

Extinction, Survivorship and Evolution of Planktic Foraminifera across the Cretaceous/Tertiary Boundary at El Kef, Tunisia

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Abstract

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An expanded sediment record at El Kef shows that the K/T boundary extinctions of planktic foraminifera extend over an interval from 25 cm below the geochemical boundary (Ir anomaly) to 7 cm above. Species extinctions appear sequential with complex, large, ornate forms disappearing first and smaller, less ornate, forms surviving longer. The 14 species extinctions below the boundary appear unrelated to an impact event.

Cretaceous species survivorship is greater than previously assumed. About 10 species survive (22%) into Subzone P1a (*Globigerina eugubina*). All Cretaceous survivors are small primitive forms which are generally smaller than their ancestors in Cretaceous sediments.

Species evolution after the K/T event occurs in two pulses. The first new Paleocene species evolve in the basal black clay (Zone PO) immediately after the major Cretaceous extinctions. Evolving species are small and primitive similar to Cretaceous survivors. The second pulse in species evolution occurs in the lower part of Subzone P1b with the appearance of larger more diverse species. The first major increase in carbonate sedimentation and productivity occurs at this time and signals the recovery of the ecosystem nearly 300,000 years after the K/T event. The species extinctions prior to the generally assumed impact event implied by the Ir anomaly, and the long recovery period of the ecosystem thereafter cannot be explained by a single impact, but suggest that multiple causes may be responsible such as climatic changes, volcanism, a sea level drop, production of warm saline bottom water and the chemical consequences associated with increased salinity.

Introduction

The El Kef section is located about 7 km west from the town of El Kef in northwest Tunisia (Fig. 1). Nannofossil studies by Perch-Nielsen (1979, 1981, a,b), Perch-Nielsen et al. (1982) and Romein and Smit (1981) and planktic foraminiferal studies by Salaj (1973, 1977) and Smit (1982) claim El Kef as the most complete K/T boundary section known to date. Both

nannofossil and foraminiferal workers have discovered one additional biostratigraphic zone at the base of the Paleocene which is not generally present in deep-sea sections with more condensed K/T boundary sequences (Perch-Nielsen, 1979; Smit, 1982). Despite recognition of El Kef as perhaps the most complete K/T boundary sequence, no detailed studies on planktic or benthic foraminifera have been published.

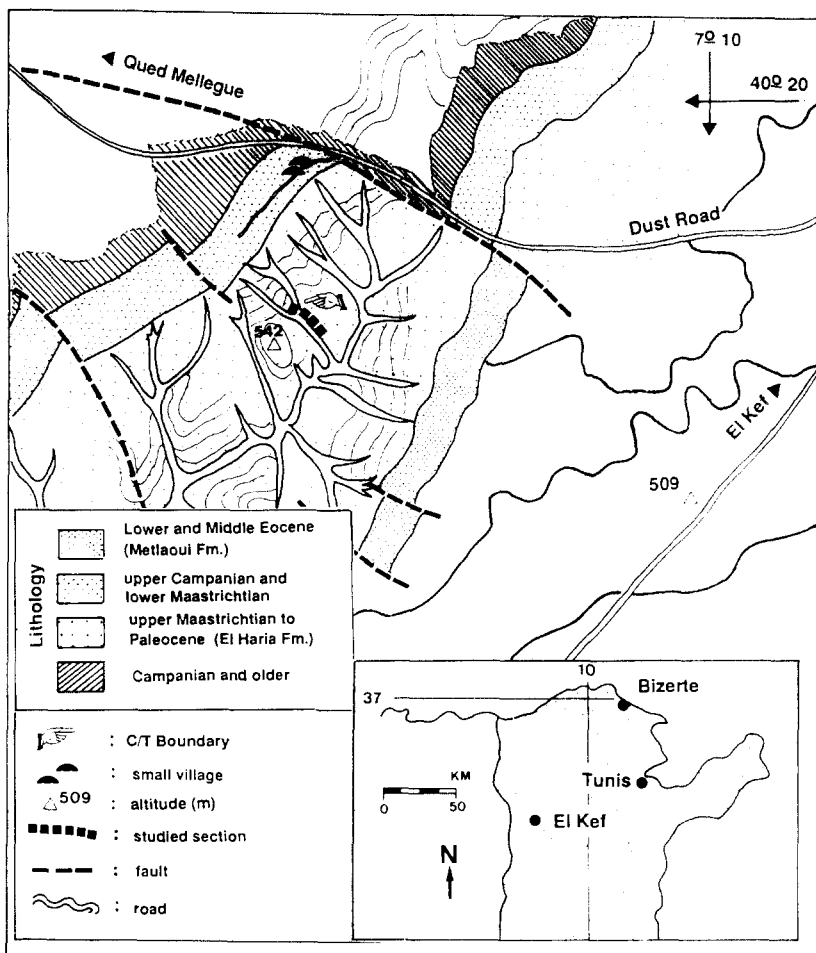


Fig. 1. Location map showing the K/T boundary section near El Kef, Tunisia along with regional distribution of sediments of Campanian to Eocene age.

This report and companion studies on benthic foraminifera (Keller, 1988a) and stable isotope stratigraphy (Keller and Lindinger, in prep.) attempt to elucidate the biotic turnover and paleoenvironmental conditions on the sea floor and in surface waters across the K/T boundary at El Kef. Benthic foraminifera show a 50% reduction in species diversity at the K/T boundary and diversity remained 37% lower during deposition of the first 3 m of the sediment above the boundary (PO to P1a Zone). Surviving species are generally tolerant of low O_2 conditions and productivity was low. Increased productivity and return to higher oxygen levels on the seafloor resumed about 4 m above the K/T

boundary (P1b Subzone, Keller, in prep.; Peyrouquet et al., 1986). Thus, the K/T boundary event profoundly affected faunas living on the sea floor of the Tunisian continental platform.

Planktic foraminifera were analyzed to obtain a complete history across the K/T boundary in a relatively protected shallow sea. The surface record of faunal changes essentially mirrors that on the sea floor, but planktic foraminifera suffered greater losses and were subjected to more stressful conditions than benthic foraminifera. Although planktic foraminifera show overall similarities with the record known from the deep-sea, fundamental differences are apparent; these, however, may be largely due to

the expanded section present at El Kef. The differences concern primarily the nature of species extinctions across the K/T boundary, species survivorship, and evolution of new species. This report primarily deals with these aspects of the K/T boundary event.

Material and methods

Samples were obtained by the Cretaceous/Paleocene Working Group of the International Committee on Stratigraphy. Sample numbers used in this report represent original numbers given by the collecting team. The section was sampled at 20-cm intervals below the K/T boundary and continuous sampling at 5-cm intervals for the first 1.60 m above the boundary, then at 20-cm intervals between 1.60–3.00 m and at 50-cm intervals between 3 and 10 m above the boundary. A total of 66 samples were analyzed for this study between 4 m below the K/T boundary to 10 m above the boundary.

Samples were processed by standard micropaleontological techniques. In general samples were not easy to disaggregate and repeated soaking in calgon with dilute H₂O₂ followed by several washings were necessary. Planktic foraminiferal preservation is generally good although recrystallization of original calcite shells is evident in lower Paleocene sediments.

Population counts were based on representative splits (using an Otto microsplitter) of about 300 specimen of the size fractions > 63 μm and > 150 μm . Two size fractions were analyzed because of the variable species sizes. The smaller size fraction (> 63 μm) best shows evolutionary trends of small species in late Cretaceous and earliest Tertiary sediments. The larger size fraction (> 150 μm) was expected to show trends of larger species, but no faunal trends could be recognized. Faunal counts for > 63 μm and > 150 μm size fractions are listed in Tables I and II. Sample depths are listed as midpoints for continuous sample intervals.

Biostratigraphy and lithology

The K/T boundary section of El Kef is contained within the El Haria Formation (Fig. 1). This formation spans upper Cretaceous to Paleocene sediments consisting of marls with sporadic limestone intercalations (Burolet, 1966). The lithology of the K/T boundary interval is characterized by five units which are discussed below in the context of the biostratigraphic zonation of Premoli Silva and Bolli (1973), Berggren (1978), Herm (1981), and modified by Salaj (1977), Smit (1982) and Smit and Romein (1985). Further modifications of this zonal system are proposed here and illustrated in Fig. 2.

Upper Maastrichtian

A white-grey clayey marl with about 40% CaCO₃ and common burrows about 2–3 cm long marks the uppermost Maastrichtian. The uppermost 4.5 m of sediment examined of this unit do not contain *Abathomphalus mayaroensis*, the index species of the latest Maastrichtian zone with the same name. Absence of this species in the El Haria Formation was earlier observed by Salaj (1980) and was also recently observed by the present author in the Negev sections of Israel and Brazos River section of Texas, and by Jones et al. (1987) in the Braggs section of Alabama. The frequently observed absence of *A. mayaroensis* from uppermost Cretaceous sediments of continental shelves indicates that this species disappears prior to the K/T boundary at least in shelf regions. For this reason the new *Pseudotextularia deformis* Zone is proposed for the latest Maastrichtian (Fig. 2).

