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Quantifying the evolutionary turnover across the K–T boundary catastrophic planktic foraminiferal extinction event at El Kef, Tunisia

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Abstract: Four metrics (extinction ratio, speciation ratio, taxonomic flux and volatility) were used to quantify the planktic foraminiferal extinction and evolutionary pattern across the Cretaceous–Tertiary (K–T) boundary at El Kef (Tunisia). They revealed a stasis episode in the terminal Maastrichtian, a K–T catastrophic mass extinction and a post-K–T evolutionary radiation. This pattern was also correlated with geochemical and isotopic data. The impact evidence and the decrease in $CaCO_3$ and $\delta^{13}C$ coincide with a period of high evolutionary volatility and significant changes in the taxonomic flux which are both very compatible with the impact theory.

Keywords: planktic foraminifera, extinction, speciation, taxonomic flux, volatility, Maastrichtian, Danian, K–T boundary.

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The richness and diversity of planktic foraminiferal species decreased drastically at the Cretaceous–Tertiary (K–T) boundary (Alvarez et al. 1980; Smit & Hertogen 1980; Smit 1982, 1990) but it remains unclear whether it occurred suddenly or gradually (Smit 1982, 1990; Keller 1988; Keller et al. 1995). In a previous attempt to resolve the controversy, four "blind" specialists were asked to examine unlabelled samples from the El Kef section (see Marine Micropaleontology, Vol. 29) but the results were contradictory (Smit & Nederbragt 1997; Keller 1997). Recent reports suggest that more than 90% of the uppermost Maastrichtian planktic foraminifera were eliminated by the K–T event, 70% of which went extinct suddenly at the K–T boundary (Molina et al. 1998; Arz et al. 1999; Arenillas et al. 2000a, 2000b).

The K–T boundary stratotype was defined at El Kef, since it is one of the most continuous and expanded K–T sections. It is also an excellent section to model the evolutionary trends in planktic foraminifera across the K–T boundary, since they are very diverse, abundant and well preserved. Here we quantify the K–T pattern using the Dean and McKinney (2001) model and the planktic foraminiferal biostratigraphic distribution at El Kef from Arenillas et al. (2000a). The results are also correlated with isotopic data from Keller and Lindinger (1989) to evaluate the magnitude of the K–T event and relate planktic foraminiferal evolutionary events with paleoclimatologic and geochemical oceanic turnovers across the K–T boundary.

Biostratigraphy and isotope stratigraphy

The biozonation applied at El Kef is based on Molina et al. (1996). We identified and analyzed the upper Maastrichtian *Plummerita hantkeninoides* Biozone (the last 12 m), the *Guembelitria cretacea* Biozone (2 m thick layer), the *Parvularugoglobigerina eugubina* Biozone (5 m thick layer), and the first 7 m of the *Parasubbotina pseudobulloides* Biozone (lower Danian). The base of the *Gb. cretacea* Biozone coincided with the K–T boundary, marked by a 2–3 mm thin rust-red clay layer with Ir anomaly, altered microtektites, Ni-rich spinels, and shocked minerals (Smit 1982; Robin & Rochia 1998). This red layer is at the base of a dark clay generally called "boundary clay", which is characterized by a low $CaCO_3$ content, a maximum of organic carbon (TOC) and a negative excursion in $\delta^{13}C$ (Keller and Lidinger 1989). The boundary clay (≈P0 by Berggren et al. 1995) is 50 cm thick with 7% $CaCO_3$ on average, compared with 35–40% $CaCO_3$ in the upper Maastrichtian and/or lower Danian marls. In addition, $CaCO_3$ is low (≈10%) in the first 2–3 m of the Danian.

