

## Family Agelasidae Verrill, 1907

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Agelasidae Verrill (Demospongiae, Agelasida) (*nomen conservandum pro* Chalinopsididae and Ectyonidae) is a monotypical family with a characteristic skeleton of spongin fibres cored and echinated by verticillate styles, occasionally oxeas. The spongin fibres are unique and morphologically quite distinct among the fibres of Demospongiae, showing arched columns and transverse bundles of collagen instead of the usual arrangement of collagen bundles aligned with the axis of the fibres. The spicules are uniquely shared with sclerosponges of the family Astroscleridae, and together the two families comprise the order Agelasida. In *Agelas* 34 nominal species have been described predominantly from the tropical Atlantic and Indo-West Pacific, with a single Mediterranean and a single South Australian species.

**Keywords:** Porifera; Demospongiae; Agelasida; Agelasidae; *Agelas*.

### DEFINITION, DIAGNOSIS, SCOPE

#### Synonymy

Chalinopsididae Schmidt, 1870: 59. Ectyonida Carter, 1875c: 133. Agelasidae Verrill, 1907: 333.

#### Definition

Agelasida with reticulation of spongin fibres, made up of transversely arranged collagen bundles; fibres cored and echinated by verticillate styles, occasionally including verticillate oxeas (Fig. 1).

#### Diagnosis

Growth form is variable, ramose, lamellate, tubular or massive. The colour is frequently orange or reddish brown and texture extremely tough but compressible. The skeleton is reticulate, very fibrous, with a well-developed system of profusely echinated spongin fibres, of which the main or ascending fibres usually contain coring spicules. The fibres are peculiar and unique in having arched transversely arranged collagen bundles. Spicules are styles with unique verticillated spines. In some species coring spicules differ geometrically from those echinating. Oxeas or strongyles may also occur along with the styles in some species. The homogeneity of skeletal characteristics makes the external growth form of great importance and utility in identification.

#### Scope

Of six nominal genera only a single valid genus is recognized, *Agelas* Duchassaing & Michelotti, 1864.

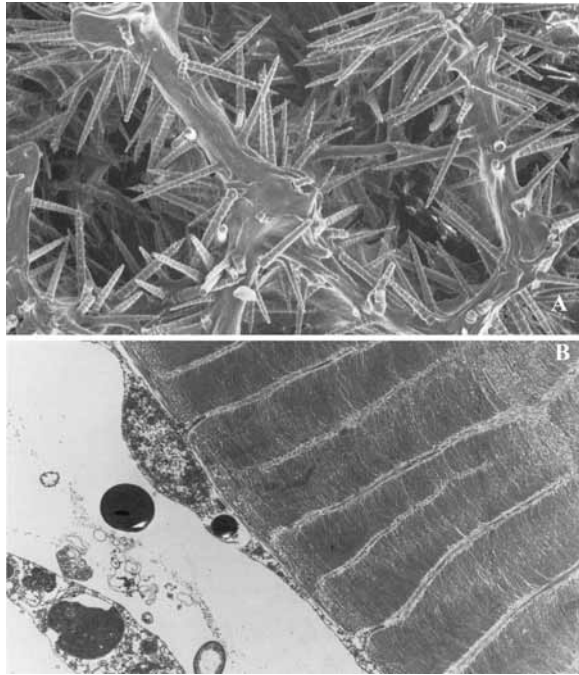
#### Remarks on synonymy

ICZN Code Article 40.2 (Anon., 1999) has to be invoked in order to be able to continue the use of the well-established family name Agelasidae Verrill, 1907: 333. The name Agelasidae was rather casually introduced by Verrill in a list of families. It is a clear junior synonym of two previously proposed names, Ectyonidae Carter

(1875c: 133, as Ectyonida) and Chalinopsididae Schmidt (1870: 59, as Chalinopsidinae). The latter name has been used subsequently only by Schmidt himself (in 1880b: 80) and by Fristedt (1885: 44; 1887: 458). Vosmaer (1887: 222) discussed the name Chalinopsididae but did not adopt it. Article 23.9.1.2 of the ICZN (Anon., 1999) clearly states the conditions under which senior unused names may be suppressed in favour of junior names in general use. The junior name must have been used at least 25 times by different authors in the past 50 years, while the senior name must not have been used since at least 1899. The latter rule precludes suppression of Ectyonidae in favour of Agelasidae since Ectyonidae was in general use before 1925. Ectyonidae may be conserved as a generally used junior synonym by suppression of the unused Chalinopsididae Schmidt, 1870 (not used after 1899, whereas Ectyonidae was used by at least 20 authors in at least 40 publications (albeit a non-exhaustive count) between 1882 and 1925). Since Chalinopsididae can be suppressed, but Ectyonidae cannot, we have to conserve the name Agelasidae under ICZN article 40.2. *Agelas* was discovered to be a senior synonym of *Ectyon* so Verrill (1907) replaced Ectyonidae by Agelasidae, and since this happened well-before 1961, and the name Agelasidae is the prevailing name, the conditions for article 40.2 are satisfied.

