

## Family Farreidae Gray, 1872

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Farreidae Gray (Hexactinellida: Hexactinosida) contains a total of 21 species in five genera, including *Aspidoscopulia* gen.nov., formed from *Claviscopulia furcillata* Lévi. Individuals of the family have been recovered from depths of 82 to over 5200 m and, with one exception, between latitudes of 55°N&S. Body form is predominately tubular, often with extensive branching and anastomosing of components, but lamellar and infundibular shapes also occur. Channelization of the dictyonal framework is typically absent, but extradictyonal epirhyses and/or aporhyses may be developed in mature stages of some species. The family is characterized by presence of scepstrules in the form of either clavules or sarules, with or without lonchioles or aspidoscopules (scopules with disk-form heads). Narrow-headed scopules typical of the Euretidae, Tretodictyidae and Aphrocallistidae have not been convincingly reported as intrinsic spicules of presently recognized members of the Farreidae. Genera are differentiated by combinations of scepstrule types. In the present treatment, body form, channelization pattern and other details of the dictyonal framework are accorded less importance than spiculation. These characters may become important in future revisions of the family.

**Keywords:** Porifera; Hexactinellida; Hexactinosida; Farreidae; Euretidae; *Aspidoscopulia*; *Aulodictyon*; *Chonodictyon*; *Claviscopulia*; *Farrea*; *Lonchiphora*; *Phyllobrochis*; *Ramella*; *Sarostegia*; *Sclerothamnopsis*.

### DEFINITION, DIAGNOSIS & SCOPE

#### Restricted synonymy

Farreidae Gray, 1872a. Euretidae, in part, Zittel, 1877. Farreidae; Schulze, 1885.

#### Definition

Hexactinosida with scepstrules including at least one form of clavule (Fig. 1A1–1A2) or sarule (Fig. 1A3–1A4), and may also include a lonchiole (Fig. 1A5) or aspidoscopule (Fig. 1A6) but without narrow-headed scopule.

#### Diagnosis

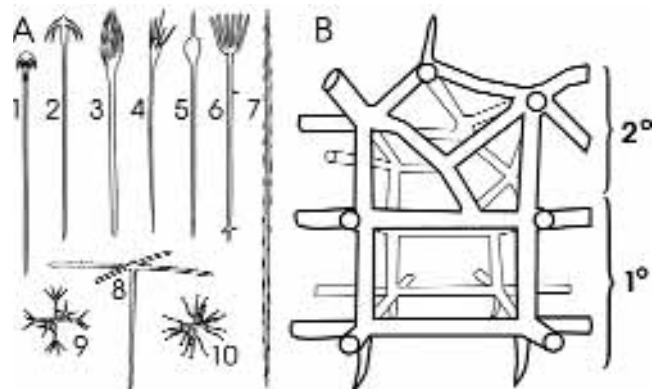
Body form within the family is variable from typical thin-walled tubular branching and anastomosing stock, to cup, funnel, flat blade or solid branching forms. The primary dictyonal skeleton is never channelized, but accreted secondary layers may contain shallow, extradictyonal epirhyses and/or aporhyses. Primary framework is fundamentally one to three layers of fused, quadrangular-meshed dictyonalia (Fig. 1B) with all nodes being true centra (with axial cross), while secondary layers have dictyonalia attached in indefinite orientation, resulting in false (non-centra bearing) nodes and triangular meshes. Dermalia and atrialia, where present, are pentactins (Fig. 1A8), either finely spined or coarsely tuberculate on outer surfaces. All members possess uncinates (Fig. 1A7) and microscleres as either oxyhexasters (Fig. 1A9) or discohexasters (Fig. 1A10) or both. Occasional microscleres may include tylohexasters, staurasters, pentasters, and diasters.

#### Scope

Five genera, including one new, are presently recognised in the family.

### History and biology

Gray (1872a) erected Farreidae to accommodate the distinctive hexactinellid genera *Farrea*, Bowerbank (erroneously attributed to Kent) and *Sympagella*, Schmidt. He characterized the taxon as having an expanded or tubular body form and a skeleton as nearly regular with four-sided meshes. Shortly thereafter, Marshall (1876) included *Farrea*, the type genus of Gray's family, among the numerous unplaced aberrant forms under his *Asynauloidea*, possibly within his *Pleionakidae*, but his intent was unclear. Zittel (1877) took *Farrea* into his new family Euretidae. Carter (1885e) supported Zittel's move, but Schulze (1885) reinstated Gray's family, with spelling corrected to Farreidae, and restricted its content to *Farrea*, transferring *Sympagella* to *Asconematidae* Gray. Schulze (1886, 1887a) solidified the distinctness of *Farrea* and the family Farreidae by erection of a special subtribe, the *Clavularia*, to accommodate only this genus. He characterized the subtribe by the



**Fig. 1.** Farreidae characters. A, spicules including clavules (1–2), sarules (3–4), lonchiole drawn from text interpretation (5), aspidoscopule (6), uncinata (7), pentactin (8), oxyhexaster (9) and discohexaster (10). B, thickened farreid dictyonal frame with two regular, quadrangular, primary layers (1°) and irregular additional secondary layers (2°) on the dermal side.

presence of clavules and within it, the single family Farreidae, by its single-layered dictyonal framework with quadrate meshes. This arrangement was widely accepted until Schulze (1899) described *Claviscopulia intermedia*, a close relative of *Farrea*, but with scopule-like spicules (sarules) in addition to *Farrea*-like clavules. Schulze felt compelled to revoke his pair of contrasting subtribes, the *Clavularia* and *Scopularia*. He also renounced support for the distinction of the family Farreidae and moved its contents, *Farrea* and his new genus *Claviscopulia*, back to the Euretidae. Throughout the early 1900's, treatment accorded the family Farreidae and its genera, now having grown to include *Sarostegia*, Topsent (1904d), was inconsistent. The farreid genera were included in Euretidae in most works (e.g., Schulze, 1904; Topsent, 1904b and others), or in Farreidae by the same authors (e.g., Schulze, 1902; Topsent, 1904d). Ijima (1927) reconciled the problems created by *Claviscopulia* by arguing (incorrectly) that the sarules of this genus were diactins rather than monactins and could not be considered modified scopules. Ijima reinstated Schulze's contrasting taxa, *Clavularia* and *Scopularia*, and re-established the distinction of the family Farreidae, now containing four genera with his added *Lonchiphora* (Ijima, 1927). All subsequent authors, with exception of Moret (1952), have followed Ijima's argument and example in recognition of the family Farreidae. Reid (1963b) argued for transfer of *Sarostegia* to the Euretidae, based upon its euretoid dictyonal framework pattern, a reasonable action from a paleontological viewpoint. This action is rejected for zoological classification of recent forms, since loose spicules share prominence with framework features in taxa diagnoses. The diagnosis used here shifts emphasis to the presence of clavules, sarules or lonchioles as sceptrules and de-emphasizes the monolayer character of the primary framework employed in earlier diagnoses when the

