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Palaeogeography, Palaeoclimatology, Palaeoecology 178 (2002) 233–255

PALAEO

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The Cretaceous–Tertiary (K–T) mass extinction in planktic foraminifera at Elles I and El Melah, Tunisia

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Received 1 July 1999; accepted 9 August 2001

Abstract

Planktic foraminiferal faunas across the K–T transition at Elles and El Melah in northwestern and northeastern Tunisia, respectively, reveal patterns of species extinctions and species survivorship similar to those found at the El Kef stratotype and the Ain Settara sections. Slightly more than 2/3 of the species disappeared at or before the K–T boundary event and slightly less than 1/3 survived into the Danian where most disappeared sequentially within zone P1a (*Parvularugoglobigerina eugubina*). Relative species abundance patterns reveal that the 13–16 K–T survivors dominated (80%) the assemblages in the latest Maastrichtian, whereas the K–T extinct species were rare and totaled less than 20% of the total assemblages.

The K–T survivors are generally small with little surface ornamentation and geographically widespread from low to high latitudes. In contrast, K–T extinct species are large, highly ornamented and geographically restricted to low latitudes. This indicates that the K–T mass extinction was selective, rather than random, and predominantly affected the less robust tropical species. With the exception of the opportunistic *Guembelitra* species which dominate the early Danian, most K–T survivor species suffered severely as is evident by the decreased species populations after the K–T event. Their eventual demise appears to have been related to post-K–T environmental changes and competition from evolving Tertiary species. These results reveal a complex mass extinction pattern that in addition to the K–T impact event is keyed to long-term environmental changes preceding and following this event. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: K–T boundary; mass extinction; Tunisia

1. Introduction

The Cretaceous–Tertiary (K–T) boundary mass extinction in planktic foraminifera is well known from the El Kef stratotype (e.g. Smit, 1982; Brinkhuis and Zachariasse, 1988; Keller, 1988,

1995; Keller et al., 1995; Ben Abdelkader, 1995; Ben Abdelkader et al., 1997) which for the most part has defined the extent of the biotic catastrophe in low latitudes. This is largely because the El Kef section has remained the most expanded and continuous sediment record of this boundary event known to date worldwide (Keller, 1996). In recent years, continued research in Tunisia has uncovered several new K–T boundary transitions, including the deeper water El Melah section

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in the northeast, the Elles and Ain Settara sections to the northwest and north of the Kasserine Island which were deposited at middle to outer neritic depths, and the inner neritic Oued Selja section south of the Kasserine Island and at the edge of the Sahara platform (e.g. Karoui et al., 1995; 1996; Keller et al., 1998; Molina et al., 1998; Dupuis et al., 1998; 2002; Karoui-Yaakoub, 1999; Zaghbib-Turki et al., 2000; 2001) (Fig. 1).

We report here on the planktic foraminiferal turnovers of two of these sections: Elles and El Melah. El Melah is unique in that it represents a deeper more open ocean environment than any of the other sections and Elles appears to have an expanded K–T transition equal to the El Kef stratotype. The propitious discovery and analysis of these new K–T transitions (by N.K.-Y.) comes at a time when the El Kef stratotype is itself endangered by oversampling and agricultural encroachment. Alternative and equally continuous K–T boundary transitions, like Elles, are therefore a necessary and welcome addition to El Kef.

The Elles sequence is located 75 km southeast of El Kef in a valley near the hamlet of Elles (Fig. 1) where sediments spanning from Campanian to lower Eocene are continuously exposed. The K–T transition outcrops in numerous places and can be traced over hundreds of meters along the slopes of the valley. Therefore, oversampling is not a concern, unlike at El Kef, nor is there any danger of obliteration due to agricultural encroachment because of the steep valley slopes. For biostratigraphers interested in the K–T mass extinction as well as environmental changes before and after this event, the Elles section offers the necessary continuous outcrops that are largely missing at the El Kef and other Tunisian sections.

The late Cretaceous to early Tertiary sequence at Elles was first reported by Pervinquier (1903) who noted the expanded Cretaceous–Tertiary sedimentary record, which was later confirmed by Said (1978) who documented the biostratigraphy based on ostracods and planktic and benthic foraminifera. Said's study was done at about 1 m intervals and consequently did not specify the K–T boundary transition. Karoui-Yaakoub (1999) and this study re-examined this section and lo-

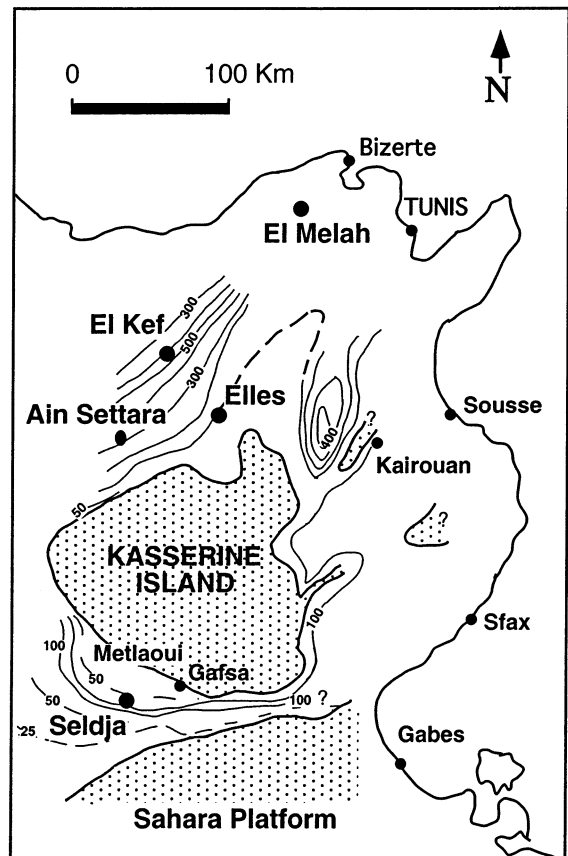


Fig. 1. Paleogeography of Tunisia during the late Maastrichtian and early Tertiary with paleolocations of the K–T boundary sections (modified after Burolet, 1967).

calated the K–T transition based on the same lithological changes and planktic foraminiferal extinctions and evolutions as at the El Kef stratotype (see also Karoui and Zaghbib-Turki, 1998), whereas Robin et al. (1998) identified the K–T spinel horizon and Rocchia (Zaghbib-Turki et al., 2000) identified the Ir anomaly. In addition, ostracods of the Elles section have been re-examined in a recent study by Said-Benzarti (1998).

This study details the planktic foraminiferal biostratigraphy, mass extinction and faunal turnover across the K–T transition at Elles from two different sample sets of the same outcrop which is here labelled Elles I. The first sample set details the species ranges from the latest Maastrichtian through the Danian. The second sample set was subsequently taken for direct comparison with El

Kef for the interval from 0.5 m below to 0.8 m above the K–T boundary. This study shows the similarities between El Kef and Elles in species extinctions, survivorship and relative abundance changes and generally confirms the pattern previously revealed at El Kef (e.g. Keller et al., 1995) and also confirmed at Ain Settara (see Luciani, 2002). In addition, we present the biostratigraphy and species ranges at El Melah.

2. Location and lithology

2.1. Elles section

The Elles section, located about 75 km south-east of the town of El Kef and near the hamlet of Elles, can be reached by the road from Maktar to Sers. About 26 km along this road is a turnoff to an unpaved road leading to the village of Elles. About 7 km along this road and prior to reaching the village, there is a house on top of Campanian limestones and behind it, the begin of a wide valley cut by the Karma river (usually dry). The Karma valley is about 4 km long. Coming up through the valley (about 3 km), one passes through thick light gray late Campanian to early Maastrichtian limestones of the Abiod Formation which are rich in inoceramids, stegasters and ichnofossils. This interval is followed by gray marls interspersed with about seven to eight 20 cm thick resistant marly limestone layers with fewer macrofossils (e.g. *Stegaster*, *Micraster* and *Holcotypoids*, see Li and Keller, 1998a; Zaghib-Turki et al., 2000). Above this interval, gray marls of the El Haria Formation continue for about 200 m where the valley forks. The right side fork has steep sides of gray marly shales with a few thin marly limestone layers. The Elles I outcrop (Karoui-Yaakoub, 1999) is located in this valley about 200 m past the fork on the left side wall. Additional K–T outcrops, including Elles II (see Keller et al., 2002) are located on the right side of the left valley fork.

The K–T transition at Elles I is exposed on the left side slope (of the right valley fork) about 12–14 m up from the valley floor and marked by dark gray shales and clays. Near the base the slope is

covered by debris and only about 7–8 m are exposed below the K–T boundary. These latest Maastrichtian sediments consist of gray shales, marly shales and several thin resistant marly limestone layers between 4 and 7 m below the K–T boundary. Although these resistant limestone layers can be traced through both valley forks, the meter distance to the K–T boundary may vary as a result of local erosion or topography.

