

## Family Euretidae Zittel, 1877

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Euretidae Zittel (Hexactinellida, Hexactinosida) contains a total of 45 extant species in 16 genera, including reinstatement of *Pityrete* Topsent pending future review of its relationship to other euretids. Subdivision of the family into two subfamilies, Euretinae and Chonelasmatinae, proposed by Reid (1958a) is accepted with slight modification of the basis and allocation of genera to the two groups. The family is distributed world-wide between depths of 90–5600 m, with few or no representatives from the North Pacific and South Atlantic basins. Body form is predominately tubular, often with extensive branching and anastomosing of components, but lamellar forms, compound cups and funnels with and without secondary lateral tubes also occur. Channelization of the dictyonal framework may be absent or consist of epirhyses with or without aporhyses, or amararhyses. The family is characterized by an euretoid dictyonal framework without diarthyses or schizorhyses and without regular alteration of epirhyses and aporhyses where these co-occur. Uncinates and scopules are characteristic free spicules in all but 2 of the 16 genera. Combinations of body form and spiculation are characters used to differentiate genera within the family. This large and diverse family deserves division at the family level, but presently available morphological data is inadequate to provide a division that is convincingly natural. This revision of the family also includes numerous lectotype and paralectotype designations.

**Keywords:** Porifera; Hexactinellida; Hexactinosida; Euretidae; Euretinae; *Calyptorete*; *Conorete*; *Endorete*; *Eurete*; *Gymmorete*; *Heterorete*; *Lefroyella*; *Pararete*; *Pityrete*; Chonelasmatinae; *Bathyxiphus*; *Chonelasma*; *Myliusia*; *Periphragella*; *Pleurochorium*; *Tretochone*; *Verrucocoeloidea*.

### DEFINITION, DIAGNOSIS & SCOPE

#### Restricted synonymy

Monakidae Marshall, 1876. Euretidae Zittel, 1877; Schulze, 1886, 1887a. Coscinoporidae (in part) Zittel, 1877. Coscinoporidae; Schulze, 1886. Maeandrospongidae (in part) Zittel, 1877. Myliusidae Schulze, 1885. Chonelasmatinae Schrammen, 1912. Wapkiosidae de Laubenfels, 1955b.

#### Definition

Hexactinosida with basic three-dimensional dictyonal framework several dictyonal layers in thickness even 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; dictyonal rays composed of series of short beams aligned to form a single strand; dictyonal beams typically composed of two (sometimes one) dictyonal rays; channelization may be absent or consist of epirhyses with or without aporhyses, or amararhyses; where epirhyses and aporhyses co-occur they are not arranged in regular, alternating, overlapping series.

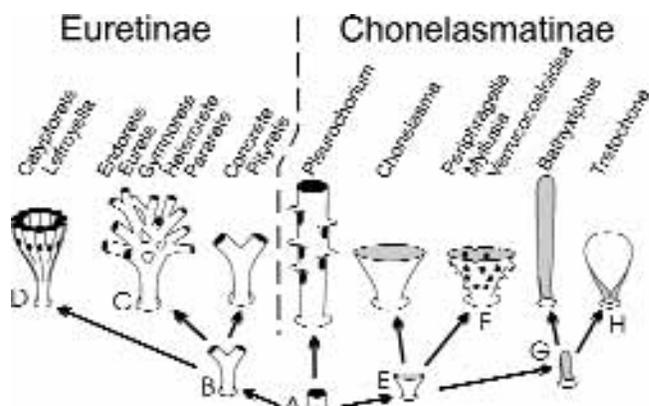
#### Diagnosis

Body form either of branching and/or anastomosing tubes, or cup-funnel formed of a ring of tubes, or of a single tube, or of a single-wall funnel with or without lateral oscula extended on marginal tubes, or blade form; dictyonal meshes mainly rectangular or triangular or irregular; meshes usually equal-sided but elongate prismatic mesh series with transverse lamellae developed in some species; dictyonal strands, if developed, oriented longitudinally;

with or without dictyonal cortices composed of primary or secondary dictyonalia; dermalia and atrialia are commonly pentactins or pinular hexactins with rays of approximately equal length, or both forms lacking; scopules and uncinates are usually present but are lacking in 2 genera; microscleres occur as oxyhexasters and/or discohexasters.

#### Remarks

Euretidae has a long history with stable focus provided by Semper's *Eurete*. The concept (range) of the family and inclusion



**Fig. 1.** Body forms and hypothetical scheme of relationships among Euretidae and its two subfamilies, Euretinae (dichotomously branching tubes B–D) and Chonelasmatinae (unbranched tube, funnel, blade and fan forms A, E–H). Terminal and lateral oscula are filled in black; atrial surfaces of funnel, blade and fan forms are filled in grey. Note reversal of curvature in *Tretochone* (H) bringing the atrial surface to the outer side of the fan body.

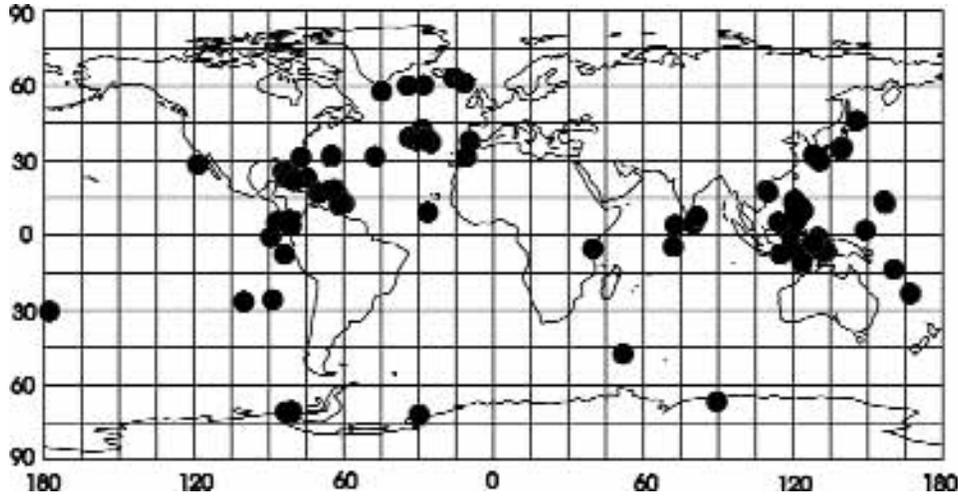


Fig. 2. Distribution of Euretidae from literature reports and additions in this work.

of taxa has varied widely, however, with early competition between the original concept of Zittel (1877), including virtually any body form, with or without channelization but with a lattice skeleton of imperforate nodes, and that of Schulze (1887a) with basic tubular body form without channelization. In spite of the difference in breadth of the two concepts, the number of extant genera in the family was small in both schemes: Schulze included only *Eurete*, *Lefroyella* and *Periphragella*. Before Ijima's (1927) reformation of the family, genera now included in the family, including both old ones (known prior to Zittel's formation) and new genera formed between 1877 and 1927, were allocated to other families which have since been repositioned or disbanded. The genera *Myliusia* and *Periphragella* were originally assigned to Maeandrospongidae but that family was ultimately recognized as lychniscosan by Schrammen (1902) and later entirely abandoned (Schrammen, 1912). Extant euretoid genera of that family were moved to Dactylocalycidae by Ijima (1903). The Dactylocalycidae was eventually disbanded by Ijima (1927) and the euretoid genera, as well as *Dactylocalyx* and *Margaritella* (here a synonym of *Iphiteon*, see Dactylocalycidae) were moved to Euretidae. Schulze originally assigned *Chonelasma* (1886) and *Bathyxiphus* (1899) to Zittel's (1877) Coscinoporidae apparently without close inspection of the basis of that family. Schrammen (1912) realized Coscinoporidae was based upon a lychniscosan type species, *C. infundibuliformis* Goldfuss, and moved the extant non-lychniscosans out to a new family, Chonelasmataidae. Ijima (1927) absorbed this family into the Euretidae without comment on its history. As a result, the Coscinoporidae has been erroneously treated as a valid hexactinosan family in some recent works (Barthel & Tendal, 1994). Ijima (1927) brought the contents of the families Euretidae, Chonelasmataidae and Dactylocalycidae together in one group, the Euretidae. Of his 15 genera, 11 are retained in the present synopsis; *Ptychodesia* was transferred by Reid (1958a) to Craticulariidae and restricted to fossil forms only; *Dactylocalyx*, *Iphiteon* and its

junior synonym *Margaritella* are here removed to the reinstated Dactylocalycidae. Ijima (1927: 164) intended to add [*Gymnodictyum*] to Euretidae, but that genus remains an undescribed *nomen nudum*. A few genera were added since Ijima's revision: *Calyptorete* Okada, 1925 (inexplicably omitted by Ijima, 1927); *Pityrete*, erected by Topsent (1928c) and immediately synonymized with *Conorete*, is reinstated pending review of Topsent's poorly defended action; *Tretochone* and *Verrucocoeloidea* were erected by Reid (1958a, 1969). Reid (1958a, 1963b) proposed reducing a number of euretoid genera which were impossible to differentiate on the basis of only body form and framework (lacking free spicules) to subgenera of *Eurete*, including *Endorete*, *Gymnorete*, *Heterorete* and *Pararete*. His argument is clearly appropriate for paleontological purposes, but since the genera are recognizable with extant material, the moves are rejected for zoological classification. Reid (1958a) also proposed subdivision of the family to two subfamilies, based upon body form: branching tubes in Euretinae and funnel or blade form in Chonelasmatinae. He provided formal diagnosis for the Euretinae but never completed treatment and diagnosis of Chonelasmatinae. We support his intent, and slightly modify the division and range of the two taxa (Fig. 1). Other genera occasionally allocated to the Euretidae (de Laubenfels, 1936a) such as *Diaretula* Schmidt, 1880b, *Hyalocaulus* Marshall and Meyer, 1877, are treated here as Hexactinosida *incertae sedis*.

**Scope**

Sixteen valid genera are presently included, of 20 nominal genera. The family is widely distributed with main diversity centers in Indonesian and Caribbean regions (Fig. 2) and few or no known representatives from the South Atlantic and North Pacific basins. They occur at depths of 90–5600 m.

**KEY TO SUBFAMILIES**

- (1) Body composed of dichotomously branching tubes (Fig. 1B–D) ..... **Euretinae**
- Body tubular, funnel-form or blade-form but without dichotomous branching (Fig. 1A, E–H) ..... **Chonelasmatinae**

**SUBFAMILY EURETINAE ZITTEL, 1877**

**Synonymy**

Euretinae Reid, 1958a: 16.

**Scope**

Nine valid genera.

**Definition**

Tubular Euretidae which grow through dichotomous subdivision of basal tube to distal tubes of approximately equal diameter and form.

**Diagnosis**

Body form may be a simple branching stock without anastomoses, a network of irregularly branching stock with anastomoses, a tube or funnel, the walls of which are constructed of a circular array of branching tubes, usually with short lateral anastomoses; channelization is typically absent but epirhyses with or without aporhyses occurs; wall gaps not related to diarthyses occur in two

genera; dermal and atrial spicules may be absent or consist of pentactins or hexactins or rarely diactins; scopules and uncinates are common, but may be lacking in two genera; microscleres are always present, either as oxyhexasters and/or discohexasters; dictyonal lamellae are not characteristic features but occur in one genus.

**Remarks**

Although Reid (1958a) clearly stated “branching tube with oscula at the end of each branch” as the basic criteria for inclusion in the subfamily, he included non-branching forms, *Pleurochorium*, *Myliusia* and *Periphragella*. He apparently did not wish to exclude lateral aperture and lateral tube formation in funnel-forms from his “branching tube” form. We feel the modification presented above and in Figure 1 to be a more logical and defensible division of the wide range of euretid forms. We have added to the subfamily *Calyptorete* and reinstated *Pityrete*, forms not considered by Reid as Euretidae and thus not available for assignment to his two subfamilies at their formulation. Presence or absence of anastomoses of tubular Euretinae indicated in Figure 1 should not be taken as definitive characters for genera; all forms pass through simple non-anastomosing stages and some species of *Eurete* are not known to exhibit anastomoses. Generic assignment within the group is based mainly upon speculation.

**KEY TO GENERA**

- (1) Body a stemmed cup or funnel with wall composed of branching tubes (Fig. 1D) ..... 2  
     Body form as non-circular array of branching tubes (Fig. 1B, C) ..... 3
- (2) Body funnel-form; lateral oscula arrayed on horizontal ridges ..... *Lefroyella*  
     Body cup-shape on stem, lateral oscula on individual tubular projections ..... *Calyptorete*
- (3) Oxyhexasters as only microscleres ..... *Eurete*  
     Discohexasters, with or without oxyhexasters as microscleres ..... 4
- (4) Dermalia as pinular hexactins ..... 5  
     Dermalia as pentactins or lacking ..... 6
- (5) Atrialia as pentactins and/or pinular hexactins ..... *Conorete*  
     Atrialia as diactins ..... *Pityrete*
- (6) Atrialia as hexactins; dermalia absent ..... *Endorete*  
     Atrialia as pentactins or absent ..... 7
- (7) Atrialia as pentactins ..... *Pararete*  
     Atrialia absent ..... 8
- (8) Uncinates and scopules present; framework uniform throughout ..... *Gymnorete*  
     Uncinates and scopules absent; framework in 2 distinct phases ..... *Heterorete*

**CALYPTORETE OKADA, 1925**

tylo- and strongyloscopules; microscleres are discohexactins and discohexasters.

**Synonymy**

*Calyptorete* Okada, 1925: 285.

**Diagnosis**

Monospecific (see type species description).

**Type species**

*Calyptorete ijimai* Okada, 1925: 285 (by monotypy).

**Remarks**

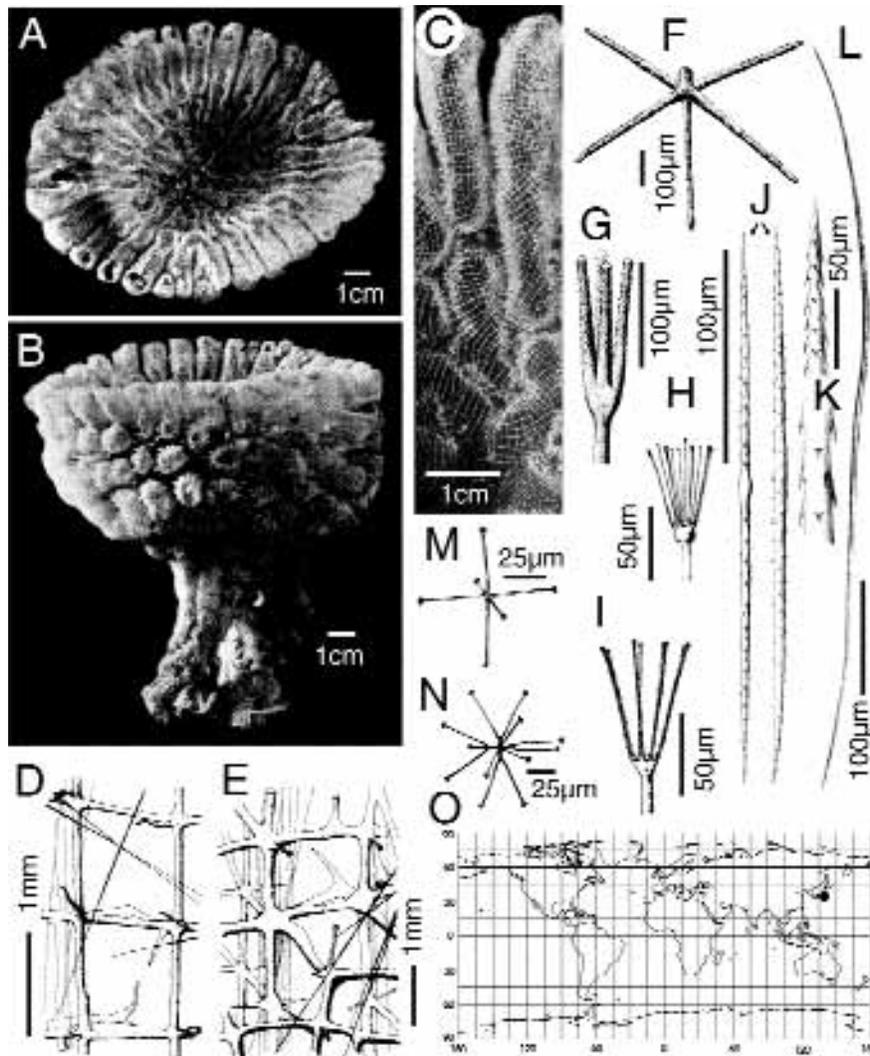
See remarks on type species.

**Definition**

Euretidae with erect, cup-shaped body composed of branching and radiating tubes supported on a tubular stalk. Framework unchannelized. Megascleres are pentactins, barbed uncinates,

**Description of type species**

*Calyptorete ijimai* Okada, 1925 (Fig. 3).



**Fig. 3.** *Calyptorete ijimai*. A–B, top and side views of lectotype. C, spicule lattice of the atrial surface. D, superficial dermal dictyonal framework. E, superficial atrial dictyonal framework. F, dermal pentactin with short rudiment of the distal ray. G, large strongyloscopule head. H, head of choanosomal tyloscopule with many tines. I, head of choanosomal tyloscopule with fewer tines. J, two complete small dermal uncينات. K, tip and mid-portion of large parenchymal uncinate. L, thin, medium-length dermal uncinate. M, discohexactin. N, discohexaster. O, geographic distribution of *Calyptorete*. (A–N, modified from Okada, 1925, pl. 1.)

**Synonymy.** *Calyptorete ijimai* Okada, 1925: 285, pl. 1, figs 1–32.

**Material examined.** None. Lectotype (here designated): specimen A of Okada (1925); entire type series probably at TIU (unconfirmed) – type locality of Sagami Sea, Japan.

**Description (from Okada, 1925).** Body calculate, or cup-shaped on 1–4 cm thick hollow stalk; total height 13–14 cm; cup portion 6–8 cm tall, 13.3 cm diam. is tightly packed radiating cluster of branching and anastomosing tubes; tubes originate from proximal stalk and open distally to exterior and proximally to atrial surface; one or both tube ends spanned by lattice membrane which also encloses inter-tube spaces in cavaedial fashion; basal plate present; primary dictyonal frame of 2–3 layers with regular meshes (1 mm width); peripheral atrial meshes irregular and smaller 0.5–0.7 mm; dictyonal strands to 0.2 mm thick oriented parallel to growth axis joined by heavily microspined transverse beams 15–60  $\mu\text{m}$  thick; nodes not swollen; spurs well developed on both surfaces, longer on dermal side (to 0.7 mm); pentactins with short

sixth-ray rudiment as dermalia (smaller) and atrialia (larger) with equal microspined rays 0.3–1.1 mm length; scopules of 3 forms: dermal strongyloscopule 0.35–0.37 mm length with 4 straight undivergent tines 0.08 mm length; choanosomal tyloscopule 0.20–0.25 mm long with 12–14 slightly divergent tines 22–27  $\mu\text{m}$  long, capitulum with four cruciately disposed knobs; second choanosomal tyloscopule of same length with 6 microspined slightly divergent tines 33–35  $\mu\text{m}$  long, capitulum slightly swollen; shaft smooth or proximally microspined; a rarely occurring oxyscopule with six, nearly parallel tines may a young stage of other scopule; barbed uncينات in 4 classes from 0.35–2.5 mm long, 12–20  $\mu\text{m}$  thick; two classes of microscleres: parenchymal discohexasters 60–80  $\mu\text{m}$  diam. with short primaries and 2–3 slightly bent secondaries, common; discohexactins 100  $\mu\text{m}$  diam. with smooth rays rare; known only from Sagami Sea, Japan (depth unknown).

**Remarks.** Okada's (1925) original description, summarized here, contains many contradictions which can only be resolved

when the type series is available for re-examination. This genus has remained virtually unknown due to its lack of inclusion in Ijima's (1927) revision of the Euretidae and Reid's (1963b) treatment of the Hexactinosida. The genus remains monospecific, known only from the type species description of Okada (1925). Okada failed to designate a holotype from among the type series, thus a lectotype is here designated; since the specimens are unavailable for study, this action has little practical utility. It is possible that the unusual diversity of spicule types described by Okada resulted from some degree of contamination with other specimens. Until the original type series is re-examined or fresh material is collected, the genus *Calypatorete* must be considered inadequately known.

## CONORETE IJIMA, 1927

### Restricted synonymy

*Conorete* Ijima, 1927: 65. *Eurete* (in part) Semper, 1868: 30. Not *Pityrete* Topsent, 1928c: 92.

### Type species

*Eurete erectum* Schulze, 1899 (by original designation).

### Definition

Tubular unchannelized Euretidae with pinular hexactins as dermalia, heavily spined pentactins and/or pinular hexactins as atrialia.

### Diagnosis

Body form erect, tubular, branched or unbranched; tubes end distally in central osculum; ornamented with accessory oscula; basal plate and stalk present; regular and irregular dictyonal framework several layers thick; reduced to one layer distally and marginally; dictyonal beams smooth; primary dictyonal strands and spurs prominent; loose spicules include dermal pinular hexactins, atrial heavily spined pentactins and/or pinular hexactins, scopules, barbed uncinates, discohexasters, oxyhexasters and onychhexasters.

### Remarks

The genus *Conorete* was erected by Ijima (1927) to include *Eurete*-like (tubular) euretids with distinct pinular hexactine dermalia and pentactine and/or pinular hexactine atrialia. Errors relating to this genus in the final list of Ijima's publication were corrected by Reischwig (1990). Topsent (1928c) realized the species he earlier (Topsent, 1904b) assigned to *Aphrocallistes* as *A. azoricus*, and had just made the type of a new genus, *Pityrete*, fit better into Ijima's *Conorete* and thus transferred it to that genus. However, *P. azoricum* lacks regularity of middle framework meshes and has diactins as atrialia, two significant factors that argue against its inclusion in *Conorete*. Until the species is re-investigated to determine its placement characters, it is here retained as the only member of the euretid genus *Pityrete* following Topsent's (1928c) first intention. Reid's (1958a) argument that *Conorete* be reduced to a subgenus of *Eurete* since it cannot be distinguished from that genus in paleontological material, is rejected for zoological classification. Following Lendenfeld's (1915)

suggestion and Ijima's (1927) action, the genus *Conorete* presently includes only two certain species, *C. erectum* (Schulze) and *C. mucronatum* (Wilson). These are known only from the Galapagos and western Panama (Pacific) from depths of 245–1693 m. Other reports of the genus from more northerly locations off North America (Talmadge, 1973; Foell & Pawson, 1986) are considered to be unconfirmed.

