DINOSAURS, EXTINCTION THEORIES FOR

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GLOSSARY

ammonites Shelled group of invertebrates related to octopus, squid, and nautilus.

amniota Taxon of vertebrates including mammals and reptiles (including birds).

archaic ungulates (or condylarths) Extinct group or grade of mammals possibly giving rise to hoofed mammals.

chondrichthyeans Sharks and their relatives.

ectotherm Animals that produce their heat from external sources such as the Sun.

endotherm Animals that produce their heat internally through metabolic means.

K/T Abbreviation for Cretaceous/Tertiary, usually in reference to the K/T boundary.

nonavian dinosaurs Dinosauria excluding birds.

ornithischians Bird-hipped dinosaurs such as horned and duck-billed dinosaurs.

palynomorphs Pollen and spores produces by plants.

saurischians Reptile-hipped dinosaurs such as theropods.

POPULAR ACCOUNTS SAY ALL DINOSAURS DIED INSTANTLY from the impact of an asteroid, comet, or meteor 65 Ma. Arguments continue to be made that dinosaurs were at the height of their taxonomic diversity at the time of their extinction. When examined in detail, the only good records we have of this extinction in North America show that the number of species of dinosaurs had declined by as much as 40% before their extinction. Dinosaurs were not alone. Of the over 100 vertebrate species (including dinosaurs) known at the time of these extinctions in North America, ~50% became extinct. Chances of survival were much lower if you were a large, terrestrial, amniotic endotherm rather than a small, freshwater, anamniotic ectotherm. Except for a recent hypothesis, none of the suggested "Dante's inferno" events accompanying the impact can explain this pattern of survival and extinction. This recent hypothesis argues that a pulse of intense thermal radiation killed any unsheltered organisms. While it is intriguing, a scenario of multiple causes (marine regression, habitat fragmentation, volcanism, and impact) better explains the pattern of extinctions at the end of the Cretaceous era, including that of nonavian dinosaurs.

Sixty-five and a half million years ago, a 10 km diameter rock from space slammed into the Earth, almost instantly annihilating over 70% of the all species, including all nonavian dinosaurs. Textbooks, the press, and many scientists have accepted some version of this Cretaceous/Tertiary (K/T) mass extinction scenario for over 20 years. Yet, even as the popularity of this single-cause explanation increased, nagging questions continued to be voiced as to the possible biologic effects of such an impact event. This is particularly true with regard to the record of plants and animals living on land and in freshwater habitats. For example, 12 clades representing about 107 species of better-studied vertebrates known from very near the K/T boundary in western North America suffered 51% extinction. Of these 12, however, only five—chondrichthyeans, lizards, marsupials, ornithischians, and saurischians (without birds)—account for 75% of the extinctions. The obvious biological question is what did sharks, lizards, opossums, and nonavian dinosaurs have in common that made them collectively more susceptible to extinction, especially from the environmental consequences of a large bolide impact? Other statistically significant patterns emerge as well (Fig. 1). Chances of survival were much lower if you were a large, terrestrial, amniotic endotherm rather than a small, freshwater, anamniotic ectotherm. None of the myriad of Dante's inferno events (e.g., sharp temperature increase, sharp temperature decrease, tsunamis, hurricanes, global wildfires, and acid rain) alleged or modeled to have occurred in the wake of this impact have been able to explain these curious extinction and survival patterns. In fact, several of these so-called inferno events have been discounted completely (e.g., acid rain, because most aquatic species survive), or are regarded as unlikely (e.g., sharp temperature decrease, because ectotherms do well) when tested against the known K/T fossil record.

