Systema Porifera: A Guide to the Classification of Sponges, Edited by John N.A. Hooper and Rob W.M. Van Soest

Family Crellidae Dendy, 1922

Rob W.M. Van Soest

Zoological Museum, University of Amsterdam, P.O. Box 94766, 1090 GT Amsterdam, Netherlands. (soest@science.uva.nl)

Crellidae Dendy (Demospongiae, Poecilosclerida) are characterized by a tangential ectosomal crust made up of acanthostyles or acanthoxeas. Prior to the present revision, Crellidae were a substantial group with 22 nominal genera. However, structural diversity appeared to be low which is reflected in only five genera and four subgenera considered valid. The crellid choaonosomal skeleton is hymedesmioid or plumose, with choanosomal megascleres consisting of peripheral tornotes and basal acanthostyles. The latter may be absent. Echinating acanthostyles are present in several species. Microscleres are commonplace arcuate isochelae (one species excepted) and sigmas, either of which may be absent. The surface of most species features prominent areolated porefields, shared with the sisterfamily Hymedesmiidae.
Keywords: Porifera; Demospongiae; Poecilosclerida; Myxillina; Crellidae; *Anisocrella*; *Crella*; *Crella* (*Crella*); *Crella* (*Pytheas*); *Crella* (*Yvesia*); *Crella* (*Grayella*); *Crellastrina*; *Crellomima*; *Spirorhabdia*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Crelleae Dendy, 1922b: 92. Crellidae Hentschel, 1923: 406.

Definition

Myxillina with a tangential crust of spined ectosomal spicules (oxeas, anisoxeas or styles), and a choanosomal plumose skeleton of smooth tornotes. A basal skeleton of acanthostyles erect on the substrate may be present. Surface provided with areolated pore fields the walls of which are built by spicules arranged in parallel. Microscleres arcuate chelae, and occasionally sigmas (the latter so far recorded in only two species).

Diagnosis

Encrusting, massive, club-shaped and branching growth forms. Choanosomal skeleton regularly reticulate or plumo-reticulate, composed of bundles of smooth oxeas. Ectosomal skeleton with a thick crust of tangentially placed acanthostyles and/or acanthoxeas. Spicules also fortify the walls of elevated surface areolae. Acanthose spicules may also be embedded erect on basal spongin (=echinating basal acanthostyles), and dispersed within the choanosome between the tracts of smooth diactines. True echination of the tornote bundles has not been recorded so far. Microscleres consist of arcuate isochelae, occasionally anisochelate, and sigmas.

Scope

23 nominal genera of which five genera are considered valid, and four subgenera: *Anisocrella, Crella, Crella* (*Crella*), *Crella* (*Pytheas*), *Crella* (*Yvesia*), *Crella* (*Grayella*), *Crellastrina, Crellomima, Spirorhabdia*.

History and biology

The family was recognized as a formal unit for the first time by Dendy (1922b), and this was followed by most later authors on account of the easily recognized surface skeleton and early attempts (e.g., by Topsent, 1892a, 1904b, 1928c) to differentiate genera sharing this feature. Crellidae are concentrated in cold-temperate and deep-water habitats, but several species, e.g., *Crella cyathophora*, are also found in tropical reef habitats. Distribution is worldwide.

Taxonomic remarks

Acanthose megascleres. The major synapomorphy for the family is the ectosomal tangential crust of spined megascleres. These are usually acanthoxeas, but they may have one or both ends blunt and then resemble acanthostyles or acanthostrongyles. Through the frequently observed intermediate spicule forms such as tapering blunt endings, often somewhat inequiended acanthoxeas, etc., it is a safe assumption that these are all a single spicule type.

Genus proliferation. This is a small family with probably only a single well-established genus, the other four being peculiar single or pairs of species. In the past, all possible combinations of presence and absence of spicule types and forms have been used to erect genera. Many of these overlapped in characters and thus it is not likely that they are natural groups. Accordingly, these are merged and we are left with only a few genera with *Crella* as the major genus. In addition, it is proposed to recognize some subgeneric units in *Crella* to facilitate classification and recognition of the large number of species.

Family status. The family shares the surface areolae with Hymedesmiidae and it may be argued that the two ought to be recognized at the level of subfamilies of a larger family uniting the two. However, in view of the distinct surface skeletons, including differential skeletal structure of the areolae (supported by acanthose spicules in Crellidae, smooth spicules in Hymedesmiidae) the two may be readily told apart and any proposal to merge them would be premature without corroboratory evidence to do so.

Previous reviews

Hentschel, 1923, Topsent, 1928c, Lévi, 1973.

KEY TO GENERA

(1) Chelae include peculiar, reduced anisochelae next to normal isochelae ..... ***Anisocrella***
Only normal isochelae or chelae absent 2
(2) Surface skeleton made up of strongly spined aster- or spiraster-like spicules which are modified acanthoxeas 3
No astrose acanthoxeas 4
(3) Basal acanthostyles absent, stylote tornotes ..... ***Crellastrina***
Basal acanthostyles present, oxeote tornotes ..... ***Spirorhabdia***
(4) Chelae normally arcuate with rounded alae or chelae absent ..... ***Crella***
Chelae polydentate-anchorate (sharp-teethed) ..... ***Crellomima***

ANISOCRELLA TOPSENT, 1927

Synonymy

Anisocrella Topsent, 1927b: 11.

Type species

Anisocrella hymedesmina Topsent, 1927b: 11 (by monotypy).

Definition

Crellidae with hymedesmioid architecture; next to normal isochelae there are peculiar reduced anisochelae.

Diagnosis

Encrusting growth form; ectosomal skeleton composed of tangential layer of acanthoxeas; choanosomal skeleton composed of smooth diactinal spicules in bundles and an erect basal layer of acanthostyles; microscleres are arcuate isochelae and reduced anisochelae.

Previous review

Boury-Esnault *et al*. (1994b).

Description of type species

Anisocrella hymedesmina Topsent, 1927b (Fig. 1A).

Synonymy. *Anisocrella hymedesmina* Topsent, 1927b: 11; Topsent, 1928c: 234, pl. VIII fig. 5; Vacelet, 1969: 198, fig. 35; Boury-Esnault *et al*., 1994b: 116, fig. 88.

Material examined. Holotype (not seen): MOM. Schizotypes: MNHN DT 1172 – 3 slides (two sections, one spicule mount) made from the holotype, labeled "St. 1349, 1902". Other material. MNHN DT 1173 – 1 slide from stn. 1420.

Description (mostly based on Topsent, 1928c). Thin smooth crusts on deep water corals, 2–3 cm^2 (Vacelet, 1969). Boury-Esnault *et al*., 1994b report areolated porefields. Greyish in alcohol (Topsent, 1928c; Vacelet, 1969), maroon in alcohol (Boury-Esnault *et al*., 1994b). Skeleton. Hymedesmioid, with acanthostyles erect on the substrate; bundles of tornotes connect the basal skeleton with the surface and carry the tangential skeleton of acanthoxeas. Spicules (Fig. 1A). Ectosomal acanthoxeas, robust, curved, heavily spined, 165–230 × 8–10 μm (Vacelet, 1969 gives only 80–115 μm); tornotes smooth, faintly polytylote, inequiended, mucronate or rounded, 130–145 × 2 μm; acanthostyles in two size categories, both entirely spined, up to 200 × 27 μm and 50–70 μm (the latter are from Vacelet, 1969). Microscleres: arcuate isochelae, small but of the usual shape, 13–15 μm; reduced, often inequiended chelae called 'anisancres arquées', 15–17 μm. Distribution and ecology. Azores, Western Mediterranean, deep water, 500–2460 m depth.

