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High stress late Maastrichtian paleoenvironment: inference from planktonic foraminifera in Tunisia

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Abstract

High resolution (~5–10 kyr) planktonic foraminiferal analysis at Elles, Tunisia, reveals major changes in the structure of the Tethyan marine ecosystem during the upper Maastrichtian. During the first 1.5 Myr of the late Maastrichtian (68.3–66.8 Ma) relatively stable environmental conditions and cool temperatures are indicated by diverse planktonic foraminiferal populations with abundant intermediate and surface dwellers. A progressive cooling trend between ~66.8–65.45 Ma resulted in the decline of globotruncanid species (intermediate dwellers). This group experienced a further decline at the climax of a rapid warm event about 300 kyr before the K–T boundary. At the same time relative abundances of long ranging dominant species fluctuated considerably reflecting the high stress environmental conditions. Times of critical high stress environments during the late Maastrichtian, and particularly at the K–T boundary, are indicated by low species diversity and blooms of the opportunistic genus *Guembelitria* at warm–cool transition intervals. During the last 100 kyr of the Maastrichtian rapid cooling is associated with accelerated species extinctions followed by the extinction of all tropical and subtropical species at the K–T boundary.

Keywords: planktonic foraminifera; biostratigraphy; upper Maastrichtian; Tunisia; paleoecology; paleoclimate

1. Introduction

Until recently most studies of Maastrichtian planktonic foraminiferal populations that aimed to describe the nature of the Cretaceous–Tertiary (K–T) boundary mass extinction focused in extraordinary detail on the K–T transition itself, which represents at best a few hundred thousand years (e.g. Smit, 1982, 1990; Keller, 1988, 1989a, 1993; Canudo et al., 1991; Keller and Benjamini, 1991; Olsson and Liu, 1993; Keller et al., 1995, 1997; Pardo et al., 1996; Appellaniz et al., l997; Luciani, 1997; Molina et al., 1998). During the last few years, it has become increasingly evident that the nature of this mass extinction cannot be effectively addressed until the background variations of populations and their relationship to environmental parameters in the Maastrichtian ecosystem are understood (e.g. Keller, 1996). To date, only a few stratigraphically well constrained studies of a more complete Maastrichtian faunal record have been published, and these concern faunas from the Brazos River, Texas (Keller, 1989b), Denmark

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(Schmitz et al., 1992), the Southern Ocean (Huber, 1992), mid-latitude South Atlantic (Li and Keller, 1998a), Tunisia (Li and Keller, 1998b), and the Negev, Israel (Abramovich et al., 1998).

These studies have shown that the deterioration of Cretaceous planktonic foraminiferal populations began in the late Maastrichtian and accelerated over the last few hundred thousand years of the Maastrichtian. The onset of the decline was accompanied by blooms of the opportunistic genus *Guembelitria* which demonstrate the instability of the pelagic ecosystem during the last few million years of the Cretaceous (Abramovich et al., 1998). The faunal decline climaxed at the K–T boundary with the mass extinction of all specialized tropical–subtropical planktonic foraminiferal species, whereas the cosmopolitan and ecologically generalist species survived into the Danian (for a summary see Keller et al., 2002).

Recent studies of the Maastrichtian stable isotopic records from DSDP Sites 525A and 21 (Li and Keller, 1998a,c) leave no doubt that global climatic deterioration occurred during the Maastrichtian, and was accompanied by significant sea level fluctuations (see also Barrera, 1994; Barrera et al., 1997; Barrera and Savin, 1999). Furthermore, the timing of these events strongly suggests that the Late Cretaceous faunal decline was triggered by environmental changes. This suggests that a bolide impact at the K–T boundary was not the sole causal mechanism for the K–T mass extinction. Further detailed high resolution records that evaluate the Maastrichtian ecosystem stress are still needed if we are to understand the relationship between environment and biotic perturbations leading up to the K–T boundary. Among the regions of high potential for obtaining high resolution records are the sections from the northern part of Tunisia.

The Upper Cretaceous sequence of northern Tunisian was deposited in a series of basins which surrounds a tectonically emergent zone, the Kasserine Island (Fig. 1), the major source for clastic material into the basins (Adatte et al., 1998; Bensalem, 1998). The sediments within the northwestern basin are characterized by abundant pelagic microfaunas deposited on the outer shelf to upper slope (Li and Keller, 1998b).

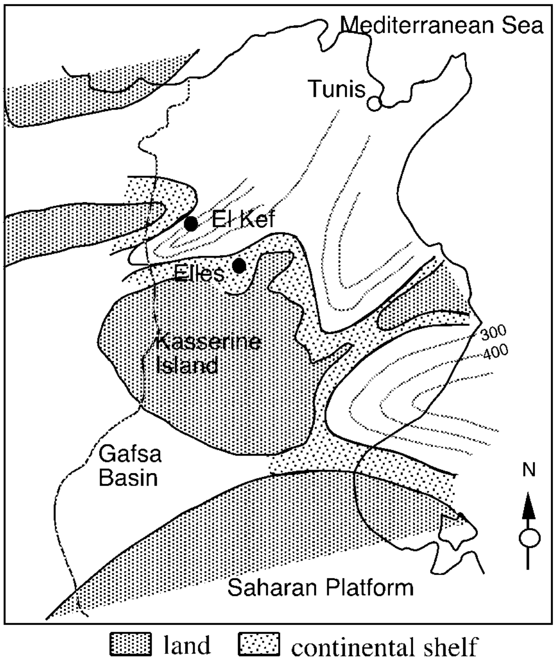

Fig. 1. Maastrichtian paleogeography of Tunisia (after Burollet, 1967). Note the paleogeographic location of the Elles section between the emergent zone of the Kasserine Island and El Kef section.

Most studies of Maastrichtian and Paleogene sections in Tunisia have concentrated on the K–T boundary transition at the El Kef stratotype (e.g. early studies summarized by Salaj (1980) and later studies by Keller et al. (1995)). High resolution microfossil and geochemical studies have generally focused on the 50–100-cm interval below and above the K–T boundary. Maastrichtian studies are few and generally of a stratigraphic nature (Salaj, 1980) with the exception of Nederbragt (1991) who studied the Heterohelicidae at El Kef. A more complete quantitative study of the entire Maastrichtian planktonic foraminiferal fauna and various geochemical analyses (stable isotopes, mineralogy, trace element geochemistry) at El Kef and Elles has recently been published by Li and Keller (1998b) and Li et al. (1999, 2000).

The objective of this study is to evaluate the late Maastrichtian faunal turnover at a section located near the hamlet of Elles in north-central

Tunisia (Fig. 1). In this section planktonic foraminiferal populations were quantitatively analyzed at 10–20-cm intervals, or on average one sample every ~5–10 kyr, for the last million years of the Maastrichtian.

2. Location, lithology and methods

The Elles section is located in the Karma valley near the hamlet of Elles, about 75 km southeast of the city of El Kef and the nearby K–T boundary stratotype section. The Maastrichtian sequence exposed in the Karma valley was deposited at middle to outer shelf depths and relatively close to the emergent zone of the Kasserine Island (Fig. 1). This position explains the high terrigenous content in Maastrichtian sediments at Elles, and the unusually high sedimentation rate (e.g. ~4 cm/1000 yr, Li and Keller, 1998b; Adatte et al., 2002). The very high sediment accumulation rate at Elles, which exceeds that of the El Kef section (Li and Keller, 1998b), has great potential for accurately evaluating the timing of environmental changes during the late Maastrichtian and particularly during the last million years of the Maastrichtian.

Lithologically, the upper Maastrichtian in northern Tunisia is represented by the El Haria Formation. Upper Maastrichtian sediments at Elles consist of relatively uniform marly shales with a 25-cm-thick resistant layer of bioturbated marly limestone at about 26 m below the K–T boundary. The K–T transition is marked by a 20-cm-thick channelized cross-bedded bioclastic layer (foraminiferal packstone), which underlies a 1-cm dark gray clay and thin rust-colored layer. The rusty layer contains an iridium anomaly and Ni-rich spinels which mark the K–T boundary (Adatte et al., 2002). A total of 191 samples were collected from the last 31 m of the Maastrichtian. Samples were collected at 10-cm intervals between 31.2 and 26.5 m, and at 20-cm intervals through the rest of the section. However, near the boundary interval samples were collected at 1-cm intervals.

