



The end-cretaceous mass extinction in the marine realm: year 2000 assessment

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Abstract

The current database indicates that the terminal decline and extinction, or near extinction, of many groups commonly attributed to an asteroid or comet impact at the Cretaceous–Tertiary (K–T) boundary (e.g., ammonites, bivalves, planktic foraminifera) began during the last 500 k.y. of the Maastrichtian. By the time of the K–T boundary, extinction-prone tropical and subtropical marine faunas and floras were almost gone, or had severely reduced species populations struggling to survive. The K–T boundary kill-effect was largely restricted to these struggling tropical and subtropical populations that accounted for 2/3 of the species among planktic foraminifera, but less than 10% of the total foraminiferal population. No significant extinctions occurred among ecological generalists that dominated across latitudes. No single kill mechanism can account for this mass extinction pattern. The last 500 k.y. of the Maastrichtian were characterized by a series of rapid and extreme climate changes characterized by 3–4 °C warming between 65.4 and 65.2 Ma, major volcanic activity between 65.4 and 65.2 Ma, a spherule-producing event between 65.3 and 65.2 Ma, and an impact at the K–T boundary (65.0 Ma). All of these events caused major environmental perturbations and biotic stresses that resulted in severe reductions in species populations and extinctions that culminated at the K–T boundary. The mass extinction pattern, and the parallel environmental changes during the last 500 k.y. of the Maastrichtian, suggest that both long-term (climate, sea-level) and short-term (impact, volcanism) events contributed to the K–T boundary mass extinction. © 2001 Elsevier Science Ltd. All rights reserved.

1. Introduction

Since the publication of the bolide impact hypothesis in 1980 (Alvarez et al., 1980), the media, the public and a large number of scientists have come to believe that a meteorite caused the global extinction of the dinosaurs and many other groups at the end of the Cretaceous. This theory unquestionably has great sex appeal. The largest and most fascinating creatures that ever roamed the Earth were wiped out in a single day in a ball of fire caused by a meteorite impact that leaves behind the crater of doom. No wonder the hypothesis captured the minds and hearts of the public.

But apart from the appeal to the imagination, the hypothesis is also supported by undeniable geochemical and geophysical evidence of a bolide impact on the Yucatan Peninsula about 65 million years ago. The existence of an impact crater alone, however, neither proves nor explains the demise of the dinosaurs, or the mass extinction of any other groups. After all, most major mass extinctions are not caused by impacts, but are more likely associated with major volcanic eruptions (Courtillet et al., 1996; MacLeod, 1998).

To ascertain whether a mass extinction was caused by the Cretaceous–Tertiary (K–T) boundary impact, we must have a paleontological database, the fossilized bones and shells of organisms that died out, and their extinction must coincide with the geochemical signals of the impact event (e.g., Ir, Pb, shocked quartz). Species extinctions and the decline in relative species abundances prior to the impact event, must be evaluated in terms of ongoing long-term changes in climate, sea-level and volcanism. To date, the paleontological database that has been amassed during the last 20 years lends insufficient support to a scenario of an impact-driven sudden mass extinction at the K–T boundary (MacLeod et al., 1997). But this database reveals a complex scenario of a long-term and accelerating decline in species diversity and extinctions during the late Maastrichtian that culminated at the K–T boundary.

Ultimately, the validity of any mass extinction hypothesis depends on how well it explains the paleontological record. Currently, the impact mass extinction hypothesis fails the test in explaining the selective nature of this mass extinction (Archibald and Bryant, 1990; Archibald, 1996; Keller, 1996), the variable latitudinal effects (Keller, 1993; Keller et al., 1993; Pardo et al., 1999), and the progressive

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extinction trend. The alternative continental flood basalt hypothesis also only partly explains the K–T mass extinction pattern. Though there is undeniable evidence that the end-Cretaceous mass extinction, as well as another eight out of ten mass extinctions during the past 300 million years, are temporally associated with flood basalt events (Courtilot et al., 1996; MacLeod, 1998; Courtilot, 1999). The environmental ramifications of flood basalt eruptions are a function of size, rate of emplacement, location and chemical composition, all variable parameters that are difficult to quantify. Nevertheless, the hypothesis gains much support from the fossil record because the timing and duration of flood basalt events often coincides with the progressive nature of the coeval mass extinctions.

Despite two decades of research into the cause(s) of the end-Cretaceous mass extinction, there is still no single hypothesis that can account for the geochemical, geophysical and paleontological database. Ever higher resolution sample collections of numerous K–T transitions in Central America (Haiti, Mexico, Guatemala, Belize) have yielded yet another puzzle. The glass spherule deposits of Haiti and Mexico that are believed to be indicative of the Chicxulub impact at the K–T boundary, consist not of one, but four distinct layers with the oldest layer in Mexico predating the K–T boundary by about 200–300 k.y. (Stinnesbeck et al., 2001). In Haiti, however, all spherule layers are in the early Danian and probably the result of reworking (Keller et al., 2001; Stinnesbeck et al., 1999). Deposition of the glass spherules thus predates the K–T boundary and appears to coincide with the global warm event followed by rapid cooling and extinctions that culminated at the K–T boundary. This new data further supports the interpretation that the end Cretaceous mass extinction was the result of a complex multi-event catastrophe brought about by the coincidence of major climate fluctuations, volcanism and impacts.

This brief review summarizes recent advances in the climatic and paleontological records of the Maastrichtian leading up to the K–T boundary mass extinction, and correlates these records with the physical and geochemical data of impact(s) and volcanism. This database makes it self-evident that an impact alone can not account for the progressive mass extinction, or the selective nature of the mass extinction, or for the warm event between 200 and 400 k.y. preceding the K–T boundary, or the initial spherule deposition at approximately that time. Ultimately, the validity of any K–T scenario depends on how well it can account for all of these disparate events.

2. Maastrichtian climate

Maastrichtian climate changes are well documented in marine sediments based on oxygen isotope measurements of planktic and benthic foraminiferal tests that record paleo-

temperatures in surface and bottom waters, respectively. The most complete late Campanian and Maastrichtian foraminiferal stable isotopic records are currently known from the middle latitude South Atlantic Site 525 (Li and Keller, 1998a), the southern high latitude Site 690 (Barrera, 1994; Barrera et al., 1997), and the tropical Pacific Site 463 (Li and Keller, 1999). These records show that the Maastrichtian global climate was significantly cooler than during the overall Late Cretaceous. Barrera (1994) and Barrera et al. (1997) estimated that deep-water temperatures from the equatorial Pacific reached 16–18°C during the Turonian–Coniacian, but only 7°C during the late Maastrichtian. The shift from relatively warm to cool deep waters at Sites 525 and 690 began at about 73 Ma during the late Campanian (Barrera et al., 1997; Li and Keller, 1998a) when deep water temperatures averaged 16°C and surface temperatures 21°C. Between 73 and 71 Ma, deep waters cooled from 16°C to 10.5°C, and surface waters cooled from 22°C to 17°C (Fig. 1, Li and Keller, 1998a). Deep-water temperatures remained cool (10.5°C) between 71.2 and 69.2 Ma, followed by rapid warming of 2–3°C between 69.0 and 69.2 Ma. These warmer though fluctuating temperatures continued until about 68.3 Ma, the early–late Maastrichtian boundary (base of C30N), when temperatures cooled again reaching a low of 10.5°C between 67.5 and 65.5 Ma. During this time, sea-surface temperatures remained variable, though with a decreasing trend (Fig. 1). The major decrease in surface and deep water temperatures reflects polar cooling associated with the formation of high-latitude cool deep waters and increased thermal gradients between equator and poles. Major sea-level regressions coincided with the major cooling phases at (C31R, 71.2–69.2 Ma and C30N, 67.3–66.5, Haq et al., 1987; Li et al., 2000).

