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Biotic effects of impacts and volcanism

Gerta Keller*

Department of Geosciences, Princeton University, Princeton, NJ 08544, USA

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Abstract

The biotic effects of late Maastrichtian mantle plume volcanism on Ninetyeast Ridge and Deccan volcanism mirror those of the Cretaceous–Tertiary (KT) mass extinction and impact event. Planktonic foraminifera responded to high stress conditions with the same impoverished and small-sized species assemblages dominated by the disaster/opportunists *Guembelitra cretacea*, which characterize the KT mass extinction worldwide. Similar high stress late Maastrichtian assemblages have recently been documented from Madagascar, Israel and Egypt. Biotic effects of volcanism cannot be differentiated from those of impacts, though every period of intense volcanism is associated with high stress assemblages, this is not the case with every impact. The most catastrophic biotic effects occurred at the KT boundary (65.0 Ma) when intense Deccan volcanism coincided with a major impact and caused the mass extinction of all tropical and subtropical species. The Chicxulub impact, which now appears to have predated the KT boundary by about 300 kyr, coincided with intense Deccan volcanism that resulted in high biotic stress and greenhouse warming, but no major extinctions. The unequivocal connection between intense volcanism and high stress assemblages during the late Maastrichtian to early Danian, and the evidence of multiple impacts, necessitates revision of current impact and mass extinction theories.

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1. Introduction

Major mass extinctions in Earth's history are generally attributed to impacts or major flood basalt volcanism and associated environmental extremes. A general consensus of impact-induced mass extinctions currently exists only for the Cretaceous–Tertiary (KT) boundary, whereas quantification of the environmental effects of major

flood volcanism (e.g. Deccan) has remained elusive. Other mass extinctions are also closely associated with flood volcanism (e.g. Permian–Triassic boundary, late Devonian [1–3]). Although the biotic effects of flood volcanism are still poorly understood, volcanogenic sulfate aerosols (acid rain), CO₂ emissions (greenhouse warming) and the dynamic effects of mantle plume activity likely contributed to the environmental extremes that led to mass extinctions [4].

Flood basalts are generally linked to hot spots, or superheated mantle plumes, which are believed to erupt over periods of 1–3 million years. Biotic effects directly attributable to flood basalts in ter-

* Tel.: +1-609-258-4117; Fax: +1-609-258-1671.

E-mail address: gkeller@princeton.edu (G. Keller).

restrial settings are difficult to evaluate, though they can easily be quantified in a marine environment due to the abundance of microfossils. One example is Deep Sea Drilling Project (DSDP) Site 216 on Ninetyeast Ridge in the Indian Ocean, which tracks the passage of the oceanic plate over a superheated mantle plume during the late Maastrichtian, resulting in lithospheric uplift, the formation of islands built to sea level [5,6], and volcanic activity lasting more than 1 million years.

DSDP Site 216 thus provides an ideal locality to evaluate the biotic and environmental effects of mantle plume activity from inception to cessation and the restoration of normal marine environments. The fact that this mantle plume activity began about 2 Myr before and ended about 500 kyr prior to the KT boundary, and involved the same biotic assemblages as at KT time, permits comparison with the KT mass extinction. Recent discoveries of high stress planktonic foraminiferal

assemblages in upper Maastrichtian sediments of Madagascar, Israel and central Egypt [7–9] revealed pre-KT biotic catastrophes of yet unknown source and paleogeographic extent that could be linked to volcanism.

This study evaluates the biotic effects of late Maastrichtian mantle plume activity at DSDP Site 216 based on disaster/opportunist and ecologic generalist planktonic foraminifera (more detailed analysis in preparation [10]) and compares these with the biotic effects observed in previous studies of Madagascar, Israel, Egypt and Tunisia (data published in [7–9,11,39] (Fig. 1). Planktonic foraminifera are unicellular species that lived in the upper water column and were highly sensitive to environmental changes. They suffered the most severe losses during the KT boundary mass extinction and are therefore ideal markers for evaluating biotic effects of catastrophic events, whether volcanism or impacts.

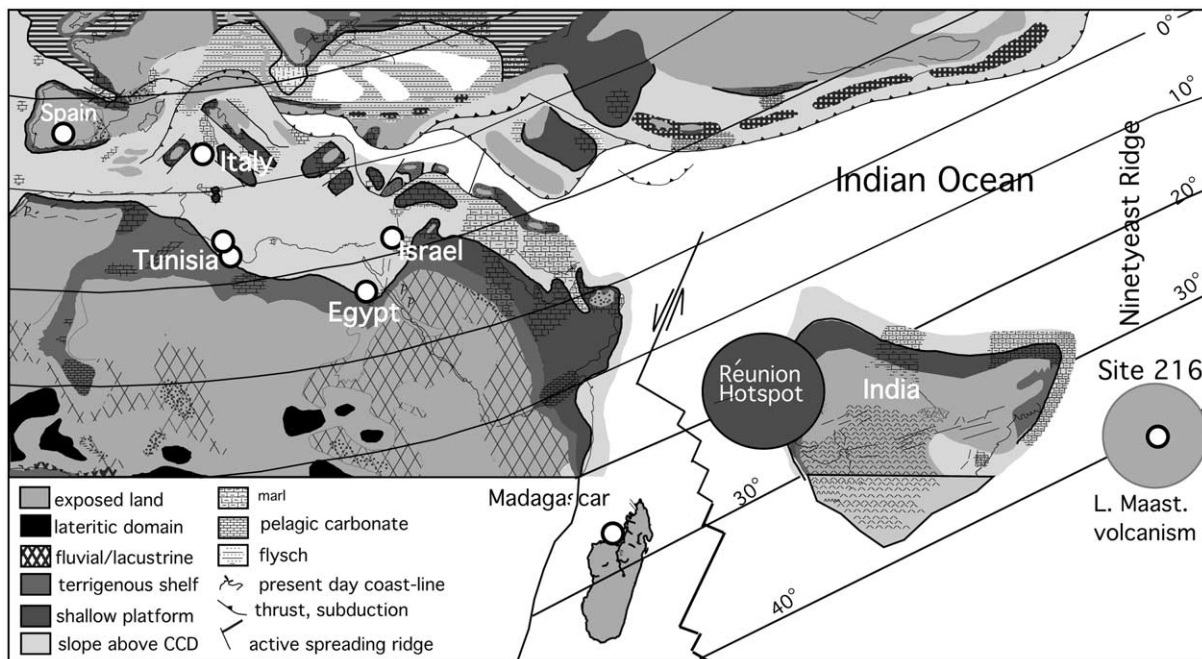


Fig. 1. Paleoenvironmental map of the Indian Ocean and eastern Tethys modified after Dercourt et al. [6] with paleolocations of studied sections (DSDP Site 216, Amboanio, Madagascar, Mishor Rotem, Israel, Qreiya, Egypt, and Elles and El Kef, Tunisia). Areas of plume activity, Reunion hotspot and Ninetyeast Ridge Site 216, are shaded. Note that biotic effects of volcanism decrease westward from the Indian Ocean to the eastern Tethys, with little expression in Tunisia and none in Spain.

