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Revision of the common Octocorallia of the Mediterranean circalittoral. I. Gorgonacea.

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ABSTRACT

Five gorgonian species are common on the rocky substratum of the Mediterranean circalittoral zone (Eunicella singularis, E. cavolinii, Lophogorgia ceratophyta, Paramuricea clavata, Corallium rubrum). Application of the priority rule of zoological nomenclature led to the renaming of two species. A complete description of all these animals is given, including colony form, morphology of the polyps, morphology and morphometry of the spicules. The latter were observed by means of light microscopy and scanning electron microscopy. Some new types of spicules were encountered. A short description of the ecology of each species is given.

Résumé

Cinq espèces de gorgones sont communs sur le substrat dur du circalittoral méditerranéen (Eunicella singularis, E. cavolinii, Lophogorgia ceratophyta, Paramuricea clavata, Corallium rubrum). L'application de la règle de priorité de la nomenclature zoologique a donné lieu à un changement de nom pour deux espèces. Une description détaillée de tous ces animaux est donnée, comprenant la morphologie des colonies entières et celle des polypes, et la morphologie et la morphométrie des spicules. Ces derniers furent observés à l'aide de deux techniques différentes: microscopie photonique et microscopie électronique à balayage. Quelques types nouveaux de spicules furent rencontrés. L'écologie de chaque espèce est abordée sommairement.

INTRODUCTION

The systematics of Octocorallia are a highly controversional and uncertain subject. Uncertainly is encountered for many species: because geographical data are lacking, because the ecology of the species is unknown or type-material is missing; in some cases it is even difficult to decide to which genus a species belongs.

The question may be put forward whether the systematical criteria that have been used up to now are the right ones. In the past, morphology of entire colonies has often led to an erroneous splitting into species, because the

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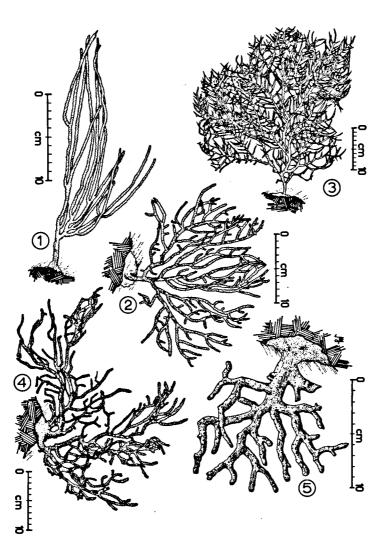


 Plate 1: Typical colony-forms for each of the species considered: 1. Eunicella singularis,
 2. E. cavolinii, 3. Lophogorgia ceratophyta, 4. Paramuricea clavata, 5. Corallium rubrum. The hatched areas indicate the substrate, and the colonies are drawn in their most characteristic natural positions.

authors failed to distinguish that gorgonians easily adapt themselves to variations of ecological factors, especially water movement (Théodor, 1963; Velimirov, 1973). It would certainly be useful, therefore, to take into consideration the ecological conditions wherein a species lives. In an earlier publication (Weinberg, 1975) we have tried to create a working method permitting to find the existing relationships between a species and several environmental factors. At present, we are pursuing this type of research. The classical and most used systematical criteria, however, remain purely morphological. Morphology, morphometry and distribution of the spicules throughout each species are most commonly used for the Octocorallia.

Notwithstanding the fact that all five species we studied are common and quite well-known, we think that this publication is justified since in many of the earlier descriptions, in spite of their respective qualities, certain data were left out. Either the figures fail to show enough detail, or they represent too small numbers of spicules, making it impossible to take into consideration the variability of this criterium within each species.

The publication by Carpine (1963), for example, contains some excellent pictures of spicules, but their number is too small. The comparison between three *Eunicella* species based upon these photographs therefore lacks objectivity, the dimensions of spicules being variable. On the other hand, the study made by Bérenguier (1954) comprises illustrations of large series of spicules for each species. Unfortunately, the quality of these drawings is very poor, so that actual comparison is impossible. Moreover, the magnification of the drawings is not given. An example of a good publication seems to be the one by Rossi (1960). The illustrations given by this author clearly show the morphology of the different types of spicules to be encountered within the three *Eunicella* species studied, as well as morphometric variation, which is obtained thanks to the study of sufficiently large series of spicules.

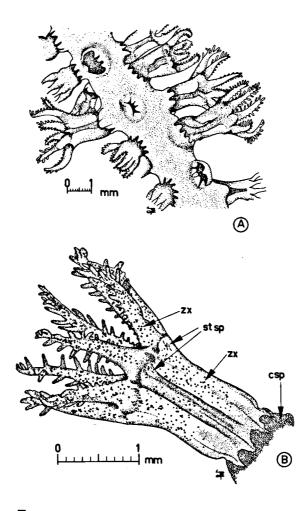
There are some other reasons which may justify the present study, the first being the fact that earlier publications often deal with only one or a few species belonging to those which are common to the circalittoral zone, and which to-day attract the attention of ecologists, physiologists and immunologists alike. As many of these publications are often quite ancient, it may be difficult for the present-day scientist to obtain some of them. We will therefore endeavour to present here a synthesis of most of the morphological and ecological criteria of these animals. Moreover, investigation of these earlier publications led to the renaming of two species.

The second reason lies in the fact that the gorgonians studied have often been described from badly preserved, or even dry material. In most of our cases we used gorgonians which were fixed with the polyps extended. In addition to this, many of these animals were observed alive. The morphology of the polyps therefore enters into consideration.

Finally, we have been able to make an extensive study of spicular morphology of the different species by means of Scanning Electron Microscopy. The results are pictures which contain more details than those presented by earlier workers.

MATERIAL AND METHODS

All specimens, which were collected by Scuba divers, were kept in



EUNICELLA SINGULARIS

Plate 2: A. Detail of a branch of *E. singularis*; note the different forms of the calyces. B. One single polyp with zooxanthellae (zx), sub-tentacular spicules (stsp) and coenenchymal spicules (csp) forming the calyx.

seawater basins until the polyps reached full extension, often after one night. Magnesium sulphate was then added, in a concentration of about 5 g/l, to anaesthetize the animals. After a few hours these were fixed with 10% formalin. Later, the colonies were transferred to jars containing 40% alcohol. All specimens are kept in the collection of the Zoological Museum of Amsterdam (ZMA).

Prior to fixation, the extremity of a branch was cut from each colony, and the soft tissues dissolved in cold and concentrated sodium-hypochlorite (Javel). The spicules settled as powder onto the bottom of the test tube.

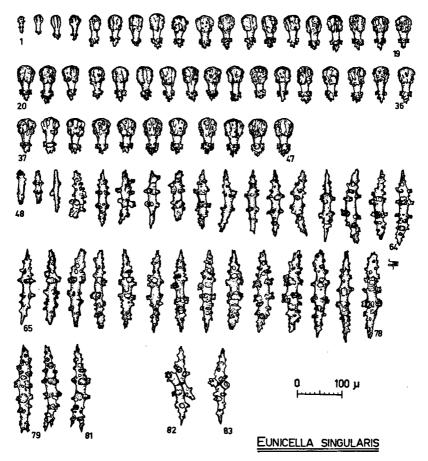


Plate 3: Spicules of *E. singularis*. 1—47: balloon-clubs from outer rind; 51—81: spindles from inner rind; 48—50: sub-tentacular spicules; 82, 83: cross-shaped spicules.

The Javel solution was then carefully sucked away with a pipette, and after several rinsings with distilled water the spicules were kept as dry powder.

The polyps were examined with a binocular microscope (Plates 2,7, 9, 13, 17).

The spicules were examined following two different techniques. The first, classical, one consists in dropping a small amount of spicule powder into a drop of water, and in mounting this drop between a cover-glass and a microscope slide. General form and colour of the spicules are thus easily observed. With this technique we have photographed large series of spicules. The pictures thus obtained, classified according to the species and according to the type of spicule, were reproduced by means of line drawings (Plates 3, 8, 10, 14, 18).

According to the second technique spicules are examined with the Scanning Electron Microscope (Stereoscan MkII, Cambridge). In order to obtain electrically conductive spicules they were covered with a layer of gold, evaporated in vacuo. This layer measuring only 200 Å in thickness, it does not dissimulate any detail. The resulting pictures contain more information than those obtained by other techniques (Plates 4, 5, 6, 11, 12, 15, 16, 19, 20).

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).

Wherever statistics are applied, we made use of SPSS (Statistical Package for the Social Sciences) programs on the Control Data 6000 computer of the Academic Computing Centre, Amsterdam.

