

Palaeoenvironmental turnover across the Cenomanian-Turonian transition in Oued Bahloul, Tunisia: Foraminifera and geochemical proxies

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Research Highlights:

Integrated analysis of foraminifera, geochemical proxies, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. > Decreasing diversity and increasing of productivity and redox proxies during OAE2. > Habitat and trophic regimes of planktic foraminiferal fluctuations during OAE2. > Enhanced productivity and poor mixing waters favored eutrophication and OMZ expansion.

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3 Bahloul, Tunisia: Foraminifera and geochemical proxies

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16 ABSTRACT

17 The integrated analysis of foraminiferal assemblages, geochemical proxies, and stable isotopes
18 in the Oued Bahloul section (Tunisia) allowed us to reconstruct the environmental turnover
19 across the Cenomanian–Turonian boundary. An increase in palaeoproductivity proxies (P/Ti,
20 U/Al, Sr/Al) and in $\delta^{13}\text{C}$ values, and a decrease in foraminiferal diversity and $\delta^{18}\text{O}$ values mark
21 the beginning of the Oceanic Anoxic Event 2 (OAE2) at the *Rotalipora cushmani* and
22 *Whiteinella archaeocretacea* biozones boundary. Eutrophic conditions at the seafloor and in the
23 water column are evidenced by high proportions of buliminids and the replacement of planktic
24 oligotrophic specialist *Rotalipora* by eutrophic opportunist *Hedbergella*. The enrichment in
25 organic matter and redox sensitive elements, together with the abundance of low-oxygen
26 tolerant benthic foraminifera, indicate dysoxic conditions in the deep-water column and at the

27 seafloor (higher U_{aut} than Mo_{aut}). Among planktic foraminifera, deep- and intermediate-dwellers
28 disappear (*Rotalipora* and *Globigerinelloides*), and surface-dwellers proliferate (*Hedbergella*).
29 The persistency of the poorly oxygenated conditions during the *W. archaeocretacea* Biozone
30 locally produced euxinic conditions where Mo_{EF} and Mo_{aut} reach high values, diversity presents
31 minimum values, and benthic foraminifera temporarily disappear. The maximum percentage of
32 heterohelicids indicates a stratified water column with a well-developed oxygen minimum zone.
33 Improved oxygen conditions returned in the upper part of the *W. archaeocretacea* Biozone and
34 *Helvetoglobotruncana helvetica* Biozone, with a slow recovery of foraminiferal assemblages,
35 decrease in eutrophic genera (*Heterohelix*) and increase in mesotrophic genera (*Whiteinella*). A
36 gradual increase in $\delta^{18}\text{O}$ values suggests decreased temperatures in surface waters. The OAE2
37 has been attributed to global temperature changes and palaeoceanographic reorganization. The
38 poor mixing of surface and deep waters and enhanced primary productivity related to global
39 warming —associated with increasing continental weathering and nutrient runoff— may have
40 favored the eutrophication of the ocean and the expansion of the oxygen minimum zone.

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42 Keywords: trophic conditions, redox conditions, ecostratigraphy, foraminifera, OAE2,

43 Cretaceous

44

45 **1. Introduction**

46

47 The Oceanic Anoxic Event 2 (OAE2), also called Bonarelli Event (e.g., Schlanger and
48 Jenkyns, 1976; Arthur et al., 1990), is represented by the worldwide deposition of organic-rich
49 facies close to the Cenomanian–Turonian (C-T) boundary. Two main hypotheses have been
50 invoked to explain the deposition of organic-rich facies during the Cretaceous: (1) oceanic
51 anoxia prevented the degradation of organic matter settling through the water column down to
52 the seafloor by decreased oxygen supply to the deep ocean due to slower oceanic circulation
53 (e.g. Erbacher et al., 2001; Tsandev and Slomp, 2009), or (2) enhanced surface water

54 productivity exceeded the oxygen availability for decaying organic matter at the seafloor (e.g.
55 Sarmiento et al., 1988; Handoh and Lenton, 2003). The OAE2 has been related to
56 palaeoceanographic and climatic changes including greenhouse warming (e.g. Huber et al.,
57 2002; Norris et al., 2002; Bornemann et al., 2008; Tsandev and Slomp, 2009; Monteiro et al.,
58 2012; Pogge von Strandmann et al., 2013), a sea-level transgression (Hallam, 1992), a
59 perturbation of the carbon cycle (e.g. Kuypers et al., 2002; Erba, 2004; Pogge von Strandmann
60 et al., 2013) and a probable massive magmatic episode (e.g. Kuroda et al., 2007; Turgeon and
61 Creaser, 2008; Erba et al., 2013). The planktic foraminiferal turnover (Coccioni and Luciani,
62 2004; Caron et al., 2006) includes the disappearance of genus *Rotalipora* close to the OAE2
63 (e.g. Hart 1996, 1999; Nederbragt and Fiorentino, 1999; Keller et al., 2001; Coccioni and
64 Luciani, 2004). Planktic foraminifera are sensitive to temperature, chemical and trophic
65 conditions of the sea water (Caron, 1983; Caron and Homewood, 1983; Petrizzo, 2002;
66 Gebhardt et al., 2004, 2010), and the ecostratigraphic analysis of their assemblages may be used
67 to reconstruct palaeoceanographic and palaeoecological changes across the OAE2. In addition,
68 the ecostratigraphic analysis of benthic foraminiferal assemblages is a useful tool to interpret
69 fluctuations in oxygen and nutrient availability (e.g. Bernhard, 1986; Nagy, 1992; Jorissen et al.,
70 1995; Van der Zwaan et al., 1999; Klein and Mutterlose, 2001; Reolid et al., 2008, 2012a, b).
71 Some authors have interpreted an extinction event affecting benthic foraminiferal assemblages
72 at the C-T boundary (e.g. Peryt and Lamolda, 1996; Kaiho, 1994, 1999; Peryt, 2004), yet there
73 is no unanimity (Holbourn and Kuhnt, 2002).

74 The analysis of redox-sensitive trace elements (such as Co, Cr, Cu, Mo, and Ni, among
75 others) has proven to be a powerful tool for interpreting redox conditions in oceans during
76 anoxic events. These elements are less soluble under reducing conditions, resulting in
77 synsedimentary enrichments under oxygen-depleted conditions (Wignall and Myers, 1988;
78 Calvert and Pedersen, 1993; Jones and Manning, 1994; Powell et al., 2003; Gallego-Torres et
79 al., 2007; Reolid et al., 2012a, b). Geochemical proxies have also been successfully applied to
80 interpret palaeoproductivity, the most extensively used being Ba/Al, Sr/Al, Ca/Al and P/Ti

81 ratios (e.g., Turgeon and Brumsack, 2006; Gallego-Torres et al., 2007; Robertson and Filippelli,
82 2008; Sun et al., 2008; Reolid and Martínez-Ruiz, 2012; Reolid et al., 2012a, b). The total
83 organic carbon (TOC) has also been employed as an indirect palaeoproductivity proxy (e.g.,
84 Gupta and Kawahata, 2006; Su et al., 2008), although enhanced TOC contents may result from
85 low bottom-water ventilation and oxygen depletion.

86 The aim of this work is to integrate planktic and benthic foraminiferal assemblages and
87 geochemical proxies to determine the palaeoenvironmental turnover across the OAE2 in the
88 Oued Bahloul section, Tunisia. The OAE2 and the C-T transition are recorded in the Bahloul
89 Formation, where numerous studies on microfacies, planktic foraminifera, organic matter and
90 stable isotopes have been carried out (e.g. Caron et al., 1999, 2006; Accarie et al., 2000;
91 Amédro et al., 2005; Zagrarni et al., 2008; Negra et al., 2011; Soua et al., 2011; for recent
92 works). Here we present the first integrated analysis of foraminiferal assemblages and
93 geochemical proxies across the C–T transition at Oued Bahloul.

94

95 **2. Geological setting and the Oued Bahloul section**

96

97 The Cretaceous palaeogeography of Tunisia consists of three main domains: the
98 Saharan Platform in the South, the Central Tunisian Platform, and the Tunisian Basin in the
99 North (Buroillet and Busson, 1983). The Central Tunisian Platform was mainly occupied by
100 outer shelf facies rich in planktic foraminifera during the C-T interval. The Bahloul Formation
101 is a widespread wedge that ranges from 23 m thick in the North to 2 m thick in the South, upon
102 the Cenomanian Central Tunisian Platform (Saïdi et al., 1997; Scott, 2003; Robaszynski et al.,
103 2010; Zaghib-Turki and Soua, 2013; Fig. 1).

104 The Oued Bahloul section was proposed by Buroillet (1956) as the type locality of the
105 Bahloul Formation. This outcrop presents the best sedimentary record of the OAE2 in the
106 southern margin of the Tethys (Robaszynski et al., 1993; Caron et al., 2006). The OAE2 is
107 marked by a strong positive shift in $\delta^{13}\text{C}$ in bulk carbonate and an increase in organic matter

108 content in the Bahloul Formation (Accarie et al., 1996; Nederbragt and Fiorentino, 1999). The
109 studied interval is 47 m thick and includes the uppermost 5 m of the Fahdène Formation, the
110 Bahloul Formation (29 m thick) and the lowermost 13 m of the Kef Formation (Fig. 1). The
111 Fahdène Formation consists of an alternation of grey-greenish marls and light-coloured
112 limestones. The Bahloul Formation is divided into two members: lower Pre-Bahloul Member
113 and upper Bahloul *s. str.* Member (Fig. 1). In turn, the Pre-Bahloul Member is 3.4 m thick and
114 its lower boundary with the Fahdène Formation is sharp and erosive. The first level (0.5 m
115 thick) is a sandy micro-conglomeratic limestone that contains phosphatic black pebbles and
116 quartz grains with well-developed graded bedding. The overlying bed is a bioclastic-rich
117 calcarenite. The upper part of the Pre-Bahloul Member consists of marls with a decreasing
118 content of quartz and bioclasts.

119 The Bahloul *s. str.* Member, in this work Bahloul Member, is composed of an
120 alternation of 2 to 5 cm thick, bedded black limestones with thin parallel lamination, and grey
121 marls. Different calcareous packages (50 cm thick) may be recognized where thin black
122 limestones dominate versus intervals with dominance of grey marls. The lamination of the black
123 limestones consists of clear laminae with abundant planktic foraminifera, and black laminae
124 with abundant pellets embedded in a dark matrix with common radiolaria, benthic foraminifera
125 (buliminids) and planktic foraminifera. The vertical transition from laminated black limestones
126 to grey marls is gradual, but the transition from grey marls to black laminated limestones is
127 abrupt. The top of the Bahloul Formation corresponds to densely bioturbated grey marls, and is
128 locally overlain by a thin limestone layer rich in ammonoid moulds with phosphate and
129 glauconite grains (Caron et al., 2006; Zagrarni et al., 2008). The overlying Annaba Member of
130 the Kef Formation consists of grey marls with interlayered marly-limestones.

131 Robaszynski et al. (1990, 1993) located a sequence boundary at the top of Fahdène
132 Formation, at the base of a channel-fill limestone bed (Ce SB5 *s.* Hardenbol et al., 1998). These
133 authors situated the transgressive contact (Ce TS5) at the top of a thicker limestone bed, and the
134 maximum flooding surface between the black laminated limestones of the Bahloul Formation

135 and the marls of the Kef Formation.

136

137 3. Material and methods

138

139 Foraminiferal and geochemical analyses were conducted across the upper Cenomanian-
140 lower Turonian at Oued Bahloul section. A total of 25 sampling levels were selected from this
141 47 m thick limestone and marly-limestone succession (Fig. 1). Micropalaeontological samples
142 were disaggregated in water with diluted H₂O₂, washed through a 63 µm sieve, and dried at
143 50°C. More endurated limestones were immersed in acetic acid (80%) during 1 h to 4 h,
144 depending on the carbonate content, then washed through a 63 µm sieve, and dried at 50°C.

145 Quantitative studies (Tables 1 and 2) were based on representative splits (using a
146 modified Otto microsplitter) of over 300 specimens of benthic foraminifera larger than 63 µm
147 and 300 specimens of planktic foraminifera larger than 100 µm per sample. The remaining
148 residue was scanned for rare species. Planktic foraminiferal taxa (Fig. 2) were also allocated to
149 biserial (*Heterohelix*), triserial (*Guembelitria*), planispiral (*Globigerinelloides*), and trochospiral
150 morphogroups (Table 3). The latter include strongly keeled (*Dicarinella*, *Rotalipora*,
151 *Thalmaninella*), weakly keeled (*Anaticinella*, *Helvetoglobotruncana*, *Praeglobotruncana*) and
152 unkeeled (*Hedbergella*, *Schackoina*, *Whiteinella*) forms (Table 3). Changes in depth
153 stratification of the water column and trophic structure, temperature and salinity are the main
154 factors controlling the composition of planktic foraminiferal assemblages. The stratification and
155 richness of nutrients in the water column is narrowly related to productivity and the behavior of
156 the planktic foraminifera. In this sense, opportunists (r-strategists) flourish in eutrophic waters
157 whereas specialists (K-strategists) proliferate in oligotrophic waters (Valentine, 1973). Depth
158 stratification favored differentiation of biotic and abiotic environmental features providing
159 distinct ecological niches and minimizing the competition among species (Hemleben et al.,
160 1989). Based on morphotype analyses (e.g. Corliss, 1985; Jones and Charnock, 1985; Corliss
161 and Chen, 1988), benthic foraminiferal taxa (Fig. 3) were allocated to infaunal, epifaunal, and

162 epifaunal/infaunal morphogroups. In general, benthic foraminifera with trochospiral,
163 planoconvex or biconvex tests are inferred to have had an epifaunal mode of life, living at the
164 sediment surface or in its upper few centimetres, while infaunal foraminifera have cylindrical or
165 flattened tapered, spherical, globular unilocular or elongated multilocular tests, and live in the
166 deeper layers of the sediment (Corliss, 1991; Reolid et al., 2008). Simple diversity (number of
167 species) and the Fisher- α diversity index (e.g. Murray, 1991) were calculated separately for
168 benthic and planktic foraminiferal assemblages.