### Description of type species

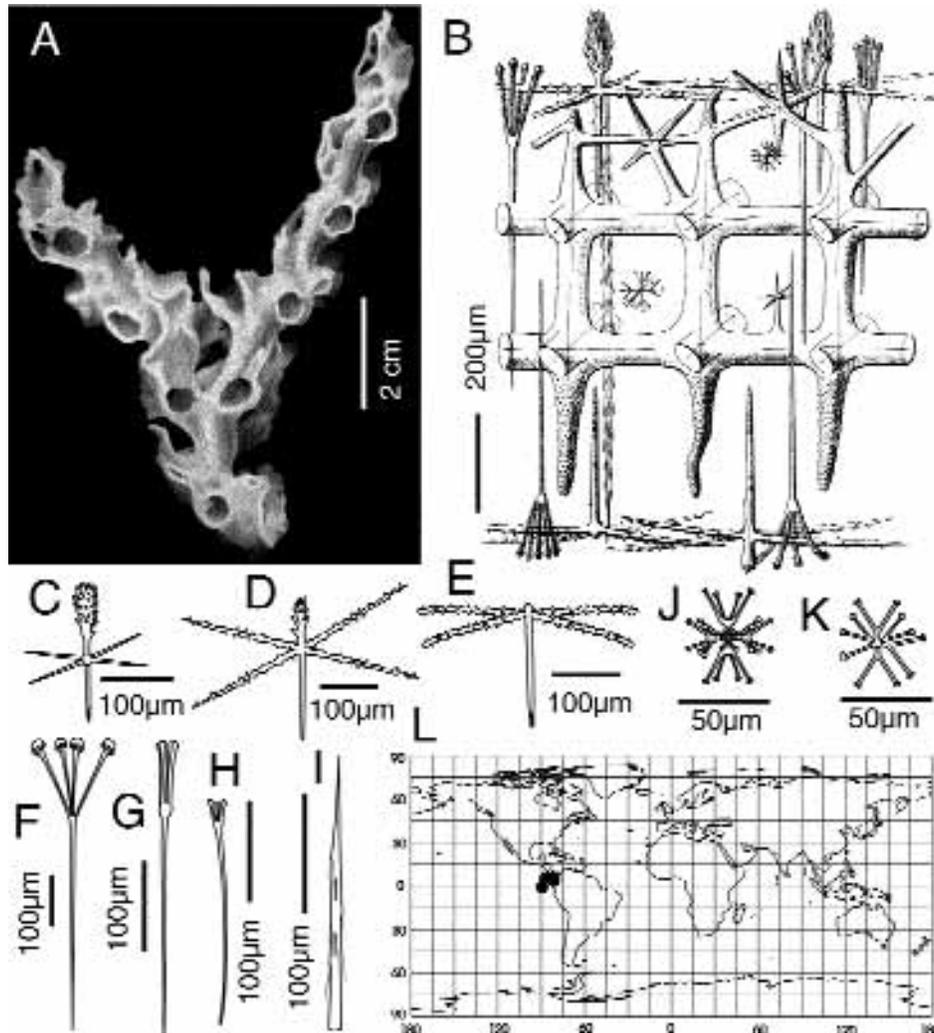
*Conorete erectum* (Schulze, 1899) (Fig. 4).

**Restricted synonymy.** *Eurete erectum* Schulze, 1899: 72, pl. 17, figs 1–3. *Conorete erectum*, Ijima, 1927: 165.

**Material examined.** Lectotype (here designated): BMNH 1908.09.24.039 – Galapagos.

**Description (measurements given as mean  $\pm$  standard deviation).** Body erect, Y-shaped; tubular; stalk (2–3 cm long; 8–10 mm diam.), fixed to substratum by basal plate; folded transversely into two hollow branches (6–8 cm height; 12 mm diam.; walls 1–1.5 mm thick); open distally as oscula; branches perforated by several (5–7) spirally arranged circular apertures (accessory oscula), with short protruding rims; skeletal framework unchannelized; three-dimensional network of hexactine megascleres; 2–3 layers thick but may be reduced to one layer distally; primary dictyonal framework regular; meshes rectangular ( $165 \pm 38 \times 311 \pm 44 \mu\text{m}$ ); dictyonal strands ( $165 \pm 38 \mu\text{m}$  apart) nearly parallel; may fan-out to surfaces; pointed and densely microspined spurs present; dermal framework irregular with triangular meshes due to intercalation of oxyhexactins (rarely spiny pentactins) to primary framework; beams thin and fragile; polyradial nodes common; atrial framework regular; meshes rectangular to triangular; intercalated hexactins rare; beams ( $60 \pm 16 \mu\text{m}$  thick) smooth throughout; nodes unswollen; dermalia as pinular hexactins with densely thorned, bushy distal rays ( $89 \pm 23 \mu\text{m}$  length), proximal ray ( $114 \pm 40 \mu\text{m}$  length) and tangential rays ( $98 \pm 22 \mu\text{m}$  length) smooth, straight and sharply pointed; atrialia as pentactins and hexactine pinule derivatives with vestigial ray ( $52\text{--}76 \mu\text{m}$  length), long ( $275 \pm 37 \mu\text{m}$ ), heavily spined, slightly bowed tangential rays bluntly tipped; proximal rays smooth, straight and pointed; scopules of two types: (1) small ( $180\text{--}265 \mu\text{m}$  long) dermal stronglylo-scopules with 3–5 straight and undivergent microspined tines with swollen, or unswollen capitulum, and (2) larger atrial tyloscopules ( $360\text{--}877 \mu\text{m}$  long) microspined with terminal tyle adorned with proximally oriented, curved spines; uncinates straight, or slightly curved ( $679 \pm 177 \mu\text{m}$  long) with long curved barbs, highly angled from shaft, common; hemidiscohexasters ( $60 \pm 8 \mu\text{m}$  diam.) with slightly swollen centra abundant; primary rays ( $6 \pm 1 \mu\text{m}$  length) with 2–3 curved secondary rays ending in small disks; same size discohexasters with weakly microspined primary rays with 4 curved secondary rays; known from the Galapagos and southwestern Panama, 717–1693 m depth.

**Remarks.** Wilson (1904) expanded Schulze's original Galapagos species description to include three additional Panamanian subspecies, *C. erectum mucronatum*, *C. erectum tubuliferum* and *C. erectum gracile*. The form was raised to species-level by Ijima (1927), following a suggestion by Lendenfeld (1915). Lendenfeld (1915) described several forms (designated by letters) from the same geographic area (western Panama) that further expanded the variation of the species, particularly in the range of scopule form. If Wilson's pattern of treatment is followed, some of Lendenfeld's forms would deserve subspecies status, but



**Fig. 4.** *Conorete erectum*. A, body form of the lectotype. B, body wall section with dictyonal frame and spicules. C, dermal pinular hexactin. D, atrial pinular hexactin. E, atrial pentactin. F, atrial tyloscopule. G, dermal strongyloscopule. H, dermal strongyloscopule. I, unciniate tip. J, discohexaster. K, hemidiscohexaster. L, geographic distribution of *Conorete*. (A–B, modified from Schulze, 1899, pl. 17, figs 1 & 3.)

alternatively, the tight geographic limits of the concerned specimens suggests that these may simply represent a single variable species population. All subspecies may have to be abandoned when more samples are carefully analyzed.

#### **ENDORETE TOPSENT, 1928**

##### **Synonymy**

*Endorete* Topsent, 1928a: 3.

##### **Type species**

*Endorete pertusum* Topsent, 1928a: 3 (by monotypy).

##### **Definition**

Euretidae with body form of thin, branching and anastomosing tubules; with alveolar or 'waffled' external surface created by framework-supported ridges circumscribing conspicuous

depressions, some of which penetrate the entire wall as parietal oscula; framework beams bearing profuse, long, often hooked spines; lacking dermalia but with pinular hexactine atrialia; microscleres as discohexasters, onychexasters, and hexactins with disco- to onycho-tips.

##### **Diagnosis**

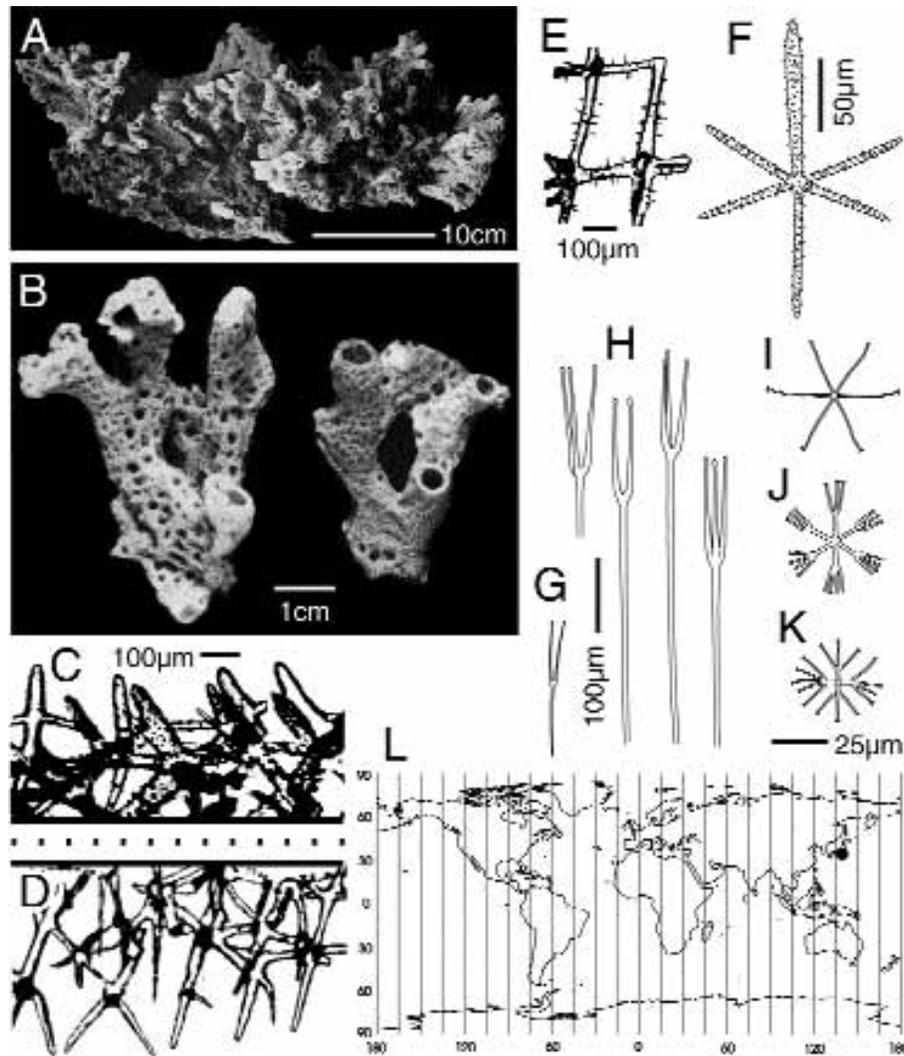
Monospecific (see type species description).

##### **Remarks**

The genus was erected shortly after Ijima's 1927 summary of Euretidae, hence it was not included in that work. Reid (1963b) considered *Endorete* to be a subgenus of *Eurete*, a subjective opinion not followed here. The lack of dermalia and distinctive parietal oscula set this taxon outside of the accepted range for *Eurete*.

##### **Description of type species**

*Endorete pertusum* Topsent, 1928a (Fig. 5).



**Fig. 5.** *Endorete pertusum* (A–K) and distribution of *Endorete* (L). A, the holotype specimen MOM 04–1970. B, fragments of the holotype. C–D, dermal and atrial surfaces, respectively, of dictyonal framework in section showing spur shape differences. E, coarsely-spined beams of internal dictyonal frame. F, pinular atrial hexactin. G, top of small subtyloscopule. H, portions of 4 larger subtyloscopules (same scale as G). I, disco/onychhexactin. J, discohexaster with long primary rays. K, discohexaster with short primary rays (same scale for all microscleres). L, geographic distribution of *Endorete*. (A–K, from Topsent, 1928d.)

**Synonymy.** *Endorete pertusum* Topsent, 1928a: 3; 1928d: 299, pl. 1, figs 1–9, pl. 3, figs 1–2.

**Material examined.** Holotype (fragment): MOM 04–1970 – Sagami Bay, Japan.

**Description.** Body is a mass of hollow, ramified and anastomosing tubes, length 40 cm, width 20 cm, height 15 cm; tubes 5–8 mm diameter, subcylindrical or flattened on one side, with free lengths rarely over 15 mm; tubules often laterally fused to form lamellae in older dead portions; atrium confluent throughout; terminal tube apertures as circular oscula; walls thin, 0.8–1.5 mm; surfaces irregular, composed of ridges outlining polygonal alveolar depressions ('waffled') often extending at their base as narrower passages, 1–1.8 mm in diameter penetrating the entire wall (interpreted by Topsent as epirhyses but here as parietal oscula); framework an irregular network of triangular and rectangular meshes with 150–175  $\mu\text{m}$  sides, tighter on external surface and wider (120–315  $\mu\text{m}$ ) and more rectangular on atrial surface; beams 20–40  $\mu\text{m}$  thick, profusely ornamented by large, pointed and often terminally hooked spines up to 45  $\mu\text{m}$  long; spurs 90–190  $\mu\text{m}$  long,

spined, shorter and more obtuse on dermal side and longer and thinner on atrial side; loose spicules: a dermal membrane containing scopules is present but typical dermalia are absent; atrialia are densely-spined, pinular hexactins 85–270  $\mu\text{m}$  in diameter with free ray not conspicuously bushy and other rays isodiametric (4–11  $\mu\text{m}$  thick); occasionally occurring as dodecactins; uncinates 400–900  $\mu\text{m}$  length, straight or slightly curved, anisoactine, with brackets but without barbs, occur singly or in bundles of 3–4 oriented perpendicular to dermal surface; subtyloscopules in 2 forms: (1) smaller subtyloscopules 350–560  $\mu\text{m}$  total length with 2–3 slightly divergent, microspined tines; head length 65–95  $\mu\text{m}$ , present on dermal and atrial surfaces; (2) larger subtyloscopule 0.7–1.0 mm length, with 2–5 nearly parallel tines microspined or covered with recurved-hooks, head length 100–120  $\mu\text{m}$ , occurs only on atrial surface; microscleres in 3 forms all disco-tipped with disks often reduced to a ring of hooks approaching onycho-form: (1) disco/onychhexactin 45–70  $\mu\text{m}$  diameter, with straight rays and 4-claw tips, (erroneously termed onychohexaster by Topsent), (2) discohexaster 35–50  $\mu\text{m}$  diameter, with long primary rays each bearing

4–7 terminals, (3) discohexaster 40 µm diameter, with short primary rays each bearing 2–4 terminals; known only from a single specimen from Sagami Bay, Japan, depth unknown.

**Remarks.** Topsent's (1928a, 1928d) descriptions of the species are authoritative and extensive, but lack details of wall framework organization (primary versus secondary layers). The fragment of the holotype available to us for resolution of some additional details, and for confirmation of the absence of dermalia, consisted of a small tubule consistent with Topsent's figure, but lacked alveolar surface and parietal oscula. Spiculation of the fragment was completely unlike Topsent's description – present were pentactine dermalia, oxyhexasters, full tyloscopules, and finely spined framework (not coarsely spined). Three possible explanations for this situation exist: (1) Topsent's original description was grossly erroneous (we consider unlikely), (2) the fragment we were supplied was not from the *E. pertusum* type specimen (we also consider unlikely), (3) the original specimen is composed of more than a single type of tubular euretoid (we consider the most likely of the alternatives). Resolution of this problem as well as confirmation and augmentation of Topsent's original description will require detailed examination of the entire holotype. Such examination must be carried out at the MOM site since transport associated with loan of the entire holotype would increase likelihood of damage and spicule mixing in the expected dual-composition specimen. At present *Endorete* must be considered an unconfirmed, but necessarily accepted genus of the Euretidae.

## EURETE SEMPER, 1868

### Restricted synonymy

*Eurete* Semper, 1868: 30.

### Type species

*Eurete simplicissima* Semper, 1868: 30 (by monotypy).

### Definition

Euretidae of branching and usually anastomosing tube form, with unchannelized walls. Spicules include dermal and atrial pentactins and oxyhexasters as the only form of microscleres.

### Diagnosis

Tubular elements of a branching and anastomosing stock bear terminal oscula and sometimes accessory lateral oscula nearly flush with the wall surface; dictyonal framework is three-dimensional throughout, consisting of several dictyonal layers at the distal margins of the growing tubes. Framework meshes basically rectangular but often subdivided to triangular shape. Beams usually smooth but occasionally slightly microspined; nodes usually unswollen but sometimes slightly swollen; microspined spurs as free rays of peripheral dictyonalia; dermalia and atrialia as pentactins; scopules and uncinates present; oxyhexasters are the only microscleres.

### Remarks

Present understanding of the genus is, in part, provisional since loose spicules of the type species, and hence the genus focus,

remain poorly known. Semper (1868) erected the genus for a washed out (spicule-free) specimen, *E. simplicissima*, obtained from the Philippines by Dr. Legaspi. Schulze (1887a) formulated the first definition of the genus, using Carter's (1877c) description of the spicule-bearing *Eurete farreopsis* as a surrogate pattern for loose spiculation of the type species. The above diagnosis and definition of *Eurete* results from Ijima's (1927) division of the genus into several new genera, assigning Carter's *E. farreopsis* (Schulze's spiculation surrogate) to *Pararete* and designating *E. bowerbanki* as the type species of *Eurete*. Although Ijima's type species designation was clearly invalid, it served to provide a new surrogate for the basic spicule pattern of *Eurete*. Both Schulze's (1887a) and Ijima's (1927) choices for spiculation of *Eurete* were subjective choices, based solely upon the need for a pattern to use in allocation of other spiculated species. Distinction of *Eurete* and *Pararete*, following Ijima (1927), is not objectively based, and clearly represents an unsatisfactory (Lévi & Lévi, 1982), but utilitarian hypothesis that cannot now be resolved (see type species remarks below). Reid (1963b) proposed re-amalgamation of Ijima's flock of daughter genera to subgenera of *Eurete*, a procedure not accepted here. The genus, as provisionally understood, includes 11 species and 2 named subspecies: *E. simplicissima* Semper, 1868; *E. schmidti* Schulze, 1886; *E. marshalli* Schulze, 1886; *E. bowerbanki* Schulze, 1886; *E. spinosum* Lendenfeld, 1915; *E. schmidti kampeni* Ijima, 1927; *E. schmidti treubi* Ijima, 1927; *E. freelandi* Ijima, 1927; *E. trachydocus* Ijima, 1927; *E. nipponica* Okada, 1932; *E. irregularis* Okada, 1932; *E. sacculiformis* Okada, 1932; *E. lamellina* Tabachnick, 1988. Known distribution is entirely Pacific, mainly western Pacific, from Japan to Indonesia, with one accepted eastern Pacific report off northern Peru; depth range is 90–4062 m.

### Description of type species

*Eurete simplicissima* Semper, 1868 (Fig. 6A–B).

**Synonymy.** *Eurete simplicissima* Semper, 1868: 30; Marshall, 1875: 181, pl. 12, fig. c, pl. 14, figs 32–41, 44–45, pl. 15, figs 47–52.

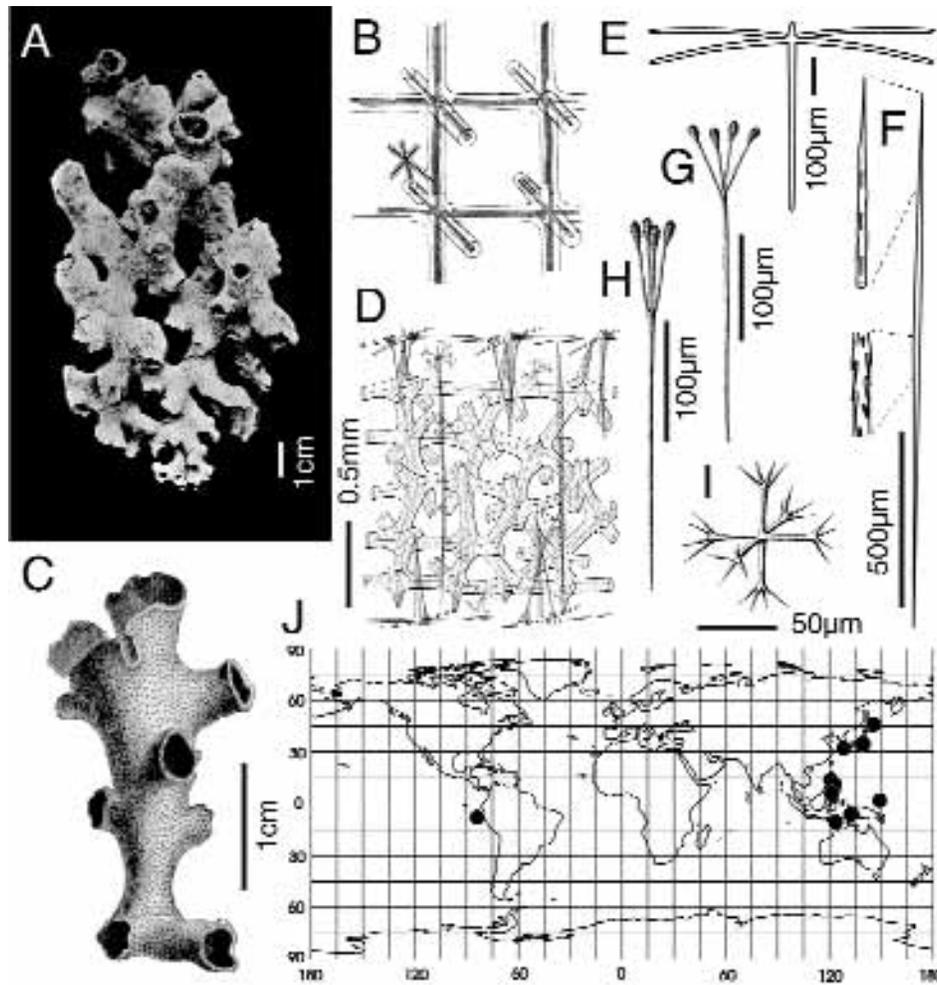
**Material examined.** None. Holotype (by monotypy) presumed lost – Philippines.