family contained only *Farrea* and *Claviscopulia*. Generic differentiation is based upon combinations of sceptrules. The transfer of *Bathyxiphus* and its single species, *B. subtilis*, from the Euretidae to the Farreidae by Mehl (1992: 57) is rejected because there was no evaluation of evidence to support the move. The specimen of *B. subtilis* was possibly contaminated by both other euretids and farreids obtained in the same dredge haul. The genus and species should remain in Euretidae until new materials are available to support a firm conclusion on placement. The genus is known only from the Pacific Ocean type locality off Baja California (Mexico); the Caribbean location cited by Mehl originated from misinterpretation of 'Guadeloupe Is.' as referring to a Caribbean location. A fifth genus, *Aspidoscopulia* gen.nov., is added here by transfer of *Claviscopulia furcillata* Lévi. The family has been collected over a depth range of 82–5200m and is considered cosmopolitan although only one report exceeds 55° latitude. The genus *Farrea* has been the focus of several important biological studies, attributable in part to the cosmopolitan distribution, relatively shallow depth occurrence, and ease of identification of members of this genus. The extensive embryological light-microscope study by Okada (1928) on *Farrea sollasi* remains a classic for the Hexactinellida. The first molecular sequence of rRNA from a hexactinellid was reported by West & Powers (1993) from *Farrea occa*. Interpretation of their data is still considered preliminary and will require confirmation and consensus with sequences from other members of the class and from other molecules. One of the still rare ultrastructural studies of tissue organization was carried out on *Farrea occa* by Reiswig & Mehl (1991). This work confirmed the general syncytial nature of the trabecular tissues and revealed greater diversity in tissue layering within the flagellated chambers among members of the Hexactinellida.

## KEY TO GENERA

- |  |                       |
|--|-----------------------|
| (1) Sceptrules include clavules (Fig. 1A1–1A2) .....                                       | 2                     |
| Sceptrules as sarules (Fig. 1A3–1A4) only, without clavules .....                          | <i>Sarostegia</i>     |
| (2) Sceptrules include forms other than clavules .....                                     | 3                     |
| Sceptrules as clavules only .....  | <i>Farrea</i>         |
| (3) Sceptrules as sarules and clavules .....   | <i>Claviscopulia</i>  |
| Sceptrules as clavules and either lonchioles (Fig. 1A5) or aspidoscopules (Fig. 1A6) ..... | 4                     |
| (4) Sceptrules as clavules and lonchioles .....  | <i>Lonchiphora</i>    |
| Sceptrules as clavules and aspidoscopules .....  | <i>Aspidoscopulia</i> |

## ASPIDOSCOPULIA GEN. NOV.

### Synonymy

*Claviscopulia*; in part, Lévi, 1990:277. *Aulodictyon*, in part, Kent, 1870b. *Farrea*, in part, Bowerbank, 1862a.

### Type species

*Claviscopulia furcillata* Lévi, 1990: 278 (here designated).

### Definition

Tubular Farreidae with sceptrules as pileate clavules and distinctive scopules (aspidoscopules) having a shield-like or discoid, flattened head; scopule tines emanate from the head in a single marginal whorl.

### Diagnosis

Monospecific (see type species description).

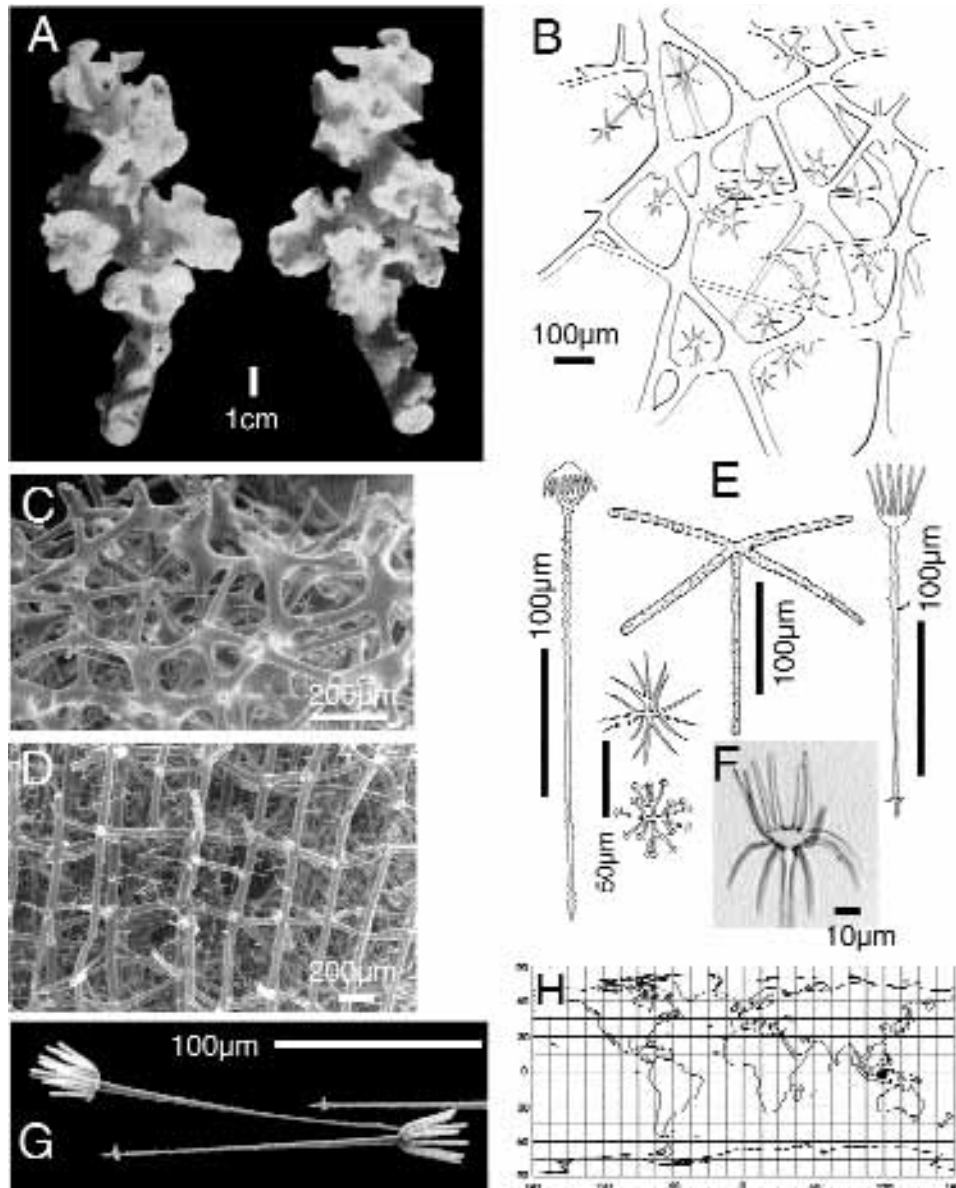
### Description of type species

*Aspidoscopulia furcillata* (Lévi, 1990) (Fig. 2).

