Mammalian extinction, survival, and recovery dynamics across the Cretaceous-Paleogene boundary in northeastern Montana, USA

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ABSTRACT

The Cretaceous-Paleogene boundary marks a critical event in mammalian evolution. Using a database of 4769 mammalian specimens from the Hell Creek and lower Fort Union formations of Garfield County, northeastern Montana, I quantified temporal patterns of diversity and community structure to evaluate faunal dynamics during the last ~1.9 m.y. of the Cretaceous, the Cretaceous-Paleogene extinction and survival, and the first ~1.2 m.y. of the early Paleocene recovery and placental radiation.

Mammalian taxonomic composition and species richness remained relatively stable for most of the last ~1.9 m.y. of the Cretaceous, but the relative abundance of metatherians and evenness of paleocommunities began declining ~500–600 k.y. before the Cretaceous-Paleogene boundary. The ecological instability implied by falling evenness may be linked to the local extinction of 75% of species at or near the Cretaceous-Paleogene boundary. The early Puercan (Pu1) survival fauna from the first ~100–200 k.y. of the Paleocene is species poor and consists of a few local “bloom taxa” and an influx of immigrants. The species-rich mid/late Puercan (Pu2/3) fauna implies mammalian recovery occurred within ~600–700 k.y. of the Cretaceous-Paleogene event. The Pu2/3 and early Torrejonian (To1) faunas signal the beginning of the placental radiation—“bloom taxa” and multitubercululates waned, richness and abundance of “archaic ungulates” and plesiadapiform primates increased, and the first appearance of taeniodonts, pantodonts, and possibly creodonts expanded the ecological diversity of local faunas. Together, the decoupled patterns of richness and relative abundances reveal the complexity of faunal dynamics during this seminal episode in mammalian history.

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INTRODUCTION

The Cretaceous-Paleogene boundary represents one of the most critical events in Earth history. It was associated with substantial changes in marine productivity and ocean chemistry (D’Hondt, 2005), the extinction of up to 76% of all species (Jablonski, 1995), dramatic restructuring of biotic communities (Norris, 2001), and long-term effects on evolutionary rates and biogeography (Krug et al., 2009). Most studies that have quantified high-resolution temporal patterns of the Cretaceous-Paleogene extinction and recovery have focused on the marine biota (e.g., Hansen et al., 1993; Marshall and Ward, 1996; Jablonski, 1998). The continental biota has received less attention, although the ecological impact of this event on land is considered to have been even more severe than in the seas (McGhee et al., 2004). It caused the collapse of dinosaur-dominated terrestrial ecosystems and led to an early Paleocene biotic recovery that transitioned into an unrivaled adaptive radiation of placental mammals and their rapid rise to ecological dominance (e.g., Simpson, 1937; Van Valen, 1978; Stucky, 1990; Maas and Krause, 1994; Alroy, 1999; Archibald, 2011). Previous quantitative studies of the Cretaceous-Paleogene extinction and recovery of continental biotas are almost entirely focused on the Western Interior of North America, unlike more global marine biota studies, and they have centered on plants (Wilf et al., 2003; Wilf and Johnson, 2004), plant-insect associations (Wilf et al., 2006), and mollusks (Hartman, 2008); few high-resolution temporal studies have quantified patterns of mammals, although they became the dominant vertebrates and primary index fossils in the ensuing Cenozoic terrestrial realm.

Among the studies that have examined mammalian evolution during this critical interval, the quantitative analyses have been based on continental-scale databases (Stucky, 1990; Maas and Krause, 1994; Alroy, 1999), whereas those that have focused at the local scale of individual basins have been largely qualitative (Archibald, 1982, 1983; Williamson, 1996; Lillegraven and Eberle, 1999; Clemens, 2002). The continental-scale approach has the advantage of increased sample sizes and greater spatial and temporal coverage, but the typically coarse bin sizes (e.g., 2.5 m.y., western North America; Alroy, 1999) can average conflicting signals or fail to detect geologically short-term, community-level processes that may be critical to understanding extinction, recovery, and radiation (Erwin, 1998; Barnosky, 2001). Studies at the local scale hold potential for higher temporal resolution, better biogeographic control, and finer ecological sensitivity than do global-scale studies, although they often lack the fossil sample sizes and the dense stratigraphic sampling necessary for robust, quantitative approaches to paleoecological and evolutionary studies (Jamniczky et al., 2007).

Here, I quantify patterns of taxonomic diversity and community structure of successive mammalian assemblages from the Hell Creek Formation and Tullock Member of the Fort Union Formation of the Williston Basin in Garfield County, northeastern (NE) Montana (Fig. 1). I measure richness, evenness, and turnover rates, and construct biostratigraphic range charts and relative abundance distributions using a database of 4769 mammalian fossil specimens. This database is derived from a dense sequence of localities that are tied into a high-resolution chronostratigraphic framework for the local composite section that spans ~3.2 m.y. across the Cretaceous-Paleogene boundary. The results from this approach shed new light on the changes in mammalian faunas in NE Montana leading up to the Cretaceous-Paleogene boundary, during the Cretaceous-Paleogene extinction and survival, and into the early Paleocene recovery and radiation of placentals. The relative abundance data, in particular, provide insights into the Cretaceous-Paleogene extinction and recovery dynamics that have not otherwise been detected from taxonomic richness data alone.
Mammalian extinction, survival, and recovery dynamics across the Cretaceous-Paleogene boundary (Clemens, 2001). In North America, the Cretaceous-Paleogene boundary approximates the boundary between the Lancian and Puercan NALMA (but see Cifelli et al. [2004] for discussion of Puercan assemblages that are questionably Late Cretaceous in age). The onset of Lancian time is poorly defined; thus, its duration is unknown but estimated at ~3 m.y. (Cifelli et al., 2004; Wilson et al., 2010). The Puercan, which is ~1 m.y. in duration, is subdivided into three interval zones (Pu1, Pu2, Pu3) on the basis of successive first appearances of mammalian taxa, and it is followed temporally by the Torrejonian NALMA (Lofgren et al., 2004). Areas in western North America that preserve Lancian and Puercan fossil localities stretch from western Canada in the north to Texas in the south. Unfortunately, few preserve fossil localities in direct superposition that include the Lancian, the Cretaceous-Paleogene boundary, and entirety of the Puercan.

The western Williston Basin in NE Montana (Fig. 1) is an exception that preserves fossil localities in stratigraphic superposition from the Lancian through Puercan and the earliest Torrejonian (To1 interval zone; Clemens and Wilson, 2009). Exposures of the Hell Creek Formation and Tullock Member of the Fort Union Formation (hereafter, referred to as the Tullock Member) in this area preserve an ~190-m-thick, nonmarine sedimentary sequence spanning ~3.2 m.y. across the Cretaceous-Paleogene boundary (see Chronostratigraphic Framework section).

History of Collecting

Paleontological and geological fieldwork in exposures of the Hell Creek Formation and Tullock Member of NE Montana began with Barnum Brown in 1902, but intensive sampling...
of vertebrate microfossil localities did not begin until the late 1960s (see Clemens, 2002; Clemens and Hartman, this volume). In 1966, Harley J. Garbani, then of the Los Angeles County Museum, discovered a prolific Paleocene vertebrate microfossil locality that prompted William A. Clemens of the UCMP to join Garbani in the field. Since 1972, Clemens has led UCMP crews in the collection of vertebrate fossils from exposures of the Hell Creek Formation and Tullock Member in the valleys of Hell Creek, Snow Creek, and Big Dry Arm (e.g., Archibald, 1982; Lofgren, 1995; Clemens, 2002; Clemens and Hartman, this volume; Wilson, 2005; see Fig. 1). These efforts were largely focused on the upper part of the Hell Creek Formation and the lower and middle parts of the Tullock Member.

In 1999, John R. Horner of Montana State University and the MOR and Nathan Myhrvold initiated the Hell Creek Project, an interdisciplinary, multi-institutional study that expanded the stratigraphic sampling. Fieldwork for the project focused on exposures of the lower part of the Hell Creek Formation near Hell Creek Bay to complement the geological and paleontological data already in place from the upper part of the formation. Under the guidance of Clemens, I led UCMP crews from 1999 to 2003 in vertebrate microfossil collecting in these exposures (Wilson, 2005). Since then, the collecting efforts of my field crews at the DMNH (2005–2007) and the University of Washington and UWBM (2008–present) have expanded to include other under-sampled strata in both the Hell Creek Formation and Tullock Member. George Bennett of the SVDM has also collected vertebrate microfossils since 2001, mostly in the upper part of the Hell Creek Formation in the Trumbo Ranch area.

These efforts have yielded over 12,000 mammalian specimens from exposures of the Hell Creek Formation and Tullock Member in Garfield County, Montana. All specimens were collected under permits from the Bureau of Land Management, Charles M. Russell National Wildlife Refuge, and Montana State Department of Natural Resources and Conservation, and with permission from private landowners. Specimens are deposited in collections at the DMNH, MOR, SVDM, UCMP, and UWBM. They consist of isolated teeth and jaw fragments and some postcranial elements. In all but easternmost Garfield County, fossil assemblages from the Hell Creek Formation are Lancian in age; they derive from both overbank (e.g., crevasse splays) and channel deposits (Archibald, 1982; Clemens, 2002; Wilson, 2005). Fossil assemblages from the Tullock Member derive from channel deposits. Those from the lowermost Tullock Member (<4 m from Cretaceous-Paleogene boundary) sample the early Puercan (Pu1; Archibald, 1982) and are separated from those of the middle of the member by ~40 m of strata. It is unclear whether the latter are middle Puercan (Pu2), late Puercan (Pu3), or temporally mixed assemblages, or if they are from a biogeographic province distinct from that on which the Puercan zonation was based (Clemens, 2002; Lofgren et al., 2004). I follow Clemens (2002) in referring to them as Pu2/3 undifferentiated. Fossil assemblages from the uppermost Tullock Member, which are ~20 m above the Pu2/3 assemblages, sample the earliest Torrejonian (To1; Clemens and Wilson, 2009).