The K–T transition is well marked by a 5–7 cm thick bioclastic packstone at Elles I. But the thickness of this bioclastic layer is laterally variable and may reach 25–30 cm in some outcrops, especially in the valley to the left of the fork (e.g. Elles II, Keller et al., 2002). Above this bioclastic layer is a 0.5–1.0 cm thick clay layer followed by a 3–4 mm thick rusty red layer associated with two thin gypsum layers. This red layer marks the K–T boundary event and contains altered spherules, spinels (enriched in Cr and Ni) and anomalous concentrations of iridium (Robin et al., 1998; Zaghib-Turki et al., 2000). Above this interval, the basal Danian consists of a 50–60 cm thick dark gray to black clay layer followed by 6 m of gradually lighter colored clayey shales and shales. Upsection, between 7.5 and 12 m gray shales are interbedded with several thin resistant marly limestone layers followed by another 8 m of marly shales which grade into rhythmically interbedded limestone and marl layers.

2.2. El Melah section

The El Melah section is located in northeastern Tunisia about 36 km west from the town of Mateur and 3 km southeast of the village of El Aouana. The section can be reached by taking the road leading from Mateur to Sejnene. About 16 km before Sejnene at a locality marked by the crossing of the Oued El Maleh river is a chalk quarry. From here onwards, the K–T section is reached on foot by following the wide valley cut by the Oued El Maleh river (rarely dry) through Campanian to early Maastrichtian light gray limestones rich in megafossils followed by alternating gray marls and marly limestone layers (Abiod Formation) similar to the Karma valley at Elles. Continuing along the valley one traverses the gray

marls of the El Haria Formation and after about 2 km reaches the darker gray shales of the K–T boundary transition. The K–T boundary horizon is marked by a thin rusty red layer similar to Elles and El Kef. A dark organic-rich clay layer of Danian age overlies the red layer. The 20 cm above and below the K–T red layer are strongly bioturbated as evident by *Thalassinoides* burrows. Upsection, gray shales and marls alternate and the first marly limestone is present at 1.80 m above the rusty red layer that marks the K–T boundary.

3. Methods

The Elles section was sampled at two different times. The first sample set (by N.K.-Y. and D.Z.-T.) shown here spans from 6 m below to 8 m above the K–T boundary. Samples were taken at about 25–30 cm intervals, except for the K–T transition from 1 m below to 2 m above the boundary where samples were taken at closer intervals of 5–10 cm and at 1–2 cm spacing across the rusty red layer. The second sample set (G.K.) was taken during a subsequent visit when the section was trenched and resampled at 5 cm intervals between 0.5 m below to 0.8 m above the K–T boundary rusty red layer in order to obtain a comparable sample set to the El Kef stratotype (see Keller et al., 1995). The results of both Elles studies are described herein. The El Melah section was generally sampled at 5–10 cm intervals except across the rusty red layer and organic-rich clay where samples were taken at 2–5 cm intervals.

Laboratory procedures differed somewhat for the two sample sets. For the first study, samples were soaked in water and dilute hydrogen peroxide and then washed through a 63 µm screen. The same procedure was followed for the subsequent more detailed K–T intervals at Elles and El Melah, except that these samples were washed through a 38 µm screen. The smaller size fraction was used because previous studies have shown that the earliest Danian species are often smaller than 63 µm (e.g. Keller, 1993; Keller et al., 1995). As a result, Danian species ranges, and conse-

quently the biozonations may differ depending on the size fraction used.

For the first study the > 63 µm size fraction of each sample was analyzed, a species census taken for biostratigraphic analysis, determination of species ranges and evaluation of the mass extinction. The same method was followed for the El Melah section. For the detailed K–T study at Elles and comparison with the El Kef stratotype, the > 38 µm size fraction was quantitatively analyzed and relative abundances determined from representative sample splits of about 250–350 specimens (Table 1).

BIOZONES: PLANKTIC FORAMINIFERA			
Stage	Datum events	Keller et al., 1995, this study	Berggren et al., 1995
Lower Paleocene (Danian)	┆ <i>P. trinidadensis</i>	P1d	P1a-P1c
	┆ <i>P. inconstans</i>		
	┆ <i>G. Conusa</i>	P1b	
	┆ <i>P. varlanta</i>		
	┆ <i>P. eugubina</i> , <i>P. longiapertura</i>	P1a(2)	
	┆ <i>G. compressa</i>		
	┆ <i>S. trivialis</i>	P0	
	┆ <i>G. pentagona</i>		
	┆ <i>P. pseudobulloides</i>	P0	
	┆ <i>S. triloculinoides</i>		
┆ <i>G. daubjergensis</i>	P0		
┆ <i>S. moskvini</i>		P0	
┆ <i>G. planocompressa</i>	P0		
┆ <i>P. taurica</i>		P0	
┆ <i>C. midwayensis</i>	P0		
U. Maestr.		┆ <i>P. eugubina</i> , <i>P. longiapertura</i>	P. hantkeninoides
	┆ <i>E. eobulloides</i>		
	┆ <i>E. edita</i> , <i>W. hornorst.</i>		
	┆ <i>E. fringa</i>		
	┆ <i>G. Conusa</i>	A. mayaroensis	
	┆ <i>P. hantkeninoides</i> , <i>A. mayaroensis</i> and extinction of tropical & subtropical species		
	┆ <i>P. hantkeninoides</i>		

Fig. 2. Planktic foraminiferal zonation of Keller et al. (1995) with some modifications by N.K.-Y. and D.Z.-T. and comparison with Berggren et al. (1995).

Table 1
Relative percent abundance data of planktic foraminifera across the K–T boundary at Elles I, Tunisia (G.K. data set)
Relative percent abundances of planktic foraminifera across the K–T boundary at Elles I, Tunisia (>63 µm)

Biozones	cm below K–T boundary										cm above base of K–T boundary clay														
	Plummerita hantkeninoides (CFI)										Pla														
	45–50	40–45	35–40	30–35	25–30	20–25	15–20	10–15	5–10	0–5	1–3	3–6	6–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–55	55–60	60–65	65–70
<i>Eoglobigerina edita</i>																									
<i>Eoglobigerina fringa</i>																									
<i>E. simplicissima</i>																									
<i>Parvularugoglobigerina eugubina</i>																									
<i>Parvularugoglobigerina longiapertura</i>																									
<i>Glogocoma conusa</i>																									
<i>G. tripartita</i>																									
<i>Planorotalites planocompressus</i>																									
<i>Woodringina hornerstowiensis</i>																									
<i>Guembelitra cretacea</i>																									
<i>Guembelitra danica</i>																									
<i>Guembelitra irregularis</i>																									
<i>Guembelitra trifolia</i>																									
<i>Globigerinelloides aspera</i>																									
<i>Globigerinella volutus</i>																									
<i>G. yaucoensis</i>																									
<i>Abathomphalus mayaroensis</i>																									
<i>Globotruncana aegyptiaca</i>																									
<i>G. arca</i>																									
<i>G. dawii</i>																									
<i>G. dupeublei</i>																									
<i>G. esnehensis</i>																									
<i>G. falsostuarti</i>																									
<i>G. insignis</i>																									
<i>G. rosetta</i>																									
<i>Globotruncanella conica</i>																									
<i>G. pettersi</i>																									

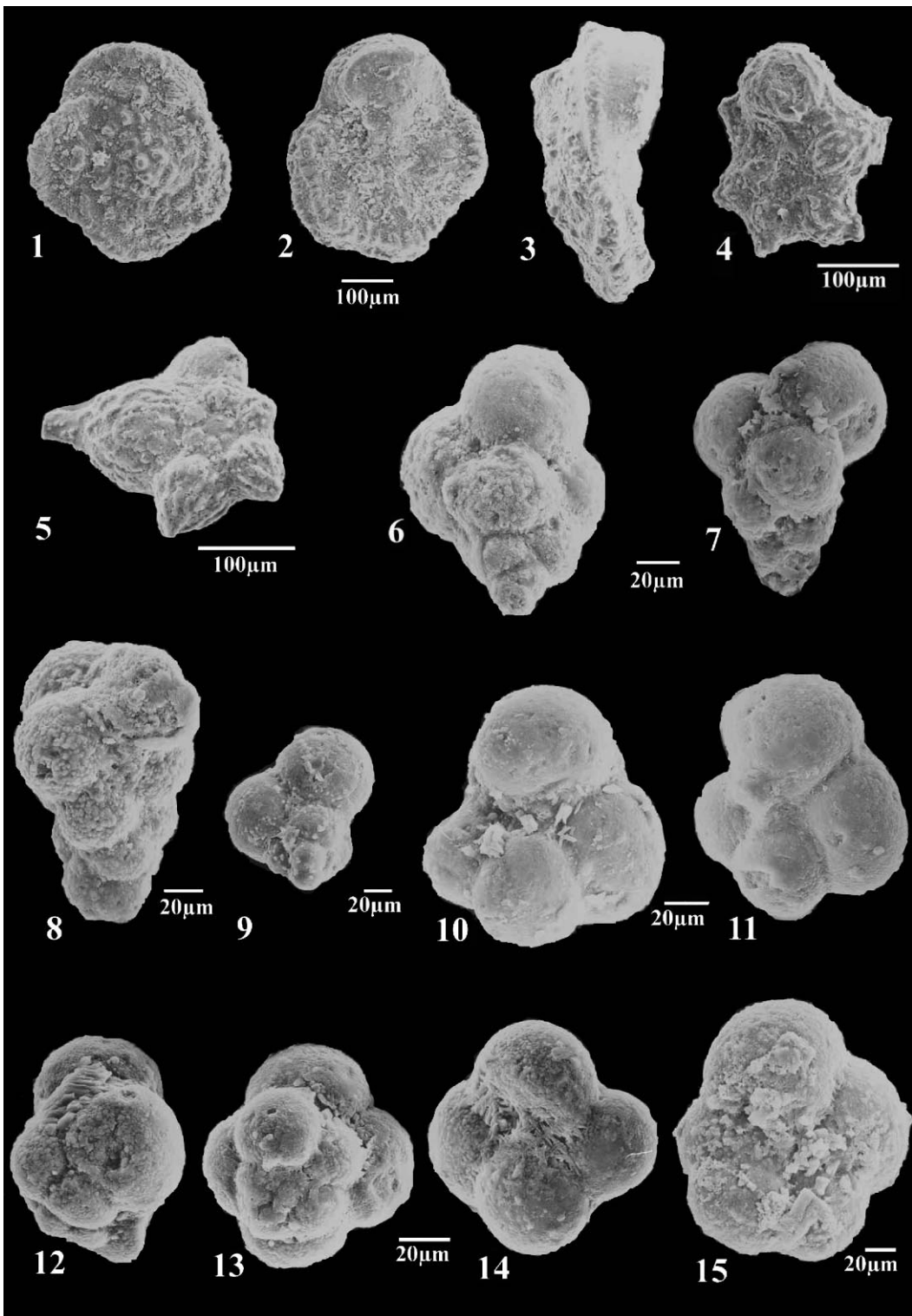
Table 1
(continued)