**Synonymy.** *Claviscopulia furcillata* Lévi, 1990: 278, textfigs 1a–e, 2, pl. 1, figs 1–2.

**Material examined.** Holotype: MNHN HCL 117 – Makassar Strait, west of Celebes (Sulawesi), Indonesia.

**Description.** Only known specimen is short spiral tube, 145 mm tall, bearing closely-spaced lateral branches, to 20 mm long, terminating as open funnels with flaring, foliaceous or pleated margins; lower 35 mm dead, broken off (assumed attached to hard substrate by basal disc); overall width 45–75 mm; exhalant openings 10–12 mm diam.; external and internal surfaces bounded

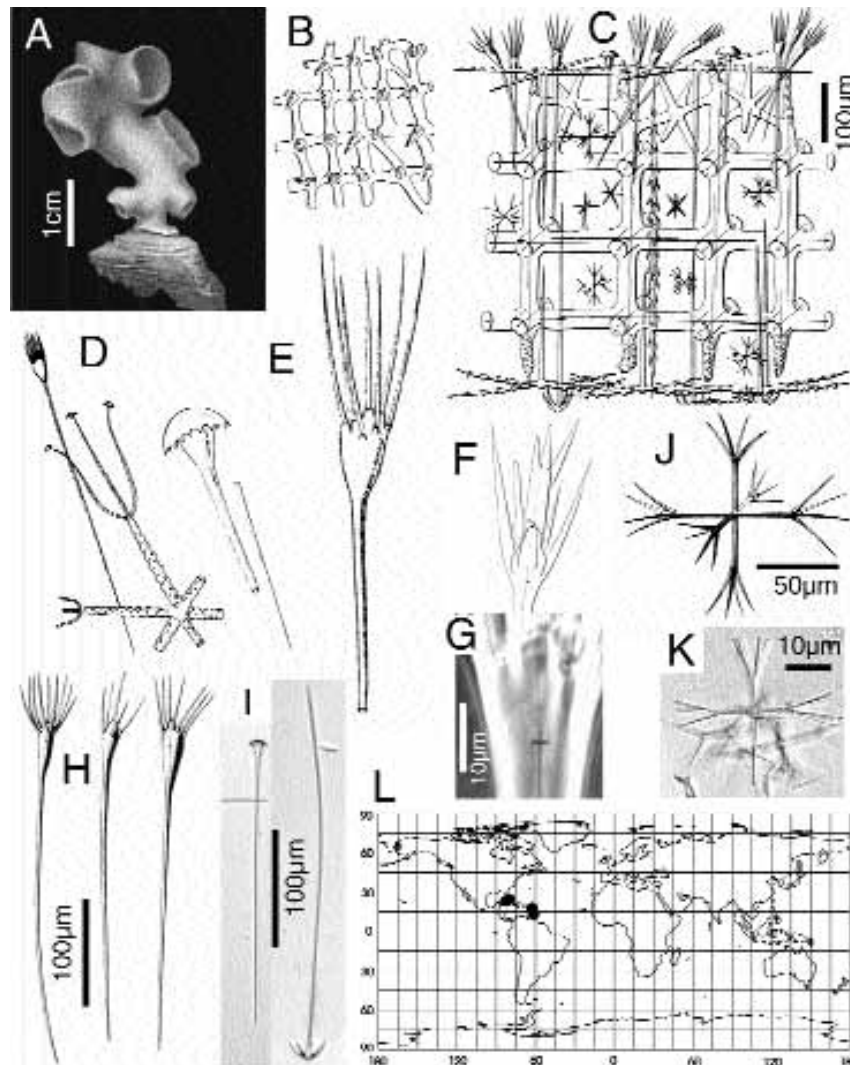


**Fig. 2.** *Aspidoscopulia furcillata*, holotype. A, body form, 2 sides (from Lévi, 1990, pl. 1, figs 1 & 2). B, diagram of framework (from Lévi, 1990, fig. 2). C, cleaned dermal framework (SEM). D, cleaned atrial framework with longitudinal strands obvious (SEM). E, major spicules: dermal pentactin, pileate clavule, aspidoscopule, oxyhexaster and discohexaster (uncinates omitted) (modified from Lévi, 1990, fig. 1). F, very rare aspidoscopule with scopule-like (anterior projecting tines) and clavule-like (posterior projecting tines) features. G, normal aspidoscopules (SEM). H, distribution of *Aspidoscopulia*.

by pentactin lattice, supplemented externally with scopules and hexasters and internally by clavules and hexasters; dictyonal skeleton very irregular; primary scaffold as coarse, rectangular-mesh without clear layering; 2–3 layers of dictyonalia irregularly appended on either or both sides; main rectangular meshes  $350 \times 600 \mu\text{m}$ ; triangular meshes  $200\text{--}500 \mu\text{m}$  sides; nodes neither swollen or ornamented; beams  $15\text{--}70 \mu\text{m}$  wide, smooth or with low rounded tubercles; abundant small oxyhexactins appended to beams or each other without pattern; loose spicules include dermal and atrial finely-spined (granular) pentactins, ray length  $140\text{--}180 \mu\text{m}$ , width  $10 \mu\text{m}$ ; atrial pileate clavules  $240\text{--}320 \mu\text{m}$  long with rough stems  $2\text{--}3 \mu\text{m}$  thick, cap  $10 \mu\text{m}$  tall by  $30 \mu\text{m}$  wide, ca. 24 marginal teeth over rough cylindrical collar; dermal aspidoscopules  $200\text{--}280 \mu\text{m}$  long with very spiny stems, often with whorl of sharp hooks just above slightly inflated tip; heads expanded as flattened

disk  $10 \mu\text{m}$  diam. bearing 12 rough marginal digitiform tines ending in rounded or abruptly pointed tips; tines run parallel or flare slightly, usually straight but occasionally curved; axial cross with same form and position as in other sceptrules; oxyhexasters  $50\text{--}55 \mu\text{m}$  diam. with 4 secondary rays, common; discohexasters  $50\text{--}60 \mu\text{m}$  diam. with 4 secondaries, common; both macro- and microuncinates are rare.

