

Porifera Hexactinellida: On *Euryplegma auriculare* Schulze, 1886, and formation of a new order

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ABSTRACT

Euryplegma auriculare, previously known off the coast of New Zealand, has recently been collected from the vicinity of New Caledonia, Fiji, Wallis and Futuna Islands. The description of spicules, structure and speculation on the origin of this species as well as reinvestigation of the related genera, *Tretopleura* and *Fieldingia*, has led to revision of the family Aulocalycidae and modification of its diagnosis. The scope of the family has been restricted to five genera: *Euryplegma*, *Aulocalyx*, *Rhabdodictyon*, *Ijimadictyon*, and *Leioplegma*. A new taxon Aulocalycoida, with the same rank as the orders Hexactinosa, Lychniscosa, Lyssacinosa, has been proposed to receive the reorganized family. It is distinguished by an aulocalycoid framework. The order Hexactinosa is thus restricted to include all of its former families except for the family Aulocalycidae. Two genera previously included in the Aulocalycidae, *Tretopleura* and *Fieldingia*, are reassigned because of their lack of an aulocalycoid framework. *Tretopleura* is referred to the hexactinose family Euretidae without a clear closest relative. *Fieldingia* (sensu stricto), still poorly known, is provisionally referred to the order Reticulosa, as incertae sedis, and possibly represents the only extant member of that group. It has some similarity to the family Stromatidiidae, but cannot be included in that taxon with the limited information now available. The position of Reticulosa in relation to the more well-known recent Hexactinellida taxa remains unclear.

RÉSUMÉ

Porifera Hexactinellida : Sur *Euryplegma auriculare* Schulze, 1886. Création d'un ordre nouveau.

Euryplegma auriculare, connu jusqu'à présent du large de la Nouvelle-Zélande, a récemment été récolté au voisinage de la Nouvelle-Calédonie et des îles Fidji, Wallis et Futuna. La description des spicules et de la structure de cette espèce, liée à des hypothèses sur son origine, ainsi que le réexamen des genres voisins *Tretopleura* et *Fieldingia*, ont conduit à une révision de la famille Aulocalycidae et à la modification de sa diagnose. Le champ de la famille a été réduit à cinq genres : *Euryplegma*, *Aulocalyx*, *Rhabdodictyon*, *Ijimadictyon* et *Leioplegma*. Un nouveau taxon Aulocalycoida, ayant le même rang que les ordres Hexactinosa, Lychniscosa, Lyssacinosa, est proposé pour recevoir la famille ainsi révisée. Il se distingue par une organisation du squelette aulocalycoïde. L'ordre Hexactinosa se trouve ainsi réduit à ses anciennes familles à l'exception de celle des Aulocalycidae. Deux genres inclus précédemment dans les Aulocalycidae, *Tretopleura* et *Fieldingia*, sont reclassés à cause de leur manque de structure aulocalycoïde. *Tretopleura* est placé, à titre provisoire, dans la famille Euretidae appartenant aux Hexactinosa, bien qu'aucune autre forme de cette famille ne lui soit clairement très proche. *Fieldingia* (sensu stricto), encore mal connu, est provisoirement rattaché à l'ordre Reticulosa, en tant qu'*incertae sedis* et représente peut-être le seul membre de ce groupe encore existant. Il possède quelques similitudes avec la famille Stromatidiidae, mais ne peut être inclus dans ce taxon avec le peu d'information dont nous disposons actuellement. La position des Reticulosa par rapport aux Hexactinellida récents, bien mieux connus, reste obscure.

A large number of interesting Hexactinellida have been collected in recent years by French expeditions in the southwestern part of the Pacific Ocean. Some of these species were previously known only by a few specimens from restricted locations. One of them — *Euryplegma auriculare* — turns out to be a common species in this area. The numerous specimens of *E. auriculare* made available by these expeditions provide opportunity to redescribe the species and to discuss the systematics of the Aulocalycidae.

Abbreviations: MNHN, Muséum national d'Histoire naturelle (Paris); NHM, The Natural History Museum (London); IORAS, Institute of Oceanology of Russian Academy of Sciences (Moscow).

1. — DESCRIPTION OF *EURYPLEGMA AURICULARE* Schulze

Genus *EURYPLEGMA* Schulze, 1886

Euryplegma Schulze, 1886: 80.

TYPE SPECIES. — *E. auriculare* Schulze, 1886.

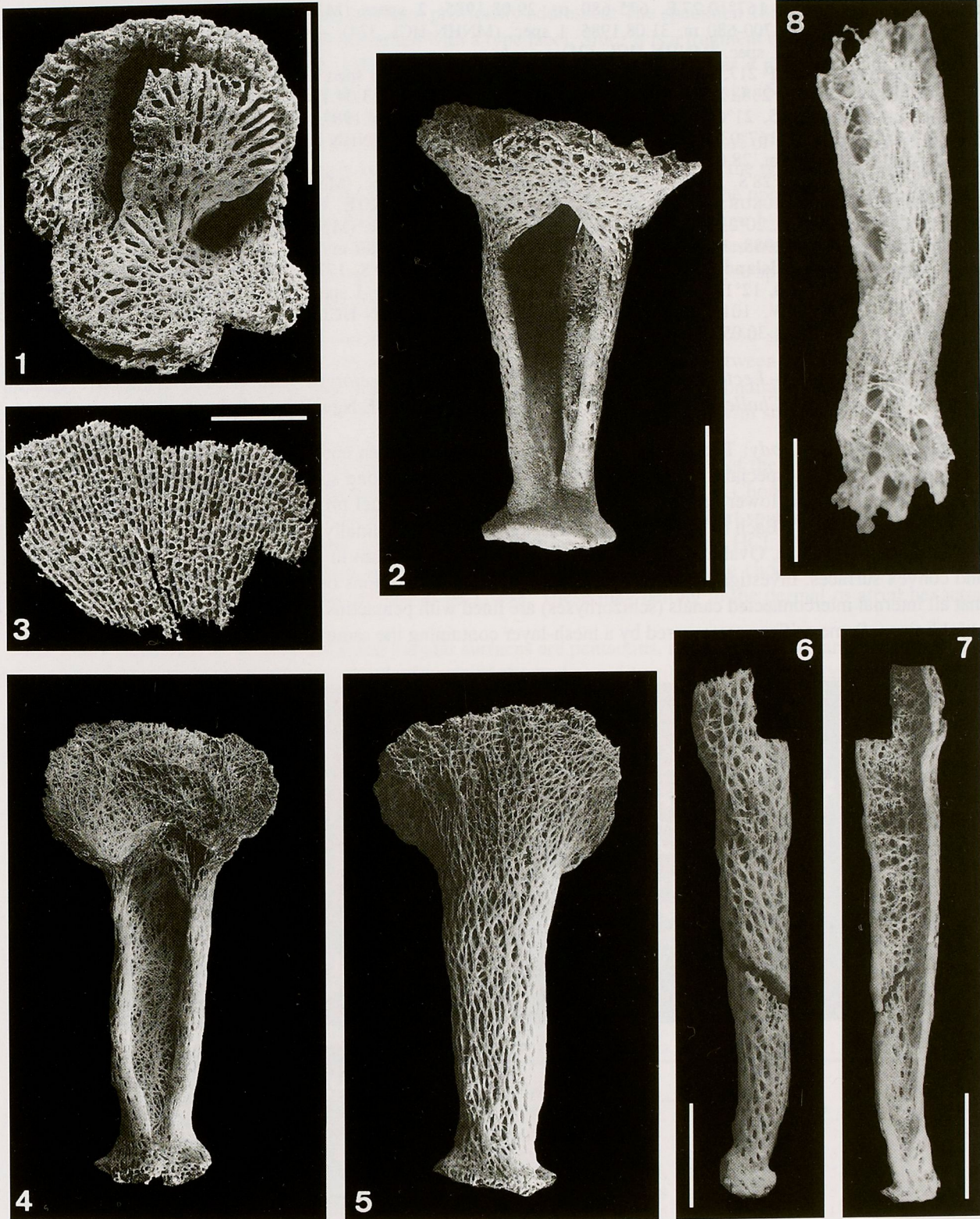
DIAGNOSIS (from SCHULZE 1887, emended here). — Fan-like, thin-walled sponge with aulocalycoïd framework of choanosomal skeleton. Dermalia and atrialia are pentactins. Loose microhexactins are rarely found in the choanosomal framework. Microscleres are discohexasters, hemidiscohexasters and sometimes discohexactins.

