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Epibiotic bryozoans on deep-water scleractinian corals from the Catalonia slope (western Mediterranean, Spain, France)*

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SUMMARY: The bryozoan fauna growing on deep-water corals (*Lophelia*, *Madrepora*) from the upper-slope of Catalonia (Blanes and Banyuls-sur-mer: NW Mediterranean Sea) was studied. Among the 36 species recorded, a new species, *Escharella acuta* sp. nov., and a new subspecies, *Escharina dutertrei protecta* ssp. nov., are described; five other species have been rarely reported or were unknown from the Mediterranean Sea (*Copidozoum exiguum*, *Amphiblestrum flemingii*, *Schizomavella neptuni*, *Smittina crystallina*, *Phylactellipora eximia*) . This epibiotic bryozoan fauna differs clearly from shallow-water assemblages and comprises a greater proportion of boreo-atlantic species.

Key words: Epibiosis, Bryozoa, deep-water corals, biogeography, western Mediterranean.

RESUMEN: BRIOZOOS EPIBIONTES DE LOS CORALES PROFUNDOS DEL TALUD CATALÁN (MEDITERRÁNEO OCCIDENTAL, ESPAÑA, FRANCIA). — Se estudia la fauna de briozoos epibiontes de los corales profundos *Lophelia* y *Madrepora* provenientes del talud continental de Cataluña (Blanes y Banyuls-sur-mer: Mediterráneo nor-occidental). Se citan 36 especies, siendo una de ellas nueva para la ciencia: *Escharella acuta*. Se describe una nueva subespecie de *Escharina dutertrei*, *E. d. protecta*. Otras cinco especies se han citado raramente o son desconocidas en el Mediterráneo (*Copidozoum exiguum*, *Amphiblestrum flemingii*, *Schizomavella neptuni*, *Smittina crystallina*, *Phylactellipora eximia*). Los corales profundos mediterráneos están colonizados por una briofauna bastante diferenciada de la que puebla las aguas más someras, y que muestra una mayor afinidad con faunas atlánticas de aguas más frías.

Palabras clave: Epibiosis, briozoos, corales profundos, Biogeografía, Mediterráneo occidental.

INTRODUCTION

The deep-water stony corals (*Lophelia*, *Madrepora*, *Desmophyllum*, etc) are widespread, important components of bathyal benthic communities (ZIBROWIUS, 1980). As passive suspension-feeders, they are preferentially distributed on topographic irregularities, such as prominent steps on canyon slopes or seamount peaks, where currents are accelerated and sedimentation rate is low (PÉRÈS, 1967). In the Atlantic, they can form mound-like reefs several meters high (WILSON, 1979). A rich motile and sessile fauna is associated with them (LE DANOIS, 1948) and they are considered to be the frame-components of a peculiar community (biocenosis of the 'white-corals': PÉRÈS and PICARD, 1964; PÉRÈS, 1967). These clumps of deep-water scleractinians are considered to be relict in the Mediterranean, while they are still flourishing in the NE Atlantic and the North Sea. Most of them are composed of dead branches or comprise only a few terminal portions that remain alive (BLANC *et al.*, 1959; PÉRÈS, 1967; TAVIANI and COLANTONI, 1979; ZIBROWIUS, 1980). This thanatocoenosis state concerns particularly *Lophelia pertusa*, which has been very seldom collected alive in the Mediterranean (ZIBROWIUS, 1980). Dead branches are covered by Fe-Mn oxides and can be filled by biomi-

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crite (DELIBRIAS and TAVIANI, 1985). The sub-fossil basal parts often bear a diverse thanatocoenosis (BLANC *et al.*, 1959; PÉRÈS, 1967; TAVIANI and COLANTONI, 1979). The composition of this dead assemblage indicates that the scleractinian clumps flourished when the Atlantic deep-water influences in the Mediterranean were stronger and the temperature colder than today (TAVIANI and COLANTONI, 1979). Datings by ^{14}C (DELIBRIAS and TAVIANI, 1985) confirmed a late Pleistocene age (15,000-30,000 yrs B.P.) for these dead Mediterranean deep-water scleractinians, corresponding to the late glacial. DELIBRIAS and TAVIANI (1985) postulated that the decline of these corals was triggered by a decrease in trophic resources associated with the water temperature increase. The occurrence of live clumps of *Madrepora oculata*, which are not infrequent on the canyon slopes of the NW Mediterranean (Provence, Cassidaigne: BOURCIER and ZIBROWIUS, 1973; Catalonia, Rech Lacaze-Duthier: REYSS, 1964), may be related to sites receiving better food inputs.

Clumps of these deep-water scleractinian corals provide a large amount of branched substrates, which are rigid, elevated in the water column (i.e. offering better access to planktonic food) and, at least partly, devoid of silt deposits. Such substrate resource, scarcely available in the deep-sea, is heavily exploited by sessile biotas, especially encrusting bryozoans. Thus, each patch of deep-water scleractinians generates a diversity peak for this invertebrate guild (HARMELIN, 1988). Rich bryozoan assemblages associated with deep-water scleractinians are reported by LE DANOIS (1948) from the Gulf of Biscay (53 spp. on *Madrepora*, *Lophelia* and *Dendrophyllia*), RYLAND (1963) from western Norway (on *Lophelia*, 90-140 m) and CHEETHAM (1971) on fossil coral mounds from the Danian of Scandinavia. In the Mediterranean, GAUTIER (1958) listed 18 species dredged in the *Dendrophyllia* zone (130-211 m) from the Gulf of Genoa (Italy); but it is not clear whether these bryozoans encrust the corals or not. This study deals with the bryozoan fauna encrusting branches of *Lophelia pertusa* (Linnaeus, 1758) and *Madrepora oculata* Linnaeus, 1758 dredged along the Spanish and French coast of Catalonia (NW Mediterranean). This material revealed a surprisingly high percentage of interesting species.

MATERIAL AND METHODS

The material studied comes from five samples made on the slopes of canyons off Blanes (Spanish Catalonia: 41°31′N, 2°2′E) and Banyuls-sur-mer (French Catalonia, Rech Lacaze-Duthiers: 42° 4′ 30 N, 3° 25′ E).

1 — Blanes Canyon: 180-350 m (trawling, 1986); about twenty dead fragments of skeleton of *Lophelia pertusa*; displaced volume: ca. 3.6 litres; external surface: ca. 2,500 cm^2.

2 — Blanes Canyon: 180-350 m (lobster trammelnet, 1986); partly alive colony of *Madrepora oculata*; volume: ca. 8.4 litres; external surface: ca. 12,800 cm^2.

3 — Rech Lacaze-Duthiers: 300 m (Manned submarine "Griffon", 19.09.1986); dead skeleton fragments of *L. pertusa* and *M. oculata*; volume: ca. 4.5 litres.

4 — Rech Lacaze-Duthiers: 340 m ("Griffon", 24.10.1987); alive and dead skeleton fragments of *M. oculata*; volume: ca. 1.5 litres.

5 — Banyuls-sur-mer: 200-300 m (trawling, 06.1984); two dead fragments of skeleton of *M. oculata*.

Fragments of corals, preserved dry, were washed in freshwater and cleaned with sodium hypochlorite. SEM observations were made on gold-coated specimens. The zooidal dimensions were measured under a stereomicroscope up to 10-15 times whenever possible on each bryozoan colony. The morphometric data given below are the grand mean of the colony means (X) and corresponding standard deviation (s.d.), the overall range, and the number of measurements (N). The abbreviations used are: Lz: length of zooid; Wz: width of zooid; Lop: length of opesia; Wop: width of opesia; Lor: length of orifice; Wor: width of orifice; Llyr: length of lyrula; Wlyr: width of lyrula; Lav: length of avicularia; Wav: width of avicularia; Lov: length of ovicell; Wov: width of ovicell. All measurements are in millimetres.

Types and specimens used for study will be deposited in the Museum of Zoology of Barcelona (MZB).

RESULTS

Thirty-six species were recorded (Cyclostomata: 19.4 %, Anasca: 27.8 %, Cribrimorpha: 8.3 %, Ascophora: 44.4 %). The distribution of the bryozoans on the skeleton fragments of *Lophelia* and *Madrepora* is clearly asymmetrical, with a concentration of the colonies on the upper side (devoid of silt deposit) of each cylindrical segment. The *Lophelia* skeletons were poorly overgrown by epibionts (cover < 30 %); the bryozoans are the dominant group (cover: ca.