169 Whole-rock analyses of major elements were carried out in 25 samples using X-ray
170 fluorescence (XRF) in a Philips PW 1040/10 spectrometer. The content of trace elements was
171 determined using an inductively coupled plasma-mass spectrometer (ICP-MS Perkin Elmer
172 Sciex-Elan 5000) at the Centro de Instrumentación Científica (CIC, Universidad de Granada).
173 Instrumental error was $\pm 2\%$ and $\pm 5\%$ for respective elemental concentrations of 50 ppm and 5
174 ppm.

175 The contents in C, N and S, as well as the total organic carbon (TOC) content, were
176 analysed analyzed with an Elemental Analyzer LECO CNS-TruSpec and an Inorganic Carbon
177 Analyzer CM5240 UIC in the laboratories of the Centro Andaluz de Medio Ambiente
178 (CEAMA, Granada). Total organic carbon was obtained as the difference between total carbon
179 and total inorganic carbon; it was measured in mg and calculated as percentage of sample
180 weight.

181 For $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analyses, and after roasting, the samples were reacted at 73°C in an
182 automated carbonate reaction system (Kiel-IV) coupled directly to the inlet of a Finnigan MAT
183 253 gas ratio mass spectrometer at the Laboratory of Stable Isotopes of the University of
184 Michigan. Isotopic ratios were corrected for ^{17}O contribution and are reported in per mil
185 notation relative to the VPDB standard. Values were calibrated using NBS 19 as the primary
186 standard, and analytical precision was monitored by daily analyses of NBS powdered carbonate
187 standards. The measured precision was maintained above 0.02‰ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$.

188 In order to compare trace-element proportions in samples with varying carbonate and
 189 clay contents, trace-element concentrations were normalized to aluminium content (Calvert and
 190 Pedersen, 1993). This technique avoids any lithological effects on trace or major element
 191 concentrations, assuming that Al content in sediments is heightened by alumino-silicates (e.g.,
 192 Calvert, 1990). The study of palaeoproductivity was carried out applying a set of proxies (Sr/Al,
 193 U/Al and P/Ti). To analyze palaeo-oxygenation, diverse redox proxies evaluating the relative
 194 increase of redox sensitive elements (Co/Al, Cr/Al, Cu/Al, Mo/Al, Ni/Al, and Th/Al) were
 195 applied throughout the section. Distinct enrichment factors (Mo and U), applied according to
 196 Zhou et al. (2012) and Tribovillard et al. (2012), included $Mo_{EF} = [Mo/Al]_{sample}/[Mo/Al]_{PAAS}$ and
 197 $U_{EF} = [U/Al]_{sample}/[U/Al]_{PAAS}$. The authigenic values of U and Mo were also calculated according
 198 to Zhou et al. (2012), as $Mo_{aut} = [Mo]_{sample} - [Mo]_{PAAS}/[Al]_{PAAS} * [Al]_{simple}$, $U_{aut} = [U]_{sample} -$
 199 $[U]_{PAAS}/[Al]_{PAAS} * [Al]_{simple}$.

200

201 4. Results

202

203 4.1. Planktic foraminifera and biostratigraphy

204

205 Planktic foraminifera dominate the assemblages in the Fahdene Formation (Fig. 4),
 206 where the P/B ratio is high (up to 93%). P/B values gradually decrease from the uppermost part
 207 of this formation towards the Bahloul Formation, with values commonly <30%, then gradually
 208 increase up to 98% towards the middle part of the Bahloul Formation (metre 17), remaining low
 209 (<30%) throughout the rest of the section and slightly increasing (up to 57%) in the lower part
 210 of the Kef Formation (Fig. 4).

211 A total of 13 genera and 31 species of planktic foraminifera were identified at Oued
 212 Bahloul (Fig. 2, Appendix 1). The species distribution allowed us to identify the *Rotalipora*
 213 *cushmani*, *Whiteinella archaeocretacea* and *Helvetoglobotruncana helvetica* biozones (Fig. 5).
 214 The upper Cenomanian *R. cushmani* Biozone corresponds to the lower part of the studied

215 interval, and is mostly represented by the Fahdène Formation (Fig. 5). This interval contains
 216 abundant keeled trochospiral forms, such as *Rotalipora cushmani*, *Thalmaninella*
 217 *greenhornensis*, *Thalmaninella brotzeni*, *Rotalipora monsalvensis* and *Anaticinella*
 218 *multiloculata* (with a poorly developed keel). The *W. archaeocretacea* Biozone is 28 m thick,
 219 and it includes the uppermost 50 cm of the Fahdène Formation and the Bahloul Formation,
 220 containing the Cenomanian-Turonian boundary. This biozone is characterised by common
 221 biserial forms such as *Heterohelix reussi* and unkeeled trochospiral forms such as *Whiteinella*
 222 *archaeocretacea*, *Whiteinella aprica*, *Hedbergella planispira* and *Hedbergella delrioensis*. The
 223 *H. helvetica* Biozone (lower Turonian) is represented in the uppermost 1.2 m of the Bahloul
 224 Formation and in the Kef Formation. This biozone is characterised by the species
 225 *Helvetoglobotruncana helvetica*, *Dicarinella imbricata*, *Shackoina bicornis* and *Whiteinella*
 226 *paradubia*.

227 The correlation of the planktic foraminiferal and ammonite (Caron et al., 1999, 2006;
 228 Amédéo et al., 2005) biozones is shown in Fig. 1C. The record of *Pseudocalycoceras*
 229 *angolaense* in the Pre-Bahloul Member and lowermost 3 m of the Bahloul Member indicates the
 230 *Metoicoceras geslinianum* Biozone (Cenomanian). The record of *Pseudaspidoceras*
 231 *pseudonodosoides* in the Bahloul Formation (12 to 29 m) indicates a late Cenomanian age (*P.*
 232 *pseudonodosoides* Biozone), and the record of *Watinoceras* and *Fagesia* in the topmost Bahloul
 233 Formation indicates early Turonian age (*Watinoceras* Biozone) (Fig. 1C). The base of the Kef
 234 Formation is lower Turonian in age: the *Pseudaspidoceras flexuosum* Biozone has been inferred
 235 by correlation with other sections (Accarie et al., 2000), and the *Thomasites rollandi* Biozone is
 236 indicated by the record of *Thomasites* sp. (Caron et al., 2006).

237 Diversity of planktic foraminiferal assemblages (Fig. 4) shows a decreasing trend from
 238 the Fahdène Formation towards the lower half of the Bahloul Formation (uppermost part of the
 239 *R. cushmani* Biozone and lower part of the *W. archaeocretacea* Biozone). Some taxa went
 240 extinct (e.g., *Globigerinelloides ultramicrus*, *Thalmaninella brotzeni*, *T. greenhornensis*,
 241 *Rotalipora cushmani*, *R. monsalvensis*), and others (e.g. *Anaticinella multicostata*, *Dicarinella*

242 spp., *Globigerinelloides bentonensis*, *Schackoina* spp.) temporarily disappeared across this
 243 interval and reappeared within the upper half of the *W. archaeocretacea* Biozone. Assemblages
 244 diversified towards the top of the section, where diversity values are similar to those in the
 245 Fahdène Formation (Fig. 4).

246 Assemblages from the lowermost part of the section include common to abundant
 247 planispiral (*Globigerinelloides bentonensis*), trochospiral (*Hedbergella delrioensis*, *H.*
 248 *planispira*, *H. simplex*) and biserial forms (*Heterohelix reussi*) (Fig. 5). Right at the base of the
 249 *Whiteinella archaeocretacea* Biozone, the abundance of *H. delrioensis* increases up to 67% of
 250 the assemblage (metre 7), and minor quantitative peaks in *Thalmaninella brotzeni* and
 251 *Whiteinella aprica* are observed (Fig. 5). Assemblages from the lower half of the Bahloul
 252 Formation are strongly dominated by *Heterohelix reussi* (up to 78% of the assemblage), whose
 253 relative abundance decreases towards the upper half of this formation, where trochospiral taxa
 254 (e.g., *W. archaeocretacea*, *W. aprica*, *W. baltica*) become common to abundant. Assemblages
 255 from the Kef Formation are similar to those from the upper Bahloul Formation, but they contain
 256 higher percentages of triserial (*Guembelitria cenomama*), trochospiral (*Hedbergella delrioensis*)
 257 and biserial morphogroups (e.g., *Globoheterohelix paraglobulosa*). A 5 m thick interval in the
 258 Kef Formation (metres 37–42) is strongly dominated by *W. aprica*, which is rapidly replaced by
 259 *Heterohelix reussi* in the uppermost part of the studied section (Fig. 5).

260

261 4.2. Benthic foraminifera

262

263 Among benthic foraminifera, calcareous taxa dominate over agglutinated ones. A total
 264 of 45 genera and 70 species were recorded throughout the Oued Bahloul section (Appendix 2).
 265 *Neobulimina*, *Gavelinella*, *Praebulimina*, *Tappanina*, and *Lenticulina* are the most common
 266 genera. *Trochammina*, *Gyroidinoides* and *Laevidentalina* are locally abundant (Fig. 6).

267 Changes in diversity of benthic foraminiferal assemblages are similar to those of
 268 planktic assemblages, showing a decreasing trend from the Fahdène Formation to the middle

269 part of the Bahloul Formation, with minimum values in metres 10–17, and gradual recovery
270 above this interval towards the top of the section (Fig. 4). Sample 17 (Bahloul Formation) is
271 barren of benthic foraminifera (Fig. 6), and very few specimens were found in samples OB-28,
272 OB-30, OB-37, OB-38 and OB-40; thus the benthic foraminiferal counts are not considered as
273 representative in these samples. While planktic foraminiferal assemblages from the uppermost
274 part of the studied section (upper part of *W. archaeocretacea* Biozone and *H. helvetica* Biozone)
275 reach diversity values similar to those in the Fahdène Formation, the diversity of benthic
276 foraminifera does not fully recover and is significantly lower at the top of the section.

277 Benthic foraminiferal assemblages from the lowermost part of the section are diverse
278 and dominated by epifaunal trochospiral forms (e.g., *Gavelinella flandrini*, *Gyroidinoides*
279 *globosus* and *Gyroidinoides lenticulus*). Spherical (*Trochammina globolaevigata*) and
280 cylindrical tapered morphogroups (*Praebulimina reussi* and *Laevidentalina* spp.) are also
281 common. The relative abundance of *Gavelinella* spp. significantly increases to the top of Pre-
282 Bahloul Member (Fig. 6), and assemblages are clearly dominated by *Gavelinella* spp.,
283 *Lenticulina gaultina*, and abundant *Globorotalites* spp. (Fig. 6).

284 The boundary between the Pre-Bahloul Member and the Bahloul Member (lower part of
285 the *W. archaeocretacea* Biozone) is characterised by an abrupt decrease in the relative
286 abundance of *Gavelinella* and *Lenticulina*, the disappearance of such taxa as *Trochammina* sp.,
287 *Globorotalites* spp. and *Lingulogavelinella frankei*, and the temporary disappearance of
288 *Laevidentalina* spp., *Laevidentalina gaultina* and *Lenticulina subgaultina* (Lazarus taxa). This
289 boundary marks a clear change in benthic assemblages, from epifauna-dominated assemblages
290 in the lower part of the section to infauna-dominated assemblages in the rest of the studied
291 section. Low-diversity assemblages from the lower half of the Bahloul Member are clearly
292 dominated by *Neobulimina albertensis* (up to 81% of the assemblages), with a minor
293 contribution of *Tappanina laciniosa* and *Coryphostoma* spp. The upper part of this member
294 contains more diversified assemblages, with abundant *Neobulimina albertensis* and *T. laciniosa*,

295 common *Laevidentalina* spp., and new taxa such as *Gavelinella rochardensis* and *Bolivina* sp.
296 (Fig. 6).

297 The lowermost 2.5 m of the *H. helvetica* Biozone are characterised by the disappearance
298 of *Astacolus* spp. and *Dorothia* spp. The Annaba Formation (*H. helvetica* Biozone) contains
299 highly variable percentages of *Neobulimina albertensis* and quantitative peaks of infaunal
300 (*Lenticulina subgaultina*, *Bolivina* spp.) and some epifaunal taxa (*Gavelinella* spp.,
301 *Gyroidinoides lenticulus*).

302

303 4.3. Geochemistry

304

305 4.3.1. Redox proxies

306 The stratigraphic distribution throughout the succession of the analysed ratios shows
307 three intervals with main changes: a) the base of the *W. archaeocretacea* Biozone, b) the middle
308 part of the *W. archaeocretacea* Biozone, and c) the *W. archaeocretacea*/*H. helvetica* biozone
309 boundary.

310 The lowermost part of the section (*R. cushmani* Biozone) is characterised by decreasing
311 Co/Al, Ni/Al and Th/Al ratios, followed by a sudden increase in all the studied proxies in the
312 Pre-Bahloul Member (base of *W. archaeocretacea* Biozone, Fig. 7). The Mo_{EF} , Mo_{aut} , U_{EF} and
313 U_{aut} ratios also increase in the Pre-Bahloul Member, with a dramatic increase in U proxies in
314 the topmost Fahdene Formation (*R. cushmani*/*W. archaeocretacea* biozone boundary),
315 immediately preceding the peaks of all other proxies. The U_{EF} values reach 8.08, which is very
316 relevant (Fig. 7). According to Tribovillard et al. (2012), values of elemental enrichment factor
317 > 3 are considerable and > 10 is considered as a strong enrichment.

