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Corresponding Author: Mr. Paris Vasileios Stefanoudis, MSc

Corresponding Author's Institution: University of Southampton

First Author: Paris Vasileios Stefanoudis, MSc

Order of Authors: Paris Vasileios Stefanoudis, MSc; Ralf Schiebel, PhD; Romain Mallet; Jennifer M Durden, MSc; Brian J Bett, PhD; Andrew J Gooday, PhD

Abstract: 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 glomeratum, Ammobaculites agglutinans, Cribrostomoides subglobosum, Cribrostomoides sp. 1, Lagenammina sp.1, four Reophax sp. and one indeterminate species) 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.

ABSTRACT

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 glomeratum, Ammobaculites agglutinans, Cribrostomoides subglobosum, Cribrostomoides* sp. 1, *Lagenammina* sp.1, four *Reophax* sp. and one indeterminate species) 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.

KEYWORDS: *abyssal hills*, *benthic foraminifera*, *elemental composition*, *morphometry*, *particle size*.

Highlights

- Agglutination patterns of benthic foraminifera from abyssal hills were compared with those on the plain
- Foraminifera selected different sized particles on hills and plains, mirroring the distinct sedimentary profiles of the two settings
- Differences in the visual appearance of the tests related to seafloor topography was confirmed by morphometric analyses
- Elemental composition of the tests was similar for all studied specimens
- In contrast abyssal hills had different elemental characteristics from the plain
- Agglutinated benthic foraminifera could be used as proxy for paleoflow dynamics

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

PARIS V. STEFANOUDIS[1,]*, RALF SCHIEBEL[2], ROMAIN MALLET[3], JENNIFER M. DURDEN[1], BRIAN J. BETT[4] & ANDREW J. GOODAY[4]

[1]Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton Waterfront Campus, European Way, Southampton SO14 3ZH, United Kingdom

[2]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

[3] SCIAM, Service Commun d'Imagerie et Analyses Microscopiques, IRIS-IBS Institut deBiologie en Santé, CHU d'Angers, LUNAM Université, 49933 Angers Cedex, France

[4]National Oceanography Centre, University of Southampton Waterfront Campus, European Way, Southampton SO14 3ZH, United Kingdom

*Corresponding author (e-mail: p.v.stefanoudis@soton.ac.uk)

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 & Holcombe, 1965; Goff & 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 & Smith, 2002; Rex & 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 & Eckman, 1990; Hasemann & Soltwedel, 2011; Warren *et al.*, 2013) but have also addressed broader scales (mesoscale, i.e. decimeters to kilometers) 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 observed apparent differences in the agglutination patterns (size and nature of the cemented particles) and morphology of benthic foraminiferal tests obtained at sites on the tops of abyssal hills and on the adjacent abyssal 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 RSS *James Cook* Cruise 062 (JC062, 24 July to 29 August 2011; Ruhl, 2012) in the vicinity of the PAPSO area. They were obtained using a Bowers and Connelly Megacorer (Gage & 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 the 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 coccoliths, while the coarser fraction (23–1000 μm) was dominated by foraminiferal tests, indicating sediments with high carbonate content (i.e. carbonate ooze). The coarser fraction constituted a higher proportion of the sediment on the abyssal hills, where pebbles to cobble-sized ice-rafted stones were also observed. 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.

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	4,851–4,853	1	4	5	1
P4	Abyssal plain	48.877	-16.293	4,849–4,851	2	19	5	2
H1	Abyssal hill	48.978	-16.728	4,669–4,679	3	16	5	1
H4	Abyssal hill	49.074	-16.243	4,339–4,388	2	26	2	1

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 *Reophax.* sp. 14). 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 & 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 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; (ii) Maximum to Minimum Diameter ratio; (iii) Perimeter to Area ratio; and (iv) Sphericity, which gives information about the roundness of the test. 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 glomeratum*, *Lagenammina* sp.1, *Reophax* sp.14 and *R.* 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 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. glomeratum*, *Lagenammina* sp.1, *R.* sp. 21, *R.* 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 & 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 & Clayton, 2009), and mechanical agitation. Detected particle sizes ranged from 0.01 to 2000 μm. The percentage of particles >63 μm in the sediments 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 & 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 the 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 (Pl. 1, figs 3–6; Pl. 2; Pl. 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 (Pl. 2, figs 5–6). However, these striking differences did not hamper the recognition of species that were common to the two settings (e.g., Pl. 2, figs 7–10; Pl., figs 3–6).

