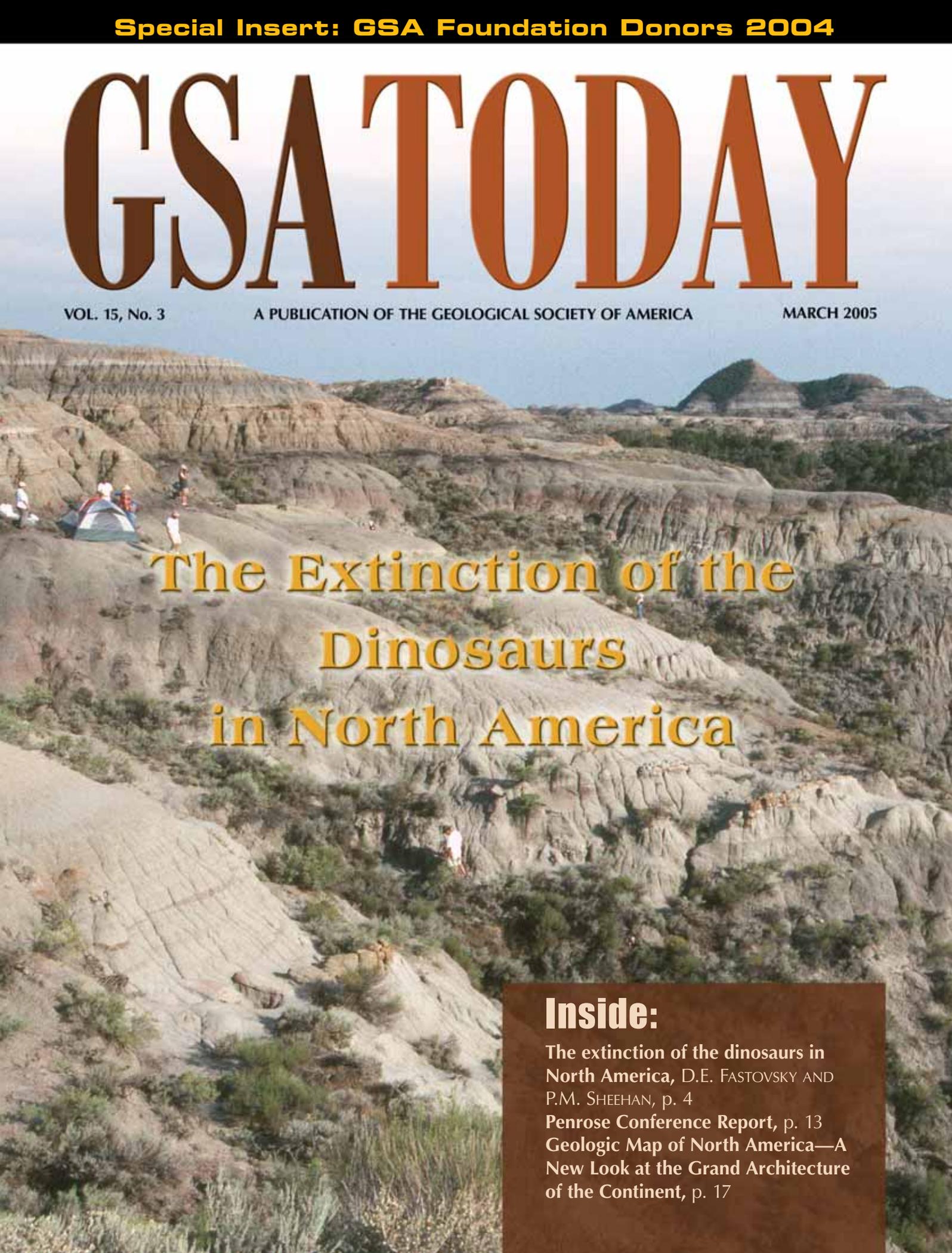


GSA TODAY

VOL. 15, No. 3

A PUBLICATION OF THE GEOLOGICAL SOCIETY OF AMERICA

MARCH 2005



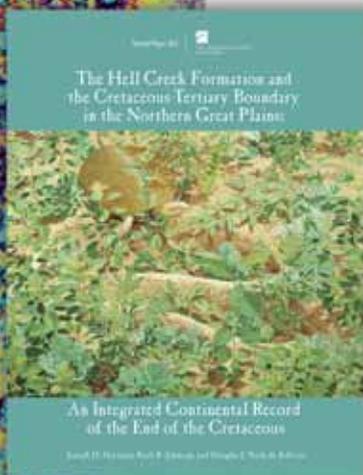
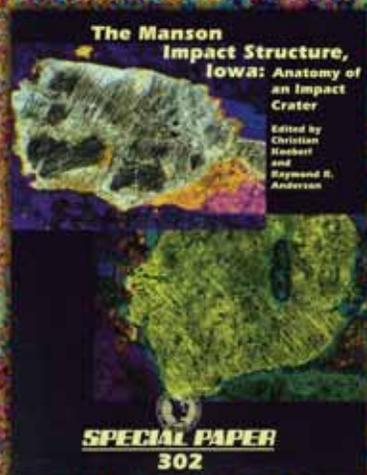
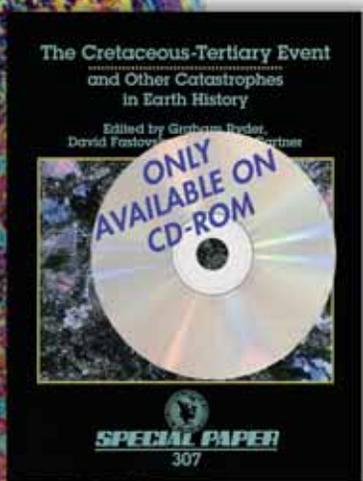
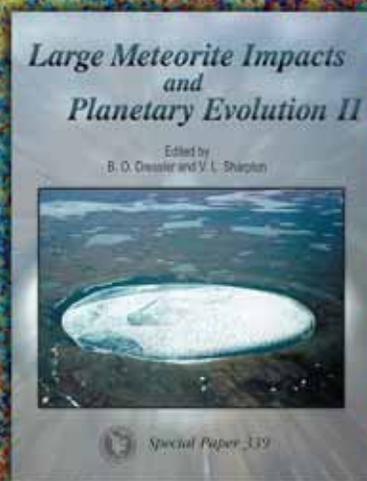
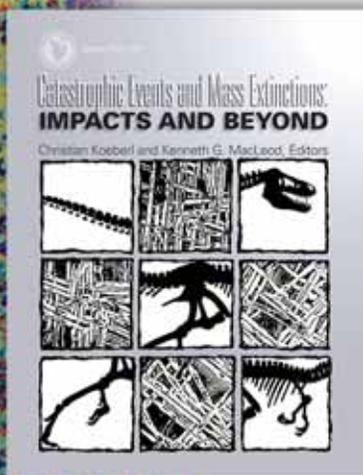
The Extinction of the Dinosaurs in North America

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GSA TODAY (ISSN 1052-5173 USPS 0456-530) is published 11 times per year, monthly, with a combined April/May issue, by The Geological Society of America, Inc., with offices at 3300 Penrose Place, Boulder, Colorado. Mailing address: P.O. Box 9140, Boulder, CO 80301-9140, USA. Periodicals postage paid at Boulder, Colorado, and at additional mailing offices. Postmaster: Send address changes to *GSA Today*, GSA Sales and Service, P.O. Box 9140, Boulder, CO 80301-9140.

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Printed in the USA using pure soy inks.

Volume 15, Number 3

March 2005

Cover: The Cretaceous–Tertiary (K–T) boundary (next to tent) at the Sand Creek Overlook, Makoshika State Park, Montana, USA. Here the K–T boundary coincides with the lithologic boundary between the Fort Union Formation and the underlying Hell Creek Formation permitting identification of both boundaries in the field. Photo by Joanne Peterson, Milwaukee Public Museum. See "The extinction of the dinosaurs in North America" by D.E. Fastovsky and P.M. Sheehan, p. 4–10.



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The Extinction of the Dinosaurs in North America

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ABSTRACT

