

1 **Paleoceanographic inferences from benthic foraminifera across the early Aptian Ocean Anoxic**
2 **Event 1a in the western Tethys**

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16 paleoceanography.

17
18 **Abstract**

19 The paleoenvironmental impact of the early Aptian Ocean Anoxic Event 1a (OAE 1a, ca. 121
20 Ma) has been investigated in detail in the Cismon Core (Lombardy Basin, western Tethys) by using
21 different geochemical and micropaleontological proxies. We provide the first high-resolution data of
22 benthic foraminiferal assemblages through the upper Barremian - lower upper Aptian stratigraphic
23 interval. Benthic foraminifera data are integrated with calcareous nannofossil and planktonic
24 foraminifera records to create a comprehensive characterization of bottom and surface waters across

25 OAE 1a. Benthic foraminiferal communities are indicative of a marked change in bottom-waters
26 around the “nannoconid decline” (latest Barremian) due to increased flux of organic matter to the
27 seafloor and intermittent dysoxic conditions probably promoted by pulses of higher productivity during
28 the initial Greater Ontong Java Event (GOJE). Benthic foraminifera experienced a marked crisis in
29 abundance (“benthic foraminiferal crisis” BFC) ca. 35 kyr before the OAE 1a, in correspondence with
30 the “nannoconid crisis” and the onset of the most intense GOJE phase. The literature survey shows that
31 the BFC is commonly recorded before the OAE 1a onset in several stratigraphic sections worldwide,
32 and therefore, it is here proposed as a global event. At Cismon, deep-water anoxia was reached at the
33 OAE 1a onset and lasted for ca. 300 kyr, promoted by higher productivity and eventually enhanced
34 water stratification during the super-greenhouse climate. The continuation of OAE 1a was marked by a
35 benthic foraminiferal repopulation event, probably resulting from the influx of relatively cooler and
36 oxygenated waters. In turn, the OAE 1a was marked by intermittent anoxic to dysoxic conditions,
37 likely in response to primary productivity sustained by N-fixing bacteria. The distribution and
38 abundance of benthic foraminifera documented in other sections across the Selli Level equivalent show
39 different features that point to local factors such as paleodepth and increased runoff. The post-OAE 1a
40 was characterized by dysoxic conditions coupled with moderate organic matter flux to the seafloor. At
41 the Cismon site and worldwide, the termination of OAE 1a coincided with the return of relatively more
42 abundant benthic taxa in response to the restoration of favorable conditions allowing the development
43 of diversified benthic foraminiferal communities.

44

45 **1. Introduction**

46 The Cretaceous was punctuated by episodes of widespread deposition of organic-rich sediments
47 (black shales) in the oceans and epicontinental seas, named Oceanic Anoxic Events (OAEs; Schlanger
48 and Jenkyns, 1976), representing major alterations in the global carbon budget (Jenkyns, 2010). The

49 early Aptian OAE 1a (ca. 120.7 Ma, Malinverno et al., 2012) coincided with global paleoclimatic and
50 paleoenvironmental perturbation that lasted for ca. 1.1 Myr (Malinverno et al., 2010) and probably
51 triggered by volcanogenic CO₂ emissions associated with the Greater Ontong Java Event (GOJE, e.g.,
52 Larson, 1991; Erba, 1994; Bralower et al., 1994; Larson and Erba, 1999; Jones and Jenkyns, 2001;
53 Leckie et al., 2002; Jenkyns, 2003; Méhay et al., 2009; Tejada et al., 2009; Bottini et al., 2012, 2015;
54 Erba et al., 2015; Naafs et al., 2016; Percival et al., 2021). The release of methane hydrates has been
55 proposed as an additional source of ¹²C-enriched carbon (Beerling et al., 2002; van Breugel et al., 2007;
56 Méhay et al., 2009; Malinverno et al., 2010; Adloff et al., 2019), which possibly further contributed to
57 the negative carbon isotope anomaly at the OAE 1a onset (e.g., Weissert, 1989; Weissert and Lini,
58 1991; Jenkyns, 1995; Bralower et al., 1999; Erba et al., 1999, 2015; Luciani et al., 2001; Price, 2003;
59 Ando et al., 2008; Méhay et al., 2009; Malkoç et al., 2010; Stein et al., 2011; Bottini et al., 2012, 2015;
60 Lübke and Mutterlose, 2016; Frau et al., 2018). The positive excursion that follows the negative shift
61 has been associated with an enhanced burial of organic carbon in marine sediments, either after
62 increased surface-water productivity or preservation of organic matter (e.g., Arthur et al., 1987, 1988;
63 Schlanger et al., 1987; Jenkyns, 2010; Robinson et al., 2017). These conditions led to the deposition of
64 marine carbon-rich sediments (primarily black shales) known as the Selli Level in the Tethys (Coccioni
65 et al., 1989), Niveau Goguel in France (Bréhéret, 1988) and Fischschiefer in the Lower Saxony Basin
66 (Mutterlose and Böckel, 1998). To date, there is a comprehensive characterization of surface-water
67 conditions during OAE 1a in the western Tethys (Premoli-Silva et al., 1999; Erba, 2004; Erba et al.,
68 2019 and references therein), and there is a general understanding of bottom-water evolution across
69 OAE 1a, including oxygenation and organic carbon flux (e.g., Kuypers et al., 2004; Pancost et al.,
70 2004). In this regard, some indications are provided by benthic foraminifera, which are controlled by
71 oxygen and food availability in bottom-waters (e.g., Sliter and Barker, 1972; Nyong and Olsson, 1984;
72 van Morkhoven et al., 1986). In particular, studies on Tethyan sites (Cobianchi et al., 1999; Coccioni et

73 al., 2006; Michalík et al., 2008; Patruno et al., 2015; Józsa et al., 2016) and sections worldwide
74 (Elkhazri et al., 2013; Bargaen and Lehmann, 2014; Zorina et al., 2017) are suggestive of a decrease in
75 benthic foraminifera abundance before OAE 1a. Several locations show scarce or absent benthic
76 specimens during OAE 1a, possibly, in response to a major paleoenvironmental perturbation at the
77 seafloor (Mutterlose and Böckel, 1998; Cobianchi et al., 1999; von Bargaen and Lehmann, 2014).
78 However, the relatively low sampling resolution adopted in these studies and/or the absence of a
79 continuous benthic foraminiferal record through OAE 1a hamper a comprehensive characterization of
80 the benthic foraminiferal response to OAE 1a. This is also verified in the Selli Level in the proposed
81 stratotype in the Umbria-Marche Basin (Gorgo a Cerbara section, central Italy), which lacks benthic
82 foraminifera (Patruno et al., 2015). Conversely, the Selli Level of the Cismon Core (Lombardy Basin,
83 western Tethys, Italy) contains benthic foraminifera and, therefore, is ideal for your investigation
84 through OAE 1a.

85 In this work, we performed a high-resolution investigation of the upper Barremian to lower upper
86 Aptian stratigraphic interval of the Cismon Core, intending to (a) reconstruct the changes in the
87 bottom-water oxygen conditions and organic carbon fluxes; (b) infer the paleobathymetry of the upper
88 Barremian-lower upper Aptian sedimentary sequence of the Cismon Core; (c) assess the impact of the
89 paleoceanographic perturbation associated with OAE 1a on the benthic foraminiferal communities; (d)
90 integrate the benthic foraminiferal record with the calcareous nannofossil and planktonic foraminiferal
91 datasets to produce a model of bottom- to surface-water changes across the OAE 1a in the Belluno
92 Basin; and (e) compare the benthic foraminiferal assemblages of the Cismon Core with the records
93 previously published from other localities to provide a comprehensive model of local vs. global
94 paleoenvironmental perturbations across OAE 1a.

95

96 **2. Geological setting and lithology**

97 The Cismon Core was drilled in the Venetian Prealps (Southern Alps, NE Italy; Fig. 1), west of
98 Feltre (Belluno Basin), along the Passo Rolle road at km 52.6 (46°02'43.46" N; 11°45'46.85" E; 398 m
99 altitude). The studied interval covers 38.75 m and is represented by the Biancone Formation (upper
100 Barremian to lowermost Aptian) and the Scaglia Variegata Formation (lower to upper Aptian).
101 Lithostratigraphically, the Biancone Formation, a local equivalent of the Maiolica Limestone, consists
102 of dominant limestones with intercalated black shales, and radiolarian-rich layers. The Scaglia
103 Variegata Formation is characterized by marlstones, marly limestones, black shales and radiolarian
104 beds (e.g., Erba and Larson, 1998; Erba et al., 1999).

105 The Selli Level equivalent corresponds to the OAE 1a in the Cismon Core and is found in the
106 Scaglia Variegata Formation between 23.67 and 18.77 m (Fig. 2). The Selli Level is lithologically
107 subdivided into three intervals: i) the lower interval (23.67 – 22.36 m) is constituted by marlstones with
108 frequent black shales and a few discrete radiolarian beds; ii) a middle interval (22.36 – 20.41 m)
109 consisting of limy marlstones with rare black shales and radiolarian beds; and iii) an upper interval
110 (20.41 – 18.77 m) characterized by alternating marlstones, common radiolarian beds and black shales
111 (Erba et al., 1999; Premoli-Silva et al., 1999). A negative $\delta^{13}\text{C}_{\text{carb}}$ shift (1 ‰) in the carbonate fraction
112 characterizes the base of the Selli Level and is followed by a complex $\delta^{13}\text{C}_{\text{carb}}$ excursion (Menegatti et
113 al., 1998; Erba et al., 1999; Bottini et al., 2015).

114 The sedimentary sequence was deposited on the Tethys southern margin (Fig. 1), on the eastward
115 deepening slope between the Trento Plateau and the Belluno Basin, at an estimated paleo-depth of
116 1000–1500 m during the Early Cretaceous (Weissert and Lini, 1991; Erba and Larson, 1998; Bernoulli
117 and Jenkyns, 2009; Erba et al., 2010).

118

119 **3. Materials and methods**

120 A total of 159 samples were studied for benthic foraminifera in the interval from 46.75 m to 8.00
121 m (Fig. 2), dated as the latest Barremian to early late Aptian (Erba et al., 1999). The benthic
122 foraminiferal studied samples are the same as those investigated by Premoli Silva et al. (1999) and
123 Barchetta (2015) for planktonic foraminifera. The sampling resolution varies from 5 to 50 cm in the
124 interval from 8 m to 31.29 m and from 12 to 170 cm in the lower part (31.29 m – 46.75 m). The studied
125 samples include different lithologies such as marly layers, radiolarian beds, marly limestones, and
126 black shales. Following the results of Premoli Silva et al. (1999), the radiolarian beds often contain
127 well preserved and relatively abundant planktonic and benthic foraminifera specimens, whereas the
128 marly layers and black shales may have rare and poorly preserved specimens.

129 Originally, samples were prepared using two methods according to the lithology (Premoli Silva et
130 al., 1999). Softer sediments were soaked in hydrogen peroxide for a few hours and then sieved through
131 a 45- μ m mesh-size to get foraminifera, while hard-siliceous samples were soaked in a 10%
132 hydrochloric solution and sieved through a 63- μ m mesh-size to extract radiolaria (Premoli Silva et al.,
133 1999; Barchetta, 2015). The whole residues of the size-fraction > 63- μ m were analyzed, and all benthic
134 foraminifera were picked in each sample. Subsequently, all specimens were identified at genus and
135 species level, counted, and stored in Plummer slides. Thin sections studied by Premoli Silva et al.
136 (1999) and Barchetta (2015) were not investigated in this work because benthic foraminifera are too
137 small to be confidently identified at species and genus level.

138 Absolute abundances of benthic foraminifera were calculated after weighing the washed residues,
139 and the results are reported as Benthic Foraminiferal Number (BFN), corresponding to the number of
140 individuals per gram of washed residue (n/g) in each sample. Species richness (S), Dominance (D), and
141 Shannon diversity (Hs; Shannon and Weaver, 1949) were calculated for each sample using the PAST
142 software (Hammer et al., 2001). A confidence interval (CI: 95%) based on the Clopper-Pearson method
143 (e.g., Suchéras-Marx et al., 2019) was applied to the benthic foraminiferal assemblages using the PAST

144 software (Hammer et al., 2001). This method assesses the statistical reliability of the analyzed data to
145 give a credible interpretation when the populations are variable. If the relative abundance is low, the CI
146 is wider, whereas high relative abundance values display a narrower CI (Fig. 2).

147 Benthic foraminifera were identified at the species level when possible, following the taxonomy
148 by Ellis and Messina (1940-2015), Mjatluk (1988), Weidich (1990), Meyn and Vespermann (1994),
149 Holbourn and Kaminski (1997), and Patruno et al. (2015). The most common taxa identified in the
150 Cismon Core were photographed using the Scanning Electron Microscopy (Jeol JSM-IT500) at the
151 Department of Earth Sciences of the Università degli Studi di Milano. Benthic foraminiferal taxa were
152 subdivided into two different morphogroups according to their life preferences: infauna and epifauna
153 (e.g., Koutsoukos, 1989; Murray and Alve 1999; Jorissen et al., 2007). A third group called epifauna–
154 infauna is here distinguished and includes opportunistic benthic foraminifera taxa adapted to variable
155 ecological niches and changing environmental conditions. We adopted the benthic foraminifera
156 paleobathymetric subdivision proposed by Nyong and Olsson (1984) and van Morkhoven et al. (1986)
157 as follows: inner-neritic (IN: 0 – 50 m), middle-neritic (MN: 50 – 100 m), outer-neritic (ON: 100 – 200
158 m), upper bathyal (UB: 200 – 500 m), middle bathyal (MB: 500 – 1000 m), and lower bathyal (LB:
159 1000 – 2000 m).

160 Planktonic foraminiferal absolute abundance data and species richness are here revised after
161 Premoli Silva et al. (1999) and Barchetta (2015). Absolute abundances in the washed residues (PFNwr)
162 were calculated as the number of individuals per gram of washed residue (n/g), whereas absolute
163 abundances in thin sections (PFNts) were obtained by counting the individuals in 40 fields of view
164 randomly chosen using a 125X magnification and corresponding to a total area of 80.4 mm².
165 Specimens analyzed in the washed residues are subdivided into morphogroups, according to the main
166 morphologies as follows: planispiral (genus *Globigerinelloides*, including species with globular and
167 radially elongate chambers; Verga and Premoli Silva, 2003a, 2003b, 2005), pseudo-planispiral (genus

168 *Leupoldina* characterized by possessing radially elongate chambers ending with close, bulb-shaped
169 extensions; Verga and Premoli Silva, 2002) and trochospiral taxa (genera *Hedbergella*, *Lilliputianella*,
170 *Gorbachikella* and *Gubkinella* characterized by having globular to radially elongate chambers; see
171 Huber et al., 2016 and references therein).