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

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

	Plains				Hills			
Species	Mean (µm)	Median (µm)	SD	>100 µm	Mean (µm)	Median (µm)	SD	>100 µm
Adercotryma glomeratum	19.0	17.2	7.9	0%	25.6	18.5	18.1	0.8%
Cribrostomoides subglobosum	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%

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

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. glomeratum* 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. 2a), 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. 2a; 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. 2b). 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. 2c), 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. 2b). 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. 2c).

Sediment samples were also clearly separated from most of the tests (Fig. 2b). 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. 2d).

Unlike the foraminiferal tests, hill and plain sediment samples showed no overlap on the MDS plot, further highlighting their different particle size compositions (Fig. 2b). 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. 2b) 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 at H4 and the apparent lack of correlation between test particle sizes 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.

At the species level, ANOSIM with 31 morphometric parameters yielded significant differences related to topography only in the case of *Adercotryma glomeratum* ($p<0.035$). *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 *R.* sp. 14 ($p=0.027$ and $p=0.048$, respectively) as well as in the maximum to minimum diameter ratio and sphericity of *R.* 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. 3a). There was no significant correlation with topographic setting for all studied material (56 tests belonging to 10 species) or for individual species (*A. glomeratum, Lagenammina* sp.1, *R.* sp. 14 and *R.* sp. 21). This was further demonstrated by the considerable overlap of species from both settings in the MDS plot (Fig. 3b). On the other hand, MDS of the sediment elemental data yielded distinct clusters for abyssal hill and abyssal plain sites, respectively (Fig. 3c). 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 plains.

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 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 & Nittrouer, 1987; Levin & 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 & 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 (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.

Our 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 (Pl. 1, figs 3–6; Pl. 2; Pl. 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. glomeratum*. 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. Pl. 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.

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 (Pl. 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 & Hedley, 1960; Wells, 1985; Thomsen & Rasmussen, 2008; du Châtelet *et al.*, 2013c; du Châtelet *et al.*, 2013b). 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 *R.* sp. 21 of the present study (see Taxonomic Appendix), were non-selective for particle size and thus exhibited wide morphological variability in different sedimentary environments.

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). 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 & 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 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 (Pl. 1, figs 3–6; Pl. 2; Pl. 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 *Adercotryma glomeratum, R.* sp. 14 and *R.* sp. 21. In the case of *A. glomeratum* it was the combined effect of all 31 morphometric parameters that drove the difference. Specimens from the plain sites were finely agglutinated with smooth and circular tests (Pl. 3, figs 1–2), similar to previous descriptions of this species (see Taxonomic Appendix), while hill specimens had a rougher surface (Pl. 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 *R.* sp. 14 from the plain sites had low convexity and sphericity values consistent with their elongate tests (Pl. 2, fig. 1), while hill specimens commonly agglutinated large, rounded to sub-rounded grains, resulting in a more spherical test (Pl. 2, fig. 2). Similarly, specimens of *R.* sp. 21 from the hills had lower maximum to minimum diameter ratios and higher sphericity than those from the plain. In this case, the incorporation of large particles obscured the basic test morphology, which often made identification more difficult (Pl. 2, figs 5–6.). We conclude that the incorporation of large grains tends to make elongate tests more spherical in shape (*R.* sp. 14, *R.* sp. 21), and make spherical tests less spherical (*A. glomeratum*).

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. 3a) 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, fig. 13A–B; fig. 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, the foraminifera in our samples had tests composed largely of quartz grains, 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 & 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 *Adercotryma glomeratum*, C*ribrostomoides* spp. or *Ammobaculites agglutinans* (Schröder, 1988), all of which are present in our study sites (Pl. 1, figs. 3–10; Pl. 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 & 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 & 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 & Charnock, 1985; Alve & Murray, 1999; Murray & Alve, 1999b, a; Murray & Alve, 2001; Murray *et al.*, 2011). Careful analysis has shown that modern agglutinated assemblages provide effective proxies for inferring past ecological conditions (Kaminski & 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 & Schröder, 1987 ; Nagy *et al.*, 1997). Certain taxa are clearly better suited to this task than others. In accordance with our findings, *Adercotryma glomeratum*, *Cribrostomoides subglobosum* 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.

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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 glomeratum (Pl. 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. glomeratum* (Brady, 1878) as illustrated in Brönniman and Whittaker (1987, figs 4a–4e), Timm (1992, pl. 4, fig. 1a), Hayward *et al.* (2010, pl. 2, fig. 20), as well as the oval-shaped morphotype of *A. glomeratum* illustrated in Gooday *et al.* (2010, fig. 15e).