K/T boundary

The K/T boundary lies between the top of the white-grey clayey marl and the overlying 50 cm thick black clay unit which has an average of 4% CaCO₃. A 2–3 mm thin rust colored ferruginous layer at the base of the black clay marks the boundary event. No burrows are observed through this layer or in the black clay.

| | Datum Events | This Report | Smit, 1982 | Premoli Silva & Bolli, 1973, Berggren, 1978 | Herm et al, 1981 |
|-----------|---|---|---------------------------------|---|----------------------------|
| PALEOCENE | <i>G. trinidadensis</i> ↓ | c <i>G. pseudo-bulloides</i> | c <i>G. pseudo-bulloides</i> | | |
| | <i>G. taurica</i> ↓ | b ₂ <i>G. taurica</i> | b <i>G. taurica</i> | b <i>G. pseudo-bulloides</i> | <i>G. pseudo-bulloides</i> |
| | <i>G. praeaequa</i> <i>S. triloculinoides</i> <i>G. eugubina</i> <i>G. moskvini</i> <i>G. pseudobulloides</i> <i>G. conusa</i> ↑ | P1 b ₁ <i>Eoglobigerina</i> spp. | P1 | P1 | |
| | <i>Eoglobigerina</i> spp. <i>G. daubjergensis</i> ↑ | a <i>G. eugubina</i> | a <i>G. eugubina</i> | a <i>G. eugubina</i> | <i>G. eugubina</i> |
| | <i>G. taurica</i> <i>G. midwayensis</i> ↑ | a <i>G. eugubina</i> | a <i>G. eugubina</i> | a <i>G. eugubina</i> | <i>G. eugubina</i> |
| | <i>G. eugubina</i> ↑ | b <i>G. conusa</i> | | | |
| | <i>G. conusa</i> , <i>E. edita</i> <i>W. hornerstownensis</i> <i>G. fringa</i> , <i>G. archeoc.</i> ↑ | PO a <i>G. cretacea</i> | PO <i>G. cretacea</i> | | <i>G. fringa</i> |
| | EXTINCTION | | | | |
| | <i>P. deformis</i> ↓ | | | | |
| | <i>A. mayaroensis</i> ↓ | M3 <i>A. mayaroensis</i> | M3 <i>A. mayaroensis</i> | <i>A. mayaroensis</i> | <i>A. mayaroensis</i> |
| MAASTRIC | | | | | |

Fig. 2. Comparison of Late Maastrichtian and early Paleocene planktic foraminiferal biozonations with biozonation of this report.

The base of the black clay layer contains positive anomalies of Ir and Os (Kuslys and Krahenbuhl, 1983). The thin ferruginous layer shows a drop in CaCO₃ to less than 1%, a maximum in organic carbon, and a negative excursion in δ¹³C (Keller and Lindinger, in prep.). At the base of the black clay layer (sample 541) are numerous compressed spherules of sanidine and hematite. These spherules were originally described by Smit (1982) as altered microtektites, but they are now shown to be authigenic in origin (Izett, 1987).

Based on planktic foraminifers the K/T boundary is generally placed at the extinction of nearly all Cretaceous species. However, the expanded K/T boundary at El Kef clearly shows that not all species went extinct simultaneously, but spread out over about 32 cm of sediment with major extinctions beginning 25 cm below the boundary (discussed below). *Globotruncana* and *Rugoglobigerina* species extinctions most closely coincide with the lithological and geochemical boundary.

Lower Paleocene

The lowermost Tertiary was originally divided into *Globigerina eugubina* (K/T boundary to FA *G. pseudobulloides*) and *G. pseudobulloides* Zones (FA of zonal marker to FA *G. trinidadensis*, Premoli Silva and Bolli, 1973). Subsequently, these zones have been divided into subzones with a numerical system beginning with PO at the boundary (Berggren, 1978; Smit, 1982). In this report a further modification of this system is proposed and illustrated in Fig. 2 along with earlier biozonations.

Zone PO — Subzones POa, (*Guembelitra cretacea*), POb (*Globoconusa conusa*)

The 50cm thick black clay unit marks the basal Paleocene. This unit contains both Cretaceous survivors and the evolution of the earliest Tertiary species, but is characterized by an abundance of *Guembelitra cretacea*. Smit (1982) defined an earliest Paleocene PO, or *G.*

cretacea Zone as ranging from the K/T boundary to the first appearance (FA) of *Globigerina minutula*. (Note, the species illustrated by Smit (1982, pl. 3) as *G. minutula* is *Globoconusa conusa* Chalilov). Based on the present faunal analysis of El Kef it is proposed that Zone PO be modified to range from the K/T boundary to the FA of *Globigerina eugubina* with a subdivision into subzones a and b. Subzone POa remains Smit's original definition of *G. cretacea* Zone. Subzone POB, or *Globoconusa conusa* ranges from the FA of *G. conusa* to the FA of *G. eugubina*. In the El Kef section *G. conusa* first appears 22 cm above the K/T boundary and *G. eugubina* appears 52 cm above the boundary near the top of the black clay unit. These two subzones provide further stratigraphic control for the K/T boundary interval. Moreover, they encompass the black boundary clay which initiates a profoundly changed ecosystem after the K/T boundary event.

Subzone P1a (G. eugubina)

Partial range subzone from FA *Globigerina eugubina* to first proliferation of *Eoglobigerina* spp. The lower boundary of this subzone is here modified from Smit (1982) who based it on the FA of *G. conusa* (*G. minutula* of Smit). Subzone P1a comprises most of *Globigerina eugubina* Zone and is characterized by dominance of *G. eugubina* common *G. conusa* and decreasing abundance of *Chiloguembelitra danica*.

At El Kef about 250 cm of sediment represent Subzone P1a. The basal 50 cm of Subzone P1a consist of dark grey clay with 6–10% CaCO₃. Few burrows are apparent. This unit grades upward into grey clay-rich shale about 200 cm thick with an average 14% CaCO₃. Above this unit carbonate increases rapidly in increasingly marly sediments.

Subzones P1b

This subzone ranges from the entry of common *Eoglobigerina* spp. to the extinction of *Globigerina eugubina*. As originally described by Salaj (1977) based on Tunisian sections this

subzone comprises the main occurrence of the *Globigerina taurica* fauna. At El Kef this fauna is most common above the extinction of *G. eugubina* (Table I). It is therefore proposed that the definition of Subzone P1b (*G. taurica*) be modified to include the main occurrence of the nominate species and that the subzone be divided into P1b₁ and P1b₂ based on the extinction of *G. eugubina*.

Subzone P1b₁ (Eoglobigerina spp.)

Partial range subzone from entry of main proliferation of *Eoglobigerina* spp. to the extinction of *G. eugubina*. At El Kef this subzone comprises 2 m of sediment from 3 to 5 m above the K/T boundary. The fauna in this interval is characterized by a rapid terminal decline in the abundance of *G. eugubina*, peak abundance of *Eoglobigerina* spp., first abundant *Chiloguembelitra taurica* and *Globigerina taurica*, and the first appearance of *G. pseudobulloides*. At El Kef Subzone P1b₁, occurs within an interval of rapidly rising carbonate (from 20 to 50%) and sharp increase in surface and bottom water productivity as indicated by a positive $\delta^{13}\text{C}$ shift of about 2‰ (Keller and Lindinger, in prep.).

Subzone P1b₂ (Globigerina taurica)

Partial range subzone from the last appearance of *G. eugubina* to the last appearance of *G. taurica*. This subzone is characterized by peak abundances of *G. taurica* and *Chiloguembelitra taurica* and common *Globoconusa daubjergensis*. At El Kef Subzone P1b₂ encompasses 4 m (+5 to +9 m) of relatively carbonate rich (~45%) marly sediments.

Sediment accumulation rates

No magnetostratigraphy has been done at El Kef. However, age estimates can be obtained from sediment accumulation rates based on datum events of foraminifers dated elsewhere. The K/T boundary lies within the reversed polarity interval between anomalies 29 and 30 (Berggren et al., 1985). Age estimates for the boundary range from 66.2 to 66.8 Ma with the best age estimated by Haq (1983) at 66.4 Ma. The first

appearances of the index species *Globigerina eugubina* and *G. pseudobulloides* have been dated at 66.35 Ma and 66.10 Ma respectively (Berggren et al., 1985). Based on these ages average sediment accumulation rates can be calculated. If we estimate the K/T boundary at 66.4 Ma, then the first 52 cm of black clay above the boundary to the first appearance of *G. eugubina* was deposited within 50,000 years, or a sedimentation rate of 1.04 cm/1000 years. The nearly 350 cm sediments of the *G. eugubina* Zone to the first appearance of *G. pseudobulloides* reflect 250,000 years, or an average sedimentation rate of 1.40 cm/1000 years. We do not have good estimates of sediment accumulation rates for the carbonate rich marls above or below the K/T boundary.

Species diversity

Total species diversity as indicator of environmental conditions is illustrated in Fig. 3 along with the number of first and last appearances of species and percent carbonate in sediments. Total species diversity is based on the actual number of species present in a sample plus species temporarily absent, but present in the samples immediately preceding and succeeding. The latter are represented by a line at the top of the histogram. This temporary absence is considered to be due to rarity of species or small sample size.

