



On the genus *Coelocalypta* (Porifera: Demospongiae) and other related fistulose halichondrid genera.

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Abstract: *Coelocalypta* is a fistulose halichondrid genus very close to others like *Ciocalypta* and *Collocalypta*. The genus has been synonymized and the species hitherto known as *Coelocalypta porrecta*, *C. aderma* and *C. hyaline* were transferred to other genera by some authors. However, after examination of several specimens of *Coelocalypta porrecta* from the Gulf of Cadiz and type material from the species *Coelocalypta porrecta*, *Coelocalypta aderma*, *Ciocalypta penicillus*, *Ciocalypta microstrongylata* and *Collocalypta digitata*, we propose the validity of these genera based on 1.- the ectosomal skeleton of the fistule: tangential in *Ciocalypta*, palisade-like in *Coelocalypta*, and absent in *Collocalypta*; 2.- the skeletal arrangement in the basal mass of the body: halichondroid-confused in *Ciocalypta/Coelocalypta* and plumose in *Collocalypta*; 3.- the presence of a tangential ectosomal skeleton in the basal mass in *Ciocalypta*, absent in *Coelocalypta/Collocalypta*. In this way, the genus *Coelocalypta* would include the species *Coelocalypta porrecta* which is here redescribed on the basis of SEM observation of new material, as well as *Coelocalypta microstrongylata* n. comb. Moreover, the new genus *Pseudohymeniacidon* is proposed to include the species *Coelocalypta aderma*.

Résumé : Le genre *Coelocalypta* (Porifera: Demospongiae) et autres genres proches d'Halichondriidae possédant des fistules. *Coelocalypta* est un genre morphologiquement très proche d'autres genres tels que *Ciocalypta* et *Collocalypta*, qui sont compris dans le groupe des Halichondriidae possédant des fistules. Le genre *Coelocalypta* a été mis en synonymie et les espèces décrites dans ce genre, *Coelocalypta porrecta*, *C. aderma* et *C. hyaline*, ont été placées dans des genres distincts. Cependant, après avoir réexaminé divers exemplaires de *Coelocalypta porrecta* du golfe de Cadix et révisé le matériel type de *Coelocalypta porrecta*, *Coelocalypta aderma*, *Ciocalypta penicillus*, *Ciocalypta microstrongylata* et *Collocalypta digitata*, nous avons conclu que les trois genres sont valides. Cette conclusion se fonde principalement sur une étude des caractéristiques du squelette ectosomal de la fistule : tangential chez *Ciocalypta*, en forme de palissade chez *Coelocalypta* et absent chez *Collocalypta*. Notre travail implique que le genre *Coelocalypta* comprend actuellement *Coelocalypta porrecta*, qui est ici redécrise sur la base d'observations en microscopie électronique à balayage du nouveau matériel récolté, et *Coelocalypta microstrongylata* n. comb. D'autre part, nous proposons le genre nouveau *Pseudohymeniacidon* pour y inclure *Coelocalypta aderma*.

Keywords: Systematic, taxonomy, Halichondriidae, Axinellidae, *Coelocalypta*, *Ciocalypta*, *Collocalypta*.

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Introduction

The halichondrids have received special attention from many authors mainly in the search of stable diagnostic characters for their classification (Topsent, 1894; Topsent, 1911; van Soest et al., 1990). Van Soest et al. (1990) showed that the Halichondrida and some Axinellida share many characteristics, and like other authors (Topsent, Burton), they associated halichondrids with axinellids, particularly with those of the family Axinellidae. The same authors suggested that reproductive adaptations should not be used at the subclass level but at lower levels. Thus, the classification based on reproductive adaptations (Lévi, 1953), which placed the axinellids in a different subclass from the halichondrids, should be abandoned. In this way, the definition of the order Halichondrida was emended to include Demospongiae with a plumoreticulate-to-confused skeletal architecture, built of interchangeable styles, oxeas and intermediate spicules of varying sizes, and not functionally localized. There have been later attempts for a classification of halichondrids either on the basis of chemotaxonomy (Pomponi et al., 1991), or on morphological and molecular data (Alvarez, 1996).

