

Material examined. Lectotype (with spicules): ZMA Por 5097 – Banda Sea, Indonesia. Paralectotype (here designated; completely macerated): ZMA Por 3435 – same locality.

Description. Body stock of irregularly branching and anastomosing tubes attached to hard substrate; tubes 5–14 mm in diameter with ovoid to sinuous-margined terminal oscula and sparse, round lateral oscula 1.5–4 mm in diameter; wall rigid and of uniform 1 mm thickness to growing margins; shallow epirhyses and aporhyses to 0.6 mm diameter throughout; dermal and atrial surfaces covered by irregular quadrate lattice of loose pentactins of 275–430 μm sides; dictyonal framework of rectangular and triangular meshes with rounded corners; longitudinal strands restricted to atrial wall, are uniaxial as single dictyonal rays extending at least 2 mm in length; dominant framework elements are secondary dictyonalia with all rays uniaxial and joined to other rays and strands laterally at any angle, never or very rarely to other dictyonal centra; beams are 40–100 μm thick and ornamented with warts or transverse ridges bearing minute spines; longitudinal strands are not differentiated from secondary dictyonalia in beam thickness or ornamentation; nodes not swollen or ornamented; synapticula are common; adherent microhexactins are absent; some surface dictyonalia have spurs, many do not; megascleres only as rough or nearly smooth dermal and atrial pentactins with tangential rays 275–400 × 13–19 μm, with proximal rays as long or longer; sceptrules and uncinates lacking; microscleres mainly perianthic spirodiscohexasters, 95–120 μm in diameter with 5–10 terminals bearing discs with 12–14 marginal teeth, and regular spherical discohexasters 30–40 μm in diameter with 5–6 terminals bearing 5–6-toothed marginal discs; hemidiscohexasters and discohexactins 75–85 μm in diameter are rare; known only from one location, S of Kur Island, Banda Sea, at 204 m depth.

Remarks. Uncinates encountered in spicule preparations of the lectotype are considered foreign. The species is known only from the original collection of 7 fragmentary specimens which might have been from a single individual. The present location of only the 2 fragments noted above is known.

LEIOPLEGMA REISWIG & TSURUMI, 1996

Synonymy

Leioplegma Reiswig & Tsurumi, 1996: 767.

