

从异地迁入的动物类群是北美西部内陆地区 古新世最早期哺乳动物群的 重要组成部分吗？

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摘要: K/T 界线绝灭事件后残存类群的迁入和地方性辐射在北美西部内陆地区的古新世最早期 (Puercan 期) 哺乳动物群的进化中所起的作用存在争议。持续的野外工作和室内研究极大地扩展和提升了我们对北美地区的白垩纪最晚期 (北美陆相哺乳动物分期的 Lancian 期) 和 Puercan 1 期 (Pu1) 的地方动物群组成的认识, 也揭示了这些地方动物群生物年代学对比的局限。总的来说, 北美西部内陆地区北部的 Pu1 地方动物群主要由多瘤齿兽类和真兽类组成, 而 Lancian 期存在的有袋类各类群绝灭。大多数的 Pu1 哺乳动物是由其他地区迁移而来, 其中许多类群在 K/T 界线后不久就迁徙到这个地区。北美洲古纬度高的地区和亚洲太平洋沿岸地区的白垩纪最晚期或者古新世最早期哺乳动物群的缺乏, 妨碍了对异地迁移到北美的哺乳动物起源于亚洲这一假说的验证。另一个假说认为, 大多数迁入北美西部内陆地区北部的 Pu1 哺乳动物可能来自北美大陆的其他地区。这一假说得到了越来越多的支持, 并且没有证据表明是错误的。

关键词: 北美西部内陆地区, 白垩纪 Lancian 期, 古新世 Puercan 期, 哺乳动物, 迁移

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WERE IMMIGRANTS A SIGNIFICANT PART OF THE EARLIEST PALEOCENE MAMMALIAN FAUNA OF THE NORTH AMERICAN WESTERN INTERIOR?

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Abstract The roles of immigration and endemic radiation of survivors of the extinctions marking the Cretaceous/Tertiary (K/T) boundary in evolution of the earliest Paleocene (Puercan) mammalian fauna of the North American Western Interior have been debated. Continued field and laboratory research has significantly expanded and refined knowledge of the compositions of North American latest Cretaceous (Lancian North American Land Mammal Age) and Puercan 1 (Pu1) local faunas. It has also revealed limitations in biochronological correlations of these local faunas. In general, Pu1 local faunas of the northern Western Interior reflect the extinction or extirpation of lineages of Lancian marsupials and consist primarily of multituberculate and eutherian mammals. The majority of Pu1 mammals were immigrants, many

dispersing into the area soon after the K/T boundary. Testing the hypothesis of Asian origins of the immigrants is hampered by lack of latest Cretaceous or earliest Paleocene mammalian local faunas particularly from high North American paleolatitudes and Pacific coastal areas of Asia. Another working hypothesis, that most, if not all, of the Pu1 immigrant mammals entering the northern Western Interior could have dispersed from other areas of the North American continent has increasing support and has yet to be falsified.

Key words Western Interior, North America; Lancian, Cretaceous; Puercan, Paleocene; Mammalia; immigration

1 Introduction

Was immigration of new species or an endemic radiation of surviving species the dominant process in evolution of earliest Paleocene mammalian faunas of the North American Western Interior after the mass extinction marking the end of the Cretaceous? Through the years, different opinions have been presented. For example, Simpson (1937:2) argued, "The Cretaceous-Paleocene transition in North America is marked by the disappearance of dinosaurs and the appearance of several orders of mammals apparently as immigrants from some unknown region."

Analyzing a larger database, Maas and Krause (1994:122) noted, "The initial radiation of mammals in the Puercan (earliest Paleocene) cannot be accounted for by dispersal of taxa from outside North America. Instead, the data for the early Paleocene are most consistent with the suggestion that the change in community structure reflected radiation of mammals into niches not occupied by mammals in the Late Cretaceous." Weil (2002) recognized the significant role of appearances of mammalian lineages previously unknown in the Western Interior in the recovery of taxonomic diversity after the K/T boundary extinctions.

Field research during the past two decades has made significant additions to the fossil record of mammalian evolution during the latest Cretaceous and early Paleocene in the Western Interior of North America, which includes fossil localities in the Canadian provinces of Alberta and Saskatchewan and the states of Montana, North and South Dakota, Wyoming, Colorado, Utah, and New Mexico (Fig. 1).

Phylogenetic analyses of some groups of these mammals, detailed studies of the geology and sedimentology of the fossiliferous strata, and paleoecologic reconstructions have added new perspectives to our understanding of the course of mammalian evolution across the K/T boundary. To set the stage for this study, the paleogeography of North America during the latest Cretaceous and earliest Paleocene is briefly described.

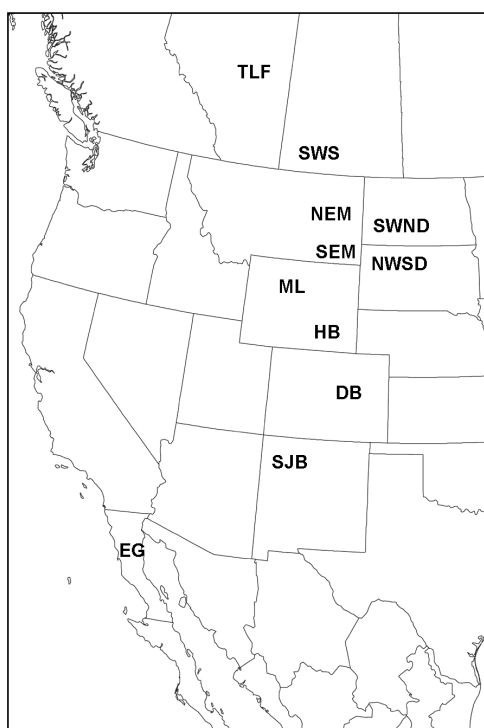


Fig. 1 Map of Western Interior of North America showing locations of localities discussed in the text. EG. El Gallo, Baja California; DB. Denver Basin, Colorado; HB. Hanna Basin, Wyoming; ML. Mantua Lentil, Wyoming; NEM. Northeastern Montana (Garfield and McCone counties); NWSD. Northwestern South Dakota; SEM. Southeastern Montana; SJB. San Juan Basin, New Mexico; SWND. Southwestern North Dakota; SWS. Southwestern Saskatchewan (Wounded Knee, Gryde, Fr-1, and MHBT (Long Fall) localities); TLF. Trochu fauna, Alberta (Modified from a United States Geological Survey base map)

Currently, local faunas of northeastern Montana still provide the most abundantly documented records of latest Cretaceous (Lancian North American Land Mammal Age = Lancian NALMA) and earliest Paleocene (Puercan NALMA, specifically its earliest interval zone, Pu1) mammalian evolution during this interval. Following a review of this record, the analysis is expanded paleogeographically to include the growing number of records of Pu1 faunas from other areas of the northern Western Interior. This provides a more complete picture of the complexity of mammalian faunal change at the beginning of the Paleocene. Finally, the question of the areas of origin of the Pu1 immigrants is addressed.

Unless otherwise indicated, McKenna and Bell's (1997) classification of mammals is followed here. University of California fossil localities are identified in the format V 74110. Additional locality information is available at <http://www.ucmp.berkeley.edu/science/index.php>. Identifications of individual teeth are in the format P3 or p4 that, respectively, identify the upper third and lower fourth premolars.

2 Paleogeography

Near the end of the Cretaceous North America was divided by the Western Interior Seaway stretching from the Arctic Ocean to what is now the Gulf of Mexico (Fig. 2). The western subcontinent was linked intermittently to eastern Asia by land extending across the area of the modern Bering Strait. Western Europe was subdivided by shallow seas into an archipelago. A global marine regression in the latest Cretaceous and early Tertiary ultimately resulted in the joining of the eastern and western subcontinents of North America. This was not a simple, steady withdrawal of the Western Interior Seaway. The regression was interrupted by episodes of transgression particularly during the Paleocene, which produced the marine Cannonball Member of the Fort Union Formation (Johnson et al., 2002). No doubt these variations in extent of the sea in the Western Interior and contemporaneous changes in oceanic sea level and patterns of circulation contributed to modification of the global climate. The marine record of the latest Cretaceous (Maastrichtian, ca. 6 my in duration) documents a general trend of significant cooling of surface and bottom waters. Approximately 300 to 400 ky before the K/T boundary this trend was reversed by a rapid short-term warming event followed by a rapid cooling just prior to the boundary (Li and Keller, 1998a,b). This terminal Cretaceous climatic oscillation also affected the

