

PLIO-PLEISTOCENE DEEP-WATER BRYOZOANS FROM RHODES, GREECE

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ABSTRACT. Twenty-one bryozoan species are recorded from the Plio-Pleistocene deep-water marls of the island of Rhodes, Greece. The faunas occur in three sections where they are represented mostly by erect colonial morphotypes belonging to the cyclostomes (11 species) and the cheilostomes (five anascans and five ascophorans). Essentially on the basis of the known bathymetric distribution of the 19 extant species, a depth of deposition of 200 to 600 m is suggested, with a shallowing occurring towards the top of the sections. This is supported by the other fossils (foraminifera, ostracodes, pteropods and trace fossils) found in the same beds. Introduction of bathyal bryozoans from the Atlantic during the late Neogene is also considered.

THE first mention of bryozoans from the Plio-Pleistocene of Rhodes was by Hedenborg (1837), who gave a list of six bryozoans (mostly determined only to genus level) under the heading 'Zoophytes'. The first real description of bryozoans from Rhodes was by Manzoni (1877). This study was based on material from the Deshayes collection, in the Ecole des Mines in Paris. The fauna consisted of 54 species, one of which, *Idmonea hedenborgi*, was new. The next description was by Pergens (1887), who described 60 species, two of which, *Filisparva delvauxi* and *Pustulopora smitti*, were new. The material for Pergens' description was probably the Hedenborg collection, which came to the Natural History Museum in Vienna in 1865, after the death of Hedenborg. It is doubtful if any of the material described by Manzoni or Pergens came from the deep-water beds mentioned here. No localities are given by Pergens, and none of the localities mentioned by Manzoni, which can be identified, comprises deep-water beds. There have been several references to the occurrence of bryozoans and 'bryozoan marl' in the geological and stratigraphical literature on Rhodes, but no actual information is given. The species described by Manzoni (1877) and Pergens (1887) have been repeatedly referred to by more recent authors, both on Recent and fossil bryozoans, but actual material from Rhodes has not been described.

The late Pliocene and Pleistocene sediments of Rhodes are well exposed, notably on the eastern coast of the island. Three deep-water sections have been studied and a number of samples were taken from various marl beds. They yielded the 21 bryozoan species that are described in this paper.

Most of the palaeoecological interpretation here is based on the known bathymetric ranges of the 19 extant bryozoan species but the distribution of the various zoarial forms is also considered. These colony morphotypes are more or less strictly related to certain environmental factors, among them depth (Stach 1936; Lagaaij and Gautier 1965; Labracherie and Prud'homme 1966; Schopf 1969a; Braga 1979; Harmelin 1988; Moissette 1988, 1993; McKinney and Jackson 1989). Bryozoan colonies belong to several erect types: vinculariiform (rigid cylindrical branches), adeoniform (rigid, narrow bilamellar branches), retoporiform (rigid reticulate branches), cellariiform (long articulated segments), and catenicelliform (very short articulated segments). Encrusting (membraniporiform), nodular (celleporiform), free-living and cup-shaped (lunulitiform), and conical (conescharelliniform) colonies are also distinguished. The pseudovinculariiform type corresponds with a membraniporiform colony forming a sleeve-like hollow tube once encrusting the stem of an unpreserved organism. Occurrence of these zoarial forms in the Plio-Pleistocene of Rhodes is variable but erect types always dominate, whereas some colony forms are completely absent.

PLIO-PLEISTOCENE STRATIGRAPHY ON RHODES

The first geologist to erect a detailed stratigraphy for these beds was Hedenborg (1837). A later manuscript edition was utilized by Bukowski (1899). Both Bukowski and other older authors regarded all the beds in question as Pliocene. Later it was realized that the younger beds also included part of the Pleistocene. This complex was named the Sguru Formation by Mutti *et al.* (1970).

Meulenkamp *et al.* (1972) introduced modern lithostratigraphical names. The marine beds were divided into the Pliocene Kritika Formation, consisting of shallow-water, often lagoonal beds, the supposedly Pleistocene Vasfi Formation, consisting mostly of open marine marls, and the youngest, Rhodos Formation, consisting mostly of bioclastic shallow-water limestones.

The field-work carried out since 1976 by the group led by Richard Bromley (Copenhagen, Denmark), Nils-Martin Hanken (Tromsø, Norway) and Stein Erik Lauritzen (Bergen, Norway) has shown that this stratigraphical scheme is too simplified. Bromley and his colleagues are working upon a revision of the stratigraphical nomenclature of these beds, and therefore no new units will be suggested here.

The deep-water beds from which the present material comes have been studied at three localities (for a detailed description, see below): Vasfi, Cape Vagia and Lindos Bay (Text-fig. 1). They are uniform lithologically, and the depth of deposition makes it reasonable to suppose that they were deposited as a continuous unit. The deep-water marls are dark bluish grey and mostly massive due to bioturbation, often with spectacular suites of trace fossils. A few horizons are finely laminated, and have a high organic content.

Palaeomagnetic studies by Løvlie *et al.* (1989) indicate that the Plio-Pleistocene boundary is found in the lower part of the deep-water beds, and thus the thickest part of it is above the boundary, of early Pleistocene age. Because of the problems with precise dating, the other localities are supposed to be of approximately the same age. The dating used here is based upon the hypothesis that, based on the Cape Vagia section, there was a rapid transgression at the end of the Pliocene, reaching its maximum just below the Plio-Pleistocene boundary, and then a slow regression punctuated by climatically induced eustatic cycles. The transgression is so great (more than 600 m) that it cannot be ascribed to ordinary eustasy, but must be a product of local tectonics. Such large vertical movements are known also from other parts of the Aegean Arc, as in Crete (Meulenkamp 1985; Peters *et al.* 1985). As a first approximation, the maximum transgression can therefore be used as a proxy for the Plio-Pleistocene boundary, even if there are some problems resulting from the incompleteness of the sections at the localities.

DEPTH INDICATORS IN THE DEEP-WATER BEDS

The sediments are extremely fine-grained clays, with more than 90 per cent. of the clastics in the clay fraction. Almost all of the material found in the washed fractions is biogenic, and also the carbonate content is almost completely biogenic, including nannofossils in the clay fraction.

The nature of the faunas in these marls indicates clearly that they were deposited in deep water (> 200 m), but it is difficult to give precise estimates of the depth. This is a consequence partly of the general lack of data about the faunal distribution in this depth interval, and partly of the peculiar local conditions.

The planktonic/benthonic ratio of foraminifera has been used as a depth indicator even if there are certain reservations, as indicated by Zwaan *et al.* (1990). Both their data, and those of Reiss *et al.* (1971) from the coast of Israel, give a depth of about 400 m for assemblages with 50 per cent. planktonic species, a figure which is common in our deep-water marls. In some, but not all the samples, the benthonic foraminifera are dominated by *Uvigerina*, which also indicates considerable depths.

As reported by many authors, the steep topography met with in many parts of the eastern Mediterranean results in extensive transport of shallow-water material down into deeper sediment.

In almost all the microfossil samples in our material, there are obvious shallow-water forms, including epiphytal ones, which evidently have been resedimented. Because of the topography of Rhodes, this is easily explained, even under conditions of much higher sea level.

The ostracodes (including *Polycope* and other deep-water forms) also indicate depths in the same range as the foraminifera, even if it must be admitted that the comparative data for the depth distribution of Mediterranean ostracodes in this depth interval is restricted. None of the true deep-water forms described by Benson (1976) has been found.

Lophelia pertusa forms typical deep-water patch-reefs in one of the localities (Vasfi), and has also been reported (Jüßen 1890) from the Lardos locality. This coral is found in about 100 m depth in the cold waters around Norway, and deeper further south. In the Mediterranean it has been reported at depths between 300 m and 800 m, in general deeper than 450 m (Blanc *et al.* 1959; Peres 1967). It should be noted that many observations are on patches of dead coral, which may have lived under other depth conditions. The other faunas found together with *Lophelia* in the Plio-Pleistocene of Rhodes indicate a depth of about 250 m. These intervals also seem to have been cold, and the presence of the corals may be the result of colder bottom water (under such circumstances *Lophelia* is known to grow at shallower depths). Another observation is that the coral patches seem to have started growing on a flat clay bottom, without a solid rock basement. This is not unusual around the coast of Norway and in the uplifted late Pleistocene of Norway, but according to Blanc *et al.* (1959) and Peres (1967) *Lophelia* patches always grow on solid rock, and on ledges in the Mediterranean. Because of these uncertainties, the presence of *Lophelia* can only be used to give a minimum value for our depth estimates.

In some of the beds, found in all three localities, there are numerous pteropods. The most easily visible is *Clio pyramidata*, but in most cases *Limacina* spp. also occur. Conventional data on the distribution of pteropod oozes (Murray and Chumley 1924) affirm that they are found between 700 and 3000 m depth. In some areas (Herman 1971, Indian Ocean) pteropods can be found at much shallower depth (up to 100 m), but the assemblages are rather different from those found in Rhodes. Reiss *et al.* (1971) have pteropods only at 550 m, and Herman (1971) indicates many cores with pteropods in the eastern Mediterranean from depths between 576 and 2897 m. Forbes (1844) reports, from some of the first deep dredging in the Aegean Sea, that white muds rich in pteropods (among them *Clio pyramidata*) are common at depths between 100 and 200 fathoms (= 180–360 m). These observations have not been repeated, but the macrofauna from the same stations has several species in common with those of the pteropod beds in Rhodes, even if many also occur in shallower water. In the fossil localities, the pteropod-rich beds also have high percentages of planktonic foraminifera (typically > 50 per cent.), and many of the foraminifera and ostracodes have recorded depth distributions deeper than 400 m.

The presence of the trace fossil *Zoophycos* which is found both in the Cape Vagia section and at Lindos Bay is also a potential indicator of considerable depth.

