



## Disaster opportunists *Guembelitrinidae*: index for environmental catastrophes

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### Abstract

Blooms of the disaster opportunist *Guembelitra* species are proxies for environmental catastrophes, whether impact or volcanism, leading to severe biotic stress crises that may range from temporary exclusion of ecological specialists and generalists to mass extinctions. During the late Maastrichtian and early Danian (zones P0 and Pl<sub>a</sub>), *Guembelitra* blooms show global distributions, but with the largest blooms (40–80% *Guembelitra*) in low and middle latitudes and only minor blooms (10–20%) in high latitudes. Late Maastrichtian *Guembelitra* blooms are, so far, known from the Indian Ocean and eastern Tethys. The most intense *Guembelitra* blooms (>60% *Guembelitra*) occurred in shallow continental shelf areas, slope/shelf margins and volcanic provinces of the Indian Ocean. What these environments have in common is high nutrient influx (eutrophication) either from continental runoff, upwelling along continental margins or volcanic input. At times of biotic crises, *Guembelitra* blooms may have spread rapidly to the exclusion of most or all other species, much like today's red tides, but with near global distributions.

A simple model can explain the ecological succession and recovery phases that follow major biotic perturbations caused by impacts or volcanism that lead to exclusion of specialist and most generalist species. Within such highly stressed environments, *Guembelitra* is the only genus to thrive, and without competition, rapidly reproduce and exponentially increase their populations. When nutrients are depleted, populations rapidly decrease, leading to ecologic niches for other generalists and ecosystem recovery. Small low-O<sub>2</sub>-tolerant heterohelicid populations mark this second stage, followed by small trochospiral and planispiral species. With further environmental recovery, increasing competition, niche development and restoration of a well-stratified water mass, oligotrophic conditions are restored, opening habitats for the highly specialized and diverse species and a return to normal diverse assemblages. This ecological succession is observed in association with mantle plume volcanism in the Indian Ocean and eastern Tethys during the late Maastrichtian, and in association with the K–T impact and volcanism during the early Tertiary.

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### 1. Introduction

Guembelitrids are a group of small-sized triserial planktic foraminiferal species that are sporadically known from the middle Cretaceous to the Recent

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and thus form one of the longest ranging plankton groups. Despite this long history, their stratigraphic record is poorly documented and their paleoecology inadequately understood. This is largely due to the very small species size (38–100  $\mu\text{m}$ ) which is generally ignored in routine foraminiferal analysis, but also the sporadic occurrence with no obvious paleoecological associations. The *Guembelitra* species record is therefore largely restricted to time intervals where larger species are absent, forcing investigators to look for clues in the smaller size fractions. This may partly account for the sporadic stratigraphic record although Kroon and Nederbragt (1990) have shown that the sporadic occurrence is real throughout the Turonian to Maastrichtian and not an artifact of selective size analysis. Similarly, Cenomanian–Turonian and Maastrichtian–Paleocene studies of small-sized species have revealed a sporadic record of *Guembelitra* abundances (Leckie, 1987; Koutsoukos, 1994, 1996; Keller et al., 2001; Abramovich et al., 1998; Abramovich and Keller, 2002; Adatte et al., 2002; Keller, 2003, 2004).

*Guembelitra* populations are best known from the aftermath of the Cretaceous–Tertiary (K–T) mass

extinction where no species larger than 100  $\mu\text{m}$  in size survived and the immediate survivors and newly evolved species are frequently smaller than 63  $\mu\text{m}$  (Koutsoukos, 1996; Keller et al., 1995, 2001). *Guembelitra* species are the sole Cretaceous long-term survivors and the sole group that thrived in the aftermath of the mass extinction when they formed major plankton blooms in middle to low latitudes that earned them the label of disaster opportunist species (Fig. 1). The frequent association of *Guembelitra* blooms with shallow water environments has suggested that they may be restricted to continental margins or upwelling areas (Leckie, 1987; Kroon and Nederbragt, 1990; D'Hondt and Keller, 1991; Koutsoukos, 1994, 1996; Keller et al., 2002), but no specific environmental conditions have been identified to date (e.g., salinity, temperature, oxygen and nutrients).

During the last decade, systematic statistical documentation of the small-sized species in upper Maastrichtian and lower Danian sediments in the world's oceans across latitudes and from shallow marginal seas to the open ocean has yielded an extensive dataset for *Guembelitra* and its environmental asso-

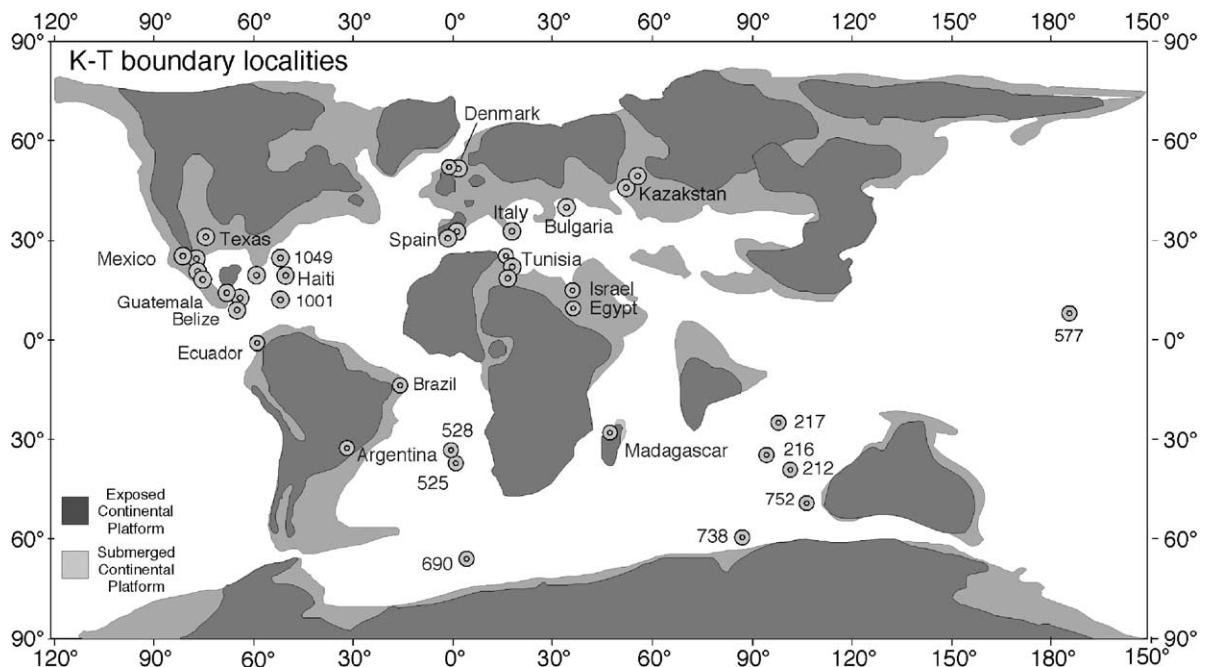


Fig. 1. Paleolocations of K–T boundary sections. Continental reconstruction after Denham and Scotese (1987) and MacLeod and Keller (1991).

ciations, along with the dominant small low-oxygen-tolerant biserial species (e.g., *Heterohelix globulosa*, *Heterohelix dentata*, *Heterohelix navarroensis*, *Zeauvigerina waiparaensis*, *Woodringina hornerstownensis*, *Woodringina claytonensis*, *Chiloguembelina midwayensis*). Quantitative records now exist from over 30 localities worldwide and spanning low to high latitudes (Fig. 1). However, most of the sections are concentrated in Central America and eastern Tethys (e.g., Tunisia, Egypt, Israel, Spain and Italy). High-latitude sections are scarce, but provide critical information on the nature and extent of the environmental crises conditions. No data are available for a vast area of the Pacific Ocean. In addition, no published reports with statistical data are known to us from onshore or offshore India, a critical area to test the biotic stress factor of volcanism.

Here, we review the *Guembelitra* blooms and low-oxygen-tolerant small biserial heterohelid species, species richness and stable isotope records from the most representative sections at various localities worldwide. This review is not intended to be comprehensive (not all records of a given locality are shown or discussed) but to highlight the most critical records, the faunal similarities and differences and the enigma of impact and volcanism signals in upper Maastrichtian, K–T boundary and lower Danian deposits. For complete faunal records and descriptions of each locality, the reader is referred to the original publications cited. This review, focusing on ecological generalist species, provides a better understanding of the foraminiferal response to biotic crises conditions and the pathway to recovery. We present a model of the biotic response to environmental perturbation that is consistent with biotic crises due to impacts or volcanism.

## 2. Dataset and methods

The data used in this study are from over 30 localities (Fig. 1) and from various published sources (Table 1). Although the statistical data was gathered over time by five different workers (e.g., G. Keller, A. Pardo, S. Abramovich, J.G. Lopez-Oliva and I. Canudo), all were trained by Keller to use the same method for quantitative data analyses and therefore the data are standardized and comparable. The fact

that similar oceanographic signals are evident in all sections testifies to the reality of an external biotic effect, rather than sample bias. The similarity in the results also indicates that there is no significant counting bias, or preservational bias unless indicated by the workers, and that any of the datasets can be reproduced using the same sample processing and analytical methods. The sample set can also be expanded by any worker with the addition of new localities for a more complete global geographic coverage, provided the same analytical methods are used. For this reason, a detailed description of the methods is given below.

About 100–200 g of sediment from each sampled interval is placed in separate heavy plastic bags and is crushed with a hammer. Sediments from each sample are then placed in beakers and labeled. Water or a dilute H<sub>2</sub>O<sub>2</sub> (3–10%) solution is added to the beakers and stirred. The samples are left to soak overnight or for several days with occasional stirring. When the sediment is disaggregated, the samples are washed through 38- and 63- $\mu$ m screen sieves. When the samples are cleaned of the clay fraction (as shown by clean water pouring through the sieve), they are decanted into a cone of filter paper which is then placed into its original labeled beaker and then placed into the oven to dry at 50 °C. (Any higher temperature will alter the test carbonate and make it useless for stable isotope analysis.) When the samples are dry, they are placed in glass vials and are labeled for analysis.

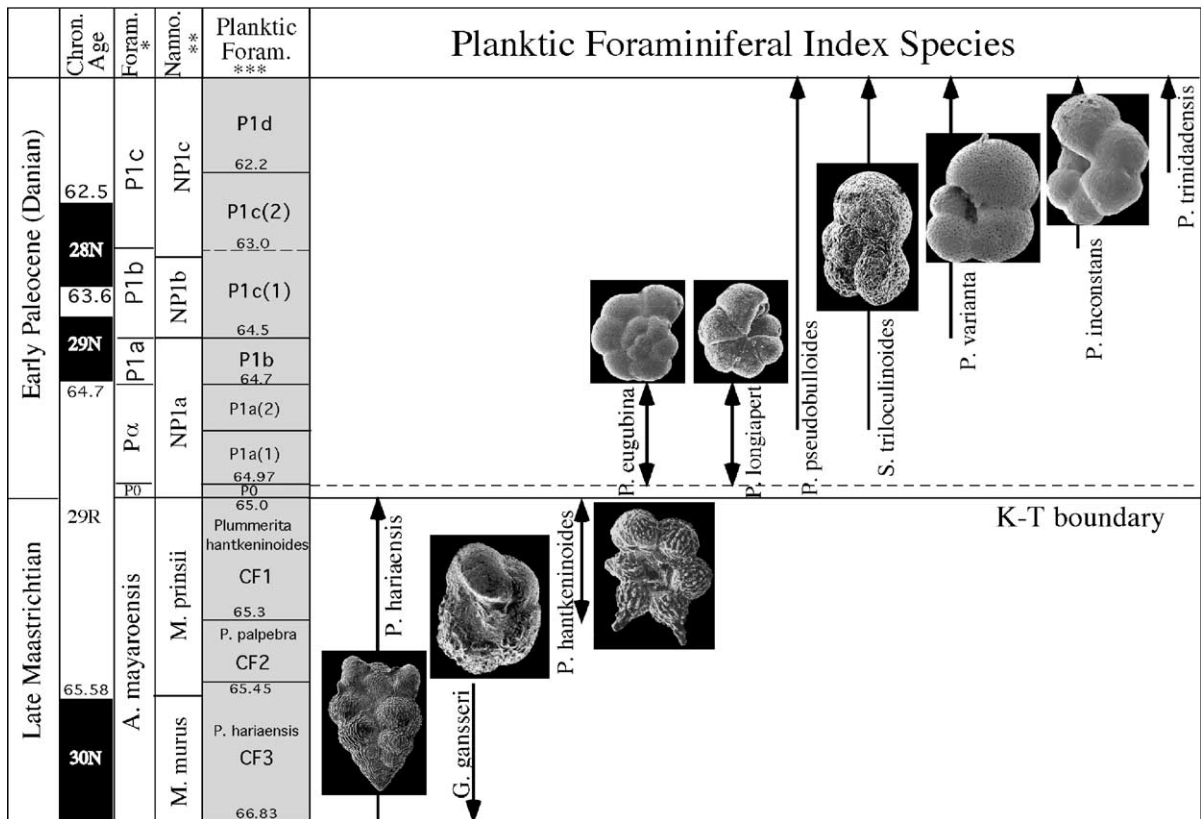
Statistical counts of planktic foraminiferal species are based on random sample splits of the >63- $\mu$ m size fraction (using an Otto microsampler) of about 150–250 specimens (average of 5–10 species) or 300 specimens for more diverse assemblages (Buzas, 1990). In clayey sediments, where species morphologies may be particularly small (dwarfed), the 38- to 100- $\mu$ m-size fraction is also analyzed to obtain a more accurate estimate of small species. The sample split (aliquot) is spread evenly on a picking tray and is examined under the microscope to evaluate that sufficient specimens are present for the statistical count. All specimens of this aliquot are counted, picked and mounted for a permanent record on microslides and archived. Because *Guembelitra* dominated assemblages reflect high-stress environments, species diversity tends to be very low and

Table 1  
K–T sections with quantitative planktic foraminifera databases

Location/Site	Section	Paleoenvironment	Literature used
<i>Tethys shelf and continental margin settings</i>			
Tunisia	El Kef	outer neritic–upper bathyal	Keller, 1988a,b, 1992; Keller and Lindinger, 1989; Keller et al., 1995, 2002; Speijer and van der Zwaan, 1996; Culver, 2003
	Elles	middle neritic	Abramovich and Keller, 2002
	Seldja	inner neritic (littoral)	Keller et al., 1998, 2002; Culver, 2003
Egypt	Qreiya	middle neritic	Luger, 1988; Keller, 2002; Tantawy, 2003;
Israel	Negev	middle-upper bathyal	Keller and Benjamini, 1991; Magaritz et al., 1992; Speijer and van der Zwaan, 1994; Abramovich et al., 1998; Keller, 1992, 2004
Spain	Agost	outer neritic, upper-middle bathyal	Canudo et al., 1991; Pardo et al., 1996; Pardo, 1999; Alegret et al., 2003
Italy	Erto	outer neritic-upper bathyal	Luciani, 1997
Southern USA	Brazos, TX	middle-inner neritic	Keller, 1989, 1992; Liu and Olsson, 1992; Barrera and Keller, 1994; Culver, 2003
Mexico	El Mimbrial and others	lower, middle, upper bathyal	Keller et al., 1994, 1997, 2002, 2003; Lopez Oliva and Keller, 1996; Alegret et al., 2001, 2002; Stinnesbeck et al., 2002; Alegret and Thomas, 2001
Haiti	Beloc	upper bathyal	Keller et al., 2001; Stueben et al., 2002
<i>Northern Tethys and high latitudes</i>			
Bulgaria	Bjala	upper bathyal	Adate et al., 2002
Kazakistan	Koshak	shallow epicontinental sea	Oberhänsli et al., 1998; Pardo, 1999; Pardo et al., 1999
	Kyzylsai	shallow epicontinental sea	Pardo, 1999
Denmark	Nye Klov	inner to middle neritic	Schmitz et al., 1992; Keller et al., 1993; Barrera and Keller, 1994
<i>Southern middle latitude</i>			
DSDP Sites 525 and 528		bathyal	Widmark and Malmgren, 1992; D'Hondt and Keller, 1991; Li and Keller, 1998a,b; Abramovich and Keller, 2003
Madagascar	Amboanio	outer neritic	Abramovich et al., 2002
Ninetyeast Ridge DSDP Site 216		volcanic ridge, subsidence, inner to outer neritic	Thompson et al., 1974; Moore et al., 1974; McGowran, 1974; Keller, 2003
<i>High-latitude Southern Ocean</i>			
ODP Sites 738 and 690		lower bathyal	Thomas, 1990a,b; Keller, 1993; Barrera and Keller, 1994

most other species, relatively rare, requiring that all specimens of the entire sample residues, may have to be picked for adequate statistical counts. Bias introduced by preservational effects (dissolution and breakage) can usually be identified based on the number of broken specimens. Because *Guembelitra* tend to be among the most fragile species, they are usually present in well-preserved assemblages, although good statistical data can be obtained from more indurated sediments, where foraminiferal tests are recrystallized and infilled with micritic carbonate which makes them more resistant to breakage and solution effects. We use species richness or the number of species present in a sample, as the simplest measure of diversity and an important measure of fluctuations in the ecosystem.

