Gradual Dinosaur Extinction and Simultaneous Ungulate Radiation in the Hell Creek Formation

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Dinosaur extinction in Montana, Alberta, and Wyoming was a gradual process that began 7 million years before the end of the Cretaceous and accelerated rapidly in the final 0.3 million years of the Cretaceous, during the interval of apparent competition from rapidly evolving immigrating ungulates. This interval involves rapid reduction in both diversity and population density of dinosaurs. The last dinosaurs known are from a channel that contains teeth of Mantuan mammals, seven species of dinosaurs, and Paleocene pollen. The top of this channel is 1.3 meters above the likely position of the iridium anomaly, the Cretaceous/Tertiary boundary.

THE CATASTROPHIC ASPECTS OF DInosaur extinction have been receiving attention recently (*1, 2*). We present new information reinforcing previous data (*3–7*) showing that dinosaur extinction was a gradual process, lasting at least 7 million years, and rapidly accelerating in the final 0.3 million years of the Cretaceous Period. Precise information on the relation of dinosaur extinction to a postulated asteroid impact is still wanting, although data from India (*8*), the Pyrenees (*9*), Peru (*10*), New Mexico (*11*), and other localities suggest that dinosaurs survived well into the early Paleocene in the tropics. Within the Hell Creek Formation of Montana we have presented data (*3*) that show the progressive reduction of taxa of dinosaurs and some mammal taxa and the progressive increase in Paleocene-like mammal taxa during the last 300,000 years of the Cretaceous. Our recent collections (Table 1) suggest that local final extinction took place about 40,000 years after the postulated asteroid impact on the basis of a channel sandstone with top 1.3 m above the lower Z coal, the local Cretaceous/Tertiary (K/T) boundary. This channel contains unreworked teeth of Mantuan mammals, seven species of dinosaurs, and Paleocene pollen.

Alvarez maintains (*1*) that an asteroid impact at the K/T boundary is the cause of dinosaur extinction. This appears to be too simplistic an explanation to agree with the available data. In the last 10 million years of the Cretaceous of Alberta, Montana, and Wyoming, there is a progressive reduction of dinosaur diversity (Fig. 1). These faunas are well dated by ammonite zones in the adjacent marine shales (*12*), by mammal and dinosaur fossils (*13–19*), magnetostratigraphy (*16, 20*), and K/Ar dates (*12, 16*). The peak diversity appears in the combined Judith River–Oldman–St. Mary River faunas of 76 to 73 million years ago with 30 genera of dinosaurs (*13, 14*), the most diverse dinosaur fauna known to date. Reduction of numbers of dinosaur genera is steady into the classic Edmonton fauna of the Horseshoe Canyon Formation of Alberta, at 23 genera from the lower part of the formation and 22 genera from the upper part (*15*) after small-sized and rare genera that occur earlier and later are added.

In the combined Lance–Hell Creek–Scollard faunas of the same area (*3, 6, 16–19*), the diversity is further reduced to a maximum of 19 genera, despite the introduction of two immigrant genera, *Leptoceratops* (*16*) from Asia and *Alamosaurus* (most likely from South America). In the uppermost 16 m of the Hell Creek Formation diversity is further reduced to 12 genera at precisely the same time that a new mammal fauna of placental and multituberculate mammals appears (*3*). This reduction is not an artifact of collection; the uppermost 30 m of the Hell Creek Formation of McCone County, Montana, have been the most intensely prospected, both for large isolated bones and for the isolated teeth that occur in the channel sand small vertebrate fossil localities. At least the multituberculate mammals migrated in from Asia where their ancestors are known from the Nemegt Formation of Mongolia (*21*). In several successive channels in this interval (BCA, BCW-SMP, HH, and FR in Fig. 2 and Table 1) rapid speciation of ungulates is observed. The peak rate of evolution is 3.85 darwins, the most rapid rate of evolution reported in the fossil record, and the number of species of ungulates successively increases from one to three to five to eight. The top of the uppermost channel of this sequence, Ferguson Ranch (FR), is located

Table 1. Presence of dinosaur genera and ungulate mammal species by channel sand small vertebrate fossil locality. Localities listed in stratigraphic order left to right (see Fig. 2). Dinosaur teeth represent the number recovered per metric ton of channel sand washed; dinosaur and mammal specimens represent the percentage of minimum number of individuals (MNI) (*3, 6*).