During the latest Cretaceous species diversity of planktic foraminifera remains relatively constant around 50 species. But during the early Tertiary the number of species averages 15–20. This represents an average decline of 78% in total species diversity as observed at El Kef, Tunisia. In contrast, benthic species diversity declined only 37% during the same time interval (Keller, 1988a). Similar to benthic faunas the decline in planktic species diversity between Cretaceous and Tertiary faunas is rapid beginning in sample 539 25 cm below the K/T boundary and reaches a maximum low of 7 species, or 86% decline in diversity, 7 cm above the

boundary. This decline occurs in stages with the maximum number of species extinct in sample 541 at the K/T boundary. Total species diversity remains very low (10 species or less) in the first 50 cm of black clay (Zone POa, b) above the K/T boundary. Above this level species diversity increases to 15–20 species and remains at this level through Subzones P1a (*G. eugubina*) and P1b.

The number of last appearances of species in Fig. 3 illustrate the rapid and sequential change occurring across the K/T boundary. In contrast, few species disappear before or after the K/T boundary event. Furthermore, there are relatively few first appearances of species and these occur in two intervals. The first pulse in evolutionary diversity occurs in the 50 cm thick black clay layer above the K/T boundary. In this interval 10 species evolve. The second pulse occurs in the lower part of Subzone P1b (*Eoglobigerina* spp.) coincident with increased carbonate sedimentation and surface productivity (Keller and Lindinger, in prep.).

There appears to be a positive correlation between high species diversity or evolutionary turnover, high carbonate in sediments and positive ^{13}C values. High species diversity correlates with high carbonate and high productivity, low species diversity correlates with low carbonate and low productivity. This suggests that species diversity is strongly linked to surface productivity.

Sequential nature of K/T boundary extinctions

Cretaceous/Tertiary boundary extinctions at El Kef do not appear to have occurred geologically instantaneously, nor do they correlate precisely with the geochemical and lithological boundary. Species extinctions begin between 25 cm below the boundary event (Ir anomaly) and end about 7 cm above. Although it is possible that bioturbation may have obscured the extinction record, this does not seem a major problem in the El Kef section. Burrows of 2–3

EL KEF, TUNISIA PLANKTIC FORAMINIFERA

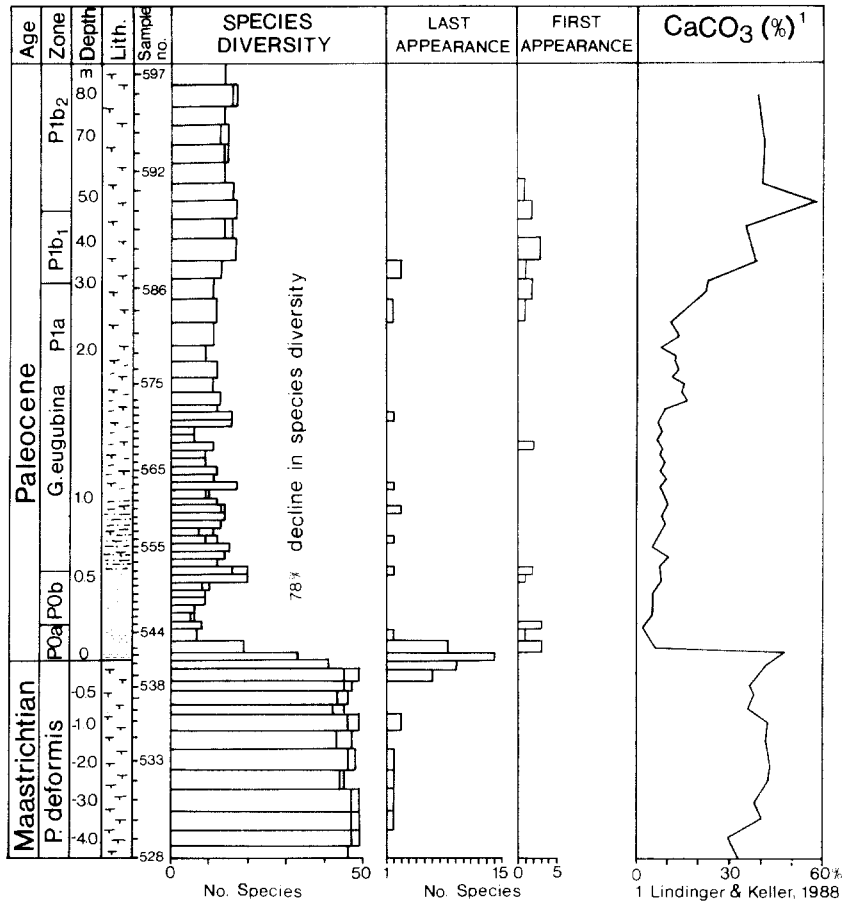


Fig. 3. Species diversity, first and last appearances of species and percent carbonate in late Maastrichtian to early Paleocene sediments at El Kef, Tunisia.

cm length were observed below the boundary clay layer, but no bioturbation was observed across the 2–3 mm thick ferruginous layer at the base of the 50 cm thick black clay or within the clay layer. Moreover, species extinctions show a systematic sequential nature which is unlikely to be caused by bioturbation.

Ranges of species are illustrated in Fig. 4. Cretaceous species found in early Tertiary samples are marked with dots; for the most part these are considered reworked specimens. Species with dots connected by a line are considered as Cretaceous survivors and will be discussed later. Six species disappeared during the latest Cretaceous between 1–4 m below the K/T boundary (Fig. 4). These species are rare

in latest Cretaceous faunas and their extinction is likely due to minor environmental perturbations unrelated to the K/T boundary event.

The K/T boundary extinctions begin in sample 539, 25 cm below the boundary clay. Six species last appear in this sample. Four of these species are morphologically similar with multiple globular chambers arranged in either biserial or multiserial fashion (*Ventrilabella eggeri*, *Racemiguembelina fructifera*, *Pseudotextularia carseyae*, *P. elegans*) (Fig. 4, Plate I). Eight species last appear in sample 540, a sample spanning 0–5 cm below the K/T boundary. Extinctions at this level appear to affect primarily the globotruncanid and globotruncanellid species (5 of 8 species) (*Globotruncana trinidaden-*

