Geological Society of America
Special Paper 361
2002

Mammals from the end of the age of dinosaurs in North Dakota and southeastern Montana, with a reappraisal of geographic differentiation among Lancian mammals

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ABSTRACT

An end-Cretaceous nonavian dinosaur extinction and an early Paleocene mammalian radiation is documented primarily in stratigraphic sequences in eastern Montana. To determine how representative these sequences are, we extended investigation of this Cretaceous-Tertiary (K-T) transition to new areas. Studies in southwestern North Dakota and southeastern Montana provide new records of mammals through the last 1.32–1.68 million years of the Cretaceous and extending into the Paleocene, allowing us to evaluate mammalian faunal differentiation across the geographic landscape of the North American Western Interior in the latest Cretaceous. In North Dakota, mammals occur at 15 horizons in the Hell Creek Formation from ~80 to 3 m below the Hell Creek–Fort Union formational contact. In southeastern Montana, where the Hell Creek Formation is ~150 m thick, mammals occur from 85 to 15 m below the formational contact, with well-sampled local faunas at 65 and 61 m. In faunal comparisons, the new study areas are closely similar to contemporaneous local faunas, but differ from those at higher latitudes in several ways. Although mammalian faunas of the northwestern coastal plain of the Western Interior Seaway (i.e., the Hell Creek Formation and its lateral equivalents) show little differentiation, differences that exist are strongly associated with geographic distance rather than latitude per se. The overlying Fort Union Formation in North Dakota and southeastern Montana has produced a few early Paleocene mammalian specimens, promising that future work in the area will contribute to knowledge of mammalian radiation after the K-T boundary.

INTRODUCTION

The end of the Cretaceous through the beginning of the Tertiary (Paleogene) was a critical time in the evolutionary history of mammals. During this interval, mammalian communities underwent profound changes in composition. In the Western Interior of North America, a Tertiary community with diverse eutherian mammals replaced a Cretaceous community dominated by primitive marsupials and the now extinct multituberculates (Archibald, 1996; Hunter, 1999). The highest rates

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Hunter, J.P., and Archibald, J.D., 2002, Mammals from the end of the age of dinosaurs in North Dakota and southeastern Montana, with a reappraisal of geographic differentiation among Lancian mammals, *in* Hartman, J.H., Johnson, K.R., and Nichols, D.J., eds., The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains: An integrated continental record of the end of the Cretaceous: Boulder, Colorado, Geological Society of America Special Paper 361, p. 191–216.

of extinction and origination, as well as the largest single increase in average body mass observed in the North American mammalian fossil record (Alroy, 1999), are associated with the Cretaceous-Tertiary (K-T) boundary Most extant orders of placental mammals first appeared in the fossil record in a dramatic Paleogene evolutionary radiation following the extinction of dinosaurs at the K-T boundary (McKenna and Bell, 1997). The temporal clustering of these ordinal appearance events (Archibald and Deutschman, 2001) and estimated preservation potential of Late Cretaceous mammals (Foote et al., 1999) demonstrate that the origin and diversification of modern placental orders deep in the Cretaceous, that is, long before the K-T boundary, is unlikely.

Unfortunately, our knowledge of the history of mammals leading up to the K-T boundary, arguably the single greatest change in mammalian communities, is restricted geographically. Although there are isolated occurrences in eastern North America (Grandstaff et al., 1992), Europe (Grigorescu and Hahn, 1987; Le Loeuff and Buffetaut, 1995), and India (Prasad et al., 1995; Krause et al., 1997), mammals from the end of the Cretaceous are best known from the North American Western Interior (Lancian North American Land Mammal Age [NALMA]) from Alberta (Lillegraven, 1969) to New Mexico (Flynn, 1986). Well-sampled stratigraphic sequences that include fossil mammals on both sides of the K-T boundary are even more restricted latitudinally to eastern Montana (Sloan and Van Valen, 1965; Archibald, 1982; Clemens, this volume) and southern Saskatchewan (Johnston, 1980; Johnston and Fox, 1984; Fox, 1989, 1997). Although similar sequences of localities occur farther south near Glendive, Montana (Hunter et al., 1997) and in the Hanna Basin of southern Wyoming (Eberle and Lillegraven, 1998a, 1998b; Lillegraven and Eberle, 1999), very earliest Paleogene mammals (Pu0 or Pu1; Archibald and Lofgren, 1990) have not been recovered near Glendive, and only a few Cretaceous mammals from the Hanna Basin.

In spite of the geographically small window of observation through which we view mammalian evolution leading up to the K-T boundary, scenarios that seek to account for mammalian turnover at the boundary have incorporated a geographic component. Differences in faunal composition among Lancian sites, e.g., an initially greater observed diversity of eutherians at higher latitudes in Lancian time (Lillegraven, 1969), have been interpreted to indicate a north-to-south sequence in the transition from Cretaceous-aspect to Paleocene-aspect vertebrate faunas, as expected with an invasion of North America by Asian immigrants (Sloan, 1969; Russell, 1975). Although some subsequent discoveries reaffirmed this interpretation (Archibald, 1982), others have rendered it less straightforward (Fox, 1989). Separating the effects of geographic, ecological, and temporal differences on the composition of Lancian mammalian local faunas has remained a problem. This difficulty has stemmed largely from the fact that no field area could boast a sequence of well-documented localities through Lancian time, by means of which at least temporal differences could be factored out (Archibald, 1982). The overall goals of this study are to move toward providing such stratigraphic sequences and to reconsider the meaning of patterns of faunal similarity among Lancian faunas.

The first specific objective of this study is to augment the known fossil record of mammals at the end of the Cretaceous, both in geographic extent and stratigraphic resolution. To this end, we first describe Late Cretaceous (Lancian) mammals from the Hell Creek Formation and Paleocene (Puercan) mammals from the Ludlow Member of the Fort Union Formation in southwestern North Dakota and adjacent South Dakota being studied by one of us (Hunter). These discoveries, primarily from North Dakota, contribute to knowledge of Lancian mammals by providing the first record of mammalian occurrences through the entire vertical extent of the Hell Creek Formation, and thus through the last ~1.32–1.68 m.y. of the Cretaceous (see Hicks et al., this volume, for estimated duration of the Hell Creek Formation of southwestern North Dakota based on a linear interpolation of sedimentation rates and a new estimate of the age of the K-T boundary). The finds derive from ongoing efforts to document Late Cretaceous and Paleocene mammalian evolution in the area (Hunter and Pearson, 1996; Hunter et al., 1997; Hunter, 1999). Second, we report on work in progress (by Archibald) on fossil mammals of the Hell Creek Formation of extreme southeastern Montana, near the town of Ekalaka in Carter County. Although these localities in Montana do not cover the stratigraphic breadth of the record in North Dakota, they nevertheless have been exhaustively sampled and likely well represent the local fauna. The third specific objective of this study is to reappraise differentiation among the well-sampled Lancian faunas, including the new ones reported here.

In this study, we follow Fox (1989, 1997) and Lillegraven and Eberle (1999) in provisionally considering the Lancian-Puercan boundary to coincide, to a first approximation, with the K-T boundary. Purportedly transitional Bug Creek assemblages in eastern Montana (Sloan and Van Valen, 1965; Lofgren, 1995) are probably best viewed as Paleocene with a reworked Late Cretaceous (i.e., Lancian) component (Lofgren, 1995). Although transitional assemblages in Saskatchewan (Fr-1 and MHBT Quarry, Long Fall horizon) might be considered Puercan on the basis of the occurrence the condylarth *Protungulatum* (Archibald and Lofgren, 1990), palynological evidence suggests that at least Fr-1 is Maastrichtian, and thus possibly in part contemporaneous with Lancian assemblages elsewhere (Fox, 1989, 1997). Although arguments based upon stratigraphy make reworking an unlikely explanation for the transitional nature of the assemblage at Long Fall (i.e., there is no obvious source for Late Cretaceous terrestrial fossils in underlying rocks nearby; Fox, 1989, 1997), interpretations other than a Late Cretaceous age remain conceivable. One possibility is that the Long Fall horizon could be Paleocene and include a component of mammalian and dinosaurian survivors from the Late Cretaceous. This scenario seems unlikely, however, because none of the dinosaurs and only one of the Lancian mammals (*Mesodma* *thompsoni*) present at Long Fall is argued to have survived the K-T boundary elsewhere (Archibald and Bryant, 1990). More probable is that the Long Fall assemblage is a time-averaged sample, as expected in any channel deposit (Behrensmeyer, 1988), and happens to span the K-T boundary. Even following Fox (1989, 1997) in considering Fr-1 and Long Fall to be Late Cretaceous (Lancian), these sites are arguably younger than other Lancian sites, and were treated as such in the Late Cretaceous mammalian time scale prepared by Hunter for use in Foote et al. (1999; see supplementary data at *www.sciencemag.org/feature/data/985988.shl.*). Accordingly, we omit both assemblages from the analytical faunal comparisons, and Fr-1 because of its small sample size. We instead include more typical and well-sampled Lancian assemblages from the same geographic area (Gryde and Wounded Knee localities).

GEOGRAPHIC AND GEOLOGIC CONTEXT

Other chapters in this volume (e.g., Murphy et al.) describe the geology of the Hell Creek Formation in the Great Plains in general and in North Dakota in particular. Nichols and Johnson (this volume) provide the palynological basis for recognizing the K-T boundary in North Dakota. The mammals described below derive from 17 localities distributed across southwestern North Dakota (Fig. 1) and an immediately adjacent area of South Dakota: 15 of these localities are in the Hell Creek Formation (~80–3 m below the K-T boundary), and two are in the Ludlow Member of the Fort Union Formation (~5.6–7.1 m above the K-T boundary; see Appendix). Each of these localities has also produced nonmammalian vertebrates. Pearson et al. (this volume) detail the collection and curation of the vertebrate specimens. See Hicks et al. (this volume), Johnson (this volume), and Nichols and Johnson (this volume) for the stratigraphic correlation of the localities from which these specimens derive. All 17 Pioneer Trails Regional Museum (PTRM) localities have been sampled by surface collection, but PTRM locality V92067 (Hunter and Pearson, 1996) has also been sampled by screen washing.

Belt et al. (1997) discussed the geology, particularly the stratigraphy, of the Hell Creek Formation of southeastern Montana, from which we report five mammalian localities comprising two local faunas, ~65 and ~61 m below the formational contact, respectively (see Appendix). All five UCMP localities have been sampled by screen washing.

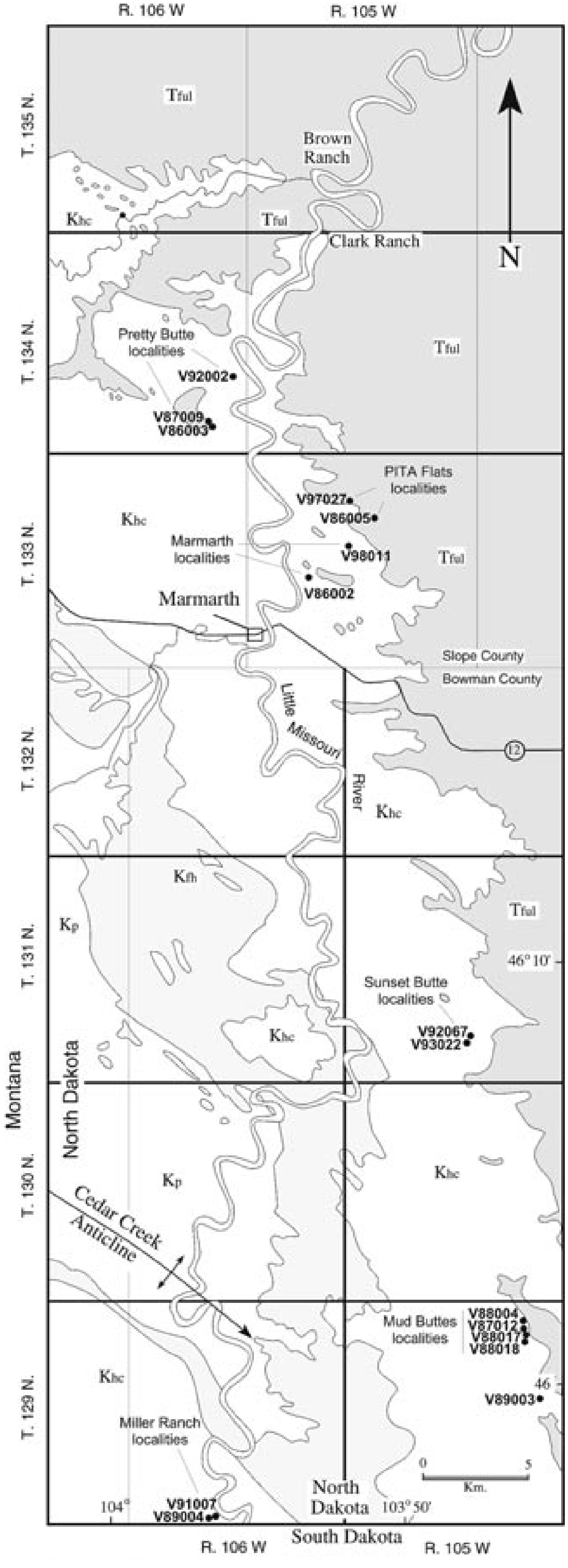

Figure 1. Map showing distribution of fossil mammal localities across study area in extreme southwestern North Dakota. Base map is adapted from Johnson (1992). All localities are identified by Pioneer Trails Regional Museum (PTRM) number. Localities in South Dakota (PTRM locality V92025) and Montana (all UCMP localities) are beyond range of map. Kfh, Fox Hills Formation; Khc, Hell Creek Formation; Kp, Pierre Formation; Tfu1, Ludlow Member of Fort Union Formation.