Late Maastrichtian climate cooling reached its maximum near the 30N/29R Chron boundary about 500 k.y. prior to the K–T boundary (Li and Keller, 1998a). During the last 500 k.y. of the Maastrichtian, extreme and rapid climate fluctuations prevailed. High-resolution (10 k.y. sample spacing) stable isotope data reveals that deep waters warmed rapidly by 3–4°C between 65.5 and 65.3 Ma, gradually cooled until 65.1 Ma, followed by accelerated cooling during the last 100 k.y. preceding the K–T boundary (Fig. 2, Li and Keller, 1998c). Similar deep-water temperature changes were also observed from Sites 690, 528, 738, El Kef and Kazakhstan (Stott and Kennett, 1990; D'Hondt and Lindinger, 1994; Barrera, 1994; Oberhänsli et al., 1998; Pardo et al., 1999). Salinity fluctuations indicate that during the short-term global warming, high-latitude deep-water production was significantly reduced and warm saline deep-waters flooded the ocean basins. These warm saline deep waters probably originated in the shallow middle and low-latitude regions of the Tethys (Li and Keller, 1998c). During the last 100 k.y. of the Maastrichtian, warm saline deep-water production ceased and cool high-latitude deep waters flooded the ocean basins. The last 500 k.y. of the Maastrichtian thus saw substantial environmental

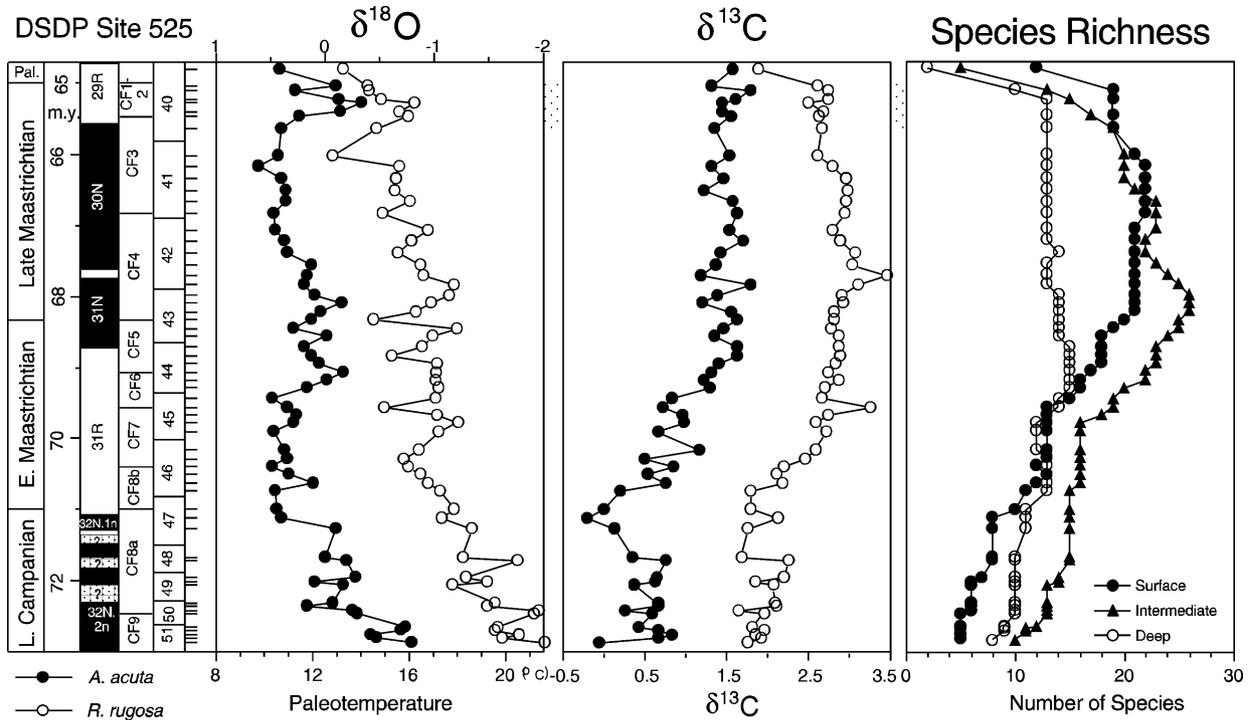


Fig. 1. Stable isotope records of surface (*Rugoglobigerina rugosa*) and intermediate water (*Anomalinoidea acuta*) foraminifera at Site 525. Note the overall gradual cooling in surface waters from 21°C to 13°C and in bottom waters from 16°C to 10.5°C by K–T boundary time. $\delta^{13}\text{C}$ values show a major negative excursion coincident with the onset of maximum cooling between 70.5 and 71 Ma and gradually increased thereafter. This increase in $\delta^{13}\text{C}$ values coincided with maximum rates of evolutionary diversification when planktic foraminiferal species richness nearly doubled. Note that species richness is given separately for groups living in surface, intermediate (thermocline depth) and deep waters. Evolutionary diversification occurred in surface and intermediate depths. (Data from Li and Keller, 1998a).

fluctuations that influenced climates from the tropics to the high latitudes.

3. Faunal turnovers

Paleontologists have generally attempted to evaluate the K–T mass extinction by studying the sediments closest to the K–T boundary and iridium anomaly. However, such short-term records can provide no insights into the biotic effects associated with long-term climatic and environmental changes preceding the K–T boundary. Could long-term environmental changes have caused severe biotic stress and predisposed faunas to eventual extinction at the end of the Cretaceous? Very few studies have detailed Maastrichtian faunal changes in either microfossils, invertebrates, or vertebrates, though a summary of published data reveals common trends as shown in this review for various invertebrate groups. A recent review of the K–T stratigraphic records of all major fossil groups was published by MacLeod et al. (1997). Summarized here are recent advances in late Cretaceous faunal turnovers in planktic foraminifera. These marine plankton suffered the most severe mass extinction across the K–T boundary. Owing to their abundance in marine sediments across latitudes, planktic foraminifera yield the most complete global high resolution database for the K–T mass extinction.

4. Planktic foraminifera

4.1. K/T record and blind test

Very few studies have examined the faunal turnovers in planktic foraminiferal populations during the Maastrichtian and most have concentrated on the last 50–100 cm (last 20–40 k.y.) interval below the K–T boundary (e.g., Smit, 1990; Canudo et al., 1991; Keller et al., 1995; 1998; Luciani, 1997; Apellaniz et al., 1997; Molina et al., 1998). Based on this short record most of the authors concluded that there were no significant pre-K–T biotic stresses that could have caused species extinctions or predisposed species to extinctions by extreme environmental stresses. To abet the ongoing controversy between those who interpret the K–T mass extinction as instantaneous vs those who interpret it as progressive, a blind test was organized with four investigators examining six samples between 50 cm below and 50 cm above the K–T boundary at the El Kef stratotype section in Tunisia. Although the results were inconclusive as to the number of species extinctions in the 50 cm below the K–T boundary, they clearly showed many Cretaceous species surviving well into the Danian (Canudo, 1997; Masters, 1997; Orue-etxebarria, 1997; Olsson, 1997). The blind test was doomed to failure from the outset because only the last 20 k.y. of the Cretaceous were examined, and because