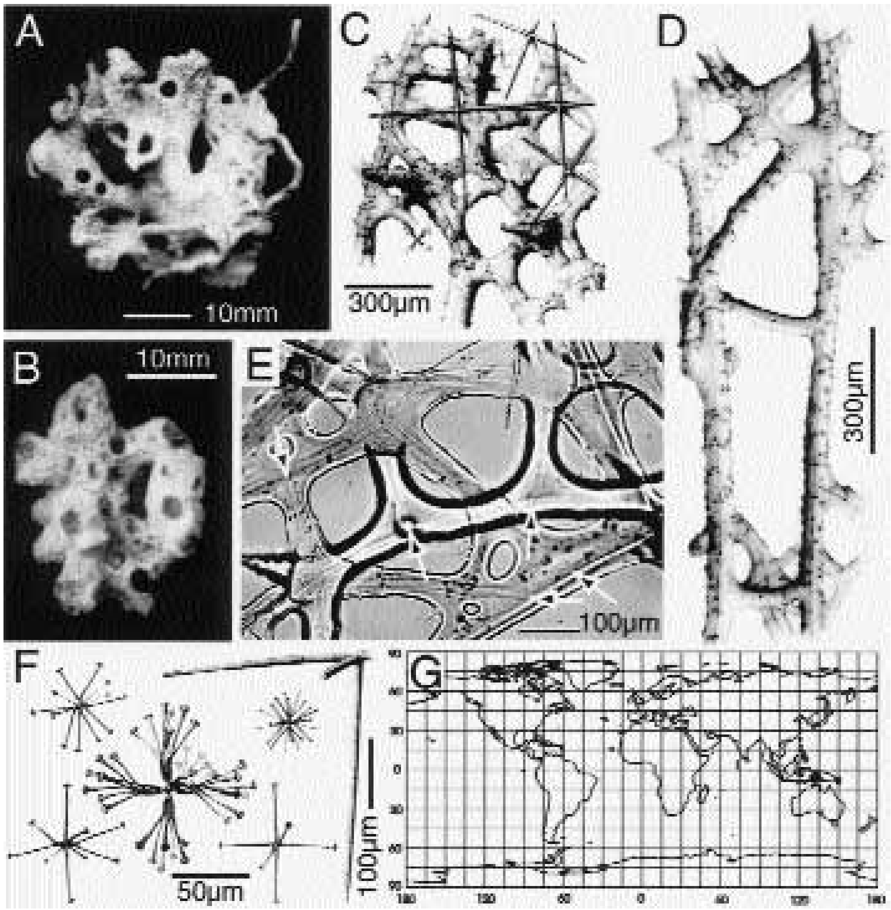

Fig. 4. *Ijimadictyum kurense*. A, lectotype ZMA Por 5097. B, paralectotype ZMA Por 3435. C, dictyonal framework viewed from dermal surface with 3 pentactins included. D, longitudinal strands of atrial framework supported by secondary dictyonalia (note single axial canals). E, framework fragment in high refractive index fluid showing 3 dictyonal centra with uniaxial rays connecting to lateral surfaces of other rays (5 arrows) and common synapticula (S). F, loose spiculation including pentactin (right), common large spirodiscohexaster and small regular discohexaster, and rare hemidiscohexasters and discohexactin. G, distribution of *Ijimadictyum*. (A–D, F, from Ijima, 1927, pl. XXIV.)

Type species

Leioplegma polyphyllon Reiswig & Tsurumi, 1996: 769 (by original designation).

Definition

Aulocalycidae with primary framework composed of longitudinal strands which run parallel to one another in a single plane without primary channelization; each strand originates as a single hexactin ray, increasing in length through longitudinal extension; strands interconnected ladder-like by synapticular bridges and irregularly attached hexactins; dermalia and atrialia as rough pentactins; choanosomal mesohexactins and perianthic (stellate) discohexasters; uncinate absent or very rare; sceptrule and oxyhexaster absent.

Diagnosis

Monospecific. See type species description.

Remarks

Leioplegma is nearly identical to *Euryplegma* in spiculation, but differs from that genus (schizorhysial) by lack of primary channelization. The genus is monospecific.

Description of type species

Leioplegma polyphyllon Reiswig & Tsurumi (Fig. 5).

Synonymy. *Leioplegma polyphyllon* Reiswig & Tsurumi, 1996: 769, figs 2–21; Tabachnick & Reiswig, 2000: 47.

Material examined. Holotype: USNM 38774 (dry); schizotypes: BMNH 1994.8.15.1; MNHN HCL 140, 141, 142; ZMA POR 10911; RMM I-7094 – 320 km ESE Charleston, South Carolina, USA. Paratypes: USNM 38771, 38938, 38941 (dry) – same locality.

Description. Fan-shaped body to 37.5 cm wide by 24 cm tall by 1.6 mm thick composed of dichotomously branching lamellae emanating from an encrusting basal plate attached to hard substrate; fusion of branches does not occur; entire specimen surface covered by continuous, irregularly-quadrate lattice of pentactins which proceeds around 1 mm thick distal edges; primary framework is single layer of longitudinally oriented, parallel aulocalycoid strands; at distal edges strands are unsupported extending ray tips spaced 150–*200*–275 µm apart, but within 1 mm of edge are stabilized by synapticular bridges and secondary hexactins fused to strands; secondary hexactins added mainly on atrial side of all strand surfaces to 500 µm thick layer but on dermal side only in central branch axes as 300 µm thick layer; slight undulation in rank of primary strands visually detectable in whole specimen; strand tips never curve towards atrial or dermal surfaces but increase in