Remarks. This is a monospecific genus, based primarily on the peculiar chelae setting it apart from mainstream *Crella*. If no further similar species will be found, it may be better to consider it a subgenus in the future. The spicule sizes quoted by Vacelet (1969) and Boury-Esnault *et al*. (1994b) differ somewhat from Topsent's specimen (acanthoxeas only up to 115 μm, tornotes up to 222 × 5 μm; anisancres up to 22 μm), but it is likely that this constitutes merely infraspecific variation. The drawings of the chelae of Boury-Esnault *et al*., 1994b remind more of palmate chelae than of arcuate chelae, but they call them 'arquées' nevertheless; also, although no acanthoxeas are drawn, these are mentioned in the description. The hymedesmioid condition of the skeleton in combination with the obvious Crellidae ectosome again demonstrates the likely polyphyletic nature of the hymedesmioid skeletal structure.

CRELLA GRAY, 1867

Synonymy

Crella Gray, 1867a. *Grayella* Carter, 1869b: 190. *Pytheas* Topsent, 1890b: 31. *Yvesia* Topsent, 1892a: 103. *Pseudoclathria* Dendy, 1897: 258. *Kowalevskyella* Swartschewsky, 1905: 40. *Crellina* Hentschel, 1914: 110. *Grella* de Laubenfels, 1936a: 64. *Tisrone* de Laubenfels, 1936a: 78. *Yvesiella* de Laubenfels, 1936a: 78. *Yvesiorbas* de Laubenfels, 1936a: 65. *Crellinspira* de Laubenfels, 1936a: 79. *Pytheilla* de Laubenfels, 1936a: 64. *Ramosichela* de Laubenfels, 1950b: 18. *Naniupi* de Laubenfels, 1950b: 19. *Crelloxea* Hechtel, 1983: 70.

Type species

Cribrella elegans Schmidt, 1862 (by original designation).

Definition

Crellidae with ectosomal acanthoxeas or acanthostyles, oxeote, strongylote or stylote tornotes; basal acanthostyles may be present; microscleres arcuate isochelae (may be absent).

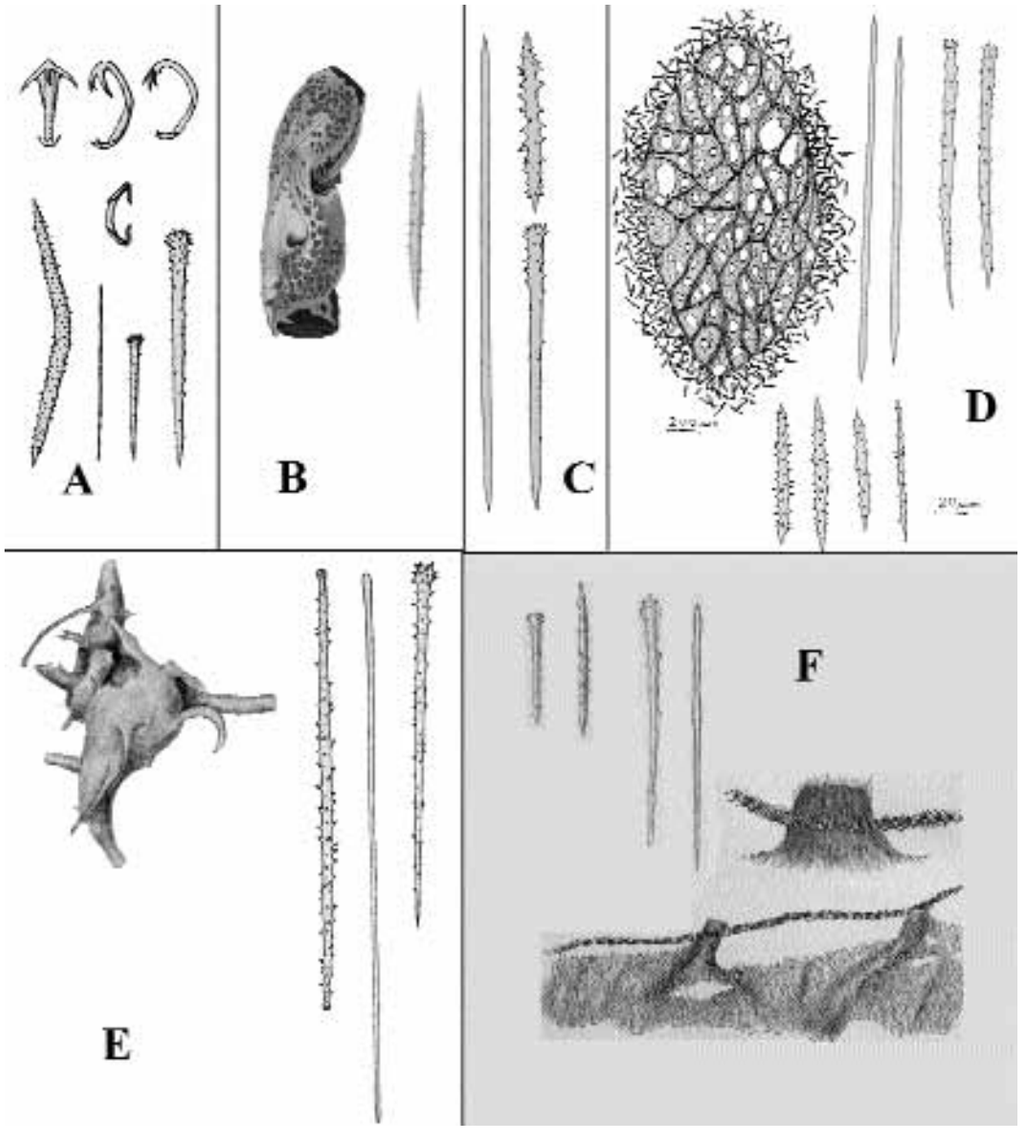

Fig. 1. A, *Anisocrella hymedesmina* Topsent, 1927b, drawing of spicules reproduced from Topsent (1928c, pl. VIII fig. 5) (sizes see text). B–D, *Crella (Crella) elegans* (Schmidt, 1862 as *Cribrella*). B, drawing of shape and acanthoxea reproduced from Schmidt (1862, pl. VII fig. 3) (scales see text). C, drawing of spicules copied from Topsent (1925c: fig. 20) (sizes see text). D, drawing of surface areola and spicules reproduced from Bibiloni, 1981, fig. 7. E, *Crella (Crella) tubifex* (Hentschel , 1914 as *Crellina*), drawing of shape and spicules reproduced from his pl. IV fig. 12, pl. VII fig. 14 (scales see text). F, *Crella (Crella) gracilis* (Swartschewsky, 1905 as *Kowalevskyella*) (=*Crella elegans*), drawing of peripheral skeleton and spicules, reproduced from Swartchewsky, 1905: pl. 7 fig. 2) (scales see text).

Diagnosis

Encrusting, lobate or pedunculate; ectosomal skeleton composed of a tangential layer of acanthoxeas or acanthostyles; choanosomal skeleton composed of smooth tornotes or strongyles arranged in tracts which may be echinated by acanthostyles, or in encrusting forms there may be an erect basal layer of acanthostyles; microscleres may include arcuate isochelae, sometimes absent, and occasionally sigmas. More than 50 species.

Previous review

Topsent (1928c).

Taxonomic remarks

The type species was originally described in the genus [*Cribrella*] Schmidt, 1862, but this is preoccupied by *Cribrella* Agassiz, 1835. [*Cribrella*] *sensu* Schmidt, 1862 is a senior preoccupied synonym of *Hamigera* (subsequent type species designation by Desqueyroux-Faúndez & Stone, 1992). A slight complication with the name *Crella* may arise from the fact that the only extant material labeled as *Cribrella elegans* in the LMJG collections is not that species (cf. below). Since there is no locality data with the LMJG specimens, and Schmidt's plate and drawing are reasonably obvious, it is almost certain that the LMJG material is not the original specimen from the Zara Canal. A neotype designation can solve this

problem. As indicated above, there are 15 generic names available covering the present concept of *Crella*. For reasons so far unclear this proliferation of genera, distinguished only on minor features as the shape of the tornotes and ectosomal acanthose megascleres, presence or absence of echinating acanthostyles and the presence or absence of chelae, exceeds the normal diversity of such artificial 'genera' distinguished in related Poecilosclerids. As usual, de Laubenfels takes care of more than half the number of synonyms. To add to the confusion, two type species of de Laubenfels's genera were attributed characters, which were not described by the original authors or were incorrectly described (genera *Pytheilla* and *Crellinspira*). Compared to other families, structural diversity of Crellidae is quite limited and the recognition of so many generic names for such trivial differences between individual species is unprecedented. For convenience sake, four of the generic names, *Crella*, *Grayella*, *Pytheas,* and *Yvesia* are here regarded as subgenera to facilitate identification of the large numbers of species. In a phylogenetic sense these subgenera are artificial, they do not comprise natural groups.

