The Cretaceous/Tertiary boundary stratotype section at El Kef, Tunisia: how catastrophic was the mass extinction?

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Abstract

The Cretaceous/Tertiary (K/T) boundary stratotype section at El Kef, Tunisia, represents the most complete and expanded sedimentary record across this important mass extinction horizon presently known. High resolution analysis of planktic foraminifera in two outcrops (El Kef I—stratotype and El Kef II) along with comparisons between planktic and benthic foraminifera, calcareous nannofossils, ostracods, pollen and spores, and dinoflagellates indicate that major changes across the K/T boundary are registered only in benthic and planktic foraminifera and calcareous nannofossils. Biotic changes in benthic foraminifera are unique to El Kef and similarly shallow continental shelf sections and appear to be the result of a sea-level regression in the latest Maastrichtian followed by a sea-level rise across the K/T boundary that was accompanied by expansion of the local oxygen minimum zone (OMZ). Biotic changes in planktic foraminifera appear partly related to these conditions also, but in general reflect more global oceanographic changes. For instance, species extinctions are gradual and selective as observed in K/T sections worldwide, rather than random and abrupt. Although there is a 69% decline in species richness between 25 cm below and 10 cm above the K/T boundary, only rare species disappeared. Their combined relative abundance constitute less than 20% of the total population. About 52% of these extinct taxa (8% of the population) are large, ornate, morphologically complex tropical–subtropical forms that lived at or below the thermocline. No planktic foraminifera from this depth range survived the K/T boundary event. All survivor taxa were surface dwellers living within the photic zone. Their relative abundance (~80%) dominates both Cretaceous and early Tertiary populations.

These data indicate that the K/T biotic record in the shallow continental shelf section at El Kef was significantly influenced by local conditions which, combined with the latest Maastrichtian sea-level regression and subsequent sea-level rise, resulted in shallowing of the local OMZ relative to the sea-surface. Shallowing of the local OMZ lead to the selective disappearance of benthic faunas and may have adversely affected the surviving photic zone dwellers. The selective nature of species extinctions, however, appear to be related partly to long-term global oceanographic changes which were accelerated at the K/T boundary possibly by a bolide impact.

1. Introduction

The El Kef section of Tunisia was officially designated the Cretaceous–Tertiary (K/T) boundary global stratotype section and point (GSSP) at the XXVIIIth International Geological Congress in Washington in 1989 with the K/T boundary defined at the base of the 50 cm thick boundary clay. Chosen for its apparently continuous and expanded sedimentary record, excellent preservation of microfossils, and geochemical and mineralogical marker horizons, the stratotype provides an

ideal boundary transition with which other sections can be compared and correlated worldwide. As such the El Kef stratotype has become the single most important K/T boundary section and the standard by which the completeness of the faunal, floral and sedimentary records are judged worldwide. Such a comparison study was recently published by MacLeod and Keller (1991a, b) based on graphic correlations of over 35 K/T boundary sections worldwide. Results show that the El Kef section indeed represents the most expanded and stratigraphically complete K/T boundary transition known to date. Similar nearly complete sections also occur at Brazos River (Texas), Agost and Caravaca (Spain), Nye Klov (Denmark), Mimbral (Mexico) and ODP Site 738C. Any interpretation of biotic and environmental events across the K/T boundary must be based on this set of stratigraphically most complete sections in order to avoid misinterpretation of spurious "mass extinctions" due to hiatuses.

The El Kef stratotype has been extensively studied with summary accounts of early studies given in Salaj (1974, 1988) and Donce et al. (1982, 1985). More detailed investigations based on closely spaced samples (in part based on a 5 cm contiguous interval sample collection sponsored by IGCP 145 and the Tunisian Geological Survey and later distributed to interested parties) were published in the following microfossil and geochemical analyses: planktic foraminifera by Smit (1982), Brinkhuis and Zachariasse (1988), Keller (1988a) and Ben Abdelkader (1992); benthic foraminifera by Keller (1988b, 1992), ostracods by Donce et al. (1982, 1985) and Peypouquet et al., (1986); nannoplankton by Perch Nielsen (1981a,b), Perch Nielsen et al. (1982), Jiang and Gartner (1986) and Pospichal (1994); dinoflagellates by Brinkhuis and Zachariasse (1988), Brinkhuis and Leereveld (1988); palynoflora by Donce et al. (1985) and Méon (1990); isotope geochemistry by Smit and Ten Kate (1982), Kuslys and Krähenbühl (1983) Keller and Lindinger (1989) and iridium and Ni-rich spinels by Robin et al. (1991).

What all of these microfossil studies of the El Kef section (except for Smit, 1982, see discussion below) have in common, is a failure to record a catastrophic mass extinction horizon centered at the K/T boundary. Instead, reported species extinctions are often gradual beginning during the late Maastrichtian and continuing well into the early Paleocene. For instance, Méon (1990, p. 93) reports that there is "no drastic modification at the Cretaceous–Tertiary boundary and hence no phenomenon of catastrophic dimension". Similar observations have been made in palynofloral studies from northern and southern high latitudes (Sweet et al., 1992; Askin, 1988, 1992). In contrast, in the U.S. western interior (Raton Basin) sharp floral changes, including a fern spore spike, are observed coincident with the K/T boundary (Nichols and Flemming, 1992). This suggests more severe environmental effects in the continental U.S. than in the Tethys region. Dinoflagellates are known to have survived through the K/T boundary virtually unscathed, and studies at El Kef confirm this observation. Brinkhuis and Leereveld (1988, p. 13) report "No sharp qualitative changes in dinoflagellate cysts associations coincide with that boundary." Nannofossil diversity (Shannon-Wiener diversity index) shows a gradual decline into the earliest Tertiary (Danian) with most Cretaceous species present well into the early Tertiary (Perch Nielson, 1981a,b; Pospichal, 1994). This record has proved difficult to interpret because nannofossils are easily reworked due to their small size and absence of unequivocal criteria that can be used to distinguish reworked from in-situ specimens. For this reason, interpretation of their continued and abundant presence above the K/T boundary is controversial and variously attributed to survival (Perch Nielson et al., 1982), reworking (Pospichal, 1994), or both (Jiang and Gartner, 1986; Gartner, in press).

Planktic foraminifera have been considered as the microplankton group that suffered virtually total extinction due to a bolide impact at K/T boundary time (e.g. Premoli Silva and McNulty, 1984; Smit, 1982, 1990). This interpretation is not supported by subsequent studies for three reasons. First, this conclusion was originally based on deep-sea sections, all of which have been subsequently shown to contain major hiatuses. MacLeod and Keller (1991a,b) and Keller et al. (1993a) demonstrated that K/T boundary hiatuses spanning from 60 to 500 kyr of the basal Tertiary are present in nearly all deep-sea sections deposited at depths

below 1000 m. In these sections extinctions and originations, spanning as much as 0.5 m.y. across the K–T transition, are concentrated at one horizon giving the appearance of a sudden catastrophic mass extinction. In contrast, shallow continental shelf sections are generally more temporally complete and show a more gradual transition. These sections are more complete primarily due to the sea-level transgression that characterizes the K/T boundary and early Danian. This transgression shifted the locus of sedimentation to continental shelf areas, leading to sediment starvation and non-deposition and/or erosion in the deep-sea (MacLeod and Keller, 1991a,b; Keller et al., 1993a).

Second, the presence of many Cretaceous taxa in lowermost Tertiary sediments has been routinely ignored based on the assumption that all Cretaceous species (except one) must have become extinct at the K/T boundary. Their presence in Danian sediments is therefore assumed to be due to reworking. For instance, at El Kef, Smit (1982, p. 329) reported that "The mass extinction event at the Cretaceous/Tertiary boundary.... exterminated all but one species of the planktic foraminifera (*Guembelitria cretacea* Cushman)." In contrast, Keller (1988a) found that about 1/3 of the Cretaceous taxa were consistently present in early Tertiary sediments at El Kef and elsewhere and their presence could not be considered due to reworking, but indicated survival. Moreover, Keller observed that "the simple morphology and small size imply that these species were generalists able to tolerate a wide range of environmental conditions" (Keller, 1988a, p. 255). Although Smit (1982, pers. comm., 1992) also observed these Cretaceous species in early Tertiary sediments at El Kef as well as at Agost and Caravaca, he chose to ignore them (no indication of their presence in range charts by Smit, 1982, nor 1990) in the belief that they were reworked. Survival of cosmopolitan taxa has since been documented in K/T boundary sections worldwide (Canudo et al., 1991; Keller, 1989a,b, 1993; Keller et al., 1993b, 1994; MacLeod and Keller, 1994; MacLeod, in press). Isotopic measurements of shell calcite of several taxa provide unequivocal evidence of their residence in Tertiary environments (Barerra and Keller, 1990,

1994; Keller et al., 1993a; MacLeod and Keller, 1994).

Third, species extinctions are often assumed to have occurred instantaneously due to a bolide impact. Additionally, Smit (1982, p. 329) stated that "the mass extinction is inferred to have occurred within 50 years and a new stable planktonic fauna re-established within 35,000 years" (see also Smit, 1990). Biostratigraphic data from El Kef, Caravaca and Agost provided by Smit (1982, fig. 5, p. 334 and 1990, fig. 3, p. 190) in support of this interpretation shows the extinction of all Cretaceous taxa (except *G. cretacea*) precisely at the K/T boundary, even though many of these same species are commonly present in overlying Danian sediments (Keller, 1988a; Canudo et al., 1991). Smit (1982, 1990) provides no data on Cretaceous species from El Kef. His study of Caravaca identified only about a dozen Cretaceous taxa (normal species richness varies between 44 and 54 for the late Cretaceous) and most of these were not identified to species level (Smit, 1982, fig. 5, p. 334). In contrast, Keller (1988a, fig. 4, p. 249) and Liu and Olsson (1992, fig. 6, p. 334) identified 48 and 44 Cretaceous species respectively in the same samples of the El Kef section and Canudo et al. (1991) identified 51 species at Caravaca. Keller also observed that species extinctions began before the K/T boundary and continued well into the early Tertiary. Keller noted that "Species extinctions appear sequential with complex, large, ornate forms disappearing first and smaller, less ornate forms surviving longer" (Keller, 1988a, p. 239). The very different results of these studies of El Kef, Caravaca and Agost are thus, at least partly, due to different levels of taxonomic resolution (extreme lumping by Smit, 1982). However, to date, no sudden extinction horizon of all, or nearly all, Cretaceous planktic foraminifera has been documented in any chronostratigraphically complete K/T boundary section (Canudo et al., 1991; Keller, 1988a, 1989a,b, 1993; Liu and Olsson, 1992; Keller et al., 1993b, 1994), although such an extinction horizon is sometimes inferred despite abundant biostratigraphic evidence to the contrary (Smit, 1982, 1990; Liu and Olsson, 1992).

Differences between Smit's (1982) and Keller's

(1988a) studies have led to re-sampling of the El Kef stratotype section, as well as sampling of a second outcrop located 600 m to the north (El Kef II) in April 1992 under the sponsorship of the Global Sedimentary Geology Program (IUGS) and the Tunisian Geological Survey. Each of these two sections was trenched and samples collected continuously at 2–5 cm intervals between 50 cm below and 50 cm above the K/T boundary. Six blind (unlabelled) samples, three from above and three from below the K/T boundary stratotype, were given to four investigators, in order to evaluate whether the mass extinction pattern is sudden, with all but one species extinct at the K/T boundary as suggested by Smit (1982, 1990), or more gradual with some species disappearing below the boundary, one-third ranging into the early Tertiary and the remaining (>50%) species extinct at or near the K/T boundary as suggested by Keller (1988a). The results show that the patterns of extinction are remarkably similar to Keller's (1988) study and the new analysis presented herein (MacLeod and Keller, in prep.).

This study presents the results of the entire 1-m interval across the K/T boundary at 5 cm sample intervals at El Kef I, the stratotype section (also known as KS), and El Kef II located 600 m to the north (also known as KD, Ben Abdelkader et al., 1992). All samples were collected during the 1992 field trip by Keller and/or the IUGS collecting team. The purpose of this study is to present a detailed, high resolution record of planktic foraminiferal events across the K/T boundary in the stratotype section, compare and contrast this record with the nearby El Kef II section, and determine the nature and tempo of species extinctions in the most complete low latitude trans-K/T boundary sedimentary record. In addition, we present direct comparisons of all microfossil records from El Kef, including planktic foraminifera, nannofossils, palynoflora, dinoflagellates, benthic foraminifera and ostracods. This study represents the first synoptic analysis of all microfossil groups and geochemical signals from a K/T boundary section. Since the El Kef section is also the K/T boundary stratotype, this study also provides a model against which data from other K/T boundary sections can be compared.

2. Location

The El Kef stratotype section is located in northwestern Tunisia about 7 km west of the town of El Kef (Fig. 1). The locality is reached by taking the road leading to Tajerouine. About 5 km along this road is a turn-off to an unpaved road leading to the village of Hamman Mellégue, which is located near the stratotype section. About 2 km along this unpaved road and prior to reaching the village is a small cement water reservoir to the south overlooking a large valley formed in Maastrichtian to Eocene limestones and marls of the El Haria Formation (Fig. 1). From this location the K/T boundary stratotype can be found by descending into the valley for about 1.5 km to reach the gray marls of the El Haria Fm. The Cretaceous–Tertiary transition of the stratotype section is on a gentle slope within the soft gray marl sequence of the El Haria Fm. marked only by a 50 cm thick black clay layer. About 600 m north of the stratotype section is a second K/T boundary outcrop with a slightly thicker clay layer. This section was originally described by Donce et al. (1982) and in this study is labeled El Kef II as compared to El Kef I, the stratotype section.

3. Methods

Samples were soaked in water and repeatedly washed through a 63 μm screen for El Kef I (stratotype) and through a 38 μm screen for El Kef II until a clean foraminiferal residue was obtained. To free foraminiferal specimens from sediment infilling, the washed residue was soaked in water and sonically agitated for 5–10 seconds. This process was repeated until clean foraminifera were obtained. The samples of El Kef I and II were washed through different size screens, in order to test whether small species are present in the 38–63 μm fraction which would be lost in the >63 μm size fraction usually analyzed. A recent study of the K/T boundary layer at ODP Site 738 revealed that many species were only present in the smaller (38–63 μm) size fraction (Keller, 1993). At El Kef only one species (*Guembelitria irregularis*) was found to be consistently smaller than
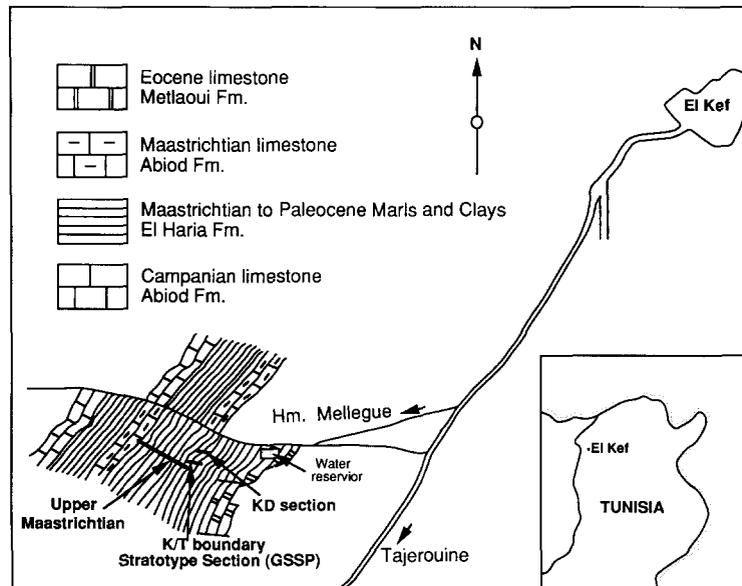
Fig. 1. Location map of the El Kef stratotype section (modified from Donce et al., 1985).