Arenillas et al. (2000a) identified 66 species in the terminal Maastrichtian at El Kef (Fig. 1). Six species (8.9%) became extinct or disappeared locally in the uppermost 12 m of the Maastrichtian, 46 (68.7%) became extinct at the K–T boundary and 15 (22.4%) ranged into the earliest Danian. This extinction pattern, in which 15 species could be cretaceous survivors, is here denominated pattern A. However, 13 out the last 15 species may not indeed have survived (see Arenillas et al. 2000a). According to recent isotope analyses, most of these species appear to be reworked (Kaiho & Lamolda 1999; MacLeod et al. 2001). Only *Gb. cretacea* and *Gb. trifolia* are certain survivors because their relative and "absolute" abundance increased in the lowermost Danian and they clearly played a role in the phylo-geny of new Danian taxa. If the other 13 species are reworked, then 90–95% of the species became extinct at the K–T boundary. This most catastrophic extinction pattern is here denominated pattern B. The K–T extinction coincides exactly with the red layer containing the impact evidence, implying a cause-effect relation between both phenomena. Some species disappeared locally below the K–T boundary (Arenillas et al. 2000a) but their disappearance hardly affects the quantified pattern proposed here. After the K–T extinction, there was an evolutionary radiation involving up to 40 new Paleocene species. Nevertheless, the species richness was generally less than 20 species.

According to the isotopic data in Keller and Lindinger (1989), there was a negative shift in $\delta^{18}O$ in the fine fraction sediment (<25 µm) above the K–T boundary (suggesting a warm event during the *Gb. cretacea* Biochron) and a sudden negative excursion in fine fraction $\delta^{13}C$ (indicating a sudden and intense decrease in biological productivity). Sediment production and $CaCO_3$ were also low during the *Gb. cretacea* Biochron and ear-

