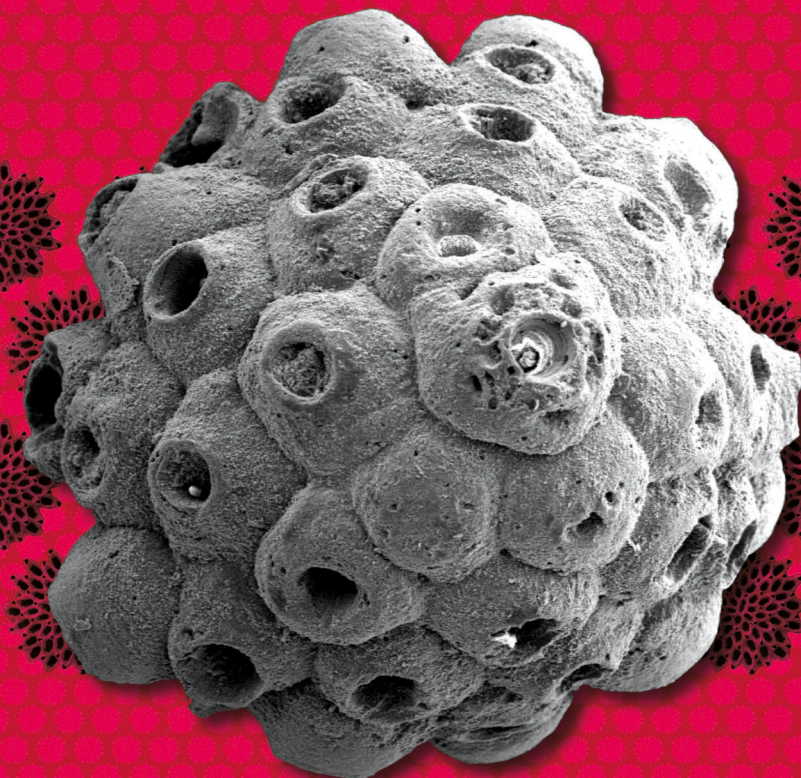


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A palaeoenvironmental case study  
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# Bryozoan faunas at the Tortonian-Messinian transition. A palaeoenvironmental case study from Crete Island, eastern Mediterranean

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## ABSTRACT

Four sedimentary sections were logged and sampled from upper Tortonian-lower Messinian outcrops on the island of Crete (Greece). The collected material yielded about 60 bryozoan species belonging to nine different colonial morphotypes. A few species are stenobathic, indicating either shallow- or deep-water environments, but most of them are eurybathic (with bathymetric ranges extending in some instances from the shelf down to several hundreds of metres). Bryozoan communities point to sea-level variations modulated by local tectonics. Deep circalittoral environments were recognized at the base of three sections (whereas the fourth section starts with infralittoral/shallow circalittoral environments passing to deep circalittoral. Shallow bathyal habitats follow upwards, succeeded in turn by assemblages indicative of deep circalittoral and subsequently shallow circalittoral/infralittoral depths. Inferred bathymetric fluctuations are diachronous throughout the island. Shallow-water species found associated, sometimes abundantly, with rarer deep-water faunas in a few levels, are interpreted as transported by currents. Several dysoxic episodes have been also detected: likely the result of water

## KEY WORDS

Bryozoa,  
palaeobathymetry,  
palaeoenvironment,  
palaeogeography,  
Late Miocene,  
Greece,  
Crete,  
Aegean Sea.

column stratification and enhanced productivity. These processes were probably boosted by a combination of changes in oceanic circulation, climate, global sea-level, and the local/regional tectonics (in Crete and/or the marine gateways between the Mediterranean and the Atlantic).

## RÉSUMÉ

*Faunes de bryozoaires à la limite Tortonien-Messinien. Étude de cas des paléoenvironnements de l'île de Crète, Méditerranée orientale.*

Quatre coupes lithostratigraphiques ont été levées et échantillonnées dans les affleurements du Tortonien supérieur-Messinien inférieur de l'île de Crète (Grèce). Le matériel prélevé a livré environ 60 espèces de bryozoaires appartenant à neuf morphotypes coloniaux différents. Quelques espèces sont sténobathes, indiquant des environnements littoraux ou profonds, mais la plupart sont eurybathes, avec des intervalles bathymétriques s'étendant parfois depuis le plateau continental jusqu'à plusieurs centaines de mètres de profondeur. Les communautés de bryozoaires révèlent des variations du niveau marin modulées par la tectonique locale. Des environnements du circalittoral profond sont reconnus à la base de trois des coupes (mais la quatrième coupe commence par l'infralittoral/circalittoral côtier, passant ensuite au circalittoral profond). Des habitats du bathyal supérieur apparaissent ensuite, suivis d'assemblages indiquant le circalittoral profond, puis le circalittoral côtier/infralittoral. Ces fluctuations bathymétriques sont fortement diachrones à travers l'île. Des espèces littorales sont par ailleurs associées, parfois en grand nombre, avec de plus rares faunes profondes dans quelques niveaux où elles ont été transportées par des courants. Plusieurs épisodes dysoxiques ont été également identifiés, résultant probablement d'une stratification croissante de la colonne d'eau et d'une augmentation de la productivité organique. Ces processus ont été vraisemblablement favorisés par une combinaison de changements dans la circulation océanique, le climat, le niveau marin global et la tectonique locale/régionale (en Crète et/ou au niveau des corridors marins entre la Méditerranée et l'Atlantique).

## MOTS CLÉS

Bryozoaires,  
paléobathymétrie,  
paléogéographie,  
paléoenvironnement,  
Miocène supérieur,  
Grèce,  
Crète,  
Mer Égée.

## INTRODUCTION

At the end of the Miocene, during the Tortonian-Messinian Transition (TMT), sea water exchanges between the Mediterranean and the Atlantic Ocean began to be restricted (e.g., Kontakiotis *et al.* 2019; Corbí *et al.* 2020). This restriction culminated by the end of the Messinian when the Betic and Rifian corridors were closed (Martín *et al.* 2001; Capella *et al.* 2017; Krijgsman *et al.* 2018). This led to the well-known Messinian Salinity Crisis (MSC) characterised by the widespread deposition of thick evaporites in deep and/or marginal sub-basins of the entire Mediterranean Sea (Hsü *et al.* 1973; Ryan *et al.* 1973; Aksu *et al.* 2018; Haq *et al.* 2020; Manzi *et al.* 2020). An abundant literature has been devoted to the timing and the causes of this event, and a consensus progressively emerged (CIESM 2008; Manzi *et al.* 2013; Roveri *et al.* 2014, 2018, 2020). To explain the large volume of evaporites, connections between the Atlantic Ocean and the Mediterranean Sea are considered necessary. Atlantic waters entered the Mediterranean either through the Betic and Rifian corridors or even the Messinian Gibraltar Corridor (Achalhi *et al.* 2016; Krijgsman *et al.* 2018). The first step of the MSC should have occurred in the 5.97-5.60 Ma interval (Gautier *et al.* 1994; Krijgsman *et al.* 1999; Manzi *et al.* 2013). During this interval, the Primary Lower Gypsum unit (PLG), the Terminal Carbonate Complex (TCC; Esteban 1979), and coeval basinal sediments were deposited. The PLG is topped by a major erosional surface which has been identified both onshore and offshore (e.g., Lofi *et al.* 2011). The second step

happened in the 5.60-5.54 Ma interval; it is characterised by the Resedimented Lower Gypsum unit (RLG) and halite deposition. The third step of the MSC occurred in the 5.54-5.33 Ma interval. It is typified by the deposition of the Upper Gypsum unit and sediments displaying freshwater influences (Lago Mare facies), prior to a marine reflooding at ca 5.33 Ma (base of the Pliocene).

The island of Crete (Aegean Sea, Greece) offers excellently exposed Miocene to Pliocene marine deposits that yielded abundant, diverse, and generally well-preserved fossil organisms. Apart from foraminifera, previous studies dealing with fossil communities are relatively few (Agiadi *et al.* 2017). Among invertebrates, bryozoans are rather common, but have not been studied in detail, even in the late Miocene (Moissette *et al.* 1993, 2018; Drinia *et al.* 2009). Bryozoans are benthic sessile invertebrates that can confidently be used for palaeoenvironmental reconstructions (e.g., Schopf 1969; Harmelin 1988; Moissette 2000; Amini *et al.* 2004; Taylor 2005). Studies on present-day Mediterranean deep-water bryozoans are scarce, but fossil communities have been the subject of much less attention (Moissette & Spjeldnaes 1995; Rosso 2005; Di Geronimo *et al.* 2005; Moissette *et al.* 2017). The purposes of this paper are thus: 1) to contribute to a better knowledge of late Miocene bryozoans and 2) use them for palaeoenvironmental reconstructions.

Four sections (Potamida, Keramoutsi, Kapariana, and Faneromeni) have been chosen (Moissette *et al.* 2018) in three different sedimentary basins (Chania, Heraklion, and Sitia) in a west-east transect along the Island of Crete, in order to

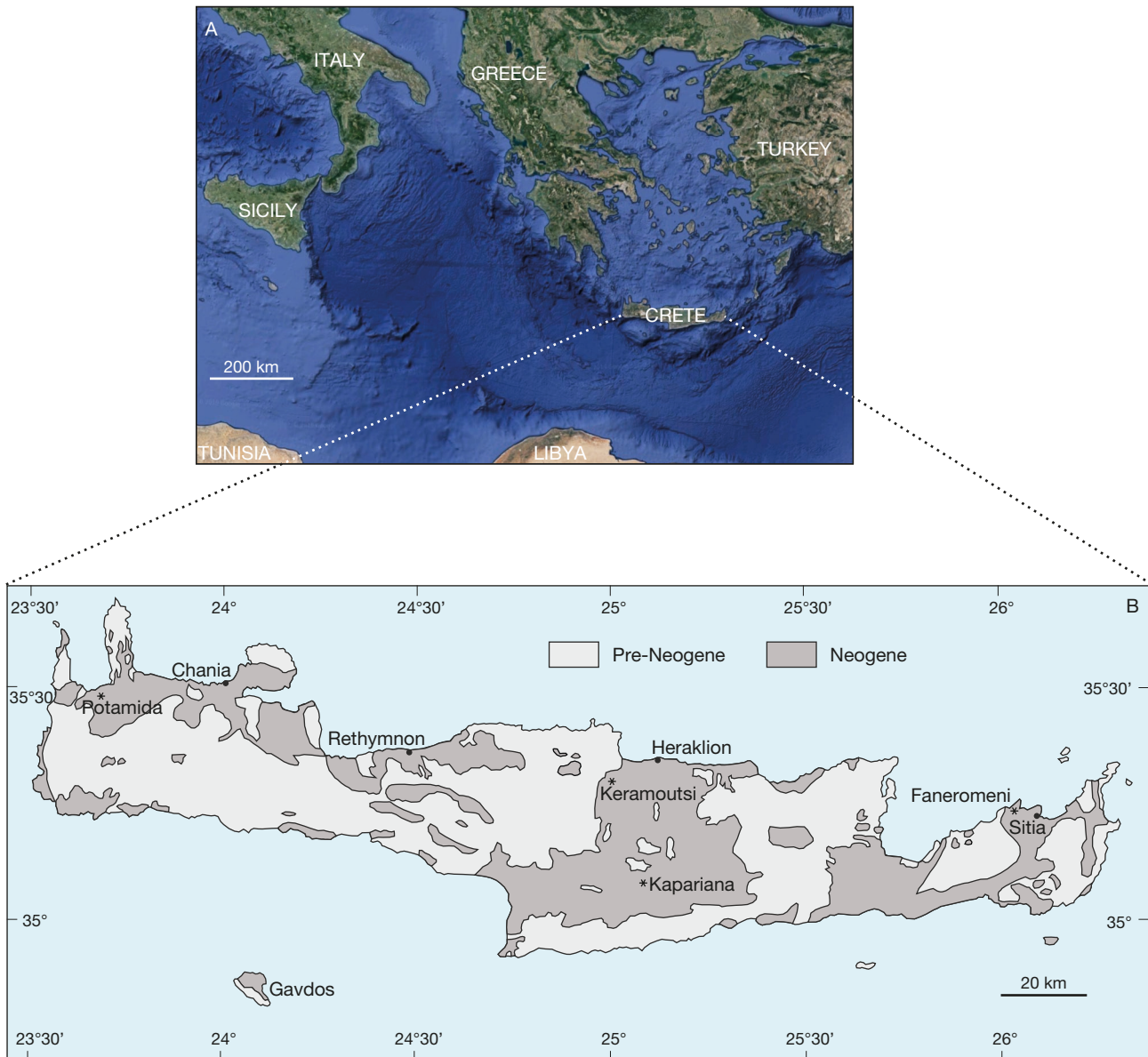


FIG. 1. — **A**, Situation map of Crete within the eastern Mediterranean; **B**, geological sketch map of the island of Crete (after Krijgsman *et al.* 1994), with location of the studied sections.

analyse the changes that occurred in bryozoan faunas before the Messinian Salinity Crisis (MSC). Our sampling starts approximately at 7.58 Ma, *c.* 220 ka after the Tortonian Salinity Crisis (TSC at 7.8 Ma; Krijgsman *et al.* 2000), and terminates at 6.72 Ma, *c.* 750 ka before the onset of the MSC (5.97 Ma; Manzi *et al.* 2013, 2018). Therefore, the studied sediments document the TMT, a crucial time interval for the palaeoceanographic history of the Mediterranean Sea.

## GEOLOGICAL BACKGROUND

Around the middle/late Miocene boundary, the area now occupied by the island of Crete (Fig. 1) became divided into a series of basins bounded by faults and filled mostly by marine

sediments (van Hinsbergen & Meulenkamp 2006; Zachariasse *et al.* 2008, 2011). During the late Miocene, marls, clayey limestones and sapropels deposited, later replaced by carbonates, diatomites and evaporites (Drinia *et al.* 2004, 2007b; Karakitsios *et al.* 2017a, b; Moissette *et al.* 2018; Antonarakou *et al.* 2019; Kontakiotis *et al.* 2019, 2020).

## MATERIAL AND METHODS

The four sections studied in this paper have been logged and sampled during several field work campaigns (Figs 2-5) and some data have been already published in Moissette *et al.* (2018). Depending mostly on outcropping conditions, an average sampling interval of approximately 1 m has been used (range

TABLE 1. — Planktonic foraminiferal bioevents identified in the four studied sections (Moissette *et al.* 2018; Kontakiotis *et al.* 2019). Abbreviations: **LO**, Last Occurrence; **LCO**, Last Common Occurrence; **FO**, First Occurrence; **FCO**, First Common Occurrence.

Stage	Planktonic Foraminiferal Bioevents	Stratigraphic level (m)				Chronostratigraphy
		Potamida	Keramoutsi	Kapariana	Faneromeni	Age (Ma)
Messinian	(10) LO <i>G. nicolae</i>	–	–	37.5	47.7	6.72
	(9) FO <i>G. nicolae</i>	34.4	65.5	33.0	41.0	6.83
	(8) LCO <i>G. scitula</i> group (sin)	–	–	31.0	32.4	7.08
	(7) FCO <i>G. miotumida</i> group	28.8	44.5	–	24.6	7.24
Tortonian	(6) Influx <i>G. menardii</i> 4 within the range of <i>G. menardii</i> 5	26.8	–	15.1	22.2	7.28
	(5) Paracme end <i>G. scitula</i> group (dex)	26.8	–	–	22.2	7.28
	(4) FO <i>G. menardii</i> 5 (dex)	7.5	–	13.2	19.4	7.36
	(3) LO <i>C. parvulus</i>	4.3	28.0	7.0	12.8	7.45
	(2) LCO <i>G. menardii</i> 4 (sin)	0.5	21.0	–	8.2	7.51
	(1) <i>G. scitula</i> group coiling change D/S	–	–	–	3.5	7.58

between about 1.6 m in Keramoutsi and 0.6 m in Potamida section). An overall number of 232 samples were collected, among which 171 yielded at least one bryozoan specimen.

For each sample, 500 g of dry sediment were soaked for several hours in diluted hydrogen peroxide and later washed under running water through five mesh sieves (2 mm, 1 mm, 0.5 mm, 0.25 mm, and 0.125 mm). The residues were oven-dried and all identifiable fossils were picked and counted under a stereomicroscope.

The time framework and the stratigraphic correlation of the studied sections was based on the qualitative and semi-quantitative analysis of the planktonic foraminifera identified in the samples (Moissette *et al.* 2018; Kontakiotis *et al.* 2019; this study). The chronology of the studied sections is based on the assemblage-based concept of the marker species, which was initially developed by Zachariasse (1975) and elaborated by several authors (e.g., Hilgen *et al.* 1995; Antonarakou *et al.* 2007; Karakitsios *et al.* 2017a; Lozar *et al.* 2018; Kontakiotis *et al.* 2019; Vasiliev *et al.* 2019; Zachariasse *et al.* 2021) in Mediterranean Neogene sections. A total of *c.* 300 specimens from the >0.125 mm size fraction of the planktonic foraminiferal assemblage were collected from the washed residue to obtain information about the abundance of marker species as a percentage of the total planktonic foraminiferal fauna. The sections were dated by using presence/absence patterns and coiling of planktonic foraminiferal marker species based on the planktonic foraminiferal biostratigraphy of Krijgsman *et al.* (1994, 1995). Ages for the planktonic foraminiferal bioevents recognized (Table 1) are derived from the astrochronology based on magnetostratigraphy and astronomical tuning of sedimentary cycle patterns (Lourens *et al.* 2004).

Each bryozoan specimen, fragment or whole colony, was counted as one unit in the >0.25 mm size fraction and a semi-quantitative representation (very rare, rare, frequent, common, abundant) was then produced (Figs 2-5). The palaeoenvironmental analysis was based on the known ecological requirements of living representatives: colonial growth forms (zoarial forms) and species (Hageman *et al.* 1998;

Moissette 2000; Amini *et al.* 2004; Taylor 2005). Selected well-preserved specimens were ultrasonically cleaned and then observed and photographed with a scanning electron microscope (JEOL JSM-6360) at the National and Kapodistrian University of Athens (Department of Historical Geology-Paleontology).