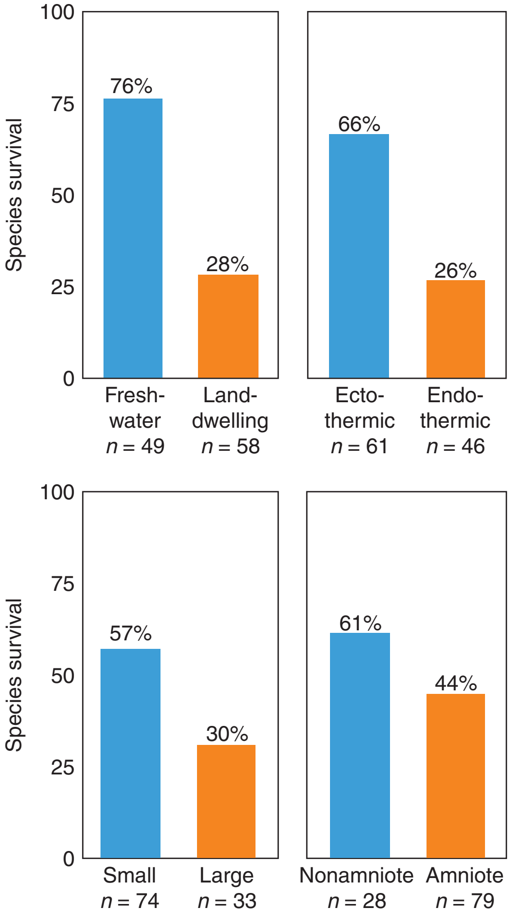

FIGURE 1 Differential patterns of vertebrate species survival at the K/T boundary (Archibald and Fastovsky, 2004). χ^2 tests of comparisons, except possibly the last, are significant (freshwater versus land-dwelling comparison and ectothermic versus endothermic comparison, $P << 0.005$, small versus large comparison, $0.010 < P < 0.025$, nonamniote versus amniote comparison $0.150 < P < 0.100$).

I. YET ANOTHER DANTE'S INFERNO

A recently proposed postimpact environmental scenario may be the first that shows some broad agreement with the vertebrate fossil record (Robertson *et al.*, 2004). This scenario postulates that, following the K/T impact, ejecta reentering the atmosphere created an intense blanket of infrared radiation that covered the planet's entire surface. Such a pulse of intense thermal radiation would kill any unsheltered organisms. The radiation scenario predicts that aquatic organisms would have been sheltered from the searing thermal pulse by a layer of water. This might explain the survival of most aquatic species. Terrestrial forms, however, would have suffered greatly unless they found shelter underground or in some sort of natural cavity. At first blush, this mechanism appears to explain why typically larger dinosaurian species faired more poorly than did some mammals. It may not actually be large size itself that was being selected against. Dinosaurs grew from a small size after hatching from eggs and some may even have been small enough after leaving any parental care to have survived in some sort of cavity. But in such cases, there would have been enough survivors to form a viable postimpact population to ensure species survival. For the smaller mammals, it is given that much larger population sizes would have predominated. Indeed, their numbers in the fossil record indicate this. By virtue of these larger population sizes, coupled with small physical size, more individuals may have been able to shelter in some sort of cavity or underground, and then emerge to reassemble their population.

This is all well and good, but how does the infrared radiation scenario explain the fact that placental mammals faired much better than marsupial mammals in North America, while in South America both groups radiated in the Early Tertiary? Similarly, under this radiation scenario, why would the clearly aquatic sharks disappear completely? In the marine realm, this scenario becomes even more unsatisfactory as it fails to account for the distinction between victims as disparate as nannoplankton, planktonic foraminifera, ammonites, and marine reptiles and survivors as disparate as benthic foraminifera, sponges, corals, lophophorates, and echinoderms. Many of these groups exhibit patterns of species-richness turnover that are not consistent with a single-event scenario located at the very end of the Cretaceous. Indeed, even the timing of impact-related event scenarios has recently been rendered much more complicated by the discovery of evidence that the Chicxulub impact may have predated the K/T boundary by as much as 300 ky.

Back on land, there are still other unresolved questions. The radiation scenario predicts that heightened infrared flux would have caused global wildfires. Whether this is a necessary correlate remains to be seen, but others have argued that the physical evidence does not support the occurrence of a global wildfire at the K/T boundary. Thus, although it is a promising mechanism, this latest Dante's inferno scenario requires much further study before postimpact reentry infrared radiation can be accepted as either a partial, or the predominant, mass-extinction killing mechanism.

