

What the dinosaur record says about extinction scenarios

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ABSTRACT

The record of dinosaurs over the last 10 m.y. of the Cretaceous, as well as surrounding the Cretaceous-Paleogene boundary, helps to define extinction scenarios. Although Late Cretaceous dinosaur fossils occur on all present-day continents, only in North America do we find a terrestrial vertebrate fossil record spanning the Cretaceous-Paleogene boundary, although promising work may yield comparable records in South America, India, China, and Europe. For the present then, the North American record represents the proxy for our knowledge of dinosaur extinction. Over the last 10 m.y. of the Cretaceous (late Campanian to late Maastrichtian) in the northern part of the western interior of North America, the number of nonavian dinosaur species dropped from 49 to 25, almost a 50% reduction, even though a 16% greater extent of fossil-bearing exposures record the last dinosaurs in the latest Cretaceous in the western interior. Important, but less-well-exposed, nonavian-dinosaur-bearing units suggest this drop occurred around, or at least commenced by, the Campanian-Maastrichtian boundary. These losses began during climatic fluctuations, occurring during and possibly in part caused by the last major regressive cycle of the Cretaceous, which also reduced the expanse of the low coastal plains inhabited by nonavian dinosaurs. The pulse of Deccan Trap emplacement that began some time later in the latest Cretaceous was also likely a major driver of climatic change. As for the dinosaur record near the Cretaceous-Paleogene boundary, even the best-known records from North America remain enigmatic and open to interpretation. Newer studies suggest some decline in at least relative abundance approaching the Cretaceous-Paleogene boundary, but the cause (or causes) for the final extinction (if it was the case) of nonavian dinosaurs remains unresolved, although the Chicxulub impact undoubtedly played a major role.

INTRODUCTION

The best-preserved and most-studied sequences of Late Cretaceous and Paleocene fossil vertebrates occur in western North America. From the latest Cretaceous of western North America alone, over 100 vertebrate species are known, representing all

major vertebrate clades. Although nonavian dinosaurs represent at most only 20% of this taxonomic diversity, interest in the possible causes and patterns of their extinction far outweighs the interest for the extinction of other species, vertebrate or not (Archibald, 1996). The study of dinosaur extinction is certainly not the most conducive for general understanding of the processes

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of extinction, quite simply because dinosaur population sizes and the environments in which they lived did not greatly favor preservation in the fossil record, with some very notable exceptions. Unfortunately, there are no such notable exceptions for any sites near the end of the Cretaceous.

Can any evidence be offered relating to the question of what the dinosaur record says about extinction scenarios, which the organizers of this volume posed as a topic to be addressed. The answer is a qualified “yes.” Specifically, the two major issues to be explored are: (1) What is the nonavian dinosaur record throughout the later Cretaceous, approximately the last 10 m.y.? (2) What is the nonavian dinosaur record like near the end of the Cretaceous, say the last half-million years leading up to the Cretaceous-Paleogene boundary? The emphasis here is by necessity on these records and less on the possible extinction scenarios, quite simply because it is easier to examine what the nonavian dinosaur record is rather than why it is this way. The questions of why are examined in the instances in which the patterns of change in nonavian dinosaur taxonomic diversity seem to address extinction scenarios.

THE LAST TEN MILLION YEARS

Most exposures in Dinosaur Provincial Park, Alberta, Canada, range from 76 to 74 m.y. old, representing the later part of the late Campanian portion of the Late Cretaceous (Currie and Koppelhus, 2005). In western North America, terrestrial, geological sections based on vertebrate fossils of this age also are known as the Judithian after the Judith River Formation, first recognized in Montana, a partial equivalent of the Dinosaur Park Formation in Canada.

Ornithischian and saurischian dinosaurs both occur commonly in the late Campanian (Judithian)-aged sediments of Dinosaur Park. Saurischians are limited to theropods, the group including both birds and the mostly large to extremely large ground-dwelling, bipedal, mostly carnivorous dinosaurs. Sauropod saurischians do not make it this far north in the Late Cretaceous, being known only as far north as southern Wyoming. Thus, the Dinosaur Park nonavian dinosaur fauna can best be grouped as ornithischians and theropods, in which ornithischians outnumber theropods by four to one. Among ornithischians, ~50% are duckbilled hadrosaurs, 25% are horned ceratopsians, and the remaining 25% mostly represent armored ankylosaurs and bone-headed pachycephalosaurs. In the park, the ornithischians comprise three genera of ankylosaurs, each with one species, three species of the pachycephalosaur genus *Stegoceras*, six species of ceratopsians belonging to four different genera, and eight hadrosaurs arrayed in six different genera. Hypsilophodontidae (a paraphyletic group including basal neornithischians and basal ornithomimids) is known only from isolated teeth in the park and thus cannot be clearly assigned to a genus or species (Table 1; references in Currie and Koppelhus, 2005; Archibald, 2011).

Theropods make up less than 10% of recovered fossils but are taxonomically quite diverse. Of the 14 families (39 genera)

of dinosaurs recognized in the park, 42% of these families (40% of the genera) are theropods (excluding birds). Thus, what theropods lack in numbers of specimens some 75 m.y. ago (Ma), they make up in diversity (Currie, 2005). This pattern of low specimen abundance but higher taxonomic diversity is echoed some 10 m.y. later, just before nonavian dinosaur extinction.

It would be best to possess good samples of nonavian dinosaur taxa at half-million-year intervals, but this is unfortunately not the case in North America. To have comparably well-sampled dinosaur faunas, we must jump to the latest Cretaceous, or the late Maastrichtian, which in North America is also called the Lancian, the terrestrial vertebrate equivalent of this age, named after the type Lance Formation of eastern Wyoming. The taxonomically most diverse Lancian-aged nonavian dinosaur fauna, with 18 species, is perhaps known from the type Lance Formation. Its upper limit is essentially the Cretaceous-Paleogene boundary at roughly 66 Ma. The base of the Lancian at 69 Ma is less well constrained (see Cifelli et al., 2004; Wilson, 2005).

