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Revision of the common Octocorallia of the Mediterranean circalittoral. III. Stolonifera

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ABSTRACT

Six stoloniferan species (*Cornularia cornucopiae, Clavularia crassa, C. ochracea, C. marioni, "Anthelia" inermis* and *Rolandia rosea*) from the Mediterranean circalittoral zone are described, nearly all of them occurring as epizoa on other organisms as well as on rocky substrata. Application of the rule of priority led to the change of one generic name, while several animals previously described as separate species were regrouped under their senior synonyms. A complete description of all these animals is given including colony form, morphology of the living polyps, morphology and morphometry of the sclerites. The latter were observed by means of light microscopy and scanning electron microscopy. A short description is given of the ecology of each species.

RÉSUMÉ

Six espèces de stolonifères (*Cornularia cornucopiae, Clavularia crassa, C. ochracea, C. marioni, "Anthelia" inermis* et *Rolandia rosea*) du circalittoral méditerranéen sont décrites, la plupart vivant soit en épibionte sur d'autres organismes, soit directement sur le substrat dur. L'application de la règle de priorité de la nomenclature zoologique a donné lieu à un changement de nom pour un genre tandis que dans d'autres cas des animaux décrits comme appartenant à des espèces distinctes ont été regroupés sous leur synonyme le plus ancien. Une description détaillée de tous ces animaux est fournie, comprenant la morphologie des colonies entières et celle des polypes vivants, et la morphologie et la morphométrie des sclérites. Ces derniers furent observés à l'aide de deux techniques différentes: microscopie photonique et microscopie électronique à balayage. L'écologie de chaque espèce est abordée sommairement.

INTRODUCTION

This is the third part of my revision of Mediterranean octocorals. Two nomenclatorial mistakes occurred in the first two parts of my revision, which I will correct here. Moreover, some additional information is included concerning the Alcyonacea which reached me after the paper dealing with this order was printed.

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a. In the first part of my revision dealing with the Gorgonacea, I failed (Weinberg, 1976: 80) to take into account Article 47a of the International code of Zoological Nomenclature, dealing with the nominate subspecies. Thus *Eunicella singularis stricta* should become *Eunicella singularis singularis*. (I thank Prof. Dr. J. H. Stock who called my attention to this error.)
b. During the 14th International Congress on Zoology in Copenhagen (Hemming, 1953) it was decided that the original spelling of a specific name remains valid, even if it contains a double *i*, unless the International Commission on Zoological Nomenclature should decide to change it. This decision still being applicable, the name *Maasella edwardsi* (see Weinberg, 1977: 149) should read *Maasella edwardsii*. (Dr. P. J. H. van Bree is kindly acknowledged for this valuable information.)
c. The subtentacular sclerites of *M. edwardsii* (see Weinberg, 1977: plate 10C) may in some cases lack the opaque oval platelets, whereas the transparent slender spindles may form a crown and points.
d. According to Schmidt (1972), in southern Italy (Strombolicchio, Aeolian Islands) *Paralcyonium spinulosum* occurs as shallow as 3 m. In this locality, the species is not always sciaphilous. I believe Schmidt mistook specimens of *Maasella edwardsii* for shallow-water ecotypes of *P. spinulosum*, especially since I found *M. edwardsii* under the same circumstances as shallow as 2 m at Cap Béar, near Banyuls-sur-Mer, which constitutes the shallowest record of this species so far.
e. I received two specimens of *M. edwardsii* from Marseilles, which grew on rhizomes of *Posidonia oceanica* in 15 m depth. Thus far *M. edwardsii* had never been found on this substratum. (I thank Miss C. Eugène and Dr. J. G. Harmelin who collected the specimens, for kindly putting them at my disposal.)
f. Also near Marseilles, *P. spinulosum* was dredged in the Canyon de la Cassidaigne as deep as 150-200 m. (I thank Dr. H. Zibrowius who provided this information.)

The order considered in the present paper, the Stolonifera, contains some of the least known shallow-water octocorals from the Mediterranean. Some species here encountered were misidentified by many authors, as will be shown below. Undoubtedly the reasons for which some of the species are so little known lie in the fact that they are so small in size that they are easily overlooked. Furthermore, the relative scarcity of many of the species means that few data on their ecology are available.

In this paper I shall use the term "sclerite" for skeletal elements rather than the previously employed "spicule". As pointed out by Bayer (personal communication), "spicule" means elongated, needle-like object. This hardly applies to most octocorallian skeletal elements.

Material and Methods

Nearly all specimens were collected by Scuba divers and observed alive in aquaria prior to fixation. Fixation took place in 10% formalin, after

anesthetization with 0.5% $MgSO_4$ in seawater. Later, the colonies were transferred to jars containing 70% aethyl-alcohol. All specimens are kept in the collections of the Zoological Museum of Amsterdam (ZMA). Additional material was examined in the Muséum National d'Histoire Naturelle of Paris (MNHN), while specimens from the Universitetets Zoologiske Museum of Copenhagen (UZMK), were also put at my disposal. Sclerites were obtained by dissolution of the soft tissues in cold and concentrated sodium-hypochlorite (Javel), and examined with a light microscope and a scanning electron microscope. In the first case, large series of sclerites have been photographed for each species. These pictures were classified according to the origin of each type of sclerite, and reproduced by means of line drawings (Plates 4, 8, 14 and 17). In the latter case, sclerites were examined with the Stereoscan MkII, from Cambridge. In order to obtain electrically conductive sclerites they were covered with a layer of gold by means of a splutter apparatus. This layer being 200 Å thick at most, it obliterates no detail; therefore the resulting pictures contain more information than those obtained by other techniques (Plates 5, 6, 9, 10, 11, 13, 15 and 18).

Underwater light measurements were made with a relative irradiance meter (Weinberg, 1974), which compares light above the water surface with light at the sites where the animals live. Measurements were carried out in the blue-green part of the spectrum (peak at 480 nm, band-width 60 nm). Light values are given in percentages as compared with the surface values. Measurements were all made during the summer and around noon in order to facilitate comparison.

Order STOLONIFERA Hickson, 1883
Family Cornulariidae Dana, 1846
Genus **Cornularia** Lamarck, 1816

Diagnosis of the genus *Cornularia:*
Small colonies with completely separate polyps connected to each other by means of tubelike stolons; no sclerites; a delicate, chitinous cuticle invests stolons and anthosteles (partly after Bayer, 1956).

Cornularia cornucopiae (Pallas, 1766)

(Collection ZMA: COEL. 7770, 7840, 7841, 7842, 7843)

Synonymy:

Tubularia cornucopiae Pallas, 1766; Esper, 1794.
Cornularia rugosa Lamarck, 1816.
Cornularia cornucopiae; Schweigger, 1820; Milne Edwards, 1857; Marion, 1882; Graeffe, 1884; Carus, 1885; Stossich, 1885; Von Koch, 1891; May, 1900; Lo Bianco, 1909; Broch, 1935; Stiasny, 1941; Pax & Müller, 1955; Abel, 1959; Pax & Müller, 1962; Tixier-Durivault & d'Hondt, 1975.

As far as we know, this is the only cornularian occurring in the Mediterranean. The genus is characterized by a chitinous outer cuticle and the absence of sclerites, two unique features among the Octocorallia [1]). The species is also the smallest octocorallian occurring in the Mediterranean. These characteristics may explain the fact that the systematics of *Cornularia cornucopiae* have not been subject to much confusion.

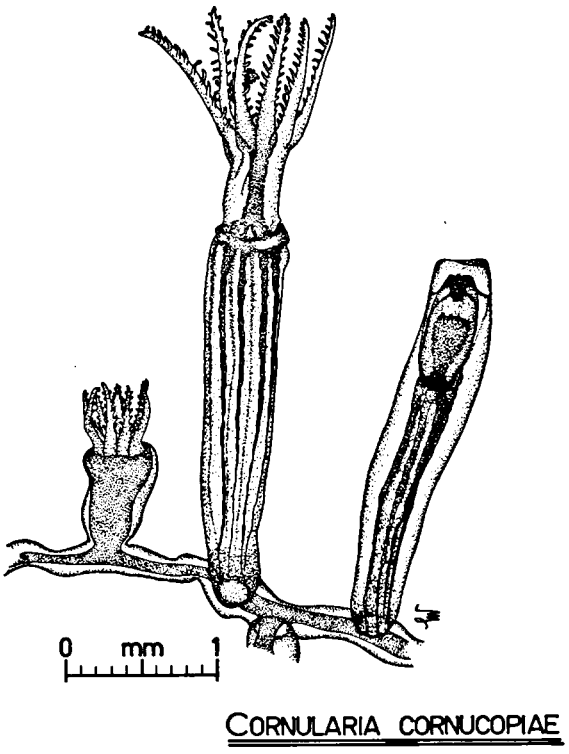


Plate 1. Stolon and polyps of *Cornularia cornucopiae*. A chitinous sheath envelopes the stolon and the lower part of the polyps.

The first description, under the name *Tubularia cornucopiae*, was given by Pallas in 1766 (p. 80, sp. 37). This was followed in 1794 by Esper's description (p. 143, sp. Tubul. 26), who also illustrated the species in two excellent figures (Tab. Tubul. XXVII, figs. 2, 3) in which the chitinous outer sheath is clearly visible, as well as the polyp bearing eight tentacles, each with 8—12 pinnules. This number is rather low, as will appear from my own description.

[1]) There seems to be one exception: *Cornularia sagamiensis*, which bears some small sclerites (Suzuki, 1971).

Lamarck (1816: 112) describes the species under the name *Cornularia rugosa,* although he does not ignore the earlier descriptions. Schweigger (1820: 425) restored the correct specific name but maintained Lamarck's genus. Since then, he has sometimes been mistaken for the author of the species (Graeffe, 1884; Carus, 1885; Broch, 1935).

In the colonies two parts may be distinguished, stolons and polyps. The tubular stolon, some 0.2 mm in diameter and of yellow or brown colour, runs over the substratum which consists of sea grass (Marion, 1882; Von Koch, 1891; Broch, 1935; personal observation) or hard matter, such as rock, stones, shells and barnacles (Graeffe, 1884; Von Koch, 1891; Broch, 1935; personal observation). The stolons, which often bifurcate, are enclosed in chitinous tubes. At regular intervals the polyps emerge from these stolons. The total height of a polyp reaches a maximum of 8 mm; the proximal 3 mm are enclosed in a cup-like prolongation of the chitinous envelope. According to Broch (1935: 2—5, fig. 1) this is not a separate cup, but merely a thickening of the ectoderm. My own observations do not confirm this, and Plate 1 clearly shows the "cup" protruding over a retracted polyp. The tentacles are some 1 mm long, with two rows of 13—15 pinnules each, whereas Pax & Müller (1962) reported some 20 pinnules.

The earlier authors found the species to be rather photophobic, although it occurred in 0—12 m depth. One of my specimens (ZMA: COEL. 7770) was found at 18 m depth, the deepest record of this species so far, under an overhanging ledge. The light reaching this spot amounts to 1.7% as compared to the surface value, which tends to confirm the photophobia of the species. Other specimens were collected near the surface (0.5—3 m) on the rhizomes of the marine angiosperm *Posidonia oceanica,* also a rather dark habitat. Schmidt (1972), however, found the species in unprotected spots as shallow as 1 m.

Cornularia cornucopiae occurs in the Adriatic Sea (Graeffe, 1884; Broch, 1935; Pax & Müller, 1962), in the Aeolian Islands (Schmidt, 1972), in the Gulf of Naples (Von Koch, 1891; Petersen, pers. comm.), near Cannes (personal observation), in the Gulf of Marseilles (Marion, 1882) and near Banyuls-sur-Mer (personal observation). The species was always thought to be exclusively Mediterranean, but recently (Tixier-Durivault & d'Hondt, 1975) it was also found in several localities at the Azores.

Little is known about the reproductive cycle. Von Koch (1891) observed larvae in the end of May, but only once. Fertilized eggs were observed from April to June by Lo Bianco (1909) and in May by Pax & Müller (1962), so that early summer appears to be the time that planulae may be expected to swarm out.

Family Clavulariidae Hickson, 1894

Genus **Clavularia** De Blainville, 1830

Diagnosis of the genus *Clavularia*:
Polyps simple, arising from bandlike or membraneous stolons; important

anthocodial armature; sclerites including simple spinous spindles, rods or clubs, and a few double forms. (After Bayer, 1956, and Tixier-Durivault, 1966.)

Clavularia crassa (Milne Edwards, 1848)

(ZMA: COEL. 7833, 7834, 7835, 7836, 7837, 7838, 7839, 7844; MNHN: type-specimen of *Clavularia steveninoae*)

Synonymy:

? Cornularia crassa Milne Edwards, 1848; Milne Edwards, 1857.
? Clavularia crassa; Kowalewsky & Marion, 1882.
Clavularia crassa (part); Marion, 1882.
Clavularia crassa; Kowalewsky & Marion, 1883; Carus, 1885; Hickson, 1895; May, 1900.
Clavularia ochracea (part); Von Koch, 1891.
Clavularia ochracea; Lo Bianco, 1909.
Anthelia crassa; Bérenguier, 1954.
Clavularia steveninoae d'Hondt & Tixier-Durivault, 1975, new synonymy.