**Description (from literature).** Body form as branching and anastomosing network of tubes 0.5–1.0 mm diam., with terminal oscula and occasional lateral oscula; wall 1 mm thick, unchannelized; meshes of dictyonal framework mainly rectangular, occasionally triangular when subdivided; beams smooth or slightly spined; nodes not swollen; axial canals of dictyonalia eroded attesting to long-dead condition; loose spicules lost although a few oxyhexasters were reported by Schulze (1887a); only specimen from Philippines, depth unknown.

**Description of comparative species.** *Eurete bowerbanki* Schulze, 1887a (spiculation reference species) (Fig. 6C–I).

**Material examined.** *E. bowerbanki* Schulze, 1887a. Type series: ZMB PO-816 & 817 – Sagami Bay, Japan, and description from the literature.

**Description.** Body erect, 'tree-like' and tubular, total height 30 mm, width 3–11 mm; consists of a primary tube which terminates distally in a funnel-shaped osculum; lateral tubes (accessory oscula) 3 mm diam. with circular apertures; attachment to substrate unknown; dictyonal framework regular and irregular; meshes rectangular or triangular, 0.3 × 0.6 mm; spurs elongate or stump-like, microspined; dictyonal strands oriented parallel to growth axis; nodes slightly swollen; beams 50–80 µm thick, finely microspined



**Fig. 6.** *Eurete simplicissima* Semper (A–B) and *E. bowerbanki* Schulze (C–I). A–B, body form and dictyonal framework of Semper's type specimen of *E. simplicissima*. C–D, body form and skeletal arrangement in wall section of *E. bowerbanki*. E, dermal pentactin. F, uncinata. G, larger tyloscopule. H, smaller tyloscopule. I, oxyhexaster. J, geographic distribution of *Eurete*. (A–B, after Marshall, 1875, pls 12, 14; C–D, modified from Schulze 1887a, pl. 79.)

throughout; dermalia and atrialia as smooth pentactins with sixth ray absent or as vestigial knob; tangential rays slightly bowed, smooth and terminally blunt; proximal ray straight with rounded tip; barbed uncinates of varying thickness and length common; short tyloscopules 70  $\mu\text{m}$  long, common, with four microspined, barely divergent tines bearing distal swelling with proximally oriented spines; capitulum unswollen; shaft straight, microspined, terminally rounded; larger tyloscopules with four divergent tines, common; one microscelere type: oxyhexaster, 90  $\mu\text{m}$  diam. with 30  $\mu\text{m}$  long primary rays ending in four sharply pointed, widely divergent, secondaries; known from Sagami Bay, 200–400 m.

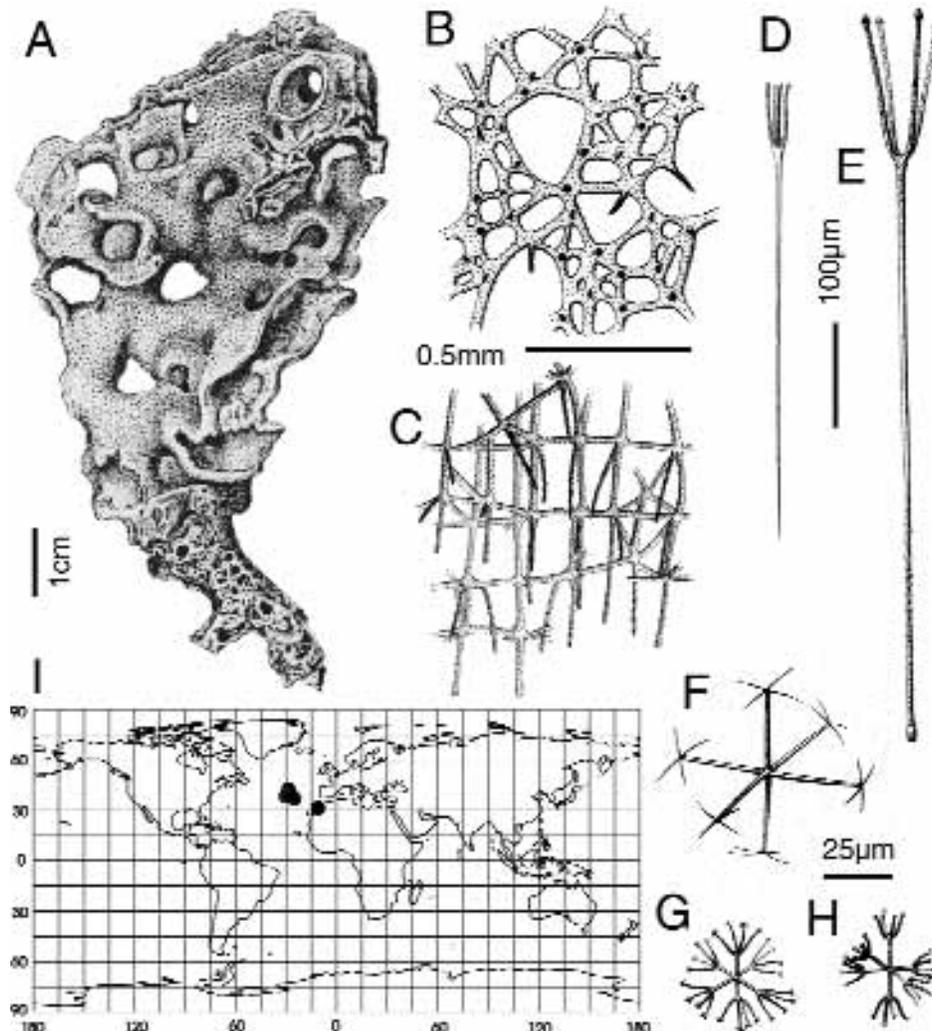
**Remarks.** Semper (1868) provided a poor description and no figures of his original specimen of the type species. It was later examined, described and figured by Marshall (1875) and again examined and briefly described by Schulze (1887a). The specimen, which provided body form and framework foci for both genus and family, cannot now be located and is presumed lost. Schulze (1887a) noted that any of his then new species of *Eurete* did not differ in any significant way from Semper's species, but he wisely decided not to assign either of them to *E. simplicissima*. Ijima's (1927) unexplained designation of *E. bowerbanki* as type for the genus was unwarranted. He was probably influenced by Schulze's

(1887a) discovery of a few oxyhexasters in Semper's original specimen, which Schulze considered of no significance. Ijima followed earlier workers in refraining from assigning a spiculated euretoid to Semper's original species, with good reason. Indeed, no spicule-bearing specimen from the Philippine area shares the few known characters of *E. simplicissima*: small caliber tubules in the form of an anastomosing network, smooth dictyonal beams, simple unornamented and unswollen dictyonal nodes. Thus, the genus and family both remain in need of a stable fixed focus for spicule characters, but a reasonable candidate for a neotype is not presently available. Until a neotype specimen for *E. simplicissima* is discovered, we retain Ijima's suggestion in using *E. bowerbanki* as spiculation surrogate. We acknowledge this as a temporary measure needed to provide an interim definition of the genus *Eurete*.

#### **GYMNORETE IJIMA, 1927**

##### **Restricted synonymy**

*Gymnorete* Ijima, 1927: 165; Reischwig, 1990: 736. *Eurete* (in part) (*Gymnorete*) Reid, 1963b: 224.



**Fig. 7.** *Gymmorete alicei*. A, lectotype. B, dermal framework in surface view with larger openings of epirhyses. C, atrial framework in lateral (section) view. D, small tyloscopule. E, large tyloscopule (same scale). F, onychexactin. G, onychexaster. H, discohexaster (all microscleres at same scale). I, geographic distribution of *Gymmorete*. (A–H, from Topsent, 1904b.)

### Type species

*Eurete alicei* Topsent, 1901c: 462 (by original designation).

### Definition

Stock a network of short hollow tubes lacking both dermalia and atrialia; with narrow epirhyses; framework coarsely thorned throughout; fine uncinates without barbs occur in small bundles at both surfaces; tyloscopules present; microscleres as onychexactins, onychexasters and discohexasters.

### Diagnosis

Monospecific (see type species description).

### Remarks

The genus was erected by Ijima (1927) for the single species, *Eurete alicei* Topsent in recognition of its lack of both dermalia and atrialia. Ijima intended to name a second species to the genus but

never published a valid description. Reid (1963b) considered the genus indistinguishable from *Eurete* for paleontological purposes and lowered it to status of a subgenus. Since the genus is zoologically recognizable, we retain it as a valid taxon.

### Description of type species

*Eurete alicei* Topsent, 1901c (Fig. 7).

**Restricted synonymy.** *Eurete alicei* Topsent, 1901c: 462; Topsent, 1904b: 45, pl. 4, fig. 8, pl. 8, fig. 5. *Gymmorete alicei* Ijima, 1927: 165.

**Material examined.** ? Lectotype (2 slides at MNHN labeled ‘*Eurete alicei* type’ probably from lectotype; see Remarks) – Azores.

**Description.** Body ear-shaped network,  $8 \times 4.5 \times 3$  cm, of short branching and anastomosing tubes; tubes 8 mm diameter with open terminal oscula; proximally, tubes reduced or absent; tube walls 0.7–0.9 mm thick; smooth, velvety outer surface profusely pocked by openings of small epirhyses 200–400  $\mu$ m in diameter; dictyonal meshes irregularly polygonal with extensive synapticulae at/near dermal surface and regularly rectangular on/near atrial surface; beams entirely covered by fairly strong conical thorns;

beams thicker on dermal surface (30  $\mu\text{m}$ ) and thinner (18  $\mu\text{m}$ ) on atrial surface; nodes not swollen; spicules: no proper dermalia or atrialia present although other surface associated spicules normally distributed; small tyloscopules to 500  $\mu\text{m}$  common on both surfaces with 4 straight, slightly divergent smooth tines to 75  $\mu\text{m}$  long terminating in small spheres; capitulum swollen ( $8 \pm 6 \mu\text{m}$  width); shaft straight, or slightly curved, proximally pointed and smooth; large tyloscopule to 800  $\mu\text{m}$  long occurs on both surfaces but more abundant atrially, with 4 straight microspined, slightly divergent tines to 150  $\mu\text{m}$  long, ending distally with marginally thorned knobs; shaft straight, microspined with a distal club-like swelling; uncinates in 2 classes: small, anisoactine, straight, or highly curved,  $509 \pm 146 \times 3 \mu\text{m}$ , forms with brackets but without barbs occur peripherally in bundles of 3–6 oriented perpendicular to surfaces; large uncinates with low-angle barbs are rare; microscleres have onycho- or disco-tips: large onychhexactins  $62 \pm 6 \mu\text{m}$  diameter abundant with long smooth primary rays  $26 \pm 5 \mu\text{m}$  bearing 3–4 slightly curved, sharp-pointed hooks 15–17  $\mu\text{m}$  long arrayed in one plane; small onychhexasters 55  $\mu\text{m}$  in diameter with 14  $\mu\text{m}$ -long primary rays and 4 14  $\mu\text{m}$ -long, rough secondary rays end in 4 small hooks; small rare discohexaster 55  $\mu\text{m}$  in diameter, has 14  $\mu\text{m}$ -long primary rays bearing 4 incurved terminals ending in small discs; known from the Azores and coast of Morocco at depths of 1130–2460 m.

**Remarks.** Topsent (1901c) based his original description upon a complete live specimen and fragments of a live specimen obtained at 'Princess Alice' stn 578 and 602 respectively. He later added more distribution data (Topsent, 1928c) but no new morphological details. We here designate as lectotype the intact specimen from stn 578 – MOM 04–0339. The fragments from stn 602 are collectively designated as paralectotype (MOM catalog number unknown). These designations are made with the purpose of clarifying the application of the name to a taxon. Review of the type specimens was not possible; review of two slides made from the type series contained several contradictions to Topsent's description. Scopules differed significantly from the descriptions and figures provided by Topsent (1901c, 1904b). Large uncinates were not found. Microscleres included the distinctive onychhexactins described and figured by Topsent, but also included some oxyhexactins and tylohexasters instead of discohexasters. We do not include these observations in the species description or figures since we cannot, at this time, be certain that they emanate from the type specimens. More important details of wall structure, depth of epirhyses penetration of primary wall, the presence/absence of aporhyses, details of beam ornamentation, etc., must await review of the type series.

## HETERORETE DENDY, 1916

### Restricted synonymy

*Heterorete* Dendy, 1916b: 214; Ijima, 1927: 165; de Laubenfels, 1936a: 187. *Eurete* (*Heterorete*) Reid, 1963b: 224.

### Type species

*Heterorete pulchra* Dendy, 1916b: 214 (by original designation).

### Definition

Euretidae with body form of branching, thick-walled tubes terminally open as oscula (anastomoses uncertain); with epirhyses

and aporhyses (questionable) penetrating nearly the entire wall; dictyonal framework profusely and coarsely spined and consisting of 2 distinct regions – a main euretoid network of normally thick beams forming irregular triangular and rectangular meshes and an atrial network of thin, loosely-fused hexactins with junctions occurring at ray-crossing points and most rays remaining free (closed meshes mostly lacking); nodes not swollen; loose spiculation entirely parenchymal, consisting of spined oxyhexactins and regular and irregular discohexasters; no surficial free spiculation (dermalia, atrialia, sceptrules) or uncinates are present.

### Diagnosis

Monospecific (see type species description).

### Remarks

The genus was erected by Dendy (1916b) to mark the significance of the biphasic dictyonal framework and the complete absence of surficial loose spicules in the single specimen of good condition. Since absence of loose spicules cannot be documented in fossil material, Reid (1963b) reduced *Heterorete* to the status of subgenus of *Eurete* for paleontological use. We reject Reid's action and, supporting Dendy's original intent, consider *Heterorete* to be a valid genus of the Euretidae for zoological purposes.

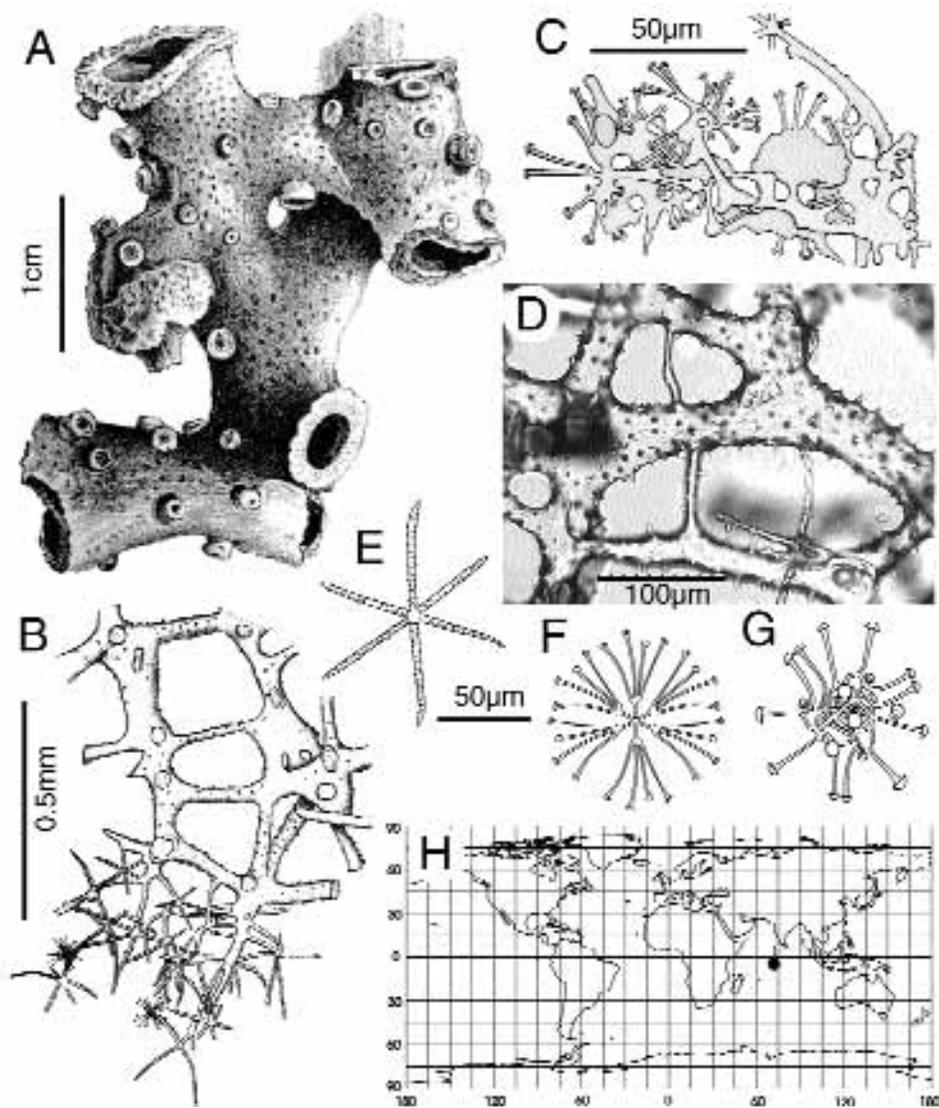
### Description of type species

*Heterorete pulchra* Dendy, 1916b (Fig. 8).

**Restricted synonymy.** *Heterorete pulchra* Dendy, 1916b: 214, pl. 41, figs 11–18; Ijima, 1927: 165.

**Material examined.** Holotype: fragment of BMNH 1920.12.09.064 – from near the Salomon Atoll, Indian Ocean, 4°10'S, 72°01'E.

**Description (measurements given as mean  $\pm$  standard deviation).** Stock as an irregularly branching system of thick-walled tubes, 3.5 cm tall without basal attachment; anastomosis of tubules not conspicuous; tubes 8 mm diameter with 2 mm thick walls; tubes terminally open as 4 mm wide oscula; outer (dermal) and inner (atrial) surfaces marked with numerous small pits as openings of epirhyses and aporhyses which penetrate nearly through the entire wall; texture stony hard but brittle; color opaque yellowish white as preserved in spirit; commensal zoanthids on outer surfaces and branching hydroid colony (*Amphibrachium infestans*) permeating the wall; dictyonal framework composed of 2 conspicuously different structural patterns: a main euretoid frame extending from dermal surface inwards as 75% of wall thickness and a secondary, loose, irregular, atrial network comprising the inner 25% of wall thickness; main framework meshes rectangular and triangular (75–225  $\mu\text{m}$ ) with gaps 241–376  $\mu\text{m}$  diameter as intradictyonal epirhyses; beams 15–57  $\mu\text{m}$  thick formed by lateral fusion of dictyonal rays (euretoid) and synaptacula, occasionally incorporating microscleres; dictyonal strands not conspicuous; beams profusely ornamented by conical, acute spines 2–11  $\mu\text{m}$  long; nodes not swollen; superficial (dermal) framework highly irregular and dense with smaller triangular meshes of 30–190  $\mu\text{m}$  sides due to synaptacula bridging and intercalation of oxyhexactins; secondary atrial framework irregular composed of thin dictyonalia loosely fused at ray crossing points (not as aligned beam pairs) with little beam thickening; indistinct triangular and rectangular meshes with sides 55–180  $\mu\text{m}$  long; aporhyses openings on



**Fig. 8.** *Heterorete pulchra*. A, holotype specimen with conspicuous zoanthid polyps distributed over the outer surface. B, vertical section of part of the main eurentoid framework (above) and the loose, non-eurentoid atrial framework (below). C, portion of the dictyonal framework where synapticular silicification has incorporated discohexasters. D, spination and synapticalae of the main framework. E, oxyhexactin. F, common discohexaster. G, rare irregular discohexaster (scale same for all spicules). H, distribution of *Heterorete*. (A–C, from Dendy, 1916b: pl. 41.)

atrial surface 284–396  $\mu\text{m}$  in diameter; loose spicules are entirely parenchymal; superficial dermalia, atrialia and sceptrules are lacking; oxyhexactins with spiny, straight or curved rays unequal in length  $54 \pm 13 \mu\text{m}$  ending in sharp or club tips; similar spicules abundantly fused to secondary framework; discohexasters  $84 \pm 12 \mu\text{m}$  diameter abundant with  $8 \pm 1 \mu\text{m}$  long primary rays supporting 3–6 out-curved secondary rays terminating in small serrated disks; irregular discohexasters (often with spiral deformations of basal portions of secondary rays) of same size, uncommon (2% of microscleres); soft tissues of the holotype are well preserved; known only from the type locality, near Salomon Atoll, Indian Ocean, 220–274 m depth.

**Remarks.** Reexamination of the holotype material confirmed Dendy's assertion that *H. pulchra* lacks surficial loose spicules and uncinates. There is no evidence that the absence of these spicules is attributable to damage during collection. We were unable to confirm the existence of channels that penetrate from the atrial surface through almost the entire wall (intradictyonal aporhyses) with the small fragment available. At present we have no basis for rejecting

Dendy's description of such channels, unique among members of the Euretidae but characteristic of Craticulariidae. We would not, however, be surprised by independent development (convergent evolution) of such deeply penetrating aporhyses in the two families.

#### **LEFROYELLA THOMSON, 1877**

##### **Restricted synonymy**

*Lefroyella* Thomson, 1877: 403; Schmidt, 1880b: 47; Schulze, 1887a: 301; Ijima, 1927: 165, 210; Reid, 1963b: 225; Reid, 1964: cxiv. *Syringidium* Schmidt, 1880b: 46; Schulze, 1887a: 15; Reid, 1963b: 225; Reid, 1964: cxiv.

##### **Type species**

*Lefroyella decora* Thomson, 1877: 403 (by monotypy).