Taxa	KS	BCA	BCW SMP	HH	FR
Dinosaurs					
Albertosaurus	X	X	X	X	X
Tyrannosaurus	X	X	X	X	
Dromaeosaurus	X	X	X	X	X
Velociraptor	X	X	X	X	
New genus and species R	X	X	X	X	X
Saurornitholestes	X	X	X		
Paronychodon	X	X	X	X	X
Thescelosaurus	X	X	X	X	X
Edmontosaurus	X	X	X	X	X
Pachycephalosaurus	X	X	X		
Stygimoloch				X	
Ankylosaurus	X	X			
Triceratops	X	X	X	X	X
Totals	12	12	11	10	7
Ungulate mammals					
Protungulatum donnae		X	X	X	X
Protungulatum gorgun			X	X	X
Mimatuta morgoth			X	X	cf.*
Mimatuta cf. *minuiel*					X
Baioconodon harbichti				X	cf.*
Baioconodon engdahli					cf.*
Oxyprimus erikseni				X	X
Oxyprimus n. sp.					X
Totals	0	1	3	5	8
Dinosaur teeth per metric ton of sediment	168.0	27.3	34.5	27.9	18.3
Dinosaurs as percent MNI	10	1.1	3.7	5.9	
Mammals as percent MNI	15	33.1	30.5	29.2	

*In standard paleontologic usage, "cf." means that the taxon is most closely compared with, but is not conspecific with, the referred taxon.

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1.3 m above the base of the lower Z coal, the highest possible position of the iridium anomaly (*22*) that defines the K/T boundary. This channel contains mammals previously defined as Mantuan, the earliest Paleocene mammal age. It also contains unreworked teeth of seven genera of dinosaurs, and Paleocene pollen has been found in carbonaceous lenses within the channel (*23*). A best estimate of its age, based on an average rate of sedimentation of 35 B (*24*), is 40,000 years after the K/T boundary. In these upper channels dinosaur-tooth abundance per metric ton of channel sandstone washed is significantly lower, about one-seventh of the abundance found in lower channels in the Hell Creek Formation [Carnosaur Flat (CF, 175 teeth per ton) and Ken's Saddle (KS, 168 teeth per ton)].

Russell argued (*23, 25*) that the Edmonton and Hell Creek local faunas are not sufficiently well known to be able to say with assurance that they are less diverse than the Oldman–Judith River faunas, which admittedly are known from many more articulated specimens. However, it is not necessary to have articulated specimen to be sure of the presence of species. A diverse mix of collecting techniques involving the collection of articulated specimens, the study of isolated bones, and the collection of loose teeth by the washing technique has increased the number of specimens to a comparable level. By combining the similar Lance, Scollard, and Hell Creek faunas the number of articulated specimens is increased to half that of the Oldman fauna. These Lancian faunas then become the second most speciose Cretaceous dinosaur faunas known.

After a century of collection of dinosaurs in the Lance and Hell Creek Formations of Wyoming and Montana, the genera that are rarest in collections are those that are small (<4 m long), just as in the collections from Dinosaur Provincial Park in Alberta. All the small theropods that are the hardest to find intact are known from partial skeletons as well as from isolated teeth and claws in mammal localities from all horizons. Ornithomimids are not easily spotted in washing