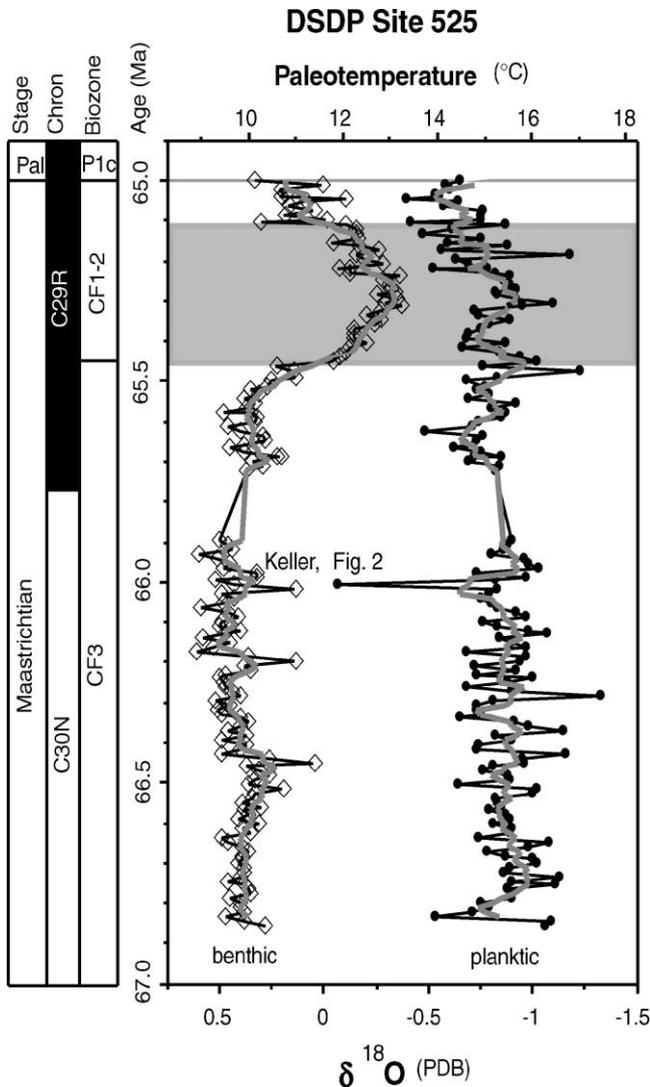


Fig. 2. High-resolution (10 k.y.) $\delta^{18}\text{O}$ and paleotemperature records of surface and intermediate waters at Site 525 for the last 1.8 million years of the Maastrichtian. Note the fluctuating surface water temperatures and the 3–4°C deep water warming between 200 and 400 k.y. before the K–T boundary. During the last 200 k.y. of the Maastrichtian both surface and deep waters cool about 2–3°C. The rapid warming may be related to a period of active global volcanism, or the spherule deposition event in Central America. (From Li and Keller, 1998c).

the test only consisted of finding the maximum number of species present in the last sample below the K–T boundary. This ignored the problems of rare species and the high potential that isolated rare specimens may be reworked (Signor and Lipps, 1982). Recent analysis of the the Elles section, located only 75 km from El Kef, demonstrates this problem. At this locality, abundant reworked specimens were found in the uppermost meter of the Maastrichtian within graded and cross-bedded sediments of a foraminiferal packstone that also indicates winnowing of sediments (Abramovich and Keller, in press). Reworked sediments and short hiatuses are ubiquitous near the top of the Maastrichtian probably due to the global cooling and intensified bottom water circulation

during the last 100 k.y. of the Maastrichtian (MacLeod and Keller, 1991a, b).

4.2. Early-to-late Maastrichtian

The Maastrichtian climate record is now well known and permits evaluation of the correlative faunal assemblages. Until very recently, the rare studies that evaluated the Maastrichtian faunal turnover patterns based on quantitative faunal analyses were restricted to the southern and northern high latitudes and Brazos River, Texas (e.g., Huber, 1992; Huber and Watkins, 1992; Hultberg and Malmgren, 1987; Keller, 1989; Schmitz et al., 1992; Keller et al., 1993). These studies revealed little of the complexities of biotic turnovers because they were based on low diversity high-latitude assemblages and low diversity shallow-water assemblages of the US Western Interior. Both of these Maastrichtian faunas consisted of stress-tolerant assemblages dominated by 4–5 species that yielded little information on the effects environmental changes had on typical high-diversity tropical and subtropical faunas.

Quantitative Maastrichtian studies of high-diversity Tethyan faunas of low and middle latitudes were recently published by Abramovich et al. (1998) and Li and Keller (1998a, b). Abramovich et al. (1998) examined tropical to subtropical assemblages in several sections of the Negev, Israel, which span upper slope to outer shelf environments. These authors concluded that 41% of the planktic foraminiferal species became extinct during the Maastrichtian, 44% at the K–T boundary, and 15% survived into the Danian. Most of the extinct species are globotruncanids and no evolutionary replacement of extinct forms was observed. Thus, Abramovich et al. (1998) concluded that the Maastrichtian suffered from both high extinction and low evolution rates, though this conclusion should have been restricted to the late Maastrichtian since they had no early Maastrichtian data. The extinction patterns observed at Sites 21, 463, 525 and El Kef and Elles in Tunisia, by Li and Keller (1998a, b, 1999) show similar late Maastrichtian faunal patterns as observed by Abramovich et al. (1998) in the Negev, though last occurrences of some species vary across this geographic region. As in the Negev study, a minor extinction of six species was observed in the early late Maastrichtian between 68.5 and 69.5 Ma, coincident with global cooling and a sea-level regression. Though this extinction phase is not evident in the species richness curves because the evolutionary increase in species richness values exceeds losses due to extinctions. However, Li and Keller's studies of the early Maastrichtian found very high evolutionary rates. In fact, the most significant event during the early Maastrichtian was the attainment of maximum species richness between 69.5 and 70 Ma. At this time, species richness nearly doubled and marked peak diversity during the entire evolutionary history of planktic foraminifera (Figs. 1 and 3).

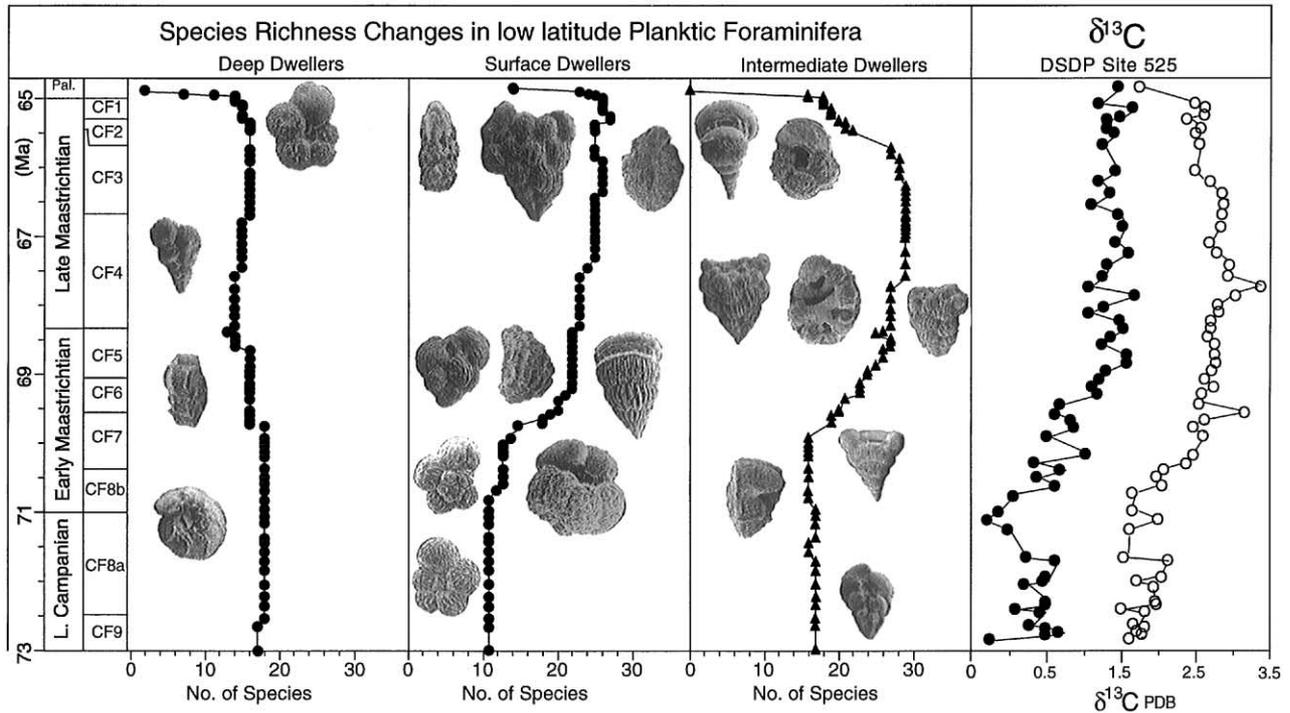


Fig. 3. Species richness of deep, intermediate and surface dwellers at El Kef compared with the paleoproductivity (carbon-13) curve of Site 525. Species richness curves reveal a selective evolution and extinction pattern depending on the particular water mass a species inhabits. Deep dwellers (below the thermocline) are the most stable. Surface and intermediate dwellers show rapid diversification in the early Maastrichtian coincident with global cooling (Fig. 1) and a major increase in paleoproductivity ($\delta^{13}\text{C}$). Intermediate dwellers suffer early extinctions coincident with global warming and decreased primary productivity. All species groups rapidly declined near the K–T boundary.