19 %), followed by serpulid polychaetes (cover: ca. 9 %); the remaining epibionts are mollusks and brachiopods (cover: ca. 1 %). The absence of sponges on *Lophelia* skeletons is noticeable. The colony of *Madrepora* from Blanes was less affected by silt deposits; it was heavily fouled (cover > 90 %), the epibiontic assemblage being dominated by polychaetes (cover: ca. 50 %), sponges (cover: ca. 30 %), and bryozoans (cover: ca. 10 %), which are mainly in cryptic positions. The live portions of the *Madrepora* colonies from Blanes and Rech Lacaze-Duthiers are devoid of epibionts. Most bryozoan colonies are small and encrusting; the most frequent growth-form is membraniporiform, whereas pauciserial creeping colonies ('runners') are surprisingly scarce. Erect colonies are represented by delicate, jointed, branching forms (*Cellaria*, *Scrupocellaria*, *Crisia*) and by small rigid forms (*Buskea*, *Palmicellaria*, *Idmidronea*). The biogeographic structure of the species stock indicates a relatively high percentage of Atlanto-boreal species (9 %) compared to that found by ZABALA (1986: 4 %) in his study of the littoral bryozoans of Catalonia. There is a high proportion (25 %) of 'deep-water' species, that is species which are distributed from the lower part of the continental shelf to the upper bathyal (roughly 100-500 m). Other species, such as *Setosella vulnerata*, *Schizomavella neptuni*, *Escharina dutertrei*, *E. hyndmanni*, *Hippothoa flagellum*, are typical crypto-bathyal species, distributed in both littoral cryptic and deep-water habitats.

LIST OF SPECIES

The species are listed according to the classification followed by ZABALA and MALUQUER (1988). The species occurrence in the five stations is indicated by the sample numbers. The asterisks indicate the deep-water species.

Class Gymnolaemata, Order Cheilostomata
Sub-order ANASCA
Gregarinidra gregaria (Heller, 1867): 1, 3, 4, 5.
Copidozoum exiguum (BARROSO, 1920): 1.
Copidozoum tenuirostre (HINCKS, 1880): 1, 2.
Callopora dumerilii (AUDOUIN, 1826): 1, 3.
Crassimarginatella crassimarginata (HINCKS, 1880): 4.
Amphiblestrum flemingii (BUSK, 1854)*: 2.
Setosella vulnerata (Busk, 1860): 1.
Cellaria salicornioides Lamouroux, 1816: 1, 4.
Scrupocellaria delilii (AUDOUIN, 1826): 2.
Scrupocellaria incurvata Waters, 1896*: 2.
Sub-order Cribrimorpha
Puellina (Cribrilaria) hincksi (Friedl, 1917): 1.
Puellina (Cribrilaria) innominata (Couch, 1844): 2, 4, 5.
Puellina (Cribrilaria) radiata (Moll, 1803): 3, 4, 5.
Sub-order Ascophora
Palmicellaria skenei (Ellis and Solander, 1786)*: 1.
Smittina crystallina (NORMAN, 1867)*: 1,2, 5.
Smittoidea ophidiana (Waters, 1879): 5.
Smittoidea reticulata (Mac Gillivray, 1842): 1, 3.
Escharella acuta sp. nov.* : 1.
Escharella octodentata (HINCKS, 1880)*: 1.
Phylactellipora eximia (HINCKS, 1860)*: 1,2, 5.
Escharina dutertrei (AUDOUIN, 1826) *protecta* ssp. nov. : 1, 3, 4, 5.
Escharina hyndmanni (JOHNSTON, 1847): 1, 2, 5.
Escharina vulgaris (Moll, 1803): 3,4.
Schizomavella linearis (Hassall, 1841): 1.
Schizomavella neptuni (JULLIEN, 1882): 2.
Fenestrulina malusii (AUDOUIN, 1826): 1, 4, 5.
Hippothoa flagellum Manzoni, 1870: 1, 3.
Buskea dichotoma (HINCKS, 1862)*: 2.
Turbicellepora coronopus (Wood, 1844): 3.
Class Stenolaemata, Order Cyclostomata
Crisia sigmoidea (Waters, 1916): 2.
"Stomatopora" gingrina JULLIEN, 1882*: 2.
Annectocyma sp.: 2.
Entalophoroecia deflexa (Couch, 1844): 1, 3, 4.
Entalophoroecia robusta HARMELIN, 1976: 1.
Plagioecia patina (LAMARCK, 1816): 2, 3, 4.
Idmidronea coerulea HARMELIN, 1976: 1.

SYSTEMATIC ACCOUNT

Copidozoum exiguum (Barroso, 1920) (Fig. 1)

Callopora exigua BARROSO, 1920: 354, fig. 1-4.
Copidozoum exiguum HAYWARD and RYLAND, 1978: 144, fig. 2A.
Copidozoum exiguum HARMELIN and D'HONDT, 1992: 34, pl. 2, A.
Material examined: More than twenty small, ovicellate, colonies mainly on *Lophelia* (Blanes).

Description: HAYWARD and RYLAND, 1978: 144.

Measurements:	Range	X	s.d.	N
Lz:	0.328-0.571	0.462	0.074	6
Wz:	0.286-0.357	0.337	0.027	5
Lop:	0.343-0.429	0.400	0.031	5
Wop:	0.286-0.357	0.305	0.027	5
Lov:	0.157-0.200	0.182	0.013	5
Wov:	0.171-0.200	0.188	0.010	5
Lav:	0.243-0.314	0.278	0.035	2
Wav:	0.128-0.143	0.135	0.007	2

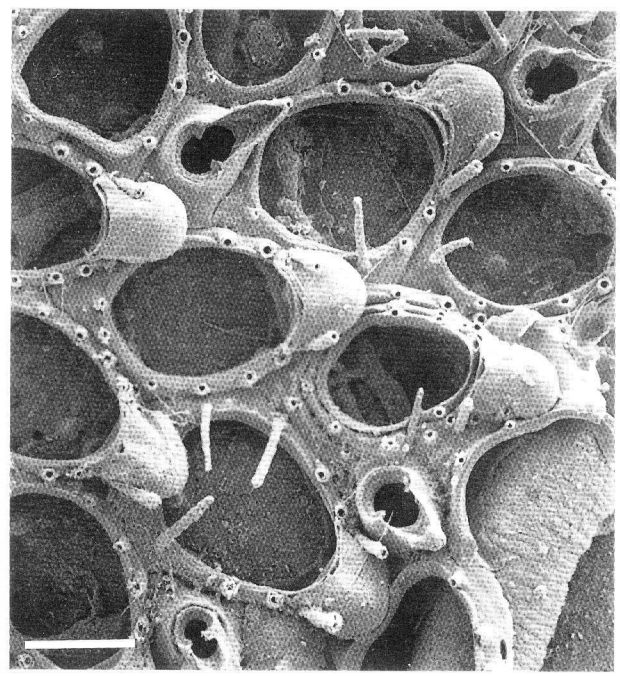

FIG. 1. — *Copidozoum exiguum*. Ovicellate zooids and avicularia. (Blanes Canyon; 180-350 m). Scale bar: 250 µm.

Remarks: This species resembles *Callopora lineata*, but the shape and size of the ovicell and the shape of the avicularia are quite different.

Distribution: *Copidozoum exiguum* is a rarely recorded, deep-water Atlanto-Mediterranean species which was described by BARROSO (1920) from material found on a beach in Santander (Northern Spain). It was recorded in the upper-bathyal of the Atlantic ocean (180-1097 m): Gulf of Biscay (HAYWARD and RYLAND, 1978), Gulf of Cadiz (HARMELIN and D'HONDT, 1992). The Mediterranean specimens come from the same depth range: Strait of Sicily and Malta (320-712 m, HARMELIN, 1979), Gulf of Lions (180 m, Harmelin, unpublished data), Alboran Sea (395 m, HARMELIN and D'HONDT, 1992).

Amphiblestrum flemingii (Busk, 1854)
(Fig. 2)

Membranipora flemingii BUSK, 1854: 58.
Membranipora flemingii HINCKS, 1880: 162; pl. 21, fig. 1-3.
Amphiblestrum flemingii PRENANT and BOBIN, 1966: 265, fig. 88.
Amphiblestrum flemingii RYLAND and HAYWARD, 1977: 104, fig. 44.
Amphiblestrum minax ZABALA and MALUQUER, 1988: pl. 3-B.
Material examined: Thirty five ovicellate colonies on *Madrepora* (Blanes).

Description: PRENANT and BOBIN, 1966: 265.

Measurements:	Range	X	s.d.	N
Lz:	0.340-0.460	0.400	0.041	5
Wz:	0.300-0.380	0.340	0.031	6
Lov:	0.180-0.200	0.185	0.008	4
Wov:	0.180-0.220	0.200	0.010	4
Lav:	0.220-0.340	0.250	0.036	9
Wav:	0.080-0.130	0.100	0.013	9

Remarks: These specimens differ from *A. flemingii* as described by PRENANT and BOBIN (1966) and RYLAND and HAYWARD (1977) in several features: the number of spines is only 4 (more rarely 6), the long, thickened spine of the proximal pair has not been observed, the opesia is only slightly trifoliate and the granular area of the ovicells is clearly triangular in shape (rounded in the original description).

Distribution: *Amphiblestrum flemingii* is a boreo-Atlantic species, which is common throughout the northern Atlantic. It has not been recorded by GAUTIER (1962) from the Mediterranean and its presence in this sea was disputed by PRENANT and BOBIN (1966).

