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).

**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; Corbi 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 (Hsiu 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., Lohf 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
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
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 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 foraminifer 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 astro-chronology 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 estimated 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).

<table>
<thead>
<tr>
<th>Stage</th>
<th>Planktonic Foraminiferal Bioevents</th>
<th>Stratigraphic level (m)</th>
<th>Chronostratigraphy</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Potamida</td>
<td>Keramoutsi</td>
</tr>
<tr>
<td>Messinian</td>
<td>(10) LO G. nicolae</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(9) FO G. nicolae</td>
<td>34.4</td>
<td>65.5</td>
</tr>
<tr>
<td></td>
<td>(8) LCO G. scitula group (sin)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(7) FCO G. miotumida group</td>
<td>28.8</td>
<td>44.5</td>
</tr>
<tr>
<td>Tortonian</td>
<td>(6) Influx G. menardii 4 within the range of G. menardii 5</td>
<td>26.8</td>
<td>15.1</td>
</tr>
<tr>
<td></td>
<td>(5) Paracme end G. scitula group (dex)</td>
<td>26.8</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(4) FO G. menardii 5 (dex)</td>
<td>7.5</td>
<td>13.2</td>
</tr>
<tr>
<td></td>
<td>(3) LO C. parvulus</td>
<td>4.3</td>
<td>28.0</td>
</tr>
<tr>
<td></td>
<td>(2) LCO G. menardii 4 (sin)</td>
<td>0.5</td>
<td>21.0</td>
</tr>
<tr>
<td></td>
<td>(1) G. scitula group coiling change D/S</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>
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 3/4 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. 2.** Schematic sedimentary log of Potamida composite section with sample location and semi-quantitative abundances of bryozoan species.

Bryozoan faunas at the Tortonian-Messinian transition

**Table:**

<table>
<thead>
<tr>
<th>Species</th>
<th>Semi-Quantitative Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Angustia verrucosa</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Annectocyma major</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Batopora rosula</td>
<td>abundant (1-5)</td>
</tr>
<tr>
<td>Biflustra savartii</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Byocryptella torquata</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Butonella muriella</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Calpensia nobilis</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Castalia rectangulata</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Cellaria salicornioides</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Celleporina canariensis</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Celleporina cf. siphuncula</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Chelioportula annulus</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Crisia aculeata</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Crisia denticulata</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Crisia sp.</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Dispora hispida</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Entalithroecia sp.</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Escharina cf. dutertrei</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Escharoides cocinea</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Exidmonea atlantica</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Laginopora leprolioides</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Margareta cereoides</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Mecynoecia delicatula</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Myriapora truncata</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Nella tenella</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Onychocella angulosa</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Orbitulipora excenrica</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Puelina sp.</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Reteporellia sp.</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Schizothyra fissa</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Scrupocellaria scrupea</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Smittina caravarii</td>
<td>very rare (1-5)</td>
</tr>
<tr>
<td>Smittina cervicornis</td>
<td>rare (6-10)</td>
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<tr>
<td>Stegnoporella montenati</td>
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<tr>
<td>Tubulipora sp.</td>
<td>rare (6-10)</td>
</tr>
<tr>
<td>Ybseloseoecia typica</td>
<td>very rare (1-5)</td>
</tr>
</tbody>
</table>
Fig. 3. — Schematic sedimentary log of Keramoutsi section with sample location and semi-quantitative abundances of bryozoan species.
Bryozoan faunas at the Tortonian-Messinian transition

