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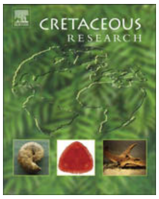

Biotic effects of environmental catastrophes at the end of the Cretaceous and early Tertiary: *Guembelitria* and *Heterohelix* blooms

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ABSTRACT

In this study we report similar biotic response patterns in planktic foraminiferal assemblages, whether in association with volcanism, impacts or climate change at the end of the Cretaceous and early Tertiary. During and after each type of catastrophe two groups dominate high stress assemblages: (1) the small *Guembelitria* species, which are interpreted as having thrived in eutrophic surface waters where other species rarely survived; and (2) the low oxygen tolerant small *Heterohelix* species, which thrived at times of an expanding oxygen minimum zone associated with high nutrients and a stratified water column. The ecosystem collapse appears to be primarily the result of high macro- and micronutrient influx (from impacts, volcanism and erosion) leading to eutrophication and phytoplankton blooms (i.e., primary producers) that result in toxic conditions for foraminifera. Once nutrients decrease due to consumption by phytoplankton, the first opportunistic foraminifera, the *Guembelitria,* appear and graze on phytoplankton, rapidly reproduce (heterochronic acceleration) and increase populations exponentially. With nutrient depletion *Guembelitria* populations rapidly decrease leading to ecologic niches for other generalists and ecosystem recovery. Small low O_2 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 watermass, oligotrophic conditions are restored opening habitats for large, highly specialized species and a return to normal diverse assemblages. Such highly stressed ecological successions are observed in association with mantle plume volcanism in the Indian Ocean, Andean volcanism in Argentina and shallow inland seas in Egypt and Madagascar during the late Maastrichtian, the K-T impact, volcanism during the early Danian, and intense upwelling and climate extremes. We present a simple model to explain the ecological succession and recovery phases that follow major biotic perturbations.

1. Introduction

Guembelitrids and small heterohelicids form two groups of small triserial and biserial planktic foraminiferal species that are sporadically known from the middle Cretaceous to the Recent and thus form some of the longest ranging plankton groups.

Small *Heterohelix* species are generally considered as tolerant of low oxygen conditions and thrived within the oxygen minimum zone (e.g., Kroon and Nederbragt, 1990; Barrera and Keller, 1994; Leckie, 1987; Leckie et al., 1998; Nederbragt et al., 1998; Keller et al., 2001; Keller and Pardo, 2004a). A relative abundance increase in these species therefore indicates an expansion of the oxygen minimum zone, which is normally associated with increased surface productivity and the depletion of oxygen in subsurface waters due to oxidation of organic carbon (Hart and Ball, 1986). Heterohelicids thus appear to have evolved to take advantage of low oxygen conditions, as evident in the oceanic anoxic event (OAE2) of the Cenomanian-Turonian transition where this group thrived to the exclusion of most other species and the shift to *Heterohelix* dominated assemblages is an important global marker of OAE2 (Leckie et al., 1998; Luciani and Cobianchi, 1999; Nederbragt and Fiorentino, 1999; Keller et al., 2001; Keller and Pardo, 2004a; Coccioni and Luciani, 2004, 2005).

In contrast to heterohelicids, little is known about environmental affinities or even the stratigraphic distributions of *Guembelitria* species. This is largely due to their small size, <100 μm or even <38 μm in extreme stress conditions (Keller et al., 1995), and generally sporadic occurrences. *Guembelitria* species are best known from the aftermath of the Cretaceous-Tertiary (K-T) mass extinction where they are the most successful longterm survivors. Because they thrived in the aftermath of the mass extinction and formed major plankton blooms, they are known as disaster

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opportunists. However, their ecology is still little understood. The frequent association of *Guembelitria* blooms with shallow water environments suggests that they may be restricted to continental margins or upwelling areas (Leckie, 1987; Kroon and Nederbragt, 1990; Koutsoukos, 1994, 1996; Schmitz et al., 1992; Keller et al., 1993, 1998, 2002a,b; El-Sabbagh et al., 2004; Adatte et al., 2005; Coccioni and Luciani, 2006), but no specific environmental conditions have been identified to date (e.g. salinity, temperature, oxygen, nutrients).

In this report we present new high latitude data that bolster the case for nutrient-rich to eutrophic environments related to volcanism and high terrestrial runoff conditions during the late Maastrichtian and early Tertiary in Argentina and compare these to published records of DSDP Site 216 (Ninetyeast Ridge, Indian Ocean) and Gebel Qreiya, Egypt. We demonstrate that *Heterohelix globulosa* and other small biserial species (e.g., *H. navarroensis, H. dentata*) invariably are the first species to thrive after environmental conditions improve and *Guembelitria* blooms decrease. In addition, we present new stable isotope data of *Guembelitria, Heterohelix globulosa, Woodringina hornerstownensis, Zeauvigerina waiparaensis* and benthic species that demonstrate nutrient-rich to eutrophic environments during the late Maastrichtian and early Danian.

2. Biostratigraphy

In this report the biozonation of Keller et al. (1995) is used for the Danian and of Pardo et al. (1996) and Li and Keller (1998a) for the Maastrichtian (Fig. 1). This zonal scheme has significantly higher age resolution for both Maastrichtian and Danian sequences than other commonly used zonations (e.g., Berggren et al., 1995; Caron, 1985). Of particular importance for this study is the subdivision of the late Maastrichtian *Abathomphalus mayaroensis* zone into four zones providing excellent correlation and age control for the *Guembelitria* and *Heterohelix* blooms. The first appearance of Danian species is an especially critical K-T boundary marker in very shallow or high latitude sequences where large, specialized tropical species that characterize the mass extinction are absent. Most of the quantitative studies used in this report have employed this zonal scheme successfully across latitudes.

3. Late Maastrichtian planktic foraminiferal assemblages: *Guembelitria* and *Heterohelix* blooms

Many workers have reported *Guembelitria* in late Maastrichtian sediments, but it was Abramovich et al. (1998) who first called attention to discrete *Guembelitria* blooms in the late Maastrichtian of the eastern Tethys (Israel). Since then, quantitative studies have confirmed the presence of *Guembelitria* blooms in numerous localities and across latitudes in Cretaceous foraminiferal (CF) zones CF4, CF3, CF2 and CF1 spanning from 68.3 to the K-T boundary (see review in Keller and Pardo, 2004b, Fig. 2A, Table 1). This indicates that catastrophic environmental conditions comparable to the K-T boundary event were intermittently approached at various times during the late Maastrichtian, but caused no species extinctions. They reveal periods of highly stressed environments that presage the terminal Cretaceous mass extinction.

A brief review of planktic foraminiferal assemblages during the late Maastrichtian and early Danian provides the context in which *Guembelitria* and *Heterohelix* blooms flourished and helps us understand the climatic and environmental evolution before and after the end-Cretaceous mass extinction. For more detailed discussions the reader is referred to Keller (2001).

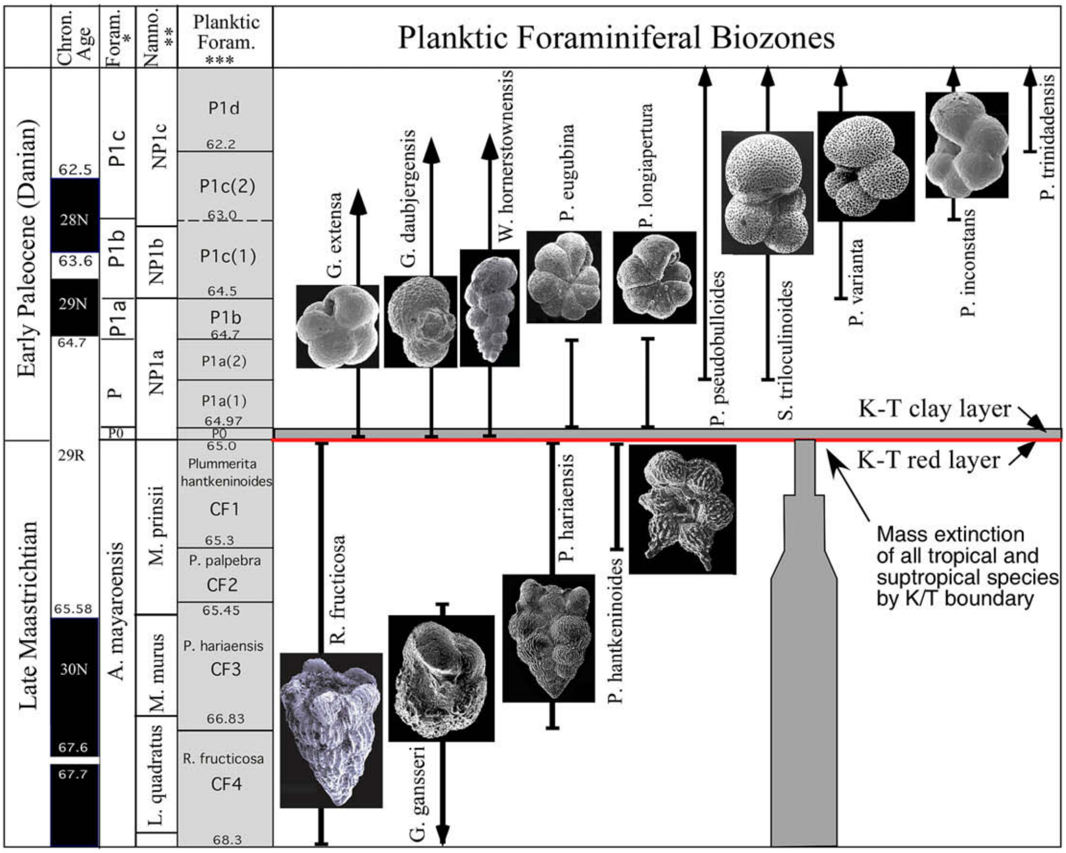

Fig. 1. High resolution planktic foraminiferal biozonation of Keller et al. (1995) and Li and Keller (1998a) used in this study and illustrations of index species. Calcareous nannofossils after Tantawy (2003). The biozonation of Berggren et al. (1995) is given for reference and correlation.