II. MULTIPLE CAUSES

Other events that clearly occurred at the K/T boundary also fit the known pattern of vertebrate extinction in western North America, notably the loss of most epicontinental seas from the middle of the continent shortly before the K/T boundary. This was the greatest such loss in the past 250 My of Earth history. How it may have contributed to the K/T extinctions is not always straightforward, with one obvious exception. Shark species that frequented the rivers of western North America would have followed the regressing seas. Thus, their absence in the earliest Paleocene of this region is no great mystery. Different shark species made a brief reappearance when the seas once again lapped interior North American shores for a short time in the Early to Middle Paleocene. Aquatic species, except the fore-mentioned sharks, generally did well across the K/T boundary as the freshwater systems expanded in the wake of the sea's retreat.

But what of the marsupials? One possibility is that the earliest archaic ungulates (or condylarths) that definitely appear in North America in the earliest Paleocene (but probably were around by the latest Cretaceous) may have out-competed the marsupials in North America. The geographic origin for these archaic ungulates is uncertain. More and more evidence, however, points to Asia. As sea level fell, archaic ungulates presumably crossed the perennially appearing Bering Land Bridge. In South America, instead of replacing the marsupials, local ungulate lineages shifted more and more to herbivory while the marsupials remained omnivores or became more carnivorous.

Latest Cretaceous dinosaurs, which are only known in any numbers from low coastal plains, would have decreased in population size as the marine regression progressed. Such habitat loss is similar to that caused by human disturbance. It is doubtful that this alone would have been sufficient to cause the demise of dinosaurs, but we do know that with this sea level regression, global environmental change caused by increased volcanism from the Deccan Traps, and the terminal Cretaceous impact, the stresses on these creatures would have been great.

III. LONG-TERM TRENDS IN DINOSAUR DIVERSITY

The events discussed thus far occurred over hundreds of thousands of years in the case of the multiple-cause hypotheses (marine regression, habitat fragmentation, volcanism, and impact), or possibly over as short a span as hours–years in the case of an impact. The problem has been that to examine these competing views more thoroughly, we need a longer record stretching back millions, if not tens of millions, of years. Nowhere is this more keenly felt than in the question of what was happening to the dinosaurs during the close of the Cretaceous. The two components of this issue are: (i) What happened during the last 10 or so million years of the Cretaceous? and (ii) What happened during the last million years or less? Although among the rarest of almost any vertebrate species in the Late Cretaceous, dinosaurs have become the poster-children for this extinction. Not surprisingly then, this group has received most of the scientific attention as well. Because its stratigraphic record is far more complete through this geological interval, once again, most work centers on western North America.

For at least the past 25 years, the general view was that the 75-million-year-old, Late Campanian beds in western North America held the richest known dinosaur fauna and that there was a substantial taxonomic decline by about 66 Ma, just before the terminal Cretaceous extinctions. There were a few who argued that this was the result of more poorly known latest Cretaceous dinosaur faunas, but the vast majority of studies found this to be a true decline in taxonomic diversity in the waning 10 My of the Cretaceous, something on the order of 40%.

A recent study has attempted to resuscitate this issue within the context of examining dinosaur diversity throughout the Mesozoic Era, in which the authors concluded that their data did not support a claim that dinosaur richness was decreasing toward extinction during the last 1 My before the K/T boundary (Fastovsky *et al.*, 2004). Separate from the issue of whether dinosaurs were decreasing toward extinction, the question at hand is how one can conclude dinosaurs were not declining in taxonomic diversity during the last 10 My of the Cretaceous. Even in such studies the results show a decline of genera going from the Late Campanian (about 75 Ma) into the Late Maastrichtian (about 65 Ma). These patterns of decline have been attempted to be explained by rarefaction analysis. Fortunately, a newly published compendium of dinosaur distribution has allowed tabulations of taxa for succeeding intervals of time.

Table I is a generic compilation from this new compendium. Comparing taxa at the generic level rather than at the species level can be problematic, but in this case most of the genera are either monotypic or only one species is known from a given fauna. Only genera identified without qualification are included in Table I. Similarly, only localities were used for which unambiguous age ranges were provided. The compilation in Table I is based on standard geological divisions of Early and Late Campanian, and Early and Late Maastrichtian.

