Journal of Mammalian Evolution, Vol. 12, Nos. 1/2, June 2005 (© 2005)
DOI: 10.1007/s10914-005-6943-4

Mammalian Faunal Dynamics During the Last 1.8 Million Years of the Cretaceous in Garfield County, Montana

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This study provides an analysis of biotic change in successive mammalian communities during the last 1.8 million years of the Cretaceous (67.3–65.58 Ma) from the Hell Creek Formation in Garfield County, Montana. Results show changes in relative abundances of species, mean individual body size, and to some extent taxonomic composition through the Hell Creek Formation. These results are interpreted as "normal" mammalian responses to fluctuating temperatures during the latest Cretaceous. By contrast, the extinction of 22–27 mammalian species at or near the Cretaceous-Tertiary (K-T) boundary cannot be explained by the coincident cooling interval alone. At the scale of temporal resolution available, these fossil data are inconsistent with an extended gradual pattern of extinction (linear-response) and are most consistent with either a non-linear response pattern for the K-T extinction, resulting from the accumulated stress of multiple long- and short-term environmental perturbations (e.g., climate change, sea-level regression, volcanism, an extraterrestrial impact), or a single, short-term cause (an extraterrestrial impact).

KEY WORDS: Late Cretaceous, Cretaceous-tertiary boundary, Mammals, Climate change, Relative abundance, Body size.

INTRODUCTION

The Cretaceous-Tertiary (K-T) mass extinction has been intensely studied and debated, especially during the past 30 years (Archibald, 1996; Sargeant and Currie, 2001). Recent studies that detail the paleoenvironment and biota leading up to this transition (Li and Keller, 1998a,b; Barrera and Savin, 1999; Pearson *et al.*, 2002; Wilf *et al.*, 2003) provide a means for evaluating competing hypotheses for the pattern (gradual vs. catastrophic) and mechanism (multiple vs. single) of this mass extinction.

High-resolution δ^{18}O data from benthic and planktic foraminifera in deep-sea and Tethyan continental shelf sediments indicate that paleotemperatures fluctuated considerably at the end of the Cretaceous (Li and Keller, 1998a; Barrera and Savin, 1999). This climatic instability was atypical for the Late Cretaceous in that it followed a long-term cooling trend from ~75 to 66.1 Ma (dates adjusted in Materials and Methods; Huber *et al.*, 2002). The general pattern of climatic instability indicates that an abrupt global cooling of 2–3°C from

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66.4 to 66.1 Ma was followed by a warming of 2–4°C from 66.1 to 65.7 Ma and a rapid cooling of 2–5°C from 65.7 to 65.58 Ma. The magnitude and absolute timing of these shifts in temperature vary with location, latitude, and paleo-ocean depth; however, the consistency of the general trends suggests that the climatic perturbations were global (Li and Keller, 1999; Stüben *et al.*, 2003). Substantial sea-level fluctuations (Li *et al.*, 2000; Adatte *et al.*, 2002), declining surface productivity ($\Delta\delta^{13}$C gradient; e.g., Li and Keller, 1998a,b; Keller *et al.*, 2002a), and changes in planktic foraminiferal species richness, relative abundances, and geographic ranges (Kucera and Malmgren, 1998; Keller *et al.*, 2002a) also accompanied these temperature shifts in various geographic regions. Pulses of Deccan trap volcanism in India from 69.5 to 64.5 Ma (Hoffman *et al.*, 2000) may have significantly increased levels of $p\mathrm{CO}_2$ and ultimately triggered the warming interval (Barrera and Savin, 1999; Nordt *et al.*, 2003).

Climatic proxy data from Hell Creek Formation megafloras in southwestern North Dakota confirm a latest Cretaceous cooling between 66.4 and 66.1 Ma, followed by a warming of 5–8°C between 66.1 and 65.7 Ma and a rapid cooling of 6–7°C that occurred during the 100,000 years (100 ky) before the K-T boundary (Wilf *et al.*, 2003). The warming interval is correlated with the boundary between the HCII to HCIII megafloral zones, which marks the extinction of megafloral taxa, the immigration of thermophillic megafloral taxa (Johnson and Hickey, 1990; Johnson, 2002), and fluctuating carbon isotopic values (Arens and Jahren, 2002). This general climatic pattern was also found using oxygen isotopic data from paleosol carbonates in Big Bend National Park, Texas (Nordt *et al.*, 2003). In sum, data from both marine and terrestrial realms suggest that global climatic perturbations and correlated biotic responses occurred prior to the K-T boundary.

Given these documented changes in Late Cretaceous climate, how might we expect mammalian communities to respond? Ecological and paleoecological studies indicate that mammals show measurable effects due to climatic change (Peters and Lovejoy, 1992; Vrba, 1995; Clyde and Gingerich, 1998). These effects may include local community changes in (1) taxonomic composition and (2) species richness due to extinction, extirpation, immigration, or speciation, (3) relative abundances of individuals within species due to shifts in important climatic parameters, and (4) body size or morphology (ecophenotypic or genetic) of individuals within species and of species within communities due to energetic considerations (Bergmann's Rule) or new competitive interactions introduced by changes in the climate regime.

Expanding on this work, Barnosky *et al.* (2003) analyzed mammalian change during four global warming episodes (Medieval Warm Period, two glacial-interglacial transitions, Mid-Miocene Climatic Optimum) that fall at the high end of the range but within background levels of climate change for the Cenozoic. They developed a generalized model for the predicted sequence of "normal" mammalian response to global warming that incorporates the rate, severity, and duration of the warming episode. First-order responses include "phenotypic and density changes in populations" (Barnosky *et al.,* 2003, p. 354). Second-order responses include "the extinction of species, noticeable changes in taxonomic composition of communities, and possibly reduction in species richness" (p. 354). Third-order responses include near-complete faunal turnover and eventually, speciation and accumulated faunal changes that may occur if the warming interval lasts 100 ky to 1 Ma. Here, I use the Barnosky *et al.* (2003) model to represent the "normal" mammalian response to background levels of climate change.

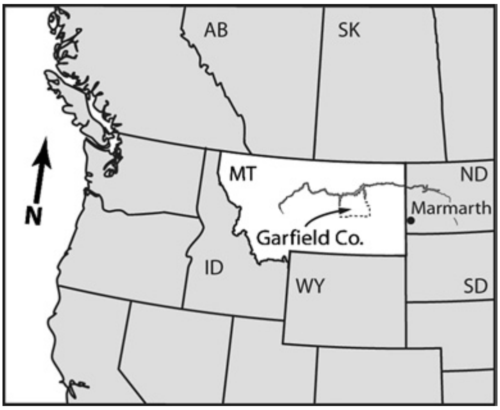

Fig. 1. Map of northwestern U.S.A. and southwestern Canada. Arrow indicates the study area in Garfield County, Montana, south of the Fort Peck Reservoir. Black dot indicates where the megafloral data of Wilf *et al.* (2003) occur in the area of Marmarth, North Dakota.

I investigated the mammalian response to climatic perturbations that occurred prior to the K-T boundary, using a well-documented and temporally constrained sequence of latest Cretaceous (Lancian North American land mammal "age") faunas from the Hell Creek Formation in Garfield County, Montana (Fig. 1; Archibald, 1982; Clemens, 2002; Wilson, 2002). Specifically, I assessed local changes in taxonomic composition, species richness, relative abundances, and mean individual body size through the formation, as they relate to climatic change during the final 1.8 million years of the Cretaceous. The aims of this study are (1) to determine whether biotic changes leading up to the K-T boundary are distinct from "normal" mammalian responses to background levels of climate change [i.e., the Barnosky *et al.* (2003) model] and (2) to relate these findings to predictions from the hypotheses for the K-T mass extinction and the results from similar efforts in the Hell Creek Formation (Pearson *et al.*, 2002; Wilf *et al.*, 2003).

MATERIALS AND METHODS

Mammalian Fossil Database

The fossil database of this study contains mammalian specimens identifiable to species, mainly jaw fragments and isolated teeth, from localities that were both surface collected and screen washed and occur in a detailed local stratigraphic framework. All specimens are housed in the University of California Museum of Paleontology (UCMP). Stratigraphic and lithologic data were compiled from Archibald (1982, Table I), UCMP field notes, and field measurements and observations (Wilson, 2004). Stratigraphic data recorded as ranges (e.g., 20–24 m above the Fox Hills-Hell Creek formational contact) were converted to averages (e.g., 22 m). The resulting fossil database consists of 1,471 specimens from 79 localities that broadly sample the Hell Creek Formation across ~60 km of Garfield County, Montana and 44 distinct horizons from 79 m of the 93-m total thickness of the formation. Sampling intensity is greatest in the uppermost Hell Creek Formation (>61 m; Fig. 2A, gray shade),