In 1848 Milne Edwards very briefly described, under the name *Cornularia crassa*, an animal from Algerian coastal waters. He claimed that it differed from *Cornularia cornucopiae* by its thick form and the fleshy consistence of the polyp. In a figure (Pl. 65, figs. 3, 3a, 3b) he showed what is unmistakably a clavularian, with both a retracted and an expanded polyp. Anthostele and stolon differ from the anthocodia, due to the tightly packed sclerites (although no detail of them was shown). Later, in 1857, he mentioned the species again, specifying its length as 4-5 mm. Unfortunately, in neither case did he mention the substratum on which the animal was found. As we will see later on, this is necessary for a firm identification of the species. Subsequently Kowalewsky & Marion (1882, 1883) and Marion (1882) mentioned the species again, placing it correctly in the genus *Clavularia*. The latest of those publications, although appearing a year after the other two, was probably written before them. This may be deduced from the fact that a new species described in the joint paper of 1883 (*Clavularia petricola*, see next section) was referred to in the "earlier" papers. In their article of 1883 they described two Mediterranean clavularian species which look very much alike, and which they would certainly have placed in one species were it not for some ecological and ethological differences. The first species was found to occur on rhizomes of the marine angiosperm *Posidonia oceanica*, the other on rocky substratum. This difference alone would not justify a separation into two species (see, for instance, *Cornularia cornucopiae* or *Maasella edwardsii*). The authors found, however, that specimens living on *Posidonia* always produced reddish eggs in the end of June. These eggs were expelled from the body cavity through the mouth, remained agglutinated on the distal part of the polyps (their Pl. 1, figs. 1, 1a) and underwent division after an initial period of rest, whereas specimens living on hard substratum produced

free-swimming planulae earlier in the same month. They called the latter species *Clavularia petricola*, conserving the older name *C. crassa* for the species living on *Posidonia*. They mentioned the name *C. ochracea*, a species established by Von Koch just before their publication, but did not possess enough data to propose a synonymy. *C. ochracea* must be considered a senior synonym of *C. petricola* as I will point out in the next section. Only twice was the name *C. ochracea* used for *C. crassa*, once by Von Koch (1891: 660) when he described the typical external development of the fertilized eggs, an exceptional feature for Octocorallia, and once by Lo Bianco (1909),

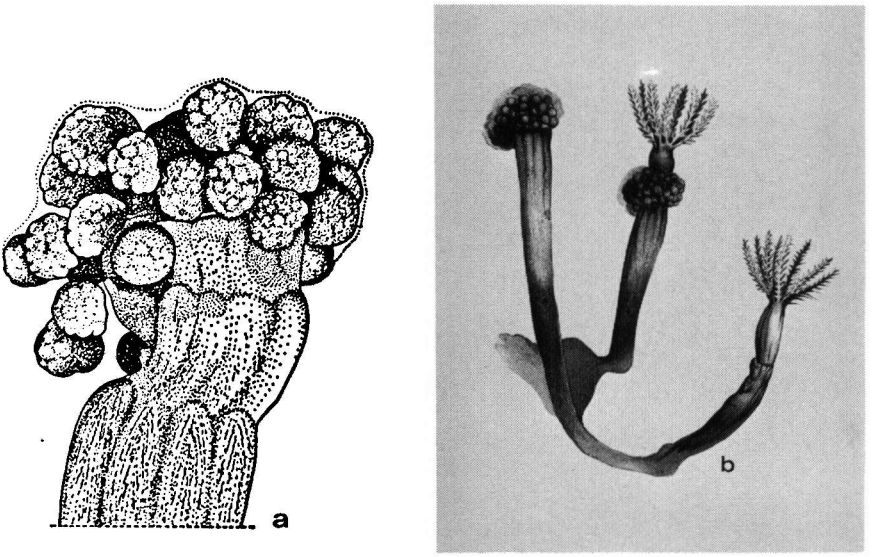


Plate 2. a: polyp of *Clavularia crassa* incubating its eggs agglutinated on its outside (from d'Hondt & Tixier-Durivault, 1975); b: similar situation as figured by Kowalewsky & Marion (1883).

who also mentions the existence of eggs on the apical part of the polyps from May to July. Bérenguier (1954) describes the species again, although placing it erroneously in the genus *Anthelia*, with all the characteristics already mentioned above. Recently, d'Hondt & Tixier-Durivault (1975) described a new species from the Mediterranean, *Clavularia steveninoae*. Their description corresponds in every respect with those of *C. crassa* given by the previous authors. The species is also a shallow-water clavularian living on the basal parts of *Posidonia*. The polyps, like those of *C. crassa*, measure up to 7 mm. Finally, the peculiar mode of reproduction of *C. crassa* is also as described for the new species; comparison of their fig. 4 (our Plate 2a) with plate 1 fig. 1A of Kowalewsky & Marion (1883) (our Plate 2b) eliminates any remaining doubt. The recent authors even failed to compare their new species with *C. crassa* as described by Kowalewsky & Marion (1883).

Moreover, they say (p. 589) that *C. steveninoae* is easily distinguished from one species (*C. marioni*) and another (*C. ochracea*) by the distribution of its polypean spicules, the size and the appearance of its different sclerites, and the number of its tentacular pinnules. The last point is contradictory, as d'Hondt & Tixier-Durivault (1975) established this number to vary from 9 to 14, with 9—11 pairs of pinnules per tentacle being found most of the time. Von Koch (1891: 659) found 10—12 pairs per tentacle for *C. ochracea* and gives no number for *C. marioni!* Another species, *C. inordinata* (see next

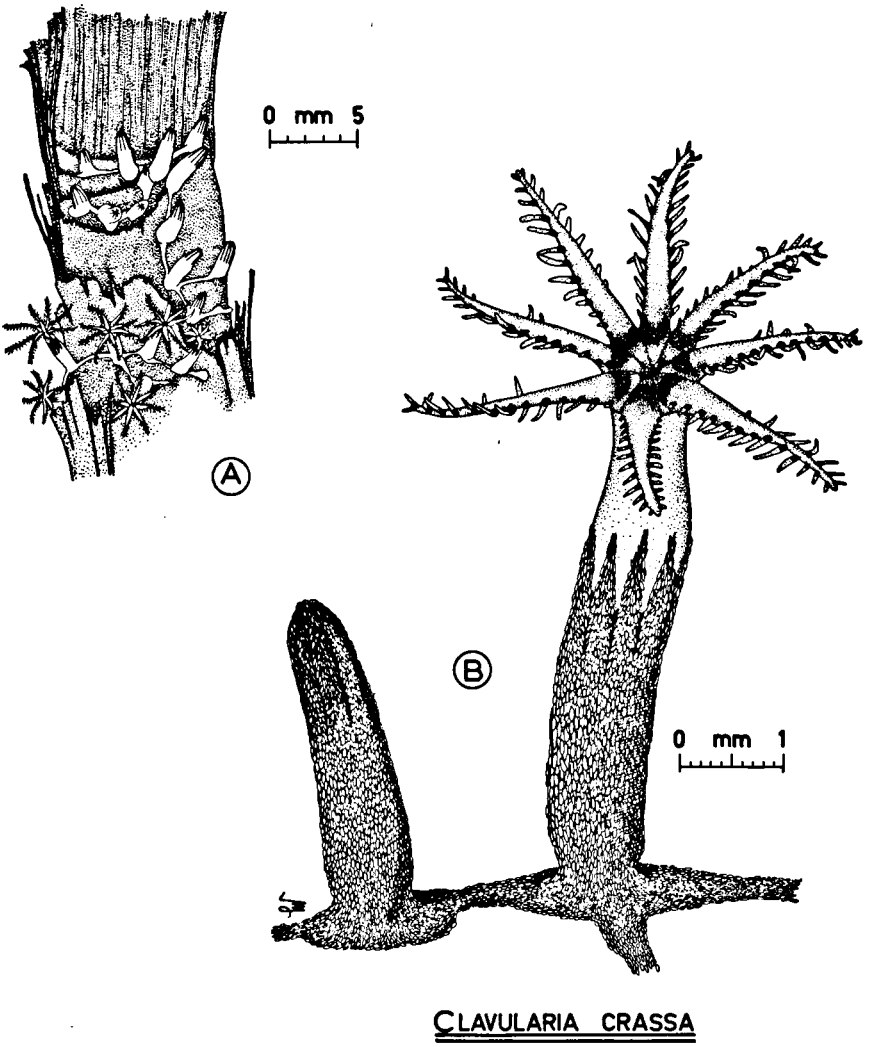


Plate 3. A: colony of *Clavularia crassa* on the basal part of the leaves of *Posidonia oceanica*. The stolons, retracted and extended polyps are clearly seen. B: detail of two polyps.

section) was described by Tixier-Durivault & Lafargue (1968) as bearing 11—12 pairs of pinnules per tentacle. Thus there seems to be a complete overlap between the species as far as this criterium is concerned. As to spiculation, I find the distinction between the Mediterranean species (*C. marioni* excepted) to be very subtle and difficult to establish, even more so because some intraspecific variation may occur.

On the grounds of the particular habitat and mode of reproduction of the species, I feel it should be referred to exclusively as *Clavularia crassa* (Milne Edwards, 1848) until a valid distinction between two or more such species can be made.

The colonies (Plate 3) consist of 0.5—2.0 mm wide, flattened stolons running over the substratum. The stolons bifurcate and anastomose from time to time. From this network polyps arise at irregular intervals, their height attaining 7 mm and their anthocodial width reaching 1.5 mm at most. The tentacles measure from 4—7 mm in length when fully extended, and bear 8—15 pairs of pinnules per tentacle. The base of each pinnule is opaque in living specimens. Opaque, crescent-shaped areas may be observed at the base of each tentacle. All these opaque areas disappear in specimens conserved in alcohol.

The stolons are covered by plump warty spindles (Plate 4 figs. 55—81) measuring from 75—185 μm, and by irregular scales (Plate 4 figs. 82—93) measuring from 130—310 μm in length. The anthosteles are stiffened by rough, rather plump, warty spindles measuring from 80—260 μm (Plate 4 figs. 28—54). Towards the distal parts of the anthosteles they form eight distinct chevrons of slender spindles, 120—320 μm in length (Plate 4 figs. 9—27). On the anthocodiae some smoother spindles, 100-210 μm in length, are found (Plate 4 figs. 1—8). Typical sclerites from the polyps and the stolons are shown in Plates 5 and 6, respectively.

The species occurs from 0.5 m (personal observation) tot 10 m depth (Miss C. Eugène, personal communication). The species has been found near Marseilles (Kowalewsky & Marion, 1883; Bérenguier, 1954; Eugène, personal communication), Cannes (d'Hondt & Tixier-Durivault, 1975; personal observation) and Naples (Von Koch, 1891; Lo Bianco, 1909; Dr. K. Petersen, personal communication).

The species may have become very rare. I searched for it in *Posidonia*-meadows near Banyuls-sur-Mer, near Le Lavandou, near Monaco and near Cannes, and succeeded in finding it only at the last locality (Pointe de la Croisette, Cannes).

Clavularia ochracea Von Koch, 1878

(Collection ZMA: COEL. 7771, 7772, 7787, 7788, 7789, 7790, 7791, 7792; MNHN: type-specimen of *C. inordinata*)

Synonymy:

Clavularia ochracea Von Koch, 1878; Von Koch, 1882; Carus, 1885; Von Koch, 1891; Von Koch, 1892; Hickson, 1895; May, 1900; Pax & Müller, 1962.

? Clavularia petricola Kowalewsky & Marion, 1882.
Clavularia petricola; Kowalewsky & Marion, 1883; Carus, 1885; Hickson, 1895; May, 1900.
Anthelia petricola; Bérenguier, 1954.
Clavularia inordinata: Tixier-Durivault & Lafargue, 1968, new synonymy.

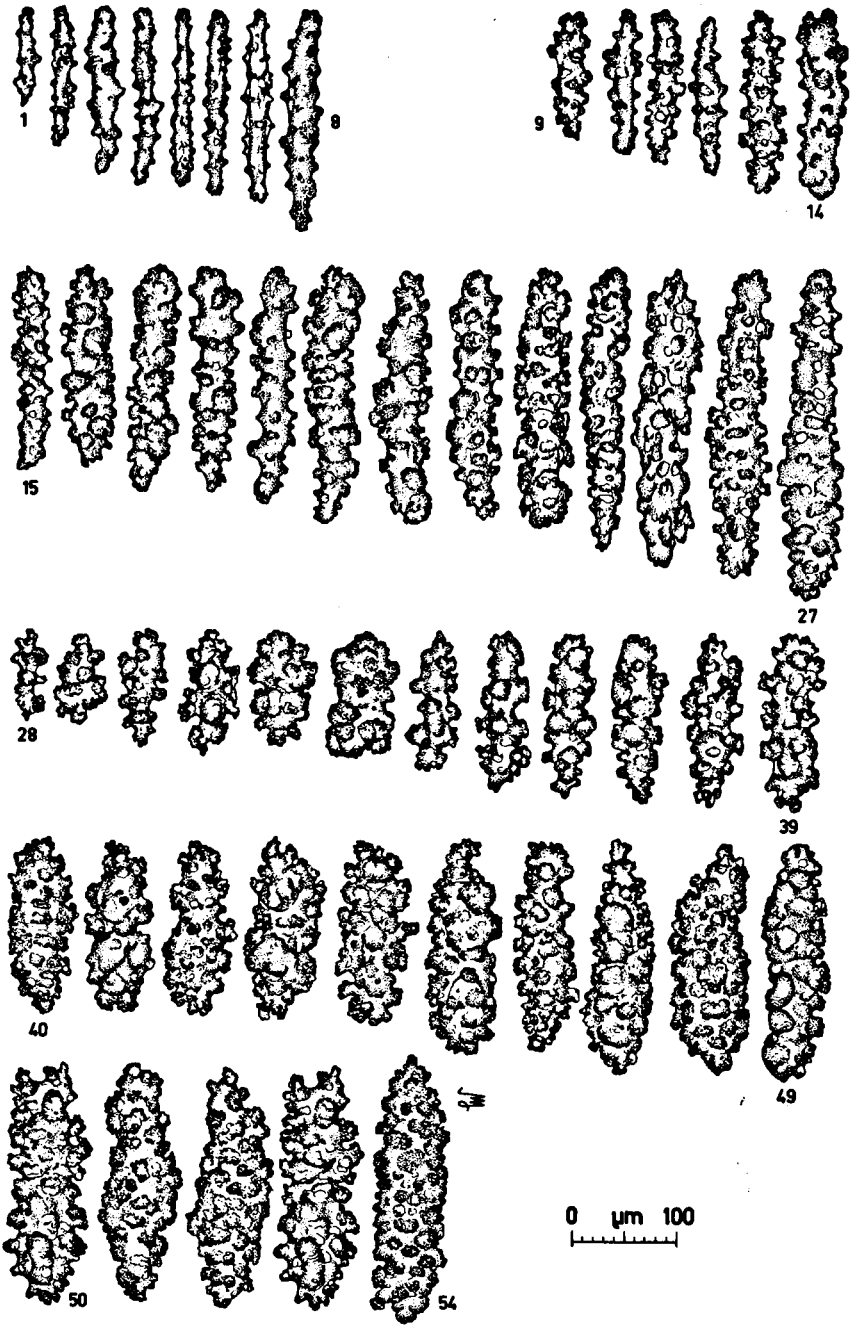


Plate 4. Sclerites of *Clavularia crassa*. 1—8: smooth spindles from anthocodia; 9—27: slender spindles from chevrons; 28—54: plump spindles from anthostele; 55—81: plump spindles from stolons; 82—93: irregular plates from stolons.