The bathymetric (bionomical) zonation used in this paper follows that of Pérès & Picard (1964). The depth limits are estimates related to light and temperature levels along latitudinal and longitudinal gradients, also depending on bottom substrate characteristics: infralittoral (0-40 m), shallow circalittoral (40-80 m), deep circalittoral (80-200 m), and upper bathyal (200-500 m). The approximate equivalent terms used by van Morkhoven *et al.* (1986) are respectively: inner shelf (inner neritic), mid shelf (mid neritic), outer shelf (outer neritic), and upper slope (upper bathyal).

## RESULTS AND INTERPRETATIONS

### BIOSTRATIGRAPHY

Most results related to the Potamida, Kapariana and Faneromeni sections have already been published by Moissette *et al.* (2018). New data for the 84-m thick Keramoutsi section (Heraklion basin; 35°16'34.77"N, 25°01'38.88"E) are given below and illustrated in Figure 3.

The planktonic foraminiferal analysis of the study sections revealed the succession of 10 planktonic bioevents (Table 1) and the Tortonian-Messinian boundary (7.24 Ma). Overall, all study sections cover the TMT spanning the time interval between 7.58 and 6.72 Ma. The Faneromeni section is slightly older than the other three sections, with the dextral to sinistral (d/s) coiling change of the *Globorotalia scitula* group recorded at the base of this section (Moissette *et al.* 2018). The biostratigraphic evidence from the top of the sections further points to an age younger than, at least, the Last Occurrence (LO) of *G. nicolae* at 6.72 Ma, for Faneromeni and Kapariana compared to Keramoutsi and Potamida sections respectively (Figs 2-5).

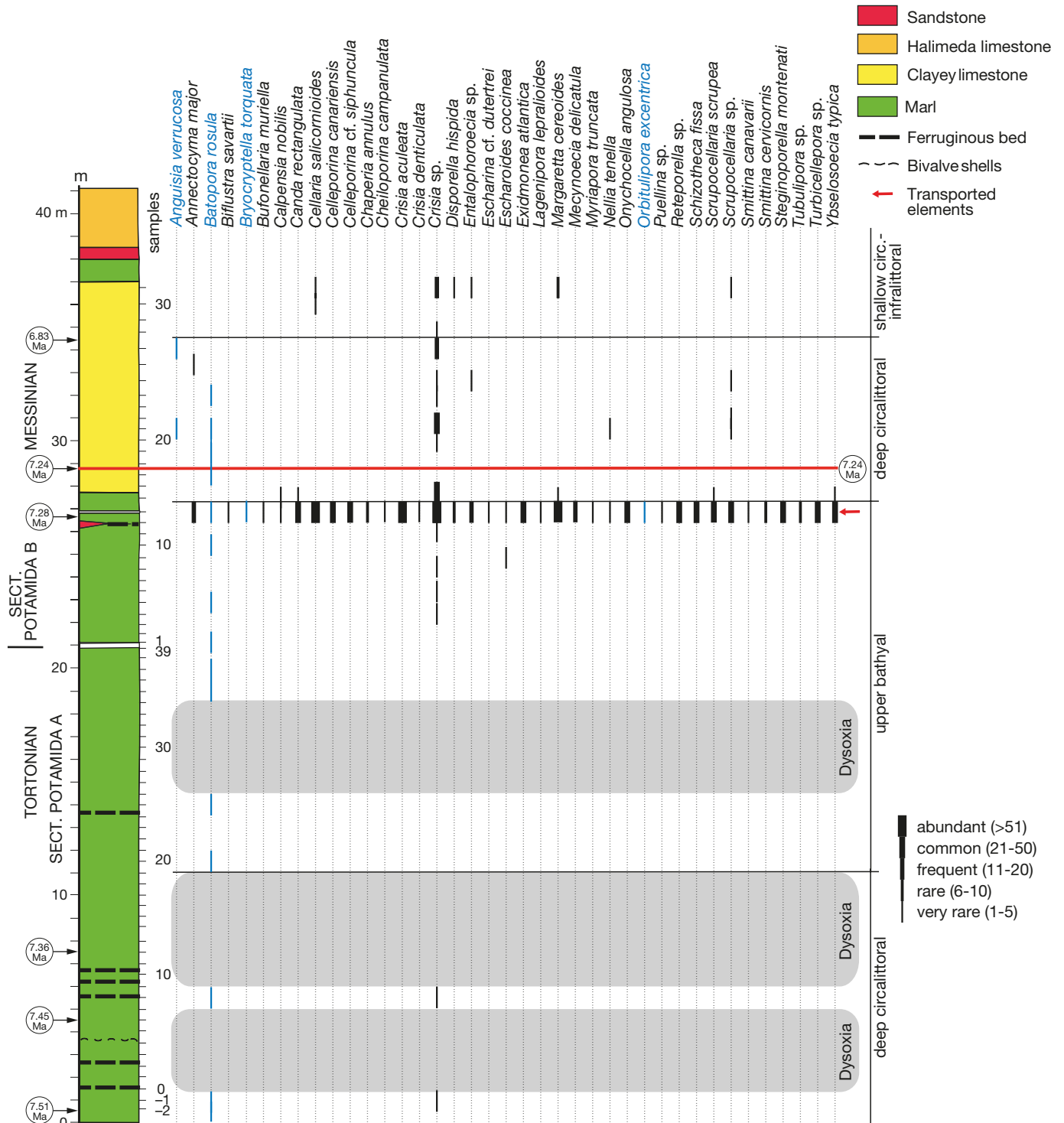


Fig. 2. — Schematic sedimentary log of Potamida composite section with sample location and semi-quantitative abundances of bryozoan species.

DESCRIPTION OF THE SECTIONS AND OF THEIR BRYOZOAN COMMUNITIES

The studied sediments are mostly composed of marls and clayey limestones. Additionally, sandstones, sandy marls, bioclastic limestones, ferruginous concretions, and bivalve shell beds are common (Moissette *et al.* 2018). The associated skeletal organisms comprise abundant foraminifera (benthic and planktonic), common to rare

bivalves, rare to very rare ostracods, echinoids, pteropods, and very rare gastropods, scaphopods, decapods, brachiopods and fishes.

Bryozoan remains occur in almost ¾ of the collected samples, but they are generally minor components with only a few fragments and species in each sample. The main results (including distribution of the species and semi-quantitative abundances) are presented in Figures 2-5.

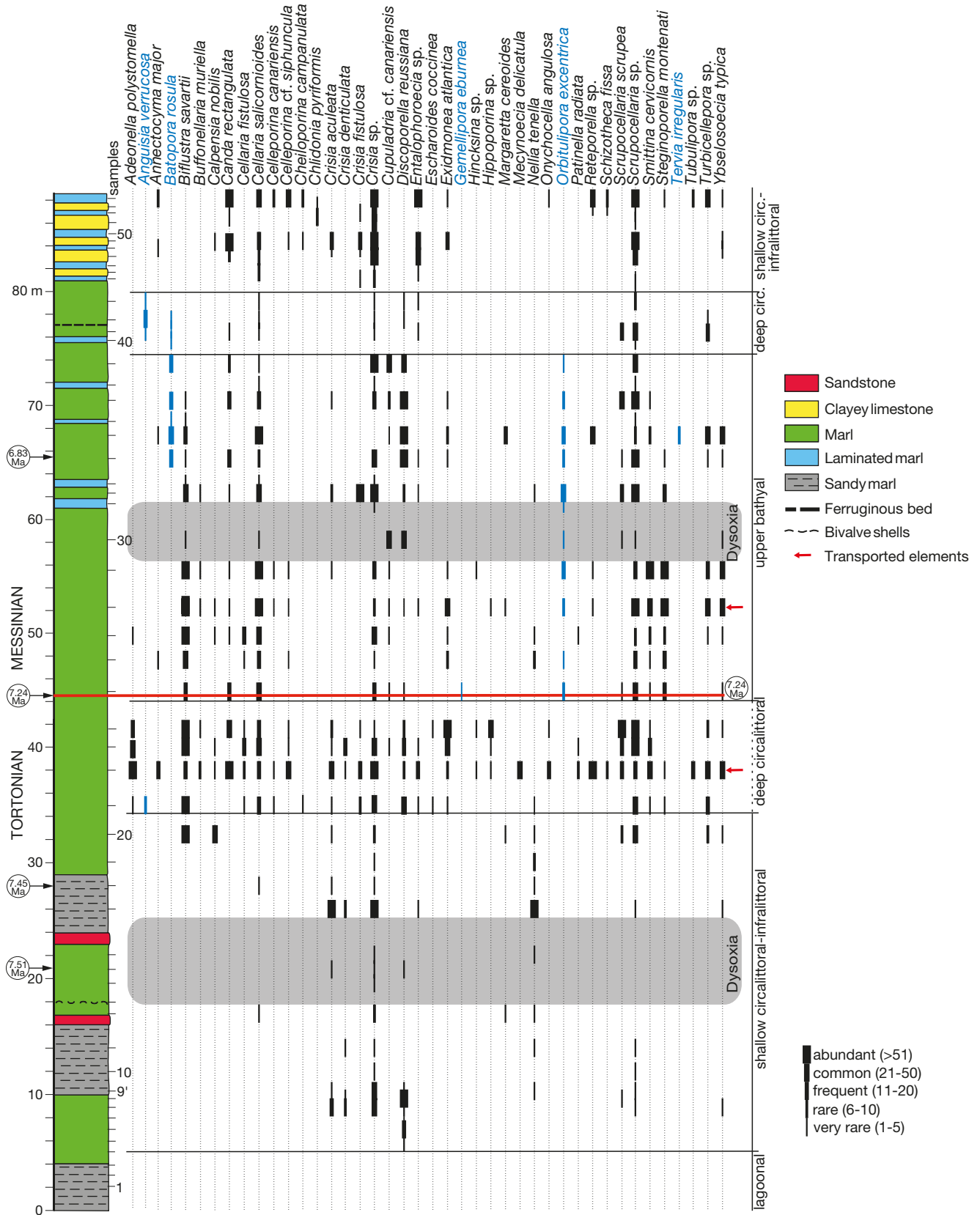


FIG. 3. — Schematic sedimentary log of Keramoutsi section with sample location and semi-quantitative abundances of bryozoan species.



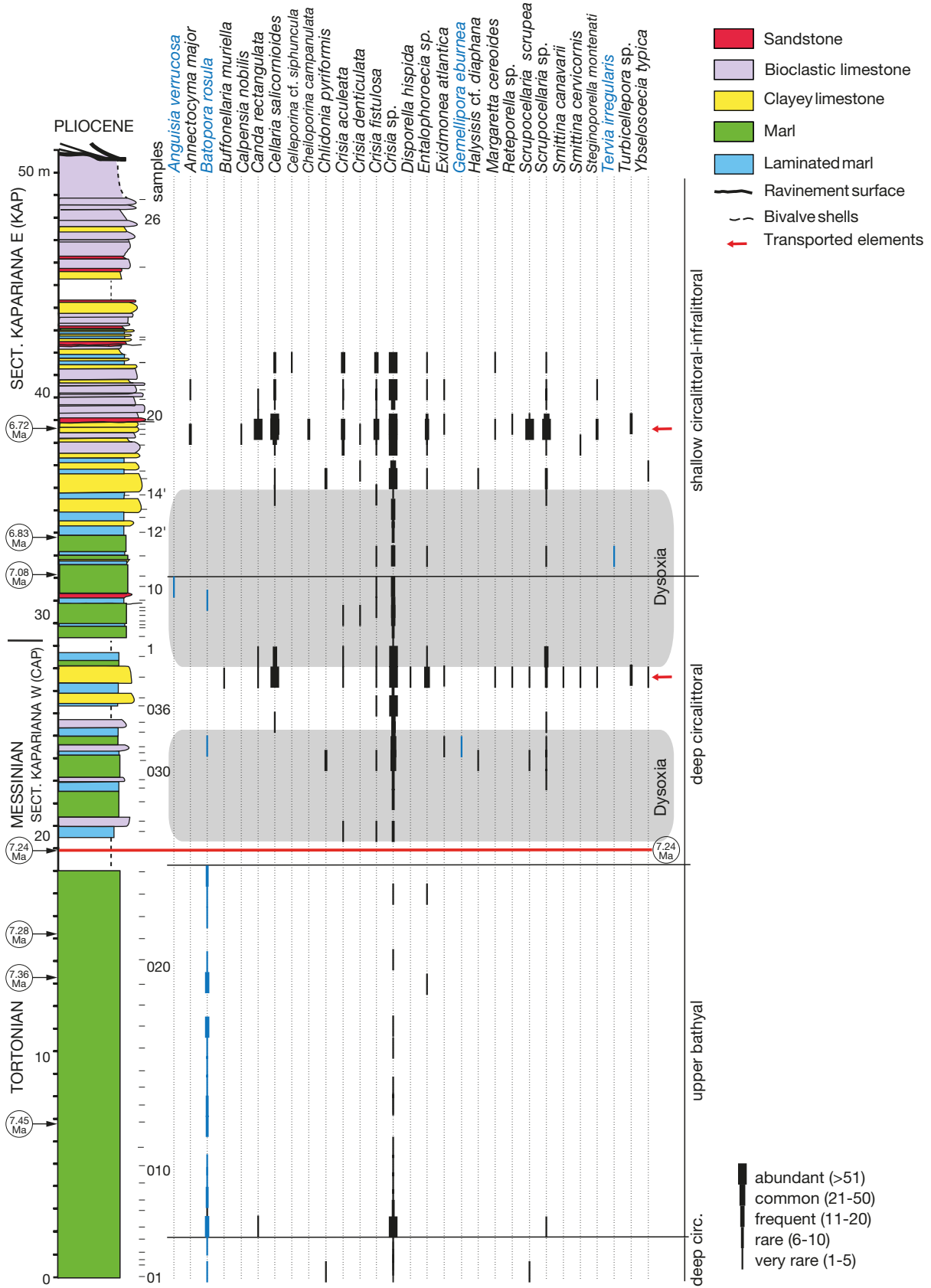


Fig. 4. — Schematic sedimentary log of Kapariana composite section with sample location and semi-quantitative abundances of bryozoan species.

TABLE 2. —List of the identified bryozoan species with indication of their zoarial morphotype and known depth range (numbers within parentheses correspond to optimum water depths, notably for the Mediterranean). The colonial morphotypes are indicated by two-letter abbreviations: **AD**, adeoniform; **CA**, catenacelliform; **CE**, cellariiform; **CO**, conescharelliniform; **CP**, celleporiform; **LU**, lunulitiform; **ME**, membraniporiform; **RE**, retetoporiform; **VI**, vinculariiform. References for environmental parameters: **1**, Harmelin 1969; **2**, Harmelin 1977; **3**, Harmelin & d'Hondt 1982; **4**, Harmelin 1976; **5**, Canu & Bassler 1929; **6**, Jullien & Calvet 1903; **7**, Berning & Kukliński 2008; **8**, Ryland & Hayward 1977; **9**, Prenant & Bobin 1966; **10**, Aristegui 1989; **11**, Hayward & McKinney 2002; **12**, Gautier 1962; **13**, Hayward & Ryland 1985; **14**, Harmelin 1990; **15**, Harmelin 1968; **16**, Reverter-Gill *et al.* 2014; **17**, Rosso *et al.* 2019; **18**, Zabala *et al.* 1993; **19**, Harmer 1957; **20**, Fransen 1986; **21**, Hayward & Ryland 1979.

