

24 and faunal events in Earth's history that have implications for the current Anthropocene
25 global warming and rapid diversity loss. Here we evaluate these two events at the
26 stratotype localities in Tunisia and Egypt based on climate warming and environmental
27 responses recorded in faunal and geochemical proxies. The KPB mass extinction is
28 commonly attributed to the Chicxulub impact, but Deccan volcanism appears as a major
29 culprit. New mercury analysis reveals that major Deccan eruptions accelerated during the
30 last 10 ky and reached the tipping point leading up to the mass extinction. During the
31 PETM, climate warmed rapidly by ~5 °C, which is mainly attributed to methane
32 degassing from seafloor sediments during global warming linked to the North Atlantic
33 Igneous Province (NAIP). Biological effects were transient, marked by temporary
34 absence of most planktic foraminifera due to ocean acidification followed by the return of
35 the pre-PETM fauna and diversification. In contrast, the current rapid rise in atmospheric
36 CO₂ and climate warming are magnitudes faster than at the KPB or PETM events leading
37 to predictions of a PETM-like response as best case scenario and rapidly approaching
38 sixth mass extinction as worst-case scenario.

39

40 **1. INTRODUCTION**

41

42 One of the greatest challenges to our planet is the looming Anthropocene mass
43 extinction commonly attributed to human activity as the dominant influence on rapid
44 climate warming and changing environments as a result of fossil fuel burning (IPCC 5th
45 Assessment Report, 2013). This climate warming is commonly compared with the rapid
46 short-term ~5 °C warming known as the Paleocene-Eocene Thermal Maximum (PETM)

47 ~55.8 Ma. However, the PETM led to opposite results: major diversification in marine
48 and terrestrial life and significant species extinctions only in deep-water benthic
49 foraminifera. A better understanding of the impending Anthropocene catastrophe can be
50 gained from the rapid warming and mass extinction culminating at the Cretaceous-
51 Paleogene boundary (KPB also known as KPgB or KTB). In this study we examine both
52 the PETM and KPB events to gain insights into potential Anthropocene scenarios.

53 The PETM event (55.8 ± 0.2 Ma) lasted ~170 ky and is commonly attributed to
54 North Atlantic Igneous Province (NAIP) volcanism and methane degassing of seafloor
55 sediments (e.g., Dickens et al., 1995; Dickens, 2000; Westerhold et al., 2009; Charles et
56 al., 2011; Wieczorek et al., 2013; Gutjahr et al., 2017). The resulting global negative $\delta^{13}\text{C}$
57 excursion of 2-6 ‰ and rapid warming of 4.5-5 °C from tropical to high latitudes was
58 accompanied by ocean acidification and shoaling of the carbonate compensation depth
59 (CCD) by ~2000 m (e.g., Kennett and Stott, 1991; Sluijs et al., 2006; Zachos et al., 2003,
60 2005, 2006; Weijers et al., 2007; McInnery and Wing, 2011; Coccioni et al., 2012;
61 Gutjahr et al., 2017). In the marine realm planktic foraminifera and calcareous
62 nannoplankton, which form the essential food chain in the oceans, temporarily
63 disappeared but returned and diversified after the PETM (Lu and Keller, 1993, 1995a, b;
64 Kelly et al., 1996, 1998; Luciani et al., 2007, 2016). Only benthic foraminifera suffered
65 significant extinctions and these were restricted to bathyal depths where an estimated 37
66 % species went extinct (Alegret and Ortiz, 2006). No other groups in marine or terrestrial
67 realms suffered significant extinctions. On land tropical and subtropical forests spread
68 into higher latitudes during the PETM (Sluijs et al., 2006) and most animals reduced in

69 size and abundance (Smith et al., 2009). Shortly after the PETM mammals migrated,
70 thrived and diversified (Smith et al., 2009).

71 The KPB mass extinction (66.02 Ma) was marked by a negative 2-3 ‰ $\delta^{13}\text{C}$ shift
72 in surface but not deep waters, leading to an inverse surface-to-deep $\delta^{13}\text{C}$ gradient
73 generally attributed to reduced primary productivity and weakening of the marine
74 biological carbon pump (e.g., Zachos et al., 1989; Kump, 1991, 2003). Rapid climate
75 warming during the last 250 ky of the Maastrichtian, prior to the KPB, and cooling
76 during the first 500 ky of the early Paleocene are linked to Deccan volcanic eruptions
77 (review Punekar et al., 2014) About 50-75 % of all terrestrial and marine taxa went
78 extinct. In the oceans, extinctions affected the base of the food chain most severely
79 causing major extinctions in calcareous nannoplankton and near total extinction (99 %) of
80 marine planktic foraminifera (e.g., Keller, 1988a, 2001; MacLeod et al., 1997; Molina et
81 al., 1998; Keller et al., 2002; Luciani, 2002), but no significant extinctions in benthic
82 foraminifera (review in Culver, 2003). The extinction of non-avian dinosaurs is the most
83 famous example of the KPB mass extinction on land while many mammals survived
84 undergoing an explosive radiation during the Paleogene (review in Feduccia, 2014;
85 Wilson, 2014). Macrofloral diversity also decreased during the late Maastrichtian
86 warming and across the mass extinction horizon (e.g., Wilf et al., 2003; Wilf and
87 Johnson, 2004).

88 Both PETM and KPB events thus recorded extreme and rapid climate changes but
89 with nearly opposite effects on marine and terrestrial life – rapid evolutionary
90 diversification following the PETM event with extinctions restricted to deep water
91 benthic foraminifera but near total mass extinction in planktic foraminifera at the KPB.

92 Understanding when rapid climate change furthers evolutionary diversification and when
93 it leads to extinctions is critical to assessing the risk of current climate warming for
94 marine and terrestrial populations including humans in the coming decades. This study
95 explores the potential reasons for the differing biotic responses associated with rapid
96 climate warming during the PETM and KPB events and compares these with the current
97 rapid climate warming and biotic response of the Anthropocene. We hypothesize that the
98 biotic response mainly depends on the rate and tempo of greenhouse gas emissions into
99 the atmosphere and that extinctions are inevitable once the tipping point or critical
100 threshold is reached, which marks the onset of irreversible climate change from which
101 even small perturbations can result in runaway effects.

102 For this study we chose the globally recognized most complete sections for the
103 KPB and PETM events. For the KPB these are the Global Stratotype Section and Point
104 (GSSP) at El Kef and the auxiliary stratotype at Elles (Molina et al., 2009) 56 km
105 southeast of the city of El Kef, Tunisia, and for the PETM, the global GSSP at the
106 Dababiya quarry in Egypt (Figs. 1, 2). We focus on four topics: 1) planktic and benthic
107 species population changes in foraminifera, the groups most strongly affected by both
108 events; 2) evidence linking mass extinctions and faunal turnovers to climate change and
109 ocean acidification; 3) evidence linking these faunal events directly to volcanism; and 4)
110 comparison of KPB and PETM with the Anthropocene and potential sixth mass
111 extinction. Analyses are based on benthic and planktic foraminifera, carbon and oxygen
112 stable isotopes, mineralogy, and mercury (Hg) anomalies. (A description of methods,
113 materials and locations and of the environmental proxies is given in Supplementary
114 Materials S1; data tables are given in Supplementary Materials S2.)

115

116 **2. KPB MASS EXTINCTION: EL KEF AND ELLES**

117

118 **2.1. KPB-Defining Criteria**

119 The KPB is one of the easiest period boundaries to identify, whether based on
120 lithological changes in the field (Fig. 3), geochemical analysis in the laboratory, or fossil
121 content. The El Kef section was officially designated in 1989 as the Global Stratotype
122 Section and Point (GSSP) and Elles (discovered in the late 1990s) designated as auxiliary
123 stratotype (Molina et al., 2009). The five KPB defining and marker criteria are: (1) mass
124 extinction in planktic foraminifera, (2) evolution of first Danian species, (3) KPB clay
125 and red layer, (4) iridium (Ir) anomaly and (5) $\delta^{13}\text{C}$ negative shift. These KPB criteria
126 have proven globally applicable and independently verifiable in over 300 KPB sequences
127 worldwide (Cowie et al., 1989; Keller et al., 1995; Remane et al., 1999). Since planktic
128 foraminifera are the only marine microfossil group that suffered near total extinction,
129 they have remained the most reliable KPB-defining criteria. All other KPB markers, such
130 as the clay and red layers, Ir anomaly and $\delta^{13}\text{C}$ shift, are not unique signals in the
131 geological record and therefore cannot define the KPB in the absence of unique
132 biomarkers (review in Keller, 2011).

133 However, proponents of the Chicxulub impact as sole cause for the mass
134 extinction eliminated the five KPB identifying criteria in favor of just the "*Ir anomaly*
135 *associated with a major extinction horizon*" (Gradstein et al., 2004, ICS website on
136 GSSPs). Based on these two criteria and the assumption that the Ir anomaly is the result
137 of the Chicxulub impact, Molina et al. (2006, p. 263) concluded that "*in this way the KPB*

138 *is marked exactly by the moment of the meteorite impact*" and that "*This definition solves*
139 *problems of correlation in the Yucatan peninsula (Mexico) and its surroundings.*" Far
140 from solving "problems of correlation", this new definition has only introduced circular
141 reasoning to support the hypothesis that the Chicxulub impact is precisely KPB in age,
142 thus ignoring contrary evidence (Keller, 2011, Supplementary Materials S3). Fortunately,
143 the El Kef and Elles KPB sections remain identified by the original five criteria that are
144 the most reliable KPB markers.

145

146 **2.2. Biostratigraphy: Planktic Foraminifera**

147 Zone definitions are based on Keller et al. (1995, 2002) and include: zone CF2
148 (last appearance (LA) of *Gansserina gansseri* near the base of magnetochron C29r to first
149 appearance (FA) of *Plummerita hantkeninoides*), zone CF1 (range of *Plummerita*
150 *hantkeninoides*, extinct at the KPB), zone P0 (from the KPB to FA of
151 *Parvularugoglobigerina eugubina*), zone P1a(1) (FA of *P. eugubina* to FAs of
152 *Parasubbotina pseudobulloides* and/or *Subbotina triloculinoides*), and zone P1a(2) (LAs
153 of *P. eugubina* and *P. longiapertura*) correlative with the top of magnetochron C29r (Fig.
154 4). Thus, zones CF2 through P1a(2) correlate with magnetochron C29r (Li and Keller,
155 1998; Pardo et al., 1996). The time interval presented in this study for El Kef spans from
156 the latest Maastrichtian zone CF1 through the early Danian zones P0, P1a(1), P1a(2) and
157 lower part of P1b and for Elles from the upper part of zone CF1 to zone P1a(1)..

158 Recent U-Pb zircon dating of Deccan Traps yielded a duration of ~750 ky for
159 C29r (Schoene et al., 2015) with 200 ky equivalent to zone CF1 below the KPB and 500
160 ky equivalent to P0, P1a(1) and P1a(2) above the KPB. The late Maastrichtian intervals

161 used in this study at El Kef and Elles span the last ~68 ky and 70 ky below the KPB and
162 first ~500 ky and ~150 ky of the early Danian, respectively, plus an unknown age interval
163 of zone P1b in C29n (Fig. 4).

164

165 **2.3. Extinctions and Survivals**

166 The mass extinction at El Kef is shown in Figure 4 based on species ranges and
167 morphologies of the different planktic foraminiferal groups. The largest most specialized
168 and highly ornamented taxa, known as K-strategists (Fig. 4 #1-10), generally lived below
169 the surface in tropical and subtropical waters, utilized specialized food sources, had few
170 offspring and lived longer (Begon et al., 1996, 1998). They suffered reduced population
171 abundances and species dwarfing during the late Maastrichtian climate warming linked to
172 Deccan volcanism in C29r, zones CF1-CF2 (Li and Keller, 1998; Olsson et al., 2001;
173 Abramovich et al., 2003, 2010; Keller and Abramovich, 2009; Punekar et al., 2014;
174 Thibault et al., 2016; Thibault and Husson, 2016).

175 Quantitative species abundances at El Kef show that during this global warming
176 complex larger specialized species decreased in abundance and diversity (Fig. 5) as also
177 observed at Elles and worldwide (Abramovich and Keller, 2002; Punekar et al., 2014;
178 Keller et al., 2016). Among this group, the robust globotruncanids (16 species) are
179 generally rare with combined abundance of 6-13 %, which demonstrates the severe toll
180 climate warming and related stresses (e.g., ocean acidification, high nutrient influx from
181 Deccan volcanism and terrestrial runoff due to increased humidity) exerted on marine
182 plankton leaving them prone to extinction.

183 A small group of species (about 1/3 of planktic foraminiferal assemblages)
184 survived relatively well during the pre-KPB C29r climate warming (zone CF1, Figs. 4,
185 5). These were relatively small species with simple biserial and trochospiral
186 morphologies, with little shell ornamentation. They were ecologically more tolerant, r-
187 strategists that thrived in varied environments from low to high latitudes, utilized diverse
188 food sources, had short life spans and reproduced rapidly with many offspring (review in
189 Keller and Abramovich, 2009). This group had high survival potential but just one
190 species survived long-term – the disaster opportunist *Guembelitra cretacea*.

191 There is general agreement that between 8-16 smaller species survived for about
192 50-150 ky into the early Danian (Figs. 4, 5) but survivorship is difficult to ascertain for
193 most species because reworked Cretaceous species are common above the KPB. This is
194 mainly due to the early Danian global cooling, lower sea level and erosion that frequently
195 resulted in hiatuses eroding the underlying KPB interval and latest Maastrichtian
196 particularly in shallow water environments (Keller et al., 2013, 2016; Mateo et al., 2017).
197 Clues to survivorship include consistent presence in Danian sediments, good
198 preservation, generally dwarfed specimens and Danian isotope values. Only *Heterohelix*
199 *globulosa*, *H. planata*, *Paraspiroplecta navarroensis*, *Pseudoguembelina costulata*,
200 *Guembelitra cretacea*, *Hedbergella monmouthensis*, *H. holmdelensis*, *Globigerinelloides*
201 *asper* and *G. yaucoensis* are proven mass extinction survivors to date (e.g., Barrera and
202 Keller, 1990; Pardo and Keller, 2008; Ashckenazi-Polivoda et al., 2011). Other species
203 are also consistently present well into the early Danian but have yet to be conclusively
204 determined as survivors (e.g., *Pseudoguembelina costellifera*, *P. kempensis*,
205 *Globigerinelloides subcarinatus*; Figs. 4-6).

206 Among the survivors, four biserial species (*P. costulata*, *H. globulosa*, *H. planata*,
207 *P. navarroensis*), at least three trochospiral species (*Hedbergella monmouthensis*, *H.*
208 *holmdelensis*, *Globigerinelloides yaucoensis*), and one triserial species (*G. cretacea*), are
209 known to tolerate low oxygen conditions. These dominate late Maastrichtian assemblages
210 and range well into the early Danian with reduced to sporadic presence (Figs. 4-6) (Pardo
211 and Keller, 2008; Ashckenazi-Polivoda et al., 2011). But they also suffered beginning in
212 the latest Maastrichtian (upper zone CF1) and into the early Danian as evident by species
213 dwarfing, deformed chambers and reduced population abundances (Fig. 6) (review in
214 Keller and Abramovich, 2009).