63 μm, but relative species abundances differ widely between the >63 μm and >38 μm size fractions. Population counts were based on representative sample splits (using an Otto microspliter) of 300–400 specimens for each section. Faunal counts are listed in Tables 1 and 2. Most taxa are illustrated by SEM to provide a guide for species identification in the stratotype as well as other sections (Plates I–IV).

4. Placement of the K/T boundary

The Cretaceous/Tertiary (K/T) boundary is easily identified in the El Kef I stratotype, as elsewhere, at the base of the boundary clay and based on the following criteria shown in Fig. 2 for El Kef I.

(1) There is a lithologic break from the chalk or marl deposition of the Cretaceous to a thin layer of dark organic-rich and $CaCO_3$ poor clay, known as the boundary clay. At El Kef I and II this clay layer is 55 cm and 65 cm thick respectively, and represents the most expanded boundary clay observed to date in any K/T boundary sections. More frequently, the boundary clay is only 4–6 cm thick (e.g. Agost, Caravaca, Stevns Klint, Nye Klov, Mimbral (Canudo et al., 1991; Smit, 1990; Schmitz et al., 1992; Keller et al., 1993b, 1994).

(2) A 2–3 mm oxidized red-layer is present at the base of the boundary clay. This red layer is present at El Kef as well as in all complete K/T boundary sections.

(3) Maximum Ir concentrations are generally concentrated in the red layer and boundary clay although they may tail several tens of centimeters above the boundary clay. At El Kef I maximum Ir concentrations are found in the red layer and values decrease 5 cm above the base of the boundary clay (Robin et al., 1991).

(4) Ni-rich spinels are frequently present in the red layer or base of the boundary clay as also observed at El Kef I (Robin et al., 1991).

(5) A negative $\delta^{13}C$ shift is found in marine calcareous plankton of low and middle latitudes (fine fraction or planktic foraminifera).

(6) The first appearance of Tertiary planktic foraminifera occurs at the base or within a few centimeters of the boundary clay, red layer, Ir anomaly and Ni-rich spinels. At El Kef I, Ben Abdelkader et al. (1992) reported the first appear-

PLATE I
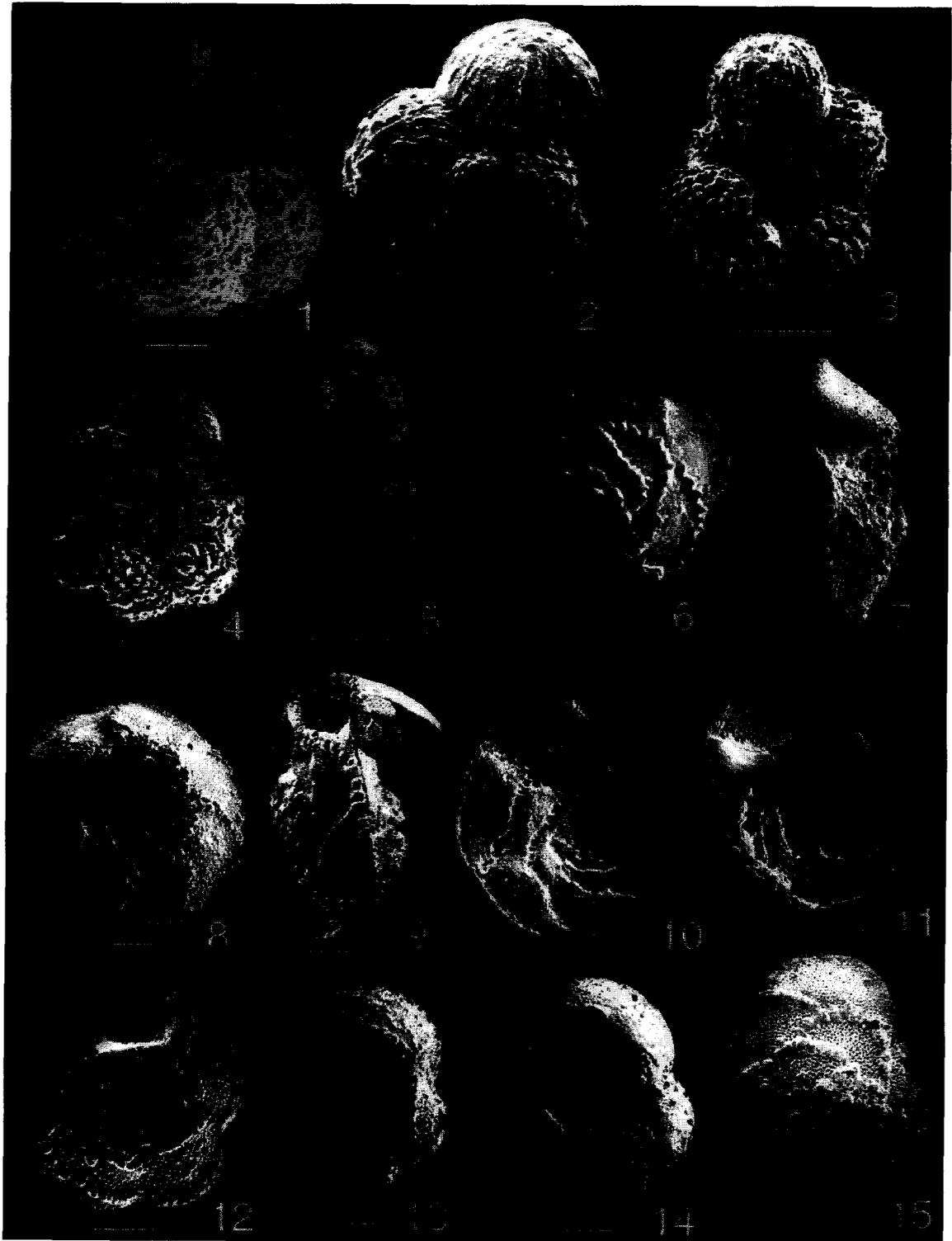
PLATE II
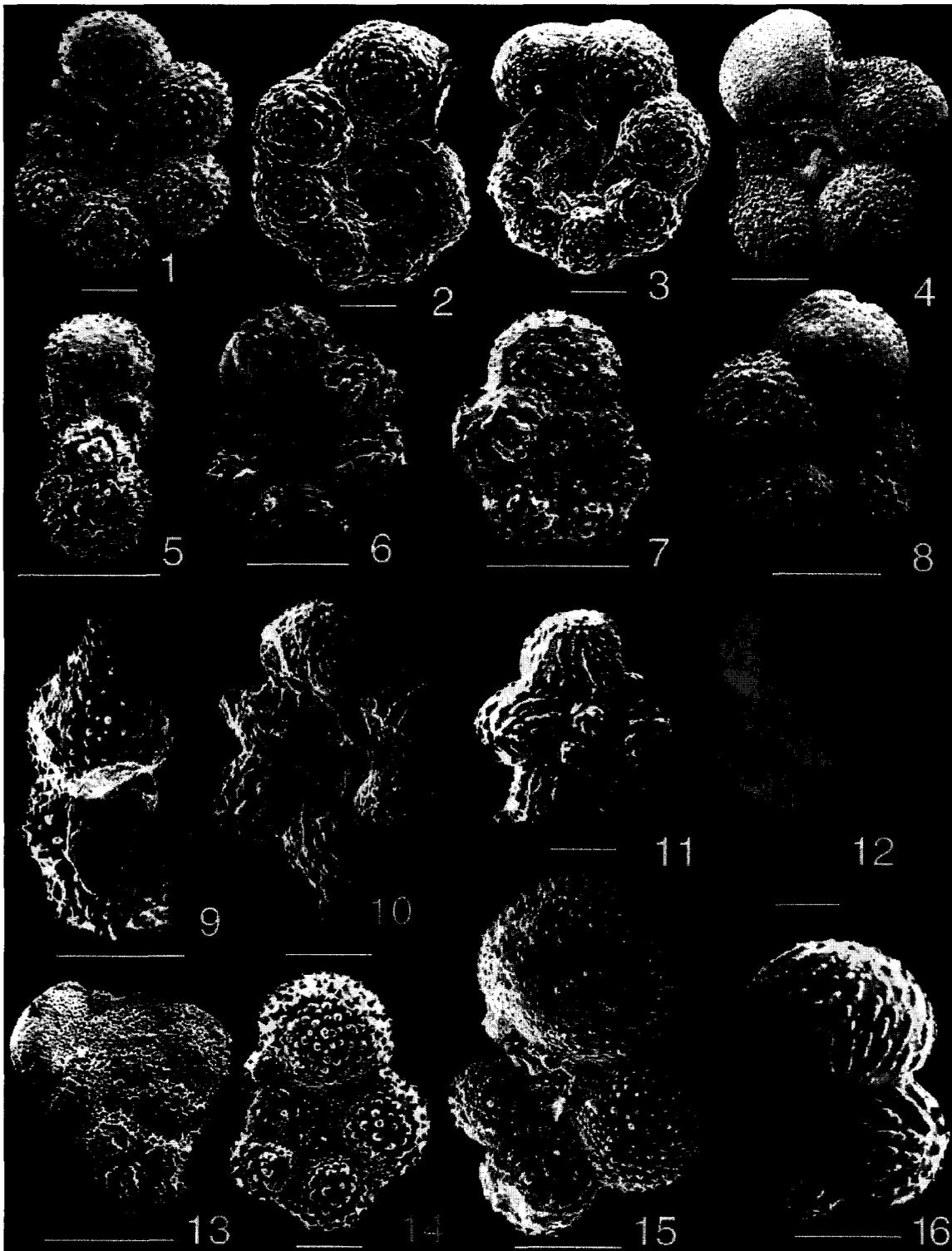
PLATE III
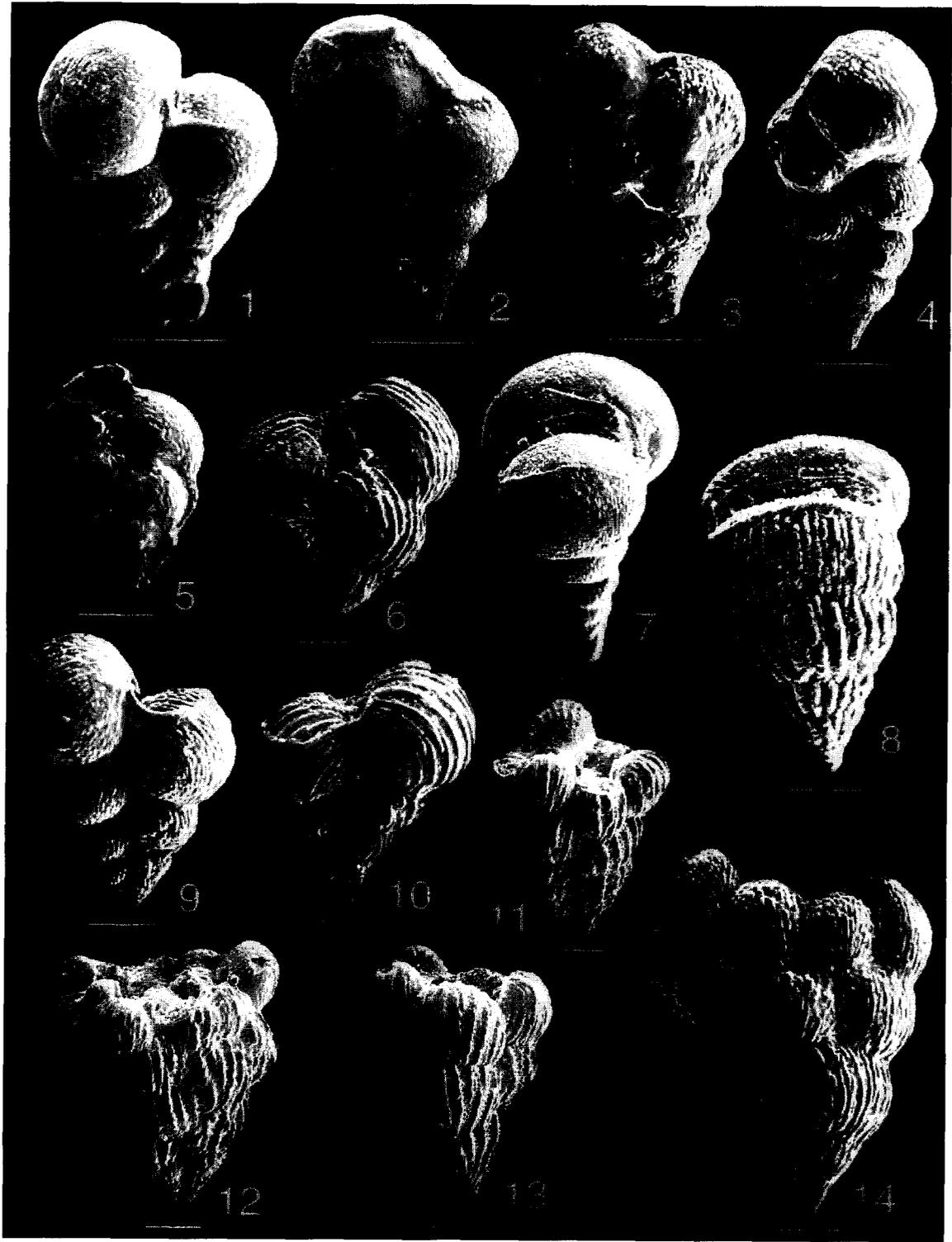
PLATE IV
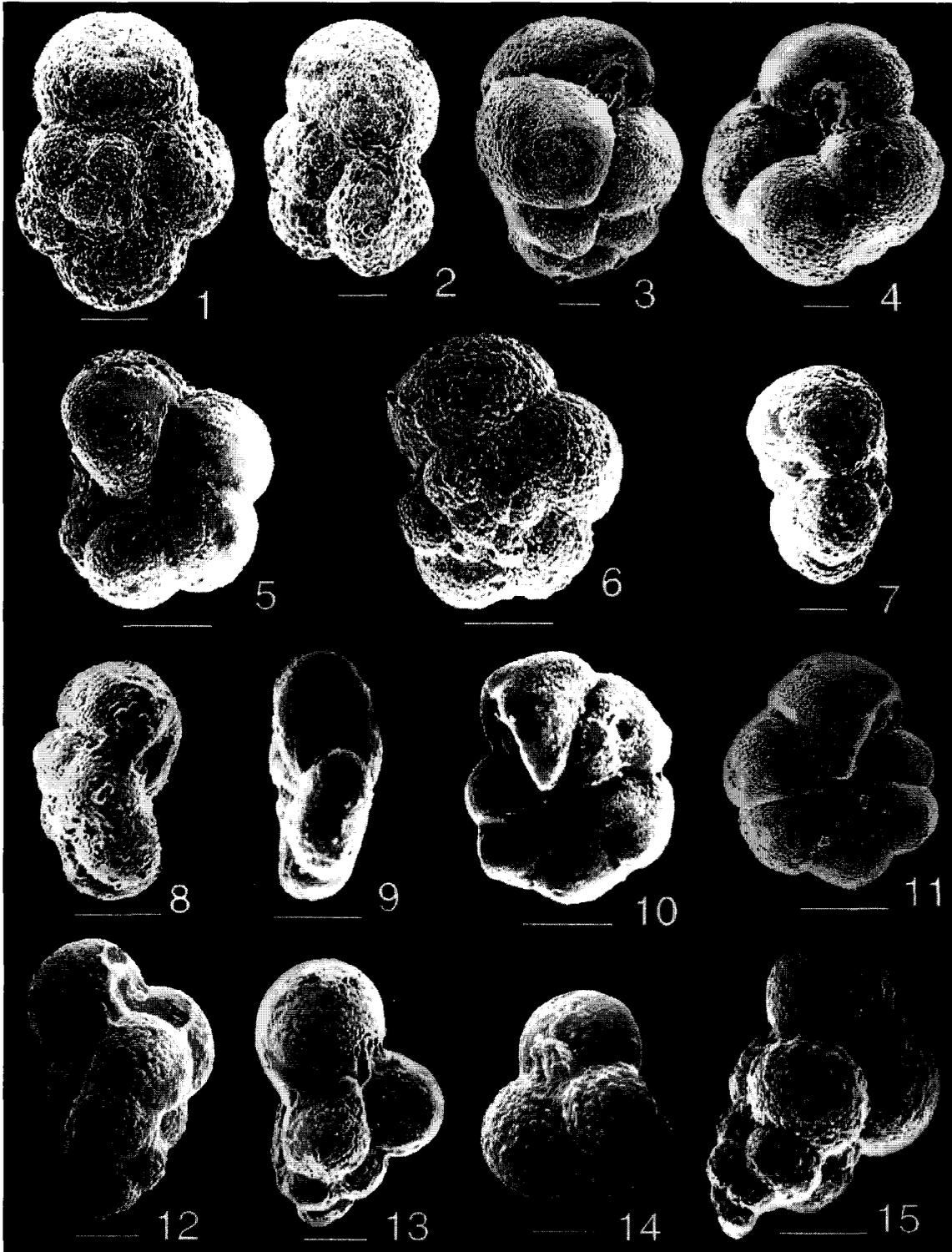
PLATE I

Scale bar = 100 μm, all specimens from El Kef I, stratotype section, Tunisia.
1.   *Rugoglobigerina rotundata* Bronnimann, 20–25 cm below the K/T boundary.
2–3.   *Rugoglobigerina rugosa* (Plummer), 10–15 cm below the K/T boundary.
4–5.   *Rugoglobigerina scotti* Bronnimann, 45–50 cm below the K/T boundary.
6–7.   *Globotruncana dupeublei* Caron, 30–35 cm below the K/T boundary.
8–10.   *Globotruncanita stuarti* (de Lapparent), 30–35 cm below the K/T boundary.
11.   *Globotruncana rosetta* (Carsey), 30–35 cm below the K/T boundary.
12.   *Globotruncana arca* (Cushman), 30–35 cm below the K/T boundary.
13.   *Globotruncana aegyptiaca* Nakkady, 30–35 cm below the K/T boundary.
14–15. *Globotruncana insignis* (Gandolfi), 30–35 cm below the K/T boundary.