Biozones	cm below K–T boundary										cm above base of K–T boundary clay																
	Plummerita hamkeninooides (CFI)										P0 (> 63 µm)										Pla						
	45–50	40–45	35–40	30–35	25–30	20–25	15–20	10–15	5–10	0–5	0–1	1–3	3–6	6–10	10–15	15–20	20–25	25–30	30–35	35–40		40–45	45–50	50–55	55–60	60–65	65–70
<i>G. stuarti</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>G. stuartiformis</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>Globotruncanella minuta</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>G. petaloidea</i>	×	1	×	1	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>G. subcarinatus</i>	×	×	×	2	×	1	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>Gublerina cuvillieri</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>G. robusta</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>Hedbergella holmdelensis</i>	2	×	2	2	2	3	3	2	1	2	2	2	2	×	1	3	5	2	2	×	×	×	×	×	×	1	
<i>H. monmouthensis</i>	3	3	2	3	3	4	1	1	1	1	5	2	3	2	2	3	3	7	7	3	2	3	1	1	1	1	
<i>Heterohelix complanata</i>	2	2	2	3	1	4	9	5	5	2	×	×	1	×	×	×	×	×	×	×	×	×	×	×	×		
<i>Heterohelix dentata</i>	18	14	24	24	19	19	23	22	24	20	11	7	5	5	3	×	1	9	16	10	4	6	4	4	6	3	
<i>H. glabrans</i>	×	×	1	×	×	1	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>H. globulosa</i>	4	4	2	4	9	3	3	9	4	6	19	2	2	×	×	1	1	4	1	×	×	×	2	1	×	×	
<i>H. moremani</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>Heterohelix navarroensis</i>	11	14	24	10	12	20	18	11	16	16	12	28	25	19	15	24	60	28	18	33	19	23	18	21	19	8	13
<i>H. planata</i>	5	8	4	2	5	6	4	2	5	7	4	1	×	1	×	×	3	×	×	×	×	×	×	×	×	×	
<i>H. pulchra</i>	2	×	×	×	×	1	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>H. punctulata</i>	3	3	1	×	1	×	3	4	3	2	2	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>H. striata</i>	×	2	1	×	×	×	×	×	2	1	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>Planoglobulina brazoensis</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>P. carseyae</i>	×	×	×	2	×	×	×	1	1	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>P. multicamerata</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>Plummerita hamkeninooides</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>P. reicheli</i>	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>Pseudoguembelina costulata</i>	21	19	16	19	16	17	12	18	13	17	26	4	7	3	2	1	7	4	2	2	2	1	1	×	2	2	
<i>P. hariaensis</i>	×	×	×	×	3	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
<i>P. kempensis</i>	4	5	3	5	6	7	4	5	9	8	4	×	3	×	1	1	2	×	×	×	×	×	×	×	×	×	
<i>P. palpebra</i>	1	2	×	×	2	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	

Table 1
(continued)

Biozones	cm below K–T boundary															cm above base of K–T boundary clay																													
	<i>Plummerita hantkeninooides</i> (CFI)															P0 (>63 µm)															P1a														
	45–50	40–45	35–40	30–35	25–30	20–25	15–20	10–15	5–10	0–5	1–3	3–6	6–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–55	55–60	60–65	65–70	70–75																			
<i>Pseudotextularia deformis</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>P. elegans</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>Racemiguembelina fructicosa</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>R. intermedia</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>R. powelli</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>Rosita contusa</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>R. plicata</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>R. walfischensis</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>Rugoglobigerina hexacamerata</i>	3	2	3	3	3	2	1	2	2	1	3	3	2	1	2	2	1	3	3	3	3	3	3	3	3	3																			
<i>R. macrocephala</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>R. rotundata</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>R. rugosa</i>	2	x	x	x	1	x	x	x	3	2	1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>R. scotti</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>Shackoina</i> sp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
<i>Zeuwigerina</i> sp.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x																			
Total number counted	356	333	388	347	408	391	337	410	429	374	370	563	461	393	340	135	78	202	333	412	376	369	414	296	263	324	275																		

63 µm, except for the P0 interval (0–20 cm above the K–T boundary) where few non-reworked and in situ specimens are present and most of the faunal assemblage is in the smaller 38–63 µm size fraction. Note that x = <2% or very rare specimens found in searching the sediment residues beyond the split used for the faunal count.



4. Biostratigraphy

The biozonation of Keller et al. (1995) is used in this study with some modifications by N.K.-Y. and D.Z.-T. (e.g. combining zones P1b and P1c as *Parasubbotina pseudobulloides* (P1b) zone and using the *Abathomphalus mayaroensis* zone to mark the latest Maastrichtian, Fig. 2). The alternative biozonation of Berggren et al. (1995) is shown for comparison. Stratigraphically important species are illustrated in Plates I and II.

A new classification of Paleocene planktic foraminifera was recently published based on wall texture (Olsson et al., 1999). This study generally follows this new classification scheme and new generic assignments with exceptions as noted below.

Previous taxonomy	Revised taxonomy (Olsson et al., 1999)
<i>Subbotina pseudobulloides</i>	<i>Parasubbotina pseudobulloides</i>
<i>Subbotina varianta</i>	<i>Parasubbotina varianta</i>
<i>Eoglobigerina trivialis</i>	<i>Subbotina trivialis</i>
<i>Globoconusa conusa</i>	<i>Parvularugoglobigerina extensa</i>
<i>Chiloguembelina waiparaensis</i>	<i>Zeauvigerina waiparaensis</i>
<i>Planorotalites compressa</i>	<i>Globanomalina compressa</i>
<i>Globigerina taurica</i>	<i>Praemurica taurica</i>
<i>Morozovella inconstans</i>	<i>Praemurica inconstans</i>
<i>Morozovella trinidadensis</i> jun.	<i>Praemurica inconstans</i>
Synonym of	

We retain the species name *Eoglobigerina fringa* for the small four-chambered early Danian morphotype which Olsson et al. (1999) now consider as part of a very widely varying *Eoglobigerina edita* population. We also retain the name *Parvu-*