Key to subgenera of *Crella*

(1) Chelae present 2
No chelae 3
(2) Basal echinating acanthostyles ..... ***Crella** (Pytheas)*
Acanthostyles either absent, or of a single kind concentrated at the surface; no basal echinating acanthostyles ..... ***Crella** (Yvesia)*
(3) Basal acanthostyles echinating the substrate present ..... ***Crella** (Crella)*
No echinating acanthostyles ..... ***Crella** (Grayella)*

SUBGENUS *CRELLA* GRAY, 1867

Synonymy

Crella Gray, 1867a. *Kowalevskyella* Swartschewsky, 1905: 40. *Crellina* Hentschel, 1914: 110.

Type species

Cribrella elegans Schmidt, 1862 (by original designation).

Definition

No chelae; basal or echinating acanthostyles present.

Description of type species

Crella (Crella) elegans (Schmidt, 1862) (Fig. 1B–D).

Synonymy. *Cribrella elegans* Schmidt, 1862: 70, pl. VII fig. 3 (Schmidt's text gives fig.1 but this represents *Tethya*). *Kowalevskyella gracilis* Swartschewsky, 1905: 40, 53, pl. II fig. 7, pl. VII fig. 2.

Material examined. Holotype: No type material could be located. Neotype (designated herein): MNHN DCl 1190 – Bay of Naples (see Topsent, 1925c). Other material. ZMA POR 54, Banyuls, 10 m, coll. G. Kleeton, VIII-1962.

Description. (largely based on Topsent, 1925c) Encrusting, smooth, colour pink. Surface provided with numerous red-coloured areolae (Fig. 1B). Consistency firm. Skeleton. Ectosomal crust of densely intercrossing acanthoxeas to form a firm leathery crust; choanosomal skeleton consisting of thick bundles of tornotes; basal acanthostyles echinate the substrate (not mentioned by Schmidt). Spicules: ectosomal acanthoxeas, densely spined all over: 70–95 × 3–15 μm; smooth, faintly polytylote, oxeote tornotes, sharply pointed, 210–250 × 3–5 μm; acanthostyles in a single category: 110–150 × 5–10 μm. Distribution and ecology: Mediterranean, NW Spain; shallow-water.

Remarks. The alleged type material in the Graz Museum, LMJG 15526 (no locality data) was reexamined and discovered to be a specimen of *Phorbas ficititius*. Prof. Lévi (*in litteris*) confirms that the Schmidt material in the Strasbourg Museum labeled as *Cribrella elegans* likewise concerns *Phorbas fictitius*. This cannot be the original material, since Schmidt's drawing of the original specimen clearly depicts an acanthoxea, which are absent in the Graz and Strasbourg Museum specimens. A neotype should be assigned to create stability in this group with so many generic names. Prof. Lévi (*in litteris*) proposed to designate as the neotype specimen the material described by Topsent (1925c) from the Bay of Naples, now housed in the Strasbourg Museum, with slides and a fragment in MNHN registered as MNHN DCl 1190. This collective material is here designated as the neotype.

Swartschewsky (1905: 40) erected the genus *Kowalevskyella* for type species (by monotypy) *Kowalevskyella gracilis* Swartschewsky, 1905: 40, pl. II fig. 7, pl. VII fig. 2 (the latter figure is here reproduced as Fig. 1F). This specimen has all the characters of *Crella elegans*, including red colour, surface areolae, lack of microscleres, and possession of oxeote tornotes, acanthoxeas and acanthostyles in the appropriate size. It is proposed here to synonymize *gracilis* with *elegans*, and thus *Kowalevskyella* becomes an objective synonym of *Crella (Crella)*.

Hentschel (1914: 110) expressly erected a genus *Crellina* for its possession of echinating acanthostyles in combination with the lack of chelae, because Schmidt's original description did not mention the acanthostyles. *Crellina* with type species (by monotypy) *C. tubifex* Hentschel (1914: 110, pl. IV fig. 12, pl. VII fig. 14) clearly falls under the definition of *Crella (Crella)*, although its type species (Fig. 1E) appears only distantly related to *C. elegans*. The type (not re-examined) is described as massive, with elongated tubes, which are possibly homologous to the surface areolae of other species. The ectosomal crust is formed by acanthostrongyles of 440–560 × 12.5–15 μm, the choanosomal skeleton consists of ill-defined bundles of tornotes of 472–650 × 7–8 μm and the acanthostyles are erect on the substrate, 176–392 × 10–11 μm. It should be noted that the material identified as *Crellina tubifex* by Burton, BMNH 1928.11.15.225 was found to belong to *Acanthorhabdus fragilis* (family Acarnidae).

SUBGENUS *GRAYELLA* CARTER, 1869

Synonymy

Grayella Carter, 1869b: 190. *Pseudoclathria* Dendy, 1897: 258. *Grella* de Laubenfels, 1936a: 64. *Yvesiorbas* de Laubenfels, 1936a: 65. *Crelloxea* Hechtel, 1989: 70.

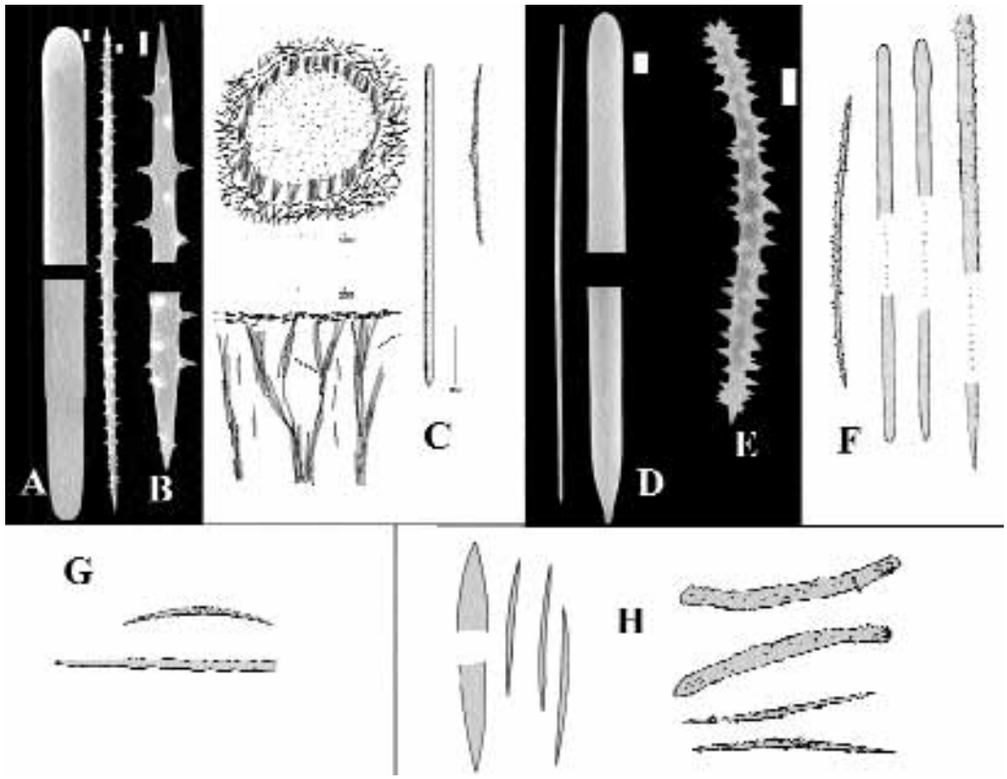

Fig. 2. *Crella (Grayella)* species. A–C, *Crella (Grayella) cyathophora* (Carter, 1881 as *Grayella*). A–B, SEM photos of spicules made from the holotype (scale 1 μm). C, drawing of skeleton and spicules made from a slide of the holotype. D–E, *Crella (Grayella) compressa* (Carter, 1886c as *Halichondria*), type of *Pseudoclathria*, SEM photos of spicules made from the holotype (scale 1 μm). F, *Crella (Grayella) pulvinar* (Schmidt, 1868 as *Myxilla*), type of *Yvesiorbas*, drawing of spicules copied from Topsent (1925c: fig. 22 as *Crella mollior*) (sizes see text). G, *Crella (Grayella) carnosa* (Topsent, 1904b, as *Yvesia*), drawing of spicules reproduced from his pl. XV fig. 19 (sizes see text). H, *Crella (Grayella) spinosa* (Hechtel, 1983 as *Crelloxea*), drawing of spicules reproduced from his fig. 11 (sizes see text).