Mammalian Fossil Database

The mammalian fossil database used here is a subset of the 12,000+ mammalian specimens from the study area that meet the following criteria: (1) They are from localities that were surface collected, screen washed, and occur in a detailed stratigraphic framework; (2) the Lancian and Pu1 specimens are identified to the species level; and (3) the Pu2/3 and To1 therian specimens are identified to at least the family level. That is, the descriptive paleontology of Pu2/3 assemblages by W.A. Clemens and Anne Weil is not yet completed; thus, analyses of relative abundances that included the Pu2/3 and poorly known To1 assemblages were performed at higher taxonomic levels only (family and above). To avoid over-representation of multituberculata from these assemblages, I included only molars and fourth premolars in the database and excluded tooth positions (e.g., upper anterior premolars, incisors) that are unlikely to be identifiable below the level of Multituberculata.

The taxonomic lists for the mammalian assemblages in the database are summarized in Table 1. The taxonomy of the Lancian assemblages is based on Archibald (1982) and Wilson (2004, 2005; 2009, personal observ.) with updates to pediomyid metatherians based on Davis (2007). Specimens previously referred to the metatherian Alphadon wilsoni by Archibald (1982) and later referred to Alphadon jasoni by Wilson (2004, 2005) are here attributed to the herpetotheriid Nortedelphys jasoni based on Case et al. (2005). A specimen of the recently described multituberculata Paressonomodon nelsoni (Wilson et al., 2010) was also identified in the collections (2009, personal observ.). The taxonomy of the Pu1 assemblages is based on Archibald (1982), with additions from Wilson (2004). The taxonomy of the Pu2/3 assemblage is based on a provisional list from Clemens (2002, 2006), Clemens (2010, personal commun.), and the UCMP online database. The taxonomy of the two To1 assemblages is based on Clemens and Wilson (2009).

Stratigraphic and lithologic data for localities were compiled from Table 1 in Archibald (1982), UCMP field notes, and field measurements and observations (Wilson, 2004, 2005; 2009, personal observ.). The stratigraphic position of the Fox Hills–Hell Creek formational contact was identified in the local section according to criteria in Jensen and Varnes (1964, p. F22), and the Hell Creek–Fort Union formational contact was placed at the lowest laterally extensive lignite in the local section, regardless of thickness (see Hartman et al., this volume; Moore et al., this volume). Stratigraphic positions recorded as ranges (e.g., 20–24 m above the Fox Hills–Hell Creek contact) were converted to arithmetic means (e.g., 22 m). It is an aim of the ongoing project to record high-accuracy stratigraphic positional data for all localities, but for the present study, the data have been acquired via methods with varying levels of accuracy, ranging from a hand level (±5 m) to a handheld Trimble 2008 GeoExplorer XH (±0.30 m).

The resulting mammalian fossil database for this study consists of 4769 specimens: 1677 from 105 Lancian localities that
**TABLE 1. MAMMALIAN FAUNAL LISTS FOR THE HELL CREEK FM. AND TULLOCK MEMBER OF GARFIELD COUNTY, NE MONTANA, USA**

<table>
<thead>
<tr>
<th>Hell Creek Formation</th>
<th>“La1”</th>
<th>“La2”</th>
<th>Pu1</th>
<th>Pu2/3</th>
<th>To1</th>
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<tbody>
<tr>
<td>Nortedelphys jasoni</td>
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<td>Alphadon marshi</td>
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<td>Protalphanodon foxi</td>
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<td>Turgidodon rhaister</td>
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<td>Pediomys elegans</td>
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<td>Leptalestes krejci</td>
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<tr>
<td>Protolambda florencae</td>
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<tr>
<td>Protolambda hatcheri</td>
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<tr>
<td>Didelphephon vorax</td>
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<tr>
<th>“Archaic Ungulates”</th>
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<tbody>
<tr>
<td>Plesiadapiform Primates</td>
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<tr>
<td>Triosodontidae</td>
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<td>Other</td>
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Note: Faunas from the upper and lower parts of the Hell Creek Formation are informally subdivided into “La1” and “La2,” respectively, of the Lancian North American land mammal age (NALMA). Faunas of the Tullock Member are assigned to the early Puercan (Pu1), undifferentiated middle/late Puercan (Pu2/3), and early Torrejonian (To1) intervals. Solid-line arrows represent the continuation of a species from one fauna to the next. Broken-line arrows represent the inferred continuation of a lineage from one fauna to the next. See text for details.
broadly sample the Hell Creek Formation, 933 from three Pu1 localities that sample the lowermost Tullock Member, 2081 (896 identified to therian family, 1185 to Multituberculata) from one Pu2/3 locality (UCMP locality V73080) that samples the middle of the Tullock Member, and 78 from four To1 localities that sample the upper part of the Tullock Member (Fig. 2). The localities stretch across ~80 km of northern Garfield County, Montana (Fig. 1). Those from the Hell Creek Formation sample 63 distinct horizons of the ~89.5 m total thickness of the formation; vertebrate microfossil concentrations have not been found in the lowest ~10 m or the highest 2.4 m of the formation. Puercan and Torrejonian localities sample three narrow stratigraphic bands in the Tullock Member. The Tullock Member was deposited in a coal-swamp environment, and most of the strata are either unfossiliferous, or the bones have been heavily damaged in the acidic environment. Preservation of vertebrate fossils is limited to channel deposits, where, one assumes, the humic and other acids were being diluted or washed away. Additional Puercan assemblages exist but are either currently under study or have not yet been tied into the stratigraphic framework. Sample sizes are largest in the uppermost Hell Creek Formation and the lower and middle parts of the Tullock Member (Fig. 2), but targeted collecting in the middle and lower parts of the Hell Creek Formation has begun to address this bias (Wilson, 2004).

Chronostratigraphic Framework

To correlate local stratigraphic sections with the global fossil and geologic record, Swisher et al. (1993) developed a chronostratigraphic framework for the Tullock Member that incorporated placement of the Cretaceous-Paleogene boundary, radiometric ages, and litho-, bio-, and magnetostratigraphic data. Radiometric ages from the framework were later recalibrated (Renne et al., 1998; Knight et al., 2003, erratum; Wilson, 2004), and magnetostratigraphic data and linear extrapolation of a sedimentation rate were used to extend the framework into the Hell Creek Formation (Wilson, 2004, 2005).

New geologic data prompt revisions to the Hell Creek Formation part of this chronostratigraphic framework. High-accuracy measurements made at the proposed type section (Hartman et al., this volume; LeCain et al., this volume) and other sections in the valley of the Hell Creek (2009, personal observ.) provide an estimate of ~89.5 m for the thickness of the formation (vs. 93 m; Wilson, 2005), though it varies slightly within the study area. Paleomagnetic analyses in the study area show variation in the placement of the C30n-C29r boundary from 7 m below the Cretaceous-Paleogene boundary (Lerbekmo, 2009), to 12–15 m below the Cretaceous-Paleogene boundary (Archibald et al., 1982; Swisher et al., 1993), and, most recently, 25 m below the Cretaceous-Paleogene boundary (LeCain et al., this volume). This discrepancy is due to depositional variation in a fluvial setting, as well as differences in stratigraphic density of paleomagnetic sampling (see discussion in LeCain et al., this volume). Also, because an unconformity of unknown duration may exist at the Fox Hills–Hell Creek formational contact (Murphy et al., 2002), strata of normal polarity that span the contact are only tentatively assigned to the same magnetochron (C30n; Lerbekmo, 2009; LeCain et al., this volume).

In accordance with these new data and uncertainties, I used two different data permutations to estimate the duration of deposition of the Hell Creek Formation. I calculated a sedimentation rate by dividing the thickness of C30n strata in the Hell Creek and Fox Hills Formations in the proposed type section (83 m; LeCain et al., this volume) by the estimated duration of C30n (1.835 m.y.; Ogg and Smith, 2004). The new rate (45 m/m.y.) is identical to that of Wilson (2005). As an alternative, I used

Figure 2. Mammalian fossil sample sizes through the Hell Creek Formation and Tullock Member in the study area. K-Pg—Cretaceous-Paleogene.
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Lerbekmo’s (figure 3 in Lerbekmo, 2009) thickness of C30n strata (~87.5 m) to calculate a sedimentation rate of 48 m/m.y. Then, using each of these sedimentation rates, the thickness of the C30n Hell Creek strata reported in the corresponding study (65 m—LeCain et al., this volume; 81 m—Lerbekmo, 2009), and the estimated duration of the Cretaceous part of C29r (~361 k.y.; Ogg and Smith, 2004), I calculated two estimates for the duration of deposition of the Hell Creek Formation in the study area (1.80 m.y. and 2.06 m.y., respectively). The arithmetic mean of these values (1.93 m.y.) is used throughout this study and related studies (Holroyd et al., this volume; Wilson et al., this volume). Although the assumption of a linear relationship between stratigraphic thickness and time is problematic in fluvial depositional environments (Kidwell and Holland, 2002), it is less so on the time scales considered here (Kirchner et al., 2001). Within the Hell Creek Formation, the chronostratigraphic framework should be considered most accurate within C29r. Tuff samples from the Hell Creek Formation that are currently being analyzed for radiometric age determinations (Renne, 2012, personal communication) should improve future iterations of this chronostratigraphic framework.

Localities were incorporated into the chronostratigraphic framework based on stratigraphic distance from the Fox Hills–Hell Creek or Hell Creek–Fort Union formation contact. In north-central Garfield County, where most localities used in this study occur, the Hell Creek–Fort Union formational contact is coincident with the Cretaceous-Paleogene boundary as identified by impact indicators (iridium anomaly, shocked mineral grains; see Moore et al., this volume) and corroborated by paleomagnetism, radiometric age determination, and biostratigraphy (Swisher et al., 1993; Hotton, 2002). Arens and colleagues (Arens and Jahren, 2002; Arens et al., this volume) have shown that stratigraphic placement of the negative carbon isotope excursion associated with the Cretaceous-Paleogene boundary may vary by ±3 m relative to the contact across Garfield and McCone Counties. However, this variation, which is due to the time-transgressive nature of the Hell Creek–Fort Union formational contact and possibly differences in criteria used to place the Hell Creek–Fort Union formational contact (see Arens et al., this volume), has for the most part little effect at the geographic scope (northern Garfield County) and stratigraphic bin sizes (5 m and 10 m) used here. Stratigraphic positions are reported in meters above or below the Cretaceous-Paleogene boundary (e.g., −35 m for a locality 35 m below the Cretaceous-Paleogene boundary).