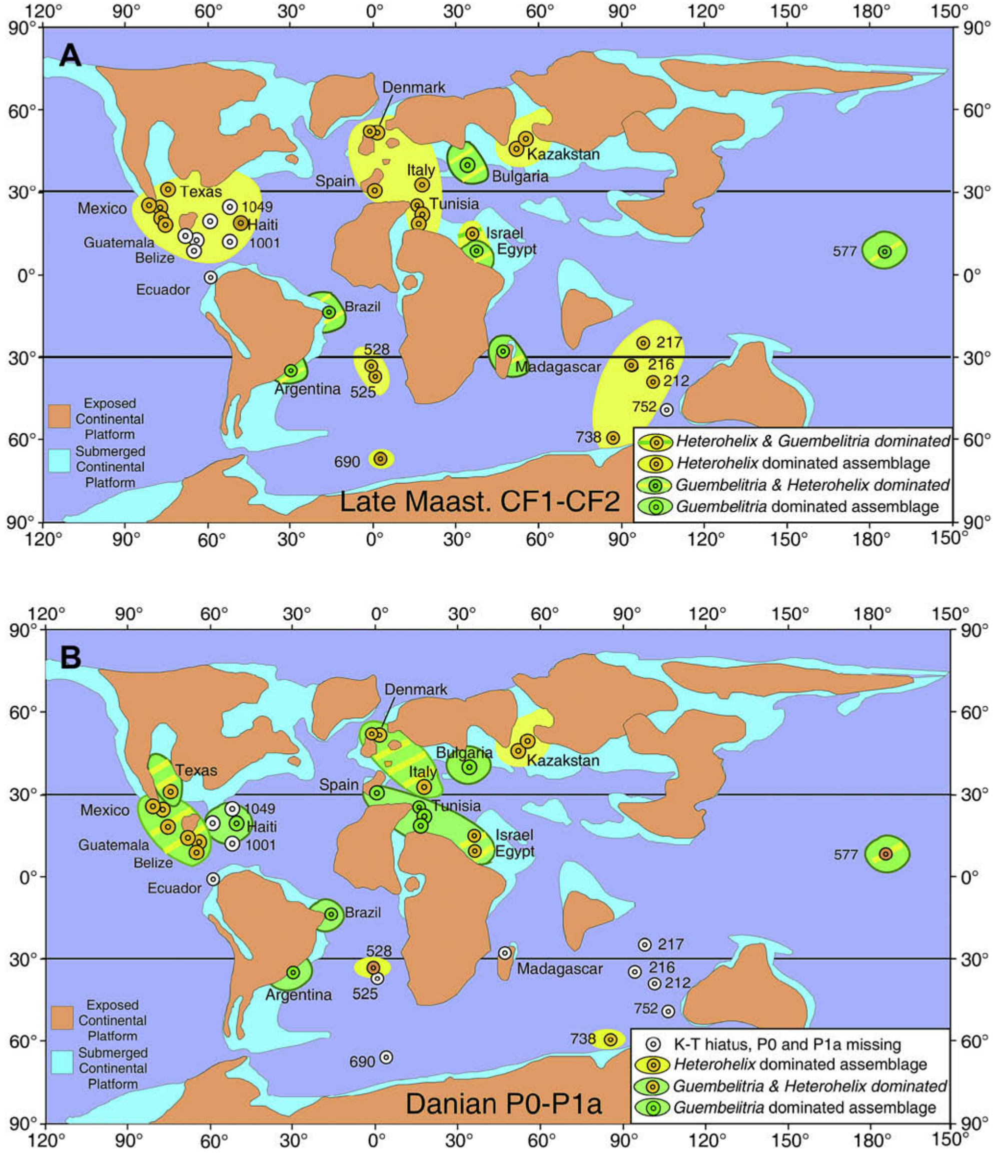

Fig. 2. A. Biogeographic distribution of *Guembelitria* and *Heterohelix* blooms during the late Maastrichtian zones CF1-CF2. Small *Heterohelix* species dominated in open marine and continental shelf areas, wheras *Guembelitria* dominated in restricted basins and upwelling areas. Modified from Keller and Pardo (2004b). For references on data set see Table 1. B. Biogeographic distribution of *Guembelitria* and *Heterohelix* blooms during the early Danian zones P0 and P1a. Note that in the aftermath of the K-T mass extinction Guembelitria dominated the Tethys Seaway, but survivor populations of *Heterohelix globulosa* (identified by their Danian δ^{13}C values) persisted in the shallow environments of Texas and Denmark. *Heterohelix* species also are commonly present in the early Danian in Mexico and Italy and may represent survivor populations. High latitudes in the north and south were dominated by heterohelicid survivors (*H. globulosa and Z. waiparaensis*). For references on data set see Table 1.

During the late Maastrichtian (zones CF4 to CF1) optimum environments for planktic foraminifera are primarily found in oligotrophic open marine settings. These environments generally show relatively high species diversity (~55–60 species in >63 μm fraction) with assemblages dominated (~60%) by small heterohelicids (*Heterohelix globulosa, H. dentata, H. navarroensis*). These heterohelicid dominated assemblages reveal the late Maastrichtian optimum environment as a well stratified ocean with a cool climate (zones CF4-CF3) and relatively high productivity, indicated by oxygen and carbon isotope data, and an expanded oxygen minimum zone (OMZ, inferred from the high abundance of low oxygen tolerant heterohelicids). In some localities late Maastrichtian assemblages contain intermittent *Guembelitria* peaks (~30%), or may even be dominated by *Guembelitria* species (e.g., Abramovich et al., 1998, 2002; Keller, 2002, 2003). These triserial foraminiferal blooms reveal periods of increased biotic stress and are generally associated with decreased species diversity and/or dramatically reduced species abundances of oligotrophic species.

During the latest Maastrichtian zones CF2-CF1 species diversity gradually decreased, apparently associated with the rapid global warming between 400–150 ky before the K-T boundary (Li and Keller, 1998b,c; Kucera and Malmgren, 1998; Olsson et al., 2001; Abramovich and Keller, 2002, 2003). At this time, globotruncanids and other large tropical and subtropical taxa (e.g., *Racemiguembelina*, some *Planoglobulina, Rugoglobigerina, Pseudoguembelina*) rapidly decreased in abundance from about 10% to <5% of the total planktic foraminiferal assemblages by K-T time. During the maximum warming most large species experienced high stress and in response reduced their sizes (Abramovich and Keller, 2003). It is largely this tropical and subtropical species group that suffered mass extinctions at the K-T boundary.

Compared with the open ocean, faunal assemblages in marginal or shallow seas and nearshore environments, as well as in high

Table 1
K-T sections with quantitative planktic foraminiferal databases, isotope stratigraphy and geochemistry

Location/Site	Section	Paleoenvironment	Literature with faunal data used in this study
Tethys shelf and continental margin settings			
TUNISIA	El Kef	outer neritic-upper bathyal	Brinkhuis and Zachariasse, 1988; Keller, 1988a,b, 1992; Keller and Lindinger, 1989; Keller et al., 1995, 2002a; Speijer and van der Zwaan, 1994; 1996; Stueben et al., 2002b; Culver, 2003
	Elles	middle neritic	Abramovich and Keller, 2002; Keller et al., 2002a; Rocchia et al., 1996
	Seldja	inner neritic (littoral)	Keller et al., 1998; Culver, 2003
	Ain Settara		Arenillas et al., 2000; Luciani, 2002
EGYPT	Qreiya	middle neritic	Luger, 1988; Keller, 2002; Keller et al., 2002b; Tantawy, 2003;
	Nezzazat, Bir El-Markha	middle neritic	El Sabbagh et al., 2004
ISRAEL	Negev Mishor Rotem, Givat Mador, Ein Mor, Hor Hahar, Ben Gurion,	middle-upper bathyal	Keller and Benjamini, 1991; Magaritz et al., 1992; Speijer and van der Zwaan, 1994; Abramovich et al., 1998; Keller, 1992, 2004; Adatte et al., 2005
SPAIN	Agost	outer neritic, upper-middle bathyal	Canudo et al., 1991; Pardo et al., 1996; Pardo, 1999; Molina et al., 1996, 2005; Alegret et al., 2003
ITALY	Erto	outer neritic-upper bathyal	Luciani, 1997
SOUTHERN USA	Brazos, TX	middle-inner neritic	Keller, 1989, 1992; Barrera and Keller, 1990; Culver, 2003
	Alabama		Rocchia et al., 1996; Liu and Olsson, 1992;
NE MEXICO	El Mimbral, El Penon, Loma Cerca, La Lahilla, La Sierrita, Coxquihui, El Mulato, Mesa Juan Perez, Los dos Plebes, Rancho Nuevo, Rancho Canales, Las Ruisas	lower, middle, upper bathyal	Keller et al., 1994, 1997a, 2002c, 2003a; Lopez Oliva and Keller, 1996; Lopez-Oliva, 1996; Rocchia et al., 1996; Alegret et al., 2002; Alegret and Thomas, 2001; Stueben et al., 2005
CENTRAL MEXICO	Tlaxcalantongo, Coxquihui		Lopez-Oliva, 1996; Lopez-Oliva and Keller, 1996 Stinnesbeck et al., 2002a
SOUTH MEXICO	Bochil, Trinitaria,		Keller et al., 2003a; Arenillas et al., 2006
GUATEMALA	El Caribe, Actela	middle and inner neritic	Stinnesbeck et al., 1995; Keller and Stinnesbeck, 2000
BELIZE	Santa Theresa, San Jose Quarry, Armenia, Albion		Keller et al., 2003b
HAITI	Beloc (4 sections)	upper bathyal	Keller et al., 2001; Stueben et al., 2002a Stinnesbeck et al., 2000b; Maurrasse et al., 2005
Northern Tethys and high latitudes			
BULGARIA	Bjala	upper bathyal	Adatte et al., 2002
KAZAKSTAN	Koshak	shallow epicontinental sea	Oberhänsli et al., 1998; Pardo, 1999; Pardo et al., 1999; Pardo and Keller, 1999
	Kyzylsai	shallow epicontinental sea	Pardo, 1999
DENMARK	Nye Klov, Stevns Klint	inner to middle neritic	Schmitz et al., 1992; Keller et al., 1993; Barrera and Keller, 1994 Hart et al., 2004, 2005
EQUATORIAL PACIFIC DSDP Site 577			D'Hondt and Keller, 1991
Southern Middle Latitudes			
DSDP Sites 525 and 528		bathyal	D'Hondt and Keller, 1991; Li and Keller, 1998b,c; Abramovich and Keller, 2003
Southern High Latitudes			
ODP Sites 738 and 690		lower bathyal	Keller, 1993; Barrera and Keller, 1994
MADAGASCAR	Amboanio, Berivotra	inner to outer neritic	Abramovich et al., 2002
NINETY E. RIDGE DSDP Site 216		inner to outer neritic	Keller, 2003, 2005
	Sites 212, 217		this study & unpublished
BRAZIL	Poty Quarry, Recife	middle neritic	Stinnesbeck and Keller, 1994; Keller and Stinnesbeck, 1996;
ARGENTINA	Neuquen Basin	middle neritic	Sasso et al., 2005; Keller et al., 2007
ECUADOR	Guaiaquil	bathyal	Keller et al., 1997b

latitudes, show strongly reduced species diversity (15–30 species) intermittently dominated by the *Heterohelix/Guembelitria* groups. These faunal assemblages indicate generally much higher stress conditions than open marine environments, with intervals dominated by *Guembelitria* bordering on biotic catastrophe conditions similar to the K-T boundary event (e.g., Keller, 2002, 2003).

The K-T mass extinction decimated planktic foraminiferal assemblages, eliminating struggling tropical and subtropical populations that account for about 2/3 of the species group, but less than 10% of the individuals in the toal foraminiferal population. The small cosmopolitan species that thrived in high latitudes and marginal marine environments generally survived for at least a couple of hundred thousand years. All but *Guembelitria* and the high latitude heterohelicid *Zeauvigerina* species gradually disappeared in the early Danian zone P1a. Their extinction was related to competition of evolving Danian species highly adapted to the changing environment (*cf.* Keller and Pardo, 2004b). Whithin this longterm trend leading up to the K-T mass extinction, guembelitrid and heterohelicid blooms reveal a sequence of environmental extremes that presages the mass extinction. After the mass extinction, their blooms reveal the continued high stress environment of the post-K-T world. It is these guembelitrid and heterohelicid blooms that are explored in this study beginning with the aftermath of the mass extinction because this is where *Guembelitria* blooms are generally recognized.

