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Paleoenvironmental and ecological changes during the Eocene-Oligocene transition based on foraminifera from the Cap Bon Peninsula in North East Tunisia

Chaima Grira, Narjess Karoui-Yaakoub, Mohamed Hédi Negra, Lucia Rivero-Cuesta, Eustoquio Molina



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1 **Paleoenvironmental and ecological changes during the Eocene-Oligocene**
2 **transition based on foraminifera from the Cap Bon Peninsula in North East**
3 **Tunisia**

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5 **Chaima Grira^a, Narjess Karoui-Yaakoub^a, Mohamed Hédi Negra^b, Lucia**
6 **Rivero-Cuesta^c, Eustoquio Molina^c**

7
8 ^a Département des Sciences de la Terre, Faculté des Sciences de Bizerte, Université Carthage, Jarzouna, Bizerte
9 7021, Tunisia.

10 ^b Unité de Recherche: Petrologie Sédimentaire et Cristalline, Faculté des Sciences de Tunis, Université El
11 Manar. Tunisia.

12 ^b Departamento de Ciencias de la Tierra and IUCA, Universidad de Zaragoza, E-50009 Zaragoza, Spain.
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15 **ABSTRACT**

16 Biostratigraphic analysis of the Eocene-Oligocene transition (E-O) at the Menzel Bou
17 Zelfa and Jhaff composite section in the Cap Bon Peninsula (North East Tunisia) allowed us
18 to recognize a continuous planktic foraminiferal biozonation: E14 *Globigerinatheka*
19 *semiinvoluta* Zone, E15 *Globigerinatheka index* Zone, E16 *Hantkenina alabamensis* Zone
20 and O1 *Pseudohastigerina nagewichiensis* Zone. A quantitative study of benthic and
21 planktic foraminifera assemblages was carried out and the richness and diversity of
22 foraminifera allowed us to reconstruct the paleoenvironmental evolution from marine to
23 terrestrial environments. From the Eocene E14 Zone, the foraminiferal association
24 characterizes a relatively warm climate with considerable oxygen content and a dominance of
25 keeled and spinose planktic foraminifera, which became extinct at the E/O boundary, possibly
26 due to cooling of the planktic environment. Nevertheless, the small benthic foraminifera do
27 not show an extinction event at the Eocene/Oligocene (E/O) boundary, indicating that the
28 benthic environment was not significantly affected. In the basal Oligocene O1 Zone, the
29 benthic environment changes to a shallower setting due to cooling of the climate. These
30 changes generated a remarkable dominance of globular forms in the planktic environment.
31 Small benthic foraminifera apparently have a gradual extinction event, or more likely a
32 gradual pattern of local disappearances, that could have been caused by the Oi1 glaciation.

33 **Keywords:** Foraminifera, Eocene/Oligocene, Extinction, Paleoenvironment, Tunisia.
34

35 1. Introduction

36

37 The E-O transition, around 34 Ma, was a pivotal time in Earth's evolution as the climate
38 shifted from Early Cenozoic greenhouse to glacial conditions with significant permanent ice
39 sheets on Antarctica (Shackleton and Kennett, 1976; Zachos et al., 1996; Wade et al., 2012;
40 Ortiz and Kaminski, 2012). This was associated with a cooling of the regions of low, medium
41 and high latitudes (Coxall and Pearson, 2007; Lear et al., 2008).

42 As the world shifted from warm Eocene climate to colder Oligocene climate, there were
43 major changes in ecology, productivity, chemistry and also probably within the vertical
44 structure of the water column. This major change under the climatic conditions is reflected by
45 similar progressive changes in the oxygen and carbon isotopes of the benthic foraminifera
46 from deep waters (Coxall et al., 2005; Coxall and Wilson, 2011) as well as in the lithology of
47 the pelagic sediments (Pälike et al., 2012), reflecting the cooling of the oceans and the
48 development of large ice sheets in Antarctica (Shackleton and Kennett, 1976; Zachos et al.,
49 1996; DeConto and Pollard, 2003; Coxall et al., 2005; Lear et al., 2008). These climate
50 changes were associated with a reduction of atmospheric carbon dioxide (Pearson et al., 2009;
51 Pagani et al., 2011), the extinction of many species of phytoplankton and zooplankton
52 (Funakawa et al., 2006; Pearson et al., 2008) a deepening of the calcite compensation depth
53 (CCD), a fall in sea level increased ocean alkalinity (Coxall et al., 2005), and the tectonic
54 changes that have opened Oceanic gateways of flows around the Antarctic (Exon et al., 2004;
55 Stickley et al., 2004; Barker et al., 2007).

56 Planktic foraminifera suffered extinction across the E/O boundary (Martínez-Gallego
57 and Molina, 1975; Molina, 1980, 1986; Molina et al., 1986, 1988, 1993, 2006; Nocchi et al.,
58 1988; Gonzalvo and Molina, 1992; Farouk et al., 2013, 2015; Pearson and Wade, 2015;
59 Karoui-Yaakoub et al., 2017). Planktic foraminifera suffered a rapid but gradual extinction
60 event, which is characterized by the extinction of the hantkeninids and turborotalids
61 (*Hantkenina primitiva*, *Hantkenina compressa*, *Hantkenina alabamensis*, *Hantkenina*
62 *nanggulanensis*, *Cribohantkenina lazzarii*, *Turborotalia cocoaensis* and *Turborotalia*
63 *cunialensis*). Furthermore, the larger *Pseudohastigerina micra* s. str. also seems to have gone
64 extinct. These species gradually became extinct in about 0.04 Myr and account for 31% of the
65 planktic assemblages (Molina, 2015). The E/O boundary was defined at the Massignano
66 section, coinciding with the extinction of the hantkeninids (Premoli Silva and Jenkins, 1993).

67 Larger foraminifera living in shallow platforms had a turnover (Orabi et al., 2015), but did
68 not suffer extinction coinciding with the E/O boundary (Molina et al., 2016), although the

69 magnitude of this turnover is not yet well known. Small benthic foraminifera, living in
70 bathyal and abyssal environments, are not so well studied as planktic and their pattern of
71 extinction at the E/O boundary is not yet known in detail. Deep-sea benthic foraminifera
72 underwent a mass but gradual extinction from the late Eocene-early Oligocene, with modern
73 type assemblages becoming established (Kaminski et al., 1989; Thomas, 1992; Thomas and
74 Gooday, 1996; Kaminski and Gradstein, 2005; Thomas and Via, 2007).

75 The aim of this work is to study the paleoenvironmental changes across the E/O
76 boundary in North East Tunisia, based on the quantitative analyses of small benthic and
77 planktic foraminiferal assemblages at the Menzel bou Zelfa and Jhaff composite section. The
78 richness of planktic foraminiferal species reflects the climatic stability of the water, and
79 therefore, varies depending on ocean circulation being greatest where redistribution of hot
80 water masses is promoted (Wade and Pearson, 2008). This causes a variety of ecological
81 habitats where the various species of life grow and proliferate. The planktic foraminiferal
82 extinction event is known to coincide with the E/O boundary, but little is known about what
83 happened at the sea bottom. Our study therefore, focuses on small benthic foraminifera in
84 order to investigate the nature and timing of the benthic foraminiferal turnover and to
85 ascertain whether the benthic extinctions coincided with the E/O boundary and the beginning
86 of the Oi1 glaciation.

87

88

89 **2. Geological and geographical setting**

90

91 The 54 m thick Menzel Bou Zelfa (MBZ) section is located in the north-eastern of
92 Tunisia in the Cap Bon peninsula. Section sampling was carried out on the NE flank of the
93 anticline Jebel Abderrahmane. The stratigraphic series is essentially composed of marls,
94 limestones and sands ranging in age from the middle Eocene to Quaternary (Fig.1). However,
95 in some places the E/O boundary interval was covered with Quaternary deposits, for which
96 reason it was decided to merge two separate sections into a single composite one. It was
97 necessary to carry out detailed sampling across the E/O boundary, which is why a better
98 exposed section in the same area about 1 Km to the south was chosen, located between the
99 coordinate points $36^{\circ} 42'16.44''\text{N}$ and $10^{\circ}41'42.5800\text{E}$. This interval of the composed section
100 is named Jhaff (J6-J13). This detailed interval was located between MBZ 26 and MBZ 25
101 (Fig. 2).

102 This section is composed of light grey marls occasionally interbedded with centimetric
103 argillaceous reddish limestone beds, rich in iron oxide and is called Unit 1. From sample Jhaff
104 11 it comprises a sandy limestone bed rich in iron oxide and is called Unit 2. This sample
105 marks a transition to a new facies characterized by grey sandy marls. This facies is overlaid
106 by dark grey marls intersected at the top by a centimetric bed of indurated marl with
107 ferruginous concretions. The units 1 and 2 are marine and belong to the Tellien Domain. The
108 top of the section is formed by light grey marl, sometimes intercalated with yellowish to
109 brownish rust, overlaid with a sandstone bed with yellow limestone cement known as Unit 3.
110 This upper unit is terrestrial and belongs to the Numidian Flysch (Boukhalfa et al., 2009).