**Taxonomic Richness**

Mammalian species richness was calculated as: (1) the raw number of species per locality; (2) the standing richness (i.e., the number of species that first appear or last appear in a stratigraphic horizon or that range through the horizon); and (3) the expected number of species in 40 specimen subsamples. The latter values were calculated for 10 localities from the Hell Creek Formation and lowermost Tullock Member with more than 40 specimens by using rarefaction analysis in Analytic Rarefaction version 1.3 (Holland, 2003), which is based on the rarefaction equations of Tipper (1979). The rarefaction values and rarefaction curves with 95% confidence intervals account for variation in sampling intensity through the section that might bias the other measures of richness (Raup, 1975; Tipper, 1979). To examine broader taxonomic patterns, standing richness values for 10 m bins were partitioned into higher-level taxa for two Hell Creek Formation bins (50–60 m and 0–10 m below the Cretaceous-Paleogene boundary) and three Tullock Member bins that correspond to the Pu1, Pu2/3, and To1 intervals. The 10 m bins represent ~200–250 k.y. intervals. Although “Insectivora” and “archaic ungulates” (traditionally called “condylarthrs”) are paraphyletic or possibly polyphyletic taxa, they were used as higher-level taxa in this study for the sake of convenience or lack of a clear alternative.

**Relative Abundances and Heterogeneity Measures**

I calculated relative abundances of individuals within mammalian species from six well-sampled localities (>50 mammal specimens) in the Hell Creek Formation and the lowermost Tullock Member (Lancian–Pu1). Because UCMP localities V73085 (Flat Creek 3) and V73087 (Flat Creek 5) are less than 40 m apart and from the same stratum, their fossil samples were combined for these analyses and treated as a single locality (Archibald, 1982). Counts are based on the number of identifiable specimens per taxon (NISP) rather than the minimum number of individuals (MNI) method, because most fossil localities in the study area derive from deposits with a low probability of association (e.g., channels, crevasse splays; Badgley, 1986). Although the fidelity of relative abundance data in the fossil record is subject to sampling and taphonomic biases (Behrensmeyer et al., 1992; Rogers and Brady, 2010), the effect of differences in taphonomic filters among assemblages is reduced when considering fossils of similar size and shape, such as small mammal teeth (Blob and Fiorillo, 1996). This is further supported by studies of vertebrate microfossil assemblages from the Hell Creek Formation that have shown that relative abundances within hydraulically equivalent elements (e.g., mammal teeth) do not differ significantly between overbank and sand channel-lag deposits (Wilson, 2005; L. Wilson, 2008).

Combining relative abundance and richness data from each of the six well-sampled localities, I calculated four heterogeneity indices (evenness, equitability, Simpson’s, and Berger-Parker) and 95% confidence intervals, using PAST (Hammer et al., 2001). These heterogeneity indices measure diversity in slightly different ways by emphasizing species richness, dominance, and rarity to varying degrees. The evenness and equitability indices are derived from Shannon’s index, which is based in information theory; they consider the relationship of the relative abundances of all species present in the sample but tend to dampen the effects of the commonest and rarest species and emphasize the richness component of diversity (Magurran, 2004). The Simpson’s and Berger-Parker indices are dominance measures that emphasize

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the abundances of the commonest species and are less influenced by species richness (Magurran, 2004).

I also constructed relative abundance distributions (RADs) for each of the six well-sampled localities. RADs show the abundances of all species in a sample as a log-linear plot of percent abundance versus rank abundance. The shallower the slope of the line formed by the plotted points, the more even is the distribution of individuals across species in the assemblage. These plots can be fit to curves that are derived from either resource-apportioning models based in ecological theory, such as the geometric series and broken-stick models, or statistical models, such as the log-normal, Zipf, and Zipf-Mandelbrot models (Magurran, 2004; McGill et al., 2007). Interpretations of RADs, which are based on ecological theory and empirical examples of the best-fit model, may reveal insights into the deterioration of communities leading up to or at the Cretaceous-Paleogene boundary and the reassembly of communities after the Cretaceous-Paleogene boundary. For example, communities with RADs best fit by a lognormal model are often highly even and from stable, high-productivity environments or in the late stages of succession, whereas those fit by a geometric series model are often more uneven and occur in harsher environmental conditions or in the early stages of succession (McGill et al., 2007). I generated the RADs and fit models to the RADs using Vegan 1.17-1 (Oksanen et al., 2010) for the statistical program R, version 2.10.1 (R Development Core Team, 2009). Akaike’s information criterion (AIC) was used to determine the most likely fit among the five models. AIC is based on log-likelihood and applies penalties to each model based on its estimated number of parameters (broken-stick = 0, geometric series = 1, lognormal and Zipf = 2, Zipf-Mandelbrot = 3; Oksanen et al., 2010).

Relative abundances of individuals within higher-level taxa (multituberculates, metatherians, and eutherians) were calculated for eleven 10 m bins through the entire section (Lancerian–To1). Despite the undesirable effect of increased time averaging, the 10 m bins were deemed necessary to increase sample sizes (>40 specimens) from the middle of the Hell Creek Formation. For relative abundances in each 10 m bin, 95% confidence intervals were calculated on the basis of sample sizes using RACINCAR (Moore et al., 2007). Temporal trends in the relative abundances were evaluated using least squares regression in JMP 8.0.1 (Sall et al., 2001). The eutherian data for two Hell Creek Formation bins (70–80 m and 0–10 m below the Cretaceous-Paleogene boundary) and three Tullock Member bins that correspond to Pu1, Pu2/3, and To1 intervals were also partitioned into finer taxonomic units (e.g., plesiadapiform primates, “Insectivora”) and plotted alongside values for metatherians and multituberculates.

Taxonomic Composition and Turnover

I tabulated biostratigraphic ranges for all species in the Hell Creek Formation and lowermost Tullock Member (Lancerian–Pu1). For the end points of the observed ranges of each taxon, 50% confidence intervals were estimated from two one-tailed calculations. These calculations were 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. Wilf and Johnson’s calculations incorporated “fossil recovery potential functions” (FRPFs; Marshall, 1997), which specify potential for fossil recovery as a function of stratigraphic position. I developed FRPFs from the number of identifiable specimens per stratigraphic interval. As a result, confidence intervals for biostratigraphic ranges adjacent to well-sampled parts of a stratigraphic section are smaller than those calculated from a random distribution method. Some confidence intervals extend indefinitely below the sampled interval or indefinitely beyond the lowermost Tullock Member.

I also calculated turnover events in 5 m stratigraphic bins up to the Pu2/3 fauna (50 m above the Cretaceous-Paleogene boundary), using biostratigraphic range data and taxonomic lists for the Pu2/3 and To1 faunas (Table 1). A species was considered present in a stratigraphic interval if it occurred in a locality from that stratigraphic interval (true occurrence) or in localities above and below that stratigraphic interval (range-through occurrence). Singletons were excluded. A range-through occurrence implies that the absence of a species 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); granted, this may not always be the case. The range-through method may produce edge effects, including artificially higher numbers of appearances and disappearances at the bottom and top of the stratigraphic section, respectively, where the method cannot be applied (Foote, 2000). These effects are minimized in this study because the fossil localities nearest the bottom and top of the section are well sampled. When possible, I distinguished among events due to cladogenesis, anagenesis, extinction, emigration, and immigration by using available phylogenetic, biogeographic, and stratigraphic information from the literature (e.g., “aliens” vs. “residents”; Weil and Clemens, 1998; Archibald, 1993; Clemens, 2010). Note that reconstructing ancestor-descendant relationships in the fossil record, especially this far back in geological time and without cladistic analyses, is challenging (see, e.g., Dayrat, 2005). When the data were ambiguous as to whether the first appearance of a new taxon was best explained as the result of an immigration event or as anagenetic or cladogenetic events within a local lineage, the latter two, which are reflective of pseudo-extinction events, were viewed as the conservative options and adopted here. Distinguishing between anagenesis and cladogenesis was not critical to calculation of turnover rates.

I calculated turnover rates at the species level as per-taxon rates per bin (Foote, 2000), with the assumption that time represented by the 5 m bins is uniform throughout the section (~108 k.y.). However, because the Pu2/3 assemblage is separated from the Pu1 assemblages by ~40 m of strata, rates were calculated as if it were in a 45 m bin (i.e., 5 m bin plus ~40 m of strata). Per-taxon turnover rates were calculated a second time after subtracting pseudo-extinction events (“corrected rates”). Estimated
per-capita turnover rates ($\lambda = \text{appearance}, \mu = \text{disappearance}$) were calculated according to Foote (2000) and corrected for pseudo-extinction events. Though less intuitive, these provide instantaneous rates and allow comparisons with results from Alroy (2000). Because temporal intervals are less than 1 m.y., rates were calculated as per-lineage per 100 k.y. Analyses of higher-level taxonomic richness and abundances (see previous) offer another view of changes in taxonomic composition through the full section.

RESULTS

The results are subdivided by the major analyses: taxonomic richness, relative abundances and heterogeneity measures, and taxonomic composition and turnover.

Taxonomic Richness

The raw number of species (filled circles, Fig. 3) per fossil locality varies through the section and even within a stratigraphic horizon. Focusing on the maximum value of raw richness for each horizon, there is a general increase from the lower to the upper part of the Hell Creek Formation, except for the two low values at the very top of the formation. In the Tullock Member, raw species richness peaks in the middle of the formation in Pu2/3 time. The temporal pattern of raw richness is corroborated by the pattern of standing richness (gray shade, Fig. 3), but both appear to be influenced by sampling. There is a significant positive correlation ($r = 0.864, p < 0.0001$) between the number of identifiable specimens per locality and the raw numbers of species per locality for both the Hell Creek Formation and Tullock Member (Fig. 4). Of the four localities outside the 95% confidence intervals, the three earliest Paleocene (Pu1) localities in the lowermost Tullock Member have fewer species than expected for their sample size, and the Pu2/3 locality from the middle Tullock Member has a greater number of species than expected for its sample size. These outliers are interpreted as biologically meaningful (see Discussion), but it should be noted that increased time averaging of a large channel deposit might also factor into the high taxonomic richness of the Pu2/3 locality. Likewise, the large drop in standing richness from the Pu2/3 locality to the To1 localities is probably overestimated, as it corresponds to an ~25-fold decrease in sample size.