## Definition

Euretidae with funnel-like, erect body form with deep atrial cavity and moderately thick walls (to 1 cm); constructed of a layer of small-caliber (1–3 mm diameter), longitudinal tubes forming longitudinal ridges separated by deep longitudinal grooves on atrial lining; tubes unchannelized and constructed of longitudinally-elongate, rectangular-mesh frame; extension of outer tube primary walls form horizontal or longitudinal ridges on outer body surface which enclose extensive cavaedial space between tubes; cavaedial space open externally by apertures on external ridges and internally to atrium by longitudinal slits between tubes; megascleres include distinctive uncinates with bushy tips, surficial pentactins to hexactins, stronglyscopules with uncinatous shafts (with barbs and brackets) and tyloscopules.

## Diagnosis

Primary framework of dictyonal strands oriented longitudinally forming long sides of rectangular mesh; short mesh sides aligned in ranks forming lamellae; all surfaces except internal tube lumina thickened by irregular-mesh cortical dictyonal layer; nodes not swollen; beams smooth or microtuberculate; microscleres consist of oxyhexasters and onychexasters to discohexasters; small smooth hexactins commonly appended to dictyonal framework in older regions.

## Remarks

Thomson (1877) erected *Lefroyella* for two washed-out 'Challenger' specimens obtained near Bermuda (uncertainty discussed below). Schmidt (1880b) described several specimens obtained by Agassiz's collections throughout the West Indies as *Syringidium zitteli*, admitting that these were probably identical to Thomson's *Lefroyella decora* and possibly to his earlier described *Dactylocalyx crispus*. Schmidt justified his action by claiming the better condition of the West Indian material, some specimens containing spicules, allowed a more accurate and useful description. He described the spiculation of his *S. zitteli* but provided no figures. Schulze (1887a), having access to the 'Challenger' material, redescribed the washed out *L. decora* specimens and considered Schmidt's *Syringidium* a probable synonym, never, however, making a firm statement to that effect. Later workers accepted *Lefroyella* as a valid genus, with no firm statement regarding status of *Syringidium* until Ijima (1927: 210) unambiguously designated *S. zitteli* as junior synonym of *L. decora*. Reid (1963b, 1964), on the basis of differences he perceived in gross framework arrangement (spaces as pseudo-channelization) between the two species and study of two new specimens, provisionally (not strongly) upheld the distinction of the two genera. In our review of 21 specimens attributable to these taxa, we obtained, by use of microporous filters (0.2 µm pore size), the set of diagnostic megascleres from 19 of them, including the supposedly washed-out type specimens of both species. On the basis of similarity of spiculation and framework, we conclude without reservation that the type species of both genera are identical, the valid name of which must be *Lefroyella decora*. The second species, *L. ceramensis*, described by Ijima (1927) from Indonesia, and reported from the neighboring open Pacific by Tabachnick (1988), remains known only from its body form and framework.

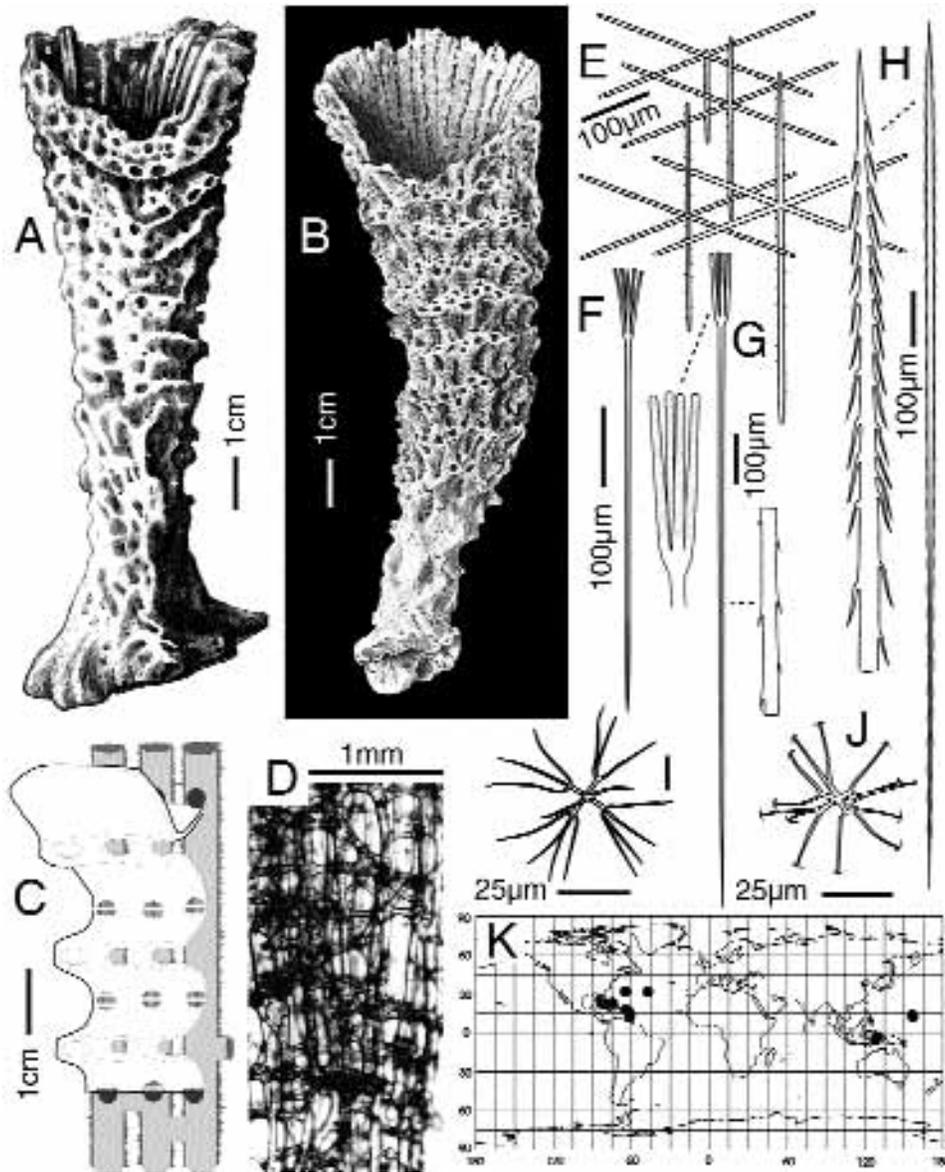
## Description of type species

*Lefroyella decora* Thomson, 1877 (Fig. 9).

**Restricted synonymy.** *Lefroyella decora* Thomson, 1877: 403, fig. 106; Schmidt, 1880b: 47; Schulze, 1887a: 301, pl. 82, fig. 1; Ijima, 1927: 210; Reid, 1964: cxiv; textfig 31b. Not *Dactylocalyx crispus* Schmidt, 1870: 19, pl. 2, figs 13–15; Schmidt, 1880b: 47. Not *Lefroyella crispa*; Van Soest & Stenotoft, 1988: 11. *Lefroyella zitteli*; Van Soest & Stenotoft, 1988: 11; *Syringidium zitteli* Schmidt, 1880b: 46, pl. 7, fig. 4; Schmidt, 1879: pl. 4, figs 9–10; Reid, 1964: cxiv, textfig. 31c.

**Material examined.** Lectotype of *Lefroyella decora* (here designated): BMNH 1887.10.20.127 – from near Bermuda or mid Atlantic (see below). Paralectotype (here designated): BMNH 1887.10.20.127a – same locality. Lectotype of (?) *Syringidium zitteli* (here designated): MCZ 6494 – Guadeloupe. Paralectotypes (here designated): BMNH 1939.2.10.15 (previously MCZ 6595) (source of spicule measurement data) – collection location unknown. MCZ 9339 & 9349 – St. Kitts. USNM 5425 (as *L. zitteli*) – Montserrat. CAS 2 uncatalogued (previously MCZ 6591 & 6592) – collection location unknown. Other material. *L. decora*: BMNH 1955.1.1.1 – St. Vincent. *S. zitteli*: UWIJ GSN 737 – Jamaica; HBOI 30-IX-89-2-001 – southwest Florida Bank; MCZ 9151, 9152 & 9157 – Cuba; MCZ 2 (uncatalogued) – St. Croix and St. Lucia; USNM (uncatalogued) – Bahamas; YPM 9339b (and 2 uncatalogued) – Cuba.

**Description (measurements given as mean ± standard deviation, range).** Erect, vase-like funnel to at least 12 cm tall; from slightly expanded basal disk sponge diameter increases from 2 cm to 4 cm at distal margin; surface of deep central atrium composed of numerous hollow, longitudinal ridges (unchannelized tubes), 2–3 mm wide numbering ca. 20 at distal edge, separated by deep longitudinal grooves of similar width; dictyonal plates extend laterally from ridge walls, often bridging across grooves, forming an incomplete, smoothed, atrial lining; longitudinal ridge number increases from base to margin; external surface bearing distinct transverse or oblique ridges (laterally fused tubular 'stumps') separated by broad grooves; closely set series of 4–5 mm diameter apertures along ridge apices open into extensive cavaedial space confluent with grooves of atrial surface; lateral growth in older specimens from ridge tops as flat sheets (flaps) extending obliquely up and out from main body wall; external grooves carry numerous round or oval apertures of variable size leading to lumina of longitudinal tubes bounding the atrial surface; lattice of surficial megascleres cover external surface and apertures in the grooves, not those on outer ridges; primary dictyonal layer of rectangular mesh, 400–900 × 150–300 µm sides, circumscribes longitudinal tubes, supports outer ridges and extension plates; long mesh sides formed by dictyonal strands; secondary cortex of smaller, irregular, triangular mesh may form on all surfaces except inner lumina of longitudinal tubes; dictyonal beams 38 ± 11 µm thickness) smooth throughout; nodes not swollen; megascleres: pentactin to regular hexactins, rays 161 ± 29 µm long, straight, sparsely spined, with parabolic or blunt tips, distal ray varies from normal length to a nub; rare large sword-hexactins, tangential and distal rays 209 ± 40 µm, proximal ray 322 ± 55 µm; large stronglyscopules 1330 ± 434 µm length with 4–6 nearly parallel tines 140 µm long, microspined except tips, outer surface of tines and entire capitulum smooth, head 145 ± 30 µm long, with tapered, pointed shaft bearing uncinatous-like thorns and brackets directed distally; tyloscopules 552 ± 157 µm long with 4–8 slightly curved micro-thorned tines and smooth tapered shaft; uncinates 1505 ± 275 µm long with barbs strongly divergent from shaft and closely spaced on anterior end (bushy); microscleres: oxyhexasters abundant, 64 ± 8 µm diameter with moderately long primary rays (5.9 ± 1.2 µm)



**Fig. 9.** *Lefroyella decora* (A–J) and distribution of *Lefroyella* (K). A, lectotype of *L. decora* (from Thomson, 1877, fig. 106). B, lectotype of *Syringidium zitteli* (from Schmidt, 1880b, pl. 4, fig. 4A). C, diagram of wall structure. D, portion of primary wall framework of A. E, range of pentactine and hexactine megascleres. F, tyloscopule. G, strongyloscopule with enlarged head and uncinatous shaft. H, uncinatous with enlarged bushy head. I, oxyhexaster. J, onychexaster. K, geographic distribution of *Lefroyella*.

bearing 3–4 smooth secondary rays; onychexasters to button-tip discohexasters  $56 \pm 11 \mu\text{m}$  diameter with 2–4 divergent secondary rays per primary ray; oxyhexactins attached to framework have straight, distally microspined rays  $40\text{--}50 \mu\text{m}$  long; occasional spherical discohexaster (not figured) may be proper; species distributed throughout the West Indies, Bermuda, and possibly central North Atlantic at 185–1966 m depth.

**Remarks.** Collection sites of *L. decora* remain partly uncertain. Thomson (1877) reported two specimens collected within sight of Bermuda. Schulze (1887a) reported a small 6-cm-long specimen from ‘Challenger’ stn 33 (close to Bermuda) and a 12-cm-long specimen from stn 56 (mid Atlantic, 1700 km from Bermuda) and in error inferred existence of a third 17-cm-long specimen due to his misreading of Thomson’s account. The 2 BMNH specimens which constitute the entire type series of

*L. decora*, bear a single label indicating both were collected at stn 56. Schulze’s location report is accepted after weighing probable sources of error. Schulze (1887a) described the basic structure of *L. decora* as composed of a ring of longitudinal tubes augmented externally with framework extensions to form hollow ridges bearing apertures into the peri-tubular spaces. Reid (1964) attempted to relate the spaces under external embellishments to a process of wall channelization and inferred the deep grooves of the atrial wall as resulting from wall plication. We consider Schulze’s interpretation to be valid and Reid’s to be unwarranted. The basic constituent tubes are unchannelized, the external framework extensions are secondary developments and there is no evidence of a plication process in wall formation. Attempts to infer direction of water flow and thus designation of ‘dermal’ and ‘atrial’ linings relative to either the presently known structure of *L. decora* or its predecessor

have been unrewarding. If the small-caliber longitudinal tubes are accepted as homologues of a farreid-euretid ancestral tube element, the lumina of these tubes are atrial and their outer surfaces dermal. The apertures confluent with those tube lumina, situated in the external grooves, should be exhalant and 'atrial' openings, rendering the entire cavaedial system, atrial slits and open apertures on the external ridges inhalant. But the only apertures certainly covered by a spicular lattice are the presumed exhalant openings in the external grooves – Reid's (1964) claim of a spicular lattice across the atrial slits has not been confirmed in any of our specimens. When other evidence is unavailable, a cover lattice over small apertures is usually taken as indication of its inhalant nature. Either we are faced with an exception to that situation in *L. decora* or the ancestral tubular homology is incorrect. Detailed examination of a well-preserved specimen with tissues in place will resolve the problem. The relationship of *Dactylocalyx crispus* to this species, based on Schmidt's (1880b) statement of mutual identity, led Van Soest and Stenfort (1988) to resurrect the earlier species as the senior synonym for the genus, *L. crista*. Examination of the of the *D. crispus* lectotype (here designated MCZ 8175A, Cuba) has shown that it is not assignable to *Lefroyella*, but its ultimate placement remains unsettled at this time.

#### PARARETE IJIMA, 1927

##### Restricted synonymy

*Pararete* Ijima, 1927: 178. *Eurete* (in part) Carter, 1877c: 121; Reid, 1963b: 224; Lévi & Lévi, 1982: 298.

##### Type species

*Eurete farreopsis* Carter, 1877c: 121 (by original designation).

##### Definition

Euretidae with body in form of a network of branching and anastomosing tubes; spicules include pentactins as dermalia and atrialia, scopules, uncinates, and discohexasters (without oxyhexasters).

##### Diagnosis

Tubular euretids with framework including rectangular-meshed primary layers and triangular-meshed secondary layers of varying thickness; narrow diarthyses-like channels may be present but epirhyses are absent; dictyonal nodes usually swollen and tubercled; dermalia and atrialia are pentactins; other megascleres include tylo- or clavisopules (club-tipped tines) and large barbed uncinates, usually accompanied by a smaller size uncinata with brackets but without barbs; microscleres consist of small discohexasters with sigmoid secondary rays and oxyhexactins often attached to framework but also as free parenchymalia; oxyhexasters are not present.

##### Remarks

The genus, as proposed by Ijima, 1927, for Euretidae with hexasters with only discoid tips as free parenchymal microscleres is retained here. Reid's (1963b) proposal to reduce *Pararete* to a subgenus of *Eurete* for paleontological purposes, is rejected in

favor of the zoological utility of its retention. Mehl (1992), indicated that several of Ijima's designated species, including the type species, *E. farreopsis*, contained oxyhexasters and were thus returnable to *Eurete*. She suggested a new species to serve as type for *Pararete* – *E. semperi* Schulze. Her suggestion may have merit, but it cannot presently be accepted without documentation of the new spicule occurrences and thorough consideration of the rules in replacement of type species. The genus *Pararete* presently includes 7 species, *P. farreopsis* (Carter), *P. gerlachi* (Topsent), *P. semperi* (Schulze), *P. carteri* (Schulze), *P. baliense* Ijima, *P. kangeanganum* Ijima, *P. freeri* Ijima, and 4 subspecies: *P. farreopsis farreopsis* (Carter), *P. farreopsis subglobosum* Ijima, *P. farreopsis jakosalemi* Ijima, and *P. farreopsis fragiferum* Ijima. The main distribution of the genus is in the Japan – Indonesian region at depths of 100–810 m.

##### Description of type species

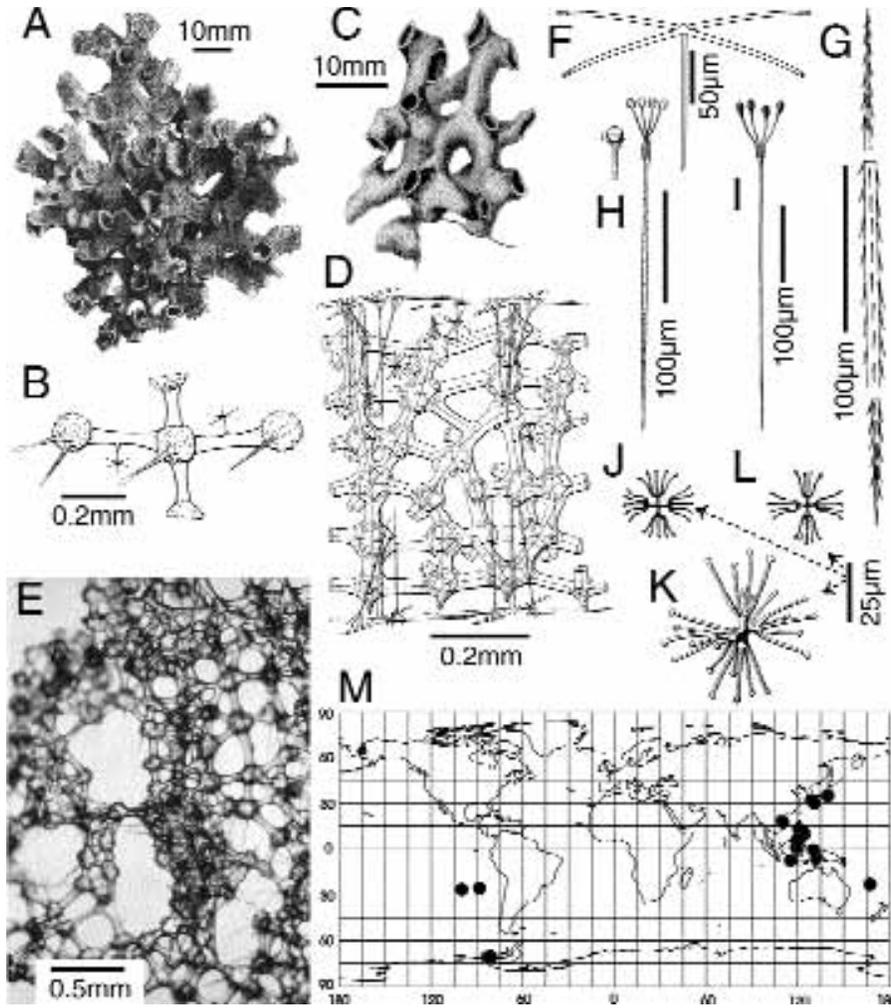
*Pararete farreopsis* (Carter, 1877c) (Fig. 10).

**Restricted synonymy.** ?*Farrea infundibularis* Carter, 1873c: 360. *Eurete farreopsis* Carter, 1877c: 121, pl. 9, figs 1–7. *Farrea farreopsis* Schmidt, 1880b: 44. *Pararete farreopsis*; Ijima, 1927: 178. Not *Aulodictyon intermedium* Marshall & Meyer, 1877: 270, pl. 75, figs 6–9.

**Material examined.** Holotype: Carter's original specimen from the Philippines cannot presently be located; it is not considered 'lost' (most likely in BMNH collections, either still unpacked or mislabelled). Other material. BMNH 1887.10.20.122 – off Little Ki Island, west of New Guinea.

**Description (measurements given as mean  $\pm$  standard deviation, taken from Little Ki Is. specimen).** The holotype is a partly macerated, bush-like form, 7.6 cm tall by 10 cm wide, composed of a complex network of branching and anastomosing tubes; tube apertures circular or funnel-shaped, 4–8 mm diam.; wall generally 0.5–1 mm thick but thicker toward base; basal attachment missing but other specimens with small basal attachment to firm substrate; channelization unknown in holotype but Little Ki Is. specimen with rounded gaps, 0.5–0.7 mm diam., in dictyonal framework as diarthyses-like channels traversing entire wall; dictyonal frame of mixed rectangular and triangular meshes, one dictyonal layer thick at margins increasing basally; dictyonal strands present; true dictyonal nodes swollen and beset with small (1–2  $\mu$ m) blunt tubercles; false nodes rarely swollen; spurs finger-like, spined; beams (52  $\pm$  11  $\mu$ m) smooth or sparsely microspined; small, smooth or rough oxyhexactins with equal-length, straight, terminally pointed, rays (38  $\pm$  24  $\mu$ m long) abundant in parenchyma and often fused to primary framework; dermalia and atrialia as pentactins with tangential rays (200  $\pm$  36  $\mu$ m long) slightly bowed, terminally rounded and microspined; proximal ray slightly shorter (169  $\pm$  48  $\mu$ m); tyloscopules as dermal and atrial accessories (209  $\pm$  32  $\mu$ m long) with 4–6 geniculate tines (49  $\pm$  8  $\mu$ m long); 2 size classes of straight to curved parenchymal uncinates; large uncinates (1.2–2.2 mm long) with prominent low barbs; small uncinates (0.25–1.1 mm long) with brackets but without barbs; microscleres as discohexasters (36  $\pm$  3  $\mu$ m diam. with 4 s-shaped secondary rays and short (4  $\pm$  1  $\mu$ m long) primary rays; oxyhexactins (mentioned above) free or attached to framework; known distribution mainly from Japan through Malaysia and Indonesia to New Caledonia, with 2 outlier locations off South America from depths of 183–810 m.