In this study, the high-resolution biozonation developed by Keller et al. (1995), Pardo et al. (1996) and Li and Keller (1998a) is used as shown in Fig. 2. Apart from first and last appearances of index species, biozones can be recognized by assemblage compositions and species abundances, particularly those of *Gansserina gansseri*, *Plummerita hantkeninoides* and *Parvularugoglobigerina eugubina* and *Parvularugoglobigerina longiapertura* (Fig. 3). In addition, there is the decrease in globotruncanids during the latest Maastrichtian and the mass extinction of all tropical and subtropical species at the K–T boundary. In addition to the mass extinction of planktic foraminifera, the K–T boundary can be identified by the evolution of the first Tertiary species, a lithological change usually marked by organic-rich clay deposi-



\*Berggren *et al.*, 1995; \*\*Tantawy, 2003; \*\*\*Keller *et al.*, 1995; Pardo *et al.*, 1996; Li and Keller, 1998a

Fig. 2. High-resolution biozonation of Keller *et al.* (1995) and Li and Keller (1998b) used in this study and illustration of planktic foraminiferal index species for biozones. The biozonation scheme by Berggren *et al.* (1995) is given for comparison. Calcareous nannofossil zones after Tantawy (2003). CF, Cretaceous Foraminifera).

tion, the presence of a thin (3–4 mm) red clay layer enriched in Ir and sometimes altered spherules and the presence of a negative excursion in the  $\delta^{13}\text{C}$  record.

### 3. Upper Maastrichtian and K–T boundary records

#### 3.1. Tethys shelf and continental margin settings

##### 3.1.1. Tunisia

The most frequently studied record is the global K–T stratotype section (GSSP) at El Kef, Tunisia. During the upper Maastrichtian, sediment deposition occurred in an outer shelf to upper slope environment (300- to 500-m depth), which shallowed to an outer to middle neritic environment in the lower Danian (Keller, 1988a, 1992; Speijer and van der Zwaan, 1996).

There is some disagreement as to the nature of sea level changes during the Maastrichtian as reviewed in Culver (2003), although this does not affect the planktonic assemblages. El Kef contains typical high-diversity upper Maastrichtian planktic foraminiferal assemblages averaging 55 species during the last 300–500 kyr of the Cretaceous (Keller *et al.*, 1995, 2002). The K–T boundary is characterized by the extinction of all tropical and subtropical species, survivorship of about a dozen ecological generalists at least for some time into the early Danian and the onset of the *Guembelitra* bloom (Fig. 4). A major negative excursion in  $\delta^{13}\text{C}$  of surface waters marks the boundary event and reflects a crash in plankton productivity, whereas  $\delta^{18}\text{O}$  values indicate climate cooling. The boundary clay is very high in total

## Age Control: Planktic Foraminifera

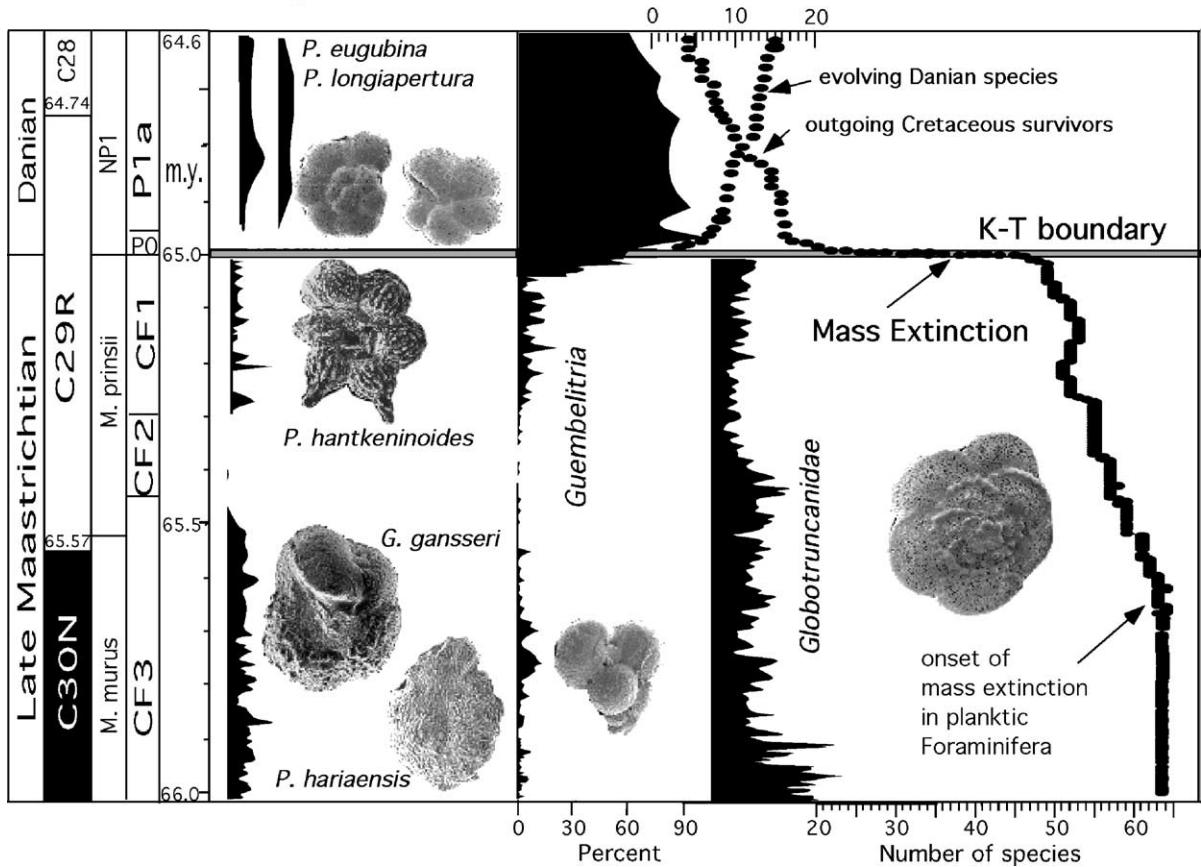


Fig. 3. Age control of the upper Maastrichtian and lower Danian by means of planktic foraminifera index species and species richness based on the K–T stratotype section at El Kef and Elles, Tunisia.

organic content (TOC, Keller and Lindinger, 1989). The *Guembelitra* bloom lasted for at least the first 100 kyr of the Tertiary, during which time, nearly all other Cretaceous survivors went extinct or became very rare. The first Tertiary species [e.g., *Globoconusa daubjergensis*, *Parvularugoglobigerina eugubina*, *P. longiapertura*, *P. extensa* (= *G. conusa*) and *Woodringina hornerstownensis*; Fig. 2] evolved immediately after the K–T boundary event, but failed to reach significant population sizes during the *Guembelitra* bloom (review in Keller et al., 2002).

The upper Maastrichtian at El Kef is dominated by small biserial species (*Heterohelix globulosa*, *Heterohelix dentata*, *Heterohelix navarroensis* (55–60%)), but *Guembelitra* are relatively rare, although increasing in the last meter below the K–T boundary. At the

nearby Elles section, three minor but distinct *Guembelitra* peaks (~10%) are identified in the upper Maastrichtian (Abramovich and Keller, 2002).

El Kef and Elles sections have the most expanded sedimentary records for the upper Maastrichtian and lower Danian known to date. The K–T boundary clay in these sections is 50- to 70-cm thick, as compared with a few centimeters in most other “complete” sections. The lower Danian *Guembelitra* blooms are therefore strongly condensed in most other marine sections including the eastern Tethys of Israel and Egypt.

The biotic effects of the K–T boundary transition in shallow water environments can be observed at Seldja in southern Tunisia at the margin of the shallow Saharan platform (Keller et al., 1998). At this locality,

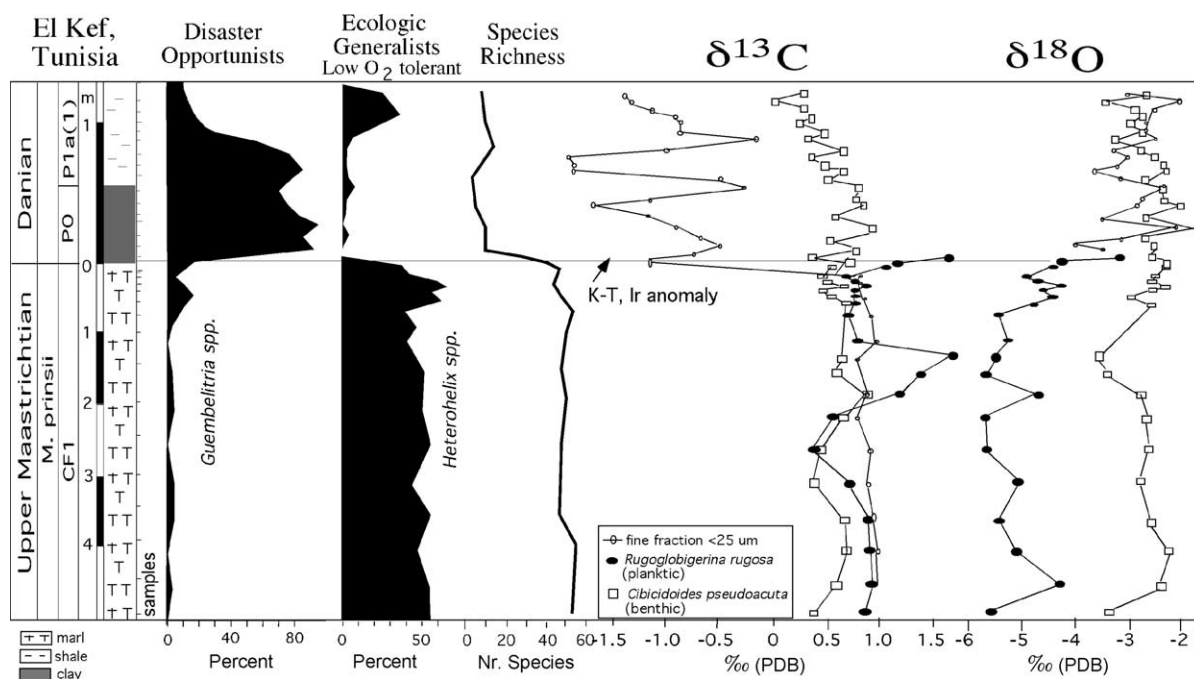


Fig. 4. Relative abundances of disaster opportunists and low oxygen tolerant ecological generalists, species richness and stable isotopes at the El Kef stratotype section in Tunisia. Data from Keller et al., 1995, 2002 and Keller and Lindinger, 1989.

deposition occurred in an inner neritic (littoral) environment and the section is marked by erosion at the K–T boundary and in the lower Danian (zone Plb and lower Plc missing; Keller et al., 1998; Fig. 5). *Guembelitra* blooms in the upper Maastrichtian zone, CF1 average >20% and >50%. At times of low *Guembelitra* abundances, *Heterohelix* species (*Heterohelix globulosa*, *Heterohelix dentata* and *Heterohelix navarroensis*) dominate, similar to the deeper sections at El Kef and Elles (Fig. 5). Just below the K–T boundary and in the early Danian zone Pla, *Guembelitra* blooms dominate to the exclusion of all other species. Species richness is very low with 15–20 species during the upper Maastrichtian and 1–3 species in the lower Danian zone Pla. Bulk rock δ<sup>13</sup>C data show no negative excursion, possibly because benthic foraminifera are abundant and the values reflect their signal. Stable isotopes, clay mineralogy and benthic foraminifera indicate shallowing to a nearshore hyposaline and hypoxic environment during the last 100–200 kyr of the Maastrichtian and a lower Danian environment of low oxygen, low salinity, high rainfall, accompanied by high erosion

and terrigenous influx (Keller et al., 1998). The *Guembelitra* blooms at Seldja may thus represent primarily the local high-stress environment.

### 3.1.2. Egypt

Sediment deposition during the upper Maastrichtian to lower Danian at Qreiya in central Egypt occurred in a middle neritic environment, similar to Elles, Tunisia (Luger, 1988; Keller et al., 2002). However, the faunal assemblages are completely different, marking strongly contrasting paleoenvironments (Keller, 2002; Keller et al., 2002; Tantawy, 2003). The K–T boundary is marked by a thin clay layer and Ir anomaly above a bioturbated marly shale with an erosional surface. Hiatuses also reduced early Danian zones Pla, Plb and Plc (Fig. 6). *Guembelitra* blooms are present in zones Pla and Plc, as also observed at El Kef (Keller, 1988a) and other Tethys sections. What sets Qreiya apart from other K–T sections are the *Guembelitra* blooms (50–70%) in the upper Maastrichtian zones CF3 and CF1. At times of low *Guembelitra* abundances, the small *Heterohelix navarroensis* dominates. Species richness is also

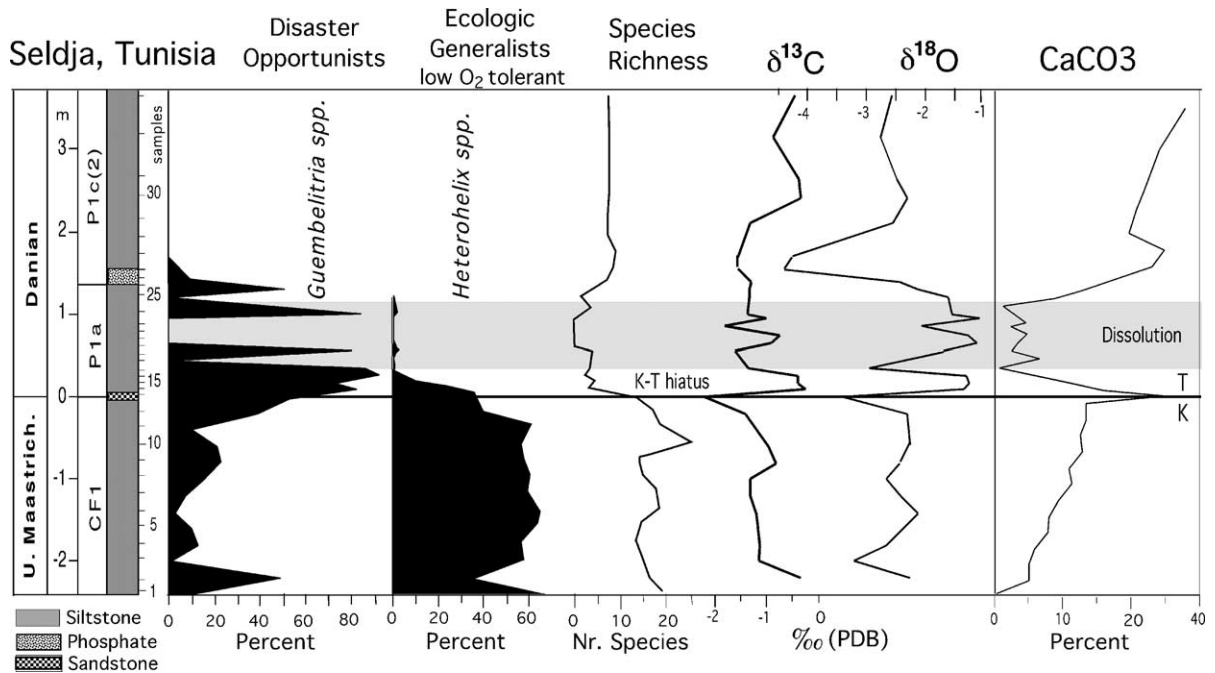


Fig. 5. Relative abundances of disaster opportunists and low oxygen tolerant ecological generalists, species richness and stable isotopes at Seldja in southern Tunisia. Data from Keller et al., 1998.

very low (25–30 species) compared with similar paleodepths at Elles (40–45 species). The *Guembelitria* blooms at Qreiya indicate that the late Maastrichtian of Egypt experienced similar high stress conditions as the lower Danian.  $\delta^{13}\text{C}$  data indicate only a minor (0.7‰) negative excursion at the K–T boundary, suggesting that primary productivity was already reduced during the upper Maastrichtian, as also indicated by the low species richness, *Guembelitria* blooms and small *Heterohelix* species. Low primary productivity is also indicated by the upper Maastrichtian reversal in the surface-to-deep  $\delta^{13}\text{C}$  gradient, which is usually associated with the K–T boundary productivity crash.