Smittina crystallina (Norman, 1867)
(Figs. 3, 4)

Lepralia crystallina NORMAN, 1867: 204.
Smittia landsborovii var. *crystallina*: HINCKS, 1880: 341, fig. 2.
Smittina crystallina HAYWARD and RYLAND, 1979: 100, fig. 35.
Smittina crystallina ZABALA and MALUQUER, 1988: 121.
Smittina crystallina HARMELIN and D'HONDT, 1992: 42; pl. V A.
Material examined: About twenty ovicellate colonies on *Madrepora* and *Lophelia* (Blanes).

Description: HAYWARD and RYLAND, 1979: 100.

Measurements:	Range	X	s.d.	N
Lz:	0.440-0.740	0.625	0.076	12
wz:	0.320-0.440	0.365	0.040	12
Lor:	0.140-0.200	0.160	0.021	12
wor:	0.140-0.180	0.151	0.012	12
Llyr:	0.060-0.100	0.080	0.014	10
wlyr:	0.060-0.100	0.075	0.009	10
Lav:	0.080-0.100	0.095	0.006	12
wav:	0.050-0.080	0.063	0.009	12
Lov:	0.220-0.240	0.228	0.008	8
wov:	0.240-0.270	0.259	0.008	8

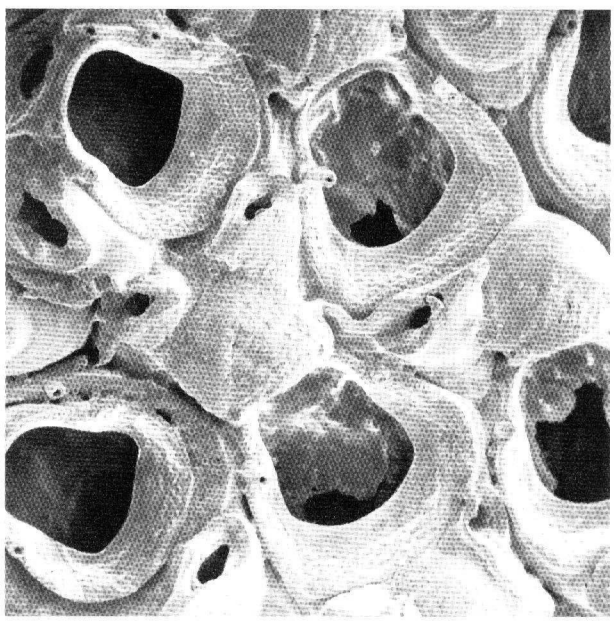

FIG. 2. — *Amphiblestrum flemingii*. Zooids with avicularia and two ovicells. (Blanes Canyon; 180-350 m).

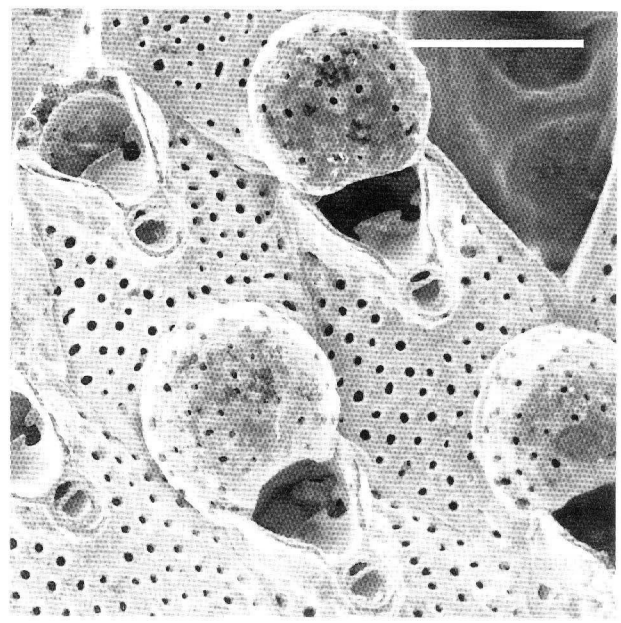

FIG. 3. — *Smittina crystallina*. Ovicellate zooids. (Blanes Canyon; 180-350 m) See the shape of the lyrula and condyles and the presence of spines on marginal zooids. Scale bar: 250 µm.

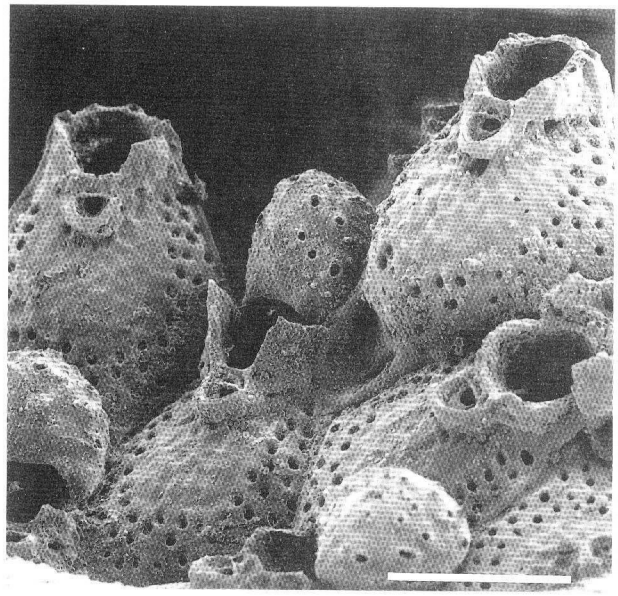

FIG. 4. — *Smittina crystallina*. Ovicellate zooids with a triangular-peristome and an extended imperforate portion of the frontal wall proximally to the orifice. Scale bar: 250 µm.

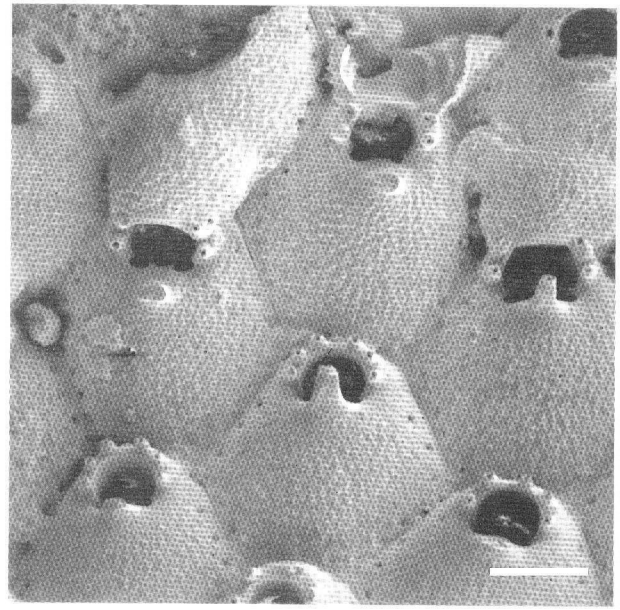

FIG. 5. — *Escharella acuta* sp. nov. Nonovicellate zooids with four, five and six oral spines and ovicellate zooids with four spines. (Blanes Canyon; 180-350 m) Scale bar: 250 µm.

Remarks: *Smittina crystallina* differs clearly from *S. landsborovii* by the presence of oral spines, by the absence of a denticulate ring on the distal margin of the orifice, and of a transverse frontal avicularium and by the shape of the lyrula. The number of oral spines is four in the Atlantic specimens of *S. crystallina* described by HAYWARD and RYLAND (1979), three to five in colonies from the Gulf of Cadiz (Balgim DR49, DW50, 521-523 m), but is only three in our material.

Distribution: As presumed by HINCKS (1880), *S. crystallina* is a upper-bathyal species. Seldom recorded from the Atlantic, it was unknown from the Mediterranean until recently (ZABALA and MALUQUER, 1988). It has been found on shells in the Gulf of Lions (Cassidaigne canyon, 200 m), in the Alboran Sea (145-195 m) and Gibraltar Strait (110 m) (HARMELIN and D'HONDT, 1992). It has also been found on *Lophelia* (?) fragments (> 275 m) in the Bay of Biscay (Hayward, Pers. Comm.).

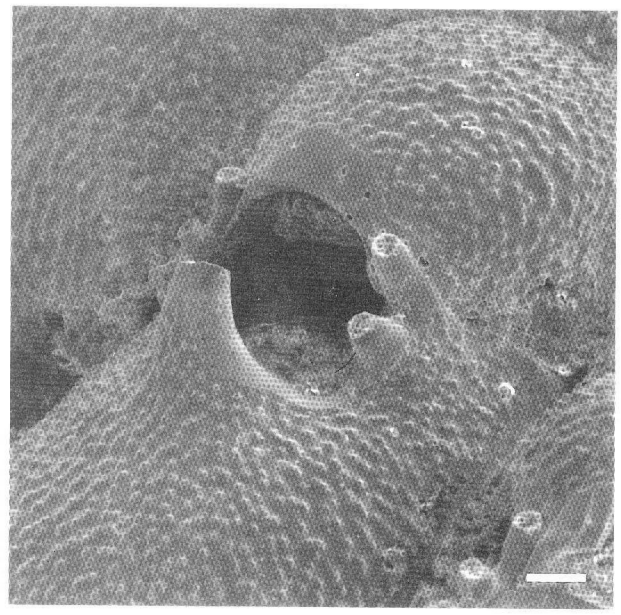

FIG. 6. — *Escharella acuta* sp. nov. Detail of an ovicellate zooid with four oral spines and acute spine-like umbo. Scale bar: 50 µm.