METHODS

Measurements (in millimeters) were taken either directly through a stereomicroscope using an optical reticle or from digital images from a Kodak MDS 120 and viewed in Adobe Photoshop. Table 1 lists the abbreviations used here. Tooth position within a tooth class (e.g., molars) is denoted by a number or by an X if position could not be ascertained.

TABLE 1. ABBREVIATIONS

AMNH	=	American Museum of Natural History, New York
PTRM	=	Pioneer Trails Regional Museum, Bowman, North Dakota
UA	=	University of Alberta
UCMP	=	University of California Museum of Paleontology, Berkeley
V	=	vertebrate
YPM	=	Yale Peabody Museum, New Haven, Connecticut
L	=	length
TALW	=	talonid width
TRGW	=	trigonid width
W	=	width
C,c	=	upper or lower canine, respectively
I,i	=	upper or lower incisor, respectively
M,m	=	upper or lower molar, respectively
P,p	=	upper or lower premolar, respectively
gen.	=	genus
indet.	=	indeterminate
sp.	=	species (singular)

SYSTEMATICS

Note that only mammalian specimens from the PTRM localities in southwestern North Dakota and South Dakota studied by Hunter are described in the following. Specimens from the UCMP localities in southeastern Montana studied by Archibald will be described elsewhere.

Class Mammalia
Order Multituberculata
Family Neoplagiaulacidae

Mesodma Jepsen 1940

Mesodma thompsoni Clemens 1964
Fig. 2, A–C

Nomenclatural summary. *Mesodma thompsoni* Clemens 1964 (p. 39).

Holotype. UCMP 47217, left p4.

Type locality. UCMP locality V5620, Lance Formation; Niobrara County, Wyoming.

Distribution. Lance Formation (Lancian), Wyoming; Hell Creek Formation (Lancian), Montana, North Dakota, and South Dakota; Scollard Formation (Lancian), Alberta. Ravenscrag Formation (Lancian and/or Puercan?), Saskatchewan. Bear Formation (Puercan), Montana; Nacimiento Formation (Puercan), New Mexico; Ravenscrag Formation (Puercan), Saskatchewan; Tornillo Formation (Puercan), Texas. Possibly also Kaiparowits Formation (Judithian), Utah; St. Mary River Formation (?Edmontonian), Alberta; Fox Hills Formation (Lancian), South Dakota; and Frenchman Formation (Lancian), Saskatchewan.

Referred specimens. Left dentary with p3–p4 (PTRM 1119) from PTRM locality V89004; left p4 (PTRM 1227) from PTRM locality V92067.

Discussion. The p4s of these specimens possess the low, arched profile with a sharp change in the slope of the serrate margin anteriorly that is typical of *Mesodma*. Specific assignment to *Mesodma thompsoni* is on the basis of size (p4 [PTRM 1119]: L = 4.33, W = 1.60), serration number (12), and profile shape (lower arched than in *M. formosa* [Marsh, 1889b] or *M. hensleighi* Lillegraven 1969).

Mesodma sp.

Referred specimens. Left P4 (PTRM 1274) and left p4 fragment (PTRM 1281) from PTRM locality V86005.

Discussion. Although these specimens are in the size range of *Mesodma thompsoni* and probably belong to that taxon, they have been identified only to the generic level because they are so fragmentary.

Family Cimolodontidae

Cimolodon Marsh 1889

Cimolodon nitidus Marsh 1889
Fig. 2, D–L

Nomenclatural summary. *Cimolodon nitidus* Marsh (1889a, p. 84–85, plate II, Figs. 5–8). See Clemens (1964, p. 56) for synonyms and a revised diagnosis.

Holotype. YPM 11776, left ml.

Type locality. Mammal locality 1 of Lull (1915); UCMP locality V5003, Lance Formation, Wyoming.

Known distribution. St. Mary River Formation (?Edmontonian), Alberta. Fox Hills Formation (Lancian), South Dakota; Scollard Formation (Lancian), Alberta; Frenchman Formation (Lancian), Saskatchewan; Hell Creek Formation (Lancian), Montana, North Dakota, and South Dakota; Lance and Ferris Formations (Lancian), Wyoming. Ravenscrag Formation (Lancian and/or Puercan?), Saskatchewan. Possibly also Prince Creek Formation (Lancian), Alaska.

Referred specimens. Left P4 (PTRM 614) from PTRM locality V89004; left M1 (PTRM 602) from PTRM locality V89003; left dentary with p4 (PTRM 3609) from PTRM locality V86002.

Discussion. These specimens (P4: L = 3.43, W = 1.69; M1: L = 4.32, W = 2.33; p4: L = 4.79, W = 2.00) are in the size range of *Cimolodon nitidus*, the only known Lancian multituberculate intermediate in size between the smaller neoplagiaulacids and the larger cimolomyids. The p4 (PTRM 3609) possesses the characteristic symmetrical arch of *C. nitidus*. P4 (PTRM 614) is bulky with a pronounced anterobuccal bulge, as in *C. nitidus*.

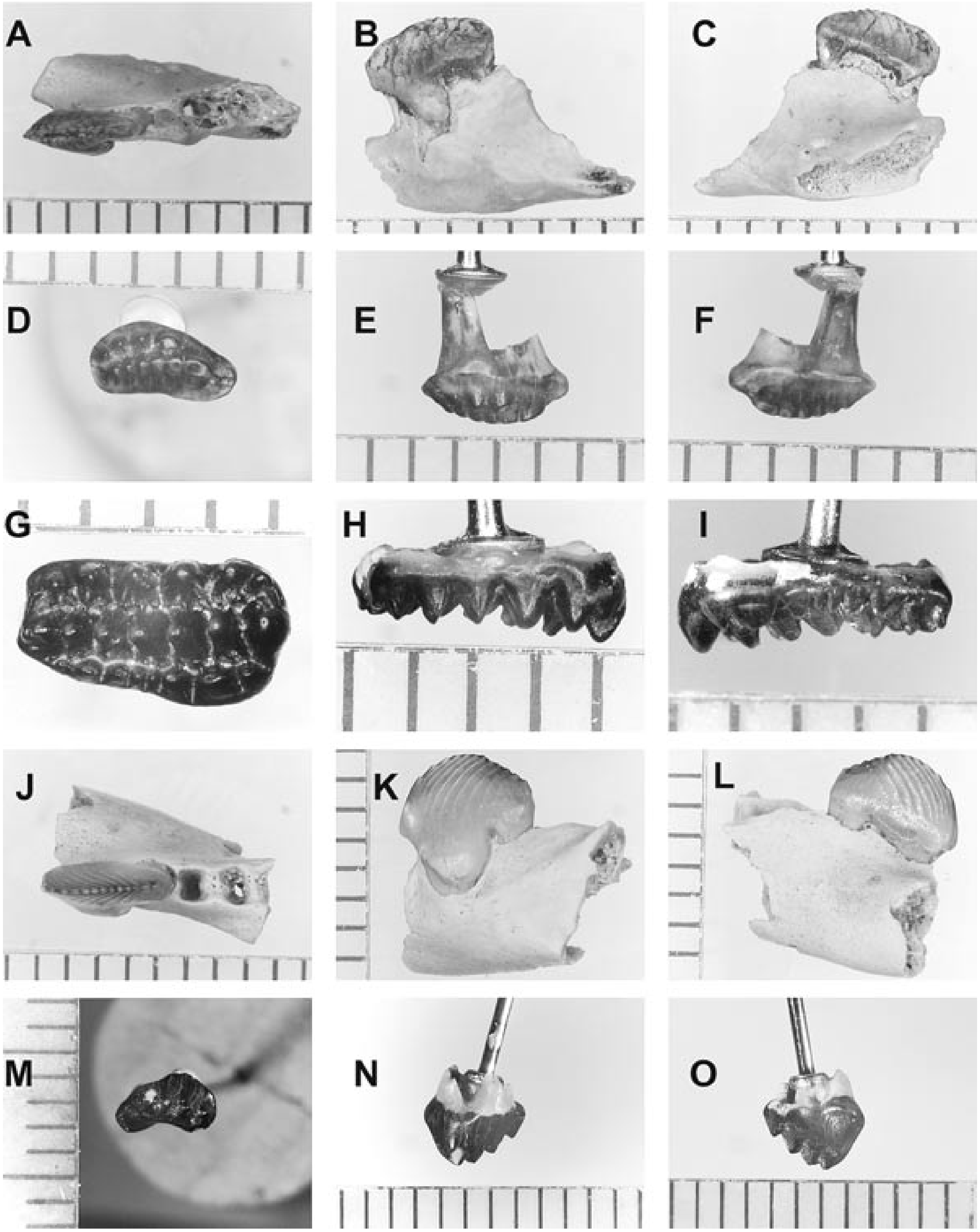

Figure 2. Photographic plate showing specimens of Late Cretaceous multituberculates from North Dakota. *Mesodma thompsoni*, left dentary with p3–p4 (PTRM 1119) from locality PTRM V89004 in occlusal (A), labial (B), and lingual (C) views. *Cimolodon nitidus*, left P4 (PTRM 614) from PTRM locality V89004 in occlusal (D), labial (E), and lingual (F) views; left M1 (PTRM 602) from PTRM locality V89003 in occlusal (G), labial (H), and lingual (I) views; left dentary with p4 (PTRM 3609) from PTRM locality V86002 in occlusal (J), labial (K), and lingual (L) views. *Meniscoessus robustus*, right P4 (PTRM 603) from PTRM locality 92002 in occlusal (M), labial (N), and lingual (O) views. Scale ruled in millimeters. PTRM is Pioneer Trails Regional Museum; for abbreviations, see Table 1.

Cimolodon sp.

Referred specimens. Left M2 (PTRM 1223) from PTRM locality V92067.

Discussion. Although this specimen is in the size range of *Cimolodon nitidus* and probably belongs to that taxon, it has been identified only to the generic level because it is so poorly preserved.

Family Cimolomyidae

Meniscoessus Cope 1882

Meniscoessus robustus (Marsh 1889)

Fig. 2, M–O; Fig. 3, A and B

Nomenclatural summary. *Dipriodon robustus* Marsh (1889a, p. 85, Plate II, Figs. 13–15). See Archibald (1982, p. 75) for synonyms and a revised diagnosis.

Holotype. YPM 11234, right m2.

Type locality. Mammal locality 2 of Lull (1915); UCMP locality V5815, Lance Formation, Wyoming.

Distribution. St. Mary River Formation, Alberta (?Edmontonian). Frenchman Formation (Lancian), Saskatchewan; Hell Creek Formation (Lancian), Montana, North Dakota, and South Dakota; Lance Formation (Lancian), Wyoming. Possibly also Frenchman and Ravenscrag Formations (Lancian and/or Puercan?), Saskatchewan.