The species richness curves of Sites 525 and El Kef illustrate this diversity maximum and also reveal selective evolution and extinction patterns depending on the particular water mass a species group inhabits (Figs. 1 and 3). Evolutionary diversification largely occurred in surface and intermediate waters where surface dwellers increased from 12 to 26 species at El Kef and from 12 to 21 species at Site 525. A similarly dramatic increase occurred among intermediate (thermocline) dwellers where species richness increased from 17 to 30 species at El Kef and from 17 to 28 at Site 525. Evolving species were ecological specialists restricted to tropical and subtropical waters and with typically large and highly ornamented tests (e.g., globotruncanids, rugoglobigerinids, racemiguembelinids, planoguembelinids). None of these ecological specialists reached relative population abundances that exceeded 10% at their maximum and none survived the K–T mass extinction (Li and Keller, 1998a, b). However, about one third of the surface dwellers are ecological generalists with smaller, sparsely ornamented biserial and trochospiral test morphologies and with wide geographic distributions across latitudes. Species richness among this group remained relatively stable. It is this group that survived the K–T mass extinction. Deep dwellers (below the thermocline) were least affected by the Maastrichtian environmental changes. These species exhibit relatively sparsely ornamented, small morphologies and low species richness, but very stable species populations from the late Campanian

through the Maastrichtian. Deep dwellers generally disappeared at or near the K–T boundary.

Possible reasons for the evolutionary activity and diversity maximum between 69.5 and 70 Ma are the changing oceanographic conditions associated with the climate change. Stable isotopic data indicate that the diversity increase coincided with global cooling in surface and deep waters and increased surface productivity (Fig. 1). This suggests that the favorable evolutionary conditions may have been due to increased upwelling and nutrient supply, as well as increased thermal gradients and water-mass stratification that accompanied the global cooling.

4.3. The last 500 k.y. of the Maastrichtian

The end-Cretaceous mass extinction began during the last 500 k.y. of the Maastrichtian and accelerated during the last 100 k.y. of the Maastrichtian (Figs. 1 and 3). Only one species (*P. hantkeninoides*) evolved during this interval. Hence extinct species were not replaced, leading to a dramatic decline in species richness (see also Abramovich et al., 1998). The first species groups affected by the K–T extinction phase were the intermediate or thermocline dwellers (e.g., globotruncanids, Figs. 1 and 3). The onset of extinctions in this group coincided with the maximum climate warming between 200 and 400 k.y. prior to the

K–T boundary. At this time, the relative abundances of all K–T “extinction-doomed” species (size fraction $> 150 \mu\text{m}$) declined from 40% to 20% (and less than 10% in the smaller $> 38 \mu\text{m}$ size fraction). Their early decline and eventual demise may have been related to increased biotic stress and changes in the watermass stratification (decreased habitats for intermediate dwellers) associated with climate warming. This is suggested by the relatively stable species richness in surface and deeper water dwellers throughout the warm pulse, though these species declined rapidly during the global cooling of the last 100 k.y. of the Maastrichtian. During this time, species extinctions were less habitat specific, affecting surface, intermediate and deeper water dwellers (Figs. 1 and 3). The combined relative abundance of tropical species declined still further ($< 10\%$ in the $> 150 \mu\text{m}$ size fraction and $< 5\%$ in the $> 38 \mu\text{m}$ size fraction) and may be related to increasing ecological stress induced by cooling. Surface-dwelling ecological generalists continued to thrive, however, and some species even increased their abundances (e.g., heterohelicids, Keller et al., 1995; Li and Keller, 1998a, b). The combined total of the survivor species exceeded 80% of the foraminiferal assemblage during the last 100–200 k.y. of the Maastrichtian. However, by K–T boundary time, all globotruncanids, rugoglobigerinids and all other tropical and subtropical species were extinct and species populations of many surface dwelling ecological generalists had declined. Most workers report a total of 60–70% of the planktic foraminiferal species extinct at and before the K–T boundary. However, it is important to note that the combined relative abundance of this species group is less than 15% of the total foraminiferal population (e.g., Keller, 1996; Canudo et al., 1991; Keller et al., 1995; Luciani, 1997; Masters, 1997; Apellaniz et al., 1997; Molina et al., 1998; Abramovich et al., 1998).

This progressive pattern of species disappearances is frequently questioned by supporters of the impact mass extinction scenario who argue that the early species disappearances are simply artifacts of the sedimentary record because the species have become too rare to be found (Signor and Lipps, 1982), yet lived until the meteorite impact caused mass destruction (Smit, 1990; Olsson and Liu, 1993; Olsson, 1997; Oure-etxebarria, 1997; Apellaniz et al., 1997; Molina et al., 1998). Unfortunately, there is no way to prove whether these early species disappearances are true extinctions, or whether the isolated (often single) specimens, found by various workers after long searches at the K–T boundary, lived up to that time, or are reworked from older sediments. What is evident from the fossil record, however, is that these species were extremely rare and endangered well before the K–T boundary and that relatively minor ecological disturbances could have caused their extinction. Whether the last member of each species population died out as a result of a bolide impact, or died out during the extreme climate fluctuations preceding this event, seems of little ecological importance.

4.4. Geographic aspects of mass extinction

Differences in the mass extinction pattern of planktic foraminifera across latitudes are now well known and documented. A summary of this global database is illustrated in Fig. 4. The mass extinction was essentially restricted to lower latitudes between 30°N and 30°S . A transitional zone (stippled, Fig. 4) with fewer subtropical and tropical species and more temperate species marked middle latitudes with reduced extinctions. No mass extinction occurred in high-latitude assemblages (which consist of ecological generalists) at or before the K–T boundary (Keller, 1993, 1996; Keller et al., 1993; Pardo et al., 1999). However, most Cretaceous species disappeared in the early Danian worldwide (MacLeod and Keller, 1994). An exception to this geographic extinction pattern is observed in the east-equatorial Pacific where cool temperate radiolarian and planktic foraminiferal assemblages dominated and the faunal pattern is similar to that observed in higher latitudes (e.g., New Zealand, Sites 738, 752 and 690; Keller et al., 1997a). The presence of these cool temperate faunas at the equator is probably the result of the proto-Humboldt current which carried cool high-latitude waters north along the coast of South America, similar to the Humboldt current today. The Ecuador section demonstrates the power of ecological and oceanographic factors in determining the fate of species.

Less well documented are the regional differences in low latitudes, as for example between eastern and western Tethyan assemblages, or near-shore and open marine environments that show pronounced variations in relative abundance changes of various species and particularly the opportunistic guembelitrid species. These tiny triserial species are best known from the K–T boundary clay and early Danian where their blooms dominate as the most successful survivor species. In Maastrichtian sediments they are generally rare, except in near-shore depositional environments where these opportunistic taxa thrived in low oxygen and variable salinity conditions (Keller et al., 1998).