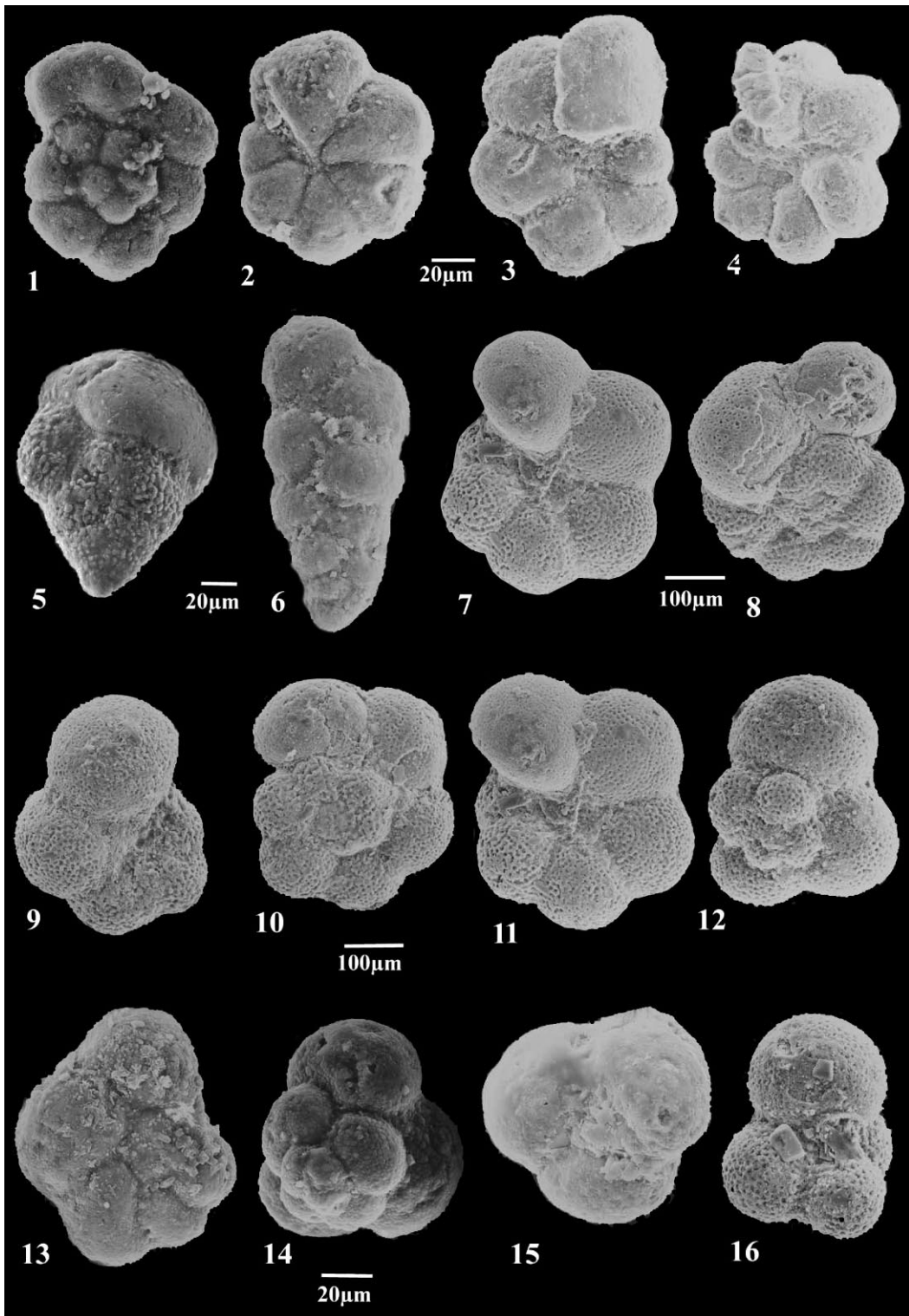
larugoglobigerina longiapertura for the very compressed five- to eight-chambered forms with long slit-like apertures which Olsson et al. (1999) include within the *Parvularugoglobigerina eugubina* population. In addition, Olsson et al. also consider all triserial species as variants of a very heterogeneous population of *Guembelitra cretacea*. We retain the species name *Guembelitra irregularis* for morphotypes with irregularly stacked chambers, *Guembelitra danica* for morphotypes with highly regularly arranged chambers and elongate spires and *Guembelitra trifolia* for the very short spired forms. These morphologies are easily distinguished from *G. cretacea* and their relative abundance distributions suggest different ecologic affinities (see Keller et al., 2002, for further discussion).

4.1. *Plummerita hantkeninoides* zone

This zone spans the range of *P. hantkeninoides* and was originally defined by Masters (1984, 1993) and subsequently by Pardo et al. (1996). At Elles I the range of *P. hantkeninoides* spans the last 7 m of the Maastrichtian and 10 m at Elles II (located in the left fork of the valley) as compared with 6 m at El Kef (Li and Keller, 1998a). The range of this excellent latest Maastrichtian marker species spans the last 300–400 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

Plate I. All specimens from Elles I, Tunisia.

1–3	<i>Abathomphalus mayaroensis</i> (BOLLI)
4	<i>Rugoglobigerina reicheli</i> (BRÖNNIMANN)
5	<i>Plummerita hantkeninoides</i> (BRÖNNIMANN)
6–7	<i>Guembelitra cretacea</i> (CUCHMAN)
8	<i>Guembelitra danica</i> (HOFKER)
9	<i>Guembelitra trifolia</i> (MOROZOVA)
10	<i>Eoglobigerina moskvini</i> (SHUTSKAY)
11	<i>Eoglobigerina fringa</i> (MOROZOVA)
12–14	<i>Globoconusa conusa</i> (CHALILOV)
15	<i>Eoglobigerina pentagona</i> (MOROZOVA)



completeness of the latest Maastrichtian interval. The *P. hantkeninoides* zone replaces the *Abathomphalus mayaroensis* zone for the top part of the Maastrichtian.

4.2. *Abathomphalus mayaroensis* zone

The total range of *A. mayaroensis* has long been used to define the late Maastrichtian. However, in recent years there has been a shift towards replacing the top of this zone by the *Plummerita hantkeninoides* zone (Plate I). There are two major reasons for this zonal change. Firstly, the range of *A. mayaroensis* is rather long (about 2 myr) and therefore the zone provides poor biostratigraphic resolution to determine how complete, or incomplete, the late Maastrichtian is. For example, although intrazonal hiatuses may be present within the 2 myr interval of the range of the zonal index, this could not be determined from the presence of the *A. mayaroensis* zone. But by identifying the short-ranging *P. hantkeninoides*, it can be determined whether the top of the Maastrichtian is present. Secondly, it is well known that *A. mayaroensis* is generally more common in high latitudes and in deeper water open ocean environments, and rare or sporadically present in low latitudes and shelf regions. For this reason, the first and last appearances of *A. mayaroensis* are often diachronous and hence unreliable for global correlations (e.g. Masters, 1984, 1993; Keller, 1988; Olsson and Liu, 1993; Pardo et al., 1996).

Nevertheless, in this study N.K.-Y. and D.Z.-T. prefer to use the last appearance of *Abathomphalus mayaroensis* to mark the latest Maastrichtian,

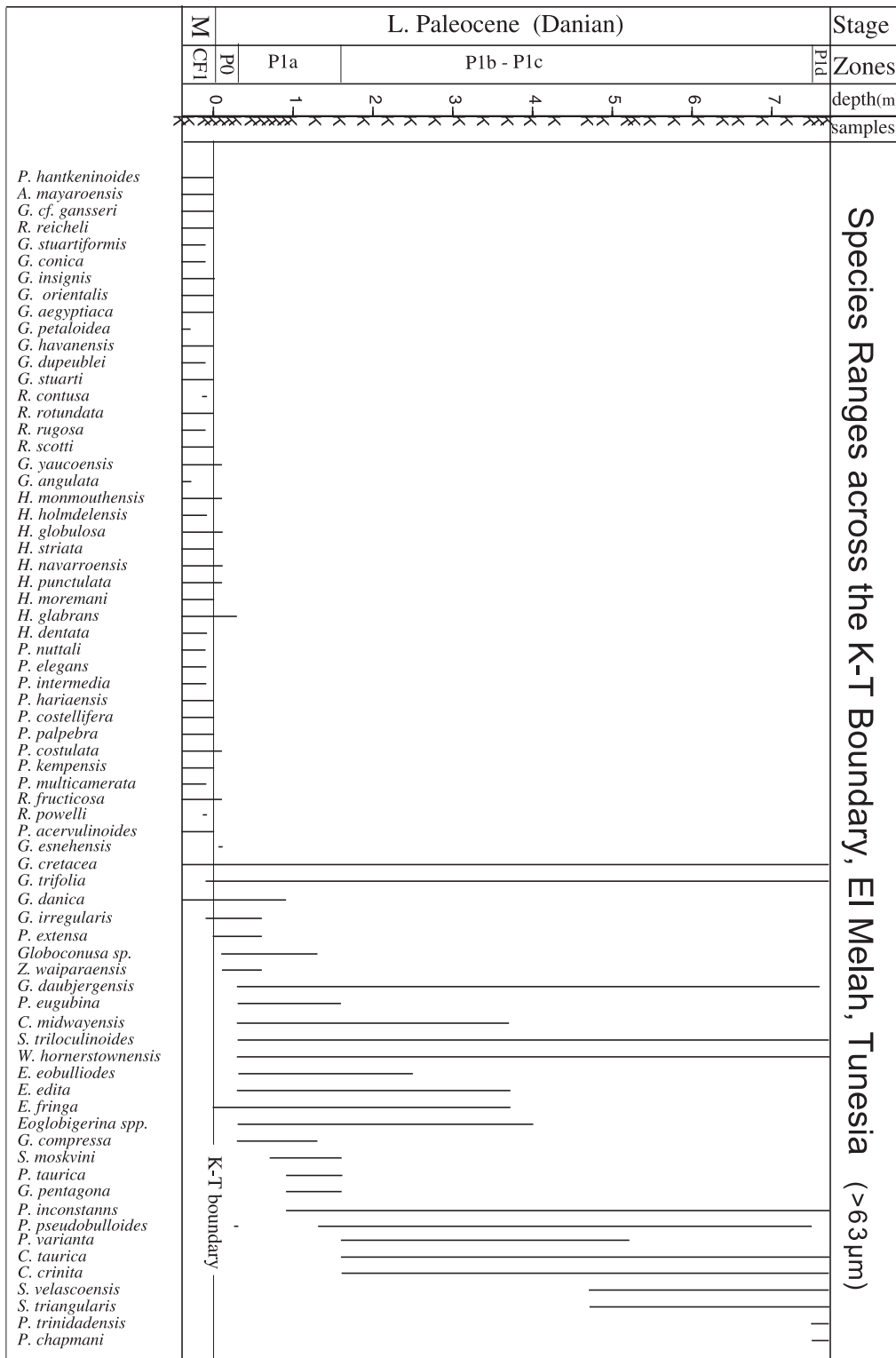
rather than the *Plummerita hantkeninoides* zone, because they did not find *P. hantkeninoides* in the last 10 cm below the red layer in their sample set of Elles I, whereas *A. mayaroensis* was present (Fig. 3). However, *P. hantkeninoides* is present in this interval in the second more closely spaced sample set of the same outcrop (Fig. 4), as well as in the nearby Elles II outcrop. Besides the consistent and common occurrence of *A. mayaroensis* reported by N.K.-Y. and D.Z.-T. is very atypical and possibly due to particular and intensive search of the species in the below K-T boundary samples. In our sample set of the same outcrop, this species is only observed at 40–45 cm below the K–T boundary (Table 1). A similarly rare and sporadic occurrence of *A. mayaroensis* is observed in the nearby Elles II outcrop (see Keller et al., 2002), as well as at El Kef and Ain Settara. At Ain Settara, isolated occurrences of *A. mayaroensis* are reported at 14 m below the K–T boundary and just below the K–T boundary (Dupuis et al., 1998; Molina et al., 1998; Luciani, 2002). At El Kef, this species is only reported as isolated occurrence at 20 m below the K–T boundary (Li and Keller, 1998a,b,c).

