

# The response of benthic foraminifera to palaeoenvironmental disturbance: A quantitative approach in turbidite-like successions

Hara Drinia and Michael D. Dermitzakis, Athens

With 5 figures

DRINIA, H. & DERMITZAKIS, M. D. (2010): The response of benthic foraminifera to palaeoenvironmental disturbance: A quantitative approach in turbidite-like successions. – N. Jb. Geol. Paläont. Abh., **258**: 325–338; Stuttgart.

Abstract: Benthic foraminifera were collected from a number of samples of a turbidite-like succession, and quantitatively investigated with the aim to describe and interpret their distributional pattern prior, during and after the turbidite events. The foraminiferal assemblages contain indigenous benthic taxa that represent combined bottom-water and bottom-sediment controlled benthic environments and allochthonous benthic shelf taxa that are transported downslope into deeper-water biotopes. Considerable differences in diversity, community organization, feeding and habitat preferences are detected among benthic foraminiferal assemblages below, across and above the turbiditic episodes. Prior to the deposition of the turbiditic sands, the benthic foraminiferal assemblage is indicative of a strong preference of environments with highly elevated food supply, but sheltered from direct disturbance. This stability was disrupted by the recurrent deposition of turbiditic sands. In the lower part of the turbiditic sequence, some specialized endobenthic forms, such as Valvulineria complanata and Nonion spp. could keep pace with high sedimentation reflecting enhanced supply of organic matter by transport. In the upper part of the turbiditic sequence, an opportunistic fauna (Bolivina spathulata assemblage), entirely composed of infaunal elements, is observed, indicating a nutrient-rich substrate. The reduction in the dominance of Bolivina spp. and the reappearance of both infaunal and epifaunal taxa reflects the recovery of the benthic ecosystem.

Key words: Early Tortonian, benthic foraminifera, turbidites, ecosystem disturbance, repopulation.

# 1. Introduction

Benthic foraminifera are unicellular organisms that are abundantly present in the marine realm. They dominate modern ocean-floor communities (e.g. GOODAY et al. 1992; GOODAY 1999) and are the most abundant benthic deep-sea organisms preserved in the fossil record. These benthic organisms are widely used as tools for the reconstruction of palaeoenvironments as they generally inhabit relatively narrow ranges of environmental conditions. Environmental factors such as energy conditions, substrate consistencies, depositional rates, oxygenation, salinity and other physicochemical conditions, all lead to discrete biological communities. For this reason, benthic foraminiferal assemblages are valuable proxies for bottom conditions, where the control on the distribution of both individual taxa and specific assemblages are becoming progressively better understood.

Colonization of new habitats by benthic foraminifera has received growing attention during the last years (for overview see ALVE 1999). A number of studies addressed the foraminiferal reactions to changing environmental parameters such as salinity, temperature, oxygen, food availability, pH, (e.g. BRADSHAW 1957, 1961; BOLTOVSKOY et al. 1991; MOODLEY & HESS 1992; ALVE & MURRAY 1999; STOUFF et al. 1999a, b; GUSTAFSSON & NORDBERG 2001; LANGER & LIPPS 2003; LE CADRE et al. 2003), contamination by trace metals (ELLISON et al. 1986; SHARIFI et al. 1991; ALVE 1991; ALVE & OLSGARDT 1999; YANKO et al. 1998; DEBENAY et al. 2001) and sewage effluents (e.g. WATKINS 1961; SCHAFER 1973). Moreover and according to ERNST et al. (2002), disturbance by turbidites is another serious parameter which affects benthic foraminiferal ecology. Turbidites are characterized by high organic carbon and low-oxygen concentration (THOMSON et al. 1984; DE LANGE 1986; WILSON et al. 1986; THOMSON et al. 1993). Recent turbidites interbedded between oxic sediments result in distinct redox boundaries at the top and bottom of a turbiditic sequence. It is therefore expected that the transportation of organic matter (food) and of clastic matter (as an agent of disturbance) into a basin would influence benthic species distribution patterns, and thus directly impact on the benthic foraminiferal assemblage.

Foraminifera have the ability to migrate or recolonize after major disturbance (e.g RICHTER 1965; KAMINSKI 1985; KAMINSKI et al. 1988; LEVIN et al. 1991; ALVE & BERNHARD 1995; LINKE et al. 1995; HESS & KUHNT 1996; ERNST et al. 2000). Recolonization of deep-sea substrates is a topic that has received increasing interest in recent years with several studies on both modern and fossil benthic foraminiferal communities following major environmental disturbances (see ALVE 1999 for a review of the topic). However, little is known about how disturbance can quantitatively affect the composition of the benthic foraminiferal assemblage.

Our specific contribution is the study of the benthic foraminiferal assemblages retrieved from a turbiditic section in southern Greece (Gavdos Island), which was undertaken to meet the following objectives: (a) to investigate the changes in foraminiferal community during intensified environmental stress and (b) to monitor the recolonization and subsequent evolution of the foraminiferal fauna following the deposition of turbidite layers.

## 2. Geological setting

Gavdos Island, Eastern Mediterranean, (Fig. 1) is located approximately 30 km south of Crete and represents the southernmost emerged part of the Hellenic arc system. The oldest rocks of Gavdos Island are represented by a Maastrichtian-Danian calcareous sequence topped by Eocene flysch (VICENTE 1970), belonging to the Pindos-Ethia geotectonic zone. Towards the northeastern part of the island, a Mesozoic volcano-sedimentary series is exposed which is thrusted above the Pindos-Ethia sequence (VICENTE 1970; SEIDEL & OKRUSCH 1978). Neogene sediments have a maximum thickness of



**Fig. 1.**  $\mathbf{a}$  – Simplified geological map of Gavdos Island (modified after TSAPARAS 2005),  $\mathbf{b}$  – Lithostratigraphical column of the Potamos section indicating the position of samples (dashes).

