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Lilliput effect in late Maastrichtian planktic foraminifera: Response to environmental stress

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ABSTRACT

The Lilliput effect marks morphologic and intraspecies size reductions in response to environmental stresses commonly associated with the aftermath of mass extinctions. This study shows that the Lilliput effect is a universal biotic response associated with greenhouse warming, mesotrophic or restricted basins, shallow marginal settings and volcanically active regions during the late Maastrichtian. Sedimentary sequences analyzed from Tunisia, Egypt, Texas, Argentina, the South Atlantic and Indian Ocean reveal that the biotic stress response appears uniform, regardless of the cause, varying only with the degree of biotic stress. Overall, late Maastrichtian environments span a continuum from optimum conditions to the catastrophic (mass extinctions) with a predictable set of biotic responses relative to the degree of stress induced by oxygen, salinity, temperature and nutrient variations as a result of climate and sea level changes and volcanism. Early stages of biotic stress result in diversity reduction and the elimination of large specialized species (k-strategists) leading to morphologic size reduction via selective extinction/disappearances and intraspecies dwarfing of survivors. Later stages of biotic stress result in the complete disappearance of k-strategists, intraspecies dwarfing of r-strategists and dominance by low oxygen tolerant small heterohelicids. At the extreme end of the biotic response are volcanically influenced environments, which cause the same detrimental biotic effects as observed in the aftermath of the K–T mass extinction, including the disappearance of most species and blooms of the disaster opportunist *Guembelitria*.

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1. Introduction

Size reduction, termed the “Lilliput effect” by Urbanek (1993), has been observed in many organisms ranging from large mammals to invertebrates and to the smallest microscopic organisms, the single-celled foraminifera. Invariably, the size changes are associated with high-stress environments, such as greenhouse warming, mesotrophic or restricted basins, shallow marginal settings and volcanically active regions. They represent a particular survival strategy most often associated with the aftermath of mass extinctions (e.g., Urbanek, 1993; Twitchett, 1999; Twitchett et al., 2001; Twitchett, 2006), and more rarely with pre-extinction or other high-stress environments (MacLeod, 1990; MacLeod et al., 2000). It is well known that the most severe biotic crises follow a predictable scenario of mass extinctions, size reduction, survival of a few small species and evolution—regardless of the cause. In the aftermath of major catastrophes, often a single disaster taxon tends to dominate for a brief time. These are generally small, unornamented species that are rare or absent in normal environments, such as the planktic foraminifer *Guembelitria* (Keller and Pardo, 2004) after the K–T boundary mass extinction, stromatolites and the inarticulate brachiopod *Lingula* before and after the Permo-Triassic mass extinction, respectively (Schubert and Bottjer, 1992; Rodland and Bottjer, 2001; Whalen et al., 2002), and graptolites in the Silurian (Urbanek, 1993). In non-crises environments, disaster taxa are geographically restricted to marginal and high-stress environments, which for *Guembelitria* include upwelling or nearshore nutrient-rich environments (Pardo and Keller, 2008).

Apart from disaster opportunists, reduced species richness and test size are characteristic of high-stress environments and particularly prominent after mass extinction events. These are two very different types of size reductions, one morphologic and the other intraspecies. One explanation for the morphologic size reduction is selective extinction of large k-strategy species during mass extinctions and survival of small r-strategists. Although this view is controversial, with arguments both for (Hayami, 1997) and against it (Jablonski, 1996), the selective nature of the K–T mass extinction supports this type of morphologic size reduction (Keller, 2001), as demonstrated in this study. The intraspecies size reduction, or dwarfing, is not necessarily selective and affects both k- and r-strategy species (Abramovich and Keller, 2003), although most reports refer to the small r-selected opportunists (e.g., MacLeod et al., 2000; Keller, 2002, 2003). In this study, the term “Lilliput effect” refers to both

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morphologic and intraspecies size reductions, whereas dwarfing refers only to the latter.

Biotic effects now labeled as Lilliput effect have been observed in foraminiferal assemblages associated with anoxic or dysoxic conditions and mass extinction boundaries since at least the 1980s and linked to environmental stress conditions (e.g., Hart and Ball, 1986; Leckie, 1987; Keller, 1989; Hart and Leary, 1991; Keller, 1993; Hart, 1996; Leckie et al., 1998, 2002; Keller, 2003; Keller et al., 2004; Coccioni et al., 2006). Some workers suggested a possible correlation between intraspecies dwarfing and the late Eocene impacts and/or climate change (MacLeod, 1990), or morphologic deformation and the K–T boundary impact (Coccioni and Luciani, 2006). Others observed species migration into higher latitudes during the late Maastrichtian greenhouse warming (Kucera and Malmgren, 1998; Olsson et al., 2001) and dwarfing of large specialized k-strategy species (Abramovich and Keller, 2003). Keller (2003, 2005a) observed severe dwarfing of all species in volcanically stressed environments, restricted basins and shallow nearshore areas (Keller, 1989; Keller et al., 2007b, 1998; Keller, 2002, 2004). The Lilliput effect has thus been observed in open marine to marginal environments where high-stress conditions were induced by various factors, including impacts, volcanism, anoxia or dysoxia, greenhouse warming, restricted basins and nearshore environments. This diversity of environments also indicates that the Lilliput effect is generally restricted to specific environments and rarely, if ever, a global phenomenon, except possibly during major mass extinctions.