2. Methods

Sediment samples from DSDP Site 216 were soaked in water, washed through 38 μm and 63 μm screens and oven dried at 50°C based on standard methods [9]. Statistical counts of planktonic foraminiferal species are based on random sample splits (using an Otto microsplitter) of about 150–250 specimens (average of 5–10 species). All specimens of this aliquot were counted, picked and mounted as permanent record on microslides and archived. Because planktonic foraminifera are relatively rare in these volcanic sediments, statistical counts in many samples are based on the entire residues of each sample with every specimen picked, counted and identified. Bias introduced by preservational effects (dissolution, breakage) appears to be minimal since the most fragile species (*Guembelitra*) are abundantly present and well preserved.

In the four sections used for regional comparison and correlation (Madagascar, Israel, Egypt and Tunisia [7–9,11,39]), data collections were based on the same methods, and two sections were analyzed by another worker (S. Abramovich). The fact that similar oceanographic signals are evident in all sections testifies to the reality of an external biotic effect, rather than sample bias.

3. DSDP Site 216

DSDP Site 216 was cored on the crest of Ninetyeast Ridge, which is currently located just north of the equator (lat. 1°27.73'N, long. 90°12.48'E) and at a water depth of 2237 m. During the late Maastrichtian Site 216 was located at about 40°S [12,13] as it passed over a mantle plume resulting in lithospheric uplift and the formation of islands, extruding amygdalar and vesicular basalt that suggest aerial or near surface lava extrusion. With the northward passage away from the mantle plume, Site 216 subsided from shallow to successively deeper marine environments. Benthic foraminifera and macrofossils indicate rapid subsidence from inner to middle neritic, outer neritic and upper bathyal depths by the end of vol-

canic deposition, and bathyal depths during the last 500 kyr of the Maastrichtian (zones CF1–2, *Micula prinsii* zone, Fig. 2). This passage is reflected first in the predominantly volcanic sediments successively followed by phosphatic and glauconitic volcanic deposits and eventually chalk deposition as Site 216 passed beyond the influence of mantle plume volcanic activity.

The onset of volcanism is difficult to date accurately due to impoverished microfossil assemblages, though a maximum age of 66.6 Ma is estimated based on the presence of the nannofossil zone *Nephrolithus frequens* [14,15] and planktonic foraminiferal zone CF3. The much younger K–Ar age of 64.1 ± 1.0 Ma reported by McDougall [16], based on a basalt sample from core 37, is likely compromised by argon loss. Volcanism ceased around 65.5 Ma, as indicated by limestone deposition with more diverse microfossil assemblages that mark zones CF1–2 and *Micula prinsii*. DSDP Site 216 was thus within the sphere of mantle plume volcanism for about 1.1 Myr, assuming that the base of zones CF3 and *N. frequens* are present. Sedimentation rates averaged about 8.5 cm/kyr, most of it due to volcanic output.

3.1. Biotic effects

Late Maastrichtian planktonic foraminifera in the volcanic-rich sediments of DSDP Site 216 are generally well preserved, with minor recrystallization and calcite infilling of test shells, and minor dissolution effects (some breakage and holes in tests), as also indicated by the great abundance of delicate small foraminiferal shells. The faunal assemblages are of very low diversity with 6–10 species in the volcanic-rich sediments and 18–25 species in the overlying chalk (Fig. 2), compared with normal diversity of 30–40 species at this latitude. The high abundance of small delicate species and relatively good preservation indicates that the low diversity is due to environmental factors, rather than an artifact of preservation, which would selectively concentrate robust larger species. Although specimens are extremely small (63–100 μm), they are fully developed adults, as indicated by overall morphology, ratio of chamber development and adult number of chambers.

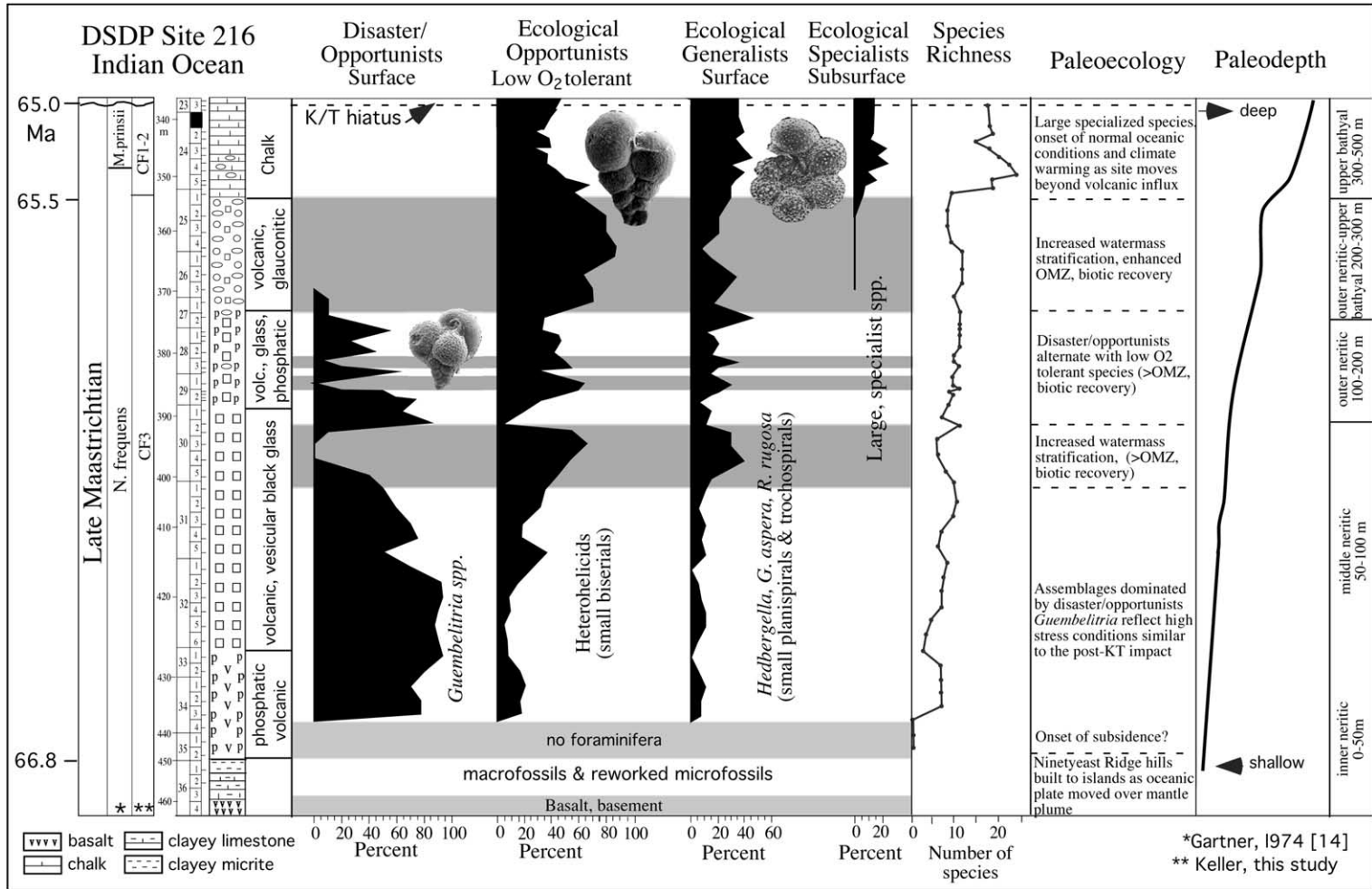


Fig. 2. Stratigraphy and paleoecology of planktonic foraminiferal assemblages at DSDP Site 216 on Ninetyeast Ridge, Indian Ocean. Note the disaster/opportunists *Guembelitra* species thrived during high stress conditions when few other species survived. At times of ecosystem recovery (decreased volcanism), *Guembelitra* nearly disappeared and low oxygen tolerant small biserial species thrived along with common small planispiral and trochospiral surface dwellers (gray shaded intervals). Normal more diverse faunal assemblages reappeared only after volcanism ceased.