**Fig. 4.** — Schematic sedimentary log of Kapariana composite section with sample location and semi-quantitative abundances of bryozoan species.
<table>
<thead>
<tr>
<th>Species</th>
<th>Zoarial forms</th>
<th>Depth</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adeonella polystomella (Reuss, 1848)</td>
<td>AD</td>
<td>20-130 m (30-60 m)</td>
<td>1</td>
</tr>
<tr>
<td>Anguisia verrucosa Julienne, 1882</td>
<td>VI</td>
<td>200-4280 m (200-1500 m)</td>
<td>2, 3</td>
</tr>
<tr>
<td>Annectocyma major (Johnston, 1847)</td>
<td>ME</td>
<td>5-200 m</td>
<td>4</td>
</tr>
<tr>
<td>Batopora rosula (Reuss, 1848)</td>
<td>CO</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Biflustra savarti (Audouin, 1826)</td>
<td>ME</td>
<td>0-100 m</td>
<td>5</td>
</tr>
<tr>
<td>Bryocryptella torquata (Julienne, 1903)</td>
<td>VI</td>
<td>80-300 m</td>
<td>6</td>
</tr>
<tr>
<td>Buffonellaria muriella Berning &amp; Kuklinshi, 2008</td>
<td>ME</td>
<td>10-50 m</td>
<td>7</td>
</tr>
<tr>
<td>Calpensia nobilis (Esper, 1796)</td>
<td>ME</td>
<td>0-60 m</td>
<td>8, 9</td>
</tr>
<tr>
<td>Candra rectangulara Uedin, 1964</td>
<td>VI</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Cellaria fistulosa (Linnaeus, 1758)</td>
<td>CE</td>
<td>30-80 m</td>
<td>8, 9</td>
</tr>
<tr>
<td>Cellaria salicornioides Lamouroux, 1816</td>
<td>CE</td>
<td>0-636 m (0-280 m)</td>
<td>8, 9</td>
</tr>
<tr>
<td>Celleporina canariensis Aristegui, 1989</td>
<td>CP</td>
<td>0-260 m</td>
<td>10</td>
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<tr>
<td>Celleporina cf. sphinctura Hayward &amp; McKinney, 2002</td>
<td>CP</td>
<td>0-35 m</td>
<td>11</td>
</tr>
<tr>
<td>Chaperia annulans Manzoni, 1878</td>
<td>ME</td>
<td>30-115 m</td>
<td>12</td>
</tr>
<tr>
<td>Cheliporina campanulata (Cipolla, 1921)</td>
<td>ME</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Chlidonina pyriformis (Bertoloni, 1810)</td>
<td>CA</td>
<td>0-40 m</td>
<td>9</td>
</tr>
<tr>
<td>Crisia aculeata Hassall, 1841</td>
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<td>50-1000 m (115-480 m)</td>
<td>13, 14</td>
</tr>
<tr>
<td>Crisia denticulata (Lamarck, 1816)</td>
<td>CE</td>
<td>0-100 m</td>
<td>14</td>
</tr>
<tr>
<td>Crisia fistulosa Heller, 1867</td>
<td>CE</td>
<td>5-100 m</td>
<td>15</td>
</tr>
<tr>
<td>Crisia sp.</td>
<td>CE</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Cupuladria cf. canariensis (Busk, 1859)</td>
<td>LU</td>
<td>5-860 m (50-300 m)</td>
<td>9</td>
</tr>
<tr>
<td>Discoporella reussiana (Manzoni, 1869)</td>
<td>LU</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Diporella hispida (Fleming, 1828)</td>
<td>ME</td>
<td>5-700 m</td>
<td>16, 17</td>
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<td>VI</td>
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<td>Escharina cf. dutertrei (Audouin, 1826)</td>
<td>ME</td>
<td>10-280 m (100-150 m)</td>
<td>18</td>
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<tr>
<td>Escharoides coccinia (Abridgida, 1806)</td>
<td>ME</td>
<td>0-100 m (30-80 m)</td>
<td>12</td>
</tr>
<tr>
<td>Exidmana atlantica (Forbes in Johnston, 1847)</td>
<td>VI</td>
<td>10-850 m (40-100 m)</td>
<td>4</td>
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<tr>
<td>Gemellipora eburnea Smitt, 1873</td>
<td>CE</td>
<td>60-3300 m</td>
<td>19</td>
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<tr>
<td>Halyssidia cf. diaphana (Busk, 1860)</td>
<td>CA</td>
<td>0-60 m</td>
<td>19</td>
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<tr>
<td>Hinckinsia sp.</td>
<td>ME</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Hippoponora sp.</td>
<td>ME</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Kionidella excelsa Koschinsky, 1885</td>
<td>CO</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Lagenipora leprailloides (Norman, 1868)</td>
<td>ME</td>
<td>10-150 m (40-80 m)</td>
<td>12</td>
</tr>
<tr>
<td>Margareta cereoides (Ellis &amp; Solander, 1786)</td>
<td>CE</td>
<td>10-90 m (10-45 m)</td>
<td>12</td>
</tr>
<tr>
<td>Mecynoecia delicatula (Busk, 1875)</td>
<td>VI</td>
<td>5-120 m</td>
<td>4</td>
</tr>
<tr>
<td>Myriapora truncata (Pallas, 1766)</td>
<td>VI</td>
<td>10-130 m (30-60 m)</td>
<td>12</td>
</tr>
<tr>
<td>Nellia tenella (Lamarck, 1816)</td>
<td>CE</td>
<td>0-250 m</td>
<td>20</td>
</tr>
<tr>
<td>Onychocella angulosa (Reuss, 1847)</td>
<td>ME</td>
<td>0-80 m (30-50 m)</td>
<td>12</td>
</tr>
<tr>
<td>Orbitulipora excentrica, 1880</td>
<td>CO</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Patinella radiata (Audouin, 1826)</td>
<td>ME</td>
<td>0-50 m</td>
<td>17</td>
</tr>
<tr>
<td>Puellina sp.</td>
<td>ME</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Reteporella sp.</td>
<td>ME</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Schizotheca fissa (Busk, 1856)</td>
<td>ME</td>
<td>20-120 m (40-120 m)</td>
<td>12</td>
</tr>
<tr>
<td>Scrupocellaria cf. elliptica (Reuss, 1847)</td>
<td>CE</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Scrupocellaria scrupea Busk, 1852</td>
<td>CE</td>
<td>0-500 m</td>
<td>9, 12</td>
</tr>
<tr>
<td>Scrupocellaria sp.</td>
<td>CE</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Smittina canavarii (Neviani, 1900)</td>
<td>ME</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Smittina cervicornis (Pallas, 1766)</td>
<td>AD</td>
<td>10-120 m (40-60 m)</td>
<td>12</td>
</tr>
<tr>
<td>Steginaund McCoy, 1972</td>
<td>ME</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Tervia irregularis (Meneghini, 1844)</td>
<td>VI</td>
<td>60-2650 m (60-300 m)</td>
<td>4</td>
</tr>
<tr>
<td>Tessaradoma boreale (Busk, 1860)</td>
<td>VI</td>
<td>60-3500 m (50-130 m)</td>
<td>12, 21</td>
</tr>
<tr>
<td>Tubulipora sp.</td>
<td>ME</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Turbicellepora sp.</td>
<td>CP</td>
<td>NA</td>
<td>–</td>
</tr>
<tr>
<td>Ysseloscoecia typica (Manzoni, 1878)</td>
<td>VI</td>
<td>NA</td>
<td>–</td>
</tr>
</tbody>
</table>