318 An increase in the Cr/Al ratio and in Mo_{EF} and Mo_{aut} values, and a minor increase in
319 Cu/Al, Ni/Al, U_{EF} and U_{aut} are recorded in sample OB-17 (metre 17, middle part of the *W.*
320 *archaeocretacea* Biozone), which is barren of benthic foraminifera (Fig. 7).

321 The Th/Al ratio remains constant throughout the rest of the section, while the other
322 proxies increase towards the top of the Bahloul Formation (*W. archaeocretacea/H. helvetica*
323 biozone boundary), where new peaks in Co/Al, Cr/Al, Cu/Al, Ni/Al and Mo_{EF} and minor
324 increases in Th/Al, Mo_{aut.}, U_{EF} and U_{aut} are observed (Fig. 7). Towards the top of the section
325 (Annaba Member), the selected ratios return to the original values recorded in the lowermost
326 part of the section (Fahdene Formation).

327

328 4.3.2. Palaeoproductivity proxies and TOC

329 In contrast to redox proxies, the selected palaeoproductivity proxies and TOC only
330 show prominent changes in the Pre-Bahloul Formation (base of the *W. archaeocretacea*
331 Biozone; Fig. 8). The U/Al and P/Ti ratios increase coinciding with the first peak in redox
332 proxies, whereas TOC reaches the maximum values (2.8 wt.%) 1 m above the U/Al and P/Ti
333 peaks. TOC values fluctuate throughout the rest of the section but never exceed the high values
334 recorded at the top of the Pre-Bahloul Formation. The Sr/Al ratio and TOC values (2.1 wt.%)
335 are higher in the *W. archaeocretacea/H. helvetica* biozone boundary than in the other biozones.
336 Apart from decreased TOC and Sr/Al values in the lower half of the Annaba Member,
337 palaeoproductivity proxies remain relatively stable up to the top of the section.

338

339 4.3.3. $\delta^{13}C$ and $\delta^{18}O$

340 Bulk rock $\delta^{13}C$ values obtained in this study have been compared to previous results by
341 Caron et al. (2006) and Zagrarni et al. (2008), and show similar trends (Fig. 9). A 2‰ increase
342 (from 1.83 – 3.76‰) in $\delta^{13}C$ is recorded at the transition from the Pre-Bahloul Member to the
343 Bahloul Member (lower part of the *W. archaeocretacea* Biozone). A marked increase in $\delta^{13}C$
344 values is a typical feature of the OAE2 (e.g. Scholle and Arthur, 1980; Schlanger et al., 1987).
345 $\delta^{13}C$ values remain high throughout most of the *W. archaeocretacea* Biozone (mean value
346 3.09‰), and decrease in its uppermost 5 m. The $\delta^{13}C$ mean value in the *H. helvetica* Biozone
347 (base of the Annaba Member) is 2.30‰.

348 The $\delta^{18}\text{O}$ values gradually decrease from the Fahdène Formation to the Bahloul Member
349 (from -4.54 to -5.31‰), and remain low (mean value -5.39‰) throughout the rest of the Bahloul
350 Formation, progressively increasing in the Annaba Member (mean value -4.55‰).

351

352 **5. Palaeoenvironmental interpretation**

353

354 *5.1. Top of the Fahdène Formation and Pre-Bahloul Member*

355

356 Analysis of redox conditions in the water column and at the seafloor is based on redox-
357 sensitive trace elements (Co, Cr, Cu, Mo, Ni, U, and Th), which tend to co-precipitate with
358 sulfides (mainly pyrite) and are usually not remobilised during diagenesis in the absence of
359 post-depositional replacement of oxidizing agents (Tribovillard et al., 2006). The enrichment in
360 redox sensitive elements (Co/Al, Cr/Al, Cu/Al, U/Al, Th/Al, Mo_{EF} , Mo_{aut} , U_{EF} and U_{aut}) points
361 to depleted oxygen conditions during deposition of the Pre-Bahloul Member (base of the *W.*
362 *archaeocretacea* Biozone). U-based proxies ($\text{U}_{\text{EF}}=8.08$; Fig. 7) and increased TOC values point
363 to depleted oxygen conditions in the lower part of the water column.

364 The P/Ti ratio is a commonly used proxy for productivity (Latimer and Filippelli, 2001;
365 Robertson and Filippelli, 2008; Reolid et al., 2012a, b). Increased values are related to higher
366 phosphorous supply to the seafloor derived from biological processes, not from terrigenous
367 components (Latimer and Filippelli, 2001; Flores et al., 2005; Sen et al., 2008). At Oued
368 Bahloul, the increase in P/Ti values at the base of the *W. archaeocretacea* Biozone (Pre-
369 Bahloul Member) indicates an abrupt increase in productivity (Fig. 8). Mort et al. (2007)
370 suggested that the increase in P-accumulation rates coinciding with the OAE2 may be related to
371 an overall increase in surface-water productivity. At Oued Bahloul, high P/Ti values coincide
372 with high U/Al and U_{EF} values (Figs. 7 and 8), and point to a productivity increase in the Pre-
373 Bahloul Member. The Sr/Al ratio, which has also been used as a palaeoproductivity proxy (Sun
374 et al., 2008; Reolid et al., 2012), shows a minor increase in the Pre-Bahloul Member (Fig. 8).

375 This interpretation is compatible with the decreased foraminiferal diversity (both in
376 planktic and benthic assemblages) and with the assemblage turnover at the base of the *W.*
377 *archaeocretacea* Biozone (Figs. 4–6). Among benthic assemblages, the percentage of
378 *Gavelinella* spp. and *Lenticulina* spp. significantly increases in the Pre-Bahloul Member, and
379 *Globorotalites* shows a minor peak (Fig. 6). *Lenticulina* is regarded as an opportunistic genus
380 that recolonizes the seafloor after redox fluctuations (Tyszka, 1994; Reolid et al., 2008; Reolid
381 et al., 2012a). *Gavelinella* spp. is a low-oxygen tolerant genus (Sliter, 1975; Gertsch et al.,
382 2010), and it occurs in shales with high organic matter levels (Holbourn et al., 2001).
383 *Globorotalites* has been observed to peak under stressful conditions at the seafloor after the
384 Cretaceous/Paleogene impact event, mostly related to changes in the type (rather than in the
385 amount) of food supply (Alegret, 2007; Alegret et al., 2012). This assemblage composition,
386 together with the disappearance of some taxa at the *R. cushmani/W. archaeocretacea* biozone
387 boundary, indicate dysoxic conditions and a high food flux to the seafloor. The disappearance
388 of *Dorothia*, *Gyroidinoides*, *Laevidentalina*, *Lingulogavelinella*, and *Pyrulinoides* may be
389 related to the dysoxic conditions in the sea-bottom. The boundary between the Pre-Bahloul
390 Member and the Bahloul Member is characterised by the disappearance or abrupt decrease in
391 relative abundance of *Lenticulina*, *Gavelinella* and *Globorotalites*, and by an abrupt increase in
392 low-oxygen tolerant forms such as epifaunal *Neobulimina* (Fig. 6).

393 The planktic foraminiferal turnover across the Pre-Bahloul Member includes the
394 disappearance of specialist, intermediate to deep-dweller species adapted to oligotrophic
395 environments (*Rotalipora monsalvensis*), along with the temporary disappearance of
396 mesotrophic, intermediate-dwellers (*Praeglobotruncana gibba*, *Dicarinella* spp.). A peak in the
397 relative abundance of the specialist intermediate-dweller *Thalmaninella brotzeni* is recorded at
398 the base of the Pre-Bahloul Member just before its disappearance (Fig. 5). The percentages of
399 the eutrophic, surface-dweller species *Hedbergella delrioensis* (and *Whiteinella aprica* to a
400 minor extent) increase towards the top of the Pre-Bahloul Member, coinciding with the peaks in
401 redox proxies (Figs. 7 and 8), the disappearance of deep-dweller species (*R. cushmani*), and the

402 temporary disappearance of surface- and intermediate-dwellers (*Globigerinelloides* spp.,
403 *Praeglobotruncana stephani*). These data suggest that the deeper and intermediate layers of the
404 water column were more severely affected than surface waters at the *R. cushmani*-*W.*
405 *archaeocretacea* biozone transition, as suggested by Coccioni and Luciani (2004). An increase
406 in surface palaeoproductivity is supported by the disappearance of the large keeled *Rotalipora*, a
407 specialist genus probably living at or below the thermocline in oligotrophic conditions
408 (Coccioni and Luciani, 2004; Table 3), and by the increase in relative abundance of small-sized
409 *Hedbergella* and *Heterohelix*, opportunistic taxa adapted to eutrophic conditions (e.g. Hart,
410 1999; Keller et al., 2001; Table 3). An increase in P content in sections from the Tethys and
411 North Atlantic has been interpreted as indicative of changes in continental input (and nutrient
412 influx) or upwelling intensification during the late Cenomanian (Mort et al., 2007). Monteiro et
413 al. (2012) suggested that a high P content could be sustained by increased chemical weathering
414 and P regeneration from anoxic sediments.

415 The increase in P/Ti and U/Al in the Pre-Bahloul Member has good stratigraphic
416 correlation with increased redox proxies (Co/Al, Cr/Al, Ni/Al, and Th/Al), and shows a short
417 delay with respect to the increase in TOC values (Figs. 7 and 8). The marine anoxia of the
418 OAE2 is thought to have been related to enhanced biological productivity (e.g. Monteiro et al.,
419 2012; Pogge von Strandmann et al., 2013). Uranium and organic matter in the sediment are
420 related, as uranium may form a complex with dissolved fulvic acid in hemipelagic sediments
421 (Nagao and Nakashima, 1992). In this sense, high values for U/Al, U_{EF} and U_{aut} are congruent
422 with the high values of P/Ti.

423 In open-ocean systems with suboxic bottom waters, U_{aut} enrichment is greater than that
424 of Mo_{aut} because U_{aut} accumulation begins at the Fe(II)-Fe(III) redox boundary (Zhou et al.,
425 2012), while Mo_{aut} accumulation becomes more important as waters become euxinic. Higher
426 values of U_{aut} recorded in the Pre-Bahloul Member are congruent with oxygen-depleted
427 conditions not only at the sea-bottom waters but also in the deeper layers of the water column,

428 where deep dwellers such as *Rotalipora* inhabited. The relative abundance of surface dwellers
429 such as *Hedbergella delrioensis* increased in the Pre-Bahloul Member.

430

431 5.2. Bahloul s. str. Member

432

433 Two intervals with significant peaks in redox proxies are recorded within the Bahloul
434 Member (Fig. 7). The first one is located in the middle part of this unit (sample OB-17), and the
435 second one is located towards its top, at the *W. archaeocretacea*/*H. helvetica* Biozone boundary
436 (Fig. 7). Some redox proxies, such as Th/Al, U_{EF} and U_{aut} , do not show any significant changes
437 across this interval.

438 In the lower half of the Bahloul Member (previous to sample OB-17), the amount of
439 dissolved oxygen in the sea-bottom waters is interpreted to have been even lower than in the
440 underlying Pre-Bahloul Member, as inferred from the disappearance of several benthic
441 foraminiferal taxa and from the very low-diversity assemblages (Figs. 2 and 6), which are
442 dominated by low-oxygen tolerant forms such as *Neobulimina* (Gertsch et al., 2010),
443 *Praebulimina*, *Coryphostoma* and *Tappanina* spp. (incl. *T. laciniosa*). The clear dominance of
444 *Neobulimina* and *Praebulimina* immediately above the extinction interval suggests that they
445 may have behaved as disaster species, as suggested by Peryt and Lamolda (1996). According to
446 these authors, disaster taxa evolved during the late, most stressful phases of an extinction
447 interval, and persisted during the survival and recovery intervals. Species of *Coryphostoma*
448 have small, tapered tests with abundant pores, and are common in dysaerobic environments
449 (e.g., Leutenegger and Hansen, 1979; Bernhard, 1986). *Coryphostoma* is a common genus in
450 low-oxygen environments during the early Danian (Coccioni et al., 1993; Alegret, 2007), and
451 *Tappanina laciniosa* is a biserial, infaunal species that has been reported from dysoxic facies in
452 highly eutrophic environments (e.g. Eicher and Worstell, 1970; Gustafsson et al., 2003;
453 Friedrich and Erbacher, 2006). Moreover, the dominance of infaunal taxa in the Bahloul

454 Member and in the Annaba Member supports the interpretation of low oxygen conditions at the
455 seafloor (Jorissen et al., 1995).

456 The decreased abundance of the surface-dweller *Hedbergella delrioensis* at the base of
457 the Bahloul Member (Fig. 5) points to oxygen-depleted eutrophic surface waters, while low-
458 oxygen conditions only affected deep and intermediate waters in the underlying Pre-Bahloul
459 Member. Only *Heterohelix reussi* —opportunistic taxon adapted to eutrophic conditions—
460 proliferates in the lower part of Baloul Member in a context of decreasing diversity of planktic
461 foraminiferal assemblages.