Escharella acuta sp. nov.
(Figs. 5, 6, 7)

Escharella n. sp.: BISHOP and HAYWARD, 1989: 32, figs. 129-131.
Holotype. MZB:1986, 14387 P.203 (Provisional cat. number), Blanes Canyon. W. Mediterranean. Paratype. MZB:1986, 14387 P.205 (Provisional cat. number), Blanes Canyon. W. Mediterranean.
Material examined: Eight ovicellate colonies on *Lophelia*.
Etymology: Acute, for the spine-like suboral umbo.

Description: Colony encrusting, irregular in shape. Zooids large, oval and markedly convex, separated by deep grooves. Frontal wall imperforate, coarsely granular with a row of marginal areolae, conspicuous when young, becoming obscured by calcification; with a narrow, acute umbo which partly hides the primary orifice. Orifice broader than long, with two strong condyles and a broad, very low, concave lyrula. Six oral spines (less frequently 4-5) in non-ovicellate zooids; four (rarely six) spines in ovicellate

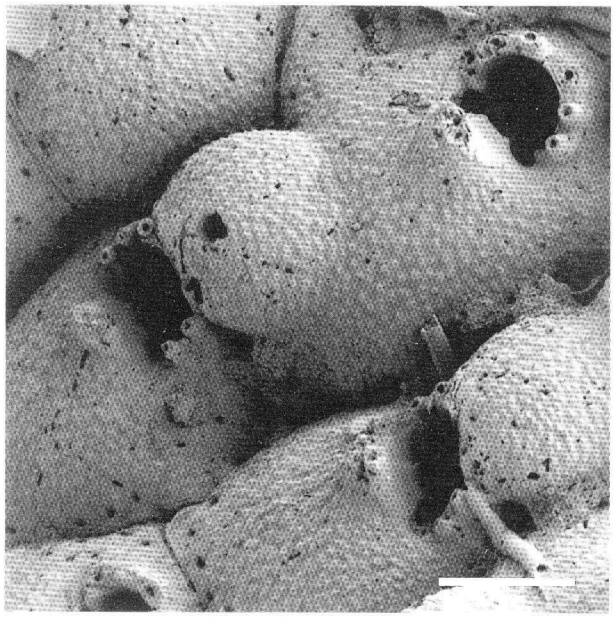

FIG. 7. — *Escharella acuta* sp. nov. Nonovicellate and ovicellate zooids with 5-6 spines. Scale bar: 250 µm.

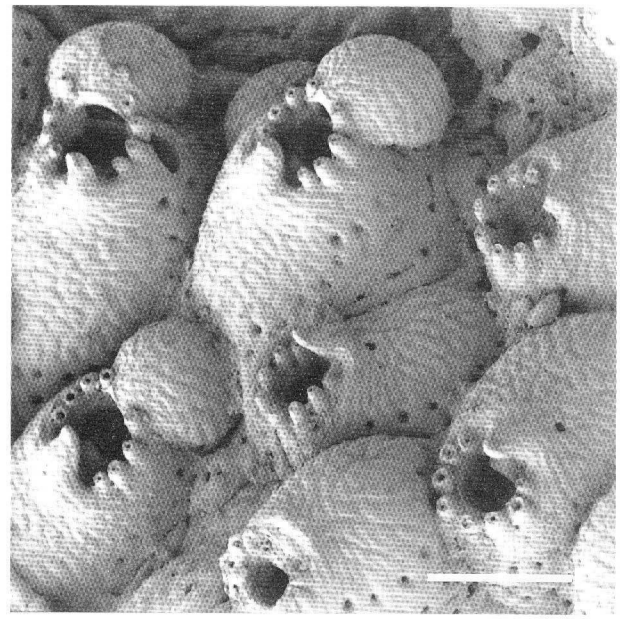

FIG. 8. — *Escharella octodentata*. Ovicellate zooids. (Blanes Canyon; 180-350 m) Scale bar: 250 µm.

zooids. Ovicell recumbent on the succeeding zooid, oval, longer than broad or slightly broader than long, coarsely granular but not perforate; not closed by the operculum. Ancestrula not observed.

Measurements:	Range	X	s.d.	N
Lz:	0.484-0.764	0.564	0.028	8
wz:	0.430-0.653	0.580	0.055	8
Lor:	0.097-0.121	0.109	0.011	8
wor:	0.121-0.149	0.137	0.005	8
wlyr:	0.058-0.080	0.068	0.013	8
Lov:	0.380-0.454	0.409	0.027	4
wov:	0.343-0.387	0.363	0.018	4

Remarks: *Escharella acuta* seems to be conspecific with the Pliocene form described by LAGAAIJ (1952) as *E. immersa* Flemming, 1828 and redescribed and figured by BISHOP and HAYWARD (1989) as an undescribed species. In spite of a similar spine number, *E. acuta* cannot be mistaken for *E. immersa* : the zooids of the later have a less convex frontal wall, conspicuous areolae, no prominent acute umbo and are smaller. *Escharella hexaespinosa* (ARISTEGUI, 1986) has a similar spine number in non-ovicellate zooids but the ovicellate zooids always have six spines; this species clearly differs from *E. acuta* by the lyrula, which is acute, and by the size and shape of the ovicells. A specimen collected in Zaffiro cave (near Naples) exhibits a very close morphology, but the lyrula is higher.

Distribution: Recent specimens are known only from the localities of the type material.

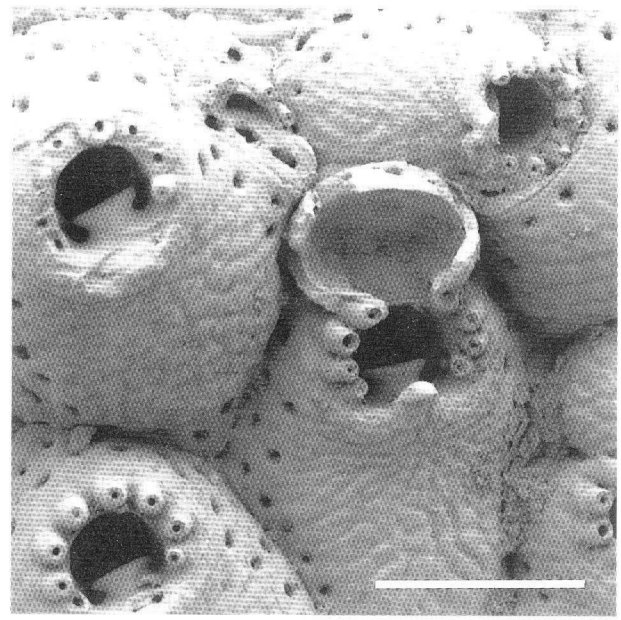

FIG. 9. — *Escharella octodentata*. Detail showing the characteristic shape of lyrula. (Blanes Canyon; 180-350 m) Scale bar: 250 µm.

Escharella octodentata (Hincks, 1880)
(Fig. 8, 9)

Mucronella peachii var. B (*octodentata*) HINCKS, 1880: 361.
Escharella immersa var. *octodentata*: GAUTIER, 1962: 213.
Escharella octodentata KLUGE, 1975: 495.
Escharella octodentata HAYWARD and RYLAND, 1979: 142.
Escharella octodentata BORONAT-TORMO, 1987: 103, pl. 5, fig. C-D.
Escharella octodentata SAGUAR and BORONAT, 1987: 399.
Material examined: Five colonies on *Lophelia* (Blanes).

Description: HAYWARD and RYLAND, 1979: 142.

Measurements:	Range	X	s.d.	N
Lz:	0.560-0.640	0.593	0.030	3
Wz:	0.420-0.500	0.460	0.020	5
Lor:	0.100-0.140	0.120	0.010	6
wor:	0.120-0.140	0.132	0.008	6
Llyr:	0.050	0.050	0.000	4
wlyr:	0.090-0.100	0.090	0.004	4

Remarks: In this material, the triangular suboral mucro appears to be noticeably more developed than in the NE Atlantic specimens figured by HINCKS (1880) and HAYWARD and RYLAND (1979); it also seems to be shorter than in the Mediterranean specimens studied by GAUTIER (1962: 'petit mucron proximal'). *Escharella octodentata* clearly differs from the other Mediterranean species of *Escharella* by the spine number, which is invariably eight in ovicellate and non-ovicellate zooids.

Distribution: The occurrence of *E. octodentata* in the Mediterranean Sea was questionable. It is considered to be a northern and deep-water species, distributed in the Barents Sea and the NE Atlantic ocean, from the Shetland Isles to the Bay of Biscay (HAYWARD and RYLAND, 1978, 1979) . The first Mediterranean record was by GAUTIER (1962) from four deep stations (85-200m) in the Alboran Sea, off Tunis and at the Hyères Islands. It was further recorded from the Alboran Sea (60-200 m) by BORONAT-TORMO (1987) and from the Columbretes Islands (60-80 m) by SAGUAR and BORONAT (1987).

