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Pauline Depuydt, Meryem Mojtahid, Christine Barras, Fatima Zohra  
Bouhdayad, Samuel Toucanne

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1           **Intermediate ocean circulation and cryosphere dynamics in**  
2           **the Northeast Atlantic during Heinrich Stadials: benthic**  
3           **foraminiferal assemblage response**

4                           Pauline DEPUYDT<sup>1,\*</sup>, Meryem MOJTAHID<sup>1</sup>, Christine BARRAS<sup>1</sup>, Fatima Zohra  
5                           BOUHDAYAD<sup>1,2</sup>, Samuel TOUCANNE<sup>3</sup>

6  
7  
8           <sup>1</sup> Univ Angers, Nantes Université, Le Mans Université, CNRS, UMR 6112, Laboratoire  
9 de Planétologie et Géosciences, F-49000 Angers, France

10           <sup>2</sup> Presently at: Institute of Geology and Mineralogy, Faculty of Mathematics and Natural  
11 Sciences, University of Cologne, Cologne, Germany

12           <sup>3</sup> Univ Brest, CNRS, Ifremer, Geo-Ocean, F-29280 Plouzane, France

13  
14           \* Corresponding author: pauline.depuydt@univ-angers.fr

15 **Abstract**

16           The interaction between ocean circulation and ice-sheet dynamics plays a key role in  
17 the Quaternary climate. Compared to the surface and deep compartments of the Atlantic  
18 Meridional Overturning Circulation (AMOC), the study of intermediate depths during key time  
19 periods, such as Heinrich Stadials (HSs), remains poorly documented, especially in the  
20 northeast Atlantic. Here we use benthic foraminiferal assemblage data to trace  
21 paleoenvironmental changes from ~32 to 14 ka cal BP at ~1000 m depth in the Bay of Biscay.  
22 Our results highlight the high sensitivity of foraminifera, with species-specific responses, to  
23 continental (European Ice Sheet dynamics) and marine (AMOC) forcing factors during the last  
24 three HSs. In general, HSs were characterized by the concomitant presence of meso-  
25 oligotrophic and anoxia indicator species and the low abundance of high-energy indicator  
26 species. This confirms an overall sluggish intermediate circulation during the three HSs in the  
27 northeast Atlantic. HS1 is distinctive by the abundance of high-organic flux indicator species  
28 during its early phase. This is consistent with the fact that HS1 was, by far, the most important  
29 period of ice-sheet retreat and meltwater release to the ocean over the studied time interval.  
30 Finally, foraminifera depict the mid-HS2 re-ventilation event due to regional glacier  
31 instabilities.

32

33 **Keywords**

34           Intermediate water masses, AMOC, European Ice Sheet, Glacial Eastern Boundary  
35 Current (GEBC), Channel River, Benthic foraminifera

36

## 37 **1. Introduction**

38 The last glacial-interglacial cycle is a critical period to understand the natural climate  
39 variability and its abrupt transitions (*e.g.* Bond *et al.*, 1993; Wang *et al.*, 2001; Clark *et al.*,  
40 2012; Denton *et al.*, 2021). Orbital forcing (solar radiation), and the feedbacks implying the  
41 atmosphere, the ocean, and the cryosphere are the main factors explaining the recorded  
42 centennial to multi-millennial climate variability over this period (Broecker and Denton, 1990;  
43 McManus *et al.*, 1999; Denton *et al.*, 2010; Lynch-Stieglitz, 2017). In the Northern Hemisphere,  
44 the climate of the last glacial period was punctuated by cold (stadials) and warm intervals  
45 (interstadials), that were coeval with periods of weakened and accelerated Atlantic Meridional  
46 Overturning Circulation (AMOC), respectively (*e.g.* Kissel *et al.*, 2008; Böhm *et al.*, 2015;  
47 Henry *et al.*, 2016; Toucanne *et al.*, 2021). Amongst the cold intervals, the most drastic are  
48 certainly the Heinrich Stadials (HSs), encompassing the Heinrich events (HEs), *i.e.* armadas of  
49 icebergs discharge issued from the dislocation of the Hudson Strait Ice stream of the Laurentide  
50 Ice Sheet (LIS) that ultimately caused the deposition of ice-rafted debris (IRD) rich sediments  
51 in the subpolar North Atlantic (Hemming, 2004). It is hypothesized that HEs were triggered by  
52 sub-surface heat (700–1100 m depth), 1-2 ka after the decline of the AMOC (Shaffer *et al.*,  
53 2004; Marcott *et al.*, 2011; Alvarez-Solas *et al.*, 2013). The initial AMOC slowdown likely  
54 requires precursor melting of North Atlantic–adjacent ice sheets and it is now accepted that the  
55 European Ice sheet (EIS) was a critical source for AMOC destabilization and the initiation of  
56 HSs conditions (Peck *et al.*, 2006; Eynaud *et al.*, 2012; Boswell *et al.*, 2019; Toucanne *et al.*,  
57 2015, 2021, 2022).

58 The present work investigates the evolution of northeast Atlantic intermediate water depth  
59 environments and their interaction with EIS dynamics during the last glacial and deglaciation  
60 periods, with a focus on HSs. This is achieved through the study of marine sediment core  
61 BOBGEO-CS05 retrieved at ~1000 m water depth in the northern Bay of Biscay (BoB) (Figure  
62 1a & 1c). This record covers the past ~32-14 ka cal BP, thus encompassing the last three HSs  
63 (HS1, HS2 and HS3). During the last glacial period and the last deglaciation, BOBGEO-CS05  
64 site was located off the Channel River, that drained EIS sediment-laden meltwaters to the  
65 northern BoB (Zaragosi *et al.*, 2001; Bourillet and Lericolais, 2003; Toucanne *et al.*, 2009,  
66 2010) (Figure 1b). At the time, the core site was also on the pathway of the Glacial Eastern  
67 Boundary Current (GEBC), the glacial analogue of the northward-flowing European Slope  
68 Current, that represents the easternmost portion of the upper branch of the AMOC (Toucanne

69 *et al.*, 2021) (Figure 1b). As such, core BOBGEO-CS05 is ideally located to track EIS melting  
70 episodes and evaluate their impact/relation to the upper branch of the AMOC.

71 The present study focuses on fossil benthic foraminifera as one of the very few biological  
72 indicator groups that are able to record the history of events on the seafloor by integrating the  
73 cumulative impacts of the changing physico-chemical habitats (*e.g.* Schmiedl and Mackensen,  
74 1997; Wollenburg *et al.*, 2001; Rodriguez-Lazaro *et al.*, 2017). A particular interest is found in  
75 documenting HS2 and HS3, which are not covered by the nearby recent foraminiferal studies  
76 (Mojtahid *et al.*, 2017; Pascual *et al.*, 2020). In addition, our aim is to establish to what extent  
77 information previously obtained from sedimentary, geochemical and surface water proxies on  
78 the interaction between the AMOC and the EIS during the HSs are consistent with our benthic  
79 biotic data. More specifically, the approach uses here foraminiferal diversity and density, and  
80 the ecological requirements of specific species to interpret several aspects of the environment  
81 on the seafloor (*e.g.* organic matter flux, bottom-water oxygenation, current, transport, water  
82 masses properties). Our findings highlight strong foraminiferal species-specific responses,  
83 particularly during HSs, with some species associations able to discriminate between  
84 EIS/continental impact and ocean circulation changes.

85

## 86 **2. Core location, present and past sedimentological and hydrographical** 87 **settings**

88 Core BOBGEO-CS05 (46°18.850'N, 5°56.988'W, 1473 cm length, 1015 m water depth) was  
89 extracted from the upper continental slope of the northern BoB (northeast Atlantic) during the  
90 BOBGEO cruise (doi.org/10.17600/9030060; R/V Pourquoi pas?; Bourillet, 2009) (Figure 1).  
91 Core BOBGEO-SC05 is mostly composed of contourite deposits (Toucanne *et al.*, 2021), *i.e.*  
92 sediments deposited or substantially reworked by the persistent action (*e.g.* selective deposition,  
93 winnowing, erosion) of bottom currents (Facies 1 and 2; Fig. 2). Silty-clayey laminations  
94 characterized the early part of the deglaciation (early HS1), ca. 18-16.7 ka (Facies 3; Figure 2),  
95 and IRD (Facies 4; Figure 2) allowed the recognition of the Heinrich layers (cf. Supplementary  
96 material S1 for the complete X-Ray radiographs).

97 Today, the sedimentation on the slope is governed by the European Slope Current (ESC),  
98 flowing along the upper slope (~500-2000 m water depth) from the northern Iberian Peninsula  
99 to the Faroe-Shetland Channel (Marsh *et al.*, 2017; Clark *et al.*, 2021; Moritz *et al.*, 2021)  
100 (Figure 1a). This current, driven by both the steep topography of the European margin and

101 large-scale meridional density gradients (Huthnance, 1984; Pingree and Cann, 1990; Friocourt  
102 *et al.*, 2007), is largely recruited from the eastern North Atlantic and is connected, north of  
103  $\sim 55^{\circ}\text{N}$  (*i.e.* Rockall Trough), to the upper part of the North Atlantic Current (NAC; that is the  
104 eastern limb of the subpolar gyre). This forms the bulk of the upper branch of the AMOC (down  
105 to  $\sim 1500$  m; Lozier *et al.*, 2019; Huthnance *et al.*, 2020). The latter (to which the ESC  
106 contributes by  $\sim 25$  %; Berx *et al.*, 2013) finally reaches the Nordic Seas convection region,  
107 where it cools and sinks to form a deeper southward return flow, the North Atlantic Deep Water  
108 (NADW), mainly found along the eastern continental margin of North America and transported  
109 by the Deep Western Boundary Current (*e.g.* Dickson and Brown, 1994) (Figure 1a).

110 The main water mass transported by the NAC into the BoB forms the Eastern North Atlantic  
111 Central Water (ENACW), found down to  $\sim 600$  m water depth (Pollard and Pu, 1985). Below,  
112 the Mediterranean Outflow Water (MOW) is present between  $\sim 600$  and  $1500$  m, flowing  
113 northward from the Gulf of Cadiz and largely entrained by the ESC north of  $\sim 45^{\circ}\text{N}$  (*e.g.* Pingree  
114 *et al.*, 1999; van Aken, 2000). Deeper, the Labrador Sea Water (LSW), centered at  $\sim 2000$  m  
115 water depth and corresponding to the upper NADW, dominates (van Aken, 2000a). fcapture of  
116 the (southward-flowing) LSW by the above (eastward-flowing) Gulf Stream – NAC system in  
117 the north-western North Atlantic (Buckley and Marshall, 2016; Zou *et al.*, 2017) (Figure 1a).