Type species

Grayella cyathophora Carter, 1869b: 190 (by monotypy).

Definition

No chelae, no basal or echinating acanthostyles.

Description of type species

Crella (Grayella) cyathophora (Carter, 1869b) (Fig. 2A–C).

Synonymy. *Grayella cyathophora* Carter, 1869b: 190, pl. VII figs 1–10; *Yvesia cyathophora*; Topsent, 1892a: 103; *Crella cyathophora*; Dendy, 1922b: 95

Material examined. Holotype (slide): BMNH 1869.6.25.48 – Gulf of Suez.

Description. Massively encrusting on rocks; type specimen 3.5 cm across, 1.25 cm thick. Surface smooth with numerous subcircular, elevated areolae. Oscules likewise elevated. The type slide contained a surface peel with three areolae and cross sections. The areolae are 1500–1800 μm in diameter are slightly raised above the surface and their walls are supported by perpendicular bundles of 4–5 tornotes. Skeleton (Fig. 2C). The surface between the areolae has a tangential crust of intercrossing acanthoxeas. The choanosomal skeleton consists of dendritic tracts of tornotes, 20–70 μm in diameter (containing 6–20 spicules). Spicules (Fig. 2A–B). Ectosomal acanthoxeas, thin, finely spined, frequently faintly centrotylote, 96–(104.5)–117 × 2–(2.6)–3 μm; choanosomal tornotes are strongyles, occasionally stylote, 279–(291.8)–306 × 2.5–(3.8)–5 μm. Distribution and ecology: Red Sea; common in the Indian Ocean; shallow-water reefs.

Remarks. The species differs from *Crella elegans* in lacking basal acanthostyles, a common enough phenomenon, not worthy of generic distinction. Topsent (1892a: 103) declared *Grayella cyathophora* a member of his genus *Yvesia* without acknowledging the fact that *Grayella* preceded *Yvesia* by 23 years. Later (1928c), he recognized *Grayella* as separate from a restricted *Yvesia*.

The genus *Pseudoclathria* Dendy (1897: 258) was erected (by original designation) for type species *Halichondria compressa* Carter (1886c: 450), redescribed by Dendy (1897) on the basis of Carter's holotype (BMNH 1886.12.15.9) and additional specimens. A further specimen BMNH 1886.12.15.392 also labeled as "*Halichondria compressa*" belongs to *Hymeniacidon*. Carter's type is an elaborate flabelliform sponge, with a broad margin bearing oscules. The surface skeleton is a crust of intercrossing acanthostyles (Fig. 2B), 108–122 × 7–9 μm, which are also scattered in the interior. The choanosomal skeleton is a system of long, infrequently branching spongin fibres with a core of thin, straight, subtylostylote tornotes (Fig. 2D), 195–225 × 4–5 μm, surrounded by a bark of acanthostyles similar to the ectosomal acanthostyles

(Fig. 2E). No echinating acanthostyles. By its elaborate shape, and by the intrusion of acanthostyles into the choanosomal bundles of tornotes, the species is an unusual *Crella (Grayella)*, but its characters fall within the definition of the subgenus.

The genus *Grella* was erected by de Laubenfels (1936a: 64) for the type species (original designation) *Yvesia carnosa* Topsent (1904b: 198). This is a thickly encrusting Azoran deep water sponge (100–1250 m) with a smooth dark coloured surface and a greyish interior. A spicule slide made of the Monaco Museum holotype was examined in MNHN, labeled D.T. 1031, '68 P.A., 1895'. The slide contains fusiform ectosomal acanthoxeas (Fig. 2G): 160–180 × 5–6 μm and smooth polytylote choanosomal anisotornotes (Fig. 2G) with mucronate apices: 600 × 10 μm. The choanosomal skeleton is described by Topsent as consisting of straight parallel tracts of tornotes up to 100 μm in diameter carrying a surface crusts of acanthoxeas; these are also scattered singly between the choanosomal tracts. Later (1928c), Topsent assigned specimens with echinating acanthostyles to this species, and this would cause it to be transferred to *Crella*.

The genus *Yvesiorbas* de Laubenfels (1936a: 65) was erected for type species (original designation) *Myxilla pulvinar* Schmidt (1868: 14, pl. II fig. 14) from Algiers, redescribed by Topsent (1939). Type slide BMNH 1868.3.2.63, from Algiers, was examined. It is a thinly encrusting crellid, with acanthoxeas of 50–80 × 1.5 μm (Pulitzer-Finali, 1978), and strongylote tornotes of 290–410 × 2–4 μm (isochelae recorded by Schmidt are foreign) (Fig. 2F). This conforms to *Grayella*; however, Schmidt's type slide contained rare acanthostyles, so some uncertainty is apparent.

The genus *Crelloxea* Hechtel, 1983 was erected for type species (by monotypy) *C. spinosa* Hechtel (1983: 70) from Brazil. This is a thinly encrusting sponge with surface crust of acanthoxeas (Fig. 2H) and acanthostrongyles, 80–140 × 2–9 μm, and choanosomal oxea-shaped tornotes (Fig. 2E), 295–407 × 10–24 μm, arranged in uni- to paucispicular tracts. The unusual feature of the sponge is the fusiform oxea-shape of the tornotes.

SUBGENUS *PYTHEAS* TOPSENT, 1890

Synonymy

Pytheas Topsent, 1890b: 31. *Crellinspira* de Laubenfels, 1936a: 79. *Ramosichela* de Laubenfels, 1936a: 18. *Naniupi* de Laubenfels, 1950b: 19.

Type species

Pytheas ater Topsent, 1890b (by monotypy).

Definition

Crella with isochelae; basal or echinating acanthostyles present.

Description of type species

Crella (Pytheas) atra(Topsent, 1890b) (Fig. 3A).

Synonymy. *Pytheas ater* Topsent, 1890b: 31; Topsent, 1892a: 110, pl. I fig. 1, pl. XI fig. 1.

Material examined. Holotype: MOM (not seen). Schizotype: MNHN DT. 996 (slide from the holotype) – labeled 'Camp. Hirondelle, 1888 No. 65, 1888:106'.

Description (based on Topsent, 1892a, 1904b). Encrusting, soft, smooth; easily detachable 'skin'. Colour black (Fig. 3A). Skeleton. The main skeleton consists of thick columns of tornotes; these carry the tangential ectosome of acanthostyles; many acanthostyles distributed singly in the interior. Spicules (Fig. 3A). Ectosomal acanthostyles, long, thin, finely spined, 375 μm; tornotes tylote, with distinct tyles, smooth, 375 μm; basal acanthostyles in the same size as the ectosomal ones, but with the lower half of the shaft smooth; microscleres arcuate isochelae, 30 μm. Distribution and ecology: Azores; deep water, 736 m depth, on coral.