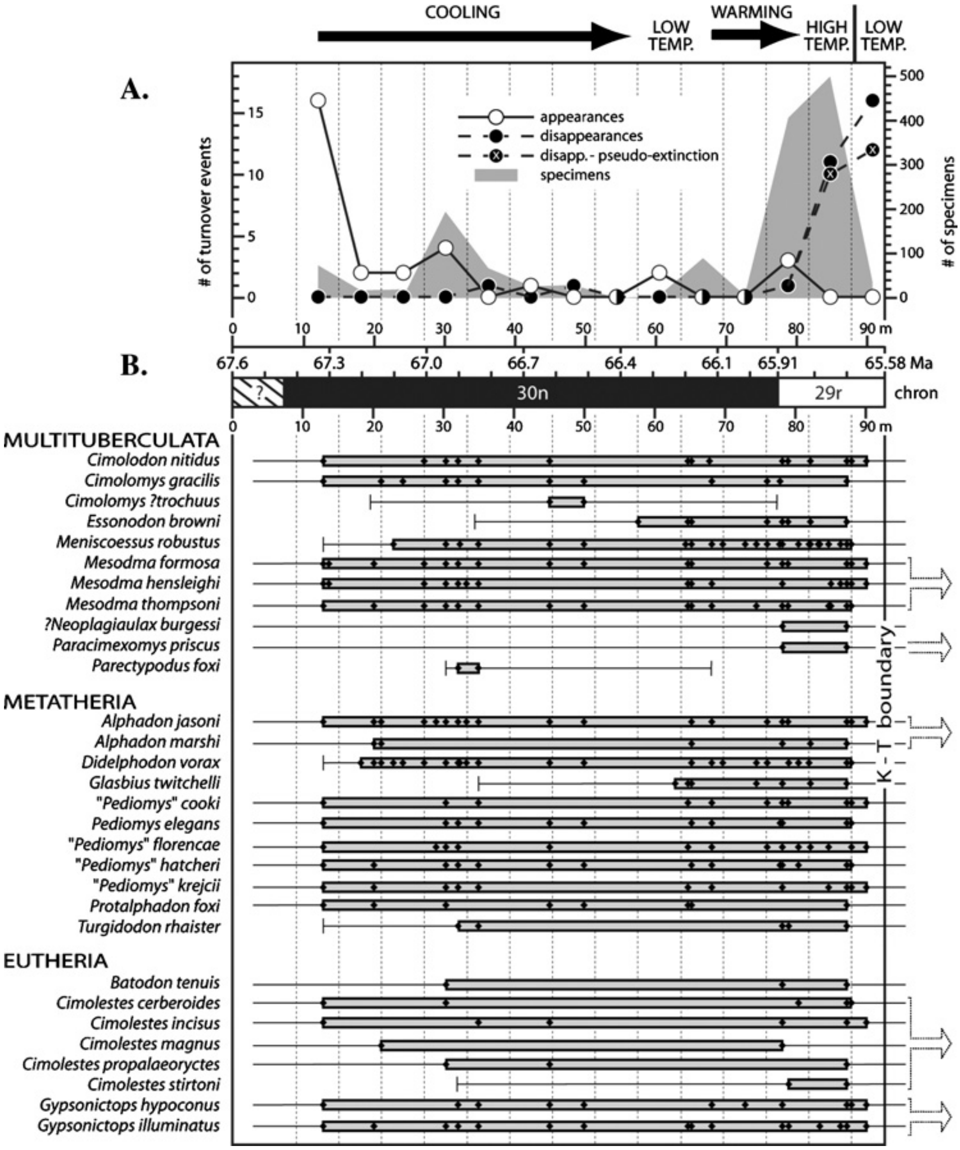

Fig. 2. Faunal turnover (A) and biostratigraphic ranges (B) for mammalian species through the Hell Creek Formation in Garfield County, Montana. Vertical dotted lines mark the 6.1-m stratigraphic intervals. (A) Black dots with an "x" for the last two intervals indicate alternate estimates for the number of disappearance events excluding hypothesized pseudo-extinction events (Weil and Clemens, 1998; Clemens, 2002). Gray shaded areas represent the number of identifiable specimens per stratigraphic interval. (B) Black diamonds represent species occurrences at that stratigraphic horizon. Thin lines with cross-bars represent the 50% stratigraphic confidence intervals. Thin lines without cross-bars indicate that the 50% stratigraphic confidence intervals extend beyond the sampled interval (see Materials and Methods). Dotted arrows indicate that the lineages may have persisted (pseudo-extinction or survivors) into the Paleocene of Garfield County. Climatic trends are from megafloral (Wilf *et al.*, 2003) and marine proxy data (e.g., Li and Keller, 1998a) and are further detailed in Figure 4A, B.

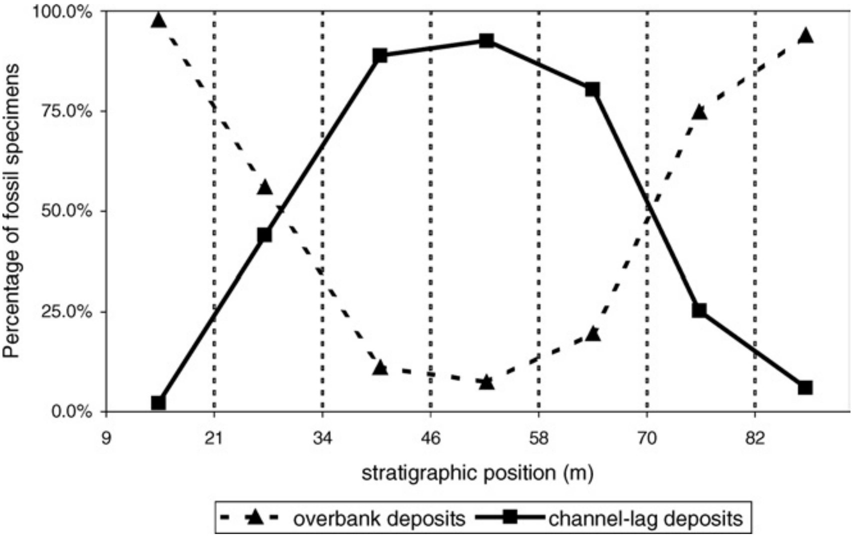

Fig. 3. Graph of the percentage of mammalian fossil specimens collected from channel-lag and overbank deposits through the Hell Creek Formation (Garfield County).

though recent collecting efforts have improved the sampling intensity lower in the section (The Hell Creek Project 1998–2003; see Wilson, 2002). Mammalian fossils have not been recovered from the lowest 10 m or highest 2.5 m of the formation. Localities derive from channel-lag and overbank deposits (Fig. 3).

Chronostratigraphic Framework

To correlate this stratigraphic section with the global record, a chronostratigraphic framework was developed from (1) a revised radiometric date of 65.58 ± 0.04 Ma for the local K-T boundary (IrZ-Coal in Garfield County; Swisher *et al.*, 1993; Renne *et al.*, 1998; Knight *et al.*, 2003 erratum); (2) magnetostratigraphic data from multiple sections in Garfield and adjacent McCone Counties, which record the magnetochron C30n to C29r transition ~15 m below the local K-T boundary (Archibald *et al.*, 1982; Swisher *et al.*, 1993); (3) a ~333 ky duration for the Cretaceous part of magnetochron C29r, based on precessional chronometry (D'Hondt *et al.*, 1996); (4) a 45 m/my sedimentation rate, based on the dates for the K-T boundary and the lower boundary of magnetochron C29r and the stratigraphic distance between these data; and (5) an estimated depositional duration of 2.1 Ma for the Hell Creek Formation, based on a linear stratigraphic extrapolation of the sedimentation rate (Wilson, 2004; also see Hicks *et al.*, 2002) and an estimated thickness of 93 m for the formation (N. C. Arens, personal communication 2002). In fluvial depositional environments, the assumption of a linear relationship between stratigraphic thickness and time is problematic (Kidwell and Holland, 2002), though less so on the time scales considered here (Kirchner *et al.*, 2001). Dates derived from extrapolation methods are provisional and most accurate within magnetochron C29r.

Localities were incorporated into the framework based on stratigraphic distance above the Fox Hills-Hell Creek formational contact. In central Garfield County, the top of the

Hell Creek Formation (the base of the IrZ-Coal) is coincident with the K-T boundary (i.e., iridium anomaly, shock mineral grains; see Clemens, 2002). For the most part, the time transgressive nature of the Hell Creek-Tullock formational contact has little effect at the geographic and temporal resolution used here (Garfield County, 6.1-m and 12.2-m intervals) except that earliest Paleocene faunas from the top meter of the formation in easternmost Garfield County are excluded. Climatic proxy data (Li and Keller, 1998a; Wilf *et al.*, 2003) and megafloral data (Wilf *et al.*, 2003) were incorporated into this framework, adjusting for differences in the dates for magnetochron boundaries and the K-T boundary.

Paleoclimate Record

Although climate consists of a suite of variables (e.g., seasonality, precipitation, humidity), climatic proxy data for the latest Cretaceous is largely restricted to mean annual temperatures, a coarse proxy for other climatic variables. Paleotemperatures were obtained from the published literature. Paleotemperatures from megafloral data (leaf-margin analysis) in North Dakota (Wilf *et al.*, 2003) may represent more coastal environments than those of northeastern Montana, but provide the best available estimate of climatic conditions in northeastern Montana (Fig. 1). Because these data were only available for the interval from 66.6 to 65.58 Ma, the paleoclimate record before 66.6 Ma was supplemented by paleotemperature trends inferred from marine $\delta^{18}O$ records. Marine proxies are sub-optimal estimates of continental paleotemperatures, but accurately reflect global trends of increasing or decreasing paleotemperatures. The record from the mid-latitude South Atlantic DSDP Site 525A (Li and Keller, 1998a) is appropriate because it densely samples the temporal interval of interest and it is from a paleolatitude similar to that of northeastern Montana.

Taxonomic Composition

Changes in taxonomic composition through time (Badgley and Gingerich, 1988) are represented by a tabulation of biostratigraphic ranges (Fig. 2B) compiled from all localities in the fossil database. Turnover events (Fig. 2A) are inferred from assessing first and last appearances of species in each 6.1-m (20-ft.) stratigraphic interval. A species was considered present in a stratigraphic interval if it occurs in a locality from that stratigraphic interval (true occurrence) or in localities both above and below that stratigraphic interval (range-through occurrence). A range-through occurrence implies that the species absence from the stratigraphic interval is more likely due to sampling error than to true short-term absence (i.e., emigration or local extinction and subsequent re-immigration), though this may not apply in all cases. The range-through method may produce edge effects, including an artifactually higher number of appearances and disappearances at the beginning and end of the stratigraphic range, respectively, where the method cannot be applied (Foote, 2000). Here, the extent of these effects is reduced because fossil localities near the bottom and top of the Hell Creek Formation are fairly well sampled (Fig. 2A, gray shade). All species are documented in at least two stratigraphic intervals (i.e., no singletons).

The accuracy of an observed biostratigraphic range is limited by sampling intensity at the ends of the true biostratigraphic range (Badgley and Gingerich, 1988) and the true relative abundance of the species (McKinney, 1996). Confidence intervals were calculated for the endpoints of the observed ranges based on the distribution of fossil localities and number of specimens recovered within the local section, using Wilf and Johnson's

(2004) expansion of the Strauss and Sadler (1989) method. The original Strauss and Sadler (1989) method assumes a random distribution of localities; Wilf and Johnson's calculations incorporate "fossil recovery potential functions" (FRPF's; Marshall, 1997), which specify potential for fossil recovery as a function of stratigraphic position. Labandeira *et al.* (2002b) and Wilf and Johnson (2004) developed FRPF's from the number of identifiable specimens per stratigraphic interval. Using this method, confidence intervals for biostratigraphic ranges adjacent to well-sampled parts of a stratigraphic section are smaller than those calculated from a random distribution method.

I calculated the 50% confidence intervals for the observed ranges with an FRPF based on the number of identifiable specimens per stratigraphic horizon (Fig. 2A, gray shade). Confidence intervals for the tops and bottoms of biostratigraphic ranges were calculated separately (two one-tailed calculations), but are shown together (Fig. 2B). Some confidence intervals extend indefinitely below the sampled interval or indefinitely beyond the K-T boundary (no cross-bar). For example, when the last appearance of a taxon occurred in the highest sampled stratigraphic horizon in the Hell Creek Formation, the 50% confidence intervals were not calculated because the numbers of identifiable specimens from horizons in the overlying Tullock Formation have not been accurately tabulated. Nevertheless, sampling intensity in the lower Tullock Formation is such that confidence intervals likely fall within the first few meters of the formation.

