Diversification and extinction in Campanian-Maastrichtian planktic foraminifera of Northwestern Tunisia

LIANGQUAN LI & GERTA KELLER

ABSTRACT

Investigation of Campanian-Maastrichtian planktic foraminifera in north Tunisia reveals that the late Maastrichtian not only ends with a mass extinction, but also attains maximum species diversity during their evolutionary history. Maximum species diversity is reached during global cooling in the early late Maastrichtian over a 600 kyr interval (69.1–69.7 Ma) when species richness nearly doubled with the evolution of many rugoglobigerinids and globotruncanids. No species extinctions occur at this time and there is little change in the relative abundance of existing species, whereas new species did not evolve into numerically large populations during the succeeding late Maastrichtian. This suggests that species originations did not result in major competition and that the early-late Maastrichtian climatic cooling may have resulted in increased habitats and nutrient supply for marine plankton. The onset of the permanent decline in Cretaceous species richness began at 65.9 Ma and accelerated during the last 50–100 kyr of the Maastrichtian, culminating in the mass extinction of all tropical and subtropical taxa at the end of the Maastrichtian. Climate changes appear to be responsible for both the rapid evolutionary activity in the early late Maastrichtian, as well as the gradual decline in species richness near the end of the Maastrichtian, although the additional stress imposed on the ecosystem by a bolide impact is the likely cause for the final demise of the tropical and subtropical fauna at the K-T boundary.

ZUSAMMENFASSUNG

Die stratigraphische Abfolge planktonischer Foraminiferen des Campan und Maastricht wurde in zwei Profilen in der SW Tethys eingehend untersucht. Demnach erreichte Artenmannngfaltigkeit im unteren Obermaastricht, vor dem Massensterben am Ende des Maastricht, ein Maximum. In nur 600 kyr (von 69.7 bis 69.1 Ma) verdoppelte sich die Anzahl der Arten durch das Erscheinen vieler neuer Rugoglobigeriniden und Globotruncaniden. Nur wenige Arten starben in diesem Zeitraum aus – die ursprüngliche planktonische Faunengemeinschaft existierte fast unverändert weiter. Die Evolution der neuen Arten erfolgte daher nicht aus einem ökologischen Wettbewerb heraus, sondern war vermutlich durch eine Abkühlung des Klimas im oberen Maastricht bedingt, die zu einer Vermehrung der ökologischen Nischen und zu einer Erhöhung des Nährstoffangebots führte. Die zahlenmässige Abnahme der Planktonforaminiferen begann um 65.9 Ma, beschleunigte sich über die letzten 50–100 kyr des Maastricht und endete mit dem Massensterben der tropischen Arten an der Kreide/Paläogengrenze. Klimatische Veränderungen sind möglicherweise für beides verantwortlich, die schnelle Vermehrung der Arten und den Beginn des Massensterbens, doch die Ursache für letzteres könnte zusätzlich auch noch der Einschlag eines Asteroiden gewesen sein.

Introduction

Most studies of late Cretaceous planktic foraminifera concentrate on their demise near the Cretaceous-Tertiary (K-T) boundary and little information exists on their diversity, abundance, or faunal turnover preceding their extinction. The scarcity of Maastrichtian studies is largely due to the interest in the K-T boundary mass extinction and the common assumption that no major climatic or environmental changes occurred during the late Cretaceous (Barron 1983). Stable isotopic data from southern oceans have shown, however, that the Maastrichtian is characterized by a long-term cooling trend that is punctuated by cooling maxima in the early-late and latest Maastrichtian followed by a short-term warming preceding the K-T boundary mass extinction (Barrera & Huber 1990; Stott & Kennett 1990; Barrera 1994; D'Hondt & Lindinger 1994; Li & Keller 1998).

There is ample evidence that Maastrichtian environmental changes caused various species extinctions among different faunal groups well before the K-T boundary event, including dinosaurs, inoceramids, rudists and ammonites (Sloan et al. 1986; MacLeod & Ward 1990; Ward et al. 1991; Stinnesbeck 1996; Archibald 1996). The effects of these environmental changes on planktic foraminifera, the group that suffered the most severe mass extinction at the K-T boundary, are still relatively unknown. Most workers have assumed that their demise at the end of the Maastrichtian was solely due to a meteorite impact and that climatic and sea-level changes had little adverse effect on their diversity. Published reports generally note increased species diversity from the early to the late Maastrichtian and a sudden extinction at the K-T boundary (e.g., Said 1978; Salaj 1980; Boersma 1981, 1984; Caron 1985; Huber

Department of Geosciences, Princeton University. Princeton, NJ 08544, USA, FAX: (609)258-1274, or E-Mail: liangli@geo.princeton.edu
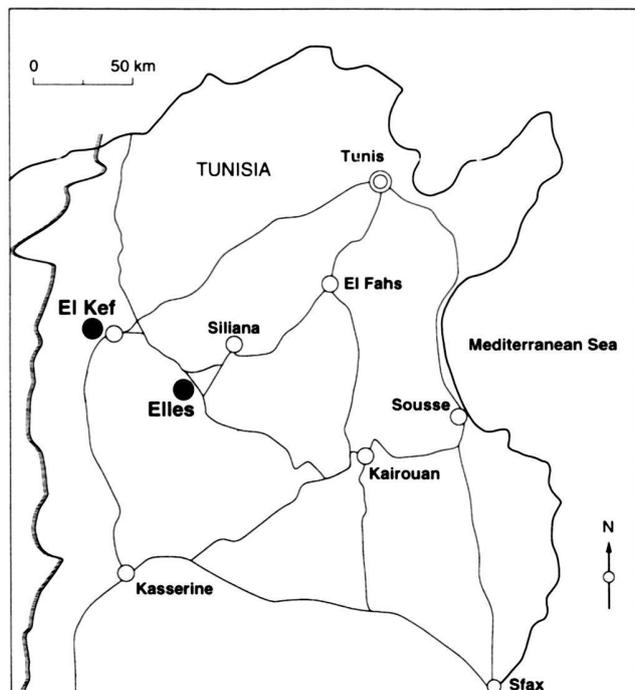
Fig. 1. Location map of the El Kef and Elles sections in northwestern Tunisia.

Fig. 2. Lithologic variations at the studied sections of El Kef and Elles, Tunisia.

1992). However, no high resolution or quantitative faunal records document faunal turnovers through the Maastrichtian. The most detailed studies to date are Nederbragt's (1991) taxonomic report of the Maastrichtian biserial planktic foraminifera at El Kef, Tunisia, and our recent reports on planktic foraminiferal diversity and climatic changes in the southern Atlantic Ocean DSDP Site 525A (Li & Keller 1998).

The current study was undertaken in order to evaluate whether the rapid evolutionary diversification observed during the early-late Maastrichtian and onset of the mass extinction during the last 300 kyr of the Maastrichtian at DSDP Site 525A was restricted to the South Atlantic or was a global phenomenon. The main objectives of this study, therefore, are to document the planktic foraminiferal diversity and turnovers in northwestern Tunisia during the late Campanian through Maastrichtian, and thereby provide a context within which to evaluate their rise to dominance followed by the mass extinction of this group. To obtain these objectives, we document species ranges and develop a high resolution planktic foraminiferal zonation, evaluate rates of evolution and extinctions, changes in total diversity, relative abundances of species and depth habitats. For this study we have chosen the El Kef and Elles sections (Fig. 1), which have excellent outcrop exposures and abundant, well-preserved planktic foraminifera. Benthic foraminifera indicate that El Kef was deposited in an upper slope to outer shelf environment, whereas Elles was situated in a shallower middle to outer shelf setting (Said 1978;

Keller 1988a; Speijer 1994). These paleodepth inferences support the paleogeographic reconstruction of Burollet (1956) and Bellier et al. (1983).

Lithology and methods

Two late Cretaceous sedimentary sequences were examined in northwestern Tunisia, with one located near the town of El Kef in a valley northwest of the El Kef K-T boundary stratotype and the other in a valley near the hamlet of Elles about 80 km to the southeast of El Kef (Fig. 1). These two sections show similar lithological sequences spanning from the Campanian to the Eocene (Fig. 2). At the El Kef section, two minor faults are present in the Maastrichtian interval at 10 m and 22 m below the K-T boundary, a slump covers an interval between 42–47 m below the K-T boundary and vegetation covers marls above the upper Campanian limestone. At Elles, the sequence is continuously exposed and no significant fault zones or slumps are present.

The lower part of the upper Campanian sediments at Elles and El Kef consists of massive light grey limestones rich in invertebrates, particularly inoceramids and rare ammonites were

Stage	Depth (m) (Elles)	Lithology (Elles)	Samples	Lithology (El Kef)	Depth (m)	Datum Events	El Kef and Elles (this study)	DSDP Site 525A (Li and Keller, 1998)	Age (Ma)	El Kef, Tunisia (Nederbragt, 1991)	Standard Zones (Caron, 1985)	Nannofossil El Kef
							K/T Boundary					
						⊤ P. hantkeninoides	P. hantkeninoides (CF1)	P. hantkeninoides (CF1) & P. palpebra (CF2)	65.00	Racemiguembelina fructicosa	Abathomphalus mayaroensis	CC26b
						⊥ P. hantkeninoides	P. palpebra (CF2)		65.30			
						⊤ G. gansseri			65.45			
						⊥ P. hariaensis	P. hariaensis (CF3)	P. hariaensis (CF3)	66.83			CC26a
						⊥ A. mayaroensis	Racemiguembelina fructicosa (CF4)	Racemiguembelina fructicosa (CF4)				
Upper Maastrichtian						⊥ R. fructicosa			68.33	Gansserina gansseri	Gansserina gansseri	CC25c
							Pseudotextularia intermedia (CF5)	Pseudotextularia intermedia (CF5)				CC25c or CC25a-b
						⊤ G. linneiana	Rosita contusa (CF6)	Rosita contusa (CF6)	69.06			
						⊥ R. contusa			69.56			CC25a-b
						⊥ G. gansseri	Gansserina gansseri (CF7)	Gansserina gansseri (CF7)	70.39			
L. Maastrichtian						⊥ G. aegyptiaca	Globotruncana aegyptiaca (CF8)	Globotruncana aegyptiaca (CF8)	72.48	Globotruncanella havanensis	Globotruncana aegyptiaca	No data
						⊤ G. calcarata	Globigerinelloides subcarinata (CF9)	Globigerinelloides subcarinata (CF9)	74.00*		Globotruncanella havanensis	
Campanian						⊥ G. calcarata	Globotruncanita calcarata (CF10)	No data	~74.8*	Globotruncanita calcarata	Globotruncanita calcarata	

▱ fault   ▱ marl   ▱ limestone   ▱ shale   ▱ slump/covered

* age estimate based on Bralower et al. (1995).

Fig. 3. Late Cretaceous planktic foraminiferal and nannofossil zonations at the El Kef and Elles sections in northwestern Tunisia. Note that the late Maastrichtian is subdivided into seven planktic foraminifera zones.

noted at El Kef. Above the limestones is a 10 m thick grey marly shale followed by a sequence of 10–25 cm thick limestone layers. These limestone layers are evenly spaced about 25 cm apart at El Kef and 1–2 m at Elles (Fig. 2). Inoceramids are still present in these limestone layers, but rare or absent in the marly shales above. Uniform grey marly shales mark the Maastrichtian above the limestone layers. The K-T boundary is well marked in both localities by a 50 cm thick dark clay layer. Samples were collected at 20 cm intervals between 12 and 20 m at El Kef and an average of 50 cm intervals throughout of the rest of the section at El Kef and Elles.

In the laboratory, samples were soaked in water for several days, sonically agitated for 15 seconds in order to separate sediment infilling from foraminiferal tests and then washed through a 63 μm sieve. This procedure was repeated several times until a clean foraminiferal residue was obtained. Planktic foraminiferal preservation is generally good, although foraminiferal tests are recrystallized. There is no evidence of

significant dissolution. Quantitative faunal analysis is based on representative sample splits (using an Otto microsplitter) of about 300 specimens in the size fraction >63 μm. All planktic foraminiferal species were picked from this size fraction, identified and mounted on microslides for a permanent record. The remaining sample residue was searched for rare species and their presence was noted. Relative abundances of planktic foraminiferal species are listed in Appendix Tables 1 and 2.

Biostratigraphy

Biostratigraphy and correlation of the Elles and El Kef sections is based on planktic foraminiferal analysis as summarized in Figure 3 along with commonly used planktic foraminiferal zonations for the upper Campanian and Maastrichtian. The nannofossil zonation of the El Kef interval by Pospichal (1994 and written communication) is included for comparison. In an earlier study, we proposed a new high resolution biozonation

for the Maastrichtian interval based on DSDP Site 525A which has excellent fossil and paleomagnetic records (Li & Keller 1998). We further develop this biozonation based on the Tunisian sections. Our new biozonation is similar to the zonations by Caron (1985) and Nederbragt (1991), except that the interval encompassed by the late Maastrichtian zones, *Gansserina gansseri* and *Abathomphalus mayaroensis* or *Racemiguembelina fructicosa*, is subdivided into seven biozones to yield higher resolution time control. For convenience each biozone has been labeled CF for Cretaceous Foraminiferal zone and numbered 1 to 10 from youngest to oldest (Fig. 3).

Age and completeness of sediment record

Two major concerns for biostratigraphers are the age and completeness of the sections analyzed. Numeric age control is generally based on magnetostratigraphy which itself is calibrated based on radiometric ages. For example, for the Maastrichtian the radiometric ages serve as cornerstones in the geomagnetic polarity for this interval and by interpolation the duration of magnetochrons are estimated (Cande & Kent 1992; Gradstein et al. 1995). The degree of uncertainty includes the error margins of the radiometric ages (both analytical and sample errors) and magnetochrons, the latter is based on the assumption of linear progression of seafloor spreading. Additional error is introduced when numeric ages are calculated based on biostratigraphic correlation (e.g., diachronous datum events) in the absence of magnetostratigraphy as is the case for the Tunisian sections. Though it is difficult to estimate the magnitude of the total error margins it may reach as high as 0.5 m.y.

For the Tunisian sections numeric ages were extrapolated based on biostratigraphic correlation with DSDP Site 525A which has an excellent paleomagnetic record (Chave 1984). The magneto- and biostratigraphy plotted vs. the standard magnetostratigraphy at Site 525A (Fig. 4A) indicate relatively continuous sedimentation through the Maastrichtian. Thus, for the new biozones (CF1 to CF10) we have extrapolated ages based on correlation of planktic foraminiferal datum events and the magnetostratigraphy of Site 525A (Fig. 3, Li & Keller 1998). However, because the low latitude index species *Plummerita hantkeninoides* is absent at Site 525A, the age for Zone CF1 was determined from magnetostratigraphy at Agost, Spain (Pardo et al. 1996). We recognize, however, that the practice of extrapolating ages for the Tunisian sections based on biostratigraphic correlation may result in significant age uncertainties (possibly as high as 0.5 m.y.) because of the lack of paleomagnetic control, potentially diachronous datum events and incomplete sediment records. Nonetheless, until paleomagnetic studies are forthcoming for the Tunisian sections, these age estimates provide a reasonable time control for the Maastrichtian zonation in this region as suggested by the depth vs. age plot (Fig. 4B). Although this plot suggests very variable sediment accumulation rates at El Kef, this is probably largely due to discontinuous sedimentation and local faults. For example, the low sediment accumulation rates in Zones CF3 and

CF4 (4.4–5.5 m/myr) coincide with an interval bounded by local fault zones and hiatuses were recognized in Zones CF10, CF8 and at the CF7/CF6 boundary.