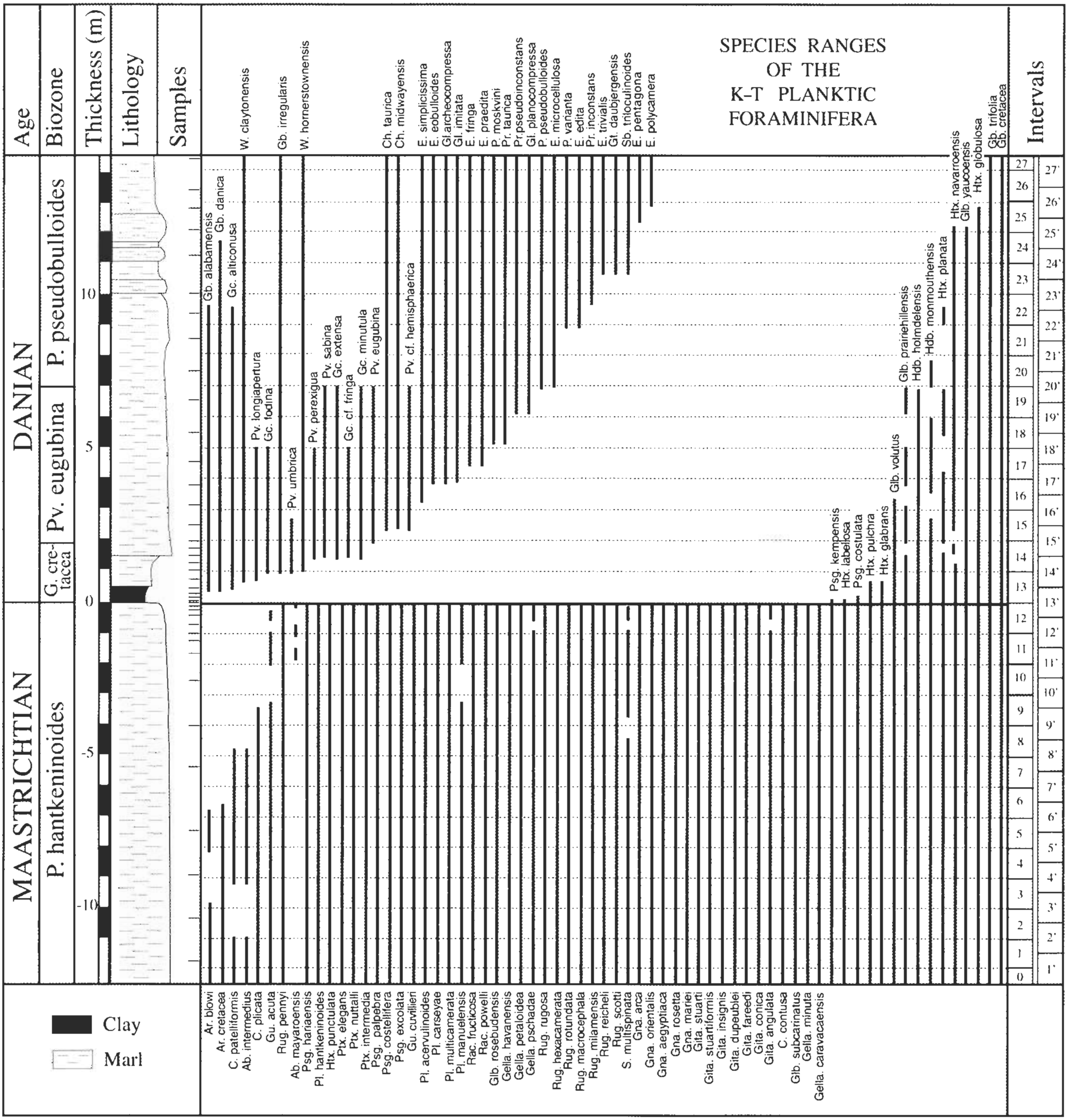

Fig. 1. The planktic foraminiferal stratigraphic range across the K–T boundary at the El Kef section (modified from Arenillas et al. 2000a) and the two series of 1 m thick intervals used to the quantified evolutionary model.

liest *P. pseudobulloides* Biochron. All these data are well explained by the impact theory (Alvarez et al. 1980), which suggests that the extinction and/or mortality of calcareous planktic microorganisms temporarily decreased the rain of calcareous biogenic material towards the sea bottom, which accounts for the low $CaCO_3$ content (boundary clay). The global negative excursion of $\delta^{13}C$ also suggests a sudden reduction in primary productivity and abrupt mass mortality. The sharp decrease of photosynthesis increased the atmospheric accumulation of CO_2, which enhanced greenhouse warming and increased the global temperature during the *G. cretacea* Biochron.

Evolutionary model and time scale

The extinction and evolution of planktic foraminifers at El Kef was quantified using the model proposed by Dean and McKinney (2001) to measure evolutionary turnover. The model includes two new metrics: taxonomic flux and a new version of volatility. They are calculated for consecutive stratigraphic intervals of approximately the same thickness and duration. The number, position, and resolution of the intervals are chosen by the researcher. In order to measure with most detail the metric turnovers, we chose two series of overlapped intervals that were 100 cm thick. The interval boundaries of the first series fall within the middle parts of the second series of intervals, and vice versa. The K–T boundary was made to coincide with the boundary between intervals 12 and 13 and with the middle part of interval 13' (Fig. 1).

Four parameters were measured in each interval (Tables 1 and 2): number of identified species (G), number of extinct species (E), number of new species (N) and number of stable species (S), all quantified from stratigraphic range data. A stable species in a particular interval is the one that persists throughout the interval. We used the K–T planktic foraminiferal biostratigraphic data from Arenillas et al. (2000a) and calculated the Dean and McKinney (2001) metrics for pattern A (15 Cretaceous survivors, Table 1) and pattern B (2 Cretaceous survivors, Table 2). The extinction (E_R) and speciation (N_R) rates in each interval were expressed as $E_R = E/G$ and $N_R = N/G$, respectively. The taxonomic flux was defined as $F = (G-E+N+S)/[S-G((E+S)/(N+S))]$ and log F was used to estimate the relative increase (positive value) or decline (negative value) in diversity in each interval. Finally, evolutionary variability was measured in terms

Table 1. Values of parameters -G, E, N and S- and metrics -E_r, N_r, F and V- in each interval for Pattern A.