This report examines the Lilliput effect in planktic foraminifera during the late Maastrichtian where numerous late Maastrichtian through K–T sequences have been quantitatively analyzed in various size fractions (e.g., <63 µm, 63–150 µm, >150 µm) and published by the authors, their students and collaborators (Fig. 1). This has yielded an internally consistent database based on the same methods and taxonomy. Here we examine the Lilliput effect in sequences from Tunisia, Egypt, Texas, Argentina, South Atlantic and Indian Ocean spanning paleoenvironments associated with volcanism, greenhouse warming, shallow marginal seas, and shallow to deep, open marine to restricted conditions. In all these environments, planktic foraminifera show a uniform response to high biotic stress—selective reduction in species richness and intraspecies size reduction among the survivors—regardless of the specific cause of the environmental stress. The late Maastrichtian to K–T mass extinction was a time of intense volcanism, climate change and impacts and provides abundant evidence of high-stress conditions in diverse environments leading up to the K–T mass extinction. But we stress that the selected database is regional or local and no claim is made that the observed Lilliput effects are global.

1.1. Species richness maxima to K–T mass extinction

The most easily identified proxy of high biotic stress conditions is the reduction in species diversity or species richness. All it requires is a tally of the number of species present in a given sample and tracing the change through a given time sequence. Of course, this method assumes that preservation is good and species are not lost due to dissolution and/or breakage. However, preservation effects are easily identified, as they tend to enhance the relative abundance of large specialized species with their thick tests and keels, which are precisely the species that disappear first in high-stress environments. Moreover, species census and preservational data are routinely provided in published biostratigraphic reports. The late Maastrichtian to K–T mass extinction provides an excellent example to illustrate the progressive nature of biotic stress and its effect on biodiversity.

Planktic foraminiferal assemblages diversified rapidly beginning in the late Campanian zone CF8 (~71 Ma) and culminating in a historic diversity maximum in the early Maastrichtian CF6 zone (~70 Ma) (Li and Keller, 1998a,b; Premoli Silva and Sliter, 1999; Keller, 2001; Abramovich and Keller, 2002) (Fig. 2). Except for a minor extinction event (extinction of *Globotruncana linneiana*, *G. plummerae*, *Archeocretacea blowi*, *A. cretacea*) in zone CF5, this diversity maximum persisted through most of the late Maastrichtian (zones CF4–CF3), or until about ~500 ky before the end-Cretaceous mass extinction. Never before or after did planktic foraminifera reach this evolutionary diversification maximum. Similar and coeval diversity maxima have been reported in palynoflora and most macrofossils, except for rudistids and inoceramids (Fig. 2) (Macellari, 1986; Méon, 1990; MacLeod and Ward, 1990; Ward and Kennedy, 1993; Johnson and Kauffman, 1996). In all groups, optimum diversity persisted until about 500 ky before the K–T mass extinction. The cause for these diversity maxima is still speculative.

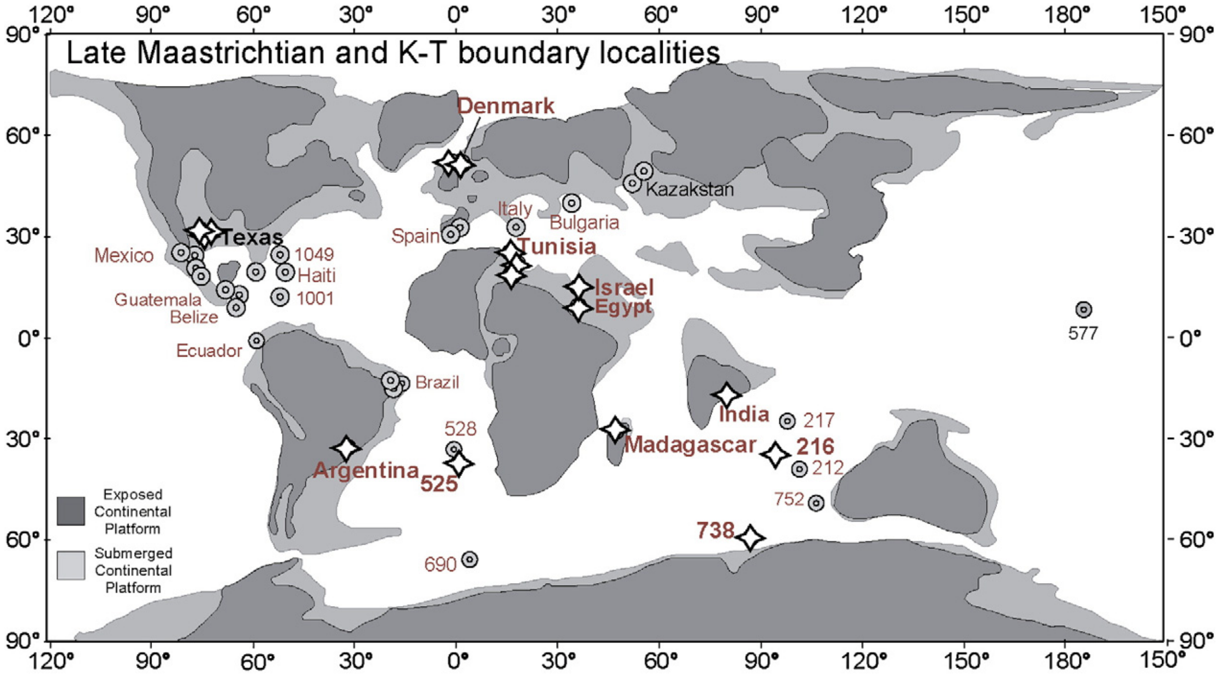

Fig. 1. Locations of late Maastrichtian and K–T sequences analyzed and published by the authors and collaborators to date. Stars mark the localities and sections discussed in this study.

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