Ammobaculites agglutinans (d' Orbigny, 1846) (Pl. 1, figs 7–8). Our specimens resemble those illustrated by Brady (1884, pl. 32, figs 19, 20, 24–26) as *Spirolina agglutinans* d'Orbigny 1846.

Cribrostomoides subglobosum (Cushman, 1910) (Pl. 1, figs 8, 9; Pl. 2, figs 7, 8). Our specimens resemble those illustrated by Brady (1884, pl. 34, figs 8–10) as *Haplophragmium latidorsatus*. This well-known species is widely reported from different oceans (Gooday & Jorissen, 2012).

Lagenammina sp. 1 (Pl. 3, figs 5–12). We included here two similar morphotypes with tests composed of mineral grains. One morphotype (Pl. 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, pl. 1, fig. 13a, b), *Lagenammina difflugiformis* of Schiebel (1992, pl. 8, fig. 9), *L. difflugiformis subsp. arenulata* (Skinner, 1961) of Wollenburg (1992, pl. 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 (Pl. 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.

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

Recurvoides sp. 9 (Pl. 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 (Pl. 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, Pl. 1, fig. 9).

Reophax dentaliniformis (Pl. 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, pl. 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.

Reophax sp. 21 (Pl. 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, pl. 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 (Pl. 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.

Supplementary files

Appendix A

List of species used for morphometric, particle size and elemental analyses.

Appendix B

Morphometric Data (31 morphometric parameter) for all 60 benthic foraminiferal tests used in this study (both for SEM and light images).

Appendix C

Elemental composition of the 56 benthic foraminiferal tests and 5 sediment samples used in this study.

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Fig. 1. Bathymetric map of the PAP-SO area showing the positions of the four study sites, P3 and P4 (abyssal plain sites), H1 and H4 (abyssal hill sites). Black triangles indicate the location of the core samples from which foraminiferal specimens were collected. Green circles and red squares indicate the location of the core samples that were used for estimating particle size distribution and elemental composition of the sediments, respectively. The inset indicates the general location of the Porcupine Abyssal Plain in the northeast Atlantic Ocean.

Explanation of 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 subglobosum*: **3–4** (P3); **5–6** (H4). **figs 7–8.** *Ammobaculites agglutinans* (H1). **figs 9–10.** *Portatrochammina murrayi* (H4). **figs 11–12.** *Reophax* sp. 9.

Explanation of Plate 2. Light and SEM photographs of *Reophax* spp. used in this study along with the site of collection. **figs 1–2.** *Reophax dentalinoformis:* **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.

Explanation of Plate 3. Light and SEM photographs of some species used in this study along with the site of collection. **figs 1–4.** *Adercotryma glomeratum*: **1–2,** (P4); **3–4,** (H4). **figs 5–10.** *Lagenammina* sp. 1: 1^{st} morphotype, **5–6,** (P4), **7–8** (H4); 2^{nd} morphotype, **9-10** (P4), **11-12** (H4). Scale bars = 100 µm.

Fig. 2. (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.

Fig. 3. (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.