### 3.1.3. Israel

The high-stress pattern observed in central Egypt is also recognized in sections from the Negev of Israel, which were deposited in deeper upper slope environments (Speijer and van der Zwaan, 1994; Abramovich et al., 1998; Keller, 2004). At the Mishor Rotem section in the Negev, the K–T boundary is marked by the characteristic thin (3–4 mm) red clay layer

enriched in iridium. A reduced zone Pla overlies the boundary clay (Fig. 7). Reworked Cretaceous species are common in the basal Danian throughout the Negev (Keller and Benjamini, 1991) and indicate erosion and transport. The *Guembelitria* bloom is reduced possibly due to preservational bias. In several other K–T sequences examined in the Negev, the lower Danian zones Pla, Plb and Plc are reduced due to hiatuses. However, a major *Guembelitria* bloom is recognized in zone Plc, similar to Qreiya and El Kef, as noted by Keller and Benjamini (1991) and Magaritz et al. (1992).

In the upper Maastrichtian, three distinct *Guembelitria* blooms are present, although they are less severe than at Qreiya as suggested by the lower percent abundance (Fig. 7). This is also indicated by the high (50–60%, although fluctuating) abundance of small *Heterohelix* species (mostly *Heterohelix globulosa*), which is more similar to El Kef than Qreiya. Species richness, however, is relatively low at 30–35 species but is still higher than at Qreiya. Israel thus experienced increased stress during the upper Maastrichtian but not as severe as Egypt.



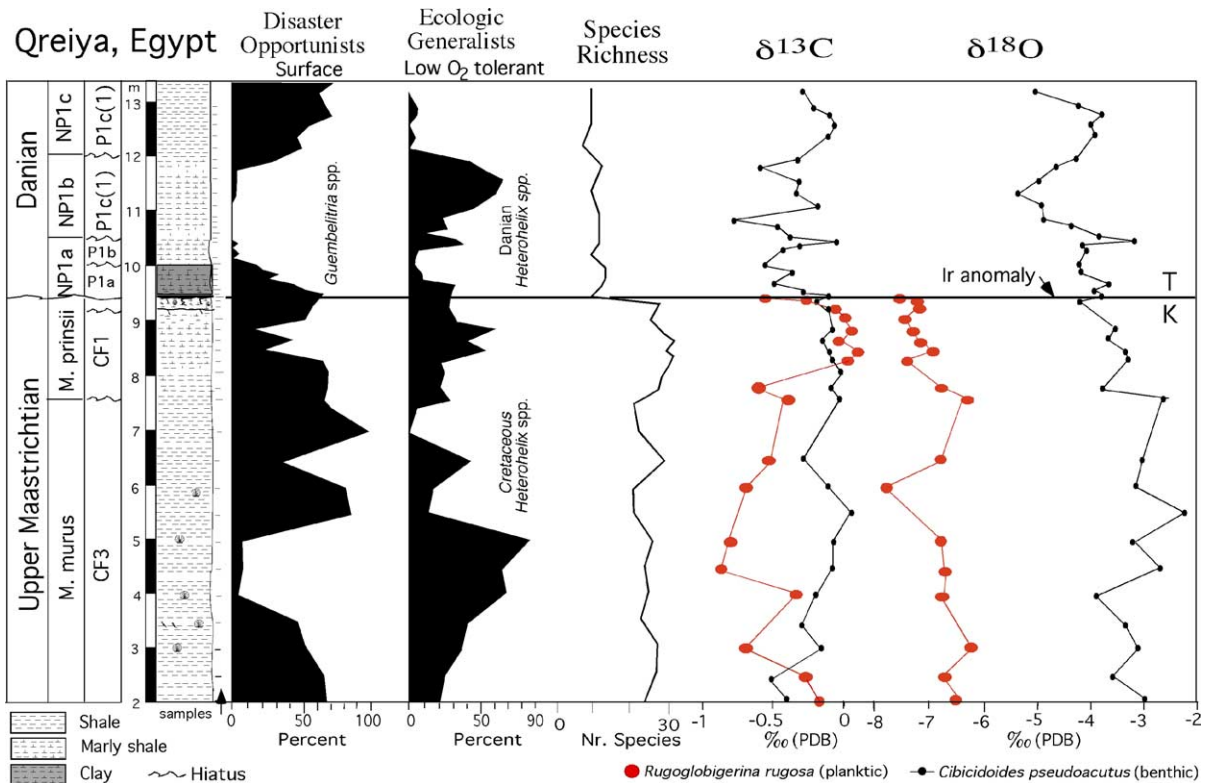


Fig. 6. Relative abundances of disaster opportunists and low oxygen tolerant ecological generalists, species richness and stable isotopes at Qreiya in central Egypt. Data from Keller, 2002 and Keller et al., 2002.

### 3.1.4. Spain and Italy

Condensed K–T transitions are also observed at Agost and Caravaca in southern Spain and Erto in northern Italy (Luciani, 1997) which were deposited in outer shelf and slope settings similar to sections in Israel and El Kef. At Agost, Alegret et al. (2003) interpreted the depositional environment as upper bathyal deepening to middle bathyal by K–T time and remaining deep into the lower Danian, whereas Pardo et al. (1996) interpreted an upper bathyal to outer neritic depth.

At the Spanish and Italian K–T localities, the boundary clay (zone P0 and Ir anomaly) is very thin (2–5 cm) and the basal Danian contains abundant reworked Cretaceous species that mask the *Guembelitra* bloom mimicking a delayed bloom in the lower part of zone P1a as shown for Agost (Fig. 8, Canudo et al., 1991; Pardo et al., 1996) and peak abundance of heterohellicids at Erto (Luciani, 1997). In general, *Heterohelix* species average 50% at Agost and 50–

60% at Erto through the upper Maastrichtian. At Agost, *Heterohelix* decreases to less than 10% in the lower Danian similar to El Kef and Elles, whereas at Erto, they gradually decrease through P1a. No isotopic analyses of the heterohellicids in the Danian of Erto have been done to evaluate, whether this unusual abundance is due to reworking or to survivorship.

### 3.1.5. Southern USA

The K–T boundary transition in Texas and Alabama occurred in relatively shallow middle to inner neritic environments, ranging from 50- to 150-m depth (see review in Culver, 2003). The K–T boundary clay zone P0 and Ir anomaly and other lower Danian zones are usually present and faunal assemblages are exceptionally well preserved (Keller, 1989; Liu and Olsson, 1992). At Brazos, Texas, a thin bioturbated clastic deposit with some spherules overlies an unconformity and major hiatus 25 cm below the K–T boundary and Ir anomaly, as discussed in

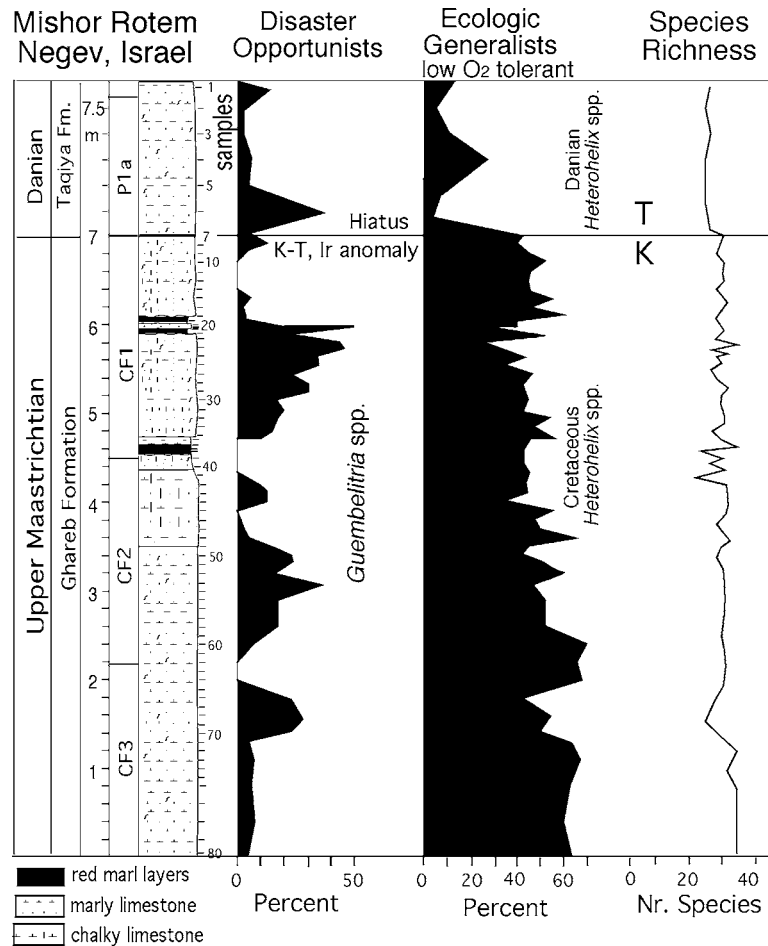


Fig. 7. Relative abundances of disaster opportunists, low oxygen tolerant ecological generalists and species richness at the Mishor Rotem section of the Negev, Israel. Data from Keller, 2004.

Keller (1989) (Fig. 9, Yancey, 1996). Species richness is low in this shallow water environment and fluctuates between 20 and 30 species during the upper Maastrichtian and about 10 species in the lower Danian. *Heterohelix globulosa* thrived averaging 60% during the upper Maastrichtian and continued to thrive into zone P0 when they rapidly decreased 20 cm above the K–T boundary and into zone P1a. *Guembelitria* are common (20%) through the upper Maastrichtian and reach 50–60% after the terminal decrease in *Heterohelix* species in the upper zone P0. Stable isotope analysis of *H. globulosa* mirrors this abundance trend with the 3‰ negative  $\delta^{13}\text{C}$  shift that marks the primary productivity crash at the K–T

transition in low to middle latitudes globally (Fig. 9).  $\delta^{18}\text{O}$  values suggest warmer waters in the lower Danian, although this may be due to the shallow water environment and salinity effects (Barrera and Keller, 1990). The Brazos section is unusual in the gradual 3‰ negative  $\delta^{13}\text{C}$  excursion at the K–T boundary, the corresponding delayed abundance decrease in *H. globulosa* and delayed onset of the *Guembelitria* bloom. Stable isotope measurements of *H. globulosa* species clearly indicate that this group survived the K–T mass extinction by adapting to the changing environment but was ultimately driven to extinction in the lower Danian by the newly evolving species.

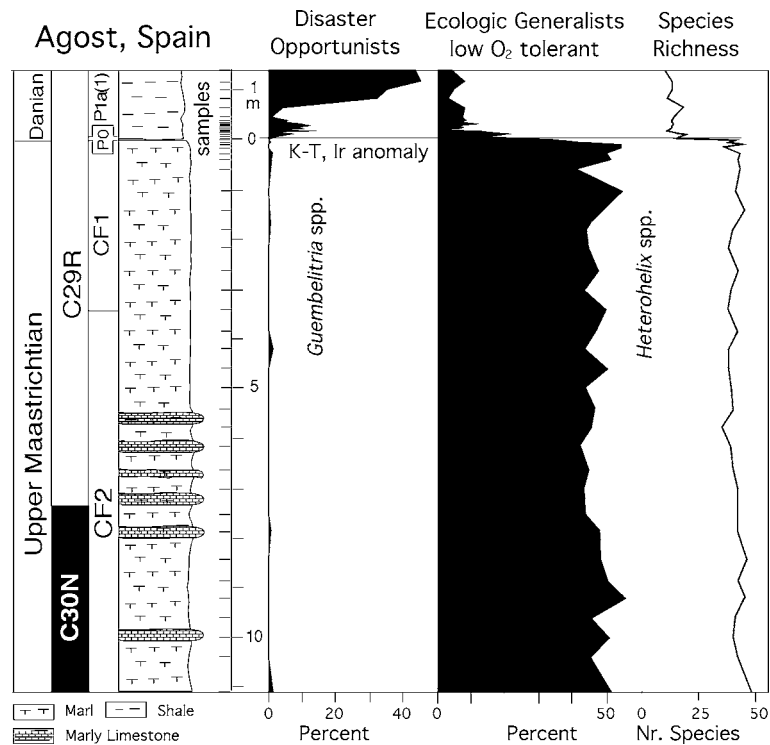


Fig. 8. Relative abundances of disaster opportunists, low oxygen tolerant ecological generalists and species richness at Agost, Spain. Data from Canudo et al., 1991 and Pardo et al., 1996.

### 3.1.6. Central America

Central American K–T sections are unique in that ejecta from the Chicxulub impact (e.g., glass spherule layers and impact breccia) are interbedded in marls of upper Maastrichtian and lower Danian age, raising doubt as to a K–T age for this impact event (review in Keller et al., 2003). At El Mimbral (Fig. 10), and over three dozen similar sections across northeastern Mexico, the K–T boundary is above a bioturbated clastic deposit that ranges from 10-cm to 8-m thick and generally overlies a glass spherule layer that ranges from 1 cm to more than 1 m in thickness (e.g., Mimbral, Lajilla, La Sierrita, El Penon, Mesa Juan Perez; Smit et al., 1992; Keller et al., 1994, 1997; Lopez Oliva and Keller, 1996; Stinnesbeck et al., 2002). Additional glass spherule layers are present in pelagic marls between 2 and 10 m below the K–T boundary in numerous outcrops (Keller et al., 2002). The stratigraphically oldest ejecta layer near the base of zone CF1 appears to be the original deposit, with subsequent layers transported from shelf areas and

redeposited on the deeper slope, possibly at times of lower sea levels.

Paleodepth of the NE Mexico K–T sections was estimated as upper bathyal by Smit et al. (1992) and Keller et al. (1994) for the Mimbral section. Alegret et al. (2001, 2002) documented paleodepths ranging from lower bathyal to middle and upper bathyal based on benthic foraminifera, with paleodepth generally shallowing to the north. Late Maastrichtian planktic foraminiferal assemblages are dominated by *H. globulosa* and *Heterohelix navarroensis* although the erratic fluctuations evident at Mimbral are due to preservational effects (Fig. 10). In well-preserved Tethyan assemblages, heterohelicids average 50–60% of the total planktic foraminiferal fauna during the late Maastrichtian (e.g., El Kef, Elles, Agost, Erto and Mishor Rotem). Poor preservation may also account for the absence of *Guembelitra* in the Maastrichtian. At Mimbral and La Sierrita, the K–T boundary is marked by a thin red layer and Ir anomaly. Reworked Maastrichtian species are com-

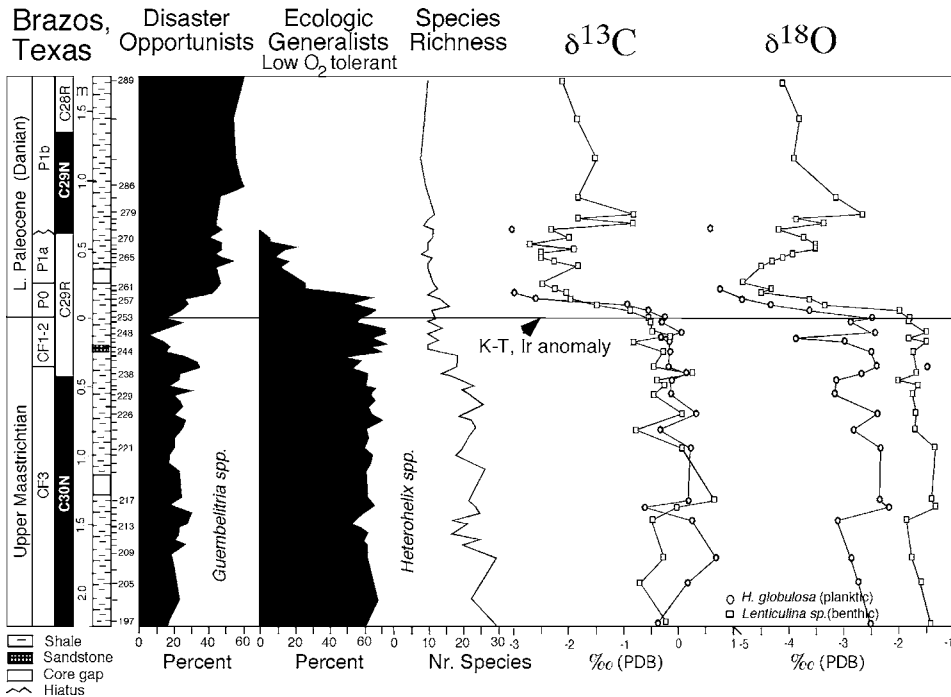


Fig. 9. Relative abundances of disaster opportunists and low oxygen tolerant ecological generalists, species richness and stable isotopes at Brazos, Texas. Data from Keller, 1989 and Barrera and Keller, 1990.

mon in the basal Danian at Mimbral, which accounts for the high heterohelid abundance and weak *Guembeltrix* signals.