Referred specimens. Right m2 (PTRM 1275) from PTRM locality 89004; right P4 (PTRM 603) from PTRM locality 92002; I2 (PTRM 1268), left P4 (PTRM 3041), two left M1s (PTRM 3001 and 3559), three right M2s (PTRM 619, 1288, and 2116), three left M2s (PTRM 1249, 1253, and 1256), right lower incisor (PTRM 3000), right p4 (PTRM 2111), two left p4s (PTRM 2119 and 2112), right m1 (PTRM 2115), two left m1s (PTRM 1248 and 1269), and four left m2s (PTRM 613, 1228, 1229, and 1252) from PTRM locality V92067; right p4 (PTRM 600) from PTRM locality V87009; left M1 (PTRM 1283) from PTRM locality V93022; left m2 (PTRM 3563) from PTRM locality 89003; right M1 (PTRM 3556), left M1 (PTRM 2117), and right m1 (PTRM 696) from PTRM locality V87012.

Discussion. *Meniscoessus robustus* from the Hell Creek Formation, North Dakota, is indistinguishable from samples of *Meniscoessus robustus* from other Lancian sites from North America but extends both the upper and lower ends of the size range of this taxon (see Hunter and Pearson, 1996).

Meniscoessus sp.

Referred specimens. Fragments of teeth from PTRM localities V89004 (PTRM 606 and 1291), V92067 (PTRM 621, 623, 624, 1226, 1231, 1232, 1247, 1264, 1287, 2120–2122, 2124, 3002, and 3042), V86003 (PTRM 3005, 3006, and 3046), V86002 (PTRM 3603), V89003 (PTRM 615), and V92025 (PTRM 1273).

Discussion. Many dental fragments most likely belong to *Meniscoessus robustus* on the basis of large size and cusp shape (e.g., extremely crescentic molar cusps), but they have been identified only to the generic level if they were too fragmentary or poorly preserved.

?*Meniscoessus* sp.

Referred specimens. Left petrosal (PTRM 1276) from PTRM locality V89004; PX fragment (PTRM 1115) from PTRM locality V86003.

Discussion. The isolated petrosal is not associated with any identifiable dental remains. Nevertheless, it is similar to isolated petrosals from the Lance Creek and Bug Creek local faunas that other workers (Kielan-Jaworowska et al., 1986; Luo, 1989; Rougier et al., 1992) have identified as belonging to either one of the large multituberculates *Meniscoessus* or *Catopsalis* Cope 1882. This petrosal will be described in a subsequent paper. The PX fragment is assigned to ?*Meniscoessus* on the basis of its large size.

Infraclass Metatheria
Order Marsupialia
Family Alphadontidae

Alphadon Simpson 1927

Alphadon marshi Simpson 1927

Fig. 3, C–E

Nomenclatural summary. *Alphadon marshi* Simpson 1927 (p. 125).

Holotype. YPM 13659, right m3.

Type locality. Lance Formation, Niobrara County, Wyoming.

Distribution. Scollard Formation (Lancian), Alberta; Lance Formation (Lancian), Wyoming; Hell Creek Formation (Lancian), Montana and North Dakota; Kirtland Formation (Lancian), New Mexico. Reported (material not yet described) from the Fox Hills and Hell Creek Formations (Lancian) of South Dakota.

Referred specimen. Right m1 (PTRM 608) from PTRM locality V89004.

Discussion. PTRM 608 possesses the twinned entoconid–hypoconulid and buccal postcingulid of primitive marsupials, and its cristid obliqua meets the middle of the posterior face of the trigonid as in other Lancian alphadontids (the cristid obliqua meets the posterior face of the protoconid in stagodontids and "pediomyids"). In size (L = 2.15, TRGW = 1.25, TALW = 1.4), the specimen is closest to *Alphadon marshi* from the Flat Creek local fauna (observed ranges: L = 2.09–2.25, TRGW = 1.05–1.35, TALW = 1.22–1.42; Archibald, 1982, Table 20), i.e., larger than known samples of *A. wilsoni* (see Fox, 1989, p. 23).

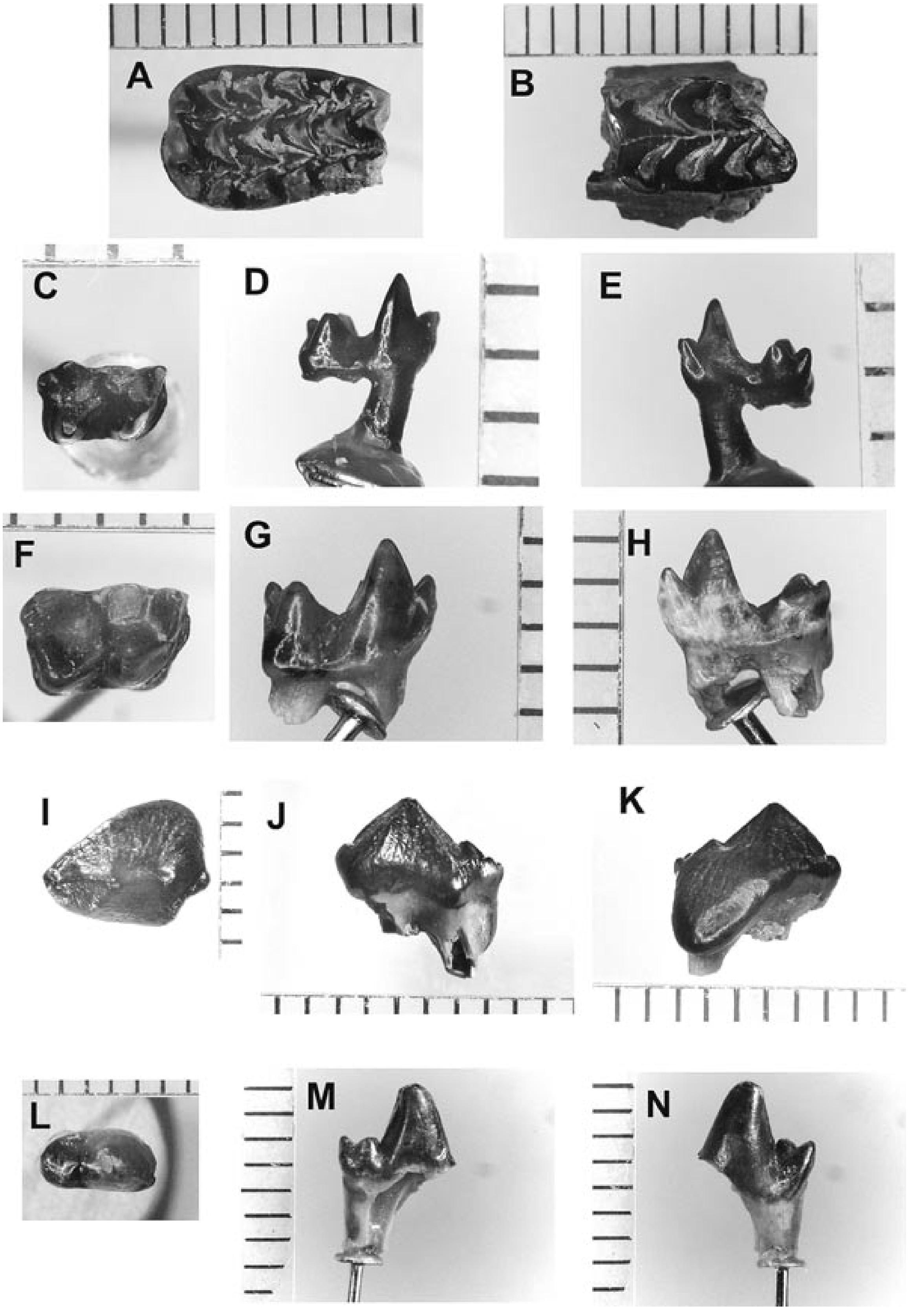

Figure 3. Photographic plate showing specimens of Late Cretaceous mammals from North Dakota. *Meniscoessus robustus*, right M1 (PTRM 3556) from PTRM locality V87012 in occlusal view (A) and left m2 (PTRM 3563) from PTRM locality 89003 in occlusal view (B). *Alphadon marshi*, right m1 (PTRM 608) from PTRM locality V89004 in occlusal (C), labial (D), and lingual (E) views. "*Pediomys*" *florencae*, right m2 (PTRM 605) from PTRM locality V89004 in occlusal (F), labial (G), and lingual (H) views. *Didelphodon vorax*, left p2 (PTRM 3012) from PTRM locality V89004 in occlusal (I), labial (J), and lingual (K) views. *Cimolestes magnus*, right p4 (PTRM 695) from PTRM locality V86002 in occlusal (L), labial (M), and lingual (N) views. Scale ruled in millimeters. PTRM is Pioneer Trails Regional Museum; for abbreviations, see Table 1.

TABLE 2. MAMMALIAN FAUNA OF THE HELL CREEK FORMATION, SOUTHWESTERN NORTH DAKOTA, AND ADJACENT SOUTH DAKOTA

- Multituberculata
  - *Mesodma thompsoni* Clemens
  - *Cimolodon nitidus* Marsh
  - *Cimolodon* sp.
  - *Meniscoessus robustus* (Marsh)
  - *Meniscoessus* sp.
  - ?*Meniscoessus* sp.
- Metatheria
  - *Alphadon marshi* Simpson
  - *Pediomys florencae* Clemens
  - *Pediomys* sp. cf. *P. florencae* Clemens
  - *Didelphodon vorax* Marsh
  - *Didelphodon* sp.
  - ?*Didelphodon* sp.
- Eutheria
  - *Gypsonictops illuminatus* Lillegraven
  - *Cimolestes magnus* Clemens and Russell

Family “Pediomyidae”

“*Pediomys*” Marsh 1889

“*Pediomys*” *florencae* Clemens 1966

Fig. 3, F–H

Nomenclatural summary. *Pediomys florencae* Clemens 1966 (p. 50).

Holotype. UCMP 51440, left maxilla with M2 and M3.

Type locality. UCMP locality V5820, Lance Formation, Wyoming.

Distribution. Hell Creek Formation (Lancian), Montana, North Dakota, and South Dakota; Lance Formation (Lancian), Wyoming.

Referred specimen. Right m2 (PTRM 605) from PTRM locality V89004.

Discussion. PTRM 605 possesses the labial cristid obliqua of “pediomyids” and stagodontids, but lacks the mesiodistally compressed trigonid of stagodontids. The metaconid has been broken, but was clearly relatively larger than the metaconid of stagodontids. In size (L = 4.2, TRGW = 2.7, TALW = 2.8) it is closest to “*Pediomys*” *florencae*, the largest known Lancian “pediomyid.”

“*Pediomys*” sp. cf. “*P*”. *florencae*

Referred specimen. Right dentary with p3, m3 (PTRM 1255) from locality V92067.

Discussion. See Hunter and Pearson (1996).

Family Stagodontidae

Didelphodon Marsh 1889

Didelphodon vorax Marsh 1889

Fig. 3, I–K

Nomenclatural summary. *Didelphodon vorax* Marsh 1889 (1889a, p. 88, Plate IV, Figs. 1–3). See Clemens (1966, p. 60) for synonyms and a revised diagnosis.

Holotype. YPM 11827, left M2.

Type locality. Mammal locality 1 of Lull (1915); 1 UCMP locality V5003, Lance Formation, Wyoming.

Distribution. Scollard Formation (Lancian), Alberta; Frenchman Formation (Lancian), Saskatchewan; Hell Creek Formation (Lancian), Montana, and North Dakota; Lance Formation (Lancian), Wyoming. Possibly also Fox Hills and Hell Creek Formations (Lancian), South Dakota.

Referred specimens. Left p2 (PTRM 3012) from PTRM locality V89004; right M2 (PTRM 599), left M2 (PTRM 1230), left M3 (PTRM 3023), right M3 fragment (PTRM 1262), left dp3 (PTRM 2106), right p3 (PTRM 2114), right mX talonid (PTRM 1250), and left mX fragment (PTRM 2118) from PTRM locality V92067; right maxillary fragment with M4 (PTRM 1290) from PTRM locality V86003; right m4 (PTRM 700) from PTRM locality V87012.