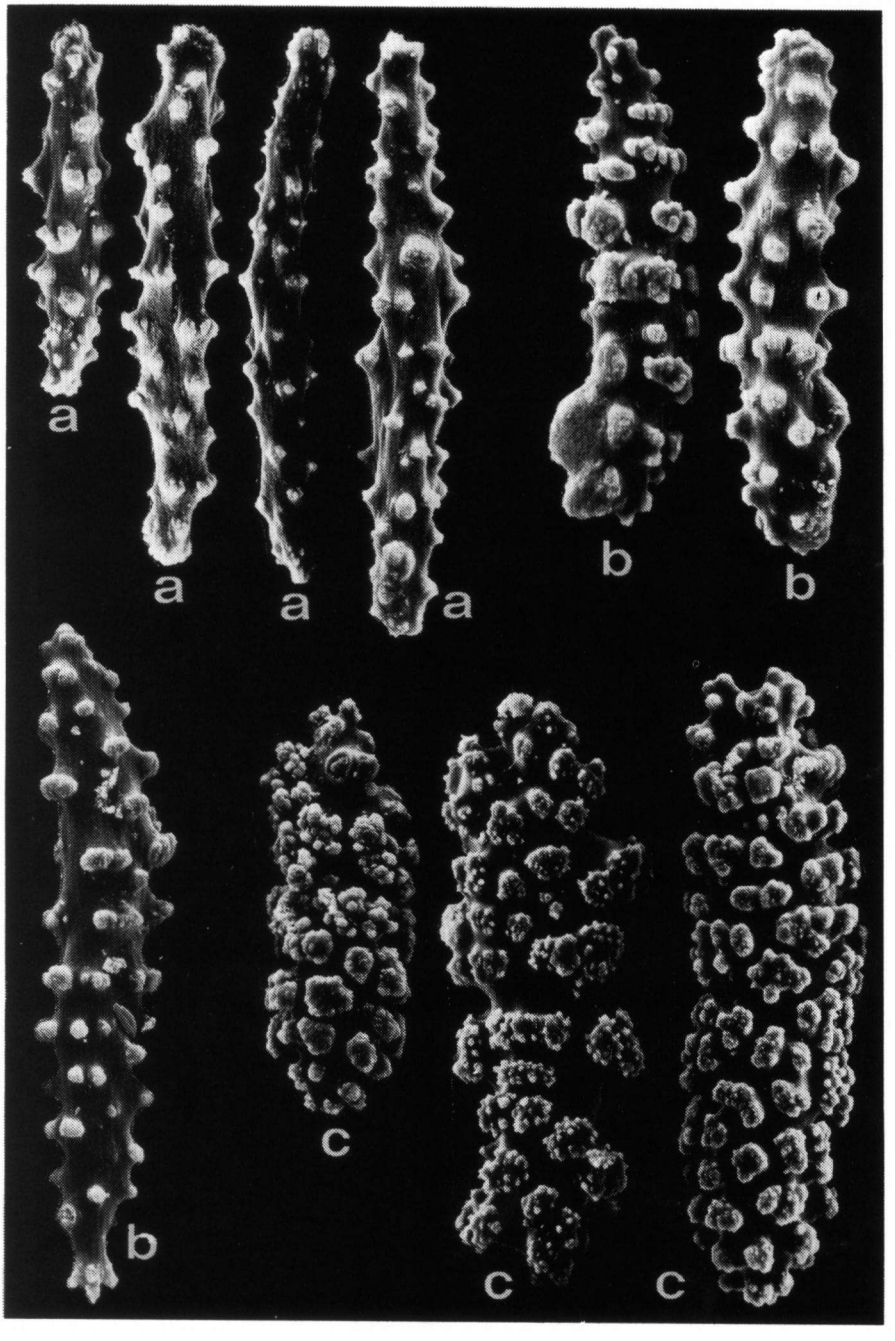


Plate 5. Sclerites from the polyps of *Clavularia crassa*. a: smooth spindles from anthocodiae; b: slender spindles from chevrons; c: plump spindles from anthostele. Magnification: 400 ×.

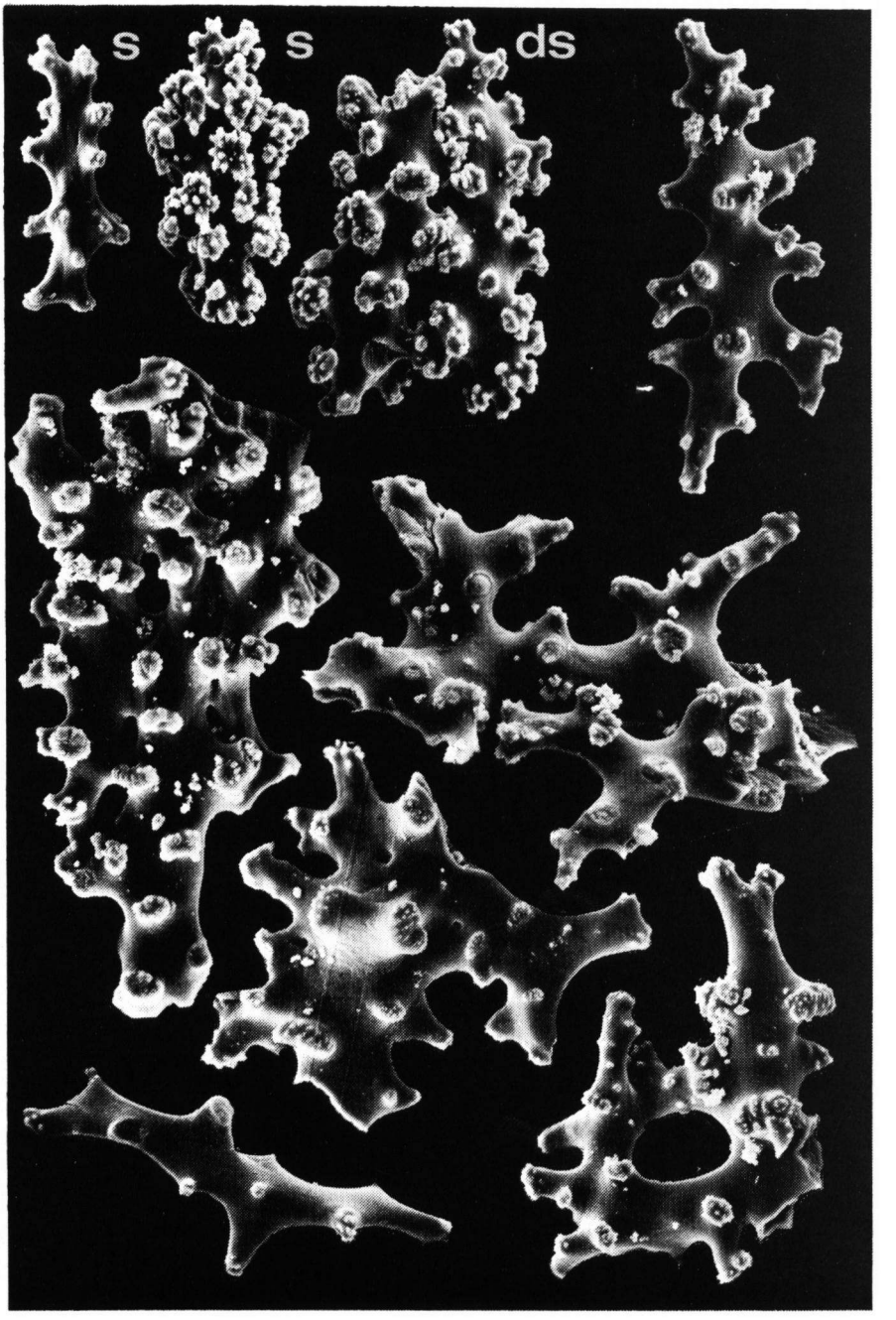


Plate 6. Sclerites from the stolons of *Clavularia crassa*. s: spindles; ds: double spindle resulting from the fusion of two spindles; irregular plates. Magnification: 400 ×.

In a publication on the clavularian skeleton, Von Koch (1878: 320) describes a new species from Naples: *Clavularia ochracea*. Some of the characters of the species are the following: upper fifth part of the extended polyp transparent and containing no sclerites; then a zone containing slender spicules with small warts, 150 μm in length; the aboral part of the polyps contains plumper sclerites with rough warts, their length ranging from 100 to 250 μm; the stolons contain irregular sclerites, often without warts, which fuse together from time to time. In a later publication (Von Koch, 1892) he gives the dimensions of the colonies; the stolon is approximately 1 mm broad and runs over the rocky substrate over several centimetres. In a detailed description (Von Koch, 1891) he describes the polyps as attaining a maximum height of 10 mm at a width of 1.5 mm, their tentacles bearing 10-12 pinnules on either side. Some pictures of the sclerites are also shown. Kowalewsky & Marion referred to the species in 1883, supposing it might be identical with their *C. crassa*. In spite of his detailed knowledge of the species, Von Koch (1891, footnote p. 658) declared that lacking more information he didn't dare to identify the species described by Marion & Kowalewsky with his one. He added, however, that if it should be impossible to distinguish *C. petricola* from *C. ochracea*, the latter name should be given priority. I fully agree with Von Koch in this respect. Unfortunately, Von Koch's type seems to be lost: Stiasny (1941) was unable to find it at the Stazione Zoologica of Naples, neither did I succeed in locating it. On the grounds that Von Koch's description corresponds in every respect with Kowalewsky & Marion's description of *C. petricola* and that comparison of type-material of the two species is not possible, I prefer to use the name *C. ochracea* for the Mediterranean shallow-water clavularian which lives on hard substratum and emits free planulae, until evidence is given that there are several such species.

The stolons of the animal are flattened, and have a diameter of 0.5 mm approximately. The polyps measure up to 10 mm in height when fully extended, the tentacles may be as long as 6 mm and bear 9—16 pinnules on either side (Plate 7A). The distal part of the anthocodia, the tentacles and the pinnules, which bear several rows of nematocysts, are in some cases virtually devoid of sclerites (Plate 7B), in others covered with minute (7—10 μm) rectangular "sclerites" (Plate 7D) and/or bigger (30—50 μm) crystalline structures (Plate 7C). In living specimens, the base of each pinnule is opaque in contrast with the glassy structure of the rest of the tentacles, which therefore appear as rows of alternating white points in incident light (black in Plates 7A, 7B). These opaque spots, as the opaque crescent-shaped areas sometimes observed at the base of each tentacle, disappear when specimens are kept in alcohol (compare with *C. crassa*, preceding paragraph).

The stolons and anthosteles bear densely packed sclerites, lying parallel to each other, and forming eight chevrons in the proximal part of the anthocodia. The lower part of each polyp is therefore a rather stiff column into which the upper part may retract completely (left polyp in Plate 7A).