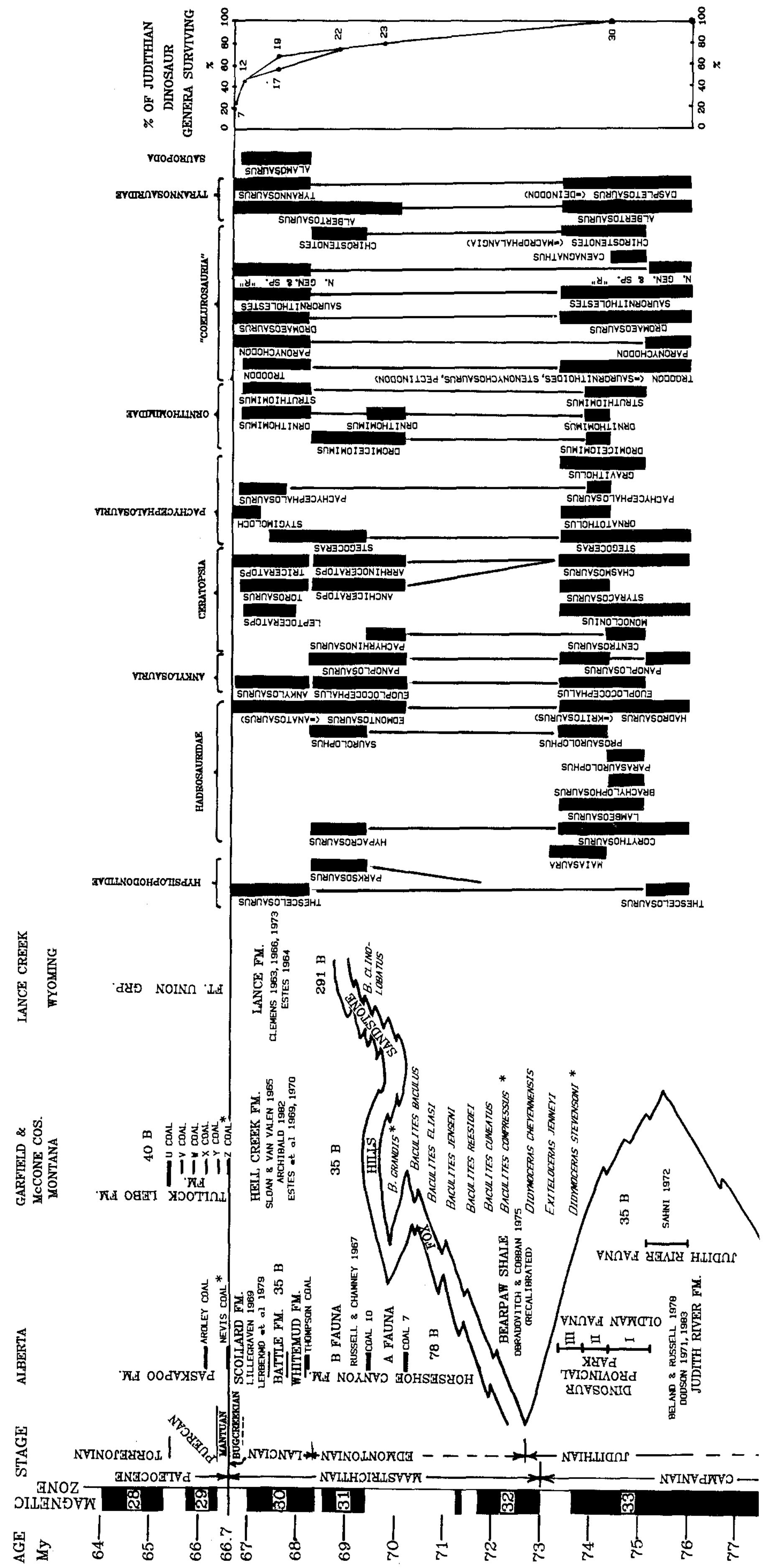

Fig. 1. Diagram showing the ages, phyletic relations, and stratigraphic occurrence of Late Cretaceous dinosaurs in Alberta, Montana, and Wyoming. The left portion of the diagram shows the stratigraphic occurrence of the dinosaur faunas, their relation to the adjacent ammonite zones of the Bearpaw Shale and the overlying Paleocene rocks, a time scale, and a magnetochron scale. The asterisk indicates a radioactive date. Solid bars indicate presence of a genus of dinosaur, and narrow connecting lines the inferred presence or ancestry. Right-hand graph shows percent of Judithian dinosaurs surviving. Sedimentation rates are in Benioff (B) units (*24*).

faunas because they are edentulous, but their claws do preserve and are distinctive.

In Fig. 1, genera based on immature dinosaurs are included with the appropriate adults. Species are not listed because of oversplitting; in most cases only one valid species per genus at a time exists for these faunas. Pseudoextinction is observed by relating each genus to its presumed descendant genus. In the entire last 7 million years of the Cretaceous, genus after genus became extinct while only two new genera migrated into the area. *Parasaurolophus* survived into the latest Maastrichtian (Lancian) in New Mexico (*26*) even though it became extinct in the northern faunas at the end of the Judithian.