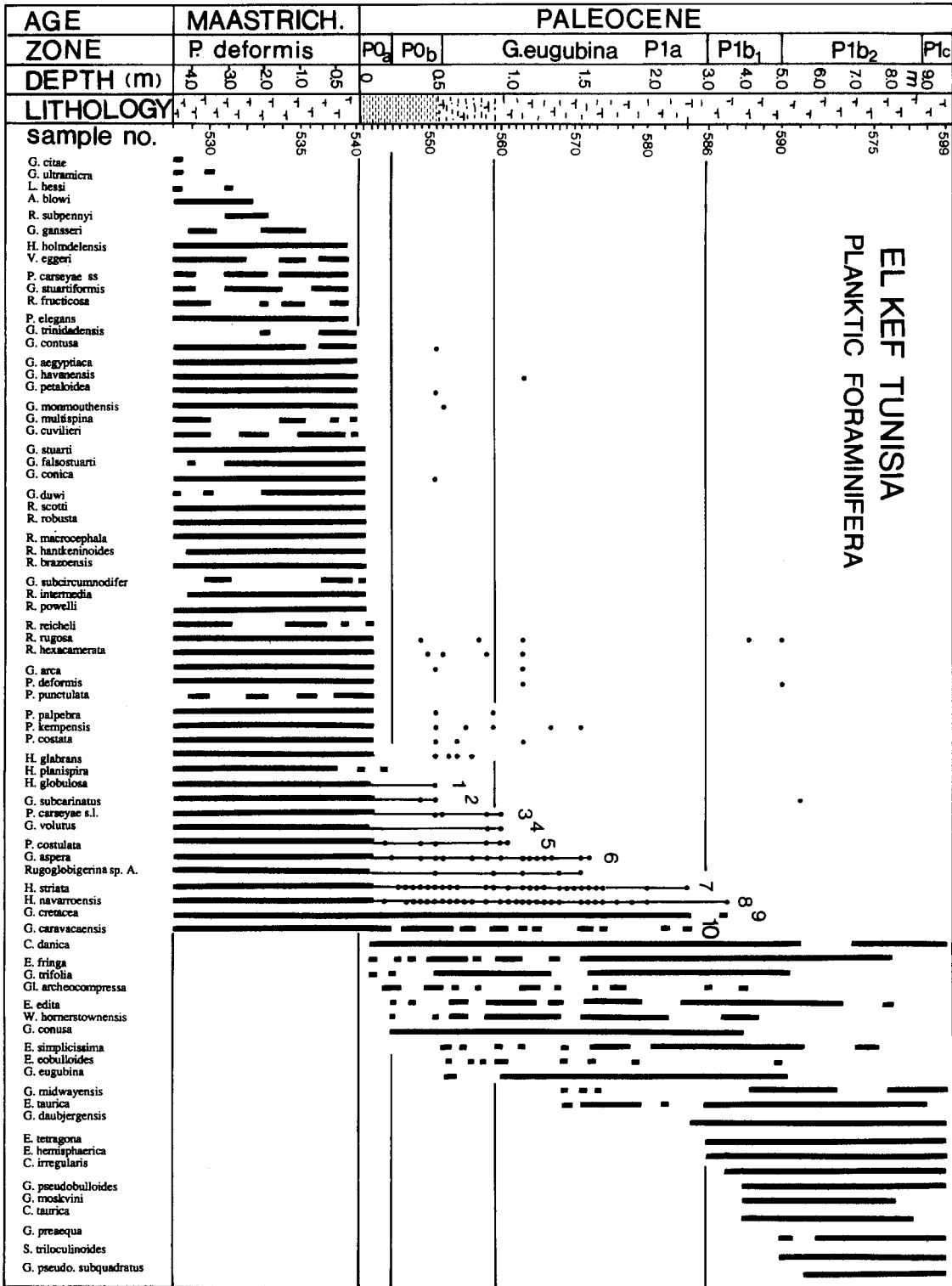
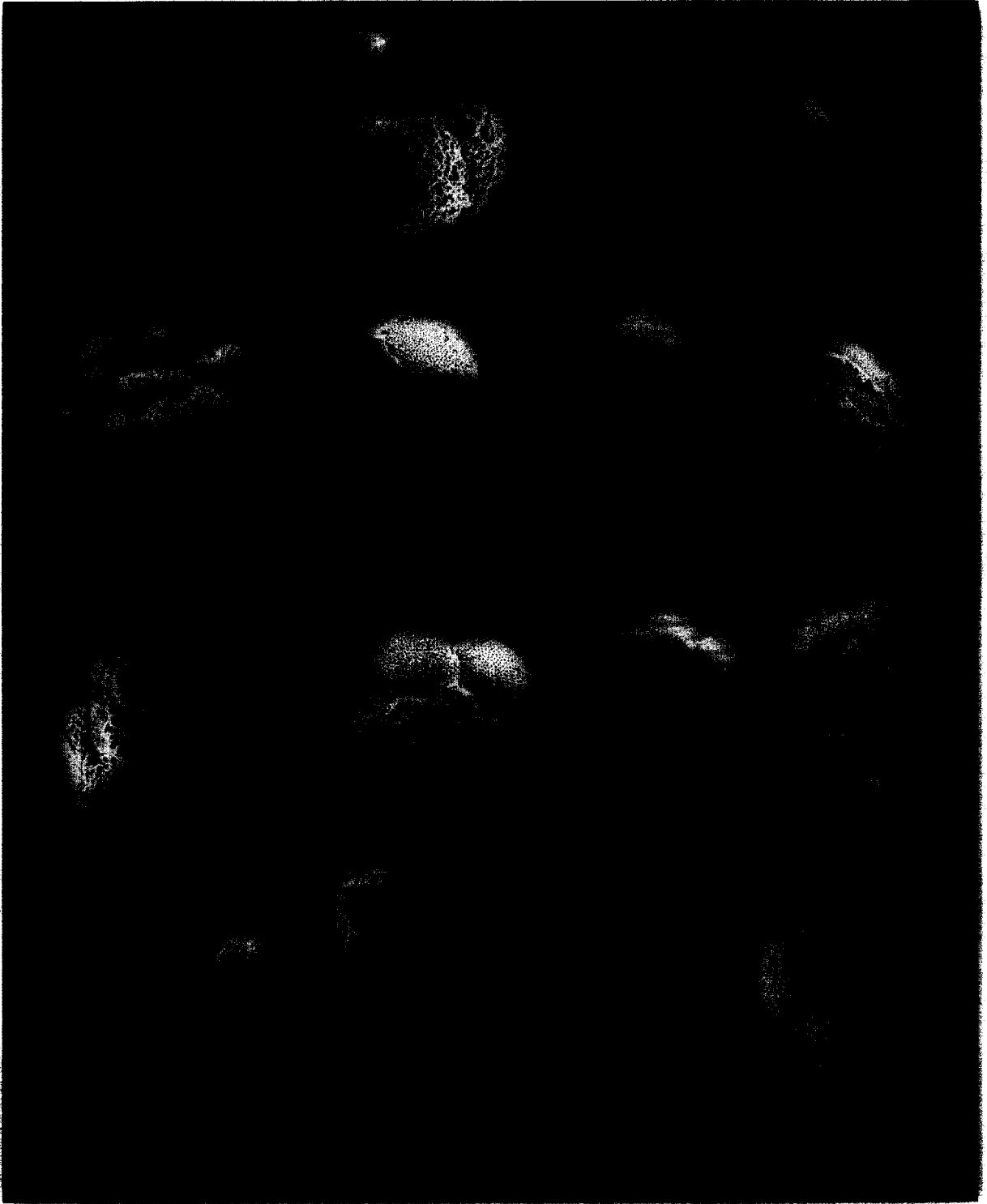


Fig. 4. Species ranges of planktic foraminifera. Note, species extinctions begin 25 cm below the K/T boundary and continue to 7 cm above the boundary. Ten Late Cretaceous species survive into the early Paleocene (dots connected by lines). Unconnected dots represent probable reworked Cretaceous species.

PLATE I



sis, *G. contusa*, *G. aegyptiaca*, *Globotruncanella havanensis*, *G. petaloidea*, Plate I, Fig. 4).

Twelve species last appear in sample 541, a sample spanning 0–5 cm above the base of the boundary clay. Major extinctions continue among the morphologies previously affected: four globotruncanid species (*G. stuarti*, *G. falsostuarti*, *G. conica*, *G. fornicata*) and three species of multichambered biserial or multiseriate morphology (*Racemiguembelina brazoensis*, *R. intermedia*, *R. powelli*). No species of the multiseriate group appears to survive this interval at El Kef. In addition to these species extinctions a new morphology, the rugoglobigerinids, are now also affected by extinctions (*Rugoglobigerina scotti*, *R. robusta*, *R. macrocephala*, *R. hantkeninoides*).

Ten species disappear in sample 542, spanning the interval 5–10 cm above the K/T boundary. The remaining rugoglobigerinid species disappear at this time (*R. reicheli*, *R. rugosa*, *R. hexacamerata*), as well as the last surviving globotruncanid species (*G. arca*). In addition, a new group, the biserial pseudotextulariids and pseudoguembelinids are now strongly affected by extinctions (*Pseudotextularia deformis*, *Pseudoguembelina punctulata*, *P.*

palpebra, *P. kempensis*, *P. costata*, Plate II, Fig. 4). In contrast, the smaller biserial heterohelicid forms decline in abundance throughout the K/T boundary extinction interval, but continue to be present in the early Tertiary where they disappear in the *Globoconusa conusa* (POb) and *G. eugubina* (P1a) Subzones (Fig. 4). In addition, *Rugoglobigerina* sp. A, a small rugosa-like form also appears to survive into the Paleocene.

Species range data from El Kef, Tunisia, thus show that the K/T boundary extinctions did not occur simultaneously, but stretched out over a considerable time period (–25 to +7 cm). Moreover, there appears to have been a systematic elimination of species groups with common morphologies suggesting that successive niche destruction occurred over this time period. It may also indicate that species with certain morphologies were more tolerant of environmental changes than other groups. Thus, the history of species extinctions at El Kef shows the early disappearance of complex large biserial to multiseriate forms followed by globotruncanid and globotruncanellid species. Most of these species are relatively rare in the upper-

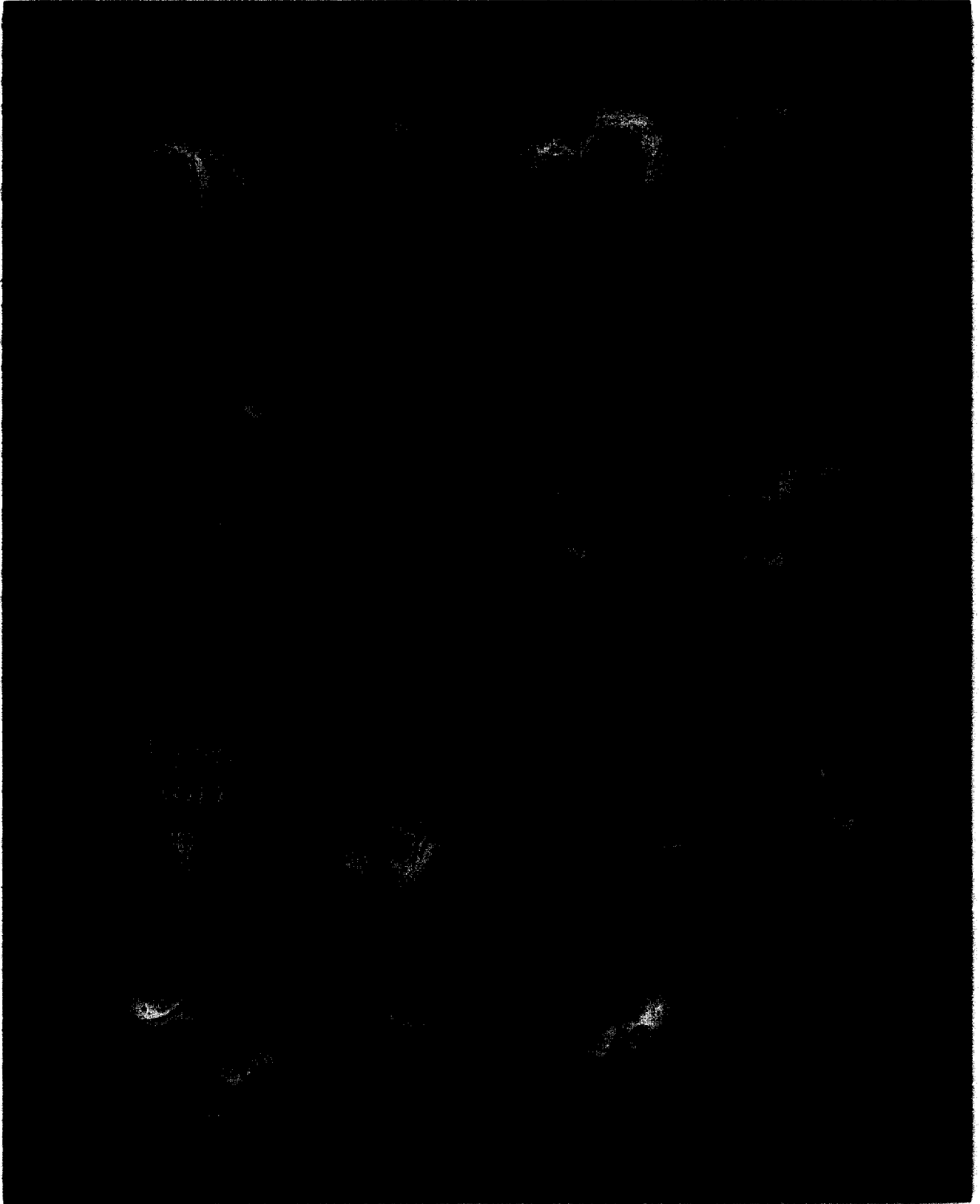
PLATE I

All Figures at 150× magnification (scale bar = 100 μm). All samples from *P. deformis* Zone. Species disappearances in the El Kef section are as follows:

Figs. 14–17, 25 cm below the K/T boundary: figs. 9–13, 5 cm below the K/T boundary: figs. 4–8 at the boundary and figs. 1–3 between 5–10 cm above the boundary.