150 m and cover about one half of the surface area of the island, overlying unconformably the Mesozoic substrate. The Neogene deposits of the island have been divided by ANASTASAKIS et al. (1995) into two formations: Potamos and Metochia. A good reconnaissance map and description of the formations is given by ANASTASAKIS et al. (1995), DRINIA et al. (2004) and TSAPARAS (2005) and need not be repeated here. ANTONARAKOU (2001) and ANTONARAKOU et al. (2007) consider that these formations are late Middle and Late Miocene in age respectively, basing their conclusions on the faunas of planktic foraminifera.

# 3. Material and methods

The early Late Miocene of Gavdos Island is well represented in the sediments encountered along Potamos Bay, located in the NNW side of the island (Fig. 1a). The Potamos section, which is 115 m thick, is composed of whitish to greyish bluish marls and sands of turbiditic origin (Fig. 1b). Previous qualitative and quantitative micropalaeontological analyses that were realised in the contained benthic microfauna showed that the section is characterized by a shallowing upwards-general trend (DRINIA 2009). In detail, bluish, fossiliferous marls with occasional lenses or layers of fine to very fine grained sands dominate mainly the basal and upper parts of the studied section and are thought to represent an open marine shelf environment.

In the middle part of the succession, thin-bedded and very fine to fine-grained sands embedded in shelf mud as well as thick-bedded, fine to medium grained, poorly sorted sands, which are laterally persistent, dominate the lithology. The thinlyinterbedded sands-marls facies is analogous to both distal storm sands deposited below storm wave base (PIRRIE 1989; ROSENTHAL & WALKER 1987) or finegrained turbidites (STOW & PIPER 1984), interbedded with lower-energy suspension sedimentation marls.

The uppermost levels of the Potamos Section consist of medium-sized partially cemented sandstone, composed of closely packed oysters more or less parallel to the bedding plane. The oysters are often very big and are stacked upon each other with a silty matrix in between. According to DEMARQ & DEMARQ (1989), the development of these banks is connected to brackish palaeoenvironmental conditions.

The section is capped by sands in which bivalves, bryozoans, irregular echinoids (Clypeaster) and large benthic foraminifera predominate (Heterostegina sp.), with minor proportions of gastropods. This skeletal material is well preserved. The skeletal content of this facies implies a fully marine shelf setting. Skeletal biota are well preserved which points to a rather quiet depositional setting below wave abrasion depth (= WAD, BRACHERT et al. 2003). The presence of Heterostegina fits a depositional environment in the lower segment of the photic zone (e.g. JAMES et al. 2001), implying warmtemperate surface temperatures (BETZLER et al. 1997, LANGER & HOTTINGER 2000). The combined lithological and micropalaeontological data suggest relatively cool and eutrophic conditions, induced by enhanced river runoff and upwelling for the Potamos shelf (DRINIA 2009). The biostratigraphy based on the planktic foraminifera assemblages analysis already allowed to confine the depositional system to the early Late Miocene (early Tortonian; DRINIA et al. 2004; ANTONARAKOU et al. 2007).

## 3.1 Micropalaeontological analyses

Quantitative analysis of benthic foraminifera has been carried out in order to document changes in benthic foraminiferal assemblages throughout the Potamos section. Samples analyzed were collected from the marly intervals. Sands above and below the marly intervals were generally not sampled or when sampled, yielded poorly preserved microfossils. Sixty nine samples were disaggregated and sieved in tap water using 63, 125 and 595 µm sieves and then dried. The 125-595 µm fraction was split into aliquots of a suitable size for census of benthic foraminiferal tests to be taken. Whole aliquots were counted and where possible at least 200 tests were identified, re-calculated as percentage values and plotted in curves to display the vertical distribution of each taxon. Species with relative frequency above 2 % were divided into three groups, according to MURRAY (1991, 2006), JORISSEN et al. (1992), BARMAWIDJAJA et al. (1992), JORISSEN (1999) and JORISSEN & WITTLING (1999): i.e. epifaunal, shallow infaunal, deep infaunal (Appendix A). Frequencies were then plotted in curves for each group. Moreover, the percentage occurrence of the well-established redox-front dwelling taxa (Globobulimina spp., Bolivina spathulata, Chilostomella spp. and Nonion spp.) which according to ROGERSON et al.



Fig. 2 (Legend see p. 329)



**Fig. 2. a** – Stratigraphic distribution of the most representative taxa belonging to epifauna group. **b** – Stratigraphic distribution of the most representative taxa belonging to the shallow infauna group. **c** – Stratigraphic distribution of the most representative taxa belonging to the deep infauna group.

(2006) is related to disturbance was also calculated. In addition, Shannon-Weaver diversity index (Hs) was recorded for each sample (Appendix B).

Finally, a statistical analysis, hierarchical cluster analysis, was performed to better describe the composition and distribution of the benthic foraminiferal assemblages. Hierarchical cluster analysis was performed on the relative percentage of frequency, per sample, by means of SPSS program version 13.0. The taxa with a frequency major than 2% were selected for this analysis. An R-mode clustering was performed, using the cluster method "Within Groups Linkage".

#### 4. Results

In the studied samples, species numbers range from 4 to 71 per sample and Shannon-Weaver diversity values range from 0.08 to 4.77 (Appendix B). At

65.5 to 85.7 m and at 87.5 m, low values of Shannon-Weaver diversity index suggest some deviation from the norm (normal marine conditions > 2.1 Shannon-Weaver diversity index) of the palaeoenvironmental parameters.