Species Richness

Species-richness data are plotted in Fig. 4C with estimated paleotemperatures (Fig. 4A and B; Li and Keller, 1998a; Wilf *et al.*, 2003) and megafloral species richness values from North Dakota (Fig. 4B; Wilf *et al.*, 2003). Mammalian species richness values were calculated as (1) the raw numbers of species per locality (black dots); (2) the number of range-through species per stratigraphic horizon (black line); and (3) the expected number of species per 12.2-m (40-ft.) stratigraphic interval based on analytic rarefaction (gray diamonds). Hereafter, specific 12.2-m stratigraphic intervals are rounded to the nearest meter. The range-through method follows the protocol used for the tabulation of turnover events and biostratigraphic ranges, except that it is applied to each stratigraphic horizon. Sample sizes from most 6.1-m stratigraphic intervals were too small for meaningful comparisons; so 12.2-m stratigraphic intervals (270 ky/interval) were used instead. The 46–58-m interval contains only 29 specimens and was excluded. The other samples were rarefied to the sample size of the 34–46-m interval (90 specimens), using the software program Analytic Rarefaction 1.3 (Holland, 2003), which is based on an analytic solution (Raup, 1975; Tipper, 1979). The individual rarefaction curves are presented in Fig. 5.

Relative Abundances

Relative abundances were determined by dividing the number of identifiable specimens per species by the total number of specimens in the sample for each stratigraphic interval (NISP method). This method is appropriate because the fossil samples derive from deposits with low probability of association (e.g., channels, crevasse splays; Badgley, 1986). Paleoecological comparisons using relative-abundance data ideally involve individual localities with similar taphonomic biases (e.g., Behrensmeyer *et al.*, 1992; Blob and Fiorillo,

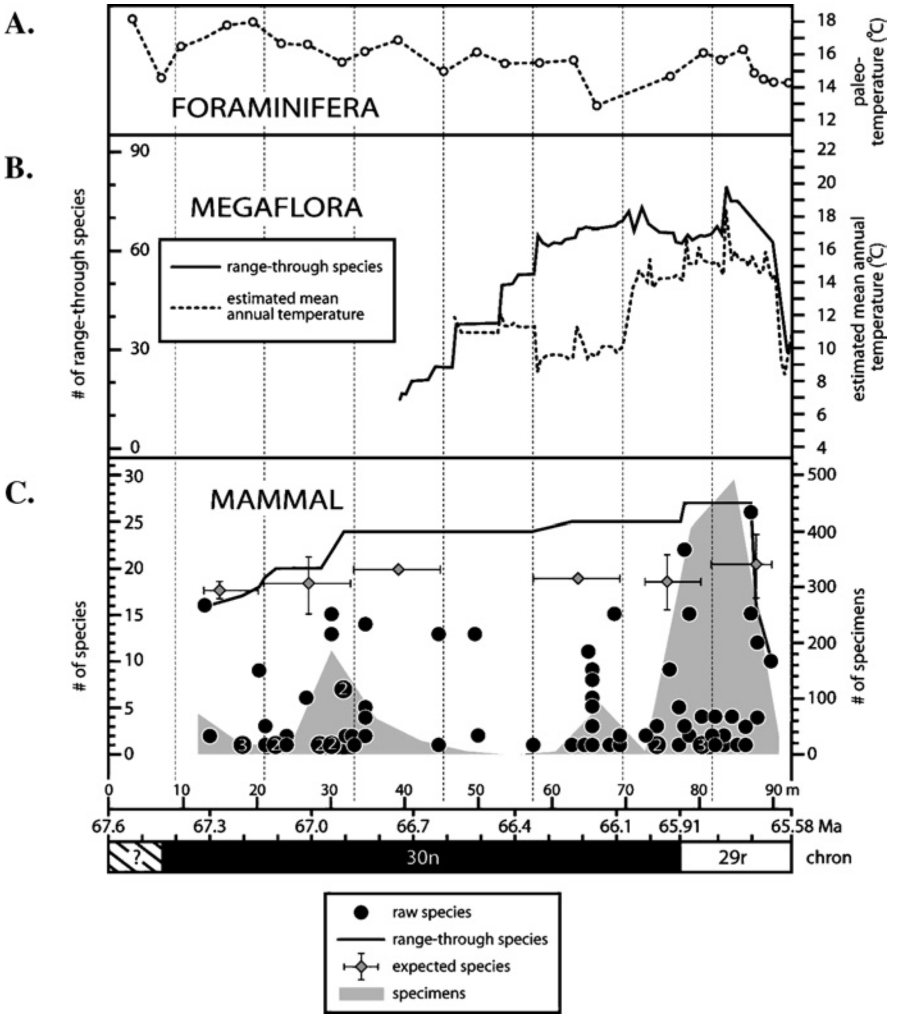

Fig. 4. (A) Surface water paleotemperatures at the mid-latitude South Atlantic DSDP Site 525A (dotted line with open circles) inferred from marine δ^{18}O records of the planktic foraminifera *Rugoglobigerina rugosa* (redrawn from Li and Keller, 1998a). (B) Estimated mean annual temperatures (dotted line) and megafloral species richness represented as the total number of range-through morphospecies (black line) through the Hell Creek Formation in the vicinity of Marmarth, North Dakota (redrawn from Wilf *et al.*, 2003). Dates for planktic foraminifera (A) and megafloral (B) data were adjusted according to Materials and Methods. (C) Mammalian species richness through the Hell Creek Formation in Garfield County, Montana represented by raw numbers of species per locality (black dots), total number of range-through species per stratigraphic horizon (black line), and expected number of species per 12.2-m stratigraphic interval (gray diamonds) for $n = 90$ specimens. Numbers inside black dots indicate that a stratigraphic horizon has multiple localities with the same raw number of species. For expected number of species, vertical bars represent 95% confidence intervals and horizontal bars represent the stratigraphic range of the data. Gray shaded areas represent the number of identifiable mammalian specimens per 6.1-m stratigraphic interval.

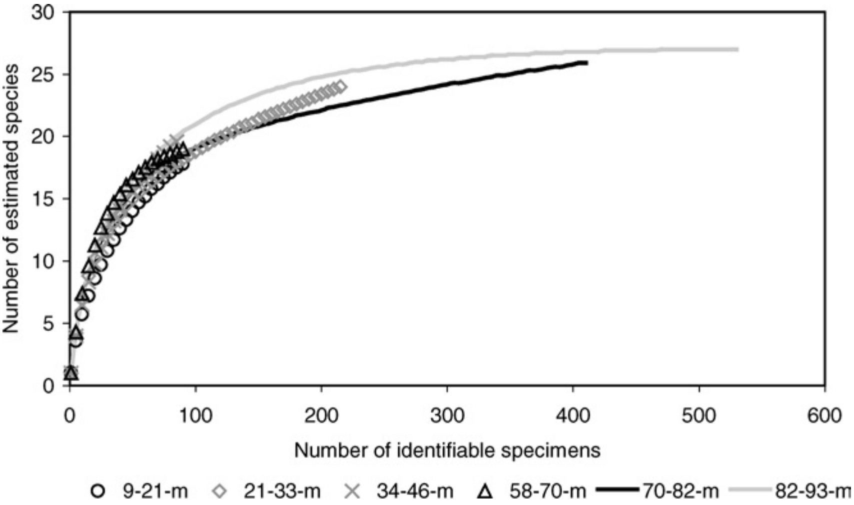

Fig. 5. Rarefaction curves for mammalian fossil samples from six 12.2-m stratigraphic intervals through the Hell Creek Formation (Garfield County). The 46–58-m stratigraphic interval was excluded due to its small sample size (29 specimens). Curves were generated using the software program Analytic Rarefaction 1.3 (Holland, 2003).

1996), but uneven sampling intensity and sampling of depositional environments through the formation rendered this approach impractical. Instead, individual localities were pooled together into 12.2-m stratigraphic intervals. This approach may cause taphonomic concerns, as 85% of specimens from the middle of the formation (34–70 m) derive from channel-lags and 87% of specimens from the bottom (9–21 m) and top of the formation (70–82, 82–93 m) derive from overbank deposits (Fig. 3).

To assess these taphonomic concerns, localities within each interval were separated into depositional-environment subsamples (channel-lag or overbank deposit). The relative abundances of species between subsamples were compared in the intervals (21–34, 70–82 m) that had a minimum of 90 specimens from both depositional environments. For these samples, "species × depositional environment" contingency tables were constructed, with cells in the tables containing specimen counts for each species in each depositional environment. The null hypothesis that the relative abundances of species are the same across depositional environments was tested using a Likelihood Ratio Chi-Square Test and a Pearson Chi-Square Test from JMP IN® software version 4.04. To reduce Type I errors, rare taxa were eliminated from the contingency tables until less than 20% of the cells had expected counts less than five (the Cochran criterion) and the average expected count for the entire table was at least 6.0 (Zar, 1999, pp. 504–505).

For the 21–34-m interval, no significant differences (Likelihood Ratio $\chi^2_{0.05,\,8} = 14.532$, $p = 0.0689$; Pearson $\chi^2_{0.05,\,8} = 14.071$, $p = 0.0799$) were found between the depositional-environment subsamples, so the null hypothesis could not be rejected. Nevertheless, because p values were low, observed counts and expected counts for each species were inspected. The two major deviations that were found are counter to predictions based on hydrodynamic sorting and may not be cause for concern in this stratigraphic interval. That is, hydrodynamic sorting would predict that the smaller-sized teeth of *Mesodma* *formosa* ($M1$ length = 2–3 mm) would have an observed count from the coarser-grain overbank deposits that was lower, not higher, than expected based on the pooled subsamples. It would also predict that the larger-sized teeth of *Cimolomys gracilis* ($M1$ length = 5–7 mm) would have an observed count from the finer-grain overbank deposits that was lower, not higher, than expected based on the pooled subsamples.

For the 70–82-m interval, significant differences (Likelihood Ratio $\chi^2_{0.05,7} = 53.580$, $p < 0.0001$; Pearson $\chi^2_{0.05,7} = 54.999$, $p = 0.0001$) were found between the depositional-environment subsamples, so the null hypothesis was rejected. Specifically, the observed counts of *Meniscoessus robustus*, a multituberculate with relatively large teeth ($M1$ length = 7–10 mm), showed a large deviation from the expected count based on the pooled subsamples that is consistent with hydrodynamic sorting. That is, for the subsample from coarser-grain channel-lag deposits, the observed count of *Meniscoessus robustus* was greater than expected based on the pooled subsamples, and vice versa for the finer-grain overbank deposit subsample.

However, if hydrodynamic sorting were driving the relative abundance patterns, one might expect subsamples from a single depositional environment (e.g., channel-lag deposits) to show little or no significant differences through the formation, assuming that grain size differs little among localities. For the four stratigraphic intervals (21–34, 34–46, 58–70, 70–82 m) with channel-lag subsamples of at least 74 specimens, "species × stratigraphic interval" contingency tables were constructed, with cells containing specimen counts for each species in a stratigraphic interval. The null hypothesis is that the relative abundances of individuals within species from channel-lag deposits are the same across stratigraphic intervals. Significant differences (Likelihood Ratio $\chi^2_{0.05,21} = 132.356$, $p < 0.0001$; Pearson $\chi^2_{0.05,21} = 122.427$, $p < 0.0001$) were found between the subsamples from the four stratigraphic intervals, so the null hypothesis was rejected, suggesting that the differences between stratigraphic intervals are not simply a function of depositional environment sampled. Further, the stratigraphic patterns of relative abundances generated from these isotaphonomic subsamples strongly resemble those generated from the pooled samples.