Discussion. These specimens are indistinguishable from material of *Didelphodon vorax* from other Lancian sites in North America. Unfortunately, a P3 has not been recovered from these sites in North Dakota. P3 is the tooth by which *D. vorax* and the poorly known *D. padanicus* (Cope 1892) are known to differ in morphology. Therefore, assignment of these specimens to *D. padanicus*, unlikely as it may be, cannot be completely ruled out.

Didelphodon sp.

Referred specimens. Right mX fragment (PTRM 3264) from locality PTRM V92067; PX fragment (PTRM 3675) from PTRM locality V89003.

Discussion. Although these specimens also probably belong to *Didelphodon vorax*, they have been identified only to the generic level because they are so fragmentary.

?*Didelphodon* sp.

Referred specimens. Edentulous jaw (PTRM 1289) from PTRM locality V87009; lower canine (PTRM 697) from PTRM locality V87012.

Discussion. Because of their large size, these specimens, which clearly belong to a therian mammal, are assigned to ?*Didelphodon*, the largest known Lancian therian mammal.

Infraclass Eutheria
Order Proteutheria
Family Gypsonictopidae

Gypsonictops Simpson 1927

Gypsonictops illuminatus Lillegraven 1969

Nomenclatural summary. *Gypsonictops illuminatus* Lillegraven 1969 (p. 51).

Holotype. UA 2447, right maxilla with P3–M3.

Type locality. Locality KUA-1, Scollard Formation, Alberta.

Distribution. Scollard Formation (Lancian), Alberta; Frenchman Formation (Lancian), Saskatchewan; Hell Creek Formation (Lancian), Montana and North Dakota. Ravenscrag Formation (Lancian and/or Puercan?), Saskatchewan.

Referred specimen. Right dentary with p3–m3 (PTRM 1254) from PTRM locality V92067.

Discussion. See Hunter and Pearson (1996).

Family Palaeoryctidae

Cimolestes Marsh 1889

Cimolestes magnus Clemens and Russell 1965

Fig. 3, L–N

Nomenclatural summary. *Cimolestes magnus* Clemens and Russell 1965 (p. 33). See Lillegraven (1969, p. 73) for a revised diagnosis.

Holotype. UA 622, left dentary with p4–m3.

Type locality. Locality KUA-1, Scollard Formation, Alberta.

Distribution. Scollard Formation (Lancian), Alberta; Frenchman Formation (Lancian), Saskatchewan; Hell Creek Formation (Lancian), Montana and North Dakota; Lance Formation (Lancian), Wyoming.

Referred specimen. Right p4 (PTRM 695) from PTRM locality V86002.

Discussion. PTRM 695 is similar in size (L = 5.5, W = 2.5, both estimated because the mesial end is missing) and shape to p4 of *Cimolestes magnus*: massive protoconid and small posterior accessory cusp. The extra cuspule posterolingual to the posterior accessory cusp is better developed than in other specimens of this species. Wear extends to the tip of the extra cuspule, not just along the posterior ridge of the protoconid and crests of the posterior accessory cusp (Lillegraven, 1969).

Order Condylarthra

Family Arctocyonidae

Protungulatum Sloan and Van Valen 1965

Protungulatum sp.

Fig. 4, A–C

Referred specimen. Left mX trigonid (PTRM 1277) from locality PTRM V86005.

Discussion. Little can be gleaned from PTRM 1277 except that its paraconid is fully lingual in position and the cusps are moderately bulbous, as in *Protungulatum donnae*.

Oxyprimus Van Valen 1978

Oxyprimus galadrielae Van Valen 1978

Fig. 4, D–F

Nomenclatural summary. *Oxyprimus galadrielae* Van Valen 1978 (p. 53, Plate I, Fig. 1. See Lofgren (1995, p. 137) for a revised diagnosis.

Holotype. PU 16866, left maxilla with P3–M3.

Type locality. Mantua Lentil locality, Polecat Bench Formation, Wyoming.

Distribution. Polecat Bench and Ferris Formations (Puercan), Wyoming; Fort Union Formation (Puercan), North Dakota.

Referred specimen. Right m3 (PTRM 3564) from PTRM locality V97027.

Discussion. L = 4.4, TRGW = 2.9, TALW = 2.3. This specimen is nearly identical to the m3 of *Oxyprimus galadrielae* (by comparison with cast of PU 16713), from the Mantua Lentil locality. PTRM 3564 differs from the material from the type locality primarily in that its talonid notch (formed on the lingual side of the tooth between the entoconid and the base of the metaconid) is slightly more closed. PTRM 3564 differs from *Protungulatum donnae* Sloan and Van Valen 1965 in its closed talonid notch, more lingual paraconid, and more vertical hypoconulid. PTRM 3564 differs from *O. erikseni* Van Valen 1978 in its wider talonid and its more complete separation of the paraconid from the metaconid.

Arctocyonidae, gen. and sp. indet.

Fig. 4, G and H

Referred specimen. Left mX trigonid (PTRM 2102) from PTRM locality V86005.

Discussion. A second species of arctocyonid occurs at locality V86005 and different from and larger than *Protungulatum* sp. (above). Its cusps are more inflated than in *Protungulatum*, comparable to the degree of inflation seen in small species of *Baioconodon* Gazin 1941 and *Loxolophus* Cope 1885.

Family Periptychidae

Oxyacodon Osborn and Earle 1895

Oxyacodon priscilla Matthew 1937

Fig. 4, I–K

Nomenclatural summary. *Oxyacodon priscilla* Matthew 1937 (p. 207–208). See Archibald et al. (1983, p. 62–63) for a revised diagnosis.

Holotype. AMNH 3547a, right dentary with p2–m3.

Type locality. Nacimiento Formation, San Juan County, New Mexico.

Distribution. Nacimiento Formation (Puercan), New Mexico; Ferris Formation (Puercan), Wyoming; Fort Union Formation (Puercan), North Dakota.

Referred specimen. Left m2 (PTRM 1396) from PTRM locality V86005.

Discussion. PTRM 1396 shares with other *Oxyacodon* m2s lack of a lingual cingulid, a poorly developed labial cingulid, a median paraconid that is reduced in size, and moderately convergent cusp tips (more than in *Mimatuta* Van Valen 1978, but less than in *Conacodon* Matthew 1897). Based on size (L = 3.3, TRGW = 2.6, TALW = 2.7), this specimen is most likely *O. priscilla* or less likely *O. ferronensis* Archibald et al. (1983).

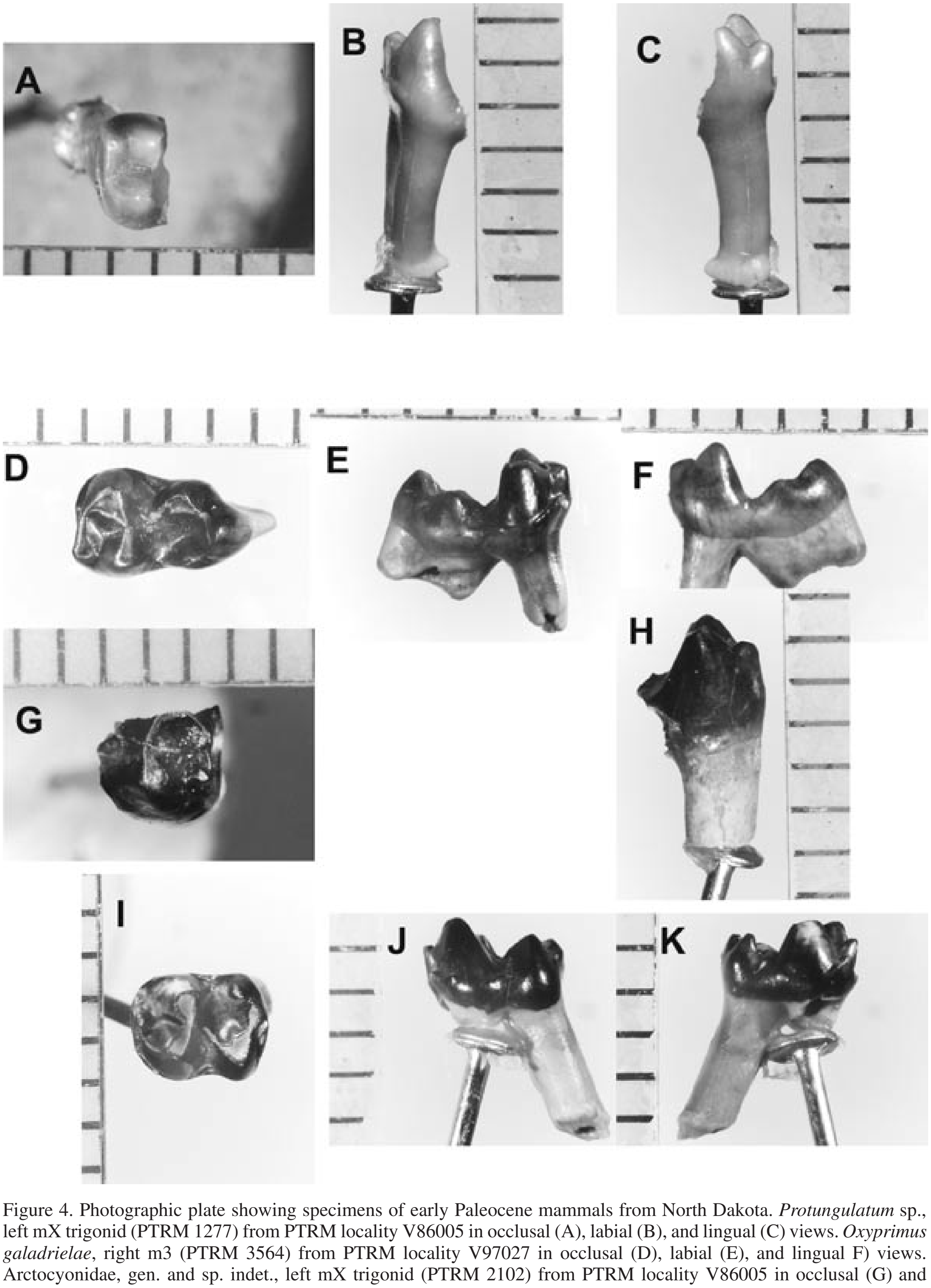

Figure 4. Photographic plate showing specimens of early Paleocene mammals from North Dakota. *Protungulatum* sp., left mX trigonid (PTRM 1277) from PTRM locality V86005 in occlusal (A), labial (B), and lingual (C) views. *Oxyprimus galadrielae*, right m3 (PTRM 3564) from PTRM locality V97027 in occlusal (D), labial (E), and lingual F) views. Arctocyonidae, gen. and sp. indet., left mX trigonid (PTRM 2102) from PTRM locality V86005 in occlusal (G) and lingual (H) views. *Oxyacodon priscilla*, left m2 (PTRM 1396) from PTRM locality V86005 in occlusal (I), labial (J), and lingual (K) views. Scale ruled in millimeters. PTRM is Pioneer Trails Regional Museum; for abbreviations, see Table 1.

MAMMALS FROM THE HELL CREEK AND FORT UNION FORMATIONS OF NORTH DAKOTA AND ADJACENT SOUTH DAKOTA

Table 2 lists the mammalian taxa recovered from the Hell Creek Formation in southwestern North Dakota and adjacent South Dakota. Table 3 lists the mammalian taxa recovered from the Ludlow Member of the Fort Union Formation of the same area. Collecting efforts have yielded 166 mammalian specimens recovered from 15 localities in the Hell Creek and 9 specimens from 2 localities in the Ludlow Member. (In this context, a mammalian specimen is any fossil that can be identified as mammalian. For teeth, further identification is usually possible to the specific or generic level. For some cranial and postcranial fragments, identification might be possible only to the ordinal level or higher.) The locality register (see Appendix) breaks down these faunal lists by locality. Figure 5 depicts the observed stratigraphic occurrences and ranges of the identified mammalian species. In southwestern North Dakota, mammalian localities occur throughout most of the vertical extent of the Hell Creek Formation, making it difficult to define isolated local faunas, and even localities that are geographically close may be separated by considerable vertical (i.e., stratigraphic) distance. We therefore name no Cretaceous local faunas here. Nevertheless, some geographic-stratigraphic clusters of localities are discernible (see Fig. 1 for placement):

1. Pretty Butte localities (40–31 m below top): PTRM localities V92002, V87009, and V86003.
2. Marmarth localities (29–6 m below top): PTRM localities V98011 and V86002.
3. Sunset Butte localities (37–25 m below top): PTRM localities V92067 and V93022.
4. Mud Buttes localities (14–3 m below top): PTRM localities V88004, V87012, V88017, and V88018.
5. Miller Ranch localities (82–73 m below top): PTRM localities V91007, V89004, and V92025.