Phylactellipora eximia (Hincks, 1860)
(Figs. 10, 11)

Lepralia eximia HINCKS, 1860: 276, pl. 30, fig. 3, 3a.
Phylactella eximia HINCKS, 1880: 359.
Phylactellipora eximia HAYWARD and RYLAND, 1979: 164.
Material examined: About sixty ovicellate colonies on *Lophelia* (Blanes) and *Madrepora* (Banyuls).

Description: HAYWARD and RYLAND, 1979: 164.

Measurements:	Range	X	s.d.	N
Lz:	0.500-0.800	0.630	0.100	10
wz:	0.380-0.480	0.430	0.030	10
Lov:	0.180-0.220	0.200	0.010	7
wov:	0.220-0.320	0.250	0.030	7

Remarks: The Mediterranean morphotype of *P. eximia* differs from the British specimens redescribed by HAYWARD and RYLAND (1979) in the constant presence of two (three in younger zooids) spines at the distal corners of the orifice. The other morphological characters of this rarely recorded species are identical, except for the ovicell, which remains apparent and not obscured by secondary calcification in Mediterranean colonies. Presence of spines seems to be a variable character in the genus *Phylactellipora* Bassler, 1953: in *P. collaris* (Norman, 1867), they are present only on some young zooids, while they were considered to be lacking in *P. eximia* (HAYWARD and RYLAND, 1979). Similarly, the genus *Phylactella* Hincks, 1879 was described without oral spines, but in the subspecies *tangerina* Harmelin and d'Hondt, 1992 of the type-species, *P. labrosa* (Busk, 1854), non-ovicellate zooids may bear one or two spines (HARMELIN and D'HONDT, 1992).

Distribution: *Phyllactellipora eximia* was known only

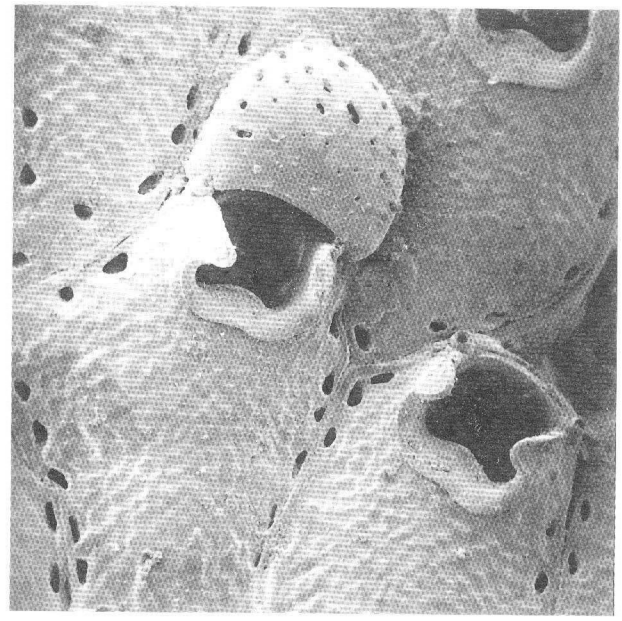

FIG. 10. — *Phylactellipora eximia*. Ovicellate zooids. (Blanes Canyon; 180-350 m).

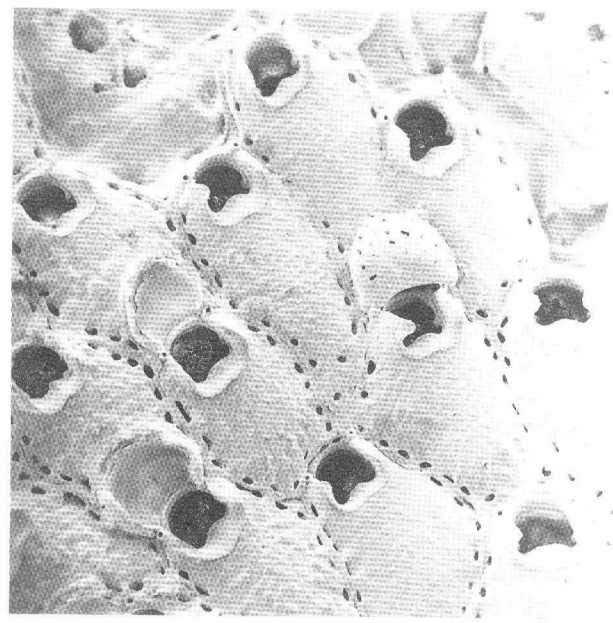

FIG. 11. — *Phylactellipora eximia*. Detail. (Blanes Canyon; 180-350 m).

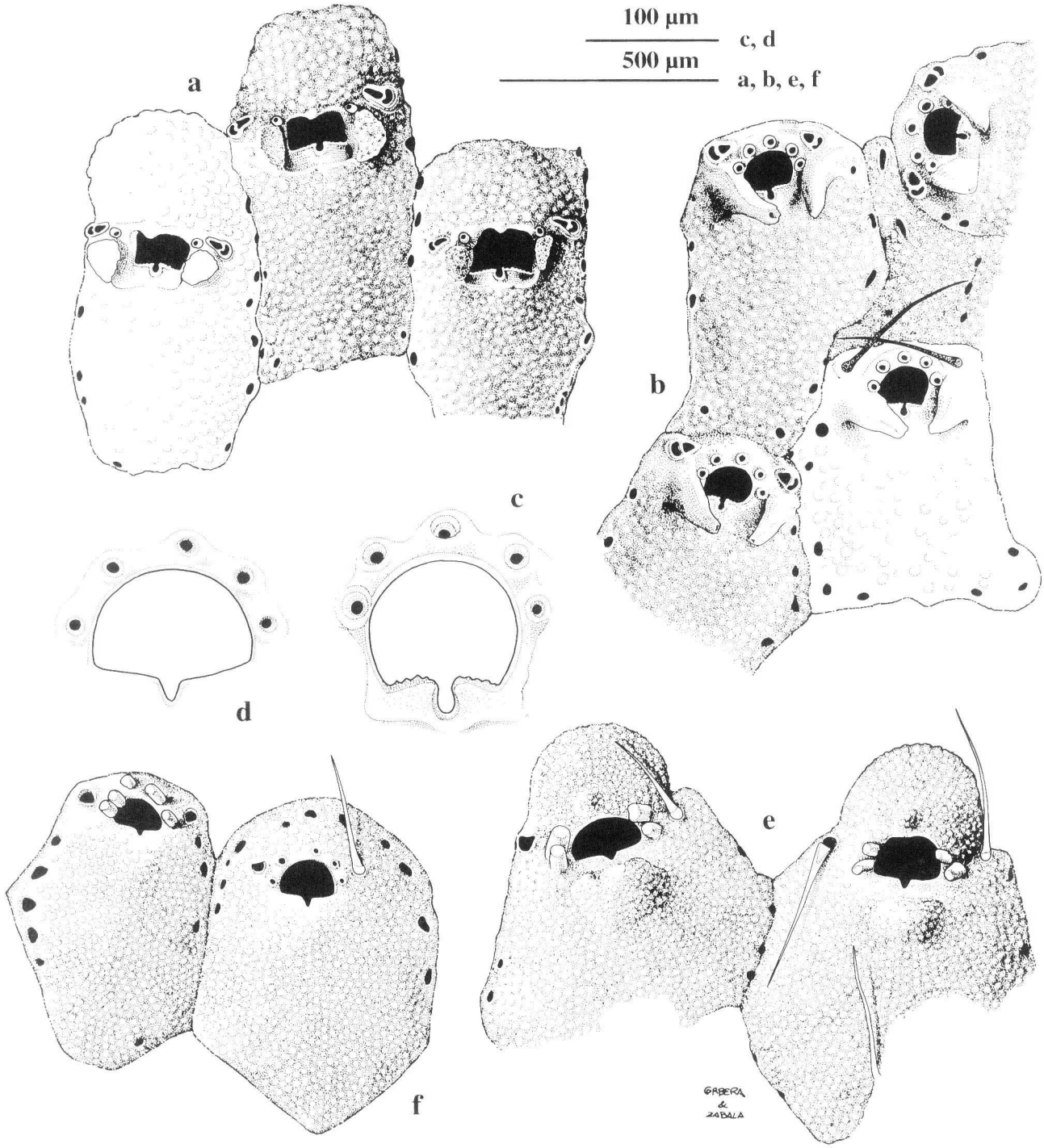

FIG. 12. — *Escharina dutertrei protecta* ssp. nov.: a: ovicellate zooids; b, nonovicellate zooids; c, orifice. *Escharina dutertrei haywardi* (Hincks, 1880): d: orifice; e, ovicellate zooids; f, nonovicellate zooids. (d,e and f drawn from the type, BMNH).

through descriptions of old material collected in British waters (HAYWARD and RYLAND, 1979). There was no recent record of this species, except for one from the Mediterranean (Provence, detritic sand, 100-200 m) by HARMELIN (1976), who listed it without description.

