

## Family Tretodictyidae Schulze, 1886

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Tretodictyidae Schulze (Hexactinellida, Hexactinosida) is defined in accordance with Ijima's 1927 formulation – basiphytous hexactinosans with a distinctive channelization pattern, schizorhyses, in a euretoid dictyonal framework. The family is revised to contain eight genera and 22 species, and many lectotype designations are made. With exception of removal of *Auloplax* to the Dactylocalycidae, this is essentially the same constituency adopted by Ijima. Genera are differentiated by a combination of body form and spiculation. Body form varies from the traditional funnel form of *Hexactinella* to cups, branching tubes, branching solid cylinders and globular forms without symmetry. The family is world wide in distribution, with a restricted depth range of (11?)–90–1917 m. The family is absent from very deep water communities, probably due to its requirement for hard bottom substrate.

**Keywords:** Porifera; Hexactinellida; Hexactinosida; Tretodictyidae; *Anomochone*; *Cyrtaulon*; *Hexactinella*; *Psilocalyx*; *Sclerothamnopsis*; *Sclerothamnus*; *Tretocalyx*; *Tretodictyum*.

### DEFINITION, DIAGNOSIS, SCOPE

#### Restricted synonymy

Sclerothamnidae Schulze, 1885. Volvulinidae Schulze, 1885. Tretodictyidae Schulze 1886. Tretocalycidae Schulze, 1904; Schrammen, 1912. Hexactinellidae; de Laubenfels, 1936a (not Schmidt, 1870).

#### Definition

Hexactinosida with three-dimensional, small-meshed, euretoid dictyonal framework several dictyonalia in thickness at the growing edge; primary dictyonal frame consists at least in part of four-sided (square or rectangular) meshes; rays of dictyonalia extend only one-mesh in length to the next adjacent dictyonal centrum; longitudinally oriented dictyonal rays aligned and fused side-by-side to form longitudinal strands; schizorhysial channelization developed by growth of framework in narrow vertical (dermal to atrial) and longitudinal oriented septa bridged by small patches of dictyonalia; such growth leaves a confluent system of small gauge channels 1–2 mm wide running mainly longitudinally, but connected transversely.

#### Diagnosis

Body form varies from branching and anastomosing solid cylinders to branching and anastomosing tubes to funnel, cup, and irregular globular forms; dictyonal frame of narrow tuberculate beams joining regular and false nodes, which are generally not swollen; lamellae have not been specifically reported; superficial cortices usually not developed but hypersilicification of dermal surfaces with swollen surface nodes occur in 3 genera; attachment of small hexactins is rare; spiculation includes stronglyloscopules in all but one genus; uncinates typically occur as intermediate sizes (300–1000 µm long) with poorly developed brackets and barbs,

often in surface brushes, but larger and smaller sizes occur in individual genera; dermalia are pentactins, hexactins or intermediates (pentactins with very short distal stub); pinule development occurs in one genus; atrialia are generally absent but occur in one genus; microscleres commonly occur in a single form, either oxyhexasters, onychexasters, onychexactins, discohexactins, but some species have two or more types.

#### Scope

Fifteen nominal genera have been included in the family of which only eight appear to be valid and correctly assigned here.

#### Remarks

Present understanding of the basic shared characters of the family, schizorhyses in an euretoid framework, was formulated by Ijima (1927) in which an unfortunate editorial mistake resulted in replacement of the term 'schizorhyses' with 'diarhyses' in all sections dealing with the family and its assigned genera. The origin of the family is clouded by Schulze's (1885) simultaneous formation of two family names: Sclerothamnidae, based on Marshall's *Sclerothamnus*, and Volvulinidae, based on Schmidt's *Volvulina*. Schulze (1886) replaced both of these families with Tretodictyidae the following year, with description of several species of *Tretodictyum*. Tretodictyidae remains the commonly used family name today. Volvulinidae was valid, but the preoccupied genus name, *Volvulina*, was replaced the following year (Schulze, 1886) by *Cyrtaulon*. It has not been used since its origin and therefore may be suppressed (ICZN Article 23; Anon, 1999). Conversely, Sclerothamnidae is valid and is clearly the senior synonym to Tretodictyidae. *Sclerothamnus* was the basis of a separate formation by Caster (1941) of a subfamily, the Sclerothamninae of the otherwise fossil Titusvillidae. It is clear that Caster was unaware of Schulze's family name. The Titusvillidae are reticulosans and

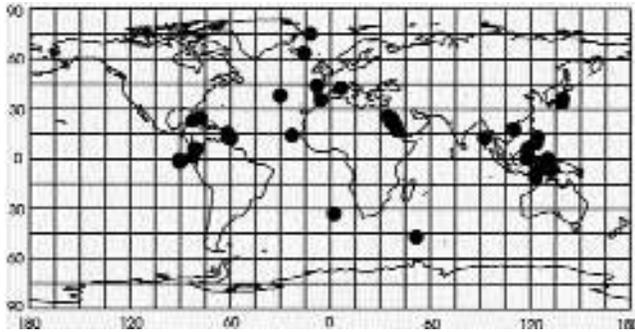


Fig. 1. Distribution of Tretodictyidae.

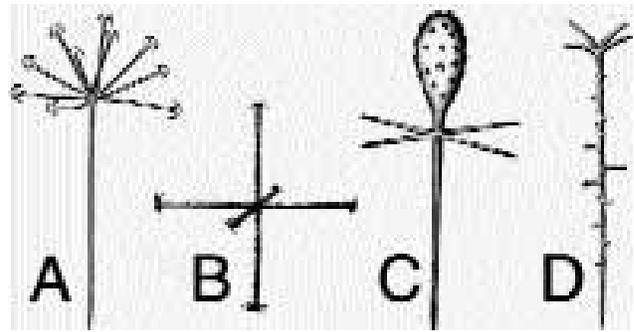


Fig. 2. Distinctive spicule forms of Tretodictyidae genera. A, mixed scepter-aster 'cyrtaulon spicule' of *Cyrtaulon*. B, onychexactin of *Tretocalyx*. C, hexactine dermalium with swollen pinulus of *Sclerothamnopsis*. D, trumpet-shape scopule of *Sclerothamnus*.

inferences of a close relationship to *Sclerothamnus* are incorrect according to Reid (1963b). Attempts here to meet ICZN criteria for direct suppression of the unused senior synonym Sclerothamnidae (used in 25 publication in the last 50 years) has been unsuccessful, the name Tretodictyidae will nevertheless be employed here as the name in common use pending result of application to ICZN for suppression of Schulze's Sclerothamnidae. Although Schulze (1887a) had moved all of his *Tretodictyum* species to *Hexactinella*, Tretodictyidae remained the family name of use until 1904. Schulze (1904) then erected Tretocalycidae as a replacement for Tretodictyidae without explanation. Tretodictyidae was eventually reinstated by Ijima (1927) on the basis of Schrammen's (1912) resurrection of *Tretodictyum*, Schulze's original genus name, for tubular members of the family. De Laubenfels (1936a) argued for use of Hexactinellidae Schmidt, as the valid family name, but Reid (1963c) very effectively showed such use of Schmidt's nomen was completely unjustified. Tretodictyidae remains the standard name of choice for the family. Fifteen genera with Recent members have been assigned to the family over the years, eight of which are here considered valid members. *Volvulina* is a preoccupied synonym of *Cyrtaulon* and *Dendrospongia* is a junior synonym of *Sclerothamnus*. *Fieldingia* Kent, a member of the family through its early years, was moved to the Aulocalycidae by Ijima (1927) and here is further removed as *Hexactinosa incertae sedis*. *Uncinatera*

Topsent was included by Schulze (1904) and Schrammen (1912) and transferred to Euretidae as a synonym of *Chonelasma* by Ijima (1927); here it is re-established as a distinct genus but moved to Aulocalycidae. *Auloplax* Schulze was assigned to the Tretodictyidae by Ijima (1927) and synonymized with *Hexactinella* by Reid (1963b); it is here resurrected as a valid genus separate from *Hexactinella* and transferred back to its original assignment in the Dactylocalycidae. *Tretorete* Ijima was originally assigned to the Craticulariidae, then moved with that entire family to Tretodictyidae by de Laubenfels (1936a); Reid (1963b) transferred *Tretorete* to the Cribrospongiidae where it remains. *Euryplegma* Schulze was moved from Aulocalycidae to Tretodictyidae by Reid (1963b) on the basis of recognized schizorhyses and uncinates; after review of framework organization and strong evidence that the uncinates were foreign, the genus was returned to Aulocalycidae by Reisinger & Tsurumi (1996). The constitution of the family accepted here, 22 species in 8 genera, is essentially that arrived at by Ijima (1927) but with *Auloplax* removed. The family is worldwide in distribution (Fig. 1) with apparent absence of reports from the north-east and entire south Pacific basins clearly attributable to inadequate publication of collections (undescribed materials from both areas are known). They occur at depths of (11?)-90–1917 m.

