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Early mammalian recovery after the end-Cretaceous mass extinction: A high-resolution view from McGuire Creek area, Montana, USA

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ABSTRACT

Changes in mammalian faunal composition and structure following the Cretaceous–Paleogene mass extinction are central to understanding not only how terrestrial communities recovered from this ecological perturbation but also the evolution of archaic groups leading to extant mammalian clades. Here, we analyzed changes in mammalian local faunas during the earliest Paleogene biotic recovery on a small spatiotemporal scale. We compiled samples of mammals from four localities in the Hell Creek Formation and Tullock Member of the Fort Union Formation, in the McGuire Creek area, McCone County, Montana, USA, and placed these localities into a high-precision chronostratigraphic framework using $^{40}Ar/^{39}Ar$ tephra ages and magnetostratigraphy. Within this framework, we quantitatively compared faunal composition, heterogeneity, and richness among McGuire Creek local faunas and made broader comparisons to other earliest Paleogene faunas from throughout the Western Interior of North America. In the first ~320 k.y. of the recovery, mammalian local faunas at McGuire Creek, all of which can be placed in the Puercan 1 North American Land Mammal Age (NALMA) interval zone, underwent modest increases in taxonomic richness and heterogeneity, indicating the beginning of biotic recovery; however, no McGuire Creek fauna reached fully recovered levels of taxonomic richness. Further, appearance of immigrant taxa such as *Purgatorius* in younger McGuire Creek faunas demonstrates important compositional changes within the Pu1 of McGuire Creek. These results highlight the difficulties with describing the nuanced mammalian recovery process using the NALMA system and emphasize the increasing importance of high-precision dating, especially when comparing faunas across large geographic distances.

INTRODUCTION

The Cretaceous–Paleogene (K-Pg) mass extinction triggered a distinct shift in terrestrial ecosystems, from vertebrate faunas dominated by dinosaurs to those dominated by mammals. Mammalian extinction levels were as high as 75%–93% of species across the K-Pg boundary (Wilson, 2014; Longrich et al., 2016), but in the aftermath, mammals rapidly increased in their range of body sizes (Alroy, 1999; Smith et al., 2010), taxonomic richness (Lillegraven, 1972; Stucky, 1990; Alroy, 1999; Wilson, 2014) and ecological disparity (Wilson, 2013; DeBey and Wilson, 2014; Halliday and Goswami, 2016; Grossnickle and Newham, 2016). Many modern clades of mammals originated around this time as well (Archibald and Deutschman, 2001; Meredith et al., 2011; O'Leary et al., 2013; dos Reis et al., 2014). This critical episode of mammalian diversification is also intimately connected to the biotic recovery from the K-Pg mass extinction. Thus, study of this event has the potential to shed light on early mammalian evolution and, more broadly, on our understanding of the process of ecosystem rebuilding following environmental devastation of the K-Pg and potentially other extinction events.

Garfield and McCone Counties in northeastern Montana, USA (Fig. 1), comprise an area particularly well suited for the study of biotic and abiotic patterns before and after the K-Pg mass extinction. Long-term paleontological and geological study of the exposures of the Hell Creek Formation and Tullock Member of the Fort Union Formation (Clemens and Hartman, 2014) have amassed abundant samples of microfossils and a high-resolution chronostratigraphy (Swisher et al., 1993; LeCain et al., 2014; Sprain et al. 2015, 2018). Previous studies that have focused on post-K-Pg mammalian faunal change in this study area (Archibald, 1982; Clemens, 2002; Wilson, 2014) have examined only two intervals of the recovery, one immediately after the mass extinction (<70 k.y.) and another ~305–780 k.y. later. Finer sampling of the recovery pattern has been hindered by a lack of mammal-bearing localities from intermediate strata.

In this study, we report on three new earliest Paleocene mammalian fossil assemblages from localities in the lower part of the Tullock Member in McCone County. These localities are all located within an area of 2 km^2 in the McGuire Creek area in McCone County and are temporally constrained by high-precision $^{40}Ar/^{39}Ar$ ages and magnetostratigraphy to the first ~320 k.y. after the K-Pg mass extinction. The restricted spatial scope of this study minimizes the influence of spatial and environmental gradients (e.g., latitudinal temperature gradients) or biogeographic provinciality that could compromise data sets for localities separated by tens or hundreds of kilometers. The fine temporal scale enables us to more precisely measure the timing and rate of changes in the mammalian local faunas under study, including changes in both taxonomic richness and faunal structure. However, we also recognize that the local McGuire Creek biotic recovery was taking place in the regional context of northeastern Montana, within the broader context of the Western Inte-

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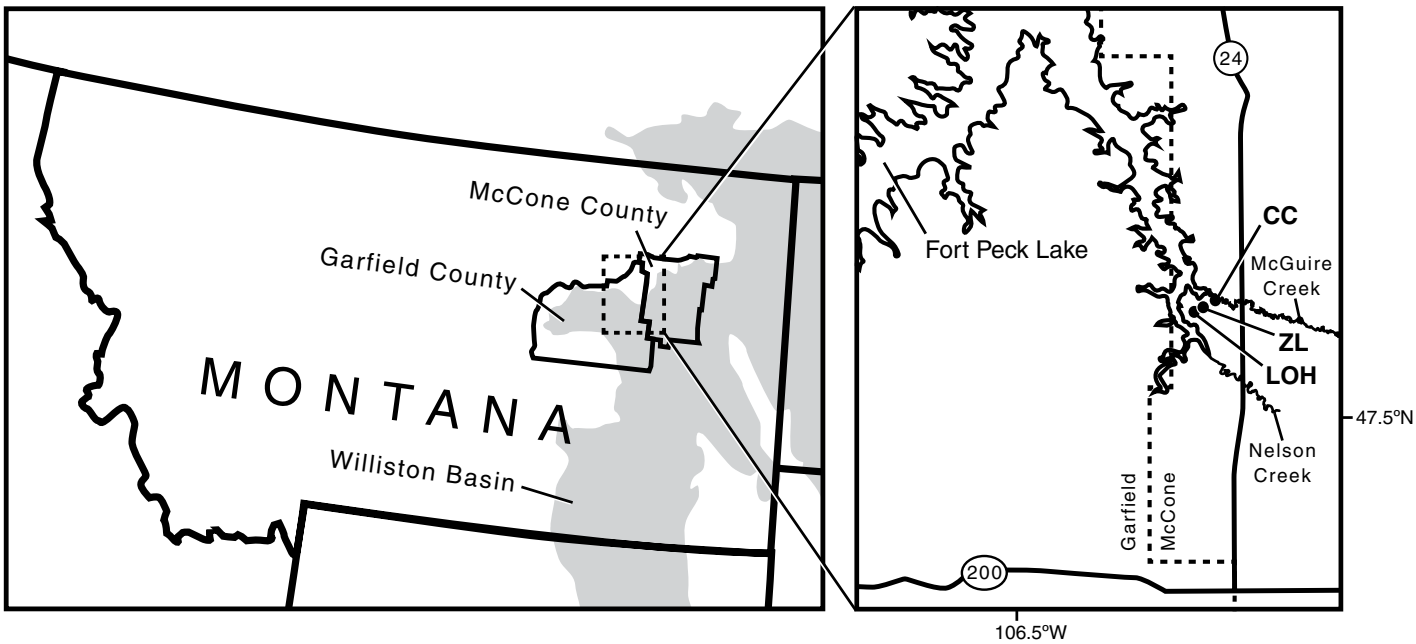

Figure 1. Map of vertebrate microfossil localities in the McGuire Creek area, McCone County, Montana, USA. ZL—Z-Line (ZLQ and ZLE, combined); LOH—Luck O Hutch; CC—Coke's Clemmys.

rior of North America as a whole. We therefore make comparisons among local, regional, and continental patterns of mammalian biotic recovery in the earliest Paleocene of North America to more fully understand the significance of McGuire Creek faunal change in relation to the bigger picture of post-K-Pg Boundary (KPB) biotic recovery. Our results add another piece of the puzzle to our growing understanding of mammalian evolution after the extinction of non-avian dinosaurs and provide new information about the spatiotemporal variability of the process of biotic recovery within the Western Interior of North America.

Research Institutions

In this study, we have linked microfossil sample localities and field crews with the associated research institutions using the following abbreviations: RAM, Raymond M. Alf Museum of Paleontology; UCMP, University of California Museum of Paleontology; and UWBM, University of Washington Burke Museum of Natural History and Culture.

GEOLOGIC SETTING

The McGuire Creek watershed is located within the northwestern portion of the Williston Basin and is a part of an area that has been extensively studied for changes around the K-Pg mass extinction, known as the Hell Creek region. Outcrops in the McGuire Creek area comprise two formations: the Hell Creek Formation (mostly Cretaceous) and the Tullock Member of the Fort Union Formation (mostly Paleogene). Both formations are broadly fluvial in origin, comprising siltstones, mudstones, lignites, and sandstones, which are common deposits representative of flood plains and channels (Gill and Cobban, 1973; Cherven and Jacob, 1985; Fastovsky, 1987). The contact between the Hell Creek and Fort Union Formations is commonly defined by the first laterally persistent lignite (Brown, 1952), known as the Z coal (Collier and Knechtel, 1939), above the highest remains of unreworked in situ non-avian dinosaurs (Calvert, 1912; Brown, 1952; Clemens and Hartman, 2014; Hartman et al., 2014; Moore et al., 2014). The contact is generally characterized by a color change from the grays of the Hell Creek Formation to yellower sediments in the Tullock Member (Archibald et al., 1982; Fastovsky and Bercovici, 2016). In the Tullock Member, variegated bedding (Fe-stained laminated siltstones), massive channel sandstones, and lignite deposits are also more common (Archibald, 1982; Fastovsky and Bercovici, 2016). All these differences suggest a change in hydraulic flux and a rise in water table associated with the formational contact (Fastovsky, 1987; Fastovsky and Bercovici, 2016). In the western portion of the Hell Creek region (central Garfield County), the formational contact is typically coincident or nearly coincident with the KPB (Moore et al., 2014; Sprain et al., 2015). There, within or just below the first laterally persistent lignite (~15 cm thick), the horizon associated with the Chicxulub impact is found within a claystone marked by an anomalously high Ir concentration. In some places this horizon also includes shocked quartz and spherules (Alvarez et al., 1980; Bohor et al., 1984; Clemens and Hartman, 2014; Moore et al., 2014). For this reason, in that area the formational contact coal has been called the Iridium Z, or IrZ, coal (Swisher et al., 1993).