PLATE II

Scale bar = 100 μm, all specimens from El Kef I, stratotype section, Tunisia.
1.   *Globigerinelloides aspera* (Bolli), 30–35 cm below the K/T boundary.
2–3.   *Globigerinelloides yaucoensis* (Pessagno), 30–35 cm below the K/T boundary.
4.   *Globotruncanella petaloidea* Gandolfi, 30–35 cm below the K/T boundary.
5–7.   *Rugoglobigerina hexacamerata* Bronnimann, 30–35 cm below the K/T boundary.
8.   *Hedbergella monmouthensis* (Olsson), 30–35 cm below the K/T boundary.
9,10,12. *Plummerita hantkeninoides* (Bronnimann), 45–50 cm below the K/T boundary.
11.   *Plummerita reicheli* (Bronnmann), 35–40 cm below the K/T boundary.
13.   *Gublerina cuvilleri* Kikoine, 45–50 cm below the K/T boundary.
14–15. *Globotruncanella subcarinatus* (Bronnimann), 30–35 cm below the K/T boundary.
16.   *Rugoglobigerina macrocephela* Bronnimann, 30–35 cm below the K/T boundary.

PLATE III

Scale bar = 100 μm, all specimens from El Kef I, stratotype section, Tunisia.
1.   *Heterohelix navarroensis* Loeblich, 20–25 cm below the K/T boundary.
2.   *Heterohelix glabrans* (Cushman), 25–30 cm below the K/T boundary.
3.   *Heterohelix pulchra* (Brotzen), 25–30 cm below the K/T boundary.
4.   *Heterohelix moremani* (Cushman), 30–35 cm below the K/T boundary.
5.   *Pseudoguembelina kempensis* Esker, 40–45 cm below the K/T boundary.
6.   *Pseudoguembelina palpebra* Bronnimann and Brown, 40–45 cm below the K/T boundary.
7.   *Pseudotextularia elegans* (Rzehak), 45–50 cm below the K/T boundary.
8.   *Pseudotextularia deformis* (Kikoine), 30–35 cm below the K/T boundary.
9.   *Heterohelix globulosa* (Ehrenberg), 25–30 cm below the K/T boundary.
10.   *Heterohelix striata* (Ehrenberg), 25–30 cm below the K/T boundary.
11.   *Racemiguembelina intermedia* (De Klasz), 10–15 cm below the K/T boundary.
12.   *Racemiguembelina fructicosa* (Egger), 45–50 cm below the K/T boundary.
13.   *Racemiguembelina powelli* (Smith and Pessagno), 20–25 cm below the K/T boundary.
14.   *Planoglobulina brazoensis* Martin, 40–45 cm below the K/T boundary.

PLATE IV

Scale bar = 100 μm, all specimens from El Kef I, stratotype section, Tunisia.
1–2.   *Eoglobigerina fringa* (Subbotina), 50–55 cm above the K/T boundary.
3–4.   *Globoconusa conusa* (Chalilov), 50–55 cm above the K/T boundary.
5–7.   *Parvularugoglobigerina eugubina* (Luterbacher and Premoli Silva), 55–60 cm above the K/T boundary.
8–11.   *Parvularugoglobigerina eugubina longiapertura* (Blow), 55–60 cm above the K/T boundary.
12.   *Guembelina danica* (Hofker), 30–35 cm below the K/T boundary.
13.   *Guembelina cretacea* (Cushman), 2–6 cm above the K/T boundary.
14.   *Guembelina trifolia* (Morozova), 20–25 cm above the K/T boundary.
15.   *Guembelina irregularis* (Morozova), 15–20 cm above the K/T boundary.
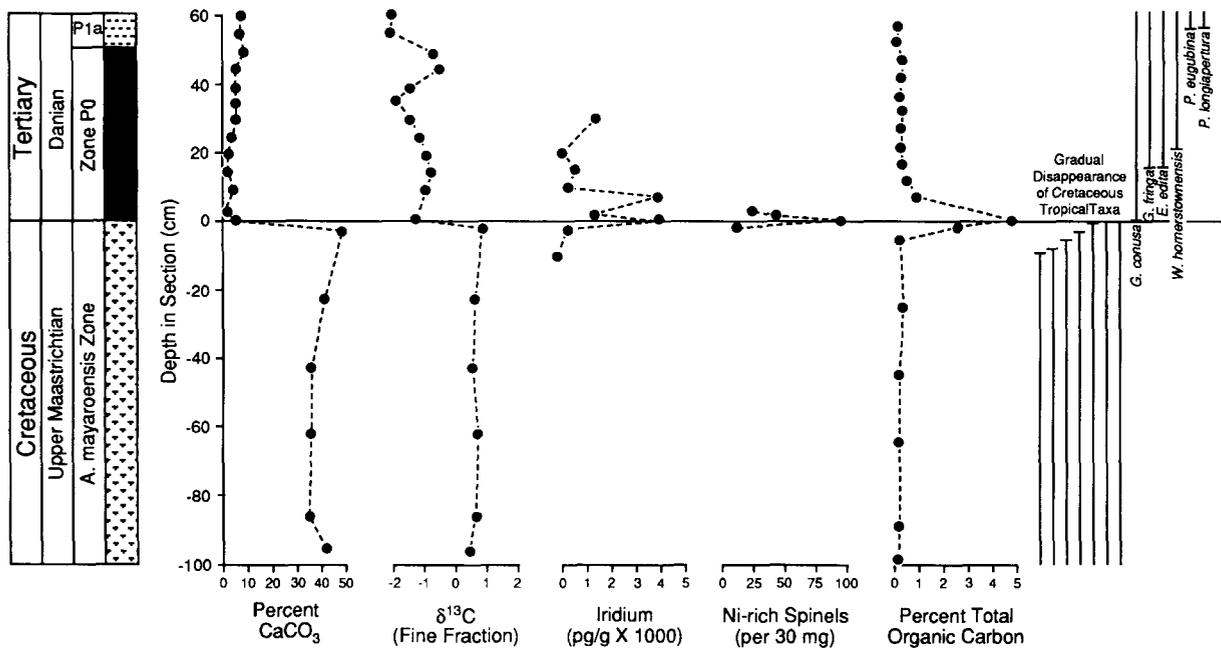
Fig. 2. El Kef I-stratotype showing criteria for placement of the K/T boundary. CaCO₃, TOC, $\delta^{13}C$ data from Keller and Lindinger (1989). Iridium and Ni-rich spinel data from Robin et al. (1991). Planktic foraminiferal data from the present study.

ance (FAD) of Tertiary species (G. conusa) at the base of the boundary clay, as confirmed in this study. In addition, we have found the FAD of Eoglobigerina fringa and E. edita and W. hornerstownensis in the lower 15–20 cm of the boundary clay.

(7) Cretaceous tropical and subtropical taxa disappear.

At El Kef all of these criteria are met. Most of them are present in all the best and most complete K/T boundary sequences (e.g., Agost, Caravaca, Nye Klov, Brazos River, Mimbral, ODP Site 738C). The coincidence of these lithological, geochemical and paleontological criteria is unique in the geological record and virtually insures that the stratigraphic placement of the K/T boundary is uniform and coeval in marine sequences across latitudes. The use of any of these criteria in isolation, however, diminishes the stratigraphic resolution of the K/T boundary.

Some workers have suggested that the sudden extinction of all species, except G. cretacea, Hedbergella monmouthensis and H. holmdelensis, should define the K/T boundary (Smit, 1982, 1990;

Berggren and Miller, 1988; Olsson and Liu, 1993; Liu and Olsson, 1992; Zachos et al., 1992). This is not reasonable since such a sudden extinction horizon has only been observed in sections with a K/T boundary hiatus (MacLeod and Keller, 1991a,b; Keller et al., 1993a). In temporally more continuous low latitude sections such as El Kef, Brazos, Mimbral, Agost and Caravaca, only specialized tropical to subtropical forms disappeared, whereas most cosmopolitan taxa survived (Keller, 1988a, 1989a,b; Keller et al., 1994; Canudo et al., 1991). Moreover, in high-latitude sections such as Nye Klov and ODP Site 738C where no tropical taxa are present, there are no significant species extinctions at the K/T boundary (Keller, 1993; Keller et al., 1993b). Equally impractical is the suggestion that the first abundance increase of Guembelitria spp. defines the K/T boundary (Smit, 1982, 1990; Liu and Olsson, 1992; Olsson and Liu, 1993), because species abundance peaks are not unique events, but rather reflect favorable environmental conditions for the particular species in those areas. For instance, at El Kef and Brazos such conditions prevailed through Zones P0 and

P1a and re-occurred in Zone P1c (Keller, 1988a, 1989a,b). At Mimbral, Agost and Caravaca the first *Guembelitria* abundance peak is near the base of Zone P1a. Maximum abundance in the Spanish sections occurs in Zone P1c (Canudo et al., 1991; Keller et al., 1994). In the high latitude Nye Klov section *Guembelitria* is abundant in the uppermost Cretaceous as well as early Tertiary Zones P0 and P1a and rare at the K/T boundary (Keller et al., 1993b). Similarly, in the southern high latitude ODP Site 738C, *Guembelitria* is rare at the boundary and common in the upper part of Zone P0 and in Zone P1a (Keller, 1993). These data indi-

cate that *Guembelitria* abundance peaks are highly unreliable markers for the K/T boundary.

Planktic foraminifera provide a high resolution biozonation for the K/T boundary transition and various zonal schemes have been proposed as shown in Fig. 3. Among these, the zonal schemes of Smit (1982), Keller (1988a, 1993; also Canudo et al., 1991) and Ben Abdelkader et al. (1992) are very similar, but differ from that proposed by Berggren and Miller (1988) in the presence of a Zone P0 marking the boundary clay and a total range Zone P1a for *Parvularugoglobigerina eugubina* (Fig. 3). The biozonation of Keller (1988a,

PLANKTIC FORAMINIFERAL ZONATION					
Datum events	Keller, 1988a, 1993 Pardo et al., in press		Abdelkader et al., 1992	Smit, 1982 Smit et al., 1992	Berggren & Miller, 1988
⊥ M. trinidadensis	P1d		P1d	P1c	P1a & P1b
⊥ M. inconstans	P1c	P1c(2)	P1c	P1b	
⊤ G. conusa ⊥ S. varianta		P1c(1)			
⊤ P. longiapertura P. eugubina	P1b		P1b		
⊥ P. compressus ⊥ E. trivialis ⊥ G. pentagona ⊥ S. pseudobulloides ⊥ S. triloculinoides ⊥ G. daubjergensis ⊥ S. moskvini ⊥ P. planocompressus ⊥ G. taurica ⊥ C. midwayensis	P1a	P1a(2)	P1a	P1a	Pα
		P1a(1)			
⊥ P. eugubina, P. longiapertura E. eobulloides E. edita, W. hornerstown. ⊥ E. fringa, E. simplicissima ⊥ G. conusa ⊤ P. hantkeninoides	P0		P0		
— K/T boundary —				P0	
⊥ P. hantkeninoides	P.hantkeni- noides		P. deformis	A. mayaro- ensis	A. mayaro- ensis
	A. mayaro- ensis		A. mayaro- ensis		

Fig. 3. Comparison of commonly used K/T boundary biozonations. Datum event sequence is based on a composite data set of 15 of the most complete K/T boundary sections (MacLeod and Keller, 1991b). Zonal index species are shown in bold type.

1993) is used in this study (see discussion of zonal definitions in Keller, 1993), with the addition of the new latest Maastrichtian *Plummerita hantkeninoides* Zone of Pardo et al. (in press). The last appearance (LAD) of *Abathomphalus mayaroensis* has generally defined the top of the Maastrichtian and the *A. mayaroensis* Zone. At El Kef *A. mayaroensis* is extremely rare and disappears below the K/T boundary. Therefore, the intervening interval to the K/T boundary was named *Pseudotextularia deformis* Zone by Keller (1988a) and Ben Abdelkader (1992). Recently, Pardo et al. (in press) have proposed a new total range biozone, *Plummerita hantkeninoides*, to mark the top of the Maastrichtian. This new biozone spans the upper half of C29R below the K/T boundary, or the last 170–200 kyr of the Maastrichtian.

5. K–T boundary mass extinction pattern

Species ranges and extinction patterns across the K/T boundary at the El Kef I stratotype section are illustrated in Fig. 4. Of 55 Cretaceous species identified, 7 species (11%) disappeared between 20 and 50 cm below the K/T boundary. Between 12 cm below and the first 1 cm of the boundary clay, 23 species (42%) disappeared.

Another 9 species (16%) disappeared 10 cm above the K/T boundary, and 16 Cretaceous species (31%) are present in Zones P0, P1a and above (see also Keller, 1988a). Many of these taxa occur only sporadically in Zone P0, or are temporarily absent and re-appear after deposition of the boundary clay. This pattern confirms, in a high resolution sequence, the gradual or extended pattern of species extinctions across the K/T boundary at El Kef that was recognized previously by Keller (1988a).