The halichondrids are characterized mainly by a confused skeletal arrangement, a simple spicule complement of oxeas and/or styles, and a differentiated ectosomal skeleton that can reach different stages of development in the different genera (Lévi, 1973; Bergquist, 1978; etc.). But the simplicity of their skeletal elements has been claimed as a basic problem from a taxonomic point of view (Díaz et al., 1990; Carballo et al., 1996).

Recently, halichondrids of the central West Atlantic were revised (Díaz et al., 1990, 1993), but we think that it is also necessary to evaluate common genera and species of halichondrids from the Atlantic-Mediterranean province. This study is the continuation of a previous revision of some genera of halichondrids and axinellids in order to study the most doubtful genera from a taxonomic point of view (Carballo et al., 1996; Carballo, 2000).

Material and methods

Characters were stated by direct examination of type specimens deposited in different Museums: *Ciocalypta penicillus* (type BMNH 1877:5:21:1069, British Museum of Natural History, London), *Ciocalypta amorphosa* (type BMNH 1887:5:2:56), *Ciocalypta microstrongylata* (type MNHN, Museum National d'Histoire Naturelle, Paris), *Coelocalypta porrecta* (type MOM, Musée Océanographique de Monaco), *Collocalypta digitata* (type BMNH 1907:2:1:89) and *Anisoxya glabra* (type MNHN LBIM n° D.T.3688, Museum National d'Histoire Naturelle, Paris).

Otherwise, the information was extracted from the literature.

Others specimens studied include material collected by the author in the Laboratorio de Biología Marina de la Universidad de Sevilla (Spain) (LBM), and material from the collection of the Centro de Estudios Avanzados de Blanes (Spain) (CEAB).

Spicule preparation followed the techniques described by Carballo (1994) and Rützler (1974) for light and electron microscopy (SEM), respectively. The pictures of microscleres were taken with a scanning electron microscope (SEM) PHILIPS XL 20, for which clean spicules were dried on a cover glass and coated with gold.

The terminology in this work (ectosomal skeleton, tangential skeleton, etc.) follows Boury-Esnault & Rützler (1997).

Results

Systematic description

Order Halichondrida

Family Halichondriidae Vosmaer, 1887

Coelocalypta Topsent, 1928

Type species: *Coelocalypta porrecta* Topsent, 1928

Diagnosis. Massive fistulose Halichondriidae, with a choanosomal skeleton formed by ill-defined, directionless spicule tracts in the basal mass. Without an ectosomal skeleton. The fistule skeleton consists of longitudinal spicule tracts, which anastomose to form a central axis. From central axis, perpendicular spicule bundles or stout fasciculi of closely packed spicules radiate out at regular distances, ending in an ectosomal palisade of tightly packed spicules. The spicules are predominantly oxeas, although styles are occasionally present. When microscleres are present, they are microstrongyles.

Coelocalypta porrecta Topsent, 1928

Material examined. Holotype MOM, and specimen LBM-107.

Diagnosis. *Coelocalypta* with oxeas, also with styles of a smaller size and thickness than the oxeas, and without microstrongyles.

Description

Basal mass (14.6 x 3.2 cm surface area and 1.4 cm thick) buried in sand. With a variable number of vertical tapering fistules (up to 5.3 cm long and 0.8 cm in diameter) with a cylindrical cross-section (Fig. 1A). Fistules with ample aquiferous cavities, thickly walled and closed at the apex. The central spicular axis of the fistule is visible through the