In the laboratory, samples were disaggregated and washed through a >63-μm sieve until a clean foraminiferal residue was recovered, which was oven-dried at 50°C. Planktonic foraminiferal tests are recrystallized, but preservation of test morphology is very good. Population counts for planktonic foraminifera are based on random sample splits using a micro-splitter. From each sample approximately 250–300 planktonic foraminifera were picked from each of two size fractions (>63 μm and >150 μm **Background Data Set**[1]). Only the larger >150-μm size fraction of the uppermost meter of the section was analyzed for this report; the smaller >63-μm size fraction was studied by Keller et al. (2002). These two size fractions were analyzed in order to obtain statistically significant representations of the smaller and larger species. At the same time, the quantitative study of two population splits reduces the bias in first and last appearances due to the Signor–Lipps effect (Signor and Lipps, 1982). Species identifications are based on descriptions of Smith and Pessagno (1973), Robaszynski et al. (1984), Caron (1985) and Nederbragt (1991).

3. Biostratigraphy

In previous studies, the upper Maastrichtian of low to middle latitude was generally assigned to the *Abathomphalus mayaroensis* Zone (Caron, 1985; Robaszynski and Caron, 1995). More recently, the interval spanning the last 200–300 kyr has been assigned to the *Plummerita hantkeninoides* Zone (Masters, 1984; Pardo et al., 1996). Li and Keller (1998a) have further subdivided the late Maastrichtian *A. mayaroensis* Zone based on Cretaceous planktonic foraminiferal assemblages and the paleomagnetic time scale of DSDP Site 525A, and applied this chronology to the Tunisian sections at El Kef and Elles (Li and Keller, 1998b). Their zonal scheme subdivides the late Maastrichtian into four zones labeled CF1 to CF4 (CF = Cretaceous Foraminifera) as applied in this study (Fig. 2).

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[1] http://www.elsevier.com/locate/palaeo

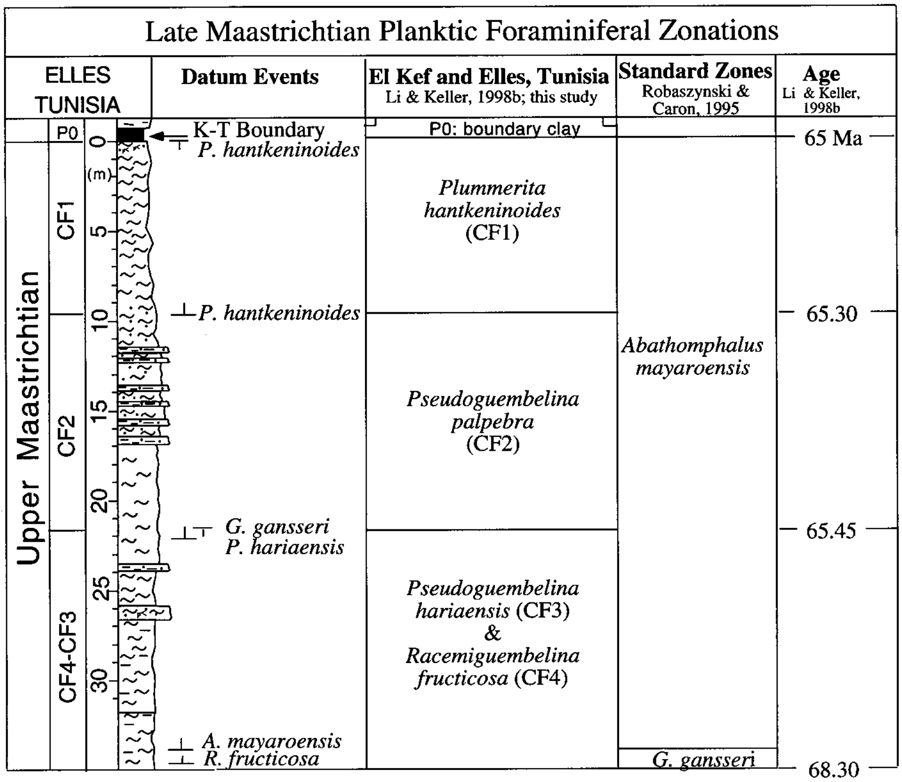


Fig. 2. Later Maastrichtian planktonic foraminiferal biozonation used in this study and comparison with the zonations of Li and Keller (1998b) and Robaszynski and Caron (1995).

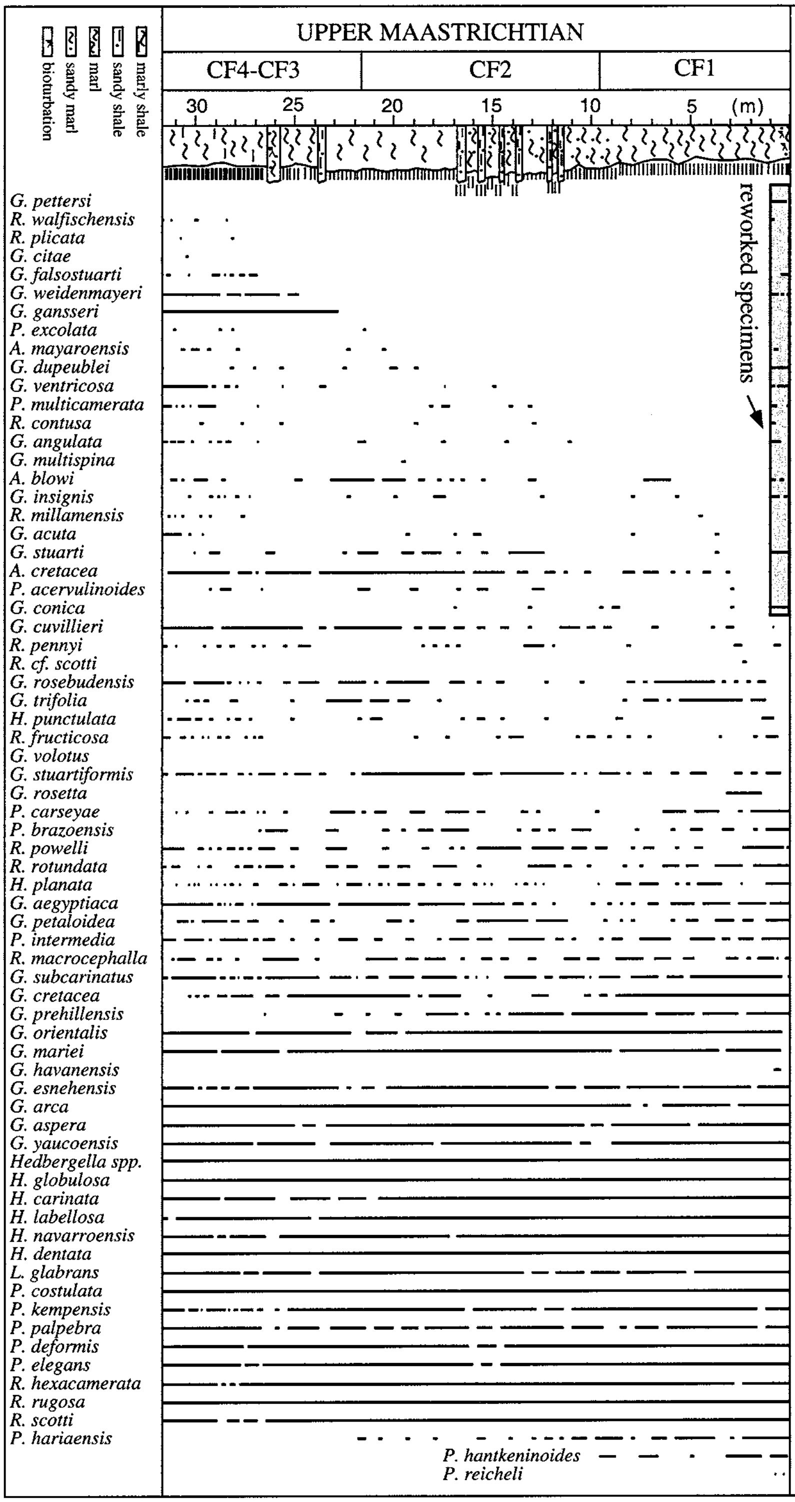
3.1. *Plummerita hantkeninoides* zone (CF1, 65–65.3 Ma)

This zone is defined by the total range of the nominate species. The zone was first defined by Masters (1984), based on sections in Egypt. Pardo et al. (1996) calibrated the age and the duration of this zone as spanning the last 200–300 kyr of the Maastrichtian based on the paleomagnetic record at Agost, Spain. At Elles, biozone CF1 spans the top 9.6 m of the Maastrichtian. This thickness represents the highest sedimentation rate (~3.2 cm/1000 yr) measured to date for this biozone. In contrast, zone CF1 at El Kef is 6 m thick, at Agost in Spain 3.8 m, and at Hor Hahar in the Negev, Israel, 8 m (Canudo et al., 1991; Abramovich et al., 1998).