Rightly or wrongly, dinosaurs are poster children for the Cretaceous-Tertiary (K-T) extinction. The rate and cause of their extinction, however, has been contentious, at least in part because of their rarity. Nonetheless, significant data have accumulated to indicate that the dinosaur extinction, in North America at least, was geologically instantaneous. The evidence comes from field studies in geologically disparate settings involving the reconstruction of dinosaur stratigraphic ranges as well as community structure in the Late Cretaceous, and from quantitative studies of the post-Cretaceous evolution of mammals.

The hypothesis of extinction by asteroid impact is concordant with what is known of the rate of the dinosaur extinction, as well as the patterns of selective vertebrate survivorship across the K-T boundary. The precise nature of the kill mechanism(s), however, remains under discussion.

INTRODUCTION

The question of what happened to the dinosaurs at the Cretaceous-Tertiary (K-T) boundary has come to exemplify the K-T extinction. Did they die out instantly, or were they gradually going extinct over millions of years? As has been noted by Clemens et al. (1981), identifying the patterns of the dinosaur extinction is a question quite separate from, but a prerequisite to, identifying the cause(s) of the extinction itself. In the last 25 years, much has been learned about the patterns of the dinosaur extinction. Ultimately, what we know about extinction pat-

terns constrains causal mechanisms, a point forcibly made by Bakker (1986). Here, we review a variety of different studies, all of which ultimately converge on the conclusion that the extinction of the dinosaurs in North America was geologically instantaneous. From this conclusion and data pertaining to the post-Cretaceous recovery, we consider potential causes of the extinction.