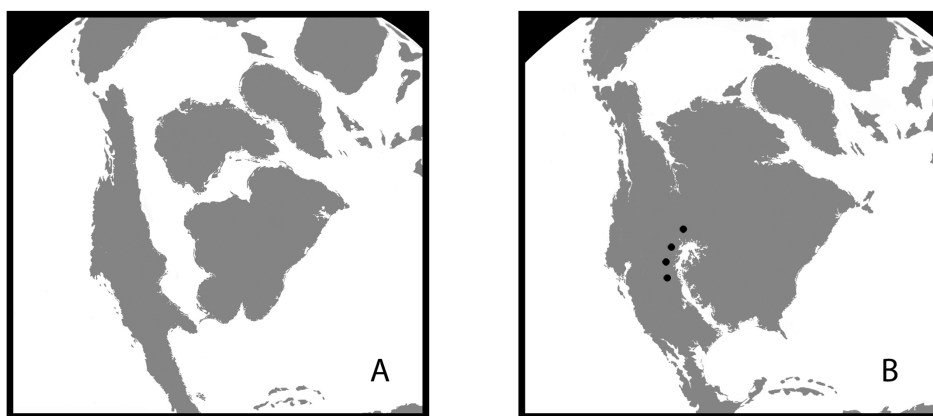


Fig. 2 Schematic restorations of North American and adjacent continental margins

A. Late Cretaceous, ca. 75 my; B. Cretaceous/Tertiary boundary, ca. 65 my; four dots approximate positions of Pu1 localities cited in the text; outlines of land masses redrawn from maps made available online by Ron Blakey (Northern Arizona University Geology)

terrestrial environment. In the northern Western Interior, the latest Cretaceous paleobotanical record is shorter, ca. 1.1 my, but it documents the brief periods of climatic warming followed by cooling at the end of the Cretaceous that continued into the earliest Paleocene (Wilf et al., 2003).

No doubt other factors were involved in modification of the environment. Volcanic eruptions in India over several million years at the end of the Cretaceous and beginning of the Paleocene produced the Deccan Traps and modified atmospheric conditions (Chenet et al., 2009 and references cited therein). Impact of an asteroid at Chicxulub in Mexico probably contributed to changes in terrestrial environments. The nature, intensity, and duration of these environmental changes, however, remain an area of discussion (e. g., Belcher, 2009). A combination of long term and short term modifications of the environment (press and pulse events) appears to have caused the terminal Cretaceous extinctions in the terrestrial biota and set the stage for its evolution in the earliest Paleocene (Arens and West, 2008).

3 Mammalian fossil record from northeastern Montana

The Hell Creek Formation in northeastern Montana has yielded a large number of Lancian mammals. Some two decades later, Simpson (1927) described the few mammalian specimens collected by Barnum Brown in 1906. Beginning in 1962, much larger samples were obtained by University of Minnesota (Sloan and Van Valen, 1965) and University of California Museum of Paleontology field parties primarily by underwater screening from localities in the upper part of the formation. Archibald (1982) provided an extensive analysis of its Lancian and Pu1 mammalian faunas. Subsequently, as part of the Hell Creek Project, field crews from the Museum of the Rockies, University of California Museum of Paleontology, and, most recently, the University of Washington emphasized collection of fossils and geological data from the lower stratigraphic levels of the Hell Creek Formation, particularly in the valley of Hell Creek. On the basis of the collections available to Archibald and new material, Wilson (2004, 2005) restudied the Lancian mammalian local faunas found at various stratigraphic levels throughout the formation, which he suggested was deposited during the last 1.8 my of the Cretaceous.

3.1 Northeastern Montana — stratigraphic setting

The lithostratigraphic boundary between the Hell Creek and overlying Tullock Formation is set at the stratigraphically lowest, geographically extensive bed of lignite (Fig. 3). In their pioneering study, Collier and Knechtel (1939) recognized that this basal lignite was part of a series of lenticular strata of lignite. They dubbed this lignite rich interval the Z coal. For many years it was assumed that initiation of the formation of the basal Z coal was essentially contemporaneous throughout northeastern Montana and marked the K/T boundary. Subsequent research by Swisher et al. (1993) revealed that in western Garfield County (Fig. 4) the basal unit of the Z coal, designated the Iridium Z coal (IrZ), is associated with a unit containing an above-background concentration of iridium, shocked quartz grains, and spherules interpreted as products of the Chicxulub impact. A recalculated $^{40}\text{Ar}/^{39}\text{Ar}$ age determination places the age of the IrZ coal and the currently recognized K/T boundary at 65.58 ± 0.04 my (see Wilson, 2005 for the basis of the recalculation). In eastern Garfield and western McCone counties the lithostratigraphic boundary between the formations, set at the McGuire Creek Z coal (McZ), is younger, 65.37 ± 0.05 my (Wilson, 2005).

The Puercan NALMA has been subdivided into three interval zones designated, from oldest to youngest; Pu1, Pu2, and Pu3 (see Lofgren et al., 2004). In western Garfield County all Pu1 local faunas are preserved at stratigraphic levels between the IrZ coal and the Hauso Flats Z coal (HFZ), which was deposited some 65.18 ± 0.07 my ago (Wilson, 2005) — an interval

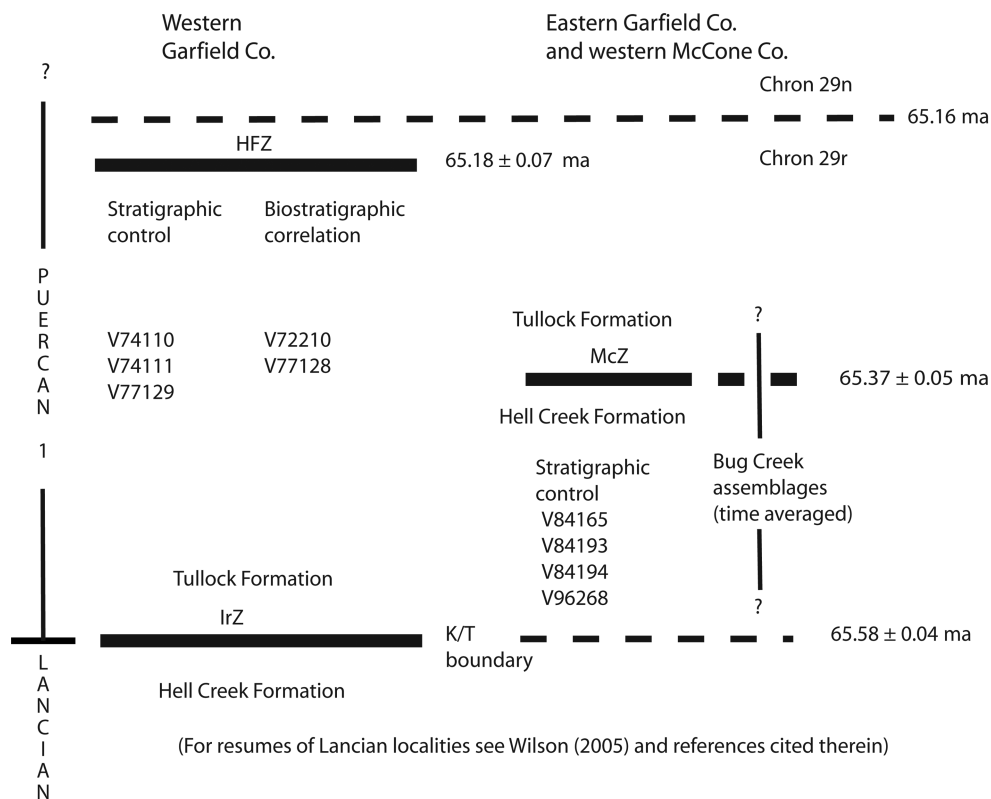


Fig. 3 Comparison of the stratigraphic section in western Garfield County with the section in eastern Garfield and western McCone counties (see Fig. 4)

Localities currently overlain by either the Hauso Flats Coal Z coal (HFZ) or McGuire Creek Z coal (McZ) are listed under the caption "stratigraphic control"; the overlying HFZ has been removed by erosion from two localities in western Garfield County listed under the caption "biostratigraphic correlation"; radiometric age determinations based on recalculations described by Wilson (2005)

of approximately 400 ky (Fig. 3). This currently is assumed to be approximately the duration of the Pu1 interval zone. In eastern Garfield County and western McCone County several Pu1 local faunas are preserved in the uppermost Hell Creek Formation and overlain by the McZ coal, which is approximately 200 ky younger than the IrZ coal and the K/T boundary. Where the magnetostratigraphy has been determined, all Pu1 local faunas are preserved in rocks deposited during Chron 29r (Swisher et al., 1993).