Intervals	G	E	N	S	Er	Nr	F	logF	V
0	66	0	0	66	0.00	0.00	1.00	0.00	0.00
1'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
1	66	0	0	66	0.00	0.00	1.00	0.00	0.00
2'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
2	66	0	0	66	0.00	0.00	1.00	0.00	0.00
3'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
3	66	0	0	66	0.00	0.00	1.00	0.00	0.00
4'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
4	66	0	0	66	0.00	0.00	1.00	0.00	0.00
5'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
5	66	0	0	66	0.00	0.00	1.00	0.00	0.00
6'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
6	66	0	0	66	0.00	0.00	1.00	0.00	0.00
7'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
7	66	0	0	66	0.00	0.00	1.00	0.00	0.00
8'	66	2	0	64	0.03	0.00	0.97	-0.01	0.00
8	66	2	0	64	0.03	0.00	0.97	-0.01	0.00
9'	64	0	0	64	0.00	0.00	1.00	0.00	0.00
9	64	0	0	64	0.00	0.00	1.00	0.00	0.00
10'	64	1	0	63	0.02	0.00	0.98	-0.01	0.02
10	64	1	0	63	0.02	0.00	0.98	-0.01	0.02
11'	63	0	0	63	0.00	0.00	1.00	0.00	0.00
11	63	0	0	63	0.00	0.00	1.00	0.00	0.00
12'	63	0	0	63	0.00	0.00	1.00	0.00	0.00
12	63	1	0	62	0.02	0.00	0.98	-0.01	0.02
13'	66	53	3	10	0.80	0.05	0.08	-1.10	0.85
13	19	5	9	5	0.26	0.47	1.51	0.18	0.74
14'	19	0	6	13	0.00	0.32	1.46	0.16	0.32
14	24	0	6	18	0.00	0.25	1.33	0.12	0.25
15'	31	0	11	20	0.00	0.35	1.55	0.19	0.35
15	30	1	5	24	0.03	0.17	1.16	0.07	0.20
16'	31	2	1	28	0.06	0.03	0.97	-0.02	0.10
16	35	1	6	28	0.03	0.17	1.18	0.07	0.20
17'	34	0	5	29	0.00	0.15	1.17	0.07	0.15
17	34	4	0	30	0.12	0.00	0.88	-0.06	0.12
18'	34	4	0	30	0.12	0.00	0.88	-0.06	0.12
18	31	0	1	30	0.00	0.03	1.03	0.01	0.03
19'	31	0	1	30	0.00	0.03	1.03	0.01	0.03
19	32	8	1	23	0.25	0.03	0.75	-0.13	0.28
20'	32	8	1	23	0.25	0.03	0.75	-0.13	0.28
20	27	1	3	23	0.04	0.11	1.09	0.04	0.15
21'	27	1	3	23	0.04	0.11	1.09	0.04	0.15
21	26	0	0	26	0.00	0.00	1.00	0.00	0.00
22'	27	0	1	26	0.00	0.04	1.04	0.02	0.04
22	31	3	3	25	0.10	0.10	1.00	0.00	0.19
23'	30	3	2	25	0.10	0.07	0.96	-0.02	0.17
23	23	0	0	23	0.00	0.00	1.00	0.00	0.00
24'	29	1	3	25	0.03	0.10	1.08	0.03	0.14
24	29	1	3	25	0.03	0.10	1.08	0.03	0.14
25'	28	2	0	26	0.07	0.00	0.93	-0.03	0.07
25	26	4	0	22	0.15	0.00	0.83	-0.08	0.15
26'	26	2	0	24	0.08	0.00	0.92	-0.04	0.08
26	24	0	0	24	0.00	0.00	1.00	0.00	0.00
27'	24	0	0	24	0.00	0.00	1.00	0.00	0.00
27	24	0	0	24	0.00	0.00	1.00	0.00	0.00

Table 2. Values of parameters -G, E, N and S- and metrics -E_r, N_r, F and V- in each interval for Pattern B.