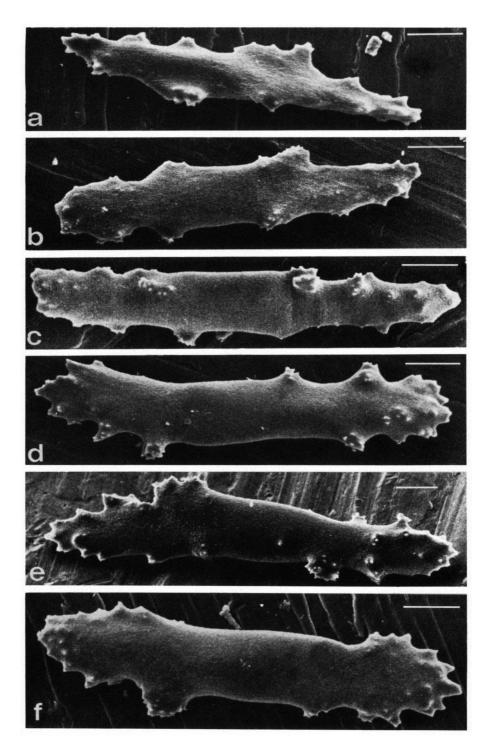
Suborder HOLAXONIA Studer, 1887 Family PLEXAURIDAE Gray, 1859 Genus Eunicella Verril, 1869

Eunicella singularis (Esper, 1794) (Collection ZMA COEL. 7468)

Synonymy:

Gorgonia viminalis var. singularis Esper, 1794 Gorgonia stricta Bertoloni, 1810 Gorgonia graminea Lamarck, 1816 Gorgonia Bertoloni Risso, 1826 Gorgonia graminea; Milne Edwards, 1857 Gorgonia verrucosa; Milne Edwards, 1857 Gorgonia graminea; Carus, 1885 Gorgonia verrucosa; v. Koch, 1887 Eunicella verrucosa; v. Koch, 1887 Eunicella stricta; Kükenthal, 1924 Eunicella verrucosa; Thomson, 1927 Eunicella verrucosa var. stricta; Stiasny, 1938 Eunicella verrucosa; Rossi, 1949 Eunicella graminea; Bérenguier, 1954 Eunicella verrucosa var. stricta; Abel, 1959 Eunicella stricta; Rossi, 1960 Eunicella verrucosa var. stricta; Pax & Müller, 1962 Eunicella stricta; Carpine, 1963 Enicella stricta stricta; Théodor, 1969 Eunicella stricta aphyta Théodor, 1969

Plate 4: Sub-tentacular spicules of *E. singularis*. Their flatness, and the minuteness of the warts is easily visible in spicules d-f. The bar represents 10µ in each of the figures.

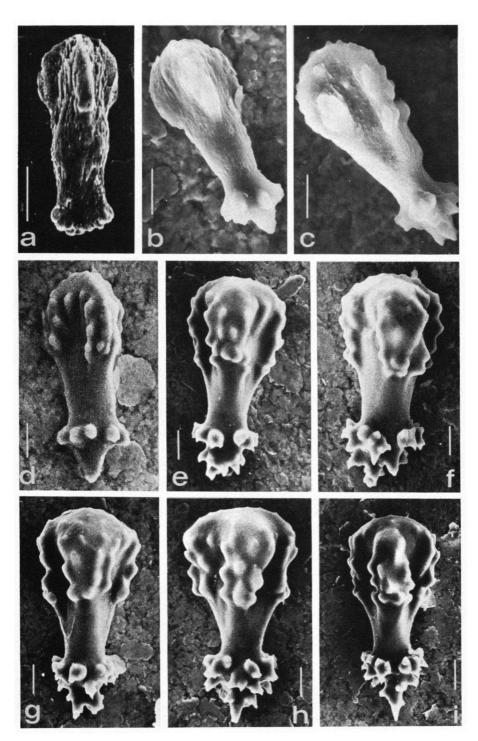


One of the first descriptions made of this species is the one by Marsilli (1725), who describes several gorgonians which he calls "litophytes". This one, called "litophyte premier", is represented in his Plate XVI fig. 80. According to Marsilli it lives in 8 to 30 fathoms (14 to 54 metres), which corresponds quite well with the depth-range as we observe it to-day by means of Scuba diving. He also says that "la substance de celle-ci semble un amas de petits grains de sel." It is very possible, therefore, that this very accurate 18th century naturalist observed the presence of spicules in the cortical layer.

In the end of that same century, Esper (1794) published the second volume of his excellent work "Die Pflanzenthiere in Abbildungen nach der Natur". In a plate (Gorg, Tab. XIA) he shows a gorgonian which is, beyond any doubt, a specimen of the dirty-white Mediterranean Eunicella species, which he calls Gorgonia viminalis var. singularis, although his G. viminalis belongs to the present-day genus Lophogorgia. Rossi (1960), in her description of the Mediterranean Eunicella, also notes Esper's G. viminalis var. singularis as a senior synonym for her Eunicella stricta. She does not apply the law of priority because she finds it impossible to establish its identity with certainty, for, as she puts it: "Malgrado ESPER abbia evidentemente raffigurato (1794; tav. IXA) [this should be XIA] una colonia di E. stricta sotto il nome di Gorgonia viminalis var. singularis, il nome singularis non può venire adottato in quanto l'A., nel testo relativo alla specie, non nomina tale varietà e viene quindi a mancare ogni precisa definizione". We believe, however, that Esper's plate XIA cannot be mistaken for another Mediterranean species. Moreover, he does consider the variety in his text, contrarily to what Rossi claims, and even doubts whether it is a mere variety of Gorgonia viminalis: "An dem Exemplar der Tab. XIA, ist sie [the cortex of G. viminalis] fast ganz verblichen, und erscheint in einer lichtgrauen kaum mercklich gilblichen Mischung. An dieser Art ist auch die äußere Fläche etwas ungleich [calyces] und in flache Krümmungen ausgeschweist, da sie an jener sich in einer geraden und gleiche Ebene hinziehet. Doch es ist bei diesen Abweichungen eine eigene Gattung zu vermuthen, und ich habe deswegen nähere Erläuterungen abzuwarten". According to Esper, the species originates in the Mediterranean. The next description is by Bertoloni (1810). His Gorgonia stricta is without any doubt the white Mediterranean Eunicella species, which since has often carried the name E. verrucosa var. stricta, or, especially during the last 15 years, Eunicella stricta.

Although we are convinced that altering the name of the species might be confusing for those used to the name of E. stricta, we believe that, for

Plate 5: Balloon-clubs from the outer rind of *E. singularis*. a-d are younger stages, e-i adult ones. The bar represents 10μ in each of the figures.

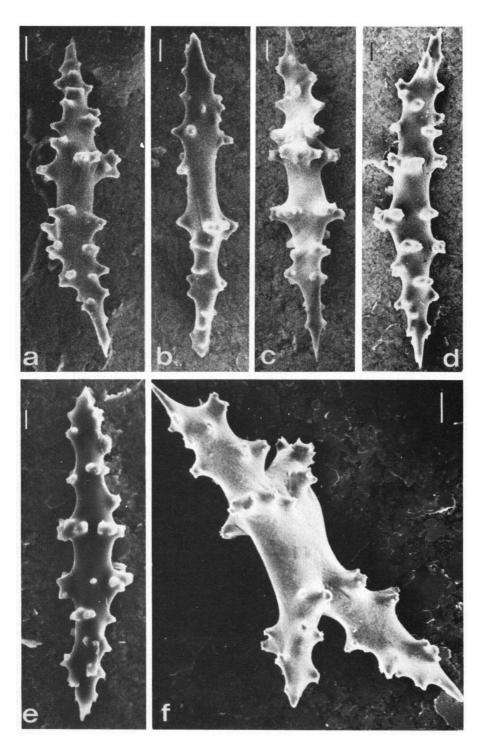


prioritary reasons, the correct name should become *Eunicella singularis* (Esper, 1794).