4. Aftermath of the K-T mass extinction: Danian zones P0 and P1a

Guembelitria blooms are best known from the aftermath of the K-T mass extinction, when they reached abundances of 80–100% in zone P0 and continued to dominate in zone Pla. At these times, various *Guembelitria species* flooded planktonic ecosystems from shallow to deep and low to middle latitudes worldwide (Fig. 2B).

However, maximum abundances (*Guembelitria* dominant) are observed in the Tethyan seaway from Israel, Egypt, Tunisia to Spain, Caribbean and southern USA. In some of these areas *Guembelitria* initially shared the environment with *Heterohelix* in the immediate aftermath of the mass extinction (e.g., Central America, Western Interior Seaway, eastern Tethys, Italy to Denmark, striped intervals in Fig. 2B). Beginning in zone P1a Cretaceous heterohelicids are replaced by Danian biserial species (e.g., *Woodringina hornerstownensis, Chiloguembelina claytonensis, C. midwayensis*), which presumably competed for the same ecologic niches as discussed below. Apart from the Tethys, *Guembelitria cretacea* also dominated in the shallow Neuquen basin of Argentina and the Paraiba basin of Brazil. All of these sequences were either deposited in very shallow nearshore areas or in upwelling regions characterized by high nutrients from upwelling, terrestrial organic matter and in some areas volcanism (e.g., Neuquen Basin of Argentina).

The record in higher latitudes is sparse because K-T hiatuses generally span the early Danian, particularly in the southern hemisphere (Keller, 1993; MacLeod and Keller, 1994). Where the early Danian zones P0-P1a are present, *Guembelitria* species are minor constituents (10–20%) and *Z. waiparaensis* is the dominant taxon of typically low diversity foraminiferal assemblages. The most intense *Guembelitria* blooms (>60% *Guembelitria*) occurred in shallow continental shelf areas, slope/shelf margins, and volcanic provinces. What all these environments have in common is high nutrient influx either from continental runoff, upwelling along continental margins, or volcanic input.

In the early 1990's, *Zeauvigerina waiparaensis,* was discovered to be the dominant species in late Maastrichtian sediments of ODP Sites 738 and 690 (Keller, 1993), showing that it thrived in the aftermath of the K-T mass extinction reaching nearly 100% in zone P0. Subsequently, *Z. waiparaensis* was also found to dominate northern high latitudes during the late Maastrichtian and early Danian (Pardo, 1999; Pardo et al., 1999; review in Keller and Pardo, 2004b). However, apart from *Z. waiparaensis* and *Guembelitria*, it is commonly assumed that most or all other Cretaceous species in the Danian must be reworked. Although reworking of Cretaceous species is common in the early Danian, there is strong evidence that about 1/3 of the Cretaceous species survived at least into zone P1a (review in MacLeod and Keller, 1994). In the shallow marine environments of Denmark and Texas (Brazos River), small heterohelicids (particularly *H. globulosa, H. dentata, H. navarroensis*) are common in the early Danian well into zone P1a (Keller, 1989; Schmitz et al., 1992; Keller et al., 1993).

The negative carbon isotope shift across the K-T boundary, provides a test for survivorsip. If δ^{13}C values of *Heterohelix* species in Danian sediments show the same signals as in the Cretaceous, they are reworked. In sections from both Denmark and Texas δ^{13}C values of *H. globulosa* show a gradual negative shift at the K-T boundary and Danian values in the upper zones P0 and Pla (Barrera and Keller, 1990; Barrera and Keller, 1994; Keller et al., 1993), showing that *Heterohelix globulosa* survived the K-T mass extinction at least for a couple of hundred thousand years. However, the adaptation to the Danian high stress environment was accompanied by dwarfing, which takes advantage of the nutrient supply by means of heterochronic acceleration (MacLeod et al., 2000).

Cretaceous heterohelicids are also common in early Danian sediments from the eastern Tethys (Negev and Sinai, Keller and Benjamini, 1991; Keller, 2004; El-Sabbagh et al., 2004), Italy (Luciani, 1997), Central America (Lopez-Oliva, 1996), and equatorial Pacific DSDP Site 577 (striped intervals in Fig. 2B, Table 1). Their presence is generally assumed to be due to reworking, though no carbon isotopic test has been done to date to assess this assumption. Sedimentary sequences with high heterohelicid abundances generally tend to have higher total organic carbon (TOC) than intervals with low heterohelicids and guembelitrids, but relatively lower TOC than intervals dominated by *Guembelitria*. This pattern reflects the nutrient-rich environments in which both *Heterohelix* and *Guembelitria* thrived.

5. Biotic effects of volcanism

The alternating *Guembelitria/Heterohelix* dominated late Maastrichtian phases that mimic the response to the K-T catastrophe and ensuing mass extinction can reveal critical factors, other than impacts, leading to environmental presssure in marine plankton. In particular, two sequences, one on Ninetyeast Ridge in the Indian Ocean and the other in the Neuquen Basin of Argentina, reveal the direct role of volcanism in environmental catastrophes.

5.1. DSDP Site 216, Ninetyeast Ridge, Indian Ocean

During the late Maastrichtian, Site 216 passed over a mantle plume leading to volcanic eruptions, islands built to sea level, followed by rapid subsidence, and catastrophic environmental conditions for planktic and benthic foraminifera (Keller, 2003, 2005). By about 500 kyr before the K-T boundary, Site 216 passed beyond the influence of mantle plume volcanism and the fauna slowly recovered - only to be hit by the K-T mass extinction. The striking correlation between late Maastrichtian volcanism and its biotic effects at Site 216 and the biotic effects of the K-T event demonstrates that volcanism and impacts can cause similar environmental catastrophes.

Ninetyeast Ridge volcanism decimated the foraminiferal populations leaving guembelitrids as dominant (>80%) survivors with small heterohelicids plus rare globigerinelloids and hedbergellids. The same species survived the K-T mass extinction. With initial improvement in environmental conditions guembelitrids decreased and heterohelicids dominated along with increasing abundance of small hedbergellids and globigerinellids (Fig. 3). Large specialized species reappeared when environmental conditions return to normal, as indicated by the absence of *Guembelitria,* decreased abundance of *Heterohelix*, diminished volcanic influx and return to limestone deposition.

The δ^{13}C isotope composition of bulk carbonate mirrors this trend, except for the high negative values in the organic-rich base of the section. These values most likely reflect ^{12}C enrichment due to diagenetic calcite formed by mineralization of organic matter. Through the high stress intervals (volcanic sediments) dominated by *Guembelitria* and *Heterohelix*, δ^{13}C values remain very low, between 0 and +0.5‰. After volcanic input ceased, δ^{13}C values in the limestone unit increased to about 2‰, which is comparable to the average values in coeval sections from similar latitudes (e.g., DSDP Site 525; Li and Keller, 1998c). The low δ^{13}C values during the high biotic stress interval thus indicate the marked reduction in primary productivity as a consequence of the toxic environmental conditions generated by the volcanic activity during passage over the mantle plume. The gradual increase to normal δ^{13}C values reflects the increase in primary productivity (Fig. 3).

This interpretation is supported by analysis of trace elements in benthic foraminiferal tests of Site 216, which revealed intense volcanic activity by the covariance of Co, Cu, Zn and Pb, Pb isotope ratios and bulk rock element contents. Of most interest to the biotic response, and in particular the *Guembelitria/Heterohelix* variations, are the micronutrients Cd and Ni, which are considered indicators for increased primary productivity (Fig. 3, factor scores of Cd and Ni calculated using the Ca-normalized trace element concentrations in foraminiferal tests of Site 216). The simultaneous increase in the concentration of these elements with the δ^{13}C values in the uppermost part of the section, and decrease of TOC is consistent with the biotic recovery and increased foraminifera productivity

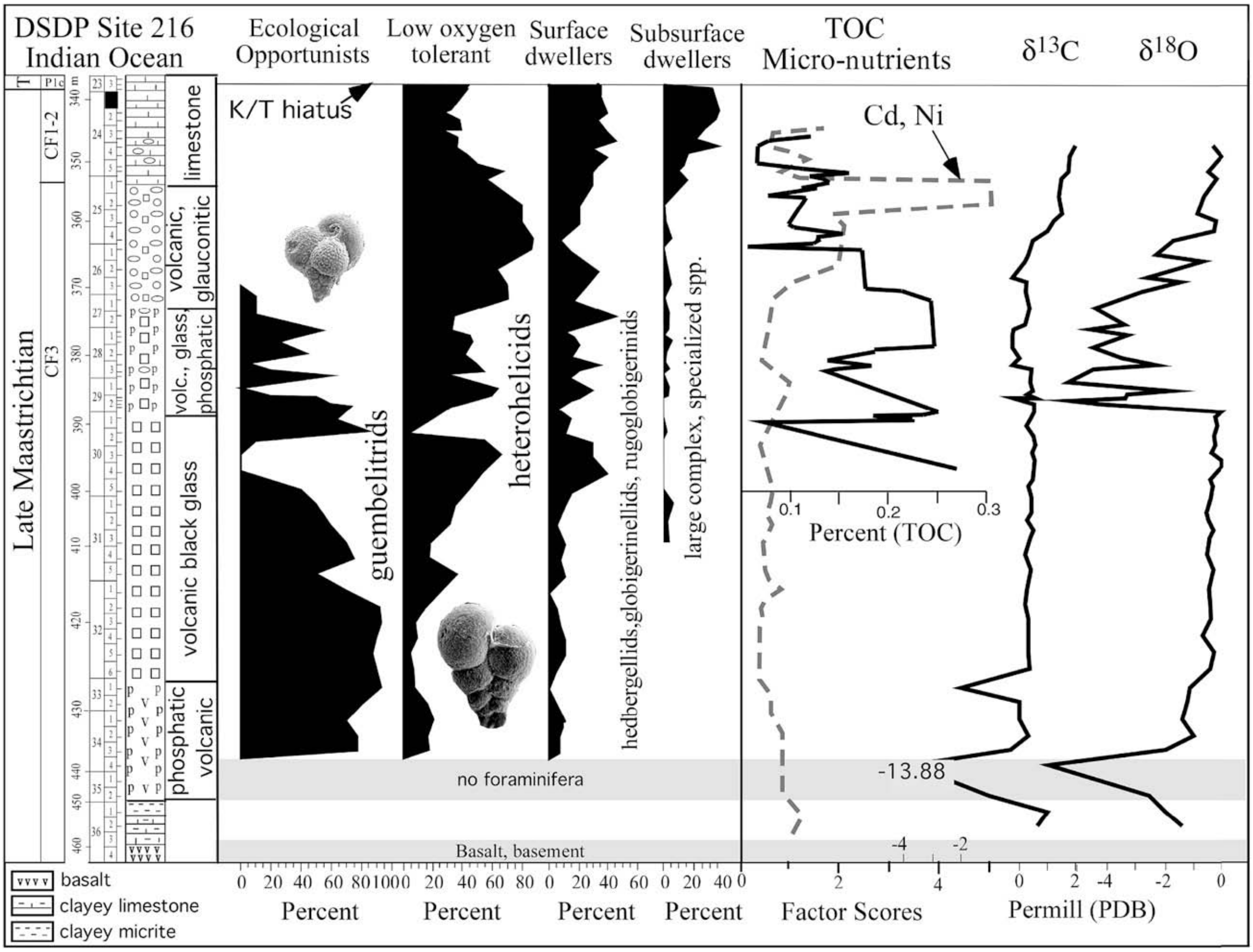

Fig. 3. Late Maastrichtian planktic foraminiferal abundances, oxygen and carbon isotopes, TOC, and micronutrients Ni and Cd (factor scores calculated using the Ca-normalized trace element concentrations in foraminifera tests). Data from Adatte (unpubl.) and Keller (2003). Note that high-stress intervals are dominated by *Guembelitria* and *Heterohelix*, low $\delta^{13}C$ values, and volcanic sediments rich in phosphate and glauconite. Return to normal biotic conditions coincides with increased $\delta^{13}C$ values (higher productivity), low TOC and increased micronutrients.

after Site 216 passed beyond the influence of Ninetyeast Ridge volcanism.