#### Taxonomic history

Until quite recently, Agelasidae (partly as Ectyonidae) was considered a member of Poecilosclerida (or equivalent earlier higher taxa) by most authors, and in the older literature it was simply defined to contain Poecilosclerida with echinating spicules. Fristedt (1885, 1887) assigned axinellid-type sponges to Chalinopsidinae, but presumably this was done in ignorance of the true nature of *Chalinopsis* and Schmidt's use of the family. Verrill's (1907) decision to erect Agelasidae as a replacement name for Ectyonidae was done without clarification and too casually to have any impact on the established use of Ectyonidae by mainstream taxonomists of the time. Topsent (1928) subdivided the former widely defined Ectyoninae into a number of families including Microcionidae (as Clathriinae), Myxillinae, Hymedesmiinae, etc., and was the first to restrict Ectyonidae to *Ectyon* (at the same time casting doubt over the synonymy with *Agelas*) and *Ectyonopsis* Carter (1883b: 315). The latter genus is not a member of Agelasidae as the spines of its spicules are not arranged in verticils, it is here considered a member



**Fig. 1.** Agelasidae characters. A, SEM photo of skeleton showing coring and echinating verticillate styles ( $\times 160$ ). B, TEM photo of spongin fibre showing transversely arranged collagen bundles ( $\times 7520$ ) (photos reproduced from De Vos *et al.*, 1992).

of Poecilosclerida: Myxillidae. Burton & Rao (1932: 355) subsequently established the synonymy of *Ectyon* with *Agelas*, and this was followed by most contemporary authors. The affinities of *Agelas* were left undecided by Burton & Rao (1932). De Laubenfels (1936a: 73) assigned *Agelas* to Verrill's Agelasidae, in turn assigned to his large assemblage of 'Phorbasiformes', and included *Acanthostylotella* (now Poecilosclerida: Raspailiidae), *Scopalina* (now Halichondrida: Dictyonellidae) and *Ophistospongia* Gray, 1867a (now Poecilosclerida: Microcionidae) in the family. The definition provided by de Laubenfels (1936a) was erroneous: he emphasized the echinating spicules and stated that coring spicules were absent. Lévi (1973) simply repeated this definition. Bergquist (1978: 168), on the basis of chemical and reproductive data, concluded that Agelasidae (stripped to a single genus *Agelas*) belonged in the order Axinellida. On similar grounds, Hartman (1980a: 29) subsequently erected a separate order Agelasida for *Agelas*.

### Biology

*Agelas* species are usually large, bright-coloured, conspicuous inhabitants of shallow-water reefs and other clear-water environments. Greatest recorded depth is 150 m (Van Soest & Stentoft, 1988). Where known, sexual reproduction is oviparous. *Agelas* species have unique secondary metabolites (bromopyrroles), which belong to a wider distributed group of molecules named pyrrole-2-carboxylic derivatives (Van Soest & Braekman, 1999).

### AGELAS DUCHASSAING & MICHELOTTI, 1864

#### Synonymy

*Agelas* Duchassaing & Michelotti, 1864: 76. *Ectyon* Gray, 1867a: 515. *Oroida* Gray, 1867a: 520. *Chalinopsis* Schmidt,

1870: 59. *Pachychalinopsis* Schmidt, 1880b: 80. *Siphonochalinopsis* Schmidt, 1880b: 80.

#### Type species

*Agelas dispar* Duchassaing & Michelotti, 1864: 76 (by subsequent designation; Burton & Rao, 1932: 355).

#### Definition

Agelasidae with skeleton of spongin fibres cored and echinated by verticillate megascleres.