The general morphology of the colonies (Plate 1, fig. 1) is quite variable, and depends largely on the hydrodynamic conditions in which the species grows (Théodor, 1963). Generally speaking, the colonies are composed of relatively long and straight branches, with rather few ramifications, running parallel to each other. In most of the cases the branches lie in one plane, but colonies growing in turbulent conditions may take on a bush-like appearance. The colour of the colonies varies from bright white (when not containing zooxanthellae) to a dirty greyish white (when they do). The diameter of the terminal branches varies from 2 to 3 mm. The polyps (3 mm long, when fully extended) are often found on all sides of the branches. They protrude from lobate calyces which in some younger stages consist of eight lobes (von Koch, 1887), three of which often join at a later stage forming calyces consisting of five smaller lobes and one big one (Plate 2A). Bérenguier (1954), who was not aware of this fact, states that the calves are composed of eight equal and regular lobes, which is rather the exception. The polyps can fully retract, the lobes of the calyces closing over them when they do. The polyps may contain zooxanthellae, and in fact they do most of the time. These unicellular algae lie in the mesogloea, and can be seen in the neck zone of the anthocodia, in the tentacles, and even in the pinnules, conferring a brown colour to the polyps, its intensity depending on the concentration of the algae. According to von Koch (1887), who first described them as "gelbe Zellen" or "Schmarotzer" (= spongers, parasites), they are characteristic of the species, and form one criterium to distinguish it from the other Mediterranean Eunicella, E. cavolinii. However, this is but partly true: as pointed out before, zooxanthellae may be completely missing from E. singularis tissues. This fact has been thoroughly investigated by Théodor (1969), who found that animals with or without symbiotic algae seem to be inherently different, and who divided the species into the subspecies stricta (with zooxanthellae) and aphyta (without zooxanthellae).

The spicules of the rind have been well-known for a long time. The outmost layer consists of balloon-clubs lying with their heads outwards, thus lending a granular appearance to the rind. It was probably those that Marsilli (1725) took for small grains of salt. The deeper layer consists of spindles. A third type of spicule, found on the anthocodia, just at the basal part of the tentacles (Plate 2B), escaped detection by nearly all of the previous authors. Bérenguier (1954) even goes as far to say that "on n'aperçoit aucune trace de spicules dans les polypes". Théodor (1971) is the only author to mention the presence of these sub-tentacular spicules. According to him their

Plate 6: Spindles from the inner rind of *E. singularis*. They possess a small middle zone, devoid of warts. In *E. cavolinii* this middle zone is less conspicuous. a-e normal spindles, f fused, cross-shaped spicule. The bar represents 10μ in each figure.



number varies greatly, ranging from 0 to 58 per polyp. Our personal observations agree with this. All three types of spicules are seen in Plate 3. We will revert to the dimensions of the spicules from the rind in a later paragraph, where the species E. singularis and E. cavolinii are compared. Plate 4 shows scanning-electron micrographs of subtentacular spicules, which have never been depicted before and consist of flat, fairly smooth

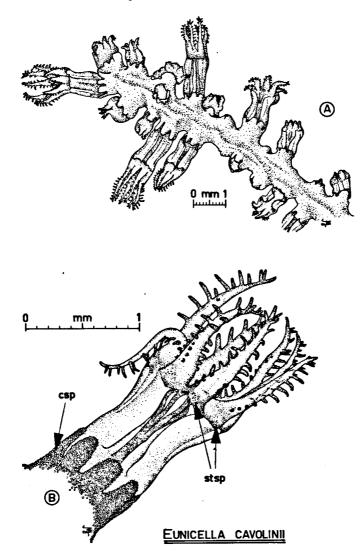


Plate 7: A. Terminal branch of *E. cavolinii*. The calyces are relatively protrusive and the rind canals appear as depressions. B. Single polyp with sub-tentacular spicules (stsp) and coenenchymal spicules (csp) forming the calyx.

structures, some six to seven times as long as they are wide, and comprising small warts, mostly concentrated in the apices of the spicules. Their average length is some $80 \,\mu\text{m}$.

Plates 5 and 6 show pictures of balloon-clubs and spindles, both from the rind, respectively. It may be clear from all these plates that the variability in form and dimensions is quite considerable, and that the species cannot be characterized by one single spicule.

The ecology of *E. singularis* has been studied by several authors. Marsilli (1725) already noted a depth range of 14 to 54 metres. We found the species from 7 metres on (Weinberg, 1975), and Théodor (1971) states that it has been seen by Reiss in a depth of 220 m. Several authors (Bérenguier, 1954; Gamulin-Brida, 1974) agree that the species is rather photophilic and lives on horizontal or subhorizontal surfaces. Our own observations (Weinberg, 1975) tend to confirm these facts. It must be borne in mind that the only cases when *E. singularis* was sighted in deep (dark) localities, specimens of *E. s. aphyta* were encountered.

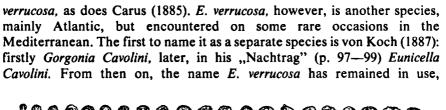
According to Pax & Müller (1962) and Weinberg (1975), the species prefers localities with strong current (> 120 m/H).

Not very commonly occurring in some localities (West coast of Corsica, Monaco), it thrives in others (Banyuls-sur-Mer) where it becomes the most important animal species of the circalittoral benthos, with densities up to fifty colonies per m².

Eunicella cavolinii (v. Koch, 1887) (Collection ZMA COEL. 7753, 7754)

Synonymy: Gorgonia verrucosa; Delle Chiaje, 1822 Gorgonia verrucosa; Carus, 1885 Gorgonia Cavolini v. Koch, 1887 Eunicella Cavolini v. Koch, 1887 Eunicella verrucosa; Thomson, 1927 Eunicella verrucosa; Thomson, 1929 Eunicella verrucosa var. typica Stiasny, 1938 Eunicella verrucosa; Rossi, 1949-1950 Eunicella cavolinii; Bérenguier, 1954 Eunicella cavolinii; Bérenguier, 1954 Eunicella cavolinii; Laborel & Vacelet, 1958 Eunicella verrucosa var. typica; Abel, 1959 Eunicella cavolinii; Rossi, 1960 Eunicella verrucosa var. typica; Pax & Müller, 1962 Eunicella cavolini; Carpine, 1963

Here again, Marsilli (1725) gave an early but unmistakable diagnosis of the species: his "litophyte troisième" is encountered in depths ranging from 11 to 54 metres, often together with Red Coral, and has a yellow colour, but it bleaches when the colonies are dried. Delle Chiaje (1822, Plate 33, figs. 4-7) gives a recognizable image of *E. cavolinii* but calls it *Gorgonia*



Y **A**ÅÅ 100 µ EUNICELLA CAVOLINII 12/

Plate 8: Spicules of *E. cavolinii*. 1-72: balloon-clubs from outer rind; 75-127: spindles from inner rind; 73, 74: sub-tentacular spicules; 128-129: cross-shaped spicules; 62-67: clubs with long spiny end; 68-72: clubs fused into "siamese twins".

sometimes the var. *typica* Stiasny, because most authors do not consider E. cavolinii a separate species. It is Bérenguier (1954) who first re-establishes its status, using the correct nomenclature E. cavolinii for the first time, followed by Rossi (1960) and Carpine (1963). After this last date it remains the only name used, but until 1962 many authors from the Austrian School continued to use the name E. verrucosa var. typica.

In the case of *E. cavolinii*, the general form of the colonies (Plate 1, fig. 2) is also variable, depending on ecological conditions, similarly as for *E. singularis*. While some authors indicate water turbulence as an important factor (Velimirov, 1973) others (Abel, 1959; Riedl, 1966) state that the growth form is light-dependent. The branches differ from those of *E. singularis* in many ways. The ramifications are more numerous, shorter, and

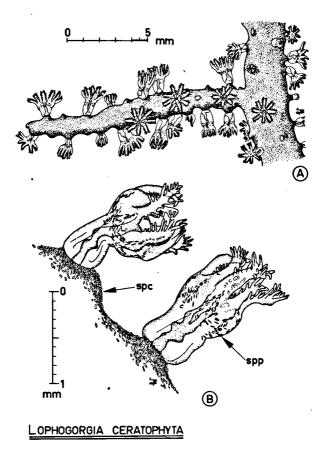


Plate 9: A. Detail of a branch of *L. ceratophyta*. Some polyps are fully retracted, showing only an oval slit in the rind. B. Detail of two polyps bearing spicules (spp); no calyces are formed by the coenenchymal spicules (spc).

they tend to be curved, pointing in many directions, not running parallel to each other, as was the case in the previous species. The colonies generally lie in one plane, but in Western Corsica (Pointe de Scandalo) we found some very stocky colonies of bush-like appearance, apparently due to the very rough water conditions in this place.