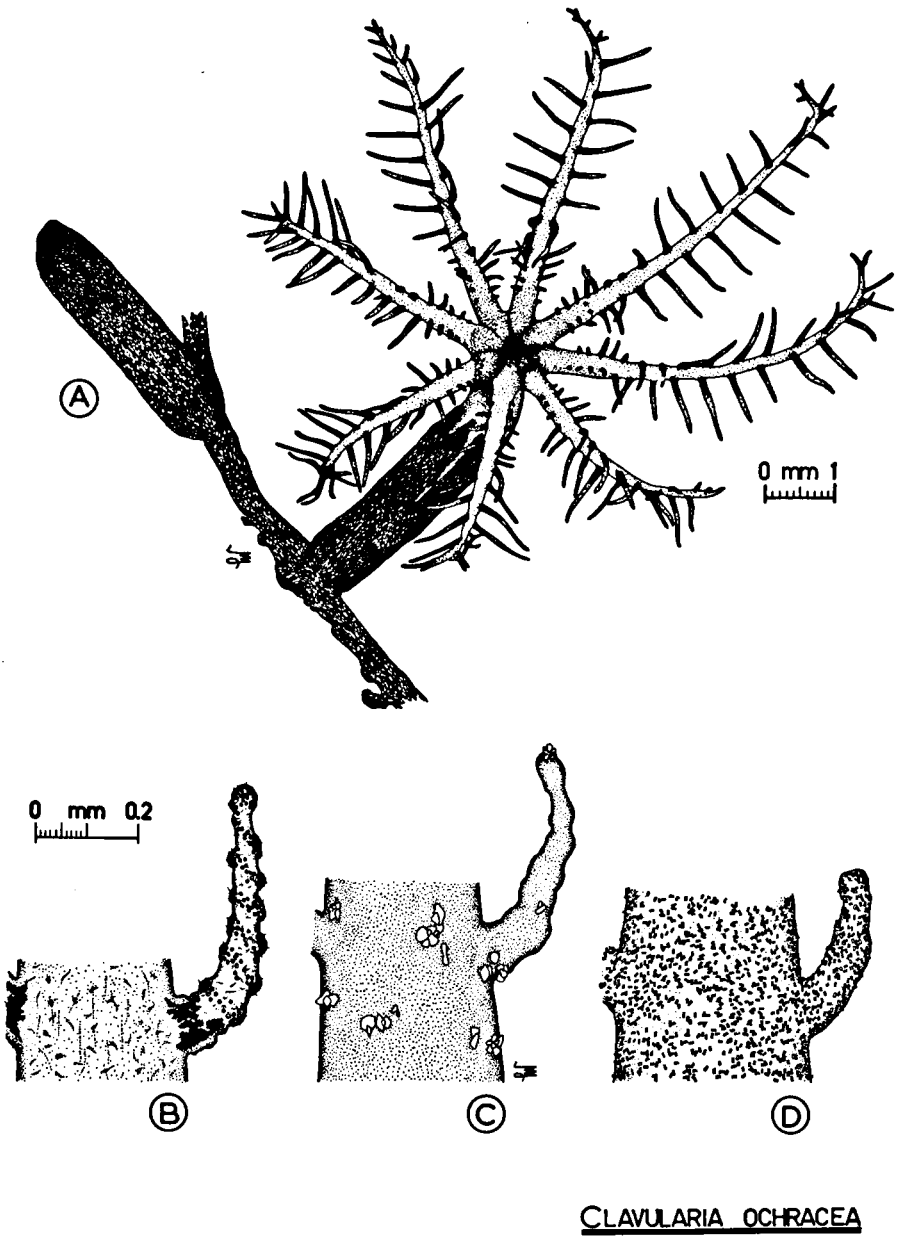


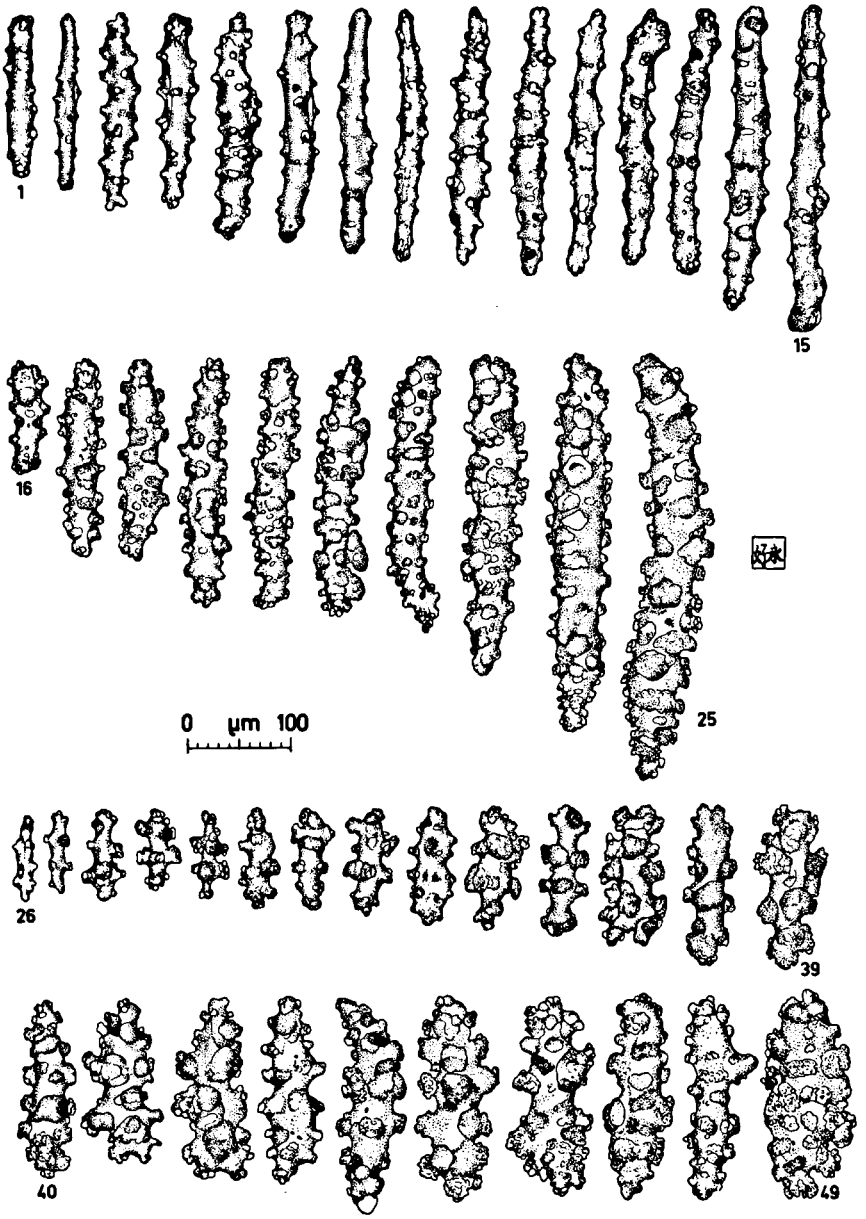
Plate 7. *Clavularia ochracea.* A: retracted and extended polyp; B: detail of living tentacle (rows of nematocysts are clearly visible as well as the opaque basis of the pinnulae); C: detail of tentacle with crystal-like objects; D: detail of tentacle with crystal-like „sclerites".

The animals are ochre to pink when alive and become a pale yellow in alcohol.

The sclerites exist in four categories:

— spindles with small warts, mainly from the chevrons in the proximal part of the anthocodia; length 155—310 µm (Plate 8, sclerites 1—15);

— slender spindles with coarse warts, mainly from the distal part of the



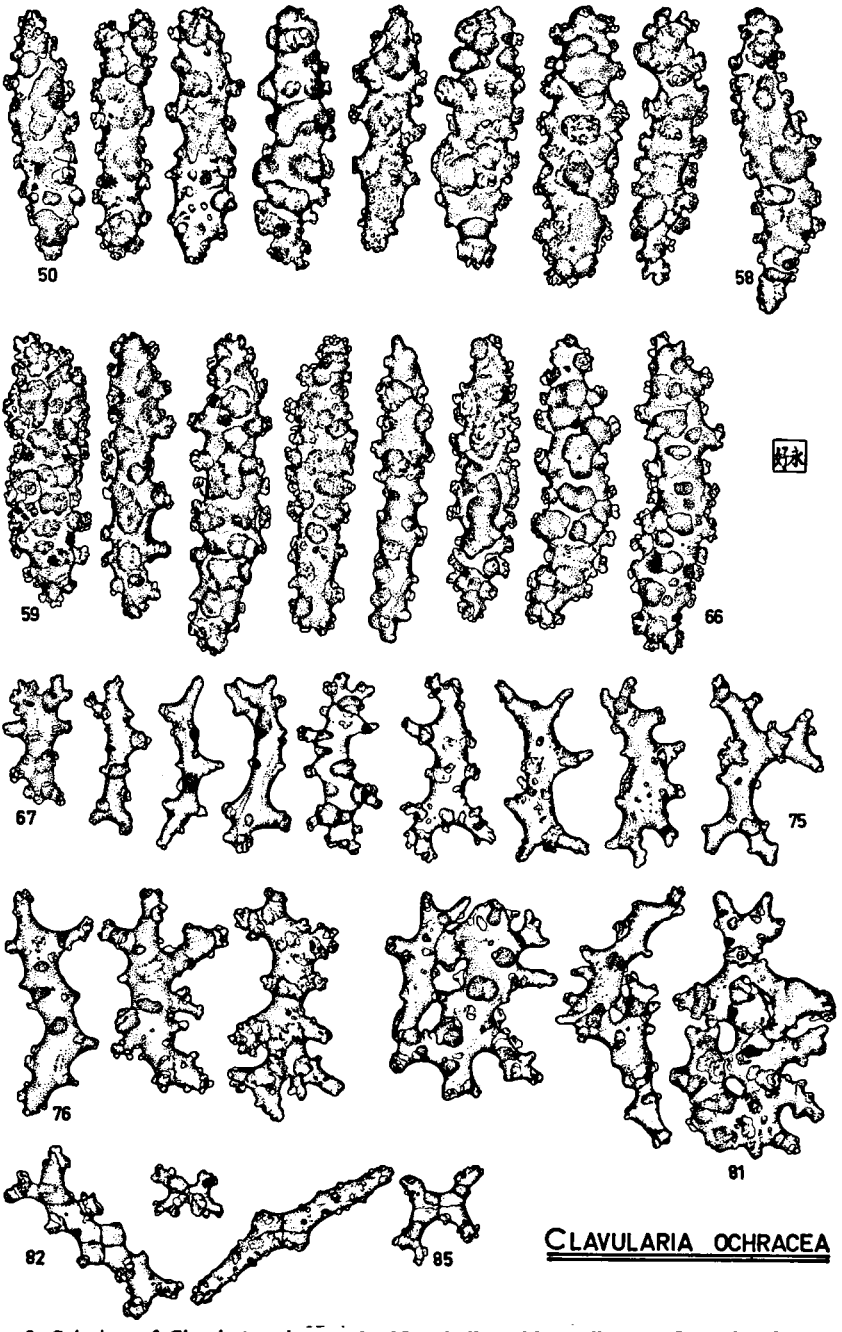


Plate 8. Sclerites of *Clavularia ochracea*. 1—15: spindles with small warts, from the chevrons; 16—25: slender spindles with coarse warts, from distal part of anthostele; 26—66: plump spindles with coarse warts, from proximal part of anthostele; 67—81: irregular plates from the stolons.

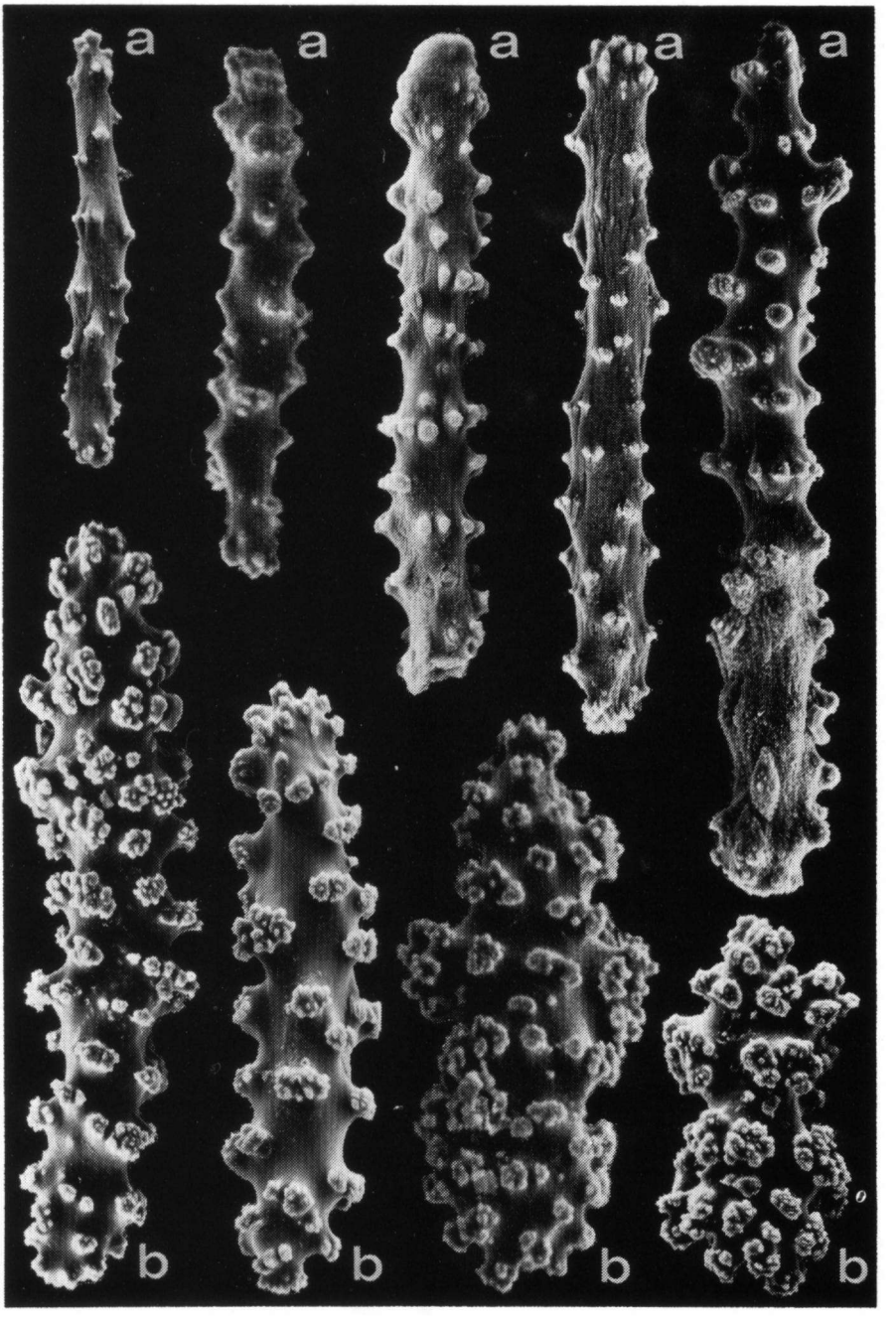


Plate 9. Sclerites from the polyps of *Clavularia ochracea*. a: sclerites from anthocodia; b sclerites from anthostele. Magnification: 400 x.