In the eastern portion of the Hell Creek region, where McGuire Creek is located, the impact claystone has not been identified, but it has been shown through $^{40}Ar/^{39}Ar$ dating that the Z coal most commonly ascribed to the formational contact is younger than the KPB, with a difference in age of 30 ± 18 ka (Sprain et al., 2015). At McGuire Creek, the formational contact, as defined by Lofgren (1995), is at the base of a thick basal Z coal (~1 m), dubbed the McGuire Creek Z (MCZ) coal (Fig. 2) for its pervasive outcropping in the McGuire Creek basin. Lofgren (1995) mapped the MCZ coal over a ~20 km^2 area extending from T22N R43E S17 in the northwest to T21N R43E S11 in the southeast (Plate 1, of Lofgren, 1995). The color change between gray and yellow sediments occurs below the MCZ coal and is roughly coincident with a ~10-cm-thick carbonaceous shale layer. This carbonaceous shale layer is also coincident with a negative carbon isotope excursion (measured near the Z-Line locality at McGuire Creek), which Arens et al. (2014) interpreted as marking the KPB; however, neither an impact

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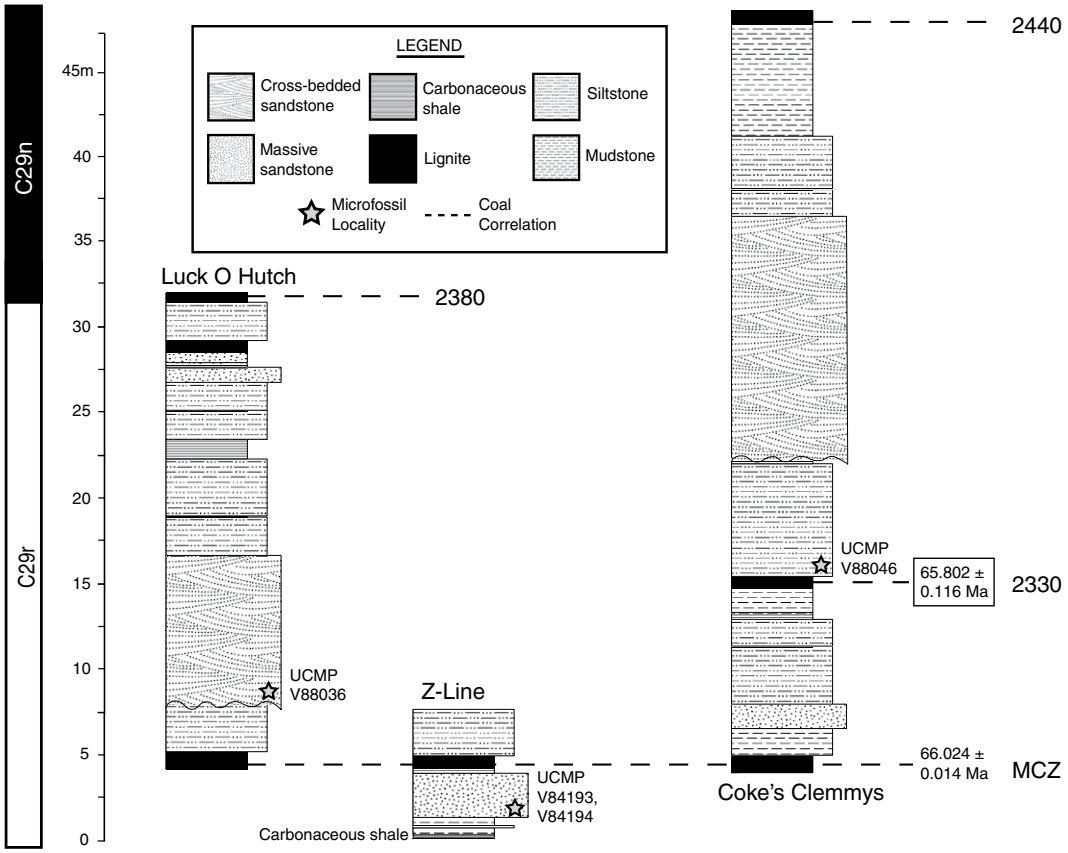

Figure 2. Composite stratigraphic section including vertebrate microfossil localities in the McGuire Creek area, McCone County, Montana, USA. (Localities are arranged according to longitude, westernmost on left to easternmost on right.) Also shown are the coals used in this study; the numbers 2330, 2380, and 2440 identify them by approximate elevation expressed in feet. The age enclosed in a rectangle is the date calculated in this study; the other age (not enclosed) is the pooled age for the McGuire Creek basal Z coal (MCZ) from Sprain et al. (2018).

claystone nor the Nirvana bentonite layer, which was derived from a tephra unique to the IrZ coal found in Garfield County (Ickert et al. (2015), is readily apparent. It is therefore possible that the carbonaceous shale layer may be roughly correlative to the IrZ coal.

The MCZ coal has been identified across the Hell Creek region on the basis of the presence of the distinctive Lerbekmo and McGuire Creek bentonites; derived from tephras, both contain phenocrysts of unique chemical and isotopic composition (Ickert et al., 2015). Sprain et al.'s (2015) dating of the McGuire Creek tephra from within this coal near the Z-Line locality yielded an age of 65.998 ± 0.044/0.061 Ma (1 sigma; slash separates analytic and systematic uncertainty), consistent with the placement of this coal above the first appearance of Paleocene pollen (Hotton, 2002). Pooling this age with other dates obtained for this tephra from across the Hell Creek region yields an inverse-variance weighted-mean age of 66.024 ± 0.014/0.044 Ma (Sprain et al., 2018). We consider this pooled age to be the best constraint on the age of the MCZ coal and will refer to it throughout the rest of the study.

Within the McGuire Creek area, three other coals above the MCZ are shown to be laterally persistent based on mapping conducted by one of us (Lofgren) in 1996. These coals are referred to by numerical designations, which roughly correspond with their altitude expressed in feet: 2330, 2380, and 2440 (Fig. 2).

MATERIALS AND METHODS

Mammalian Fossil Localities: Geological Descriptions

During the summers of 2014, 2015, and 2016, we revisited four vertebrate microfossil localities in the McGuire Creek area: UCMP V84193/UWBM C2366 (Z-Line Quarry, ZLQ), UCMP V84194/UWBM C2554 (Z-Line Quarry East, ZLE), UCMP V88036/UWBM C1700 (Luck O Hutch, LOH), and UCMP V88046/UWBM C1908 (Coke's Clemmys, CC) (Figs. 1 and 2).

The Z-Line localities (ZLQ and ZLE, or collectively referred to as ZL) are stratigraphically between the carbonaceous shale layer and the MCZ coal. The carbonaceous shale layer there is ~10 cm thick, dark gray, and very fissile. It grades laterally into coal, and ~4 cm from the top of the layer is a 1–2-cm-thick fine-grained pink (Munsell color 5 R 6/2) siltstone. This carbonaceous shale layer can be visually traced to the carbonaceous shale measured by Arens et al. (2014) where the negative carbon isotope excursion was identified. A 1–2-cm-thick, light-gray to pink claystone forms the lower bound to the carbonaceous shale. This claystone does not have any obvious indicators of the impact layer, such as spherules. Approximately 4 m above the carbonaceous shale is the MCZ coal. There the coal is ~70 cm thick and contains both the Lerbekmo and McGuire Creek bentonites (Ickert et al., 2015). Between the carbonaceous shale and the MCZ coal is the Z-Line channel deposit, containing both ZLQ and ZLE fossil localities, which are both near the base of the channel deposit and ~3 m below the MCZ coal but are ~12 m laterally apart from each other. The fossil-bearing horizon at ZLE is a ~12 cm thick, poorly sorted, brown to tan fine-grained sandstone that includes carbonaceous plant hash as well as vertebrate fossils. The fossil-bearing horizon at ZLQ is similar to that at ZLE, in that fossils occur at the base of the sandstone, directly above the carbonaceous shale (Fig. 2). Lateral to the Z-Line channel deposit, a series of light-gray to buff mudstones, siltstones, and fine-grained sandstones crop out between the carbonaceous shale layer and the MCZ coal.

The LOH is ~2.3 m above the MCZ coal at the base of a ~9 m-thick channel deposit called Jack's Channel, which consists of a medium- to

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fine-grained gray sandstone (Fig. 2). Large indurated blocks within the channel show bedding planes that are both horizontal and cross-bedded. The base of the channel deposit is erosive and locally occurs between 2.0 and 2.7 m above the MCZ coal. An indurated Fe-stained layer that is laterally variable in thickness occurs at the base of the channel deposit. Vertebrate fossils occur in laterally discontinuous lenses within that layer, although the fossils are not numerous. These lenses include numerous Fe concretions, carbonaceous plant material, and small pieces of coal. The 2380 coal is exposed ~14.5 m above the top of Jack's Channel. That coal here is ~0.5 m thick and contains a thin tephra (bentonite) layer (~2 mm thick) ~1 cm below the top of the coal. Another coal layer crops out ~2 m below the 2380. Based on mapping and altitude, we do not believe this coal to be the 2330 coal and instead believe that Jack's Channel cut out the 2330 coal. Sprain et al. (2018) collected paleomagnetic samples around the 2380 coal at this location and showed that the C29r/C29n reversal, dated at 65.724 ± 0.013/0.044 Ma, occurs right around the 2380 coal and significantly above the fossil locality.

The Coke's Clemmys fossil locality (CC) is ~10.3 m above the top of the MCZ coal and is directly on top of the 2330 coal (Fig. 2). Between the MCZ and the 2330 coal at this locality is ~10 m of alternating siltstone and mudstone layers with a 1.4-m-thick sandstone layer exposed ~1.5 m above the MCZ coal. CC is within a ~6.5-m-thick channel deposit that mostly consists of siltstone. The fossil-bearing horizon falls within a cross-bedded sandstone at the base of the channel deposit. The channel locally cuts down into the 2330 coal, which here is ~0.5 m thick and contains one tephra (bentonite) layer that was sampled for $^{40}Ar/^{39}Ar$ analysis (Fig. 3). The tephra layer occurs ~5 cm below the top of the coal. It is 2 cm thick, red/brown (10 R 3/4), and largely unconsolidated. Euhedral grains of feldspar are identifiable. The tephra is laterally discontinuous and locally is cut out by the CC channel. Around 1 kg of tephra was collected for analysis. About 0.5 m above the top of the CC channel is a larger channel deposit, ~14 m thick, that consists of fine- to medium-grained sandstone (litharenite). This larger channel has an erosive base, apparent cross-bedding, and large indurated blocks. Eleven meters above the top of the large channel deposit, the 2440 coal crops out, ~32 m stratigraphically above CC. Although the 2380 coal is not exposed here, mapping shows that it is cut out by the large channel fill above CC, whose base is ~10 m above the 2330 coal in the NE1/4, SW1/4, S3, T21N, R43E. This large channel fill can be observed to contact the 2380 coal and is overlain by strata that are capped by the 2440 coal. Thus, there is little doubt that the CC channel was once capped by the 2380 coal.

