Research paper

Agglutination of benthic foraminifera in relation to mesoscale bathymetric features in the abyssal NE Atlantic (Porcupine Abyssal Plain)

Paris V. Stefanoudis [a,*], Ralf Schiebel [b], Romain Mallet [c], Jennifer M. Durden [a], Brian J. Bett [d], Andrew J. Gooday [d]

[a] Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton Waterfront Campus, European Way, Southampton SO14 3ZH, United Kingdom
[b] LUNAM Université, Université d'Angers, UMR-CNRS 6112, LPGN-BIAF, Laboratoire des Bio-Indicateurs Actuels et Fossiles, 2 Boulevard Lavoisier, 49045 Angers CEDEX 01, France
[c] SCIAM, Service Commun d'Imagerie et Analyses Microscopiques, IRIS-IBS Institut deBiologie en Santé, CHU d'Angers, LUNAM Université, 49933 Angers Cedex, France
[d] National Oceanography Centre, University of Southampton Waterfront Campus, European Way, Southampton SO14 3ZH, United Kingdom

A R T I C L E   I N F O

A B S T R A C T

Abyssal hills, small topographic features rising above the abyssal seafloor (<1000 m altitude), have distinct environmental characteristics compared to abyssal plains, notably the presence of coarser-grained sediments. As a result, they are a major source of habitat heterogeneity in the deep sea. The aim of this study was to investigate whether there is a link between abyssal hills and the test characteristics of selected agglutinated benthic foraminiferal species. We analysed 1) the overall morphometry, and 2) the granulometric and chemical (elemental) characteristics of the agglutinated tests of ten common foraminiferal species (*Adercotryma glomerata*, *Ammobaculites agglutinans*, *Cribrostomoides subglobosus*, *Lagenammina* sp.1, *Nodulina dentaliniformis*, *Portatrochammina murrayi*, three *Reophax* sp. and *Recurvoides* sp. 9) at four sites (two on top of abyssal hills and two on the adjacent plain) in the area of the Porcupine Abyssal Plain Sustained Observatory, northeast Atlantic. The foraminiferal test data were compared with the particle size distribution and elemental composition of sediments from the study sites in order to explore possible grain size and mineral selectivity. We found differences in the visual appearance of the tests (i.e. the degree of irregularity in their shape), which was confirmed by morphometric analyses, related to seafloor topography. The agglutinated foraminifera selected different sized particles on hills and plains, reflecting the distinct granulometric characteristics of these settings. These characteristics (incorporation of coarse particles, test morphometry) could provide evidence for the recognition of ancient abyssal hill environments, as well as other palaeoceanographic settings that were characterised by enhanced current flow. Furthermore, analyses of sediment samples from the hill and plain sites using wavelength dispersive X-ray fluorescence (WD-XRF) yielded different elemental profiles from the plains, probably a result of winnowing on the hills, although all samples were carbonate-rich. In contrast, the majority of the agglutinated tests were rich in silica, suggesting a preferential selection for quartz.

1. Introduction

Abyssal plains are vast areas of the ocean floor situated at water depths between 3500 and 6500 m. They make up almost two-thirds of the Earth's surface (Watling et al., 2013), yet despite their immense size they have received disproportionately little scientific attention compared to other ocean habitats (Stuart et al., 2008). Often regarded as topographically homogeneous, abyssal plains are populated by abyssal hills, typically up to a few hundred meters in height and a few kilometres in width. These represent one of the most important geomorphic features in the oceans (Heezen et al., 1959; Heezen and Holcombe, 1965; Goff and Arbic, 2010). Abyssal hills share many environmental characteristics with larger underwater features such as submarine knolls and seamounts (Yesson et al., 2011), which led to the term seamount being applied to any topographic rise >100 m high (Pitcher et al., 2007; Clark et al., 2010). However, here we retain the term 'abyssal hills' for relatively low (<1000 m) topographic rises located on the abyssal seafloor, and treat them as distinct topographic entities. Abyssal hills increase habitat complexity on the seafloor and may potentially alter benthic faunal patterns and diversity (Snelgrove and Smith, 2002; Rex and Etter, 2010). There is an extensive literature on the effects of habitat heterogeneity on benthic diversity patterns. Studies have focussed mainly on the finer spatial scales (centimeters to meters) represented by biogenic structures and the patchy distribution of organic matter (Gooday, 1986; Levin et al., 1986; Thistle and Eckman, 1990; Hasemann and Soltwedel, 2011; Warren et al., 2013) but have also

* Corresponding author.
E-mail address: p.v.stefanoudis@soton.ac.uk (P.V. Stefanoudis).

addressed broader scales (mesoscale, i.e. decimetres to kilometres) by comparing assemblages from environmentally contrasting sites (Thistle, 1983; Kaminski, 1985; Gage et al., 1995; Baldrighi et al., 2014). However, very few studies (e.g., Durden et al., 2015) have explored the impacts of abyssal hills on deep-sea communities and none has dealt with meiofaunal groups such as the foraminifera.

Benthic foraminifera are a successful group of largely marine testate protists within the Rhizaria (Adl et al., 2012; Ruggiero et al., 2015). The 'tests' (shells) of some species are preserved in marine sediments and represent important proxies in palaeoceanography. They are a major component of modern soft-bottom meio- and macro-faunal communities on abyssal plains and play an important role in ecological processes on the ocean floor (Gooday et al., 1992). During the analysis of foraminiferal samples collected in the area of the Porcupine Abyssal Plain Sustained Observatory (PAP-SO; Hartman et al., 2012) in the northeast Atlantic (4800 m water depth), we found variation in the community composition of benthic foraminiferal assemblages obtained at sites on the tops of abyssal hills and on the adjacent abyssal plain (Stefanoudis et al., 2015). In addition, we observed apparent differences in the agglutination patterns (size and nature of the cemented particles) and morphology of benthic foraminiferal tests in relation to these two topographic settings (i.e. hills vs. plain). The overall aim of this study was to investigate whether and how environmental differences between the hills and the plain affect the construction of agglutinated benthic foraminiferal tests in this region. Specifically, we were interested in 1) whether the same species select particles of different (a) sizes and (b) composition in these two settings, and 2) the extent to which any differences in particle selection influences the test morphology. To address these questions we analysed the overall morphometry as well as the granulometric and chemical (elemental) characteristics of the agglutinated tests of selected common foraminiferal species in the PAP-SO area.

2. Materials and methods

2.1. Sample collection and study site

Samples were collected during RRS James Cook Cruise 062 (JC062, 24 July to 29 August 2011; Ruhl, 2012) in the vicinity of the PAP-SO area. They were obtained using a Bowers and Connelly Megacorer (Gage and Bett, 2005) equipped with core tubes (59 mm internal diameter) from two abyssal plain sites (P1, P2) and two abyssal hill sites (H1, H4) (Fig. 1; Table 1). Distances between sites were in the range of tens of kilometres. On board the ship the cores were sliced into 0.5-cm-thick layers down to 2-cm sediment depth, followed by 1-cm-thick layers from 2 to 10-cm depth, and each slice fixed in 10% Borax buffered formalin. The present contribution is based on material retained on a 150-μm sieve from the 0–1 cm sediment horizon of eight samples. Sixty-five foraminiferal specimens (23 from abyssal plain sites, and 42 from abyssal hill sites) belonging to 10 agglutinated taxa were included in the analysis (Table 1). The selection of species was based on their numerical abundance and an initial assessment of the variability in the size and nature of the agglutinated particles that constituted their tests. The species, the number of specimens of each examined, and the types of analyses employed, are detailed in Appendix A. A brief description of the species is given in section Taxonomic Appendix.

Durden et al. (2015) present data on the physical characteristics for our sampling sites. Particle size distribution (0–5 cm sediment horizon) at all sites was bimodal, with peaks at 4 and 200 μm and a trough at 22.9 μm. The fine sediment fraction (<23 μm) comprised mainly
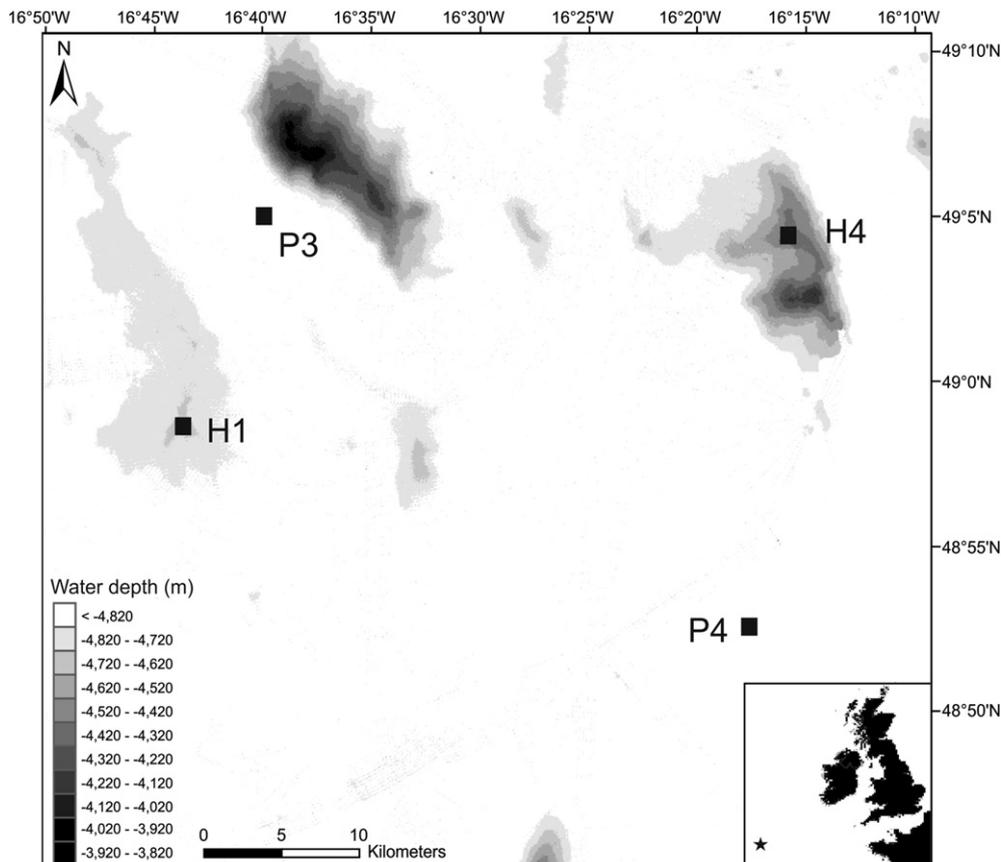
Fig. 1. Bathymetric map of the PAP-SO area indicating the location of the four study sites, P3 and P4 (abyssal plain sites), H1 and H4 (abyssal hill sites). The inset indicates the general location of the Porcupine Abyssal Plain in the northeast Atlantic Ocean.

Table 1
Locality data. N_1 = number of replicate samples from which foraminiferal specimens have been collected and used in this study. N_2 = number of specimens analysed from each site. N_3 = Number of sediment samples for particle size analysis. N_4 = Number of sediment samples for elemental analysis. For geographical position of sites consult Fig. 1.

Site	Topography	Centre latitude (N)	Centre longitude (W)	Water depth (m)	N_1	N_2	N_3	N_4
P3	Abyssal plain	49.083	−16.667	4851–4853	1	4	5	1
P4	Abyssal plain	48.877	−16.293	4849–4851	2	19	5	2
H1	Abyssal hill	48.978	−16.728	4669–4679	3	16	5	1
H4	Abyssal hill	49.074	−16.243	4339–4388	2	26	2	1

coccoliths, while the coarser fraction (23–1000 μm) was dominated by foraminiferal tests, indicating sediments with high carbonate content (i.e. carbonate ooze). The size contrast between the two sediment components generated the bimodal particle-size distribution observed in all samples. The coarser fraction constituted a higher proportion of the sediment on the abyssal hills, where larger mineral grains, including pebbles to cobble-sized ice-rafted stones were also observed, enhancing the larger of the two size peaks. Median seabed slope was greater and more variable at the abyssal hill sites compared to the plain sites, and the slope of H4 (8.6°) was more than double that of H1 (4.0°). Organic matter input estimated from seabed images and expressed either as the percentage of the seafloor covered by phytodetritus or as median detritus aggregate size, did not vary spatially in the PAP-SO area.