1. *Rugoglobigerina scotti* (Bronnimann), sample 540.
2. *Rugoglobigerina robusta* Bronnimann, sample 540.
3. *Rugoglobigerina macrocephala* Bronnimann, sample 540.
4. *Globotruncana stuarti* (Lapparent), sample 540.
5. *Planoglobulina brazoensis* Martin, sample 539.
6. *Globotruncana aegyptiaca* Nakkady, sample 540.
- 7, 8. *Globotruncana arca* (Cushman), sample 540.
9. *Globotruncana contusa* (Cushman), sample 539.
10. *Globotruncanella havanensis* (Voorwijk), sample 539.
11. *Globotruncana arca* (Cushman), sample 539.
- 12,13. *Globotruncanella petaloidea* (Gandolfi), sample 540.
14. *Ventriabellina eggeri* (Cushman), sample 539.
15. *Racemiguembelina fructicosa* (Egger), sample 539.
16. *Planoglobulina carseyae* (Plummer), sample 539.
17. *Pseudotextularia elegans* (Rzehak), sample 539.

PLATE II



most Maastrichtian of El Kef. These extinctions are followed by the somewhat more robust and more common rugoglobigerinid and smaller, simpler biserial pseudotextularid species extinctions. The small biserial heterohelicids as well as some globigerinellids, hedbergellids and guembelitrids survived longest and appear to have been best adapted for survival.

Plates I and II illustrate the characteristic morphologies of species extinct across the K/T boundary. All scanning electron micrographs (SEM) were taken at the same magnification for Late Cretaceous species, except for the small K/T boundary survivors, to show size changes. Because K/T boundary survivors and early Danian species are extremely small, these species are illustrated at over three times the magnification of Late Cretaceous species (Plates I and II). The following characteristics are immediately obvious: large species disappear earlier than small species, complex morphologies disappear first, and simple morphologies survive longest. Thus, large, complex overspecialized morphologies are unsuited for adaptation in a rapidly changing environment, whereas generalists with simple morphologies are best suited for survival. This illustrates what has long been known in theory and was observed among late Cretaceous invertebrates by Kauff-

man (1984). However, this selective nature of species extinctions has not been demonstrated before for the K/T boundary extinction event. The K/T boundary extinctions are generally believed to have occurred too rapidly for selective species extinctions to occur. This study of El Kef faunas shows that even in a very rapidly or catastrophically changing environment, the theory of selectivity in species extinctions holds.

Species survivorship

Foraminiferal workers commonly report the near extinction of all planktic species at the Cretaceous/Tertiary boundary. However, a few authors have observed an impoverished relict faunule composed of dwarfed Late Cretaceous genera such as *Rugoglobigerina*, *Planomalina*, *Globigerinelloides* and *Hedbergella* (Berggren, 1965; Hofker, 1978; Blow, 1979). Although many other workers have observed the presence of small Cretaceous species in early Tertiary sediments, they have generally assumed that their presence was a result of bioturbation or reworking of older sediments. Reworked specimens are difficult and often impossible to identify especially if they are not discolored or show differential preservation and are obviously anomalous in age with the rest of the

PLATE II

Figs. 1-8 represent Late Cretaceous survivors, magnified $500\times$ (scale bar-10 μm). Figs. 9-17 represent species extinct about 7 cm above the K/T boundary and magnified $150\times$ (scale bar=100 μm). Note the smaller size of Cretaceous survivors which are actually less than 1/3 the size of average Cretaceous species.

1. *Guembelitria cretacea* (Cushman), POa, *G. cretacea* Subzone, sample 544.
2. *Globigerinelloides subcarinatus* (Bronnimann), P1a, *G. eugubina* Subzone, sample 552.
- 3, 4. *Globotruncanella caravacaensis* Smit, P1a, *G. eugubina* Subzone, sample 556.
5. *Heterohelix navarroensis* Loeblich, POB, *G. conusa* Subzone, sample 548.
6. *Heterohelix striata* (Ehrenberg), POB, *G. conusa* Subzone, sample 548.
- 7, 8. *Globigerinelloides aspera*, Bolli, Pla, *G. eugubina* Subzone, sample 558.
9. *Pseudotextularia deformis* (Kikoine), *P. deformis* Zone, sample 541.
10. *Pseudoguembelina punctulata* (Cushman), *P. deformis* Zone, sample 538.
11. *Pseudoguembelina palpebra* (Bronnimann and Brown), *P. deformis* Zone, sample 538.
12. *Pseudoguembelina kempensis* (Esker), *P. deformis* Zone, sample 538.
13. *Pseudoguembelina costata* (Carsey), *P. deformis* Zone, sample 538.
14. *Rugoglobigerina rugosa* (Plummer), *P. deformis* Zone, sample 539.
15. *Rugoglobigerina reicheli* (Bronnimann), *P. deformis* Zone, sample 539.
- 16,17. *Rugoglobigerina hexacamerata* (Bronnimann), *P. deformis* Zone, sample 539.

faunal assemblage. The early Danian fauna at El Kef clearly contains some intervals with reworked Cretaceous specimens, particularly globotruncanids (Fig. 4). However, many samples contain the smaller heterohelicid, pseudotextularid and hedbergellid species without other characteristic Cretaceous species. This suggests that at least some of these species may be Cretaceous survivors.

Ranges of ten species believed to be Cretaceous survivors are illustrated in Fig. 4 and numbered 1–10 with lines connecting their occurrences (dots) in specific samples above the K/T boundary. These species are believed to be Cretaceous survivors because of their frequent presence in early Tertiary samples in absence of other characteristic Cretaceous species, comparable preservation to early Tertiary fauna, and generally smaller overall size when compared with the same species in Cretaceous sediments. Moreover, the same ten species have also been found in coeval early Tertiary sediments from Brazos River, Texas (Keller, unpublished data). A graphic correlation plot based on first and last appearances of species at El Kef plotted against the same species at Brazos River indicates that these species disappeared at about the same time in both regions. This coincidence is unlikely to be the result of reworking of Cretaceous sediments. It strongly suggests that more species survived the K/T boundary event than generally assumed. A preliminary ^{13}C analysis of some Brazos River survivors (*H. striata*, *G. cretacea*) reveals nearly a 2‰ difference in values before and after the K/T boundary (Keller and Lindinger, unpublished data). This isotopic difference clearly shows that the early Tertiary specimens are not from reworked Cretaceous sediments. El Kef species have not been analyzed isotopically because insufficient specimens are present.

Species survivorship among calcareous nannoplankton across the K/T boundary has been observed earlier by Thierstein (1982) from deep-sea sections and by Perch-Nielsen (1981a,b) from El Kef, Tunisia. Recently, Jiang

and Gartner (1986) reported that a significant number of nannoplankton species also survived the K/T boundary at Brazos River, Texas.

Some of the ten Cretaceous planktic foraminiferal species which appear to have survived into the early Tertiary are illustrated in Plate II. Their disappearances in early Tertiary sediments occurs gradually over about 300,000 years or 300 cm of sedimentation at El Kef, Tunisia. Of these species *Heterohelix globulosa* and *Globigerinelloides subcarinatus* disappear at the top of POb (*G. conusa*) Subzone. *Heterohelix planata*, *Globigerinelloides volutus* and *Pseudotextularia costulata* disappear in the lower part of Subzone P1a (*G. eugubina*). *Globigerinelloides aspera* and *Rugoglobigerina* sp. A disappear within Subzone P1a. The remaining three Cretaceous survivors (*H. navarroensis*, *H. striata*, *G. cretacea*, *G. caravacaensis*) disappear near the top of Subzone P1a, or in the early part of Subzone P1b (Fig. 4).

It is possible that other small Cretaceous species also survived into the early Tertiary, as for instance minute specimens of *Rugoglobigerina hexacamerata*, *Heterohelix glabrans*, *Pseudotextularia costata* and *P. kempensis*. These species have also been found in early Tertiary sediments of both El Kef, Tunisia and Brazos River, Texas, but their disappearances in these sections are not coeval. It will be necessary to study other sections in different parts of the world in order to confirm the nature and extent of survivorship of these species.