Juvenile forms are present in the smaller size fraction (38–63 μm). Similarly dwarfed species assemblages are well known from the KT boundary [17,18].

Immediately above the basement basalt at Site 216 are clayey limestone and micrite layers that contain abundant macrofossil fragments (bivalves, gastropods, echinoid spines, ostracods), few poorly preserved reworked planktonic foraminifera of normal large size ($> 150 \mu\text{m}$), and a mixed assemblage of shallow and deepwater benthic foraminifera dominated by shallow water species *Anomalinoidea newmaniae* and *Epistominella minima*. This assemblage indicates deposition in a shallow inner neritic or subtidal environment with common reworking and transport of older deeper water sediments. The absence of in situ planktonic foraminifera also suggests very shallow (lagoonal/subtidal) or adverse marine conditions.

In the overlying volcanic phosphate-rich clay (core 35 to 34-4, Fig. 2), benthic and planktonic foraminifera are rare or absent, probably due to adverse conditions. Cores 34-3 through 31 contain unusually impoverished and very small (63–100 μm) high stress assemblages dominated (~ 60 –80%) by the ecological opportunist and disaster species *Guembelitra* [18]. In cores 30-2 to 30-5 *Guembelitra* are nearly absent and the low O_2 tolerant ecologic generalists dominate (e.g. small biserial species *Heterohelix dentata*, *H. globulosa*, *Zeauvigerina waiparaensis*), along with common small planispiral and trochospiral ecologic generalists in surface waters (e.g. *Hedbergella*, *Rugoglobigerina* and *Globigerinelloides* [10,18]). This indicates increased water mass stratification, an enhanced oxygen minimum zone (OMZ), and more favorable surface ecosystem.

In the volcanic and phosphate-rich micritic carbonate of cores 27–29, disaster/opportunists and low O_2 tolerant generalists alternate in abundance, though all species are still extremely small (63–100 μm). These rapid variations may be related to on–off volcanic activity. Opportunists (*Guembelitra*) are absent in the volcanic and glauconite-rich micritic carbonate of cores 25–26 where small low O_2 tolerant generalists dominate and surface generalists are common, indicating an improved ecosystem with enhanced OMZ, though

species richness remained very low and large specialist species are absent (Fig. 2).

Further environmental improvement is indicated in the chalks of core 24 where *Guembelitra* opportunists are absent, low O_2 tolerant heterohelids decrease in abundance, small surface dwelling generalists increase and large subsurface dwellers are a significant component for the first time and suggest increased water mass stratification. Species richness more than doubled to 18–25 species, though still short of normal diversity (30–40 species) at this latitude. The increased diversity appears to be primarily due to a short-term influx of species from low latitudes (e.g. globotruncanids, gublerinids, racemiguembelinids, and pseudotextularids), which may reflect the climate warming between 65.4 and 65.2 Ma [19]. Stress tolerant species continue to dominate faunal assemblages. No comparison can be made with the KT mass extinction because a major hiatus (Danian zone P1c (core 23-3, 98 cm)) overlies upper Maastrichtian sediments (core 23-3, 140 cm) and spans the basal 500 kyr of the Danian (zones P0, P1a, P1b) and part of the uppermost Maastrichtian.

The late Maastrichtian succession of high stress assemblages at Site 216 is clearly associated with mantle plume volcanic activity. Maximum biotic stress, indicated by dominance of the disaster/opportunists *Guembelitra*, occurred during the early part of volcanic activity. The same *Guembelitra* dominated assemblages characterize the earliest Danian after the KT impact event. Increased water mass stratification and expanded OMZ (biserial dominance) mark the initial recovery of the ecosystem. After volcanic influx ceased and normal pelagic sedimentation resumed as Site 216 passed beyond the reach of mantle plume activity, small stress tolerant assemblages still dominate, though reflecting increased water mass stratification, and there is an influx of more specialized low latitude species. Similar successions of high stress assemblages can be observed in Madagascar.

4. Amboanio, Madagascar

The Amboanio section is located in a cement

quarry near the village of Amboanio about 28 km south of the city of Mahajanga. During the late Maastrichtian, Amboanio was located at about 28°S latitude (Fig. 1). The base of the section may be as much as 1 Myr older (zone CF4) than at DSDP Site 216 (zone CF3), though dating is uncertain [7]. In the lower part of the section (CF4) sediment deposition occurred in an outer shelf environment (200–300 m), followed by middle shelf (150–200 m) deposition in the upper part (CF3–CF1). Three major hiatuses are present and mark eustatic sea level lowstands at 67 Ma (CF4/CF3 boundary), 65.5 Ma (CF3/CF2 boundary) and KT boundary (hiatus 64.5–65.2 Ma, Fig. 3

[7,20,21]. Each biozone is therefore incomplete, though the faunal assemblages can be correlated with DSDP Site 216.

During the late Maastrichtian at Amboanio the overall faunal diversity was low, varying between 15 and 27 species, and dominated by the disaster/opportunist *Guembelitra* and low O₂ tolerant small heterohelicids (Fig. 3). However, over the entire interval there are rare single specimen isolated occurrences of an additional 40 species of mostly tropical to subtropical affinity that appear to be migrants and suggest an open ocean envi-