Remarks. The slide of the holotype examined did not contain an obvious second category of acanthostyles, but Topsent reports a second category of the same size as the ectosomal ones, but with the lower half smooth. These are assumed to be a different category from the ectosomal spicules, echinating the substrate.

The genus *Crellinspira* de Laubenfels (1936a: 79) was erected for type species (original designation) *Crella donsi* Burton (1931c: 136, fig. 1), a 1 mm thin encrustation collected under a stone at the low water mark at the Lofoten in northern Norway. The type is in the Trondheim Museum, but microscopical slides of the holotype are in the Natural History Museum, London, BMNH 1931.10.28.30a and these were re-examined. The sponge has the usual crust of acanthose megascleres leaving contracted areoles charged with microscleres; the choanosome has plumose bundles of smooth tornotes and scattered single acanthostyles similar to those of the ectosomal crust. At the base of the sponge there are long acanthostyles echinating the substrate (Fig. 3B). Spicules (Fig. 3B). Smooth oxeote tornotes, sometimes faintly polytylote, with sharp or occasionally mucronate ends, 171–(204.0)–243 × 2.5–(3.2)–4 μm; ectosomal acanthostyles (acanthostyles II), thickest some distance from the blunt end, fully spined, 69–(84.1)–98 × 3–(4.0)–5 μm; long echinating acanthostyles, 153–(178.0)–210 × 5–(5.8)–7 μm; arcuate isochelae, not reported by Burton ('microscleres absent') but nevertheless definitely present (dozens of similar chelae were observed in situ in the sections), 18–(20.1)–24 μm. Thus, the type species of *Crellinspira* does not conform to the definition given by de Laubenfels. It clearly falls into the synonymy of *Pytheas*. Some sigmas were also noted, but these were probably foreign.

The genus *Ramosichela* de Laubenfels (1950b: 18) was erected for type species (by original designation) *Grayella akraleitae* Brøndsted (1932: 14, fig. 7). This is a thinly encrusting deep-water sponge (not re-examined) on hydroids. The ectosomal skeleton is a crust of acanthostyles, around 100 × 4 μm; the choanosomal skeleton consists of bundles of polytylote, stylote tornotes (fig. 3C), 340–420 × 6–7 μm; basal acanthostyles up to 280 × 8 μm. The arcuate chelae are about 38 μm. It conforms closely to *Pytheas*.

The genus *Naniupi* de Laubenfels, 1950b was erected for type species (by monotypy) *N. ula* de Laubenfels (1950b: 19, fig. 11). The holotype USNM 22740 was re-examined. It is a thin encrustation. It has ectosomal acanthoxeas (Fig. 3D) of 110 × 4 μm, choanosomal stylote tornotes of 190 × 4 μm, echinating acanthostyles of 130 × 7 μm and arcuate chelae of about 2 μm. In addition it has some of the acanthoxeas curled in such a way that de Laubenfels deemed them sufficient reason for erecting a new genus. They are uncommon and obviously derived from normal-shaped acanthoxeas. The only difference with the type of *Pytheas* is the fact that it has ectosomal acanthoxeas instead of acanthostyles.

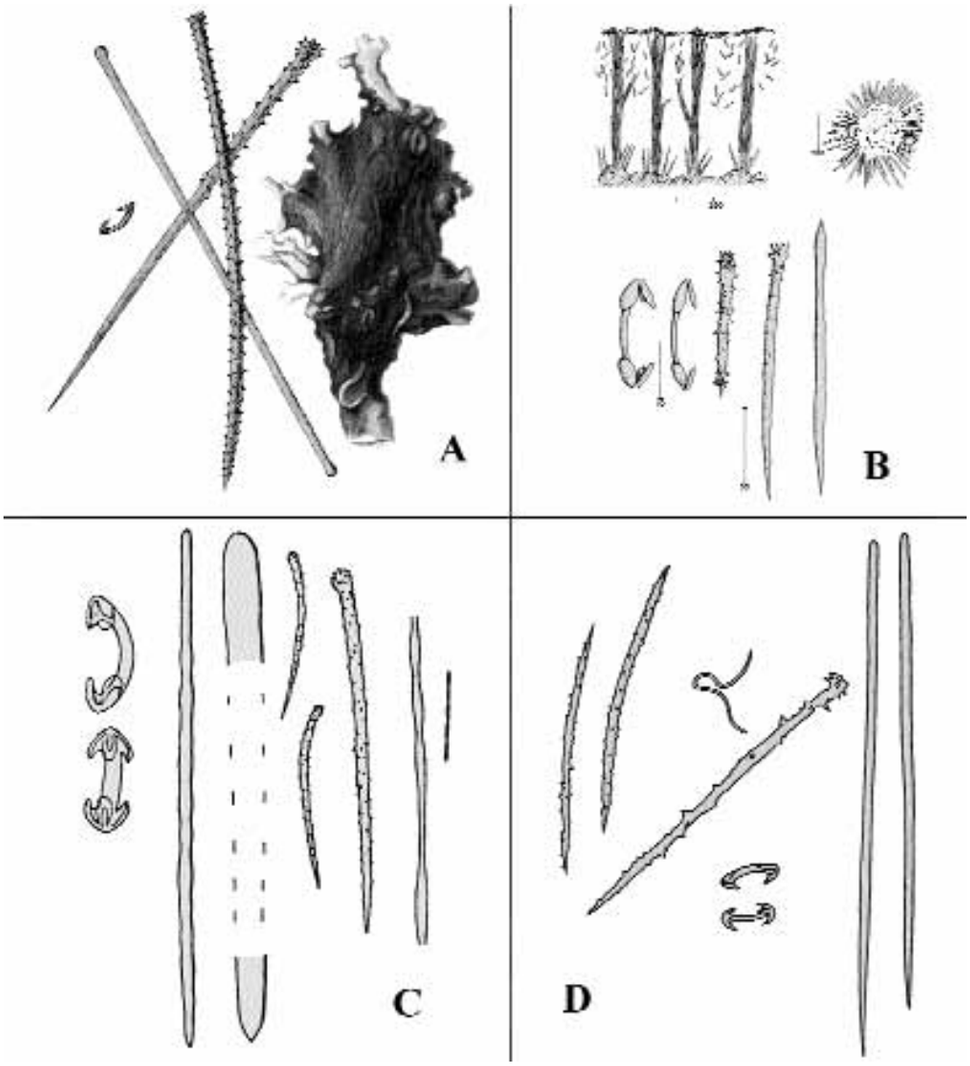

Fig. 3. *Crella (Pytheas)* species. A, *Crella (Pytheas) atra* (Topsent, 1890b as *Pytheas*), drawing of shape and spicules, reproduced from Topsent (1892a pl. I fig. 1 and pl. XI fig. 1) (scales see text). B, *Crella (Pytheas) donsi* Burton (1931), type of *Crellinspira*, drawing of skeleton and spicules made from a slide of the holotype. C, *Crella (Pytheas) akraleitae*(Brøndsted, 1932 as *Grayella*), type of *Ramosichela*, drawing of spicules reproduced from his fig. 7 (sizes see text). D, *Crella (Pytheas) ula* (de Laubenfels, 1950b as *Naniupi*), drawing of spicules reproduced from his fig. 11 (sizes see text).

SUBGENUS *YVESIA* TOPSENT, 1892

Synonymy

Yvesia Topsent, 1892a: 103. *Pytheilla* de Laubenfels, 1936a: 64. *Tisrone* de Laubenfels, 1936a: 78. *Yvesiella* de Laubenfels, 1936a: 78.

Type species

Halichondria albula Bowerbank, 1866 (by subsequent designation; Topsent, 1928c: 51).

Definition

Crella with chelae; no basal echinating acanthostyles.

Description of type species

Crella (Yvesia) albula (Bowerbank, 1866) (Fig. 4A–D).