462 Relatively higher TOC values (mean 1.42 wt.%) and high $\delta^{13}\text{C}$ are recorded in the
463 Bahloul Member (Fig. 8), suggesting higher productivity than in the other units and high
464 accumulation of organic matter derived from surface primary productivity (Schlanger and
465 Jenkyns, 1976; Arthur et al., 1990; Ingall et al., 1993; Van Cappellen and Ingall, 1994; Mort et
466 al., 2007). TOC values have been used as an indirect palaeoproductivity proxy by various
467 authors (e.g., Calvert and Fontugne, 2001; Gupta and Kawahata, 2006; Plewa et al., 2006; Su et
468 al., 2008; Reolid et al., 2012a) when TOC is related to phytodetritus associated with
469 phytoplankton or dinoflagellate remains. Nevertheless, because high TOC values may result
470 from low bottom-water ventilation and oxygen depletion, they are not necessarily related to
471 high surface productivity. According to Tribovillard et al. (2006), the TOC is generally
472 proportional to surface-water productivity and constitutes a useful palaeoproductivity proxy in
473 spite of certain complications attributable to efficient organic recycling, export productivity,
474 delivery to the sediment-water interface and final burial. The maximum TOC values (2.82
475 wt.%) are recorded at the base of this unit (Fig. 8), coeval with high percentages of *Heterohelix*
476 *reussi*, *Heterohelix moremani* and *Hedbergella planispira* (Fig. 5), which are thought to be
477 indicative of eutrophic environments (Table 3). These results are compatible with the analyses
478 of organic matter carried out by Farrimond et al. (1990), who reported abundant algal-derived
479 biological markers across the Cenomanian-Turonian transition at Oued Bahloul, suggesting high
480 surface productivity. High TOC values are also correlated to high percentages of *Neobulimina*

481 and other buliminids (Fig. 6), which are considered to be indicators of high-food and/or low
482 oxygenation at the seafloor in the modern oceans (e.g., Fontanier et al., 2002; Gooday, 2003).
483 The dominance of buliminids is also compatible with the proposed conditions, given that high
484 proportions of buliminids indicate eutrophic conditions (Sprong et al., 2013). These results point
485 to a high export productivity and poor oxygenation at the sea-bottom waters during deposition
486 of the lower part of the Bahloul Member; and combined with the high TOC and $\delta^{13}\text{C}$ values
487 (Figs. 8 and 9), they suggest a major climatic and palaeoceanographic perturbation in a
488 transgressive context (e.g. Zagrarni et al., 2008). In addition, Caron et al. (1999) and Soua et al.
489 (2011) documented the proliferation of radiolarians (mainly Nassellarian) and diatoms at the
490 base of the *Whiteinella archaeocretacea* Biozone (from the uppermost Pre-Bahloul Member), in
491 coincidence with an increased abundance of *Heterohelix* during the deposition of dark laminated
492 limestones. These authors interpreted the proliferation of radiolarians as indicative of renewal of
493 nutrient-rich oceanic waters and increase in water depth.

494 An increase in Mo_{EF} and Mo_{aut} , and a minor increase in Cu/Al , Cr/Al and Ni/Al are
495 observed in bed OB-17 (Fig. 7). High Mo_{EF} and Mo_{aut} values require the presence of H_2S
496 (euxinic conditions) (Tribovillard et al., 2012; Zhou et al., 2012). The gradual increase in Mo_{EF}
497 and Mo_{aut} across the lower half of the studied section indicates a progressive decrease in oxygen
498 availability towards euxinic conditions. Other authors have reported euxinic conditions from the
499 OAE2 (e.g. Wang et al., 2001; Scopelliti et al., 2004). The progressive accentuation of oxygen-
500 depleted conditions from the Pre-Bahloul Member towards the lower half of the Bahloul
501 Member is compatible with the disappearance of benthic taxa that flourished at the beginning of
502 the suboxic conditions (e.g., *Lenticulina*, *Gavelinella*, *Globorotalites*), and with the proliferation
503 of the disaster genus *Neobulimina* (low oxygen tolerant form, Friedrich et al., 2009), which has
504 been documented from other sections during the Cenomanian–Turonian event (e.g. Gebhardt et
505 al., 2004). Finally, the interpretation of anoxia/euxinia is compatible with the lack of benthic
506 foraminifera and very low diversity of planktic assemblages in sample OB-17. The bed OB-17
507 represents a benthic barren level. Unfavorable conditions also affected the water column during

508 this interval, as inferred from the dramatic decrease in the percentage of the opportunistic
509 surface dweller *Hedbergella delrioensis* and the increase in opportunistic surface to
510 intermediate dwellers (*Heterohelix* spp.). The highest relative abundances of heterohelicids (*H.*
511 *reussi*) occur in OB-17 (Fig. 5), where maximum values of Mo_{EF} and Mo_{aut} are recorded (Fig.
512 7). *Heterohelix* has been interpreted as a low-oxygen tolerant genus that bloomed in stratified
513 open marine settings with a well-developed oxygen minimum zone (e.g. Leckie et al., 1998;
514 Premoli Silva and Sliter, 1999; Keller et al., 2001; Keller and Pardo, 2004).

515 Redox proxies indicate the return to normal oxygen conditions across the upper half of
516 the Bahloul Member, but the palaeoenvironmental perturbation induced slow recovery of the
517 foraminiferal assemblages, as reflected by the dominance of the opportunistic *Heterohelix* and
518 *Whiteinella* in intermediate and surface waters, respectively. Diversity of benthic assemblages
519 slightly increases through this interval, and assemblages are dominated by buliminids
520 (*Neobulimina* and *Praebulimina*), with higher percentages of *Gavelinella rochardensis*,
521 *Laevidentalina* and *T. laciniosa* towards the upper part of the Bahloul Formation. The species *T.*
522 *laciniosa* and the genera *Gavelinella*, *Neobulimina* and *Praebulimina* have been reported from
523 dysoxic facies in highly eutrophic environments and high organic-matter fluxes (e.g. Eicher and
524 Worstell, 1970; Coccioni et al., 1993; Gustafsson et al., 2003; Gebhardt et al., 2004; Friedrich
525 and Erbacher, 2006; Friedrich et al., 2009). This assemblage suggests that the repopulation
526 phase at the seafloor occurred in the upper half of the Bahloul Formation. Among planktic
527 foraminifera, the opportunistic surface dweller *Whiteinella* proliferated in this interval, together
528 with the intermediate dweller *H. reussi*, as previously reported from the Tethys area (Coccioni
529 and Luciani, 2004). Non-opportunist forms including *Praeglobotruncana* and *Dicarinella* are
530 recorded in the upper part of the *W. archaeocretacea* Biozone, whereas deep dweller specialists
531 as *Rotalipora* are definitively extinct and there are no genera occupying this ecologic niche.

532 A positive peak in redox proxies (Mo_{EF} , Cu/Al, Co/Al, Cr/Al, Ni/Al ratios) and a minor
533 increase in some palaeoproductivity proxies have been recorded at the *W. archaeocretacea/H.*
534 *helvetica* biozone boundary (sample OB-33), coinciding with an increase in the percentage of

535 buliminids and *Guembelitra cenomana*. *Guembelitra* is interpreted as an opportunist surface
536 dweller adapted to poorly oxygenated, eutrophic waters (Table 3) or to variable salinity and
537 nutrient levels (Keller and Pardo, 2004). The obtained data indicate high productivity and low-
538 oxygen conditions both in surface waters and at the seafloor towards the top of the *W*.
539 *archaeocretacea* Biozone. According to Souza et al. (2011), the composition of radiolarian
540 assemblages also experiments a turnover related to low-oxygen conditions with a drastic
541 decrease of nassellarians and an abundance and diversification of spumellarians.

542

543 5.3. Base of the Kef Formation

544

545 A progressive increase in the diversity of planktic assemblages, together with the co-
546 occurrence of surface and intermediate-to-deep dwellers indicates partial recovery of the
547 assemblages at the beginning of the *H. helvetica* Biozone. The most common taxa (*Whiteinella*,
548 *Heterohelix*, *Hedbergella*) are indicative of eutrophic, oxygenated to poorly oxygenated surface
549 and intermediate waters. Deep dwellers such as the intermediate to specialist
550 *Helvetoglobotruncana* (Table 3) make only a minor contribution to the assemblages. Just after
551 the last suboxic pulse of the top of Bahloul Member (level OB-33), *Whiteinella* proliferates
552 again in the assemblage as a rapid response to improved conditions.

553 In benthic microhabitats, the beginning of the *H. helvetica* Biozone is marked by an
554 increase in relative abundance of *Gyroidinoides*, *Lenticulina* and *Planularia*, and a decrease in
555 *Tappanina* and *Gavelinella*. Diversity of the benthic assemblages remains low, and the
556 dominance of buliminids (*Praebulimina* and *Neobulimina*) indicates a high food supply or low-
557 oxygen conditions at the seafloor (Jorissen et al., 1995; Widmark and Speijer, 1997; Fontanier
558 et al., 2002).

559

560 6. Climatic and palaeoceanographic changes across the Cenomanian–Turonian boundary

561

562 Analyses of $\delta^{18}\text{O}$ in bulk rock show a ~ 1.5 ‰ decrease from the base of the section
563 towards the Bahoul Member, followed by a gradual recovery above this unit (Fig. 9). Assuming
564 these results have not been strongly altered by diagenesis, we infer significantly warmer ($\sim 6^\circ\text{C}$)
565 temperatures during deposition of the organic rich facies of the Bahoul Member (*W.*
566 *archaeocretacea* Biozone), coeval with the disappearance of specialist planktic foraminifera
567 (e.g. *Rotalipora*) and with the proliferation of opportunistic, eutrophic forms such as
568 *Heterohelix* and *Hedbergella*. These results suggest a narrow link between the development of
569 the anoxic event and eutrophic conditions with changes in the ocean-atmosphere system. Some
570 authors have identified a short term cooling during the OAE2 (e.g. Jarvis et al., 2011; Gavrilov
571 et al., 2013; Zheng et al., 2013), which we were not able to recognize in our record from Oued
572 Bahloul at the present resolution.

573 In the transgressive context of the Cenomanian–Turonian boundary (e.g. Zagrarni et al.,
574 2008), the enhanced fertility resulting in high primary productivity and eutrophication was
575 favored by nutrient inputs by leaching from flooded shelves (Erbacher et al., 2001) or enhanced
576 continental supply of nutrients (Föllmi, 1995; Handoh and Lenton, 2003). According to Wagner
577 et al. (2007), the warm humid climate contributes to an intensified hydrological cycle and
578 enhanced export of nutrient-rich weathered material from land to the ocean, as also suggested
579 for the Paleocene-Eocene Thermal Maximum (see refs. in Arreguín-Rodríguez et al., 2014). For
580 the end of Cenomanian, another hypothesis was developed by Caron et al. (1999): the
581 alternation of climatic fluctuations, with evaporation/precipitation in low latitude areas and the
582 formation of dense, hypersaline sea waters.

583 Calcareous nannofossil turnover has been interpreted in terms of enhanced fertility and
584 increased temperatures, pointing to an eutrophication event (Erba, 2004; Hardas and Mutterlose,
585 2007). P-cycling models for Cretaceous Anoxic Events, however, indicate that enhanced
586 primary productivity is not enough for producing anoxic conditions in the bottom waters if
587 water circulation exists (Tsandev and Slomp, 2009). According to these authors, the global
588 ocean has to be sufficiently stagnant (low mixing) to allow the system to achieve oxygen

589 depletion in the deep sea. In general, the thermohaline circulation during the Cretaceous is
590 believed to have been slower due to reduced thermal gradients between the tropics and poles
591 (e.g. Shlanger and Jenkyns, 1976; Fischer and Arthur, 1977), and the wider extension of
592 continental shelves (e.g. Bjerrum et al., 2006). In this context, increased P supply from flooded
593 shelves and weathered continental areas may have triggered enhanced primary production and
594 anoxia in a stagnant ocean. In the Oued Bahloul section, a significant increase in P has been
595 observed in the Pre-Bahloul Member coeval with high dominance of *Hedbergella* and the
596 extinction of *Rotalipora*. The progressive decrease in oxygenation of bottom- and deep-waters
597 towards anoxic conditions in the Bahloul Member (metre 17, OB-17) represents the most
598 stressing conditions for the foraminiferal assemblages, with the disappearance of benthic
599 foraminifera, the expansion of the oxygen minimum zone coincident with maximum values of
600 *Heterohelix*, and probably euxinic conditions in the low water column as indicated by increased
601 Mo_{EF} and Mo_{aut} .

602

603 7. Conclusions

604

605 The integrated analysis of planktic and benthic foraminiferal assemblages, geochemical
606 proxies, TOC and $\delta^{13}C$ and $\delta^{18}O$ from the classic locality of the Oued Bahloul section allowed
607 us to interpret: (a) the redox and palaeoproductivity fluctuations related to the C/T boundary,
608 and (b) the ecostratigraphic changes of foraminiferal associations across the OAE2.

609 Significant changes were recorded across the *R. cushmani*/*W. archaeocretacea*
610 boundary, and planktic and benthic foraminiferal diversity decreased. The disappearance of the
611 planktic genera *Rotalipora*, *Praeglobotruncana*, *Globigerinelloides* and *Thalmaninella*, and
612 the occurrence of the opportunist genus *Hedbergella*, together with the proliferation of
613 buliminids and the increase in palaeoproductivity proxies (P/Ti, U/Al, Sr/Al), indicate eutrophic
614 conditions both in the water column and at the seafloor. The abundance of low-oxygen tolerant
615 genera of benthic foraminifera at the base of *W. archaeocretacea* Biozone is compatible with

616 the enrichment in redox proxies indicating dysoxic conditions in sediment pore water. Deep
617 waters were also oxygen-depleted, as deduced from higher values of U_{aut} than Mo_{aut} , favouring
618 the disappearance of *Rotalipora* and *Globigerinelloides* and the proliferation of surface-dweller
619 *Hedbergella*. The maximum TOC values registered in the lower part of the *W. archaeocretacea*
620 Biozone indicate an abrupt increase in organic matter coeval with an increase in
621 palaeoproductivity and redox proxies.

622 The persistence of the poorly oxygenated conditions in the *W. archaeocretacea* Biozone
623 probably produced euxinic conditions, as indicated by high Mo_{EF} and Mo_{aut} values, minimum
624 diversity and the local disappearance of benthic forms. The decrease in abundance of
625 opportunist surface dwellers (*Hedbergella*) and the increase in opportunist intermediate dwellers
626 (heterohelicids), together with maximum values of Mo_{EF} and Mo_{aut} , indicate stressed conditions
627 and stratified open marine settings with a well-developed oxygen minimum zone.