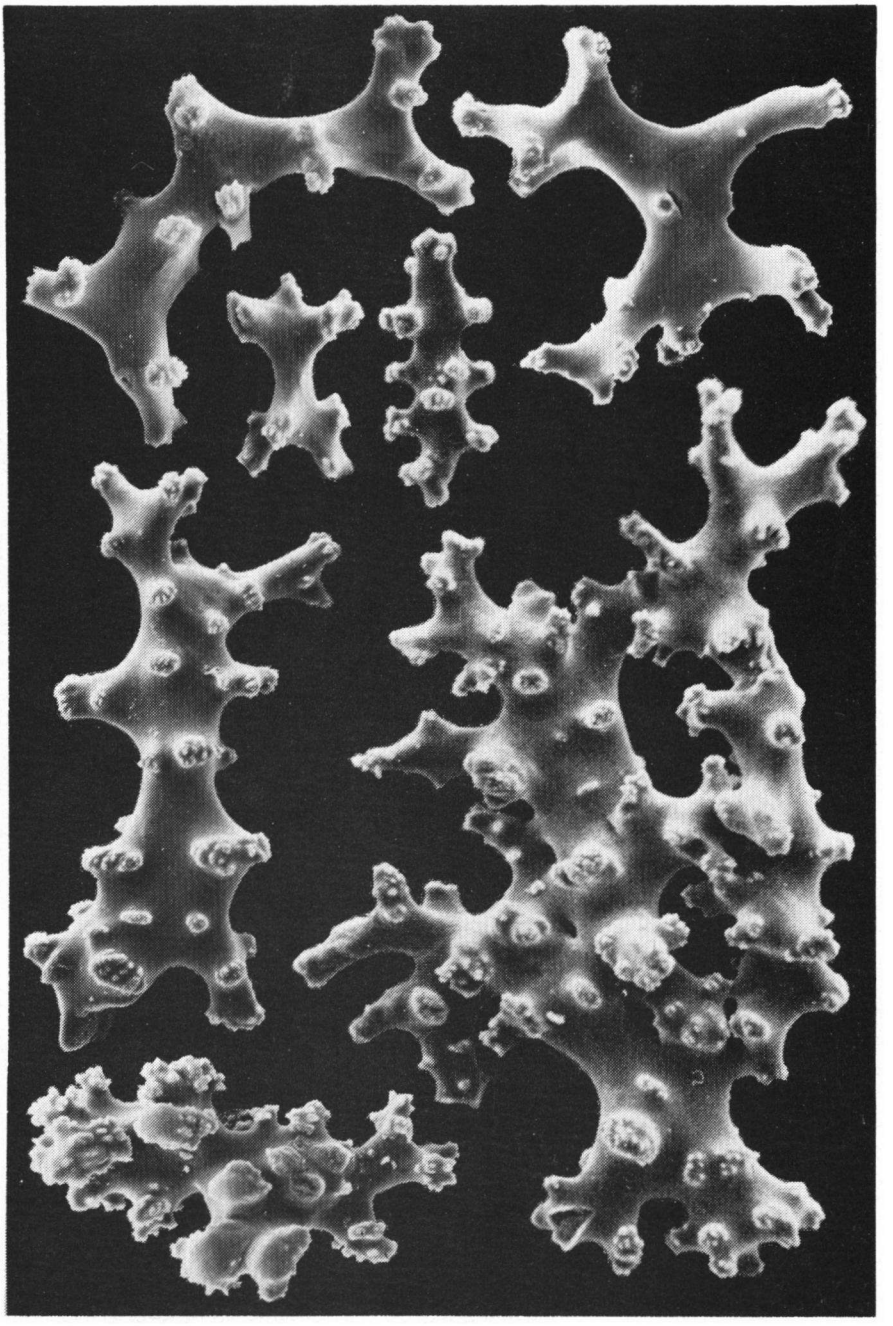


Plate 10. Sclerites from the stolons of *Clavularia ochracea*. Note how complex forms arise when several sclerites fuse together. Magnification: 400 ×.

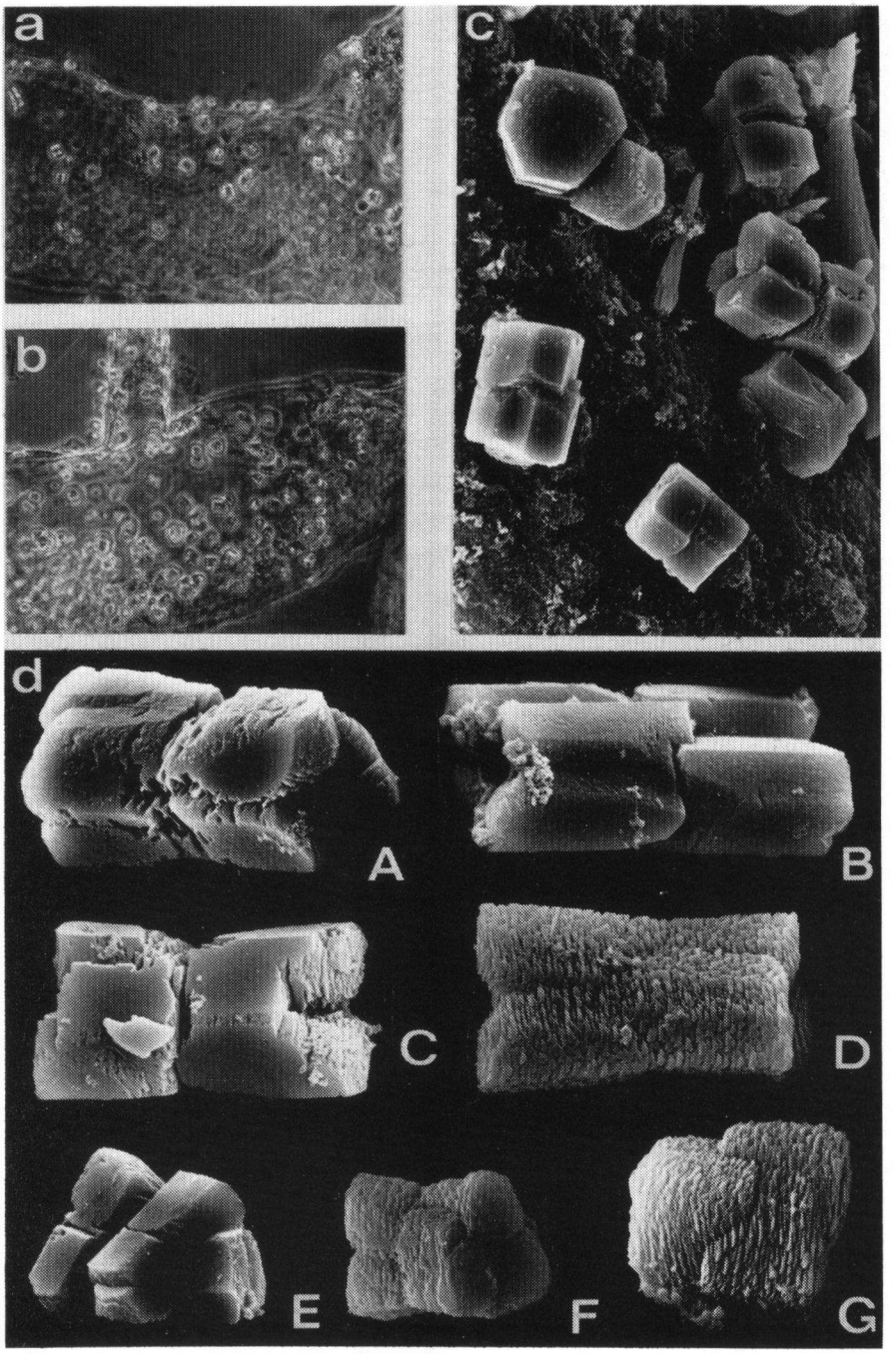


Plate 11. Rectangular, crystal-like "sclerites" from *Clavularia ochracea*. a, b: as seen by light-microscopy on the tentacles (180 ×); c: the same as seen by Scanning Electron Microscopy (1600 ×); d: details of some "sclerites", all consisting of two halves of three parts each, some of them being smooth (A, B, C, E) while others (D, F, G) consist of crystalline sub-units (3000 ×).

anthostele; length 110—140 µm (Plate 8, sclerites 16—25);
— plump spindles with coarse warts, mainly from the proximal part of the anthostele; length 80—310 µm (Plate 8, sclerites 26—66);
— irregular flattened sclerites, sometimes fused together, mainly from the stolons; length 125—260 µm (Plate 8, sclerites 67—81).

Some scanning electron micrographs of typical sclerites are shown in plates 9 and 10.

Quite recently, Tixier-Durivault & Lafargue (1968) described a new clavularian species from 12 m depth at Banyuls-sur-Mer, the same locality where my specimens of *C. ochracea* were found. The ecology of their species, *C. inordinata,* corresponds exactly with that of *C. ochracea.* I often found the species from Banyuls under overhanging rock ledges, in some cases together with *Cornularia cornucopiae.* It is interesting to quote Von Koch (1891) in this respect: "*Cornularia cornucopiae* kommt im Golf von Neapel häufig vor und zwar immer in geringer Tiefe und meist gesellschaftlich mit *Clavularia ochracea* . . .". As to the morphology of the species, contrarily to what is claimed by Tixier-Durivault & Lafargue (1968) *C. inordinata* differs very little, if at all, from Von Koch's species. They mentioned 11—12 pairs of pinnules per tentacle, against 10—12 mentioned for *C. ochracea* (cf. Von Koch, 1891). The sclerites also correspond with those described for *C. ochradea* (cf. Von Koch, 1891), for *C. petricola* (cf. Kowalewsky & Marion, 1883), and with my own description (see above), in form as well as in size. Table I sums up the size ranges for sclerites from the polyps (anthostele and anthocodia), and those for sclerites from the stolons, as quoted and/or depicted by the various authors. It should be pointed out that the size of octocorallian sclerites being extremely variable, only the approximate size can be taken into consideration when comparing small numbers of sclerites.

Table I. Comparison of the length of sclerites from the polyps and the stolons of *C. petricola* (Kowalewsky & Marion, 1883) (1), *C. ochracea* (Von Koch, 1878, 1891) (2), *C. inordinata* (Tixier-Durivault & Lafargue, 1968) (3) with those of our own specimens of *C. ochracea* (4).

	polyps	stolons
1	80-250 µm	110-135 µm
2	100-250 µm	90-170 µm
3	110-290 µm	150-180 µm
4	80-410 µm	125-260 µm

The only difference lies in the fact that according to Tixier-Durivault & Lafargue (1968) the anthocodia, tentacles and pinnules of *C. inordinata* were entirely covered with minute (10—20 µm) oval sclerites. This would rather indicate a similarity with *C. marioni* (see next section). In some of our specimens these small "sclerites" were also observed, but although very numerous in some specimens (Plate 7D), they were absent in others (Plate 7B). Detailed observation of these "sclerites" showed that they are small

rectangular crystals (Plate 11). I do not know whether these crystals are of biologic origin (excretion, Protozoa?), or whether they should be looked upon as artifacts. I have not encountered these structures on the live tentacles (Plate 7B) that I have observed, but on the other hand they are also absent in many of the preserved animals. Larger crystalline structures were also observed (Plate 7D). The extreme variability of this character (compare with the subtentacular sclerites of *Eunicella* in Weinberg, 1976) makes it useless as a specific character.

I must therefore conclude that the species *C. inordinata* is not valid, and should be placed in synonymy with *C. ochracea* Von Koch, 1882.

The species occurs from 0.5 m (Kowalewsky & Marion, 1883; personal observation) to 25 m depth (personal observation). So far it has only been found in Naples (Von Koch, 1882, 1891), Marseilles (Kowalewsky & Marion, 1883; Bérenguier, 1954; Mr. J. Marinopoulos, personal communication), and Banyuls (Tixier-Durivault & Lafargue (1968), personal observation), but it may occur in other localities as well.

Kowalewsky & Marion (1883) observed planulae in June; the specimens described by Tixier-Durivault & Lafargue (1968), which were collected in the second half of June, contained eggs, as did some of my own specimens collected during the same period.

I wish to stress the fact that the separation of the species *C. crassa* and *C. ochracea*, their morphology being very similar, is based mainly upon Kowalewsky & Marion's (1883) observations on their different modes of reproduction. The rather peculiar way in which *C. crassa* incubates its eggs has recently been observed by d'Hondt & Tixier-Durivault (1975). However, reconfirmation of planulae emission by *C. ochracea* is needed to establish the validity of two distinct species with certainty.

Clavularia marioni Von Koch, 1891

(Collection ZMA: COEL. 7831)

Synonymy:
Clavularia Marioni Von Koch, 1891; Thomson, 1927
Clavularia marioni; Hickson, 1895; Tixier-Durivault & d'Hondt, 1975.
? Clavularia arctica; Bérenguier, 1954.