172

173 **4. Results**

174 **4.1 Benthic foraminiferal abundance and diversity**

175 A total of 73 taxa (29 genera and 44 species) of benthic foraminifera were identified in the upper
176 Barremian – upper Aptian interval of the Cismon Core (Supplementary Table S1). The BFN ranges
177 from 1/g to 323/g, with an exception in sample 44.53 m that contains 1359/g (Fig. 2). Samples
178 comprised between the base of the studied interval (46.75 m) and the base of the Selli Level (23.67 m)
179 show an average BFN of 67/g. Within the Selli Level, the interval between 23.67 m and 21.89 m is
180 barren of benthic foraminifera, while the overlaying interval of the Selli Level from 21.77 m to 18.83 m
181 shows an average BFN of 3/g. The BFN above the Selli Level (18.43 to 8.20 m) is relatively low, with
182 an average value of 12/g. The S fluctuates between 1 taxon in most samples and a maximum of 26 taxa
183 in sample 15.98 m. The average S value in the studied section is 4 taxa (Fig. 2). The D ranges from
184 0.12 to 1 (Fig. 2): low values were mainly recorded in the upper Barremian (from 46.75 m to 32.30 m).
185 Higher values are characteristic of the lower Aptian interval (below the Selli Level, from 27.19 m to
186 24.33 m), and the samples from above the barren interval, until the top of the studied stratigraphic
187 section (from 21.77 m to 8.87 m). The H_s shows values from 0 to 2.2 (Fig. 2): most samples display
188 low values, especially in the lower Aptian below the Selli Level (from 29.06 m to 23.66 m) and above
189 the barren interval till the top of the studied stratigraphic section (from 21.77 m to 8.87 m).

190 Agglutinated foraminifera (AF) are recorded in 82% of the studied samples and constitute the
191 most abundant group, varying from 1/g to 1365/g in abundance. Higher abundance values are detected

192 in the upper Barremian (from 46.75 m to 39.65 m), with a peak in sample 44.53 m containing 1365/g.
193 Lower abundances of AF are observed from 21.77 m to the top of the studied interval. The calcareous
194 benthic foraminifera (CF) are present in 66% of the samples, although with a limited abundance of 1/g
195 (in most samples) to 55/g in sample 21.46 m. The relative abundance of CF ranges from 0.6% (35.02
196 m) to 100% in most of the Selli Level samples (above the barren interval; Fig. 2).

197 The epifaunal morphogroup fluctuates from 1/g (16.44 m) to 704/g (44.53 m) and its relative
198 abundance varies from 3.9% (30.63 m) to 100% (in samples 27.34 m, 26.07 m, 25.65 m, 25.25 m,
199 24.64 m, 24.33 m, 11.02 m, 10.76 m). This morphogroup shows the highest abundances (up to 800/g)
200 from 46.75 m to 24.12 m. A decrease in abundance of the epifaunal morphogroup is recorded in sample
201 21.77 m, and the average abundance decreases toward the top of the studied interval. The exception is a
202 peak value of 123/g at 15.98 m (Fig. 2). The infaunal morphogroup ranges from 1/g (16.44 m) to 133/g
203 (26.59 m) and is more abundant in the upper Barremian and lowermost Aptian interval (mean value:
204 16/g). Above the Selli Level, the infaunal morphogroup displays very low abundances, reaching a
205 maximum value of 8/g (Fig. 2). The relative abundance of the infaunal morphogroup ranges from 1.2%
206 (15.98 m) to 100%, the latter abundance being observed in samples 28.85 m, 24.99 m, 20.53 m, 19.68
207 m, 19.01 m, 18.83 m, 9.72 m, and 9.31 m.

208 The opportunistic taxa included within the epifauna-infauna group fluctuate from 1/g (16.44 m)
209 to 583/g (44.53 m). An increase in abundance (up to 583/g) of this group is recorded in the upper
210 Barremian (44.53 m, 43.92 m, 43.41 m) and lower Aptian (15.98 m) interval. The relative abundance
211 of this group ranges from 3.1% (30.85 m) to 100% (in samples 20.47 m, 20.27 m, 19.53 m, 17.08 m,
212 18.86 m, 14.39 m; Fig. 2).

213 Six benthic foraminiferal intervals (BFI) were identified according to the variations in BFN, D,
214 and H_S (Fig. 2). From the base to the top, the BFIs are described as follows:

- 215 • BFI-I (46.75 m – 42.48 m) is characterized by moderate to high BFN and moderate H_S and D.

- 216 • BFI-II (42.48 m – 30.85 m) shows lower BFN, contains a few barren samples, and displays
217 intermediate Hs and low D.
- 218 • BFI-III (30.85 m – 24.12 m) displays slightly higher BFN, intermediate Hs, and higher D.
- 219 • BFI-IV (24.12 – 21.77 m) is characterized by a marked decrease in BFN and Hs, but relatively high
220 D just below the base of the Selli Level, while benthic foraminifera are absent in the Selli Level.
- 221 • BFI-V (21.77 m – 18.77 m) shows low BFN with intercalated barren samples, low Hs, and high D.
- 222 • BFI-VI (18.77 m – 8.20 m) shows intermediate BFN with few barren samples and is characterized
223 by moderate Hs and intermediate to high D.

224

225 **4.2 Composition of the benthic foraminiferal assemblages**

226 Agglutinated and calcareous benthic foraminifera, recorded in the Cismon Core (Figs. 2, 3, and
227 4), were grouped according to their paleoecological affinities and abundances (Fig. 5 and Table 1).

228

229 **4.2.1 Agglutinated benthic foraminifera (AF)**

230 Two genera of agglutinated foraminifera are dominant in the Cismon Core (Fig. 5), *Rhizammina*
231 and *Verneuilinoides*. The absolute abundance of *Rhizammina* ranges from 1/g (16.44 m) to 694/g
232 (44.53 m). The highest abundances are recorded in the BFI-I (mean 85/g). The BFI-II shows lower
233 abundance values of *Rhizammina*, although a minor increase is detected in the uppermost part of the
234 interval. A few minor peaks are detected in the BFI-III, reaching 80/g (sample 32.30 m). The genus
235 *Rhizammina* is absent in the Selli Level except for a few specimens found immediately above the
236 barren interval. Low abundances of *Rhizammina* (mean value: 7/g) are recorded above the Selli Level
237 (BFI-VI) except for a peak of 93/g observed at 15.98 m.

238 The genus *Verneuilinoides* is mainly represented by *Verneuilinoides* cf. *V. neocomiensis*, which
239 displays an absolute abundance of 1/g (45.07 m) to 115/g (26.59 m). This species occurs only in the
240 upper Barremian (BFI – I, II, and III). Peaks in abundance of *Verneuilinoides* cf. *V. neocomiensis* are
241 recorded in a few samples from BFI-II (samples 36.66 m and 34.21 m) and BFI-III (samples 30.63 m,
242 29.42 m, 26.82 m, and 26.59 m).

243 Other agglutinated foraminifera displaying intermediate to low absolute abundances are
244 documented in the Cismon Core. The genus *Ammodiscus* (*A. cretaceous*, *A. infimus*) is characterized by
245 low absolute values varying from 1/g (18.78 m) to 6/g (15.18 m). Peaks in abundance of *Ammodiscus*
246 are reported: in BF-I, at the top of BFI-II, in the middle of BFI-III, and in BFI-VI. The genus
247 *Bathysiphon* (*B. brosgiei*, *B. vitta*) ranged from 1/g (18.78 m) to 10/g (44.53 m) and was sporadically
248 found throughout all the BFIs. This genus reaches the highest abundance in BFI-I (44.53 m). The genus
249 *Dorothia* ranges from 1/g (25.09 m) to 16/g (26.59 m). The most significant increases in abundance of
250 *Dorothia* are observed in one sample of BFI-I (43.41 m) displaying 14/g and in BFI-III (26.82 m and
251 26.59 m) with 10/g and 16/g, respectively.

252 *Glomospira charoides* and *Glomospira gordialis* are recorded in the BFI-I, BFI-II, and BFI-VI.
253 *Glomospira charoides* displays low absolute abundances ranging from 2/g (BFI-I: 39.86 m) to 12/g
254 (BFI-V: 15.98 m) and is the rarest taxon of the assemblages. On the contrary, *G. gordialis* displays
255 more fluctuations in the absolute abundance with values comprised between 1/g (29.95 m) and 229/g
256 (44.53 m). The maximum increases in abundance of *G. gordialis* are recorded in the BFI-I and BFI-II,
257 but their peak in abundance is observed at 15.98 m (BFI-VI).

258 The genus *Haplophragmoides* (*H. kirki*, *H. gigas gigas*, *H. gigas minor*) was recorded in the BFI-
259 I, BFI-II, BFI-III, and BFI-VI, varying in abundance values from 1/g (45.07 m, 35.02 m) to 120/g
260 (43.41 m), and displaying peaks mainly in the BFI-I (46.75 m – 42.48 m). *Hippocrepina depressa*

261 shows low abundances ranging from 1/g (15.11 m) to 6/g (27.34 m) in the BFI-II, BFI-III, and BFI-VI.
262 The highest abundance (6 /g; 27.34 m) of this species was recorded in the BFI-III.

263 The genus *Reophax* (*R. helveticus*, *R. liasicus*) displays low absolute abundances of 1/g (21.77 m)
264 to 78/g (44.53 m). It is distributed through all BFIs, being more abundant in the BFI-I (44.53 m). The
265 absolute abundance of Textularids shows values from 1/g (26.59 m) to 248/g (44.53 m) in the BFI-I,
266 BFI-II, and BFI-III and registers the highest values in the BFI-I (44.53 m).

267 Other agglutinated taxa include *Ammobaculites* sp., *Binominela entis*, *Gaudryina dividens*,
268 *Scherochorella minuta*, *Spiroplectinata lata*, *Tolypamma* sp., and *Tritaxia pyramidata*, all
269 characterized by low absolute abundances (Supplementary Table S1).

270

271 **4.2.2 Calcareous benthic foraminifera (CF)**

272 The genus *Astacolus* (*A. calliopsis*, *A. humilis*, *A. planiusculus*) was recorded in the BFI-I, BFI-
273 III, BFI-V and BFI-VI intervals, with low absolute abundance values ranging from 1/g (17.78 m) to 6/g
274 (15.98 m). This genus is recorded in the BFI-V, and BFI-VI (21.77 m – 8.20 m) within and above the
275 Selli Level, with the highest abundance (6/g) observed at 15.98 m (Fig. 5).

276 *Gavelinella barremiana* displays intermediate absolute abundance, varying from 1/g (35.02 m) to
277 45/g (26.82 m) across all BFIs. Increases in the abundance of *G. barremiana* were observed in the BFI-
278 III. Conversely, *Gavelinella intermedia* was detected in the BFI-V and is characterized by low absolute
279 abundance values ranging from 1/g (18.90 m) to 12/g (15.98 m). *Gyroidina nítida* displays low
280 abundances across the BFI-III, BFI-V and BFI-VI intervals and, particularly below and above the Selli
281 Level, varying from 1/g (15.11 m) to 6/g (24.12 m). The genus *Lenticulina* (*L. macrodisca*, *L.*
282 *muensteri*, *L. pulchella*, *L. subgaultina*, *L. turgidula*) was detected in all BFIs, showing intermediate
283 abundance values from 1/g (45.07 m) to 47/g (21.46 m), with the highest abundance in the Selli Level
284 (21.46 m).

285 The genus *Laevidentalina* (*L. distincta*, *L. linearis*, *L. soluta*) was exclusively observed in the
286 BFI-III, BFI-V, and BFI-VI and displayed low absolute abundances ranging from 1/g (samples 21.23
287 m, 20.87 m, 19.01 m, 16.91 m) to 6/g (30.33 m).

288 Other calcareous taxa, such as *Dentalina comunis*, *Dentalina gracilis*, *Dentalina guttifera*,
289 *Globulina Prisca*, *Guttulina* sp., *Gyroidina globosa*, *Lingulina* sp., *Lingulonodosaria nodosaria*,
290 *Nodosaria* sp., *Pleurostomella reussi*, *Pyrulina* sp., *Saracenaria* spp., *Stilostomella* sp., and
291 *Vaginulinopsis* spp., are characterized by low absolute abundance (Supplementary Table S1).

292

293 **5. Discussion**

294 **5.1 Paleobathymetry of the Cismon Core based on benthic foraminifera**

295 Benthic foraminiferal habitats are defined by the abundance of genera and/or marker species that
296 thrive at specific water depths. Cretaceous benthic foraminiferal assemblages are thought to indicate
297 water depths, similar to modern ocean assemblage composition, and their association with mega- and
298 microfauna, which are also linked to sedimentary features (Sliter and Barker, 1972). The taxa found in
299 the Cismon Core are divided into four groups based on the maximum paleo-depth range reported in the
300 literature (Table 2).

301 **Group 1** includes taxa documented down to abyssal settings (3000 m), such as agglutinated
302 foraminifera *Rhizammina* and *Verneuilinoides neocomiensis* that were adapted to upper bathyal to
303 abyssal paleo-water depths (200 m – 3000 m). *Dorothia*, *Ammodiscus*, *Astacolus*, and *Bathisyphon* are
304 inferred to have populated inner neritic to abyssal settings (0 – >3000 m), while *G. charoides* (50 –
305 3000 m) and *Gyroidina globosa* are documented from outer neritic to abyssal environments (100 –
306 3000 m).

307 **Group 2** consists of taxa that lived in upper bathyal to lower bathyal environments (up to 2000
308 m), such as *Lenticulina*, *Haplophragmoides*, and *Reophax*, that are supposed to have thrived between 0

309 – 2000 m. The genus *Gavelinella* and *G. gordialis* are interpreted to have thrived in outer neritic to
310 lower bathyal (50 – 2000 m) environments.

311 **Group 3** includes taxa that live in lower bathyal environments (1500 m), such as *Gavelinella*
312 *intermedia* and *Gyroidina nitida*.

313 **Group 4** includes taxa that live down to 1000 m, such as *Dentalina* (0 – 1000 m),
314 *Laevidentalina*, and *Pleurostomella* (50 m – 1000 m).

315 The benthic foraminifera taxa of Group 2 and Group 3 are the most abundant in the studied
316 interval and indicate a lower bathyal paleo-water depth of about 1500 m. The presence of taxa
317 belonging to Group 4 eventually constrains the paleo-depth at the Cismon site to 1000 m (Table 2), but
318 due to the rarity of taxa belonging to Group 4, we conclude that the Cismon site was probably
319 deposited at a paleo-depth of between 1000 and 1500 m (lower bathyal). This result is consistent with
320 previous studies, which indicated a paleo-water depth of 1000 – 1500 m (e.g., Weissert and Lini, 1991;
321 Erba and Larson, 1998; Erba et al., 1999).

322 Among the taxa identified in the Cismon Core, remarkable is the identification of *Gavelinella*
323 *barremiana* in the assemblages, which suggests that this species was probably adapted to thrive in
324 deeper water than previously reported (middle neritic to upper bathyal; e.g., Koutsoukos, 1989;
325 Riegraf, 1989; Frenzel, 2000; Tyszka, 2006).