One of the Miller Ranch sites, PTRM locality V92025, is in South Dakota outside the range of the map used in Figure 1. PTRM locality V89003 (~8 m below the K-T boundary) is treated as an isolated occurrence southeast of the nearby Mud Buttes area.

Three species of mammals (*Alphadon marshi, Gypsonictops illuminatus*, and *Cimolestes magnus*) of the eight that have been found in the Hell Creek Formation in southwestern North Dakota occur at a single stratigraphic horizon each. Because only one specimen of each of these species has been recovered from the study area, however, little can be said except that these species occur. The recovery of these species may be largely a result of their occurrence in well-sampled vertebrate faunules: *Alphadon marshi* at PTRM locality V89004 (980 vertebrate specimens), *Gypsonictops illuminatus* at PTRM locality V92067 (3243 vertebrate specimens), and *Cimolestes magnus* at PTRM locality 86002 (1180 vertebrate specimens). (In this context, a vertebrate specimen is any vertebrate fossil that can be identified to the specific, generic, or familial level, exclusive of repeated elements such as gar scales, turtle shell fragments, and crocodilian osteoscutes; see Pearson et al., this volume.) Although the metatherian species *"Pediomys" florencae* is also known locally from only one specimen recovered ~82 m below the K-T boundary (PTRM locality V89004), material referred to "*Pediomys*" sp. cf. *P. florencae* ~37 m below the K-T boundary (PTRM locality V92067) may also belong to the same species (Hunter and Pearson, 1996).

Slightly more commonly recovered are two species of multituberculates (*Cimolodon nitidus* and *Mesodma thompsoni*) that have extensive stratigraphic ranges; however, their distributions within those ranges have been strongly influenced by the vagaries of sampling. Although *Cimolodon nitidus* is known locally with certainty from only three specimens recovered from better sampled faunules (one each from PTRM localities V89004, V86002, and V89003), its stratigraphic range spans most of the (locally 100 m thick) Hell Creek Formation from ~82 m (PTRM locality V89004) to ~8 m below the K-T boundary (PTRM locality V89003). Similarly, *Mesodma thompsoni*, a species known to have survived the K-T boundary elsewhere in the Western Interior (Archibald and Bryant, 1990), occurs as low as ~82 m below the K-T boundary and may extend as high as ~5.6–7.1 m above the boundary in the study area.

The two species of mammals most commonly recovered locally, *Didelphodon vorax* and *Meniscoessus robustus*, but not known to have survived the K-T boundary (Archibald and Bryant, 1990), occur throughout the Hell Creek Formation. To some extent, these two species may be the most commonly recovered because they are the two largest mammals in the sample and because surface collections are almost certainly biased toward recovering large specimens. Nevertheless, these two species are relatively rare at many other Lancian local faunas, particularly *Meniscoessus robustus* at higher latitudes (Lillegraven, 1969; Fox, 1989; Storer, 1991), and so their numerical dominance locally in the Hell Creek Formation of southeastern North Dakota, where *Meniscoessus robustus* composes ~58% and *Didelphodon vorax* composes ~22% of the mammalian fauna, is an unusual and significant observation.

Early Paleocene (Puercan NALMA) mammals recovered from the Ludlow Member of the Fort Union Formation occur at two localities within a single channel system and stratigraphic horizon. This assemblage of fossils has been named the

TABLE 3. MAMMALIAN FAUNA OF THE LUDLOW MEMBER OF THE FORT UNION FORMATION, SOUTHWESTERN NORTH DAKOTA

- Multituberculata
  - *Mesodma* sp.
- Eutheria
  - *Protungulatum* sp.
  - *Oxyprimus galadrielae* Van Valen
  - Arctocyonidae, gen & sp. indet.
  - *Oxyacodon priscilla* Matthew

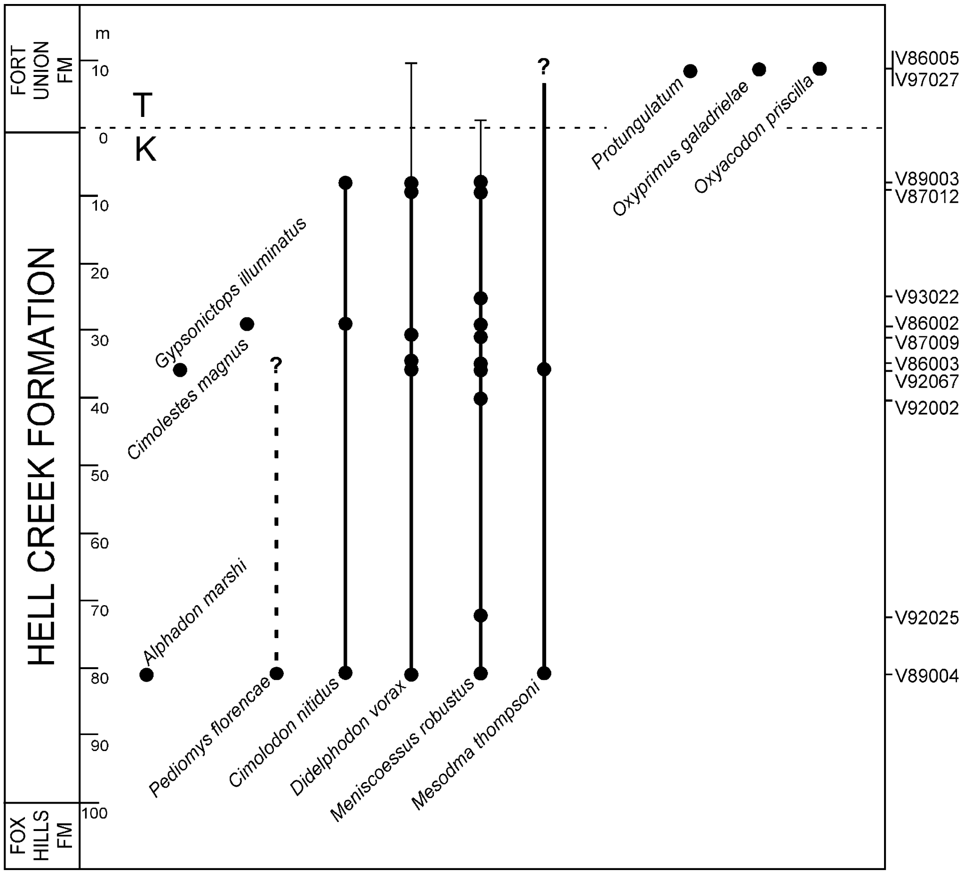

Figure 5. Chart of stratigraphic ranges of mammalian taxa in Hell Creek and Fort Union Formations (FM), southwestern North Dakota. T, K, Tertiary, Cretaceous. Local observed range of "*Pediomys*" *florencae* extends further if "*Pediomys*" sp. cf. "*P.*" *florencae* belongs to this species. *Mesodma thompsoni* may be present in Fort Union locally, but this occurrence is not unexpected given that species is known to occur in Paleocene strata outside of study area (Archibald and Bryant, 1990). One-tailed classical confidence limits (Strauss and Sadler, 1989; Marshall, 1990) have been added (thin lines) to observed ranges of *Didelphodon vorax* and *Meniscoessus robustus* to indicate degree of confidence that can be placed on highest observed local occurrences of these taxa. Only 12 localities that have produced mammalian fossils that are diagnostic to generic or specific level have been included.

PITA Flats local fauna on the basis of the faunule at PTRM locality V86005 (Hunter, 1999). This locality occurs ~8 m above the contact between the Hell Creek and Fort Union Formations. Although the K-T boundary has not been precisely identified near PTRM locality V86005, Cretaceous pollen occurs in the lowest 0.86 m of the Ludlow in the PITA Flats measured section, whereas ~0.8 km away Cretaceous pollen occurs in the lowest 2.37 m of the Ludlow in the North Dakota Academy of Science measured section (Johnson, this volume, Table A2). Given that the K-T boundary must occur at least this high, an estimate of ~5.6–7.1 m above the K-T boundary for PITA Flats seems reasonable.

Originally, one of us (Hunter, 1999, p. 142) advanced a Pu2–Pu3 age for this local fauna based on the occurrence of the condylarth *Oxyacodon priscilla*, which is known only from the Pu2 and Pu3 interval zones of the Puercan NALMA (Archibald et al., 1987; Williamson, 1996; Eberle and Lillegraven, 1998b). Two lines of evidence suggest that the PITA Flats local fauna may be older than other local faunas assigned to the Pu2–Pu3 interval zones. First, a second site (PTRM locality V97027), within the same channel system and almost assuredly the same stratigraphic horizon as PTRM locality V86005, has produced a specimen of the condylarth *Oxyprimus galadrielae*, which is know elsewhere only from the Pu1 interval zone (Van Valen, 1978; Eberle and Lillegraven, 1998b). Second, the stratigraphic position of both PITA Flats localities ~5.6–7.1 m above the K-T boundary places the PITA Flats local fauna within magnetochron 29R based on stratigraphic thickness (see Hicks et al., this volume). Known local faunas of Pu1 age elsewhere occur within C29R, whereas those of Pu2 and Pu3 age occur within the overlying C29N (Archibald et al., 1987; Swisher et al., 1993). On current evidence, the PITA Flats local fauna is clearly close to the transition between the Pu1 and Pu2 interval zones.

MAMMALS FROM THE HELL CREEK FORMATION, SOUTHEASTERN MONTANA

Table 4 lists the mammalian species recovered from the Hell Creek Formation of extreme southeastern Montana, Carter County, in the vicinity of the town of Ekalaka. Collecting efforts have yielded 874 mammalian specimens recovered from five localities. The locality register (see Appendix) breaks down this faunal list by locality. Unlike the localities in North Dakota, those in southeastern Montana are clustered stratigraphically and geographically into a Claw Butte Anthills local fauna (UCMP localities V86081–4) ~65 m and a Spigot-Bottle local fauna (UCMP locality V88007) ~61 m below the Hell Creek–

TABLE 4. MAMMALIAN FAUNA OF THE HELL CREEK FORMATION, CARTER COUNTY, SOUTHEASTERN MONTANA

- Multituberculata
  - *Cimolodon nitidus* Marsh
  - *Cimolomys gracilis* Marsh
  - *Essonodon browni* Simpson
  - *Meniscoessus robustus* (Marsh)
  - *Mesodma formosa* (Marsh)
  - *Mesodma hensleighi* Lillegraven
  - *Mesodma thompsoni* Clemens
- Metatheria
  - *Alphadon marshi* Simpson
  - *Alphadon wilsoni* Lillegraven
  - *Didelphodon vorax* Marsh
  - *Glasbius twitchelli* Archibald
  - *Pediomys cooki* Clemens
  - *Pediomys elegans* Marsh
  - *Pediomys florencae* Clemens
  - *Pediomys hatcheri* Osborn
  - *Pediomys krejcii* Clemens
  - *Protalphadon lulli* (Clemens)
  - *Turgidodon rhaister* (Clemens)
- Eutheria
  - *Batodon tenuis* Marsh
  - *Cimolestes incisus* Marsh
  - *Cimolestes propalaeoryctes* Lillegraven
  - *Cimolestes stirtoni* Clemens
  - *Gypsonictops hypoconus* Simpson

Fort Union formational contact. Note, however, that the Hell Creek Formation is considerably thicker near Ekalaka (~150 m) than it is in southwestern North Dakota (~100 m) (Belt et al., 1997), and so vertical distance below the formational contact cannot be compared directly between the two regions. The actual fossil material from these localities will be described elsewhere.