Von Koch (1891) described a new species which he called *Clavularia Marioni*. According to his description, it differed in some anatomical respects from *C. ochracea:* the tentacles are densely covered with small sclerites (whereas those of *C. ochracea,* according to him, contained only a few), and the sclerites from the stolons differ in form and size (Plate XXV figs. 4, 5 and 9). Moreover, *C. marioni* lives in deeper water, whereas *C. ochracea* is encountered in shallow depths. Since then, many authors have considered the two species to be identical, possibly ecotypes living in different depths. The only times that *C. marioni* was mentioned in the past fifty years,

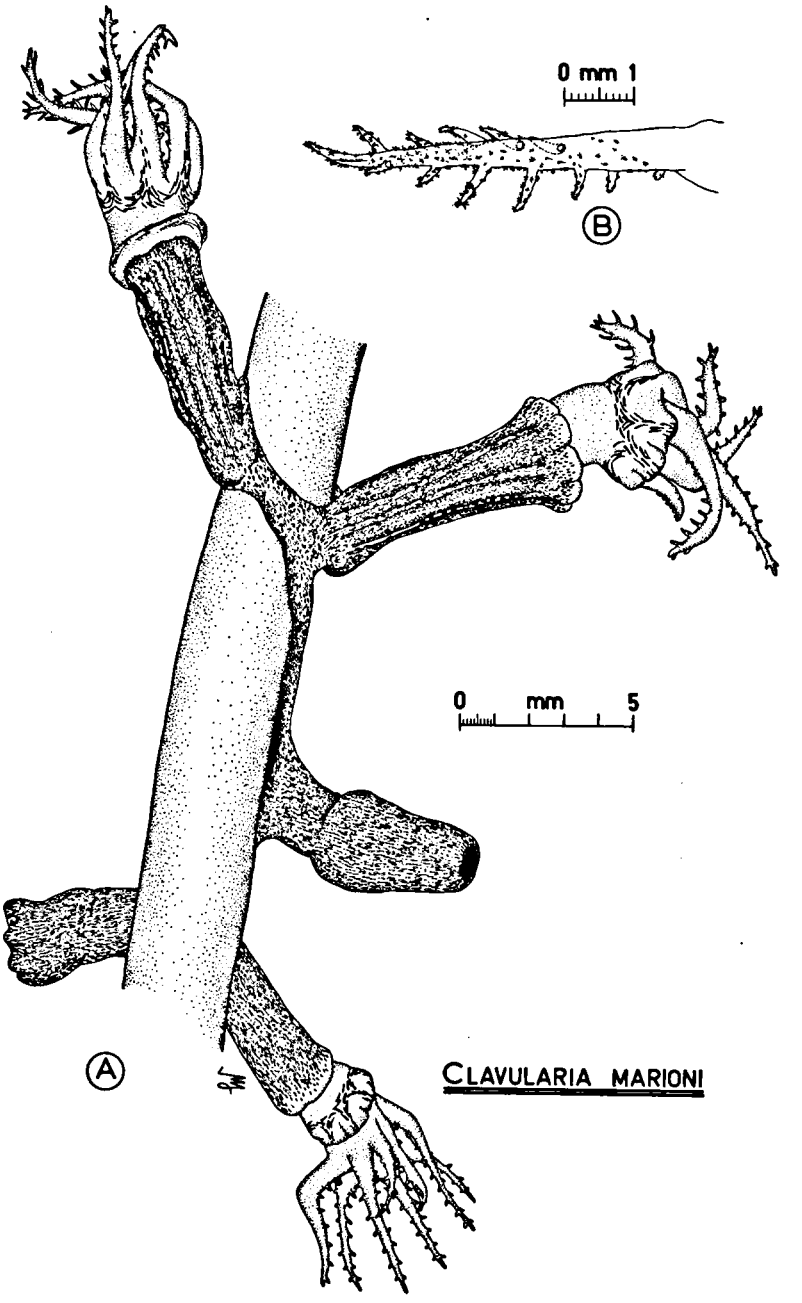


Plate 12. A: colony of *Clavularia marioni* growing on the stem of a brown alga; B: detail of a tentacle bearing small needle-like crystals.

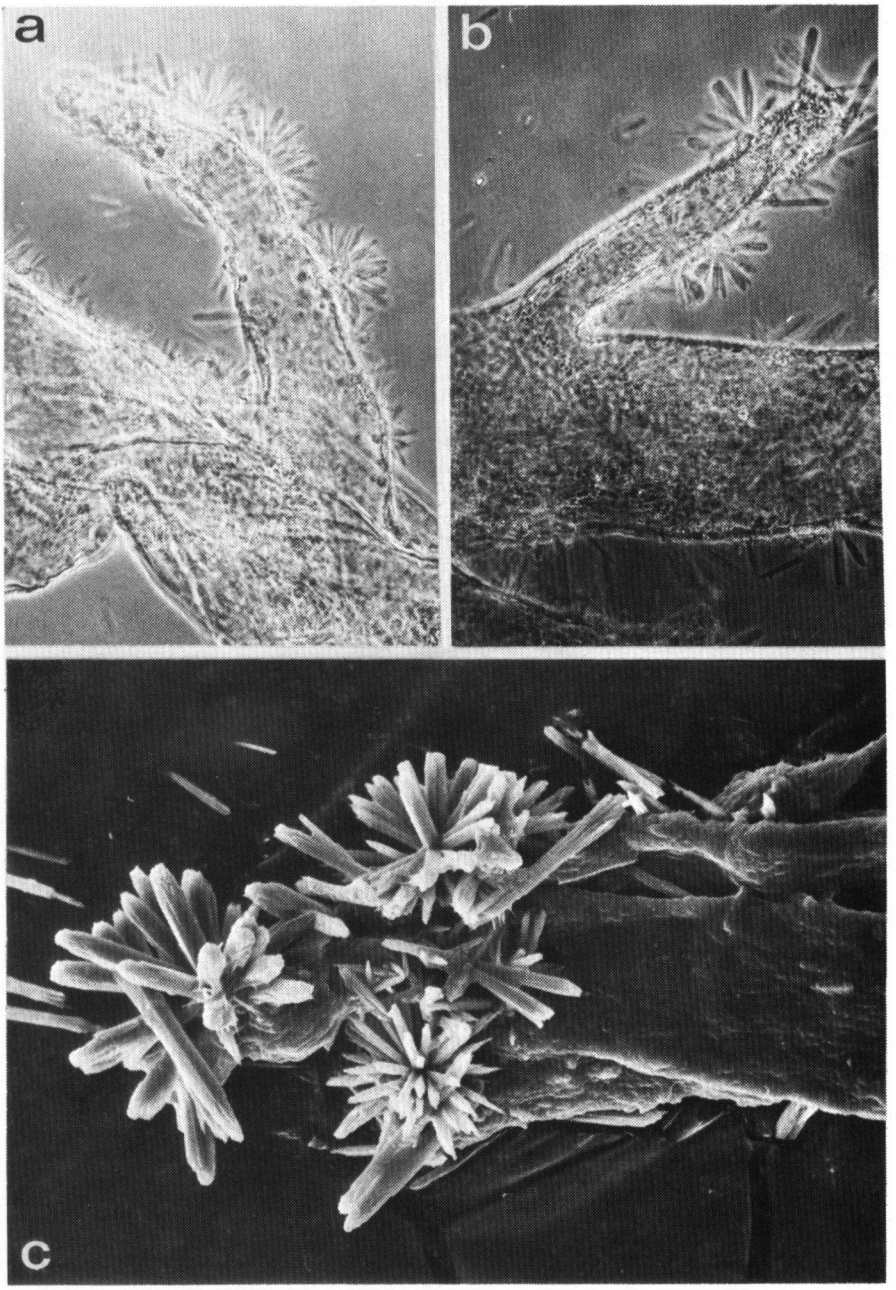


Plate 13. Details of "nests" of crystals on the tentacles of *Clavularia marioni*. a, b: light microscopy (185 ×); c: Scanning Electron Microscopy (540 ×).

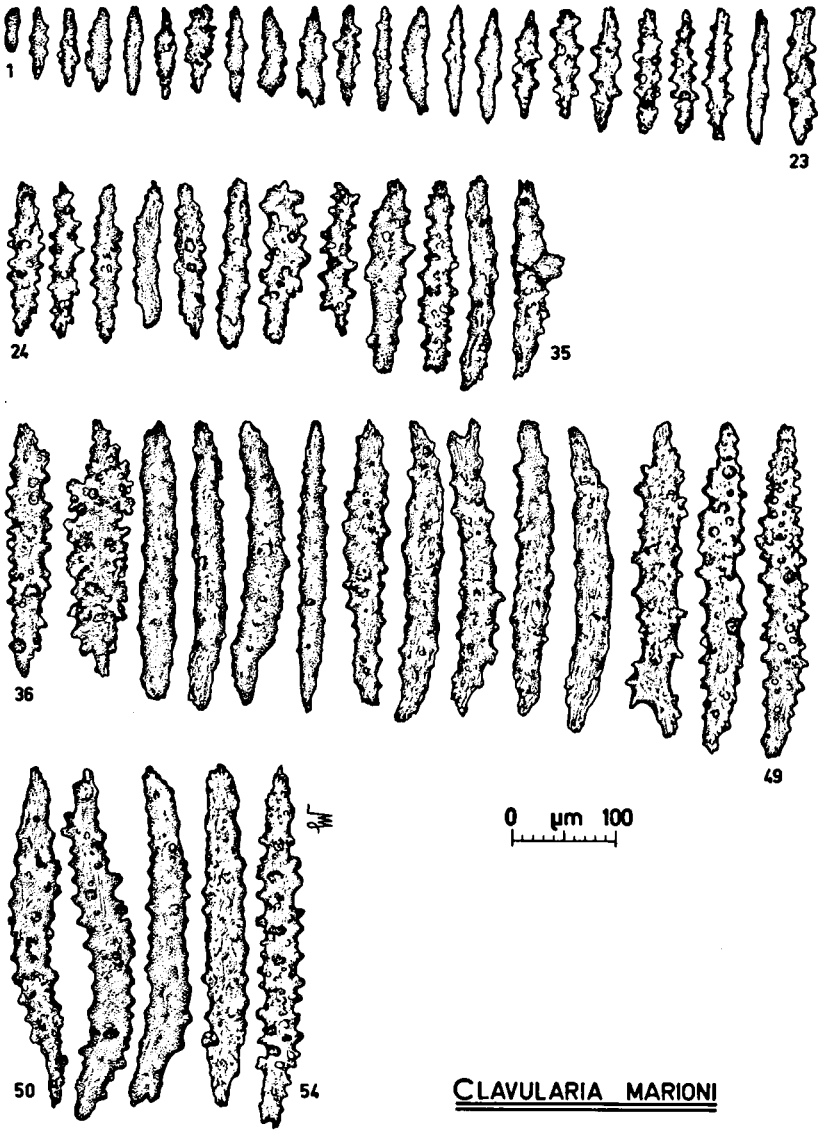


Plate 14. Sclerites of *Clavularia marioni*. 1—35: spindles from anthocodia; 36—54: spindles from stolons.

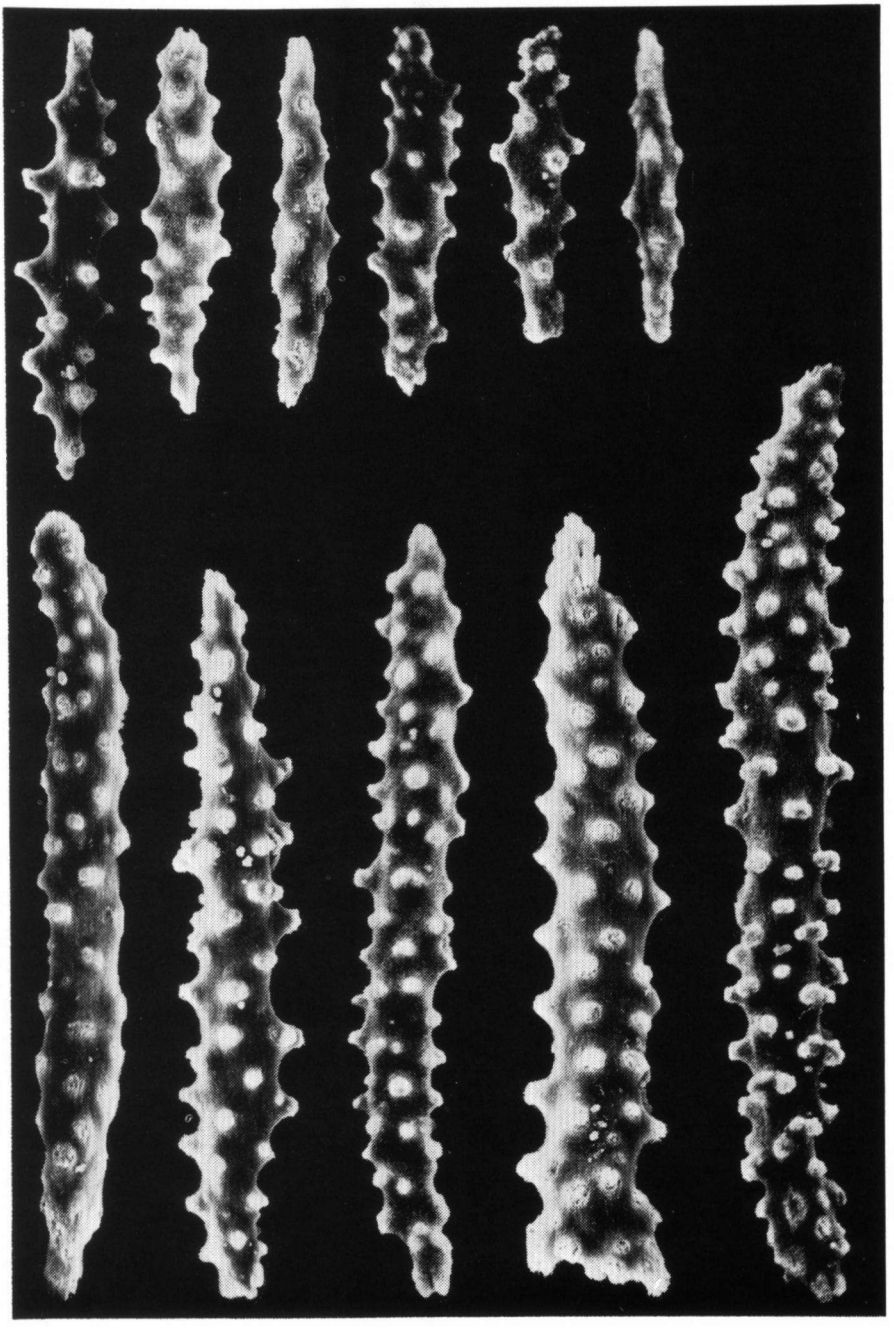


Plate 15. Sclerites of *Clavularia marioni*. Upper row: spindles from anthocodia; lower row spindles from stolons. Magnification: 400 ×.

specimens from greater depths were found: at 845—2165 m (Thomson, 1927) and 1735 m (Tixier-Durivault & d'Hondt, 1975). Bérenguier (1954) also described specimens from deep water, which she identified as belonging to *C. arctica*. It may well be, however, that in this case it was also *C. marioni* that was found (no material of Bérenguier subsists at the Station Marine d'Endoume, Marseilles). Comparison of the stolonal sclerites of *C. arctica* (cf. Bérenguier, 1954; pl. IV) with those of *C. marioni* (cf. Von Koch, 1891; pl. XXV fig. 9) strongly suggests this possibility. I failed to obtain Von Koch's type-material at the Stazione Zoologica of Naples, but a specimen was sent to me (ZMA: COEL. 7831) bearing the following label: "Bocca Piccola, Napoli, — 70 m 15/03/1956". According to the depth mentioned, it was found in the circalittoral zone as defined by us (Weinberg, 1977: footnote p. 132). I therefore include the species in my revision, and a brief description of the only specimen in the ZMA-collection will follow.