326

327 **5.2 Bottom-water dynamics across OAE 1a**

328 The Cismon Core is characterized by epifaunal and infaunal benthic foraminifera, indicating
329 variations in bottom-water conditions (nutrient and oxygen availability) during the late Barremian-early
330 late Aptian time interval according to the TROX model (Trophic conditions and oxygen
331 concentrations; Jorissen et al., 1995; De Stigter, 1996; van der Zwaan et al., 1999; Jorissen et al.,
332 2007). In particular, benthic foraminifera developed different test morphologies (planispiral,

333 trochospiral, biserial, etc.) that are used to identify morphogroups corresponding to specific
334 microhabitats (e.g., Corliss, 1985; Corliss and Chen, 1988; Koutsoukos and Hart, 1990; Tyska, 1994)
335 (Table 1). The epifaunal morphogroup is composed of benthic foraminifera that thrived under well-
336 oxygenated conditions such as *Rhizammina* and *Gavelinella*. *Rhizammina* is considered an indicator of
337 low organic-flux (Koutsoukos, 1989; Koutsoukos and Hart, 1990; Tyska, 1994; Nagy et al., 1995;
338 Kaminski and Kuhnt, 1995; van der Ekker et al., 2000; Rückheim et al., 2006; Patruno et al., 2015) and
339 high oxygen conditions in different oligotrophic settings (Koutsoukos, 1989; Koutsoukos and Hart,
340 1990; Kaminski and Kuhnt, 1995; Szarek et al., 2000; Rückheim et al., 2006; Patruno et al., 2015).
341 However, *Rhizammina* is also considered an opportunistic taxon as, in some records, there is evidence
342 that it thrived under low oxygen content (e.g., Kaminski and Kuhnt, 1995; Cetean et al., 2008).
343 *Gavelinella* also shows a wide range of habitats and has been interpreted to have thrived in
344 oligotrophic-mesotrophic environments in both well and poorly oxygenated conditions (Koutsoukos,
345 1989; Koutsoukos and Hart, 1990; Friedrich and Erbacher, 2006; Friedrich and Hemleben, 2007).

346 Infaunal taxa are thought to tolerate oxygen-depleted conditions and, in some cases, high organic
347 fluxes. The main component of the infaunal morphogroup is the agglutinated genus *Verneuilinoides*
348 (e.g., Rückheim et al., 2006; Patruno et al., 2015), which was also recorded in well-oxygenated
349 environments (Kuhnt, 1995; Szarek et al., 2000), and *Reophax* (Koutsoukos, 1989; Tyska, 1994; van
350 Den Akker et al., 2000; Rückheim et al., 2006; Reolid et al., 2008; Cetean et al., 2011; Reolid and
351 Ruiz, 2012). The genera *Laevidentalina* (Holbourn et al., 2001; Friedrich and Hemleben, 2007; Koch
352 and Friedrich, 2012) and *Pleurostomella* are thought to have inhabited low oxygen water masses
353 (Koutsoukos, 1989; Frenzel, 2000; Kaiho, 1994; Holbourn et al., 2001).

354 Some taxa of the epifaunal or shallow infaunal morphogroups are considered opportunistic due to
355 tolerated high- to low-oxygen conditions (Jorissen et al., 2007). This opportunistic groups include the
356 genera *Haplophragmoides*, *Glomospira* (Kuhnt and Kaminski, 1989; Koutsoukos and Hart, 1990;

357 Rückheim et al., 2006; Cetean et al., 2008; Reolid et al., 2008), and *Lenticulina* (Koutsoukos, 1989;
358 Tyska, 1994; Kaiho, 1994; Frenzel, 2000; Holbourn et al., 2001; Reolid et al., 2008; Koch and
359 Friedrich, 2012).

360 The dominance of the genus *Rhizammina* in the upper Barremian (BFI-I) indicates temporary
361 oxic–dysoxic conditions at the seafloor under low to moderate organic carbon flux (Figs. 2, 5, 6). In the
362 BFI-II, benthic foraminifera experienced a decrease in abundance, also indicated by the presence of
363 several barren samples and a reduction in Hs and D values. The BFI-II is also coeval with the decline in
364 abundance of *Rhizammina* and increased abundances of *Verneuilinoides* and *Glomospira* (Figs. 5, 6),
365 suggesting interludes of lower oxygen levels (dysoxic conditions) and increased organic carbon flux at
366 the water-sediment interface.

367 Benthic foraminiferal assemblages in the BFI-I and BFI-II were investigated only in centimetric
368 marly beds; therefore, the interpretation of the bottom water conditions does not refer to the limestones
369 of the Biancone Formation, which dominate the BFI-I and BFI-II. Thus, the marly beds are attributed
370 to the episodic reduction of oxygen concentrations in bottom water during generally well-oxygenated
371 conditions. The further decrease in benthic foraminiferal abundance values, diversity, and dominance is
372 interpreted as intermittent dysoxic conditions and high organic flux at the seafloor during the BFI-III
373 (Figs. 2, 6). In particular, we infer from the benthic foraminiferal assemblages of BFI-III that, in the
374 latest Barremian-earliest Aptian, oxygenated conditions were interrupted by short-lived interludes of
375 reduced oxygen levels in bottom waters and elevated organic matter flux. The low total organic carbon
376 content (< 1 wt. %) in the BFI-II, and BFI-III, supports this interpretation. Isolated TOC peaks (e.g.,
377 3.8 wt. % at 42.91 m and 1.8 wt. % at 41.56 m) coincide with darker, centimetric marlstone layers
378 marked by impoverished benthic foraminiferal assemblages.

379 A pronounced decrease in benthic foraminiferal abundance, here named “benthic foraminiferal
380 crisis” (BFC; near the base of the BFI-IV at 23.89 m, Figs. 6, 7), is recorded just before the OAE 1a

381 onset. From the BFC toward the base of the Selli Level, rare specimens belonging to *Bathysiphon*,
382 *Gavelinella*, *Gyroidina nitida*, *Rhizammina*, and *Reophax* are found, suggesting a deterioration of
383 bottom-water conditions coupled with the progressive decrease of the oxygen content (dysoxic–anoxic)
384 and high organic carbon flux. Benthic foraminifera are absent from the base of the carbon isotopic
385 segment Ap3 up to the lowermost part of segment Ap5 (Bottini et al., 2015; C3-C5 *sensu* Menegatti et
386 al., 1998), possibly in response to anoxic bottom-water conditions, which promoted the organic matter
387 preservation of the Selli Level black shales, as also testified by TOC enrichments (up to 6 wt%) (Figs.
388 6, 7). These episodes were probably intermittent, as evidenced by bioturbation patterns recorded by
389 Menegatti et al. (1998).

390 At the base of the BFI-V, in correspondence with the beginning of isotopic segment Ap5 (Bottini
391 et al., 2015; C5-C6 *sensu* Menegatti et al., 1998), benthic foraminifera document the onset of a
392 repopulation event (*sensu* Friedrich, 2010). The presence of the genera *Astacolus*, *Lenticulina*,
393 *Laevidentalina*, *Rhizammina* and *Reophax* indicates a moderate, but significant, re-oxygenation of the
394 seafloor during OAE 1a, despite the persistence of intermittent anoxic to dysoxic conditions that
395 favored the organic matter preservation in black shales enriched in TOC content (up to 8 wt %) (Figs.
396 6, 7).

397 The relatively higher benthic foraminiferal abundance, lower Hs, and high D detected above the
398 Selli Level (Fig. 2; BFI-VI) are interpreted to reflect attenuated organic carbon flux and relatively
399 oxygenated bottom-water conditions, although not fully oxygenated (Figs. 6, 7). The samples from
400 BFI-VI mostly correspond to radiolarian layers and, consequently, are not representative of the whole
401 Scaglia Variegata Formation and probably reflect interludes of relatively higher productivity and
402 moderate organic flux (Premoli Silva et al., 1999).

403

404 **5.3 Late Barremian – early late Aptian paleoenvironmental changes in the western Tethys**

405 The benthic foraminifera data collected from the Cismon Core are used to trace the
406 development of deep-water conditions in response to the paleoenvironmental perturbations associated
407 with OAE 1a. The integration of benthic foraminifera with calcareous nannofossil and planktonic
408 foraminifera data contributes to a comprehensive characterization of the paleoclimatic and
409 paleoceanographic conditions of the late Barremian to the early-late Aptian time interval in the western
410 Tethys.

411

412 **5.3.1 The late Barremian – earliest Aptian time interval**

413 The benthic foraminiferal assemblages of the BFI-I indicate that, in the late Barremian, the
414 Cismon site was characterized by oxic–dysoxic conditions and low to moderate organic carbon flux at
415 the seafloor. The change in benthic foraminiferal abundance and assemblage composition in the BFI-II
416 indicate that temporary phases of moderate instability at the seafloor took place during the deposition
417 of the upper Barremian pelagic limestones. In particular, there is evidence of short-lived interludes of
418 relatively higher organic flux and dysoxia that led to the deposition of millimetric to centimetric dark
419 grey-black marlstone layers (Figs. 2, 6).

420 A pronounced general impoverishment in the total benthic foraminiferal abundance occurred ca.
421 1 m.y. before the OAE 1a onset (BFI-III) and, remarkably, corresponds to the “nannoconid decline” at
422 31.50 m (NC, Figs. 2, 6, 7), a globally recognized biohorizon, which represents the onset of a
423 nannoplankton crisis (Erba and Tremolada, 2004).

424 Several studies have found a link between the "nannoconid decline" and the onset of an early
425 volcanic phase of the GOJE (Erba et al., 2015, and references therein), most likely as a result of
426 combined surface-water acidification and pulses of higher surface-water fertility caused by injections
427 of volcanogenic CO₂ and biolimiting trace metals (Larson, 1991; Erba, 1994; Larson and Erba, 1999;

428 Tejada et al., 2009; Méhay et al., 2009; Bottini et al., 2012, 2015; Erba et al., 2015; Charbonnier et al.,
429 2016).

430 The benthic foraminifera data gathered in this study suggest that interludes of increased surface-
431 water fertility probably also had a significant impact on the seafloor, promoting the organic matter flux
432 and inducing temporary phases of expanded oxygen minimum zone with consequent impoverishment
433 of the benthic foraminiferal population (BFI-III; Figs. 6, 8). It is not excluded that benthic foraminifera
434 also directly suffered higher concentrations of toxic metals, as this happens in modern benthic
435 foraminifera (e.g., Frontalini and Coccioni, 2012; Munsel et al., 2010; Munsel 2013). However, we
436 underline that the Cismon site was distant from reconstructed hydrothermal sources (GOJE) and metal
437 concentrations detected in the sediments are relatively low compared to GOJE-near sites (e.g., DSDP
438 Site 463, see Erba et al., 2015).

439 The temporal matching of benthos and plankton responses detected in the upper Barremian of the
440 Cismon Core is the first evidence that the GOJE-induced paleoenvironmental perturbation affected
441 bottom- and surface-water biota concurrently (Figs. 6, 7, 8). This observation may suggest a supra-
442 regional to global cause for the benthic foraminifera decline in abundance detected in the Cismon Core,
443 which should be proved by examining other records worldwide.

444 So far, a correlatable change in the benthic foraminiferal assemblages and associated turnover has
445 been documented only at Gorgo a Cerbara in the Umbria-Marche Basin (Italy) (Patrino et al., 2015), as
446 time-interval equivalent sections studied elsewhere have been investigated at low sampling resolution
447 (Fig. 9). At Gorgo a Cerbara and Cismon Core, benthic foraminifera assemblage composition and
448 abundance show a marked increase in infaunal benthic species (e.g., *Verneulinoides*) during the latest
449 Barremian, especially in the marly strata (Supplementary Figure 1). Specifically, at Gorgo a Cerbara,
450 Patrino et al. (2015) identified a “*Verneulinoides acme*” from the topmost part of the magnetochron
451 M0 up to the “nannoconid crisis”. The correspondence between the “*Verneulinoides acme*” and the

452 nanofossil “pentaliths peak” was interpreted to reflect higher nutrient–recycling after increased
453 freshwater input through runoff (Bellanca et al., 2002; Bersezio et al., 2002; Erba and Tremolada,
454 2004; Patruno et al., 2015). In the Cismon Core, abundant *Verneuilinoides* are detected in the middle
455 part of the BFI-II and, similarly to Gorgo a Cerbara, in the BFI-III up to the “nannoconid crisis” (Fig.
456 2, and Supplementary material). Indeed, this interval corresponds to pulses of increased surface-water
457 fertility (Bottini et al., 2015) and pentalith peaks (Erba and Tremolada, 2004). Moreover, the
458 planktonic foraminiferal assemblages analyzed in the washed residues confirm meso-to eutrophic
459 conditions in the surface waters based on the occurrence of abundant opportunistic trochospiral taxa,
460 which cyclically alternate with rare leupoldinids and with a few planispirals, the latter inferred to be
461 indicative of more mesotrophic regimes (Premoli Silva et al., 1999; Coccioni et al., 2006) (Figs. 6, 7).

462

463 **5.3.2 The benthic foraminifera crisis and repopulation across OAE 1a**

464 Benthic foraminifera display a marked decrease in the absolute abundance (BFC), just before the
465 OAE 1a onset, and are absent from the base of the Selli Level up to the lowermost part of the carbon
466 isotope segment Ap5 (BFI-IV; Figs. 6, 7). The onset of the BFC correlates with a GOJE volcanic pulse
467 at the OAE 1a onset (e.g., Méhay et al., 2009; Kuroda et al., 2011; Bottini et al., 2012; Erba et al.,
468 2015), responsible for a stepwise accumulation of volcanogenic CO₂ in the atmosphere, paralleled by
469 nutrient enrichment, progressive warming (Bottini et al., 2015; Bottini and Erba, 2018), and trace metal
470 spikes (e.g., V, Zn, and Cu; Erba et al., 2015; Figs. 6, 7, 8). Remarkably, the BFC occurred almost
471 contemporaneously with the “nannoconid crisis” (NC), as the difference in the stratigraphic level (1
472 cm) is due to the different sampling resolutions used for nanofossil and benthic foraminiferal
473 analyses. This correspondence, also identified at Gorgo a Cerbara (Patruno et al., 2015; Fig. 9,
474 Supplementary Fig. 1), testifies to the onset of highly fertile surface-water conditions, which favored
475 higher photic zone coccoliths at the expense of nannoconids (Erba, 2004; Bottini et al., 2015; Bottini

476 and Erba, 2018) and initiated dysoxic/mesotrophic conditions under higher organic carbon flux to the
477 seafloor.

478 During this phase, from the BFC (23.89 m) and the “nannoconid crisis” (23.90 m) to just above
479 the base of the Selli level, planktonic foraminifera seem not to be affected and show an increase of 52/g
480 in the washed residues and 12 specimens/FOV in thin sections at 23.66 m and 23.57 m, respectively
481 (Fig. 6). Specifically, the integration of the data obtained from washed residues and thin sections
482 increases the resolution of the planktonic foraminiferal record and documents a peak in the absolute
483 abundance 10 cm above the base of the Selli level (23.67 cm). This value is immediately followed by
484 an interval characterized by a marked decrease in abundance of planktonic foraminifera coupled with a
485 change in the assemblage composition, which results in the assemblage being almost solely
486 characterized by leopoldinids (Fig. 6, 7), interpreted to be tolerant taxa. The delay in the response of
487 the planktonic foraminifera, compared to the benthic foraminifera and nannoconids, could be related to
488 the composition of lower Aptian planktonic assemblages. These are characterized by the lack of
489 oligotrophic and specialized taxa, being only composed of mesotrophic to eutrophic species (Coccioni
490 et al., 2006). The interval marked by scarce to absent planktonic foraminifera correlates with the core
491 of the interval barren of benthic foraminifera and coincides with the temporary absence of nannofossils
492 (Fig. 7; Erba et al., 2010). Quantitative and morphometric analyses of calcareous nannofossils
493 evidenced that the volcanogenic CO₂ emissions at the “nannoconid crisis” started a progressive
494 increase in surface-water acidification and a shallowing of the calcite lysocline (Erba et al., 2010).
495 After ~75 kyr from the beginning of the $\delta^{13}\text{C}$ negative shift (core of carbon isotope segment Ap3), the
496 calcite lysocline reached ~1200 m of paleowater depth with consequent severe dissolution at the
497 sediment/water interface and an absence of calcareous nannofossils, which lasted for ~70 kyr (Erba et
498 al., 2010; Figs. 6, 7, 8), during the most intense GOJE volcanism (Tejada et al., 2009; Bottini et al.,
499 2012; Charbonnier et al., 2016; Percival et al., 2021). Therefore, it may be plausible that ocean

500 acidification contributed to the abrupt decline in planktonic foraminiferal abundance recorded at 23.41
501 cm as well as to the temporary absence of benthic foraminifera (Figs. 6, 7, 8).