The $\delta^{18}O$ data roughly parallel the $\delta^{13}C$ values in the lower part of the section, with the remarkably stable values (0 and −0.5‰) comparable Site 525 (e.g., Li and Keller, 1998c) and the extreme low value due to diagenetic alteration. In the upper volcanic and phosphate-rich unit, a sharp drop in the isotope records from 0.0 to −4.8‰, followed by strong fluctuations suggests a periodic influx of warm hydrothermal fluids into the seawater during deposition. The gradual $\delta^{18}O$ increase in the glauconite-rich unit marks the onset of a general recovery, as also indicated by the increased $\delta^{13}C$ values, decrease in *Heterohelix* abundance at the top coincident with the re-appearance of large specialized species (Fig. 3).

5.2. Bajada de Jaguel, Neuquén Basin, Argentina

During the Maastrichtian an extensive marine transgression flooded the Neuquén Basin in west-central Argentina. The transgression was connected to the opening of the South Atlantic to the east and reached the area of the present Andes to the west. In the southeastern part of the Neuquén Basin, marine environments persisted into the Paleogene. Towards the west contemporaneous volcanic activity led to emergence in the area of the present Andes, which separated the Neuquén basin from the Pacific (Uliana and Biddle, 1988).

The K-T sections of this region were first reported by Bertels (1970, 1980) followed by more detailed microfossil studies by Concheyro and Nañez (1994), Scasso et al. (2005) and integrated studies of planktic foraminifera, stable isotopes and mineralogy by Keller et al. (2007). Late Maastrichtian sediments in the Neuquén basin consist of claystones and silty claystones with four prominent volcanic-rich layers. Abundant smectite throughout the section appears partly derived from argillized submarine volcanic rocks from the nearby volcanic arc. Total organic carbon (TOC) is relatively low in the late Maastrichtian (0.15–0.5%) with higher values corresponding with higher species diversity. Consistently higher TOC values (0.5–0.6%) occur in the Danian. The relatively low TOC values are likely due to weathering, as indicated also by the high marine productivity reflected in $\delta^{13}C$ values (Fig. 4). A significant and relatively constant nutrient input into the Neuquén Basin occurred from the Atlantic and surrounding extensive land areas, including an active volcanic arc to the West. Volcaniclastic input and the presence of dominant smectite suggest continuous volcanic activity with several major volcanic eruptions during the late Maastrichtian. Deposition occurred in a relatively shallow middle shelf environment (Scasso et al., 2005; Keller et al., 2007).

Planktic foraminiferal assemblages are dominated by alternating abundances of very small *Guembelitria* and *Heterohelix*, each of which reached ∼80% during dominant phases (Fig. 4). Species richness is lowest during *Guembelitria* dominance with only 2–4 species (2 *Guembelitria*, 1-2 *Heterohelix*), and higher during

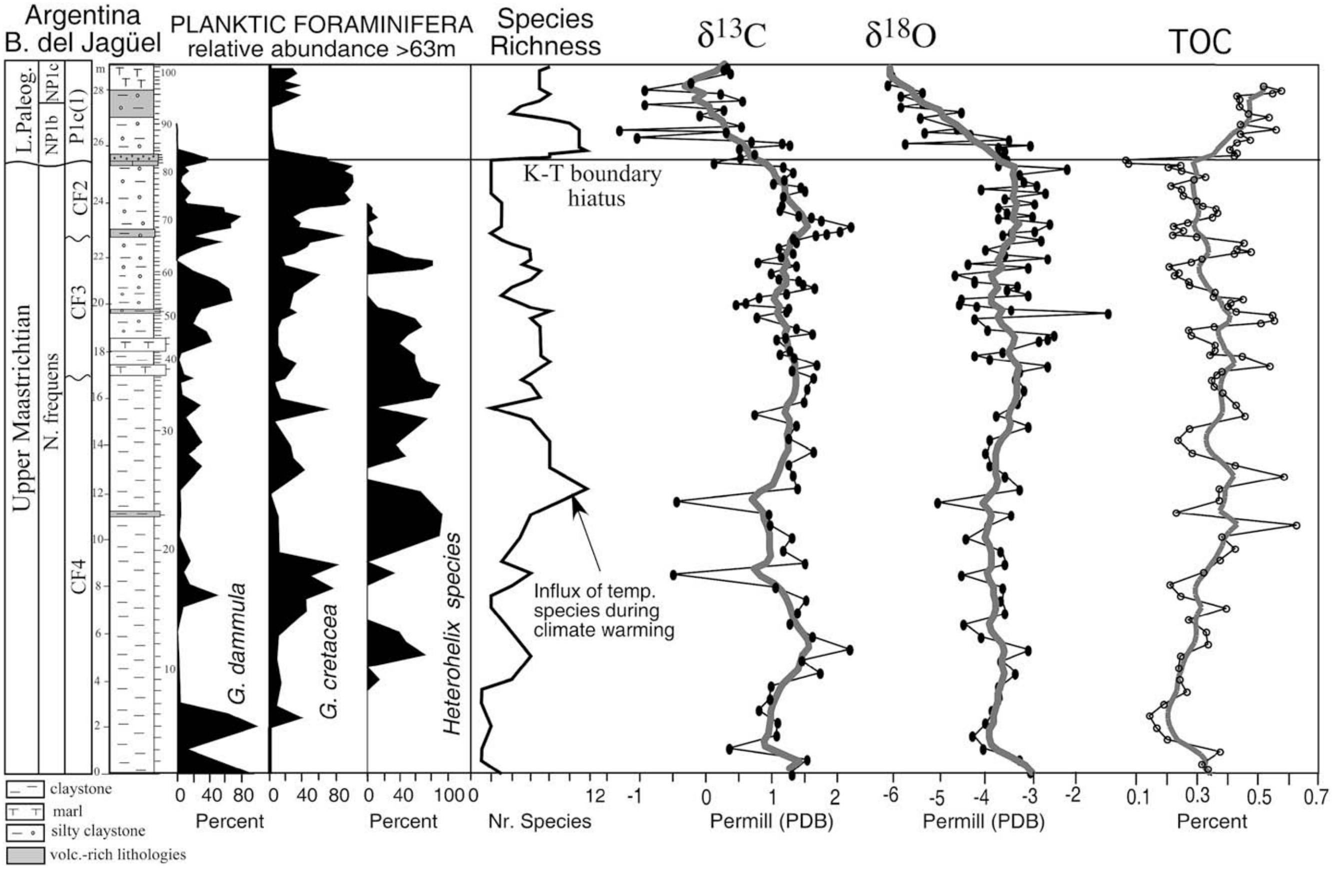

Fig. 4. *Guembelitria* and *Heterohelix* abundances, oxygen and carbon isotope records in the late Maastrichtian and early Danian of the Bajada de Jagüel section in the Neuquen Basin, Argentina. Maximum species richness in zone CF4 reflects an influx of temperate species during climate warming. Zones CF1, P0, P1a, and P1b are missing due to a major hiatus.

Heterohelix dominance reaching a maximum of 8 species (2 *Guembelitria*, 4 *heterohelicids, 1-2 Hedbergella).* Only during a short interval of climate warming in zone CF4 is there a significant increase in species size and species richness (max.12 species) due to an influx of warm temperate species (e.g., *Globotruncana arca, G. aegyptiaca, Gansserina gansseri, Rugoglobigera rugosa*. At this time both *Heterohelix* and *Guembelitria* temporarily decrease to near zero. Stable isotope data reveal this zone CF4 climate warming also in DSDP Site 525A and Site 463 (Li and Keller, 1998c, 1999).

6. Biotic effects of shallow basin and nearshore settings

Volcanism and impacts are not the only causes for the severe biotic crises reflected by *Guembelitria*/*Heterohelix* fluctuations. Some shallow nearshore areas reveal the same late Maastrichtian zone CF4-CF1 patterns with no volcanic influence or impact(s) evident, as for example in Madagascar, Bulgaria, southern Tunisia and Central Egypt (Abramovich et al., 2002; Adatte et al., 2002; Keller, 2002; Keller et al., 1998, 2002a,b; Table 1). The Gebel Qreiya section of the Asiut Basin of central Egypt is an extreme case of late Maastrichtian (zone CF3-CF1) planktic foraminiferal assemblages experiencing high stress conditions comparable to those associated with the K-T mass extinction. At this locality monotonous shale deposition in the Asiut Basin was interrupted by periods of erosion due to local tectonic activity and sea level fluctuations (Keller et al., 2002b). In zone CF3 (66.8–65.4 Ma) the region experienced a prolonged breakdown of the biologically mediated surface-to-bottom gradient of the $^{13}C/^{12}C$ ratio with planktic values 0.2–0.8‰ $\delta^{13}C$ lighter than benthic values (Keller et al., 2002b). This is akin to the inverse gradient observed at the K-T boundary worldwide, which lasted for more than a million years. The late Maastrichtian breakdown in primary productivity occurred during a time of global cooling and sea level regression, though clay mineralogy indicates that locally warm, wet, tropical-subtropical conditions prevailed, as also observed in Israel (Adatte et al., 2005). A normal carbon isotope gradient was re-established during the global warming and rising sea level in zone CF1, between 400–150 kyr prior to the K-T boundary.

This environmental condition is accompanied by generally high, but variable biotic stress, similar to the Bajada de Jaguel section of the Neuquén Basin, though species diversity is significantly higher in Egypt, between 25–30 species, probably due to its low latitude location. *Guembelitria cretacea* reached 80–90% in zone CF3, similar to Site 216, and Bajada de Jaguel. Intervals with low *Guembelitria* are dominated (~80%) by small heterohelicids (mostly *H. navarroensis*). During the zone CF1 climate warming, *Guembelitria* decreased and a more diverse assemblage of heterohelicids dominated along with significant *Plummerita, Rugoglobigerina, Hedbergella* and *Pseudoguembelina costulata* populations (Keller, 2002). This increased diversity signals the return to a normally stratified ocean, as also observed in the return of a normal surface-to-deep $\delta^{13}C$ gradient.