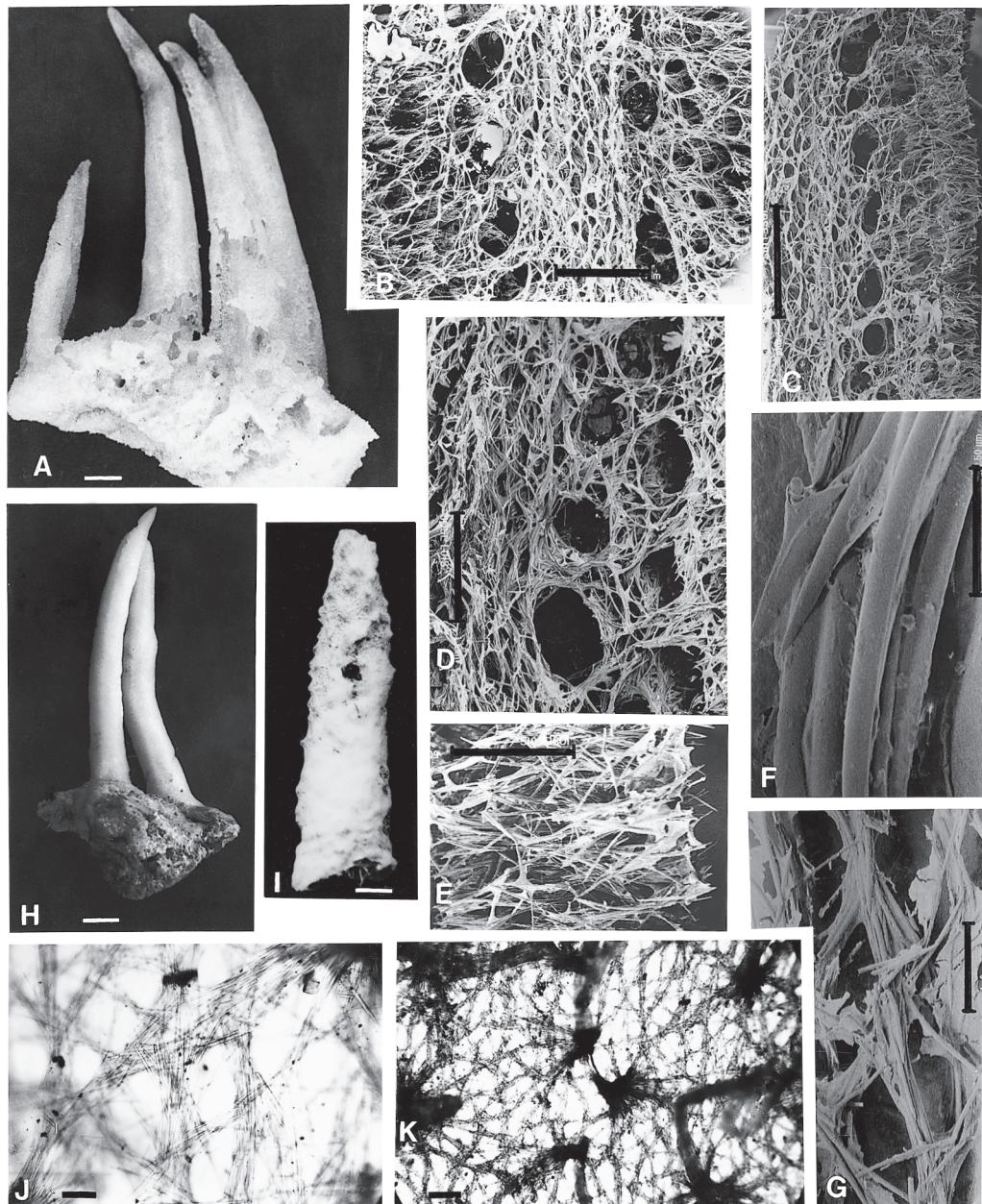


Figure 1. **A.** *Coelocalypta porrecta* (Gulf of Cádiz). **B.** Longitudinal section of centre of fistule showing skeletal architecture. **C.** Longitudinal section of centre of fistule showing spicule brushes of peripheral ectosomal skeleton. **D.** Longitudinal section showing axially condensed reticulate skeleton from which tracts crossing ample subdermic spaces start. **E.** Spicule brushes of peripheral ectosomal skeleton. **F.** Detail of one spicular tract of the fistular axial support. **G.** Central spicular tracts where a reticular arrangement skeleton is observed. **H.** *Coelocalypta microstrongylata* holotype. **I.** *Ciocalypta penicillus* holotype. **J.** Ectosomal tangential skeleton in *Ciocalypta penicillus*. **K.** The same showing chaanosomal axes. Scale bars: A, H: 6 mm; B, D: 1mm; C: 2 mm; E: 500 µm; F: 50 µm; G: 200 µm; I: 4 mm; J: 260 µm; K: 500 µm.