**Remarks.** Spiculation of the type species has been poorly figured in historic treatments. Carter (1877c) was unable to provide



**Fig. 10.** *Pararete farreopsis* and distribution of *Pararete*. A, body form of Carter's holotype from the Philippines. B, fragment of holotype framework with tuberculate swollen nodes. C, body form of Little Ki Is. specimen. D, wall section of Little Ki Is. specimen with spicules. E, surface of cleaned framework of Little Ki Is. specimen with diarhyses-like gaps. F, pentactin. G, large uncinata. H, tyloscopule of holotype (from Carter). I, tyloscopule from Little Ki Is. specimen (from Schulze). J, discohexaster of holotype (from Carter). K, tylohexaster from Little Ki Is. specimen (from Schulze). L, discohexaster of another Little Ki Is. specimen (from Ijima, 1927, pl. 16). M, geographic distribution of *Pararete*. (A, B, G, H & J, from Carter, 1877c, pl. 9; C, D, I & K, from Schulze, 1887a, pl. 79.)

figures for dermalia and atrialia but rendered the tyloscopule, uncinata and small discohexaster fairly well. His larger spherical discohexaster (pl. 9, fig. 3g) has not been noted in other specimens of this species and is considered dubious. Schulze's (1887a) figures of both the tyloscopule and discohexaster of the 'Challenger' Little Ki Is. specimen (copied here as Fig. 10I & K) are misleading, the latter in both shape and size. Both Carter's (1877c) and Ijima's (1927) renditions of the perianth-form small discohexaster are close to that of the Little Ki Is. specimen, but err in terminal disc form. Review of the specimen showed that the single class of small hexasters possess typical marginally-toothed discs, not terminal tyles as often stated and/or figured. The type species consists of the typical subspecies and three subspecies named by Ijima (1927) for forms differing slightly, all located within the Indonesian region. It is probable that these are variants of a variable species rather than genetically distinct populations. Lévi & Lévi (1982) speculated that many or all of the Indonesian *Pararete* species may be conspecific. The extent of occurrence and the significance of the diarhyses present in the Little Ki Is. specimen deserves further attention. Ijima (1927) noted numerous roundish pores (to 0.5 mm diam.) in the 'Siboga' specimens of this species, but described them as

openings to superficial pits. He made no assessment of them as dictyonal channels.

#### *PITYRETE* TOPSENT, 1928

##### Synonymy

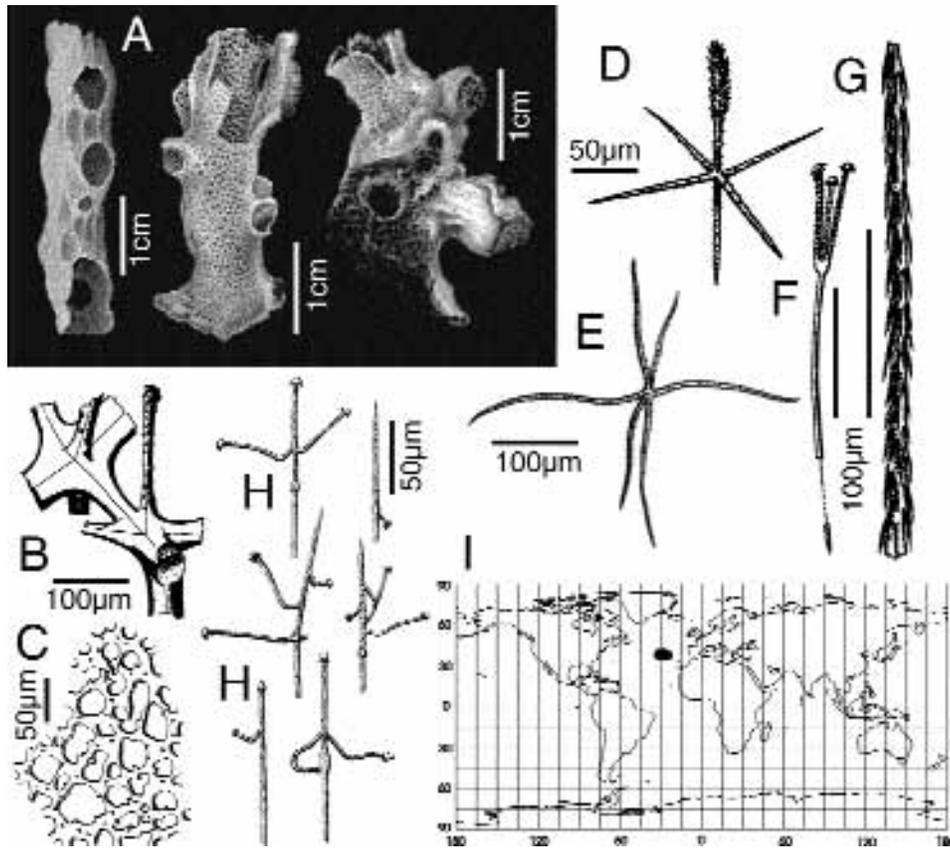
*Pityrete* Topsent, 1928c: 92. *Aphrocallistes* (in part) Topsent, 1901c: 455. *Conorete* (in part) Topsent, 1928c: 48.

##### Type species

*Aphrocallistes azoricus* Topsent, 1901c: 455 (by monotypy).

##### Definition

Euretidae of branching tubular stock with pinular hexactins as dermalia, diactins as atrialia, discoscopules, uncinates and parenchymal hexactins with flexuous rays; microscleres are oxyhexasters and discohexasters.



**Fig. 11.** *Pityrete azoricus* and distribution of *Pityrete*. A, three of the four type specimens. B, a fragment of the superficial dictyonal framework with spined spurs. C, portion of the basal plate. D, dermal pinular hexactin. E, parenchymal hexactin. F, regular scopule. G, segment of an uncinat. H, series of six abnormal scopules. I, distribution of *Pityrete*. (A (left), B, D–G, from Topsent, 1892a, pls 5 & 7; A (middle and right), C & H, from Topsent, 1904a, pls 5 & 7.)

### Diagnosis

Monospecific (see type species description).

### Remarks

See remarks for type species.

### Description of type species

*Pityrete azoricus* (Topsent, 1892a) (Fig. 11).

**Synonymy.** *Aphrocallistes ramosus*; Topsent, 1892a: 32, pl. 5, fig. 1, pl. 7, fig. 10 (non Schulze, 1886: 75). *Aphrocallistes azoricus* Topsent, 1901c: 455; Topsent 1904b: 48, pl. 5, figs 7–8, pl. 7, fig. 1. *Pityrete azoricus* Topsent 1928c: 92. *Conorete azoricum* Topsent, 1928c: 337.

**Material examined.** None. Lectotype (here designated): MOM 04 0318 – Azores. Paralectotypes (here designated): MOM 04 0076, 04 0411 – Azores.

**Description (from the literature).** Erect, thin-walled branching tubular form, main tube 6–12 mm diameter from which smaller secondary tubes 2.5–5 mm diameter branch at right angles; wall 0.3–0.6 mm thick penetrated by small channels 0.2–0.3 mm diameter of uncertain nature (? diarhyses); dictyonal framework smooth excepting heavily spined digitate spurs; beams 40  $\mu\text{m}$  wide; mesh shape and size unknown; megascleres: dermalia as finely-spined pinular hexactins with pinulus and tangential rays 100  $\mu\text{m}$  long, proximal ray 80  $\mu\text{m}$  long; dermal discoscopules 415–440  $\mu\text{m}$  long

with 3 entirely spined tines bearing discs with serrated margins; shaft gradually increasing in thickness distally but terminally tapering to a point; scopules absent from atrial lining; atrialia as sparsely-spined diactins 500–800  $\mu\text{m}$  long with 4-tubercled centrum located eccentrically and heavily-spined, abruptly tapered tips; parenchymal oxyhexactins with spiny flexuous rays 170  $\times$  3–4  $\mu\text{m}$ ; uncinates 1–1.5 mm long  $\times$  5–8  $\mu\text{m}$  thick; irregular scopules with 1–4 tines, often bent, arise from different positions on the shaft; microscleres: oxyhexasters 60  $\mu\text{m}$  diameter with long (20  $\mu\text{m}$ ) primary rays bearing 2 out-curved secondaries; discohexasters 30–36  $\mu\text{m}$  diameter with short (3–4  $\mu\text{m}$ ) primaries bearing 2–5 secondaries; known only from the Azores, North Atlantic 523–927 m depths.

**Remarks.** The first fragmentary specimen obtained by ‘Prince Albert de Monaco’ from the Azores was misidentified by Topsent (1892a) as *Aphrocallistes ramosus*. After obtaining new and better fragments of the form, Topsent (1901c) decided it constituted a new species, and described it as *Aphrocallistes azoricus*. From 1904 through 1927, the species was incorrectly treated as a synonym of *Aphrocallistes beatrix* by many workers due mainly to the lack of description of its dictyonal frame arrangement. With more careful scrutiny, Topsent (1928c) finally decided that it did not belong to *Aphrocallistes*, but was a member of the Euretidae. Because of its pinular dermalia, a rare feature among Euretidae at the time Topsent (1928c) found it necessary to erect a new genus, *Pityrete*, for the species. He strongly implied inclusion of *Eurete erectum*, a form also bearing pinular hexactine dermalia, in the new genus. During final editing of his report, Topsent learned of Ijima’s (1927) formation of *Conorete*, with *Eurete erectum* as type species,

for euretids with pinular hexactine dermalia. Topsent added as addendum to his 1928 work, that his *Pityrete* was synonymous with Ijima's *Conorete*, and the Azores sponge should be referred to as *Conorete azoricum*. The decision taken at that time was based upon the single feature: presence of pinular dermalia in the two genera. Such dermalia are now known to be more common in Euretidae (e.g., *Bathyxiphus* and *Tretochone*). Decision to join two groups in a single genus should be based upon additional shared similarities and absence of significant differences. The two type species, *Aphrocallistes azoricus* and *Eurete erectum*, differ in having in the former (vs. latter) diactin atrialia (vs. pinular hexactine atrialia), parenchymal hexactins (vs. none) and dermal-only scopules (vs. dermal and atrial scopules). The framework is basically rectangular-meshed in *Eurete erectum*, but undescribed and unknown in *A. azoricus*. Because many of the known differences are significant, and the very important character of framework arrangement is yet to be determined for *A. azoricus*, we reject Topsent's synonymy and retain *Pityrete* as a distinct genus until all characters of two type species are reassessed.

### SUBFAMILY CHONELASMATINAE SCHRAMMEN, 1912

#### Synonymy

Chonelasmatinae Reid, 1958a: 15.

#### Scope

Seven valid genera.

#### KEY TO GENERA

- |   |                         |
|---|-------------------------|
| (1) Tubular body form, without branching (Fig. 1A) .....                | <i>Pleurochorium</i>    |
| Funnel, blade or fan form body (Fig. 1E–H) .....                        | 2                       |
| (2) Funnel (or plate form in fragments; Fig. 1E, F) .....               | 3                       |
| Blade (Fig. 1G) or fan form body with surfaces reversed (Fig. 1H) ..... | 6                       |
| (3) Without lateral oscula (Fig. 1G) .....                              | <i>Chonelasma</i>       |
| With lateral oscula (Fig. 1F) .....                                     | 4                       |
| (4) Without elongate primary meshes, uncinates and scopules .....       | <i>Myliusia</i>         |
| With elongate primary meshes, uncinates and scopules .....              | 5                       |
| (5) With secondary branching tubes as lateral extensions .....          | <i>Periphragella</i>    |
| Without secondary branching tubes on lateral surface .....              | <i>Verrucocoeloidea</i> |
| (6) Thin, blade-form body .....   | <i>Bathyxiphus</i>      |
| Fan or ear-shaped body with horizontal ridges on inner surface .....    | <i>Tretochone</i>       |

### *BATHYXIPHUS* SCHULZE, 1899

#### Synonymy

*Bathyxiphus* Schulze, 1899: 82.

#### Type species

*Bathyxiphus subtilis* Schulze, 1899: 82 (by monotypy).

#### Definition

Euretidae with long, thin, blade-like, body, lenticular in cross section; without indication of tubular tendency; without channelization. Spicules include superficial pinular hexactins (and possibly

#### Definition

Euretidae with basic body form of a tube, funnel or blade, with or without lateral oscula sometimes on projections of body wall but without dichotomous branching of the main body axis.

#### Diagnosis

Primary oscula are represented by terminal aperture of tube or funnel body forms, or the expanded exhalant surface of blade- or fan-shaped forms; accessory oscula may be apertures flush on the lateral body or projected as short or extended, sometimes branching tubule systems; channelization may be absent or consist of epirhyses with or without aporhyses, or amararhyses in one genus; very elongate rectangular dictyonal meshes and conspicuous transverse lamellae are common in most genera but may be absent in some; dermalia and atrialia (where differentiable) are pentactins or pinular hexactins; uncinates and scopules are present in all but one genus; microscleres occur as oxyhexasters and/or discohexasters.

#### Remarks

Reid (1958a) suggested formation of the subfamily for euretids with funnel-like or asymmetric growth form but he failed to include the clearly funnel-form genera *Myliusia* and *Periphragella*, added here. Since 'branching tube' was the criterion for membership in Euretinae, we have taken the phrase literally to move the tubular but non-branching *Pleurochorium* to the Chonelasmatinae. The only new euretid genus erected since Reid's subfamily formation, *Verrucocoeloidea*, is appropriately added to this subfamily.

pentactins), barbed uncinates, tylo- and subtyloscopules, pileate clavules (possibly foreign), microxyhexactins and long-primaried oxyhexasters.

#### Diagnosis

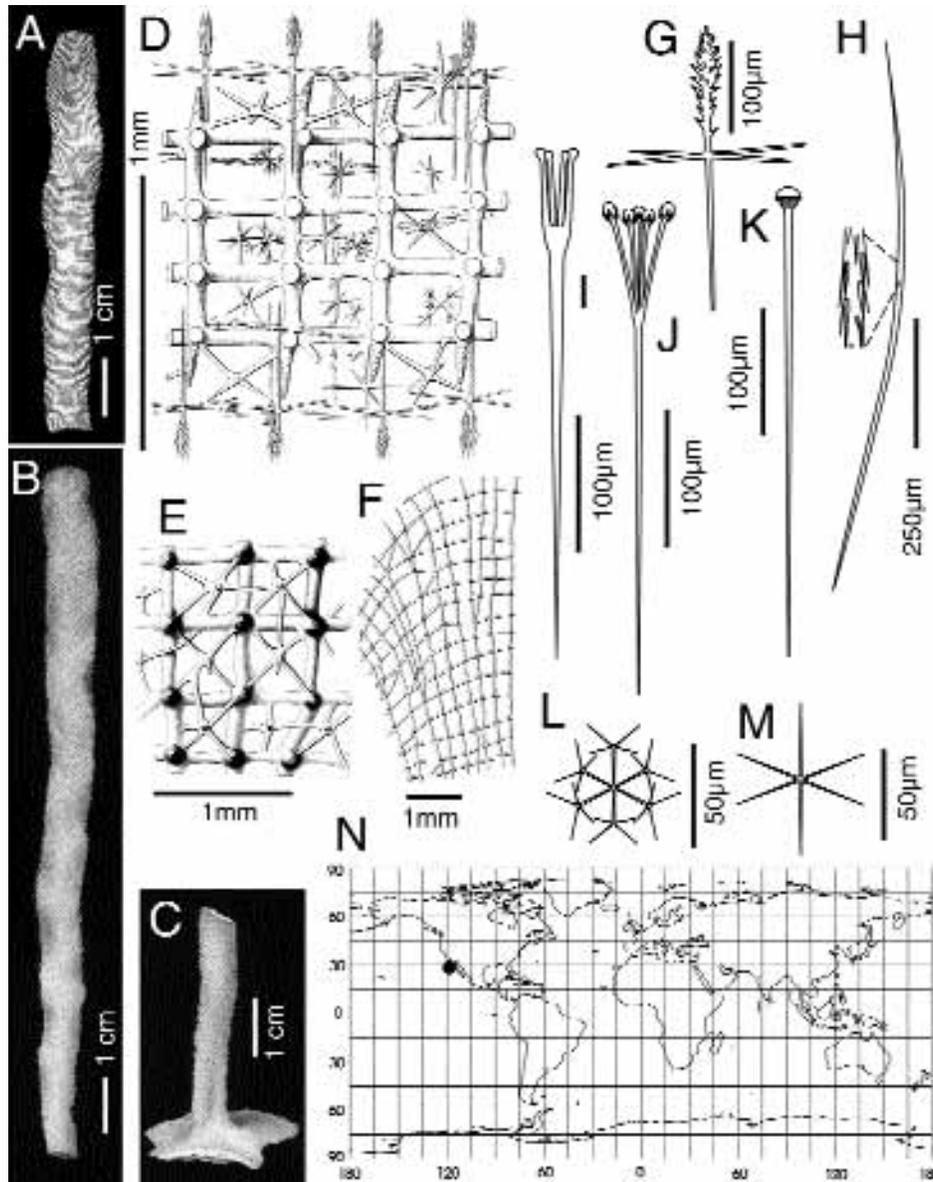
Monospecific (see type species description).

#### Remarks.

See remarks for type species.

#### Description of type species

*Bathyxiphus subtilis* Schulze, 1899 (Fig. 12).



**Fig. 12.** *Bathyxiphus subtilis* and distribution of *Bathyxiphus*. A–C, body form of holotype in 3 fragments, distal to basal. D, skeletal framework and spicule positions in a cross section. E, surface view of the dictyonal framework with intercalated hexactins. F, middle dictyonal framework in longitudinal section of specimen's major plane. G, pinular hexactin. H, uncinates with enlarged segment. I, subtyloscopule. J, tyloscopule. K, pileate clavule (of possible foreign origin). L, oxyhexaster. M, microxyhexactin. N, geographic distribution of *Bathyxiphus* (unconfirmed reports excluded). (A–F, from Schulze, 1899, pls 17–18.)

**Synonymy.** *Bathyxiphus subtilis* Schulze, 1899: 82, pl. 17, figs 4–5, pl. 18, figs 1–2.

**Material examined.** Holotype: USNM 7528 – south of Guadeloupe Island, off Lower California, Mexico (Pacific Ocean).

**Description (measurements given as mean  $\pm$  standard deviation).** Holotype length 30 cm (in 3 pieces); tapering from 5–10 mm in width and 2–5 mm in thickness from narrow, thick base to broad, thin tip; body form elongate, blade-like; lenticular in cross-section; sides sharpened and slightly wavy; basal plate 2–3 mm thick and 2 square cm in area; dermal and atrial surfaces indistinguishable; internally, primary framework comprised of smooth beams ( $46.3 \pm 9.3 \mu\text{m}$  thick), connected by regular, unswollen, six-rayed nodes, in roughly regular cubic meshwork ( $362 \pm 111 \mu\text{m}$

width); distal and extreme edges of both margins consist of one layer of primary skeleton, increasing to 4–5 at body center; primary dictyonal strands ( $289 \pm 39 \mu\text{m}$  apart) oriented parallel to growth axis, fanning out to lateral margins; microscleres and uncinate often soldered to beams forming dense and irregularly-shaped secondary framework; spurs present; external secondary, often false nodes not swollen; basal sections thicker and denser than distal portions by intercallation of oxyhexactins; no osculum, tubes or channelization; megascleres consist of pinulate hexactins, pentactins (uncertain if proper), uncinate, and two types of scopules; pinulate hexactins ( $300\text{--}400 \mu\text{m}$  total length) occur on both surfaces, tangential rays smooth ( $150 \times 6 \mu\text{m}$ ); superficial pentactins may be foreign (mentioned but not figured by Schulze, 1899, and unconfirmed in recent review of holotype fragments),

with smooth proximal ray and occasional vestigial knob of distal ray; uncinates ( $1025 \pm 234 \mu\text{m}$  length) with moderately long barbs, significantly spreading from shaft, common; subtyloscopules ( $308\text{--}403 \mu\text{m}$  length) with 2–4 straight undivergent microspined tines (tines and capitulum  $57 \pm 16 \mu\text{m}$  long), capitulum unswollen ( $9.8 \pm 2.4 \mu\text{m}$  width), shaft weakly microspined, straight and pointed; tyloscopules ( $298\text{--}313 \mu\text{m}$  length) with five, slightly divergent and weakly bent tines, tines microspined and distally thorned; capitulum unswollen; pileate clavules (of possible foreign origin) weakly microspined ( $574 \pm 380 \mu\text{m}$  length) with distinctly serrated cap margins; oxyhexasters ( $76 \pm 20 \mu\text{m}$  diameter) with primary rays ( $19 \pm 6.8 \mu\text{m}$  long) terminating distally in four sharply pointed slightly divergent secondary rays; smooth oxyhexactins with slightly swollen nodes ( $6.1 \pm 1.9 \mu\text{m}$  diameter) abundant; rays equal length ( $30.2 \pm 3.1 \mu\text{m}$ ), straight, and pointed; hemioxyhexasters rare; known with certainty only from the type locality, northeastern Pacific Ocean, 1251 m depth.

**Remarks.** Records show specimens of *Eurete* sp. and *Farrea occa* Bowerbank were collected together with *B. subtilis* at the type locality, and may have been sources of pentactin and clavule spicule contamination. Reexamination of holotype material has not resolved the true spicule complement of *B. subtilis*. Although pinules, oxyhexactins, uncinates, scopules, clavules and oxyhexasters were observed, none of Schulze's (1899) complete 'gastral-like' pentactins were found. An uncontaminated specimen is needed to determine the intrinsic or foreign source of the clavules. Report of washed-out fragments of this genus as *Bathyxiphus* sp. from the Antarctic (Schulze & Kirkpatrick, 1911: 53) cannot be accepted as confirmed species occurrence since spicule evidence was unavailable. Other reports from the eastern Pacific off Columbia (as *Bathyxiphus* sp.; Wilson, 1904) and off northern California (as *B. subtilis*; Talmage, 1973), are more likely locations for this species but they cannot be treated as valid occurrences since, in the former, spicules were washed out, and in the latter, identity of the spicule-bearing specimen, now presumed lost, was never confirmed by a specialist.

### CHONELASMA SCHULZE, 1886

#### Restricted synonymy

*Chonelasma* Schulze, 1886: 76; Schulze, 1887a: 320; Ijima, 1927: 165; Reiswig, 1990: 742; Reiswig & Mehl, 1994: 153. *Leptophragmella* Reid, 1963b: 226.