For many years it has been said that dinosaurs were waning in number and diversity over the last 10 m.y. of the Cretaceous (the Campanian-Maastrichtian interval). A typical statement of this viewpoint can be found in Dodson (1996) who notes, "[Among dinosaurs] I see a pattern of dwindling. Ten million years before the end [the K-T boundary] there were two subfamilies of ceratopsids. ...At the end, only the chasmosaurines were left. Ten million years before the end, there were two families of hadrosaurs. ...At the end, only the hadrosaurines were left. Ten million years before the end, there were two families of armoured dinosaurs. ...At the end, only the ankylosaurids were left" (p. 280).

This apparent drop in diversity looks to us to be comparable to other Late Cretaceous fluctuations in the imperfect dinosaur record. Considered in the context of all dinosaur diversity fluctuations throughout the Late Cretaceous, this drop in diversity over the last 10 m.y. does not appear remarkable, either for North America or globally (Fastovsky et al., 2004). Consequently, we focus here on the final two m.y. of the dinosaur record as key to the rate and mechanism of their extinction.

It would be ideal to be able to resolve the precise duration of the North American dinosaur extinction, no matter what its length. At a temporal distance of 65 m.y. and beset by a fragmentary terrestrial record, however, we can only characterize events as geologically instantaneous, by which we mean encompassing time-scales of tens of thousands of years (or less). Nonetheless, this allows us to distinguish between processes and events that occurred on such time-scales (or less) and those that occurred on longer ones.

Global databases for dinosaurs exist (e.g., Weishampel et al., 2004), and fluxes in dinosaur diversity have been reconstructed from them (e.g., Dodson, 1990; Fastovsky et al., 2004); yet, the North American record remains uniquely suited to understanding the rate of the dinosaur extinction. This is because only in North America are there dinosaur-bearing exposures with a high level of stratigraphic resolution that preserve a terrestrial K-T boundary *and* that have been studied quantitatively.

SEDIMENTARY ENVIRONMENTS THAT PRESERVE THE LATE HISTORY OF THE DINOSAURS

In the latest Cretaceous of the North American Western Interior, dinosaurs such as *Triceratops*, *Tyrannosaurus*, and *Edmontosaurus* (and a host of lesser luminaries) roamed upland and coastal plain settings (Lehman, 1987) that formed during the Laramide phase of the Rocky Mountain uplift (Peterson, 1986). Dinosaur-bearing units that have been the subjects of studies sufficiently detailed to resolve the nature of the extinction are preserved in the structurally complicated Hanna Basin, an intermontane basin in southern Wyoming (Eberle and Lillegraven, 1998; Lillegraven et al., 2004), and undeformed sediments of the Williston Basin, an intracratonic basin extending through eastern Montana and western North and South Dakota (Peterson, 1986) (Fig. 1).

In the Hanna Basin, the K-T boundary is found within the Ferris Formation,

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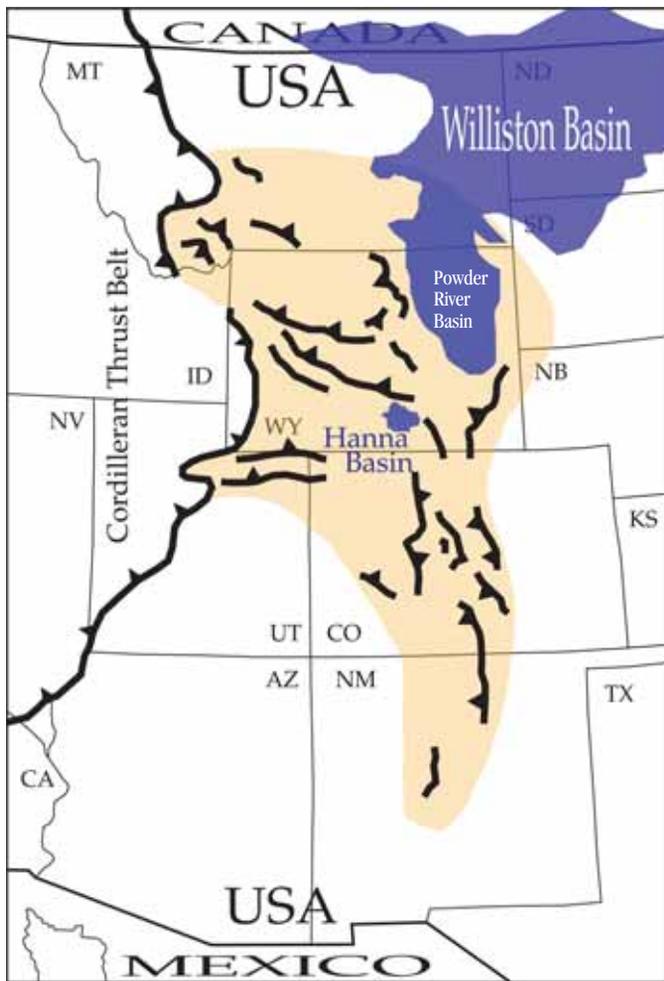