A few observations on the nature of Cretaceous survivorship can be made however from this study of El Kef faunas. The Cretaceous survivors are all small species which are not common in late Cretaceous faunas except for *H. globulosa* and *H. striata*. Without exception the Cretaceous survivors are of a basic primitive morphology consisting of small globular chambers arranged either in uniserial coiled fashion (globigerinellids, hedbergellids), or biserial (heterohelicids and pseudotextularids) and triserial fashion (such as Guembelitria). Apertures are simple and there is little wall or-

namentation (Plate II). The simple morphology and small size imply that these species were generalists able to tolerate a wide range of environmental conditions. During the late Cretaceous when niche partitioning was at its height, as seen in the highly diverse faunas, this ecologic tolerance appears to have been a hindrance to developing large populations of individual species. But after the destruction of the late Cretaceous ecosystem, this tolerance aided their survival.

To understand why some Cretaceous species survived it will be necessary to study their populations in late Cretaceous and early Tertiary deposits by means of quantitative stratigraphy, morphometrics and stable isotopes. Stable isotope analysis of survivors in relationship to non-survivors is expected to yield clues to their ecologic habitat and changes in watermass stratification across the K/T boundary.

Early Tertiary evolution

The evolution of the early Tertiary fauna after the K/T boundary extinctions is still largely a mystery. The problem lies primarily in the paucity of sections with a complete sedimentary record and high sedimentation rates. For instance, K/T boundary sections from the deep-sea generally lack Zone PO and frequently also Subzone P1a (*G. eugubina*). Thus, 50,000–300,000 years of the earliest Tertiary history is either missing or condensed into a few centimeters of sediment. The most expanded history for this interval is present at El Kef, Tunisia where 50 cm of black clay records Zone PO and 2.5 m record Subzone P1a. A similarly high sedimentation rate is observed at Brazos River, Texas (Keller, 1988b). Both sections represent shelf sequences deposited at about 150–350 m depth. Thus, early Tertiary radiation can be uniquely studied in two widely separated regions of the world.

Smit (1982) earlier studied planktic foraminiferal evolution in early Tertiary sediments at Caravaca, Spain and El Kef, Tunisia. The pres-

ent author also studied the Carvaca section, but found preservation of planktic foraminifers too poor for positive species identification for the purpose of evolutionary studies. Smit's observation of a monospecific assemblage of *Guembelitra cretacea* at the base of the Tertiary at El Kef could not be confirmed in this study (see Fig. 4, Table I).

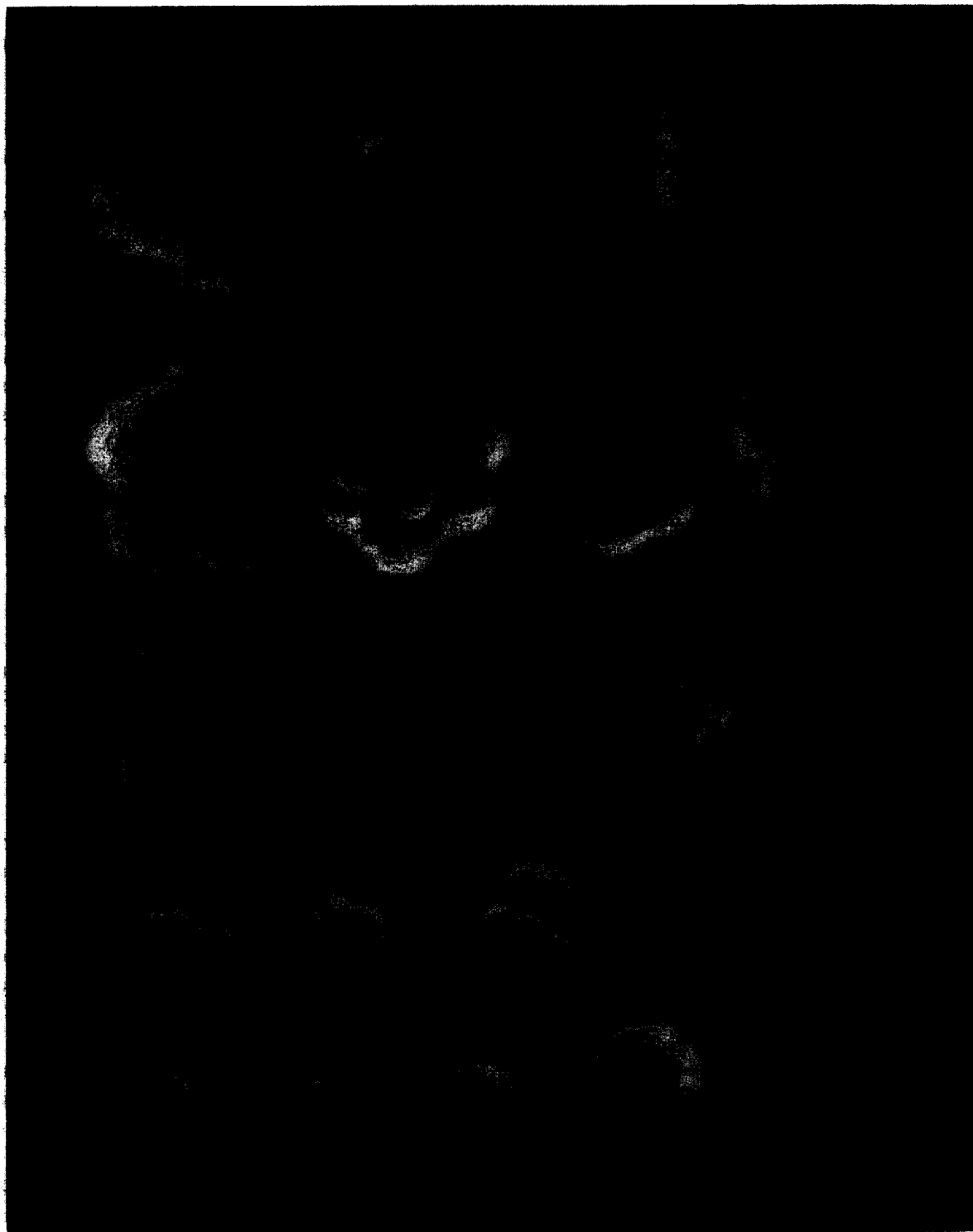
First appearances (FA) and ranges of new early Tertiary species at El Kef are shown in Fig. 4 and illustrated in Plate III. It is apparent that species evolution was most active immediately after the K/T boundary event in the 50 cm of black clay overlying the 2–3 mm thick ferruginous boundary layer. The black clay layer represents deposition over about 50,000 years (K/T boundary to FA *G. eugubina*). The next major pulse in species evolution occurs about 250,000 years later (FA *G. eugubina* 66.35 Ma to FA *G. pseudobulloides* 66.1 Ma) in Subzone P1b, (*Eoglobigerina* spp.) during a rapid increase in carbonate deposition.

The earliest new Tertiary species (*Guembelitra trifolia*, *Chiloguembelitra danica*, *Globigerina fringa*) appear in sample 542, 7 cm (about 7000 years) above the K/T boundary. Both *G. trifolia* and *Ch. danica* evolved from *G. cretacea* and specimens of similar morphology can be found occasionally among *G. cretacea* populations of the late Cretaceous. Therefore, its evolutionary first appearance may occur earlier. *Woodringina hornerstownensis*, *Eoglobigerina edita*, *Globoconusa conusa* and *Globorotalia archeocompressa* first appear 17–22 cm (~20,000 years) above the K/T boundary. Three new species appear near the top of the black clay layer (*G. eugubina*, *E. eobulloides*, *E. simplicissima*).

Species populations remain relatively stable and there is little evolutionary diversity during deposition of the 250 cm of sediment representing Subzone P1a (*G. eugubina*). Only two species appear at this time (*G. midwayensis* and *Eoglobigerina taurica*).

The second pulse in evolutionary diversity in Subzone P1b₁ (*Eoglobigerina* spp.) marks the

PLATE III



entry of *Globorotalia pseudobulloides* and related species (*G. moskvini*, *G. pseudobulloides subquadratus*), the diversification of the *G.(E.) taurica* group (*E. tetragona*, *E. hemisphaerica*), the first appearances of *Chiloguembelitra taurica*, *Globoconusa daubjergensis*, *Subbotina triloculinoides*, and *Globorotalia praeaequa*. The remaining Cretaceous survivors and *G. eugubina* become extinct at this time.

Thus, early Danian faunas show two major pulses of species diversification. The first pulse is recorded in the 50 cm of black clay above the K/T boundary and immediately follows the major Cretaceous species extinctions. This evolutionary diversification occurs at a time of extremely low species diversity, less than 5% CaCO₃ in sediments, very low productivity as indicated by low ¹³C values and generally cool fluctuating temperatures (Keller and Lindinger, in prep.). The species that evolved under these stressful conditions were very small (lack of nutrients?) and of simple morphology with small globular chamber arranged in uniserial coiled fashion (*Globorotalia archeocompressa*, *Globigerina eugubina*), biserial (*Woodringina hornerstownensis*), triserial (*Guembelitra trifolia*), quadriserial (*Globoconusa conusa*) or globigerinid. Although the basic morphologies of evolving species is the same as those of Cretaceous survivors there is no obvious ancestor-descendent relationship between these groups

except among biserial and multiserial forms (D'Hondt and Keller, 1987).