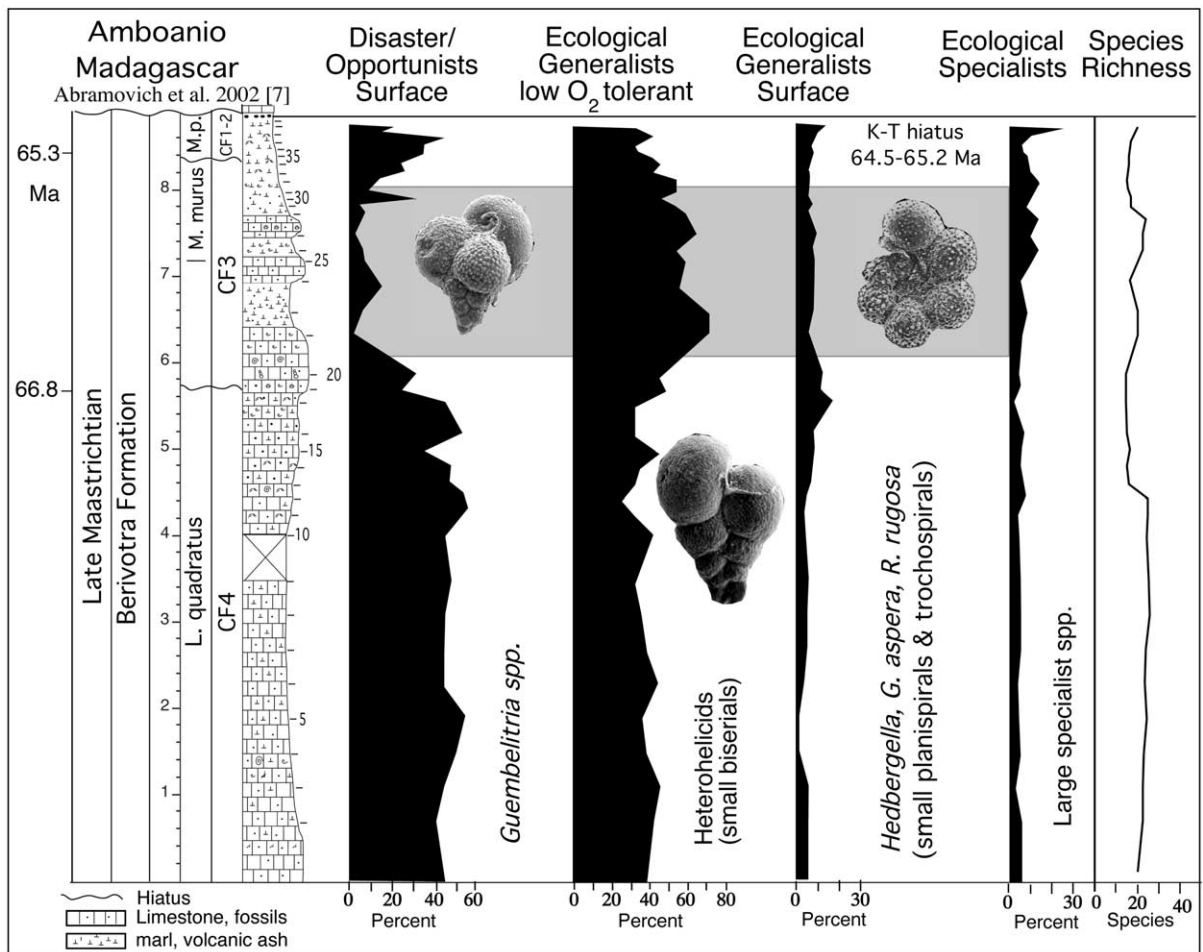


Fig. 3. Stratigraphy and paleoecology of planktonic foraminiferal assemblages at Amboanio, Madagascar. Note that the dominance of the disaster/opportunists *Guembelitra* during the late Maastrichtian reflects high stress conditions. Ecosystem recovery in zone CF3 is accompanied by dominance of low oxygen tolerant small biserial species (gray shaded intervals). Note zones CF1–2 and CF3 are incomplete due to hiatuses.

ronment. Adding these migrants to the species richness curve will increase the overall diversity between 25 and 38 species [7].

Faunal assemblages are dominated by the same small species as at DSDP Site 216 and reveal a similar alternating succession of ecological opportunists and generalists (Fig. 3). In zone CF4 the disaster/opportunist *Guembelitra* and low O₂ tolerant small biserial ecologic generalists dominate with 40–50% and 30–40% respectively. This suggests a high stress surface environment and well developed OMZ. The relatively deep open ocean marine environment argues against stress induced

by a shallow nearshore setting. The absence of ash layers in this interval may be due to diagenetic alteration [7].

Most of zone CF3 is missing due to a hiatus, but the part present is dominated by low O₂ tolerant species (60–70%), few *Guembelitra* (<10%), a minor increase in generalist surface dwellers (<10%) and ecologic specialists (10–15%). This interval reflects increased water mass stratification, expanded OMZ and more favorable surface and deeper water environments for planktonic foraminifera. The coeval interval at DSDP Site 216 is likely the lower expanded OMZ in zone

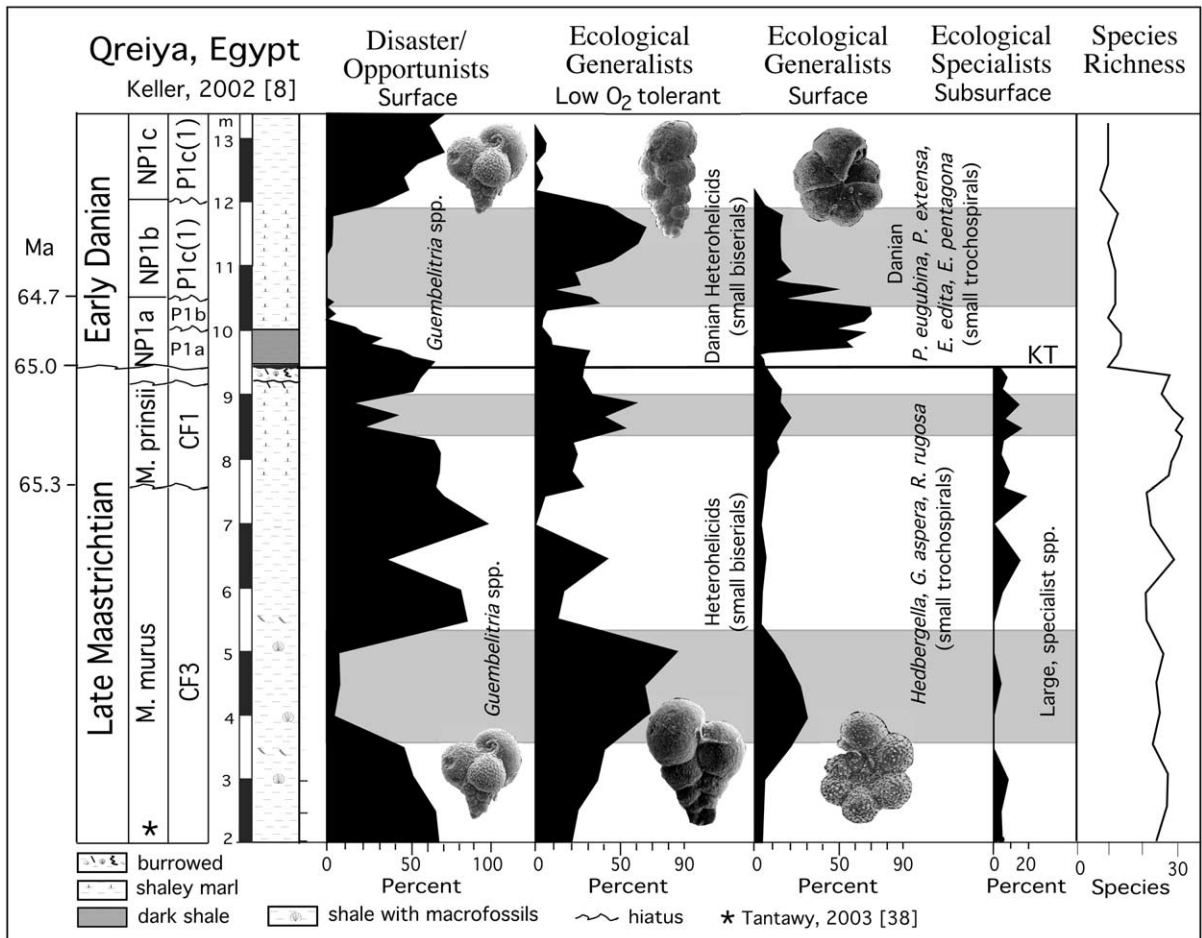


Fig. 4. Stratigraphy and paleoecology of planktonic foraminiferal assemblages at Qreiya, Egypt. Note that the disaster/opportunist *Guembelitra* species, which thrived during high stress conditions, alternate with low oxygen tolerant small biserial species and increased ecologic generalists in surface waters at times of ecosystem recovery during the late Maastrichtian and early Danian (gray shaded intervals). Note hiatuses at CF3/CF1 (CF2 missing), the KT boundary, and early Danian P1a/P1b, P1b/P1c zones. Data at asterisk from Tantawy [38].