Figure 1. The Western Interior of North America, showing in blue the Cretaceous-Tertiary Hanna, Williston, and contiguous Powder River (not discussed here) basins. Area shown in tan exhibits Laramide deformation; Laramide-age thrust faults shown as barbed lines. Redrawn from Hamilton (1988) and Lillegraven and Eberle (1999).

a 1.2-km-thick sequence of sandstones and mudstones interpreted to represent fluvial deposition. A well-developed braided river system bisects the Cretaceous part of the formation, giving way (~300 m below the K-T boundary) to a meandering fluvial system with lacustrine subenvironments (Eberle and Lillegraven, 1998; Wroblewski, 2003, 2004). In the Williston Basin, the latest Cretaceous is represented by the Hell Creek Formation, a unit that consists of ~100 m of mudstones interbedded with sandstones, interpreted as the remnants of ancient, meandering, aggradational fluvial systems (Fastovsky, 1987; Murphy et al., 2002).

Like some great cosmic joke designed to frustrate paleontologists, the K-T boundary is rarely found in a thick sequence of strata unambiguously representing continuous deposition in a single paleoenvironmental setting. In the Hanna Basin, the K-T boundary probably occurs adjacent to or within a disconformity-bounded, 8-m-thick, complexly channeled sandstone, the so-called “zone of uncertainty” of Lillegraven and Eberle (1999). By contrast, in the Williston Basin, the boundary interval is characterized by a facies

change in which the interbedded mudstones and sandstones of the Hell Creek Formation generally give way to extensive laminated siltstones and coal deposits of the basal part of the Fort Union Formation (Fastovsky, 1987; Lofgren, 1995). The lithostratigraphic contact between the Hell Creek and Fort Union Formations is not precisely isochronous, but varies by as much as 3 m above or below the palynologically identified K-T boundary (see Fastovsky, 1987; Johnson, 1992; Lund et al., 2002; Nichols and Johnson, 2002; Pearson et al., 2002). The low density of dinosaur preservation (an estimated 0.000056 dinosaurs/m² of exposure; White et al., 1998) means that in practice, the facies change is commonly (but certainly not always) associated with the dinosaur extinction.

RECONSTRUCTING FLUXES IN DINOSAUR DIVERSITY AT THE K-T BOUNDARY

Over the past 15 years, three studies, by three different research groups using different approaches, have produced stratigraphically refined, quantitative data bearing upon the rate of the Late Cretaceous dinosaur extinction in western North America.

Hanna Basin

Dinosaur distributions in the Hanna Basin were studied by determining, with maximum refinement, the stratigraphic ranges of taxa preserved in the Ferris Formation. Stratigraphic relations were established using a combination of palynostratigraphy and North American Land Mammal “Ages” (Cifelli et al., 2004; Lofgren et al., 2004; see also Grimaldi et al., 2000). Seventy-six vertebrate-bearing localities contributed to the results of the study (Fig. 2). Regarding the pattern of dinosaur extinction, Lillegraven and Eberle (1999, p. 702) concluded “there exists little evidence for progressive reductions in taxonomic diversity of the local dinosaurian fauna... Indeed, our collections show that, exclusive of the rare forms, most species of dinosaurs from the Ferris Formation are represented up [to] ... the eight meter thick zone of complexly channeled sandstone that is uncertain in age. ... The late history of local dinosaurs seemed to have a sudden termination. That is, high taxonomic diversity persisted late into the [latest Cretaceous]...”

The authors thus identified a geologically instantaneous extinction, but, given the issues of temporal resolution described above, noted that their study could not distinguish between events that took place on 1000 to 10,000 year time-scales and those that are much shorter.

Williston Basin

Sheehan et al. (1991) divided the Hell Creek into three sequential stratigraphic windows to test whether community-level changes among dinosaur assemblages were compatible with long-term extinction scenarios. A methodologically controlled census of dinosaur remains through the thickness of the formation produced a minimum number of 556 in situ, precisely located individuals within the Hell Creek Formation. Using rarefaction to compare the communities among the three windows, Sheehan et al. (1991) found that the number, rank order, and relative proportions of families were unchanged, indicating stable communities through the formation, and concluded that “there is no statistically meaningful drop in the ecological diversity of dinosaurs through