215 The KPB mass extinction has just one long-term survivor, *G. cretacea*, which is
216 known as a disaster opportunist. This species thrived during maximum stress conditions
217 and dominated faunal assemblages of the latest Maastrichtian and early Danian (>90 %)
218 at El Kef and Elles (Figs. 5, 6) (Pardo and Keller, 2008; Punekar et al., 2014).
219 *Guembelitria cretacea* was the smallest planktic foraminifer (63-100 μm) and responded
220 to high-stress conditions by dwarfing (size reduction to 38-63 μm), irregular deformed
221 chambers (Coccioni and Luciani, 2006), and less frequently gigantism (Keller, 2014).
222 During optimal environmental conditions, this disaster opportunist disappeared from
223 open marine assemblages but survived in high-stress near-shore refugia.

224

225 **2.4. Species Dwarfing**

226 Species dwarfing, also known as the Lilliput effect, marks morphologic and
227 intraspecies size reductions in response to environmental stresses commonly associated
228 with, but not restricted to, the aftermath of mass extinctions (Keller and Abramovich,

229 2009). In addition to planktic foraminifera across the KPB mass extinction, the Lilliput
230 effect has been observed in many groups, including ostracods, mollusks and bivalves, of
231 the Permo-Triassic mass extinction (Payne, 2005; Twitchett, 2007; Chu et al., 2015),
232 shelly faunas and microbial carbonates preceding the end-Devonian mass extinction
233 (Whalen et al., 2002; Bosetti et al., 2010), crinoids of the end-Ordovician mass extinction
234 (Borths and Ausich, 2011) and graptolites of the upper Silurian (Urbanek, 1993). This
235 suggests a universal biotic response to environmental stress, regardless of cause, timing
236 or nature of organisms.

237 High-stress environments are associated with rapid climate change, mesotrophic
238 or restricted basins, shallow marginal settings and volcanically active regions. For
239 example, Large Igneous Province (LIP) volcanism is currently associated with four of the
240 five Phanerozoic mass extinctions, whereas Hg anomalies, a proxy for volcanism, are
241 reported from all five (da Silva et al., 2008; Grasby et al., 2013; Percival et al., 2015;
242 Thibodeau et al., 2016; Font et al., 2016; Gong et al., 2017). Second order volcanic
243 events (e.g., Ninetyeast Ridge and Andean volcanism) are at least in part related to the
244 early late Maastrichtian faunal turnover (Keller, 2003; Keller et al., 2007; Mateo et al.,
245 2017).

246 Among planktic foraminifera the sequence of responses to increasingly high
247 environmental stress developed in 5 stages that form a stress continuum from optimum
248 open marine conditions to increasingly stressful environments associated with rapid
249 climate warming and volcanic activity leading to catastrophe (Fig. 7). The five stages of
250 this stress continuum include: (1) elimination of large specialized species (K-strategists),
251 (2) intraspecies dwarfing, (3) dominance of low oxygen tolerant small heterohelicids (r-

252 strategists), (4) decline of heterohelicids and (5) dominance of disaster opportunist
253 *Guembelitra* species (Keller and Abramovich, 2009).

254 This sequence of stress-induced biotic events is demonstrated at El Kef and Elles,
255 as well as in all continuous KPB sequences worldwide (Pardo and Keller, 2008; Keller
256 and Abramovich, 2009). Stages 1-2 are evident by the dramatic reduction in large K-
257 strategist species populations and dwarfing of survivors, which was first linked to global
258 warming caused by Deccan volcanism in magnetochron C29r at South Atlantic DSDP
259 Site 525A (Abramovich and Keller, 2003). Stage 3 marks the rising dominance of r-
260 strategists, followed by dwarfing in stage 4 and declining populations. Stage 5 marks
261 maximum stress resulting in decreased populations of r-strategists and dominance of the
262 disaster opportunist *Guembelitra*.

263 Figure 6 shows the effects of species dwarfing across the KPB transition based on
264 $>63 \mu\text{m}$ and $38\text{-}63 \mu\text{m}$ size fractions at Elles. In the $>63 \mu\text{m}$ size fraction below the KPB,
265 the same four biserial taxa dominate the assemblage as at El Kef and *Guembelitra*
266 *cretacea* is rare (Fig. 6A). After the mass extinction, *G. cretacea* dominates ($>95\%$) but
267 the interval between 7 cm to 80 cm above the KPB is barren in the $>63 \mu\text{m}$ size fraction
268 with species abruptly reappearing above (Fig. 6A).

269 Analysis of the smaller size fraction ($38\text{-}63 \mu\text{m}$) reveals the missing fauna as
270 dwarfed due to increased stress (Fig. 6B). The most notable difference is the dominance
271 of dwarfed disaster opportunist *G. cretacea* and low oxygen tolerant *P. navarroensis* and
272 *H. planata*. Dwarfed *Guembelitra* populations up to 90 % of the total foraminiferal
273 assemblages are frequently observed below the KPB in shallow shelf to open marine and
274 in volcanically stressed environments (review in Pardo and Keller, 2008). Similar

275 *Guembelitra* blooms dominated (~90 %) after the KPB mass extinction, although they
276 are generally not dwarfed. This suggests that environmental stress was higher before the
277 mass extinction than in its aftermath.

278

279 **2.5. Evolution and Delayed Recovery**

280 Evolution of new species began in zone P0 immediately after the mass extinction
281 (Fig. 8). The first new species were very small (38-63 μm), unornamented, with simple
282 globular chamber arrangements in biserial, triserial and trochospiral morphologies (Figs.
283 4-6). Low diversity assemblages of 10 to 15 species with slightly larger (63-100 μm)
284 morphologies persisted for the first 500 ky (zones P1a(1)-P1a(2)) after the mass
285 extinction, marking a long crisis interval. Cretaceous survivor species gradually
286 disappeared in zone P1a(1) (Fig. 8). Dwarfing, slow evolution, simple small species
287 morphology and gradual disappearance of dwarfed survivor species during the early
288 Danian mark continued high-stress environments dominated by the disaster opportunist
289 *Guembelitra* and the new crisis opportunists *Parvularugoglobigerina eugubina* and *P.*
290 *longiapertura* (Figs. 5, 6).

291 A clue to the nature of this crisis interval is seen in the negative 2-3 ‰ $\delta^{13}\text{C}$
292 excursion at the KPB that represents a sudden drop in primary marine productivity at the
293 mass extinction horizon (Fig. 5). During the early Danian, planktic $\delta^{13}\text{C}$ values at El Kef
294 and Elles remained 1-2 ‰ below benthic values for the first ~500 ky correlative with the
295 delayed recovery in marine plankton (Keller and Lindinger, 1989; Stüben et al., 2003).
296 This interval is followed by the rapid positive 2 ‰ $\delta^{13}\text{C}$ excursion at the P1a(2)/P1b zone
297 boundary (C29r/C29n) that signals the onset of recovery coincident with the end of the

298 main phase of Deccan volcanism (Fig. 5). Thus the delayed recovery appears to be due to
299 continued volcanic eruptions. For marine plankton, the $\delta^{13}\text{C}$ recovery lead to a major re-
300 organization, including the near disappearance of the disaster opportunist *Guembelitra*
301 (Fig. 5), extinction of the dominant crisis interval taxa (*P. eugubina*, *P. longiapertura*, *P.*
302 *extensa*), dominance of *Praemurica taurica* and small biserial low oxygen tolerant
303 species (*Chiloguembelina morsei*, *Woodringina hornerstownensis*, *W. claytonensis*),
304 increased diversity and gradual appearance of larger morphotypes particularly in zone
305 P1c (Fig. 8).

306

307 **2.6. Benthic Foraminifera**

308 There is no mass extinction in benthic foraminifera across the KPB globally but
309 they suffered a severe and prolonged faunal turnover (Fig. 9). At El Kef, 42 % (21
310 species) of 50 calcareous benthic species identified disappeared at the KPB and remained
311 absent through the early Danian zone P1a-P1b interval analyzed (>500 ky) (Keller
312 1988b). During the early Danian P0-P1a high-stress interval, 16 % (8 species)
313 temporarily disappeared, 30 % (15 species) ranged through with *Anomalinoides acutus*
314 dominant in the high-stress P1a interval and 12 % (6 species) appeared in the early
315 Danian. Correlative with this faunal turnover is the drop in CaCO_3 from ~50 % (pre-
316 KPB) to <10 % (post-KPB) in the sediments, high terrestrial organic influx (due to
317 enhanced weathering) and low oxygen in the water column and seafloor sediments
318 (Keller and Lindinger, 1989). These high nutrient conditions favored epifaunal
319 assemblages dominated by *A. acutus* scavenging food on the seafloor. Infaunal
320 assemblages largely disappeared returning with increased oxygen in sediments in zone

321 P1b (Fig. 9). Speijer and Van der Zwaan (1996) also analyzed El Kef benthic
322 foraminifera. Their faunal turnover results slightly differ from Keller (1988b) with the
323 main difference being the larger number of disappearing and temporarily absent species,
324 which is largely due to their inclusion of agglutinated and non-specified genera
325 groupings.

326 How representative is the El Kef benthic faunal turnover pattern on a global
327 basis? Culver (2003, p. 214) reviewed published reports across latitudes and palaeodepths
328 and concluded: "*if the percentage data are taken at face value and averaged for shallow,*
329 *intermediate and deep water, the results come out as follows: shallow, 40 % disappear;*
330 *intermediate, 35 % maximum, 29 % minimum disappear; deep, 29 % maximum, 19 %*
331 *minimum disappear.*" Note that "disappear" means that most or all of these taxa returned
332 after the stress event in the aftermath of the KPB mass extinction. Although these data are
333 incomplete and percentage values may have large errors, a major environmental change
334 is evident on the seafloor across latitudes and palaeodepths but no mass extinction is
335 recorded.

336

337 **3. ENVIRONMENTAL PROXIES: KPB**

338

339 During the late Maastrichtian, rapid and extreme climate warming, interrupted by
340 short cool events, began in the lower half of zone CF2, coincident with the onset of major
341 Deccan volcanic eruptions near the base of C29r about 350 ky prior to the mass
342 extinction (Li and Keller, 1998; Punekar et al., 2014; Thibault et al., 2016). Figure 10
343 shows climate changes ($\delta^{18}\text{O}$) and Hg anomalies (proxy for Deccan volcanism) during

344 the last 70 ky of the Maastrichtian leading up to the mass extinction at Elles. No
345 temperatures have been calculated from this $\delta^{18}\text{O}$ data because diagenetic alteration of
346 foraminiferal shell calcite shifts values negative though temperature trends are preserved
347 (see Supplementary Materials S4). Hg in sediments is a byproduct of explosive
348 volcanism and has a residence time of 1-2 years in the atmosphere during which it is
349 distributed by winds worldwide before fallout and accumulation in sediments (Grasby et
350 al., 2013; Thibodeau and Bergquist, 2017). Since Hg is commonly concentrated in
351 organic carbon, it is typically normalized and shown as the ratio of Hg to total organic
352 carbon (Hg/TOC).

353 The Elles $\delta^{18}\text{O}$ record indicates a relatively cool climate from 70-40 ky pre-KPB
354 during a volcanically quiet period (Fig. 10). About 40 ky pre-KPB, surface water rapidly
355 warmed coincident with major Deccan eruptions but warming in bottom waters is
356 delayed by several thousand years. During the last 10 ky pre-KPB, climate remained
357 warm and Hg/TOC ratios remained high. Through this interval Hg/TOC ratios mark peak
358 volcanic activity with accelerating eruptions reaching maximum values at the KPB mass
359 extinction (2498 ppb/wt%; 1291 ppb/wt% at El Kef).

360 We interpret the Hg/TOC ratios at Elles as recording Deccan eruptions with the
361 high ratios indicating larger or more explosive eruptions. Maximum climate warming and
362 accelerating massive Deccan eruptions during the last 10 ky may mark the tipping point
363 for planktic foraminifera. From this point on, extinctions are rapid culminating at the
364 KPB. Faunal assemblages during this interval are dominated by stress-tolerant and
365 generally dwarfed survivor taxa with the disaster opportunist *G. cretacea* being the most
366 abundant (Figs. 5, 6A,B). At El Kef, faunal proxies indicate diversity loss, decreasing

367 P/B ratio, increasing fragmentation in planktic foraminifera due to dissolution and high
368 abundance of dwarfed *Guembelitra* populations (Fig. 11). Similar faunal extinctions,
369 disaster opportunists and dissolution coincident with high Hg/TOC ratios have been
370 recorded during the last 30-50 ky pre-KPB in France, Austria and Spain and interpreted
371 as ocean acidification (Font et al., 2016; Punekar et al., 2016).

372 Ocean acidification linked to Large Igneous Province (LIP) volcanism has been
373 identified for the PETM and mass extinctions at the KPB, end-Triassic and end-Permian
374 (Hönisch et al., 2012). CO₂ emissions into the atmosphere from LIP volcanism can
375 severely perturb the carbon cycle. If the rate of atmospheric *p*CO₂ increase overtakes the
376 buffering time/capacity of the ocean (~1000 yrs; Zeebe, 2012), seawater carbonate
377 chemistry can be seriously altered resulting in the lowering of carbonate ion
378 concentration ([CO₃²⁻]) and the surface ocean pH (Kump et al., 2009). Ocean
379 acidification leads to calcification crises in shelly organisms, such as nannofossils,
380 foraminifera, bivalves, gastropods and pteropods, and has increasingly been identified as
381 an important mechanism linking major volcanic episodes, including the PETM and KPB,
382 with faunal turnovers and mass extinction events (Hönisch et al., 2012; Font et al., 2016;
383 Punekar et al., 2016; Bond and Wignall, 2016).

384 The most characteristic KPB signals, apart from the Ir anomaly and mass
385 extinction, are the drop in CaCO₃ to near 0 %, the Hg anomalies and high Hg/TOC ratios,
386 and the 2-3 ‰ drop in δ¹³C, which is attributed to the mass extinction, loss of primary
387 productivity and collapse of the biological carbon pump (Fig. 11). All faunal proxies
388 indicate continued high-stress conditions through the early Danian C29r (~500 ky). The
389 inverse surface-to-deep δ¹³C gradient persisted for ~1 Myr into C29n and CaCO₃

390 remained low (<10 %). During these stress conditions the disaster opportunist
391 *Guembelitria* dominated but alternated with the evolving short-ranging opportunist *P.*
392 *longiapertura* (Fig. 5). The onset of recovery resulted in the extinction of the latter, near
393 disappearance of the former, increased abundance of earlier taxa and evolution of new
394 species. The recovery is led by a gradual return to higher productivity ($\delta^{13}\text{C}$) and
395 increased CaCO_3 (>30 %) (Fig. 11). The cause for this delayed recovery has long
396 remained an enigma. The answer appears to be continued Deccan volcanism after the
397 mass extinction as indicated by Hg/TOC anomalies.

398

399 **4. PALEOCENE-EOCENE THERMAL MAXIMUM (PETM): DABABIYA (GSSP)**

400

401 The Dababiya GSSP is located on the eastern side of the upper Nile Valley and 35
402 km southeast of Luxor at 25°30'N, 32°31'E (Fig. 2). Sediment deposition occurred at
403 outer shelf depth between 150-200 m (Alegret et al., 2005) in a submarine channel (Fig.
404 12A-C). The outcrop is fragile because it forms a precarious point jutting out at the
405 turning point between eastern and northwestern parts of the channel and a vertical
406 fracture runs through it. The section was sampled at 50 m to the northwest and 25 m to
407 the east of the turning point, which partially collapsed in the spring of 2016 along the
408 vertical fracture (Fig. 12C).