Synonymy. *Halichondria albula* Bowerbank, 1866: 268; Bowerbank, 1874b: 112, pl. XLV figs 21–24; *Dendoryx albula*; Gray, 1867a: 536; *Myxilla albula*; Vosmaer, 1880: 128. *Myxilla exigua* Hansen, 1885: 11, pl. II fig. 2; *Grayella albula*; Lundbeck, 1910: 37; *Yvesia albula*; Topsent, 1892a: 103; *Crella albula*; Burton, 1930a: 494, 506, fig. 5.

Material examined. Holotype: BMNH 1930.7.3.242 – from Shetland.

Description. Very thinly encrusting (on a shell), not exceeding 1 cm in widest expansion; whitish sponge. Surface smooth. Oscules (or pore fields) scattered. Skeleton (Fig. 4D). Ectosomal skeleton a tangential crust of acanthostyles; choanosomal skeleton irregular bundles of tornotes. Spicules (Fig. 4A–D). Ectosomal

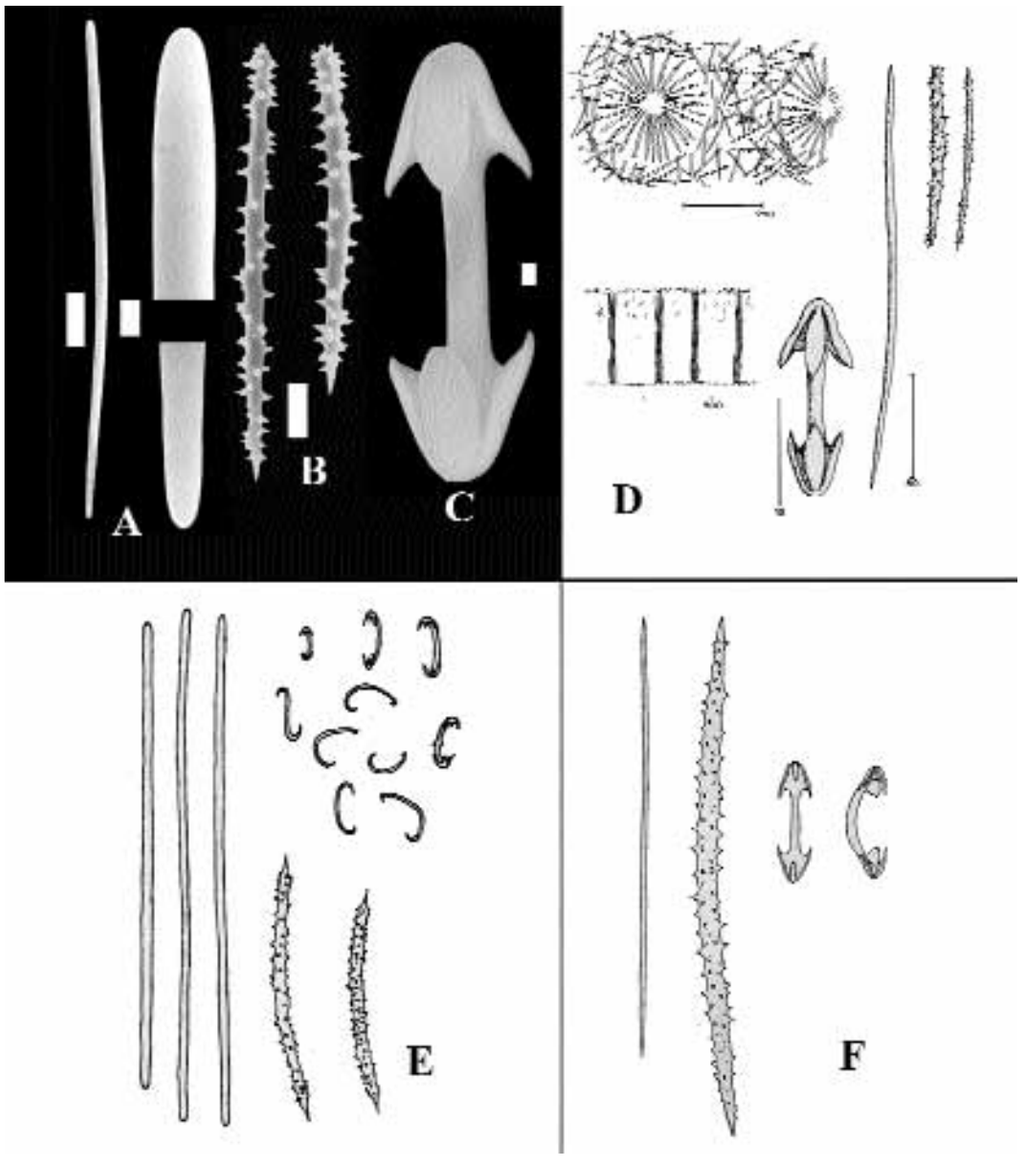

Fig. 4. *Crella (Yvesia)* species. A–D, *Crella (Yvesia) albula* (Bowerbank, 1866 as *Halichondria*). A–C, SEM photos of spicules from the holotype (scales: A left and B, 10 μm; A right and C, 1 μm). D, drawing of skeleton and spicules made from a slide of the holotype. E, *Crella (Yvesia) topsenti* (Babiç, 1922 as *Grayella*), type of *Pytheilla*, drawing of spicules reproduced from his fig. U (sizes see text). F, *Crella (Yvesia) spinulata* (Hentschel, 1911 as *Grayella*), type of *Tisrone*, drawing of spicules reproduced from his fig. 29 (sizes see text).

acanthostyles (Fig. 4B,D), some verging towards acanthoxeas, curved, 100–120 × 2–3 μm; tornotes (Fig. 4A, D) are style-like with a rounded and a pointed end, smooth, straight, 210–360 × 2–6 μm; arcuate isochelae (Fig. 4C, D), 18–28 μm. Distribution and ecology. Shetland and Norway, mostly deep water, 7–180 m depth.

Remarks. The genus *Yvesia* Topsent, 1892a was originally erected for *Crella s.l.*, but later (1928c), Topsent designated *Halichondria albula* Bowerbank (1866) as type species, and restricted its use for species with chelae, stylote tornotes and acanthostyles. Here the definition is widened again to include diactinal tornotes and ectosomal spicules, in accordance with the tendency in the type species to have variable endings of these spicules. It is distinct from *Pytheas* in lacking basal echinating acanthostyles.

The genus *Pytheilla* de Laubenfels, 1936a: 64 was erected for type species (by original designation) *Grayella topsenti* Babiç (1922: 246, text-fig. U, here reproduced in Fig. 4E). This is encrusting other sponges or various substrates. Colour rose-violet or yellowish violet. Skeleton consisting of an ectosomal crust of acanthoxeas, 80–133 × 4–5 μm, carried by choanosomal bundles of tornotes, 185–300 × 4–7 μm. In contrast to what de Laubenfels writes, Babiç does not report the occurrence of echinating spicules and thus the grounds for maintaining a (sub-)genus *Pytheilla* separate from *Yvesia* are lacking. Microscleres: unguiferate arcuate isochelae, 12–19 μm, and sigmas, 12–35 μm.