4.3. K–T boundary and mass extinction

This boundary is defined by the coincidence of several characteristic lithological and geochemical criteria: a lithological change from marls or shales to dark gray or black clay; a 2–4 mm thin rusty red layer at the base of the clay; the presence of spherules, spinels and anomalous concentrations of iridium and other platinum group elements in the rusty red layer. Paleontological criteria in-

Plate II. All specimens from Elles I, Tunisia.

- 1–4 *Parvularugoglobigerina eugubina* (LUTTERBACHER and PREMOLI SILVA)
- 5 *Chiloguembelina midwayensis* (CUCHMAN)
- 6 *Chiloguembelina taurica* (MOROZOVA)
- 7–8 *Praemurica inconstans* (SUBBOTINA)
- 9 *Parasubbotina pseudobulloides* (PLUMMER)
- 10–11 *Praemurica trinidadensis* (BOLLI)
- 12, 16 *Subbotina triloculinoides* (PLUMMER)
- 13 *Praemurica taurica* (MOROZOVA)
- 14–15 *Globoconusa daubjergensis* (BRÖNNIMANN)



clude the extinction of all ornate large tropical and subtropical species, including all globotruncanids, racemiguembelinids and rugoglobigerinids 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 clay (e.g. *Globoconusa conusa*, *Eoglobigerina fringa*, *Eoglobigerina edita*, *Eoglobigerina eobulloides*, *Woodringina hornerstownensis*, Plates I and II; Keller et al., 1995). The survivors are Cretaceous ecological generalists, characterized by small size, little or no test ornamentation and wide geographic ranges. The K–T boundary is marked by these criteria in both the Elles I and El Melah sections, as also observed at El Kef and Ain Settara (Keller, 1988; Keller et al., 1995; Molina et al., 1998; Luciani, 2002).

4.4. 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* (Plate II). 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). However, new studies based on the smaller 38–63 size fraction suggest that P0 may be restricted to the lower part of this black clay layer. At El Melah, zone P0 is condensed, about 10 cm thick, and spans the dark clay interval. At Elles I, zone P0 spans the clay layer (66 cm) in N.K.-Y.'s sample set, but is restricted to the lower part of this interval (20–25 cm) in G.K.'s sample set due to the presence of tiny *P. eugubina* and *P. longiapertura* in the smaller size fraction as discussed below. Zone P0 is characterized by abundant triserial species (*Guembelitra cretacea*, *Guembelitra trifolia*, *Guembelitra danica*, Plate I).

4.5. P1a zone

This range zone spans from the first appearance of *Parvularugoglobigerina eugubina* and/or *longiapertura* to the extinction of these taxa. At El Melah, the first *P. eugubina* (lumped with *P. longiapertura*) were observed 10 cm above the K–T boundary red layer and zone P1a spans 140 cm (Fig. 3, Plate II). At Elles I, the P1a zone is 5.6 m thick and comparable to the 4.5 m observed at El Kef (Keller, 1988, Fig. 6). Zone P1a can be subdivided into P1a(1) and P1a(2) based on the first appearance (FA) of *Subbotina pseudobulloides* (Fig. 2).

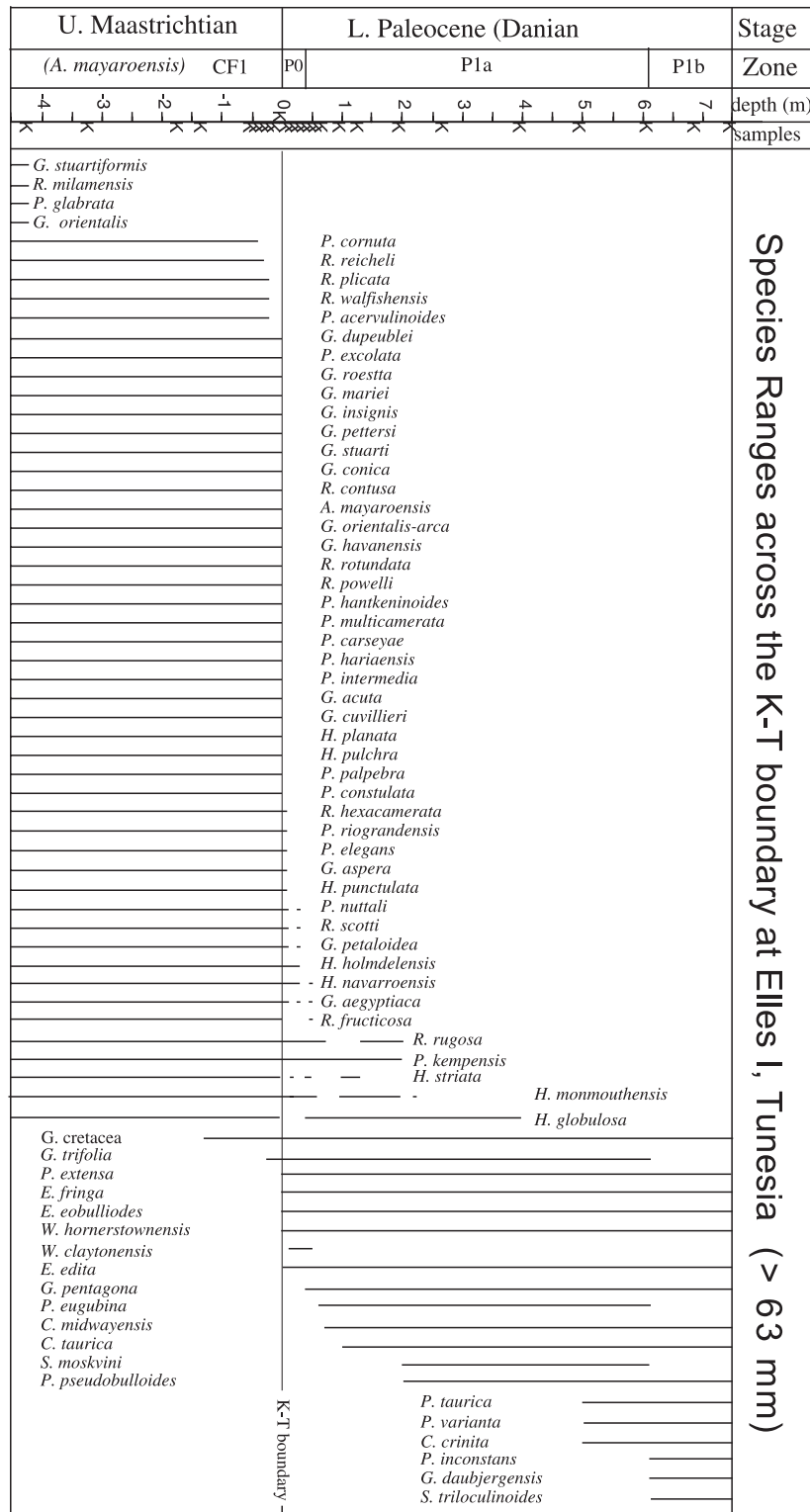
The first appearances of *Parvularugoglobigerina eugubina* and/or *Parvularugoglobigerina longiapertura* differ in the two different sample sets and different size fractions analyzed at Elles I. In the first sample set (long section, Fig. 4), based on the >63 μm size fraction, *P. eugubina* (lumped with *P. longiapertura*) first appears at 66 cm above the K–T boundary near the top of the organic-rich clay. But in the second sample set based on the 38–63 μm size fraction (Fig. 5), the first *P. longiapertura* and *P. eugubina* appear at 20–25 cm and 40–45 cm, respectively, above the red layer and K–T boundary. This suggests that in the early evolutionary range *P. longiapertura* and *P. eugubina* remained morphologically small species (<63 μm), but generally increased in size above the organic-rich clay layer. It further suggests that the origination of *P. longiapertura* morphotype may precede that of *P. eugubina*, though this was not observed at El Kef by Keller et al. (1995).