502 The new benthic foraminifera data at the Cismon site show that the OAE 1a paleoenvironmental
503 perturbation, related to the GOJE volcanism, including not only maximum warming (e.g., Price 2003;
504 Ando et al., 2008; Mutterlose et al., 2014; Bottini et al., 2015; Bottini and Erba, 2018), surface-water
505 acidification (Wissler et al., 2003; Weisser and Erba, 2004; Erba et al., 2010), and trace-metal release
506 (Erba et al., 2015), but also imposed deep-water anoxic “inhabitable” conditions for ca. 300 kyr in the
507 earliest part of OAE 1a (adopting the time scale of Malinverno et al., 2010; Figs. 6, 7, 8). This is
508 consistent with rapid oceanic deoxygenation evidenced by combined redox-sensitive geochemical
509 proxies (Bauer et al., 2021). The GOJE activity probably induced chemical and physical changes in
510 surface waters, stimulating primary productivity and consuming oxygen through organic matter
511 oxidation, hence promoting dysoxic to anoxic conditions at the seafloor. Evidence of increased surface-
512 water fertility is based on the calcareous nannoplankton Nutrient Index (NI: Bottini et al., 2015; Bottini
513 and Erba, 2018) and is confirmed by the composition of planktonic foraminiferal assemblages that, as
514 mentioned above, register the absence of the mesotrophic and specialized planispiral taxa (Coccioni et
515 al., 2006) and the rarity of the more opportunistic trochospiral taxa (Premoli Silva et al., 1999), both
516 balanced by the common occurrence of the eutrophic and low oxygen tolerant leupoldinids (Fig. 6 TOC
517 spikes further suggest higher organic matter preservation in this interval (Fig. 6; Erba et al., 1999). We
518 infer that the increased primary productivity generated a higher organic flux to the seafloor coupled
519 with oxygen depletion after organic matter degradation. A contribution to surface-water fertility could
520 have also come from hydrothermal trace metal enrichments (V, Zn, and Cu; Erba et al., 2015), riverine
521 runoff as suggested by palynomorph assemblages (Hochuli et al., 1999), and accelerated weathering
522 rates, as documented by the increase in siliciclastic sedimentation (Weissert, 1990) and by radiogenic
523 osmium isotopic composition of seawater (Tejada et al., 2009; Bottini et al., 2012; Fig. 7, 8).

524 Consequently, bottom-water anoxia could have been promoted by enhanced water stratification
525 following increased precipitation and continental runoff.

526 Benthic foraminifera indicate that after ca. 300 kyr of bottom-water anoxia, alternating anoxic to
527 dysoxic conditions prevailed at the Cismon site until the end of OAE 1a (BFI-V; Figs. 6, 7) and favored
528 the deposition of organic-rich sediments, as also testified by relatively high TOC content (up to 6 wt.
529 %). The benthic foraminifera repopulation detected in the Cismon Core reflects the ability of several
530 taxa (*Gavelinella*, *Gyroidina*, *Laevidentalina*, *Lenticulina*, *Pleurostomella*, *Reophax*, *Rhizammina*) to
531 adapt to ameliorated but still unstable conditions, with alternating phases of anoxia and dysoxia at the
532 seafloor (Figs. 6, 7, 8). The repopulation event was preceded by a relative cooling coincident with the
533 end of the carbon isotope segment Ap3, the establishment of an intermediate temperature and the end
534 of surface-water acidification (Erba et al., 2010; Bottini et al., 2015; Jenkyns, 2018; Huck and
535 Heimhofer, 2021; Fig. 7). These changes in climatic and paleoenvironmental conditions were possibly
536 favored by temporary inputs of relatively colder and more oxygenated waters, thereby inducing the
537 benthic foraminifera return. Interludes of higher productivity were probably sustained by N-fixing
538 cyanobacteria rather than by nanoplankton during BFI-V (see Kuypers et al., 2004; Dumitrescu and
539 Brassell, 2006; Bottini et al., 2015), explaining the low nannofossil NI and the low abundances of the
540 leupoldinids (Fig. 6).

541 In the Cismon Core, the benthic foraminiferal repopulation event coincides with a still low
542 abundance of planktonic foraminifera, although a slight increase in species richness is registered (Fig.
543 6). Alternated anoxic to dysoxic conditions at the seafloor in the BFI-V interval were paralleled by
544 changes in nutrient levels in surface waters, as testified by the composition of the planktonic
545 foraminiferal assemblages. Specifically, the opportunistic trochospiral taxa dominating the assemblages
546 cyclically fluctuated in abundance, alternating either with the specialized planispirals or with the
547 opportunistic and eutrophic leupoldinids. This reveals a complex paleoceanographic scenario

548 characterized by high variability in the surface-water stratification. The benthic foraminiferal
549 repopulation coincides with relatively high calcareous nannofossil average abundance, similar to pre-
550 OAE 1a values in the photic zone (Fig. 7). The nannofossil assemblages indicate low fertility under
551 alternating minor cooler and warmer phases (Bottini et al., 2015).

552 Benthic foraminiferal repopulation events were documented for other OAEs, such as OAE 1b and
553 OAE 2, in response to moderate influxes of oxygen to the seafloor, temporarily interrupting anoxic
554 conditions (Eicher and Worstell, 1970; Erbacher et al., 1999; Holbourn and Kuhnt, 2001; Holbourn et
555 al., 2001; Friedrich et al., 2005, 2006; Friedrich, 2010). However, it is not possible to exclude that
556 benthic foraminifera were adapted to thrive in anoxic settings. This has been documented in new
557 studies of modern benthic foraminifera, which show their metabolic capacity to respire nitrate under
558 anoxic conditions (Risgaard-Petersen et al., 2006; Piña-Ochoa et al., 2010), allowing survival in anoxic
559 waters for weeks to months through denitrification (LeKieffre et al., 2017). Benthic foraminifera from
560 the Peruvian oxygen minimum zone also display a metabolic preference for denitrification over O₂
561 respiration (Glock et al., 2019). In the geological record, there are some examples of benthic
562 foraminifera that could survive long-term anoxic to dysoxic bottom-water conditions in denitrified
563 environments (Schneider-Mor et al., 2012; Quan et al., 2013; Belanger and Garcia, 2014; Meilijson et
564 al., 2015, 2018). Indeed, the benthic foraminiferal repopulation is concomitant with a period of
565 denitrification documented in the Cismon Core (Kuypers et al., 2004). This suggests an increase in the
566 nitrate and/or oxygen concentration in bottom-waters, favoring the return of benthic foraminifera even
567 under almost anoxic conditions.

568

569 **5.3.3 The post-OAE 1a phase**

570 The BFI-VI above the Selli Level (Figs. 7, 8) is characterized by the re-establishment of
571 oxygenated conditions at the seafloor, as indicated by a slight increase in the abundance of benthic

572 foraminifera. Meanwhile, in surface-waters, planktonic foraminifera display a marked increase in
573 abundance and nannofossils also increase in abundance with the return of the nannoconids, indicating
574 cooler and more oligotrophic surface-water conditions (Bottini et al., 2015). Similarly, abundant
575 specialized planispiral taxa (Coccioni et al., 2006), which dominated over the trochospiral taxa and the
576 leupoldinids, suggest more stable conditions and meso-to oligotrophic waters (Figs. 6, 7, 8). Our
577 updated dataset, thus, advocates for a post-OAE 1a phase of coeval nannoplankton, planktonic
578 foraminifera, and benthic foraminifera recovery under colder oligo-mesotrophic surface waters and
579 more oxygenated conditions at the seafloor. The end of the GOJE volcanism and the burial of organic
580 matter during OAE 1a — progressively acting as storage for excess CO₂ — most probably concurred to
581 terminate OAE 1a and promote lower temperatures (Heimhofer et al., 2004; Bottini et al., 2015; Erba et
582 al., 2015).

583

584 **5.4 The worldwide benthic foraminiferal record across OAE 1a**

585 The comparison of the benthic foraminiferal data of the Cismon Core with benthic foraminiferal
586 records across OAE 1a from different localities (Coccioni et al., 1992; Mutterlose and Böckel 1998;
587 Cobianchi et al., 1999; Rückheim et al., 2006; Michalík et al., 2008; Barga and Lehmann 2014;
588 Patruno et al., 2015; Moullade et al., 2015; Zorina et al., 2017) shows similarities and differences as
589 discussed below (Fig. 9).

590 Several sites show a marked decrease in abundance (or disappearance) of benthic foraminifera
591 before the OAE 1a onset (Coccioni et al., 1992; Mutterlose and Böckel 1998; Cobianchi et al., 1999;
592 Rückheim et al., 2006; Barga and Lehmann 2014; Patruno et al., 2015; Moullade et al., 2015; Zorina
593 et al., 2017; Michalík et al., 2008), which correlates with the marked decrease in abundance (BFC)
594 identified in the Cismon Core (Fig. 9). We infer that the BFC was a global event that may have
595 occurred in response to the paleoenvironmental perturbation initiated just before the OAE 1a.

596 Contrarily, during OAE 1a, the benthic foraminifera abundance and composition were diverse in the
597 studied localities (Fig. 9). The Cismon Core is the only section that displays an interval barren of
598 benthic foraminifera in the early phase of OAE 1a, followed by a repopulation event occurring in the
599 middle of OAE 1a. The Selli Level equivalent of some stratigraphic sections is entirely barren of
600 benthic foraminifera (e.g., Coccioni et al., 1992; Michalík et al., 2008; Patruno et al., 2015; Zorina et
601 al., 2017), whereas other sites are characterized by scarce specimens (Gargano: Cobianchi et al., 1999;
602 Lower Saxony Basin, German: Mutterlose and Böckel 1998; Bergen and Lehmann 2014). Conversely,
603 the Jebel Ammar section (Tunisia: Elkhazri et al., 2013) contains relatively common benthic
604 foraminifera specimens, although the section only starts above segment Ap4 (Elkhazri et al., 2013). In
605 the Lower Saxony Basin, higher benthic foraminifera abundances are reported at the end of the carbon
606 isotope segment C6, close to the termination of OAE 1a (Mutterlose and Böckel 1998; Rückeim et al.,
607 2006; Bergen and Lehmann 2014). The La Bedoule section in the Vocontian Basin (France) is the only
608 site characterized by relatively frequent benthic foraminifera throughout the Niveau Goguel (Moullade
609 et al., 2015), probably because anoxic conditions were never reached at this locality (Moullade et al.,
610 2015).

611 Based on the high variability in the distribution of benthic foraminifera, we conclude that, during
612 OAE 1a, the benthic community was primarily controlled by local factors. Remarkably, the benthic
613 foraminifera record across the Selli Level in the Cismon Core also differs from other sections located in
614 the western Tethys basins, such as the Umbria–Marche Basin (Gorgo a Cerbara section, central Italy:
615 Coccioni et al., 1992; Patruno et al., 2015) and the Gargano Promontory (southern Italy: Cobianchi et
616 al., 1999), further indicating that local environmental factors, possibly influenced by global
617 paleoenvironmental changes related to OAE 1a, control the bottom-water oxygenation during OAE 1a.

618 The post-OAE 1a phase was instead marked by a typical response of the benthic foraminifera
619 communities. Many stratigraphic sections display a recovery in benthic foraminiferal abundances

620 around the base of the carbon isotopic segment Ap7 indicative of restored oxygenated conditions at the
621 seafloor after the termination of the OAE 1a (Coccioni et al., 1992; Mutterlose and Böckel 1998;
622 Cobianchi et al., 1999; Elkhazri et al., 2013; Rückheim et al., 2006; Michalík et al., 2008; Józsa et al.,
623 2016; von Bargen and Lehmann 2014; Patruno et al., 2015; Zorina et al., 2017; Fig. 9).

624

625 **6. Conclusions**

626 The study of the benthic foraminiferal assemblages in the Cismón Core provides, for the first time, a
627 high-resolution record of bottom-water paleoceanographic conditions across the late Barremian to the
628 early late Aptian time interval. The composition and abundance of the benthic foraminiferal
629 assemblages confirm a paleowater depth for the Cismón Core of ca. 1000-1500 m (lower bathyal). The
630 late Barremian was characterized by oxygenated conditions interrupted by short interludes of bottom-
631 water dysoxia and high organic flux to the seafloor. In surface waters, the increase in fertilization
632 caused a progressive decrease of the oligotrophic nannoconids (“nannoconid decline”) and induced
633 alternated phases of decrease and increase in abundance of the more specialized planispiral planktonic
634 foraminiferal taxa. Before OAE 1a (ca. 35 kyr), benthic foraminifera were affected by a marked
635 decrease in abundance, here named “benthic foraminifera crisis,” coincident with the “nannoconid
636 crisis” and contemporaneous with the initiation of the most intense GOJE volcanic phase. A profound
637 change in the paleoenvironmental conditions occurred at the benthic and nannoconid crises level,
638 including surface-water ocean acidification, progressive warming, increased surface-water fertility, and
639 established deep-water dysoxia.

640 Bottom-water anoxia was reached at the OAE 1a onset, probably promoted by higher productivity
641 under a super-greenhouse climate. Increased precipitation and continental runoff as a result of an
642 accelerated hydrological cycle may also have contributed to an oxygen deficiency at the seafloor via
643 enhanced water stratification. The anoxia caused the temporary absence of benthic foraminifera for ca.

644 300 kyr. Increased surface-water fertility also affected calcareous nannofossils and planktonic
645 foraminifera assemblage composition but not their abundance. A benthic foraminifera repopulation
646 event occurred after ca. 300 kyr from the OAE 1a onset, probably favored by the influx of relatively
647 cooler and oxygenated waters. Intermittent anoxic to dysoxic conditions at the seafloor characterized
648 the continuation of OAE 1a. Possibly, the interludes of higher productivity were sustained by N-fixing
649 bacteria rather than by calcareous nanoplankton, indicating lower surface-water fertility. Accordingly,
650 surface-water planktonic foraminifera show a change in the composition of their assemblages with the
651 dominance of the opportunistic trochospiral taxa. The post-OAE 1a interval was characterized by the
652 return of relatively abundant benthic foraminifera on a global scale, in response to the restoration of
653 favorable conditions for the development of diversified communities of benthic foraminifera.

654

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661

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663 **Victor M. Giraldo-Gómez:** Conceptualization, Investigation, Data curation, Formal analysis,
664 Visualization, Writing- original draft preparation, Writing - review & editing. **Maria Rose Petrizzo:**
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668

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1243 **Appendix A**

1244 **Taxonomic appendix**

1245 Taxonomic list of the benthic foraminifera taxa cited in the text is based on Ellis and Messina (1940-
1246 2015), Mjatliuk (1988), Weidich (1990), Meyn and Vespermann (1994), Holbourn and Kaminski
1247 (1997), Patruno et al. (2015).