KEY TO GENERA

- (1) Body funnel or cup-shaped with accessory lateral oscula ..... *Anomochone*  
 Body form otherwise ..... 2
- (2) With distinctive 'cyrtaulon spicules' (Fig. 2A) ..... *Cyrtaulon*  
 Without 'cyrtaulon spicules' ..... 3
- (3) All microscleres as onychexactins (Fig. 2B) ..... *Tretocalyx*  
 Microscleres otherwise, never as onychexactins ..... 4
- (4) Dermalia as hexactins with swollen pinulus (Fig. 2C) ..... *Sclerothamnopsis*  
 Dermalia without swollen pinulus or unknown ..... 5
- (5) With distinctive trumpet-shape scopule with digitate shaft processes (Fig. 2D) ..... *Sclerothamnus*  
 Without distinctive floriscopules with shaft processes ..... 6
- (6) Microscleres as oxyhexasters only ..... *Tretodictyum*  
 Microscleres mainly discohexasters; oxyhexasters may occur ..... 7
- (7) Cup-shape body with swollen surface dictyonal nodes ..... *Psilocalyx*  
 Funnel to tubular body without swollen surface dictyonal nodes ..... *Hexactinella*

**ANOMOCHONE** IJIMA, 1927**Synonymy**

*Anomochone* Ijima, 1927: 268.

**Type species**

*Anomochone expansa* Ijima, 1927: 269 (by original designation).

**Definition**

Tretodictyidae of either irregular, thin-walled funnel-form body with tendency to extreme lateral plication (branching) or thick-walled globose body, both with deep atrium either wide or narrow, respectively; with large terminal osculum and small lateral oscula; dictyonal framework of triangular meshes and multiradiate nodes very swollen in dermal layer.

**Diagnosis**

Attached to solid substrate by narrow basal disc; with typical schizorhyses opening by surface grooves in upper marginal regions but obscured in main and lower body parts by dictyonal encroachment into channels; framework entirely sparsely spined; dictyonal spurs as short sharp spikes; poorly known spiculation includes stronglyloscopules and two sizes of uncinates; surface spicules and microscleres are unknown to date.

**Remarks**

The genus was erected by Ijima (1927) for two species of tretodictyids, *A. expansa* and *A. globosa*, collected by the 'Siboga' at two stations in the Banda Sea from depths of 90–204 m. Most specimens were completely macerated – only one of the nine specimens contained a few spicules. No subsequent material has been reported since the original account. Present rudimentary data on spiculation prevents placement of the genus with respect to the other members of the Tretodictyidae. Ijima's diagnosis and description of the genus and constituent species was adequate, but many errors occurred during posthumous editing. Most significant for this genus was the inexplicable notation of its channelization as 'diarhyses' instead of the obvious schizorhyses present here. Reid (1963b) did not mention the genus in his review of the Hexactinosida.

**Description of type species**

*Anomochone expansa* Ijima (Fig. 3).

**Synonymy.** *Anomochone expansa* Ijima, 1927: 269, pl. 20, figs 9–16, textfigs 33–34.

**Material examined.** None. Lectotype (here designated): ZMA 3398 – south of Kur Island, Banda Sea. Paralectotypes (here designated): ZMA 3428 and 5090 – same location.

**Description (from literature).** Thin-wall, irregular funnel-form body to 7 cm tall by 6.3 cm wide strongly pleated to form branch-like extensions of upper margin; deep atrium spanned by cross bridges between deepest inner pleats of body wall; attached to solid substrate by narrow basal disc; atrium widely open above by main osculum and through body wall by small round lateral oscula to 4 mm diameter borne on short tubes oriented downwards (in type specimen) or laterally; wall 2–4 mm thick penetrated by schizorhyses opening in upper body region by longitudinal branching grooves to

0.5 mm wide separated by dictyonal septa 1–2 mm wide; in middle and lower body regions schizorhysial openings restricted to smaller round apertures by dictyonal encroachment; dictyonal framework triangular in mesh with 110–275  $\mu\text{m}$  long sides throughout, with no dictyonal strands or lamellae; nodes multiradiate with 8–9 connecting beams; dermal nodes strongly swollen, 100–140  $\mu\text{m}$  diameter; all framework beams and nodes sparsely spined; beams generally 30–50  $\mu\text{m}$  thick; spurs on surface nodes as short sharp spikes; atrial framework very irregular with narrow beams down to 20  $\mu\text{m}$  thick and nodes not swollen; small rough hexactins (50  $\mu\text{m}$  ray length) and larger pentactins (110–170  $\mu\text{m}$  ray length) commonly fused to framework; free spicules (incompletely known) include large uncinates 1.5 mm long by 16  $\mu\text{m}$  thick; small oxydiactins (microuncinates?) to 300  $\mu\text{m}$  long; stronglyloscopules 460–550  $\mu\text{m}$  long with 5–6 rough tines 45–55  $\mu\text{m}$  long; dermalia and microscleres remain undetected.

**Remarks.** The species remains understood only from the original, mostly macerated type collection and Ijima's original description. New specimens with intact spiculation are needed to determine the species relationships with other Tretodictyidae.

**Distribution**

Known only from the Banda Sea, Indonesia, at 90–204 m depths.

**CYRTAULON** SCHULZE, 1886**Synonymy**

[*Volvulina*] Schmidt, 1880b: 58 (preocc.). *Cyrtaulon* Schulze, 1886: 81, Schulze, 1887a: 332.

**Type species**

*Volvulina sigsbeeii* Schmidt, 1880b: 58 (by monotypy).

**Definition**

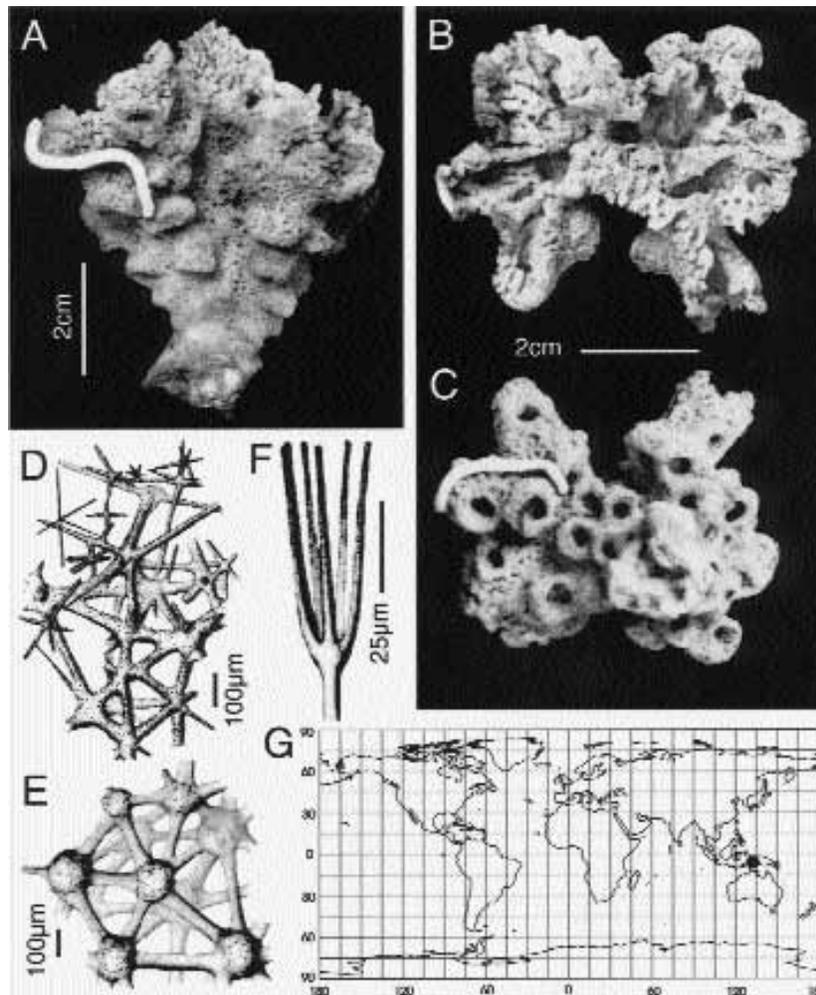
Tretodictyidae with distinctive 'cyrtaulon-spicule' consisting of a discohexaster-like centrum, from which extends a sceptrule-like style.

**Diagnosis**

Body cup-form or cylindrical without atrial cavity; superficial dictyonal nodes and beams may be hypersilicified (swollen) or not; dermalia as pentactins, with or without hexactins; regular scopules may or may not be present; medium-size uncinates present, with or without a central swelling; in addition to the 'cyrtaulon-spicule', there are either only discohexasters or no other microscleres present.

**Remarks**

Ijima's (1927: 219) choice of *C. solutus* as type species for the genus is contrary to ICZN rules. Since *Cyrtaulon* Schulze is not a new taxon but a replacement for *Volvulina* Schmidt, the type species of the genus remains unchanged as *Volvulina sigsbeeii* Schmidt. Reid (1963b) made no comment on the genus at all in his review of Hexactinosida. The genus contains two species: *C. sigsbeeii* (Schmidt) and *C. solutus* Schulze, distributed in the two west tropical regions, the West Indies and Indonesian areas, respectively, from depths between 183 and 838 m.



**Fig. 3.** *Anomochone expansa* (A–F) and distribution of *Anomochone* (G). A–C, lectotype viewed from side, top, and bottom, respectively. D, fragment of the dictyonal framework from the atrial surface. E, fragment of the dermal dictyonal framework. F, stronglyloscopule. G, distribution of *Anomochone*. (A–F, from Ijima, 1927, pl. 20, figs 9–11, 14–16).

### Description of type species

*Cyrtaulon sigsbeeii* (Schmidt) (Fig. 4).