The Claw Butte Anthills local fauna, named for the anthills at the top of Claw Butte, was recovered from localities at the top of the Claw Butte channel belt described by Belt et al. (1997, their Fig. 12). Most material was screen washed from an in situ channel fill composed of silty sand with a very small proportion also obtained by screening the anthills. Although sediments do not directly overlie Claw Butte, Belt et al. (1997, their Fig. 7) were able to trace the beds at Claw Butte, on the basis of sedimentology, to the Blacktail Creek area ~10 km to the northeast, where the overlying formational and K-T boundaries are found. Therefore, the Claw Butte Anthill local fauna is estimated to be 65 m below the Hell Creek–Fort Union contact. The Spigot-Bottle local fauna, named for a nearby spigot and broken bottles littering the surface, was recovered from localities near the top of the Toe Bone meander belt described by Belt et al. (1997, their Fig. 12). Although there are several Spigot localities, they are far less rich than Spigot-Bottle and thus are not described further. As with Claw Butte, the sediment at Spigot-Bottle is silty sand. Although the preliminary faunal analysis presented here indicates that these two local faunas are not clearly separable on the basis of fauna, they were first named at a time when their faunal content and stratigraphic content were not well known. Accordingly, we retain them as separate local faunas but consider them as a single unit in the much broader analysis presented in this chapter.

In addition to the taxa listed in Table 4, two other records of Late Cretaceous or early Paleocene mammals from the Ekalaka area, but not from either the Claw Butte Anthills or Spigot-Bottle local faunas, are notable. Clemens (1973) reported the occurrence of *Cimolestes magnus* in the Hell Creek Formation near Ekalaka, and we have added this species to the overall faunal list for the Hell Creek Formation, Ekalaka area, used in the following faunal comparisons. Simmons (1987) described a new species of multituberculate, *Taeniolabis lamberti*, from the Fort Union Formation of the Ekalaka area, documenting the occurrence of early Paleocene mammals there.

COMPARISONS AMONG LANCIAN MAMMALIAN FAUNAS

The discovery of Lancian mammals in southwestern North Dakota and southeastern Montana augments the density of the geographic record of Lancian North American mammals and provides an opportunity to reevaluate patterns of similarity among approximately contemporaneous mammalian faunas. Previous workers have commented on putative differences in faunal composition among Lancian mammalian faunas, arguably associated with latitude. Lillegraven (1969) pointed out a higher diversity of eutherians, particularly palaeoryctoids, in the Trochu local fauna in central Alberta (1 in Fig. 6) than were known in the Lance local fauna in eastern Wyoming (7 in Fig. 6). Sloan (1969) and Russell (1975) suggested that this difference might indicate an invasion of North America by eutherian immigrants from Asia, which had not yet been completed by Lancian time. This view assumes that the Trochu and Lance local faunas were contemporaneous. Alternatively, the slightly more progressive aspect of the Trochu fauna, given that eutherians underwent a marked evolutionary radiation after the Cretaceous, could also be a result of temporal differences, the Trochu local fauna being somewhat younger than the Lance fauna. A third possibility is that local ecological differences could account for the differences in composition. Archibald (1982) described mammals from the Hell Creek Formation of eastern Montana, noting that at this intermediate latitude (i.e., between the Trochu local fauna to the north and the Lance local fauna to the south) the fauna was intermediate in taxonomic composition as well. Others have since described more Lancian faunas at intermediate latitudes (Fig. 6), and Fox (1989) and Hunter et al. (1997) discussed the general problem of separating the effects of time, latitude, and local ecology on the composition of Lancian local faunas.

Although we are not yet able to completely resolve these issues, we discuss here the more modest goal of establishing whether there are geographic patterns in the composition and abundance of Lancian mammals. To simplify, we assume that all the described Lancian local faunas are approximately contemporaneous, and therefore time has not been important in

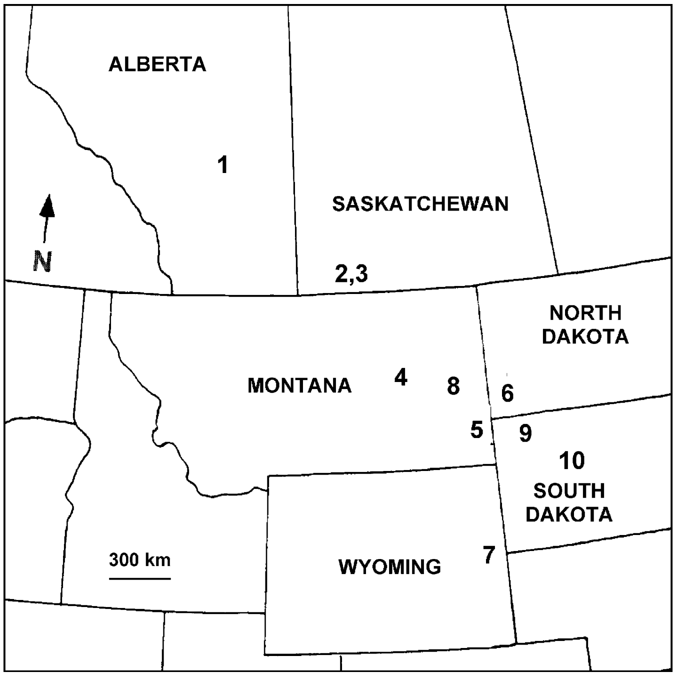

Figure 6. Map showing distribution of well-sampled Lancian mammalian faunas compared here. Base map is adapted from Archibald et al. (1987). 1, Trochu local fauna, Scollard Formation, Alberta; 2, Gryde local fauna, Frenchman Formation, Saskatchewan; 3, Wounded Knee local fauna, Frenchman Formation, Saskatchewan; 4, Hell Creek fauna, Garfield County, Montana; 5, Hell Creek fauna, Carter County, Montana; 6, Hell Creek fauna, southwestern North Dakota; 7, Lance local fauna, Wyoming; 8, Muddy Tork local fauna, Hell Creek Formation, Dawson County, Montana; 9, Hell Creek fauna, South Dakota; 10, Red Owl local fauna, Fox Hills Formation, South Dakota.

establishing faunal differences. This is a reasonable assumption for two reasons. First, all of these local faunas occur in approximately laterally equivalent lithostratigraphic units (Gill and Cobban, 1973; Cherven and Jacob, 1985; Belt et al., 1997), the upper bounds of which in some cases approximate the K-T boundary (to within a few meters; e.g., Swisher et al., 1993; Hunter et al., 1997; Nichols and Johnson, this volume). Although Lancian faunas can be correlated approximately to upper Maastrichtian marine ammonite zones (Lillegraven and Ostresh, 1990) that represent approximately the last 4 m.y. of the Cretaceous (Gradstein et al., 1995), the finds reported here from southwestern North Dakota seem to be restricted to the last 1.32–1.68 m.y. of the Cretaceous (Hicks et al., this volume), and a similar restriction may be valid for other faunas in our comparisons (but see below regarding the Fox Hills Formation of South Dakota). Second, in the course of compiling faunal data from the literature, localities at all stratigraphic levels were pooled within the same formation and area of study to arrive at a single faunal list and set of abundances for each formation study area (Tables 5 and 6). Thus we use analytically time averaged and approximately contemporaneous (or at least temporally overlapping) samples, which should minimize any temporal pattern (i.e., difference in faunal composition correlated with difference in time) among the samples. This procedure is further justified by the fact that we observed no mammalian biostratigraphic changes through the Hell Creek Formation in our respective study areas. Nevertheless, the mammalian occurrences in the Fox Hills Formation of South Dakota (the Red Owl locality) are probably stratigraphically lower than the other occurrences and therefore probably older (Foote et al., 1999, supplementary data, *www.sciencemag.org/feature/data/985988.shl*).

In compiling data on the taxonomic composition of Lancian faunas, as presented in Tables 5 and 6, we made several decisions. First, in order to include only those faunas that have been sampled moderately well to thoroughly, so that we could assume that the known samples reflect local composition, we omitted faunas that include fewer than 8 species or 40 specimens. Unfortunately, this decision had the undesired effect of restricting the geographic scope of this study. We were forced to disregard poorly sampled Lancian, or possibly Lancian, local faunas from Alaska (Clemens and Nelms, 1993), Wyoming (Breithaupt, 1982; Eberle and Lillegraven, 1998a, 1998b; Lillegraven and Eberle, 1999), Colorado (Carpenter, 1979), Utah (Cifelli et al., 1999), and New Mexico (Flynn, 1986). We also omitted assemblages Fr-1 and the Long Fall horizon of the MHBT Quarry in Saskatchewan (Johnston, 1980; Johnston and Fox, 1984; Fox, 1989, 1997) because of their age and transitional nature, and Fr-1 further because of its small sample size, but we were able to include the more typical and well-sampled Gryde and Wounded Knee faunas from the same geographic area.

Second, we were able to include local faunas from South Dakota (Wilson, 1983, 1987) in the comparisons using presence-absence data (Table 6), but not in the comparisons using abundance data (Table 5) because only taxonomic faunal lists for the localities in the Hell Creek Formation of South Dakota have been published (Wilson, 1983) and because only multituberculates, but not therians, have been described from the Fox Hills Formation (Wilson, 1987). Moreover, precise geographic coordinates have not been published for any of these localities in South Dakota. Because of the limited geographic information available about these sites, faunal lists were pooled into two master lists, one for the Hell Creek and another for the Fox Hills, and their geographic placements (Table 7) were approximated as the towns of Buffalo and Red Owl, South Dakota, respectively. We encountered a similar problem inferring the geographic position of the Wounded Knee locality (Fox, 1989) because precise coordinates have not been published. Therefore, we assigned geographic coordinates to Wounded Knee corresponding to 3.4 km north of the Gryde locality, as described by Storer (1991).

Third, taxonomic problems in discriminating among small-bodied species of the marsupial *Alphadon* (i.e., *A. marshi, A. wilsoni*, and *A. jasoni*) somewhat complicate determining the abundance and even the occurrence of these species at Lancian

TABLE 5. NUMBER OF IDENTIFIABLE SPECIMENS (ABUNDANCE) OF MAMMALIAN SPECIES AT LANCIAN-AGE LOCAL FAUNAS IN THE WESTERN INTERIOR

	Scollard[*]	Gryde[†]	WK[§]	HC Garfield[#]	HC Ekalaka[**]	HC ND[††]	Lance[§§]	HC MT[##]
Alostera saskatachewanensis	1	1	3	0	0	0	0	0
Alphadon jasoni	27	309	44	13	0	0	3	0
Alphadon marshi (incl. *wilsoni*)	26	0	3	3	33	1	17	0
Batodon tenuis	9	7	0	4	3	0	1	0
Cimexomys minor	0	0	0	0	0	0	7	0
Cimolestes cerberoides	88	0	0	1	0	0	0	0
Cimolestes incisus	0	28	4	3	10	0	35	0
Cimolestes magnus	61	11	0	0	1	1	4	0
Cimolestes propalaeoryctes	19	0	2	1	4	0	0	0
Cimolestes stirtoni	0	0	2	3	5	0	13	0
Cimolodon nitidus	66	4	3	27	36	3	450	0
Cimolomys gracilis	7	18	0	7	6	0	89	0
Cimolomys trochuus	3	0	0	0	0	0	0	0
Clemensodon megaloba	0	0	0	0	0	0	3	0
Didelphodon vorax	11	3	1	16	9	11	196	6
Essonodon browni	0	0	1	10	6	0	1	0
Glasbius intricatus	0	0	0	0	0	0	16	0
Glasbius twitchelli	0	0	1	35	3	0	0	0
Gypsonictops hypoconus	8	0	0	0	78	0	314	0
Gypsonictops illuminatus	102	102	15	18	0	1	0	0
Meniscoessus robustus	0	2	2	41	55	29	186	24
Mesodma formosa	105	341	10	18	148	0	170	0
Mesodma hensleighi	34	92	0	38	34	0	26	0
Mesodma thompsoni	29	40	4	19	207	2	117	3
Neoplagiaulax burgessi	0	0	0	5	0	0	0	0
Paracimexomys priscus	9	1	2	15	0	0	0	0
Parectypodus foxi	0	4	0	0	0	0	0	0
Pediomys cooki	0	0	0	1	26	0	130	0
Pediomys elegans	9	30	3	4	106	0	152	2
Pediomys florencae	0	0	0	10	27	2	79	3
Pediomys hatcheri	2	6	0	3	33	0	73	2
Pediomys krejcii	26	28	0	9	1	0	26	1
Protalphadon lulli	0	0	0	3	3	0	19	0
Turgidodon petiminis	0	17	0	0	0	0	0	0
Turgidodon rhaister	8	0	0	4	12	0	14	1