4.6. P1b zone

This zone marks the interval from the last appearance of *Parvularugoglobigerina eugubina* to the first appearance of *Parasubbotina varianta* (Keller et al., 1995). At El Melah, *P. varianta* is first observed at 250–300 cm above the K–T boundary and zone P1b spans 100 cm (Fig. 3). At Elles I, the first appearance of *P. varianta* is nearly coincident with the disappearance of *P. eugubina* which is marked by a major faunal turnover just below a limestone layer (Figs. 3, 6). A

Fig. 3. Planktic foraminiferal species ranges across the K–T transition at El Melah based on the >63 μm size fraction.

Fig. 4. Planktic foraminiferal species ranges across the K–T transition at Elles I based on the > 63 µm size fraction analyzed by N.K.-Y. Note the differences between the species census data of the two separate sample sets in Fig. 6A and B.



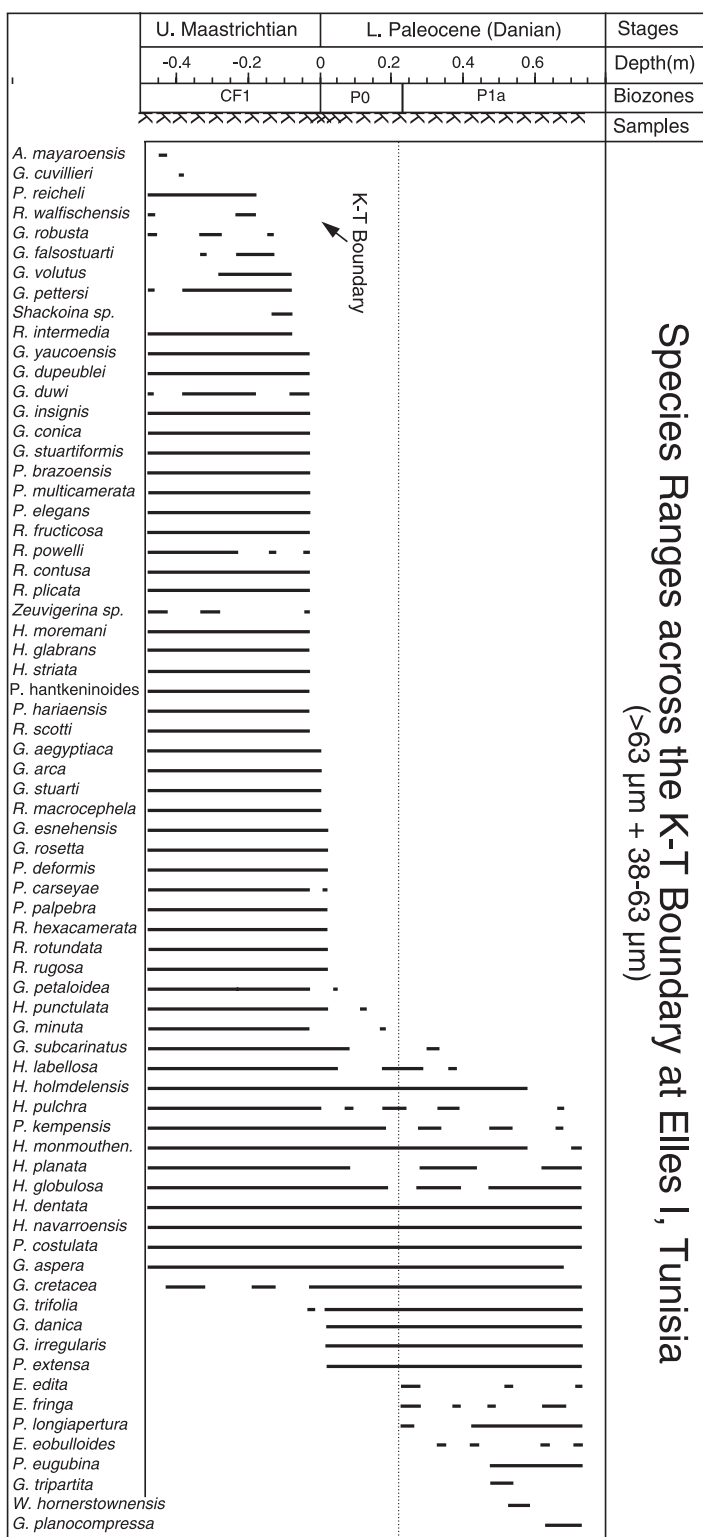


Fig. 5. Planktic foraminiferal species ranges across the K-T transition at Elles I based on the > 38 µm size fraction and analyzed by G.K. Note the differences between species ranges and species census data are partly attributable to differences in sampling procedures, laboratory and analytical techniques (e.g. size fraction analyzed), reworking and bioturbation (possible sampling of burrows), and taxonomic views (e.g. identification as well as lumping or splitting of species). See text for discussion.

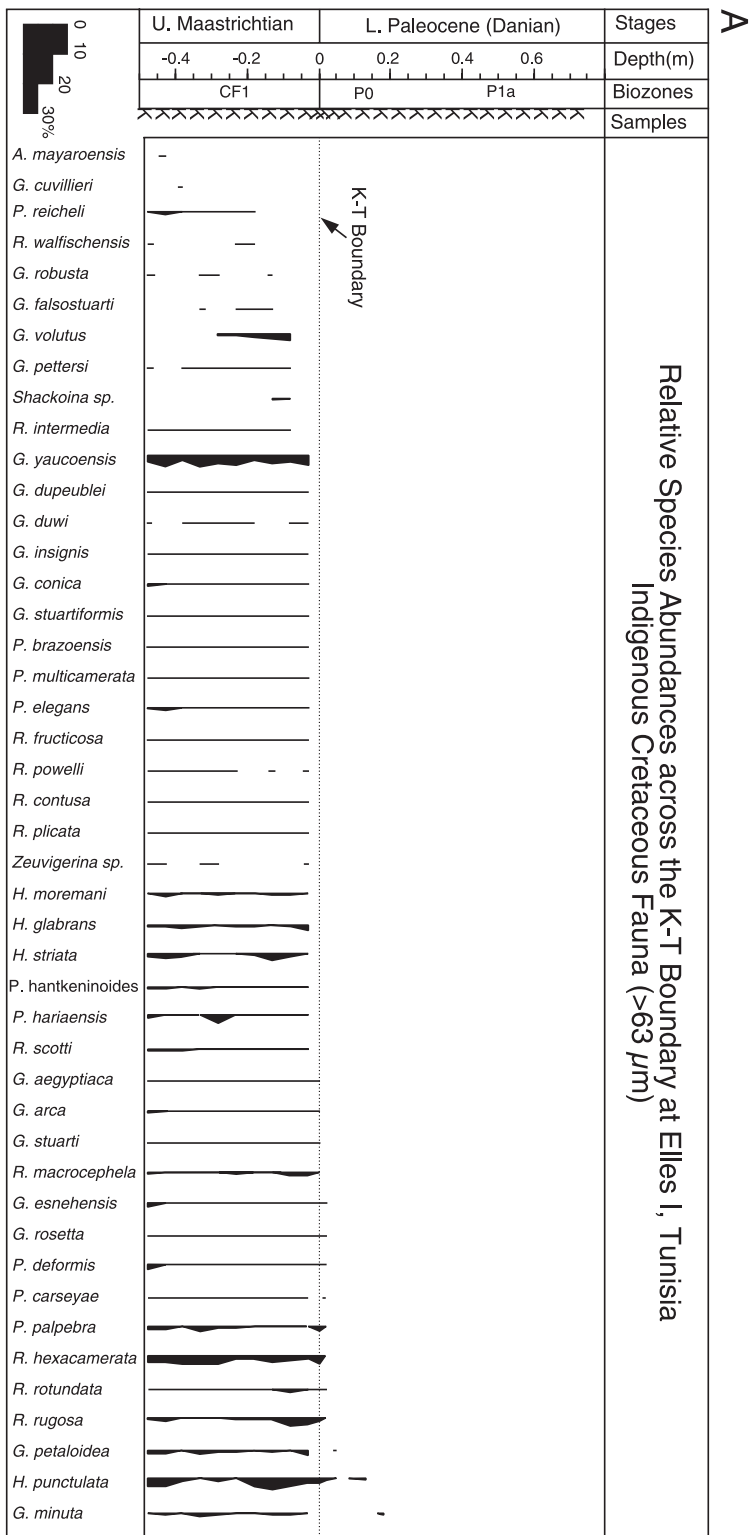


Fig. 6. (A) Relative species abundances of the indigenous Cretaceous planktic foraminiferal across the K–T boundary at Elles I in the > 63 μm size fraction. Note that all of these species, which are considered extinct at or near the K–T boundary, are tropical to subtropical and rare to few or only sporadically present near the end 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 planktic foraminifera in latest Maastrichtian and early Danian sediments at Elles I. Faunal counts are based on the > 63 μm size fraction, except for the P0 interval where most of the species are dwarfed and present only in the smaller 38–63 μm size fraction. Note the unusually high abundance of biserial species in the early Danian is considered reworked.