Euryplegma auriculare Schulze, 1886

Figs 1-13; Table 1

MATERIAL EXAMINED. — **New Zealand.** "Challenger", stn 170 A, off Raoul or Sandy islands, 29°45'S, 178°11'W, 1120 m: *Lectotype* (BMNH 1887.10.20.075), *paralectotype* (BMNH 1887.10.20.075A).

New Caledonia. BIOCAL: stn CP 17, 20°34.54'S, 167°24.68'E, 3680 m, 14.08.1985: 2 specs (MNHN-HCL 366-368). — Stn CP 26, 22°39.66'S, 166°27.41'E, 1618-1740 m, 28.08.1985: 2 specs (MNHN-HCL 369-370). —



FIGS 1-8. — Fragments of *Euryplegma auriculare*: 1-2, MNHN-HCL 369, upper and side view (scale 2 cm); 3-5, MNHN-HCL 395, upper part side view and lower parts from two sides (scale 1 cm); 6-7, MNHN-HCL 392, lower parts, views from 2 sides (scale 2 cm); 8, MNHN-HCL 392, basal part (scale 1 cm).

Stn DW 33, 23°09.71'S, 167°10.27'E, 675-680 m, 29.08.1985: 2 specs (MNHN-HCL 372-373). — Stn DW 51, 23°05.27'S, 167°44.95'E, 700-680 m, 31.08.1985: 1 spec. (MNHN-HCL 374). — Stn CP 52, 23°05.79'S, 167°46.54'E, 600-540 m, 31.08.1985: 1 spec. (MNHN-HCL 371).

MUSORSTOM 4: stn CP 217, 22°3.60'S, 167°27'E, 850 m, 29.09.1985: 1 spec. (MNHN-HCL 396).

BIOGEOCAL: stn CP 238, 21°27.64'S, 166°23.41'E, 1300-1260 m, 13.04.1987: 10 specs (MNHN-HCL 375-382, 384-385). — Stn CP 265, 21°04.09'S, 167°00.40'E, 1760-1870 m, 18.04.1987: 6 specs (MNHN-HCL 386-391). — Stn CP 290, 20°36.91'S, 167°03.34'E, 920-760 m, 27.04.1987: 1 spec. (MNHN-HCL 392). — Stn CP 297, 20°38.64'S, 167°10.77'E, 1230-1240 m, 28.04.1987: 2 specs (MNHN-HCL 393-394).

CALSUB: Dive 12, 21°28'S, 166°21.50'E, 1265-700 m, 3.03.1989: 1 spec. (MNHN-HCL 395)

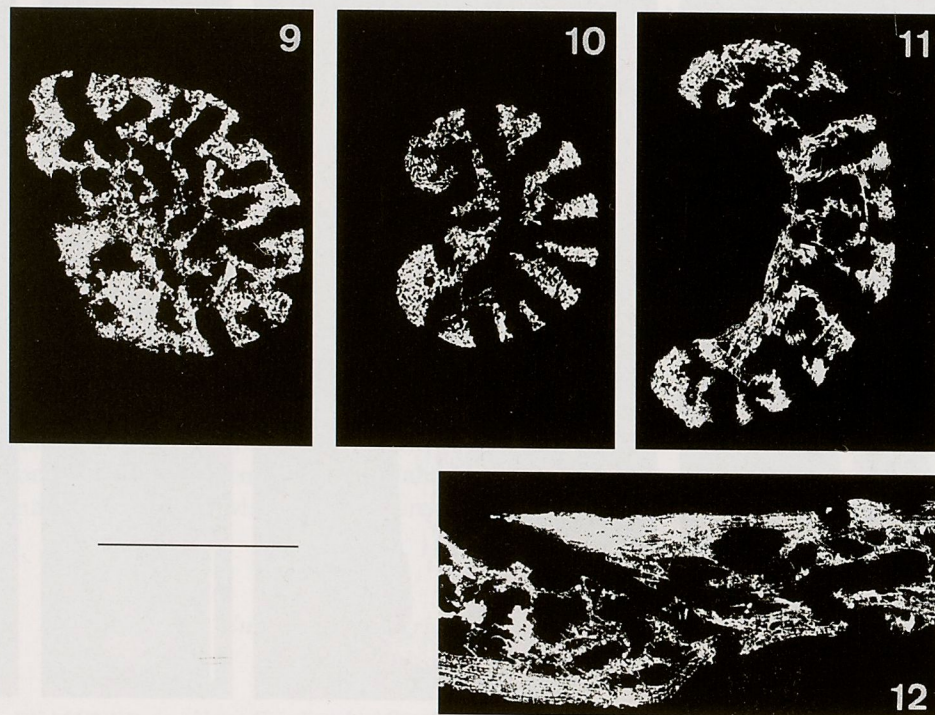
Loyalty Islands. MUSORSTOM 6: stn CP 427, 20°23.35'S, 166°20'E, 800 m, 17.02.1989: 1 spec. (MNHN-HCL398). — Stn CP 438, 20°23'S, 166°20.10'E, 780 m, 18.02.1989: 1 spec. (MNHN-HCL 397).