The hiatus at the CF7/CF6 Zone boundary is marked by the simultaneous first appearances of ten species (Figs. 5 and 6). In Zone CF8 a hiatus is marked by abundant trace fossils of *Zoophycos* and *Ophiomorpha*, and abundant fragments of mollusks and echinoids, at the top of the limestone layers (Figs. 3 and 4B). In the lower part of the section at Elles, a hiatus was recognized by the presence of a hardground, abundant inoceramids, *Stegaster*, wood fragments and horizontal burrows of *Ophiomorpha* at the limestone to marl transition in Zone CF10. Benthic foraminifera indicate that these two hiatuses are associated with low sea-levels and erosion or non-deposition (Li et al. in prep.). Thus, sediment accumulation at El Kef and Elles is not continuous from the late Campanian through the Maastrichtian. Nevertheless, the sections are *stratigraphically complete* because all biozones are present; this means that the missing intervals are within a biozone or span parts of two biozones.

Campanian-Maastrichtian boundary

The Campanian-Maastrichtian boundary has not been formally defined, though at the Second International Symposium on Cretaceous Stage Boundaries in Brussels (Sept., 1995), organized by the Subcommission on Cretaceous Stratigraphy of ICS, the section at Tercis near Dax in Aquitaine, southwestern France, was proposed as the new boundary stratotype and the ammonite *Pachydiscus neubergicus* (FA) was the preferred candidate for defining this boundary (Odin 1996). However, no studies are known to us that correlate this datum event to planktic foraminiferal datum events within the same section. Informal reports suggest that the FA of *P. neubergicus* predates the FA of *Gansserina gansseri* and postdates the LA of *Globotruncanita calcarata* (Stinnesbeck, personal communication 1996). However, in published literature the Campanian-Maastrichtian boundary is generally placed at the LA of *G. calcarata* which in some studies is placed at the FA of *P. neubergicus* (e.g., Robaszynski et al. 1983–1984). Considering the uncertainties in defining this boundary, we follow the current practice of placing the Campanian-Maastrichtian boundary at the LA of *G. calcarata*. Future integrative ammonite and planktic foraminiferal studies are necessary to determine the stratigraphic relationships.

The numeric age for the Campanian/Maastrichtian boundary has been variously placed at 74.5 Ma (Cande & Kent 1992), 74 Ma (Bralower et al. 1995) or 71.3 Ma (Gradstein et al. 1995). The younger age assignment of 71.3 Ma is largely based on linear interpolation of K/Ar ages of two bentonites; one in the early Maastrichtian *Baculites grandis* Zone dated at 70.1 ± 0.7 Ma and the other in the late Campanian *Baculites compressus* Zone dated at 73.2 ± 0.7 Ma (Obradovich 1988, 1993). Gradstein et al. (1995) correlate the 71.3 Ma age to the boundary between these two ammonite zones. The older 74 or

Fig. 4A. Magneto- and biostratigraphy of DSDP Site 525A plotted against the Geomagnetic Polarity Time Scale. Ages for datum events and sedimentation rates were extrapolated based on this timescale (see Li & Keller 1997) and applied to the Tunisian sections.

Fig. 4B. Age vs. depth correlations at the El Kef and Elles sections based on the numeric ages extrapolated from the paleomagnetic time scale at Site 525A. Note the relatively low sedimentation rates in Zones CF3, CF4, CF8 and CF9 suggest hiatuses as also indicated by faults, hardgrounds, trace fossil and lithological changes. Sedimentation rates are calculated for each biozone. Figures in parentheses indicate sedimentation rates at Elles. The age estimate for the top of *G. cal-carata* at 74.0 Ma (see also text) is based on Bralower et al. (1995).

Species Ranges of Planktic Foraminifera at Elles, Tunisia

Fig. 5. Planktic foraminiferal species ranges from the late Campanian to the late Maastrichtian at Elles, Tunisia. Note that species evolution is gradual during the early Maastrichtian followed by a rapid diversification in the early late Maastrichtian (Zones CF8–CF6).

Fig. 6. Planktic foraminiferal species ranges during the Maastrichtian at El Kef, Tunisia. Note the rapid species diversification in the early late Maastrichtian (Zones CF8– CF6).
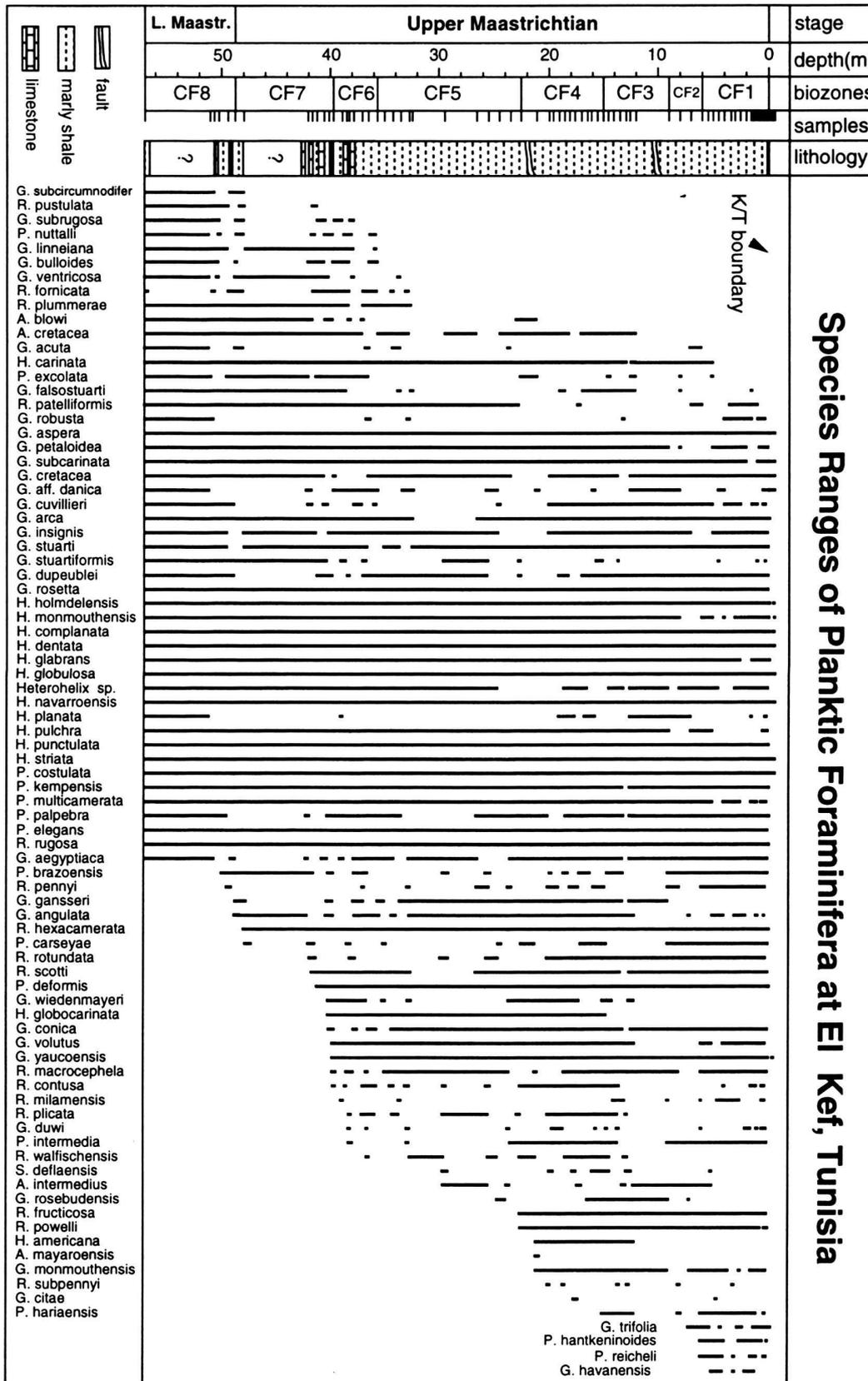
74.5 Ma age assignments are based on magnetostratigraphic correlation of the *G. calcarata* LA datum event in the Gubbio section, Italy, where this datum occurs in the upper part of C33N (Alvarez et al. 1977). We prefer to follow Cande and Kent (1992) and Bralower et al. (1995) in using the older age, because the correlation between microfossil datums and the two ammonite zones is unknown. Note, however, that the placement of the Campanian/Maastrichtian boundary, whether at 71.3 Ma, 74 Ma, or some other age, does not change the chron boundary ages. Therefore, our age extrapolations for the foraminiferal zones for Site 525, El Kef and Elles are not affected by the choice of the older 74 Ma age.

At the Second International Symposium on Cretaceous Stage Boundaries in Brussels it was also recommended that the Maastrichtian stage be formally divided into two substages (Lower and Upper), though, "there was no agreement on the boundary-criterion for the base of the Upper Maastrichtian" (Odin 1996, p. 115). It was suggested that the problem be further studied. Planktic foraminiferal workers have generally placed the Lower-Upper Maastrichtian boundary at the FA of *G. gansseri* (Robaszynski et al. 1983–84; Caron 1985) or at the FA of *A. mayaroensis* (Boersma 1984; Huber 1990). In this study we followed the informal practice of placing the Lower-Upper Maastrichtian boundary at the FA of *G. gansseri*.

Biozonation

The ***Plummerita hantkeninoides*** Zone (**CF1**), marks the uppermost Cretaceous foraminiferal biozone and is defined by the total range of the nominate taxon (Pl. I, Figs. 2; Pardo et al. 1996). The top of this zone also marks the K-T boundary and is characterized by the mass extinction of tropical-subtropical planktic foraminifera (Fig. 5) and an Ir anomaly at the base of the overlying clay layer (Keller et al. 1996). At El Kef, Zone CF1 spans the top six meters of the Maastrichtian. This interval is estimated to encompass the last ~300–400 kyr of the Maastrichtian, based on biostratigraphic correlation of El Kef and Agost, Spain, and the revised timescale of Berggren et al. (1995).

The ***Pseudoguembelina palpebra*** Zone (**CF2**), is defined by the last appearance (LA) of *Gansserina gansseri* at the base and the first appearance (FA) of *P. hantkeninoides* at the top (Pl. I, Fig. 3). At El Kef, this zone spans 3 m (from 6 m to 9 m), though a local fault truncates the base and suggests that Zone CF2 may be incomplete. Based on the paleomagnetic record at Site 525A, Zone CF2 spans about 150 kyr.

The ***Pseudoguembelina hariaensis*** Zone (**CF3**), is defined by the FA of *P. hariaensis* at the base and the LA of *G. gansseri* at the top (Pl. I, Fig. 4). At El Kef, *P. hariaensis* first appears 15.0 m below the K-T boundary. A fault zone occurs at 10 m, indicating that part of this zone is missing. At Site 525A, Zone CF3 spans about 1.4 myr within chron 30N (Li & Keller 1998).

The ***Racemiguembelina fructicosa*** Zone (**CF4**), marks the interval between the FA's of *R. fructicosa* at the base and *P.*

hariaensis at the top (Pl. I, Fig. 5). At El Kef, *R. fructicosa* first appears at 22.5 m and just below a minor fault zone. The low sedimentation rate (~5.5 m/myr) within Zone CF4 suggests that part of this zone is missing at El Kef (Fig. 4B). Based on DSDP Site 525A, Zone CF4 has a duration of 1.5 myr.

The ***Pseudotextularia intermedia*** Zone (**CF5**), defines the interval from the LA of *G. linneiana* to the FA of *R. fructicosa* (Pl. I, Figs. 6–8). At El Kef, this Zone spans from 35.7 to 22.5 m and at Elles from 41 to 48 m (Figs. 5 and 6). Zone CF5 is named after *P. intermedia*, which first appears in Zone CF6 at El Kef and at the top of CF7 at Elles, but well-developed typical morphotypes of this species are characteristic of Zone CF5. Based on graphic correlation of El Kef and Site 525A, Zone CF5 spans ~700 kyr in the upper chron 31R and lower chron 31N.

The ***Rosita contusa*** Zone (**CF6**), is defined by the FA of *R. contusa* at the base and the LA of *G. linneiana* at the top (Pl. I, Figs. 9–10). At El Kef, Zone CF6 spans an interval of 4.1 m and at Elles 4.5 m. At Site 525A this zone occurs within chron 31R and is about 500 kyr long. The near simultaneous first appearance of these species at the limestone/marl transition suggests the presence of a short hiatus or condensed interval.

The ***Gansserina gansseri*** Zone (**CF7**), is defined by the FA's of *G. gansseri* at the base and *R. contusa* at the top (Pl. I, Figs. 12–13). At El Kef, *G. gansseri* first appears between limestone layers (48.8 m) below a covered interval (Fig. 5). At Elles, where outcrop exposures are more continuous, *G. gansseri* first appears in the marls above the limestone layers that appear stratigraphically equivalent to the *G. gansseri*-bearing limestone layers at El Kef. It is therefore possible that the true first appearance of *G. gansseri* was not recovered at Elles, as also suggested by the simultaneous first appearances of *G. gansseri* and *P. palpebra* at the base of CF7, whereas at El Kef *P. palpebra* is present below this interval (Figs. 5 and 6). At Site 525A, Zone CF7 occurs within chron 31R and spans ~800 kyr (Fig. 4A).

The ***Globotruncana aegyptiaca*** Zone (**CF8**), is defined by the FA's of *G. aegyptiaca* at the base and *G. gansseri* at the top (Pl. I, Figs. 14–15). This zone is equivalent to the *G. aegyptiaca* Zone of Caron (1985, Fig. 3). At El Kef, the base of this zone was not sampled. At Elles, Zone CF8 spans 14 m (from 15.8 to 29.8 m, Figs. 3 and 6). Field observations indicate the presence of a hiatus at the limestone/marl transition within Zone CF8 at Elles as also suggested by the low sedimentation rates (6.4 m/myr, Fig. 4B). At Site 525A, Zone CF8 spans an interval of 2.1 myr from chron 32N to the base of chron 31R (Fig. 4A).