3.2. *Pseudoguembelina palpebra* zone (CF2, 65.3–65.45 Ma)

The base of this zone is defined by the LA (last appearance) of *Gansserina gansseri*, and the top by the FA (first appearance) of *Plummerita hantkeninoides*. At Elles zone CF2 spans 12 m (from 21.6 to 9.6 m) and represents the highest sedimentation rate (~8 cm/1000 yr) measured to date for this interval. At the nearby El Kef section zone CF2 is only 3 m thick due to a local fault that truncates the base of the zone (Li and Keller,

Fig. 3. Planktonic foraminiferal species census data at Elles arranged in order of last appearances. Note that two-thirds of the upper Maastrichtian species are rare and sporadically present. These are tropical to subtropical species with large complex morphologies. Among these species, extinctions are progressive with 17 species disappearing during the late Maastrichtian. Sediment reworking is evident within the 50–100 cm below the K–T boundary where 12 of these species temporarily reappear.



Species Ranges of Planktic Foraminifera at Elles, Tunisia

1998b). Based on the paleomagnetic records at Site 525A and Agost, Zone CF2 spans about 150 kyr (Li and Keller, 1998a), though this correlation is tentative and needs further calibration at other localities.

3.3. *Pseudoguembelina hariaensis zone (CF3, 65.45–66.8 Ma)*

This zone is defined by the FA of *Pseudoguembelina hariaensis* at the base and the LA of *Gansserina gansseri* at the top. At the Elles section, the FA of *P. hariaensis* almost coincides with the LA of *G. gansseri* (20 cm below). The absence of the index species may be interpreted as either representing a hiatus, or ecological exclusion due to adverse environmental conditions. Since there are no structural or sedimentological changes (fault, lithological changes, hardground, and bioturbation), or abrupt faunal changes, indicative of a hiatus, we prefer the latter explanation, though the possibility of a hiatus cannot be excluded. This interpretation is supported by the rarity of *P. hariaensis* in the part of its stratigraphic range below Zone CF2, which was also observed at El Kef (Nederbragt, 1991; Li and Keller, 1998b). For this reason we have not subdivided Zones CF3 and CF4 based on the FA of *P. hariaensis*.

3.4. *Racemiguembelina fructicosa zone (CF4, 66.8–68.3 Ma)*

This zone is defined by the FA of *Racemiguembelina fructicosa* at the base and the FA of *Pseudoguembelina hariaensis* at the top. Only the upper part of the Zone is included in this study. The lower part of the zone was studied by Li and Keller (1998b).

4. Species ranges

The temporal range of a species is defined from its evolutionary first appearance to its last appearance or extinction. During its range, a species may only be intermittently or sporadically present, or have a truncated range as compared with other localities due to ecological, preservational or sedimentological factors. Outside its preferred habitat, ecological stress may result in shortened species ranges or sporadic occurrences. Species which are rare and only sporadically present may not be encountered in standard biostratigraphic analysis and therefore result in bias towards shortened species ranges, also known as the Signor–Lipps effect (Signor and Lipps, l982). But species ranges in the sediment record can also be biased towards prolonged ranges beyond that of the biological occurrence by bioturbation and reworking.

A total of 75 planktonic foraminiferal species were identified in upper Maastrichtian sediments at Elles. About 25 of these species have relatively continuous occurrences throughout the upper Maastrichtian (Fig. 3). They are generally abundant, small and simple morphotypes characteristic of ecological generalists that tolerate a wide range of environments across latitudes (e.g. hedbergellids, heterohelicids, guembelitrids). But two-thirds of the species are only sporadically present and generally few in numbers. These species have generally more complex morphologies (e.g. trochospiral, multiserial), narrow tolerance limits, and generally restricted to lower latitude environments. Similar species range patterns were observed at El Kef (Li and Keller, 1998b), and the Negev (Abramovich et al., 1998).

Of particular interest in the species census data at Elles is the progressive disappearance of 17 species (mostly globotruncanids) in the upper Maastrichtian preceding the K–T boundary extinction event (e.g. *Abathomphalus mayaroensis*, *Archaeoglobigerina blowi*, *Gansserina gansseri*, *Gansserina wiedenmayeri*, *Globotruncanita pettersi*, *Globotruncanita angulata*, *Globotruncana duepeblei*, *Globotruncana falsostuarti*, *Globotruncana insignis*, *Globotruncana ventricosa*, *Globigerinelloides multispina*, *Globotruncanella citae*, *Planoglobulina multicamerata*, *Pseudoguembelina excolata*, *Rosita contusa*, *Rosita plicata*, and *Rosita walfishensis*). A similar late Maastrichtian decrease in species richness (presumably due to extinction or high stress environment) was observed at El Kef (Li and Keller, 1998b) and the Negev (Abramovich et al., 1998). However, at Elles 12 of these species temporarily reappear in the uppermost meter of the Maastrichtian (upper Zone CF1, see Fig. 3), after

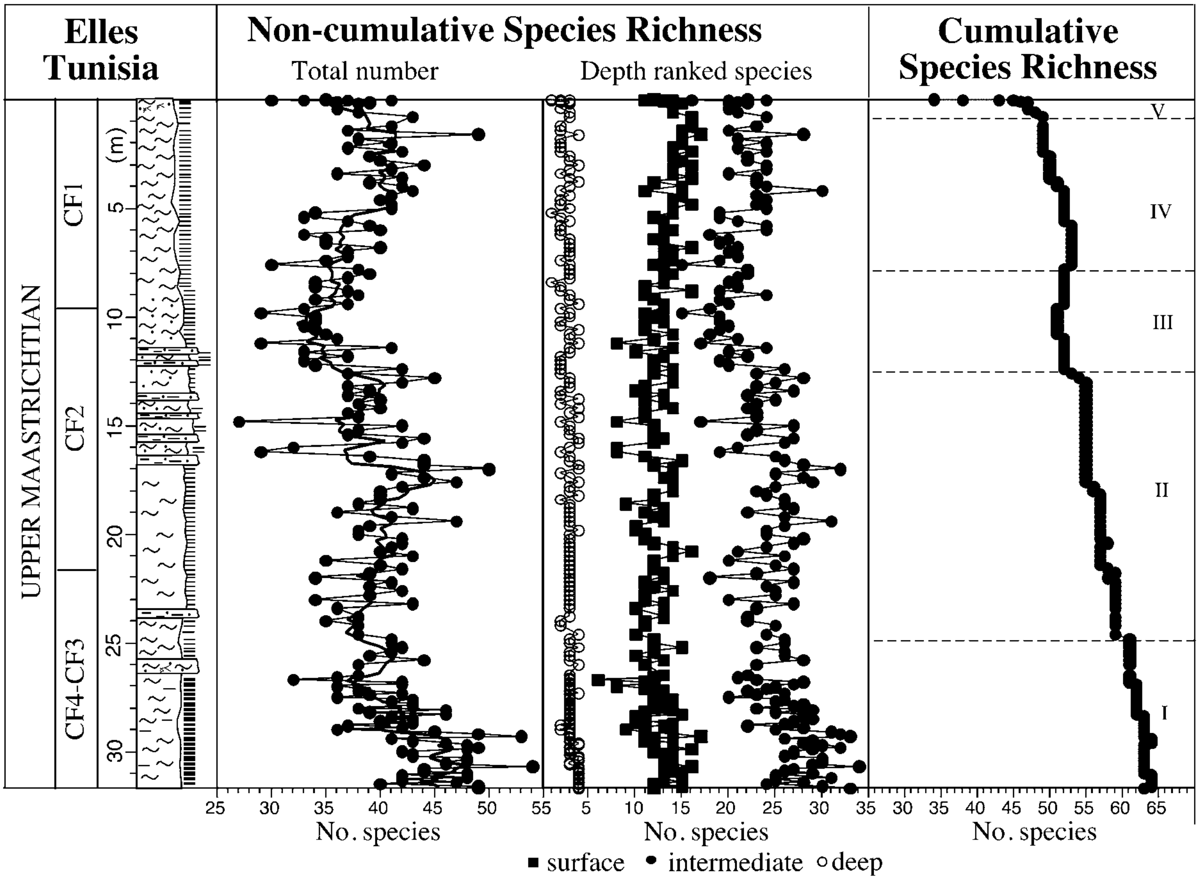


Fig. 4. Planktonic foraminiferal species richness patterns of the late Maastrichtian at Elles, in terms of cumulative and non-cumulative species richness (black line marks five points running average). Non-cumulative species richness is further divided based on three depth ranked foraminiferal groups: surface, intermediate, and deep dwellers. Cumulative species richness shows a gradual decline with accelerated species extinctions during the last meter below the K–T boundary, and reflects the evolutionary response to global environmental stress. Non-cumulative species richness shows a decreasing trend with strong sinusoidal variations mainly within intermediate dwellers that reflect the local response to changes in climate and watermass stratification.