The second pulse in species diversification occurs under more favorable environmental conditions evidenced by a return of carbonate in sediment to pre-K/T levels, higher productivity as seen by a 2‰ positive ¹³C shift, warmer more stable water temperatures and increased water mass stratification (Keller and Lindinger, in prep.). The morphologies evolving at this time are larger and more complex globigerine and globorotalid forms. This implies that more equitable environmental conditions returned after the *G. eugubina* Subzone (P1a) or about 300,000 years after the K/T boundary event.

Population turnover

Quantitative faunal analysis reveals trends in species dominance that yield clues to the nature of faunal assemblages and stability of the environment. However, late Cretaceous faunas with their wide variations in species sizes yield unique problems. To observe dominant species trends in both small and larger forms both the > 63 μm and > 150 μm size fractions were analyzed. It was found that the > 63 μm size fraction provided the most informative data on faunal turnover and evolution across the K/T boundary. Figure 5 illustrates this data for the most common species. The commonly studied > 150 μm size fraction was found to bias to-

PLATE III

Figs. 1-7, 11 are magnified 300× (scale bar-100 μm). Figs. 8-10, 12-20 are magnified 500× (scale bar-10 μm). Note, in actual size species of Subzone P1b are nearly twice as large as those of Subzones P1a and PO.

1. *Globigerina moskvini* Shutskaya, P1b₂, *E. taurica* Subzone sample 596.
2. *Globigerina pseudobulloides* Plummer, P1a, *G. pseudobulloides* Subzone, sample 599.
3. *Chiloguembelitra taurica* Morozova, P1a, *G. pseudobulloides* Subzone, sample 599.
- 4, 5. *Globigerina (Eoglobigerina) taurica* Morozova, P1b₂, *E. taurica* Subzone, sample 591.
- 6, 7, 11. *Globigerina (Eoglobigerina) hemisphaerica* Morozova, P1b₂, *E. taurica* Subzone, sample 592.
- 8-10. *Globigerina eugubina* Luterbacher and Premoli Silva, P1a, *G. eugubina* Subzone, sample 565.
- 12-14. *Globoconusa conusa* Chalilov, POB, *G. conusa* Subzone, sample 548.
15. *Woodringina hornerstownensis* Olsson, P1a, *G. eugubina* Subzone, sample 553.
- 16, 17. *Globigerina fringa* Subbotina, POB, *G. conusa* Subzone, sample 548.
18. *Globigerina cf edita* Subbotina, POB, *G. conusa* Subzone, sample 548.
- 19, 20. *Globorotalia archeocompressa* Blow, P1a, *G. eugubina* Subzone, sample 554.

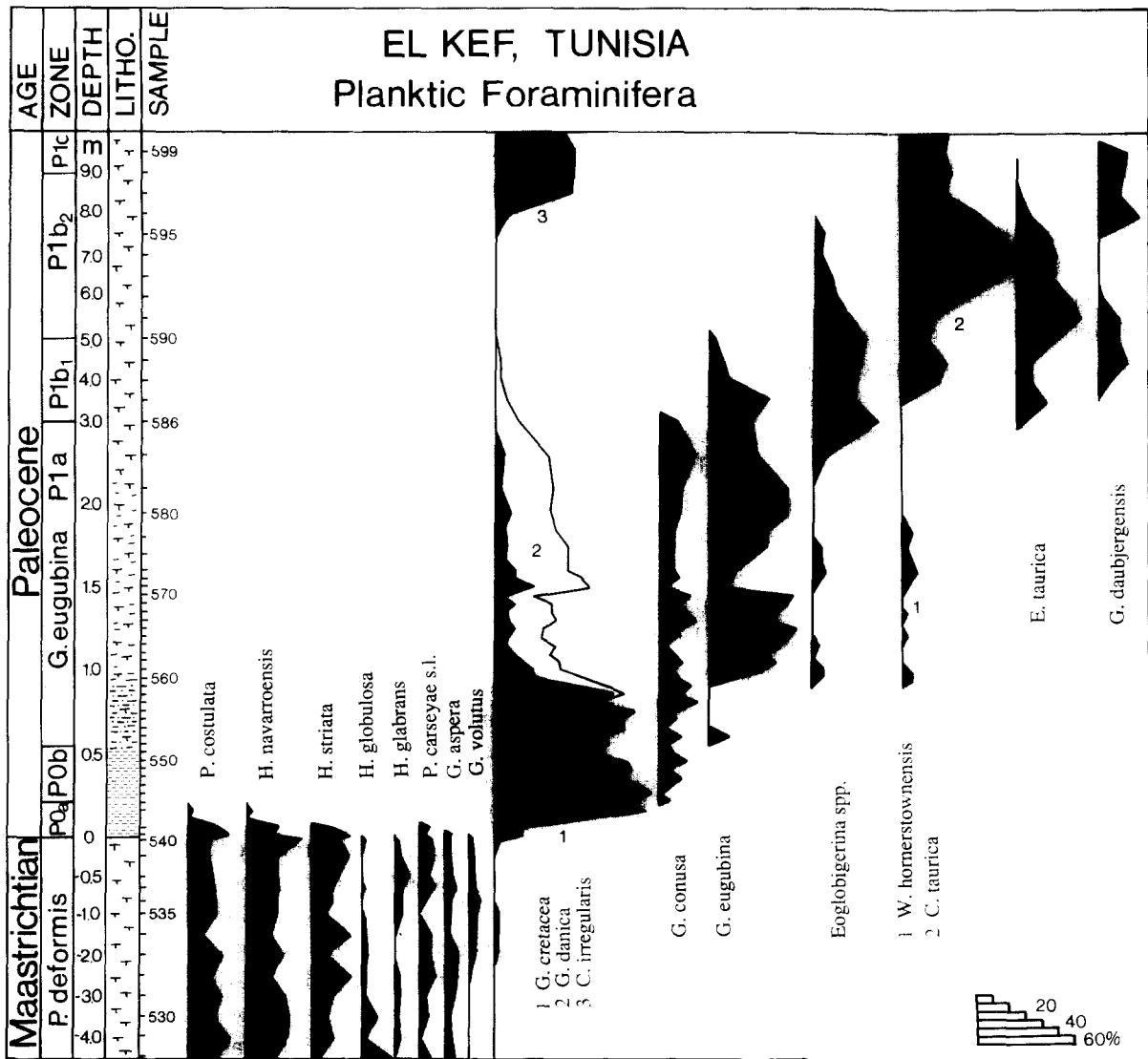


Fig. 5. Relative population abundances of common species in the size fraction $> 63 \mu\text{m}$. Note, only small biserial or planispiral species are common in uppermost Maastrichtian sediments. In the early Paleocene species dominance of any one species is short lived each being successively replaced by another (competing?) species. Low species diversity and short lived populations indicate highly unstable stressed conditions.

wards large species without showing recognizable trends (Fig. 6). For spot samples the $> 105 \mu\text{m}$ size fraction was also analyzed for the latest Cretaceous and early Tertiary Subzone P1b. The results were not significantly different from the smaller size fraction ($> 63 \mu\text{m}$). The still smaller size fraction ($> 32 \mu\text{m}$) was also examined, but was found to be impractical for quantitative studies because of the large num-

bers of juveniles present which could not be identified to species level with the light microscope. Thus, for biostratigraphic resolution, ecologic and evolutionary studies the $> 63 \mu\text{m}$ size fraction was found to provide the best results for the K/T boundary interval. Nevertheless, major faunal successions can also be recognized in the $> 150 \mu\text{m}$ size fraction as illustrated by Gerstel et al. (1986, 1987). Species

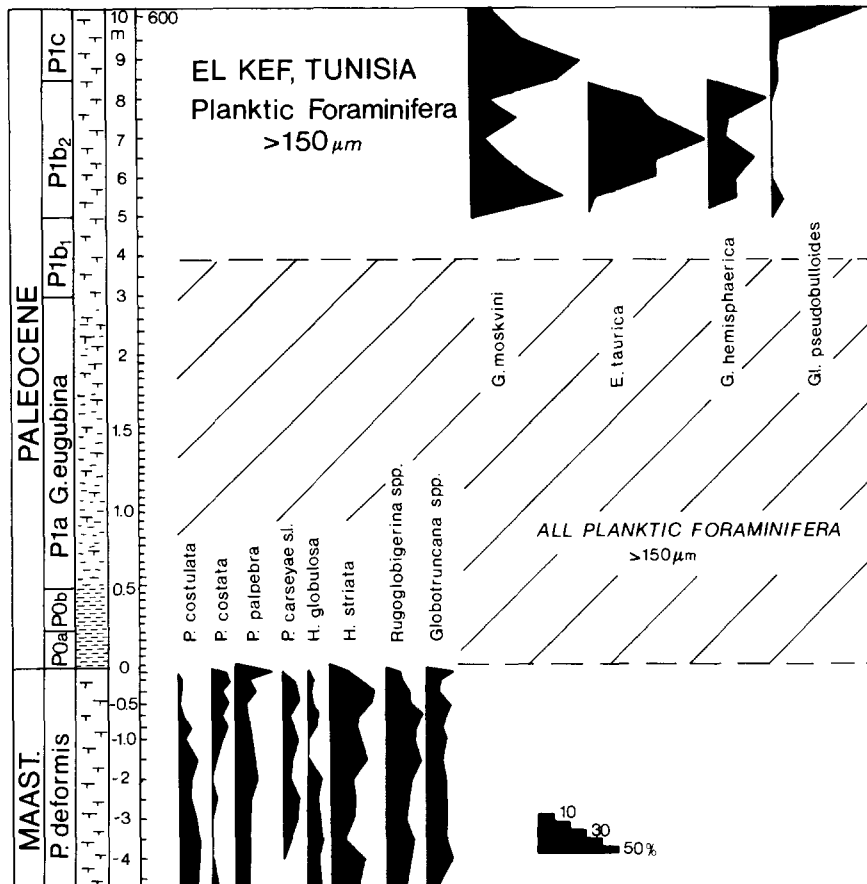


Fig. 6. Relative population abundances of common species in the size fraction $> 150 \mu\text{m}$. Note the similarity in common species below the K/T boundary, absence of foraminifers above the boundary and return of species in the $> 150 \mu\text{m}$ size fraction in Subzone P1b. The latter represents a major loss of information when compared with Fig. 5.

abundance curves illustrated in Figs. 5 and 6 have error bars of $\pm 1.5\%$ as tested by duplicate faunal counts.