Comparing the Dinosaur Park and Lance Formations, the former represents about 2 m.y. and the latter between 2 and 3 m.y., respectively. Being terrestrial, largely fluvially derived units, we must keep in mind that although both formations span the times indicated, they do not preserve events through the entirety of these interval, but rather represent time-averaged packets. Most terrestrially derived fossils are from such time-averaged occurrences. Both formations represent similar depositional histories, preserving floodplain and coastal fluvial deposits draining easterly into the Pierre or Western Interior Seaway. The western continent of Laramidia lay to the west, and the eastern continent of Appalachia lay to the east of this seaway (Archibald, 1996), transgressing and regressing some four times during the last 35 m.y. of the Late Cretaceous (Fig. 1). The last incarnation of this epicontinental sea at its greatest width might have reached 1000 km wide and up to five times as long. Such seaways inundated almost all continents during the Late Cretaceous, equivalent to an area probably approximately the size of modern Africa. Nothing comparable in size exists today, although Hudson Bay, the North Sea, the Baltic Sea, and the Red Sea all have been proposed as smaller examples.

In a comparison of the nonavian dinosaur faunas, the Lance Formation, although quite rich, does not match the older Dinosaur Park Formation nonavian dinosaur fauna: Dinosaur Park has 39 species, whereas the Lance Formation has 18 species. This means a drop of over 50% species abundance during the last 10 m.y. of the Cretaceous in North America (Table 1). Additional Judithian- and Lancian-aged nonavian dinosaur faunas in western North America add further support in showing this decline is real. Other major Judithian-aged formations in the northern western interior are the Judith River and Two Medicine Formations in central Montana; the other major formation of Lancian age is the Hell Creek Formation of eastern Montana and western North and South Dakota. Adding these additional records to augment the Dinosaur Park and Lance Formations, we find a loss of dinosaur species of almost 50%, still a considerable decline (Table 1).

TABLE 1. GENERIC AND SPECIES COUNTS OF LATE CAMPANIAN THROUGH LATE MAASTRICHTIAN NONAVIAN DINOSAURS FROM NORTHERN LARAMIDIA (CURRIE, 2005; EBERTH ET AL., 2005; RYAN AND EVANS, 2005; LONGRICH AND CURRIE, 2009; WEISHAMPEL ET AL., 2004)

Dinosaur Park Formation (Judithian, late Campanian)*	Horseshoe Canyon Formation (Edmontonian, Campanian– Maastrichtian)	Lance Formation (Lancian, late Maastrichtian)#	Change in no. of species (with J, T, M, and D) between late Camp. and late Maast.
Genus	Genus	Genus	
No. species (J and T)	No. species	No. species (M and D)	
Theropoda	Theropoda	Theropoda	-9 (-4)
<i>Albertosaurus</i> (J)	<i>Albertonykus</i>	<i>Albertosaurus</i>	1
<i>Bambiraptor</i> (T)	<i>Albertosaurus</i>	<i>Caenagnathus</i> (D)	(1)
<i>Caenagnathus</i>	<i>Atrociraptor</i>	<i>Chirostenotes</i> (M, D) [§]	(1)
<i>Chirostenotes</i>	cf. <i>Dromaeosaurus</i>	<i>Dromaeosaurus</i>	1
<i>Daspletosaurus</i>	<i>Epichirostenotes</i> [§]	<i>Elmisaurus</i> (M, D) [§]	(1)
<i>Dromaeosaurus</i>	<i>Ornithomimus</i>	<i>Nanotyrannus</i> (M)	(1)
<i>Dromiceiomimus</i>	cf. <i>Paronychodont</i> [†]	<i>Ornithomimus</i>	1
<i>Elmisaurus</i> [§]	cf. <i>Richardoestesia</i> [†]	<i>Paronychodont</i> [†]	1
<i>Gorgosaurus</i>	<i>Struthiomimus</i>	<i>Richardoestesia</i> [†]	1
<i>Hesperonychus</i>	<i>Troodon</i>	<i>Saurornitholestes</i>	1
<i>Ornithomimus</i>		<i>Struthiomimus</i> (D)	(1)
<i>Paronychodont</i> [†]		<i>Troodon</i>	1
<i>Richardoestesia</i> [†]		<i>Tyrannosaurus</i>	1
<i>Saurornitholestes</i>			
<i>Struthiomimus</i>			
<i>Therizinosaurid</i>			
<i>Troodon</i>			
Ankylosauria	Ankylosauria	Ankylosauria	-1(-2)
<i>Edmontonia</i> (1 is from J)	<i>Edmontonia</i>	<i>Ankylosaurus</i>	1
<i>Euoplocephalus</i>	<i>Euoplocephalus</i>	<i>Edmontonia</i>	1
<i>Panoplosaurus</i>			
Euornithopoda	Euornithopoda	Euornithopoda	+1(0)
<i>Hypsilophodontid</i>	<i>Parksosaurus</i>	<i>Bugenasaura</i>	1
<i>Orodromeus</i> (T)		<i>Thescelosaurus</i>	1
Hadrosauridae	Hadrosauridae	Hadrosauridae	-6 (-9)
<i>Brachylophosaurus</i>	<i>Edmontosaurus</i>	<i>Edmontosaurus</i>	2
<i>Corythosaurus</i>	<i>Hypacrosaurus</i>		
<i>Gryposaurus</i>	<i>Saurolophus</i>		
<i>Hypacrosaurus</i> (T)			
<i>Lambeosaurus</i>			
<i>Maiasaura</i> (T)			
<i>Parasaurolophus</i> (1 is from T)			
<i>Prosaurolophus</i>			

(Continued)

TABLE 1. GENERIC AND SPECIES COUNTS OF LATE CAMPANIAN THROUGH LATE MAASTRICHTIAN NONAVIAN DINOSAURS FROM NORTHERN LARAMIDIA (CURRIE, 2005; EBERTH ET AL., 2005; RYAN AND EVANS, 2005; LONGRICH AND CURRIE, 2009; WEISHAMPEL ET AL., 2004) (Continued)

Genus	No. species (J and T)	Horseshoe Canyon Formation (Edmontonian, Campanian–Maastrichtian) Genus	No. species	Lance Formation (Lancian, late Maastrichtian) [#] Genus	No. species (M and D)	Change in no. of species (with J, T, M, and D) between late Camp. and late Maast.
Pachycephalosauria		Pachycephalosauria		Pachycephalosauria		-1 (+1)
Stegoceras	3	cf. <i>Colepiocephale</i> Sphaerolitholus	1 1	Pachycephalosaurus Stegoceras (M, D) Sphaerolitholus (M) Stygmoloch	1 (1) (1) 1	
Ceratopsia		Ceratopsia		Ceratopsia		-3 (-6)
<i>Achelosaurus</i> (T)	(1)	Anchiceratops	1	Diceratops (or Diceratus)	1	
<i>Avaceratops</i> (J)	(1)	Arrhinoceratops	1	Leptoceratops	1	
<i>Anchiceratops</i> **	1	Eotriceratops	1	Triceratops	2††	
Centrosaurus	1	Montanoceratops	1			
Chasmosaurus	3	Pachyrhinosaurus	1			
<i>Elnisaurus</i> (T)	(1)					
Leptoceratops	1					
Styracosaurus	1					
Total numbers of species	39 (49)		23		18 (25)	-19 (-24)

*Additional genera from the Judith River (J) and Two Medicine (T) Formations of central Montana.