The colour of the colonies varies from light ochre to a warm yelloworange, but it vanishes when the colonies are dried, and bleaches considerably when they are preserved in alcohol. This colour is due to the living tissue, and not to the spicules which are colourless. The diameter of the terminal branches varies from 1 to 3 mm. The polyps (Plate 7A) are mostly found at opposite sides of the branches, lying in the plane of the entire colony. Stem canals and gastrodermal solenia are visible through the rind, even in dried specimens, as gutter-like depressions. The calyces resemble those of *E. singularis*, with 8 small lobes, often developing into 5 smaller lobes plus 1 bigger one. Their height, however, seems more important than in the previous species, and with fully extended polyps they may reach 1.2 mm. In dried colonies, or colonies with the polyps fully retracted, this leads to a more warty appearance of the rind.

Zooxanthellae are never encountered in *E. cavolinii*, and the polyps (2 mm long, when fully extended) have a slightly opaque, light-yellow appearance.

The spiculation of the species closely resembles that of E. singularis, as will be seen in the next paragraph. In this species sub-tentacular spicules were also found (Plate 7B), a fact thus far never noticed. Their number seems to be smaller then in E. singularis, ranging from 0 to 29 per polyp. The spicules of this species, depicted in Plate 8, differ so little from those of the previous one that no scanning-electron micrographs are shown in this case. In the case of the balloon-clubs, "siamese twins" were encountered from time to time (Plate 8, nos. 68—72), a type we never saw with E. singularis.

The ecology of E. cavolinii is quite well-known. The species is found in depths ranging from 8 metres (Velimirov, 1975) to 150 metres (Carpine, 1963). Many authors are agreed on the fact that E. cavolinii lives almost exclusively on vertical or overhanging rock ledges (von Koch, 1887; Bérenguier, 1954; Laborel & Vacelet, 1958; Carpine, 1963; Gamulin-Brida, 1974; Velimirov, 1975), a fact confirmed by our own observations. Riedl (1966) even found it to be present in caves. The species is rather photophobic, as is proved by an experiment of Velimirov (1975). This author took some colonies of *E. cavolinii* from a vertical wall, and placed them on a horizontal substrate. In one case, with the colonies fully exposed to incident light, the living tissue died and disappeared within eight days, leaving only the naked horny skeleton. In the other one, with the colonies placed horizontally but in the shadow of a vertical wall, they remained healthy even for a period of 16 months. Our own observations confirm the photophobia of the species, as will be demonstrated in the next paragraph. The animal seems to be very tolerant to hydrodynamic conditions.

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Plate 10: Spicules of *L. ceratophyta.* 6–88: rough warty spindles from the coenenchyme; 89–129: flat spicules and smooth warty spindles, partly from the polyps, partly from the rind; 1–5: spiny spindles, a new type, probably from the rind.

Very common in the Eastern part of the Western basin of the Mediterranean (French coast East of Marseilles, Italy, Adriatic), it is very rare, and sometimes virtually absent, West of Marseilles.

Comparison of E. singularis and E. cavolinii

Several authors refused to consider the two animals to belong to different

species. Others claimed that differences could be established on both morphological and ecological data.

We have seen that the external appearance of the colonies is different. E. singularis is either bright white with transparent colourless polyps when not containing zooxanthellae (E. s. aphyta), or dirty white with brown polyps when these algae are present (E. s. stricta). E. cavolinii is yellow or orange, which colour also applies to the polyps which seem to be a little opaque.

The colonies of *E. singularis* consist of long, straight branches, which are slightly granular on all sides because of the calyces, and which run parallel to each other. Those of *E. cavolinii*, on the other hand, are more ramified, the ramifications being curved and pointing in many directions although lying in one plane. The calyces are more protruding but generally lie only on opposite sides of the branches, in which the stem canals can clearly be seen. The height of the polyps of *E. singularis* reaches 3 mm, as compared to 2 mm with *E. cavolinii*. Those differences enable the diving scientist to tell them apart in the field.

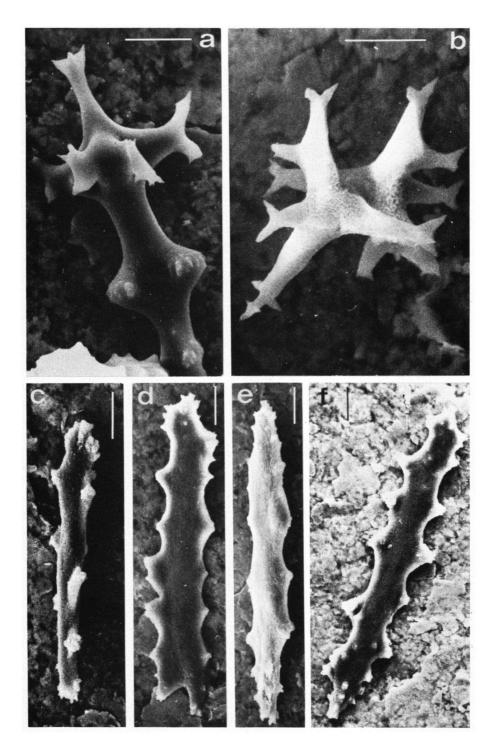
With regard to the spicules many authors have told many things, but a statistical comparison, based upon large series of spicules, has never been undertaken. In an attempt to clarify this question we measured over 600 spicules, 245 belonging to *E. singularis*, 357 belonging to *E. cavolinii*. A total of eight colonies was observed, originating from three different localities. For the data cf. table I.

The balloon-clubs were characterized by means of four measured parameters: total length of the clubs (LC), maximum width of the clubs (WC), width of the "collar" of the clubs (CC), and width of the "spiny end" of the clubs (SpC). Additional parameters were computed for each spicule; the "slenderness" of the clubs (SC) was defined in the following way:

Specimen no.	Species	Locality	number of clubs examined	number of spindles examined		
1	E. singularis stricta	Banyuls s/Mer		33		
2	E. singularis stricta	Banyuls s/Mer	23	20		
3	E. singularis aphyta	Banyuls s/Mer	46	27		
4	E. singularis stricta	Cap Revellata	25	25		
5	E. cavolinii	Cap Revellata	19	16		
6	E. cavolinii	Cap Revellata	35	11 -		
7	E. cavolinii	Monaco	92	92		
8	E. cavolinii	Monaco	60	32		

 TABLE I. Number of balloon-clubs and spindles per specimen and per locality for a statistical comparison between the species Eunicella singularis and Eunicella cavolinii.

Plate 11: Spicules of L. ceratophyta. a-b: spiny spindles; c-f: smooth warty spindles and flat spicules from the polyps. The bar represents 10µ in each figure.



SC = WC/LC and the "uniformity" of the clubs (UC) was computed as: UC = (WC.SpC)/(LC.CC). The spindles were measured by length (LS) and width (WS), and their "slenderness" was also computed as SS = WS/LS. How the different parameters were measured is shown in fig. 1.

In a first attempt, the mean and the 95%-confidence intervals were computed for each specimen and for each parameter. The results are shown in fig. 2. It seems obvious from the graphs that the difference between individuals (specimens) is very large, and that natural groups as species groups (specimen 1-4 vs. specimen 5-8) or locality groups (specimen 1-3, specimen 4-6, specimen 7-8) do not appear. Variance analysis with the specimens considered separately confirmed this chaotic appearance; H_0 (uniformity) was rejected for every parameter with a probable error of 0.1% or less.

We took the specimens together as species groups in a second run, and again calculated mean and 95%-confidence intervals of each parameter, this time per species. In this way (see also fig. 2) some differences began to occur. Variance analysis enabled us to reject H_0 (uniformity of the species) with a probable error percentage indicated in the lower left of each graph. Very significant differences are observed for the clubs (error 0.1% or less). Those of *E. singularis* are longer and have a much wider collar and a much wider spiny end then those of *E. cavolinii*. Their width, slenderness and uniformity, however, concord very much in both species.

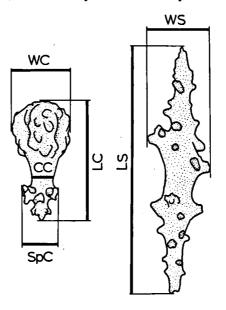


Fig. 1: The different parameters that were measured to compare the rind spicules of *E. singularis* with those of *E. cavolinii*. Balloon clubs: LC = length, WC = max. width, CC = collar width, SpC = width spiny end. Spindles: LS = length, WS = max. width.

