

# Hypothesis testing on the planktic foraminiferal survival model after the KPB mass extinction: evidence from Tunisia and Algeria

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## Abstract

A historical review of the extinction, survival, and evolutionary models of planktic foraminifera proposed for the Cretaceous/Paleogene boundary (KPB) mass extinction event sometimes leaves the impression that there is still no conclusive evidence to support any single one of them. Two main models have been put forward: i) catastrophic mass extinction, almost total for some authors, compatible with the geologically instantaneous paleoenvironmental effects of a large meteorite impact (Chicxulub impact, Mexico); and ii) gradual mass extinction, compatible with the paleoenvironmental effects of massive, long-lasting volcanism (Deccan Traps, India). Over the years, a lot of evidence has been proposed supporting one hypothesis or the other, highlighting isotopic ( $\delta^{18}\text{O}$ ,  $\delta^{13}\text{C}$ ,  $^{87}\text{Sr}/^{86}\text{Sr}$ ) as well as taphonomic, biostratigraphic, quantitative (relative and/or absolute abundance), phylogenetic, and even teratological. We review previous planktic foraminiferal and stable isotope studies, and provide new quantitative and statistical tests from two pelagic sections: the El Kef section (Tunisia), recognized as the most continuous and expanded lowermost Danian section worldwide, and the Sidi Ziane section (Algeria), affected by relevant hiatus in the lower Danian. The results indicate that all the latest Maastrichtian planktic foraminiferal species except those of *Guembelitra* went extinct exactly at the KPB, supporting the hypothesis of an almost total extinction. In the light of this new evidence, we maintain that the Maastrichtian planktic foraminiferal specimens found worldwide in lower Danian samples could be the result of similar reworking and vertical mixing processes to those at El Kef and Sidi Ziane.

## Key Words

catastrophic mass extinction, biostratigraphy, Danian, Maastrichtian, reworking

## 1. Introduction

The accuracy of planktic foraminiferal extinction models across the Cretaceous/Paleogene boundary (KPB) has been a matter of controversy since the 1980s. The mass extinction event was initially described in the Caravaca (Spain) and El Kef (Tunisia) sections as being sudden and almost total (Smit 1982), except for the survival of the disaster opportunist *Guembelitra cretacea*. The near-complete extinction model was questioned by Keller (1988), who pointed out that, at El Kef, 12 Maastrichtian species

went extinct before the KPB, 31 species disappeared near the KPB, and at least 11 species survived into the early Danian. To resolve the dispute, four specialists (Canudo 1997; Masters 1997; Olsson 1997; Orue-Etxebarria 1997) blindly examined unlabeled samples from the El Kef stratotype (Smit and Nederbragt 1997). The El Kef blind test was an admirable attempt to resolve the controversy (Lipps 1997; Ginsburg 1997a). However, both Smit (Smit and Nederbragt 1997) and Keller (Keller 1997) claimed that the outcome supported their own views. Ginsburg (1997b) concluded that the blind test had failed, among

other reasons, due to differences in the taxonomic naming of the species among those carrying out the test, as well as an inability to discriminate between in situ and ex situ (reworked) specimens.

In accordance with Smit (1982, 1990), the so-called catastrophist hypothesis was supported by many other specialists in planktic foraminifera in the 1990s (KPB–catastrophists from now on), albeit proposing slightly different extinction models in which a greater number of surviving species were suggested (e.g., Arz et al. 1996b, 1999a; Huber 1996; Koutsoukos 1996; Molina et al. 1996, 1998; Apellaniz et al. 1997; Kaiho and Lamolda 1999). KPB–catastrophists argue that a geologically instantaneous extinction can only be explained by the abrupt environmental effects caused by the impact of a large asteroid, which is linked to the Chicxulub impact in the Yucatan Peninsula, Mexico (see Hildebrand et al. 1991; Schulte et al. 2010 and references therein).

After defending the idea that a wider range of Maastrichtian species went extinct before or after the KPB, the supporters of so-called gradualist hypothesis (KPB–gradualists from now on) suggest that a gradual mass extinction can only be explained by long-lasting environmental changes not directly related to the Chicxulub impact (e.g., Keller et al. 1993, 1995; MacLeod and Keller 1994; Luciani 1997). A gradual extinction extending for hundreds of thousands of years across the KPB would be more consistent with the hypothesis of global climate changes triggered by massive volcanism linked to the flood basalt emplacement of the Deccan Traps in west-central India (Officer and Drake 1985; Courtillot et al. 1988; Keller et al. 2010, and references herein). Alternatively, KPB–gradualists have proposed the hypothesis of multiple causes, which combines the three major extinction factors postulated for that time: massive volcanism, a sea-level fall, and a large meteorite impact, via climate change (Canudo et al. 1991; Li and Keller 1998).

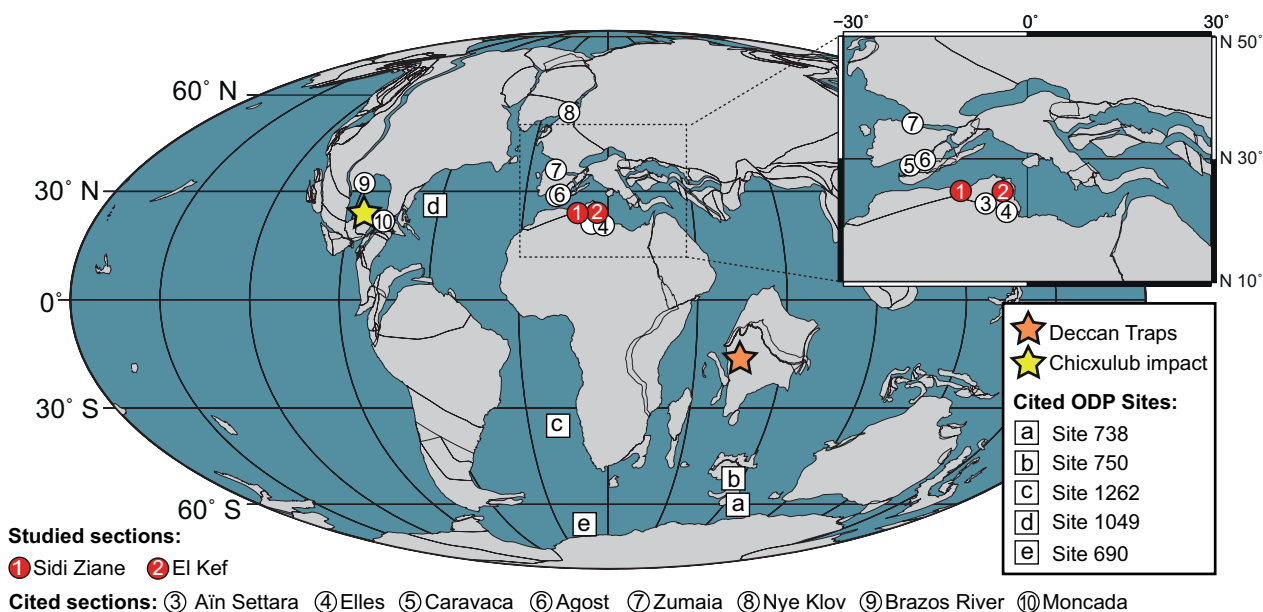
KPB–catastrophists have pointed out that the latest Maastrichtian planktic foraminiferal extinctions are in fact an artefact of the Signor–Lipps effect, due to the low intensity in the search for the scarcest species (Signor and Lipps 1982; Molina 1995). The Signor–Lipps effect might lead to the erroneous interpretation that the stratigraphic ranges of some Maastrichtian planktic foraminiferal species do not reach the KPB. Nevertheless, KPB–gradualists have continued to hold that the micropaleontological data agreed with their claim that the extinction began in the last 500 kyr of the Maastrichtian and continued in the earliest Danian (Keller 2001, and references herein). On the other hand, Smit (1982, 1990) warned that the presence of Maastrichtian species in Danian samples may be the result of reworking processes, and not the result of their survival from the KPB extinction. However, KPB–gradualists considered these to be surviving species (Keller 2001, and references herein). In the 1990s,  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  analyses of Maastrichtian planktic foraminiferal species identified in the lower Danian also failed to distinguish clearly between the surviving

taxa and reworked specimens (e.g., Stott and Kennett 1990; Zachos et al. 1992; Keller et al. 1993; Barrera and Keller 1994; Kaiho and Lamolda 1999), so the debate on the magnitude and extension of the KPB mass extinction event seemed to resist all attempts at solution.

In the last twenty years, KPB specialists have focused on determining which of two alleged factors (asteroid impact or massive volcanism) was the main contributor to the extinction (Keller et al. 2010, 2020; Schulte et al. 2010; Vellekoop et al. 2014, 2016; Arenillas et al. 2018; Lowery et al. 2018, 2020; MacLeod et al. 2018; Renne et al. 2018; Henehan et al. 2019; Hull et al. 2020; Gilabert et al. 2021a, 2021b), as well as ascertaining the precise timing of both the Chicxulub impact and the main Deccan volcanic phases (Renne et al. 2013, 2015; Schoene et al. 2015, 2019; Sprain et al. 2019; Gilabert et al. 2022). Because the dispute among KPB specialists focused on the controversy over the causes of the extinction, the debate on the presence of “reworked specimens vs. survivor taxa” in lowermost Danian samples waned in the 2000s, and virtually nothing else was published in the 2010s, with only a few exceptions (e.g., Gallala et al. 2009; Gallala 2013, 2014; Punekar et al. 2014; Molina 2015). However, this is a relevant issue both for the verification or refutation of the two main hypotheses about the causes of the KPB extinction (asteroid impact vs. massive volcanism) and for the reconstruction of the phylogenetic relationships among early Danian planktic foraminifera (e.g., Koutsoukos 2014). In order to provide new evidence that might clear up how many species survived the KPB mass extinction event, we have first reviewed biostratigraphic and isotopic studies of planktic foraminifera previously carried out in some relevant KPB pelagic sections and Ocean Drilling Program (ODP) sites around the world (Fig. 1). In addition, we have quantitatively and statistically analyzed the planktic foraminiferal survival patterns after the KPB extinction in two western Tethyan localities: El Kef (Tunisia) and Sidi Ziane (Algeria).

## 2. Geographical and geological setting

The El Kef section is located 5–6 km southwest of the city of El Kef, northwestern Tunisia. The KPB lies in the upper Maastrichtian to Paleocene El Haria Formation (Salaj 1974). It was chosen to define the Global Boundary Stratotype Section and Point (GSSP) for the base of the Danian Stage, or KPB, because it is the most continuous, complete, and expanded section worldwide (Remane et al. 1999; Molina et al. 2006). The GSSP for the KPB was defined as the lowermost part of what is informally known as the dark KPB Clay, specifically as the base of a 2–5 mm thick rust clay layer (airfall layer) that has anomalous iridium concentrations and is rich in impact ejecta (impact glasses, Ni-spinels, shocked quartz, etc.). The base of this airfall layer at El Kef is the same stratigraphic level as the planktic foraminiferal extinction horizon (Arenillas et al. 2000b; Molina et al. 2006).



**Figure 1.** Paleogeographic reconstruction of the KPBB (66.00 Ma), with the localities cited in this study (after [https://www.odsn.de/odsn/services/paleomap/adv\\_map.html](https://www.odsn.de/odsn/services/paleomap/adv_map.html)). ODP – Ocean Drilling Program.

