THIRTY

Dinosaur Extinction

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The disappearance of nonavian dinosaurs is probably the most notorious extinction event of all time, yet it is only a small part of a greater class of extinctions known as "mass extinctions." Mass extinctions are global events characterized by unusually high rates of extinction. The magnitude of these rates is usually unspecified but it is generally significantly higher than the rate of so-called "background extinctions;" that is, extinctions that occur constantly through geologic time (Raup and Sepkoski 1982). Mass extinctions are also characterized by geologically short timescales and by a significant diminution in the number of surviving taxa, as well as in their diversity. Although background extinctions may account for more than 95% of all extinctions through geologic history, it appears that mass extinctions reset the evolutionary clock, as it were, allowing one major taxonomic group to replace another in a given environment.

Five episodes of mass extinctions are generally regarded as the most significant in Earth history. These are (in order of decreasing magnitude) the Permo-Triassic extinction (245 mya), the Late Ordovician extinction (~439 mya), the Late Devonian extinction (~367 mya), the Triassic-Jurassic extinction (208 mya), and the Cretaceous-Tertiary (K/T) extinction (65 mya). Surprisingly, little is known about most of these events; however, glaciation is generally believed to have been the driving force behind the Late Ordovician event (e.g., Sheehan 1988; Brenchley et al. 1994).

The Permo-Triassic and K/T events have been extensively studied, with mixed results. The Permo-Triassic extinction was termed by Erwin (1996) the "mother of all mass extinctions;" a whopping 95% of all marine species (57% of the families) are estimated to have become extinct at that time (Erwin 1993). By this standard, the K/T extinction was somewhat less severe, with about 50% of the genera and about 20% of the families becoming extinct (Sepkoski 1993), but nonetheless, it constituted a major reorganization of much of Earth's biota.

The focus of this chapter is the Cretaceous/Tertiary (K/T) extinction. During the latter half of the Cretaceous (~97–65 mya), Earth underwent a variety of complicated changes, culminating in the extinction of nonavian dinosaurs (Dinosauria excluding Aves) and many other life forms at or somewhat before the K/T boundary. To merely consider nonavian dinosaurs without an understanding of all that was going on during this time would be myopic. For this reason, we consider here both the patterns of geologic and biotic changes that occurred at that time.

Although much is agreed upon regarding the changes that characterize the latter half of the Cretaceous, considerable controversy remains. Much of this controversy is rooted in differing interpretations of the geologic and fossil records. As authors of this chapter there is much on which we agree, but there are also issues on which we hold differing interpretations, as was the case in an earlier dialog between Russell and Dodson (1997) on dinosaur extinction. Thus, in each section, we highlight the similarities and differences of interpretation as they arise. Finally, we conclude with two short scenarios explaining our differing views on how the extinction of dinosaurs and their contemporaries may have transpired.

Geologic Events at or Near the K/T Boundary

Our search for a cause or causes of the extinctions requires us to be aware of events that might have occurred at approximately the same time as the extinctions occurred. We can identify three major, probably unrelated geologic events occurring at or surrounding the K/T boundary. Here we describe these three events and outline the evidence for each, starting with the longest (volcanism) and ending with the shortest (asteroid impact) event. We also list the various physical corollaries that will be discussed later.

Before we discuss these three geologic events, we first comment briefly on longer-term climatic trends across the K/T boundary. No single pattern has emerged, so we do not discuss this subject in detail. Although there are some stratigraphic problems, estimates suggest that the regional, if not the global, climate gradually cooled a few degrees from mid-Cretaceous (~90 mya) highs through the K/T transition into the Paleocene. Most estimates place the change across the boundary between 2 and 3°C (Sigurdsson et al. 1992), although some estimates have placed it as high as 8°C locally (Lécuyer et al. 1993). There is no unambiguous evidence for a precipitous drop in temperature across the boundary. Other factors, including marine regression, would have also contributed to longer-term cooling.

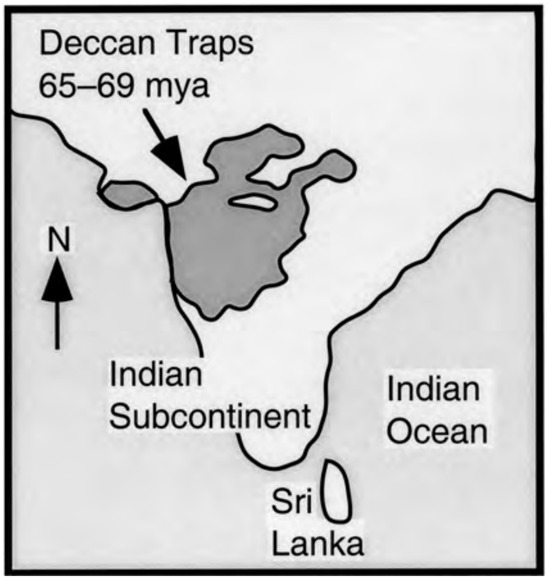

FIGURE 30.1. Geographic extent of latest Cretaceous and earliest Paleocene Deccan Traps. (After Courtillot 1990.)

Volcanism

The latest Cretaceous was a time of significant tectonic activity; this brought with it arc volcanism, particularly in the Pacific. In addition, one of the greatest episodes of nonpyroclastic volcanism since the Permian brackets the K/T boundary. These flood basalts, known as the Deccan Traps, cover an immense part of both modern day India and Pakistan (fig. 30.1). Individual flows in the sequence cover almost 10,000 km^2, with a volume exceeding 10,000 km^3. Individual flows average 10–50 m thick, sometimes reaching 150 m. In western India, the accumulation of lava flows is 2,400 m. Flows originally may have covered almost two million km^2, with a volume possibly exceeding two million km^3 (Courtillot 1990).

The age estimates for emplacement of the Deccan Traps run from about 69 to 63 mya (Venkatesan et al. 1993; Prasad et al. 1994), which, on the magnetostratigraphic time scale, spans from near the end of 30 normal into the commencement of 29 normal (Courtillot 1990). The eruptions were episodic, not continuous, possibly with a peak eruption surrounding the K/T boundary (Courtillot 1990; Courtillot et al. 1996), which occurs in 29 reversed on the magnetostratigraphic time scale (Courtillot 1990). It not certain how close to the K/T boundary individual episodes can be placed, and thus it is not clear that one can estimate magnitudes with any certainty. It is, however, clear that the eruptions bracket the K/T boundary. Based on radiometric dating, paleomagnetism, and vertebrate biostratigraphy, the bulk of the eruptions were centered around the K/T boundary, during a reversal in Earth's magnetic poles known as 29R (Courtillot 1990; Prasad et al. 1994). Although one cannot eliminate the possibility of sudden, violent eruptions, most of the Deccan Traps were viscous flood basalts, more like the Hawaiian volcanoes than Mt. St. Helens. Regardless, the six-million-year episode of Deccan Traps volcanism dwarfs both of these more modern eruptions.

Corollary physical effects for such sustained eruptions are not well understood. If modern pyroclastic volcanism is any guide, an increase in particulate matter in the atmosphere probably took place. Moreover, the potential to produce significant amounts of atmospheric CO_2 may have existed. Whether increased CO_2 caused warming through a greenhouse effect or the increased particulate matter resulted in cooling is not known. If the latter scenario is correct, the longer-term effects, over a million years or more, could have been global cooling.

Global Marine Regression

As was the case with other mass extinctions, there is a regression associated with the K/T extinctions. In terms of subaerial exposure, it may have been significantly larger by comparison to any other regression since the end of the Permian (Smith et al. 1994; fig. 30.2).

Although the regression was global in extent, the North American Western Interior contains the best-studied record of latest Cretaceous dinosaurs; thus, most of our comments on marine regression deal with this continent. In this region, the regression is well represented by the Fox Hills Sandstone (Montana and North Dakota, United States), a regressive barrier-bar sequence (Gill and Cobban 1973). A terrestrial unit, the dinosaur-bearing Hell Creek Formation, prograded over the Fox Hills Sandstone to form a low coastal plain, built by aggrading, meandering rivers (Fastovsky 1987). Several lines of evidence suggest that maximum regression was just prior to the end of the Cretaceous. Keller and Stinnesbeck (1996) suggest that the global maximal regression occurred sometime between 3×10^5 and 1×10^5 years before the end of the Cretaceous. The presence of elasmobranchs (sharks and relatives) in Hell Creek freshwater deposits may indicate close proximity to marine conditions. Elasmobranchs are known throughout the entire Hell Creek Formation, are absent from the basal portion of the unit above the Hell Creek Formation (the Tullock Formation), but again appear (different taxa) in the middle of the Tullock (or Fort Union Formation). This suggests that the seaway had regressed by earliest Paleocene times, if not earlier. The Tullock Formation has indications of extensive ponded water in its basal sections (Fastovsky 1987), suggesting the rise of base level and the last-gasp reincursion of the last Western Interior Sea. There is thus a facies/paleoenvironmental shift at the lithostratigraphic Hell Creek/Tullock boundary, going from slightly better drainage to poor drainage and flooding (ponds). Together, these data argue for maximum regression just before the Hell Creek/Tullock lithostratigraphic contact, with transgression in the region commencing at or just before the time of the Hell Creek/Tullock contact.