In DSDP Site 216 and the Neuquén Basin of Argentina, the late Maastrichtian high stress conditions can be explained by high volcanic influx and its associated high nutrients leading to nutrient-rich or eutrophic waters. Similarly, in the Mishor Rotem section of the Negev, intensified stress conditions can be linked to volcanic influx and climatic changes. But in the Asiut Basin of Egypt, and Bjala section of Bulgaria, no volcanic influx is detected, though detrital influx is high. This suggests that in Central Egypt the late

Maastrichtian high biotic stress environment of zones CF1-CF3 was primarily linked to the existing shallow shelf setting and possibly local tectonic activity and restricted circulation. This could have led to high nutrient influx and eutrophic waters. Total organic carbon (TOC) is low in these sediments due to sediment dilution, oxidizing bottom waters, and post-depositional alteration evident by the low hydrogen index and high oxygen index values, which suggest that most of the TOC was altered and partly destroyed (Keller et al., 2002b).

7. Stable isotope ranking of *Guembelitria* and *Heterohelix*

Oxygen and carbon stable isotope ranking of planktic foraminiferal species permits determination of the relative depth stratification within the ocean's upper water masses and traces various biological paleo-activities including nutrition. The accuracy and reliability of these interpretations primarily depend on the quality of the analyzed material (e.g. preservation, diagenesis) and effects of environmental variability upon isotopic signals. In contrast, species abundance data quantify a species response to the environmental changes recorded in the stable isotope data. Thus the combination of stable isotope and quantitative species analyses provides a powerful tool for paleoenvironmental studies during the late Cretaceous as recently demonstrated by Abramovich et al. (2003).

Depth ranking of planktic foraminifera is based on the principle that δ^{18}O values of foraminiferal calcite generally increase with depth in the water column due to decreasing temperatures (Fairbanks et al., 1982; Hemleben et al., 1989). In contrast, in normal marine environments δ^{13}C values decrease with depth due to selective removal of ^{12}C by photosynthesis in the euphotic zone and accumulation of ^{12}C in deeper water due to organic matter decay (Bouvier-Soumagnac and Duplessy, 1985). Accordingly, deep planktic foraminiferal species are expected to display the heaviest δ^{18}O and lightest δ^{13}C values, characteristic of cold and respiration-dominated environments below the thermocline (Fairbanks et al., 1982; Hemleben et al., 1989; D'Hondt and Arthur, 1995; Abramovich et al., 2003). However, in eutrophic environments surface waters are highly enriched in ^{12}C due to photosynthesis and phytoplanktic grazers such as plankton foraminifera therefore will display the lightest δ^{13}C values.

It is well documented that K-T boundary sequences in low to middle latitudes show a reversed δ^{13}C surface-to-deep gradient in the early Danian. The fact that in many sequences this reversal already occurred during the late Maastrichtian is less well known and has been an enigma. In the early Danian the reversed gradient is commonly interpreted as the result of the mass extinction and resultant nutrient enrichment leading to a drop of 2–3‰ in δ^{13}C values at the K-T boundary (e.g., Zachos et al., 1989). However, in numerous sections this δ^{13}C excursion occurs gradually (e.g.,

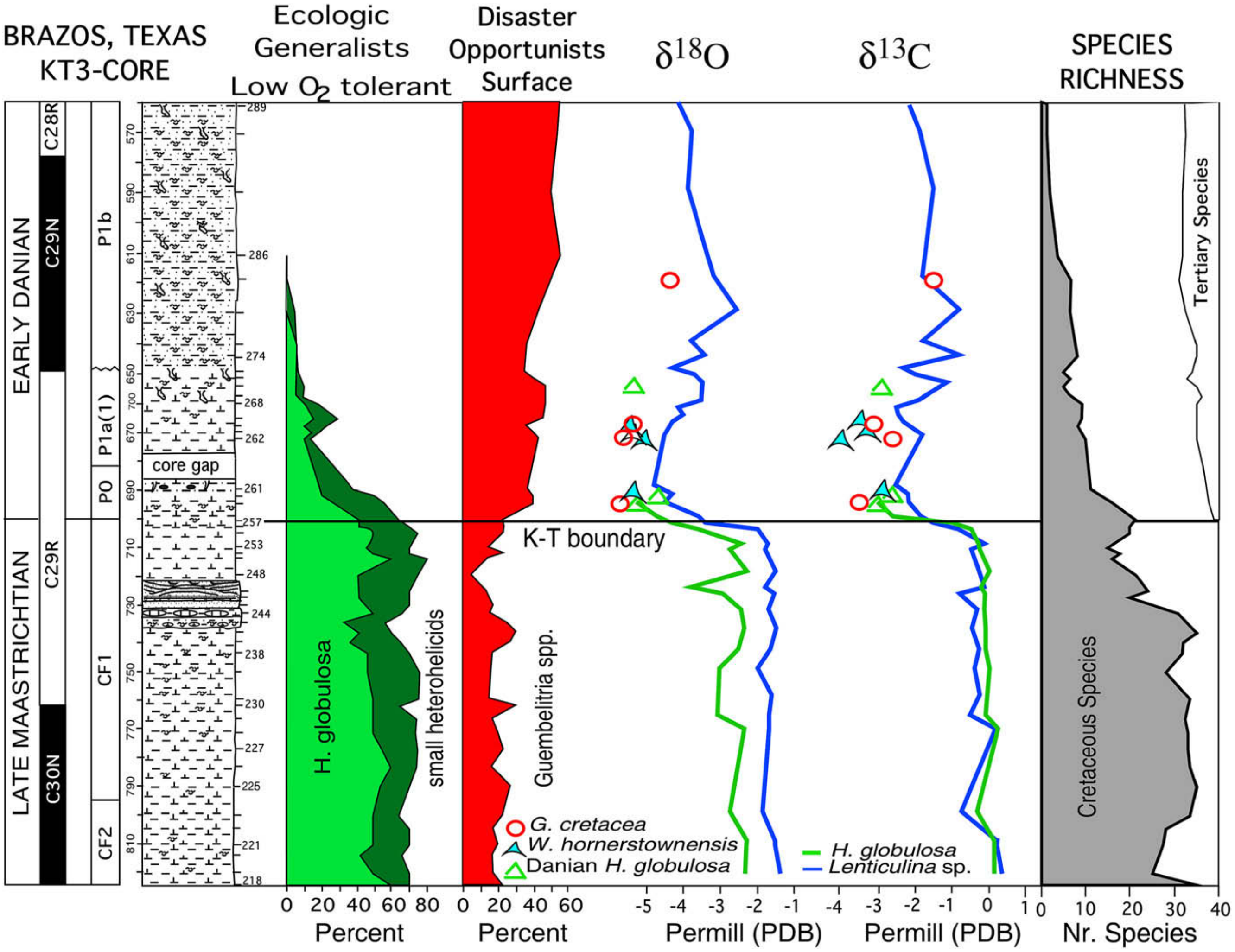

Fig. 5. *Guembelitria* and *Heterohelix* abundances, species richness, oxygen and carbon isotopes from the Brazos KT-3 core (data from Keller, 1989; Barrera and Keller, 1990). Note that survivorship of *H. globulosa* and *Guembelitria* in the early Danian is demonstrated by the Danian isotope values of these species, similar to *Woodringina hornerstownensis*.

Brazos, Texas, Denmark, Egypt) and can therefore not be the result of a geologically instantaneous mass dying. Moreover, in high latitudes the δ^{13}C excursion is relatively minor (~0.5‰) suggesting diminished environmental effects (Barrera and Keller, 1994; Pardo et al., 1999). Here we explore the possibility that the reversed δ^{13}C gradient during the K-T transition may be the result of nutrient-rich to eutropic environments, which depressed plankton productivity. Comparison of stable isotope ranking of heterohelicids and guembelitrids in late Maastrichtian and early Danian sequences lend support to this idea. Stable isotope analysis was performed on well preserved individual species of selected sequences based on methods described in Barrera and Keller (1994).

7.1. Brazos River, Texas

Stable isotopes from well-preserved *Guembelitria cretacea*, *Heterohelix globulosa*, *Woodringina hornerstownensis* and the benthic *Lenticulina* from the KT-3 core along the Brazos River, Texas, were analyzed for the late Maastrichtian zones CF1-CF2 and early Danian zones P0, P1a and P1b. The environmental and geological setting of the Brazos River area has been discussed in numerous sections (e.g., Hansen et al., 1987; Keller, 1989; Barrera and Keller, 1990; Yancey, 1996; Heymann et al., 1998; Schulte et al., 2006; Gale, 2006). At this locality, *Heterohelix globulosa* populations dominate late Maastrichtian assemblages and gradually decrease in the early Danian zones P0 and P1a, coincident with the decrease in δ^{13}C values of *H. globulosa* and the benthic *Lenticulina* species (Fig. 5). It is noteworthy that Danian *H. globulosa* populations record Danian isotopic values, which clearly mark them as K/T survivors, as also observed in the Nye Klov section of Denmark (Barrera and Keller, 1990, 1994; Keller et al., 1993). These data demonstrate that *H. globulosa* survived the K/T mass extinction along with *G. cretacea* and several other Cretaceous species, as also indicated by their paleogeographic distribution (MacLeod and Keller, 1994).

At the Brazos River, planktic δ^{13}C values drop below benthic values in the basal Danian, as is consistently observed in low to middle latitudes (Fig. 5). This reverse surface-to-deep gradient persists through the early Danian zones P0, P1a and P1b with *Guembelitria*, *Woodringina hornerstownensis* and *H. globulosa* survivors consistently recording more negative δ^{13}C values than benthic foraminifera. A δ^{13}C/δ^{18}O plot for each biozone shows that during the late Maastrichtian zones CF1-CF2 δ^{13}C values for benthic *Lenticulina* sp. and *H. globulosa* are similar, though δ^{18}O values are consistently more negative reflecting warmer temperatures (Fig. 6). In the early Danian Zones P0-P1b, *Lenticulina* and *H. globulosa* δ^{13}C values consistently average 2‰ lighter. *Guembelitria cretacea* and *W. hornerstownensis* record the lightest values in zones P0 and P1a, and slightly heavier values in zone Plb.

The inverse surface-to-deep δ^{13}C gradient reflects the nutrient-rich environment and low bioproductivity after the K-T mass extinction. The delay in recovery may partly be due to the sea level fall, more humid conditions and increased terrigenous influx during the early Danian. The trend towards heavier δ^{13}C values in zone Plb reflects the improving environmental conditions. Only in zone P1c are normal conditions re-established. This slow recovery after the mass extinction has been observed worldwide (e.g., Keller and Lindinger, 1989; Zachos et al., 1989).

7.2. Nye Klov, Denmark

At Nye Klov *Heterohelix globulosa* is also dominant and *Guembelitria* species never reached the blooms characteristic of other post-K-T boundary sequences (Fig. 7). This suggests that environmental conditions were less severe than in lower latitudes, which is also indicated by the much smaller negative δ^{13}C excursion of 0.6‰ as compared with 2–3‰ in lower latitudes (Schmitz et al., 1992; Keller et al., 1993; Hart et al., 2004, 2005). Moreover, δ^{13}C values of *H. globulosa* are consistently lighter than for the benthic species *Cibicidoides pseudoacutus* in both late Maastrichtian and early Danian sediments, as also observed for early Danian taxa, thus showing an inverse relationship (i.e. suggesting lower productivity in the upper water column than on seafloor).