Figure 1. **A.** *Coelocalypta porrecta* (golfe de Cadix). **B.** Coupe longitudinale du centre de la fistule. **C.** Coupe longitudinale du centre de la fistule montrant le squelette ectosomique en forme de palissade. **D.** Section longitudinale montrant la disposition réticulée au centre de la fistule. **E.** Faisceaux de spicules du squelette ectosomique périphérique. **F.** Détail d'un faisceau de spicules au centre de la fistule. **G.** Faisceaux de spicules de l'axe de la fistule montrant une disposition réticulaire. **H.** *Coelocalypta microstrongylata*, holotype. **I.** *Ciocalypta penicillus*, holotype. **J.** Squelette ectosomal tangentiel chez *Ciocalypta penicillus*. **K.** Idem, montrant les faisceaux qui partent du chaanosome. Echelles : A, H : 6 mm ; B, D : 1 mm ; C : 2 mm ; E : 500 µm ; F : 50 µm ; G : 200 µm ; I : 4 mm ; J : 260 µm ; K : 500 µm.

semitransparent walls. Consistency of fistules is very delicate and fragile. The surface is fairly even, slightly hispid in some zones, with a characteristic pattern of subectosomal aquiferous grooves distributed over the sponge basal part. The ectosome is very delicate, transparent and not detachable. Oscula have not been observed. Colour is pale orange in life and white with translucent fistule parts in alcohol.

Skeletal arrangement (Fig. 1A-G)

The main skeleton in the basal mass is halichondroid-confused with ill-defined, directionless spicule tracts. The fistule skeleton consists of a central axis (0.8 to 1.4 mm wide) (Fig. 1B,1C) formed by somewhat dense spicule tracts (4 to 7 spicules) (Fig. 1F) which set out in an irregular reticular manner (1G). From these, stout fasciculi of closely packed spicula radiate out, and then cross wide, slightly oval subectosomal cavities, 230 to 875 µm in diameter (1D). These spicular tracts join together as they approach the external surface, where they are all tightly packed together in a palisade 475 to 610 µm wide (1E). There is no tangential ectosomal skeleton.

Spicule complement

Oxeas are slightly curved and have occasionally stair-stepped ends (Fig. 2A): 213-690 x 0.9-19.4 µm (280-1000 x 4-50 µm in holotype). Styles of a smaller size and thickness than the oxeas also appear (Fig. 2B).

Distribution. Atlantic Ocean. Madeira, Gulf of Cadiz (South of Spain).

Habitat. Rock, sandy sublittoral bottoms, 10 to 95 m depth.

Remarks

We did not observe terminal oscules in the fistules of the specimens examined; we suggest, in accordance with the study conducted by Weerding & Sánchez (1991) on the genus *Oceanapia*, that the inhalant current enters through the fistules which open out above the sediment surface, and the processed water leaves the body of the sponge which is embedded in the sediment. This can be further supported by the presence of the subectosomal canals in the body of the sponge, as we have previously mentioned.

Pseudohymeniacidon genus nov.

Type species: *Coelocalypta aderma* Lévi & Vacelet, 1958

Diagnosis. Halichondriidae compressible, with a fleshy consistency. The ectosome is thin, membranous, detachable, without an ectosomal skeleton. Conulose surface. Choanosomal skeleton consists of ill-defined multisporular ascending tracts. Spicule are oxeas not separable in size categories, sometimes bent once or twice.