Thus, the degree to which taphonomic processes have affected the relative abundance data is unclear. Combining the subsamples from channel-lag and overbank deposits for each stratigraphic interval may dampen or accentuate the signal from a depositional environment, but it seems to reliably reflect the trends for each taxon (increasing or decreasing relative abundance). Also, the effects of differential size sorting between non-isotaphonomic localities are reduced among fossils of a narrow size (1–11 mm) and shape range, such as the Late Cretaceous mammal teeth in this study (Blob and Fiorillo, 1996). In sum, pooling samples from different depositional environments was considered acceptable for tracking general trends in the relative abundances of mammalian species leading up to the K-T boundary.

Relative abundances are represented as percentages and ranks (Fig. 6). The use of rank-order abundance minimizes effects due to variation in the abundance of the most common taxa (Brinkman, 1990) and the depositional environment sampled. Studies of extant communities suggest that common species tend to show the least spatial-temporal variation in abundance (Maurer, 1994; Brown, 1995), thus providing a more conservative measure of change through time. A species was considered common if it fell in the top abundance quartile in at least one stratigraphic interval (the quartile definition, Gaston,

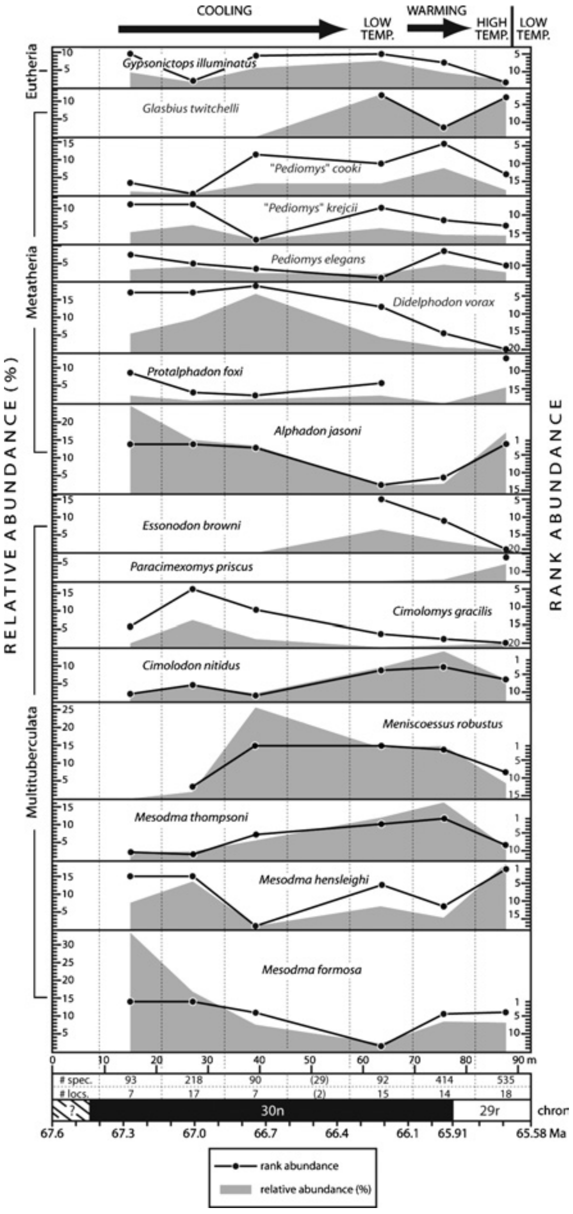

Fig. 6. Relative abundances represented as ranks (line and dots) and percentages (gray) for the common mammalian species (i.e., 16 of the 30 species) through the Hell Creek Formation in Garfield County, Montana (see Materials and Methods). The number of identifiable specimens per stratigraphic interval (12.2 m) and number of localities per interval are provided at the bottom. The number of identifiable specimens for the 46–58-m stratigraphic interval was small and excluded from the analysis. Climatic trends are from megafloral (Wilf *et al*., 2003) and marine proxy data (e.g., Li and Keller, 1998a) and are further detailed in Fig. 4A and B.

1994). Although relative abundances were calculated for all taxa, only those for the common species (i.e., 16 of 30 species) are illustrated in Fig. 6. Significance of secular changes in relative abundances of mammalian species was determined using a Likelihood Ratio Chi-Square Test and a Pearson Chi-Square Test from JMP IN® software version 4.04.

Mean Individual Body Size

Mean individual body size, which measures the numerical importance of different-sized species in a sample (Clyde and Gingerich, 1998), was calculated by summing the body size of each individual in a 12-m stratigraphic interval and dividing by the total number of individuals in that interval. Another informative measure, mean species body size, was not calculated because taxonomic composition changed little through the formation.

Body size can be estimated in extinct mammals via regression equations that relate molar area to body mass in living mammals. I used taxon-specific lower first molar (*m*1) regression equations whenever possible (for eutherians, Bloch *et al.*, 1998; for metatherians, Gordon, 2003), however, multituberculates have no living representatives from which to develop such an equation. Nevertheless, results from McDermott *et al.* (2002) suggest that the *m*1 regression equation for all mammals (Legendre, 1989) may provide a reasonable estimate of body mass for multituberculates.

The *m*1 areas were calculated for most species in the Hell Creek Formation from averages of length and width measurements of specimens in the fossil database. For a few species, *m*1's were either unavailable for measurement or unknown, in which case measurements were taken from the published literature (Clemens, 1964, 1973; Lillegraven, 1969) or estimated from the size of other tooth positions. For example, because the lower fourth premolars of *Neoplagiaulax burgessi* and *Mesodma formosa* are similar in size, I assumed that their m1's are also similar in size. The *m*1 areas for each species were used to calculate body mass estimates for individuals in samples from each 12.2-m stratigraphic interval. Because sample sizes are small and measurements are not available for all specimens, intra-species changes in body size were not considered here. Mean individual body sizes were also calculated for *Mesodma* and *Pediomys* to investigate intrageneric patterns of body sizes through time. The results with their 95% confidence intervals are presented in Fig. 7.

RESULTS AND DISCUSSION

Taxonomic Composition

The biostratigraphic range chart (Fig. 2B) illustrates that most of the 30 mammalian species persist throughout the Hell Creek Formation, providing few indications of change in taxonomic composition before the K-T boundary (Wilson, 2002).

However, the 50% stratigraphic confidence intervals for the multituberculate *Essonodon browni* and metatherian *Glasbius twitchelli* suggest that the absence of these species from the lower part of the Hell Creek Formation (Fig. 2B) is not sampling artifact. Their relative abundances in the upper part of the Hell Creek Formation (average rank = 12.3, 5.7, respectively; Fig. 6) further suggest that sample sizes in the lower part of the Hell Creek Formation are sufficient to document their occurrence, if present in similar abundances. Isolated teeth of *Essonodon browni* are also large by Late Cretaceous standards (*M*1 length

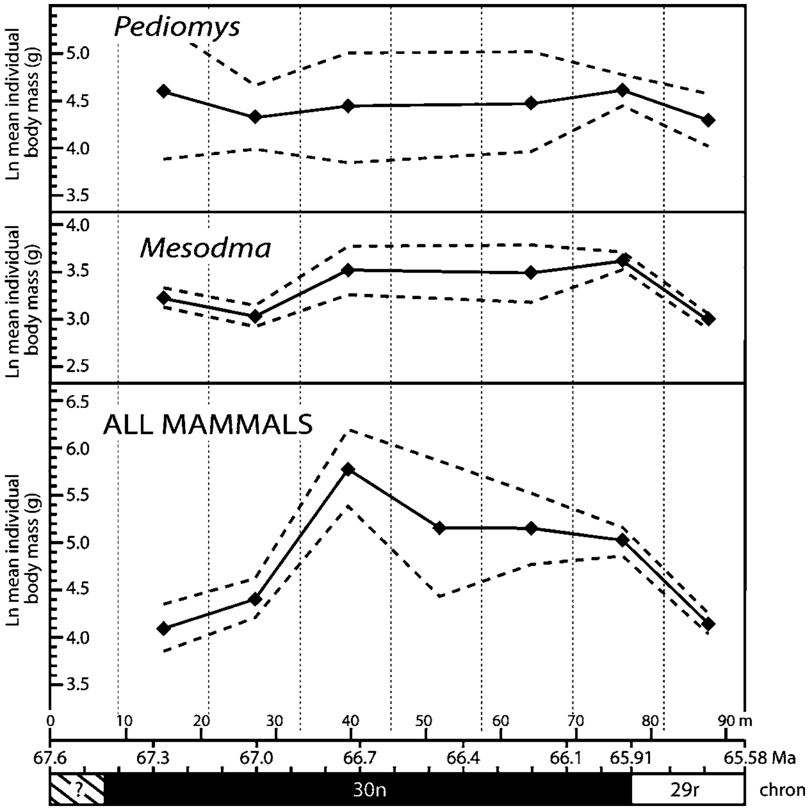

Fig. 7. Mean individual body size for all mammalian species, for species of *Mesodma*, and for species of *Pediomys* through the Hell Creek Formation in Garfield County, Montana. Vertical dotted lines mark the 12.2-m stratigraphic intervals. Bold dashed lines represent the 95% confidence intervals. Body mass estimates were calculated as described in the Materials and Methods.

~7.5 mm), and both taxa have distinctive dental morphologies, such that fragmentary specimens are easily identified.

Two multituberculates (*Cimolomys ?trochuus*, *Parectypodus foxi*) are documented by only four specimens, but their 50% stratigraphic confidence intervals also suggest that their absence from the upper part of the formation (Fig. 2B) is not sampling artifact. By contrast, the restricted biostratigraphic ranges of the eutherian *Cimolestes magnus* and metatherian *Turgidodon rhaister* are likely sampling artifacts.

The multituberculate *Paracimexomys priscus* has only been recovered from three localities (Fig. 2B), but in two of them, it ranks relatively high in abundance (rank = 7, 6; Fig. 6). Its restricted stratigraphic range in the upper part of the formation co-occurs with that of the multituberculates *?Neoplagiaulax burgessi* and eutherian *Cimolestes stirtoni*, but the stratigraphic confidence intervals for *P. priscus* and *?N. burgessi* extend to the bottom of the formation.

The stratigraphic distribution of some or all of these rare taxa may expand with increased sampling intensity, but their restricted biostratigraphic ranges may also be climate related. Although a causal link rarely can be proven in natural environments, ecologists (Peters and Lovejoy, 1992) and paleontologists (Graham, 1992; Vrba, 1995; Clyde and Gingerich, 1998) have accumulated data that strongly suggest that mammal species alter abundances within local populations as a first-order response to climatic change, and through that process change their geographic ranges. Depending on the climatic tolerances of individuals within species and the tolerances of the biota upon which they depend (e.g., plants), geographic ranges of mammalian species contract, expand, shift, or exhibit no change at all. While climate consists of a suite of variables (e.g., seasonality, precipitation, humidity), here it is necessarily generalized to mean annual temperatures. As mean annual temperatures increased, one might expect that some warm-adapted species from southerly regions expanded or shifted their geographic ranges northward, perhaps resulting in first appearances in northeastern Montana; whereas some cool-adapted species contracted or shifted their geographic ranges northward, perhaps resulting in extirpation from northeastern Montana; and vice versa as mean annual temperatures decreased (Vrba, 1995).