409 Khozyem et al. (2014, 2015) published geochemical and stratigraphic studies of
410 the two sampled sequences. Earlier publications reported on mineralogy and
411 geochemistry (Dupuis et al., 2003; Soliman et al., 2006; Schulte et al., 2011), and
412 planktic and benthic foraminifera (Speijer et al., 1995; Speijer and Schmitz, 1998; Speijer

413 and Wagner, 2002; Berggren and Ouda, 2003; Alegret et al., 2005; Alegret and Ortiz,
414 2006). Here we present new quantitative data on the planktic foraminiferal response to
415 the PETM event at the section 25 m east from the GSSP cliff compared with benthic
416 foraminifera and previously published stable isotope records (Alegret and Ortiz, 2006;
417 Dupuis et al, 2003) (Fig. 12B, C).

418

419 **4.1. PEB-Defining Criteria**

420 The PEB is defined based on: (1) global $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{13}\text{C}_{\text{carb}}$ isotope excursions
421 (CIE), (2) disappearance of the deep water benthic foraminifer *Stensioina beccariiformis*,
422 (3) transient occurrence of planktic foraminifera (*Acarinina africana*, *A. sibiyaensis*,
423 *Morozovella allisonensis*) during the $\delta^{13}\text{C}$ excursions, (4) transient occurrence of the
424 nannofossil *Rhomboaster* spp. – *Discoaster araneus* assemblage and (5) acme of the
425 dinoflagellate *Apectodinium* (Aubry et al., 2007). At our Dababiya section 25 m east of
426 the GSSP cliff, these PEB defining characteristics are identified. Lithology and
427 geochemistry are discussed in Khozyem et al. (2014, 2015).

428

429 **4.2. Biostratigraphy: Planktic Foraminifera**

430 Biostratigraphy for the Dababiya section is based on high-resolution planktic
431 foraminifera and the standard biozonation scheme by Olsson et al. (1999) and Pearson et
432 al. (2006) (Fig. 13A). The sampled interval spans zones P4c, P5, E1 and E2 covering an
433 estimated time span of 2 Myr (54.5-56.5 Ma). Zone P4c marks the base of the section as
434 indicated by the last appearance (LA) of the index species *Globanomalina*
435 *pseudomenardii* and an assemblage dominated by *Igorina tadjikistanensis*, *Acarinina*

436 *soldadoensis*, *Subbotina hornibrooki*, *Morozovella acuta* and *M. aequa*. The interval
437 from the extinction of *Gl. pseudomenardii* to the first appearance (FA) of *Acarinina*
438 *sibaiyaensis* defines zone P5 and the top of the Paleocene. At Dababiya, zone P5 marks
439 the onset of the PETM with a 40 % increase in species diversity (from 21 to 35 species)
440 and decreased abundance of the dominant zone P5 species correlative with a gradual
441 decrease in $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{13}\text{C}_{\text{carb}}$ values culminating at the PEB (Fig. 13A).

442 Above the PEB, zone E1 spans 1 m with the basal 42 cm a barren clay devoid of
443 CaCO_3 marking dissolution/ocean acidification (Fig. 13A). Between 42-47 cm is a 5 cm
444 thick radiolarian-rich interval with the transient PETM fauna dominated by *A.*
445 *sibaiyaensis* and *A. africana* and FA of *A. africana* and *Morozovella allisonensis*. The 50
446 cm above mark the onset of recovery with increasing $\delta^{13}\text{C}$ values and rare foraminifera in
447 the upper 20 cm. The E1/E2 boundary is placed at the first continuous occurrence of
448 *Pseudohastingerina wilcoxensis* 1 m above the PEB coincident with the reappearance of
449 diverse assemblages that existed already during the latest Paleocene. Just four species
450 disappeared as they morphed into new species - a phenomenon known as
451 pseudoextinction. Returning species have generally larger shell sizes than before their
452 temporary disappearance, show morphological diversification and speciation (Lu and
453 Keller, 1993, 1995a, b; Lu et al., 1998; Kaiho et al., 2006; Kelly et al., 1996, 1998; Pardo
454 et al., 1999; Berggren and Ouda, 2003; Luciani et al., 2007, 2016; Khozyem et al., 2014).
455 Thus, despite major climate warming, decreased productivity and ocean acidification, the
456 PETM caused no significant species extinctions, likely due to migration into higher
457 latitudes during warming, and fostered major diversification in its aftermath.

458

459 **4.3. Benthic Extinction and Faunal Turnover Event**

460 Alegret et al. (2005, Alegret and Ortiz, 2006) reported a major benthic faunal
461 turnover at the Dababiya section (Fig. 13B) but only 7 species (18 %) went extinct, 82 %
462 were survivors that reappeared after the PETM acidification event, and 26 % new species
463 evolved during environmental recovery. Similar observations are reported from marginal
464 and epicontinental seas (Speijer and Schmitz, 1998; Speijer and Wagner, 2002). But in
465 lower bathyal to abyssal environments (e.g., Alamedilla, Spain) species extinctions
466 reached ~37 % (Alegret et al., 2009), which is in the lower estimate of the previously
467 reported extinction ranging between 30-50 % (Thomas, 1998). Thus, significant benthic
468 extinctions were restricted to deep-water environments and generally concentrated at the
469 onset of the PETM event. This can be explained by the observed shoaling of the CCD by
470 2000 m during the PETM (Zachos et al., 2008).

471

472 **5. ENVIRONMENTAL PROXIES: PEB**

473

474 The PETM is marked by a global temperature increase of 5-9 °C over an interval
475 variously estimated ~10 ky or ~30 ky and estimated loading of 2,000 Gt of isotopically
476 light carbon to the atmosphere and oceans (Zachos et al., 2003, 2005, 2006; Sluijs et al.,
477 2006; Weijers et al., 2007). A low correlation coefficient of CaCO₃ vs. $\delta^{13}\text{C}_{\text{carb}}$ ($R^2 =$
478 0.025) indicates limited diagenetic overprinting on the $\delta^{13}\text{C}_{\text{carb}}$ values but $\delta^{18}\text{O}$ data are
479 strongly affected by diagenesis (see Supplementary Materials S4, Fig. S11).

480 Faunal, geochemical and volcanic proxies illustrate the high-stress conditions
481 across the PETM (Fig. 14). At the base of the section (zone P4C), a short dissolution

482 event is marked by near-absence of planktic species, decreased CaCO₃ from 50 % to 40
483 % and maximum Hg/TOC ratios. In contrast, benthic species are well preserved. This
484 suggests surface ocean acidification as a result of peak volcanic emissions (NAIP).
485 Above this interval planktic and benthic species show dissolution effects with just 1/3
486 well-preserved ‘good’ planktic and between 20-60 % ‘good’ benthic foraminifera.
487 Hg/TOC ratios as well as $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{org}}$ values gradually decreased reaching
488 minimum values 20 cm below the PEB and at the PEB, respectively (Fig. 14).

489 A similar gradual $\delta^{13}\text{C}_{\text{org}}$ decrease has been reported from Alamedilla, Spain, (Lu
490 et al., 1996) and Spitsbergen, Norway, with the latter linked to North Atlantic Igneous
491 Province (NAIP) volcanism (Wieczorek et al., 2013). At Dababiya Hg/TOC ratios
492 (ppb/wt%) also link this interval to NAIP. At all three sites the isotopic records are
493 interpreted as gradually increasing ocean temperatures due to atmospheric CO₂ loading
494 linked to NAIP (Speijer and Wagner, 2002; Sluijs et al., 2008; Bowen and Zachos, 2010;
495 Khozyem et al., 2015).

496 At the PEB planktic foraminifera suddenly disappeared and calcite decreased to
497 near 0 % for 42 cm in the lower part of zone E1 followed by a brief reappearance of
498 calcite (35 %) and small opportunistic new foraminiferal species and radiolarians (Figs.
499 13A, 14). Above this interval calcite varies between 10-30 % but planktic foraminifera
500 are generally rare to absent and reappearing only with calcite content >40 % at the top of
501 zone E1 (Fig. 14).

502 The sudden calcite drop at the PEB from 50 % to near 0 % coincides with onset of
503 high detrital input during the PETM interval that spans zone E1 (Figs. 13, 14). Khozyem
504 et al. (2015, p. 127) argued that “*detrital input negatively affects the calcite content*

505 *resulting in minimum values that could be due to leaching of carbonate contents under*
506 *acid conditions and/or dilution by increased detrital input.*” The high terrigenous input at
507 Dababiya due to climate and sea level changes supports this interpretation (e.g.,
508 Khozyem et al., 2015; Schulte et al., 2011; Speijer and Wagner, 2002). The temporary
509 absence of benthic and planktic foraminifera and near absence of nannofossils during the
510 PETM coupled with shoaling of the CCD by 2000 m indicates ocean acidification likely
511 due to a huge rapid input of CO₂ from methane degassing (e.g., Zachos et al., 2008;
512 Westerhold et al., 2011) and/or from NAIP volcanism (Gutjahr et al., 2017).

513

514 **6. DISCUSSION**

515

516 **6.1. PETM Event**

517 During the Paleocene-Eocene transition two major volcanic events temporally
518 precede and overlap the PETM ($\sim 55.8 \pm 0.2$ Ma; Westerhold et al., 2009; Charles et al.,
519 2011; Wiczeorek et al., 2013) (Fig. 1B): (1) the North Atlantic Igneous Province (NAIP)
520 formed during the opening of the northern part of the North Atlantic ocean ~ 61 Ma with
521 maximum activity between 57 and 54 Ma (Hirschman et al., 1997; Svensen et al., 2004,
522 2010; Storey et al., 2007); and (2) Central American circum-Caribbean volcanism linked
523 to enhanced tectonic activity that began ~ 56 -55.5 Ma in the proto Greater Antilles
524 (Sigurdsson et al., 1997). Thus the nature of NAIP volcanism associated with the PETM
525 event was fundamentally different from the continental flood basalt Deccan Traps
526 eruptions.

527 Support for NAIP as driver for the PETM comes from a large drop in $^{187}\text{Os}/^{188}\text{Os}$
528 and ash deposits dated ~24 ky before the maximum $\delta^{13}\text{C}$ excursion in Core BH9/05
529 (Spitsbergen, Svalbard Archipelago, Norway) (Wieczorek et al., 2013) and from an Earth
530 system model pairing ocean surface pH data and a carbon isotope record from the
531 northeast Atlantic Ocean (Gutjahr et al., 2017). Recent discovery of Hg anomalies in
532 North Atlantic, Spain and Egypt provide further evidence linking NAIP to the PETM
533 event by initiating the warming that likely led to the release of methane gases from
534 organic-rich sediments (Svensen et al., 2004, 2010; Maclennan and Jones, 2006;
535 Wieczorek et al., 2013).

536 The PETM event was a short-term and isolated event possibly triggered by an
537 estimated ~2000 Gt of CO_2 from volcanic activity (NAIP, Sinton and Duncan, 1998;
538 Westerhold et al., 2011) and ~1500 Gt of methane carbon from gas hydrates released into
539 the atmosphere (Dickens et al., 1995; Dickens, 2003). (These CO_2 estimates are based on
540 the $\delta^{13}\text{C}$ isotope excursion, which may have large uncertainties.) The resulting rapid
541 global warming is thought to have occurred over about ~10 ky with the entire event
542 lasting ~170 ky. This suggests rapid injection of carbon and slow subsequent removal
543 given that the average residence time of carbon in the ocean is about 100 ky (Zachos et
544 al., 2005, 2008). Boron-based ($\delta^{11}\text{B}$ and B/Ca) proxies for surface ocean carbonate
545 chemistry indicate an estimated ~0.3 units drop in the pH of surface and thermocline
546 seawater sustained over ~70 ky during the PETM (Penman et al., 2014). Model
547 simulations suggest that this duration is consistent with a scenario of rapid initial pulse of
548 carbon loading followed by continued slow, gradual release of carbon likely due to
549 feedbacks (Panchuk et al., 2008; Zeebe et al., 2009; Zeebe, 2012).

550 The PETM coincides with ocean acidification and shoaling of the CCD by 2000
551 m (Zachos et al., 2005, 2008; Speijer and Wagner, 2002; Sluijs et al., 2008; Gutjahr et al.,
552 2017); the latter may account for benthic foraminifera extinctions in deep waters
553 (Thomas, 1998; Alegret et al., 2006). Planktic foraminifera and calcareous nannofossils
554 temporarily disappeared from tropical and subtropical oceans (suggesting warming and
555 surface ocean acidification) by migrating into higher latitudes. Assemblages returned
556 after the PETM with no significant extinctions and underwent evolutionary
557 diversification (Lu and Keller, 1993, 1995a, b; Kelly et al., 1996, 1998; Luciani et al.,
558 2007, 2016; Khozyem et al., 2014). On land extreme climate warming resulted in
559 decreased abundances and dwarfing ranging from soil dwelling species (e.g., burrowers,
560 crayfish, mollusks, Smith et al., 2009) to mammals (D'Ambrosia et al., 2017). But the
561 great mammal migration, diversification and geographic dispersal began shortly after the
562 PETM (Koch et al., 1992, 1995; Hooker, 1998; Clyde and Gingrich, 1998; Clyde et al.,
563 2003; Tong and Wang, 2006; Smith et al., 2006; Rose et al., 2008; Punekar and
564 Saraswati, 2010; Smith, 2012).

565

566 **6.2. KPB Event**

567 The main phase of Deccan volcanism spans magnetochron C29r (Chenet et al.,
568 2008, 2009) dated ~750 ky during which time an estimated >1.1 million km³ of basalt
569 erupted (Schoene et al., 2015). The KPB is at 66.021±0.024 Ma, ~350 ky after the onset
570 of eruptions at the base of C29r. Hg anomalies and Hg/TOC ratios at Elles indicate that
571 volcanic eruptions accelerated during the last 40 ky before the mass extinction (Fig. 10).
572 In the field in India, Deccan eruptions near the end of the Maastrichtian resulted in 3-4

573 lava megaflows that flowed over 1000 km across India into the Bay of Bengal (Keller et
574 al., 2011a; Self et al., 2008) (Fig. 1A). The mass extinction of planktic foraminifera was
575 documented directly in sediments between these lava megaflows in cores 2500-3500 m
576 below the surface in the Krishna-Godavari Basin (Keller et al., 2011a, 2012). Danian
577 (zone P1a) sediments overlie the megaflows and constrain the age of the KPB mass
578 extinction to peak volcanic activity, as now confirmed by the large Hg/TOC ratios at
579 Elles (Fig. 10). An estimated cumulative loading of 12,000-28,000 Gt of volcanogenic
580 CO₂ spewed into the end-Cretaceous atmosphere within less than 350 ky and
581 significantly increased atmospheric *p*CO₂ (Courtilot and Fluteau, 2014; Self et al., 2014).
582 Volcanic eruptions continued intermittently through the early Danian C29r with the last
583 phase of eruptions in the lower part of C29n (Fig. 11). Mercury analysis in marine and
584 terrestrial sediments worldwide mark late Maastrichtian and early Danian Deccan
585 eruptions linked directly to the KPB mass extinction (Font et al., 2016; this study).