Species	Zoarial forms	Depth	References
<i>Adeonella polystomella</i> (Reuss, 1848)	AD	20-130 m (30-60 m)	1
<i>Anguisia verrucosa</i> Jullien, 1882	VI	200-4280 m (200-1500 m)	2, 3
<i>Annectocyma major</i> (Johnston, 1847)	ME	5-200 m	4
<i>Batopora rosula</i> (Reuss, 1848)	CO	NA	—
<i>Biflustra savartii</i> (Audouin, 1826)	ME	0-100 m	5
<i>Bryocryptella torquata</i> (Jullien, 1903)	VI	80-300 m	6
<i>Buffonellaria muriella</i> Berning & Kukliński, 2008	ME	10-50 m	7
<i>Calpensia nobilis</i> (Esper, 1796).	ME	0-60 m	8, 9
<i>Canda rectangulata</i> Udin, 1964	VI	NA	—
<i>Cellaria fistulosa</i> (Linnaeus, 1758)	CE	30-80 m	8, 9
<i>Cellaria salicornioides</i> Lamouroux, 1816	CE	0-636 m (0-280 m)	8, 9
<i>Celleporina canariensis</i> Aristegui, 1989	CP	0-260 m	10
<i>Celleporina cf. siphuncula</i> Hayward & McKinney, 2002	CP	0-35 m	11
<i>Chaperia annulus</i> Manzoni, 1878	ME	30-115 m	12
<i>Cheiloporina campanulata</i> (Cipolla, 1921)	ME	NA	—
<i>Chlidonia pyriformis</i> (Bertoloni, 1810)	CA	0-40 m	9
<i>Crisia aculeata</i> Hassall, 1841	CE	50-1000 m (115-480 m)	13, 14
<i>Crisia denticulata</i> (Lamarck, 1816)	CE	0-100 m	14
<i>Crisia fistulosa</i> Heller, 1867	CE	5-100 m	15
<i>Crisia</i> sp.	CE	NA	—
<i>Cupuladria cf. canariensis</i> (Busk, 1859)	LU	5-860 m (50-300 m)	9
<i>Discoporella reussiana</i> (Manzoni, 1869)	LU	NA	—
<i>Disporella hispida</i> (Fleming, 1828)	ME	5-700 m	16, 17
<i>Entalophoroecia</i> sp.	VI	NA	—
<i>Escharina cf. dutertrei</i> (Audouin, 1826)	ME	10-280 m (100-150 m)	18
<i>Escharoides coccinea</i> (Abildgaard, 1806)	ME	0-100 m (30-80 m)	12
<i>Exidmonea atlantica</i> (Forbes in Johnston, 1847)	VI	10-850 m (40-100 m)	4
<i>Gemellipora eburnea</i> Smitt, 1873	CE	60-3300 m	19
<i>Halysisis cf. diaphana</i> (Busk, 1860)	CA	0-60 m	19
<i>Hincksina</i> sp.	ME	NA	—
<i>Hippoporina</i> sp.	ME	NA	—
<i>Kionidella excelsa</i> Koschinsky, 1885	CO	NA	—
<i>Lagenipora lepralioides</i> (Norman, 1868)	ME	10-150 m (40-80 m)	12
<i>Margaretta cereoides</i> (Ellis & Solander, 1786)	CE	10-90 m (10-45 m)	12
<i>Mecynoecia delicatula</i> (Busk, 1875)	VI	5-120 m	4
<i>Myriapora truncata</i> (Pallas, 1766)	VI	10-130 m (30-60 m)	12
<i>Nellia tenella</i> (Lamarck, 1816)	CE	0-250 m	20
<i>Onychoecella angulosa</i> (Reuss, 1847)	ME	0-80 m (30-50 m)	12
<i>Orbitulipora excentrica</i> Seguenza, 1880	CO	NA	—
<i>Patinella radiata</i> (Audouin, 1826)	ME	0-50 m	17
<i>Puellina</i> sp.	ME	NA	—
<i>Reteporella</i> sp.	RE	NA	—
<i>Schizotheca fissa</i> (Busk, 1856)	ME	20-120 m (40-120 m)	12
<i>Scrupocellaria cf. elliptica</i> (Reuss, 1847)	CE	NA	—
<i>Scrupocellaria scrupea</i> Busk, 1852	CE	0-500 m	9, 12
<i>Scrupocellaria</i> sp.	CE	NA	—
<i>Smittina canavarii</i> (Neviani, 1900)	ME	NA	—
<i>Smittina cervicornis</i> (Pallas, 1766)	AD	10-120 m (40-60 m)	12
<i>Steginoporella montenati</i> David & Pouyet, 1972	ME	NA	—
<i>Tervia irregularis</i> (Meneghini, 1844)	VI	60-2650 m (60-300 m)	4
<i>Tessaradoma boreale</i> (Busk, 1860)	VI	60-3500 m (50-1300 m)	12, 21
<i>Tubulipora</i> sp.	ME	NA	—
<i>Turbicellepora</i> sp.	CP	NA	—
<i>Ybselosoecia typica</i> (Manzoni, 1878)	VI	NA	—

*Potamida composite section*

This section (73 samples) is about 40 m thick and is comprised of two subsections separated by a thin observational gap (log interval 20.9-21.1 m): Potamida A at the base and Potamida B at the top (Fig. 2). Most samples are totally devoid

of bryozoan remains or yielded only a few specimens. Level 13 (subsection B) is an exception, characterised by the accumulation of numerous fragments belonging to 38 bryozoan species. A total of 34 genera of bryozoans are represented by 39 species in the Potamida section.

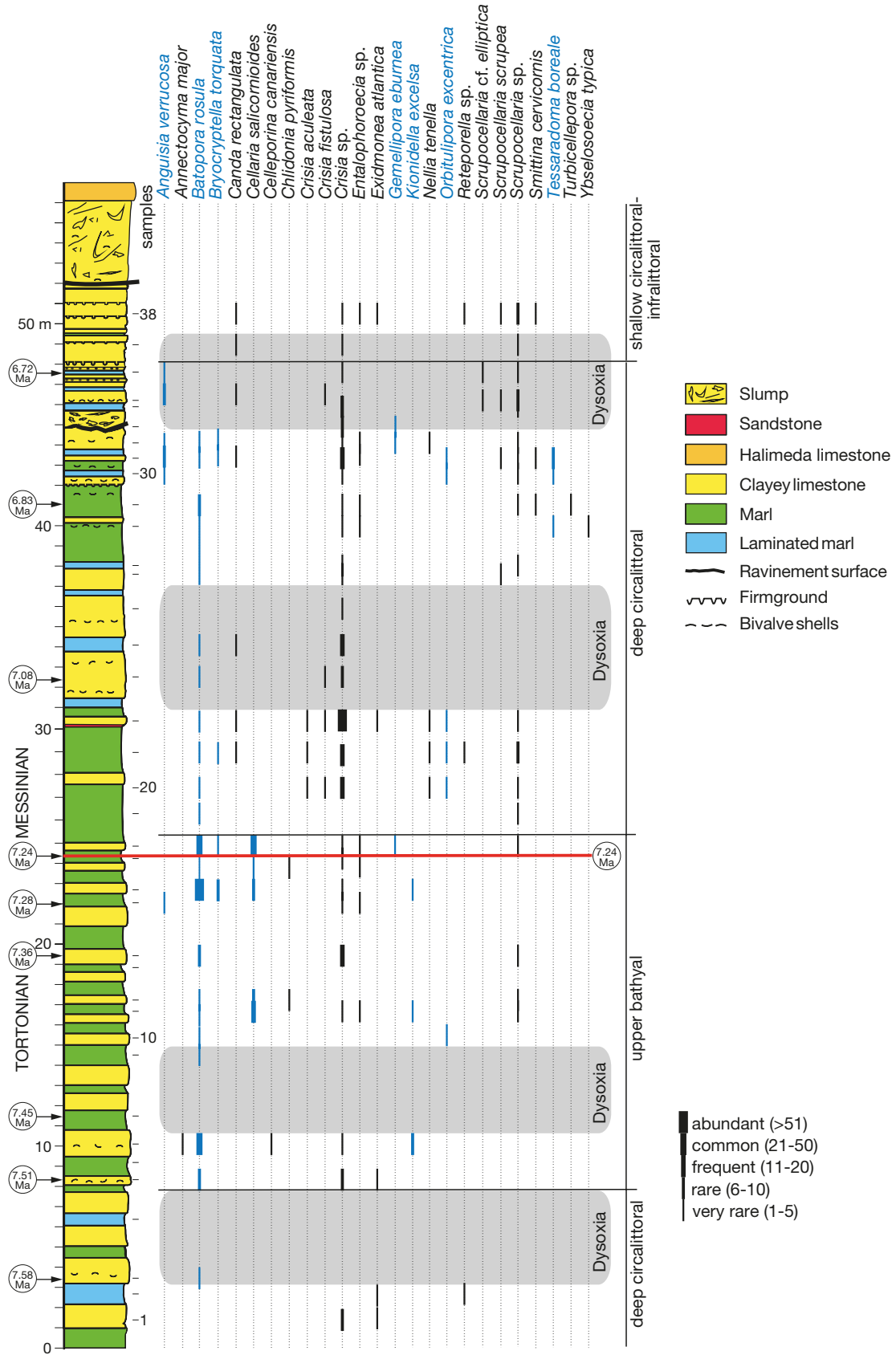


Fig. 5. — Schematic sedimentary log of Faneromeni section with sample location and semi-quantitative abundances of bryozoan species.

#### *Keramoutsi section*

With 84 m of sediments, this section (55 samples) is the thickest one (Fig. 3). Bryozoan specimens are present and even abundant in most samples, except at the base (samples 1-20) and in two short intervals (sample 30 and samples 40-45) where they are often lacking or relatively rare. Thirty six genera of bryozoans are represented by 42 species.

#### *Kapariana composite section*

This 50 m thick section (66 samples) consists of two subsections: Kapariana W at the base (samples CAP01 to 038) and Kapariana E (sample KAP1 to 26) at the top (Fig. 4). Four short observational gaps exist near steep topographic areas. Specimens are relatively abundant, especially in the upper part of the section. They are however relatively rare in two intervals and completely absent in the uppermost part (samples KAP23 to 26). Twenty four genera of bryozoans are represented by 29 species.

#### *Faneromeni section*

This section (38 samples) is almost 57 m thick (Fig. 5). The specimens occurring in each sample are relatively rare, especially in four intervals (two near the base and two in the upper part of the section) where they can even be completely absent. Twenty one genera of bryozoans are represented by 25 species.

### GENERAL CHARACTERISTICS

#### OF THE BRYOZOAN COMMUNITIES

A total of 46 genera and 54 species have been identified in the study material (Table 2). They belong to nine different colonial morphotypes or zoarial forms.

#### *Adeoniform*

Erect, rigid, colonies with bilamellar branches. They characterise moderately deep environments. Only two species represent this colonial type (*Adeonella polystomella* and *Smitina cervicornis*).

#### *Catenicelliform*

Erect flexible zoarial type, with colonies attached to the substratum by chitinous rootlets, each articulated segment comprising only one or two individuals. This morphotype typically characterises shallow-water settings. It is represented here by very rare specimens belonging to only two species (*Halysis cf. diaphana* and *Chlidonia pyriformis*).

#### *Cellariiform*

Erect flexible colonies attached to the substratum by chitinous rootlets and with segments (constituted by numerous individuals) articulated by chitinous joints. They live in different types of environments and at various depths. In the studied material, this is the most abundant (numerous specimens) and diverse group (12 species, predominantly belonging to three genera: *Cellaria*, *Crisia*, and *Scrupocellaria*). A fourth genus is represented by *Gemellipora eburnea*, essentially a deep species (60-3300 m, with an optimum depth of about 700 m).

#### *Celleporiform*

Nodular colonies formed by irregular frontal budding, often around soft, flexible substrates. They are also predominant in shallow-water environments. They are represented here by rare fragments belonging to only three species (*Celleporina canariensis*, *C. cf. siphuncula*, and *Turbicellepora* sp.).

#### *Conescharelliniform*

Conical (conescharelliniform *sensu stricto*) to discoidal (orbituliporiform) rooted colonies. They are typical of deep-water muddy bottoms. Recent *Batopora* colonies are found at depths of 285-805 m (Cook & Lagaaij 1976). Mono- to oligo-specific assemblages with relatively numerous *Batopora rosula* colonies are considered as indicating shallow bathyal environments (Moissette 1996). This morphotype is represented in the studied sections by three species (*B. rosula*, *Kionidella excelsa*, and *Orbitulipora excentrica*).

#### *Lunulitiform*

Free-living, cup-shaped colonies. This morphotype is characteristic of muddy to sandy bottoms at moderate depths. They occur only in the Keramoutsi section where they are represented by two species (*Cupuladria cf. canariensis* and *Discoporella reussiana*).

#### *Membraniporiform*

Encrusting, normally unilaminar colonies growing mostly on hard substrates. They largely predominate in shallow-water settings (although skeletons of bathyal corals may be colonised by numerous encrusting bryozoans). This morphotype is represented here by 19 species, but none of them is abundant.

#### *Reteporiform*

Erect rigid fenestrate colonies. They predominate in shallow-water settings, but some species may occur deeper. They are represented here by only one species, *Reteporella* sp.

#### *Vinculariiform*

Erect rigid colonies with cylindrical branches. Their presence indicates relatively deep environments. This is the case for extant species such as *Tervia irregularis* (60-300 m in the Mediterranean), *Tessaradoma boreale* (50-1300 m in the Mediterranean), and *Bryocryptella torquata* (80-300 m). This morphotype is represented in the study material by ten species.

### BATHYMETRIC RANGES

As indicated in the systematic part (Table 2), most species have a relatively broad bathymetric distribution. However, some of them show relatively more restricted depth ranges or are more or less constantly associated and may thus provide insights into palaeoenvironmental conditions, especially water depth.

#### *Shallow-water species*

About 20 species belong to this group. Most of them have a present-day distribution in the upper 100 m and some of these genera or species (e.g., *Biflustra savartii*, *Steginoporella*) live in tropical to subtropical environments. In the framework of the

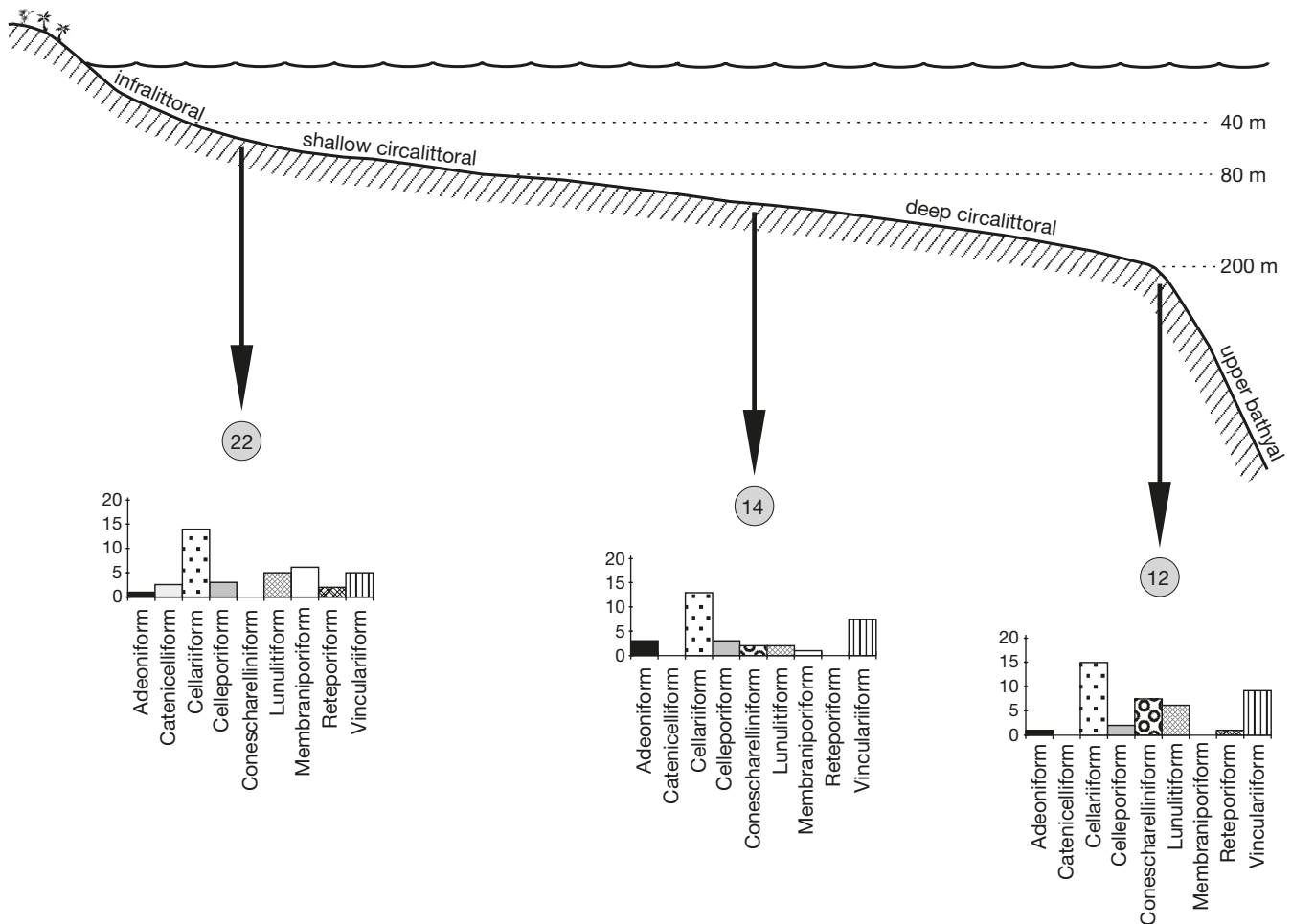


FIG. 6. — Theoretical zonation in a transect from coastal to upper bathyal palaeoenvironments following Pérès & Picard (1964). This bionomic depth zonation illustrates the situation on flat muddy bottoms in areas with very clear waters, like in the oligotrophic (eastern) Mediterranean Sea. The distribution of bryozoan growth-form assemblages (in average number of fragments per sample) and the average number of species in each assemblage is indicated in a grey circle (partly inspired from Moissette 2000).

present study, these taxa are mostly regarded as transported from shallow into deeper waters, as sometimes indicated by a number of yellowish and abraded fragments, excepted at the top of the Potamida, Kapariana and Faneromeni sections as well as at the base and top of the Keramoutsi section. However, a few species, although recorded predominantly from moderate depths, have been found also exceptionally in deeper settings (e.g., *Smittina cervicornis*: 10-120 m, but down to 306 m in the Adriatic Bari Canyon; Sanfilippo *et al.* 2013, Rueda *et al.* 2019).

#### Deep-water species

Living from the deep circalittoral (at depths of at least 80-100 m) to the upper bathyal, they are represented here by a few extant species (*Anguisia verrucosa*, *Bryocryptella torquata*, *Gemellipora eburnea*, *Tervia irregularis*, and *Tessaradoma boreale*). Based on their present-day close relatives, colonial morphotype, and frequent association with certain Recent species, a number of fossil taxa are also regarded as deep-water indicators (*Batopora rosula*, *Kionidella excelsa*, and *Orbitulipora excentrica*). All these species may be considered as autochthonous.

#### *Eurybathic species*

They have wide bathymetric ranges, extending from the shallow infralittoral down to several hundred metres (Table 2). A few of them, especially some plastic species, although not normally considered as deep-sea organisms, may sometimes be found associated with deep taxa: *Annectocyma major*, *Cellaria salicorniooides*, *Celleporina canariensis*, *Cupuladria canariensis*, *Disporella hispida*, *Exidmonea atlantica*, and *Nellia tenella*.

#### PALAEOENVIRONMENTAL INDICATORS

Several bryozoan species and colonial morphotypes, occurring alone or together may be considered characteristic of certain palaeoenvironments (Hageman *et al.* 1998; Moissette 2000; Taylor 2005). The main feature observed in all Recent or fossil deep-water bryozoan assemblages is low diversity, with each species represented by relatively few specimens (Schopf 1968; Cook 1981; Moissette & Spjeldnaes 1995; Rosso 2005). However, this general observation is mostly valid for flat muddy bottoms (as is the case in this study), without hard substrates such as shells or cold-water coral skeletons. On the contrary, shallow-water communities show higher diversities with con-

comitant greater abundance of colonies (or fragments). This is similarly observable in the studied assemblages.