The Sidi Ziane section is located 4 km south of the village of Sidi Ziane in the Souagui District of Médéa Province, northern Algeria, which is approximately 75 km southwest of Algiers and 47 km southeast of Médéa, the capital city of the province of the same name. The area is characterized by thick allochthonous deposits of Cretaceous to Eocene age (Kieken 1974). The KPBB lies in Unit I of Kieken (1974), consisting of clayey marls in the upper Maastrichtian and an alternation of clayey marls and marly limestones in the lower Danian. The thickness of the last planktic foraminiferal biozone of the Maastrichtian (*Plummerita hantkeninoides* Zone) at Sidi Ziane is 13.5 m, making it one of the thickest identified to date, suggesting that the uppermost Maastrichtian is complete and continuous. Based on graphic correlation, it has been determined that the sedimentation rate of the Maastrichtian in Sidi Ziane is 8.98 cm/kyr, which is comparable with the most expanded and continuous sections worldwide, such as the El Kef and Ain Settara sections in Tunisia (Metsana-Oussaid et al. 2019). However, the absence of the dark KPBB Clay and the first Danian biozones at Sidi Ziane indicates a hiatus affecting the first few hundred thousand years of the Danian (Metsana-Oussaid et al. 2019).

### 3. Material and methods

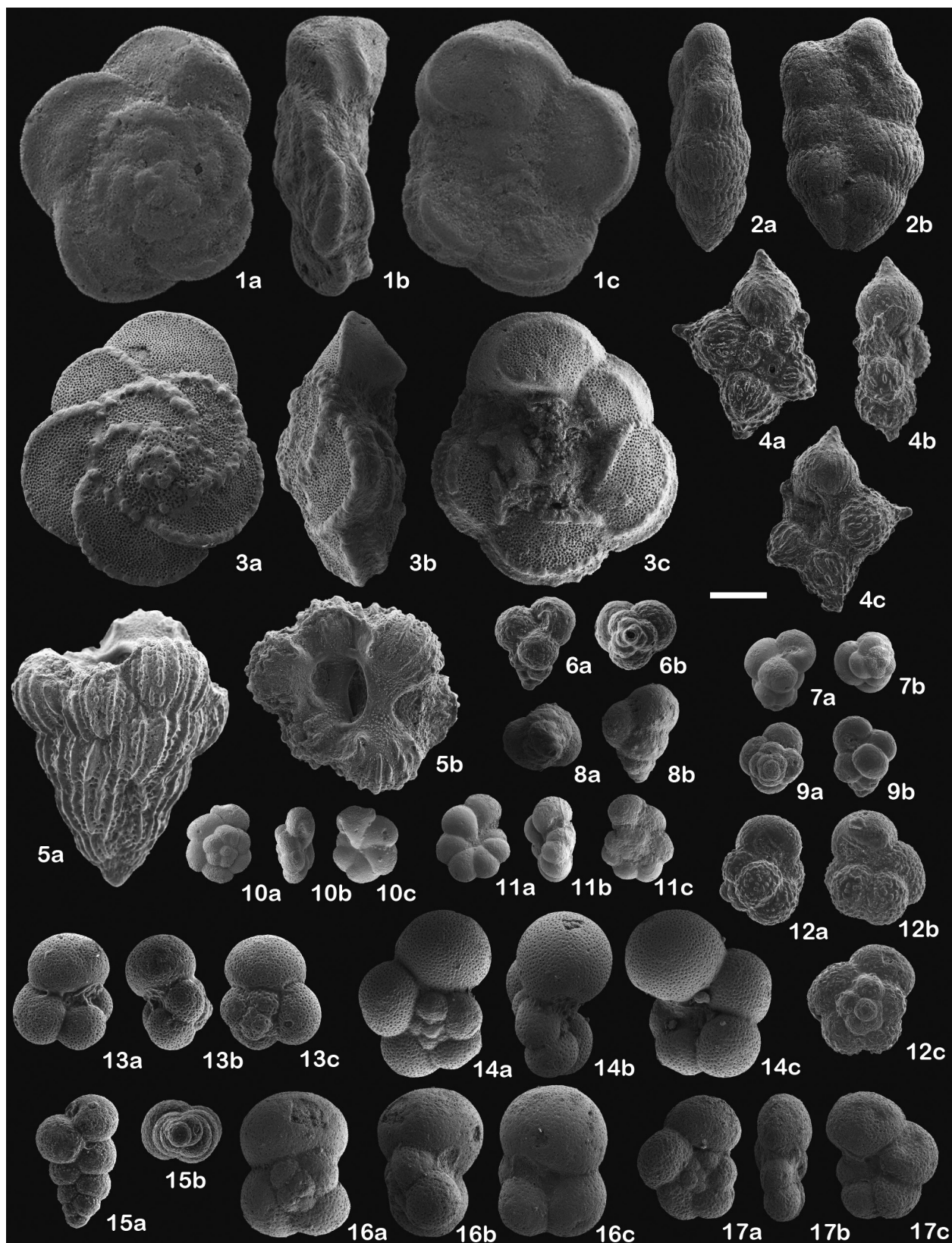
For biostratigraphic and taphonomic interpretations, we selected 40 samples from El Kef and 47 samples from Sidi Ziane across the critical KPBB interval from the set of samples collected in both sections. All studied rock samples were disaggregated in water with diluted  $H_2O_2$ , washed through a 63  $\mu m$  sieve, and then oven dried at 50 °C. The planktic foraminiferal species of the upper Maastrichtian were intensively searched in all samples from the  $\geq 63 \mu m$  size fraction in order to minimize the

Signor–Lipps effect. The quantitative analyses (relative abundance counts at species level) were based on representative aliquots, obtained by microsplitter, of approximately 300 specimens per sample (Suppl. material 2: Table S1, Suppl. material 3: Table S2). Some relevant planktic foraminiferal specimens were picked from the residues and selected for scanning electron microscopy (SEM), using a Zeiss MERLIN FE-SEM of the Electron Microscopy Service of the Universidad de Zaragoza (Spain). SEM photographs of some species are provided in Figs 2–4.

In order to minimize the reworking effect and determine the planktic foraminiferal survival patterns at El Kef and Sidi Ziane, we drew on quantitative and statistical analyses. For these analyses, we followed two methods.

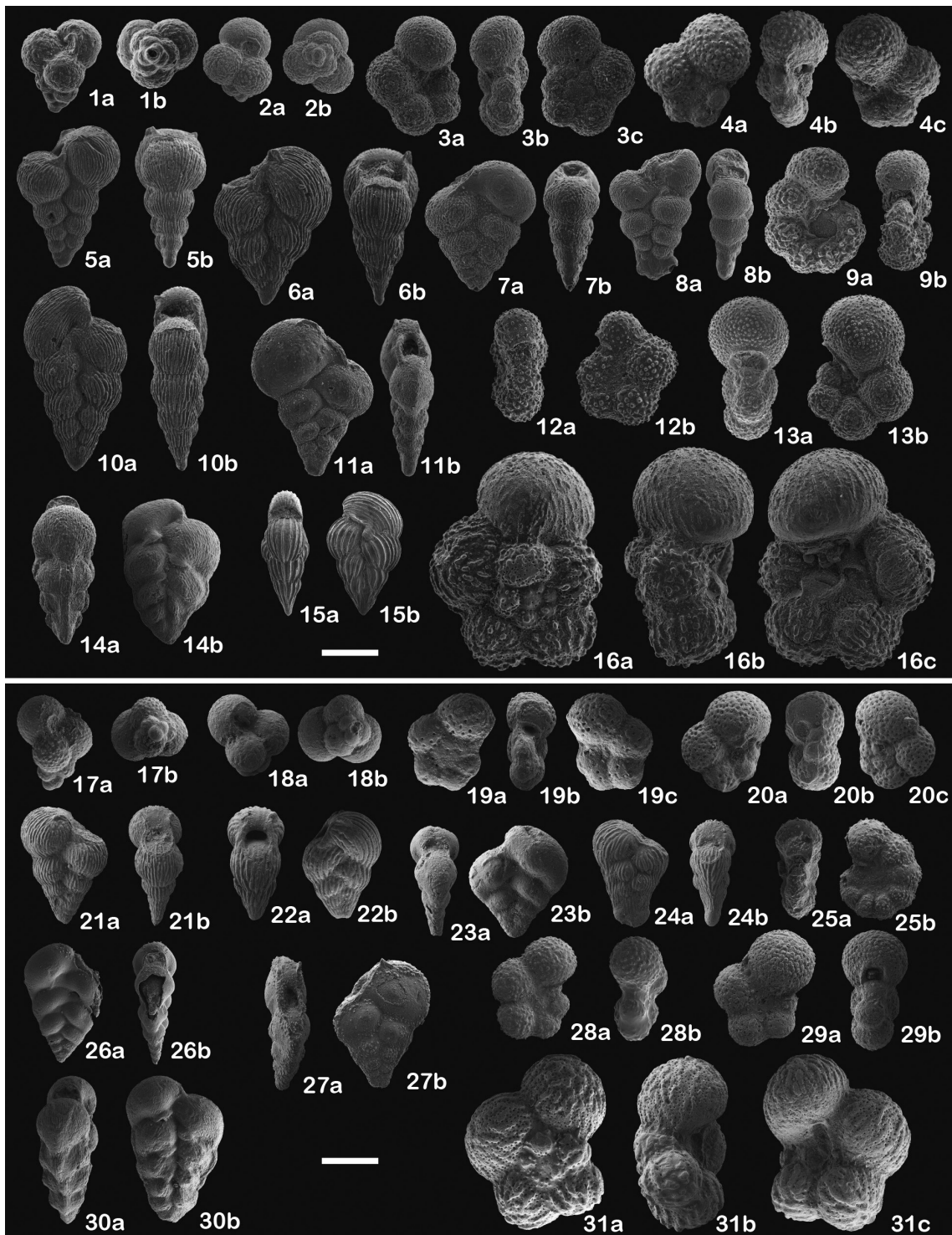
First, we performed nonlinear regression analyses using least squares to find equations/functions that fit two data sets of the lowermost Danian in both the El Kef and Sidi Ziane sections:  $y = \text{relative abundance (\%)} \text{ of Maastrichtian specimens with respect to the total planktic foraminiferal specimens}$ , and  $x = \text{number of sample (cm above the KPBB)}$ . The data were fitted by a method of successive approximations, following Levenberg-Marquardt optimization. In order to select which function or model best fits the  $x$ - $y$  data, the Akaike Information Criterion (Akaike IC) was used; lower values for the Akaike IC imply a better fit. Two nonlinear functions were selected: exponential and power functions. Other nonlinear functions were also tested, but they did not give good results since very high Akaike IC values were obtained. To fit data to exponential functions (exponential curve  $y = ae^{bx} + c$ ), an initial guess by linearization (log-transforming  $y$ ), followed by nonlinear optimization, was performed. To fit data to power functions (power curve  $y = ax^b + c$ ), an initial guess by log-log transformation and linear regression, i.e.  $c = 0$ , followed by nonlinear optimization,