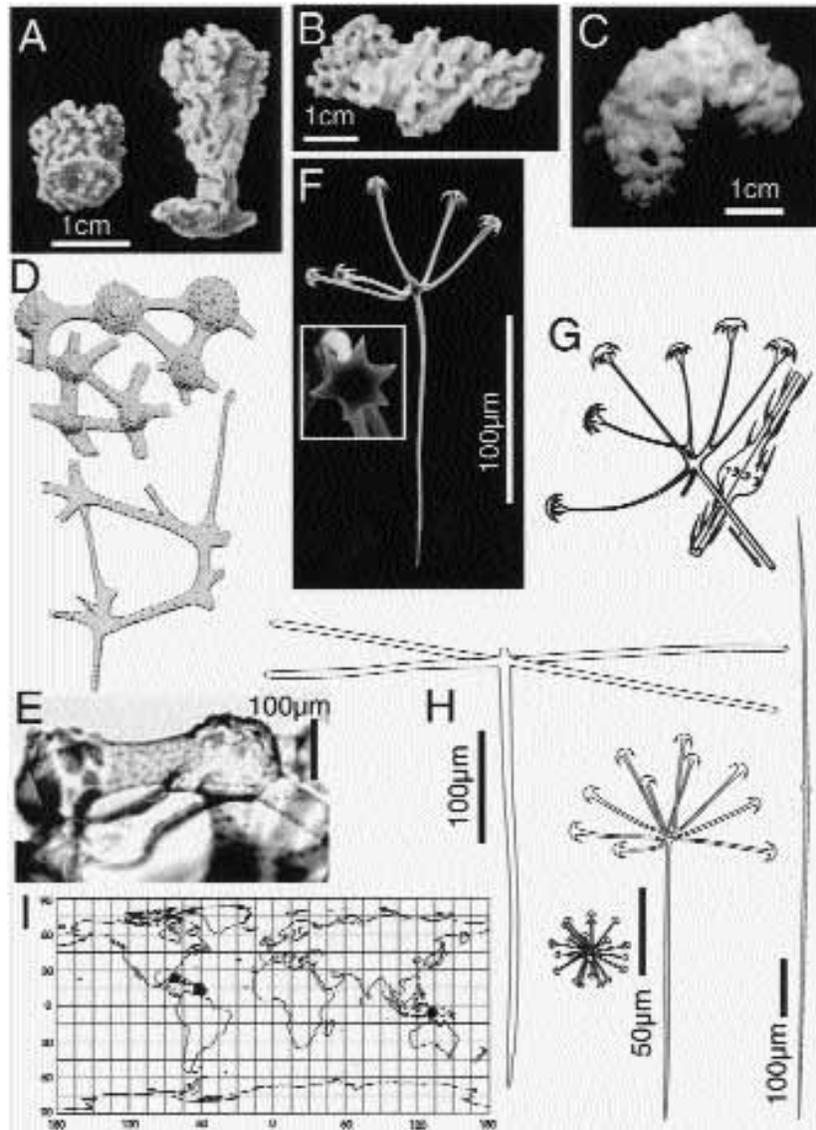
**Synonymy.** *Volvulina sigsbeeii* Schmidt, 1880b: 58, pl. 3, figs 14–15, pl. 4, fig. 6. pl. 5, fig. 7; pl. 6, fig. 6. *Cyrtaulon sigsbeeii* Schulze, 1886: 81; Schulze, 1887a: 333, pl. 92, fig. 9; van Soest & Stenotoft, 1988: 9, pl. 1, figs 3–4; Desqueroux-Faundez & Stone, 1992: 91.

**Material examined.** Lectotype: MCZ 6652 (here designated) – St. Vincent, Western Antilles. Other material. MCZ 6721r – Florida-Cuba. MCZ 8169 (part) – Guadeloupe. MCZ (2 uncatalogued specimens) – Barbados. YPM 9341a & b – Caribbean. RMM RMI-2540 – Barbados.

**Description.** Shape variable, a simple cylindrical stump with paragaster when small, attaining cup-form to 4.5 cm tall by 3 cm wide, with marginal paragasters; outer surface hispid and tubercular, consisting of 1 mm wide digitate processes when young (small), coalescing to 1–2 mm wide sinuous ridges and grooves (schizorhysial entrances) in intermediate size forms to an irregularly shallow-grooved surface with 1–3 mm diameter pores opening under short, imbricating canopies (half-tubes) in larger specimens; paragaster in smaller forms, 3–4 mm diameter,

confluent with schizorhysial channels; surface grooves probably covered by very delicate lattice of dermalia in life but present evidence poor; consistency hard and fragile; framework constructed of 0.3–3 mm wide strands (sheets and cords) joined together by small bundles of junctional beams, thereby circumscribing a network of obliquely-running, tortuous channels (schizorhyses?) penetrating the entire width of wall; dictyonal meshes are irregular, a few rectangular but most polygonal or triangular, with 50–400 μm sides; beams 10–40 μm thick, tuberculate but some areas smooth in same specimen; striking hypersilicification of external layer results in swollen surface nodes ornamented with warts and tubercles and thickened tuberculate beams; internal nodes usually not swollen or ornamented; spurs absent from most external nodes; megascleres: (1) pentactins with cylindrical rays, tangential rays 140–201–290 μm long, proximal rays 184–251–391 μm long, distal stub to 10 μm long, (2) fine-barbed uncinates with sharply swollen centrum 737–941–1142 × 3.8–5.5–8.0 μm; mesosclere: tylodiscohexaster ('cyrtaulon-spicule') aster radius 58–69–81 μm, style length 126–158–190 μm; microsclere: spherical discohexaster, diameter 33–43–60 μm.

**Remarks.** This species remains poorly understood mainly because of Schmidt's original lack of rigor in identification and limited availability of well-preserved specimens. Of nine



**Fig. 4.** *Cyrtaulon sigsbeei* (A–H) and distribution of *Cyrtaulon* (I). A, body form from Schmidt (1879, pl. 4, fig. 6) may not be this species. B, body form from Schulze (1887a, pl. 92, fig. 9) is probably correct determination but the specimen was macerated. C, body form of lectotype MCZ 6652 viewed from upper margin. D, dictyonal frame fragments by Schmidt (1879, pl. 3, figs 14–15) is inaccurate indication of conical spines rather than warts on surface nodes. E, warted surface nodes and ornamented beams of MCZ 6652. F, SEM of ‘cyrtaulon-spicule’ of RMM RMI-2540 with disc face as insert (photo: H. Browman). G, ‘cyrtaulon-spicule’ and center of uncinates (Schmidt, 1880b, pl. 6, fig. 6). H, spicules: dermal pentactin, ‘cyrtaulon-spicule’, uncinates and discohexaster from MCZ 6652. I, distribution of *Cyrtaulon*.

specimens surveyed from MCZ and USNM collections labelled ‘*Volvulina sigsbeei*, cotype’, only one bore cyrtaulon-spicules, two were washed out but probably belonged to this species; the other six were clearly not *C. sigsbeei*. Additional small fragments with type labels exist at MZUS but their identifications have not yet been confirmed. None of them will qualify as lectotype, but some may be accorded paralectotype status. Many characters such as body form, hypersilicification, node warting, surface texture and channelization pattern may be subject to ontogenetic and/or geographic variation.

#### Distribution

The species is restricted to the West Indies at depths of 183–838 m.

#### HEXACTINELLA CARTER, 1885

##### Synonymy

*Hexactinella* Carter, 1885e: 397; Schulze, 1887a: 327, 398 [in part]. *Tretodictyum* Schulze, 1886: 78 [in part].

##### Type species

*Hexactinella ventilabrum* Carter, 1885e: 397 (by monotypy).

##### Definition

Tretodictyidae of variable shape from simple vase- or bowl-like to branching tubules; entire external surface including

labyrinthic schizorhysial entrances covered by a dermal lattice of loose pentactins and subhexactins; discohexasters or variant always present; oxyhexasters present or absent.

### Diagnosis

Choanosomal channelization as cleft-form to labyrinthine schizorhyses delimited by radial septa oriented mainly longitudinally; dictyonal beams microtuberculate either scattered or in transverse rows; funnel or tube body internally lined by an atrial layer which is not continuous over exhalant apertures; scopule usually stronglyliform but tylote and oxyote tine tips occur; raphidial uncinates common with or without indications of brackets and barbs; spicules still unknown for several species.

### Remarks

Unaware of Carter's (1885e) description of *H. ventilabrum* and erection of the genus, Schulze (1886) described the same species as *Tretodictyum cyathus*. Realizing his error, Schulze (1887a) dropped his entire genus *Tretodictyum* to a junior synonym of *Hexactinella* Carter. This synonymy held until Schrammen (1912) decided that distinction between *Hexactinella* and *Tretodictyum* was justified, thereby removing only *H. tubulosum* from *Hexactinella* in resurrection of *Tretodictyum*. The species described by Dendy & Burton (1926) as *H. minor* is here transferred to *Tretodictyum* to preserve Ijima's (1927) distinction between the two main genera based upon microscleres: discohexasters in all *Hexactinella* and oxyhexasters in all *Tretodictyum*. Ijima's (1927) suggestions that *H. monticularis* Lendenfeld be reassigned to *Tretocalyx* is rejected since arguments were not presented and the species fits well within the definition of *Hexactinella*. Ijima's (1927) ambiguous suggestion that *H. labyrinthica* Wilson be removed from *Hexactinella*, taken by Reiswig (1990) as transfer to *Tretodictyum*, is also rejected; *H. labyrinthica* must remain in *Hexactinella* by virtue of its discohexaster microscleres. Reid's (1963b) transfers of *Tretocalyx* and *Auloplax* to synonymy with *Hexactinella* are not accepted here. Members of *Tretocalyx*, with only onychhexasters as microscleres, are easily distinguished from all known *Hexactinella* species. *Auloplax*, which completely lacks schizorhyses, has here been transferred to the Dactylocalycidae. Its only similarity with *Hexactinella* and other Tretodictyidae appears to be its loose spiculation. How Reid (1963b) came to suggest synonymy with *Hexactinella* remains a mystery. Reid's (1963b) further suggestion that *Hexactinella* be divided into two unequal subgenera on the basis of body form, *Parahexactinella* for the branching tubular *H. lata* (Schulze) and *Hexactinella s.s.* for all other species, has no zoological utility and is not followed here. The genus *Hexactinella* presently contains 10 species, *H. divergens* Tabachnick, *H. grimaldi* Topsent, *H. labyrinthica* Wilson, *H. lata* (Schulze), *H. lingua* Ijima, *H. rugosa* Ijima, *H. monticularis* Lendenfeld, *H. spongiosa* Ijima, *H. ventilabrum* Carter and *H. vermiculosa* Ijima, distributed world-wide at depths of 11–1917 m. Several species are poorly known and will require reassignment when spicule characters become available.