111

112

113 3. Materials and methods

114

115 In the field it was possible to select a complete section, which was accessible and
116 presented the best outcrop. An initial scatter sampling was performed during the first visit to
117 identify the location of the boundaries, followed by a second more detailed sampling to
118 further characterize them.

119 The marly samples were washed in the laboratory. Each sample was soaked in tap water
120 for few days, adding diluted H₂O₂ for some very compacted samples. These samples were
121 then washed through a column of three interlocking sieves, with meshes 250µm, 150µm and
122 63µm. The washed residue was collected in Petri dishes and dried in a stove at a temperature
123 of 50°C.

124 The residues were sorted and observed under a binocular microscope in order to identify
125 the foraminifera. The quantitative and taxonomic studies were based on representative splits
126 of >300 specimens of the 63 and 150-µm fraction combined, obtained with an Otto
127 microsplitter and the rest of the sample was scanned to look for rare species. Relative
128 abundance of common taxa was calculated, together with faunal indices commonly used in
129 ecology and paleoenvironmental reconstruction. The most representative taxa were
130 photographed using the Scanning Electron Microscope at the ETAP (Tunisian National Oil
131 Company).

132 The biostratigraphy of this section was previously studied and published by the present
133 authors (Karoui-Yaakoub et al., 2017) with planktic foraminifera biozonation based on
134 Pearson et al. (2006). The last occurrence (LO) of the index taxon *Globigerinatheka*
135 *semiinvoluta* was used to recognize E14, the LO of *Globigerinatheka index* to mark E15, the

136 LO of *Hantkenina alabamensis* to locate the E16/O1 boundary, and the LO of
137 *Pseudohastigerina naguewichiensis* to mark the first biozone of the Rupelian (Fig 2).

138 Benthic fauna occupies numerous and diverse ecological niches. Indeed, it yields a
139 considerable amount of information about the conditions of the bottom of the ocean and has
140 played an important role over the years in interpreting these conditions. Furthermore,
141 determining the micro-habitat of benthic foraminifera is fundamental as it allows us to specify
142 the ecological requirements of each species. This work has used quantitative analysis based
143 primarily on the nature of foraminifera tests, whether calcitic, agglutinated or porcelaneous
144 (Fontanier, 2003).

145

146

147 **4. Results**

148

149 In this work the association of planktic foraminifera in the middle and upper Eocene
150 sediments reflects a considerable number of individuals (about 500 individuals), belonging to
151 around 25 species. This number of planktic foraminifera is relatively small compared to the
152 number of species of benthic foraminifera (see below). Major turnovers of planktic
153 foraminifera occur across the E/O boundary; the quantitative analysis revealed that planktic
154 foraminifera are very numerous but not very diversified (about 7 species). Furthermore, it
155 showed low diversity of benthic foraminifera (about 15 species) and represented by a
156 relatively small number of individuals (Fig. 2).

157 The planktic foraminifera are present in all samples of the middle Eocene to the lower
158 Oligocene succession interval and show a variation of the assemblage composition and
159 relative abundance. A faunal turnover occurred during the E/O transition interval and includes
160 major extinctions of some species such as the extinction of all species of the genus
161 *Hantkenina* and three species of *Turborotalia* (*T. cerroazulensis* Cole, *T. cocoaensis*
162 Cushman, *T. cunialensis* Toumarkine and Bolli). At the same time, species such as
163 *Pseudohastigerina micra* Cole, *P. naguewichiensis* Myatliuk, *Chilguembelina ototara* Finlay,
164 *Streptochilus martini* Pijpers, and *Tenuitella praegemma* Li dominate the assemblages.

165 Above the E/O boundary, there is a gradual decrease in the influence of pelagic realm
166 signaled by a decreased number of planktic foraminifera and a micro-faunistic undiversified
167 association announced by a low value of species richness, 10 to 15 species per sample.
168 According to Wade and Pearson (2008), a minor change in temperature can have an important

169 effect on planktic foraminifera as their niches are closely grouped together and depend on the
170 stratification of the water column.

171 Benthic foraminiferal species richness varies from 30 to 50 species per sample,
172 represented mainly by calcitic test species such as *Bolivinooides floridana* Cushman, *Brizalina*
173 *antegressa* Subbotina, *Globocassidulina subglobosa* Brady, *Cibicidoides mundulus* Brady,
174 Parker and Jones, *C. praemundulus* Berggren and Miller, *Oridorsalis umbonatus* Reuss and
175 *Gyroidina girardana* Reuss. Indeed, the extinction of only two species (*Nuttallides truempyi*
176 Nuttall and *Angulogerina muralis* Terquem) was observed across the E/O transition interval.

177 The dominance of the benthic foraminifera especially with the calcitic test, is recorded
178 throughout the section (Fig. 3), such as *B. floridana*, *Br. antegressa* Subbotina, *Gl.*
179 *Subglobosa* Brady, *C. mundulus* Brady, *C. praemundulus* Berggren and Miller, *O. umbonatus*
180 Reuss, *G. girardana* Reuss, *C. eocaenus* Gümbel, *C. mexicanus* Nuttall, and representative
181 species of tri-serial tests groups such as *Bulimina jarvisi* Cushman and Parker, *Bu. macilenta*
182 Cushman and Parker, *Bu. jacksonensis* Cushman, *Bu. thanetensis* Cushman and Parker and
183 *Bu. secaensis* Cushman and Stainforth.

184 On the other hand, the agglutinated test forms are less abundant (around 10%) and are
185 represented by the species *Reticulophragmium amplexens* Gzybowski, *Valvulina peruviana*
186 Cushman and Stainforth, *Rhadbamina samunica* Berry, *Ammodiscus* sp., *Karrierella* sp. The
187 Miliolidae with porcelaneous tests are represented mainly by Spiroloculinidae and are very
188 rare throughout the section.

189

190

191 5. Discussion

192

193 As foraminifera constitute the major protists in many marine ecosystems (Murray,
194 1991), we will discuss their role in the reconstruction of the paleoenvironment. Their potential
195 for fossilization makes them good indicators of the physicochemical conditions of deposition
196 environment where they were buried. Changes in relative abundances and diversity have been
197 used to infer changes in carbonate saturation state, oxygenation and food supply (Gooday,
198 2003).

199 The calcitic test assemblages found are typical of bathyal and abyssal environments;
200 generally, the Bolivinidae, Buliminidae, Uvigerinidae and Cibicidoidae genera require bathyal
201 environments (Holbourn et al., 2013). On the contrary, Gyroidinoidinae indicates an abyssal
202 domain. We also noticed the coexistence of several species such as *C. mexicanus* Nuttall, *Bu.*

203 *Jarvisi* Cushman and Parker, *C. grimsdalei* Nuttall, indicators of a low to median bathyal
204 environment (Holbourn et al., 2013) (Fig.3).

205 Furthermore, we identified cosmopolitan species which thrive in deep sea basins such as
206 *Nuttallides umboniferus* rarely found on the Oligocene sediment, *Epistominella exigua* which
207 was also rarely found on the Eocene and Oligocene sediment, and *Cibicidoides wuellerstorfi*
208 which are distributed all along the section (Jorissen et al., 2007). However, below the E/O
209 boundary we recorded the LO of the species *Nuttallides truempyi* which is proposed to reflect
210 fluctuations in organic matter flux to the seafloor (meso- to eutrophic) under oxygenated
211 bottom-water conditions. Indeed, it is one of the dominant lower bathyal-abyssal taxa with an
212 age range of Late Cretaceous (Maastrichtian) to latest Eocene, which was reported in Molina
213 et al. (2006), Berggren and Miller (1989) and Holbourn et al. (2013). *Angulogerina muralis*,
214 which refer to the Eocene (Ortiz and Thomas, 2006; Molina et al., 2006) was also found in
215 this section and we marked the LO close to the E/O which was also reported in the Fuente
216 Caldera section in Spain (Molina et al. 2006) (Fig. 3a).

217 The assemblages of small benthic foraminifera in Menzel Bou Zelfa and Jhaff sections
218 are very diverse. Species with calcitic test are significantly the most dominant and have a very
219 high frequency ranging from 85.63 to 100%. This percentage reflects sedimentation above the
220 CCD. The quantitative study of benthic foraminifera species immediately below the E/O
221 boundary (Fig. 4) shows the abundance of bathyal forms, the most important among them
222 being *Br. antegressa* (around 8%) and *B. floridana* (around 6%). Moreover, we cannot
223 exclude the presence of some foraminifera with calcitic test but typical of neritic environment
224 such as Lagenidae and Lenticulininae (around 0.1 to 0.7%). Their presence is interpreted as
225 the result of erosion of the shallow levels and thus transport from the platform to the bathyal
226 environment. On the other hand, we noticed the presence of some agglutinated forms mostly
227 represented by clavulinids, *Ammodiscus*, *Karrierella*, vulvulinids, and *Plectina* such as
228 *Cyclamina cancellata*, *Ammodiscus incertus* and *Reticulophragmium amplexans*, which
229 coincide with Alano section NE Italy (Agnini et al., 2011). These forms show relatively small
230 percentages (about 0.05%).