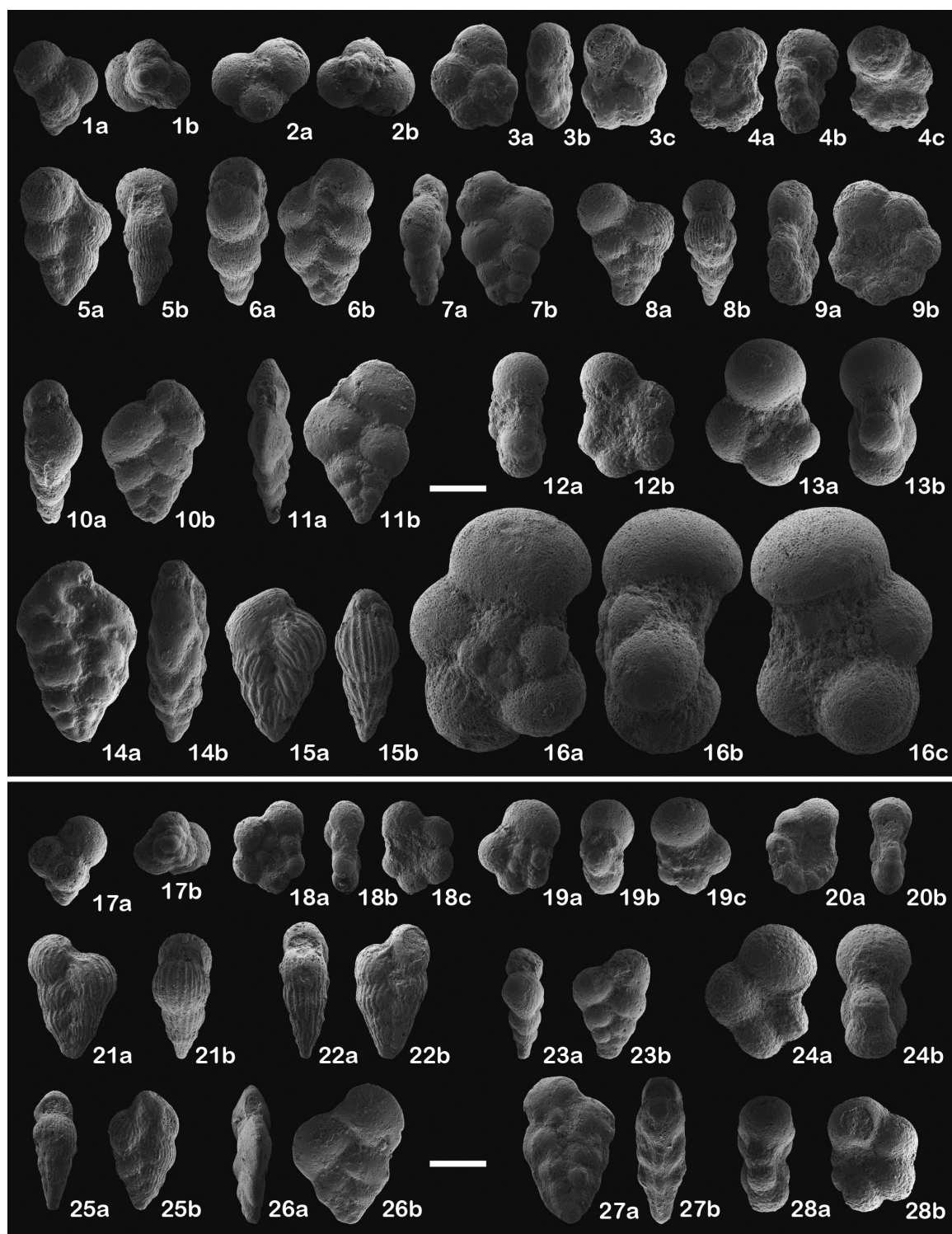


**Figure 2.** SEM photographs of the planktic foraminiferal index species and some other relevant species from the Maastrichtian and Danian. Samples K and SZ numbered in cm from the KP/B. **1.** *Abathomphalus mayaroensis* (SZ-350); **2.** *Pseudoguembelina hariaensis* (SZ-1550); **3.** *Globotruncana arca* (K-1200); **4.** *Plummerita hantkeninoides* (sample K-400); **5.** *Racemiguembelina fructicosa* (K-400); **6.** *Guembelitra cretacea* (K-100); **7.** *Pseudocaucasina antecessor* (K+70); **8.** *Chiloguembelitra danica* (SZ+1); **9.** *Palaeoglobigerina alticonusa* (K+450); **10.** *Parvularugoglobigerina longiapertura* (K+100); **11.** *Parvularugoglobigerina eugubina* (K+200); **12.** *Trochoguembelitra liuae* (K+850); **13.** *Eoglobigerina simplicissima* (sample K+550); **14.** *Parasubbotina pseudobulloides* (K+1110); **15.** *Woodringina hornerstownensis* (K+650); **16.** *Subbotina triloculinoides* (SZ+30); **17.** *Globanomalina compressa* (SZ+445). Scale bar: 100  $\mu$ m.





**Figure 3.** SEM photographs of the Maastrichtian planktic foraminiferal species usually considered to be putative survivors of the KPBB extinction. Specimen comparison from upper Maastrichtian and lower Danian samples at El Kef. Samples K numbered in cm from the KPBB. Specimens in Maastrichtian samples: **1.** *Guembelitra cretacea* (K-100); **2.** *Guembelitra blowi* (K-750); **3.** *Muricohedbergella holmdelensis* (K-400); **4.** *Muricohedbergella monmouthensis* (K-70); **5.** *Heterohelix globulosa* (K-400); **6.** *Heterohelix labellosa* (K-400); **7.** *Heterohelix planata* (K-400); **8.** *Heterohelix navarroensis* (K-400); **9.** *Globigerinelloides yaucoensis* (K-400); **10.** *Pseudoguembelina costulata* (sample K-400); **11.** *Laeviheterohelix glabrans* (K-400); **12.** *Globigerinelloides prairiehillensis* (K-1100); **13.** *Globigerinelloides volutus* (sample K-400); **14.** *Pseudoguembelina kempensis* (sample K-400); **15.** *Pseudoguembelina costulata* (K-400); **16.** *Rugoglobigerina rugosa* (K-400). Specimens in Danian samples: **17.** *Guembelitra cretacea* (K+5); **18.** *Guembelitra blowi* (K+5); **19.** *Muricohedbergella holmdelensis* (K+5); **20.** *Muricohedbergella monmouthensis* (K+70); **21.** *Heterohelix globulosa* (K+5); **22.** *Heterohelix labellosa* (K+5); **23.** *Heterohelix planata* (K+20); **24.** *Heterohelix navarroensis* (K+5); **25.** *Globigerinelloides yaucoensis* (K+5); **26.** *Laeviheterohelix pulchra* (K+5); **27.** *Laeviheterohelix glabrans* (K+5); **28.** *Globigerinelloides prairiehillensis* (K+10); **29.** *Globigerinelloides volutus* (K+5); **30.** *Pseudoguembelina kempensis* (K+10); **31.** *Rugoglobigerina rugosa* (K+5). Scale bars: 100  $\mu\text{m}$ .



**Figure 4.** SEM photographs of the Maastrichtian species usually considered to be putative survivors of the KPb extinction. Specimen comparison from upper Maastrichtian and lower Danian samples at Sidi Ziane. Samples SZ numbered in cm from the KPb. Specimens in Maastrichtian samples: **1.** *Guembelitra cretacea* (SZ-40); **2.** *Guembelitra blowi* (SZ-40); **3.** *Muricohedbergella holmdelensis* (SZ-40); **4.** *Muricohedbergella monmouthensis* (SZ-850); **5.** *Heterohelix globulosa* (SZ-40); **6.** *Heterohelix labellosa* (SZ-40); **7.** *Heterohelix planata* (SZ-40); **8.** *Heterohelix navarroensis* (SZ-40); **9.** *Globigerinelloides yaucoensis* (SZ-820); **10.** *Laeviheterohelix pulchra* (SZ-40); **11.** *Laeviheterohelix glabrans* (SZ-40); **12.** *Globigerinelloides prairiehillensis* (SZ-40); **13.** *Globigerinelloides volutus* (SZ-40); **14.** *Pseudoguembelina kempensis* (SZ-40); **15.** *Pseudoguembelina costulata* (SZ-40); **16.** *Rugoglobigerina rugosa* (SZ-80). Specimens in Danian samples (from *Globanomalina compressa* Subzone, or Subbiozone P1c): **17.** *Guembelitra cretacea* (SZ+1); **18.** *Muricohedbergella holmdelensis* (SZ+1); **19.** *Muricohedbergella monmouthensis* (SZ+1); **20.** *Globigerinelloides yaucoensis* (SZ+1); **21.** *Heterohelix globulosa* (SZ+1); **22.** *Heterohelix labellosa* (SZ+1); **23.** *Heterohelix navarroensis* (SZ+1); **24.** *Globigerinelloides volutus* (SZ+1); **25.** *Pseudoguembelina costulata* (SZ+1); **26.** *Laeviheterohelix glabrans* (SZ+1); **27.** *Pseudoguembelina kempensis* (SZ+1); **28.** *Globigerinelloides prairiehillensis* (SZ+1). Scale bars: 100  $\mu$ m.



was performed. 95% confidence intervals, based on 1999 bootstrap replicates, were calculated and added in scatter graphs of both exponential and power curves. The software used was the program PAST, version 4.04 for Mac (Hammer et al. 2001).

Second, we used counts of the average relative abundance (%) of the most relevant and/or abundant Maastrichtian planktic foraminiferal taxa in uppermost Maastrichtian and lowermost Danian samples from both the El Kef and Sidi Ziane sections (Suppl. material 2: Table S1, Suppl. material 3: Table S2). These counts were carried out at the genus and species levels and were used to determine the relative abundance distribution (RAD) of Maastrichtian species and genera in both upper Maastrichtian and lower Danian samples. Incoming Danian taxa were excluded from the calculation of the relative abundances in Danian samples. For the lower Danian, average relative abundances were calculated for two sample sets: i) all Danian samples, and ii) samples from the first 20 cm of Danian. In the El Kef section, average relative abundances of *Guembelitra* in the lower Danian were calculated with respect to: i) the total specimen number of both Maastrichtian and Danian species, and ii) the total specimen number of only Maastrichtian species.

#### 4. Planktic foraminiferal biostratigraphy and biochronology

The stratigraphic ranges of planktic foraminiferal species in the El Kef section (Fig. 5) are based on Arenillas et al. (2000b) and subsequent revisions (see Arenillas and Arz 2017). Here we include data from the uppermost Maastrichtian biozone (Biozone CF1 of Li and Keller 1998, or *Plummerita hantkeninoides* Subzone of Arz and Molina 2002) and the first Danian biozones. The latter include the *Guembelitra cretacea* Zone (*Muricohedbergella holmdelensis* and *Parvularugoglobigerina longiapertura* Subzones), the *Parvularugoglobigerina eugubina* Zone (*Parvularugoglobigerina sabina* and *Eoglobigerina simplicissima* Subzones), and the *Parasubbotina pseudobulloides* Zone (*Eoglobigerina trivialis*, *Subbotina triloculinoides*, and *Globanomalina compressa* Subzones) of Arenillas et al. (2004). These are approximately equivalent to the most standardized Biozones P0 and Pa, and Subbiozones P1a, P1b, and P1c of Wade et al. (2011). According to Gilabert et al. (2022), the *Plummerita hantkeninoides* Subzone spans the last 99 kyr of the Maastrichtian. The bases of the lower Danian subzones of Arenillas et al. (2004) have recently been astronomically calibrated by Gilabert et al. (2022) to 0, 7, 18, 26, 68, 210, and 473 kyr after the KPBB, respectively. The dark bed of the KPBB Clay roughly coincides with the *Muricohedbergella holmdelensis* Subzone (Biozone P0). The stratigraphic ranges of planktic foraminiferal species in the Sidi Ziane section (Fig. 6) are based on Metsana-Oussaid et al. (2019), who recognized a relevant hiatus in the lower Danian, affecting the *Gb. cretacea* and *Pv. eugubina*

