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Paleoecology of the Cretaceous–Tertiary mass extinction in planktonic foraminifera

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Abstract

Paleobiogeographic patterns of the Cretaceous–Tertiary (K–T) mass extinction in planktonic foraminifera in Tunisia, spanning environments from open marine upper bathyal, to shelf and shallow marginal settings, indicate a surprisingly selective and environmentally mediated mass extinction. This selectivity is apparent in all of the environmental proxies used to evaluate the mass extinction, including species richness, ecological generalists, ecological specialists, surface and subsurface dwellers, whether based on the number of species or the relative percent abundances of species. The following conclusions can be reached for shallow to deep environments: about three quarters of the species disappeared at or near the K–T boundary and only ecological generalists able to tolerate wide variations in temperature, nutrients, salinity and oxygen survived. Among the ecological generalists (heterohelicids, guembelitrids, hedbergellids and globigerinellids), only surface dwellers survived. Ecological generalists which largely consisted of two morphogroups of opportunistic biserial and triserial species also suffered selectively. Biserials thrived during the latest Maastrichtian in well stratified open marine settings and dramatically declined in relative abundances in the early Danian. Triserials thrived only in shallow marginal marine environments, or similarly stressed ecosystems, during the latest Maastrichtian, but dominated both open marine and restricted marginal settings in the early Danian. This highly selective mass extinction pattern reflects dramatic changes in temperature, salinity, oxygen and nutrients across the K–T boundary in the low latitude Tethys ocean which appear to be the result of both long-term environmental changes (e.g., climate, sea level, volcanism) and short-term effects (bolide impact).

Keywords: Tunisia; paleoecology; K–T planktonic foraminifera

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1. Introduction

The mass extinction in planktonic foraminifera across the Cretaceous–Tertiary (K–T) transition is one of the most severe biotic effects generally at-

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tributed to a large extraterrestrial impact near Chicxulub on the Yucatan Peninsula, Mexico, though the end of the Cretaceous was also a time of extremely stressful environmental conditions for any living organism due to the culmination of long-term climatic changes, such as the ∼6–7°C cooling during the Maastrichtian followed by rapid warming of ∼3–4°C between 400 and 200 kyr before the K–T boundary and subsequent cooling of ∼2–3°C during the last 100–200 kyr of the Maastrichtian (e.g., Barrera, 1994; Li and Keller, 1998a,c). Few studies, however, have addressed the biotic effects that accompanied these long-term environmental changes and the effect this may have had in pre-disposing high stress assemblages to eventual extinction (e.g., Abramovich et al., 1998, 2002; Li and Keller, 1998b,c; Kucera and Malmgren, 1998; Olsson et al., 2001).

Most K–T boundary studies on planktonic foraminifera have concentrated on documenting the pattern of species extinctions immediately below and above the lithological change and geochemical anomalies that mark the boundary event. A few studies have attempted to evaluate some aspects of this mass extinction event on a regional or global scale, including hiatus distribution (MacLeod and Keller, 199l), species survivorship (MacLeod and Keller, 1994), pre-K–T species extinctions in the Negev (Abramovich et al., 1998) and extinctions in northern Spain (Apellanize et al., 1997) and the northern Tethys (Pardo et al., 1999). The absence of more comphrehensive integrated summary results is largely because most K–T sections are scattered far apart and direct comparisons are difficult due to still unknown regional effects.

Recent studies of several new K–T boundary sections in Tunisia now provide the opportunity to evaluate the mass extinction pattern in the low latitude Tethys region. The Tunisian sections, which include the El Kef stratotype, are known to have the most continuous sediment accumulation records across the K–T boundary and generally well preserved planktonic foraminiferal assemblages. The Elles locality, about 75 km southeast of El Kef, has an even more expanded K–T transition than the stratotype section and differs from the latter in the presence of an event deposit consisting of a 20 cm thick, cross-bedded foraminiferal packstone just below the K–T boundary. Here we detail the K–T transition of Elles II, the most expanded of the Elles outcrops (see Elles I in Karoui-Yaakoub et al., 2002). We consider the faunal turnover in this section, as well as that of El Kef, as representative of the mass extinction in the open marine low latitude Tethys environment.

We then present a regional paleoecological evaluation of the mass extinction in Tunisia based on five sections which span from the shallow Sahara Platform in the south to the open marine environment of the north (Fig. 1). The database consists of the planktonic foraminiferal species census and relative species abundances of these sections and the analysis contrasts faunal assemblages before and after the K–T boundary based on two time slices, the latest Maastrichtian (upper CF1) and early Danian (P0 to lower P1a). Specific parameters are evaluated and mapped, including species richness, ecological generalists, ecological

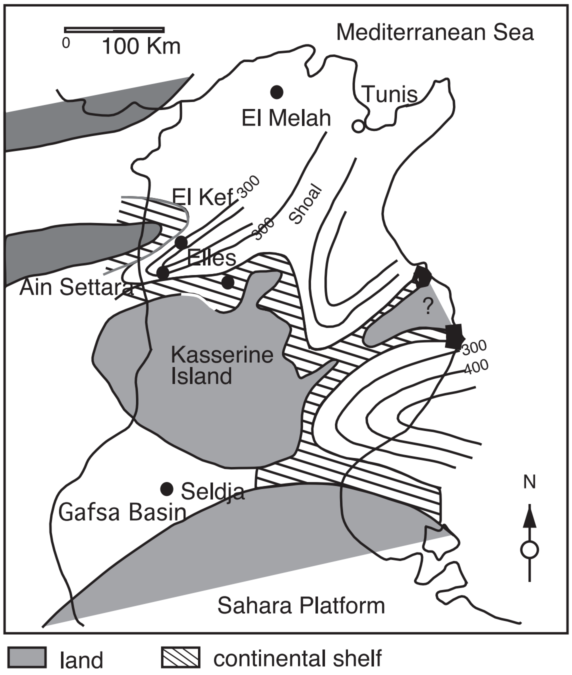

Fig. 1. Paleogeography of Tunisia during the late Maastrichtian and early Tertiary with paleolocations of the K–T boundary sections (modified after Burollet, 1967).

specialists, opportunists, and surface vs. subsurface dwellers. This allows us to evaluate the biotic effects in assemblages ranging from shallow marginal to open marine settings in the low latitude Tethys region.

1.1. Paleogeography of Tunisia

The paleogeographic and tectonic setting of Tunisian sections during the late Maastrichtian to early Paleocene is shown in Fig. 1 (modified from Burollet, 1967). The Seldja section was deposited in the shallow water Gafsa Basin which was connected to the Sahara Platform to the south, but separated from the Tethyan realm to the north by the Kasserine Island. Interchange with the open sea was therefore restricted by the Kasserine Island and probably also by small uplifted areas to the east and west that acted as barriers to circulation (Burollet, 1956; Burollet and Oudin, 1980; Sassi, 1974). Sediment deposition occurred largely in restricted seas that fluctuated between inner neritic and coastal environments. Tectonic activity and erosion of the Kasserine Island contributed to a constant though variable terrigenous influx of sediments (Adatte et al., 2002). Planktonic foraminiferal faunas provide a rare glimpse of marine life in shallow near-shore environments during the K–T transition (Keller et al., 1998).

The El Kef, Elles and Ain Settara sections are located to the north of the Kasserine Island. Sediment deposition occurred at upper bathyal to outer neritic depths at El Kef and middle to outer neritic depths at Elles and Ain Settara, as indicated by benthic foraminifera (Galeotti and Coccioni, 2002, Fig. 2). All three sections indicate similar depositional environments in open marine conditions, but with variable terrigenous influx from the Kasserine Island (see Adatte et al., 2002). At Elles and Ain Settara, terrigenous influx is generally higher than at El Kef with episodes of bioclastic or terrigenous transport just below and above the K–T boundary. Elles and El Kef have comparable sediment records, whereas Ain Settara has a condensed boundary clay and possibly a short hiatus (zone P0 is only a few centimeters thick; Luciani, 2002).

About 150 km to the north of El Kef is the El Melah section which represents the northernmost of the Tunisian K–T boundary outcrops. Sediment deposition occurred at a deeper upper bathyal depth than at El Kef and terrigenous influx was low (Adatte et al., 2002). As a result, sediment accumulation is significantly lower than at El Kef and Elles (Karoui-Yaakoub et al., 2002).

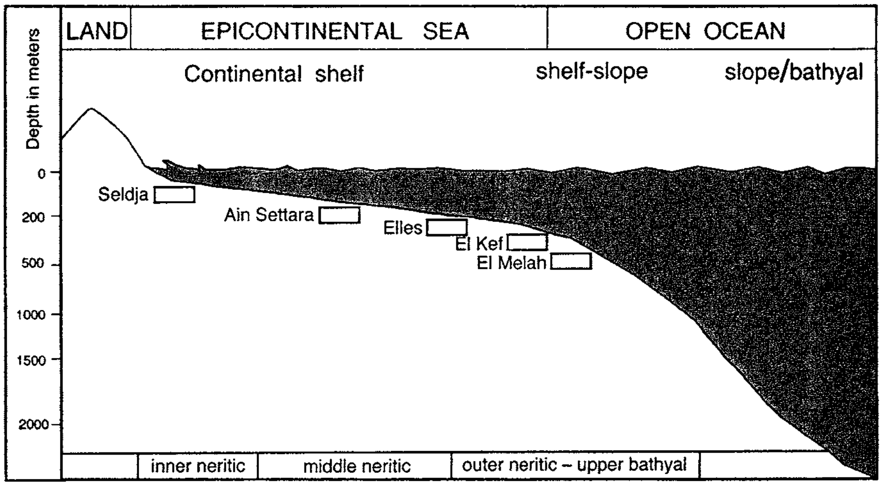

Fig. 2. Paleoenvironmental settings of five Tunisian K–T sections spanning from the restricted shallow Gafsa Basin Seldja section at the edge of the Sahara to the middle and outer shelf depths of the El Kef, Elles and Ain Settara sections just north of the Kasserine Island and to the upper bathyal El Melah section to the north (see Fig. 1 for paleolocalities).

With the exception of Seldja where beds are tilted, sediment layers at the other four Tunisian K–T boundary localities are essentially horizontal and without structural complexities. There is easy access to the sections and foraminiferal preservation is very good to excellent. Together these five sections provide an ideal transect representing paleodepositional environments from the shallow inner neritic, to middle and outer neritic, and upper slope environments (Fig. 2) that may be characteristic of the low latitude Tethyan realm in general.

1.2. Previous work and database

A number of high resolution quantitative planktonic foraminiferal studies have recently been completed for the Tunisian K–T sections, including El Kef (Keller et al., 1995; Molina et al., 1998), Ain Settara (Molina et al., 1998; Luciani, 2002), Elles and El Melah (Karoui-Yaakoub et al., 2002 and this study) and Seldja (Keller et al., 1998, Fig. 1). Though these studies were done independently by different workers, in all but one (Molina et al., 1998) the same or similar species concepts and methods were used and the database of these workers is thus internally consistent and forms the basis for the Tunisian paleobiogeography of the K–T mass extinction.

There are few taxonomic differences between Keller and Luciani (see Luciani, 1997, 2002), and the differences between Keller and Karoui-Yaakoub in the species census data are due to lumper and splitter effects (see discussion in Karoui-Yaakoub et al., 2002). Therefore for the Elles section, only the results of Keller's analysis (this study) are used, though both Elles outcrop localities show nearly identical species census and faunal assemblage changes. The quantitative data for this report are based on Keller's and Luciani's studies for all Tunisian sections.

1.3. Methods

Samples from all five Tunisian sections were collected by the same team using the same methods. The sections were cleaned from surface contamination by digging a trench to fresh bedrock. Samples were then taken at 5–10-cm intervals in general, and at closer 1–2-cm intervals across the boundary clay layer. For each section, the same sample set was used for faunal, geochemical and mineralogical studies to insure direct comparison of results (Adatte et al., 2002; Stüben et al., 2002).

Laboratory and analytical methods for planktonic foraminiferal studies have been described in Keller et al. (1995). Population counts were based on sample splits of about 300 specimens from each of two size fractions (38–63 μm and >63 μm). Duplicate analyses of two size fractions were done because there is a significant difference between the first appearances of the earliest Danian species in the two size fractions, with earlier first occurrences in the small <63-μm size fraction. This affects the biostratigraphic results of biozones P0 and P1a. In addition, the relative abundances of small species is significantly larger in the smaller size fraction because they tend to fall through the larger sieve size (>63 μm). Conversely, the larger size fraction (>63 μm) was analyzed because larger species tend to be underrepresented in the smaller size fraction. Quantitative results of the two size fractions are shown for the Elles II outcrop (Tables 1 and 2). For the biogeographic maps, relative abundances of the >63-μm size fraction was used. Species identifications are based on Robaszynski et al. (1983/84), Caron (1985), Nederbragt (1991), Keller et al. (1995) and Olsson et al. (1999).

2. Results I

2.1. Elles II

The biostratigraphy and faunal turnover of Elles II are discussed and illustrated here as characteristic of the species richness and relative species abundances of the K–T transition in Tunisia, and in the low latitude Tethys in general. The lithostratigraphy of this expanded sequence is characteristic of Tunisian sections, but may also be relevant in other regions, assuming that the K–T transition evident in Tunisia records global, rather than local trends.

Elles II is located about 75 km southeast of El Kef near the hamlet of Elles in a valley cut by the

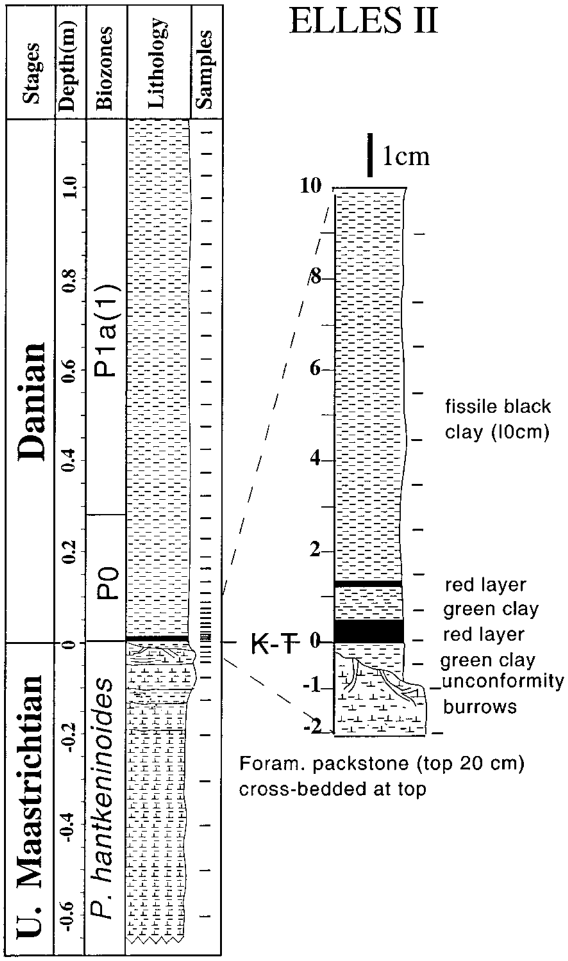

Fig. 3. Lithology across the K–T transition at Elles II. Note the 25–30 cm thick foraminiferal packstone and cross-bedded unit just below the K–T boundary.

Karma river. Following the river upsection to where the valley forks, Elles I is located in the right side valley fork (see Karoui-Yaakoub et al., 2002) and Elles II in the left side valley fork. Elles II differs from Elles I primarily in the more expanded K–T transition and the presence of a 20–25 cm thick bioclastic bed with ripple marks below the K–T boundary clay and red layer.

2.2. Lithology and lithostratigraphy

The uppermost Maastrichtian at Elles II consists of monotonous gray marls and silty shales. An important sedimentological change occurs in the 25–30 cm thick interval directly underlying the K–T boundary red layer (Fig. 3). In this interval gray marls first grade into gray calcareous siltstones and then into gray calcarenites, both of which form layers of 5 cm and 8 cm thick respectively. Overlying this interval is a 5–7 cm thick yellow calcarenite consisting primarily of planktonic foraminiferal tests (foraminiferal packstone). The foraminiferal packstone is yellowish, cross-bedded and burrowed. Burrows are about 5 mm in diameter, unbranched and reach a length of a few centimeters. Most of the burrows are horizontal or oblique, but a few are almost vertical with the upper end at the top of the packstone layer. All of the burrows are infilled with the yellow marly sediment and none with the green clay that overlies the foraminiferal packstone. This indicates that colonization and infilling of burrows occurred before deposition of the green clay layer. Because the upper surface of the packstone is also an undulating erosional surface, an unconformity is present between the top of the packstone and the green clay. However, this hiatus appears to be very short as suggested by the presence of the most expanded zone CF1 known to date (10 m at Elles as compared with 6 m at El Kef; Pardo et al., 1996; Abramovich et al., 2002).