Intervals	G	E	N	S	Er	Nr	F	logF	V
0	66	0	0	66	0.00	0.00	1.00	0.00	0.00
1'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
1	66	0	0	66	0.00	0.00	1.00	0.00	0.00
2'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
2	66	0	0	66	0.00	0.00	1.00	0.00	0.00
3'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
3	66	0	0	66	0.00	0.00	1.00	0.00	0.00
4'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
4	66	0	0	66	0.00	0.00	1.00	0.00	0.00
5'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
5	66	0	0	66	0.00	0.00	1.00	0.00	0.00
6'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
6	66	0	0	66	0.00	0.00	1.00	0.00	0.00
7'	66	0	0	66	0.00	0.00	1.00	0.00	0.00
7	66	0	0	66	0.00	0.00	1.00	0.00	0.00
8'	66	2	0	64	0.03	0.00	1.03	-0.01	0.03
8	66	2	0	64	0.03	0.00	0.97	-0.01	0.03
9'	64	0	0	64	0.00	0.00	0.97	0.00	0.00
9	64	0	0	64	0.00	0.00	1.00	0.00	0.00
10'	64	1	0	63	0.02	0.00	0.98	-0.01	0.02
10	64	1	0	63	0.02	0.00	0.98	-0.01	0.02
11'	63	0	0	63	0.00	0.00	1.00	0.00	0.00
11	63	0	0	63	0.00	0.00	1.00	0.00	0.00
12'	63	0	0	63	0.00	0.00	1.00	0.00	0.00
12	63	1	0	62	0.05	0.00	1.98	-0.01	0.02
13'	66	61	3	2	0.92	0.05	0.01	-1.92	0.97
13	14	0	9	5	0.00	0.64	2.80	0.45	0.64
14'	19	0	6	13	0.00	0.32	1.46	0.16	0.32
14	16	0	6	10	0.00	0.38	1.60	0.20	0.38
15'	23	0	11	12	0.00	0.48	1.92	0.28	0.48
15	22	1	5	16	0.05	0.23	1.24	0.09	0.27
16'	22	1	1	20	0.05	0.05	1.00	0.00	0.09
16	27	0	6	21	0.00	0.22	1.29	0.11	0.22
17'	25	0	3	22	0.00	0.12	1.14	0.06	0.12
17	27	4	0	23	0.15	0.00	0.84	-0.08	0.15
18'	27	4	0	23	0.15	0.00	0.84	-0.08	0.15
18	24	0	1	23	0.00	0.04	1.04	0.02	0.04
19'	24	0	1	23	0.00	0.04	1.04	0.02	0.04
19	25	6	1	18	0.24	0.04	0.77	-0.12	0.28
20'	25	6	1	18	0.24	0.04	0.77	-0.12	0.28
20	22	0	3	19	0.00	0.14	1.16	0.06	0.14
21'	22	0	3	19	0.00	0.14	1.16	0.06	0.14
21	22	0	0	22	0.00	0.00	1.00	0.00	0.00
22'	23	0	1	22	0.00	0.04	1.05	0.02	0.04
22	26	2	3	21	0.08	0.12	1.05	0.02	0.19
23'	27	3	2	22	0.11	0.07	0.96	-0.02	0.19
23	20	0	0	20	0.00	0.00	1.00	0.00	0.00
24'	26	1	3	22	0.04	0.12	1.09	0.04	0.15
24	26	1	3	22	0.04	0.12	1.09	0.04	0.15
25'	25	2	0	23	0.08	0.00	0.92	-0.04	0.08
25	23	1	0	22	0.04	0.00	0.96	-0.02	0.04
26'	23	1	0	22	0.04	0.00	0.96	-0.02	0.04
26	22	0	0	22	0.00	0.00	1.00	0.00	0.00
27'	22	0	0	22	0.00	0.00	1.00	0.00	0.00
27	22	0	0	22	0.00	0.00	1.00	0.00	0.00