prolonged absence. There are two likely explanations for this phenomenon. (1) The reappearance of these species represents their true evolutionary ranges, whereas their observed early extinction is an artifact of rare species (e.g. Signor–Lipps effect, rare and sporadic occurrences that could be missed in the sample analyzed). This is a real possibility for any environmentally sensitive species in stressed environments. (2) Sediment reworking by currents and redeposition into younger sediments is a very common way to produce the observed pattern of isolated species occurrences.

Though it is often difficult to separate reworked species, especially if reworking of extant species is involved, there are some clues, including poor preservation as compared with in situ specimens, occurrences restricted to specific intervals marked by bioturbation, hardground, and lithological changes. In addition, reworked sediments generally preserve large, robust and thick-shelled specimens as a result of transport and winnowing. In contrast, isolated occurrences due to the Signor–Lipps effect show no preservation preference – large and small, fragile and robust specimens

Table 1
Relative percent abundances of planktonic foraminifera in the 63–150-μm size fraction at Elles, Tunisia

Depth (m) below the KTB Biozones	4.20 CF1	4.00	3.80	3.60	3.40	3.20	3.00	2.80	2.60	2.40	2.20	2.00	1.80	1.60	1.40	1.20
A. blowi																
A. cretacea																
Guembelitria cretacea	1	6	6	2	3	5	7	3	4	4	1	1	2	5	1	1
G. trifolia	1	3	4	x	6	4	4	1	6	4		2	1	3	1	1
Globigerinelloides aspera	1	2	x	x	2	1	1	3	1	x	1	2	1	1	1	1
G. prehillensis	x			1										x	x	x
G. volutus		x			1					1						
G. subcarinatus	1	2	3	x	3	2	1	3	2	x	x	1		x	1	1
G. rosebudensis	x	x			2	1		1	1		1	1		x	x	1
G. multispina																
G. yaucoensis	4	2	2	4	3	2	1	2	2	2	2	2	2	2	1	1
Abathomphalus mayaroensis																
Globotruncana aegyptica				x								1	x			
G. orientalis	x			1	x	1										
G. arca	x							1				x				
G. esnehensis								x						x		
G. falsostuarti																
G. mariei			x	1	x	1								x		
G. insignis											x					
G. ventricosa																
G. rosetta						x			x							
Globotruncanita conica																
G. angulata																
G. pettersi																
G. stuarti																
G. stuartiformis					x											
G. petaloidea	x		x							x			x			
G. citae																
G. havanensis	x	1	2	1	x		x	1		x	1	1		x		
Gublerina cuvilieri							x									
G. acuta																
Gansserina gansseri																
G. wiedenmayeri																
Hedbergella	4	9	8	8	5	6	9	7	5	10	4	5	8	6	5	4
L. glabrans	2	2	1	3	1	2	4	4	3	3	2	2	x	2	2	3
H. globulosa	28	20	19	19	12	19	18	22	22	18	18	16	13	16	24	29
H. carinata	6	2	4	4	1	4	1	4	5	3	4	3	3	4	4	5
H. labellosa	x							x		x	1	x		x		1
H. navarroensis	10	19	17	16	18	15	23	9	17	14	11	8	21	15	7	10
H. dentata	15	15	15	11	19	11	15	15	14	14	21	25	30	23	28	13
H. planata	1	1	1	2	2					x					1	1
H. punctulata																
Plummerita hantkeninoides					1			x	x			x		1		x
P. reicheli																
Pseudoguembelina costulata	16	13	14	20	17	16	13	18	15	19	28	19	16	16	16	22
P. hariaensis		x									1	x	x		x	1
P. kempensis	2	1	1	1	2	1	1	2	1	2	1	1	2	1	1	1
P. palpebra			x	x			x					x		x		
Pseudotextularia deformis				1										x	x	x
P. intermedia																
P. elegans	x		1	1	1	2	x	1		x		x	x	1	1	1
Rugoglobigerina hexacamerata	1	x		1	1	1	1	1	x	x	1	2		x	1	

Table 1 (*continued*)

Depth (m) below the KTB Biozones	4.20 CF1	4.00	3.80	3.60	3.40	3.20	3.00	2.80	2.60	2.40	2.20	2.00	1.80	1.60	1.40	1.20
R. macrocephala									x	x						
R. rotundata																
R. pennyi																
R. rugosa	2	2	1	1	1	3	1	2	1	1	2	4	x	3	3	3
R. scotti	x	xx	1	1	x	1					x	1		1		1
R. cf scotti																
Total number counted	412	264	331	339	325	241	270	302	331	229	323	299	270	554	335	336

x = < 1%, xx = very rare.

should be represented. Most of the suspect species, which are reappearing in the uppermost meter at Elles well after their last continuous occurrences, show characteristics of reworked specimens. In addition, field and laboratory sedimentological and mineralogical observations indicate various features characteristic of reworking and current transport, including cross-bedding, size gradation, and the presence of a foraminiferal packstone (see Adatte et al., 2002). These features strongly indicate that the reappearance of the suspect species (stippled interval, Fig. 3) is an artifact of sediment reworking.

5. Species richness

Species richness, or the number of species present within a sample, is the simplest measure of diversity and an important tool for understanding fluctuations in the structure of an ecosystem. There are two measures of species richness: simple species richness and cumulative species richness. Simple species richness is the number of species physically present in any given sample. It measures the species flux in and out of a given ecosystem. As such it is a measure of ecological variability, of climatic changes, of short-term availability of nutrients, of oxygen and salinity fluctuations. In short, it is an index of climatic, ecological, geographic and overall environmental variability. In contrast, cumulative species richness is the number of species theoretically present in any given sample. It assumes that a species is present from its first evolutionary appearance to its extinction and ignores any temporary absence in the sediment record due to adverse environmental fluctuations. Cumulative species richness thus expresses the evolutionary response of species to long-term changes in the environment over time.

5.1. Cumulative species richness

The cumulative species richness pattern at Elles shows a gradual decline through the upper Maastrichtian followed by accelerated species extinctions during the top 1 m below the K–T boundary (Fig. 4). The lower part of the section (lower CF4–3 interval, part I) shows a diverse planktonic foraminiferal community with a maximum of 63 species. This species community gradually decreased to 53 species by the upper Zone CF2 (part II). Species richness remained low during the transition between CF2 and CF1 (part III) and decreased by three species in the middle to upper Zone CF1 (part IV). A rapid decrease in species richness by 18 species occurred in the uppermost Maastrichtian, last meter below the K–T boundary (part V), followed by the extinction of all remaining tropical and subtropical species at or near the K–T boundary (Fig. 4, Tables 1 and 2 **Background Data Set**[1]). This cumulative species richness pattern reflects the decreased evolutionary diversity during the late Maastrichtian and the accelerated rate of extinction approaching the K–T boundary event. Similar patterns were observed from sections at El Kef and the Negev, Israel (Li and Keller, 1998b; Abramovich et al., 1998). High biotic stress induced by rapidly changing climatic conditions near the end of the Maastricthian are the likely causal factors for this species richness decrease (Li and Keller, 1998c).