In Fig. 2 the stratigraphic distributional patterns of the major epifaunal, shallow infaunal and deep infaunal species are displayed. Among the epifaunal group (Fig. 2a), *Cibicides lobatulus* is present with significant frequencies throughout the record apart from the stratigraphic interval at 58.5 to 90 m which is characterized by thick turbidite layers. Similar stratigraphic trends are documented for the species *Planulina ariminensis, Heterolepa dutemplei* and *Cibicidoides* spp., yet present with lower abundance values.

Among the shallow infauna (Fig. 2b), Bolivinidae, with *Bolivina spathulata* as their main representative, are always present with frequencies less than 25%, apart from the upper part of the turbidite sequence, from 58.5 to 90 m. In this interval, this group of species shows the maximum abundance and is dominant. From the rest of the species, Buliminidae, *Valvulineria complanata*, *Gyroidina soldanii* and *Nonion* spp. show their maximum abundance values before and across the lower part of the turbidite sequence, are almost absent in the statigraphic level above turbidites but they re-appear in the upper part of the record, yet with lower frequency values.

In the upper part of the record, at 110.9 m, a dramatic change takes place. High relative abundance of the shallow infaunal Ammonia beccarii (84.7%) and an overall benthic foraminiferal abundance decline indicates that an estuarine environment offered suitable conditions for this species (DRINIA et al. 2004). The most significant deep infaunal species is Globobulimina spp. (Fig. 2c). It is more abundant across the turbidite layers and decreases in the stratigraphic portion above these. At around 90 m it reappears again showing a decreasing trend up to top of the record. In Fig. 3 the distribution of the microhabitat groups is plotted together with H(s) values and the percentage of the redox-front dwelling fauna. From this graph it is evident that going upwards through the turbidite layers, the epifaunal group strongly decreases in abundance and the assemblages are characterized by a great number of individuals, belonging to the shallow infaunal species B. spathulata. In the same interval, the abundance of the redox-front dwelling taxa in the assemblage shows maximum values (up to 98%). These maxima coin-



**Fig. 3.** Distribution pattern of the microhabitat preferences in the succession, plotted with Shannon Diversity and the percentage of the Redox-front dwelling taxa. It is evident that during the early stage of the ecosystem colonization (shadowed area) the abundance of the redox-front dwelling taxa in the assemblage shows maximum values (up to 98 %), which coincide with strong minima in the Shannon-Weaver diversity (as low as 0.08).

cide with strong minima in the Shannon-Weaver diversity (as low as 0.08), an index sensitive to single-taxon dominance. These patterns typify samples that are heavily dominated by *B. spathulata*.

Inspection of the R-mode cluster analysis dendrogram (Fig. 4) allows the identification of six benthic foraminiferal associations. In Fig. 5, the cumulative plots of these associations are plotted. Cluster I represents a mixed fauna composed of allochthonous taxa (Elphidium spp., A. beccarii and C. lobatulus) which may represent the bedload transport of (turbidity) currents, sweeping material off the shelf into bathyal depths. The abundance of these species is considered as an indication of erosional processes from shallow shelf seas and therefore not a part of the fossil community. The stratigraphic interval from 110.9 to 112.5 m is dominated by abundant Ammonia beccarii with subsidiary Elphidium spp. In this part of the record, the assemblage points to a somewhat restricted environment, as may deduced from the dominance of Ammonia and the low diversity of the assemblage. Furthermore, the large numbers of

A. *beccarii* point to a fresh water supply to the system.

Cluster II is characterized by a great number of individuals, belonging to the shallow infaunal species *B. dilatata* and *B. spathulata* and it is recorded from 65.5 to 85.7 m and from 87.5 to 88.4 m. In the interval from 65.5 to 85.7 m of the record, *B. spathulata* and *B. dilatata* are the sole benthic species. *Bolivina spathulata* is a shallow infaunal species, mostly regulated by oxygen concentration (e.g. DERMITZAKIS & KOUROUNI 1982). For this reason, the effect of mixing of the sediment and the subsequent induced migration of this species affects its survival (VAN DER ZWAAN 1982; VERHALLEN 1991; JORISSEN et al. 1992).

Cluster III is persistently present throughout the studied record exhibiting moderate to high frequency values of the range of 60%, yet it is nearly absent in the stratigraphic levels where species of Cluster II dominate. This assemblage is mainly composed of *B*. *costata* and *C*. *laevigata*. These taxa prefer a shallow infaunal microhabitat, common in environments





with moderate oxygen depletions and medium/ high trophic levels (JORISSEN 1987; BERGAMIN et al. 1999; SCHMIEDL et al. 2003). Particularly, *B. costata* shows a tolerance to dysoxia (SEN GUPTA & MACHAIN-CASTILLO 1993). The presence of *C. laevi*- gata exclusively within energy minimum zones indicates a strong preference of this species to environments with highly elevated food supply, but that are sheltered form direct disturbance.



**Fig. 5.** Cumulative plots of Clusters I to VI. A remarkable pattern characterizes the post-turbiditic interval (shadowed area) where Cluster II (dominated by *B. spathulata*) strongly prevails in the foraminiferal assemblage.

Cluster IV consists of *Globobulimina* spp., a group of species with deep infaunal microhabitat especially resistant to very low oxygen conditions. In the studied succession, it is represented with low frequency values apart from the stratigraphic intervals at 21.2 m (39 %), 85.20 m (49.5 %) and 86 m (47 %) indicating high primary productivity and low oxygen conditions in bottom and/or pore waters.

Cluster V groups V. complanata with Nonion spp. This assemblage shows strong fluctuations exhibiting maximum values at 29.35 and 39.80 m constituting 56% and 73% of the total population respectively. Valvulineria complanata is considered to be an epifaunal to shallow infaunal species whereas Nonion spp. is considered to be an infaunal species. However, both species occupy a shallow infaunal position in the turbiditic sediments.