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 (samples 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 *Smittina 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 (*Halypsis 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.*).

**Conescharcelliniform**
Conical (*conescharcelliniform sensu stricto*) to discoidal (*orbitu-liporiform*) rooted colonies. They are typical of deep-water muddy bottoms. Recent *Batpora* colonies are found at depths of 285-805 m (Cook & Lagaaij 1976). Mono- to oligo-specific assemblages with relatively numerous *Batpora 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.*

**Vinculariform**
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.

**BATHMETRIC 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
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 tongtua, Gemellipora eburnea, Terva irregularis, and Tesaradoma borea). 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 salicornioides, 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-

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).
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 tortuata*, *Kionidella excelsa* and subordinate *Teretia irregularis* and *Tessadoma 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 conescharelliform 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 vinculariforms (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 tortuata*, *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 conescharelliform 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 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 PALAEONTOLOGY**

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=taxdetails&id=146142 on 2019-09-18).

The origin of the material has been indicated with the following abbreviations: Potamida (POTA, POTB), Kapariana (CAP), 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.

*Anguisia verrucosa* Jullien, 1882

(Fig. 7A, B)

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

**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).
REM A R K S
The gonozooid, characteristic of the genus, consisting of a single elongated chamber with a terminal tubular ooe ciostome (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


**Genus Exidmonea** David, Mongereau & Pouyet, 1972

*Exidmonea atlantica* (Forbes in Johnston, 1847)


This list of fossil records concerns *Idmonea-Idmironosa-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**

Vinculariform 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 ooe ciostome was not observed.

Family TERYIIDAE Canu & Bassler, 1920


**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

*Ybselosoecia typica* (Manzoni, 1878)

(Fig. 7E-G)

**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.

Description
Vinculariform colony. Dichotomous branches mostly flattened. Frontal smooth, zoetal 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. Ooeicostome with flared, transverse and convoluted rim.

Suborder ARTICULINA Busk, 1859
Family CRISIDAE Johnston, 1838
Genus CRISIA Lamouroux, 1812

CRISIA ACULEATA Hassall, 1841
(Fig. 8A-C)


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 ramifications arise from the third zooid. Pseudopores elongate and relatively rare. Gonozooid pyriform with a discrete ooeicostome 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. churnea (Linnæus) 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.