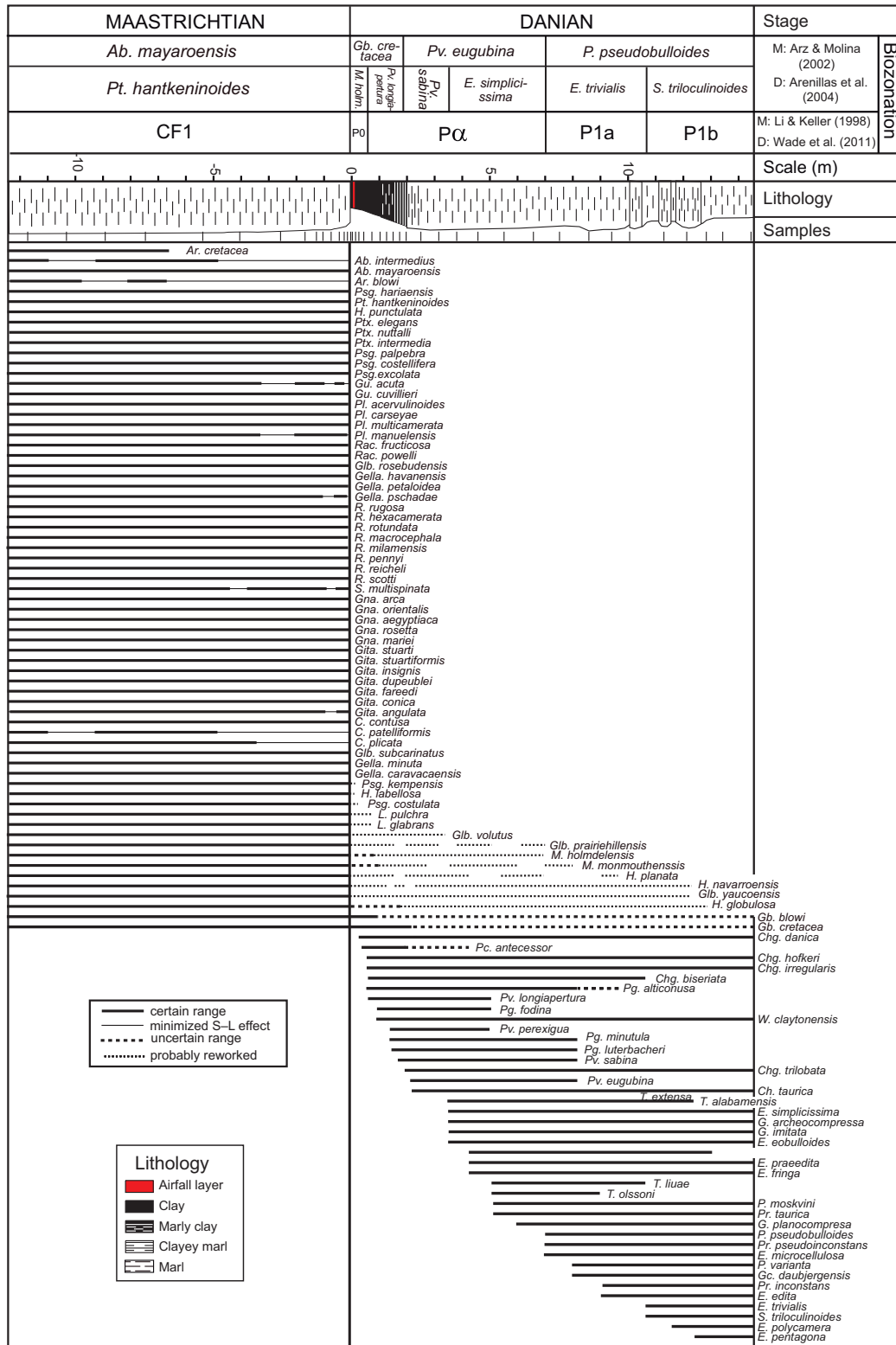
Zones and *E. trivialis* and *S. triloculinoides* Subzones. According to the age model of Gilabert et al. (2022), the hiatus at Sidi Ziane spans approximately the first 500 kyr of the Danian.

#### 5. Isotopic evidence a proxy for distinguishing of reworked specimens vs. survivor taxa

To infer the survival pattern that best fits what is observed in each KPBB section, and before inferring the global survival model, which is part of the extinction model, the species that survived the KPBB mass extinction must be identified. With a few exceptions, taphonomic evidence is hard to recognize in planktic foraminiferal specimens in lowermost Danian samples because it is difficult to find a simple visual criterion to distinguish reworked specimens. Only a few criteria have been cited, such as the differences in the preservation and coloration of reworked specimens compared to those of in situ specimens (Zumaia; Arz et al. 1999b), or the differences in the coloration of test infill in reworked specimens (ODP Site 1049; Huber et al. 2002). Isotopic evidence has been considered the most objective tool for testing the hypotheses on planktic foraminiferal extinction and survival models across the KPBB. Comparison of the values of planktic foraminiferal  $\delta^{18}\text{O}$ ,  $\delta^{13}\text{C}$ , and  $^{87}\text{Sr}/^{86}\text{Sr}$  in Maastrichtian and Danian samples makes it possible to discern whether the Maastrichtian specimens found above the KPBB are in situ or ex situ. If the tests of a particular Maastrichtian species have a Danian isotopic signal, differing significantly from the one they have in the Maastrichtian, they can be considered specimens in situ and consequently survivors, unless the isotopic signal is altered by diagenesis.

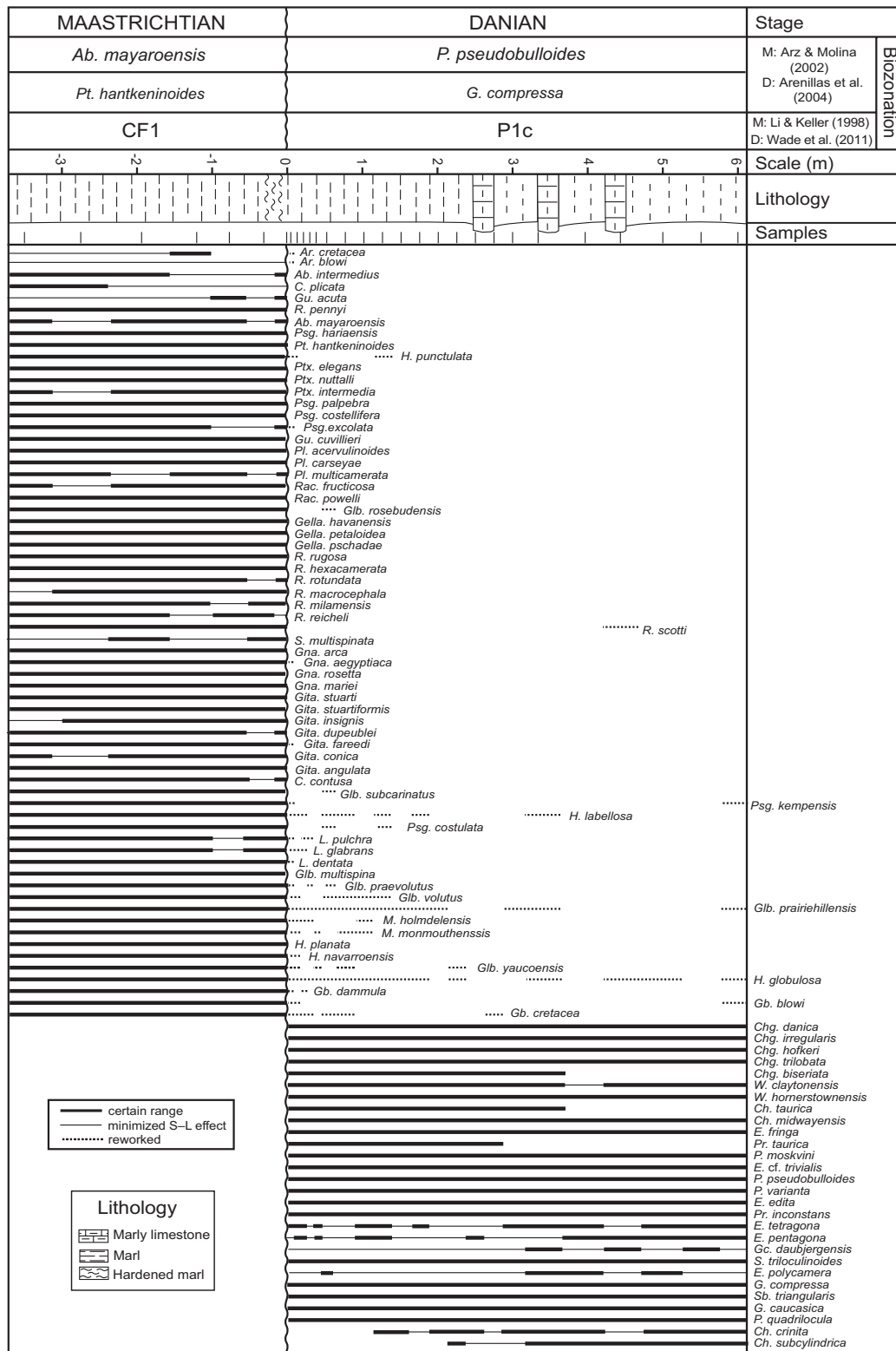
The first species to be considered a survivor based on isotopic evidence was *Heterohelix globulosa*, after analysis of its  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values in both Maastrichtian and Danian from Brazos River (Barrera and Keller 1990; MacLeod and Keller 1994) and Nye Klov (Keller et al. 1993; Barrera and Keller 1994). However, other specialists raised doubts about this evidence, since the *H. globulosa*  $\delta^{13}\text{C}$  values in the Maastrichtian and the Danian exhibited great similarity at ODP Sites 690 (Maud Rise; South Atlantic) and 750 (Kerguelen Plateau; Indian Ocean), suggesting that *H. globulosa* specimens are reworked in the Danian samples (Stott and Kennett 1990; Zachos et al. 1992). Barrera and Keller (1994) admitted that such isotopic similarity also occurred at ODP Site 738.

The second species to be recognized as a potential survivor based on isotopic evidence was *Rugoglobigerina rugosa*, following its isotopic analysis at Nye Klov (Keller et al. 1993). However, as in the case of *H. globulosa*, subsequent stable isotope studies again called this evidence into question (Huber 1996; MacLeod and Huber 1996; Kaiho and Lamolda 1999). For example, Huber (1996) noted that the  $\delta^{13}\text{C}$  values of the *R. rugosa* (as well as *H. globulosa*) reported at Nye Klov by Keller et al.



**Figure 5.** Stratigraphic ranges of the planktic foraminiferal species across the KPb in the El Kef section. Certain range = known stratigraphic range according to Arenillas et al. (2000b); minimized S-L effect = stratigraphic range after minimizing the Signor–Lipps effect and comparing with the stratigraphic ranges from other sections; uncertain range = doubtful stratigraphic ranges according to Arenillas and Arz (2017) and Arenillas et al. (2008); probably reworked = stratigraphic range based on probably reworked specimens (identified in the representative aliquot). M: Biozonation for the upper Maastrichtian; D: Biozonation for the lower Danian. Ar. – *Archaeoglobigerina*; Ab. – *Abathomphalus*; Psg. – *Pseudoguembelina*; Pt. – *Plummerita*; H. – *Heterohelix*; Ptx. – *Pseudotextularia*; Gu. – *Gublerina*; Pl. – *Planoglobulina*; Rac. – *Racemiguembelina*; Glb. – *Globigerinelloides*; Gella. – *Globotruncanella*; R. – *Rugoglobigerina*; S. – *Schackoina*; Gna. – *Globotruncana*; Gita. – *Globotruncanita*; C. – *Contusotruncana*; L. – *Laeviheterohelix*; M. – *Muricohedbergella*; Gb. – *Guembelitria*; Chg. – *Chiloguembelitria*; Pc. – *Pseudocausasia*; Pg. – *Palaeoglobigerina*; Pv. – *Parvularuoglobigerina*; W. – *Woodringina*; T. – *Trochoguembelitria*; E. – *Eoglobigerina*; G. – *Globanomalina*; P. – *Parasubbotina*; Gc. – *Globoconusa*; Pr. – *Praemurica*; S. – *Subbotina*.