Rarefied richness values (diamonds, Fig. 3) account for variation in sampling through the section. Within the Hell Creek Formation, rarefied richness peaks in the middle of the formation and decreases slightly in the upper part of the formation, but in all cases the 95% confidence intervals overlap. The rarefied richness of the lowermost Tullock Member Pu1 locality (UCMP locality V74111) is lower than those for all of the Lancian Hell Creek Formation localities, and its upper 95% confidence limit overlaps with only the lower 95% confidence limit of the low-

Figure 3. Mammalian species richness through the Hell Creek Formation and Tullock Member of Garfield County, NE Montana, represented as (1) raw numbers of species at individual localities (dark-gray circles; if more than one locality at the same horizon has the same richness, the number of localities is listed within the circle); (2) standing richness through the section (light-gray shade); and (3) expected numbers of species (open diamonds and 95% confidence intervals) from rarefaction analysis of 40-specimen samples from select localities. The chronostratigraphic framework is based on the following data: Ar/Ar radiometric ages (*), ages for magnetostratigraphic boundaries (†), and an estimated age of the base of the Hell Creek Formation (‡). See text for details. K-Pg—Cretaceous-Paleogene; NALMA—North American land mammal age.
Figure 4. Log-linear correlation of mammalian fossil sample sizes and species richness of localities from the Hell Creek Formation and Tullock Member (Lancian–To1) of Garfield County, NE Montana ($r = 0.864$, $p < 0.0001$). The 95% confidence intervals are shaded gray. University of California Museum of Paleontology (UCMP) locality number and stratigraphic position are listed for outliers.

Figure 5. Rarefaction curves for five Lancian mammalian assemblages from the Hell Creek Formation (V99220, V99370, V99368, V77130, V73085 + V73087) and one Puercan (Pu1) mammalian assemblage (V74111) from the lowermost Tullock Member of Garfield County, NE Montana. Bold lines represent the expected number of species, and thin lines represent 95% confidence intervals. University of California Museum of Paleontology (UCMP) locality number and stratigraphic position are listed.
Figure 6. Higher-level taxonomic patterns of (A) species richness and (B) relative abundances of individuals through the Hell Creek (HC) Formation and Tullock Member (Lancian–To1) of Garfield County, NE Montana, for Multituberculata (black), Metatheria (red), and Eutheria (blue). Relative abundances for Pantodonta, Taeniodonta, and Creodonta in the Pu2/3 interval are less than 1%. K-Pg—Cretaceous-Paleogene.
the Pu1 interval, “archaic ungulates” have seven species. Their richness increases through the section, from nine species in the Pu2/3 interval to 12 species in the To1 interval; as a proportion of total richness, this is a 28% increase from the Pu2/3 to the To1 interval. Other higher-level taxa (i.e., plesiadapiform primates, triisodontids, creodonts, taeniodonts, and pantodonts) first appear in the study area in the Pu2/3 interval, but they never attain substantial levels of richness in the section. From the Pu2/3 to To1 interval, plesiadapiform primates increase from three to four species, triisodontids maintain two species, and the other taxa, which had two or fewer species in the Pu2/3 interval, are not recorded in the small samples from the To1 localities.

Relative Abundances and Heterogeneity Measures

The four heterogeneity indices show a common pattern of diversity leading up to and across the Cretaceous-Paleogene boundary. Diversity, as measured by the heterogeneity indices, increases from the lower to the middle part of the Hell Creek Formation and then drops from the upper-middle Hell Creek Formation to the lowermost Tullock Member (Fig. 7). The pattern is more pronounced among the information indices (Fig. 7, evenness [squares], equitability [circles]) than it is among the dominance measures (Fig. 7, Simpson’s [triangles], Berger-Parker [diamonds]), which tend to be more robust to low sample sizes (Magurran, 2004). The 95% confidence intervals imply that statistical support for the trend is fairly robust but varies according to index. All but the Berger-Parker point to the Lancian fauna from the lowermost Hell Creek Formation (UCMP locality V99220) as significantly less diverse than the two middle Hell Creek faunas (UCMP localities V99370, V99368). According to the dominance indices (Simpson, Berger-Parker), the lowermost Hell Creek fauna is also statistically distinct from the two upper Hell Creek faunas (UCMP localities V77130, V73085, and V73087). The information indices indicate that one or both of these upper Hell Creek faunas are not significantly different from the lowermost Hell Creek fauna but are less diverse than one or both of the middle Hell Creek faunas. Across the Cretaceous-Paleogene boundary, the statistical support is more consistent. Diversity of the Pu1 fauna from the lowermost Tullock Member (UCMP locality V74111) is significantly lower than that for all of the Lancian faunas but that from the lowermost Hell Creek Formation.

The RADs also show a clear difference in community structure across the Cretaceous-Paleogene boundary (Fig. 8). Most notably, within Lancian faunas, the differences between the percent abundances of species of successive rank tend to be much smaller than those in the Pu1 fauna. The fitted curve for the Pu1 fauna (UCMP locality V74111) is as a consequence much steeper than those for the Lancian faunas. The models that best fit the abundance data vary by locality (Table 2) without any discernible pattern. The Zipf model fits the lowest Lancian fauna (UCMP locality V99220) slightly better than the Zipf-Mandelbrot model does. The Broken-stick model is the best fit for the stratigraphically higher UCMP locality V99370, although all of the models have a decent fit of the data. The relative abundance data of Lancian faunas from the middle and upper Hell Creek Formation (UCMP localities V99368 and V77130, respectively) are best fit by the Geometric series model. The Zipf-Mandelbrot model provides the best fit for the Lancian fauna from the uppermost Hell Creek Formation (UCMP localities V73085 and V73087) and the Pu1 fauna from the lowermost Tullock Member (UCMP locality V74111). In most Lancian faunas from the Hell Creek Formation, the metatherian Nortedelphys jasoni and at least one species of the multituberculate Mesodma are among the most abundant species. The exception is the fauna from the middle of the Hell Creek Formation (UCMP locality V99368), in which Meniscoessus robustus, Gypsonictops hypoconus, and Protolamda hatcheri are the most abundant species. The sample from this locality is small (N = 54) and might be biased toward larger surface-collected specimens (e.g., M. robustus, P. hatcheri). Glasbius twitchelli, which does not occur in the lower Hell Creek Formation, is among the most abundant species in the uppermost Hell Creek fauna (UCMP localities V73085 and V73087). In the lowermost Tullock Member Pu1 fauna, the “insectivoran” eutherian Procerberus formicarum, the multituberculate Mesodma thompsoni, and the metatherian Peradectes cf. P. pusillus are the most ecologically abundant. All three are considered local survivors of the Cretaceous-Paleogene event (see Results: Taxonomic Composition).

Results from the higher-level taxonomic patterns of relative abundances (Fig. 9) show that eutherians (Fig. 9, blue squares) had only a minor contribution of individuals to the mammalian fauna (~6%–21%) through the Lancian-age Hell Creek Formation. During the same interval, multituberculates (Fig. 9, black circles) and metatherians (Fig. 9, red triangles) each input between ~26% and 61% of the individuals (Fig. 9). Whereas the relative abundance of multituberculates fluctuates up and down through the formation, metatherians have a significant negative trend in abundance (r = 0.840, p < 0.0001) that continues across the Cretaceous-Paleogene boundary and through the Tullock Member. Multituberculates remain ecologically abundant through the Puercan (Pu1–Pu2/3), but their abundance falls to 10% in the To1 interval. In contrast, eutherian relative abundance surges to ~42% immediately after the Cretaceous-Paleogene boundary, where it holds steady during the Puercan and reaches 90% in the To1 interval. Among the eutherians, “insectivorans” are the sole representatives through the Hell Creek Formation (Fig. 6B); they have low relative abundances (~6%–21%) during the Lancian, but they reach a peak abundance of 32% in the Pu1 interval of the lowermost Tullock Member. Thereafter, they are only a small fraction of mammalian individuals (~5%). “Archaic ungulates” have modest relative abundances in the Pu1 and Pu2/3 intervals (10% and 12%, respectively) but rise to ~30% relative abundance in To1. Upon their first appearance in Pu2/3, plesiadapiform primates are the most ecologically abundant eutherians (25%), and, by To1, they make up nearly half of all mammalian individuals. Triisodontid,
Figure 7. Heterogeneity indices and 95% confidence intervals for mammalian assemblages from the Hell Creek Formation (Lancian) and lowermost Tullock Member (Pu1) of Garfield County, NE Montana. The chronostratigraphic framework is based on the following data: Ar/Ar radiometric ages (*), ages for magnetochron boundaries (‡), and an estimated age of the base of the Hell Creek Formation (†). See text for details. K-Pg—Cretaceous-Paleogene; NALMA—North American land mammal age.
Figure 8. Relative abundance distributions (RADs) for mammalian assemblages from the Hell Creek Formation (Lancian) and lowermost Tullock Member (Pu1) of the study area. The three most abundant species and the total fossil sample size (N) are listed for each locality. University of California Museum of Paleontology (UCMP) locality number and stratigraphic position are listed.

<table>
<thead>
<tr>
<th>UCMP locality number</th>
<th>S</th>
<th>N</th>
<th>Broken-stick</th>
<th>Lognormal</th>
<th>Geometric</th>
<th>Zipf</th>
<th>Zipf-Mandelbrot</th>
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<tr>
<td>V99220 (-76 m)</td>
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<td>92</td>
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<td>71.56</td>
<td>78.40</td>
<td>65.50</td>
<td>65.76</td>
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<td>91</td>
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<td>62.65</td>
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<td>51.85</td>
<td>50.30</td>
<td>53.83</td>
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<tr>
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<td>289</td>
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<td>469</td>
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<td>131.38</td>
<td>124.84</td>
<td>164.72</td>
<td>165.07</td>
</tr>
</tbody>
</table>

Note: Measure of model fit for relative abundance distributions (RADs) for mammalian assemblages from the Hell Creek Formation (Lancian) and lowermost Tullock Member (Pu1) of the study area. University of California Museum of Paleontology (UCMP) locality number, raw species richness (S), number of specimens (N), and Akaike’s information criterion (AIC) value for the five models are listed. The best-fit model (bold) was determined by the lowest AIC value.
creodont, taeniodont, and pantodont eutherians never exceed relative abundances of 5% in the study area.