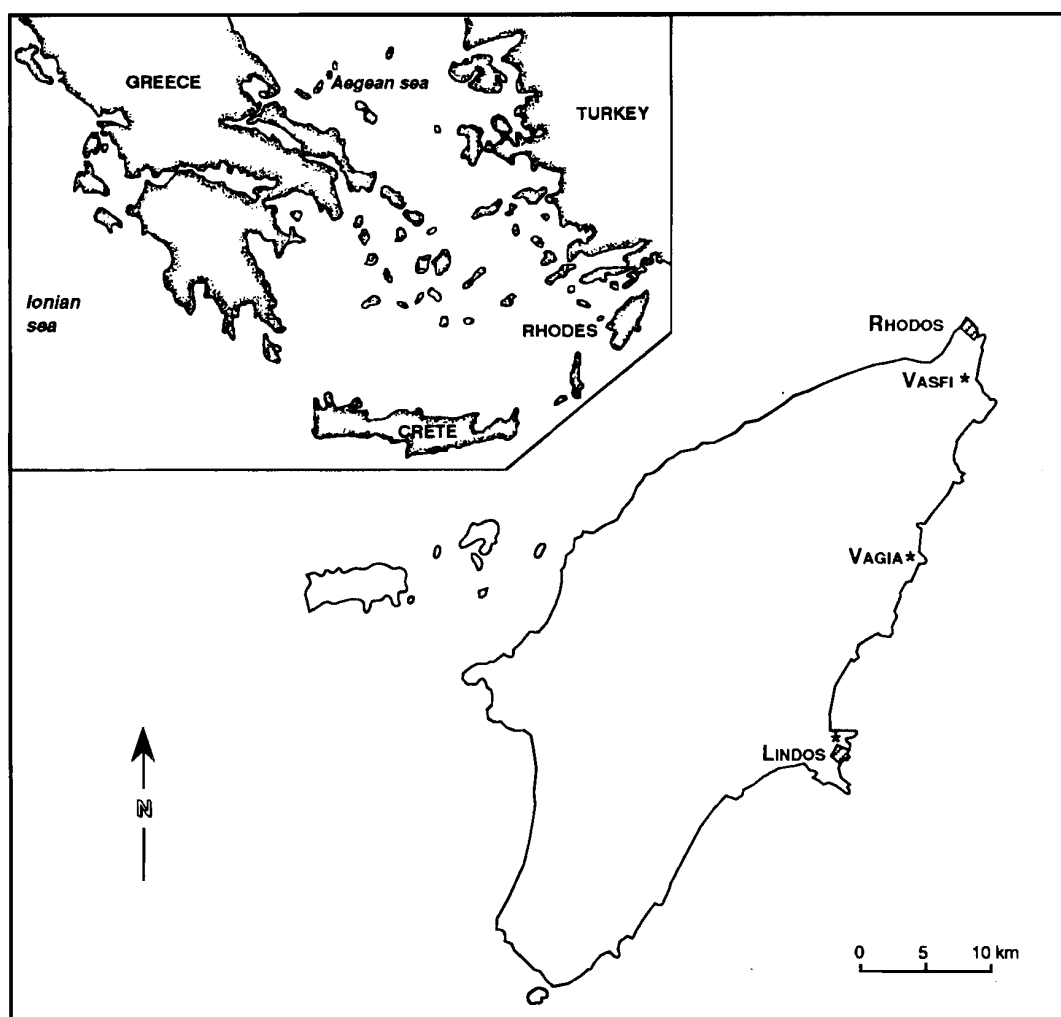
Even if the absolute depth figures are uncertain, the relative values seem to be well established. We regard the pteropod beds to be the deepest (about 600 m), the typical marls to be between 450 and 250 m (based on known depth distribution of foraminifera, ostracodes, and bryozoans), and the *Lophelia* beds are estimated to indicate a depth of about 250 m.

DESCRIPTION OF THE SECTIONS

The Vasfi section

This section, situated along the eastern coast of Rhodes about 6 km south of Rhodes City (Text-fig. 1), was described by Orombelli and Montanari (1967), Zaccaria (1968), and Sørensen (1984). It was the best known section in the Plio-Pleistocene of Rhodes, and was mentioned repeatedly in the literature, e.g. by Keraudern (1971).

The upper part of the section was logged in detail by one of the authors (NS) and his students in 1976, but shortly afterwards the section was built over by the construction of an hotel. Now only a short section (about 1 m) is exposed at the contact between the coquina and the marl.



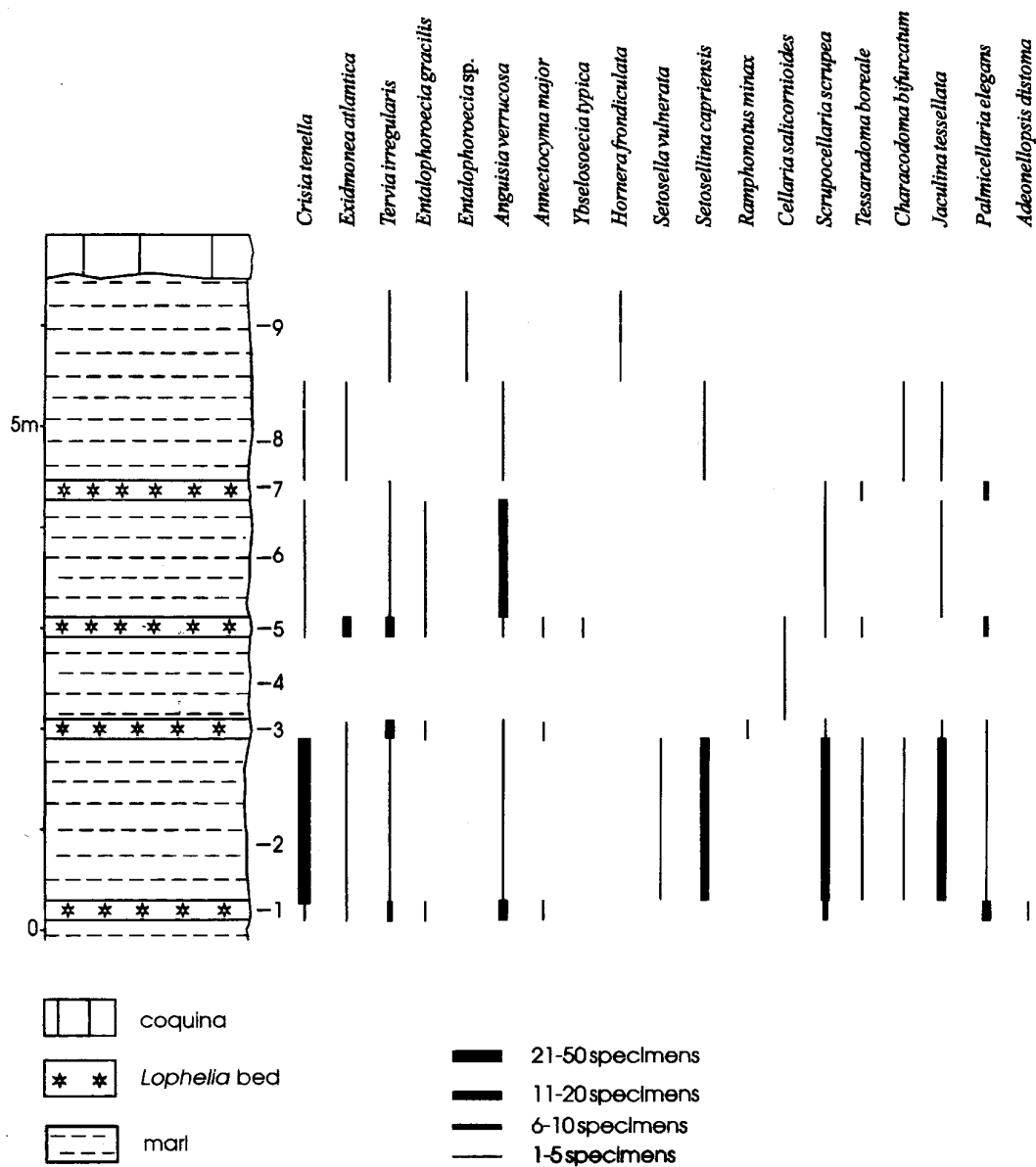
TEXT-FIG. 1. Location map of the three sections on the island of Rhodes.

The lower, unlogged part of the section consists of about 7 m of bluish-grey marl, with a fauna of small molluscs – mostly bivalves – some scaphopods and single corals. This is the typical fauna of these deep-water marls in Rhodes. There are also numerous trace fossils, especially echinoid burrows and *Chondrites*.

The logged section (Text-fig. 2) consists of the same marl, but with four beds of *Lophelia*-thickets. On top, there is a coquinal, impure limestone which grades into a beach-rock. The contact is disconformable, and cuts down into the marl towards the east.

The comparatively sparse macrofauna found in the *Lophelia* patches in Vasfi is also different from that mentioned by Peres (1967) for Recent patches in the Mediterranean. Studies on the microfauna (foraminifera and ostracodes) indicate that the *Lophelia*-beds were deposited at shallower depth, and in colder temperatures than the intervening marls.

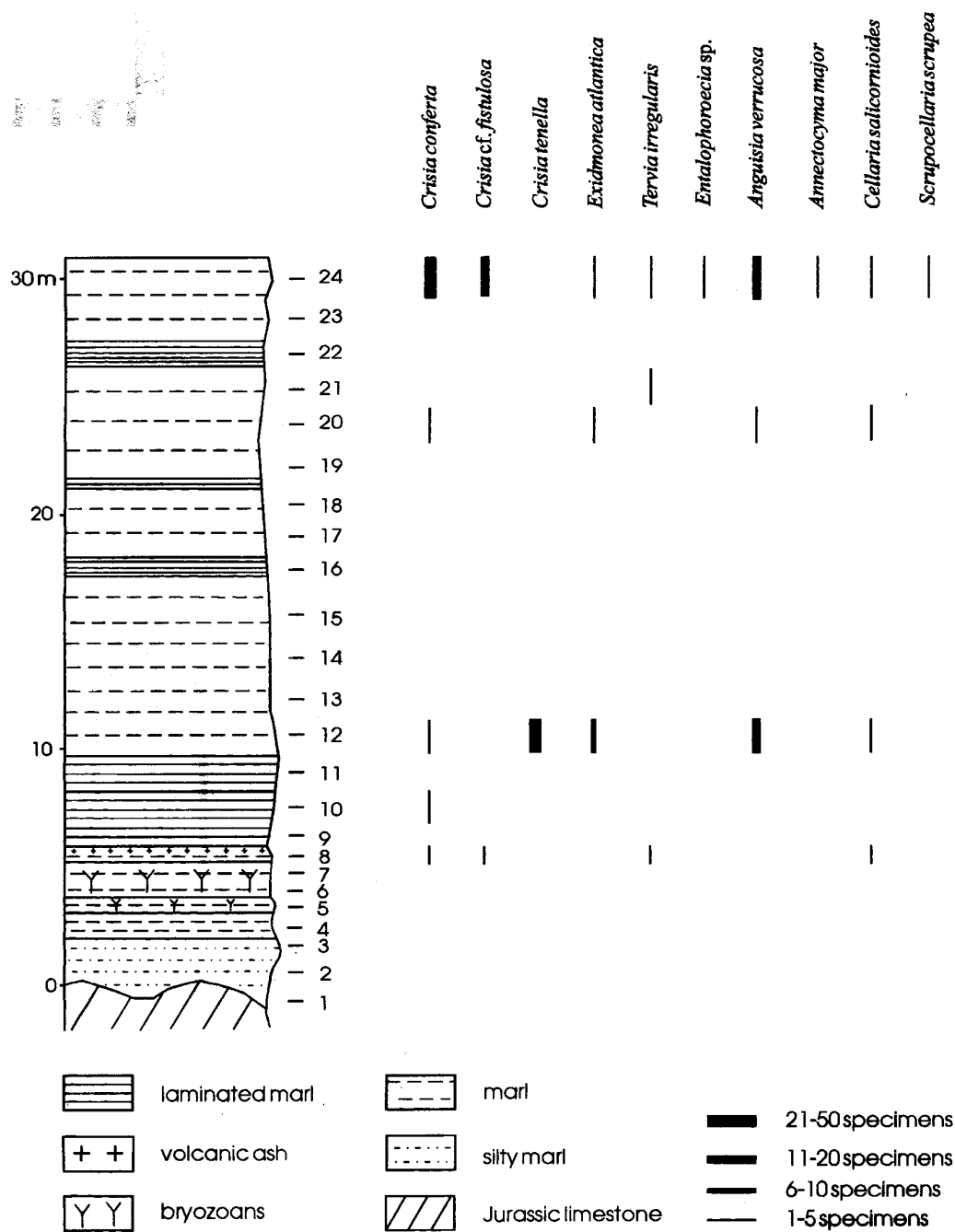
The topmost marl beds (about 1–2 m maximum thickness) contain numerous pteropods, and this, in combination with the microfossil data (a high percentage of planktonic foraminifera, with



TEXT-FIG. 2. Distribution of bryozoans in the Vasfi section.

many deep-water forms), indicates deposition at a depth of approximately 600 m. For the other parts of the marl, a depth of about 400 m is estimated, and for the *Lophelia* patches, about 250 m.