231 Approaching the E/O boundary, the abundance of these agglutinated forms shows a
232 slight increase, particularly of the species *Cyclamina cancellata*, which shows a maximum
233 value 0.68% (Tab. 1). This increase is negligible compared to percentages of forms of hyaline
234 tests that showed considerable ability to survive and thrive during the limit. While the
235 frequency of species with hyaline tests increased steadily up to the upper part of the O1 Zone
236 reaching a high frequency of around 98.3%.

237 This mixture of foraminifera, comprising 3 types of test, could be indicative of a
238 decrease in sea level and an increase in erosion that caused the transport of certain non-native
239 species from the platform to the bathyal domain. This decrease could be linked to the cooling
240 and global glaciation characterizing the E-O transition (Molina et al., 2006). Approaches
241 based on micro-organisms for the estimation of paleo-depth have been developed by
242 determining the index of oceanity which normally increases with depth (Bellier et al., 2010).
243 The density of planktic foraminifera is therefore maximal in open marine environments.
244 Moreover, we have also used some species of benthic foraminifera considered to be indicator
245 species for paleobathymetry (Nyong and Olsson, 1984; Van Morkhoven et al., 1986; Culver,
246 2003; Alegret and Thomas, 2004).

247 The index of oceanity shows values close to 80% (fig.5) at the base of the series,
248 decreasing to 40% at sample Jhaff 10. Indeed, the index marks some fluctuations in the last 30
249 m (from sample MBZ 26). The percentages of around 80% recorded at the base of the series
250 indicate sedimentation in nearby bathymetries 200 m and more precisely the upper bathyal
251 domain. This is confirmed by the presence of an association of planktic foraminifera typical
252 of the surface dwellings and intermediate environments (Molina et al., 2006) such as *T.*
253 *cunialensis*, *T. cocoaensis*, *Cr. inflata*, *H. alabamensis*, *S. linaperta*, *S. corpulenta*, *S. eocaena*
254 that showed a relative abundance at the base of this series (Fig. 5). However, it should be
255 noted that values below 80% indicating low bathymetries are probably related to a fall in the
256 number of planktic foraminifera and therefore the state of preservation of these
257 microorganisms. This reflects a disturbance of stratification of the water column caused by
258 the decline in sea level. Moreover, the upheaval in the behavior of foraminifera is essentially
259 due to the disappearance of the latest keeled forms and therefore a fall in the index of oceanity
260 at the E/O boundary. However, this change is followed by the development of typical forms
261 of deep dwellings such as *D. pseudovenezuelana*, *D. tripartita*, *C. unicavus*, *Gl. suteri*. At the
262 same time, we note that the assemblages of benthic foraminifera are dominated by the calcitic
263 test forms of the upper bathyal domain such as *B. floridana*, *Br. antegressa*, *Gl. subglobosa*,
264 *C. mundulus*, *O. umbonatus*.

265 The abundance of benthic forms is continuous throughout the series, causing the
266 decrease of the index of oceanity, showing the eustatic variation during the late Eocene and
267 the base of Oligocene. The relative fall of this index at the E/O boundary could indicate a
268 decrease in sea level, from the decline of the sea spawned during global cooling.

269 Foraminifera have a rapid adaptation to environmental changes, a potential for
270 fossilization and a strong correlation with the latitudinal distributions of surface temperatures,

271 and the use of approaches based on the morphology of their test could provide an estimation
272 of the paleotemperature and paleobathymetry (Murray, 1991). The change in the water
273 column structure is mainly due to the variation of the thermocline, which is defined as the
274 depth where we find the highest temperature transition. Even in the general case, the warm
275 surface waters or deep thermocline favors the establishment of shallow dwellings with warm
276 waters. However, the reduction in depth of the thermocline favors deep niches and forms that
277 thrive in cold waters (Wade and Pearson, 2008).

278 In the section of Menzel Bou Zelfa and Jhaff, planktic foraminifera present a well-
279 preserved test in all samples. At the base of the section, precisely in the E14, E15 biozones of
280 *Gl. semivoluta* and *Gl. index*, we notice a major faunal change in the history of the evolution
281 of planktic foraminifera, which involves paleoenvironmental implications in determining the
282 Bartonian/Priabonian boundary (Fig. 5). These changes are manifested by the absence of
283 keeled forms such as *Morozovelloides* and *Acarinina* that are abundant in low and middle
284 latitudes (Agnini et al., 2011). In fact, these forms normally record the low values of $\delta^{18}\text{O}$ and
285 the greatest values of $\delta^{13}\text{C}$ and are typical of warm waters (Pearson et al., 1993; Norris, 1996;
286 Pearson et al., 2001). The absence of these typical forms of surface water, with no disruption
287 of those living in deeper waters, generally reflects a drop in temperature or more precisely the
288 cooling of surface waters.

289 According to Wade (2004), the extinction of these keeled forms may result from the
290 destruction of their dwellings, due initially to sudden cooling of the thermocline. In addition,
291 the drop in temperature is accompanied mainly by a decrease in the depth of the thermocline.
292 These forms are therefore disturbed by the installation of a low temperature zone, meaning an
293 inability to adapt to these conditions caused their major extinction. This structural change in
294 the water column may also have impacts on the reproductive side of foraminifera, leading to a
295 gradually decreasing frequency. This change was followed by the invasion of the mixed level
296 by the genera *Hantkenina*, *Turborotalia* and *Subbotina* at the reduced level of the
297 thermocline, and thus the change in the depth of their niches (Wade, 2004).

298 This extinction can be associated with several factors including the main cause, which is
299 the inability of *acarininids* to overcome this temperature decrease. A small increase in the
300 number of keeled forms on the upper Eocene at samples (J6, J7, J8, J9, MBZ 26, MBZ27,
301 MBZ28, MBZ 29) could be explained by a particular abundance of the species: *T. cunialensis*,
302 *T. cocoaensis* *T. cerroazulensis*, *H. primitiva*, *H. compressa*.

303 The top of the Eocene, precisely the top of the E16 zone, is characterized by the last
304 appearance of five species of the genus *Hantkenina*, typical of surface dwellings; *H.*

305 *compressa*, *H. primitiva*, *H. nanggulanensis*, *H. alabamensis* and *Cribrohantkenina lazzarii*,
306 is associated with the extinction of *T. cerroazulensis* *T. cunialensis* and *T. cocoaensis*.
307 According to Coxall and Pearson (2007), these species require the establishment of a warm
308 climate with considerable oxygen levels, which explains their development during the Middle
309 to Upper Eocene. In addition, Molina et al. (2006) pointed out that these species would be
310 linked to a lower rate of $\delta^{18}\text{O}$ and a high rate of $\delta^{13}\text{C}$, belonging to the group of low and
311 middle latitudes reflecting a mixed level of warm water. Thus, the species which survived the
312 beginning of the cooling would subsequently be affected by this event.

313 From the boundary, this extinction of tropical and subtropical forms is followed by an
314 increase in the number of species belonging to the families Globigerinidae, Globoquadrinidae
315 and the species *T. ampliapertura*. However, at the base of the Oligocene the species *S.*
316 *corpulenta* and *S. eocaena* and the Globoquadrinidae *Dentoglobigerina galavisi*,
317 *Dentoglobigerina pseudovenezuelana* constantly increase in number. According to Wade and
318 Pearson (2008), these species show high values of $\delta^{18}\text{O}$ which reflect dwellings belonging to a
319 deep cold thermocline. It should be noted that *Catapsydrax unicavus* which appears on the
320 lower Eocene is one of the species that has shown a considerable abundance after the E/O
321 boundary and is considered a good indicator of deep, cold environments (sub thermocline)
322 (Pearson et al., 2001). Based on these data, some species are indicators of cold deep water.
323 These species have survived despite the crisis by adapting to the new way of life; the others
324 were not able to survive and underwent a major extinction.

325 However, we noticed the existence of a third group of foraminifera that was affected by
326 this crisis but was able to adapt to these conditions, these are the *Pseudohastigerina* group.
327 According to Wade and Pearson (2008), the species *Ps. naguewichiensis* is associated with
328 values depleted in $\delta^{18}\text{O}$, indicating that it has been calcified in the mixed levels. Indeed we
329 notice the existence of this species in the samples above the E/O boundary, but in the fractions
330 less than 150 μm , meaning it suffered an actual reduction in size. Furthermore, the species *Ps.*
331 *micra* has been able also adapt to these conditions using a different strategy. Indeed, they are
332 smaller than 150 μm and are considered *Pseudohastigerina cf. micra*.