586 Rapid climate warming of 3-4 °C during massive Deccan eruptions resulted in
587 dwarfed planktic foraminifera and reduced abundances of all but a few stress-resistant
588 taxa dominated by a single disaster opportunist and sole long-term survivor *Guembelitra*
589 *cretacea* (Keller and Abramovich, 2009). On land, non-avian dinosaurs, mammals,
590 amphibians, plants and insects (e.g., MacLeod et al., 1997; Labandeira et al., 2002; Wilf
591 and Johnson, 2004; Wilson et al., 2005, 2014; Nichols and Johnson, 2008; Longrich et
592 al., 2011, 2012; Wilson, 2014; Vajda and Bercovici, 2014; Donovan et al., 2016) also
593 recorded a prolonged ecological decline, reduced diversity and turnovers during climate
594 instability associated with Deccan volcanism preceding the KPB (e.g., Wilf and Johnson,
595 2004; Wilson, 2005, 2014; Wilson et al., 2014; Archibald, 1996, 2011).

596 The similar patterns of long-term stress and decline in marine and terrestrial
597 faunas and flora during the late Maastrichtian C29r warming parallels massive Deccan
598 volcanism that accelerated during the last 10 ky leading to further warming and probably
599 reaching threshold conditions. Maximum volcanic eruptions in rapid succession during
600 the last few thousand years culminated with the KPb mass extinction (Fig. 10). The
601 subsequent delayed recovery in marine plankton and on land can now be shown to
602 coincide with continued though less frequent Deccan volcanic eruptions keeping stress
603 conditions high (Fig. 11). Deccan volcanism is thus a major culprit for climate warming,
604 biotic stresses and the mass extinction.

605 The Chicxulub impact is commonly believed to be the sole cause for the KPb
606 mass extinction based primarily on the Ir anomaly in the KPb clay layer, the imPACT
607 CRATER IN MEXICO AND IMPACT GLASS SPHERULES FREQUENTLY FOUND IN
608 SEDIMENTS AT, BELOW OR ABOVE THE KPb, WHICH HAS BEEN THE SOURCE OF
609 CONTROVERSY (SCHULTE ET AL., 2010; KELLER ET AL., 2011B). (SEE
610 SUPPLEMENTARY MATERIALS S3 FOR A DISCUSSION OF THIS CONTROVERSY.)
611 HOWEVER, OVER THE PAST 10 YEARS, INCREASING EVIDENCE LINKING THE MASS
612 EXTINCTION TO DECCAN VOLCANISM REVEALS THE NEED FOR RE-EVALUATION
613 OF THE IMPACT THEORY. CRITICAL EVIDENCE LINKING THE MASS EXTINCTION
614 DIRECTLY TO DECCAN VOLCANISM INCLUDES: (1) THE MASS EXTINCTION
615 DOCUMENTED BETWEEN MASSIVE LAVA FLOWS IN INDIA DIRECTLY BELOW THE
616 KPb (KELLER ET AL., 2008, 2009, 2011A, 2012), (2) U-Pb AGE DATING OF ASH
617 LAYERS AND RED BOLE INTERTRAPPEAN SEDIMENTS THAT SPAN C29R (SCHOENE
618 ET AL., 2015), AND (3) Hg ANOMALIES THAT MARK ATMOSPHERIC FALLOUT
619 FROM DECCAN ERUPTIONS WORLDWIDE (SILVA ET AL., 2013; FONT ET AL., 2016;

620 THIS STUDY). AS A RESULT, THE IMPACT THEORY IS ALREADY BEING MODIFIED
621 BY IMPACT PROPONENTS SUGGESTING THAT THE IMPACT TRIGGERED DECCAN
622 VOLCANISM (RICHARDS ET AL., 2015), OR ACCELERATED DECCAN VOLCANISM
623 LEADING TO EXTINCTIONS (RENNE ET AL., 2015). THE PRECISE AGE OF THE
624 CHICXULUB IMPACT IS CURRENTLY UNDER INVESTIGATION BASED ON NEW
625 AR/AR DATING OF IMPACT SPHERULES BY THREE LABORATORIES. THE PRECISE
626 ROLE THE IMPACT PLAYED IN THE MASS EXTINCTION ALSO STILL REMAINS TO BE
627 DETERMINED IN LIGHT OF NEW DECCAN VOLCANISM DATA. WHAT IS CERTAIN IS
628 THAT THIS IMPACT ADDED A SIGNIFICANT BLOW TO AN ALREADY WEAKENED
629 AND STRESSED ENVIRONMENT REGARDLESS OF THE PRECISE AGE. BUT IT WAS A
630 ONE-TIME BLOW AT THE LEVEL OF TOTAL CO₂ AND SO₂ GAS OUTPUT
631 COMPARABLE TO ONE MAJOR DECCAN ERUPTION PULSE OF WHICH THERE ARE
632 MANY (CHENET ET AL., 2008; COURTILOT AND FLUTEAU, 2014).

633 At present we can confidently evaluate the PETM and KPB catastrophes based on
634 the response by planktic foraminifera, which are an essential part of the food chain, and
635 new Hg anomaly data now link these global faunal records to NAIP and Deccan
636 volcanism. The fundamentally different biotic responses to these catastrophes lie in the
637 nature of volcanic eruptions. During the PETM, NAIP volcanism due to rifting of the
638 North Atlantic led to relatively short-term gradual warming that likely triggered the
639 postulated methane release and rapid warming. Absence of Hg anomalies after the PETM
640 indicates no significant NAIP eruptions, climate cooled and biotic recovery was rapid. In
641 contrast, Deccan Traps are continental flood basalt eruptions that began ~350 ky before
642 the KPB mass extinction causing long-term warming. Accelerating eruptions during the

643 last ~10 ky reached the tipping point and mass extinction. Thereafter, intermittent Deccan
644 eruptions delayed recovery for over 500 ky.

645

646 **6.3. Anthropocene: The Sixth Mass Extinction?**

647 Scientists increasingly recognize the accelerating rate of modern species
648 extinctions and sounding alarm that humans are now causing the sixth mass extinction
649 (e.g., Leakey and Lewin, 1992; Dirzo and Raven, 2003; Wake and Vredenburg, 2008;
650 Barnosky et al., 2011; Glikson, 2014). Evidence of an impending catastrophe is all
651 around us in the increasing rate of species extinctions and those endangered on the verge
652 of extinction. Climate warming due to fossil fuel burning is attributed to the increasing
653 rate of extreme climate events, melting of polar glaciers and rapidly rising sea level.
654 Despite all this, it is hard to fathom that we are living in the midst of a mass extinction.

655 We can glimpse our future from comparison with extreme events in the past,
656 particularly the hyperthermal warming (PETM) of the Paleocene-Eocene boundary (PEB,
657 55.8 Ma) and rapid extreme warming leading to the end-Cretaceous mass extinction
658 (KPB, 66.0 Ma) (Table 1). Both PEB and KPB catastrophes are largely the results of
659 massive rapid emissions of greenhouse gases leading to the tipping point. At one
660 extreme, scientists suggest the tipping point may have already been reached at the current
661 CO₂ level (407 ppm) and that just 1 °C additional warming may result in runaway
662 warming, ocean acidification and the sixth mass extinction (Glikson, 2014). At the other
663 extreme are those who deny the existence of current climate change.

664 Projecting current and/or increasing Anthropocene warming into the future has
665 the potential to follow the path of the PETM hyper-warming and faunal turnover, as

666 frequently suggested by scientists, or it could end in a mass extinction similar to the KP
667 as suggested by predictions of the sixth mass extinction. Global climate warming due to
668 massive input of greenhouse gases is the leading cause for all three events even if the
669 sources differ (Table 1). Critical is the rapid rate of climate warming that is vastly (12 to
670 16 times) more rapid for the Anthropocene. The tipping point may be around 5 °C and
671 just 1 °C off from the current overall temperature rise (Hay, 2011).

672 Ocean acidification and acid rain on land had catastrophic effects for PETM and
673 KP events and similar effects are already ongoing today. For example, seasonal
674 aragonite undersaturation observed in surface waters of the Southern Ocean already have
675 harmful effects on live pteropods (Bednarsek et al., 2012; Hunt et al., 2008; Sunday et al.,
676 2014). By 2030 undersaturation is predicted to spread to ~30 % of the Southern Ocean
677 and >70 % by 2100 as a result of anthropogenic CO₂, thus severely affecting the marine
678 food chain (McNeil and Matear, 2008; Hauri et al., 2016).

679 A cartoon illustrates the nature of the three events (Fig. 15). Climate warming and
680 the end-Cretaceous mass extinction are closely linked to the Chicxulub impact and
681 Deccan volcanism (Fig. 15A). The latter emitted huge quantities of aerosols and
682 greenhouse gases (CO₂, SO₂) into the atmosphere over 350 ky and the impact added in a
683 single instant a quantity about equal to one major Deccan eruption pulse (Chenet et al.,
684 2008; Courtillot and Fluteau, 2014). Accelerating large volcanic eruptions during the last
685 10 ky prior to the mass extinction led to increased warming and the tipping point
686 resulting in the rapid mass extinction of 66 % planktic foraminiferal species during the
687 last few thousand years of the Cretaceous, followed by another 33 % within 50-150 ky in

688 the early Danian. Continued eruptions in the early Danian delayed full recovery for over
689 500 ky.

690 The PEB event can be attributed to NAIP volcanism and climate warming that
691 likely set the conditions for the abrupt release of methane (CH₄) stored in organic-rich
692 sediments on land and continental shelves resulting in the rapid PETM warming of 5 °C
693 within ~10 ky (Fig. 15B). Methane, partially oxidized in the water column leading to
694 ocean acidification during the relatively short but intense PETM event (~170 ky) raising
695 the CCD by 2000 m. Prevailing hot-humid conditions on land and recovery of carbonate
696 deposition via CO₂ drawdown by organic matter burial in the oceans are likely causes for
697 the rapid return/recovery and diversification of marine faunas after the PETM (Bains et
698 al., 2000).

699 Current rapid warming is the result of huge inputs of greenhouse gases (CO₂,
700 CH₄) linked to human activities and fossil fuel burning during the Anthropocene (Fig.
701 15C). The input rate of greenhouse gases exceeds those at the PETM and KPB by orders
702 of magnitude. Ozone depletion and particle pollution from fossil fuel burning and other
703 human activities result in dust clouds that trap solar radiation in Earth's atmosphere with
704 little reflected back into space, thus contributing to Earth's rising temperature. Similar to
705 PEB and KPB events, today's CO₂ from the atmosphere is absorbed in the oceans and has
706 already lowered the pH; ocean acidification is already affecting shelly organisms at the
707 base of the food chain (e.g., pteropods, corals) and endangering all life up the food chain.
708 At the current trend of greenhouse gas emissions, the prediction is that Cretaceous-like
709 climate could be reached by 2070 setting us well on the way to the sixth mass extinction
710 within as little as a couple of hundred years (Hay, 2011; Hauri et al., 2016).

711 The worst-case scenario could thus be similar to the KPB mass extinction but
712 with a faster rate of extinctions; this is currently predicted as the Anthropocene mass
713 extinction – or sixth mass extinction. The best-case scenario could be similar to the
714 PETM event: We escape mass extinctions but suffer through a period of extreme
715 environmental stress marked by intense heat, extreme climate events, rising sea level and
716 severe food shortages reducing populations and forcing migration to higher latitudes for
717 survival. This scenario depends on dramatically reducing greenhouse gas input thus
718 slowing the rate of global warming and its dire long-term consequences.

719

720 **7. CONCLUSIONS**

721

722 The PETM extreme warming is a commonly used analogue and predicted best-
723 case scenario for the current rapid climate warming in the coming decades and centuries.
724 If this is our fate, survival is possible although in reduced populations with the best
725 chances for survival in higher latitudes. The predicted worst-case scenario for the current
726 climate trend is the sixth mass extinction. The KPB mass extinction is a good analogue
727 for this catastrophic scenario because accelerating Deccan volcanic eruptions and
728 increasing greenhouse gas input into the atmosphere can have similar effects on the
729 biosphere as current fossil-fuel burning. Perhaps all it takes to realize the sixth mass
730 extinction scenario is continued or increasing greenhouse gas input reaching the tipping
731 point. It is unclear whether current climate warming will follow the PETM or KPB
732 analogue, or a completely different model of biosphere destruction unseen in Phanerozoic
733 mass extinctions.

734

735

736

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1406

1407 **FIGURE CAPTIONS**

1408

1409 **Figure 1:** (A) Paleogeography at the KPB (66.02 Ma) and paleolocations of El Kef and
1410 Elles sections, Reunion hotspot, Deccan volcanism and Chicxulub impact site. (B)
1411 Paleogeography at the PEB (55.8 Ma) and paleolocations of the Dababiya section, North
1412 Atlantic Igneous Province and circum-Caribbean volcanism. Paleomaps from Scotese
1413 (2013a, b).

1414

1415 **Figure 2:** Locations of the Cretaceous-Paleogene boundary (KPB) GSSP El Kef and
1416 Elles, Tunisia, and the Paleocene-Eocene boundary (PEB) GSSP at Dababiya, Egypt.

1417

1418 **Figure 3:** (A) The KPB event at Elles, Tunisia, is well exposed across the hillside
1419 marked by a lithological change from gray shale of the Maastrichtian to dark gray clay of
1420 the early Danian weathered to a light brownish color. (B) A 1-2 cm thick rusty "red layer"
1421 at the base of the KPB clay layer contains maximum Ir concentrations and marks the
1422 mass extinction. (C) A blow-up of this red layer shows the sharp contact with the
1423 Maastrichtian marl below and dark Danian clay of zone P0 above.

1424

1425 **Figure 4:** KPB extinction pattern at El Kef, Tunisia, shows all large tropical to
1426 subtropical species extinct at or near the KPB (2/3 of all species, SEM illustrations 1-10,
1427 numbers keyed to species), the short-term survivorship of small ecologically more
1428 tolerant species (1/3 of the species, SEMs 11-18) including a single long-term survivor
1429 (*Guembelitria cretacea*, SEM 14). Early Danian evolution begins within a few thousand

1430 years of the mass extinction but diversity remains low and species small (SEMs 1-9)
1431 marking high-stress conditions over ~500 ky of the earliest Danian. SEM illustrations are
1432 shown in relative species sizes in the assemblages. Faunal data updated from Keller
1433 (1988a).

1434

1435 **Figure 5:** El Kef, Tunisia, relative abundances of planktic foraminifera across the KPB
1436 (>63 μm size fraction for all species except 38-63 μm for *Guembelitra*) with SEM
1437 illustrations of marker species (numbers keyed to species names and abundance data).
1438 Carbon stable isotopes of bulk rock and benthic species *Anomalinoidea acutus* across the
1439 KPB transition. Note the abrupt diversity change that marks the KPB mass extinction and
1440 the $\delta^{13}\text{C}$ negative shift that signals the collapse of primary productivity. Faunal data from
1441 Keller (1988a, updated), isotope data from Keller and Lindinger (1989).