Table 2
Relative percent abundances of planktonic foraminifera in the size fraction >150 μm at Elles, Tunisia

Depth (m) below the KTB	0.18	0.13	0.08	0.04	0.03	0.02	0.01	0.00
Biozones	CF1							
Archaeoglobigerina blowi	x		x		x	x		x
A. cretacea								
Globigerinelloides aspera	1	1	1	1	x	1		
G. prehillensis		x			4		x	x
G. rosebudensis		x						
G. multispina								
G. subcarinatus	x	x	1			x		
G. volutus								
G. yaucoensis		2	x		x			
Abathomphalus mayaroensis								
Globotruncana aegyptica		1	1	1	1	x	1	2
G. arca	2	2	3	2	3	5	5	7
G. orientalis	3	1	1	1	2	3	2	2
G. dupeublei	x		x	x	x	x		x
G. esnehensis	x	1	1	1	1	2	1	1
G. ventricosa	x		1	1		x	x	1
G. angulata						x	x	1
G. falsostuarti				x	x	x	x	1
G. mariei	4	3	1	1	2	3	3	2
G. insignis	x			x	x	x		
G. rosetta	1						1	1
Globotruncanita conica	1				x	1	1	1
G. pettersi	x	x	x					
G. stuarti	x	1	1		x	x	1	1
G. stuartiformis	2	x	2	1	x	4	x	2
G. petaloidea	1	1	1	1	x	x	x	x
G. citae								
G. havanensis	3	1	2	3	2	3	3	
Gublerina cuvilieri	1	x						
Gublerina acuta						1		
Gansserina gansseri								
G. wiedenmayeri	x		x		x	x		
Heterohelix globulosa	34	38	37	46	37	28	35	30
H. punctulata		x			1	x	x	
H. labellosa	4	3	2	2	4	4	6	8
L. glabrans	1	1	1		1	x	x	
Planoglobulina brazoensis						x	1	1
P. carseyae		x	1			x		1
P. acervulinoides			x		x		x	
P. multicamerata	x	x				x	x	
Plummerita hantkeninoides	x	1	x					
P. reicheli				x				
Pseudoguembelina costulata	5	8	7	6	4	2	3	4
P. excolata								
P. hariaensis	3	3	2	4	5	4	3	2
P. kempensis	1	x	x		1		1	x
P. palpebra	3	1	1	2	2	3	2	1
Pseudotextularia deformis	3	1	3	3	6	7	7	7
P. intermedia	x		1	x		1	x	
P. elegans	8	7	12	8	8	6	4	4
Racemiguembelina fructicosa	1	x				x		1
R. powelli	1	1		x	1	2	1	1

Table 2 (*continued*)

Depth (m) below the KTB Biozones	0.18 CF1	0.13	0.08	0.04	0.03	0.02	0.01	0.00
Rosita contusa						x		
R. patelliformis								
R. plicata								
R. walfischensis	x							
Rugoglobigerina hexacamerata	2	3	x	1	1	1	4	2
R. miliamerensis		x				1		
R. macrocephala	3	1	2	1	2	1	3	2
R. rotundata	1		1	1			1	1
R. pennyi	x		x			1		
R. rugosa	8	13	12	10	11	10	6	5
R. scotti	5	3	2	4	3	2	4	5
R. cf scotti				1				
Total number counted	314	351	330	312	309	269	272	293

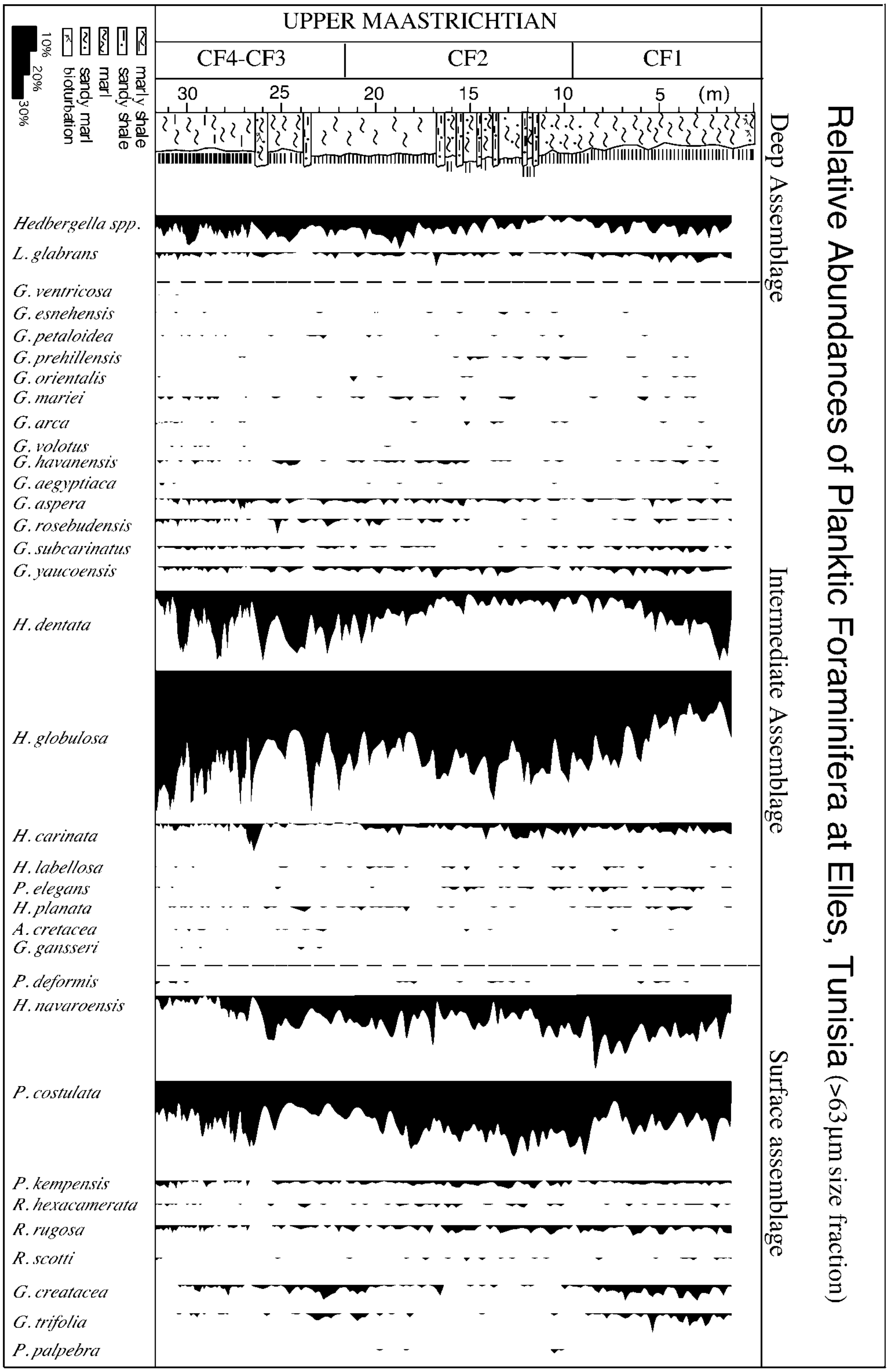
x = < 1%

5.2. Non-cumulative species richness (total number)

The non-cumulative species richness (total number) shows a very different pattern from that of the cumulative species richness (Fig. 4). Where the latter shows a linear acceleration of the evolutionary decrease, the former shows a decreasing trend with strong sinusoidal variations. The maximum species diversity (∼50–54 species) is found in the lowermost part of the CF4–3 interval, but decreased rapidly to 37–40 species in the upper CF4–3. In the lower part of Zone CF2, species richness values at first increased by seven species, then decreased to 32–35 species in the upper CF2 to lower CF1 Zones. In the lower-middle CF1, species richness temporarily increased by five species, and then decreased rapidly to 30–35 species towards the K–T boundary prior to the extinction of all tropical and subtropical forms (for changes across the K–T transition see Keller et al., 2002). These broad-based sinusoidal variations likely reflect changes in climate and watermass stratification, though no climate data based on stable isotopes are available at this time.

5.3. Non-cumulative species richness (depth ranked)

More environmental information can be gained by evaluating the non-cumulative species richness patterns based on groups living at specific depth habitats (e.g. surface mixed layer, intermediate or thermocline depth, and deep dwellers below thermocline, Fig. 4). Depth habitats of planktonic foraminifera, inferred from stable isotopic data of individual species, provide a solid basis for reconstructing species life habitats and stratification of the water column (D'Hondt and Arthur, 1995; Li and Keller, 1998b). Species richness depth habitat patterns show that surface and deeper dwellers remained relatively stable throughout the upper Maastrichtian. Though at the end of the Maastrichtian (uppermost meter), the species richness of surface dwellers decreased. Thus, the non-cumulative diversity fluctuations noted above primarily occurred within the intermediate dwellers which lived within the thermocline layer. In today's oceans a well-developed thermocline layer characterized by high productivity supports the highest diversity of planktonic foraminifera. This is largely due to the high nutrient content recycled from deeper waters, and hence an abundant food supply (e.g. phytoplankton and other zooplankton, Hemleben et al., 1989). The strength of the thermocline layer primarily depends on the temperature gradient and therefore reflects mostly climate and oceanic circulation. The depth ranked species richness curves thus also reflect significantly accelerating biotic stress induced by climate changes.