333 In conclusion, we can note a remarkable dominance of globular forms during the late
334 Eocene to the Oligocene, adapting to the cold climate (Fig. 6). This can be explained by the
335 instability of the environment in the tropical zones caused mainly by the decrease in
336 temperature and thus the paleoecological changes of the foraminiferal habitat. These changes
337 would likely be in conjunction with the predominance of glaciation in the high latitudes and a
338 change in the circulation of deep waters (Wade and Pearson, 2008).

339 Due to their lifestyle, their ubiquity and richness in marine environments as well as their
340 potential fossilization, benthic foraminifera are good markers of paleo-depth due to their
341 ability to rapidly respond to environmental parameters. Based on the results obtained, it is
342 noted that the benthic foraminifera assemblages reflect the variations in their relative
343 abundances along the section, reacting to the cooling which starts at the upper Eocene. Below
344 the boundary, there is a dominance of infaunal species characterized by percentage around
345 80%, due particularly to the high frequency of Buliminids and Bolivinids. Their high
346 abundance could be related to a significant transfer of the organic matter to the bottom of the
347 sea as they proliferate in these environments (Molina et al., 2006; Alegret et al., 2008; Fenero
348 et al., 2012).

349 As we approach to the E/O boundary, we notice that the diversity of the assemblages
350 decline, reaching the lowest values. This decrease is partly due to a decline in relative
351 abundance of rectilinear species with complex apertures (Pleurostomella, Buliminidae, etc.)
352 (Thomas and Via, 2007; Bordiga et al., 2015). We noticed also a temporary decrease in
353 abundance of buliminids reaching 1.03 %, also reported by Miller et al. (1985), Thomas
354 (1992), and Coccioni and Galeotti (2003) in the Massignano section.

355 The presence of infauna increases after the boundary, reaching a maximum value of
356 about 89%. This abundance of infauna is due to the proliferation of the Bi and Tri-serial forms
357 (Fig. 6). Therefore, we interpret a high relative abundance of the infaunal, triserial buliminids
358 as indicative of a high food supply (Gooday, 2003; Bordiga et al., 2015). They are represented
359 mainly by small size forms and smooth test or lightly ornamented by longitudinal costae,
360 which generally explains a significant transfer of the potent supply to the bottom of the sea.
361 Indeed, two peaks (around 50%) of Bolivinidae are recorded during the upper Eocene and at
362 the E/O boundary. These peaks in fact correspond to an increase in the percentage of the
363 species *Br. antegressa* and *B. floridana*, which are representative of bathyal domain. We
364 suggest that this remarkable increase in the percentage of bolivinids is the response of benthic
365 foraminifera to a local increase in the flux of organic matter to the sea floor. In parallel with
366 the dominance of the infaunal group recorded throughout the section, we notice the presence
367 of some epifaunal species also characteristic of bathyal domain such as *C. eocaenus*, *C.*
368 *mexicanus*, *Planulina wuellerstorfi* and *Alabamina dissonata*.

369 This high influence of infaunal species typical of bathyal domains, markers of the
370 environments with minimum oxygen and an important flow of organic matter (Gooday, 2003)
371 such as *Bu. macilenta*, *Bu. jacksonensis*, *Bu. jarvisi*, *Br. antegressa*, *B. floridana*, *U. spinulosa*

372 and *Glo. subglobosa* associated with a small percentage of epifaunal foraminifera (about
373 20%), undoubtedly indicates a bathyal environment with eutrophic conditions.

374 The assemblages of the benthic foraminifera found are the result of an accumulation of
375 autochthonous and allochthonous forms, the latter being typical of neritic domains towards
376 the deeper levels such *L. inornata*, *La. sulcata*, *Si. tenuis*, as well as the distribution of the
377 organic substances in the bathyal zone. This mixture of forms could be related to the decrease
378 in sea level at the beginning of the Oi1 glaciation, facilitating the transport of this shallow
379 species towards deeper environments. The retreat of the sea is also accompanied by an
380 increase in detrital elements observed from the sample MBZ 12.

381 Small benthic foraminifera do not show an extinction event at the E/O boundary,
382 indicating that the benthic environment was not significantly affected. The extinction of *N.*
383 *truempyi* is similarly not recorded up to the boundary, although it was considered a marker for
384 the E/O boundary (Molina et al., 2006), possibly because the environment was not yet enough
385 deep for this species to live in the section studied.

386 In the basal Oligocene O1 Zone, the small benthic foraminifera shows an apparently
387 gradual pattern of extinction, which more likely could be a pattern of local disappearances
388 caused by the decrease in temperature and depth. This pattern was not previously reported
389 (Bolli et al., 1994; among others), although Hayward et al. (2010) suggested that it could be a
390 benthic faunal turnover after the rapid E-O cooling event. The maximum glacial conditions
391 occurred about 200 k.y. after the E/O boundary (Pearson et al., 2008). Consequently, this
392 pattern of extinctions or disappearances could be caused by the Oi1 glaciation.

393

394

395 **6. Conclusions**

396

397 The detailed micropaleontological study of the samples of the Menzel Bou Zelfa and
398 Jhaff section allowed us to establish different characteristics of the planktic and benthic
399 associations of foraminifera, which meant we could reconstruct the paleoenvironment and
400 highlight the global and regional eustatic changes.

401 The exploitation of all the micropaleontological data for planktic foraminifera led us to
402 establish a regional scale of biozonation which we used to highlight the biological events
403 recorded in the deposits of the E-O transition in accordance with the differential behavior of
404 planktic and benthic foraminifera. In the biostratigraphic paper, we were able to recognize in
405 the of Menzel Bou Zelfa and Jhaff section the following zones: E14. *Globigerinatheka*

406 *semiinvoluta*, E15. *Globigerinatheka index*, E16. *Hantkenina alabamensis* for the late Eocene
407 and zone O1. *Pseudohastigerina naguwichiensis* for the lower Oligocene.

408 Based on a quantitative analysis and paleoecological preferences for planktic and
409 benthic foraminifera, we have established a general paleoenvironment reconstruction during
410 the Eocene. From the base to the top of the Menzel Bou Zelfa and Jhaff section, these
411 analyses revealed that the associations of foraminifera are characteristic of a relatively warm
412 climate with considerable oxygen content during the middle to late Eocene, whereas at base of
413 Oligocene the data indicates a cooling of the climate.

414 The diversity of foraminifera reveals that the top of the Eocene is marked by a massive
415 extinction event of a distinctive group of planktic foraminifera, probably caused by the
416 decrease in temperature, bathymetry and reduction in depth of the thermocline. Nevertheless,
417 the small benthic foraminifera do not show an extinction event at the E/O boundary,
418 indicating that the benthic environment was not significantly affected. Similarly, the
419 extinction of *N. truempyi*, which is considered a marker for the E/O boundary, is recorded at
420 the boundary due to bathymetry.

421 In the basal Oligocene a clear dominance of infaunal morphotypes with calcitic test,
422 especially the bolivinids, indicates bathyal domains with cold-water, eutrophic seas and
423 oxygen minimum. In the basal Oligocene O1 Zone, the benthic environment is apparently
424 affected by a gradual extinction event that could be caused by the Oi1 glaciation. The small
425 benthic foraminifera show a gradual pattern of extinction, which more likely could be local
426 disappearances caused by the decrease in temperature and depth. Consequently, further
427 studies are necessary to confirm whether this pattern is a global extinction event or just a local
428 pattern of disappearances.

429

430

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432

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442

443

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445

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623
624

625 **Figure captions**

626

627 Figure 1: Geographical and geological location of the Menzel Bou Zelfa and Jhaff sections.

628 Figure 2: Planktic foraminiferal biostratigraphy and specific richness of foraminifera.

629 Figure 3a: Stratigraphic distribution of benthic foraminifera species.

630 Figure 3b: Stratigraphic distribution of benthic foraminifera species.

631 Figure 4a: Relative abundances of the most common benthic foraminifera species

632 Figure 4b: Relative abundances of the most common benthic foraminifera species

633 Figure 5: Relative abundance of muricate and globular taxa, calcareous, agglutinated and
634 porcelaneous taxa and the oceanity index.

635 Figure 6: Relative abundance of infaunal and epifaunal morphogroups.

636

637 **Plate captions**

638 Plate 1:

639 1-3: *Globigerinatheka semiinvoluta* KEIJZER. Zone E14. Sample MBZ30. 4-5:
 640 *Globigerinatheka index* FINLAY. Sample MBZ29. Zone E15. 6: *Globigerinatheka index*
 641 FINLAY. Sample MBZ29. Zone E15. 7: *Hantkenina alabamensis* CUSHMAN. Sample MBZ
 642 27. Zone E16. 8: *Cribohantkenina inflata* HOWE. Sample MBZ 27. Zone E16. 9:
 643 *Cribohantkenina lazzarii*. Sample Jhaff 8. Zone E16. 10: *Pseudohastigerina micra* COLE.
 644 Sample MBZ 12. Zone O1. 11: *Pseudohastigerina naguewichiensis* MYATLIUK. Sample
 645 MBZ 12. Zone O1. 12: *Streptochilus martini* PIJPERS. Sample MBZ 27. Zone E16.