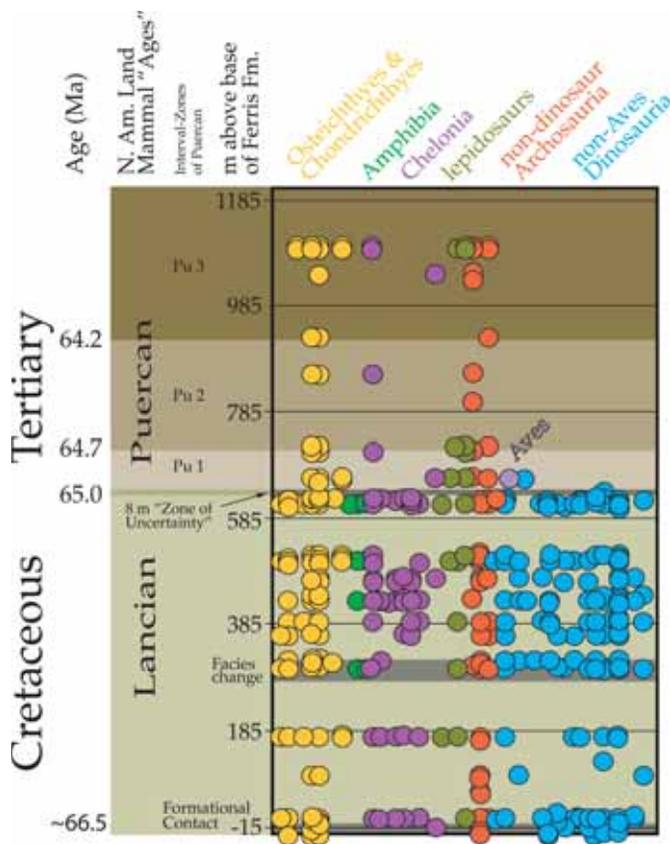


Figure 2. Stratigraphic range chart showing the distribution of non-mammalian fossil vertebrate specimens in the Ferris Formation in the Hanna Basin (data from Lillegraven and Eberle, 1999). Dinosaurs essentially disappear at the base of the 8-m-thick, largely unfossiliferous, "zone of uncertainty" (see text). Three exceptions to this are an isolated tooth found within the "zone of uncertainty" and two water-worn specimens, interpreted by Lillegraven and Eberle (1999) as Cretaceous material reworked in earliest Tertiary time. Formation thickness and key lithological changes, biostratigraphic zonations (North American Land Mammal "Ages" and "Interval Zones"), and geochronology (Ma) are shown on left. Dates are ± 0.1 m.y. (interpolated from Lofgren et al., 2004; basal date from Grimaldi et al., 2000).

the Hell Creek. [O]ur data are compatible with abrupt extinction scenarios" (p. 838). The Sheehan et al. (1991) study was criticized for its use of rarefaction by Hurlbert and Archibald (1995), who noted that the technique was "only weakly related to ... variables such as absolute numbers of dinosaur taxa, population densities, or extinction rates" (p. 881). Sheehan et al. (1996) countered that the critique was misdirected because these variables were not the ones under consideration. They noted that absence of a taxonomic decline was established without rarefaction (number and rank order of taxa were unchanged) and affirmed that the statistical treatment was only an effort to search for a community-level reorganization such as might indicate a deteriorating ecosystem.

Approaching the question from a biostratigraphic perspective, Pearson et al. (2002) undertook a 10-year effort to determine the stratigraphic distribution of taxa in the Hell Creek (Fig. 3). At each of the 82 sites distributed among 20 localities that they studied, they identified the K-T boundary via pollen and then surveyed the vertebrate faunas found in each locality. Their database included 2233 dinosaur specimens

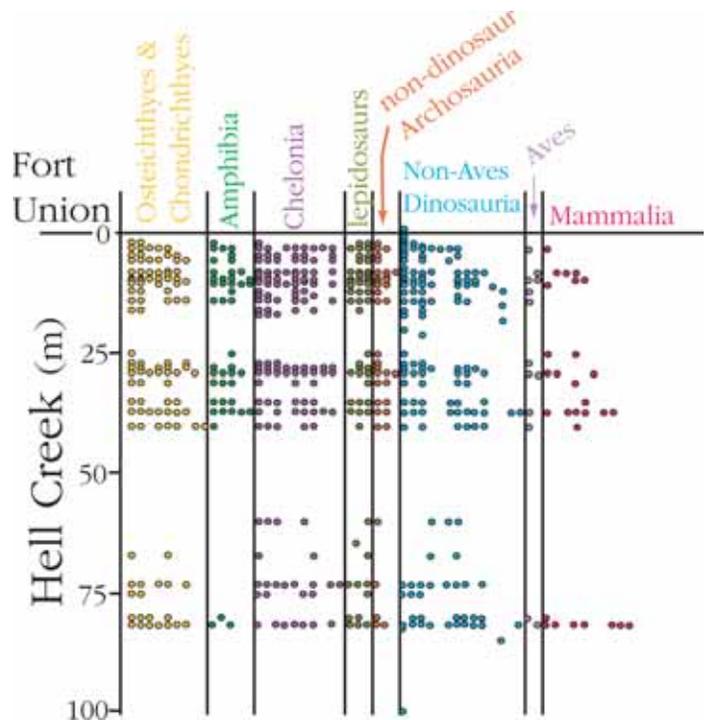


Figure 3. Composite stratigraphic range chart showing the distribution of identifiable fossil vertebrate specimens in the Hell Creek Formation, which records the last 1.4 m.y. of the Cretaceous in the Williston Basin. In the case of dinosaurs, no decrease in diversity could be found. A single non-avian dinosaur in the basal part of the Fort Union Formation demonstrates the diachroneity of the lithostratigraphic contact between the Hell Creek and Fort Union, reaffirming that in places, the basal Fort Union is Cretaceous in age. Redrawn from Pearson et al. (2002).