In central and southern Mexico, Guatemala, Belize and Haiti, early Danian sediments overlie pelagic sediments or breccias of carbonate platform origin that are interpreted as impact breccias (Smit, 1999), or collapse breccias (Stinnesbeck et al., 1997; Fourcade et al., 1998). The Danian sediments of zone Pla are generally interbedded with spherule deposits that may be reworked from the upper Maastrichtian zone CF1 spherule deposits observed in northeastern Mexico (see review in Keller et al., 2003). For example, at Coxquihui in central Mexico, the clastic deposit below the K–T boundary is only 5-cm thick with a 2-cm-thick glass spherule layer above it. However, 20 cm above the K–T boundary is a 60-cm-thick spherule layer followed by an Ir anomaly and *Guembeltrix* bloom well within zone Pla (Stinnesbeck et al., 2002).

In Haiti, the glass spherule layer disconformably overlies Maastrichtian limestone followed by spher-

ules interbedded in marly and bioclastic limestones of zone Pla (Fig. 11). Above the spherule deposits in Pla is a red shale layer with an Ir anomaly of chondritic origin that indicates a lower Danian impact (Keller et al., 2001; Stueben et al., 2002). A major *Guembeltrix* bloom (>70%, Fig. 11) is associated with this interval. Similarly, at Bochil, southern Mexico, and at Actela, Guatemala, spherule deposits are interbedded in the lower parts of zone Pla and an Ir anomaly is present above it associated with a *Guembeltrix* bloom (review in Keller et al., 2003). An early Danian zone Pla Ir anomaly was first observed in the southern ocean ODP Site 752 by Michel et al. (1991).

### 3.1.7. *Tethys ocean-deep sea*

In the deep sea, early Danian sediments are always condensed, with reduced thickness of zone Pla overlying Maastrichtian sediments in the most complete sequences (e.g., Sites 577, 528, 1049, 1001; MacLeod and Keller, 1991; Norris et al., 2000; Huber et al., 2002; Keller et al., 2003), or

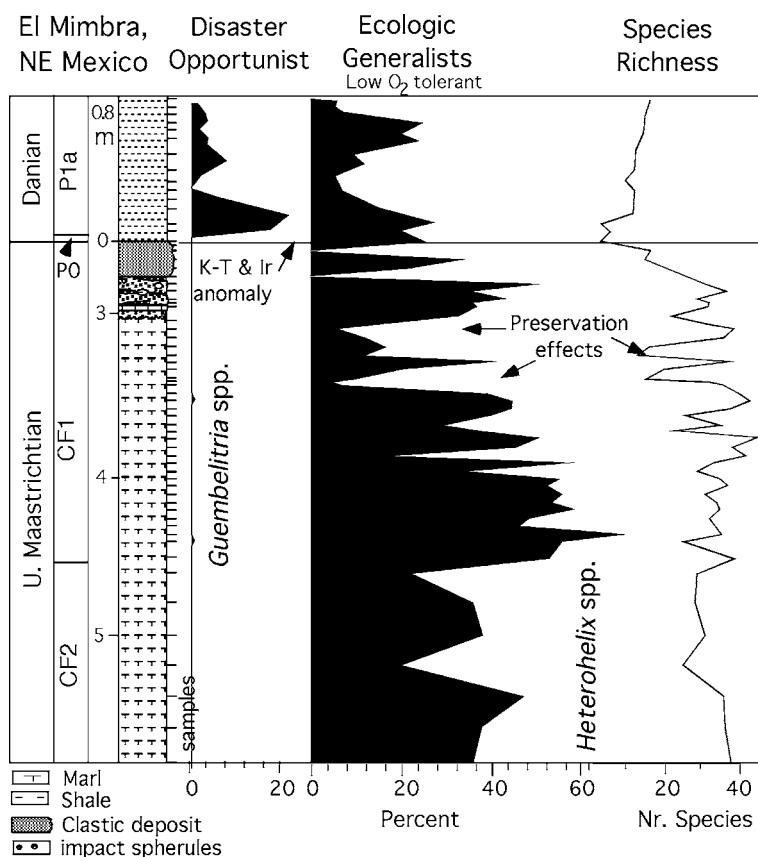


Fig. 10. Relative abundances of disaster opportunists, low oxygen tolerant ecological generalists and species richness at El Mimbral in northeastern Mexico. Data from Keller et al., 1994 and Lopez Oliva and Keller, 1996.

major hiatuses with zones Pla, Plb and at least part of Plc missing (e.g., Sites, 525, 690; Keller, 1993; D'Hondt and Keller, 1991). In the low-latitude Tethys, there is little quantitative data available for zone Pla *Guembelitra* blooms, except for Site 577 where *Guembelitra* dominates (>60%) in zone Pla and into Plb (D'Hondt and Keller, 1991). Down-core contamination prevents statistical estimates of species abundances in these upper Maastrichtian sediments.

### 3.2. Northern Tethys and high latitudes

There are relatively few sections with quantitative data from the northern Tethys (Fig. 1) and they all show very different faunal assemblage compositions and reduced  $\delta^{13}\text{C}$  excursions from those of the lower

Tethys Ocean, suggesting latitudinal variations in biotic effects of stress conditions.

#### 3.2.1. Bulgaria

An unusual faunal assemblage is present in an upper slope environment at Bjala, Bulgaria, where *Guembelitra* (mostly *Guembelitra dammula* and *Guembelitra cretacea*; Plate 1) dominated (60–80%) in the upper Maastrichtian, and *Heterohelix* species are a minor component (20%, Fig. 12; Rögle et al., 1996; Adatte et al., 2002). Nevertheless, species richness is high averaging 40 species. At the K–T boundary, *G. dammula* nearly disappeared and the usual *G. cretacea* blooms mark zone Pla. Although a thin boundary clay and Ir anomaly are present, zone Pla is reduced and incomplete with zone Plb missing. This may explain the relatively low abundance (50%)

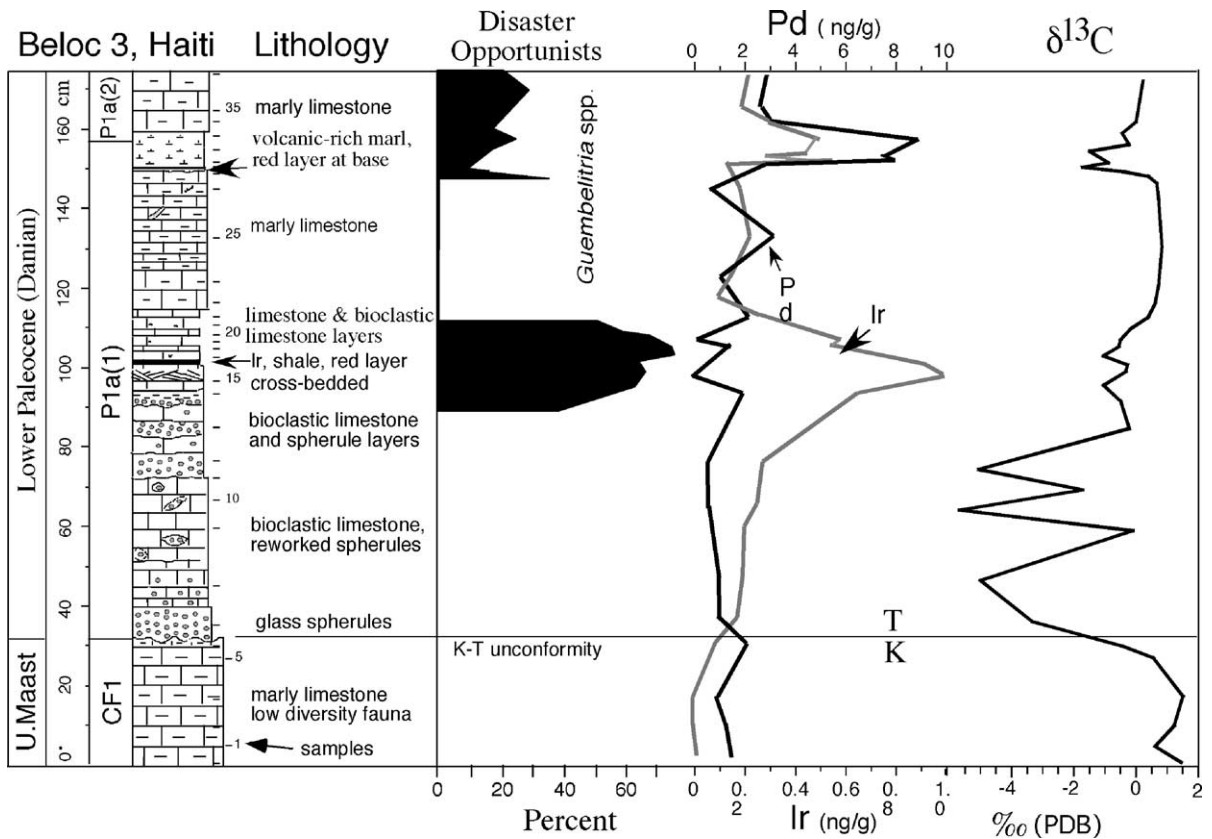


Fig. 11. Relative abundances of disaster opportunists, carbon isotopes, Ir and Pd anomalies in the early Danian at Beloc, Haiti. Data from Keller et al., 2001 and Stueben et al., 2002.

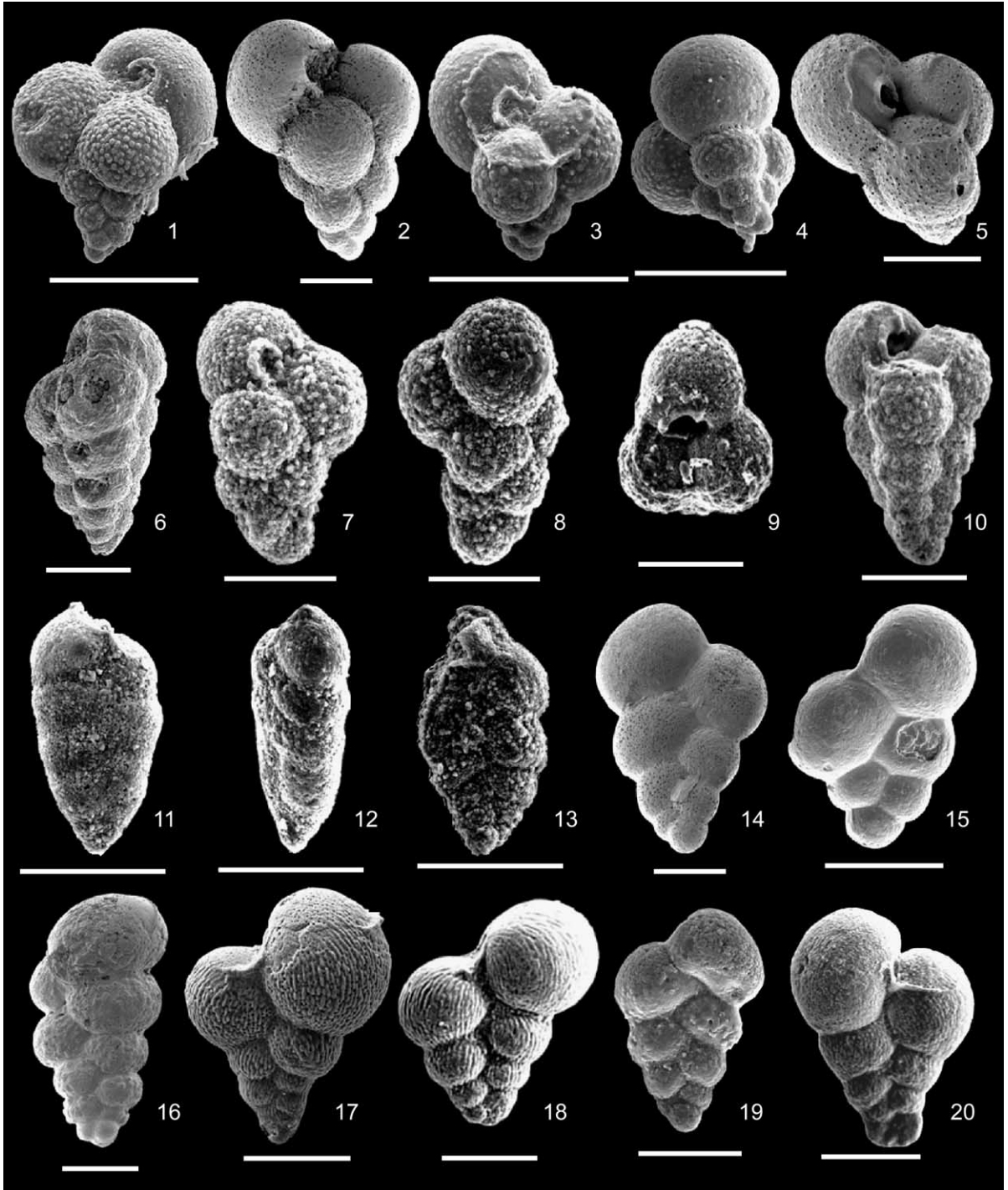
of the *Guembelitra* bloom in Pla.  $\delta^{13}\text{C}$  values are also unusual in that the K–T negative shift is only 0.5‰, as compared with 2–3‰ at El Kef and elsewhere. The reduced  $\delta^{13}\text{C}$  shift is consistent with other high-latitude sequences and suggests a diminished effect into higher latitudes.  $\delta^{18}\text{O}$  values indicate

an early Danian cooling as elsewhere in normal marine environments.

### 3.2.2. Kazakstan

The Koshak and Kyzylsai K–T sections in Kazakstan reveal typical high-latitude low-diversity faunal

Plate 1. Scanning electron micrographs of ecological generalists that mark the first and second recovery phases of biotic crises conditions. Phase 1 is characterized by the disaster opportunist *Guembelitra* species (Figs. 1–10), and phase 2 by low-oxygen-tolerant heterohelicids (Figs. 11–20). All disaster and low-oxygen-tolerant generalist species are thin-walled and lack surface ornamentation. (1) *Guembelitra cretacea* (Cushman), El Kef, Tunisia. Zone Pla, scale bar = 100  $\mu\text{m}$ . (2) *Guembelitra cretacea* (Cushman), Qreiya, Egypt. Zone CF1, scale bar = 50  $\mu\text{m}$ . (3–4) *Guembelitra trifolia* (Morozova), El Kef, Tunisia. Zone Pla, scale bar = 100  $\mu\text{m}$ . (5) *Guembelitra trifolia* (Morozova), Qreiya, Egypt. Zone CF1, scale bar = 50  $\mu\text{m}$ . (6) *Guembelitra dammula* (Voloshina), Amboanio, Madagascar. Zone CF1-2, scale bar = 50  $\mu\text{m}$ . (7–8) *Guembelitra irregularis* (Morozova), Koshak, Kazakstan. Zone CF1, scale bar = 50  $\mu\text{m}$ . (9–10) *Guembelitra danica* (Hofker), Koshak, Kazakstan. Zone CF1, scale bar = 50  $\mu\text{m}$ . (11–12) *Zeauvigerina waiparaensis* (Jenkins), Koshak, Kazakstan. Zone CF1, scale bar = 50  $\mu\text{m}$ . (13) *Zeauvigerina parri* (Finlay), Koshak, Kazakstan. Zone CF1, scale bar = 50  $\mu\text{m}$ . (14) *Chiloguembelina midwayensis* (Cushman), Qreiya, Egypt. Zone Plc, scale bar = 50  $\mu\text{m}$ . (15) *Chiloguembelina claytonensis* (Loeblich and Tappan), Qreiya, Egypt. Zone Plc, scale bar = 50  $\mu\text{m}$ . (16) *Woodringina hornerstownensis* (Olson), Qreiya, Egypt. Zone Plc, scale bar = 50  $\mu\text{m}$ . (17–18) *Heterohelix globulosa* (Ehrenberg), El Kef, Tunisia. Zone CF1, scale bar = 100  $\mu\text{m}$ . (19) *Heterohelix dentata* (Stenestad), El Kef, Tunisia. Zone CF1, scale bar = 50  $\mu\text{m}$ . (20) *Heterohelix navarroensis* (Loeblich), El Kef, Tunisia. Zone CF1, scale bar = 100  $\mu\text{m}$ .