Relative Abundances of Planktic Foraminifera at Elles, Tunisia (>63µm size fraction)
UPPER MAASTRICHTIAN
CF4-CF3
CF2
CF1
30
25
20
15
10
5
(m)
marly shale
sandy shale
marl
sandy marl
bioturbation
10%
20%
30%
Deep Assemblage
Intermediate Assemblage
Surface assemblage
Hedbergella spp.
L. glabrans
G. ventricosa
G. esnehensis
G. petaloidea
G. prehillensis
G. orientalis
G. mariei
G. arca
G. volotus
G. havanensis
G. aegyptiaca
G. aspera
G. rosebudensis
G. subcarinatus
G. yaucoensis
H. dentata
H. globulosa
H. carinata
H. labellosa
P. elegans
H. planata
A. cretacea
G. gansseri
P. deformis
H. navaroensis
P. costulata
P. kempensis
R. hexacamerata
R. rugosa
R. scotti
G. creatacea
G. trifolia
P. palpebra

6. Relative abundance changes

6.1. Heterohelicids

The planktonic foraminiferal populations of the upper Maastrichtian at Elles are typical of the Tethyan pelagic upper slope and outer shelf environments (Figs. 5 and 6). Long-ranging biserial heterohelicid species dominate (generally >70%) in the two size fractions analyzed (>63 μm and >150 μm). Heterohelicid populations in the smaller (>63 μm) size fraction comprise mainly four species (*Heterohelix globulosa*, *Heterohelix dentata*, *Heterohelix navarroensis*, and *Pseudoguembelina costulata*), whereas in the larger (>150 μm) size fraction three species dominate (*H. globulosa*, *Pseudotextularia elegans*, and *Pseudotextularia deformis*). Hence, with the exception of *H. globulosa*, heterohelicid species are specific to the smaller size fraction. All other Maastrichtian taxa are much less abundant, especially in the smaller (>63 μm) size fraction (Fig. 5).

Within the heterohelicids of the >63 μm size fraction, *Heterohelix dentata* gradually decreased in the lower part of Zone CF2 (from ~30% to ~10%), and increased again towards the upper part of CF1 (~30%). *Pseudoguembelina costulata* decreased in the upper part of CF4–3 (~30 to ~10%, Fig. 5), and increased again (~30%) in the lower part of CF2. *Heterohelix navarroensis* significantly increased from the lower to the upper part of CF4–3 (from ~5% to ~20%, Fig. 5). The relative abundance of *Heterohelix globulosa* fluctuated in Zone CF4–3, and stabilized in CF2 with high average values of ~40%. The terminal decline of *H. globulosa* began in the upper part of CF1 (~20%). In the larger (>150 μm) size fraction the most significant biotic change within the heterohelicids is the sharp abundance decline of *Pseudotextularia deformis* in the upper part of CF2 which coincided with the sharp increase in *Pseudotextularia elegans* (Fig. 6).

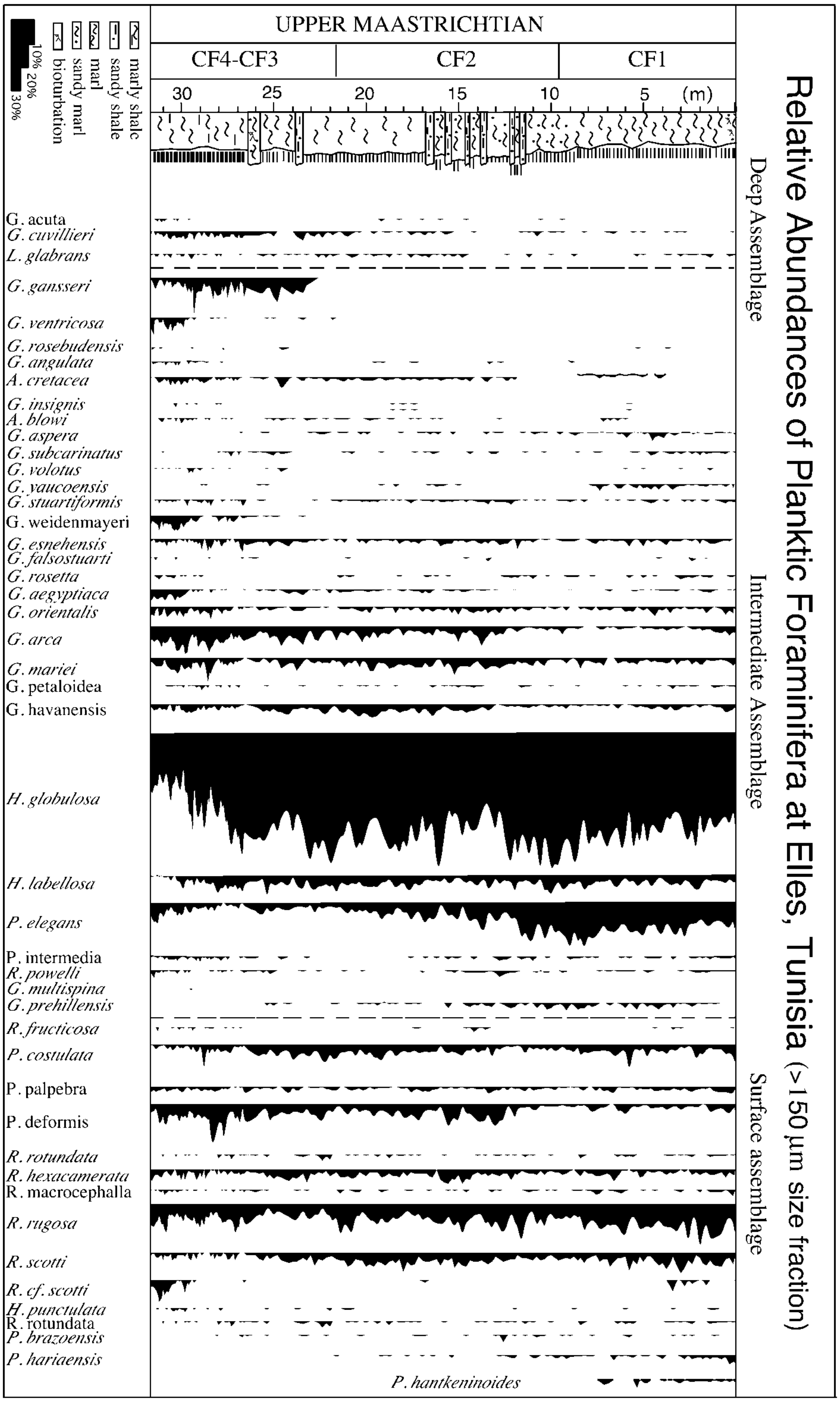
6.2. Guembelitrids

Two separate *Guembelitria* blooms (*G. cretacea* and *G. trifolia*) occurred in the upper Maastrichtian as observed in the >63-μm size fraction (Fig. 5). The first *Guembelitria* bloom occurred in the interval between the upper part of Zone CF4–3 and the lower part of Zone CF2, with the combined relative abundance of the two species reaching a maximum of 8.5% (see Fig. 7). The second *Guembelitria* bloom occurred in Zone CF1 where it reached a maximum level of 13.6%. These blooms are not observed at the nearby El Kef section (Li and Keller, 1998b), probably due to the lower sample resolution.

In previous studies of the Maastrichtian, *Guembelitria* has been reported in low abundances in outer shelf and deep sea environments (D'Hondt and Keller, 1991; Keller, 1996), and relatively high abundances in shallow shelf regions (e.g. Brazos River (Keller, 1989a,b), Stevns Klint (Schmitz et al., 1992), Seldja, Tunisia (Keller et al., 1998). High *Guembelitria* abundances in the pelagic marine environment have been described so far only from the earliest Danian (Smit, 1982, 1990; Keller and Benjamini, 1991; Schmitz et al., 1992; Keller et al., 1993, 1995; Pardo et al., 1996), and in the upper Maastrichtian of the Negev (Abramovich et al., 1998).