1442

1443 **Figure 6:** (A) Relative abundances of planktic foraminifera (>63 μm) across the KPB at
1444 Elles, Tunisia, reveal low diversity assemblages dominated by small biserial species, but
1445 not *Guembelitra*, during the climate warming of the latest Maastrichtian and an interval
1446 of the early Danian. (B) Relative abundances of planktic foraminifera in the smaller (38-
1447 63 μm) size fraction reveals abundant dwarfed species in the earliest Danian as well as
1448 peak abundances (40 %) during the latest Maastrichtian preceding the mass extinction.
1449 This indicates that dwarfing of the disaster opportunist *Guembelitra* is a response to
1450 extreme environmental stress. SEM illustrations (numbers keyed to species names) are
1451 shown in relative species sizes in the assemblages. Faunal data from Keller et al. (2002).

1452

1453 **Figure 7:** Effects of increasing environmental stress upon planktic foraminiferal
1454 assemblages from optimum to catastrophe conditions. Note the successive elimination of
1455 large, specialized k-strategy species during climate warming, particularly in restricted
1456 basins and marginal marine environments, and the survival of small r-strategy species
1457 commonly associated with volcanic activity. Disaster opportunists flood the environment
1458 during catastrophes. Modified from Keller and Abramovich (2009).

1459

1460 **Figure 8:** Early Danian evolution and decline in Cretaceous survivor species illustrate
1461 high-stress environments. Small dwarfed species and low diversity mark delayed marine
1462 recovery in magnetochron C29r from zones P0 through P1a(2) correlative with
1463 decreasing abundance and gradual extinction of dwarfed survivor species. The last phase
1464 of Deccan volcanism began near the zone P1a/P1b boundary (C29r/C29n) and marks the
1465 extinction of two dominant zone P1a index species (*Parvularugoglobigerina eugubina*,
1466 *P. longiapertura*). Marine recovery begins after this last volcanic phase and is marked by
1467 higher diversity and increasing species sizes. Note the number of the same specimens in
1468 each column indicates relative abundance. From Punekar et al. (2014).

1469

1470 **Figure 9:** Relative abundances of benthic foraminifera (>63 μm) and carbon stable
1471 isotopes of bulk rock and benthic species *Anomalinoides acutus* across the KPB transition
1472 at El Kef, Tunisia. Note the major faunal turnover across the KPB with up to 48 %
1473 species disappearing over 500 ky with many of them reappearing after environmental
1474 recovery. Faunal data from Keller (1988b); stable isotope data from Keller and Lindinger
1475 (1989).

1476

1477 **Figure 10:** Paleoenvironmental proxies (oxygen isotopes, mercury and disaster
1478 opportunist species) across the KPB at Elles, Tunisia. Note climate warming during the
1479 last 10 ky of the Maastrichtian coincides with increased Deccan volcanism (Hg/TOC
1480 ratio), which accelerates during the last thousand years and culminates with the KPB
1481 mass extinction. Hg and TOC data in Supplementary Materials S2, Table S2.

1482

1483 **Figure 11:** Paleoenvironmental proxies for the KPB transition at El Kef, Tunisia. The
1484 interval analyzed spans part of the latest Maastrichtian warming (zone CF1) marked by
1485 ocean acidification and high dissolution effects (FI), and 500 ky of the early Danian
1486 zones P0-P1a(2) marked by continuous high-stress low oxygen conditions and ends with
1487 the onset of recovery in P1b (base C29n). Data table (Table S1) in Supplementary
1488 Materials S2.

1489

1490 **Figure 12:** (A) Dababiya outcrop with GSSP designated cliff to the right and our
1491 sampled location 25 m to the left (East). (B) Sampling of the section using a ladder. (C)
1492 Contiguous outcrop between the GSSP cliff and our sampled section at 25 m east permits
1493 tracing the lithology bed by bed. Note the GSSP outcrop collapsed in the spring of 2016
1494 at the vertical crack seen in C across the label "PEB". Armed guards protected the
1495 outcrop from eagerly sampling geologists.

1496

1497 **Figure 13:** (A) Relative abundances of planktic foraminifera, carbon stable isotopes and
1498 species richness at Dababiya, Egypt, 25 m east of the GSSP outcrop. The PETM interval

1499 spans from its gradual onset 75 cm below to 1 m above the PEB and is marked by near
1500 total carbonate dissolution. Another strong dissolution interval at the base of the section
1501 has common benthic species but only rare planktics. Faunal data from this study, isotope
1502 data from Khozyem et al. (2014, 2015). (B) Relative abundances of benthic foraminifera
1503 show a major faunal turnover but few species extinctions (18 %, 7 species). Faunal data
1504 from Alegret and Ortiz (2006).

1505

1506 **Figure 14:** Paleoenvironmental proxies for the PETM transition at Dababiya, Egypt.
1507 Dissolution first appears in zone P4C coincident with high Hg/TOC values. The onset of
1508 the PETM begins with gradually decreasing $\delta^{13}\text{C}$ values in zone P5 that reached
1509 maximum at the PEB. Near total CaCO_3 dissolution in the lower part of zone E1 and
1510 strong dissolution in the upper part marks an interval nearly devoid of marine calcareous
1511 plankton during the PETM and signals strong ocean acidification despite the onset of
1512 recovery in $\delta^{13}\text{C}$ and CaCO_3 . Faunal recovery begins in zone E2 with increasing $\delta^{13}\text{C}$
1513 values and CaCO_3 reaching 60 %. Data table (Table S3) in Supplementary Materials S2.

1514

1515 **Figure 15:** Illustration of the KPB mass extinction, the PETM and Anthropocene climate
1516 warming. (A) During the latest Maastrichtian environmental devastation is mainly due to
1517 volcanism (ash, aerosols and greenhouse gases), resulting in rapid climate changes, acid
1518 rains and ocean acidification that is exacerbated by the Chicxulub impact, thus impeding
1519 calcification by marine plankton at the base of the food chain. (B) During the latest
1520 Paleocene to early Eocene: Gradual climate warming preceding the PEB is attributed to
1521 North Atlantic Igneous Province volcanism (NAIP), but the rapid warming of 5 °C

1522 (PETM) is linked to methane hydrates released from continental shelves resulting in acid
1523 rain on land and ocean acidification (~170 ky). (C) During the Anthropocene large
1524 inputs of greenhouse gases (CO₂, SO₂, N₂O) linked to human activities and fossil fuel
1525 burning leads to rapid warming and ocean acidification at a rate exceeding those at the
1526 PETM and KPB by orders of magnitude. Global carbon budget data for the Anthropocene
1527 from Le Quéré et al. (2013). Illustration modified from Glikson (2014).

1528

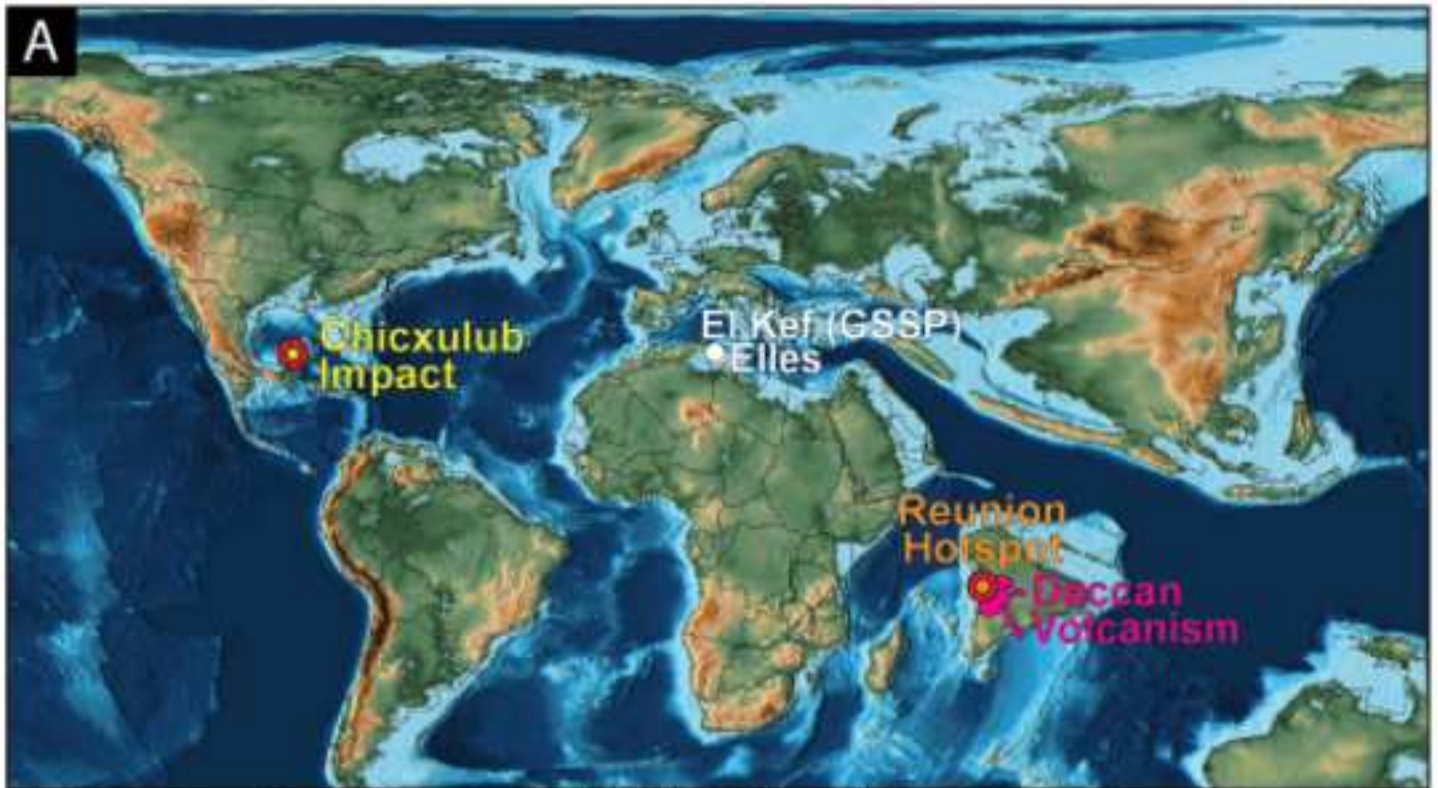
1529 **TABLE CAPTIONS**

1530

1531 **Table 1:** Comparison of KPB, PETM and Anthropocene events based on climate and
1532 environmental changes shows great similarities, except that the Anthropocene warming is
1533 orders of magnitude more rapid than the PETM and KPB warming. The rate of faunal
1534 turnover and particularly extinctions is very difficult to estimate and contains the largest
1535 potential errors. At the current rate of CO₂ input into the atmosphere, the Anthropocene
1536 extinction is estimated to reach the 75 % mass extinction level within the next 250-500
1537 ky.

1538

Figure 1



Cretaceous/Paleogene Boundary (66 Ma): End-Cretaceous Mass Extinction



Paleocene/Eocene Boundary (55.8 Ma): P/E Thermal Maximum (PETM)