The lithostratigraphic boundary between the Hell Creek and Tullock formations is recognizable by this facies change, as well as by the presence of localized coal deposits. These localized coal deposits were at one time considered of greater stratigraphic importance than they are now, and were labeled in inverse alphabetic order, with the lowest, or "Z" coal, marking the lithostratigraphic contact. It has been shown that the coals do not always precisely correlate with the K/T biostratigraphic boundary as identified by iridium (Fastovsky 1987) and pollen, and may diverge by as much as 5 m (Johnson 1992).

A number of consequences have been suggested as occurring at the time of maximum marine regression: decrease in coastal and marine habitats, fragmentation of remaining habitats, establishment of land bridges, and lengthening of stream systems. These are discussed in the section dealing with the patterns and tempo of biotic change.

Asteroid Impact

Although its affects on the biota are still being debated—here, as in other studies—the fact of an asteroid impact at the end of the

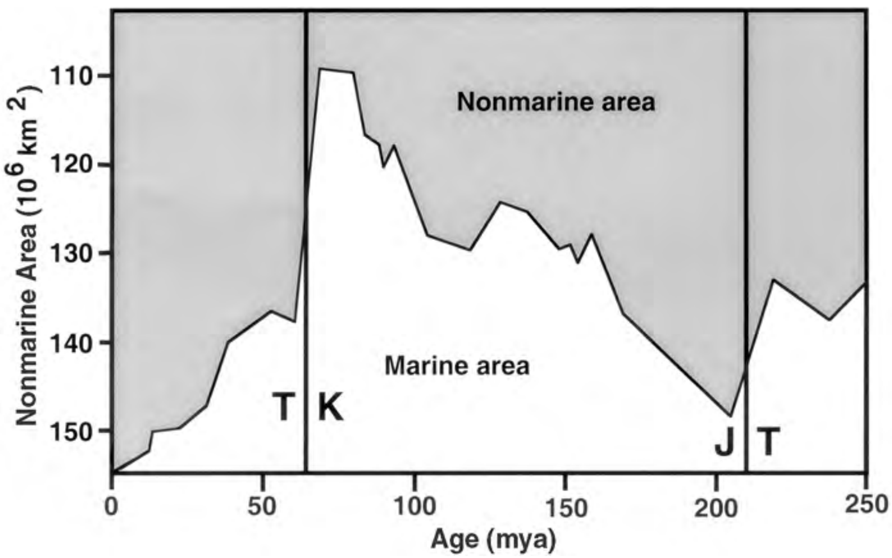

FIGURE 30.2. Comparison of marine and nonmarine areas for the past 250 million years. Note marked additions of nonmarine areas surrounding the Triassic/Jurassic and K/T boundaries. (After Smith et al. 1994.)

Cretaceous is beyond doubt for most geologists (but see Officer and Page 1996). As is well known, in 1980, Alvarez et al. proposed that an asteroid struck Earth 65 mya and caused the K/T extinctions. The evidence that they produced was largely based on the presence of anomalously high concentrations of platinum group metals (the most famous and significant of which was iridium) at the paleontologically identified K/T boundary in three marine sections in Italy, Denmark, and New Zealand (fig. 30.3). A fourth locality in Spain was identified virtually simultaneously by other workers, who had come to the same conclusion (Smit and Hertogen 1980).

Because iridium is not common at Earth's surface, but is known from iron-rich meteors (chondrites), the Alvarez team assumed that the iridium came from an extraterrestrial source. From this supposition, it was calculated that an asteroid with a diameter of 10 km would have been necessary to spread iridium globally in the quantities observed. The presumed exact coincidence of the impact layer with the K/T extinction forced the conclusion that the asteroid and the biotic event were causally linked. Observations derived from the 1883 volcanic eruption of Krakatoa proved to be a readily available model. Thus in the 1980 paper, the Alvarez team postulated that not only did an asteroid strike Earth 65 mya, but that the dust driven into the atmosphere from its impact blocked off the sunlight and produced the extinctions. Luis Alvarez (1983:627) put it thus:

> When the asteroid hit, it threw up a great cloud of dust that quickly circled the globe. It is now seen worldwide, typically as a clay layer a few centimeters thick in which we see a relatively high concentration of the element iridium—this element is very common in meteorites, and presumably in asteroids, but is very rare on earth. The evidence that we have is largely from chemical analyses of the material in this clay layer. In fact, meteoric iridium content is more than that of crustal material by a factor of more than 10^4. . . . Iridium is depleted in the earth's crust, relative to normal solar system material, because when the earth heated up and the molten iron sank to the core it "scrubbed out" the platinum group elements in an alloying process and took them "downstairs."

The history of the acceptance of asteroid-induced extinctions at the K/T boundary is well known and need not be recited here (Raup 1986; Alvarez 1997; Powell 1998). What is critical is that the idea was testable: that high concentrations of iridium should be found globally, in terrestrial as well as marine sedimentary rocks, and that if other features of impacts became known, these too should be present globally. The idea that an impact occurred at the K/T boundary has gained broad credibility exactly because it has resisted falsification and because discoveries at the K/T boundary have been of the type that it predicted. For example, if the K/T asteroid impact were truly a global phenomenon, it should have had global effects. In fact, just short of 110 K/T boundary, sites are now known globally with anomalous concentrations of iridium (Alvarez, pers. comm.). The discovery—first made in 1983—of terrestrial sequences throughout the Western Interior of the United States and Canada that contain high platinum-group metal concentrations sustained the prediction that iridium was not simply some by-product of marine sedimentation.

Because impacts are instantaneous, high-pressure events, it came to be recognized that they leave signatures reflecting their nature. Perhaps the most distinctive of these is so-called "shocked quartz," quartz that has literally begun to fracture and reorganize itself into the high-pressure mineral stishovite. Other indicators include droplets of molten crustal material that have cooled instantaneously in the atmosphere (tektites) and then rained down as impact glass. All of these features are known to be associated with impacts generally, and with the K/T impact in particular.

In 1990, a crater near the town of Chicxulub in the Yucatan Peninsula of Mexico was rediscovered (see Powell [1998] for a discussion of this history; fig. 30.4). Despite claims that the crater was actually derived from volcanic activity (Officer et al. 1992), it has generally been acknowledged in the years since its rediscovery that it is an impact crater (Hildebrand and Boynton 1991). Dating of the melt rock produced a date of almost exactly 65 mya (Swisher et al. 1992), and the size of the crater, 170 km in diameter (Hildebrand et al. 1991), corresponds to estimates of crater sizes that would be produced by an impact of 10 km in diameter. The timing, geochemistry, and location (Schultz and D'Hondt 1996) of this crater all are concordant with the one that might have been expected from the end-of-Cretaceous asteroid.

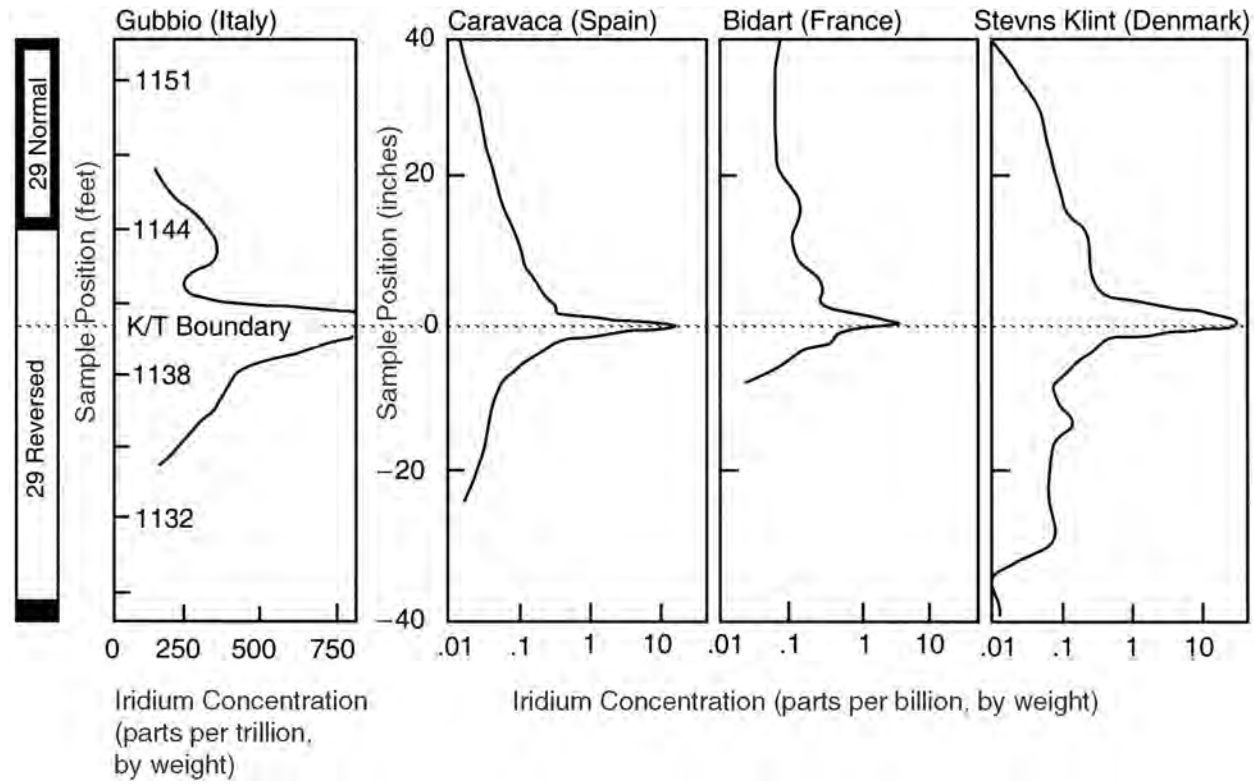

FIGURE 30.3. Anomalous levels of iridium at the K/T boundary compared with the background levels for various sites around the world. The portion of magnetostratigraphic column bracketing the K/T boundary is on the left. (after Courtillot 1990.)