For comparison, stratigraphic ranges of planktic foraminifera at El Kef II are illustrated in Fig. 5 in the same species order as at El Kef I. At this location, 58 Cretaceous species were identified; three more than at El Kef I. These three species constitute a single occurrence of *Abathomphalus mayaroensis* and rare occurrences of *Rosita walfishensis* and *Globotruncana falsostuarti* (Fig. 5, Table 2). Apart from these minor differences, the sections differ mainly in that more taxa disappeared between 12 cm below and the first 1 cm of the boundary clay (58% as compared to 42% at El Kef I). This difference is primarily the result of greater dissolution in the boundary clay at El Kef II and therefore the absence of many species which are present at El Kef I. Although this could be interpreted as a more sudden extinction at El Kef
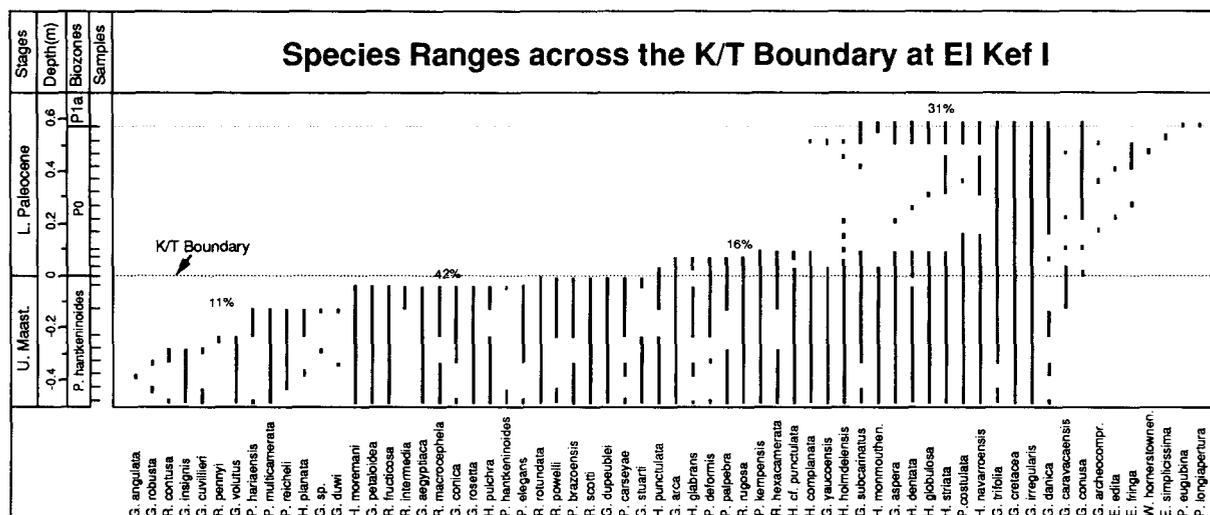
Fig. 4. Biostratigraphic ranges of planktic foraminifera across the K/T boundary at the El Kef I-stratotype.
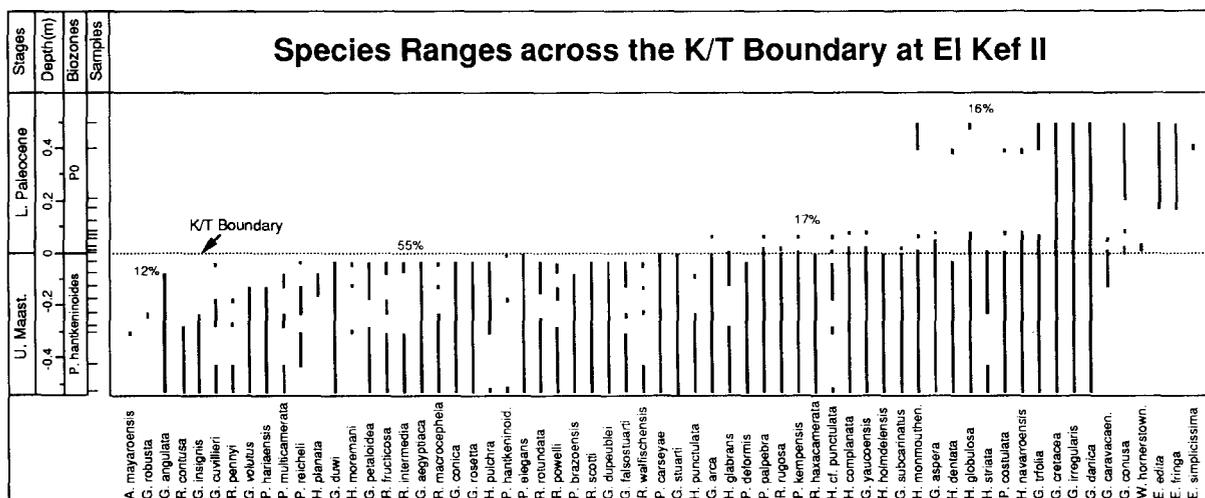
Fig. 5. Biostratigraphic ranges of planktic foraminifera across the K/T boundary at El Kef II.

II, graphic correlation indicates otherwise. Fig. 6 shows that the additional species missing at or near the K/T boundary at El Kef II are the result of either dissolution and a very condensed topmost Maastrichtian (dotted line in Fig. 6), or a short hiatus that removed the topmost Maastrichtian (solid line in Fig. 6). Our biostratigraphic analysis thus suggests that the El Kef I stratotype section has a more complete uppermost Maastrichtian than the nearby El Kef II section. This accounts for the minor differences observed in their last appearance patterns.

A condensed interval or short hiatus at El Kef II is also suggested by the species richness and faunal turnover patterns shown in Figs. 7 and 8. In both sections, species richness begins to decline about 30 cm below the K/T boundary and reaches minimum low values 10 cm above the K/T boundary. But the decline is more gradual in the stratotype section than at El Kef II. This is further illustrated by the number of last appearances (LADs) per sample interval which shows a broad distribution at El Kef I that peaks in the two samples that straddle the boundary, whereas at El Kef II the majority of LADs occur in the sample just below the K/T boundary (Figs. 7 and 8). The difference in the extinction patterns indicates either a short hiatus at El Kef II, or bioturbation and reworking restricted only to El Kef I. The latter is

unlikely since the two sections are only 600 m apart and there is no bioturbation observed across the K/T boundary clay in either section. The data indicate that the stratotype section, El Kef I, is more complete than the nearby El Kef II section.

6. How catastrophic was the mass extinction at El Kef?

The severity of a mass extinction is generally measured by the number of species extinct giving equal weight to extinction of species that are very rare or only sporadically present as to those which dominate the assemblage while ignoring dramatic changes in relative abundances of species that survived. A more reliable measure of the catastrophic nature of the biotic crisis would include measurement of the relative abundance of species extinct and the relative abundance changes of survivors because the extinction of rare, and especially tropical-subtropical taxa, may be caused by relatively minor environmental perturbations. Here we evaluate the severity of the K/T boundary biotic crisis at El Kef based on the relative abundances of species in the size fractions >63 μm for El Kef I and >38 μm for El Kef II (Figs. 9, 10). These two size fractions were chosen in order to evaluate the potential loss of information in the
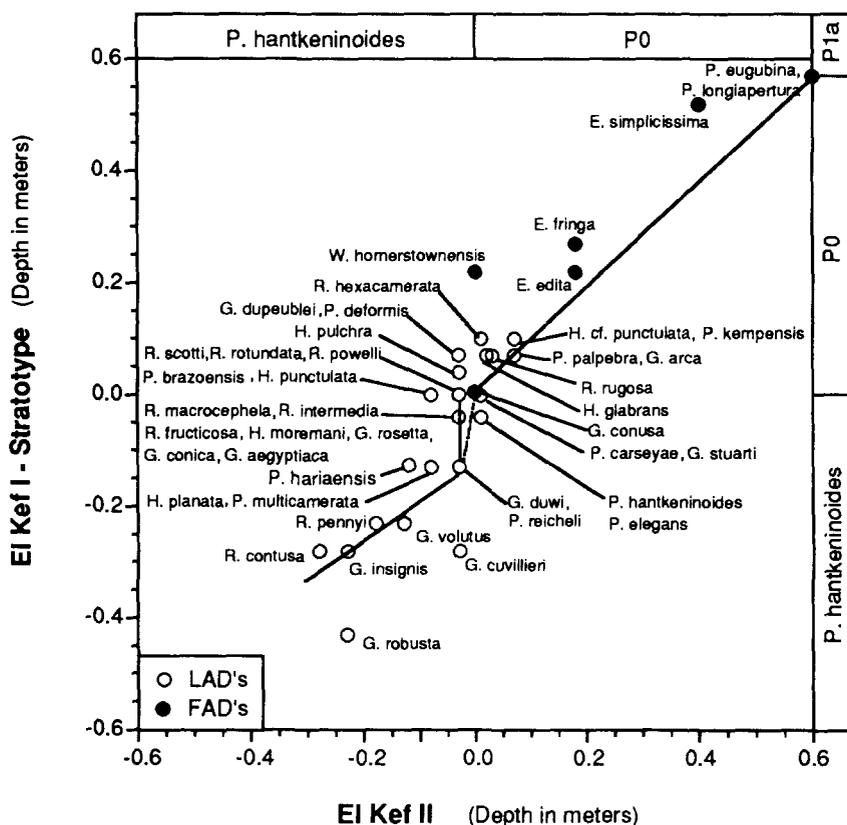
Fig. 6. Graphic correlation of El Kef I and El Kef II sections. Note that El Kef II has either a very condensed topmost Maastrichtian (dotted line) or a short hiatus (solid line).

larger (>63 μm) standard size fraction. As expected, the results show a substantial increase in the relative abundance of very small species in the >38 μm size fraction.

How catastrophic was the demise of the tropical–subtropical fauna of the planktic foraminiferal assemblage? Relative species abundance changes reveal that all 31–33 species, or 58% of the total assemblage disappearing at or below the K/T boundary at El Kef I and II respectively are rare, with relative species abundances generally between 0.1% and 1% (Figs. 9A, 10A). In fact, the combined relative abundance of this disappearing species group averages less than 8% of the total fauna. Moreover, with few exceptions (5 species or 9%), these species are complex, large, ornamented tropical to subtropical taxa of the genera *Globotruncana, Globotruncanita, Rugoglobigerina,*

Planoglobulina, Pseudotextularia and *Racemiguembelina* (Plates I–III). The nine species (17%) disappearing within the first 10–20 cm of the Tertiary are primarily mid-sized taxa of the genus *Pseudoguembelina* (Plate III). These species vary in relative abundances between 1% and 6% for a combined relative abundance of about 12% (Tables 1, 2). The relative abundances of all of these species extinctions (a total of 69% of the species assemblage) combined, thus account for an average of less than 20% of the planktic foraminiferal population (see relative abundance of LAD's in Figs. 7, 8). While this certainly represents a major environmental change, it is not the catastrophic mass extinction of nearly the entire population as generally implied in the literature.

What was the effect of the K/T boundary event upon the survivors? Figs. 9B and 10B illustrate
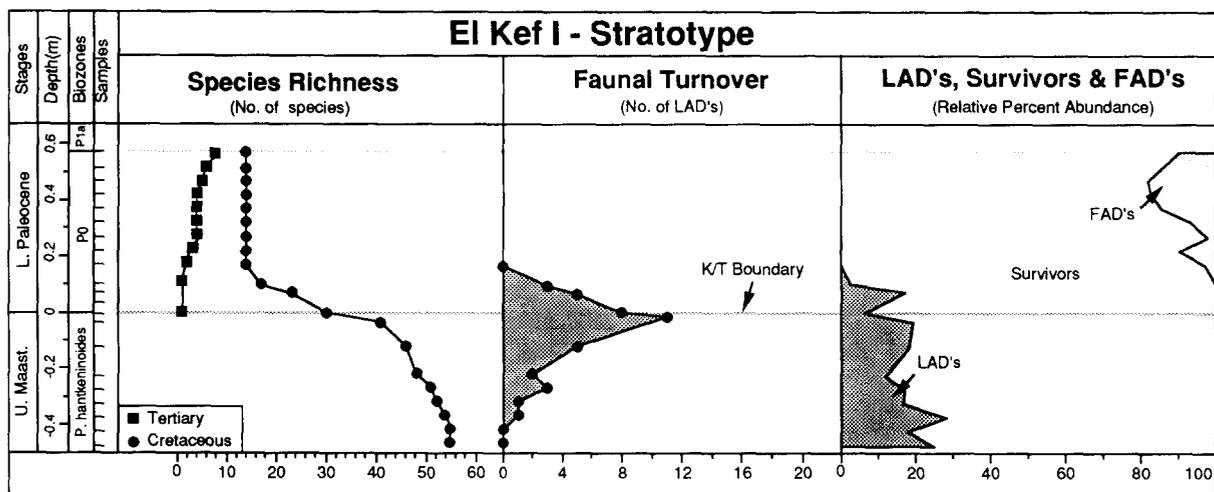
Fig. 7. Biotic effects of planktic foraminifera in terms of species richness, faunal turnover (no. of LAD's) and relative abundances of first appearances (FAD's) and last appearances (LAD's) of species across the K/T boundary at El Kef I-stratotype. Note the gradual change in species richness and faunal turnover across the K/T boundary.
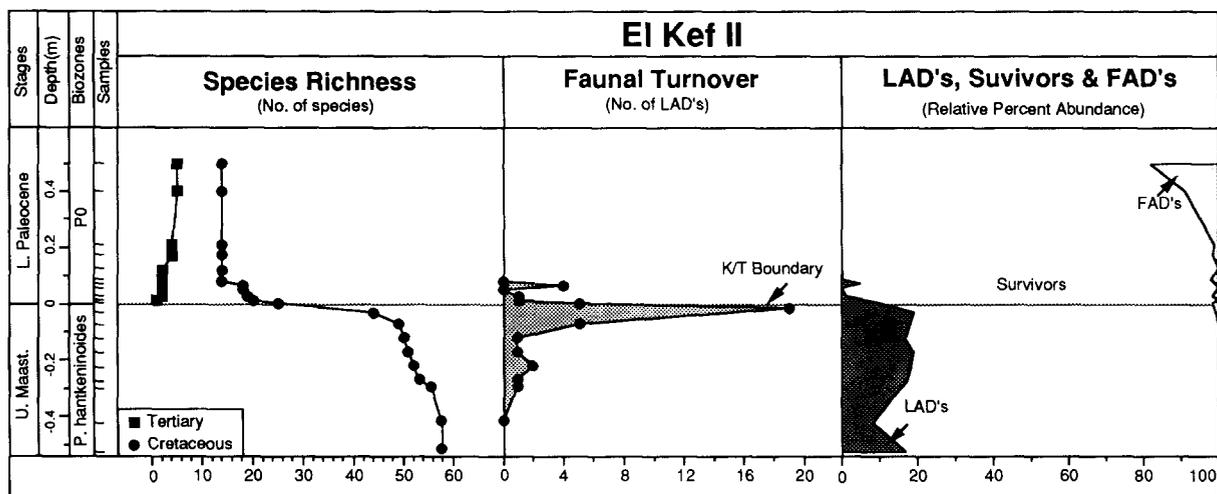
Fig. 8. Biotic effects of planktic foraminifera in terms of species richness, faunal turnover (no. of LAD's) and relative abundances of first appearances (FAD's) and last appearances (LAD's) of species across the K/T boundary at El Kef I-stratotype. Note the more sudden faunal turnover as compared with the El Kef I stratotype section which appears to be due to a short hiatus or condensed interval below the boundary clay (see Fig. 6).

the relative abundance changes of Cretaceous survivor taxa and the evolving Tertiary species at El Kef I and II, respectively. Note that the major differences in the relative species abundances between the two sections is due to the smaller size fraction (>38 μm) analyzed at El Kef II. This was done in order to test whether certain very small

taxa would be lost by analyzing the >63 μm size fraction and whether the relative abundances of the taxa present differ appreciably. The most extreme example of both of these differences is the very small (<63 μm) species *Guembelitria irregularis* (Plate IV, Fig. 10B) which dominates the fauna in the boundary clay (Zone P0) in the

Table 1

Relative percent abundances across the K/T boundary at the El Kef I, stratotype section ($\pm$ = <1%)