The ***Globigerinelloides subcarinata*** Zone (**CF9**), is defined by the LA of *Globotruncanita calcarata* at the base and the FA of *G. aegyptiaca* at the top (Pl. I, Fig. 14–15). This zone is equivalent to the *Globotruncanella havanensis* Zone of Caron (1985), but has been renamed because *G. havanensis* was not observed in this interval at Elles (Fig. 3). Zone CF9 spans 6.1 m (from 9.7 to 15.8 m) in the Elles section. Based on age estimates by Bralower et al. (1995), the top of the *G. calcarata* Zone is at 74 Ma. This age estimate is close to that de-

Species Richness
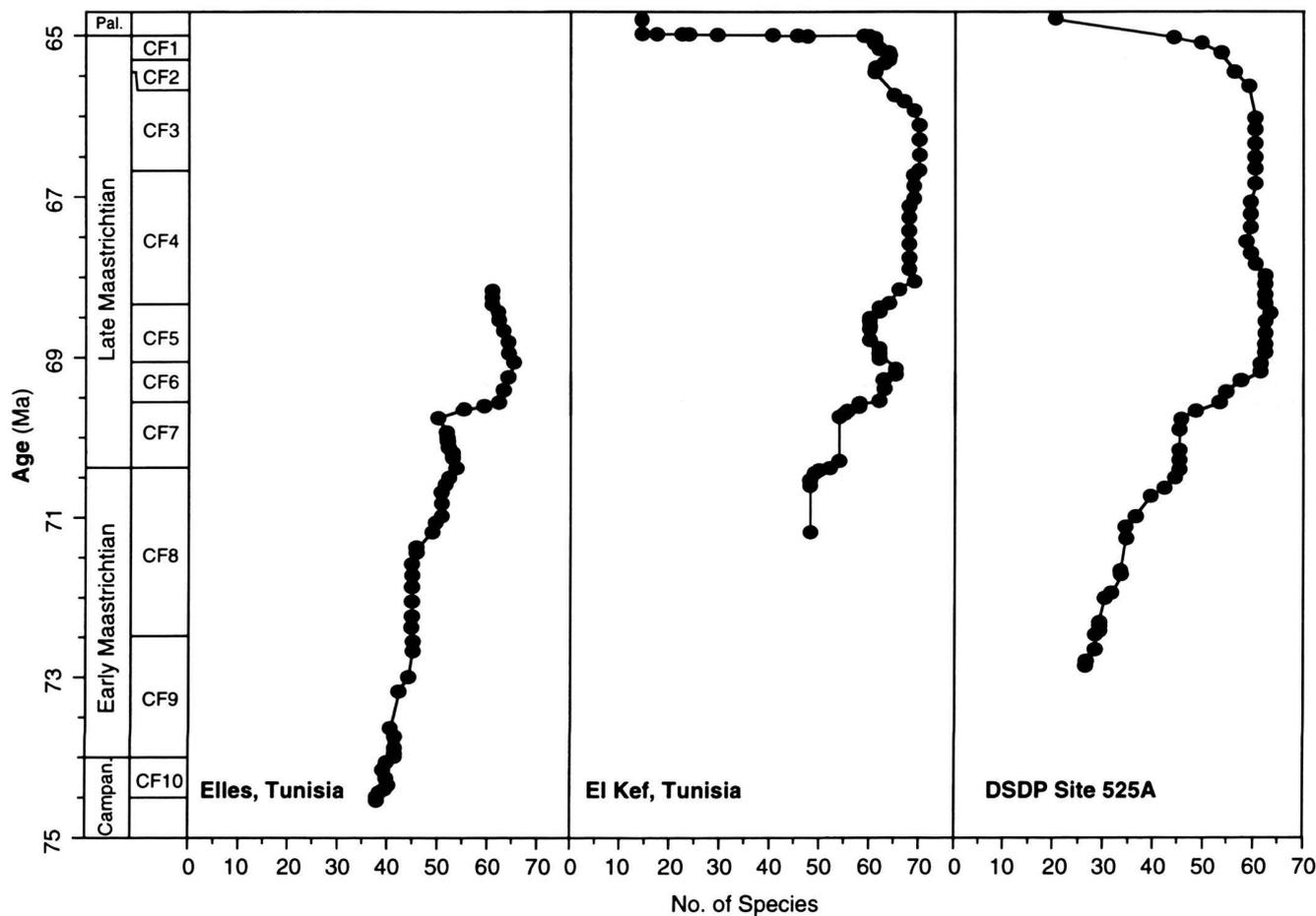
Fig. 7. Maastrichtian species richness in planktic foraminifera of low (El Kef and Elles) and middle latitudes (Site 525A). Note that maximum species richness was attained rapidly during a short period of only about 600 kyr. The mass extinction of planktic foraminifera also occurred very rapidly during the last 400 kyr of the Maastrichtian.

termined for this biostratigraphic marker at Elles based on the assumption of constant sedimentation rates between Zones CF8 and CF9 (Fig. 4B).

The **Globotruncanita calcarata** Zone (**CF10**), is defined by the total range of *G. calcarata* (Pl. I, Fig. 1). This biozone is only observed at the Elles section. Bralower et al. (1995) estimated that *G. calcarata* first appears at ~74.8 Ma.

Species richness

The occurrences and ranges of all species identified at Elles and El Kef illustrate an increasing trend of species richness during the late Maastrichtian (Figs. 5 and 6). For example, during the late Campanian Zone CF10 (*G. calcarata*), species richness was relatively low (38–40 species at Elles) and dominated

by globotruncanid and biserial taxa (Fig. 5). During the early Maastrichtian, species richness increased to 45 species (Figs. 5–7). Beginning at about 71 Ma (upper Zone CF8) species richness gradually increased and at the CF7–CF6 transition rapidly expanded from 45 to 54 species at both Elles and El Kef. A similar increase (from 35 to 45 species) is observed at the South Atlantic Site 525A (Fig. 7). During the following 500 kyr (Zone CF7), species richness temporarily decreased at Elles with the disappearances of *Globigerinelloides minuta*, *Globotruncana subcircumnodifer*, *Rugoglobigerina pustulata*, and *Globotruncana subrugosa* (Fig. 5). This decline is less pronounced at El Kef because much of Zone CF7 was not exposed (Fig. 6). However, at Site 525A no net change in species richness occurred in this interval (Fig. 7) because these species are not present.
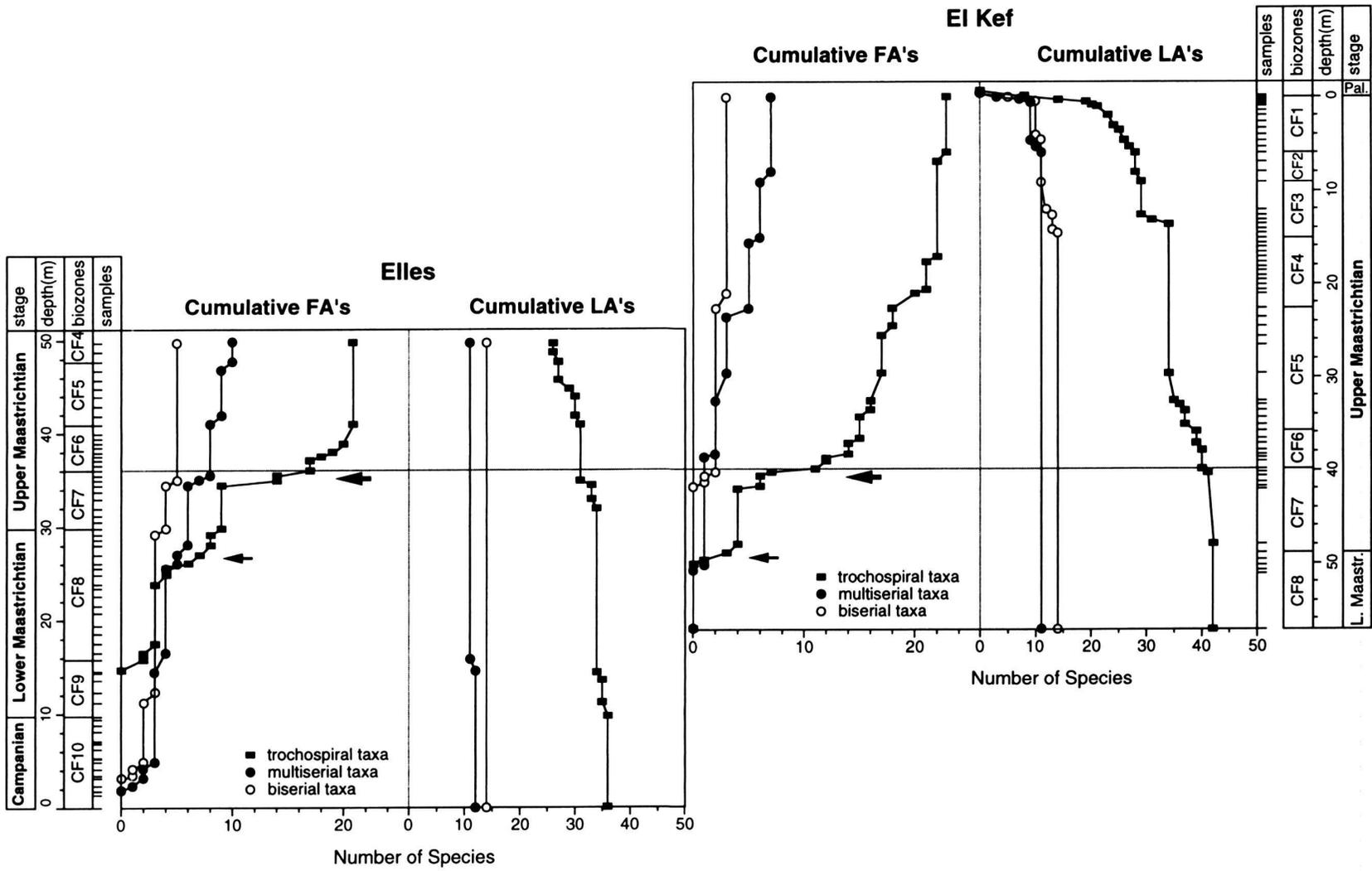
Fig. 8. Faunal changes viewed in terms of cumulative first (FA's) and last (LA's) appearances of species at Elles and El Kef. The El Kef and Elles sections are correlated based on the CF7–CF6 Zone boundary. Arrows mark the onset of diversification in trochospiral taxa near the CF8–CF7 and the CF7–CF6 transitions. Note that trochospiral taxa both drive evolutionary diversification and the mass extinction. This group gradually declined during the last 400 kyr of the Maastrichtian and suffered rapid extinction at the K-T boundary.
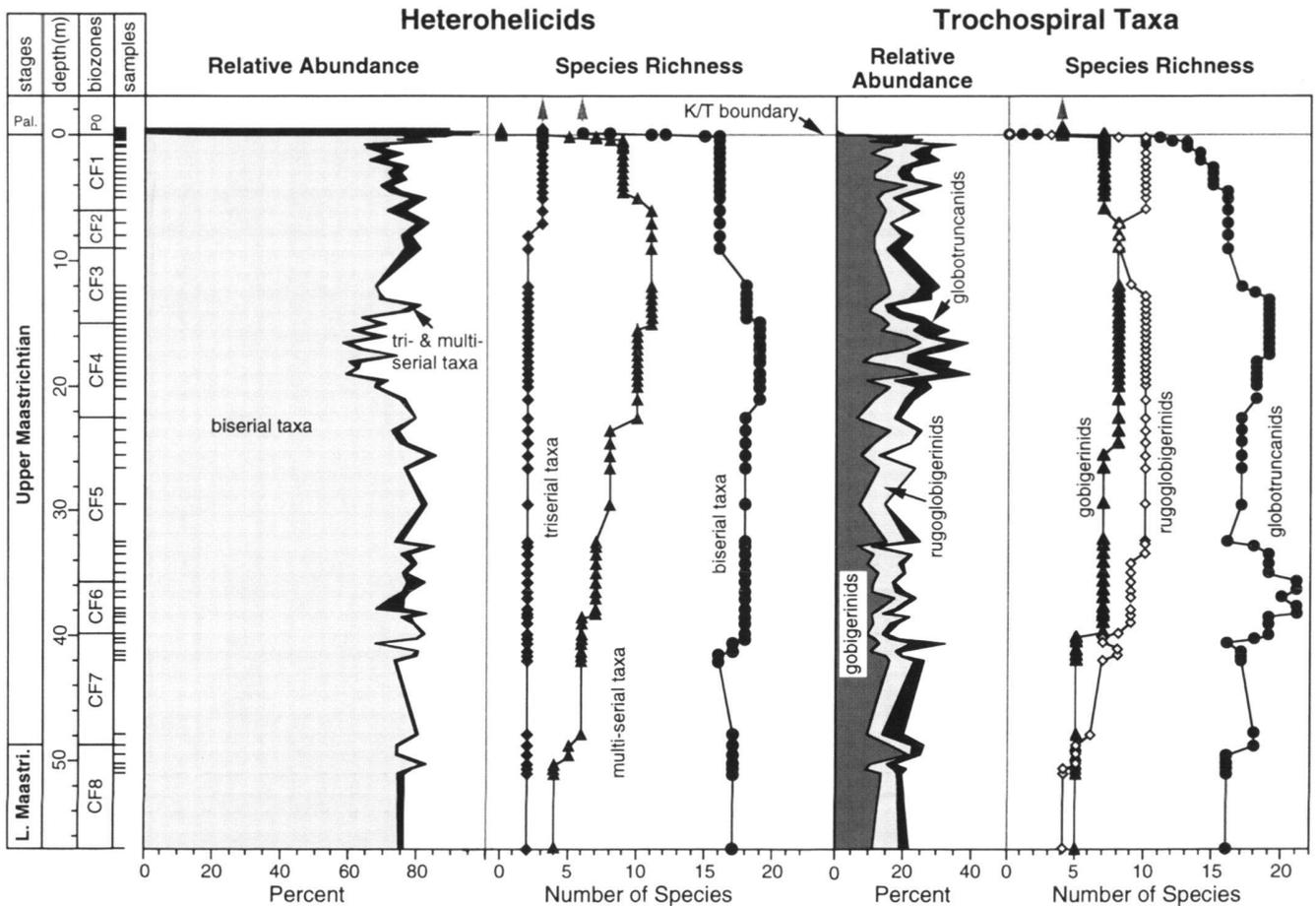
Fig. 9. Species richness and relative abundances grouped by morphological characteristics at the El Kef section. Note that species richness changes occurred mainly in morphologically complex taxa (e.g., rugoglobigerinids, globotruncanids and multi-serial taxa), whereas morphologically simple taxa remained stable and many survived the mass extinction (e.g., triserial, biserial and globigerid taxa).

A second rapid increase in species diversification began at 69.7 Ma in the uppermost part of Zone CF7 and continued through Zone CF6. By 69.1 Ma, species richness reached a maximum of 65 species. This rapid diversification is similar at El Kef and Elles and most new species appear within similar stratigraphic intervals at both localities (Figs. 5 and 6). Slight differences in the first appearance of some species above or below the CF7–CF6 boundary are likely due to rarity of taxa, diachronous occurrence of some species, or a short hiatus particularly at Elles. This remarkably rapid change resulted in maximum diversity of both globotruncanids and rugoglobigerinids for the Maastrichtian. Moreover, it was a time when maximum global species richness was attained as suggested by peak species richness in both Tunisian sections and DSDP Site 525A (Fig. 7).

During the following 2 myr (Zones CF5 and CF4), species richness declined by four to six species in the Tunisian sections with the disappearances of *Pseudotextularia nuttalli*,

Globotruncana linneiana, G. ventricosa, G. bulloides, Rosita plummerae, and *R. fornicata* (Fig. 6). However, this decrease was not observed until later in Zone CF4 at the South Atlantic Site 525A (Fig. 7). At El Kef species richness reached a maximum of 70 species by 68 Ma (Zone CF3) with the appearance of several species in Zone CF4 (e.g., *Racemiguembelina fructicosa, R. powelli, Heterohelix americana, A. mayaroensis, G.* cf. *monmouthensis,* and *Rugotruncana subpennyi,* Fig. 6), although some of these may be local first appearances. Between 68 and 65.9 Ma species richness remained at an all-time high of 70 species at El Kef and at 60–65 species at Site 525A (Figs. 6 and 7).