628 The redox proxies indicate a return to normal oxygen conditions in the upper part of the
629 *W. archaeocretacea* Biozone, with a slow recovery of foraminiferal assemblages. The genus
630 *Whiteinella*, characteristic of mesotrophic environments, becomes more abundant upward in the
631 section. The subsequent colonization of the bottom after the anoxic event was produced by
632 *Praebulimina* (disaster genus), *Gavelinella*, *Neobulimina* and *Tappanina*. These genera are
633 low-oxygen tolerant and related to high organic matter fluxes, thus representing the
634 repopulation episode of the bottom after the benthic barren interval.

635 The *W. archaeocretacea*/*H. helvetica* biozone boundary is characterized by increasing
636 values of redox proxies, coeval with a new peak of *Praebulimina*, a decrease in *Whiteinella* and
637 the record of opportunist *Guembelitria*.

638 The beginning of the *H. helvetica* Biozone indicates a partial recovery of the planktic
639 foraminiferal assemblage due to a persistent dominance of opportunists (*Whiteinella* and
640 *Hedbergella* in surface waters, and *Heterohelix* in intermediate waters). In benthic
641 microhabitats, the beginning of the *H. helvetica* Biozone is marked by an increase in relative
642 abundance of *Neobulimina*, *Lenticulina*, and *Gyroidinoides*, and a decrease in *Tappanina*.

643 Temperature changes and palaeoceanographic reorganization have been inferred across
644 the OAE2. This entailed a low mixing of surface and deep waters (poor ocean ventilation) and
645 enhanced primary productivity related to global warming, increasing continental weathering and
646 nutrient input to the ocean. The expansion of the oxygen minimum zone and the eutrophication
647 led to a reduced diversity of foraminifera and the planktic foraminiferal shift, showing a
648 dominance of genera with low-oxygen tolerance typical of high mesotrophic to eutrophic
649 conditions.

650

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652

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666 **References**

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1014

1015 **Appendix 1: Planktic foraminiferal species**

- 1016 *Anaticinella multiloculata* (Morrow, 1934)
- 1017 *Dicarinella algeriana* (Caron, 1966)
- 1018 *Dicarinella hagni* (Scheibnerova, 1962)
- 1019 *Dicarinella imbricata* (Mornod, 1950)
- 1020 *Globigerinelloides bentonensis* (Morrow, 1934)
- 1021 *Globigerinelloides ultramicrus* (Subbotina, 1949)
- 1022 *Globoheterohelix paraglobulosa* Georgescu and Huber, 2009
- 1023 *Guembelitria cenomana* (Keller, 1935)
- 1024 *Hedbergella delrioensis* (Carsey, 1926)
- 1025 *Hedbergella planispira* (Tappan, 1940)
- 1026 *Hedbergella simplex* (Morrow, 1934)
- 1027 *Helvetoglobotruncana helvetica* (Bolli, 1945)
- 1028 *Helvetoglobotruncana praehelvetica* (Trujillo, 1960)

- 1029 *Heterohelix moremani* (Cushman, 1938)
- 1030 *Heterohelix pulchra* (Brotzen, 1936)
- 1031 *Heterohelix reussi* (Cushman, 1938)
- 1032 *Praeglobotruncana gibba* Klaus, 1960
- 1033 *Praeglobotruncana stephani* (Gandolfi, 1942)
- 1034 *Rotalipora cushmani* (Morrow, 1934)
- 1035 *Rotalipora monsalvensis* (Mornod, 1950)
- 1036 *Shackoina bicornis* (Reichel, 1948)
- 1037 *Schackoina cenomana* (Shacko, 1897)
- 1038 *Thalmaninella brotzeni* (Sigal, 1948)
- 1039 *Thalmaninella greenhornensis* (Morrow, 1934)
- 1040 *Whiteinella aprica* (Loeblich and Tappan, 1961)
- 1041 *Whiteinella archaeocretacea* Pesaggio, 1967
- 1042 *Whiteinella aumalensis* (Sigal, 1952)
- 1043 *Whiteinella baltica* Douglas and Rankin, 1969
- 1044 *Whiteinella brittonensis* (Loeblich and Tappan, 1961)
- 1045 *Whiteinella paradubia* (Sigal, 1952)
- 1046 *Whiteinella* sp.
- 1047
- 1048 **Appendix 2: Benthic foraminiferal species**
- 1049 *Ammodiscus* spp.
- 1050 *Arenobulimina* spp.
- 1051 *Astacolus* spp.
- 1052 *Bathysiphon* spp.
- 1053 *Bigenerina* sp.
- 1054 *Bolivina* sp.
- 1055 *Bolivinopsis* sp.

- 1056 *Brunsvigella thoenensis* (Bartenstein and Brand, 1951)
- 1057 *Charltonina australis* Scheibnerová, 1978
- 1058 *Charltonina* sp.
- 1059 *Conorotalites* sp.
- 1060 *Coryphostoma* spp.
- 1061 *Dorothia pupa* (Reuss, 1860)
- 1062 *Dorothia* spp.
- 1063 *Frondicularia* sp.
- 1064 *Gaudryina pyramidata* Cushman, 1926
- 1065 *Gaudryina* spp.
- 1066 *Gavelinella barremiana* Bettenstaedt, 1952
- 1067 *Gavelinella cenomanica* (Brotzen, 1945)
- 1068 *Gavelinella flandrini* Moullade. 1960
- 1069 *Gavelinella intermedia* (Berthelin, 1880)
- 1070 *Gavelinella rochardensis* Beckmann, 1991
- 1071 *Gavelinella* spp.
- 1072 *Glandulina* sp.
- 1073 *Globorotalites* sp.
- 1074 *Globulina* spp.
- 1075 *Gyroidinoides beisseli* (White, 1928)
- 1076 *Gyroidinoides globosus* (Hagenow, 1842)
- 1077 *Gyroidinoides lenticulus* (Reuss, 1845)
- 1078 *Gyroidinoides* spp.
- 1079 *Gyroidinoides subglobosus* Dailey, 1970
- 1080 *Laevidentalina* spp.
- 1081 *Lagena* spp.
- 1082 *Lenticulina gaultina* (Berthelin, 1880)

- 1083 *Lenticulina* spp.
- 1084 *Lenticulina subgaultina* Bartenstein, 1962
- 1085 *Lingulina* sp.
- 1086 *Lingulina taylorana* Cushman, 1938
- 1087 *Lingulogavelinella frankei* (Bykova, 1953)
- 1088 *Lingulogavelinella* sp.
- 1089 *Marssonella oxycona* (Reuss, 1860)
- 1090 *Neobulimina albertensis* (Stelck and Wall, 1954)
- 1091 *Neobulimina irregularis* Cushman and Parker, 1936
- 1092 *Neobulimina* spp.
- 1093 *Neobulimina subregularis* (de Klasz, Magné and Rérat, 1963)
- 1094 *Neoflabellina* sp.
- 1095 *Palmula* sp.
- 1096 *Planularia advena* Cushman and Jarvis, 1932
- 1097 *Planularia dissona* Plummer, 1931
- 1098 *Planularia* sp.
- 1099 *Praebulimina* cf. *exigua* Cushman and Parker, 1935
- 1100 *Praebulimina nannina* (Tappan, 1940)
- 1101 *Praebulimina reussi* (Morrow, 1934)
- 1102 *Praebulimina* spp.
- 1103 *Pyrulina* spp.
- 1104 *Pyrulinoides* spp.
- 1105 *Quadrimorphina* sp.
- 1106 *Quasispiroplectammina* spp.
- 1107 *Ramulina* spp.
- 1108 *Reophax* sp.
- 1109 *Repmanina charoides* (Jones and Parker, 1860)

- 1110 *Saracenaria* sp.
 1111 *Spiroplectammina* sp.
 1112 *Stensioeina exsculpta* (Reuss, 1860)
 1113 *Tappanina laciniosa* Eicher and Worstell, 1970
 1114 *Tappanina* sp.
 1115 *Textularia* sp.
 1116 *Trochammina globolaevigata* Beckmann, 1991
 1117 *Vaginulina* sp.
 1118 *Valvulineria* sp.

1119
 1120
 1121

1122 **Figure caption.**

1123

1124 **Fig. 1.** (A) Geological setting, (B) palaeogeographic reconstruction of Western Tethys after
 1125 Thierry (2000) and (C) Oued Bahloul section. Ammonite biostratigraphy according to
 1126 Caron et al. (1999, 2006), Accarie et al. (2000), Amédro et al. (2005) and Zagarni et al.
 1127 (2008).

1128 **Fig. 2.** Planktic foraminiferal species in the Oued Bahloul section: **1-** *Globigerinelloides*
 1129 *bentonensis* (OB-3.5). **2-** *Globoheterohelix paraglobulosa* (OB-42). **3-** *Guembelitra*
 1130 *cenomana* (OB-24). **4-** *Hedbergella delrioensis* (OB-42). **5-** *Hedbergella planispira* (OB-
 1131 22). **6-** *Hedbergella simplex* (OB-3). **7-8** *Helvetoglobotruncana helvetica* (7: OB-44, 8: OB-
 1132 35). **9-** *Heterohelix moremani* (OB-13). **10-** *Heterohelix reussi* (OB-22). **11-**
 1133 *Praeglobotruncana gibba* (OB-3). **12-** *Praeglobotruncana stephani* (OB-3.5). **13-**
 1134 *Rotalipora cushmani* (OB-3). **14-** *Rotalipora brotzeni* (OB-3.5). **15-** *Rotalipora*
 1135 *greenhornensis* (OB-3.5). **16-** *Whiteinella archaeocretacea* (OB-20). **17-** *Whiteinella aprica*
 1136 (OB-37). **18** *Whiteinella brittonensis* (OB-28). Scale bars: 0.1 mm.

1137 **Fig. 3.** Benthic foraminiferal species in the Oued Bahloul section: **1-** *Neobulimina albertensis*
 1138 (OB-10). **2-** *Neobulimina subregularis* (OB-10). **3-** *Praebulimina prolixa* (OB-24). **4-**
 1139 *Lenticulina gaultina* (OB-2). **5-** *Gyroidinoides lenticulus* (OB-2). **6-** *Gyroidinoides globosus*
 1140 (OB-2). **7-** *Praebulimina nannina* (OB-2). **8-** *Gaudryina pyramidata* (OB-3). **9-**
 1141 *Marssonella oxycona* (OB-3). **10-** *Lenticulina* sp (OB-3). **11-** *Trochammina globolaevigata*
 1142 (OB-3). **12-** *Praebulimina* sp (OB-8). **13-** *Praebulimina reussi* (OB-8). **14-** *Gavelinella*
 1143 *rochardensis* (OB-8). **15-** *Planularia advena* (OB-35.5). **16-** *Tappanina laciniosa* (OB-33).
 1144 **17-** *Gavelinella* cf. *rochardensis* (OB-22). **18-** *Astacolus* ? sp. (OB-35). Scale bars: 0.1 mm

1145 **Fig. 4.** Stratigraphic distribution of planktic/benthic ratio and diversity of planktic and benthic
 1146 foraminifera.

1147 **Fig. 5.** Stratigraphic distribution of planktic foraminiferal assemblages.

1148 **Fig. 6.** Stratigraphic distribution of benthic foraminiferal assemblages.

1149 **Fig. 7.** Stratigraphic fluctuations of geochemical redox proxies and U- and Mo-based proxies
 1150 (enrichment factor and authigenic content).

1151 **Fig. 8.** Stratigraphic fluctuations of CO₃Ca content, TOC and geochemical palaeoproductivity
 1152 proxies.

1153 **Fig. 9.** Stratigraphic fluctuations of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ and comparison with previous $\delta^{13}\text{C}$ curves of
 1154 Caron et al. (2006) (dashed line) and Zagrarni et al. (2008) (dotted line).

1155 **Fig. 10.** Evolution of trophic conditions, productivity and oxygenation in the water column and
 1156 the seafloor (sea-bottom waters) inferred from foraminiferal assemblages and geochemical
 1157 proxies.

1158

1159

1160 **Table caption**

1161 Table 1. Planktic foraminiferal counts per sampling level.

1162 Table 2. Benthic foraminiferal counts per sampling level.

1163 Table 3. Planktic forms and inferred life style including redox and trophic requirements of
1164 planktic foraminifera from Ouled Bahloul section based on Hart and Bailey (1979), Hart
1165 (1999), Keller et al. (2001) and Coccioni and Luciani (2005).