For example, a possibility is that the taxa absent from the upper part of the Hell Creek Formation (*Cimolomys ?trochuus*, *Parectypodus foxi*) were cool-adapted and had climatic-tolerance thresholds that forced them to shift their geographic ranges northward in response to the warming interval 500 ky before the K-T boundary. Interestingly, these taxa are otherwise only known from two Lancian local faunas, both from Canada (Trochu and Gryde local faunas) and one (Trochu) known to be younger than the occurrences in Montana (Lillegraven, 1969; Lerbekmo, 1985; Storer, 1991). This geographic and temporal relationship is consistent with a climatically driven geographic range shift. This interpretation is also consistent with Bergmann's rule (Searcy, 1980), which would predict a northward range shift for the larger body-size *Cimolomys ?trochuus* while the smaller body-size, more common congener *Cimolomys gracilis* persisted in Montana during the warming interval. Denser geographic and temporal sampling of vertebrate faunas is needed before this interpretation can be considered more than exploratory.

The pattern of mammalian faunal turnover through the Hell Creek Formation (Fig. 2A) documents the appearance of 16 species in the first 6.1-m stratigraphic interval (9–15 m), followed by the modest appearance of two, two, and four species in successive intervals that are likely attributable to an edge effect. Subsequent intervals record additional appearance events (40–45, 58–64, 76–82 m) with the largest bringing three taxa. Curiously, the 82–88-m stratigraphic interval has the largest sample size (Fig. 2A, gray shade), but does not record a first appearance event, suggesting that (1) appearances are not driven by sample size alone and (2) species did not accumulate up until the mass extinction at or near the K-T boundary.

Disappearance events occur infrequently through the Hell Creek Formation (Fig. 2B). *Parectypodus foxi* and *Cimolomys ?trochuus* disappear before the upper part of the formation, while 27 of the remaining 28 species disappear in the upper 5 m of the formation (i.e., last ∼115 ky of the Cretaceous). More precisely, 11 disappear in the 82–88-m interval and 16 disappear in the 88–93-m interval, a pattern which is consistent with a stepwise extinction or extirpation or both prior to the K-T boundary and correlated with the rapid cooling from 65.7 to 65.58 Ma. However, caution must accompany interpretations, as pseudo-extinction artificially inflates the number of disappearances in the upper 5 m of the formation (Archibald, 1993, 1996). At least five Cretaceous lineages that seem to disappear actually persist into the Paleocene of Garfield County as descendant species (Archibald, 1993; Weil and Clemens, 1998). Conversely, low sampling intensity in the upper 5 m of the formation (36 specimens) suggests that edge effects or the Signor-Lipps effect may mask a pattern of disappearance that is concentrated even higher in the section and indicative of a sudden not gradual extinction.

Species Richness

The pattern of mammalian species richness (Fig. 4C) is positively correlated with that from the North Dakota megafloral data (Fig. 4B; Wilf *et al.*, 2003), but differences between datasets may affect interpretations. Whereas the megafloral data, which were arranged into 1-m intervals, provide greater temporal resolution than the mammalian data, the mammalian data extend deeper into the latest Cretaceous than the megafloral data (67.3 Ma vs. 66.7 Ma). Consequently, the pattern of megafloral species richness before 66.3 Ma may be subject to edge effects (Wilf *et al.*, 2003). For the mammalian range-through data, edge effects are probably negligible after 66.9 Ma. In both datasets, sampling intensity is greatest near the K-T boundary. Wilf and Johnson (2004) accounted for this possible bias through rarefaction analysis, as was done with the mammalian data (Fig. 4, gray diamonds).

Although an interesting correspondence exists between raw counts, range-through data, and megafloral data (Fig. 4B and C), the peak in mammalian species richness by these metrics reflects the larger sample sizes in the highest stratigraphic intervals. Adjusting for this imbalance through rarefaction analysis produces rarefaction curves for these intervals (70–82, 82–93 m) that begin leveling off at 200–300 specimens (Fig. 5). The rarefaction curves for other intervals have strongly positive trajectories, indicating that these intervals will likely accumulate new species with further sampling. When sample sizes are set to 90 specimens, the expected number of mammalian species for each interval (Fig. 4C, gray diamonds) does not support the pattern illustrated by the raw counts and range-through data. Instead, the expected number of mammalian species ranges from 17.7 to 20.3 species and in most cases, the 95% confidence intervals clearly overlap. Thus, there is little statistical evidence that mammalian species richness changed during the sampled interval in northeastern Montana, results which agree with Alroy *et al.* (2000) and Barnosky and Carrasco (2002), who found little correlation between global temperature change and species richness during other temporal intervals.

Relative Abundances and Mean Individual Body Size

Relative abundances (Fig. 6) fluctuated significantly leading up to the K-T boundary (Likelihood Ratio $\chi^2_{0.05,50} = 554.121$, $p < 0.0001$; Pearson $\chi^2_{0.05,50} = 537.118$, $p < 0.0001$). A conspicuous pattern among both ranks and percentages is that some species (e.g., *Meniscoessus robustus*, *Mesodma thompsoni*, *Didelphodon vorax*) have relative abundances that are high in one or more middle stratigraphic intervals (34–46, 58–70, 70–82 m) and low in the lower- and uppermost stratigraphic intervals (9–21, 21–34, 82–93 m). Other species (e.g., *Mesodma formosa*, *Mesodma hensleighi*, *Alphadon jasoni*) show the complementary pattern. The correspondence between these data and the climatic proxy data (Fig. 4A and B) suggest that changes in relative abundances of mammalian species co-occur with changes in temperatures leading up to the K-T boundary. Wilf *et al.* (2003) did not present climatic proxy data corresponding to the first three stratigraphic intervals used here; so high-resolution marine climatic proxy data (Li and Keller, 1998a, Fig. 12) were substituted. The dramatic cooling from 65.7 to 65.58 Ma that corresponds to the upper part of the 82–93-m stratigraphic interval is largely ignored because most fossil specimens in the mammalian database were collected in the lower half of this interval, corresponding to a warm period.

Similar patterns of co-occurring shifts in paleotemperature and relative abundances have been documented in a variety of communities and on a variety of time scales (Hadly, 1997; Barnosky *et al.*, 2003) and have commonly been interpreted as responses to climate change. The pattern of fluctuating relative abundances of mammalian species through the Hell Creek Formation may be similarly interpreted. From an ecological standpoint, it follows that species with high relative abundances between 66.9 and 65.8 Ma (34–46, 58–70, 70–82 m) likely thrived in cooler climates; whereas those with high relative abundances between 67.4 and 66.9 Ma (9–21, 21–34 m) and between 65.8 and 65.58 Ma (82–93 m) likely thrived in warmer climates.

Mean individual body size results are consistent with these inferences (Fig. 7). During cool intervals, a substantial proportion of species with high abundances of individuals were of large-body size relative to other latest Cretaceous mammals (e.g., *Meniscoessus robustus*, *Didelphodon vorax*) and vice versa during warm intervals. This pattern follows Bergmann's rule, which recognizes a negative correlation between temperature and body size (Searcy, 1980). Similarly, among species of *Mesodma*, the largest in size, *M. thompsoni*, was most abundant during cool intervals, whereas the smallest in size, *M. hensleighi*, was most abundant during warm intervals. The pattern for species of *Pediomys* is inconclusive.

Alternative explanations for the relative abundance and mean individual body size patterns cannot be excluded. A shift in the depositional environment sampled (Fig. 3) co-occurs with the shifts in relative abundances, mean individual body size, and paleotemperatures. If hydrodynamic sorting differentially affected samples from the two depositional environments, the shift in dominant depositional environment sampled, not the shift in paleotemperatures, may explain the pattern of fluctuating relative abundances and mean individual body size. Nevertheless, this taphonomic concern does not appear to drive the observed patterns, as subsamples from channel-lag deposits yield a pattern of fluctuating relative abundances resembling that from the pooled data (see Materials and Methods). However, because sample sizes are small and other taphonomic differences may exist through the section (e.g., agents of mortality; geographic area sampled; fossil material surface collected versus screen washed), the temporal patterns of relative abundances and mean individual body size must be approached with caution.

Patterns of increasing or decreasing relative abundance for higher mammalian taxa (multituberculates, metatherians, eutherians) were not identified, suggesting that foreshadowing of metatherian extinction at the K-T boundary and eutherian diversification following the K-T boundary is not evident in the Hell Creek Formation (Garfield County).

Comparisons with Mammalian Response to Background Levels of Climate Change

These results demonstrate that there may be temporal changes in mean individual body size, relative abundances of species, and to some extent taxonomic composition within the Late Cretaceous mammalian fauna of the Hell Creek Formation (Garfield County). Intriguingly, some of these biotic changes co-occur with shifts in paleotemperature proxies. Before exploring the broader implications of these data, it is important to determine whether these changes differ from "normal" mammalian responses to background levels of climate change. According to the Barnosky *et al.* (2003) model, changes in mean individual body size and relative abundances of mammalian species leading up to the K-T boundary are consistent with "normal" first-order responses to background levels of climate change (see Introduction). Similarly, minor changes in mammalian taxonomic composition are consistent with "normal" first- or possibly second-order responses to background levels of climate change.

The extinction or pseudo-extinction of up to 27 species at or near the K-T boundary (65.7–65.58 Ma) is a different situation. Sampling issues (e.g., Signor-Lipps effect) render the apparent step-wise pattern (Fig. 2A) indistinguishable from one of sudden extinction at the K-T boundary, but in either case, the turnover is beyond the predicted biotic response to background levels of climate change. At best, it would be consistent with a third-order response to climate change of considerable magnitude, rate, and duration (see Introduction). However, the actual climate change does not match that description. Estimates of continental paleotemperatures in nearby North Dakota suggest a decrease of 6–8°C over the course of $\sim$100 ky (Wilf *et al.*, 2003). Among per-100-year temperature-changes for the Cenozoic (see Barnosky *et al.*, 2003, Fig. 2), this cooling interval lies on the high end of the range for background levels of climate change but is not qualitatively exceptional. Thus, it is unlikely that the dramatic extinction of 22–27 mammalian species at or near the K-T boundary was caused by the cooling interval alone.