646

647 Plate 2:

648 1-2: *Cibicidoides mexicanus* NUTTALL. Sample MBZ15. Zone O1. 3: *Pseudoglandulina*
 649 *manifesta* REUSS. Sample MBZ29. Zone E15. 4: *Gyroidina girardana* REUSS. Sample
 650 MBZ29. Zone E15. 5: *Lenticulina inornata* D'ORBIGNY. Sample J12. Zone O1. 6:
 651 *Cyclamina cancellata* BRADY. Sample MBZ14. Zone O1. 7: *Globocassidulina subglobosa*
 652 BRADY. Sample MBZ16. Zone O1. 8: *Planulina wuellerstorfi* SCHWAGER. Sample J12.
 653 Zone O1. 9: *Reticulophragmium amplexens* GRZYBOWSKI. Sample MBZ12. Zone O1. 10:
 654 *Pullenia quinqueloba* REUSS. Sample MBZ28. Zone E15. 11-12: *Oridorsalis umbonatus*
 655 REUSS Cole. Sample J12. Zone O1. 13: *Favulina squamosa* MONTAGU. Sample MBZ30.
 656 Zone E14. 14: *Plectina nuttalli* CUSHMAN & STAINFORTH. Sample MBZ11. Zone O1.
 657 15: *Plectina nuttalli* CUSHMAN & STAINFORTH. Sample MBZ11. Zone O1. 16:
 658 *Cassidulina caudriae* CUSHMAN & STAINFORTH. Sample MBZ13. Zone O1. 17:
 659 *Sigmoilina tenuis* CZJZEK. Sample J7. Zone E16. 18: *Clavulinoides eucarinatus* CUSHMAN
 660 & BERMUDEZ. Sample MBZ17. Zone O1. 19: *Coryphostoma midwayensis* CUSHMAN.
 661 Sample MBZ22. Zone O1. 20: *Bulimina macilenta* CUSHMAN & PARKER. Sample J12.
 662 Zone O1. 21: *Bulimina secaensis* CUSHMAN & STAINFORTH. Sample MBZ27. Zone E15.
 663 22: *Stilostomella subspinosa* CUSHMAN. Sample MBZ22. Zone O1. 23: *Stilostomella*
 664 *paleocenica* CUSHMAN & TODD. Sample MBZ19. Zone O1. 24: *Brizalina antegressa*
 665 SUBBOTINA. Sample MBZ24. Zone O1. 25: *Entosolenia flintiana* CUSHMAN. Sample J8.
 666 Zone E16.

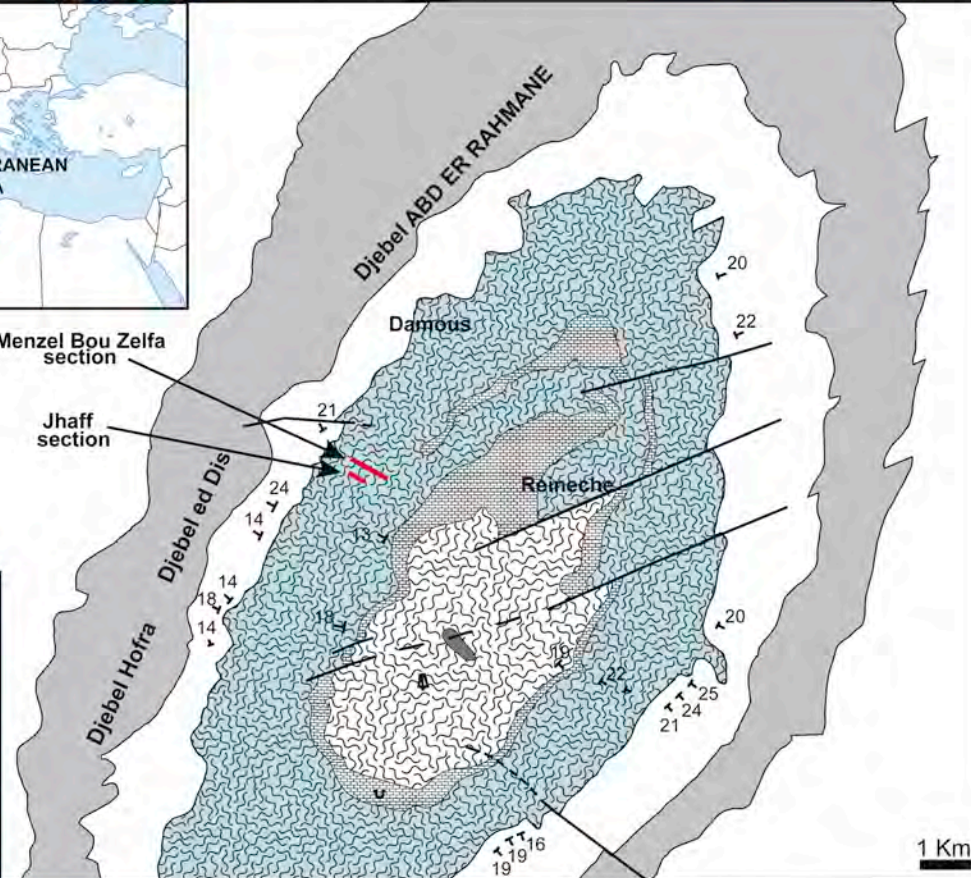
667

668 **Tablescaption**

669

670 Table 1: Percentages of small benthic foraminifera.

	<i>Uvigerina pigmea</i>	<i>Bulimina macilentata</i>	<i>Ramulina pulchra</i>	<i>Lagena perlucida</i>	<i>Bulimina jacksonensis</i>	<i>Osangularia mexicana</i>	<i>Sigmoilina tenuis</i>	<i>Anomatina subbadensis</i>	<i>Chrysalogonium elongatum</i>	<i>Marginulinopsis aff. tuberculata</i>	<i>Dentalina eocaena</i>	<i>Lagena striata</i>	<i>Spiroplectamina nuttalli</i>	<i>Stilostomella nuttalli</i>	<i>Stilostomella subspinosa</i>
MBZ1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MBZ2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MBZ3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MBZ4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MBZ5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MBZ6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MBZ7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MBZ8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MBZ9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MBZ10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MBZ11	0	0,95	0	0	1,71	0	0	0	0	0	0	0	0	0	1,14
MBZ12	0	0,84	0	0	0,25	0	0,08	0	0	0	0	0	0	0,08	1,09
MBZ13	0	0,00	0	0	0	0,35	0,53	0	0	0	0	0	0	0	0,35
MBZ14	0	1,58	0	0	0,39	0	1,18	0	1,18	0	0	0	0	0	0,39
MBZ15	0	0,00	0,11	0	0,11	0,11	0,11	0	0,22	0	0	0	0	0	1,02
MBZ16	0	0,00	0	0	0	0	0	0	0	0	0	0	0	0,48	2,42
MBZ17	0	0,84	0	0	0,55	0	0,27	0,27	0,83	0	1,4	0,55	0	0,27	2,23
MBZ18	0	0,34	0	0	2,72	0	2,041	0	1,02	0	0	0	0	0	0,34
MBZ19	0	0,18	0	0	0,73	0	0,37	0	0	0	0,74	0	1,1	0,92	1,29
MBZ21	0	0,77	0	0	1,27	0	1,27	0	0	0	0	0	1,02	1,53	4,34
MBZ22	0	0,64	0	0	0	0	0,64	0	0,32	0	0,32	0	0,64	1,92	4,5
MBZ23	0	0,00	0	0	1,93	0	0,32	0	0	0	0	0	0	0	7,09
MBZ24	0	0,00	0	0	0,77	0	1,16	0	0,38	0	1,56	0	0	0	8,17
MBZ25	0	0,00	0	0	1,53	0	2,15	0	0,61	0	0	0	0	4	0
Jhaff13	0	0,31	0	0	0	0	0,18	0	0	0	0	0	0	0	0,81
Jhaff12	0	0,45	0	0	0,19	0	0,64	0	0	0,06	0	0,13	0	0	1,23
Jhaff10	0	0,11	0	0	0,44	0	0,11	0	0	0	0	0	0	0	2,78
Jhaff9	0	1,57	0	0	0	0	0,31	0	0	0,09	0	0,09	0	0	2,02
Jhaff8	0	0,83	0	0	0,05	0	0,16	0	0	0	0	0,22	0,05	0	0,88
Jhaff7	0	1,87	0	0	0,62	0	0,67	0	0	0	0	0,41	1,19	0	2,08
Jhaff6	0	0,00	0	0	1,19	0	0,25	0	0,15	0,05	0	0	0,25	0	0
MBZ26	0	0,27	0,27	0,82	0,41	0	1,09	0	0	0,13	0	0,27	0	0	1,09
MBZ27	0	0,64	0	0	0,85	0,85	0	0	0,21	0	0	0	0	0	0
MBZ28	0	0,00	0,17	0	1,24	0,35	0,17	0	0,35	0	0,36	0	0	0	0
MBZ29	0,3	0,30	0	0	1,36	0	0	0	0,45	0	0	0	0	0	0
MBZ30	1,61	0,32	0,32	0,32	1,29	0,32	0,32	1,29	0,96	0,32	0,65	0,32	0,64	0,96	3,87