2.2. Test morphometry

Initially, all 65 specimens were photographed under an incident light microscope (Leica Z16-APO). The majority (56) were then examined by scanning electron microscopy (SEM) using an environmental Zeiss EVO LS10 at variable pressure. The number of SEM images was lower than the number of light microscope images because some delicately agglutinated species collapsed upon transfer to SEM stubs (mostly specimens of *Nodulina dentaliniformis*). Subsequently, both sets of images were processed and a total of 31 morphometric parameters were obtained using image analysis software (analySIS version 5.0, Olympus Soft Imaging Solutions). The resulting morphometric data from both sets of microscopic images were compared for consistency. As there were no significant statistical differences, the light transmission microscopy dataset, which was based on a larger number of specimens (65 compared to 56 SEM images), was selected for further analyses of the overall test morphometry (see Appendix A). Tests incorporating long spicules (mostly belonging to *Reophax* sp. 28) were not included in the analysis as the image analysis software overestimated their surface area, lowering the total number of specimens suitable for morphometric comparisons to 60 (see Appendix A).

Multivariate assessment of the data was computed using PRIMER 6 (Clarke and Gorley, 2006). Euclidean distance similarity matrices were created for the morphometric data and their relation to topography was explored using Multi-dimensional Scaling (MDS) and Analysis of Similarities (ANOSIM). We first worked on the complete set of morphometric parameters before focusing on the following reduced set of four parameters (see Fig. 2) that seemed to drive most variation in the data: (i) Convexity, defined as the ratio between the actual measured test area (an irregular surface) and an imaginary smooth envelope that encloses the test (Fig. 2a); (ii) Maximum to Minimum Diameter ratio (Fig. 2b); (iii) Perimeter to Area ratio (Fig. 2c); and (iv) Sphericity, which gives information about the roundness of the test (Fig. 2d). In general, specimens with more irregular, "bumpier" morphologies will tend to have lower convexity and sphericity values, and higher perimeter to area and maximum to minimum diameter ratios, while the opposite will hold true for specimens with smooth surfaces and a more circular appearance. We assessed the effect of individual parameters using the Student's t and Mann–Whitney U tests, for normally and non-normally distributed data respectively (Shapiro–Wilk test; $p < 0.05$).

The relationship of these parameters to topography was assessed using morphometric data from all species as well as focusing on four species (*Adercotryma glomerata*, *Lagenammina* sp.1, *N. dentaliniformis* and *Reophax* sp. 21) that were represented by enough specimens (≥3) in both settings to permit statistical comparisons (see Appendix A).

2.3. Particle size

Test particle size was measured from a set of 56 SEM images. Initially, an automated counting procedure was used, similar to the one described in Armynot du Châtelet et al. (2013a). However, it could not cope well with the heterogeneous nature of the particles found in the foraminiferal tests and therefore its use was discontinued. Instead, measurements were made manually using ImageJ (Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997–2014), and restricted to particles ≥10 μm. Size was determined as the longest axis dimension of the grains. In order to relate particle size to topography, the data were divided into 25 size classes based on the geometric mean particle diameter, spanning grain sizes from 10 to 295 μm, and the resulting particle size distributions were compared. The effect of topography could be tested further for four species (*A. glomerata*, *Lagenammina* sp.1, *Reophax* sp. 21, *Reophax* sp. 28) that were represented by sufficient specimens (≥3) in both settings.

Grain size characteristics for the four study sites were assessed from seventeen samples (Fig. 1; Table 1) that were obtained using a Bowers and Connelly Megacorer equipped with multiple core tubes (59 and 100 mm internal diameter) (Gage and Bett, 2005). On board the ship the cores were sliced in three layers (0–1, 1–3, 3–5 cm) and each slice was stored in plastic bags with no preservative for later analysis. Sediment particle size distributions were measured by laser diffraction using a Malvern Mastersizer, after homogenisation (particles >2 mm removed), dispersal in a 0.05% $(NaPO_3)_6$ solution (Abbireddy and Clayton, 2009), and mechanical agitation. Detected particle sizes ranged from 0.01 to 2000 μm. The percentage of particles >63 μm in the sediments
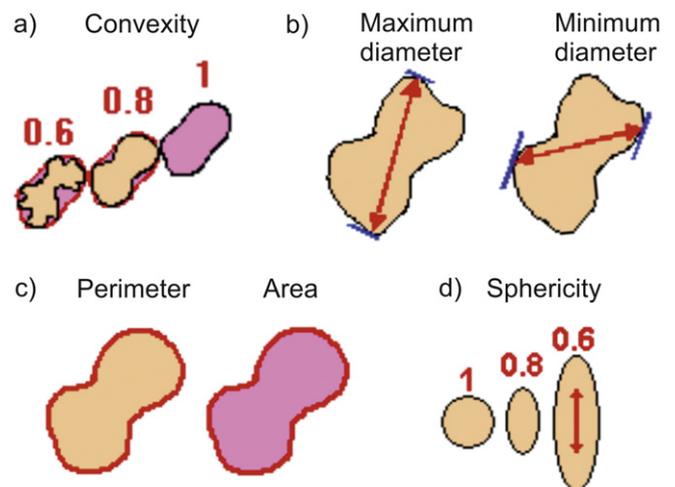
Fig. 2. The four morphometric descriptors driving most variation in the data (iconography from analySIS version 5.0, Olympus Soft Imaging Solutions). (a) Convexity. (b) Maximum to Minimum Diameter ratio. (c) Perimeter to Area ratio. **(d)** Sphericity.

of each site and topographic setting was also estimated, as in deep-sea sediments it can serve as a proxy of current activity (McCave et al., 1995; McCave and Hall, 2006). The present contribution is based on material from the 0–1 cm sediment horizon. In order to test for particle size selectivity by the foraminifera, we compared particle-size distribution data from the tests and the sediment samples, focusing on particles within the 10 to 295 μm range, which covers the same 25 size classes used to analyse foraminiferal grains.

2.4. Elemental composition

Quantitative estimates of the elemental composition of 56 benthic foraminiferal tests (see Appendix A) were carried out using an Environmental Scanning Electron Microscope (ESEM) (Zeiss EVO LS10) equipped with an Energy-Dispersive Spectroscopy (EDS) device (X-Max, Oxford Instruments).

The elemental composition of sediments from the hills and plains was determined by applying wavelength-dispersive X-ray fluorescence (WD-XRF) techniques to five samples, three from the plains and two from the hills (Table 1). Major elements were determined in fused beads obtained following fusion with a pure lithium borate flux in a Pt–Au vessel at c. 1100 °C. Lithium tetraborate (Fluxana, Germany) was used to dissolve the samples prior to major element determinations. Trace elements were analysed using pressed powder pellets. A Philips MAGIX-PRO automatic sequential WD X-ray fluorescence spectrometer was used to determine element concentrations. The elements were excited by means of a 4 kW Rh end-window X-ray tube. The instrument was calibrated using a wide range of international geochemical reference samples; accuracy was typically within 5% of the consensus value when an international reference sample was run as an unknown. The 2σ precision is typically 1–5%. Following conventional practice in geochemistry, the major element compositions were expressed as oxides. We then calculated the proportion of each element separately based on their atomic number in order to compare sediment elemental data with the elemental composition of the tests.

3. Results

3.1. Visual comparison of agglutinated foraminifera tests from hill and plains

The ten species used in this study are illustrated in Plates 1–3 and brief descriptions given in section Taxonomic Appendix. There were clear differences in the visual appearance of tests from topographically high and low sites. Specimens from the hills incorporated a higher number of larger particles (i.e. >100 μm) (Table 2) in their test walls, which gave them a more or less irregular ('lumpier') appearance with rougher surfaces than those from the plain sites (Plates 1, Figs. 3–6; 2; 3). In certain species, notably *Reophax* sp. 21, which utilised some conspicuously large grains (up to almost 300 μm in size), the effect of these larger particles on the shape and appearance of the test was particularly evident (Plate 2, Figs. 5–6). However, these striking differences did not hamper the recognition of species that were common to the two settings (e.g., Plate 2, Figs. 3–10).

3.2. Particle size analysis

A summary of test particle size data for the agglutinated foraminifera is given in Table 2. In general, the average size and standard deviation of test particles was higher for hill specimens, although median values were comparable between hills and plains. ANOSIM results showed that the overall particle size composition of the tests (i.e. taking into account all 25 particle size classes) was not related (p > 0.05) to the topographic setting. At the species level, only *A. glomerata* showed significant differences in particle size (ANOSIM, p = 0.048), with abyssal hill specimens utilising coarser particles on average (Table 2).

Sediment particle size distributions for the four studied sites were bimodal with peaks at approximately 4 μm and 200 μm (Fig. 3a), although on average the abyssal hills had a greater proportion of coarser material (>63 μm) compared to the plain sites (Student's t, p < 0.05) (Fig. 3a; Table 3). Within the 10–295 μm size range, which spanned the data we used to test for particle size selectivity by the foraminifera, ANOSIM found statistically significant differences (p < 0.01) in particle size composition between hill and plain sediments.

An MDS ordination based on the particle size data derived from all ten species (56 specimens) and four sites (17 sediment samples) revealed differences between test and sediment samples (Fig. 3b). On an MDS plot the distance between two points corresponds to their degree of similarity in composition (i.e. closely spaced points are compositionally similar). Box–Whisker plots of the MDS x and y-ordinates against topography indicated that foraminiferal tests from the two hills contained particles that spanned a wider size range than those from the plain (Fig. 3c), reflecting the greater abundance of coarse particles available in these settings. Consistent with the above-mentioned ANOSIM results, hill and plain specimens did not form well-defined groupings and had significant overlap (Fig. 3b). Sediment samples from the four sites exhibited lower levels of particle size variability compared to the tests. In the case of the plain sediments this was particularly evident from plots of the MDS x and y-ordinates against topography (Fig. 3c). Sediment samples were also clearly separated from most of the tests (Fig. 3b). This was to be expected, as the sediment particle data used extends several size classes below and above the studied size range (10–295 μm). Consequently, sediment samples had higher proportions of coarser particles compared to the foraminifera, which always included only a few coarse grains in their tests (Fig. 3d).

Unlike the foraminiferal tests, hill and plain sediment samples showed no overlap on the MDS plot, further highlighting their different particle size compositions (Fig. 3b). Interestingly, H1 sediment samples were positioned between the plain (P3, P4) and the H4 samples, indicating an intermediate composition. In order to explore this further, an additional ANOSIM of sediment particle data against study site was performed. Initial results were significant (p < 0.01), and further pairwise comparisons revealed that the particle size composition was similar between the two plain samples (P3, P4), but significantly different from the hill site H1 (P3 vs. H1, p = 0.016; P4 vs. H1, p < 0.01). Unfortunately, the low number of sediment samples (2) from H4 did not permit pairwise comparisons with the rest of the sites, but based on their positioning on the ordination plot (Fig. 3b) we assume that the particle-size composition is different from both plain samples, and perhaps from H1 as well.

In the light of these findings, we wanted to explore the inconsistency between the coarser sediments on the hills (especially at H4) and the apparent lack of correlation between test particle size and topographic setting. To do this we performed an additional ANOSIM on particle size data from all 56 tests against the study sites P4, H1 and H4 (P3 had particle data only from two specimens and thus could not be compared). This analysis yielded significant results (p = 0.021). Additional pairwise comparisons demonstrated that specimens from H4 had significantly different particle size composition compared to specimens from P4 (p < 0.01) as well as H1 (p = 0.036), whereas H1 specimens were not different from P4.