**Taxonomic Composition and Turnover**

The species composition of the Lancian mammalian fauna is relatively stable through the Hell Creek Formation (Fig. 10). Only four of the 30 nonsingleton mammalian species from the Hell Creek Formation have restricted biostratigraphic ranges. The multituberculate *Parectypodus foxi* is only found in the middle of the formation (−58 m to −54 m), though its upper stratigraphic confidence limit extends to −28 m. The eutherian *Cimolestes magnus* is rare as well. It is only found in three stratigraphic horizons (between −68 m and −13.7 m); nevertheless, its upper stratigraphic confidence limit suggests that it disappeared from the local section ~5 m below the Cretaceous-Paleogene boundary. The multituberculate *Essodon brownii* and the metatherian *Glasius twitchelli* are limited to the upper half of the formation (above −35 m), but their lower stratigraphic confidence limits extend to −48 m. Two multituberculates that only appear in the middle of the formation, *Cimolomys trochoius* and the newly recognized *Paressodon nelsoni*, are only known from single specimens; thus, their biostratigraphic ranges cannot be accurately determined. *Cimexomys minor*, *Neoplagaiaulax burgessi*, and *Paracimexomys priscus* are multituberculates that occur in the upper 20 m of the formation; however, because they are rare, their lower stratigraphic confidence limits extend to the bottom of the formation, implying that their absence lower in the section could be an artifact of sampling.

The Pu1 mammalian fauna from the lowermost Tullock Member shares two species in common with the Lancian fauna from the Hell Creek Formation, the multituberculates *Mesodma thompsoni* and *Cimexomys minor*. Five others from the Pu1 mammalian fauna appear to represent the anagenetic or cladogenetic continuation of Hell Creek lineages across the Cretaceous-Paleogene boundary. (1) *Mesodma garfieldensis* is descended from one of the three species of *Mesodma* that occur in the Hell Creek Formation. (2) One of five Hell Creek species of *Cimolestes* likely gave rise to *Cimolestes* sp. A from the lowermost Tullock Member. (3) *Procerberus formicarum* is also included in the Cimolestidae (McKenna and Bell, 1997; Kielan-Jaworowska et al., 2004; Wible et al., 2007, 2009) and has been proposed as a likely descendant of *Cimolestes* (e.g., Lillegraven, 1973; Novacek, 1986) or possibly *Batodon tenuis* (Williamson et al., 2011). (4) *Gypsonictops* is not considered a leptictid, but it has been put forward as the most recent ancestor of leptictids (Lillegraven, 1969; Clemens, 1973; Novacek, 1986) or possibly *Batodon tenuis* (Williamson et al., 2011). (5) The ancestor of *Peradectes* possibly lies among “alphadontids,” two of which (*Alphadon, Protalphadon*) are found in the uppermost Hell Creek Formation (Clemens, 1966). This hypothesized ancestry has recently been questioned (Johnson, 1996a; Clemens, 2006;
Figure 10. Biostratigraphic ranges with 50% confidence intervals for mammalian species from the Hell Creek Formation and lowermost Tullock Member of Garfield County, NE Montana. Diamonds represent occurrences, thick lines represent inferred range-through occurrences, thick lines with fading tails represent inferred occurrence of the lineage in older deposits (see discussion of pseudo-extinction), thin lines with cross bars represent 50% confidence intervals, and thin lines without cross bars indicate that the calculated confidence limit extends beyond the sampled interval. The chronostratigraphic framework is based on the following data: Ar/Ar radiometric ages (‡), ages for magnetochron boundaries (†), and an estimated age of the base of the Hell Creek Formation (‘). See text for details. K-Pg—Cretaceous-Paleogene; NALMA—North American land mammal age.
Korth, 2007; Horowitz et al., 2009). Opposing arguments hinge on a phylogenetic analysis by Johanson (1996b), in which her preferred cladogram (figure 3 in Johanson, 1996b) places Alphadon, Turgidodon, and Peradectes–Peratherium in an unresolved polytomy. Recent analyses relevant to the argument have included additional taxa and morphological characters, but none has specifically evaluated phylogenetic relationships among “alphadontids,” peradectids, and herpetotheriids (Martin et al., 2005; Sánchez-Villagra et al., 2007; Horowitz et al., 2009). Until this issue is resolved, the most parsimonious hypothesis is that the ancestry of Peradectes is among “alphadontids.” Of the remaining 10 species from the lowestmost Tullock Member, which include archaic ungulates and taeniolabidid, eucoosmodontid, and microcosmodontid multituberculates, none has a credible ancestor in Lancian faunas from the underlying Hell Creek Formation of the study area or, for the most part, from equivalent deposits in the Western Interior of North America. A single confirmed specimen of an archaic ungulate (Protungulatum coombsi) among nearly 1200 other specimens from the Lancian Spigot Bottle local fauna of southeastern Montana (Archibald et al., 2011) lends support to a more regional source area, possibly upland environments, for archaic ungulates, but archaic ungulates and the other taxa are still considered earliest Paleocene immigrants to the study area. Proposed pseudo-extinction events for the other intervals are shown in Table 1 (dashed arrows).

Faunal turnover is minimal through much of the Hell Creek Formation (Fig. 11). The high appearance rates at the base of the formation are an artifact of the method. The minor fluctuations in appearance rates between −30 m and −10 m are a mix of meaningful appearance events (Glasius, Essonodon) and the first occurrences of rare taxa (Placodontomys, ?Neoplagiaulax) that likely range to the base of the formation. Per-taxon disappearance rates spike in the topmost bins of the Hell Creek Formation (39% and 88% per bin, respectively), even after correcting for pseudo-extinctions (39% and 59% per bin, respectively). Across the Cretaceous-Paleogene boundary, the corrected disappearance rate in the lowermost Tullock Member remains high (33% per bin), and the corrected appearance rate jumps to 61% per bin. Appearance and disappearance rates fall to ~10% in the Pu2/3 interval. The pattern of estimated per-capita rates largely mirrors that for per-taxon rates, except that the per-capita rate of disappearance in the Pu1 interval is zero; this is because per-capita rates only consider boundary-crossers, and among those taxa that crossed the Cretaceous-Paleogene boundary, all persist into the Pu2/3 interval.

**DISCUSSION**

The Cretaceous-Paleogene mass extinction is a key event in Earth history—it wiped out dinosaur-dominated ecosystems and led to the radiation of most lineages of extant placental mammals. However, important issues regarding this event remain unresolved. Specifically, researchers are divided on the timing and causes of the Cretaceous-Paleogene mass extinction event, with some arguing for a single cause (bolide impact) at the Cretaceous-Paleogene boundary (see Schulte et al., 2010) and others arguing for multiple causes (e.g., bolide impact, climate change, volcanism, marine regression) that combined over long (>10 k.y.) and short temporal scales (1 d–10 k.y.; see Archibald et al., 2010). The details of the ensuing recovery and placental radiation also remain uncertain. Although several studies have focused on early Cenozoic patterns of mammalian diversity (e.g., Stucky, 1990; Alroy, 1999), few have examined the patterns and processes of biotic recovery and diversification from the perspective of paleocommunities. The results from the analyses in this study provide insight into both of these issues. In this section, I discuss these implications in temporal sequence from the lead-up to the Cretaceous-Paleogene boundary, to the Cretaceous-Paleogene extinction and survival, and, lastly, the early Paleocene recovery and radiation of placental.

**Lead-Up to the Cretaceous-Paleogene Boundary: Two Waves of Change**

During the last ~1.9 m.y. of the Cretaceous, changes in the taxonomic diversity and community structure of mammalian faunas in the study area occurred in two waves. The first wave began in the middle to upper third of the Hell Creek Formation (~30 m), less than 650 k.y. before the Cretaceous-Paleogene boundary. In quantity and magnitude, the changes were subtle, but in timing and character, they may be causally related to events at the Cretaceous-Paleogene boundary. The changes include: (1) three turnover events, a last appearance (Parectypodus foxi) and two first appearances (Essonodon browni, Glasbius twitchelli); (2) a trend of decreasing richness and evenness of mammalian faunas, though only that for evenness is statistically significant; (3) a trend of decreasing relative abundances of metatherians; and (4) as reported in Wilson (2005, figure 7 therein), a trend of decreasing mean individual body size of mammalian faunas. Corresponding changes in the diversity of salamander faunas reinforce these results (Wilson et al., this volume). The taxonomic composition of salamander faunas changed little through the Hell Creek Formation, but evenness began declining in the middle to upper third of the formation.

The initiation of these local faunal changes temporally overlaps with the onset of an episode of increased atmospheric pCO2 and estimated mean annual temperatures (e.g., Li and Keller, 1998), referred to as the late Maastrichtian event (Nordt et al., 2003). The late Maastrichtian event, which interrupted a general Maastrichtian cooling trend (Barrera and Savin, 1999), has been recorded globally in marine deposits via stable isotopic analysis (δ13C) of foraminifera (Li and Keller, 1998; MacLeod et al., 2005) and macrofauna (Tobin et al., 2012) and regionally in terrestrial deposits of western North America via isotopic analysis of paleosol carbonates (Nordt et al., 2003) and leaf margin analysis of paleofloras (Wilf et al., 2003). Although estimates of its timing and magnitude vary with ocean depth, geography, and climate proxy, data from paleofloras of North Dakota suggest...
that the warming event, which may have been precipitated by CO$_2$ released from Deccan volcanism (see Ravizza and Peucker-Ehrenbrink, 2003; Sefl et al., 2006; Chenet et al., 2009; Tobin et al., 2012), began ~500–600 k.y. before the Cretaceous-Paleogene boundary. Temperatures remained elevated by ~5–6 °C until a dramatic cooling interval lowered temperatures by ~7 °C within the last ~100 k.y. of the Cretaceous (Wilf et al., 2003). Peak warming occurred ~200–300 k.y. before the Cretaceous-Paleogene boundary coincident with the transition from the HC II megaforal zone to what has been interpreted as the “immigration of the rich, thermophilic HCIII flora” (Wilf et al., 2003, p. 602). From the marine realm, high-resolution changes in the species richness, relative abundances, and geographic ranges of planktic foraminifers and extinctions in mollusks have been temporally correlated with the late Maastrichtian event (Kucera and Malmgren, 1998; Tobin et al., 2012).