The coquina beds above the marl indicate a deposition in shallow water (< 50 m), and a definite Pleistocene age. The age of the marls themselves is either earliest Pleistocene or latest Pliocene. None of the significant guide fossils are found among the microfossils, and *Hyalinea baltica* which is regarded as the guide fossil for the beginning of the Pleistocene, is found only in the coquinal beds,



TEXT-FIG. 3. Distribution of bryozoans in the Cape Vagia section (samples 1 to 7 include numerous shallow to moderately deep water bryozoans not treated in this paper).

and (probably as an admixture due to burrowing) in the topmost part of the pteropod-rich marl. If the pteropod-rich beds are taken as indicating the maximum transgression, a comparison with the Cape Vagia section would indicate that the whole section at Vasfi was in the uppermost Pliocene, just below the Plio-Pleistocene boundary. On the other hand, the oscillation in temperature and possibly also depth indicated by the *Lophelia*-beds seem stronger than would be expected from the known late Pliocene glaciations. The stronger oscillations are found only in the upper Pleistocene, and that would be too young for these beds.

The Cape Vagia section

This locality is a small, south-facing basin on the eastern coast of Rhodes (Text-fig. 1). At the base of the section are Jurassic limestones, intensively bored by *Lithophaga* and other organisms. The lower part of the sequence (Text-fig. 3) consists of marl with fossils (mostly fragmentary) between the boulders and irregularities in the basement, followed by an impure limestone with numerous fossils. Some marl-rich bands are found, and there are numerous trace fossil-horizons. At about 3–4 m above the base there are beds rich in bryozoans, echinoids, brachiopods, and molluscs, especially pectinids. Much material has been washed in from shallower water, including large, bored blocks of limestone (up to 1 m in diameter), fragments of oyster, and red algae, and for this reason, samples 1 to 7 are not studied in this paper.

Above these beds, the clay content increases rapidly, and the top marl includes beds rich in pteropods, and with a high (> 50 per cent.) percentage of planktonic foraminifera. The beds contain some spectacular trace fossils, including *Zoophycos*, found by R. G. Bromley and N.-M. Hanken. These trace fossils are taken to indicate deep water, and in this case the top of the *Zoophycos* is in the pteropod-rich beds, which are estimated to show a depth of about 600 m. They penetrate down into beds which were probably deposited in much shallower depth (about 150–200 m).

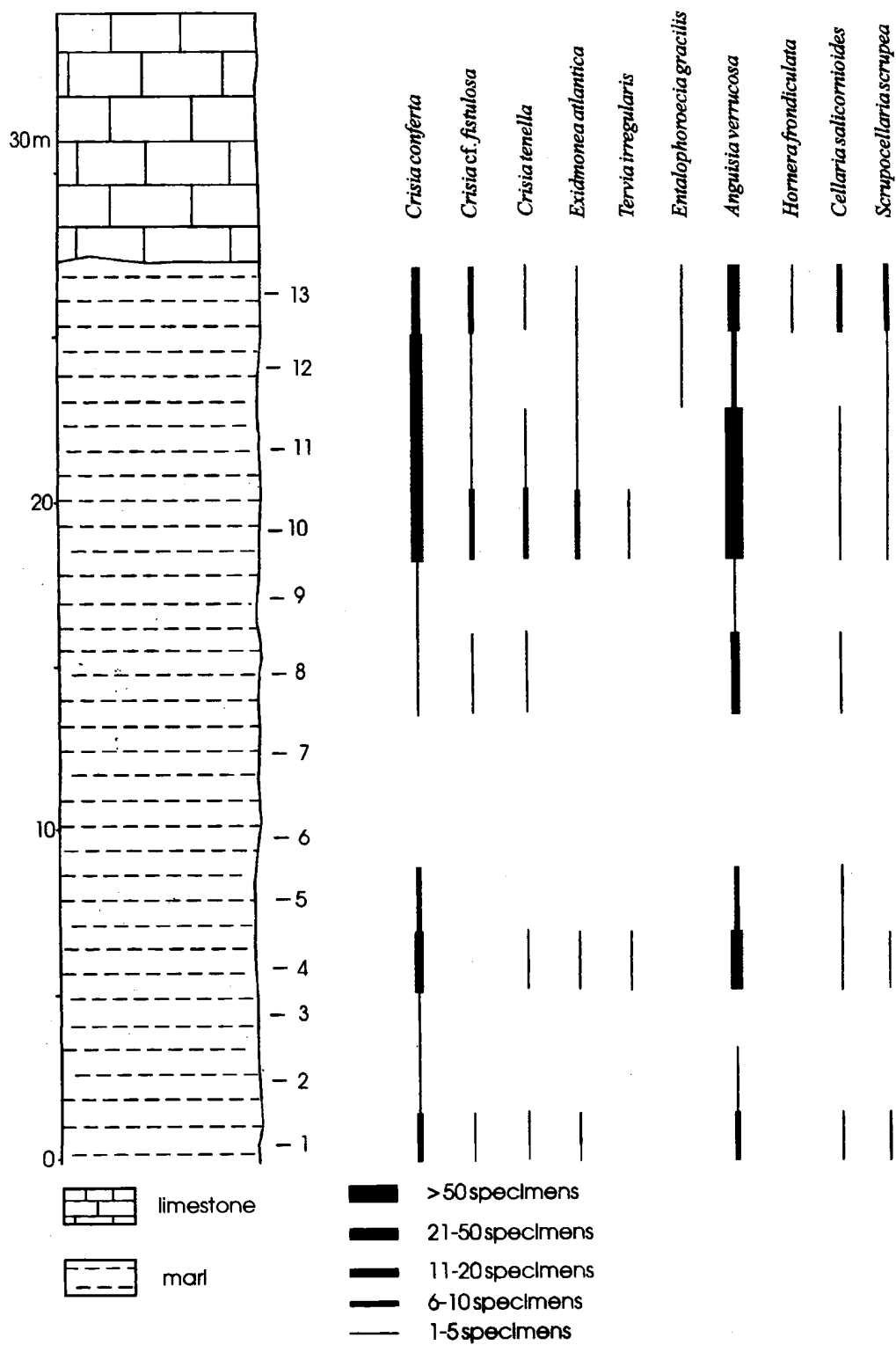
A thin (2–4 mm) red bed, probably a basaltic volcanic ash (Løvlie *et al.* 1989), overlies the *Zoophycos* bed. In the following bed, there are decimetric intervals of laminated, organic-rich beds, some of them with macroscopic plant remains, mostly *Pinus* wood. Most of the section consists of bioturbated marl, with a deep-water fauna dominated by bivalves, scaphopods, solitary corals, and brachiopods. The suggested depth of the lower part of the marl beds is approximately 400 m, decreasing upwards to about 250 m. As usual, there are many microfossils which have been washed in from shallower water, including epiphytic foraminifera.

From the palaeomagnetic results of Løvlie *et al.* (1989) the Plio-Pleistocene boundary should be about 5 m above the ash bed (about 10 m above the base of the section in Text-fig. 3). This indicates that the lower beds and the pteropod-rich beds marking the maximum transgression are youngest Pliocene, and the upper part of the section is Pleistocene. If it is accepted that the normal interval in the top of the section is the Brunhes Chron, this part of the section will be younger than 0.8 Ma.

The model developed from the palaeomagnetic results in this section, which may also be used for correlation with the other sections, demonstrates that the major transgression, which must have been very rapid and of a magnitude which exceeds usual eustatic sea-level changes, started in the very latest Pliocene, reached its maximum (at least 600 m higher than at present), just before the Plio-Pleistocene boundary, and was followed by a very slow, gradual regression.

The Lindos Bay section

Lindos Bay is situated along the eastern coast of Rhodes, a few km north of the town of Lindos (Text-fig. 1). Beginning just above present-day sea-level, the section consists of about 28 m of bluish-grey marl, rich in pteropods and trace fossils (*Zoophycos*). Foraminifera, bivalves, scaphopods and ostracodes are also present, together with decapod, echinoid and fish remains.



TEXT-FIG. 4. Distribution of bryozoans in the Lindos Bay section.

Locally laminated, the marl is mainly massive and well bioturbated. Massive coquinal and bryozoan-rich limestones cap the section, in disconformable contact with the marl (Text-fig. 4).

By comparison with the previous sections, the marls are considered to be uppermost Pliocene. A decrease upwards in the number of pteropod shells and *Zoophycos*, lacking in the last three levels, suggests a progressive shallowing of the deposits from depths around 400 m to approximately 200 m. The coquinal beds above the marl indicate shallow water and a Pleistocene age.

MATERIAL AND METHODS

For this study a total number of 39 samples (samples 1–7 of the Vagia section are not considered here) were collected from the marl levels of the three sections. For Vagia and Lindos, 500 g of sediment was weighed and then washed and sieved for each sample, whereas in Vasfi only an approximate weight of sediment was used, c. 100 g. Only 26 samples yielded bryozoans whose fragments were hand-picked from dried residues. The number of specimens belonging to each identified species was counted, and is given in parenthesis in the systematic description ('Material') after each sample number. This results in a semi-quantitative representation of the distribution of the species in the section (Text-figs 2–4).

Repository. Figured specimens are housed in the Institute of Earth Sciences, University of Lyon, France (prefixed FSL).

SYSTEMATIC PALAEOLOGY

Class STENOLAEMATA Borg, 1926

Order TUBULIPORATA Johnston, 1847 (= CYCLOSTOMATA Busk, 1852)

Sub-order ARTICULATA Busk, 1859

Family CRISIIDAE Johnston, 1847

Genus CRISIA Lamouroux, 1812

Crisia conferta Busk, 1875

Plate 1, figures 1–2

1875 *Crisia conferta* Busk, p. 7, pl. 6A, fig. 5.