Figure 01
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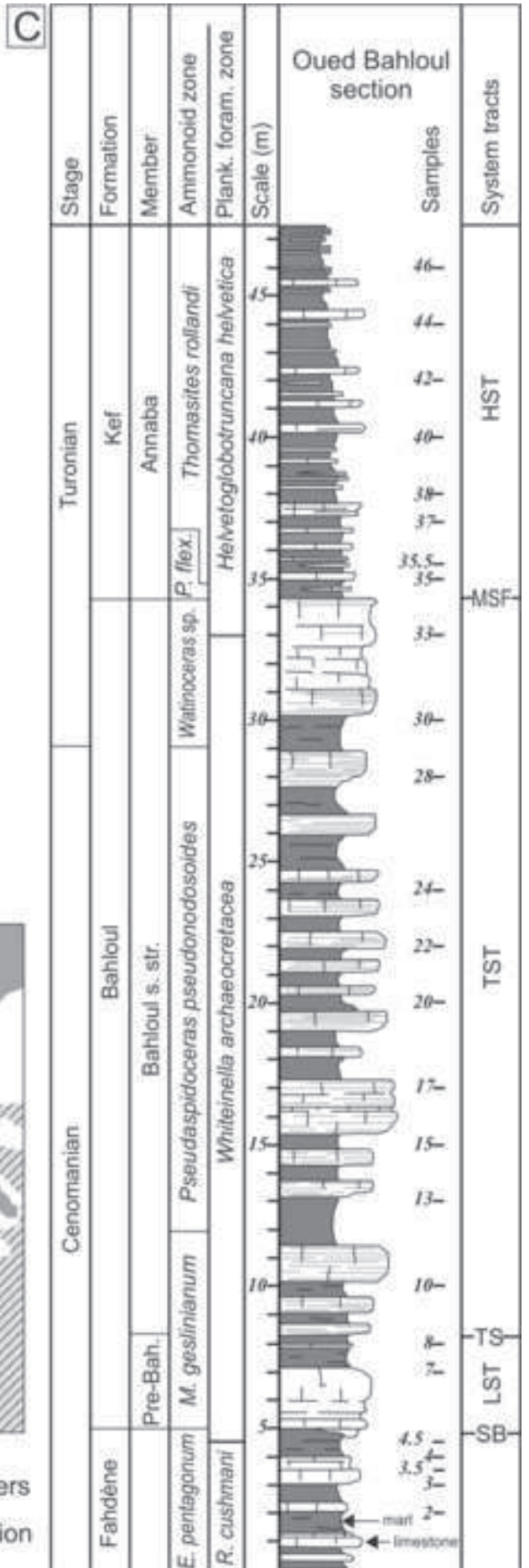


Figure 02
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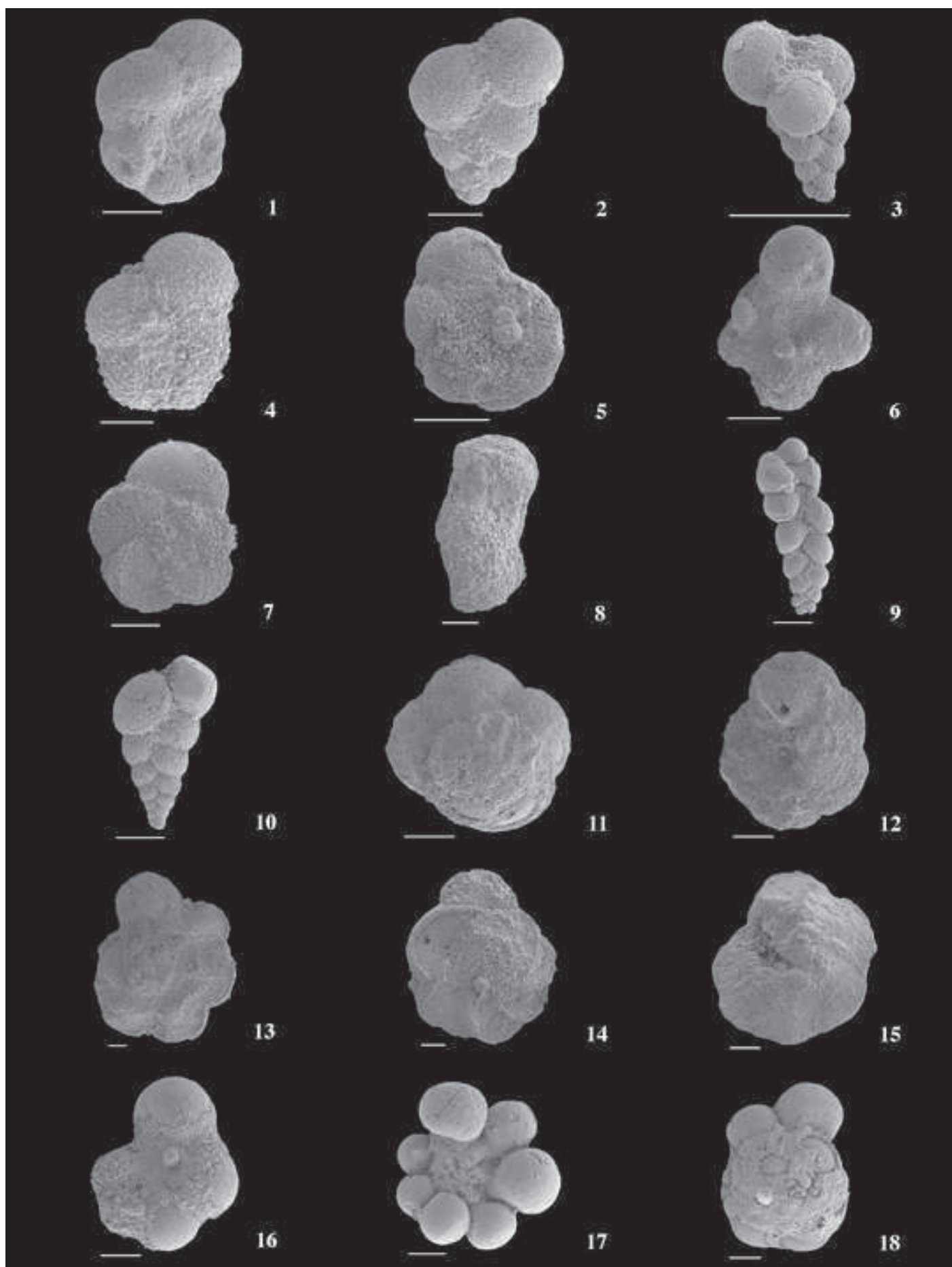


Figure 03
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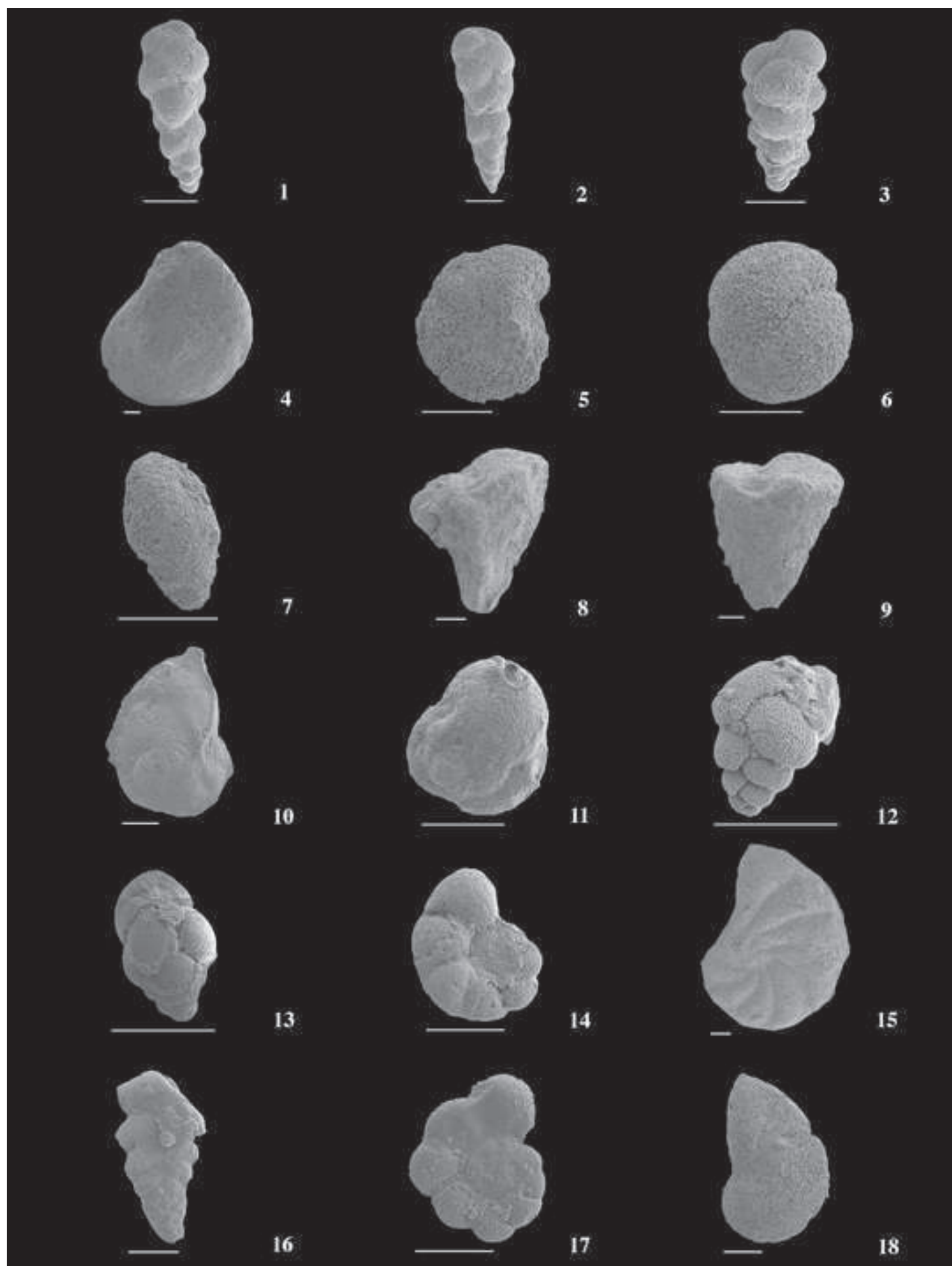


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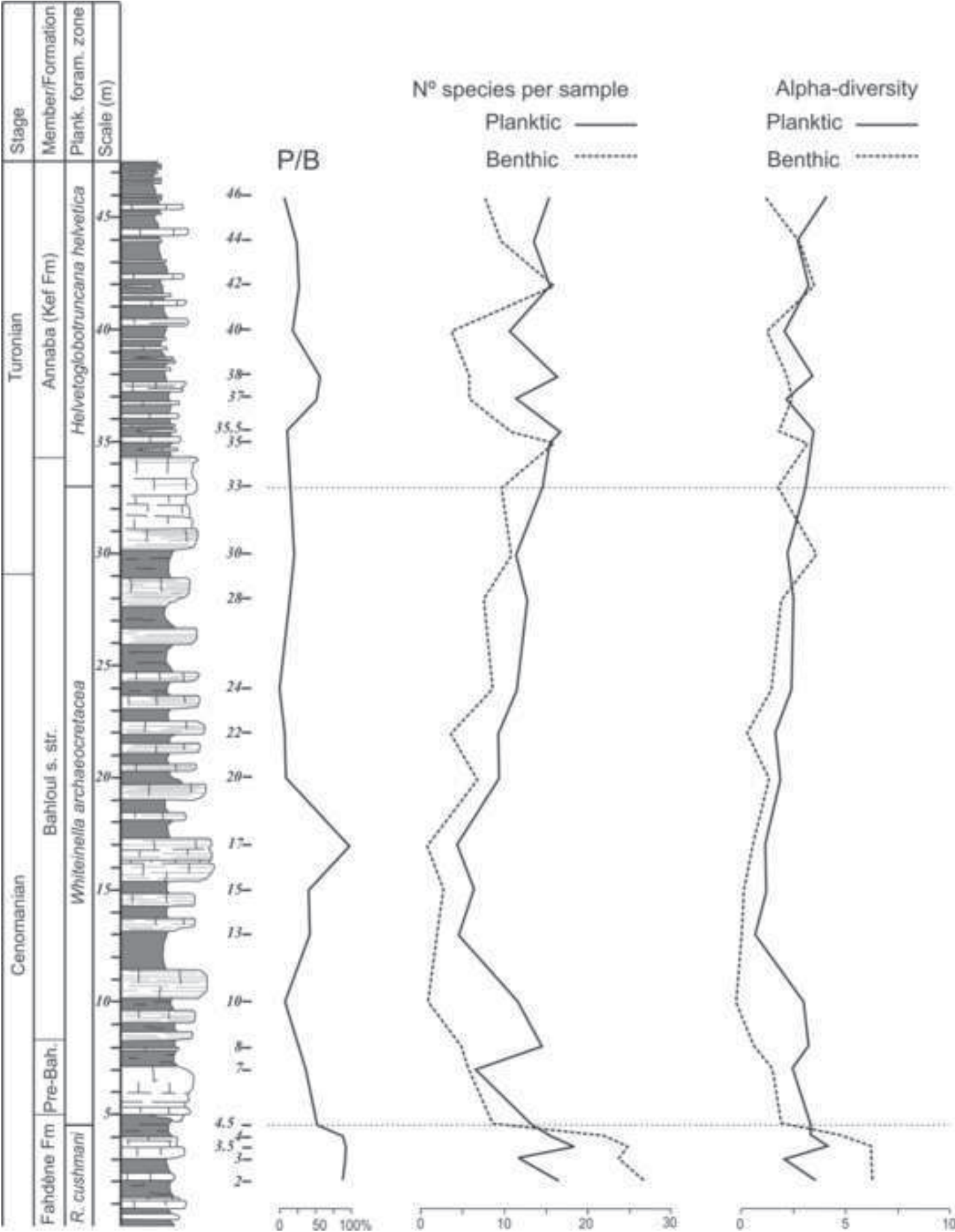