Sloan and Van Valen (1965) described collections of vertebrate fossils from large channel infillings in the valley of Bug Creek and adjacent areas (the Bug Creek Anthills, Bug Creek West, and Harbicht Hill localities) in western McCone County. They considered them to be of latest Cretaceous age and documenting a gradual change in the composition of the terrestrial fauna. Lofgren's (1995) analysis of the stratigraphy and composition of these and other localities in the McGuire Creek region led to the current interpretation that these large channel infillings preserve time-averaged assemblages containing mixtures of Pu1 and reworked Lancian fossils deposited during the Pu1 interval zone (Lofgren et al., 2004).

3.2 Localities considered, northeastern Montana

Previous analyses of Pu1 local faunas revealed that over half of the mammalian taxa lack

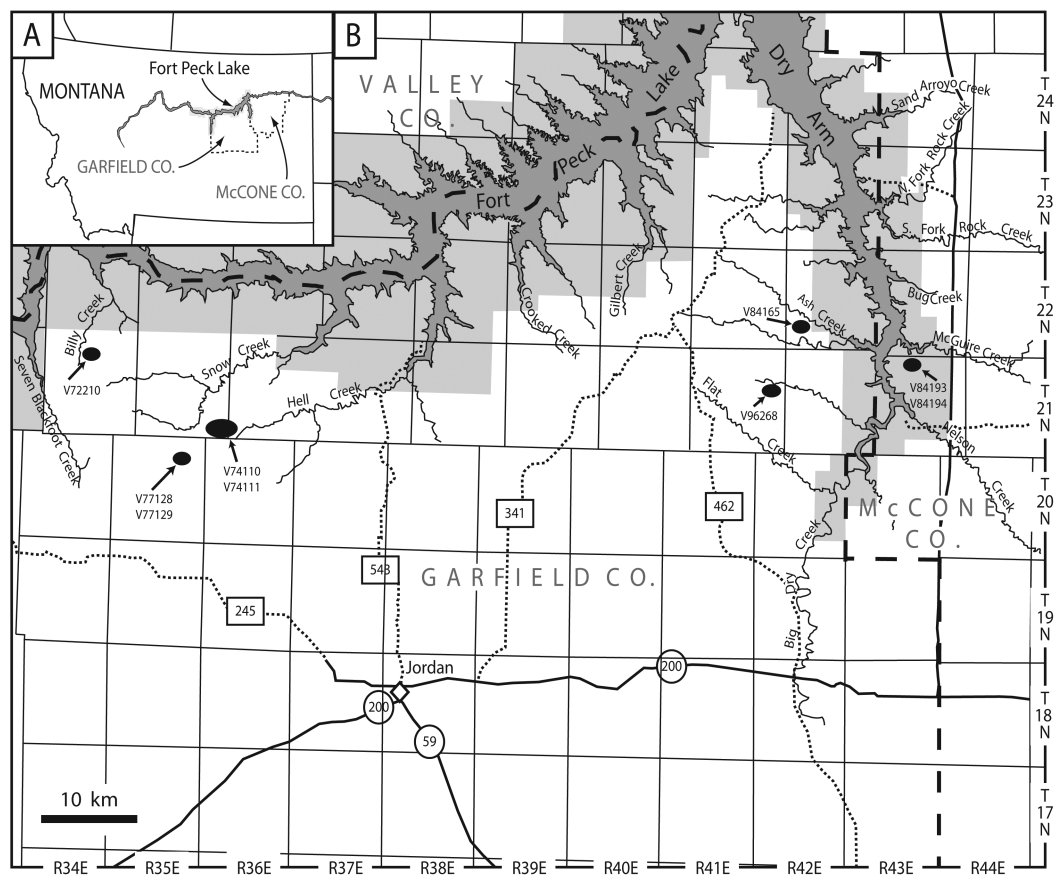


Fig. 4 Map showing the locations of University of California Museum of Paleontology localities in western Garfield County and in eastern Garfield and western McCone counties. The land included in the Charles M. Russell National Wildlife Refuge is shaded in light gray; base map provided by Gregory Wilson.

ancestors or closely related sister groups in Lancian local faunas of the northern Western Interior (Weil and Clemens, 1998; Weil, 1999; Clemens, 2002). In these studies, composite faunas from localities ranging from the Late Cretaceous Judithian NALMA through the Puercan were considered. Taxa were classified as residents if they were present or their lineage was represented during the preceding biochronologic unit. Immigrants (aliens) were taxa that lacked ancestors or closely related sister groups in the preceding biochronologic unit. A limitation of these analyses came from drawing faunal data from a variety of sites thus masking the biogeographic variation in composition of Pu1 local faunas. Here the initial focus is narrowed to a consideration of the role of immigration in evolution of Pu1 local faunas in a relatively small area in north-eastern Montana that has yielded large samples of Lancian and Pu1 local faunas. In broad terms, the evolutionary history documented in this area is typical of the northern Western Interior. However, as noted below, there are significant differences in taxonomic composition of Lancian and Pu1 local faunas in other parts of the northern Western Interior.

Composition of the Lancian mammalian fauna of the Hell Creek Formation in western Garfield County as documented by Wilson (2005) is used as a basis for comparison (Appendix 1). The lack of fossil localities just below the IrZ coal in the uppermost one to three meters of the Hell Creek Formation has resulted in a gap in the data on mammalian faunal change at the

close of the Cretaceous.

In western Garfield County, localities in the drainage of Snow Creek, just west of Hell Creek (Fig. 4), have produced an extensive sample of the Pu1 fauna (Archibald, 1982). Taxonomic revisions were made by Lofgren (1995) and additional material has been collected since their research. The faunal list for western Garfield County (Appendix 1) is based primarily on a collection totaling approximately 1700 mammalian specimens (mostly isolated teeth) from three localities (V 74110, V 74111, and V 77129) overlain by the HFZ coal. Two other Pu1 localities correlated biostratigraphically (V 72210 and V 77128) have yielded approximately 350 additional mammalian specimens (again mostly isolated teeth). Radiometric age determinations of the IrZ and HFZ coals (Wilson, 2005) show that these localities document the Pu1 fauna at times during the first ca. 400 ky of the Paleocene.

A composite faunal list for four localities (V 84165, V 84193, V 84194, and V 96268) in eastern Garfield County and western McCone County is included in Appendix 1. The IrZ coal and strata containing an above-background concentration of iridium, shocked quartz grains, and spherules interpreted as products of the Chicxulub impact have not been found in this area. Here the boundary between the Hell Creek and Tullock formations is placed at the base of the McZ coal. Two localities (V 84193 and V 84194) are in the valley of McGuire Creek in western McCone County and were analyzed in detail by Lofgren (1995). Stratigraphically these localities are above the last local occurrences of unreworked nonavian dinosaur remains and overlie palynofloras of Paleocene age. Both localities lack reworked teeth or fragmentary bones of nonavian dinosaurs, have yielded Pu1 mammalian local faunas, and are overlain by the McZ coal. Lofgren's study (1995) was in press and did not benefit from the radiometric age determination of the age of the McZ coal obtained by Swisher et al. (1993), which confirms Lofgren's determination of their age.

The other two localities (V 84165 and V 96268) are in eastern Garfield County some 10 and 16 km west of the valley of McGuire Creek (Fig. 4). They also are overlain by the McZ coal, lack reworked fossils of nonavian dinosaurs, and have yielded Pu1 mammalian local faunas. The combined sample of mammals from these four localities is small (approximately 250 specimens, mostly isolated teeth) relative to the combined sample from western Garfield County, but it is of significance in documenting the presence of several mammalian genera within the first ca. 200 ky of the Paleocene.

Lofgren (1995) also provided detailed analyses of the stratigraphy and time-averaged mammalian assemblages found in the region of McGuire Creek. The mammals from these localities are known from approximately 1800 specimens (mostly isolated teeth). At the generic level, all of the immigrant taxa found in the Pu1 localities in western Garfield County, except the rare multituberculate *Acheronodon*, are present in the local faunas of eastern Garfield and western McCone counties (Appendix 1). There are differences at the specific level; for example, *Baioconodon engdahli* is present in western Garfield County, while *B. nordicum* occurs in western McCone County. Also, Pu1 immigrant mammals in the McCone County local faunas are taxonomically more diverse with two species each of *Catopsalis*, *Mimatuta*, and *Protungulatum*. The samples from these two areas are essentially the same size, and in both areas the majority of the fossils were obtained by underwater screening. Although by current standards these samples are large, the differences in their compositions still might be the product of vagaries in collecting. Probably to some degree they also reflect an unknown combination of differences in age, environment, and taphonomy.