3.3. Morphometric analysis

Multivariate analysis of morphometric data (31 parameters) did not reveal significant differences in test morphology between foraminiferal tests from abyssal hills and plains. Further analyses using a reduced set of four parameters (convexity, maximum to minimum diameter ratio, perimeter to area ratio and sphericity) produced significant results (ANOSIM, p < 0.01), although further tests did not attribute this variation to any single morphometric character.
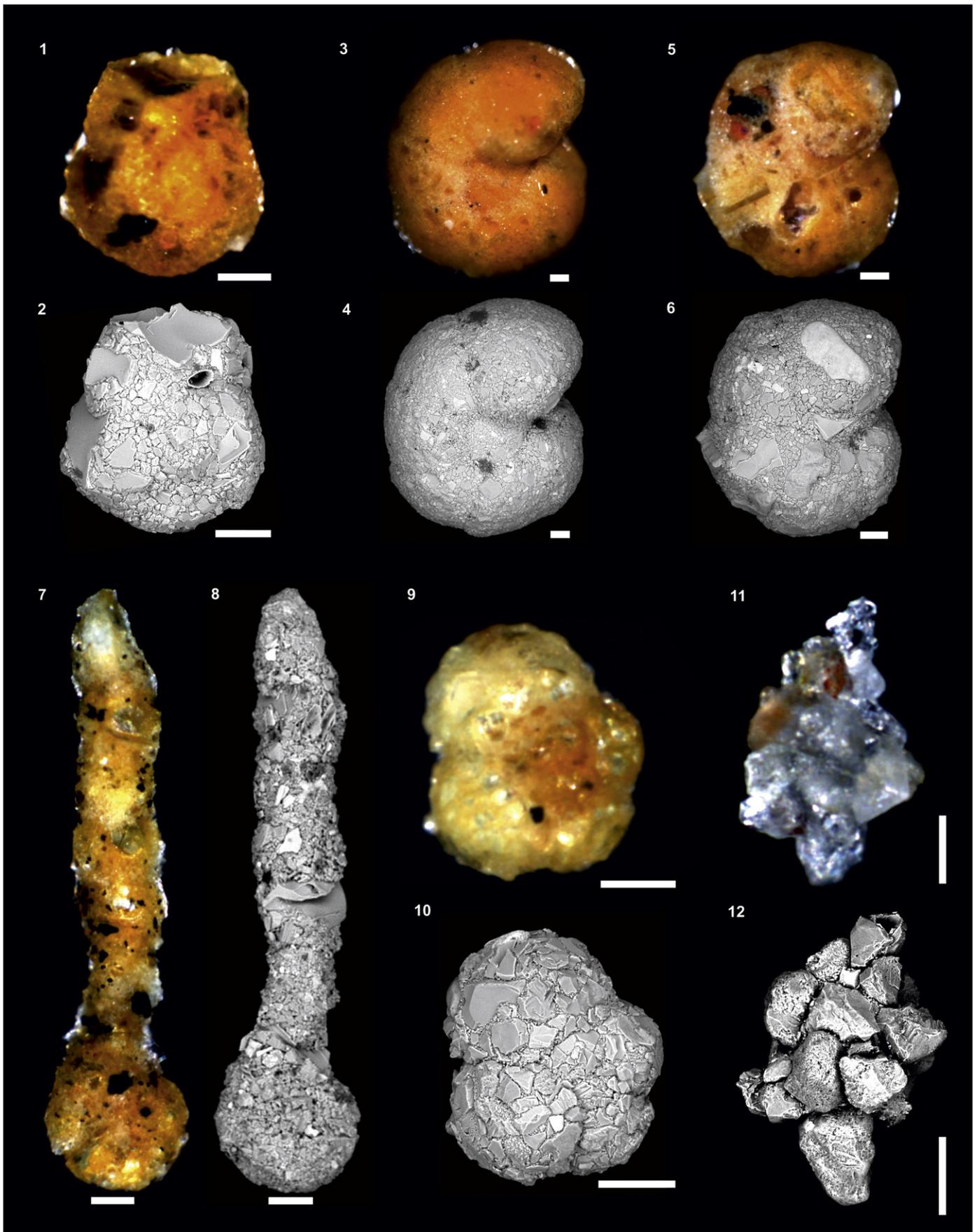
Plate 1. Light and SEM photographs of some species used in this study along with the site of collection. **Figs. 1–2**. *Recurvoides* sp. 9 (H1). **Figs. 3–6**. *Cribrostomoides subglobosus*: **3–4** (P3); **5–6** (H4). **Figs. 7–8**. *Ammobaculites agglutinans* (H1). **Figs. 9–10**. *Portatrochammina murrayi* (H4). **Figs. 11–12**. *Reophax* sp. 9 (H4).Scale bars = 100 μm.
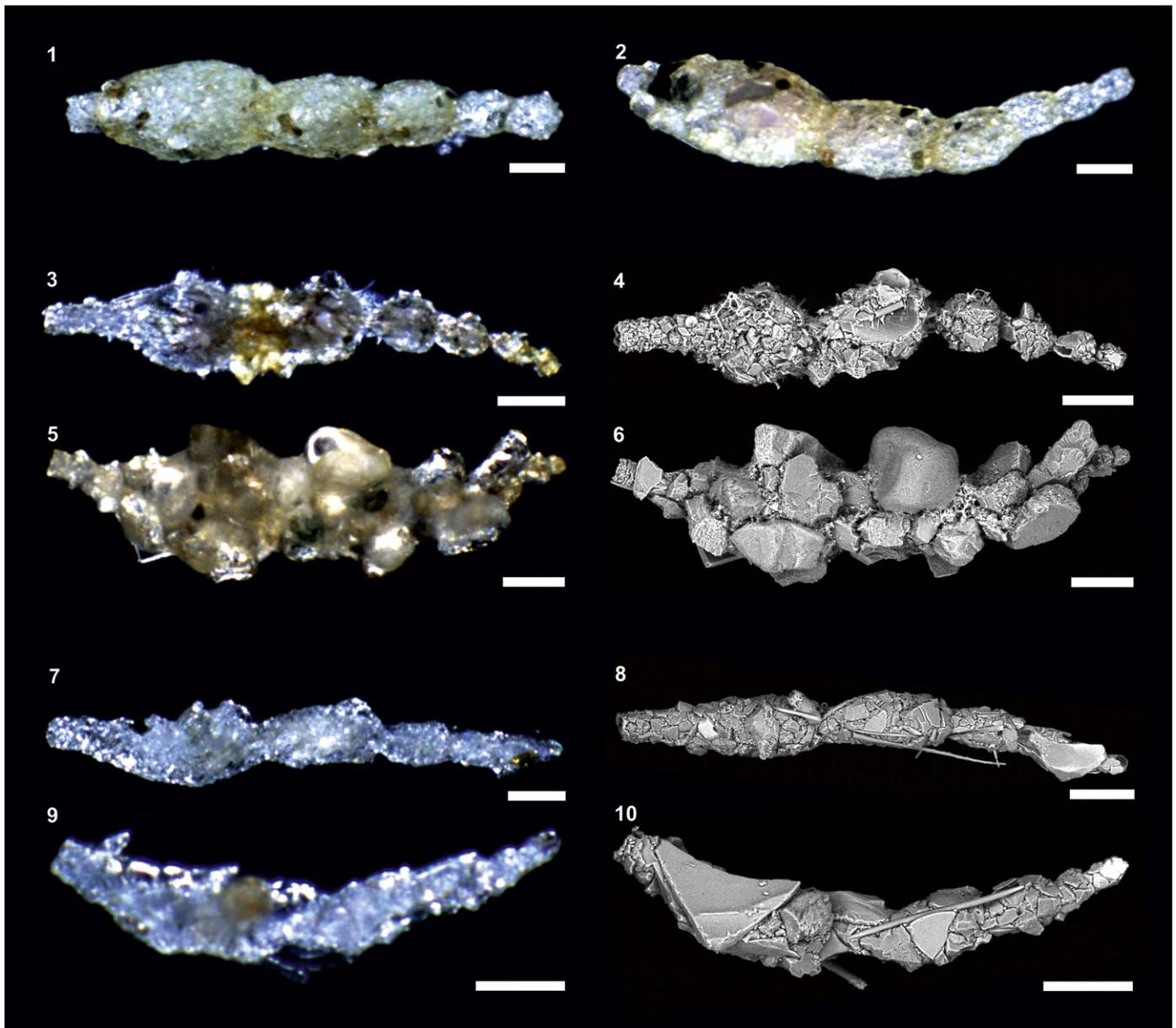
Plate 2. Light and SEM photographs of some species used in this study along with the site of collection. **Figs. 1–2.** *Nodulina dentaliniformis*: **1,** (P4); **2,** (H4). **Figs. 3–6.** *Reophax* sp. 21: **3–4**, (P4); **5–6**, (H4). **Figs. 7–10.** *Reophax* sp. 28: **7–8**, (P4); **9–10**, (H1). Scale bars = 100 μm.

At the species level, ANOSIM with 31 morphometric parameters yielded significant differences related to topography only in the case of *A. glomerata* (p < 0.035). *Reophax* sp. 21 showed variation in test morphometry between hills and plains only when taking into account the reduced set of four parameters (ANOSIM, p < 0.018). Furthermore, Student's t and Mann–Whitney U tests identified differences in the convexity and sphericity of *N. dentaliniformis* (p = 0.027 and p = 0.048, respectively) as well as in the maximum to minimum diameter ratio and sphericity of *Reophax* sp.21 (p < 0.01 in both cases).

All the morphometric characters estimated for the studied specimens can be found in Appendix B.

3.4. Elemental analysis

ESEM–EDS identified a total of 16 elements (10 major and 6 trace) from 56 benthic foraminiferal tests. Silica (Si) was by far

the most abundant element, reflecting high quartz content, consistent with peaks in Si and oxygen (O) in most EDS spectra. WD-XRF identified a total of 11 major elements and 21 trace elements in the five sediment samples taken from the four study sites. Ca was the dominant element, with CaO constituting approximately 39% in all samples (41% and 37% in hill and plains samples, respectively) reflecting the presence of carbonate oozes at the PAP-SO. The next most abundant element was Si, with SiO constituting approximately 15% in all samples (14% and 17% in hill and plain samples, respectively).

The elemental composition of the foraminiferal tests was markedly different from that of the sediment samples (ANOSIM, p < 0.01; Fig. 4a). There was no significant correlation with topographic setting for all studied material (56 tests belonging to 10 species) or for individual species (*A. glomerata*, *Lagenammina* sp.1, *N. dentaliniformis* and *Reophax* sp. 21). This was further demonstrated by the considerable