Depth (cm)	Above K/T boundary													Below K/T boundary							
	55–60	50–55	45–50	40–45	35–40	30 35	25–30	20–25	15–20	8–13	6–10	2–6	0–1	(−)1–6	(−)10–15	(−)20–25	(−)25–30	(−)30–35	(−)35–40	(−)40–45	(−)45–50
Eoglobigerina edita				1				1													
E. fringa		2	1	1			1														
E. simplicissima		2																			
Parvularugoglobigerina eugubina	1																				
P. longiapertura	1																					
Globoconusa conusa	7	11	17	15	9	7	1	7		×		×									
Globigerinelloides aspera		1						1		1	3	×	2	3	5	6	5	4	6	3	4
G. volutus																1	×	×	1	1	1
G. yaucoensis			1								×	2	2	5	5	3	2	2	3	1
"Globorotalia" archeocompressa		1			1				3												
Globotruncana aegyptiaca														×	×	×	×	×	×	×	×
G. arca											×	×	×	×	×	×	×	×	×	×	×
G. duwi															×						
G. insignis																×	×	×		×	×
G. dupeublei												×		×	×	×	×	×	×	×	×
G. rosetta														×	×	×	×	1		1	×
Globotruncanella caravacaensis			2					1		2	×	×	×	×	×						
G. monmouthonensis															×			×			
G. petaloidea														2	1	×	1	×	1	1	1
G. subcarinatus				1						1	1	×	1	1	2	×	×	×		2	1
Globotruncanita angulata																			×		
G. conica														×	×	×	×	×			×
G. stuarti												×		×		×	×	×	×	×	×
Gublerina cuvillieri																		×		×	×
G. robusta																		×		×	
Guembelitria cretacea	75	67	70	73	76	78	83	77	82	76	18	58	16	1	1	1	1	1	1		1
G. danica	2	×	3	3	2	1	1	1	2		×	2			×	1		1	×		×
G. irregularis	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
G. trifolia	1	2	5	4	4	10	14	10	8	3	1	3	1	1	×	1	1	1		×	1
Hedbergella holmdelensis		1	2			1		1	2	2	2	1	2	1	1	2	2	1	2	1	1
H. monmouthensis	1										2	2	2	2	6	4	4	5	4	5	5
Heterohelix complanata	1	2								2	8	1	5	6	2	3	1	3	6	4	6
H. dentata	1	2					1			1	9	1		30	24	29	26	34	13	22	8
H. glabrans											1	1		2	1	2		1	3		5
H. globulosa	4	1				1				7	12	7	22	8	7	5	10	5	8	10	9
H. moremani														1	×	×	1	3	3	1	6
H. navarroensis	1	×	2	1	2	1			2	3	15	17	14	12	17	22	13	10	9	7	21
H. planata															1	1			×		
H. pulchra														1	1		2	1	×	1	1
H. punctulata											×	×		2	×		1	2	4	2	2
H. cf. punctulata										×	1	2		6	7	6	6	2	4	4	4
H. striata	4	7	1	1	1					×	1	1	1	2	3	3	7	5	10	9	4
Planoglobulina brazoensis													×	×	×	×		×	×	×	×
P. carseyae													2	×	×	×		×	×		×
P. multicamerata															×		×	×	×	×	×
Plummerita hantkeninoides														×						×	×
P. reicheli															1	1		×	2	×	×
Pseudoguembelina costulata	1	2			2				2	3	13	2	24	12	9	7	9	11	11	15	14
P. hariaensis															×	×					
P. kempensis										×	6	1	4	2	3	1	1	1	1	2	2
P. palpebra											5	×	×	1	1		1	1	×	×	1
Pseudotextularia deformis											1	×	×	1	×	×		×			×
P. elegans														1	×	×	×	×			×
Racemiguembelina fructicosa														×	×	×	×	×	×	×	×
R. intermedia														×	×						
R. powelli												×		×	×	×				×	×
Rosita contusa																	×				
Rugoglobigerina hexacamerata										×	×			×	×		1	1	1	1	1
R. macrocephala														×	×	×		×	×	×	×
R. pennyi																×					
R. rotundata												×		×	×	×		×	×		×
R. rugosa											×		×	×	2	1	3	2	6	2	1
R. scotti													×	×	×	×	×	×	×	1	1
Woodringina hornerstownensis			1					1													
juveniles no identification													1								
Total Number Counted	176	158	189	157	120	67	138	97	100	276	235	305	250	396	342	298	300	287	278	279	297

Table 2

Relative percent abundance across the K/T boundary at the El Kef II section

Depth (cm)	Above K/T boundary											Below K/T boundary								
	50	40	19–23	15–20	10–15	7–10	6–8	4–7	2–4	1–2	0–1	(−)1–5	(−)5–10	(−)10–15	(−)15–20	(−)20–25	(−)25–30	(−)30–40	(−)40–45	(−)50–55
Abathomphalus mayaroensis																		×		
Eogloberina edita	2	3		1																
E. fringa	3	1	×	1																
E. simplicissima		×																		
Globigerinelloides aspera							2		×	1	×	1	2	2	1	3	2	1	1	3
G. volutus														1	1	1	2	×	×	1
G. yaucoensis		×					×	×		1	×	4	3	2	4	5	1	1	1	3
Globoconusa conusa	13	4	1			2			1		1									
Globotruncana aegyptiaca												×	×	×	×	×	×	×	×	×
G. arca							1				×	×	×	×	×	×	×	×	×	
G. duwi												×	×		×		×		×	
G. falsostuarti												×	×	×			×		×	×
G. insignis																×	×	×	×	×
G. dupeublei												×	×	×	×	×	×	×	×	×
G. rosetta												×	×	×	×	×	×	×	×	1
Globotruncanella caravacaensis							×			×	×	×	×	×						
G. citae																				
G. petaloides												×	×	×	×		1	1	×	×
G. subcarinatus										×		1	1	×	1	1	1	1	1	×
Globotruncanita angulata													×	×	×	×	1	×	×	×
G. conica												×	×	×	×	×	×	×	×	×
G. stuarti											×	×	×	×	×	×	×	×	×	×
Gublerina cuvillieri												×			×	×	×		×	×
G. robusta																×				
Guembelitria cretacea	9	12	12	7	5	9	23	19	24	12	16	10	4	5	5	4	4	3	7	3
G. danica	2	7	5	4	2	2	2	×	×	1			1		1	2	2	1	1	
G. trifolia	2	2					5	1	2	4	3	4	4	6	4	3	4	5	6	2
G. irregularis	68	66	82	88	93	86	55	78	70	66	39	4	11	7	6	10	9	11	16	12
Hedbergella holmdelensis										×	1	2	3	3	2	2	4	4	4	2
H. monmouthensis	×	×					2			1	3	4	4	4	4	3	5	3	6	7
Heterohelix complanata							×			1	×	3	4	4	2	2	3	2	2	3
H. dentata		1								4		7	6	7	7		7	5	3	4
H. glabrans								~		1	3	×	1	2		1	2	2	5
H. globulosa	×						3	1	×	1	6	10	7	9	12	11	12	14	12	12
H. moremani												1		1						
H. navarroensis		4				1	4		1	4	13	25	26	23	21	31	19	26	25	20
H. planata													1	2						
H. pulchra												4	4	1	4	3	4	1		×
H. punctulata													1			×	1	1	×	
H. cf. punctulata							2			1	2	2	2	3	1		1	×		×
H. striata										2	1	1	1	1	2				×	3
Planoglobulina brazoensis													×	×	×	×	×	×	×	×
P. carseyae											×	×	×	×	1	×	×	×	×	×
P. multicamerata													×	×		×	×		×	×
Plummerita hantkeninoides											×				×					×
P. reicheli												1		×	1	1		1		
Pseudoguembelina costuluta		×					2				6	8	11	15	14	11	14	10	10	12
P. hariaensis														×	×	×	×	×	×	×
P. kempensis							1			×	1	1	2	2	2	2	2	3	×	1
P. palpebra							×				×	1	×	×	×	1	×	×		×
Pseudotextularia deformis												×	×	×	×	×	×	×	×	×
P. elegans											1	×	×	×	×	×	×	×	×	×
Racemiguembelina fructicosa												×	×		×	×		×	×	
R. intermedia												×	×					×	×	×
R. powelli												×	×		×	×		×	×	×
Rosita contusa																	×	×	×	×
R. walfishensis												×			×	×		×	×	×
Rugoglobigerina hexacamerata											×	×	1	1	2	2	1	2	2	2
R. macrocephala												×		×		×	×	×	×	×
R. pennyi														×			×		×	×
R. rotundata												×	×	×	×		×	×	×	×
R. rugosa									×		×	2		1	1	×	1	1	×	1
R. scotti												×	×		×	×	×	×	×	×
Woodringina hornerstownensis										×										
Total Number Counted	337	387	289	162	157	190	399	370	237	290	415	414	372	396	350	287	304	320	415	325
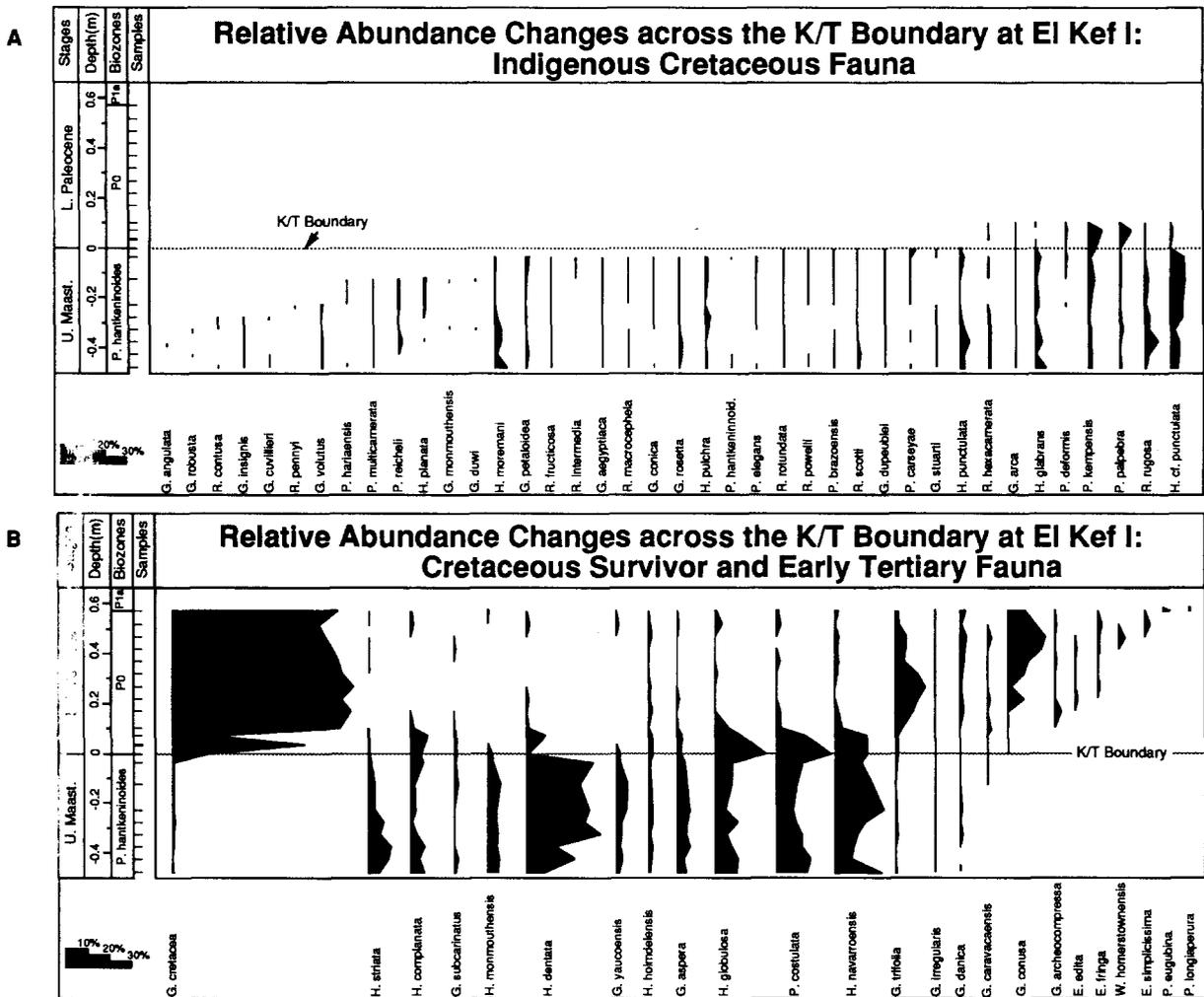
Fig. 9. Relative species abundances of planktic foraminifera in the >63 μm size fraction at El Kef I-stratotype. Note the gradual extinction pattern across the K/T boundary (11A) and the relative abundance changes of Cretaceous survivor taxa (11B).

smaller size fraction, but is rarely present in the larger (>63 μm) size fraction (Figs. 9B, 10B). Another small species, *Heterohelix navarroensis* (Plate III, 1) also exhibits higher abundances in the smaller size fraction. In contrast, the slightly larger species *Guembelitria cretacea* (Plate IV, 13) dominates in the >63 μm size fraction and its relative abundance is greatly reduced in the smaller size fraction similar to *Heterohelix dentata* (Figs. 9B, 10B). Beyond these differences, relative abundance trends in the two size fractions are very similar. It should be noted, however, that species

differences between the El Kef I and II sections at 50–60 cm above the K/T boundary are also due to the fact that the boundary clay (Zone P0) at El Kef II is 10 cm thicker than at El Kef I, and hence the reappearance of some species at the base of Zone P1a observed at El Kef I is just beyond the limits of the Fig. 10 graph.

With the information provided above, we can now evaluate the effect of the K/T boundary event on the survivor fauna of El Kef as illustrated in Figs. 9B and 10B. But first it is important to note that the 16 survivor species (31% of all taxa at El
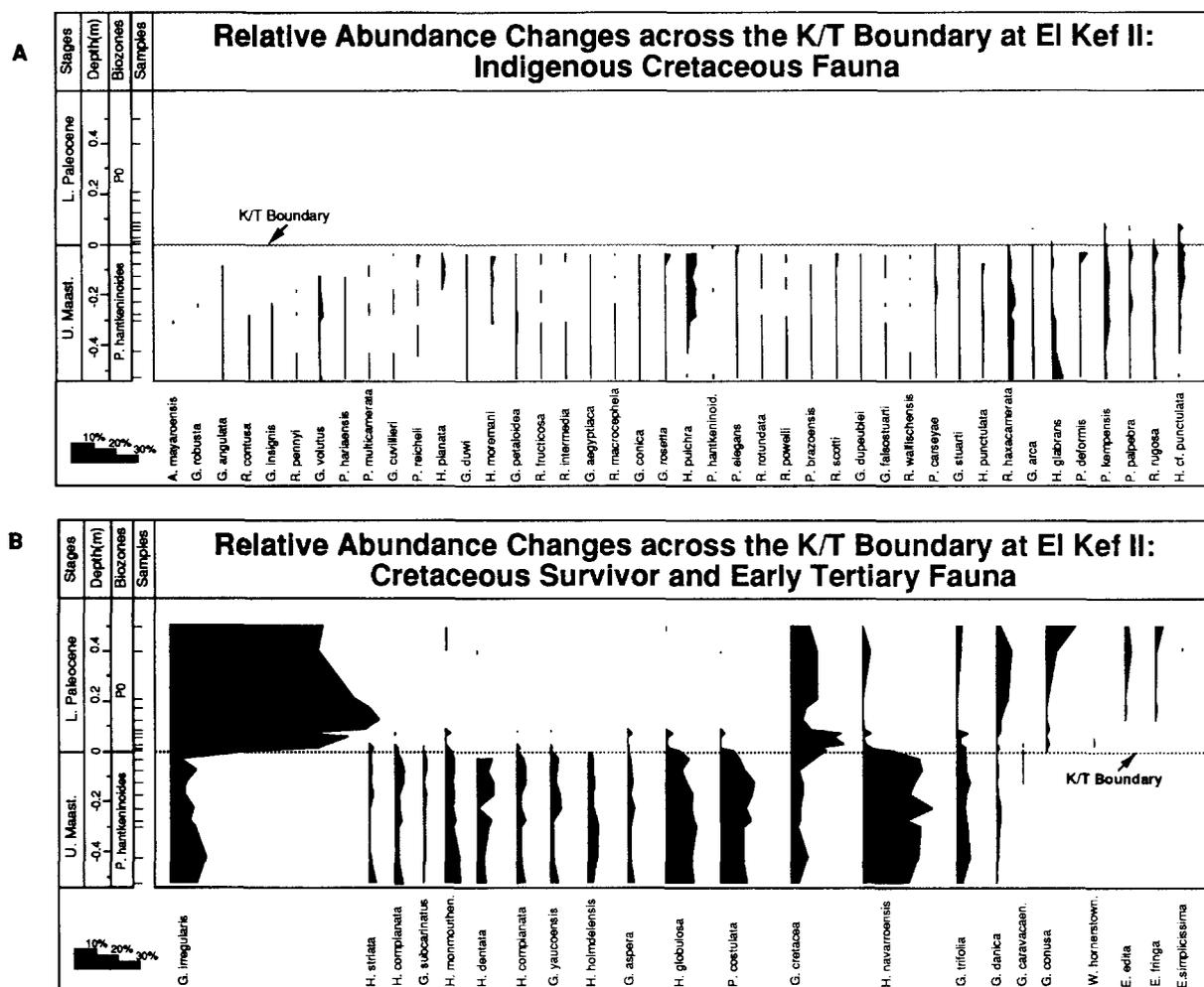
Fig. 10. Relative species abundances of planktic foraminifera in the >38 μm size fraction at El Kef II. Note the greater number of Cretaceous species extinctions centered at the K/T boundary (12A) as compared to El Kef I and the relative abundance changes of Cretaceous survivor taxa (12B).