#### Upper bathyal environment

Upper bathyal depths (Fig. 6) are indicated by a maximum number of fragments/colonies of *Batopora rosula*, accompanied by few other deep-water species (oligo- to mono-specific assemblages of Moissette 1996) such as *Orbitulipora excentrica*, *Bryocryptella torquata*, *Kionidella excelsa* and subordinate *Tervia irregularis* and *Tessaradoma boreale* (e.g., Kapariana section, samples CAP06-024; Faneromeni section, samples 5-18). A number of erect eurybathic taxa, sometimes represented by abundant specimens, are constantly found associated with these depth indicators: *Cellaria salicornioides*, *Crisia*, *Exidmonea atlantica*, *Mecynoecia*, *Nellia tenella*, and *Scrupocellaria*. The conescharelliniform colonial morphotype is the most characteristic element of this assemblage, accompanied by cellariiform species (mostly *Crisia* sp. and *Scrupocellaria* sp. with relatively numerous fragments) and scarcer vinculariiforms (Moissette 1996). The lunulitiform morphotype is also relatively well represented in some samples from the Keramoutsi section interpreted as deposited in deep-water settings.

#### Deep circalittoral environment

Deep circalittoral settings (Fig. 6) are characterised by less abundant *Batopora rosula* colonies coupled with species like *Anguisia verrucosa* and *Gemellipora eburnea* (with these two species, usually considered as bathyal markers, here mostly associated with deep circalittoral settings). Less distinctive species (*Bryocryptella torquata*, *Kionidella excelsa*, and *Orbitulipora excentrica*) add to this assemblage (e.g., Potamida section, samples 15-27; Faneromeni section, samples 19-37). As previously documented in the upper bathyal community, approximately the same eurybathic erect taxa also occur here (e.g., *Cellaria salicornioides*, *Crisia* sp., *Exidmonea atlantica*, *Scrupocellaria* sp.). The colonial morphotype assemblage is similar to its deeper-water counterpart, but with less abundant conescharelliniform colony fragments.

#### Infralittoral to shallow circalittoral environments

Shallow (infralittoral) to moderately deep (shallow circalittoral) environments (Fig. 6) are recognized near the top of all sections (e.g., Keramoutsi section, samples 40-54; Kapariana section, samples KAP11-22). The sediments characteristically contain substantial amounts of sandy and bioclastic material (sometimes with abundant calcified segments of the green alga *Halimeda*, such as in Potamida and Faneromeni). These settings are characterised by the absence of deep-water bryozoans and by the occurrence of numerous and abundant shallow-water taxa (e.g., *Biflustra savartii*, *Calpensia nobilis*, *Margaretta cereoides*, *Onychocella angulosa*, *Patinella radiata*, and *Steginoporella montenati*). Membraniporiform and celleporiform colonial morphotypes are here slightly predominant, whereas conescharelliniform colonies are completely lacking. Erect species, either rigid (adeoniform, retoporiform, vinculariiform) or flexible (cellariiform) are also relatively well represented. Very rare segments of catenelliform species occur in a few samples.

A clear distinction between shallow circalittoral and infralittoral environments is difficult to establish here on the basis of bryozoan

communities only. They have consequently been grouped together (Figs 2-5). Even when bryozoans are absent or poorly represented, shallow marine environments are clearly recognisable at/near the top of each sections by the presence of other characteristic organisms (Moissette *et al.* 2018 and references therein). Among them are calcareous green algae (*Halimeda*), benthic foraminifera (e.g., *Elphidium* spp.), bivalves (e.g., *Anomia ephippium* and *Limaria* sp.), and ostracods (e.g., *Aurila* spp., *Cnestocythere truncata*, and *Pokornyyella italica*). However, even in these shallow-water areas, abundant and diverse planktonic (and benthic) foraminiferal assemblages occur (except at the very top of the Kapariana section in samples KAP23-26), indicating open marine conditions.

Finally, brackish-water (lagoonal) settings have even been documented at the very base of the Keramoutsi section (samples 1-3) where benthic foraminifera, bivalves, gastropods and ostracods occur together with coal fragments and gyrogonites of characean green algae. Bryozoans are here absent.

## SYSTEMATIC PALAEOLOGY

Only species considered as deep-dwelling (either stenobathic or eurybathic, but found associated with deep-water taxa, at depths of at least 80-100 m) are taken into account and described in this systematic part. Synonymic lists for species frequently encountered in the literature have been restricted to reports, with descriptions and illustrations, from the Mediterranean. References from the Paratethys and the NE Atlantic have sometimes also been given.

The systematic classification used in this paper is based on the current taxonomic position of the species according to the Bryozoa Home Page edited by Bock (<http://bryozoa.net/indexes.html>), and World Register of Marine Species (WoRMS; <http://www.marinespecies.org/aphia.php?p=tax-details&id=146142> on 2019-09-18).

The origin of the material has been indicated with the following abbreviations: Potamida (POTA, POTB), Kapariana (CAP, KAP), Keramoutsi (KER), and Faneromeni (FAN). The investigated samples are housed in the collections of the Athens Museum of Paleontology and Geology-Invertebrates: AMPG(IV). Complete information about the studied material (inventory numbers, list of species, samples, number of specimens, and SEM photo references) is provided as online additional data.

Class STENOLAEMATA Borg, 1926  
Order CYCLOSTOMATIDA Busk, 1852  
Suborder TUBULIPORINA Milne-Edwards, 1838  
Family ONCOUSOECIIDAE Canu, 1918  
Genus *Anguisia* Jullien, 1882

*Anguisia verrucosa* Jullien, 1882  
(Fig. 7A, B)

*Anguisia verrucosa* Jullien, 1882: 497, pl. 13, figs 1-2. — Harmelin 1977: 1058, figs 1-2; pl. I, figs 1, 3. — Harmelin 1979b: 414, pl. 2, fig. 3. — Harmelin & d'Hondt 1982: 7, pl. I, figs 3-4. — Moissette & Spjeldnaes 1995: 783, pl. 2, figs 1-2.



FIG. 7. — **A, B**, *Anguisia verrucosa* Jullien, 1882; **A**, bifurcating branch, FAN36: AMPG(IV) 3471; **B**, encrusting base (left) and erect peristome of the encrusting proximal zooid of a running branch (right), FAN35: AMPG(IV) 3470; **C, D**, *Exidmonea atlantica* (Forbes in Johnston, 1847); **C**, fragment of a branch, frontal view (with a gonozooid on the left upper part), POTB13: AMPG(IV) 2853a; **D**, fragment of a branch, dorsal view, POTB13: AMPG(IV) 2853b; **E-G**, *Ybseosoecia typica* (Manzoni, 1878); **E**, fragment of a branch (with a large gonozooid), frontal view, POTB13: AMPG(IV) 2881a; **F**, detail of the oecioostome of another gonozooid, POTB13: AMPG(IV) 2881b; **G**, fragment of a branch, dorsal view, POTB13: AMPG(IV) 2881c. Scale bars: A, D, 200  $\mu$ m; B, G, 100  $\mu$ m; C-E, 500  $\mu$ m.

*Anguisia jullieni* Neviani, 1895: 129, pl. 6, figs 39-40.

**OCCURRENCE.** — Pleistocene: Sicily, Calabria (Rosso 2005), Rhodes (Moissette & Spjeldnaes 1995). Recent: Eastern Atlantic (200-2018 m), Mediterranean (500-1525 m).

#### DESCRIPTION

Erect, tubular fragile colony, arising from an encrusting uniserial basis. Zooids forming slender bifurcating cylindrical branches, ornamented by thin growth lines and scattered slightly prominent verrucae (pseudopores).

REMARKS

The gonozooid, characteristic of the genus, consisting of a simple elongated chamber with a terminal tubular oeciostome (J.-G. Harmelin, personal communication), was not observed. The encrusting basis is visible in some of the studied specimens (Fig. 6B). The species created by Neviani (1895) from the Pliocene/Pleistocene of northern Italy, *A. jullieni* most probably corresponds to the encrusting basis of *A. verrucosa*. However, the homonymous *A. jullieni* described by Ostrovsky (1998) from the present-day Antarctic is a different species. Peristome diameter and length are smaller in *A. verrucosa* and the prominent verrucae associated with the pseudopores are absent in *A. jullieni*.

Family TUBULIPORIDAE Johnston, 1838

TYPE GENUS. — *Exidmonea* David, Mongereau & Pouyet, 1972, by subsequent designation of Mongereau (1969: 212).

Genus *Exidmonea* David, Mongereau & Pouyet, 1972

*Exidmonea atlantica* (Forbes in Johnston, 1847)  
(Fig. 7C, D)

*Idmonea atlantica* Forbes in Johnston, 1847: 278, pl. 48, fig. 3. — Buge 1966: 5, pl. B, figs 1-2.

*Idmidronea atlantica* – Harmelin 1976: 182, pl. 32, figs 1-11. — Vávra 1983: 73, pl. 1, figs 1-4. — Zabala 1986: 658, text-figs 235a-d; pl. 28, fig. E. — Zabala & Maluquer 1988: 174, text-figs 569-572; pl. 33, fig. A. — El Hajjaji 1992: 44, pl. 2, fig. 11. — Haddadi-Hamdane 1996: p. 45, pl. 1, fig. 8, pl. 2, fig. 4.

*Exidmonea atlantica* – Mongereau 1970: 30, pl. 1, fig. 1; pl. 2, figs 1, 5. — David *et al.* 1972: 84. — Moissette 1988: 48, pl. 6, figs 6-7. — Pouyet & Moissette 1992: 24, pl. 1, figs 7-8. — Moissette *et al.* 1993: 84, figs 3i-j. — Moissette & Spjeldnaes 1995: 780, pl. 1, fig. 11.

*Exidmonea triforis* – Hayward & McKinney 2002: 104, fig. 49A-H, 50.

OCCURRENCE. — Eocene: Italy, Austria, Hungary, Romania (Zágoršek 2003). Oligocene: Germany, Italy (Braga 2008). Early Miocene: France, Italy, Egypt (El Safori & El-Sorogy 1999). Middle Miocene: Austria, Hungary, Poland, France, Libya (Vávra 1983). Late Miocene: Algeria (Moissette 1988), Morocco (El Hajjaji 1992), Tunisia (Moissette 1997), Crete. Pliocene: France, Sicily (Pouyet & Moissette 1992), Algeria (Haddadi-Hamdane 1996), Tunisia. Pleistocene: Sicily (Di Geronimo *et al.* 1997; Rosso 2005), Rhodes (Moissette & Spjeldnaes 1995).

This list of fossil records concerns *Idmonea-Idmidronea-Exidmonea*-like species, i.e. a group of species with the same growth form without consideration of the species-specific morphological criteria which cannot be, in most cases, preserved in fossils (J.-G. Harmelin, personal communication). Recent: Eastern Atlantic (North Sea to Angola) and Mediterranean, at depths ranging from 10 to 850 m. In the Mediterranean, this species is particularly abundant between 40 and 100 m (Harmelin 1976).

DESCRIPTION

Vinculariiform colony. Frontal surface showing zoecial tubes alternating in two series of 4-5 tubes. Dorsal flattened or

slightly concave, ornamented by thin inverted U-shaped growth lines. Gonozooid (brood-chamber) elongate, situated along the axis of a branch, between peristomes.

REMARKS

The oeciostome was not observed.

Family TERVIIDAE Canu & Bassler, 1920  
Genus *Tervia* Jullien, 1882

*Tervia irregularis* (Meneghini, 1844)

*Idmonea irregularis* Meneghini, 1845: 128.

*Tervia irregularis* – Malecki 1963: 71, text-fig. 30; pl. 3, fig. 11. — Vávra 1975: p. 523, pl. 2, figs 3-4. — Harmelin 1976: 163, pl. 26, figs 1-11. — Harmelin & d'Hondt 1982: 9, pl. 3, fig. 4. — Zabala 1986: 656, text-fig. 234. — Moissette 1988: 49, pl. 6, figs 10-12. — Zabala & Maluquer 1988: 174, text-figs 563-568. — Pouyet & Moissette 1992: 25, pl. 1, figs 11-12. — El Hajjaji 1992: p. 48, pl. 2, fig. 10. — Moissette *et al.* 1993: 85, fig. 3h, l. — Moissette & Spjeldnaes 1995: 782, pl. 1, figs 9, 12. — Haddadi-Hamdane 1996: 46, pl. 1, fig. 10, pl. 2, figs 3, 8.

OCCURRENCE. — Eocene: Poland, Hungary, Spain (Malecki 1963). Oligocene: Germany (Malecki 1963). Early Miocene: France (Buge 1957). Middle Miocene: Austria, Hungary (Moissette *et al.* 2006), France. Late Miocene: Algeria (Moissette 1988), Morocco (El Hajjaji 1992), Crete (Moissette *et al.* 1993). Pliocene: Netherlands (Lagaaij 1952), Belgium, France, Algeria, Sicily (Pouyet & Moissette 1992). Pleistocene: Rhodes (Moissette & Spjeldnaes 1995), Karpathos (Moissette *et al.* 2017). Recent: Eastern Atlantic (down to a depth of 2650 m in the Bay of Biscay), Mediterranean (60-300 m), Pacific, Indian Ocean.

REMARKS

Only a few fragments have been found in two samples. This easily recognizable species is not illustrated here because of the relatively poor preservation state of the rare recovered specimens.

Family DIAPEROECIIDAE Canu, 1918  
Genus *Ybselosoecia* Canu & Lecointre, 1933

*Ybselosoecia typica* (Manzoni, 1878)  
(Fig. 7E-G)

*Filisparsa typica* Manzoni, 1878: 10, pl. 8, fig. 30. — Canu 1909: 115, pl. 14, figs 25-26.

*Ybselosoecia typica* – Buge 1956: 13, pl. 1, figs 3-4; pl. 2, figs 3-4. — Malecki 1963: 76, fig. 33; pl. 5, fig. 1. — Mongereau 1965: 317, fig. 1. — Vávra 1974: 362, pl. 2, figs 9-10. — Vávra 1984: 226, pl. 1, figs 2-3. — Moissette 1988: 56, pl. 7, figs 9, 13; 1997: 188, pl. 1, fig. 6. — El Hajjaji 1992: 56, pl. 2, figs 2-3. — Pouyet & Moissette 1992: 28, pl. 2, fig. 4. — Moissette *et al.* 1993: 87. — Moissette & Spjeldnaes 1995: 784, pl. 2, fig. 4. — Haddadi-Hamdane 1996: 51, pl. 1, figs 11-12; pl. 2, fig. 11. — Pouyet 1997: 26, pl. 1, figs 1-4. — Zágoršek 2003: 119, pl. 4, figs 5-6. — Zágoršek 2010a: 31, pl. 15, figs 1-5. — Zágoršek *et al.* 2017: 115, fig. 2J.





FIG. 8. — **A-C**, *Crisia aculeata* Hassall, 1841; **A**, internode, frontal view, POTB13: AMPG(IV) 2828a; **B**, internode, dorsal view, POTB13 2828b: AMPG(IV); **C**, internode with gonozooid, KAP22: AMPG(IV) 3339. **D-F**, *Crisia denticulata* (Lamarck, 1816); **D**, internode, frontal view, POTB13: AMPG(IV) 2829a; **E**, internode dorsal view, POTB13: AMPG(IV) 2829b; **F**, gonozooid, POTB13: AMPG(IV) 2829c. Scale bars: A, 500  $\mu$ m; B-F, 200  $\mu$ m.

**OCCURRENCE.** — Eocene: France, Italy, Germany, Austria, Romania, Poland (Malecki 1963; Zágoršek 2003). Oligocene: France (Buge 1964). Oligo-Miocene: Iran (Zágoršek *et al.* 2017). Early Miocene: France (Mongereau 1965). Middle Miocene: France, Austria, Hungary, Romania, Czech Republic, Poland (Vávra 1984; Moissette *et al.* 2006). Late Miocene: Morocco, Algeria (Moissette 1988), Tunisia (Moissette 1997), Crete (Moissette *et al.* 1993). Pliocene: Netherlands, France, Sicily (Pouyet & Moissette 1992), Algeria (Haddadi-Hamdane 1996), Tunisia (Buge 1956). Pleistocene: Rhodes (Moissette & Spjeldnaes 1995). This fossil species has mostly been recorded from the Mediterranean

and Paratethys basins. It has been recovered in a few instances together with deep-water bryozoan faunas: Messinian of western Algeria (Moissette 2000) and Pleistocene of Rhodes (Moissette & Spjeldnaes 1995).

#### DESCRIPTION

Vinculariiform colony. Dichotomous branches mostly flattened. Frontal smooth, zoecial tubes indistinct, quincuncially arranged and isolated, with well-developed sub-circular peristomes. Dorsal slightly convex, with thin transversal growth

lines and perforated by small pseudopores. Gonozooid enlarged, also perforated by small pseudopores, occupying the whole width of a branch and encompassing up to ten zoecial tubes. Ooeciostome with flared, transverse and convoluted rim.

Suborder ARTICULINA Busk, 1859  
Family CRISIIDAE Johnston, 1838  
Genus *Crisia* Lamouroux, 1812

*Crisia aculeata* Hassall, 1841  
(Fig. 8A-C)

*Crisia aculeata* Hassall, 1841: 170, pl. 7, figs 3-4. — Harmer 1891: 132, pl. 12, fig. 4. — Hayward & Ryland 1985: 50, fig. 14. — Harmelin 1990: 1602, figs 2, 3-6.

OCCURRENCE. — Recent: Eastern Atlantic (50-60 m in the North Sea, much deeper in Norway, the Bay of Biscay and Morocco: 135-1000 m) and Mediterranean (115-480 m).

#### DESCRIPTION

Cellariiform colony. Internodes short (8-12 zooids). The first ramification arises from the third zooid. Pseudopores elongate and relatively rare. Gonozooid pyriform with a discrete ooeciostome situated near the base of the following zooid.

#### REMARKS

This species is poorly known and has rarely been illustrated. It has often been considered as a variety of *C. eburnea* (Linnaeus) to which it resembles. Harmelin (1990) distinguished a northern (Atlantic) and a southern form (Atlantic coast of Morocco, Mediterranean). The main differences are a higher number of zooids (9-12) per internode and a mitre-shaped gonozooid in the southern form.