Escharina dutertrei (Audouin,1826)
(Figs. 12, 13, 14, 15, 16, 17)

Flustra dutertrei AUDOUIN, 1826: 67; SAVIGNY (in AUDOUIN, 1826) pl. 9, fig. 2.
Mastigophora dutertrei HINCKS, 1880: 279, pl. 37, fig. 1-2.
Escharina dutertrei GAUTIER, 1962: 157.
Escharina dutertrei HARMELIN, 1976: 215.
Escharina dutertrei HAYWARD and RYLAND, 1979: 198, fig. 83.
Escharina dutertrei ZABALA, 1986: 454, fig. 152 a-c.
Escharina dutertrei MOISSETTE, 1988: 131, pl. 21, fig. 5, 7.

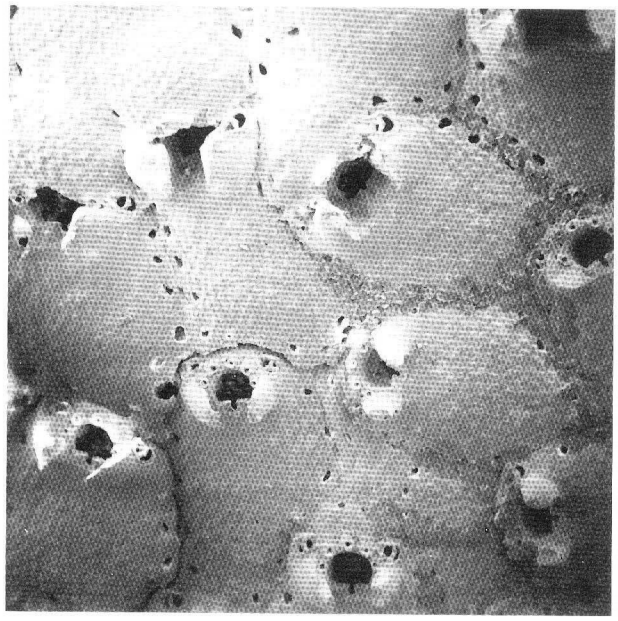

FIG. 13. — *Escharina dutertrei protecta* ssp. nov. Ovicellate zooids from Blanes Canyon (180-350 m) with the characteristic wing-shaped peristome. See a kenozooid in the lower right corner.

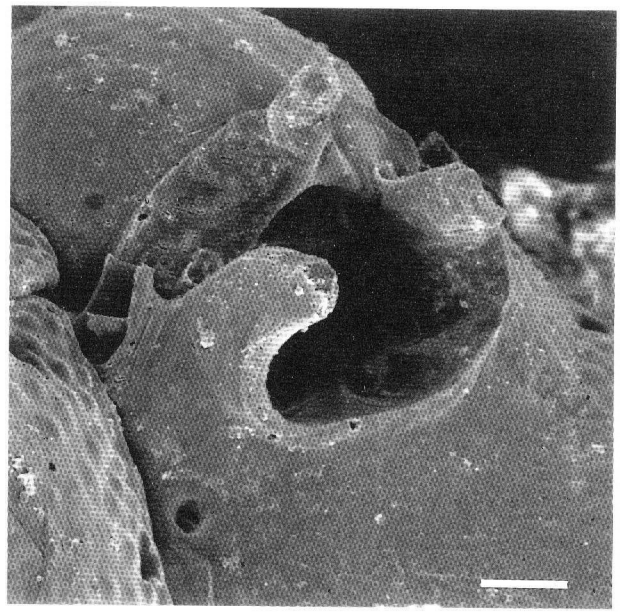

FIG. 15. — *Escharina dutertrei protecta* ssp. nov. Detail of an ovicellate zooid from Blanes Canyon (180-350 m) showing the acute mucro of the ovicell and the wing-shaped lobes of the peristome. Scale bar: 50 µm.

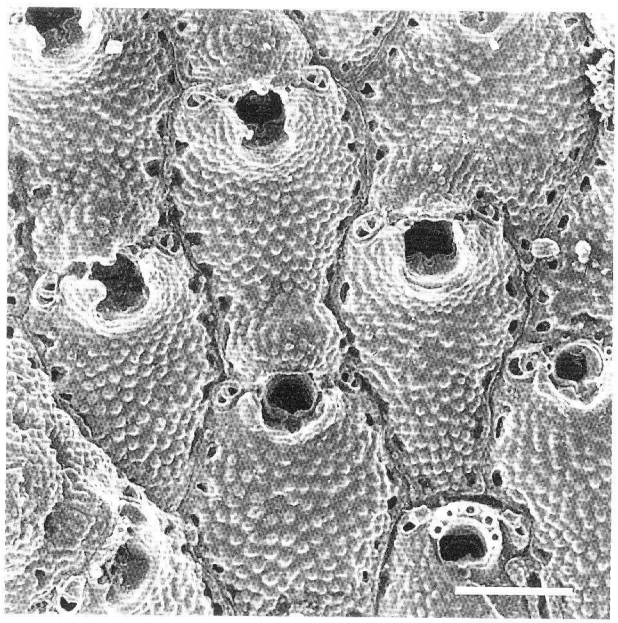

FIG. 14. — *Escharina dutertrei protecta* ssp. nov. Ovicellate zooids from Açores Islands (Sta. Maria, 120-130 m). Scale bar: 250 µm.

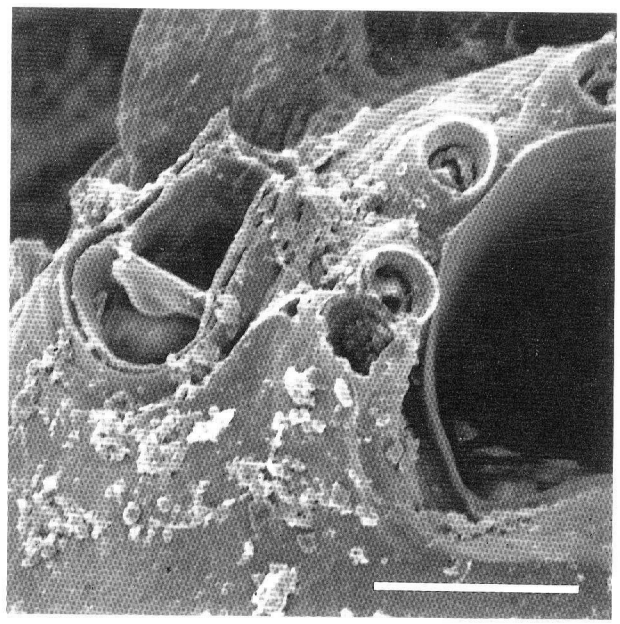

FIG. 16. — *Escharina dutertrei protecta* ssp. nov. Detail of an avicularium. (Blanes Canyon; 180-350 m). Scale bar: 50 µm.

Escharina dutertrei protecta ssp. nov.

Holotype. MZB.1986 14387 A.200. (Provisional cat. number). Blanes Canyon, W. Mediterranean.
Paratype. MZB.1986 14387 A.201 (Provisional cat. number). Blanes Canyon, W. Mediterranean.
Material examined: Nine small, ovicellate colonies on *Lophelia* (Blanes); several other specimens on *Madrepora* (Banyuls, 200-300 m). Many other colonies from Mediterranean shallow-water cryptic habitats (dark caves and underfaces of stones: Catalonia, Provence, 6-25 m) or shelf margin (Provence, 150 m). Several colonies from Açores: Santa Maria Island, 120-130 m, RV "Pt Théodore Tissier", st. 423; 110 m, RV "Jean Charcot", Biaçores st. 225; Flores, 105 m, Biaçores st. 106.
Etymology: *protecta*: protected, reference to the two flat peristomial lobes overarching the orifice.
Museum material: three small ovicellate colonies from the Hincks' collection (BMNH n° 1911.10.1.1198A and 1911.10.1.1199A).