Plate 3. Light and SEM photographs of some species used in this study along with the site of collection. **Figs. 1–4.** *Adercotryma glomerata*: **1–2,** (P4); **3–4,** (H4). **Figs. 5–10.** *Lagenammina* sp. 1: 1st morphotype, **5–6,** (P4); **7–8** (H4); 2nd morphotype, **9–10** (P4), **11–12** (H4). Scale bars = 100 μm.
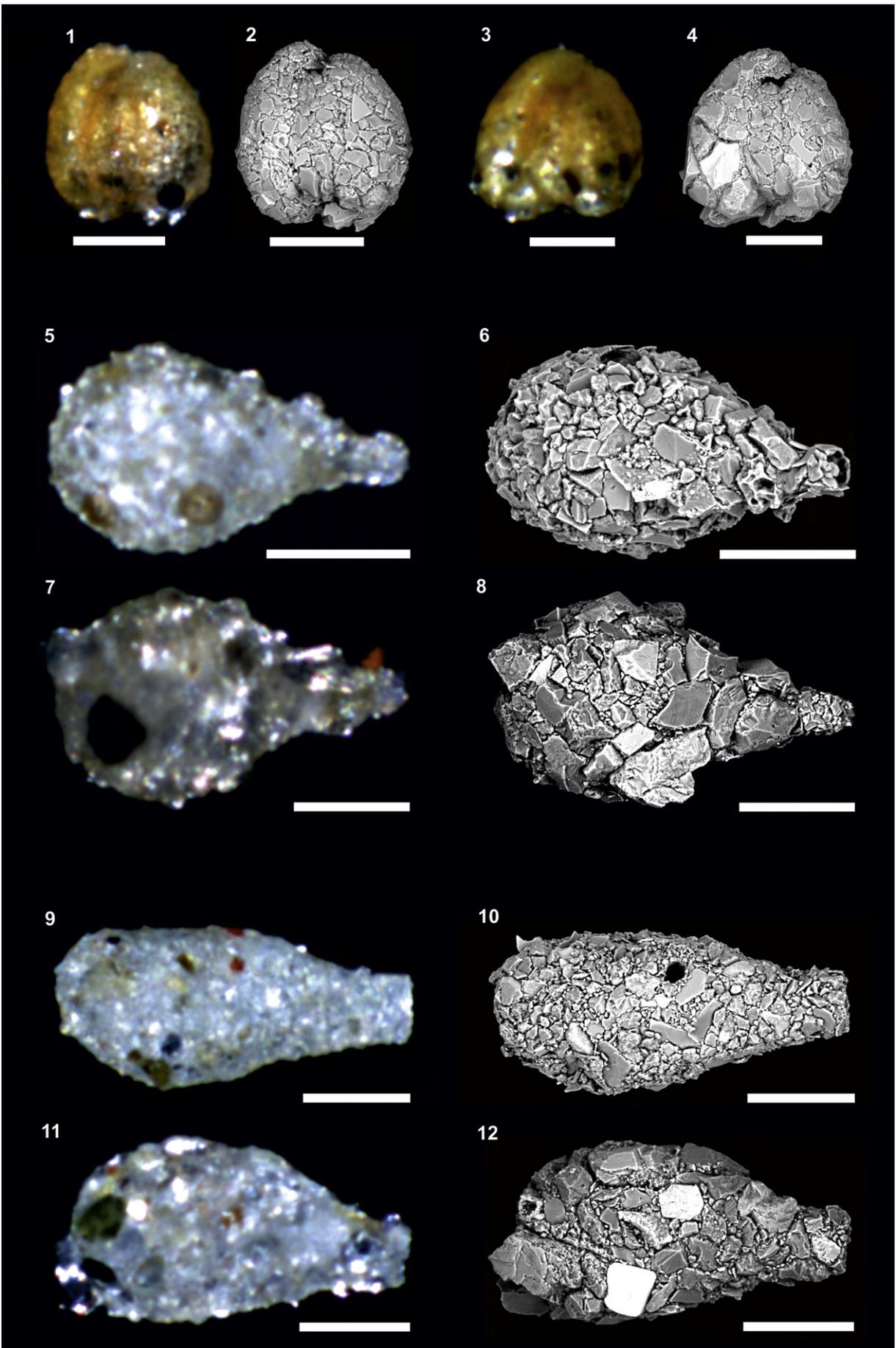
overlap of species from both settings in the MDS plot (Fig. 4b). On the other hand, MDS of the sediment elemental data yielded distinct clusters for abyssal hill and abyssal plain sites, respectively (Fig. 4c). An additional t-test on the MDS X-ordinate of the five sediment samples was significant (p < 0.01), indicating distinct elemental profiles for abyssal hills and plain.

All the data used for the elemental analysis can be found in Appendix C.

4. Discussion

4.1. Limitations of dataset

As our samples were fixed in formalin, we could not obtain molecular data to support our contention that the same foraminiferal species occur at the hill and plain sites. However, we took considerable care to compare specimens using light and scanning electron microscopy and are confident that similar specimens can be considered conspecific on the basis of morphological characters (see section Taxonomic Appendix).

The particle size analysis of the agglutinated tests was based on two-dimensional SEM images in which only one side of each specimen was visible. In addition, particles <10 μm were too small to be reliably measured from SEM images and therefore this finest sediment fraction could not be included in the analysis. Creating an automated, accurate and high-resolution (sub-micron scale) method for counting the entire range of agglutinated particles in benthic foraminiferal tests remains a challenge for the future.

4.2. Do agglutinated foraminifera utilize different sized particles in hill and plain settings?

In the deep sea, areas with elevated current activity have been shown to consist of coarse-grained sediments as a result of winnowing processes (Kaminski, 1985; Schröder, 1988; Aller, 1989); these areas include topographic high points such as seamounts (Genin et al., 1986; Levin and Nittrouer, 1987; Levin and Thomas, 1989). Although we lack current-meter data for our specific study sites, sediment grain-size distributions provide some indication of the hydrodynamic regime at our study sites. In the deep sea, sediments of the 10–63 μm range (sortable silt) are thought to be most easily eroded by current activity (McCave et al., 1995; McCave and Hall, 2006). Thus, higher proportions of particles >63 μm should be an indicator of enhanced current flow. This has been empirically established for a large abyssal hill (height >900 m) in the PAP-SO area, where numerical modelling predictions of higher flow intensity above parts of the topographic feature correlated well with actual grain-size patterns (i.e. higher proportions of particles >63 μm) found the sedimentary record (Turnewitsch et al., 2004; Turnewitsch et al., 2013). The sediments on the abyssal hills that we sampled consisted, on average, of greater proportions of particles >63 μm compared to the adjacent abyssal plain (Fig. 3a; Table 3). In addition, hill sites from this area (including H1 and H4), were found to have greater median seabed slope compared to plain sites (including P3 and P4) (Durden et al., 2015). Considering the above, substantial hydrographic differences between our hill and plain sites (i.e. elevated current activity above the hills) are likely. These differences were found to have a significant effect on the faunal composition of benthic foraminifera from the same sites (Stefanoudis et al., 2015) and are going to be discussed in more detail on a future publication (Stefanoudis et al., in prep).

Our present results suggest that differences in sediment granulometry between our plain and hill sites are reflected in differences in foraminiferal test agglutination. Specimens collected from abyssal hills agglutinated larger particles, mirroring the coarser nature of the surrounding sediments. This was evident simply from a visual comparison of specimens from the hill and plain settings, with the latter having a more irregular morphology than the former (Plates 1, Figs. 3–6; 2; 3), although those differences were not confirmed by numerical analyses. Similarly, at the species level statistical analyses revealed no significant differences in test particle size composition with topography for the rest of the species, except in the case of A. glomerata. This is probably because the number of large agglutinated grains (>100 μm) was low in relation to the finer-grained component. A few coarse grains incorporated in an otherwise finely agglutinated foraminiferal test can have a disproportionate effect on its overall shape and appearance (e.g. Plate 2, Figs. 3–6). Another factor may be that we grouped together the two abyssal hill sites (H1 and H4), despite their significant bathymetric differences (see Table 1). H4 was located at the top of the highest and steepest hill and was characterised by a much larger fraction of particles >63 μm compared to H1 (Table 3). Similarly, pairwise comparisons using ANOSIM revealed that specimens from H4 had significantly coarser agglutination than those from H1. By amalgamating data from these two topographic high sites and comparing them to the plain, statistical differences in test particle size composition of foraminifera became insignificant.

Previous studies have suggested that particle selection by size occurs in some species of agglutinated foraminifera (Sliter, 1968; Salami, 1976; Bowser and Bernhard, 1993; Gooday et al., 1995; Allen et al., 1999; Bowser et al., 2002; Bartholdy et al., 2005). However, based on visual inspection of the specimens combined with statistical tests, we conclude that the agglutinated foraminiferal species included in this study were not selecting for particular particle sizes. Instead, the composition of their tests reflected the sedimentary environment in which they resided. In some early culture experiments, Slama (1954) observed that Ammobaculites, a genus included in the present study (Plate 3, Figs. 7–8), indiscriminately agglutinated particles of different composition and size. Since then, further studies have demonstrated non-selectivity for particle size in some agglutinated foraminifera (Buchanan and Hedley, 1960; Wells, 1985; Thomsen and Rasmussen, 2008; Armynot du Châtelet et al., 2013b, 2013c). In a comparative study of benthic foraminiferal assemblages between two deep-sea habitats in the central north Pacific and western north Atlantic, Schröder (1986) and Schröder et al. (1988) found that certain species, including their Reophax scorpiurus, which resembles Reophax sp. 21 of the present study (see section Taxonomic Appendix), were non-selective for particle size and thus exhibited wide morphological variability in different sedimentary environments. Moreover, Cyclammina pusilla that usually uses small quartz grains for test construction was found to also incorporate volcanic ash grains in its test, as soon as these particles became prevalent in the sediments following the 1991 Mt Pinatubo eruption (Hess et al., 2000).

4.3. Does the composition of the substratum affect test morphometry?

To our knowledge, only a few studies have examined the relationship between substratum and the test morphometry of agglutinated foraminifera. Hada (1957) observed that foraminifera living in coarser sediments have coarser test surfaces. Haake (1977) noted that tests of Textularia pseudogamen become broader (i.e. higher width/length ratio) on coarser sediments. Schröder (1986) and Schröder et al. (1988) commented on the intraspecific morphological variability of Reophax species as a reponse to different substratum characteristics (see previous section). Recently, Mancin et al. (2015) noted changes in the wall thickness of some agglutinated foraminifera that were linked to tephra deposits. With the exception of Haake (1977), the results from the rest of the studies were qualitative as they were mainly based on visual observation of the tests. Such approaches can be informative and have been successfully applied in paleoenvironmental studies (e.g. Kaminski and Schröder, 1987). However, in order to detect trends in the shape of agglutinated tests under different environmental conditions, quantitative morphometric data are necessary. The present work is the first to investigate changes in test morphology related to different

Table 2
Summary statistics of test particle size composition for species found in both hills and plains and all species for each setting combined.

Species	Plains				Hills			
	Mean (µm)	Median (µm)	SD	>100 µm	Mean (µm)	Median (µm)	SD	>100 µm
Adercotryma glomerata	19.0	17.2	7.9	0%	25.6	18.5	18.1	0.8%
Cribrostomoides subglobosus	25.1	22.1	12.3	0.1%	24	19.3	22.7	1.7%
Lagenammina sp. 1	22.6	19.7	11.4	0.2%	28.8	21.1	21.8	1.6%
Recurvoides sp. 9	15.7	14.3	5.5	0.0%	24.8	19.6	16.1	0.3%
Reophax sp. 21	21.1	17.1	15.7	0.3%	33.6	19.3	35.9	6.3%
Reophax sp. 28	21.7	18.6	13.2	0.3%	25.3	18.5	23.2	1.4%
All species	22.1	19.3	12.0	0.1%	27	19.3	23.8	2%

sedimentary environments both qualitatively (i.e. visual observation of tests) and quantitatively (i.e. by using a range of morphometric parameters).

We failed to find clear evidence for differences in particle size selection between the agglutinated foraminiferal tests from the hill and plain sites, despite the different granulometric profiles of the two topographic settings. Nevertheless, all species that could be compared directly had more irregularly shaped tests at the highest site (H4) as a result of the incorporation of a relatively few large grains (Plates 1, Figs. 3–6; 2; 3). This was particularly evident in the case of *Reophax* sp. 21. These

obvious visual differences were confirmed by morphometric analyses. A comparison of all agglutinated tests between abyssal hill and plain sites demonstrated that there is a systematic morphometric difference that could not be expressed in terms of a single character. Instead, a combination of four parameters (convexity, maximum to minimum diameter ratio, perimeter to area ratio and sphericity) was more effective in differentiating tests from the two settings.