In sum, the localities studied here are in sandstone channel-fill deposits of the basal part of the Tullock Member except for the Z-Line localities, which occur in the last few meters of the upper-most Hell Creek Formation. ZLQ and ZLE are stratigraphically the lowest of the four localities and occur at approximately the same level; LOH and CC are stratigraphically higher than both ZLQ and ZLE, but their relative stratigraphic order remains unresolved.

Mammalian Fossil Collection

The mammalian fossil collection compiled for this study consists of specimens of isolated teeth and fragmentary jaws. We recovered specimens from the four vertebrate microfossil localities described above (ZLQ, ZLE, LOH, and CC) via surface collection and underwater screenwashing of fossiliferous sediment over the course of several field seasons (in the 1980s and early 1990s by UCMP and RAM field crews led by Lofgren and in the 2010s by UWBM field crews led by Smith and Wilson). Similar techniques were used in all collecting events, to minimize bias among samples. Only specimens that we could confidently identify to the genus level or lower were included in our data set, with a few exceptions: four specimens referred to Metatheria, indeterminate; two specimens referred to the metatherian family Alphadontidae, and one specimen referred to the eutherian Periptychidae (a family of archaic ungulates). Although these specimens are not complete enough to identify to the genus level, we included them in our data set because they represent taxa that are unique in the sample (see Systematic Paleontology in the GSA Data Repository[1]). The excluded specimens include small fragments of multituberculate teeth, single cusps of therian teeth, or specimens otherwise too worn to preserve genus-level diagnostic features.

Terminology

Fauna Versus Local Fauna

We use the term "local fauna" sensu Woodburne (2004, p. xiii), after Tedford (1970), as a group of fossil species that "have a limited distribution in time from a number of closely grouped localities in a limited geographic area." For example, we use "Z-Line local fauna" in reference to the mammalian species present at ZLQ and ZLE. We also use the term "fauna" sensu Woodburne (2004, p. xii), after Tedford (1970): "… vertebrate fossils of similar taxonomic composition obtained from a small number of sites considered to have a limited temporal range…commonly composed of a number of local faunas." As used here, "fauna" has a greater spatiotemporal scope than "local fauna." For example, we use "Ferris Formation Pu1 fauna" to refer to the sample including all local faunas of Pu1 age in the Ferris Formation.

Assemblage or Sample Versus Local Fauna

We use the terms "assemblage" and "sample" interchangeably, to refer to the collection of fossil specimens recovered from a particular locality, whereas "local fauna" refers to the biological entities (e.g., species) represented by those specimens. The Z-Line assemblage consists of specimens from the two localities ZLQ and ZLE; likewise, the Z-Line local fauna includes species found at either or both localities.

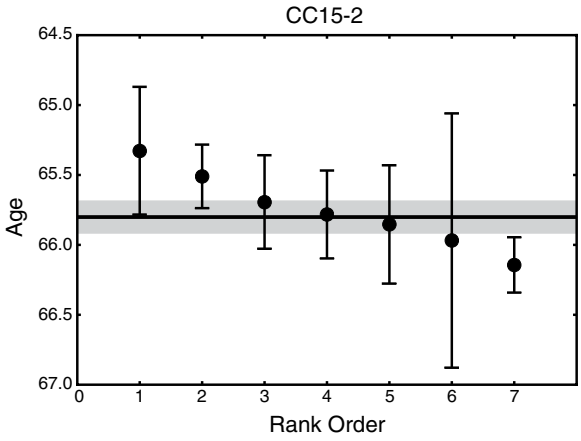

Figure 3. Single-crystal $^{40}Ar/^{39}Ar$ results for 2330 tephra (sample CC15-2). Individual ages are shown in rank order with analytical uncertainty limits of 1σ. The thick horizontal line indicates the weighted mean age with the 1σ uncertainty shown by the gray box.

[1]GSA Data Repository item 2018182, two supplemental data tables from geochronology analysis (as spreadsheets); and one supplemental pdf, which includes systematic descriptions of mammalian fossils, and raw data for correspondence and cluster analyses, is available at http://www.geosociety.org/datarepository/2018 or by request to editing@geosociety.org.

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Taxonomic Diversity Metrics, Similarity, Shareholder Quorum Subsampling, and Rarefaction

All quantitative analyses were conducted in R version 3.3.2 (R Core Team, 2017; http://www.r-project.org); unless stated otherwise, all diversity metrics were calculated using appropriate functions from the community ecology package vegan, version 2.4-2 (Oksanen et al., 2017).

Relative Abundances and Taxonomic Richness

We calculated relative abundance of individuals within mammalian taxa as the number of identifiable specimens (NISP) for a taxon divided by the total number of specimens of all taxa in the sample; NISP is the most appropriate counting method for fluvially transported assemblages, such as those described here (Badgley, 1986). We assessed taxonomic richness in each mammalian local fauna via three metrics: raw richness, subsampled rarefied richness, and subsampled richness using shareholder quorum subsampling (SQS) (Alroy, 2010). For each metric, we calculated taxonomic richness at the genus level as well as the species level. The genus-level calculation was used to account for the difficulties in assigning isolated teeth of *Mesodma* and *Mimatuta* to species (Novacek and Clemens, 1977; Van Valen, 1978; Lofgren, 1995; Smith and Wilson, 2017); see the Data Repository for further information concerning those genera.

Two specimens in our samples (RAM 4045, Periptychidae indet., Fig. S15; RAM 4058, ?*Baioconodon* sp., Fig. S12 [see footnote 1]) could not be confidently assigned to genus or species, but because each represents a taxon distinct from all others in the sample, we included them in the genus- and species-level analyses. Of the 17 metatherian specimens in the Z-Line assemblage, 4 could be assigned only to Metatheria indet. and 2 only to Alphadontidae indet. Because it is unclear how many genera and species those specimens represent, we provisionally treated them as a single taxon ("Metatheria indet.") and represented them by a single specimen in our analyses. To include more than one specimen as "Metatheria indet." in the analyses would assume that everything in that category belonged to a single taxon (genus or species), but we do not have sufficient evidence to make such an assumption. Although it might artificially inflate the relative abundance of other taxa in the assemblage, this choice requires the fewest additional assumptions regarding taxonomic identity (i.e., there is no need to determine if what we count as one genus in our genus-level analyses includes more than one species), and it still allows the taxon some representation in our analyses. We chose this approach as an intermediate between excluding all specimens of "Metatheria indet." and including all of them as distinct genera and species. This decision could artificially depress taxonomic richness in the ZL assemblage but accurately reflects our understanding that there is at least one additional metatherian taxon present in the sample.

We conducted SQS at the genus and species level using John Alroy's R script SQS version 3.3 (http://bio.mq.edu.au/~jalroy/SQS-3-3.R) (Alroy, 2010). We ran 2000 trials, both with and without correction for evenness, achieved by excluding the most common taxon (Alroy, 2010), and chose our quorum level (q) to accommodate the assemblage with the lowest value for Good's u (coverage) (Good, 1953), which was LOH in every case. We also calculated rarefied richness using the function rarefy() from package vegan, which uses the subsampling methodology of Hurlbert (1971). We estimated 95% confidence intervals for the rarefied-richness values, using the formula 95% confidence interval = mean value ± 1.96*standard error. We ran rarefaction with sampling level N = (sample size of assemblage with the smallest sample) – 1. Additionally, we compared the McGuire Creek richness values to values obtained by Wilson (2014) for the Worm Coulee 1 (WC1) assemblage (UCMP V74111/UWBM C1369), which is similar in age to ZL but located in nearby Garfield County (Fig. 1). We also compared richness specifically between ZL and WC1. This analysis used a higher quorum level (q) based on the coverage (u) at ZL rather than the coverage at LOH.

Taxonomic Diversity Indices

We also calculated three other taxonomic diversity indices that incorporate richness and relative-abundance data in various ways: Berger–Parker dominance index (1–d; Berger and Parker, 1970), Simpson's index (1–D; Simpson, 1949), and Pielou's evenness (J'; Pielou, 1966). These indices are relatively easy to interpret, are biologically meaningful, and emphasize different aspects of abundance structure (e.g., Berger–Parker index emphasizes the most common taxon, whereas Pielou's evenness places more emphasis on rarer taxa). Pielou's evenness (J') is subject to many of the same biases as Shannon's H' (Magurran, 2004) but includes a correction for the number of species present in the assemblage: $J' = H'/H_{max} = H'/\ln S$, where S is raw taxonomic richness (Hammer and Harper, 2008). The 95% confidence intervals were generated for each index using a custom bootstrapping function (1000 replicates).

Faunal Similarity Analysis

We assessed similarity in faunal composition among McGuire Creek assemblages using two distance metrics that incorporate relative abundance data: the Bray–Curtis similarity metric (BC) (Bray and Curtis, 1957) and the Canberra distance metric (CM) (Lance and Williams, 1967). These two distance metrics perform well at small sample sizes with low species richness (Krebs, 1989). Whereas BC is strongly affected by abundant taxa, CM places greater emphasis on rare taxa (Krebs, 1989); thus, including both helps to balance our interpretations. To further balance the influence of common and rare taxa in these analyses, we (1) square-root transformed our raw abundance data, and (2) standardized values for each species to equal maximum abundance (Faith et al., 1987; Krebs, 1989).

To broaden our comparative context, we also conducted similarity analyses of earliest Paleocene (Puercan) mammalian faunas across the Western Interior of North America. We compiled genus-level presence/absence data for 16 faunas from Saskatchewan, Canada, to New Mexico, USA (Table 1). We excluded several faunas (e.g., Long Fall Horizon and Frenchman 1, Saskatchewan; Gas Tank Hill, Utah) that are poorly constrained temporally (Cifelli et al., 2004; Lofgren et al., 2004, 2005; Redman et al., 2015; Clemens, 2017). When data sources listed a taxonomic occurrence modified with "cf." or "?", or when the taxon was shown as present only as a range-through occurrence, we alternately considered that taxon as absent (0) in one permutation of the data set and present (1) in a second permutation of the data set. We conducted correspondence analysis (which groups taxa [R-mode] and samples [Q-mode] via chi-square distance) on both permutations of the data set using the function ca() from package ca (Nenadic and Greenacre, 2007). We also calculated the Sørensen-Dice index (Dice, 1945; Sørensen, 1948) for both permutations of the data set to measure faunal similarity. Because this index normalizes to the average number of taxa rather than the total number of taxa in the two samples being compared, it has the advantage of being less sensitive to differences in sample size compared to the Jaccard index (Hammer and Harper, 2008). We constructed a dendrogram (see Faunal Analyses in the Data Repository) using the resulting distance matrix and the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) function hlclust (method = "average") (Sokal and Michener, 1958) from the package ade4 (Dray and Dufour, 2007).