distributed among 14 taxa and located to precise stratigraphic horizon. The results showed no obvious change in diversity through the Hell Creek, an inference that they statistically tested via rarefaction. They concluded, "there is no evidence for a decreasing trend [in diversity] through the formation ... these results are not compatible with gradual extinction at the end of the Cretaceous" (p. 164-165).

All published, quantitative, stratigraphically refined, field-based studies involving dinosaurs are sending the same clear signal of geologically instantaneous extinction.

THE RECOVERY

One may also approach this problem from a quite different perspective: A catastrophic perturbation to the ecosystem, as has been proposed, ought to leave some kind of mark in the fossil record, reflected in the subsequent recovery of the ecosystem. And indeed, it has been common knowledge almost since dinosaurs were first identified as Mesozoic beasts that the terrestrial K-T boundary is characterized by a stunning ecosystemic turnover marked by the extinction of dinosaurs and the radiation of mammals. The nature of these early mammals has also long been well known: they were small, presumably omnivorous, generalists (e.g., Lillegraven et al., 1979; Maas and Krause, 1994). While their connection to more recent mammals is becoming manifest (e.g., Archibald et al., 2001; Archibald, 2002, 2003), and while modern clades of placental mammals may have roots prior to the K-T boundary,

there is little comparison to be made between the *appearance* of modern mammalian clades during Late Cretaceous time and the *radiation* that followed the K-T boundary.

Like the dinosaur extinction, mammalian evolution in the early Tertiary of North America has been evaluated quantitatively (Maas and Krause, 1994; Alroy, 1999; Archibald and Deutschman, 2001). All agree that earliest Tertiary mammals underwent high rates of speciation leading to a steep increase in rates of diversification during the first 5 m.y. of the Tertiary (Fig. 4). Indeed, seventeen of the eighteen orders of extant placental mammals did not exist before the K-T boundary (Archibald, 2002).

A range of evolutionary specializations took place during the early Tertiary, as mammals invaded ecospace abandoned by dinosaurs. As noted by Alroy (1998), "... the data are compatible with the idea that the extinction of large terrestrial vertebrates such as dinosaurs at the K-T boundary opened up the larger end of the body size spectrum for occupation by mammals" (p. 733).

Just how quickly did the post-K-T mammalian radiation proceed? Eberle and Lillegraven (1998) record increasing body sizes among primitive eutherian mammals (condylarths) within 400,000 yr of the K-T boundary in the Hanna Basin. Still, Maas and Krause (1994) report that it took mammals 3–5 m.y. to develop the broad range of body sizes and diversity of ecological specializations that have characterized all successive, stable, mammalian faunas throughout the Cenozoic (e.g., Janis et al., 1998). An even longer estimate was provided by Kirchner and Weil (2000), who suggested that the recovery took as long as 10 m.y.

Rates of evolution were evidently fueled by multiple waves of immigration (Weil and Clemens, 1998; Lillegraven and Eberle, 1999; Clemens, 2002). Clemens (2002) summarizes

this viewpoint: "Recovery of the terrestrial vertebrate fauna [in eastern Montana] was not simply the product of an explosive evolutionary radiation of a few surviving stocks. Immigration from other areas played a major role in reconstitution of mammalian diversity" (p. 240).

Interestingly, all accounts suggest that the timing of the post-K-T radiation of mammals lags somewhat behind that observed by d'Hondt et al. (1996, 1998) for planktonic foraminifera after the K-T boundary. However, these estimates of mammalian recovery intervals are in the range of those for other organisms following other mass extinction events (Jablonski, 1991).

The record of earliest Tertiary mammals, with its high rates of speciation and diversification and generally delayed onset of broad morphological specializations and size disparities, appears very much like the kinds of faunas and floras that typically develop after ecological traumas: the so-called "disaster species" (Brenchley and Harper, 1998). Indeed, evolutionary patterns in the earliest Tertiary are generally termed a *recovery* (but see Lillegraven and Eberle, 1999), signaling that there was something from which to recover.

CAUSES: SO WHAT KILLED THE DINOSAURS?