The samples of the time-averaged (Lancian and Pu1) Bug Creek assemblage, particularly those from the Bug Creek Anthills locality, are not fully considered here. Beyond faunal lists or citations in stratigraphic studies (e. g., Sloan and Van Valen, 1965; Sloan et al., 1986; and Rigby et al., 1987), only a few thorough analyses of constituent taxa (e. g., Novacek and

Clemens, 1977; Luo, 1991; Lofgren, 1995) have been published. Specimens from these samples, however, have been cited as holotypes or referred specimens in studies of particular taxa (e. g., *Stygimys kuszmauli* (Sloan and Van Valen, 1965), *Nortedelphys minimus* (Case et al., 2005), and *Alostera saskatchewanensis* (Fox, 1989)). These taxa will be cited below where pertinent in discussing the possible areas of origin of the Pu1 faunas of the Western Interior.

3.3 Recovery of taxonomic diversity of the Pu1 local faunas, northeastern Montana

Multituberculata: During the Cretaceous multituberculates underwent a major evolutionary radiation, but their taxonomic diversity appears to have been reduced by extinctions at the end of the period. Five families were present in North America during the Paleocene: Eucosmodontidae, Microcosmodontidae, Taeniolabididae, Ptilodontidae, and Neoplagiaulacidae. *Cimexomys* represents a sixth surviving lineage and is placed *incertae sedis* within Cimolodonta (Weil and Krause, 2008). Because many of the species and some genera are known only from isolated teeth or fragmentary mandibles or maxillae, phylogenetic analyses have yet to clearly reveal the interrelationships of multituberculates known from Lancian and Pu1 local faunas (Weil, 1999; Weil and Krause, 2008). Recognizing this uncertainty and attendant difficulties in distinguishing biological extinctions and nomenclatorial pseudoextinctions, it appears that multituberculate taxonomic diversity was depressed by perhaps 50% over the K/T boundary (Archibald, 1996).

No member of the Ptilodontidae has been recovered from Lancian or Pu1 local faunas in northeastern Montana. In contrast, both the Neoplagiaulacidae and the *Cimexomys* lineage are represented in both Lancian and Pu1 local faunas. At the generic level, the neoplagiaulacid *Mesodma* is abundantly represented (Lofgren et al., 2005), while *Cimexomys* is not as common.

Currently, no member of the Taeniolabididae is known from Lancian local faunas in northeastern Montana; however *Bubodens*, a probable taeniolabidid represented by a single molar from the Lancian Red Owl local fauna, South Dakota, documents the presence of the family in the Western Interior (Wilson, 1987; Weil and Krause, 2008). Two immigrant species of *Catopsalis* appear in Pu1 local faunas of northeastern Montana. Earlier, *Catopsalis* was thought to be a member of local faunas in both the Western Interior and Asia (Mongolia). The Asian occurrence has since been recognized as a misidentification (Weil and Krause, 2008).

Members of the Eucosmodontidae are not known in Lancian local faunas of northeastern Montana, but the family is represented by *Stygimys* in Pu1 local faunas (Lofgren et al., 2005). *Stygimys* might be present in a Judithian (Campanian) local fauna of the Western Interior (Weil, 1999). A species of *Stygimys* is a member of the El Gallo fauna, Baja California, which is probably of Campanian age (Lillegraven, 1972; Lofgren et al., 2005). These occurrences strongly suggest that the appearance of *Stygimys* in Pu1 local faunas of the northern Western Interior was a product of dispersal from another area within North America.

The microcosmodontid *Acheronodon garbanii* was based on a p4 from locality V 74111 in western Garfield County (Archibald, 1982; Weil, 1998). The family is not represented in Lancian local faunas of northeastern Montana. Fox (2004), however, reported the presence of a microcosmodontid in the Medicine Hat Brick and Tile Quarry at the Long Fall horizon (MHB-T (Long Fall)) in southern Saskatchewan.

Metatheria: The end of the Cretaceous saw a crash in taxonomic diversity of metatherians in the northern Western Interior. In northeastern Montana, 11 species were either locally extirpated or became extinct. The latter group includes species of the non-marsupial metatherians *Didelphodon*, *Pediomys*, "*Pediomys*" spp. (four species following Davis, 2007), *Protalphadon*, and *Turgidodon*. Only one species of marsupial, *Peradectes* cf. *P. pusillus*, is known in Pu1 local faunas of the area (Clemens, 2006). Clemens (1966) suggested that *Peradectes* was

derived from a latest Cretaceous species of *Alphadon* or a metatherian with a similar dentition. Based on a cladistic analysis, Johanson (1996a) concluded that a polytomy linked the *Peradectes*–*Peratherium* clade, the *Turgidodon* clade, and a clade including three species of *Alphadon* (*A. jasoni*, *A. marshi*, and *A. halleyi*). Provisionally, *Alphadon* and *Peradectes* are assumed to be sister taxa or have an ancestor-descendant relationship. In this analysis, *Peradectes* is tentatively classified as a resident taxon.

Additional complexity and uncertainty concerning the fate of metatherians across the K/T boundary was added by Case et al. (2005), who reviewed collections of molars of *Alphadon marshi* and a probably synonymous species, *A. wilsoni*, from various Lancian and time-averaged Lancian and Pu1 localities in Alberta, Montana, Wyoming, and South Dakota. They established three species of the new genus *Nortedelphys*, which was allocated to the Herpetotheriidae. The holotypes of two of these species, *N. intermedius* and *N. minimus*, are isolated molars from the Bug Creek Anthills locality and the Tedrow Quarry D (V 87072) respectively (Lofgren, 1995). Both preserve time-averaged Lancian and Pu1 fossil assemblages, thus opening the possibility that these species were based on specimens of Pu1 age. In the same year, another herpetotheriid, *Maastrichtidelphys meurismeti*, based on an isolated molar from the latest Cretaceous Maastricht Formation of the Netherlands was described by Martin et al. (2005). The authors hypothesized the Laurasian origin of herpetotheriids with their range extending from the Western Interior to Europe during the Late Cretaceous. Herpetotheriids have yet to be discovered in Puercan local faunas of the Western Interior but reappear during the early mid-Paleocene Torrejonian NALMA (Johanson, 1996b).

Species of the Lancian genus *Glasbius* were widespread in the Western Interior, ranging from southern Saskatchewan (Fox, 1997) to the San Juan Basin, New Mexico (Williamson and Weil, 2008) but are unknown in Pu1 local faunas. A number of authors have suggested close phylogenetic relationships of *Glasbius* with members of the South American paucituberculatan family Caroloameghiniidae. Case et al. (2005) proposed a new Lancian taxon, *Hatcheritherium alpha*, based on an isolated molar from the Lance Formation, Wyoming, and allied it with *Glasbius* in the Hatcheriformes, a basal group of the largely South American Polydolopimorpha. They hypothesized that both the peradectids and polydolopimorphans differentiated during the Late Cretaceous in western North America and then the latter group dispersed into South America.

Eutheria: Three genera of eutherians are recorded in Lancian local faunas of northeastern Montana: *Batodon*, *Cimolestes* and *Gypsonictops*. *Batodon tenuis* is a rare, minute eutherian of debated phylogenetic affinities and possibly includes representatives of two species (Polly et al., 2005). It was assigned to the Cimolestidae by Keilan-Jaworowska et al. (2004), but McKenna and Bell (1997) included it in the soricomorph family Geolabididae. A phylogenetic analysis by Bloch et al. (1998) supported the latter assignment and indicated *Cimolestes* was a closely related sister group of the geolabidids. Most recently Wible et al. (2009) supported inclusion of *Batodon* in the Cimolestidae but discounted its purported soricomorph affinities. *Batodon* has yet to be found in Pu1 localities in northeastern Montana.

Cimolestes is represented by five species in Lancian faunas of northeastern Montana while only two cimolestids (*Procerberus formicarum* and *Cimolestes* sp.) are present in the Pu1 local faunas of the area. Recent studies (Gunnell et al., 2008; Strauss, 2007) suggest that the ancestry of *P. formicarum* is to be found in a species of *Cimolestes*, possibly *C. incisus*. Wilson (2004) described an isolated lower molar from a Pu1 locality in western Garfield County (V 72210). It is intermediate in size between *C. incisus* and *C. stirtoni* and is listed here as *Cimolestes* sp.

In the Western Interior, species of *Gypsonictops* have a long chronological range (Judithian to Lancian NALMAs) and a wide geographic range extending from New Mexico into Alberta.

Gypsonictops is currently placed in a separate family, Gypsonictopidae, of the Leptictida, which also includes the family Leptictidae (McKenna and Bell, 1997). The phylogenetic relationships of *Gypsonictops*, leptictids, and various Tertiary groups have been discussed at length (see Kielan-Jaworowska et al., 2004). The hypothesis advanced by Novacek (1977) that *Gypsonictops* was closely related, but not ancestral, to Tertiary leptictids has yet to be falsified.