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TABLE 1. NORTH AMERICAN PUERCAN MAMMAL FAUNAS

Name	Abbrev.	Formation	State or Province	References	NALMA
Alexander Locality	alCO	Denver (Denver Basin)	Colorado	Middleton (1983); Eberle (2003); Middleton and Dewar (2004)	Pu1/Pu2
Coke's Clemmys	ccMT	Tullock Member (Williston Basin)	Montana	This study	Pu1
Corral Bluffs	coblCO	Denver (Denver Basin)	Colorado	Eberle (2003)	Pu2/Pu3
DMNH 2560	dahlCO	Denver (Denver Basin)	Colorado	Dahlberg et al. (2016)	Pu1
Ferris Pu1	fpu1WY	Ferris (Hanna Basin)	Wyoming	Eberle and Lillegraven (1998); Lillegraven and Eberle (1999)	Pu1
Ferris Pu2	fpu2WY	Ferris (Hanna Basin)	Wyoming	Eberle and Lillegraven (1998); Lillegraven and Eberle (1999)	Pu2
Ferris Pu3	fpu3WY	Ferris (Hanna Basin)	Wyoming	Eberle and Lillegraven (1998); Lillegraven and Eberle (1999)	Pu3
Garbani Channel Harley's High	garMT	Tullock Member (Williston Basin)	Montana	Clemens (2002, 2004, 2006); Wilson (2014)	Pu3
Luck O Hutch	lohMT	Tullock Member (Williston Basin)	Montana	This study	Pu1
Nacimiento Pu2	pu2NM	Nacimiento (San Juan Basin)	New Mexico	Sloan (1981); Williamson (1996); Clemens and Williamson (2005); Williamson et al. (2011)	Pu2
Nacimiento Pu3	pu3NM	Nacimiento (San Juan Basin)	New Mexico	Sloan (1981); Williamson and Lucas (1993); Williamson (1996); Williamson and Weil (2011); Williamson et al. (2011)	Pu3
Ravenscrag W-1	ravSK	Ravenscrag (Cypress Hills Plateau)	Saskatchewan	Johnston and Fox (1984); Fox (1990); Fox and Youzwyshyn (1994); Fox et al. (2010); Fox and Scott (2011)	Pu3
Hiatt Local	seMT	Fort Union (Williston Basin)	Montana	Hunter et al. (1997)	Pu2
Wagonroad	wagUT	North Horn (Wasatch Plateau)	Utah	Gazin (1941); Robison (1986); Cifelli et al. (1999)	Pu3
Worm Coulee 1	wc1MT	Tullock Member (Williston Basin)	Montana	Wilson (2014)	Pu1
Z-Line	zlMT	Hell Creek (Williston Basin)	Montana	This study	Pu1

Note: Faunas listed here are those included in correspondence analysis (Fig. 8) and cluster analysis (see Data Repository [footnote 1]). NALMA—North American land mammal age.

$^{40}Ar/^{39}Ar$ Geochronology

Sample Prep

Feldspars for $^{40}Ar/^{39}Ar$ analysis were separated from a ~1-kg sample of the CC15-2 tephra, which is within the 2330 coal directly below the CC locality. First the sample was disaggregated using water suspension and was subsequently washed and sieved. To further concentrate feldspar, the sample underwent magnetic and density separations in addition to ultrasonic cleaning in 7% hydrofluoric acid. Because some of the feldspars showed evidence of alteration, the sample underwent further treatment with hydrofluoric acid in order to remove the altered material. This sample also required a treatment of hydrogen peroxide to remove excess coal. Clear euhedral grains were picked preferentially.

Analysis

Analyses were performed at the Berkeley Geochronology Center (California). The sample was subjected to a 50 h irradiation in the Cadmium-Lined In-Core Irradiation Tube facility of the Oregon State University Triga reactor. The sample was loaded into an Al disk figured in Renne et al. (2015, their fig. S2) for irradiation. The fast-neutron fluence, monitored by the J parameter, was calculated by analyzing crystals of the standard Fish Canyon sanidine (Morgan et al., 2014) by single-crystal total fusion for each of the six positions that spanned the disk. The J value for all unknowns was determined by interpolation within a planar fit to J values determined from the Fish Canyon sanidine. The precision on J was better than 0.04%.

Renne et al. (2013) described the methods and facilities used for mass spectrometry. In summary, single sanidine crystals were analyzed by total fusion with a CO_2 laser on an extraction line connected to a MAP 215C mass spectrometer with a Nier-type ion source and analog electron multiplier detector. Argon isotopes (^{40}Ar, ^{39}Ar, ^{38}Ar, ^{37}Ar, and ^{36}Ar) were measured by peak-hopping, which was accomplished by magnetic-field switching on a single detector. Each isotope was measured in 15 cycles. Blanks were determined every three unknowns, and air pipets were measured throughout the run to properly determine mass discrimination (see Table DR1 in the Data Repository).

The final age was determined from blank-, discrimination-, and decay-corrected Ar isotope data. Argon isotope data are presented within Table DR2 (see footnote 1). Corrections for reactor interferences were determined from Fe-doped $KAlSiO_4$ glass (Renne et al., 2013) for K and from fluorite (Renne et al., 2015) for Ca. Age uncertainty (Fig. 3) is reported at 1 sigma and is stated as X/Y where X is analytical uncertainty and Y is systematic uncertainty arising from calibration. Calibration from Renne et al. (2011) was used.

RESULTS

Mammalian Relative Abundances

In each assemblage, the most abundant genus is the multituberculate *Mesodma*, with *M. thompsoni* being the most common species (Table 2). *Cimexomys*, the only other multituberculate genus in our samples, was not recovered from the Z-Line (ZL) localities, but two *Cimexomys* species occur in both the Luck O Hutch (LOH) and Coke's Clemmys (CC) assemblages. Metatherians are relatively abundant in ZL, at 15% of specimens, but are absent from LOH and CC. Of the metatherians in ZL, the majority are attributable to *Thylacodon montanensis*, but ?*Leptalestes cooki* and the Alphadontidae are also represented; also recovered were some metatherian dental fragments that are morphologically distinct from the other three metatherian taxa but not identifiable at the family or genus level (see Data Repository [footnote 1]). Eutherians make up 12% of specimens at ZL and are dominated by the cimolestid *Procerberus formicarum* and the periptychid archaic ungulate *Mimatuta*. Eutherians are relatively abundant in LOH (27%) and CC (24%), with archaic ungulates being the most common eutherians both in number of species and number of specimens. Both LOH and CC assemblages include 2%–7% of each of the archaic ungulates *Oxyprimus erikseni*, *Protungulatum donnae*, and *Mimatuta* sp. LOH also includes singletons of two other archaic ungulate taxa (*Baioconodon* sp. and a relatively large, unidentified periptychid), the leptictid *Prodiacodon crustulum*, and two specimens of *Procerberus* cf. *P. grandis*. CC has three specimens (5%) of the purgatoriid *Purgatorius* cf. *P. coracis*.

Raw and Subsampled Taxonomic Richness

By both subsampling methods used (rarefaction and SQS), LOH and CC richness values are closer to one another than either is to that of ZL (Fig. 4; Tables 3 and 4), a pattern that is more distinct at the species level (Fig. 4B). ZL has the lowest value for both generic and species richness across all four richness measures. In raw generic richness, all three assemblages are similar, but at the species level, LOH (12 spp.) is slightly greater than CC (10 spp.) and nearly twice that of ZL (7 spp.). The difference in genus-level rarefied richness is statistically significant both between LOH and ZL and between LOH and CC but not between ZL

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TABLE 2. RELATIVE ABUNDANCE OF MAMMALS PRESENT AT MCGUIRE CREEK FOSSIL LOCALITIES

Taxon	V84193 (ZLQ)	V84194 (ZLE)	ZLQ+ZLE (ZL)	V88036 (LOH)	V88046 (CC)
Multituberculata					
Mesodma hensleighi	–	–	–	1 (0.02)	3 (0.05)
Mesodma formosa	11 (0.35)	16 (0.19)	27 (0.23)	11 (0.20)	9 (0.16)
Mesodma thompsoni	12 (0.39)	30 (0.35)	42 (0.36)	16 (0.29)	14 (0.24)
Mesodma sp.	3 (0.10)	14 (0.16)	17 (0.15)	9 (0.16)	15 (0.26)
Cimexomys minor	–	–	–	1 (0.02)	2 (0.03)
Cimexomys gratus	–	–	–	3 (0.05)	1 (0.02)
Metatheria					
Thylacodon montanensis	–	10 (0.12)	10 (0.09)	–	–
?*Leptalestes cooki*	–	1 (0.01)	1 (0.01)	–	–
Alphadontidae indet.	–	2 (0.02)	2 (0.02)	–	–
Metatheria indet.	–	4 (0.05)	4 (0.03)	–	–
Eutheria					
Procerberus formicarum	3 (0.10)	6 (0.07)	9 (0.08)	1 (0.02)	4 (0.07)
Procerberus cf. *P. grandis*	–	–	–	2 (0.04)	–
?*Ambilestes cerberoides*	–	1 (0.01)	1 (0.01)	–	–
?*Prodiacodon crustulum*	–	–	–	1 (0.02)	–
Protungulatum donnae	–	–	–	4 (0.07)	1 (0.02)
Oxyprimus erikseni	–	–	–	2 (0.04)	2 (0.03)
Baioconodon sp.	–	–	–	1 (0.02)	–
Mimatuta morgoth	–	–	–	1 (0.02)	–
Mimatuta minuial	–	–	–	–	1 (0.02)
Mimatuta sp.	2 (0.06)	1 (0.01)	3 (0.03)	1 (0.02)	3 (0.05)
Periptychidae indet.	–	–	–	1 (0.02)	–
Purgatorius cf. *P. coracis*	–	–	–	–	3 (0.05)
TOTAL N	31	85	116	55	58

Note: Raw values are listed first, then relative abundance in parentheses. Also included for convenience are combined values for the complete Z-Line assemblage (ZLQ+ZLE). LOH—Luck O Hutch; CC—Coke's Clemmys; N—number of specimens.

and CC; the difference in species-level rarefied richness is statistically significant both between LOH and ZL and between CC and ZL but not between LOH and CC (95% confidence intervals) (Fig. 4). All three rarefaction curves (Fig. 5) show that sampling of the McGuire Creek local faunas is incomplete (not horizontal at maximum sample size); however, because the ZL curve is tending toward being level whereas the LOH and CC curves are strongly inclined, it is likely that further sampling would magnify the observed differences in taxonomic richness between ZL and the two younger assemblages.