†*Paronychodon* and *Richardoestesia* are tooth taxa and accordingly not recognized by some workers.

‡There is no consensus as to how many genera are represented by *Chirostenotes*, *Elmisaurus*, and *Epichirostenotes*. All are recognized here.

#Additional genera from the Hell Creek Formation of eastern Montana (M) and western part of the Dakotas (D).

**Found south, outside of Dinosaur Park.

††The number of species of *Triceratops* is uncertain. I use the higher number of two. Further, according to Scannella (2009), *Torosaurus latus* from the Lance Formation represents older individuals of *Triceratops*.

What the dinosaur record says about extinction scenarios

Some have argued that the Dinosaur Park Formation and Lance Formation are not ecologically equivalent but have offered no data to support this claim, going so far as to call such an assessment absurd (Fastovsky et al., 2005). Others have even attempted without success to statistically discount this very real decline (Fastovsky et al., 2005; Wang and Dodson, 2006; Lloyd et al., 2008). In agreement with the results presented here, a study by Barrett et al. (2009) compiled genus-richness estimates for three Mesozoic dinosaur clades, noting a marked decline in dinosaur generic richness in the final stages of the Cretaceous, which indicates that the clade decreased in diversity for several million years

before its final extinction at the Cretaceous-Paleogene boundary. The authors of this study show that many fluctuations in dinosaur diversity through the Mesozoic found in previous studies are likely not real but are artifacts of fossil preservation. These authors further found that when biases in fossil preservation are taken into account, several genuine diversity signals are present; the most intriguing of these, according to these authors, shows that both ornithischian and theropod dinosaur lineages began to decline several million years prior to the Cretaceous-Paleogene extinction event, again in accord with the results discussed here.

In 2012, Brusatte et al. (2012) calculated what they termed the morphological disparity or anatomical variability found in seven major dinosaur groups during the latest Cretaceous. They found both geographic and clade-specific heterogeneity. The morphological disparity declined for large-bodied herbivores (ceratopsids and hadrosauroids) and some North American taxa during the final two stages of the Cretaceous. At the same time, carnivorous dinosaurs, mid-sized herbivores, and some Asian taxa did not decrease in morphological disparity. These authors argued that the pattern of Late Cretaceous dinosaur evolution was complex and that there was no universal biodiversity trend. As with earlier studies, Brusatte et al. (2012) found that some dinosaur groups endured long-term declines in morphological variability before their final extinction at the end of the Cretaceous.

The data presented here as well as by Barrett et al. (2009) and Brusatte et al. (2012) indicate that the Late Cretaceous vertebrate fossil record in western North America is quite good and by all measures is reliable in providing proportional changes, if not absolute changes, between Judithian and Lancian, and Lancian and Cretaceous-Paleogene boundary sites. Nevertheless, Fastovsky et al. (2005, e75) repeated one of the common canards against comparison of the Dinosaur Park and Lance Formation nonavian dinosaur faunas: "There is no reason to suppose that the richest formations of each time interval are spatially equivalent or preserve faunas with equal fidelity." If by a possible lack of "spatial equivalence" of the rock units yielding these dinosaurs bones, they mean the two are not equivalent in areal exposure, they are correct, but certainly not in the way they implied. The argument here basically is that if you have more exposure, everything else being equal, you should also have more species of dinosaurs preserved. Following their reasoning, if the much greater taxonomic richness of the Dinosaur Park Formation could be attributed to a greater geologic exposure, these authors might have a case. Such is in fact, not the case.

Eberth (2005, p. 58) noted that "the bedrock exposures in the [Dinosaur Provincial] Park comprise Canada's largest area of badlands, covering approximately 75 km²." The Dinosaur Park