Single Versus Multiple Causes for the K-T Extinction

How do these findings relate to hypotheses for the pattern and mechanism of the K-T extinction? Evidence supporting the occurrence of an extraterrestrial impact at the K-T boundary [e.g., iridium anomaly, shocked quartz, an impact crater; see Archibald (1996) and Sargeant and Currie (2001) for reviews] has become widely accepted in the scientific literature (but see Keller *et al.*, 2002b, 2004). However, hypotheses to explain the K-T mass extinction remain hotly debated. Some workers advocate a single-cause hypothesis, in which the extraterrestrial impact led to global wildfire, acid rain, a thermal pulse, periods of darkness (Alvarez, 1986), and catastrophic biological consequences (but see e.g., Pope, 2002; Belcher *et al.*, 2003). Other workers advocate a multiple-cause hypothesis, in which causes purportedly operated over both long (10 ky–1 my) and short (1 day–100 yrs) temporal scales. Long-term environmental perturbations, such as climatic fluctuations, habitat fragmentation, marine regression, and volcanic degassing, stressed biotic communities leading up to and at the K-T boundary. In turn, mounting ecological instability rendered biotic communities vulnerable to a short-term "knock-out blow," such as an extraterrestrial impact or surge of volcanism (Archibald, 1996; MacLeod *et al.*, 1997; Li and Keller, 1998b; Clemens, 2002). To evaluate these hypotheses, one must assess change in biotic communities over long temporal intervals leading up to and across the K-T boundary.

Although most studies of terrestrial vertebrate faunas have focused attention immediately across the K-T boundary (Archibald and Bryant, 1990; Clemens, 2002), there are a few notable exceptions. Sheehan *et al.* (1991) sampled dinosaur fossils from the Hell Creek Formation in Glendive, Montana and Marmarth, North Dakota. Samples were binned into three distinct stratigraphic intervals, representing $\sim$730 ky each. No significant changes in either taxonomic richness or ecological diversity (via Shannon index and rarefaction) of dinosaur families were found leading up to the K-T boundary. Accordingly, they rejected a gradual pattern of extinction for non-avian dinosaurs and the role of long-term causes. Their study led to considerable debate, mainly questioning whether the taxonomic and temporal resolution of their data was capable of detecting ecologically meaningful change (Clemens *et al.*, 1992; Williams, 1994; Hunter, 1994; Hurlbert and Archibald, 1995).

Recent studies by Pearson *et al.* (2001, 2002) also analyzed change in terrestrial vertebrate faunas leading up to the K-T boundary, using an impressive fossil database (>10,000 specimens) from the well-constrained framework of the Hell Creek Formation in southwestern North Dakota and northwestern South Dakota. In agreement with Sheehan *et al.* (1991, 2000), their results showed that most taxa persist through the formation, and non-avian dinosaurs, in particular, are found in their highest well-sampled localities. Their rarefied fossil data also indicate that in the study area, taxonomic diversity of terrestrial vertebrates and non-avian dinosaurs, in particular, did not decline leading up to the K-T boundary.

The study presented here provides an additional pattern of biotic change leading up to the K-T boundary. The taxonomic and temporal resolution is finer than that of Sheehan *et al.* (1991) and compares well with that of Pearson *et al.* (2002), although the Hell Creek Formation in Montana may represent a longer temporal interval than sections in North Dakota (~2.06 Ma vs. ~1.36 Ma; Hicks *et al.*, 2002). Data from Pearson *et al.* (2002) include mammals as well as other vertebrates, but were amassed largely from surface collections. Consequently, their mammalian data are sparse, consisting of only 50 specimens identifiable to species (Hunter and Archibald, 2002, Table 5).

While this study's results differ from those of Sheehan *et al.* (1991) and Pearson *et al.* (2002) in that they document biotic changes leading up to the K-T boundary, these changes are likely "normal" mammalian responses to background levels of climate change. The megafloral record from North Dakota also shows pre-K-T changes in composition of megafloras (Johnson and Hickey, 1990; Johnson, 2002; Wilf *et al.*, 2003) and insect herbivores (Labandeira *et al.*, 2002a, b), which have been interpreted as "normal" responses to climate change. By contrast, the dramatic extinction or pseudo-extinction of 22 to 27 mammalian species at or near the K-T boundary (65.7–65.58 Ma) cannot be explained by climate change alone, a result that is consistent with Sheehan *et al.* (1991) and Pearson *et al.* (2002).

The question then becomes—what patterns in the fossil record would support or falsify each causal hypothesis? Because an extraterrestrial impact occurred at the K-T boundary, the single-cause hypothesis predicts only background levels of biotic change leading up to the K-T boundary, followed by dramatic levels of biotic change at the K-T boundary. Thus, a pre-K-T pattern of extinction or ecological instability that exceeds background levels would falsify this hypothesis.

However, the converse pattern of no substantial extinction or ecological instability prior to the K-T boundary may not necessarily falsify the multiple-cause hypothesis. First, the patterns predicted by the multiple-cause hypothesis are often oversimplified. The presumption that biotic communities respond linearly to environmental perturbations (i.e., in proportion to and shortly after) overlooks ecological and Holocene paleoecological studies that suggest populations may exhibit inertia or resistance to environmental stresses (Underwood, 1989). High-inertia populations may not initially respond to environmental perturbations, leaving few "early-warning signals" of the stresses incurred by environmental perturbations (Scheffer *et al.*, 2001). However, once stress-tolerance thresholds of populations are reached through additive or synergistic effects of either simultaneous or accumulated stresses (Parsons, 1990; Brown *et al.*, 1997), populations may respond suddenly and non-linearly (i.e., disproportionate to any one of the individual stresses).

If these ecological processes also operate on or translate to geological time scales, the multiple-cause hypothesis may offer a spectrum of predicted patterns. On one end of this spectrum, lineages or communities may have exhibited "early-warning signals" as environmental perturbations built up approaching the K-T boundary. The accompanying pattern (linear response pattern) would document increasing levels of biotic change leading up to and at the K-T boundary, exceeding levels expected from background climate change or environmental perturbations [i.e., Barnosky *et al.* (2003) model]. On the other end of this spectrum, lineages or communities may not have exhibited detectable "early-warning signals" leading up to the K-T boundary, but instead exhibited dramatic levels of biotic change more suddenly at or near the K-T boundary as mounting environmental perturbations exceeded stress-tolerance thresholds. The accompanying pattern (non-linear response pattern) would document levels of biotic change (1) leading up to the K-T boundary that differ little from levels expected from background climate change or environmental perturbations and (2) at or near the K-T boundary that differ dramatically from levels expected from background climate change or environmental perturbations.

The second issue is whether the fossil record can adequately test the predictions of these hypotheses. Although the non-linear response pattern of the multiple-cause hypothesis does not seem readily distinguishable from the pattern predicted by the single-cause hypothesis, stress-tolerance thresholds likely varied between biotic communities or lineages (e.g., foraminifera vs. mammals) and the effects of environmental perturbations varied between geographic regions. However, if the "knock-out blow" was an extraterrestrial impact, it was severely felt on a global scale, leading many biotic communities and lineages to exceed their stress-tolerance thresholds in a geologically instantaneous fashion. Thus, the non-linear response pattern of the multiple-cause hypothesis may not be detectably different from the predicted pattern of the single-cause hypothesis. Even the linear response pattern (i.e., gradual pattern) may not be distinguishable from the pattern predicted by the single-cause hypothesis. The K-T fossil record from the terrestrial realm, in particular, may not have the temporal resolution to distinguish between causes operating over 10–100 ky and those operating over shorter temporal intervals (1 day–100 yrs.). Additionally, the geographic sampling of the K-T fossil record is sparse. Well-sampled terrestrial vertebrate faunas leading up to and across the K-T boundary are only known from the northern Western Interior of North America (Pearson *et al.*, 2002), perhaps providing a myopic view of the K-T extinction (Clemens, 2002; Wilf and Johnson, 2004). The more broadly sampled marine record shows that the rate, timing, and magnitude of the extinction may vary between geographic areas and biological groups (see MacLeod *et al.*, 1997).

CONCLUSIONS

This analysis presents a detailed study of temporal change in mammalian communities through the Lancian portion of the Late Cretaceous, an important step toward teasing apart temporal and biogeographic differences in Lancian faunas (e.g., Hunter and Archibald, 2002). It also represents the first integration of these data with megafloral and paleoclimatic proxy data to understand changes in mammalian communities leading up to the K-T boundary. Species richness remained constant through this interval, whereas changes in taxonomic composition, relative abundances, and mean individual body size were found and correlate temporally with changes in paleotemperature. Although taphonomic causes cannot be entirely excluded, results suggest that mammalian communities responded to changes in global climate or coincident changes in other abiotic or biotic aspects of the latest Cretaceous environment (e.g., sea-level, vegetation) or both.

With the exception of Pearson *et al.* (2002), previous studies of terrestrial vertebrate communities across the K-T boundary have been limited by the need for deeper temporal context, finer temporal resolution, and larger fossil sample sizes. Those studies that pinpointed changes immediately across the K-T boundary were unable to fully explore hypotheses for gradual versus catastrophic extinction, whereas those with a coarser temporal perspective were unable to resolve the effects of environmental perturbations operating on finer temporal scales. Although this study offers ecologically meaningful temporal context to questions regarding the pattern and mechanism of the K-T extinction, the need for improved temporal resolution and sampling intensity still exists. Nevertheless, for a period of ∼1.6 Ma (67.3–65.7 Ma), latest Cretaceous mammalian communities from Garfield County, Montana were relatively stable, as indicated by their "normal" response to background levels of environmental change. Then, less than ∼115 ky before the K-T boundary (65.7–65.58 Ma), mammalian communities became relatively unstable, as indicated by their dramatic turnover.

Because the step-wise extinction pattern cannot be distinguished from a more sudden extinction, these fossil data do not support an extended linear-response pattern of the multiple-cause hypothesis at the scale of temporal resolution available. These fossil data are consistent with either a non-linear response pattern of the multiple-cause hypothesis or the pattern predicted by the single-cause hypothesis. However, until the role of the other environmental factors can be excluded, the hypothesis for the singular role of an extraterrestrial impact in the K-T extinction should not represent the null hypothesis, especially in light of other extraterrestrial impacts unassociated with biological catastrophes (Tsujita, 2001; Alroy, 2003). Some may claim that the multiple-cause hypothesis is more complex than a single-cause hypothesis, but others would posit that so are natural systems (Williams, 1994; Tsujita, 2001). Lastly, this study represents a biotic pattern from one vertebrate group and one study area. Additional studies leading up to and across the K-T boundary from various geographic regions, paleoenvironments, and taxonomic groups will refine our view of this critical transition in earth's history.

ACKNOWLEDGMENTS

This study is dedicated to Bill Clemens who has made tremendous contributions to our understanding of the Cretaceous-Tertiary boundary. Bill also introduced me to Jordan, Montana—a place that he and many of his students hold dearly for its fossils and people. For this and his patient and thoughtful guidance and friendship, I am truly grateful. I acknowledge the help of many students and volunteers from the UCMP's tradition of fieldwork in northeastern Montana, especially that of M. Ames, A. Ballerini, N. Beranek, I. Cara, N. Chauhan, B. Farrell, B. Friedman, J. Herbeck, J. Lee, J. Mason, H. Morey, R. Sayaman, M. de Sosa, D. Stewart, T. Stidham, A. Weil, M. Wilson, and P. Wilson.