#### Diagnosis

Massive-lobate, encrusting, tubular, branching or flabellate sponges, often of considerable size, with smooth surface provided with small rounded and/or key-hole shaped apertures. Colour usually orange or brownish orange. Consistency toughly compressible, firm. No ectosomal specialization. Choanosomal skeleton is an isotropic or anisotropic, occasionally irregular, system of spongin fibres. The main fibres are distinguishable by a core of megascleres, both main and interconnecting fibres are profusely echinated by megascleres. Spicules verticillate styles or oxeas. 34 nominal species distributed over most tropical waters; a single species occurs in the Mediterranean. The genus has not been recorded from the tropical East Pacific and tropical West Africa.

#### Previous reviews

Wiedenmayer (1977b), Assmann *et al.* (2001).

#### Description of type species

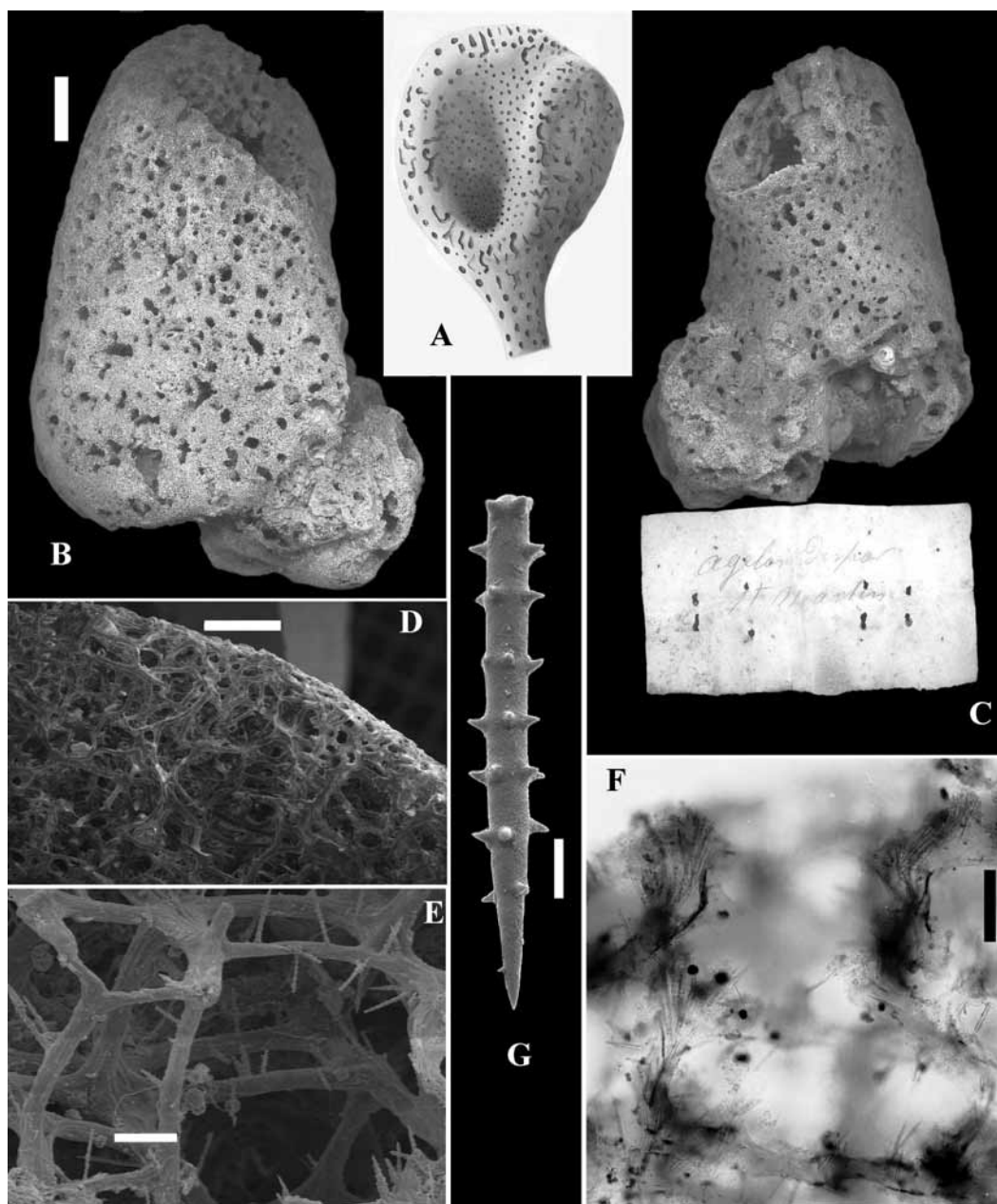
*Agelas dispar* Duchassaing & Michelotti, 1864 (Fig. 2A–F).