Figure 2

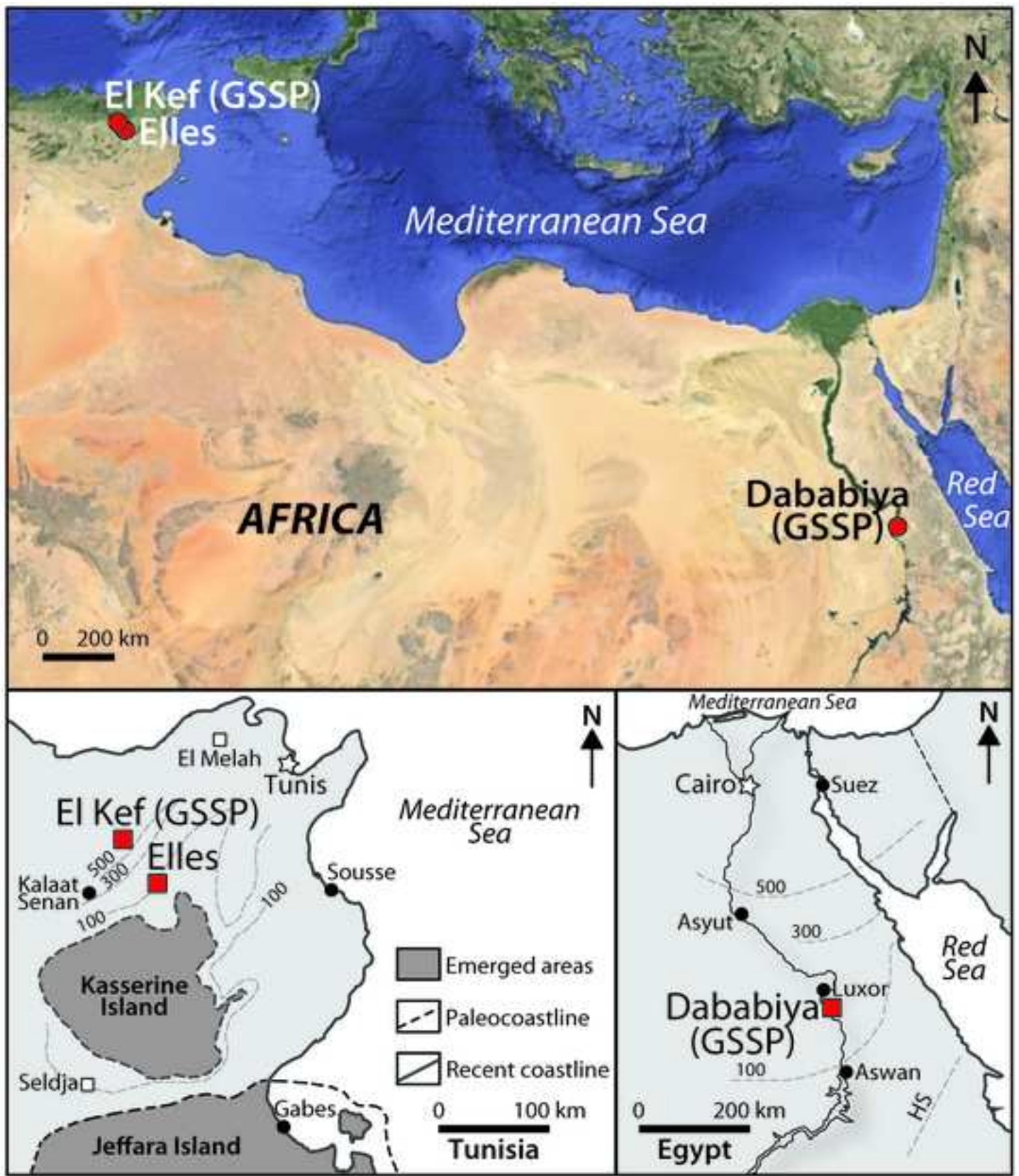


Figure 3



Figure 4

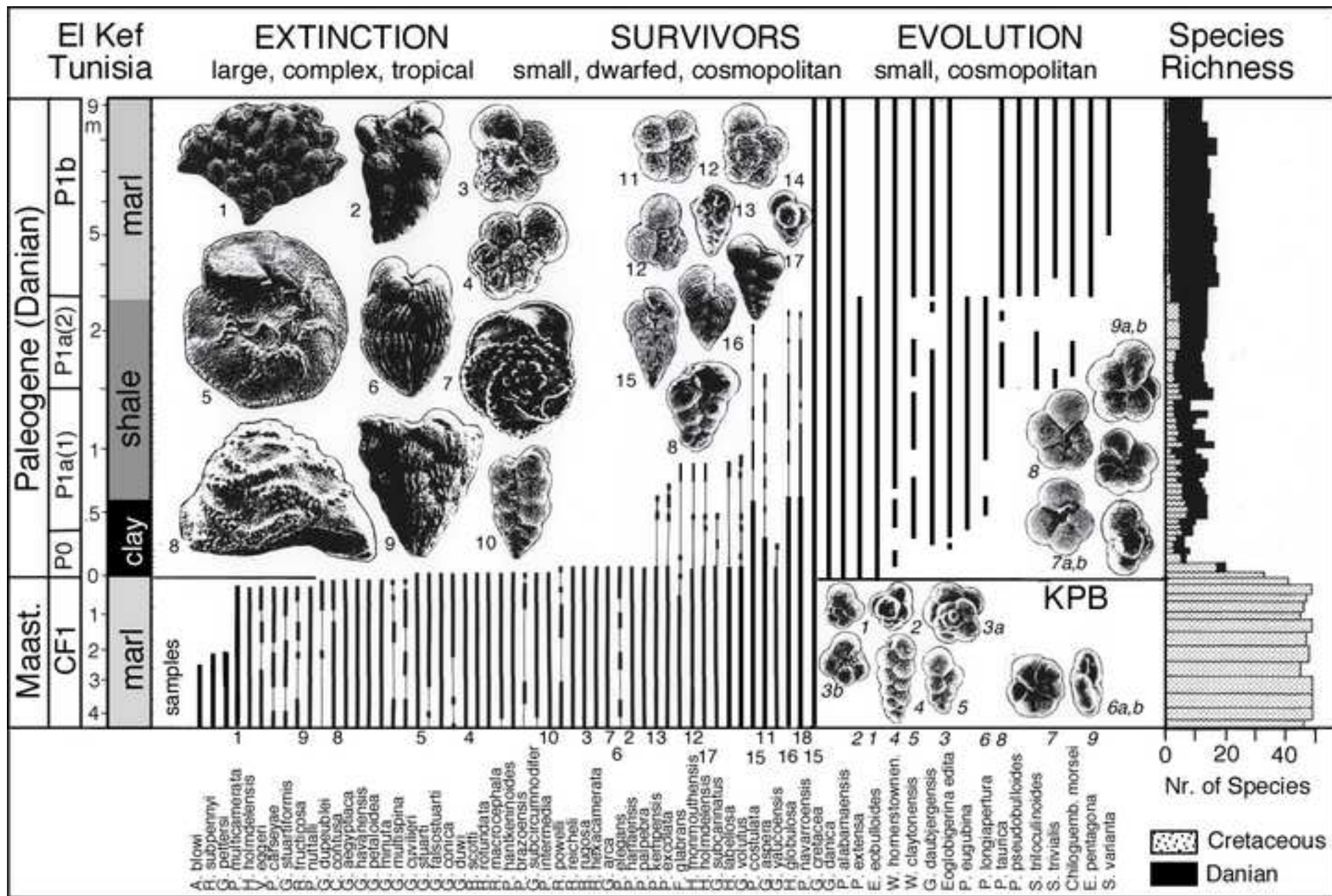
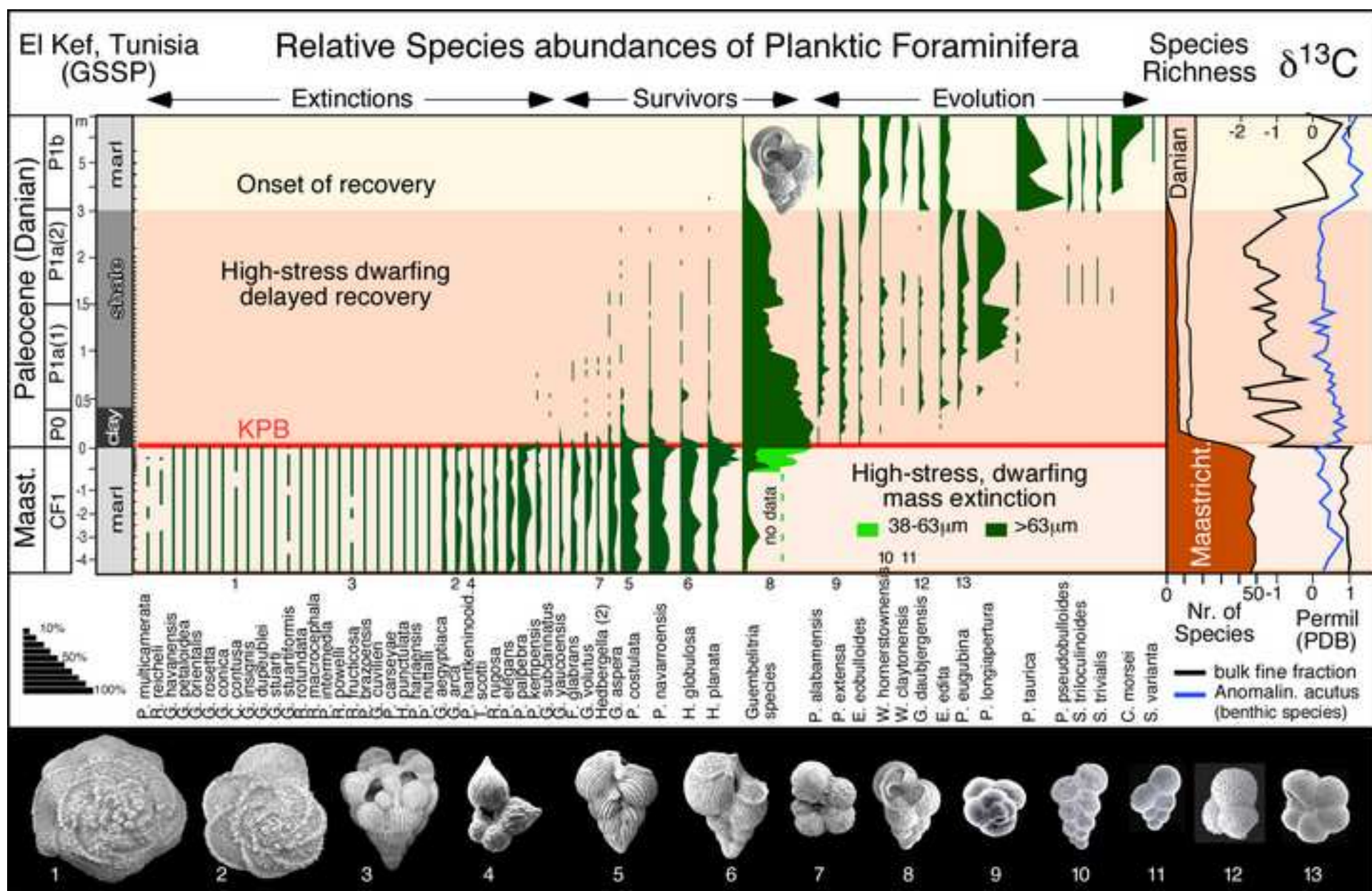