I also thank the Charles M. Russell Wildlife Refuge, the Bureau of Land Management, the Montana Fish Wildlife and Parks, and J. Horner, J. H. Hartman, N. C. Arens, M. B. Goodwin, and other members of the Hell Creek Project, and special thanks to Harley and Mary Garbani, the Engdahl's, the Twitchell's, and the community of Jordan. A. D. Barnosky, W. A. Clemens, P. A. Holroyd, F. C. Howell, D. R. Lindberg, N. D. Pyenson, C. A. E. Strömberg, L. Wilson, J. A. Wilson, and two anonymous reviewers provided helpful reviews. Financial support comes from a NSF Graduate Research Fellowship, Department of Integrative Biology Summer Block Grants, UCMP Graduate Student Support Grants, Nathan Myhrvold and other donors to the Hell Creek Project, and a grant to J. H. Hartman from the U.S. Department of Energy to the University of North Dakota Energy & Environmental Research Center. This is UCMP contribution no. 1868.

LITERATURE CITED

Adatte, T., Keller, G., and Stinnesbeck, W. (2002). Late Cretaceous to early Paleocene climate and sea-level fluctuations: The Tunisian record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **178:** 165–196.

Alroy, J. (2003). Cenozoic bolide impacts and biotic change in North American mammals. *Astrobiology* **3:** 119–132.

Alroy, J., Koch, P. L., and Zachos, J. C. (2000). Global climate change and North American mammalian evolution. In: *Deep Time: Paleobiology's Perspective*, D. H. Erwin and S. L. Wing, eds., pp. 259–288, The Paleontological Society, Lawrence, Kansas.

Alvarez, W. (1986). Toward a theory of impact crises. *Eos* **67:** 649, 653–655, 658.

Archibald, J. D. (1982). A study of Mammalia and geology across the Cretaceous-Tertiary boundary in Garfield County, Montana. *Univ. Calif. Publ. Geol. Sci.* **122:** 1–286.

Archibald, J. D. (1993). The importance of phylogenetic analysis for the assessment of species turnover: A case history of Paleocene mammals in North America. *Paleobiology* **19:** 1–27.

Archibald, J. D. (1996). *Dinosaur Extinction and the End of an Era: What the Fossils Say*, Columbia University Press, New York.

Archibald, J. D., and Bryant, L. J. (1990). Differential Cretaceous/Tertiary extinctions of nonmarine vertebrates; Evidence from northeastern Montana. In: *Global Catastrophes in Earth history: An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality*, V. L. Sharpton and P. D. Ward, eds., pp. 549–562, Geological Society of America Special Paper 247, Boulder, Colorado.

Archibald, J. D., Butler, R. F., Lindsay, E. H., Clemens, W. A., and Dingus, L. (1982). Upper Cretaceous-Paleocene biostratigraphy and magnetostratigraphy, Hell Creek and Tullock Formations, northeastern Montana. *Geology* **10:** 153–159.

Arens, N. C., and Jahren, A. H. (2002). Chemostratigraphic correlation of four fossil-bearing sections in southwestern North Dakota. In: *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, J. H. Hartman, K. R. Johnson, and D. J. Nichols, eds., pp. 75–93, Geological Society of America Special Paper 361, Boulder, Colorado.

Badgley, C. (1986). Counting individuals in mammalian fossil assemblages from fluvial environments. *Palaios* **1:** 328–338.

Badgley, C., and Gingerich, P. D. (1988). Sampling and faunal turnover in Early Eocene mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **63:** 141–157.

Barnosky, A. D., and Carrasco, M. A. (2002). Effects of Oligo-Miocene global climate changes on mammalian species richness in the northwestern quarter of the USA. *Evol. Ecol. Res.* **4:** 811–841.

Barnosky, A. D., Hadly, E. A., and Bell, C. J. (2003). Mammalian response to global warming on varied temporal scales. *J. Mammal.* **84:** 354–368.

Barrera, E., and Savin, S. M. (1999). Evolution of late Campanian-Maastrichtian marine climates and oceans. In: *Evolution of the Cretaceous Ocean-Climate System*, E. Barrera and C. C. Johnson, eds., pp. 245–282, Geological Society of America Special Paper 332, Boulder, Colorado.

Behrensmeyer, A. K., Hook, R. W., Badgley, C., Boy, J. A., Chapman, R. E., Dodson, P., Gastaldo, R. A., Graham, R. W., Martin, L. D., Olsen, P. E., Spicer, R. A., Taggart, R. E., and Wilson, M. V. H. (1992). Paleoenvironmental contexts and taphonomic modes. In: *Terrestrial Ecosystems Through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals*, A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H.-D. Sues, and S. L. Wing, eds., pp. 15–136, University of Chicago Press, Chicago.

Belcher, C. M., Collinson, M. E., Sweet, A. R., Hildebrand, A. R., and Scott, A. C. (2003). Fireball passes and nothing burns-The role of thermal radiation in the Cretaceous-Tertiary event: Evidence from the charcoal record of North America. *Geology* **31:** 1061–1064.

Blob, R. W., and Fiorillo, A. R. (1996). The significance of vertebrate microfossil size and shape distributions for faunal abundance reconstructions: A Late Cretaceous example. *Paleobiology* **22:** 422–435.

Bloch, J. I., Rose, K. D., and Gingerich, P. D. (1998). New species of *Batodonoides* (Lipotyphla, Geolabididae) from the Early Eocene of Wyoming: Smallest known mammal? *J. Mammal.* **79:** 804–827.

Brown, J. H. (1995). *Macroecology*, University of Chicago, Chicago.

Brown, J. H., Valone, T. J., and Curtin, C. G. (1997). Reorganization of an arid ecosystem in response to recent climate change. *Proc. Natl. Acad. Sci. U.S.A.* **94:** 9729–9733.

Clemens, W. A. (1964). Fossil mammals of the type Lance Formation, Wyoming: Part I. Introduction and Multituberculata. *Univ. Calif. Publ. Geol. Sci.* **48:** 1–105.

Clemens, W. A. (1973). Fossil mammals of the type Lance Formation, Wyoming: Part III. Eutheria and summary. *Univ. Calif. Publ. Geol. Sci.* **94:** 1–102.

Clemens, W. A. (2002). Evolution of the mammalian fauna across the Cretaceous-Tertiary boundary in northeastern Montana and other areas of the Western Interior. In: *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, J. H. Hartman, K. R. Johnson, and D. J. Nichols, eds., pp. 217–245, Geological Society of America Special Paper 361, Boulder, Colorado.

Clemens, W. A., Archibald, J. D., Sheehan, P. M., Fastovsky, D. E., Hoffman, R. G., Berghaus, C. B., and Gabriel, D. L. (1992). Dinosaur diversity and extinction; discussions and reply. *Science* **256:** 159–161.

Clyde, W. C., and Gingerich, P. D. (1998). Mammalian community response to the latest Paleocene thermal maximum: An isotaphonomic study in the northern Bighorn Basin, Wyoming. *Geology* **26:** 1011–1014.

D'Hondt, S., Herbert, T. D., King, J., and Gibson, C. (1996). Planktic foraminifera, asteroids, and marine production: Death and recovery at the Cretaceous-Tertiary boundary. In: *The Cretaceous-Tertiary Event and Other Catastrophes in Earth History*, G. Ryder, D. Fastovsky, and S. Gartner, eds., pp. 303–317, Geological Society of America Special Paper 307, Boulder, Colorado.

Foote, M. (2000). Origination and extinction components of taxonomic diversity: General problems. In: *Deep Time: Paleobiology's Perspective*, D. H. Erwin and S. L. Wing, eds., pp. 74–102, The Paleontological Society, Lawrence, Kansas.

Gaston, K. J. (1994). *Rarity*, Chapman and Hall, London.

Gordon, C. L. (2003). A first look at estimating body size in dentally conservative marsupials. *J. Mamm. Evol.* **10:** 1–21.

Graham, R. W. (1992). Late Pleistocene faunal changes as a guide to understanding effects of greenhouse warming on the mammalian fauna of North America. In: *Global Warming and Biological Diversity*, R. L. Peters and T. E. Lovejoy, eds., pp. 76–87, Yale University Press, New Haven.

Hadly, E. A. (1997). Evolutionary and ecological response of pocket gophers (*Thomomys talpoides*) to late-Holocene climatic change. *Biol. J. Linn. Soc.* **60:** 277–296.

Hicks, J. F., Johnson, K. R., Obradovich, J. D., Tauxe, L., and Clark, D. (2002). Magnetostratigraphy and geochronology of the Hell Creek and basal Fort Union Formations of southwestern North Dakota and a recalibration of the age of the Cretaceous-Tertiary boundary. In: *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, J. H. Hartman, K. R. Johnson, and D. J. Nichols, eds., pp. 35–55, Geological Society of America Special Paper 361, Boulder, Colorado.

Hoffman, C., Féraud, G., and Courtillot, V. (2000). ^{40}Ar/^{39}Ar dating of mineral separates and whole rocks from the Western Ghats lava pile: Further constraints on duration and age of the Deccan traps. *Earth Planet. Sci. Lett.* **180:** 13–27.

Holland, S. M. (2003). Analytic Rarefaction 1.3. http://www.uga.edu/∼strata/software/.

Huber, B. T., Norris, R. D., and MacLeod, K. G. (2002). Deep-sea paleotemperature record of extreme warmth during the Cretaceous. *Geology* **30:** 123–126.

Hunter, J. (1994). Lack of a high body count at the K-T boundary. *J. Paleontol.* **68:** 1158.

Hunter, J. P., and Archibald, J. D. (2002). Mammals from the end of the age of dinosaurs in North Dakota and southeastern Montana, with a reappraisal of geographic differentiation among Lancian mammals. In: *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, J. H. Hartman, K. R. Johnson, and D. J. Nichols, eds., pp. 191–216, Geological Society of America Special Paper 361, Boulder, Colorado.

Hurlbert, S. H., and Archibald, J. D. (1995). No statistical support for sudden (or gradual) extinction of dinosaurs. *Geology* **23:** 881–884.

Johnson, K. R. (2002). Megaflora of the Hell Creek and lower Fort Union Formations in the western Dakotas: Vegetational response to climate change, the Cretaceous-Tertiary boundary event, and rapid marine transgression. In: *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains:*

An Integrated Continental Record of the End of the Cretaceous, J. H. Hartman, K. R. Johnson, and D. J. Nichols, eds., pp. 329–391, Geological Society of America Special Paper 361, Boulder, Colorado.

Johnson, K. R., and Hickey, L. J. (1990). Megafloral change across the Cretaceous/Tertiary boundary in the northern Great Plains and Rocky Mountains, U.S.A. In: *Global catastrophes in Earth history: An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality*, V. L. Sharpton and P. D. Ward, eds., pp. 433–444, Geological Soceity of America Special Paper 247, Boulder, Colorado.