The overlying plastic green clay varies between 0.2 to 1 cm thick and fills the depressions in the packstone. Above the green clay is the 2–4 mm thick rusty red layer that generally marks the K–T boundary event and contains maximum concentrations of Ir- and Ni-rich spinels (Rocchia et al., 1995; Robin et al., 1995). No burrows are observed across the red and green layers. Overlying the red layer is another 1–2 cm thick plastic green clay layer with a second very thin red layer (Fig. 3). No burrows are observed in this couplet either.

Upsection, the green clay grades into fissile clays with small Fe concretions. The lowermost 10 cm of the clay are black, rich in organic matter and contain rare casts of nuculanid bivalves. The black clays grade into dark gray shaley clays overlain by gray shales which are less fissile. Bioturbation was noted at 50 cm above the K–T boundary (Fig. 3).

Table 1A
Relative percent abundances of planktonic foraminifera (>63 μm) below the K–T boundary at Elles II, Tunisia (X = rare)

Biozones	*Plummerita hantkeninoides*															
Samples: cm below K–T	0	0–0.5	0.5–1.5	1.5–2.5	2.5–3.5	7.5–8.5	11.5–15	15–20	25–30	35–40	45–50	55–60	65–70	75–80	85–90	95–100
Abathomphalus mayaroensis					X											X
Archeoglobigerina blowi	X	X			X	1			X	X	X		X	X	X	X
Gansserina wiedenmayeri	X	X	X		X	X	X		X	1		X	X	X	X	
Globigerinelloides aspera	4	4	2	X	3	2	1	5	2	3	3	2	4	4	2	1
G. subcarinatus			X								X	1				
G. yaucoensis	1	3	3	4	3	2	1	2	2	3	4	3	1	1	1	2
G. volutus	X			X		1	2	X		1	X	X		X		X
Globotruncanella petaloidea	X	X	X	X	1	1	1	X	1	X	1	X	X	3	1	X
G. minuta	2	X	1		X	1	1	1	X	X	1	X	X	1	X	X
Globotruncana arca	X	X	X		X		1	X	X	1	1	X	1	1	1	1
G. aegyptiaca	X	1		X	X	X	X	X	X	X	X	X	X	1	X	X
G. duwi				X	X	X	1	X	X	1	X	X	X	X	X	
G. esnehensis		X			X	X	X	X	1	X			X	X	X	X
G. falsostuarti	X	X	X	X	X	X	X	X	X	X						
G. insignis	X	X			X	X	X	X	X		X	X	X	X	X	X
G. dupeublei	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
G. rosetta	X	X	X	X	X	X	X	X	X	1	X	X	X	1	1	X
Globotruncanita angulata										X	X	X		X	X	X
G. conica	X	X	X	X	X	X	X	X	X	X	X	X	X	4	X	X
G. pettersi				X			X	X	1	1	X	X	1	X	X	X
G. stuarti	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
G. stuartiformis	X	X	X		X	X	X	X	X	X		X	X	X	X	X
Gublerina cuvilieri																X
G. robusta							X			X				X	X	X
Guembelitria cretacea	X	X	9	2	2	1		1	X	1	1	1		1	X	X
G. danica	X		1	X												
G. irregularis	X		2	1												
G. trifolia		X	X	X												
Hedbergella holmdelensis	4	1	1	X	1	X	X	1	1	2	2	X	3	2	X	2
H. monmouthensis	4	1	6	4	1	1	2	2	2	2	2	1	2	1	3	3
Heterohelix carinata	1	1	X	1	2	3	1	2	7	5	6	4	3	1	3	7
H. dentata	11	X	8	19	16	15	22	12	16	21	13	14	10	12	16	13
H. globulosa	22	17	16	10	12	9	12	11	16	9	9	10	11	12	13	10
H. labellosa	2	3	2	3	4	6	6	6	3	3	1	2	3	3	2	5
H. moremani					X	X	X			X	2	2	1	X		
H. navarroensis	26	30	23	23	21	15	18	19	10	14	20	17	21	11	8	19
H. planata	3	6	1	2	6	7	6	6	7	6	7	6	6	7	6	8
H. pulchra			1	1	2	1	1	2	2	2	1	3	1	1	1	X
H. striata		3					X				X	X	X	2	X	X

Table 1A
(*continued*)

Biozones	*Plummerita hantkeninoides*															
Samples: cm below K–T	0	0–0.5	0.5–1.5	1.5–2.5	2.5–3.5	7.5–8.5	11.5–15	15–20	25–30	35–40	45–50	55–60	65–70	75–80	85–90	95–100
Planoglobulina carseyae	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
P. multicamerata				X	X	X		X		X		X	X	X	X	X
P. brazoensis				X	X	X	X	X	X	X	X	X	X	X	X	X
Plummerita hantkeninoides	X	X				X	X	1	X		X	X	X	1	X	X
Pseudoguembelina costulata	12	21	16	20	16	18	16	19	16	12	16	15	21	18	21	16
P. hariaensis	X	1	X	X	1	x	1	X	1	1	X	X	X	X	x	1
P. kempensis	3	2	2	2	5	5	2	3	4	2	1	7	5	4	7	4
P. palpebra	X	X	X	1	X	X	1	X	1	X	X	X	1	1	X	X
P. punctulata	2	5	2	2	3	7	1	3	4	2	1	7	5	4	7	4
Pseudotextularia deformis	X	X	X	X	X	X	X	X	X	X	X	X	1	1	X	X
P. elegans	X	X	X	X	X	X	X	X	X	X	X	X	X	1	X	X
Racemiguembelina intermedia	X	X	X	X	X		X	X	X	X		X	X	X		X
R. powelli	X	X		X	X		X		X	X	X	X			X	X
R. fructicosa	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Rosita contusa			X			X	X				X		X	X	X	X
R. patelliformis	X	X	X	X	X	X	X	X	X	X	X			X	X	X
R. walfischensis											X			X	X	
Rugoglobigerina hexacamerata	X	X	1	X		X	1	1	2	1	4	X	1	3	4	1
R. macrocephala	X	X	X	1	1	X	X	X				X		X		
Rugoglobigerina reicheli								X		X				X		
R. rotundata	1		1	X	X	1	1	1	X	X	X	X	X	1	X	X
R. rugosa	1	1	X	X	1	1	2	2	X	3	2	1	X	2	2	1
R. scotti	X		X	X	X	1	X	X	X	1	1	X	X	1	X	X

Table 1B
Relative percent abundances of planktonic foraminifera (> 63 μm) above the K–T boundary at Elles II Tunisia (X = rare)

Biozones	P0							P1a								
Samples: cm above K–T	0–0.5	1–2	3–4	4–5	8–10	12–15	18–20	25–30	35–40	45–50	55–60	65–70	75–80	85–90	95–100	105–110
Globigerinelloides aspera	4	X	1	X	X				X					X		
G. subcarinatus	1		1													
G. yaucoensis	2	1	1	X	X									X		
G. volutus	X		X		X									X		
Globotruncanella petaloidea	X	X	X													
G. minuta	X	X		X												
Globotruncana arca	X	X	X													
G. aegyptiaca	X	X	X													
G. esnehensis	X	X					X									
G. rosetta	X	1														
Globotruncanita stuarti	X		X													
Guembelitria cretacea	11	26	38	75	84	X	X	X	X	X	X	X	40	32	65	21
G. danica	2	X	X	10	4	X	X	X		X	X	X	8	6	X	3
G. irregularis	1	X	X	5	7	X	X	X	X	X	X	X	2	7	6	4
G. trifolia	1	7	2	3		X	X	X	X				2			
Hedbergella holmdelensis	1	4	2	X	X									1		2
H. monmouthensis	2	1	2	X	X								1			
Heterohelix carinata	X	X	1	X												
H. dentata	20	18	14	2	1		X	X	X				2	3		1
H. globulosa	11	7	5	1	1		X			X			2			
H. labellosa	5	2	4													
H. navarroensis	16	14	14	2	1		X	X	X					2	1	1
H. planata	3	4	4	1	X		X	X	X							
Planoglobulina carseyae	X	X														
Pseudoguembelina costulata	9	8	4	X	X		X	X	X				3			
P. hariaensis		X		X												
P. kempensis	2	2	2		X		X	X	X							
P. palpebra	1	X	X													
P. punctulata	4	2	1		X											
Pseudotextularia deformis	X	1														
P. elegans	X															
Racemiguembelina intermedia			X													
R. fructicosa			X													
Rugoglobigerina hexacamerata	X	X	X		X											
R. macrocephala	2	1	X		1										1	
R. rugosa	1	X	1	X	X											
Globoconusa daubjergensis														1		
Eoglobigerina eobulloides														1		
E. edita														3		
E. fringa													1	1		

Table 1B
(*continued*)

Biozones	P0							P1a								
Samples: cm above K–T	0–0.5	1–2	3–4	4–5	8–10	12–15	18–20	25–30	35–40	45–50	55–60	65–70	75–80	85–90	95–100	105–110
S. trivialis														1	1	
Parvularugogloberina eugubina														1	3	1
P. extensa										X			24	12	3	1
Total counted	266	250	226	122	137	0	0	0	0	0	0	0	125	135	77	89

Table 2A
Relative percent abundances of planktonic foraminifera in the size fraction 38–63μm below the K–T boundary at Elles II, Tunisia

Biozones	*Plummerita hantkeninoides*											
Samples: cm below K–T	0–0.5	0.5–1.5	1.5–2.5	2.5–3.5	7.5–8.5	11.5–15	15–20	25–30	35–40	45–50	55–60	65–70
Globigerinelloides yaucoensis	3	2	3	5	7	4	3	5	2	1	4	1
Guembelitria cretacea	23	23	21	15	22	19	39	20	13	18	31	29
G. danica	4	2	3	4	4	3	2	1		2		2
G. irregularis	3	6	9	3	3	6	5	2	6	8		2
G. trifolia	3	2	1	3	3	1	1	1	5	5		
Hedbergella holmdelensis				3	2	2	5	9	4	4	11	6
H. monmouthensis	12	9	7	6	6	8	5	7	5	2	5	4
Heterohelix dentata	12	10	13	14	16	31	17	18	20	16	23	15
H. globulosa	9	10	5	3	2			2				
H. planata			3	2	2							
H. navarroensis	22	30	25	37	27	26	20	30	34	35	24	37
Pseudoguembelina costulata	6	4	8	5	6			3	6			
Heterohelicid juveniles	3	2	2				3	2	5	9	2	4
Total counted	232	267	267	295	311	256	183	304	248	148	229	222

Table 2B
Relative percent abundances of planktonic foraminifera in the size fraction 38–63μm above the K–T boundary at Elles II Tunisia (X = rare)

Biozones	P0								P1a								
Samples: cm above K–T	0–0.5	0.5–1.0	1–2	3–4	4–5	8–10	12–15	18–20	25–30	35–40	45–50	55–60	65–70	75–80	85–90	95–100	105–110
Globigerinelloides aspera	1	2	1	1	X	1				X				X	X		X
G. subcarinatus		X						X									
G. yaucoensis	1	1	1		X									X			
G. volutus	1			X		1									X		
Globotruncanella petaloidea	X			X													
G. minuta	X	X	X		X												
Globotruncana arca	X	X	X														
G. aegyptiaca	X	X	X	X													
G. duwi		X															
G. esnehensis	X	X	X					X									
G. rosetta	X	X	X														
Globotruncanita stuarti	X			X													
Guembelitria cretacea	20	23	40	31	37	39	67	45	61	53	53	53	57	48	50	43	36
G. danica	4	2	5	6	6	11	8	10	8	6	3	4	1	5	5	5	4
G. irregularis	25	17	30	49	43	34	12	29	14	20	22	20	12	12	10	13	18
G. trifolia	4	7	8	6	7	5	2	6	2	1	1	1	3	3	3	2	1
Hedbergella holmdelensis	3	2	1	X	1	1		1				X					X
H. monmouthensis	2	2	X	1	1	1				X							X
Heterohelix carinata	1	1	1	X	X			X									
H. dentata	13	11	6	1	1	1		X	1	1		X		X	X		1
H. globulosa	6	4	2	1		2		1	X	1		X			X		
H. labellosa	1	1										X			X		
H. navarroensis	10	15	4	1	X	2		X	1	2							1
H. planata	1	2	X	1		X			X	X							
H. pulchra	X	X															
Planoglobulina carseyae	X		X														
Pseudoguembelina costulata	4	5	X	1	2	1		X	X	X				X	X		
P. hariaensis			X		X												
P. kempensis	1	1	1			1		X	X	X							
P. palpebra	X	X	X	X													
P. punctulata	1	1	X	X		X											
Pseudotextularia deformis	X	X	X														
P. elegans	X																
Racemiguembelina intermedia		X															
Rugoglobigerina hexacamerata	X		X			X		X									
R. macrocephala		X	X	X													
R. rugosa	X	X			X	X											
Globoconusa daubjergensis							5	5	3								
Eoglobigerina eobulloides						1	1	X	1				1	1	1	2	2

Table 2B
(continued)

Biozones	P0								P1a								
Samples: cm above K–T	0–0.5	0.5–1.0	1–2	3-4	4-5	8–10	12–15	18–20	25–30	35–40	45–50	55–60	65–70	75–80	85–90	95–100	105–110
E. edita								1	2	5	5	3	10	12	9	10	11
E. fringa									1	X	2	2	2	5	3	3	6
S. trivialis																X	
Parvularugogloberina eugubina									2	2	4	10	4	4	4	4	4
P. extensa		1	1	1	1	X	5	X	4	8	10	6	5	4	6	11	8
Globanomalina compressa												X	1		1	X	X
Total counted	383	410	358	414	270	383	126	240	291	412	392	415	368	332	448	326	365

2.3. Biostratigraphy

2.3.1. Taxonomic notes

Recently, a new classification of Paleocene planktonic foraminifera based on wall texture was published (Olsson et al., 1999). This study generally follows this new classification scheme for the early Danian species though with some exceptions that are explained below.

Parasubbotina pseudobulloides (Plummer, 1926): This well-known species is characterized by 5 chambers in the last whorl (rarely 6) and rapidly increasing chamber size. Well-developed large (> 150 μm) morphotypes first appear after the extinction of *Parvularugoglobigerina eugubina*. But forms with 4.5–5 chambers appear earlier in the upper half of the *P. eugubina* range (zone P1a) and later coexist with the well-developed *pseudobulloides* morphotypes. The first appearance of this morphotype marks the subdivision of zone P1a (Fig. 4). Olsson et al. (1999) assign these specimens to a separate group *P.* aff. *pseudobulloides*. However, since these forms appear to be part of a continuous variation within the *pseudobulloides* population and separation is difficult at best, we retain this early morphotype within *P. pseudobulloides*.

Subbotina triloculinoides (Plummer, 1926): This is another well-known species with 3.5 globose chambers in the last whorl and the last chamber characteristically enveloping the upper half of the test. This morphotype first appears in the middle of zone P1a nearly coincident with *Parasubbotina pseudobulloides* and marks the subdivision of zone P1a (Fig. 4), though, as with the latter species, large morphotypes (> 150 μm) of *S. triloculinoides* do not appear until after the extinction of *Parvularugoglobigerina eugubina*. Olsson et al. (1999) recognize only the larger morphotypes which they date as first appearing at 64.5 Ma.

Guembelitria cretacea Cushman, 1933; Olsson et al. (1999) group all triserial morphotypes within the species *G. cretacea*, including the high-spired *danica*, the irregularly stacked chambers of *irregularis* and the short-spired *trifolia*. Although we agree that all three morphotypes share the same finely perforate wall texture, globular chambers and overall triserial chamber arrangement, they are also very distinct and easily identified morphotypes which differ in their relative abundance distributions geographically and through time. They may represent either different species or ecological variants. We continue to separate these morphotypes in order to evaluate their stratigraphic and ecological affinities.

Parvularugoglobigerina eugubina (Luterbacher and Premoli Silva, 1964): This small species was originally defined as a 5–6 (rarely 8) chambered form with inflated subglobular chambers and high open aperture. Blow (1979) described a small species with 5–8 compressed chambers and slit-like narrow aperture, with a similar stratigraphic range, as *longiapertura*. Olsson et al. (1999) consider this form a variant of *P. eugubina*. We retain the separation of these two distinct morphotypes because their geographic distribution may eventually provide paleoecological information.

Parvularugoglobigerina extensa (Blow, 1979); Olsson et al. (1999) consider the species formerly classified as *Globoconusa conusa* (Khalilov) a junior synonym of *P. extensa* and we follow this convention.