On this basis, I suggest that the changes in mammalian faunas that began in the middle to upper third of the Hell Creek Formation may have been in response to the late Maastrichtian event and its associated environmental changes. As discussed in Wilson (2005), the turnover events were possibly the result of shifts in the geographic ranges of the taxa involved, which in turn were a function

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**Figure 11.** (A) Per-capita rates and (B) proportional rates of mammalian turnover for 5 m bins through the Hell Creek Formation and Tullock Member of Garfield County, NE Montana. Per-capita rates (diamonds) are in per-lineage per 100 k.y. units, and are corrected for inferred pseudo-extinction. Proportional rates (circles) are presented as uncorrected (unbroken lines) and corrected (broken lines) for inferred pseudo-extinction. K-Pg—Cretaceous-Paleogene; NALMA—North American land mammal age. The chronostratigraphic framework is based on the following data: Ar/Ar radiometric ages (*), ages for magnetochron boundaries (‡), and an estimated age of the base of the Hell Creek Formation (†).
of their climatic tolerances and those of the taxa on which they depended (e.g., plants; Wilf et al., 2003). The decreasing mean individual body size of mammalian faunas may be a community-level manifestation of Bergmann’s rule extended over geologic time (Blackburn et al., 1999); as paleotemperatures increased during the late Maastrichtian event, larger congeners or closely related species became less abundant than small-bodied congeners or closely related species. This pattern has also been recorded in the mammalian faunas of the Bighorn Basin, Wyoming, across the Paleocene-Eocene thermal maximum (Clyde and Gingerich, 1998). The decreasing evenness of mammalian faunas, as measured by heterogeneity indices, and the declining relative abundances of metatherians are also revealing. In modern ecology, low evenness of communities often reflects ecological instability or stress from environmental disturbance (Magurran, 2004). As such, the trends in mammalian and amphibian communities through the Hell Creek Formation in NE Montana suggest a level of environmental instability prior to the Cretaceous-Paleogene boundary, which is consistent with interpretations of fluctuating δ13C values from sedimentary organic material recorded in the upper Hell Creek Formation of nearby North Dakota (Arens and Jahren, 2002).

The second wave of changes in Lancian mammalian faunas of NE Montana is localized in the upper 10 m of the Hell Creek Formation, corresponding to the last ~200 k.y. of the Cretaceous. These more marked changes punctuated the subtler and more protracted trends that began in the middle to upper third of the Formation. As the relative abundances of metatherians and the evenness of mammalian faunas continued to decline, disappearances spiked in the two highest bins of the Hell Creek Formation (Fig. 11B: 39% and 59%, respectively). A literal interpretation of these data implies that a stepwise pattern of extinction and extirpation occurred among mammalian faunas in NE Montana within the last ~200 k.y. of the Cretaceous. If so, this mammalian turnover would temporally correlate with the global and regional cooling event (up to ~7 °C) that followed the late Maastrichtian event (Wilf et al., 2003; Nordt et al., 2003; Tobin et al., 2012). Alternatively, the pattern of mammalian turnover may appear to be stepwise due to sampling artifacts, namely, the Signor-Lipps effect (Signor and Lipps, 1982). In this case, the true pattern of faunal turnover would be concentrated near or at the Cretaceous-Paleogene boundary. Unfortunately, the sampling profile through this interval does not provide a clear resolution. The highest stratigraphic bin in the Hell Creek Formation (~10 m to ~5 m) is well sampled and includes over 500 specimens, whereas the stratigraphically highest bin (~5 m to 0 m) consists of only 13 specimens, all from one locality (UCMP locality V75162). Recent collecting efforts have targeted this interval, but, for now, the spike in mammalian turnover can only be constrained to the last ~200 k.y. of the Cretaceous.

**Cretaceous-Paleogene Extinction: A Complex Scenario**

Despite uncertainties regarding the timing of this event, the turnover at or near the Cretaceous-Paleogene boundary had enormous influence on mammalian faunas of NE Montana. Of the 28 mammalian lineages present in the upper 10 m of the Hell Creek Formation (a more restrictive stratigraphic bin then La2 in Table 1), 75% did not survive the Cretaceous-Paleogene extinction in any form (e.g., daughter species); they either went extinct or emigrated outside the sampled region of the Western Interior of North America (Lofgren et al., 2004). Metatherians were the hardest hit by this event (91% of lineages), but taxonomic selectivity is not statistically significant among mammals (r = 0.0956, p > 0.2219): 70% of multituberculate lineages and 57% of eutherian lineages also disappeared from the region. Statistical analysis of body mass estimates of victims and local survivors provides evidence of body-size selectivity among mammals across the Cretaceous-Paleogene event (Wilson, 2013). The mean body mass of Lancian mammals from the study area is 112 g (a maximum of ~1.7 kg for Didelphodon vorax), whereas the mean body mass of local survivors is 61 g. Selectivity among feeding ecologies was also apparently at play in the Cretaceous-Paleogene extinction. Lancian therians have traditionally been classified as insectivores, almost by default (e.g., Kielen-Jaworowska et al., 2004). Only a few Lancian mammals have been considered otherwise: *Didelphodon* as a durophagivore-omnivore (Clemens, 1966), *Glasbius* as a frugivore (Clemens, 1966; Wing and Tiffney, 1987), *Essonodon* and *Bubodens* as herbivores (Kielen-Jaworowska et al., 2004; Wilson et al., 2012), and *Cimolestes magnus* and *Nanocuris improvida* as carnivores (Clemens, 1973; Fox et al., 2007; Wilson and Riedel, 2010). More rigorous attempts to infer feeding ecologies of Lancian mammals have largely upheld these characterizations (Hunter, 1997; Gordon, 2003; Wilson, 2004, 2013; Wilson and Self, 2011; Calede and Wilson, 2011; Wilson et al., 2012). In a study of quantifying dental morphology patterns across the Cretaceous-Paleogene boundary in NE Montana, Wilson (2013) classified all of the local survivors as insectivores or animal-dominated omnivores. Although non-insectivores were only a small component of Lancian faunas to begin with, Wilson (2013) argued that this pattern demonstrated selectivity against strict carnivores and taxa with plant-based diets. Locomotion of Lancian mammals has received less research attention, although this aspect of life habit was central to the Cretaceous-Paleogene extinction selection filter forwarded by Robertson et al. (2004). They argued that a severe global pulse of infrared radiation would have occurred in the first few hours after the extraterrestrial impact, and survivors would have found shelter from its effects in water or below ground surface, though they need not have been semi aquatic or burrowing specialists. Preliminary analysis of a collection of mammalian postcranial fragments from Lancian faunas does not support this hypothesis (Borths and Hunter, 2008); rather, it appears that most local survivors were locomotor generalists. Additional research into the locomotor ecologies of the Cretaceous-Paleogene victims and survivors is currently under way by L. DeBey (formerly L. Berg, 2011).

What are the implications of these results on Cretaceous-Paleogene extinction scenarios? On one hand, they show a staggering pattern of 75% local extinction of mammalian species at
or very near the Cretaceous-Paleogene boundary, which, on its own, might be interpreted as the effects of a single, rapid cause, such as a bolide impact. On the other hand, the results show declining trends in the evenness of mammalian communities and relative abundances of metatherians in the ~500–600 k.y. leading up to the Cretaceous-Paleogene boundary, which may be interpreted as signs of ecological instability brought on by the temporally correlated and possibly causally linked late Maastrichtian event and Deccan volcanism. Together, these patterns may reflect a complex scenario for the Cretaceous-Paleogene extinction, in which longer-term environmental disturbances, such as volcanism and climate change, destabilized biotic communities in advance of the “knockout blow” from the bolide impact at the Cretaceous-Paleogene boundary. Several other studies have provided similar indications of biotic change before the Cretaceous-Paleogene boundary that support this interpretation (Marshall and Ward, 1996; MacLeod et al., 1997; Kucera and Malgnen, 1998; Tobin et al., 2012; Wilson et al., this volume). As such, it seems premature to discount the possible role of pre–Cretaceous-Paleogene boundary environmental disturbances (e.g., volcanism, marine regression, climate change) in the mass extinction event and accept evidence of a Cretaceous-Paleogene bolide impact as the lone “smoking gun” (contra Schulte et al., 2010). Indeed, studies have shown that bolide impacts as well as volcanism and climate change are individually poorly correlated with various measures of mammalian change in the Cenozoic fossil record (Alroy, 2003; Prothero, 2004). Arens and West (2008) instead found that, in the Mesozoic and Cenozoic, levels of extinction were elevated when volcanism and impacts co-occurred in the same interval, leading them to argue that mass extinction events most likely result from a combination of press events (volcanism, climate change, marine regression) and pulse events (bolide impact) in close succession, rather than either type of event in isolation. Whereas volcanism and the bolide impact have been central to Cretaceous-Paleogene extinction scenarios, a study by Peters (2008) highlights the important influence of sea-level changes on rates of extinction and extinction selectivity of marine animals during the Phanerozoic. Thus, future studies should focus on the correlation between biotic change in all its forms (e.g., relative abundances) and all possible environmental perturbations in order to better understand what is likely a complex interaction among multiple causes.