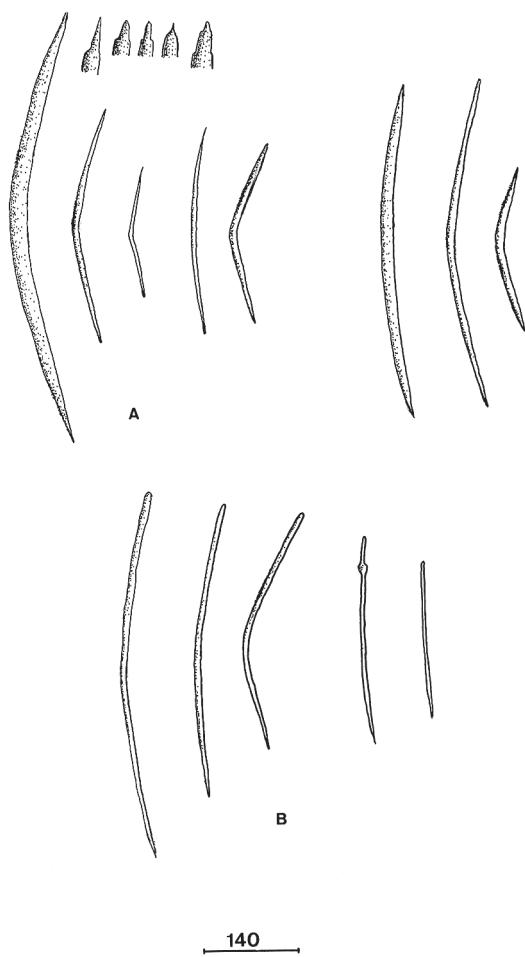


Figure 2. Spicules of *Coelocalypta porrecta*. A. Oxeas and apexes. B. Styles. Scale bar: 140 µm.

Figure 2. Spicules de *Coelocalypta porrecta*. A. Oxeas et apex. B. Styles. Echelle : 140 µm.

Pseudohymeniacidon aderma n. comb. *Coelocalypta aderma* Lévi & Vacelet, 1958

Material examined. Holotype *Coelocalypta aderma* MNHN (without number).

Description

Massive subspherical sponge 4.8 cm in maximum diameter, with two lateral projections 2.6-4 cm long (Fig. 3A). Surface minutely conulose. Ectosome smooth and bright, easy to detach, without spicules. Consistency compressible and fleshy. No visible oscules. No spongin has been observed. Colour in life was "marron-clair jaunâtre" according to Lévi & Vacelet, 1958; dark brown in alcohol.

Skeletal arrangement

Spicules are strewn in confusion (Fig. 3F), or grouped in directionless loose tracts (irregular network of loose