Two species of *Gypsonictops* are present in Lancian faunas of northeastern Montana. Archibald (1982) and Lofgren (1995) found that *Gypsonictops* was commonly represented in time-averaged Lancian–Pu1 assemblages, but neither this genus nor a leptictid was present in the samples of Pu1 local faunas they analyzed. Currently the first incontrovertible record of the Leptictidae is *Prodiacodon crustulum*, which is known from several localities in the Garbani Channel deposits of undifferentiated Pu2–Pu3 age in northeastern Montana (see Clemens, 2002). Wilson (2004) described isolated leptictidan lower molars from Pu1 localities in western (V 74110 and the probably stratigraphically equivalent V 80021) and eastern Garfield County (V 96268). Morphologically these teeth are similar to the m1 or m2 of *Gypsonictops* and *Prodiacodon*, but their crowns do not provide characters distinctive enough to assign them to one or the other genus. Provisionally the occurrences of these teeth are interpreted as records of an immigrant taxon.

At least four genera of archaic ungulates (“condylarths”) were present in the Pu1 local faunas of northeastern Montana. These include the basal archaic ungulate *Protungulatum*, whose first appearance defines the onset of the Pu1 interval zone (Lofgren et al., 2004). Also making their first appearance are the oxyclaenid *Oxyprimus*, arctocyonid *Baioconodon*, and anisonchine peripitychid *Mimatuta*. In spite of the current uncertainties concerning their phylogenetic relationships (e. g., Archibald, 1998), the appearance of these four genera in Pu1 local faunas strongly suggests the evolutionary radiation of archaic ungulates began prior to the Pu1 interval zone in some other area.

Finally, Fox (1989) described *Alostera saskatchewanensis* based on material from the Canadian Lancian Wounded Knee local fauna, the Gryde local fauna, and a locality in the Scollard Formation as well as a series of isolated teeth from the time-averaged Bug Creek Anthills assemblage in northeastern Montana. The genus has not been found in any strictly Lancian or Pu1 local faunas in the latter area. *Alostera* has been recognized as a member of the “Zhelestidae,” a primarily Cretaceous group of stem eutherians or basal laurasiatherian placentals (Archibald and Averianov, 2007). Their occurrences in some areas of the northern Western Interior may well represent relicts of a radiation earlier in the Late Cretaceous.

In summary, as currently known, the Pu1 multituberculate fauna of northeastern Montana consisted of eight species representing five genera. Of these, four species (*Acheronodon garbani*, *Catopsalis alexanderi*, *C. joyneri*, and *Stygimys kuszmauli*) were immigrants into the area. The record of *Stygimys* in a Campanian local fauna in Baja California strongly suggests its appearance in Pu1 local faunas of the northern Western Interior was a product of dispersal from another area of North America, possibly from its Pacific Coast. There is no compelling evidence that any of these species dispersed from eastern Asia at the beginning of the Paleocene. Weil and Krause (2008) supported the interpretation initially advanced by Fox (1968) that these immigrants were derived from stocks living in as yet unsampled upland environments in the Western Interior during the Late Cretaceous.

New collections and recent studies of Cretaceous and Pu1 localities in northeastern Montana have not modified the interpretation that extinction or extirpation greatly reduced metatherian diversity at the end of the Cretaceous. Only the lineage leading to *Peradectes* cf. *P. pusillus* is thought to have survived in northeastern Montana. Although known from time-averaged Lancian–Pu1 localities, for example Bug Creek Anthills, neither species of *Glasbius* nor *Nortedelphys* have been found in strictly Pu1 localities. Case et al. (2005) hypothesized that *Glasbius* was

closely related to the ancestors of the Tertiary radiation of South American marsupials and *Nortedelphys* was a member of the lineage that gave rise to Tertiary Laurasian herpetotheriids. If these hypotheses prove to be correct, the absences of *Gasbius* and *Nortedelphys* from Pu1 local faunas of northeastern Montana were the result of local extirpations.

As is the case with multituberculates, phylogenetic analyses have yet to clearly reveal the interrelationships of eutherians represented in Lancian and Pu1 local faunas of northeastern Montana. Recent studies suggest that the lineages represented by the Lancian eutherians *Batodon* and *Gypsonictops* continued on into the Paleocene, although apparently *Gypsonictops* was not ancestral to Tertiary leptictids. Lancian species of *Cimolestes* have been suggested to have been ancestral stocks for a variety of placental clades, but many of these hypotheses are vigorously debated (e. g., Wible et al., 2009). What does seem clear is that the Pu1 cimolestids in northeastern Montana, *Cimolestes* sp. and *Procerberus* were derived from the Lancian *C. incisus* or a closely related species. In contrast, the archaic ungulates *Protungulatum*, *Oxyprimus*, *Baioconodon*, and *Mimatuta* lack closely related sister groups or ancestors in the Lancian local faunas of northeastern Montana and clearly were immigrants. Although there is disagreement about the exact suprageneric reference of these taxa, there is agreement that they represent several families. This suggests their differentiation occurred at least in the Lancian, if not earlier. The records of the “zhelestid” *Alostera* come from the time-averaged Bug Creek assemblage and, at the moment, there are no criteria to determine if these records are of Lancian and/or Pu1 age.

4 Records of Pu1 immigrants in other areas

Full analysis of Pu1 local faunas found in areas outside northeastern Montana is beyond the scope of this study. However, several taxa unknown in northeastern Montana appear to be immigrants entering other areas of the northern Western Interior during the Pu1 interval zone. Citation of these taxa helps to illustrate the full range of the impact of immigration in evolution of its earliest Paleocene mammalian fauna.

4.1 Other regions in Montana, North Dakota, South Dakota (Fig. 1, NWSD, SEM, SWND)

Lancian local faunas of southwestern North Dakota and southeastern Montana were described in detail by Hunter and Archibald (2002 and references cited therein). Wilson (1983, 1987) reported on the Lancian mammals of the Red Owl local fauna found in northwestern South Dakota. Preserved in sediments referred to the Fox Hills Formation, the Red Owl mammals might well be older than those found in the Lancian localities in eastern Wyoming and Montana and southwestern North Dakota (Cifelli et al., 2004). Samples of most of these Lancian local faunas are smaller than and not as diverse taxonomically as those from northeastern Montana. The exception is the large sample collected from the Hell Creek Formation near Ekalaka in southeastern Montana. Hunter and Archibald (2002) report the presence of 23 mammalian species in this local fauna as compared to 26 found in the Hell Creek Formation in Garfield and McCone counties. The majority of the species represented in this and the local faunas in North and South Dakota are present in the Lancian local faunas of northeastern Montana. A significant exception is *Bubodens magnus*, the only known Lancian taeniolabidid multituberculate, represented by a single molar in the sample of the Red Owl local fauna (Wilson, 1987). Hunter and Archibald (2002) analyzed the biogeographic variation in Lancian local faunas from Wyoming in the south to Alberta in the north. They uncovered some differences that were strongly associated with geographic distance rather than latitude per se.

In contrast to the multiple records of Lancian mammals, the Puercan, particularly the Pu1 record, is scanty. Hunter and Archibald (2002) argued that the PITA Flats localities in south-

western North Dakota, which have yielded remains of *Mesodma* sp., *Protungulatum* sp., *Oxyprimus galadriellae*, *Oxyacodon priscilla*, and Arctocyonidae, gen. & sp. indet., might be of Pu1 age. Weinstein (2009) announced the discovery of a lower jaw of the large cimolestid *Alveugena* at an unidentified Pu1 locality in North Dakota.

4.2 Wyoming and Colorado (Fig. 1, ML, HB, DB)

Localities in two areas in Wyoming have yielded records of Lancian and Pu1 local faunas. Local faunas of Lancian (Dumbell Hill), Puercan (Mantua Lentil) and Torrejonian (Rock Bench) have been recovered from exposures on the eastern side of Polecat Bench, north of Powell, northwestern Wyoming. The sample of the Dumbell Hill local fauna is small but includes records of four species of multituberculates, a metatherian, and, possibly, a leptictoid (Gingerich et al., 1980). As far as can be determined, all are representatives of taxa present in the Lance Formation of eastern Wyoming and the Hell Creek Formation of northeastern Montana. Similarly, the sample of Lancian mammals from the Hanna Basin, south-central Wyoming, is small but documents the presence of four species of multituberculates, three metatherians, and two eutherians (Eberle and Lillegraven, 1998a,b). With the exception of recognition of a new species of *Meniscoessus*, *M. seminoensis*, as far as can be determined the other mammals do not differ from taxa present in the Lance Formation of eastern Wyoming and the Hell Creek Formation of northeastern Montana.