Figure 5



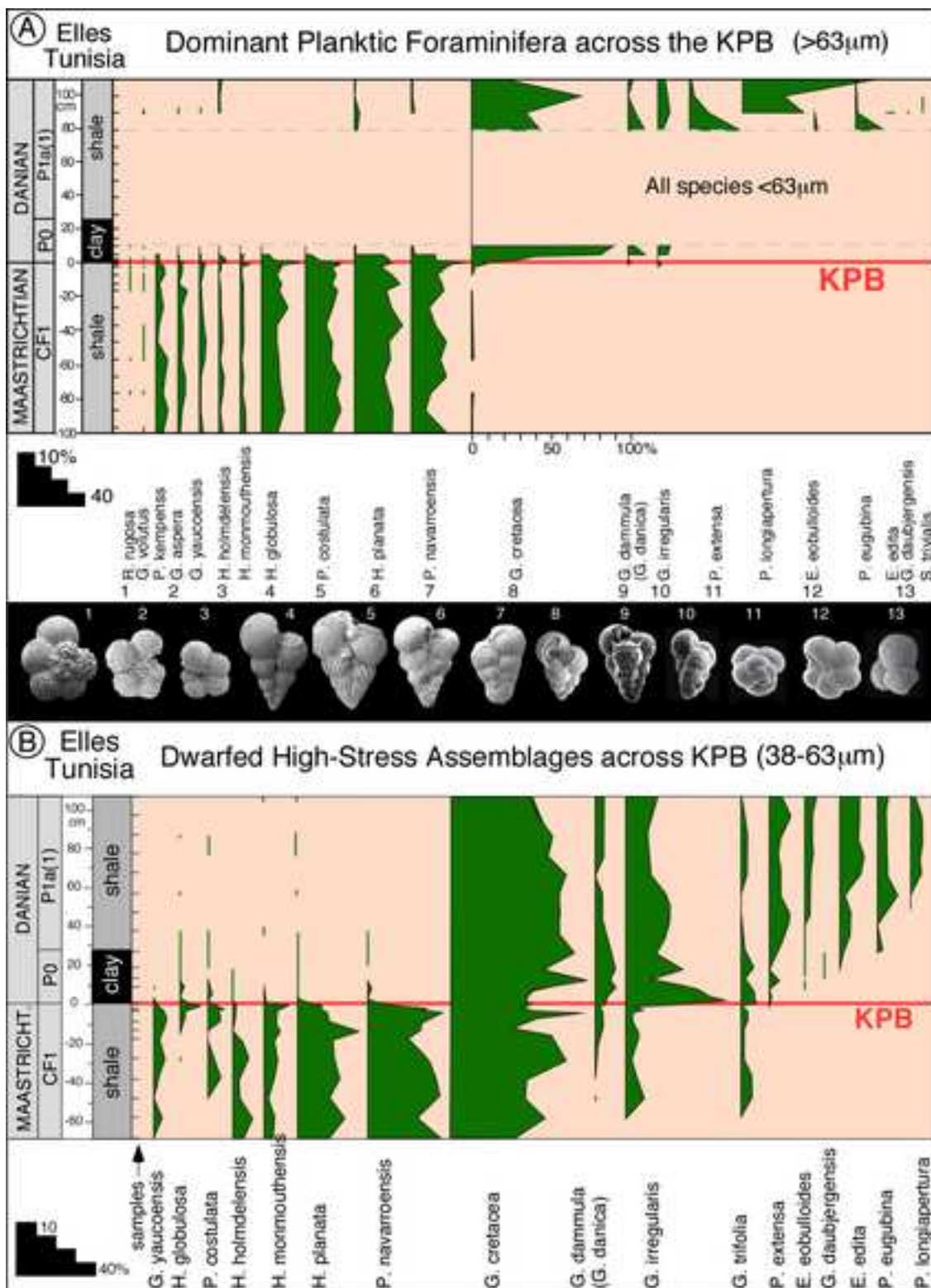


Figure 7

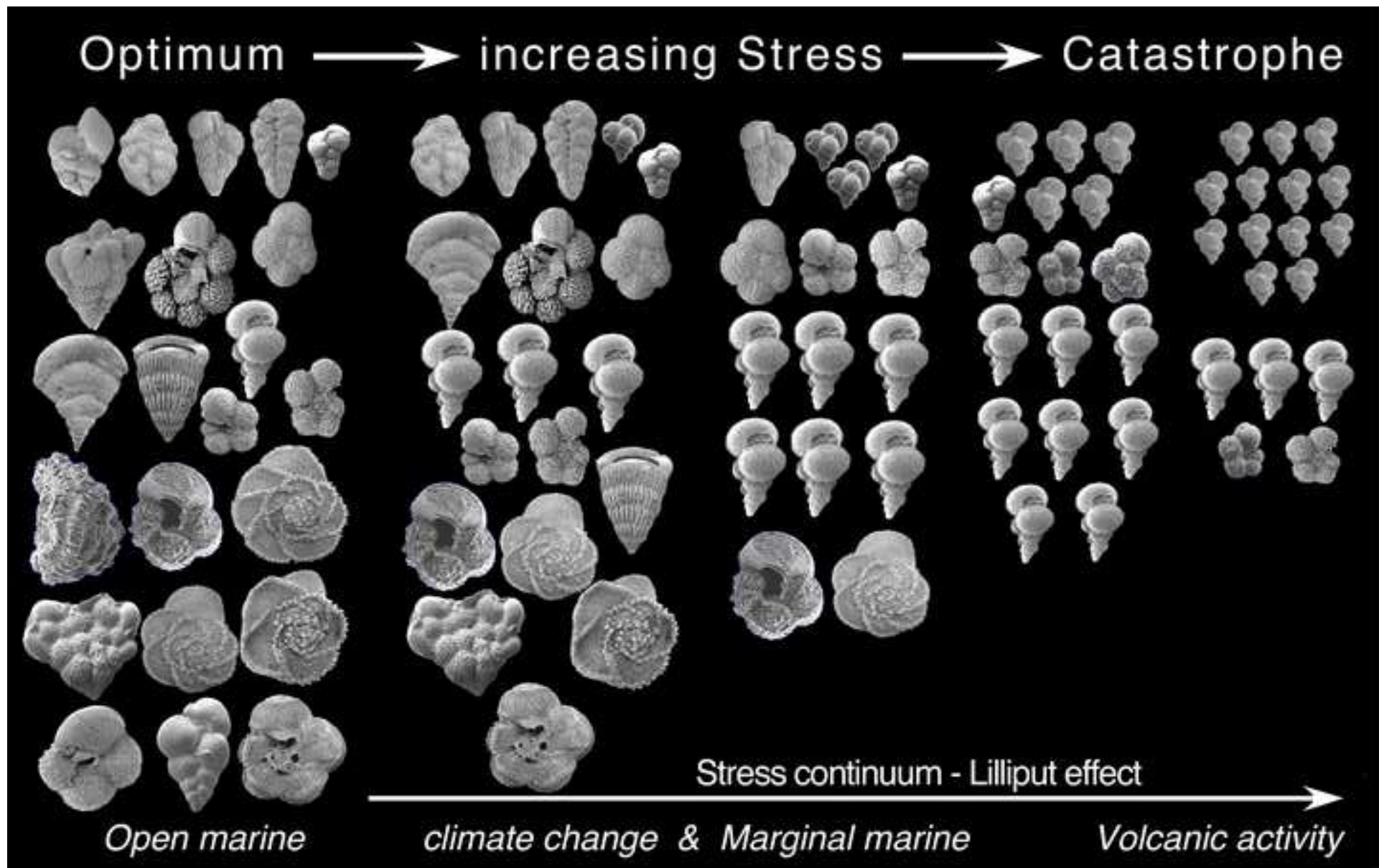


Figure 8

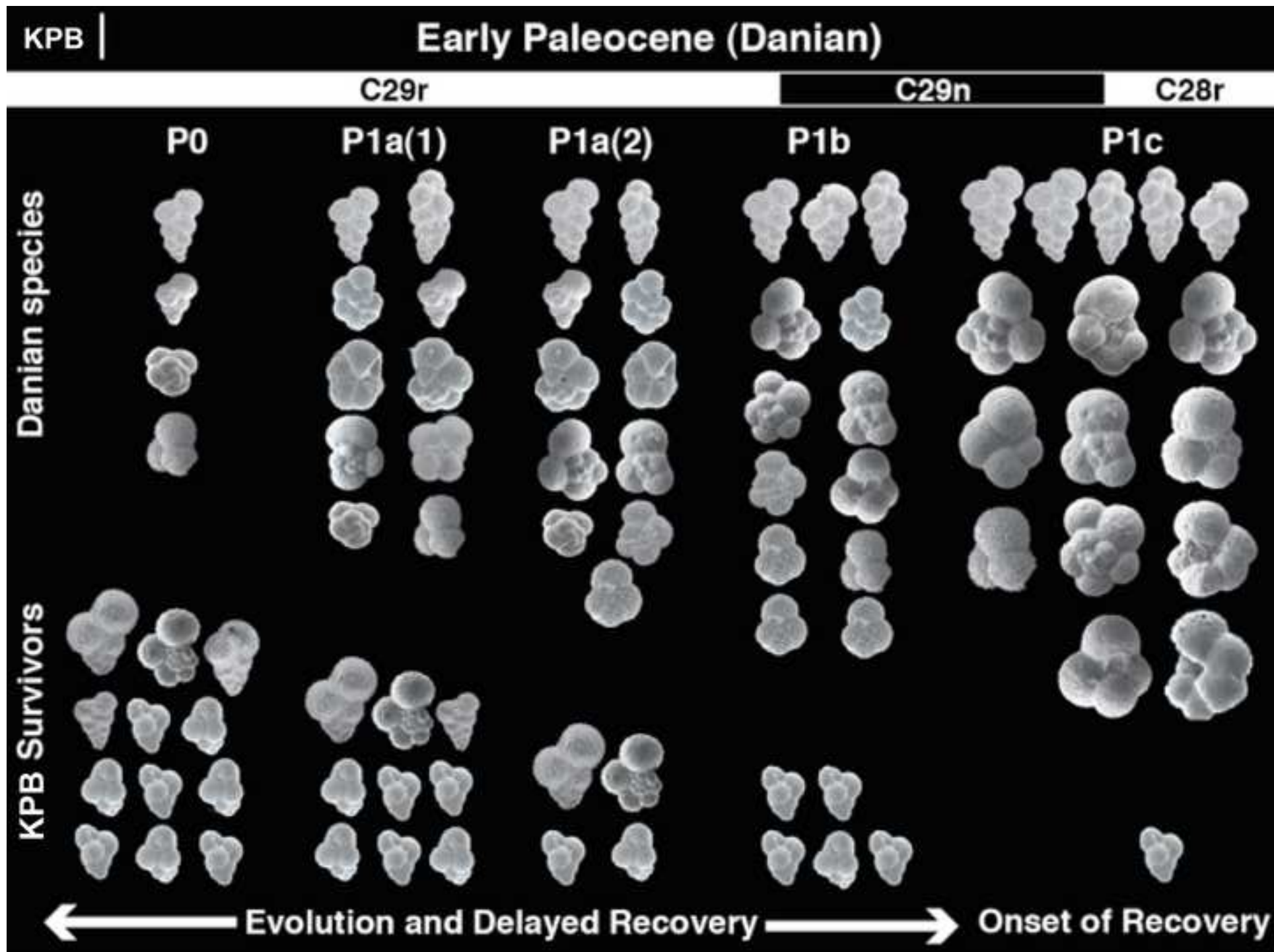


Figure 9

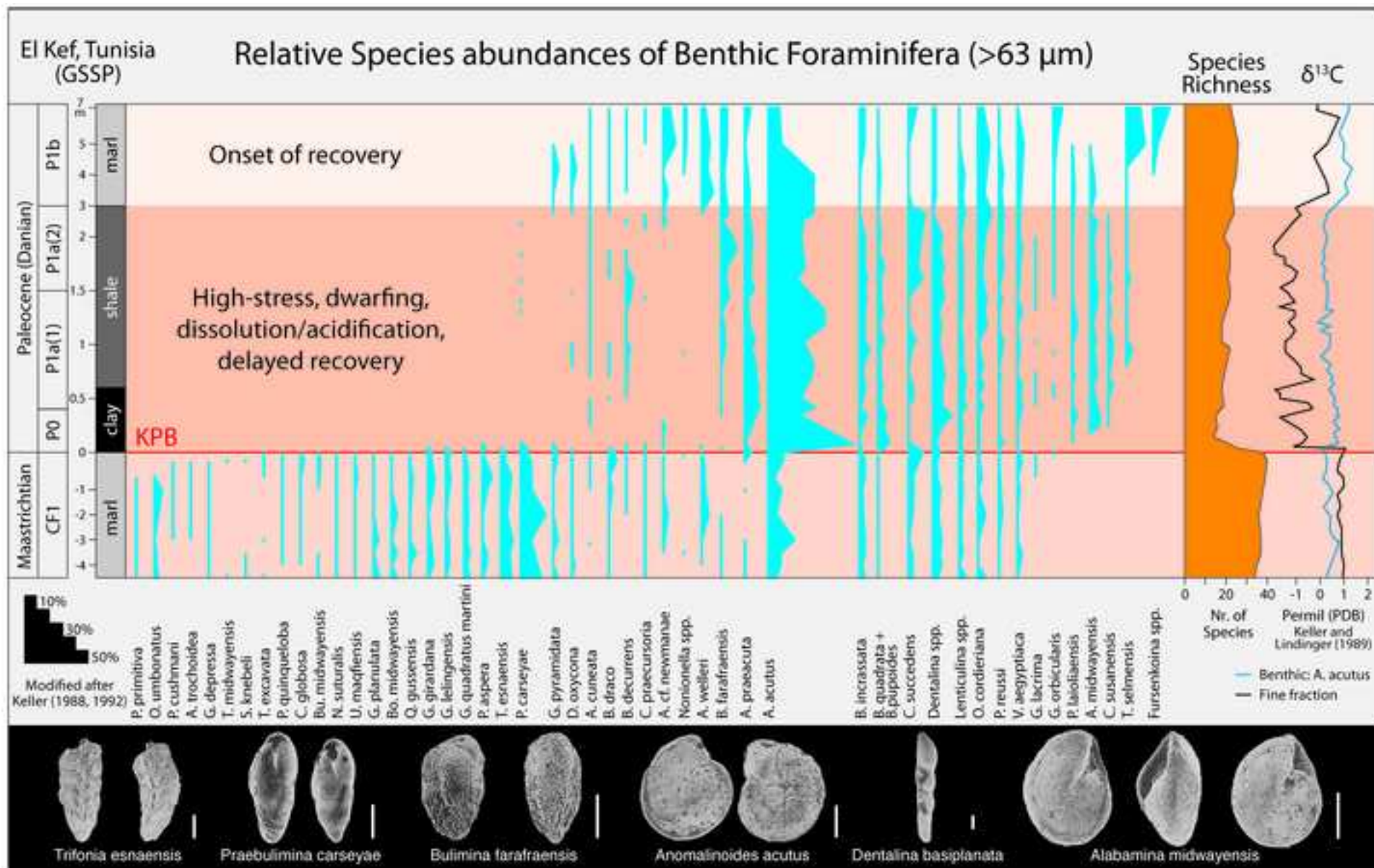


Figure 10

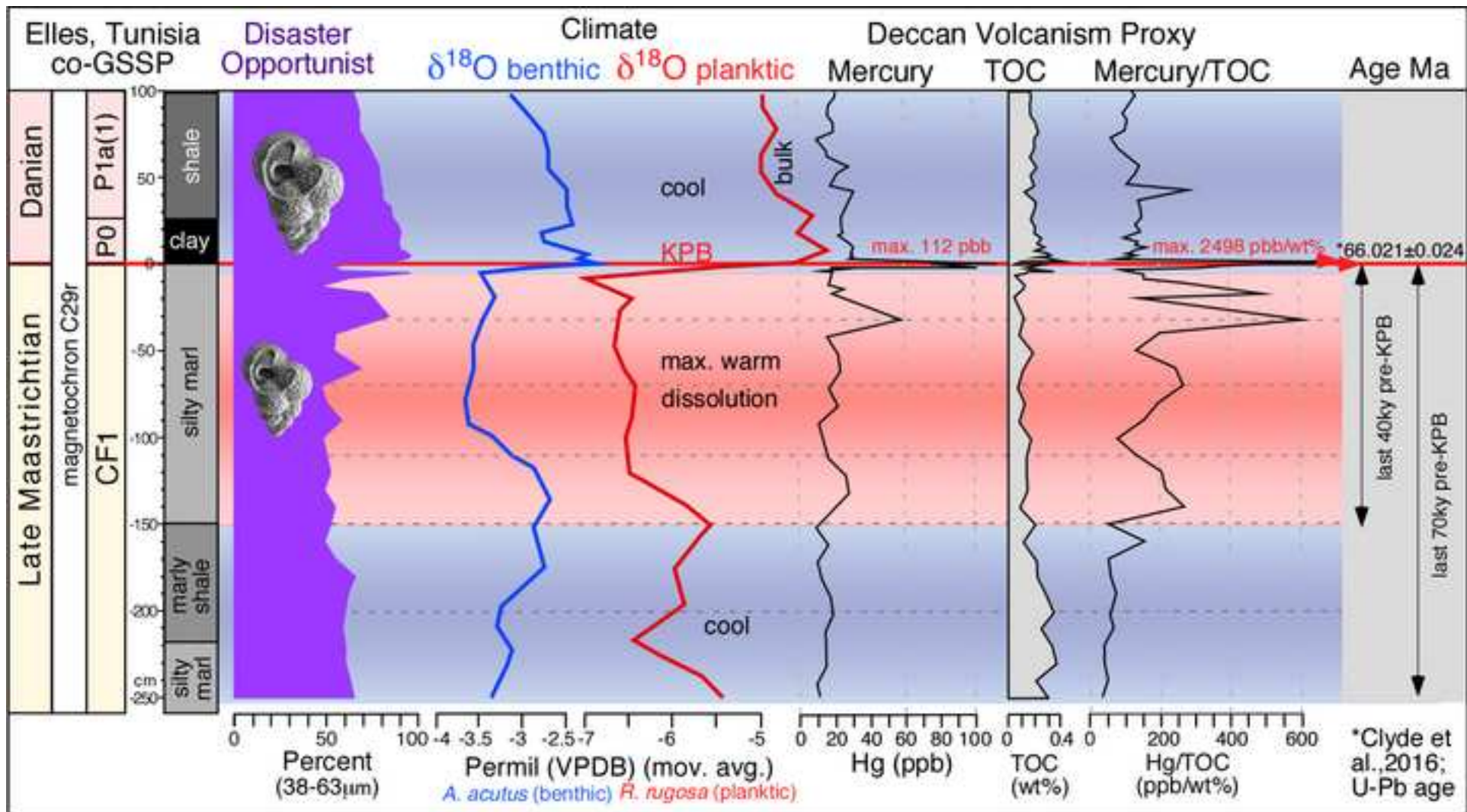


Figure 11

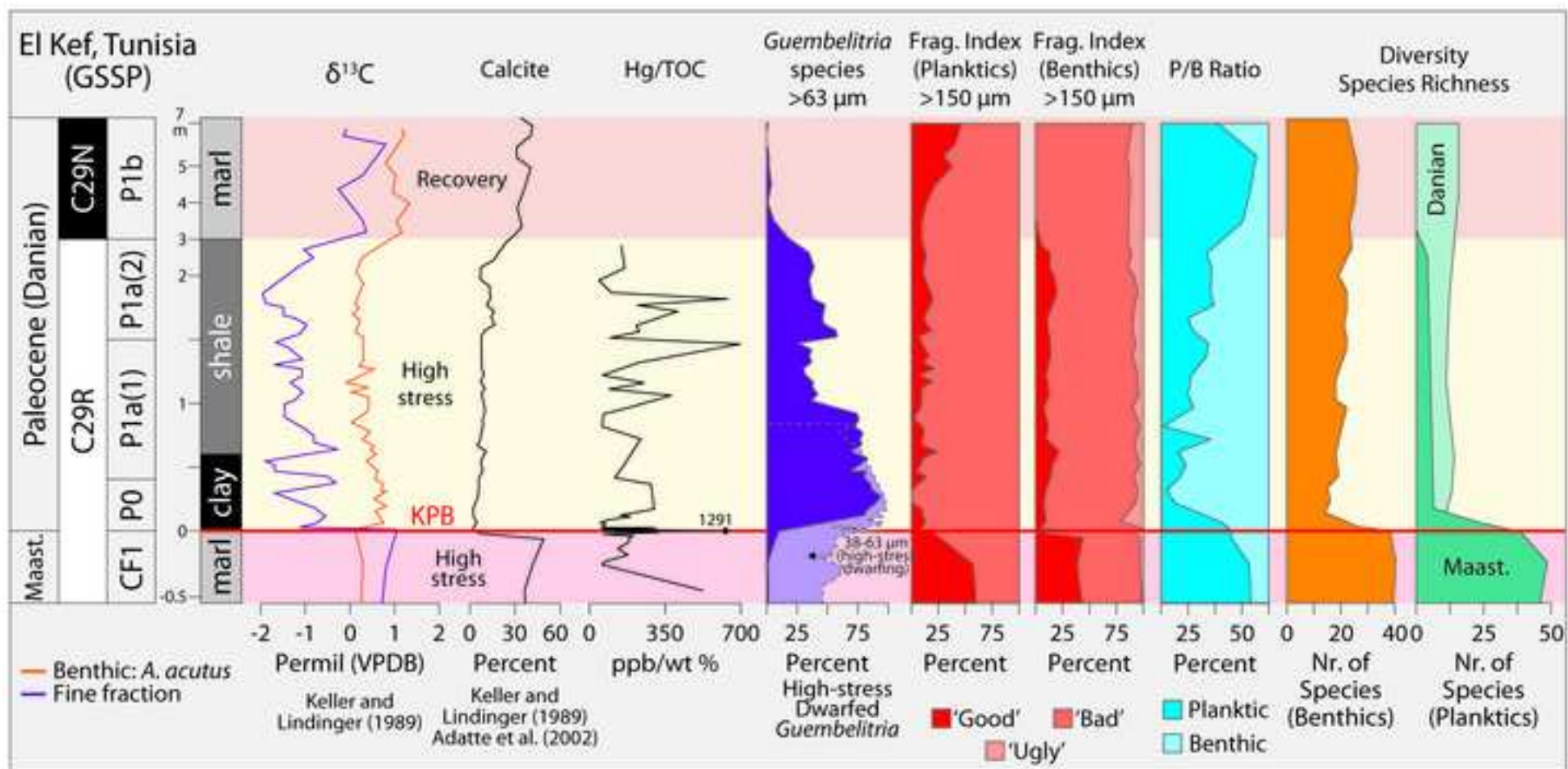


Figure 12



Figure 13

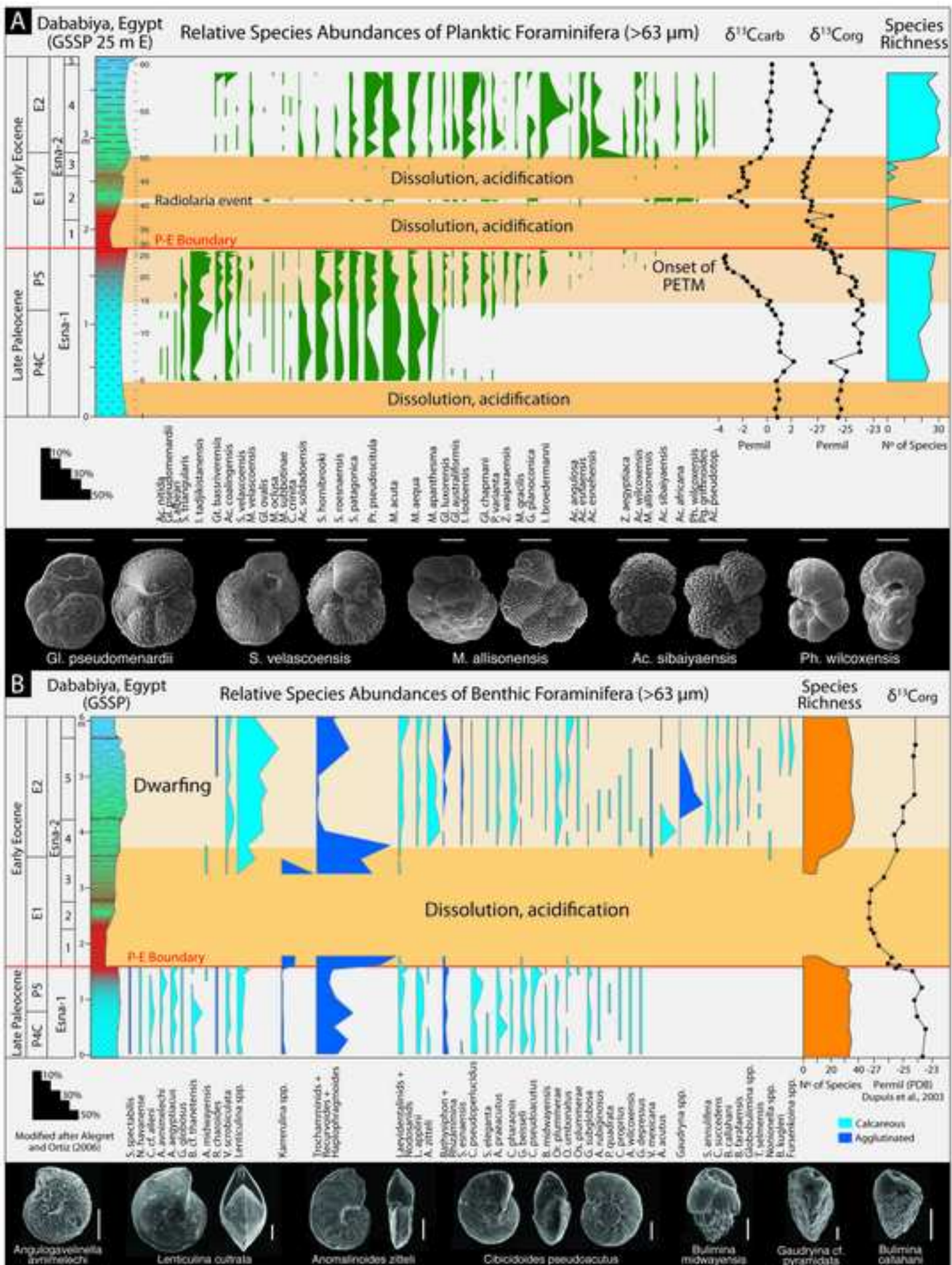


Figure 14

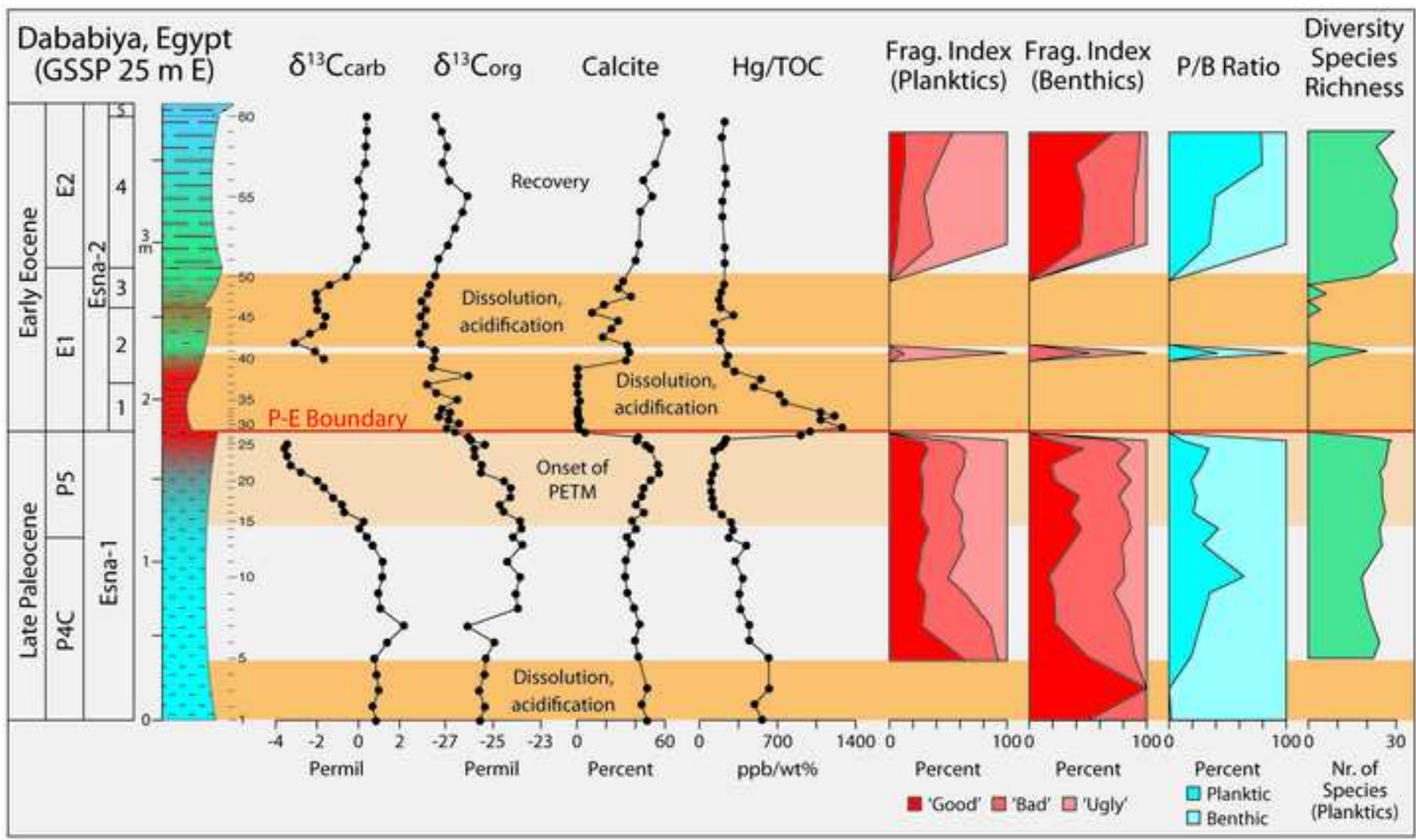


Figure 15

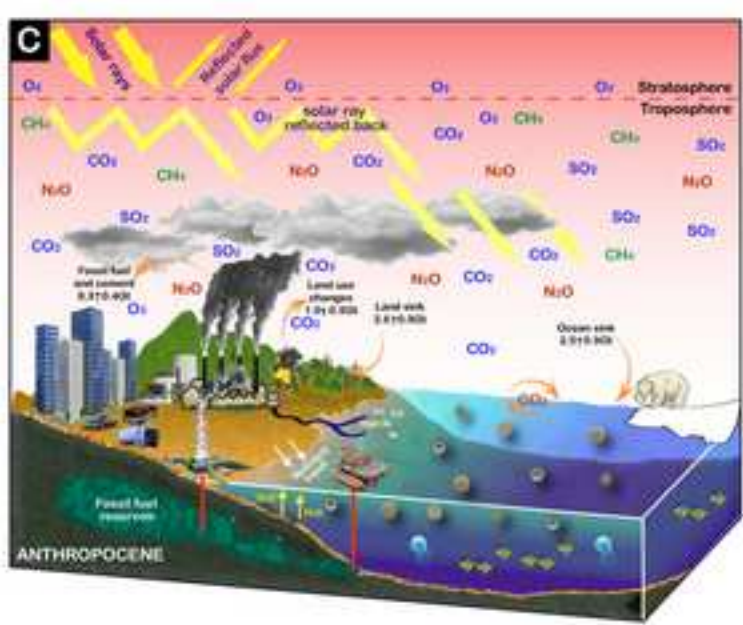
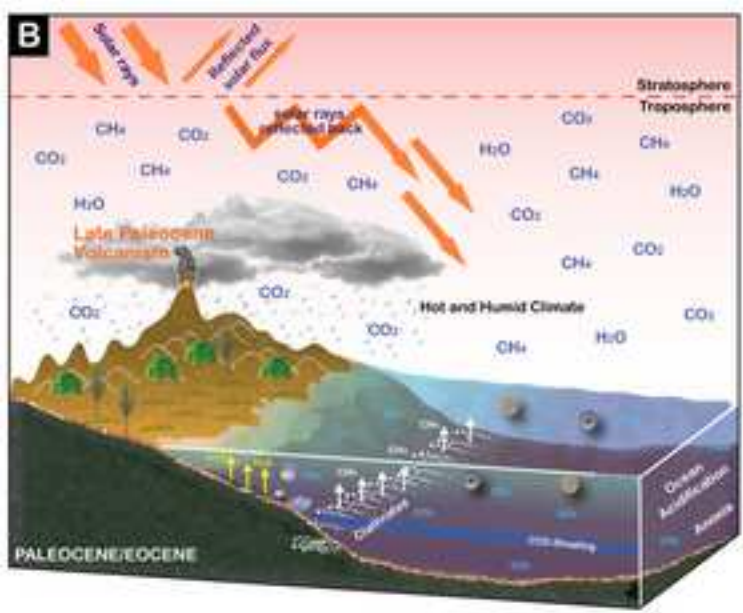
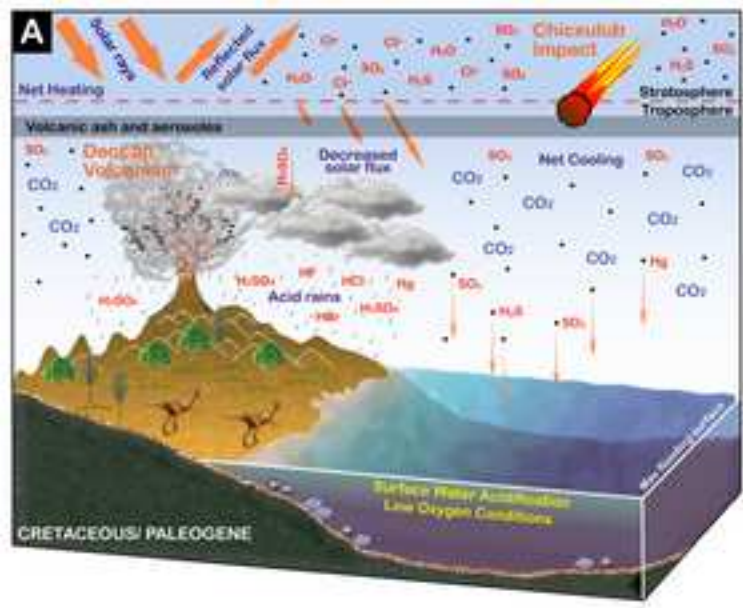


Table 1

Events	Anthropocene: Mass Extinction?	Paleocene/Eocene: PETM	End-Cretaceous: Mass Extinction
Age (Ma)	Ongoing, predicted by ~2250-2500 ¹	55.8±0.2 Ma	66.021±0.024 Ma
Faunal turnover	Ongoing extinctions	Extinctions/originations	Mass extinction
Mass extinctions	In progress	Minor ²	~50% genera, ~75% species
Rate of extinctions	In accelerating phase 20-50X background rates ¹	Rapid at max. warming 6-12X background rates in benthic foraminifera ²	Rapid over ~1000 years ~220X background rate in planktic foraminifera ³
Benthic foram extinctions	Yes, ongoing	30-50% species	Minor
Planktic foram extinctions	Yes, ongoing	Minor	99% species
Vertebrate extinctions	Yes, ongoing	Minor, migration	Major
Terrestrial extinctions	Yes, ongoing	Minor	Major
Recovery	-----	Rapid after PETM	Delayed >500 ky
Pre-event climate	Gradual warming	Gradual warming	Rapid warm-cool changes over 350 ky ⁴
Climate (greenhouse gases)	Rapid warming	Rapid warming	Rapid warming
Warming: rate	1-4 °C/100 yrs, 2-10 °C next 200-300 yrs	0.025 °C/100 yrs, total 5 °C ⁵	Oceans 3-4 °C ⁴ Land 6-8 °C ⁶
Warming: max duration	Decades to 100's of years	Tens of thousands of years	Tens of thousands of years
Tippling point temperature increase >4°C	~4 °C possibly reached by 2020	5 °C	~5 °C
Sea-level	Rapid rise (1-2 m) ⁷	Rapid rise (3-5 m)	Rise ~50 m over 100 ky
Anoxia/ dysoxia	Yes	Yes, continental shelf	Dysoxia in water column