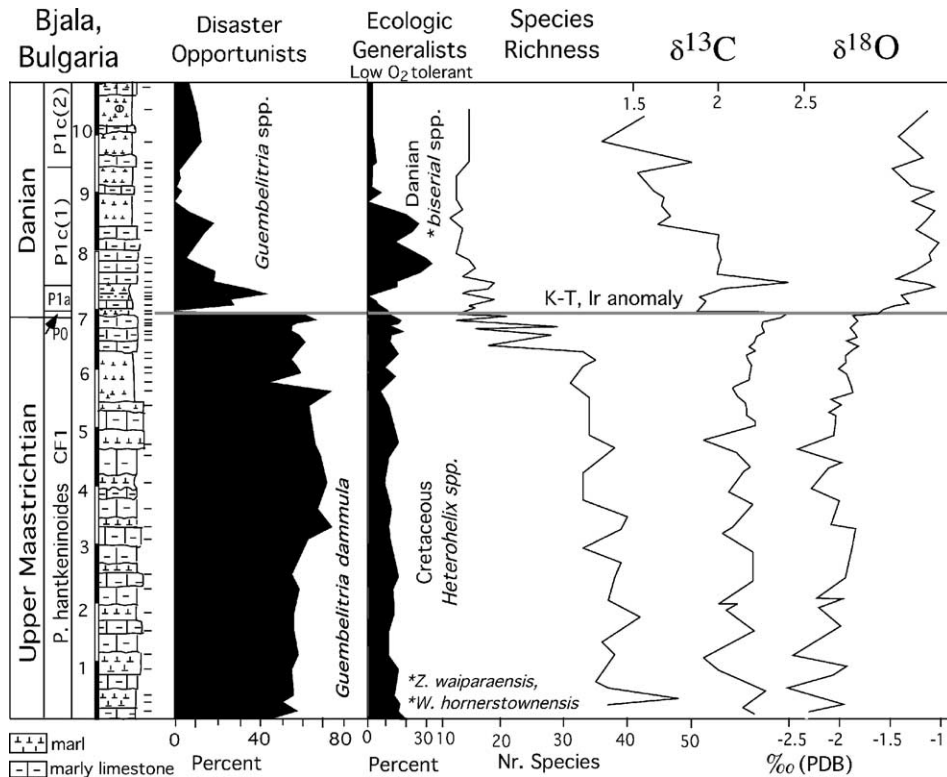


Fig. 12. Relative abundances of disaster opportunists, low oxygen tolerant ecological generalists, species richness and stable isotopes at Bjala, Bulgaria. Data from Adatte et al., 2002.

assemblages with reduced biotic effects (Pardo, 1999; Pardo et al., 1999). In both localities, the assemblages predominantly consist of small heterohelicids. In the upper Maastrichtian, *Zeauvigerina waiparaensis* dominates (90%) and guembelitrids average less than 10% (Figs. 13 and 14). The *Z. waiparaensis* dominance continues into the Danian and marks this species as a thriving survivor similar to *Guembelitra* in lower latitudes. At Koshak, *Z. waiparaensis* and Danian biserials (*Woodringina*, *Chiloguembelina*) completely replace Cretaceous *Heterohelix* species in the early Danian, unlike Denmark where *Heterohelix globulosa* survives well into the early Tertiary (Keller et al., 1993). At Kyzylsai, small biserial heterohelicids are reduced to between 40% and 60% in the early Danian, with *Guembelitra* blooms <20%. In both sections, *Guembelitra* increases in the lower part of zone P1a to 15–20%. At Koshak, *Guembelitra* averages <10% in the early Danian P1a, but at 45 cm above the K–T boundary, *Guembelitra* bloom to the virtual exclusion

of other species (Fig. 14). Unfortunately, this tantalizing evidence of high-stress conditions in zone P1a could not be further investigated because the sections were not sampled for the Danian.

$\delta^{13}\text{C}$  data (fine fraction carbonate) at Kyzylsai reveal a 1.3‰ negative shift at the K–T boundary and a major cooling (Fig. 13; Pardo, 1999), consistent with the diminished  $\delta^{13}\text{C}$  effect in higher latitudes and the global cooling. Late Maastrichtian  $\delta^{18}\text{O}$  values show climate warming followed by cooling just below the K–T boundary, a pattern that is also consistent with global records of climate change during zone CF1 (Li and Keller, 1998b). Stable isotope data, similar to planktic foraminiferal assemblages, indicate a different K–T environment at Koshak. Bulk rock and benthic  $\delta^{13}\text{C}$  data show only a minor change to more negative values across the K–T boundary (Fig. 14). In contrast, the low-oxygen-tolerant planktic foraminifer *Zeauvigerina waiparaensis* indicates a 0.5‰ positive shift, suggesting increased productivity



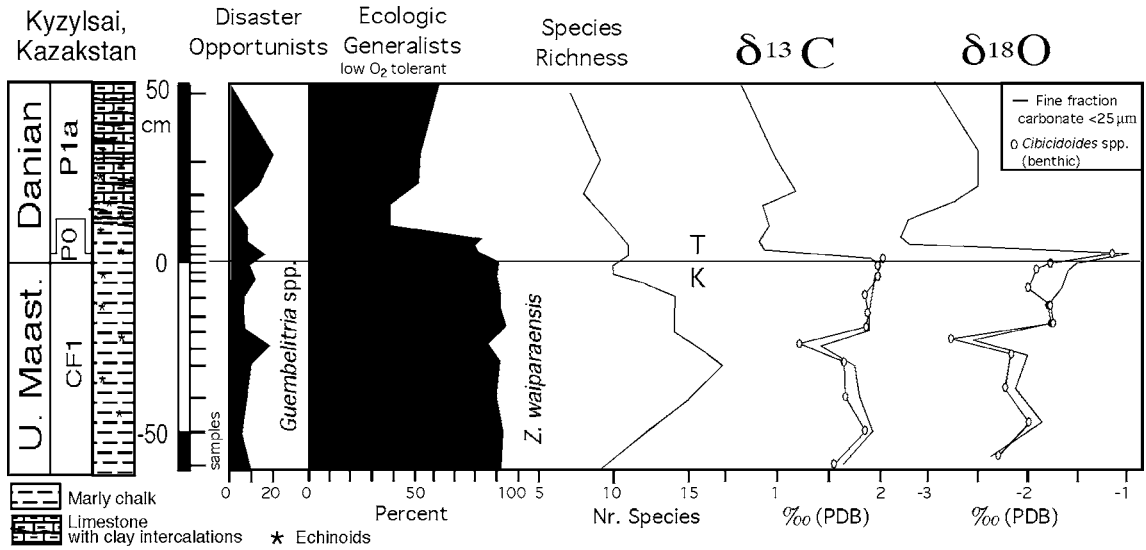


Fig. 13. Relative abundances of disaster opportunists and low oxygen tolerant ecological generalists, species richness and stable isotopes at Kyzylsai, Kazakstan. Data from Pardo, 1999 and Pardo et al., 1999.

(Oberhänsli et al., 1998; Pardo, 1999). A positive  $\delta^{13}C$  shift has also been observed in the southern high-latitude Site 738 (Barrera and Keller, 1994). Bulk rock  $\delta^{18}O$  data show the zone CF1 warm event followed by cooling at the end of the Maastrichtian,

similar to Kyzylsai. But there is significant warming indicated in the lower Danian by benthic and planktic foraminifera and bulk rock  $\delta^{18}O$  data.

The stable isotope data indicate that the late Maastrichtian experienced similar environmental

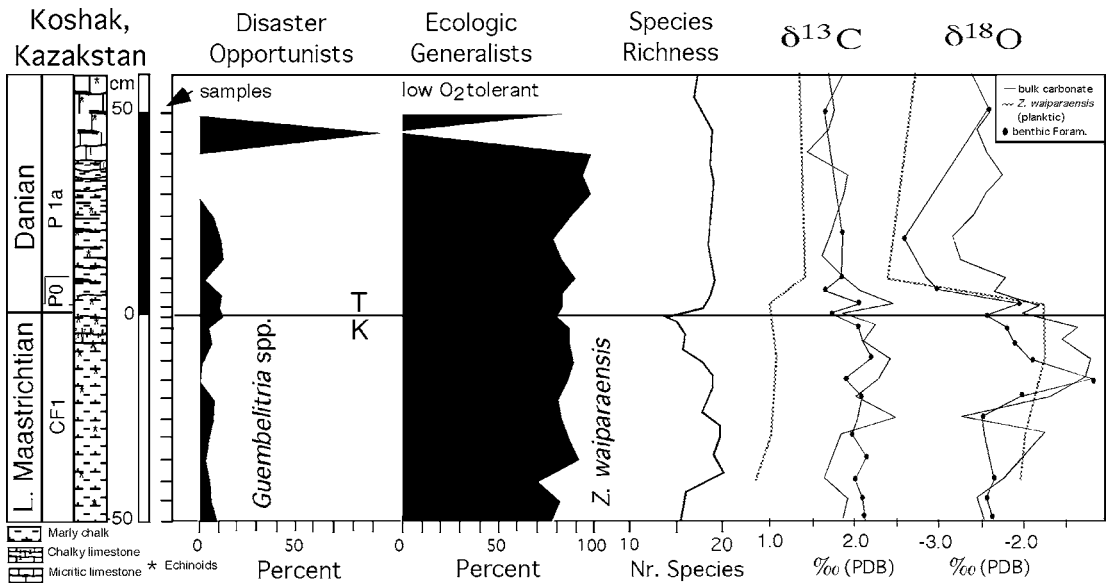


Fig. 14. Relative abundances of disaster opportunists and low oxygen tolerant ecological generalists, species richness and stable isotopes at Koshak, Kazakstan. Data from Pardo, 1999 and Pardo et al., 1999.

conditions at Koshak and Kyzylsai including the effects of the CF1 global warming, followed by end Maastrichtian cooling. The global warming is also indicated by the brief incursion of lower latitude species (e.g., *Globotruncana arca*, *Globotruncanella petaloidea*, *Globotruncanella caravacaensis*). However, the K–T catastrophe affected the two localities differently. Kyzylsai experienced a weaker effect of the global crisis in lower latitudes. But at Koshak, environmental conditions appear to have remained more stable, possibly with even increased productivity and generally warmer temperatures or salinity effects. This difference may be explained by regional variations, such as a shallower marine environment at Kyzylsai with little or no surface-to-deep gradient, higher terrigenous influx than that at Koshak and greater variations in nutrient and salinity fluctuations.

### 3.2.3. Denmark

The Danish sections at Stevns Klint and Nye Klov and the Koshak and Kyzylsai sections have very similar planktic foraminiferal assemblages and stable isotope signals as shown in Fig. 15 for Nye Klov. This section was deposited in an inner to middle neritic environment (Keller et al., 1993). The upper Maastrichtian is dominated (70–80%) by *Heterohelix* species (mainly *Heterohelix globulosa*). *Guembeltria* are a minor component, except for the last 2 m below the K–T boundary when they reach 25%, suggesting increased biotic stress. Beginning at the K–T boundary, *H. globulosa* populations gradually decrease through zone P1a and P1b. This pattern of *H. globulosa* survivorship has also been observed at the similarly shallow Brazos section of Texas (Fig. 9). *Guembeltria* blooms reach 35% in the early Danian. Species richness during the upper Maastrichtian is very low

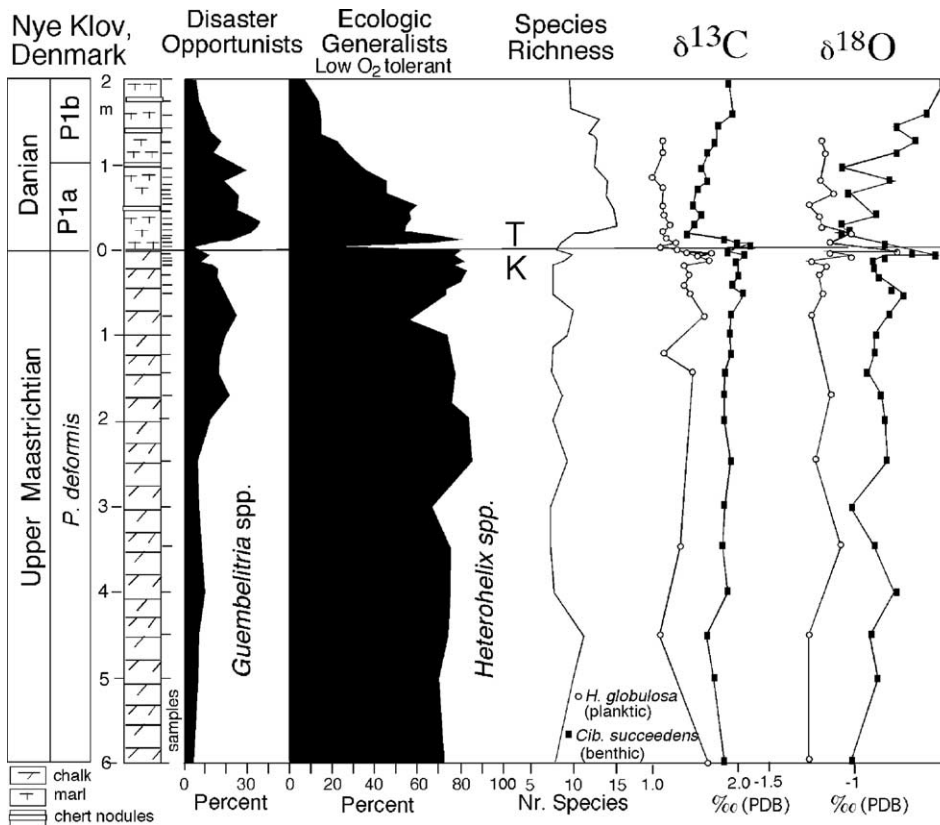


Fig. 15. Relative abundances of disaster opportunists and low oxygen tolerant ecological generalists, species richness and stable isotopes at Nye Klov, Denmark. Data from Keller et al., 1993 and Barrera and Keller, 1994.

between 6 and 10 species, but increased in the lower Danian to 12–15 species because of survivors and the evolution of new species. The lower Danian species richness is comparable to that in the lower Tethys region. However, the low upper Maastrichtian diversity is at the minimum, observed anywhere.  $\delta^{13}\text{C}$  data of both benthic foraminifera and the planktic *H. globulosa* indicate a 0.5‰ negative excursion at the K–T boundary (Fig. 15; Barrera and Keller, 1994).  $\delta^{18}\text{O}$  data suggest cooling followed by warming or salinity effects. The negative excursion  $\delta^{13}\text{C}$  in *H. globulosa* in the early Danian not only reveals this species as a K–T survivor but also indicates adaptation to the changing environment, as also observed for this species at Brazos, Texas (Barrera and Keller, 1990).

The northern high-latitude faunal data thus reveal relatively stable high heterohelid populations in all localities during the upper Maastrichtian, although with a significant percentage of *Guembelitra* (10–25%), except for Bulgaria where *Guembelitra dammula* dominates. Heterohelids continued their dominance into the early Danian, and post-K–T *Guembelitra* blooms are of relatively low magnitude. Similarly, the negative  $\delta^{13}\text{C}$  excursion in higher latitudes is significantly reduced. This suggests that higher latitudes experienced lower biotic stress than the lower latitude Tethys Ocean, which can be explained by at least three factors:

- (1) diminishing biotic effects of the catastrophe into higher latitudes,
- (2) high-latitude ecological generalists are more capable of adapting and tolerating variable environmental conditions, and
- (3) mitigating influence of nearby terrestrial environments.

### 3.3. Southern middle latitudes

#### 3.3.1. DSDP sites 525 and 528

Sites 525 and 528 are located on Walvis Ridge in the South Atlantic. During the upper Maastrichtian, sediment deposition occurred at bathyal depths variously estimated at 1100 or 1500 m (Widmark and Malmgren, 1992; Li and Keller, 1998a). As in most deep-sea sections, the K–T transition is condensed with zone Pla very reduced. Just above the K–T

boundary, *Guembelitra* are rare and lower Danian heterohelids dominate which indicates that the basal Danian zones P0 and lower part of Pla [Pla(l), no. 1; Fig. 3] are missing (D’Hondt and Keller, 1991). Small heterohelids (mostly *Heterohelix globulosa*, *Heterohelix dentata*) dominate the upper Maastrichtian.

At Site 525, the lower Danian P0–Plb interval is missing due to a hiatus, but a continuous upper Maastrichtian record is preserved (Li and Keller, 1998a,b). High-resolution analysis of this record reveals the major global warming in zone CF1 between 65.45 and 65.1 Ma (Fig. 16, Li and Keller, 1998b). During this global warming, species diversity decreased and larger specialized species (e.g., globotruncanids, pseudotextulariids and rugoglobigerinids), which are relatively abundant (~40%), are dwarfed in response to increased biotic stress conditions (Abramovich and Keller, 2003). Minor populations of *Guembelitra* also appear at this time and reflect the heightened stress environment. Small heterohelids (mostly *Heterohelix dentata* and *Heterohelix globulosa*) dominate before and after the warming. The global warming in CF1 and related biotic stress environment has been observed globally and coincides with a major pulse in Deccan volcanism and probably the Chicxulub impact event (Keller et al., 2002, 2003).