Fiji. DK-88-4-NBF, 1988, 12-13, stn 29, 16°39.89'S, 173°49.32'E, 2580 m (MNHN-HCL 383)

Wallis and Futuna Islands. MUSORSTOM 7: stn DW 539, 12°27.30'S, 177°27.30'W, 700 m, 17.05.1992: 1 spec. (ZMMU). — Stn CP 550, 12°14.80'S, 177°28'W, 800-810 m, 18.05.1992: 1 spec (MNHN-HCL 399). — Stn CP 564, 11°46.10'S, 178°27.40'W, 1015-1020 m, 20.05.1992: 2 spec. (MNHN-HCL 400-401). — Stn 636, 13°39.40'S, 179°55.50'W, 650-700 m, 30.05.1992: 1 spec. (MNHN-HCL 402).

TYPE MATERIAL. — *Lectotype* (BMNH 1887.10.20.075). *Paralectotype* (BMNH 1887.10.20.075A). Both collected by the HMS "Challenger", stn 170 A, 29°45'S, 178°11'W, NE New Zealand, depth 1120 m.

DESCRIPTION. — *Body*: The sponge is tongue-like or similar to an ear-shaped plate; flabellate. Sections of most specimens, and especially the upper parts, are sickle-like with one surface convex and the other concave. Some fragments of the lower part of the body have a secondary funnel produced by ingrowth and union of the opposite edges (Fig. 1). Each of these fragments has a narrow, longitudinally directed slit enclosed by the union of the ingrown parts above. Oval and round orifices approximately 1-3 mm in diameter are located on both concave and convex surfaces. Investigation of transverse and longitudinal sections of specimen MNHN-HCL 395 showed that all internal interconnected canals (schizorhyses) are lined with pentactins identical with those of the dermal and atrial linings. Some orifices are covered by a mesh-layer containing the same pentactins.



FIGS 9-12. — Sections of *Eurylegma auriculare*: 9-11, transverse sections through basal and upper parts; 12, longitudinal section.

Status of existing type specimens has not been previously addressed. The specimen 1887.10.20.075A stored in The Natural History Museum (London) is marked with a type label. Since it is a fragment of macerated skeleton of the lower part of the body (SCHULZE, 1887, pl. 102, fig. 2) it is here designated as a paralectotype. The other specimen 1887.10.20.075 is 80 mm in length. It consists of the lower part of a sponge (SCHULZE, 1887, pl. 102, fig. 1) and contains the loose spicules. It is here designated as the lectotype.

The newly collected specimens are all fragments of the lower part of sponges. Some of them are represented by macerated skeletons, while others contain loose spicules which correspond in size to the type material. The largest complete fragment (MNHN-HCL 400) is over 140 mm in length. The thickness of the upper lamellar-like parts is 3-9 mm. The most complete specimen (MNHN-HCL 395) was broken during capture by the manipulator of the submersible. The lower part is 50 mm in length while the rest of the body part is represented by numerous flexible laminae 3-5 mm in thickness. The specimens contain none of the allochthonous loose spicules which have been reported from the type materials by REID (1957).

Spiculation: The choanosomal skeleton consists of a framework of aulocalycoid skeleton with numerous synapticular junctions. All central spicule nodes are hexaradiate. Since the walls between internal canals are thin (1-3 mm), most rays are bent to lie in a single plane, as occurs in framework dictyonalia of *Aphrocallistes*. The diameter of the aulocalycoid beams is 0.03-0.11 mm. They are smooth or covered with short spines. Free rays of these hexactins have rough tips or they are entirely rough.

The loose hexactins are numerous in the lectotype but are less abundant in all of the new specimens. These small hexactins are never fused to the framework as in most Farreidae and Euretidae. Choanosomal hexactins have rays 0.023-0.084 mm — probably up to 0.266/0.002-0.005 mm — covered with short spines. These choanosomal hexactins are numerous in the lectotype, common in the specimens HCL 387 and HCL 388, rare in HCL 395, HCL 389, HCL 392 and apparently absent in HCL 372, HCL 396. Only one large choanosomal hexactin was found in the lectotype while there were several in HCL 395. These may belong to the dermal or atrial hexactin population.

Spicules underlying the dermal, atrial and canalar surfaces are pentactins, rarely stauractins and sometimes the hexactins mentioned above. Pentactins from all parts of the body are identical in range of shape and size. The tangential rays are 0.080-0.448 mm long; the proximal rays are 0.068-0.669 mm long; their diameter near the base is 0.007-0.034 mm. The rays are more or less spinous, but always have dense short spines ornamenting their ends. Pentactins from concave and convex surfaces of specimens HCL 387 and HCL 389 were compared — they are indistinguishable in most dimensions (Table 1).

	1887.10.20.075				HCL 385				HCL 387				HCL 389				
	n	avg	min	max	n	avg	min	max	n	avg	min	max	n	avg	min	max	
L pentactin of concave surface, tangential ray									15	.136	.084	.266	15	.188	.106	.289	
L pentactin of concave surface, ray proximal									15	.241	.106	.638	15	.334	.137	.441	
L pentactin of convex surface, tangential ray									16	.156	.099	.198	16	.181	.129	.220	
L pentactin of convex surface, ray proximal									16	.257	.106	.410	16	.336	.122	.418	
L dermal and atrial pentactin, tangential ray	26	.146	.084	.220	30	.234	.114	.342	31	.147	.084	.266	31	.184	.106	.289	
L dermal and atrial pentactin, ray proximal	26	.305	.068	.593	30	.387	.137	.669	31	.249	.106	.638	31	.335	.122	.441	
D discohexaster	24	.046	.031	.065	32	.066	.036	.180	31	.041	.029	.058	30	.043	.032	.061	
D dicohexaster's primary rosette	24	.012	.007	.018	32	.009	.004	.022	31	.010	.005	.018	30	.010	.007	.018	
D dicohexactin	1	.029	.029	.029	7	.052	.043	.061									
L choanosomal hexactin, ray	25	.069	.032	.152	3	.208	.144	.266	12	.073	.061	.084	1	.076	.076	.076	
		HCL 388				HCL 392				HCL 372				HCL 396			
		n	avg	min	max	n	avg	min	max	n	avg	min	max	n	avg	min	max
L dermal and atrial pentactin, tangential ray	25	.160	.080	.289	13	.174	.106	.258					15	.228	.129	.448	
L dermal and atrial pentactin, proximal	25	.275	.152	.388	13	.313	.190	.418					15	.421	.182	.555	
D discohexaster	25	.045	.032	.061	6	.055	.047	.068	8	.090	.076	.122	15	.088	.058	.108	
D discohexaster's primary rosette	25	.010	.007	.018	6	.011	.007	.018	8	.017	.011	.022	15	.015	.007	.020	
D dicohexactin					2	.086	.083	.088	15	.070	.065	.083	1	.072	.072	.072	
L choanosomal hexactin, ray	8	.093	.068	.137	3	.058	.038	.084									

TABLE 1. — Some measurements of the spicules of *Euryplegma auriculare* (in mm). L: length. — D: diameter.