118 During the last glacial maximum (LGM) ca. 23-18 ka cal BP (Mix *et al.*, 2001), the Gulf  
119 Stream – NAC system and more generally the upper branch of the AMOC certainly had a  
120 different geometry (*i.e.* positioned southward) because of the (southward) expansion of ice  
121 sheets over North America (Keffer *et al.*, 1988; Otto-Bliesner *et al.*, 2006; Brady and Otto-  
122 Bliesner, 2011; Löffverström *et al.*, 2014) (Figure 1b). The NADW was likely replaced by a  
123 shallower, northern-sourced nutrient-poor water mass, namely the Glacial North Atlantic  
124 Intermediate Water (GNAIW), dominant above  $2000$  m depth and overlaying a more nutrient-  
125 rich water of southern origin below  $2000$  m (*i.e.* a glacial analog of Antarctic Bottom Water)  
126 (*e.g.* Lynch-Stieglitz *et al.*, 2007). The recirculation of the GNAIW by the glacial Gulf Stream  
127 – NAC system certainly explains GNAIW signatures recorded in the NE Atlantic basin and the  
128 BoB basin during the last glacial period (Zahn *et al.*, 1997; Peck *et al.*, 2006, 2007a; Toucanne  
129 *et al.*, 2021). At the same time, the Mediterranean-Atlantic water exchange was reduced by  
130  $\sim 50$  %, and the MOW was certainly restricted to the southern Iberian margin (*e.g.* Rogerson *et*  
131 *al.*, 2012). On the other hand, the presence of Antarctic Intermediate waters (AAIW) along the  
132 European margin as far north as the South Iceland Rise was hypothesized (Rickaby and  
133 Elderfield, 2005; Thornalley *et al.*, 2010) but the recent studies of Thornalley *et al.* (2015) then

134 Crocker *et al.* (2016) concluded that mid-depth in the NE Atlantic was never ventilated by  
135 southern-sourced waters during the last glacial period. During late HS1 (~17 ka cal BP), and  
136 the near shutdown of the AMOC (McManus *et al.*, 2004; Ng *et al.*, 2018), Mojtahid *et al.* (2017)  
137 recorded low foraminiferal Sr/Ca ratios (*i.e.* carbonate system proxy; Yu *et al.*, 2014; Allen *et*  
138 *al.*, 2016; Keul *et al.*, 2017), indicative of a change in water mass chemistry and origin in the  
139 BoB. At the same time, Mojtahid *et al.* (2017) recorded increasing benthic foraminiferal Mg/Ca  
140 ratios, indicating a warming of intermediate water masses. This is interpreted as the northward  
141 conveyance of the subsurface warming originating from the low latitudes (Rühlemann *et al.*,  
142 2004; Shaffer *et al.*, 2004) by the glacial NAC (GNAC) and the GEBC (Figure 1b) (Toucanne  
143 *et al.*, 2021). This reinforces the view that the water mass structure in the glacial NE Atlantic  
144 could have changed rapidly through time.

145

### 146 **3. Materials and Methods**

#### 147 **3.1. Chronology**

148 The chronostratigraphic framework of core BOBGEO-CS05 (Figure 2) is detailed in  
149 Toucanne *et al.* (2021). In short, the final age model is based on XRF-Ca/Ti data  
150 synchronization with the nearby well-dated core MD95-2002 (Figure 2a). Twenty-one XRF tie-  
151 points based on the recognition of millennial-scale oscillations were determined. The final age  
152 model indicates that core BOBGEO-CS05 covers a period extending from ca. 32 to  
153 14 ka cal BP (Figure 2), thus encompassing the end of MIS 3 (ca. 57-29 ka cal BP) and MIS 2  
154 (ca. 29-14.7 ka cal BP). The accuracy of the age model is supported first by the good match  
155 between the percentages of the polar planktonic taxon *N. pachyderma* in core BOBGEO-CS05  
156 and MD95-2002 (Figure 2c), and second, by the overall concordance with the new radiocarbon  
157 dates (n=12; Table 1; Figure 2b). The top core <sup>14</sup>C dates show older ages (~15.7 cal ka BP) than  
158 the final XRF-Ca/Ti based age model (~14 cal ka BP) (Figure 2b). The low percentages of the  
159 polar taxon *N. pachyderma* at the core top (Figure 2c) indicate that we are out of the Heinrich  
160 Stadial, making the core top <sup>14</sup>C ages unreliable. Such incoherencies in <sup>14</sup>C dates (including the  
161 few outliers; Figure 2b) are certainly linked to physical sediment mixing and bioturbation that  
162 are common in contourite deposits.

163 The final age model clearly shows a sedimentary hiatus after ~14 cal ka BP, in concordance  
164 with previous studies in similar environments in the BoB (Mojtahid *et al.*, 2017; Toucanne *et*  
165 *al.*, 2021). The lack of sedimentation is due to increased erosion of the shelf deposits in response

166 to the significant sea-level rise and the embayment of the English Channel (e.g., Bourillet *et al.*,  
167 2003; Toucanne *et al.*, 2012).

168 Core BOBGEO-CS05 shows sedimentation rates of 50-150 cm.ka<sup>-1</sup> (Figure 2b). As such,  
169 core BOBGEO-CS05 offers a unique opportunity to study at high time resolution the later part  
170 of the last glacial period and the last three HSs.

171

### 172 **3.2. Foraminiferal analyses**

173 For benthic foraminiferal analyses, 56 samples were investigated (~320 years resolution).  
174 The samples were washed through 63 and 150 µm mesh size sieves. The >150 µm fraction was  
175 splitted with a dry Otto microsplitter (when necessary) until obtaining at least 250-  
176 300 specimens in the final split. Then, all foraminifera were picked out from the split and  
177 mounted on Plummer cell slides for taxonomic determination. To verify the relevance of small-  
178 sized benthic species, 16 out of the 56 samples were investigated from the 63-150 µm size  
179 fraction. Foraminifera were picked out from 3 out of the 16 samples, put in Plummer cell slides  
180 and determined taxonomically. For the rest of the 63-150 µm samples, foraminifera were  
181 counted and determined directly under the stereomicroscope. Similarly to the >150 µm fraction,  
182 samples (63-150 µm) were splitted with a dry Otto microsplitter until obtaining at least 250-  
183 300 specimens in the final split. The benthic foraminiferal accumulation rate (ind.cm<sup>-2</sup>.ka<sup>-1</sup>)  
184 (BFAR), used as paleo-productivity proxy (Herguera and Berger, 1991; Herguera, 1992;  
185 Gooday, 2003; Jorissen *et al.*, 2007), was calculated for both the >150 µm and >63 µm (63-150  
186 + >150 µm) fractions as: number of individuals per gram of dry sediment × linear sedimentation  
187 rate (cm.ka<sup>-1</sup>) × Dry Bulk Density (g.cm<sup>-3</sup>) (Herguera and Berger, 1991). The Dry Bulk Density  
188 (DBD) was calculated following the relation:  $DBD = 2.65 \times (1.024 - D_{wet}) / (1.024 - 2.65)$ , where  
189 2.65 g.cm<sup>-3</sup> is the grain density and 1.024 g.cm<sup>-3</sup> is the interstitial water density (Auffret *et al.*,  
190 2002). Wet bulk densities ( $D_{wet}$ ) were derived from gamma-ray attenuation density  
191 measurements obtained from a 'Geotek Multi Sensor Core Logger' (MSCL).

192 The relative abundances of benthic species (% of the total foraminiferal abundances) were  
193 calculated for the >150 µm fraction for the 56 samples and for the >63 µm fraction (63-150 µm  
194 + >150 µm) for the selected 16 samples. The error bars of the relative abundances were  
195 computed with the binomial standard error  $\sqrt{(p(1-p))/n}$  (Buzas, 1990; Fatela and Taborda,  
196 2002), where p is the species proportion estimate (number of counted individuals for a given  
197 species/n). The diversity of the 56 samples (>150 µm) was calculated with the Shannon index  
198 (entropy, H; Hayek and Buzas, 1997) using the PAST software (PAleontological STatistics;



199 Version 2.14; Hammer *et al.*, 2001). Error bars representing 95 % confidence interval were  
200 computed with a bootstrap procedure. In this study, we discuss mainly the most dominant  
201 species with relative abundance >10 % showing the highest variability. All species with relative  
202 abundance between 5 and 10 % in at least one sample are presented in supplementary material  
203 S2, and their ecological interpretations summarized in Table 2. The complete raw data set is  
204 available as supplementary material S3 and in SEANOE data repository  
205 (<https://doi.org/10.17882/88029>). Scanning Electron Microscope (SEM) photographs were  
206 obtained at LPG (Angers University, France) using a Tabletop Microscope Hitachi  
207 TM4000Plus.

208 For the counts of the planktonic taxon *N. pachyderma*, the >150  $\mu\text{m}$  fraction were used  
209 and the relative abundances were determined using a minimum of 300 planktonic foraminiferal  
210 tests from single sample splits. Counting was performed at University of Bordeaux (France).

211

#### 212 **4. Results**

213 Average BFAR values from the >150  $\mu\text{m}$  fraction are  $\sim 12 \cdot 10^3 \text{ ind.cm}^{-2} \cdot \text{ka}^{-1}$  and from the  
214 >63  $\mu\text{m}$  are  $\sim 7.5 \cdot 10^6 \text{ ind.cm}^{-2} \cdot \text{ka}^{-1}$  (Figure 3a). The values from the >150  $\mu\text{m}$  fraction are  
215 minimal during the three HSs ( $\sim 1 \cdot 10^3 \text{ ind.cm}^{-2} \cdot \text{ka}^{-1}$ ) and are more important during the  
216 interstadial periods ( $\sim 30 \cdot 10^3 \text{ ind.cm}^{-2} \cdot \text{ka}^{-1}$ ). From  $\sim 32$  to 14 ka cal BP, the Shannon (H) index  
217 (Figure 3b) shows an overall increase of diversity, with values ranging from  $\sim 2$  to 3.2.

218 The eight most dominant species (>10 %) showing the highest variability are illustrated in  
219 Plate 1 and their relative abundances are presented in Figure 3 (c-j). *Elphidium* spp.,  
220 *Cassidulina crassa* and *Cibicides lobatulus* are dominant along the record and account together  
221 for 12.7 to 74.3 % of the total fauna. In this study, *Elphidium* spp. includes mainly *E. excavatum*  
222 (*i.e.* *E. excavatum* f. *clavatum*) with pyritized shells (Plate 2a) and other species of the genus  
223 *Elphidium* (e.g., *E. gerthi*, *E. macellum*). *Elphidium* spp. show maximum values (>30 %)   
224 between 30.7 and 28.9 ka cal BP (*i.e.* HS3) and minimum values (<10 %) between 17.5 and  
225 16.5 ka cal BP (*i.e.* Early HS1; Figure 3c). Before HS2, *C. crassa* accounts in average for about  
226  $\sim 21$  % of the total fauna (Figure 3d). The highest values are recorded during HS2, with  
227 maximum percentages (40 %) just before HE2 followed by a sharp decrease. After HS2, the  
228 relative density of this species remains stable around  $\sim 8$  %. *Cibicides lobatulus* exhibits a  
229 different pattern in comparison with the previously mentioned species. Generally, this species  
230 is present with lower proportions during HS periods (around 5-10 %), except at 24.2 ka cal BP

231 (during HE2) and 17.2 ka cal BP (during HS1). Between HS3 and HS2 (ca. 29-26 ka cal BP)  
232 and during the LGM (ca. 23-18 ka cal BP), *C. lobatulus* accounts for ~22 % of the total fauna  
233 (Figure 3e). *Trifarina angulosa* shows the same trend as *C. lobatulus* (Figure 3f) but with  
234 overall lower proportions (maximum values around 10 %). The remaining dominant species  
235 (>10 %) present a discontinuous evolution. *Cassidulina carinata*, *Bolivina* spp. and  
236 *Globobulimina* spp. exhibit high relative abundances (up to 42 %, 24 % and 18 % respectively),  
237 with high variability, during early HS1 (Figure 3g, 3h & 3i). Before HS1, *Globobulimina*  
238 species are almost absent except in samples from HS3 and HS2 (average of ~5 % and 7.5 %,  
239 respectively). *Cibicidoides pachyderma* is also present mainly during the three HSs reaching  
240 12.5 % at 29.3 ka cal BP (*i.e.* during HS3), 20 % at 25.3 ka cal BP (*i.e.* during HS2) and varying  
241 around 10 % at ~HS1 (Figure 3j). Here, *C. pachyderma* encompasses several morphotypes  
242 spanning from *C. pachyderma* sensu stricto (pronounced carina) to *Cibicidoides kullenbergi*  
243 sensu stricto (less pronounced carina) (Plate 2b). The presence of several intermediate  
244 morphotypes hampered the taxonomical differentiation between *C. pachyderma* and *C.*  
245 *kullenbergi*, and as such were lumped together as *C. pachyderma*.