**Remarks.** Lévi (1990) provisionally assigned his new species, *furcillata*, to *Claviscopulia*, noting the considerable differences between the scopules of this species and the sceptrules of the other members of the genus. He was unable to resolve details of the axial canal system and thus the potential homology between scopules of this new form and those typical of the Scopularia. The axial cross has here been resolved; it is similar in position and form to those of both the clavules and scopules of other hexactinosans.



**Fig. 3.** *Claviscopulia facunda*. A, body form of neotype (from Schulze, 1899, pl. 16, fig. 3). B, framework fragment (Schmidt, 1870, pl. 1, fig. 13). C, cross section of wall (Schulze, 1899, pl. 16, fig. 4). D, spicules from original description (Schmidt, 1870, pl. 1, figs 19–20). E, sarule (Schmidt, 1870, pl. 1, fig. 18). F, sarule head with axial cross (Schmidt, 1880, pl. 5, fig. 8). G, sarule with axial cross, from neotype. H, sarules from neotype (Schulze, 1899, pl. 16, figs 5–7). I, dermal pileate and atrial anchorate clavules from neotype. J, oxyhexaster (Schulze, 1899, pl. 16, fig. 8). K, tylohexaster from neotype. L, distribution of *Claviscopulia*.

In view of the disc-like capitulum of the scopule in *C. furcillata*, it is here considered to be sufficiently distinct from the scepterules of both *C. facunda* and *S. oculata*, to form the basis of a new genus, *Aspidoscopulia* (aspid, Gk. = shield). The new genus is retained within the family Farreidae, following the suggestion by Lévi (1990) because of its typical farreid clavules. The genus is known only from Sulawesi, Indonesia (798 m).

### CLAVISCOPULIA SCHULZE, 1899

#### Restricted Synonymy

*Claviscopulia* Schulze, 1899: 76.

#### Type species

*Farrea facunda* Schmidt, 1870: 16 (by monotypy).

#### Definition

Tubular Farreidae with both clavules and sarules as scepterules.

#### Diagnosis

Monospecific genus (see type species description).

#### Description of type species

*Claviscopulia facunda* (Schmidt, 1870) (Fig. 3).

**Restricted Synonymy.** *Farrea facunda* Schmidt, 1870: 16, pl. 1, figs 13–20, pl. 2, fig. 10; *Aulodictyon facunda*; Kent, 1870b:250; *Claviscopulia facunda*; Reid, 1958b: 3; *Claviscopulia facunda*; Van Soest & Stentoft, 1988: 11 (*lapsus*). *Claviscopulia intermedia* Schulze, 1899: 76, pl. 16, figs 3–8.

**Material examined.** Neotype: MCZ 6742 – St. Vincent, West Indies (selected by Schulze, 1899: 76 as holotype, by monotypy, of

*C. intermedia*). Other material. MCZ 6429wa (old 70a) – Cuba. MCZ 6429wj (old 70j) – Cuba. MCZ 6429r (old 116) – Florida Strait. MCZ 6711 – St. Vincent, West Indies. USNM 23333 – Puerto Rico, West Indies. BMNH 1 slide uncatalogued, tray 4/77.

**Description.** Irregularly dichotomously branching tubes 2–10 mm diam. with wide open ends, arising from a spreading basal plate attached to hard substrate; wall thickness to 1 mm; dictyonal framework of 1–3 regular, rectangular-mesh tiers, sides 90–235  $\mu\text{m}$  long, with addition of 1–3 irregularly arranged dictyonal layers with triangular meshes on the external (dermal) face; beams smooth, 33  $\mu\text{m}$  diam.; nodes not thickened; external spurs evenly conical and tuberculate; smooth oxyhexactins (80–120  $\mu\text{m}$  diam.) are commonly attached to beams by single rays in lower parts; dermalia and atrialia are pentactins with hastate, rounded or clavate ray terminations (200  $\mu\text{m}$  tangential ray length) with outer and lateral surfaces ornamented by widely-spaced tubercles (knobs) in the largest (most mature) forms; regular uncinates oriented perpendicular to wall surfaces; dermal scepstrules include pileate clavules (200  $\mu\text{m}$  length with 18  $\mu\text{m}$  diam. disc with 15 teeth) and sarules (150–450  $\mu\text{m}$  length with 6–10 sharp spines projecting apically); atrial scepstrules are only anchorate clavules (150  $\mu\text{m}$  length) with 4 large gently recurved spines; microscleres include oxyhexasters (120–150  $\mu\text{m}$  diam.) with 3–4 moderately diverging terminals and less common discohexasters with small, marginally serrate discs; tropical western Atlantic, 161–823 m.

**Remarks.** The genus *Claviscopulia* is closely related to *Farrea* by shared features of body form, dictyonal framework and clavule shapes. Schulze (1887a) considered Schmidt's *Farrea facunda* to be insufficiently defined for acceptance because Schmidt designated no holotype and many of the specimens bearing Schmidt's handwritten labels proved to be mixtures of a variety of farreids, euretids and aulocystids, all badly contaminated with spicules from each other. Most *Farrea facunda* labelled specimens, including many labelled by O. Schmidt himself, belong to other species or are unidentifiable, including: – MCZ 6208, 6209, 6225, 6711i, 6711q, 6721a; USNM 980; 8 of 9 BMNH slides in tray 4/77. Moreover, Schmidt's extended description of *F. facunda* in 1880 included spicules that were not consistently found in specimens bearing the distinctive broom spicules with acute spines (sarules, Fig. 3E). Schulze (1899) felt compelled to resolve the species by choosing one specimen with sarules among those bearing Schmidt's handwritten labels. He apparently could not find an acceptable specimen from the original collection (nor could I in recent surveys: 1870 and earlier from between Florida and Cuba, 234–823 m) and selected a specimen clearly NOT from the type series, collected in 1879 from St. Vincent, W.I. Since he did not base his revision on type material of the original species, Schulze (1899) resolved the problem by erecting a new genus and species *C. intermedia*, to replace Schmidt's *Farrea facunda*. However, Schmidt's *F. facunda* was, and remains, clearly recognizable on the basis its sarule (broom spicule), thus Schulze's *C. intermedia* is a junior synonym. Schulze (1899) first interpreted Schmidt's broom spicule to be a peculiar scopule. He considered this spicule to be intermediate between a clavule and scopule, and the organism forming it to be intermediate between the genera *Farrea* and *Eurete*. Topsent (1904d) rejected the 'scopule' affinity for the distinctive *Claviscopulia* spicule and applied the new neutral term "sarule" to this and to the scepstrule of his new *Sarostegia oculata*. Ijima (1927) agreed with Topsent, and considered the sarule as distinct from the typical euretoid scopule, arguing that the form of axial crosses indicated that the sarule was a diactin (anisodiactin) and the scopule a monactin. He based this