Description: Colony encrusting, yellowish, small and lobed. Zooids large, flat or slightly convex. Frontal wall thick, coarsely granular, with a row of marginal

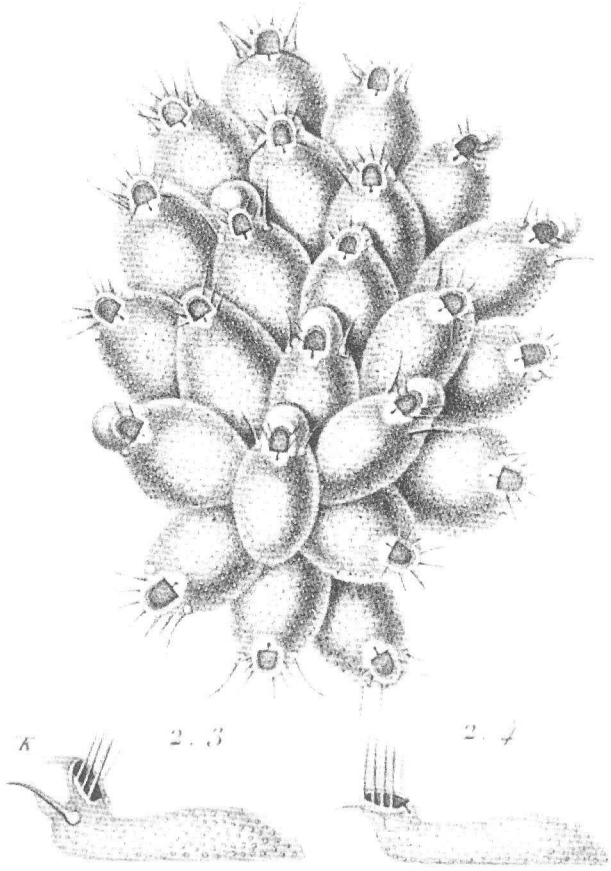

FIG. 17. — Enlarged photograph of the original illustration by SAVIGNY (in AUDOUIN, 1826) of *Flustra dutertrei* Audouin (1826).

pores variable in size and shape. Primary orifice semicircular, broader than long; straight or slightly convex proximal border, irregularly denticulate and indented by a narrow U-shaped sinus. Five to six (up to 7 in some cases) thick, short spines around the disto-lateral margins of the orifice of non ovicellate zooids, only two persisting in ovicellate zooids. Peristome with two lateral flat lips, wing-shaped when fully developed, partly overarching the orifice. Avicularia paired, symmetrical, disto-lateral to the orifice, with a short, truncated rostrum directed disto-centrally; long setiform mandible. Ovicell wider than long, protected laterally by the peristomial lobes; surface imperforate, coarsely granular, with a conspicuous mucro on the proximal edge, over the orifice. Kenozooids infrequent similar in size and shape to the autozooids but without orifice. Ancestrula not observed.

Measurements:	Range	X	s.d.	N
Lz:	0.600-0.757	0.681	0.070	4
wz:	0.454-0.530	0.484	0.030	4
Lor:	0.091-0.121	0.106	0.009	5
wor:	0.091-0.121	0.106	0.009	5
Lav:	0.058-0.070	0.062	0.008	8
wav:	0.040-0.056	0.045	0.012	8

DISCUSSION

E. dutertrei was originally described from the Red Sea (AUDOUIN, 1826) and it is reputed to be widespread in the Mediterranean and along the East Atlantic coasts, from Madeira to the Shetland Isles (HAYWARD and RYLAND, 1979). The present material shows that the Mediterranean specimens differ from the boreo-atlantic form described by HINCKS (1880) and HAYWARD and RYLAND (1979) in several features : 1) the orifice has a convex, frequently crenulate, (only visible by SEM) proximal border and a deeper, round-ended sinus; 2) the spine number in ovicellate zooids is always two instead of four; 3) the orifice is flanked by two peristomial, raised, wing-shaped lobes; 4) there is no umbo proximal to the orifice.

These distinctive characters of the Mediterranean morphotype were recognized in all Mediterranean specimens examined, although being more or less variable. The number of oral spines in ovicellate zooids and the occurrence of flattened peristomial lobes are constant. On the other hand, the spine number of non-ovicellate zooids, the height of the peristomial lobes, and the crenulation of the orifice vary according to the habitat. In deep-water colonies living on *Lophelia* and *Madrepora*, or other substrates (150-350 m), the most frequent number of oral spines is five, the proximal border of the orifice is clearly crenulated and the peristomial wings are tall. In shallow-water colonies (6-10 m, underfaces of piled stones), the spine number is frequently six (up to 7), the crenulation of the orifice is less pronounced or not apparent, and the peristomial wings are short. These Mediterranean characters were also observed in colonies from Açores islands (Santa Maria, 120-130 m).

The differences between the Mediterranean and the boreo-Atlantic specimens seem to be sufficient criteria for separating them taxonomically (P.J. Hayward, pers. comm.).

The Red Sea specimen illustrated by SAVIGNY (in AUDOUIN, 1826)(pl. 9, fig. 2), and named *Flustra dutertrei* by AUDOUIN (1826), seems to belong to a third morphotype, different from the Mediterranean and the Atlantic forms. The Savigny's illustrations clearly show (1) five ovicellate zooids with two pairs of oral spines (general view of the colony) and an ovicellate zooid (lateral view, fig. 2.3), with three spines on one side; (2) the absence of a well-developed peristome; (3) non-ovicellate zooids with 6 spines (4 spines on one side on a zooid in lateral view); (4) the absence of suboral umbo. In spite of the difficulty of interpreting Savigny's illustrations, it seems obvious that the Red

Sea specimen for which Audouin created the specific name of *dutertrei* clearly differs from the Mediterranean morphotype at least by the number of spines in ovicellate zooids and the absence of a peristome.

Thus, it seems preferable to establish three subspecies-names for these geographic morphotypes:

(1) *E. dutertrei dutertrei* ssp. nov. for the Red Sea form, which should be redescribed;

(2) *E. dutertrei haywardi* ssp. nov. for the boreo-Atlantic form described by HINCKS (1880) and HAYWARD and RYLAND (1979), with the specimens BMNH n.° 1911.10.1.1198A as holotype, and BMNH n.° 1911.10.1.1199A as paratype;

(3) *E. dutertrei protecta* ssp. nov. for the Mediterranean and Azorean form, as described above.

General distribution: Recent: north-east Atlantic (British Islands, Açores, Madeira), Mediterranean, Red Sea, ? Pacific Ocean. Fossil: Eocene to Pleistocene in Europe (*cf.* MOISSETTE, 1988)

Escharina hyndmanni (Johnston, 1847)
(Fig. 18)

Lepralia hyndmanni JOHNSTON, 1847: 306.
Herentia hyndmanni GAUTIER, 1962: 159.
Herentia (Herentia) hyndmanni DAVID and POUYET, 1978.
Escharina hyndmanni HAYWARD and RYLAND, 1979: 196.
Material examined: Several colonies on *Lophelia* (Blanes) and *Madrepora* (Blanes, Banyuls).

Description: HAYWARD and RYLAND, 1979: 196.

Measurements:	Range	X	s.d.	N
Lz:	0.560-0.700	0.610	0.040	5
wz:	0.400-0.500	0.456	0.030	5
Lov:	0.100-0.160	0.130	0.030	2
wov:	0.200-0.240	0.220	0.020	2

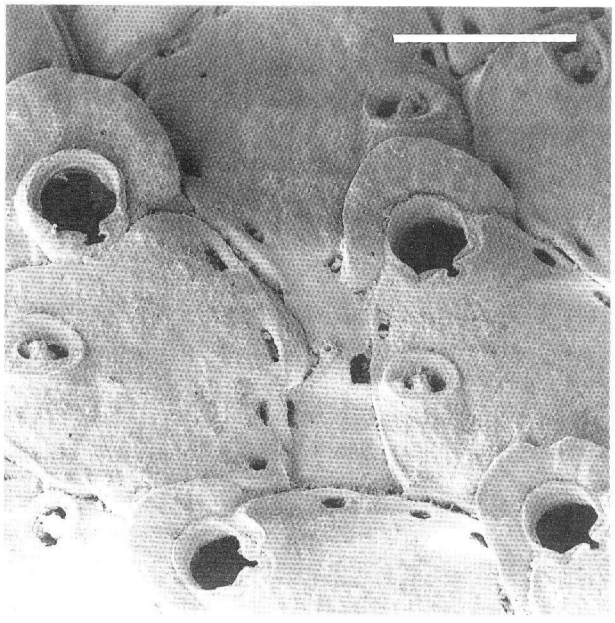

FIG. 18. — *Escharina hyndmanni*. Ovicellate zooids. (Blanes Canyon; 180-350 m) Scale bar: 250 µm.

Remarks: In his description of *Escharina hyndmanni*, GAUTIER (1962) probably included specimens of *E. porosa* (Smitt), which differs from the former by a perforate frontal wall (subgenus *Therenia* DAVID and POUYET, 1978 of *Herentia* Gray, 1848). Several species and subspecies closely related to *E. hyndmanni* were described by DAVID and POUYET (1978) from Neogene and Recent material of Europe. A reevaluation of these taxa, together with the available material attributed to *E. hyndmanni*, is necessary. In the Mediterranean, *E. hyndmanni* is relatively common, particularly on small substrates from deep water (> 100 m) and in littoral cryptic habitats (dark caves and stone underfaces).

Distribution: East Atlantic (Shetland Isles to Madeira) and Mediterranean Sea.

Schizomavella neptuni (Jullien, 1882)
(Figs. 19, 20)

Schizoporella neptuni JULLIEN, 1882: 511, pl. 14, fig. 34.
Schizoporella neptuni JULLIEN and CALVET, 1903: 80.
Schizoporella neptuni CALVET, 1906: 421, pl. 27, fig. 14.
Schizoporella neptuni ZABALA and MALUQUER, 1988: 133, pl. 18 F.
Schizomavella neptuni HARMELIN and D'HONDT, 1992: 46, pl 6 C.
Material examined: Four small ovicellate colonies on *Madrepora* (Blanes).