The terminal decline in Cretaceous species richness began at 65.9 Ma in the Tethys as well as in the South Atlantic and greatly accelerated during the last 300 kyr of the Maastrichtian (Fig. 7). The decline began in Zone CF3 with the disappearance of *Archaeoglobigerina cretacea, Gublerina acuta, Heterohelix carinata, Pseudoguembelina excolata,* and *Globotruncana*
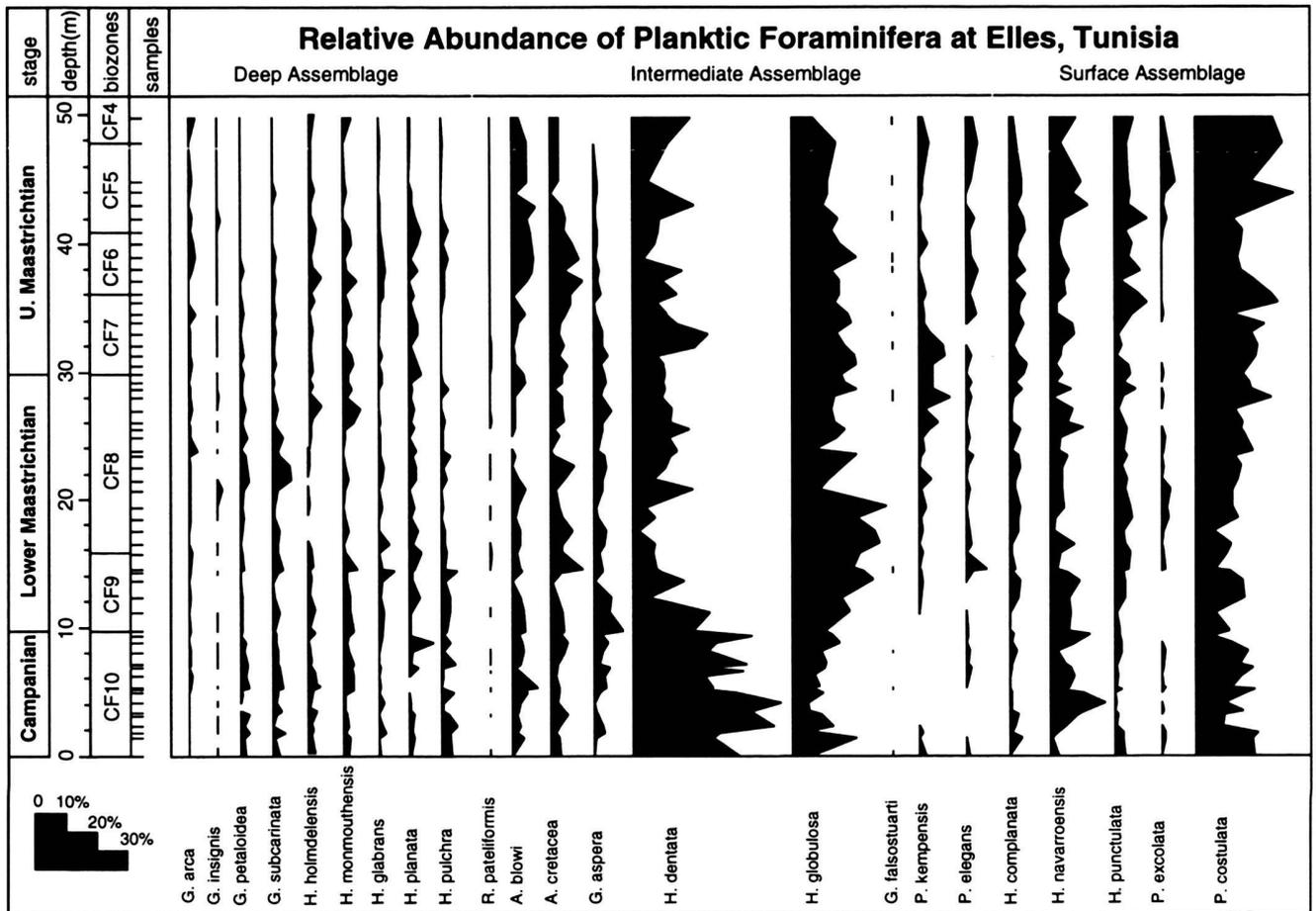
Fig. 10. Relative abundances of species that ranged through most of the late Campanian and Maastrichtian at Elles. Heterohelicids are the dominant and stable fauna with a major population shift at the Campanian-Maastrichtian transition (e.g., 20% decrease in *H. dentata* and ~20% increase in *H. globulosa*).

falsostuarti (Fig. 6). However, in Zone CF1 species disappearances are offset by the evolution of *Plummerita reicheli* and *P. hantkeninoides*. At the K-T boundary, virtually all tropical and subtropical species disappeared globally (see Keller et al. 1996 for more details of the K-T event).

What was the nature and tempo of the evolutionary diversification and mass extinction during the late Maastrichtian? Morphologic groupings of species into trochospiral and heterohelicid taxa indicate that the rapid rise in species richness to their all-time global maximum between 69 and 71 Ma (upper

CF8 through CF6) was due primarily to the evolutionary diversification in trochospiral taxa (Fig. 8). The rate of evolutionary increase in this morphologic group averaged one species/myr during the late Campanian and early Maastrichtian, increased to nine species/myr between 70 and 71 Ma, and tripled to 15 species between 69.1–69.7 Ma (see cumulative FA's, Fig. 8). In contrast, the evolutionary rate in biserial and multiserial taxa was moderate and steady, doubling from one to two species per million years during the same two million year interval.

Fig. 11. Relative abundance of species that ranged through the Maastrichtian at El Kef. Heterohelicids are the dominant and stable fauna with major changes at the CF3–CF2 boundary (65.5 Ma) and during the last 500–100 kyr of the Maastrichtian.
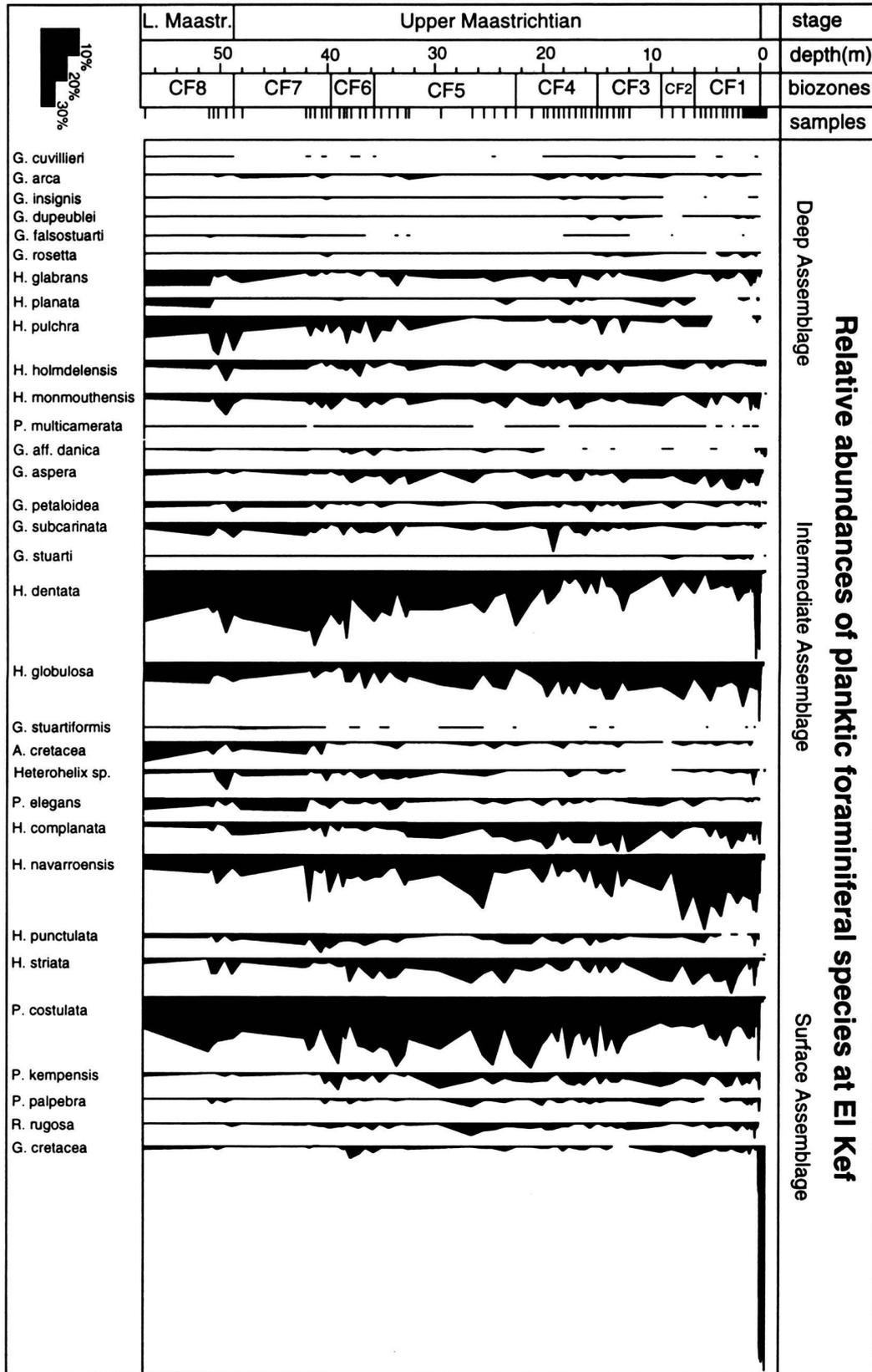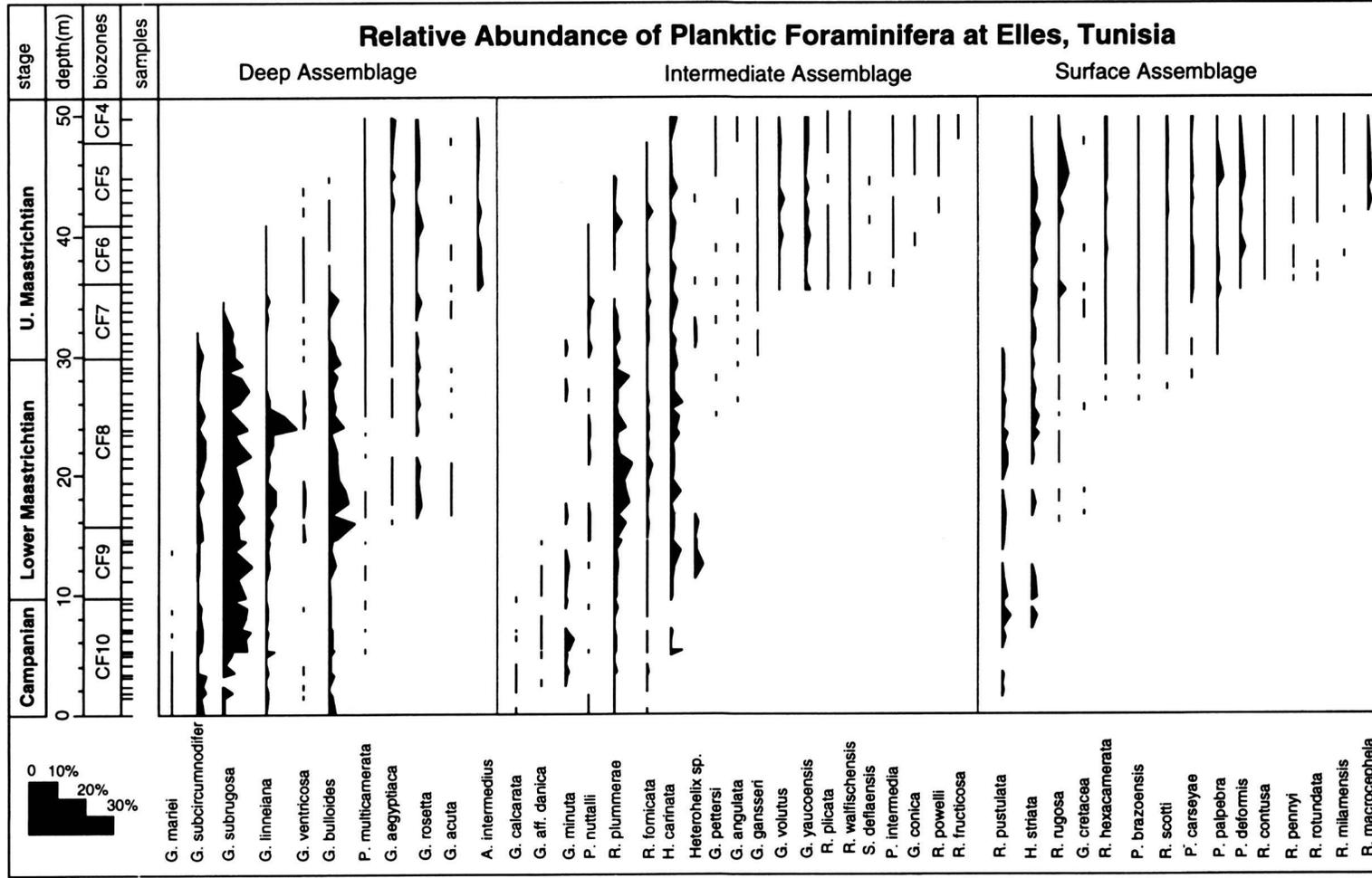
Fig. 12. Relative abundances of species which originate or disappear within the late Campanian to the Maastrichtian at Elles. Note that most of these species are rare or sporadically present throughout their ranges.

Fig. 13. Relative abundance of species which originate or disappear within the Maastrichtian at Elles. Note that most of these species are rare or sporadically present throughout their ranges.
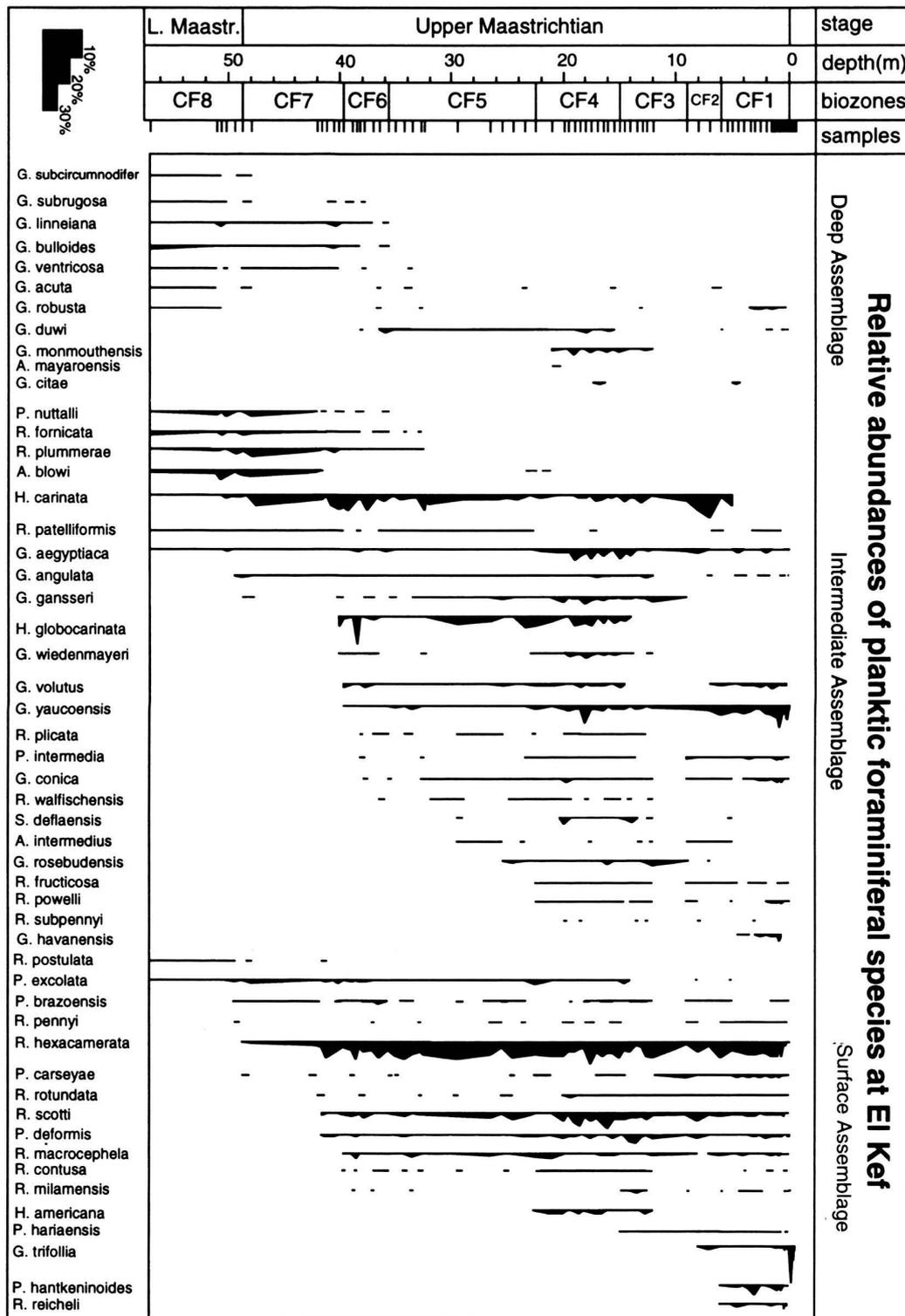
Tab. 1A. Depth ranking of Maastrichtian planktic foraminiferal species based on published stable isotopic data.