CF3 (shaded intervals in Fig. 2), because the upper part of CF3 is missing at Amboanio.

The uppermost Maastrichtian is only partially present at Amboanio, but differs from Site 216 in that *Guembelitra* is abundant (40%) indicating high stress conditions. The presence of ash layers in this interval indicates a volcanic source [7]. Similarly high stress assemblages are observed in Egypt.

5. Qreiya, central Egypt

During the late Maastrichtian, Qreiya was located in the Asyut Basin of central Egypt at a paleodepth of 150–300 m. Similar to Amboanio, Madagascar, erosional surfaces bound most biozones as a result of sea level lowstands, though all biozones, except CF2, are present and the KT boundary event is preserved in a thin clay layer and Ir anomaly [8]. The early Danian is present albeit fragmented due to erosion as a result of sea level fluctuations (Fig. 4). Limited outcrop exposure prevents evaluation of the lower part of zone CF3 and zone CF4.

Late Maastrichtian faunal assemblages are remarkably similar to coeval assemblages at DSDP Site 216 and Amboanio. Species assemblages are of low diversity (20–30 species) and dominated by the disaster/opportunist *Guembelitra* (70–90%), which alternates with low O₂ tolerant ecologic generalists. One interval in zone CF3 is characterized by low O₂ tolerant generalists, increased surface generalists (small planispiral and trochospiral species, 20–30%), and near absence of opportunists. This interval is correlative with similar faunal assemblages of zone CF3 at Site 216 and at Amboanio (gray intervals, Figs. 2–4). The upper parts of zones CF3 and CF2 are missing at Qreiya due to a hiatus and sea level lowstand at 65.5 Ma [21].

The latest Maastrichtian zone CF1 (65.0–65.3 Ma) is incomplete at Qreiya, Amboanio and DSDP Site 216 due to hiatuses. Nevertheless, some comparisons can be made. In all three sections, low O₂ tolerant ecologic generalists average about 40%, surface generalists 10–30%, disaster/opportunists are absent in Site 216 and greatly

reduced in the other sections and large specialist species vary from 5 to 20%. These assemblages reveal relatively improved ecological conditions during the last 300 kyr of the Maastrichtian, but still reflect high stress at these localities. During the early Danian, the succession of disaster/opportunists and generalists at Qreiya is temporally and quantitatively similar to Israel and Tunisia, although more condensed due to hiatuses as discussed below.

6. Mishor Rotem, Israel

The Mishor Rotem section is located on the Rotem syncline of the Syrian Arc structural province near Dimona in the Negev of Israel [22]. During the late Maastrichtian the Rotem syncline was submerged at outer neritic to upper bathyal depths (300–500 m [9]). Sediments are characterized by three distinct red clay layers with Pd, Pt and minor Ir anomalies, which are interbedded in chalk and marl of the upper Maastrichtian zone CF1. The KT boundary is marked by a 3 mm thin red clay layer, altered impact spherules and Ir anomaly. This section thus contains evidence of the KT impact event as well as pre-KT events possibly related to volcanism [9,23,24].

Late Maastrichtian planktonic foraminiferal species richness is unusually low (25–35 species) for a Tethyan pelagic assemblage (Fig. 5), similar to Qreiya in Egypt [8]. Low O₂ tolerant, small, biserial ecologic generalists dominate (>50%) the assemblages, surface dwelling ecologic generalists average 15%, and large specialist species (globotruncanids) are rare or absent. The disaster/opportunist *Guembelitra* appears in distinct peaks of 30–40% in upper zone CF3, zones CF2, CF1 and lower Danian zone P1a. Correlative *Guembelitra* peaks can be observed at Elles and El Kef in Tunisia.

7. El Kef and Elles, Tunisia

The best-known and most expanded KT boundary records are known from the El Kef global stratotype and point (GSSP) and Elles lo-

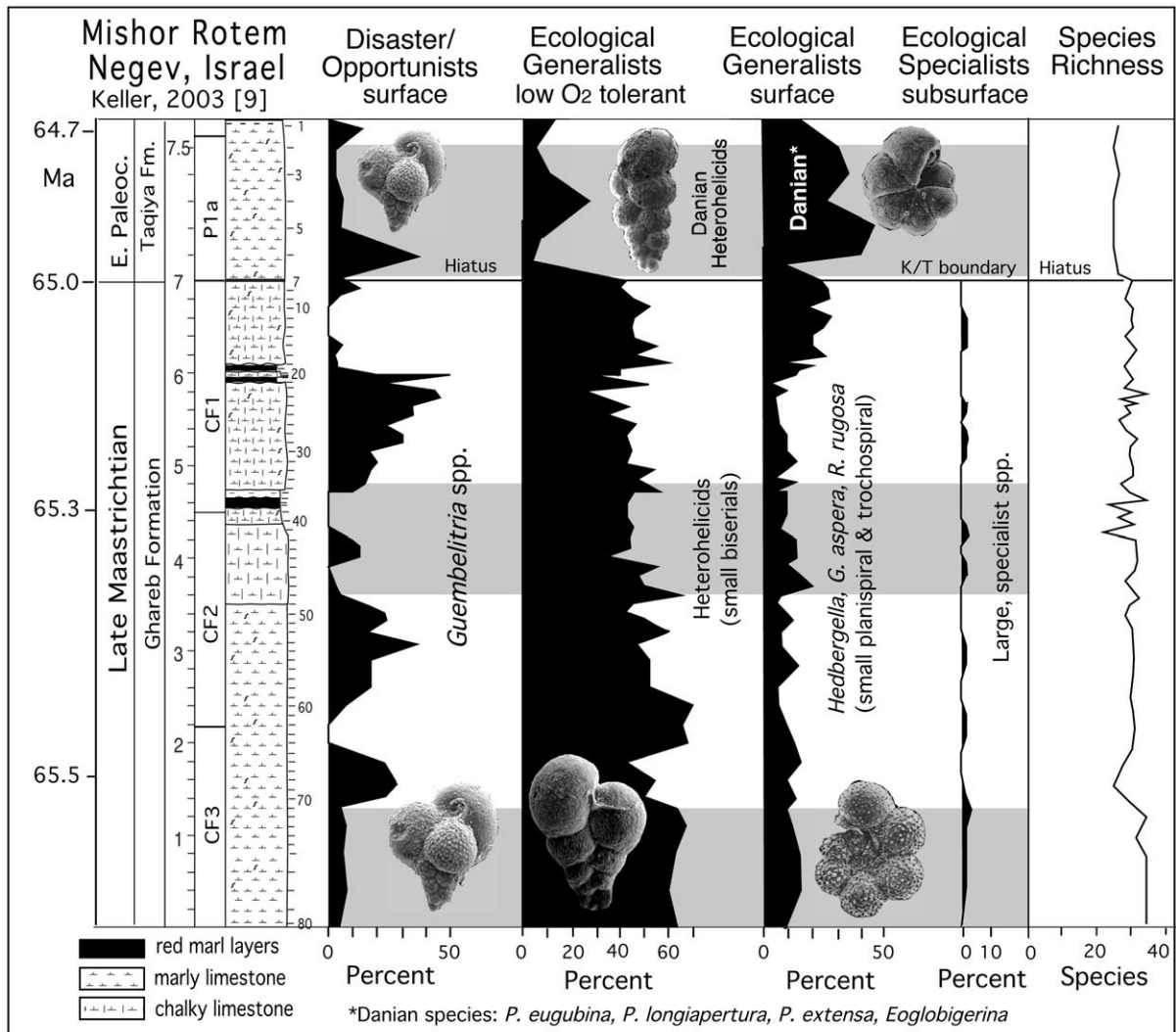


Fig. 5. Stratigraphy and paleoecology of planktonic foraminiferal assemblages at Mishor Rotem in the Negev, Israel. Note that the disaster/opportunists *Guembeltria* species are significantly less abundant than in Egypt, Madagascar, or Site 216, but occur in distinct abundance peaks correlative with maximum abundances in those sections. Low oxygen tolerant small biserial species dominate during the late Maastrichtian and indicate an enhanced OMZ and well-stratified ocean (gray intervals). Note that the three red marl layers in the late Maastrichtian zone CF1 are enriched in platinum group elements with a significant Ir enrichment in the lowermost red marl layer, correlative with an Ir enrichment in Oman [8,31].