We have spent much of this article reviewing aspects of the pattern (in this case, the rate) of the North American dinosaur extinction. Causal factors are necessarily much more difficult to identify, because while events can potentially be shown to be coincident, the demonstration of causality is far more problematical. Indeed, the extinction of the dinosaurs has a notorious, ongoing history of insouciant proposals unfettered by data (see Fastovsky and Weishampel, 2005).

Our interest, however, is in published models that are grounded in data and that are potentially testable. In this category, Archibald and Bryant (1990) and Archibald (1996, 1997), basing their interpretations upon patterns of vertebrate survivorship, proposed marine regression with associated habitat fragmentation as the ultimate cause of the K-T extinctions. In this model, multiplication and lengthening of river systems due to a marine regression led to a diminution and fragmentation of coastal plain habitats, in turn causing range reductions and eventual extinction. A variation on this model was proposed by Dingus and Rowe (1997), who suggested that the regression in combination with latest Cretaceous igneous activity *and* the asteroid impact caused the extinction of the dinosaurs.

The conclusion that the extinction of the dinosaurs was geologically instantaneous precludes longer-term causes (e.g., events on million to ten-million-year timescales). So, although survivorship patterns may be in accord with habitat fragmentation-based models, habitat fragmentation as the driving force for the dinosaur extinction is problematical, because it is linked in this case to a marine regression that occurred over a million or more years. Moreover, recent stratigraphic work summarized in Johnson et al. (2002) suggests that the Hell Creek was deposited rather quickly (over ~1.4 m.y.; Hicks et al., 1999, 2002) in a transgressive setting (the final transgression of the North American Western Interior Sea). This interpretation is concordant with a previously inferred rise in the water table (Fastovsky and McSweeney, 1987). The transgressive geological setting is antithetical to the proposed

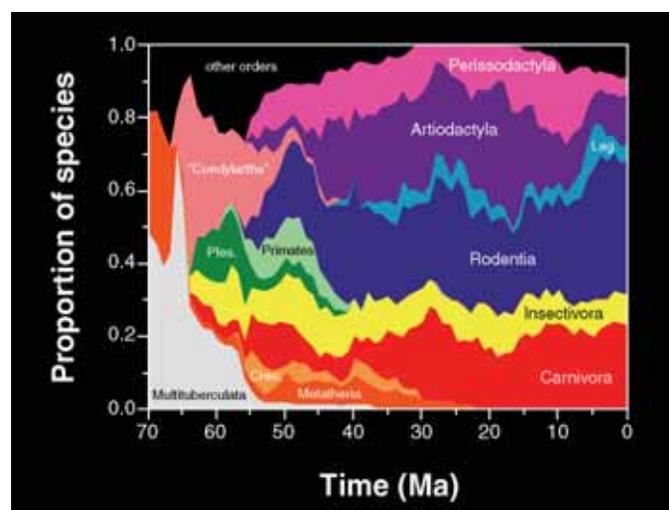


Figure 4. Cenozoic mammalian ordinal diversity plotted as a function of time. Note the sharp rises in the diversity of condylarths at 65 Ma and the secondary evolutionary bursts of Plesiadapiformes ("Ples.") and insectivores at 62–63 Ma. By 55 Ma, all of these orders of mammals started to become far less dominant as the larger, more diversified perissodactyls, artiodactyls, carnivorans, and rodents became important parts of successive global mammalian faunas. (From Alroy, 1999; also at <http://www.nceas.ucsb.edu/~alroy/mammalorders.gif>).

fluvial lengthening associated with the habitat fragmentation scenario and suggests that it was not likely a factor in the North American dinosaur extinction.

Death by Asteroid

The current “alternative hypothesis” for the cause of the extinction of the dinosaurs is, of course, an asteroid impact with Earth. Schultz and d’Hondt (1996), using the morphology of the crater as an indicator of the angle and direction of the impact, proposed that the Western Interior of North America would bear the brunt of impact effects. In all scenarios, wholesale extinctions on extremely short timescales are presumed to be a consequence of such an event. While the extinction cannot be shown to have occurred within hours, days, or weeks, extinction timescales can be constrained to a few tens of thousands of years *or less*. For this reason, what is known of the rate of the dinosaur extinction in North America is concordant with the predicted effects of an asteroid.

In this brave new world of an asteroid blight, how did some organisms survive and others become extinct? A number of workers (e.g., Weil, 1994; Archibald and Bryant, 1990; Archibald, 1996, 1997; Dingus and Rowe, 1997) have argued that the patterns of survivorship are not concordant with the expected effects of an asteroid impact. Such effects include global wildfires (Wolbach et al., 1988; Ivany and Salawich, 1993), acid rain (Prinn and Fegley, 1987; Zahnle, 1990; Retallack, 2004), and atmospheric dust (Alvarez et al., 1980).¹