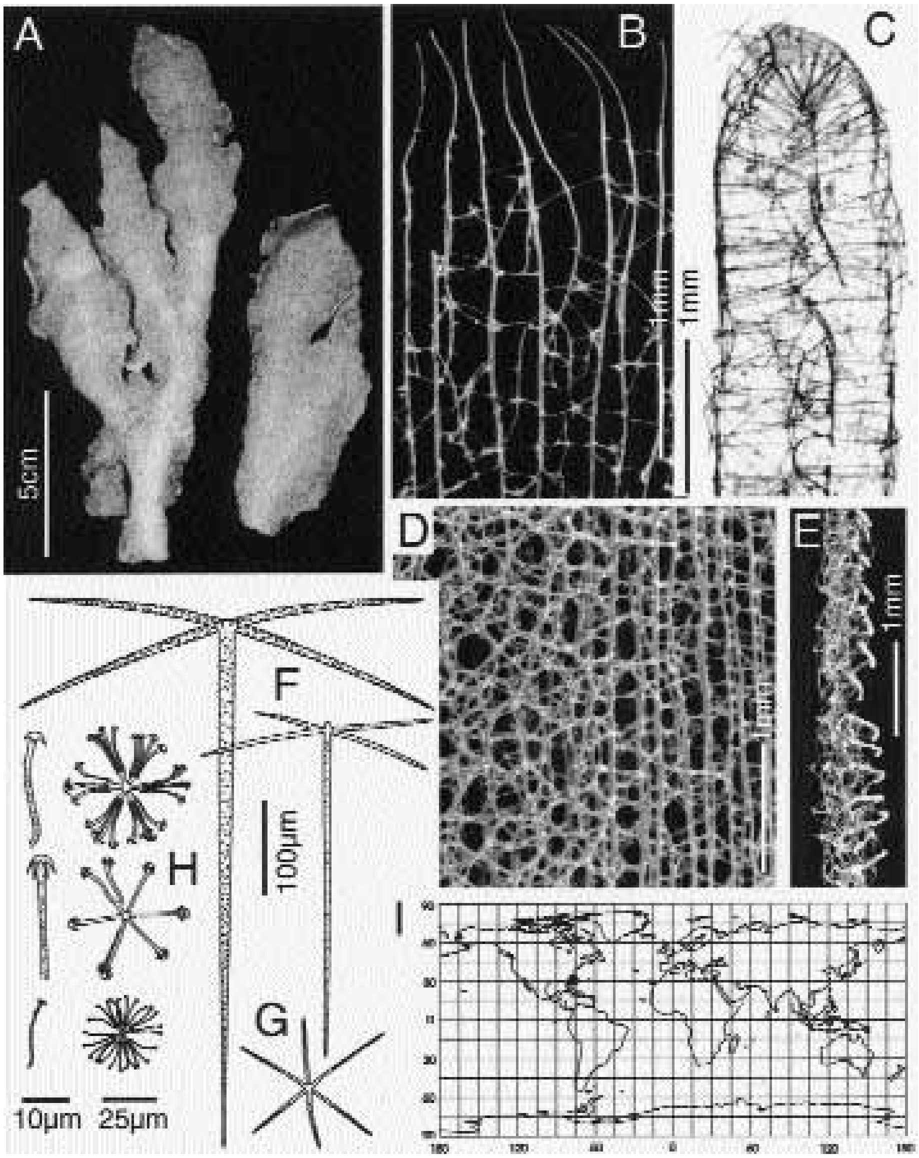

Fig. 5. *Leioplegma polyphyllon*, all from holotype. A, main fragments showing lamellate branch form. B, cleaned skeletal framework of the growing margin (above) with primary strands and stabilizing synapticula and secondary hexactins (SEM). C, transverse section of margin with pentactin lattice in place (LM). D, dermal surface view of medial branch framework with secondary hexactin layer added onto older medial axial strands (left) and no secondary hexactins on peripheral lateral strands (right) (SEM). E, transverse section of branch from distal end showing slight undulation of primary strands and addition of secondary hexactins on atrial side of strands (SEM). F, two surface pentactins. G, oxyhexactin. H, three discohexaster variants, most common form above, with magnified ray tips. I, distribution of *Leioplegma*. (A–H, from Reiswig & Tsurumi, 1996.)