argument on Schmidt's figure (1880: pl. 5, fig. 8) of the sarule of *Farrea facunda* and Schulze's figure (1899: pl. 16, figs 5–7) of the sarule of *Claviscopulia intermedia*, both of which show the axial filament of the distal ray as considerably longer than those of the undeveloped transverse rays. Inspection of sarules of the type specimen of *C. intermedia* and of two *F. facunda* specimens, indicates these figures are erroneous. The distal axial filament is not significantly longer than those of the transverse filaments (as shown in Mehl, 1992: pl. 6, fig. 2), thus the sarules of both *Claviscopulia* and *Sarostegia* must be considered monactins. The distal extensions of both sarules are not accompanied by extension of the axial filament, and, as such, cannot be considered to be a primary ray structures. The distal extensions are secondary silicifications. Topsent's (1904d) proposal to include *Farrea clavigera* Schulze, 1886, in *Claviscopulia*, and thereby modify the concept of the genus and of the sarule, was rejected by Ijima (1927) and has had no later support. Lévi (1990) modified the concept and diagnosis of *Claviscopulia* by inclusion of a new scopule-bearing farreid, *C. furcillata*. This species is here considered sufficiently different from *C. facunda* to warrant erection of a separate genus, thereby returning *Claviscopulia* to its former content and diagnosis. Reid's (1963b) suggestion that *Claviscopulia* be considered a subgenus of *Farrea*, a perspective useful for paleontological purposes, is rejected for zoological use. Suggestion that the sarule occurs in other non-clavularian hexactinellids (Mehl, 1992) such as *Hertwigia falcifera* and *Pleurochorium annandalei* are based upon faulty original attribution of foreign spicules by Schmidt (1880) in the former and misinterpretation of superficially similar spicule morphology (scopule) in the latter. The genus is known only from the Caribbean (161–823 m).

## **FARREA BOWERBANK, 1862**

### **Restricted Synonymy**

*Farrea* Bowerbank, 1862b: 1118. *Aulodictyon* Kent, 1870b: 249. *Chonodictyon* Reid, 1958b: 4. *Phyllobrochis* Reid, 1958b: 9.

### **Type species**

*Farrea occa* Bowerbank, 1862b: 1118 (by monotypy).

### **Definition**

Farreidae with clavules as the only scepstrule form.

### **Diagnosis**

Scepstrules as clavules; dermalia and atrialia as pentactins; microscleres as oxyhexasters with long primary rays with or without discohexasters; tylohexasters, pentasters, staurasters and diasters may occasionally occur; attached to hard substrate by spreading basal plate; body form varies from typical dichotomously branching and anastomosing tubes with open lateral branches to broad funnel to laterally undulated flat blade, and intermediates; primary dictyonal wall, seen in distal growing edges, as a regular, rectangular-meshed monolayer with dictyonal strands oriented longitudinally; primary wall not channelized; secondary dictyonalia added basally as one or more duplications of the organized primary layer or as irregularly joined dictyonalia; secondary layers may contain shallow epirhyses and/or aporhyses.

**Remarks**

Schulze (1887a: 266), in summarizing the history of *Farrea*, deftly avoided its controversial origin. Before setting down formal definition of *Farrea occa*, Bowerbank (1862a) had clear understanding of two distinct types of siliceous framework fragments from the root of Owen's (1857) *Euplectella cucumer* collected near Comoros. One was canaliculated [hollow, eroded], coarsely tuberculate [an eurentoid framework in modern terms] and was referred to as "*Farrea MS*" in both text and figure (Bowerbank, 1862a, pl. 28, fig. 11); the other was solid, smooth, and "harrow-like" [a farreoid framework in modern terms], and was undesignated by name (Bowerbank, 1862a, pl. 33, fig. 7). Bowerbank explicitly chose the former of the two, the canaliculated and tuberculate [eurentoid] form, as the object of his first description of *Farrea occa* (Bowerbank, 1862b:1118) and made reference to the figure of the eurentid (with typographic error of plate number). In choosing the name '*occa*' (harrow), he contradicted his stated characters of the species. Subsequently Bowerbank (1864) repeatedly mixed application of his name, *Farrea occa*, between frameworks of the two types – the tuberculate framework (1864: 13, 80, fig. 277), and the smooth, harrow-like framework (1864: 19, 104, fig. 311). He finally accepted both under that name (1864: 288), considering the former to have been internal and the latter (the harrow) to have been superficial parts of the same specimen (Bowerbank, 1869c: 339). This constituted a modification of his original description, by amplification. Kent's (1870b) report of a complete, but macerated, specimen of *F. occa* from the coast of Portugal added to the problem; his specimen was composed entirely of a one-layer farreoid framework, but was tuberculate throughout and thus could not be a representative of Bowerbank's species. In description of another specimen, his new genus and species, *Aulodictyon woodwardi*, Kent unknowingly provided the first figures of the authentic spiculation of the genus *Farrea*. Carter (1873c: 445), acting as first reviser, selected the quadrangular, monolayered, harrow-like framework (Bowerbank, 1869c, pl. 24, fig. 7, reproduced here as Fig. 4D) among Bowerbank's many different representations of *F. occa*, as the characteristic feature of the species, a decision that established the modern concept of the dictyonal frame of *F. occa* and for the genus *Farrea*. He renamed the tuberculate frame fragment, the form taken originally as *F. occa* by Bowerbank, as *F. densa*. Present understanding of spiculation of *F. occa* stems from Carter's (1885e) description of a specimen from near Misaki, Sagami Sea, Japan, which he felt free to assign to Bowerbank's *F. occa*, in spite of the source being quite remote from the Comoros type locality. The second authoritative report of *F. occa* spiculation followed shortly in Schulze's reports of the 'Challenger' collections (Schulze, 1885, 1886, 1887a). Reid (1958b) suggested partition of the genus *Farrea* on the basis of body form. This would provide paleontologists with the ability to differentiate taxa that shared the same dictyonal framework pattern, but where loose spicules were unavailable. He proposed subdivision of the genus into *Farrea* for tubular stocks, *Chonodictyon* for funnel-form stocks and *Phyllobrochis* for blade-form stocks. He later (1963b) reduced these to subgenera of *Farrea*. Reid's taxa, being based solely on body form, cannot be accepted as valid taxa for zoological purposes and are considered junior synonyms of *Farrea*. Significant body form variation is known to exist within a single species as defined by loose spicule patterns. The genus presently contains 17 recognized species with overall cosmopolitan distribution, tropics to high boreal, reported only once beyond 55° latitude (Topsent, 1901d), with a depth range 82–5218 m (the small fragment reported from

11m depth off Borneo by Ijima, 1927: 161 is considered a dubious record).