Surface Assemblage	Intermediate Assemblage	Deep Assemblage
Guembelitria cretacea	Gansserina gansseri	Abathomphalus mayaroensis
G. trifolia	Globigerinelloides aspera*	Globotruncanella citae
Heterohelix navarroensis	G. petaloides	Gublerina actua
H. striata	G. subcarinata	G. cuvillieri
Planoglobulina brazoensis	Globotruncana aegyptiaca	G. aff. ultramicrus
Pseudoguembelina costulata	G. arca	Hedbergella holmdelensis
P. excolata	G. falsostuarti	H. monmouthensis
P. palpebra	Globotruncanita angulata	Heterohelix glabrans
Pseudotextularia deformis	G. conica	H. planata
Rosita contusa	G. stuarti	H. pulchra
Rugoglobigerina rotundata	G. stuartiformis**	Planoglobulina multicamerata
R. rugosa	Heterohelix dentata	
R. scotti	H. globulosa*	
	Pseudotextularia elegans	
	P. intermedia	
	Racemiguembelina fructicosa	
	R. powelli	

Tab. 1B. Depth ranking based on similar morphology.

Surface Assemblage	Intermediate Assemblage	Deep Assemblage
Heterohelix americana	Archaeoglobigerina blowi	Abathomphalus intermedius
H. complanata	A. cretacea	Globotruncana bulloides
H. punctulata	Gansserina wiedenmayeri	G. dupeublei
Planoglobulina carseyae	Globigerinelloides rosebudensis	G. duwi
Plummerita hantkeninoides	G. volutus	G. insignis
P. reicheli	G. yaucoensis	G. linneiana
Pseudoguembelina hariaensis	Globotruncanita calcarata	G. mariei
P. kempensis	Guembelitria danica	G. rosetta
Rugoglobigerina hexacamerata	Heterohelix carinata	G. subcircumnodifer
R. macrocephala	H. globocarinata	G. subrugosa
R. milamensis	H. kempensis	G. ventricosa
R. pennyi	Pseudotextularia nuttalli	Gublerina robusta
R. postulata	Rosita fornicata	
	R. patelliformis	
	R. plicata	
	R. plummerae	
	R. walfischensis	
	Sigalia deflaensis	

* surface in shallow water, intermediate in open ocean.
** indeterminate.

Just as the rapid rise to maximum diversity was due primarily to trochospiral taxa, so was the rapid terminal decline during the last 300 kyr of the Maastrichtian primarily due to changes among trochospiral taxa. The cumulative LA curves at El Kef for the three morphologic groups mark the onset of this terminal decline in trochospiral taxa near the CF3–CF2 boundary (65.9 Ma), but no significant change occurred during Zone CF2 (Fig. 9). However, in Zone CF1 trochospiral species richness rapidly declined and reached near zero at the K-T boundary (only two hedbergellid and two globigerinellid species survived). In contrast, biserial and multiserial species declined more slowly and many more species survived (6 biserial and all

triserial species, Fig. 8; for more details of the K-T interval, see Keller et al. 1996).

Evaluation of the species richness within various generic and morphologic groups provides further clues to the nature of the late Maastrichtian species richness maximum followed by the terminal decline and extinction at the K-T boundary. For example, multiserial taxa doubled in species richness (from four to 11 species) during the late Maastrichtian, began to decline at 300 kyr before the K-T boundary (CF2–CF1) and disappeared at or near the K-T boundary (Fig. 9). This morphologic group is relatively rare (<5%) through the Maastrichtian. Biserial morphotypes remained relatively stable through the

Maastrichtian increasing only by two species (from 17 to 19 species). Their decline began about 500 kyr (CF3) before the K-T boundary, but species richness remained unchanged at 16 species during the last 400 kyr of the Maastrichtian (CF2–CF1) and rapidly dropped to six species at the K-T boundary. Biserial taxa dominated Maastrichtian faunas, averaging 75% except during Zones CF4 to CF3 (Fig. 9). Triserial morphotypes neither diversified nor suffered extinctions. This group thrived after the K-T boundary.

Species richness patterns in various trochospiral groups reveal that rapid evolutionary diversification of globotruncanids, more than any other group, is responsible for the rapid rise to the Cretaceous species richness maximum, rapid decline and mass extinction during the last 300 kyr of the Maastrichtian (Fig. 9). Globotruncanids increased from 16 to 21 species by the CF6–CF5 boundary (69 Ma), temporarily decreased to 16 species in Zone CF5, but increased again to 19 species in Zones CF3–CF4. During the last 300 kyr of the Maastrichtian (CF1), globotruncanids declined from 16 to nine species and the remaining taxa became extinct at the K-T boundary. It is possible that the disappearance pattern of globotruncanids during the last 300 kyr is partly influenced by the rarity of these species. Globotruncanids averaged less than 10% of the total foraminiferal population at this time and they rarely exceeded 10% during the Maastrichtian.

Like globotruncanids, rugoglobigerinids also rapidly diversified (from six to nine species) in Zone CF6. This group remained relatively constant in both species richness and relative abundance (10–15%) through the late Maastrichtian and disappeared at the K-T boundary. In contrast, the small morphotypes of the globigerinid group (hedbergellids, globigerinellids, and globotruncanellids) changed only gradually through the Maastrichtian (from 4 to 8 species) and half of these survived into the Danian (hedbergellids and globigerinellids).

Relative abundance changes

Clues to environmental changes can also be gained from variations in relative abundances of species. For example, relative abundances of long-ranging species (e.g., species that ranged through the Campanian-Maastrichtian intervals at Elles and El Kef, Figs. 10 and 11) show little change. Most taxa contribute less than 10% of the total population through the Campanian and Maastrichtian. But a few species dominate and all of these are heterohelicids (e.g., *Heterohelix complanata*, *H. dentata*, *H. globulosa*, *H. navarroensis*, *H. striata* and *P. costulata*). The combined relative abundance of these heterohelicids averages 70–80% (Fig. 10). Within this group, *H. dentata* dominated during the late Campanian (>60%), declined (~20%) during the early to the early late Maastrichtian, coincident with a temporary increase in *H. globulosa* (>30%, Fig. 10). *Heterohelix dentata* further declined by about 10% during the latest Maastrichtian (CF4 to CF1, Fig. 11). In the last 50 cm (~25 kyr) of the Maastrichtian, *H. dentata* sharply rose to 35% along with a

sharp increase in relative abundance of *H. globulosa* and *P. costulata* (Fig. 11). Moreover, within the last 300 kyr (Zone CF1) of the Maastrichtian, *H. navarroensis* increased from 10% to 20–30%.

Thus, long-ranging species indicate major abundance changes in the earliest Maastrichtian (~72–74 Ma, Zones CF9–CF8) and during the last 300 kyr of the Maastrichtian (CF1) including the last 50–100 kyr. However, the major rapid increase in species richness in the early part of the late Maastrichtian (69.7–69.1 Ma, CF6) appears to have had no short- or long-term effects on this group.

Short-ranging species (e.g., species that first appeared or disappeared within the late Campanian-Maastrichtian intervals) show greater abundance variations and evolutionary diversification, and extinctions. At El Kef and Elles, more than half of the species are short-ranging, but most of them are rare and none exceed 10% (Figs. 12 and 13). Within this group, major changes are indicated by the onset of diversification in Zones CF8 and CF7 and the rapid diversification in Zone CF6 accompanied by several species extinctions. A major change is also indicated in Zone CF3 by the disappearance of six species and in Zones CF2 and CF1 by eight species disappearances (Fig. 13). It is interesting that none of the evolving Maastrichtian species succeeded in establishing dominant populations and only *Rugoglobigerina hexacamerata* reached 10% in relative abundance (Fig. 12). This may be due to the unusually high species turnover rate during the late Maastrichtian and hence competition.

Discussion

Changes in the watermass stratification of the surface ocean may be responsible for the faunal turnovers in the early and late Maastrichtian, though not necessarily for the K-T boundary event. Such changes can be inferred from species richness and the relative abundances of assemblages living at different depths in surface, intermediate (thermocline), or deep waters (below thermocline) as inferred from stable isotopic ranking of species as demonstrated by various studies for the late Cretaceous to Paleogene (e.g., Douglas & Savin 1978; Boersma & Shackleton 1981; Barrera & Keller 1994; D'Hondt & Arthur 1995; Huber et al. 1995). Depth ranking based on stable isotopes has been accomplished for about half of the Maastrichtian planktic foraminiferal species as summarized in Table 1A. For species which have not yet been ranked isotopically, we have tentatively inferred depth ranking from biofacies studies of epicontinental seas (Table 1B; Sliter 1972; Hart & Bailey 1979; Leckie 1987) and morphologic studies (Hart 1980; Caron & Homewood 1983). Although isotopic depth ranking of Maastrichtian planktic foraminiferal species is still tentative, clues to the nature of the Maastrichtian faunal turnover and environmental changes can be gained.

Late Campanian-Early Maastrichtian: Depth ranked assemblages at Elles and El Kef indicate that deep dwellers re-

Depth Ranking of Planktic Foraminifera
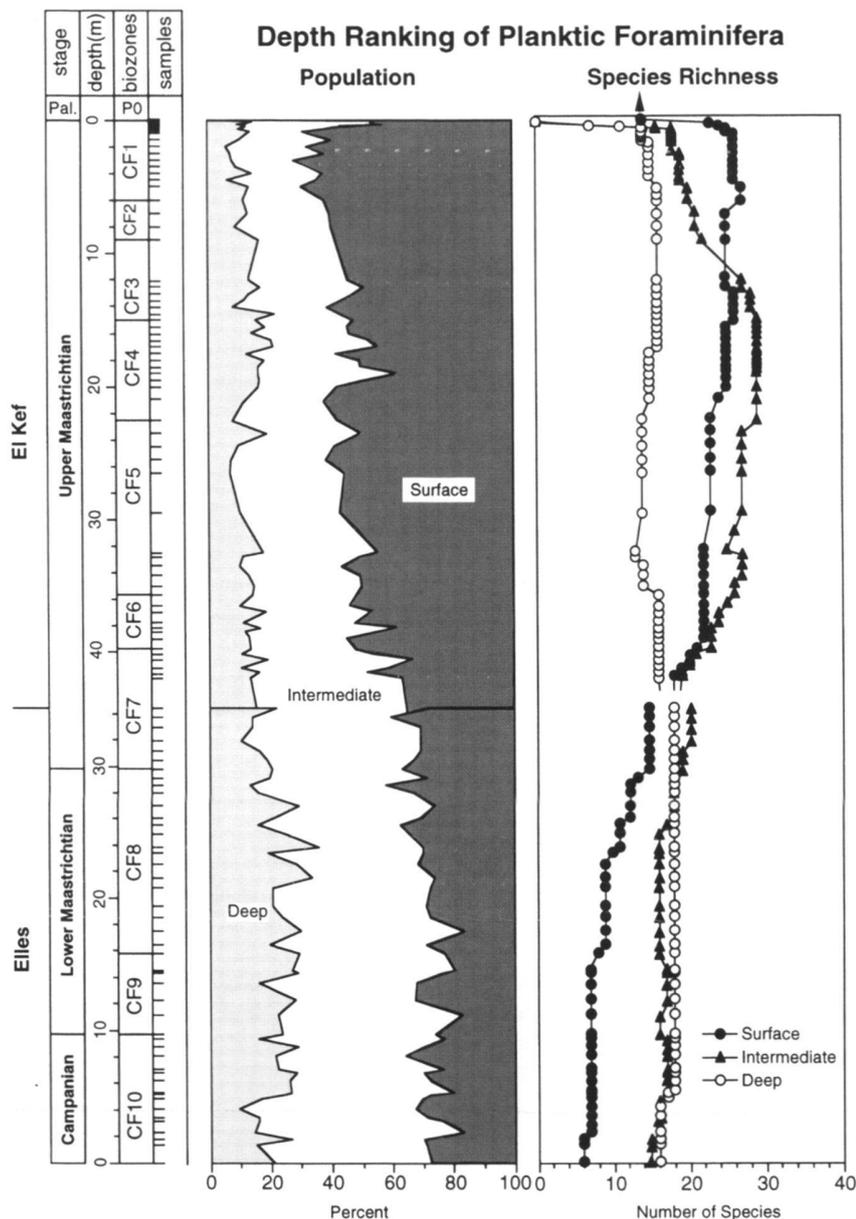
Fig. 14. Relative abundances and species richness grouped by inferred dwelling habitats in surface, intermediate (thermocline) and deeper waters during the late Campanian through Maastrichtian at Elles and El Kef. Note that no major changes occur in either species richness or relative abundances during the late Campanian and early Maastrichtian. Major faunal changes occur in the early late Maastrichtian (~69.7 Ma) and during the last 0.5 myr of the Maastrichtian.

mained stable at about 18 species and slightly more species than intermediate dwellers during the late Campanian and early Maastrichtian (Figs. 11–14). Their combined relative abundance averaged only 20% (Fig. 14). Intermediate dwellers contributed 50% on average, or 2.5 times more than deep dwellers during the same time interval, although they are represented only 16 to 20 species (Fig. 14). Surface dwellers averaged only seven species during the late Campanian and gradually increased to 12 species during the early Maastrichtian. This assemblage, however, averaged 30% in combined relative abundance throughout this interval.

These data suggest that there was little change in the watermass stratification of the southwestern Tethys during the late Campanian and most of the early Maastrichtian. However, the increased species richness in surface and intermediate dwellers beginning at about 71.5 Ma (middle of Zone CF8) suggest the onset of changes in surface and thermoclinal depths. Oxygen isotopic temperature records from southern ocean ODP Site 690C and DSDP Site 525A indicate major global cooling and possibly ice formation at this time (Spicer & Parrish, 1990; Barrera, 1994; Li & Keller 1998). It is possible that the onset of this global cooling resulted in increased up-

welling of nutrient-rich waters in the Tethys region, or nutrient influx due to enhanced weathering and erosion during a low sea-level. A major sea-level lowstand is well documented at this time (Haq et al. 1987).

Late Maastrichtian: The late Maastrichtian was a time of extreme upheaval among planktic foraminifera, a time when species richness reached the maximum in their evolutionary history and plunged to near extinction near the end of the Maastrichtian (Fig. 6). Depth ranking of species indicates that the rapid rise to maximum species richness in the late Maastrichtian (69.7–69.1 Ma) was due to diversification in surface and intermediate dwellers (from 12 to 22 species and from 18 to 27 species, respectively; Figs. 12–14). During this time, species richness in deep dwellers remained stable, though their combined relative abundance decreased from an average of 20% to 10%. At the same time, the combined relative abundance of intermediate dwellers also decreased from 50% to 30%, whereas surface dwellers increased from 30% to 60% (Fig. 14). Species richness thus indicates that the changes that led to maximum species richness occurred in the surface water and at thermoclinal depths. Species richness remained at maximum levels between 66.5 and 69 Ma (CF5–CF4) and neither depth ranking nor relative abundances of species indicate major environmental changes.

At Elles and El Kef the decrease in the combined abundance of intermediate dwellers (despite their increased species richness) is primarily due to decreased abundance of biserial species, a group believed to be tolerant of low oxygen condition (Boersma & Premoli Silva 1989; Keller 1993; Barrera & Keller 1994). Their decreased abundance implies a more restricted oxygen minimum zone relative to the late Campanian and early Maastrichtian. The increased abundance of surface dwellers suggests increased upwelling and nutrient supply. Oxygen isotopic data from Sites 690C and 525A indicate cool deep and surface water temperatures accompanied by increased productivity at this time (Barrera 1994; Li & Keller 1998).