The WC1 assemblage has a slightly greater taxonomic richness than ZL, according to both rarefaction and SQS results, although richness estimates for corrected SQS at the genus level are nearly identical (Table 5; Fig. 6). Unlike in McGuire Creek comparisons, where corrected SQS gave consistently higher richness estimates than uncorrected SQS (Tables 3 and 4; Fig. 4), this set of analyses yielded a lower estimate from corrected SQS with the exception of ZL at the genus level (Table 5).

Taxonomic Diversity Indices

LOH and CC have slightly higher diversity values than ZL for every index, although these differences are not statistically significant (Fig. 7). LOH has the highest values (corresponding to lower dominance and higher evenness) in genus-level analyses (Fig. 7A), and CC has the highest values in species-level analyses (Fig. 7B). Although indices were selected to minimize biases due to differences in sample size (Magurran, 2004), we suspect that the large discrepancy in sample sizes (ZL is approximately twice that of both LOH and CC) affects our results. To investigate this possibility, we conducted a second set of bootstrap analyses for all three indices at both genus and species level: we subsampled each locality to 55 specimens for the genus-level analyses and 40 specimens for the species-level analyses, corresponding to the lowest sample size in each case. The resulting second set of bootstrap 95% confidence intervals (dotted vertical lines in Fig. 7) are lower than measured values of both Simpson's 1–*D* and Berger–Parker index at ZL, suggesting that evenness of ZL may be artificially inflated relative to LOH and CC.

Faunal Similarity, Cluster Analysis, and Correspondence Analysis

LOH and CC are more similar to each other in taxonomic composition and relative abundance structure than either is to ZL, at both the genus and species level and regardless of distance metric used (BC or CM) (Table 6). In all four comparisons, CC is slightly more similar to ZL than LOH is to ZL.

In our correspondence analysis (Fig. 8), Dimension 1 represents 19.8% of variance and Dimension 2 represents 14.3% of variance; higher dimensions represent ~10% or less of variance and are not considered here. Pu1 faunas cluster in the upper-left quadrant; Pu2 and Pu3 faunas from New Mexico, Wyoming,

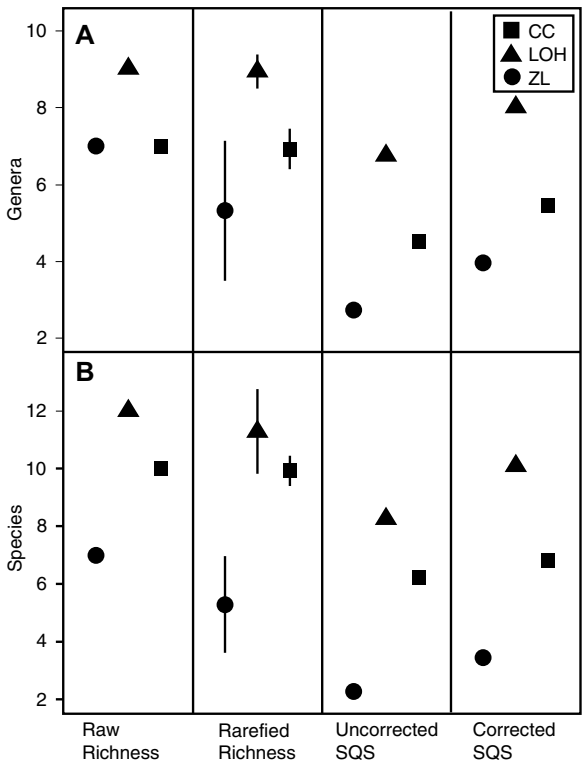

Figure 4. Raw, rarefied, and SQS richness for McGuire Creek mammalian assemblages, at genus level (A) and species level (B). ZL—Z-Line; LOH—Luck O Hutch; CC—Coke's Clemmys; SQS—shareholder quorum subsampling. Rarefied richness values are shown with 95% confidence intervals (calculated using standard error). Uncorrected SQS values were obtained by sampling the entire assemblage, whereas corrected SQS values were obtained using Alroy's (2010) evenness correction.

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TABLE 3. GENUS-LEVEL RICHNESS FOR MCGUIRE CREEK LOCALITIES AND WC1 (UCMP V74111)

Assemblage	N	Raw Richness	Good's u		Subsampled Richness		Rarefied Richness
			uncorrected	corrected	uncorrected	corrected	
ZLE+ZLQ	111	7	0.97	0.88	2.73	3.96	5.32
LOH	55	9	0.95	0.83	6.76	8.04	8.95
CC	58	7	0.98	0.94	4.53	5.43	6.93
WC1	883	13	0.99	0.99	4.63	3.68	7.34

Note: Richness estimated by shareholder quorum subsampling (SQS) and rarefaction. For uncorrected SQS, q (quorum level) = 0.9; for corrected SQS, q = 0.8; for rarefaction, N = 54 specimens. All specimens not identified to at least genus were excluded. Rarefaction curves are shown in Figures 5A and 6A. ZLE+ZLQ—Z-Line; LOH—Luck O Hutch; CC—Coke's Clemmys; WC1—Worm Coulee 1.

TABLE 4. SPECIES-LEVEL RICHNESS FOR MCGUIRE CREEK LOCALITIES AND WC1 (UCMP V74111)

Assemblage	N	Raw Richness	Good's u		Subsampled Richness		Rarefied Richness
			uncorrected	corrected	uncorrected	corrected	
ZLE+ZLQ	91	7	0.97	0.94	2.48	3.46	5.28
LOH	44	12	0.86	0.78	8.24	10.11	11.30
CC	40	10	0.93	0.88	6.25	6.85	9.93
WC1	883	18	0.99	0.99	3.17	3.37	7.43

Note: Richness estimated by shareholder quorum subsampling (SQS) and rarefaction. For uncorrected SQS, q (quorum level) = 0.8; for corrected SQS, q = 0.75. For rarefaction, N = 39 specimens. All specimens not identified to species were excluded. Rarefaction curves are shown in Figures 5B and 6B. ZLE+ZLQ—Z-Line; LOH—Luck O Hutch; CC—Coke's Clemmys; WC1—Worm Coulee 1.

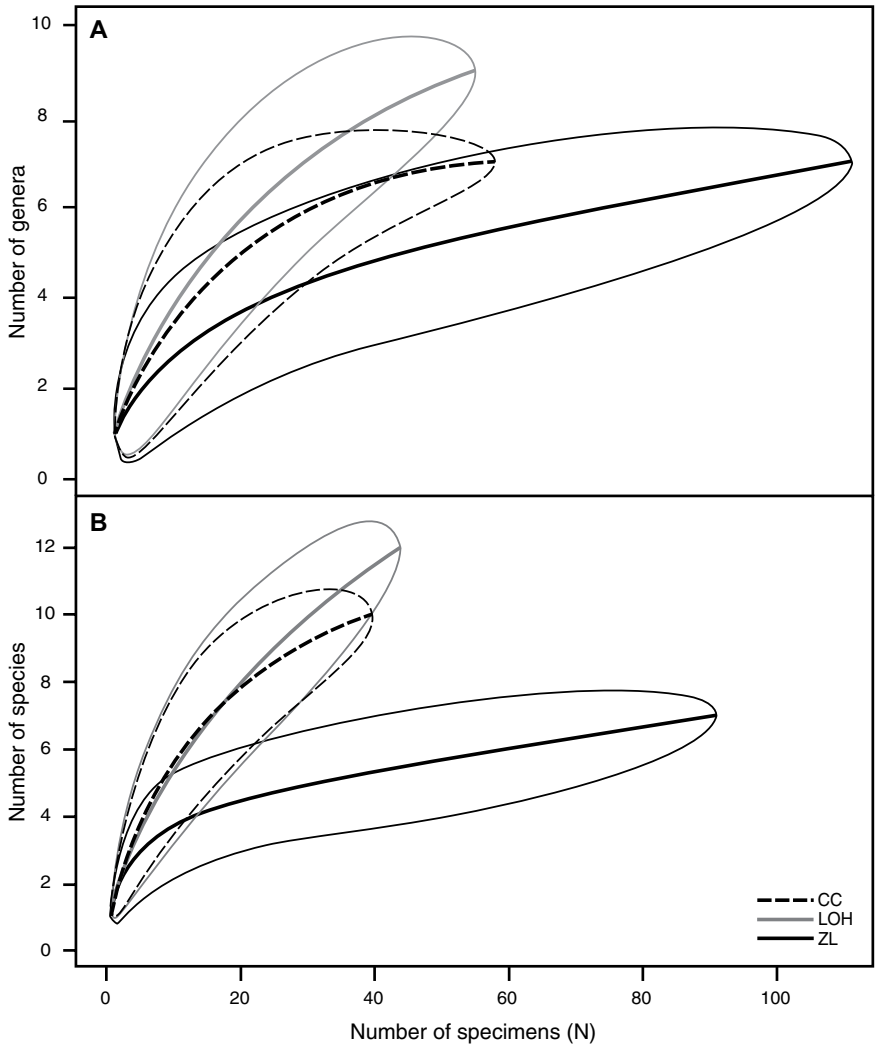

Figure 5. Rarefaction curves with 95% confidence intervals for McGuire Creek assemblages at genus level (A) and species level (B). ZL—Z-Line; LOH—Luck O Hutch; CC—Coke's Clemmys.

Colorado, and Utah cluster in the upper-right quadrant; and Pu2 and Pu3 faunas from Montana and Saskatchewan cluster in the lower-right quadrant. The Pu1 group is united by the presence of several common Pu1 taxa, including *Oxyprimus*, *Mimatuta*, *Mesodma*, and *Cimexomys*. *Periptychus* and other archaic ungulates, such as *Conacodon*, unify the southern/central grouping of Pu2 and Pu3 faunas (upper-right quadrant), whereas the northern grouping of Pu2 and Pu3 faunas (lower-right quadrant) is united by *Carcinodon* and *Stygimys*. *Purgatorius*, which is present in the two northernmost Pu3 local faunas (garMT and ravSK), is also present in the Pu1 ccMT local fauna but does not cause these three to group near one another in the correspondence analysis. Taxa such as *Taeniolabis* and *Loxolophus* are shared across many local faunas on both the upper- and lower-right sides of the plot (Pu2 and Pu3 faunas). The location of faunas relative to one another is largely unchanged when uncertain occurrences are treated as absences; the three main groupings mentioned above remain intact. Results of cluster analysis mirror those of correspondence analysis (see Data Repository [footnote 1]).