1248

1249 **Agglutinated foraminifera:**

1250 *Ammobaculites* sp. Cushman, 1910

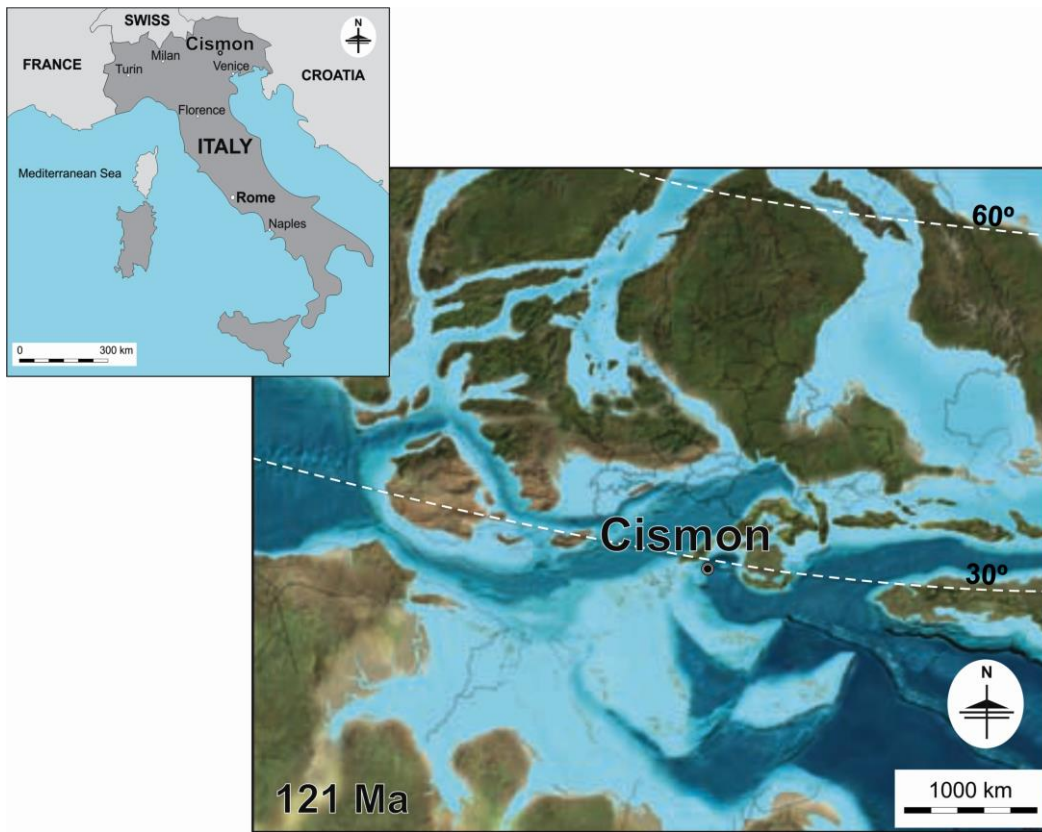
1251 *Ammodiscus* sp. Reuss, 1862

- 1252 *Ammodiscus cretaceus* (Reuss, 1845)
- 1253 *Ammodiscus infimus* Franke, 1936
- 1254 *Bathysiphon* sp. Sars, 1872
- 1255 *Bathysiphon brosgei* Tappan, 1957
- 1256 *Bathysiphon vitta* Nauss, 1947
- 1257 *Bimonilina* Eicher, 1960
- 1258 *Bimonilina entis* Mjatluk, 1988
- 1259 *Dorothia* sp. Plummer, 1931
- 1260 *Dorothia hyperconica* Risch, 1970
- 1261 *Gaudryina* sp. d'Orbigny, 1839
- 1262 *Gaudryina dividens* Grabert, 1959
- 1263 *Glomospira* sp. Rzehak, 1885
- 1264 *Glomospira gordialis* (Jones and Parker, 1860)
- 1265 *Glomospira charoides* (Jones and Parker, 1860).
- 1266 *Glomospirella* sp. Plummer, 1945
- 1267 *Haplophragmoides* sp. Cushman, 1910
- 1268 *Haplophragmoides kirki* Wickenden, 1932
- 1269 *Haplophragmoides gigas gigas* Cushman, 1927
- 1270 *Haplophragmoides gigas minor* Nauss, 1947
- 1271 *Hippocrepina* Parker, 1870
- 1272 *Hippocrepina depressa* Vašíček, 1947
- 1273 *Reophax* sp. Montfort, 1808
- 1274 *Reophax helveticus* (Haeusler, 1881)
- 1275 *Reophax liasicus* Franke, 1936
- 1276 *Rhizammina* sp. Brady, 1879

- 1277 *Scherochorella* Loeblich and Tappan, 1984
- 1278 *Scherochorella minuta* Tappan, 1940 = *Reophax minutus* Tappan, 1940
- 1279 *Spiroplectinata* sp. Cushman, 1927
- 1280 *Spiroplectinata lata* Grabert, 1959
- 1281 *Tolypammina* sp. Rhumbler, 1895
- 1282 *Tritaxia* Reuss, 1860
- 1283 *Tritaxia pyramidata* Reuss, 1863
- 1284 *Verneuilinoides* sp. Loeblich & Tappan, 1949
- 1285 *Verneuilinoides* cf. *neocomiensis* (Mjatliuk, 1939)
- 1286
- 1287 **Calcareous foraminifera:**
- 1288 *Astacolus* sp. Montfort, 1808
- 1289 *Astacolus calliopsis* (Reuss, 1863)
- 1290 *Astacolus humilis* (Reuss, 1863)
- 1291 *Astacolus planiusculus* (Reuss, 1863).
- 1292 *Dentalina* sp. Risso, 1826
- 1293 *Dentalina comunis* (d'Orbigny, 1826) = *Laevidentalina comunis* (d'Orbigny, 1826)
- 1294 *Dentalina gracilis* d'Orbigny, 1840
- 1295 *Dentalina guttifera* (d'Orbigny, 1846) = *Laevidentalina guttifera* (d'Orbigny, 1846)
- 1296 *Gavelinella* sp. Brotzen, 1942
- 1297 *Gavelinella barremiana* Bettenstaedt, 1952
- 1298 *Gavelinella berthelini* Fuchs, 1967
- 1299 *Gavelinella intermedia intermedia* = *Berthelina intermedia* (Berthelin, 1880)
- 1300 *Globulina* sp. d'Orbigny, 1839
- 1301 *Globulina prisca* (Reuss, 1863)

- 1302 *Guttulina* sp. d'Orbigny, 1839
- 1303 *Gyroidina* sp. d'Orbigny, 1826
- 1304 *Gyroidina globosa* (Hagenow 1842) = *Gyroidinoides globosa* (Hagenow 1842)
- 1305 *Gyroidina nitida* (Reuss, 1850) = *Gyroidinoides nitida* (Reuss, 1844)
- 1306 *Laevidentalina* sp. Loeblich & Tappan, 1986
- 1307 *Laevidentalina distincta* (Reuss, 1960) = *Dentalina distincta* (Reuss, 1860)
- 1308 *Laevidentalina linearis* (Roemer, 1841)
- 1309 *Laevidentalina soluta* (Reuss, 1851)
- 1310 *Lenticulina* sp. Lamarck, 1804
- 1311 *Lenticulina macrodisca* (Reuss, 1863)
- 1312 *Lenticulina muensteri* (Roemer, 1839)
- 1313 *Lenticulina pulchella* (Reuss, 1863)
- 1314 *Lenticulina subgaultina* Bartenstein, 1962
- 1315 *Lenticulina turgidula* (Reuss, 1863)
- 1316 *Lingulonodosaria* Silvestri, 1903
- 1317 *Lingulonodosaria nodosaria* (Reuss, 1863)
- 1318 *Lingulina* sp. d'Orbigny, 1826
- 1319 *Nodosaria* sp. Lamarck, 1816
- 1320 *Pleurostomella* sp. Reuss, 1860
- 1321 *Pleurostomella reussi* Berthelin, 1880 = *Pleurostomella subnodosa* (Reuss, 1851)
- 1322 *Pseudonodosaria* sp. Boomgaart, 1949
- 1323 *Pseudonodosaria humilis* (Roemer, 1841)
- 1324 *Pyrulina* sp. d'Orbigny, 1839
- 1325 *Saracenaria* sp. Defrance, 1824
- 1326 *Saracenaria* sp1.

- 1327 *Saracenaria* sp2.
- 1328 *Stilostomella* sp. Guppy, 1894
- 1329 *Vaginulinopsis* sp. Silvestri, 1904
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- 1350 **Figures**



1351

1352 **Fig. 1.** Location of the Cismon today (upper left) and in the early Aptian (ca. 121 Ma).
 1353 Paleogeographical map of the western Tethys modified from Blakey (2012), NAU Geology.
 1354 <http://jan.ucc.nau.edu/~rcb7/>.

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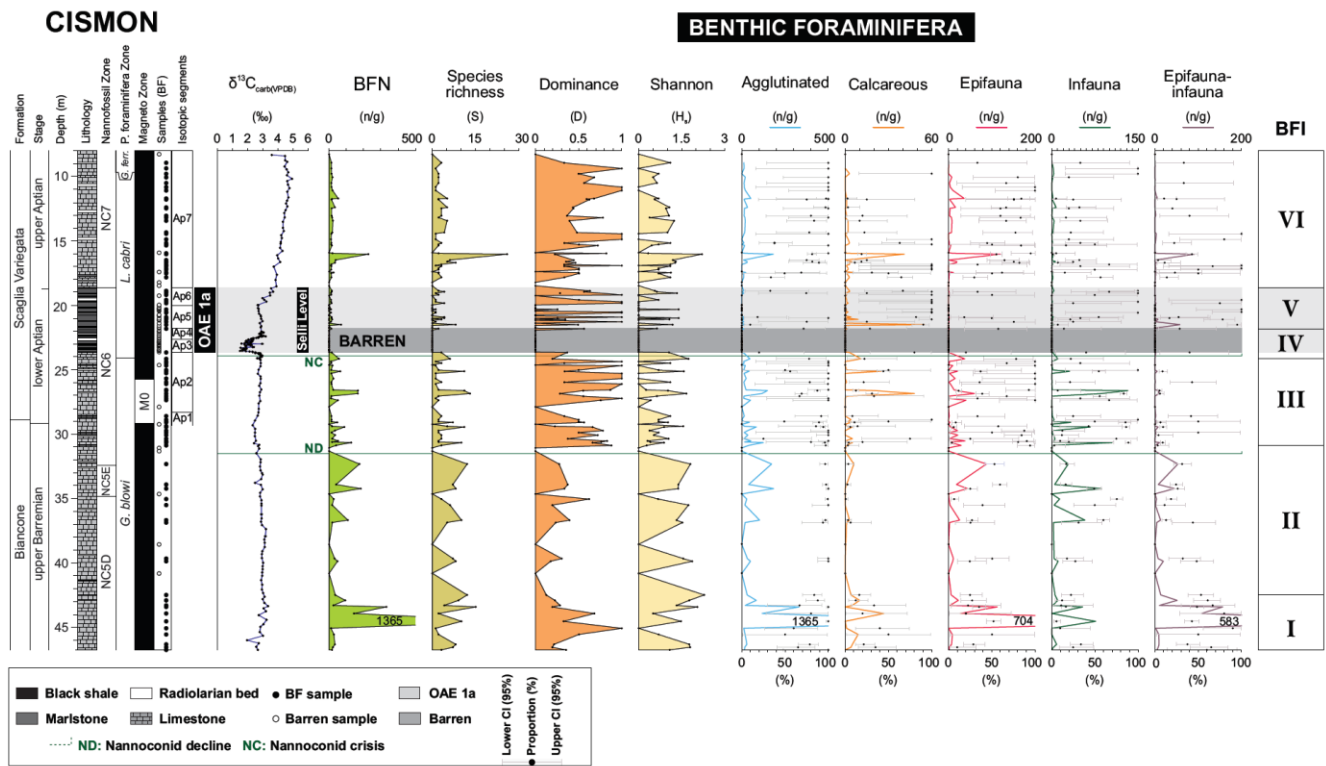
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1365 **Fig. 2.** Benthic foraminifera distribution in the upper Barremian-upper Aptian interval of the Cision
 1366 Core. The benthic foraminifera number (BFN), species richness (S), Shannon index (Hs), Dominance
 1367 (D), confidence interval (CI%), relative (%), and absolute (number of specimens per gram of washed
 1368 residue = n/g) abundances of the agglutinated foraminifera, calcareous foraminifera, epifauna and
 1369 infauna morphogroups, and epifauna-infauna are reported. The Benthic Foraminifera Intervals (BFI)
 1370 identified in this work are displayed. Lithology, planktonic foraminifera, and nannofossil
 1371 biostratigraphy are after Erba et al. (1999) and Bottini et al. (2015). ND = nannoconid decline at 31.50
 1372 m; NC = nannoconid crisis at 23.90 m. Magnetostratigraphy is from Channell et al. (2000). $\delta^{13}\text{C}_{\text{carb}}$
 1373 data are from Erba et al. (1999) and Méhay et al. (2009). The isotopic segments Ap1-Ap7 are after
 1374 Bottini et al. (2015). TOC is after Erba et al. (1999) and Bottini et al. (2012).