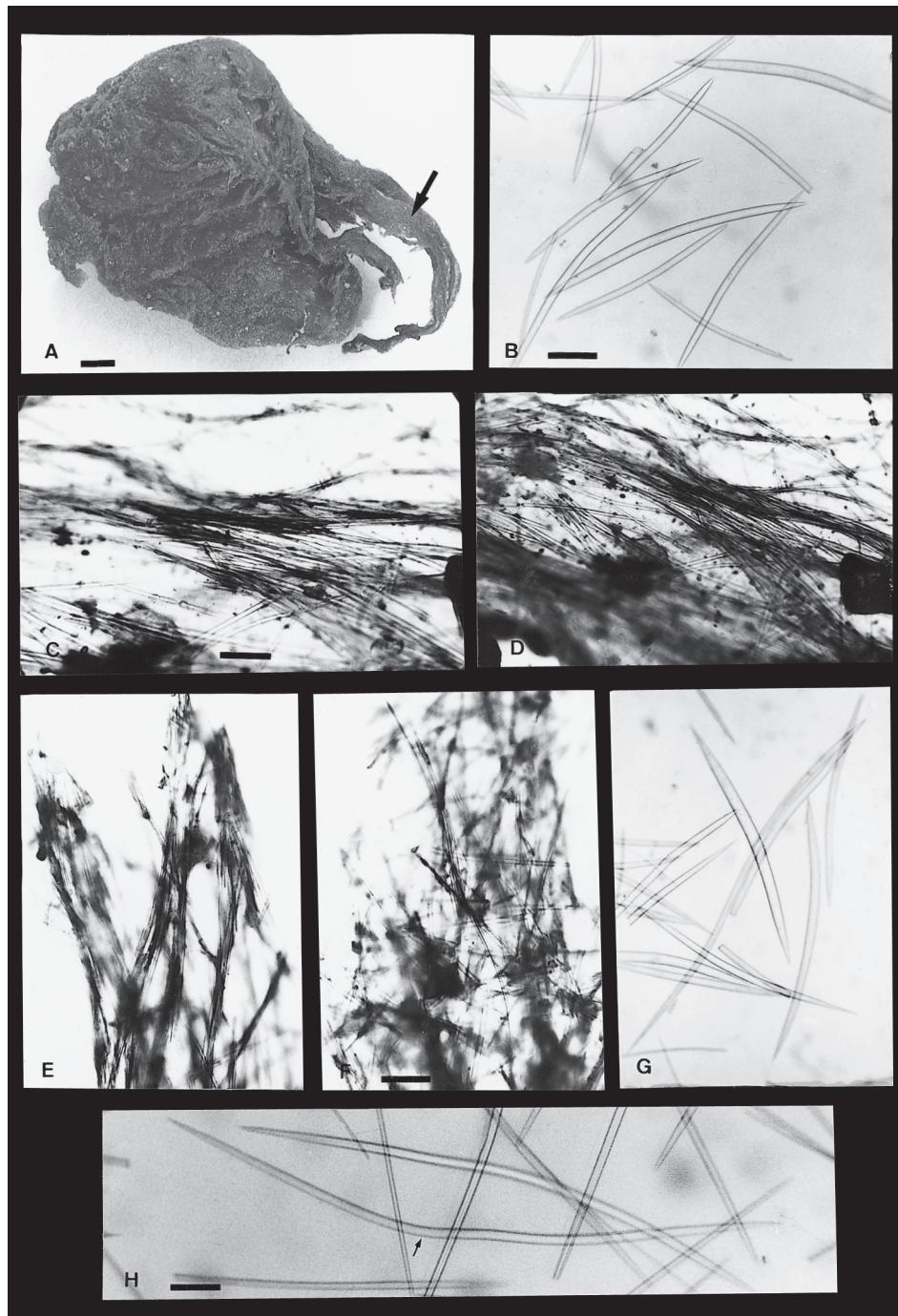


Figure 3. *Pseudohymeniacion aderma* A. Holotype. Arrow shows two lateral projections. B. Spicules of the projection. C. Skeletal arrangement of the projections showing well-developed spicule tracts, which can cross each other. D. Skeletal arrangement of the projections. E. Spicules grouped in directionless loose tracts in the choanosome. F. In other places the choanosomal skeleton is strewn in confusion. G. Spicules of the body. H. Sometimes spicules are curved twice. Scale bars: A: 5 mm; B, G: 125 µm; C, D, E: 150 µm; F: 230 µm; H: 50 µm.

Figure 3. *Pseudohymeniacion aderma* A. Holotype. La flèche indique deux projections latérales. B. Spicules de la projection. C. Disposition du squelette dans les projections, montrant des faisceaux de spicules bien développés. D. Disposition du squelette dans les projections. E. Spicules groupés sans direction dans le choanosome. F. Faisceaux de spicules du choanosome. G. Spicules du corps de l'éponge. H. Spicules présentant une double courbe. Echelles : A : 5 mm ; B, G : 125 µm ; C, D, E : 150 µm ; F : 230 µm ; H : 50 µm.

polyspicular fibres) in the choanosome (Fig. 3C-3E). The two lateral projections are a continuation of the choanosomal skeleton.

Spicule complement

The megascleres are exclusively oxeas measuring 850-1000 x 9-22 µm, evenly or irregularly curved, and sometimes sinuous or doubly curved (Fig. 3B, 3G, 3H, and Fig. 4).