**Synonymy.** *Agelas dispar* Duchassaing & Michelotti, 1864: 76, pl. XV fig. 1.

**Material examined.** Holotype: ZMA POR. 607 – original label 'Agelas Dispar/St. Martin' (cf. Fig. 2C).

**Description.** The holotype (only extant type) is an erect lobe of 9 cm high and 5 cm in diameter, with an apical depression of 2.5 cm in diameter (Fig. 2B–C). The colour according to Duchassaing & Michelotti's description and plate, is pale orange-brown. The dry holotype is greyish brown. Surface smooth, with scattered small rounded and keyhole-shaped apertures. Larger rounded openings are concentrated in the apical depression. Interior strongly cavernous-clathrate. Skeleton a tight-meshed reticulation of spongin fibres (Fig. 2D). Main fibres of 70–110  $\mu\text{m}$  in thickness, cored by 0–8 spicules, lie at distances of 180–350  $\mu\text{m}$ . Interconnecting fibre of 20–70  $\mu\text{m}$  in thickness are uncored and are 200–350  $\mu\text{m}$  apart (Fig. 2F). Both main and interconnecting fibres are echinated by 1–4 spicules over 500  $\mu\text{m}$  fibre length (Fig. 2E). Spicules verticillate styles 70–150  $\times$  2.5–7.5  $\mu\text{m}$  with 7–12 whorls of spines (Fig. 2G). Distribution and ecology. West Indian region, shallow-water reefs.

**Remarks.** The holotype is the only specimen that can be attributed with certainty to this species, most other records need verification in view of the confusion over the extent to which the shape and colour of the species is variable. Duchassaing & Michelotti's water colour of this species, though crude, is obviously not a representation of the holotype (here reproduced as Fig. 2A), so we must assume some of the type material has become lost.