1990 *Crisia conferta* Busk; Harmelin, p. 1607, figs 2, 12–14.

Material. Vagia 8 (2), 10 (3), 12 (4), 20 (1), 24 (31); Lindos 1 (9), 2 (2), 3 (1), 4 (11), 5 (6), 8 (1), 9 (5), 10 (28).

Morphology. Colony cellariiform; internodes rather wide, with eight to twelve zooecia; top of gonozooid generally flattened but sometimes rounded. In some cases, the gonozooid is subdivided into a basal part with flat top, followed by a rounded upper part (Pl. 1, fig. 2). Ooeciostome is of the same diameter but slightly shorter than the periostome of the next distal zooid, both tubes being adjacent or coalescent at their base. Harmelin (1990) noted that *C. conferta* and *C. sigmoidea* Waters, 1916 are probably identical and considered them to be two geographical forms of the same species.

Occurrence. Eastern Atlantic (Angola to the Bay of Biscay) at depths from 130 to 850 m, Mediterranean (Gibraltar area) at 110 m. The Mediterranean form, *C. sigmoidea*, has a shallower range: from 5 m in caves to 30 m in coralligenous biocoenosis. This is the first time that *C. conferta* (and *C. sigmoidea*) is reported as a fossil.

Crisia cf. fistulosa Heller, 1867

Plate 1, figures 3–4

1867 *Crisia fistulosa* Heller, p. 118, pl. 3, fig. 5.

1879 *Crisia fistulosa* Heller; Waters, p. 268, pl. 23, fig. 3.

1955 *Crisia fistulosa* Heller; Gautier, p. 268.

1968 *Crisia fistulosa* Heller; Harmelin, p. 427, fig. 4: 3–4.

1986 *Crisia fistulosa* Heller; Zabala, p. 607, text-fig. 215.

Material. Vagia 8 (3), 24 (12); Lindos 1 (2), 8 (1), 10 (6), 11 (3), 12 (3), 13 (6).

Morphology. Colony cellariiform; internodes narrow, each with a small number (three to eight) of long zooecia; gonozooid cylindrical; ooeciostome terminal. The specimens from Rhodes are never very well preserved and the specific identification remains uncertain. The possibility that this species was transported from shallower water cannot be excluded. As noted by several authors (Heller 1867; Harmelin 1968; Zabala 1986) *Crisia fistulosa* closely resembles *Filicrisia geniculata* (Milne-Edwards, 1838).

Occurrence. Eastern Atlantic (Madeira) but mostly Mediterranean, at shallow depths from 5 to 40 m. This species has never been reported before as a fossil but some citations of *Filicrisia geniculata* (late Oligocene to Recent) may in fact deal with *Crisia fistulosa*.

Crisia tenella Calvet, 1906b

Plate 1, figures 5–6

1906b *Crisia tenella* Calvet, p. 219.

1906c *Crisia tenella* Calvet; Calvet, p. 460, figs 1–2.

1982 *Crisia tenella* Calvet; Harmelin and Hondt, p. 5, pl. 1, fig. 2.

1990 *Crisia tenella* Calvet; Harmelin, p. 1611, figs 2, 15–17, 21.

Material. Vasfi 1 (1), 2 (35), 5 (1), 6 (4), 8 (1); Vagia 12 (32); Lindos 1 (1), 4 (4), 8 (3), 10 (8), 11 (2), 13 (2).

Morphology. Colony cellariiform; internodes very narrow, each comprising three to twelve zooecia, but five to seven in most cases; basis rami short and thin, always numerous; gonozooid rounded, beginning with a narrow base, erect and oblique to the internode; ooeciostome short, dorsal and terminal. Present in all three sections, this species is generally well preserved and is even abundant in some of the samples.

Occurrence. Eastern Atlantic (Cape Verde Islands to the Bay of Biscay) at depths from 150 to 1696 m, Mediterranean (Alboran Sea) from 70 to 480 m. This species is also reported here as a fossil for the first time.

Sub-order TUBULIPORINA Milne-Edwards, 1838

Family TUBULIPORIDAE Johnston, 1838

Genus EXIDMONEA Mongereau, 1970

Exidmonea atlantica Mongereau, 1970

Plate 1, figure 11

1847 *Idmonea atlantica* Forbes in Johnston, p. 278, pl. 48, fig. 3.

1966 *Idmonea atlantica* Forbes; Buge, p. 5, pl. B, figs 1–2.

EXPLANATION OF PLATE 1

Figs 1–2. *Crisia conferta*. 1, FSL 490.046, internode, frontal view; Vagia 12, $\times 33$. 2, FSL 490.047, internode with gonozooid; Vagia 12, $\times 51$.

Figs 3–4. *Crisia* cf. *fistulosa*. 3, FSL 490.048, internode, frontal view; Vagia 24, $\times 48$. 4, FSL 490.049, internode with gonozooid; Vagia 24, $\times 51$.

Figs 5–6. *Crisia tenella*. 5, FSL 490.050, internode, frontal view; Vasfi 2, $\times 24$. 6, 490.051, internode with gonozooid; Vasfi 2, $\times 73$.

Figs 7–8 *Entalophoroecia gracilis*. 7, FSL 490.052, branch bearing a gonozooid; Vasfi 1, $\times 48$. 8, FSL 490.053, fragment of a branch; Vasfi 3, $\times 26$.

Figs 9, 12. *Tervia irregularis*. 9, FSL 490.054, fragment of a branch, frontal view; Vasfi 1, $\times 51$. 12, FSL 490.055, detail of the gonozooid with its elliptical ooeciostome; Vasfi 1, $\times 66$.

Fig. 10. *Entalophoroecia* sp., FSL 490.056, fragment of a branch; Vasfi 9, $\times 36$.

Fig. 11. *Exidmonea atlantica*, FSL 490.057, fragment of a branch, frontal view; Vasfi 5, $\times 40$.



MOISSETTE and SPJELDNAES, Plio-Pleistocene Bryozoa

- 1970 *Exidmonea atlantica* Mongereau, p. 30, pl. 1, fig. 1; pl. 2, figs 1, 5.
 1976 *Idmidronea atlantica* (Forbes); Harmelin, p. 182, pl. 32, figs 1–11.
 1983 *Idmidronea atlantica* (Forbes); Vávra, p. 73, pl. 1, figs 1–4.
 1986 *Idmidronea atlantica* (Forbes); Zabala, p. 658, text-fig. 235a–d; pl. 28, fig. E.
 1988 *Idmidronea atlantica* (Forbes); Moissette, p. 48, pl. 6, figs 6–7.
 1988 *Idmidronea atlantica* (Forbes); Zabala and Maluquer, p. 174, text-figs 569–572; pl. 33, fig. A.
 1992 *Exidmonea atlantica* (Forbes); Pouyet and Moissette, p. 24, pl. 1, figs 7–8.
 1992 *Idmidronea atlantica* (Forbes); El Hajjaji, p. 44, pl. 2, fig. 11.
 1993 *Exidmonea atlantica* (Forbes); Moissette *et al.*, p. 84, figs 3i–j.

Material. Vasfi 1 (3), 2 (1), 3 (3), 5 (20), 8 (94); Vagia 12 (7), 20 (5), 24 (1); Lindos 1 (1), 4 (2), 10 (6), 11 (1), 12 (1), 13 (1).

Morphology. Colony vinculariiform; fascicles alternating on each side of the median crest, each comprising three to four salient zooecial tubes; dorsal flattened or slightly concave. Although the gonozoid has not been observed, *Exidmonea atlantica* is easily identifiable.

Occurrence. Almost cosmopolitan in distribution, this species has been recorded from depths of 10 to 850 m. It has a long stratigraphical range, from the Eocene to the Recent and is particularly well represented in the Mediterranean Neogene.

Family TERVIIDAE Canu and Bassler, 1920

Genus TERVIA Jullien, 1882

Tervia irregularis (Meneghini, 1845)

Plate 1, figures 9, 12

- 1845 *Idmonea irregularis* Meneghini, p. 128.
 1963 *Tervia irregularis* (Meneghini); Malecki, p. 71, text-fig. 30; pl. 3, fig. 11.
 1972 *Tervia irregularis* (Meneghini); Mongereau, p. 342, pl. 9, fig. 9.
 1975 *Tervia irregularis* (Meneghini); Vávra, p. 523, pl. 2, figs 3–4.
 1976 *Tervia irregularis* (Meneghini); Harmelin, p. 163, pl. 26, figs 1–11.
 1982 *Tervia irregularis* (Meneghini); Harmelin and Hondt, p. 8, pl. 3, fig. 4.
 1986 *Tervia irregularis* (Meneghini); Zabala, p. 656, text-fig. 234.
 1988 *Tervia irregularis* (Meneghini); Moissette, p. 49, pl. 6, figs 10–12.
 1988 *Tervia irregularis* (Meneghini); Zabala and Maluquer, p. 174, text-figs 563–568.
 1992 *Tervia irregularis* (Meneghini); Pouyet and Moissette, p. 25, pl. 1, figs 11–12.
 1992 *Tervia irregularis* (Meneghini); El Hajjaji, p. 48, pl. 2, fig. 10.
 1993 *Tervia irregularis* (Meneghini); Moissette *et al.*, p. 85, fig. 3h, l.

Material. Vasfi 1 (9), 2 (1), 3 (14), 5 (11), 6 (1), 7 (2), 9 (1); Vagia 8 (4), 21 (1), 24 (1); Lindos 4 (1), 10 (2).

Morphology. Colony vinculariiform; zooecial tubes and their peristomes isolated or clustered in groups of three to five; dorsal convex, with longitudinal lines corresponding with the limits of tubes; gonozoid dorsal, rounded and elongated; ooeciostome terminal, elliptical, adjacent to the dorsal, with a curved upper lip. This species is easily identifiable by the clustering of the tubes, the dorsal side, and the gonozoid.

Occurrence. Harmelin (1976) considers *Tervia irregularis* as a typical deep-water species, never found above 60 m (60–300 m in the Mediterranean) and even reaching a depth of 2650 m in the Bay of Biscay. It has a vast geographical distribution: eastern Atlantic (Senegal to the Bay of Biscay), Mediterranean, Pacific (Australia) and Indian Ocean (East Africa). It is known from as early as the Eocene from a number of deposits, especially in the Mediterranean realm.

Family ENTALOPHORIDAE Reuss, 1869

Genus ENTALOPHOROECIA Harmelin, 1976

Entalophoroecia gracilis Harmelin, 1976

Plate 1, figures 7–8

- 1976 *Entalophoroecia gracilis* Harmelin, p. 100, pl. 7, figs 1–8; pl. 11, figs 1–6.