At the species level, differences in test morphology related to topography were significant for *A. glomerata*, *N. dentaliniformis* and *Reophax* sp. 21. In the case of *A. glomerata* it was the combined effect of all 31
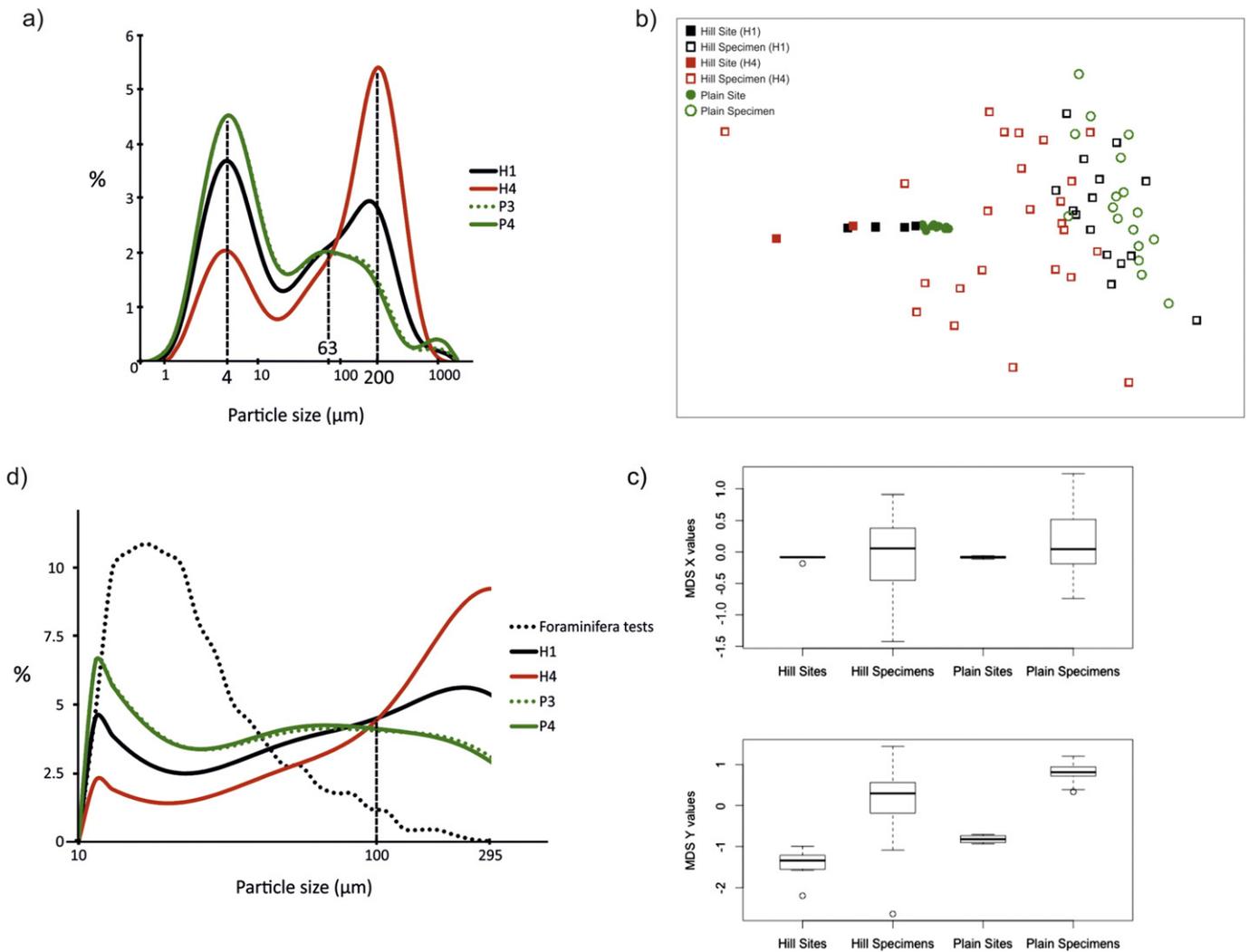
Fig. 3. (a) Mean particle size distribution (0–1 cm sediment horizon) of sediment samples from the four study sites. (b) MDS on the particle size distribution of 56 benthic foraminiferal tests and seventeen sediment samples from four sites. (c) Box–Whisker plots of the MDS x- and y-ordinate for the sediment samples and foraminiferal tests against topography. d) Mean particle size distribution (0–1 cm sediment horizon) of the foraminiferal tests and sediment samples from the four study sites.

Table 3
Mean percentages of the coarse sediment particle fraction (>63 μm) against the whole range of measured particles (0.01–2000 μm) for each of the four study sites and topographic settings.

Site	>63 μm (%)
P3	24.8
P4	24.9
H1	38.2
H4	63

morphometric parameters that drove the difference. Specimens from the plain sites were finely agglutinated with smooth and circular tests (Plate 3, Figs. 1–2), similar to previous descriptions of this species (see section Taxonomic Appendix), while hill specimens had a rougher surface (Plate 3, Figs. 3–4), a reflection of the coarser sediment fractions present in these settings. However, their general shape and outline remained recognisable in both cases and there was little doubt that they represented the same morphospecies. Specimens of *N. dentaliniformis* from the plain sites had low convexity and sphericity values consistent with their elongate tests (Plate 2, Fig. 1), while hill specimens commonly agglutinated large, rounded to sub-rounded grains, resulting in a more spherical test (Plate 2, Fig. 2). Similarly, specimens of *Reophax* sp. 21 from the hills had lower maximum to minimum diameter ratios and higher sphericity than those

Fig. 4. (a) MDS on the elemental composition (13 common elements: 10 major, 3 trace) of 56 benthic foraminiferal tests and five sediment samples from four sites. (b) MDS on the elemental composition (16 elements: 10 major, 6 trace) of the 56 benthic foraminiferal tests. (c) MDS on the elemental (32 elements: 11 major, 21 trace) composition of the five sediment samples.

from the plain. In this case, the incorporation of large particles obscured the basic test morphology, which often made identification more difficult (Plate 2, Figs. 5–6.). We conclude that the incorporation of large grains tends to make elongate tests more spherical in shape (*N. dentaliniformis*, *Reophax* sp. 21), and make spherical tests less spherical (*A. glomerata*).

4.4. Evidence of mineral selectivity

ESEM–EDS analyses revealed significant overlaps in the elemental composition of agglutinated tests in relation to topographic setting. In contrast, the elemental composition of hill and plain sediments was different when using the MDS x-ordinate as a variable in a Student's t-test ($p < 0.01$), most likely as result of the different environmental conditions prevalent in the two settings. For example, Turnewitsch et al. (2004) demonstrated hydrodynamic near-bottom sorting and selective deposition/erosion of particles of differing sizes and chemical composition on a large abyssal hill in the PAP-SO area. They concluded that area of increasing near-bottom flow (erosiveness) tended to have higher concentrations of large and heavy particles (e.g. Zircon) than more quiescent sites. In our case, sediments from the hill sites are subject to winnowing processes that preferentially remove the finer particles (e.g. coccoliths, small quartz grains) from the hilltops and deposit them on the adjacent plain, leaving the hill sediments enriched with coarser material (e.g. dead planktonic foraminifera tests, pebble to cobble-sized ice-rafted stones). It is likely that such processes are responsible for the distinct elemental profiles in the two settings.

The clear differences in the elemental composition of the tests and the sediments (Fig. 4a) indicated that foraminiferans favour certain minerals. The sediment at the PAP-SO is a carbonate ooze and as a result, many species found in the same area have tests made of planktonic foraminifera shells, including species of *Reophax* and *Lagenammina* (Gooday et al., 2010, Figs. 13A–B; 14F). Thus the presence of agglutinated taxa with tests made exclusively of mineral grains indicates a certain degree of mineral selection. Based on EDS spectra, all of the foraminifera in our samples had tests composed largely of quartz grains that were held together by organic cement (Bender and Hemleben, 1988; Bender, 1989, 1995) regardless of species or site of origin. Quartz has been identified as the main test component of agglutinated foraminifera in marginal marine settings (Allen et al., 1999), the deep sea (Gooday, 1986; Gooday and Claugher, 1989) and in ancient marine environments (Mancin, 2001; Mancin et al., 2012), including carbonate-dominated habitats where this mineral occurred only in negligible amounts (Jørgensen, 1977). The selection of a quartz as a test component must confer certain benefits for the agglutinated foraminifera. Quartz is a stable mineral, with a consistent density and high resistance to weathering (Drever, 1985). Its use could help to make agglutinated foraminiferal tests more robust (Mancin et al., 2012), at least in the case of species with firmly cemented tests like *A. glomerata*, *Cribrostomoides* spp. or *Ammobaculites agglutinans* (Schröder, 1988), all of which are present in our study sites (Plates 1, Figs. 3–10; 3, Figs. 1–4). Benthic foraminifera (mainly calcareous) living in physically stressed coastal habitats have stronger tests than those from nearby more tranquil localities (Wetmore, 1987). It is possible that a similar relationship applies in hydrographically different deep-sea settings.

4.5. Paleoceanographic significance

The rich fossil record of benthic foraminifera makes them ideal tools for paleoenvironmental reconstructions. Traditionally, there has been an emphasis on calcareous taxa due to their high fossilization potential (Gooday, 2003; Rohling and Cooke, 2003; Jorissen et al., 2007). However, agglutinated foraminifera are sometimes a major component of fossil assemblages, especially in "flysch-type" or "high latitude slope deep-water agglutinated foraminifera" faunas (Brouwer, 1965; Gradstein and Berggren, 1981; Kaminski et al., 1989a; Kaminski et al.,
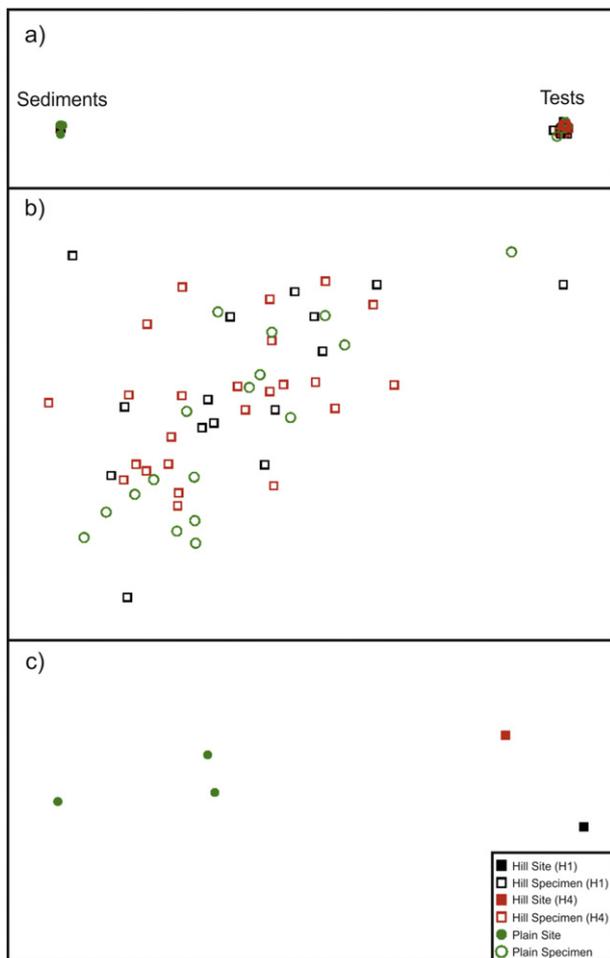
1989b; Kaminski et al., 1995; Nagy et al., 1997; Peryt et al., 1997; Nagy et al., 2000; Peryt et al., 2004; Reolid et al., 2008; Reolid et al., 2010; Setoyama et al., 2011; Waskowska, 2011) and can convey important palaeoecological information (Jones and Charnock, 1985; Alve and Murray, 1999; Murray and Alve, 1999a, 1999b; Murray and Alve, 2001; Murray et al., 2011). Careful analysis has shown that modern agglutinated assemblages provide effective proxies for inferring past ecological conditions (Kaminski and Schröder, 1987; Nagy, 1992; Jones, 1999; Preece et al., 1999; Jones et al., 2005; Kender et al., 2008). Additional studies on modern agglutinated foraminiferal faunas will help to refine their use in paleoceanography. The present results indicate that some abyssal NE Atlantic species are fairly consistent in terms of their test elemental composition, and hence presumably their selection of particular minerals (predominately quartz). Although we found no statistical support for selection of particles in terms of size, there were differences in terms of the visual appearance and overall morphometry of the tests, which were more irregularly shaped ('lumpier') at the hill sites, H4 in particular. These characteristics (incorporation of coarse particles, test morphometry) could provide evidence for the recognition of ancient abyssal hills environments, as well as other palaeoceanographic settings that were characterised by enhanced current flow (Kaminski, 1985; Kaminski and Schröder, 1987; Nagy et al., 1997). Certain taxa are clearly better suited to this task than others. In accordance with our findings, *A. glomerata*, *Cribrostomoides subglobosus* and species of the genus *Reophax* have been elsewhere reported to reflect the nature of the surrounding sediments (Schröder et al., 1988). These taxa, which are an important component of modern foraminiferal assemblages in the PAP-SO area, could be potential indicators of ancient environments exposed to enhanced near-bottom flow, complementing proxies based the analysis of sediment characteristics.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.marmicro.2015.12.005.

Taxonomic Appendix

The following notes include all named species and all open nomenclature species. For named species, we give the author, the original generic designation, and references to representative illustrations. Open nomenclature species are briefly characterized and compared, where possible, to a published illustration.