Figure 06a
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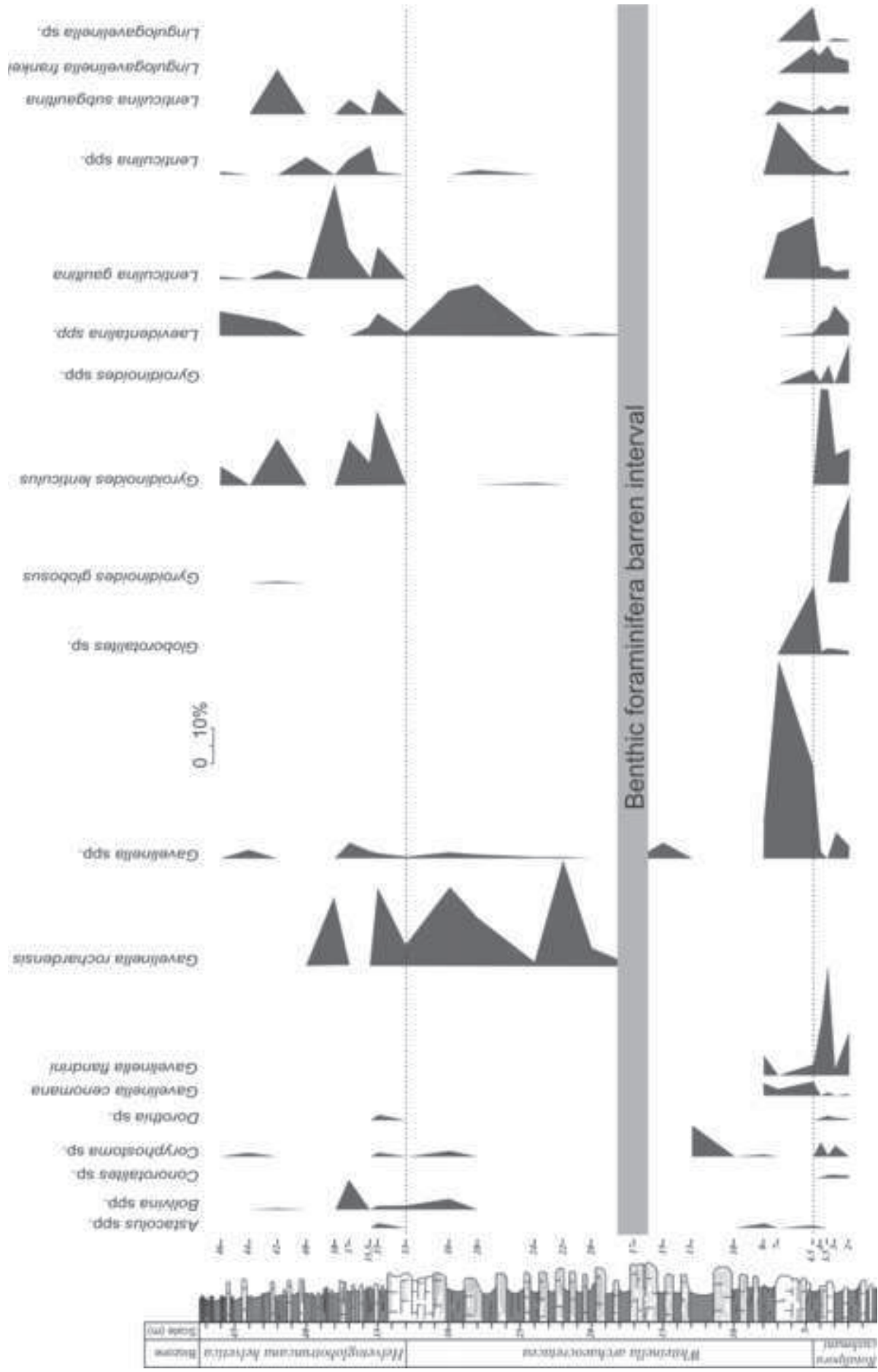


Figure 06b
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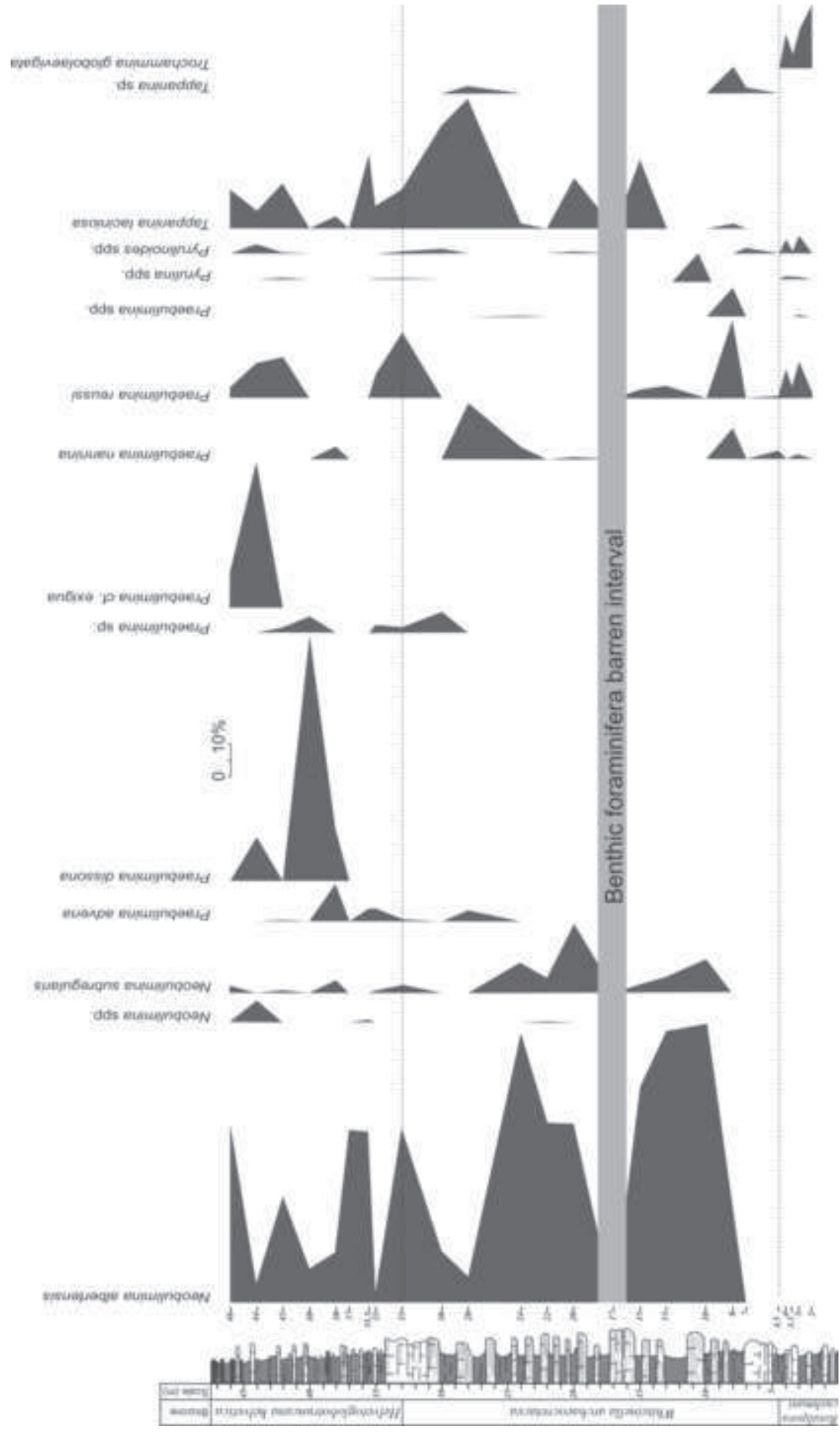


Figure 07
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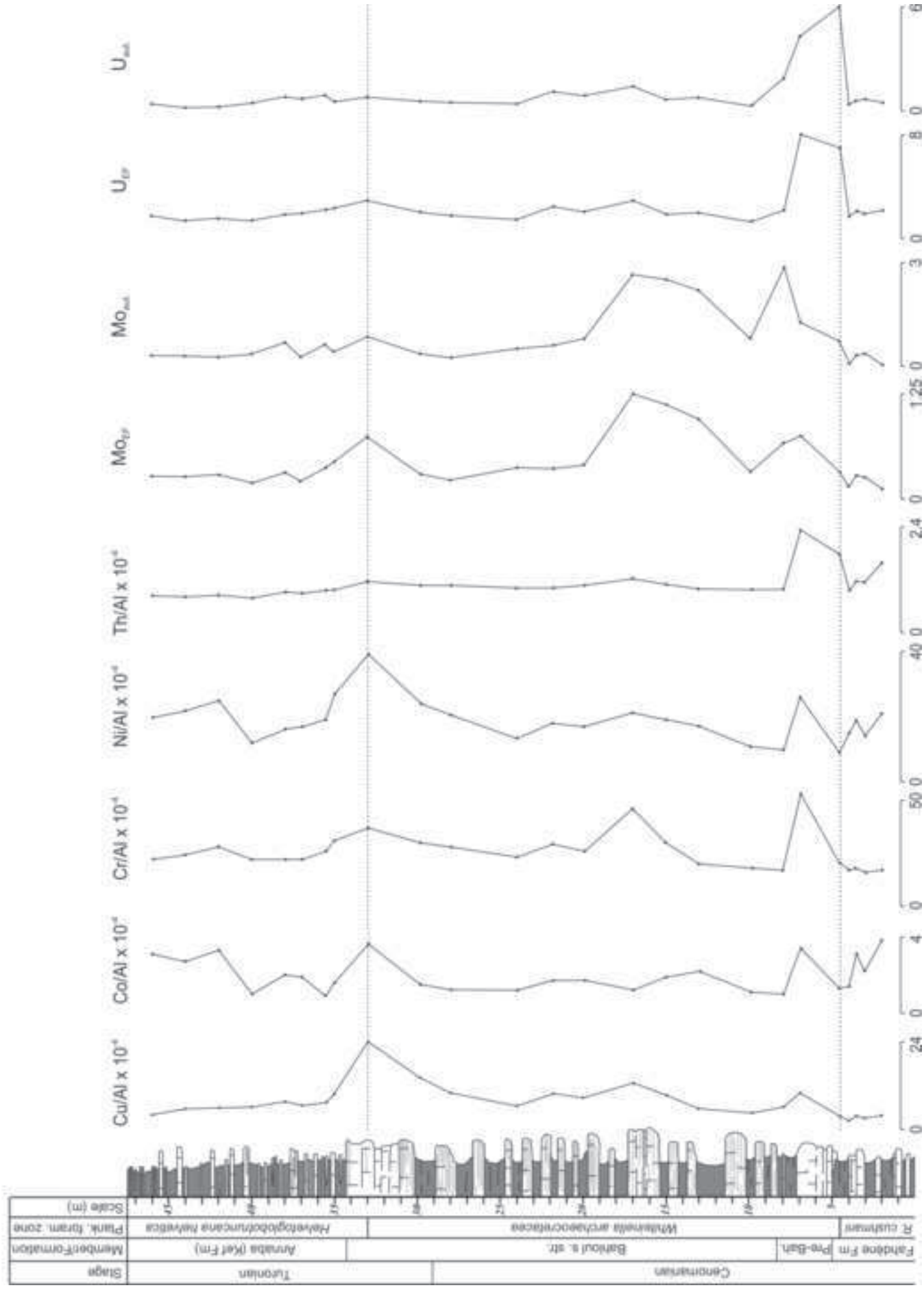


Figure 08
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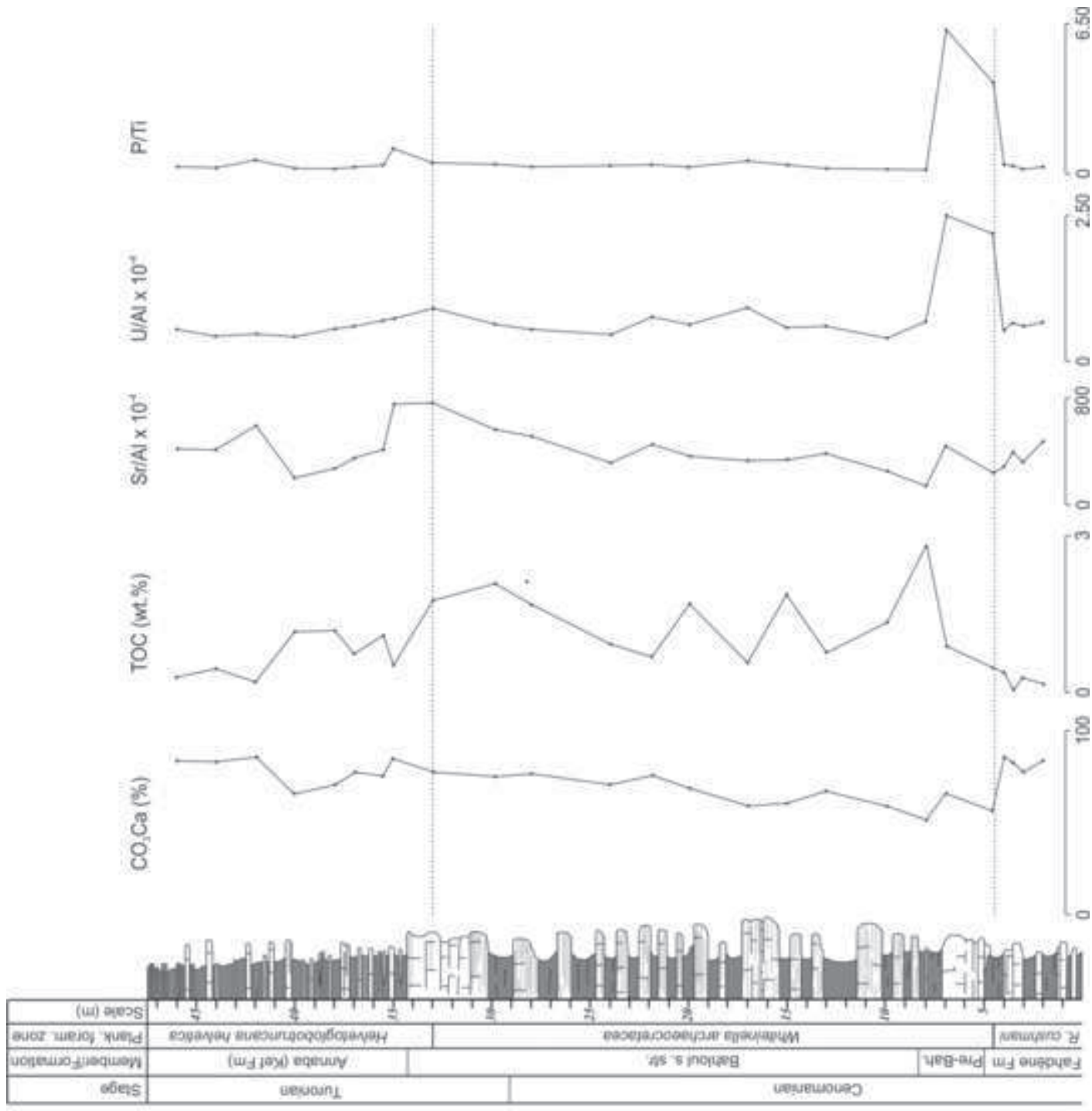