number to provide plumose support strands to lateral branch margins and to increase strand density (100–*125*–140 µm spacing) in central branch axes by initiation of new strands from secondary hexactins added into plane of primary strands, not by branching of existing strands; primary framework unchannelized but indistinct epirhyses and aporhyses present as extradictyonal gaps in secondary hexactin layers of thickened central areas of branches; strands distally smooth, 18–*22*–26 µm thick increasing medially in thickness to 50–*63*–80 µm and spine density; strands commonly contact and fuse in condensed branch axes; all framework elements including secondary dictyonalia and synapticula finely spined; spurs of framework almost non-existent due to extension, curvature and fusion of most secondary hexactin rays; dermal and atrial pentactins uniformly microtuberculate, highly variable in size, dermalia larger than atrialia, tangential ray length 99–*225*–300 µm, proximal ray length 316–*554*–741 µm, ray thickness 6–*11*–18 µm; rough parenchymal mesohexactins with ray length 41–*77*–138 µm, ray thickness 1.5–*2.9*–4.7 µm; few uncinates 1.7 mm long occur only in branch axes appear proper; short-primaried stellate discohexasters of one variable class, including hemihexastrous and hexactin variants, 20–*50*–75 µm diameter, mostly with 4–*5*–7 terminal rays in lophoid plumes; known as a single specimen from Blake Ridge, 320 km ESE of Charleston, South Carolina from 2200 m depth.

Remarks. During review of the holotype a few complete uncinates, not noted in the original species description, were found only in axial areas of branches. They may have originated as contaminants from co-collected *Farrea*, but their restricted position suggests an intrinsic source. The species is convergent in lamellar form to the euretid *Bathyxiphus subtilis*, and the uncinaterid *Tretopleura styloformis*.