#### 3.3.2. Madagascar

The Amboanio section from the Mahajanga Basin of northwestern Madagascar was deposited in an outer neritic environment, which shallowed to middle neritic depths near the end of the Maastrichtian (Abramovich et al., 2002). Major hiatuses are present between zones CF4 and CF3, or between *Laburruus quadratus* and *Micula murus* zones (Tantawy, written communication, 2002), with most of CF3 missing and between CF3 and CF1-2, or between *M. murus* and *Micula prinsii* zones, with most of CF2 missing. These hiatuses correspond to sea level lowstands at 65.5 and 67 Ma. During the upper Maastrichtian, in zone CF4, *Guembelitra* species dominate (*Guembelitra cretacea* 40%, *Guembelitra dammula* 10–15%) along with *Heterohelix* species (*Heterohelix dentata* 20–25%, *Heterohelix globulosa* (8–15%), *Heterohelix navarroensis* 5%; Fig. 17). In zone CF3, *Heterohelix* species (mainly *Heterohelix dentata*) reach 80% and *Guembelitra* average 10%. Near the end of the

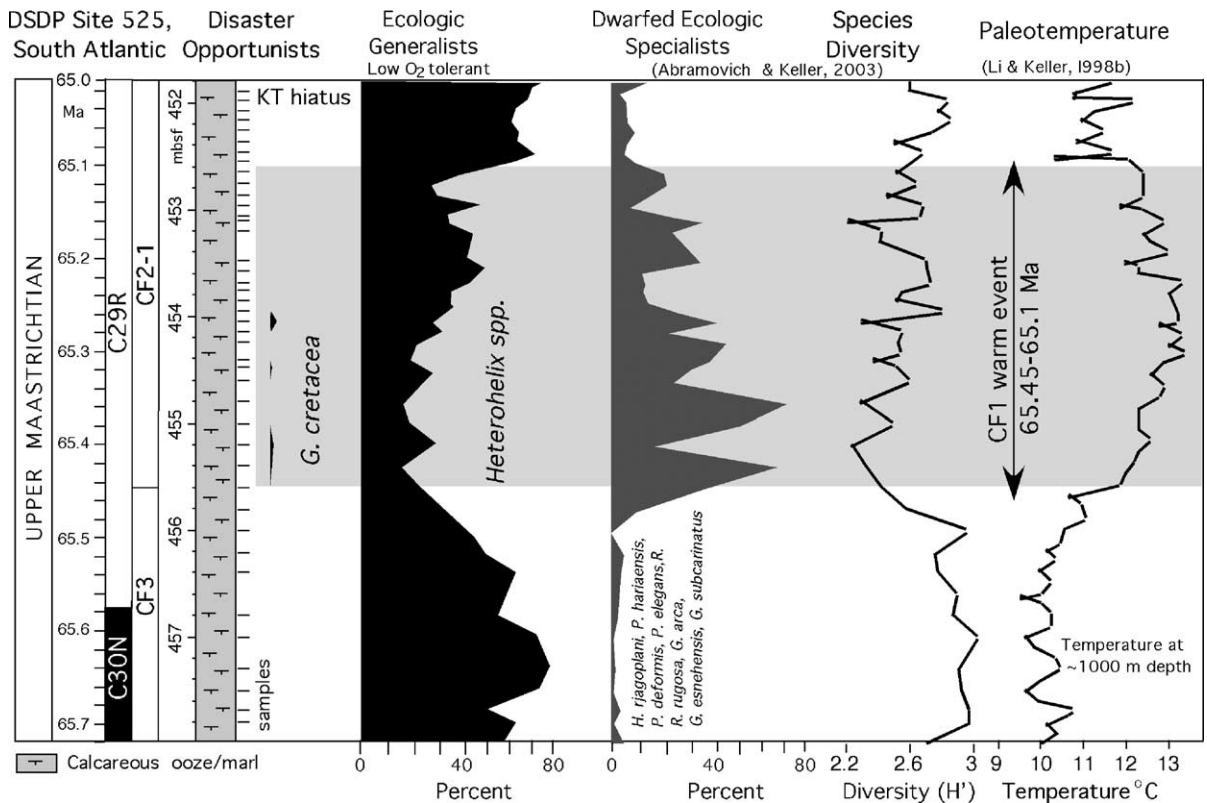


Fig. 16. Relative abundances of disaster opportunists and low oxygen tolerant ecological generalists, species diversity (Shannon Weaver index) and benthic stable isotope temperature curve at DSDP Site 525. Data from Li and Keller, 1998b and Abramovich and Keller, 2003.

Maastrichtian, in zone CF1, *Guembelitra* blooms reach 40%. A hiatus marks the K–T boundary.  $\delta^{13}\text{C}$  data of benthic and planktic foraminifera show gradually decreasing values during zone CF3. Relatively warm temperatures and a good surface-to-deep gradient are indicated in the  $\delta^{18}\text{O}$  data.

The very high and prolonged *Guembelitra* abundances in zone CF4 (66.8–68.3 Ma) are an enigma. No similar records have been reported to date although this may be due to lack of investigations of small size fractions for this interval. Volcanism is the most likely cause for such prolonged crisis conditions (see Site 216).

### 3.3.3. Ninetyeast Ridge DSDP Site 216

During the late Maastrichtian, DSDP Site 216 was located at a paleolatitude of about  $40^\circ\text{S}$  on the crest of Ninetyeast Ridge, Indian Ocean, which consisted of islands built to sea level as the oceanic plate moved

over a mantle plume resulting in lithospheric uplift and volcanic deposition (Thompson et al., 1974; Moore et al., 1974). After passage over the mantle plume, the site rapidly subsided and deepened from shallow to deeper marine below the photic zone, as Site 216 passed beyond the influence of mantle plume volcanism and chalk deposition resumed during the last 500 kyr of the Maastrichtian. Microfossils associated with these volcanic-rich sediments reveal unusually low diversity and small size, which was originally attributed to a high-latitude location and dissolution effects (McGowran, 1974), but restudy of the small size fraction reveals a high-stress fauna related to mantle plume volcanism (Keller, 2003).

The K–T boundary is marked by a hiatus that spans the early Danian zones P0 to the lower part of Plc and possibly the uppermost part of the Maastrichtian. The chinks below the K–T boundary contain planktic foraminiferal and nannofossil assemblages

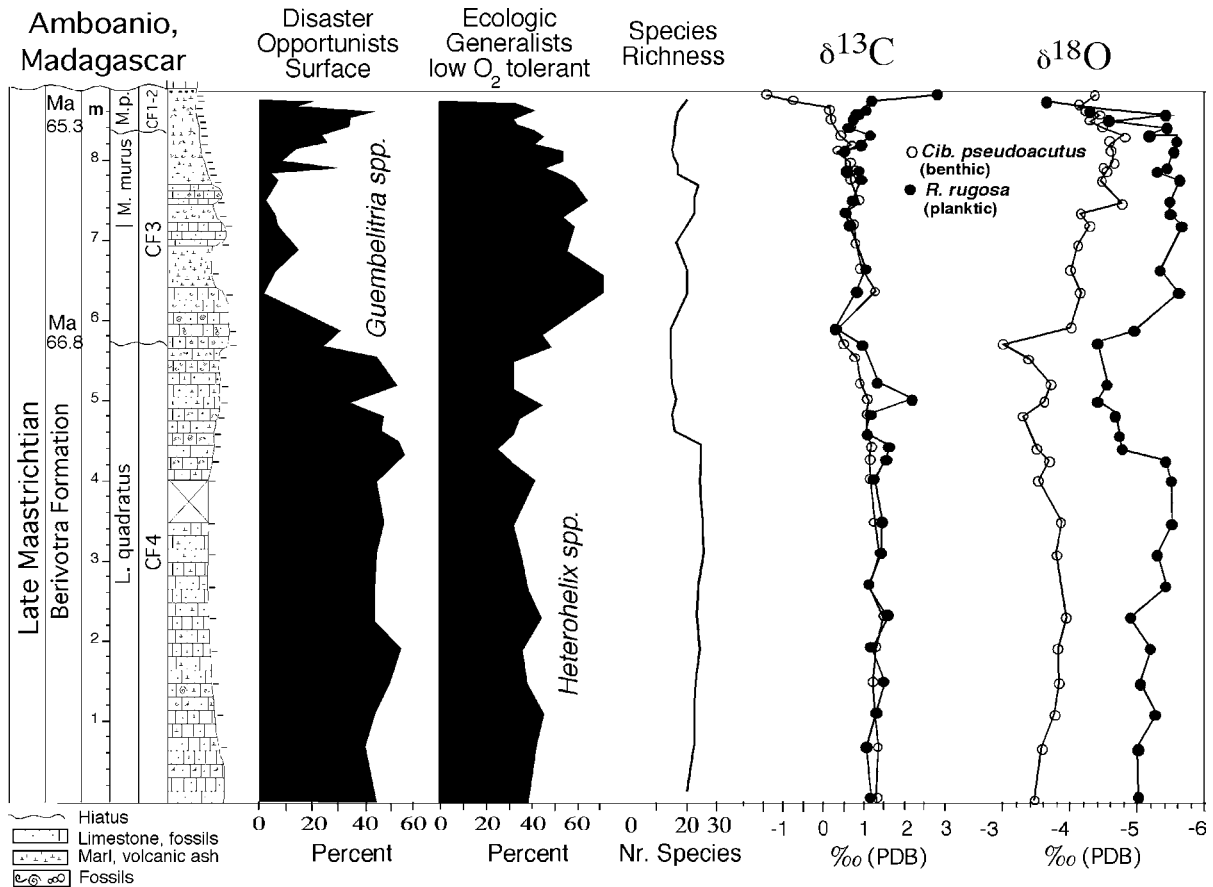


Fig. 17. Relative abundances of disaster opportunists and low oxygen tolerant ecological generalists, species richness and stable isotopes at Amboanio, Mahajanga Basin, Madagascar. Data from Abramovich et al., 2002.

characteristic of the zone CF1-CF2 and *Micula prinsii* interval (Tantawy, written communication, 2003; Fig. 18). The abrupt transition from chalk to volcanic-rich deposition is marked by a hiatus and correlates with the sea level lowstand at 65.5 Ma. Widespread erosion at this sea level lowstand is also observed in Madagascar, Israel and Egypt (Abramovich et al., 2002; Keller, 2002, 2003).

Upper Maastrichtian planktic foraminiferal assemblages in the volcanic-rich sediments at Site 216 are characterized by unusually low diversity (6–10 species), very small adult species sizes (<100  $\mu\text{m}$ ) and low abundances compared with assemblages at similar middle to high latitudes, except for the unusually high abundances (>80%) of the disaster/opportunist *Guembelitra cretacea* (Fig. 18). More diverse species as-

semblages with normal adult species sizes first appear in the chalk near the top of the section and above the volcanic-rich sediments. Low-oxygen-tolerant small heterohelids (mostly *Heterohelix dentata*, *Heterohelix globulosa*) dominate at times of low *Guembelitra* abundances. Preservational effects cannot account for these unusual assemblages because foraminiferal tests are generally well preserved. Dissolution effects are minor (some breakage and holes in tests) as evident in the high abundance of small delicate species. Moreover, the absence of other more dissolution resistant species indicates that these assemblages are not the result of preservational bias. These unusual high-stress assemblages thus appear to be directly related to the passage of the oceanic plate over a mantle

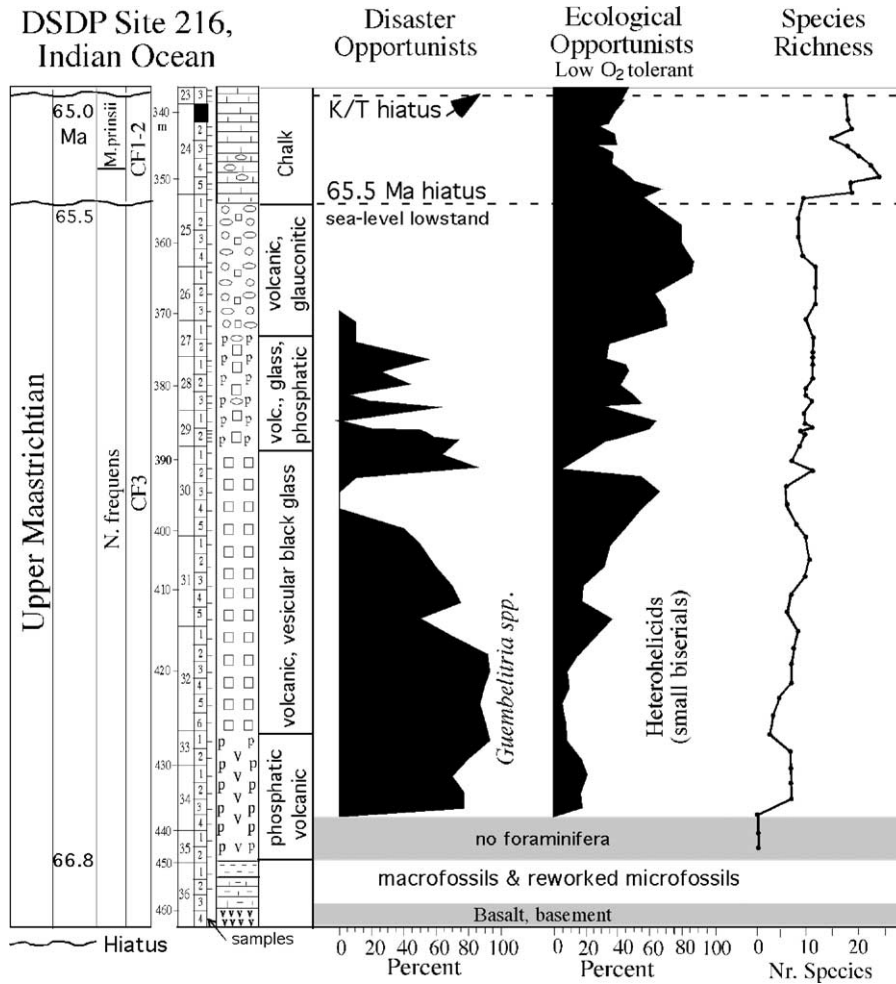


Fig. 18. Relative abundances of disaster opportunists, low oxygen tolerant ecological generalists and species richness at DSDP Site 216 on Ninetyeast Ridge, Indian Ocean. Data from Keller, 2003.

plume and consequent volcanic activity. The full geographic extent of the biotic effects of Ninetyeast Ridge mantle plume activity is still to be investigated.

### 3.4. High-latitude southern ocean

#### 3.4.1. ODP Sites 738 and 690

Planktic foraminiferal assemblages in the southern high-latitude ocean show similar aspects to the northern high latitudes. ODP Site 738 was deposited at about 1000-m depth. Upper Maastrichtian and early Paleocene sediments consist of chalks and carbonate ooze, with the K–T boundary transition in clay-rich

laminated interval with the Ir anomaly at 2cm above the base of this clay (Keller, 1993; Schmitz et al., 1992). The late Maastrichtian is dominated (50–60%) by heterohelicids, predominantly *Heterohelix globulosa* and <10% *Zeauvigerina waiparaensis* (Fig. 19). *Guembelitria* are rare. Near the end of the Maastrichtian, *Z. waiparaensis* populations rapidly increase to 80% and continue to dominate in the early Danian. A minor *Guembelitria* bloom occurred in zone P0–P1a. Species richness is very low during the upper Maastrichtian (10–15 species), except for a short incursion of lower latitude species during the global warm event. In the early Danian, species richness is com-

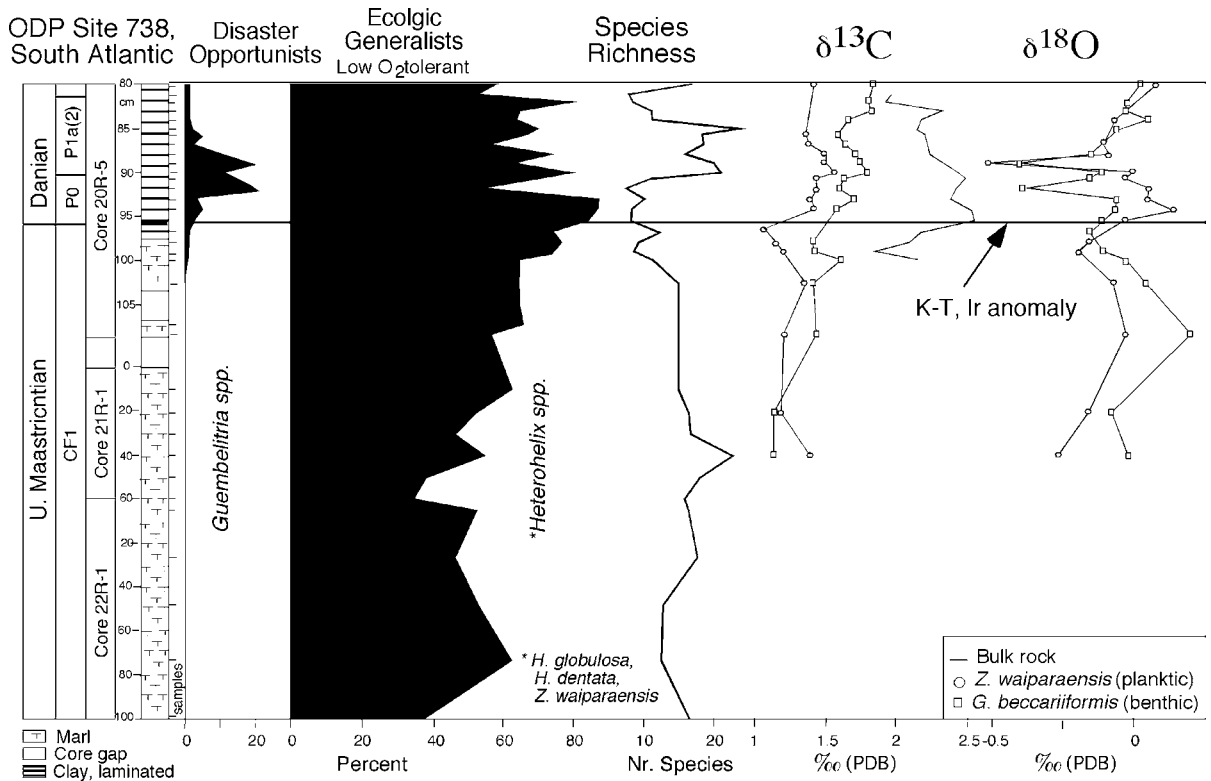


Fig. 19. Relative abundances of disaster opportunists and low-oxygen-tolerant ecological generalists, species richness and stable isotopes at ODP Site 738. Data from Keller, 1993 and Barrera and Keller, 1994.

parable to low latitudes with the evolution of new Tertiary species.