Keller, G., Adatte, T., Burns, S. J., and Tantawy, A. A. (2002a). High-stress paleoenvironment during the late Maastrichtian to early Paleocene in Central Egypt. *Palaeogeogr. Palaeoclimatol. Palaeoecol***. 187:** 35–60.

Keller, G., Adatte, T., Stinnesbeck, W., Affolter, M., Schilli, L., and Lopez-Oliva, J. G. (2002b). Multiple spherule layers in the late Maastrichtian of northeastern Mexico. In: *Catastrophic Events and Mass Extinctions: Impacts and Beyond*, C. Koeberl and K. G. MacLeod, eds., pp. 145–162, Geological Society of America Special Paper 356, Boulder, Colorado.

Keller, G., Adatte, T., Stinnesbeck, W., Rebolledo-Vieyra, M., Fucugauchi, J. U., Kramar, U., and Stüben, D. (2004). Chicxulub impact predates the K-T boundary mass extinction. *Proc. Natl. Acad. Sci. U.S.A.* **101:** 3753–3758.

Kidwell, S. M., and Holland, S. M. (2002). The quality of the fossil record: Implications for evolutionary analyses. *Ann. Rev. Ecol. Syst.* **33:** 561–588.

Kirchner, J. W., Finkel, R. C., Riebe, C. S., Granger, D. E., Clayton, J. L., King, J. G., and Megahan, W. F. (2001). Mountain erosion over 10 yr, 10 k.y., and 10 m.y. time scales. *Geology* **29:** 591–594.

Knight, K. B., Renne, P. R., Halkett, A., and White, N. (2003). ^{40}Ar/^{39}Ar dating of the Rajahmundry Traps, Eastern India and their relationship to the Deccan Traps. *Earth Planet. Sci. Lett.* **208:** 85–99.

Kucera, M., and Malmgren, B. (1998). Terminal Cretaceous warming event in the mid-latitude South Atlantic Ocean: Evidence from poleward migration of *Contusotruncana contusa* (planktonic foraminifera) morphotypes. *Palaeogeogr. Palaeoclimatol. Palaeoecol***. 138:** 1–15.

Labandeira, C. C., Johnson, K. R., and Lang, P. (2002a). Preliminary assessment of insect herbivory across the Cretaceous-Tertiary boundary: Major extinction and minimum rebound. In: *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, J. H. Hartman, K. R. Johnson, and D. J. Nichols, eds., pp. 297–327, Geological Society of America Special Paper 361, Boulder, Colorado.

Labandeira, C. C., Johnson, K. R., and Wilf, P. (2002b). Impact of the terminal Cretaceous event on plant-insect associations. *Proc. Natl. Acad. Sci. U.S.A.* **99:** 2061–2066.

Lerbekmo, J. F. (1985). Magnetostratigraphic and biostratigraphic correlations of Maastrichtian to early Paleocene strata between south-central Alberta and southwestern Saskatchewan. *Bull. Canad. Petro. Geol.* **33:** 213–226.

Li, L., and Keller, G. (1998a). Maastrichtian climate, productivity and faunal turnovers in planktic foraminifera in South Atlantic DSDP sites 525A and 21. *Mar. Micropaleontol.* **33:** 55–86.

Li, L., and Keller, G. (1998b). Abrupt deep-sea warming at the end of the Cretaceous. *Geology* **26:** 995–999.

Li, L., and Keller, G. (1999). Variability in Late Cretaceous climate and deep waters: Evidence from stable isotopes. *Mar. Geol.* **161:** 171–190.

Li, L., Keller, G., Adatte, T., and Stinnesbeck, W. (2000). Late Cretaceous sea-level changes in Tunisia: A multi-disciplinary approach. *J. Geol. Soc. Lond.* **157:** 447–458.

Lillegraven, J. A. (1969). Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. *Univ. Kansas Paleontol. Contr.* **50:** 1–122.

MacLeod, N., Rawson, P. F., Forey, P. L., Banner, F. T., Boudagher-Fadel, M. K., Bown, P. R., Burnett, J. A., Chambers, P., Culver, S., Evans, S. E., Jeffery, C., Kaminski, M. A., Lord, A. R., Milner, A. C., Milner, A. R., Morris, N., Owen, E., Rosen, B. R., Smith, B., Taylor, P. D., Urquhart, E., and Young, J. R. (1997). The Cretaceous-Tertiary biotic transition. *J. Geol. Soc. Lond.* **154:** 265–292.

Marshall, C. R. (1997). Confidence intervals on stratigraphic ranges with nonrandom distribution of fossil horizons. *Paleobiology* **23:** 1997.

Maurer, B. A. (1994). *Geographical population analysis: Tools for the Analysis of Biodiversity*, Blackwell, London.

McDermott, B., Hunter, J., and Alroy, J. (2002). Estimating body mass of multituberculate mammals. *J. Vertebr. Paleontol.* **22:** 86A.

McKinney, M. L. (1996). The biology of fossil abundance. *Revista Española de Paleontología* **11:** 125–133.

Nordt, L., Atchley, S., and Dworkin, S. (2003). Terrestrial evidence for two greenhouse events in the latest Cretaceous. *GSA Today* **13:** 4–9.

Parsons, P. A. (1990). The metabolic cost of multiple environmental stresses: Implications for climatic change and conservation. *Trends Ecol. Evol.* **5:** 315–317.

Pearson, D. A., Schaefer, T., Johnson, K. R., and Nichols, D. J. (2001). Palynologically calibrated vertebrate record from North Dakota consistent with abrupt dinosaur extinction at the Cretaceous-Tertiary boundary. *Geology* **29:** 39–42.

Pearson, D. A., Schaefer, T., Johnson, K. R., Nichols, D. J., and Hunter, J. P. (2002). Vertebrate biostratigraphy of the Hell Creek Formation in southwestern North Dakota and northwestern South Dakota. In: *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, J. H. Hartman, K. R. Johnson, and D. J. Nichols, eds., pp. 145–167, Geological Society of America Special Paper 361, Boulder, Colorado.

Peters, R. L., and Lovejoy, T. E. (1992). *Global Warming and Biological Diversity*, Yale University Press, New Haven.

Pope, K. O. (2002). Impact dust not the cause of the Cretaceous-Tertiary mass extinction. *Geology* **30:** 99–102.

Raup, D. M. (1975). Taxonomic diversity estimation using rarefaction. *Paleobiology* **1:** 333–342.

Renne, P. R., Swisher, C. C. I., Deino, A. L., Karner, D. B., Owens, T. L., and DePaolo, D. J. (1998). Intercalibration of standards, absolute ages and uncertainties in ^{40}Ar/^{39}Ar dating. *Chem. Geol. (Isotope Geoscience section)* **145:** 117–152.

Sargeant, W. A. S., and Currie, P. J. (2001). The "Great Extinction" that never happened: The demise of dinosaurs considered. *Canad. J. Earth Sci.* **38:** 239–247.

Scheffer, M., Carpenter, S., Foley, J., Folke, C., and Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature* **413:** 591–596.

Searcy, W. A. (1980). Optimum body sizes at different ambient temperatures: An energetics explanation of Bergmann's Rule. *J. Theoret. Biol.* **83:** 579–593.

Sheehan, P. M., Fastovsky, D. E., Barreto, C., and Hoffman, R. G. (2000). Dinosaur abundance was not declining in a "3 m gap" at the top of the Hell Creek Formation, Montana and North Dakota. *Geology* **28:** 523–526.

Sheehan, P. M., Fastovsky, D. E., Hoffman, R. G., Berghaus, C. B., and Gabriel, D. L. (1991). Sudden extinction of the dinosaurs: Latest Cretaceous, upper Great Plains, U. S. A. *Science* **254:** 835–839.

Storer, J. E. (1991). The mammals of the Gryde Local Fauna, Frenchman Formation (Maastrichtian: Lancian), Saskatchewan. *J. Vertebr. Paleontol.* **11:** 350–369.

Strauss, D., and Sadler, P. M. (1989). Classical confidence intervals and bayesian probability estimates for ends of local taxon ranges. *Math. Geol.* **21:** 411–427.

Stüben, D., Kramar, U., Berner, Z. A., Meudt, M., Keller, G., Abramovich, S., Adatte, T., Hambach, U., and Stinnesbeck, W. (2003). Late Maastrichtian paleoclimatic and paleoceanographic changes inferred from Sr/Ca ratio and stable isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **199:** 107–127.

Swisher, C. C. I., Dingus, L., and Butler, R. F. (1993). ^{40}Ar/^{39}Ar dating and magnetostratigraphic correlation of the terrestrial Cretaceous-Paleogene boundary and Puercan Mammal Age, Hell Creek-Tullock formations, eastern Montana. *Canad. J. Earth Sci.* **30:** 1981–1986.

Tipper, J. C. (1979). Rarefaction and rarefiction: The use and abuse of a method in paleoecology. *Paleobiology* **5:** 423–434.

Tsujita, C. (2001). The significance of multiple causes and coincidence in the geological record: From clam clusters to Cretaceous catastrophe. *Canad. J. Earth Sci.* **38:** 271–292.

Underwood, A. J. (1989). The analysis of stress in natural populations. *Biol. J. Linn. Soc.* **37:** 51–78.

Vrba, E. S. (1995). On the connections between paleoclimate and evolution. In: *Paleoclimate and Evolution, with Emphasis on Human Origins*, E. S. Vrba, G. H. Denton, T. C. Partridge, and L. H. Burckle, eds., pp. 24–45, Yale University Press, New Haven.

Weil, A., and Clemens, W. A. (1998). Aliens in Montana: Phylogenetically and biogeographically diverse lineages contributed to an earliest Cenozoic community. *Geological Society of America, Abstracts with Programs* **30:** 69–70.

Wilf, P., and Johnson, K. R. (2004). Land plant extinction at the end of the Cretaceous: A quantitative analysis of the North Dakota megafloral record. *Paleobiology* **30:** 347–368.

Wilf, P., Johnson, K. R., and Huber, B. T. (2003). Correlated terrestrial and marine evidence for global climate changes before mass extinction at the Cretaceous-Paleogene boundary. *Proc. Natl. Acad. Sci. U.S.A.* **100:** 599–604.

Williams, M. E. (1994). Catastrophic versus noncatastrophic extinction of the dinosaurs: Testing, falsifiability, and the burden of proof. *J. Paleontol.* **68:** 183–190.

Wilson, G. P. (2002). Mammalian faunal stasis: New data from the lower portion of the Hell Creek Formation in Garfield County, Montana. *J. Vertebr. Paleontol.* **22:** 120A.

Wilson, G. P. (2004). A quantitative assessment of mammalian change leading up to and across the Cretaceous-Tertiary boundary in northeastern Montana, Ph.D. dissertation, University of California, Berkeley.

Zar, J. H. (1999). *Biostatistical Analysis*, Prentice Hall, New York.