Guembelitria are ecological opportunists as indicated by the very low $\delta^{13}C$ values associated with the early Danian blooms that indicate a drastic reduction in primary productivity (Keller, 1996; Keller et al., 2002). The presence of two *Guembelitria* blooms in the upper Maastrichtian at Elles reflects the instability of the planktonic population structure at this time. The relative strength of environmental stress is indicated by the magnitude of the *Guembelitria* blooms. By this measure, the environmental stress at Elles is lower than in the Negev where coeval *Guembelitria* blooms reached a maximum of ~80% as

Fig. 5. Relative abundances of planktonic foraminifera in the smaller (>63 μm) size fraction at Elles. Note that only about five species dominate the assemblages and four of these species are biserial morphotypes and the fifth is a hedbergellid. There are short-term (Milankovitch) fluctuations and long-term trends. Intervals of environmental crises during the late Maastrichtian can be identified based on two separate blooms of the opportunistic *Guembelitria* species (*G. cretacea*, and *G. trifolia*) in zones CF1 and CF3–4.


Relative Abundances of Planktic Foraminifera at Elles, Tunisia (>150 μm size fraction)
UPPER MAASTRICHTIAN
CF4-CF3
CF2
CF1
30
25
20
15
10
5
(m)
marly shale
sandy shale
marl
sandy marl
bioturbation
10%
20%
30%
Deep Assemblage
Intermediate Assemblage
Surface assemblage
G. acuta
G. cuvillieri
L. glabrans
G. gansseri
G. ventricosa
G. rosebudensis
G. angulata
A. cretacea
G. insignis
A. blowi
G. aspera
G. subcarinatus
G. volutus
G. yaucoensis
G. stuartiformis
G. weidenmayeri
G. esnehensis
G. falsostuarti
G. rosetta
G. aegyptiaca
G. orientalis
G. arca
G. mariei
G. petaloidea
G. havanensis
H. globulosa
H. labellosa
P. elegans
P. intermedia
R. powelli
G. multispina
G. prehillensis
R. fructicosa
P. costulata
P. palpebra
P. deformis
R. rotundata
R. hexacamerata
R. macrocephalla
R. rugosa
R. scotti
R. cf. scotti
H. punctulata
R. rotundata
P. brazoensis
P. hariaensis
P. hantkeninoides

compared with 13.6% at Elles (Abramovich et al., 1998). Thus the biotic response to the environmental stress induced by climatic perturbation in different parts of the Tethys may be of the same nature, but of different magnitude.

6.3. Globotruncanids

In the larger (>150 μm) size fraction, major biotic changes took place between the upper CF4–3 and the upper CF2 Zones when many globotruncanids decreased in relative abundance (*Gansserina gansseri*, *G. wiedenmayeri*, *G. arca*, *G. orientalis*, *G. mariei*, and *G. havanensis*, Fig. 6). This decrease demonstrates that the upper Maastrichtian decline of globotruncanids was expressed not only by decreased species richness, but also by decreased population abundance. A similar decrease in globorotaliids was observed in the Negev sections, Israel (Abramovich et al., 1998). However, because globorotaliid are large species and generally few to rare, this decrease is not evident when counting only the smaller (>63 μm) size fraction (Fig. 5), and hence Li and Keller (1998b) who analyzed only the smaller size fraction, failed to note it.

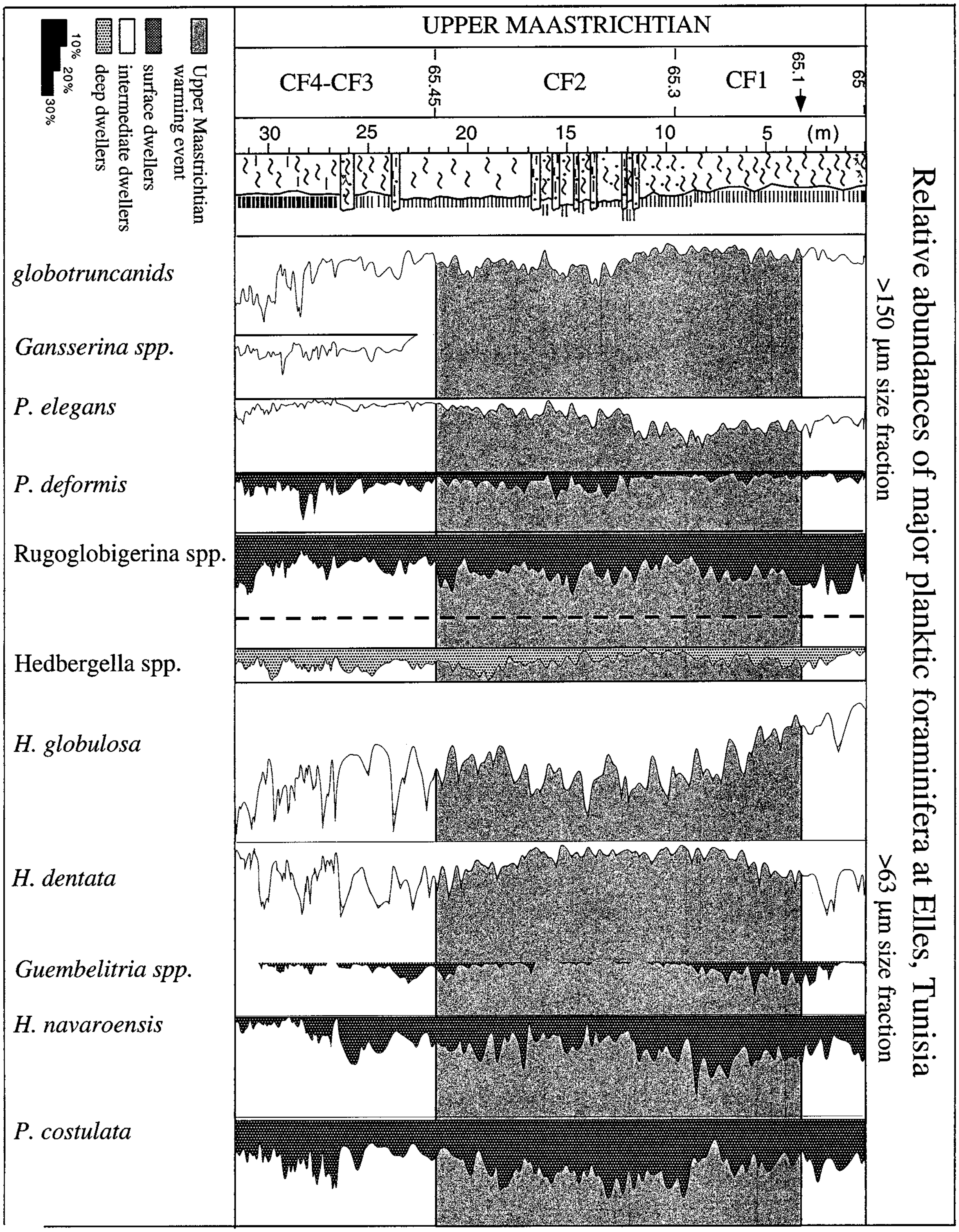
Globotruncanids are usually regarded as intermediate to deep dwellers and geographically limited to the Tethyan tropical–subtropical belt during the Cretaceous. All globotruncanid species were extinct before or at the K–T boundary. The limited distribution of globotruncanids and their characteristic complex morphologies illustrate both their specific requirements for stable undisturbed environmental conditions (mainly well stratified watermass with constant food supply, and stable temperatures) and their specialized life strategy as many modern analogous forms of today's tropics indicate (Caron and Homewood, 1983; Leckie, 1989; Keller et al., 1995; Keller, 1996). Therefore, their decline during the late Maastrichtian at Elles demonstrates biotic stress induced by instability in the Tethyan tropic belt environment preceding the K–T boundary (Fig. 4).

7. Late Maastrichtian paleoenvironment in Tunisia

The biotic response to climatic perturbations is reflected by relative abundance changes in species populations, species census data and species richness patterns (both cumulative and non-cumulative). At Elles all of these parameters show significant variations during the late Maastrichtian and a progressively accelerating decrease in species richness during the last 300 kyr of the Maastrichtian. In addition, biotic stress is indicated by the decline in relative abundances of dominant species, sporadic blooms of opportunistic species, and abundance fluctuations in populations of long-ranging species. Interpreting these records in terms of specific climate changes, such as warm and cool events, variations in temperature gradients and watermass stratification, remains a challenge. In Tunisian sections, this task is further complicated by oxygen isotope records of foraminifera that are often compromised by diagenetic alteration and therefore allow no temperature interpretations (e.g. El Kef, Keller and Lindinger, 1989).