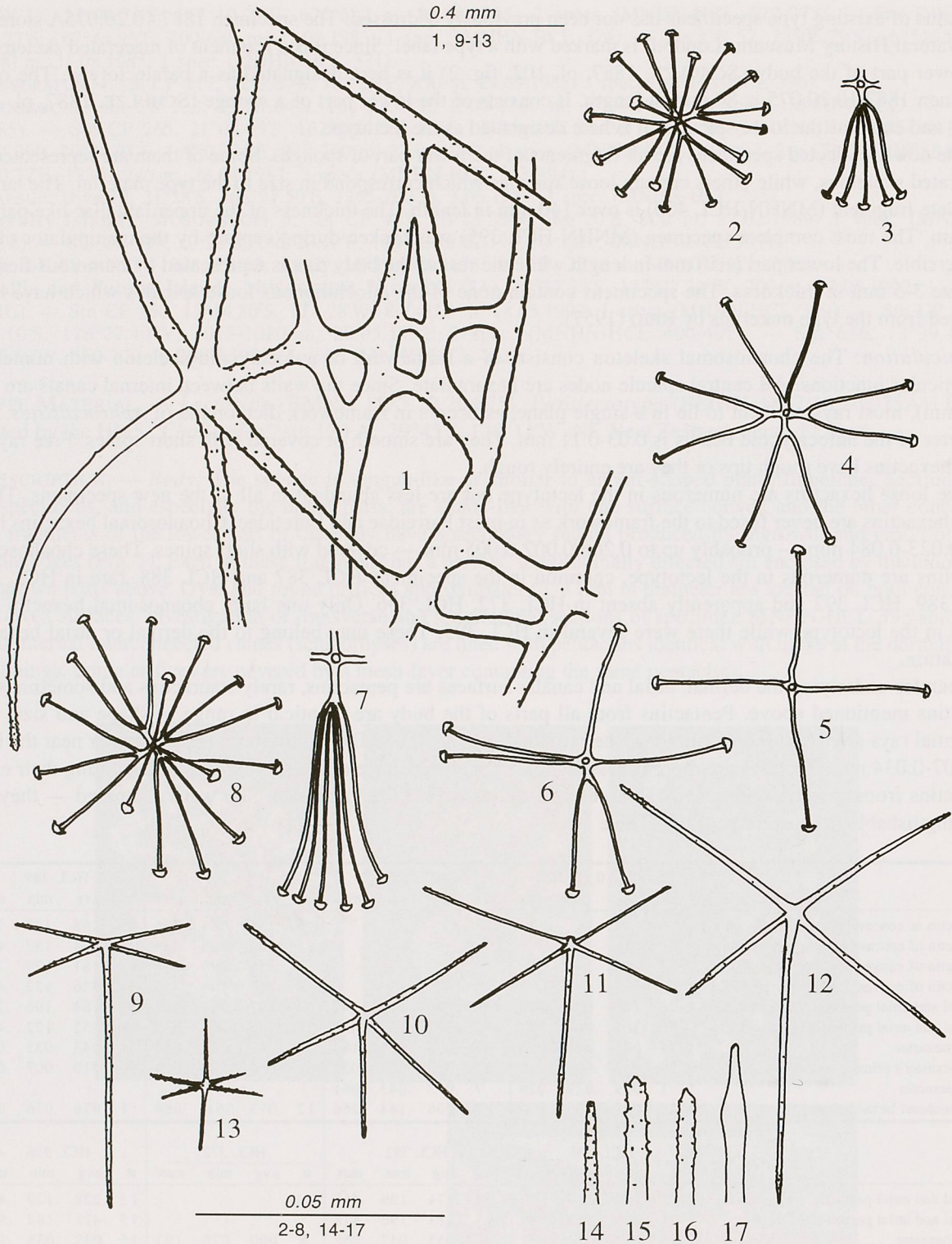


FIG. 13. — Spicules of *Euryplegma auriculare*: 1, portion of choanosomal aulocalycoid skeleton (MNHN-HCL 395); 2, spherical discohexasphere (NHM 1887.10.20.075); 3, stellate discohexasphere (NHM 1887.10.20.075); 4, 8, spherical discohexasphere (MNHN-HCL 395); 5, discohexasphere; 6-7, stellate discohexasphere (MNHN-HCL 395); 9, pentactin (NMH 1887.10.20.075); 10-12, pentactins (MNHN-HCL 395); 13, choanosomal hexactin (NHM 1887.10.20.075); 14-17, tips of pentactin tangential rays (MNHN-HCL 395).

Microscleres: Discohexasters usually prevail over the other types of microscleres with discoidal ends — hemidiscohexasters and discohexactins. Regular discohexasters 0.029-0.180 mm in diameter often have stellate form, i.e. their secondary rays are arrayed in rather compact tufts, or they sometimes have secondary rays organized in broad tufts, rendering their external form spherical. Discohexactins 0.029-0.088 mm in diameter are almost absent in the lectotype, rare in some specimens e.g. HCL 392, HCL 396, HCL 395 and predominant in HCL 372. The hemidiscohexasters are rare or entirely absent in most specimens but they were regularly observed in HCL 372. The uncinates (spicules important for taxonomy) found in the type material by REID (1957) were absent in the sponge HCL 372 captured by submersible. It is now possible to confirm the suggestion of REISWIG and TSURUMI (1996) that these spicules have an allochthonous origin.

2. — THE AULOCALYCOID STRUCTURE OF *EURYPLEGMA*

The taxonomic position of *Euryplegma* has been changed many times. SCHULZE (1886) described and first referred his new genus to the family Tretodictyidae, but the next year he (SCHULZE, 1887) reassigned it to the Rossellidae. IJIMA (1898) included *Euryplegma* in his Leucopsacinae, which, at that time, was a subfamily of Rossellidae. Not long after, SCHULZE (1904) again changed the position of the genus, assigning it to the Dactylocalycidae. Later IJIMA (1927) created a new family Aulocalycidae and included the genus *Euryplegma* in it. The features of *Euryplegma*, described by SCHULZE (1887), i.e. the presence of epirhyses and aporhyses, are reflected in IJIMA's differential key characters, but he did not provide a generic diagnosis. LAUBENFELS (1955) proposed a special family, Euryplegmatidae, for this genus but it had no diagnostic difference from the previous Aulocalycidae and thus, no reasonable basis could be found to distinguish it. REID (1957) reinvestigated the type materials and found uncinates, which he considered to be autochthonous, and schizorhyses instead of epirhyses and aporhyses. These features led him to transfer the genus to the family Tretodictyidae. REISWIG & TSURUMI (1996) dismissed the autochthonous nature of the uncinates and changed the diagnosis of Aulocalycidae by adding the possibility of schizorhyses in order to include *Euryplegma* here. With the new specimens, we can now determine the exact set of spicules and confirm the suggestion made by REISWIG & TSURUMI (1996) on the spicules of *Euryplegma*. However, the mode of wall canalization casts doubt on the present taxonomic position of the genus and requires special analysis. Unfortunately the juvenile features and young stages of *E. auriculare* are unknown, hence speculation on the structure of this genus have to be based mainly on theoretical considerations. We present 3 schemes of interpretation of origin and nature of the internal canals of *Euryplegma* (Fig. 14).