The colony, growing on the stem of a brown alga (Plate 12A), consists of five polyps connected to each other by means of a flat, broad (up to 1.1 mm) stolon. The polyps measure up tot 14 mm in height, the tentacles are about 5 mm long, bearing 8 to 10 pinnules on either side. According to Von Koch (1891), the tentacles as well as the pinnules are densely covered with sclerites. I did not find those on my specimen. Instead, crystalline structures strongly suggesting aragonite were found (Plates 12B, 13). Again (see preceding paragraph) these may be of biological origin (compare with the radiolarian *Sticholonche zanclea*, for instance), or be an artifact (smaller "nests" of these needle-like crystals were found on other Octocorallia, but also on different substrata, such as algae).

The anthocodiae are covered by small spindles, their length ranging from 40—210 μm (mean: 123.8 μm) and their width being comprised between 10—40 μm (mean: 25.4 μm). Form and size correspond with those given by Von Koch (1891: Plate 25), so that in spite of the absence of tentacular sclerites, I believe my specimen to belong to the species *C. marioni*.

The sclerites from the stolons are slender spindles with small warts, their length ranging from 240—350 μm (mean: 295.3 μm) and their width ranging from 25—65 μm (mean: 43.7 μm). Both types of sclerites appear in Plates 14 and 15.

"Anthelia" inermis Bérenguier, 1954

Synonymy:
Anthelia inermis Bérenguier, 1954

The species was described only once, by Bérenguier (1954: 61; Plate IIC, D). According to this author, it lives under stones in a depth of only 50 cm. The stolons are membranaceous and are covered by a mucous veil. The extremely transparent polyps occur either isolated or in groups. When completely retracted, they have a globular appearance, and are protected by a sheath of different agglomerated particles. On the ground of these

characters, I do not think that Bérenguier saw specimens of *Cornularia cornucopiae*. No sclerites are found. On the ground of the retractility of the polyps, the species does not belong to the genus *Anthelia*. The other species described by Bérenguier as belonging to *Anthelia* were representatives of *Clavularia* (see preceeding sections). But if this species does not possess sclerites, it does not belong to the latter genus either. If specimens of *inermis* are to be found again, it might turn out to belong to a genus of its own. So far, I have not been able to find the species, nor did I find any material in several European Museums. *A. inermis* therefore remains rather enigmatic. As even no type-material could be traced (it was probably thrown away by Bérenguier!), I can give no more details than the above résumé of Bérenguier's text. The reproduction of *A. inermis* is different from the other Mediterranean Stolonifera, as it is oviparous. Eggs are expulsed in May-June. So far, the species has only been found near Marseilles.

Genus **Rolandia** De Lacaze-Duthiers, 1900

The genus *Rolandia* was created by De Lacaze-Duthiers (1900) for a Mediterranean species which he called *Rolandia coralloïdes* (sic). Subsequently, some authors (Müller, 1910; Pax & Müller, 1962; Laubier, 1966) demonstrated the species to be a junior synonym of *Evagora rosea* Philippi, 1842 (see below). Since its discovery, the species has been shifted from one genus to another; some of these genera were new ones erected to fit the characteristics of the species (*Evagora, Rolandia*), whereas others were already existing genera to which the species was thought to belong (*Rhizoxenia, Clavularia, Sarcodictyon, Zoantha*).

By application of the priority rule of zoological nomenclature, Pax & Müller (1955) established the genus *Zoantha* as being the correct one by saying that: ". . . il genere di Stoloniferi Zoantha (Lesson, 1830) ha la priorità sul genere degli Zoantari Zoantha (Dana, 1849)". This, however, is not correct. The zoantharian genus *Zoantha* was not erected by Dana, 1849 but by Lamarck, 1801. The stoloniferan generic name *Zoantha* Lesson, 1830 is therefore invalid, since it is preoccupied. Furthermore, the type-species, *Zoantha thalassantos* (Lesson, 1830; sp. 52, p. 87) is a typical clavularian (Lesson, 1826; Pl. I fig. 2). Hickson (1895) and May (1900) therefore reunited the genera *Zoantha* and *Clavularia*. Müller (1910), on the other hand, maintained *Rhizoxenia* (see below) as a separate genus. This genus was erected in 1834 by Ehrenberg to replace the name *Zoantha* Lesson. As was pointed out above, the type-species *Zoantha* (*Rhizoxenia*) *thalassanthos* should probably become *Clavularia thalassanthos*. Whether this is the case or not, the Mediterranean species described by Philippi (1842) and De Lacaze-Duthiers (1900) does not belong to the genus *Rhizoxenia*, its habitus being entirely different: the species *R. thalassanthos* possesses high anthosteles stiffened by sclerites, the Mediterranean species lacks sclerites in the polyps. The generic name *Evagora* Philippi, 1842 is invalid, being twice preoccupied

by *Evagora* Péron & Lesueur, 1810 (Hydrozoa) and *Evagora* Laporte & Gory, 1839 (Coleoptera). The genera *Zoantha*, *Rhizoxenia* and *Evagora* being ruled out, we still have to consider *Clavularia*, *Sarcodictyon* and *Rolandia*.

Diagnosis of the genus *Clavularia* De Blainville, 1830: "Polyps simple, arising from bandlike or membranous stolons; important anthocodial armature; sclerites including simple spinous spindles, rods or clubs, and a few double forms" (after Bayer, 1956 and Tixier-Durivault, 1966). The Mediterranean species that we will deal with below possesses very characteristic plate-like coenenchymal sclerites, the anthocodiae being devoid of skeletal elements.

Diagnosis of the genus *Sarcodictyon* Forbes, 1847: "Stolons form anastomosing network; anthosteles low and conical; spicules irregular rods, stars or crosses solidly fused together. Anthocodial armature of 8 triangular fields of spindles" (after Deichmann, 1936 and Bayer, 1956). The sclerites of our species are not fused together at all, the anthocodiae, as mentioned before, are practically devoid of sclerites. Besides, Hickson (1930) had already decided against synonymy of *Sarcodictyon* with *Rhizoxenia*.

It appears, therefore, that the only remaining generic name, *Rolandia* De Lacaze-Duthiers, 1900, should be employed for the species which will be described below. Diagnosis of the genus *Rolandia:* "Stolons simple or anastomosing to form thick membranes; coenenchyme fleshy, composed of an outer layer with and an inner layer without sclerites; polyps fully retractile, devoid of sclerites; coenenchymal sclerites irregular biscuit-like platelets covered with minute asperities; many cross-shaped double forms". Type species: *Rolandia rosea* (Philippi, 1842), by monotypy.

Rolandia rosea (Philippi, 1842)

(Collection ZMA: COEL. 2, 7773, 7775, 7776, 7777, 7783, 7784, 7785 (dredged), 7786)

Synonymy:

Evagora rosea Philippi, 1842
Rhizoxenia rosea; Dana, 1846
Rhizoxenia rosea; Milne Edwards, 1857
Rhizoxenia rosea; Marion, 1882
Rhizoxenia rosea; Graeffe, 1884
Rhizoxenia rosea; Carus, 1885
Rhizoxenia rosea; Stossich, 1885
Rhizoxenia rosea; Von Koch, 1891
Clavularia danae Hickson, 1895
Rolandia coralloïdes De Lacaze-Duthiers, 1900
Rhizoxenia rosea; Lo Bianco, 1909
Rhizoxenia rosea; Thomson, 1927
Evagora rosea; Molander, 1929
Evagora corii Broch, 1935
Rhizoxenia rosea; Stiasny, 1941
Sarcodictyon catenatum; Bérenguier, 1954
Zoantha rosea; Pax & Müller, 1955
Rolandia coralloides; Rossi, 1958
Zoantha rosea; Pax & Müller, 1962
Zoantha corii; Pax & Müller, 1962
Zoantha rosea; Laubier, 1966

The species was first described as *Evagora rosea* by Philippi (1842). We translate part of his original description: "The individual polyps measure hardly 3‴ [= 6.3 mm] in length and ⅔‴ [= 1.4 mm] in width when fully

extended. Basal part firm, almost leathery, and the upper part may retract completely in this basal part. Lives [. . .] on barnacles and dead oyster shells, adhering by its base, from which grow narrow sprouts which are easily overlooked, at the end of which new polyps arise, and so on, but it is rare to find more than six to ten polyps clinging to each other this way". This description corresponds with the mode of growth depicted in my Plate 16B. The author also gave a figure, but it is too small to give precise information. He concluded with the question whether the species should be considered to belong to Ehrenberg's genus *Rhizoxenia*. I have ruled out this possibility in the discussion concerning the genus (see above).

The next extensive description, as *Rhizoxenia rosea*, is the one by Von Koch (1891). Some parts of his text follow: "Die festeren Theile, basale Abschnitte der Polypen ("Kelche") und Stolonen sind carminroth, welche Farbe durch eine überliegende farblose Schicht eigenthümlich gedämpft wird, und die weichen einziehbaren, oralen Abschnitte der Polypen sind zart rosa oder ganz farblos. [. . .]. Die Polypen sind ausserordentlich contractil, was sich durch das Fehlen der Kalkkörper in dem grössten Theil der Wandung erklärt. Die Tentakel [. . .] stülpen sich ähnlich wie die von Corallium theilweise um. [. . .]. Die Form [of the spicules] ist am einfachsten als Cylinder mit je 3 in Quincunx gestellten Fortsätzen an beiden Enden zu bezeichnen, auch lassen sich Abweichungen von diesem Typus fast alle als Abplattungen auffassen. [. . .]. Auf der Oberfläche sitzen kleine conische Wärzchen. Die Farbe ist gelbroth. Die Länge beträgt ca. 0.05 mm. [. . .]. Auf grösseren Flächen, wie [. . .] Steinen, Muschelschalen etc. [. . .] stehen die Polypen oft in grosser Entfernung von einander und sind dann durch nahezu gerade, schmale Stolonen mit einander verbunden [see my Plate 16B]. [. . .]. Auf Gorgonienachsen, die von Rhizoxenia sehr gern bewohnt werden [. . .] sind [. . .] die Stolonen verbreitert und so mit einander verschmolzen, dass sie über weite Strecken hin einen gleichmässigen Überzug bilden, auf dem [. . .] die Polypen mehr oder weniger regelmässiger vertheilt, aber ziemlich dicht bei einander stehen [see my Plate 16A]".

The next, and most complete, description is the one given by De Lacaze-Duthiers (1900). He created *Rolandia coralloïdes* n.gen., n.spec.. It is astonishing that he should not have read Von Koch's paper, because his description resembles item by item that of the German author: "Mais un caractère général du zoanthodème [. . .], c'est que la couleur semble voilée par une légère couche blanchâtre, formant une membrane [. . .]. Dans l'état de contraction absolue, [. . .] (J'ai déjà [. . .] décrit cet état pour la Polype du Corail) les tentacules n'étant pas doublés par des corpuscules solides sont d'autant plus flexibles et peuvent s'invaginer dans la cavité périoesophagienne qui leur correspond. [. . .]. La forme la plus générale des spicules [. . .] est [. . .] celle d'un biscuit à la cuiller, c'est à dire d'un corps allongé à extrémités arrondies et un peu étranglé dans le milieu de sa longueur. [. . .]. La largeur moyenne [. . .] est de 45 à 50 μm. [. . .]. Sarcosome étalé en

lame envahissante, parasite, surtout sur les axes des Gorgones".

I insist upon a comparison of both texts, because it is only by establishing with certainty that *Rolandia coralloides* is a junior synonym of *Rhizoxenia* (*Evagora*) *rosea* that the name *Rolandia rosea* becomes justified. As after these extensive quotations a complete description of the species seems hardly necessary, I will briefly summarize its main characteristics.