*Crisia denticulata* (Lamarck, 1816)  
(Fig. 8D-F)

*Cellaria denticulata* Lamarck, 1816: 137.

*Crisia denticulata* – Vávra 1975: 523, pl. 1, fig. 1. — Hayward & Ryland 1985: 54, fig. 16. — Poluzzi *et al.* 1988: 64, figs 15b-d. — Poluzzi & Rosso 1988: 99, pl. 1, fig. 1. — Zabala & Maluquer 1988: 165, text-figs 480-482, pl. 29B. — Bobies 1958: 153, pl. 13, figs 5-7. — Marcopoulou-Diacantoni & Wuest 1999: 552, pl. 2, fig. 6.

OCCURRENCE. — Middle Miocene: Austria, Hungary, Czech Republic (Bobies 1958; Vávra 1975). Late Miocene: Sardinia, Sicily (Moissette *et al.* 2002). Pliocene: UK, Netherlands (Lagaaij 1952), Belgium, Crete (Marcopoulou-Diacantoni & Wuest 1999). Pleistocene: Sicily (Rosso 1987). Recent: western and eastern Atlantic (Canada to Gulf of Mexico, Madeira, Azores, Norway to Ghana), Mediterranean. This species lives at depths between 0 and 100 m, but it is associated with deep-water-corals in Norway (Sula Reef: 275-295 m; Mortensen & Fosså 2006) and in the Bay of Biscay (Calvet 1896).

#### REMARKS

*C. denticulata* closely resembles the fossil species *C. hoernesii* Reuss, which however has a greater number of zooids per internode (14-16).

Class GYMNOLAEMATA Allman, 1856  
Order CHEILOSTOMATIDA Busk, 1852  
Suborder FLUSTRINA Smitt, 1868  
Superfamily CALLOPOROIDEA Norman, 1903  
Family QUADRICELLARIIDAE Gordon, 1984  
Genus *Nellia* Busk, 1852

*Nellia tenella* (Lamarck, 1816)  
(Fig. 9E)

*Cellaria tenella* Lamarck, 1816: 135.

*Nellia oculata* – Busk 1852: 18, pl. 64, fig. 6; pl. 65 (bis), fig. 4. — Moissette *et al.* 1993: 98, fig. 5i. — Moissette 1997: 192, pl. 2, figs 5-6.

*Nellia tenella* – Ziko *et al.* 2016: 18, pl. 2, fig. 6.

OCCURRENCE. — Eocene: UK, France, Italy, Germany, Romania (Braga 2008). Oligocene: USA, Malta, Libya (El Safori & Muftah 2007), UAE (Braga & Bahr 2003). Early Miocene: USA (Di Martino *et al.* 2017), Dominican Republic, France, Portugal, Egypt (El Safori & El-Sorogy 1999). Middle Miocene: Jamaica, Hungary (Moissette *et al.* 2006), Austria, France, Portugal, Egypt (Ziko *et al.* 2016). Late Miocene: Morocco (El Hajjaji 1992), Algeria (Moissette 1988), Crete, Turkey, Tunisia (Moissette 1997). Pliocene: Costa Rica, Panama, Dominican Republic, Jamaica (Taylor & Foster 1998; Cheetham *et al.* 1999). Pleistocene: Rhodes (PM, pers. obs.). Recent: eastern and western Atlantic, Indian Ocean, Pacific. This species is widely distributed in tropical to subtropical waters around the world. It lives at depths between 0 and 250 m (Fransen 1986).

#### DESCRIPTION

Colony cellariiform. Internodes straight with quadrangular section and elongate zooids separated by shallow grooves. Opesia oval, occupying the greatest part of the zooidal frontal wall. Gymnocyst and cryptocyst well-developed proximally. Two small avicularia occur on the proximal part of the gymnocyst. Ovicells not observed.

#### REMARKS

*Nellia oculata* Busk is now regarded as a junior synonym of *N. tenella* (Lamarck). However, their very broad ecological, geographical and stratigraphical records may indicate either a "living fossil" species or a "cryptic species complex" (Winston *et al.* 2014; Di Martino *et al.* 2017).

Family CUPULADRIIDAE Lagaaij, 1952  
Genus *Cupuladria* Canu & Bassler, 1919

*Cupuladria* cf. *canariensis* (Busk, 1859)  
(Fig. 9A, B)

*Cupularia canariensis* Busk, 1859: 66, pl. 23, figs 6-9.

*Cupuladria canariensis* – Manzoni 1869, p. 26, pl. 2, fig. 17; 1877: 72, pl. 17, figs 56a-c. — Cipolla 1921: 31, pl. 2, figs 22-24. — Lagaaij 1952: 33, pl. 2, figs 1a-b. — Buge 1957: 139, pl. 9, fig. 5. — Annoscia 1963: 225, pl. 9, fig. 1; pl. 10, fig. 1; pl. 11, figs 1a-b; pl. 12, figs 1a-b. — Cook 1965: 197, text-figs 1a-f, pl. 1, fig. 1; pl. 3, fig. 4. — Prenant & Bobin 1966: 307, figs 101-102. — Baluk & Radwansky 1984: 21, pl. 1, figs 1-4; pl. 8, figs 1-4. — Zabala & Maluquer 1988: 89, fig. 112-

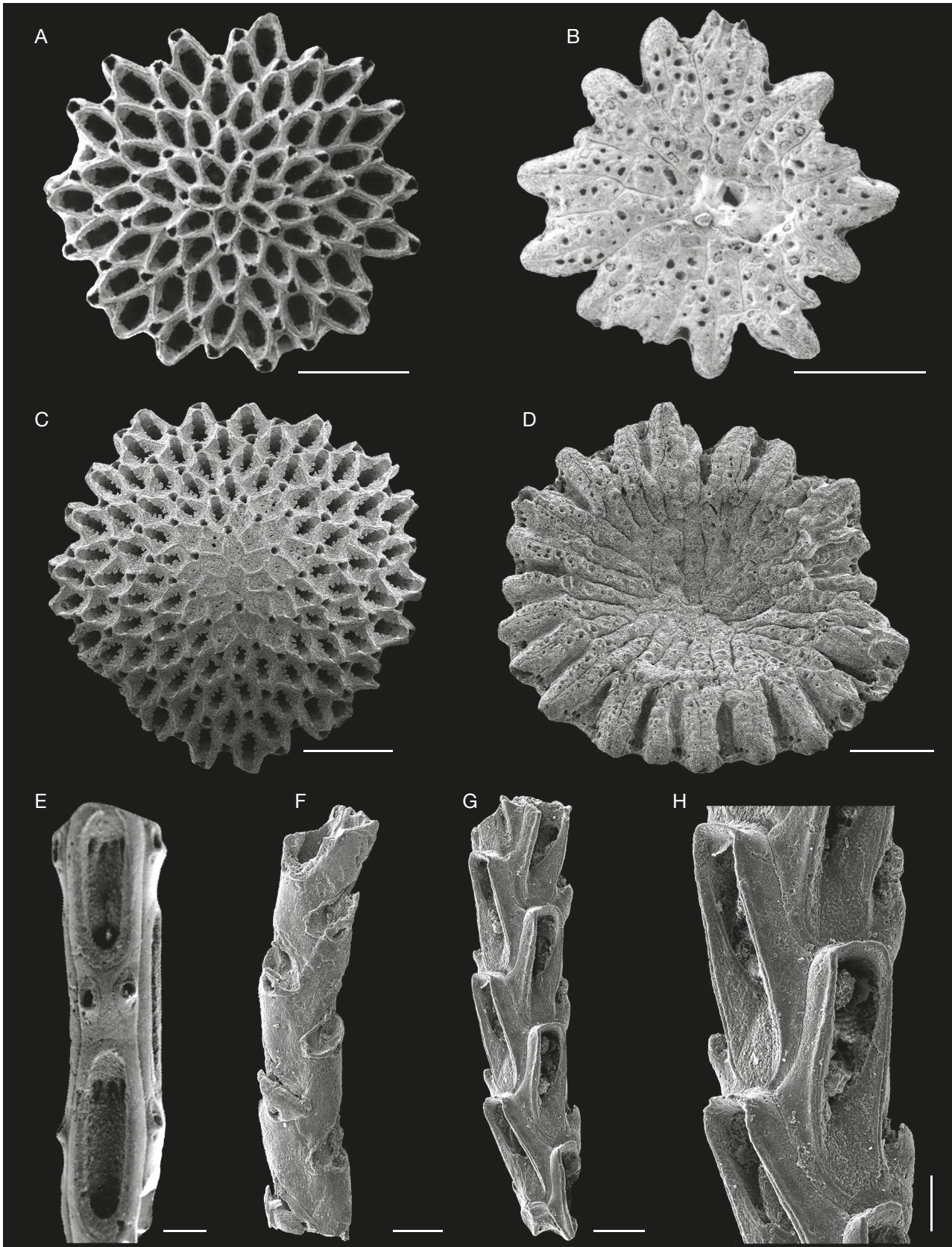


FIG. 9. — **A, B**, *Cupuladria cf. canariensis* (Busk, 1859); **A**, frontal view of a whole colony, KER39: AMPG(IV) 3078a; **B**, dorsal view of a whole colony, KER39: AMPG(IV) 3078b; **C, D**, *Discoporella reussiana* (Manzoni, 1869); **C**, frontal view of a whole colony, KER30: AMPG(IV) 3102; **D**, dorsal view of a whole colony, KER30: AMPG(IV) 3101; **E**, *Nellia tenella* (Lamarck, 1816), detail of an internode showing two zooids in frontal view, KER17: AMPG(IV) 3150a; **F-H**, *Canda rectangulata* Udin, 1964; **F**, dorsal view of an internode fragment, FAN35: AMPG(IV) 3506a; **G**, frontal view of an internode fragment, FAN35: AMPG(IV) 3506b; **H**, Detail of the same fragment, FAN35: AMPG(IV) 3506b. Scale bars: A-D, 1 mm; E, H, 100  $\mu$ m; F-G, 200  $\mu$ m.

114. — Pouyet & Moissette 1992: 33, pl. 3, figs 4-5. — Moissette *et al.* 1993: 92, figs 4g-i. — Haddadi-Hamdane 1996: 65, pl. 5, figs 1, 4. — Marcopoulou-Diacantoni & Wuest 1999: 555, pl. 3, fig. 1.

**OCCURRENCE.** — Middle Miocene: France, Spain, Austria, Poland (Baluk & Radwansky 1984). Late Miocene: Germany, Italy, Crete (Moissette *et al.* 1993). Pliocene: UK, Netherlands, Sicily (Pouyet & Moissette 1992), Algeria (Haddadi-Hamdane 1996), Crete (Marcopoulou-Diacantoni & Wuest 1999). Pleistocene: Sicily (Rosso 1987), Rhodes (Moissette 2012). Recent: eastern Pacific (Ecuador to northern Mexico), western and eastern Atlantic (Brazil, Caribbean, Gabon, Azores, Madeira and Canary islands to southern Portugal), southern Mediterranean (Rosso & Di Martino 2016). This warm-water species lives on sandy, more or less muddy bottoms at depths between 50 and 300 m (Prenant & Bobin 1966). But it has also been found in much shallower (5-50 m) and much deeper waters (down to 860 m in the Sargasso Sea; Lagaaij 1963). Following Cadée (1979, 1981), *C. canariensis* seems however mostly a western Atlantic species. Records with this name must consequently be carefully checked, eliminating possible misidentifications (A. Rosso, personal communication).

**REMARKS**

Due to possible confusion with two other species of the same genus (*C. biporosa* (Canu & Bassler, 1923) and *C. vindobonensis* Baluk & Radwanski, 1984) a systematic revision is needed. Cadée (1979) also created a new subspecies, *Cupuladria canariensis cavernosa*, for Mio-Pliocene European specimens with intermediate characteristics between *C. biporosa* and *C. canariensis* (Cadée 1979, 1981).

Genus *Discoporella* d'Orbigny, 1852

*Discoporella reussiana* (Manzoni, 1869)  
(Fig. 9C, D)

*Cupularia reussiana* Manzoni, 1869: 27, pl. 2, fig. 19.

*Cupuladria reussiana* – Annoscia 1963: 226, pl. 9, fig. 2; pl. 10, fig. 2; pl. 13, fig. 1; pl. 14, fig. 1a-b. — Prenant & Bobin 1966: 316, fig. 104. — Reguant 1969: 38, figs 1-3.

*Reussirella reussiana* – Baluk & Radwansky 1984: 27, pl. 11, figs 1-2.

*Discoporella reussiana* – Cook 1965: 219, text-fig. 2f; pl. 3, fig. 1. — Poluzzi 1975: 52, pl. 18, figs 1a-m, 2, 3. — Pouyet & Moissette 1992: 44, pl. 5, fig. 4-6. — Moissette *et al.* 1993: 96, figs 5c-d. — Haddadi-Hamdane 1996: 66, pl. 5, figs 2, 3, 8.

**OCCURRENCE.** — Middle Miocene: Austria (Baluk & Radwansky 1984). Late Miocene: Italy, Crete (Moissette *et al.* 1993). Pliocene: Algeria (Haddadi-Hamdane 1996), Sicily (Pouyet & Moissette 1992). Pleistocene: Spain (Reguant 1969), Sicily, Umbria, central Italy (Bizzarri *et al.* 2015). Recent: the present-day occurrence of this species is doubtful (Cook 1965; Prenant & Bobin 1966). The nearest living species, *R. doma*, lives in tropical to subtropical waters of the Atlantic and Mediterranean, on sandy to muddy bottoms at depths of 10 to 370 m (Cook 1965; Prenant & Bobin 1966).

**DESCRIPTION**

Lunulitiform colony. Frontal surface with alternating radial series of rhomboidal zooids, each bearing a distal vibraculum. The six cryptocystal denticles do not fuse in the middle of the opesia. The apical zone of the colony shows zooids covered

by a calcified lamina. Basal surface depressed in the centre, displaying marked radial grooves and strong tubercles.

**REMARKS**

*D. reussiana* resembles very much *Reussirella doma* (d'Orbigny, 1851) to which it has been confused (Prenant & Bobin 1966). According to Cook (1965), the unfused cryptocystal denticles are especially characteristic of the western African *Reussirella owenii* (Gray, 1828).

Superfamily BUGULOIDEA Gray, 1848

Family CANDIDAE d'Orbigny, 1851

Genus *Canda* Lamouroux, 1816

*Canda rectangulata* Udin, 1964  
(Fig. 9F-H)

*Canda rectangulata* Udin, 1964: 393, pl. 1, fig. 3. — Vávra 1979: 599, pl. 1, figs a, d, g; 1980: 58, pl. 2, figs 5-6. — Schmid 1989: 25, pl. 6, figs 1-5, 8. — Moissette 1997: 193, pl. 2, figs 11-12.

**OCCURRENCE.** — Middle Miocene: Austria (Schmid 1989), Hungary (Moissette *et al.* 2007). Late Miocene: Tunisia (Moissette 1997).

**DESCRIPTION**

Colony vinculariiform. Frontal showing rectangular zooids organized in two alternating series with prominent distal and lateral edges. Cryptocyst concave, proximally well-developed and thus resulting in an elongate V-shaped opesia. Dorsal displaying enlarged triangular vibracularia with long setal grooves and large radicular pore. Frontal avicularia and ovicells not observed.

**REMARKS**

The closeness with the Recent *Canda retiformis* Pourtalès has been emphasized since the creation of *C. rectangulata*. A revision of both fossil and Recent material of the genus *Canda* is desirable.

Genus *Scrupocellaria* van Beneden, 1845

*Scrupocellaria* cf. *elliptica* (Reuss, 1847)  
(Fig. 10A-C)

*Bactridium ellipticum* Reuss, 1847: 56, pl. 9, fig. 7-8.

*Scrupocellaria elliptica* – Reuss 1874: 148, pl. 11, figs 1-9. — Moissette 1988: 106, pl. 16, figs 5, 8. — Schmid 1989: 23, pl. 5, figs 1-7. — Zágoršek 2010a: 46, pl. 52, figs 1-6.

*Scrupocellaria* sp. – Berning 2006: 32, figs 27-29.

**OCCURRENCE.** — Middle Miocene: Austria (Schmid 1989), Czech Republic (Zágoršek 2010a). Late Miocene: Algeria (Moissette 1988), Spain (Berning 2006).

**DESCRIPTION**

Cellariiform colony. Each segment consists of two alternating series of about five zooids. Gymnocyst smooth. Oval opesia

occupying approximately one half of the zooecial length. Two large septula are discernible in the distal part of the opesia margin. Four spine bases occur on the outer distal part of the opesia and three on the inner angle, accompanied by one slightly larger scutal spine (scutum rarely preserved, covering almost half the opesia). No frontal avicularium. Lateral avicularia triangular and well developed. Dorsal surface showing small triangular vibracularia and radicular pores. No observed ovicells.

## REMARKS

As noted by Schmid (1989) and Berning (2006), many fossil *Scrupocellaria* specimens have been mistakenly assigned to *S. elliptica*. Partly due to a frequent poor state of preservation this has been accompanied by insufficient description and illustration, notably concerning the presence and number of spine bases. Spines are not alluded to in Reuss (1847), but mentioned and partly illustrated in Reuss (1874). Although not reported, spines are visible on some specimens of the late Miocene of Algeria (Moissette 1988: pl. 16, fig. 8) on. Scutum and spines (at least 5) are clearly observable on the middle Miocene material (Schmid 1989: pl. 5, fig. 2 and fig. 4, respectively). Six spines (+scutum) are reported and illustrated by Berning (2006). Zágorský (2010b) describes “spines often arranged in 4-5 pairs”. A revision of Neogene Mediterranean/Paratethys *Scrupocellaria* is thus strongly necessary, notably to confirm the attribution of specimens with seven oral spines to *S. elliptica*. A new approach to the taxonomy of the polyphyletic genus *Scrupocellaria* has been presented by Vieira *et al.* (2014).