Kef I, Fig. 9B) have significantly higher relative abundances in the topmost Maastrichtian than the 39 species (69%) exiting (Fig. 9A). Their combined relative abundance averages 80% of the total fauna as compared with the 20% of the exiting species group (Figs. 7, 8). Second, all of the 16 survivor taxa are small, simple and relatively unornamented morphotypes. Third, these survivor taxa are generally dwarfed in early Tertiary sediments, often sexually maturing at half their Maastrichtian size (MacLeod and Keller, 1992). And fourth, all survivor taxa are cosmopolitan and consistently

present from high to low latitudes. Thus, biotic effects of the K/T boundary event upon this cosmopolitan survivor group can be systematically evaluated across latitudes. Here we evaluate these effects at El Kef, Tunisia which represents one low latitude area that does not appear to be representative of low latitudes in general as will be discussed below.

At El Kef, the major relative abundance change of all survivor taxa coincides with the K/T boundary and the base of the boundary clay (base of Zone P0, Figs. 9B, 10B). In the boundary clay,

Guembelitria cretacea and *G. irregularis* abundance suddenly increases from a few percent in the topmost Maastrichtian to over 80% in the boundary clay. This is unique to El Kef and has not been observed at any other K/T boundary section. All other taxa sharply decrease to a few percent and some even temporarily disappear only to reappear again in Zones P1a, P1b and P1c (Keller, 1988a). These relative abundance patterns show a dramatic adverse effect of the K/T boundary event on all survivor species at El Kef. Only two species, *G. cretacea* and *G. irregularis*, thrived during these adverse conditions. Because of these two thriving opportunistic taxa, the combined relative abundance of survivor species changes little (Figs. 7, 8). This unique pattern of faunal abundance changes at the K/T boundary at El Kef, however, must be viewed in the context of other K/T boundary sections in order to determine whether they represent the biotic effects of a bolide impact or local environmental conditions.

Based on the data presented for El Kef, we might conclude that the biotic effects of the K/T boundary event were catastrophic for all Cretaceous planktic foraminifera leading to the extinction of over 2/3 of all species and dramatic terminal abundance declines for the remainder. Moreover, we might conclude that the primary cause for these biotic changes was a bolide impact at K/T boundary time, even though species extinctions appear to be gradual beginning below the K/T boundary as illustrated in Fig. 9 for the El Kef I stratotype. These conclusions, based on a single location, would be premature. Comparisons between El Kef and similarly continuous low latitude K/T boundary sections in Spain, Mexico and Texas confirm that all large, complex, and ornamented tropical to subtropical taxa do indeed disappear at or below the K/T boundary with the combined relative abundance of all exiting taxa being less than 20% of the total population similar to El Kef (Canudo et al., 1991; Keller, 1989a,b; Keller et al., 1994). Thus, as at El Kef, the loss of this low latitude faunal component was not that catastrophic for planktic foraminiferal populations and could have resulted from relatively minor environmental perturbations in temperature, salinity, oxygen or water mass stratification.

It is the survivor fauna which dominates late Maastrichtian planktic foraminiferal assemblages that provides the best clue to the nature and severity of the K/T boundary event. This survivor fauna does not show similarly catastrophic effects at K/T boundary time in Texas or northeastern Mexico, nearer to the proposed impact location on Yucatan, as at El Kef (Keller et al., 1994). At the El Mimbral section in NE Mexico, the cosmopolitan survivor taxa show no major change in their relative abundances at the K/T boundary or well into Zone P1a about 100–200 kyr into the early Tertiary, except for a gradual decline (Keller et al., 1994). At this location the disappearance of the tropical taxa (<18% of the population) could at best, be attributed to a K/T boundary event. This, however, is not the severe catastrophic biotic effect expected from a major bolide impact. At Brazos River Texas, few of the large complex tropical morphotypes are present because the depositional environment was very shallow (<100 m) at K/T boundary time and these taxa are generally deeper water dwellers (see discussion below). However, cosmopolitan taxa which either dwell in surface waters, or are tolerant of various depth habitats, are abundant. Similar to El Mimbral, they show no major changes in their relative abundances at the K/T boundary and no catastrophic biotic effects can be directly attributed with any confidence to a bolide impact.

At high latitudes, cosmopolitan taxa dominate and tropical taxa are absent. The section examined at Nye Klov has very similar relative abundance patterns as at Brazos River and El Mimbral with no sudden changes in the relative abundances of Cretaceous survivors at the K/T boundary (Keller et al., 1993b). At the southern high latitude ODP Site 738C, Cretaceous survivor taxa show no significant adverse biotic effects directly at the K/T boundary, but begin their abundance decline below the K/T boundary coincident with a rapid increase and dominance of the Cretaceous survivor *Chiloguembelina waiparaensis* (Keller, 1993). In all of these sections, cosmopolitan taxa seemingly survived the K/T boundary event unscathed. Their abundances generally declined in Zone P1a about 100–200 kyr into the Tertiary (except for Site 738C) and seem related to the rise and increasing

competition of the evolving new Tertiary fauna and climatic changes. These data do not support the predicted global catastrophic mass extinction of nearly all taxa at the K/T boundary, but suggest long term environmental changes superimposed by the K/T boundary event. Long-term environmental changes are also suggested by the selectivity of habitats destroyed.

6.1. Were planktic habitats selectively destroyed?

Most living planktic foraminifera live in the upper 200–400 m of the water column and, within this interval, can be grouped into surface, intermediate or deep dwellers based on their oxygen and carbon isotope ranking and the assumption that they grew their shells in isotopic equilibrium with the surrounding sea water in which they lived (Douglas and Savin, 1978; Boersma and Shackleton, 1981; Keller, 1985; Stott and Kennett, 1989; Barrera and Huber, 1990; Lu and Keller, 1993; D'Hondt and Zachos, 1993). Species living in surface waters have the lightest $\delta^{18}O$ and heaviest $\delta^{13}C$ values, whereas species living in deeper, cooler waters have successively heavier $\delta^{18}O$ and lighter $\delta^{13}C$ values.

Because stable isotope ranking of Cretaceous species is still preliminary, Table 3 groups species by genus, and only into surface and deeper dwellers. Future isotope analyses are expected to show, however, that not all species within a genus inhabited the same depth environment (see MacLeod, 1993), or that some species calcified their shells in disequilibrium with the sea water in which they grew. *Heterohelix globulosa* is one example of a

species that calcified in isotopic disequilibrium or changed its habitat over time. In the Cretaceous, this species has been reported with relatively heavy $\delta^{18}O$ values in the open ocean (although other heterohelicid species have light values) indicating that it lived within thermocline depths (Boersma and Shackleton, 1981). However, in the shallow water (< 100 m) Brazos sections where this species is dominant throughout the late Cretaceous and into the early Tertiary (Keller, 1989b), this species apparently adapted to living in a shallower environment. The same pattern has been observed in the shallow water Stevns Klint and Nye Klov sections (Schmitz et al., 1992; Keller et al., 1993b). For this reason, *H. globulosa* has been grouped with surface dwellers. The same appears to be the case for *Hedbergella*, although isotopic values of this genus generally rank it deeper than *Heterohelix*.

Table 3 shows that all deeper-dwelling genera disappeared by K/T boundary time whereas surface dwellers survived with the exception of rugoglobigerinids (the isotopically lightest surface dwellers) and pseudotextularids (*P. elegans and P. deformis*). Moreover, of the deep-dwelling genera all species disappeared with the possible exception of *Globotruncanella subcarinatus*. In contrast, many species of the surface-dwelling genera survived (except for *Rugoglobigerina* and *Pseudotextularia*).

Figure 11 shows that of the 69% of the species disappearing at El Kef I below or at the K/T boundary and in the first 10 cm of the boundary clay (Zone P0), 52% are deeper water dwellers all of which disappeared by K/T boundary time, except for *Globotruncana arca* which is frequently

Table 3
Preliminary isotopic ranking of Cretaceous planktic foraminifera

Surface			Deep		
Rugoglobigerina	extinct	C	Globotruncana	extinct	T-S
Guembelitria	survivor	C	Globotruncanita	extinct	T-S
Heterohelix	survivor	C	Globotruncanella	extinct	T-S
Globigerinelloides	survivor	C	Racemiguembelina	extinct	T-S
Hedbergella	survivor	C	Planoglobulina	extinct	T-S
Pseudoguembelina	survivor	C	Gublerina	extinct	T-S
Pseudotextularia	extinct	C	Rugotruncana	extinct	T-S

C = cosmopolitan, T-S = tropical-subtropical.
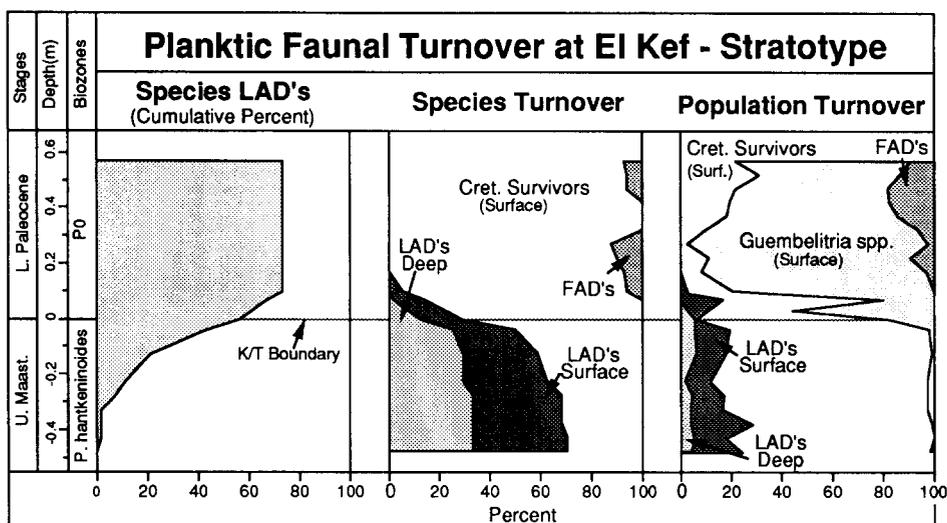
Fig. 11. Selectivity in planktic foraminiferal species extinction and survivorship patterns across the K/T boundary at El Kef I-stratotype. See text for discussion.

found in the boundary clay (MacLeod and Keller, 1994). Note that all deep water dwellers combined comprise less than 8% of the total population. Of the surface dwellers, rugoglobigerinids are the largest group disappearing below and at the K/T boundary with *R. rugosa* and *R. hexacamerata* frequently observed in the boundary clay (MacLeod and Keller, 1994). Other taxa disappearing in this interval are pseudotextularids (*P. elegans, P. deformis*), pseudoguembelinids and a few heterohelicids. All disappearing surface dwellers combined account for less than 12% of the population (Fig. 11).

The survivor fauna consists of surface dwellers only and is dominated by *Guembelitria*, with smaller abundances of *Heterohelix, Hedbergella*, and *Globigerinelloides* (Fig. 11). Note that this group dominates the latest Maastrichtian foraminiferal population. However, a major environmental change is apparent within the surface population beginning at K/T boundary time by the apparent takeover of *Guembelitria* spp. (Fig. 11).

This pattern of species last appearances and survivors is not random, but indicates a systematic and complete elimination of deeper dwelling species by K/T boundary time. This selective and

preferential disappearance of deep dwellers is related at least in part to the sea-level regression which lowered sea-levels from 300–400 m to less than 200 m depth at El Kef (Donce et al., 1985; Peypouquet et al., 1986; Keller, 1988b, 1992). This shallow neritic environment would have excluded habitats for deeper water dwellers. Surface dwellers which also disappeared may have been sensitive to temperature, oxygen and salinity fluctuations. A possible scenario for the extinctions will be discussed below.

7. What are the biotic effects on other microorganisms at El Kef?

In order to evaluate the biotic effects of the K/T boundary event on other microfossil groups at El Kef, we have plotted species richness, species extinctions and species originations for planktic and benthic foraminifera, calcareous nannofossils, pollen and spores, ostracods and dinoflagellates (Figs. 12–14). Results are illuminating and potentially far reaching for our understanding of the nature and cause of the K/T boundary event. For instance, planktic and benthic foraminifera and calcareous nannofossils responded more strongly
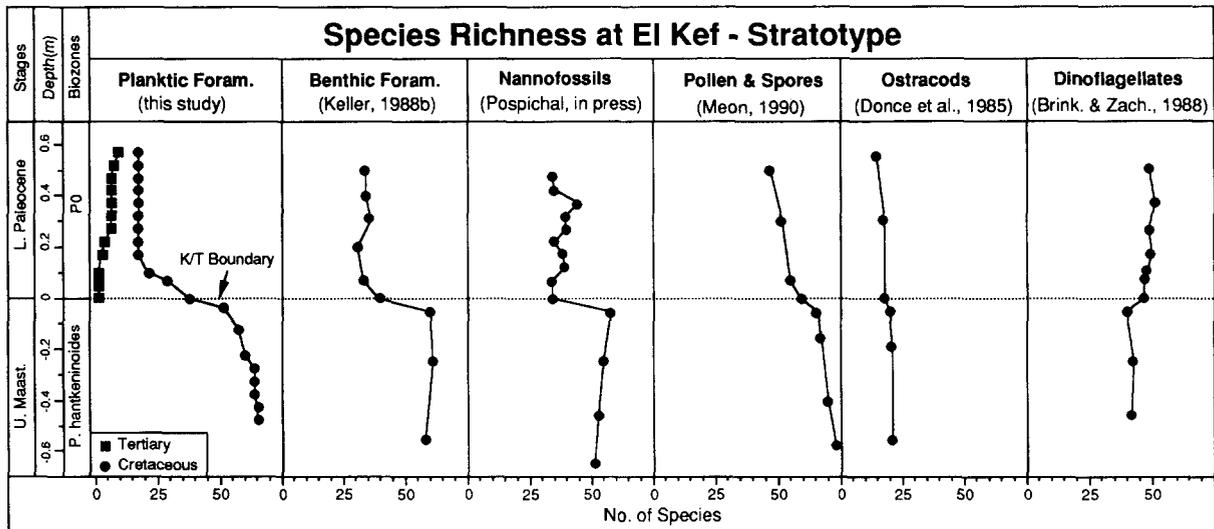
Fig. 12. Species richness patterns in six microfossil groups across the K/T boundary at El Kef I-stratotype. Note that major changes are apparent only in planktic and benthic foraminifera and nannofossils.

to the K/T boundary environmental changes than other microfossil groups with a maximum decrease in species richness of 69%, 45% and 58% respectively (Fig. 12). In contrast, species richness in pollen and spores as well as ostracods decreased gradually and only by 8% and 10% respectively, whereas for dinoflagellates there is an 18% increase in species richness (Fig. 12).