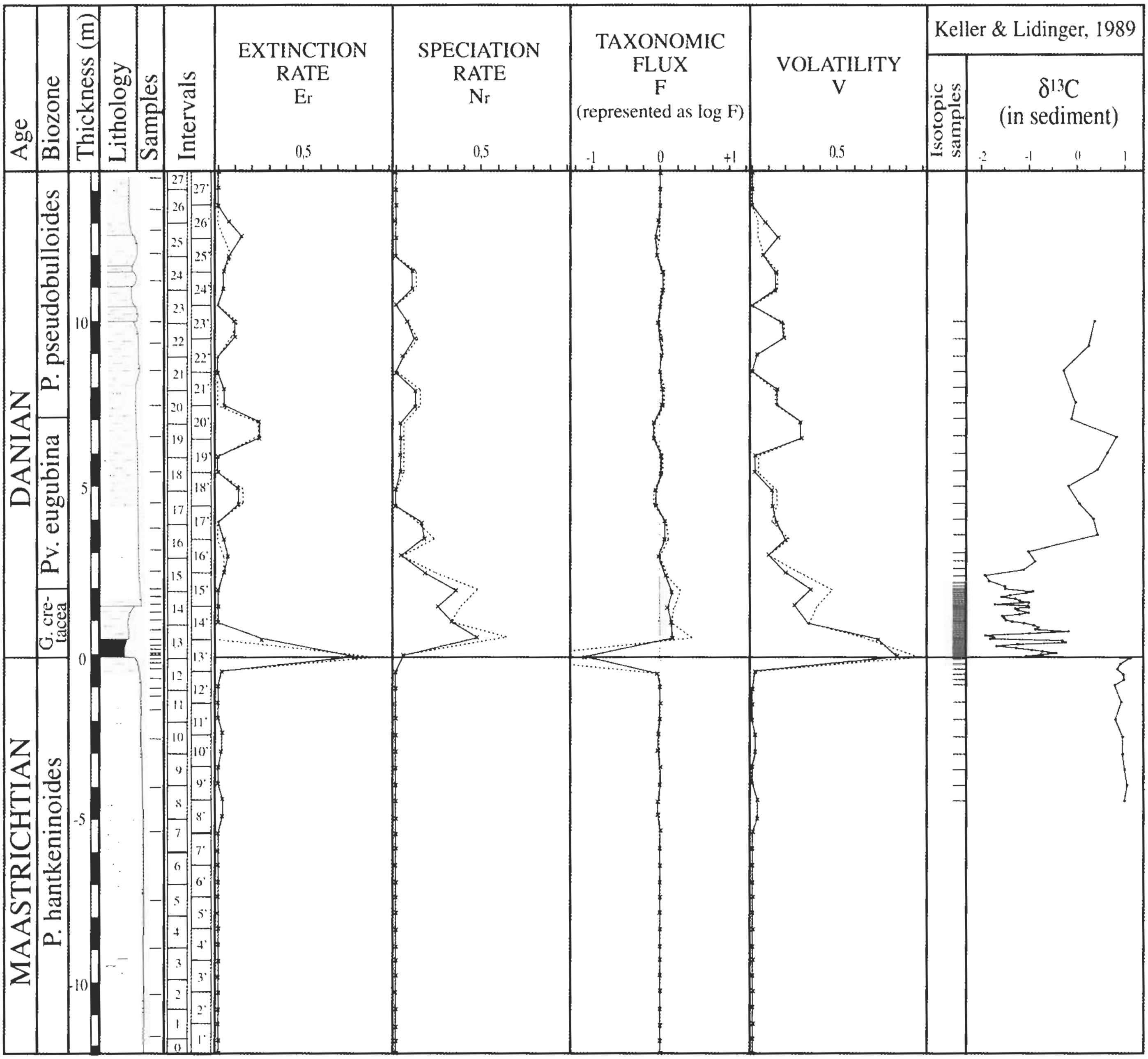

Fig. 2. Metric turnovers at El Kef and their correlation with $\delta^{13}C$ data (solid line = hypothesis A; dotted line = hypothesis B).

of volatility, V = (G–S)/G, where low values indicate evolutionary stability and high values imply evolutionary turnovers.