Adercotryma glomerata (Brady, 1878) (Plate 3, Figs. 1–4). The specimens included here are more or less rounded, almost circular in shape with four chambers in the final whorl. The almost circular shape is more pronounced in specimens from the abyssal plain than those from hill sites. In general, they closely resemble *A. glomerata* as illustrated in Brönnimann, and Whittaker (1987, Fig. 4a–e), Timm (1992, Plate 4, Fig. 1a); Hayward et al. (2010, Plate 2, Fig. 20), as well as the oval-shaped morphotype of *A. glomerata* illustrated in Gooday et al. (2010, Fig. 15e).

Ammobaculites agglutinans (d' Orbigny, 1846) (Plate 1, Figs. 7–8). Our specimen resembles those illustrated by Brady (1884, Plate 32, Figs. 19–20, 24–26) as *Spirolina agglutinans* d'Orbigny 1846. Kaminski and Kuhnt (1991) noted that specimens of this species from abyssal calcareous oozes are larger in size and usually possess more uniserial chambers compared to specimens from shallower depths on the continental margin.

Cribrostomoides subglobosus (Cushman, 1910) (Plate 1, Figs. 3–6). Our specimens resemble those illustrated by Brady (1884, Plate 34, Figs. 8–10) as *Haplophragmium latidorsatus*, and Kaminski and Gradstein (2005) as *Cribrostomoides subglobosus subglobosus*. This well-known species is widely reported from different oceans (Kaminski and Gradstein, 2005; Gooday and Jorissen, 2012).

Lagenammina sp. 1 (Plate 3, Figs. 5–12). We included here two similar morphotypes with tests composed of mineral grains. One morphotype (Plate 3, Figs. 5–8) has an oval-shaped chamber with a relatively narrow apertural neck and is probably conspecific with *Reophax* cf. *difflugiformis* Brady 1879 of Timm (1992, Plate 1, Fig. 13a–b), *Lagenammina difflugiformis* of Schiebel (1992, Plate 8, Fig. 9), *L. difflugiformis subsp. arenulata* (Skinner, 1961) of Wollenburg (1992, Plate 2, Fig. 3), as well as the 'morphotype resembling *L. difflugiformis*' of Gooday et al. (2010, Fig. 13c) from the PAP-SO central site. The other morphotype has a generally more elongate test with a relatively wider apertural neck (Plate 3, Figs. 9–12) and resembles another of the *Lagenammina* species illustrated by Gooday et al. (2010, Fig. 13f). The two forms could not be separated consistently, as in the case of specimens from the abyssal hills the shape of the test was partly or completely obscured by coarse mineral grains. Consequently, we regarded both morphotypes as being the same species. Length up to 650 μm.

Nodulina dentaliniformis (Brady, 1881) (Plate 2, Figs. 1–2). Test long and slender, consisting of up to seven clearly defined chambers arranged along a straight or slightly curved axis. Chambers are clearly defined and become larger and more elongate distally, although never parallel-sided. Final chamber elongate with a short apertural neck. Test wall consists of mineral grains. Specimens from abyssal hills slightly deviate from the typical morphology of this species, due to the coarser material they agglutinate. Length up to 1400 μm.

Remarks: This species closely resembles *Reophax dentaliniformis* of Brady (1884, Plate 30, Figs. 21–22) in both the number and shape of the chambers. The final chamber lacks the almost cylindrical (parallel-sided) shape shown in Brady's Fig. 22, but the specimens on the type slide (ZF265) in the Natural History Museum, London, exhibit quite a lot of variability in this respect.

Portatrochammina murrayi Brönnimann and Zaninetti, 1984 (Plate 1, Figs. 9–10). Our specimens illustrate those described in Brönnimann and Zaninetti, 1984 (Plate 5, Figs. 7, 12–15), Gooday (1986, Fig. 100, P) and Dorst & Schönfeld (2015, Figs. 3a, b and 4a, b). This species has a wide bathymetric range (Murray and Alve, 2011).

Recurvoides sp. 9 (Plate 1, Figs. 1–2). Test sub-rounded, streptospirally coiled, occasionally incorporating large quartz grains. Last whorl consists of four to five chambers, which gradually increase in size. The aperture is small, simple, oval-shaped, and placed on the base of the final chamber. The wall is semi-opaque and its colour ranges from orange to yellowish brown. Length ~420 μm.

Reophax sp. 9 (Plate 1, Figs. 11–12). Test comprising two to three chambers, the final being substantially larger than the previous ones,

and produced into a pronounced apertural neck. Wall is composed predominantly of mineral grains, which can be quite coarse in the case of specimens from abyssal hills. Length up to 370 μm.

Remarks. This species closely resembles *Reophax* sp. 112/113 of Gooday et al. (2010, Fig. 14A) from the PAP-SO central site, *Reophax* sp. 14 of Cornelius & Gooday (2004, Fig. 5c) and *Reophax* sp. PS2214-4 of Wollenburg & Mackensen (1998, Plate 1, Fig. 9).

Reophax sp. 21 (Plate 1, Figs. 3–6) Test rather elongate, occasionally slightly curved, comprising 4–6 more or less globular chambers, sometimes connected by short necks. Chambers increase in size distally; final chamber with a relatively long apertural neck. Wall consists predominantly of mineral grains. This species is easy to recognise, despite the incorporation of large grains by specimens from the abyssal hills. Length up to 880 μm.

Remarks. This species closely resembles *Reophax* sp. 116 of Gooday et al. (2010, Fig. 14E) from the PAP-SO central site. In addition, it looks similar to *Reophax scorpiurus* in Schröder et al. (1988, Plate 5, Figs. 1–2). However, given the range of test morphologies illustrated by Schröder (1986), it is possible that their concept of this species encompassed several genetically distinct entities.

Reophax sp. 28 (Plate 1, Figs. 7–10) Test elongate, more or less straight, comprising four to five slim chambers, which gradually increase in size. The wall is largely made of mineral grains and it often incorporates a small number of long spicules. The final chamber is often particularly elongated and has a thin apertural neck. Length up to 830 μm.

Remarks. This species closely resembles *Reophax* sp. 117 of Gooday et al. (2010, Fig. 14C) from the PAP-SO central site.

References

Abbireddy, C.O.R., Clayton, C.R.I., 2009. A review of modern particle sizing methods. Proc. Inst. Civ. Eng. Geotech. Eng. 162 (4), 193–201. http://dx.doi.org/10.1680/Geng.2009. 162.4.193.

Adl, S.M., Simpson, A.G.B., Lane, C.E., Lukes, J., Bass, D., Bowser, S.S., Brown, M.W., Burki, F., Dunthorn, M., Hampl, V., Heiss, A., Hoppenrath, M., Lara, E., le Gall, L., Lynn, D.H., McManus, H., Mitchell, E.A.D., Mozley-Stanridge, S.E., Parfrey, L.W., Pawlowski, J., Rueckert, S., Shadwick, L., Schoch, C.L., Smirnov, A., Spiegel, F.W., 2012. The revised classification of eukaryotes. J. Eukaryot. Microbiol. 59 (5), 429–493. http://dx.doi.org/10.1111/J.1550-7408.2012.00644.X.

Allen, K., Roberts, S., Murray, J.W., 1999. Marginal marine agglutinated foraminifera: affinities for mineral phases. J. Micropalaeontol. 18, 183–191.

Aller, J.Y., 1989. Quantifying sediment disturbance by bottom currents and its effect on benthic communities in a deep-sea western boundary zone. Deep Sea Res. Part A 36 (6), 901–934. http://dx.doi.org/10.1016/0198-0149(89)90035-6.

Alve, E., Murray, J.W., 1999. Marginal marine environments of the Skagerrak and Kattegat: a baseline study of living (stained) benthic foraminiferal ecology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 146 (1–4), 171–193. http://dx.doi.org/10.1016/S0031-0182(98)00131-X.

Armynot du Châtelet, E., Noiriel, C., Delaine, M., 2013a. Three-dimensional morphological and mineralogical characterization of testate amebae. Microsc. Microanal. 19 (6), 1511–1522. http://dx.doi.org/10.1017/S1431927613013226.

Armynot du Châtelet, E., Frontalini, F., Guillot, F., Recourt, P., Ventalon, S., 2013b. Surface analysis of agglutinated benthic foraminifera through ESEM–EDS and Raman analyses: an expeditious approach for tracing mineral diversity. Mar. Micropaleontol. 105, 18–29. http://dx.doi.org/10.1016/J.Marmicro.2013.10.001.

Armynot du Châtelet, E., Bout-Roumazeilles, V., Coccioni, R., Frontalini, F., Guillot, F., Kaminski, M.A., Recourt, P., Riboulleau, A., Trentesaux, A., Tribovillard, N., Ventalon, S., 2013c. Environmental control on shell structure and composition of agglutinated foraminifera along a proximal–distal transect in the Marmara Sea. Mar. Geol. 335, 114–128. http://dx.doi.org/10.1016/J.Margeo.2012.10.013.

Baldrighi, E., Lavaleye, M., Aliani, S., Conversi, A., Manini, E., 2014. Large spatial scale variability in Bathyal Macrobenthos abundance, biomass, alpha- and beta-diversity along the Mediterranean Continental Margin. PLoS One 9 (9), e107261. http://dx.doi.org/10.1371/journal.pone.0107261.

Bartholdy, J., Leipe, T., Frenzel, P., Tauber, F., Bahlo, R., 2005. High resolution single particle analysis by scanning electron microscopy: a new tool to investigate the mineral composition of agglutinated foraminifers. Methods Appl. Micropaleontol. 124, 53–65.

Bender, H., 1989. Gehäuseaufbau, Gehäusegenese und Biologie agglutinierter Foraminiferen (Sarcodina, Textulariina). Jahrb. Geol. Bundesanst. 133, 259–347.

Bender, H., 1995. Test structure and classification in agglutinated foraminifera. In: Kaminski, M.A., Geroch, S., Gasinski, M.A. (Eds.), Proceedings of the Fourth International Workshop on Agglutinated Foraminifera, Grzybowski Foundation Special Publication, pp. 27–70.

Bender, H., Hemleben, C., 1988. Constructional aspects in test formation of some agglutinated foraminifera. Abh. Geol. Bundesanst. 41, 13-12.

Bowser, S.S., Bernhard, J.M., 1993. Structure, bioadhesive distribution and elastic properties of the agglutinated test of *Astrammina rara* (protozoa, foraminiferida). J. Eukaryot. Microbiol. 40 (2), 121–131. http://dx.doi.org/10.1111/J.1550-7408. 1993.Tb04891.X.

Bowser, S.S., Bernhard, J.M., Habura, A., Gooday, A.J., 2002. Structure, taxonomy and ecology of *Astrammina triangularis* (Earland), an allogromiid-like agglutinated foraminifer from explorers cove, Antarctica. J. Foraminifer. Res. 32 (4), 364–374. http://dx.doi.org/10.2113/0320364.

Brady, H.B., 1884. Report on the foraminifera dredged by H.M.S. Challenger during the years 1873–1876: report of the scientific results of the voyage of H.M.S. Challenger, 1873–1876. Zoology 9, 1–814.

Brönnimann, P., Zaninetti, L., 1984. Agglutinated foraminifera mainly Trochamminacea from the Baia de Sepetiba, near Rio de Janeiro, Brazil. Rev. Paléobiol. 3, 63–115.

Brouwer, J., 1965. Agglutinated foraminiferal faunas from some turbiditic sequences I, II. Proc. K. Ned. Akad. Wet. Ser. B 68 (5), 309–334.

Brönnimann, P., Whittaker, J.E., 1987. A revision of the foraminiferal genus Adercotryma Loeblich & Tappan, with a description of A. wrighti sp. nov. from British waters. Bull Br Mus Nat Hist Zool 52, 19–28.

Buchanan, J.B., Hedley, R.H., 1960. A contribution to the biology of *Astrorhiza limicola* (Foraminifera). J. Mar. Biol. Assoc. U. K. 39 (3), 549–560.

Clark, M.R., Rowden, A.A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K.I., Rogers, A.D., O'Hara, T.D., White, M., Shank, T.M., Hall-Spencer, J.M., 2010. The ecology of seamounts: structure, function, and human impacts. Ann. Rev. Mar. Sci. 2, 253–278. http://dx.doi.org/10.1146/Annurev-Marine-120308-081109.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth, UK.