FIGURE 30.4. Possible extent of the Chicxulub crater in the Yucatan Peninsula. (After Archibald 1996a.)

In short, it is believed that the crater produced by the terminal-Cretaceous asteroid impact has now been found.

A number of physical events (corollaries) stemming from the impact have been proposed: acid rain, sudden temperature drops, sudden temperature increases, tsunamis, and global wildfire. These are discussed in the next section.

Patterns and Tempo of Biotic Change

We start with a viewpoint shared by almost all vertebrate paleontologists: the remains of nonavian dinosaurs are not found in sediments younger than the K/T boundary, a moment in time most reliably dated at around 65 mya. The conclusion, again shared by almost all vertebrate paleontologists, is that nonavian dinosaurs became extinct at or before this time. Despite these widely held views, there remains some confusion. Even in the very unlikely event that the undisputed remains of a few nonavian dinosaurs are found above the K/T boundary, the current evidence strongly indicates that the ultimate cause(s) of nonavian dinosaur extinction occurred at or before the K/T boundary. This is because organisms may linger in isolated refugia well after the vast majority of their species has disappeared.

The K/T extinctions resulted in a profound biotic turnover involving both marine and nonmarine organisms. As mammals, humans have a particular interest in the K/T events, because the extinction of most, if not all, medium to large (over ~10 kg) terrestrial vertebrates—mostly nonavian dinosaurs—opened an ecological space that mammals, including our primate ancestors, began to fill within a million years or less.

For some groups of organisms, a global pattern of biotic turnover is known or is emerging for the K/T boundary. For nonmarine (freshwater and terrestrial) vertebrates, including nonavian dinosaurs, the fossil record is far more geographically restricted. For most of the Late Cretaceous, the record of dinosaurs is nearly global in extent (fig. 30.5A), but near the K/T boundary, the well-studied record is restricted to the Western Interior of North America (fig. 30.5B). Recent discoveries of Late Cretaceous dinosaurs in South America, China, Europe, Siberia, and India hold promise as additional K/T boundary sections, but for

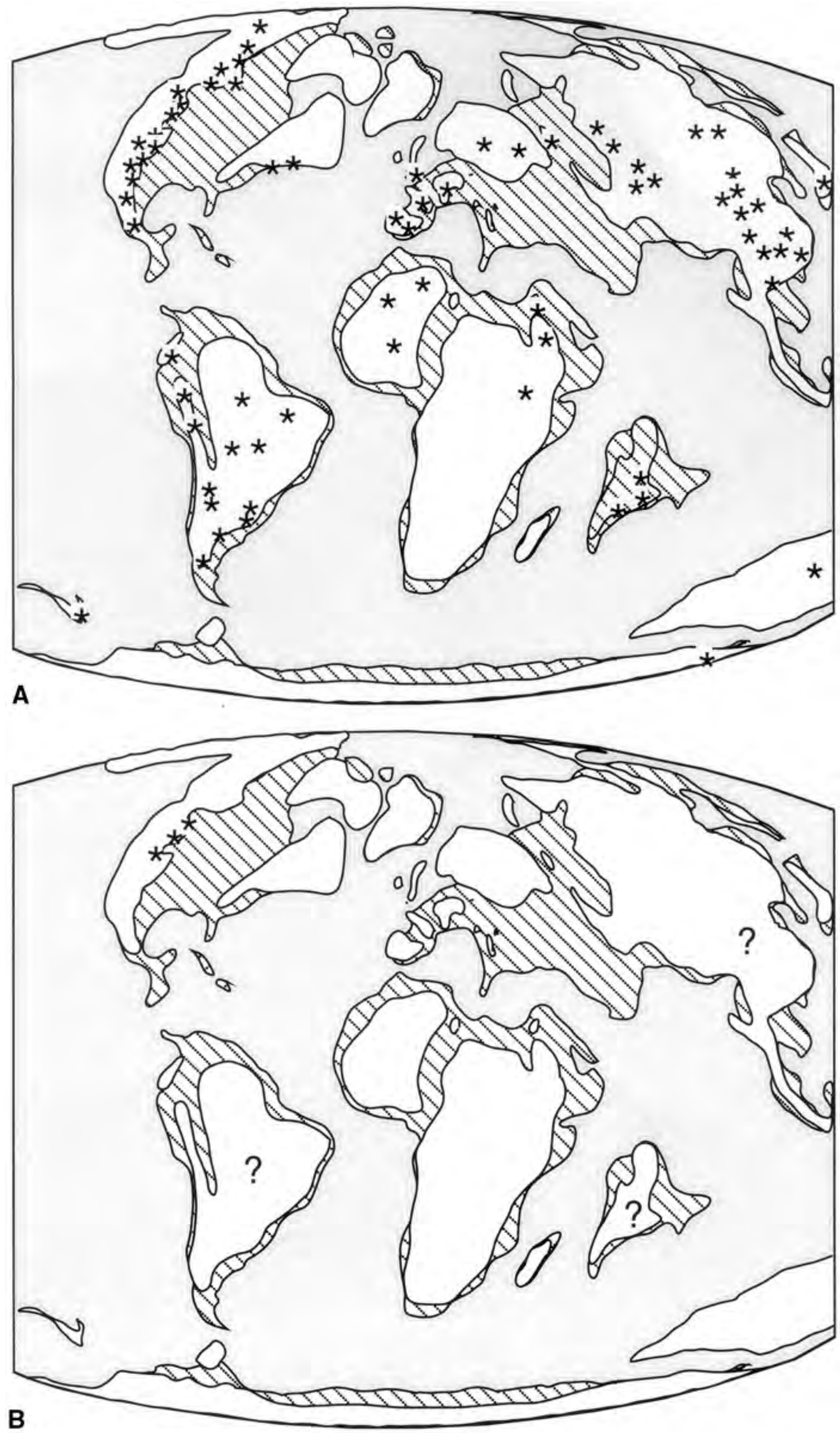

FIGURE 30.5. A, record of nonavian dinosaurs for the Late Cretaceous (asterisks). B, record of nonavian dinosaurs at the K/T boundary (asterisks) and new areas (question marks) possibly preserving a similar record. Shaded areas represent marine environments covering continental plates. (After Archibald 1996a.)

now, we must content ourselves with what is known from the Western Interior.

Dinosaur Diversity during the Last Ten Million Years of the Cretaceous

Opinions vary on what happened to dinosaur diversity during the last ten million years of the Cretaceous in the Western Interior. The most widely accepted view is that the number of genera and species declined considerably over these ten million years (e.g., Sullivan 1998a). This assessment is based on the two best-known dinosaur faunas in the Late Cretaceous of the Western Interior: the ~75 my Judith River and ~65 my Hell Creek faunas. From the Judith River to the Hell Creek fauna, the absolute generic diversity of dinosaurs decreased by 40% (dropping from 32 to 19). Most important was the dramatic reduction of the large, probably herding ceratopsids (five down to two) and hadrosaurids (seven down to two). Notably, it was the more common taxa (ornithischians) that show the greatest decline rather than the much rarer saurischians (Archibald 1996a). Although this reading of the fossil record argues that the number of taxa declined, there is no evidence as to whether the number of individuals declined, remained the same, or even increased.

Another view for the same ten-million-year interval suggests that dinosaur diversity remained the same or even increased. Advocates of this view (e.g., Russell 1984b, 1984c) argue that the Judith River Formation is much better sampled than the Hell Creek Formation, and thus, any apparent decline is the result of a discrepancy in the sampling effort. Moreover, a comparison of faunas that preceded the Judith River, as well as those that succeeded it, suggests that the Judith River possesses an anomalously diverse dinosaur fauna. According to this reading of the fossil record, one would need to normalize for the number of localities in the Judith River as well as in the Hell Creek to obtain meaningful comparative data between these fossil-bearing units. Dodson (1990b:7612), in the only quantitative study to attempt to obtain data on the total number of nonavian dinosaurs during their 160-million-year tenure on Earth, concluded, “The decisive role of dinosaurs in the terminal Cretaceous mass extinctions is open to question. The data presented . . . lend support to neither a gradual nor an abrupt disappearance of the dinosaurs. Nonetheless, there is nothing to suggest that dinosaurs in the Campanian or the Maastrichtian were a group that had passed its prime and were in a state of decline.”