*Scrupocellaria scrupea* Busk, 1852

(Fig. 10D-E)

*Scrupocellaria scrupea* Busk, 1852: 83, pl. 9, figs 11-12. — Hincks 1880: 50, pl. 7, figs 11-14. — Prenant & Bobin 1966: 432, text-fig. 143. — Ryland & Hayward 1977: 138, text-fig. 66. — Zabala & Maluquer 1988: 99, text-figs 167-168. — Moissette & Spjeldnaes 1995: 788, pl. 3, figs 2-4. — Hayward & McKinney 2002: 27, fig. 11A-E.

OCCURRENCE. — Pliocene: Calabria (Neviani 1900). Pleistocene: Calabria (Di Geronimo *et al.* 1997), Rhodes (Moissette & Spjeldnaes 1995). Recent: eastern Atlantic and Mediterranean from the surface to 150 m (and down to 500 m in the Gulf of Gascony: Jullien & Calvet 1903).

## DESCRIPTION

Cellariiform colony. Internodes comprising two alternating series of zooids. Gymnocyst smooth. Oval opesia occupying slightly more than half of the zooecial length with two large septula in the distal part of the opesia margin. Five spine bases on the distal rim (three on the outer edge and two on the inner part), accompanied by one slightly larger scutal basis on the internal edge. The scutum itself, rarely preserved, is rather large and its proximal lobe is more developed. Prominent triangular lateral avicularia. When present, the frontal avicularia are small and always located near the internal distal part of the ovicells, which are rounded, smooth and exhibit a small proximal fenestra. Dorsal surface with small triangular vibracularia.

## REMARKS

The number of spine bases is relatively constant, but one of them, on the distal rim, is occasionally lacking. Only two spines are observable on ovicellate zooids.

## Superfamily CELLARIOIDEA Lamouroux, 1821

Family CELLARIIDAE Hincks, 1880

Genus *Cellaria* Ellis & Solander, 1786*Cellaria salicornioides* Lamouroux, 1816

(Fig. 10F-H)

*Cellaria salicornioides* Lamouroux, 1816: 127. — Audouin 1826: 236; Savigny 1817: pl. 6, fig. 7. — Prenant & Bobin 1966: 382, text-fig. 124. — Ryland & Hayward 1977: 124, text-figs 56A, 59. — Poluzzi & Padovani 1984: 109, fig. 5d. — Zabala 1986: 307, text-fig. 84:3a-e; pl. 3, figs E-F. — Moissette 1988: 104, pl. 17, figs 1-2. — Zabala & Maluquer 1988: 94, text-figs 137-140; pl. 2, fig. H. — Schmid 1989: 18, pl. 4, figs 3-6. — El Hajjaji 1992: 129, pl. 6, fig. 7. — Moissette & Spjeldnaes 1995: 788, pl. 3, fig. 1. — Haddadi-Hamdane 1996: 71, pl. 6, figs 12-13. — López de la Cuadra & García-Gómez 1996: 158, figs 1C, 3A-F, 4.

OCCURRENCE. — Early Miocene: France (Pouyet 1991). Middle Miocene: Austria (Schmid 1989), Hungary (Moissette *et al.* 2006), Czech Republic, Poland (Pouyet 1997). Late Miocene: Morocco (El Hajjaji 1992), Algeria (Moissette 1988). Pliocene: Algeria (Haddadi-Hamdane 1996), Crete. Pleistocene: Sicily (Poluzzi & Padovani 1984), Rhodes (Moissette & Spjeldnaes 1995). Recent: eastern Atlantic (Morocco, Madeira, up to the Shetland Islands), Mediterranean, Red Sea. The species has been recorded from the Atlantic at depths of 0-360 m (and even down to 636 m in Morocco). In the Mediterranean, it occurs from the shallow infralittoral down to 280 m.

## REMARKS

A number of specimens, especially those from the Phanerozoic section, resemble *C. salicornioides* var. *normani*, a variety created by Hastings (1946) and considered as a distinct species, *C. normani*, by Prenant & Bobin (1966). However, López de la Cuadra & García-Gómez (1996) considered that the slight morphological differences (more slender internodes and larger avicularia in *C. normani*) do not justify the erection of a distinct taxon.

## Suborder ASCOPHORA Levensen, 1909

Infraorder HIPPOTHOOMORPHA Gordon, 1989

## Superfamily HIPPOTHOOIDEA Busk, 1859

Family PASYTHEIDAE Davis, 1934

Genus *Gemellipora* Smitt, 1873*Gemellipora eburnea* Smitt, 1873

(Fig. 10I)

*Gemellipora eburnea* Smitt, 1873: 35, pl. 7, figs 152-156. — Harmer 1957: 994, pl. 69, figs 28-29. — Moissette 1988: 190, pl. 30, figs 6, 9, 12.

*Gemellaria punctata* – Seguenza 1880: 127, pl. 12, figs 14-14a. — Neviani 1900: 148, pl. 16, figs 89.

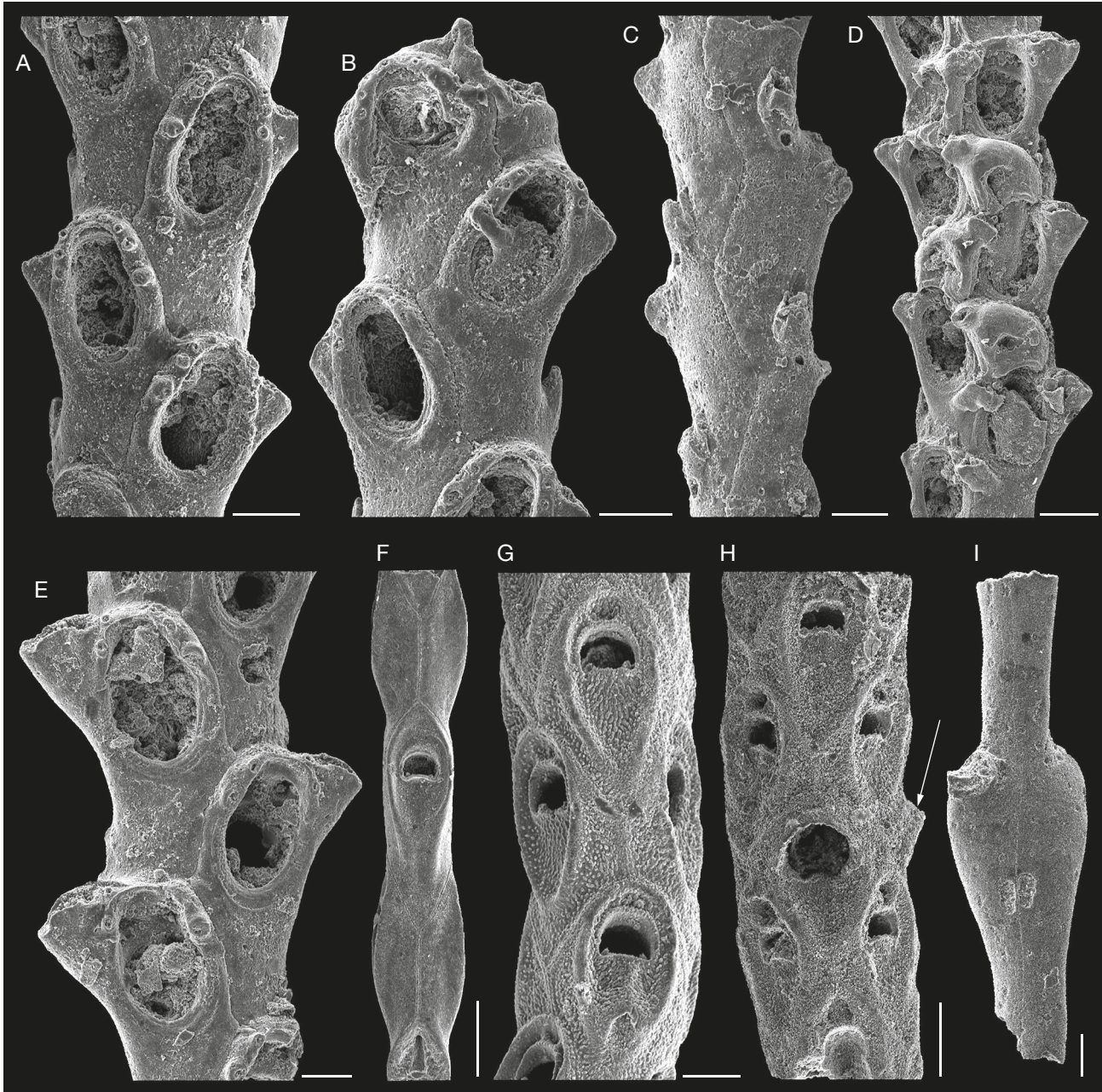


FIG. 10. — **A-C**, *Scrupocellaria* cf. *elliptica* (Reuss, 1847); **A**, view of some zoids showing opesia with 4 spine bases on the outer distal part and 3 spine bases + 1 scutal spine on the inner distal rim, FAN36: AMPG(IV) 3587; **B**, zoids with 7 spine bases and the scutum, FAN35: AMPG(IV) 3586a; **C**, dorsal surface of a colony fragment with small vibracularia and radicular pores, FAN35: AMPG(IV) 3586b; **D, E**, *Scrupocellaria scrupea* Busk, 1852; **D**, ovicellate colony fragment, FAN35: AMPG(IV) 3590a; **E**, detail frontal view showing opesia with five spine bases, FAN35: AMPG(IV) 3590b; **F-H**, *Cellaria salicornioides* Lamouroux, 1816; **F**, part of a slender internode, FAN18: AMPG(IV) 3513a; **G**, detail view showing denticles and endotoichal ovicells, POTB13: AMPG(IV) 2821a; **H**, avicularia in frontal and lateral view (arrow), POTB13: AMPG(IV) 2821b; **I**, *Gemellipora eburnea* Smitt, 1873, broken internode showing two zoids with two oval scars separated by a thin interzoidal groove, CAP032: AMPG(IV) 3426. Scale bars: A-E, G, I, 100 µm; F, H, 200 µm.

*Pasythea eburnea* – Busk 1884: 5, pl. 34, fig. 1a-f. — Canu & Bassler 1928: 151, pl. 8, figs 11-12.

**OCCURRENCE.** — Early Miocene: Indonesia (Di Martino & Taylor 2014). Middle Miocene: Hungary (Moissette *et al.* 2006). Late Miocene: Dominican Republic (Cheetham *et al.* 1999), Algeria (Moissette 1988), Calabria. Pliocene: Sicily (Rosso 2002). Pleistocene: Calabria, Sicily (Rosso & Di Geronimo 1998; Rosso 2005), Rhodes (Moissette & Spjeldnaes 1995), Karpathos (Moissette *et al.* 2017). Holocene: southern Italy (Di Geronimo *et al.* 2001). Recent: western and eastern Atlantic (Brazil, Caribbean, Azores, Madeira, Bay of

Biscay, Gulf of Cadiz), Indian Ocean (Indonesia), Pacific (Hawaii, New Zealand). This is a deep-water species found in the Atlantic at depths between 60 m and 3300 m (Harmer 1957; Harmelin 1977).

**DESCRIPTION**

Cellariiform colony. Internodes made of one to four pairs of zoids. In each pair, the zoids are separated by a thin groove, placed back to back, slightly twisted from one another, and oriented at about 90 degrees of the previous/

following pair. Zooids elongate, displaying a smooth frontal surface with scarce inconspicuous pores. A few zooids bear in their central part a small oval scar (separated by the thin groove dividing two zooids) corresponding to the start of a lateral branch. Apertures almost circular with two very small indentations on the proximal corners. Neither avicularia nor ovicells.

## REMARKS

Smitt (1873) describes an encrusting base (Smitt 1873: pl. 7, fig. 152) from which the erect, typical form arises. Another creeping colony (Smitt 1873: pl. 9, fig. 178) is erroneously attributed by the same author to *G. eburnea*. The confusion was evidenced by Canu & Bassler (1928).

Infraorder UMBONULOMORPHA Gordon, 1989  
Superfamily LEPRALIELLOIDEA Vigneaux, 1949  
Family BRYOCRYPTELLIDAE Vigneaux, 1949  
Genus *Bryocryptella* Cossman, 1906

*Bryocryptella torquata* (Jullien, 1903)  
(Fig. 11A-C)

*Cryptella torquata* Jullien in Jullien & Calvet, 1903: 77, pl. 7, fig. 5a-c.

*Porella torquata* – Norman 1909: 300, pl. 39, figs 5-8. — Barroso 1912: 33, figs 6, 6a-e.

*Bryocryptella torquata* – Álvarez 1991: 93, fig. 5; pl. 10, figs A-E.

OCCURRENCE. — Recent: eastern Atlantic (Gulf of Gascony, Madeira). Deep-water species recorded at depths from 80 m to 300 m (Álvarez 1991).

## DESCRIPTION

Colony vinculariiform. Narrow subcylindrical branches formed by 3-4 alternating longitudinal rows of zooids opening on the same frontal side. Zooids hexagonal separated by deep furrows. Frontal ventricose with about 20 large pores. Aperture subcircular; a small avicularium is sometimes present on its proximal edge. Peristome more or less developed, devoid of pores. Dorsal slightly convex showing marked grooves corresponding to zooecial limits and a few pores. Ovicells not observed.

## REMARKS

This species was erroneously identified as *Characodoma* sp. in Moissette *et al.* (2018).

Family TESSARADOMIDAE Jullien & Calvet, 1903  
Genus *Tessaradoma* Norman, 1869

*Tessaradoma boreale* (Busk, 1860)  
(Fig. 11D)

*Onchopora borealis* Busk, 1860: 213, pl. 28, figs 6-7.

*Porina borealis* – Hincks 1880: 229, pl. 31, figs 4-6. — Neviani 1891: 120, pl. 4, figs 4-5.

*Tessaradoma boreale* – Gautier 1962: 222. — Hayward & Ryland 1979: 242, text-fig. 104. — Moissette 1988: 123, pl. 20, fig. 5. — Zabala & Maluquer 1988: 142, text-fig. 343. — El Hajjaji 1992: 225, pl. 13, fig. 2. — Pouyet & Moissette 1992: 53, pl. 7, fig. 3. — Moissette & Spjeldnaes 1995: 790, pl. 3, fig. 5.

OCCURRENCE. — Middle Miocene: France. Late Miocene: Morocco (El Hajjaji 1992), Algeria (Moissette 1988), Calabria. Pliocene: northern Italy, Sicily (Pouyet & Moissette 1992). Pleistocene: Sicily, Calabria (Rosso 2005), Rhodes (Moissette & Spjeldnaes 1995), Karpathos (Moissette *et al.* 2017). Recent: Atlantic (western, but mostly eastern), Arctic, Mediterranean. *T. boreale* is predominantly a deep-water (Cheetham 1972), cryophilic (max. 13° C) species (60-3500 m in the Atlantic, 50-1300 m in the Mediterranean).

## DESCRIPTION

Vinculariiform colony. Slender cylindrical branches. Oval, elongate zooids arranged in alternating series. Frontal smooth and finely striated, with a row of marginal pores. A spiramen is situated proximally to the semicircular aperture, which bears a short tubular peristome. Avicularia (1-3) and ovicell not observed.

## REMARKS

*T. gracile* (Sars) is generally considered as a synonym of *T. boreale*.

Family ASCOSIIDAE Jullien, 1883  
Genus *Kionidella* Koschinsky, 1885

*Kionidella excelsa* Koschinsky, 1885  
(Fig. 11E-F)

*Kionidella excelsa* Koschinsky, 1885: 68, pl. 7, figs 5-12. — Malceki 1963: 133, fig. 58, pl. 15, fig. 1. — Braga 1975, p. 147, pl. 3, fig. 67. — Moissette 1988: 192, pl. 31, figs 4-6. — Zágóršek 2001: 554, pl. 19, fig. 4. — Zágóršek 2003: 176, pl. 28, fig. 6.

*Fedora excelsa* – Waters 1891: 29, pl. 4, fig. 6.

OCCURRENCE. — Eocene: Germany, Austria, Italy, Slovakia, Hungary, Romania, Poland (Zágóršek 2003). Late Miocene: Algeria (Moissette 1988).

## DESCRIPTION

Small conical, hollow and rather elongated coneschareliniform colonies. Hexagonal zooids arranged in alternating radial series. Smooth convex frontal.

Pear-shaped aperture with a large anter separated by two strong cardelles from a smaller poster. One or two well-developed oval avicularia are generally present on the lateral sides of the zooid. Ovicell not observed.

## REMARKS

As noted by several authors (e.g., Zágóršek 2003), the avicularia are more or less developed and may either occur in pairs, or alone, or lack completely. The ovicells have rarely been observed.