Alvarez (*1*) argued that there is no reduction in dinosaur density within the Hell Creek Formation. But the largest body of information available to us suggests strongly that just such a reduction in density did occur. Our earlier statements on density were based mainly on the observed time between finding specimens at different horizons, and limitations of fieldwork made it difficult to be more quantitative. However, the Milwaukee Public Museum (MPM) Dig-A-Dinosaur project of 1977 to 1981 supplies a large quantitative base supplemented by the American Museum collections of 1906 to 1909, the University of Michigan collections of the 1930's, and the University of Minnesota collections of the past 20 years (Fig. 2).

Alvarez used only the vertical position of found specimens as a guide to abundance. In McCone County, at least, this is not sufficient. There is much more badland outcrop for the uppermost Hell Creek Formation than for lower levels. Consequently, much more prospecting has taken place in the uppermost 30 m than in comparable thicknesses of lower levels. A more appropriate measure of dinosaur abundance (density) is number of specimens per meter of section per square kilometer of badland exposure. The location and horizon or elevation of all these specimens were known from field records. Bell had mapped the Z coal beds, the mappable K/T boundary, on aerial photographs at a scale of 1/20,000 (*5*). These data were transferred to the same topographic maps on which the MPM data were plotted, and the distance to the K/T boundary was calculated for each specimen. The area of available badlands exposure was calculated for each prospecting area from the same aerial photos. Specimens were then grouped into 9-m stratigraphic intervals (to ensure adequate samples) and the number of individuals per 9-m interval of section per square kilometer was calculated. Results (Table 2) show a significant reduction in abundance in the uppermost Hell Creek Formation, as earlier stated on less quantitative data. Despite the fact that much more prospecting has been done just below the Z coal (the K/T boundary), dinosaurs are less common in the top 9 m than in any other part of the Hell Creek Formation. A striking fact is that only 7.45 km^2 have been prospected in McCone County. This may seem very small, but this small area occurs in 51 km^2 of land, and examination of aerial photographs shows that the actual density of exposed upper Hell Creek Formation is only 15 percent or less, the rest of the area being covered with grass, as is most of the lower part of the formation.

A similar reduction in diversity takes place in sporopollen taxa. This was previously pointed out for the Garfield County localities (*27*). Oltz (*4*) repeated the Garfield