Pattern of Vertebrate Turnover at the K/T Boundary

There is agreement on the general pattern of species-level vertebrate turnover in the Western Interior at the K/T boundary, although there are some differences in interpretation. The greatest differences of interpretation are in the timing (and thus causes) of the extinctions. We first examine the general pattern and then discuss the much more controversial issue of the timing and causes of these extinctions in the next section.

The best snapshot of species-level diversity in terrestrial ecosystems just before and after the K/T boundary comes from the uppermost Cretaceous Hell Creek and lower Tullock formations in eastern Montana. Archibald (1996a) argued that some 107 species are well enough known to be used in a discussion of turnover. Archibald and Bryant (1990) and Archibald (1996a) asked the basic question: which of these 107 species known from the Hell Creek Formation survived into the lower Paleocene, as represented by specimens in Tullock Formation localities? In such an analysis, one always runs the risk of overstating the importance of the absence of data. Poorly represented taxa had already been eliminated from the sample of 107 species, and the localities from the two formations are believed by Archibald and Bryant (1990) and Archibald (1996a) to be of comparable richness and of similar enough ecology to use the absence of data with a degree of confidence.

The only major taxa not included were birds and pterosaurs. The patchy fossil bird record does not allow the timing of these extinctions to be documented precisely, nor does it permit a good estimate of the amount of extinction. Although what are regarded as stem taxa for modern birds are recognized before the boundary, only four modern lineages extend through the boundary (Dingus and Rowe 1998). One view, based on cladistic analysis (Dingus and Rowe 1998), holds that this suggests a significant pre-Tertiary avian radiation. Another view, based upon fossil gap analysis (Bleiweiss 1998), holds that extant bird orders arose and radiated after the K/T boundary.

A single pterosaur family, Azdarchidae, which included the largest known pterosaur, is known from the Hell Creek. The overall record of pterosaurs suggests a decline toward the end of the Cretaceous, but the record is simply too poor to determine the pattern.

Table 30.1 (column A) shows the pattern of survival for the other 12 major monophyletic taxa, as interpreted by Archibald (1996a). Of these 12, elasmobranchs, squamates, metattherians, and ornithischian and saurischian (without Aves) dinosaurs show very low levels of survival, ranging from zero to only 30% species survival. According to Archibald (1996a), these five taxa account for about 75% of all the vertebrate extinctions. Archibald noted four particular patterns of survival: freshwater (76% survival) versus land-dwelling (28% survival), ectothermic (61%) versus endothermic (26%), small (74%) versus large (33%), and nonamniote (61%) versus amniote (44%). Except for possibly the last comparison, chi-square tests confirm the differences among these factors (fig. 30.6). The biological significance of these differences is more difficult to demonstrate, but these comparisons emphasize that the K/T vertebrate pattern of extinction and survival was differential (Archibald 1996a; Archibald and Bryant 1990).

Using vertebrate data from Archibald and Bryant (1990), Sheehan and Fastovsky (1992) came to a somewhat different conclusion (table 30.1, column B). Notably, Sheehan and Fastovsky treated the data on elasmobranchs and mammals differently. Archibald (1996a; Archibald and Bryant 1990) treated elasmobranchs as part of the Hell Creek fauna, because they occur at the same localities and are not reworked. Elasmobranchs, like some bony fishes, spend much of their life in a marine setting. Under this interpretation, Archibald (1996a; Archibald and Bryant 1990) treated the loss of all five elasmobranchs as disappearances. The comparable ecology with close proximity to marine conditions is absent in the overlying basal Tullock, but occurs again in the middle of the formation. Because of these ecological differences, Sheehan and Fastovsky (1992) argued that the elasmobranchs should not be included in extinction/survival counts at the K/T boundary, because the sediments at and near the boundary are exclusively nonmarine. Regardless, a recent study by Hoganson (2000) suggests that the elasmobranch extinction may have occurred at the K/T boundary.

Among the mammals, there are three major monophyletic clades—multituberculates, metatherians, and placentals (table 30.1). Fifty percent (or more) of the ten multituberculate species disappear, with at least four of the five survivors known by the

TABLE 30.1

Survival of Vertebrate Species across the K/T Boundary

Major Clades from the Upper Cretaceous Hell Creek Formation, Eastern Montana	*Species Survival*	
	A	*B*
Elasmobranchii	0 of 5 (0)	Not included
Actinopterygii	9 of 15 (60)	5 of 6 (83)
Amphibia	8 of 8 (100)	5 of 5 (100)
Mammalia		
Multituberculata	5 of 10 (50)	0 of 7 (0)
Eutheria (placentals)	6 of 6 (100)	0 of 1 (0)
Metatheria	1 of 11 (9)	0 of 5 (0)
Reptilia		
Testudines	15 of 17 (88)	14 of 16 (88)
Squamata	3 of 10 (30)	3 of 7 (43)
Choristodera (Champsosauridae)	1 of 1 (100)	1 of 1 (100)
Crocodilia	4 of 5 (80)	3 of 4 (75)
Ornithischia	0 of 10 (0)	0 of 4 (0)
Saurischia	0 of 9 (0)	0 of 7 (0)
Total	52 of 107 (49)	31 of 63 (49)

Note: Column A is after Archibald (1996a); column B is after Sheehan and Fastovsky (1992). The lower total number of species in column B reflects only the use of the most common species as given in Archibald and Bryant (1990). The numbers in parentheses are the percentages of surviving species.

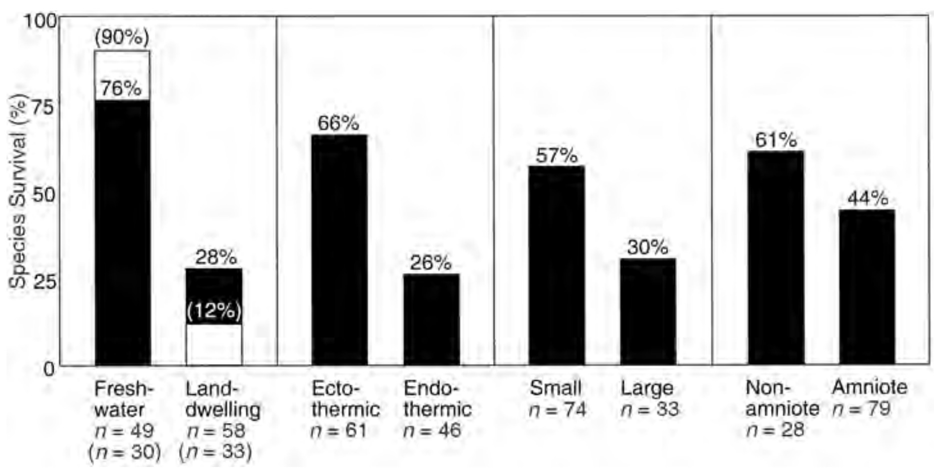

FIGURE 30.6. Factors showing patterns of differential vertebrate species survival at the K/T boundary. Chi-square tests show all of comparisons, except possibly the last, are significant (freshwater versus land-dwelling comparison and ectothermic versus endothermic comparison, $P << 0.005$; small versus large comparison, $0.010 < P < 0.025$; nonamniote versus amniote comparison, $0.150 < P < 0.100$). The white histograms (percentages and numbers in parentheses) on the far left show a similar pattern for freshwater versus land-dwelling species. (The four factors shown as black histograms from Archibald 1996a; white histograms from Sheehan and Fastovsky 1992).

same species or genus in the early Tertiary. All 11 marsupial species disappear across the boundary, with one a possible ancestor for an early Tertiary species in North America. Two to three North American species are argued by some to belong to or be stem taxa for some Tertiary marsupials in South America (Marshall et al. 1990), where marsupials fared much better during the Tertiary. As is the case for most other Late Cretaceous mammals, placentals have low rates of evolutionary change compared with the earliest Tertiary mammals. Placentals do increase in relative diversity near the end of the Cretaceous, but with the possible exception of Lipotyphla, none of the extant 18 orders of placentals is known from before the boundary. Of the six placental species in the Hell Creek, one is thought to be in the Paleocene, and the other five are argued by various authors (see Archibald and Bryant [1990] for references) to be stem taxa for extinct or extant orders. The radiation of placentals in the early Tertiary is the greatest in the history of the group, with 16 of 18 extant orders, along with a number of extinct orders, appearing in the first 16 million years of the Cenozoic. In this interpretation, followed by Archibald (1996a) and Archibald and Bryant (1990), five of six placentals are not known by the same species in the earliest Tertiary but are considered as survivals, because of proposed phylogenetic relations with Tertiary taxa. Sheehan and Fastovsky (1992) argued that most of the mammals should be treated as extinctions, and thus they found zero percent survival for mammals, whereas Archibald (1996a) found 44% survival. The difference in interpretation is a result of whether one considers just the study area (Sheehan and Fastovsky 1992) or includes other areas in the Western Interior (Archibald 1996a).