Cluster VI consists of *Cibicidoides* spp., *O. umbonatus*, *G. soldanii* and *Uvigerina* spp. All these taxa have an epifaunal to shallow infaunal microhabitat preference (MURRAY 1991). *Cibicidoides* spp. assemblage is mainly present in the basal part of the section. Scattered occurrences of this assemblage are reported at 37.4 m, 96.5 m and 106.5 m of the record. This epifaunal taxa with planoconvex or biconvex trochospiral tests, is considered indicative of oxic environments (e.g. CORLISS 1991; KAIHO 1994). The co-existence with *Uvigerina* spp., which is assumed to tolerate increased nutrient supply, indicates meso- to oligotrophic conditions for this assemblage.

### 5. Discussion

In the studied sediments, the preservation of the foraminiferal assemblages was most certainly influenced by the sedimentological regime. The area was subjected to episodic storms and floods alternating with periods of quiescence. Thin pelagic marls are interbedded with turbidites. These beds are generally thin (10 to 20 cm) but occasionally reach 2 to 3 m. The pelagics interbedded with turbidites suggest that occasionally pelagic sedimentation took place between the turbidity flows. Often the flows were too close in time to allow thick pelagic sediments to accumulate. The small amount that was deposited was eroded by the next flow. Yet this rapid succession of turbidites was occasionally interrupted. These conditions seriously affected the preservation of foraminifera and undoubtedly

account for much of the patchiness of foraminiferal distribution and diversity.

Remarkable oscillations between benthic foraminiferal assemblages are apparent. Assemblages associated with non-turbiditic sediments are dominated by taxa typical of stable environmental conditions. Those associated with the turbiditic sediments are dominated by indigenous benthic taxa that represent combined bottom-water and bottom-sediment controlled benthic environments, and by allochthonous benthic taxa that are transported as displaced populations. Between the pulses of high energy bottom currents that deposit the sand, benthic environments reflect low current energy, poor oxygenation of bottom water and sediments, and increased detrital components such as clays and marine or terrestrial organic matter. These unique and contrasting environments support diverse diagnostic assemblages of indigenous benthic foraminifera that provide us with opportunities to make very detailed interpretations of depositional variables in complex marine settings.

There are four main intervals (I to IV) during which the turbiditic sequence was deposited:

Interval I (Environmental Stability): Prior to the deposition of the turbidite layers, the benthic foraminiferal assemblage is indicative of a certain environmental stability as indicated by the relatively minor fluctuations in the measured faunal parameters. The composition of the pre-turbidite assemblage (first 9 m of the record) is characterized by high diversity and numerous different morphotypes. Sessile suspension feeders such as *Cibicidoides* spp. occur along with infaunal detritus feeders. All ecological niches were occupied, signifying that the oxygen penetration within the sediment column reached several centimeters (LOUBÈRE 1997) and the redox zone was deep.

Interval II (Early stage of ecosystem disturbance): The environmental stability of Interval I is disrupted by the deposition of the turbidite layers. During the early stage of the disturbance of the system, in the form of an excess of the input of food, the well-defined micro niches of Interval I seem to collapse. Apart from the reworked species (*C. lobatulus, Elphidium* spp., *A. beccarii*), the turbidites of this part of the record which have maximum thickness 15 cm, contain some specialized infaunal taxa which utilize organic matter in the turbidite

layer. The increased organic matter is bioturbated downward into the sediment column, enabling infauna foraminifera to occur outside their typical microhabitat, or induce a trigger for infaunal foraminifera to migrate to shallower zones. Infaunal species such as *V. complanata*, able to cope with refractory material, are found to enlarge their microhabitats to deeper zone. According to RATHBURN & CORLISS (1994), *Valvulineria* can possibly be regarded as a dysoxic-tolerant species adapted to turbiditedisturbed environments, feeding on the organic matter delivered with turbidites. In this case, this species has the same microhabitat preference, cooccurring with *Globobulimina* spp. and *Nonion* spp.

Across the turbidite layers, the foraminiferal assemblage is characterised by relatively high diversity, indicating that the increase of the deep infauna is not accompanied by the disappearance of the less resistant taxa. This may be due to the fact that turbidites were either insufficient or not sustained long enough to destroy the benthic foraminiferal assemblages. Yet, they are likely that they supported a large number of nutrients which attracted foraminiferal and accounted for the enrichment in foraminiferal population. Thus the relatively high diversity of the foraminiferal assemblages across the turbiditic levels are relicts of both the environmental conditions (at the time of deposition) and of preservation biases.

Interval III (Late stage of ecosystem disturbance): A remarkable pattern that can be interpreted as evidence of ongoing disturbance characterised the sea floor from 55 to 98 m of the record. In this part of the record, an oligotypic assemblage prevails. The fauna is mostly composed of B. spathulata, making up to 90 % of the total benthic assemblage. The very low diversity of foraminiferal assemblages can be related to prevailing strong physical disturbance, in the form of fast current speeds, high sedimentation rates and frequent sediment resuspension, leading to an unstable sediment substrate. The *Bolivina* spp. occurring in this part of the record can be regarded as a highly opportunistic recolonizer, thriving under eutrophic conditions, possessing sufficient tolerance for oxygen deficiency and therefore it does not need to migrate to escape the environmental hostility in the deeper sediment layers. These taxa displayed rapid migration to the upper sediment layers presumably to find more favourable microhabitats and are thus reasonable reflectors of the redox state of the sediment. On the contrary, a number of so-called epifaunal taxa experience considerable population loss, probably indicating that the redox conditions became hostile.

Interval IV (Return of Ecosystem Stability): In this part of the record, *Bolivina spathulata*. is diminishing, and a number of epifaunal taxa follow the recovery. Deeper living taxa (*Globobulimina* spp.) also re-appear indicating the re-establishment of the redox condition.