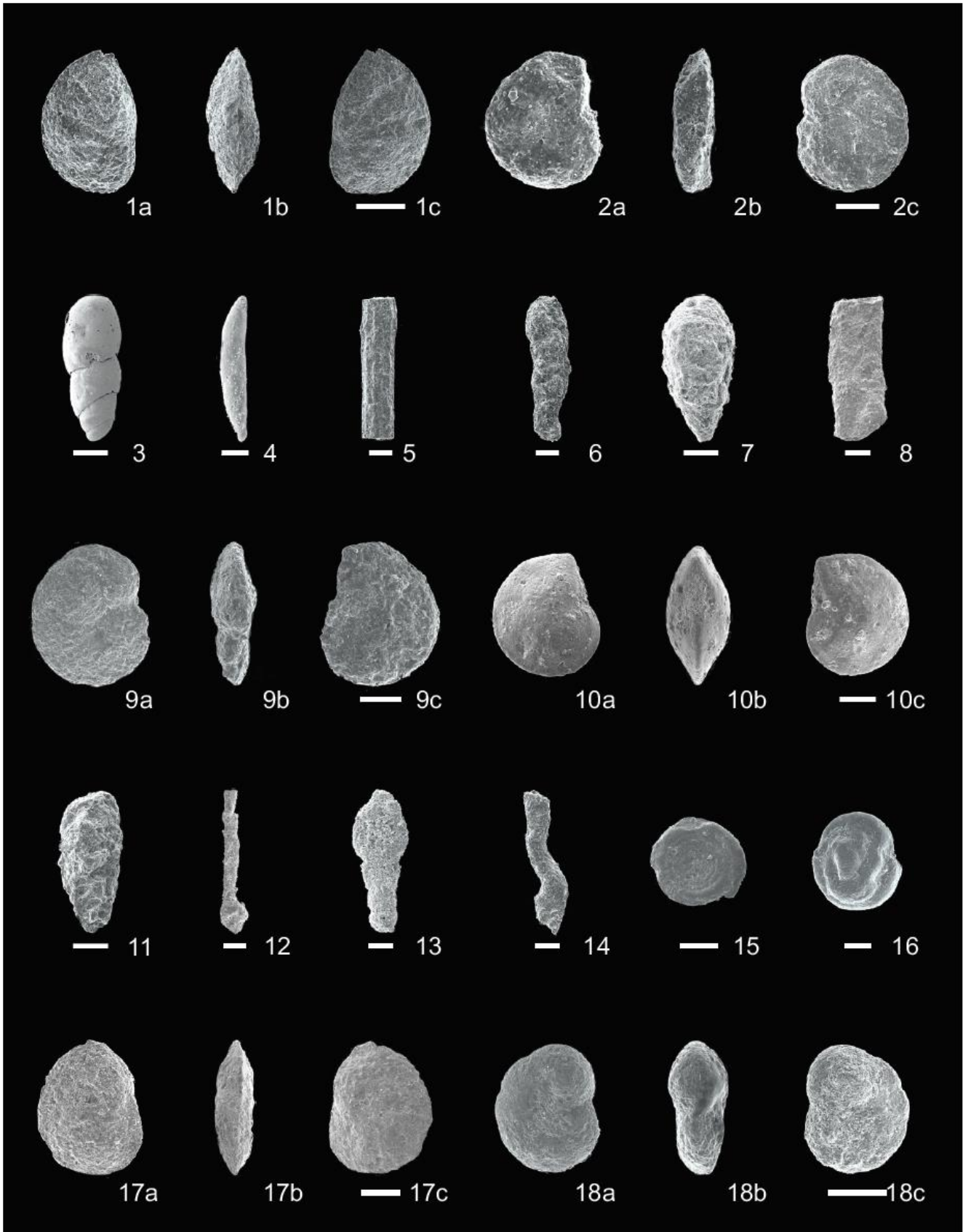
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1381 **Fig. 3.** Benthic foraminifera of the Cismon Core. Scale-bars are 100 μ m. **1.** a/b/c *Astacolus*
1382 *planiusculus* (core 12 – 12/162; 15.98 m); **2.** *Gavelinella* sp.(core 12 – 12/162; 15.98 m); **3.**
1383 *Lingulonodosaria nodosaria* (core 13 – Rad 35; 17.78 m); **4.** *Laevidentalina soluta* (core 13 – Rad 35;
1384 17.78 m); **5.** *Bathysiphon brosgiei* (core 12 – 12/162; 15.98 m); **6.** *Scherochorella minuta* (core 162 –
1385 16/99; 26.82 m); **7.** *Dorothia hyperconica* (core 17 – 17/211; 30.63 m); **8.** *Rhizammina* sp. (core 23 –
1386 23/38; 44.53 m); **9.** a/b/c *Gavelinella barremiana* (core 12 – 12/162; 15.98 m); **10.** a/b/c *Lenticulina*
1387 *muensteri* (core 14 – 14/167; 21.46 m); **11.** *Bimonilina entis* (core 16 – 16/79; 30.63 m); **12.**
1388 *Tolypamma* sp. (core 14 – Rad 53; 21.23 m); **13.** *Reophax helveticus* (core 15 – Rad 75; 24.12 m); **14.**
1389 *Rhizammina* sp. (core 12 – 12/162; 15.98 m); **15.** *Ammodiscus cretaceus* (core 12 – 12/162; 15.98 m);
1390 **16.** *Glomospira charoides* (core 12 – 12/162; 15.98 m); **17.** a/b/c *Astacolus calliopsis* (core 12 –
1391 12/162; 15.98 m); **18.** a/b/c *Gavelinella intermedia* (core 15 – 15/124; 25.09 m).

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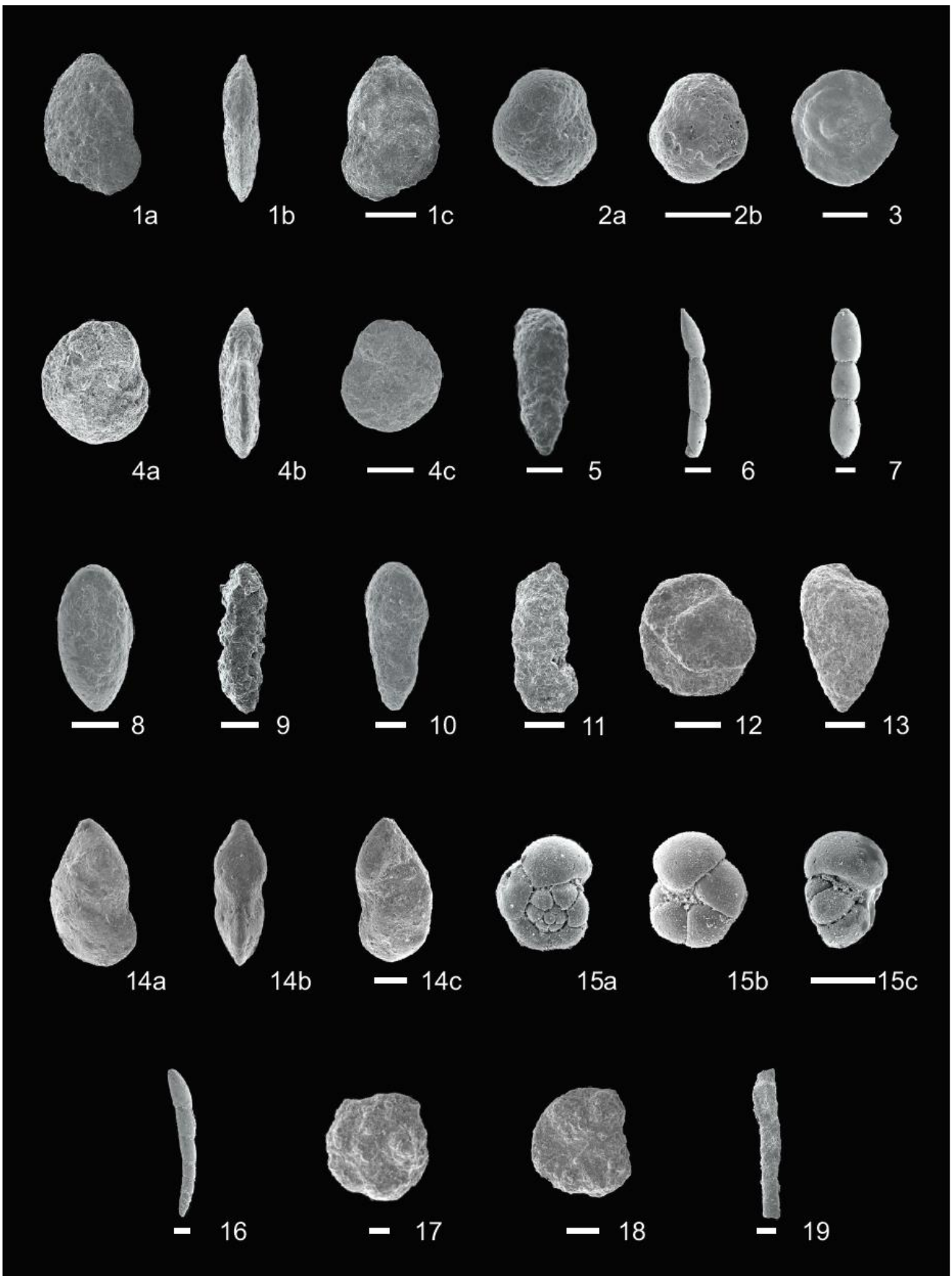
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1408 **Fig. 4.** Benthic foraminifera of the Cismon Core. Scale-bars are 100 μm . **1.** a/b/c *Lenticulina*
1409 *subgaultina* (core 12 – 12/162; 15.98 m); **2.** a/b *Gyroidina globosa* (core 15 – 15/124; 25.09 m); **3.**
1410 *Glomospira gordialis* (core 12 – 12/162; 15.98 m); **4.** a/b/c *Gavelinella barremiana* (core 16 – 16/98;
1411 26.82 m); **5.** *Verneuilinoides cf. neocomiensis* (core 17 – 17/211; 30.63 m); **6.** *Laevidentalina distincta*
1412 (core 13 – Rad 35; 17.78 m); **7.** *Pleurostomella reussi* (core 14 – Rad 50; 20.87 m); **8.** *Globulina prisca*
1413 (core 15 – 15/124; 25.09 m); **9.** *Verneuilinoides* sp. (core 17 – 17/211; 30.63 m); **10.** *Verneuilinoides*
1414 *cf. neocomiensis* (core 15 – 15/124; 25.09 m); **11.** *Reophax liasicus* (core 18 – 18/265; 33.89 m); **12.**
1415 *Haplophragmoides kirki* (core 22 – 22/224; 21.23 m); **13.** *Dorothia hyperconica* (core 16 – 16/79;
1416 42.90 m); **14.** a/b/c *Vaginulinopsis* sp. (core 1 – 14/167W; 21.46 m); **15.** a/b/c *Gyroidina nitida* (core
1417 12 – Rad 27; 16.78 m); **16.** *Dentalina gracilis* (core 16 – 16/79; 26.59 m); **17.** *Haplophragmoides gigas*
1418 *minor* (core 22 – 22/170; 33.89 m); **18.** *Haplophragmoides gigas gigas* (core 22 – 22/224; 43.41 m);
1419 **19.** *Bathysiphon vitta* (core 11 – Rad 16; 14.29 m).

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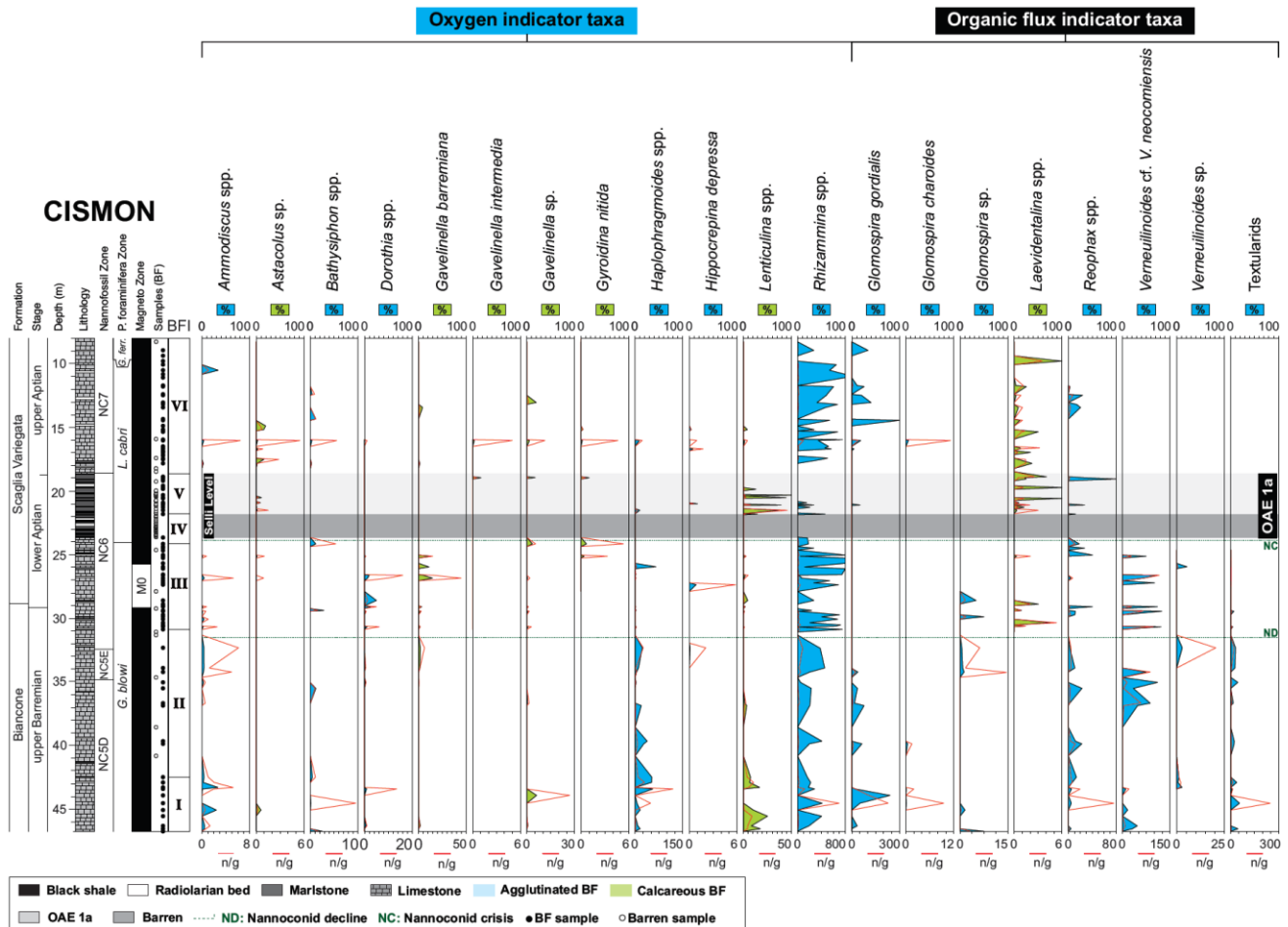
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1436 **Fig. 5.** Relative (%) and absolute (number of specimens per gram of washed residue = n/g) abundances
 1437 of the most common benthic foraminiferal taxa (grouped at genus level) identified in the Cison Core.
 1438 BFI = Benthic foraminifera intervals. Lithology, planktonic foraminifera, and nannofossil
 1439 biostratigraphy are after Erba et al. (1999) and Bottini et al. (2015). ND = nannoconid decline at 31.50
 1440 m; NC = nannoconid crisis at 23.90 m. Magnetostratigraphy is from Channell et al. (2000).