Species extinction plots mirror the same variability with the maximum number of species extinctions in planktic and benthic foraminifera culminating at or just below the K/T boundary (Fig. 13). There are relatively minor increases in species extinctions in pollen and spores, and ostracods. No dinoflagellate species extinctions coincide with the K/T boundary. For calcareous nannofossils, it is impossible to evaluate the number of species extinct because all Cretaceous taxa are present or reappear above the K/T boundary and it is unclear whether all or most are present because of reworking (Jiang and Gartner, 1986; Pospichal, 1994; Gartner, in press).

These species richness and species extinction data point towards environmental effects selectively affecting specific groups, such as calcareous nannofossils and planktic and benthic foramini-

fera. However, no microfossil groups, except dinoflagellates, thrived during the K/T boundary transition. This is evident from the species origination plot (Fig. 14) which shows that no species evolved in ostracods or pollen and spores; only one nannofossils species evolved and few benthic and planktic foraminifera (Fig. 14).

Why is it that at El Kef both the planktic and benthic foraminiferal faunas and calcareous nannofossils show nearly catastrophic biotic effects near the K/T boundary, whereas other microfossil groups show no major biotic effects? Because of the uncertainty in reworked vs. Cretaceous survivor taxa in nannofossil assemblages, we will not address their extinction pattern further. Clues may be gained from planktic and benthic foraminifera. For instance, with the exception of the extinction of the tropical–subtropical planktic foraminifera neither the adverse biotic effects on the cosmopolitan survivor taxa, nor the adverse biotic effects on the benthic foraminifera can be confirmed outside El Kef at other low latitude localities (Keller, 1989a,b, 1992; Thomas, 1990a,b; Kaiho, 1988; Nomura, 1991). This suggests that the apparent sudden faunal change among the survivor group was largely due to regional, rather than global
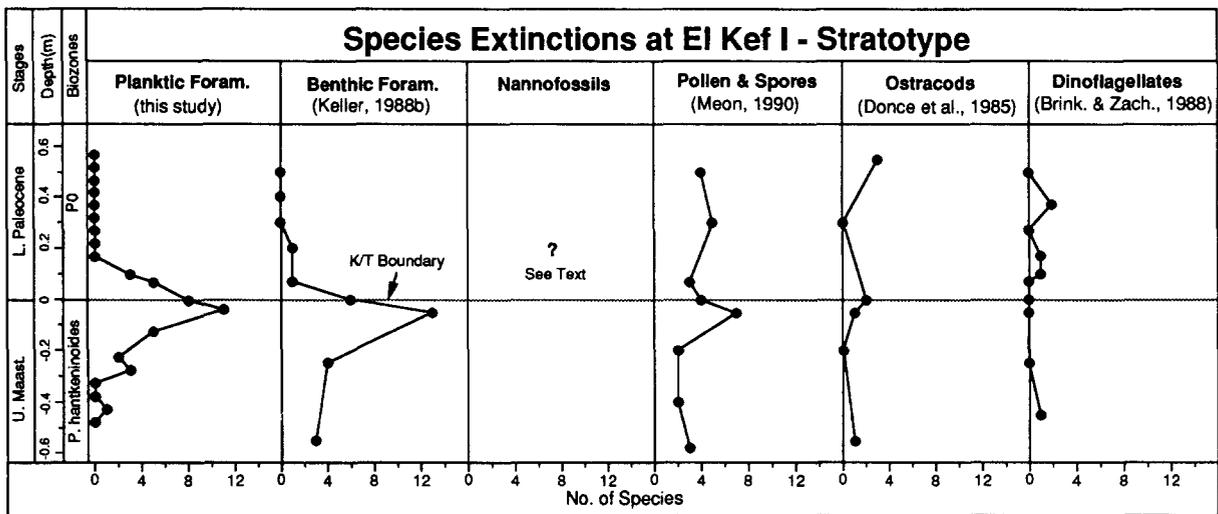
Fig. 13. Species extinction patterns in six microfossil groups across the K/T boundary at El Kef I-stratotype. Note that only benthic and planktic foraminifera show major extinctions. Nannofossil extinctions are uncertain due to reworking.
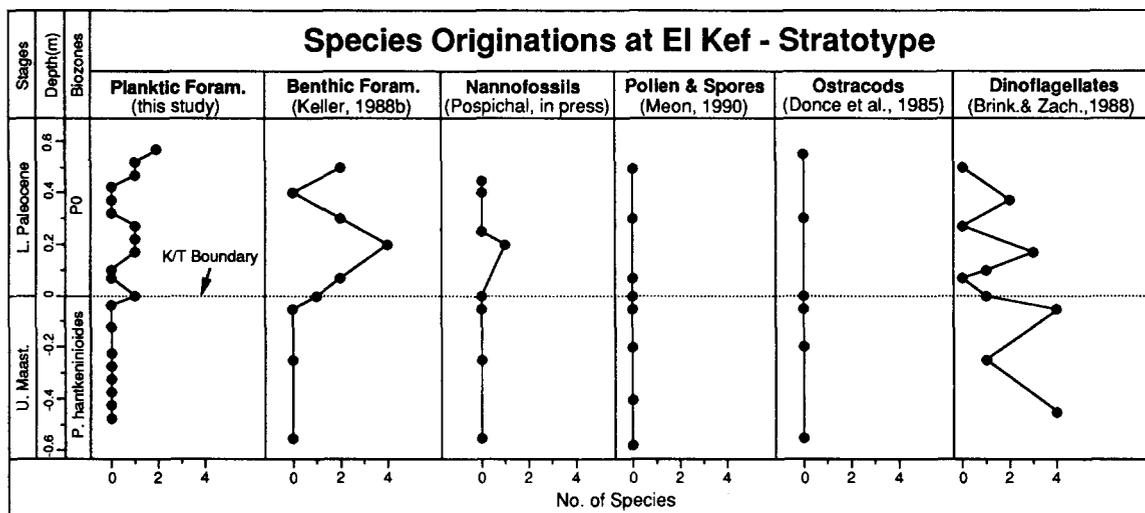
Fig. 14. Species origination patterns in six microfossil groups across the K/T boundary at El Kef I-stratotype. Note that dinoflagellates, which show no extinctions across the K/T boundary, thrived.

environmental conditions. Note that Coccioni and Galeotti (1994) reported catastrophic extinctions in benthic foraminifera from Caravaca, Spain. However, the apparent more sudden faunal turnover is largely a function of the very condensed K/T boundary transition with a 7 cm thick boundary clay at Caravaca, as compared to a 50 cm

thick boundary clay at El Kef (see also Keller, 1992), and their assumption that the thin clay layer was deposited within five to six thousand years. However, the boundary clay is generally considered to have been deposited within 40–50 thousand years (see MacLeod and Keller, 1991a,b and references therein).

8. El Kef extinction patterns: local or global changes?

El Kef is located on the North African platform, a region strongly influenced by sea-level fluctuations and variations in the oxygen minimum zone, both of which most strongly affect bottom dwellers (ostracods and benthic foraminifera) and deeper dwelling planktic foraminifera. A global sea-level regression maximum about 200–300 kyr prior to the K/T boundary is well documented (e.g. Haq et al., 1987; Donovan et al., 1988; Schmitz et al., 1992; Keller et al., 1993b; Keller and Stinnesbeck, in press; Pardo et al., in press). Based on ostracods, Donce et al. (1985) and Peypouquet et al. (1986) estimated that at El Kef sea-level shallowed from upper bathyal to neritic depths. Based on benthic foraminifera Keller (1988b, 1992) and Pardo et al. (in press) estimated shallowing of about 70–100 m during the lastest Maastrichtian followed by deepening during the last 100 kyr of the Maastrichtian and into the earliest Tertiary (Keller, 1992). Based on dinocysts, Brinkhuis and Zachariasse (1988) also calculated a major sea-level regression beginning in the uppermost Maastrichtian and culminating near the K/T boundary followed by generally rising, though fluctuating sea-levels in the earliest Tertiary. This same pattern of sea-level fluctuations has since been confirmed at Stevns Klint and Nye Klov based on benthic and planktic foraminifera and stable isotopes (Schmitz et al., 1992; Keller et al., 1993b). In these Danish sections the sea-level regression maximum also occurs in the latest Maastrichtian followed by maximum sea-level transgression across the K/T boundary that is marked by deposition of the boundary clay. This may also have been the case at El Kef.

The strong biotic responses of benthic and planktic foraminifera in the El Kef region are also observed at Agost in southern Spain. In both localities benthic foraminifera indicate that the sea-level transgression is associated with an expanded oxygen minimum zone with the maximum transgression marked by deposition of the boundary clay (Zone P0). Low oxygen conditions prevailed through Zone P1a (Donce et al., 1985; Peypouquet et al., 1986; Keller, 1988b, 1992;

Rohling et al., 1993). The combined effects of a major sea-level drop during the lastest Maastrichtian followed by a sea-level rise and stagnant low oxygen conditions appear to be primarily responsible for the observed adverse biotic effects in benthic foraminifera.

Fig. 15 illustrates the species and population turnover in benthic foraminifera at El Kef. Although only about 20% of the species disappeared (LAD's) by K/T boundary time, they are relatively abundant comprising 40% of the population. These species represent primarily upper bathyal to outer shelf depths. Their disappearance seems related to the latest Maastrichtian sea-level regression and then the onset of transgression and an expanded oxygen minimum zone at the K/T boundary. This interpretation is supported by the temporary disappearance of several taxa (e.g., *Gaudryina pyramidata, Bolivinoides draco, Cibicidoides praecursoria, Anomalinoides newmanae, A. welleri*) during the low sea levels and low oxygen conditions in Zones P0 and P1a and their reappearance thereafter at the top of Zone P1a and P1b with the return of more oxygenated waters (Keller, 1988b, 1992). During the low oxygen interval, the epifaunal *Anomalinoides acuta* dominates (>60% of the population) similar to *Guembelitria cretacea* in surface waters, and other thriving or new incoming taxa are generally low oxygen tolerant morphotypes (e.g., *Alabamina midwayensis, Bulimina kugleri, B. farafraensis, B. pupoides, B. quadrata, B. reussi, B. lajollaensis*, Keller, 1988b). These benthic foraminiferal changes are thus directly related to the sea-level regression and subsequent transgression associated with stagnant, low oxygen conditions. Benthic faunal turnovers in other K/T boundary sections show similar changes related to sea-level and oxygen conditions, although generally less severe than at El Kef (Kaiho, 1988; Nomura, 1991; Thomas, 1990a,b; Keller, 1992; Pardo et al., in press). Because of the ongoing sea-level fluctuations and associated variations in the oxygen minimum zone, it seems impossible to evaluate and separate the biotic effects of a bolide impact from those of ongoing environmental changes (Figs. 16, 17).

The extinction of the tropical-subtropical deeper
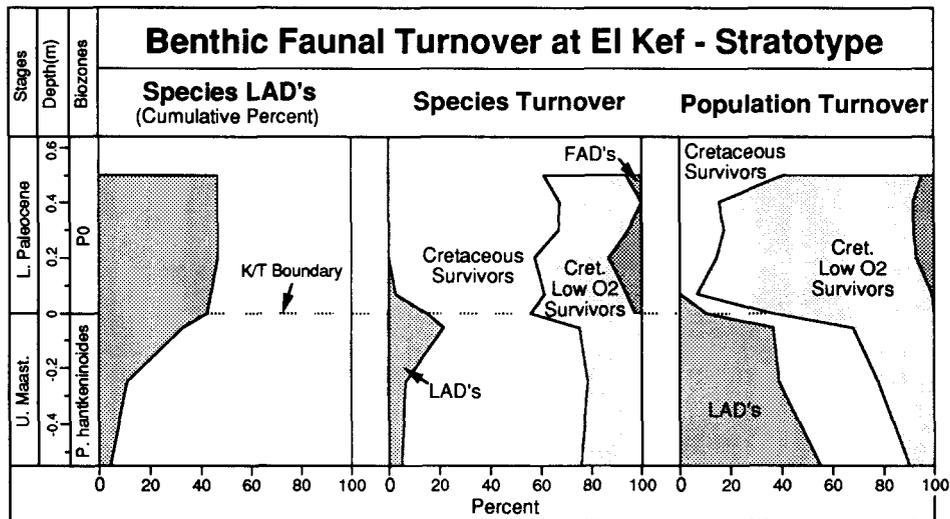
Fig. 15. Selectivity in benthic foraminiferal species extinction and survivorship patterns across the K/T boundary at El Kef I-stratotype. Note the increase in the relative abundance of the low oxygen tolerant population above the K/T boundary signals an expanded oxygen minimum zone.

dwelling planktic foraminifera at or below the K/T boundary also can be explained in part by long-term changing environmental conditions. During the late Maastrichtian, the ocean was chemically and thermally well-stratified supporting a large diversity of species. As sea levels dropped, this stratification diminished with increased mixing due to upwelling and higher current intensity, thus eliminating many taxa. In shallow areas, such as El Kef where sea-levels dropped below 200 m depth, this could have caused the disappearance of the deeper water dwellers. However, since the same tropical–subtropical taxa disappeared globally in continental shelf as well as open ocean environments, global changes in thermal and chemical stratification must have accompanied the sea-level regression and transgression. Moreover, their demise was probably hastened by a global lateral and vertical expansion of the oxygen minimum zone at K/T boundary time that is evident by the deposition of the boundary clay worldwide.

As noted earlier, the most dramatic faunal changes and unique to El Kef are the sudden decline in the cosmopolitan surface dwellers at the base of the boundary clay and the concurrent major increase in the triserial *Guembelitria* group (Figs. 9, 10). Since these biotic effects on the

survivor taxa have not been observed at other low latitude localities, they appear to have been caused by local rather than global environmental conditions. The coincidence of these faunal changes with the onset of clay deposition and low oxygen conditions evident in ostracod and benthic foraminiferal faunas, suggests that it is due to a major expansion of the oxygen minimum zone into the photic zone. The *Guembelitria* group may have thrived during this time because they are shallow surface and near-shore surface dwellers. As with benthic foraminifera, it is difficult to separate the biotic effects due to long-term environmental changes from those due to a bolide impact. Although it appears that the regression/transgression and associated circulation and watermass changes may have been sufficient to cause the observed faunal changes, a bolide impact may have hastened the demise of the already declining tropical–subtropical fauna.