Quaternary
Crust and crusting

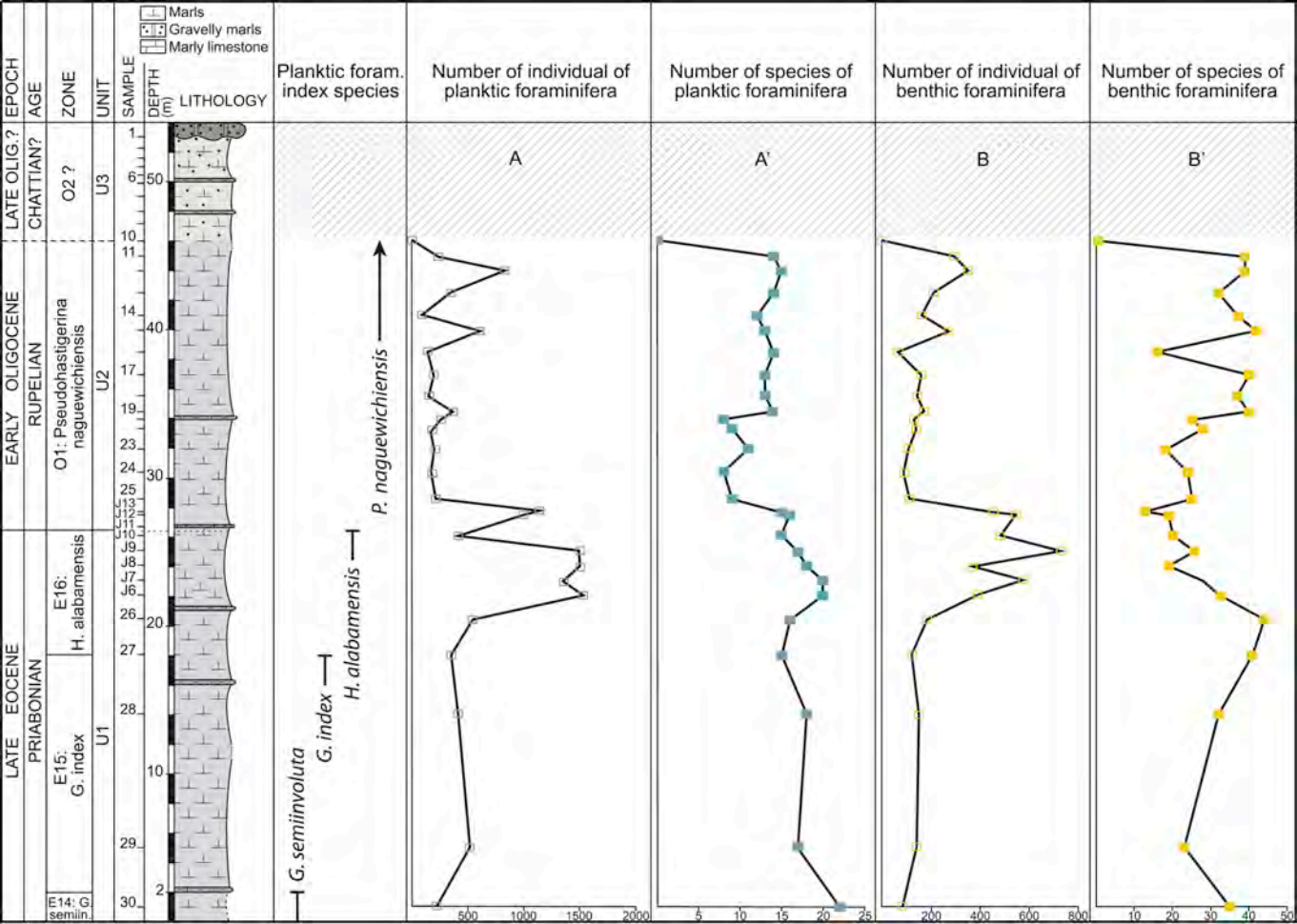
Aquitanian-Burdigalian
Haouaria unit

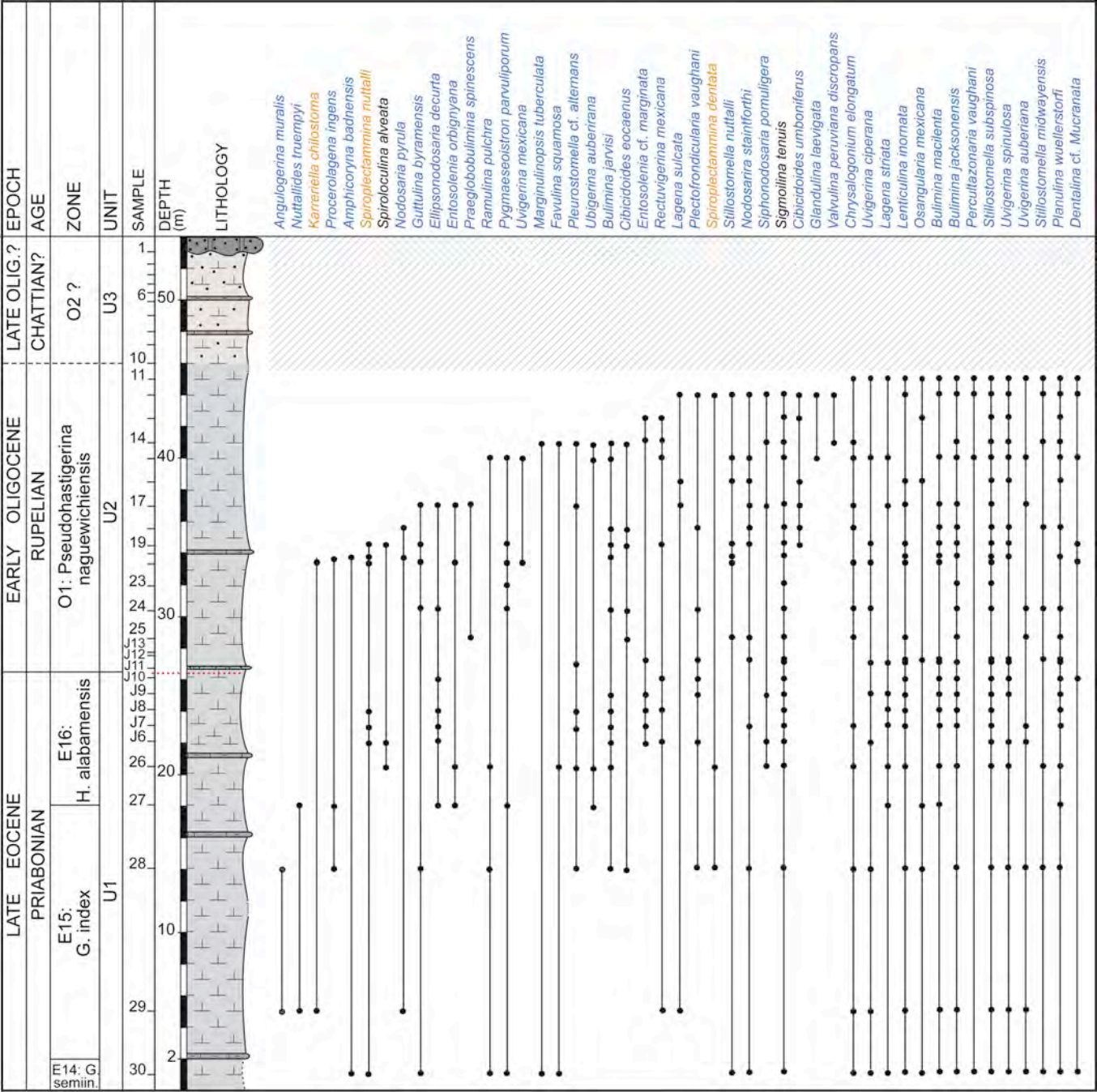
Oligocene
Sandstone: Korboous
Unit

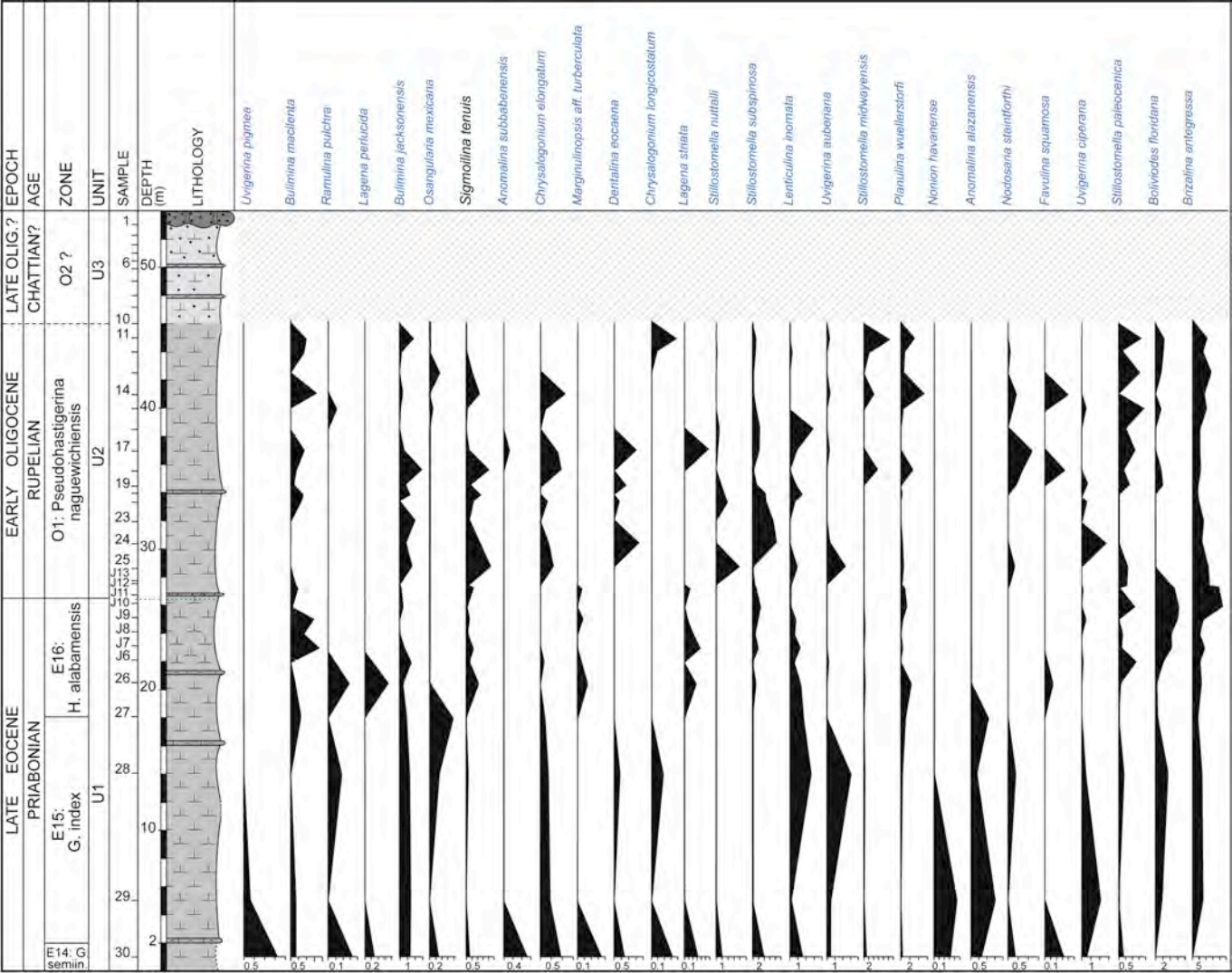
Late Lutetian
Early Clay

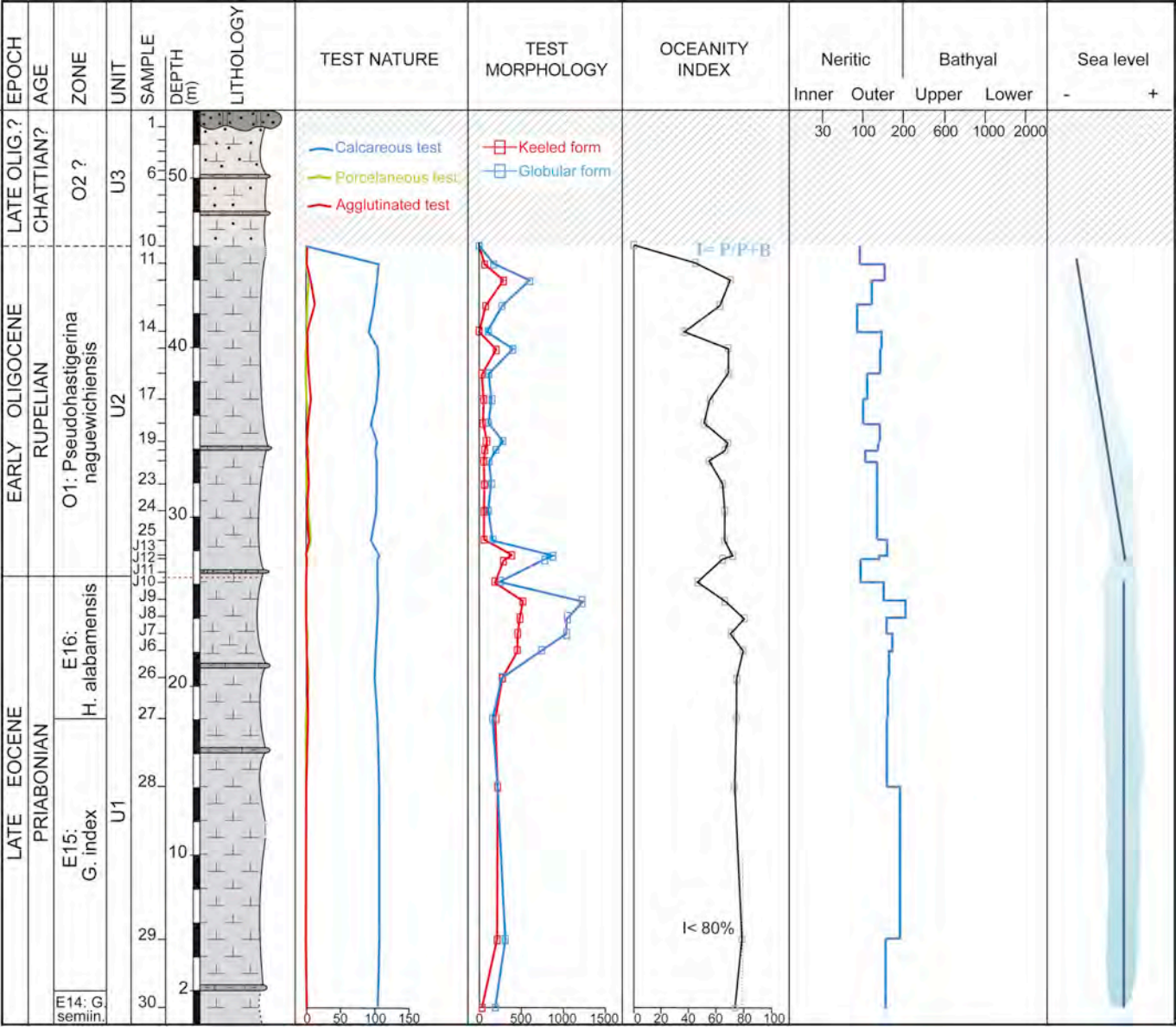
Late Lutetian
Reineche limestone

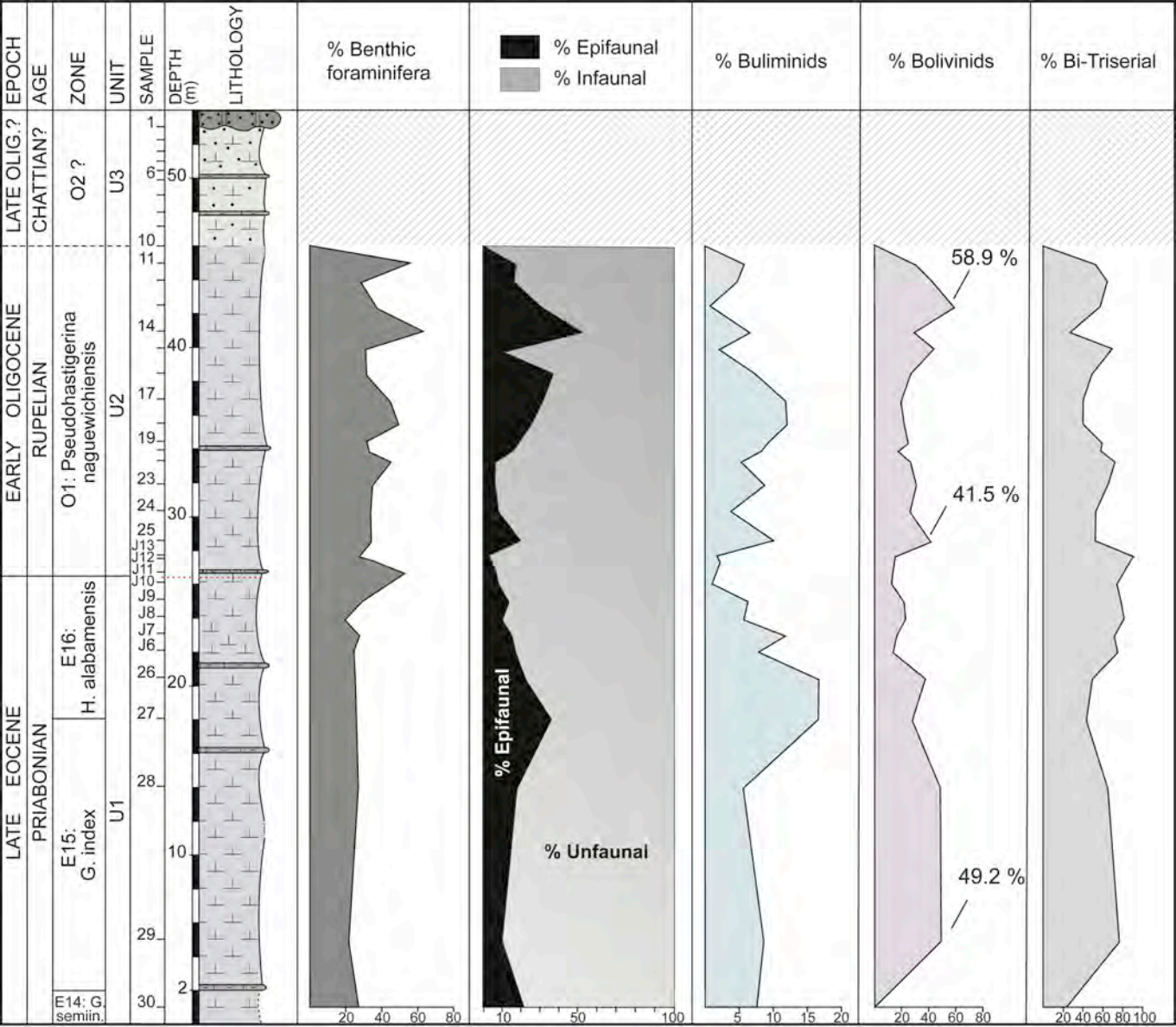
Late Lutetian-
Priabonian