**Description of type species**

*Farrea occa* Bowerbank, 1862b (Fig. 4).

**Restricted Synonymy.** *Euplectella cucumer*, in part, Owen, 1857, pl. 21, figs 9–9a; Bowerbank, 1862a, pl. 32, fig. 7 (Not pl. 28, fig. 11). *Farrea occa* Bowerbank, 1862b: 1118; Carter, 1873c: 445; Carter, 1885e: 388, pl. 12, pl. 13, figs 1–11.

**Material examined.** Holotype: BMNH 1877.5.21.1466, 1 slide, Bk 1466, R1304, slide tray 4/77 – Comoro, Indian Ocean (frequently reported origin 'Seychelles' is incorrect). Reference non-type specimen: BMNH 1885.12.31.10 & 12 (mixture), dry fragments – Enoshima, Japan (main specimens at IMC, unverified).

**Description of holotype.** The holotype is a framework fragment without indication of body form or loose spiculation; beams smooth, 32–42µm thick; rectangular meshes with sides 93–167 × 148–231µm in single plane; spurs rough, pointed, 102–157µm long project from both sides of intersections.

**Description of Carter's non-type reference specimen.** Body form as branching and anastomosing system of tubes, to 12 cm tall, attached to solid substrate by a spreading basal plate; tube diam. 0.5–1.0–2+ cm, increases distally; terminal tube openings as simple or foliate-edged oscula and growth margins; walls thin, ca. 1 mm, consist partly or completely (distally) of primary monolayer of dictyonalia fused to form longitudinal primary strands joined by lateral beams; regular rectangular meshes of 250–500µm sides; unattached rays project on both surfaces as rough, conical spurs to 400µm long; irregularly-arranged, secondary dictyonalia added to dermal and, less commonly, atrial surface; primary wall unchanneled but shallow epirhysis and/or aporhysis may occur in secondary wall layers; beams 50–65µm diam., smooth; nodes not swollen; affixed microxyhexactins common in older areas, but synapticalae very rare; dermalia and atrialia as pentactins with coarse spination on outer surfaces, tangential ray length 185–250µm; dermal scepstrules predominately pileate clavules oriented head-out in bundles of 4 to 10 around dermalia; atrial scepstrules usually anchorate clavules with 4–10 strong recurved hooks, total length 190–360µm; uncinates abundant, oriented perpendicular to surfaces; microscleres 75–110µm diam. as smooth, long-primaried oxyhexasters with 4 secondaries per primary; rough discohexasters may occur.

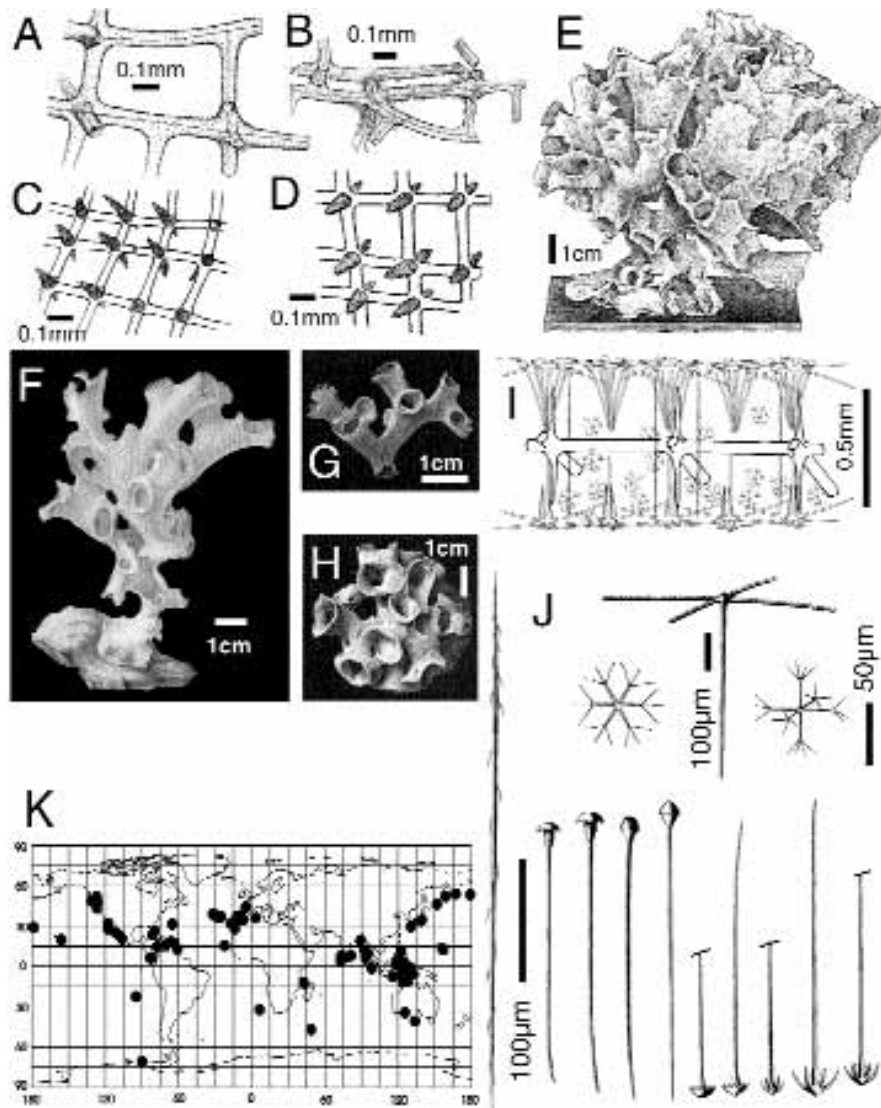
**Remarks.** The species presently contains nine subspecies in addition to the typical form. Thus body shape (frondose to funnel-form), tube branching pattern (including monopodial form), tube diam., details of framework structure, spicule sizes, beam ornamentation and microsclere form are quite variable within *Farrea occa*. The unifying specific combination is: dermal pileate clavules and atrial anchorate clavules.

**LONCHIPHORA IJIMA, 1927****Synonymy**

*Lonchiphora* Ijima, 1927: 130.

**Type species**

*Lonchiphora inversa* Ijima, 1927: 138 (by monotypy).