2.3.2. Biozonation

The biozonation of Keller et al. (1995) is used in this study (Fig. 4). Berggren et al.'s (1995) revised zonation uses the same index species for the two lowermost Danian zones, but call Keller et al.'s P1a zone Pα. Keller et al. (1995) subdivide zone P1a (range of *Parvularugoglobigerina eugubina*) based on the first appearances of *Parasubbotina pseudobulloides* (*P.* aff. *pseudobulloides* of Olsson et al., 1999) and/or *Subbotina triloculinoides*.

2.3.2.1. Plummerita hantkeninoides Zone

This zone marks the end of the Maastrichtian and spans the range of *Plummerita hantkeninoides* as defined by Masters (1984, 1993) and subsequently by Pardo et al. (1996) (Fig. 4). At Elles II, as well as other Tunisian sections, *P. hantkeninoides* is consistently present (except for two samples), whereas only two occurrences of *Abathomphalus mayaroensis* (the alternative late Maastrichtian marker species) were noted (at the K–T boundary and at 1 m below, Fig. 5). At Elles I and Elles II the range of *P. hantkeninoides* spans the last 7 m and 10 m of the Maastrichtian respectively (Abramovich and Keller, 2002) as compared with 6 m at El Kef (Li and Keller, 1998a). Agewise the range of this excellent latest Maastrichtian marker species spans the last 300 kyr of the Maastrichtian, or most of chron 29R below the K–T boundary, as estimated from the paleomagnetic record at Agost (see Pardo et al., 1996; Groot et al., 1989). This species is easily identified by its long apical spines and is common in Tunisian sections where its stratigraphic range (generally > 6 m) provides a good estimate of the completeness of the latest Maastrichtian interval. The *P. hantkeninoides* Zone replaces the *A. mayaroensis* Zone for the top part of the Maastrichtian.

2.3.2.2. K–T boundary

This boundary is defined by the coincidence of several characteristic lithological and geochemical criteria in all sections in Tunisia (e.g., Fig. 3) and worldwide including: a lithological change from marls or shales to dark gray or black organic-rich clay; a 2–4 mm thin rusty red layer at the base of the clay; the presence of spherules, spinels and anomalous concentrations of Ir and other plantinum group elements in the rusty red layer.

Paleontological criteria include the extinction of all ornate large tropical and subtropical species, including all globotruncanids, racemiguembelinids and rugoglobigerinids (with the possible exception of *Rugoglobigerina macrocephala*) below the red layer and organic-rich clay layer. This extinction horizon is followed by the first appearance of Danian species at or near the base of the organic-rich black clay (e.g., *Parvularugoglobigerina extensa, Eoglobigerina fringa, Eoglobigerina edita, Eoglobigerina eobulloides, Woodringina hornerstownensis*).

2.3.2.3. P0 zone

This zone spans the part of the basal Danian organic-rich black clay layer from the extinction of the tropical–subtropical species group (at the rusty red layer) to the first appearance of *Parvularugoglobigerina eugubina* and/or *Parvularugoglobigerina longiapertura* (Fig. 4). In many earlier studies zone P0 was considered to span the organic-rich clay layer (e.g., Smit, 1982; Keller, 1988;

Olsson and Liu, 1993; Molina et al., 1998). This is also supported by the first occurrence of the marker species in the > 63-µm size fraction near the top of the clay layer (at 65 cm above the red layer) at Elles I and Elles II (Table 2A, Fig. 5). However, new studies based on the smaller 36–63-µm size fraction at Elles I and Elles II indicate small *P. eugubina* first appear 25–30 cm above the red layer, whereas small *P. longiapertura* first appear at 45–50 cm (Fig. 6, Table 2B, see also Karoui-Yaakoub et al., 2002). This suggests that P0 may be restricted to the lower half of this black clay layer. Zone P0 is noteworthy for its common presence of reworked Cretaceous tropical species and large abundance of triserial species.

2.3.2.4. P1a zone

This range zone spans from the first appearance of *Parvularugoglobigerina eugubina* and/or *Parvularugoglobigerina longiapertura* to the extinction of these taxa. Due to the increased terrigenous influx from the nearby Kasserine Island at Elles I and II, as well as at Ain Settara, the P1a zone is about 5–6 m thick and hence more expanded than the 4.5 m observed at El Kef (Keller, 1988). At the more distant and deeper water locality of El Melah, zone P1a is condensed and only 1.4 m thick. Zone P1a can be subdivided into P1a(1) and P1a(2) based on the first appearance (FA) of *Parasubbotina pseudobulloides* (Fig. 4).

2.3.3. Faunal turnover

2.3.3.1. Species extinctions

A total of 60 Cretaceous species are present in the last 100 cm of the Elles II section in

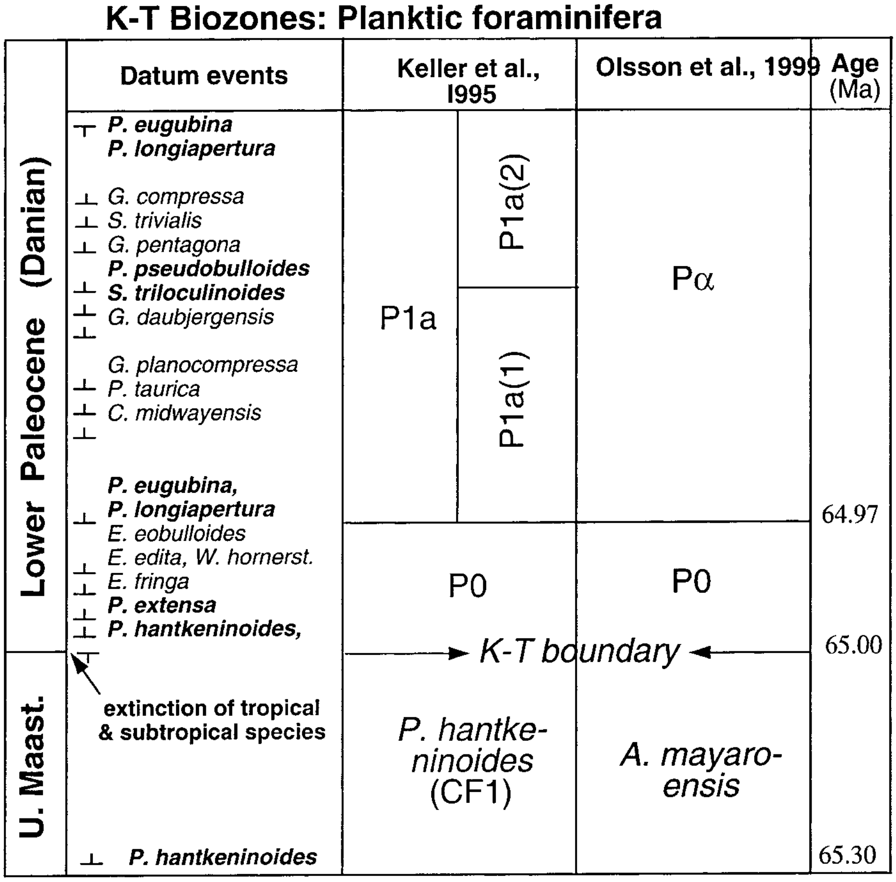

Fig. 4. Planktonic foraminiferal zonation of Keller et al. (1995) and comparison with Berggren et al. (1995).

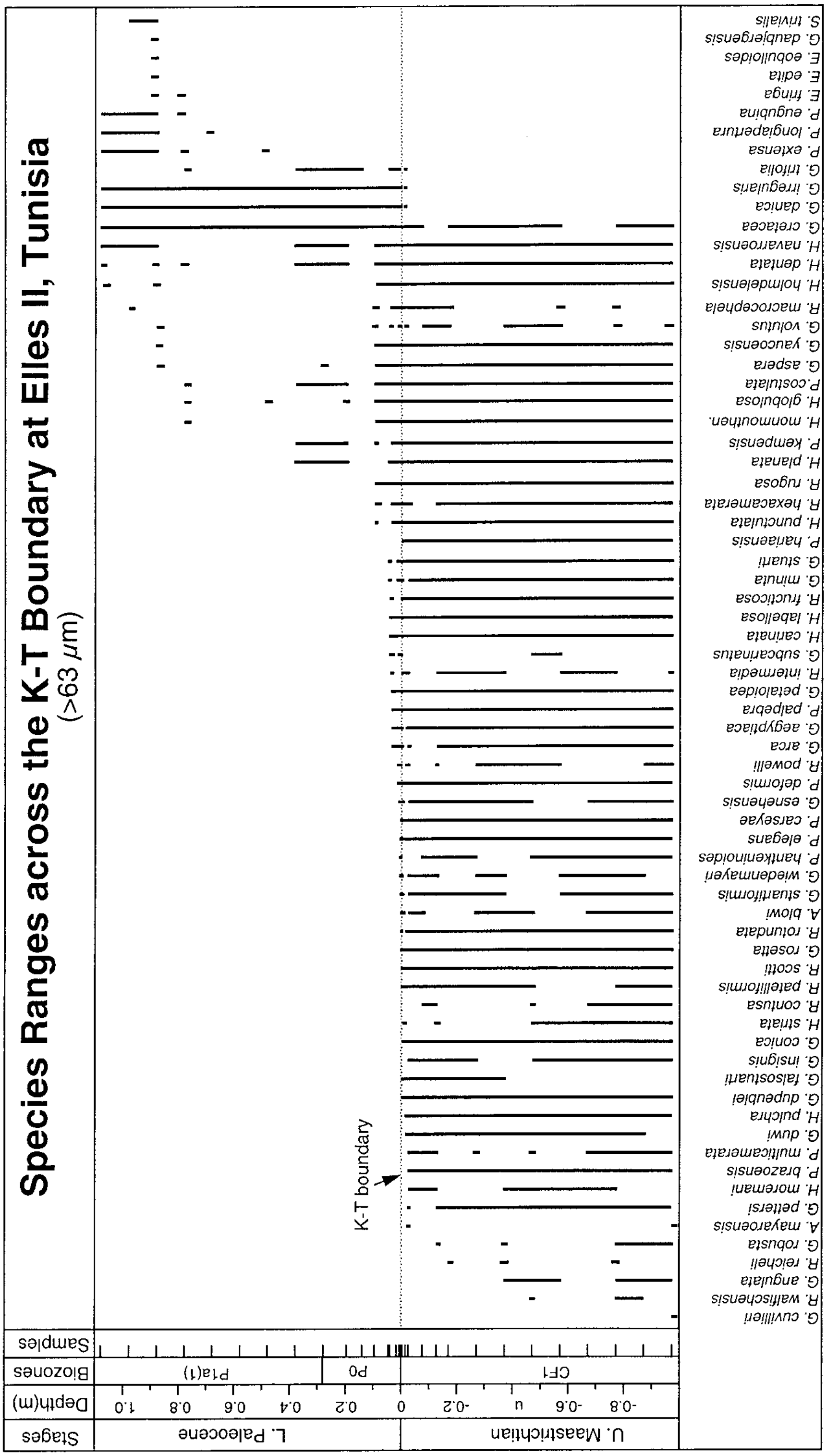

Fig. 5. Planktonic foraminiferal species ranges across the K–T transition at Elles II based on the > 63-μm size fraction.

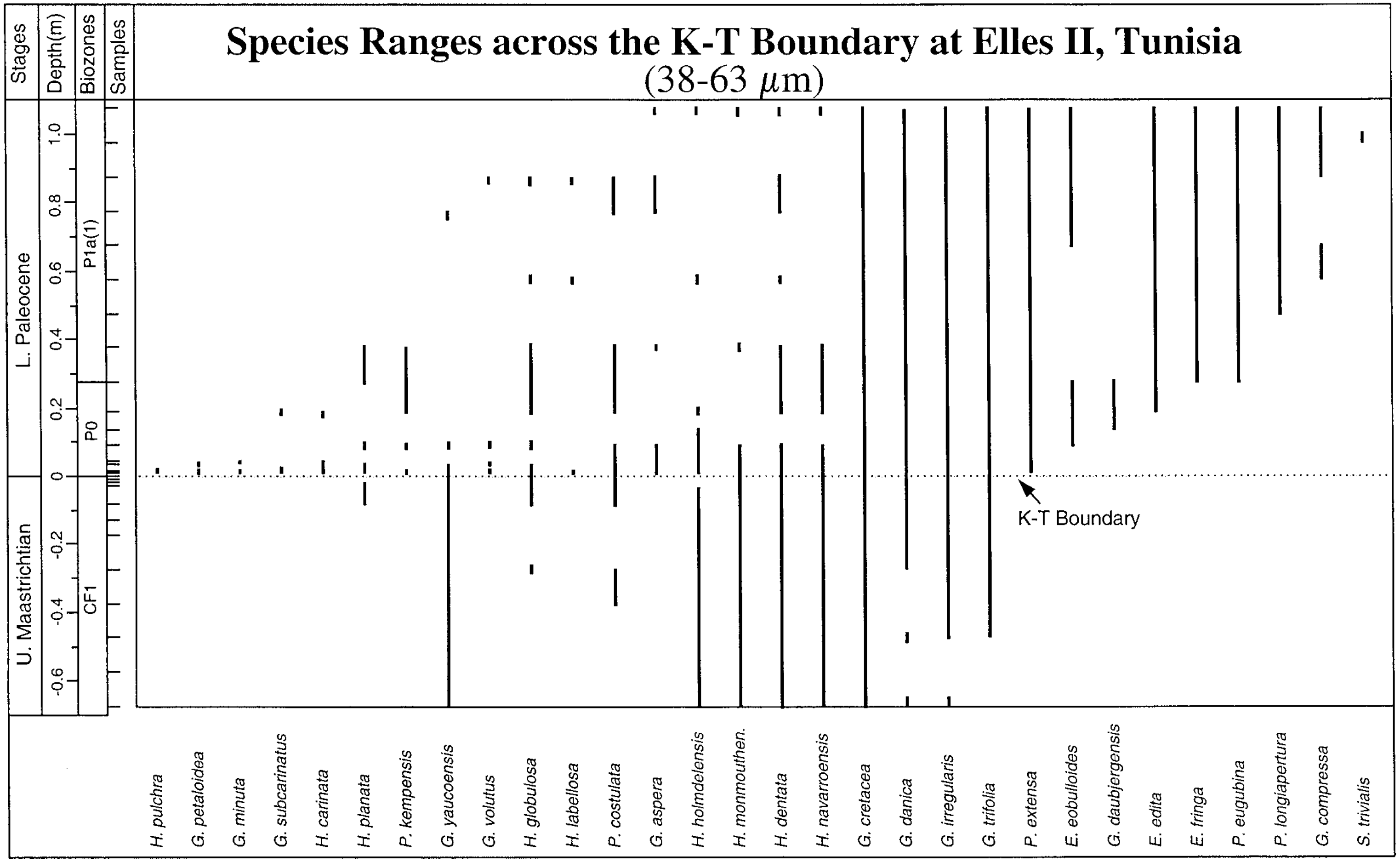

Fig. 6. Planktonic foraminiferal species ranges across the K–T transition at Elles II based on the 36-63-µm size fraction. Note the differences between the species census data of the two size fractions in Figs. 5 and 6.