Even with these differences, however, both Archibald (1996a) and Sheehan and Fastovsky (1992) found total extinction levels of near 50% for vertebrates across the K/T boundary. Sheehan and Fastovsky (1992) also argued that the extinction pattern was differential (fig. 30.6), but considered the differences to be largely attributable to much higher survival levels for freshwater (90%) versus land-dwelling vertebrates (12%), rather than to the multiple factors argued by Archibald (1996a). Thus, these authors agreed that the pattern is one of differential survival and extinction, with at least ornithischians, saurischians (without birds), lizards, and marsupials showing very high greatest percentages of extinction. The possible causes for this differential pattern are discussed in the two concluding scenarios.

Tempo of Vertebrate Turnover at the K/T Boundary

The greatest controversy regarding vertebrate turnover does not concern the overall pattern, but the tempo at which the turnover occurred. Three basic interpretations of turnover have been proposed. Although these three interpretations might apply to all vertebrates, the analyses centered on the tempo of nonavian dinosaur extinction. The first alternative (Sloan et al. 1986) argued that the number of species of dinosaurs was declining in the last few million years of the Cretaceous. This was based on counting the taxa and numbers of dinosaurs from typical Hell Creek Formation sediments through the Bug Creek sequence, just east of Fort Peck Reservoir. Subsequently, it has been shown that most, if not all, of the Bug Creek sequence is Paleocene in age, having cut down into the underlying Hell Creek Formation (Lofgren 1995). Thus, dinosaur teeth in the Bug Creek sequence are usually regarded as having been reworked, and any decrease at subsequently higher localities would simply be the result of fewer reworked teeth (Zombie taxa of Archibald [1996a]).

The second alternative argues that the number of species of dinosaurs shows no decline in the last few million years of the Cretaceous (Sheehan et al. 1991). This study was based on surface collecting through the basal, middle, and upper third of the Hell Creek Formation at sites in Montana and North Dakota. Because of the fragmentary nature of most material, fossils were identified only to the family level. Using several statistical analyses, the authors concluded that the proportions of the various families did not change from the bottom to the top third of the formation. The authors concluded that these findings are commensurate with a catastrophic extinction of dinosaurs.

The third alternative (Hurlbert and Archibald 1995) argued that the quality of the fossil record (particularly, the scarcity of identifiable dinosaur specimens) does not permit us to determine whether the number of species of dinosaurs shows any decline or was stable in the last few million years of the Cretaceous. These authors came to the conclusion, after re-examining the statistical analyses of Sheehan et al. (1991), that the statistical tests were inappropriately applied and that up to 40% of dinosaur species could be lost before any change in proportions of families would be detected.

The question of the pace of dinosaur turnover at the K/T boundary remains unresolved. In part, this is a result of the so-called "Signor-Lipps effect"—the observation by Philip Signor and Jere Lipps in 1982 that, as one approaches any arbitrary boundary (such as an extinction), the overall diversity of groups decreases with decreasing distance from that boundary (Signor and Lipps 1982; see also Fastovsky and Weishampel 1986). What this means, in essence, is that even in the case of an abrupt extinction, the pattern of extinctions leading to the boundary will *appear* gradual. This is because as one approaches the boundary, less diversity is preserved, regardless of whether the diversity truly decreases. The interpretation of any observed decrease in diversity, therefore, must incorporate the Signor-Lipps effect and can be as much a judgment call as an unimpeachable scientific conclusion.

Corollaries of Marine Regression

Some corollaries that have been suggested as occurring at the time of maximum marine regression are a decrease in coastal and marine habitats, establishment of land bridges, fragmentation of remaining habitats, and lengthening of stream systems. Although this is argued to be a worldwide phenomenon, most discussion has centered on North America, where the K/T record of vertebrate turnover is best known.

There is evidence for the establishment of land bridges, especially based on faunal similarities. There may have been some contact with parts of Europe through Greenland. North and South America were probably not fully joined, but certainly the number and proximity of intervening islands increased. Also the western Laramidia and eastern Appalachia continents rejoined to form North America (fig. 30.7). Faunal similarities between Asia and North America are seen during various parts of the latter half of the Cretaceous (e.g., Weishampel 1990b; Fastovsky and Weishampel 1996), suggesting that there were intermittent connections between these continents throughout this time interval. The re-establishment of the Bering land bridge near the K/T boundary appears to have brought a wave of placental mammals into western North America from Asia (Nessov et al. 1998). Most important for our discussion here were archaic ungulates ("condylarths"), the very early relatives of modern ungulates and whales (Archibald 1996c, 1998). Their appearance in North America coincides with the very rapid decline of marsupials. Within a million years of the K/T boundary, 30 species of these archaic ungulates are known in North America, and their numbers continued to increase. The archaic ungulate invaders had dentitions very similar to contemporary marsupials and presumably had a similar diet. Its seems more than coincidence that marsupials did well in North America for about 20 million years, only to almost disappear with the appearance of the ungulate clade. It is ironic that both marsupials and ungulates invaded South America at about the time of the K/T boundary. Their dentitions were already beginning to show differentiation, with the marsupials headed toward carnivory and ungulates toward herbivory. These two clades survived throughout most of the Tertiary in South America.

With the draining of epicontinental seas, there is no doubt that total subaerial exposures increased (Smith et al. 1994). The areal extent of low coastal plains and shallow nearshore environments, however, would have decreased, simply because of the reduction in the total amount of coastline. Archibald (1996a) argued that with the reduction in size of various terrestrial and nearshore habitats, there would have also been a fragmentation of these habitats and concomitant reduction in biotic diversity. He analogized this process with the human-caused reduction and fragmentation of habitats in the Rift Valley System of modern

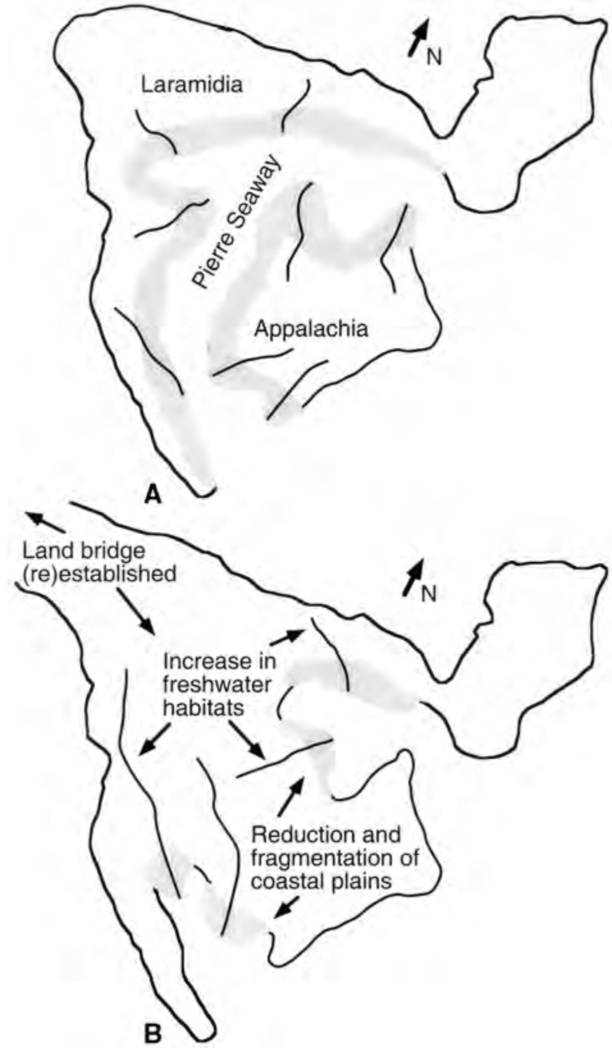

FIGURE 30.7. A, North America divided into two continents (Laramidia and Appalachia) by a midcontinental seaway throughout much of the Late Cretaceous. B, North America reunited as single continent in latest Cretaceous or early Tertiary, showing some possible results of this event. Exact positions of most streams and coastal plains are not known. (After Archibald 1996a.)

East Africa that first impacts larger vertebrates, especially mammals. Although not well known in geologic circles, habitat fragmentation is widely recognized by ecologists as a major contributing factor to extinction (e.g., Bolger et al. 1991). Some earth scientists have argued, however, that there is no evidence for these kinds of changes in the rock record of the North American Western Interior (Fastovsky and Sheehan 1997).