OCCURRENCE. — Middle Miocene: Austria, Hungary, Czech Republic (Bobies 1958; Vavara 1975), Late Miocene: Sardinia, Sicily (Moissette et al. 2002), 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 & Fossa 2006) and in the Bay of Biscay (Calvet 1896).

REMARKS
C. denticulata closely resembles the fossil species C. hoernesi Reuss, which however has a greater number of zooids per internode (14-16).
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 µm; F-G, 200 µm.
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: 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; Lagaaï 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 & Basler, 1923) and *C. vindobonensis* Baluk & Radwansky, 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 Discoparella** d’Orbigny, 1852

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

*Cupuladria 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.

**Discoparella 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 5-c-d. — Haddadi-Hamdane 1996: 66, pl. 5, figs 2, 3, 8.


**Description**

Lunuliform 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
occupying approximately one half of the zooecial length. Two large septula are discernible in the distal part of the opesial 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). Zágoršek (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)*


**Occurrence.** — Pliocene: Calabria (Neviani 1900). Pleistocene: Calabria (Di Geronimo *et al.* 1997), Rhodes (Moissette & Spijeldnaes 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 zoecial length with two large septula in the distal part of the opesial 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.
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 zooids. In each pair, the zooids 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** LEPROLIOIDEA Vigneaux, 1949  
**Family** BRYOCRYPTELLIDAE Vigneaux, 1949  
**Genus** Bryocryptella Cosman, 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.

**Description**
Colony vinculariform. 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 zoecial 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.
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, Kio nidella 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 µm; B, E, 200 µm; C, F, 100 µm; D, 1 mm.
Superfamily Conescharellainoidea 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.


Description
Small conical conescharellaiform 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 & Lagaaij 1976; Pizzaferri & Braga 2000).

Family Orbituliporidace Canu & Bassler, 1923
Genus Orbitulipora Stolickza, 1862

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


Description
Discoidal 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 oovicells (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 zoocoral frontal.

Discussion
Taphonomy
Most bryozoans (and other skeletal organisms) are well preserved, except a number of yellowish, abraded fragments of littoral species (e.g., Adrenella polytomella, Margareta 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.

Palaeanoenvirornmental 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.
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, Onychocella 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
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 – Vasilev 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; Kontakiotis et al. 1999; Drinia et al. 2007; Kontakiotis et al. 2019; Vasilev et al. 2019; Zacharias 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, Kapariana, 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, Vasilev 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 dysxia 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; Freiwalld 2019). This is further supported by changes in faunas (replacement of ophi- philic by stress-resistant benthic taxa: Kouwenhoven et al. 1999, 2003; dwarf planktonic species: Corbi et al. 2016, 2020; growth and size variations in planktonic foraminifera: Brachert et al. 2015), lithology (replacement of sапропель 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, sапропель, and diatomites (e.g., Hsiü et al. 1973; Schenau et al. 2000; Drinia et al. 2004; Karakitsios et al. 2017a; Pellegrino et al. 2018; Carnevale et al. 2019; Freiwalld 2019; Kontakiotis et al. 2019; Vasilev 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 Kapariana 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*, *Cri sia aculeata*, *C. denticulata*, *C. fistulosa*, *Exidendra atlantica*, *Orbitulipora excentrica*, *Scrupocellaria scupea*, and *Tesaradoma boreale*. The second most important group is endemic to the Mediterranean-Paratethys region: *Batopora rosula*, *Canda rectangulata*, *Discoporella reussiana*, *Kionidella excelsa*, *Scrupocellaria elliptica*, and *Ybsolesosia typica*. The third group comprises “cosmopolitan” species: *Tervia irregularis*, *Nellia tenella*, and *Gemmellipora 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*, *Cephalopora canariensis*, *Chapera annulata*, *Myriapora truncata*, and *Onychocella angulosa*. Additionally, three fossil species are considered endemic to the Mediterranean: *Chelaptorina campanulata*, *Smititina canavarrii*, 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 Ybelosooecia 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; Vàvra 1975), the Czech Republic (e.g., Zágoršek 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 excavicentra* (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: *Anquisia 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: *Anquisia 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 and Calabria, very abundant in some samples in Karpathos, scarcer in Rhodes), 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 ehematypic 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 verniformis*), while others remained (e.g., *jaculina tesellata, Palmicellaria elegans, and Reteporella sparreri*). 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 Pliocene 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*, *Tereya 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 (Keramoutsi 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 coneschelliforminum (three species), which is constantly associated with a few erect rigid (viculariiform) 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 (lunuliform) 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.