We estimated a sedimentation rate of 15 cm/k.y. in the basal part of the Danian (Arenillas et al. 2002), based on the geologic time scale proposed by Berggren et al. (1995) and Röhl et al. (2001). The sedimentation rate in the uppermost Maastrichtian was assumed to be similar to the lowermost Danian marls based on similar $CaCO_3$ content (on average 35–40 wt%) in both intervals. Therefore, each interval approximately represents 6–7 k.y. Nevertheless, the boundary clay has only 7% $CaCO_3$ on average, suggesting that sedimentation was slower in the boundary clay than in the Maastrichtian and Danian marls. Considering constant depositional flux of the residual mineral matrix across the K–T boundary, sedimentation rate may have been 9–10 cm/k.y. in the first 2 meters of the Danian (including the boundary clay). Thus, intervals 13 and 14 were slightly longer (about 10–11 k.y.). This small error is not significant, and the reason why we have considered that all selected intervals approximately represent the same time.

The Signor-Lipps effect (Signor & Lipps 1982) can influence the values of the Dean and McKinney (2001) metrics. According to Signor and Lipps (1982), a not intensively sampling could be responsible for incomplete species ranges. Even if the samplings are sufficiently detailed, a similar effect occurs if the sample residue is not intensively scanned. The range of an uncommon species could seem discontinuous due to the Signor-Lipps effect when single samples are studied. However, the Signor-Lipps effect is minimized or even completely avoided by using short-time intervals. Identifying the species in one sample of a particular interval is enough for considering it as an identified species in the interval and including it in the G parameter. The Dean and McKinney (2001) model uses the maximum species range irrespective of discontinuity. This may only cause a problem for very extended Signor-Lipps effects, where the true first and last appearance data may not have been recognized. To avoid this, we scanned the samples more than once to find all uncommon species.

Results

Values of E_R, N_R, F and V were plotted on a stratigraphic scale after applying the Dean and McKinney (2001) metrics (Fig. 2). At the K–T boundary obtained values are $E_R = 0.80$ and $\log F = -1.10$ for pattern A and $E_R = 0.92$ and $\log F = -1.92$ for pattern B (after eliminating doubtful survivors). The E_R maximum represents the highest extinction rate in planktic foraminiferal evolutionary history (close to total extinction, $E_R = 1$), while the F values suggest a strong decrease in diversity. The situation changes completely in the next interval where $N_R = 0.47$ and $\log F = 0.18$ (pattern A) or $N_R = 0.64$ and $\log F = 0.45$ (pattern B). Species diversity increased significantly after the K–T event, and there was a sudden evolutionary radiation of new species. According to pattern B, these two consecutive events raised the volatility ($V = 0.97$ and 0.64) to maximum levels (close to total extinction or the first radiation of a taxon, $V = 1$).

According to the volatility curve, there were four main periods in the evolutionary model across the K–T boundary at El Kef:

(1) Uppermost Maastrichtian: V is near or equal to 0, indicating high evolutionary stability. It only increases slightly due to background extinction and local disappearances in some intervals.

(2) K–T event (*Gb. cretacea* Biozone): V approaches maximum values (very high evolutionary instability) in a short time interval fluctuating between 0.9 and 0.4.

(3) Lowermost Danian (*Pv. eugubina* Biozone and lower part of *P. pseudobulloides* Biozone): V remains high (about 0.2), suggesting continuing evolutionary instability.

(4) Upper part of *P. pseudobulloides* Biozone: V decreases to about 0.1, indicating increased evolutionary stability (not shown in Fig. 2).