Although we do not have a definitive map of drainage for the Western Interior, extensive work has been done on the sedimentology and drainage patterns for specific latest Cretaceous and early Tertiary stream systems in the eastern part of Laramidia (Belt et al. 1997). Even without accurate paleodrainage maps for all of the Western Interior, however, freshwater stream systems must have increased in length as the marine regression progressed. Thus, it is no surprise that with the bolstering of freshwater habitats, all aquatic vertebrates did well, except for those with close marine ties—sharks and some bony fishes. Such fishes may need to spend at least a portion of their life in a marine environment, in some instances, to reproduce. The major group most likely to suffer would have been the elasmobranchs. In fact, all five species disappear. New species of elasmobranchs did not occur in the area until a smaller transgression (Cannonball Sea) reached the Western Interior at or just before middle Paleocene times (Bryant 1989).

Corollaries of Asteroid Impact

We have no first hand experience as to the kinds and magnitude of climatic and environmental changes that might be wrought by the impact of a 10-km-diameter asteroid. This is simply not within human experience. In the absence of precedent, therefore, scientists have relied on scaling up the observed results of smaller impacts, volcanoes, and nuclear explosions to inform their opinions about what happened when the K/T asteroid hit.

As is evident from the earlier Alvarez (1983) quote, the original idea was that, based upon the atmospheric residence time of fine-grained particulate matter generated in the Krakatoa eruption, sunlight would have been blocked. This was supposed to have caused a multiple-month (later, reckoned to be three-month) episode of darkness (e.g., Pollock et al. 1983). Recently, however, the very concept of large amounts of dust ejected into the atmosphere has itself become controversial. Primarily based on theoretical calculations, Pope (2002) concluded that the amount of dust that was injected into the atmosphere as a result of the asteroid impact was overestimated by two orders of magnitude. He concluded that the shutdown of photosynthesis by atmospheric dust is not a viable scenario.

Assuming darkness arose as a result of some dust in the atmosphere, it has been hypothesized that atmospheric cooling would also have occurred as a result of the darkness. Regardless of whether this actually occurred, the idea remains largely untestable, because of the difficulty of identifying so short an interval of time in the fossil record. What may be testable, however, is whether the extinctions in the fossil record conform to any of these putative byproducts of the impact. Two views have been presented; not surprisingly, one is that the patterns of extinctions reflect what one might expect from an impact, and the other is that they do not.

In support of the idea that Earth underwent an approximately three-month period of darkness, Sheehan and Fastovsky (1992) observed that the survival of aquatic tetrapods (and the extinction of land-based tetrapods) fits the hypothesis of prolonged darkness. Land-based tetrapods, they note, function within food chains that are primary productivity-based; that is, herbivores require fresh plant material as the immediate source of all nutrition. Aquatic vertebrate ecosystems require living plants as the ultimate source of all energy; however, these ecosystems can be buffered by detritus feeding. Even with a temporary stoppage of primary production, these animals can survive for extended periods based on detritus that originated from land-based ecosystems. Interestingly enough, this pattern of survivorship of detritus-based food chains has also been observed in the marine realm. Organisms that are dependent upon primary production—planktonic marine organisms, ammonites and other cephalopods, and a variety of other mollusks—were harder hit by extinction than organisms in detritus-based food chains (Sheehan and Hansen 1986).

As we have seen, it is clear that at the K/T boundary, organisms in freshwater ecosystems were less affected, whereas those in land-based ecosystems were hardest hit (see fig. 30.6). Sheehan and Fastovsky's (1992) conclusion was, therefore, that this is exactly the pattern of survival and extinction that one might observe if photosynthesis were temporarily impeded. In support of this idea is the observation that in the terrestrial realm, plants, the ultimate source of primary production, underwent a 79% extinction (Johnson and Hickey 1990), at least at low to middle latitudes. Moreover, in the marine realm, primary production is thought to have dipped temporarily to near-zero levels (e.g., Zachos et al. 1989).

It has been argued that if tremendous amounts of dust were injected into the atmosphere after a large impact, the darkness would not only suppress photosynthesis but would also produce extremely cold temperatures. This hypothesized condition has become known as "impact winter." The hypothesis states that, following a large impact, ocean temperatures would decrease only a few degrees because of the huge heat capacity of the oceans, but on the continents, temperatures would be subfreezing for a period of 45 days to six months (Toon et al. 1982). The temperature would remain subfreezing for about twice as long as the period of darkness caused by the dust. This idea, however, remains largely untestable, because of the difficulty of identifying so short a time interval in the fossil record.

One can, however, compare survivorship records with this potential means of extinction. The fossil record does not reveal an extinction induced by cold alone. With the exception of a 70% decline in lizards, ectothermic tetrapods (frogs, salamanders, turtles, champsosaurs, crocodilians) did very well across the K/T boundary. Moreover, a latest (but not terminal) Cretaceous vertebrate fauna from northern Alaska strengthens the evidence that a hypothesized sudden temperature drop was not a likely cause of K/T boundary extinctions. Although the Alaskan dinosaur fauna is similar to the Montana faunas (although smaller and with fewer species), the Alaskan fauna completely lacks amphibians, turtles, lizards, champsosaurs, and crocodilians. If the estimated balmy temperature range of 2–8 °C for Late Cretaceous Alaska (Clemens and Nelms 1993) was enough to exclude ectothermic tetrapods, a severe temperature drop to below subfreezing temperatures at the K/T boundary should have devastated the rich ectothermic tetrapod faunas at mid-latitudes. These species flourished. The hypothesis of a sudden temperature decrease simply does not fit with the vertebrate data at the K/T boundary.

A second proposed byproduct of the asteroid impact was acid rain. The most commonly cited acid to be produced by an impact event is nitric acid; some workers have also claimed that sulfuric acid could be produced. It has been argued that nitric acid would have been produced by the combination of atmospheric nitrogen and oxygen as a result of the tremendous energy released by an impact (Prinn and Fegley 1987). Sulfuric acid, it has been suggested, could have been produced as large amounts of sulfur dioxide were vaporized from evaporites at the impact site (Sigurdsson et al. 1992). These acids were presumed to have precipitated as rain. Estimates of the pH of these acid rains vary, but estimates reach as low as 0–1 near the impact site and ~4–5 globally.

Today, rain with a pH as low as 2.4 has been recorded, but annual averages in areas affected by acid rain range from 3.8 to 4.4 (Cox 1993). Acid fogs and clouds with pH levels from 2.1 to 2.2 have been recorded in southern California and have been known to bathe spruce-fir forest in North Carolina (Cox 1993).

Death-and-doom scenarios based on acid rain are now questioned by geologists as well as paleontologists. Calculations of global acid production indicate that not enough acid would have been produced to acidify ponds to the extent that life would have been affected (e.g., D'Hondt et al. 1994). Retallack (1996) argues that in the Hell Creek, at least, the K/T boundary couplet shows the effects of acidification, but it fortuitously served as a buffer, protecting life. Archibald (1996b) pointed out that these interpretations were based on a single geologic section and that Retallack's claims of a trauma for herbivorous vertebrates are not borne out by the fossil record.

Regardless, the survivorship pattern in the biota does not show the presumed affects of an acid rain (Weil 1994). And, given what we know of our modern biota's reaction to acid rain, aquatic animals should have been devastated if acid rain were a significant factor at the K/T boundary. The biological consequences of such low pH values vary from one vertebrate group to another but are always detrimental. Aquatic species (fish, amphibians, and some reptiles) are the first and most drastically affected; with those reproducing in water being the first to suffer. If pH becomes lower than about 3.0, adults often die. The affects on aquatic vertebrates across the K/T boundary would have been very bad if a pH of 3.0 was reached and truly horrendous if it hit 0.0, as suggested by some of the authors noted above. Of all the aquatic species, only elasmobranchs show a drastic drop in eastern Montana. Thus, vertebrate indicators do not reflect any evidence of an acid rain; whatever acid rain occurred did not leave a discernable effect in the vertebrate record.

Also associated with the impact hypothesis was the claim that Earth underwent massive global wildfires (Wolbach et al. 1988; Ivany and Salawitch 1993). Soot and charcoal have been reported from several sites at the K/T boundary coincident with the enrichment of iridium noted earlier. It was argued that the isotopic signature of the charcoal and soot is unique and must therefore have come from the essentially synchronous burning of vegetation equivalent to half of all the modern forests. Other scenarios argue that some 25% of the aboveground biomass burned at the end of the Cretaceous (Ivany and Salawitch 1993).

Such a global conflagration is really beyond our comprehension. In such an apocalyptic global wildfire, much of the aboveground biomass all over the world would have been reduced to ashes. In fresh water, those plants and animals not boiled outright would have faced a rain of organic and inorganic matter unparalleled in human experience. These organisms could have literally choked on the debris or suffocated as oxygen was suddenly depleted with the tremendous influx of organic matter. For some scientists, it thus is no surprise that the global-wildfire scenario appears to be one of equal-opportunity losers and thus does not show any significant agreement with the differential pattern of vertebrate extinction and survival at the K/T boundary. For other scientists, however, the aquatic realm may have been just the place to optimize survival, and it is thus not surprising that survivorship among aquatic organisms was favored.