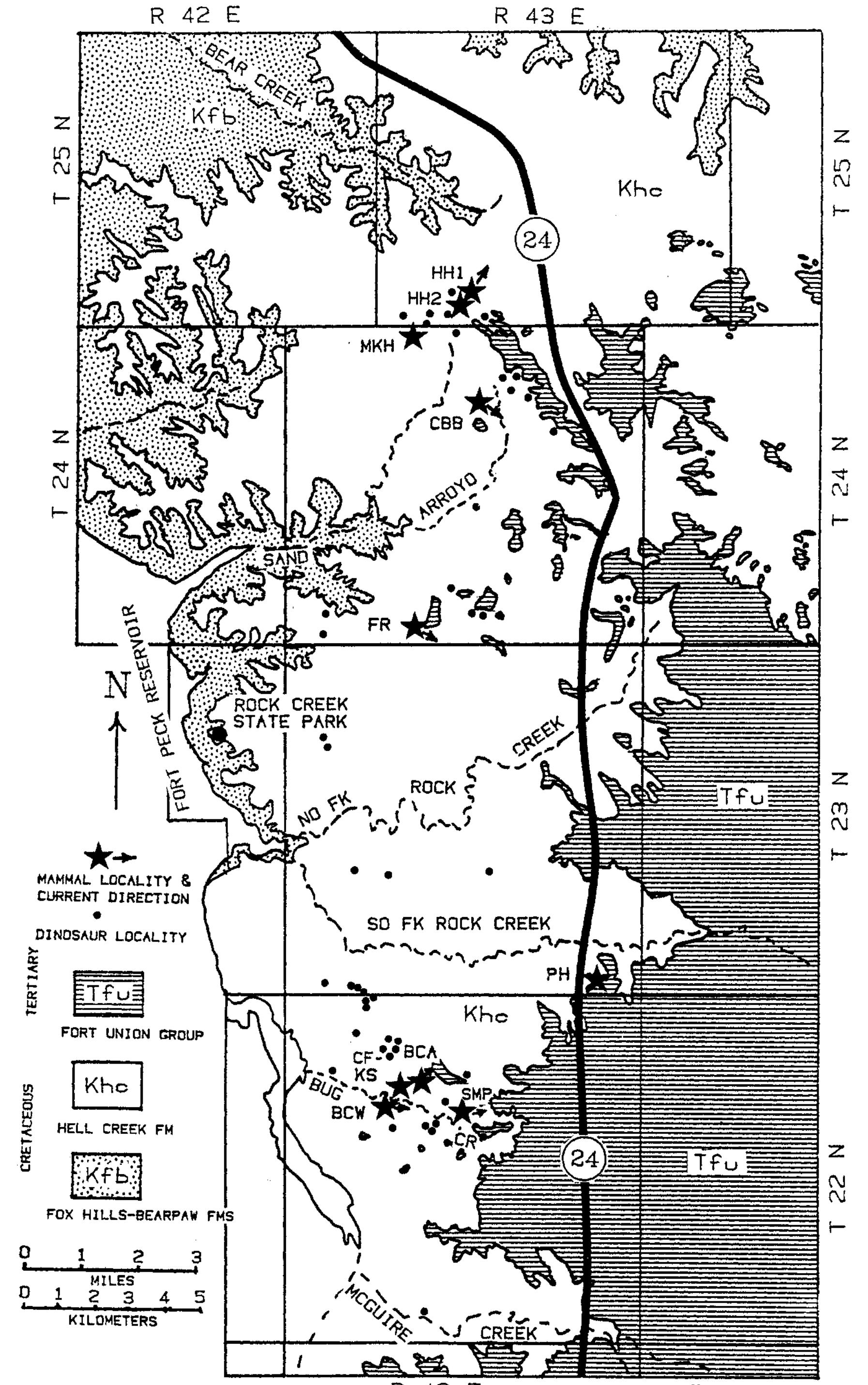

Fig. 2. Geologic map of the Fort Peck Fossil Field, McCone County, Montana, showing dinosaur and mammal localities. Geology after Bell (*5*).

County studies on the McCone County sequence with the same results; again the reduction in plant diversity takes place well below the K/T boundary. As in the earlier studies of Norton and Hall (*27*), pollen diversity was greatest in the middle Hell Creek Formation, where 114 sporopollen taxa were found, and began to drop off well below the K/T boundary; in the upper 12 m of the formation there are only 84 taxa. Only 64 taxa were present at the base of the early Paleocene Tullock Formation; 19 new taxa were added higher in the formation. Data from both Garfield and McCone counties agree with Hickey's (*28*) hypothesis of gradual floral change, not with the catastrophic scenario of Alvarez.

Data supporting the beginning of the ungulate radiation well in advance of dinosaur extinction, the end of the Cretaceous, and the impact "extinction" event are substantial and conflict with the account of Smit and van der Kaars (*2*). They conclude that the Bugcreekian time interval does not exist, on the basis of distinct faunal characteristics, that dinosaur extinction was sharp and catastrophic, and that the principal radiation of ungulates took place entirely after the extinction of dinosaurs.

A principal part of their evidence hinges on the identity and stratigraphic placement of the Bug Creek Anthills (BCA) channel sand (*3, 6*). They include a diagrammatic, nonscale cross section that confuses at least three channels of distinctly different faunas and ages, KS, BCA, and BCW-SMP. This is perhaps not surprising, since the upper 25 m of the Hell Creek Formation is 35 percent channel sandstone in north-south cross section, in distinct contrast to both the lower Hell Creek Formation and the Tullock Formation. In the Tullock Formation the proportion of channel sandstones is only 15 percent. We presume this difference is related to global eustacy with steeper stream gradient during the (Hell Creek) late Maastrichtian regression and gentler stream gradient during the (Tullock) Danian transgression.