Both the Early Campanian and Early Maastrichtian have a quite low diversity, which are almost certainly artifactual. This is supported by the fact that five genera (*Avisaurus*, *Leptoceratops*, *Pachycephalosaurus*, *Pentaceratop*, and *Troodon*) reported from the Late Campanian and Late Maastrichtian are not identified from the intervening Early Maastrichtian. The Late Campanian and Late Maastrichtian of North America are much better sampled intervals, with an obvious decline from 48 to 32 genera—a 33% drop. This is the case even though there are four more localities and 27 more repeated generic samplings for the North American Late Maastrichtian compared with the Late Campanian.

Although the drop in generic richness is clear, one could argue that such broad-brush geographic comparisons are not ecologically meaningful. To examine this concern, one can compare more clearly delineated faunas rather than make comparisons across the board (Table II). For the Late Campanian, the richest dinosaurian fauna is from the Dinosaur Park Formation, Alberta, which includes 31 genera and 38 to 42 species. A recent reassessment of this fauna's age brackets it between about 76.5 and 74.2 Ma within Dinosaur Provincial Park, Alberta, with the actual span of time represented by this dinosaur fauna being somewhat shorter, by about 2 My. For the Late Maastrichtian, the richest fauna is from the Lance Formation, Wyoming, which contains 20 genera and 21 to 22 species. Although ages are not well known for the Lance Formation, the nearby biostratigraphically comparable Hell Creek Formation in Montana spans about the last 1.7 My of the Cretaceous. Comparing these figures shows that, although the Dinosaur Park and Lance Formations sample a similar magnitude of time, there is a 35% generic decline, and up to a 50% species decline between the Dinosaur Park (Late Campanian) and the Lance (Late Maastrichtian) faunas.

What is of particular ecological interest is that this decline is not especially high among the rarer carnivorous theropods, but rather among the more common hadrosaurid and ceratopsian genera. From six hadrosaurid and six ceratopsian genera in the Dinosaur Park fauna, we see a decline to only one hadrosaurid and four ceratopsian genera in the Lance fauna (Table II). Comparable changes have been reported for the similarly aged Hell Creek Formation, but they are less well known for the Scollard Formation, Alberta. Thus for all the cases known, the percent generic and species declines are still over 30 and near 50, respectively, during the last 10 My of the Cretaceous.

IV. SHORT-TERM TRENDS IN DINOSAUR DIVERSITY

The question of what happened to vertebrates—and especially to dinosaurs—during the last million years or

TABLE I

Dinosaur generic counts through the Campanian and Maastrichtian of North America[a, b] (Weishampel *et al.*, 2004)

E. Campanian 7 localities		L. Campanian 14 localities		E. Maastrichtian 3 localities		L. Maastrichtian 18 localities	
Hesperornis	4	*Achelousaurus*	1	*Albertosaurus*	2	*Alamosaurus*	7
Hadrosaurus	2	*Albertosaurus*	1	*Anchiceratops*	2	*Albertosaurus*	2
Ricardoestesia	1	*Anchiceratops*	1	*Arrhinoceratops*	1	*Ankylosaurus*	4
Troodon	1	*Apatornis*	1	*Aublysodon*	1	*Avisaurus*	1
4 genera	8	*Aublysodon*	2	*Caenagnathus*	1	*Bugenasaura*	2
		Avaceratops	1	*Chirostenotes*	1	*Caenagnathus*	1
		Avimimus	1	*Daspletosaurus*	1	*Chirostenotes*	2
		Avisaurus[b]	1	*Dromaeosaurus*	2	*Diceratops*	1
		Bambiraptor	1	*Edmontonia*	3	*Dromaeosaurus*	7
		Baptornis	2	*Edmontosaurus*	3	*Edmontonia*	6
		Brachyceratops	1	*Euoplocephalus*	1	*Edmontosaurus*	9
		Brachylophosaurus	3	*Hypacrosaurus*	1	*Leptoceratops*	3
		Centrosaurus	2	*Maiasaura*	1	*Montanoceratops*	1
		Chasmosaurus	1	*Montanoceratops*	2	*Nanotyrannus*	1
		Chirostenotes	2	*Ornithomimus*	1	*Ornithomimus*	5
		Coniornis	1	*Pachyrhinosaurus*	2	*Pachycephalosaurus*	4
		Corythosaurus	1	*Panoplosaurus*	1	*Pachyrhinosaurus*	1
		Daspletosaurus	3	*Parksosaurus*	1	*Palintropus*	1
		Dromaeosaurus	4	*Ricardoestesia*	1	*Parksosaurus*	1
		Dryptosaurus	1	*Saurolophus*	1	*Pentaceratops*	1
		Edmontonia	4	*Saurornitholestes*	1	*Potamornis*	1
		Einiosaurus	1	*Stegoceras*	1	*Ricardoestesia*	3
		Euoplocephalus	3	*Struthiomimus*	1	*Saurornitholestes*	6
		Gorgosaurus	2	23 genera	32	*Sphaerotholus*	1
		Gravitholus	1			*Stegoceras*	2
		Gryposaurus	2			*Struthiomimus*	1
		Hadrosaurus	1			*Stygimoloch*	4
		Hesperornis	2			*Thescelosaurus*	6
		Hypacrosaurus	2			*Torosaurus*	8
		Lambeosaurus	1			*Triceratops*	9
		Leptoceratops[b]	2			*Troodon*	6
		Maiasaura	1			*Tyrannosaurus*	12
		Monoclonius	2			32 genera	119
		Montanoceratops	1				
		Ornatotholus	1				
		Ornithomimus	3				
		Orodromeus	3				
		Pachycephalosaurus[b]	2				
		Panoplosaurus	1				
		Parasaurolophus	2				
		Pentaceratops[b]	1				
		Prosaurolophus	2				
		Ricardoestesia	4				
		Saurornitholestes	6				
		Stegoceras	4				
		Struthiomimus	1				
		Styracosaurus	1				
		Troodon[b]	5				
		48 genera	92				