The geochemical and isotopic data closely reflected the evolutionary turnover of planktic foraminifera across the K–T boundary at El Kef. The relationship between the Dean and McKinney indices and $d^{13}C$ (Fig. 2) indicates that evolutionary stability in the upper Maastrichtian paralleled $d^{13}C$ stability. Evolutionary and isotopic data suggest an episode stasis in the terminal Maastrichtian. The peaks in E_R and log F (in interval 13') coincide with the K–T extinction, the impact evidence and the sudden decrease in $d^{13}C$ and $CaCO_3$. These maxima are the result of the planktic foraminiferal catastrophic mass extinction and suggest that the K–T extinction was severe, sudden and drastically reduced biological productivity.

Volatility remained high during the rest of period 2 due to post-K–T planktic foraminiferal evolutionary radiation which was very intense and rapid. It has been observed worldwide (see Arenillas et al. 2000a), and coincides with the evolution of small species of *Parvularugoglobigerina* and *Globoconusa* when sediment $\delta^{13}C$ and $CaCO_3$ were still very low. These new species evolved in oligotrophic conditions and must be considered r-strategist and cosmopolitans that adapted to an environment with low nutrient supply. The absence of biological competitors, empty ecological niches and warming by greenhouse effect could have favoured this rapid evolution.

Period 3 coincided with a second radiation of new Tertiary species that were larger and had cancellate walls (*Eoglobigerina*, *Parasubbotina*, *Praemurica* and *Subbotina*). It lasted longer than the first radiation so N_R values are lower ($N_R \approx 0.1$). However, the gradual extinction of the small species that proliferated after the K–T event ($E_R \approx 0.1$), induced fluctuations in log F and increased V. The significant increase in calcareous plankton significantly enhanced $CaCO_3$ in pelagic sediments. The rise in $\delta^{13}C$ suggests a slow recovery of photosynthesis and productivity which increased the nutrient flux from oligotrophic to mesotrophic. In general, the ecological conditions stabilized and the planktic foraminifers adapted to the new conditions and recolonized vacant niches.

Period 3 marks the end of the post-K–T greenhouse event (period 2). The rapid increase in planktic foraminifera (and calcareous nannoplankton) could have played a very important role in decreasing greenhouse warming. Atmospheric greenhouse CO_2 gas would have decreased after the increased input of biogenic calcium carbonate to the sea bottom and carbon fixing in pelagic sediments. According to isotopic data from El Kef (Keller and Lindinger 1989), the productivity and temperature were lower in period 3 than in the upper Maastrichtian, conditions that were probably maintained during the lower and middle Danian (period 4). Evolutionary stability returned to upper Maastrichtian values, although the planktic foraminiferal species richness and diversity never recovered.

Similar results could be obtained by applying the Dean and McKinney (2001) model with 1 m-thick intervals (≈6–10 ky) to the biostratigraphic data in Keller (1988) and Keller et al. (1995). Nevertheless their V and F values would be slightly lower and the anomalous values would begin slightly before the K–T boundary since their data suffer from a generalized Signor-Lipps effect (Arenillas et al. 2000a). In fact, the isotopic data in Keller and Lindinger (1989) provide evidence for a sudden, catastrophic, paleobiological and paleoclimatic event coinciding with the K–T boundary, which is not very compatible with the gradual hypothesis.

Conclusions

Four metrics (extinction ratio, speciation ratio, taxonomic flux and volatility) of the Dean and McKinney (2001) model suggest sudden planktic foraminiferal evolutionary turnover across the Cretaceous–Tertiary (K–T) boundary at El Kef (Tunisia). Two possible patterns have been considered depending on the survivor cretaceous species number, 15 species in pattern A and only 2 in pattern B. Both quantified patterns revealed a stasis episode in the terminal Maastrichtian, a K–T catastrophic mass extinction and a post-K–T evolutionary radiation. The evolutionary stability across the uppermost Maastrichtian contrasts with the high volatility across the lowermost Danian. The impact evidence and the decrease in $CaCO_3$ and $d^{13}C$ coincide with the period of high evolutionary volatility and significant changes in the taxonomic flux which are both very compatible with the impact theory.

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