246 The evolution through time of the minor species (*i.e.* present only few times with percentages  
247 >5 %) is represented in **Erreur ! Source du renvoi introuvable.** *Gavelinopsis praegeri* and  
248 *Planorbulina mediterranensis* mainly appear just after 24.2 ka cal BP, between HE2 and the  
249 end of HS2. *Chilostomella oolina*, *Pullenia quinqueloba*, *Textularia sagittula* occur just one  
250 time with relative densities >5 % at 16.8 ka cal BP, 16.5 ka cal BP, 17.2 ka cal BP respectively  
251 while *Hoeglundina elegans* occurs only at 14 ka cal BP. *Nonionella turgida* become dominant  
252 only after HE1 (~6 %).

253 In the small fraction (63-150  $\mu$ m), the identified species were similar to the ones found in  
254 the larger size fraction (>150  $\mu$ m). When considering the small and large fractions together  
255 (>63  $\mu$ m), six major species >5 % are present: *Elphidium* spp., *C. crassa*, *C. lobatulus*, *C.*  
256 *carinata*, *Bolivina* spp. and *T. angulosa*. These species, also identified as major species when  
257 considering only the >150  $\mu$ m size fraction, exhibit approximately similar trends (black dashed  
258 line; Fig. 3 c-h). Only *C. crassa* presents much higher proportions in the >63  $\mu$ m fraction with  
259 abundances ranging from 15 to 60 % of the total fauna.

260

## 261 **5. Discussion**

### 262 **5.1. Regional inter-comparison of benthic foraminiferal faunas**

263 Most of the dominant foraminiferal taxa in core BOBGEO-CS05 (*e.g.* *C. pachyderma*, *C.*  
264 *carinata*, *C. crassa*, *Bolivina* spp., *Globobulimina* spp.) inhabit the modern upper slope  
265 environments of the BoB (*e.g.* Murray, 1970; Fontanier *et al.*, 2006; Mojtahid *et al.*, 2010;  
266 Duros *et al.*, 2011, 2012; Dorst and Schönfeld, 2013), and/or are found in the regional benthic  
267 fossil (*i.e.* last glacial) records of intermediate waters depths (Figure 1c; Mojtahid *et al.*, 2017;  
268 Pascual *et al.*, 2020). However, some discrepancies are observed and detailed hereafter:

269

#### 270 **5.1.1. High-energy indicator species**

271 *Cibicides lobatulus* (also known as *Lobatula lobatula*) is highly dominant in our record (~4-  
272 30 %). This species is also present, but with overall lower percentages (~10 %), at site MD99-  
273 2328, north of our study site (Figure 1), that covers the time interval from 23 to 16 ka cal BP  
274 (Mojtahid *et al.*, 2017) (Figure 3). However, this epibenthic species is absent today from the  
275 BoB modern foraminiferal communities at ~1000 m depth (*e.g.* Fontanier *et al.*, 2002;  
276 Fontanier *et al.*, 2006; Mojtahid *et al.*, 2010; Duros *et al.*, 2011, 2012). This discrepancy can be  
277 explained by different environmental conditions (*e.g.* food source, hydrodynamics) during the  
278 last glacial period allowing their settlement at intermediate water depths in the area. Indeed, *C.*  
279 *lobatulus* is a suspension-feeder that inhabits moderate-to-strong hydrodynamic environments  
280 of the modern northeast Atlantic. These include shelf environments (*e.g.* Basque shelf; Pascual  
281 *et al.*, 2008) and upper slope settings swept by strong bottom currents and characterized by  
282 coarse substrate and/or cold-water coral mounds and reefs trapping abundant food particles (*e.g.*  
283 Gulf of Cadiz, Porcupine and Rockall Banks; Schönfeld, 1997, 2002a, 2002b; Margreth *et al.*,  
284 2009; Spezzaferri *et al.*, 2015). As such, the high presence of *C. lobatulus* in the BOBGEO-  
285 CS05 glacial record might indicate stronger currents than today. The depicted link between *C.*  
286 *lobatulus* and strong energy environments is further supported in our record by its co-variation  
287 with: i) the abundance of *Trifarina angulosa* ( $r^2 = 0.78$ ) (Figure 3e & 3f) which is commonly  
288 associated with shelf-edge to upper-slope areas swept by vigorous bottom currents (*e.g.*  
289 southwest Norway, Rockall Trough ; Mackensen *et al.*, 1985; Austin and Evans, 2000; Gooday  
290 and Hughes, 2002), and ii) the “sortable silt” mean size  $\overline{SS}$  (*i.e.* the mean grain size of the  
291 carbonate-free terrigenous silt fraction) at BOBGEO-CS05 (Figure 4f; Toucanne *et al.*, 2021)  
292 that provides a direct constraint on the rate of past bottom flows (McCave *et al.*, 1995). As such,  
293 our biotic data independently support the presence of strong bottom currents on the upper slope

294 of the BoB, and by extent the presence of the GEBC along the French Atlantic margin  
295 (Toucanne *et al.*, 2021). Based on the above, we summed the percentages of *C. lobatulus* and  
296 *T. angulosa* to constitute the group of high-energy indicator species. The latter will be used to  
297 examine the hydrodynamics variability in the study area throughout the ca. 32-14 ka cal BP  
298 interval, and more specifically during the HSs (cf. Section 5.2).

299

### 300 **5.1.2. Glacier-proximal species**

301 The high dominance (up to ~40 % in the late MIS 3 and ~20 % thereafter) of elphidiids in  
302 core BOBGEO-CS05 is peculiar as this group is presently found in coastal, shelf and estuarine  
303 environments of the northeast Atlantic (*e.g.* Pujos, 1976; Murray, 2014; Mojtahid *et al.*, 2016).  
304 In the modern benthic foraminiferal assemblage of the upper Whittard region (northern BoB,  
305 ~1000 m depth; Duros *et al.*, 2012), *Elphidium* spp. are found only in the dead faunas, and as  
306 such, were considered as transported from shallower settings. Mojtahid *et al.* (2017) report  
307 high abundances of *Elphidium* spp. in core MD99-2328 especially during the late HS1 (16.7-  
308 16 ka cal BP; up to ~70 %) and hypothesized their transport to these intermediate depths by the  
309 EIS icebergs and/or shelf ice. This would be also a possibility for BOBGEO-CS05 since  
310 *Elphidium* shells show pyritization marks (Plate 2a) that may indicate a potential reworking and  
311 transport. However, it is interesting to note that modern elphidiids may extend their habitats to  
312 deeper settings (several hundred meters) in cold, arctic environments, usually in connection  
313 with freshwater river outflow (*e.g.* Bergsten, 1994; Polyak *et al.*, 2002). Therefore, another  
314 explanation for the high abundance of elphidiids in the glacial BOBGEO-CS05 record could  
315 simply be an adaptation to cold glacial conditions and meltwater inputs in the BoB. This is  
316 supported by the presence of *E. excavatum* f. *clavatum*, the dominant elphidiids species in our  
317 assemblages (~75 %), frequently found today in glacier-proximal environments (*e.g.* Jennings  
318 *et al.*, 2004; Murray, 2006; Darling *et al.*, 2016; Fossile *et al.*, 2020). The modern conditions in  
319 the polar regions where this species lives today are close to the conditions prevailing during the  
320 last glacial period in our study area since the EIS invaded the western European shelf (cf. ice-  
321 sheet and polar fronts limits in Figure 1) and the Channel River channeled huge amounts of  
322 meltwaters to the northern BoB.

323 *Cassidulina crassa* occurs concomitantly to *E. excavatum* f. *clavatum* in our record ( $r^2 =$   
324 0.85). Similarly to *Elphidium* spp., modern upper slope foraminiferal studies from the BoB  
325 reported that *C. crassa* is either only encountered in the dead faunas or very rarely present in

326 the living faunas (*e.g.* Fontanier *et al.*, 2002 , 2006; Mojtahid *et al.*, 2010; Duros *et al.*, 2012).  
327 It is therefore probable that this species has been transported to the study site, although *C. crassa*  
328 tests are rather intact (Plate 1) compared to *E. excavatum* f. *clavatum* (Plate 2a). It must be noted  
329 that the morphospecies identified here as *C. crassa* (d'Orbigny, 1839) has a variant that is very  
330 close morphologically and was described first as *Cassidulina crassa* var. *reniforme* Nørvang,  
331 1945, and later elevated to the species rank as *C. reniforme*. *Cassidulina reniforme*  
332 morphospecies is mainly reported from arctic regions as typical of near-glacier environments  
333 (Hansen and Knudsen, 1995; Korsun *et al.*, 1995; Murray, 2006). Thus, it is highly possible  
334 that *C. crassa* from BOBGEO-CS05 is actually the same morphospecies than the one reported  
335 from arctic regions. We therefore assume that the *C. crassa* - *E. excavatum* f. *clavatum*  
336 association in our record is coherent with near-glacier environments. This is further  
337 corroborated by the absence of these species in the upper slope glacial record PP10-12 from the  
338 southeast BoB (Pascual *et al.*, 2020), far from both the ice sheet extent limit and the Channel  
339 River mouth. Based on the above, we summed the percentages of *E. excavatum* f. *clavatum* and  
340 *C. crassa* to constitute the group of glacier-proximal indicator species. The latter will be used  
341 to examine the EIS dynamics (*cf.* Section 5.2).

342

### 343 **5.1.3. Holocene indicator species**

344 One of the most striking features of our benthic foraminiferal record is the absence of  
345 uvigerinids (*e.g.* *U. peregrina*, *U. mediterranea*), whereas they dominate the modern benthic  
346 foraminiferal assemblages of the BoB between ~500 and 2000 m water depth (*e.g.*, Schönfeld,  
347 2006; Barras *et al.*, 2010; Mojtahid *et al.*, 2010; Duros *et al.*, 2011, 2012). This absence is also  
348 the case in the glacial part of the MD99-2328 record (Mojtahid *et al.*, 2017). We assume  
349 therefore that uvigerinids might not be tolerant to the glacial-related conditions on the BoB  
350 seafloor (Mojtahid *et al.*, 2013; Pascual *et al.*, 2020; Rodriguez-Lazaro *et al.*, 2017). Schönfeld  
351 and Altenbach (2005) hypothesized a widespread change from glacial to modern surface  
352 productivity configuration (*e.g.* nature of primary producers, seasonality in phytoplankton  
353 blooms) that may have triggered the Holocene settlement of *U. peregrina* in the northeast  
354 Atlantic. It is also interesting to note that *U. peregrina* and *U. mediterranea* are very abundant  
355 in bathyal depths (~200-1500 m) of the Mediterranean and the BoB bathed by the MOW (*e.g.*  
356 De Rijk *et al.*, 2000; Schmiedl *et al.*, 2000; Fontanier *et al.*, 2003). The possible link between  
357 water masses and specific fauna has been progressively abandoned in favor of organic matter  
358 and oxygen as major controlling environmental parameters (Jorissen *et al.*, 2007). Yet, the

359 settlement of uvigerinids in the BoB in the end of deglaciation - early Holocene (Garcia *et al.*,  
360 2013; Mojtahid *et al.*, 2013; Pascual *et al.*, 2020) seems to coincide with the significant increase  
361 in the influx of the MOW into the North Atlantic and along the European margin (Rogerson *et*  
362 *al.*, 2012; Lebreiro *et al.*, 2018). This is coherent with what Mojtahid *et al.* (2017) observed in  
363 core MD99-2328 where they record the appearance of uvigerinids (although with low  
364 abundances) only in the Holocene portion of the record.