Clay and marl

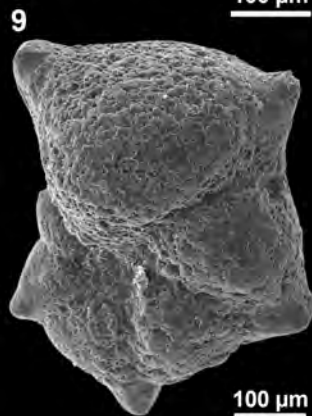
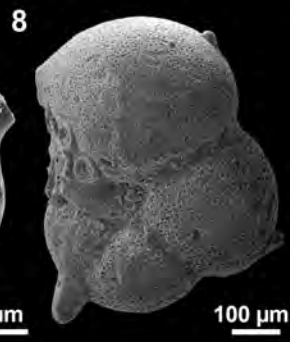
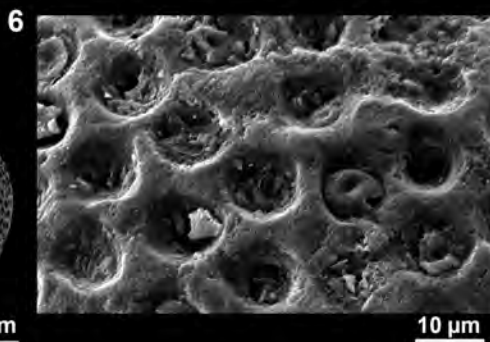
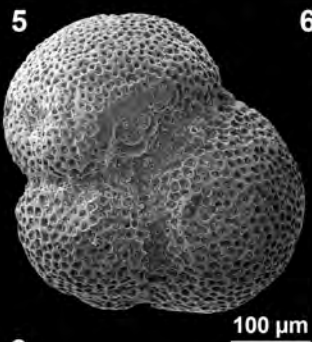
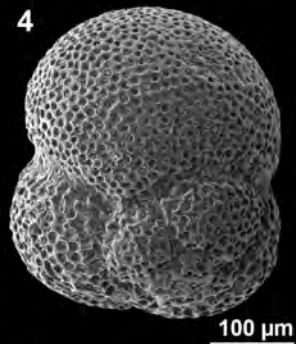
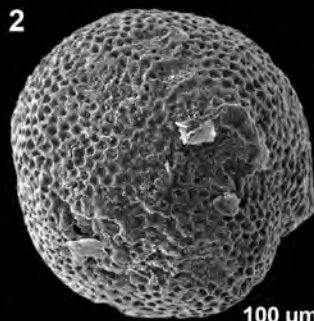
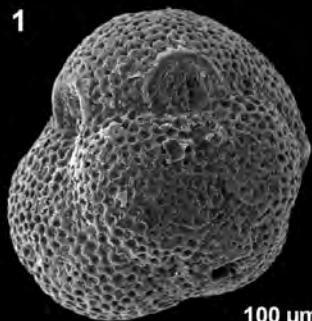


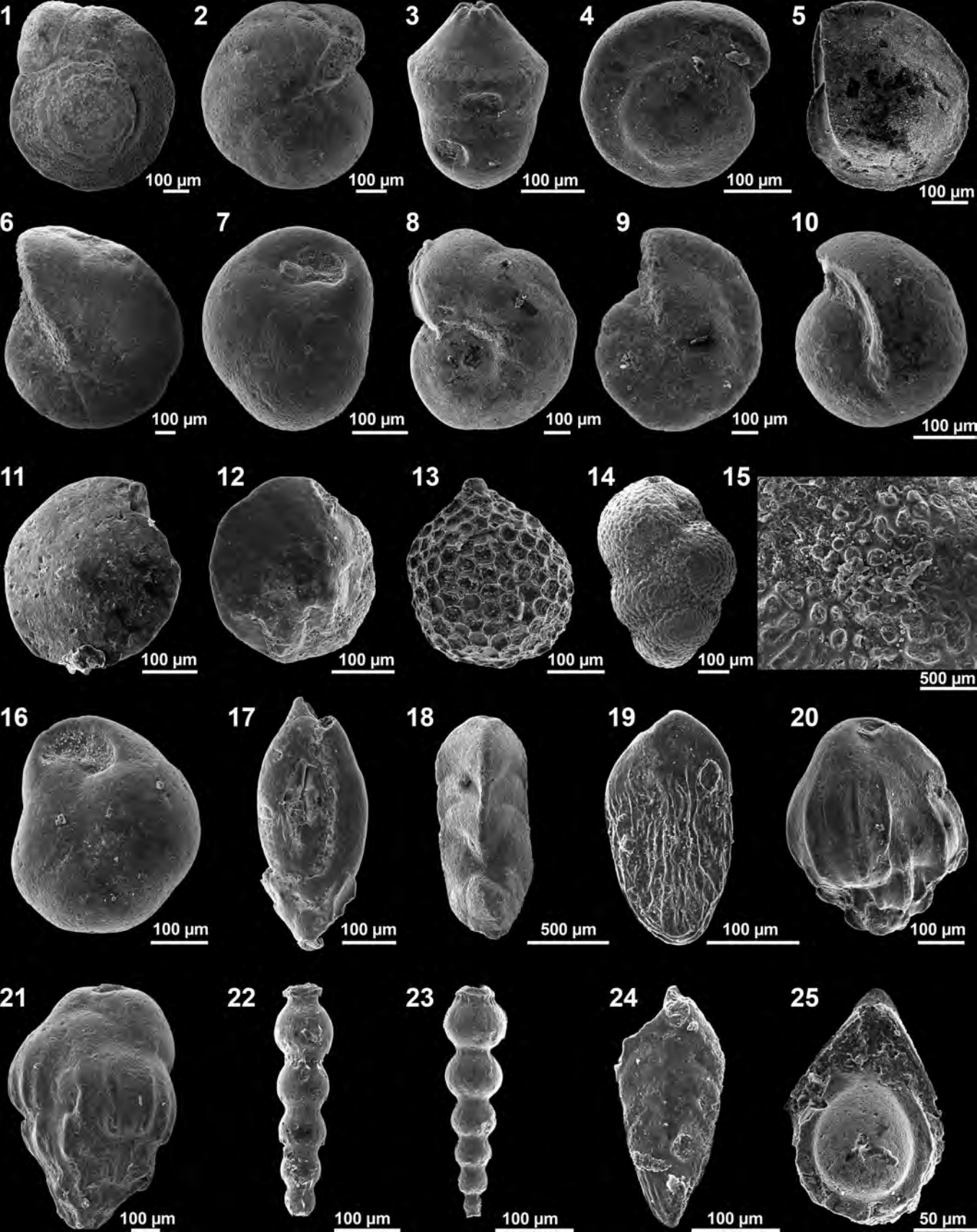












Highlights

Paleoenvironmental and ecological changes at E14, E15, E16, O1 Zones are identified.

Planktic foraminifera had an extinction event at the E/O boundary reflecting a surface cooling.

Small benthic foraminifera did not suffer an extinction event at the E/O boundary.

The benthic environment was not significantly affected at the E/O boundary.

At the basal Oligocene benthic foraminifera were affected by the Oi1 glaciation.