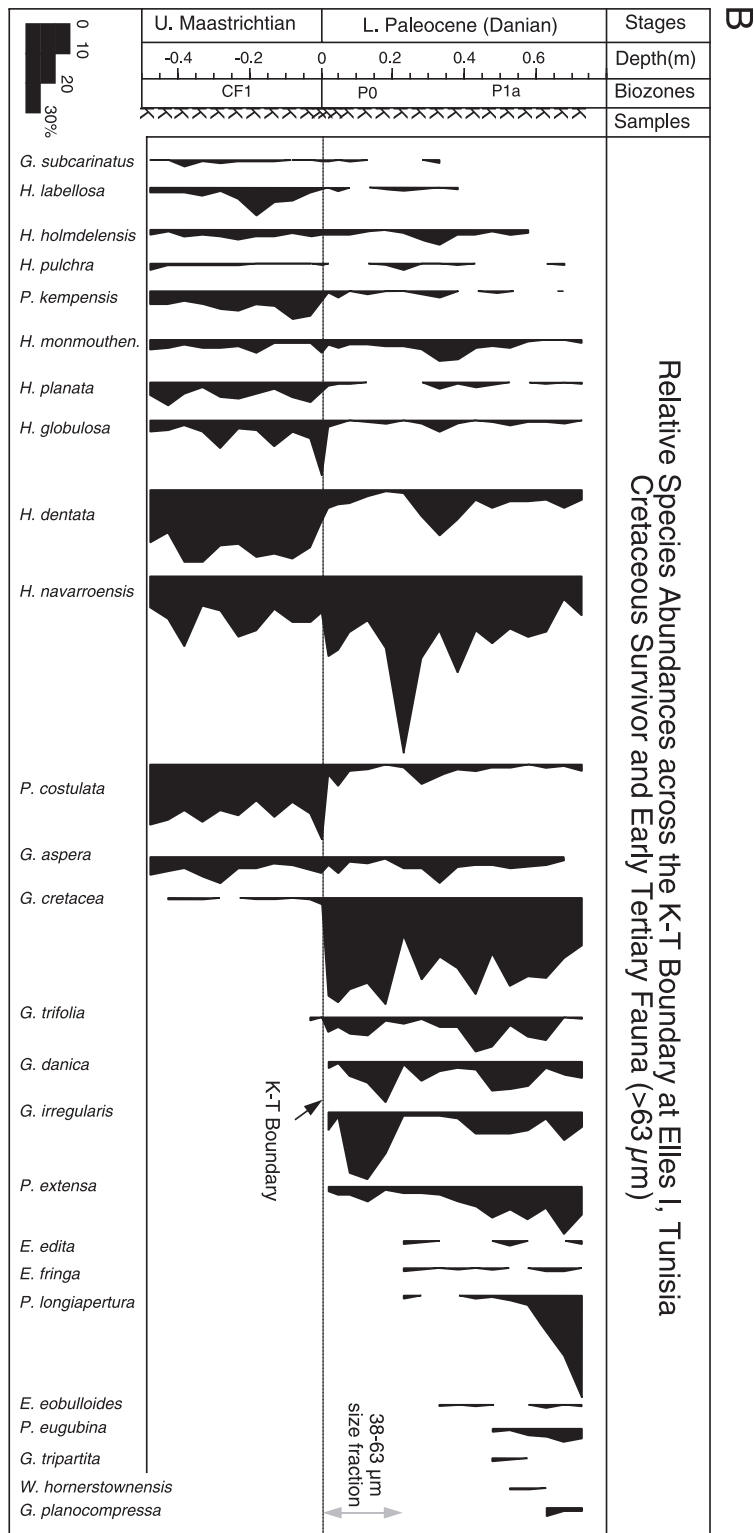


Fig. 6. (continued).

similar faunal turnover is observed at Ain Settara where Molina et al. (1998) also note the FA of *P. varianta* near the extinction of *P. eugubina* and nearly coincident with the simultaneous appearance of seven new species and disappearance of six. At El Kef, a major faunal turnover also coincides with the extinction of *P. eugubina*, in addition to an abrupt increase in the size of Danian species (Keller, 1988). This suggests that zone P1b is condensed or missing in these sections.

Though earlier studies of El Kef and Ain Settara considered the early Danian interval to be complete, the abrupt faunal turnover marked by several species extinctions (e.g. *Parvularugoglobigerina eugubina*, *Parvularugoglobigerina longiapertura*, *Globoconusa conusa*) and originations (e.g. *Globanomalina planocompressa*, *Parasubbotina varianta*, *Subbotina trivialis*, *S. triloculinoidea*, *Globoconusa daubjergensis*, *Praemurica inconstans*, Plates I and II), the abrupt decline in species populations, and the abrupt change to large morphotypes (> 150 µm, see fig. 6 in Keller, 1988) all suggest the presence of a hiatus. Hiatuses are common in Danian sections at the P1a/P1b interval as noted in sections worldwide (MacLeod and Keller, 1991). In Tunisian sections, this hiatus is apparently also present, though the stratigraphic extent may vary depending on paleodepth, topography and currents. For example, the shallow Sahara platform section at Oued Selja has a hiatus that spans from P1c(1) to near the top of P1a (Keller et al., 1998). This erosive event may express itself as a short hiatus or condensed interval at the Ain Settara, Elles and El Kef localities to the north.

4.7. P1c zone

This zone spans the interval from the first appearance of *Parasubbotina varianta* to the first appearance of *Praemurica trinidadensis*. At Elles this interval spans about 10 m (Fig. 6), whereas at El Melah zone P1c spans 5 m (Figs. 3, 4). Zone P1c can be subdivided based on the first occurrence of *Praemurica inconstans* which at Elles and Ain Settara nearly coincides with the extinction of *Parvularugoglobigerina eugubina*. As noted above the major faunal turnover at this interval suggests a

hiatus with P1b and the lower part of P1c(1) missing.

Alternative zone P1b: N.K.-Y. and D.Z.-T. prefer to use a *Parasubbotina pseudobulloides* (P1b) zone to mark the interval from the extinction of *Parvularugoglobigerina eugubina* to the first appearance of *Praemurica trinidadensis*; this zone is equivalent to zones P1b and P1c of Keller et al. (1995) (Fig. 2).

5. Analytical reproducibility

Can faunal and biostratigraphic analyses of one worker be reproduced reliably by another worker? Perhaps most of the controversies surrounding the K–T boundary mass extinction in planktic foraminifera, or indeed in all fossil groups, may be resolved if uniform species concepts and the same analytical methods could be employed by all workers. Unfortunately, this is still an unrealized dream among paleontologists. As a result, the data set of one worker is generally difficult to reproduce by another worker. Nevertheless, there is significant progress with very similar results obtained when the same analytical techniques and species concepts are employed (e.g. compare Keller et al., 1995, 2002, with Luciani, 1997, 2002).

The El Kef foraminiferal blind test was designed to test the reproducibility of planktic foraminiferal species census data and thereby resolve the continuing controversy regarding the mass extinction pattern. This test failed. It was initiated during the Snowbird II Conference (1988) to resolve a disagreement between Smit and Keller regarding the mass extinction pattern at El Kef in particular. Smit (1982, 1990) argued that planktic foraminifera exhibit a pattern of abrupt and simultaneous disappearance for all but one species (*Guembelitra cretacea*) at the K–T boundary with no reductions of species or species abundances below the boundary. He interpreted this extinction pattern as indicative of a geologically instantaneous mass kill effect as a result of a bolide impact. Keller (1988) and Keller et al. (1995) reported local disappearances of about 10% of the Cretaceous species within the last 50 cm below the

K–T boundary and about 30% of the Cretaceous species surviving into the Danian. She interpreted this progressive mass extinction pattern as the result of late Maastrichtian environmental changes with accelerated extinctions of tropical species at the K–T boundary possibly due to a bolide impact and the survivorship of ecological generalists into the Danian. Many recent publications have supported the Keller scenario of survivorship, though the percentage of species extinctions before the K–T boundary remains a controversial issue (e.g. Luciani, 1997; Apellaniz et al., 1997; Molina et al., 1998). The blind test failed to generate closely comparable results of replicate samples and hence failed to resolve the controversy (see Canudo, 1997; Masters, 1997; Olsson, 1997; Smit and Nederbragt, 1997; Keller, 1997; MacLeod, 1996a,b; 1998).

MacLeod (1998) (p. 43) noted that although the blind test failed to resolve the controversy, it highlighted the need for studies that address the issue of paleontological data reproducibility at both the empirical and theoretical levels. He noted that paleontologists must either improve the reproducibility of systematic results, or develop methods to incorporate relatively high levels of uncertainty in both qualitative and quantitative analyses. We agree with this assessment, but note that the major problems may well be due to systematics and the different conceptual approaches between lumpers and splitters. This report offers another example of this problem.