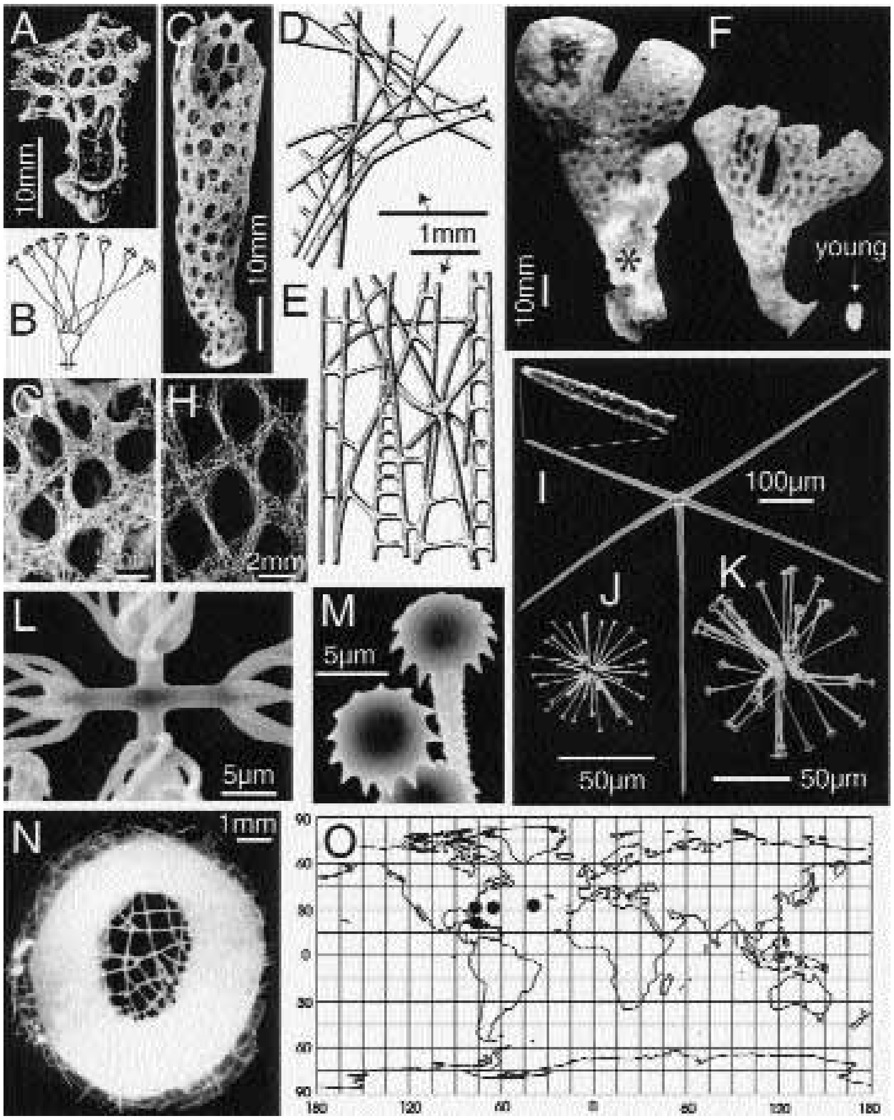

Fig. 6. *Rhabdodictyum delicatum*. A, holotype, MCZ 6428B. B, Schmidt's original spirodiscohexaster drawing. C, macerated 'Challenger' specimen from near Bermuda. D–E, dictyonal framework fragments from the Bermuda specimen. F, recent specimens from the Blake Plateau, from left, USNM 51550, 51551, 51554 (*surface obscured by residual adherent demosponge tissues). G–H, parietal gaps of lateral wall of the worn holotype (left) and alive-at-collection USNM 51550 (SEM). I, dermal pentactin with magnified ray tip. J, spherical discohexaster. K, spirodiscohexaster. L, central part of a spirodiscohexaster. M, discs of spirodiscohexaster. N, young specimen with sparse veil and sieve grid intact (USNM 51553). O, distribution of *Rhabdodictyum*. (A–B, from Schmidt, 1880b, pls VI & VII; C–E, from Schulze, 1887, pl. XX.)

RHABDODICTYUM SCHMIDT, 1880

Synonymy

[*Rhabdodictyon*] Schmidt, 1880b: 46. *Rhabdodictyum* Zittel, 1883: 180.

Type species

Rhabdodictyon delicatum Schmidt, 1880b: 46 (by monotypy).

Definition

Aulocalycidae of dichotomously branching tubular stock with terminal oscula and regularly arrayed parietal oscula; primary framework composed of longitudinal strands of sinuous form passing around and between parietal gaps; framework not channelized; microscleres include spirodiscohexasters; uncinate absent or very rare; sceptrule and oxyhexaster absent.

Diagnosis

Monospecific. See type species description.

Remarks

Like most present members of the Aulocalycidae, *Rhabdodictyum* has been regarded alternately as a hexactinosan or lyssacinosan. Zittel (1883) first assigned Schmidt's new genus to Euretidae, but most early authors followed Schulze's (1885, 1886,

1887) reassignment of it to Euplectellidae. Ijima (1927) transferred the genus to his newly formed hexactinosan family Aulocalycidae, where it remains. Tabachnick & Reiswig (2000) recently recognized the group as a separate hexasterophoran order, Aulocalycoida, distinct from both hexactinosan and lyssacinosan groups. Besides the type species, only *R. kurense* Ijima has been assigned to the genus. Following Mehl's (1992) transfer of *R. kurense* to a newly formed genus *Ijimadictyon, Rhabdodictyum* once more became monospecific.

Description of type species

Rhabdodictyum delicatum Schmidt (Fig. 6).

Synonymy. *Rhabdodictyon delicatum* Schmidt, 1880b: 46, pl. vi, fig. 1, pl. vii, fig. 3B; Schulze, 1887: 107, pl. xx, figs 1–4. *Rhabdodictyum delineatum* (*lapsus calami*) Schulze, 1887: 491.

Material examined. Holotype: MCZ 6428B (dry) – N of eastern Cuba, 76°33′W, 21°43′N, 1827 m depth. Other material. USNM 51547–51554 – all 320 km ESE of Charleston, South Carolina.