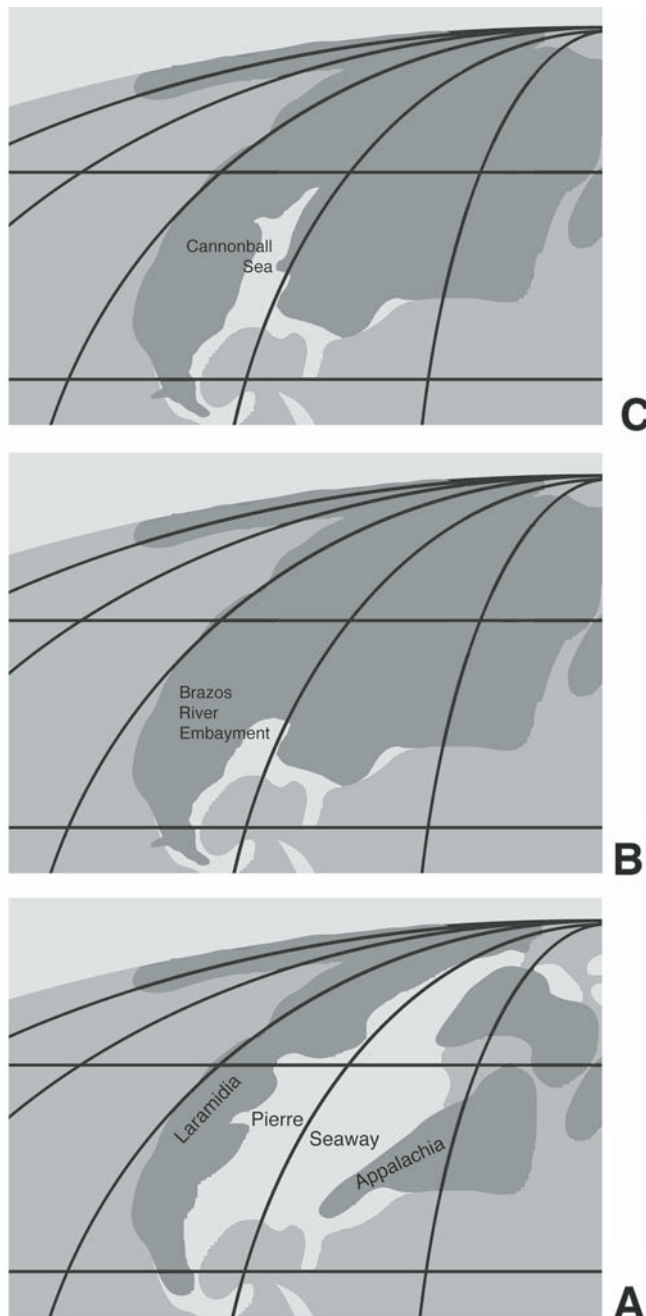


Figure 1. (A) North American biogeography during the latter part of the Cretaceous showing the major western continent of Laramidia and the eastern continent of Appalachia separated by the epicontinental Pierre Seaway. (B) The same region near the Cretaceous-Paleogene boundary showing the Brazos River Embayment. (C) The same region near the mid-Paleocene showing the Cannonball Sea (after Archibald, 2011).

Formation comprises a large portion of this area, and as noted above, has produced 39 species of nonavian dinosaur. More broadly, the Dinosaur Park Formation in Alberta and Saskatchewan plus the equivalently aged Judith River and Two Medicine Formations to the south in Montana are mapped as covering something like 48,000 km² (Archibald, 2011). Doing this, an additional 10 nonavian dinosaur taxa can be added to the 39 already known in and near Dinosaur Provincial Park, giving a total of 49 late Campanian (Judithian) nonavian dinosaurs from these three formations. By comparison, the late Maastrichtian (Lancian)-aged Lance Formation of Wyoming and the Hell Creek Formation of eastern Montana and western North and South Dakota are mapped as covering at least 57,000 km²; yet at most five additional dinosaur species can be added, yielding perhaps 25 species of nonavian dinosaurs for this interval (Archibald, 2011). Clearly, the late Campanian (Judithian) nonavian-dinosaur-bearing formations in western North America have less exposure than late Maastrichtian (Lancian) nonavian dinosaur-bearing formations in western North America (Fig. 2). Although the late Campanian faunas are known from 16% fewer exposures than those faunas from the late Maastrichtian faunas, the former have produced almost double the number of species. Barrett et al. (2009) echoed such a percentage drop in dinosaur diversity.

The second claim by Fastovsky et al. (2005), that the dinosaur faunas of the Judithian and Lancian are not preserved with equal fidelity, cannot be justified other than possibly by statistical

machinations. The issue of whether the Dinosaur Park and age-equivalent formations and the Lance and age-equivalent formations are equally rich in the number of identifiable specimens that each has yielded cannot be addressed as definitively as the question concerning “spatial equivalence.” There are no complete lists of the identifiable specimens that have been removed over the past 100 yr and more from these units. Many museums around the world have nonavian dinosaurs from especially the Lance and Hell Creek Formations. It is fair to say that both sets of formations have yielded countless nonavian dinosaur specimens, thus it is up to naysayers such as Fastovsky and his colleagues to demonstrate that there is a significant preservational bias between these two sets of formations. Barring this, the argument of preservational bias between the Dinosaur Park and Lance Formations must be treated as a red herring.

Yet another clear pattern of change in the last 10 m.y. of the Cretaceous shows that the decline in dinosaur species abundance is most certainly real. This concerns the patterns of change over the last 10 m.y. for more common hadrosaurids and ceratopsians compared to the far rarer theropods. If the Lance nonavian dinosaur fauna were more poorly sampled than the Dinosaur Park fauna, it would show first in a depauperate nonavian theropod fauna. The rarer theropods should be the first to disappear from the record, if it is a matter of sampling. This is decidedly not the case. For Dinosaur Park, nonavian theropods comprise ~44% of the species abundance and account for only 10% of the specimens. By the time of the Lance Formation, whereas nonavian theropods are equally rare as specimens, if anything, they may have relatively increased taxonomically, ranging from 44% to 52% of the nonavian dinosaur species abundance. Their numbers of species, however, declined between 32% and 53% compared to those of theropods from the Dinosaur Park faunas (Table 1). This is further strong evidence indicating that comparative sampling is not an issue. The decline of nonavian theropods in the last 10 m.y. of the Cretaceous in western North America is most certainly real.

The most-striking pattern of decline concerns the most common nonavian dinosaurs in the faunas from the Dinosaur Park and Lance–Hell Creek Formations, namely, the hadrosaurids and ceratopsians. Recall that for the Dinosaur Park fauna, among the ornithischians, hadrosaurs (50%) and ceratopsians (25%) account for 75% of the specimens. For Lance–Hell Creek Formations, this percentage is, if anything, higher, yet hadrosaurids declined taxonomically by 80% and the ceratopsians declined by 40% between these two faunas. Even with this precipitous taxonomic decline, by end of the Cretaceous in western North America, hadrosaurids and ceratopsians remain very common as specimens. Unequivocally, hadrosaurids and ceratopsians declined in taxonomic diversity in the western interior of North America during the last 10 m.y. of the Cretaceous. These patterns of change demonstrate that it was the most common hadrosaurids and, to a lesser extent, ceratopsians rather than the rarer theropod taxa that suffered the greatest taxonomic decline during the last 10 m.y. of the Cretaceous in western North America. No statistical special pleading can explain away these patterns of decline.