The repopulation of the nutrient-rich substrate by the low-diversity *Bolivina spathulata* assemblage is replaced by species that are capable to occupy a wider range of ecological niches (the shallow infaunal *Valvulineria*, *Uvigerina* and the epifaunal *Cibicidoides* spp.). The reduction in the dominance of *Bolivina* spp. and the reappearance of both infaunal and epifaunal taxa reflects the recovery of the benthic ecosystem and the concurrent greater stability of the redox zones.

This study shows that the environmental disturbance by turbidites results in various stages of trophic levels that are exploited by different assemblages of foraminiferal communities. However, the distinction between epibenthos and endobenthos across the turbiditic levels becomes obscure, the species distribution being essentially controlled by the redox profile. The adaptive ability of some foraminiferal species (e.g. *Valvulineria*) to move into higher or lower microhabitats apparently plays a particularly significant role in the foraminiferal colonization of turbiditic-like sediments.

The palaeoenvironmental conditions of the Potamos section reflect the biotic recovery of the benthic ecosystem, after a period of intense turbidity activity. The vertical evolution of the benthic foraminiferal assemblages indicates a succession from (a) a predisturbance deposit to (b) a disturbance deposit followed by (c) the post disturbance deposit (sensu ALVE 1999). According to ALVE (1999), units (a) and (c) may contain in situ fossils whereas (b) will be either unfossiliferous or contain transported fossils (although they may contain post-disturbance, infaunal taxa which utilize organic matter in the turbidite layers (RATHBURN & CORLISS 1994)).

#### 6. Conclusions

Significant differences in diversity, community structure, feeding and habitat preferences are observed among benthic foraminiferal assemblages below and above turbidite layers in Potamos section, Gavdos Island, Greece.

Prior to the deposition of the turbiditic sands, the benthic foraminiferal assemblage is indicative of a certain environmental stability as indicated by the relatively minor fluctuations in the measured faunal parameters. This stability was disrupted by the recurrent deposition of turbiditic sands. Some specialized endobenthic forms, such as *Valvulineria complanata* and *Nonion* spp. could keep pace with high sedimentation in this high-energy regime, taking advantage of the food supplied by the strong bottom currents.

A remarkable pattern that can be interpreted as evidence of the ongoing ecosystem disturbance characterized the sea-floor. An assemblage of opportunistic taxa (*Bolivina spathulata* assemblage) is the only survivor. This oligotypic fauna is replaced later by a more-diversified fauna which is capable to occupy a wider range of ecological niches, indicating the return to ecosystem stability.

#### Acknowledgements

This work is part of a project undertaken by the Faculty of Geology and Geoenvironment of the University of Athens focussed on the Neogene development of Gavdos Island. The authors would like to express their gratitude to Dr. NIKOS TSAPARAS for his interest and invaluable notions on the work. Special thanks are due to the University of Athens for providing financial support (Project No 70/4/7612). An anonymous reviewer is thanked for his valuable criticism and remarks on the manuscript.

#### References

- ALVE, E. (1991): Benthic foraminifera in sediment cores reflecting heavy metal pollution in Soerfjord, Western Norway. – Journal of Foraminiferal Research, 21: 1-19.
- (1999): Colonization of new habitats by benthic foraminifera: a review. – Earth-Science Reviews, 46: 167-185.
- ALVE, E. & BERNHARD, J. M. (1995): Vertical migratory response of benthic foraminifera to controlled oxygen concentrations in an experimental mesocosm. – Marine Ecology Progress Series, **116**: 137-151.
- ALVE, E. & MURRAY, J. W. (1999): Marginal marine environments of the Skagerrak and Kattegat: a baseline

study of living (stained) benthic foraminifera. – Palaeogeography Palaeoclimatology Palaeoecology, **146**: 171-193.

- ALVE, E. & OLSGARDT, F. (1999): Benthic foraminiferal colonisation in experiments with copper-contaminated sediments. – Journal of Foraminifera Research, 29: 186-195.
- ANASTASAKIS, G. C., DERMITZAKIS, M. & TRIANTAPHYLLOU, M. (1995): Stratigraphic framework of the Gavdos Island Neogene sediments. – Newsletters on Stratigraphy, 32: 1-15.
- ANTONARAKOU, A. (2001): Biostratigraphic and paleoenvironmental implications on Miocene sediments of Eastern Mediterranean (Gavdos Island). – PhD Thesis, Athens University. – 180 pp.
- ANTONARAKOU, A., DRINIA, H., TSAPARAS, N. & DER-MITZAKIS, M. D. (2007): Assessment of micropaleontological sedimentary parameters as proxies of surface water properties and paleoclimate, in Gavdos Island, Eastern Mediterranean. – Geodiversitas, 29: 379-399.
- BARMAWIDJAJA, D. M., JORISSEN, F. J., PUSKARIC, S. & VAN DER ZWAAN, G. J. (1992): Microhabitat selection by benthic foraminifera in the northern Adriatic Sea. – Journal of Foraminiferal Research, 22: 297-317.
- BERGAMIN, L., DI BELLA, L. & CARBONI, M. G. (1999): Valvulineria bradyana (Fornasini) in organic matterenriched environment (Ombrone River Mouth, Central Italy). – Il Quaternario, **12**: 51-56.
- BETZLER, C., BRACHERT, T. C. & NEBELSICK, J. (1997): The warm-temperate carbonate province – a review of the facies, zonations and delimitations. – Courier Forschungsinstitut Senckenberg, **201**: 83-99.
- BOLTOVSKOY, E., SCOTT, D. B. & MEDIOLI, F. S. (1991): Morphological variations of benthic foraminiferal tests in response to changes in ecological parameters: a review. – Journal of Paleontology, **65**: 175-185.
- BRADSHAW, J. (1957): Laboratory studies on the rate of growth of the foraminifer "*Streblus beccarri* (LINNÉ) var. *tepida* (CUSHMAN)". – Journal of Paleontology, **31**: 1138-1147.
- BRADSHAW, J. (1961): Laboratory experiments on the ecology of foraminifera. – Contributions from the Cushman Foundation for Foraminiferal Research, 7: 87-106.
- BRACHERT, T. C., FORST, M. H., PAIS, J. J., LEGOINHA, P. & REIJMER, J. J. G. (2003): Lowstand carbonates, highstand sandstones. – Sedimentary Geology, 155: 1-12.
- CORLISS, B. H. (1991): Morphology and microhabitat preferences of benthic foraminifera from the Northwest Atlantic Ocean. – Marine Micropaleontology, 17: 195-236.
- DE LANGE G. J. (1986): Chemical composition of interstitial water in cores from the Nares abyssal plain (Western North Atlantic). – Oceanologica Acta, 9: 159-168.
- DEBENAY, J.-P., TSAKIRIDIS, E., SOULARD, R. & GROSSEL, H. (2001): Factors determining the distribution of foraminiferal assemblages in Port Joinville Harbour (lle d'Yeu, France): the influence of pollution. – Marine Micropaleontology, 43: 75-118.