Heterohelix globulosa in early Danian sediments records Danian δ^{13}C values, similar to *Guembelitria* species (*G. cretacea* and *G. danica*), *Woodringina hornerstownensis* and *Zeauvigerina waiparaensis,* demonstrating that this is a survivor taxon (Fig. 7). At Stevns Klint this inverse relationship was also observed above the hardground and interpreted as possibly related to the sea level fall accompanied by intensified water mass stratification and cooling (Schmitz et al., 1992; Hart et al., 2004, 2005). Alternatively, this may reflect a nutrient-rich environment (e.g., increased terrigenous influx associated with low sea level) with an expanded oxygen

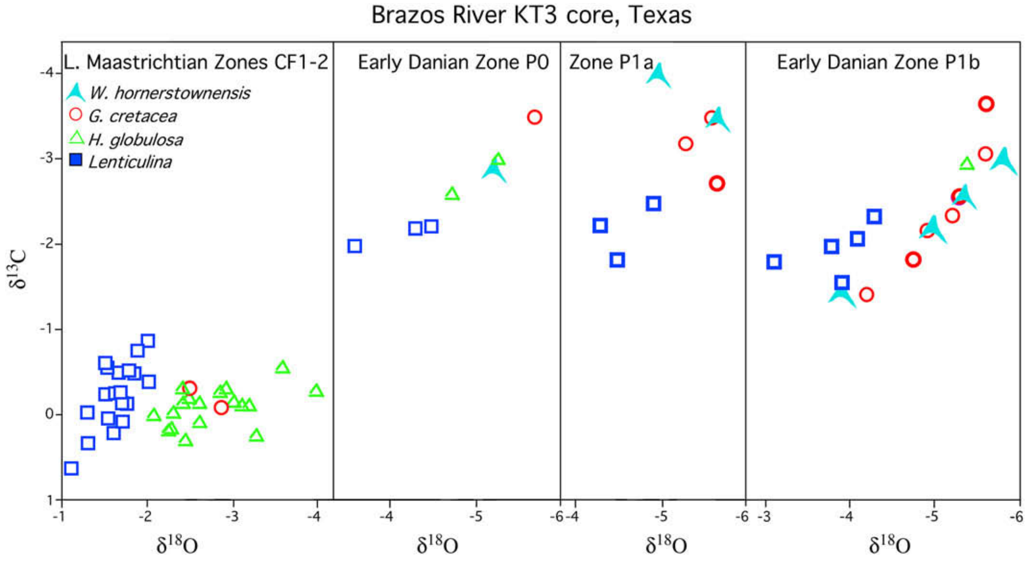

Fig. 6. Stable isotope ranking of selected species in late Maastrichtian and early Danian sediments of Brazos core KT-3. Note the 2–3 permill δ^{13}C shift across the K-T boundary. *Guembelitria*, *Heterohelix globulosa and W. hornerstownensis* are isotopically the lightest in both δ^{13}C and δ^{18}O values, suggesting that these species lived in surface waters.

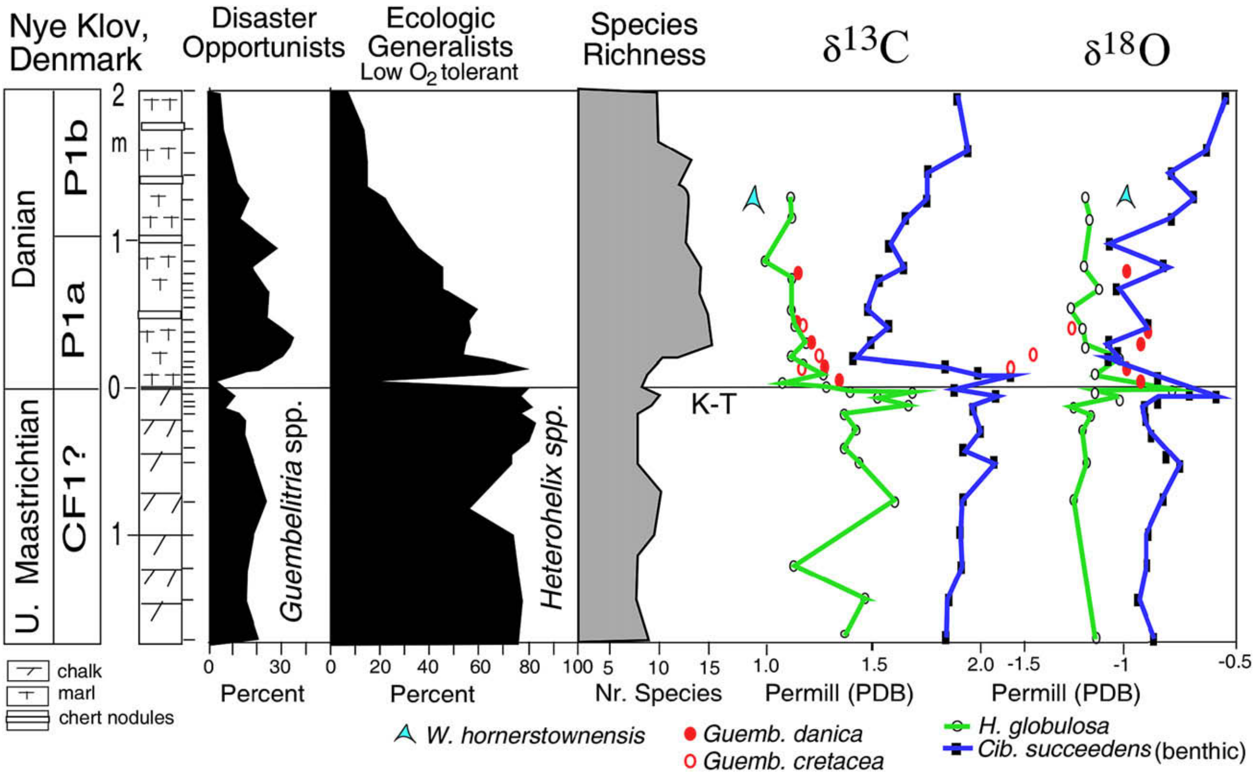

Fig. 7. *Guembelitria* and *Heterohelix* abundances, species richness, oxygen and carbon isotopes from Nye Klov, Denmark (data from Keller et al., 1993). Note that survivorship of *H. globulosa* and *Guembelitria* in the early Danian is demonstrated by the Danian isotope values of these species. The $\delta^{13}C$ shift across the K-T boundary is reduced in high latitudes, marking the dimished effect in primary productivity (Barrera and Keller, 1994).

minimum zone, as suggested by the *Heterohelix* dominance (~80%) in the late Maastrichtian, akin to the *Heterohelix* dominance during the Cenomanian/Turonian anoxic event (Leckie et al., 1998; Keller et al., 2001, 2004; Keller and Pardo, 2004a).

A $\delta^{13}C/\delta^{18}O$ plot of individual species data for the late Maastrichtian shows the expected stratification with *Rugoglobigerina rugosa* and *Globigerinelloides aspera* as heaviest in $\delta^{13}C$ and lightest in $\delta^{18}O$ reflecting the near surface habitat and high productivity and a clear surface-to-deep gradient (Fig. 8). But the reversed gradient is apparent between the benthic *Cibicidoides succeedens* and *H. globulosa* and *Guembelitria* species in the late Maastrichtian and early Danian. This may be explained by watermass stratification with the low oxygen tolerant *H. globulosa* thriving in the OMZ and *Guembelitria* species in nutrient-rich surface waters. *Heterohelix globulosa* $\delta^{18}O$ values are generally heavier than *G. cretacea,* but lighter than *G. danica*. In the early Danian zones P1a-P1b, benthic and *H. globulosa* average lighter $\delta^{13}C$ values than in the late Maastrichtian, revealing an adaptive change and possibly narrower ecological niche. In contrast, *Guembelitria* species (*G. cretacea* and *G. danica*) show no significant changes suggesting that these species are uniquely adjusted to variable environmental conditions in the late Maastrichtian and early Danian. The evolving biserial species *Woodringina hornerstownensis* and *Zeauvigerina waiparaensis,* which replaced *H. globulosa* and other small Cretaceous biserials, show the lightest $\delta^{13}C$ values.

7.3. Gebel Qreiya, Asiut Basin, central Egypt

At Gebel Qreiya, the $\delta^{13}C/\delta^{18}O$ plots of individual planktic and benthic species reflect the high stress environment evident in the *Guembelitria/Heterohelix* abundance fluctuations (Fig. 9; Keller, 2002; Keller et al., 2002b). The $\delta^{13}C$ values of the benthic *Cibicidoides pseudoacutus* range between 0.3 and −0.5‰ during the late Maastrichtian zones CF1-CF3 and early Danian zones P1a-P1c. *Rugoglobigerina rugosa* is highly variable ranging from 0.1 to −0.9‰ during the late Maastrichtian and reflects the variable surface-to-deep gradient ranging from normal to inverse (Fig. 9). In the early Danian zones P1a-P1b only few datapoints are available of *Guembelitria* due to its low abundance. However, two of the three datapoints show very light values consistent with other localities. In zone P1c, *Guembelitria* $\delta^{13}C$ values are generally light, particularly during high abundance peaks. Notably heavier $\delta^{13}C$ values are recorded by *Subbotina triloculinoides* in zone P1c. The first common occurrence of this species in zone P1c reflects the return to more equitable marine conditions and the heavier $\delta^{13}C$ values indicate increased primary productivity. Zone P1c marks the return to normal marine conditions worldwide accompanied by a major increase in species diversity, larger species sizes and in the upper part of this zone the disappearance of *Guembelitria* and *Heterohelix* blooms.

8. Discussion

8.1. Eutrophic environments

High nutrient content is a common factor in each of the K-T boundary and late Maastrichtian environments discussed above, either due to direct volcanic influx (Site 216), direct volcanic plus terrigenous influx (Argentina, Israel), direct impact plus terrigenous influx at the K-T event or terrigenous influx and restricted circulation in nearshore settings (Egypt, Denmark, Bulgaria, Texas). In each case, the biotic response of planktic foraminifera is similar: highly reduced species diversity dominated by *Guembelitria* and *Heterohelix* species. Previous studies have indicated that *Guembelitria* thrived principally in environments that are generally toxic to other species, possibly because of eutrophic conditions, which may