#### Type species

*Chonelasma lamella* Schulze, 1886: 76 (by subsequent designation, Ijima, 1927: 165).

#### Definition

Euretidae of funnel-like body form with walls composed of a middle primary layer with elongate rectangular meshes and nodes aligned transversely to form dictyonal lamellae; an irregular-meshed, channelized (by epirhyses) cortical layer always present on dermal side but the atrial surface may bear either a rudimentary, unchannelized or fully formed, channelized (aporhytic) cortex; dermalia and atrialia usually pentactins bearing conspicuous spination on the outer surfaces.

#### Diagnosis

Dictyonal beams sparsely spined but thicker strands often smooth; spiny mesohexactins present in all species examined (unknown in one species); typical barbed uncinates and scopules with indistinct swellings on tine tips in all species; microscleres include oxyhexactins and oxyhexasters and/or discohexactins and discohexasters grading to onychhexactins and onychhexasters.

#### Remarks

The genus *Chonelasma* was erected by Schulze (1886) to accommodate several hexactinosan species grouped by similarity of body form – either smooth plates of unknown larger bodies or funnel-form cups. No specific details of dictyonal framework or spiculation were stated characters of the genus. Schrammen (1924a) moved *C. doederleini* to *Ptychodesia*, an action supported by Ijima (1927). Ijima (1927) provided the first skeleton-based diagnosis of *Chonelasma*, stressing rectangular meshes of the middle dictyonal framework and greatly restricting scope of the genus. He reassigned three species to his new genus *Heterochone* and synonymized *C. schulzei* to *Periphragella lusitanica*, leaving only *C. lamella lamella*, *C. lamella choanoides* and *C. ijimai* as members. Reid (1958a) very effectively rejected Schrammen's earlier transfer of *C. doederleini* to *Ptychodesia*, and, though not stated, effectively returned that species to *Chonelasma*. In 1963, Reid raised *C. lamella choanoides* to species level and employed it as type species for his new craticulariid genus *Leptophragmella*. Reiswig & Mehl (1994) demonstrated that *L. choanoides* shared dictyonal lamellae and spiculation details with *C. lamella*. They synonymized Reid's *Leptophragmella*, returning *C. choanoides* to *Chonelasma*, and provided a new diagnosis for the genus. *Chonelasma* presently contains four species: *C. lamella* Schulze, *C. doederleini* Schulze, *C. ijimai* Topsent and *C. choanoides* Schulze & Kirkpatrick. Membership of *C. doederleini*, with pinular hexactine dermalia instead of the distal-spined pentactins in all other species, remains problematic. The genus ranges worldwide, with reports concentrated mainly in the North Atlantic and Antarctic from depths of 823–5600 m; unreported from Indian Ocean and eastern Pacific.

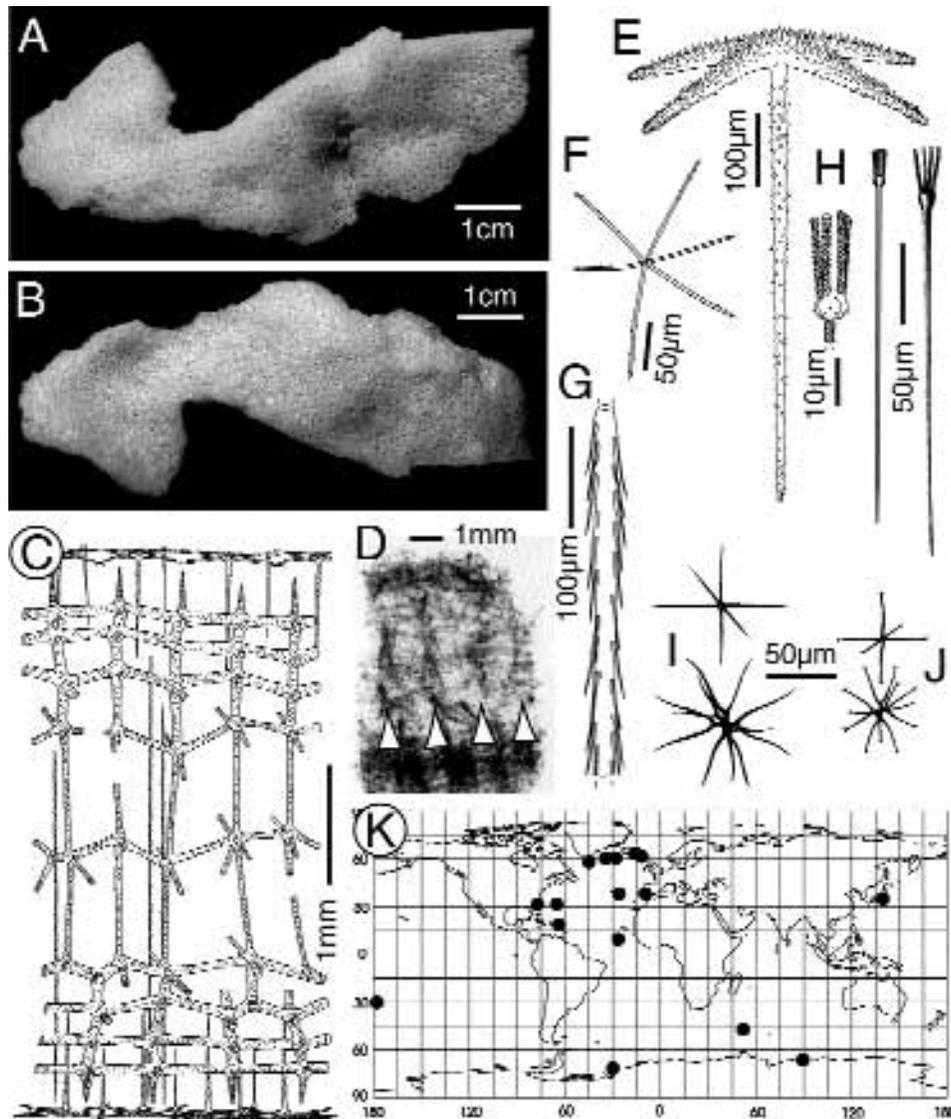
#### Description of type species

*Chonelasma lamella* Schulze, 1886 (Fig. 13).

**Restricted synonymy.** *Chonelasma lamella* Schulze, 1886: 76; Schulze, 1887a: 321, pl. 88 (not pl. 87); Ijima, 1927: 165; Reid, 1964: xcvi; Reiswig & Mehl, 1994: 153, figs 1–4, 9, tables 1–2.

**Material examined.** Lectotype: BMNH 1887.10.20.135 – from near Kermadec Islands, north of New Zealand.

**Description (measurements given as mean  $\pm$  standard deviation, range).** The preserved fragment: a flat, uneven plate  $8.1 \times 12.0$  cm size, 7.7–12.5 mm thickness; from a specimen of unknown body form and size; both surfaces covered by a pentactin-supported, porous tissue membrane beneath which dictyonal channels penetrate vertically through dense cortical layers and end in a looser middle layer; dermal and atrial surfaces undistinguishable; unchannelized middle layer (4.5 mm thick) with transverse, slightly arched lamellae (1.38 mm spacing) perpendicular to growth axis; middle-layer meshes elongate-rectangular, locally obscured by intercalated small hexactins, uncinates and dictyonal spurs; cortical layers 1.4–6.5 mm thick penetrated by cylindrical



**Fig. 13.** *Chonelasma lamella* and distribution of *Chonelasma*. A–B, the two surfaces of the lectotype. C, wall section showing dictyonal framework and position of most megascleres. D, photograph of thick wall section showing dictyonal lamellae (arrowheads) of middle layer. E, pentactin. F, mesohexactin. G, portion of uncinates. H, scopule from original description (right) and recent review (left, with head magnified). I, oxyhexactin and oxyhexaster. J, discohexactin and discohexaster. K, distribution of *Chonelasma*. (A–B, D–H–left, from Reising & Mehl, 1994; C, from Barthel & Tendal, 1994; H–right, I–J, re-scaled from Schulze, 1887a.)

channels,  $0.9 \pm 0.2$  mm diameter, bounded by tight, triangular and rectangular dictyonal meshwork; channels (epirhyses and aporhyses), extend to, and terminate openly at wide-meshed middle layer; dictyonal beams uniformly finely spined; pentactins of both surfaces similar and highly variable in size with coarsely spined outer faces of tangential rays; tangential rays ( $176 \pm 46$ , 91–280  $\mu\text{m}$  length;  $15.2 \pm 6.2$   $\mu\text{m}$  width) terminate bluntly with proclined spines on distal end; proximal ray long ( $384 \pm 201$ , 63–849  $\mu\text{m}$  length;  $16.4 \pm 6.0$   $\mu\text{m}$  width); scopules ( $219 \pm 27$   $\mu\text{m}$  length) located below dermal and atrial surfaces similar; 3–4–7 straight, slightly divergent tines tipped by indistinct serrated caps and arising from 4-lobed capitulum; tines and shaft finely thorned; uncinates oriented perpendicular to surfaces ( $3.6 \pm 0.8$  mm length;  $18 \pm 3$   $\mu\text{m}$  width) with long barbs slightly spreading from shaft; mesohexactines (rays  $123 \pm 34$   $\mu\text{m}$  length) not abundant; rays finely thorned throughout; thorns proclined; microscleres with

finely roughened surfaces predominately oxy-hexactins (59%) and -hemihexasters (16%),  $92 \pm 10$   $\mu\text{m}$  diameter; disco-hexactins, -hexasters and -hemihexasters grading to onycho-hexactins, -hexasters and -hemihexasters less common (total 9%),  $65 \pm 11$   $\mu\text{m}$  diameter; irregular forms (triactins, tetractins, pentactins, spiral forms, etc., 16%); known only from off the Kermadec Is., eastern Pacific Ocean, 1152 m depth.

**Remarks.** Schulze (1886, 1887) declared no type specimen for *C. lamella* and based his description upon several specimens, all of which, except the Kermadec Is. specimen, were assigned by Reid (1964) to *C. lamella choanoides*. In Reid's (1963b) reformation of the species, he raised the subspecies to species level, *C. choanoides*, and transferred the latter to *Leptophragmella*, an action later refuted by Reising and Mehl (1994). Reid (1964) appropriately designated the Kermadec Is. specimen, still the only certainly known representative of the species, as lectotype.

**MYLIUSIA GRAY, 1859****Restricted synonymy**

*Myliusia* Gray, 1859: 439; Gray, 1867a: 506; Schulze, 1887a: 87; Ijima, 1903: 25; Ijima, 1927: 165; de Laubenfels, 1955b: E82; Reid, 1963b: 224. Not *Myliusia* Bowerbank, 1869b: 76; Bowerbank, 1869c: 334; Schmidt, 1880b: 52. *Dactylocalyx* (in part) Thomson, 1868: 119.

**Type species**

*Myliusia callocyathus* Gray, 1859: 439 (by monotypy).

**Definition**

Body cup-shape when young, flaring to bowl-shape in older specimens, with cylindrical or widely open atrial cavity; fundamental wall folded and rejoined to form short radial tubes opening both on outer surface and to atrial cavity; adjacent tube walls often fused; tubes circumscribe external interchannel or cavaedial spaces; dictyonal framework not arranged in rectangular network; frame profusely spined; spines on beams in transverse rows; nodes polyradial, swollen, with conspicuous spined warts; lacking dictyonal spurs, dictyonal strands, scepstrules and uncinates.

**Diagnosis**

Fundamental wall 2–6 meshes thick; forms with thicker walls have nodes in ranks (arranged in transverse lamellae) and irregular epirhyses and aporhyses; mesh triangular or rectangular; loose spicules as club- or acute-tipped sword-shaped and regular hexactins; pentactins; and discohexasters.

**Remarks**

The early convoluted history of the genus is detailed by Schulze (1887a). Gray (1859), in erecting the genus for the single West Indian specimen and species, *M. callocyathes*, provided an excellent figure and sparse description of body form, but no information on spiculation. Thomson (1868, 1869) synonymized the genus to *Dactylocalyx*, supported by many later workers. Bowerbank (1869b, c) moved Gray's species to *Iphiteon*, then, with very unfortunate consequences, reused Gray's genus name, *Myliusia*, for an outwardly similar, but structurally very different specimen, *M. grayii*, which was indeed the first of the known living lychniscosan hexactinellids – now known as *Neoaulocystis*. Bowerbank's ill-advised action was accepted by many workers, resulting in widespread contradictory use of *Myliusia* for many years. Schulze (1887a) corrected the problem, replacing Bowerbank's *Myliusia* with *Aulocystis* and reinstating Gray's valid focus of the genus, with spelling corrected, as *M. callocyathus*. Schulze (1887a) ill-advisedly assigned Indo-Pacific specimens obtained by the 'Challenger' to the West Indian type species, *M. callocyathus*, and described the first spiculation pattern for the genus as being of that species. He did not state that the spicule pattern was derived solely from the Indonesian specimens. Our review of spiculation of both populations (that of *M. callocyathus* detailed below) show distinct differences between them; the West Indian population has megascleres with club-end tangential rays and 2 types of discohexasters while the Indonesian population has

acute-tip megascleres and only one type of discohexaster. Schulze's (1887a) claim of oxyhexactins and oxyhexasters is incorrect and is attributable to contamination. On this basis we rename the Indonesian specimens assigned to *M. callocyathus* by Schulze (1887a) and Ijima (1927) as *M. challengerii* sp.nov. (etymology – after the collecting vessel, 'H.M.S. Challenger'), and assign as holotype specimen BMNH 1887.10.20.151 (Little Kei Is.) and as paratype BMNH 1887.10.20.152 (Timor). The genus presently contains four species: *M. callocyathus* Gray, 1859 (West Indies), *M. challengerii* sp.nov. (Indo-Pacific), *M. verrucosa* Ijima, 1927 (Indo-Pacific) and *M. conica* (Schmidt, 1880b) (West Indies). Spiculation of the latter two species remains unknown. Many other species assigned to the genus in the past have been reassigned to other genera. Review of the type specimen of *Dactylocalyx subglobosus* Gray, 1867a, has shown that Ijima's (1927) assignment of the species to *Myliusia* is unsupported; the specimen is a good *Dactylocalyx*, and is West Indian in origin (the 'Malacca?' label is incorrect).

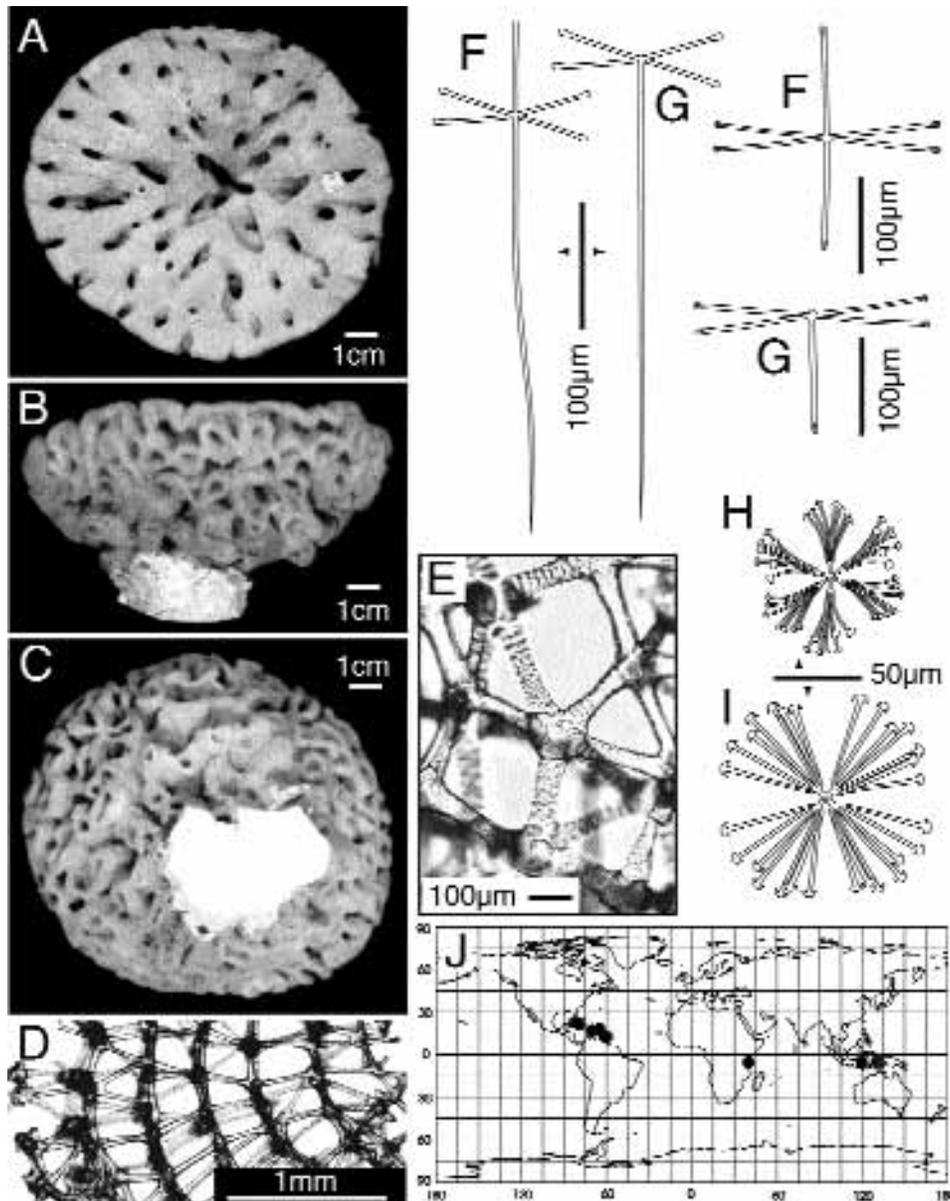
**Description of type species**

*Myliusia callocyathus* Gray, 1859 (Fig. 14).

**Restricted synonymy.** *Myliusia callocyathes* Gray, 1859: 439, pl. 16; Gray, 1860: 497; Gray, 1867a: 506. *Myliusia callocyathus*; Schulze (in part), 1887a: 354, not pl. 103; Ijima (in part) 1927: 214; not de Laubenfels, 1955b: E82, fig. 65: 2. *Dactylocalyx callocyathes*; Thomson, 1868: 119; Thomson, 1869: 713. *Dactylocalyx callocyathus*; Schmidt, 1880b: 54, pl. 8, figs 1–3. *Iphiteon callocyathes*; Bowerbank, 1869b: 76; Bowerbank, 1869c: 333, pl. 23, figs 4, 5, 7.

**Material examined.** Holotype: BMNH 1988.6.27.1 – West Indies. **Other material.** BMNH 1886.6.14.3 – Barbados. USNM 994 – St. Vincent, West Indies. USNM 5423 – Barbados. MCZ 6622I – Grenada. MCZ 6346, 9180, 9181 – Cuba. MCZ 6347 – St. Lucia. MCZ 6348, 6351, 6353, 6359, 9025 – Barbados. MCZ 6356 – location unknown. MCZ 6358 – St. Vincent. MCZ 8174 – Martinique. UWIJ EST 474, 474A – Jamaica.

**Description (measurements given as mean  $\pm$  standard deviation (range)).** Cup or funnel shape body with total wall thickness to 3.5 cm; diameter of distal margin to 11.25 cm; height to 6.7 cm; body comprised of thin fundamental wall 2–2.5 mm thick, marginally folded and fused during growth to form an irregular series of short radial parietal tubes 2.2–3.2–3.7 mm internal diameter, 5.6–8.3–9.4 mm outside diameter, to 3.3 cm long, open distally and atrially; atrium bearing apertures to radial tubes, occasional parietal oscula 1.3–1.7–2.2 mm diameter through the wall, and sparse aporhyses 0.4–0.8 mm diameter in radial lines; external (dermal) surface consists of parietal tubes whose round or ovoid aperture margins are slightly flared and often fused to adjacent tubes, bounded by a convoluted system of dermal grooves and pits representing cavaedial or interchannel spaces; dermal epirhyses of same dimensions as aporhyses; dictyonal framework entirely spined; wall 4–6 dictyonalia in thickness, constructed of polyradial nodes each bearing 6–10 beams not aligned in straight rays through nodes; meshes irregularly square to triangular; nodes aligned in transverse lamellae but not aligned in longitudinal strands; internal nodes swollen and ornamented with spined warts; beams  $45 \pm 7.4$  (27–61)  $\mu\text{m}$  thick,  $271 \pm 55$  (149–370)  $\mu\text{m}$  long, bearing spines in transverse rows; thin cortical layer of 1–2 dictyonalia in thickness covers all wall surfaces with thickened beams and nodes not aligned with internal wall structure, with triangular rotular meshes



**Fig. 14.** *Myliusia callocyathus* and distribution of *Myliusia*. A–C, upper, lateral and bottom views of the holotype (base encased in plaster of Paris for display attachment). D, longitudinal section of main wall showing alignment of dictyonal nodes in layers; growth direction to left. E, inner dictyonal framework nodes with warts and beams in transverse rows. F, sword-like and regular hexactine megascleres. G, pentactins with long and short proximal rays. H, flori-discohexaster. I, straight-rayed discohexaster with 2 rays omitted for clarity. J, distribution of *Myliusia*.

and without spurs; megascleres: hexactins with isodiametric rough rays in two forms: sword-shaped form with club-tip tangential rays  $103 \pm 23$  (59–161)  $\mu\text{m}$  long, round-tip distal ray  $98 \pm 26$  (17–149)  $\mu\text{m}$  long, sharp-tip proximal ray  $392 \pm 154$  (131–670)  $\mu\text{m}$  long; regular hexactins with all rays club-tipped and equal to tangential rays of sword-form; similar-size pentactins occur sparsely; microscleres in 2 forms of discohexasters, both with short primary rays and 5–8 secondary rays per group: flori-discohexaster  $83 \pm 18$  (46–136)  $\mu\text{m}$  diameter and straight-rayed, nearly spherical discohexaster  $128 \pm 19$  (84–159)  $\mu\text{m}$  diameter; known from throughout the West Indies from depths of 209–1957 m.