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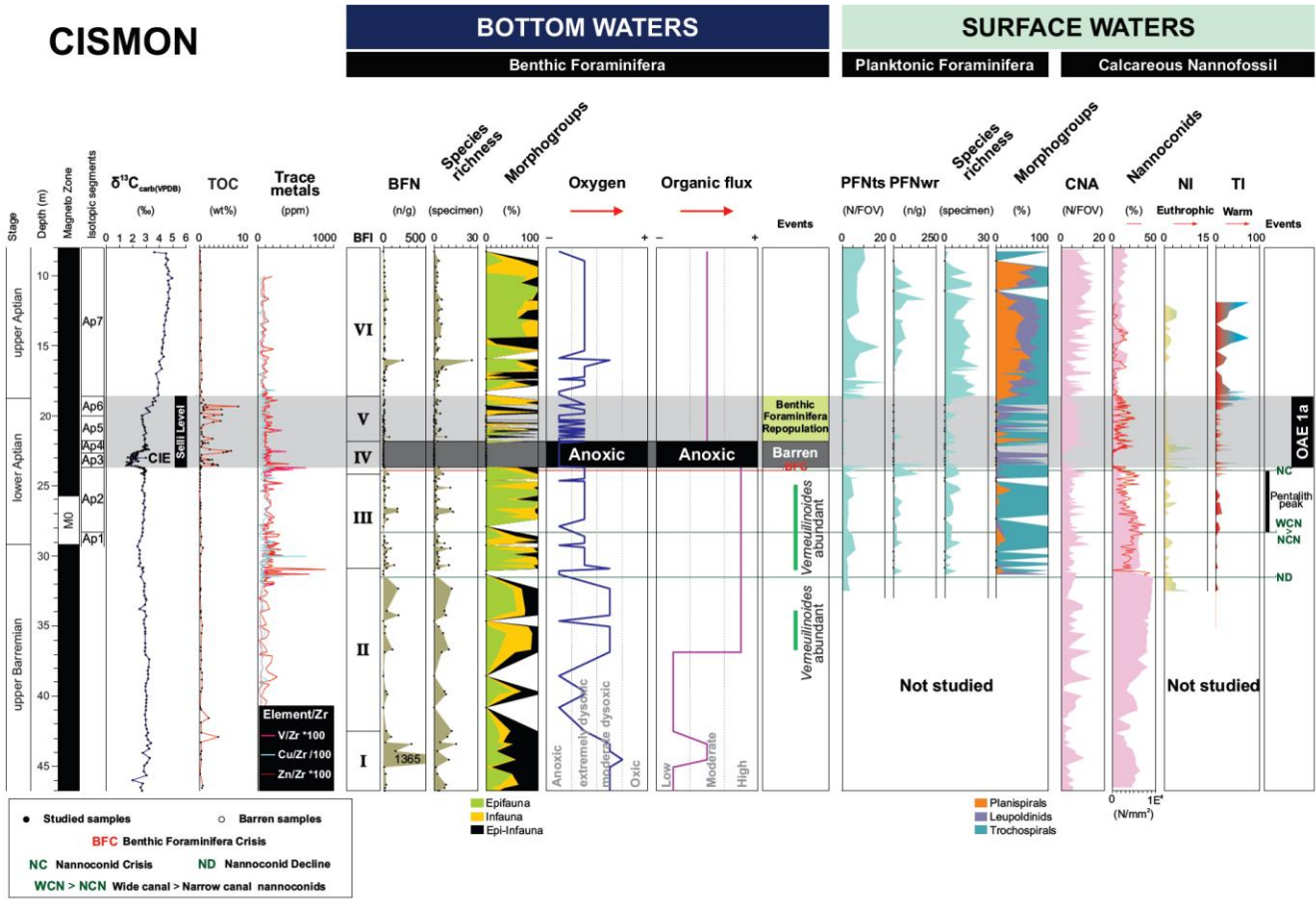
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1448 **Fig. 6.** Paleoenvironmental interpretation of the bottom-water and surface-water conditions based on
 1449 benthic foraminifera (this study), calcareous nannofossils (Erba and Tremolada, 2004; Erba et al.,
 1450 2010; Bottini et al., 2015) and planktonic foraminifera (Barchetta, 2015; this study) through the upper
 1451 Barremian-lower upper Aptian sedimentary sequence in the Cismon Core. Paleoenvironmental
 1452 interpretation of bottom-water conditions based on benthic foraminiferal assemblages (this work).
 1453 Magnetostratigraphy is from Channell et al. (2000). $\delta^{13}\text{C}_{\text{carb}}$ data are after Erba et al. (1999) and Méhay
 1454 et al. (2009). The isotopic segments Ap1-Ap7 are after Bottini et al. (2015). TOC is after Erba et al.
 1455 (1999) and Bottini et al. (2012). Trace metal abundances are after Erba et al. (2015). The Nannofossil
 1456 Nutrient Index (NI) and Temperature Index (TI) are from Bottini et al. (2015). BFI = Benthic
 1457 Foraminifera Intervals; BFN = benthic foraminifera absolute abundance; PFNwr = planktonic
 1458 foraminifera absolute abundance in washed residues n/40 field of view; n/g = number of specimens per
 1459 gram of washed residue; PFNts = planktonic foraminifera absolute abundance in thin sections; CNA =
 1460 calcareous nannofossils abundance; N/FOV = number of specimens per fields of view; ND =

1461 nannoconid decline at 31.50 m; NCN = narrow canal nannoconids; WCN= wide canal nannoconids;
1462 NC = nannoconid crisis at 23.90 m; BFC = benthic foraminifera crisis at 23.89 m.

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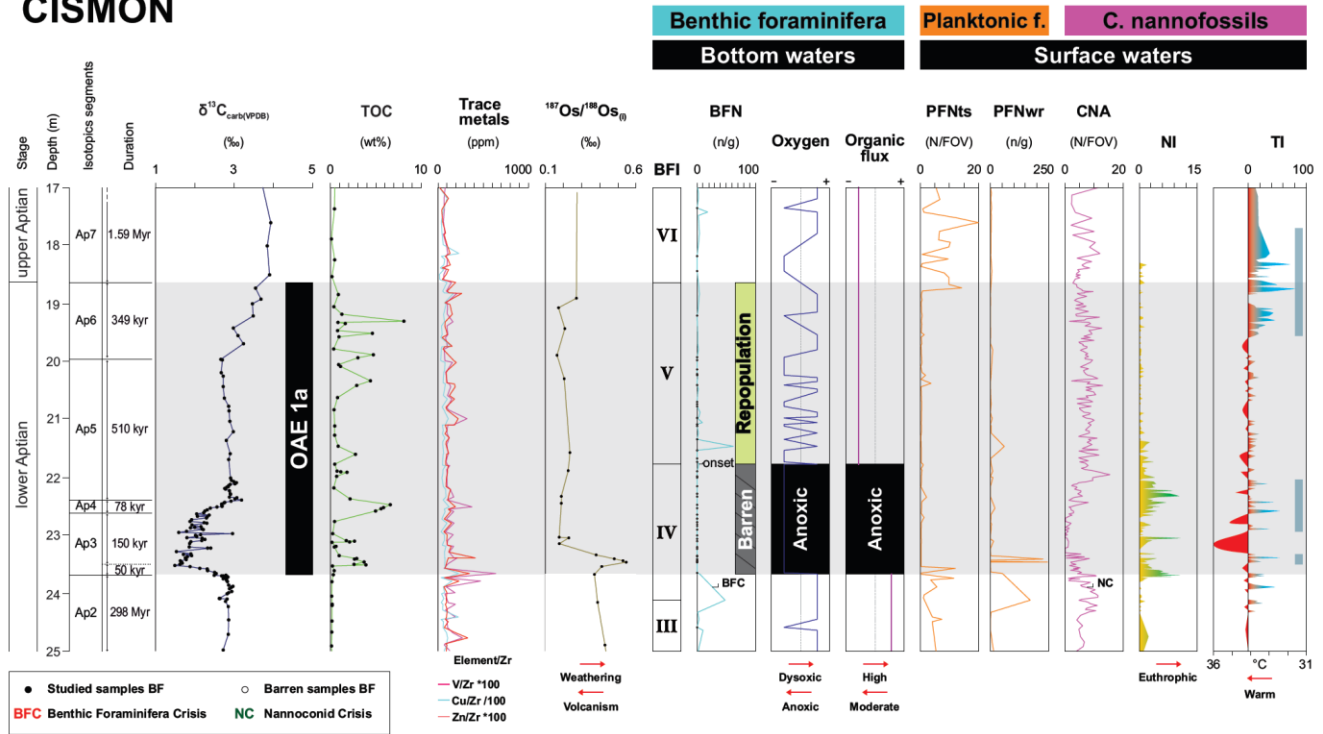
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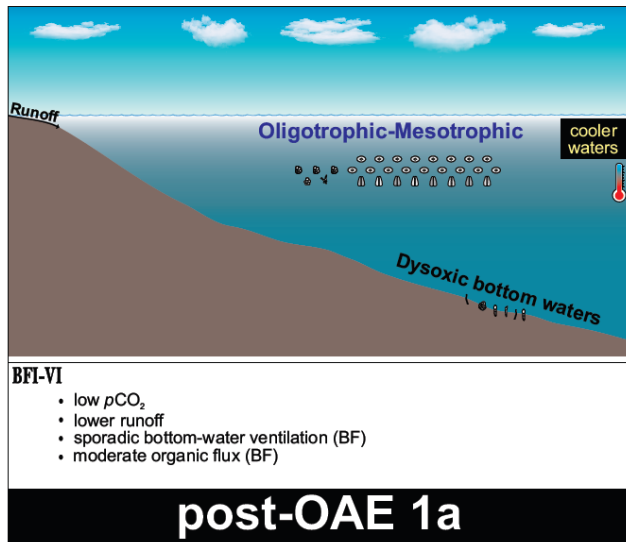
1486 **Fig. 7.** OAE 1a closeup in the Cismon Core. $\delta^{13}\text{C}_{\text{carb}}$ data are after Erba et al. (1999) and Méhay et al.
 1487 (2009). The isotopic segments Ap2-Ap7 after Bottini et al. (2015). Duration of the isotopic segments
 1488 according to Malinverno et al. (2010). TOC is after Erba et al. (1999) and Bottini et al. (2012). Trace
 1489 metal abundances are from Erba et al. (2015). The Os-isotope curve is after Bottini et al. (2012).
 1490 Benthic foraminiferal data (oxygen, organic flux) are from this study. Planktonic foraminiferal data are
 1491 after Barchetta (2015) and this study. Calcareous nannofossil data are after Erba et al. (1999) and
 1492 Bottini et al. (2015). The Nannofossil Nutrient Index (NI) and Temperature Index (TI) are from Bottini
 1493 et al. (2015). BFI = Benthic Foraminifera Intervals; BFN = benthic foraminifera absolute abundance;
 1494 PFNwr = planktonic foraminifera absolute abundance in washed residues, n/g = number of specimens
 1495 per gram of washed residue; PFNts = planktonic foraminifera absolute abundance in thin sections;
 1496 CNA = calcareous nannofossils abundance; N/FOV = number of specimens per fields of view; NC =
 1497 nannoconids crisis at 23.90 m, BFC = benthic foraminifera crisis at 23.89 m.

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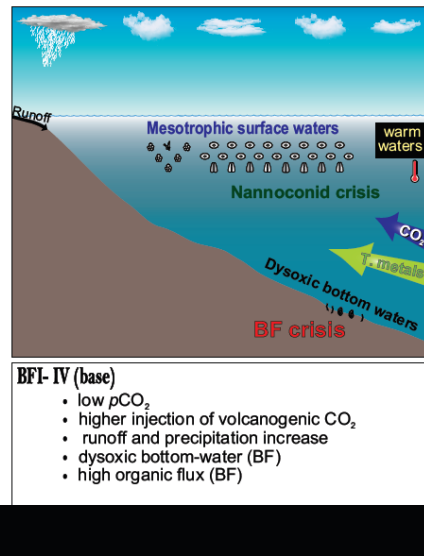
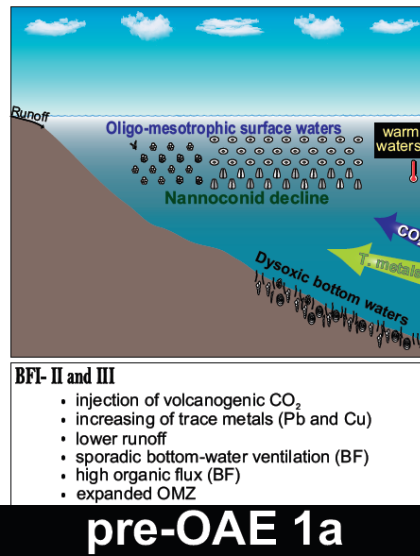
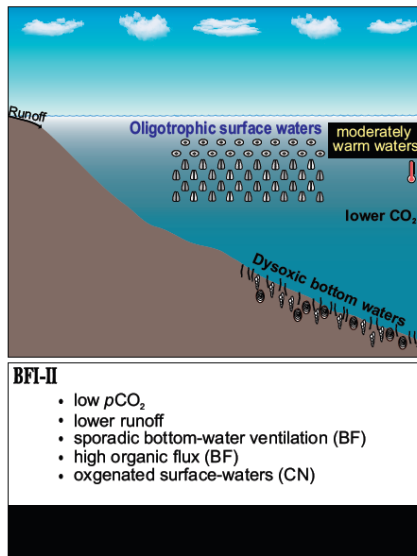
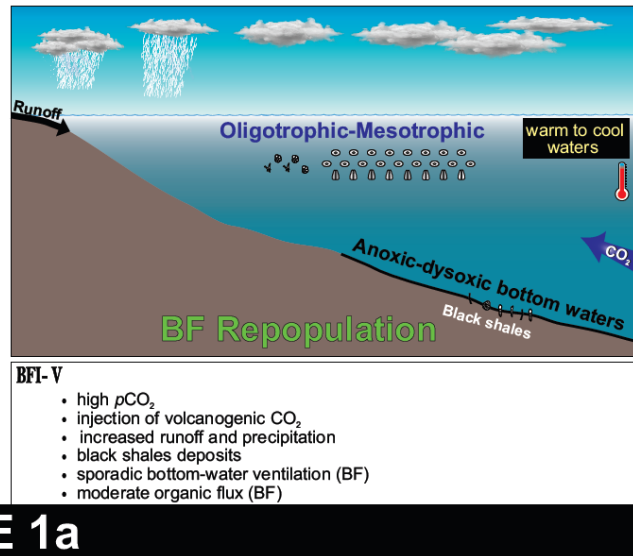
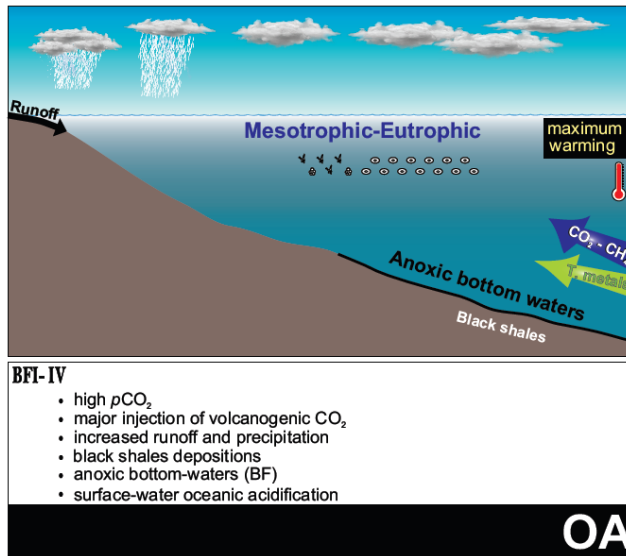
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Benthic foraminifera (BF)	
⌋ Bathysiphon	⌋ <i>Pleurostomella</i>
⊙ Glomospira	⌋ <i>Rhizammina</i>
⊗ Lenticulina	⌋ <i>Vermeuilinoides</i>
⌋ Laevidentalina	

Planktonic foraminifera (PK)	Calcareous nannofossils
⊗ Planispiral	⊙ Coccoliths
⊗ Trochospiral	⌋ Narrow-canal Nannoconids
⌋ Pseudo-planispiral	⌋ Wide-canal Nannoconids



pre-OAE 1a

1503 **Fig. 8.** Paleoceanographic reconstruction of bottom- and surface-water conditions in the Cismon Core
1504 from the late Barremian to the early late Aptian. See text for explanations.