Cretaceous-Paleogene Survival: Bloom Taxa and Immigrants

The survival fauna of NE Montana derives from localities less than ~3 m above the Cretaceous-Paleogene boundary, which provide a view of the first ~100–200 k.y. of the Paleocene. The most striking feature of this Pu1 fauna is that it has significantly fewer species (18 spp., Pu1 in Table 1) than the Lancian faunas (30 spp., La2 in Table 1), notwithstanding its far greater sample size (933 specimens; Figs. 3 and 5). This low species richness is typical of Pu1 faunas from the region. Lillegraven and Eberle (1999) recorded 17 Pu1 species from the Ferris Formation in the Hanna Basin of Wyoming, and only 13 species are documented from the Pu1 Mantua Lentil local fauna in the Bighorn Basin of Wyoming (Jepsen, 1940; Van Valen, 1978). This drop in richness would be even more pronounced were it not for the large influx of species during the Pu1 interval (61% corrected appearance rate, 4.99 per-lineage per 100 k.y.). These appearances are almost entirely due to immigration into the area, not in situ evolution (Weil and Clemens, 1998; Clemens, 2010). The source area for these invaders is less certain, but Asia, Baja California, and unsampled upland environments have all been proposed (see Weil, 1999; Clemens, 2010; Archibald et al., 2011). As a result of the extinction and ensuing immigration, the Pu1 fauna of NE Montana is dramatically different from the preceding Lancian faunas. Multituberculate diversity was the least affected. Despite a severe loss of species at the Cretaceous-Paleogene event (70% of lineages), multituberculate richness was buoyed by the immigration of four lineages into the area, including the first eucosmodontid, taeniolabidid, and microcosmodontid. As relative abundances dipped only slightly to 40% (Fig. 9), multituberculates remained an ecologically abundant component of the Pu1 fauna. Metatherians did not fare quite so well. As foreshadowed by their pre–Cretaceous-Paleogene drop in relative abundance, their local richness was decimated by the Cretaceous-Paleogene event (91% of lineages) and was not buffered by subsequent immigration into the area. The sole surviving metatherian lineage Peradectes cf. P. pusillus nevertheless attained a moderately high relative abundance (18%, rank 3) in the Pu1 fauna, indicating that metatherians, even with their declining richness and abundance, remained ecologically important during the survival interval. Eutherians benefited the most from the Cretaceous-Paleogene event. Despite having had the lowest species richness and relative abundances in Lancian faunas and suffering 57% species extinction at the Cretaceous-Paleogene boundary, eutherians became the most species-rich and ecologically abundant members of the Pu1 fauna. Their rebound was largely fueled by the immigration of seven “archaic ungulate” species, representing two families, the Arctocyonidae and Periphytichidae. Similar levels of relative abundances did not immediately accompany this apparent taxonomic radiation of “archaic ungulates” (Van Valen, 1978; Archibald, 1983). Among Pu1 mammals, “archaic ungulates” represent only 10% of the individuals; Procerberus formicarum, a resident “insectivoran” lineage, had the highest relative abundance among mammals (32%). This temporal discordance between richness and relative abundance of “archaic ungulates” mirrors that found among bryozoan clades following the Cretaceous-Paleogene extinction (McKinney et al., 1998) and stresses the importance of abundance data in teasing apart macroevolutionary patterns in the fossil record.

Community structure of the Pu1 fauna strongly diverges from that of Lancian faunas in the study area. Evenness of the Pu1 fauna, as inferred from heterogeneity indices, is significantly lower than those of the Lancian faunas (Fig. 7), and the RAD for the Pu1 locality (UCMP locality V74111) is much steeper than
those for the Lancian localities (Fig. 8), indicating that the Pu1 fauna is composed of a few ecologically abundant species and many rare species. Hunter (1997) also calculated relative abundances and RADs among mammalian assemblages across the Cretaceous-Paleogene boundary, although the main focus of his study was the putative competitive displacement of marsupials by “archaic ungulates.” Due, in part, to the level of taxonomic resolution and time averaging of some localities used in his study, abundance patterns across the Cretaceous-Paleogene boundary were inconclusive. The abundance patterns found in the present study are reminiscent of those found among modern communities after an ecological disturbance or early in ecological succession (Magurran, 2004). They also closely match descriptions of survival biotas in the “standard model” of postextinction biotic recovery (Erwin, 1998, 2001; Solé et al., 2002): The Pu1 mammalian fauna of NE Montana is taxonomically impoverished, supplemented by an influx of immigrants, and predominated by a few opportunistic generalists or bloom taxa. Bloom taxa have been reported from other post–Cretaceous-Paleogene survival biotas, such as that represented by the “fern spike” from the floral record (e.g., Fleming and Nichols, 1990), Guenelbitria cretacea among planktic foraminiferans (D’Hondt, 2005), and Litiopa among molluscan faunas (Hansen et al., 1993). However, the structure of recoveries differs among geographic regions; the bloom taxa may differ (Sweet and Braman, 1992) or not exist at all (Jablonski, 1998), or the level of invasion by immigrants may vary (Jablonski, 1998). Among mammals, “archaic ungulates,” which immigrated into the region, have traditionally been viewed as the post–Cretaceous-Paleogene bloom taxa by virtue of their relatively high species richness in early Puercan faunas in North America (Van Valen, 1978; Archibald, 1983; Maas and Krause, 1994). However, the relative abundance results clearly show that, in the study area, local incumbents of broad taxonomic representation were the first to thrive in the aftermath of the Cretaceous-Paleogene extinction. These bloom taxa were the “insectivoran” Procerberus formicarum, the multituberculate Mesodma thompsoni, and the metatherian Peradectes cf. P. pusillus (Fig. 8). Perhaps the combination of their status as local incumbents (Jablonski, 2000) and small-bodied insectivores within a detritus-based food chain (Sheehan and Hansen, 1986; Wilson, 2013) allowed them to ecologically preempt resources during the survival interval. In contrast, presumed low primary productivity during a protracted floral recovery (Wing et al., 1995; Hotton, 2002; Wilf and Johnson, 2004) might not have been able to support large colonizing populations of omnivorous “archaic ungulates.” Low diversity of early Paleocene plant-insect associations in the leaf damage record also implies prolonged food-web disturbance that would support this scenario (Labandeira et al., 2002; Wilf et al., 2006).

Early Paleocene Recovery and Placental Radiation: Major Faunal Reorganization

The Pu2/3 mammalian fauna from the middle of the Tullock Member reflects the major taxonomic and ecological reorganization that took place during the transition from the survival interval to later phases of recovery. Interpolation between two radiometric ages that bracket UCMP locality V73080 indicate that the Pu2/3 fauna is from ~600–700 k.y. after the Cretaceous-Paleogene extinction (Fig. 3). A considerable amount of turnover occurred between the Pu1 and Pu2/3 mammalian faunas. The corrected rate of disappearances in the Pu1 interval is 33%. It is significantly less than that across the Cretaceous-Paleogene boundary, but nevertheless it implies that several of taxa from the Pu1 survival fauna were short-lived. Among them, “insectivorans” and metatherians of NE Montana are prime examples of what Jablonski (2002) coined “dead clades walking,” which are taxa that survive mass extinctions but decline in richness, become marginalized, or simply fail to diversify during the recovery interval. The “insectivoran” Procerberus and the metatherian Peradectes were bloom taxa in the Pu1 survival fauna. Both genera persisted into the Pu2/3 interval, but the relative abundances of their parent taxa plummeted to 1%, and the richness of their parent taxa never rose above three species in the remainder of the local section (Fig. 6). The traits that promoted their evolutionary fitness during the Cretaceous-Paleogene interval were perhaps no longer advantageous in the face of changing environmental conditions or increased competition later in recovery. The corrected appearance rate for the Pu2/3 interval was not large after accounting for the estimated amount of time between Pu1 and Pu2/3 assemblages (~600 k.y.), but mammalian richness more than doubled from the Pu1 to Pu2/3 interval (Fig. 3). The Pu2/3 assemblage is known from an extensive collection of more than 2000 specimens, but the number of species in it (40 spp.) is still significantly greater than expected for its sample size (Fig. 4). In fact, the richness of the Pu2/3 fauna exceeds levels attained by all Lancian faunas in the study area (e.g., 26 spp., UCMP locality V73087) and elsewhere in the region (Stucky, 1990; Alroy, 1999; Cifelli et al., 2004). This doubling of species richness mirrors the pattern in the Hanna Basin, where there are 27 species in the Pu2 interval versus 13 in the Pu1 interval (Lillegraven and Eberle, 1999). Although there is no single definition of biotic recovery, this pattern satisfies at least one common measure—the return to pre-extinction levels of richness (Erwin, 1998). The evenness of the fauna would also be expected to return to pre-extinction levels during the course of recovery. Unfortunately, species-level abundance data are not yet available for the Pu2/3 assemblage (UCMP locality V73080); however, among the specimens from this assemblage that have been identified to the genus level, the distribution of relative abundances appears to be more even (data not shown) than that of the Pu1 survival fauna and similar to those of the Lancian faunas from the study area (Fig. 8).

These results suggest that the mammalian fauna of NE Montana recovered, at least in taxonomic diversity, by ~600–700 k.y. after the Cretaceous-Paleogene extinction, and as collecting efforts fill in the ~40 m stratigraphic gap that separates the Pu1 fauna from the Pu2/3 recovery fauna, the nature and timing of this recovery will become more precise. Whereas it is commonly held that the duration of the recovery lag positively correlates
with the severity of the extinction event (Erwin, 1998, 2001), Kirchner and Weil (2000) in a time-series analysis of the Phanerozoic marine fossil record showed that origination rates peak ~10 m.y. after extinction rates peak, regardless of the severity of the event. In contrast, empirical data from the Cretaceous-Paleogene event show tremendous variation in duration of recovery lags. In the marine realm, both planktic foraminifera and calcareous nanoplanckton assemblages suffered more than 90% species extinction across the Cretaceous-Paleogene boundary, yet their recovery lags were no more than a few hundred thousand years (D’Hondt, 2005; Jiang et al., 2010). In contrast, isotopic evidence suggests that the return of pre–Cretaceous-Paleogene levels of marine productivity and export of organic carbon from surface to deep waters occurred somewhat later—500 k.y. to 2 m.y. after the extinction event (D’Hondt, 2005). In the terrestrial realm, plants incurred more moderate levels of extinction across the Cretaceous-Paleogene boundary (57% of leaf morphospecies; Wilf and Johnson, 2004), but they experienced a more prolonged recovery interval. Floras in the Western Interior of North America remained low in diversity for nearly the entire Paleocene (Wing et al., 1995; Wilf and Johnson, 2004; Wilf et al., 2006); one exception is the high-diversity early Paleocene tropical rain forest from Castle Rock, Colorado, which hints at the physiographic complexities of recovery (Johnson and Ellis, 2002). The Paleocene record of insect damage diversity largely mirrors the floral pattern (Wilf et al., 2006). Thus, the recovery of mammalian faunas in NE Montana, as measured by taxonomic diversity and community structure, occurred more quickly than other aspects of terrestrial ecosystems (flora, insects) but in step with aspects of the marine biota.

The considerable amount of variability among patterns of Cretaceous-Paleogene recovery likely reflects (1) actual variation in the severity of the extinction as experienced by each of these taxonomic groups in each geographic region and environment; (2) the highly complex and variable processes of ecological recovery and reassembly of communities and food webs; (3) divergent methods and proxies as well as inherent difficulties of measuring biotic recovery in the fossil record; or (4) some combination of these factors.