Figure 5 illustrates that among small late Cretaceous species the heterohelicid, pseudoguembelinid and globigerinellid survivors were most abundant. However, the abundance of each species declined immediately after the K/T boundary to less than 2% and is therefore too small to show on Fig. 5. Among the $> 150 \mu\text{m}$ fauna this group, except globigerinellids, is also most abundant (Fig. 6). Most surprising however, is the high species diversity, but overall low abundance among the larger species of *Rugoglobigerina* and *Globotruncana*. Thus, no additional information was gained by analyzing

this size fraction in the latest Cretaceous.

All species in the earliest Tertiary assemblages are smaller than $150 \mu\text{m}$. The fauna after the K/T event is dominated by *Guembelitra cretacea* through the 50 cm black clay and 50 cm dark grey clay. Only *Globoconusa conusa* coexists in relative abundance at this time. The subsequent rise in *G. eugubina* is associated with a permanent decline in *G. cretacea* suggesting niche competition or destruction. *Globigerina eugubina*, *G. conusa* and *C. danica* dominate Subzone P1a (*G. eugubina*). These rapid successive species replacements suggest highly stressed unstable environmental conditions related to low surface productivity (Keller and Lindinger, in prep.). Similarly stressed condi-

tions were observed by Gerstel et al. (1987) from DSDP Site 577 who concluded that low productivity adversely affected faunal stability. Dramatic productivity changes in the early Danian have been observed by other authors including Hsu and McKenzie (1985) and Zachos et al. (1986).

The first major faunal change in the early Tertiary occurs during Subzone P1b₁ (*Eoglobigerina* spp., Fig. 5) and marks the first recovery of the ecosystem after the K/T boundary event. Major environmental changes are implied by the increased evolutionary diversity and the first appearance of larger species (> 150 μm , see Fig. 6, Plate I). Perhaps the most significant change at this time was a major increase in surface water productivity as indicated by increased carbonate sedimentation and a 2‰ positive shift in ¹³C. Although carbonate sedimentation reached pre-K/T boundary levels, surface productivity remained well below. Oxygen isotope ratios indicate that temperatures were more stable, but remained cool at this time (Keller and Lindinger, in prep.). The change in faunal diversity also suggests an increase in watermass stratification.

Discussion and conclusions

The Cretaceous/Tertiary boundary section at El Kef, Tunisia illustrates that high resolution stratigraphic control is possible in continental shelf sections with high sedimentation rates. But it is not clear whether the faunal sequence is representative of open oceanic conditions where the K/T boundary interval is much more condensed and hence stratigraphic resolution is lost. Detailed studies of deep-sea sequences (on a cm scale or less) will be necessary to correlate and compare continental shelf with oceanic environments.

The K/T boundary extinctions at El Kef begin about 25 cm below the lithologic and geochemical boundary (Ir anomaly and base of black clay layer) and continue through 7 cm above the boundary. Why did major species ex-

tinctions start before the K/T boundary event? The early disappearance of complex species suggests a changing environment preceding and thus unrelated to, a K/T boundary impact. There is also selectivity in species extinctions before and after the K/T boundary event (Ir anomaly). Complex larger species disappear before smaller less ornate species and primitive small species survive longest. This selectivity in species extinctions suggests sequential elimination of less tolerant species.

Habitats of Cretaceous species are relatively unknown; however, a clue can be obtained from oxygen isotope ranking of planktic foraminifera. Isotopically light species generally live in surface waters whereas isotopically heavier species live in deeper waters (Boersma and Shackleton, 1981; Keller, 1985). Unfortunately, not all late Cretaceous species have been isotopically ranked, but work by Boersma and Shackleton (1983) and Keller and Thierstein (unpublished data) imply that large complex species including globotruncanids live in relatively deeper waters whereas rugoglobigerinids and pseudotextularids are surface dwellers. This suggests that pre-K/T boundary extinctions largely affected deeper dwelling planktic species first and surface dwellers survived longest. This implies changes in the water mass structure, temperature or chemical conditions of subsurface waters prior to the K/T boundary event.

A clue to pre-K/T boundary species extinctions may also be found in the convergent oxygen isotopic trends of bottom and surface waters at El Kef (Keller and Lindinger, in prep.). This convergent trend is primarily due to more negative benthic oxygen isotope values suggesting an influx of warm saline bottom water. A similar convergent oxygen isotopic trend was observed by E. Barrera (pers. comm., 1987) from DSDP Sites 689,690 and Seymour Island. This implies that warm saline bottom waters may have affected oceanic circulation globally. Increased production of saline waters may have occurred in low latitude marginal seas (Brass

et al., 1982) possibly triggered by a lowered eustatic sea level (Peypouquet et al., 1986; Keller, 1988a). It is likely that increased salinity and its chemical consequences are responsible for the pre-K/T boundary species extinctions.

The K/T boundary event marked by Ir and Os anomalies (Kushlys and Krahenbuhl, 1983), maximum total organic carbon, a dramatic decrease in CaCO_3 to less than 1% and drop in surface productivity (Keller and Lindinger, in prep.) also coincides with maximum species extinctions. Primarily surface dwellers are affected at this time (rugoglobigerinids, pseudotextularids). This event appears to be unrelated to, but superimposed upon the adverse environmental trend and associated species extinctions that began during the late Maastrichtian. The geologically instantaneous geochemical changes at the boundary point towards a catastrophic event such as a large extraterrestrial impact (Alvarez et al., 1980), but large scale volcanism cannot be excluded (McLean, 1985; Officer and Drake, 1985).

El Kef data show that the ecosystem did not recover for nearly 300,000 years after the K/T boundary event (Subzone P1b, FA *G. pseudobulloides*) and full recovery was not reached until about 1.5 m.y. after the boundary event (Zachos and Arthur, 1986; Arthur et al., 1987; Gerstel et al., 1987). During this time faunal assemblages remain simple, primitive and of very low diversity. Generally low oxygen conditions prevailed on the ocean floor (Peypouquet et al., 1986; Keller, 1988a). Stable oxygen and carbon isotopic data indicate highly stressed environmental conditions with low surface productivity, generally cool fluctuating temperatures and a very low surface to bottom temperature gradient (Keller and Lindinger, in prep.). The post-K/T boundary recovery starts in Subzone P1b₁ just before the first appearance of *Globorotalia pseudobulloides*, dated at 66.35 Ma. The recovery is relatively rapid with an increase in carbonate sedimentation to pre-K/T levels and a major increase in surface and bottom water productivity as indicated by a po-

sitive shift of about 2‰ in ^{13}C . Productivity, however, stabilized below pre-K/T boundary levels at this time.

The Cretaceous/Tertiary boundary section of El Kef has shown this mass extinction event to be more complex than previously thought. Although the findings of this study clarify many aspects of the K/T boundary event, such as the nature of extinctions and species survivorship, subsequent radiation of early Tertiary species and the recovery of the ecosystem, many new questions are raised. For instance, why did the ecosystem not recover from the K/T boundary shock for so long? Can a single impact explain such a long recovery period? The effects of an impact event, with an increase in atmospheric dust and possible warming due to the greenhouse effect, are likely to be much shorter. At the present time there is evidence (Ir anomaly, shocked quartz) for only one impact event at the K/T boundary. An immediate but short lasting surface water warming seems to be associated with the K/T boundary event at El Kef (Lindinger and Keller, in press) which lends support to the theory of a greenhouse effect, but does not explain the long recovery period.

Were there repeated shocks to the ecosystem before and after the K/T boundary event as for instance from a major episode of volcanism or multiple impacts? El Kef data of pre-K/T boundary extinctions and long period of depressed environmental conditions suggests that multiple causes were involved, but there is no evidence of multiple impacts or major volcanism. The present study suggests a multi-cause scenario including pre-K/T boundary extinctions possibly related to production of warm saline bottom waters and its geochemical consequences, a geologically instantaneous catastrophe at the K/T boundary possibly caused by a bolide impact followed by prolonged environmental stress perhaps due to a disrupted climatic regime and CO_2 fluctuations. Further detailed geochemical and faunal studies of other K/T boundary sections with continuous sedimentation, high sedimentation rates and good

faunal preservation will be necessary to test this scenario.

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