**Figure 6.** Stratigraphic ranges of the planktic foraminiferal species across the KPb in the Sidi Ziane section. Certain range = known stratigraphic range based on Metsana-Oussaid et al. (2019); minimized S-L effect = stratigraphic range after minimizing the Signor–Lipps effect and comparing with the stratigraphic ranges from other sections; reworked = stratigraphic range based on reworked Maastrichtian specimens (identified in the representative aliquot). M: Biozonation for the upper Maastrichtian; D: Biozonation for the lower Danian. Ar. – *Archaeoglobigerina*; Ab. – *Abathomphalus*; Psg. – *Pseudoguembelina*; Pt. – *Plummerita*; H. – *Heterohelix*; Ptx. – *Pseudotextularia*; Gu. – *Gublerina*; Pl. – *Planoglobulina*; Rac. – *Racemiguembelina*; Glb. – *Globigerinelloides*; Gella. – *Globotruncanella*; R. – *Rugoglobigerina*; S. – *Schackoina*; Gna. – *Globotruncana*; Gita. – *Globotruncanita*; C. – *Contusotruncana*; L. – *Laeviheterohelix*; M. – *Muricohedbergella*; Gb. – *Guembelitra*; Chg. – *Chiloguembelitra*; Pc. – *Pseudocaucasina*; Pg. – *Palaeoglobigerina*; Pv. – *Parvularuoglobigerina*; W. – *Woodringina*; T. – *Trochoguembelitra*; E. – *Eoglobigerina*; G. – *Globanomalina*; P. – *Parasubbotina*; Gc. – *Globoconusa*; Pr. – *Praemurica*; S. – *Subbotina*.

(1993) and Barrera and Keller (1994) do not exhibit any significant change across the KPB.

The next species to be isotopically proposed as survivors were those belonging to disaster opportunist *Guembelitra*. At Nye Klov, Barrera and Keller (1994) suggested that *Gb. cretacea*, *Gb. blowi* (called *Gb. trifolia* by these authors), and *Gb. dammula* (called *Gb. danica* by these authors) are survivors. Given that all planktic foraminiferal taxonomists and biostratigraphers agree that *Guembelitra* survived (Smit 1982; Keller 1988; Molina et al. 1996; Olsson et al. 1999; Arenillas et al. 2000a, 2000b, 2006, 2018; Huber et al. 2002; Keller and Pardo 2004; Birch et al. 2016; Lowery et al. 2018, 2020), this isotopic evidence can be considered a verification. However, we must note some taxonomic details. Arz et al. (2010) and Arenillas et al. (2017) warned of the existence of pseudocryptic species in the lowermost Danian among *Guembelitra* and *Chiloguembelitra* (*Gb. cretacea* vs. *Chg. danica*; *Gb. blowi* vs. *Chg. trilobata*; *Gb. dammula* vs. *Chg. hofkeri*), which are only differentiated by the position of the aperture and mainly by the wall texture. Therefore, many isotopic analyses on putative *Guembelitra* tests of the lower Danian were most likely performed on *Chiloguembelitra* tests. For this reason, Arenillas et al. (2017) raised doubts as to whether at least one of the *Guembelitra* species, *Gb. dammula*, was indeed a survivor.

Another species to be recognized as a survivor was *Zeauvigerina waiparaensis* (Huber and Boersma 1994; Olsson et al. 1999). Barrera and Keller (1994) obtained isotopic evidence at ODP Site 738 (Kerguelen Plateau; Indian Ocean), where *Z. waiparaensis*, which they called *Chiloguembelina waiparaensis*, became the dominant species of the early Danian foraminiferal assemblages. However, there are many doubts as to whether this species is planktic or benthic (Arenillas 2012; Lowery et al. 2020). Its planktic life-form was inferred by Huber and Boersma (1994) based on relative abundance counts, after discovering that, in the pelagic sections they studied, the relative abundance of *Z. waiparaensis* was higher than that of all the benthic species (see also Olsson et al. 1999). However, Huber and Boersma (1994) indicated that *Z. waiparaensis* yields stable isotopic values that are closer to benthic foraminiferal values than to planktic ones, raising doubts about its planktic life-form. Barrera and Keller (1994) also reported that the *Z. waiparaensis*  $\delta^{13}\text{C}$  values are similar to benthic foraminiferal ones, although they used them as evidence of its deeper water habitat. These isotopic data could be more compatible with the hypothesis that *Z. waiparaensis* had a benthic life-form and was a disaster opportunist. A similar case could be *Rectoguembelina cretacea*, which is also considered a planktic species that survived the extinction event (Huber and Boersma 1994; Olsson et al. 1999).

Furthermore, Huber (1996) noted that, in addition to *Gb. cretacea* and *Z. waiparaensis*, there are other Maastrichtian species, such as *Muricohedbergella holmdelensis* and *Muricohedbergella monmouthensis*, that are considered survivors and ancestral to Cenozoic planktic foraminiferal lineages (Liu and Olsson 1992, 1994; Olsson et al. 1992, 1999; Aze et al. 2011; Lowery et al. 2018, 2020).

Recently, Birch et al. (2016) contributed to the discussion by demonstrating with isotopic evidence that *M. holmdelensis* was a survivor. After reporting a relevant decrease in the  $\delta^{13}\text{C}$  values of its test after the KPB at ODP Site 1262 (Walvis Ridge; South Atlantic), they concluded that the specimens of *M. holmdelensis* above the KPB had a Danian isotopic signal. Nevertheless, this evidence was based on a very low-resolution sampling, taking measurements on just four samples, of which only one was from the lowermost Danian. Consequently, more isotopic evidence will be needed before it can be concluded that *Muricohedbergella* was a Maastrichtian survivor like *Guembelitra*.

Subsequently, Keller (1997) also claimed to have isotopically demonstrated that *Globigerinelloides asper* was a survivor, although we have not been able to find any such evidence in the references cited by the author (Barrera and Keller 1990; Keller 1993; Keller et al. 1993). The latter only reported the high abundance of this species in the lower Danian of Brazos River, Nye Klov, and ODP Site 738C as evidence of its survival. Keller (1988, 1989a, 1989b), Huber (1991), and Barrera and Keller (1994) also noted the high relative abundance of other species of *Globigerinelloides*, such as *Glb. multispinus*, in the lower Danian, which could indicate that these survived the KPB extinction. However, Stott and Kennett (1990), Zachos et al. (1992), Barrera and Keller (1994), and Huber (1996) ruled this out, because the isotopic values showed very little difference below and above the KPB in the studied localities and were consistently very different from in situ specimens of co-occurring Danian species.

Most of the  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  studies have not been able to demonstrate that the Maastrichtian species found in Danian samples, except for *Gb. cretacea* and the allegedly planktic *Z. waiparaensis* and *Rec. cretacea*, were survivors. Conversely, there is much isotopic evidence showing that most of the Maastrichtian specimens found in the lowermost Danian are reworked (e.g., Stott and Kennett 1990; Zachos et al. 1992; Barrera and Keller 1994; Huber 1996; MacLeod and Huber 1996). The most extensive isotopic analysis of taxon-specific tests across the KPB was probably that conducted by Kaiho and Lamolda (1999) at Caravaca. They analyzed  $\delta^{13}\text{C}$  values from specimens of 12 Maastrichtian species belonging to the genera *Globotruncana*, *Rugoglobigerina* (including *R. rugosa*), *Racemiguembelina*, *Pseudotextularia*, *Pseudoguembelina*, *Globigerinelloides* (including *Glb. asper*), and *Heterohelix* (including *H. globulosa*), which constituted > 99% of the total specimens (in the  $\geq 63\ \mu\text{m}$  size fraction) collected across the KPB. Their results were similar to those obtained by Zachos et al. (1992) and Huber (1996) for *H. globulosa* and *Globigerinelloides* spp. at ODP Sites 690, 738, and 750. Based on this isotopic evidence and the sharp decline in the relative and absolute abundance of these species, Kaiho and Lamolda (1999) concluded that most planktic foraminiferal species, except *Gb. cretacea*, did not survive and abruptly went extinct at the KPB.

Complementary studies of the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios of taxon-specific tests at ODP Site 738 suggested an extensive and pervasive reworking across the KPB and led to the

conclusion that there were likely to be few, if any, survivors after the KPB extinction event (MacLeod and Huber 1996). The results also implied that several methods for evaluating survival patterns (e.g., Keller 1993; Keller et al. 1993; MacLeod and Keller 1994) are flawed insofar as they fail to recognize extensive reworking.

In summary, isotopic evidence has been used to support both catastrophic and gradual hypotheses on planktic foraminiferal extinction and survival patterns across the KPB. This evidence may be flawed for several main reasons. First, diagenesis may have destroyed the original geochemical signature of the calcareous tests, and samples may not be suitable for isotopic studies. Second, the lower Danian specimens of Maastrichtian species used for isotopic analysis could be small, juvenile forms due to taphonomic selection by size, as already pointed out by Smit and Nederbragt (1997). In this case, they will always yield a different isotopic signal from those of the Maastrichtian regardless of whether they are survivors or reworked. Third, taxonomic assignment errors could lead to the use of specimens belonging to Danian species for isotopic analysis after erroneously assigning them to the analyzed Maastrichtian species, especially when the selection of tests was performed in samples from the < 63 µm size fraction.

## 6. Quantitatively and statistically testing the survival model

Quantitative data on relative abundances have also been used as a criterion to ascertain the survival model. The relative abundances of all Maastrichtian species except those of *Guembelitra* consistently decrease in the first cm of Danian in pelagic sections, so this could be used as a criterion for recognizing reworked specimens (e.g., Olsson 1997; Arenillas et al. 2000a, 2000b, 2006, 2016; Krahl et al. 2017; Gilabert et al. 2021b, 2022). However, because there are no incoming Danian species or their abundance is still very low, Maastrichtian species remain proportionally dominant in the basal part of the Danian, so this has also been used as evidence of survival (Keller 1988; Keller et al. 1995; Orue-Etxebarria 1997).