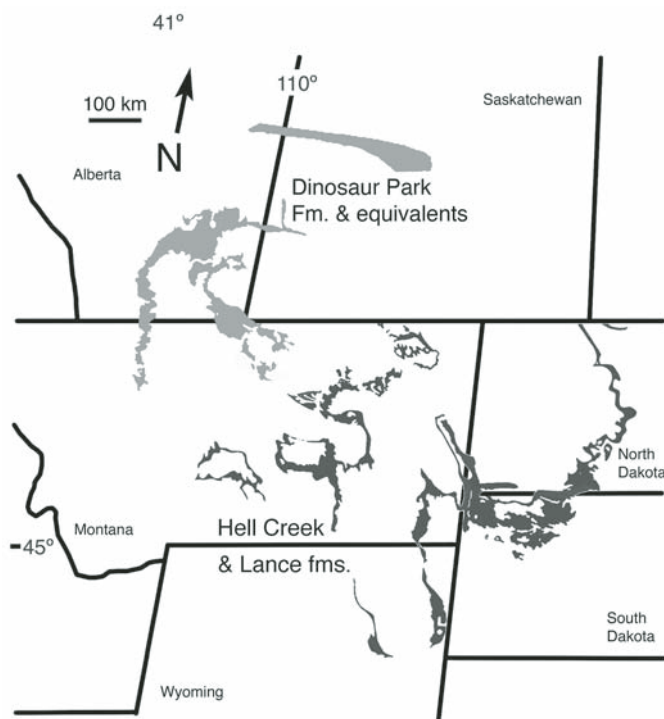


Figure 2. The mapped area of the late Campanian (ca. 75 Ma) Dinosaur Park Formation and its equivalents (48,000 km²) compared to the mapped areas of late Maastrichtian (ca. 66 Ma) Lance and Hell Creek Formations (with 57,000 km²; after Archibald, 2011).

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Determining the causes of these taxonomic declines is harder to do. A possibility noted earlier concerns the fact that the deposition of the Lance and Hell Creek Formations occurred as part of the last and most massive regression of the Pierre Seaway leading to near the Cretaceous-Paleogene boundary. The fossil vertebrate evidence available for the four transgressions and regressions in North America during the 35 m.y. of the Late Cretaceous suggests that during times of transgressions, freshwater vertebrates suffered but land-dwelling species, including nonavian dinosaurs, fared better, even showing a taxonomic increase. The opposite occurred during regressions, and, at best, land-dwelling species show taxonomic stasis, such as for the Dinosaur Park Formation, or decline during the much greater regression that occurred when the Lance–Hell Creek vertebrate faunas lived (Archibald, 1996).

Some parallels can be drawn between the changes that occurred between the Dinosaur Park and Lance–Hell Creek nonavian dinosaur faunas and differences we see in extant mammalian biotas. The single Lance–Hell Creek genus of hadrosaurid, *Edmontosaurus*, is arguably represented by more identifiable remains than any of the seven hadrosaurids from Dinosaur Park. Although the number of hadrosaurid species dramatically declined in the last 10 m.y. of the Cretaceous, the one or two species that replaced them were quite common. This is similar to the pattern of African savannah ungulates compared to ungulates of pre-European human invasion of North America. In Africa, there are as many as 60 medium (above 25 kg) to large grazers and browsers (elephants, rhinoceroses, zebra, pigs, hippopotamuses, deer, giraffes, antelope, sheep, goats, cattle-like bovids; Haltenorth and Diller, 1992), whereas in North America, there are only 12 such mammals (peccaries, deer, elk, moose, caribou, sheep, goats, bison, pronghorns; Whitaker, 1980). In Africa, some large migrating mammals such as zebras and wildebeest have prodigious numbers, but other herbivorous species are not uncommon. The migratory populations of wildebeest in the Serengeti-Mara have been measured as high as 1.3 million individuals, and single concentrations can range from 10,000 to 20,000 animals but are usually smaller (Kingdon, 1982). Whereas in North America, the bison was far and away the most numerous large grazing mammal when Europeans arrived some 500 yr ago. In the fifteenth century, 60 million bison roamed North America in massive migrations. Hornaday (1886) estimated in one area that a migrating herd reached over four million animals! By 1900, only 1000 animals remained, but this has now grown to over 30,000 individuals (Whitaker, 1980). North America had a large biomass of large ungulates, but it was dominated by a single species. It is possible that a trend toward lower diversity, but still with a large biomass, transpired for large herbivorous nonavian dinosaurs in the waning 10 m.y. of the Cretaceous in North America.

This likely scenario does not explain why the diversity of the carnivorous and scavenging theropods did not decline as dramatically over the same 10 m.y. Although the numbers of potential prey species clearly declined, as suggested in the comparison of Lancian hadrosaurs and North American bison, likely the total numbers of individuals remained similar over the same 10 m.y.

Another possibility is that because the vast majority of these theropods are ostrich size or smaller, with a diversity of diets, a decline in the larger hadrosaurid and ceratopsian diversity would not have affected these smaller theropods as dramatically.

Given that the decline in dinosaur taxonomic diversity between the late Campanian (Judithian) and the late Maastrichtian (Lancian) is real, when did these declines occur and why? These questions may be addressed as more intermediate-aged nonavian-dinosaur-bearing sites are studied. One such study by Eberth et al. (2013) examined the dinosaur biostratigraphy of the Edmonton Group in Alberta, Canada, in considerable detail, encompassing beds ranging in age from ca. 72.5 to 65.5 Ma, or the latest Campanian into the early Paleogene. The upper portion, the Scollard Formation, includes the Cretaceous-Paleogene boundary, with the late Maastrichtian (Lancian) portion including the same dinosaur species known further to the south in the Lance and Hell Creek Formations. Below this, there is the Horseshoe Canyon Formation, which spans the Campanian-Maastrichtian (Edmontonian) boundary, including the best-known nonavian dinosaur fauna of this age in the northern part of present-day North America. The Eberth et al. (2013) study included occurrences and biostratigraphic distributions of the nonavian dinosaurs from the Horseshoe Canyon and Scollard Formations, which record the regressive phase of the Bearpaw transgressive-regressive (T-R) cycle and the Fox Hills T-R cycle. Comparing the areas of the Horseshoe Canyon Formation outcrops shown in their figure 1 to those of the older and younger beds shown here in Figure 1, it is clear the Horseshoe Canyon Formation represents considerably less exposure yet has produced 23 genera of nonavian dinosaurs. The middle two columns in Table 1 list these genera. As seen in this table, the taxonomic diversity of nonavian dinosaurs from the Horseshoe Canyon Formation rivals that of the younger Lance–Hell Creek Formations.

Two factors, however, suggest that nonavian dinosaurs are underrepresented from this intermediate interval. First, as noted, the Horseshoe Canyon Formation exposures, although extensive, are far less so than the earlier and later nonavian-dinosaur-producing exposures in northern Laramidia, likely in part yielding this lower taxonomic diversity. Second, when taxa are compared across the three time intervals shown in Table 1, one finds that there may be as many as six genera found both in the older Dinosaur Park and the younger Lance–Hell Creek Formations not known from the intermediate Horseshoe Canyon Formation. This follows the same pattern found for all of North America by Archibald and MacLeod (2007). If these Lazarus taxa are added to those known from the Horseshoe Canyon Formation, this interval would have upwards of 29 nonavian dinosaur genera, surpassing that of the much more greatly exposed late Maastrichtian Lance–Hell Creek Formations, but still considerably less than the late Campanian Dinosaur Park Formation.