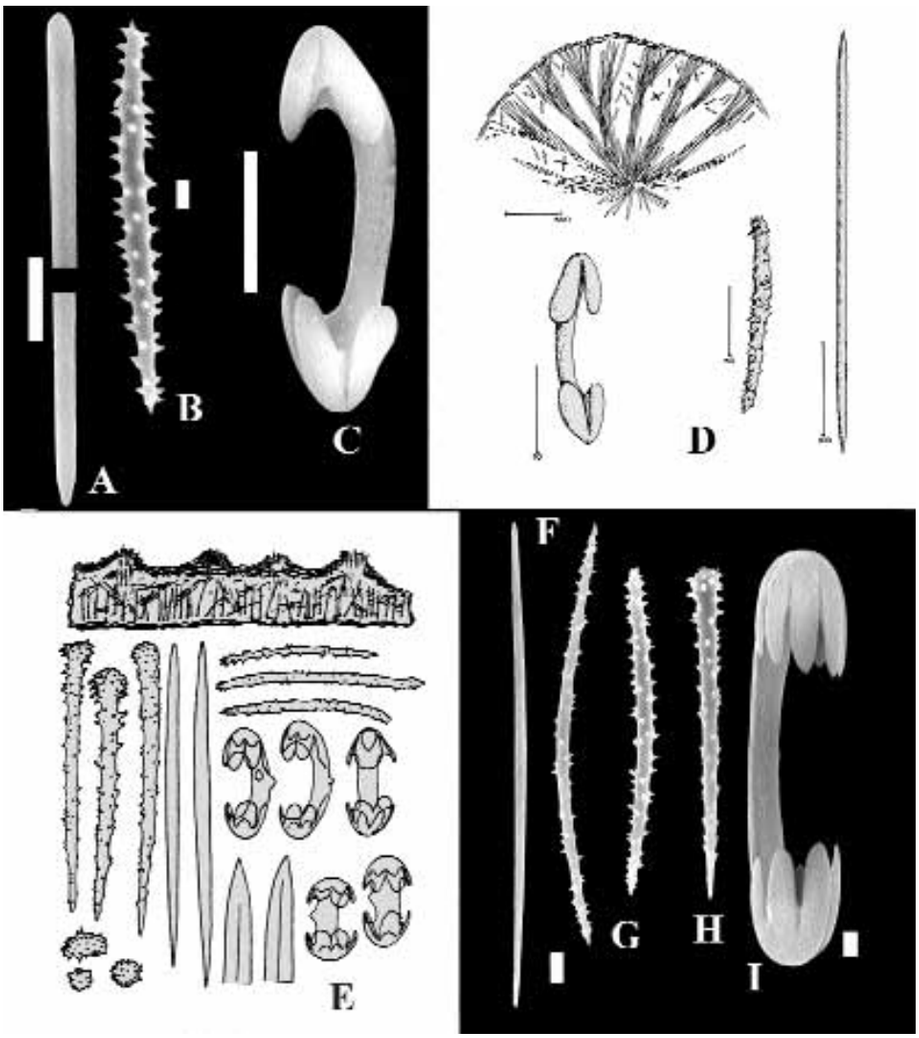

Fig. 5. A–D, *Crella (Yvesia) pyrula* (Carter, 1876 as *Cometella*), type of *Yvesiella*. A–C, SEM photos of spicules made from the holotype (scale 10 μm). D, drawing of skeleton and spicules made from a slide of the holotype. E, *Crellomima imparidens* Rezvoi (1925), drawing of skeleton and spicules reproduced from his fig. 4 (scales see text). F–I, *Crellomima incrustans* Hentschel (1929), type of *Damonilla*, SEM photos of spicules made from a specimen in BMNH (scales: 10 μm, except I, 1 μm).

The genus *Tisrone* de Laubenfels (1936a: 78) was erected for type species (by original designation) *Grayella spinulata* Hentschel (1911: 340, fig. 29, here reproduced in Fig. 4F). The type (not re-examined) is an encrusting-lobate sponge, with surface covered in porefields; colour orange-red or grey-violet (alcohol). Skeleton the usual dermal crust of acanthoxeas, 120–152 × 4–5 μm, and choanosomal tracts of oxeote tornotes, 264–328 × 3–5 μm, mixed with acanthoxeas. Microscleres arcuate isochelae, 16–20 μm. This combination of characters clearly conforms to *Yvesia*.

The genus *Yvesiella* de Laubenfels, 1936a: 78 was erected for the pedunculate type species (original designation) *Cometella pyrula* Carter (1876: 388, pl. XIV fig. 20, pl. XV fig. 38) from deep water (512 m) in the North Atlantic. The type BMNH 1882.7.2.8.11, was re-examined. It has a thick (30–50 μm) multilayered crust of acanthose megascleres (acanthostyles). The choanosomal skeleton (Fig. 5D) consists of a 800–1000 μm thick peripheral zone in which thick bundles of tornotes (100 μm at the periphery thickening to 200 μm in the centre of the sponge) carry the surface skeleton. These bundles converge into the centre of the sponge where they form the axis of the stalk. Several embryos of 200–300 μm long are present in the slides at the base of the peripheral zone. Spicules (Fig. 5A–D): smooth tornotes with blunt (Fig. 5A) or sharp ends (Fig. 5D), occasionally faintly polytylote: 423–(521.8)–586 × 7–(8.7)–11 μm; ectosomal acanthostyles (Fig. 5B, D), thickest some distance away from the blunt end, fully spined: 123–(146.7)–166 × 8–(11.2)–14 μm; arcuate isochelae (Fig. 5C,D), middle part of the shaft occasionally swollen: 21–(23.4)–26 μm. These characters conform to those of *Yvesia*. This species was recorded from several deep water localities along the coasts of Europe and North Africa (Boury-Esnault *et al*., 1994b).

GENUS *CRELLOMIMA* REZVOI, 1925

Synonymy

Crellomima Rezvoi, 1925: 198. *Damonilla* de Laubenfels, 1936a: 65.

Type species

Crellomima imparidens Rezvoi, 1925: 198 (by monotypy).

Definition

Crellidae with anchorate chelae.

Diagnosis

Encrusting, with hymedesmioid skeleton of acanthostyles with heads embedded in a basal layer of spongin; choanosomal skeleton of bundles of smooth tornotes; ectosomal skeleton the usual crust of acanthose megascleres; microscleres tridentate, quadridentate or polydentate anchorate chelae. Two species.

Description of type species

Crellomima imparidens Rezvoi, 1925 (Fig. 5E).

Synonymy. *Crellomima imparidens* Rezvoi, 1925: 198, fig. 4; Koltun, 1959: 172, fig. 132.

Material examined. None. Whereabouts of the type are unknown.

Description. Thinly encrusting, smooth, with leathery surface (Fig. 5E), covered with small (0.5 mm) papillae spaced 1–1.5 mm apart. Colour bright rose. Skeleton. Ectosomal skeleton a crust of acanthostyles tangentially arranged. Choanosomal skeleton of obliquely arranged bundles of tornotes; at the base there are single acanthostyles erect on the substrate. Spicules (Fig. 5E). Ectosomal acanthostyles, 93–190 × 4–7 μm; oxeote tornotes, polytylote, 160–240 × 5–7 μm (Koltun gives 200–416 × 4–8 μm); basal acanthostyles, 92–214 × 6–15 μm; spatulate tridentate or quadridentate anchorate chelae, 16–22 μm. Distribution and ecology. Arctic, 8–320 m depth.

Remarks. The type species is clearly described by Rezvoi, and it was recorded again by Koltun, but cannot be considered well known. The possession of anchorate chelae (the drawing of Rezvoi cannot be interpreted otherwise) is an exception in the family Crellidae, and if this family is considered the sister family to Hymedesmiidae, then the anchorate chelae are even more unusual. This diminishes the value of chela micromorphology as a marker for this group of sponges, unless the *Crellomima* chelae are regarded as a separate independent conversion from ancestral arcuate chelae. Close relationship with *Ectyomyxilla (Crellomyxilla)* (cf. family Myxillidae) is not likely because the skeletal architecture of that group is reticulate and the arrangement of the ectosomal acanthostyles is perpendicular, not tangential.

De Laubenfels (1936a: 65) erected *Damonilla* for type species (by original designation) *Crellomima incrustans* Hentschel (1929: 889, pl. XIII fig. 4). This thinly encrusting sponge has irregular surface, made up of a crust of acanthostrongyles and acanthostyles of 113–156 × 6–7 μm; choanosomal oxeote tornotes are 210–280 × 4–7 μm, basal acanthostyles are 145–224 × 6–11 μm, and microscleres are polydentate (5–7 teeth) chelae of 16–21 μm. A specimen and a slide labeled *Damonilla incrustans* in The Natural History Museum London collection, BMNH 1936.11.20.14, from 'between Franz-Joseph Land and Lenin land, Zool. Inst. Acd. Sci. Leningrad' appears to belong to this species. It is a hard yellow crust, with soft interior. It has the structure and contains the spicules (Fig. 5F–I) recorded by Hentschel, including the polydentate anchorate chelae (Fig. 5I), but some other spicules, presumably belonging to a species of *Iotroata*, are found in cuts of the specimen. Some doubts about the true nature of this sponge remain, and a reliable fresh record of the species is much needed. Nevertheless, it is clear that *Damonilla* is a junior synonym of *Crellomima*.