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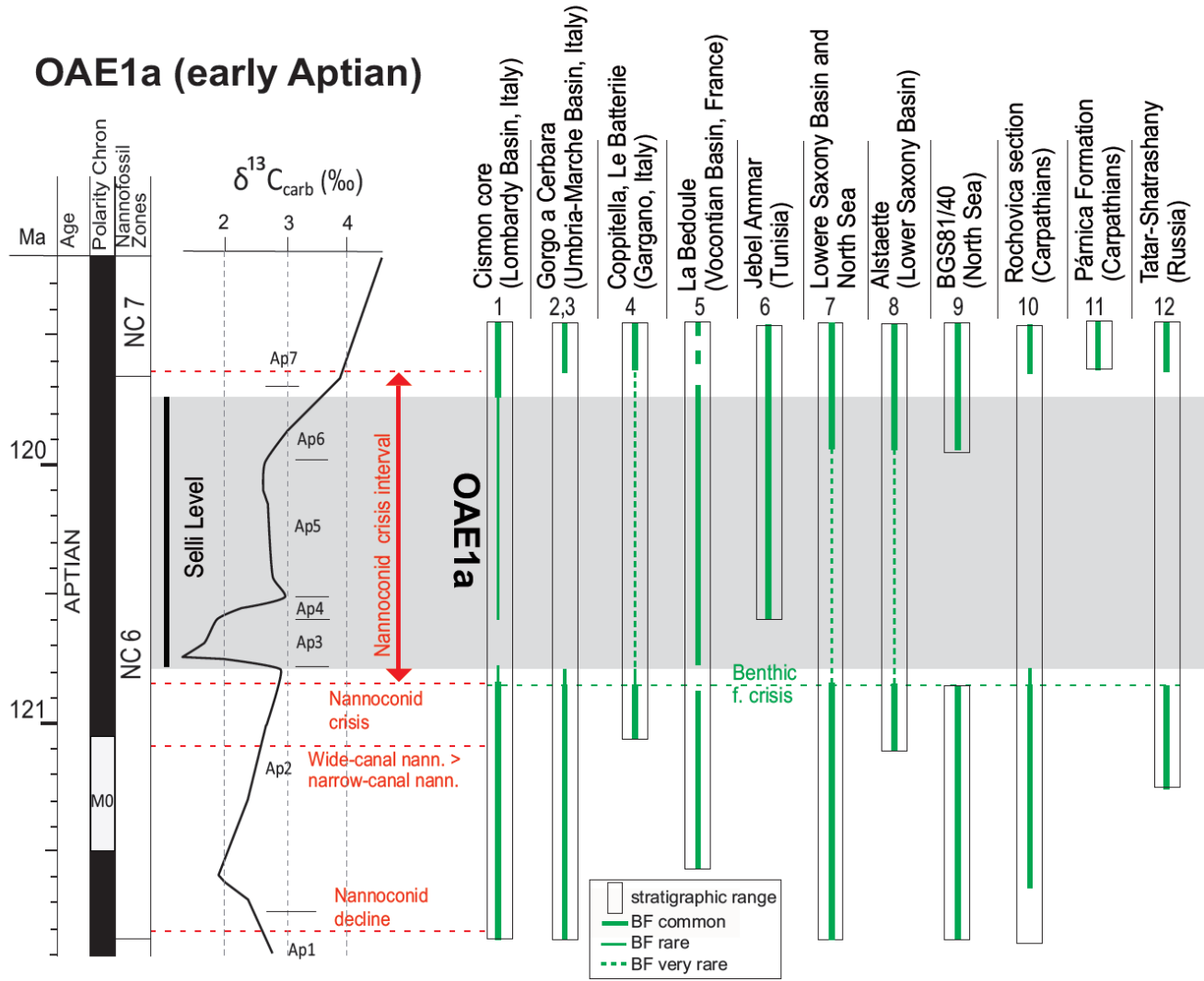
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OAE1a (early Aptian)



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1528 **Fig. 9.** Synthesis of the benthic foraminiferal abundance data across OAE 1a according to this study
 1529 and data from the literature, as follows: 1) this study; 2) Coccioni et al., 1992; 3) Patruno et al., 2015;
 1530 4) Cobianchi et al., 1999; 5) Moullade et al., 2015; 6) Elkhazri et al., 2013; 7) Mutterlose and Böckel,
 1531 1998; 8) von Bargen and Lehmann, 2014; 9) Rückheim et al., 2006; 10) Michalík et al., 2008; 11)
 1532 Józsa et al., 2016; 12) Zorina et al., 2017.

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BENTHIC FORAMINIFERA	MORPHOGROUPS				OXYGEN			ORGANIC FLUX			REFERENCES
	Epifauna	Shallow Epifauna	Shallow Infauna	Infauna	Low	Middle	High	Low	Middle	High	
<i>Ammodiscus</i>	X	X	X								1, 6, 9, 10, 11, 13, 17, 18
<i>Astacolus</i>	X		X	X							1, 12, 13, 18, 20
<i>Bathysiphon</i>	X										1, 6, 9, 10, 13, 19, 20
<i>Dentalina</i>	X		X								1, 4, 18
<i>Dorothia</i>				X							1, 3, 10, 19, 20
<i>Gavelinella</i>	X										1, 3, 10, 14, 15, 17, 20
<i>Glomospira</i>	X	X	X								1, 2, 3, 9, 10, 13, 17, 19
<i>Gyroidina</i>	X		X								1, 10, 15
<i>Haplophragmoides</i>		X	X	X							2, 3, 6, 13, 15, 17, 18, 19
<i>Hippocrepina</i>	X										6, 7
<i>Laevidentalina</i>			X	X							5, 12, 13, 14, 15, 16, 18, 20
<i>Lenticulina</i>	X		X	X							1, 4, 10, 12, 13, 18, 20
<i>Pleurostomella</i>			X								1, 4, 10, 12, 13, 19
<i>Reophax</i>			X	X							1, 5, 9, 13, 15, 18, 19, 21
<i>Rhizammina</i>	X										1, 2, 3, 5, 6, 8, 9, 11, 13, 15, 17, 23
<i>Verneuilinoides</i>				X							3, 7, 9, 11, 15, 22, 23

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1539 **Table 1.** Paleoecological preferences of benthic foraminifera according to their morphogroups based
1540 on previous studies, as follows: Koutsoukos, (1989)¹; Kuhnt and Kaminski, (1989)²; Koutsoukos and
1541 Hart, (1990)³; Kaiho, (1994)⁴; Tyszka, (1994)⁵; Nagy et al. (1995)⁶; Kuhnt, (1995)⁷; Kaminski and
1542 Kuhnt, (1995)⁸; van Den Akker et al. (2000)⁹; Frenzel, (2000)¹⁰; Szarek et al. (2000)¹¹; Holbourn et al.
1543 (2001)¹²; Alegret et al. (2003)¹³; Friedrich and Erbacher, (2006)¹⁴; Rückheim et al. (2006)¹⁵; Friedrich
1544 and Hemleben, (2007)¹⁶; Cetean et al. (2008)¹⁷; Reolid et al. (2008)¹⁸; Cetean et al. (2011)¹⁹; Koch and
1545 Friedrich, (2012)²⁰; Reolid and Ruiz, (2012)²¹; Patruno et al. (2015)²²; Józsa, (2017)²³.

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Group	BENTHIC FORAMINIFERA	PALEODEPTH											REFERENCES				
		0 E	IN	50	MN	100	ON	200	UB	500	MB	1000		LB	2000	AB	3000
I	<i>Ammodiscus</i>																4, 5,12
	<i>Astacolus</i>																5, 7,12,17
	<i>Bathysiphon</i>																4, 5, 8,12,13
	<i>Dorothia</i>																1, 4, 5,12
	<i>Glomospira charoides</i>																2, 3, 4, 5,16, 18
	<i>Gyroidina globosa</i>																7,15,19, 23
	<i>Rhizammina</i>																5,13,14
	<i>Verneuilinoides</i>																10,16
	<i>V. neocomiensis</i>																9, 22
II	<i>Glomospira</i>																2, 3, 4, 5,16, 18
	<i>G. gordialis</i>																2, 5, 18
	<i>Gavelinella</i>																1, 4, 5,12
	<i>Haplophragmoides</i>																5
	<i>H. gigas</i>																18
	<i>H. kirki</i>																24
	<i>Lenticulina</i>																4, 5,12, 14, 23
	<i>Reophax</i>																5,13,14
III	<i>Gavelinella intermedia</i>																3,14
	<i>Gyroidina nitida</i>																3,11, 23
IV	<i>Dentalina</i>																5,12
	<i>Gavelinella barremiana</i>																5, 6, 20
	<i>Laevidentalina</i>																14, 23
	<i>Pleurostomella</i>																4, 5,12
	<i>P. reussi</i>																16

1553

1554 **Table 2.** Paleobathymetric preferences of benthic foraminiferal taxa identified in the Cismon Core
1555 based on different sources, as follows: Sliter and Baker, (1972)¹; Bock, (1979)²; Nygon and Olson,
1556 (1984)³; De Azevedo et al. (1987)⁴; Koutsoukos, (1989)⁵; Riegraf, (1989)⁶; Saint-Marc, (1992)⁷; Nagy
1557 et al. (1995)⁸; Kuhnt, (1995)⁹; Kaminski et al. (1999)¹⁰; Schnack, (2000)¹¹; Frenzel, (2000)¹²; van Den
1558 Akker, et al. (2000)¹³; Holbourn et al. (2001)¹⁴; Alegret et al. (2003)¹⁵; Szydło, (2004)¹⁶; Haig,
1559 (2005)¹⁷; Kaminski and Gradstein, (2005)¹⁸; Moullade et al. (2005)¹⁹; Tyszka, (2006)²⁰; Bindu et al.
1560 (2013)²¹; Holbourn et al. (2013)²²; Aschckenazi-Polivoda et al. (2018)²³. For this study will be adopted
1561 the paleobathymetric subdivision (Nyong and Olsson, 1984 and van Morkhoven et al., 1986): inner-
1562 neritic (IN: 0–50 m), middle-neritic (MN: 50–100 m), outer-neritic (ON: 100–200 m), upper bathyal
1563 (UB: 200–500 m), middle bathyal (MB: 500–1000 m), lower bathyal (LB: 1000–2000 m) and abyssal

1564 (AB: > 3000 m). The grey band indicates the inferred paleobathymetry for the Cismon Core based on
1565 the composition of the benthic foraminiferal assemblages.

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1595 **Supplementary Data**

1596 *Comparison between the benthic foraminifera and calcareous plankton records the Cismon*
1597 *Core and the Gorgo a Cerbara section (see Figure S1)*

1598 Here we provide a comparison of the most important bioevents detected in benthic foraminifera,
1599 planktonic foraminifera, and calcareous nannofossils across the OAE 1a at Gorgo a Cerbara and
1600 Cismon Core. The two sections show many similarities that can be extrapolated from Supplementary
1601 Figure 1 and a few main differences that are commented as follows:

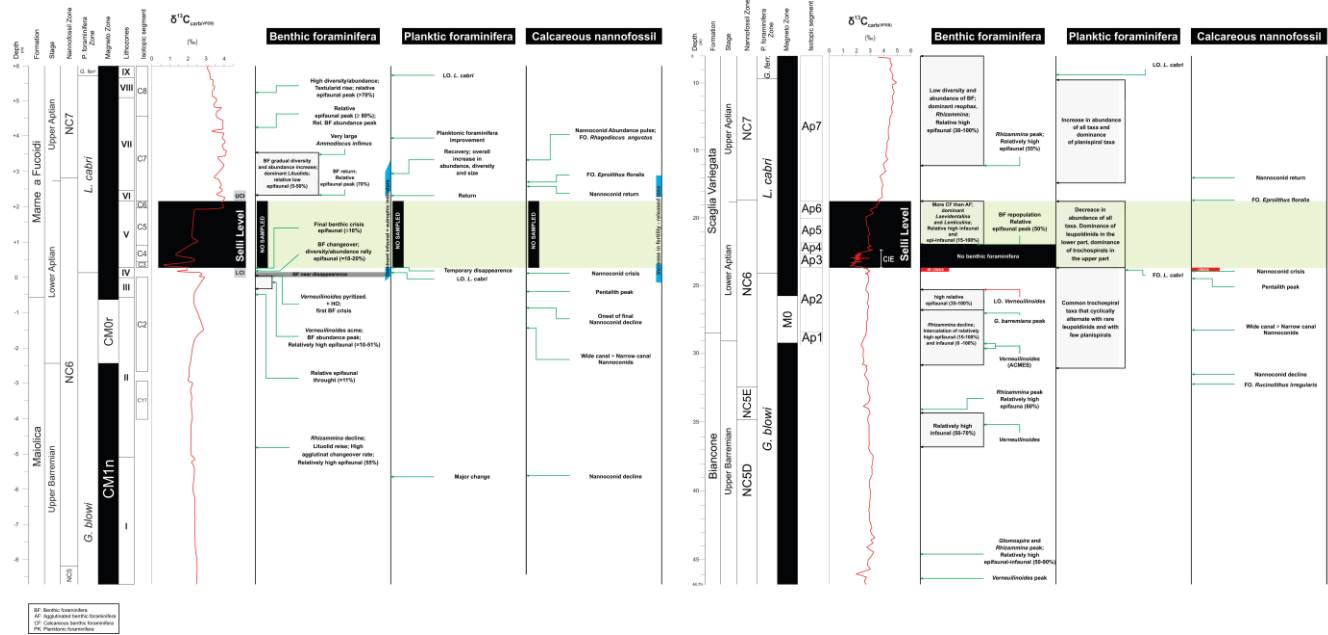
- 1602 1) The sampling resolution and the methodology adopted for the benthic foraminifera study are
1603 different. The benthic foraminiferal sampling resolution applied at Cismon along a 38.05 m
1604 thick section (159 samples) is from 5 to 50 cm (from 8 m to 31.29 m) and from 12 to 170 cm in
1605 the lower part (31.29 m – 46.75 m). Thus, it is higher compared to the 42 samples along the
1606 33.06 m-thick section at Gorgo a Cerbara.
- 1607 2) The size-fractions of the washed residues studied for benthic foraminifera are smaller for the
1608 Cismon ($> 63 \mu\text{m}$) compared to the Gorgo Cerbara ($> 125 \mu\text{m}$). This observation could explain
1609 the distribution of the genus *Verneuilinoides*, which is more abundant in the small-sized fraction
1610 $> 63 \mu\text{m}$ of the upper Barremian samples of the Cismon Core compared to the equivalent
1611 stratigraphic interval at Gorgo a Cerbara.
- 1612 3) In the Cismon Core, planktonic foraminifera are present within the Selli Level, although in low
1613 numbers and few samples are barren, whereas they are completely absent in the Selli Level at
1614 Gorgo a Cerbara (Coccioni et al., 1992; Coccioni, 2019). Moreover, at Gorgo a Cerbara, the 26
1615 cm-thick-interval below the Selli level is characterized by a marked decrease in the planktonic
1616 foraminiferal abundance and diversity, and the assemblage is composed of only poorly
1617 preserved trochospiral hedbergellids (lower critical interval: Coccioni et al., 1992). On the
1618 contrary, in the equivalent stratigraphic interval in the Cismon Core, planktonic foraminifera do

1619 not show a significant decrease in abundance, although, similar to Gorgo a Cerbara, the
 1620 assemblage is dominated by common trochospiral taxa.

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GORGO A CERBARA

CISMON



1622

1623 **Supplementary data, Figure S1.** Comparison of the benthic foraminifera, planktonic foraminifera and
 1624 calcareous nannofossil assemblage data across the Barremian-Aptian interval from the Gorgo a Cerbara
 1625 section (Italy) and the Cison Core (Italy, this study). Data from Gorgo a Cerbara: benthic
 1626 foraminifera, planktonic foraminifera, and calcareous nannofossil after Coccioni et al. (1992); Patruno
 1627 et al. (2015) and Coccioni (2019). $\delta^{13}\text{C}_{\text{carb}}$ data are after Stein et al. (2011) and Li et al. (2016). The
 1628 carbon isotopic segments Ap1 to Ap7 are after Bottini et al. (2015). Data from Cison: benthic
 1629 foraminifera (this work), planktonic foraminifera after Barchetta (2015) and this study, calcareous
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1674 **Supplementary data, Table S1.** Distribution chart of benthic foraminifera at Cismon Core (xls.).

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