Description. Spherical to ovoid sponges when young, developing into dichotomously branching tubular mature forms to 10 cm tall attached to hard substrate by small base; branching in one plane; tube units slightly flattened in plane of branching, 5–24 mm diameter, to 40 mm wide at branch points; terminal oscula 2–14 mm diameter covered by sieve plate of 0.6 × 0.9 mm meshes constructed of pentactins with short (30–100 µm long) proximal rays; lateral walls penetrated by parietal oscula 1.0–*1.4*–2.2 mm diameter (soft tissues) situated over hexagonally-arranged, ovoid, parietal wall gaps (skeletal) of minor and major diameters 1.6–*2.6*–3.5 × 1.8–*3.3*–4.7 mm, strikingly manifest in dried and macerated specimens; framework septa between adjacent parietal gaps 0.3–*0.8*–1.7 mm wide; unchannelized walls 1–6.5 mm thick; texture delicate and fragile; surface even bearing sparse veil of pentactins 0.4–0.7 mm above general surface and penetrated by sparse prostal spines to 1 cm long consisting partly of distal ends of longitudinal dictyonal strands and partly of extended proximal rays of pentactins in which distal end is broken off; main framework of sinuous longitudinal strands (extended hexactin rays) interwoven through parietal septa, delineating parietal gaps; frame stabilized by strand fusion at contacts, connected at non-contacts by synapticular bridges and fused secondary hexactins; wall thickened by addition of 2–3 layers of longitudinal strands internal (atrial) to main dermal strands; rays of secondary hexactins form a palisade of secondary dictyonal strands projecting perpendicularly outwards from margins of parietal gaps; beams smooth, 8–*40*–90 µm thick; nodes simple; dictyonal meshes highly irregular without characteristic size; dermal and atrial pentactins smooth with rough tips or entirely rough, tangential ray length 202–*487*–955 µm, proximal ray length 157–*642*–1232 µm; oscular sieve pentactins similar but with short proximal ray; accessory rough hexactins occur basally in most specimens, ray length 126–*178*–231 µm; microscleres as spirodiscohexasters and regular spherical discohexasters; spirodiscohexasters 105–*146*–164 µm diameter with 6–9 secondary rays per terminal ending in discs with 12–16 marginal teeth; regular spherical discohexasters 49–*94*–134 µm diameter with 7–10 secondary rays per terminal with similar discs; sceptrules absent; few uncinates may be foreign or rare proper spicules; distribution entirely North Atlantic, from mid-ocean west of Azores to Cuba at depths of 1827–2422 m.

Remarks. Site of origin of the holotype has been repeatedly and incorrectly reported as Bequia (West Indies), the only location Schmidt (1880b) provided. This was indeed the site of Schmidt's original 'A' specimen, later referred to *Dictyocalyx gracilis* by Schulze (1887). Label of Schmidt's original 'B' specimen, the eventual holotype of *Rhabdodictyum delicatum*, includes the Cuban co-ordinates reported above but never published. Previously known spiculation of the species derives only from the partial spirodiscohexaster drawing in Schmidt's (1880b) original description. All subsequent specimens assigned to the species were macerated frameworks (Schulze, 1887; Topsent, 1928c). Such reports from the North Atlantic are accepted here as probably correct, but macerated specimens from the Indian Ocean referred here by Schulze (1895, 1902) cannot be accepted as relating to this species, and can only be considered Aulocalycidae, gen. et sp. indeterm. Topsent's earlier reports (1890b, 1892a) of the species from the Azores was later corrected (Topsent, 1904b) with reassignment of the specimen to *Regadrella*. Recent discovery of a rich population of young and mature *R. delicatum* on the 1857 shipwreck of the SS 'Central America' on the Blake Ridge off South Carolina (Herdendorf *et al.*, 1995, as *Rhabdodictyum* sp.) has finally enabled resolution of the complete spiculation of the species, and determination of the soft-tissue relationships of the parietal oscula. Surprising variation in spicule complements were found in the four specimens examined in detail. Medium-size accessory hexactins were present in only two specimens, one large and one young (ca. 10 mm total length). Spheric (non-spiralled) discohexasters composed a varying proportion of all discohexasters in each specimen: 0, 5%, 30%, 50%, the highest proportions in the young specimens. Such variation was first interpreted to suggest two distinct species might be present at the site, but the wreck represents a very restricted hard substrate patch on a coarse pteropod-sand plateau, populated by several hexactinellids, including several thousand *R. delicatum*. Evidence that these are samples of a single genetically-interwoven species population is very strong.