Bulk rock  $\delta^{13}\text{C}$  data show a positive excursion beginning below the K–T boundary and continuing through the lower Danian zone P1a, suggesting increased nutrient input. Benthic foraminifera show gradually increasing values. The planktic foraminifer *Zeauvigerina waiparaensis* shows surprisingly light  $\delta^{13}\text{C}$  data values, suggesting nutrient-enriched surface waters and/or oxygen depletion (Barrera and Keller, 1994).

In the Weddell Sea ODP Site 690, heterohelicids also dominate (40%, *Heterohelix globulosa* and *Heterohelix planata*) the late Maastrichtian, but the high-stress indicators *Guembelitra* and *Zeauvigerina waiparaensis* are absent (Keller, 1993). The K–T boundary is marked by a hiatus with the lower Danian zones P0 through P1a missing.

One of the most interesting results of the southern ocean  $\delta^{13}\text{C}$  data (ODP Sites 690, 738 and 750) is the

negative excursion about 200 kyr after the K–T boundary. A similar negative excursion has been observed in benthic  $\delta^{13}\text{C}$  data of DSDP Sites 577 (Zachos et al., 1989, 1992) and 527 (Shackleton et al., 1994) and suggests a regional shift in the carbon isotope composition of oceanic total dissolved carbon (TDC; Barrera and Keller, 1994).

### 3.5. Paleobiogeography of *Guembelitra*

Blooms of the disaster opportunist *Guembelitra* species are best known from the aftermath of the K–T boundary mass extinction where they characterize the early Danian zone P0 and lower part of zone P1a in all oceans and across latitudes. The intensity of this bloom, as measured based on relative abundance with respect to other species, is variable ranging from as little as 10% to as much as 100% although this variability is at least in part due to preservational effects and condensed or incomplete sections. How-

ever, there is a clear geographic demarcation between dominant blooms, here identified as abundances of 40–80% or greater and lesser blooms of 10–20%. The dominant blooms occur in low to middle latitudes, whereas the lesser blooms are restricted to northern and southern high latitudes (Fig. 20). This indicates that low and middle latitudes experienced the most intense biotic stress during the post-K–T mass extinction. This is independently supported by the mass extinction pattern which shows all tropical and subtropical species extinct, but the survival of ecologic generalists adapted to environmental changes (Koutsoukos, 1996; Keller, 2001). This pattern is also independently supported by benthic, planktic and bulk rock  $\delta^{13}\text{C}$  records, which show a 2–3‰ negative shift in low to middle latitudes, but only 0.5‰ to 1.0‰, or even a positive shift, in high latitudes (e.g., Denmark, Kazakstan, Bulgaria and ODP Site 738). Low latitudes thus experienced the major productivity crash and the most severe biotic consequences. In contrast, high latitudes experienced reduced bioproductivity and biotic stress.

However, there are also regional coeval blooms in the Danian, as well as in the upper Maastrichtian,

which indicate recurring biotic crises conditions unrelated to the K–T boundary event. Review of the statistical data of *Guembelitra* blooms and small heterohelicids presented in the preceding section shows that their temporal and geographic distribution is complex and variable. Apart from the well-known post-K–T bloom, there are additional *Guembelitra* blooms in early Danian zones Pla and Plc (e.g., Tunisia, Egypt, Israel, Kazakstan, Bulgaria, Haiti and Guatemala; Fig. 21). In addition, three or more *Guembelitra* blooms have been identified in the upper Maastrichtian (e.g., Israel, Egypt, Tunisia (at Elles), Madagascar and Site 216). Most of the apparent variability and complexity in these *Guembelitra* bloom patterns may be due to incomplete sedimentary records as a result of widespread hiatuses related to sea level fluctuations. These hiatuses can be identified based on planktic and benthic faunas and lithologic features, particularly in continental shelf sequences (Li et al., 2000). High-resolution quantitative studies and the use of planktic foraminiferal and calcareous nannofossil biozonations help identify intrazonal hiatuses and aid in correlation of blooms as illustrated in Fig. 21.

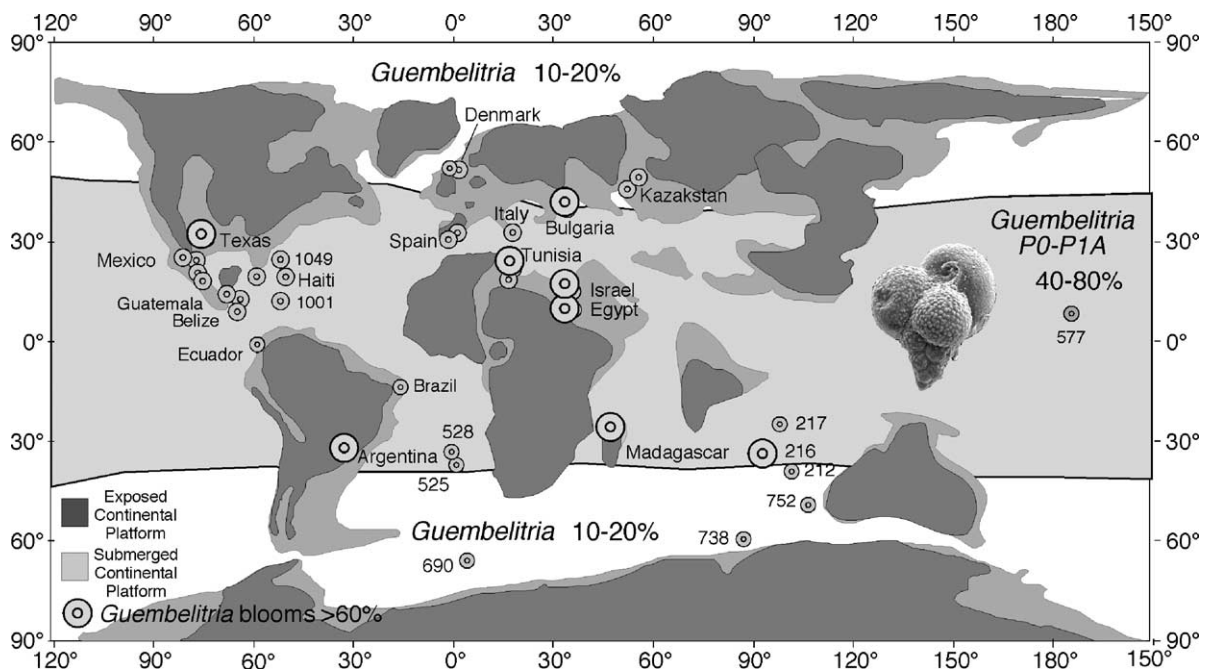
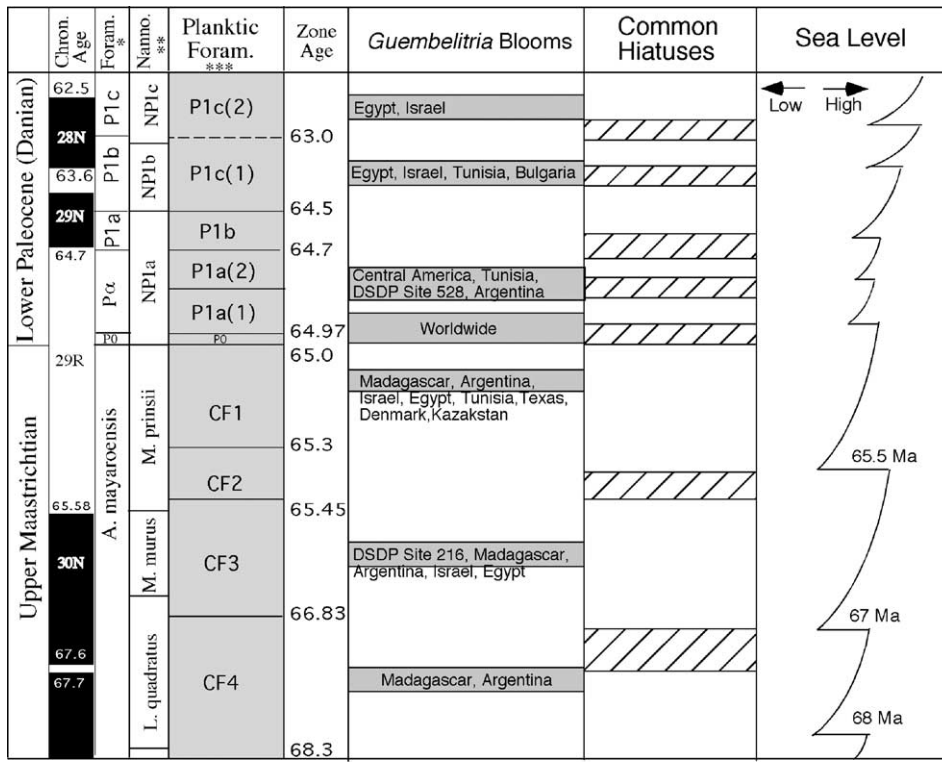


Fig. 20. Biogeographic distribution of the early Danian *Guembelitra* blooms.





\*Berggren et al., 1995; \*\*Tantawy, 2003; \*\*\*Keller et al., 1995; Pardo et al., 1996; Li and Keller, 1998a

Fig. 21. Stratigraphic ages of *Guembelitra* blooms. Sea level data from Li et al., 2000. See Fig. 3 for explanation of biozonation.

### 3.6. *Guembelitra* blooms and eutrophic waters

Are the most intense (>60%) *Guembelitra* blooms associated with particular paleoenvironments? The answer appears to be yes. The most intense *Guembelitra* blooms (>60%) of the late Maastrichtian, post-K–T and Danian occurred on shallow continental shelf environments, upper bathyal environments of continental margins and on areas of intense volcanism (Fig. 20). All of these environments have one common factor—high nutrient influx either from continental runoff (Brinkhuis and Zachariasse, 1998; Adatte et al., 2002; Keller et al., 2002), upwelling or volcanic input. A large meteorite impact could temporarily have the same effect causing increased nutrient influx from fallout and erosion, associated with postimpact climate cooling. Planktic foraminiferal diversity, which is at the maximum in oligotrophic and well-stratified oceans (Lipps, 1979), significantly decreases in such nutrient-rich environments. Kout-

soukos (1996) discussed the unusual phytoplankton blooms associated with these nutrient-rich environments in the early Danian and suggested that *Guembelitra* were probably passive grazers.

*Guembelitra* blooms show a consistent affinity with nutrient-rich oceanic environments throughout the late Maastrichtian and early Tertiary and indeed since their evolution in the middle Cretaceous (Kroon and Nederbragt, 1990; Koutsoukos, 1996; Keller, 2002, 2003). In this respect, modern representatives of *Guembelitra* appear to have retained this same affinity for high-nutrient environments, as they are most abundant in upwelling areas with highly variable conditions where few other species thrive (Kroon and Nederbragt, 1990). Times of biotic crises may thus be related to a number of different factors, all of which lead to increased nutrient influx including impacts, volcanism, restricted shelf environments and upwelling along continental margins. Preliminary stable isotopic ranking of *Guembelitra* species seems to

support this observation. *Guembelitra* species consistently rank the lightest in  $\delta^{13}\text{C}$  values relative to other species (Barrera and Keller, 1994; unpublished data), probably because they thrive in surface waters with high nutrients (Koutsoukos, 1996).

### 3.7. Biotic crisis and recovery model

The biotic response to any major environmental catastrophe appears to be universal and can be expressed by a simple model (Fig. 22). A climatic or optimum ecological assemblage consists of high diversity of K-strategy species (e.g., large, complex and specialized taxa) and a background of low-diversity R-strategy species (e.g., small ecologic generalists). A major environmental perturbation, such as a large impact or prolonged intense volcanism, dramatically alters the ecosystem, increases the nutrient influx leading to eutrophication and obliterates the specialized niches of K-strategy species and most of the R-strategists resulting in mass mortality. This may result in mass extinction (e.g., K–T boundary) or

temporary local or regional exclusion of all large complex species and many ecological generalists (e.g., DSDP Site 216). The critical factor in mass mortality is eutrophication which leads to a phytoplankton bloom (e.g., primary producers such as in the modern red tide) and toxic conditions for foraminifera, whether photosymbiotic species, carnivores (spinose cancellate-walled globigerinids), herbivores or passive grazers (nospinose including *Guembelitra*; Koutsoukos, 1996; Abramovich et al., 2003). Once the organic matter decreases due to consumption by phytoplankton, the first opportunistic foraminifera, the *Guembelitra*, appear and graze on phytoplankton.

Stratigraphic evidence and the biogeographic distribution of *Guembelitra* (Plate 1, Figs. 1–10) indicate that this group is the most stress tolerant, as well as the first opportunists to thrive after an environmental catastrophe. The wide fundamental niche of these organisms enables adaptation to variable environmental conditions and hence permits the niche drift that assures survival of these stress-tolerant species (Koutsoukos, 1996; Begon et al., 1998). Their adaptation to

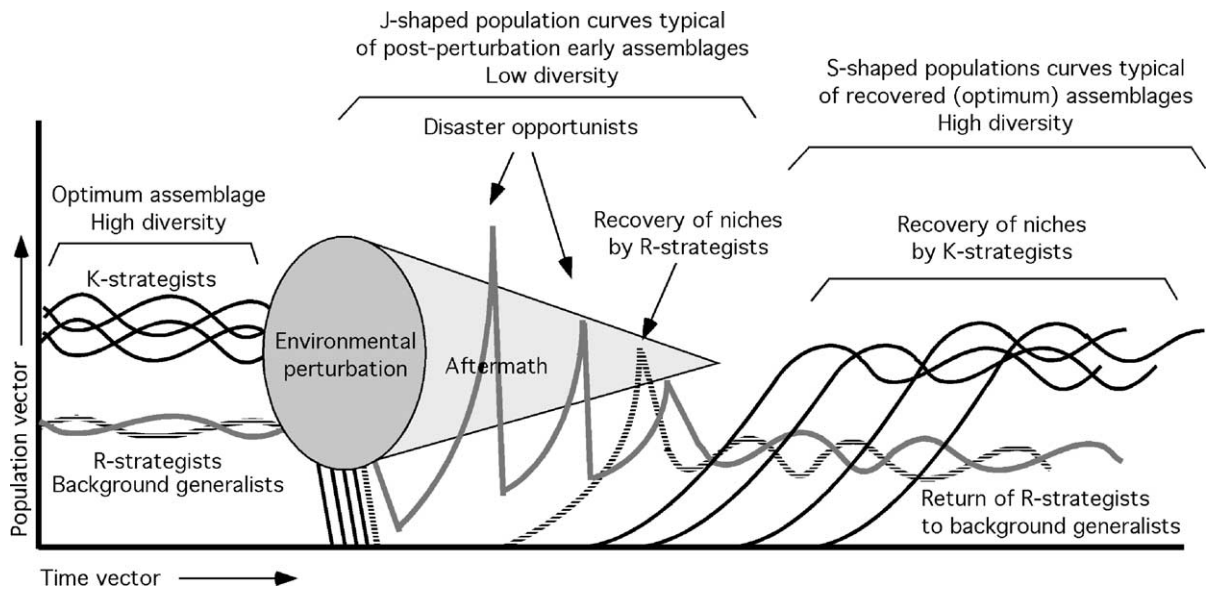


Fig. 22. Model illustrating the ecological succession after a major environmental perturbation. The perturbation eliminates all K-strategists (specialist species) and most R-strategists (generalists) of the optimum assemblage, leaving the disaster opportunist *Guembelitra* as sole thriving group. In the first phase, *Guembelitra* rapidly reproduce, leading to exponential population (J-shaped) growth, then crash when nutrients are depleted and the environment changes from eutrophic to mesotrophic. In the second phase, low- $\text{O}_2$ -tolerant heterohelicids and other generalists thrive, further depleting nutrients and changing towards oligotrophic conditions, increased water-mass stratification and niche competition. With increased competition, species populations switch from J-shaped crisis mode to the more stable S-shaped mode. With the re-establishment of high-diversity K-strategy species assemblages, R-strategy generalists are again displaced (background assemblage).

high-stress disturbed environments includes dwarfing which is an ecological response for taking advantage of the nutrient supply by means of heterochronic acceleration (i.e., early sexual maturation and faster reproduction, e.g., MacLeod et al., 2000). Without interference from competitors, these species rapidly reproduce and increase their populations exponentially (J-shaped curve), much like the red tide algae blooms in the modern ocean. *Guembelitra* thus exhibits a well-developed R-strategy that allows these organisms to take full advantage from stressed and disturbed habitats. When nutrient levels become insufficient to sustain this population growth, they cease, thus opening niches to other ecologic generalists.