### Description of type species

*Hexactinella ventilabrum* Carter (Fig. 5).

**Synonymy.** *Hexactinella ventilabrum* Carter, 1885e: 397, pl. 14, figs 1–10; Schulze, 1887a: 331, pl. 96, figs 1–9. *Tretodictyum cyathus* Schulze, 1886: 79.

**Material examined.** Holotype: BMNH 1885.12.31.013 – off Misaki, entrance to Tokyo Bay, Japan.

**Description.** Shape is a compressed bowl, boat-like, on a short compressed stalk attached to solid substrate; the extended margins may be undulate (wavy) and in large specimens may fold locally to circumscribe marginal funnels with surface reversal: dermal inside and atrial outside; wall fragile, to 10 mm thick and total specimen diameter to 70 cm; outer dermal surface continuously covered by a loose spicule lattice of pentactins, scopules and smooth uncinates overlying a schizorhysial groove-and-ridge form of dictyonal framework with both grooves and ridges about 1 mm wide; atrial surface with similar spicular lattice covering the frame; atrial ridges extend laterally as thin dictyonal membranes from the ridges to circumscribe circular openings 1–4 mm wide; some atrial apertures are not covered by the atrial spicule lattice; the dermal labyrinthal schizorhysial grooves (interseptal slits) are continuous and mostly oriented longitudinally (toward growth margin), but basally the frame septa gradually thicken, reducing grooves to isolated pits; externally the ridges divide at low angles to maintain the spacing pattern distally; superficial schizorhysial slits extend internally obliquely and basally toward the middle wall layer and there intercommunicate with each other and with the channels opening on the atrial surface; schizorhysial channels thus form a net-like system throughout the wall but whether these reflect water passages or are occluded by soft tissue structures remains unknown; a thin layer of longitudinal dictyonal strands at mid-wall level gives rise to strands arching out to both surfaces in the septa, forming an overall plumose pattern; dictyonal meshes are square with 300 μm sides; nodes are mostly true hexactine centra, not swollen; beams 30–100 μm thick with tubercles uniformly scattered or tending to transverse rows; megascleres are dermal and atrial pentactins with swelling or occasional short peg as sixth-ray rudiment, tangential rays 347 × 30 μm; stronglyliform scopules with 2–4 tines, microspined only at spicule ends, 458 μm long, occur in dermal and atrial surfaces; thin moniliform oxydiactins (smooth uncinates?) occur in perpendicular brushes along with scopules in both surface lattices; uncinates (700–833 × 3–14 μm) with fine barbs are parenchymalia; 2 microsclere types are common: oxyhexasters with short primary rays (58–89, rarely to 170 μm diameter) and long-primaries (tylo?) discohexasters (58–70 μm diameter) with ca. 10 short secondaries in compact tufts; a third microsclere, short-primaries discohexasters (55 μm diameter) with 3–5 slightly S-form terminals is rare.

**Remarks.** Specimens from the eastern Pacific (Wilson, 1904) cannot be confirmed to species due to original macerated condition.

### Distribution

Known certainly only from off Japan, depths indefinite.

### PSILOCALYX IJIMA, 1927

#### Synonymy

*Psilocalyx* Ijima, 1927: 265. ? *Nitidus* de Laubenfels, 1955b: E86.

#### Type species

*Psilocalyx wilsoni* Ijima, 1927: 265 (by monotypy).

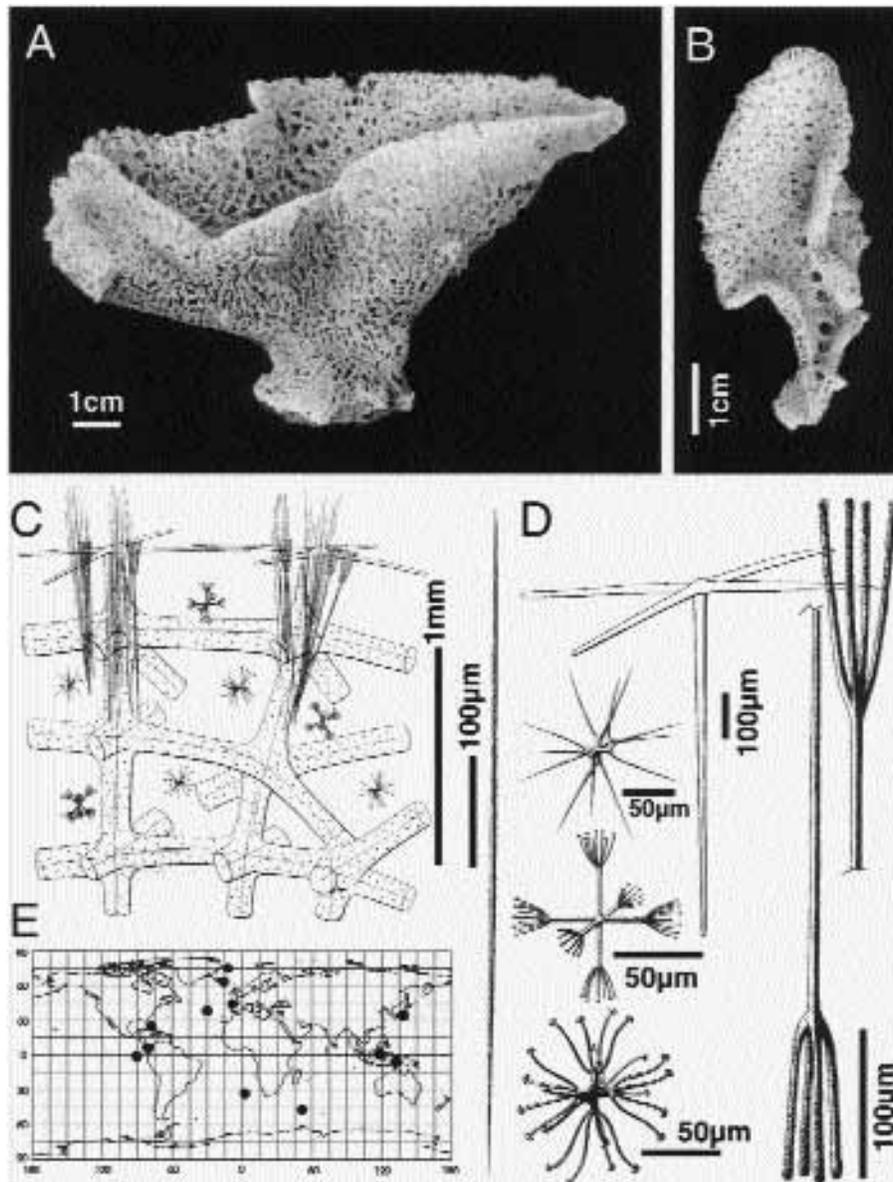


Fig. 5. *Hexactinella ventilabrum* (A–D) and distribution of *Hexactinella* (E). A, lateral view and B, superior view of dried non-type specimens. C, transverse section of outer wall. D, spicules: dermal pentactin, dermal and atrial scopule ends, uncinates, oxyhexaster and common (upper) and rare (lower) dischexasters. E, distribution of *Hexactinella*. (A–D, from Schulze, 1887a, pl. 96.)

### Definition

Tretodictyidae of thick-walled cup shape with wide labyrinthic schizorhyses opening dermally and atrially by rounded apertures; external dictyonal skeleton hypersilicified as a crust-like cortex; lacking a dermal spicule lattice; spicules: thin uncinates, strongyloscopules and long-principalled strongylhexasters.

### Diagnosis

Monospecific – see type species description.

### Remarks

The genus includes only the single extant type species. The long-principalled hexaster occurring in *Hexactinella ventilabrum*,

*Sclerothamnopsis schulzei* and here has been considered a possible synapomorphy of these genera by Mehl (1992). Reid (1963b, 1964) proposed the fossil *Nitidus* de Laubenfels (1955b) be considered a junior synonym of *Psilocalyx*.