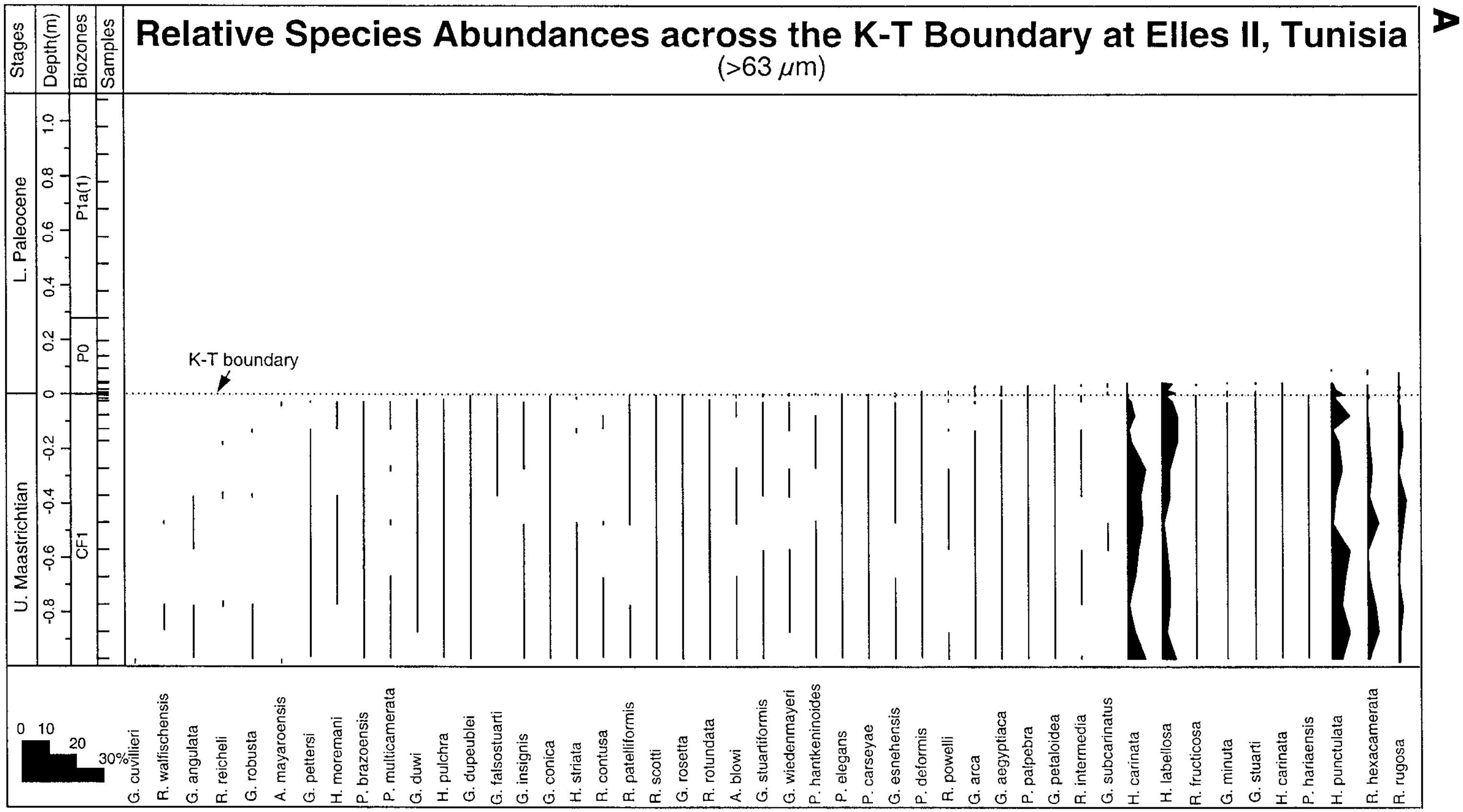

Fig. 7. (A) Relative species abundances of the indigenous Cretaceous planktonic foraminifera across the K–T boundary at Elles II in the > 63-μm size fraction. Note that all of these species, which are considered extinct at or near the K–T boundary, are tropical to subtropical and are rare to few or only sporadically present directly below the top of the Maastrichtian. Their combined total abundance is less than 20% of the Cretaceous assemblage. Thus, the K–T boundary mass extinction selectively eliminated these subtropical to tropical ecological specialists. (B) Relative species abundances of Cretaceous survivors and evolving early Tertiary planktonic foraminifera in uppermost Maastrichtian and lowermost Danian sediments at Elles II. Faunal counts are based on the > 63-μm size fraction. Note that species in P0 and the lower part of P1a(1) are nearly absent in this size fraction because they are dwarfed due to high stress conditions and therefore only common in the smaller 36–63-μm size fraction (Fig. 8).

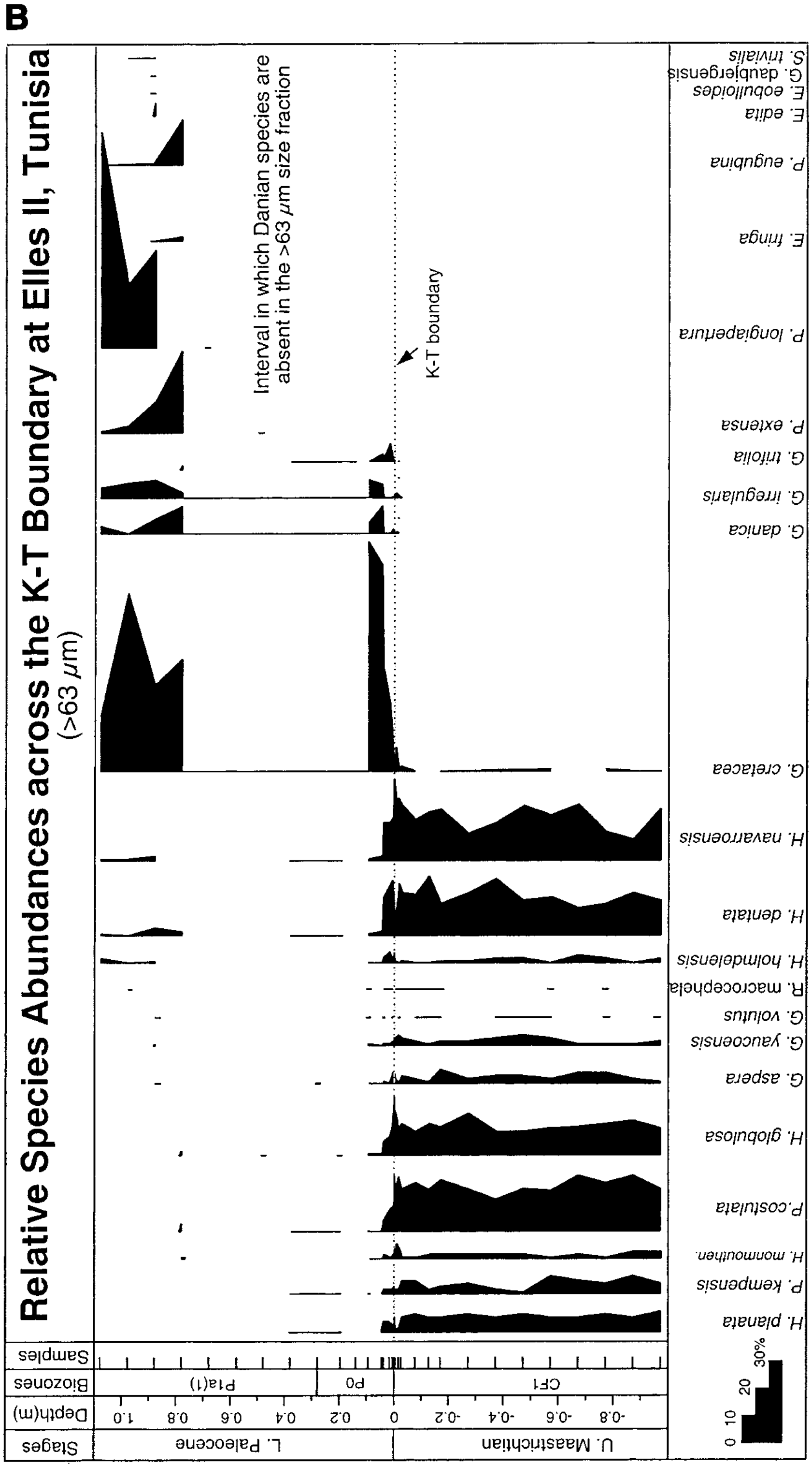

Fig. 7 (continued).

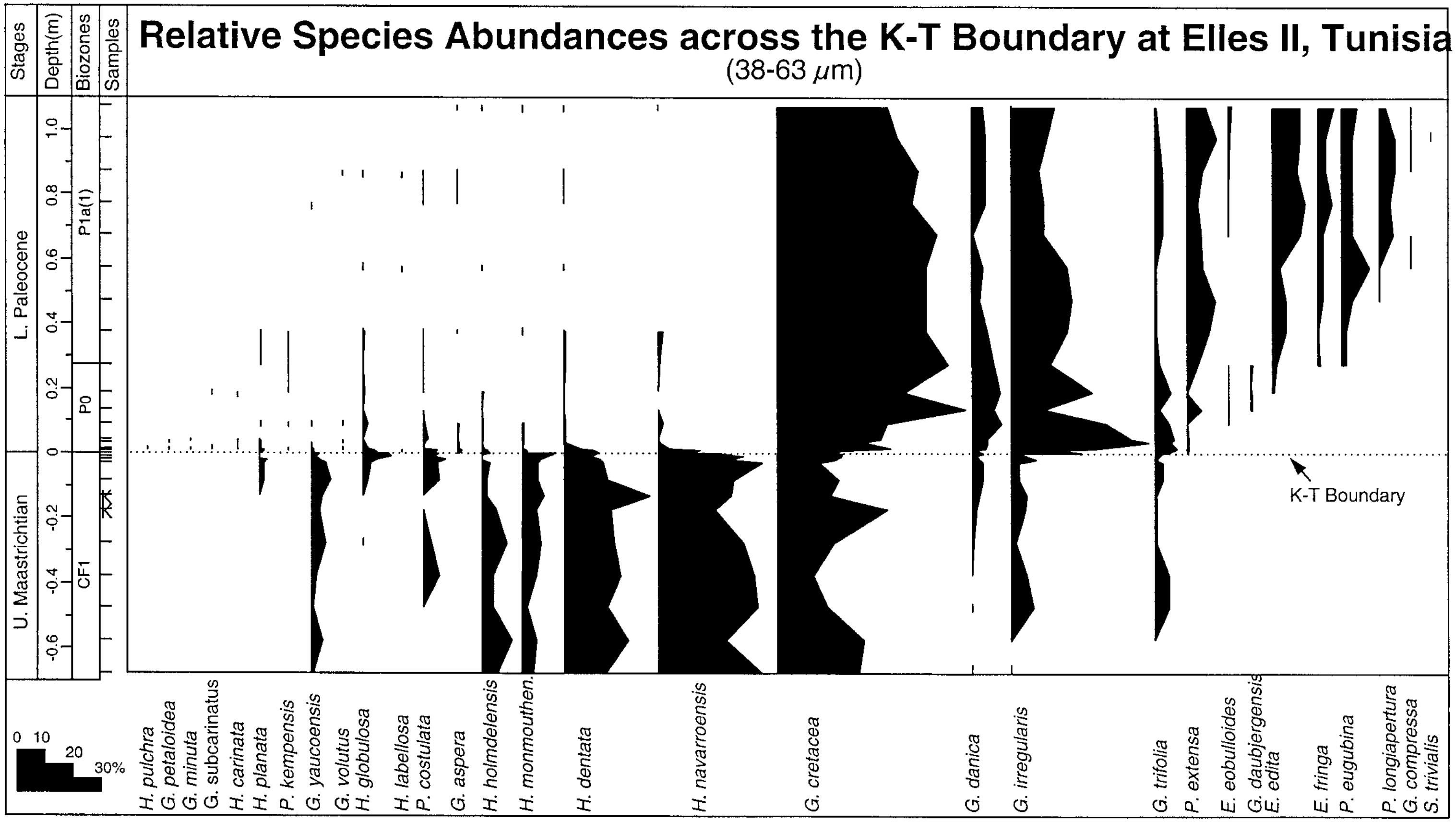

Fig. 8. Relative species abundances of Cretaceous survivors and evolving early Tertiary planktonic foraminifera in uppermost Maastrichtian and lowermost Danian sediments at Elles II in the 36–63-μm size fraction. Note that this small size fraction contains abundant high stress, dwarfed species which are generally not found in the larger (> 63-μm) size fraction. For this reason, the small 38–63-μm size fraction has to be examined for the K–T transition interval to determine the presence and absence of Danian species as well as the faunal turnover.

the $>$63-μm size fraction (Fig. 5) and another three species are present only in the smaller (38–63-μm) size fraction (*Guembelitria danica, Guembelitria irregularis, Guembelitria trifolia*, Fig. 6). A comparable number of species was identified at El Kef (57 species, Keller et al., 1995; Keller, 1996), Ain Settara (Luciani, 2002) and El Melah (this study). Most species range through the last meter interval below the K–T boundary. Though only a few species were not observed in the top 10 cm below the K–T boundary (e.g., *Gublerina cuvilieri, Rosita walfishensis, Globotruncanita angulata, Rugoglobigerina reicheli*), many species reappear in the top 25 cm (Fig. 5) within the foraminiferal packstone layer marked by cross-bedding. This suggests that there is significant transportation and reworking of older assemblages within the packstone and for this reason we excluded the packstone from our paleobiogeographic database.

Though most species disappear at or below the K–T boundary, 16 species (*Heterohelix carinata* to *Rugoglobigerina rugosa*, Fig. 5) are also present in the lower zone P0 (Fig. 5); these are considered reworked because many of the specimens show differential preservation or are broken. In sections globally, these species generally disappear near the K–T boundary (MacLeod and Keller, 1994). A total of 16 Cretaceous species range well into the early Danian and are considered as survivors as discussed below.

Thus, we consider all but 16 species, or 75%, as extinct at or near the K–T boundary (*Gublerina cuvilieri* to *Rugoglobigerina rugosa* in Fig. 5); though the combined relative abundance of this group averages less than 20% of the total assemblage (Fig. 7A,B). The same species extinction and relative abundance pattern was observed at El Kef (Keller et al., 1995, fig. 11, p. 243) and at Ain Settara (Luciani, 2002). Nearly all of the extinct species have large morphologies, highly ornamented tests, and their geographic distributions are restricted to low and middle latitudes. We consider these taxa as ecological specialists well adapted to tropical and subtropical environments, but intolerant of environmental changes, including fluctuations in temperature, nutrients, oxygen and salinity as discussed below.

2.3.3.2. Survivors

The fact that the mass extinction eliminated only ecological specialists having relatively narrow ecological habitats points to a selective mass extinction pattern. The group of 16 species (or 25%) which range into the lower Danian zones P0 and P1a are generally common to abundant ($>$80%) in the upper Maastrichtian (Fig. 5, *Heterohelix planata* to *Guembelitria trifolia*; see also Fig. 6 for ranges of small species in the 38–63-μm size fraction, Figs. 7A,B and 8). A similar number of Cretaceous species range well into the lower Danian at El Kef, El Melah and Ain Settara (16 species). These species are considered Cretaceous survivors because they have been observed to be consistently present in early Danian sediments of sections worldwide, do not show differential preservation as compared with Danian species, and many have Danian stable isotope signals (Barrera and Keller, 1990, 1994; Keller et al., 1993; MacLeod and Keller, 1994).

Among these 16 species, *Pseudoguembelina costulata*, and *Pseudoguembelina kempensis* were not previously considered survivors, but are tentatively included here because of their consistent occurrence in Danian sediments; though further studies are necessary to determine their extinction datum. All the survivor taxa are biserial (mostly heterohelicids), triserial (guembelitrids), trochospiral (hedbergellids) and planispiral (globigerinellids). Morphologically, these taxa are generally small with little or no surface ornamentation. They are geographically widespread and for the most part common to abundant. We consider them ecological generalists, able to tolerate fluctuations in temperature, nutrients, oxygen and salinity.

It is noteworthy that in the examination of the $>$63-μm size fraction, the new Danian species as well as most of the Cretaceous survivors are absent in an interval spaning part of P0 and the lowermost part of P1a (Fig. 7B) as also observed earlier at El Kef (Keller, 1988; Keller et al., 1995), ODP Site 738 (Keller, 1993) and Haiti (Keller et al., 2001). Nevertheless, in the smaller size fraction (38–63 μm) these species are common to abundant (Fig. 8, Tables 1 and 2). This reflects the dwarfing of species in environmentally stressed habitats (see MacLeod et al., 2000). However, it also illustrates that biostratigraphic and faunal turnover conclusions based solely on the > 63-μm size fraction are in error.

2.3.3.3. Opportunists

The populations of most Cretaceous survivors dramatically decline in the lower Danian zones P0 and P1a and never recover. Some Cretaceous species, however, thrive after the mass extinction of tropical and subtropical species and the decline of the ecological generalist survivors. These are the triserial *Guembelitria* species in low to middle latitudes and the biserial *Zeauvigerina waiparaensis* in high latitudes (Keller, 1993; Pardo and Keller, 1999). These biserial and triserial taxa dominated (> 95%) the faunal assemblages during the early Danian in the absence of ecological competition as a result of the mass extinction and decline of survivor species, and prior to the establishment of the newly evolving Danian assemblages.

Guembelitria species are generally present in very low abundances (< 1%) in Cretaceous faunal assemblages of normal open marine conditions and more abundant (> 10–25%) in shallow neritic near-shore environments characteristic of variable temperature, oxygen, salinity and nutrient conditions (see Keller et al., 1998). However, whenever open marine environmental conditions reach a crisis level and reduce normal population diversity they produce opportunistic blooms (e.g., K–T boundary, Cenomanian–Turonian boundary, and three blooms in the late Maastrichtian, Abramovich et al., 1998; Keller et al., 2001). In open marine conditions, such an opportunistic *Guembelitria* bloom began in zone P0 and continued through P1a, though tapering off in the later part of P1a (Keller et al., 1994; Luciani, 1997; Molina et al., 1998; Olsson and Liu 1993; Apellaniz et al., 1997). However, in near-shore shallow neritic environments, such as Seldja on the Sahara Platform or Brazos River in Texas, the *Guembelitria* blooms began in the latest Maastrichtian suggesting that adverse environmental conditions began well prior to the K–T boundary event (Keller, 1989; Keller et al., 1998).