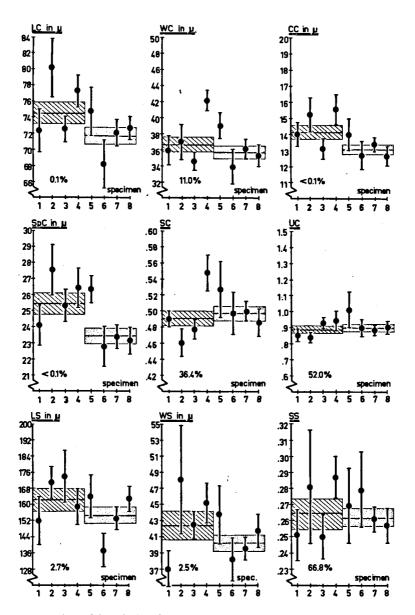


Fig. 2: Comparison of the spicules of *E. singularis* with those of *E. cavolinii*. LC = length clubs, WC = width clubs, CC = collar-width clubs, SpC = width spiny end clubs, SC = slenderness clubs, UC = uniformity clubs, LS = length spindles, WS = width spindles, SS = slenderness spindles. Black dots mark the mean value for each specimen, vertical bars the 95%-confidence interval. Horizontal bars mark the mean for each species, accompanied by their 95%-confidence intervals (hatched areas for *E. singularis*, stippled areas for *E. cavolinii*). The percentages in the lower left of each graph indicate the probability that the species are the same, according to the parameter considered.

As to the spindles, with a probable error of less than 3% it is permitted to state that those of *E. singularis* are both longer and wider than those of *E. cavolinii*. Their slenderness, on the other hand, is very much the same. If again we compare Plates 3 and 8, we may see that at a first glance it is not evident that differences between the species can be demonstrated. Only the observation of very large series of spicules and a thorough statistical analysis made it possible to outline differences objectively.

A last point of comparison lies in the ecology of both species. *E. singularis* lives mostly on (sub)horizontal surfaces, *E. cavolinii* on (sub)vertical ones. Light measurements enabled us to define in what range of percentages (relative to surface irradiance) both species are to be found. All measurements were made during the summer months, mostly around noon, and are therefore quite comparable. A total of 39 measurements were made involving *E. singularis* populations, and 24 for populations of *E. cavolinii*.

The first species was found in a minimum 0.60% and a maximum of 23.60% relative irradiance with a mean of 7.83% and a 95%-confidence interval going from 6.03% to 9.60%.

The second species occurred from a minimum of 0.12% to a maximum of 4.71%, with a mean of 1.80% and a 95%-confidence interval ranging from 1.20% to 2.41%.

These ecological differences are striking, and together with the morphological ones presented above may reconfirm the validity of both species.

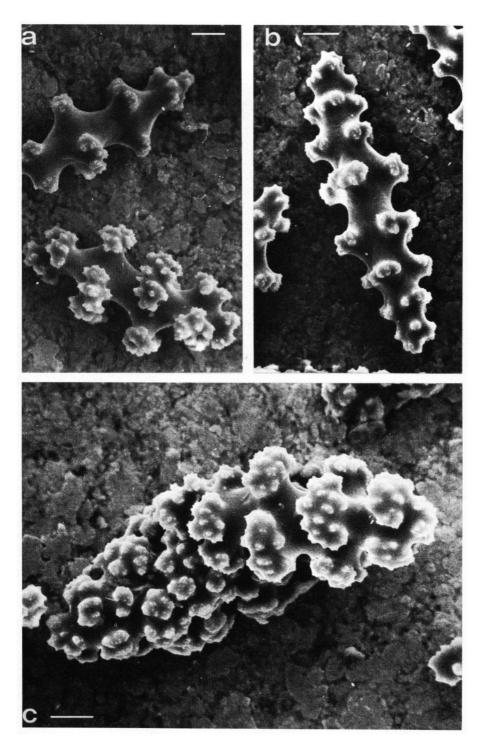
Family GORGONIIDAE Lamouroux, 1812 Genus Lophogorgia Milne Edwards & Haime, 1857

Lophogorgia ceratophyta (Linnaeus, 1758) (Coll. ZMA COEL. 7467).

Synonymy:

? Gorgonia ceratophyta Linnaeus, 1758
Gorgonia ceratophyta; Pallas, 1766
? Gorgonia viminalis Pallas, 1766
Gorgonia ceratophyta; Linnaeus, 1767
Gorgonia ceratophyta; Esper, 1794
non Gorgonia sarmentosa Esper, 1794
? Gorgonia viminalis; Esper, 1794
Gorgonia rosea Lamarck, 1816
Gorgonia ceratophyta; Lamarck, 1816
Gorgonia ceratophyta; Delle Chiaje, 1822
Gorgonia viminalis; Delle Chiaje, 1822

Plate 12: Coenenchymal rough warty spindles of L. ceratophyta. a-b: typical spicules; c: spicule with many fusing warts, approaching the form typical for Leptogorgia. The bar represents 10µ in each figure.



Gorgonia ceratophyta; Risso, 1826 Gorgonia sarmentosa; Risso, 1826 Gorgonella sarmentosa; Milne-Edwards, 1857 Gorgonella sarmentosa; Carus, 1885 ? Leptogorgia cauliculus Carus, 1885 ? Leptogorgia viminalis; Carus; 1885 Gorgonella sarmentosa; v. Koch, 1887 Leptogorgia sarmentosa; v. Koch, 1887 Leptogorgia sarmentosa; Kükenthal, 1924 Leptogorgia sarmentosa; Carpine, 1963 Lophogorgia sarmentosa; Théodor, 1967 Lophogorgia sarmentosa; Weinberg, 1975

Although many of the earlier authors (between 1758 and 1797) give very diverging descriptions, Marsilli (1725) collected specimens of *Lophogorgia ceratophyta* which he describes as his "litophyte quatrième" in the following way: "Hauteur maximale 2 pieds. Cette plante est toute pleine de rameaux capillaires, l'écorce sortant de l'eau est de la couleur de terre cuite". Of course, he makes the error, proper to his time, to treat the species as a plant. But as unequivocal a description as his is not to be found for many years after him.

In the tenth edition of his "Systema Naturae", Linnaeus (1758) mentions Gorgonia ceratophyta. There follow some conflicting indications: "habitat in Indiis et M. Adriatico. Crusta alba membranacea". Apparently he means a white gorgonian, living in two very different localities. But in his list of synonyms he quotes Catesby: "cortice flavo perforato" (a yellow gorgonian then ?), and the Virga sanguinea of Rumphius. Upon investigation we found this species in Rumphius (1750, Ch. 12, p.233, Tab. 83) to be a red gorgonian from the Indonesian archipelago, and comprising relatively few ramifications. So neither colour nor locality are well defined by Linnaeus. The next mention of G. ceratophyta is made by Pallas (1766). He describes a red specimen from Gibraltar, and yellow ones with many branches. The description fits the Mediterranean Lophogorgia very well. According to Pallas, his species grows in the Mediterranean, in the Atlantic, and near America. The confusion increases when he quotes Seba and Knorr for il-Seba (1759, Tab. 107, fig. 3) shows a purple-red lustrations. "Titanokeratophyton" with few branches, coming from Cape of Good Hope. The species represented by Knorr (1771, Tab. A5, fig. 2) closely resembles the pink variety of Eunicella verrucosa (although our edition of Knorr is a later one than the one mentioned by Pallas, the plates certainly coincide). As far as we can judge, Pallas observed gorgonians from different localities, and believed them all to belong to the same species. There is a species living in the Western Atlantic, which has often been thought (Milne-Edwards, 1857; Kükenthal, 1924; Bayer, 1961) to be (partly) synonymous with G. ceratophyta, but which actually is Leptogorgia virgulata (Lamarck, 1815).