- DEMARQ, G. & DEMARQ, H. (1989): Biostrome à Crassostrea du Quaternaire récent (Sénégal), comparaison avec ceux du Miocène (bassin rhodanien). – Géologie Méditerranéenne, **16**: 3-15.
- DERMITZAKIS, M. D. & KOUROUNI, E. (1982): Stratigraphic survey and environmental interpretation of the Neogene deposits of Keratokampos (Viannou District, central Crete). – Annales Geologiques des Pays Helleniques, **31**: 271-332.
- DRINIA, H. (2009): Foraminiferal biofacies and paleoenvironmental implications of the Early Tortonian deposits of Gavdos Island (Eastern Mediterranean). – Revue de Micropaleontology, **52**: 15-29.
- DRINIA, H., ANTONARAKOU, A., TSAPARAS, N., DERMIT-ZAKIS, M. D. & DOUKAS, C. (2004): Foraminiferal sequence eco-biostratigraphy of the Middle-early Late Miocene Potamos Section from Gavdos Island, Greece. – Courier Forschungsinstitut Senckenberg, 249: 29-43.
- ELLISON, R., BROOME, R. & OGILVIE, R. (1986): Foraminiferal response to trace metal contamination in the Patapsco River and Baltimore Harbour, Maryland. – Marine Pollution, (B), **17**: 419-423.
- ERNST, S. R., DUIJNSTEE, I. A. P., JANNINK, N. T. & VAN DER ZWAAN, G. J. (2000): An experimental mesocosm study of microhabitat preferences and mobility in benthic foraminifera: preliminary results. – In: HART, M. B., KAMINSKI, M. A. & SMART, C. W. (Eds.): Proceedings of the Fifth International Workshop on Agglutinated Foraminifera. – Crzybowski Foundation, Special Publication, 101-104.
- ERNST, S. R., DUIJNSTEE, I. A. P. & VAN DER ZWAAN, G. J. (2002): The dynamics of the benthic foraminiferal microhabitat: recovery after experimental disturbance. – Marine Micropaleontology, 46: 343-361.
- GOODAY, A. J. (1999): Biodiversity of Foraminifera and other protists in the deep sea: scales and patterns. – In: MEES, J. (Ed.): Proceedings of the 5th Benelux Congress of Zoology Gent, 6-7 November 1998. – Belgian Journal of Zoology, **129**: 61-80.
- GOODAY, A. J., LEVIN, L. A., LINKE, P. & HEEGER, T. (1992): The role of benthic foraminifera in deep-sea food webs and carbon cycling. – In: ROWE, G. T. & PARIENTE, V. (Eds): Deep-sea food chains and the global carbon cycle, 63-91; Amsterdam (Kluwer).
- GUSTAFSSON, M. & NORDBERG, K. (2001): Living (stained) benthic foraminiferal response to primary production and hydrography in the deepest part of the Gullmar Fjord, Swedish west coast, with comparison to Hoeglund's 1927 material. – Journal of Foraminiferal Research, **31**: 2-11.
- HESS, S. & KUHNT, W. (1996): Deep-sea benthic foraminiferal recolonization of the 1991 Mt. Pinatubo ash layer in the South China Sea. – Marine Micropaleontology, 28: 171-197.
- JAMES, N. P., BONE, Y., COLLINS, L. B. & KYSER, T. K. (2001): Surficial sediments of the Great Australian Bight: facies dynamics and oceanography on a vast cool-water carbonate shelf. – Journal of Foraminiferal Research, **71**: 549-567.