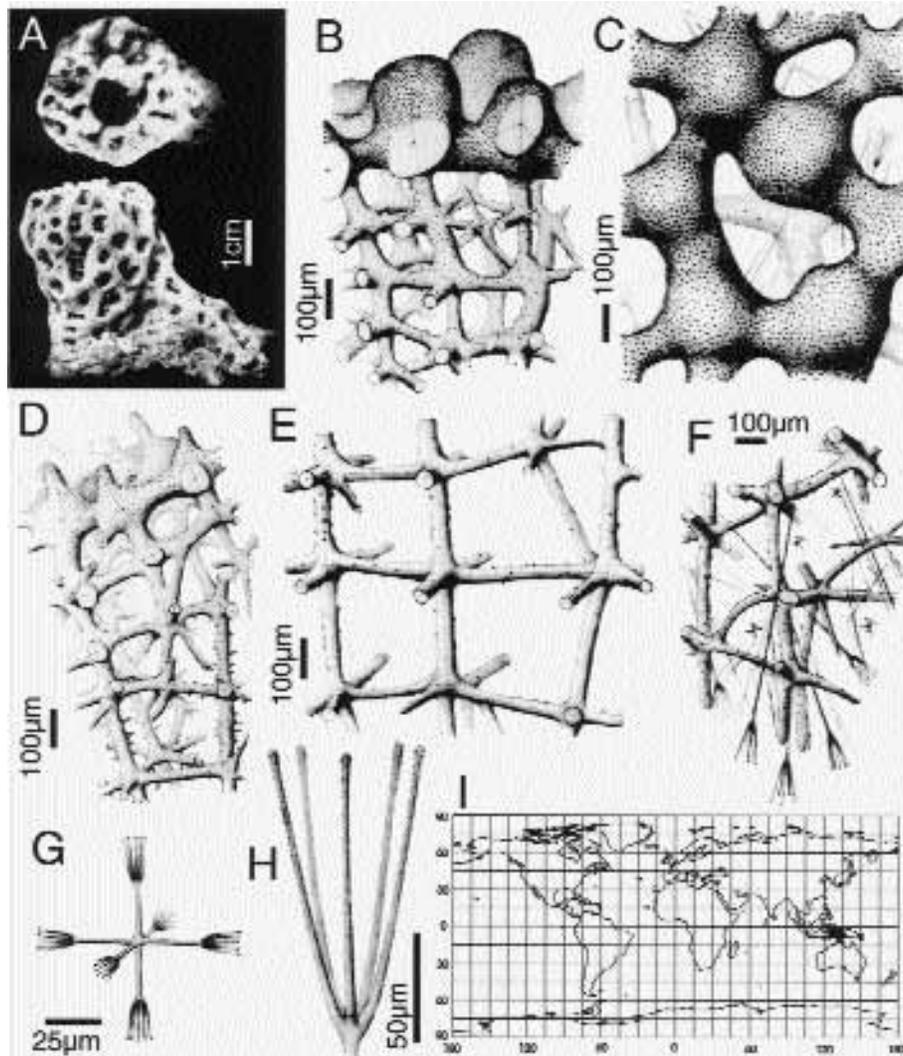
### Description of type species

*Psilocalyx wilsoni* Ijima (Fig. 6).

**Synonymy.** *Psilocalyx wilsoni* Ijima, 1927: 265, pl. 23, figs 1–9; Mehl, 1992: 62, pl. 7, figs 5–6.

**Material examined.** None. Holotype: ZMA 3402 – Arafura Sea, Indonesia. Paratypes: ZMA 4729 – Arafura Sea. ZMA 4699 – Banda Sea.

**Description (from literature).** Small thick-walled cup or short tube attached by broad base to hard substrate; superior round osculum, 10 mm diameter, terminates a deep pit-like atrial cavity



**Fig. 6.** *Psilocalyx wilsoni*. A, holotype, ZMA 3402. B, section of dictyonal framework perpendicular to surface. C, surface view of external cortex. D, transverse section of schizorhysal septum just within an external aperture (channel surface above). E, dictyonal frame within schizorhysal septum. F, transverse section at atrial lining (below). G, long-principalled strongylohexaster. H, strongyloscopule. I, distribution of *Psilocalyx*. (A–H, from Ijima, 1927, pl. 23.)

narrowing basally; body to 38 mm tall, 32 mm wide, 10–14 mm wall thickness; external surface permeated by 1.5–3.5 mm wide, irregular to ovoid apertures with rounded corners as openings into labyrinthic schizorhyses; no dermal spicule lattice present but dermal membrane, supported by scopules and uncinates, is depressed at the dictyonal surface and just within the schizorhysal apertures; ridges of external dictyonal surface between schizorhyses composed of crust-like hypersilicified beams, nodes and spurs, forming a dense, knobby cortex; texture stony, hard; internal schizorhysal channels 2–4 mm diameter delimited by irregularly branching and anastomosing skeletal trabeculae 1.5–3 mm thick; internal dictyonal meshes subrectangular, 165–400 µm sides, becoming irregular towards the surface where meshes reduced by beam/node thickening to 35–275 µm diameter; internal beams 20–50 µm thick, densely tuberculated, occasionally coarsely spined; internal nodes not swollen; external beams, nodes and spurs hypersilicified 60–250 µm thick and evenly tuberculated on outer and lateral surfaces; megascleres: (1) strongyloscopules with 5–6 rough tines, 800–1000 µm total length, head 100–130 µm long; (2) small uncinates with brackets and barbs,

120 × 8 µm (parenchymal?); (3) longer filiform uncinates with bracket indications but without barbs, 300–800 × 1–5 µm in perpendicular bundles in surface membranes; dermalia and atrialia unknown (lost or absent); only one microsclere type: long-principalled strongylohexaster, 70–90 µm diameter, primaries 20–30 µm long bearing bushes of 8–16 short digitate terminals.

**Remarks.** The species is known only from the type collection obtained by the ‘Siboga’ Expedition maintained at ZMA.

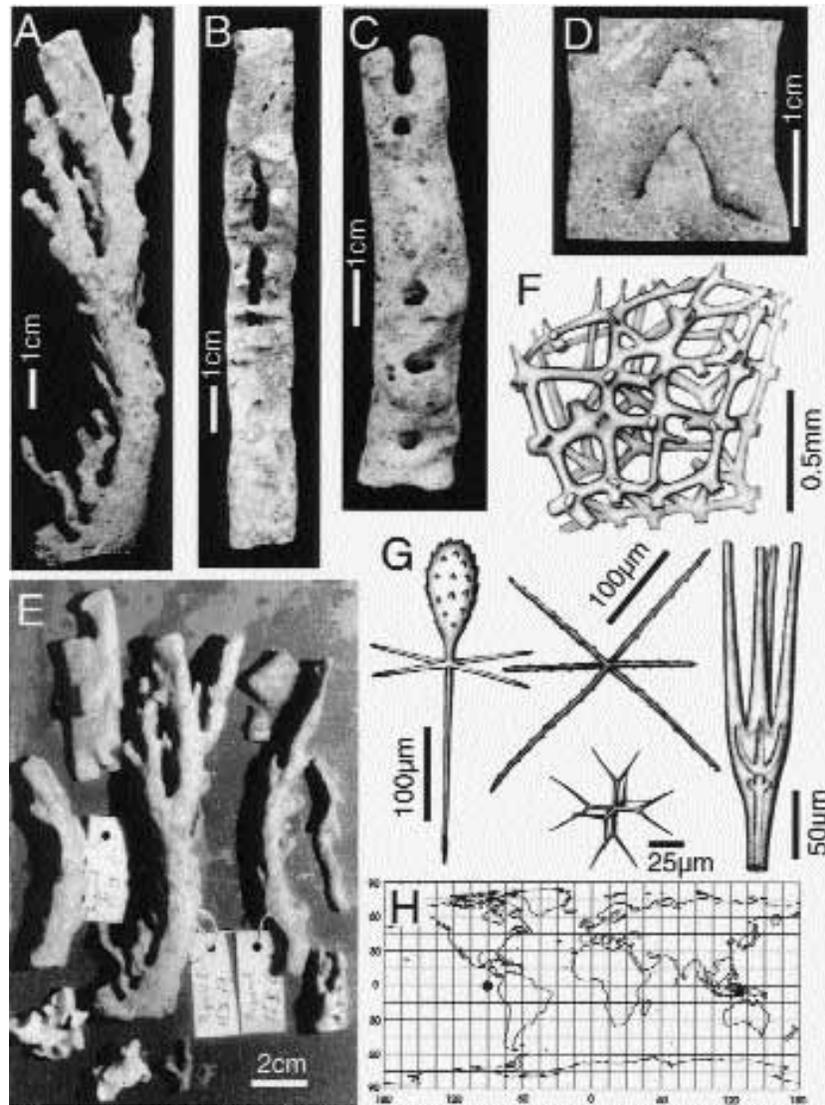
#### Distribution

Arafura and Banda Seas, Indonesia, 984–1595 m depth.

#### *SCLEROTHAMNOPSIS WILSON, 1904*

#### Synonymy

*Sclerothamnopsis* Wilson, 1904: 84.



**Fig. 7.** *Sclerothamnopsis compressa* (A–G) and distribution of *Sclerothamnopsis* (H). A, lectotype of *S. compressa*. B, broad face of branch bearing slit oscula. C, broad face of branch bearing round oscula. D, broad branch face bearing incipient branches. E, USNM 8320, lectotype and paralectotype series, on 11 Aug. 1987, including 2 small fragments unlikely to belong to this species. F, perpendicular section of the dictyonal framework, surface at top. G, megascleres including dermal pinule, intermedial hexactin, axially eroded scopule head and oxyhexaster. H, distribution of *Sclerothamnopsis*. (A–D, F–G, from Wilson, 1904, pls 9–10.)

#### Type species

*Sclerothamnopsis compressa* Wilson, 1904: 84 (by monotypy).

#### Definition

Tretodictyidae of branching habit, pinnate-monopodial or dichotomous, rarely anastomosing; branches more-or-less solid or tubular; walls penetrated by vermicular schizorhysial channels; dermal hexactins with grossly swollen, spinous pinulus; microscleres always include long-principalled oxyhexaster.