cated 75 km east of El Kef, Tunisia [11,18,39]. Sediment deposition occurred in a middle to outer neritic environment (150–250 m) at Elles and outer neritic–upper bathyal environment (250–500 m) at El Kef. Fig. 6 shows the more complete Elles record for the late Maastrichtian, and the early Danian of El Kef. Late Maastrichtian species richness varies between 35 and 45 species and is

significantly higher than diversity at similar paleodepths at Qreiya in Egypt or the deeper Mishor Rotem section of Israel. Danian species richness patterns are the same in all sections.

During the late Maastrichtian small biserial species dominated, varying between 60 and 90%, small planispiral and trochospiral species varied between 3 and 15% and large specialized species

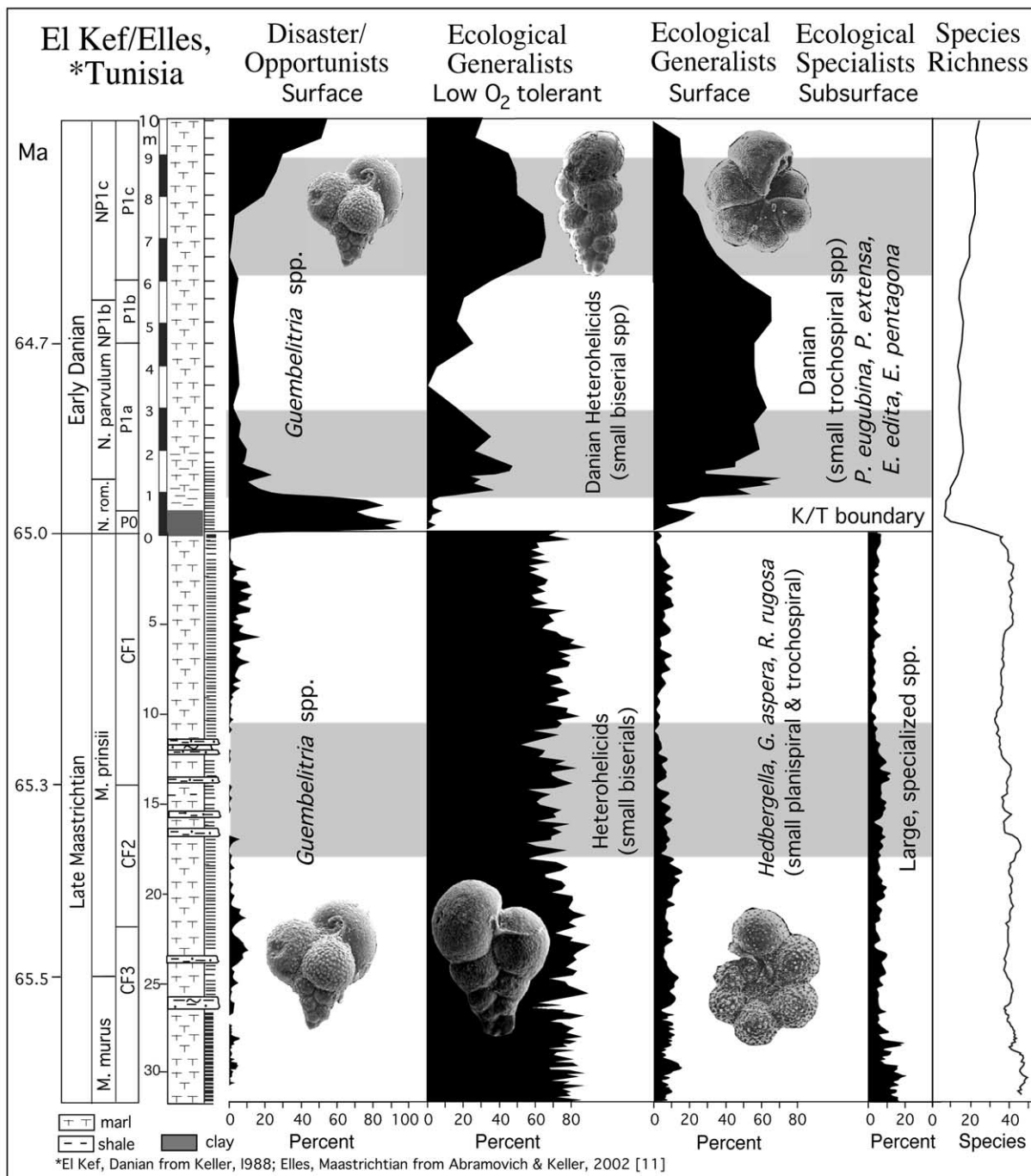


Fig. 6. Stratigraphy and paleoecology of planktonic foraminiferal assemblages at Elles (late Maastrichtian) and El Kef (Danian), Tunisia. Note that the disaster/opportunist *Guembeltria* species show only a minor abundance increase correlative with abundance peaks in Israel. This indicates a further westward decrease in biotic effects during the late Maastrichtian. During the KT and early Danian *Guembeltria* is dominant, subsequently it is replaced by low oxygen tolerant biserials, followed by surface dwelling ecologic generalists.