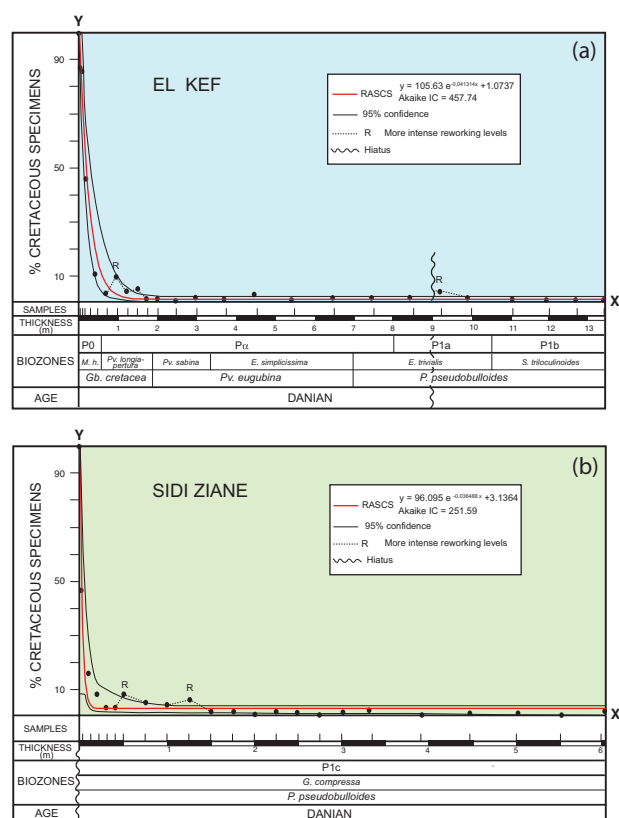
At Elles (Tunisia), Agost (Spain), and Caravaca (Spain), Arz et al. (1999a, 2000) observed in the lower Danian a sharp decrease in the relative abundance of all Maastrichtian species with the exception of *Guembelitra* spp. The decreases in these sections fitted well with a polynomial function, following a descending curve that they called the RASCS curve (Relative Abundance of the “Surviving” Cretaceous Species, or ARECS in the Spanish acronym). Arz et al. (1999a) interpreted the RASCS curve from Elles and Agost as the product of the progressive decrease in the abundance of Maastrichtian survivors as they were gradually replaced by the incoming Danian species. However, Arz et al. (2000) were not able to confirm the validity of this interpretation with dependable evidence at Caravaca. The late Maastrichtian species identified in the lower Danian samples were precisely the most abundant

species in the Maastrichtian, and they seemed to disappear in an order corresponding almost exactly to their relative abundance in the late Maastrichtian, leading the authors to suspect the existence of a statistical relationship between the two terms (Arz et al. 1999a). The RASCS curves might simply represent the progressive decline of reworked Maastrichtian specimens across the lowermost Danian.

To delve further into this topic, we propose two types of tests to verify or refute whether the Maastrichtian species found in the lower Danian of El Kef and Sidi Ziane are in situ or ex situ: a statistical test based on nonlinear regression analyses to find equations that fit the downward curves of relative abundance in Maastrichtian specimens, and a quantitative test to calculate the average relative abundance distribution (RAD) of Maastrichtian species in both upper Maastrichtian and lower Danian samples.

### 6.1. Statistical tests (comparison of RASCS curves)

At El Kef, the asymptotic decrease in the relative abundance of Maastrichtian specimens, excluding *Guembelitra* spp., across the lower Danian (the RASCS curve) fits better with an exponential function (Akaike IC = 457.74) than a power function (Akaike IC = 5340.7). The RASCS curve at El Kef is fitted with the exponential equation  $y = 105.63 e^{-0.041314x} + 1.0737$  (Fig. 7A) and the power equation  $y = 9313.9 x^{-0.0011128} - 9247$  (Suppl. material 1:



**Figure 7.** RASCS curves (relative abundance of the “surviving” Cretaceous species), fitted to an exponential function, across the lower Danian at (A) El Kef and (B) Sidi Ziane.



Fig. S1A). In both cases, but especially for the exponential model, all the  $x$ - $y$  data fall within the 95% confidence interval, except the sample to 9.25 m above the KPB, which belongs to the *E. trivialis* Subzone (~ Subbiozone P1a). This sample appears to represent a level of more intense reworking and may be related to an erosive hiatus (Fig. 7A and Suppl. material 1: Fig. S1A). The thickness of the *E. trivialis* Subzone at El Kef is proportionally less than in other Tethyan localities (see Arenillas et al. 2004, and Molina et al. 2009), which could corroborate the existence of this short hiatus at El Kef. In the nearby Elles section, Arz et al. (1999a) also identified a hiatus affecting the *E. trivialis* Subzone, which is absent.

As at El Kef, the RASCS curve at Sidi Ziane is also better fitted to an exponential function (Akaike IC = 251.59) (Fig. 7B) than to a power function (Akaike IC = 455.09) (Suppl. material 1: Fig. S1B). It is fitted with the exponential equation  $y = 96.095 e^{-0.34886x} + 3.1364$  and the power equation  $y = 63.925 x^{-0.15091} - 26.598$ . In both cases, but especially for the power model, all the  $x$ - $y$  data fall within the 95% confidence interval, except for two samples in the lower part of the *G. compressa* Subzone (~ Subbiozone P1c), which have been attributed to levels of more intense reworking (Fig. 7B and Suppl. material 1: Fig. S1B).

As suggested by Arz et al. (1999a) for Elles and Agost, the RASCS curves (exponential and power) from El Kef could still be interpreted as the result of the gradual decline of Maastrichtian species due to their progressive replacement by the incoming Danian species, which were probably better adapted to the new and stressed environmental conditions after the KPB. However, this hypothesis is impossible to apply to the RASCS curves from Sidi Ziane, which are suspiciously similar to those of El Kef, both being better fitted with an exponential function. The RASCS curves in the Sidi Ziane section undoubtedly reflect the decrease in abundance of reworked Maastrichtian specimens in the Danian samples, including, unlike at El Kef, those of *Guembelitria*. This is so because the biostratigraphic interval that includes the *Gb. cretacea* Zone, the *Pv. eugubina* Zone, the *E. trivialis* Subzone and a large part of the *S. triloculinoides* Subzone, in which the extinctions of all supposedly surviving Maastrichtian species are recorded (e.g., Olsson et al. 1999; Arenillas et al. 2017, 2018), is missing at Sidi Ziane. The similarity of the RASCS curves in both sections suggests that those from El Kef are also the result of the progressive decrease in abundance of reworked Maastrichtian specimens in the lower Danian samples, i.e., in the time interval in which the planktic foraminiferal assemblages were progressively recovering and contributing more and more tests to the ocean bottom.

This interpretation was already suggested by Olsson (1997), who noted that, after the KPB catastrophic mass extinction event, the seafloor would be littered with Maastrichtian planktic foraminiferal tests, which would be easily remobilized until their final burial in Danian samples. Based on the vertical mixing model of Berger and Health (1968) for pelagic sediments, Olsson (1997) observed that the asymptotic decrease in the abundance of Maastrichtian spe-

cies in the lowermost Danian (similar to the RASCS curves, but in terms of absolute abundance) fits with the mixing curve expected from reworking. Given certain assumptions for their model, Berger and Health (1968) demonstrated that the specimen concentration of a particular species decreases gradually in pelagic sediments upon its extinction, following an approximately exponential function.

## 6.2. Quantitative tests (comparison of RADs)

This type of test aims to quantitatively compare the Maastrichtian assemblages present in upper Maastrichtian samples and those present in lower Danian samples in order to identify differences or similarities in their relative abundance distribution (RAD). The RADs were estimated at genus and species levels, analyzing especially those genera and species that are more abundant or more relevant to the debate on the relative importance of reworked reworked specimens vs. survivor taxa (Suppl. material 2: Table S1, Suppl. material 3: Table S2). If numerous Maastrichtian species survived, the sudden environmental crisis triggered by the Chicxulub impact and its aftermath would have forced a sharp change in their RAD after the KPB boundary. We can assume therefore that, if the RADs are very similar before and after the KPB, the Maastrichtian specimens found in lowermost Danian samples were reworked as a result of vertical mixing by remobilization from older sediments. Additionally, bioturbation can foster the redistribution of microfossils, as well as abiotic components, in burrows further down or even up the KPB, which can influence interpretation of the extinction/survivorship patterns (Rodríguez-Tovar and Uchman 2008).

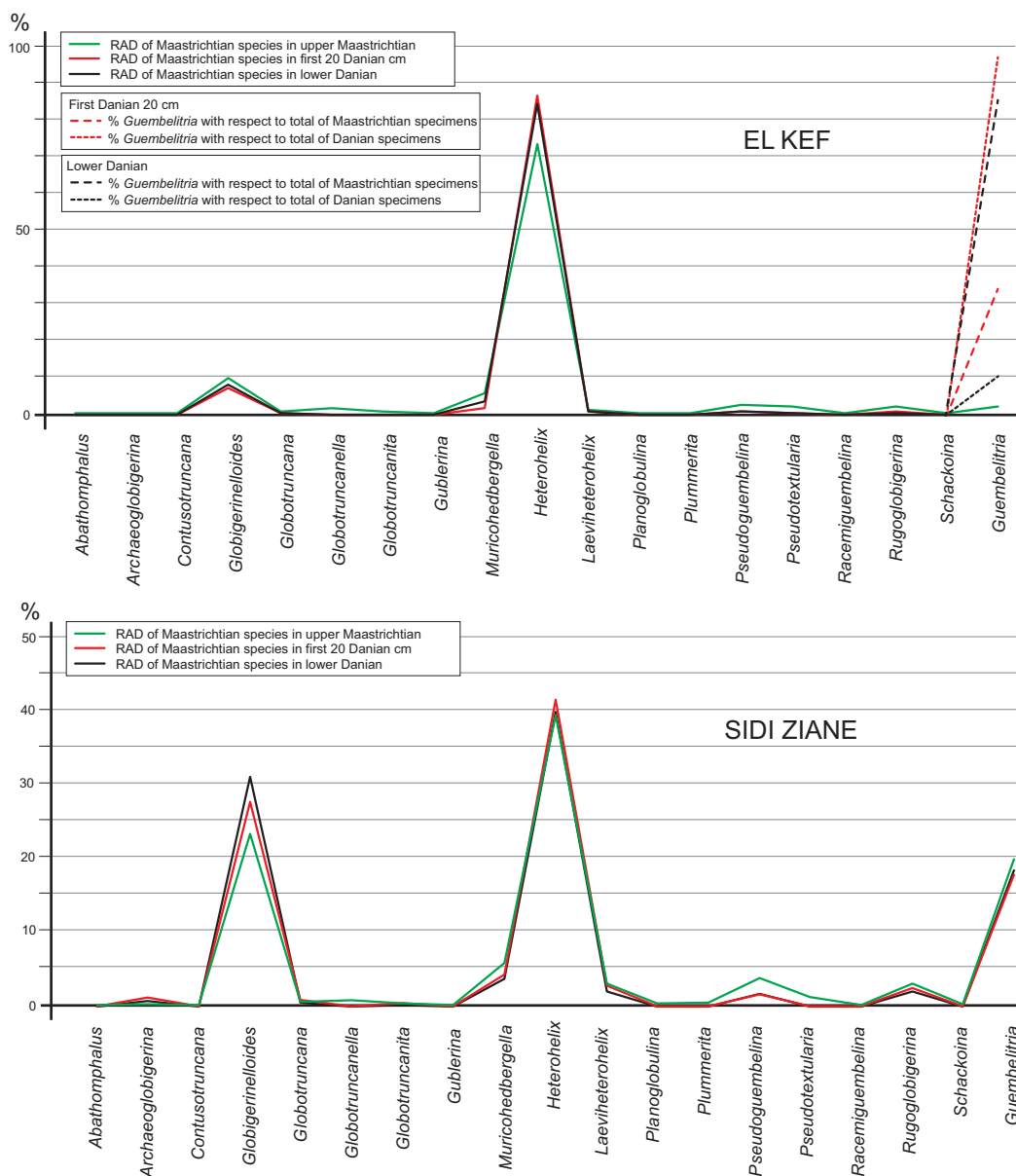
At El Kef (Arenillas et al. 2000b, 2018), the Maastrichtian species identified in lowermost Danian samples with a relative abundance high enough to be considered survivors were, ordered according to their alleged extinction horizon, the following: *Pseudoguembelina kempensis*, *Heterohelix labellosa*, *Pseudoguembelina costulata*, *Laeviheterohelix pulchra*, *L. glabrans*, *Globigerinelloides volutus*, *Glb. prairiehillensis*, *Muricohedbergella holmdelensis*, *M. monmouthensis*, *H. planata*, *H. navarroensis*, *Glb. yaucensis*, *H. globulosa*, *Guembelitria blowi*, and *Gb. cretacea* (Figs 3, 5). Additionally, we have included *R. rugosa* because it is also frequently identified in lower Danian samples. The rest of the species are either very scarce or absent in the representative aliquot studied in each Danian sample (i.e., they can only be found after an intensive search to minimize the Signor–Lipps effect), so their presence in the Danian of El Kef was eliminated from Fig. 5. At Sidi Ziane, the Maastrichtian species identified in lowermost Danian samples are similar to those identified at El Kef (Fig. 6). The differences in the lower Danian stratigraphic ranges of the Maastrichtian species presumed surviving appear to be a reflection of the different Maastrichtian RADs between the two sections (Suppl. material 2: Table S1, Suppl. material 3: Table S2). The abundance of all the Maastrichtian genera identified in the upper Maastrichtian

and the lower Danian samples is shown in Fig. 8 in order to visualize the RADs of Maastrichtian genera in the three chosen stratigraphic intervals (upper Maastrichtian, first 20 cm of Danian, and lower Danian).