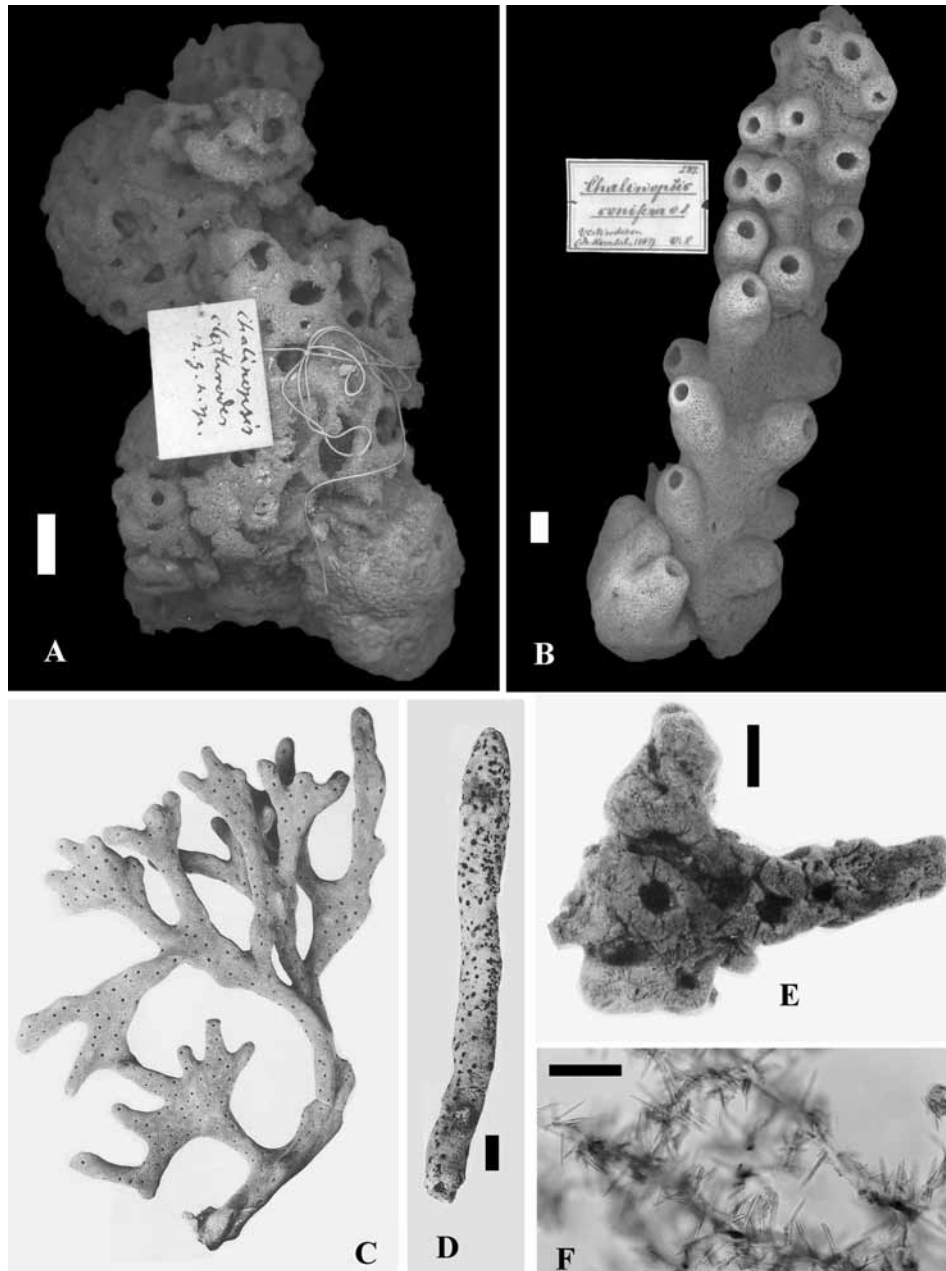


**Fig. 2.** *Agelas dispar*. A, Duchassaing & Michelotti's plate XV fig. 1. B–C, holotype ZMA Por. 607 photographed from two sides (scale 1 cm). D–E, SEM images of skeleton of holotype (scales: D, 500  $\mu\text{m}$ ; E, 100  $\mu\text{m}$ ). F, photomicrograph of skeleton of holotype showing coring of ascending fibres (scale 100  $\mu\text{m}$ ). G, verticillate style of holotype (scale 10  $\mu\text{m}$ ).

The genus *Ectyon* Gray, 1867a: 515 was erected for the Caribbean *Ectyon sparsus* Gray, 1867a: 515 (by subsequent designation; de Laubenfels, 1936a: 74). The type specimen (BMNH 1845.5.12.123) was re-examined, consisting of two halves of an extensive specimen of approximately 15 $\times$ 12 $\times$ 4 cm each. The skeleton is tight-meshed, anisotropic at the surface with main fibres of 50–90  $\mu\text{m}$  thickness cored by 2–3 spicules and secondary fibres of 30–50  $\mu\text{m}$  thickness uncored. The fibre system gradually becomes isotropic in the interior, with little distinction of primary and secondary fibres. Rounded meshes measure 150–300  $\mu\text{m}$ , echination of fibres is sparse with 0–5 spicules over a distance of 500  $\mu\text{m}$ . Verticillate styles 120–180  $\times$  7–11  $\mu\text{m}$ , with 11–13 whorls of spines. This material has been described and figured by Carter (1871c: 270, pl. XVII figs 1–3). Wiedenmayer

(1977b) considered *E. sparsus* a junior synonym of *Agelas dispar*, but it could also quite possibly be a specimen of *Agelas dilatata* Duchassaing & Michelotti (1864: 77, pl. II fig. F, pl. XIV fig. 1), the original material of which is lost. A recent record (Assmann *et al.*, 2001) of *A. dilatata* confirmed the specific distinctness of this species. In any case, *Ectyon* is a clear junior synonym of *Agelas* as it shares with *Agelas dispar* the possession of verticillate styles coring and echinating a skeleton of spongin fibres.

The genus *Oroidea* Gray, 1867a: 520 was erected for type species (by monotypy) *Oroidea adriatica* Gray, 1867a: 520. The definition provided by Gray leaves no doubt that he was referring to the species now known as *Agelas oroides* (Schmidt, 1864: 35, pl. IV figs 1–2, as *Clathria*). *Clathria oroides* (holotype LMJG 15957, here reproduced in Fig. 3E, copied from



**Fig. 3.** *Agelas* type specimens. A, lectotype of *Chalinopsis clathrodes* Schmidt, 1870 from ZMUC (scale 1 cm). B, lectotype of *Chalinopsis conifera* Schmidt, 1870 from ZMUC (scale 100  $\mu\text{m}$ ). C, lectotype of *Spongia arborescens* Lamarck, 1814 (reproduced from Topsent, 1932a). D, lectotype of *Alcyonium sceptrum* Lamarck, 1814 (reproduced from Topsent, 1933, scale 1 cm). E, lectotype of *Clathria oroides* Schmidt, 1864 (reproduced from Desqueyroux-Faúndez & Stone, 1992, scale 1 cm). F, photomicrograph of skeleton of a Jamaican specimen of *Agelas conifera* (ZMA Por 12778) to show coring and echination of spongin fibres (scale 250  $\mu\text{m}$ ).