At Stevns Klint, Denmark, one of the localities where the soot layer was first reported, the physical basis for such an event may be suspect (Officer and Ekdale 1986). It has been argued that there is a global charcoal and soot layer that coincides with the K/T boundary, whose emplacement is measured in months (Wolbach et al. 1990). This also assumes that the sedimentary layer encasing the charcoal and soot was also deposited in only months. This is not the case at Stevns Klint section on the coast of Denmark. Ichnologists Ekdale and Bromley (1984) have described it as a laterally discontinuous, complexly layered and burrowed clay. According to Officer and Ekdale (1986) this unit could not be the result of less than a year of deposition caused by an impact-induced global wildfire. Thus, despite its uniform isotopic signature, the carbon accumulation near the K/T boundary at Stevns Klint, at least, has been interpreted as possibly the result of much longer-term accumulation (Officer and Ekdale 1986).

The Plant Record

The record for plants at and near the K/T boundary is usually distinguished as megafloral (including leaves and fruiting bodies) and palynological (including pollen and spores). The palynological record is commonly easier to sample over a greater geographic range but may not allow as great a taxonomic resolution as the megafloral remains. Although more global in extent than the vertebrate record, the plant record also is best known in the northern hemisphere, particularly in North America. Unlike for vertebrates, it has been possible to recognize four megafloral zones in the Hell Creek (three zones) and lower Fort Union (one zone) formations (Johnson and Hickey 1990; Johnson 1992). Although best studied near Marmarth in southwestern North Dakota, this megaflora also has been studied in eastern Montana, eastern Wyoming and western portions of South Dakota. Between each of the four successive megafloras, extinctions were 59%, 75%, and 79% (Johnson and Hickey 1990; Johnson 1992). The last figure of 79% extinction is for extinction at the K/T boundary.

Above and beyond the megafloral extinction, a fern spore "spike" occurs just above the iridium-bearing clay at the K/T boundary. This is believed to have been caused by a brief flourishing of spore-bearing ferns at the K/T boundary (Orth et al. 1981; Tschudy et al. 1984a).

More recent, finer-grained sampling of palynomorphs in eastern Montana suggests that plant communities were changing before the K/T boundary, possibly reflecting a transition from more open to more closed and moist habitats (Stromberg et al. 1998). To the north, in Canada, palynomorphs (Sweet et al. 1993) have also been argued to show a more gradual change. On the opposite side of the globe, in such places as New Zealand, which was much farther south than it is today, and in Antarctica, the palynofloral record does not record any biotic upheaval (Askin et al. 1994; Johnson 1993). The picture that is emerging is one of considerable extinction at lower latitudes compared with higher latitudes.

The Marine Record

The marine record of invertebrates, in both geographic and stratigraphic coverage, is more complete than either the marine or terrestrial vertebrate record. Nonetheless, the patterns of extinction in many groups are poorly understood, and only hint at the nature of the boundary event(s).

Arguably the most profound change in the biota at the K/T boundary is recorded in marine records obtained through the Deep Sea Drilling and Oceanic Drilling programs. In these deposits, stable isotope records (^{13}C) from foraminiferans indicate that the normal (~4–5 permil) difference in ^{13}C between the benthic and planktic organisms effectively collapsed, so that there was virtually no difference between the isotopic signatures of the surface and bottom of the oceans (Hsü et al. 1982; Arthur et al. 1987; Zachos et al. 1989). This extraordinary event was once considered to have resulted from a cessation in primary productivity, popularized by Hsü et al. (1982) as the "Strangelove Ocean." In the intervening years, it has been noted that the stable isotope record can be equally explained by a reduction in surface-dwelling carbon export to the deep oceans (D'Hondt et al. 1996). Either explanation (or both) may be correct; regardless, the data suggest that a profound perturbation of oceanic primary productivity occurred at the K/T boundary. Carbon export from the surface waters to deep waters in the oceans appears to have been shut down for an approximately three-million-year period just after the K/T boundary (Luttenberg et al. 1995; D'Hondt et al. 1996).

Interestingly enough, although there has been little disagreement about the isotopic record, the fossil record of Foraminifera (from whence the stable isotopes are obtained) remains controversial. All agree that there was a major foraminiferal extinction, but the question is whether it was abrupt at the boundary or spread out across the K/T transition. The issue revolves around the question of whether the record can be read literally. If so, it would suggest a slower paced extinction. If there was mechanical turbation of the samples, as claimed by many workers (e.g., D'Hondt et al. 1996; Huber 1996), some Cretaceous Foraminifera could have been reworked into lower Paleocene samples and a record that appeared gradual would actually have been abrupt. The issue came to a head in a "blind test;" a test in which paleontologists from both factions were given unknown samples from the El Kef, Tunisia, K/T section, to identify and analyze. The results of even this test were ambiguous (Ginsburg 1997). Up-to-date statements claiming an abrupt foraminiferal extinction may be found in D'Hondt et al. (1996), Huber (1996), and Norris et al. (1999); the view that the extinction was gradual is presented in Keller and MacLeod (1995) and MacLeod (1996). Pospichal (1994; 1996) has reconstructed nannoplankton extinctions as having undergone an unambiguously abrupt and synchronous extinction.

Data regarding macroinvertebrates are less definitive. Sixty-three percent of bivalves became extinct sometime during the last ten million years of the Cretaceous (Raup and Jablonski 1993) but how abrupt or gradual that extinction was is unclear; rudists apparently went out somewhat before the boundary. Inoceramids are known to have undergone an asynchronous, global mid-Late Cretaceous (mid-Maastrichtian) extinction (MacLeod et al. 1996).

Ammonites have been traditional indicators of biotic crises in the marine world, and their fortunes have waxed and waned since their appearance during the Devonian (Clarkson 1986). The latest Cretaceous record of ammonites is complicated by a sea-level-driven extinction that occurred somewhat before the boundary. Possibly the most detailed study to date is that for the region of Zumaya, Spain. Marshall and Ward (1996) concluded that of 28 species of ammonites, six became extinct well before the K/T boundary, another three to ten either disappeared before (possibly from a major regression) or survived until the K/T boundary, and the remaining 12 species probably survived until the K/T boundary.

The record of marine fishes remains largely unknown; however, among marine amniotes, plesiosaurs and mosasaurs are noteworthy. Both are known from the latter part of the Late Cretaceous, but neither is known from the early Tertiary. Their pace of extinction, however, is not well understood. Both may or may not have been undergoing decline. In North America, where these matters have been best studied, marine beds of K/T age are uncommon, because of the Late Cretaceous regression.

Scenarios of Extinction at the K/T Boundary

In the previous sections, we reviewed the physical and biotic events before and through the K/T boundary. There is an emerging consensus on many points, but as we discussed, there remains considerable controversy as to how each of the physical events (volcanism, marine regression, and asteroid impact) may have contributed to the extinctions, including the pace of extinctions. To highlight these differences, each of us, as representatives of differing schools of thought on the cause or causes of the K/T extinctions, conclude by presenting two alternatives of what may have happened some 65 mya.

Multiple Causes for the K/T Extinctions

There are two major arguments for considering the K/T extinctions as the result of multiple causes rather than any single cause. First, as discussed in this chapter, no single pattern of extinction and survival is seen at the K/T boundary. The very great phylogenetic and ecological differences in survival are a strong indication that no single cause is sufficient. Together, however, volcanism, marine regression, and asteroid impact can explain this differential pattern of survival. Literally almost everything that could go wrong did so surrounding the K/T boundary. Second, some events offered as a single cause for the K/T extinctions are either not associated with other mass extinctions or have occurred at other times without causing mass extinction. For example, the essentially contemporaneous, 35.7-million-year-old, 100-km-wide Siberian Popigai and 85-km-wide Chesapeake Bay craters (Bottomley et al. 1997) do not correlate with any mass extinction. Further, of the five widely accepted mass extinctions, only that at the end of the Cretaceous correlates with a large impact. Interestingly, all five major mass extinctions do correlate with global marine regressions (Hallam and Wignall 1997), and extinctions at the terminal Jurassic and terminal Cretaceous are associated with by far the greatest marine regressions since the beginning of the Triassic about 250 mya (Smith et al. 1994).

The following scenario of the K/T extinctions modified after Archibald (1996a) is one of multiple causes—volcanism, marine regression, and asteroid impact. Each may have been necessary for these extinctions, but none was sufficient to cause the decidedly differential pattern of extinctions seen in the fossil record of vertebrates from western North America. It is an account of more than one kind of biotic stress leading to extinction.

To understand this biotic upheaval, one must start at least ten million years before the boundary. Because the record of vertebrate change during this time is largely limited to the Western Interior, the scenario must be similarly limited in scope. How much more widely it can be applied remains a paleontologic puzzle.

The scene approximately 75 mya is of an open plain with scattered trees on the eastern shore of Laramidia (Western Interior of North America). Rivers of moderate size meander across the landscape. In the distance, the plains are lapped gently by a shallow sea stretching to the horizon. The scene is dominated by vast herds of several species of duck-billed and horned dinosaurs, analogous to the herds of animals found on the Serengeti Plain of Africa today. Other ornithischian dinosaurs and the infrequent meat-eating theropods cross the landscape. The streams are populated by numerous species of turtles, amphibians, crocodilians, and fish, including the occasional skate or shark swimming up from the nearby sea. It is daytime; mouse and rat-sized mammals are asleep in their dens.