On the other hand, Sheehan and Hansen (1986) first proposed, for both marine and terrestrial faunas, that buffering against the effects of the K-T extinction might accrue from detritus feeding because animals in detritus-based food chains appear to have fared better than those dependent upon primary production. Sheehan and Fastovsky (1992) and Archibald (1993, 1996), using data from eastern Montana first presented in Archibald

and Bryant (1990), demonstrated that in the terrestrial realm, aquatic organisms fared better than their fully terrestrial counterparts. Sheehan and Fastovsky (1992) proposed that aquatic organisms were generally more likely than exclusively terrestrial organisms to be in detritus-based food chains (see also Retallack, 2004) and that among terrestrial animals, those able to feed in detritus-based food chains (e.g., mammals) were more likely to survive than animals in food chains dependent on primary production (e.g., dinosaurs). In Sheehan and Fastovsky’s (1992) scenario, as in the original Alvarez et al. (1980) scenario, sunlight was blocked for an extended period of time, causing a collapse in primary production and holding out the hope of survivorship to only those who could live exclusively from detritus.

These ideas were recently revisited by Robertson et al. (2004), who quantified a previously proposed infrared thermal pulse from a global rain of hot spherules (splashed from the K-T impact), reassessed the patterns of biotic survivorship, and suggested that the short-term (hours-long), global pulse of intense infrared radiation was the primary killing agent. It would have caused severe thermal stress and ignited global wildfires that incinerated anything that could not shelter itself: “sheltering underground, within natural cavities, or in water was the fundamental means to survival during the first few hours of the Cenozoic. Shelter was by itself not enough to guarantee survival, but lack of shelter would have been lethal” (Robertson et al., 2004, p. 760). This model differs from its antecedents because a heat pulse (and subsequent wildfires) rather than the cessation of photosynthesis, was the primary killing agent, and thermal sheltering, rather than detritus feeding, allowed survival.

We sincerely doubt that we have reported the last word on the cause of the extinction of the dinosaurs. This is in part because, as we have seen, the

number of studies reconstructing the pattern of the extinction is sparse and the temporal resolution of the data is limited. Moreover, in the case of the asteroid impact, although the enormous energy released by the impact made disastrous environmental consequences inevitable, a generally accepted model for all the environmental changes associated with the K-T impact has not yet emerged. Indeed, each of the potential effects of an asteroid impact has been the subject of considerable discussion. Among the putative effects to have undergone reconsideration are global wild fires (Belcher et al., 2003), acid rain (d’Hondt et al., 1994; Maruoka and Koeberl, 2003), and darkness, which may have been caused by aerosols rather than dust (Pope, 2002). Nonetheless, the extinction of the dinosaurs has been characterized by a rich intellectual debate as new methods of extracting highly refined stratigraphic data from sections are pioneered, as new interpretations of global events are entertained, and as an understanding of catastrophic events in earth history (e.g., Powell, 1998) is forged.

CONCLUSIONS

In the 25 years since Alvarez et al. (1980) first proposed that an impact was responsible for the K-T extinctions, stratigraphic and paleoecologic evidence have come together to present a reasonably cohesive picture of a quick demise of the dinosaurs. Evidence from the rates of dinosaur extinction suggests that the extinction was geologically instantaneous; this conclusion in combination with the nature of the post-Cretaceous biologic recovery suggests that the extinction occurred on an extremely short, irresolvable timescale. While the exact killing mechanisms may or may not yet have been identified, all the data—including the rate of extinction, the nature of the recovery, and the patterns of survivorship—are concordant with the hypothesis of extinction by asteroid impact.

¹To review the most pervasively cited example: Since amphibians are particularly sensitive to pH conditions, and they passed through the boundary largely unscathed, the asteroid impact could not have had a significant involvement in the extinction, because one of its predicted side effects—acid rain—would surely have affected amphibian survivorship (Weil, 1994; Archibald, 1996, 1997). In fact, a significant body of work suggests that the survival of amphibians is good evidence that deadly acid rain was not a major effect of the impact (see also d’Hondt et al., 1994; Maruoka and Koeberl, 2003; Retallack, 2004).

ACKNOWLEDGMENTS

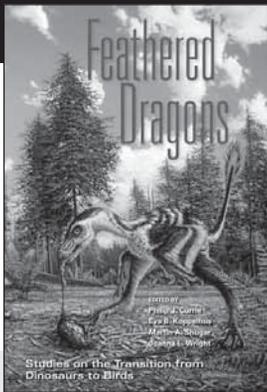
Grateful thanks are due to J.D.

Archibald, D.A. Eberth, K. Howard, J.A. Lillegraven, G.J. Retallack, and A. Sweet, all of whom reviewed earlier drafts of this manuscript and contributed immensely to its improvement.

However, the viewpoints expressed here are not necessarily those of the reviewers. This work was supported in part by the Instituto de Geología, Universidad Nacional Autónoma de México, and by a Fulbright Garcia-Robles Award.

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*Manuscript received October 11, 2004;
accepted December 22, 2004. ♦*



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