#### Diagnosis

Oscula on branch tips or faces open into local or continuous axial atrial cavity; skeletal septa thin or undetectable; stronglylo-scopule present; tylohexaster may occur along with oxyhexaster.

#### Remarks

Dendy's (1916b) suggestion that *Sclerothamnopsis* was merely a junior synonym of *Sarostegia* Topsent fortunately never gained support. Recognition of schizorhysial channelization in partially solid stocks such as *Sclerothamnopsis*, is problematic since an atrial cavity is absent. Alternate recognition of the channels as epirhyses and assignment to Euretidae is possible but a poor second choice for structure interpretation here. They are presently retained in the Tretodictyidae by weak negative, rather than strong positive characters. The genus presently contains two species, *S. compressa* Wilson from the Galapagos at 1008 m and *S. schulzei* Ijima from the Banda Sea at 1595 m.

#### Description of type species

*Sclerothamnopsis compressa* Wilson (Fig. 7).

**Synonymy.** *Sclerothamnopsis compressa* Wilson, 1904: 84, pl. 9, figs 2, 4, 6–8, 10–11, pl. 10, figs 1, 3.

**Material examined.** Lectotype (here designated): largest fragment of USNM 8320 – Galapagos. Paralectotypes: remaining fragments of USNM 8320 – same location. MCZ 6801 – Galapagos.

**Description.** Shrub-like habitus inferred from fragments of branches; base unknown; branching irregular or alternating from a main stem, uniplanar; stems and branches distinctly flattened in the plane perpendicular to branching, hence branching occurs from broader faces; broad faces of main stem and branches bear round or slit apertures 3–6 mm wide as openings of channels passing obliquely into or entirely through branch, considered as local atrial systems and openings as oscula; smaller openings ca. 0.5 mm diameter abundant, open into poorly defined network of small-calibre internal channels considered schizorhyses; overall texture stony hard, porous, not fragile; dictyonal framework very tight-mesh, septa and lamellae not detectable; dictyonal strands detectable in smaller branches, run longitudinal and curve-to-surfaces and lining of larger channels (atria) but obscured in older parts by intercalation of dictyonalia into mesh spaces and thickening of all rays; meshes rectangular only in subsurface layer, elsewhere irregular with rounded corners; beams and superficial short-conic or finger-like spurs smooth, usually 50 µm thick; nodes not thickened; megascleres: (1) dermal pinule with bulb-like, spined-swollen pinulus 130 µm long, tangentials 100 × 4–5 µm long, proximal ray 212 µm long; (2) scopule with 4 parallel, strongylote tines 130 µm long, shaft 700 µm long; (3) spiny inter-medial hexactins probably incipient dictyonalia, rays 100–180 × 4–5 µm (4) oxydiactin (uncinate) with tylote swelling at 1/3 length, with barely detectable brackets but no barbs, 550 × 4 µm; microscleres smooth, long-principalled oxyhexasters with 2 terminals per principal, 80–95 µm diameter.

**Remarks.** The type species is represented only by the original type collection, a series of fragments which had been dead for some time but retain eroded proper spicules on/in the dense-meshed, eroded skeletal framework.

#### Distribution

Known only from the Galapagos Is. at 1008 m depth.

#### *SCLEROTHAMNUS* MARSHALL, 1875

##### Synonymy

*Sclerothamnus* Marshall, 1875: 171. *Dendrospongia* Murie, 1877: 228; Carter, 1877b: 231. Not [*Dendrospongia*] Hyatt, 1875: 400 (preocc., de Laubenfels, 1948: 127).

##### Type species

*Sclerothamnus clausi* Marshall, 1875: 171 (by monotypy).

##### Definition

Tretodictyidae of branching bush-like body form expanding three-dimensionally (not planar) from a base attached to hard substrate; branches solid but permeated by vague labyrinthic schizorhyses; branches terminally bearing spiral and annular ridges circumscribing deep intervening grooves; scopules include

a regular form and a distinctive trumpet-shape scopule bearing conspicuous perpendicular processes extending from the shaft.

##### Diagnosis

Monospecific genus (see type species description).

##### Remarks

Caster (1941) suggested that *Sclerothamnus* be included in the Paleozoic Titusvillidae Caster, but Reid (1963b) pointed out that, although the forms share a similar dichotomous branching habitus, the bases of their framework construction (hexactinosan vs. reticulosan) are quite different. The genus is monospecific.

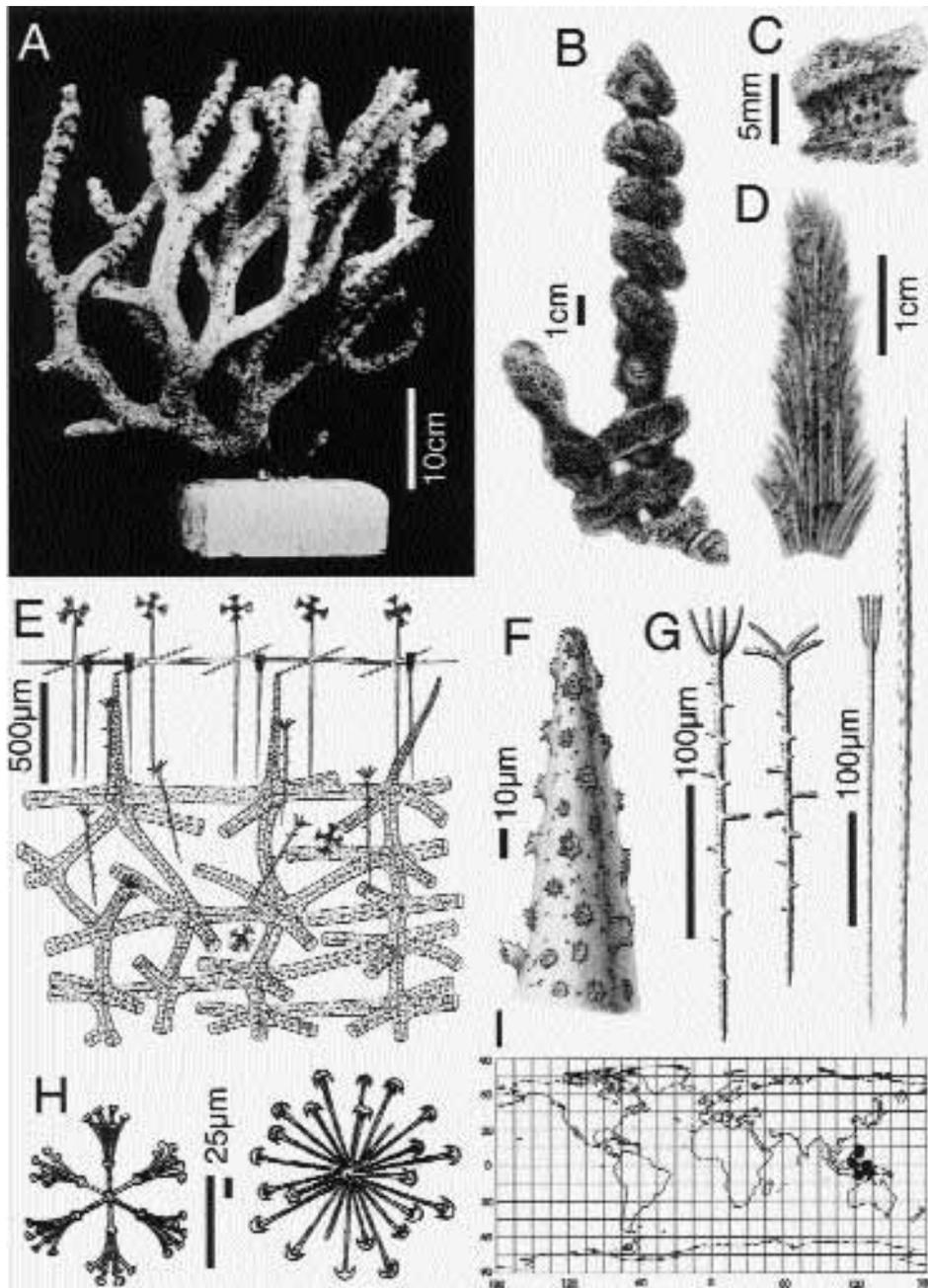
##### Description of type species

*Sclerothamnus clausi* Marshall (Fig. 8).

**Synonymy.** ? *Farrea densa* Carter, 1873c: 463, pl. 17, figs 5–6. *Sclerothamnus clausii* Marshall, 1875: 171, pl. 11, pl. 13, figs 1, 10–11; Schulze, 1887a: 339, pl. 98, figs 1–11; Ijima, 1927: 253, textfigs 29–32, pl. 33, figs 10–13. *Dendrospongia steerii* Murie, 1877: 228, textfigs 1–2, pl. 36, figs 1–4, pl. 37 figs 5–27; Carter, 1877b: 231.

**Material examined.** Holotype: RMNH 029 m – source unknown. Holotype (fragment) of *D. steerii*: BMNH 1903.6.26.1 – Philippines. Other material. *S. clausi*: BMNH 1887.10.24.6 – Banda Is.