Although there are differences in species represented, both the Pu1 Mantua Lentil (Appendix 2) and Pu1 local faunas in northeastern Montana contain representatives of *Oxyprimus*, *Baiocodon*, and *Mimatuta*. Immigrant taxa not represented in northeastern Montana include the conacodontine peripitychid *Oxyacodon josephi*, the peripitychine peripitychid *Maiorana noctiluca*, and the triisodontid *Eoconodon copanus*. Taxonomically, the Pu1 fauna preserved in the Ferris Formation of the Hanna Basin (Eberle and Lillegraven, 1998a,b) is more diverse. It includes a greater diversity of species of *Mesodma*, but the immigrant multituberculates *Stygimys* and *Catopsalis* have yet to be recorded. Two species of *Protungulatum* and species of *Oxyprimus*, *Mimatuta*, *Maiorana*, and *Eoconodon* are interpreted as immigrant taxa in this fauna.

Collecting in the Cheyenne Basin, Colorado, has expanded documentation of Lancian local faunas to the southeast of the Hanna Basin. On the basis of fragmentary material, Carpenter (1979) reported the occurrence of three genera of mammals (*Cimolomys*, *Meniscoessus*, and *Gypsonictops*) typically represented in Lancian local faunas to the north. Further field work in the basin resulted in discovery of a long stratigraphic sequence (ca. 300 m) containing Late Cretaceous fossil localities (Wilson et al., 2010). The stratigraphically lowest is Carpenter's discovery locality. Subsequent research (Diem, 1999) resulted in reference of the record of *Meniscoessus* sp. to *M. collomensis*, which might indicate an "Edmontonian" age of this local fauna. For the most part the superjacent localities yielded typical Lancian mammals. The significant exception is the stratigraphically highest locality that is the type locality of two new multituberculates, *Parikimys carpenteri* and *Paressonodon nelsoni* (Wilson et al., 2010).

Local faunas of Pu1 age have yet to be found in the Cheyenne Basin. Lancian localities have yet to be discovered in the adjacent Denver Basin, but several fossil localities yielding Pu1 mammals have been discovered there. The collections from these localities have been treated as representing a single fauna, the Littleton local fauna (Dewar, 2003; Eberle, 2003; Middleton and Dewar, 2004). The most productive locality, the Alexander locality, and some other localities where the magnetostratigraphy has been determined are in rocks deposited during Chron 29r as are the Pu1 local faunas in northeastern Montana (Eberle, 2003). In taxonomic composition, the Littleton local fauna is distinctly different from the local faunas in northeastern Montana. Many of the mammalian genera recognized as residents in northeastern Montana are represented by different species (e. g., *Cimexomys arapahoensis*, *Procerberus andesiticus*, and *P.*

grandis). New immigrant taxa include *Kimbetohia? mziae*, which might be the earliest record of the Ptilodontidae in the Western Interior, and the neoplagiaulacid *Xyonomys robinsoni*. The local fauna also stands apart in the taxonomic diversity of its immigrant archaic ungulates (“condylarths”); 13 species represent eight genera that are currently referred to three families (Appendix 2). Eberle (2003) suggested two working hypotheses to account for this diversity, particularly among the peripitychids, which account for six of the species and five of the genera. Although a Pu1 fauna preserved in sediments deposited during magnetostratigraphic Chron 29r, the Littleton local fauna might be younger than Pu1 faunas to the north and document a later stage in radiation of the archaic ungulates. Another hypothesis recognized the lack of discovery of a Pu1 fauna in the San Juan Basin, New Mexico. The typifying Pu2 and Pu3 faunas come from this basin, and a Lancian local fauna has just been described by Williamson and Weil (2008). All three show distinct differences from contemporaneous faunas to the north (note Weil, 1999). The archaic ungulates in the Littleton local fauna might be immigrants from a Pu1 or earlier radiation of these lineages in the San Juan Basin or other areas of the southern Western Interior.

4.3 Alberta and Saskatchewan (Fig. 1, SWS, TLF)

Three major local faunas of Lancian age are known from Canada: the Trochu local fauna (Lillegraven, 1969) in Alberta (Appendix 3) and the Wounded Knee (Fox, 1989, 1997) and Gryde (Storer, 1991) local faunas in Saskatchewan. These mammalian local faunas are made up mostly of genera also known from Lancian faunas to the south, but there are significant differences. Since Lillegraven’s (1969) study of the Trochu local fauna, Fox (1989) recognized the presence of the “zhelestid” *Alostera saskatchewanensis* in all three local faunas. Subsequently Fox and Naylor (2003) added the taeniodont *Schowalteria clemensi* to the Trochu local fauna.

Two Canadian local faunas, Fr-1 in the Frenchman Formation and the local fauna from the Long Fall horizon exposed in the Medicine Hat Brick and Tile Quarry (MHBT (Long Fall)) in the Ravenscrag Formation, are of particular pertinence to this analysis (Appendix 3). Fox (1997) noted that in the greater taxonomic diversity of eutherians and, in some cases, their high relative abundance, the Wounded Knee and Gryde local faunas show a greater resemblance to Pu1 rather than Lancian faunas to the south. Whether these local faunas are of Cretaceous or Paleocene age or are referable to the Lancian or Pu1 interval zone has been contested (see Fox, 1997; Lillegraven and Eberle, 1999; Cifelli et al., 2004; and references cited therein). In part, this reflects a difference in criteria for definition of the boundary between the Lancian and Pu1. Fox equated, “...the end of the continental Cretaceous with the end of the Lancian...” (Fox, 1997:70). Other workers (e.g., Cifelli et al., 2004; Lillegraven and Eberle, 1999; Lofgren et al., 2004) mark the boundary between the Lancian and Pu1 at the first appearance of *Protungulatum*. The stratigraphy and limited palynological evidence from these two sites suggest that both were deposited during the Cretaceous and there was not extensive reworking as is found in the Bug Creek assemblages (see discussion in Cifelli et al., 2004). The presence of *Protungulatum* cf. *P. donnae* in both localities indicates their local faunas are referable to the Pu1 interval zone. If the Cretaceous age determinations of the Fr-1, the MHBT (Long Fall), or new localities yielding local faunas of similar compositions are supported, the boundary between the Lancian and Puercan NALMA in the Western Interior is time transgressive. This would indicate that many taxa of multituberculates and eutherians identified as immigrants in Pu1 local faunas to the south were already present in southern Canada in the latest Cretaceous and expanded their ranges southward in the earliest Paleocene. If these Canadian local faunas are time-averaged assemblages similar in origin to the Bug Creek assemblages, the hypothesis that the Cretaceous/Tertiary boundary approximates the Lancian/Puercan boundary is not challenged

and the pattern of faunal change in Saskatchewan might not differ significantly from that found in areas to the south.

5 Records from other continents

There is evidence of mammalian dispersal between North America and Europe as well as South America during the Lancian, if not earlier (e. g., Case et al., 2005). Currently there is no persuasive evidence suggesting that any of the recognized Pu1 immigrants into the Western Interior originated from either of these continents. Records of mammalian dispersal between Asia and North America throughout the Cretaceous were summarized by Cifelli (2000). The Asian Campanian and Maastrichtian fossil record is heavily biased in favor of Mongolian localities probably of Campanian age. The mammals from these localities were dominantly endemics adapted to the arid environments of the area. Most likely dispersal eastward from Asia during or prior to the Campanian brought the “zhelestids” to North America where they were members of Late Cretaceous local faunas in Alberta, Baja California, Montana, Saskatchewan, Texas, and Utah (Kielan-Jaworowska et al., 2004). Wible et al. (2007, 2009) concluded that the Campanian, Mongolian *Maelestes gobiensis* is a member of the Cimolestidae. The other two cimolestids included in these analyses, *Cimolestes* and *Batodon*, were members of Lancian local faunas suggesting dispersal between North America and Asia occurred earlier. The two Mongolian mammals of possible Maastrichtian age come from localities in Mongolia, the multituberculate *Buginbaatar* and an unnamed deltatheridiid (Kielan-Jaworowska et al., 2004). Kielan-Jaworowska and Hurum (2001) tentatively referred *Buginbaatar* to the otherwise Late Cretaceous North American family Cimolomyidae. The unnamed deltatheridiid, based on the “Guriliin Tsav skull,” probably documents an early phase of metatherian evolution (Kielan-Jaworowska et al., 2004). Although indicating an earlier common ancestry with North American lineages and a Campanian or earlier interchange, there is no direct evidence of dispersal of mammals from this part of Asia contributing to the Pu1 faunas of the North American Western Interior.