- 1986 *Entalophoroecia gracilis* Harmelin; Zabala, p. 633, text-fig. 225; pl. 24, fig. E.
 1992 *Entalophoroecia gracilis* Harmelin; Harmelin and Hondt, p. 614, fig. 1; pl. 2, figs B–C.

Material. Vasfi 1 (2), 3 (2), 5 (1), 6 (1); Lindos 12 (2), 13 (3).

Morphology. Colony vinculariiform, always slender; zooecial tubes more or less rugose, opening on all sides of the branches; gonozooid forming a simple bulge, generally at the end of a branch; ooeciostome terminal, of a smaller diameter than the peristomes. This species was only encountered in its erect form, corresponding with deeper habitats than the semi-erect pustuloporian or the creeping stomatoporian colonies (Harmelin 1976).

Occurrence. Eastern Atlantic (from the Gulf of Guinea to Brittany) at depths down to 610 m, Mediterranean from 70 to 480 m. This species is reported as a fossil for the first time.

Entalophoroecia sp.

Plate 1, figure 10

Material. Vasfi 9 (1); Vagia 24 (1).

Morphology. Colony vinculariiform; zooecial tubes isolated, always small in number. This species is only represented by two specimens without gonozooids. Specific identification is impossible.

Genus *ANGUISIA* Jullien, 1882

Anguisia verrucosa Jullien, 1882

Plate 2, figures 1–2

- 1882 *Anguisia verrucosa* Jullien, p. 497, pl. 13, figs 1–2.
 1977 *Anguisia verrucosa* Jullien; Harmelin, p. 1058, figs 1–2; pl. 1, figs 1, 3.
 1979 *Anguisia verrucosa* Jullien; Harmelin, p. 414, pl. 2, fig. 3.
 1982 *Anguisia verrucosa* Jullien; Harmelin and Hondt, p. 7, pl. 1, figs 3–4.

Material. Vasfi 1 (11), 2 (3), 3 (2), 5 (3), 6 (18), 8 (3); Vagia 12 (11), 20 (1), 24 (14); Lindos 1 (10), 2 (2), 4 (24), 5 (7), 8 (12), 9 (4), 10 (63), 11 (61), 12 (9), 13 (21).

Morphology. Colony vinculariiform, arising from an encrusting uniserial basis; zooecial tubes forming slender bifurcating branches, striated by thin growth lines and verrucous (pseudopores).

Occurrence. Eastern Atlantic (200–2018 m) and Mediterranean (500–1525 m). The species created by Neviani (1895) from the Pleistocene of Italy, *A. jullieni*, probably corresponds with an encrusting basis of *A. verrucosa*.

Family ANNECTOCYMIIDAE Hayward and Ryland, 1985

Genus ANNECTOCYMA Hayward and Ryland, 1985

Annectocyma major (Johnston, 1847)

Plate 2, figure 3

- 1847 *Alecto major* Johnston, p. 281, pl. 49, figs 3–4.
 1956 *Diaperoecia major* (Johnston); Buge, p. 11, pl. 1, figs 5–6.
 1976 *Diaperoecia major* (Johnston); Harmelin, p. 79, pl. 1, figs 1–11; pl. 2, figs 1–9; pl. 13, figs 1–10; pl. 14, figs 1–10.
 1984 *Diaperoecia major* (Johnston); Poluzzi and Padovani, p. 104, fig. 4d.

- 1985 *Annectocyma major* (Johnston); Hayward and Ryland, p. 1077, fig. 1C-D.
 1986 *Diaperoecia major* (Johnston); Zabala, p. 623, fig. 222.
 1988 *Diaperoecia major* (Johnston); Moissette, p. 53, pl. 7, fig. 4.
 1988 *Annectocyma major* (Johnston); Zabala and Maluquer, p. 167, figs 492-494; pl. 30, figs A-B.
 1992 *Annectocyma major* (Johnston); El Hajjaji, p. 54, pl. 2, figs 4-5.
 1992 *Annectocyma major* (Johnston); Pouyet and Moissette, p. 27, pl. 1, fig. 12.
 1993 *Annectocyma major* (Johnston); Moissette *et al.*, p. 87.

Material. Vasfi 1 (3), 3 (3), 5 (2); Vagia 24 (2).

Morphology. Colony membraniporiform, forming irregular dichotomous branches with rugose surface; zooecial tubes often clustered in series of two to four; peristomes moderately protruding. Generally encrusting, this species may also give rise to erect branches, and confusion with *Entalophoroecia* species is then possible (Harmelin 1976).

Occurrence. This species has wide geographical and stratigraphical distributions: western and eastern Atlantic (Brazil; Cape Verde Islands to Norway), Mediterranean, and possibly Pacific in the Recent; Mediterranean and eastern Atlantic from the Middle Miocene to the Pleistocene. Its bathymetric range is from 3 to 205 m in the Mediterranean, deeper in the Atlantic (to 362 m off the Spanish-Moroccan coast).

Genus YBSELOSOECIA Canu and Lecointre, 1933

Ybselosoecia typica (Manzoni, 1878)

Plate 2, figure 4

- 1878 *Filisparsa typica* Manzoni, p. 10, pl. 8, fig. 30.
 1909 *Filisparsa typica* Manzoni; Canu, p. 115, pl. 14, figs 25-26.
 1956 *Ybselosoecia typica* (Manzoni); Buge, p. 13, pl. 1, figs 3-4; pl. 2, figs 3-4.
 1963 *Ybselosoecia typica* (Manzoni); Malecki, p. 76, fig. 33; pl. 5, fig. 1.
 1965 *Ybselosoecia typica* (Manzoni); Mongereau, p. 317, fig. 1.
 1974 *Ybselosoecia typica* (Manzoni); Vávra, p. 362, pl. 2, figs 9-10.
 1984 *Ybselosoecia typica* (Manzoni); Vávra, p. 226, pl. 1, figs 2-3.
 1988 *Ybselosoecia typica* (Manzoni); Moissette, p. 56, pl. 7, figs 9, 13.
 1992 *Ybselosoecia typica* (Manzoni); El Hajjaji, p. 56, pl. 2, figs 2-3.
 1992 *Ybselosoecia typica* (Manzoni); Pouyet and Moissette, p. 28, pl. 2, fig. 4.
 1993 *Ybselosoecia typica* (Manzoni); Moissette *et al.*, p. 87.

Material. Vasfi 5 (1).

Morphology. Colony vinculariiform, forming dichotomous and more or less flattened branches; zooecial tubes indistinct, terminated by isolated peristomes of a large diameter; dorsal wall slightly convex, with thin growth lines. This fossil species is easily identifiable by its slightly flattened branches and large peristomes.

Occurrence. Eocene to Pliocene, mostly from Mediterranean regions.

EXPLANATION OF PLATE 2

- Figs 1-2. *Anguisia verrucosa*. 1, FSL 490.058, bifurcating branch; Vasfi 1, $\times 24$. 2, FSL 490.059, detail of a branch; Vasfi 1, $\times 165$.
 Fig. 3. *Annectocyma major*, FSL 490.060, zoarium with clustered tubes; Vasfi 3, $\times 32$.
 Fig. 4. *Ybselosoecia typica*, FSL 490.061, fragment of a branch, frontal view; Vasfi 5, $\times 51$.
 Figs 5-6. *Hornera frondiculata*. 5, FSL 490.062, fragment of a branch, frontal view; Vasfi 9, $\times 24$. 6, FSL 490.063, fragment of a branch, dorsal view; Vasfi 9, $\times 26$.
 Fig. 7. *Ramphonotus minax*, FSL 490.064, fragment of a pseudovinculariiform branch with ovicellate zooecia; Vasfi 3, $\times 51$.
 Fig. 8. *Setosella vulnerata*, FSL 490.065, colony growing in a spiral around the ancestrule on a small shell fragment; Vasfi 2, $\times 62$.
 Fig. 9. *Setosellina capriensis*, FSL 490.066, ancestrular area of a small colony; Vasfi 8, $\times 94$.



MOISSETTE and SPJELDNAES, Plio-Pleistocene Bryozoa

Sub-order CANCELLATA Gregory, 1896

Family HORNERIDAE Gregory, 1899

Genus HORNERA Lamouroux, 1821

Hornera frondiculata Lamouroux, 1821

Plate 2, figures 5–6

- 1821 *Hornera frondiculata* Lamouroux, p. 41, pl. 74, figs 7–9.
 1963 *Hornera frondiculata* Lamouroux; Malecki, p. 80, pl. 5, fig. 2a–b.
 1972 *Hornera frondiculata* Auct. forme *frondiculata* Mongereau, p. 329, pl. 5, figs 1–3; pl. 7, figs 1–2.
 1972 *Hornera frondiculata* Auct. forme *striata* Mongereau, p. 345, pl. 5, figs 8–9; pl. 6, figs 1–4, 6; pl. 7, figs 5–8.
 1986 *Hornera frondiculata* Lamouroux; Zabala, p. 686, text-fig. 243.
 1988 *Hornera frondiculata* Auct. forme *frondiculata* Mongereau; Moissette, p. 61, pl. 8, fig. 11.
 1988 *Hornera frondiculata* Auct. forme *striata* Mongereau; Moissette, p. 62, pl. 8, fig. 10.
 1988 *Hornera frondiculata* Lamouroux; Zabala and Maluquer, p. 182, text-figs 625–629; pl. 36, figs A–B.
 1992 *Hornera frondiculata* Auct. forme *frondiculata* Mongereau; El Hajjaji, p. 65, pl. 2, figs 15–16.
 1992 *Hornera frondiculata* Auct. forme *striata* Mongereau; El Hajjaji, p. 66, pl. 3, figs 1–2.
 1992 *Hornera frondiculata* Lamouroux; Pouyet and Moissette, p. 30, pl. 2, figs 10–11.
 1993 *Hornera frondiculata* Lamouroux; Moissette *et al.*, p. 88.

Material. Vasfi 9 (1); Lindos 13 (5).

Morphology. Colony vinculariiform; zooecial tubes separated by sulci, a vacuole at each end of the protruding peristomes; dorsal sulci little salient, with series of small vacuoles in-between. Depending upon the degree of calcification, two forms of *Hornera frondiculata* were recognized by Mongereau (1972); they are now generally reunited. This species is represented here by a small number of fragments, and only in the highest level of the Vasfi and Lindos sections. Its presence there could be due to a reworking, possibly by bioturbation, of the younger (and shallower) beds of the coquina limestones.

Occurrence. Known from the eastern Atlantic (Cape Verde Islands to the Bay of Biscay) and the Mediterranean, *Hornera frondiculata* has been recorded from depths of 30 to 200 m. It has a large stratigraphical range, from the Eocene to the Recent, notably in the Mediterranean realm.