**Description.** Tree or bush like body composed of solid cylindrical branches extending to 50 cm height in three dimensions from a basal plate attached to hard substrate; branching mostly dichotomously but some trichotomies occur; main branches 4 cm diameter and somewhat flattened; distal branches 2.5 cm diameter and terminally bearing spiral or occasional annular ridge and groove system of 1–1.5 cm width; texture stony hard but fragile; surface of ridges hirsute but may be covered in life by a delicate dermal lattice; surface of grooves smooth and lined by usually retained dermal lattice of square 175–240 µm mesh sides; numerous scattered surface openings in the dictyonal framework, 1–5 mm diameter, have been interpreted as ostia (lattice covered) and oscula (never covered) but likely represent entrances to the permeating, labyrinthic schizorhysial channel system; internal channels 0.5–1 mm diameter run longitudinally but unite profusely with each other and oblique channels extending to the surfaces of both grooves and ridges; dictyonal meshes mainly rectangular but irregular transverse ray curvature results in irregular meshes; nodes not swollen; beams 14–141 µm diameter, occasionally to over 200 µm by lateral fusion, ornamented mainly by profuse, scattered, sharp-conical spines, but younger areas and spurs of the distal branches bear distinctive polydentulate tubercles; small hexactins fused to dictyonal beams are abundant; megascleres: (1) rough dermal hexactins with 165–220 µm long tangential rays, 55–80 µm unspecialized distal ray, and intermediate length proximal ray; (2) uncinat 1–2 mm × 11–38 µm, (3) regular rough scopule with 2–4–8 nearly parallel strongylote tines 40–120 µm long, total length 300–770 µm; (4) distinctive trumpet-shape scopule covered with fine recurved spines and bearing 3–5 outwardly, occasional inwardly, curved strongylote tines 70–80 µm long, shaft bearing several perpendicular extensions to 23 µm long, total length 175–400 µm; microscleres are two types of discohexasters: a very abundant small flori-form (often erroneously termed tylo- or spherohexaster) 32–42–50 µm in diameter with moderately long primary rays and 7–9 secondaries bearing a toothed disc; the larger spherodiscohexaster,



**Fig. 8.** *Sclerothamnus clausi*. A, holotype (after Marshall, 1877, pl. 11). B, branch tip with spiral groove (after Murie, 1877, pl. 36, fig. 2). C, groove magnified (after Murie, 1877, pl. 36, fig. 3). D, section of branch tip (after Murie, 1877, pl. 36, fig. 4). E, transverse section of outer wall (after Schulze, 1887a, pl. 98, fig. 5). F, tip of dictyonal frame with polyspined tubercles (after Schulze, 1887a, pl. 98, fig. 11). G, megascleres: a scopule with procurved tines, a trumpet-form scopule distinctive of *Sclerothamnus* (both with transverse stem processes), a regular scopule and uncinata (after Schulze, 1887a, pl. 98, figs 7–10). H, two discohexaster forms (after Murie, 1877, pl. 37, figs 24–25). I, distribution map of *Sclerothamnus*.

220–410  $\mu\text{m}$  diameter, is rare, has very short primaries which each bear 3–5 terminally toothed secondary rays.

**Remarks.** Marshall (1875) originally reported two specimens at the Leiden Museum; both are apparently included under the single catalog number.

#### Distribution

Known only from the Philippine-Indonesian region, at depths of 11(?)–659 m.

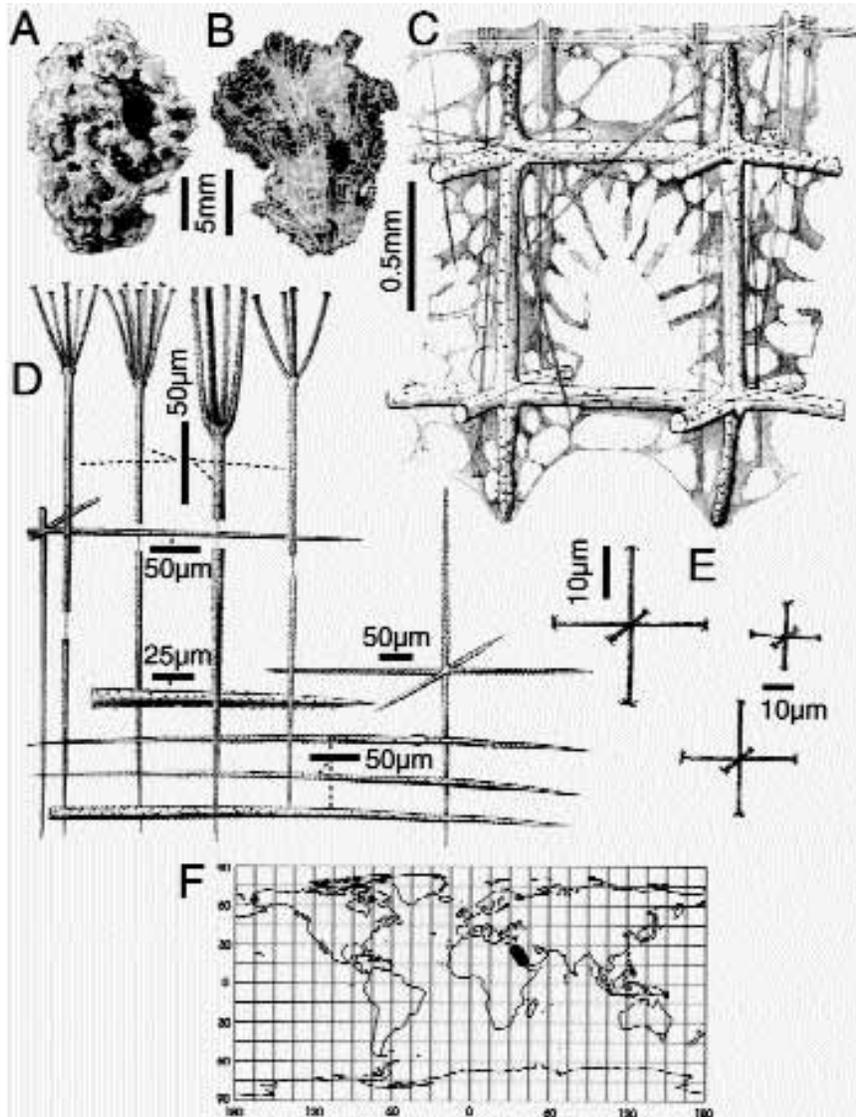
#### TRETOCALYX SCHULZE, 1900

#### Synonymy

*Tretocalyx* Schulze, 1900: 319; Reid, 1963c: 241. *Hexactinella*; Reid, 1963b: 228.

#### Type species

*Tretocalyx polae* Schulze, 1900: 319 (by monotypy).



**Fig. 9.** *Tretocalyx polae*. A, short-cup body form, oblique view. B, view of internal atrial surface of macerated specimen in longitudinal section. C, transverse section through a schizorhysial septum (combination figure). D, megascleres including 4 scopules, a dermal subhexactin, a parenchymal hexactin, 3 complete uncinates and a magnified uncinat tip. E, 3 onychexactin microscleres. F, distribution of *Tretocalyx* (A–E, after Schulze, 1900, pl. 3).

### Definition

Tretodictyidae with microscleres consisting solely of onychexactins.

### Diagnosis

Monospecific (see type species description).

### Remarks

Schulze's (1900) original description, made before criteria for schizorhyses had been established, should be considered incomplete, as Schulze himself acknowledged. His composite microscopic section (reproduced here) was also oversimplified; it is consistent with a euretoid organization but incompatible with present tretodictyid placement of the species in lacking any indication of channelization. The genus is here retained in Tretodictyidae with

reservation. Ijima (1927) suggested transfer of *Hexactinella monticularis* Lendenfeld, 1915, to *Tretocalyx*, but he gave only an authoritarian statement without reasons supporting the move. Since the irregular spiny hexactins of *H. monticularis* may not be microscleres, are only suggestive of onychexactins, and since discohexasters are present, Ijima's suggestion is rejected; *H. monticularis* is retained in *Hexactinella*. *Tretocalyx* is thus a monospecific genus of obscure relationship to the other Tretodictyidae. Reid (1963c: 241) considered the genus dubious; his demotion and transfer (Reid, 1963b: 228) of the genus to a subgenus of *Hexactinella* was unaccompanied by argument, and is thus rejected.

### Description of type species

*Tretocalyx polae* Schulze (Fig. 9).

**Synonymy.** *Tretocalyx polae* Schulze, 1900: 319, pl. 3, figs 1–16. *Hexactinella polae* Reid, 1963b: 228.

**Material examined.** None. Lectotype here designated: ZMB 3664. Paralectotypes: ZMB 5742, ZMB 5743 – all from 'Pola' Expedition, Red Sea.

**Description (from literature).** Small, compact, thick-wall cup to 3 cm tall with single round superior to subapical osculum opening into a narrow atrial cavity; attached by short, thick stem to hard substrate; texture stony hard but fragile; external intact surface poorly known but presumed (from fragments) to consist of smooth dermal lattice spanning across the irregular groove-ridge framework; pattern of framework channel system uncertain and originally described as interdigitating epirhyses and aporhyses but most likely schizorhysial (still unverified); framework formed externally as irregularly oriented system of 1 mm wide ridges (septa) circumscribing irregular system of 2–3 mm wide tubes (grooves); atrial surface composed of similar ridges and grooves oriented longitudinally; confluence of the dermal and atrial channel systems neither confirmed or rejected; trains of longitudinal dictyonal strands in atrial ridges give rise to secondary strands which curve out toward the dermal surface into dermal ridges; entire framework finely tuberculate with tubercles irregularly distributed; meshes rectangular with 200–400  $\mu\text{m}$  sides; nodes not swollen; free dictyonal spurs are digitate and copiously tuberculate; beams 4–40  $\mu\text{m}$  wide; megascleres are (1) rough dermal pentactins with terminal swelling and rough subhexactins with distal ray to 40  $\mu\text{m}$  long, tangential rays 600+  $\mu\text{m}$  (2) rare, rough, dermal stauractins with 400  $\mu\text{m}$  rays, (3) rough, regular parenchymal hexactins as predictyonalia in superficial locations, (4) two forms of rough scopules with terminal discs; smaller form to 300  $\mu\text{m}$  long with 4–8 divergent tines; larger form to 700  $\mu\text{m}$  long with nearly parallel tines, (5) parenchymal uncinates 500–1000  $\times$  4  $\mu\text{m}$  with or without a near-central swelling; atrialia are lacking; microscleres as only rough, subdermal onychexactins 16–32  $\mu\text{m}$  diameter with 4 (rarely more) 2–4  $\mu\text{m}$  long claws at tips.