Cornelius, N., Gooday, A.J., 2004. 'Live' (stained) deep-sea benthic foraminiferans in the western Weddell Sea: trends in abundance, diversity and taxonomic composition along a depth transect. Deep-Sea Res. II Top. Stud. Oceanogr. 51 (14–16), 1571–1602. http://dx.doi.org/10.1016/J.Dsr2.2004.06.024.

Dorst, S., Schonfeld, J., 2015. Taxonomic notes on recent benthic foraminiferal species of the family trochamminidae from the Celtic Sea. J. Foraminifer. Res. 45 (2), 167–189.

Drever, J.I., 1985. The Chemistry of Weathering. Reidel, New York.

Durden, J.M., Bett, B.J., Jones, D.O.B., Huvenne, V.A.I., Ruhl, H.A., 2015. Abyssal hills — hidden source of increased habitat heterogeneity, benthic megafaunal biomass and diversity in the deep sea. Prog. Oceanogr. http://dx.doi.org/10.1016/j.pocean.2015.06.006.

Gage, E.J.D., Bett, B.J., 2005. Deep-sea benthic sampling. In: Eleftheriou, A., MacIntyre, A. (Eds.), Methods for the Study of Marine Benthos, third ed. Blackwell Scientific, Oxford, UK, pp. 273–325.

Gage, J.D., Lamont, P.A., Tyler, P.A., 1995. Deep-sea macrobenthic communities at contrasting sites off Portugal, preliminary-results. 1. Introduction and diversity comparisons. Int. Rev. Gesamten Hydrobiol. 80 (2), 235–250. http://dx.doi.org/10.1002/Iroh. 19950800211.

Genin, A., Dayton, P.K., Lonsdale, P.F., Spiess, F.N., 1986. Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature 322 (6074), 59–61. http://dx.doi.org/10.1038/322059a0.

Goff, J.A., Arbic, B.K., 2010. Global prediction of abyssal hill roughness statistics for use in ocean models from digital maps of paleo-spreading rate, paleo-ridge orientation, and sediment thickness. Ocean Model. 32 (1-2), 36–43. http://dx.doi.org/10.1016/J. Ocemod.2009.10.001.

Gooday, A.J., 1986. Meiofaunal foraminiferans from the bathyal Porcupine-Seabight (northeast Atlantic): size structure, standing stock, taxonomic composition, species-diversity and vertical-distribution in the sediment. Deep Sea Res. Part A 33 (10), 1345–1373. http://dx.doi.org/10.1016/0198-0149(86)90040-3.

Gooday, A.J., 2003. Benthic foraminifera (protista) as tools in deep-water palaeoceanography: environmental influences on faunal characteristics. Adv. Mar. Biol. 46, 1–90. http://dx.doi.org/10.1016/S0065-2881(03)46002-1.

Gooday, A.J., Claugher, D., 1989. The genus Bathysiphon (Protista, Foraminiferida) in the northeast Atlantic — SEM observations on the wall structure of 7 species. J. Nat. Hist. 23 (3), 591–611. http://dx.doi.org/10.1080/00222938900770331.

Gooday, A.J., Jorissen, F.J., 2012. Benthic foraminiferal biogeography: controls on global distribution patterns in deep-water settings. Ann. Rev. Mar. Sci. 4, 237–262. http://dx.doi.org/10.1146/Annurev-Marine-120709-142737.

Gooday, A.J., Levin, L.A., Linke, P., Heeger, T., 1992. The role of benthic Foraminifera in deep-sea food webs and carbon cycling. Deep-Sea Food Chains Glob. Carbon Cycle 360, 63–91.

Gooday, A.J., Nott, J.A., Davis, S., Mann, S., 1995. Apatite particles in the test wall of the large agglutinated foraminifer *Bathysiphon major* (Protista). J. Mar. Biol. Assoc. U. K. 75 (2), 469–481.

Gooday, A.J., Malzone, M.G., Bett, B.J., Lamont, P.A., 2010. Decadal-scale changes in shallow-infaunal foraminiferal assemblages at the Porcupine Abyssal Plain, NE Atlantic. Deep-Sea Res. II Top. Stud. Oceanogr. 57, 1362–1382. http://dx.doi.org/10.1016/j.dsr2.2010.01.012.

Gradstein, F.M., Berggren, W.A., 1981. Flysch-type agglutinated foraminifera and the maestrichtian to paleogene history of the labrador and north seas. Mar. Micropaleontol. 6 (3), 211–268.

Haake, F.-W., 1977. Living Foraminifera in the Adriatic Sea: influence of water depth and sediment. J. Foraminifer. Res. 7 (1), 62–75.

Hada, Y., 1957. Biology of the arenaceous Foraminifera. J. Sci. Suzugamine Women's Coll. Hiroshima Jpn. 3 (B), 31–50.

Hartman, S.E., Lampitt, R.S., Larkin, K.E., Pagnani, M., Campbell, J., Gkritzalis, T., Jiang, Z.P., Pebody, C.A., Ruhl, H.A., Gooday, A.J., Bett, B.J., Billett, D.S.M., Provost, P., McLachlan, R.,

Turton, J.D., Lankester, S., 2012. The Porcupine Abyssal Plain Fixed-point Sustained Observatory (PAP-SO): variations and trends from the Northeast Atlantic fixed-point time-series. ICES J. Mar. Sci. 69 (5), 776–783. http://dx.doi.org/10.1093/Icesjms/Fss077.

Hasemann, C., Soltwedel, T., 2011. Small-scale heterogeneity in deep-sea nematode communities around biogenic structures. plos one 6 (12), e29152. http://dx.doi.org/10.1371/journal.pone.0029152.

Hayward, B.W., Grenfell, H.R., Sabaa, A.T., Neil, H.L., Buzas, M.A., 2010. Recent New Zealand Deep-Water Benthic Foraminifera: Taxonomy, Ecologic Distribution, Biogeography, and Use in Paleoenvironmental Assessment. Lower Hutt, New Zealand.

Heezen, B.C., Holcombe, T.L., 1965. Geographic Distribution of Bottom Roughness in the North Atlantic. Columbia University, Lamont Geological Observatory.

Heezen, B.C., Tharp, M., Ewing, M., 1959. The floors of the oceans: I. The North Atlantic. Geol. Soc. Am. Spec. Pap. 65, 1–126.

Hess, S., Kuhnt, W., Spivey, B., Kaminski, M.A., Whittaker, J.E., 2000. Ash grains of the 1991 Mt Pinatubo eruption as a tracer in Rose Bengal stained deep sea agglutinated foraminifera: how old is Freddy? In: Hart, M.B., Kaminski, M.A., Smart, C.W. (Eds.), Proceedings of the Fifth International Workshop on Agglutinated Foraminifera. Grzybowski Foundation Special Publication 7, p. 126

Jones, R.W., 1999. Forties field (North Sea) revisited: a demonstration of the value of historical micropalaeontological data. Biostratigraphy Prod. Dev. Geol. 152, 185–200. http://dx.doi.org/10.1144/Gsl.Sp.1999.152.01.11.

Jones, R.W., Charnock, M.A., 1985. Morphogroups of agglutinated foraminifera. Their life positions and feeding habits and potential applicability in (paleo)ecological studies. Rev. Paléobiol. 4 (2), 311–320.

Jones, R.W., Pickering, K.T., Boudagher-Fadel, M., Matthews, S., 2005. Preliminary observations on the micropalaeontological characterization of submarine fan/channel sub-environments, Ainsa system, south-central Pyrenees, Spain. Recent Dev. Appl. Biostratigraphy 55–68.

Jørgensen, N.O., 1977. Wall structure of some arenaceous foraminifera from the Maastrictian White Chalk (Denmark). J. Foraminifer. Res. 7, 313–321.

Jorissen, F.J., Fontanier, C., Thomas, E., 2007. Paleoceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics. In: Hillaire-Marcel, C., de Vernal, A. (Eds.), Proxies in Late Cenozoic Paleoceanography: Part. 2: Biological Tracers and Biomarkers, pp. 263–326.

Kaminski, M.A., 1985. Evidence for control of abyssal agglutinated foraminiferal community structure by substrate disturbance — results from the Hebble area. Mar. Geol. 66 (1–4), 113–131. http://dx.doi.org/10.1016/0025-3227(85)90025-8.

Kaminski, M.A., Gradstein, F.M., 2005. Atlas of Paleogene Cosmopolitan Deep-water Agglutinated Foraminifera.

Kaminski, M.A., Kuhnt, W., 1991. Depth-related shape variation in *Ammobaculites agglutinans*. Ann. Soc. Geol. Pol. 61, 221–230.

Kaminski, M.A., Schröder, C.J., 1987. Environmental analysis of deep-sea agglutinated foraminifera: can we distinguish tranquil from disturbed environments? Gulf Coast Section SEPM Foundation Eighth Annual Research Conference. Selected Papers and Illustrated Abstracts, pp. 90–93

Kaminski, M.A., Gradstein, F.M., Berggren, W.A., 1989a. Paleogene benthic foraminifer biostratigraphy and paleoecology at Site 647, southern Labrador Sea. Proc. Ocean Drill. Program Sci. Results 105, 705–730.

Kaminski, M.A., Gradstein, F.M., Scott, D.B., Mackinnon, K.D., 1989b. Neogene benthic foraminiferal stratigraphy and deep water history of Sites 645, 646, and 647, Baffin Bay and Labrador Sea. Proc. Ocean Drill. Program Sci. Results 105, 731–756.

Kaminski, M.A., Boersma, M., Tyszka, J., Holbourn, A.E.L., 1995. Response of deep-water agglutinated foraminifera to dysoxic conditions in the California borderland basins. In: Kaminski, M.A., Geroch, S., Gasifski, M.A. (Eds.), Proceedings of the Fourth International Workshop on Agglutinated Foraminifera, Kraków, Poland, September 12–19, 1993. Grzybowski Foundation Special Publication 3, pp. 131–140.

Kender, S., Kaminski, M.A., Jones, R.W., 2008. Early to middle Miocene foraminifera from the deep-sea Congo Fan, offshore Angola. Micropaleontology 54 (6), 477–568.

Levin, L.A., Nittrouer, C.A., 1987. Textural characteristics of sediments on deep seamounts in the eastern Pacific Ocean between 10 N and 30 N. Seamounts Islands Atolls 43, 187–203.

Levin, L.A., Thomas, C.L., 1989. The influence of hydrodynamic regime on infaunal assemblages inhabiting carbonate sediments on central Pacific seamounts. Deep Sea Res. Part A 36 (12), 1897–1915. http://dx.doi.org/10.1016/0198-0149(89)90117-9.

Levin, L.A., Demaster, D.J., Mccann, L.D., Thomas, C.L., 1986. Effects of giant protozoans (Class Xenophyophorea) on deep-seamount benthos. Mar. Ecol. Prog. Ser. 29 (1), 99–104. http://dx.doi.org/10.3354/Meps029099.

Mancin, N., 2001. Agglutinated foraminifera from the Epiligurian succession (Middle Eocene/Lower Miocene, Northern Apennines, Italy): Scanning electron microscopic characterization and paleoenvironmental implications. J. Foraminifer. Res. 31 (4), 294–308. http://dx.doi.org/10.2113/0310294.

Mancin, N., Basso, E., Pirini, C., Kaminski, M.A., 2012. Selective mineral composition, functional test morphology and paleoecology of the agglutinated foraminiferal genus Colominella Popescu, 1998 in the Mediterranean Pliocene (Liguria, Italy). Geol. Carpath. 63 (6), 491–502. http://dx.doi.org/10.2478/V10096-012-0038-Y.

Mancin, N., Basso, E., Lupi, C., Cobianchi, M., Kaminski, M.A., Hayward, B.W., 2015. The agglutinated Foraminifera from the SW Pacific bathyal sediments of the last 550 kyr: relationship with the deposition of tephra layers. Mar. Micropaleontol. 115, 39–58. http://dx.doi.org/10.1016/j.marmicro.2014.12.004.

McCave, I.N., Hall, I.R., 2006. Size sorting in marine muds: processes, pitfalls, and prospects for paleoflow-speed proxies. Geochem. Geophys. Geosyst. 7. http://dx.doi.org/10.1029/2006gc001284.