Geochronology of the 2330 Coal

From sample CC15-2 of the 2330 coal at CC, 72 grains were analyzed. A majority of these grains were xenocrysts (reworked grains with distinctly older ages >3 sigma from the mean), quartz (little to no gas), and plagioclase (based on K/Ca < 1). Although many of the feldspars analyzed were xenocrystic, we identified a distinctly younger mode based on analyses of seven single crystals of K-feldspar (determined from K/Ca ratios); they yielded a weighted mean age of 65.802 ± 0.116/0.125 Ma with 0.99 as the mean square of weighted deviates (Fig. 3).

DISCUSSION

Biotic recovery is a complex evolutionary and ecological process; it perhaps follows that the associated terminology (e.g., "recovery" and "recovered") has been used variously in the literature and sometimes without clear definition or scope (e.g., MacMahon et al., 1989; Del Moral, 1998; Sepkoski, 1998; Sahney and Benton, 2008; Payne et al., 2011; Hull, 2015). Here, we broadly define "biotic recovery" as the overall process of rebound immediately following peak extinction up until the return to pre-extinction or similar conditions (Erwin, 1998). The rebound most often involves increases in taxonomic richness (via *in situ* speciation and immigration), increases in evenness, and ecological restructuring (Erwin, 1998). The pattern resulting from this process has

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TABLE 5. GENUS- AND SPECIES-LEVEL RICHNESS FOR WC1 AND Z-LINE LOCALITIES

Assemblage	N	Raw Richness	Good's u		Subsampled Richness		Rarefied Richness
			uncorrected	corrected	uncorrected	corrected	
Genus level							
ZLE+ZLQ	111	7	0.97	0.88	3.81	4.35	6.97
WC1	883	13	0.99	0.99	6.44	4.51	8.57
Species level							
ZLE+ZLQ	91	7	0.96	0.97	4.12	3.52	6.97
WC1	883	18	0.99	0.99	8.33	7.08	10.00

Note: Richness estimated by shareholder quorum subsampling (SQS) and rarefaction. For uncorrected SQS, q (quorum level) = 0.95; for corrected SQS, q = 0.85 for genus level, q = 0.90 for species level. For rarefaction, N = 110 specimens for genus level, 90 specimens for species level. Rarefaction curves are shown in Figure 6. ZLE+ZLQ—ZL or Z-Line; WC1—Worm Coulee 1.

been characterized as a three-phase model, which we use hereafter: the immediate post-extinction "disaster" or "survival" phase, when local biotas have highly uneven relative abundance structure and consist mostly of ecological generalists (eurytopic taxa), opportunists, and species from refugia (immigrants); a "recovery" phase, which coincides with increasing taxonomic richness (*in situ* evolution and immigrants) and often includes the appearance of more ecological specialists and a decrease in the relative abundance of generalists and opportunists; and the "fully recovered" phase, when pre-extinction levels of richness, evenness, or some other measure of ecological stability has been reached (Kauffman and Harries, 1996; Erwin, 1998).

Empirical evidence largely agrees with this general model, but the exact pattern and the rate of biotic recovery varies depending on taxonomic group, ecology, environment, and extinction severity (e.g., Zhuravlev, 1996; Jablonski, 1998; Sepúlveda et al., 2009; Chen and Benton, 2012; Donovan et al., 2016); moreover, the process is complicated by the trophic interactions among recovering groups (Solé et al., 2010). Most studies of post-K-Pg mammalian recovery have tracked changes in taxonomic diversity and composition at the temporal resolution of North American land mammal age (NALMA) interval zones (e.g., Pu1, Pu2, Pu3; Archibald, 1983; Clemens, 2002; Wilson, 2014), which correspond to ~200–400-k.y. intervals of the earliest Paleogene (Lofgren et al., 2004; Sprain et al., 2015). In the following sections, we integrate the geochronology results of this study and previous studies with the results of our faunal analyses from the McGuire Creek assemblages to build a local picture of the post-K-Pg mammalian recovery dynamics within the first ~320 k.y. of the Paleogene; then, we compare that local view to the broader and coarser view from regional and continental scales.

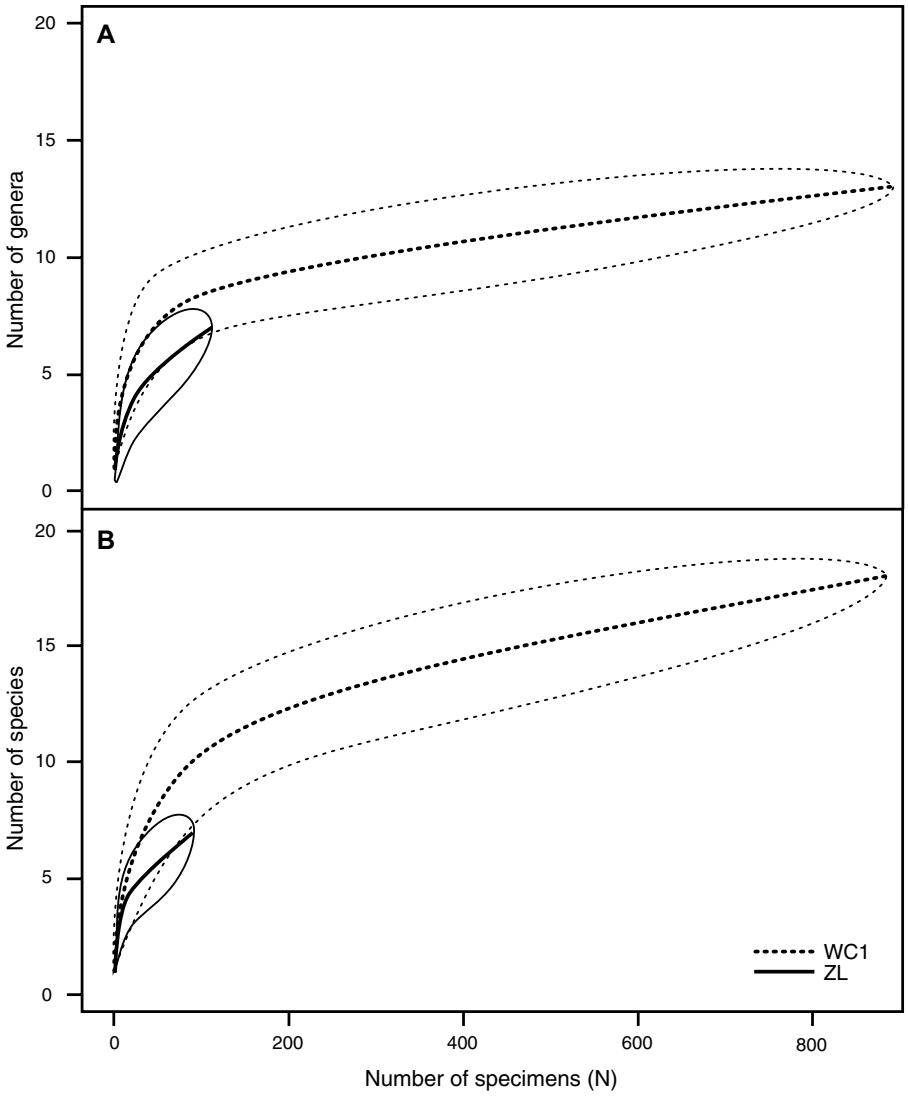

Figure 6. Rarefaction curves with 95% confidence intervals for Z-Line (ZL) and Worm Coulee 1 (WC1) assemblages, at genus level (A) and species level (B).

A High-Resolution Temporal Framework for the McGuire Creek Local Faunas

We combined our geochronological results with previous results to better constrain the age of the McGuire Creek local faunas. Both the Z-Line Quarry and Z-Line Quarry East localities (ZL local fauna) occur below the MCZ and above the carbonaceous shale that contains a negative carbon isotope excursion interpreted to mark the KPB (Fig. 2) (Arens et al., 2014); the age of the KPB is based on the Nirvana bentonite in the IrZ coal found in Garfield County. Accordingly, the age of the ZL local fauna is bracketed between the pooled IrZ age 66.052 ± 0.008/0.043 Ma (Sprain et al., 2018) and the pooled Z coal age 66.024 ± 0.014/0.044 Ma (Sprain et al., 2018), at most 28 ± 16 k.y. after the KPB. Both the LOH and CC localities are stratigraphically above the MCZ coal, so they must be younger than 66.024 ± 0.014/0.044 Ma (Fig. 2). At CC, we have an additional constraint for the maximum age of the local fauna from our new date for the 2330 coal, which is 65.802 ± 0.116/0.125 Ma. Mapping of the 2330 coal by one of us (Lofgren) indicates that Jack's Channel, which contains LOH, cuts out the 2330 coal; accordingly, the

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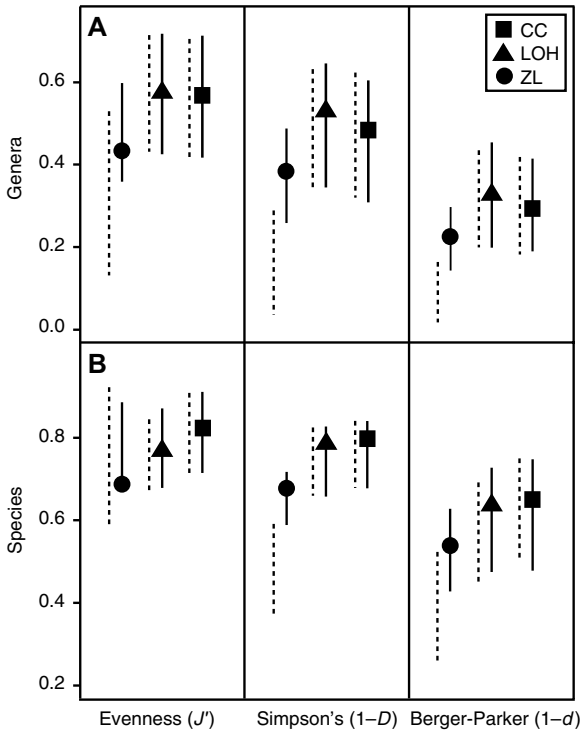