**Remarks.** The spiculation of *M. callocyathus* has been partially reported upon by Bowerbank (1869c), Carter (1873c), Schmidt (1880b), but never as a complete set. Our review of the

holotype (all measurements from that specimen) and 18 additional specimens assigned to this species allowed unambiguous determination of the complete spiculation of the species. As noted above, the spiculation described by Schulze (1887a) is inapplicable to *M. callocyathus*, and is now appropriate to *M. challengerii* sp. nov. The two species, *M. callocyathus* and *M. challengerii* are close relatives, sharing similarity of wall: 2 mm or more and six or more dictyonalia in thickness with nodes arranged in conspicuous lamellae. The other two species, *M. verrucosa* and *M. conica*, form walls less than 1 mm and 2–3 dictyonalia in thickness, precluding detectable lamellae. These features allow easy determination of washed out skeletons from the appropriate geographic locations. Many specimens in museum collections are incorrectly identified as belonging to this species.

**PERIPHRAELLA MARSHALL, 1875****Restricted synonymy**

*Periphragella* Marshall, 1875: 177; Carter 1885e: 394; Schulze, 1887a: 299; Ijima, 1927: 203.

**Type species**

*Periphragella elisae* Marshall, 1875: 177 (by monotypy).

**Definition**

Club-shaped body composed of thin-walled deep atrial cavity from which emanate thin-walled radial tubes; the latter branch and anastomose externally forming a poorly defined thick body wall; atrium developed directly from expanded lumen of originating tubular unit with primary unchanneled dictyonal wall composed of elongate rectangular meshes; long beams form longitudinal strands; connecting beams aligned in transverse laminae; secondary dictyonal structures of irregular mesh; beams uniformly microspined; megascleres include pentactins or hexactins with short distal ray as dermalia and atrialia, tyloscopules and uncinates; microscleres include oxyhexasters with or without discohexasters.

**Diagnosis**

Spicule form variable between species, specimens and within specimens; scopule tyles vary from conspicuous to just detectable; scopule tines vary from geniculate to straight; scopule shafts may be distally swollen to acute-tipped; ray tips of dermalia and atrialia may or may not be swollen in different species; mean number of oxyhexactin secondary rays ranges from 2 to 4 in different species.

**Remarks**

The genus was formed by Marshall (1877) for his new species, *P. elisae* from the Moluccas. Topsent (1890b) added *P. lusitanica* from the Azores, and later synonymized *Chonelasma schulzei* to it. Ijima (1927) reassigned an unnamed form described by Schulze (1887a) as *P. challengerii* and added *P. parva* and *P. irregularis*, all from Indonesia, to complete the present complement of five species. Paleontologically the genus cannot be differentiated from *Verrucocoelia* Etallon, 1859 (Reid, 1969; Rigby & Mohanti, 1993) and, although these may be synonyms, practice is to assign recent specimens to *Periphragella* and fossil forms to *Verrucocoelia*. The genus is distributed throughout eastern Indonesia to Japan in the western Pacific Ocean and the Azores in the Atlantic Ocean, at depths of 256–1919 m.

**Description of type species.**

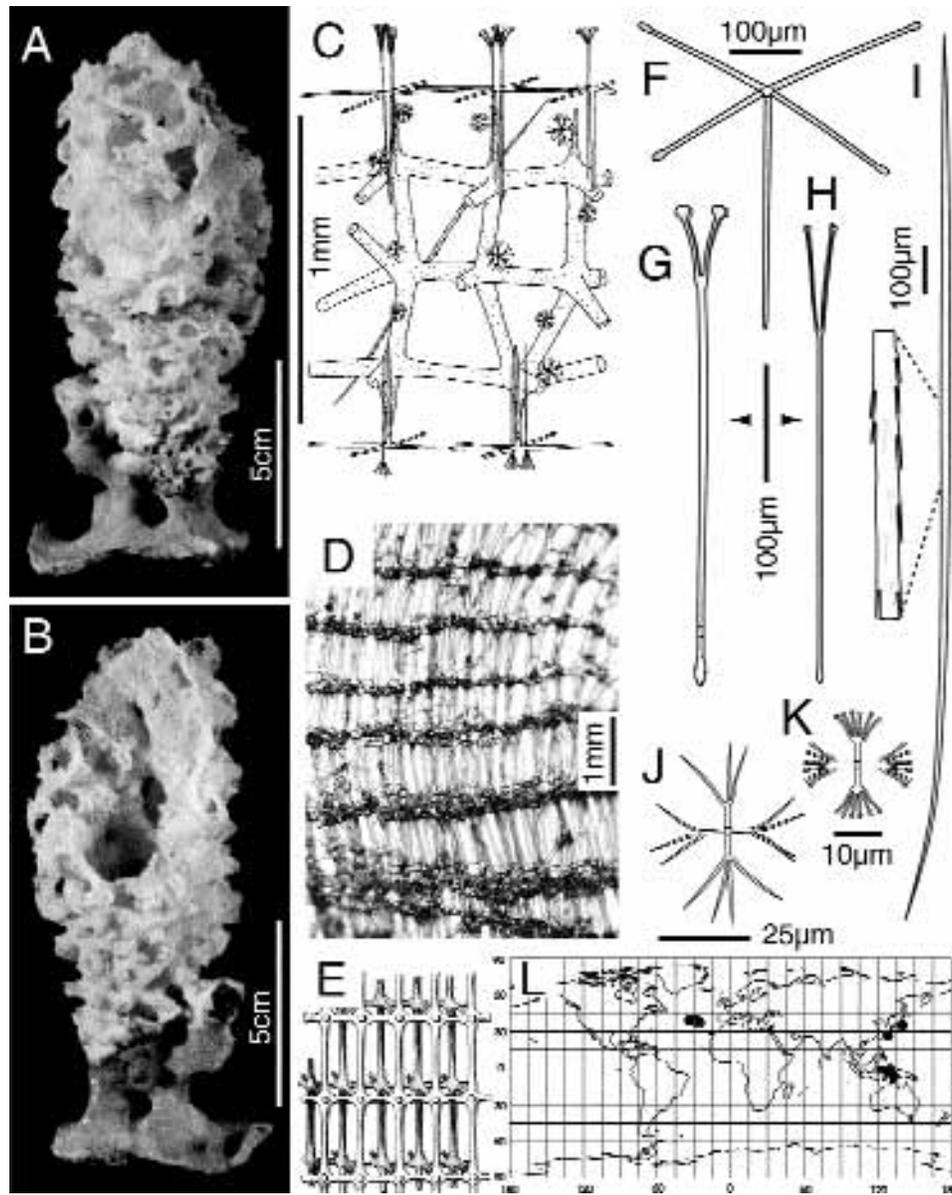
*Periphragella elisae* Marshall, 1875 (Fig. 15).

**Restricted synonymy.** *Periphragella elisae* Marshall, 1875: 177, pl. 12, fig. B, pl. 13, figs 24–25, pl. 14, figs 26–31; Carter, 1885e: 394; Schulze, 1887a: 394, pl. 80, figs 1–2, pl. 81, figs 1–10; Ijima, 1927: 204; Okada, 1932: 50; Reid, 1964: lxxx, textfig. 43a–c.

**Material examined.** Holotype: RMNH Porifera no 28 – Moluccas. **Other material.** USNM 22135 – Japan. BMNH 1898.12.19.23, 1921.11.5.10 – Japan. MCZ 6621, 9027 – unknown location and Japan, resp. BPBM C350a,b,c; 351a, b; 352 – Ryukyu Is.

**Description (measurements given as mean  $\pm$  standard deviation (and range), taken from holotype).** Erect funnel with poorly-defined, thick outer wall composed of branching and anastomosing tubes of highly variable diameter; body to 15 cm tall by 5 cm diameter with central smooth-surfaced atrium 10.5 cm long by 3 cm diameter at margin; secured to hard substrate by large spreading basal plate; texture firm but elastic; atrium derived from original thin-wall tubule by upward expansion; primary wall 2.5 mm thick basally, 1.0 mm thick marginally, composed of 3–4 dictyonal layers of regular, elongate, rectangular meshes ( $936 \pm 28 \mu\text{m}$  long by  $418 \pm 102 \mu\text{m}$  wide) with longitudinal beams forming dictyonal strands and connecting beams aligned in ranks forming conspicuous lamellae perpendicular to inner atrial wall; atrial wall projected radially as short, large-diameter tubes open on both lateral body surface and atrium; outer (dermal) surface of primary walls of main funnel and lateral tubes thickened by addition of 1–many layers of irregular-mesh secondary dictyonalia; lateral walls of main radial tubules (5–15 mm diameter) give rise by secondary branching to small–2–4 mm diameter tubules which branch and anastomose on outer body wall between main radial tubes, thickening the overall body wall to 1–4 cm, and ultimately open on the outer body surface by small 2–4 mm diameter apertures; all discrete apertures of atrium and lateral body surface are exhalant and constitute the terminations of the continuous atrial surface; dermal surface as outer surfaces of radial tubes, tubules and the lining of the lateral cavaedial spaces under and between those tubules; dictyonal beams ( $65 \pm 17 \mu\text{m}$  thick) uniformly microspined throughout; dictyonal nodes smooth and not swollen; spurs finger-like and spined; framework meshes subdivided by synapticulae and intercalated hexactins; megascleres: pentactins on dermal and atrial surfaces similar of varying size, tangential rays  $181 \pm 31$  ( $121$ – $250$ )  $\mu\text{m}$  long, uniformly microspined, slightly bowed and terminally swollen; proximal ray  $266 \pm 55$  ( $146$ – $421$ )  $\mu\text{m}$  long, straight or curved, terminally blunt tapered; vestigial 6th ray as knob-like swelling; tyloscopules  $375 \pm 105$  ( $155$ – $590$ )  $\mu\text{m}$  long; on both surfaces; with 4 slightly divergent, straight, microspined tines  $67 \pm 17$  ( $10$ – $115$ )  $\mu\text{m}$  long, shaft smooth, rarely uncinata-like or spined, terminates proximally with distinct swelling; uncinates are rare,  $1.8 \pm 0.4$  ( $0.8$ – $2.5$ ) mm long (measurements pooled from 5 specimens) with barbs not inclined from spicule surface; microscleres: oxyhexasters  $45 \pm 7$  ( $27$ – $69$ )  $\mu\text{m}$  diameter with 6–8  $\mu\text{m}$  long smooth primary rays each bearing 2–8 rough sharply-pointed, curved or occasionally straight, secondary rays; disco- or stronglylohexasters  $23 \pm 4$  ( $13$ – $34$ )  $\mu\text{m}$  diameter with smooth short  $4 \pm 1 \mu\text{m}$  long primary rays each bearing 5–7–10 thorned, short, curved or straight secondary rays tipped with barely discernable serrated disks; known from western Pacific, Moluccas to Japan, from 183–675 meter depths.

**Remarks.** In his review of the genus, Ijima (1927) concluded that specimens attributed to *P. elisae* from Japan (Carter, 1885e; Schulze, 1887a) were distinct from Marshall's Moluccas type specimen and suggested denoting them as *P. elisae japonica*, the typical form defaulting to *P. elisae elisae*. The Japan forms were thought to differ from the typical form in having smaller discohexasters and scopules with bent tines and rough shafts. Similarity of spiculation of a new 'Albatross' specimen to the Moluccas holotype prompted Okada (1932) to suggest that all earlier Japan specimens assigned to *P. elisae japonica* by Ijima be designated a distinct species (Okada suggested no name). No later worker has commented on these actions and suggestions. Our review of the Mollucas holotype, and specimens from Ryukyu and Japan (not including Carter's and Schulze's specimens) indicate all



**Fig. 15.** *Periphragella elisae* and distribution of *Periphragella*. A–B, two sides of the holotype as of 9/1998. C, dictyonal frame and spicule distribution in a wall section of smaller tubule of non-type specimen (redrawn from Schulze, 1887a, pl. 81, fig. 2). D, facial view of main atrial framework showing transverse lamellae and elongate meshes (non-type specimen from Ryukyu Is.). E, lamellate frame with elongate mesh of holotype (from Marshall, 1885). F, dermal pentactin (all spicules from the holotype). G, large-tyle scopule with curved tines. H, small-tyle scopule with straight tines. I, uncinata. J, oxyhexaster (axis perpendicular to page omitted for clarity). K, small disco- or stronglylohexaster (ditto). L, distribution of *Periphragella*.

of these forms are indistinguishable. Differences in descriptions by the involved workers can be attributed to the great variation in size, form and spination of spicules and to the lack of review of Marshall's type specimen. We find no basis for the differences claimed by Ijima (1927) and Okada (1932) and conclude that no recognizable subspecific taxa exist in this species.

#### **PLEUROCHORIUM SCHRAMMEN, 1912**

##### **Restricted synonymy**

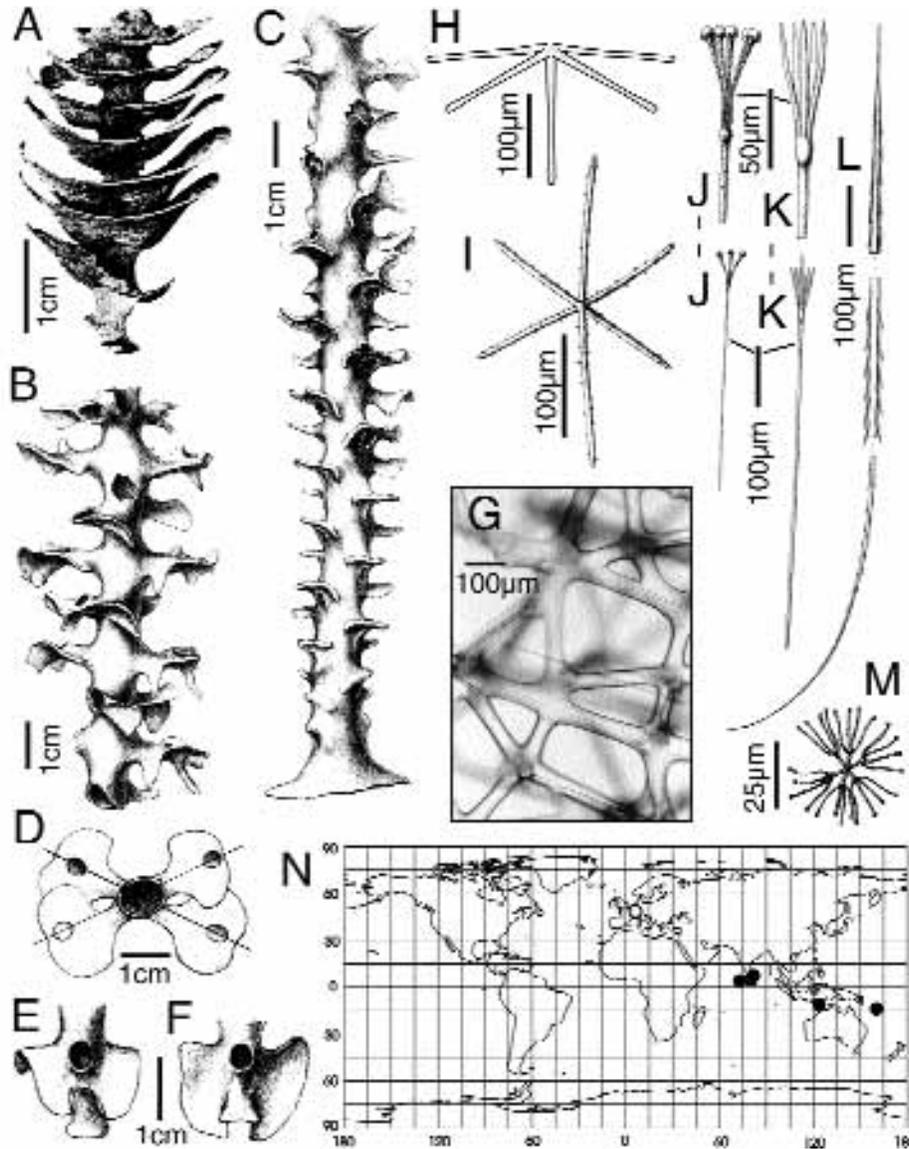
*Pleurochorium* Schrammen, 1912: 251. *Eurete* (in part) Kirkpatrick, 1908a: 21. *Pararete*; (in part) Reid, 1964: cxlvi.

##### **Type species**

*Pleurochorium schulzei* Schrammen, 1912: 251 (by monotypy).

##### **Definition**

Euretidae with form of an unchannelized, erect, axial tube bearing longitudinal series of lateral oscula, opening either under conspicuous solid, plate-like extensions projecting perpendicularly from lateral tube surfaces, or opening on tubular bases of such extensions; dermalia and atrialia as pentactins; other spicules include scopules, barbed uncinate and small discohexasters.



**Fig. 16.** *Pleurochorium*. A, *P. schulzei*† lateral view of lectotype. B–M, *P. amandalei*. B–C, lectotype and paralectotype. D, cross section of lectotype showing offset angle of lateral appendages. E, upper, and F, lower views of appendages. G, superficial dictyonal frame with mostly triangular meshes. H, dermal pentactin from Maldives specimen. I, hexactin from lectotype. J, tyloscopules from lectotype. K, oxyscopules from lectotype. L, uncinates from lectotype. M, discohexaster from lectotype. N, distribution of *Pleurochorium*: fossil type locality as open circle; Recent specimens as filled circles. (A, from Schrammen, 1912, pl. 27, fig. 4; B–F, I–M, from Kirkpatrick, 1908a, pl. 1.)

### Diagnosis

Axial tube open at terminal osculum; lateral oscula in various patterns from a single spiral series to 2 opposite series to 4 alternating opposite series; lateral oscula open either directly from axial tube or from short lateral tubes which form bases of perpendicular projections; internal dictyonal meshes quadrangular while superficial meshes are triangular; nodes not swollen; scopules where known always include tyloscopules but may also include oxyscopules or discoscopules.

### Remarks

The genus was originally erected for the fossil species *P. schulzei*. Two recent species, *Eurete amandalei* Kirkpatrick

(1908a), and *P. cornutum* Ijima (1927) were later assigned here by Ijima (1927). Reid (1964) and Lévi & Lévi (1982) supported synonymy of *Pleurochorium* with the closely related genus *Pararete* since loose spicules of the two are almost indistinguishable. However, absence of swollen nodes and distinctive body form of *Pleurochorium* are here considered adequate differences to maintain distinction between the genera. The spiculation pattern of the genus, absent in the fossil type species, is necessarily based upon the recent members, *P. amandalei* and *P. cornutum*. The genus is known from the Upper Cretaceous (Germany) to the Recent (tropical Indo-Pacific). Recent forms are reported from 520–1207 m depth.

### Description of type species

*Pleurochorium schulzei* Schrammen, 1912 (Fig. 16A).

**Restricted synonymy.** *Pleurochorium schulzei* Schrammen, 1912: 251, pl. 27, figs 3–5, pl. 41, figs 1–2; textpl. 10, fig. 8. *P. feschulzei* (err.); de Laubenfels, 1955b: E86, fig. 67: 1.

**Material examined.** None. Type series (7 fragments) originally in Schrammen's collection; syntypes (4) at IMGP Göttingen reassigned here as lectotype: 432–18 (Schrammen 1912, pl. 27, fig. 4); paralectotypes: 432–19 (ibid., fig. 3), 432–54 (ibid., fig. 5), 432–69 (not figured).

**Description.** Fossil material. Thin-wall axial tube compressed in one plane; tube (2–4 × 6–8 mm diam.), bearing series of thin (0.2–0.3 mm) perpendicular, sheet-like extensions (wings) at regular intervals (4 mm); main wall thickness 0.3 mm; solid extensions arise from and encircle axial tube and extend in plane of compression to 2.5 cm outward and upward as bowl-like flanges; lateral oscula also located in the compression plane at lower intersection of tube and extensions in 2 opposite series; wall unchannelized; dictyonal meshes rectangular in interior and triangular in surface layers; nodes not thickened; beams tuberculate; dictyonal strands in lateral extensions oriented longitudinally, radially and circularly; loose spicules unknown; Upper Cretaceous of Germany.

**Description of comparative species.** *Pleurochorium annandalei* (Kirkpatrick, 1908a) (Fig. 16B–M).

**Restricted synonymy.** *Eurete annandalei* Kirkpatrick, 1908a: 21, pl. 1, figs 1–13. *Pleurochorium annandalei* Ijima, 1927: 196.

**Material examined.** Lectotype (here designated): BMNH 1907.8.9.3 (fragments of IM specimen, catalogue number unknown) – Bay of Bengal ('Investigator'), eastern Indian Ocean. Paralectotypes: BMNH 1907.8.9.1, 1907.8.9.2 – same locality. Other material. BMNH 1936.3.4.6 – Maldives ('Mahabis'), north-central Indian Ocean.

**Description (measurements given as mean ± standard deviation).** Erect cylindrical, hollow tube 9 cm height, 7–10 mm diam., with fourteen vertical lateral lamellar branch-like appendages (total width 3.5–4.5 cm); lateral appendages perpendicular to central tube; arranged in four longitudinal series; in opposite pairs; lateral appendages saddle-shaped (2–5 mm thick, 1.5–2 cm wide and long); lateral edges curving downwards; with well-defined round orifices (3–4 mm diam.) on both upper and lower surfaces (lateral oscula); appendages distally solid but connected to central tube by means of a short, hollow, tubular stem; internal dictyonal framework meshes regular-quadrant; superficial meshes irregular-triangular; wall thickness 0.5–0.7 mm; layering not apparent; dictyonal strands prominent; nodes not swollen, mixture of true and false types; external nodes with curved spurs; beams (49 ± 8 μm diam.) smooth; synaptical common; dermalia and atrialia as pentactins (unknown in 'Investigator' specimens but present in Murray Expedition specimens), weakly spined; tangential rays (135–231 × 7–15 μm) bent about 10° down from perpendicular; proximal ray same size; hexactins (400–450 μm ray length) uniformly microspined, straight or curved; terminally rounded; large (436 μm length) dermal tyloscopules with 4–5 tines (62 μm length) geniculate and microspined, distal bulbs beset with numerous recurved thorns; capitulum microspined and slightly swollen; smooth shaft straight or curved, terminally microspined and bluntly pointed; larger (694 μm length) dermal oxyscopules with 5 smooth, lanceolate tines (82 μm length), capitulum microspined, slightly swollen; curved uncinates (1300 μm length) with prominent low-angled barbs; parenchymal discohexasters (45 μm diam.) with short (6.3 μm long) primary rays each bearing 4 s-shaped secondary rays (16 μm length) distally tipped with minute disks; distributed in tropical Indo-Pacific from 878–1207 m depth.