5. Invertebrate faunas

Although planktic foraminifera suffered a major mass extinction in tropical and subtropical assemblages over a couple of hundred thousand years, the maximum species extinctions centered at the K–T boundary. How similar is this extinction pattern in invertebrate faunas? The marine invertebrate record is somewhat sketchy because there are not many localities with well-preserved invertebrate faunas across the K–T boundary. A number of excellent studies exist from Seymour Island, Antarctica (Macellari, 1986; Zinsmeister et al., 1989; Zinsmeister and Feldmann, 1996), Chile (Stinnesbeck, 1996), the Bay of

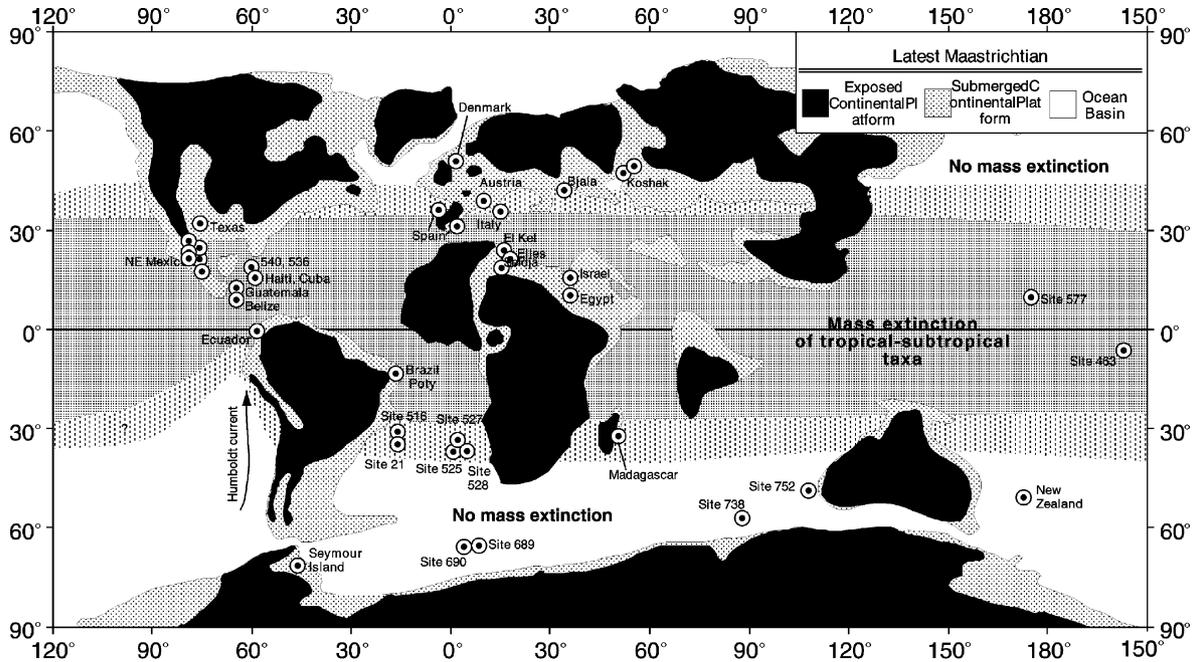


Fig. 4. Paleolocations of Cretaceous–Tertiary (K–T) boundary sections with good planktic foraminiferal faunas across the K–T boundary transition. Stippled, grey and white patterns distinguish tropical–subtropical, transitional warm–temperate, and cool high latitude assemblages. The K–T mass extinction was restricted to tropical–subtropical faunas and no significant species extinctions occurred in higher latitudes. Note that in sections in Ecuador no mass extinction was observed largely because of the reduced effects of the eastern boundary current setting and the presence of temperate faunas at these tropical latitudes (Keller et al., 1997a).

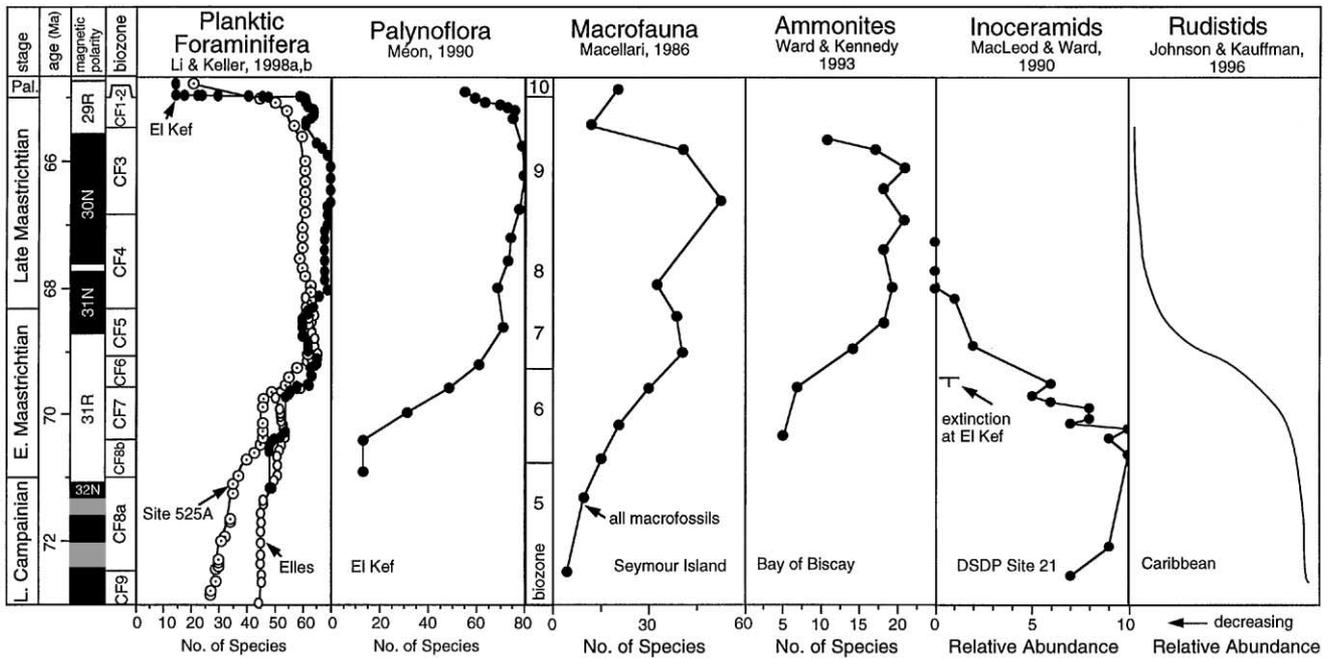


Fig. 5. Late Campanian–Maastrichtian faunal and floral turnovers. Note the rapid increase in species richness in the early Maastrichtian in all fossil groups, except inoceramids and rudistids which dramatically declined to near extinction. Only one inoceramid species survived to the K–T boundary, and rudistids disappeared 100–250 k.y. before the K–T boundary (Johnson and Kauffman, 1996). Note also the terminal decrease in invertebrates, palynoflora and planktic foraminifera during the last 400–500 k.y. of the Maastrichtian. The pre-K–T extinctions are related to rapid climate changes.

Biscay in northern Spain (Ward and Kennedy, 1993), and various deep-sea sites (MacLeod and Ward, 1990). The species richness data from these studies is summarized in Fig. 5 and plotted against the planktic foraminiferal zonation and paleomagnetic time scale of Site 525 (Li and Keller, 1998a). The inferred correlation between planktic foraminifera and ammonite zones is based on Gradstein et al. (1995).