Ken's Saddle (KS) (*3*) is a rich channel sand deposit with a standard Lance–Hell Creek fauna of dinosaurs and marsupial and multituberculate mammals; it lacks the new mammals typical of Bug Creek Anthills. At the very top of that butte a second channel cuts into it; this channel, Ken's Apex (KA) has a fauna that duplicates BCA.

The Bug Creek Anthills sandbody is a channel sandstone 11 m thick that trends north 30° east with the top 16 m below the lower Z coal. The cross bedding in the main quarry is of channel scour type, dips to the southeast, and marks the northwest edge of the channel. This channel has a well-known

Table 2. Number of dinosaur specimens per square kilometer of outcrop per 9 m interval of stratigraphic section (exclusive of washing localities).

Stratigraphic interval below Z coal (m)	Number of dinosaur skeletons or large bones	Area prospected (km²/9 m)	Dinosaurs per square kilometer
0–9	6	4.18	1.44*
10–18	13	4.18	3.1
19–27	9	3.93	2.29
28–36	14	2.76	5.07
37–45	4	2.31	1.73
46–54	6	2.42	2.48

*The prospecting success in the highest level differs significantly [χ^2 test; $P < 0.05$] from the combined others, holding the observed areas and total number of specimens constant. The highest level was thought from other evidence (*3*) to show a decline in dinosaur abundance.

fauna (*3, 6*) with a single species of ungulate. We have collected or know of the collection of some 65 tons of sediment from the quarries in this sand; the only ungulate from this sand is *Protungulatum donnae*. The main channel disappears under floodplain silts just below the road leading to Bug Creek in the north half of section 9. These floodplain clays and silts lie beneath and lateral to another channel. This later channel has its top 2 m below the merged upper Z and lower Z coals at bench mark "Bug" and is separated from the coals by floodplain silts. The northern margin of this higher channel lies just above a bend in the Bug Creek road, 50 m south of the northern edge of the BCA channel. This higher channel is the channel Smit and van der Kaars (*2*) traced into the west half of section 10. A mammal locality in the upper channel, Scmenge Point (SMP), which has a fauna exactly identical in ungulate species to Bug Creek West (BCW) was found by J.K.R. Immediately below bench mark "Bug," Oltz (*4*) recovered abundant well-preserved specimens of the diagnostic Cretaceous pollen grains *Aquillapollenites amplus* and *A. delicatus* from the base of the combined Z coals above both the BCA and BCW-SMP channels.

Orth (*22*) found a slightly enriched zone of iridium just above a thin charcoal streak that varies from 0.6 m to a maximum of 1.8 m below the base of the lowest Z coal in the basin, 7 km east of SMP. The Z coals merge near the southeast margin of the BCW-SMP channel and dip into a swale trending northeast over the margin of the upper channel. The Z coals frequently merge, especially over a high channel sand in the Hell Creek Formation. We interpret this phenomenon to represent differential compaction and deposition of channel sands and floodplain shales in the early Paleocene, Mantuan, time interval between the deposition of the upper and lower Z coals.

We interpret these data to mean BCA and BCW-SMP channels are of different ages, and that at least BCA is Cretaceous in age. Other mammal localities with Bugcreekian faunas in this area (Fig. 2) are Harbicht Hill (HH) 1 and 2, and Chris's Bone Bed (CBB) (*7*). The top of the Harbicht Hill channel is 14 m below the projected level of the lower Z coal. The CBB channel is oriented south 30° east and points directly at the wall of the Sand Arroyo badlands, which has a continuous exposure of both upper and lower Z coals; this channel does not cut them. Many dinosaurs have been collected above this locality by parties of the American Museum of Natural History, the Milwaukee Public Museum, and the Universities of Michigan and Minnesota. The Ferguson Ranch locality is in the southwest quarter of section 33, T 24 N, R 43 E. It is in the extreme southern edge of a channel oriented south 50° east. It has younger fauna than Harbicht Hill that is comparable in age to the Worm Coulee and Hell Hollow localities of Archibald (*18*) in Garfield County to the west. The particular species of *Baioconodon* [formerly *Ragnarok* (*29*)] and *Oxyprimus* have only been recovered from Mantuan, earliest Paleocene localities.