To date, the most detailed and least diagenetically compromised stable isotope paleotemperature record for the late Maastrichtian is from middle latitude DSDP Site 525A. This record indicates that relatively cool temperatures prevailed during the first 3 Myr of the late Maastrichtian (CF4–3 interval) with intermediate water temperatures about 6–7°C cooler than in the early Maastrichtian and surface temperatures cool but variable (Li and Keller, 1998a,c). This long-term cooling trend continued throughout the CF4–3 interval and reached minimum temperatures in the upper part of CF3 coincident with a hiatus at El Kef at 65.5 Ma (Li and Keller, 1998c). At

Fig. 6. Relative abundances of planktonic foraminifera in the larger (>150 μm) size fraction at Elles. Note that biserial taxa are still dominant in this size fraction, but rugoglobigerinids are also common. Globotruncanids (mainly tropical complex morphologies) are significantly more common than in the smaller size fraction, but decrease significantly near the top of CF3–4 and CF2.


Relative abundances of major planktic foraminifera at Elles, Tunisia

Elles, the environmental parameters of planktonic foraminifera for the equivalent late Maastrichtian interval (CF4–3) indicate a well-stratified water column characteristic of a cooler climate in which deeper water habitats are well populated, particularly in the lower part of the CF4–3 interval. These conditions are mainly demonstrated by the high species richness and the relative abundance of species with complex trochospiral shells (globotruncanids), and biserial species that inhabit the intermediate to deeper waters (e.g. at or below the thermocline, Fig. 7). However, towards the upper part of the Zone CF4–3 interval globotruncanids began to decline (from ~30% to ~20%, see Fig. 7) and species richness decreased by 10 species, resulting in depleted intermediate water communities (Fig. 4). This decline may reflect a decrease in water temperatures below the optimal tolerance range for globotruncanid species. In general, the geographic restriction of most globotruncanid species to low latitudes, their relatively low abundance at middle latitudes, and near absence in higher latitudes reflects a narrow temperature tolerance range. Alternatively, it is possible that the onset of the subsequent warming in CF2–1 (Li and Keller, 1998a,c) began earlier in the Tethys resulting in decreased thermal gradients and hence habitats for subsurface populations. Stable isotope data of the eastern Tethys are still needed to evaluate which scenario is most likely.

In middle to high southern latitudes, the long-term late Maastrichtian cooling was interrupted by a short-term warming of 3–4°C in both surface and intermediate waters (e.g. Sites 690 and 525A, Barrera, 1994; Li and Keller, 1998a,c). This warming began 450 kyr before the K–T boundary (base of Zone CF2), reached a maximum at 65.3 Ma (base of Zone CF1) and ended 100 kyr before the K–T boundary (Li and Keller, 1998c). During the last 100 kyr of the Maastrichtian temperatures dropped rapidly, and returned to the previous low level. The biotic effect of this warm event on the Tethyan ecosystem is well demonstrated at Elles (Fig. 7). Globotruncanids, which began to decline in the upper part of the CF4–3 interval, experienced another decline during the maximum warming (lower to middle part of Zone CF1) when their combined relative abundance decreased by another 10%, and the species richness decreased by ca. five species. The same response was also observed in the Negev sections (Abramovich et al., 1998). *Heterohelix dentata* (a biserial intermediate dweller) was also affected by this event. During the warm interval the relative abundance of this species decreased by ~30%, and with the return to cooler temperatures the relative abundance increased again. The two species of the genus *Pseudotextularia* (*P. elegans*, and *P. deformis*) also seem to respond to this climatic change. When the relative abundance of the surface dweller, *P. deformis*, decreased near the base of Zone CF1, the relative abundance of the intermediate dweller *P. elegans* increased (Fig. 7). The fluctuation in the relative abundances of other major species, such as *Pseudoguembelina costulata*, *Rugoglobigerina* spp., *Heterohelix navarroensis*, and *Hedbergella* spp., does not seem to correspond to major temperature changes.

It is interesting to note that some species, which respond in the same way to climatic changes, do not share the same habitat. Also, some species that share the same habitat show opposite responses to climatic changes. For example, both the intermediate dwelling globotruncanids and the surface dweller *Pseudotextularia deformis* declined during the maximum warming. But the intermediate dweller *Heterohelix globulosa* increased during the warming, whereas the intermediate dweller *Heterohelix dentata* decreased. This dem-

Fig. 7. Summary of relative abundances of dominant planktonic foraminiferal species and genera from the two size fractions (>150 μm and >63 μm) at Elles. Abundance changes reflect planktonic foraminiferal response to climatic instability. Shaded interval marks the late Maastrichtian warm event (age estimate based on biostratigraphic correlation with the warm event at Site 525A, Li and Keller, 1998c). Note the species turnover within the biserial population in response to the warm event; the biserial species *Heterohelix dentata*, and *Pseudotextularia deformis* decreased, whereas the biserial species *Heterohelix globulosa*, *Pseudotextularia elegans* and *Pseudotextularia costulata* increased. Globotruncanids also decreased preceding and during the warm event.

onstrates that a given change in the environment can have different effects on species that share the same habitat depth zone. Consequently, species that inhabit the same depth habitats do not necessarily have the same requirements for resources, or the same tolerance for environmental changes. For example, the intermediate dwelling heterohelicids are considered to have a high tolerance for low oxygen conditions (Premoli Silva and Boersma, 1989; Keller, 1993; Barrera and Keller, 1994), but intermediate dwelling globotruncanids clearly do not, they decrease or disappear during times of expanded low oxygen conditions (e.g. Almogi-Labin et al., 1993). The small triserial *Guembelitria*, best known as disaster species that thrived after the mass extinction of tropical and subtropical species at the K–T boundary, generally thrived at times of major biotic stress associated with major climate transitions. In addition to the K–T boundary, two blooms of these disaster species were observed during the upper Maastrichtian at Elles and in the eastern Tethys (Abramovich et al., 1998).

8. Conclusions

Upper Maastrichtian planktonic foraminiferal assemblages at Elles reveal major faunal turnovers that reflect the global long-term climate cooling followed by rapid and extreme warming between 200 and 400 kyr before the K–T boundary, and a return to a cooler climate during the last 100 kyr of the Maastrichtian. Although there are still few studies that evaluate the association of specific Cretaceous species with particular environmental changes, preliminary results are encouraging and promise that this approach will reveal much about the environmental changes and biotic stresses that accompany major climate transitions.

From the Elles study a number of preliminary conclusions can be reached.

(1) Cumulative species richness data (total number of species living), which reflect evolutionary trends, show a gradual decrease in diversity through the last 3 Myr of the Maastrichtian with a rapid decrease during the last 100 kyr of the Maastrichtian.

(2) Non-cumulative species richness data (actual number of species present), which reflect environmental changes, show major broad-based fluctuations that mirror climate changes and associated variations in ocean circulation, thermal gradients and watermass stratification. The Elles records indicate that environmental changes were particularly strong during the last 500 kyr of the Maastrichtian.

(3) Non-cumulative depth ranked (surface, intermediate, deep dwellers) species richness data reveal the particular habitat most severely affected by ongoing climate and environmental changes. At Elles, the intermediate dwellers living within thermocline depths drove both the long-term evolutionary trends and the response to short-term environmental changes. Surface and deeper dweller groups remained relatively stable.

(4) Species census data (individual species ranges) also reveal environmental flux. At Elles, 17 species (intermediate dwellers) gradually disappeared during the upper Maastrichtian and reflect the increasing environmental stress during the last 2 Myr of the Cretaceous.

(5) Globotruncanids are the most sensitive indicators of Maastrichtian climate changes. This group of thermocline dwellers (intermediate) thrived during relatively cool climates and a well-stratified water column. But their temperature tolerance limit is relatively low and they are prone to extinctions when temperatures are either too cool or too warm.

(6) Guembelitrids are useful indicators for environmental extremes and high biotic stress, particularly at transitions from warm to cold climates and vice versa. During these times, *Guembelitria* species responded with opportunistic blooms that reflect the high stress and unstable planktonic population structure.

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