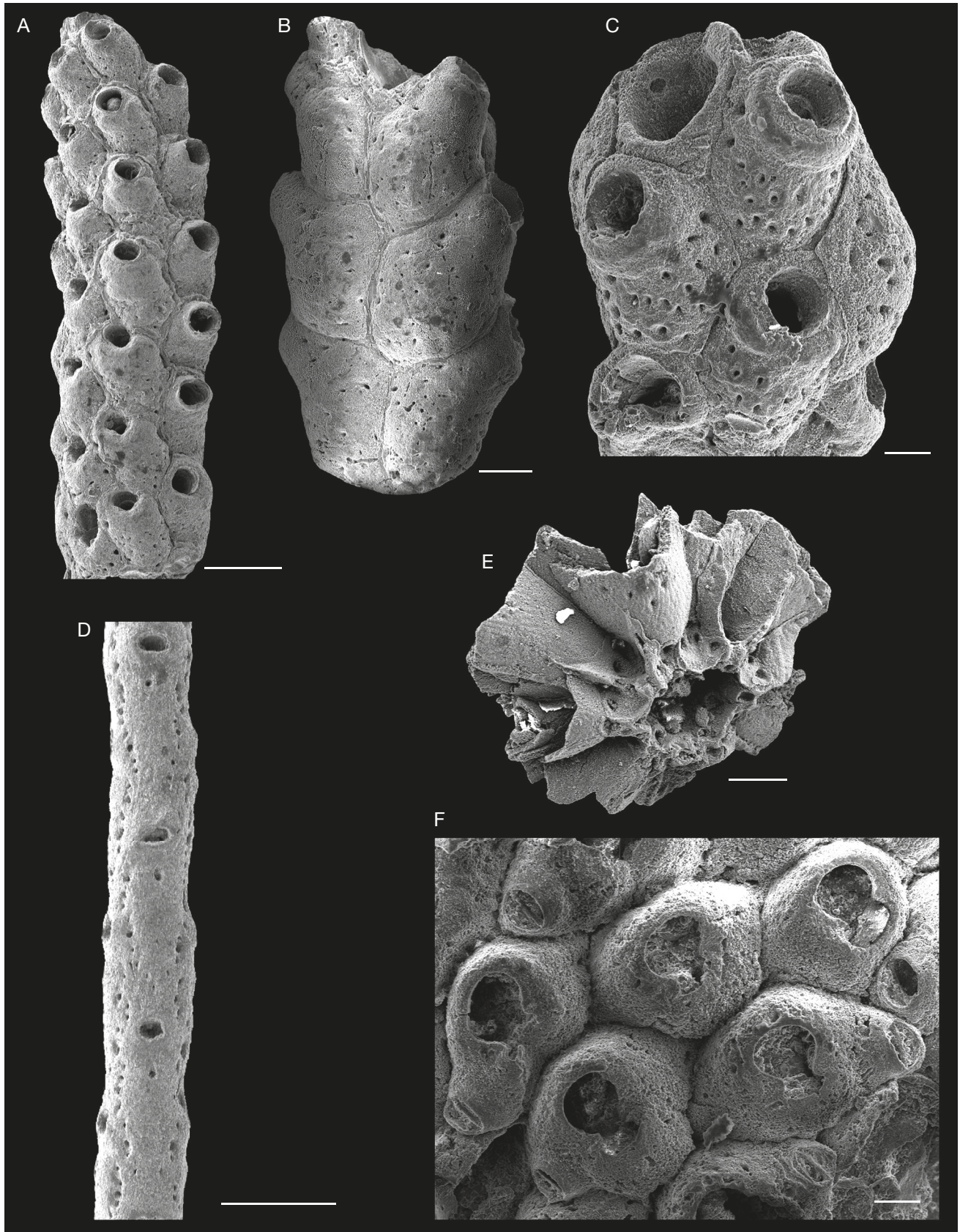


FIG. 11. — **A-C**, *Bryocryptella torquata* (Jullien, 1903); **A**, colony fragment, frontal view, POTB13: AMPG(IV) 2815a; **B**, colony fragment, dorsal view, POTB13: AMPG(IV) 2815b; **C**, detail view of zooids, FAN31: AMPG(IV) 3500a; **D**, *Tessaradoma boreale* (Busk, 1860), colony fragment, FAN28: AMPG(IV) 3613. **E-F**, *Kionidella excelsa* Koschinsky, 1885; **E**, colony fragment, basal view, FAN7: AMPG(IV)3570a; **F**, frontal view of a few zooids, FAN16: AMPG(IV) 3572. Scale bars: A, 500  $\mu$ m; B, E, 200  $\mu$ m; C, F, 100  $\mu$ m; D, 1 mm.



Superfamily CONESCHARELLINOIDEA Levinsen, 1909  
 Family BATOPORIDAE Neviani, 1900  
 Genus *Batopora* Reuss, 1867

*Batopora rosula* (Reuss, 1847)  
 (Fig. 12A-G)

*Cellepora rosula* Reuss, 1847: 78, pl. 9, fig. 17; 1867: pl. 1, fig. 7a-c; pl. 2, fig. 1a-c.

*Batopora rosula* – Manzoni 1877: 54, pl. 2, fig. 6. — Malecki 1963: 135, pl. 15, fig. 4. — Braga 1975: 147, pl. 3, figs 10-11. — Cook & Lagaij 1976: 351, pl. 3, figs 2-3; pl. 4, figs 1-2. — Moissette *et al.* 1993: 113, figs 7g-i. — Haddadi-Hamdane 1996: 121, pl. 2, fig. 4. — Moissette 1996: 193, figs 1A-C. — Pizzaferrri & Braga 2000: 61, fig. 2. — Zágóršek 2010b: 168, pl. 83, fig. 4.

*Lacrimula* sp. – Moissette 1988: 193, pl. 31, figs 7-9.

**OCCURRENCE.** — Eocene: Italy, Romania (Malecki 1963; Braga 1975). Early Miocene: Spain, Corsica, Italy, Malta (Moissette 1996). Middle Miocene: Austria, Hungary (Moissette *et al.* 2006), Czech Republic (Zágóršek 2010b), northern Italy, Calabria, Malta (Moissette 1996). Late Miocene: Algeria (Moissette 1988), Sardinia, Sicily, Calabria (Pizzaferrri & Braga 2000), Malta (PM, pers. obs.), Crete (Moissette *et al.* 1993). Pliocene: Spain, Algeria (Haddadi-Hamdane 1996), northern Italy, Sicily, Crete (PM, pers. obs.), Karpathos (PM, pers. obs.). Pleistocene: Rhodes (PM, pers. obs.). This fossil species has exclusively been recorded from the Mediterranean-Paratethys realm (Moissette 1996). Three present-day *Batopora* species are known from the Indo-Pacific at depths between 285 and 880 m (Cook & Lagaij 1976; Hayward & Cook 1979).

**DESCRIPTION**

Small conical conescharelliniform colonies with a flattened base an apical tube comprised of kenozooids and terminated by a small pit. Hexagonal zooids arranged in concentric alternating series. Frontal convex with fairly large pores. Large circular aperture located in the distal part of each zooid. No avicularia. Rare small broken hyperstomial ovicells are visible (Fig. 12A).

**REMARKS**

A few juvenile colonies are present in a fair number of samples. This was also observed by several authors (Cook & Lagaij 1976; Pizzaferrri & Braga 2000).

Family ORBITULIPORIDAE Canu & Bassler, 1923  
 Genus *Orbitulipora* Stolickza, 1862

*Orbitulipora excentrica* Seguenza, 1880  
 (Fig. 12H-I)

*Orbitulipora excentrica* Seguenza, 1880: 130, pl. 12, figs 22-22a. — Neviani 1900: 188, pl. 17, figs 15-16. — Waters 1919: 90, text-fig. 2a-c. — Rosso & Sanfilippo 1991: 202, pl. 1, figs 1-5; pl. 2, figs 1-8. — Moissette *et al.* 1993: 113, figs a-c.

**OCCURRENCE.** — Late Eocene: Italy (Waters 1919). Early Miocene: Sardinia (Rosso & Sanfilippo 1991). Late Miocene: Calabria (Rosso & Sanfilippo 1991), Crete (Moissette *et al.* 1993). *Orbitulipora* and the orbituliporiform morphotype (fossil and Recent) are considered as deep-water markers and living representatives as typical of muddy bottoms (Cook 1981; Rosso & Sanfilippo 1991).

**DESCRIPTION**

Discooidal bilaminar morphology (orbituliporiform). A short kenozooidal tube occurs at the apical part of each colony. Subcircular to subhexagonal zooids arranged in irregular concentric series and progressively increasing in size from the apex to the base. Frontal convex with relatively large pores. Very large circular aperture located in the centre of each zooid. No avicularia. A few ovicells (or their scars) are visible at the growing edge of some colonies. They are hyperstomial, spherical, as large as a zooid and perforated by pores similar to those of the zooecial frontal.

**DISCUSSION**

**TAPHONOMY**

Most bryozoans (and other skeletal organisms) are well preserved, except a number of yellowish, abraded fragments of littoral species (e.g., *Adeonella polystomella*, *Margaretta cereoides*, *Reteporella* sp., *Smittina cervicornis*, and *Steginoporella montenati*) indicating transport from shallow to deep waters. Examples of such transported material are found in three sections but only in a few beds (among which Potamida B13; Kapariana CAP18; Keramoutsi KER22, KER28), where numerous shallow-water bryozoan remains are found together with fewer deeper water elements.

**PALAEOENVIRONMENTAL SIGNIFICANCE  
 OF THE LATE MIOCENE BRYOZOANS OF CRETE**

*Depth*

A general trend is observed in all studied sections (Figs 2-5). Starting in the late Tortonian, a relatively deep basal assemblage (deep circalittoral) is later replaced by an upper bathyal one. A shallowing-upward sequence follows, with deeper circalittoral conditions succeeded by shallow circalittoral to infralittoral ones. A slight dissimilarity is observed in the Keramoutsi section with very shallow settings (infralittoral-lagoonal) at the base, overlain by shallow circalittoral environments and later the same sequence as in the other three sections. This pattern (Fig. 6), within different sub-basins, is interpreted as resulting mostly from the stepped closure of the Betic-Rifian corridors. It is validated by the analysis of the associated benthic faunas of foraminifera, bivalves, and ostracods (Moissette *et al.* 2018). However, slight differences are noticed between the two results with the recognition in the present paper of shallower environments (deep circalittoral) at the base of all sections.

Correlations between the provided planktonic foraminiferal biostratigraphic zonation and the palaeoenvironmental scheme based on bryozoan (and other) faunas are difficult. The position of the bathymetric events is markedly diachronic, probably because of differential vertical motions in separate sub-basins (Fig. 13). The upper bathyal (deepest) assemblage is however located in the latest Tortonian in three sections (Potamida, Kapariana, and Faneromeni) and in the earliest Messinian in the Keramoutsi section.

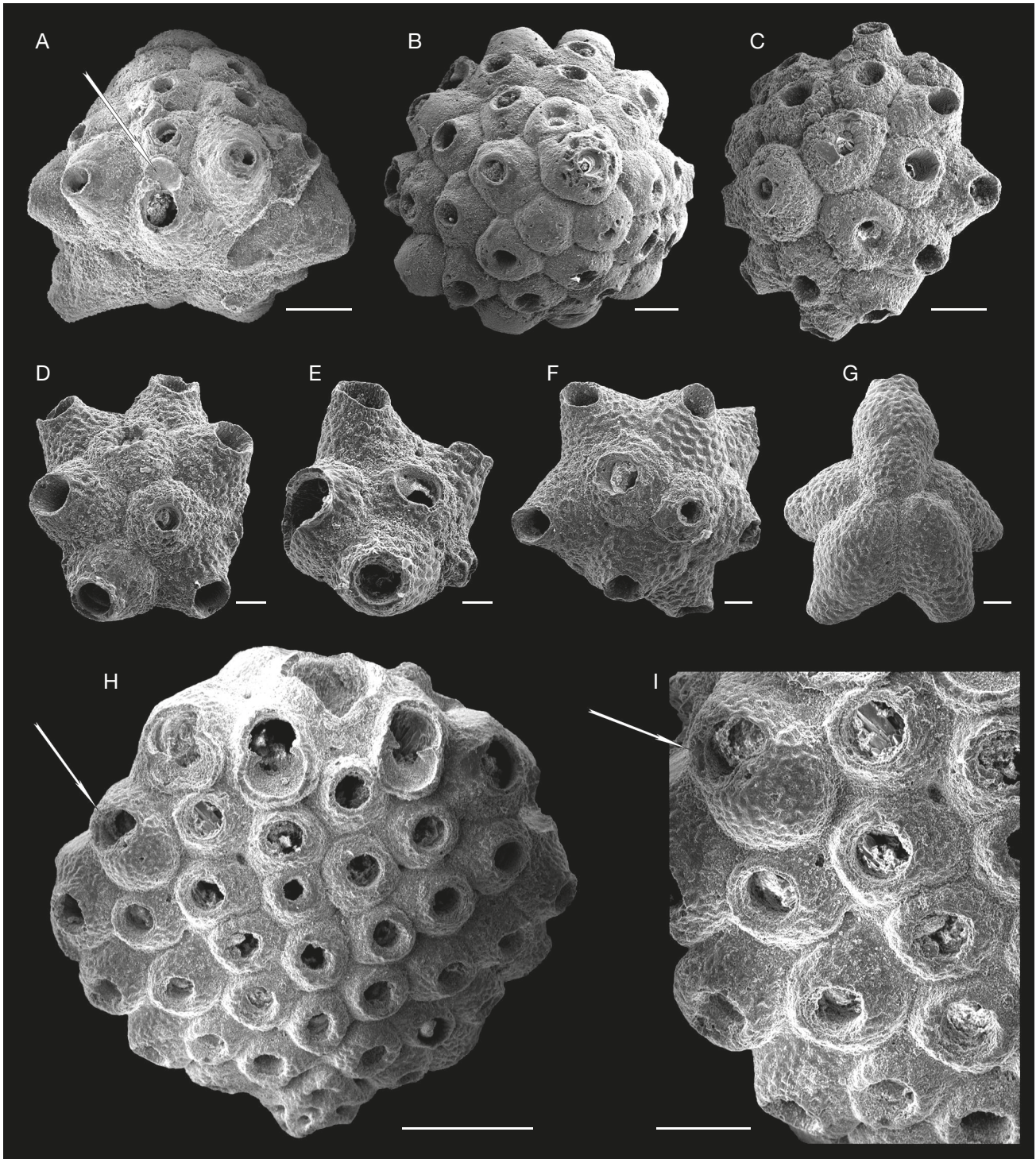


FIG. 12. — **A-G**, *Batopora rosula* (Reuss, 1847); **A**, colony, basal-lateral view (arrow indicates the scar of an ovicellate zooid), FAN7: AMPG(IV) 3475a; **B**, colony, apical view, FAN7: AMPG(IV) 3475b; **C**, colony, lateral-apical view, FAN7: AMPG(IV) 3475c; **D-G**, juvenile forms (**G**, basal view), FAN18: AMPG(IV)a-d; **H-I**, *Orbitulipora excentrica* Seguenza, 1880; **H**, whole colony, FAN22: AMPG(IV) 3580a; **I**, detail view of the left part of the same colony (arrows indicate ovicellate zooids), FAN22: AMPG(IV) 3580a. Scale bars: H, 500 µm; A-C, I, 200 µm; D-G, 100 µm.

### Temperature

A number of fossil and extant shallow-water, eurybathic species and/or genera, and even some deep-water taxa, are confined to the tropical-subtropical climatic zone: *Batopora*, *Biflustra savartii*, *Canda*, *Cupuladria canariensis*,

*Celleporina canariensis*, *Discoporella*, *Gemellipora eburnea*, *Nellia tenella*, *Onyhocella angulosa*, and *Steginoporella*. This climate-related observations fit well with the known Late Miocene climate configuration (Tzanova *et al.* 2015; Kontakiotis *et al.* 2019; Vasiliev *et al.* 2019), indicating

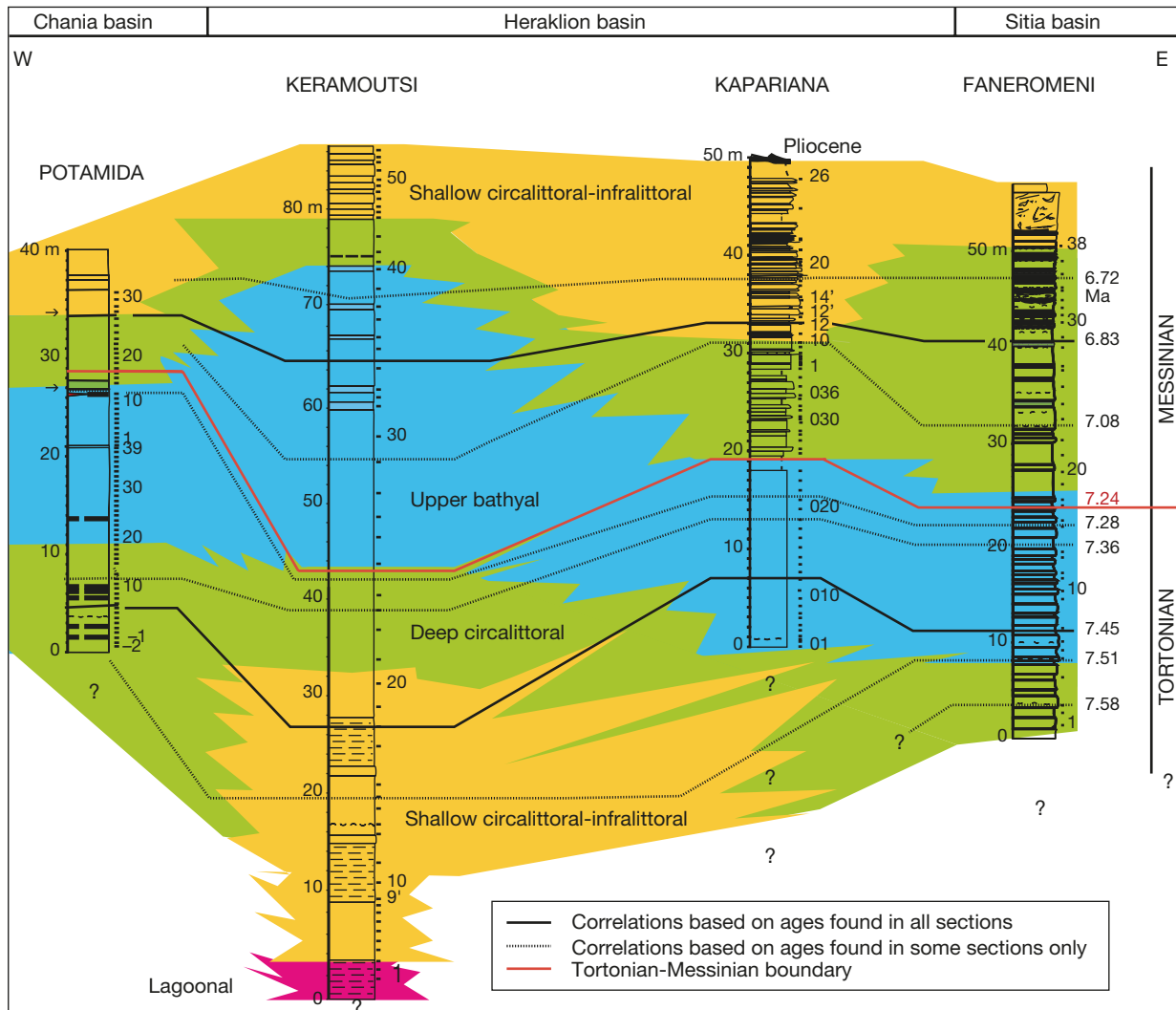


FIG. 13. — Bathymetric reconstruction and correlations between sections.

that the sea surface temperatures (SST) over this interval in the eastern Mediterranean was as warm as “warm pool” regions of the modern ocean. Particularly for the Crete Island, average Sr/Ca foraminiferal derived temperatures of 25.2 and 20.2°C for the latest Tortonian and earliest Messinian, respectively, have been documented (Kontakiotis *et al.* 2019). Such SST estimates are well in line with published seasonal (*c.* 19°C in winter) and annual SST (*c.* 23°C) estimates based on annual skeletal growth rates in *Porites* from the study area (Brachert *et al.* 2006; Mertz-Kraus *et al.* 2009a,b). Overall, SST values, although approaching or even exceeding the present-day average surface temperatures of *c.* 21°C in Crete (Locarnini *et al.* 2018), are significantly cooler than the tropical-like UK’37 temperatures (*c.* 28–30°C) for the oldest time period (12.9–8.0 Ma; Tzanova *et al.* 2015) in the Mediterranean Sea. This supports the transitional character from the “warmhouse” (Middle Miocene) towards the “glacial-interglacial” (Pliocene-Pleistocene) climate mode and cryospheric circulation system (Böhme *et al.* 2008).