IJIMA (1927) interpreted the wall structures of *Euryplegma* as epirhyses and aporhyses, apparently solely on the basis of the description and figure provided by SCHULZE (1887). The structure of the reviewed material does not agree with this interpretation. REID's (1957) opinion, supported by REISWIG & TSURUMI (1996), on the development of true schizorhyses is more reliable (Scheme A, Fig. 14). The initially tubular archetype or unknown ancestor became tongue-like due to asymmetrical growth of a tube's sector. Walls became thicker to provide greater support for an extended body. Thickened walls required elaboration of an internal aquiferous system hence the system of extensive canals were developed. The formation of the tongue-like body which is sickle-like in section, is the result of the increase in longitudinal rigidity of whole sponge. In this case the convex side is dermal while the opposite concave-atrial, similar to other bilateral-symmetrical forms of Hexactinellida. The secondary funnel sometimes, but not always, present in the lower part of a sponge is produced by ingrowth and union of the opposite edges of the a tongue-like growth. This enclosed, narrow, longitudinally-directed slit must be considered, in this scheme, as a parietal osculum. Some objections can be raised against Scheme A (Fig. 14A). All of the internal wall passages observed in sections of *Euryplegma* are lined with pentactins similar to those of the exposed convex and concave surfaces. Are these specific canalaria equivalent to dermal and atrial spicules? Such canalaria are unknown in other Hexactinellida, moreover true schizorhyses are "subdermal canals always covered with dermal layer" (IJIMA, 1927). Thus the interpretation of structure and derivation by Scheme A (Fig. 14), a pattern consistent for Tretodictyidae, does not seem to be applicable to *Euryplegma*.

Scheme B of Fig. 14 suggests an interpretation of body form and canalization by development of schizorhyses which are lined with surface tissues originating from both dermal and atrial layers. This process began with

asymmetrical growth of only a sector of an ancestral tubular form as in the previous scheme (A). Walls of a tongue-like sponge became thicker, its opposite surfaces developed small furrows and depressions which included dermal and atrial layers. Some depressions became connected with those directly opposite and also with internal cavities forming the structure typical of the genus *Euryplegma*. In this case dermal and atrial spicules are situated on the concave and convex surfaces of the tongue-like sponge and, in addition, underlie the linings of the structures similar to schizorhyses. The occurrence of the secondary funnel in the lower part of a body does not change the location of layers of the initial structure. The canal-like structures in this case are not homologous to true schizorhyses of Tretodictyidae and instead are specific aulocalycoid structures, interpretable as tortuous oscula — orifices between dermal and atrial layers. This interpretation is improbable since intermediate forms of such "pseudocanalization" are so far unknown. The primitive canalization of *Tretopleura* with superficial epirhyses and aporhyses is considered unrelated to that of *Euryplegma* and offers no support here. If Scheme B is accepted, then the family Aulocalycidae possesses unique "pseudocanal" structures.

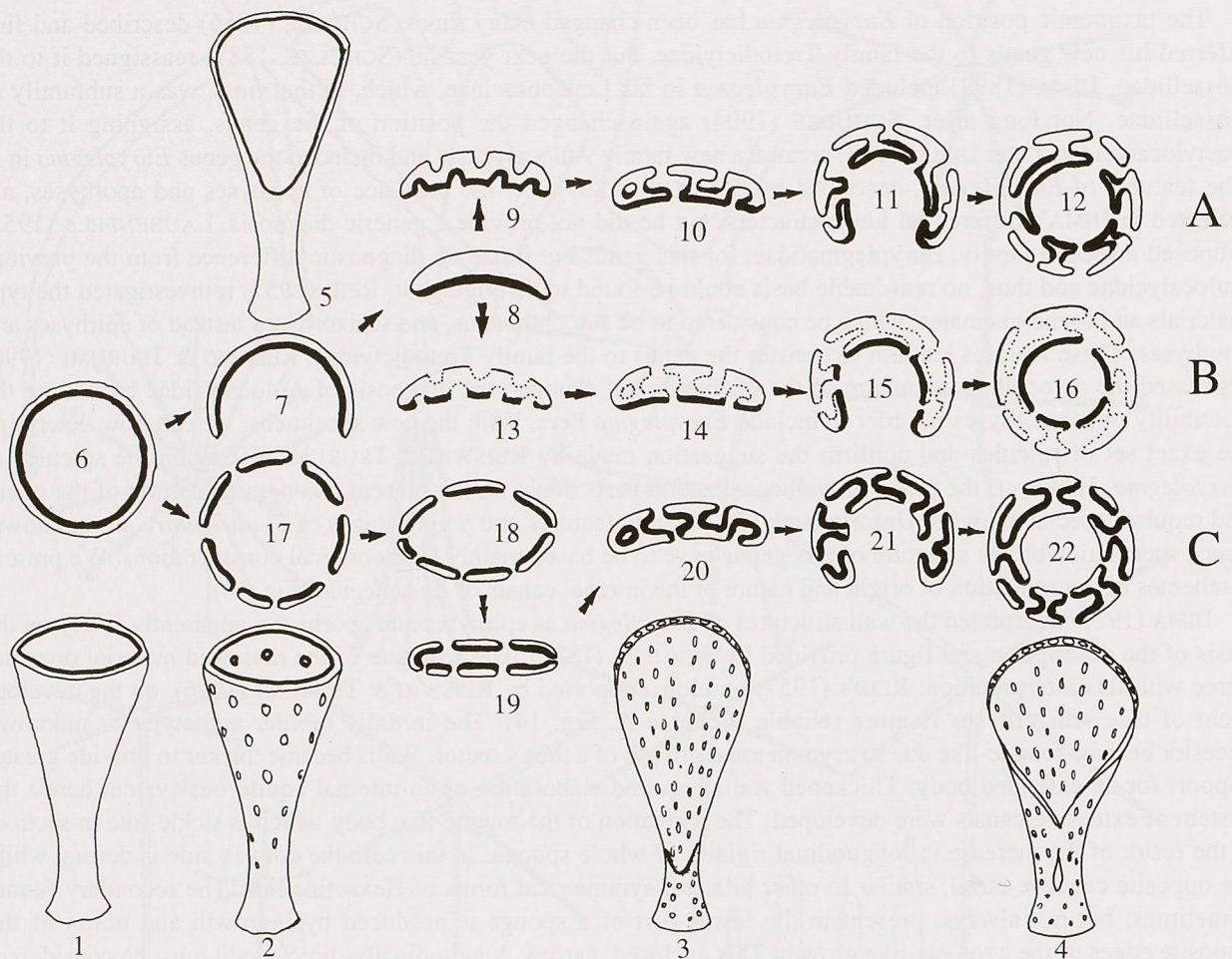


FIG. 14. — Schemes of morphogenesis of *Euryplegma* (thin line: dermalia; thick line: atrialia; dotted line: canalaria): **A**, scheme of development through wall canalization of an asymmetrical form. **B**, scheme of development through wall "pseudocanalization" of an asymmetrical form. **C**, Scheme of development through flattening of a tubular form with lateral parietal oscula and marginal oscula.