In northern and southern high latitude sections, such as in Kazakstan and ODP Site 738, the *Guembelitria* bloom in the lower Danian is much reduced (∼20–30%) and the biserial species *Zeauvigerina waiparaensis* takes its place as the dominant opportunistic species (Keller, 1993; Pardo and Keller, 1999). *Zeauvigerina waiparaensis* Jenkins was originally considered a Danian species, but was found to be common (∼20%) in the upper Maastrichtian of Site 738 (Keller, 1993), as well as in northern high latitude sections (Pardo and Keller, 1999). Opportunistic blooms of this species began below the K–T boundary and increased to 80% in P0 and P1a. This *waiparaensis* bloom may be linked to a tolerance for low oxygen conditions in the increasingly high nutrient environment of the early Danian in high latitudes as suggested by increased Ba, a proxy for nu-

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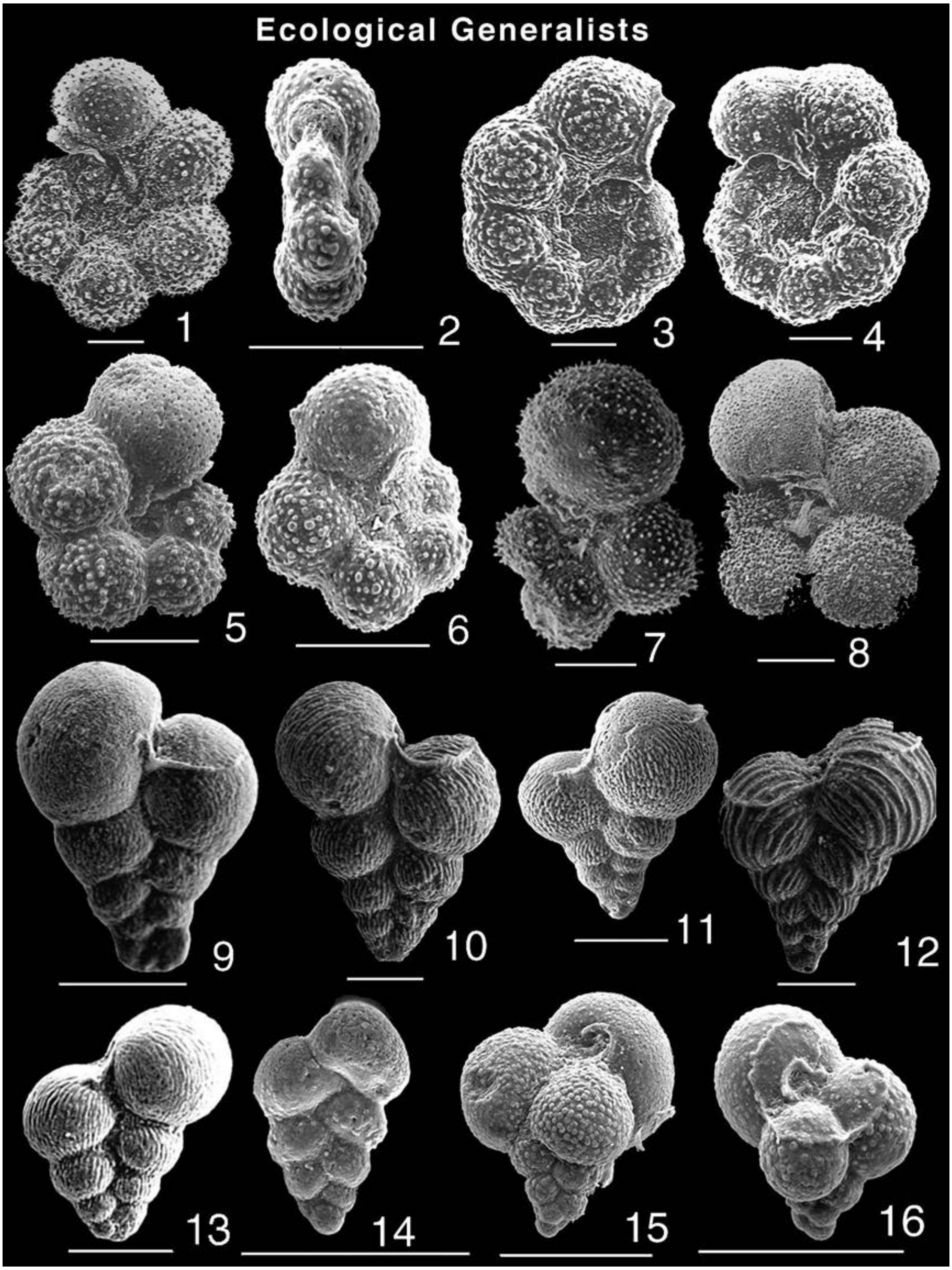
Plate I. Ecological generalists. This group is characterized by species of small morphology, weak surface ornamentation, and biserial, triserial, trochospiral or planispiral chamber arrangement. All specimens from the top 50 cm below the K–T boundary at El Kef and Ain Settara. Scale bar = 100 μm.

1, 2.	*Globigerinelloides aspera* (Bolli)
3, 4.	*Globigerinelloides yaucoensis* (Pessagno)
5, 6.	*Hedbergella monmouthensis* (Olsson)
7.	*Globotruncanella subcarinatus* Bronnimann
8.	*Globotruncanella petaloidea* Gandolfi
9.	*Heterohelix navarroensis* Loeblich
10–13.	*Heterohelix globulosa* (Ehrenberg)
14.	Heterohelix dentata Stenestad
15, 16.	*Guembelitria cretacea* (Cushman).


Ecological Generalists
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trients, and the absence of a major negative carbon-13 shift (Barrera and Keller, 1994). This species is very rare in low latitudes possibly because very low nutrient conditions prevailed in the early Danian as suggested by the 2–3‰ carbon-13 shift (Keller and Lindinger, 1989; Zachos et al. 1989; Oberhänsli et al., 1998).

2.3.3.4. K–T faunal turnover

The overall mass extinction pattern at Elles II is similar to that observed at El Kef (Keller et al., 1995), Ain Settara (Luciani, 2002), Mexico (Lopez-Oliva and Keller, 1996), Haiti (Keller et al., in preparation), Italy (Luciani, 1997), Spain (Canudo et al., 1991; Apellaniz et al., 1997) and other low latitude regions. Over two thirds of the species disappeared at or near the K–T boundary and nearly one third of the species survived into the early Danian. The K–T extinct species group (which here includes species which are rare and may have disappeared earlier) consists of ecological specialists which includes all tropical and subtropical species. These ecological specialists are generally characterized by highly ornamented, large multiserial or keeled morphologies. Their combined relative abundance is less than 20% of the total planktonic foraminiferal assemblages (Fig. 8). In contrast, the K–T survivor group consists of ecological generalists, characterized by small biserial, triserial, trochospiral or planispiral morphologies with little surface ornamentation. Ecological generalists dominate the latest Maastrichtian oceans and their combined relative abundance may exceed 80% (Fig. 8).

3. Results II

3.1. K–T paleoecology

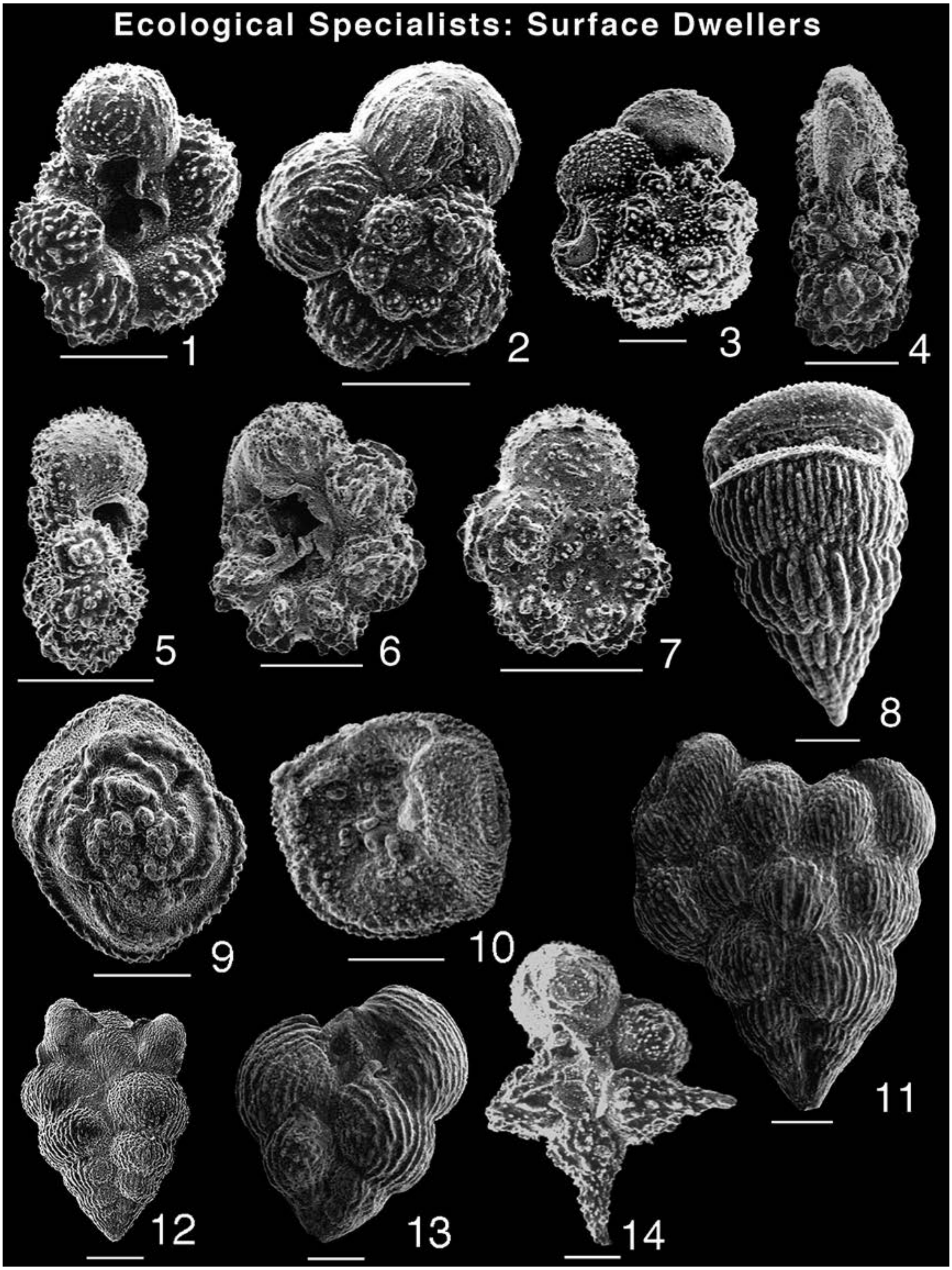
Planktonic foraminiferal assemblages of Tunisian sections representing paleodepths between inner neritic (~10–20 m, Sedja), middle neritic to outer neritic (100–250 m, Elles and Ain Settara), outer neritic to upper bathyal (200–500 m, El Kef), and predominantly upper bathyal (>250 m, El Melah, Fig. 2) reveal consistent differences between shallow restricted marine and open marine environments both before and after the K–T boundary mass extinction. Moreover, Cretaceous foraminiferal assemblages in shallow restricted and open marine environments responded differently to the environmental stresses that led to the mass extinction. In contrast, there is little difference in the evolving early Danian assemblages between open marine and shallow restricted marginal environments. A number of different proxies, including species richness, ecological generalists, specialists and opportunists, and depth ranking, can be used to evaluate the extent and nature of the K–T mass extinction.

3.1.1. Time slice selection

To facilitate comparison of the pre-K–T and post-K–T planktonic foraminiferal assemblages, two time slices were chosen. The pre-K–T time slice is represented by the top 50–100 cm of the uppermost Maastrichtian zone CF1 (*Plummerita hantkeninoides*). The entire zone CF1 is estimated to span the last 300 kyr of the Maastrichtian (part

Plate II. Ecological specialists: surface dwellers. This group is heterogeneous and includes trochospiral, biserial and multiserial taxa which are highly ornamented, of predominantly medium sized morphologies, though a few larger species are also surface dwellers. All specimens from the top 50 cm below the K–T boundary at El Kef. Scale bar = 100 μm.

1, 2.	*Rugoglobigerina rugosa* (Plumber)
3, 4.	*Rugoglobigerina scotti* Bronnimann
5–7.	*Rugoglobigerina hexacamerata* Bronnimann
8.	*Pseudotextularia deformis* (Kikoine)
9, 10.	*Rosita contusa* (Cushman)
11.	*Planoglobulina brazoensis* Martin
12.	*Pseudoguembelina hariaensis* Nederbragt
13.	*Pseudoguembelina palpebra* Bronnimann and Brown


Ecological Specialists: Surface Dwellers
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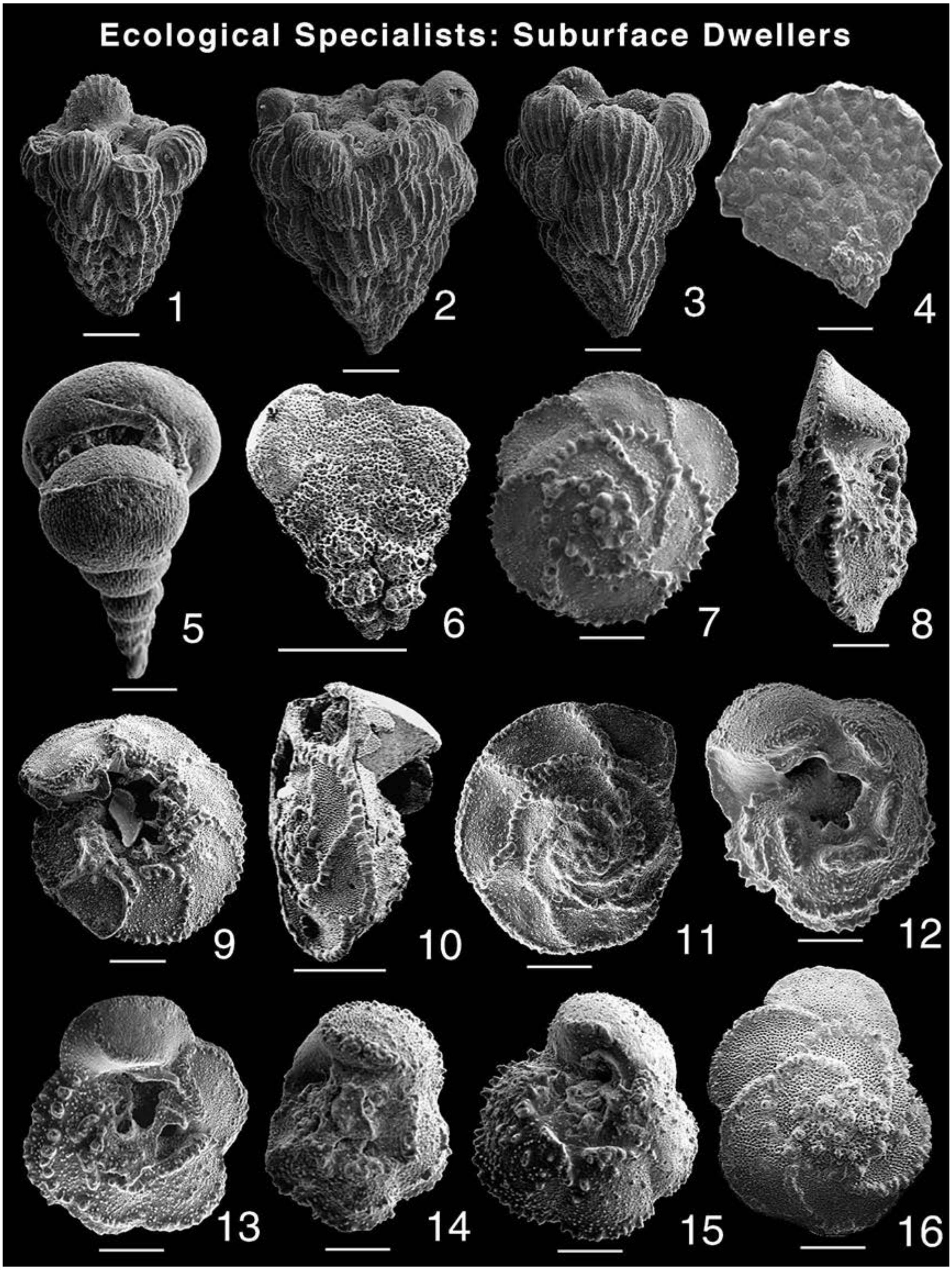
Ecological Specialists: Suburface Dwellers
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of chron 29R below the K–T boundary; Pardo and Keller, 1999) and the time slice chosen spans approximately the last 25–50 kyr of the Maastrichtian, assuming that no hiatus is present and that sediment accumulation was constant. *Plummerita hantkeninoides*, the index species for zone CF1, is easily identified and present in all low latitude sections. Within this time slice interval, relative species abundances are averaged to reduce bias of extreme fluctuations.