**Fig. 4.** *Farrea occa*. A–B, frame fragments from the *Euplectella cucumer* root tuft from the Comoros labelled as this species but not belonging to the eventual selected form (Bowerbank, 1862a, pl. 28, fig. 11; 1869c, pl. 24, fig. 1). C–D, the harrow-form which became the basis of the species and genus (Bowerbank, 1862a, pl. 32, fig. 7 & 1869c, pl. 24, fig. 7). E, body form of the Tokyo Bay reference specimen (Carter, 1885e, pl. 12). F–H, body forms (Schulze, 1887a, pl. 71, figs 1–2, pl. 72, fig. 1). I, transverse section of body wall (after Schulze 1887a, pl. 71, fig. 3). J, spicules including dermal pentactin, uncinates, dermal and atrial clavules, oxyhexaster (Schulze, 1887a, pl. 71) and combination figure, part oxyhexaster and part discohexaster (Carter, 1885e, pl. 13, fig. 9). K, distribution map of *Farrea*.

**Definition**

Farreidae with sceptrules as clavules and lonchioles.

**Diagnosis**

Monospecific genus (see type species description).

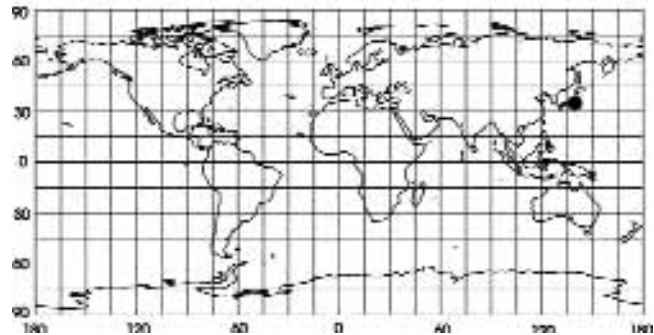
**Description of type species**

*Lonchiphora inversa* Ijima, 1927 (Fig. 5).

**Synonymy.** *Lonchiphora inversa* Ijima, 1927: 162.

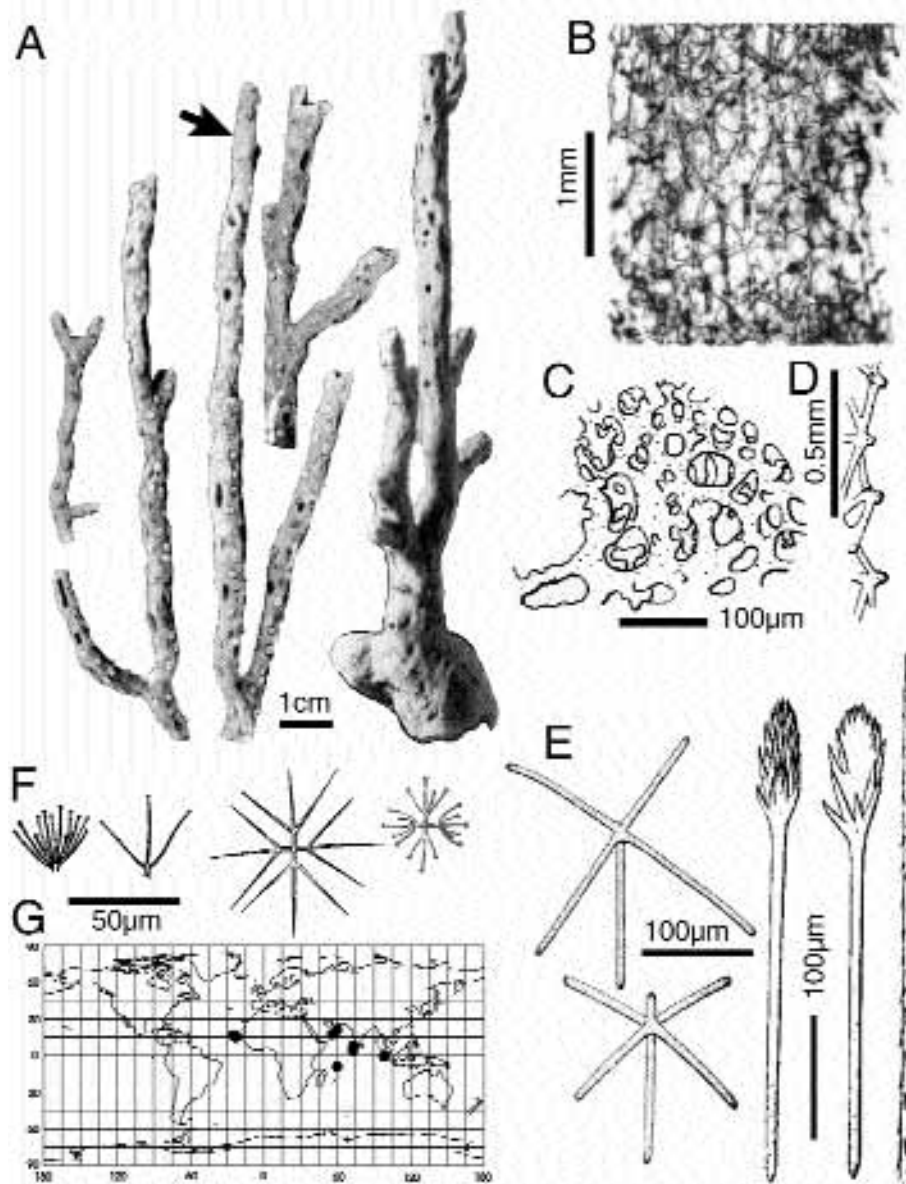
**Material examined.** None. Holotype presently unknown, probably at TIU – Sagami Bay, Japan.

**Description (from the literature).** The limited descriptive information derives from Ijima’s (1927: 162) confusing comparison with a ‘Siboga’ fragment: a more-or-less horizontally expanded and undulating plate with tubular outgrowths, with atrial surface on



**Fig. 5.** *Lonchiphora* distribution.

the outside and dermal surface on the inside. Atrial sceptrules are lonchioles (a monactin with a single apical spine, authentic figures unavailable, see Fig. 1A5); dermal sceptrules are presumably only anchorate clavules; form of dermalia, atrialia and microscleres unknown.



**Fig. 6.** *Sarostegia oculata*. A, part of the type series from Cape Verde Is. including 4 fragments collected alive (left, arrow indicates lectotype) and a macerated skeleton with base (right) (from Topsent, 1928c, pl. 1, figs 11–12). B, dermal view of the dictyonal framework. C, fragment of the basal plate lattice. D, profile view of external dictyonal frame with short, blunt spurs. E, megascleres: atrial pentactin, dermal hexactin, two sarules and part of an uncinata. F, microscleres: oxyhexaster and discohexaster with variety of secondary tufts. G, distribution of *Sarostegia*. (B–F from Topsent, 1928c, pl. 4, fig. 5.)