Latest Maastrichtian: The onset of the first permanent decline in species richness began at about 500 kyr before the K-T boundary and coincided with a temperature minimum for the Maastrichtian (Barrera 1994; Li & Keller 1998) and a major sea-level fall. At this time, species richness decreased among intermediate (thermocline) dwellers from 29 to 21 species (Figs. 13 and 14) and many tropical and subtropical species declined in abundance and became very rare during the last 400 kyr of the Maastrichtian (Figs. 11 and 13). At or near the K-T boundary, all remaining tropical and subtropical species disappeared marking the mass extinction of the Cretaceous fauna. Only small cosmopolitan and environmentally tolerant species survived the K-T boundary event (Keller 1988b, 1989, 1993, 1997; MacLeod & Keller 1994; Keller et al. 1996; Masters 1997).

The observed species richness pattern during the last 500 kyr of the Maastrichtian provides strong evidence in support of major environmental changes preceding the K-T boundary.

Though it may be argued that the exact point of disappearance of any rare species is questionable (e.g., Signor-Lipps effect, Signor & Lipps 1982), statistically the overall pattern can not be attributed to artifacts of rarity and preservation (MacLeod 1996). Evidence for environmental changes is also strongly indicated by a sharp decline of six species (intermediate dwellers) at the top of Zone CF3 and subsequent rarity of most tropical and subtropical taxa (Fig. 14). In contrast, there are no species extinctions in surface or deep dwellers in this interval. During the last 300 kyr (Zone CF1) of the Maastrichtian, the combined relative abundance of intermediate dwellers decreased, whereas the combined relative abundance of surface dwellers reached an all-time maximum of 75%, up from an average of 50% during the preceding Zone CF5–CF3 interval (Fig. 14). The increase is largely due to the increased abundance of heterohelicids (*H. navarroensis*, Fig. 11). During the last 50–100 kyr (top 1 m) of the Maastrichtian, surface dwellers rapidly declined to 40% and intermediate dwellers (*H. dentata* and *H. globulosa*) dominate (Figs. 11 and 14).

Global climatic changes are the most likely cause for the decline in species richness beginning at about 65.5 Ma. Coincident with the declining species richness at the top of Zone CF3 at El Kef, Maastrichtian cooling reached its maximum in both surface and deep waters at Sites 690C and 525A (Barrera 1994; Li & Keller 1998). Beginning at about 65.4 Ma and continuing to 65.1 Ma, surface and deep waters rapidly warmed, coincident with the decline in relative abundance of most tropical and subtropical taxa. At the same time, biserials increased in relative abundance from 60% to 75% at El Kef (Zone CF1, Fig. 14). During the last 50–100 kyr of the Maastrichtian, temperature cooled rapidly in middle and southern high latitudes in both surface and deep waters (Barrera 1994; Li & Keller 1998) accompanied by a further decline in species richness. By K-T boundary time all tropical species disappeared globally, whereas environmentally more tolerant cosmopolitan species survived. The observed species extinction pattern is thus consistent with a highly stressful marine environment during the last 500 kyr of the Maastrichtian. However, the sudden extinction of all remaining tropical and subtropical species at the K-T boundary was likely caused by the additional stress imposed on the ecosystem by a bolide impact.

Conclusions

1. The late Maastrichtian was the most tumultuous time in the evolutionary history of planktic foraminifera: species richness reached a historical maximum within only 600 kyr (between 69.7–69.1 Ma) and four million years later a mass extinction decimated the population.

2. The rapid rise in species richness was driven primarily by diversification in surface and intermediate depths and was led by rugoglobigerinids, globigerinids and heterohelicids. Populations of deeper water dwellers (e.g., some globotruncanids) remained stable through the late Campanian and Maastrichtian.

Plate I.
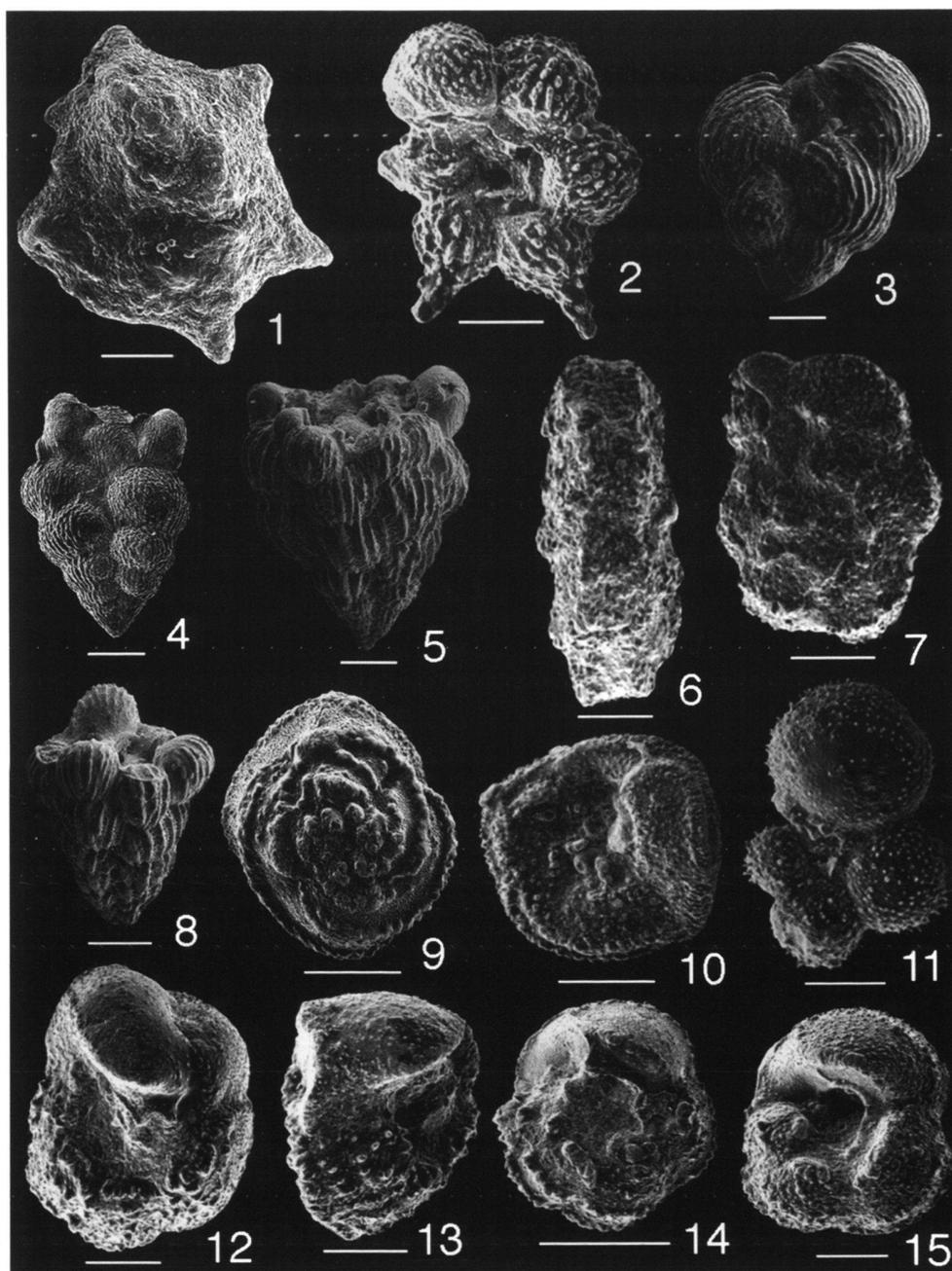
Scale bar = 100 μm, all specimens from Tunisia.

Fig. 1.   *Globotruncanita calcarata* (Cushman), from the sample at 3.4 m, Elles.
Fig. 2.   *Plummerita hantkeninoides* (Brönnimann), 45–50 cm below the K/T boundary, El Kef.
Fig. 3.   *Pseudoguembelina palpebra* Brönnimann & Brown, 40–45 cm below the K/T boundary, El Kef.
Fig. 4.   *Pseudoguembelina hariaensis* Nederbragt, 5 m below the K/T boundary, El Kef.
Fig. 5.   *Racemiguembelina fructicosa* (Egger), 45–50 cm below the K/T boundary, El Kef.
Figs. 6–7. *Globotruncana linneiana* (d'Orbigny), 41.2 m below the K/T boundary, El Kef.
Fig. 8.   *Racemiguembelina intermedia* (De Klasz), 10–15 cm below the K/T boundary, El Kef.
Figs. 9–10. *Rosita contusa* (Cushman), 18 m below the K/T boundary, El Kef.
Fig. 11.   *Globigerinelloides subcarinata* (Brönnimann), 30–35 cm below the K/T boundary, El Kef.
Figs. 12–13. *Gansserina gansseri* (Bolli), 18 m below the K/T boundary, El Kef.
Figs. 14–15. *Globotruncana aegyptiaca* Nakkady, 18 m below the K/T boundary, El Kef.

3. The terminal decline in species richness began in Zone CF3 with the disappearance of some intermediate dwellers, whereas surface and deeper dwellers remained unaffected.
4. Extinction of tropical and subtropical taxa (mainly globotruncanids) accelerated during the global cooling in the last 100 kyr of the Maastrichtian and ended in their extinction at the K-T boundary possibly as the result of the additional stress imposed by a bolide impact.

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Appendix

Tab. 1. Relative percent abundance of planktic foraminiferal species at Elles, Tunisia. X = < 2%, xx = rare species. + = present in samples not included in quantitative analysis.

Depth (m)	49,7	48,7	47,7	44,8	44,4	43,9	43,4	42,9	42,4	41,9	41,4	40,9	40,4	39,9	39,4	38,9	38,4	37,9	37,5	37,1	36,5	36	35,4	34,9
Abathomphalus intermedius		+	X	xx	+	xx	+	xx	+	X	+	X				X		X		X		2	X	
Archaeoglobigerina blowi	3	+	5	5	+	X	+	8	+	5	+	7	+	7	+	7	+	7	+	5	+	X	3	+
A. cretacea	3	+	3	3	+	X	+	4	+	5	+	5	+	8	+	10	+	5	+	11	+	7	7	+
Gansserina gansseri	xx	+	X	xx	+		+	xx	+	xx	+	xx	+	xx	+	X	+	X	+	xx	+	xx	xx	+
Globigerinelloides aspera	X	+	X	X	+	X	+	X	+	X	+	X	+	X	+	X	+	2	+	X	+	3		+
G. multispina																								
G. rosebudensis	X	+		X	+	X										X								
G. volutus	X	+	X		+	X	+	2	+	X	+		+	X	+		+	X	+	X	+	X	X	+
G. yaucoensis	X		X		+	X	+	X	+	X	+	2	+	X	+	X	+	X	+	X		X	2	+
Globotruncana aegyptiaca	2		X	xx	+	X	+		+	X	+	X	+	2	+	2	+	xx	+	X	+	X		+
G. arca	2		X	X	+	X	+	X	+	X	+	X	+	2	+	2	+	X	+	X	+	xx	xx	+
G. bulloides				X	+	X	+	X	+	2	+	3	+	3	+		+	2	+		+	xx	X	
G. falsostuarti	X		X																					+
G. insignis	X		X			xx		xx		X				X		xx		X				xx	xx	+
G. linneiana												X		X		2				X		X	X	+
G. rosetta	X		2	X						X		2		X		X				xx			xx	+
G. ventricosa						X				X				X		xx		xx		X		xx	xx	+
Globotruncanella petaloidea						X				X						X				X		X	X	+
G. subcarinata	X		X	X		X		X		X		X		X		X				X		X	X	+
Globotruncanita angulata	X		X					xx		X				xx									xx	+
G. conica	X		xx	X										xx										
G. pettersi	xx		xx	X												X								
G. stuarti	X		xx	2				xx		X		X		X		X		X		X		X		+
G. stuartiformis	xx			xx				xx																
Gublerina actua			xx					xx								X		X					X	
G. cuvillieri				xx						xx						xx				xx				xx
Guembelitria cretacea			X																					X
Hedbergella holmdelensis	2	+	X	X	+	2	+	X	+	X	+	3	+	2	+	X	+	X	+	4	+	X	2	+
H. monmouthensis	3	+	X	X	+	X	+	X	+	X	+	2	+	3	+	X	+	X	+	5	+	X	2	+
Heterohelix carinata	3	+	X		+	2	+		+		+	2	+	xx	+		+		+	2	+	X	X	+
H. complanata	X	+	2	4	+	4	+	2	+	5	+	5	+	3	+	3	+	5	+	X	+	5	4	+
H. dentata	19	+	11	5	+	12	+	20	+	9	+	8	+	7	+	3	+	16	+	10	+	15	8	+
H. glabrans		+	X		+		+	X	+	X	+	X	+	2	+	2	+	2	+	2		X		+
H. globulosa	7	+	15	12	+	12	+	10	+	15	+	13	+	16	+	21	+	13	+	16	+	16	14	+
H. navarroensis	9	+	4	10	+	7	+	13	+	4	+	3	+	3	+	4	+	6	+	5	+	5	3	+
H. planata	X	+	X	X	+	X	+	X	+	3	+	4	+	3	+	X	+	3	+		+	2	X	+
H. pulchra	X	+	X		+		+	X	+	X	+	2	+	X	+	2	+	X	+	X	+	X	X	+
H. punctulata	6	+	4	4	+	5	+	5	+	11	+	4	+	6	+	5	+	9	+	2	+	8	11	+
H. striata	xx	+	xx	X	+	X	+	X	+	X	+	3	+	X	+	X	+	2	+		+		2	+
Planoglobulina brazoensis	xx	+	xx		+	X	+	xx	+	X	+	X	+	xx	+	xx	+	X	+	xx		xx	xx	+
P. carseyae	X	+	X	X	+	xx	+	X	+	X	+	xx	+		+	X	+	X	+	X	+	X	X	+
P. multicamerata	xx	+	X	xx	+		+	xx	+	xx	+	X	+	xx	+	xx	+	X	+	X	+	xx		+
Pseudoguembelina costuluta	26	+	29	18	+	32	+	23	+	12	+	16	+	15	+	14	+	15	+	20	+	25	28	+
P. excolata	X	+	2	5	+	X	+	X	+	2	+	X	+	X	+	X	+	xx	+		+	xx	xx	+
P. kempensis	X	+	4	X	+	X	+	X	+	X	+	X	+	3	+		+		+	X	+	2	X	+
P. palpebra	xx	+	X	2	+		+	X	+	xx	+		+	X	+	xx	+	X	+	X	+	xx	X	+
Pseudotextularia deformis	X	+	X	2	+	X	+		+	X	+		+	X	+	2	+	xx	+	xx	+	xx	xx	+
P. elegans	2	+	4	2	+		+	xx	+	3	+	2	+	2	+	3	+	4	+	3	+	X	3	+
P. intermedia	xx	+	X		+		+	xx	+	xx	+		+	X	+	xx	+	xx	+		+	xx	xx	+
P. nuttalli											+	X	+	X	+	xx	+	xx	+	xx	+	xx	xx	+
Racemiguembelina fructicosa	xx	+	xx																					
R. powelli	X	+	xx	X	+		+	xx	+	xx														
Rosita contusa	xx	+	xx	X	+	xx	+	xx	+	xx	+	xx	+	xx	+	xx	+	xx	+	xx	+	xx		+
R. fornicata				xx	+	xx	+	xx	+	2	+	xx	+	X	+	X	+	X	+	X	+	xx	X	+
R. patelliformis	xx	+	xx					xx				X		xx		X		xx		X		xx	xx	+
R. plicata	xx	+	xx	xx	+		+	X	+	xx	+	X	+	xx	+	xx	+	X	+	xx		xx		
R. plummerae				X	+	X	+		+	X	+	6	+	X	+	3	+	X	+	X	+	xx		+
R. walfischensis	X	+	xx	xx	+	xx	+	xx	+		+	xx	+		+	xx	+	xx	+		+	xx	xx	
Rugoglobigerina hexacamerata	X	+	X	X	+	X	+	X	+	X	+	X	+		+	X						X		+
R. macrocephela	xx	+	X	X	+		+	X	+		+	X												
R. milamensis	xx	+	xx		+		+		+		+								+	xx				
R. pennyi	X	+						X	+	X	+	xx							+	xx	+	X		xx
R. rotundata	xx	+		xx	+		+			xx	+	xx						+		xx	+	xx		
R. rugosa	X	+	2	6	+	5	+	X	+	3	+	X		xx	+	xx	+	xx	+	X	+	X	2	+
R. scotti	X	+	X	2	+	X	+	2	+	2	+	X	+	X	+	xx	+	X	+	xx				+
Sigalia deflaensis														xx			+		+	xx	+	xx	xx	
Total Number Counted	313		324	302		304		300		305		320		302		305		303		306		296	304	