#### Substrates

Soft-bottom habitats (clayey, more or less calcareous and sandy/silty muds) predominate throughout the sedimentary successions. Hard bottoms (bivalve shells, gravels) are scarce. Although rare on deep-water fine-grained sediments, skeletal remains are often used as “benthic islands” for communities normally living on hard substrates.

#### Salinity

Bryozoans are essentially stenohaline organisms, restricted to salinities between about 32 and 40 PSU. As noted by Harmelin & d’Hondt (1993), the high salinity of the Recent Mediterranean deep water is an exclusion factor for many Atlantic species. It is especially true for the eastern Mediterranean where salinities reach and even exceed 39 PSU. An example is given by the lunulitiform *Cupuladria canariensis*, which is absent from this present-day region (Lagaaij 1963). The current distributional data were further reinforced by the salinity variability (34–44 PSU; Vasiliev *et al.* 2019; Kontakiotis *et al.* 2019) recorded during this time interval in the eastern Mediterranean Sea (Kalamaki

section, Zakynthos Island – Vasiliev *et al.* 2019; Faneromeni section – Kontakiotis *et al.* 2019). According to the above sea surface salinity reconstructions, there were periods within the study time span when salinity values were approaching or even exceeding 40 PSU. Moreover, size measurements on the planktonic foraminifera *Orbulina universa* at Moni Gorgolaini section (central Crete) have shown that local seawater must have been enriched by evaporation during that time (Brachert *et al.* 2015). Maximum evaporation (high salinity) intervals were strongly associated with rare occurrences of smaller and heavier planktonic shells due to the increasing density of sea water (Zarkogiannis *et al.* 2019). For instance, evidence of small size *O. universa* in Moni Gorgolaini section (Brachert *et al.* 2015) and low shell mass of *Globigerinoides obliquus* in Faneromeni section (Kontakiotis *et al.* 2019) have been interpreted as primarily produced by high water density (28.5 g/l), with a salinity of 40.5 PSU at 22°C. These high salinity and subsequent water density values inferred from both faunal and geochemical data correspond to a major restriction for most of the biota, and possibly represent a sound explanation for their generally low absolute numbers. For instance, declining benthic and planktonic foraminiferal diversity and mass occurrences of phyto- and zoo-plankton adapted to high salinity in the Mediterranean all evidence fluctuating and increasing salinity stress prior to the MSC (Santarelli *et al.* 1998; Kouwenhoven *et al.* 1999; Brachert *et al.* 2007; Kontakiotis *et al.* 2019; Vasiliev *et al.* 2019; Zachariasse *et al.* 2021).

Consequently, and with the exception of the lowermost levels of the Keramoutsi section, where extremely rare brackish-water elements occur, all bryozoans, invertebrates and foraminifera are indicative of normal marine conditions characterised by strong salinity fluctuations (with mostly high salinity conditions) in the Messinian of Crete. In this regard, brine pools intermittently developed, and this scenario also involves the occurrence of possible refugia for stenohaline biota to survive and recover after episodes of environmental restriction.

#### Oxygen content

Bryozoans are either very rare (Keramoutsi, Kaparariana, and Faneromeni sections) or completely absent (Potamida section) in a number of samples. Other benthic organisms (foraminifera, bivalves, and ostracods) are also scarce or lacking in some of these layers, although ostracods are often better represented than the other groups (Moissette *et al.* 2018). The classical explanation for this phenomenon is episodic hypoxia or dysoxia in the benthos, most probably due to a combination of multiple factors, among which water stratification (Kouwenhoven *et al.* 1999, 2003; Kontakiotis *et al.* 2019). This hydrographic feature may have been caused by restricted communications with the Atlantic (closure of the straits; Krijgsman *et al.* 1999, 2018), leading to falling sea level and consequently to reduced deep-water ventilation in semi-enclosed sub-basins as the result of obstructed outflow of deeper waters (Kouwenhoven & van der Zwaan 2006), increasing residence time of water masses and accumulation of light organic carbon (Capella *et al.* 2019). Constriction of the Atlantic-Mediterranean connections, together with the

enhanced influence of the climate (Kontakiotis *et al.* 2019, Vasiliev *et al.* 2019; Mancini *et al.* 2020), could further contribute to hydrological variations characterised by increasing salinity, enhanced primary productivity, and water column stratification. The establishment of stressed marine conditions is characterised by increasing dysoxia due to deep-water stagnation and high supply of organic matter (Seidenkrantz *et al.* 2000; Kouwenhoven *et al.* 2003; Antonarakou *et al.* 2007; Drinia *et al.* 2007a, 2014; Freiwald 2019). This is further supported by changes in faunas (replacement of oxyphilic by stress-resistant benthic taxa: Kouwenhoven *et al.* 1999, 2003; dwarf planktonic species: Corbí *et al.* 2016, 2020; growth and size variations in planktonic foraminifera: Brachert *et al.* 2015), lithology (replacement of sapropels by diatomites: Pérez-Folgado *et al.* 2003; Drinia *et al.* 2007b), and sedimentation rates (“Early Messinian Sediment starvation Event”: Santarelli *et al.* 1998). Hypoxic to dysoxic episodes are indicated in the Messinian sediments of Crete (and other regions) by laminated marls, black shales, sapropels, and diatomite levels (e.g., Hsü *et al.* 1973; Schenau *et al.* 2000; Drinia *et al.* 2004; Karakitsios *et al.* 2017a; Pellegrino *et al.* 2018; Carnevale *et al.* 2019; Freiwald 2019; Kontakiotis *et al.* 2019; Vasiliev *et al.* 2019). These characteristic deposits are all related to water stratification and oxygen depletion in the bottom layers of the basins. In the study sections some of the laminated marl layers contain fewer benthic fossils, particularly bryozoans, than massive beds. However, correlations between lamination, sparsity of skeletal remains and hypoxia/dysoxia should be made with caution. This is mostly observable in the Kaparariana section, much less in the other sections and some massive beds, with poorer benthic communities, may also be indicative of lower oxygen conditions.

#### PALAEOBIOGEOGRAPHY OF THE LATE MIOCENE BRYOZOANS OF CRETE

Among the deep-water (stenobathic or not) extant or fossil species found in the studied material, most belong to an Atlantic (typically eastern)-Mediterranean group: *Anguisia verrucosa*, *Bryocryptella torquata*, *Cellaria salicornioides*, *Crisia aculeata*, *C. denticulata*, *C. fistulosa*, *Exidmonea atlantica*, *Orbitulipora excentrica*, *Scrupocellaria scrupea*, and *Tessaradoma boreale*. The second most important group is endemic to the Mediterranean-Paratethys region: *Batopora rosula*, *Canda rectangularata*, *Discoporella reussiana*, *Kionidella excelsa*, *Scrupocellaria elliptica*, and *Ybselesoecia typica*. The third group comprises “cosmopolitan” species: *Tervia irregularis*, *Nellia tenella*, and *Gemellipora eburnea* (but nearly all fossil records of this last species are from the Mediterranean and the Paratethys).

The shallow or strictly eurybathic bryozoan species fall approximately into the same biogeographical categories and with the same proportions. Some of the species are particularly characteristic of the present-day Mediterranean: *Calpensia nobilis*, *Celleporina canariensis*, *Chaperia annulus*, *Myriapora truncata*, and *Onychoecella angulosa*. Additionally, three fossil species are considered endemic to the Mediterranean: *Cheiloporina campanulata*, *Smittina canavarii*, and *Steginoporella montenati*.

Although the number of bryozoan species (54) found in this study is relatively low, the general pattern points to the modern character of these communities. Most of the 35 extant species belong to a group having an Eastern Atlantic/Mediterranean origin. Moreover, six fossil taxa are members of the Mediterranean/Paratethys basin system. The evolution of bryozoan (and other invertebrate) faunas from the Miocene to the present was in fact strongly conditioned by climate and palaeogeographic changes (e.g., Moissette & Pouyet 1987).

#### COMPARISON WITH OTHER MEDITERRANEAN (AND PARATETHYS) DEEP-WATER BRYOZOAN FAUNAS

Although poorly studied, bryozoan remains occur in Miocene (especially Tortonian-Messinian) to Recent marine deposits. A number of genera and species disappeared progressively from the Mediterranean during the late Miocene, the Pliocene and then the Pleistocene (Moissette & Pouyet 1987). Some may have subsisted elsewhere or in the Mediterranean, but have not (yet) been recorded in present-day habitats (e.g., *Bryocryptella torquata*, *Discoporella reussiana*, *Gemellipora eburnea*, *Nellia tenella*). A common stock of stenobathic deep-water species and more or less eurybathic species occur in practically all basins/stratigraphical intervals: *Annectocyma major*, *Cellaria salicornioides*, *Exidmonea atlantica*, *Nellia tenella*, *Tervia irregularis*, *Tessaradoma boreale*, and *Ybseosoecia typica*.

#### Middle Miocene of the Paratethys

The bryozoan faunas of the Badenian (Langhian-Serravallian) of the Central Paratethys are relatively well known, especially those of Austria (e.g., David & Pouyet 1974; Vávra 1975), the Czech Republic (e.g., Zágorský 2010a, b), and Hungary (e.g., Moissette *et al.* 2006, 2007). Among them, deep-water taxa have been recognized and a fair number of them are common with the Messinian of Crete. This is notably the case with well-represented species such as *Batopora rosula*, *Gemellipora eburnea*, and *Tervia irregularis*.

#### Late Miocene

Deep-water sediments occur onshore and offshore throughout the Mediterranean, but relatively few have been studied for their palaeontological content. The best outcrops for the purposes of this study are observed in western Algeria (Moissette 1988, 2000), Malta (PM, pers. obs.), Sardinia (PM, pers. obs.), Calabria (Neviani 1900; Rosso & Sanfilippo 1991; Di Geronimo *et al.* 1992), and Crete (Moissette *et al.* 1993, 2018). Among the most characteristic species, the following are to be mentioned: *Batopora rosula* (Algeria, Calabria, Sardinia, and Malta), *Gemellipora eburnea* (Algeria, Calabria), *Kionidella excelsa* (Algeria), *Orbitulipora excentrica* (Calabria), *Tervia irregularis* (Algeria, Sardinia), and *Tessaradoma boreale* (Algeria, Sardinia).

#### Pliocene

Good quality field exposures are available in Algeria (Haddadi-Hamdane 1996; PM, pers. obs.), Calabria (Barrier *et al.* 1987), Crete (PM, pers. obs.), and Karpathos (PM, pers. obs.). The most distinctive species are: *Anguisia verrucosa* (often abundant

in Karpathos), *Batopora rosula* (well represented in Sicily and Crete, scarcer in Algeria, Calabria, and Karpathos), *Gemellipora eburnea* (relatively abundant in Sicily and Karpathos), *Tervia irregularis* (common in Algeria, Calabria, Crete and Karpathos), and *Tessaradoma boreale* (common in Calabria and Karpathos).

#### Pleistocene

The best examples are those of Sicily and Calabria (Barrier *et al.* 1987; Di Geronimo *et al.* 1997; Rosso 1998, 2002, 2005; Rosso & Di Geronimo 1998; Di Geronimo *et al.* 2005), Rhodes (Moissette & Spjeldnaes 1995; PM pers. obs.), and Karpathos (Moissette *et al.* 2017). Many of the deep-water bryozoan taxa occurring in the Messinian of Crete are also present in the Italian and Greek deposits. Among them, the most frequent are: *Anguisia verrucosa* (common to abundant in Sicily, Calabria, Rhodes and Karpathos), *Batopora rosula* (extremely rare in Rhodes, which most probably constitutes its last occurrence), and *Gemellipora eburnea* (common in Sicily and Calabria, very abundant in some samples in Karpathos, scarcer in Rhodes), *Tervia irregularis* (common in Sicily, Calabria, Rhodes, and Karpathos), and *Tessaradoma boreale* (common in Sicily, Calabria, Rhodes, and Karpathos).

However, the Pleistocene deep-water bryozoan faunas are generally more diverse than those of the Messinian. Two main reasons may be suggested for this. First, larger hard substrates such as ahermatypic scleractinian corals (Italy and Greece) and rocky blocks (Italy) are relatively frequent (Di Geronimo *et al.* 2005; Rosso 2005; Moissette *et al.* 2017; Rosso & Sciuto 2019). Second, “boreal guests” entered the Mediterranean from the Atlantic during the Pleistocene when sea-water temperatures decreased (Di Geronimo *et al.* 1996, 2005; Rosso & Di Geronimo 1998; Rosso & Sciuto 2019).

#### Recent

Information on present-day deep-water Mediterranean bryozoan communities is relatively sparse and is principally focused on the western and central parts of the basin (Lagaaij & Gautier 1965; Harmelin 1979a; Harmelin & d’Hondt 1982, 1992a, b, 1993; Zabala *et al.* 1993; Mastrototaro *et al.* 2010; Rosso *et al.* 2010; Madurell *et al.* 2013; D’Onghia *et al.* 2015; Rosso & Di Martino 2016). The richest and better studied deep-sea bryozoan communities occur on cold-water coral skeletons where encrusting species largely predominate (Zabala *et al.* 1993; Mastrototaro *et al.* 2010; Rosso *et al.* 2010; Rueda *et al.* 2019). Compared with those of the Pleistocene, the Recent deep-water faunas are impoverished. Some species are absent from the present-day Mediterranean, but are living in the eastern Atlantic Ocean. Among the species common to southern Italy and eastern Greece, a number of “boreal guests” thus disappeared (e.g., *Bugulella elegans*, *Canda ligata*, and *Euginoma vermiformis*), while others remained (e.g., *Jaculina tessellata*, *Palmicellaria elegans*, and *Reteporella sparteli*). These changes are assumed to be mostly due to climate and hydrological fluctuations with deep waters becoming warmer after the

Plio-Pleistocene glacial episodes. Other factors such as lower trophic resources and higher salinities in the present-day Mediterranean (especially in the eastern part) may also have played important roles (Harmelin 1992; Harmelin & d'Hondt 1993; Di Geronimo *et al.* 2005).

One of the most representative taxa is *Gemellipora eburnea*, which is common in Miocene and Pleistocene deposits and found in Holocene sediments off north-eastern Sicily, but is absent from the Recent Mediterranean (Di Geronimo *et al.* 2001). Other deep-sea Atlantic species occur in the present-day Mediterranean: *Anguisia verrucosa*, *Tervia irregularis*, and *Tessaradoma boreale* (although these last two species are very rare in the collected material, they are common in other Messinian basins).

## CONCLUSIONS

A study of the bryozoan assemblages from the upper Miocene deposits of Crete revealed an overall shallowing-up sequence in all sections, with diminishing number of deep-water species and fragments, which later disappear completely. This general trend actually starts with shallow-water (infralittoral) deposits (Keramoutsis section only) and is followed by deeper (circalittoral) and then upper bathyal marls. This first sequence is succeeded by circalittoral marls and clayey limestones, capped by infralittoral carbonates and rarer sandstones. Apart from these sea-level variations, there is also some evidence that various shallow-water species were transported by currents to greater depths. The deep-water assemblages (deep circalittoral to upper bathyal) are characterised by the presence of rare bryozoan remains and species belonging to a few colonial morphotypes. In terms of abundance of specimens, the predominant and distinctive growth form is the conescharelliniform (three species), which is constantly associated with a few erect rigid (vinculariiform) and more diverse and numerous erect flexible (cellariiform) colonies (but a bias is introduced by the easy disarticulation of this colonial type). Fragments of the free-living morphotype (lunulitiform) also occur, but more rarely and less characteristically.

As previously noted, these bathymetric changes are diachronous throughout the region. Another major change indicated by the studied assemblages is the occurrence of several episodes of dysoxia suggesting water stratification together with increased productivity. All these phenomena result from relative sea-level fluctuations that are most probably a combination of changes in oceanic circulation, climate, global sea-level variations, and local tectonics (in Crete and/or near the Betic-Rifian corridors). The marine gateways were almost completely closed between 7.35 and 6.0 Ma, well within the time span of the studied sections (base and top dated at about 7.58 Ma and 6.72 Ma respectively). The palaeogeographic controls upon Mediterranean environments and biological communities were accordingly already in place, well before the onset of the salinity crisis itself at about 5.9–5.6 Ma.

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APPENDIX 1. — List of the material housed in the Museum of Palaeontology and Geology of the University of Athens (XLSX file): [https://doi.org/10.5852/g2021v43a26\\_s1](https://doi.org/10.5852/g2021v43a26_s1).