- JORISSEN, F. J. (1987): The Distribution of Benthic Foraminifera in the Adriatic Sea. – Marine Micropaleontology, 12: 21-48.
- (1999): Benthic foraminiferal successions across Late Quaternary Mediterranean sapropels. – Marine Micropaleontology, 153: 91-101.
- JORISSEN, F. J., BARMAWIDJAJA, D., PUSKARIC, C. & VAN DER ZWAAN, G. J. (1992): Vertical distribution of benthic foraminifera in the northern Adriatic Sea; the relation with the organic flux. – Marine Micropaleontology, 19: 131-146.
- JORISSEN, F. J. & WITTLING, I. (1999): Ecological evidence from taphonomical studies; living-dead comparisons of benthic foraminiferal faunas off Cape Blanc (NW Africa). – Palaeogeography, Palaeoclimatology, Palaeoecology, 149: 151-170.
- KAIHO, K. (1994): Benthonic foraminiferal dissolvedoxygen index and dissolved levels in the modern ocean. – Geology, 22: 719-722.
- KAMINSKI, M. A. (1985): Evidence for control of abyssal agglutinated foraminiferal community structure by substrate disturbance. – Marine Geology, 66: 113-131.
- KAMINSKI, M. A., GRASSLE, J. F. & WHITLATCH, R. D. (1988): Life History and recolonization among agglutinated foraminifera in the Panama Basin. – Proceedings of the. Second Workshop on Agglutinated Foraminifera, Vienna, Austria, June 23-26, 1986. – Abhandlungen der Geologischen Bundesanstalt, 41: 228-244.
- LANGER, M. R. & HOTTINGER, L. (2000): Biogeography of selected larger foraminifera. – In: LEE, J. J. (Ed.): Biology of Foraminifera. 46, Suppl. 1: 105-126; New York (Micropaleontology Press).
- LANGER, M. R. & LIPPS, J. H. (2003): Foraminiferal distribution and diversity, Madang Reef and Lagoon, Papua New Guinea. – Coral Reefs, 22: 143-154.
- LE CADRE, V., DEBENAY, J.-P. & LESOURD, M. (2003): Low pH effects on *Ammonia beccarii* test deformation: implications for using test deformations as a pollution indicator. – Journal of Foraminiferal Research, **33**: 1-9.
- LEVIN, L. A., CHILDERS, S. & SMITH, C. R. (1991): Epibenthic, agglutinating foraminiferans in the Santa Catalina Basin and their response to disturbance. – Deep-Sea Research, 38: 465-483.
- LINKE, P., ALTENBACH, A. V., GRAF, G. & HEEGER, T. (1995): Response of deep-sea benthic foraminifera to a simulated sedimentation event. – Journal of Foraminiferal Research, 25: 75-82.
- LOUBÈRE, P. (1997): Benthic foraminiferal assemblage formation, organic carbon flux and oxygen concentrations on the outer continental shelf and slope. – Journal of Foraminiferal Research, **27**: 93-100.
- MOODLEY, L. & HESS, CH. (1992): Tolerance of infaunal benthic foraminifera for low and high oxygen concentrations. – The Biological Bulletin, **183**: 94-98.
- MURRAY, J. W. (1991): Ecology and Palaeoecology of Benthic Foraminifera. 397 pp.; Harlow (Longman).
- (2006): Ecology and Applications of Benthic Foraminifera. – 426 pp.; Cambridge (Cambridge University Press).

- PIRRIE, D. (1989): Shallow marine sedimentation within an active margin basin, James Ross Island, Antarctica. – Sedimentary Geology, 63: 61-82.
- RATHBURN, A. E. & CORLISS, B. H. (1994): The ecology of living (stained) deep-sea benthic foraminifera from the Sulu Sea. – Paleoceanography, 9: 87-150.
- RICHTER, G. (1965): Zur Ökologie der Foraminiferen: III Verdriftung und Transport in der Gezeitenzone. – Natur und Museum, 95: 51-62.
- ROGERSON, M., KOUWENHOVEN, T. J., VAN DER ZWAAN, G. J., O'NEILL, B. J., VAN DER ZWAAN, C. J., POSTMA, G., KLEVERLAAN, K. & TIJBOSCH, H. (2006): Benthic foraminifera of a Miocene canyon and fan. – Marine Micropaleontology, **60**: 295-318.
- ROSENTHAL, L. R. P. & WALKER, R. G. (1987): Lateral and vertical facies sequences in the Upper Cretaceous Chungo Member, Wapiabi Formation, southern Alberta. – Canadian Journal of Earth Sciences, 24: 771-783.
- SCHAFER, C. T. (1973): Distribution of foraminifera near pollution sources in Chaleur Bay. – Water Air Soil Pollution, 2: 219-233.
- SCHMIEDL, G., MITSCHELE, A., BECK, S., WELDEAB, S., SCHULZ, H., HEMLEBEN, C., SPERLING, M. & EMEIS, K.-C. (2003): Benthic foraminiferal record of ecosystem variability in the eastern Mediterranean Sea during times of sapropel S5 and S6 formation. – Palaeogeography, Palaeoclimatology, Palaeoecology, 190: 139-164.
- SEIDEL, E. & OKRUSCH, M. (1978): Regional distribution of critical metamorphic minerals in Crete. – In: CLOSS, H., ROEDER, H. D. & SCHMIDT, K. E. (Eds.): Alps, Apennines, Hellenides, 448-452; Stuttgart (Schweizerbart).
- SEN GUPTA, B. K. & MACHAIN-CASTILLO, M. L. (1993): Benthic foraminifera in oxygen-poor habitats. – Marine Micropaleontology, 20:183-201.
- SHARIFI, A. R., CROUDACE, L. W. & AUSTIN, R. L. (1991): Benthic foraminiferids as pollution indicators in Southampton Water, southern England, United Kingdom. – Journal of Micropaleontology, **10**: 109-113.
- STOUFF, V., DEBENAY, J.-P. & LESOURD, M. (1999a): Origin of double and multiple tests in benthic foraminifera: observations in laboratory cultures. – Marine Micropaleontology, 36: 189-204.
- STOUFF, V., GESLIN, E., DEBENAY, J.-P. & LESOURD, M. (1999b): Origin of morphological abnormalities in *Ammonia* (Foraminifera): studies in laboratory and natural environments. – Journal of Foraminifera Research, 29: 152-170.
- STOW, D. A. V. & PIPER, D. J. W. (1984): Deep water finegrained sediments: Facies models. – In: STOW, D. A. V. & PIPER, D. J. W. (Eds.): Fine Grained Sediments: Deep Water Processes and Facies. – Geological Society of London, Special Publications, 15: 611-646.