Figure 1

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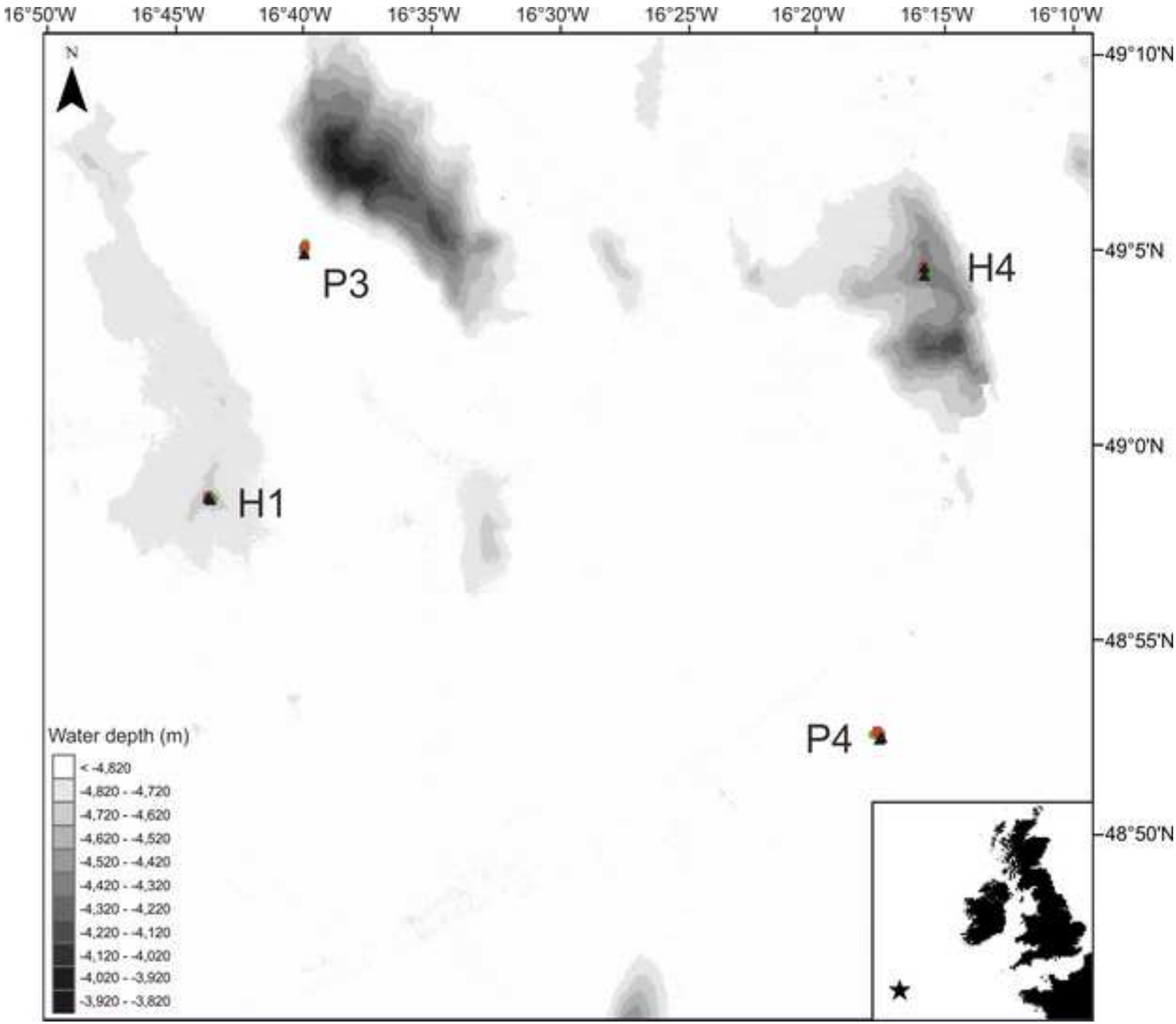