The post-K–T time slice is represented by the lowest Danian zones P0 and lower part of P1a (*Parvularugoglobigerina eugubina*, basal 50–100 cm of the Danian), and is estimated to span the first 50–75 kyr of the Danian (part of chron 29R above the K–T boundary), assuming constant sediment accumulation. As in the CF1 time slice, relative species abundances are averaged within this time slice to reduce bias of extreme fluctuations. Though the first Danian zone P0 represents the early Danian time slice, this thin zone commonly contains reworked Cretaceous species and may be absent or very thin (a few centimeters at Ain Settara). Reworked specimens are identified by their differential preservation, discoloration, or isolated occurrences and have been excluded in the species richness dataset.

3.2. Paleoenvironment based on species richness

Species richness (the number of species present in any given sample) is a measure of ecological diversity and is the most commonly used proxy for evaluating mass extinctions. However, this proxy makes no distinction between a species that is rare (often only one specimen), and one that is abundant. It is therefore only a first approximation of a mass extinction. For example, the presence or absence of a species in any given sample is also dependent on its numerical abundance; rare species may not be observed and their absence interpreted as extinctions (e.g., Signor–Lipps effect). Alternatively, the presence of rare and isolated specimens may be due to reworking. These problems have resulted in the controversial interpretations of sudden vs progressive mass extinction patterns.

In order to avoid this controversy, we estimate species richness for the two time slices as the maximum number of species present in any sample irrespective of where the last occurrence was noted. This means that any species which is noted only at the base of the time slice, or is an isolated occurrence, is counted as present throughout the time slice (up to the K–T boundary without consideration of the reworking potential). This will tend to exaggerate the mass extinction effect and bias it towards a more catastrophic interpretation. The alternative option of excluding these species would result in the opposite bias. Since there is no way to evaluate the true species richness, we prefer to err on the side of the maximum mass extinction effect. Any bias introduced by the presence of very rare and isolated species will be

Plate III. Ecological specialists: subsurface dwellers. This group is characterized by generally large and highly ornamented morphologies, heavily encrusted tests with nods, ridges and keels (globotruncanids, racemiguembelinids). All specimens from the top 50 cm below the K–T boundary at El Kef, except for number 4 which is from Ain Settara. Scale bar = 100 μm.

1. *Racemiguembelina intermedia* (De Klasz)
2. *Racemiguembelina fructicosa* (Egger)
3. *Racemiguembelina powelli* (Smith and Pessagno)
4. *Planoglobulina multicamerata* (Plummer)
5. *Pseudotextularia elegans* (Rzehak)
6. *Gublerina cuvilieri* Kikoine

7, 8. *Globotruncana dupeublei* Caron

9–11. *Globotruncanita stuarti* (de Lapparent)

12. *Globotruncana rosetta* (Carsey)
13. *Globotruncana arca* (Cushman)
14. *Globotruncana aegyptiaca* Nakkady

15, 16. *Globotruncana insignis* (Gandolfi)

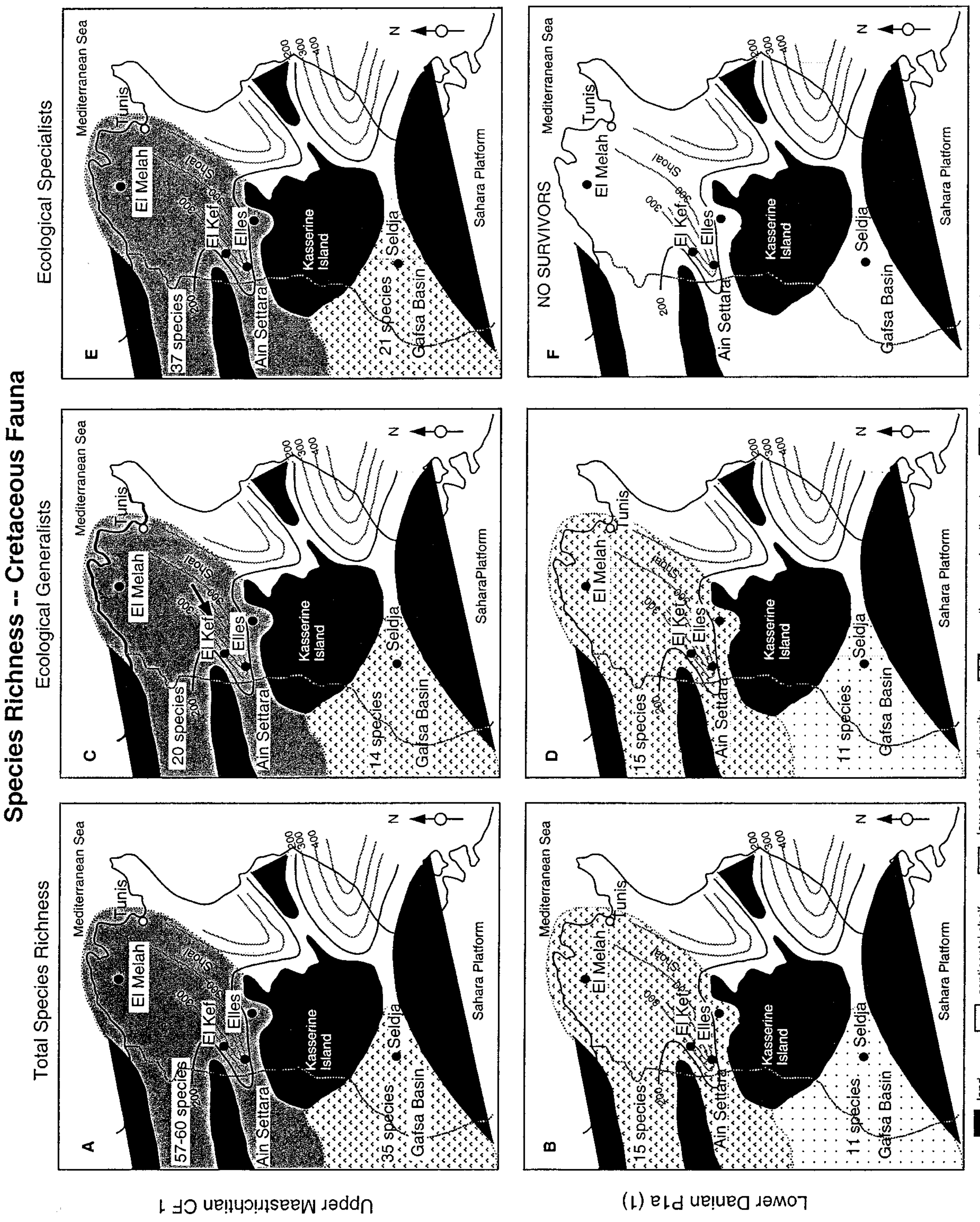
Species Richness -- Cretaceous Fauna
Total Species Richness
Ecological Generalists
Ecological Specialists
Upper Maastrichtian CF 1
Lower Danian P1a (1)
A
B
C
D
E
F
57-60 species
35 species
20 species
14 species
37 species
21 species
15 species
11 species
NO SURVIVORS
Mediterranean Sea
Tunis
El Melah
El Kef
Elles
Ain Settara
Seldja
Gafsa Basin
Kasserine Island
Sahara Platform
Shoal
200
300
400
N
land
continental shelf
low species diversity
medium species diversity
high species diversity

Fig. 9. K–T paleobiogeography of Tunisia based on species richness of Cretaceous planktonic foraminifera of inner neritic, middle and outer shelf and upper bathyal environments. Pre- and post-K–T environments are compared based on averaged samples of time slices in the upper zone CF1 (last 25–50 kyr of Maastrichtian) and earliest Danian zone P1a(1) (lower *Parvularugoglobigerina eugubina* zone, first 50–75 kyr of Danian. (Age estimates are based on the assumption of constant sedimentation rates and no hiatus.) Note that the major faunal changes in each species richness group occurred across the K–T boundary with no survivors among ecological specialists. In contrast, ecological generalists (e.g., small heterohelicids, hedbergellids, globigerinellids and guembelitrids) suffered the least with about 25% extinct at this time.

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obvious in the biogeographic distribution of the relative abundances of all species extinct.

3.2.1. Species richness patterns

Near the end of the Maastrichtian (zone CF1), planktonic foraminifera in middle neritic to upper bathyal depths are diverse averaging 57–60 species with no significant differences (Fig. 9A). In contrast, the restricted shallow marine environment of the Gafsa Basin has a lower diversity of 35 species, 17 of which are present in most samples. Another 18 species, which include predominantly open marine surface and subsurface dwellers (e.g., globotruncanids (*Globotruncana arca, Globotruncana esnehensis, Globotruncana aegyptiaca, Globotruncanita stuarti, Globotruncana rosetta*), *Gublerina robusta, Racemiguembelina fructicosa, Rugoglobigerina scotti*, Keller et al., 1998) are present in few samples. The presence of these latter taxa in the Gafsa Basin is likely due to a marine incursion as a result of a rising sea level (climate warming in chron 29R; see Li and Keller, 1998c), or local tectonic activity of the Kasserine Island.

In the early Danian P1a(1) (lower part of *Parvularugoglobigerina eugubina* range, Fig. 4), Cretaceous species richness of open marine environments was reduced to about 15 species (Fig. 5) and in shallow restricted marine environments to about 11 species (Fig. 9B). In both environments, however, the Cretaceous species assemblages are similar consisting of heterohelicids, globigerinellids, guembelitrids and hedbergellids. Thus there was a greater mass extinction in open marine environments than in near-shore environments, and extinctions were selective as is evident when species richness is divided by ecological proxies.

3.2.2. Ecological generalists

This group includes a relatively small number of species having a nearly global paleogeographic range (~15–20 species, including heterohelicids, globigerinellids, hedbergellids, globotruncanellids and guembelitrids, Plate I). All of these species are of relatively small size and simple morphology, and their tests have little or no surface ornamentation. During the late Maastrichtian, the small biserial heterohelicids (*Heterohelix globulosa, Heterohelix navarroensis, Heterohelix dentata*) generally dominated (70–80%) planktonic foraminiferal assemblages and hedbergellids were common. In the early Danian, many of these species were consistently present, though reduced to a few percent and generally dwarfed (~30–50% smaller than Cretaceous populations; Keller, 1988; MacLeod et al., 2000). The exception are the triserial *Guembelitria* species which were rare in open marine environments during the Maastrichtian, but common to abundant in shallow restricted environments, and dominated both open marine and shallow restricted environments in the early Danian. The consistent presence of these Cretaceous species in early Danian sediments in Tunisian sections, as well as globally (MacLeod and Keller, 1994), indicates that these species were survivors (see discussion above) as well as ecological generalists able to tolerate significant fluctuations in temperature, salinity, oxygen and nutrients.

Species richness of ecological generalists in the latest Maastrichtian CF1 zone averaged 20 species in open marine and 14 species in restricted shallow marine environments (Fig. 9C,D). In the early Danian P1a(1) zone, 15 and 11 species were present in these environments respectively. Thus, when viewed solely on the basis of species extinctions (ignoring the relative abundances of species), the mass extinction had a relatively small effect on ecological generalists. Moreover, there appears to have been no significant difference in the species

Table 3
Depth ranking of planktonic foraminifera based on stable isotopes (+) and morphology

Surface			Subsurface		
ΔΩ	*Guembelitria*	*cretacea*+	Δ	*Heterohelix*	*glabrans*+
ΔΩ		*danica*	Δ		*planata*+
ΔΩ		*irregularis*+	Δ		*pulchra*+
ΔΩ		*trifolia*+	Δ	*Globotruncanella*	*petalloidea*+
ΔΩ	*Heterohelix*	*globulosa*+*	Δ		*subcarinatus*+
ΔΩ		*dentata**	◇	*Globotruncana*	*aegyptiaca*+
ΔΩ		*navarroensis*+	◇		*arca*+
Δ		*labellosa*	◇		*conica*+
Δ?		*punctulata*	◇		*falsostuarti*+
Δ		*striata*+	◇		*duwi*
Δ	*Pseudoguembelina*	*costulata*+	◇		*dupeublei*
		excolata+	◇		*insignis*
Δ?		*kempensis*	◇		*mariei*
◇		*palpebra*+	◇		*rosetta*
◇		*hariaensis*	◇	*Globotruncanita*	*angulata*+
◇	*Planoglobulina*	*brazoensis*+	◇		*conica*+
◇		*carseyae*	◇		*stuarti*+
◇	*Pseudotextularia*	*deformis*+	◇		*stuartiformis*+
◇	*Rosita*	*contusa*+	◇	*Abathomphalus*	*mayaroensis*+
◇	*Rugoglobigerina*	*rugosa*+	◇		*intermedius*
◇		*rotundata*+	◇	*Globotruncanella*	*citae*+
◇		*scotti*+	◇	*Rosita*	*patelliformis*
◇		*hexacamerata*	◇		*plicata*
Δ?		*macrocephala*	◇		*walfishensis*
◇		*milamensis*	◇	*Pseudotextularia*	*elegans*+
◇		*pennyi*	◇	*Racemiguembelina*	*fructicosa*+
◇		*reicheli*	◇		*powelli*+
◇	*Plummerita*	*hantkeninoides*	◇		*intermedia*+
			◇	*Planoglobulina*	*multicamerata*
			◇	*Gublerina*	*acuta*+
			◇		*cuvilieri*+
			◇		*robusta*
Surface or subsurface					
Δ	*Hedbergella*	*monmouthensis*+*			
Δ		*holmdelensis*+*			
ΔΩ	*Heterohelix*	*globulosa*+*			
ΔΩ		*dentata**			
Δ	*Globigerinelloides*	*aspera*+			
Δ		*yaucoensis*			
Δ		*volutus*			

Some species may have adapted to surface waters in shallow environments and subsurface waters in deeper open marine environments as indicated by their isotopic ranking as well as geographic distribution (*). Species are grouped into ecological generalists (Δ) able to tolerate wide variations in temperature, salinity, oxygen and nutrients; some of these can be classified as ecological opportunists (Ω) able to thrive in adverse conditions; ecological specialists (◇) are adapted to narrowly restricted environments and include most tropical-subtropical species, but also some taxa thriving in higher latitudes.

extinction rate between open marine and shallow restricted environments. Ecological generalists that disappeared at or near the K–T boundary included various small heterohelicids (e.g., *Heterohelix carinata, Heterohelix moremani, Heterohelix pulchra, Heterohelix labellosa, Heterohelix striata*).