Class GYMNOLEAEMATA Allman, 1856

Order CHEILOSTOMATA Busk, 1852

Sub-order ANASCA Levinsen, 1909

Family SETOSELLIDAE Levinsen, 1909

Genus SETOSELLA Hincks, 1877

Setosella vulnerata (Busk, 1860)

Plate 2, figure 8

- 1860 *Membranipora vulnerata* Busk, p. 124, pl. 25, fig. 3.
 1880 *Setosella vulnerata* (Busk); Hincks, p. 181, pl. 21, fig. 7.
 1882 *Setosella vulnerata* (Busk); Jullien, p. 524, pl. 17, fig. 66.
 1962 *Setosella vulnerata* (Busk); Gautier, p. 68.
 1966 *Setosella vulnerata* (Busk); Prenant Bobin, p. 358, text-fig. 117I–IV.
 1977 *Setosella vulnerata* (Busk); Ryland and Hayward, p. 118, text-fig. 55.
 1977 *Setosella vulnerata* (Busk); Harmelin, p. 1064, text-figs 13–15; pl. 1, fig. 6.
 1988 *Setosella vulnerata* (Busk); Zabala and Maluquer, p. 92, text-fig. 133; pl. 2E.
 1992 *Setosella vulnerata* (Busk); Reguant and Maluquer, p. 144, pl. 1, fig. 6.
 1993 *Setosella vulnerata* (Busk); Moissette *et al.*, p. 97, fig. 6a–b.

Material. Vasfi 2 (2).

Morphology. Colony membraniporiform; autozooezia suboval; cryptocyst smooth with a narrow opesiular slit on each side, a little below the semi-circular opesia. A small distal vibraculum is always present over each autozooezium. Two colonies were found in the Vasfi section. They had encrusted small shell fragments and grew in a spiral around the ancestrula (with trifoliate opesia).

Occurrence. Western and eastern Atlantic (Gulf of Mexico; Cape Verde Islands to Shetland and Norway), Mediterranean, Indian Ocean (Gulf of Aden). Although presenting a wide bathymetric distribution (30 to 3700 m), this species is typical of deep waters.

Genus SETOSELLINA Calvet, 1906a

Setosellina capriensis (Waters, 1926)

Plate 2, figure 9

- 1926 *Cupularia capriensis* Waters, p. 432, pl. 18, figs 8–9.
- 1965 *Setosellina capriensis* (Waters); Cook, p. 182, pl. 1, figs 5–6.
- 1966 *Setosellina capriensis* (Waters); Prenant and Bobin, p. 301.
- 1988 *Setosellina capriensis* (Waters); Zabala and Maluquer, p. 88, text-fig. 111.
- 1992 *Setosellina capriensis* (Waters); Reguant and Maluquer, p. 143, pl. 1, fig. 1.

Material. Vasfi 2 (11), 8 (1).

Morphology. Colony membraniporiform; autozooezia suboval with a gymnocyst developed in the proximal part only and forming a salient frame around the opesia; opesia oval, surrounded by a granular cryptocyst absent from the more distal part; each autozooezium bears in its distal part a small median vibraculum. The autozooezia of the ancestrular area are almost completely occluded by a calcareous lamina, leaving only a small central pore. This species closely resembles *Setosellina roulei* (Calvet, 1906a). The differences are a smaller zooecial size, a narrower cryptocyst, and a deeper habitat (200 to 2330 m) for *S. roulei*.

Occurrence. Eastern Atlantic (Azores and Canary Islands) and Mediterranean, at depths from 55 to 240 m.

Family CALLOPORIDAE Norman, 1903

Genus RAMPHONOTUS Norman, 1894

Ramphonotus minax (Busk, 1860)

Plate 2, figure 7

- 1860 *Membranipora minax* Busk, p. 125, pl. 25, fig. 1.
- 1906c *Membranipora minax* Busk; Calvet, p. 388, pl. 26, fig. 2.
- 1962 *Ramphonotus minax* (Busk); Gautier, p. 45.
- 1966 *Ramphonotus minax* (Busk); Prenant and Bobin, p. 271, text-fig. 90.
- 1977 *Amphiblestrum minax* (Busk); Ryland and Hayward, p. 106, text-fig. 46.
- 1986 *Amphiblestrum minax* (Busk); Zabala, p. 263, text-fig. 66.
- 1988 *Ramphonotus minax* (Busk); Moissette, p. 85, pl. 13, figs 4–5.
- 1989 *Amphiblestrum minax* (Busk); Zabala and Maluquer, p. 82, text-fig. 93; pl. 3, fig. B.
- 1992 *Ramphonotus minax* (Busk); El Hajjaji, p. 101, pl. 4, fig. 11.
- 1992 *Ramphonotus minax* (Busk); Pouyet and Moissette, p. 38.

Material. Vasfi 3 (1).

Morphology. Colony pseudovinculariiform; autozooezia rhomboidal to subhexagonal; gymnocyst and cryptocyst granular, separated by a thin ridge; opesia trapezoidal and rounded. A small avicularium is situated in the centre of the proximal part of the cryptocyst; hyperstomial ovicell globular, with a granular surface and a frontal triangular to circular area. Although generally occurring in its membraniporiform zoarial type, this species is represented here by a small fragment of pseudovinculariiform colony, perhaps corresponding with a deeper habitat. As in Recent material, the specimen from Rhodes presents only one avicularium, whereas other fossil material often shows two avicularia in the distal part of ovicellate autozooezia.

Occurrence. Western and eastern Atlantic (Canada and Greenland; Bay of Biscay to Norway), Arctic Ocean, Mediterranean. It is a boreal species widespread in the Atlantic from depths of 25 to 300 m. In the Mediterranean, it occurs between 80 and 145 m. From the fossil record, it is known in the Middle Miocene to the Pliocene, mainly in the Mediterranean region.

Family CELLARIIDAE Hincks, 1880
Genus CELLARIA Ellis and Solander, 1786
Cellaria salicornioides Lamouroux, 1816

Plate 3, figure 1

- 1816 *Cellaria salicornioides* Lamouroux, p. 127.
1826 *Cellaria salicornioides* Lamouroux; Audouin, p. 236; Savigny, 1827, pl. 6, fig. 7.
1962 *Cellaria salicornioides* Audouin; Gautier, p. 72.
1966 *Cellaria salicornioides* ?Lamouroux, Savigny-Audouin; Prenant and Bobin, p. 382, text-fig. 124.
1977 *Cellaria salicornioides* Lamouroux; Ryland and Hayward, p. 124, text-fig. 59.
1984 *Cellaria salicornioides* Lamouroux; Poluzzi and Padovani, p. 109, fig. 5d.
1986 *Cellaria salicornioides* Audouin; Zabala, p. 307, text-fig. 84:3a-e; pl. 3, figs E-F.
1988 *Cellaria salicornioides* Lamouroux; Moissette, p. 104, pl. 17, figs 1-2.
1988 *Cellaria salicornioides* Audouin; Zabala and Maluquer, p. 94, text-figs 137-140; pl. 2, fig. H.
1992 *Cellaria salicornioides* Lamouroux; El Hajjaji, p. 129, pl. 6, fig. 7.

Material. Vasfi 4 (1), 5 (1); Vagia 8 (1), 12 (4), 20 (4), 24 (1); Lindos 1 (1), 4 (4), 5 (2), 8 (3), 10 (2), 11 (1), 13 (10).

Morphology. Colony cellariiform; slender branches with four longitudinal series of autozooeceia; autozooeceia subhexagonal, alternating in adjacent series and separated by a thin groove; cryptocyst depressed, finely granular, with a raised marginal rim; opesia semicircular, showing two short lateral denticles on the convex proximal edge; endotoichal ovicell with a small round opening distal to the opesia. The interzooeceial avicularium has not been observed on the studied material; however, it is always rare in this species.

Occurrence. Eastern Atlantic (from Madeira to Shetland), Mediterranean, Red Sea. It has been recorded from the Atlantic at depths of 0 to 362 m. In the Mediterranean, it occurs between 0 and 150 m. It is known from the fossil record back to the Middle Miocene, essentially in the Mediterranean region, but also in England and Portugal.

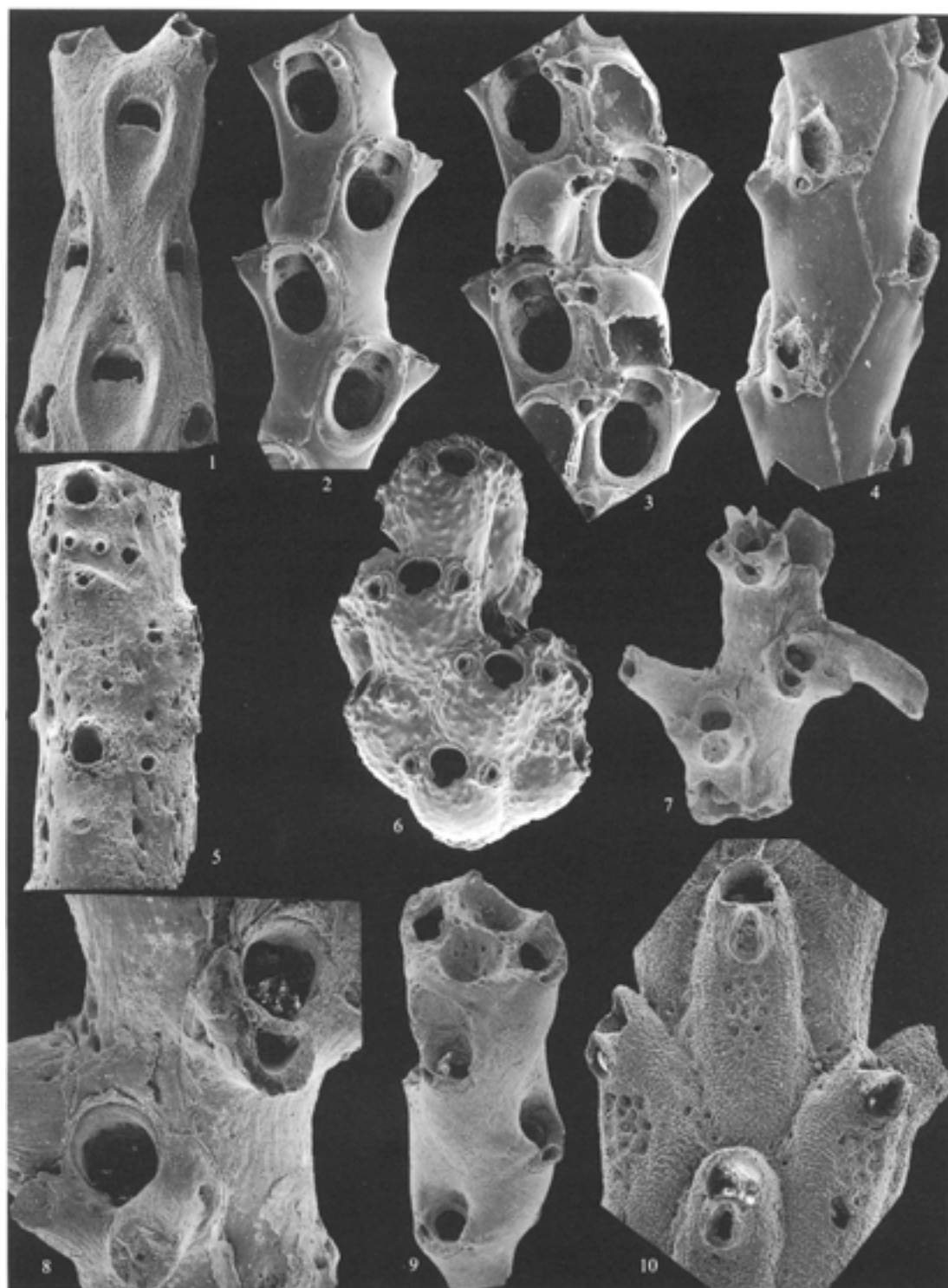
Family SCRUPOCELLARIIDAE Levinsen, 1909
Genus SCRUPOCELLARIA Beneden, 1845
Scrupocellaria scrupea Busk, 1851

Plate 3, figures 2-4

- 1851 *Scrupocellaria scrupea* Busk, p. 83, pl. 9, figs 11-12.