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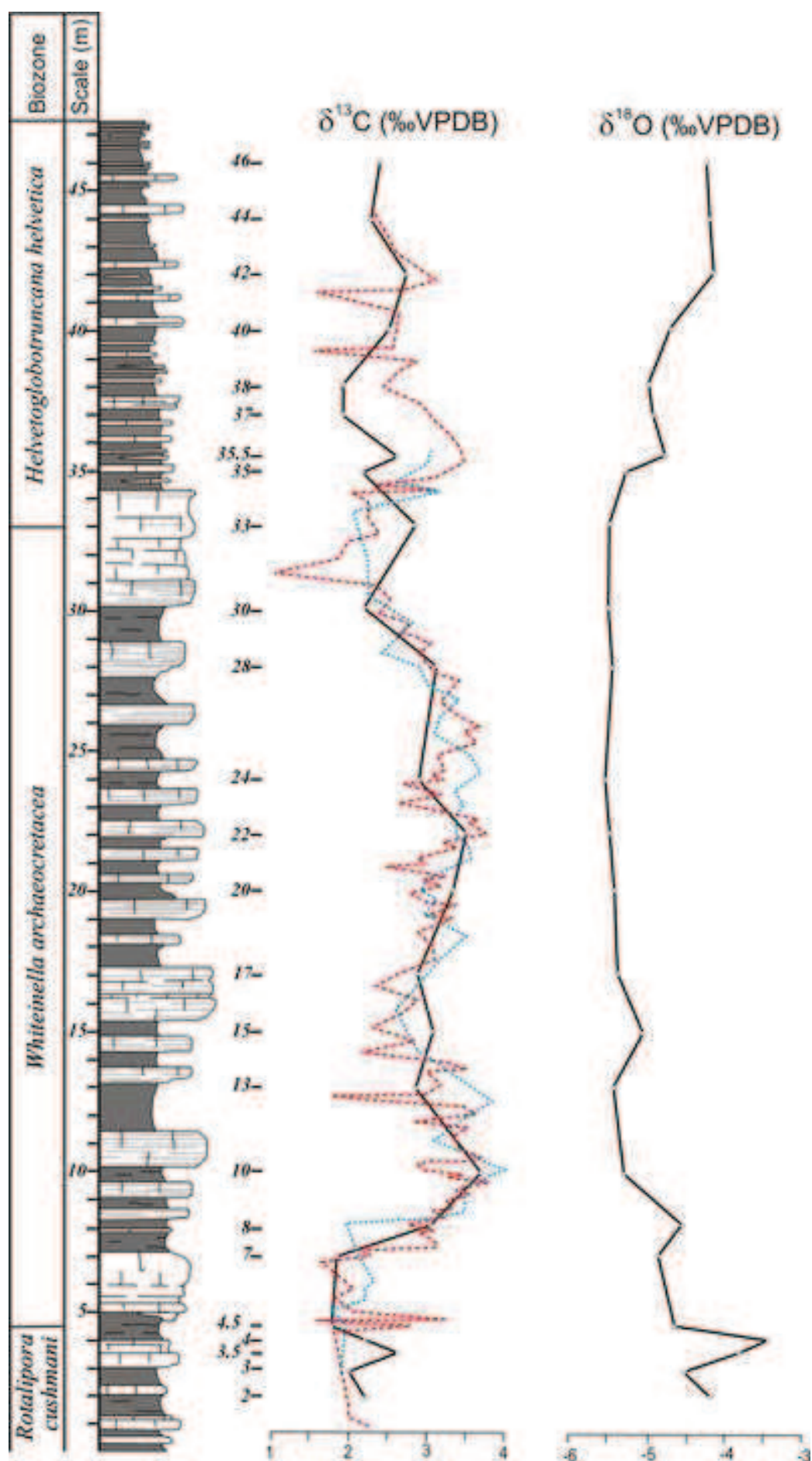


Figure 10
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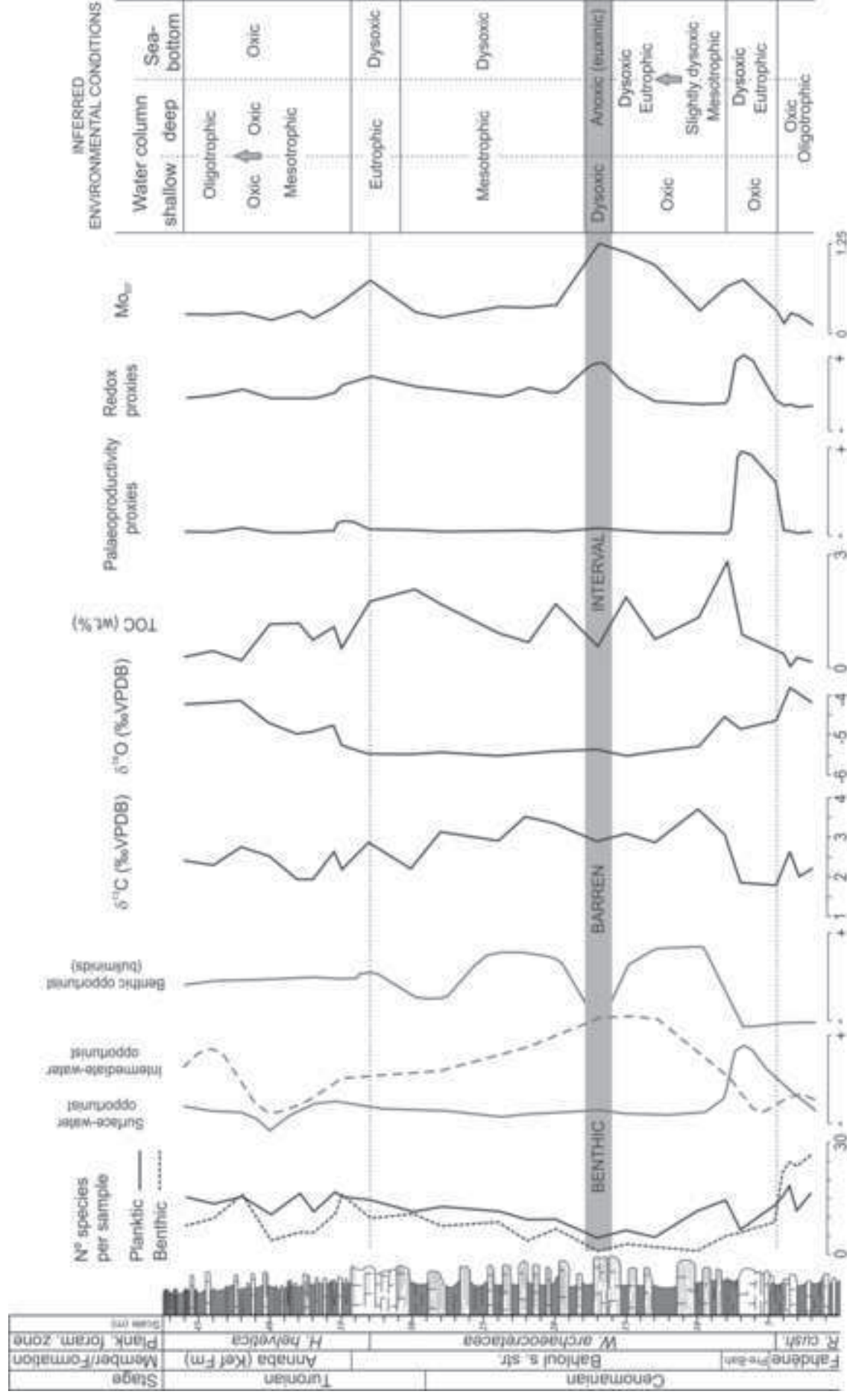


Table 01
[Click here to download Table: Table 1.xlsx](#)

SAMPLE \ SPECIES	<i>Anaticinella multiloculata</i>				<i>Dicarinella algeriana</i>	<i>Dicarinella hagni</i>	<i>Dicarinella imbricata</i>	<i>Globigerinelloides bentonensis</i>	<i>Globigerinelloides ultramicrus</i>			<i>Globoheterohelix paraglobulosa</i>		<i>Guembelitria cenomana</i>	<i>Hedbergella delrioensis</i>	<i>Hedbergella planispira</i>	<i>Hedbergella simplex</i>	<i>Helvetoglobotruncana helvetica</i>		<i>Helvetoglobotruncana praehelvetica</i>	<i>Heterohelix moremani</i>
OB10-46	0	4	0	0	0	0	0	0	26	0	82	19	4	1	26	6					
OB10-44	0	3	0	0	0	0	0	0	66	6	19	8	1	0	13	4					
OB10-42	0	5	0	0	0	0	0	0	37	17	57	5	3	3	11	0					
OB10-40	0	0	0	0	0	0	0	0	3	0	0	0	0	1	2	0					
OB10-38	0	3	1	0	0	0	0	0	10	21	41	38	3	8	11	4					
OB10-37	0	0	0	0	0	0	0	0	15	0	31	7	5	25	22	0					
OB10-35.5	0	0	0	0	0	0	0	0	20	68	73	17	17	3	2	4					
OB10-35	0	5	3	1	0	0	0	0	19	25	61	15	0	7	20	3					
OB10-33	0	1	2	0	0	0	0	0	27	70	21	19	0	3	15	2					
OB10-30	0	0	0	0	0	0	0	0	32	8	25	17	0	0	10	5					
OB10-28	0	0	0	0	2	0	0	0	0	7	22	23	0	0	7	1					
OB10-24	0	0	0	0	0	0	0	0	0	4	4	20	0	0	23	8					
OB10-22	0	0	0	0	0	0	0	0	0	7	14	27	0	0	2	38					
OB10-20	0	0	0	0	0	0	0	0	0	12	7	35	0	0	18	13					
OB10-17	0	0	0	0	0	0	0	0	0	0	4	10	0	0	0	1					
OB10-15	0	0	0	0	0	0	0	0	1	2	4	30	0	0	0	18					
OB10-13	0	0	0	0	0	0	0	0	0	0	4	40	4	0	0	35					
OB10-10	0	0	0	0	0	0	0	0	11	0	17	21	0	0	3	10					
OB10-8	0	0	0	0	3	2	0	14	89	22	12	0	1	4							
OB10-7	0	0	0	0	1	1	0	0	22	1	0	0	0	0	0	0					
OB10-4.5	0	0	0	0	14	1	0	0	57	27	5	0	0	0	0	0					
OB10-4	0	0	0	0	47	3	0	0	143	12	17	0	0	0	3						
OB10-3.5	1	1	0	0	78	8	0	0	90	25	25	0	0	0	3						
OB10-3	0	0	0	0	80	16	0	0	42	123	34	0	0	0	5						
OB10-2	0	0	1	0	32	31	0	5	89	80	38	0	0	0	6						

Table 02
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SAMPLE / SPECIES																
	<i>Ammodiscus</i> spp.	<i>Arenobulimina</i> spp.	<i>Astacolus</i> spp.	<i>Bathysiphon</i> spp.	<i>Bigenerina</i> sp.	<i>Bolivina</i> sp.	<i>Boliviniopsis</i> sp.	<i>Brunsvigella thoerensis</i>	<i>Charltonina australis</i>	<i>Charltonina</i> sp.	<i>Conorotalites</i> sp.	<i>Coryphostoma</i> spp.	<i>Dorothia pupa</i>	<i>Dorothia</i> spp.	<i>Fronicularia</i> sp.	<i>Gaudryina pyramidata</i>
OB10-46	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
OB10-44	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
OB10-42	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	
OB10-40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
OB10-38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
OB10-37	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	
OB10-35.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
OB10-35	0	0	5	0	0	4	0	0	0	0	0	4	0	6	2	
OB10-33	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	
OB10-30	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	
OB10-28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
OB10-24	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	
OB10-22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
OB10-20	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	
OB10-17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
OB10-15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
OB10-13	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	
OB10-10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
OB10-8	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	
OB10-7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
OB10-4.5	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	
OB10-4	1	0	1	0	0	0	0	0	7	0	1	14	0	2	0	
OB10-3.5	2	0	0	1	0	0	2	0	1	0	3	1	0	4	2	
OB10-3	0	0	0	0	0	0	0	0	0	0	3	8	3	2	2	
OB10-2	1	0	0	0	0	0	0	0	2	1	3	0	2	1	0	

Table 03

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Morphology	Genera	Habitat	Mode
Strongly keeled trochospiral	<i>Dicarinella</i>	Intermediate-dweller	Intermediate
	<i>Rotalipora</i>	Intermediate to deep-	Specialist
	<i>Thalmaninella</i>	Intermediate to deep-	Specialist
Weakly keeled trochospiral	<i>Anaticinella</i>	Intermediate-dweller	Intermediate
	<i>Helvetoglobotruncana</i>	Intermediate to deep-dweller	Intermediate to specialist
	<i>Praeglobotruncana</i>	Intermediate-dweller	Intermediate
Unkeeled trochospiral	<i>Hedbergella</i>	Surface-dweller	Opportunist
	<i>Shackoina</i>	Intermediate-dweller	Intermediate
	<i>Whiteinella</i>	Surface-dweller	Opportunist
Planispiral	<i>Globigerinelloides</i>	Surface to intermediate-dweller	Opportunist to Intermediate
Biserial	<i>Heterohelix</i>	Surface to intermediate-dweller	Opportunist
Triserial	<i>Guembelitra</i>	Surface-dweller	Opportunist