Invertebrate species richness patterns of macrofossils and ammonites are remarkably similar to those of planktic foraminifera and also palynofloras from Tunisia, but differ significantly for inoceramids and rudistids (Fig. 5). As among planktic foraminifera and palynoflora, the species diversity in the late Campanian is generally low for macrofossils on Seymour Island and ammonites in the Bay of Biscay. But species diversity rapidly increased beginning in the early late Maastrichtian and remained high well into the late Maastrichtian. Ammonites in the Bay of Biscay increased from 5 to 20 species, bivalves on Seymour Island increased from less than 5–12 species, whereas all macrofossils increased from 10 to over 40 species. At the same time, however, inoceramids and rudistids rapidly decreased and became extinct (MacLeod and Ward, 1990; MacLeod, 1994).

Johnson and Kauffman (1996) report that despite climate cooling, rudistid-dominated reefs reached their peak in diversity and ecological complexity during the early Maastrichtian, which corresponds to the latest Campanian based on the revised Campanian/Maastrichtian boundary (see Gradstein et al., 1995) used in this study. Globally, this diversity peak coincided with gradual cooling of surface waters from 21°C to 16°C (Fig. 1, zones CF9 to CF8). Dramatic extinctions occurred within the tropical carbonate platform facies during the early Maastrichtian (CF7–CF5, *G. gansseri* zone), though temperate-adapted species and ecological generalists survived to within 100–250 k.y. of the K–T boundary (Johnson and Kauffman, 1996). The extinction of inoceramids at a time of major evolutionary diversification among most other marine organisms is enigmatic and has eluded explanation (MacLeod, 1994). It is possible that this group was adversely affected by the influx of cooler more oxygenated and nutrient-rich bottom water from higher latitudes.

The terminal decline in all invertebrate faunas began near the top of Chron 30N about 400–500 k.y. before the K–T boundary and coincided with the end of the long-term Maastrichtian global cooling and onset of rapid warming (Figs. 2 and 5). Most invertebrate groups decreased rapidly during the last 300–400 k.y. of the Maastrichtian and were nearly extinct well before the K–T boundary. On Seymour Island, Antarctica, Zinsmeister and Feldmann (1996) report the presence of four ammonite species as ranging up to the K–T boundary and long-ranging ammonites have also been reported near the K–T boundary in the Bay of Biscay (Ward and Kennedy, 1993).

6. Discussion

6.1. K–T mass extinction and climate

Paleontological records unequivocally show similar patterns of evolutionary diversity and extinctions during the Maastrichtian that can be related to the records of global climate change. Two major orthogonally opposed biotic events mark the Maastrichtian. One event is the attainment of maximum diversity in marine plankton and invertebrates between 69.5 and 68.5 Ma, except for the extinction of inoceramids and the terminal decline of rudistids (Fig. 5). This evolutionary diversity event follows the global cooling at 71 Ma and is associated with increased $\delta^{13}\text{C}$ values reflecting increased primary productivity, increased watermass stratification and ecological niche creation, and increased CO_2 and nutrients (Figs. 1 and 3; Barrera, 1994; Li and Keller, 1998a, b). For the most part, the high species richness attained by planktic foraminifera, terrestrial floras, and invertebrates after the early Maastrichtian cooling maximum remained stable during the early late Maastrichtian cooling, or until about 500 k.y. before the K–T boundary (see Figs. 3 and 5; and references therein).

The second event is the mass extinction that began during the last 500 k.y. of the Maastrichtian and also seems to be directly related to climate changes—at least prior to the K–T boundary event itself (Figs. 2 and 5; Li and Keller, 1998c). During this time, invertebrate diversity rapidly decreased and only a few species survived until the last 100 k.y. of the Maastrichtian. Current age control is insufficient to determine whether this diversity decline in invertebrates is associated with the global climate warming or the subsequent cooling or both. However, the planktic foraminiferal record is unequivocal. The decrease in diversity began when climate rapidly warmed by 3–4°C between 65.4 and 65.2 Ma and the diversity decline continued during the subsequent 3°C surface water cooling of the last 100 k.y. before the K–T boundary (Li and Keller, 1998a–c). Overall species diversity among terrestrial floras also decreased during the rapid climate changes at the end of the Maastrichtian. The onset of the terminal decline in evolutionary diversity in the marine realm was associated with strongly reduced surface-to-deep $\delta^{13}\text{C}$ and thermal gradients indicating loss of ecological niches and lower watermass stratification. The resultant increased competition and inhospitable environmental conditions, rather than climate change per se, are the likely causal factors for the onset of the terminal decline of the late Maastrichtian fauna and flora.

From the fossil record it is difficult to find strong support for the scenario of a sudden impact-caused mass extinction at the end of the Cretaceous as the sole causal mechanism (see also MacLeod et al., 1997; MacLeod, 1998). Though the extinction of all tropical and subtropical planktic foraminifera that survived to the K–T boundary lends support to such an event as the *final* killing mechanism. However, since tropical and subtropical planktic foraminiferal populations were

already highly stressed and averaged less than 10–15% of the planktic foraminiferal population at this time, a relatively minor event may have caused their demise. The excellent paleontological evidence for a progressive mass extinction over several 100,000 years creates a challenge to identify the possible multi-event extinction mechanism. Although geochemical and mineralogical studies clearly identify dramatic climate and sea-level changes, episodes of accelerated volcanism, and a major bolide impact during the last 500 k.y. of the Maastrichtian, there is no evidence in the fossil record that any one of these events alone acted as the sole, or even primary mass extinction mechanism. However, it is possible that the cumulative effects of climatic, volcanic and impact events exceeded biotic stress levels and resulted in the mass extinction. But how do we differentiate between these potential causal mechanisms?

We can rule out the argument that global cooling and sea-level regressions alone caused the mass extinction. Global cooling may result in extinction of tropical species, but during the early Maastrichtian it triggered a major increase in evolutionary diversity primarily as a result of increased nutrient cycling and increased watermass stratification that made available more ecological niches. Sea-level regressions may have caused some terrestrial extinctions as a result of shrinking habitats and increased competition (Archibald, 1996), but there is no evidence that any of the Maastrichtian sea-level changes are associated with major extinctions, let alone a mass extinction, in the marine realm (Li et al., 1998b, 1999). We can also rule out that volcanism alone caused the K–T mass extinction. However, we agree with Courtillot et al. (1996) that volcanism and the associated climate changes may have been the major triggering factors leading to environmental changes that eventually caused the end-Cretaceous mass extinction. The accelerated rate of species extinctions associated with climate changes and major Deccan Traps volcanic eruptions now dated between 65.4 and 65.2 Ma lends strong support to this argument (Hoffmann et al., 2000). Finally we can rule out an impact at the K–T boundary as the sole killing mechanism because major faunal turnovers preceded the impact. But is it possible that some other catastrophic event occurred during the latest Maastrichtian? Or that the Chicxulub event may not be of precisely K–T boundary age at all? New evidence points in this direction.

6.2. Glass spherule deposits—evidence of chicxulub impact?

It is widely accepted that precisely at K–T boundary time an asteroid or comet impacted the Earth near Chicxulub on the Yucatan Peninsula, Mexico. However, the age of the Chicxulub structure is still unknown (Ward et al., 1995), and currently inferred to be of K–T age largely based on the assumption that the Haiti and Mexican spherule layers are of precisely K–T age and originated as a result of the

Chicxulub impact (Smit et al., 1996). In support of this assumption are similar $^{40}\text{Ar}/^{39}\text{Ar}$ ages of the Haiti and Mexico glass spherules and Chicxulub glass. However, the margins of error for the radiometric ages span the last 500 k.y. and therefore can not differentiate whether the impact event occurred at 65.0, 65.3 or 65.5 Ma (e.g., from 64.98 ± 0.05 to 65.2 ± 0.4 Ma, Izett et al., 1991; Sharpton et al., 1992; Swisher, 1992). Moreover, recent studies have shown that neither the Haiti or Mexico spherule layers may be of K–T age. The Haiti spherule layer(s) are within the early Danian (*Parvularugoglobigerina eugubina* zone), and it is still unclear whether they represent a reworked K–T or latest Maastrichtian deposit, or even a Danian spherule producing event (Stinnesbeck et al., 1999; Keller et al., 2001). The originally discovered Mexican spherule layer is at the base of a siliciclastic deposit that is stratigraphically well below the K–T boundary (Keller et al., 1997b; Ekdale and Stinnesbeck, 1998). Though a pre-K–T age has been disputed based on the assumption that the siliciclastic deposit represents an impact-generated tsunami deposit (Smit et al., 1996). However, this interpretation is erroneous because several horizons of trace fossils (e.g., *Thalassinoides*, *Chondrites*) within this deposit indicate that colonization of the ocean floor occurred repeatedly during its deposition, which thus must have occurred over an extended period of time (years), well exceeding the hours or days of a tsunami event.