EXPLANATION OF PLATE 3

- Fig. 1. *Cellaria salicornioides*, FSL 490.067, extremity of a branch; Vagia 1, $\times 79$.
Figs 2-4. *Scrupocellaria scrupea*. 2, FSL 490.068, fragment of a branch, frontal view. 3, FSL 490.069, ovicellate zooecia. 4, FSL 490.070, fragment of a branch, dorsal view. All Vasfi 1, $\times 73$.
Fig. 5. *Tessaradoma boreale*, FSL 490.071, fragment of a branch, with spiramen and avicularia; Vasfi 5, $\times 51$.
Fig. 6. *Characodoma bifurcatum*, FSL 490.072; Vasfi 8, $\times 73$.
Figs 7-8. *Jaculina tessellata*. 7, FSL 490.073, fragment of the reteporiform zoarium; Vasfi 8, $\times 33$. 8, FSL 490.073, detail view of the zooecia and their apertures; Vasfi 8, $\times 79$.
Fig. 9. *Palmicellaria elegans*, FSL 490.074, fragment of a branch showing the cross section; Vasfi 1, $\times 46$.
Fig. 10. *Aeonellopsis distoma*, FSL 490.075; Vasfi 1, $\times 73$.



MOISSETTE and SPJELDNAES, Plio-Pleistocene Bryozoa

- 1852 *Scrupocellaria scrupea* Busk; Busk, p. 24, pl. 21, figs 1–2.
 1880 *Scrupocellaria scrupea* Busk; Hincks, p. 50, pl. 7, figs 11–14.
 1962 *Scrupocellaria scrupea* Busk; Gautier, p. 90.
 1966 *Scrupocellaria scrupea* Busk; Prenant and Bobin, p. 432, text-fig. 143.
 1977 *Scrupocellaria scrupea* Busk; Ryland and Hayward, p. 138, text-fig. 66.

Material. Vasfi 1 (6), 2 (15), 3 (3), 5 (2), 6 (2), 7 (2); Vagia 24 (2); Lindos 1 (1), 4 (2), 10 (5), 11 (1), 12 (1), 13 (8).

Morphology. Colony cellariiform; flattened branches with two alternating series of elongated subquadrangular autozooezia; opesia oval, occupying nearly one-half of the zooecium and surrounded by a narrow rim bearing five distal spines (three on the external edge, two on the internal edge); lateral avicularium large and constant; frontal avicularium small and inconstant, mostly associated with ovicells; ovicell rounded, with a smooth surface and a small proximal fenestra; dorsal slightly convex, with a proximal vibraculum on each zooecium. The number of spines is fairly constant on the recovered material. When associated with an ovicell, the frontal avicularium is well developed and in a slightly transverse position.

Occurrence. Eastern Atlantic (from Cape Verde Islands to the North Sea), Mediterranean, Indian and Pacific Oceans. This species has a wide bathymetric distribution: from 0 to 500 m in the Atlantic and from 0 to 150 m in the Mediterranean. In the fossil record, it has only been reported before from the Pleistocene of Italy (Neviani 1904).

Sub-order ASCOPHORA Levinsen, 1909
 Family TESSARADOMIDAE Jullien and Calvet, 1903
 Genus TESSARADOMA Norman, 1869

Tessaradoma boreale (Busk, 1860)

Plate 3, figure 5

- 1860 *Onchopora boreale* Busk, p. 213, pl. 28, figs 6–7.
 1880 *Porina borealis* (Busk); Hincks, p. 229, pl. 31, figs 4–6.
 1962 *Tessaradoma boreale* (Busk); Gautier, p. 222.
 1979 *Tessaradoma boreale* (Busk); Hayward and Ryland, p. 242, text-fig. 104.
 1988 *Tessaradoma boreale* (Busk); Moissette, p. 123, pl. 20, fig. 5.
 1988 *Tessaradoma boreale* (Busk); Zabala and Maluquer, p. 142, text-fig. 343.
 1992 *Tessaradoma boreale* (Busk); El Hajjaji, p. 225, pl. 13, fig. 2.
 1992 *Tessaradoma boreale* (Busk); Pouyet and Moissette, p. 53, pl. 7, fig. 3.

Material. Vasfi 2 (2), 5 (5), 7 (5).

Morphology. Colony vinculariiform; autozooezia oval and more or less elongate, the granular frontal bordered by a row of marginal pores; spiramen immediately proximal to the orbicular aperture. Two pairs of small frontal avicularia are generally present: one lateral to the spiramen, the other near the marginal pores. This species varies mainly in the degree of calcification and in the number and position of the avicularia.

Occurrence. Western and eastern Atlantic (Florida, West Indies; Cape Verde Islands to Spitzbergen), Arctic, Mediterranean. It occurs at depths of 50 to 3700 m in the Atlantic and down to 1300 m in the Mediterranean. From the fossil record, it is known back to the Upper Miocene, especially in the Mediterranean region.

Family SCHIZOPORELLIDAE Jullien in Jullien and Calvet, 1903
 Genus CHARACODOMA Maplestone, 1900
Characodoma bifurcatum (Waters, 1918)

Plate 3, figure 6

- 1918 *Lepralia bifurcata* Waters, p. 96, pl. 12, figs 2–4.
 1957 *Characodoma bifurcatum* (Waters); Harmer, p. 1006, text-fig. 109; pl. 68, figs 34–36.

Material. Vasfi 2 (2), 8 (1).

Morphology. Colony vinculariiform; autozooezia quadrangular, with granular frontal; aperture subcircular, limited by two small cardelles in its lower part. One small rounded avicularium is situated on each side of the aperture.

Occurrence. *C. bifurcatum* has only been reported before from the Mediterranean, at depths of about 90 m (Waters 1918; Poluzzi and Rosso 1988) and from the Pacific Ocean (Indonesia), at depths of 59–82 m (Harmer 1957). It is most probably a very rare species, both as a fossil and in the Recent.

Family ESCHARELLIDAE Levinsen, 1909
Genus JACULINA Jullien in Jullien and Calvet, 1903

Jaculina tessellata Hayward, 1979

Plate 3, figures 7–8

1979 *Jaculina tessellata* Hayward, p. 64.

1981 *Jaculina tessellata* Hayward; Hondt, p. 36, pl. 5, figs 4–6.

Material. Vasfi 2 (19), 3 (1), 6 (2), 8 (1).

Morphology. Colony reteporiform; cylindrical biserial branches joined by thin transverse tubular trabecules; autozooezia subrectangular with a smooth frontal wall; aperture orbicular, incised by a small round sinus. A long and thin mucro is situated on the proximal lip; it bears a small avicularium near its base; dorsal wall smooth, with rare small elliptical avicularia.

Occurrence. Eastern Atlantic (Bay of Biscay and Gulf of Cadiz, at depths between 355 and 463 m), Mediterranean (500–509 m). It has only been reported once as fossil, from a Mediterranean Würmian thanatocoenosis (Rosso 1990). This species has not been described before by many authors. Its ecology is also little known.

Genus PALMICELLARIA Alder, 1864

Palmicellaria elegans Alder, 1864

Plate 3, figure 9

1864 *Palmicellaria elegans* Alder, p. 100, pl. 2, figs 1–4.

1880 *Palmicellaria elegans* Alder; Hincks, p. 378, pl. 31, figs 7–9.

1962 *Palmicellaria elegans* Alder; Gautier, p. 203.

1979 *Palmicellaria elegans* Alder; Hayward and Ryland, p. 130, text-fig. 50.

1986 *Palmicellaria elegans* Alder; Zabala, p. 409, text-fig. 135.

1992 *Palmicellaria elegans* Alder; Reguant and Maluquer, p. 148, pl. 2, figs 1–2.

Material. Vasfi 1 (17), 2 (3), 5 (6), 7 (8).

Morphology. Colony vinculariiform; branches composed of two pairs of alternating elongate autozooezia; frontal wall smooth; aperture hidden by a flared peristome with a pointed mucro bearing a small elliptical avicularium on its upper lip. In the fossil material, the peristome is often worn and only the trace of the avicularium is visible near the sunken aperture.

Occurrence. Eastern Atlantic (Bay of Biscay, Shetland), Mediterranean. In the Mediterranean it occurs at depths of 50 to 1000 m. As a fossil, this species has been reported before only from the Holocene of Spain (Reguant and Maluquer 1992).

Family ADEONIDAE Jullien, 1903
Genus ADEONELLOPSIS MacGillivray, 1886

Adeonellopsis distoma (Busk, 1858)

Plate 3, figure 10

1858 *Lepralia distoma* Busk, p. 127, pl. 18, fig. 1.

- 1962 *Adeonellopsis distoma* (Busk); Gautier, p. 221.
 1970 *Adeonellopsis distoma* (Busk); Hondt, p. 241, text-fig. 7.
 1985 *Adeonellopsis distoma* (Busk); Aristegui, p. 425, text-fig. 2.
 1986 *Adeonellopsis distoma* (Busk); Zabala, p. 391, text-fig. 126; pl. 5, figs E-F.
 1989 *Adeonellopsis distoma* (Busk); Bishop and Hayward, p. 42, text-figs 172-176.
 1992 *Adeonellopsis distoma* (Busk); Reguant and Maluquer, p. 145, pl. 1, fig. 9.

Material. Vasfi 1 (1).

Morphology. Colony adeoniform; autozoecia oval, with one row of marginal pores; primary aperture hidden by a distally developed peristome; frontal wall granular, with a median depression perforated by one ascopore subdivided into eight to twelve small pores; triangular avicularium on the proximal lip of the peristome. The only specimen recovered shows a higher number of ascopores than noted by several authors (eight to twelve instead of five to ten) but the other features are identical. For Gautier (1962), the fossil species *A. imbricata* (Philippi, 1844) and *A. coscinophora* (Reuss, 1848) could be identical to *A. distoma*.