365 In summary, we have shown that the upper slope benthic foraminifera assemblage found at  
366 site BOBGEO-CS05 reflect the complex, highly dynamic and variable environmental  
367 conditions in the northern BoB during the last glacial period, including high bottom water  
368 currents, glacier-proximal settings, and southern retreat of the MOW. Since benthic  
369 foraminifera respond greatly to these various environmental parameters, they present a great  
370 potential to better constrain glacial intermediate bottom water characteristics during HSs.

371

## 372 ***5.2. Environmental particularities of Heinrich Stadials depicted by benthic*** 373 ***foraminifera***

### 374 **5.2.1. What do the last three Heinrich Stadials have in common in the Bay of** 375 **Biscay?**

376 In general, HS3 (~31-29 ka cal BP), HS2 (~26-23 ka cal BP) and HS1 (~18-15.5 ka cal BP)  
377 in core BOBGEO-CS05 are characterized by a systematic drop in BFAR values (Fig. 3a). This  
378 may indicate unfavorable conditions (*e.g.* low quality/quantity of the organic matter, low  
379 oxygenation) for the growth and reproduction of foraminifera. In the same intervals, we record  
380 the highest occurrence of *Cibicidoides pachyderma* and *Globobulimina* spp. (Figure 3j & 3i).  
381 *Cibicidoides pachyderma* is usually found in meso-oligotrophic open-slope environments, as  
382 in the modern BoB (Schmiedl *et al.*, 2000; Mojtahid *et al.*, 2010; Duros *et al.*, 2012).  
383 *Globobulimina* spp., on the other hand, are deep infaunal species that tolerate hypoxia and  
384 anoxia (Risgaard-Petersen *et al.*, 2006; Pina-Ochoa *et al.*, 2010; Koho *et al.*, 2011). Hence, we  
385 interpret the *C. pachyderma* - *Globobulimina* spp. association (*i.e.* meso-oligotrophic species;  
386 see Figure 4h) during HSs, together with the low BFAR, as indicating meso-oligotrophic  
387 conditions, with moderate to low export of organic matter to the seafloor, and reduced bottom-  
388 water ventilation. The latter is supported by the concomitant decrease in the proportions of  
389 high-energy indicator species *T. angulosa* and *C. lobatulus* during each of the HSs (Figure 4g).  
390 The weak hydrodynamics during the HSs is independently supported by the low  $\overline{SS}$  values at

391 BOBGEO-CS05 and at many sites along the French Atlantic margin (Toucanne *et al.*, 2021).  
392 As such, biotic and sedimentological data indicate reduced near-bottom flow speed (*i.e.*  
393 weakened GEBC) and, by extension, a sluggish AMOC during the three HSs.

394 The glacier-proximal species (*E. excavatum* f. *clavatum*. and *C. crassa*), although present all  
395 along the BOBGEO-CS05 record, display the highest percentages during the HSs, especially  
396 during HS3 and HS2 (Figure 4b). In their modern habitats in the Arctic fjords, these species are  
397 impacted by seasonal melting of marine-terminating glaciers (Schroder-Adams *et al.*, 1990;  
398 Wollenburg and Mackensen, 1998; Wollenburg and Kuhnt, 2000; Wollenburg *et al.*, 2004).  
399 Since enhanced EIS meltwaters influx to the BoB are described during HSs (Toucanne *et al.*,  
400 2015), increased densities of these species might be indicative of such meltwater inputs. The  
401 concomitant presence of meso-oligotrophic species (*e.g.* *C. pachyderma*) indicates a low to  
402 moderate export of organic matter to the seafloor, especially during HS2 and HS3. This will be  
403 further discussed when addressing the specificities of each HS (*cf.* Sections 5.2.2. and 5.3).

404

#### 405 **5.2.2. The difference between the early HS1 and the other HSs**

406 In core BOBGEO-CS05, HS1 is very distinct from HS2 and HS3 by displaying a high  
407 presence (~60 %) of opportunistic and high-organic flux indicator species (*C. carinata* and  
408 *Bolivina* spp.; Schmiedl *et al.*, 1997; Fontanier *et al.*, 2003; Duros *et al.*, 2011) during its early  
409 phase ca. ~18-16.7 ka cal BP (Figure 4d). This is coherent with the findings of Mojtahid *et al.*  
410 (2017) at the same time period at site MD99-2328. Conversely, during HS2 and HS3, these  
411 species were present with much lower abundances (< 10 %; Figure 4d). Thus, we assume that  
412 limited organic material inputs reached the BOBGEO-CS05 site during HS3 and HS2, then  
413 substantially increased during the early HS1. This difference is further corroborated by the  
414 positive correlation between the abundance of the high-organic flux indicator species during  
415 early HS1 at our site and both the BIT index at site MD95-2002 (Figure 4c; Ménot *et al.*, 2006)  
416 and the turbidite (*i.e.* flood-related deposits) flux in the deep BoB (Zaragosi *et al.*, 2006;  
417 Toucanne *et al.*, 2008, 2012). It has been suggested that these differences in organic material  
418 inputs through time could result from complex interactions between climate conditions, and ice  
419 and vegetation cover (Ménot *et al.*, 2006). Our data cannot resolve this issue, but it certainly  
420 highlights the paroxysmal phase of EIS melting in response to increasing boreal insolation  
421 during HS1, and the concomitant rapid progradation of a large outer-shelf delta that ultimately  
422 improved the connection between the BOBGEO-CS05 site and the Channel River system  
423 (Toucanne *et al.*, 2012). That said, because *C. carinata* and *Bolivina* spp. are very abundant in

424 shallower settings in the BoB (140-550 m depth; Duros *et al.*, 2011 ; Fontanier *et al.*, 2003), we  
425 cannot discard that their presence in our record is a result of downslope transport. Even so, the  
426 abundance of these species still indicates increased organic fluxes in their source habitats.

427 Interestingly, in the upper slope BOBGEO-CS05 and MD99-2328 cores, the dominance of  
428 the anoxia indicator species (representing the sum of *Globobulimina* spp. and *Chilostomella*  
429 *oolina*) at HS1 occurs early within this interval, before HE1 event *sensu stricto* (Figure 4i).  
430 According to Mojtahid *et al.* (2017), the presence of these indicator species during early HS1  
431 is indicative of organically-enriched and/or oxygen-depleted benthic environments, and their  
432 absence during HE1 event, together with high  $\overline{SS}$  (Figure 4i & 4f) indicate well-ventilated  
433 intermediate waters. In deeper sediment cores from the BoB (>2000 m depth), the HE1 event  
434 is characterized by the presence of authigenic carbonates indicating anoxic bottom waters (*e.g.*  
435 Auffret *et al.*, 1996; Toucanne *et al.*, 2015). Because these anoxia markers are not observed in  
436 the shallower cores BOBGEO-CS05 and MD99-2328 and because all proxies ( $\overline{SS}$  and  
437 foraminifera; Figure 4) indicate well-ventilated bottom waters, we can hypothesize a  
438 decoupling between a vigorous intermediate water depth circulation during HE1 and a still  
439 sluggish circulation at >2000 m in the northeast Atlantic, as reported by the Bermuda rise  
440  $^{231}\text{Pa}/^{230}\text{Th}$  data from the deep northwest Atlantic (Figure 4e). A similar pattern is found in the  
441 equatorial Atlantic where a better ventilation of mid-depth waters in late HS1 is recorded while  
442 the deep sites remained poorly ventilated (Chen *et al.*, 2015).

443

### 444 **5.3. Foraminiferal evidence for mid-HS2 re-ventilation event**

445 During HS2 (Figure 5), the overall meso-oligotrophic conditions and the low bottom-water  
446 ventilation depicted by both the low BFAR and the *C. pachyderma* - *Globobulimina* spp.  
447 association (*i.e.* meso-oligotrophic species) were interrupted around 24.3 ka cal BP (Figure 5d  
448 & 5e). At the same time, low percentages of the polar planktonic species *N. pachyderma* (Figure  
449 5a) indicate a a warming of the sea-surface conditions and therefore a cessation of meltwater  
450 input in the northern BoB. This surface water warming is recorded in several sedimentary  
451 records along the European margin (*e.g.* Scourse *et al.*, 2009; Austin *et al.*, 2012; Waelbroeck  
452 *et al.*, 2019). This warm event interrupting HS2 seems to be coeval with a well-known  
453 atmospheric decrease in dust flux at high latitudes (Rasmussen *et al.*, 2008; Austin *et al.*, 2012).  
454 During this sea-surface warming event, the re-appearance of the high-energy indicator species  
455 (Figure 5c) and the drop in the anoxia indicator species (Figure 5f) strongly suggests a



456 reactivation of bottom water currents at site BOBGEO-CS05. This is supported by the increase  
457 in the  $\overline{SS}$  values at our site and, more generally, in the northern part of the French Atlantic  
458 margin (Figure 5b). Our biotic data, although covering this millennial-scale event at low  
459 sampling resolution, thus indicate, together with the  $\overline{SS}$  proxy, enhanced vigor of the GEBC  
460 and, by extension, of the AMOC during the mid-HS2. This re-acceleration of the GEBC  
461 continues to about 100 yrs before the iceberg debacle of the LIS (*i.e.* HE2 *sensu stricto* at  
462 24.2 ka cal BP), when our biotic and sedimentological proxies show a rapid return to meso-  
463 oligotrophic conditions at the sea-floor and weak bottom currents.

464

## 465 **6. Conclusions**

466 Benthic foraminiferal assemblage data allowed us to reconstruct the paleoenvironmental  
467 evolution of the upper slope of the BoB (site BOBGEO-CS05) over the ca. 32-14 ka cal BP  
468 period. In general, species-specific responses reflect the complex, highly dynamic and variable  
469 environmental conditions in the northern BoB during the last glacial period, including  
470 fluctuations in the bottom water current and the GEBC, changes in organic matter fluxes and  
471 Channel River discharges, and latitudinal changes of the MOW.

472 The three HSs (HS3, HS2 and HS1) present some common features. They are all  
473 characterized by an overall low proportion of high-energy indicator species (*i.e.* *Cibicides*  
474 *lobatulus* and *Trifarina angulosa*), and a significant presence of meso-oligotrophic indicator  
475 species (*Cibicoides pachyderma*), anoxia indicator species (*Globobulimina* spp. and *C.*  
476 *oolina*), and glacier-proximal species (*E. excavatum* f. *clavatum* and *Cassidulina crassa*). In  
477 agreement with previously published sedimentological and geochemical proxies, this reflects  
478 overall low organic matter fluxes to the seafloor and a low bottom water ventilation during the  
479 HSs.

480 Detailed investigation of the benthic foraminifera reveals some specificities of the HSs in  
481 the northeast Atlantic. First, the high abundance of high-organic flux indicator species  
482 (*Cassidulina carinata* and *Bolivina* spp.) during early HS1, compared to their near absence  
483 during HS2 and HS3, reveals a millennial-scale peak in terrestrial organic material in the BoB  
484 resulting from the significant EIS melting and Channel River meltwater floods. Second, benthic  
485 foraminiferal species depict a short-term mid-depth re-ventilation event during HS2, indicated  
486 by a decrease in the proportions of anoxia indicator species and an increase in the abundance  
487 of high-energy indicator species. This short-term reactivation of the GEBC along the French

488 Atlantic margin, and of the AMOC, is coherent with the cessation of the EIS meltwater input  
489 in the northern BoB, and more generally, with a warming of the sea-surface conditions in the  
490 northeast Atlantic. This result strongly emphasizes the connection between the intermediate  
491 ocean circulation and the cryosphere dynamics in the northeast Atlantic during the Heinrich  
492 Stadials.

493

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505

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**Table 1.**  $^{14}\text{C}$  dates of core BOBGEO-CS05.