The dinosaur teeth from the Ferguson Ranch locality are in a channel whose top occurs between the upper and lower Z coals, presumably after the deposition of the iridium layer and thus are earliest Paleocene or Mantuan age. The lower Z coal is indeed cut by the channel. Lenses of clay in the base of the channel contain Paleocene pollen (*22*). Teeth of seven species of dinosaurs have been recovered from this channel (Table 1). The question arises: Were these dinosaurs living after the end of the Cretaceous, or are they reworked from older sediments (*30*)?

We do not think that they were reworked, for several reasons. They were not transported very far, because postmortem stream abrasion on these teeth is minimal. The teeth are all shed teeth, some with unabraded sharp basal edges resulting from dentine root resorption before shedding. The likelihood of concentrating these teeth by eroding the floodplain sediments adjacent to the channel is very low in view of the rare occurrence in the clays of isolated teeth or other small vertebrate fragments. The hollow cavity of the base of the teeth is unfilled with floodplain silts or clay but instead is empty or filled with channel sand. It is even less likely that they were eroded from older channel sands because the usual occurrence in channel sands is near the base of the sand and this is a very thin channel—it did not cut deeply enough into lower channels to rework many teeth. The surface of the teeth shows no abrasion; the very tiny and sharp denticles of the theropod teeth show only occlusal attritional wear. Finally, were they to be reworked, one would also expect to find Cretaceous species of *Baioconodon* and *Oxyprimus* that are far more numerous than dinosaur teeth in the only channels from which the dinosaur teeth could possibly be reworked. The most reasonable conclusion is that these are indeed early Paleocene dinosaurs.

It thus appears on present data that KS and BCA are definitely Cretaceous, BCW-SMP may be Cretaceous or Paleocene, and FR is definitely Paleocene. Of the 30 dinosaur genera present in the area 8 million years before the end of the Cretaceous, a maximum of 12 were present just before the K/T boundary event, and between 7 and 11 genera survived into the Paleocene. Depending on the precise level of the K/T boundary with respect to these faunas, all that can be ascribed to the asteroid impact is the extinction of from one to three genera. The remaining genera either became extinct significantly earlier or later.

If dinosaur extinction is not solely due to an asteroid impact (we are convinced it did not help them), what are the other factors? We continue (*3*) to suggest a concurrence of several factors: global temperature lowering over the last 15 million years of the Cretaceous, lowering of sea level during the late Maastrichtian and consequent increase in seasonality, major deterioration of the flora as a result of these two causes, and diffuse competition from new mammalian herbivores most likely introduced to this continent from Asia.

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Crystal Structure Analysis of Deamino-Oxytocin: Conformational Flexibility and Receptor Binding

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Two crystal structures of deamino-oxytocin have been determined at better than 1.1 Å resolution from isomorphous replacement and anomalous scattering x-ray measurements. In each of two crystal forms there are two closely related conformers with disulfide bridges of different chirality, which may be important in receptor recognition and activation.

The neurohypophyseal hormone oxytocin (Fig. 1) elicits smooth muscle contraction, causing milk ejection and uterine contractions in mammals. The synthesis of oxytocin (*1*) led to a systematic study of the relation of primary structure to biological activity, and more recent studies have highlighted the additive nature of modifications that favor certain pharmacological effects. This has resulted in the design of highly selective, long-acting superagonists and antagonists of therapeutic potential (*2, 3*). One synthetic analogue of particular interest is deamino-oxytocin (1-mercaptopropionateoxytocin), which was the first to be found more active in most tests than the natural hormone (*4*).

Spectroscopic studies such as nuclear magnetic resonance (NMR), laser Raman, and circular dichroism have shown that oxytocin can exist in several conformations although certain well-defined intramolecular hydrogen bonds characterize most conformers in solution (*5, 6*). In view of this inherent flexibility, it is necessary to examine the conformation and dynamics of the hormone and its analogues not only in aqueous conditions, but also in other environments that are models for the hormone in its complex with the receptor. Although crystals of oxytocin were first reported in 1952 (*7*), the crystal structure has proved elusive. In 1965, crystal data for deamino-oxytocin were reported by Low and Chen (*8*) and an active

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