[*] Trochu local fauna, Scollard Formation, Alberta: Lillegraven (1969), Lillegraven and McKenna (1986) Fox (1989, 1997).
[†] Gryde local fauna, Frenchman Formation, Saskatchewan: Storer (1991)
[§] Wounded Knee local fauna, Frenchman Formation, Saskatchewan: Fox (1989, 1997).
[#] Hell Creek Formation, Garfield County, near Jordan, Montana (incl. Flat Creek local fauna): Archibald (1982), Lillegraven and McKenna (1986), Johanson (1996).
[**] Hell Creek Formation, Carter County, near Ekalaka, Montana: this paper.
[††] Hell Creek Formation, southwestern North Dakota: Hunter and Pearson (1996) and this paper.
[§§] Lance Formation, Wyoming: Clemens (1964, 1966, 1973), Lillegraven and McKenna (1986), Krause (1992).
[##] Muddy Tork local fauna, Hell Creek Formation, Dawson County, Makoshika State Park, Glendive, Montana: Hunter et al. (1997).

sites. Clemens (1966) originally recognized only *A. marshi* in the Lance local fauna. After Lillegraven (1969) had named *A. wilsoni* based on material in the Trochu local fauna, Clemens (1973) reported that *A. wilsoni* also occurs in the Lance local fauna but did not report the exact number of *A. wilsoni* specimens recovered. Storer (1991) named *A. jasoni*, documenting its presence at the Gryde locality and also suggesting that it also occurred at the Wounded Knee and Bug Creek Anthills localities. Thus, as originally conceived, *A. jasoni* would have a clearly northern distribution, possibly replacing *A. marshi* and *A. wilsoni* locally. However, Johanson (1996), in revising *Alphadon*, argued that *A. wilsoni* is a junior synonym of *A. marshi* and that *A. jasoni* includes some specimens formerly identified as *A. marshi* and *A. wilsoni*. If correct, it would mean that *A. jasoni* occurs in several additional local faunas (including the Trochu, Flat Creek, and Lance) in the presence of at least *A. marshi*. Regardless of the actual status of *A. wilsoni*, we had to pool this species with *A. marshi* in order to include the Lance local fauna because published accounts do not distinguish between the two species in terms of the number of actual specimens recovered. In addition, we provisionally follow Johanson (1996) regarding specimen assignments to *A. jasoni* because they result in greater overlap between the geographic distributions of *A. jasoni* and the pooled sample of *A. marshi* + *A. wilsoni*, which is conservative relative to the hypothesis of faunal differentiation. We treated less certainly identified species (e.g., *Meniscoessus* sp. cf. *M. robustus*) as actual occurrences of these species for the sake of comparison.

Because the originally hypothesized difference among Lancian local faunas was that of a greater diversity of eutherians

TABLE 6. PRESENCE (1)/ABSENCE (0) OF MAMMALIAN SPECIES AT LANCIAN LOCAL FAUNAS IN THE WESTERN INTERIOR

	Scollard[*]	Gryde[†]	WK[§]	HC Garfield[#]	HC Ekalaka[**]	HC ND[††]	Lance[§§]	HC MT[##]	HC SD[***]	Fox Hills[†††]
Alostera saskatachewanensis	1	1	1	0	0	0	0	0	0	0
Alphadon jasoni	1	1	1	1	0	0	1	0	0	0
Alphadon marshi(incl. *wilsoni*)	1	0	1	1	1	1	1	0	1	1
Batodon tenuis	1	1	0	1	1	0	1	0	0	0
Cimexomys minor	0	0	0	0	0	0	1	0	0	0
Cimolestes cerberoides	1	0	0	1	0	0	0	0	0	0
Cimolestes incisus	0	1	1	1	1	0	1	0	0	0
Cimolestes magnus	1	1	0	0	1	1	1	0	0	0
Cimolestes propalaeoryctes	1	0	1	1	1	0	0	0	0	0
Cimolestes stirtoni	0	0	1	1	1	0	1	0	0	0
Cimolodon nitidus	1	1	1	1	1	1	1	0	1	1
Cimolomys gracilis	1	1	0	1	1	0	1	0	1	0
Cimolomys trochuus	1	0	0	0	0	0	0	0	0	0
Clemensodon megaloba	0	0	0	0	0	0	1	0	0	0
Didelphodon vorax	1	1	1	1	1	1	1	1	1	1
Essonodon browni	0	0	1	1	1	0	1	0	0	0
Glasbius intricatus	0	0	0	0	0	0	1	0	0	0
Glasbius twitchelli	0	0	1	1	1	0	0	0	0	0
Gypsonictops hypoconus	1	0	0	0	1	0	1	0	1	1
Gypsonictops illuminatus	1	1	1	1	0	1	0	0	0	0
Meniscoessus robustus	0	1	1	1	1	1	1	1	1	1
Mesodma formosa	1	1	1	1	1	0	1	0	0	1
Mesodma hensleighi	1	1	0	1	1	0	1	0	0	1
Mesodma thompsoni	1	1	1	1	1	1	1	1	0	1
Neoplagiaulax burgessi	0	0	0	1	0	0	0	0	0	0
Paracimexomys priscus	1	1	1	1	0	0	0	0	0	0
Parectypodus foxi	0	1	0	0	0	0	0	0	0	0
Pediomys cooki	0	0	0	1	1	0	1	0	0	1
Pediomys elegans	1	1	1	1	1	0	1	1	1	0
Pediomys florencae	0	0	0	1	1	1	1	1	1	0
Pediomys hatcheri	1	1	0	1	1	0	1	1	1	1
Pediomys krejcii	1	1	0	1	1	0	1	1	1	1
Protalphadon lulli	0	0	0	1	1	0	1	0	0	1
Turgidodon petiminis	0	1	0	0	0	0	0	0	0	0
Turgidodon rhaister	1	0	0	1	1	0	1	1	0	0

[*] Trochu local fauna, Scollard Formation, Alberta: Lillegraven (1969), Lillegraven and McKenna (1986) Fox (1989, 1997).

[†] Gryde local fauna, Frenchman Formation, Saskatchewan: Storer (1991).

[§] Wounded Knee local fauna, Frenchman Formation, Saskatchewan: Fox (1989, 1997).

[#] Hell Creek Formation, Garfield County, near Jordan, Montana (incl. Flat Creek local fauna): Archibald (1982), Lillegraven and McKenna (1986), Johanson (1996).

[**] Hell Creek Formation, Carter County, near Ekalaka, Montana: this paper.

[††] Hell Creek Formation, southwestern North Dakota: Hunter and Pearson (1996) and this paper.

[§§] Lance Formation, Wyoming: Clemens (1964, 1966, 1973), Lillegraven and McKenna (1986), Krause (1992).

[##] Muddy Tork local fauna, Hell Creek Formation, Dawson County, Makoshika State Park, Glendive, Montana: Hunter et al. (1997).

[***] Hell Creek Formation, Eureka Quarry and vicinity, and Joe Painter Quarry, South Dakota: Wilson (1983).

[†††] Fox Hills Formation, Red Owl local fauna, South Dakota: Wilson (1983, 1987).

TABLE 7. APPROXIMATE GEOGRAPHIC COORDINATES OF LANCIAN-AGE LOCAL FAUNAS

Local Fauna	Latitude	Longitude
Scollard	51.92	112.95
Gryde	49.31	108.42
Wounded Knee	49.34	108.42
Hell Creek Garfield	47.52	106.41
Hell Creek Ekalaka	45.86	104.87
Hell Creek North Dakota	46.14	103.80
Lance	43.20	104.55
Muddy Tork	47.09	104.72
Hell Creek South Dakota	45.35	103.32
Fox Hills, South Dakota	44.43	102.31

at higher latitudes, we first examine the number of species of multituberculates, metatherians, and eutherians among the faunas (Table 8). A simple G-test (Sokal and Rohlf, 1995, p. 724–743) establishes that there is no significant difference in the proportion of species within each higher taxon across all of the samples ($G = 12.6359$, $p = 0.8127$, degrees of freedom $= 18$). Moreover, results presented here on the distribution of individual species suggest that, with few exceptions, eutherians do not contribute to significant geographic patterning among Lancian faunas.

In order to summarize the variation in composition among the faunas, we examined the abundance (Table 5) and presence and/or absence data (Table 6) with correspondence analysis (CA) using NTSYS-pc (Rohlf, 1999). CA is better suited to

TABLE 8. NUMBERS OF SPECIES IN THE THREE MAJOR HIGHER TAXA OF MAMMALS AT LANCIAN-AGE LOCAL FAUNAS IN THE WESTERN INTERIOR

	Scollard	Gryde	Wounded Knee	Hell Creek Garfield	Hell Creek Ekalaka	Hell Creek North Dakota	Lance	Muddy Tork	Hell Creek South Dakota	Fox Hills
Multituberculata	7	8	6	9	7	3	9	2	3	5
Metatheria	7	6	5	11	10	3	11	6	6	6
Eutheria	7	5	5	6	6	2	5	0	1	1

species data than other ordination techniques (e.g., principal component analysis) because it characterizes relationships among rows and columns (here, species and faunal lists) using the chi-square (χ^2) distance, the metric preserved in contingency tables (Legendre and Legendre, 1998, p. 451–452). The χ^2 distance excludes double-zeros, i.e., the absence of a species from both of a pair of sites, thereby avoiding the species abundance paradox that plagues many distance metrics, including euclidean distance (Legendre and Legendre, 1998, p. 276–286). CA is equally suitable for abundance and presence and/or absence data on species. In the abundance data, rows and columns (species and faunal lists) are strongly nonindependent across the overall data table ($\chi^2 = 6328.187$, degrees of freedom = 238, $p < 0.0001$). The first CA axis explains 43.35% of the variance (eigenvalue = 0.5291), the second axis explains 21.17% (eigenvalue = 0.2584), the third axis explains 15.38% (eigenvalue = 0.1878), and the fourth axis explains 10.81% (eigenvalue = 0.1319) for a cumulative 90.17% of the variance explained by the first four axes. Figure 7 shows the projections for eight Lancian sites, for which abundance data were available, along the first two CA axes. We do not show the projections for species because of the large number (N = 35) involved. CA axis 1 recovers geographically correlated variation in pattern of species abundance, specifically correlated with latitude; localities at higher latitudes score higher along CA axis 1 than those at lower latitudes. This observation is significant by Spearman's rank order correlation (r_S, = 0.7857, $0.05 > p$; see Siegel, 1956, Table P, for critical values of r_S for $n \leq 30$) and by an exact test, systematically enumerating all 8! permutations of latitude, each time recalculating the correlation coefficient ($r = 0.7769$, $p = 0.0119$).

Unlike the abundance data, in the presence and/or absence data, independence of the rows and columns (species and sites) could not be rejected across the data table ($\chi^2 = 154.464$, not significant, degrees of freedom = 306). Accordingly, CA was also less effective in capturing variation overall in the presence and/or absence data than in the abundance data. The first CA axis explains 23.37% of the variance (eigenvalue = 0.2148), the second axis explains 17.42% (eigenvalue = 0.1602), the third axis explains 14.73% (eigenvalue = 0.1354), and the fourth axis explains 12.05% (eigenvalue = 0.1108) for a cumulative 67.56% of the variance explained by the first four axes. Figure 8 shows the projections for 10 Lancian sites along the first two CA axes, again omitting the species projections. Although CA has been less satisfactory as an ordination technique for the presence and/or absence data, CA axis 1 appears to have captured some geographically correlated variation in faunal composition, as localities at higher latitudes score higher along CA axis 1 than those at lower latitudes. This result is significant by Spearman's rank order correlation ($r_S = 0.9030$, $p < 0.01$; see Siegel, 1956, Table P, for critical values of r_S when $n \leq 30$) and by a randomization test ($r = 0.7769$, $p = 0.0123$ in 10,000 trials, 9999 random permutations of latitude plus observed).