Core label	Depth (cm)	Lab. Number <sup>a</sup>	Species	$^{14}\text{C}$ age (yr BP)	error (1 $\sigma$ )	Reservoir correction <sup>b</sup> ( $^{14}\text{C}$ yr)	error <sup>b</sup> (1 $\sigma$ )	$^{14}\text{C}$ age corrected for reservoir <sup>c</sup> ( $^{14}\text{C}$ yr BP)	error <sup>d</sup> (1 $\sigma$ )	Calendar age range <sup>e</sup> (yr BP, 2 $\sigma$ )
BOBGEO-CS05	0	Poz-73846	<i>N. pachyderma</i>	14100	80	970	200	13130	215	15133-16357
BOBGEO-CS05	10	Poz-42911	bulk planktonic	14770	70	970	200	13800	212	16132-17333
BOBGEO-CS05	305-309	Beta-478193	<i>G. bulloides</i>	15270	40	400	200	14870	204	17550-18661
BOBGEO-CS05	446	SacA-29355	bulk planktonic	18090	60	400	200	17690	209	20890-22026
BOBGEO-CS05	500-505	Beta-478194	<i>G. bulloides</i>	17140	50	400	200	16740	206	19773-20716
BOBGEO-CS05	660	SacA-29356	bulk planktonic	21140	200	400	200	20740	283	24238-25672
BOBGEO-CS05	796-800	Beta-478195	<i>G. bulloides</i>	19680	60	400	200	19280	209	22885-23789
BOBGEO-CS05	933-935	Beta-478196	<i>G. bulloides</i>	20430	70	400	200	20030	212	23727-24665
BOBGEO-CS05	1030-1033	Beta-478197	<i>G. bulloides</i>	21830	70	400	200	21430	212	25220-26049
BOBGEO-CS05	1230	Poz-45912	bulk planktonic	24510	240	400	200	24110	312	27726-28959
BOBGEO-CS05	1350	SacA-29357	bulk planktonic	24220	100	400	200	23820	224	27624-28628
BOBGEO-CS05	1460	Poz-73848	<i>N. pachyderma</i>	26130	230	400	200	25730	305	29237-30490

a: Poz- (Poznan Radiocarbon Lab., Poland); Beta- (Beta Analytic, USA); SacA- (SMA Artemis, France)

b: Reservoir correction inferred from Stern et Lisieki (2013); see Toucanne et al. (2015) for details

c: Corrected  $^{14}\text{C}$  ages are obtained by subtracting the reservoir correction to the original  $^{14}\text{C}$  age

d: Errors associated to the corrected  $^{14}\text{C}$  were propagated through the quadratic sum

e: Corrected  $^{14}\text{C}$  ages were calibrated using the atmospheric calibration curve IntCal20 (Reimer et al., 2020)

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**Table 2.** Taxonomic reference list, microhabitat and ecological preferences for the dominant benthic species (>5 %) and the corresponding bibliographic references.

Species	References with images	Microhabitat	Ecological preferences	Plate 1	Plate 2
<i>Bolivina</i> spp.		Shallow infaunal (John W. Murray, 2006)	<i>Bolivina</i> spp. have opportunistic behaviour (Schmiedl <i>et al.</i> , 2000) and ecological preferences for phytodetritus enriched deposits (Duros <i>et al.</i> , 2017, 2011)	5-6	
<i>Cassidulina carinata</i> Silvestri, 1896	Phleger <i>et al.</i> (1953), p1. 9, Figs. 32–37	Epifaunal to shallow infaunal (Jorissen, 1987; Altenbach <i>et al.</i> , 1999)	<i>Cassidulina carinata</i> is an opportunistic species (Fontanier <i>et al.</i> , 2003; Duros <i>et al.</i> , 2011) that lives in OM-enriched sediments (Hess <i>et al.</i> , 2005; Hess and Jorissen, 2009).	7	
<i>Cassidulina crassa</i> d'Orbigny, 1839	Jorissen (1987), pl. 1, Fig. 3	Shallow infaunal (de Stigter <i>et al.</i> , 1998; Fontanier <i>et al.</i> , 2005)	In our case, <i>Cassidulina crassa</i> could be a morphospecies of <i>Cassidulina reniforme</i> . This latter is often transported from the continental shelf, and redeposited on glacial marine sediments (Mackensen <i>et al.</i> , 1985), until 1000m water depth in Arctic (Wollenburg and Mackensen, 2009).	8	
<i>Cibicides lobatulus</i> Walker and Jacob, 1798	Jones and Brady (1994), pl. 93, Fig. 1	Epifaunal (John W. Murray, 2006)	<i>Cibicides lobatulus</i> live at shallow depth, attached on seagrass and algae (Véneç-Peyré and Le Calvez, 1988; John W. Murray, 2006). Even if, they were described as transported species, they can be found alive in deep and high energy environments ( <i>e.g.</i> Schönfeld, 1997, 2002b, 2002a; Margreth <i>et al.</i> , 2009; Spezzaferri <i>et al.</i> , 2015)	13	
<i>Cibicidoides pachyderma</i> Rzehak, 1886	Jones and Brady (1994), pl. 94, Fig. 9	Shallow infaunal (Fontanier <i>et al.</i> , 2003, 2002)	<i>Cibicidoides pachyderma</i> live in meso-oligotrophic conditions (Fontanier <i>et al.</i> , 2003; Mojtahid <i>et al.</i> , 2009). They prefer low nutrients waters (Schmiedl <i>et al.</i> , 2000).	11-12	b
<i>Chilostomella oolina</i> Schwager, 1878	Jones and Brady (1994), pl. 55, Fig. 12-14	Deep Infaunal (Corliss and Emerson, 1990; Bernhard, 1992; Jorissen <i>et al.</i> , 1998)	<i>Chilostomella oolina</i> is adapted to anoxic or suboxic conditions (Fontanier <i>et al.</i> , 2002; Bernhard and Sen Gupta, 2003). They may be replaced by <i>Globobulimina</i> spp. when the degraded OM quality decreases (Fontanier <i>et al.</i> , 2002)	4	
<i>Elphidium clavatum</i> Cushman, 1930	Darling <i>et al.</i> (2016), Fig. 4, S4	Infaunal–epifaunal (John W. Murray, 2006)	<i>Elphidium clavatum</i> is a widespread taxon, mainly distributed in the Arctic, and frequent in glacier-proximal environments. It is found living down to several hundreds of meters depths in the Arctic and in the Baltic (Jennings <i>et al.</i> , 2004; John W. Murray, 2006; Darling <i>et al.</i> , 2016; Fossile <i>et al.</i> , 2020). In the nearby study of Mojtahid <i>et al.</i> (2017), <i>Elphidium</i> species found at 1000 m depth during the last deglaciation were interpreted as being possibly transported from shallower settings.	10	a
<i>Elphidium gerthi</i> van Voorthuysen, 1957	Mendes <i>et al.</i> (2012), Fig. 4, 8		<i>Elphidium gerthi</i> is a subtidal to intertidal species, very common along the western European coasts . In the nearby study of Mojtahid <i>et al.</i> (2017), <i>Elphidium</i> species found at 1000 m depth during the last deglaciation were interpreted as being possibly transported from shallower settings.	9	

<i>Species</i>	References with images	Microhabitat	<i>Ecological preferences</i>	Plate 1	Plate 2
<i>Globobulimina</i> spp.		Deep infaunal (John W. Murray, 2006)	<i>Globobulimina</i> spp. live in organically-enriched and/or oxygen-depleted sediments (e.g. Jorissen, 1999; Schmiedl <i>et al.</i> , 2003; Mojtahid <i>et al.</i> , 2010). They can live in anoxic sediments by respiring nitrates (Risgaard-Petersen <i>et al.</i> , 2006).	3	
<i>Gavelinopsis praegeri</i> Heron-Allen & Earland, 1913	Jorissen (1987), pl. 3, Fig. 13	Epifaunal (Jorissen, 1987)	<i>Gavelinopsis praegeri</i> is an epiphytic species living in a wide range of water depths in marine environments (John W. Murray, 2006). They are found down to 1200m water depth (de Stigter, 1996) and prefers more oxic conditions (Dorst <i>et al.</i> , 2015).	16	
<i>Hoeglundina elegans</i> d'Orbigny, 1826	Milker and Schmiedl, (2012), pl. 19, Fig. 15	Epifaunal; shallow infaunal (Jorissen <i>et al.</i> , 1998; Fontanier <i>et al.</i> , 2002)	<i>Hoeglundina elegans</i> is described as indicator of low organic carbon environments (Fontanier <i>et al.</i> , 2002; Morigi <i>et al.</i> , 2001).	17	
<i>Nonionella turgida</i> Williamson, 1858	Milker and Schmiedl, (2012), pl. 26, Figs. 1-5	Deep infaunal (Corliss, 1991)	<i>Nonionella turgida</i> is an opportunistic species, tolerant to low oxygen conditions and high nutrient level (Van der Zwaan and Jorissen, 1991).	2	
<i>Planorbulina mediterraneensis</i> d'Orbigny, 1826	Jones and Brady (1994), pl. 92, Fig. 1	Epifaunal (Murray, 2006)	<i>Planorbulina mediterraneensis</i> is an epiphytic species and lives at shallow depths (Murray, 2006).	15	
<i>Pullenia quinqueloba</i> Reuss, 1851	Jones and Brady (1994), pl. 84, Fig. 14	Intermediate infaunal (Corliss, 1991; C. Fontanier <i>et al.</i> , 2008)	<i>Pullenia quinqueloba</i> can live in low-organic carbon conditions (Gupta, 1999).	18	
<i>Textularia sagittula</i> DeFrance, 1824	Jorissen (1987), pl. 3, Fig. 12	Epifaunal (Murray, 2006)	<i>Textularia sagittula</i> is an agglutinated species (Murray, 2006). They are dominant in shallow water depths, on sandy sediments (Murray, 2014)	1	
<i>Trifarina angulosa</i> Williamson, 1858	Jones and Brady (1994), pl. 74, Fig. 15	Shallow infaunal (Hess and Jorissen, 2009)	<i>Trifarina angulosa</i> have been observed in phytodetritus-enriched sediment (e.g. Hess and Jorissen, 2009; Duros <i>et al.</i> , 2011). They are often associated with <i>C. lobatulus</i> to strong bottom currents and can be observed until 1000m water depth (Mackensen <i>et al.</i> , 1985).	14	

1052

1053 **9. Tables caption**

1054 **Table 3.**  $^{14}\text{C}$  dates of core BOBGEO-CS05.

1055 **Table 4.** Taxonomic reference list, microhabitat and ecological preferences for the dominant  
1056 benthic species (>5 %) and the corresponding bibliographic references.

1057

1058 **10. Figures caption**

1059 **Figure 1.** Location of the study area. a) 3D representation (N-S, W-E and in water depth) of  
1060 the modern oceanic circulation in the North Atlantic representing the main currents (acronyms  
1061 written in black), water masses (acronyms written in colors) and the Subpolar (in blue) and  
1062 Subtropical (in red) gyres in the North Atlantic. b) Bathymetric map representing the  
1063 paleogeographic and paleoceanographic configuration (i.e. ice sheets, the Channel River,  
1064 currents, and water masses) of the North Atlantic during the Last Glacial Stadials according to  
1065 Toucanne et al. (2021). The angulous shapes represent the icebergs. c) Bathymetric map  
1066 focussing on the study area and showing the location of our study core BOBGEO-CS05 (violet  
1067 star), together with nearby cores at 1000 m water depth (black stars): MD95-2002 (Eynaud et  
1068 al., 2012; Ménot et al., 2006; Toucanne et al., 2015), MD99-2328 (Mojtahid et al., 2017), PP10-  
1069 12 (Pascual et al., 2020). For the detailed description of the general modern and glacial  
1070 circulation in the North Atlantic and in the study area, the reader is referred to the text (Section  
1071 2). LGM: Last Glacial Maximum.