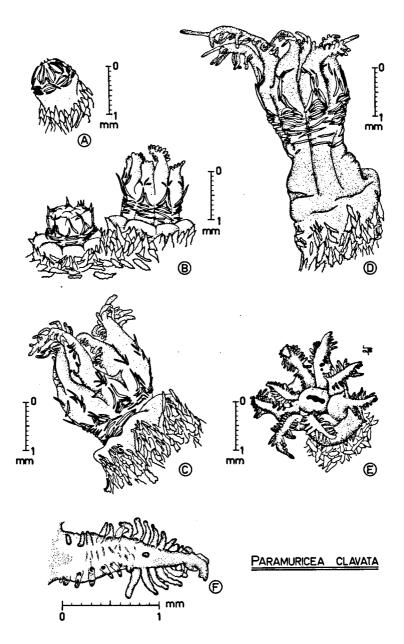
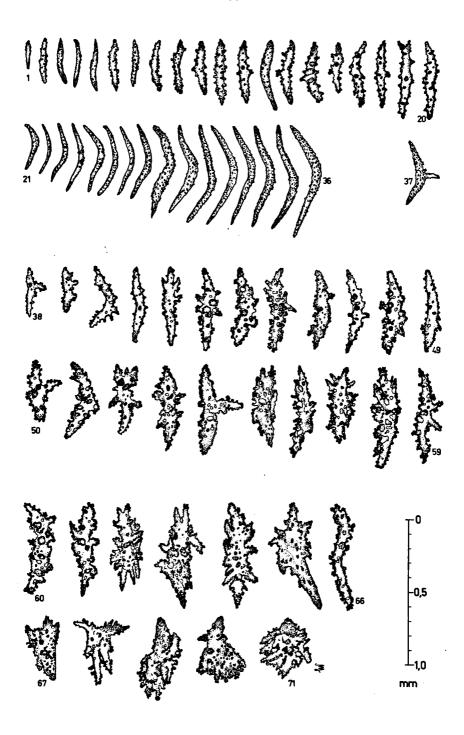


Plate 13: Polyps of P. clavata. The left polyp in B is fully contracted; through A, the right polyp in B, and C, we finally observe a fully extended polyp in D. The anthocodial scaphoids form a collaret of about four rows in A and about eight in D. Upon the transverse collaret rest points of "en chevron" scaphoids. The coenenchymal thorn scales are clearly seen. In E, the oral disk is clearly visible, with the slit-like mouth. F shows the detail of a tentacle.



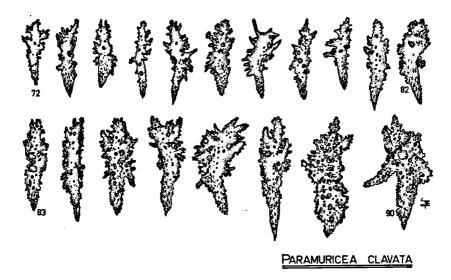


Plate 14: Spicules of *P. clavata*. 1-20: spindles belonging partly to the anthocodial points, partly to the coenenchyme; 21-37: anthocodial scaphoids; 38-90: irregular spicules from the rind. The most developed thorn scales come from the calyces.

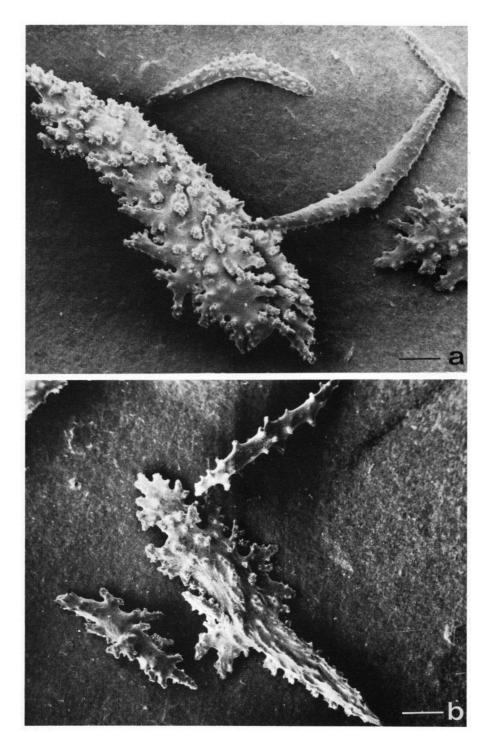
A very important indication that the Mediterranean specimens described by Pallas belong to our species, lies in the fact that he quotes Marsilli's "litophyte quatrième", which we mentioned in the beginning of this chapter. So does Linnaeus (1767, p. 1290, sp. 6) who describes G. ceratophyta as follows: Gorgonia subdichotoma, axillis divaricatis, ramis virgatis bisulcatis, cortice rubro poris bisariis. Habitat O. Atlantico, Americano". The geographical statement contrasts synonymy with the specimen described by Marsilli, who never worked outside the Mediterranean. The confusion does not end here. Esper (1794, p. 78, sp. 17, Gorg. Tab. XIX) shows what may be a small pink specimen of Lophogorgia under the name G. ceratophyta, saying: ,,die Wohnplätze sind sowohl das atlantische, mittelländische als auch das südliche amerikanische Meer". The shell, belonging to the genus Spondylus¹), upon which the gorgonian grows, gives no clue as to its origin. Pink specimens, although rather rare, do occur in the Mediterranean Lophogorgia. We therefore may be induced to think that at least part of the animals described under the name Gorgonia ceratophyta belonged to this species. As the specific name ceratophyta is not used for the other possible synonym, Leptogorgia virgulata, we believe it correct to call the Mediterranean species Lophogorgia ceratophyta (Linnaeus, 1758) instead of L. sarmentosa (Esper, 1794). One might object to this that the name L. sarmentosa has been in use for quite a time. The first time that Esper (1794) described Gorgonia sarmentosa, however, he was not dealing with a

¹) We wish to thank Dr. H. E. Coomans for identification

specimen of the Mediterranean species, although his plate (Gorg. Tab. XXI) closely resembles it. We reproduce part of his text (p. 85): "Auch diese Horncoralle, so bekannt sie etwa sein möchte, ist noch in keinem Verzeichnis eingetragen. Vielleicht wurde sie für eine Abänderung der G. ceratophyta erklärt, von der sie aber in der Bauart der Aeste, ihrer Rinde und der Poren, ganz verschieden ist. Sie kommt von den Ostindischen Meeren, die genau bestimmteren Wohnplätze aber, hatte ich zur Zeit noch nicht erfahren können". The specimen shown is cream-coloured, a colour we never observed in the Mediterranean species. Some years later, Esper (1797, p. 165-erroneously numbered 265, Tab. Gorg. XLV) shows another G. sarmentosa Variet. This bright yellow specimen from Naples doubtless belongs to the species considered here. But the name sarmentosa under which the species has been generally known for about a century, was not adopted immediately. Several authors continued to use the Linnaean name ceratophyta for our species. Delle Chiaje (1822, Tav. LXV) shows two specimens of this Lophogorgia, a red one, which he calls Gorgonia ceratophyta, and a yellow one by the name of G. viminalis. Risso (1826) also describes these two colour varieties as distinct species. Gorgonia ceratophyta (p. 328, sp. 59): "rameaux grêles, allongés, sillonnés, presque dichotomes, d'un rouge de laque; polypes blancs, épars, à huit tentacules. Profondeurs coralligènes". Gorgonia sarmentosa (p. 329, sp. 62): "rameaux lâches, allongés, flexibles et sillonnés, à écorce crétacée, lisse, d'un jaune orange, couverte de polypes nombreux, disposés presque en séries. Profondeurs coralligenes". The two descriptions do not differ very much, except for the colour of the colonies. Von Koch (1887), who looked also at the spicules, recognized that yellow, orange or red specimens all belong to the same species, which he calls Gorgonella sarmentosa, obviously ignoring the earlier name ceratophyta. He later places the species in the genus Leptogorgia, and only recently Carpine (1963) mentions the fact that according to the systematics of Bayer (1956, 1961) the species belongs to the genus Lophogorgia. The systematics in this article follow the system of Bayer (1956), hence the name Lophogorgia ceratophyta.

The colonies (Plate 1, fig. 3) are composed of many short, straight and slender ramifications, ramifying in an almost dichotomous manner. The terminal branches measure hardly more than one millimetre in diameter, and are often terminated by a sharp apex. The colonies grow mostly in one plane, and may reach one metre in height. The colour of the colonies is yellow, orange or brick-red, in some very rare cases pink. The polyps lie either randomly distributed (Plate 9A) or follow eachother at regular intervals on either sides of the branches, in the same plane as the entire colony.

Plate 15: Spicules of *P. clavata*. a: Calycular thorn scale and anthocodial scaphoids; b: coenenchymal spicules. The bar represents 100µ in both figures.



These differences (compare with the quotes from Risso, 1826!) may be due to differences in hydrodynamic conditions during growth (turbulent water conditions in the first case, laminar current in the second one). The coenenchyme contains symmetrical warty spindles which according to Bayer (1956) are characteristic for the genus. These spicules (Plate 9B) give their colour to the colonies. The polyps also carry spicules. These structures, much smoother than the previous ones, lying perpendicular to the axis of the polyps in the distal part of the anthocodia and parallel to it in the basal part of the tentacles (Plate 9B), are red according to von Koch (1887) and Carpine (1963). However, in the specimens examined by us they are pale yellow.