In this study, N.K.-Y. with D.Z.-T. and G.K. independently analyzed two different sample sets of the same Elles I section for a narrow interval spanning the K–T boundary (Figs. 4, 5). The methods employed differ (species census vs. quantitative analyses of assemblages) and species concepts also differ for a number of species. Therefore, the results vary in detail, but are comparable in general. For example, N.K.-Y. identified 56 Cretaceous species at Elles I (Fig. 4). 76% (43 species) of these are in common with G.K.'s species list of the same section, but from a different sample set (Fig. 5). The species which are not represented in G.K.'s study are generally included in closely related species morphologies and can be attributed to the lumper-splitter effect (e.g. *Clavi-*

hedbergella–*Shackoina*, *R. milamensis*–*R. rotundata*–*R. penny*–*R. robusta*, *G. orientalis*–*G. arca*, *G. acuta*–*G. robusta*, *Globigerinella volutus*–*Globigerinelloides aspera*, *P. nuttali*–*Pseudotextularia deformis*–*P. riograndensis*–*Planoglobulina brazoensis*, *P. excolata*–*Pseudoguembelina costulata*, *G. havanensis*–*G. petaloidea*), and four were not observed (*P. glabrata*, *P. cornuta*, *P. acervulinoides*, *G. mariei*).

G.K. identified 61 Cretaceous species for the same section (different sample set). 66% (41 species) of these are also present in N.K.-Y.'s study. Of the 20 species which are not present in N.K.-Y.'s study, all but one species (*Zeuvigerina*), are probably lumped with other species and hence can be attributed to the lumper-splitter effect (e.g. *Globigerinelloides volutus*–*G. yaucoensis*–*Globigerinelloides aspera*, *G. subcarinatus*–*G. petaloidea*, *Heterohelix dentata*–*H. globulosa*–*H. moremani*, *G. stuartiformis*–*G. falsostuarti*–*G. stuarti*, *Planoglobulina brazoensis*–*P. riograndensis*, *H. glabrans*–*H. pulchra*–*Heterohelix complanata*, *G. arca*–*G. orientalis*–*G. esnehensis*, *Pseudotextularia deformis*–*P. nuttali*, *Shackoina*–*Clavihedbergella*).

Because of the lumper-splitter dichotomy, a high degree of reproducibility between workers is only possible if they share the same taxonomic concepts. Since this is frequently not the case, analytical reproducibility even in the same section has very high variability as seen in the example of the Elles I section. Therefore, one would assume that the reproducibility would be better, even between different sections and regardless of the specific worker, as long as the same taxonomic concepts are used. For example, a study by Luciani (1997, 2002) of the Erto section in Italy and Ain Settara section in Tunisia shows very similar results to those earlier obtained from the El Kef and Elles sections by Keller et al. (1995, 2002). This suggests that these workers have independently used the same species concepts based solely on comparisons of published illustrations.

Many factors influence the reproducibility of species range data, including field sampling techniques (e.g. sample spacing, size of samples, sample contamination at outcrops), methods of sample processing (e.g. mechanical breakage, acid treatment causing dissolution, sieve size used),

sample analysis (size fraction analyzed, time spent searching for rare species, qualitative vs. quantitative analysis, problems in recognizing reworked species), systematics (species concepts of outlier species) and ecological variations in species distributions. Given all these variables, it is perhaps more surprising that the mass extinction pattern is so consistent, than that there are still some arguments over the finer points of the mass extinction pattern.

6. K–T faunal turnover

The K–T mass extinction pattern in planktic foraminifera at Elles I analyzed for the two sample sets differs in some details. For example, the N.K.-Y. sample set (Fig. 4) shows an unusual presence of many large tropical species above the K–T boundary (zones P0 and P1a(1)), which are known to be extinct at or near the boundary (*P. multicamerata*, *P. palpebra*, *Rugoglobigerina hexacamerata*, *R. scotti*, *P. riograndoensis*, *P. elegans*, *P. nutalli*, *G. aegyptiaca*, *Racemiguembelina fructicosa*, *R. rugosa*, *P. kempensis*). Their presence is likely a result of reworking and bioturbation as suggested by discolored, abraided and broken tests, as well as the common presence of *Thalassinoides* burrows above and below the red layer. In the second sample set where burrows were carefully avoided wherever possible (Fig. 5), only a few of these tropical species are present at the base of P0 and are attributed to reworking. Though *P. kempensis* and *Pseudoguembelina costulata* are consistently present in the early Danian at Elles I as well as the nearby Elles II and Ain Settara sections (Keller et al., 2002; Luciani, 2002). Thus these species may also have survived the K–T event.

The overall extinction patterns of both Elles I studies are similar to those observed in other Tunisian sections. Some species (~16%) are very rare or sporadically present and not observed to range up to the K–T boundary. Their true extinction level can not be determined. This is especially evident in that the species with early disappearances differ between the two sample sets analyzed (Figs. 4, 5). For many species, single isolated oc-

currences are reported within the last 10 cm below the K–T boundary, an interval that consists of a foraminiferal packstone. At Elles II, where this foraminiferal packstone is about 25–30 cm thick, cross-bedding is apparent and indicates a transported and probably reworked older assemblage. For this reason, no conclusions can be drawn regarding the extinction level of species that are only sporadically present below this foraminiferal packstone.

Nevertheless, the overall mass extinction pattern at Elles I is similar to that observed at El Kef (Keller et al., 1995), Ain Settara (Luciani, 2002), Mexico (Keller et al., 1994; Lopez-Oliva and Keller, 1996; Keller, 1996), Italy (Luciani, 1997) and other localities with tropical to subtropical planktic foraminiferal assemblages. Nearly 2/3 of the species disappeared at or near the K–T boundary and about 1/3 of the species survived into the early Danian. The K–T extinct species group (which here includes species which are rare and appear to disappear 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 planktic foraminiferal assemblages (Fig. 6A,B). In contrast, the K–T survivor group consists of ecological generalists. They are 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. 6B).

Above the K–T boundary, triserial species (*Guembelitra*) dominate (~80–90%) in the small 38–63 μm size fraction, but are relatively few (<10%) in the larger >63 μm size fraction. This is likely a result of the high stress post-K–T boundary environment (MacLeod, 1993; MacLeod and Keller, 1994; MacLeod et al., 2000). Curiously, Cretaceous survivor species are rather common in zone P1a above the K–T boundary, especially the relative abundance of *Heterohelix navarroensis* which appears to increase. In fact, a peak of the latter species reaches 60% at the P0/

P1a boundary (Fig. 6B). This is very unusual. In general, survivor species strongly decrease in the early Danian zones P0 and P1a in all Tunisian sections, including at Elles II which was collected only 200 m distant from Elles I (see Keller et al., 2002). The anomalous abundance of small Cretaceous survivors at Elles I can therefore not be attributed to differential local ecological conditions, but is likely due to locally abundant reworked sediments as also suggested by the common presence of obviously reworked large tropical species (Fig. 4).

7. Discussion and conclusions

The progressive extinction pattern at Elles I is overall similar to that observed previously for the same interval at outcrops at El Kef and Ain Set-tara (Keller, 1988, 1996; Keller et al., 1995; Molina et al., 1998; Luciani, 2002), as well as in sections in Israel, Spain, Italy, Lattengebirge, Mexico and Brazil (Canudo et al., 1991; Keller and Benjamini, 1991; Peryt et al., 1993; Keller et al., 1993, 1994; Lopez-Oliva and Keller, 1996; Abramovich et al., 1998; Luciani, 1997; Apellaniz et al., 1997). Although in each of these localities the overall extinction pattern of specialists and survivorship of generalists is similar, there are enough differences to fuel a continuing controversy about the nature of the K–T mass extinction, whether progressive or instantaneous. One part of the controversy centers over whether there are pre-K–T extinctions that foreshadow stressful environmental changes during the latest Maastrichtian, or whether a bolide impact at the K–T boundary was solely responsible for the mass extinction. The other part centers over the nature and number of Cretaceous species survivorship.

These arguments are unlikely to be solved based on a narrow interval spanning the K–T boundary. Most K–T studies have concentrated on an interval of 50–100 cm below and above the boundary, or included at most the topmost few meters of the Maastrichtian, and few have examined environmental and faunal changes during the entire late Maastrichtian. However, stable isotope studies demonstrate profound climatic

changes during the last 500 kyr of the Maastrichtian (Stott and Kennett, 1990; Barrera and Keller, 1990, 1994; Barrera, 1994; Li and Keller, 1998a,b). High resolution studies are needed to determine the nature of the progressive biotic effects associated with climatic and environmental changes before the K–T boundary event.

Acknowledgements

We gratefully acknowledge Dr. N. Ben Haj Ali, Director of the Geological Survey of Tunisia, Tunis, and Dr. H. Ben Salem, for their tremendous logistical and transportation support for the field excursion and Workshop of May 1998 on Tunisian K–T boundary sections. Fieldwork for the Elles and El Melah sections was a joint effort with Thierry Adatte and Wolfgang Stinnesbeck and we gratefully acknowledge their collaboration. We thank H.P. Luterbacher and one anonymous reviewer for their comments and suggestions. This study was supported by NSF-INT 95-04309.

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