1072 **Figure 2.** Age model of core BOBGEO-CS05. a) Chronostratigraphic framework of core  
1073 BOBGEO-CS05 based on the synchronisation of XRF-Ca/Ti ratios with cores MD95-2002 and  
1074 MD99-2328 (Zaragosi et al., 2006; Mojtahid et al., 2017; Toucanne et al., 2021). b) Sediment  
1075 Accumulation Rate (SAR; full line) and  $^{14}\text{C}$  dates (orange triangles) with associated errors in  
1076 core BOBGEO-CS05. The  $^{14}\text{C}$  dates represented by empty triangles are outliers (cf. section  
1077 3.1. for further details). In red is represented the final age model based on XRF-Ca/Ti  
1078 synchronisation (cf. Fig. 2a). c) Test of the robustness of the age model with the percentages of  
1079 the polar planktonic species *N. pachyderma* in core BOBGEO-CS05 (this study) with core  
1080 MD95-2002 (Grousset et al., 2000) and MD99-2328 (Mojtahid et al., 2017). d) NGRIP  $\delta^{18}\text{O}$   
1081 (GICCS05 chronology; Rasmussen et al., 2006, 2014). f) X-Ray photographs (cf.  
1082 Supplementary material S1 for the whole core) showing the four observed facies. Blue triangles:  
1083  $^{14}\text{C}$  dates of core MD95-2002 (Toucanne et al., 2021); Orange and empty triangles:  $^{14}\text{C}$  dates

1084 of core BOBGEO-CS05; Blue bands: Heinrich Stadials (HSs); Gray bands: Heinrich Events  
1085 (HEs); Greenland Interstadial (GI); Last Glacial Maximum (LGM); Marine Isotope Stage  
1086 (MIS).

1087 **Figure 3.** Benthic foraminiferal data from core BOBGEO-CS05. a) Benthic Foraminiferal  
1088 Accumulation Rates (BFAR; ind.cm<sup>-3</sup>.ka<sup>-1</sup>) for the >150 µm (full line) and the >63 µm fraction  
1089 (dashed line). b) Shannon index (H). c-j) Relative abundances (%) of the eight most  
1090 representative benthic foraminiferal species (>10 %). Full lines and dashed lines represent  
1091 respectively the > 150 µm and >63 µm fractions. Brown lines represent data from the >150 µm  
1092 fraction of core MD99-2328 (Mojtahid et al., 2017). Yellow bands: Greenland Interstadials  
1093 (GI); gray bands: Heinrich Events (HEs); blues bands: Heinrich Stadial (HSs). Marine Isotope  
1094 Stage (MIS). The vertical dashed grey line represents the limit between early HS1 (ca. 18.2 -  
1095 16.7 cal ka BP) and late HS1 (ca. 16.7 – 14.7 cal ka BP). To better highlight the variations of  
1096 the different species groups, the scale of the ordinate axis is not constant.

1097  
1098 **Figure 4.** Benthic foraminiferal response to ice-sheet/AMOC dynamics. a) Relative abundance  
1099 of *N. pachyderma* in core BOBGEO-CS05. b) Relative abundances of glacier-proximal  
1100 indicator species (% *Elphidium excavatum* f. *clavatum* + % *C. crassa*) in core BOBGEO-CS05.  
1101 c) BIT-index at site MD95-2002 as a proxy for continental-derived material input (Ménot et al.,  
1102 2006). d) Relative abundances of high-organic flux indicator species (% *C. carinata* +  
1103 % *Bolivina* spp.) in core BOBGEO-CS05. e) Bermuda Rise <sup>231</sup>Pa/<sup>230</sup>Th compilation as a proxy  
1104 for AMOC export at >2 000 m depth (McManus et al., 2004; Böhm et al., 2015; Henry et al.,  
1105 2016). f) XRF-Zr/Rb (violet line) and  $\overline{SS}$  (pink line) composite records from the northeast  
1106 Atlantic including BOBGEO-CS05 as proxies for the reconstruction of GEBIC flow speed  
1107 changes (Toucanne et al., 2021). g) Relative abundances of high-energy indicator species (% *C.*  
1108 *lobatulus* + % *T. angulosa*) in core BOBGEO-CS05. h) Relative abundances of meso-  
1109 oligotrophic indicator species (% *C. pachyderma*) in core BOBGEO-CS05. i) Relative  
1110 abundances of anoxia indicator species (% *Globobulimina* spp. + % *C. oolina*). To better  
1111 highlight the variations of the different species groups, the scale of the ordinate axis is not  
1112 constant. The main events and climatic phases are reported similarly to Figure 3.

1113  
1114 **Figure 5.** Focus on HS2. a) Relative abundances of the planktonic species *N. pachyderma* in  
1115 core BOBGEO-CS05 (black line; this study) and MD95-2002 (blue line; Grousset et al., 2000).

1116 b) XRF-Zr/Rb (violet line) and  $\overline{SS}$  (pink line) composite records from the northeast Atlantic  
1117 (including BOBGEO-CS05) as proxies for the reconstruction of GEBC flow speed changes  
1118 (Toucanne et al., 2021). c) Relative abundances of high-energy indicator species (% *C.*  
1119 *lobatulus* + % *T. angulosa*) in core BOBGEO-CS05. d) Benthic Foraminiferal Accumulation  
1120 Rates (BFAR; ind.cm<sup>-3</sup>.ka<sup>-1</sup>) for the >150  $\mu$ m in core BOBGEO-CS05. e) Relative abundances  
1121 of meso-oligotrophic indicator species (% *C. pachyderma*) in core BOBGEO-CS05. f) Relative  
1122 abundances of anoxia indicator species (% *Globobulimina* spp. + % *C. oolina*) in core  
1123 BOBGEO-CS05. Dashed vertical line: Heinrich Event 2 (HE2) sensu stricto according to the  
1124 regional Ca/Ti synchronisation (cf. Table S2 in Toucanne et al., 2021); blue bands: the HS2a,b  
1125 cold events (Bard et al., 2000); yellow band: the mid-HS2 re-ventilation event. To better  
1126 highlight the variations of the different species groups, the scale of the ordinate axis is not  
1127 constant.

1128

## 1129 **11. Plates caption**

1130 **Plate 1.** SEM photographs of the dominant benthic species (>5 % in at least one sample): 1)  
1131 *Textularia sagittula* ; 2) *Nonionella turgida* ; 3) *Globobulimina affinis* ; 4) *Chilostomella oolina*  
1132 ; 5) *Bolivina subaenariensis*; 6) *Bolivina albatrossi*; 7) *Cassidulina carinata*; 8) *Cassidulina*  
1133 *crassa*; 9) *Elphidium gerthi* ; 10) *Elphidium excavatum* f. *clavatum* ; 11) *Cibicidoides*  
1134 *pachyderma* ; 12) *Cibicides lobatulus*; 13) *Trifarina angulosa*; 14) *Planorbulina*  
1135 *mediterraneensis*; 15) *Gavelinopsis praegeri* ; 16) *Hoeglundina elegans* ; 17) *Pullenia*  
1136 *quineloba*. Scale bar = 100 $\mu$ m.

1137

1138 **Plate 2.** a) Natural light photographs of *Elphidium excavatum* f. *clavatum* showing pyritised  
1139 and altered shells. b) SEM photographs showing the variability of the morphotypes (in lateral  
1140 view) lumped into *Cibicidoides pachyderma* in this study.

1141

## 1142 **12. Supplementary materials caption**

1143 **S1.** X-Ray imagery of core BOBGEO-CS05

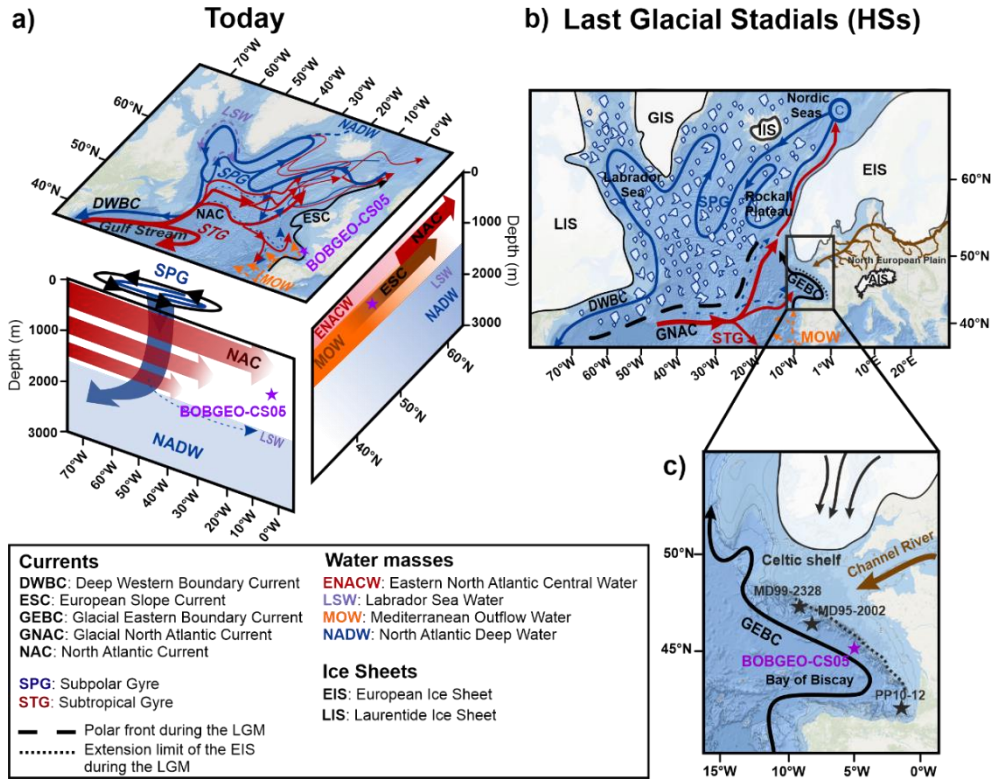
1144 **S2.** Figure representing the relative abundances of taxa present between 5 and 10 % in at least  
1145 one sample

1146 **S3.** Raw foraminiferal counts

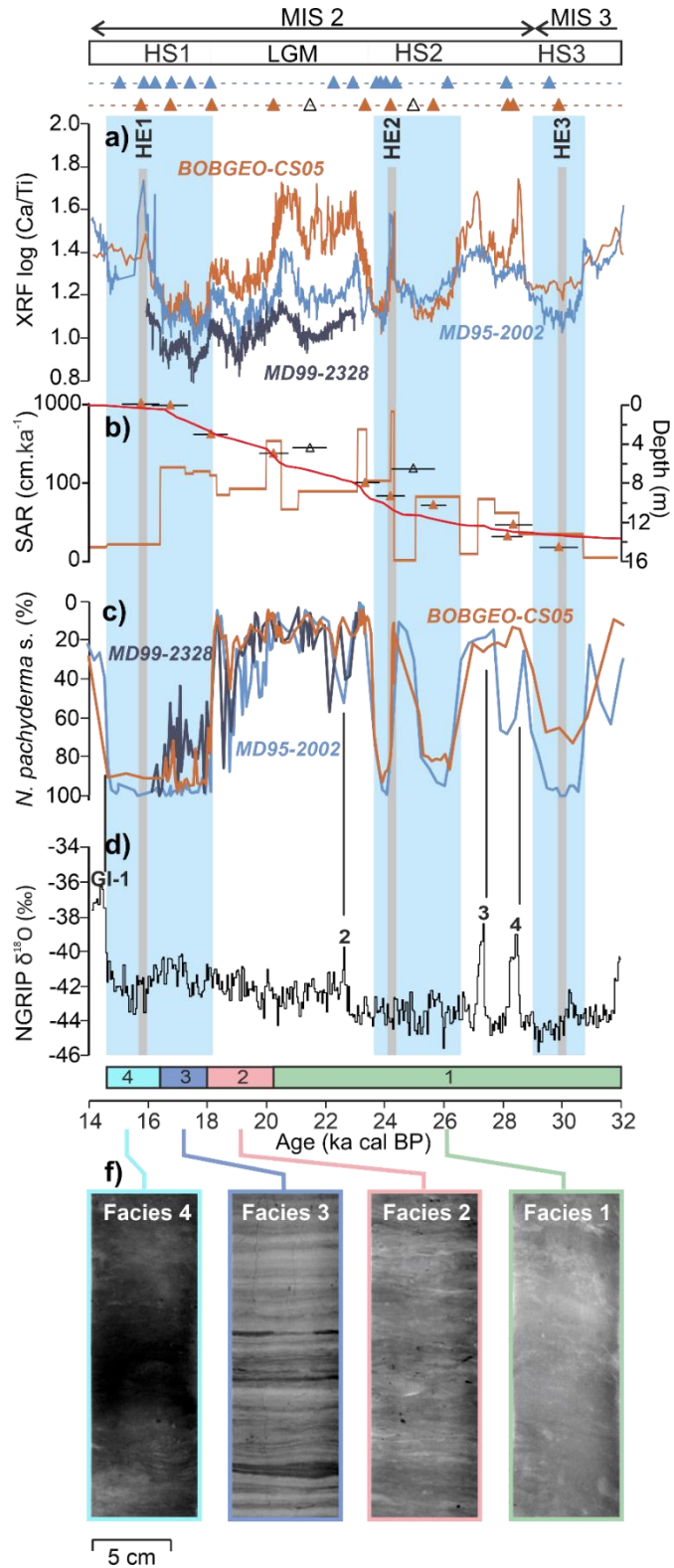
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**Figure 1**