**Remarks.** The species is known only from the Red Sea, depth 341–820 m.

### TRETODICTYUM SCHULZE, 1886

#### Synonymy

[*Tretodictyum*] Schulze, 1885: 451 (*nomen nudum*). *Tretodictyum* Schulze, 1886: 78; Schrammen, 1912: 225; Ijima, 1927: 220. *Hexactinella*; Schulze, 1887a: 327 [in part]; not de Laubenfels, 1936a: 185.

#### Type species

*Tretodictyum tubulosum* Schulze, 1886: 78 (by monotypy).

#### Definition

Tretodictyidae with body form of tubular, branching and anastomosing network or stumpy fused mass of tubules; with oxyhexaster microscleres.

#### Diagnosis

Ostia located terminally or laterally, opening into pit-like or elongate-cylindrical but discontinuous atrial cavities; labyrinthic or cleft-like schizorhyses covered externally by dermal spicule lattice; dermalia pentactin to pinular subhexactins; scopules stronglyliform;

oxyhexasters with long principal rays; uncinates lacking or with weakly developed barbs.

#### Remarks

Schulze (1886), unaware of Carter's (1885e) prior erection of *Hexactinella* for *H. ventilabrum*, erected *Tretodictyum* for three new species, *T. tubulosum*, *T. latum* and *T. cyathus*. Recognizing his *T. cyathus* to be congeneric with *H. ventilabrum*, Schulze (1887a) dropped *Tretodictyum* to a junior synonym of *Hexactinella* Carter, and reassigned all of his *Tretodictyum* species there. Schrammen (1912) recognized the distinction between *T. tubulosum* and the focus of *Hexactinella*, *H. ventilabrum*, and resurrected Schulze's *Tretodictyum* as a valid genus, encompassing only *T. tubulosum* Schulze at that time. In his rationalization of generic assignments of Tretodictyidae species, Ijima (1927) never resolved placement of *H. labyrinthica* Wilson. He removed it from *Hexactinella* but could not assign it to *Tretodictyum* because it possessed only discohexasters. Reiswig (1990: 736) accepted Ijima's statement as proposal to move the species to *Tretodictyum*. It is now clear that Wilson's species must return to *Hexactinella* if present generic diagnoses are to be supported. The genus thus contains only three species: *T. punicosum* Ijima, *T. schrammeni* Ijima and *T. tubulosum* Schulze.

#### Description of type species

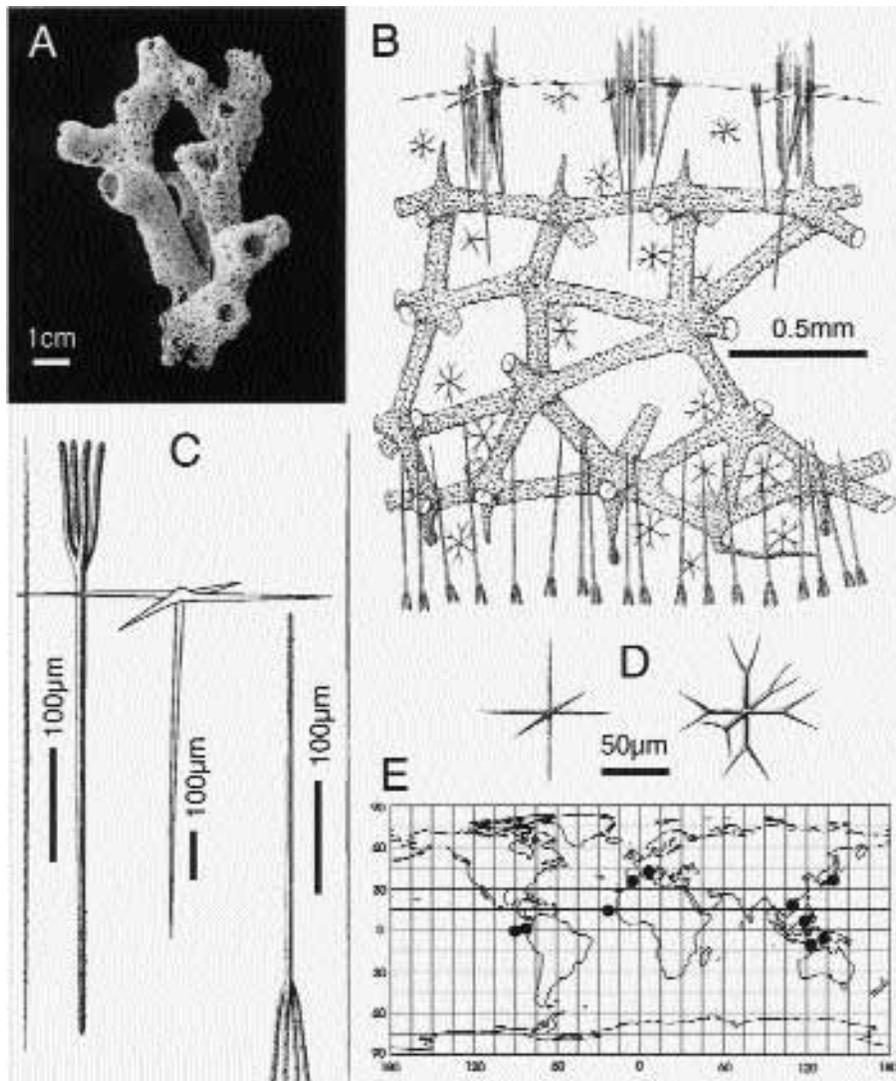
*Tretodictyum tubulosum* Schulze (Fig. 10).

**Synonymy.** *Tretodictyum tubulosum* Schulze, 1885: 451 [nomen nudum]; Schulze, 1886: 78; Ijima, 1927: 221, pl. 19, figs 1–4, textfig. 24; Vacelet, 1969: 163, fig. 10. *Hexactinella tubulosa* Schulze, 1887a: 328, 398, pl. 93, figs 1–8; Wilson, 1904: 83; Topsent, 1928c: 96, pl. 1, figs 6, 10.

**Material examined.** None. Lectotype (here designated): MZUS PO-917. Paralectotypes (here designated): MZUS PO-916, -918, -828 – all off Enoshima, Japan.

**Description (from literature).** Shape as simple or dichotomously branching and occasionally anastomosing mass of tubes 10–15 mm in diameter, with 2–3 mm thick walls, arising from a crust-like spreading base attached to hard substrate or loose clay and reaching over 10 cm in overall size; terminal oscula with simple smooth margins open into atrial cavities which do not extend through the entire stock; external lattice of loose dermalia covering an irregular frame of ridges and 1–2 mm wide grooves representing the septa separating the channel openings of labyrinthic schizorhyses; dictyonal framework at mid-depth contains longitudinal and transverse strands producing square meshes with 275  $\mu\text{m}$  sides; meshes irregular and partly triangular in superficial and atrial boundaries; dictyonal nodes not thickened; beams 35–130  $\mu\text{m}$  thick ornamented with tubercles distributed uniformly or aligned in transverse rows; megascleres include dermal pentactins with tangential rays 115–400  $\times$  6–40  $\mu\text{m}$ ; delicate parenchymal uncinates (oxydiactins) with or without very fine barbs to 715  $\times$  2  $\mu\text{m}$  arrayed in projecting tufts around dermalia; atrialia absent; stronglyliform scopules to 825  $\mu\text{m}$  length in dermal and atrial surfaces, with 2–4–9 weakly S-shaped, rough tines; microscleres as small rough oxyhexactins and long-primaried oxyhexasters with hemihexaster variants 81–100–143  $\mu\text{m}$  diameter.

**Remarks.** Only those reports of *T. tubulosum* from Japan and the China Sea, depth 328–656 m, are here considered valid occurrences of this species. Reports from other areas, based mostly upon macerated specimens, are considered questionable (unlikely) identifications. Specimens reported from



**Fig. 10.** *Tretodictyum tubulosum* (A–D) and distribution of *Tretodictyum* (E). A, lectotype. B, transverse section of tubule wall. C, megascleres: dermal pentactin, dermal and atrial scopules, uncinates (left) and oxydiactin (right). D, microscleres: oxyhexactin and oxyhexaster. E, distribution of *Tretodictyum*. (A–D, after Schulze, 1887a, pl. 93).

Cape Verde-Mediterranean locations, depth 306–875 m (Topsent, 1928c; Vacelet, 1969; Boury-Esnault *et al.*, 1994b) contain hexactine dermalia with very short distal ray and probably represent a distinct species yet to be named, verification of which is beyond the present study. It can best be referred to as *Tretodictyum* sp. until its distinctive characters and taxonomic status are established.

#### Distribution

The genus is worldwide, tropical and temperate in overall distribution, but there remain no confirmed reports from the Indian Ocean, NW Pacific, and higher latitudes beyond 45°N and 15°S. They have been reported from 90–1645 m depths.