Plate 1

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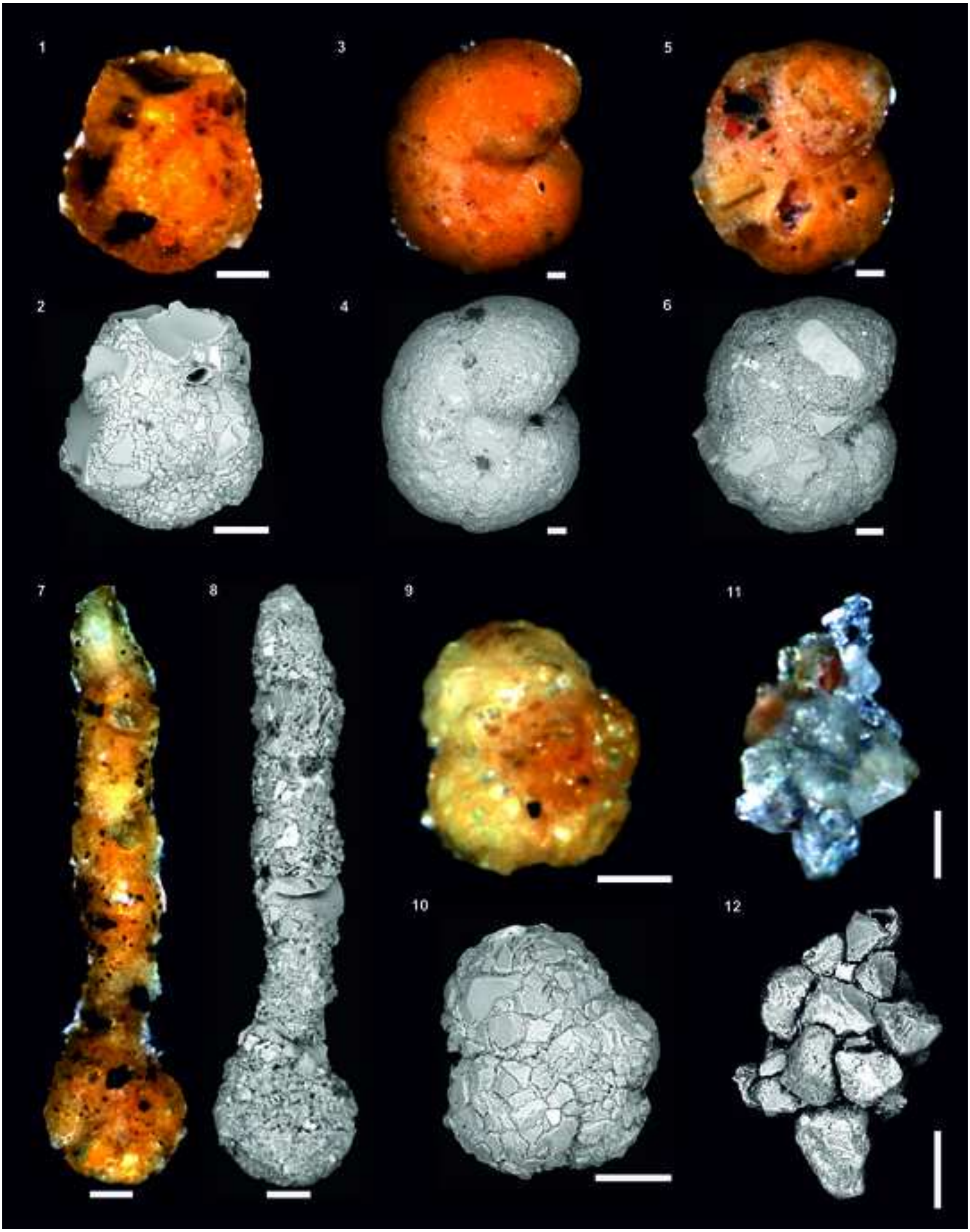

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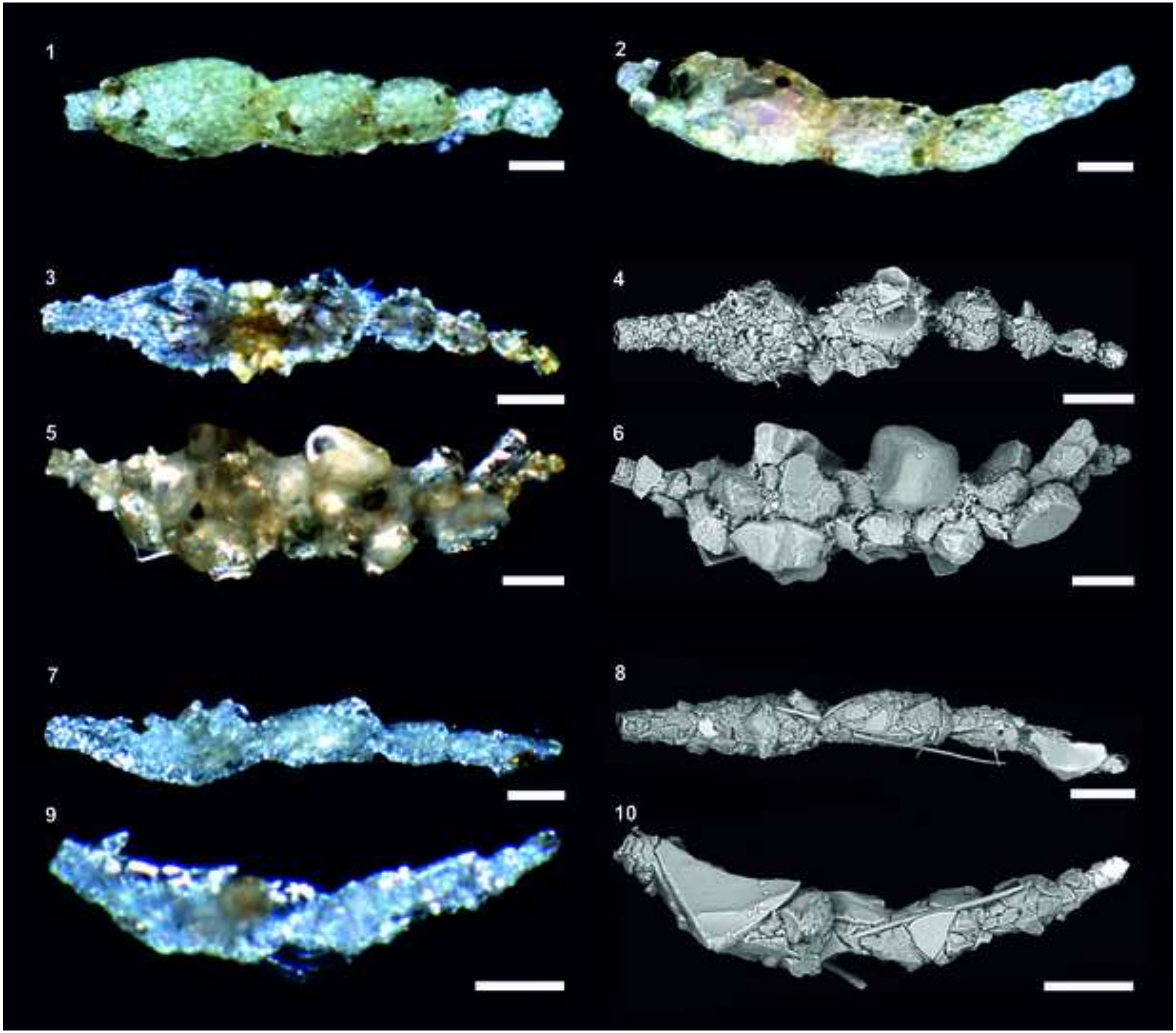