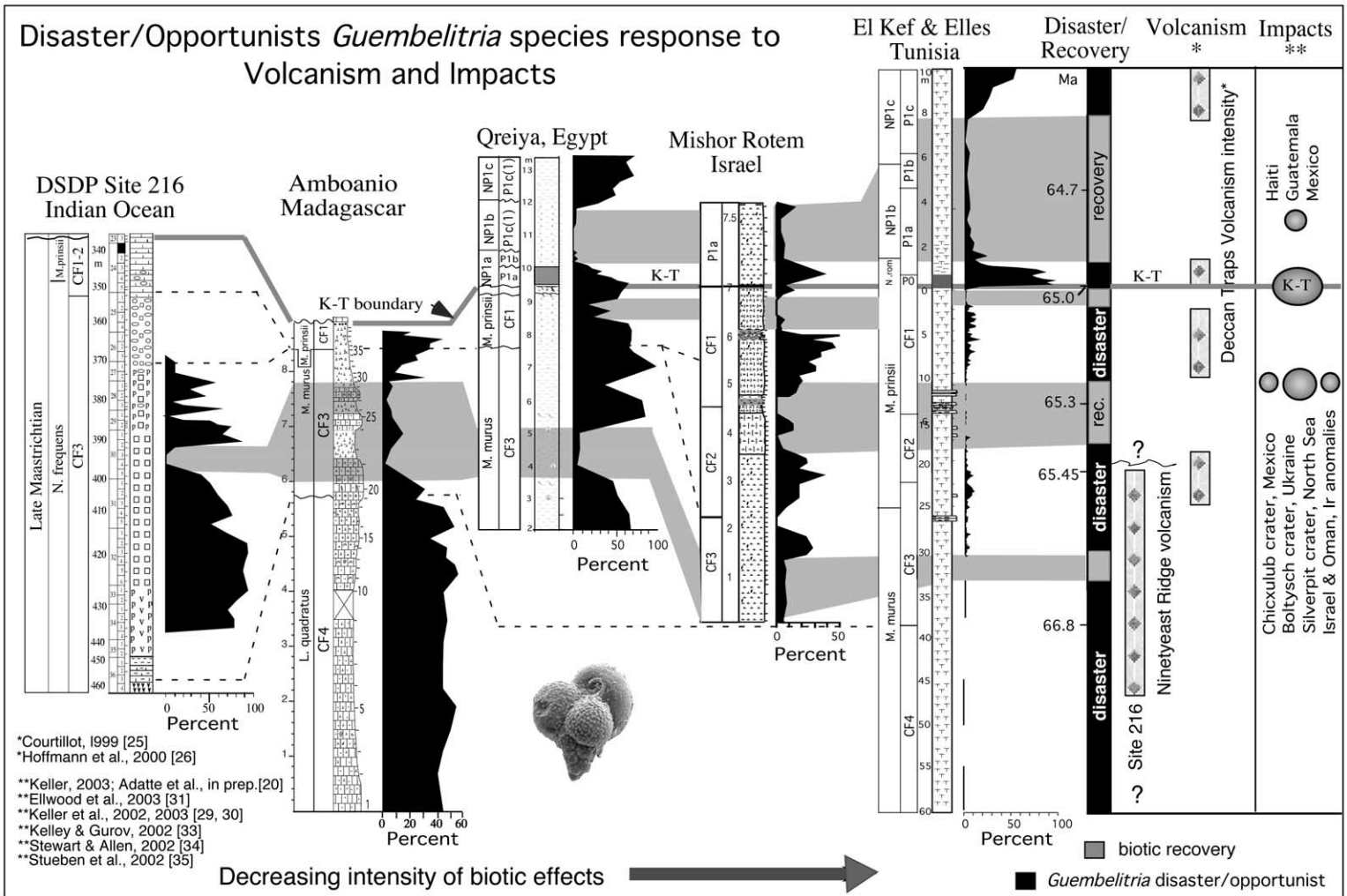


Fig. 7. Correlation of the disaster/opportunist *Guembeltria* species in sections spanning the Indian Ocean and eastern Tethys. Correlation is based on planktonic foraminiferal biozones (dashed lines) and initial recovery intervals (gray shaded). Note the westward decrease in biotic effects. Disaster and recovery intervals are summarized for comparison with periods of intense volcanic activity at Site 216 and Deccan Traps [25,26], and multiple impact events [20,29-31,35]. Note that all periods of intense volcanism correspond with disaster/opportunist, but not all impact events do. See text for discussion.

gradually decreased from 15% to 4%. These assemblages reflect a well-stratified marine environment with enhanced OMZ on the Tunisian margin of the Tethys during the late Maastrichtian. The disaster/opportunist *Guembelitra* species reached about 10% in zone CF1 and the upper zone CF3 (Fig. 6), as compared with 30–40% in the Negev. In Egypt and Madagascar, the equivalent intervals (though reduced due to hiatuses) are dominated (60–90%) by the disaster/opportunist *Guembelitra*. The reduced *Guembelitra* abundance at Mishor Rotem and further reduction at El Kef and Elles appear to reflect decreased biotic effects towards the west (Fig. 7). Between *Guembelitra* enriched intervals heterohelicids generally increased along with small trochospiral and large specialist species, reflecting increased water mass stratification, similar to the initial recovery phases observed at Qreiya, Amboanio and Site 216.

An abrupt faunal change marks the KT boundary mass extinction. All large, complex species, as well as the small trochospiral taxa, except for the hedbergellids, disappeared [18]. Maastrichtian biserial species decreased dramatically and together with hedbergellids disappeared in the early Danian. Only the disaster/opportunist *Guembelitra* thrived after the mass extinction, dominating (80–90%) in zones P0 to early P1a and again in P1c. With initial ecosystem recovery newly evolving small biserial low O₂ tolerant generalists (*Woodringina hornerstownensis*, *W. claytonensis*, *Chiloguembelina taurica*) succeeded disaster/opportunists (*Guembelitra*, gray intervals, Fig. 6). Further ecosystem recovery led to dominance of the newly evolved small trochospiral ecologic generalists (*Parvularugoglobigerina eugubina*, *P. longiapertura*, *P. extensa*, *Eoglobigerina edita*, *E. pentagona*).

The early Danian at El Kef and Elles [18] thus shows the same succession of disaster/opportunists followed by low O₂ tolerant ecologic generalists (gray interval, Fig. 6) as at DSDP Site 216, Amboanio, and Qreiya during the late Maastrichtian zone CF3. The foraminiferal response is thus very similar, although both the timing (early Danian vs. late Maastrichtian) and causes (impact vs. volcanism) for the high stress conditions may differ.

8. Discussion

8.1. High stress biotic environments

Most previous studies have associated planktonic foraminiferal blooms of the disaster/opportunist *Guembelitra* exclusively with the KT mass extinction. This study shows that high stress environments are always characterized by *Guembelitra* blooms, which may arise at any time (late Maastrichtian to early Tertiary) or place (near-shore to open ocean) and last from thousands to several hundred thousand years (Fig. 7). Planktonic foraminifera show the same biotic response to high stress environments during the late Maastrichtian in the Indian Ocean DSDP Site 216, Madagascar, Israel and Egypt as in the post-KT mass extinction recovery phase in Tunisia, Egypt, Israel and worldwide. Moreover, the biotic response is the same, a single species (*Guembelitra cretacea*) generally dominates (70–90%) during maximum stress, though the timing and cause(s) for the high stress conditions may differ.

With the first abatement of stress conditions, the disaster/opportunists give way to small ecologic generalists in surface waters (planispiral and trochospiral species) and the OMZ (small biserial species). Only with the return to normal marine conditions are diverse planktonic foraminiferal communities with ecological specialists restored. This pattern of disaster and initial recovery (Disaster/Recovery, Fig. 7) repeats itself through the late Maastrichtian and early Danian and indicates statistical universality in the planktonic foraminiferal response to high stress environments independent of time or cause(s).

What triggers this statistical universality in response to high stress conditions appears to be a throwback to the simplest morphologies of these unicellular microplankton: small globular chambers arranged in either triserial or biserial form and adaptation to opportunistic or generalist life strategies – also known as r-strategy. The triserial *Guembelitra* species are the disaster/opportunists of planktonic foraminiferal assemblages with fast reproduction, very small size (often 35–60 μm), large numbers of offspring, the ability to endure a wide range of environmental conditions, and

rapid increase in populations as opportunity arises [25,26]. Opportunists are typically smaller than non-opportunist species, inefficient in utilizing food and incapable of competing with more advanced species when food resources are scarce.