McCave, I.N., Manighetti, B., Robinson, S.G., 1995. Sortable silt and fine sediment size composition slicing — parameters for paleocurrent speed and paleoceanography. Paleoceanography 10 (3), 593–610. http://dx.doi.org/10.1029/94pa03039.

Murray, J.W., Alve, E., 1999a. Natural dissolution of modern shallow water benthic foraminifera: taphonomic effects on the palaeoecological record. Palaeogeogr. Palaeoclimatol. Palaeoecol. 146 (1–4), 195–209. http://dx.doi.org/10.1016/S0031-0182(98)00132-1.

Murray, J.W., Alve, E., 1999b. Taphonomic experiments on marginal marine foraminiferal assemblages: how much ecological information is preserved? Palaeogeogr. Palaeoclimatol. Palaeoecol. 149 (1–4), 183–197. http://dx.doi.org/10.1016/S0031-0182(98)00200-4.

Murray, J.W., Alve, E., 2001. Do calcareous dominated shelf foraminiferal assemblages leave worthwhile ecological information after their dissolution? In: Hart, M.B., Kaminski, M.A., Smart, C.W. (Eds.), Proceedings of the Fifth International Workshop on Agglutinated Foraminifera, Plymouth, U.K., September 6–16, 1997. Grzybowski Foundation Special Publication 7, pp. 311–331.

Murray, J.W., Alve, E., 2011. The distribution of agglutinated foraminifera in NW European seas: baseline data for the interpretation of fossil assemblages. Palaeontol. Electron. 14 (2), 1–41.

Murray, J.W., Alve, E., Jones, B.W., 2011. A new look at modern agglutinated benthic foraminiferal morphogroups: their value in palaeoecological interpretation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 309 (3–4), 229–241. http://dx.doi.org/10.1016/J.Palaeo.2011.06.006.

Nagy, J., 1992. Environmental significance of foraminiferal morphogroups in Jurassic north-sea deltas. Palaeogeogr. Palaeoclimatol. Palaeoecol. 95 (1–2), 111–134. http://dx.doi.org/10.1016/0031-0182(92)90168-5.

Nagy, J., Kaminski, M.A., Johnsen, K., Mitlehner, A.G., 1997. Foraminiferal, palynomorph, and diatom biostratigraphy and paleoenvironments of the Tork formation: a reference section for the Paleocene–Eocene transition in the western Barents Sea. In: Hass, H.C., Kaminski, M.A. (Eds.), Contributions to the Micropaleontology and Paleoceanography of the Northern North Atlantic. Grzybowski Foundation Special Publication 5, pp. 15–38.

Nagy, J., Kaminski, M.A., Kuhnt, W., Bremer, M.A., 2000. Agglutinated foraminifera from neritic to bathyal facies in the Palaeogene of Spitsbergen and the Barents Sea. In: Hart, M.B., Kaminski, M.A., Smart, C.W. (Eds.), Proceedings of the Fifth International Workshop on Agglutinated Foraminifera. Grzybowski Foundation Special Publication 7, pp. 333–361.

Peryt, D., Lahodynsky, R., Durakiewicz, T., 1997. Deep-water agglutinated foraminiferal changes and stable isotope profiles across the Cretaceous–Paleogene boundary in the Rotwandgraben section, Eastern Alps (Austria). Palaeogeogr. Palaeoclimatol. Palaeoecol. 132 (1–4), 287–307. http://dx.doi.org/10.1016/S0031-0182(97)00056-4.

Peryt, D., Alegret, L., Molina, E., 2004. Agglutinated foraminifers and their response to the Cretaceous/Paleogene (K/P) boundary event at Aïn Settara, Tunisia. In: Bubík, M., Kaminski, M.A. (Eds.), Proceedings of the Sixth International Workshop on Agglutinated Foraminifera. Grzybowski Foundation Special Publication 8, pp. 393–412.

Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S., 2007. Seamounts: Ecology, Fisheries, and Conservation. Blackwell, Oxford, UK.

Preece, R.C., Kaminski, M.A., Dignes, T.W., 1999. Miocene benthonic foraminiferal morphogroups in an oxygen minimum zone, offshore Cabinda. In: Cameron, N.R., Bate, R.H., Clure, V.S. (Eds.), The oil and gas habitats of the South Atlantic. Geological Society Special Publication 153, pp. 267–282.

Reolid, M., Rodriguez-Tovar, F.J., Nagy, J., Oloriz, F., 2008. Benthic foraminiferal morphogroups of mid to outer shelf environments of the Late Jurassic (Prebetic Zone, southern Spain): Characterization of biofacies and environmental significance. Palaeogeogr. Palaeoclimatol. Palaeoecol. 261 (3–4), 280–299. http://dx.doi.org/10.1016/J.Palaeo.2008.01.021.

Reolid, M., Nagy, J., Rodriguez-Tovar, F.J., 2010. Ecostratigraphic trends of Jurassic agglutinated foraminiferal assemblages as a response to sea-level changes in shelf deposits of Svalbard (Norway). Palaeogeogr. Palaeoclimatol. Palaeoecol. 293 (1–2), 184–196. http://dx.doi.org/10.1016/J.Palaeo.2010.05.019.

Rex, M.A., Etter, R.J., 2010. Deep-sea Biodiversity: Pattern and Scale. Harvard University Press, Cambridge, MA.

Rohling, E.J., Cooke, S., 2003. Stable oxygen and carbon isotopes in foraminiferal carbonate shells. In: Gupta, B.K.S. (Ed.), Modern Foraminifera. Springer Netherlands, pp. 239–258.

Ruggiero, M., Gordon, D.P., Orrell, T.M., Bailly, N., Bourgoin, T., Brusca, R.C., Cavalier-Smith, T., Guiry, M.D., Kirk, P.M., 2015. A higher level classification of all living organisms. PLoS One 10 (4), 1–60. http://dx.doi.org/10.1371/journal.pone.0119248.

Ruhl, H., 2012. RRS James Cook Cruise 62, 24 Jul–29 Aug 2011. Porcupine Abyssal Plain-Sustained Observatory Research. National Oceanography Centre, Southampton.

Salami, M.B., 1976. Biology of *Trochammina* cf. *T. quadriloba* Hoglund (1947), an agglutinating foraminifer. J. Foraminifer. Res. 6, 142–153.

Schiebel, R., 1992. Rezente benthische Foraminiferen in Sedimenten des Schelfes un oberen Kontinentalhanges im Golf von Guinea (Westafrika). Ber. Rep. Geol.-Pälontol. Inst. Univ. Kiel. 51, 1–179.

Schröder, C.J., 1986. Deep-water arenaceous Foraminifera in the northwest Atlantic Ocean. Can. Tech. Rep. Hydrography Ocean Sci. 1, 1–191.

Schröder, C.J., 1988. Subsurface preservation of agglutinated foraminifera in the Northwest Atlantic Ocean. Abh. Geol. Bundesanst. 41, 325–336.

Schröder, C.J., Scott, D.B., Medioli, F.S., Bernstein, B.B., Hessler, R.R., 1988. Larger agglutinated Foraminifera: comparison of assemblages from central North Pacific and Western North Atlantic (Nares Abyssal Plain). J. Foraminifer. Res. 18 (1), 25–41.

Setoyama, E., Kaminski, M.A., Tyszka, J., 2011. The Late Cretaceous–Early Paleocene palaeobathymetric trends in the southwestern Barents Sea — palaeoenvironmental implications of benthic foraminiferal assemblage analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 307 (1–4), 44–58. http://dx.doi.org/10.1016/J.Palaeo.2011.04.021.

Slama, D.C., 1954. Arenaceous tests in foraminifera: an experiment. Micropaleontologist 8, 33–34.

Sliter, W.V., 1968. Shell material variation in the agglutinated foraminifer *Trochammina pacifica* Cushman. Tulane Stud. Geol. Paleontol. 6, 80–84.

Snelgrove, P.V.R., Smith, C.R., 2002. A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor. Oceanogr. Mar. Biol. 40, 311–342.

Stefanoudis, P.V., Bett, B.J., Gooday, A.J., 2015. Hills and plains: the influence of topography on deep-sea benthic foraminiferal assemblages. 14th Deep-Sea Biology Symposium. UA Editora, Universidade De Aveiro, pp. 174–175.

Stuart, C.T., Arbizu, P.M., Smith, C.R., Molodtsova, T., Brandt, A., Etter, R.J., Escobar-Briones, E., Fabri, M.C., Rex, M.A., 2008. CeDAMar global database of abyssal biological sampling. Aquat. Biol. 4 (2), 143–145. http://dx.doi.org/10.3354/Ab00097.

Thistle, D., 1983. The stability time hypothesis as a predictor of diversity in deep-sea soft-bottom communities — a test. Deep Sea Res. Part A 30 (3), 267–277. http://dx.doi.org/10.1016/0198-0149(83)90010-9.

Thistle, D., Eckman, J.E., 1990. The effect of a biologically produced structure on the benthic copepods of a deep-sea site. Deep Sea Res. Part A 37 (4), 541–554. http://dx.doi.org/10.1016/0198-0149(90)90089-E.

Thomsen, E., Rasmussen, T.L., 2008. Coccolith-agglutinating Foraminifera from the early Cretaceous and how they constructed their tests. J. Foraminifer. Res. 38 (3), 193–214. http://dx.doi.org/10.2113/Gsjfr.38.3.193.

Timm, S., 1992. Rezente Tiefsee-Benthosforaminiferen aus Oberflächen-sedimenten des Golfes von Guinea (Westafrika) — Taxonomie, Verbreitung, Ökologie und Korngrössenfraktionen. Ber. Rep. Geol.-Päontol. Inst. Christ.-Albrechts-Univ. Kiel. 59, 1–155.

Turnewitsch, R., Reyss, J.L., Chapman, D.C., Thomson, J., Lampitt, R.S., 2004. Evidence for a sedimentary fingerprint of an asymmetric flow field surrounding a short seamount. Earth Planet. Sci. Lett. 222 (3–4), 1023–1036. http://dx.doi.org/10.1016/J.Epsl.2004.03.042.

Turnewitsch, R., Falahat, S., Nycander, J., Dale, A., Scott, R.B., Furnival, D., 2013. Deep-sea fluid and sediment dynamics-influence of hill- to seamount-scale seafloor topography. Earth Sci. Rev. 127, 203–241. http://dx.doi.org/10.1016/J.Earscirev.2013.10.005.

Warren, R., VanDerWal, J., Price, J., Welbergen, J.A., Atkinson, I., Ramirez-Villegas, J., Osborn, T.J., Jarvis, A., Shoo, L.P., Williams, S.E., 2013. Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. Nat. Clim. Chang. 3, 678–682.

Waskowska, A., 2011. Response of Early Eocene deep-water benthic foraminifera to volcanic ash falls in the Polish Outer Carpathians: palaeoecological implications. Palaeogeogr. Palaeoclimatol. Palaeoecol. 305 (1–4), 50–64. http://dx.doi.org/10.1016/J.Palaeo.2011.02.012.

Watling, L., Guinotte, J., Clark, M.R., Smith, C.R., 2013. A proposed biogeography of the deep ocean floor. Prog. Oceanogr. 111, 91–112.

Wells, P.E., 1985. Recent agglutinated benthonic Foraminifera (Suborder Textulariina) of Wellington Harbor, New-Zealand. N. Z. J. Mar. Freshw. Res. 19 (4), 575–599.

Wetmore, K.L., 1987. Correlations between test strength, morphology and habitat in some benthic Foraminifera from the coast of Washington. J. Foraminifer. Res. 17 (1), 1–13.

Wollenburg, J.E., 1992. Zur Taxonomie von resented benthischen Foraminiferen aus dem Nansen Becken, Arktischer Ozean. Ber. Polarforsch. 112, 1–137.

Wollenburg, J.E., Mackensen, A., 1998. Living benthic foraminifers from the central Arctic Ocean: faunal composition, standing stock and diversity. Mar. Micropaleontol. 34 (3), 153–185.

Yesson, C., Clark, M.R., Taylor, M.L., Rogers, A.D., 2011. The global distribution of seamounts based on 30 arc seconds bathymetry data. Deep-Sea Res. I Oceanogr. Res. Pap. 58 (4), 442–453. http://dx.doi.org/10.1016/J.Dsr.2011.02.004.