Description: Colony encrusting, unilaminar, small (20-30 zooids), white. Zooids quadrate, flat. Frontal wall vitreous, coarsely granular, with very few small, proximo-lateral pores, irregularly distributed, and a row of marginal areolae. Primary orifice orbicular, longer than broad, with a very deep and narrow sinus; operculum well chitinized. Eight oral spines,

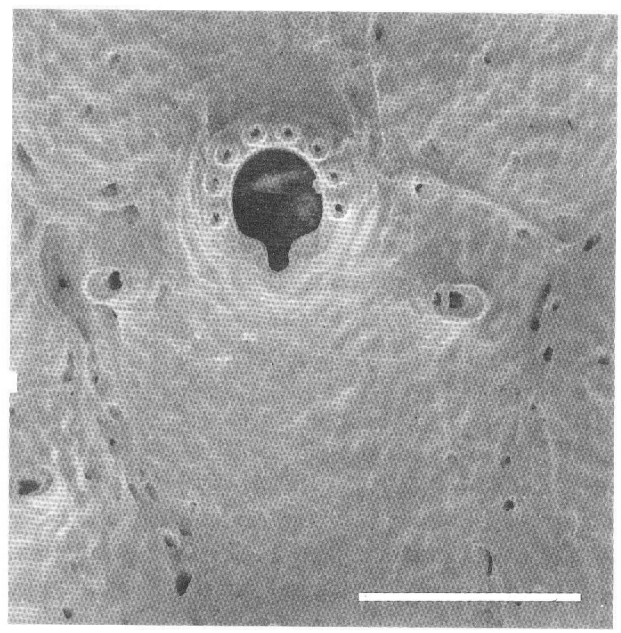

FIG. 19. — *Schizomavella neptuni*. Nonovicellate zooid (Blanes Canyon; 180-350 m). Scale bar: 250 µm.

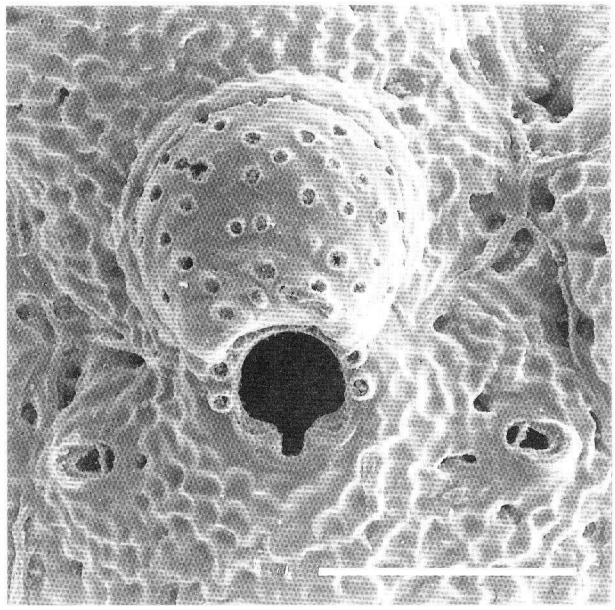

FIG. 20. — *Schizomavella neptuni*. Ovicellate zooid: persistence of the spine bases under the ovicell orifice (Malta, 350-900 m; 'Suroit' Escarmed 3). Scale bar: 250 µm.

four apparent in ovicellate zooids. Avicularia small, paired or sometimes single, at sinus level or proximal to the orifice on the lateral borders of the zooid, directed proximo-laterally, oblique to the frontal surface of the zooid; rostrum oval or slightly spatulate. Ovicell recumbent on the succeeding zooid, broader than long, irregularly perforated by large pores, not closed by the operculum. Embryos and ancestrula not observed.

Measurements:	Range	X	s.d.	N
Lz:	0.565-0.726	0.629	0.063	4
wz:	0.387-0.484	0.439	0.038	4
Lor:	0.097-0.129	0.117	0.013	4
wor:	0.081-0.097	0.089	0.089	4
Lov:	0.161-0.177	0.169	0.008	2
wov:	0.242-0.258	0.250	0.008	2
Lav:	0.053-0.065	0.061	0.004	4
wav:	0.032-0.042	0.034	0.004	4

Distribution: This rare species, typically from the upper-slope of the Atlanto-Mediterranean region, was first described from the Gulf of Biscay by JULLIEN (1882). It was reported later from the NE Atlantic Ocean (Britain to Açores and Gulf of Cadiz; 150-1068 m) by JULLIEN and CALVET (1903), CALVET (1906), HAYWARD and RYLAND, 1978, HARMELIN and D'HONDT, 1992. In the Mediterranean, it was found on deep rocks in the Strait of Sicily and Malta (320-900 m; HARMELIN, 1979), Tyrrhenian Sea (700 m; Sonne 58 DC; Harmelin, unpublished), and on dead shells off the Provence coast (120-180 m; Braprov 3A.29; J.G.H., unpublished). The only shallow-water record of *S. neptuni* is from the rocky floor of a Catalonian submarine cave (Medes Islands, 20 m; ZABALA and MALUQUER, 1988). GORDON (1987) reported *S. neptuni* from the Pacific Ocean: Kermadec Ridge (290 m); his description and S.E.M. micrograph indicate avicularia different in shape and number from that observed in our material.

Plagioecia patina (Lamarck, 1816)
(Fig. 21)

Tubulipora patina LAMARCK, 1816: 163.
Plagioecia patina HARMELIN, 1976: 129; pl. 8, figs. 5-9; pl. 18, figs. 4-9; pl.19, figs. 1-5.
Plagioecia patina HAYWARD and RYLAND, 1985: 97, figs. 5A, B, 6E-G, 33.
Material examined: More than fifty colonies on *Madrepora* (Blanes and Banyuls).

Description: Deep-water morphotype characterized by adnate growth and compound zoarium. Daughter colonies (up to 6-7) closely piled and budded centrally. Compound colony convex to dome-shaped (5-8 mm in diameter, without the marginal lamina). Superposed daughter colonies show only slight differences in diameter, which tends to decrease upwardly. Marginal lamina much developed (width: 2.5-3.5 mm) and fragile. Feeding zooids restricted to a unique peripheral row corresponding to the growing edge. The other zooids, more or less arranged in radiating rows, are closed by planar diaphragms, punctured with pseudopores, and without erect peristome. Gonozooid crescent-shaped, large (width: 2-

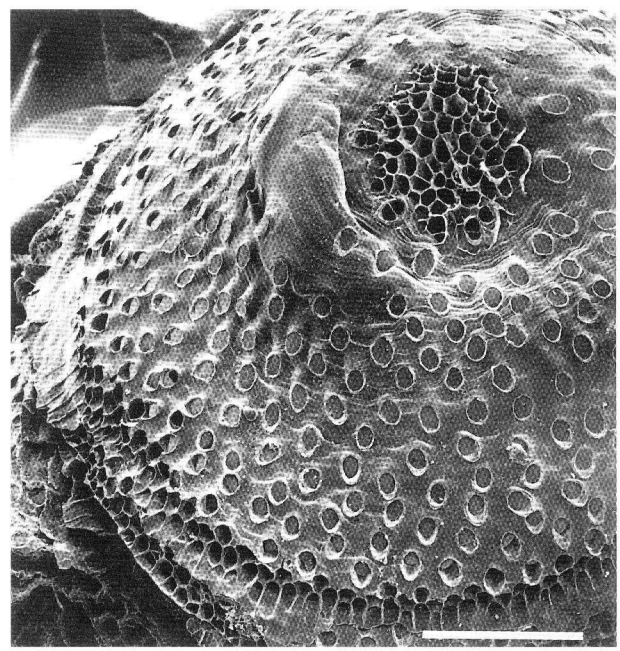

FIG. 21. — *Plagioecia patina*. Compound fertile colony showing the central budding zone. (Lacaze-Duthiers Canyon; 300 m). Scale bar: 1 mm.

3.3 mm, length: 0.6-0.8 mm) with a rather central (upper) position on the zoarium, partly enveloping some autozooid orifices at the periphery. Ooeciostome short, compressed (90-120 × 145-160 μm), bent proximally, located on the middle of the distal border of the gonozooid.

Remarks: This deep-water morphotype differs from the shallower typical growth-form (HARMELIN, 1976; HAYWARD and RYLAND, 1985) mainly by its entirely adnate growth, constancy of the compound structure of the zoarium, and central budding of the daughter colonies. In colonies from intermediate depths, such as that figured by HARMELIN (1976, pl. 18, figs. 5, 6, 8; st. 72-37: Marseille, 55 m), both peripheral and central budding of daughter colonies can occur simultaneously. Constant central zoarial budding characterizes *P. inoedificata* (JULLIEN, 1882) and *P. platydiscus* Harmelin, 1976. Daughter colonies of the former are generally cup-shaped and attached by the central region of the basal wall. *Plagioecia platydiscus* resembles the deep-water morphotype of *P. patina* also in its adnate growth and lack of peristomes, but differs in the gonozooid shape and presence of autozooid diaphragms opening by a central tubule.

Distribution: *Plagioecia patina* is common in the Atlanto-Mediterranean region from shallow-water to upper-slope habitats; it is reputed to have a cosmopolitan distribution.

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