The second ecological generalists to recover are a group of low-oxygen-tolerant small biserial species (Plate 1, Figs. 11–20), followed by a third group, the small planispiral and trochospiral species. These two groups of ecological generalists further feed on the phytoplankton blooms and gradually change the environment from eutrophic to mesotrophic conditions. *Guembelitra* dominance may alternate with biserial populations over time depending on nutrient influx (e.g., variable intensity of volcanism at Site 216) and the associated phytoplankton blooms. The increasing niche competition among the second stage generalists eventually switches their population growth curve from J-shaped to a more stable S-shape population curve (Fig. 22). *Guembelitra* blooms thus represent the first stage of a new ecological succession and are succeeded by low-oxygen-tolerant small heterohelids during the second stage that characterizes the initial recovery of environmental conditions.

With improving stable environmental conditions, increasing competition, niche development and restoration of a well-stratified water mass, oligotrophic conditions are restored opening habitats for the highly specialized and diverse K-strategists (Hallock, 1987, 1996; Hallock et al., 1991; Koutsoukos, 1996). K-strategy species, which are more suited to high interspecific competition, displace R-strategy species to the background assemblage. The reestablishment of this highly diverse and mature assemblage represents the full recovery of the ecological succession after a major environmental perturbation. The recovery period may be short (<100,000 year) or prolonged over several 100,000 years. At the K–T boundary event, full recovery was delayed for about 3 myr.

D'Hondt et al. (1998) proposed an alternate scenario to explain the delayed ecologic recovery after the K–T mass extinction. They propose that during the early Danian, the delayed recovery was not due to lower biological production, as commonly thought, but to decreased organic flux to the deep ocean. They argue that the delay in recovery could have been due to the high rate of phytoplankton production and low rate of relatively large grazers that facilitate the biomass sinking in the form of fecal pellets. This would keep essential nutrients in easily remineralized form (such as tiny microbially grazed plankton) in the euphotic zone and increase the rate of nutrient recycling and open ocean biomass production (D'Hondt et al., 1998, p. 278). This scenario, based on carbon isotopes, in principle, agrees with our model (Fig. 22) which shows the gradual return of more diverse and larger species with ecosystem recovery. However, their scenario is based on the post-K–T impact recovery and requires a catastrophic event, such as the mass extinction, to produce the *Guembelitra* and phytoplankton blooms. Our data demonstrates that much smaller environmental shocks can produce the same biotic effects and delayed recovery periods. A case in point is the Qreiya section of central Egypt (Fig. 6) where the planktic  $\delta^{13}\text{C}$  values decrease or even drop to below benthic values during the late Maastrichtian accompanied by *Guembelitra* blooms. These stress conditions may be related to Deccan volcanism.

An important test of the photoeutrophic nutrient cycling hypothesis is the organic content of marine origin in sediments. One would expect the organic content of marine origin to be very low in sediments associated with high-stress conditions and *Guembelitra* blooms, reflecting the nearly absent transfer of biomass to the ocean bottom. A preliminary survey suggests some support for this idea at Qreiya, Egypt (Keller et al., 2002), where the organic content is very low (0.2%) in the upper Maastrichtian and lower Danian (Fig. 6). Similarly at DSDP Site 216, the marine organic matter content is nearly absent (unpublished data). However, the organic matter content is generally high in the basal Danian clayey sediments. In most of these clays, the total organic matter has been analyzed but not the portion of marine origin. A study detailing the marine organic matter content in K–T sections is needed to further test the idea of photoeutrophic nutrient cycling in crisis conditions.

## 4. Discussion

### 4.1. Biotic effects of volcanism

The biotic response of *Guembelitra* to the K–T impact catastrophe is well documented, whereas the biotic response to intense volcanism is still relatively unknown.

However, a recent study of DSDP Site 216 on Ninetyeast Ridge, Indian Ocean, has shown that the biotic effects of impacts and volcanism are substantially the same (Fig. 18). Planktic foraminifera in the volcanic-rich late Maastrichtian sediments of Site 216 are dominated by *Guembelitra* (80–90%), which alternate with *Heterohelix* species when conditions improve. Species are generally dwarfed, and species assemblages very impoverished (Keller, 2003). Only when volcanic influx (predominantly ash) ceased is there a return of more diverse and normal sized species. Trace element analyses of foraminiferal tests indicate a strong micronutrient increase related to volcanism (e.g., Mn, Mg, Fe; Meudt et al., 2003). This is also evident in the volcanic-rich sediments which are rich in phosphate and glauconite. However, preliminary analysis has shown that there is almost no organic flux of marine origin. This lends support to the hypothesis of nutrient recycling of D'Hondt et al. in the eutrophic zone.

### 4.2. Separating biotic effects of impacts and volcanism

The relative environmental stress can be determined based on the degree of the biotic response such as the dominance of the disaster opportunists *Guembelitra* and *Zeauvigerina* (exclusion of other species) and their temporal and geographic distribution. To determine the cause for the biotic effects requires other environmental evidence such as volcanic sediments or impact ejecta (anomalous concentrations of iridium, glass spherules and melt rock in breccias). The biotic response to a large impact should be sudden and correlate with the impact evidence, as for example, the mass extinction of species coincident with an Ir anomaly as at the K–T boundary. However, one would expect the environment to recover relatively rapidly which is not the case in the early

Tertiary where biotic stress conditions lasted for several hundred thousand years and suggest subsequent repeated environmental perturbations unrelated to the K–T impact. Coccioni and Luciani (in preparation) recently studied the morphological abnormalities in *Guembelitra irregularis* during the early Danian and concluded that these represented high-stress conditions possibly induced by the K–T boundary impact. Although we agree that the high abundance of guembelitrids reflects high-stress conditions, attributing abnormalities in individual species to the specific effects of an impact seems premature without further evidence.

We argue that with the increasing evidence of multiple impacts (Keller et al., 2003), the popular K–T impact mass extinction scenario with Chicxulub as the impact location has lost some of its luster. The new evidence from late Maastrichtian microtektite layers in northeastern Mexico (Keller et al., 2002, 2003) and the new drill core within the Chicxulub crater (Keller et al., 2004) indicate that this impact predates the K–T boundary by about 300 kyr although this finding is still under discussion. In addition, the crater now appears to be only about 145 km in diameter, rather than the 180–300 km originally thought (Hildebrand et al., 1991; Sharpton et al., 1992; Dressler et al., 2003). Impacts of similar magnitude during the late Eocene (e.g., Popigai) did not cause any species extinctions or major environmental changes (Keller et al., 1983; Hallam and Wignall, 1997). Increasingly, Chicxulub appears to be just one of a series of smaller impacts during the late Maastrichtian including the Boltysch crater in the Ukraine estimated to be about 200,000 years prior to the K–T boundary (Kelley and Gurov, 2002). An impact also appears likely in the early Danian about 100–200 kyr after the K–T boundary, as suggested by Ir anomalies in Haiti, Guatemala and Mexico (Keller et al., 2003) as well as in ODP Site 752 (Michel et al., 1991).

These impacts, along with the yet to be found K–T impact crater, may have caused or contributed to a prolonged period of biotic stress but no specific short-term biotic events can be correlated with either the late Maastrichtian or early Danian intervals. On the other hand, there appears to be a good correlation with periods of intensified volcanic activity (Courtilot, 1999; Hoffmann et al., 2000; Stueben et al., 2002).

The well-documented global warming between 65.2 and 65.4 Ma appears to be related to intensified Deccan volcanism and also correlates to the onset of a gradual decrease in species diversity and dwarfing of specialized large species (Fig. 16; Li and Keller, 1998b; Abramovich and Keller, 2003). This study points towards India and the Indian Ocean and its hotspot or mantle plume volcanism as the source of biotic stress at least during the late Maastrichtian and probably also during the early Danian.

#### 4.3. Further studies

*Guembelitra* blooms are reliable proxies for environmental catastrophes, whether regional or global, during the late Maastrichtian and post-K–T early Danian, particularly in low and middle latitudes. Quantifying these easily identifiable small species thus provides a simple method for locating times of high environmental stress. The first-order investigation should concern the temporal and geographic distribution of *Guembelitra* blooms during the late Maastrichtian and K–T boundary and its association with flood basalts and/or impacts. In particular, data are needed for India and the Indian Ocean to determine the biotic effects associated with Deccan flood basalts. There is also the possibility that India may have been the K–T boundary impact location. The Shiva crater has been proposed as the K–T impact crater (Chatterjee et al., 2003). The combination of a major impact superimposed over ongoing Deccan volcanism would produce a powerful biotic catastrophe.

Although the geographic distribution of *Guembelitra* blooms is well documented for the K–T boundary event, little is known of their spatial and temporal distribution in other time intervals, particularly during the late Maastrichtian. This is largely because routine species analysis is generally done on the >150- $\mu\text{m}$  size fraction and does not include the small *Guembelitra* species which are generally found in the <100- $\mu\text{m}$  size fraction, along with several small low-O<sub>2</sub>-tolerant biserial species. A major effort is required to investigate the small size fraction (38–100  $\mu\text{m}$  and/or >63  $\mu\text{m}$ ) for the late Maastrichtian across latitudes to reveal background levels, crisis response and latitudinal distribution of these species.

Because *Guembelitra* species are very long ranging and appear to have remained a disaster opportunist

group, this proxy can identify environmental catastrophes from the middle Cretaceous to the Recent. A systematic analysis of species in the small size fraction in marine sequences from the late Cretaceous should reveal additional environmental catastrophes, as for example, during the Albian, the Cenomanian–Turonian transition and the Campanian (Kroon and Nederbragt, 1990; Keller et al., 2001).

Little is known of the environmental conditions that lead to *Guembelitra* blooms. Preliminary  $\delta^{13}\text{C}$  species ranking suggests that *Guembelitra* species are among the isotopically lightest species, along with *Zeuvingerina waiparaensis* in high latitudes (Barrera and Keller, 1994; Pardo et al., 1999) and both groups lived and thrived in eutrophic surface waters. Further geochemical studies are needed to determine the paleoecology of these species including:

- (1) stable isotope ranking of *Guembelitra* species relative to other species in order to determine depth habitat, productivity and temperature conditions,
- (2) trace element analysis of benthic and planktic foraminiferal tests to determine toxicity levels that may have proved lethal for specialized species, and
- (3) nutrient, salinity, temperature and oxygen variations evaluation within crises intervals.

## 5. Conclusions

Blooms of the disaster opportunist *Guembelitra* group are proxies for environmental catastrophes leading to severe biotic stress conditions that may range from temporary exclusion of ecological specialists (K-strategists) and generalists (R-strategists) to mass extinctions. *Guembelitra* species seem to be well-adapted R-strategists that maximize their full ecological potential in areas and at times of major sudden increases in nutrient contents of marine surface waters resulting in phytoplankton blooms. The origins of these extreme eutrophic conditions range from continental runoff, to upwelling and massive volcanism, both subaerial and submarine.

The ecological generalists consisting of small biserial species (*Heterohelix globulosa*, *Heterohelix nav-*

*arroensis*, *Heterohelix dentata*, *Heterohelix planata*) are reliable proxies for low O<sub>2</sub> conditions and generally mark initial recovery after peak eutrophic conditions passed. In high latitudes, the small biserial *Zeauvigerina waiparaensis* is a Cretaceous survivor (Keller, 1993; Pardo, 1999) and thrives in the post-K–T high stress environment.

The biogeography of *Guembelitra* blooms in the early Danian zones P0 and Pla(1) reveals a global distribution but with the largest blooms (40–80% *Guembelitra*) in low and middle latitudes. Only minor *Guembelitra* blooms (10–20%) occurred in high latitudes. The most intense *Guembelitra* blooms (>60% *Guembelitra*) occurred in shallow continental shelf areas, slope/shelf margins and volcanic provinces of the Indian Ocean although their temporal and geographic distributions are still poorly known.

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## Appendix A

### A.1. Taxonomic Notes

*Guembelitra cretacea* (Cushman, 1933). This is the most common and easily recognized species of the genus *Guembelitra* in low and middle latitudes. *G. cretacea* is a small triserial, with globular chambers, depressed sutures, finely perforate wall and semicircular aperture.

*Guembelitra trifolia* (Morozova, 1961) is distinguished from *Guembelitra cretacea* by its smaller size, very low spire and rapid chamber increase. This morphotype is often lumped with *G. cretacea*. Its sporadic occurrence suggests an ecologic affinity.

*Guembelitra irregularis* (Morozova, 1961) is characterized by its high spire and irregular stacking of chambers. This species is very common in some Danian and Maastrichtian environments.

*Guembelitra dammula* (Voloshina, 1961) is characterized by its very high spire and very regular stacking of chambers. In some cool to temperate Maastrichtian environments (e.g., Bulgaria, Madagascar), this species dominates.

*Guembelitra danica* (Hofker, 1978) is also characterized by a high spire and regular stacking of chambers, but is generally smaller than *Guembelitra dammula*. *G. danica* is abundant in the Danian of Denmark. It is possible that this is a morphotype of *G. dammula*.

*Zeauvigerina waiparaensis* (Jenkins, 1966). This species has a small biserial test, sometimes slightly twisted, with weakly inflated chambers and a broad outline. Chambers increase slowly and evenly in size, with 4–7 pairs of overlapping chambers. The final pair of chambers is usually compressed and the oval aperture rimmed by a narrow lip. The test surface is characteristically covered by pustules, except for the final pair of chambers. A full treatment of the genus *Zeauvigerina* and the *waiparaensis* morphotypes is given by Huber and Boersma (1994).

Remarks: *Zeauvigerina waiparaensis* was originally described from the lower Paleocene of New Zealand (Jenkins, 1966) and was considered restricted to the Tertiary. Subsequently, Keller (1993) found this species to be abundant in upper Maastrichtian sediments of the South Atlantic DSDP Site 783. Since then, the species has been reported from many southern and northern high latitude sequences. Huber and Boersma (1994) report its earliest appearance just below the FAD of *Abathomphalus mayaroensis* on Lord Howe Rise, DSDP Site 208.

*Zeauvigerina parri* (Finlay, 1939). This morphotype is very similar to *Zeauvigerina waiparaensis* but with the final chambers much reduced.

*Chiloguembelina midwayensis* (Cushman, 1940). This is a distinctive small, compressed biserial species with rounded periphery and rapidly increasing chambers. This species first appears in the early Danian zone Pla.

*Chiloguembelina claytonensis* (Loeblich and Tappan, 1957). This small species has 3 to 4 pairs of

chambers, a slightly twisted test and a characteristic low slit-like aperture.

*Woodringina hornerstownensis* (Olsson, 1960). This species is characterized by 5–6 pairs of inflated chambers, a highly arched aperture and strongly twisted test.

*Heterohelix globulosa* (Ehrenberg, 1854). This common biserial species has a highly variable size, globular chambers and semicircular aperture. It is abundant in Maastrichtian sediments and survived into the early Danian zone Pla (Barrera and Keller, 1990; Keller et al., 1993).

*Heterohelix dentata* (Stenestad, 1968). This small species has compressed chambers and angular periphery. It is distinguished from *Heterohelix navarroensis* by the absence of an initial coil.

*Heterohelix navarroensis* (Loeblich, 1951). This small, compressed biserial species is easily identified by its coiled initial chambers. The species is common to abundant in some late Maastrichtian sequences.

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