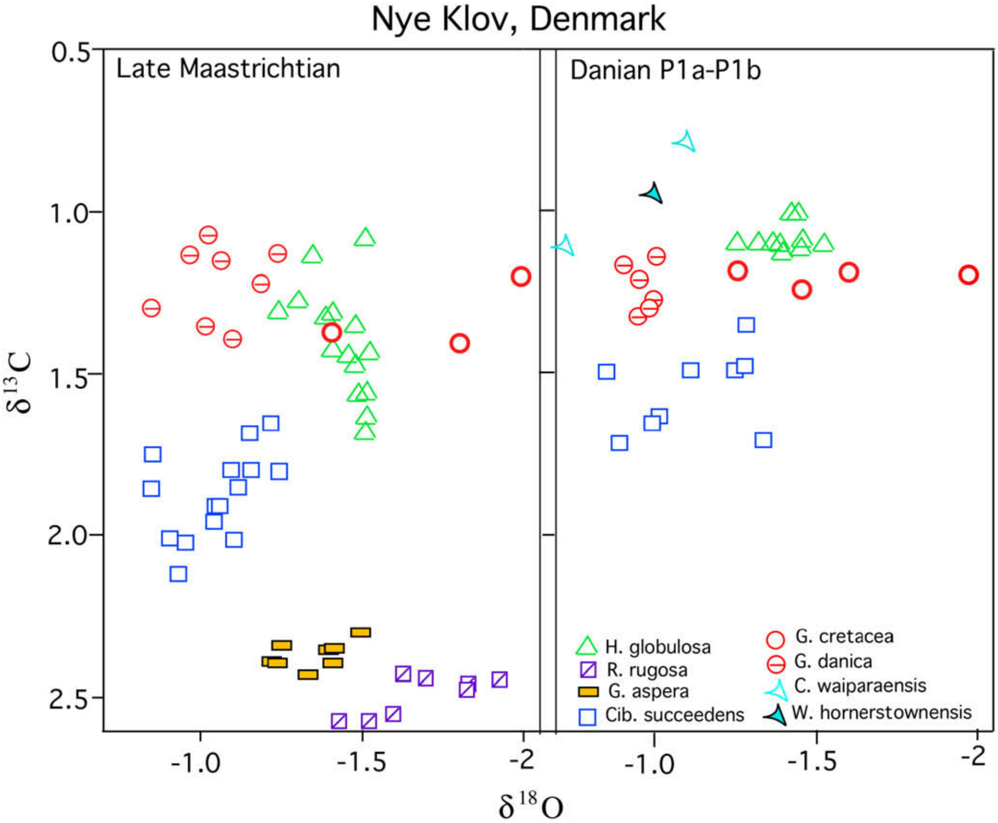

Fig. 8. Stable isotope ranking of selected species in late Maastrichtian and early Danian sediments of Nye Klov, Denmark. Note the reduced δ^{13}C shift across the K-T boundary relative to Brazos,Texas shown in Fig. 5. (Data from Keller et al., 1993; Barrera and Keller, 1994).

result from high terrigenous runoff, upwelling of nutrient-rich waters, phosphorus input from volcanism, or any combination thereof (e.g., Keller, 2002, 2003; Keller and Pardo, 2004b; Adatte et al., 2005). In general, *Guembelitria* thrived in nearshore environments with high terrigenous nutrient input, but could thrive in any nutrient-rich environment, whether shallow or deep, high or low latitudes. The generally very light δ^{13}C values of *Guembelitria* and the inverse surface-to-deep gradient these species project supports nutrient-rich to eutrophic habitats.

Guembelitria blooms are generally followed by blooms of biserial low oxygen tolerant species (*Heterohelix globulosa* and/or *H. dentata*), which subsequently yield to small trochospiral forms (*Globigerinelloides, Hedbergella*), followed by the return of more diverse, larger species as the environment gradually returns to

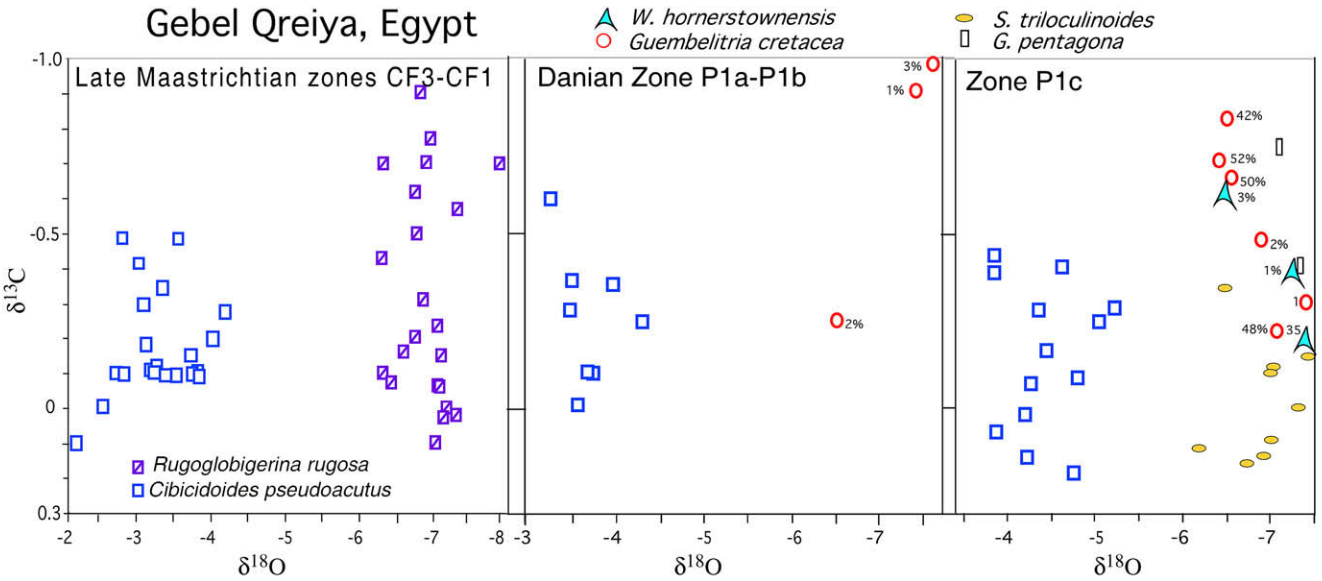

Fig. 9. Stable isotope ranking of selected species in late Maastrichtian and early Danian sediments of Gebel Qreiya, Central Egypt. *Guembelitria* and *W. hornerstownensis* are isotopically the lightest in both δ^{13}C and δ^{18}O values in the early Danian zone P1c, suggesting that these species lived in surface waters. *Subbotina triloculinodes* is substantially heavier in δ^{13}C. Data from Keller, 2002; Keller et al., 2002b).

normal (oligotrophic) conditions (Keller and Pardo, 2004b). *Heterohelix* species generally thrived in subsurface low oxygen environments and their blooms thus indicate oxygen depletion, expansion of the OMZ and/or increased watermass stratification.

Since *Guembelitria* favored nearshore eutrophic environments and *Heterohelix* thrived in the deeper oxygen depleted subsurface waters, sea level fluctuations may have been partly responsible for the alternating blooms. The benthic/planktic ratio generally supports this interpretation in the Neuquén (Argentina) and Asiut (Egypt) basins where low benthic abundances correspond to higher sea levels during *Heterohelix* blooms, and high benthic abundances correspond with low sea levels during *Guembelitria* blooms. Moreover, in these basins low sea levels are generally associated with variable abundance of framboidal pyrite, dysoxic conditions, low *Heterohelix* abundance, and a eutrophic surface mixed layer where only *Guembelitria* thrived. During high sea levels benthic foraminiferal abundance is generally low due to variable dysoxic to anoxic conditions and high abundance of framboidal pyrite. Thus, *Heterohelix* blooms reflect an expanded OMZ, *Guembelitria* blooms reflect highly nutrient-rich to eutrophic waters, and increased diversity of surface dwellers reflects a comparatively thick layer of normally oxygenated surface mixed layer.

8.2. Biotic crisis and recovery model

Biotic responses and strategies by opportunistic species to environmental crises have been widely studied in modern aquatic and terrestrial ecosystems (e.g., Olson, 1958; MacArthur and Wilson, 1967; Connel and Slayter, 1977; Sousa, 1979; Margalef, 1981; Begon et al., 1998). From these studies it appears that the biotic response to any major environmental catastrophe is universal and can be expressed by a simple model (Fig. 10). For example, a climactic or optimum ecological assemblage usually consists of a polytaxic community with high diversity of *K*-strategy species (e.g., large, complex, specialized taxa) and a background of low diversity *r*-strategy species (e.g., small ecologic generalists (MacArthur and Wilson, 1967; Begon et al., 1998). When a major environmental perturbation dramatically alters the ecosystem and increases the nutrient influx, it may lead to eutrophication and toxic levels of trace elements from fallout (volcanism or impact), which would lead to toxic condition for foraminifera and hence cause mass mortality (a cartoon illustrates this conditions in Fig. 11A). Higly nutrient-rich environments lead to euphotic phytoplankton blooms, which further increase the toxicity for foraminifera and lead to ecological inhibition (Connel and Slayter,

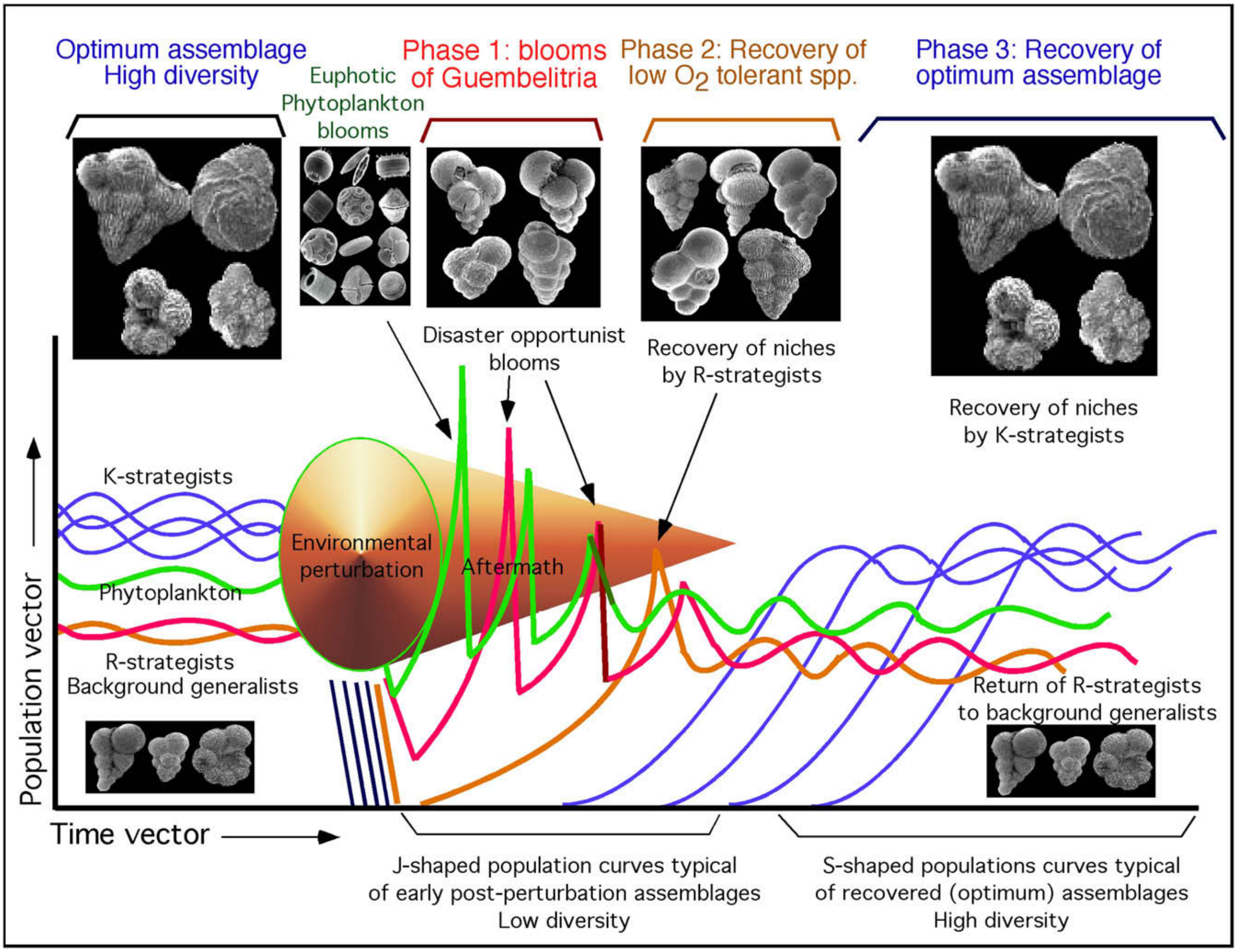

Fig. 10. Model illustrating the ecological succession after a major environmental perturbation which eliminates all *K*-strategists (specialists) and most or all *r*-strategists (generalists) of the optimum assemblage leading to eutrophic phytoplankton blooms (modified from Keller and Pardo, 2004b). The disaster opportunist *Guembelitria* are the first planktic foraminifera to appear in phase-1; they rapidly reproduce leading to exponential population (J-shaped) growth, then crash when nutrients are depleted and the environment changes from eutrophic to mesotrophic. At this time (phase 2) the low O_2 tolerant heterohelicids and other generalists thrive, further depleting nutrients and resulting in oligotrophic conditions, increased watermass stratification, niche competition. With increased competition, species populations switch from J-shaped crisis mode to the more stable S-shaped mode (phase 3). With the re-establishment of high diversity *K*-strategy species assemblages, *r*-strategy generalists are again displaced to background assemblage.