The taxonomic diversity trends of mammalian faunas of NE Montana, from the Pu1 interval through the To1 interval (~1.2 m.y. after the Cretaceous-Paleogene boundary), also record early stages of placental radiation, although the diversity of Pu1 immigrants implies the radiation was initiated elsewhere during the Cretaceous. Prior to the Cretaceous-Paleogene boundary, multituberculates were the most diverse group of mammals in Lancian faunas in the study area. Their diversity remained relatively steady across the Cretaceous-Paleogene boundary, increased in the Pu2/3 interval, and fell sharply in the To1 interval (4 species, 10% relative abundance). Large-scale studies of multituberculate diversity in the Western Interior of North America have also shown a decline in relative abundances from the Puerkan to Torrejonian, although the drop was more modest than recorded here (Van Valen and Sloan, 1966; Krause, 1986). Moreover, in these studies and in a global study (Wilson et al., 2012), multituberculate generic richness remained high through most of the Paleocene and only dropped off between the Tiffanian and Clarkforkian NALMAs, ~8 m.y. later than in NE Montana. This discrepancy could be explained in several ways: (1) The low multituberculate richness in the To1 fauna of NE Montana is an artifact of relatively small fossil sample sizes (78 total specimens vs. 2081 total specimens for the Pu2/3 assemblage); (2) the low multituberculate richness in the To1 fauna of NE Montana is accurate but is an oddity among early and mid-Paleocene mammalian faunas of the region; or (3) the high multituberculate richness at the regional scale is accurate but reflects a mid-Paleocene increase in beta diversity that masks a concurrent drop in alpha diversity. Increased sampling of the To1 fauna of NE Montana will likely increase the number of mammalian species sampled as suggested by item 1; however, it is unlikely that it would substantially change the proportional representation of higher-level taxa, including multituberculates. As for items 2 and 3, these explanations cannot be fully evaluated yet.

Although workers have suggested and in some cases demonstrated latitudinal provinciality among early and mid-Paleocene mammalian faunas of western North America (Stucky, 1990; Weil, 1999), the To1 interval remains poorly sampled outside of the San Juan Basin of New Mexico (Lofgren et al., 2004). For now, I contend that the To1 assemblages of NE Montana at minimum accurately reflect a general declining trend of multituberculate diversity in the local section. Concurrently, eutherians became increasingly more diverse through the local section. In the Pu1 and Pu2/3 intervals, they represented about half of all mammalian species, and by the To1 interval, they make up nearly 85% of all mammalian species, with relative abundances closely tracking this pattern.

Among eutherians, “insectivorans” played an important role as local survivors and bloom taxa in the Pu1 interval, but their role in terms of richness and relative abundance significantly diminished in subsequent intervals. Instead, “archaic ungulates” and plesiadapiform primates, in different ways, dominated the initial phase of the placental radiation in the local section. The evolutionary radiation of “archaic ungulates” was seeded with the immigration of seven species into the study area immediately after the Cretaceous-Paleogene extinction (Pu1 interval). Despite increasing levels of richness during the Puerkan, “archaic ungulates” remained numerically marginal members of local mammalian communities (10%–12% of all individuals) until the To1 interval. In the To1 interval, they represented 50% of all species and 29% of all individuals. In contrast, Archibald (1983) suggested that “archaic ungulates” might have competitively displaced latest Cretaceous metatherians based on a “double wedge” pattern of species richness and guild occupancy. In a detailed study, Hunter (1997) found little evidence for competition between metatherians and “archaic ungulates,” although recognized uncertainties in the ages of some localities hampered his analyses. Relative abundance patterns of metatherians and “archaic ungulates” from the present study support Hunter’s conclusion.
In contrast to “archaic ungulates,” plesiadapiform primates did not immigrate into the study area until the Pu2/3 interval and then with only three species; however, upon their first arrival, they were ecologically abundant members of local mammalian communities (25% of all individuals). By the To1 interval, plesiadapiforms were even more abundant, consisting of nearly half of all individuals, though they were still only represented by four species. Despite divergent patterns of diversification and abundance, early Paleocene “archaic ungulates” and plesiadapiforms share dental traits indicative of trends toward omnivorous and herbivorous dietary habits (e.g., low rounded molar cusps, broad talonid basins). Other higher-level taxa that went on to contribute to the early radiation of placentals also made their first appearance in the local section in the Pu2/3 interval (trisodontids, creodonts, taeniodonts, and pantodons). These taxa do not attain high-levels of species richness in the local section, but they substantially expand the range of ecomorphologies within mammalian communities of NE Montana. They include carnivores, herbivores, and rooters of medium body size (5–9 kg body mass) (Archibald, 1983; Maas and Krause, 1994). Thus, it seems that the taxonomic diversification and increasing ecological abundance of placentals were accompanied by ecological diversification and an increasingly complex trophic structure (quantification of this pattern is currently under way; Wilson and Self, 2011; Calede and Wilson, 2011; Wilson, 2013), indicating that in the study area, the early Cenozoic placental radiation was in full swing less than 1 m.y. after the Cretaceous-Paleogene event.

These results amplify the results of previous studies (Archibald, 1983; Stucky, 1990; Maas and Krause, 1994; Alroy, 1999, 2000). Using a data set from western North America that was partitioned into 1 m.y. bins, Alroy (2000) found that rates of species origination were significantly higher in the first 1 m.y. bin immediately after the Cretaceous-Paleogene boundary than at any other time in the Cenozoic. Converting his instantaneous turnover rates (supplemental Table 2 in Alroy, 2000) into per-lineage per 100 k.y. units for comparison with this study, the origination rate for his first Paleocene interval is 0.174 per-lineage per 100 k.y. In the present study, the available temporal resolution allowed me to partition Alroy’s first Paleocene interval into two unequal bins. The per-capita appearance rate in the first 100 k.y. of the Paleocene was 0.499 per-lineage per 100 k.y., which is nearly three times higher than Alroy’s rate. The origination rate in the next 700 k.y. of the Paleocene dropped to 0.111 per-lineage per 100 k.y., but was still higher than all bins except the first 1 m.y. bin in Alroy’s data set (supplemental Table 2 in Alroy, 2000). Archibald (1983) also calculated post–Cretaceous-Paleogene mammalian rates of turnover from the study area in NE Montana; however, he used a slightly different data set, age model, and rate formula than used here. Nevertheless, his results also show a particularly high appearance rate in the Pu1 interval, followed by a decreased but still elevated rate in the Pu2/3 interval. Stucky (1990) and Maas and Krause (1994), analyzing data sets from western North America and at the temporal scale of NALMA zones, also recovered exceptional early Paleocene origination rates that closely correspond to the results presented here.

The Cretaceous-Paleogene boundary was clearly a watershed moment for placental mammals in western North America. Whereas paleontologists (e.g., Simpson, 1937; Maas and Krause, 1994) and molecular systematists (Bininda-Emonds et al., 2007) agree that the Paleocene-Eocene interval was the inflection point for the diversification of extant placental lineages, this study and others show that, within ~1 m.y. of the Cretaceous-Paleogene boundary, mammalian communities, whether composed of extant or “archaic” lineages, underwent a dramatic increase in taxonomic diversity, ecological abundance, and ecomorphological diversity of placentals. This resulted from an exceptionally high rate of appearance that was initially driven by immigration and later by both speciation and immigration (contra Maas and Krause, 1994). Although the Paleocene–Eocene transition of mammalian communities included some ecological restructuring, it was mainly a continuation of trends initiated in the earliest Paleocene, with “modern” placentals increasingly filling the roles previously held by “archaic” placentals and multituberculates (e.g., Simpson, 1937; Maas and Krause, 1994). This Cretaceous-Paleogene transition was almost certainly spurred by factors associated with the mass extinction event, such as ecological release, vacated ecospace, dislodged incumbents, or more indirect effects (e.g., changes in vegetation structure); testing these hypotheses is a challenge for future studies. Paradoxically, the placental radiation began during the early Paleocene while floral diversity in the Western Interior of North America remained largely depressed, suggesting that mammalian recovery and placental radiation may have tracked other aspects of Paleocene floral change, such as the hypothesized shift from a more open to a more closed vegetation structure, as has been proposed elsewhere (Wing and Tiffney, 1987; Stucky, 1990) but should be more fully explored.

CONCLUSIONS AND PROSPECTUS

This study provided high-resolution temporal patterns of mammalian diversity and community structure during arguably the most critical episode in mammalian evolution. Despite a long history of work on the Cretaceous-Paleogene events, the results of this study are unique in that they incorporate assemblage-based relative abundance data—a source of ecological information that is often neglected in paleontological studies because they are difficult to obtain, and their fidelity in the fossil record is subject to sampling and taphonomic biases. In other studies, key insights about extinction and recovery dynamics have been revealed through decoupled or discordant patterns of relative abundances and taxonomic richness (McKinney et al., 1998; Wagner et al., 2006). In this study, the resulting patterns of diversity and community structure shed light on the complexity of the Cretaceous-Paleogene events in the following ways: (1) Declines in the evenness of mammalian faunas and relative abundances of metatherians that predate the Cretaceous-Paleogene boundary.
provide support for causal mechanisms of the extinction that account for ecological instability before the bolide impact (e.g., Deccan volcanism); (2) the highly uneven, species-poor earliest Paleocene mammalian fauna, which has a few incumbent species of high abundances and many “archaic ungulate” immigrant species of low abundances, validates characterizations of postdisaster survival biotas based in ecological theory (Solé et al., 2002); and (3) the decoupled but individual patterns of early Paleocene richness and relative abundances of “archaic ungulates” and plesiadapiform primates show the variable paths that make up the early evolutionary radiation of placental...

Projects currently under way and being planned within this study hold promise for further refining our views of the Cretaceous-Paleogene events; they include fossil collecting to fill critical key stratigraphic gaps (e.g., between Pu1 and Pu2/3 faunas) and quantitative approaches to characterize ecomorphologies (e.g., dental complexity, microwear) and model food webs across this interval. Nevertheless, it should be stated that analysis of the Cretaceous-Paleogene extinction and recovery of the continental biota presently suffers from a myopic geographic scope. Vertebrate fossil data are almost entirely drawn from the northern Western Interior of North America with only a few of these areas providing a subformational succession of fossil localities (see Wilson et al., 2010; Donohue et al., 2013). In light of the spatial complexity of mass extinctions and recoveries (Jablonski, 1998), broad generalizations of the Cretaceous-Paleogene extinction and recovery should be approached with caution until we have a wider geographic handle on the events during this interval. It follows that future efforts to develop parallel study systems in other geographic areas, examine other taxonomic groups, and integrate data sets for a more complete view of terrestrial ecosystems will yield substantial gains in our understanding of the Cretaceous-Paleogene events.

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