Figure 7. Evenness and dominance for McGuire Creek mammalian assemblages, at genus level (A) and species level (B). All values are shown with 95% confidence intervals obtained from 1000 bootstrap replicates. Dotted lines are bootstrap replicates conducted at sampling level for least-well-sampled locality (N = 55 specimens for A, N = 40 specimens for B). Simpson's and Berger-Parker indices are expressed as the inverse of their dominance measures (1-D and 1-d, respectively). ZL—Z-Line; LOH—Luck O Hutch; CC—Coke's Clemmys.

channel incision is likewise younger than 65.802 ± 0.116/0.125 Ma. However, according to hypotheses for the origin of vertebrate microfossil bonebeds (Rogers and Brady, 2010; Rogers et al., 2017), LOH fossils could have been liberated from any of the older strata cut by Jack's Channel; thus, the age of the MCZ coal, not the age of the 2330 coal, should be used as a maximum age of LOH. Near LOH, the C29r/C29n reversal occurs ~20 cm above the 2380 coal and ~5.5 m below the 2440 coal (Sprain et al., 2018). At LOH, the 2380 coal crops out ~10 m above Jack's Channel, and at CC, the 2440 coal crops out ~20 m above the top of CC channel (Fig. 2). Accordingly, we infer that both local faunas occur within the Paleogene portion of C29r, and are consequently bracketed by the age of the C29r/C29n reversal, which Sprain et al. (2018) calculated to be 65.724 ± 0.013/0.044 Ma. Therefore, the CC local fauna is constrained to between 328 ± 15 k.y. and 250 ± 116 k.y. after the KPB, and the LOH local fauna is constrained to between 328 ± 15 k.y. and 28 ± 16 k.y. after the KPB. We are unable to further constrain relative ages of LOH and CC; however, both are distinctly younger than ZL.

The Beginning of Post-K-Pg Mammalian Recovery at McGuire Creek

All three McGuire Creek local faunas are assigned to the Pu1 NALMA interval zone on the basis of the presence of typical Pu1 taxa (e.g., *Procerberus* and *Mimatuta*) according to Lofgren et al. (2004) and this study (see below); however, differences among these local faunas in age, taxonomic occurrences, and relative abundances suggest that they represent at least two different phases in early post-K-Pg mammalian recovery, resulting in a more granular view of this interval than previously possible (Archibald, 1982; Lillegraven and Eberle, 1999; Clemens, 2002; Wilson, 2014).

Disaster phase. The ZL local fauna, which is constrained to the first ~25 k.y. after the KPB (Fig. 2), is largely consistent with previous characterizations of the disaster phase of biotic recovery in general (e.g., Payne et al., 2011; Chen and Benton, 2012; Ruta et al., 2013) and of the post-K-Pg mammalian recovery in particular (Wilson, 2014). It is taxonomically depauperate (7 spp.) and highly uneven, primarily due to the high relative abundance of three genera (*Mesodma*, *Thylacodon*, and *Procerberus*) (Table 2; Figs. 4–7). These opportunistic taxa, or bloom taxa (Wilson, 2014), have been interpreted as local survivors (Clemens, 2002, 2010), a view summarized by Wilson (2013) and opposed by Williamson et al. (2012) regarding *Thylacodon montanensis*; as insectivores (*T. montanensis* and *Procerberus formicarum*); or as insectivores or animal-dominated omnivores (*M. thompsoni*) (Wilson, 2013). If insectivores are considered to be dietary specialists, their relative abundance in the disaster fauna appears to contradict the idea that eurytopic taxa are the most common post-extinction bloom taxa (Kauffman and Harries, 1996; Erwin, 1998). However, these mammals were small bodied and likely relied on a detritus-based food web (Sheehan and Hansen, 1986; Wilson, 2013, 2014), which perhaps shielded them from any deleterious effects of dietary specialization in the aftermath of the mass extinction. We further note that differences in factors such as extinction selectivity and ecological context could lead to higher abundance of specialists in post-extinction faunas (Jablonski, 1998; Solé et al., 2010). For example, the most notable disaster taxon from the end-Permian mass extinction, the dicynodont *Lystrosaurus* (relative abundance of ~90%) (Benton, 1983; Chen and Benton, 2012), was hardly a eurytopic taxon—it was adapted for high-fiber herbivory (King et al., 1989; Jasinoski et al., 2009).

The ZL local disaster fauna also includes two typically Cretaceous metatherian taxa: a single specimen of the Lancian-aspect *Leptalestes* and two specimens that we refer to the Alphadontidae. Their presence in ZL might indicate (1) a low level of local survival into the earliest Puercan for these typically Lancian taxa, as is seen in some palynological assemblages (Bercovici et al., 2009); or (2) post-depositional reworking of latest Cretaceous fossils resulting from the Z-Line channel cutting into lower strata. If the latter interpretation is correct, we might expect to find non-avian dinosaur fossils intermingled with Puercan taxa. At present, no such dinosaur fossils have been recovered from ZL, which distinguishes it from the temporally mixed assemblages of Bug Creek Anthills and other temporally mixed localities near McGuire Creek (Archibald and Lofgren, 1990; Lofgren, 1995). Thus, in conjunction with Arens et al.'s (2014) evidence for the KPB carbon isotope excursion stratigraphically below the Z-Line channel, we interpret the presence of these mammals as evidence of limited range extension of some Lancian-aspect metatherians into the earliest Puercan. If correct, these taxa would be considered "dead clades walking" (Jablonski, 2002) because their survival across the KPB was relatively short lived. Two other taxa, *Procerberus* and *Thylacodon* (both bloom taxa) previously

TABLE 6. DISSIMILARITY AMONG MCGUIRE CREEK LOCALITIES

	Genus level			Species level		
	ZL	LOH	CC	ZL	LOH	CC
ZL	–	0.74	0.65	–	0.82	0.76
LOH	0.81	–	0.37	0.88	–	0.48
CC	0.77	0.47	–	0.84	0.56	–

Note: Upper right corner of each table section (genus- or species-level analysis) is Bray-Curtis Measure; lower left corner is Canberra Metric. ZL—Z-Line; LOH—Luck O Hutch; CC—Coke's Clemmys.

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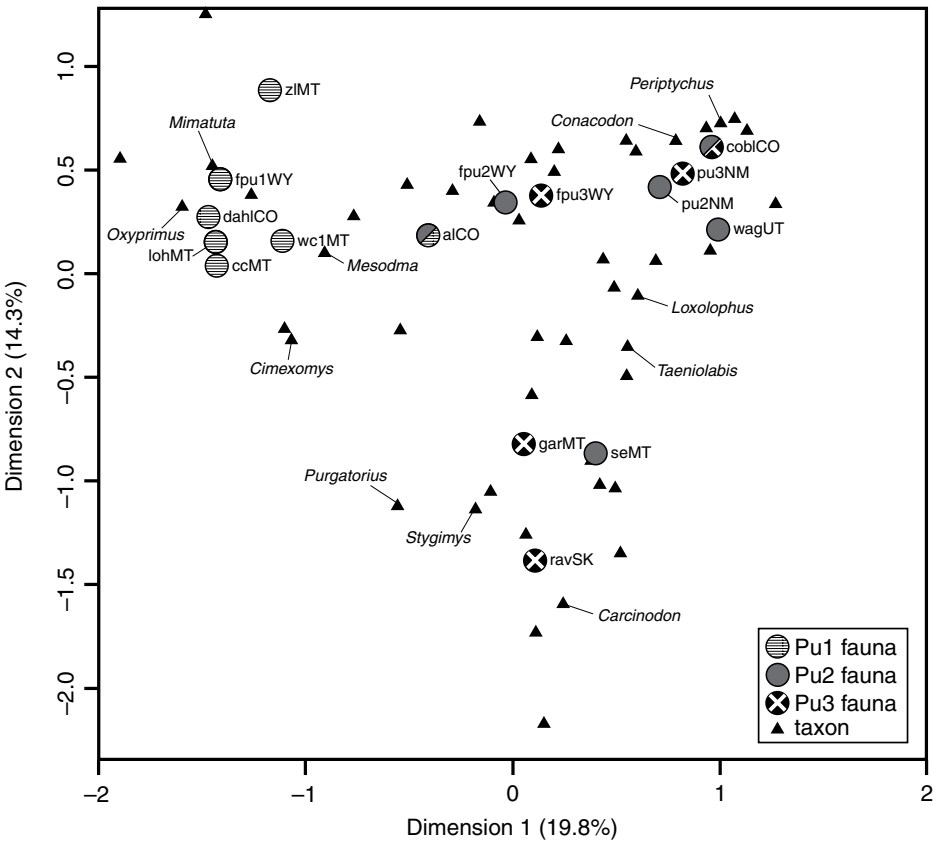

Figure 8. Correspondence analysis of North American mammalian faunas. Abbreviations for faunas are listed in Table 1. Filled circle next to the name of each fauna corresponds to North American land mammal age (NALMA). Split circles indicate a transitional fauna (e.g., Pu2–3).

also were identified as "dead clades walking" because of their hypothesized ancestors in the Lancian (Wilson, 2014), but their local decline occurred over a relatively longer time span in the Puercan.

The ZL local disaster fauna shows some similarities with the broadly contemporaneous WC1 local fauna (UCMP V74111/UWBM C1369), another disaster fauna (Wilson, 2014) from farther west, in central Garfield County, in the Hell Creek region. The WC1 assemblage is from the Hell Hollow Channel sandstone, which is less than 3 m above the IrZ, our proxy for the KPB, at 66.052 ± 0.008/0.043 Ma (Sprain et al., 2018) and 11.9 m below the Hauso Flats Z coal, dated at 65.973 ± 0.020/0.047 Ma (Sprain et al., 2015). On the basis of sediment accumulation rate, Sprain et al. (2018) estimated that the Hell Hollow Channel sandstone was deposited within ~16 k.y. after the KPB (66.036 ± 0.008/0.036 Ma). Among the 883 mammalian specimens from WC1 that were identifiable to species, *Mesodma thompsoni*, *Thylacodon montanensis*, and *Procerberus formicarum* were the three most common taxa (i.e., bloom taxa) (Wilson, 2014) and are the same as those in ZL despite the large difference in sample size. The subsampled generic richness of these disaster local faunas is also nearly identical (Table 5) when we account for evenness in SQS analyses.