1, 6, hypothetical tubular form, side view and section. 5, 7, 9, 13, hypothetical tubular form with lateral parietal oscula, side view and section. 2, 17-19, hypothetical tubular form with lateral oscula, side view and section. 3, real tongue-like form, side view. 4, 10, 11, 14, 15, 20, 21, real tongue-like forms with secondary funnel in lower part, side view and upper section. 12, 16, 22, sections through the lower secondary funnel of form 4.

According to Scheme C (Fig. 14) the ancestral tubular form developed numerous lateral parietal oscula. Bilateral compression produced a tongue-like sponge. To increase local rigidity the walls on opposite sides of the atrial surfaces were connected by broad anastomoses. The sickle-like form in transverse section of the tongue-like sponge developed to increase longitudinal rigidity of the entire organism. Also the secondary funnel in the base of some specimens was produced by ingrowth and union of the opposite edges of a tongue-like body. According to this interpretation, the convex and concave (or the inner and the outer) surfaces are lined with dermalia. The parietal slit enclosed in the secondary funnel by union of the ingrown parts is not homologous to a parietal osculum, but is an inter-cavaedium — an entrance into a dermally-lined cavity (term of REID, 1964, for some Euretidae). The atrial cavity in this form must be situated between convex and concave surfaces, subdivided into a system of branching canals. The primary osculum of *Euryplegma* must also be subdivided into numerous apertures at the growing edge of the tongue-like sponge. The functions of the atrial cavity and the oscula have presumably been altered as a result of this major shape change. Water flow might maintain its original pattern, moving into the walls from all exposed surfaces, and transported to the distal edge within the atrial canal system. Alternately water flow might have been grossly modified to pass from one dermal surface to the other across the now internalized atrial cavity, as in the simple ear-like processes of "metameric" claviscopulid described as *Chonelasma* (TABACHNICK, 1988, 1991). These alternatives can only be decided when live specimens are directly examined or specimens with very well-fixed tissues are analyzed histologically.

The three schemes presented should be viewed as hypotheses of possible derivation of the specialized *Euryplegma* body form. At present there is no strong evidence, or known intermediate, to suggest that Scheme C, calling for body flattening and atrial bridging, is more likely scenario than Scheme B. The canals of *Euryplegma* are still termed schizorhyses, with the understanding that they are unlikely to be homologous with the similar canals of the Tretodictyidae.

3. — THE SCOPE OF THE FAMILY AULOCALYCIDAE

The family Aulocalycidae was created by IJIMA (1927). It included 5 genera; *Aulocalyx*, with two species *A. irregularis* Schulze, 1887, and *A. serialis* Dendy, 1916; *Rhabdodictyon*, with two species *R. delicatum* Schmidt, 1880, and *R. kurense* Ijima, 1927, and three monospecific genera, *Tretopleura candelabrum* Ijima, 1927, *Euryplegma auriculare* Schulze, 1886, and *Fieldingia lagettoides* Kent, 1870. Only two taxa were added later: *Tretopleura styloformis* Tabachnick, 1988, and *Leioplegma polyphyllon* Reiswig & Tsurumi, 1996. *R. kurense* was formally transferred to a new genus *Ijimadictyum* Mehl, 1992. The family, according to IJIMA (1927), was determined by an irregular-meshed skeletal framework (later denoted as "aulocalycoid" by REID, 1963); the presence of scopules and uncinates was permitted, as well as epirhyses and aporhyses in *Tretopleura* and *Euryplegma*. The diagnosis of the family given by BARTHEL and TENDAL (1994) was simplified to the aulocalycoid skeleton without any other features and without speculations on the scope of the family. REISWIG and TSURUMI (1996) clarified the misunderstood distinction of the aulocalycoid skeleton and suggested an expanded diagnosis which also allowed uncinates and scopules. Thus the family Aulocalycidae is presently contained within Scopularia and includes forms with a great range of canalization modes where other Scopularia have one special mode, or perhaps two modes, within a family. The mode of canalization is generally regarded as the most significant feature in the family definition - e.g., families Euretidae (sensu IJIMA) or Euretidae and Coscinoporidae (sensu ZITTEL, 1877; BARTHEL & TENDAL, 1994) and Tretodictyidae. Instances of body-form complication by development of inter-cavaedia or atrial expansion in sponges such as *Myliusia* (REID, 1964) are usually not reflected in the diagnosis of families.

Except for the aulocalycoid type of skeleton, there is no other character authentically defining the family. The obligatory presence of dermal and atrial pentactins are common in other Scopularia. From the contributions of IJIMA (1927), MEHL (1992), REISWIG & TSURUMI (1996), the genera recognized until the present as constituents of the Aulocalycidae can be characterized by the following specific features (except choanosomal skeleton and dermal and atrial pentactins):

1. *Euryplegma* - see above.

2. *Aulocalyx* is a tubular stellate form with vertically directed folds bearing lateral oscula; microscleres are distinctive rhopalasters and various discohexasters.

3. *Rhabdodictyon* is a cup-like or tubular sponge with lateral oscula (similar to e.g., *Regadrella* in shape), microscleres are discohexasters, spirodiscohexasters, hemidiscohexasters and discohexactins.

4. *Fieldingia*, as originally described by KENT (1870), is an incomplete sponge represented by a minute and thin lamellar fragment composed of pentactins, rarely stauractins and hexactins; these spicules are fused to each other by tangential rays and numerous synapticalae.

5. *Tretopleura* is a fan-like elongate sponge. Only this genus of Aulocalycidae (*sensu* IJIMA) has epirhyses and aporhyses (IJIMA, 1927), scopules, uncinates and often hexactins (rarely pentactins) among dermalia and atrialia (TABACHNICK, 1988).

6. *Ijimadictyum* is composed of branching and anastomosing tubes provided with additional lateral oscula, microscleres are discohexasters, spirodiscohexasters, hemidiscohexasters and discohexactins.

7. *Leioplegma* is fan-like with dichotomously branching lobate processes; microscleres are discohexasters and hemidiscohexasters.

Loose choanosomal hexactins have been reported from some specimens of *Euryplegma*, from *Aulocalyx serialis* and from *Leioplegma polyphyllon*. It is worth noting that they are always loose, never fused to the aulocalycoid framework.

Of these seven genera, five of them, *Euryplegma*, *Aulocalyx*, *Rhabdodictyon*, *Ijimadictyum* and *Leioplegma*, form a well distinguished group of taxa and it is suggested here that the family Aulocalycidae be limited to this group. An emended family diagnosis, based upon those given by IJIMA (1927) and REISWIG & TSURUMI (1996), is offered here.