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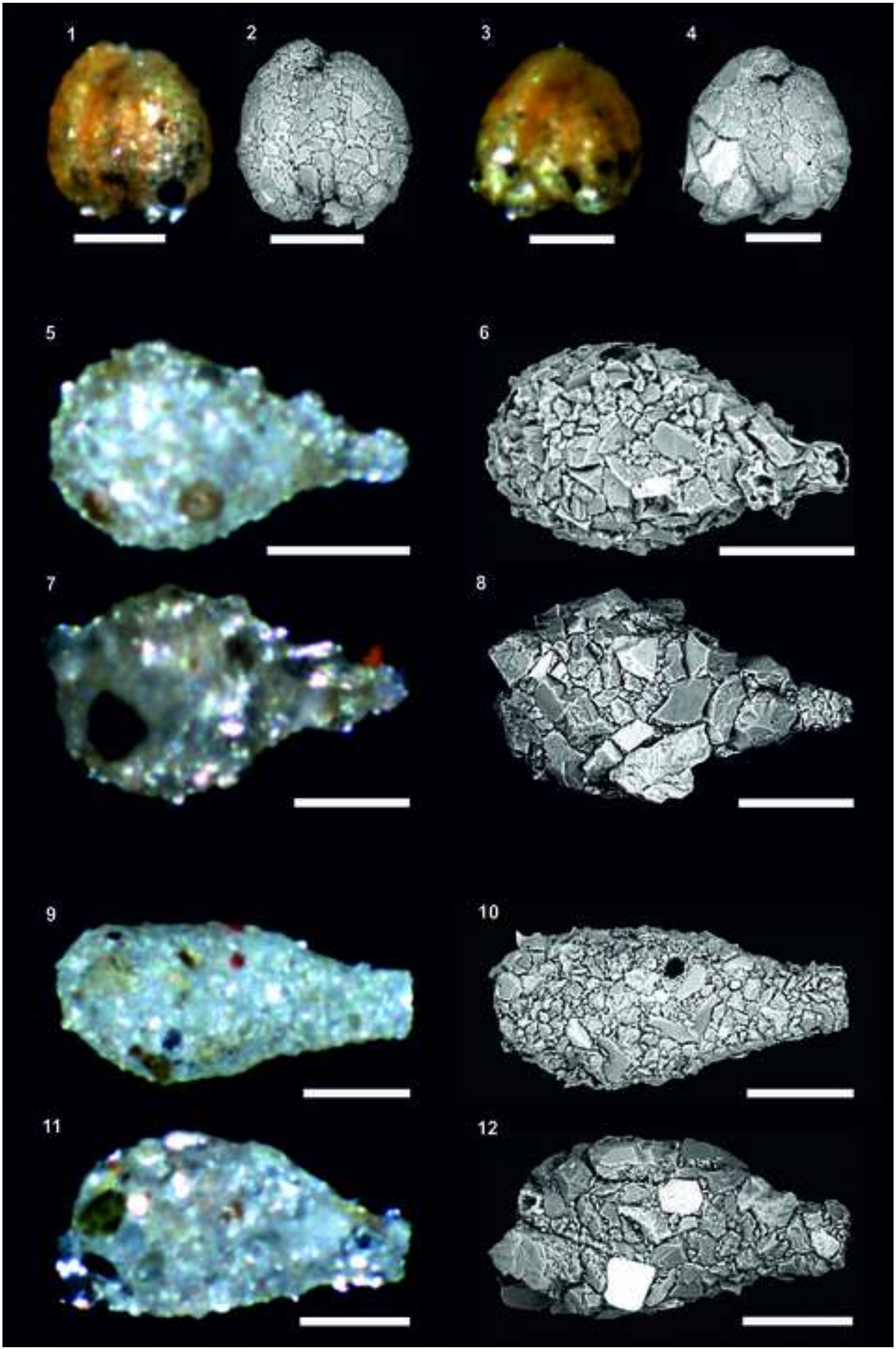