Although the dip in dinosaurian taxonomic diversity in the latest Campanian and early Maastrichtian is almost certainly in part artificial, caused by the nature of the fossil record, some of it is certainly real, suggesting that whatever the cause(s) of

the decline between the late Campanian and late Maastrichtian, much of the decline may have begun or occurred by the Campanian-Maastrichtian transition. Eberth et al. (2013) noted that there is no evidence of significant climatic changes in the older, but relatively shorter expanse of the Dinosaur Park Formation, whereas each of the members of the Horseshoe Canyon Formation, being as long as the entire duration of the Dinosaur Park Formation, shows considerable climatic change. Compared to the Dinosaur Park Formation ornithischians, those in the Horseshoe Canyon Formation show longer-term morphological stasis and major climate-change-driven nonavian dinosaur migration into and out of the area. In the Horseshoe Canyon Formation interval, the authors detail climatic shifts involving a shift from warm and wet to cool and seasonally dry and back again, and finally to a warm and seasonally dry climate in the overlying latest Cretaceous Scollard Formation.

Some of these regional climatic changes appear to have been tectonically driven, but some changes may also have been more global in scale. What the results of these global changes might have been is not yet clear, but the longer-term pattern of regression commencing in earnest ca. 73 Ma, with a much shorter interval of transgression during the latest Campanian into the Maastrichtian (Eberth et al., 2013), might have been in part responsible for these climatic fluctuations. This regression also diminished the expanse of low coastal plains that the nonavian dinosaurs inhabited, as well as provided new avenues of intercontinental migrations (Archibald, 1996, 2011). Still later, ca. 67.4 Ma, the first but smallest of the three pulses of Deccan volcanism may have also contributed to climatic fluctuations, with the second, much larger pulse near the Cretaceous-Paleogene boundary contributing even further to climatic change. A smaller third pulse occurred in early Paleogene (Keller et al., 2012).

APPROACHING THE CRETACEOUS-PALEOGENE BOUNDARY

Although there is little question that at least in North America, nonavian dinosaur species abundance declined by at least 50% over the last 10 m.y. of the Cretaceous, the record becomes more problematic as one approaches the Cretaceous-Paleogene boundary. In order to examine this boundary interval, we must utilize the latest Cretaceous Hell Creek Formation and the overlying early Paleocene Tullock Formation of eastern Montana as well as parts of western North and South Dakota. This is because the records of all vertebrates, not just nonavian dinosaurs, have been more thoroughly studied in these areas, the Cretaceous-Paleogene boundary is better known, and at least in eastern Montana, there is a reasonably good vertebrate record in the overlying Paleocene beds.

Several studies have attempted to determine the diversity of nonavian dinosaurs in the Hell Creek Formation. One study (Sheehan et al., 1991) examined what happened to familial-level diversity of nonavian dinosaurs in a three-part partitioning of the Hell Creek Formation, arguing that the pattern was commensu-

rate with sudden extinction. Unfortunately, one could not detect changes below the family level, which was a level too coarse to detect if there had been any decline within the families (Hurlbert and Archibald, 1995).

In some recent studies, Pearson et al. (2001; see also Pearson et al., 2002) identified over 10,000 specimens of very small to very large vertebrates of 61 vertebrate taxa from a 100 m section of Hell Creek Formation exposed mostly in southwestern North Dakota. One of their major conclusions seems well justified, namely, that there is no evidence for a decline in overall vertebrate diversity through the vertical extent of the formation. Problems arise with their second conclusion; there is no evidence for a decline of nonavian dinosaur diversity in the 3 m below the Cretaceous-Paleogene boundary. There is scarce evidence for any vertebrate fossils in at least the last 1.77 m of their section (Fig. 3). The single specimen they identified that constitutes this record is identified as an indeterminate ceratopsid. Of the over 10,000 specimens they collected, there are only three nonavian dinosaurs identified between 2 and 3 m below the Cretaceous-Paleogene boundary. These consist of an indeterminate ceratopsid, an indeterminate hadrosaurine, and the theropod tooth taxon *Richardoestesia*. Moving down section, according to their figures, one encounters five nonavian dinosaur taxa just below 3 m and eight taxa just below 8 m. Does this mean that, counter to their arguments, in fact we see a decline from eight to five to three to one and finally to zero by 1.77 m below the Cretaceous-Paleogene boundary. I think not.

The left side of Figure 3 is after their figure 2, whereas the right side shows their record for nonavian dinosaurs recast as a spindle or minaret-shaped diagram. In the spindle diagram, numbers show the nonavian dinosaur taxa either collected at that level or implied by their lines connecting occurrences below and above. If this record is to be believed, there is relative taxonomic stability until about the 4 m mark, when numbers start to drop, reaching zero before the Cretaceous-Paleogene boundary. This record would seem to indicate a gradual disappearance of dinosaurs in these sections. The authors argue that this is artificial and that in reality this dinosaur record is commensurate with a catastrophic extinction. This argument mostly derives from the so-called Signor-Lipps effect, which argues that because the fossil record is never complete, we should not expect to have found the first or the last fossil records of any particular species or higher group of organisms. Invoking the Signor-Lipps effect means, however, that one can claim that catastrophic, gradual, or some other pattern of extinction is commensurate with the fossil record. The authors note that possibly the gap near the top of the Hell Creek Formation is a function of depositional conditions associated with the transitions between formations rather than reflecting true terminal Cretaceous faunal diversity, an assessment with which I agree.