Two areas in northern Asian coastal areas, which might have been more similar environmentally to the northern Western Interior of North America, offer very limited pertinent information, but have great potential for future discoveries. One is the Amur (Heilongjiang) River valley in northeastern China and southeastern Russia. On the basis of a fragment of posterior end of a p4, Averianov et al. (2002) reported the occurrence of a cimolodontan multituberculate in the late Maastrichtian Kundur local fauna in the Amur River region of southeastern Russia. The fragment shows some resemblances to p4s of the eucosmodontid *Stygmys* and microcosmodontids. The dinosaurian fauna from this area is markedly different from the late Maastrichtian faunas known from northeastern Siberia suggesting provincialism in this part of Asia (Godefroit et al., 2009, and references cited therein). Godefroit et al. (2009) recently described a latest Cretaceous (late Maastrichtian) vertebrate microfossil locality at Kakanaut at a high paleolatitude in northeastern Russia. Unfortunately, no mammalian material was recovered in screen washing sediments from this site. The local fauna resembles the somewhat older local fauna from the Prince Creek Formation in Alaska in the diversity of dinosaurs and absence of amphibians and turtles, crocodilians, and other non-dinosaurian reptiles, which are common in Campanian and Maastrichtian faunas farther to the south in the Western Interior (Clemens and Nelms, 1993).

The Chinese record of latest Cretaceous mammals is limited to Nei Mongol (Inner Mongolia). The mammals so far described appear to be related to members of the Campanian assemblages of Mongolia, particularly the Djadokhta fauna. To the south, a series of rift basins in southeastern China contain some highly fossiliferous sediments documenting early Paleocene mammalian faunas (Ting, 1998; Wang et al., 1998). Pertinent here are the oldest local faunas

that form the basis for definition of the Shanghuan Land Mammal Age, which has been divided into two interval zones: the older *Bemalambda* Interval Zone and the *Archeolambda* Interval Zone (Ting, 1998). Shanghuan faunas are dominated by Asian endemics including anagalids, eurymylids, mimotomids, and didymoconids. As noted by Lucas and Williamson (1995), they also include mesonychids, viverravids, pantodonts, and tillodonts. Members of these groups dispersed eastward making their first appearances in North American Torrejonian faunas. The limited bases for correlation of the Shanghuan with parts of the Puercan and Torrejonian NAL-MAs were thoroughly and favorably evaluated by Wang et al. (1998).

The Triisodontidae is essentially North American in known distribution with the gigantic *Andrewsarchus* from the Eocene of Asia added in some classifications (e. g. McKenna and Bell, 1997). The most primitive triisodontid, *Eoconodon*, makes its appearance in North America in the Pu1 and could well be the progenitor of the radiation of triisodontids later in the Paleocene. Phylogenetic analyses suggest that triisodontids were a sister group (e. g., Geisler and Uhen, 2005) or possibly ancestral to mesonychids. If this hypothesis is correct, what was the paleobiogeographic range of the common ancestor of triisodontids and mesonychids? Could *Eoconodon* be an Asian immigrant into the Western Interior at the beginning of the Puercan?

6 Discussion and conclusions

Was immigration of new species or an endemic radiation of surviving species the dominant process in evolution of earliest Paleocene mammalian faunas of the North American Western Interior after the mass extinction marking the end of the Cretaceous? Previous analyses of the origins of Pu1 faunas in the northern Western Interior have focused on a short time scale, and classified Pu1 taxa as residents or immigrants according to presence or absence of the taxon, of a sister group of the taxon, or a potential ancestor in Lancian faunas of this area. These interpretations can change when the scope of faunal evidence is increased to include longer temporal ranges (older or younger) or from wider paleogeographic areas. For example, as far as currently known *Stygmimys* was not present in the Lancian fauna of northeastern Montana and dispersed into the area at or near the beginning of the Pu1 interval zone. In this limited temporal and paleogeographic context, it was a Pu1 immigrant. Adopting a longer time scale and enlarging the paleogeographic area to include what is now Baja California reveals that *Stygmimys* or a closely related eucosmodontid had been a resident of western North America since the Campanian.

Analyses of limited paleogeographic and temporal scope indicated that in the northeastern Montana immigrant taxa were primarily archaic ungulates (“condylarths”) and to a lesser extent multituberculates. At the generic level immigrants outnumber residents by nine to five; at the specific level the ratio is twelve to six (Appendix 1). Expanding the paleogeographic area to include the Mantua Lentil and Hanna Basin faunas of Wyoming (Appendix 2) the same pattern is evident. Immigrants dominate in these Pu1 local faunas, however an immigrant unknown in northeastern Montana, *Eoconodon*, made its appearance.

To the south, the Pu1 Littleton fauna of the Denver Basin stands apart in the taxonomic diversity of its archaic ungulates, particularly peripitychids. As Eberle (2003) noted this difference might reflect a different source area for the immigrant archaic ungulates or the Littleton fauna might be younger and sampling a more recent stage of diversification of Pu1 faunas than found in Pu1 localities in Wyoming and Montana.

To the north, in general composition, the Trochu local fauna in Alberta (Appendix 3) and the Wounded Knee and Gryde local faunas in Saskatchewan (see Fox, 1997) resemble Lancian local faunas in Montana and Wyoming. As noted by Lillegraven (1969) and subsequent workers (e. g., Fox, 1997) they differ in the greater taxonomic diversity of eutherians and, in some cases, their high relative abundance. *Alostera*, probably a relict “zhelestid,” is present in all

three local faunas, and *Schowalteria*, a primitive taeniodont — a group that radiated in the Paleogene — is a member of the Trochu local fauna.

Because of their compositions and uncertainty concerning their age the Fr-1 and MHB (Long Fall) local faunas of southern Saskatchewan (Appendix 3) are of particular interest. In composition they resemble the Bug Creek assemblages of northeastern Montana in a mixture of what have been taken to be typical Lancian and Pu1 taxa. The stratigraphy and limited palynological evidence from the Fr-1 and MHB (Long Fall) localities suggest that both were deposited during the Cretaceous, and there was not extensive reworking as characterizes the Bug Creek assemblages (Lofgren, 1995). Because of the presence of *Protungulatum* cf. *P. donnae*, they are referable to the Pu1 interval zone. If the Cretaceous age of these local faunas is supported by future field work, the boundary between the Lancian and Puercan NALMA in the Western Interior is time transgressive relative to the K/T boundary. This would indicate that many of the taxa of multituberculates and eutherians identified as immigrants in Pu1 local faunas to the south were already present in southern Canada in the latest Cretaceous and simply expanded their ranges southward after the end of the Cretaceous.

There is evidence of mammalian dispersal from Asia in the Campanian and probably earlier in the Cretaceous (Cifelli, 2000, Wible et al., 2009). Maastrichtian and earliest Paleocene fossil records from these areas are very limited and not particularly informative concerning the origins of the Pu1 immigrants in faunas of the Western Interior. Given the magnitude of the marine regression at the end of the Cretaceous (Fig. 2), the possibility of dispersal of mammals at this time from eastern North America and Europe cannot be excluded.

In summary, analyses of known Lancian and Pu1 local faunas of the northern Western Interior strongly suggest that immigration was the dominate process in origin of its Pu1 local faunas. Currently, it appears likely that many, if not the majority, of these immigrants came from other areas in North America. The discovery of local faunas of Lancian and Puercan or equivalent ages in yet to be sampled areas of North America, particularly at high northern paleolatitudes, and the Pacific coastal area of Asia, will provide data for testing this hypothesis. As is so often the case in paleontology, discovery and analysis of additional fossils and stratigraphic information has brought to light more complexity and raised more questions concerning the course of mammalian evolution across the K/T boundary.

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Appendix 1 Lancian and Puercan 1 mammals from northeastern Montana