3.2.3. Ecological specialists

This proxy includes all tropical and subtropical

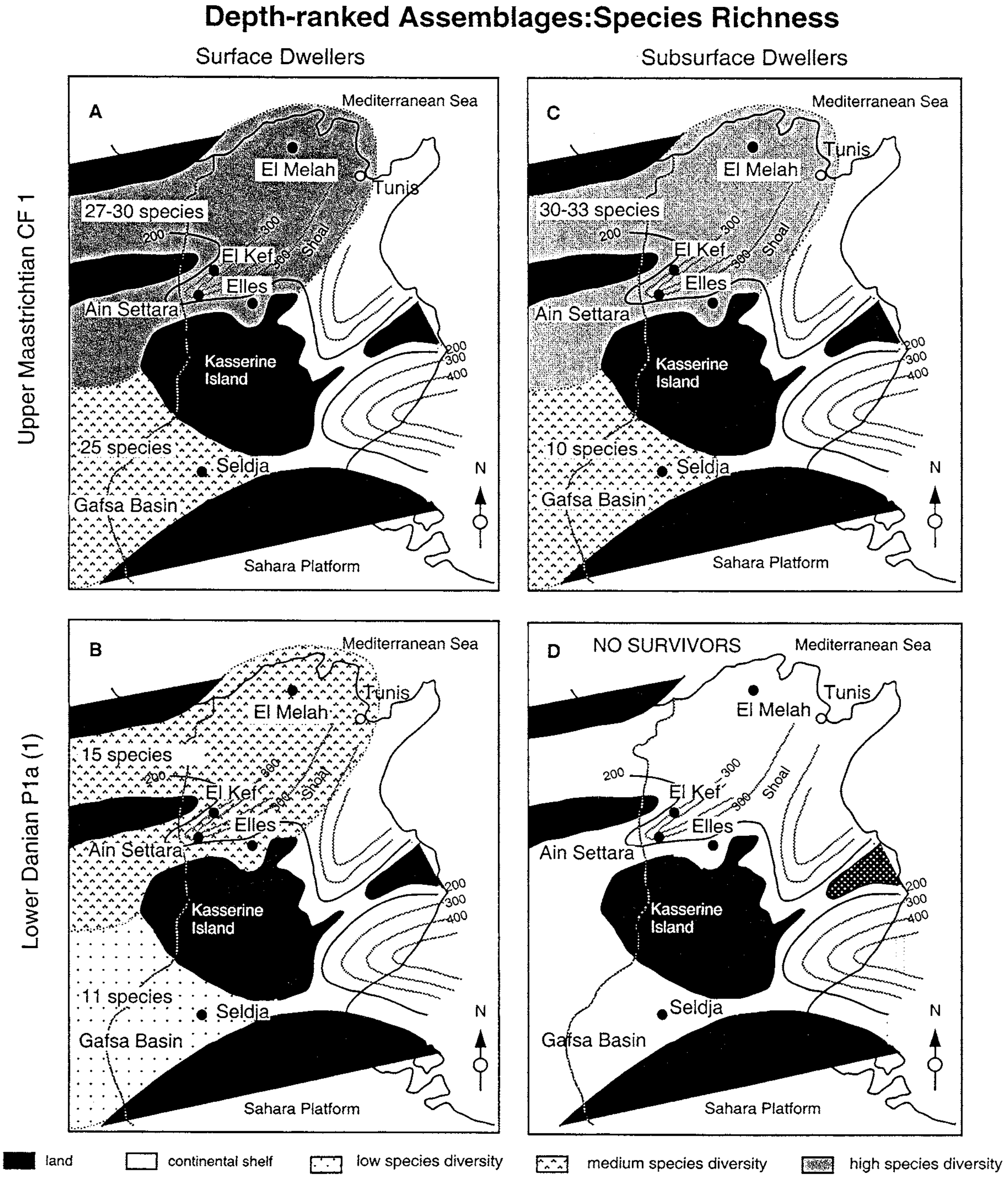

Fig. 10. K–T paleobiogeography of Tunisia based on depth ranked species richness of planktonic foraminifera (see Fig. 9 for complete caption). Note that only surface dwellers survived the K–T mass extinction in either open marine or restricted marginal marine environments.

species (Plates II and III). They are characterized by restricted paleogeographic range and generally narrow tolerance limits for temperature, salinity, oxygen and nutrients. Ecological specialists are generally of large size, complex morphology, and with highly ornamented tests; they may have keels, ridges, spines, and generally large numbers of chambers, large apertures, and most have heavily calcified tests (e.g., globotruncanids, racemiguembelinids, planoglobulinids, rugoglobigerinids, pseudotextularids, Plates II and III). None of these species dominate foraminiferal population during the Maastrichtian and their relative abundances were generally less than 5% (Li and Keller, 1998a,b). The diversity of ecological specialists was highest in tropical and subtropical environments, but these species may have migrated outside these regions during times of climate warming. As a result, they may be found as temporary incursions into higher latitudes during warm climates.

During the latest Maastrichtian zone CF1, species richness was dominated by ecological specialists (∼60%). An average of 37 ecological specialist species were present in open marine environments and 21 in the shallow Gafsa Basin (Fig. 9E,F), but only four of these were consistently present (Fig. 9E, *Plummerita hantkeninoides, Rugoglobigerina reicheli, Rugoglobigerina rugosa, Planoglobulina carseyae*, Keller et al., 1998). The other 17 species were sporadically present and probably reflect marine incursions. There were no survivors in this group; all disappeared at or before the K–T boundary. This pattern characterizes the highly selective nature of the mass extinction in planktonic foraminifera.

3.2.4. Species depth ranking

Depth ranking of species into surface and subsurface (thermocline and deeper dwellers) based on stable isotopes is a proxy for watermass stratification. Species can be depth ranked based on their stable isotope values, though less than half of the Maastrichtian species have been isotopically depth ranked at this time; for the remaining species, depth ranking has been inferred from morphological characteristics, which is therefore more subjective (Table 3; discussion in Li and Keller, 1998a).

3.2.5. Ecological generalists – surface or subsurface dwellers?

Most ecological generalists are surface dwellers, or able to live in either surface or subsurface conditions depending on the marine environment. Such species include the ecological generalists *Heterohelix globulosa* and *Heterohelix dentata,* and possibly also *Hedbergella holmdelensis*, *Hedbergella monmouthensis* and *Globigerinelloides yaucoensis*. Other species which may also fall into this group include the small, flat and thin-walled heterohelicids *Heterohelix glabrans, Heterohelix. planata*, and *Heterohelix pulchra*, and the small planispiral *Globigerinelloides aspera, Globigerinelloides volutus*, *Globotruncanella subcarinatus* and *Globotruncanella petaloidea*. Taxa which are primarily considered as surface dwellers are marked with an asterisk in Table 3 and included as surface dwellers in Fig. 10.

3.2.6. Surface dwellers – ecological specialists

This group is distinct from the surface dwelling ecological generalists by their larger size, more complex and ornamented morphology, and generally restricted paleogeographic distribution. They are distinct from subsurface dwellers in that they include generally smaller morphologies, less heavily ornamented and thinner tests (e.g., all rugoglobigerinids, some large biserial species), and no heavily calcified thickened keels (Plate II). However, there are exceptions; some keeled forms such as *Rosita contusa* are isotopically light and hence surface dwellers.

Surface dwellers, with ecological specialists and generalists combined, were nearly half of the species assemblage (27–30 species) in open marine environments during the late Maastrichtian in Tunisia suggesting a well-stratified water column. Though in the restricted Gafsa Basin, surface dwellers dominated with 25 out of a maximum of 30 species (Fig. 10A). But 11 of the surface dwellers were rare and only sporadically present (Keller et al., 1998). They probably reflect an influx of open marine species with periodic marine incursions into the shallow Gafsa Basin.

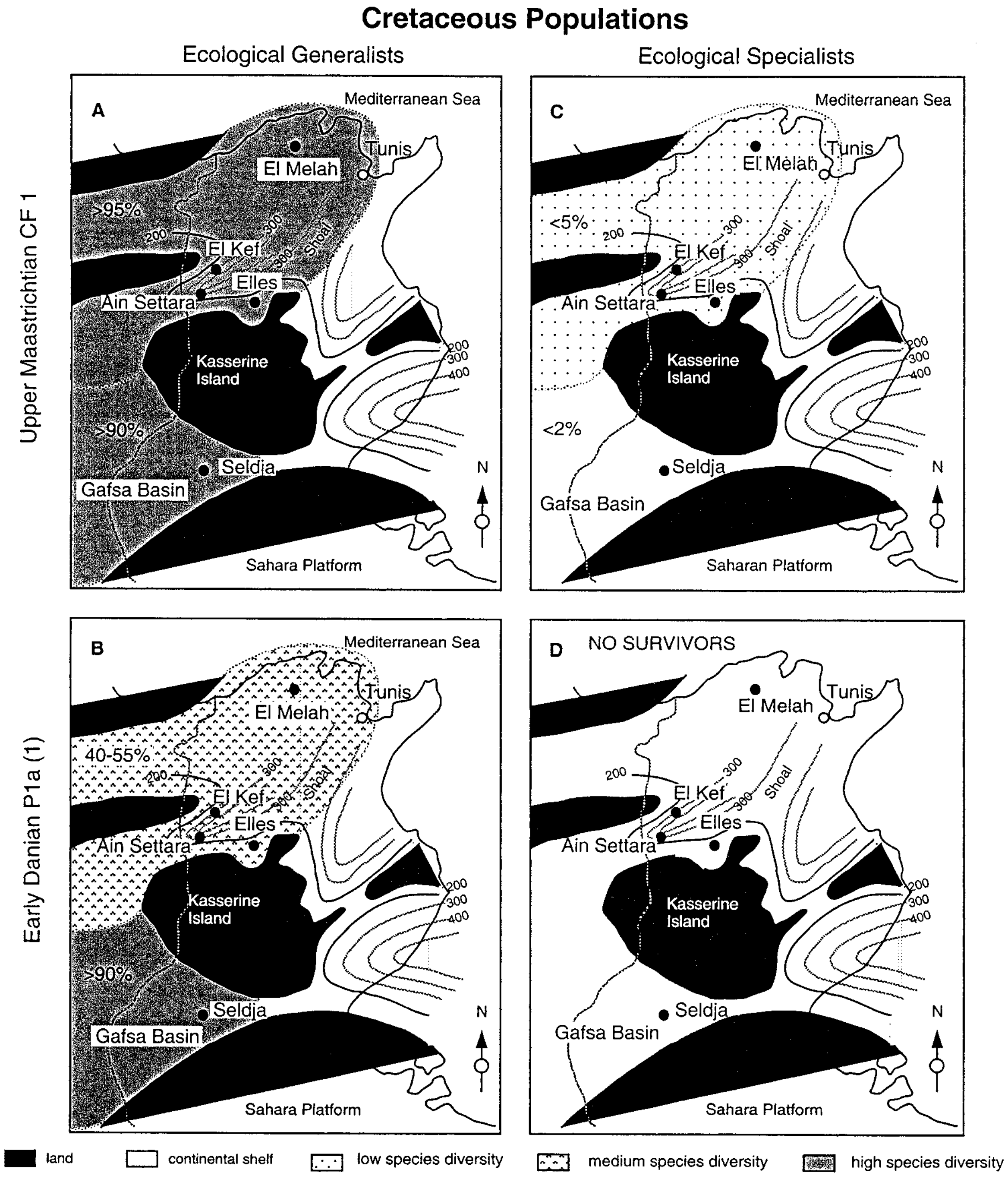

Fig. 11. K–T paleobiogeography of Tunisia based on relative percent abundances of Cretaceous planktonic foraminiferal populations grouped into ecological generalists and ecological specialists (see Fig. 9 for complete caption). Note that ecological specialists were rare (< 5%) near the end of the Maastrichtian and did not survive the K–T boundary event, whereas ecological generalists were abundant before and after the K–T event.

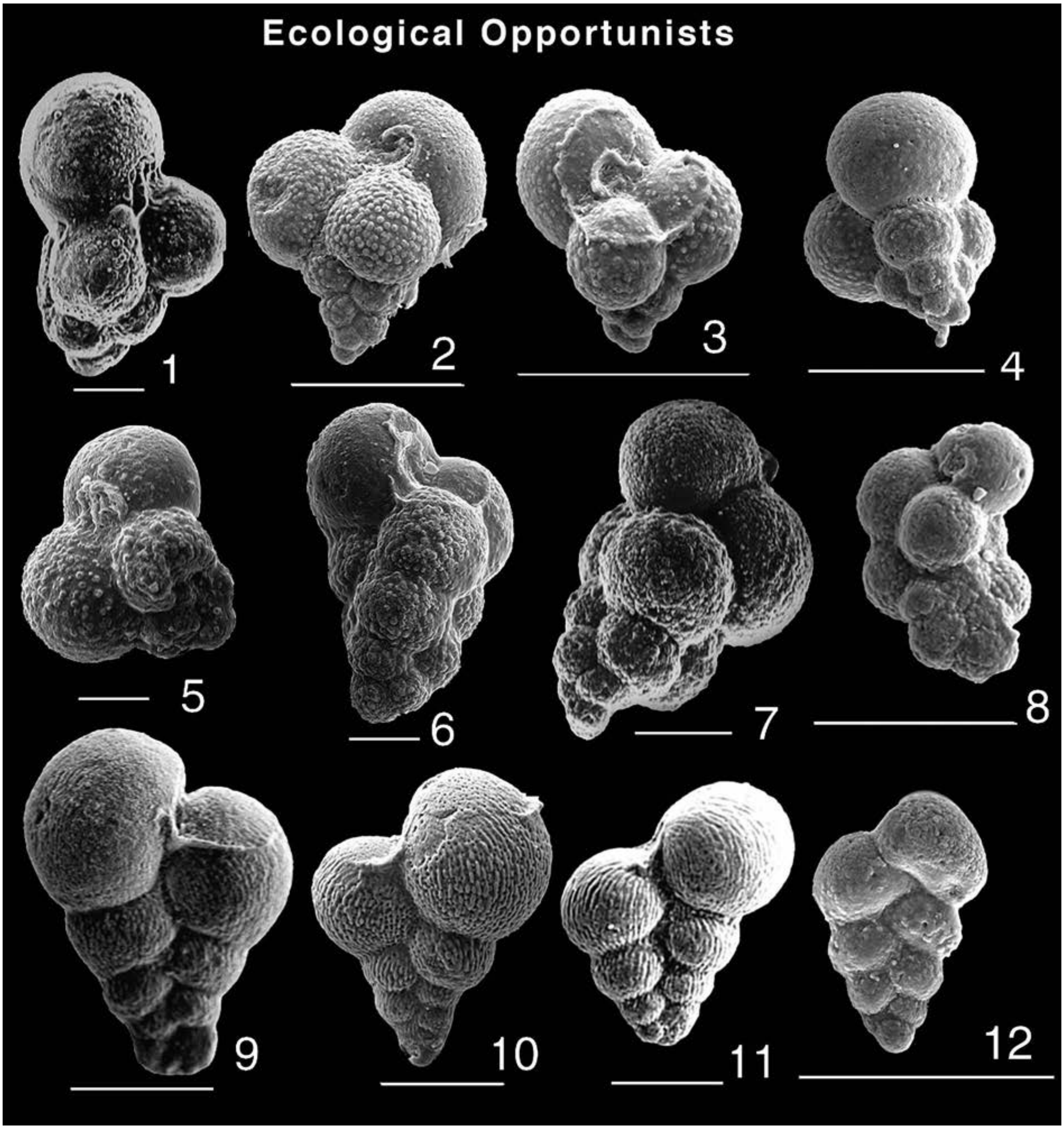

Plate IV. Ecological opportunists. This group is characterized by the triserial guembelitrids and small biserial heterohelicids. Both morphotypes are small, thin-walled and have little or no surface ornamentation. All specimens from zone P0 at El Kef and Ain Settara. Scale bar = 100 μm.

1–5.	*Guembelina cretacea* (Cushman)
6.	*Guembelina danica* (Hofker)
7, 8.	*Guembelina irregularis* (Morozova)
9.	*Heterohelix navarroensis* Loeblich
10, 11.	*Heterohelix globulosa* (Ehrenberg)
12.	*Heterohelix dentata* Stenestad

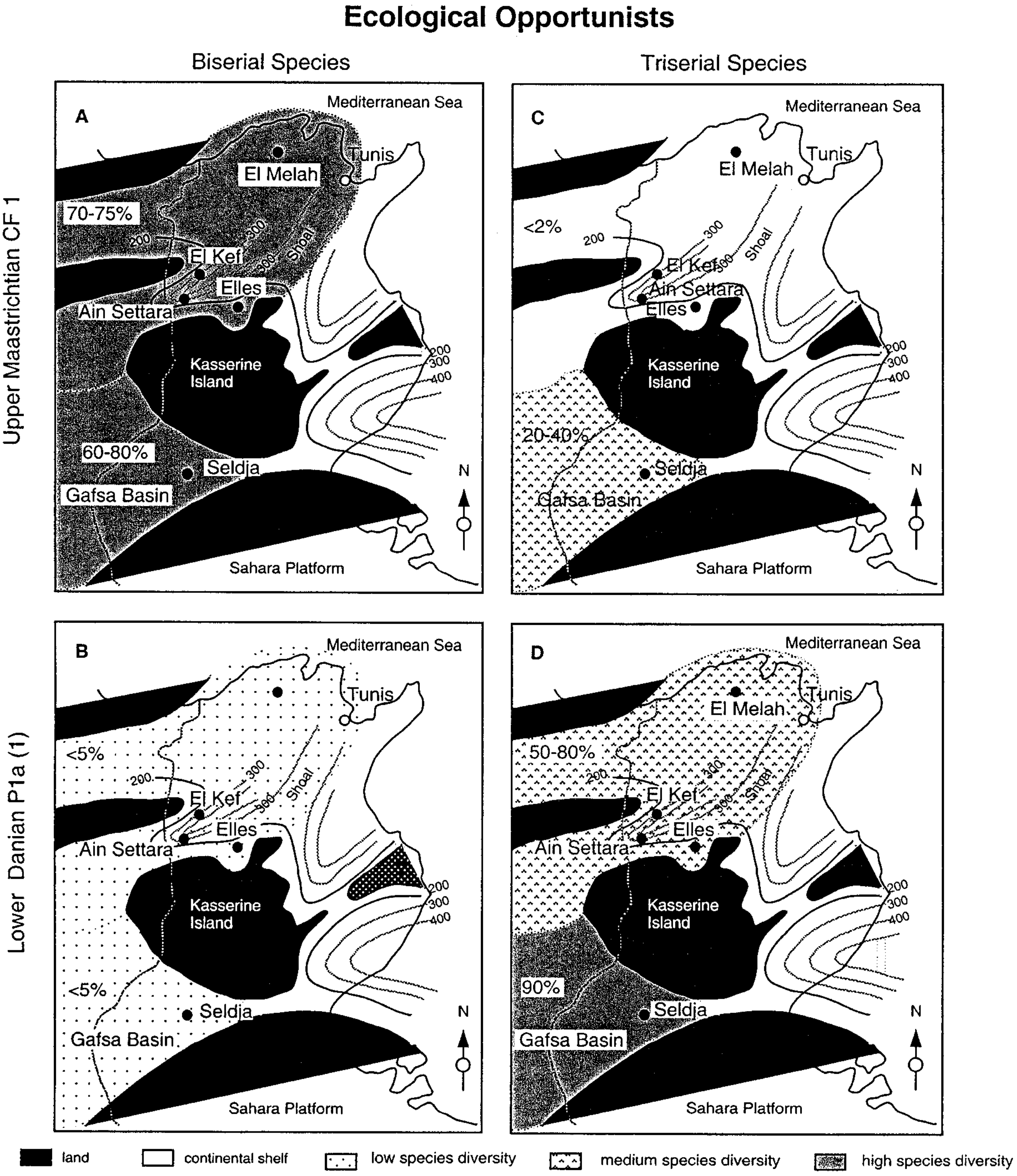

Fig. 12. K–T paleobiogeography of Tunisia based on ecological opportunists grouped into biserial (heterohelicids) and triserial (guembelitrids) populations (see Fig. 9 for complete caption). Note that biserials dominated the latest Maastrichtian with less than 5% surviving into the early Danian. Opportunistic triserial species thrived only in shallow marginal marine environments during the latest Maastrichtian, but dominated both open marine and restricted marginal settings in the early Danian.