Figure 2

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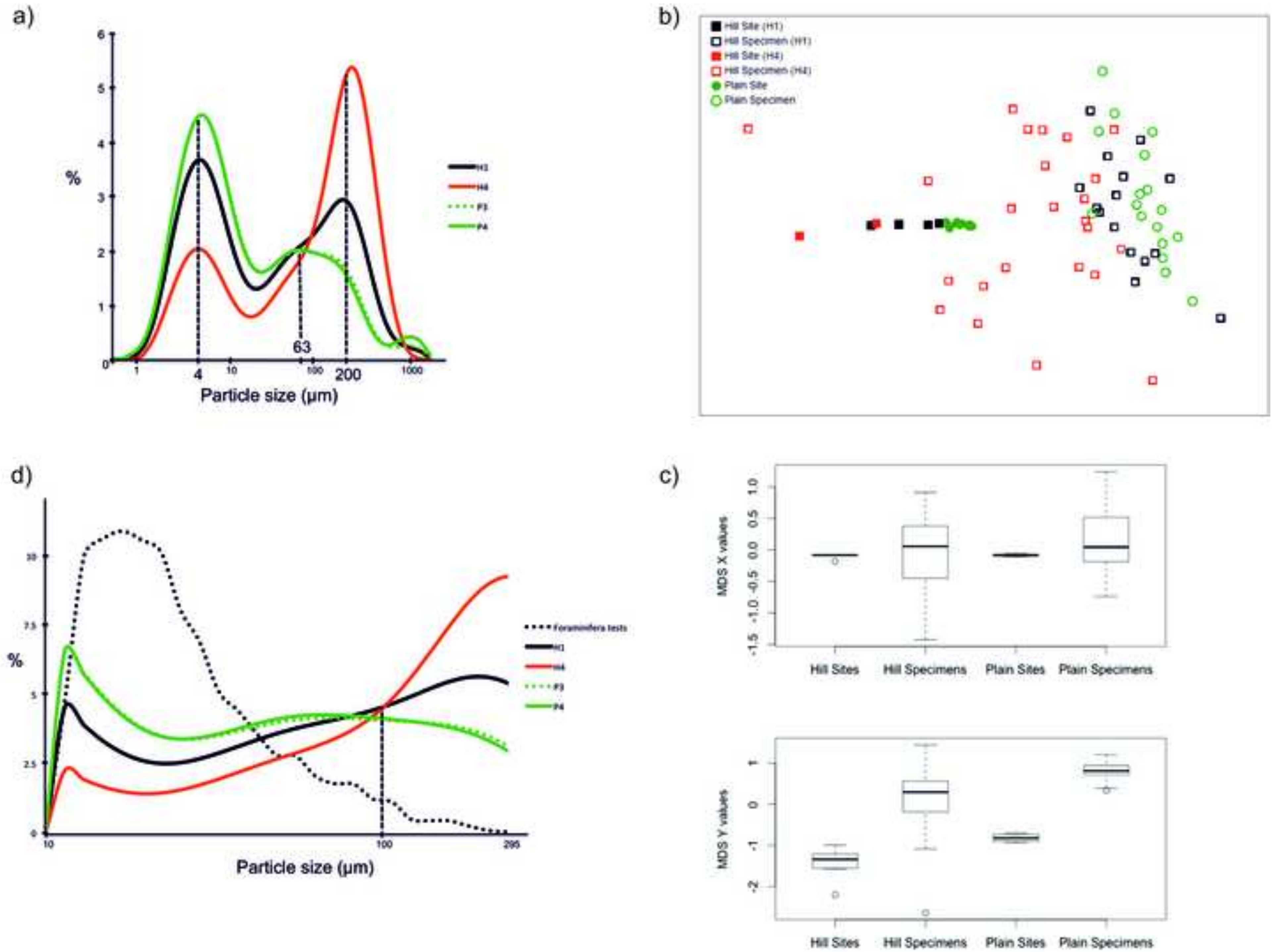