Garfield County Lancian	Western Garfield County Pu1	Eastern Garfield & western McCone Co. Pu1	Western McCone Co. (time-averaged Lancian and Pu1 assemblage) Immigrant taxa only
MULTITUBERCULATA	Residents	Resident	
<i>Cimolodon nitidus</i>	<i>Cimexomys minor</i>		
<i>Cimolomys gracilis</i>	<i>Cimexomys gratus</i>		
<i>Essonodon browni</i>			
<i>Meniscoessus robustus</i>			
<i>Mesodma formosa</i>	<i>Mesodma garfieldensis</i>	<i>Mesodma thompsoni</i>	
<i>Mesodma thompsoni</i>			
? <i>Neoplagauiax burgessi</i>	Immigrants	Immigrants	Immigrants
<i>Paracimexomys priscus</i>			
<i>Parectypodus foxi</i>	<i>Acheronodon garbanii</i>		<i>Catopsalis joyneri</i>
	<i>Catopsalis</i> cf. <i>C. alexanderi</i>		<i>Catopsalis alexanderi</i>
	<i>Stygimys kuszmauli</i>	<i>Stygimys kuszmauli</i>	<i>Stygimys kuszmauli</i>
METATHERIA	Resident	Resident	
<i>Alphadon jasoni</i>	<i>Peradectes</i> cf. <i>P. pusillus</i>	<i>Peradectes</i> cf. <i>P. pusillus</i>	
<i>Alphadon marshi</i>			
<i>Didelphodon vorax</i>			
<i>Glasbius twitchelli</i>			
" <i>Pedimys</i> " <i>cooki</i>			
<i>Pedimys elegans</i>			
" <i>Pedimys</i> " <i>florencae</i>			
" <i>Pedimys</i> " <i>hatcheri</i>			
" <i>Pedimys</i> " <i>krejci</i>			
<i>Protalphadon foxi</i>			
<i>Turgidodon rhaister</i>			
EUTHERIA	Resident	Resident	
<i>Batodon tenuis</i>	<i>Cimolestes</i> sp.		
<i>Cimolestes cerberoides</i>	<i>Procerberus formicarum</i>	<i>Procerberus formicarum</i>	
<i>Cimolestes incisus</i>			
<i>Cimolestes magnus</i>			
<i>Cimolestes propalaeoryctes</i>	Immigrants	Immigrants	Immigrants
<i>Cimolestes stirtoni</i>			
<i>Gypsonictops hypoconus</i>	Leptictidan	Leptictidan	
<i>Gypsonictops illuminatus</i>	<i>Baioconodon engdahli</i>	<i>Baioconodon</i> sp.	<i>Baioconodon nordicum</i>
	<i>Mimatuta morgoth</i>	<i>Mimatuta</i> sp.	<i>Mimatuta morgoth</i>
			<i>Mimatuta minuial</i>
	<i>Oxyprimus erikseni</i>	<i>Oxyprimus</i> sp.	<i>Oxyprimus erikseni</i>
	<i>Protungulatum donnae</i>		<i>Protungulatum donnae</i>
			<i>Protungulatum gorgon</i>
	?Periptychidae gen. et sp. nov.		

Note: As a base for comparison the Garfield County Lancian NALMA faunal list is reproduced from Wilson (2005). The Western Garfield County Pu1 faunal list is based on the work of Archibald (1982) with modifications by Lofgren (1995) and new collections. The Eastern Garfield and western McCone County faunal list is based on Lofgren's (1995) analyses of localities V 84193 and V 84194 and new collections from localities V 84165 and V 96268. The Western McCone County (time-averaged Lancian and Pu1) assemblage list is taken from Lofgren (1995) and includes only the taxa interpreted to be Pu1 mammalian immigrants into northeastern Montana.

Appendix 2 Puercan 1 mammalian faunas from Wyoming (Mantua Lentil and Hanna Basin) and Colorado (Denver Basin)

Mantua local fauna Pu1	Hanna Basin Pu1	Denver Basin Pu1
MULTITUBERCULATA		
<i>Mesodma ambigua</i>	<i>Mesodma formosa</i> <i>Mesodma ambigua</i> <i>Mesodma hensleighi</i> <i>Mesodma</i> cf. <i>M. garfieldensis</i> <i>Mesodma</i> sp. indet. ? <i>Mesodma</i> sp. Neoplagiulacidae gen. et sp. indet.	<i>Mesodma</i> cf. <i>M. ambigua</i>
<i>Stygimys kuszmauli</i>		<i>Xyronomys robinsoni</i> <i>Kimbetohia</i> ? <i>mziae</i> <i>Catopsalis alexanderi</i> <i>Cimexomys arapahoensis</i> <i>Cimexomys minor</i>
<i>Cimexomys gratus</i>		
METATHERIA		
	<i>Peradectes</i> cf. <i>P. pusillus</i>	<i>Peradectes pusillus</i>
EUTHERIA		
	Palaeoryctidae gen. et sp. indet. Proteutheria family indet.	Proteutheria indet.
<i>Procerberus</i> spp.	<i>Protungulatum donnae</i> <i>Protungulatum sloani</i>	<i>Procerberus andesiticus</i> <i>Protungulatum donnae</i> <i>Procerberus grandis</i> <i>Oxyciaenus subbituminus</i> <i>Oxyciaenus</i> cf. <i>O. simplex</i> <i>Oxyprimus</i> cf. <i>O. galadrielae</i>
<i>Oxyprimus galadrielae</i> <i>Oxyprimus putoris</i> <i>Baioconodon nordicum</i>	<i>Oxyprimus galadrielae</i> <i>Oxyprimus</i> sp. indet.	<i>Baioconodon denverensis</i> <i>Baioconodon cannoni</i> <i>Baioconodon jeffersonensis</i> Aretocyonidae gen. et sp. indet.
<i>Mimatuta minuial</i> <i>Mimatuta undomiel</i> <i>Maiorana noctiluca</i>	<i>Mimatuta</i> sp. indet. <i>Maiorana ferrisensis</i>	
<i>Oxyacodon josephi</i>		<i>Alticonus gazini</i> <i>Ampliconus browni</i> <i>Auraria urbana</i> <i>Conacodon harbourae</i> <i>Conacodon matthewi</i> <i>Oxyacodon archibaldi</i> Periptychidae n. gen. et sp.
<i>Eoconodon copanus</i>	<i>Eoconodon</i> sp.	

Note: The Mantua Lentil faunal list is based on the work of Jepsen (1940), Van Valen (1978), Gingerich et al. (1980), and Lofgren (1995). The monographic studies by Eberle and Lillegraven (1998a,b) are the source of the Pu1 faunal list for the Hanna Basin. The faunal list for the Denver Basin is based on a compilation of studies by Middleton and Dewar (2004) and Eberle (2003).

Appendix 3 Lancian and Puercan 1 mammals from Alberta and Saskatchewan, Canada

Trochu local fauna	Fr-1	MHBT (Long Fall)
Lancian	Pu1 (Cretaceous)	Pu1 (Cretaceous)
MULTITUBERCULATA		
	<i>Catopsalis</i> cf. <i>C. joyneri</i>	<i>Catopsalis johnstoni</i> <i>Catopsalis</i> cf. <i>C. joyneri</i> <i>Cimexomys minor</i> <i>Cimexomys</i> cf. <i>C. hausoi</i>
<i>Cimolodon nitidus</i>	<i>Cimolodon</i> cf. <i>C. nitidus</i>	<i>Cimolodon nitidus</i>
<i>Cimolomys gracilis</i>		<i>Cimolomys</i> cf. <i>C. gracilis</i>
<i>Cimolomys trochuus</i>		
	<i>Meniscoessus</i> cf. <i>M. robustus</i>	<i>Meniscoessus</i> cf. <i>M. robustus</i>
<i>Mesodma formosa</i>	<i>Mesodma</i> sp.	
<i>Mesodma hensleighi</i>		<i>Mesodma thompsoni</i>
<i>Mesodma thompsoni</i>		microcosmodontid
<i>Paracimexomys priscus</i>		<i>Stygimys cupressus</i>
METATHERIA		
<i>Alphadon jasoni</i>	<i>Alphadon jasoni</i>	<i>Alphadon</i> sp.
<i>Alphadon marshi</i> (incl. <i>A. wilsoni</i>)		
<i>Didelphodon vorax</i>		
<i>Pediomys elegans</i>		<i>Pediomys elegans</i>
" <i>Pediomys</i> " <i>hatcheri</i>		
" <i>Pediomys</i> " <i>krejci</i>		
<i>Turgidodon rhaister</i>		
EUTHERIA		
<i>Alostera saskatchewanensis</i>		
<i>Batodon tenuis</i>		
		<i>Baioconodon</i> sp.
<i>Cimolestes cerberoides</i>	<i>Cimolestes</i> cf. <i>C. cerberoides</i>	<i>Cimolestes</i> cf. <i>C. cerberoides</i>
<i>Cimolestes magnus</i>		
<i>Cimolestes propalaeoryctes</i>		<i>Cimolestes</i> cf. <i>C. stirtoni</i>
<i>Gypsonictops hypoconus</i>		<i>Gypsonictops illuminatus</i>
<i>Gypsonictops illuminatus</i>		hyopsodontid <i>Mimatuta</i> sp. <i>Oxyprimus</i> cf. <i>O. erikseni</i> <i>Procerberus</i> cf. <i>P. formicarum</i> <i>Protungulatum</i> cf. <i>P. donnae</i> <i>?periptychid</i>
	<i>Protungulatum</i> cf. <i>P. donnae</i> <i>?periptychid</i>	
<i>Schowalteria clemensi</i>		

Note: As a base for comparison the Lancian Trochu local faunal list is compiled from the studies of Lillegraven (1969), Hunter and Archibald (2002), and Fox and Naylor (2003). Faunal lists for the Fr-1 and MHBT (Long Fall) (=Long Fall horizon in the Medicine Hat Brick and Tile Quarry) localities were taken from the compilation provided by Fox (1997).