Remarkable new discoveries have recently been made in northeastern Mexico by a team of researchers who found that there is not one spherule layer, but four (Stinnesbeck et al., 2001; Keller et al., in press). The additional three newly discovered spherule layers are all within the late Maastrichtian, within the marls of the Mendez Formation, and 6–10 m below the siliciclastic deposit that marks the interval just below the K–T boundary in northeastern Mexico (Fig. 6). The spherule layers range from 20 cm to 1 m in thickness. To date, they have been traced and mapped in over two dozen sections spanning over 20 km (Stinnesbeck et al., 2001). Planktic foraminifera indicate that stratigraphically the lower spherule layers are in the lower third of the *Plummerita hantkeninoides* Zone that spans the last 300 k.y. of the Maastrichtian. Moreover, planktic foraminifera above the spherule layer indicate a significantly warmer climate, indicating that deposition of the spherule layer either preceded, or was part of, the early global warming shown in Fig. 2. Stable isotope data from bulk rock carbonates reveal normal Cretaceous carbon-13 values with effects of diagenetic alteration within the spherule layers. There is no evidence of chaotic deposition. Similarly, granulometric analysis of insoluble residues show uniform small grain sizes ($< 16 \mu\text{m}$, Fig. 6), except for the spherule deposits, and indicate normal pelagic deposition of the Mendez marls. This is also indicated by the generally mottled character of the marls, the presence of bioturbation and trace fossils, and the absence of erosional surfaces, mud clasts, or lithological changes.

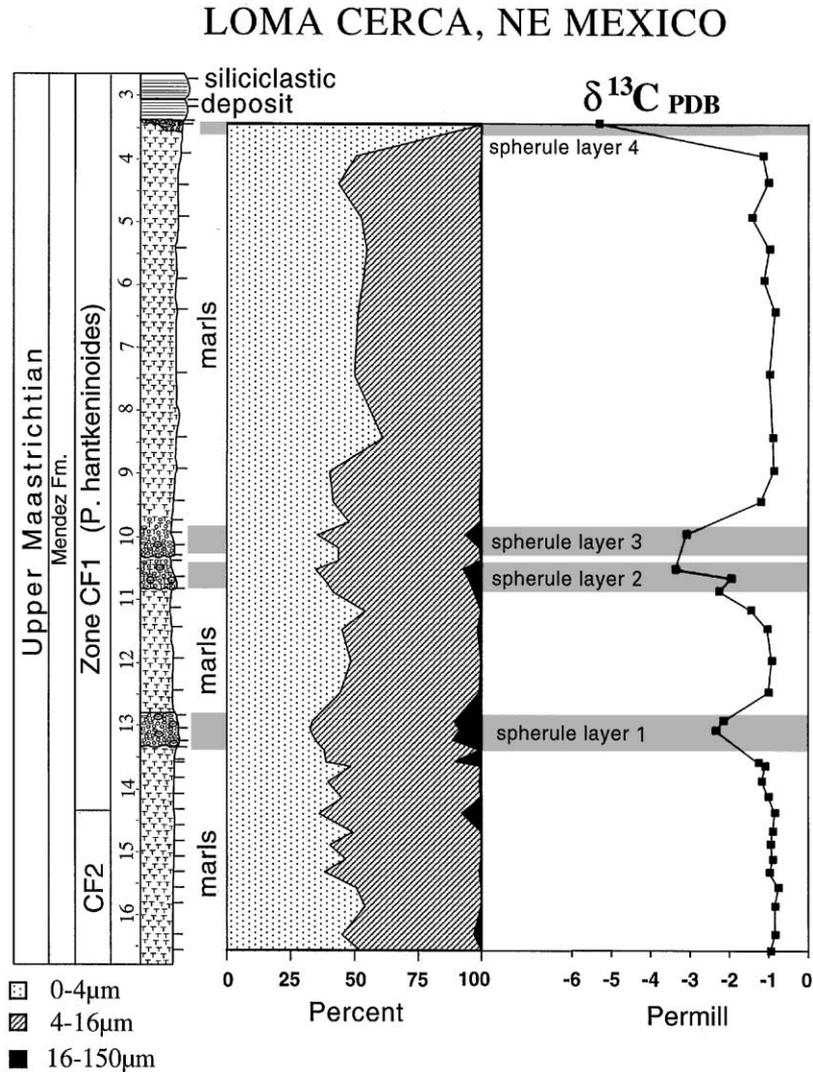


Fig. 6. Lithology, spherule layers, grain-size distribution and $\delta^{13}\text{C}$ record at the Loma Cerca section in northeastern Mexico. Note that the marly sediments are very uniform and contain bioturbation and trace fossils that indicate deposition occurred under normal pelagic conditions. This is also apparent in the uniform grain size values and the stable isotopes that show variations only within the spherule layers (SRD-1 to SRD-4). Note that the age of the oldest spherule deposit is near the base of Zone CF1 that spans the last 300 k.y. of the Maastrichtian. Assuming that SRD-2, 3 and SRD-4 are reworked from SRD-1, the original spherule deposition event occurred between 200 and 300 k.y. before the K–T boundary.

The spherule layers contain abundant light to dark brown and some green partially to wholly de-vitrified glassy spherules that are up to 5 mm in diameter, and glassy, angular, elongated fragments. Most spherules contain large vesicles that make up 75% of the spherule volume and are infilled with blocky calcite (Stinnesbeck et al., 2001). The lowermost layer consists essentially of spherules, some of which are welded together, which suggests deposition occurred while the glass was still hot and ductile. This appears to have been the original event deposition (Keller et al., in press). Non-glass fragments, marl clasts or foraminifera are rare or absent. In contrast, the spherule layers upsection contain abundant foraminifera, marl clasts and terrigenous fragments, that suggests reworking and redeposition of these layers at a later time. There is no evidence of Ir enrichment,

or enrichment of any other platinum group elements. The age of the original spherule event can be estimated between 200 and 300 k.y. before the K–T boundary based on the stratigraphic deposition near the base of the *P. hantkeninoides* Zone.