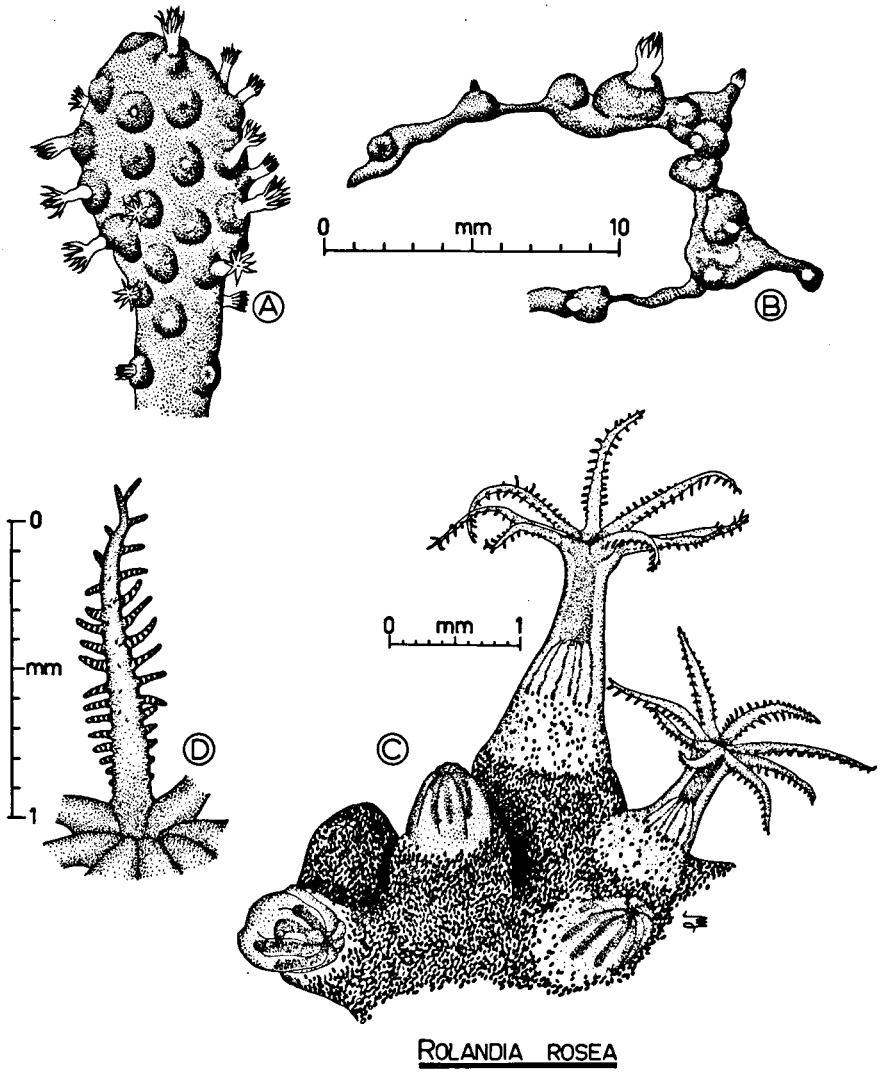


Plate 16. *Rolandia rosea.* A: colony encrusting the branch of a dead gorgonian; B: colony consisting of a stolon and single polyps growing on rock; C: detail of polyps (note retracted polyps invaginate their tentacles); D: detail of a tentacle.

The colonies consist either of rows of polyps arising at irregular intervals from the stolons (Plate 16B), or the stolons fuse to form thick membranes from which the polyps arise at short distances from each other (Plate 16A), mostly on nude gorgonian axes. These differences probably have an ecological origin: few organisms seem able to cover gorgonian axes (*Parerythropodium coralloides* has a similar mode of growth, see Weinberg, 1975, 1977) and spatial concurrence is therefore very limited on this substratum, enabling the species to reach its maximum development. On other substrata, the concurrence by algae, sponges, bryozoans and synascidians is more important. I found one colony, however, forming a membrane covering a stone over an area of approximately 40 cm² (ZMA: COEL. 7783).

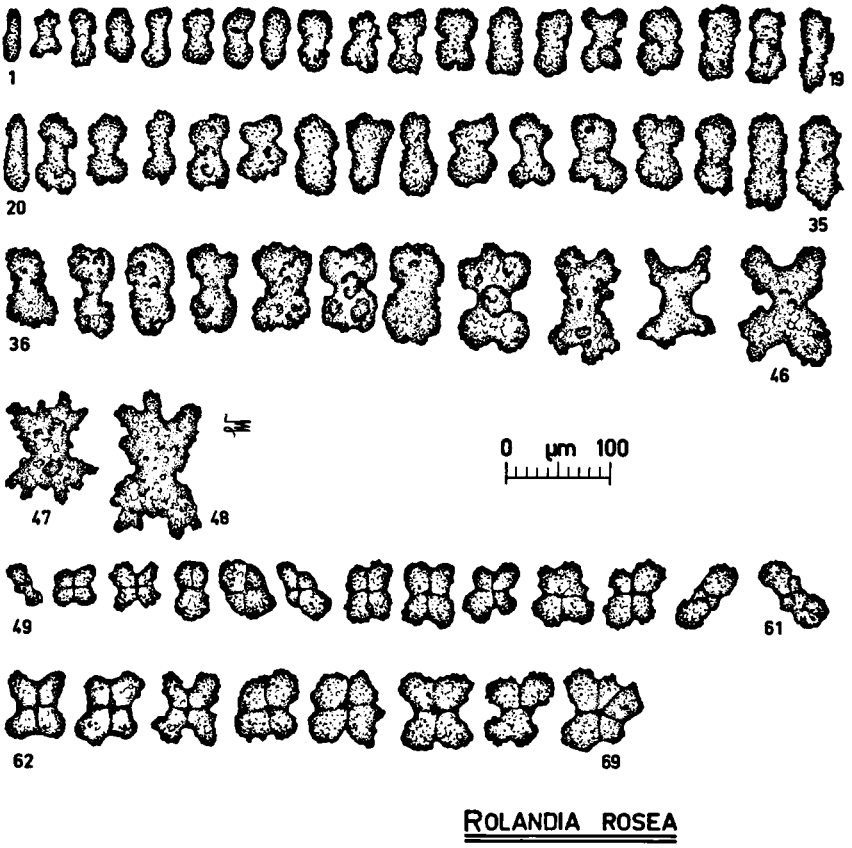


Plate 17. Sclerites of *Rolandia rosea*. 1—48: flattened double clubs; 49—69: fused "quadruplets".

The rather thick coenenchyme is composed of two distinct layers of equal thickness, an outer one containing brown-red sclerites, and an inner one lacking skeletal elements. The outer surface of living colonies is covered by a

thin mucous veil, which weakens their colour to a pinkish red. The polyps (Plate 16C) measure up to 2.5 mm in height when fully extended. The basal part of the anthostele takes on a rather inflated appearance in extended polyps, and is covered by sclerites. These diminish rapidly in number upwards, and fail completely in the anthocodiae and tentacles. The latter are very delicate and contain two rows of 15—18 pinnules each, which have a banded appearance due to concentrations of nematocysts (Plate 16D). The

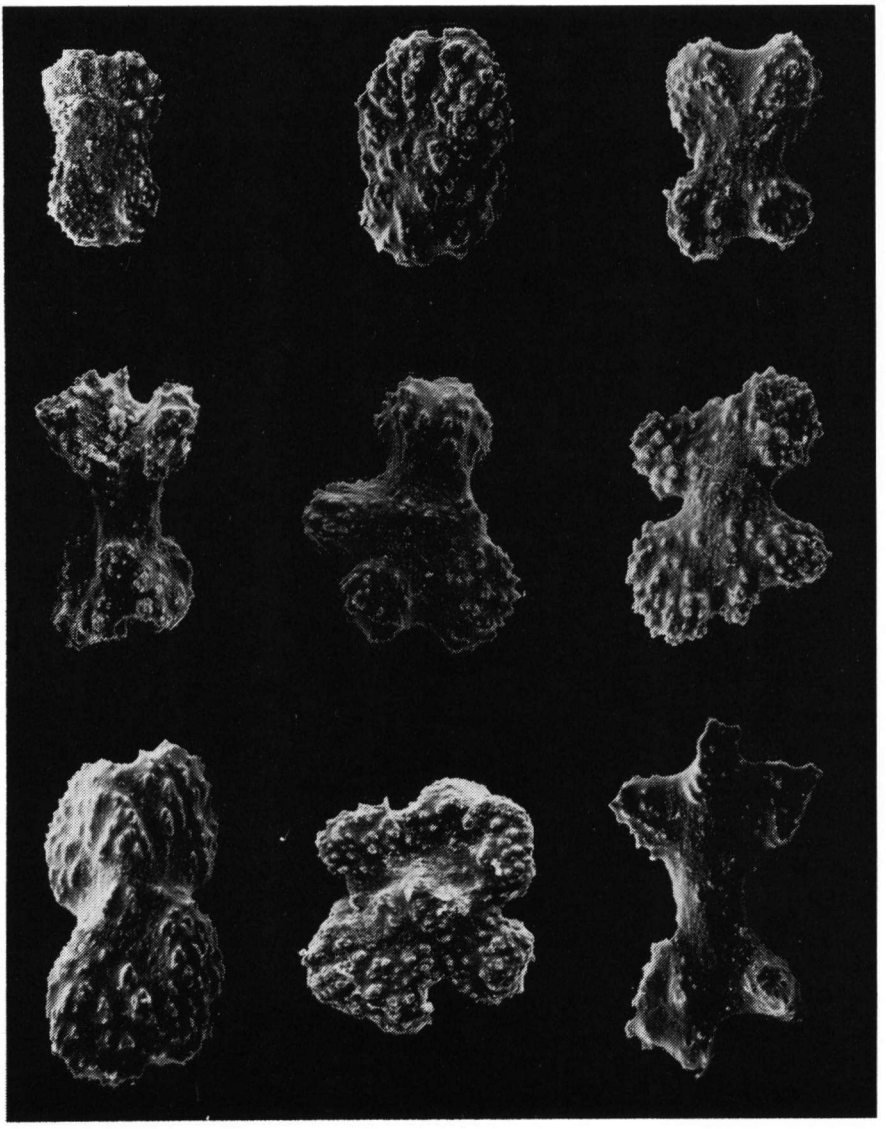


Plate 18. Sclerites of *Rolandia rosea*. Magnification: 500 ×.

polyps can retract completely, invaginating their tentacles into their gastrovascular cavities (see Plate 16C). The sclerites (Plates 17, 18) are irregular plates, often consisting of flattened double clubs. This type of sclerite is very rare among Octocorallia, and may explain why Von Koch (1891: 663) considered them to be flattened modifications of the cylindrous (?) sclerites he depicted as being the usual type in his fig. 13. De Lacaze-Duthiers (1900), on the other hand, figures (Plate XV fig. 11) the sclerites correctly. Their size (Plate 17) ranges from 40 to 110 μm. Numerous fused "quadruplets" are also present. Plate 18 shows some SEM-photographs of typical sclerites.

Bérenguier (1954) described the two growth forms of *Rolandia rosea*, coming to the right conclusion that both forms belong to the same species. Unfortunately she calls it *Sarcodictyon catenatum*, although Thomson (1927) had already noticed that this species differs from *"Rhizoxenia rosea"* by their "entirely different spicules". The sclerites drawn for both forms by Bérenguier (1954) (Plates VI, VII) correspond exactly with those figured by De Lacaze-Duthiers (1900), and not with those drawn by Herdman (1885) in his very thorough study of *Sarcodictyon catenatum*. Tixier-Durivault (1964) is therefore wrong when she remarks that the sclerites figured by Bérenguier (1954) are typical for *S. catenatum* and differ completely from those of *R. coralloides* (= *R. rosea*).

Broch (1935: 5—8, fig. 2) created a new species, *Evagora corii*, the description of which is analogous in all respects with the one I have given for *R. rosea*, although the author stated that his species is not identical with *Rhizoxenia rosea* Philippi sensu Sars. He was misled by the description of *R. rosea* given by Sars, who mistook it for *Clavularia crassa*. This confusion continued with Pax & Müller (1962), who maintained *Zoantha rosea* and *Z. corii* to be separate species. Sars' error is partially repeated in their paper (p. 262—264). The inconsistency of the description given by Sars with the one of Von Koch is noted by the authors, but they fail to reach any conclusion. I consider *Evagora corii* Broch, 1935, to be a junior synonym of *Rolandia rosea* (Philippi, 1842).

Finally, it is necessary to point out here that Molander (1929) makes two false statements, the first being (p. 7—8): "*Cornularia crassa* ist wahrscheinlich mit *Evagora rosea* [. . .] identisch". The fallacy of this statement, which was also made by Sars, becomes obvious when we compare the original description by Milne Edwards (1848) and Philippi (1842). The second error is (p. 41—42): "Der Versuch R. Müller's (1910) *Rolandia coralloides* mit *Evagora rosea* zu identifizieren ist nicht glücklich, denn die Spicula beider Arten sind sehr verschieden". We have shown in the present paper that the identity of both species is genuine. Molander (1929) concluded that *Rolandia coralloides* is synonymous with *Corallium rubrum*, which is definitely wrong.

Rolandia rosea is found on different substrata: stones, rock, shells, barnacles, rhizomes of *Posidonia*, the ascidian *Microcosmus sabatieri*, the gorgonian *Eunicella singularis*, in depths ranging from just below the surface

(Marion, 1882) to 200 m (Lo Bianco, 1909). My specimens come from 15 m (Pier Port Vendres, ZMA: COEL. 2) to 90 m (on a *Microcosmus* dredged off Banyuls, ZMA: COEL. 7785). I encountered the species in light intensities ranging from 1—11% as compared to surface values.

Rolandia rosea occurs in the Adriatic Sea (Graeffe, 1884; Stossich, 1885; Broch, 1935; Pax & Müller, 1962), in the Gulf of Naples (Von Koch, 1891; Lo Bianco, 1909), in the Gulf of Marseilles (Marion, 1882; Bérenguier, 1954), near Banyuls-sur-Mer (De Lacaze-Duthiers, 1900; personal observation) and near Algeria (De Lacaze-Duthiers, 1900).

Lo Bianco (1909) noted the finding of eggs in September. In some of my specimens, collected in July, eggs were also observed. Planulae were seen by Graeffe (1884) from May till June.

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