Tab. 1 continued

Depth (m)	34.4	33.7	33	31.9	31.2	30.5	29.8	29.1	28.6	28	27	26	25.5	24.8	23.8	23.4	22.5	21.5	20.7	19.4	18.5	17.5	16.5
Archaeoglobigerina blowi	5	2	2	X	2	X	4	4	4	X	X	2	X	X	X	X	X	3	5	2	X	3	3
A. cretacea	5	3	3	4	3	6	4	4	X	4	4	5	2	3		X	8	5	2	3	5	7	4
Gansserina gansseri	xx	xx		xx	xx	xx																	
Globigerinelloides aspera	X	2	3	3	5	2	3	4	3	2	6	3	3	3	X	4	4	3	3	X	X	4	4
G. minuta						X		X		X							X						X
G. multispina	X			X																			
Globotruncana aegyptiaca	xx	xx	xx	xx	xx	xx	xx	xx		X	X	X	X	X			X	X	X	X	X		
G. arca	2	xx	X	X	X	2	X		X	X	X		X	X	3	X	X	X	X	X	X	X	X
G. bulloides	3	2				2	2	4	X	2	X	2	2	X	5	X	X	3	3	3	5	7	X
G. falsostuarti											xx												
G. insignis	X	xx	X	X	X		X	xx	xx	X		X	X		X		xx		2	X	X		xx
G. linneiana	X		X		X		X				X	2	2	6	11	3	3	X	X		4	4	X
G. mariei																							
G. rosetta	2	X	X		X	X	X	X		X		X		X	X		X	X	X	X	2		
G. subcircumnodifer				X	2			2	X	X	3	X	2	2	X	X	X	2	X	2	X	X	
G. subrugosa	4	3	3	4	3	4	4	7	X	6	9	6	2	5	9	4	6	10	4	6	7	4	7
G. ventricosa			X		X		X				X	X	X	X	X				X	X	X	X	
G. petaloidea	X	X	X	X	X	X	X	X	X	X	X	2	X	X	2	X	2	3	3	X	X	X	X
G. subcarinata	X	X	X	X	X	X		X		X	2	X	2	3	2	2	6	6	2	X	X	3	2
Globotruncanita angulata	X							xx				xx											
G. calcarata																							
G. pettersi			X								X			X									
G. stuarti	X	xx	X	X	X	xx		xx	xx		xx	X		X	X	X	X	X	2		X		X
G. stuartiformis		X	xx			xx	X				xx	xx											
Gublerina actua	X								X			xx			X		xx		X	X	X	X	X
Guembelitria cretacea	X	X	X											X					2	X			X
Guembelitria sp.																							
Hedbergella holmdelensis		X	X	X	X	X	2	X	X	X	4	X	X	X		X	X	X		X		X	
H. monmouthensis	3	X	X	X	3	4	2	2	3	2	6	3	X	X		X	X	2	X		X	2	
Heterohelix carinata	3	2	X		2	2	2	2	X	X	X	4		3	2	3	X	X	X	X	3	X	X
H. complanata	3	5	3	2	3	6	5	2	4	X	X	4	4	3	X	3	4	3	4	2	3	3	X
H. dentata	11	14	25	20	8	10	11	10	11	10	13	13	19	12	14	13	11	7	20	4	8	2	7
H. glabrans	X	X			2		X	X			X	X		X	X	X	2	X		2			3
H. globulosa	18	20	15	17	21	21	16	17	21	14	13	14	17	15	7	21	17	12	9	31	21	27	29
H. navarroensis	2	7	8	4	4	2	4	2	7	X	7	6	11	3	3	6	4	4	4	5	2	X	8
H. planata	2	3	3	X	2	3	4	X	X	X	2	X	2		2	X	2	3		2	X	3	X
H. pulchra	X	X		X	X		X	X	2			2	X	X	X	3	X	2	X	X	X	X	X
H. punctulata	6	4	2	2	X	5	5	3	7	3	X	3	4	3	3	4	3	4	4	5	6	3	3
H. striata	X			X	X	X	X	X				X	X	X	2	X	2		X	X		X	
Heterohelix sp.				X	X																X		
Planoglobulina brazoensis	xx	xx	X	X	X	xx	X	X		xx		xx											
P. carseyae	X			X	xx	X		X	X														
P. multicamerata	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	X	xx	xx	xx	X		xx		xx			xx	xx
Pseudoguembelina costuluta	12	23	18	21	20	18	15	18	19	25	13	16	15	17	19	13	15	14	12	13	14	6	12
P. excolata	X				X	X				X				X	X	X	X		3	2	2	X	X
P. kempensis	2	2	4	8	8	5	5	5	5	10	2	6	4	X	2	X	X	4	X	2	X	X	
P. palpebra	xx	xx	xx	xx		xx	xx																
Pseudotextularia elegans	4	xx	xx	xx	2	X	xx	2	X	2	X	xx	X	X	xx	3	X	xx	X	xx	X	X	2
P. nuttalli	2	X	X			X		X							X	X	X	X	X			X	X
Rosita fornicata	X	X			X	X	X	X	X	X	X	X	X	xx	X	3	xx	xx	X	X	X	X	X
R. patelliformis	X	xx	X	X	X	X	X	xx	xx	xx	X	X	xx			xx	X	X		X	X		X
R. plummerae			X	X	2	xx	X	2	X	5	X	X	X	X	4	X	X	2	6	4	4	5	X
Rugoglobigerina hexacamerata	xx	xx	xx	xx	xx	xx	xx	xx			X												
R. pustulata	xx		xx	X			X	X	X	X		2	X	X		2	X	2	2		X	X	X
R. rugosa	xx	xx	xx	xx	xx	xx	xx	xx		X	X	X		X		X	xx	xx	X		xx	xx	
R. scotti	xx	xx	xx	xx	xx	xx	xx				X												
Total Number Counted	360	288	317	316	383	327	297	312	295	326	334	326	333	347	294	307	304	310	291	332	301	340	288

Tab. 1 continued

Depth (m)	15,8	14,5	14,3	13,6	12,3	11,2	9,7	9,4	8,8	8,1	7,1	6,8	6,5	6,2	5,3	5,2	4,8	4,1	3,4	3,1	2,3	1,8	1,3	0
Archaeoglobigerina blowi	2	3	3	X	3	4	5	2	4	4	3	X	4	4	8	5	5	3	2	2	3	2	4	X
A. cretacea	4	11	3	X	2	4	4	3	6	5	3	3	4	2	3	3	3	3	5	6	3	2	3	4
Gansserina gansseri																								
Globigernelloides aspera	2	3	3	X	6	5	10	3	4	3	2	5	X	4	4	4	2	X	X	X	3	4	X	X
G. minuta					2	X		X				X			3	X		X		X	X			
G. multispina																								
Globotruncana aegyptiaca	xx																							
G. arca	X	X	X	xx	X	xx	X		X	X	X	xx	xx	X	X	X	xx	xx	X	xx	xx		X	xx
G. bulloides	9	3	X	X	2		X	X	X	X	X	X	X	X	X	2	X	X	X	X			X	2
G. falsostuarti		X	X							X						X								X
G. insignis	X		X			xx	X		xx	X	xx	X			xx			xx		xx	xx	xx		xx
G. linneiana	2	X	X	X	2				X	X		X	X	X	xx	3	X	X	X	X		X	X	
G. mariei				xx					xx			xx	xx		X	3	X	X	X	xx	xx	X	xx	2
G. rosetta		X	X													X								
G. subcircumnodifer	X	X			X	X						X	X	X	X	X		X	X	X			X	X
G. subrugosa	5	6	8	4	10	5	8	4	6	8	6	10	9	8	9	4	3	X	4			4	X	X
G. ventricosa		X	X	X	X		X	X		X	X								X					
G. petaloidea	X	X	X	X	X	X	X	X	2	X	2	2	3	2	3	X	X		X	3	X	3	X	2
G. subcarinata	2	3	2	X	X	3	X	X	X	2	2	2	3	3	3	2	2	X	3	X	X	4	X	2
Globotruncanita angulata																								
G. calcarata							X	xx				xx		X					xx	X	xx	xx	xx	X
G. pettersi							X																	
G. stuarti	X		X						xx			xx	xx	xx		X	X	xx		X	xx	xx	X	xx
G. stuartiformis																								
Gublerina actua																								
Guembelitria cretacea		X	X	X			X	X	X	X				X	X		X				X			
Guembelitria sp.			xx		X	xx	X			X	xx	X	X	xx	xx	X	xx	X			X			
Hedbergella holmdelensis	X	2	X	X	X	2	X	3		X	X	X	X	3	3	4	2	X	X	3	X	2	X	2
H. monmouthensis	X	4	2	X	2	3	3	2	X	2	3	3	2	4	3	3	X	X	X	X	2	X	3	2
Heterohelix carinata	X	X	X	4	2	X	X					X		X	X	4								
H. complanata	X	2		4	3			X	X	2		X	4				X	X		3	2	X	4	
H. dentata	7	8	9	17	5	25	20	39	20	22	35	18	34	23	26	23	34	48	39	40	46	29	26	35
H. glabrans		X	5	2	X	2	X	X	X			X		X	X	X		2		X	X	3		X
H. globulosa	23	20	23	27	16	19	11	13	4	10	11	11	12	7	9	6	10	5	6	9	14	6	21	8
H. navarroensis	4	2	6	10	6	7	7	13	8	2	5	7	2	8	6	3	11	18	10	8	5	2	X	3
H. planata	4	2	X	2	4	X	X	X	8	X	X	3	2					X	X	2	X	X	2	X
H. pulchra	2	X	5	2	3	3	2	X	3	X	4	X	3	X		X	4	X	X	2	5	3	3	4
H. punctulata	5	5	3	3	4	X	2	2	2	2	X	X	3	X	X	2	X	X	xx	X	X	3	3	3
H. striata						X	2			2					X	X			X					
Heterohelix sp.	X		X	X	3																			
Planoglobulina brazoensis																								
P. carseyae																								
P. multicamerata	xx		xx		xx	xx		xx	xx			xx		xx		xx								
Pseudoguembelina costuluta	10	6	11	16	16	6	11	5	11	18	15	19	12	15	12	20	17	10	16	10	9	3	19	20
P. excolata	X	X	X				X	X		X	X	X	xx		X	X		X	X	X		X	X	
P. kempensis	X		X	2	X					X												X		2
P. palpebra																								
Pseudotextularia elegans		7	2		X	X	X	X	xx	X	X	2	xx	X					X			xx	X	X
P. nuttalli	X	X			X				xx							xx							xx	
Rosita fornicata	X	xx	X	xx	X	xx	X	xx	xx		xx	X	xx	X	xx	X				xx	xx	xx		
R. patelliformis	X					xx				X	X		xx			X				xx				xx
R. plummerae	4	X	3	X	2	X	X	xx	X	X	xx	xx	xx	X	X	X			X	xx	xx		xx	X
Rugoglobigerina hexacamerata																								
R. pustulata	X	X	X		X	X	2	X	X	3	X	X		X			X			X	X		xx	xx
R. rugosa	xx																							
R. scotti																								
Total Number Counted	372	362	378	332	326	312	292	306	309	285	317	349	296	347	355	293	330	310	369	286	291	298	310	301

Tab. 2. Relative percent abundance of planktic foraminiferal species at El Kef, Tunisia. X = < 2% and xx = rare species.

Depth (m) below KTB	0,00	0,04	0,13	0,23	0,28	0,33	0,38	0,43	0,53	0,65	0,85	1	1,5	2	2,5	3	3,5	4	4,5	5	6	7	8	9
Abathomphalus intermedius																				X	X	xx	X	X
Ganserina gansseri																								X
Globigerinelloides aspera	2	3	5	6	5	4	6	3	4	4	4	4	2	7	7	6	3	5	6	2	5	4	2	3
G. multispina																	X							
G. rosebudensis																							X	X
G. volutus				X	X	X	X	X	X	X	X	X	2	X	X	X	X	X		X	X			
G. yaucoensis	2	2	5	5	3	2	2	3	X	5	8	5	4	3	X	X	2	3	2	2	3	2	2	X
Globotruncana aegyptiaca		X	X	X	X	X	X	X	X			X	X	X	X	X	X	X	X	X	X	X	X	X
G. arca	X	X	X	X	X	X	X	X	xx	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
G. duwi			X										X	X							X			
G. falsostuarti													X										X	
G. insignis			X			X	X	X	X	X	X		X	X	X	X	X	X	X	X		X	X	X
G. dupeublei	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
G. rosetta		X	X	X	X	X	X	X	X	X	X	X	2	X	X	X	X	X	X	X	X	X	X	X
Globotruncanella citae																			X					
G. havanensis										X	3	X	X		X		X	X	X					
G. monmouthensis			X	X		X	X				X		X			X	X	X		X	X	X		X
G. petaloidea		2	X	X	X	X	X	X	X		X			X	X	X	X	2	X	X			2	
G. subcarinata	X	X	2	X	X	X		2	X	X		X		X	X	X	X	X	X	X	2	2	X	X
Globotruncanita angulata							X						X	X	X		X	X	X	X	X	X		
G. conica		X	X	X	X	X			X	X	X	X	X	X	X	X	X	X		X	X	X	X	X
G. stuarti	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
G. stuartiformis			X										X						X					
Gublerina acuta																					X	X		
G. cuvillieri				X			X	X					X	X		X	X	X	X		X	X	X	X
G. robusta						X		X					X	X	X	X	X	X						
Guembelitria cretacea	16	X	X	X	X	X	X		X	X	3	X	2	2	X	2	2	X	2	2	4	2	2	3
G. danica		X	X		X	X		X	X											X	X		X	X
G. trifollia	X	X	X	X	X	X		X	X	X		X		X	X			X		X	X	X		
Hedbergella holmdelensis	2	X	X	2	2	X	2	X	X	X	X	X	X	X	X	X	2	X	3	X	X	3	2	X
H. monmouthensis	2	2	6	4	4	5	4	5	5	X	6	X	X	4	2	X		4		5	2		X	5
Heterohelix carinata																				2	X	10	6	3
H. complanata	5	6	2	3	X	3	6	4	6	2	4	2	7	6	10	4	6	X	5	2	X	3	6	3
H. dentata		30	24	29	26	34	13	22	8	8	3	8	12	5	6	6	5	6	7	X	8	4	10	X
H. glabrans		2	X	2		X	3		5	4	6	4	X		3	3	2	4	2	X	X	2	3	4
H. globulosa	22	8	7	5	10	5	8	10	9	10	9	10	17	9	7	8	9	9	15	11	6	14	12	9
H. navarroensis	14	12	17	22	13	10	9	7	21	16	17	16	15	18	15	14	24	20	19	29	15	25	6	14
H. planata		X	X										X										2	3
H. pulchra		X	X		2	X	X	X												4	4	4		2
H. punctulata	X	2	X	6	X	2	4	2	2	X	3	X	X	X	X	X	X	X	X	3	2	X	2	X
H. striata	X	2	3	3	7	5	10	9	4	X	4	X	4	7	13	7	8	8	5	6	10	2	9	8
Heterohelix sp.		X	X	X		3	3	X	6	X	X	X	X	X	X		X		X		1	X	X	
Planoglobulina brazoensis	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X
P. carseyae	2	X	X	X		X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
P. multicamerata		X	X	X	X	X	X	X	X	X	X		X	X		X	X	X	X		X	X	X	X
Plummerita hantkeninoides		X				X	X	X	X	2	X	2	X	X		4	X	X	X	X	X			
P. reicheli		X	X		X	2	X	X	X		X	X					X			X	X	X	X	
Pseudoguembelina costulata	24	12	9	7	9	11	11	15	14	15	16	15	11	11	13	19	14	16	15	10	11	11	11	9
P. excolata																				X			X	
P. hariaensis			X						X				X	X	X	X	X	X	X	X	X		X	
P. kempensis	4	2	3	X	X	X	X	2	2	3	4	3	5	X	4	5	3	X	2	5	2	2	4	5
P. palpebra	X	X		X	X	X	X	X	2	X	2	X	X	X	2	X	X		X	X	X	X	X	3
Pseudotextularia deformis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	2	X
P. elegans		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	3	X	X	3
P. intermedia		X	X	X				X	X		X	X		X	X	X	X	X	X	X	X	X	X	X
Racemiguembelina fructicosa		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
R. powelli	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X
Rosita contusa				X									X	X					X					
R. patelliformis													X	X	X	X	X					X	X	
Rugoglobigerina hexacamerata		X	X		X	X	X	X	X	5	X	5	5	4	4	5	5	4	3	3	6	2	4	X
R. macrocephela		X	X	X		X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X		X
R. milamensis			X					X						X	X	X	X	X		X				X
R. pennyi			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	X		X	X
R. rotundata	X	X	X	X		X	xx		X											X	X	X	X	X
R. rugosa	X	X	2	X	3	2	6	2	X	2	X	2		3	X	X	X	X	2	X	2	X		X
R. scotti	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	3	X
Rugotruntata subpennyi																	X							X
Sigalia deflaensis																				X				
Total number counted	250	396	342	298	300	287	278	279	297	409	389	406	409	434	468	376	370	470	504	261	324	263	252	277