If the single indeterminate ceratopsid noted above is discounted, the 1.77 m becomes a 2.37 m fossil gap in this data set. This gap has also sometimes been referred to as the 3 m or 10 ft gap. Some 30 yr ago, this notoriously unfossiliferous gap

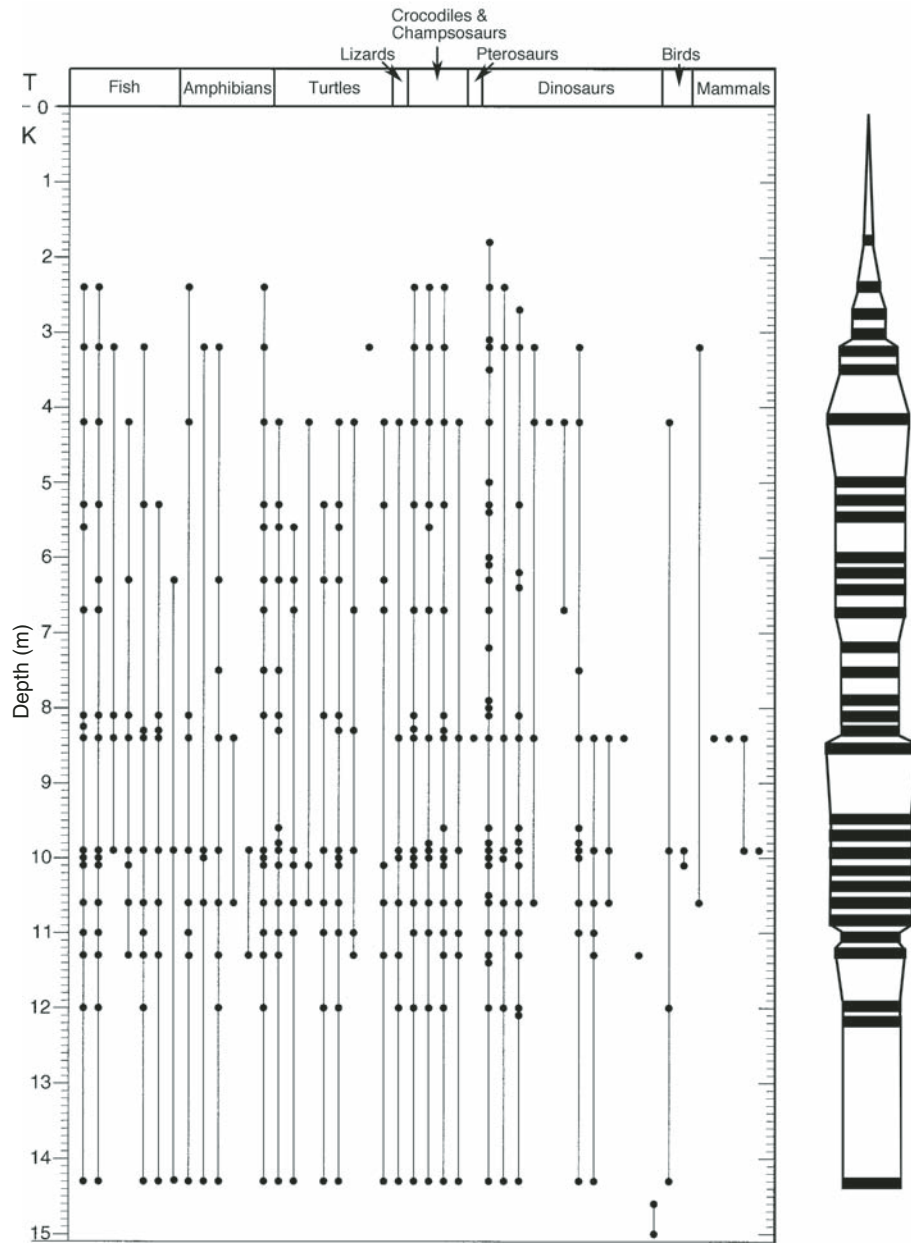
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Figure 3. Isolated occurrences of taxa (dots) are identified within clades connected by vertical lines within the upper 15 m of the Hell Creek Formation, exposed mostly in southwestern North Dakota (after Pearson et al., 2001). Spindle diagram to the right shows repeating occurrences of dinosaurs at the various levels and interpolates the presence of a taxon if it was recovered above and below that level (after Archibald, 2011). Note the decline from seven to zero taxa in the last 4 m and the total lack of any vertebrates in the uppermost 1.77 m. K—Cretaceous; T—Tertiary.

was first thought possibly to represent the level at which dinosaur extinction occurred. This gap occurs below the Cretaceous-Paleogene boundary, based on the much more easily and better-sampled plant pollen record and the iridium-enriched level thought to mark the Chicxulub impact. Even before the advent of the impact theory of extinction, it was realized that although not completely barren, it is a generally unfossiliferous zone for vertebrate fossils. Thus, for over 30 yr, no one seriously argued that the base of this gap represented the level of final extinction for nonavian dinosaurs.

Unfortunately, this fact was lost on the authors of a paper in 2011 (Lyson et al., 2011) claiming to show that a chunk of a ceratopsian brow horn found 13 cm below what they identified

as the Cretaceous-Paleogene boundary proved (p. 14) “that a gap devoid of non-avian dinosaur fossils does not exist and is inconsistent with the hypothesis that non-avian dinosaurs were extinct prior to the K-T boundary impact event.” Even taking the conclusions of their field evidence for this occurrence at face value, it simply represents one more rare occurrence of a bone, dinosaur or otherwise, in this quite unfossiliferous gap in fossil representation near the top of the Hell Creek Formation.

Not surprisingly, this very real gap creates considerable problems in gauging what was happening not just to dinosaurs, but all vertebrates during this nearly barren interval. Some, such as Pearson et al. (2001) and Lyson et al. (2011), have tried to argue this gap away, basically saying that because no decline

in vertebrate diversity can be detected, no such decline, especially for dinosaurs, occurred in the 3 m below the Cretaceous-Paleogene boundary. Given that this 3 m (or 2.37 m) gap in the records compiled by Pearson et al. (2001) is by far the largest gap in the upper 12 m of the Hell Creek Formation, such a claim is not warranted. There is no evidence supporting a catastrophic (bang) or gradual (whimper) extinction in these last 2 to 3 m of the Hell Creek Formation.

This unfossiliferous gap is vexing. Why is there such a gap at all? The views vary, and frankly all explanations seem to have some merit, but choosing one over another is problematic. One suggestion is that a lack of channel deposits within this 3 m interval may explain the absence of fossil localities. The vast majority of both small and large fossil vertebrates in the Hell Creek Formation are associated with fluvial or riverlain deposits. These can be the channels themselves, sand bars that breached the channels during flood events, or more rarely floodplain deposits on the margins of the streams. Especially compared to the overlying Paleocene Tullock (or Fort Union as it is referred to in the Dakotas) Formation, the Hell Creek Formation tends to preserve smaller streams or at least muddier streams in its upper reaches, although very large channels certainly are not present. The upper reaches of the Hell Creek Formation for the most part lack larger channel deposits, although most of the sediment still appears to be fluvially related, and thus the rarity of channel deposits to explain the absence of fossil localities in the last 3 m seems to have merit.