Distribution. Atlantic. Known only from the type locality (Azores Islands, 95 m depth).

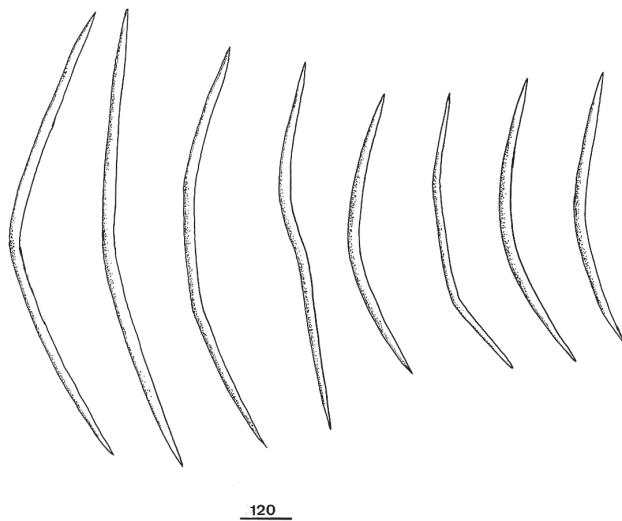


Figure 4. Spicules of *Pseudohymeniacidon aderma*. Scale bar: 120 µm.

Figure 4. Spicules de *Pseudohymeniacidon aderma*. Echelle : 120 µm.

Remarks

The new genus *Pseudohymeniacidon* is proposed in order to harbour *Coelocalypta aderma* and other species which are currently in the genus *Halichondria* but which do not have an ectosomal skeleton. *Pseudohymeniacidon* is like a fleshy *Halichondria* but without an ectosomal skeleton, or like a *Hymeniacidon* but with oxeas instead of styles. Besides the lack of an ectosomal skeleton, another common feature of these *Halichondria* species is the presence of a choanosomal skeleton consisting of an irregular network of loose polyspicular fibres (de Laubenfels, 1936). *Halichondria oblonga* (Armauer Hansen, 1885 as *Reniera oblonga*) and *Halichondria tenuiderma* Lundbeck, 1902, two species with a North-Atlantic distribution, both have an ectosome without spicules, and a choanosomal skeleton consisting of an irregular network of loose fibres

(Lundbeck, 1902), and therefore, they should be transferred to the new genus *Pseudohymeniacidon*. This new genus is clearly different from other halichondrid genera without an ectosomal skeleton and with a similar choanosomal skeleton, such as *Hymeniacidon* (styles), *Hemimycale* (styles/strongyles), and *Stylorella* (styles/strongyles). *Pseudohymeniacidon* is also close to *Axynissa*-species devoid of an ectosomal skeleton, by the presence of a disorganized choanosomal skeleton with spicules strewn in confusion or forming loose bundles, with spicule tracts protruding through the surface to produce conules. However, the spicules in *Axynissa* are oxeas, strongyloxeas or styles usually of only one size class (Carballo et al., 1996; Carballo, 2000).

Discussion

The presence of fistules is a very common feature in some groups of sponges such as the halichondrids, where various genera (*Coelocalypta*, *Ciocalypta*, *Collocalypta*, etc.), typical of soft bottoms, have developed these structures as an evolutive adaptation to their habitat (Fig. 1A, 1H, 1I). The external morphology of these genera is so similar that they can only be differentiated by studying their skeletal elements, their fistules, and their position in the sponge body. Van Soest et al. (1990) suggest that "the fistular habit of this type of sponge seems a clear adaptation to life on a sandy bottom and there may well be no other way to build a fistule with the confused spicular arrangement found in the Halichondriidae". These authors consider that both features are subject to environmental pressure and represent convergent characters. However it seems unlikely that fistules with very different and complicated architecture, as they occur in these halichondrid genera, could be constructed following a basic plan, attributed solely to environmental conditions without considering the genetic determination inherent to each species. There are other genera close to Halichondriidae that form fistules similar to the genera *Ciocalypta* and *Coelocalypta*, but with a very different fistulous skeleton, which give us an idea of the large amount of morphological diversity to be found in the ectosomal skeleton of the fistule. The growth form and the habitat of these genera are similar, and there is an outside possibility that these are closely related, but we have no doubts that sufficient morphological differences exist to maintain them as valid genera.