[a] Number following each genus is the number of localities at which a particular genus occurs.

[b] Taxa occur in L. Campanian and L. Masstrichtian, but not intervening E. Maastrichtian.

TABLE II

Generic and species counts of dinosaurs for Dinosaur Park Formation (Late Campanian) and Lance Formation (Late Maastrichtian) of North America (Weishampel *et al.*, 2004)

Dinosaur Park Formation		Lance Formation	
Genus	No. of species	Genus	No. of species
Theropoda		Theropoda	
Avimimus	1	*Albertosaurus*	1
Baptornis	1	*Dromaeosaurus*	1
Chirostenotes	2	*Palintropus*	1
Daspletosaurus	1	*Ornithomimus*	1
Dromaeosaurus	1–2	*Potamornis*	1
Gorgosaurus	1	*Ricardoestesia*	1
Ornithomimus	1	*Saurornitholestes*	1
Ricardoestesia	2	*Troodon*	1
Saurornitholestes	1	*Tyrannosaurus*	1
Struthiomimus	1		
Troodon	1		
Ankylosauria		Ankylosauria	
Edmontonia	2	*Ankylosaurus*	1
Euoplocephalus	1	*Edmontonia*	1
Panoplosaurus	1		
Euornithopoda		Euornithopoda	
Orodromeus	1	*Bugenasaura*	1
		Thescelosaurus	1
Hadrosauridae		Hadrosauridae	
Brachylophosaurus	1	*Edmontosaurus*	2
Corythosaurus	1		
Gryposaurus	2		
Lambeosaurus	2		
Parasaurolophus	1		
Prosaurolophus	1		
Pachycephalosauria		Pachycephalosauria	
Gravitholus	1	*Pachycephalosaurus*	1
Ornatotholus	1	*Stygimoloch*	1
Pachycephalosaurus	1		
Stegoceras	1		
Ceratopsia		Ceratopsia	
Anchiceratops	1	*Diceratops*	1
Centrosaurus	1–2	*Leptoceratops*	1
Chasmosaurus	3–4	*Torosaurus*	1
Leptoceratops	1	*Triceratops*	1–2
Monoclonius	1–2	20 genera	21–22
Styracosaurus	1		
31 genera	38–42		

so of the Cretaceous is a less tractable problem. Unlike the broader question of patterns characteristic of last 10 My of the Cretaceous, in tracking a much finer scale pattern we are now asking much more of the fossil record. The first attempt at quantification of this question counted the number of dinosaur teeth per metric ton of sediment recovered from screen washing samples collected in eastern Montana. Results showed a gradual decrease of dinosaurs leading up to the K/T boundary. As it turned out, all but the lowest sample were from the earliest Paleocene. Consequently, the dinosaur teeth were largely zombie taxa (i.e., taxa reworked from latest Cretaceous sediments). In 1992, another study examined surface-collected dinosaur material within the lower, middle, and upper third of the Hell Creek Formation, North Dakota. No changes in the dinosaur faunas were found throughout the section. Unfortunately, as this study was conducted at the relatively crude taxonomic level of family, a 40% loss of dinosaur species could have occurred without being detected.