These observations and the ubiquitous abundance of *Guembelitra* in shallow nearshore post-KT environments have long suggested a preference for eutrophic conditions, possibly due to riverine nutrient influx and the opportunity of vacated ecologic niches due to the mass extinction [18]. However, *Guembelitra* blooms are equally abundant in post-KT deepwater marine environments where riverine nutrient influx is not a contributing factor, suggesting that other still unknown factors play a key role. This study shows that *Guembelitra* blooms in late Maastrichtian deep marine environments of the Indian Ocean, Madagascar, Israel and Egypt are proxies for environmental catastrophes, whether due to impacts, volcanism or any other type of catastrophe.

8.1.1. Further studies

The environmental conditions that triggered *Guembelitra* blooms still need to be investigated. While the geographic distribution of this disaster opportunist is well documented for the KT boundary event, little is known of its spatial and temporal distribution in other time intervals. This is largely because routine species analysis does not include the small size fraction (38–100 μm) that contains *Guembelitra* or several other small low O_2 tolerant biserial species. A major effort is required to investigate the small size fraction for the late Maastrichtian across latitudes to reveal background levels, crisis response, and latitudinal distribution of this species. Temporal and spatial distributions in volcanic provinces and at times of impacts need to be investigated and mapped to gain a better understanding of the biotic effects. Preliminary $\delta^{13}\text{C}$ species ranking suggests that *Guembelitra* is one of the isotopically lightest species living in the upper few meters of surface waters, and thrived in eutrophic waters. Further geochemical studies, including stable isotope and trace element analyses, are required on *Guembelitra* tests to investigate toxicity levels that proved

lethal for specialized species, as well as nutrients, salinity, temperature and oxygen variations.

8.2. Volcanism

Mantle plume volcanism (amygdalar and vesicular basalt) at DSDP Site 216 directly correlates with the disaster opportunist *Guembelitra* blooms or dominance during the late Maastrichtian zone CF3 and ends with their disappearance in the uppermost part of this zone (Fig. 2). This suggests a cause-and-effect relationship between volcanism and high stress environments. Stress conditions are variable with *Guembelitra* blooms alternating with low O_2 tolerant species signaling early recovery. The first major and apparently unique recovery event in CF3 represents a correlatable horizon in Madagascar, Egypt and Israel, but is not recognized in Tunisia (shaded interval in Fig. 7) suggesting a westward decrease in the intensity of environmental effects. Three such disaster/recovery horizons have previously been recognized in late Maastrichtian (zones CF1–CF3) sediments of Israel [9,27] and Tunisia [11,39], two in Egypt where the middle recovery event (zone CF2) is missing due to a hiatus [8], but only one is present (zone CF3) in Madagascar due to hiatuses [7] (Fig. 7). The same alternating disaster/recovery pattern is repeated in the early Danian.

Periods of intense Deccan volcanism [4,28,29] correlate well with periods dominated by disaster opportunists (Fig. 7). This pattern suggests that *Guembelitra* blooms are directly related to the intensity of volcanism with recovery periods related to decreased volcanic input. The nature of this cause and effect relationship is uncertain and needs to be investigated. Studies of trace elements incorporated in foraminiferal shells during the organism's life cycle may yield clues to toxic levels lethal to most species.

8.3. Multiple impacts

The KT boundary impact is well documented and generally recognized as the cause for the end-Cretaceous mass extinction. This study shows that periods of intense volcanism caused similar biotic effects during the late Maastrichtian and early

Danian. What sets the KT boundary and basal Danian apart from these other high stress periods is the mass extinction of all specialized larger species [18]. The coincidence of this mass extinction and the impact event is the primary evidence that supports a cause and effect scenario. However, the current data indicate that the mass extinction was likely caused by the coincidence of intense volcanism and a large impact.

To separate the biotic effects of impacts from those of volcanism documented in this study is difficult, if not impossible. This task is further complicated by the recent discoveries of multiple impacts across the KT boundary [30]. The new core Yaxcopoil-1 drilled inside the Chicxulub crater revealed late Maastrichtian planktonic foraminiferal assemblages of zone CF1 in dolomitic limestones overlying the impact breccia and underlying a KT hiatus [31]. This reveals that Chicxulub is not the KT boundary impact crater, but an earlier pre-KT impact, and the crater was probably much smaller (<120 km) than previously estimated [32]. An alternative interpretation explains these late Maastrichtian dolomitic limestones as backwash after the impact and cratering event [32]. However, this interpretation cannot explain the absence of reworked breccia clasts, or clasts from shallow water limestones, gypsum and anhydrite underlying the breccia, or the absence of size grading and sorting, or the origin of pelagic planktonic foraminifera which did not exist in the lagoonal to subtidal Yucatan platform prior to the impact [31].

The recent discovery of three or four microtektite layers interbedded in up to 10 m of late Maastrichtian marls (zone CF1) in numerous sections throughout northeastern Mexico also indicates that the Chicxulub impact predates the KT boundary [33]. The oldest microtektite layer is near the base of zone CF1 and indicates the impact occurred about 300 kyr prior to the KT boundary. The younger microtektite layers are likely reworked, as suggested by reworked marl clasts and shallow water benthic foraminifera. An alternative interpretation is that these multiple microtektite layers are slump structures due to seismic shaking after the impact. However, only small local slumps have been found and the geo-

graphic distribution and similar patterns of the multiple microtektite layers is more consistent with repeated reworking episodes of spherule deposits in shallow waters and transport into the deeper upper bathyal setting where they rest. Although these new findings are still controversial, perhaps mainly due to the entrenched view that Chicxulub is the KT impact crater, they reveal a consistent pattern of a pre-KT age that is difficult to ignore.

There is mounting evidence of multiple impacts in Late Maastrichtian and KT sediments. In Oman [34] two distinct Ir anomalies mark the KT and pre-KT impacts. In addition, there is evidence for two small impact craters during the late Maastrichtian. One is the 24 km wide Boltsh crater of Ukraine dated at 65.2 ± 0.6 Ma [35] and the other is the 12 km wide Silverpit crater of the North Sea [36]. Neither of these smaller craters likely had long-term biotic effects, though they suggest a period of comet showers associated with the KT mass extinction and volcanism (Fig. 7). There also appears to have been an impact in the early Danian. An Ir anomaly has been documented in the *Parvularugoglobigerina eugubina* zone (P1a) in five Central American localities (Bochil, Coxquihui and Trinitaria in Mexico, Actela, Guatemala, and Beloc, Haiti) and is tentatively identified as an impact event at about 64.9 Ma [30,37]. This impact event is not associated with the disaster/opportunist *Guembelitria* and appears to have had a relatively minor biotic effect.

9. Conclusions

Although both impacts and volcanism can cause high biotic stress conditions characterized by blooms of the disaster/opportunist *Guembelitria* species, not every impact does. In contrast, every period of intense volcanism is associated with a high stress environment. The geographic distribution of high stress environments depends on the cause and nature of the catastrophes, and may be global or regional and associated with impacts or volcanism. Based on the current data, the biotic effects of volcanism cannot be distinguished from those of impacts, but the co-

incidence of volcanism and impact(s) caused the most severe biotic effects. Thus the most catastrophic biotic effects occurred at the KT boundary where intense Deccan volcanism coincided with a major impact and caused the mass extinction of all tropical and subtropical species. The pre-KT boundary Deccan volcanism and impact(s) about 300 kyr before the end of the Cretaceous resulted in high biotic stress and greenhouse warming, but no major extinctions. No significant biotic stress or volcanism is associated with the early Danian impact (64.9 Ma), though it may have contributed to the delayed recovery in productivity and evolutionary diversity.

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