Fig. 13. K–T paleobiogeography of Tunisia based on relative percent abundances of depth ranked assemblages grouped into surface and subsurface dwellers (see Fig. 9 for complete caption). Note that surface dwellers dominated (>90%) before and after the K–T event, whereas relatively few (5–10%) subsurface dwellers were present in open marine environments and none survived the K–T event.

During the early Danian zone P1a(1), as many as 15 Cretaceous species, all of them surface dwellers and ecological generalists of the genera *Heterohelix, Guembelitria, Hedbergella*, *Globigerinelloides* and *Pseudoguembelina* (*Pseudoguembelina costulata*) may have survived in open marine environments (Fig. 10B, Table 3). Eleven of these species may also have survived in the restricted Gafsa Basin; the exception are the globigerinellids which were rare and may not be survivors in this environment (Keller et al., 1998).

3.2.7. Subsurface dwellers – ecological specialists

Subsurface dwellers are a distinct group characterized by their heavily calcified tests with extra calcite in test ornamentation, thickened keels and large size (Plate III). This group includes most globotruncanids, all racemiguembelinids and various other large biserial and multiserial taxa (Table 3). As noted above, a few ecological generalists may have been subsurface dwellers. These species are generally small and thin-walled and may have been able to adapt to either surface or subsurface environments (Table 3).

During the latest Maastrichtian zone CF1, subsurface dwellers (including ecological generalists) were slightly more diverse than surface dwellers in the open marine environments of Tunisia (Fig. 10C). This suggests a well-stratified water column. But there were only 10 subsurface dwelling species in the Gafsa Basin and all of these were rare or sporadically present, suggesting periodic marine incursions. There were no survivors in this group in the early Danian in either open marine or restricted shallow environments (Fig. 10D). This indicates that surface dwellers, and particularly the ecological generalists among them, were generally more adapted for survival, probably because of their greater tolerance for changes in temperature, oxygen, nutrients and salinity.

3.3. Paleoecology based on relative species abundances

Overall, the relative percent abundance of a species or species group is a better proxy of environmental change than the presence or absence of a species or species group. This is evident in a comparison of the two types of proxies. For example, the strong species richness trends observed among ecological generalists and specialists, or surface and subsurface dwellers, are even more pronounced when the relative percent abundances of the species are taken into consideration.

3.3.1. Generalists versus specialists

During the latest Maastrichtian zone CF1, the relative abundance of ecological generalists in open marine and restricted shallow basin environments averaged over 95% of the total planktonic foraminiferal assemblages. In contrast, ecological specialists (including surface and subsurface dwellers) averaged less than 5% in open marine, and $<2\%$ in the Gafsa Basin (Fig. 11A,C). This indicates that already prior to the K–T boundary event, ecological specialists were a rare and endangered group with very high diversity and very low numerical abundance. These overspecialized species were thus prone to extinction.

During the early Danian zone P1a(1) Cretaceous ecological generalists decreased to 40–50% in open marine environments (Fig. 11B), and the remaining assemblage consisted of the evolving early Danian species. In the shallow restricted Gafsa Basin, the Cretaceous ecological generalists remained dominant ($>90\%$). Ecological specialists did not survive (Fig. 11D). This indicates that although the K–T mass extinction was restricted to ecological specialists, most Cretaceous generalists also died out, though much later in the early Danian. Species populations of generalists declined dramatically in open marine environments, but not in the restricted shallow Gafsa Basin. Though this generalization is somewhat misleading as is evident when the ecological generalist group is further evaluated below.

3.3.2. Ecological opportunists

Ecological generalists were dominated by two groups of ecological opportunists: (a) the small biserial heterohelicids generally tolerant of low-oxygen environments (*Heterohelix globulosa, Heterohelix dentata, Heterohelix navarroensis, Pseudoguembelina costulata*) and (b) the very small triserial guembelitrids (*Guembelitria cretacea, Guembelitria trifolia, Guembelitria irregularis,* *Guembelitria danica*) generally thriving in high stress near-shore environments (Plate IV). Using these two groups as proxies reveals that the biserial opportunists dominated both in open marine (70–75%) and shallow restricted basins (60–80%) in Tunisia, but relative abundances are more variable in the latter (Fig. 12A). All biserials suffered strong declines in the early Danian (from 70–75% to < 5%, Fig. 12A,B) and all were extinct by the end of P1a or in P1c (MacLeod and Keller, 1994). This suggests that a well-stratified ocean prevailed in CF1 with a well-developed oxygen minimum zone, but in the early Danian this ecological niche was reduced probably as a result of a cooler well-mixed watermass.

The triserial opportunists are also revealing. During the latest Maastrichtian CF1 they were rare (< 2%) in open marine environments, but rather abundant in the shallow restricted Gafsa Basin (20–40%, Fig. 12C). But in the early Danian P1a(1) (and particularly zone P0) they dominated, though still maintained a preference for shallow near-shore environments (90%) as compared to open marine (50–80%, Fig. 12D). The amplitude difference in the fluctuations is probably due to greater competition with evolving Danian species in more open marine environments. The preferred environmental conditions of triserial guembelitrid species are not yet well understood, though there appears to be a high tolerance for salinity, nutrient and temperature fluctuations. In the Gafsa Basin guembelitrid dominance is associated with a warm humid climate, high rainfall, low salinity and high organic matter influx (Keller et al., 1998).

3.3.3. Relative abundances in depth ranked assemblages

The overall percent abundance of surface dwellers during the latest Maastrichtian was nearly the same in open marine (90–95%) and the restricted Gafsa Basin (98%) and this group continued its relative abundance into the early Danian (Fig. 13A,B). As noted above, surface dwellers before and after the K–T boundary were dominated by different opportunistic taxa: the low oxygen tolerant heterohelicids thrived in open marine environments and the guembelitrids thrived in shallow marginal marine environments. Although this proxy suggests there was little change in the relative abundance of surface dwellers across the K–T boundary, in fact, guembelitrids replaced heterohelicids (see Fig. 12). In contrast, subsurface dwellers were a minor component of open marine (5–10%) environments during the latest Maastrichtian and there were no survivors in the early Danian (Fig. 13C,D).

Surface and subsurface dwellers thus reflect relatively consistent high stress environments in open marine as well as shallow restricted basin environments before and after the K–T boundary. Ecological opportunists suggest that in open marine environments high stress conditions probably included an expanding oxygen minimum zone, whereas in shallow restricted basins they included salinity, temperature and nutrient fluctuations.

4. Discussion

4.1. Species survivorship and reworking

Foraminiferal experts generally agree that a major mass extinction occurred across the K–T boundary in low to middle latitudes. But they disagree about the nature of the mass extinction pattern. Some workers contend that all but one to three species became extinct as a result of the bolide impact and that the presence of other Cretaceous species in Danian sediments is due to reworking (e.g., Olsson and Liu, 1993; Peryt et al., 1993; Olsson, 1997). Other workers contend that many more species survived, though they also agree that reworking is significant in Danian sediments (e.g., MacLeod, 1996a,b; Luciani, 1997).

The survivorship of Cretaceous species has been discussed in many publications (MacLeod and Keller, 1994; MacLeod, 1996c; Keller, 1996), and also addressed in the El Kef blind test (e.g., MacLeod, 1996a,b; Canudo, 1997; Masters, 1997; Orue-Etxebarria, 1997; Keller, 1997; Olsson, 1997; Smit and Nederbragt, 1997). At issue here is not whether many Cretaceous species are present in Danian sediments; nearly all workers have reported their presence, but whether they are survivors or reworked. Keller (1988) first noted that at El Kef the large ornamented tropical species disappeared at or near the K–T boundary, whereas the small weakly ornamented ecological generalists ranged well into the lower Danian zone P1a and appeared to be K–T survivors (see also Keller et al., 1995). Since that time, this pattern has been substantiated in many low latitude sections worldwide and the question is no longer whether, but how many, of the ecological generalists survived. Current estimates range from as low as three to five (Smit and Nederbragt, 1997; Olsson, 1997) to as many as 16 species (e.g., MacLeod and Keller, 1994; Luciani, 1997, 2002; Apellaniz et al., 1997; Molina et al., 1998; Pardo et al., 2002; Karoui-Yaakoub et al., 2002).

Cretaceous species survivorship is also substantiated based on carbon and oxygen isotope measurements of species. In low latitudes, where the carbon isotope shift is between 2–3‰ across the K–T boundary, many Cretaceous species that lived in the Danian have a significantly greater negative isotopic shift than those that lived in the Maastrichtian (e.g., Barrera and Keller, 1990, 1994; Keller et al., 1993). At higher latitudes, where the carbon isotopic change is small, this test is less reliable. In these sections, the continued and consistent presence of certain Cretaceous species in Danian sediments, but absence of others, is a good indicator of survivorship.

However, the stable isotope test for species survivorship has its pitfalls and must be applied with great care. For example, recently Kaiho and Lamolda (1999) claimed that, based on stable isotope measurements of individual species at Caravaca, Spain, there is no evidence of Cretaceous species survivorship. Details of their data, however, reveal that the specimens analyzed were taken within the first 5 cm of the Danian zone P0 at three intervals: at the K–T boundary, at 2 cm and 5 cm above the boundary. This interval (zone P0) contains an abundance of reworked Cretaceous species as discussed by Canudo et al. (199l). Moreover, numerous studies have shown that the basal Danian zone P0 almost always contains many reworked Cretaceous specimens, which generally cannot be distinguished from in situ specimens, and hence should be avoided when testing for Cretaceous survivors. Kaiho and Lamolda (1999) thus unwittingly analyzed reworked Cretaceous specimens and correctly obtained a Cretaceous signal which they correctly interpreted as reworked. But they incorrectly concluded that their analysis of these reworked specimens provided evidence against survivorship of Cretaceous species and for a catastrophic mass extinction of nearly all species at the K–T boundary.

During the last decade, the argument for significant survivorship among Cretaceous ecological generalists into the Danian (Keller, 1988, 1989; Keller et al., 1995) has gained much support, largely due to the accumulation of a global empirical database that documents the consistent presence of Cretaceous ecological generalists in the Danian (MacLeod and Keller, 1994; Keller, 1993; MacLeod, 1996a,b; Luciani, 1997, 2002; Apellaniz et al., 1997; Molina et al., 1998). In addition, Tertiary stable isotope signals obtained from individual Cretaceous species in Danian sediments have provided convincing evidence of survivorship for many species (Barrera and Keller, 1990; Keller et al., 1993). Although there is still no agreement as to the total number of species that survived, about 15 species may now be counted as K–T survivors (*Globotruncanella subcarinatus, Globigerinelloides aspera, Heterohelix globulosa, Heterohelix complanata (=Heterohelix lamellosa), Heterohelix navarroensis, Heterohelix dentata, Heterohelix planata, Hedbergella monmouthensis, Hedbergella holmdelensis, Pseudoguembelina costulata, Pseudoguembelina kempensis (?), Guembelitria cretacea, Guembelitria trifolia, Guembelitria danica, Guembelitria irregularis)*.

4.2. Pre-K–T extinction?

Still highly controversial is the pre-K–T species extinction pattern and, in fact, some workers question whether there is any foreshadowing of the boundary extinction event (Smit, 1982, 1990; Olsson and Liu, 1993; Molina et al., 1998; Apellaniz et al., 1997; Luciani, 1977). It is generally argued that the species which are shown to disappear below the K–T boundary at Elles I and II and also at El Kef I and II, are simply extremely rare, but in fact survived up to the boundary event. A time-consuming multiple hour search for each of these species in a sample just below the K–T boundary by two El Kef blind test investigators is reported to have revealed at least one specimen of each species (Olsson, 1997; Orue-Etxebarria, 1997). It is suggested that these rare occurrences of isolated specimens at the K–T boundary prove that these species also survived up to the K–T boundary event. However, no consideration has been given to the fact that isolated specimens may equally well be present due to reworking as is evident at Elles I and Elles II in the foraminiferal packstone. Even though the reworking argument is generally rejected for isolated specimens below or at the K–T boundary, this same argument is commonly used to interpret the presence of Cretaceous species in Danian sediments as reworked.

In our paleobiogeographic distribution study we avoided arguments regarding pre-K–T extinctions by taking the worst-case scenario, namely that all species present in the CF1 time slice interval were extinct by K–T boundary time. The argument regarding pre-K–T extinctions is unlikely to be solved based on the narrow interval of 50–100 cm below and above the boundary that most workers choose to analyze and we used in this study. Few workers have examined the environmental and faunal changes during the late Maastrichtian. Though, stable isotope studies demonstrate profound climatic changes during the last 500 kyr of the Maastrichtian with maximum cooling near the chron 30N/29R boundary about 500 kyr before the K–T boundary followed by rapid 3–4°C warming between 200 and 400 kyr before the K–T boundary and cooling during the last 200 kyr of the Maastrichtian (Stott and Kennett, 1990; Barrera, 1994; Li and Keller, 1998a,b). Recent studies by Li and Keller (1998a,c) at El Kef and DSDP Site 528, by Abramovich et al. (1998) in Israeli sections and at Elles II have demonstrated major biotic turnovers that mark the progressive biotic effects associated with these rapid climatic changes.

5. Conclusions

Paleoecologic patterns of the K–T mass extinction in planktonic foraminifera in Tunisia, spanning environments from open marine upper bathyal, to shelf and shallow marginal settings, indicate a surprisingly selective and environmentally mediated mass extinction. This selectivity is apparent in all of the environmental proxies used to evaluate the mass extinction, including species richness, ecological generalists, ecological specialists, surface and subsurface dwellers, whether based on the number of species or the relative percent abundances of species. The following conclusions can be reached for shallow to deep environments:

- About three quarters of the species disappeared at or near the K–T boundary.
- Only ecological generalists, able to tolerate wide variations in temperature, nutrients, salinity and oxygen, survived.
- Among the ecological generalists, only surface dwellers survived.
- Ecological opportunists survived (biserial and triserial morphotypes).
- Only selected ecological opportunists survived.
- Opportunistic biserial species thrived during the latest Maastrichtian in well stratified open marine settings, but dramatically declined in relative abundances in the early Danian.
- Opportunistic triserial species thrived only in shallow marginal marine environments during the latest Maastrichtian, but dominated both open marine and restricted marginal settings in the early Danian.

This highly selective mass extinction pattern reflects dramatic changes in temperature, salinity, oxygen and nutrients across the K–T boundary in the low latitude Tethys ocean. Are these environmental changes solely the result of a major meteor or comet impact on Yucatan at the K–T boundary? Or are they the cumulative result of rapid climatic changes, major volcanism and impact(s) across the K–T transition? Though an answer to these questions is beyond the scope of this study, the single impact scenario can not explain why the ecosystem did not recover for several hundred thousand years after the K–T boundary, or why high stress conditions began long before the K–T boundary. New studies of the Haiti and

Mexican K–T sections suggest a multi-event scenario of impacts, volcanism and climatic changes beginning in the late Maastrichtian and continuing well into the early Danian (Stinnesbeck et al., 1999, 2001; Stüben et al., 2002; Keller et al., in preparation).

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