Plate 10 shows the typical coenenchymal spindles (nos. 6-88) with rough warts. Their average length is 102.8 μ with a 95%-confidence interval ranging from 95.2 μ to 110.3 μ . Average width 32.7 μ (95%-c.i.: 31.6 μ -33.9 μ). Average slenderness (width/length) 0.345 (95%-c.i.: 0.325-0.366).

The anthocodial spicules possess smooth warts (Plate 10, nos. 89–129). Average length 108.4 μ (95%-c.i.: 98.3 μ -118.5 μ). Average width 23.5 μ (95%-c.i.: 21.7 μ -25.3 μ). Average slenderness 0.226 (95%-c.i.: 0.210-0.241).

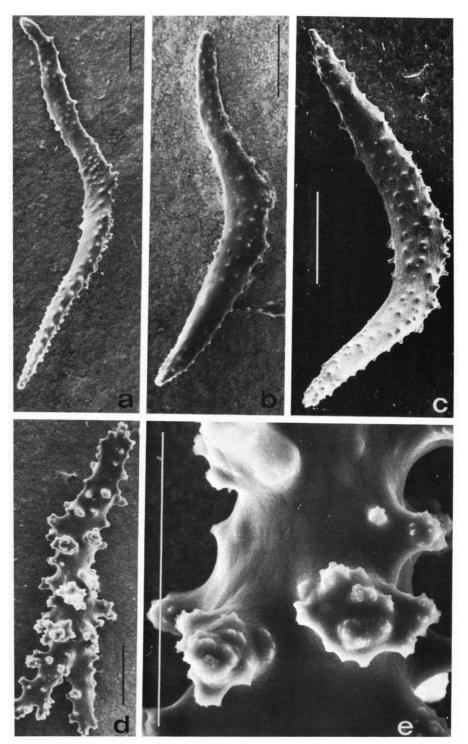
The first five spicules of Plate 10 belong to a type never previously observed in *Lophogorgia ceratophyta*. They are colourless, and probably originate from the coenenchyme. Plate 11, figs. a and b show scanning-electron micrographs of these spicules. The previously described spindles are also depicted in plate 11 and 12.

Marsilli (1725) found the species in 54 to 72 metres. Pax & Müller (1962) mention depths ranging from 20 to 40 metres, and according to Carpine (1963) *Lophogorgia ceratophyta* is to be found between 25 and 200 metres, on loose stones or rocks lying burrowed in sediment. The latter author also says that the colonies seldom occur in groups, and that although they live near coralligenous rocky substratum they only occasionally grow on it. Our own observations (Weinberg, 1975) belie this statement. We often found *L. ceratophyta* populations on hard substratum (up to 12 colonies per m²), at a minimum depth of 18 metres.

The animals are found in a big range of current velocities but have a preference for strong currents (> 300 m/H).

Fourteen light measurements at different localities with *L. ceratophyta* yielded the following results: minimum 1.8%, maximum 12.4%, mean 7.39% (95%-c.i.: 5.23%-9.54%). The animal may therefore be expected to occur in the same places as *Eunicella singularis*, which is in fact often the case in areas where both species are present. The species does not occur as much as Eunicella, however, and although seemingly present in the whole Western

Plate 16: Spicules of *P. clavata*. a-c: anthocodial scaphoids; d: irregular spicule from the rind; e: detail of the previous one showing the morphology of the warts. The bar represents 100µ in each figure.



basin of the Mediterranean, it has only been spotted by us in massive quantities in the neighbourhood of Banyuls-sur-Mer.

Family PARAMURICEIDAE Bayer, 1956 Genus Paramuricea Kölliker, 1865

Paramuricea clavata (Risso, 1826) (Coll. ZMA COEL. 7470)

Synonymy:

Gorgonia placomus Pallas, 1766 Gorgonia placomus; Esper, 1794 Gorgonia placomus; Esper, 1794 Gorgonia clavata Risso, 1826 Muricea chamaeleon var. sanguinea Carus, 1885 Muricea chamaeleon var. sulphurea Carus, 1885 Gorgonia Rissoana Carus, 1885 Gorgonia clavata Carus, 1885 Muricea chamaeleon v. Koch, 1887 Anthomuricea chamaeleon; v. Koch, 1887 Clematissa chamaeleon; Thomson, 1927 Clematissa chamaeleon; Thomson, 1929 Paramuricea chamaeleon; Pax & Müller, 1962 Paramuricea clavata; Carpine, 1963

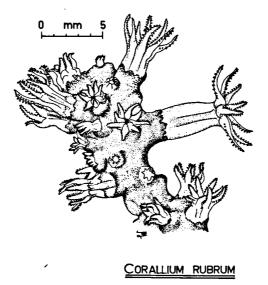


Plate 17: Terminal branch of *C. rubrum*, with polyps in different degrees of extension. Spicules are found in the coenenchyme and calyces only, none are present in the polyps.



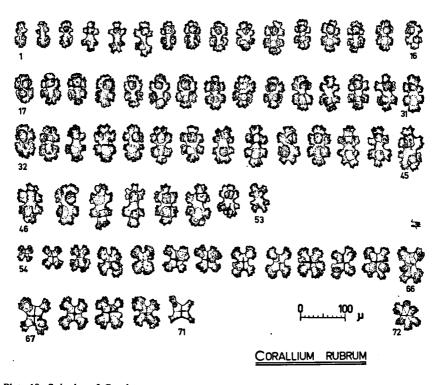


Plate 18: Spicules of C. rubrum. 1—53 coenenchymal capstans; 54—71: cross-shaped spicules with two planes of fusion; 72: the same with three planes of fusion.

This gorgonian also was described in an unmistakable way by Marsilli (1725, p. 93, Pl. XVII, fig. 81) as a species he found at Riou (an islet in the vicinity of Marseilles). This is what he says about his "Litophyte second": "... jusqu'à quatre pieds de haut et deux pouces de large vers le pied. Son écorce sortant de la Mer, a les vessies pleines d'une Glu rouge comme du vin chargé, [...] seché la plante devient d'une couleur terrestre et noirâtre".

Pallas (1766, p. 201, sp. 129), Esper (1794, p. 113, sp. 27, Tab. Gorg. XXX-III, XXXIV, XXXIV A) and Lamarck (1816, p. 316) described the species under the name *Gorgonia placomus*. To-day, however, *Paramuricea placomus* is considered a different, mainly Atlantic species. Risso (1826, p. 330, sp. 64, Pl. VIII, fig. 41, 42) gives an excellent description, and is to be considered the author of the species. In 1887 v. Koch describes it as a new species, which he calls *Muricea chamaeleon*, then *Anthomuricea chamaeleon*.

Subsequently, the species has been shifted from one genus to the other, but its specific name remained unchanged, until Carpine (1963) restores the name *clavata* by application of the law of priority.

The colonies (Plate 1, fig, 4) are large (up to 1 m) with thick irregularly ramifying branches which carry many polyps on all their sides. When these

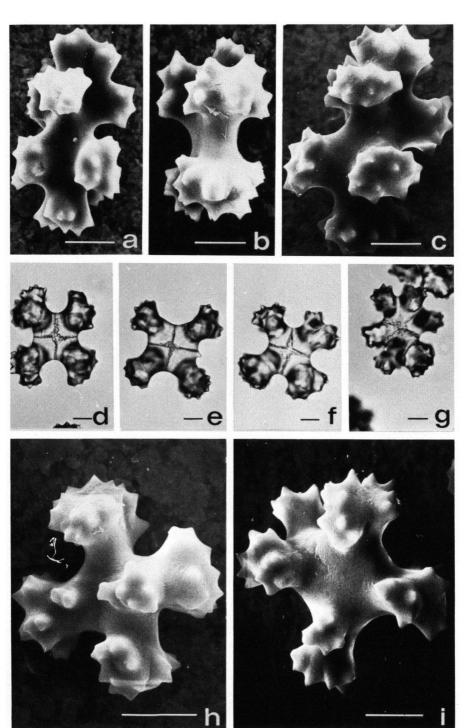
large (up to 8 mm) polyps are fully extended, they lend to the colonies a beautiful, fluffy appearance. Their colour is a deep purple most of the time, sometimes bright yellow, and in some cases both colours are found in the same colony. In the latter case, the transition is very gradual, and as far as we know always concerns purple colonies with yellow extremities, never the other way round. The coloration is due to the living tissue (the spicules are colour-less) and is found in the polyps as well. When dried, the colonies rapidly shrink, loosing their former beauty, and become a dull grey, reminding one of burnt matches. In alcohol, the colour rapidly turns to light green or brown, and eventually vanishes entirely. The polyps (Plate 13) comprise an anthocodial armature of "en chevron" points, which rest upon a transverse collaret. These spicules are mostly scaphoids, and close as a hatch over the polyps when they retract. In dried colonies the anthocodial spicules form conspicuous warts on the rind.