**Remarks.** Ijima (1927:130) introduced *Lonchiphora* in his key of the Recent Farreidae. He noted later (1927: 162), in comments on a fragmentary, macerated ‘*Siboga*’ specimen, that he would soon publish a complete description of the new genus, a task he never completed. He did, however, produce a verbal description of the distinctive scepterule, the ‘lonchirole’ (1927: 124), and described a few morphological features of the only species, *L. inversa*. Although the type species has thus never been formally described or figured in publication, Ijima’s brief characterization has been accepted as a sufficient indication by de Laubenfels (1936a) and Reid (1958a,b, 1963b) to accord the taxon recognition. The genus *Lonchiphora* is here recognized as a valid, but poorly known, member of the Farreidae. In the absence of an authentic figure of a lonchirole, the single distinctive character of the genus, Reid (1958a: xxxi, fig. 21d) created a representation of it from

Ijima’s description. The genus is known only from Sagami Bay, Japan (depth unknown).

**SAROSTEGIA TOPSENT, 1904**

**Restricted Synonymy**

*Sarostegia* Topsent, 1904d:4; Topsent, 1904e: 378. *Ramella* Schulze, 1904: 38. Not *Sclerothamnopsis* Wilson, 1904: 84.

**Type species**

*Sarostegia oculata* Topsent, 1904d: 4 (by monotypy).



**Definition**

Tubular Farreidae with thick wall and narrow atrial channel; framework eurentoid; with only sarules as scepstrules.

**Diagnosis**

Monospecific genus (see type species description).

**Description of type species**

*Sarostegia oculata* Topsent, 1904 (Fig. 6).

**Synonymy.** *Sarostegia oculata* Topsent, 1904d: 4, figs 1–3; Topsent, 1904e: 378. *Ramella tubulosa* Schulze, 1904: 38, pl. 14, figs 7–10.

**Material examined.** Lectotype (here designated): MOM 13 0066 (in part, see Fig. 6A) – Cape Verde Islands, stn 1193. Paralectotypes: MOM 13 0066 (in part, several fragments) – same location. MOM 13 0062 – Cape Verde Is, stn 1144. Other material. BMNH 1920.12.9.65 – Saya de Malha Group, Indian Ocean. BMNH 1936.3.4.5 – Maldives, Indian Ocean.

**Description.** Body tubular, arborescent, more-or-less dichotomously branching, rarely anastomosing, mostly uniplanar, to 21 cm tall, attached to hard substrate by a basal plate; very brittle; branches cylindrical to subcylindrical, 2–10 mm diam. tapering gradually from the thickest parts basally; axial atrial cavity 2–5 mm diam. extends as lumen through most of body, occasionally occluded by wall ingrowth; walls 1/2–2 mm thick perforated by slit-like, elongate parietal oscula 2–6 mm long at intervals of 6–15 mm along sides of branches in the plane of growth; color alive yellow-rose; very pale brown when preserved in alcohol or formalin; surface of living specimens occupied by colonies of the orange, symbiotic zoanthid, *Thoracactis topsenti* Gravier; dictyonal framework of hexactins, dense-meshed, irregular with mixed triangular and quadrangular meshes; without longitudinal strands evident; mesh sides 100–280  $\mu\text{m}$ ; beams with granular surfaces, 12–33–50  $\mu\text{m}$  diam.; nodes polyradial, solid, not swollen; peripheral spurs short, blunt, bearing few small tubercles; basal plate as thin perforate siliceous film; small spiny hexactins commonly affixed to beams; flat facets or shallow pits on outer skeletal surface underlie zoantharian zooids; dermal and atrial megascleres are entirely microspined (rough), bear rounded or knob-tipped rays, arrayed in quadrangular lattice; dermal

hexactins with very short distal ray; atrial pentactin equal-rayed, tangential rays of both 100–250  $\times$  10–18  $\mu\text{m}$ ; proximal ray of dermalia to 325  $\mu\text{m}$ ; sarules with extended, bushy head and robust stem mainly perpendicular to dermal surface, rarely atrial, length 365–430  $\mu\text{m}$ , head length 120  $\mu\text{m}$ , axial cross at base of head with only proximal axis extended (a monactin); uncinates oriented parallel to branch and permeate framework, 630–1000  $\times$  4–7  $\mu\text{m}$ ; oxyhexasters 70–75  $\mu\text{m}$  diam. with short primary rays and 3–2 secondary rays; discohexasters 35–55  $\mu\text{m}$  diam. with 3–6–12 secondary rays.

**Remarks.** The genus erected by Topsent (1904d) remains monospecific. Ijima (1927) considered this genus to be related to *Claviscopulia* because of the presence of sarules as scepstrules and lack of scopules in both. It was thus indirectly linked to *Farrea* and placed within the Clavularia. Topsent (1928c) was not swayed by the similarity of sarule form, but placed *Sarostegia* in the Eurentidae on the basis of its eurentid-like dictyonal framework. Reid (1958b, 1963b) argued that *Sarostegia* could not remain within the Clavularia because of the non-farreid but eurentid form of its dictyonal framework, the absence of clavules, and the lack of correspondence of the sarules of *Sarostegia* (monactins) with those of *Claviscopulia* (diactins) as claimed by Ijima (1927) from his inspection of the axial filament system in *Sarostegia* and reliance on Schulze's (1899) figure of the sarule of *Claviscopulia*. Reid (1958b) suggested placement in the family Eurentidae, subfamily Eurentinae, but left them unplaced as to family in his later arrangements (Reid, 1963b; 1964). Reinspection of the axial crosses of the two sarule types and the form of the immature stages of *Sarostegia* sarules contradict Ijima's claim of difference and Reid's acceptance of that claim. The distal ray of the axial system is equally undeveloped in both spicules, hence both sarules are monactins. The early stages of sarule formation in *S. oculata* exhibit minimal extension of the distal cap, a feature formed during maturation. Thus, one of Reid's important arguments – the lack of homology of the two sarule types – is not accepted. The genus is retained within the family Farreidae pending more convincing arguments for its removal. Dendy's (1916b) claim that atrialia (gastralia) are hexactins in the 'Sealark' samples was not substantiated by inspection of 'Sealark' and 'Mabahiss' specimens. Synonymy of *Sclerothamnopsis* Wilson suggested by Dendy (1916b) has been consistently rejected (Ijima, 1927; Topsent, 1928c) without convincing argument. The genus is known from the Atlantic and Indian Oceans, Cape Verde Is. to Indonesia, 256–1829 m.