In 2002, the results of a study conducted largely by an amateur paleontologist provided the first well-documented sampling of vertebrates through the entire thickness of the Hell Creek Formation in North and South Dakota. Despite a somewhat coarse-level sampling scheme, this study did not find any obvious changes in taxonomic diversity throughout the formation. These results have been used by some as evidence for abrupt dinosaur extinction. In fact, neither the stratigraphic nor the taxonomic levels of resolution employed in these studies are fine enough to address, let alone answer, this question. For example, this study reported that there are 2233 dinosaurian specimens representing 14 taxa. In the 3 m interval below the K/T boundary, there are only 26 dinosaurian specimens representing just three taxa. Within the upper 5 m of the Hell Creek only two dinosaurs (*Ricardoestesia* and *Tyrannosaurus*) were identified at the generic level. The next higher occurrences of dinosaur genera occur 8 m or lower within the Hell Creek Formation. What of the other 18 or so dinosaur genera that are known to have occurred in the Hell Creek Formation? Such a record is obviously much too poor to say anything about whether the local dinosaur extinction was instantaneous or gradual on a scale of tens to hundreds of thousands of years.

V. OUT WITH A WHIMPER, A BANG, OR BOTH?

If questions of rate and taxonomic magnitude of terrestrial extinctions are to be addressed and possibly answered, a much finer scale of both stratigraphic and taxonomic sampling will be required. One study (Fig. 2) that specifically addressed changes within the turtle community in the Hell Creek Formation during the last 1.7 My of the Cretaceous found that for turtles, as well as for mammals and plants, taxonomic richness was lower in the formation and dropped immediately before the K/T boundary. The maximum diversities in these three groups were correlated with the maximum latest Cretaceous warming and the drop in richness was correlated to a rapid drop in paleotemperature. In a detailed study of only the mammals from this same sequence, the observed change in climate was deemed insufficient to explain the extinction or pseudoextinction (disappearance resulting from speciation) of up to 27 species of mammal near or at the K/T boundary. A longer, gradual turnover pattern could be ruled out based on this analysis, but the time resolution of these data was not able to differentiate between stepwise and sudden extinction.

Until recently, the well-sampled megafloral (leaves and fruits rather than pollen) record had indicated as much as a 79% plant extinction at the K/T boundary in the northern western interior of the United States and even higher (84%) farther to the south in the United States. With much tighter stratigraphic control, however, this estimate has recently been downgraded to a minimum of 30% extinction based on palynomorphs that have higher stratigraphic but lower taxonomic resolution, compared with a maximum of 57% extinction based on megaflora that disappear within 5 m or less of the K/T boundary. This flora was interpreted then to have suffered between 30% and 57% extinction at the K/T boundary, while other floral extinctions were spread out within the 50 m of the upper part of the Hell Creek Formation. Certainly, there is a dynamic floral turnover throughout the Cretaceous part of the section, a sharp shift near the K/T boundary, and virtual stasis during the Paleocene; a pattern interpreted as being commensurate with "sudden ecosystem collapse, presumably caused by the Chicxulub impact." Once again, though, while the fact of the taxic richness decline is clear, the time interval over which this decline occurred, and its correlation to alternative sources of global environmental change, are not.