DIAGNOSIS OF THE FAMILY AULOCALYCIDAE (from IJIMA, 1927 emended). — Funnel-like, or tubular dichotomously branching-fusing, or fan-like thin-walled sponges with or without lateral oscula. The choanosomal skeleton is of aulocalycoid type — irregular-meshed framework made of hexactins which are orientated irregularly and have elongate rays, usually curved, intersecting at various angles and fusing at intersections and by synaptical junctions. Dermalia and atrialia are pentactins. Canalization is usually lacking but may include unique schizorhyses. Microscleres have spined club ends (rhopalaster) or discoidal ends (discohexasters, hemidiscohexasters and discohexactins).

REMARKS. — The following features seem to be absent in the suggested list of the representatives of the family Aulocalycidae: no sceptrules (scopules or clavules), no uncinates. Except for the schizorhyses canalization of *Euryplegma*, true wall canalization appears to be absent in the other members of the family. Dermalia and atrialia could include some stauractins or even hexactins. Rather small loose choanosomal hexactins could be present within the meshes of the choanosomal framework. The wide spectrum of external body shape does not seem to be an extraordinary feature of Aulocalycidae as it also occurs in the close families, Euretidae and Euplectellidae.

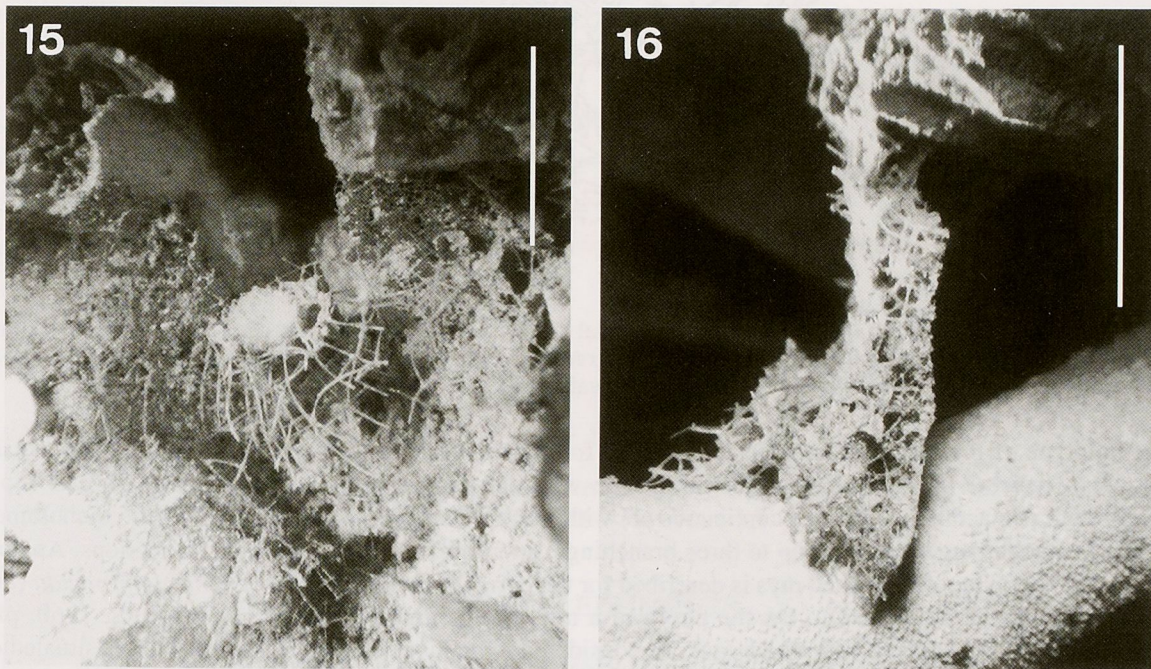
4. — PLACEMENT OF *TRETOPLEURA* AND *FIELDINGIA*

Two genera, *Tretopleura* Ijima and *Fieldingia* Kent, presently members of the family Aulocalycidae, lack the required aulocalycoid choanosomal skeleton. They are to be transferred to other families.

We propose referring *Tretopleura* to the Euretidae (or Coscinoporidae if one chooses to accept division of the former family). Both species of *Tretopleura* have small hexactins fused to the framework similar to representatives of the Euretidae and Farreidae. The genus is poorly investigated and it remains uncertain whether the skeleton of primary regular framework known in the Euretidae/Coscinoporidae representatives (REID, 1958a, 1958b, 1961) can be demonstrated in the type species, *T. candelabrum*. The skeleton in the central, thicker part of *T. styloformis* is fairly regular and may be considered as euretoid. Since the latter is subjectively assigned to *Tretopleura*, its characters cannot be used to set the characters of the genus. The spicule composition and overall body form of *Tretopleura*, necessarily set by its type species, remains unknown; canalization includes extradictyonal epirhyses

and aporhyses. Spiculation, body form and canalization of *T. styloformis* are similar to those of *Bathyxiphus*, differing only in microscleres. We prefer to maintain the genus as a distinct taxon pending finding the type specimen and comparing its characters to those of the other genera of Euretidae.

The genus *Fieldingia* has been described twice. The holotype of *F. lagettoides* is a poor fragment described by KENT (1870) from the Atlantic ocean, the remnants stored as NHM 1872.2.3.178 (Figs 15-17). It does not correspond to the other specimen from the Pacific ocean described under the same species name by SCHULZE (1887), 1887.10.20.127. The characters of the specimen described by KENT are summarized above (3. 4). It is impossible to decide whether junctions between the tangential rays of the dermal pentactins begin as sympodial ray branching, spines produced only in the tangential plane, or simply represent synapticular junctions; these alternatives may only be extreme examples of a continuous spectrum of secondary silicification processes. We cannot even be certain that small stauractins are not involved as well. If this latter feature is true, the skeleton may resemble (in plane view) some skeletons of *Reticulosa* composed of stauractins of several orders of size. "The largest are arranged so as to enclose square meshes, and the smaller grades lie within these meshes so as to subdivide them regularly" (REID, 1958a) - into so-called "quadrules" (HALL & CLARKE, 1898). In spite of the fact that *Reticulosa* are considered to be lyssacine sponges, some members of this group may have had spicules cemented together (REID, 1958a).



FIGS 15-16. — *Fieldingia lagettoides*: holotype, attached to coral (scale 5 mm).

Small spherical aggregations of fused hexactins are also sporadically found attached to the main skeleton of *F. lagettoides*. These spherical bodies are similar to the siliceous aggregations which have been reported from diactins of some Rossellidae (e.g., so called "small basidictyonal masses" in *Staurocalyptus glaber* Ijima 1904, pl. 15, fig. 13), and are also likely to have an allochthonous origin.

The specimen described by SCHULZE as a second representative of *F. lagettoides* is a fragment of fused irregular framework of large and small hexaradiate spicules with numerous thick spherical aggregations probably having autochthonous origin. These spherical aggregations must be simple knots of the main spicule framework. The loose spicules are scopules, uncinates, diactins; microscleres are discohexasters, hemihexasters and hexactins. It is impossible to find similarities shared by these fragmentary specimens of KENT and SCHULZE, except for the spherical siliceous bodies which indeed differ in detail in the two forms. Hence SCHULZE's specimen cannot even

be considered a representative of *Fieldingia*. According to its skeleton and spicules, some of which seem to have allochthonous origin, it could not be referred to any existing genus or family and its allocation must await a more detailed analysis of the specimen.