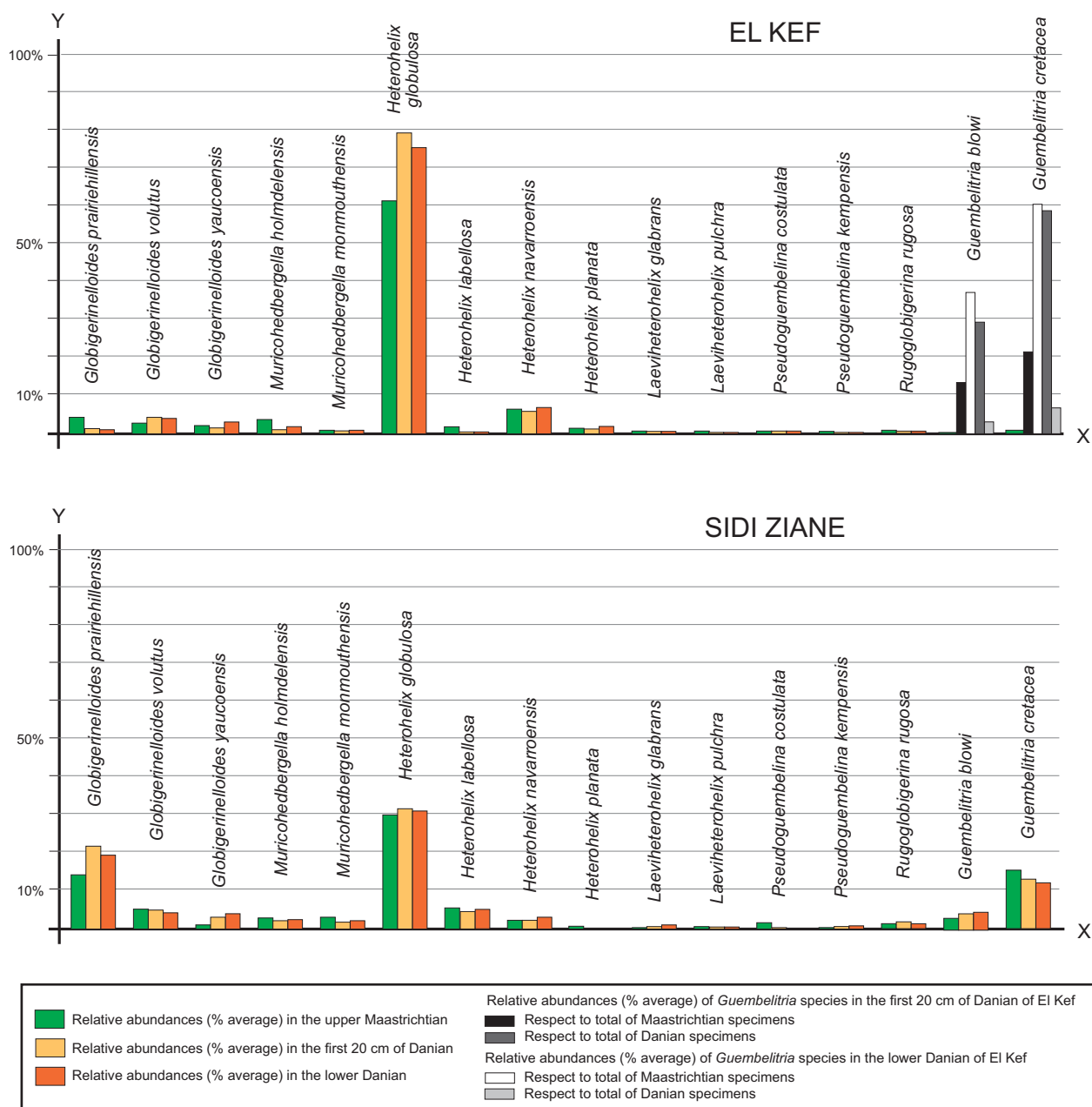
The quantitative data show that at El Kef (Fig. 8; Suppl. material 2: Table S1) the late Maastrichtian assemblages are dominated by *Heterohelix* (72.4% average), followed by *Globigerinelloides* (9.8% average) and *Muricohedbergella* (5.3% average). The relative abundance of each other genus is always < 3% average, including *Guembelitra*, *Pseudoguembelina*, and *Rugoglobigerina*. In terms of species (Fig. 9; Suppl. material 2: Table S1), the most abundant by far is *Heterohelix globulosa* (61.6% average), followed by *H. navarroensis* (6.2% average), *Globigerinelloides prairiehillensis* (4% average), and *Muricohedbergella holmdelensis* (3.8% average). At

Sidi Ziane (Fig. 8; Suppl. material 3: Table S2), the late Maastrichtian assemblages exhibit some differences with respect to those at El Kef. *Heterohelix* is also the predominant genus (41.3% average), but the relative abundances of *Globigerinelloides* (21.3% average) and *Guembelitra* (18.6% average) are proportionally much higher. The rest of the genera have an average abundance similar to those at El Kef, albeit slightly higher in *Muricohedbergella* (5.7% average), *Pseudoguembelina* (3.9% average), and *Rugoglobigerina* (2.9% average).

When the upper Maastrichtian and lower Danian RADs of Maastrichtian species are compared, a strong similarity can be observed in both sections (Figs 8, 9; Suppl. material 2: Table S1, Suppl. material 3: Table S2), indicating that all the Maastrichtian specimens are reworked in the Danian samples, except those of *Guembelitra* at El Kef.



**Figure 8.** Comparison of the relative abundance distributions (RADs) of Maastrichtian genera in Maastrichtian (green color) and Danian (red-black colors) samples from El Kef and Sidi Ziane.



**Figure 9.** Comparison of the relative abundance of some Maastrichtian species in Maastrichtian and Danian samples from El Kef and Sidi Ziane. At El Kef, *Guembelitra* spp. were excluded from the count in Danian samples.

## 7. Evidence for the survival of Maastrichtian taxa

Many biostratigraphers have concluded that, if the aforementioned Signor–Lipps and reworking effects are minimized, the planktic foraminiferal extinction model is more compatible with a catastrophic mass extinction event occurring exactly at the KPB (e.g., Smit 1990; Molina et al. 1996, 1998; Olsson 1997; Smit and Nederbragt 1997; Arenillas et al. 2000a, 2000b; Arz et al. 2000; Koutsoukos 2014; Molina 2015; Lowery et al. 2018; Gilabert et al. 2021b, 2022). Next, we analyze the genera that are most often considered to be survivors, especially *Guembelitra*, *Heterohelix* s.l., and *Muricohedbergella*, with a

view to verifying or refuting the catastrophic hypothesis. All the average relative abundances mentioned below are exclusively with respect to the total Maastrichtian planktic foraminiferal specimens (excluding the incoming Danian taxa), both in Maastrichtian and Danian samples.

### 7.1. Survival of *Guembelitra*

*Guembelitra* was undoubtedly a survivor given the amount of evidence that has been reported, not only isotopic (Barrera and Keller 1994; Birch et al. 2016) but also quantitative and phylogenetic. Two of its species, *Gb. cretacea* and *Gb. blowi*, may in fact be the only species surviving the KPB extinction event (Arenillas and



Arz 2017; Arenillas et al. 2018). It has also been widely demonstrated that the abundance of *Guembelitra* increased after the KPB (e.g., Smit 1982; Molina et al. 1996; Smit and Nederbragt 1997; Arenillas et al. 1998, 2000a, 2000b; Punekar et al. 2014; Lowery et al. 2018; Krahl et al. 2020; Gilabert et al. 2021b, 2022). In addition, *Guembelitra* played a relevant role in the phylogeny of Danian taxa (Olsson et al. 1999), having been widely shown to be the ancestor, through *Chiloguembelitra*, of two Danian lineages: the biserial lineage that groups together *Woodringina* and *Chiloguembelina*, and the trochospiral lineage that groups *Trochoguembelitra* and *Globoconusa* (see Arenillas and Arz 2017).

The survival of *Guembelitra* is again verified in the quantitative analysis carried out at El Kef. Its relative abundance increases abruptly in the first 20 cm of Danian, with an average of 34.3% if we only take Maastrichtian species into account, or 97.1% if we only take Danian species into account, which contrasts with its average relative abundance (1.8%) in the upper Maastrichtian (Fig. 8; Suppl. material 2: Table S1). If we consider all the samples from the lower Danian, the average relative abundance of *Guembelitra* increases to 86.6% for the total Maastrichtian specimens but drops to 10.2% when we consider only Danian specimens. There are two reasons for the latter: i) incoming Danian taxa increase in abundance across the lower Danian, and ii) the genus *Chiloguembelitra* has been taxonomically differentiated from *Guembelitra*. At Sidi Ziane, unlike at El Kef, the average relative abundances of *Guembelitra* both in the lower Danian (18.4%) and the first 20 cm of Danian (17.7%) are very similar to those in the upper Maastrichtian (18.6%) (Fig. 9; Suppl. material 3: Table S2), evidencing that, as expected given the hiatus in the lower Danian, the *Guembelitra* specimens found in the Danian of Sidi Ziane are reworked.

## 7.2. Survival of *Heterohelix* s.l.?

One of the genera most commonly considered a survivor is *Heterohelix* s.l. (*Heterohelix* and *Laeviheterohelix*), especially *H. globulosa* but also *H. navarroensis*, *H. planata*, *H. labellosa*, *L. pulchra*, and *L. glabrans*. Phylogenetic evidence has been proposed to support this, since *Heterohelix* has on occasion been considered the ancestor of the Paleogene genus *Chiloguembelina* (e.g., Apellaniz et al. 2002). However, this proposal has been rejected in most phylogenetic studies (e.g., Olsson et al. 1999), since it has been demonstrated that *Chiloguembelina* is a descendant of *Woodringina*, and this in turn of *Chiloguembelitra* (Arenillas et al. 2017).