Ocean Acidification (rate)	Yes (0.3 units/100 yrs) ⁸	Yes (0.3 units/20 ky) ⁹	Yes ¹⁰
Clathrates (CH₄)	No (possible in future)	Yes	None confirmed
Volcanism (LIPs)	No	North Atlantic Igneous Province (NAIP)	Deccan Traps
Global warming: main underlying cause(s)	CO ₂ : fossil fuel burning CH ₄ : peat, coal, permafrost	CO ₂ : volcanoes, CH ₄ : clathrates, peat, coal, permafrost	CO ₂ : volcanoes CH ₄ : no data
Impacts	No	Unconfirmed	Chicxulub 180 km

¹ Anthropocene extinctions are predicted to reach the 75 % mass extinction level within the next 250 to 500 ky (conservative estimate) based on projection of current rates of extinctions and current rates of fossil fuel burning (e.g. May et al., 1995; Hughes et al., 1997; Ceballos and Ehrlich, 2002; Pereira et al., 2010; Barnosky et al., 2011).

² For the PETM event extinctions are limited to benthic foraminifera in the marine realm; with maximum 50 % extinct over 170 ky (estimated duration of PETM event), the rate of extinction estimated from El Kef is 0.12 species/ky or about 12-24 background rates at 1-2 species/100 ky (this study).

³ Estimated from planktic foraminifera: 66 % (44 species) extinct over about 10 ky, an average of 4.4 species/ky; background rates are 1-2 species/100 ky or 0.01-0.02/ky. This means that the rate of extinction is at least 220 times background. About 33 % go extinct within 50-100 ky after the KPBS leaving a single survivor species (this study).

⁴ e.g., Stüben et al. (2003), Li and Keller (1998), Abramovich and Keller (2003), Punekar et al. (2014)

⁵ Zachos et al. (2005, 2006)

⁶ Wilf et al. (2003), Nordt et al. (2003)

⁷ IPCC 5th Assessment Report (2013), conservative estimate

⁸ e.g., Sluijs et al. (2008), IPCC 4th Assessment Report (2007), projected global average pH surface ocean, between 2000-2100

⁹ Penman et al. (2014), comparison of $\delta^{11}\text{B}$ data and LOSCAR model simulation

¹⁰ Font et al. (2011, 2014), Punekar et al. (2016)