***CRELLASTRINA* TOPSENT, 1927**

Synonymy

Crellastrina Topsent, 1927b. *Aaaba* de Laubenfels, 1936a: 65.

Type species

Yvesia alecto Topsent, 1898b: 248 (by original designation).

Definition

Crellidae with peculiar astrose derivations of spined oxeas forming a tangential crust; no chelae.

Diagnosis

Encrusting, with an ectosomal crust of acanthoxeas and astrose derivations; choanosomal skeleton of strongylote or stylote tornotes; no acanthostyles, no microscleres. One species.

Description of the type species

Crellastrina alecto (Topsent, 1898b) (Fig. 6A).

Synonymy. *Yvsia alecto* Topsent, 1898b: 248; Topsent, 1904b: 196, pl. XV fig. 16; *Crellastrina alecto*; Topsent, 1928c: 51; *Aaaba alecto* de Laubenfels, 1936a: 65.

Material examined. Holotype: MOM (not seen). Schizotype: MNHN DT 1023 – slide of the holotype, labeled "Yvesia alecto n.sp. PA 1897,111".

Description (based on Topsent, 1904b). Small crust on a deep water coral, thin, translucent, smooth, parchment-like. Colour grey in alcohol (brown interior). Skeleton. The acanthoxeas and asters form a detachable tangential crust, carried by bundles of tornotes. Spicules (Fig. 6A). Ectosomal acanthoxeas, curved, with the entire surface provided with long conical spines or tubercles, often partly finely spined or rugose, 120 × 6 μm (without spines), spines 15–18 μm long; asters of various shapes, looking similar to the spined oxeas and probably reduced derivations thereof: 27–30 μm in diameter; tornotes are strongyles with unequal endings, maybe to be called strongylostyles, with one end often with a slight tyle: 540 × 7 μm. Distribution and ecology. Azores, deep water, 600 m depth.

Remarks. This is a monospecific genus based on very peculiar derivations of the ectosomal acanthoxeas. Some of the asters appear deceptively like true asters and they may take in extreme forms a shape not unlike those of *Jaspis* or Hemiasterellidae, for example. Some of the acanthoxeas also resemble to some extent the peculiar spiraster-like spicules of the latrunculiid genus *Sceptrintrus* and their possible close relationship cannot be excluded. The assignment to Crellidae or even Poecilosclerida is tentative as no chelae or other microscleres, nor acanthostyles are found. Thus, this genus lacks any of the Poecilosclerida synapomorphies. However, the crellid nature of the genus is strengthened

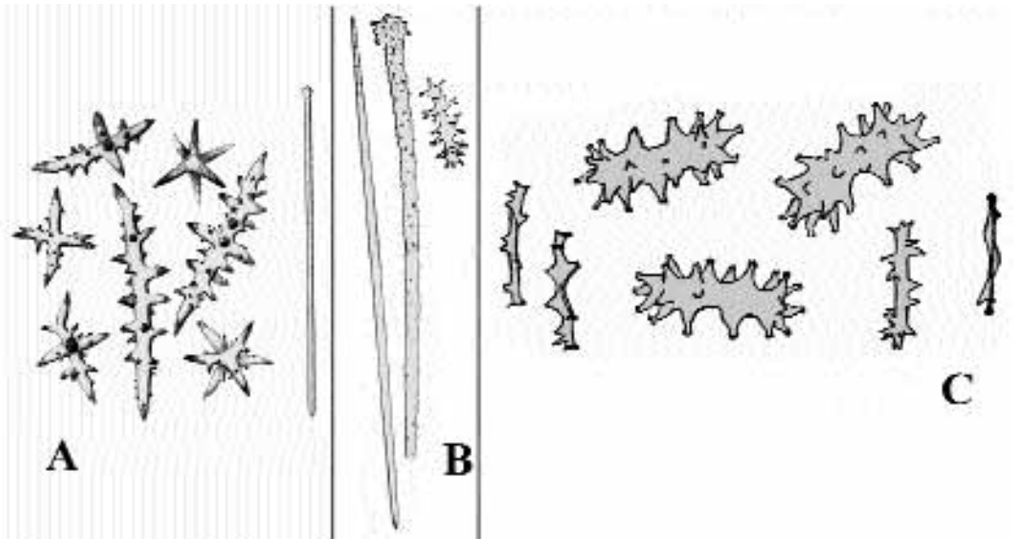

Fig. 6. A, *Crellastrina alecto* (Topsent, 1898b as *Yvesia*), drawing of spicules reproduced from Topsent (1904b, pl. XV fig. 16). B–C, *Spirorhabdia vidua* (Schmidt, 1875 as *Spirastrella*). B, drawing of spicules made from a slide of the holotype, reproduced from Thiele (1903b, fig. 27). C, drawing of spined spicules reproduced from Topsent (1918, fig. xvi) (sizes see text).

by the occurrence of species like *Spirorhabdia vidua* (cf. below) showing similarities to it, but possessing basal acanthostyles.

The genus *Aaaba* de Laubenfels, 1936a: 65 is an objective synonym because it has the same type species (by original designation) as *Crellastrina*.

SPIRORHABDIA TOPSENT, 1918

Spirorhabdia Topsent, 1918: 556.

Type species

Spirastrella vidua Schmidt, 1875: 120 (by original designation).

Definition

Crellidae with polytylote ectosomal oxeote tornotes, basal acanthostyles, and profusedly spined rhabds in an ectosomal crust.

Diagnosis

Thinly encrusting, with dense ectosomal cover of acanthorhabds, carried by bundles of choanosomal oxeote tornotes; basal acanthostyles echinate the substrate. No microscleres. One species.

Description of type species

Spirorhabdia vidua (Schmidt, 1875) (Fig. 6B–C).

Synonymy. *Spirastrella vidua* Schmidt, 1875: 120. *Spirastrella aculeata* Topsent, 1892a: 127, pl. VIII fig. 10; *Hymedesmia vidua*; Thiele, 1903b: 393, fig. 27 *Spirorhabdia vidua*; Topsent, 1918: 556, fig. xvi.

Material examined. None.

Description (from Thiele, 1903b). Thinly encrusting, size about 1 cm^2, smooth and even surface. Colour whitish. Skeleton. Hymedesmioid with acanthostyles erect on the substrate, and bundles of tornotes. Ectosome a tight mass of spined rhabds forming a coherent surface crust. Spicules (Fig. 6B). Ectosomal acanthorhabds, spines or thorns conical, with a terminal thickening, 45–50 × 5–8 μm; tornotes, faintly polytylote, oxeote, 340–350 × 6 μm; acanthostyles, spined all over, up to 350 × 15 μm. Distribution and ecology. Norway, Azores, deep water, below 190 m depth.

Remarks. This is a monospecific genus based on very peculiar derivations of the ectosomal acanthoxeas. It is here assigned to Crellidae for the first time; previous asignment was to Hymedesmiidae, but the surface crust of acanthose spicules of admittedly peculiar shape, fits Crellidae much better than Hymedesmiidae. Thiele (1903b) re-examined Schmidt's type material and expressly stated that the spines of the acanthorhabds were not spirally arranged; however, Topsent (1918) suggested that developmental forms demonstrated spiral arrangement, and he proposed to call these spicules 'spirorhabds', likening them to the spicules of *Latrunculia* and *Sceptrintus*. In view of the presence of acanthostyles, the spirorhabds are unlikely to be homologous to spirasters of *Spirastrella*, but affinity with *Latrunculia* cannot be excluded, since that enigmatic genus shows poecilosclerid affinities in its chemistry (similar to that of *Zyzzya* and *Mycale*).