Despite those similarities, some notable differences between the ZL and WC1 local faunas point to variability in the disaster phase of post-K-Pg mammalian recovery. For example, the multituberculate *Stygimys kuszmauli* is absent from ZL (and LOH and CC) but is present in WC1 and is a fairly common taxon among Pu1 mammalian assemblages in other nearby localities in McCone County (UCMP localities V87072, V87037, V87038, etc.) (Lofgren, 1995) as well as across the Western Interior of North America, according to Lofgren et al.'s (2005) review of the genus. Also absent from ZL but present in WC1 are the common Pu1 archaic ungulates *Baioconodon nordicum*, *Oxyprimus erikseni*, and *Protungulatum donnae*. Despite very rare genus-level occurrence of *Baioconodon* and *Protungulatum* in latest Cretaceous localities in southwestern Montana (Archibald et al., 2011; Kelly, 2014), these archaic ungulates and *Stygimys kuszmauli* have been considered post-KPB immigrants into the area (Clemens, 2010; Wilson, 2014). Thus, the relative lack of immigrant taxa and retention of Lancian-aspect metatherians in ZL might imply that it represents a slightly earlier phase of recovery than WC1. That said, the Constenius locality of eastern Garfield County (UCMP V96268/UWBM C1665) (Clemens, 2002), which, like ZL, is stratigraphically between the KPB, as determined by the negative carbon isotope excursion (Arens et al., 2014), and the MCZ coal, has assemblages that are very similar in taxonomic composition to those of WC1. Though the Constenius fauna is not yet formally described, *Stygimys* and typical Pu1 archaic ungulates are well represented. These differences between localities might be due to preservational bias against larger, more-fragile fossils at ZL; for example, the Constenius locality frequently produces well-preserved dentulous jaws, whereas ZL produces almost exclusively small, isolated teeth. Additionally, these differences between ZL and WC1 + Constenius might be due to some combination of differences in sampling intensity, paleohabitat, or spatial heterogeneity. As such, our evolutionary interpretation of the compositional differences between ZL and WC1 (namely, that ZL represents a slightly earlier disaster phase) should be treated as a provisional working hypothesis, pending additional fossil sampling and analysis of depositional environments at ZL.

Early recovery phase. The LOH and CC local faunas are younger than the ZL local disaster fauna; LOH is temporally constrained between ~28 k.y. and ~328 k.y. after the KPB (66.024 ± 0.014/0.044 Ma and 65.724 ± 0.013/0.044 Ma), and CC is between ~250 k.y. and ~328 k.y. after the KPB (65.802 ± 0.116/0.125 Ma and 65.724 ± 0.013/0.044 Ma) (Fig. 2) (Sprain et al., 2018). It thus follows that they show a greater degree of recovery from the K-Pg mass extinction than ZL does. Although the increase in evenness from ZL to LOH and from ZL to CC is slight (Fig. 7), there are differences in taxonomic composition (Table 2). The Lancian-aspect metatherians present in the ZL local fauna and the metatherian bloom taxon *Thylacodon montanensis* are absent from LOH and CC. Another typical bloom taxon, *Procerberus formicarum*, is supplanted by *Protungulatum donnae* as the most abundant therian taxon in LOH. This pattern of decline in bloom taxa and increase in relative abundance of archaic ungulates in LOH and CC (Table 2) characterizes the departure from the disaster phase of post-K-Pg mammalian faunal change and the onset of recovery.

This early part of the recovery phase is also characterized by the appearance of several

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new taxa in LOH and/or CC, including typical Pu1 archaic ungulates (e.g., *Protungulatum, Oxyprimus*); a large, unidentified periptychid archaic ungulate (cf. *Hemithlaeus* and *Tinuviel*) (see the Data Repository); the plesiadapiform *Purgatorius* cf. *P. coracis*; the leptictid ?*Prodiacodon crustulum*; and the cimolestid *Procerberus* cf. *P. grandis*. *Purgatorius* and *Prodiacodon* are otherwise known only from Pu2 and Pu3 local faunas in the northern portion of western North America (Fig. 8) (Johnston and Fox, 1984; Fox, 1990; Clemens, 2002, 2017; Clemens and Wilson, 2012; Lofgren et al., 2004; Wilson, 2014), but Pu1- and Pu2-aspect faunas were possibly concurrent (Fox and Scott, 2011). Similarly, *Hemithlaeus* and *Tinuviel* are otherwise known only from the Pu2 and Pu3 of New Mexico and southeastern Montana (Williamson, 1996; Hunter et al., 1997). These occurrences at LOH and CC suggest that new taxa appeared in the McGuire Creek area throughout Pu1, resulting in gradual rather than abrupt faunal turnover during the earliest recovery period; this pattern indicates that mammalian biotic recovery proceeded at a finer temporal scale than our current mammalian biochronology system (NALMAs) allows us to express. Indeed, this has been previously observed in areas other than northeastern Montana. The Alexander Locality from the Denver Basin (alCO) (Fig. 8), which has been referred to Pu1 based on the presence of several classic Pu1 taxa, is compositionally more similar to Pu2 faunas from the San Juan and Hanna Basins (Middleton, 1983; Eberle, 2003; Lofgren et al., 2004; Middleton and Dewar, 2004). In our correspondence analysis plot (Fig. 8), alCO is intermediate to the main cluster of Pu1 faunas and the cluster of Pu2–3 faunas from Colorado, Wyoming, Utah, and New Mexico. These results support the hypothesis that alCO represents a transitional Pu1–2 fauna (Middleton, 1983; Eberle, 2003; Lofgren et al., 2004; Middleton and Dewar, 2004) that cannot be convincingly assigned to either Pu1 or Pu2 to the exclusion of the other. In combination with these results from alCO, our McGuire Creek results indicate that as temporal gaps in our sampling of the early Paleogene are filled, we will need more precise age constraints, such as those from geochronological and paleomagnetic data, to better understand and describe the nuances of the mammalian biotic recovery.

Late recovery phase. Comparison with younger local faunas from the Hell Creek region reveals that a major increase in regional taxonomic richness occurred between LOH/CC and the Garbani Channel local fauna (garMT, Fig. 8). Sprain et al. (2018) used sediment accumulation rates to estimate that the Garbani Channel local fauna occurred between ~375 k.y. and ~850 k.y. after the KPB; age data for sample GC12–2 (Sprain et al., 2015) and more recent work (Sprain et al., 2018) together constrain these estimated ages to 65.677 ± 0.041/0.059 Ma and 65.202 ± 0.057/0.114 Ma, respectively. Even with conservative estimates of the number of taxa in garMT (Wilson, 2014), there are more than twice as many species in garMT than any McGuire Creek local fauna. Current estimates of generic richness from faunal studies around the Western Interior (see Data Repository [footnote 1]) show that garMT is similar in richness to Pu2 and Pu3 faunas from New Mexico and Wyoming. Although the Garbani Channel local fauna is still under study, preliminary work indicates a distinct uptick in the number of archaic ungulate, multituberculate, and plesiadapiform taxa from LOH/CC to garMT. As such, we infer that the new taxa appearing in LOH and CC are merely the beginning of a shift toward more taxonomically diverse, recovered faunas. Most local taxonomic diversity accumulated between ~328 k.y. and ~850 k.y. after the KPB (ages 65.724 ± 0.013/0.044 Ma and 65.202 ± 0.057/0.114 Ma, respectively). Because the temporal gap between LOH/CC and garMT is substantial and because the time averaging represented by the thick Garbani Channel deposit (~20 m) is possibly substantial, the local progression of late-recovery faunas is not yet well resolved.

Results from our correspondence analysis reveal a broader spatiotemporal context to the biotic recovery documented at McGuire Creek and in northeastern Montana. Early Puercan (Pu1) faunas, including all McGuire Creek local faunas, have some compositional differences among them but are largely similar across Montana, Wyoming, and Colorado (Fig. 8); Pu1 faunas are not known from farther south, and faunas from Alberta and Saskatchewan that have sometimes been assigned to Pu1 (e.g., Long Fall Horizon and Frenchman 1) were excluded from our analyses because of age uncertainties (Cifelli et al., 2004; Lofgren et al., 2004; Redman et al., 2015; Clemens, 2017). In contrast, the Pu2 and Pu3 faunas are compositionally separated into northern and southern groups (Fig. 8). This implies that by the Pu2 at the latest, northern and southern biogeographic provinces had formed; however, because of the lack of Pu1 faunas south of Colorado and Utah, we cannot rule out the possibility that this provinciality arose earlier than Pu2. Eberle and Lillegraven (1998) similarly proposed that north–south differentiation of North American mammalian faunas began in Pu2, although their hypothesis was on qualitative grounds. They noted a closer similarity in faunal composition between Pu2–Pu3 faunas of the Ferris Formation and other faunas to the south, as we find here. A north–south pattern of faunal differentiation in Pu2 and Pu3 was also proposed by Williamson (1996) and quantitatively investigated by Weil (1999). This pattern could be driven by a latitudinal climate gradient or the formation of discrete geographic barriers between the northern and southern portions of the Western Interior, such as a temporary western incursion of the Western Interior Seaway (Boyd and Lillegraven, 2011). This pattern could also reflect diachroneity of Pu2–3 faunas in the northern part of the continent and those in the south; more precise ages for Pu2–3 localities would be required to test this hypothesis.

CONCLUSION

Our findings here add to the increasing body of knowledge regarding the spatiotemporal variability of biotic recovery. Previous studies (e.g., Jablonski, 1998; Donovan et al., 2016) have shown striking geographic variation in patterns of biotic recovery across continents; we have shown spatial variation in recovery pattern even at our more restricted geographic scale within North America. On a local scale within our McGuire Creek study area, mammalian biotic recovery is underway within the first ~320 k.y. after the KPB. Although the changes in taxonomic richness, evenness, dominance, and faunal composition between our oldest local fauna, ZL (minimum age, 66.024 ± 0.014/0.044 Ma), and our two younger local faunas, LOH and CC (maximum age, 65.802 ± 0.116/0.125 Ma; minimum age, 65.724 ± 0.013/0.044 Ma), are slight, they do reflect turnover from the disaster local fauna at ZL to the early-recovery faunas at LOH and CC. The appearance of several new taxa, coupled with higher overall taxonomic richness and decreased relative abundance of bloom taxa, distinguish LOH and CC from ZL. Yet all three McGuire Creek local faunas differ considerably from the younger, nearby Garbani Channel local fauna, which has much higher levels of richness. The three McGuire Creek local faunas reported here broadly resemble other North American Pu1 faunas, which are relatively homogeneous throughout the Western Interior. Yet the presence of younger aspect taxa, such as *Purgatorius*, aligns the LOH and CC McGuire Creek local faunas with younger faunas in the northern half of the continent. Future studies should seek to capture more snapshots of both the early and late recovery periods across the Western Interior, in order to (1) better resolve local and regional faunal changes, and (2) assemble a more unified temporal framework for the succession of mammals across regions and throughout the recovery process.

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