Coelocalypta (Topsent, 1928) has been a problematic genus from a taxonomic point of view given its similarity to the genus *Ciocalypta* (Bowerbank, 1864). The basic difference that clearly separates these genera is the presence of a tangential ectosomal layer of spicules which is well developed in *Ciocalypta* (Fig. 1J, 1K), yet absent in

Coelocalypta. Formerly, in a revision of the genus *Ciocalypta*, Ridley & Dendy (1887) commented on the doubtful inclusion in *Ciocalypta* of the species *C. calva* Ridley, 1881, due to the lack of the tangential ectosomal skeleton, characteristic of the genus. However, we have not included the species *Ciocalypta calva* in the genus *Coelocalypta*, because of the presence of horny fibres giving a clear chalinoid appearance, according to its own author (Ridley & Dendy, 1887), and as also previously noted by Ridley (1881).

On the other hand, the genus *Coelocalypta* has been often misinterpreted and synonymized with *Topsentia* by van Soest & Stenroft (1988), Díaz et al. (1990) and van Soest et al. (1990). We have also examined the holotype of *Topsentia* (as *Anisoxya glabra*) and, in our opinion, both genera are unquestionably morphologically distinct. Moreover, these authors commented that the genus *Coelocalypta* was erected for fistulose forms with size-class differentiated oxea, and this is not really true; Topsent erected the genus *Coelocalypta* for a specimen similar to *Ciocalypta*-species, but without an ectosomal skeleton. The skeletal architecture of the genus *Coelocalypta* is very different from that of other fistulose-genera (Fig.1) and, if we follow the same logic, we could also interpret the genus *Ciocalypta* as *Halichondria* with fistules since *Ciocalypta* specimens with only oxeas have been described (Pulitzer-Finali, 1978). More recently, Vacelet et al. (1976) described a new species of *Ciocalypta*, *C. microstrongylata* (Fig. 1H), which presents oxeas and microstrongyles. The authors state that this species does not match the genus *Ciocalypta* very well due to the absence of a tangential ectosomal skeleton and the presence of microscleres. After examination of the holotype of *Ciocalypta microstrongylata* we have concluded that the skeletal architecture is identical to that of the genus *Coelocalypta*. Therefore, the genus *Coelocalypta* comprises the species *Coelocalypta porrecta* Topsent, 1928, and *Coelocalypta microstrongylata* (Vacelet et al., 1976), which is clearly different from the former due to the presence of microstrongyles.

Moreover, van Soest et al. (1990) included the species *Coelocalypta aderma* in the genus *Collocalypta* (Dendy, 1905) without providing an argument to support this decision. These specimens are completely different from each other: the fistule of *Collocalypta digitata* Dendy, 1905 has no ectosomal skeleton; it is not tangential like in *Ciocalypta* nor palisade like in *Coelocalypta*, but in this case, spicular tracts are independently constructed departing from the central axis of the fistule; they are set at a straight angle without touching each other and protrude like tufts directly to the exterior. Moreover the choanosomal skeleton consists of a basal portion of erect plumose columns of megascleres that match perfectly that of an Axinellidae (Carballo, 2000), and are very different from *Ciocalypta*

species, or *Coelocalypta aderma*, which has now been included in the new genus *Pseudohymeniacidon*.

We couldn't study the holotype of the species *Coelocalypta hyalina* Pulitzer-Finali (1978) conserved in the BMNH (1977:7:6:10) due to the minuscule size of the only fragment available. However, according to the original description, this species presents some structural characteristics which clearly exclude it from the genus *Coelocalypta*.

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