9. Conclusions

High resolution planktic foraminiferal analysis across the K/T boundary at El Kef and comparison with benthic foraminifera, calcareous nanno-
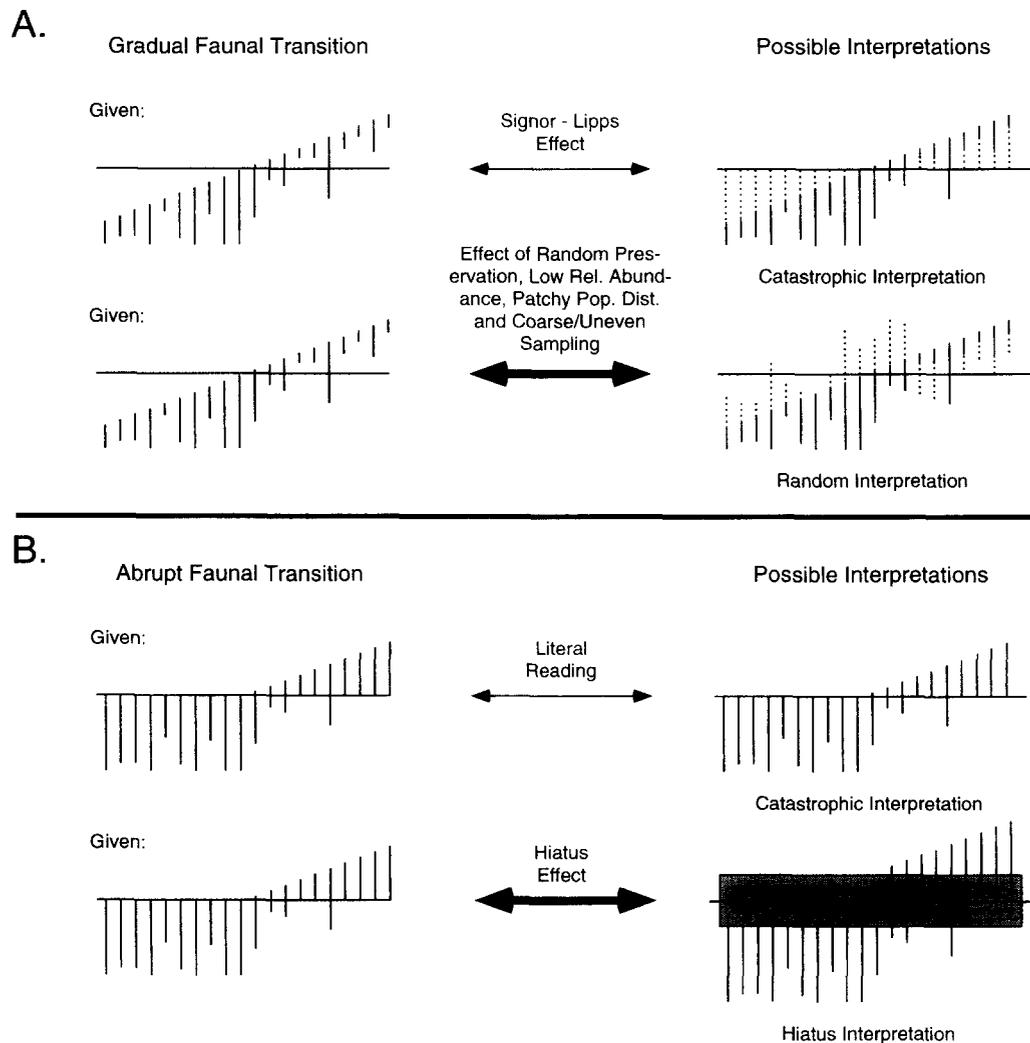
Fig. 16. Possible interpretations of gradual (A) and abrupt (B) faunal turnover patterns. See text for discussion.

fossils, ostracods, pollen and spores and dinoflagellates indicate that major biotic changes are registered only in benthic and planktic foraminifera and calcareous nannofossils. Pollen and spores and ostracods record relatively minor gradual changes in species richness across the K/T boundary, whereas dinoflagellates thrive with increasing species richness.

Among calcareous nannofossils, species richness declined by 58% at the base of the boundary clay. However, since nearly all of the Cretaceous taxa reappear in early Tertiary sediments above the

boundary clay and their presence is suspected to be due to reworking, further evaluation of the biotic effects of this microfossil group awaits positive identification of reworked vs. survivor taxa.

Among planktic foraminifera, a 69% decline in species richness across the K/T boundary is primarily the result of a disappearing tropical–subtropical fauna with a combined relative abundance of less than 20% of the total population. The extinction pattern at El Kef strongly suggests an extended period of extinctions beginning below and ending above the K/T boundary. Extinctions
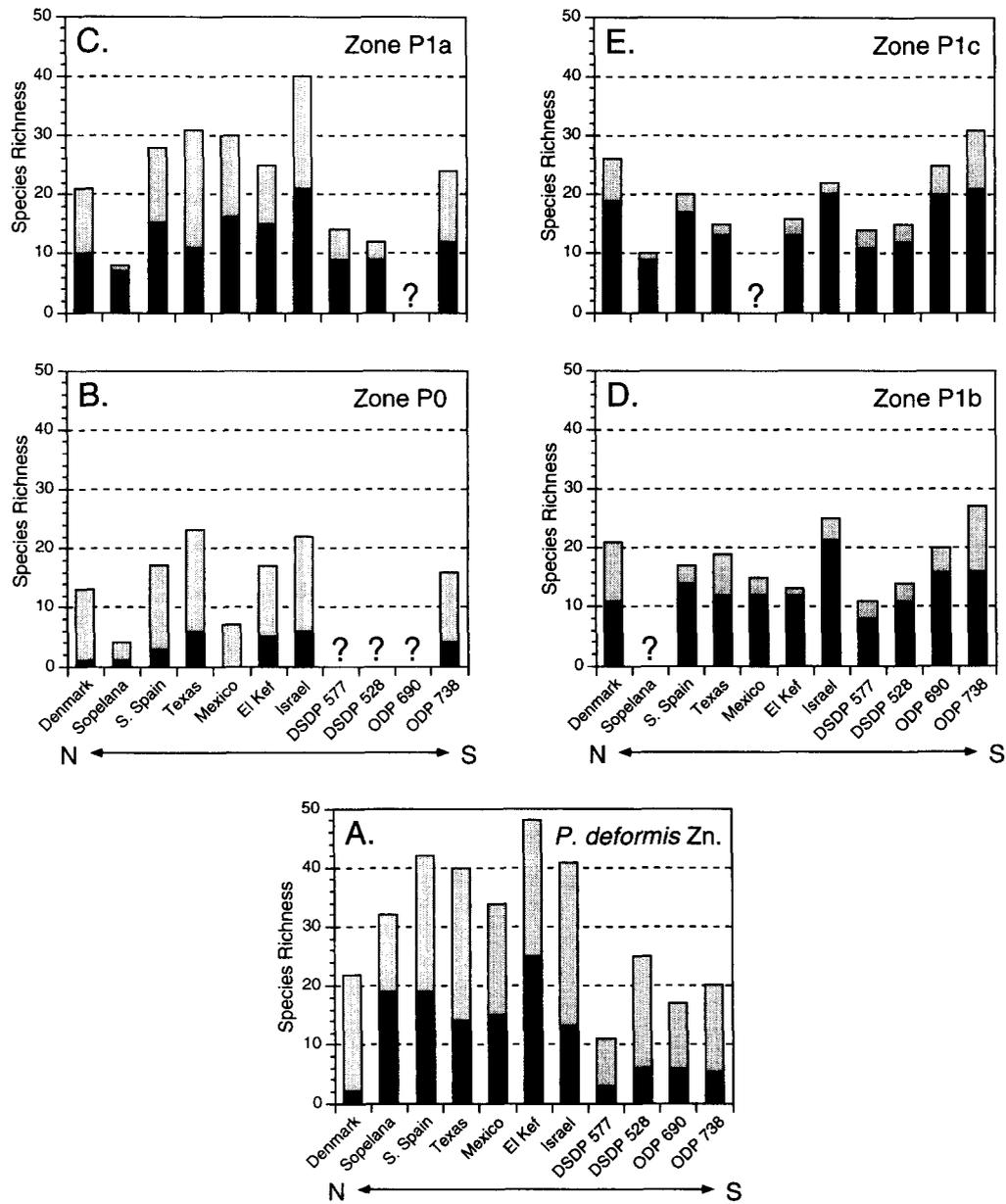
Fig. 17. Geographic patterns of variations in species richness values for composite planktic foraminiferal faunas of the latest Maastrichtian *P. deformis* Zone and the earliest Paleocene P0, Pla, Plb and Plc Zones. Localities are arrayed along a north–south transect. Black pattern marks Cretaceous taxa in Fig. 10A and Tertiary taxa in Fig. 10B–10E, stipple pattern marks Cretaceous survivor species. Question marks indicate biozone is missing in that particular region (from MacLeod and Keller, 1994).

are selective, rather than random as would be expected from a large bolide impact. Only rare species disappeared. About 52% of these taxa are large, ornate, complex tropical–subtropical forms

that lived in well stratified waters at or below the thermocline. Their combined abundance, however, constitutes less than 8% of the planktic foraminiferal population. Remaining extinct taxa are sur-

face dwellers that constitute less than 12% of the total population. All survivors are surface dwellers living within the photic zone. Their sharp relative abundance decrease at the base of the boundary clay is unique to El Kef and has not been observed elsewhere. For this reason it cannot be attributed to a global biotic effect of the bolide impact, but must be due to local environmental changes such as the expansion of the oxygen minimum zone indicated by benthic foraminifera, and ostracods.

Benthic foraminifera show a 45% decline in species richness that is primarily the result of a disappearing upper bathyal to outer neritic fauna during the latest Maastrichtian sea-level regression and the subsequent expanded oxygen minimum zone that accompanied the sea-level rise across the K/T boundary. An expanded oxygen minimum zone is indicated by the dominance of low oxygen tolerant taxa in the boundary clay (Zone P0) and the succeeding Zone P1a (*P. eugubina*). Since the strong benthic foraminiferal turnover at El Kef is not observed elsewhere in the Tethys or globally, it must be largely due to local environmental conditions.

We conclude that the El Kef stratotype section represents the most complete and most expanded sedimentary record across the K/T boundary known to date worldwide. The unique environmental conditions that preserved this complete stratigraphic record at El Kef, however, are largely due to its shallow continental shelf depth and a local maximum expansion of the oxygen minimum zone. But, these conditions also imprinted a unique biotic response upon bottom dwellers (benthic foraminifera and ostracods), and marine microplankton (planktic foraminifera) that is not representative of global environmental changes. Therefore, the biotic response at El Kef reflects a combination of local environmental and global oceanographic conditions that cannot be used directly to evaluate the global biotic response to the K/T boundary event.

Acknowledgments

Appendix

Signor-Lipps Effect

Is it possible that the entire gradual extinction pattern at the El Kef I stratotype section is an artifact of sampling (Signor and Lipps, 1982) and reworking? For species disappearing below the K/T boundary it is frequently argued that if you look hard enough, eventually you will find all upper Maastrichtian species ranging exactly up to the K/T boundary. For species ranging above the K/T boundary, it is argued that all but a few must be reworked. These arguments a priori assume that there must be one catastrophic extinction horizon. Fig. 16 illustrates the possible interpretations of gradual and abrupt extinction patterns and their pitfalls taking into consideration the Signor-Lipps Effect. We demonstrate that the possibility of preservational bias does not predict or support the interpretation of a gradual extinction pattern as one of catastrophic extinctions at a single horizon.

Given a gradual pattern of faunal turnover across an a priori-defined stratigraphic horizon (Fig. 16A), the possibility that one or more taxa whose last appearance datum (LAD) falls below, or whose first appearance datum (FAD) falls above the horizon actually became extinct (or originated) at the horizon cannot be ruled out. This uncertainty stems from intrinsic differences in species' preservation potentials resulting in their intermittent occurrence in local sections or cores, low relative abundances and patchy population distributions during initial radiation or terminal decline, and coarse or uneven sampling. Signor and Lipps (1982) used this well-known stratigraphic principle to point out that a catastrophic faunal turnover pattern might appear gradual in local stratigraphic sequences. However, the Signor-Lipps Effect is a statement of possibility, not probability. More to the point, recognition of the possibility of this bias by itself is of absolutely no use in predicting what the true sequence of LAD's and FAD's may be. Given these data alone, the most catastrophic interpretation of the Signor-Lipps effect, in which all pre-boundary LAD's and post boundary FAD's are arbitrarily extended to the boundary is an extremely limiting condition that, in the absence of independent biotic evidence, must be regarded as having an exceedingly low probability of being the correct interpretation (Fig. 16A, thin arrow). A more likely interpretation would

regard the true positions of species' FAD's and LAD's in a random manner, (Fig. 16A, thick arrow). Similarly, the stratigraphic record of an abrupt extinction event (Fig. 16B) should not be taken at face value. This situation also may be accommodated by two end-member interpretations; a literal (catastrophic) turnover (Fig. 16B, thin arrow), and recognition of a hiatus, in which the true turnover pattern remains uncertain at the level of the local sequence (Fig. 16B, thick arrow). Once again, the catastrophic interpretation represents the extreme end-member of a wide spectrum of possible turnover patterns and, for that reason, must be regarded as having a low probability of being correct. Neither of these faunal turnover patterns can be unambiguously interpreted unless their study is approached in a comparative manner that integrates information from a wide variety of coeval stratigraphic sequences.

Cretaceous species survivorship

The argument that all but a few Cretaceous species present in early Tertiary sediments are reworked has an equally diminished probability. Reworking and redeposition of older sediments is always a possibility throughout the sedimentary column and especially near hiatuses where intensified currents tend to erode sediments. But for no other stratigraphic interval has it been argued that the presence of all but one or a few species of a prior stage fauna must be due to reworking.

Reworked specimens can often, although not always, be identified by their different preservation or coloration. Such reworked specimens are also present in early Danian deposits. However, about 1/3 of the Cretaceous species are consistently present in early Danian sediments globally. For the most part these are small cosmopolitan taxa (heterohelicids, hedbergellids, globigerinellids, guembelitrids) that show none of the telltale discolorations, recrystallized surfaces, or breaks associated with reworking. Their range and biogeographic distribution patterns are also not random, as would be expected from random reworking. Instead, these patterns are systematic and similar to those that would be expected from a living fauna (Keller et al., 1993b; MacLeod and Keller, 1994; MacLeod, in press). Even these species' relative abundance distributions are often similar in widely separated regions such as Brazos River, Texas and Nye Klov, Denmark (Keller et al., 1993b). MacLeod and Keller (1994 and MacLeod, in press) have analyzed the species richness patterns of uppermost Maastrichtian (*P. deformis* Zone) and Danian Zones P0–P1c globally in 11 localities representing 19 K/T boundary sections (Fig. 17). These results show high species richness in low to middle latitudes (>40 species) and low species richness in high latitudes (~20 species). By K/T boundary time about 1/2 to 2/3 of the species have disappeared in low to middle latitudes and 1/3 to 1/2 of the species generally continue into the early Tertiary (shaded area in Fig. 17A). In contrast in high latitudes where tropical to subtropical species are absent, nearly all Cretaceous species survived into the early Tertiary. Moreover, during the early Tertiary Zones P0–P1c, there is a systematic presence of Cretaceous cosmopolitan taxa in all sections across latitudes (Fig. 17B). No random sediment reworking process could produce such systematic similarities in species abundance and distribution patterns across the world oceans.

Fortunately, there is another independent, objective and definitive test of species survival based on $\delta^{13}C$ isotopes of the species in question. $\delta^{13}C$ values between the Cretaceous and Tertiary differ by 2–3 ‰ in low and middle latitudes (but not in high latitudes, see Keller, 1993; Keller et al., 1993b). Therefore, if the Cretaceous species present in earliest Tertiary sediments are reworked, they should have Cretaceous isotopic signals; if they lived, they should have Tertiary signals. This test unequivocally marks Cretaceous species in early Tertiary sediments as either in-situ or reworked. The following Cretaceous species have been isotopically measured and found to be Cretaceous survivors: *Heterohelix globulosa, H. navarroensis, Guembelitria cretacea, G. trifolia, G. danica, Chiloguembelina waiparaensis* (Barrera and Keller, 1990, 1994; Keller et al., 1993b; Keller, 1993). Other Cretaceous species believed to be survivors based on their constant presence and geographic distribution are: *Hedbergella holmdelensis, H. monmouthensis, Globigerinelloides aspera, G. yaucoensis, Heterohelix dentata, H. striata, H. costulata, H. complanata, Globotruncanella subcarinatus* (Plates II, III).

Stable isotopic tests for species survival should never be applied to Cretaceous species that are poorly preserved, rare or sporadically present, or present only in isolated intervals at or near a hiatus, because such specimens may have been reworked. Zachos et al. (1992) measured Cretaceous species found in early Tertiary sediments at Site 750 and, finding their isotopic signals similar to those of Cretaceous taxa, concluded that there is no evidence for Cretaceous species survival. Since Site 750 contains a major hiatus (with Zones P0, P1a and probably Zone P1b missing; Barrera and Keller, 1994), specimens measured are from Zone P1c where few Cretaceous survivors are present. Moreover, since in high latitudes the $\delta^{13}C$ shift is very small or absent (Keller, 1993; Keller et al., 1993b; Barrera and Keller, 1994) the absence of a $\delta^{13}C$ shift does not prove that the species are reworked and of Cretaceous origin. For instance, at Nye Klov the Cretaceous survivor *H. globulosa* registers only a 0.5‰ change at the K/T boundary whereas in low latitudes (Brazos River) it registers over 3‰ (Barrera and Keller, 1990; Keller et al., 1993b). Also at Site 738C, *Chiloguembelina waiparaensis*, previously known only from the early Tertiary, registers no significant change across the K/T boundary (Keller, 1993; Barrera and Keller, 1994).

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