Tab. 2 continued

Depth (m) below KTB	12	12,5	13	13,5	14	14,5	15	15,5	16	16,5	17	17,5	18	18,5	19	19,5	20	21	22,5	23,5	24,5	25,5	26,5	29,5	32,5
Abathomphalus intermedius	x		x									x								x		x	x	x	
A. mayaroensis																			x						
Archaeoglobigerina blowi																			x	x	x				
A. cretacea		x	x	x	x		x	x	x	x	x		2	x	x	x	x	x	x	x	2	x	x	x	x
Gansserina gansseri	2	x	x	x	x	x	x	x	x	2	x	x	2	x	x	x	2	x	x	x	x	x	x	x	x
G. wiedenmayeri	x	x			x	x	x	x		x	x	x	2	x	x	x	x	x	x	x					x
Globigerinelloides aspera	3	5	3	x	x	2	2	2	x	3	4	x	x	3	3	x	2	3		x	x	x	4	x	5
G. multispina														x											
G. rosebudensis	2	x						x	x												x				
G. volutus			x	x	x		x	x		x	x	x		2	x		x	x	x			x			
G. yaucoensis	x	2	x	2	2	2	3	2	6	4	2	3	x	5	3		3	x	x	x	2		2	x	x
Globotruncana aegyptiaca	x	x	x	x	x	2	2	4	x	x	2	x	4	2	3	4	x	x	x	x			x		x
G. arca	x	x	x	x	x	2	x	2	x	x	x	x	x	x	x	2	x	x	x	x	x	x	x		2
G. dupeublei	x	x	x	x	x	x	x	x	x	x	x		x	x	x				x			x	x	x	x
G. duwi				x		x		x		x				x	x	x				x					x
G. falsostuarti	x	x	x	x	x	x	x	x	x	x	x			x	x										x
G. insignis		x	x		x		x	x	x		x	x	x	x	x	x	x				x	x	x	x	x
G. rosetta	x		x	x	x	2	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Globotruncanella citae												x													
G. monmouthensis		x					x	x		x	x	x	x			3		x							
G. petaloidea	2	2	x	x	x	2		4	x	x	x	x	x	2	x	x	x	x	2	2	x	x	x	x	x
G. subcarinata	2	x	2	x	3	2	3	x	5	4	4	x	x	2	11	2	2	x	2	3	2	x	2	x	x
Globotruncanita angulata	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
G. conica	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x	x	x				x	
G. stuarti	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
G. stuartiformis				x				x	x					x	x					x			x	x	x
Gublerina acuta								x												x					
G. cuvillieri	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x				x				
G. robusta			x																						
Guembelitria cretacea				x		x		x	2	x			2	x	x	x	x			2	x	x	x	x	x
G. danica			x					x									x			x	2				x
Hedbergella holmdelensis	2	2	4	2	x	3	3	2	3	6	2	x	3	2	3	x	3	x	3	2	x	2	x	4	4
H. monmouthensis	3	3	2	3	2	2	2	3	4	5	6	2	2	3		3	5	4	x	5	2	4	2	2	4
Heterohelix americana		x								x	x	x		2	x		x	x							
H. carinata	4		x	5	x	x	3	x	x	x	2	2		x	x	x			x	x	2	2	2	2	4
H. complanata	11	2	11	7	8	8	3	8	7	7	7	4	6	2	8	9	7	6	7	5	5	2	3	6	5
H. dentata	9	15	9	6	6		8	4	9	5	2	4	3	8	10	12	6	11	21	8	10	16	12	15	15
H. glabrans	2	x		2		2	3	2	2	2	6	3	3	3	3	2	4	2	2	3	4	2	3	3	2
H. globocarinata							2	x	2		2		4	2	4	4							2	3	
H. globulosa	11	7	10	14	14	9	10	10	8	7	12	8	12	7	9	13	9	5	2	10	9	4	10	8	5
H. navarroensis	9	12	3	15	13	9	12	4	10	7	4	6	6	8	x	8	10	5	6	7	6	20	15	7	10
H. planata	x							x		x			3	x	x	x				3					
H. pulchra	2	7	x		2	7	2		2	3	2	x	3	2	3		x	2	2	2	x	x	x	2	5
H. punctulata	x	x	2	x	2	3	x	4	x	2	x	2	4	2	3	x		4	3	4	2	2	x		x
H. striata	3	x	4	5	2	5	x	5	4	x	x	4	5	4	3	x	3	5	4	9	4	6	9	5	4
Heterohelix sp.		x		x	x				x	2	2		x						x	2	2	x	3
Planoglobulina brazoensis	x	x	x	x	x			x	x	x	x		x	x		x				x		x	
P. carseyae				x	x	x	x			x			x					x	x		x				
P. multicamerata	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x			x	x	x
Plummerita spinosa			x	x		x	x					x							x	x	x			x	
Pseudoguembelina costulata	15	17	21	15	20	7	22	13	18	13	15	23	9	17	13	16	17	27	21	11	26	22	12	20	16
P. excolata		x			x													x	2	x					
P. hariaensis	xx	xx	xx	xx	xx	xx	xx																		
P. kempensis	2	2	3	3	4	x	2	x	2	5	3	4	4	2	x	3	3	4	3	2	4	x	3	6	
P. palpebra	x	x	x	x	x	2	4	x	2	x	x	x	x	2	x		2		x	x	x	x	3		
Pseudotextularia deformis	x	x	x	3	3	x	x	x	x	x	x	x	x	x	x		x	x	x	x		x		x	
P. elegans	x	x	x	x		x	x	x		x	2	x	3			x	2		x	2	x	2	x	x	x
P. intermedia				x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x				
P. nuttalli																									
Racemiguembelina fructicosa	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x						
R. powelli	x	x	x	x	x		x	x	x	x	x	x	x	x	x		x	x	x						
Rosita contusa				x	x		x	x	x	x	x	x	x	x	x	x	x	x	x		x		x		
R. patelliformis														x					x	x	x	x	x	x	x
R. plicata		x			x	x	x	x	x	x	x	x	x	x	x	x	x		x			x	x	x	
R. plummerae																									x
R. walfischensis		x	x		x	x	x	x	x	x	x	x	x	x					x	x		x	x	x	x
Rugoglobigerina hexacamerata	6	5	2	x	3	3	6	4	4	5	3	8	3	3	3	3	5	5	5	5	6	2	4	6	5
R. milamensis		x	x	x										x											
R. penny				x			x		x		x	x		x	x	x				x		x	x		
R. rotundata		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x				x	x	x		
R. rugosa	3	x	2	x	x	x	x	2		x	x	x	x	2	2	3	x	2	x	x	2	3	4	x	x
R. scotti	x	x	x	x	x	x	x	2	x	x	x	x	6	x	x	2	x	x	x	x	x	x	x		x
Rugotruncana subpennyi		x		x										x		x									
Sigalia deflaensis			2	x		x						x				2								x	
Total number counted	274	250	396	283	268	254	261	364	288	330	290	272	267	260	318	274	278	279	268	268	313	254	249	246	276

Tab. 2 continued

Depth (m) below KTB	32,8	33,5	34,2	35	35,7	36,5	37	37,8	38,2	38,5	39	39,8	40,2	40,6	41,2	41,6	42	47,9	48,8	49,5	50,2	50,7	51	57
Archaeoglobigerina blowi							x		x			x	x	x		x	x	2	2	x	2	4	x	x
A. cretacea	x	2	x	x	x	x	x	x	x	x	x	x		4	x	2	5	2	3	x	3	5	3	7
Gansserina gansseri	x	x	x	x	x		x	x				x	x					x	x					
G. wiedenmayeri	x			x			x	x		x	x	x	x											
Globigerinelloides aspera	2	3	5	2	2	2	3	5	3	2	2		x	x	2	x	2			x	x	2	x	2
G. impensus													3	3		3	x	x	x	2	x	x	x	x
G. rosebudensis															x									
G. volutus							x	x				x												
G. yaucoensis	x	x	x	x	x	x	x	2	x	x	x	x												
Globotruncana aegyptiaca	x		x	x	x	x	x	x			x		x	x			x		x			x	x	x
G. arca	x	x	x	x	x	x	x	x	x	x	x	x	x	2	x		x	x	x	x	x	x	x	x
G. bulloides									x	x	x	x		x	x	x	x		x		x	x	x	x
G. dupeublei	x	x	x	x	x	x	x		x			x	x	x	x			x	x	x	x	x	x	x
G. duwi	x		x			x			x															
G. falsostuarti		x				x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
G. insignis	x	x			x	x	x	x	x	x	x		x		x	x	x	x		x	x	x	x	x
G. linneiana				x				x	x	x	x	x	x	x	x	x	x			x	x	x	x	x
G. rosetta	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x
G. subcircumnodifer																		xx	xx		xx	xx	x	x
G. subrugosa					xx	xx			xx	xx		xx	xx	xx		x		xx	xx			xx	x	x
G. ventricosa		x							x				x	x	x	x	x	x	x		x		x	x
G. petaloidea		x	x	2		x	x	x	x		x	x	x	2	x	x	2	2	3	x	x	x	x	2
G. subcarinata	x	5		3	4	3	4	x	2	4	x	x	2	x	4	3	4	2	5	3	x	4	4	2
Globotruncanita angulata	x		x		x	x	x	x				x	x			x	x	x						
G. conica	x				x	x		x				x	x											
G. stuarti		x	x	x		x	x	x	x	x	x		x	x	x	x	x	x		x	x	x	x	x
G. stuartiformis					x	x				x	x		x	x	x	x	x	x	x	x	x	x	x	x
Gublerina acuta		x	x			x												x	x				x	x
G. cuvillieri					x		x	x					x	x		x	x		x	x	x	x	x	x
G. robusta	x					x																	x	x
Guembelitria cretacea	x	x	x	x	3	x	3	5	x	x		x				x					x	x	x	x
G. danica	x	x			3		x	2	x	2						x	x						x	x
Hedbergella holmdelensis	2	2	x	x	3	x	6	2	4	3	3	x	2	x	2	2	3	3	3	7	x	2	3	2
H. monmouthensis	2	x	2	4	2	5	3	2	x	2	3	6	3	5	2	4	3	2	4	8	5	x	4	2
Heterohelix carinata	3	x	2	2	x	2	2	2	3	2	2	6	5	5	4	x	2	4	x	x	x	2	x	x
H. complanata	4	2	2	2	2	3	2	2	2		3		5	x	5	x	2	5	4	x	x	3	2	x
H. dentata	17	8	17	15	19	16	14	10	25	17	20	15	19	22	29	22	22	18	16	23	14	16	13	19
H. glabrans	x	6	3	2			2	x	x	x	x		x	x	2	2	x	4	4	x	2	x	6	6
H. globocarinata		x					x			10		x	4											
H. globulosa	8	6	3	8	3	9	2	8	7	3	x	4	3	4	6	3	4	6	7	6	5	5	8	7
H. navarroensis	11	5	5	9	8	10	8	9	8	12	5	13	4	7	5	18	4	8	4	7	11	5	7	5
H. planata										x													4	3
H. pulchra	4		6	5	9	x	6	5	10	5	3	6	x	6	3	7	3	6	13	5	15	13	6	8
H. punctulata	x	3	2	2	3	4	3	2	2	2	3	5	4	7	4	x	4	2	2		3	x	x	x
H. striata	3	7	7	4	7	5	2	9	2	3	3	x	2	2	x	3	4	x	6		5	6	x	2
Heterohelix sp.	3	3	3	3	x	2	3	x	x	2	x	x	4	x	x		2	3		8	4		x	x
Planoglobulina brazoensis							x	x	x			x												
P. carseyae						x						x												
P. multicamerata	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x
Plummerita spinosa		x																						
Pseudoguembelina costulata	22	27	21	18	21	19	18	10	16	13	25	19	15	11	18	20	15	13	16	16	17	18	21	12
P. excolata							x	x	x	x	x	x	x	x		x		x	x	x	x		x	x
P. kempensis	2	x		3		3	2	2	x	2	6	2	4		x		x	x		x		x		
P. palpebra		x	x	x		x		2		x	x		2			x			x	x	2	x	x
Pseudotextularia deformis		x		x		x			x		x	x	x	x										
P. elegans	x	4	4	x	2	x	2	2	x	x	x	3	2	2	x		4	4	x	2		3	2	4
P. intermedia	x						x	x																
P. nuttalli																x		2	x		2		x	x
Rosita contusa	x		x		x	x	x			x		x												
R. fornicata	x		x		x	x	x	x	x	x	x	x	x	x		x	x	x		x		x	x	
R. patelliformis	x	x	x	x	x	x	x	x	x	x	x	x	x	2	x	x	x	x	x	x	x	x	x	x
R. plicata		x	x		x	x	x		x															
R. plummerae	x	x	x	x	x	x	x		x	x	x	x	x	x		x	x	3	x	2	x	x	x	
R. walfischensis	x				x																			
Rugoglobigerina hexacamerata	3	6	6	5	3	6	3	3	2	6	3	2	3	4	6	2	x	x						
R. milamensis		x					x	x			x													
R. penny							x																	
R. rotundata	x						x	x																
R. rugosa	x	2	3	x	3	x	2	x	x	x	x	2	x	x	x	x	x	x	x	x	x	x	x	x
R. scotti		x	x	x	x		x	x	x	x	x	x			x	x								
Total number counted	262	267	260	300	315	318	284	288	318	328	292	243	280	271	322	250	292	312	274	277	255	256	268	273