The new discovery of the older (late Maastrichtian) spherule layers, calls for a re-evaluation of the age of the Chicxulub event. Chicxulub is currently assumed to be of precisely K–T age based primarily on variable Ar/Ar ages and the stratigraphic position of the previously known single spherule layer just below the siliciclastic deposit. The new discovery indicates that the age of this spherule event (and by inference Chicxulub) predates the K–T boundary by 200–300 k.y. Alternatively, the spherule event may have no relationship to Chicxulub and represents another earlier

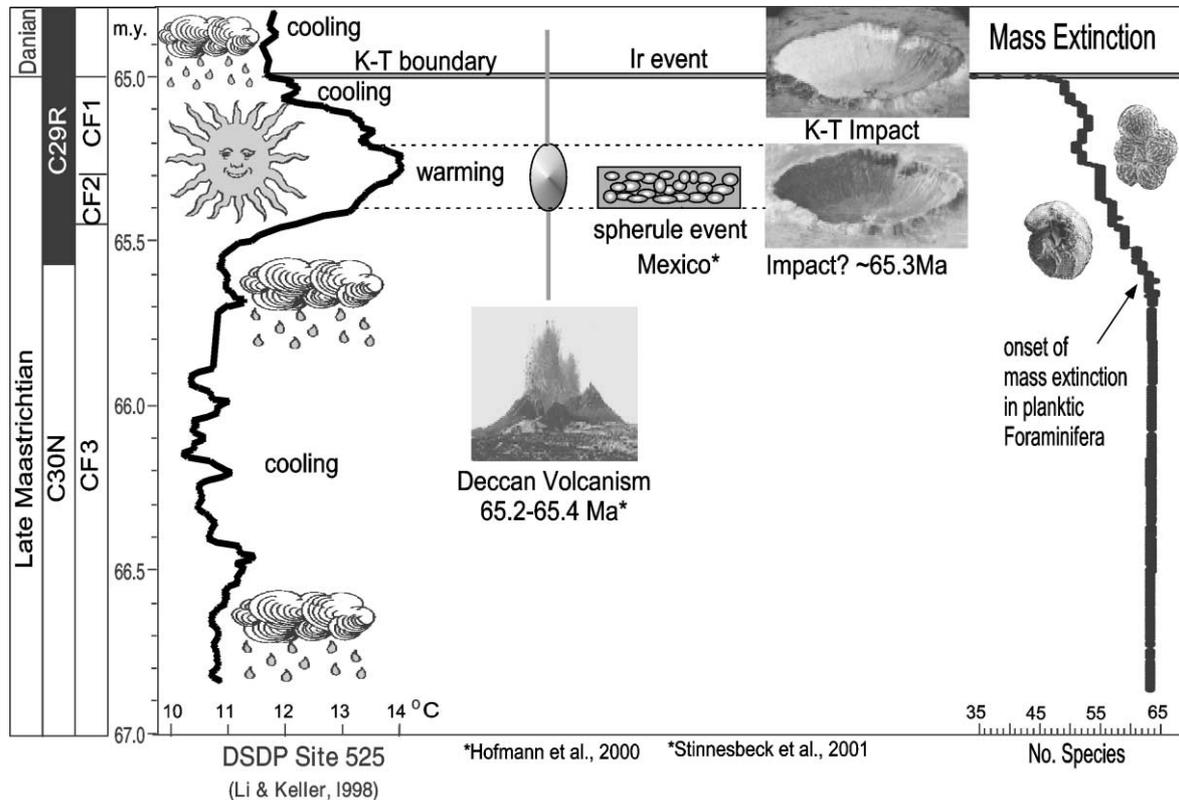


Fig. 7. Cartoon illustrating the sequence of climatic, volcanic and impact events plotted next to the bottom water temperature curve of DSDP Site 525 (Data from Li and Keller, 1998c). Note that based on new discovery of spherule layers, the original spherule deposition event predated the K–T boundary by 200–300 k.y. Assuming that the spherules are of impact origin, we postulate a pre-K–T impact at about 65.3 Ma. Alternatively, if the spherules are of volcanic origin, a major volcanic eruption should have occurred in Central America around this time. There is evidence of major volcanic eruptions in India between 65.4 and 65.2 Ma (Hoffmann et al., 2000).

catastrophic event—a pre-K–T impact, or volcanism? There is now strong evidence that the major Deccan volcanic eruptions occurred between 65.2 and 65.4 Ma (Hoffmann et al., 2000), making volcanism a strong contender for the coeval global warming. However, there is still no evidence of major volcanism in Central America at this time that could be linked to the spherule layer(s). Whatever the cause for the spherule-producing event may have been, the fact is that it coincided with rapid global warming of 3–4°C in surface and deeper waters (Fig. 2, 7), decreased surface-to-deep $\delta^{13}\text{C}$ gradients, and decreased watermass stratification. These factors resulted in a decrease in ecological niches and a high-stress environment for marine biotas that accelerated species extinctions.

7. Multi-event mass extinction scenario

The faunal record clearly shows that we can rule out that any single event (e.g., climate change, sea-level regression, volcanism, or comet/asteroid impact) can account for the progressive pattern of the K–T mass extinction. But the combined effects of climate change, volcanism and impacts are the likely killing mechanisms (e.g., the whole is greater than

the sum of its parts). This multi-event sequence started about 400–500 k.y. before the K–T boundary, at the transition that marks the end of the long-term Maastrichtian global cooling trend and the onset of rapid warming as illustrated in the summary cartoon of Fig. 7. At this time, tropical planktic foraminiferal species populations were severely stressed with most species rare and the overall populations strongly reduced. Temperate species and ecologic generalists dominated in the (now) humid temperate tropics and subtropics and ecologic generalists thrived from low to high latitudes. Marine invertebrate populations were also stressed in the tropics and subtropics, with decreasing diversity possibly exacerbated by shrinking shelf habitats and increased competition due to the sea-level regression at 65.5 Ma (Keller and Stinnesbeck, 1996).

Beginning about 450 k.y. before the K–T boundary, climate rapidly warmed by 3–4°C in surface and deep waters over a period of a few thousand years and vertical temperature gradients decreased by 2.7°C (Li and Keller, 1998c). At the same time, carbon-13 values in surface and deep water decreased by 0.6 permil (Li and Keller, 1998c). Temperatures remained warm between 200 and 400 k.y. before the K–T boundary (Fig. 7) and carbon-13 values gradually recovered. This warm event may have been linked to

increased atmospheric CO₂ due to volcanic eruptions, or an impact event. There is ample evidence of intense volcanism in India during the latest Maastrichtian (Deccan Traps, (Courtillot et al., 1996; McLean, 1991; Basu et al., 1993; Bhandari et al., 1995; Venkatesan et al., 1993, 1996), and the major pulse of Deccan volcanism is now dated between 65.4 and 65.2 Ma (Hoffmann et al., 2000). Now there is also evidence of a major spherule-producing event in Central America between 65.3 and 65.2 Ma, the time of maximum warming (Stinnesbeck et al., 2001; Keller et al., in press).

Despite these extreme climatic conditions, Late Cretaceous tropical and subtropical faunas and floras made a comeback from the brink of extinction at least for a brief time. In the marine realm, tropical and subtropical planktic foraminifera invaded higher latitudes carried by warm surface currents. Their invasion was short-lived, but was evident in marine sediments deposited at latitudes up to 50–60° north and south (Keller et al., 1993; Pardo et al., 1999). However, not all tropical species fared well. Those living within the thermocline suffered extinctions as a result of reduced thermal gradients and hence competition with surface dwellers whose habitat was expanding. Several prominent marine invertebrate groups never recovered and continued their rapid decline to extinction, possibly as a result of the invasion of warm saline bottom waters into their habitat (Fig. 6).

During the last 100 k.y. of the Maastrichtian, climate cooled rapidly by 2–3°C in surface and bottom waters across latitudes (Fig. 7). This rapid cooling resulted in severe biotic stress for tropical and subtropical marine faunas, which rapidly decreased in diversity and their total combined relative abundance dropped to less than 10%. At the same time ecological generalists dominated and a few opportunistic species thrived (e.g., *Guembeltria* and *Chiloquembelina waiparaensis*). At the K–T boundary all tropical and subtropical species disappeared. This group totaled about 2/3 of the planktic foraminiferal species, but their combined relative abundance averaged only 5–10% of the total population. In contrast, ecological generalists that dominated across latitudes survived well into the early Danian. Thus, the environmental effect of the extinctions directly associated with the K–T boundary impact itself was relatively small and restricted to the tropics and subtropics. However, the long-term effects of the climate change, and particularly the continued cooling into the early Danian and dramatically reduced primary productivity, coupled with increased competition of newly evolving species, resulted in the rapid decline of the ecological generalist populations and led to the extinction of most K–T survivors within the first 200,000 years of the early Danian.

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