According to Pax & Müller (1962) the species *P. chamaeleon* (= *P. clavata*) and *P. placomus* both occur in the Mediterranean and can be told from each other by the number of rows forming the collaret. Diagnosis of *P. clavata*: "Skleritenring des Polypen 5—8 reihig" (as to 4 for *P. placomus*). Our plate 13A shows that 4 rows of scaphoids may also be encountered in *P. clavata*, which confirms Thomson's description (1927): "trois ou quatre rangées d'arcs font la couronne".

Another diagnosis of *P. clavata* (Pax & Müller, 1962) is based upon the morphology of the scaphoids: "Ringnadeln auf der concaven Seite glatt, auf der convexen Seite mit dichtstehenden, ziemlich hohen konischen Warzen besetzt" (as to small warts on all sides for *P. placomus*). Our specimens, on the other hand, contained only scaphoids of the latter type (Plate 14, figs. 21-36; Plate 15a; Plate 16a-c). It would therefore seem to us that a critical comparison between both species should be carried out, a recommendation already made by Stiasny (1941).

The ecology of the species closely resembles that of *Eunicella cavolinii* (in Corsica we often found assemblages containing both species). It also grows on vertical or overhanging ledges (Carpine, 1963; Gamulin-Brida, 1974; Weinberg, 1975). The light preferences of *P. clavata* also show great resemblance to those of *E. cavolinii*. According to True (1970) at Ile Plane (near Marseilles) *P. clavata* is more sciaphilic than *E. cavolinii*, and tolerates light-intensities which are lower than those normally encountered for the species. Statements like this lack objectivity, however, for they are based upon visual observations, and we know from practice that it is very hard to evaluate light intensities, because of the accomodation of the eye. 16 light measurements carried out in different populations of *P. clavata* yielded the

Plate 19: Spicules of C. rubrum. a-c: typical capstans; d-g: cross-shaped spicules as seen in light microscopy; h-i: the same as seen in scanning-electron microscopy. The bar represents 20µ in each figure.



following results: minimum relative irradiance: 0.17%, maximum: 6.0%, mean: 1.94%, 95%-c.i.: 1.07%-2.81%. The species is found in the entire Western basin of the Mediterranean, sometimes in very dense populations (46 colonies/m² at Banyuls s/Mer).

Suborder SCLERAXONIA Studer, 1887 Family CORALLIIDAE Lamouroux, 1802 Genus Corallium Cuvier, 1798

Corallium rubrum (Linnaeus, 1758) (Coll. ZMA COEL. 7466)

Synonymy:

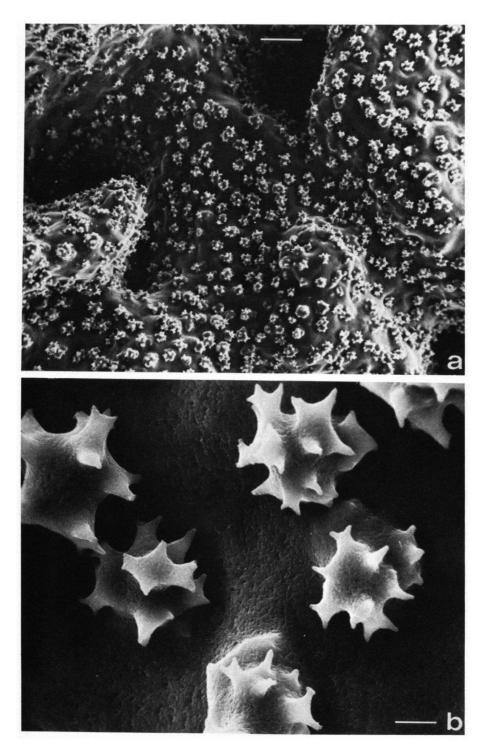
Madrepora rubra Linnaeus, 1758 Isis nobilis Pallas, 1766 Isis nobilis; Linnaeus, 1767 Gorgonia nobilis; Linnaeus, 1789 Isis nobilis; Esper, 1791 Corallium rubrum; Lamarck, 1816 Corallium rubrum; Delle Chiaje, 1822 Corallium rubrum; Carus, 1885 Corallium rubrum; Carus, 1885 Corallium rubrum; v. Koch, 1891 Corallium rubrum; Müller, 1910 Corallium rubrum; Pax & Müller, 1962

The "red" or "noble" coral attracted the attention of Mediterranean people since antiquity, since it was used in jewelry. It was fished by means of pieces of net that dangled from a wooden cross (called "faubert" in french) and were slowly dragged over the sea-bottom. The branches of coral were thus broken off and got entangled in the nets. To-day this practice is still carried out by a small flotilla of Italian (mostly Sardinian) fishermen, but gets gradually replaced by Scuba-divers, who risk their lives for the "red gold" in depths up to 140 metres.

Marsilli was one of the first men to take a scientific interest in the species. He was the first person (Marsilli, 1707) to observe octocorallian polyps, which he very accurately describes as retractile "flowers" with eight equal rays. He also concluded from some of the specimens brought up by his fishermen that the species lives on the ceiling of caves "with its roots upside, and its branches directed to the center of the earth" (Marsilli, 1725, p. 108, Plate XXII, figs. 105, 106).

The coral also gave rise to a fierce debate between 18th century scientists

Plate 20: a. Detail of the axis of C. rubrum, with spicules embedded in its calcareous mass. The bar represents 100μ. b. Detail of a. The bar represents 10μ.



The following quote (Donati, 1750) may sum up the indecision of that time: "Voi qui vedete vegetazione di pianta, e propagazione d'animale".

Some French (Bérenguier, 1954; Laborel & Vacelet, 1961) and Italian (Barletta & Vighi, 1968) authors have erroneously considered Lamarck (1816) the author of the species, which was already described by Linnaeus (1758) under the name *Madrepora rubra*.

The colonies (Plate 1, fig. 5) are tree-like, their ramifications often lying in one plane, but bush-like colonies are not seldom. The average height of the colonies as they are brought up by fishermen or divers, is 10—30cm. We have seen one single bush-like specimen, however, which filled a pail. Barletta et al. (1968) found a colony which weighed 1.2 kg and Pax & Müller (1962) claim the existence of colonies over 1 m high with a weight of more than 30 kg.

The polyps, or autozooids, which carry no spicules, protrude from calyces with eight regular lobes (Plate 17). They are white, can reach 1 cm when fully extended, and contrast beautifully with the branches. A second type of modified polyps, bearing no tentacles and called siphonozooids, is also found (v. Koch, 1891). They appear in the rind as small white orifices.

The orange-red rind contains mostly capstans, but cross-shaped spicules are not seldom (Plates 18,19). The mean length of the capstans is 77.9μ (95%-c.i.: 74.8μ -81.0 μ), their mean width 44.7μ (95%-c.i.: 42.8μ -46.7 μ) and their mean slenderness 0.574 (95%-c.i.: 0.562-0.586).

The axis is not horny as in the Holaxonia, but consists of a very hard, blood-red calcareous mass, in which coenenchymal spicules are embedded (v. Koch, 1891; Müller, 1910). This fact is clearly illustrated in Plate 20.

The ecology of the species was already known to medieval coral-fishers who knew where and how to drag their "fauberts". It lives in caves or under overhanging rocks. With increasing depth the species becomes more acrophilic (Laborel & Vacelet, 1961). This fact was confirmed to us by a Sardinian coral-diver, who said that in depths of over 100 m he found the colonies on every side of the rocks, even on top.

All authors agree on the photophobia of C. rubrum (Laborel & Vacelet, 1958; Gamulin-Brida, 1974; Weinberg, 1975). We have carried out 8 light measurements, and found the species between 0.04% and 0.50% relative irradiance, with a mean of 0.18% and a 95%-c.i. of 0.11% to 0.26%.

The depths in which the species can be found go from 16 m (personal observation) to over 200 m (according to some fishermen). The species is common in the whole Western basin of the Mediterranean and forms massive populations near the Algerian coast (Lacaze-Duthiers, 1864), in the Adriatic Sea (Pax & Müller, 1962) and in the Straits of Bonifacio (Barletta et al., 1968).

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