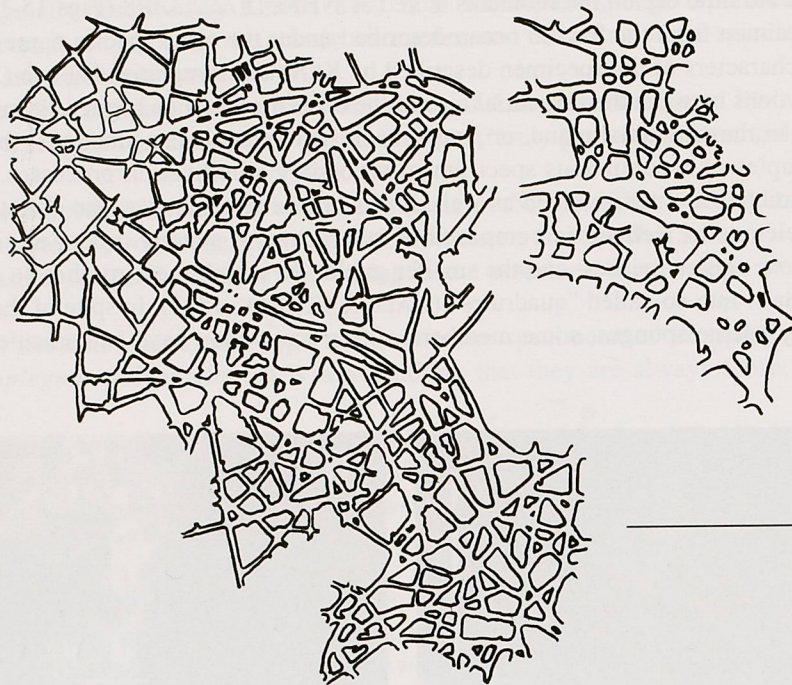


FIG. 17. — "Quadrules" of *Fieldingia lagettoides* (tangential surface). The large spicules are pentactins or hexactins, the small ones are stauractines and synapticalae. This diagram, made from the NHM slide of the holotype described by KENT, resembles the figured skeletons of reticulosans (scale 1 mm).

The holotype of *Fieldingia* is somewhat similar to fossil *Stromatidium* Girty, 1908, which contains a single species — *S. typicale* Girty. It is a cylindrical sponge with one osculum and walls built with several separate layers of rough pentactins fused into a continuous net within each layer. The fusion is formed with dichotomously branching pentactin tangential rays (up to three branchings) and probably with synapticular junctions. Analogous dichotomous branching of tangential rays is described for the dermal pentactins of *Aulochone clathroclada* (family Rossellidae) (LÉVI & LÉVI, 1982). On the photo of a non-type fragment of *S. typicale* (FINKS, 1960, pl. 44, fig. 7), the first inner spicular layer, which must be considered to be juvenile or neanic and which is situated close to the atrial cavity, appears to be composed of fused stauractins. This fact is omitted in the description and should be reviewed in both the photographed non-type fragment and GIRTY's type specimens. Dermal pentactin fusion is known also for *Lychniscosa* (MEHL, personal communication). FINKS (1960) suggested a new family Stromatidiidae for this unique genus and the family itself is tentatively included into his superfamily Brachiospongioidae. In our opinion both of REID's systems (1958b), one developed chiefly from IJIMA's system and the other from that of SCHRAMMEN, offer more suitable placement for Stromatidiidae. It may be included into the order Reticulosa, characterized as having a skeleton of "coherent or connected megascleres of dermal origin or partly dermal origin" (REID, 1958b). The similarity of *Fieldingia* to *Stromatidium* may be only superficial in that there is an internal dictyonal framework of hexactins in *Fieldingia* but no such component in *Stromatidium* or other Reticulosa. For the present, we consider *Fieldingia* doubtful member of the order Reticulosa, possibly related to Stromatidiidae but not able to be placed within that family on the basis of limited knowledge of both groups. The Reticulosa may be a hexasterophoran group with the same range as Lyssacinosa, Hexactinosa and Lychniscosa or a separate stock with the range equal to Hexasterophora and Amphidiscophora.

5. — THE CLASSIFICATION OF HEXASTEROPHORA

Since the Aulocalycidae are distinguished from the other Hexactinosa by a distinct pattern of framework construction, their removal from that order results in the formation of two coherent and consistent taxa, the Aulocalycoida for the family Aulocalycidae, and the Hexactinosa for the remaining members. The Aulocalycoida should have the same rank as IJIMA's (1927) tribes or REID's (1958b, 1961) orders: Hexactinosa, Lyssacinosa and Lychniscosa. The new taxon, order Aulocalycoida, can be characterized by the diagnosis of Aulocalycidae without specific description of loose spicules. Hence the Aulocalycoida is offered for sponges with specific aulocalycoid skeleton in which uncinates and scepstrules are absent. The diagnosis of the Hexactinosa should be reformed to delimit its scope. Hexactinosa were defined by REID (1958a) as "dictyonina in which the connected hexactins are all simple". Thus sponges with lychniscosan skeletons (all Lychniscosa) and sponges with basidictyonalia (some Lyssacinosa) do not belong to Hexactinosa. The major diagnostic character separating the members of the Hexactinosa from the removed group would be "with farreoid or euretoid type of primary dictyonal skeleton". There is some defense for adding the presence of scepstrules and/or uncinates to the Hexactinosa diagnosis but this would only restrict forms like *Dactylocalyx* Gray, 1867, from this taxon. The modified higher classification of Hexactinellida is presented in Fig. 18.

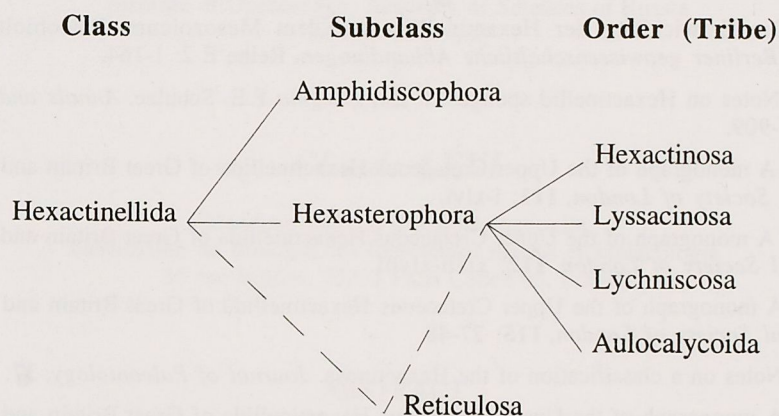


FIG. 18. — Taxonomic scheme of highest taxa of recent Hexactinellida. Complete lines denote well supported relationships; dashed lines indicate uncertain relationships.

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