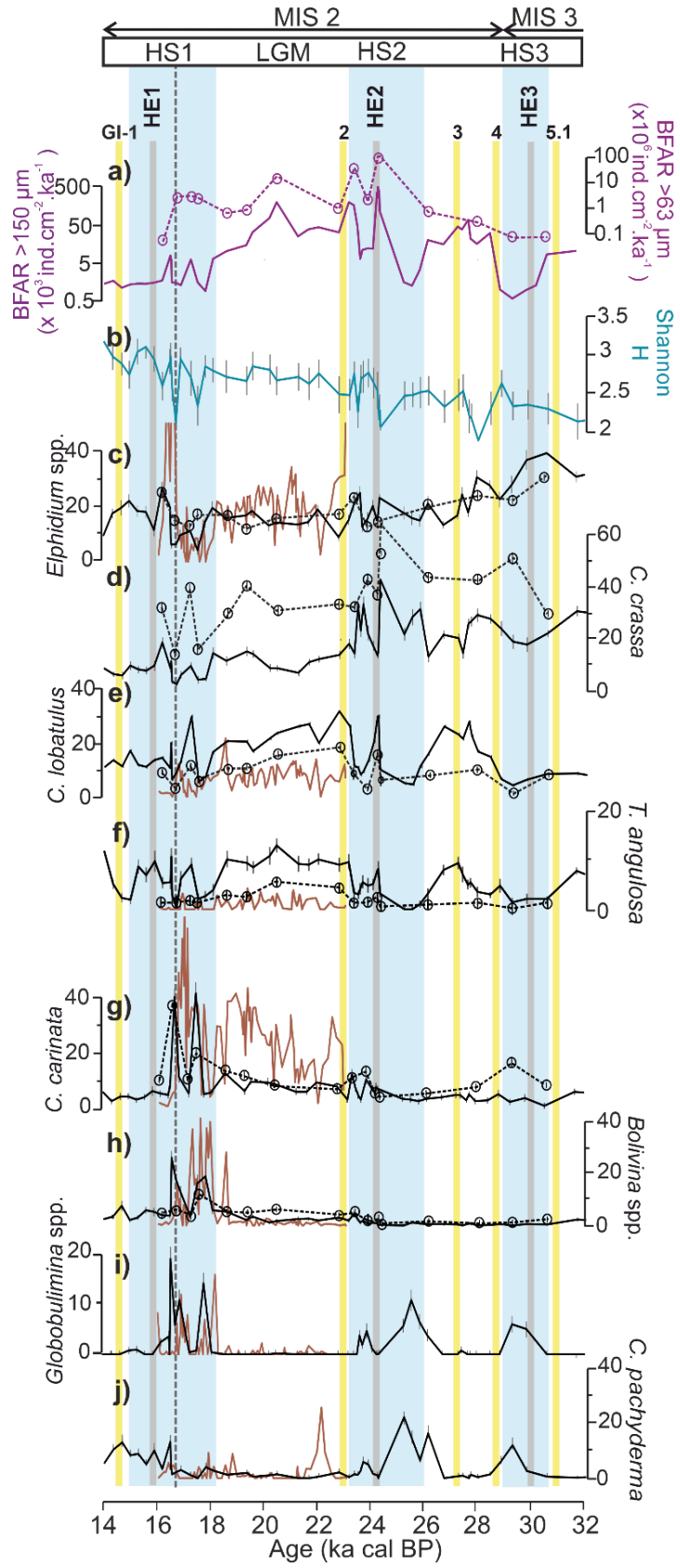


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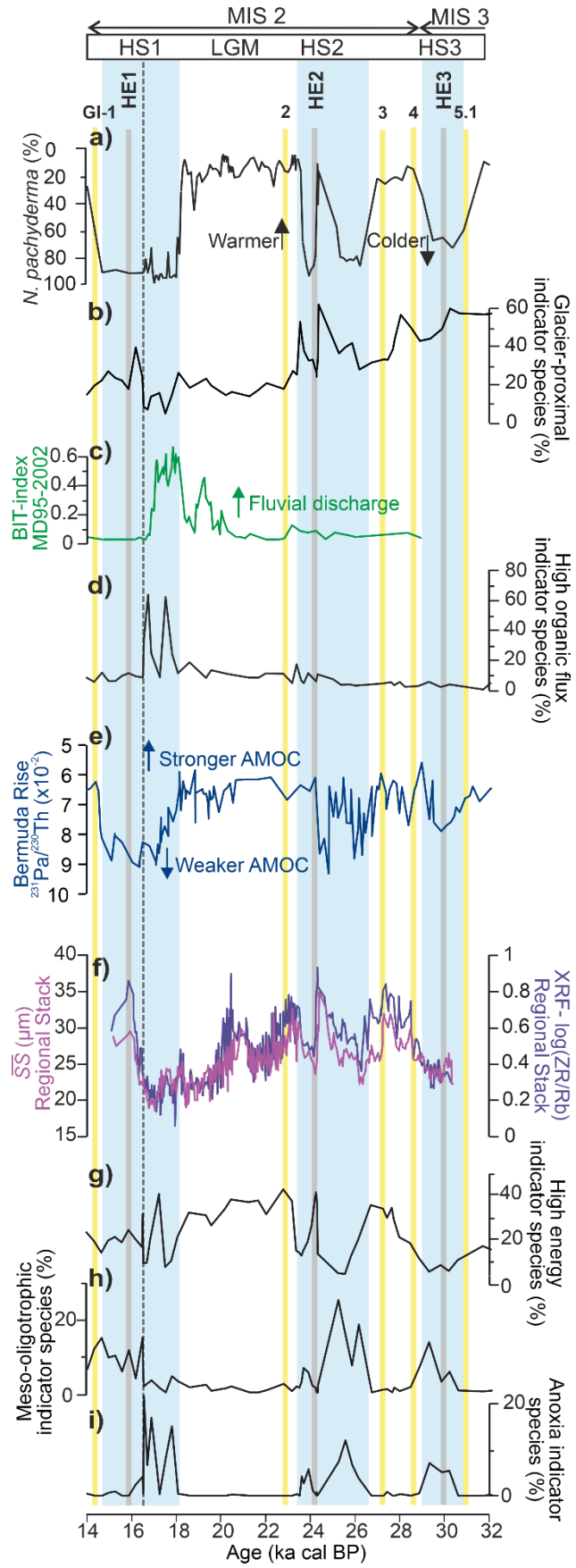


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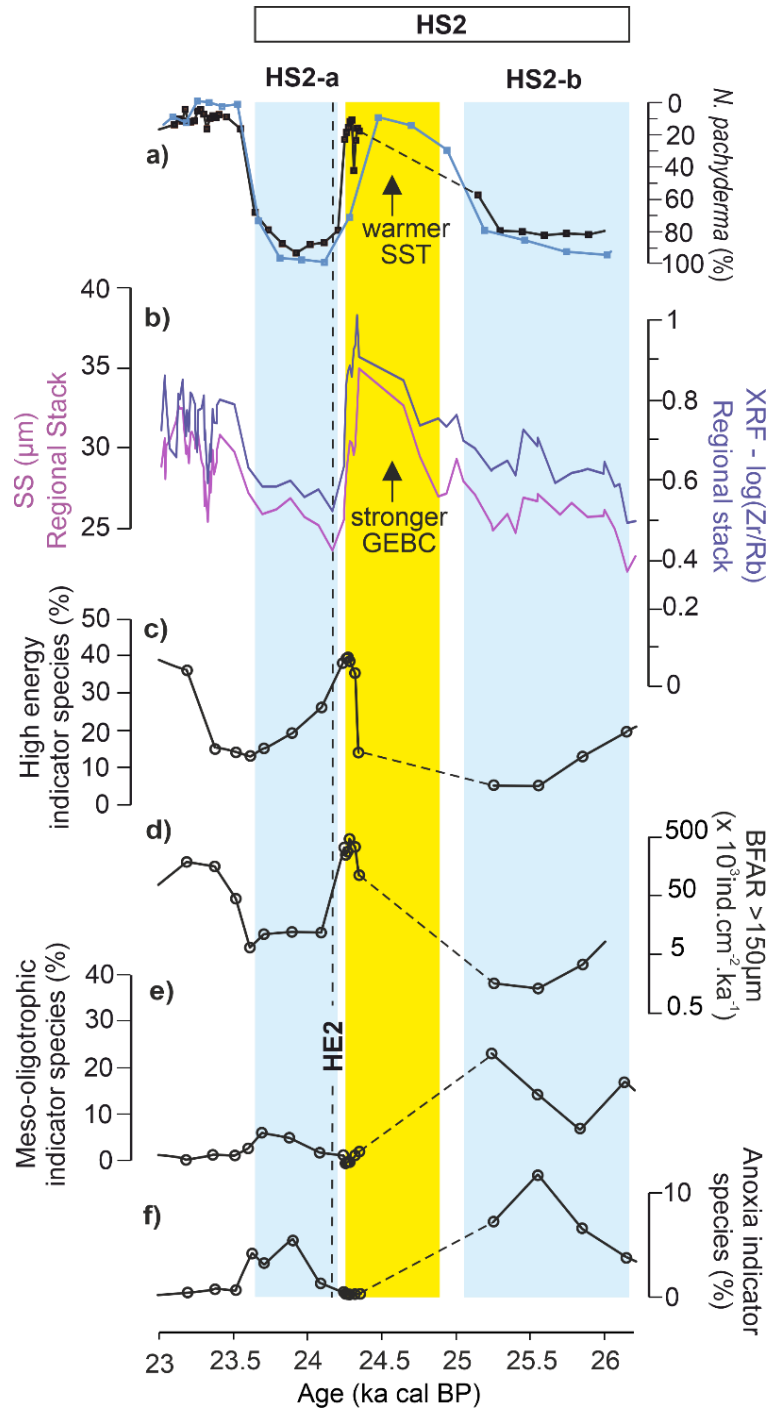
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Figure 5