VI. CONCLUSIONS

The newest generation of studies on the K/T and dinosaur extinctions shows that extinction levels for plants and animals, on land and in fresh water, are not as great as once thought. Instead of species extinction levels as high as 80%, newer studies range from a possible low of 30% to a high of, at the most, 60%. Dinosaurs clearly declined in taxonomic richness during the last 10 My of the Cretaceous, at least in North America where they are best known. This is true whether broader geographic taxonomic counts or specific dinosaurian faunas are compared. But the dinosaur record remains too poor to determine what occurred in the last few tens or hundreds of thousands of years of the Cretaceous. The record is better for other terrestrial groups. Taxonomic

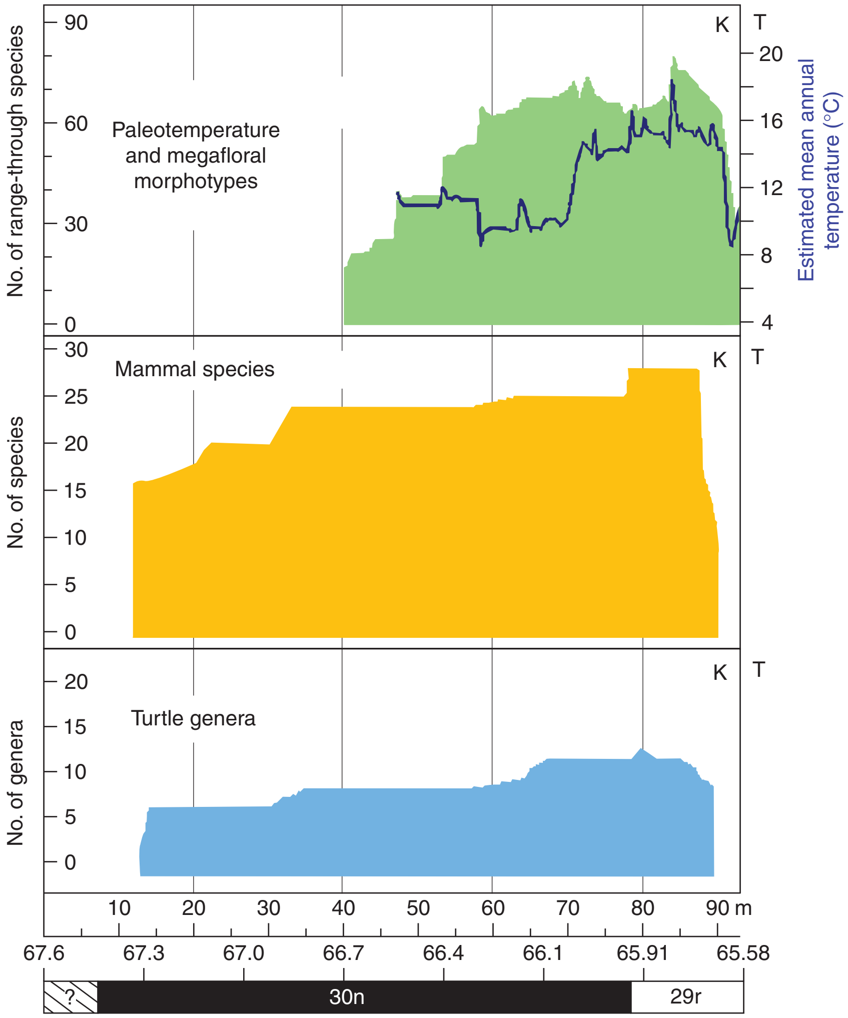

FIGURE 2 Compiled taxonomic richness data for plants, mammals, and turtles in the Hell Creek Formation. Independent of taxonomic level, taxonomic richness is lower in the early portion of the Late Maastrichtian and it drops immediately before the K/T boundary. The greatest taxonomic diversity is associated with maximum warmth, while the latest Maastrichtian drop is correlated with a rapid drop in paleotemperature. After Hutchison *et al.* (2004).

richness for both plants, and vertebrates—at least turtles and mammals—tracks the climb to a warm maximum and then a sudden plunge in temperature just before the K/T boundary. These records appear sufficient to eliminate a long-term, gradual pattern of extinction leading up to the K/T boundary, but whether the extinctions were stepwise over hundreds of thousands of years, or sudden over as little as a few years cannot be determined, given the record currently available. Moreover, given the certain knowledge that a number of major environmental changes were operating in this latest Maastrichtian interval, singling out of any one cause is more a matter of speculation than fact.

See Also the Following Articles

EXTINCTION, CAUSES OF • MASS EXTINCTIONS, CONCEPT OF • MASS EXTINCTIONS, NOTABLE EXAMPLES OF

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