Another suggestion is that as a result of the Chicxulub impact at the Cretaceous-Paleogene boundary, the resulting global acid rain fallout likely caused the destruction of microfossils immediately underlying the impact layer (Bailey et al., 2005). At first an appealing idea, the survival of most aquatic vertebrate species belies the idea of a very low pH acid rain. The possibility of the dissolution of most teeth and bones in the upper 3 m of the Hell Creek Formation may yet prove to be true, but not from acid rain. Rather, the carbonaceous and lignitic coals that most often overlie the top of the Hell Creek Formation could have caused the leaching near the top of the Hell Creek Formation. This admittedly more prosaic explanation seems more likely to have been the cause.

Finding and thoroughly exploring other terrestrial Cretaceous-Paleogene sections will help to determine if this gap is a regionally driven phenomenon or is more global in extent. Finding a single bone in a single section, such as done by Lyson et al. (2011), does not begin to address the issue or answer any question about the rapidity of dinosaur extinction. Similarly, although not concerned with the subject of this paper (i.e., non-avian dinosaur extinction), two recent papers dealing with extinctions of other vertebrate groups misrepresent the nature of the vertebrate fossil record near and at the Cretaceous-Paleogene boundary. One study shows the fossil record of lizards and snakes extending exactly to the Cretaceous-Paleogene boundary (Longrich et al., 2012). The second, and more egregious in its misrepresentation of the fossil record, shows the record for birds as sin-

gle dots immediately below the Cretaceous-Paleogene boundary (Longrich et al., 2011). Although some species of snakes, lizards, and birds may have become extinct at the Cretaceous-Paleogene boundary, to my knowledge, there is no record of any of these taxa within 2 to 3 m of the Cretaceous-Paleogene boundary. The problem with all of these studies is the impression of a sudden extinction, when in fact such evidence is completely lacking.

Another approach to examining what was occurring leading up to and across the Cretaceous-Paleogene boundary has used large samples of vertebrate microfossils amassed over almost 40 yr, mostly by crews often under the direction of W.A. Clemens from the Museum of Paleontology at the University of California, Berkeley, working in the late Maastrichtian (Lancian) Hell Creek Formation and early Paleocene Tullock Member of northeastern Montana. One more recent approach by Wilson and colleagues (Hutchison et al., 2004; Wilson, 2005) placed vertebrate localities into a temporal framework utilizing stratigraphic position. Although their work did not address dinosaur records, it is relevant to understanding possible broader climatic changes that certainly would have affected dinosaurs. These authors noted changes in the better-sampled amphibian, turtle, and mammalian paleocommunities approaching the Cretaceous-Paleogene boundary. They compared these data with those for published paleofloral and paleoclimatic data. Echoing the findings of Pearson and colleagues, Wilson and colleagues did not find any evidence of long-term changes within paleocommunities leading up to the Cretaceous-Paleogene boundary, although they did find some changes in relative abundances, taxonomic composition, and body sizes that likely reflect normal responses to background levels of climate change. However, unlike Pearson and colleagues, Wilson and colleagues did find dramatic changes in turtle and mammalian paleocommunities within the last 100 k.y. of the Cretaceous. These authors went on to write that while their results are consistent with a sudden extinction, such as from an extraterrestrial impact, the response was nonlinear, so that long-term causes or multiple short-term causes cannot be rejected. They further wrote that their assessments will improve with increased temporal resolution of the chronostratigraphic framework, improvement of the density of fossil sampling, the incorporation of other fossil taxa such as plants and mollusks, and comparisons with other study areas.

This work shows that during the last 2 m.y. of the Cretaceous, maximum diversities of turtles, mammals, and plants correlate with the maximum latest Cretaceous warming trend, while the drop in taxonomic richness of these three groups correlates to a rapid drop in paleotemperature in the last 100,000 yr of the Cretaceous of the same region (Hutchison et al., 2004; Wilson, 2005). If verified by further studies, these results clearly point to factors driving climatic change well before an extraterrestrial impact that would be expected to have affected dinosaur relative abundances and/or taxonomic diversity in some fashion.

Finally, a more recent approach by Horner et al. (2011) examined in considerable detail the stratigraphic distribution of nonavian dinosaur skeletons and individual bones in the Hell

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Creek Formation of northeastern Montana. Whereas up to six genera are known in the lower two thirds based on skeletons and individual bones (*Triceratops*, *Tyrannosaurus*, *Edmontosaurus*, *Thescelosaurus*, *Ornithomimus*, *Pachycephalosaurus*, and *Ankylosaurus*), only three genera (*Triceratops*, *Tyrannosaurus*, *Edmontosaurus*) are known in the upper one third, and this portion is dominated by a single taxon—*Triceratops*. The evidence then, if it shows anything, is that there was a decline in relative abundance, if not dinosaur diversity, in the upper Hell Creek Formation.

CONCLUSIONS

The lack of well-studied, fossiliferous Cretaceous–Paleogene terrestrial sections on all continents except western North America means that the records from these North American locations must for now act as proxy for our knowledge of dinosaur extinction. During the last 10 m.y. of the Cretaceous, in at least the northern part of the western interior of North America, nonavian dinosaur species dropped from 49 to 25, almost a 50% decline. This is the case even though the latest Cretaceous vertebrate-bearing beds are represented by a 16% greater areal extent than beds some 10 m.y. earlier in the same region. This decrease in nonavian dinosaur taxonomic diversity commenced near the Campanian–Maastrichtian boundary and likely continued during the greatest marine regression to occur in the past 250 m.y. and later during phases of Deccan Trap emplacement. Resulting climatic changes and loss of habitat likely contributed to this decline. The nonavian dinosaur record near the Cretaceous–Paleogene boundary, even for the best-known records from North America, remains enigmatic and open to interpretation. Newer studies suggest some decline in at least relative abundance of nonavian dinosaurs as one approaches the Cretaceous–Paleogene boundary, but the cause (or causes) for their final extinction (if it was the case) remains unresolved, although the Chicxulub impact undoubtedly played a major role following upon the effects of longer-term regression and volcanism.

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