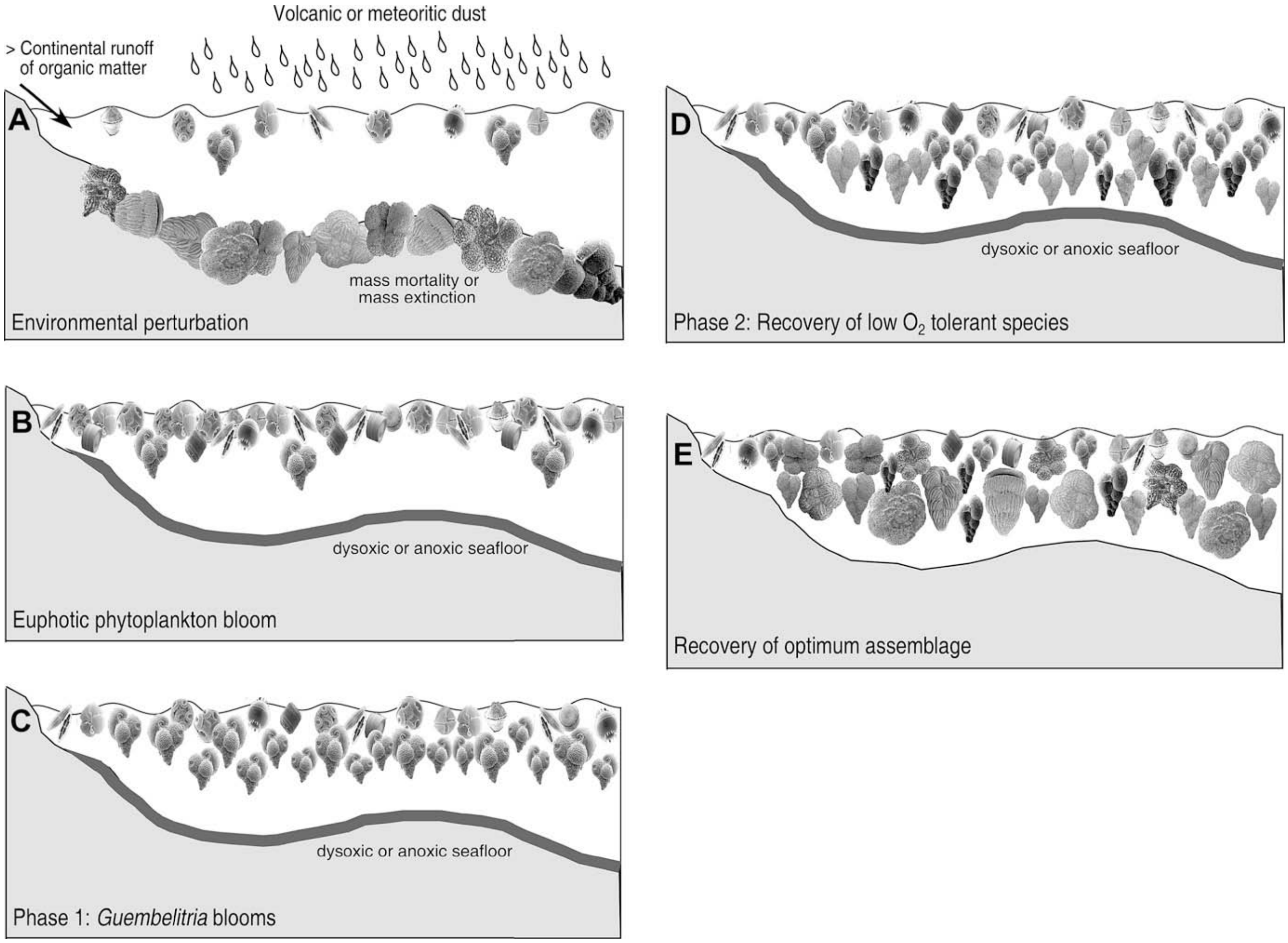

Fig. 11. Schematic illustration of biotic effects after a major environmental perturbation. A, Increased continental runoff and fallout from volcanism or impacts result in eutrophication and possibly toxic levels of trace elements in the water column leading to mass mortality or mass extinction. B, Eutrophic conditions are toxic to most foraminifera (except possibly *Guembelitria*) and lead to phytoplankton blooms. C, As phytoplankton consume excess organic matter, it opens opportunity for *Guembelitria*, which graze on phytoplankton and begin the recovery. D, When nutrient input returns to normal low levels, *Guembelitria* blooms retreat opening niches to *R*-strategists, the low oxygen tolerant heterohelicids, followed by small planispiral surface dwellers. E, With improving stable environmental conditions, increasing competition, niche development, and restoration of a well-stratified watermass, oligotrophic conditions are restored paving the way for recovery of the optimum assemblage of highly specialized and diverse *K*-strategists.

1977; Koutsoukos, 1996). The result is the obliteration not only of *K*-strategy species, but also most of the *r*-strategists (Figs. 10, 11B).

The severity of this critical environmental stress may vary from mass extinction to temporary local or regional exclusion of all large complex species and many ecological generalists (Abramovich et al., 2003; Keller and Pardo, 2004a). As excess organic matter decreases due to consumption by phytoplankton, the first opportunistic foraminifera, the *Guembelitria*, overcome the ecologic inhibition produced by phytoplankton (Connel and Slayter, 1977) and graze on phytoplankton (Fig. 10 Phase I, Fig. 11C).

Stratigraphic evidence and the biogeographic distribution of *Guembelitria* species (Figs. 2–3) indicate that this group is the most stress tolerant, as well as the first opportunists to thrive after an environmental catastrophe (review in Keller and Pardo, 2004b). 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 (MacArthur and Wilson, 1967; Koutsoukos, 1996; Begon et al., 1998). Their adaptation to high-stress disturbed environments includes heterochronic acceleration (e.g., MacLeod et al., 2000). Without interference from competitors, these species rapidly reproduce and increase their populations exponentially followed by mass mortalities that replicates over time as the population of opportunist species surpasses the feeding capacity of primary producers (Fig. 10, J-shaped curve; Begon et al., 1996). *Guembelitria* thus exhibit a well-developed *r*-strategy that allows these organisms to take full advantage from stressed and disturbed habitats. When nutrient input returns to normal low levels, which are insufficient to sustain *Guembelitria* population growth, disaster opportunist communities retreat. This allows the opening of niches to other ecologic generalists.

Low oxygen tolerant small biserial species are the next group of ecological generalists to recover (Fig. 10, Phase 2, Fig. 11D), followed by a third group, the small planispiral and trochospiral species. These two groups further feed on the phytoplankton blooms and gradually change the environment from eutrophic to mesotrophic conditions, similar to today's aquatic ecosystems (Barnes and Mann, 1980; Carpenter and Kitchell, 1984; Carpenter et al., 1985). *Guembelitria* dominance may alternate with biserial populations over time depending on nutrient influx and the associated phytoplankton blooms (Keller, 2003, 2005; Keller and Pardo, 2004b). 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 (Begon et al., 1996; Fig. 10, end Phase 2, Fig. 11D). *Guembelitria* blooms thus represent the first phase of a new ecological succession and are succeeded in the second phase by low oxygen tolerant small heterohelicids that characterizes the initial ecosystem recovery.

With improving of stable environmental conditions, increasing competition, niche development, and restoration of a well-stratified watermass, oligotrophic conditions are re-established opening niches for the highly specialized and diverse *K*-strategists (Hallock, 1987, 1996; Hallock et al., 1991; Koutsoukos, 1996; Fig. 10, Phase 3, Fig. 11E). *K*-strategy species, which are more suited to high interspecific competition, displace *R*-strategy species to the background assemblage. The return of this polytaxic and mature assemblage represents the full recovery of the ecological succession after a major environmental perturbation (Whittaker, 1953). The recovery period may be short (<100,000 year), or prolonged over several 100,000 to more than a million years, as after the K-T boundary event.

9. Conclusions

Biogeographic distribution patterns reveal *Guembelitria* blooms after each major environmental catastrophe, whether impact, volcanism or rapid climate change (Fig. 2). The most intense blooms are generally associated with nearshore environments, isolated basins and upwelling areas. *Guembelitria* 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 subaereal and submarine. *Guembelitria* blooms are thus proxies for severe biotic stress conditions that may range from temporary exclusion of ecological specialists (*K*-strategists) and generalists (*R*-strategists) to mass extinctions.

In contrast, *Heterohelix* species dominated the late Maastrichtian in open marine and nearshore areas, except for isolated high stress environments (Fig. 2). These ecological generalists (e.g., small biserial species *Heterohelix globulosa, H. navarroensis, H. dentata*, *H. planate, Zeauvigerina waiparaensis)* are reliable proxies for low O_2 conditions and generally mark initial recovery after peak eutrophic conditions passed and *Guembelitria* blooms abate.

A simple model explains the succession of planktic foraminiferal recovery after major environmental perturbations followed by phytoplankton blooms (Fig. 10). In this model, phase 1 is characterized by abrupt guembelitrid blooms (J-shaped curve pattern), which reflect high-stress disturbed environments and adaptations, such as dwarfing, by means of heterochronic acceleration. Phase 2 is marked by dominance of low oxygen tolerant small biserial species, followed by the small planispiral and trochospiral species. During this phase *Guembelitria* dominance may alternate with biserial populations over time depending on nutrient influx and the associated phytoplankton blooms. The increasing niche competition among the phase-2 generalists eventually switches the J-shaped population growth curve to a more stable S-shape (Fig. 10).

Phase 3 represents full recovery of the ecological succession after a major environmental perturbation. The restoration of oligotrophic conditions opens habitats for the highly specialized and diverse *K*-strategy species, which are more suited to high interspecific competition, and thus displace *r*-strategy species to the background assemblage. According to data derived from the analyzed interval, the recovery period may be short (<100,000 year), or prolonged (> 100,000 years, > 1 m.y).

Such ecological successions are observed in association with mantle plume volcanism in the Indian Ocean, Andean volcanism in Argentina and shallow inland seas in Egypt and Madagascar during the late Maastrichtian, the K-T impact, the early Danian and intense upwelling and climate extremes.

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