- THOMSON, J., HIGGS, N. C., CROUDACE, I. W., COLLEY, S. & HYDES, D. J. (1993): Redox zonation of elements at an oxic/post-oxic boundary in deep-sea sediments. – Geochimica et Cosmochimica Acta, 57: 579-595.
- THOMSON, J., WILSON, T. R. S., CULKIN, F. & HYDES, D. J. (1984): Non-steady state diagenetic record in eastern equatorial Atlantic sediments. – Earth and Planetary Science Letters, **71**: 23-30.
- TSAPARAS, N. (2005): Contribution to the history of sedimentation of the Upper Cenozoic marine formations in Gavdos Island. – PhD Thesis, University of Athens.
- VAN DER ZWAAN, G. J. (1982): Paleoecology of Late Miocene foraminifera. – Utrecht Micropaleontological Bulletins, 25: 1-201.
- VERHALLEN, P. J. J. M. (1991): Late Pliocene to early Pleistocene Mediterranean mud-dwelling foraminifera; influence of a changing environment on community structure and evolution. – Utrecht Micropaleontological Bulletins, 40: 1-219.
- VICENTE, E. (1970): Eturde géologique de l'île de Gavdos (Grèce), la plus méridional de l'Europe. – Bulletin de la Société géologique de France, 7: 481-485.
- WATKINS, J. G. (1961): Foraminiferal ecology around the Orange County, California, ocean sewer outfall. – Micropaleontology, 7: 199-206.
- WILSON, T. R. S, THOMSON, J., HYDES, D. J., COLLEY, S., CULKIN, F. & SØRENSEN, J. (1986): Oxidation fronts in pelagic sediments: diagenetic formation of metal-rich layers. – Science, 232: 972-975.
- YANKO, V., AHMAD, M. & KAMINSKI, M. (1998): Morphological deformities of benthic foraminiferal tests in response to pollution by heavy metals: implications for pollution monitoring. – Journal of Foraminiferal Research, 28: 177-200.

Manuscript received: September 15th, 2009. Revised version accepted by the Bonn editor: November 5th, 2009.

#### Addresses of the authors:

HARA DRINIA, MICHAEL D. DERMITZAKIS, National and Kapodistrian University of Athens, Faculty of Geology and Geoenvironment, Department of Historical Geology and Palaeontology, Panepistimiopolis, 157 84, Athens, Greece;

e-mails: cntrinia@geol.uoa.gr; mdermi@geol.uoa.gr

Epifaunal taxa	Shallow infauna taxa	Deep infauna taxa
Asterigerinata planorbis	Ammonia beccarii	Amphicoryna scalaris
Cibicides lobatulus	Astrononion stelligerum	Globocassidulina subglobosa
Cibicidoides spp.	Bolivinidae	Globobulimina spp.
<i>Elphidium</i> spp.	Buliminidae	
Heterolepa spp.	Cassidulina laevigata	
Lenticulina spp.	Gyroidina soldanii	
Oridorsalis umbonatus	Nonion sp.	
<i>Planulina</i> spp.	Pullenia spp.	
	Uvigerina spp.	
	Valvulineria complanata	

# Appendix A – Taxa encountered in this study grouped according to microhabitat preferences

# Appendix B – Diversity indices of the studied samples from the Potamos section

Stratigraphic level (m)	Taxa_S	Dominance_D	Shannon_H
0.75	23	0.13	2.72
1.5	24	0.15	2.60
2	26	0.15	2.80
2.5	22	0.13	2.75
3	55	0.08	4.59
4.75	27	0.10	3.08
6	57	0.10	4.06
7.5	20	0.21	2.39
9.5	36	0.11	3.42
10.7	50	0.06	4.17
11.5	43	0.07	3.96
12	20	0.17	2.71
12.5	21	0.11	2.88
13	22	0.13	2.76
13.25	42	0.10	4.02
13.5	26	0.18	2.89
13.8	23	0.12	2.99
13.95	42	0.10	3.79
14.12	26	0.11	2.87
15	15	0.15	2.41
16	22	0.09	2.87
16.15	19	0.19	2.40
16.32	25	0.28	2.34
18.5	17	0.18	2.63
20.8	46	0.11	3.65
21	50	0.08	3.81
21.2	22	0.23	2.36
22.2	18	0.19	2.34
27.5	17	0.18	2.38
29.35	24	0.42	2.08
30	15	0.25	1.86
31.5	16	0.24	2.30
32.5	17	0.25	2.01
35.9	21	0.18	2.70
37.4	32	0.08	3.54
39.8	12	0.66	1.14
53	15	0.17	2.29
53.2	35	0.10	3.38
58.1	28	0.17	2.89
65.5	4	1.01	0.08

# Appendix B (cont.)

75.6	14	0.80	0.75
83.1	6	0.83	0.52
83.5	13	0.64	1.20
83.7	22	0.23	2.22
84	7	0.93	0.31
84.8	6	0.98	0.20
85.2	5	0.47	0.92
85.7	19	0.34	1.79
86	15	0.31	1.99
87	27	0.14	2.84
87.5	6	0.48	0.94
88.4	20	0.28	2.24
89.5	20	0.16	2.50
90.8	19	0.15	2.48
93.7	33	0.17	2.83
94.2	27	0.15	2.72
94.8	33	0.10	3.43
96.5	71	0.08	4.77
99.3	27	0.10	3.11
100	35	0.08	3.39
100.9	29	0.11	3.15
103.1	40	0.17	3.05
104	27	0.11	3.05
106.5	31	0.09	3.23
107	24	0.09	2.89
107.2	34	0.11	3.24
107.7	29	0.12	3.11
110.9	14	0.84	0.63
112.5	11	0.61	0.88