**Remarks.** Kirkpatrick (1908a) was able to obtain some spicule information from the original type series of seven partly macerated specimens, but he was unable to establish dermal and atrial spicules. Specimens obtained by the Murray Expedition from Maldives were in much better condition but Burton (1959a) failed to provide any spicule description in his assignment of these to *E. annandalei*. Superficial pentactins extracted from fragments of the Maldives specimens are included here for completion of the species (*P. annandalei*) and genus spicule descriptions. Similar pentactins are known from *P. cornutum* Ijima.

## TRETOCHONE REID, 1958

### Synonymy

*Ptychodesia*; (in part) Ijima, 1927: 165 (not Schrammen, 1912: 252). *Tretochone* Reid, 1958a: 11; Reid, 1962: 739; Reid, 1963b: 225; Reid, 1964: cxlvi.

### Type species

*Ptychodesia duplicata* Topsent, 1928a: 1 (by original designation).

### Definition

Euretidae of erect curved sheet or broad tongue form with edges fused basally to form oblique cone; with transverse ridges and papillae on internal surface and longitudinal slits on external surface; internal and external surfaces anatomically inverted relative to normal sponges; middle dictyonal layer constructed of elongate prismatic meshes and transverse lamellae; channelized with amarrhyses, epirhyses and aporrhyses; megascleres include pinulated hexactins, regular hexactins, pentactins, scopules and uncinates; microscleres as oxyhexactins to hemioxyhexasters and disco- to stronglylohexasters with slight button tips.

### Diagnosis

Monospecific (see type species description).

### Remarks

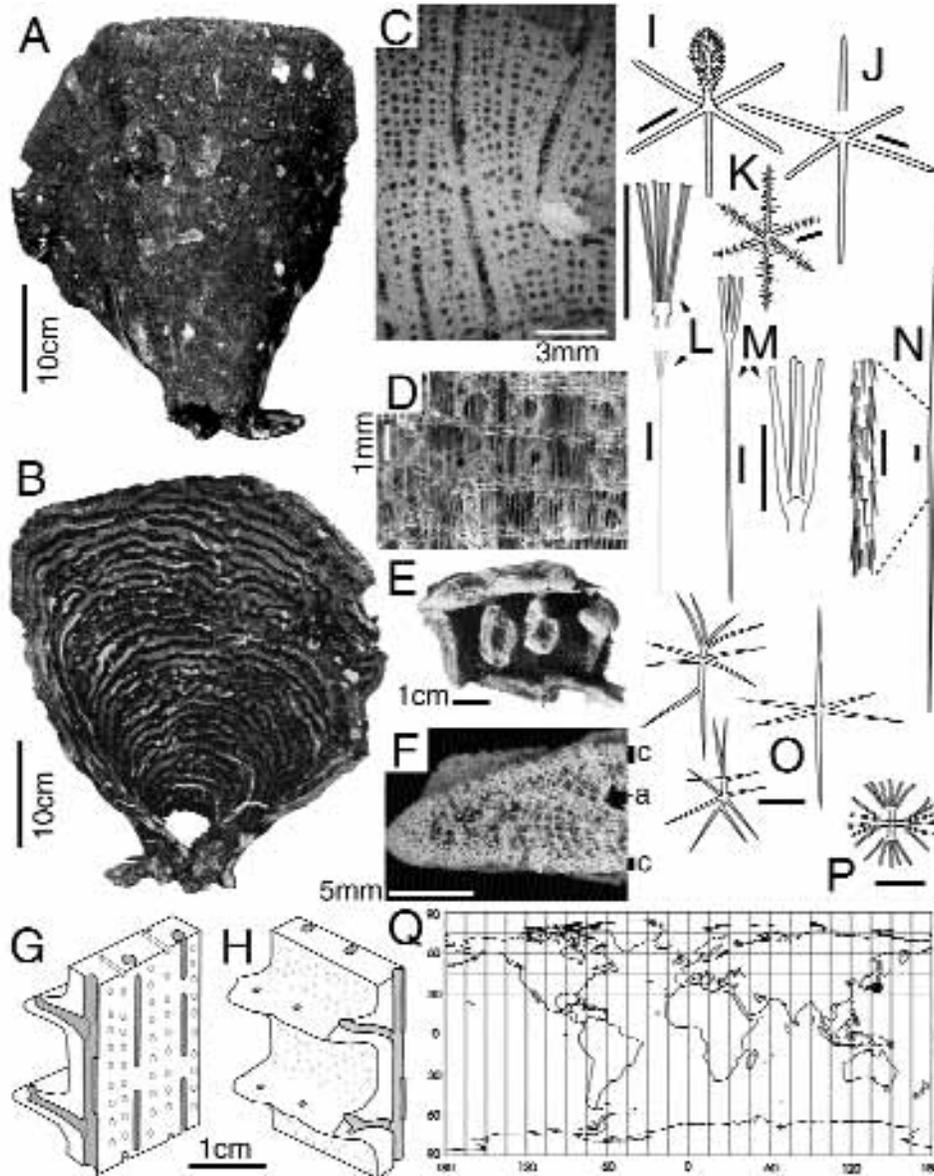
See remarks for type species.

### Description of type species

*Tretochone duplicata* (Topsent, 1928a) (Fig. 17).

**Synonymy.** *Ptychodesia duplicata* Topsent, 1928a: 1; Topsent 1928d: 302, pl. 2, figs 1–6, pl. 3, fig. 3. *Ptychodesia doederleini*; Ijima, 1927: 165 (not *Chonelasma doederleini* Schulze, 1886). *Tretochone duplicata* Reid, 1958a: 11; Reid, 1962: 739; Reid, 1964: liii, textfigs 44, 52.

**Material examined.** Holotype: MOM 04 1971 (fragment MNHN P. 4676) – off Misaki, Japan. **Other material.** MCZ 26908 (label *Hexactinella lorica*) – Japan. BMNH 1925.11.01.681 (label *Chonelasma doederleini*) – unknown origin. BMNH 1898.12.19.8 (label *Hexactinella lorica*; all spicule data reported below from this specimen) – Japan. BMNH uncatalogued (label *Hexactinella lorica*) – Japan.



**Fig. 17.** *Tretochone duplicata*. A–B, holotype; view of convex (above) and concave (below) surfaces. C, external surface with aporhyses and slits. D, tangential view of middle framework layer after removal of external cortex, showing lamellae and walls of aporhytic channels. E, ridges and papillae of holotype fragment concave surface. F, section through dermal ridge with cortical layers (c) and amaranthesis (a) and arched lamellae in middle framework layer. G–H, diagrams of main wall with view of outer (left) and inner (right) surfaces; amaranthesis, indicated by gray shading, connected to exterior by slits (outer side) and accessory oscula on upper ridge surfaces (inner side). I, pinular hexactin. J, rough hexactin and pentactin. K, thorned hexactin. L, small discoscopule. M, stronglyloscopule. N, uncinata. O, oxyhexactine and 2 hemioxyhexactine microscleres. P, stronglylohexaster. Q, geographic distribution. (A–B, E, from Topsent, 1928d, pl. 2); C–D, F, from MCZ 26908; scales: megascleres 50  $\mu$ m, microscleres 20  $\mu$ m.)

**Description (measurements given as mean (and range)).**

Erect, thin (4–5 mm thick) curved plate (to 40 cm tall by 50 cm wide) with basal lateral margins enrolled and fused to produce a basal cone or funnel; attached to hard substrate by broad, thin basal plate; surfaces reversed relative to normal tubular euretoid organization – here internal surface inhalant or dermal and external surface exhalant and equivalent to atrial surface of normal stocks; concave surface bearing parallel transverse ridges (spacing interval 1.1 cm) and papillae to 2 cm high bearing sparse openings as accessory oscula, 1.26 (0.92–1.67) mm diameter, on apices or upper surfaces, and densely crowded openings of epirhyses, 0.65 (0.43–0.92) mm diameter on main wall and all surfaces of ridges/papillae; outer concave surface with conspicuous exhalant slits 1.35

(0.68–2.00) mm wide and usually 20–50 mm long, oriented mainly longitudinally but often radiating in fields – not closely corresponding with ridges/papillae on opposing face; areas between slits bear round aporhytic apertures 0.79 (0.41–1.41) mm diameter, arranged in rows parallel to slits; dictyonal frame of 3 layers: low-density middle layer bounded by dense cortical layers; middle layer of elongate rectangular or prismatic meshes (0.8–1.1 mm  $\times$  0.4–0.5 mm sides), elongate beams forming longitudinal strands, short beams aligned in transverse lamellae arched distally, ending tangentially on outer surfaces; middle layer extends into ridges/papillae; dense cortical layer (0.8–2 mm thick) of smaller rectangular and triangular meshes (0.22–0.34 mm sides) and thickened beams covers all surfaces of the middle layer, including ridges and

papillae; cortex represents close-spaced, tangential extensions of middle layer lamellae, hence part of primary wall (not secondary addition); epirhyses of main body wall penetrate cortical layer and open into middle layer without continuation as discrete channels; aporhyses of main body wall penetrate cortical layer and continue through middle layer to opposite cortex; defined in middle layer by triangular-meshed dictyonal walls but channels are traversed by longitudinal beams of middle layer (not empty gaps); channelization of ridges/papillae probably mixture of epirhyses and aporhyses; amararhyses as system of separate longitudinal channels 2.3 (1.9–3.1) mm diameter lying within middle layer just under cortex of concave surface; each amararhysis extends from base to growing distal margin and branches only into ridges/papillae to open by accessory oscula on concave surface and by longitudinal slits on convex surface; adjacent amararhythic units not connected; amararhyses surfaces consist of openings of channels homologous to aporhyses; external nodes with spurs well developed only on concave (dermal) surface; dictyonal beams (50  $\mu\text{m}$  thick) uniformly microspined (spines 2–4  $\mu\text{m}$  height); longitudinal strands not thickened; synaptacula present; nodes not swollen, primarily regular but some nodes polyradial in cortices; megascleres (locations undetermined) fine-spined pinular hexactins with club-shape pinule ray 90 (51–127)  $\mu\text{m}$  long, sharp-tipped tangential rays 104 (75–126)  $\mu\text{m}$  long and proximal rays 121 (70–339)  $\mu\text{m}$  long; rough hexactins with round-ended rays 99 (58–152)  $\mu\text{m}$  length; similar rough pentactins with tangential rays 144 (65–253)  $\mu\text{m}$  long, proximal rays 170 (80–387)  $\mu\text{m}$  long; thorned hexactins with pointed rays 105 (66–152)  $\mu\text{m}$  long bearing spines to 13  $\mu\text{m}$ -long; smaller disco- to subtyloscopules 309 (217–411)  $\mu\text{m}$  total length, head 54 (32–68)  $\mu\text{m}$  long with sharp 4-lobed basal inflation bearing 3–8 retrospined tines bearing small discoid terminal buttons, and straight shaft with fine uncinatous ornamentation; larger stronglylscopule 442 (315–585)  $\mu\text{m}$  total length, head 93 (53–125)  $\mu\text{m}$  long bearing 3–5 stout microspined tines, with straight shaft ornamented with insignificant uncinatous spines; uncinat 2.96 (1.65–3.90) mm long bearing moderately inclined barbs; microscleres: microxyhexactins to irregular hemioxyhexasters 82 (53–106)  $\mu\text{m}$  diameter with very finely rough secondary rays; disco- to stronglylohexasters with highly variable lengths of primary and secondary rays, 36 (22–57)  $\mu\text{m}$  diameter, with rough secondary rays ending in very small discoid terminal buttons or blunt ends; known only from Sagami Sea, Japan at unknown depth.

**Remarks.** Early history of the genus and species was reviewed by Topsent (1928d) and Reid (1962). The species was well known to Ijima as dead frameworks used by other hexactinellids for attachment. He referred to the form in early publications (Ijima, 1898, 1903, 1904) as *Hexactinella lorica*, a *nomen nudum* (Reid, 1962), borne by many museum specimens. Ijima, after consulting with Schrammen, accepted his advice to assign the sponge to Schrammen's *Ptychodesia* (Topsent, 1928d), but incorrectly determined the species to be Schulze's (1886) *Chonelasma doederleini*. The form was thus first described as *Ptychodesia doederleini*, within Euretidae, in Ijima's posthumous 1927 publication. Topsent accepted the family and generic position but, realizing the form was distinct from Schulze's species, redescribed it as *Ptychodesia duplicata* (1928a, 1928d). After comparing *P. duplicata* with Schrammen's fossil type species, *P. papillata*†, Reid (1958a) decided that the two forms differed in basic structure, prompting his reassignment of *Ptychodesia* (with only fossil members) to Craticulariidae and creation of a new eurentid genus, *Tretochone*, for *P. duplicata*. Topsent recognized epirhyses,

aporhyses and amararhyses as skeletal channels in his original description, but Reid (1962) inexplicably considered the two smaller apertures to be ostia and postica and concluded that true epirhyses and aporhyses were absent. In *Tretochone*, these elements penetrate the cortical layers of the primary dictyonal framework as gaps in the silicified structure – they are true channels and not simply apertures. The apertures on the convex surface lead to channels that traverse the entire middle wall layer – they are not complete gaps in the primary framework, but are circumscribed by special sets of dictyonalia forming recognizable bounding walls. We consider these to be true epirhyses and aporhyses, necessitating a modification of the definition of the family Euretidae. The physical robustness and persistence of the main framework after death, due to the strong cortices, explains the near ubiquity of heavily encrusted, washed-out specimens in museum collections and the lack of data on spiculation in descriptions of this species. The first figures and spicule measurements provided here are consistent with all previous mentions of occasional spicule occurrences.

### **VERRUCOCOELOIDEA REID, 1969**

#### **Synonymy**

*Verrucocoeloidea* Reid, 1969: 485.

#### **Type species**

*Verrucocoeloidea burtoni* Reid, 1969: 485 (by original designation).

#### **Definition**

Euretidae in the form of a plicate funnel, terminally open, with tubular, lateral outgrowths from external wall; central atrium invaded by longitudinal series of ingrowths which spread apically (internally) to form a discontinuous secondary atrial lining, thereby defining a ring of interconnected subatrial longitudinal tunnels; loose spicules include pentactins, hexactins, tyloscopules, uncinates, oxyhexasters and discohexasters.

#### **Diagnosis**

Monospecific (see type species description).

#### **Remarks**

See remarks for type species.

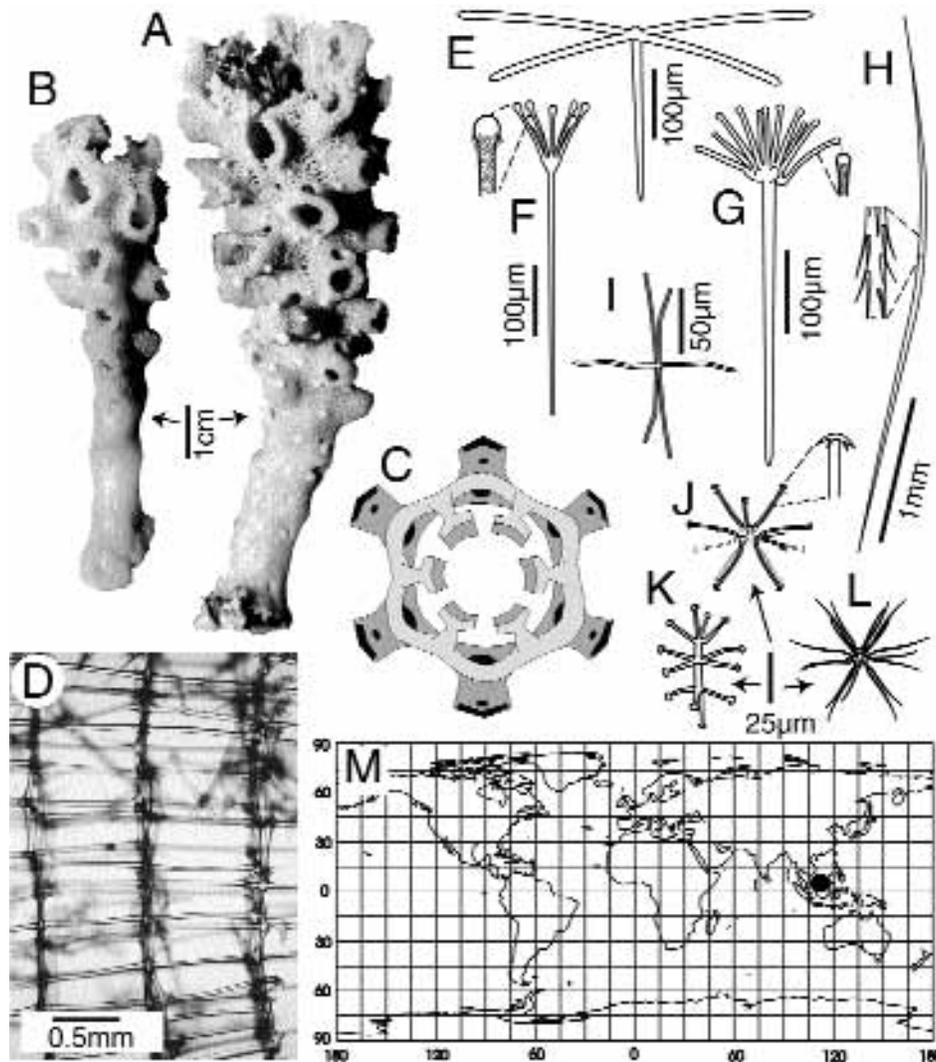
#### **Description of type species**

*Verrucocoeloidea burtoni* Reid, 1969 (Fig. 18).

**Synonymy.** *Verrucocoeloidea burtoni* Reid, 1969: 485, figs 1–8.

**Material examined.** Holotype: BMNH 1967.5.23.1 – off Brunei, Borneo. Paratype: BMNH 1967.5.23.2 – same locality.

**Description (measurements given as mean  $\pm$  standard deviation).** Holotype is erect funnel 11 cm tall; 2.9 cm wide; secured to substrate by basal plate from which extends nearly smooth, conical stalk grading into main body funnel; external surface with prominent, tubular lateral outgrowths, 5–9 mm diam., open distally



**Fig. 18.** *Verrucocoeloidea burtoni*. A–B, lateral view of holotype (A) and paratype (B). C, diagram of cross-sectional segment showing relation of atrial ingrowths to main body wall (light surface). D, photograph of dictyonal framework including 3 lamellae (growth direction to left). E, dermal pentactin. F, most common subtyloscopule with enlarged subtyle showing thorns. G, less common irregular subtyloscopule. H, uncinata. I, small hexactin. J, regular discohexaster. K, hemidiscohexaster (diaster). L, oxyhexaster. M, geographic distribution.

as accessory oscula; arranged in 5–6 nearly longitudinal series; lateral outgrowths rudimentary and hood-like just above stalk; color dull orange; epirhyses to 1 mm diam. present only in superficial secondary layers over outer grooves of plicate body wall; within atrium, inner edges of wall plications bear longitudinal series of ingrowths 4–6 mm wide, extending ca. 5 mm into atrium lumen forming incomplete secondary atrial lining; primary dictyonal framework with prominent longitudinal strands gradually spreading (curving) to wall surfaces, regular, layered (2–3 layers) with longitudinal elongate rectangular meshes,  $940 \times 320 \mu\text{m}$ ; mixed rectangular/triangular meshes in transverse lamellar sheets; regularity obscured in places by intercalated small hexactins; secondary external dictyonal meshes of surfaces less regular, with common synapticula and triangular meshes; dictyonal strands prominent; orientation parallel to axis of growth, often with slight lateral spreading; beams connecting dictyonal strands arranged to form transverse lamellae; nodes not swollen or ornamented; dictyonal beams smooth, rarely microspined,  $20\text{--}85 \mu\text{m}$  diam.; external spurs finger-like, microspined; atrial spurs to  $600 \mu\text{m}$  long;

dermalia and atrialia as pentactins with unequal length ( $266 \pm 44 \mu\text{m}$ ) tangential rays slightly bowed, microspined and terminally blunt; proximal ray smooth or microspined,  $150\text{--}250 \mu\text{m}$  length, terminally blunt; free hexactins with straight or slightly curved rays unequal in length  $60 \pm 20 \mu\text{m}$ , microspined and terminally blunt; subtyloscopules  $429 \pm 62 \mu\text{m}$  length, in dermal and atrial surfaces, with six to eleven divergent, straight, microspined tines  $96 \pm 14 \mu\text{m}$  length, terminate as club heavily beset with numerous, proximally directed, curved thorns; shaft smooth, straight, capitulum slightly swollen, smooth  $14 \pm 3 \mu\text{m}$  wide but occasionally nearly discoid in form; straight or curved uncينات,  $3.6 \pm 0.7 \text{ mm}$  length, with barbs outwardly curved, divergent from shaft; regular discohexasters abundant  $48 \pm 12 \mu\text{m}$  diam. with short ( $6 \pm 1 \mu\text{m}$ ) primary rays bearing 2–4 slightly curved secondary rays tipped with minute four-pronged disks; irregular hemidiscohexasters with full primary and secondary rays developed in only one axis (diasters of Reid, 1969), common; oxyhexasters  $58 \pm 28 \mu\text{m}$  diam. with 2–4 curved, secondary rays; primary rays short  $5 \pm 1 \mu\text{m}$ ; known only from off Borneo, 200 m.

**Remarks.** Reexamination of holotype material confirms Reid's (1969) original description and suggests that the spicules he referred to as "irregular variants approaching diasters" are less common than intimated. Reid's suggestion that *V. burtoni* is very closely related to the extinct genus *Verrucocoelia* and to Recent species of *Periphragella* is accepted, but the unique atrial extensions in

*V. burtoni* allow the living forms to be easily distinguished. Mehl (1992), after reemphasizing the great similarity between *Verrucocoeloidea* and *Periphragella* in body form and dictyonal frame organization, noted the similarity of discohexaster variations in *Verrucocoeloidea* and *Aphrocallistes*. The genus is known only from the type locality, northwest of Borneo.