Desqueyroux-Faúndez & Stone (1992); there is also a slide in BMNH 1868.3.2.22, from Algiers) shares the possession of verticillate styles coring and echinating a skeleton of spongin fibres with *Agelas dispar*. It is a lobate sponge with irregular surface. The interior is densely organic with very few larger canals or cavities. The skeleton is an irregular reticulation of spongin fibres, without a clear distinction between primary ascending and secondary interconnecting fibres, all fibres being 30–70  $\mu\text{m}$  in diameter. Some are cored by 1–5 spicules, so presumably are primary fibres. Echination prominent and uniformly 3–4 spicules over 500  $\mu\text{m}$  fibre length. Meshes

60–700  $\mu\text{m}$ . Verticillate styles 93–163  $\times$  5–10  $\mu\text{m}$ , with 10–14 whorls of spines.

The genus *Chalinopsis* Schmidt, 1870: 59 was erected for *Chalinopsis cervicornis* Schmidt (1870: 60, pl. V fig. 2a), subsequently designated type species by de Laubenfels 1936a: 7, and *C. clathrodes* Schmidt (1870: 60) and *C. conifera* Schmidt (1870: 60, pl. V fig. 2b). There is a junior homonym, *Chalinopsis* Lendenfeld, 1887c, which belongs to Callyspongiidae (Haplosclerida). The type material of Schmidt's type species appears to be lost (Desqueyroux-Faúndez & Stone, 1992), the figure of Schmidt is

a non-informative drawing of a spicule, and the description is too short to be certain of its identity in modern context. Schmidt's type is generally considered a junior synonym of *Spongia arborescens sensu* Lamarck, 1814 (not Pallas, 1766). Topsent (1932a: 104, pl. V fig. 2, as *Ectyon cervicornis*, here reproduced as Fig. 3C) redescribed Lamarck's type specimen. It has an antler-like growth form with flattened smooth branches which become plate-like forms lower down though fusion. Oscules are regularly distributed and flush. The overall resemblance with Schmidt's description of *C. cervicornis* is compelling. The verticillate styles are stated to be  $90\text{--}210 \times 4.5\text{--}9 \mu\text{m}$ , with 19–23 whorls of spines. Zea (1987: 215), quoting a personal communication from Dr Klaus Rützler, synonymized *Chalinopsis cervicornis* with *Alcyonium sceptrum* Lamarck (1814: 163). The type of this was redescribed by Topsent (1933: 33, pl. II fig. 5, as *Ectyon*, here reproduced as Fig. 3D). It is a single long branch of 25 cm long and 2.5 cm diameter. Oscules are numerous and flush with the surface. Thickest fibres are  $70 \mu\text{m}$ .

Verticillate styles  $120\text{--}164 \times 9\text{--}10 \mu\text{m}$ , with 11–13 whorls of spines. Topsent noted that the description of *Ectyon cylindricus* Carter, 1883b: 314 is very similar. Examination of Carter's type, BMNH 1884.5.26.6, confirmed this both macroscopically and microscopically. It appears likely that *Agelas sceptrum* (long single branches and low number of verticils) and *Agelas cervicornis* (ramose, flattened, with high number of verticils) are distinct species. Further proof that Schmidt's *Chalinopsis* is indeed a junior synonym of *Agelas* are the lectotype specimens (designation herein) of both *Chalinopsis clathrodes* and *C. conifera*, which are still extant in ZMUC, and both contain the typical features of *Agelas*. They are here illustrated in Fig. 3A (*C. clathrodes*) and Fig. 3B (*C. conifera*). A representative photomicrograph taken from the skeleton of a recent specimen of *Agelas conifera* is shown in Fig. 3F.

The genera *Pachychalinopsis* Schmidt, 1880b: 80 and *Siphonochalinopsis* Schmidt, 1880b: 80 were erected without naming any species and thus are *nomina nuda*.