The high relative abundance of *Heterohelix* s.l. in lowermost Danian samples has been put forward as among the strongest evidence for its survival (e.g., Pardo and Keller 2008). Here, however, we refute this evidence. In both El Kef and Sidi Ziane, the average relative abundance of *Heterohelix* s.l. in the Danian samples is similar to, or

only slightly higher than, that in the Maastrichtian samples, both in the first 20 cm of Danian and in the Danian interval studied as a whole. At El Kef, its average relative abundance goes up slightly to ~ 85% but, at Sidi Ziane, it remains stable at around 40% (Fig. 8; Suppl. material 2: Table S1). This quantitative pattern across the KPB is repeated when we observe the average relative abundances of the dominant species *H. globulosa* (Fig. 9). At Sidi Ziane, the average relative abundance of *Heterohelix* s.l. in lower Danian samples seems to reflect that of the total Maastrichtian samples (Fig. 8; Suppl. material 3: Table S2). The survival of *Heterohelix* s.l. appears to be refuted since its quantitative pattern across the KPB in El Kef is very similar to that in Sidi Ziane, where it is obvious that the *Heterohelix* s.l. specimens are reworked.

## 7.3. Survival of *Muricohedbergella*?

Another of the genera whose survival has been most frequently asserted is *Muricohedbergella* (Huber 1996; Olsson 1997; Olsson et al. 1999; Huber et al. 2002; Koutsoukos 2014; Birch et al. 2016; Lowery et al. 2018, 2020), including the species *M. holmdelensis* and *M. monmouthensis*. *Muricohedbergella* is also commonly considered the ancestor of two Danian lineages (e.g., Olsson et al. 1999; Aze et al. 2011): the spinose lineage that groups together *Eoglobigerina*, *Parasubbotina*, and *Subbotina*, and the non-spinose lineage that groups *Globanomalina* and *Praemurica*. As in the case of *Gb. cretacea*, Huber (1996), Olsson (1997) and Koutsoukos (2014) proposed that *Muricohedbergella* should also be considered a survivor based on this phylogenetic evidence, by contrast with the original proposal made by Smit (1982). After ascertaining that the biostratigraphic ranges of *Muricohedbergella* and the spinose and non-spinose lineages do not overlap in the lower Danian (Arenillas et al. 2000a, 2000b), Arenillas and Arz (2000) disproved the claim that *Muricohedbergella* was the ancestral form of these lineages, proposing instead that it was the ancestor of parvularugoglobigerinids. However, this latter phylogenetic proposal was also refuted by Arenillas and Arz (2017). Based on Brinkhuis and Zachariasse (1988), these authors proposed that the parvularugoglobigerinids, which are the most probable ancestor of the spinose and non-spinose lineages (Arenillas et al. 2018, and references herein), evolved from the benthic genus *Caucasina*, which exhibits a similar microperforate, smooth wall texture, *Pseudocaucasina antecessor* being its first representative. If verified, this hypothesis implies not only that the main Cenozoic lineages of trochospiral planktic foraminifera, whose descendants have reached the present day, could have a benthic origin after the KPB, but also that the phylogenetic evidence for the survival of *Muricohedbergella* is disproved.

The new quantitative data obtained at El Kef likewise appear not to support the survival of *Muricohedbergella*. At El Kef (Figs 8, 9; Suppl. material 2: Table S1), the

average relative abundance of *Muricohedbergella* decreases in Danian samples (3.5%) relative to the Maastrichtian (5.3%), especially in the first 20 cm of Danian (2%). If incoming Danian species are taken into account, the relative abundance of *Muricohedbergella* tends to zero in the first 20 cm of Danian, as with the other Maastrichtian genera except *Guembelitra*. At Sidi Ziane (Figs 8, 9; Suppl. material 3: Table S2), the abundance of *Muricohedbergella* in Danian samples also decreases, albeit more slightly (from 5.6% to ~4%). This very similar quantitative pattern in both sections seems to refute the idea that *Muricohedbergella* was a survivor. Unlike *Guembelitra*, the relative and/or absolute abundance of *Muricohedbergella* declined abruptly after the KPB until its supposed extinction in the earliest Danian, just the opposite of what might be expected of generalist taxa in a period of environmental recovery (Arenillas et al. 2000a, 2000b, 2018).

#### 7.4. Survival of other Maastrichtian taxa?

Interpretations similar to those for *Heterohelix* s.l. and *Muricohedbergella* are derived from the quantitative patterns for *Globigerinelloides*, *Pseudoguembelina*, and *Rugoglobigerina* at El Kef and Sidi Ziane. In both sections, their average relative abundances in Danian sediments are similar to those in Maastrichtian sediments (Figs 8, 9; Suppl. material 2: Table S1, Suppl. material 3: Table S2). Only of *Globigerinelloides* does the relative abundance appear to increase significantly at Sidi Ziane in Danian samples (~30%) with respect to Maastrichtian samples (~23%). However, this increase may be due to the significantly higher abundance of this genus in the last 400 Maastrichtian centimeters (Suppl. material 3: Table S2). There is also no quantitative evidence of survival at El Kef and Sidi Ziane for other Maastrichtian genera such as *Abathomphalus*, *Archaeoglobigerina*, *Contusotruncana*, *Globotruncana*, *Globotruncanella*, *Globotruncanita*, *Gublerina*, *Planoglobulina*, *Plummerita*, *Pseudotextularia*, *Racemiguembelina*, and *Schackoia*, and the species they contain (Figs 8, 9; Suppl. material 2: Table S1, Suppl. material 3: Table S2).

The quantitative and statistical evidence from El Kef and Sidi Ziane refuting the survival of all the Maastrichtian taxa except *Guembelitra* agrees with independent quantitative evidence reported by Arenillas et al. (2018) from El Kef and Aïn Settara (Tunisia), based on calculations of the relative abundance of specimens with abnormal morphologies. The authors observed in the lowermost Danian a strong increase in aberrant forms (>10%) among *Guembelitra* and incoming Danian species, and attributed this to huge environmental changes induced mainly by the Chicxulub impact. Gilabert et al. (2021b) reported similar increases in aberrant forms of *Guembelitra* and other Danian species in the lowermost Danian of Caravaca. These findings contrasted with very low percentages (<1%) of aberrant Maastrichtian specimens,

including those of *Heterohelix* s.l. and *Muricohedbergella*, in the lowermost Danian samples, which were very similar to the percentages of aberrant specimens estimated in Maastrichtian samples. This teratological evidence suggests that, except for *Guembelitra*, all Maastrichtian specimens (aberrants and non-aberrants alike) found in the lowermost Danian of El Kef, Aïn Settara, and Caravaca are in fact reworked.

The hypothesis of a single surviving genus (*Guembelitra*) is also in agreement with the biostratigraphic data reported by Arenillas et al. (2016) in the Moncada section (Cuba), which was located in the middle to upper slope of the eastern Yucatan continental margin when the Chicxulub asteroid impacted (Tada et al. 2002). This KPB section is characterized by a 2 m thick, ejecta-rich clastic deposit, locally named the Moncada Formation, which disconformably overlies the Albian micritic limestones of the Pons Formation, and unconformably underlies the earliest Danian marly limestones of the Ancón Formation (Tada et al. 2002; Arenillas et al. 2016). The Moncada section offered an excellent opportunity to test the survival of Maastrichtian taxa because it is continuous and complete in the lowermost Danian, and the underlying Upper Cretaceous sediments were removed by the huge Chicxulub impact-triggered debris flow, which transported them towards deeper locations. After analyzing the first 125 cm of Danian of the Moncada section in detail, Arenillas et al. (2016) revealed the lack of Maastrichtian taxa in the Danian samples, including the generalist and cosmopolitan *Heterohelix* s.l. and *Muricohedbergella*, unlike what happens in most pelagic sections worldwide such as El Kef and Sidi Ziane. Only specimens of the opportunist *Guembelitra* were found in the Danian, its relative abundance reaching 100% of the planktic foraminiferal assemblages. The previous erosion and disappearance of Maastrichtian deposits by the Chicxulub-linked sedimentological disturbances at the eastern Yucatan continental margin may have minimized the tendency for reworked Maastrichtian specimens to arrive in the Moncada area, preventing their presence in the lowermost Danian. This finding was relevant because it supports the hypothesis that only *Guembelitra* survived the KPB mass extinction triggered by the Chicxulub impact.

## 8. Conclusions

After reviewing the planktic foraminiferal extinction models and the causes proposed for the Cretaceous/Paleogene boundary (KPB) mass extinction event, it can give the wrong impression that there is still no conclusive evidence to support any single one of them. One of the main disputes focuses on the severity of the KPB extinction, i.e. on the proportion of surviving species after the KPB event (survival model). This dispute is grounded in the controversy over the relative importance of “reworked specimens vs. survivor taxa”, i.e. the question how many Maastrichtian species identified in the lower Danian of pe-

lagic sections were survivors and how many were the result of reworking processes. New quantitative and statistical evidence from the El Kef stratotype section (Tunisia), recognized as the most continuous, complete, and expanded lower Danian section worldwide, and the Sidi Ziane section (Algeria), affected by a relevant hiatus in the lower Danian, supports the notion that all the latest Maastrichtian species, except those of *Guembelitra*, went extinct exactly at the KPB. Nonlinear regression analyses indicate that the equation that best fits the asymptotically decreasing curve of the relative abundance of Maastrichtian specimens in lower Danian samples (the RASCS curve) is an exponential equation in both El Kef and Sidi Ziane, adjusting well to the vertical mixing curve expected by reworking processes. The similar relative abundance distribution (RAD) of the Maastrichtian planktic foraminiferal assemblages recorded in the upper Maastrichtian and the lower Danian of El Kef and Sidi Ziane indicates that all the Maastrichtian specimens found in Danian samples, except those of *Guembelitra*, are reworked. The obvious Maastrichtian paleobiological signal of the RADs of the Maastrichtian species in the lower Danian of El Kef leads one to conclude that the survival model of the Maastrichtian planktic foraminiferal species after the KPB event is definitely compatible with a model of almost total catastrophic extinction caused by the Chicxulub impact.

## Data availability

All data and supplementary figures are included as supplementary materials.

## Author contributions

IA led the writing and organization of the manuscript. IA and JAA performed the biostratigraphy and quantitatively analyzed the micropaleontological samples from El Kef and Sidi Ziane. FMD and DB sampled and stratigraphically analyzed the Sidi Ziane section. VG provided magnetostratigraphical and astronomical calibrations and reviewed the quantitative and statistical analyses. All co-authors assisted with the conceptualization and writing of the manuscript.

## Competing interests

The authors declare that they have no conflict of interest.

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## Supplementary material 1

### Figure S1

- Authors: Ignacio Arenillas, José A. Arz, Fariza Metsana-Oussaid, Vicente Gilabert, Djelloul Belhai
- Data type: pdf file
- Explanation note: RASCS curves (relative abundance of the "surviving" Cretaceous species), fitted to a power function, across the lower Danian at (A) El Kef and (B) Sidi Ziane.
- Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
- Link: <https://doi.org/10.3897/fr.25.79958.suppl1>

## Supplementary material 2

### Table S1

- Authors: Ignacio Arenillas, José A. Arz, Fariza Metsana-Oussaid, Vicente Gilabert, Djelloul Belhai
- Data type: Quantitative dataset Table
- Explanation note: Relative abundance of Maastrichtian planktic foraminiferal species and genera in both Maastrichtian and Danian samples of the El Kef section.
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- Link: <https://doi.org/10.3897/fr.25.79958.suppl2>

## Supplementary material 3

### Table S2

- Authors: Ignacio Arenillas, José A. Arz, Fariza Metsana-Oussaid, Vicente Gilabert, Djelloul Belhai
- Data type: Quantitative dataset Table
- Explanation note: Relative abundance of Maastrichtian planktic foraminiferal species and genera in both Maastrichtian and Danian samples of the Sidi Ziane section.
- Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
- Link: <https://doi.org/10.3897/fr.25.79958.suppl3>