Figure 3
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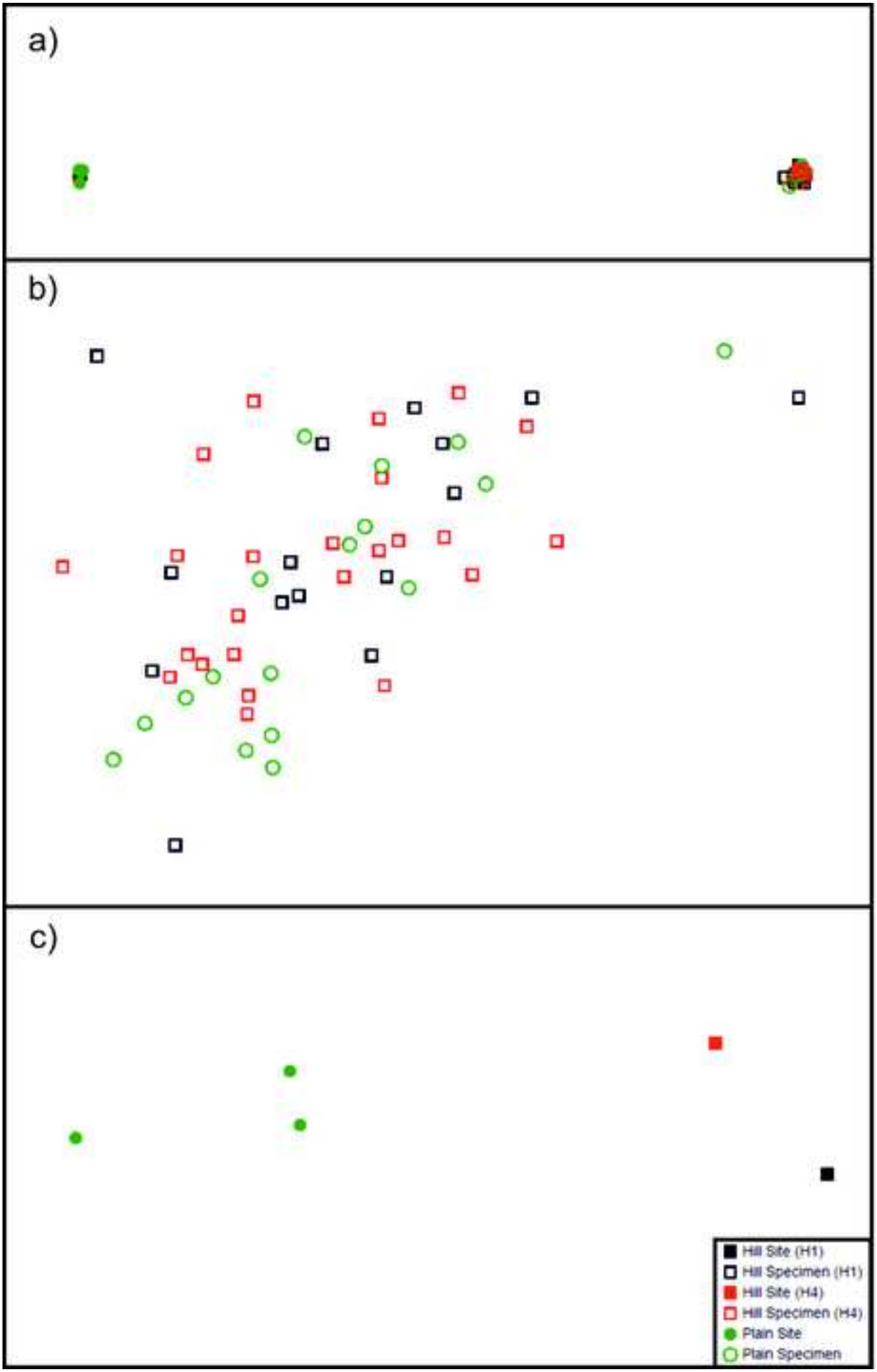

Appendix A

Appendix B

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Appendix C

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