Fast forward to about 66 mya. The shallow seaway has begun to slip away to the south and east. As the exiting seaways reach lower-lying, flatter terrain, the rate of exodus quickens with the final stages of withdrawal occurring in, at most, tens of thousands of years. So, too, have followed the great herds of duck-billed and horned dinosaurs. But as their dwindling refugia of low coastal plains rapidly decreases, first one, then another of the species dwindles until the great herds are reduced to at most two or three remaining species, much like the herds of bison that once roamed North America. Dinosaurs, like large vertebrates everywhere and at all times, are the first to experience biotic stresses leading to decline and disappearance.

We do not know what was happening to vertebrates in more inland areas just before the K/T boundary, as few such areas are well preserved and none has been studied. The coastal plains dinosaurs certainly were capable of migrating from one shrinking coastal habitat to another, but even this could not stop further declines in population sizes—just like the relentless encroachments of increasing human populations that are causing many biotas to shrink today. Other large vertebrates suffered. The Komodo Dragon-sized lizards and the single exclusively terrestrial turtle, *Boremys,* also experienced declines. Populations of smaller terrestrial vertebrates were also declining, but because of shorter life spans and quicker turnover rates, they adapted more quickly to the environmental stresses caused by the loss and fragmentation of the coastal plains.

Marsupials had flourished for some 25 million years in North America. Newly emerging land bridges appeared as the seas retreated. Invaders appeared. In North America, these were the newly arriving diminutive archaic ungulates, probably from Asia. In the Western Interior, at least, they successfully competed with the marsupials for dwindling resources. In South America, events were different. Both groups of mammals appeared in South America soon after the K/T boundary, where they divided into guilds, with marsupials becoming the carnivores and the ungulates the herbivores. This co-evolutionary arrangement lasted for almost 50 million years in South America, with only an infusion of rodents and primates from the outside world.

Unlike the terrestrial vertebrates, freshwater species faced far less stress, largely because the size of their habitat was at least holding its own as the lengthening streams followed the retreating seas. Not all aquatic vertebrates fared so well. With the loss of close ties to the seas in areas like eastern Montana, sharks and skates ventured into the rivers in the area less and less frequently, as the distance to the sea expanded from tens to thousands of miles, eventually reaching Texas to the south.

Plants and nearshore species also showed added stresses as their respective habitats shrank. Certainly, some species must have done well as new habitats were formed as the seas regressed. As with vertebrates, however, we do not have any clear record of these environments away from the coastal areas.

Even before the seas began to retreat, the waxing and waning of the eruptions of the Deccan Traps added further stresses. One such stress was the added particulate matter in the atmosphere that very slowly began to cool and dry some areas of the globe.

Suddenly, a literally Earth-shattering event magnified the differences between the “have” and “have not” species. A 10-km-wide asteroid struck what today we call the Yucatan Peninsula. Material injected into the upper atmosphere formed a cover of darkness, blanketing the sun to the point that photosynthesis either ceased or diminished for many weeks, depending upon location. The effects were especially acute at lower latitudes and closer to the impact, such as in North America. Plants unaccustomed to lower light regimes caused by the seasonal changes in the Sun’s position were especially hard hit. Higher latitude plants accustomed to seasonally lower light regimes were better able to survive, as were the animals that fed upon them. The effects on higher latitude plants and animals were tempered by which season they were experiencing when impact occurred. Extinction rates for coastal plants in North America soared because of the cumulative effects of continued habitat loss, drought, and loss of sunlight.

Except for the elasmobranchs, which had already departed or become extinct as the seas regressed, all ectothermic aquatic vertebrate species (bony fishes, amphibians, turtles, champsosaurs, and crocodilians) weathered the impact well in their still-flourishing freshwater habitats (80% or 37 out of 46 taxa survival rate).

With the added loss of more plant species, and the reduction of biomass that the impact brought in the already highly stressed ecosystem on land, other vertebrate species rapidly succumbed. Most notable were the last of the large herbivorous nonavian dinosaurs. The remaining predaceous, nonavian dinosaurs followed very soon, with the larger species disappearing first. In some places on the globe, the great saurians may have lingered a while longer, but finally, for the first time in more than 150 million years, no large land vertebrates graced Earth. The landscape was open and waiting for evolution's next gambit—mammals.

A Single Cause for the K/T Extinctions

The single-cause argument for the K/T extinctions is fundamentally a parsimony argument. Fastovsky and Weishampel (1996) have noted that any hypothesis purporting to explain events at the K/T boundary must meet two criteria: (1) the hypothesis must be testable, and (2) the hypothesis must be able to explain as much of what is known about the boundary as is possible.

In this sense, the argument that a variety of causes (asteroid impacts, volcanism, regression) produced a variety of effects on a variety of different organisms is unsatisfying. If more "causes" were known, would we then be better able to explain the effects? The multiple-causes–multiple-effects viewpoint is a default: simply because these events are known to have occurred is not a priori reason to consider them causes. Many of these events occurred many times pervasively—even in conjunction—and did not cause a mass extinction.

esta ility of the asteroid impact hypothesis. Is the asteroid impact hypothesis testable? Unquestionably so, not only in terms of the predictions that it makes for the ubiquity and synchroneity of deposits left by the impact, but also in terms of the prediction that it makes with regard to the biota.

The asteroid hypothesis predicts that the K/T extinction will be found globally to have been abrupt and synchronous. This is fundamentally distinct from the claim that has been made (e.g., Archibald 1996a) that the biota does not show in its extinction patterns the by-products of an asteroid impact, such as acid rain. It is interesting that these by-products have been hypothesized and researched, but they should not be confused for predictions of the asteroid impact hypothesis. Our current understanding is such that the only legitimate prediction for the asteroid impact hypothesis is that the pattern of extinction must be abrupt and synchronous.

Given this assertion, the general pattern for our understanding of the extinctions is that they were synchronous and abrupt in both the terrestrial and marine realms. Over the past 18 years, the trend has been that groups once thought to have become extinct gradually have come to be recognized as having undergone an abrupt extinction. Ammonites, Foraminifera, and angiosperms are among the most well-documented examples of this. For other groups—most notoriously, dinosaurs—many workers are convinced by the data that an abrupt extinction occurred. To date, all field-based studies whose sole design and intent were to reconstruct the fluxes of vertebrate populations across the K/T boundary (e.g., Sheehan et al. 1991; Buffetaut 1997; Pearson et al. 2001, 2002) are compatible with an impact scenario. The single-cause extinction viewpoint prediction is that groups whose extinction patterns are currently uncertain will be shown to have become extinct abruptly and synchronously. In the case of the dinosaurs, the study of terrestrial K/T boundaries in China, India, Spain, France, and Romania (see Buffetaut 1997) may provide the keys to reconstructing dinosaur population fluxes in the Latest Cretaceous.

E planation of all the data. Both the single-cause and multiple-cause viewpoints agree that the K/T extinctions touched a variety of taxa, both terrestrial and marine. We know that primary production dropped globally. Along with the extinctions, we know that Earth's ecosystems were significantly and globally disrupted. We know that this disruption—as reflected in the extinctions—was globally synchronous. Rather than postulating a variety of unconnected causes as somehow coalescing at the K/T boundary, it is much more parsimonious to postulate that the synchroneity is because the extinctions were caused by a single event. It is reasonable to do this, particularly when there is—at this time—no doubt that an exceptionally rare event (the asteroid impact) that was big enough to do the job also took place at that time. Why accumulate other mechanisms—none of which was enough to do the job by itself—and concatenate them, when a sufficiently powerful means of killing exists?

The exact mechanism of the asteroid's destruction remains unclear, although the power released by such an impact is undoubted. As noted above, if sunlight were reduced and/or cut off over a period of several months, primary production (via photosynthesis) could be shut off. Clearly, one of the dominant signatures of the extinctions at the K/T boundary was the cessation of primary productivity, and so this correlates well with a pattern that might be expected from a cessation and/or reduction of incoming sunlight.

Recently, Schultz and D'Hondt (1996) have produced an interesting suggestion. Basing their analysis on asymmetries in subsurface features of the Chicxulub crater (observed via geophysical methods), they determined that the impact must have occurred at a low angle (~30°) from the southeast. That being the case, they predicted that the greatest devastation should have occurred in the Northern Hemisphere at relatively low latitudes. Indeed, what is known of the pattern of extinctions approximates this hypothesis.

Thus, the key features of the single-cause hypothesis are the parsimony of the argument, and the secure sense that the asteroid impact was powerful enough to cause the extinction. Attempts to develop precise scenarios appear, in this viewpoint, difficult to sustain. This is because the ramifications of massive impacts are poorly understood, the vagaries of the fossil record do not allow a mechanistic reading of it, and, in the chaotic and catastrophic scenario that must have resulted from the impact, survivorship at least in part depended upon luck, thus defying retrodiction. We can be sure that whatever else is true, the last word has not yet been said vis-à-vis the extinctions at the end of the Mesozoic.