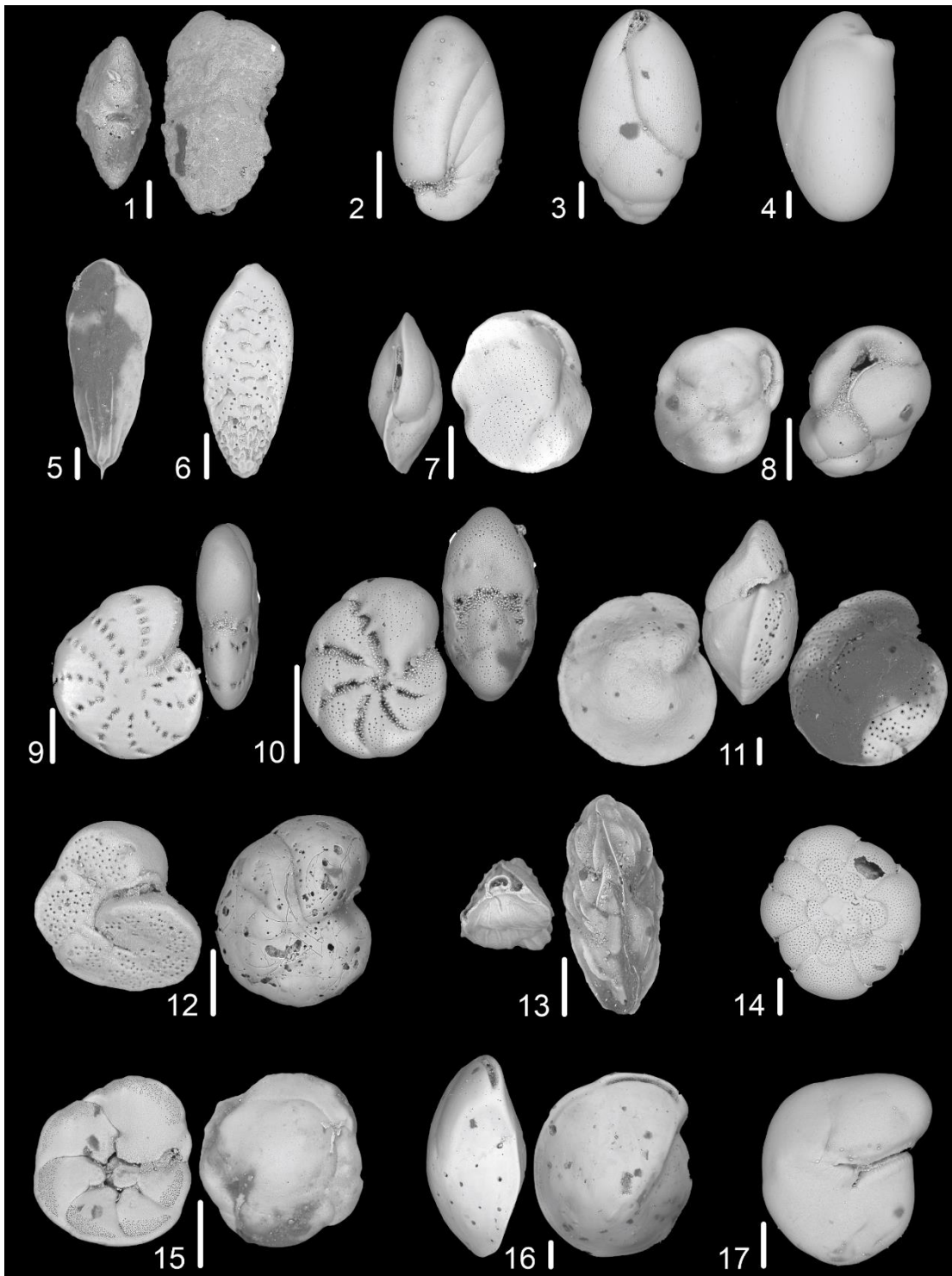


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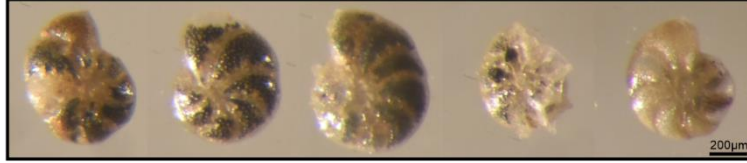


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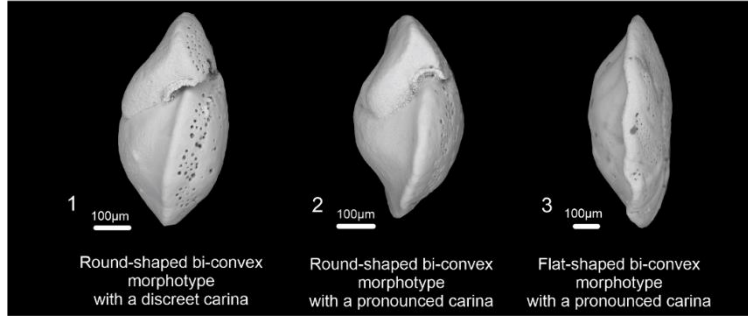
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**Plate 2**

**a) *Elphidium excavatum* cf. *clavatum***



**b) Morphotypes of *C. pachyderma***



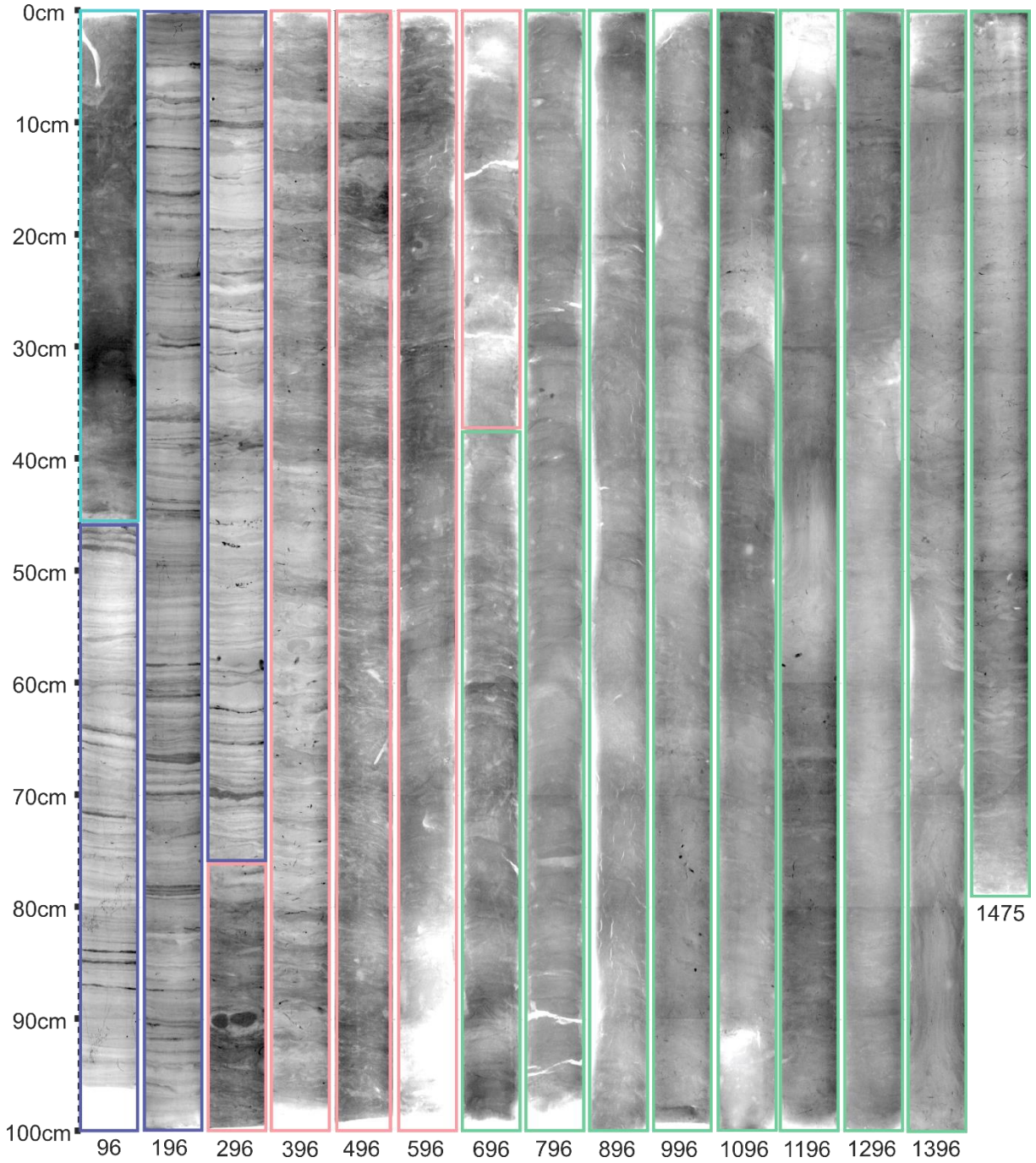
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1180 **Supplementary material**

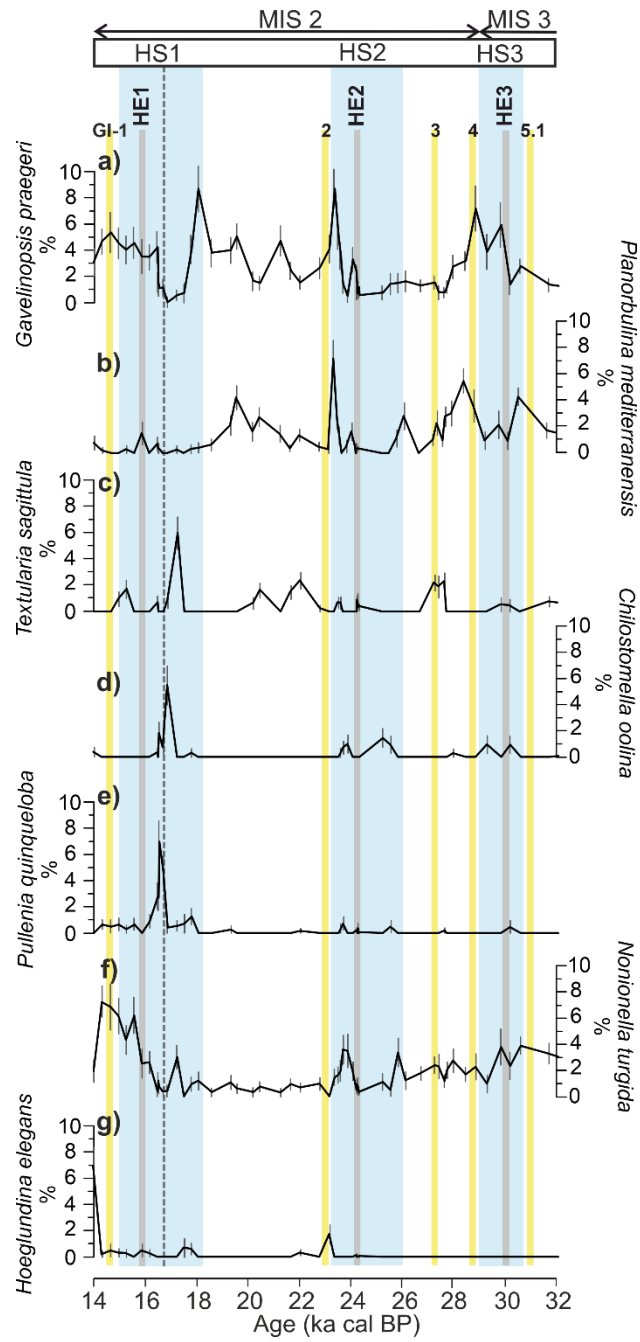
1181 **S1**



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S2



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S3. Raw foraminiferal counts available in <https://doi.org/10.17882/88029>