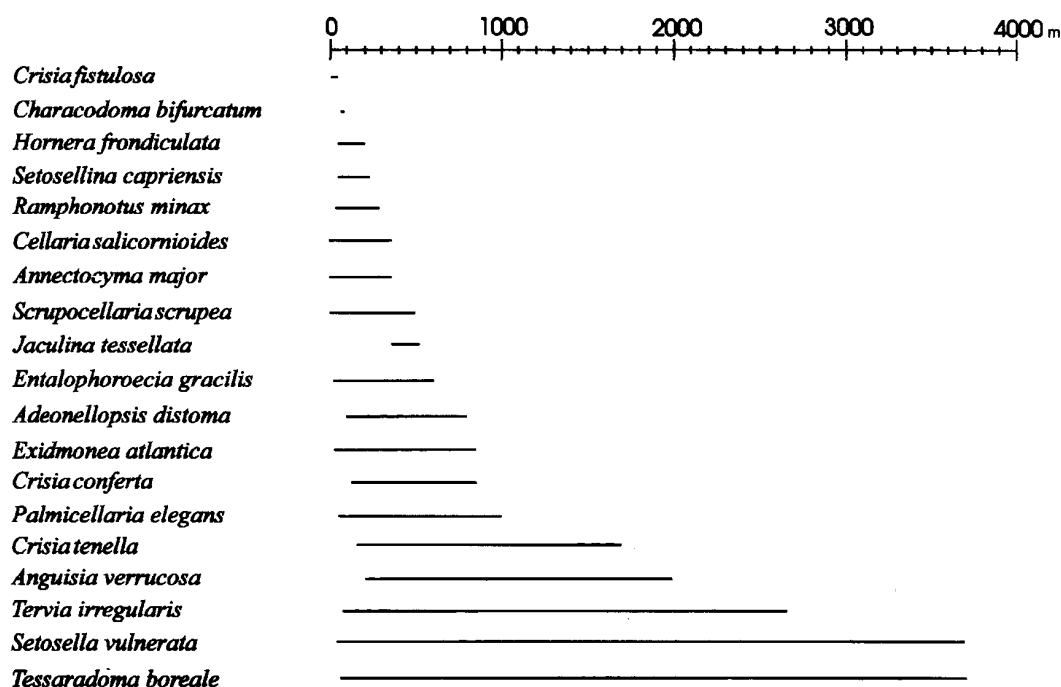
Occurrence. Eastern Atlantic (from Madeira to Brittany), Mediterranean, Indian Ocean. This species was found in the Atlantic at depths from 94 to 787 m. In the Mediterranean it is from somewhat shallower depths (100 to 480 m). In the fossil record, it has been reported from the Pliocene of the North Sea basin and from the Holocene of Spain.

BRYOZOAN DISTRIBUTION IN THE SECTIONS AND BATHYMETRY

A total of 39 samples was taken from the deep-water marls of the three sections and many of them yielded at least some bryozoan fragments. Only 21 species were found in the collected material: 11 cyclostomes, five anascan cheilostomes, and five ascophoran cheilostomes. Although most of the 19 extant species have a wide bathymetric range (Text-fig. 5) information about depth of deposition may be gathered when combining data for each species (presence/absence and abundance).

In the Vasfi section, all samples yielded at least some bryozoan fragments (Text-fig. 2), but sample four is very poor with only one specimen belonging to *Cellaria salicornioides*. The number of species (19) is moderate: nine cyclostomes, five anascan cheilostomes, and five ascophoran cheilostomes. Erect zoarial types largely predominate with 11 vinculariiforms (*Ramphonotus minax* is in fact a pseudovinculariiform), three cellariiforms, one adeoniform, and one reteporiform, but three membraniporiforms, also occur with very few specimens. The best represented are *Crisia tenella*, *Anguisia verrucosa*, *Scrupocellaria scruposa* and *Jaculina tessellata*. Four other species are less abundant: *Tervia irregularis*, *Setosellina capriensis*, *Palmicellaria elegans* and *Exidmonea atlantica*. Some of the species are only present, or best represented in the *Lophelia* beds: *Tervia irregularis*, *Entalophoroecia gracilis*, *Annectocyma major*, *Tessaradoma boreale* and *Palmicellaria elegans*. From the known bathymetric ranges of the extant species, depths of about 500 to 600 m are inferred for the marl beds, and about 300 to 400 m for the intervening *Lophelia* beds (*Annectocyma major*, a shallower water species, occurs only there). A shallowing probably occurred during the deposition of the upper part of the topmost marl bed (sample eight) with reduction in the number of fragments belonging to deeper water species and appearance of *Hornera frondiculata* (but this species could also have been reworked by bioturbation from the coquina).

In the deep-water part of Cape Vagia section (samples eight to twenty-four of Text-fig. 3) bryozoans are not common and ten samples (most of them corresponding with laminated marl) are barren. The ten species found in this section (eight cyclostomes and two anascan cheilostomes) are represented by a small number of fragments. With the exception of one membraniporiform species (*Annectocyma major*, very poorly represented in the last sample), only erect zoarial types occur: five cellariiforms and four vinculariiforms. Four species are relatively abundant: *Anguisia verrucosa*, *Crisia conferta*, *Crisia* cf. *fistulosa* and *Crisia tenella*. On the basis of the known bathymetric ranges of extant bryozoan species, a depth of 300 to 500 m is suggested for the deposition of the major part



TEXT-FIG. 5. Known bathymetric ranges of the extant bryozoan species found in the Plio-Pleistocene deep-water marls of Rhodes.

of the marls, a shallowing occurring near the top of the section (with shallower water species like *Crisia* cf. *fistulosa* and *Annectocyma major*).

Among the 13 samples taken from the marls in Lindos Bay section, two are completely barren of bryozoans (samples six and seven in Text-fig. 4) and only ten species were found (eight cyclostomes and two anascan cheilostomes). All belong to erect types: vinculariiform (five) and cellariiform (five). Two species (*Anguisia verrucosa* and *Crisia conferta*) are relatively abundant and occur in all or almost all samples. Depths of deposition of 300 to 500 m are indicated by the extant species, with a shallowing to about 200–300 m near the top of the section (presence of *Hornera frondiculata*, and increase in the number of fragments belonging to *Cellaria salicornioides* and *Scrupocellaria scrupaea* in the topmost sample).

The indications given by some of the species are dubious, however, since they may either have been displaced from relatively shallow waters (*Hornera frondiculata* is an example), or their exact bathymetric distribution is not properly known. This could be the case of *Crisia* cf. *fistulosa*, *Setosellina capriensis* and *Characodoma bifurcatum*. The reported depth range of *Crisia fistulosa* (5 to 40 m) is definitely too shallow for these deposits, but the corresponding specimens have not been identified with certainty and, if not transported, could belong to another, deeper species or, alternatively, the inferior limit would be lowered with new records for deep-water stations. The depth ranges of *Setosellina capriensis* (55–240 m) and *Characodoma bifurcatum* (59–90 m) are relatively limited and other findings of these rare species could indeed widen their real bathymetric distribution.

DISCUSSION

The main features of the deep-water bryozoan faunas studied may be summarized as the following:

- small number of species (one to 11) and fragments (one to 63 but mostly about five) in each 100–500 g sample;
- predominance of the cyclostomes over the cheilostomes (in number of species, eleven to ten, but above all in number of fragments);
- equal number of anascan and ascophoran cheilostomes species;
- strong predominance of erect colonies, rigid or articulated (mainly vinculariiform and cellariiform, but also adeoniform and reteporiform);
- very small number of encrusting species and colonies (setoselliniform and rarer membraniporiform);
- complete absence of mostly shallow-water zoarial forms (cateniceform and celleporiform, but also lunulitiform);
- lack of conescharelliniform species.

Recent bathyal and abyssal bryozoans (Schopf 1969b; Hayward 1979; Cook 1981; David and Pouyet 1986; Gordon 1987) are also represented mainly by erect zoarial forms, with rooted species (cellariiform and conescharelliniform) predominating on the particulate substrates generally occurring in deep-water settings. In the absence of adequate hard substrates, typical encrusting colonies (membraniporiform) are rare and are instead replaced by the deeper setoselliniform morphotype with spiral growth on sand grains or small shell fragments. Among the cheilostomes, anascans are, however, more numerous than ascophorans, and cheilostomes always considerably outnumber cyclostomes, especially in deeper stations (> 1000 m).

Various features of the deep-water Plio-Pleistocene bryozoan fauna from Rhodes (notably abundant cyclostomes and anascan cheilostomes) suggest that deposition took place in the upper-bathyal zone, not deeper than 600 m. Although often found in deep-water assemblages from the Miocene and early Pliocene (Cook 1981; Moissette 1993), conescharelliniform species later disappear from the Mediterranean and so are absent here.

It is difficult to give an absolute depth for the faunas described here, because of the incomplete information about the Recent depth distribution of many of the bryozoans. It is also noteworthy that among the 19 extant species from Rhodes, almost all have a wide bathymetric range: from a few tens of metres to several hundred or even thousand metres (Text-fig. 5). The sporadic occurrence of shallow-water species is best explained by the washing in of such forms from the steep coast; Rhodes does not have a real shelf; depths of 4000 m are commonly found close to the coast, and this makes it difficult to use depth criteria developed for more normal coastal profiles. These species are therefore disregarded in the calculation of the depth of deposition. The relative abundance in a number of samples of mostly deep-water species such as *Crisia tenella*, *Anguisia verrucosa* and *Jaculina tessellata* is considered however to indicate depths of about 200–600 m. Moreover, no deep stenobathic species were found here, as are generally reported from greater depths (> 600 m) in various oceans (Hondt 1975, 1981; Hondt and Schopf 1984; David and Pouyet 1986; Gordon 1987). On the other hand, some indicators (high percentage of planktonic foraminifera, presence of *Lophelia*, *Zoophycos*, and numerous pteropods) point to deeper waters than suggested here.

Harmelin and Hondt (1993) noted that in the Mediterranean there is an upward shift in the depth distribution for some bryozoans. This is particularly the case here since most of the 19 extant species show a deeper depth range in the Atlantic than in the present-day Mediterranean (Harmelin and Hondt 1993). In the Recent, trophic factors, temperature and salinity are responsible for the partial exclusion of deep Atlantic species from the Mediterranean. However, during certain periods of time during the Pliocene and the Pleistocene, exchange of water through the Straits of Gibraltar may have been easier, thus permitting the penetration of bathyal species even into the eastern Mediterranean, where they were able to descend to greater depths. This phenomenon is also observed in various calcified anthozoans, molluscs, brachiopods, crinoids, and serpulid worms, and could be the result of massive cold-water influxes from the Atlantic into the Mediterranean during lower temperature episodes of the Pliocene and Pleistocene, at times when the Mediterranean presented different hydrological features, and when the Straits of Gibraltar were deeper and wider (Barrier *et al.* 1989).

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