In order to test for spatial patterning among sites in faunal abundance and composition, as suggested by the CA ordination among sites, we performed a series of Mantel tests between matrices of geographic distance and faunal distance between sites. We treated geographic distance initially both as surface distance by great circle route (Table 9) and latitudinal difference between sites. Although surface distance and latitudinal difference are obviously correlated (they are both derived from the same geographic coordinates), they are not completely redundant; there is some east-west spread among the sites. In addition, because the original hypothesis of faunal differentiation was phrased in terms of latitude, we present results for the overall faunal comparisons employing both geographical distances. Subsequently, we study the partial correlation structure of each of the measures of geographic distance with faunal distance and argue that faunal composition varies in ways more directly related to simple geographic separation than to latitude (see following). Rather than presenting actual Mantel statistics, z, which vary from problem to problem, we list the more familiar coefficient of matrix correlation (Smouse et al., 1986) and evaluate its significance by randomization test. In comparisons using the abundance data, which were available for eight faunas, testing is by systematic enumeration of all 8! permutations of one of the faunal distance matrix, recalculating z each time, with p being the proportion of z statistics obtained by randomization greater than or equal to observed z, using Matlab (Mathworks, 1999). Because exact tests would have been impractical in the presence and/or absence comparisons for all 10! permutations of the faunal distance matrix among 10 faunas, p was determined by 10000 trials, 9999 random permutations and one observed. All tests are one-tailed and in the positive direction because negative correlation in this context, corresponding to a "repulsed" distribution across the landscape, lacks an obvious biological interpretation. We set the arbitrary threshold for sig-

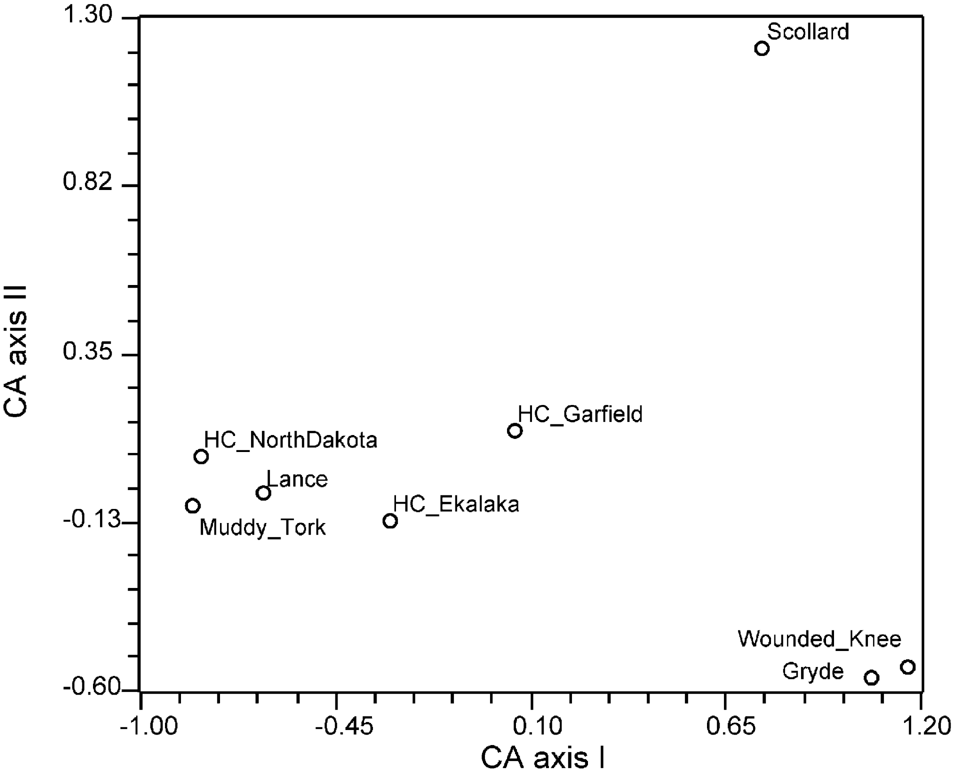

Figure 7. Ordination of Lancian mammalian faunas along first two correspondence analysis (CA) axes, comparing patterns of species abundance. See text for explanation and Table 5 for abbreviations.

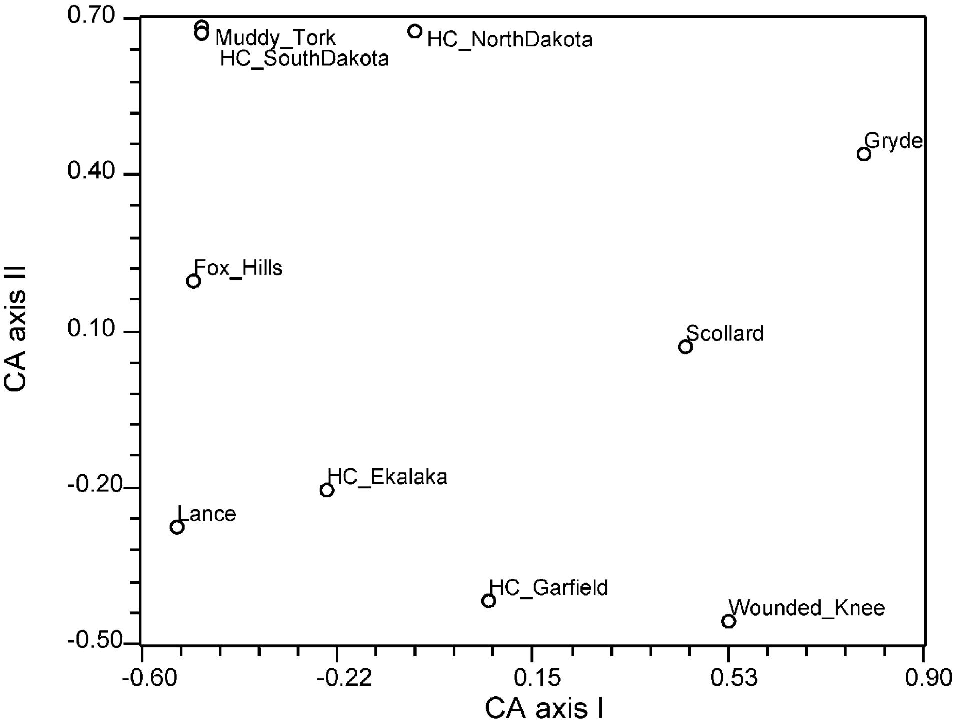

Figure 8. Ordination of Lancian mammalian faunas along first two correspondence analysis (CA) axes, comparing patterns of species presence and absence. See text for explanation and Table 6 for abbreviations.

TABLE 9. GEOGRAPHIC DISTANCES BETWEEN PAIRS OF LANCIAN-AGE LOCAL FAUNAS

	Scollard	Gryde	Wounded Knee	HC Garfield	HC Ekalaka	HC North Dakota	Lance	Muddy Tork	HC South Dakota
Gryde	431.3								
Wounded Knee	428.9	3.4							
HC Garfield	677.7	248.2	251.0						
HC Ekalaka	895.0	467.2	469.9	219.1					
HC North Dakota	925.5	494.2	496.6	251.7	88.8				
Lance	1154.9	742.0	745.1	502.3	296.9	332.2			
Muddy Tork	800.6	369.6	371.8	136.7	137.0	126.8	432.5		
HC South Dakota	1015.2	584.3	586.8	338.1	133.1	94.8	258.5	220.7	
Fox Hills, SD	1144.5	713.7	716.2	467.2	255.9	222.2	226.2	349.0	129.4

Note: Distances in kilometers, HC in Hell Creek. SD is South Dakota.

nificance at the conventional $p < 0.05$ level, but given the exploratory nature of this study and the small sample sizes ($N = 8$ or 10 faunas), we consider any $p < 0.1$ as marginally significant.

The upper half of Table 10 shows the results for χ^2 distance as the faunal distance metric between sites, taking into account variation in all 35 species. None of the tests of association between χ^2 distance based on all species and geographic distance was significant. We interpret this result to indicate great similarity among Lancian faunas in composition, with little differentiation or geographic patterning overall. Nevertheless, the existence of some latitudinal patterning is suggested by the CA ordination, at least along CA axis 1. Therefore, we also investigated faunal distance within the reduced dimensionality of the CA space. The lower half of Table 10 shows the results for a distance simply called faunal dissimilarity that we define as the euclidean distance among sites within the ordination space delimited by the first four CA axes. Such distances in the space of the principal axes should be euclidean after rotation (Legendre and Legendre, 1998, p. 452), and proper scaling of the axes results in weighting projections along the first axis higher than the second, the second higher than the third, and so forth. All of the tests of association between geographic distance and faunal dissimilarity, thus defined, are significant (Table 10, lower half). In spite of the great overall similarity in composition among these faunas, the major axes of variation among them, as summarized by CA, are related to geography.

TABLE 10. MANTEL TESTS OF ASSOCIATION BETWEEN GEOGRAPHIC OR LATITUDINAL (DEGREES) DISTANCE, AND CHI SQUARED DISTANCE OR FAUNAL DISSIMILARITY* BETWEEN LOCALITIES

	r_M†	p§
Chi Squared Distance between Localities		
Abundance Data		
X Geographic Distance	0.1667	0.1869
X Latitudinal Distance	0.0401	0.4244
Presence and/or Absence Data		
X Geographic Distance	0.10318	0.2298
X Latitudinal Distance	0.05282	0.3190
Faunal Dissimilarity between Localities		
Abundance Data		
X Geographic Distance	0.5298	0.0055
X Latitudinal Distance	0.4248	0.0169
Presence and/or Absence Data		
X Geographic Distance	0.43494	0.0104
X Latitudinal Distance	0.42181	0.0106

Note: Distance in kilometers.

*Faunal dissimilarity: euclidean distance between projections of objects (localities) along the first four correspondence analysis axes (see text for explanation)

†r_M, matrix correlation

§p, one-tailed probability of obtaining random $Z \geq$ observed Z, from systematic enumeration of all 8! permutations of the faunal distances (abundance data) or from 10 000 enumerations (9999 random permutations + observed; presence/absence data).

We decided to study the strength of the association of each of these two measures of geographic distance (surface distance and latitudinal difference) with faunal dissimilarity by studying their partial correlation structure (Smouse et al., 1986). Faunal dissimilarity (f, calculated on the abundance data) is correlated both with surface distance, s ($r_{fs} = 0.5298$, $p = 0.0055$), and with latitudinal difference, l ($r_{fl} = 0.4248$, $p = 0.0169$), between sites (Table 10). Furthermore, the partial correlation of faunal dissimilarity and surface distance, with latitudinal difference held constant, is significantly positive (partial correlation, $r_{fs\,l} = 0.5358$, $p = 0.0076$) by an exact test, permutating faunal dissimilarity while keeping the geographic distance matrices fixed, by the method described by Smouse et al. (1986). In contrast, the partial correlation of faunal dissimilarity and latitudinal difference, with surface distance held constant, is actually negative (partial correlation, $r_{fl\,s} = -0.4332$). Negative correlation here lacks an obvious biological explanation, and we simply consider it to be nonsignificant. We interpret these results to indicate that considerable residual association remains between overall surface distance and faunal distance after correcting for the effect of latitude, presumably caused by some east-west differentiation. No association remains, however, between faunal distance and latitudinal difference after correcting for overall surface distance, meaning that the observed latitudinal patterning in the faunal distances (Table 10) is accounted for by simple geographic separation. For this reason, remaining comparisons are made using only surface distance.

In order to determine which species distributions are most affected by geographic separation, we performed a series of Mantel tests between geographic and faunal distance between sites, but with each species considered separately (Table 11). Because we could not calculate χ^2 distance without complete column totals (i.e., without other species from the same fauna), we instead calculated faunal distance as the Bray-Curtis distance, for the log (Y + 1) transformed abundance data, and as 1—the simple matching coefficient (SM), for the presence and/or absence data. Although SM as a similarity measure is not recommended for species data because double-zeros contribute to it (Sokal and Sneath, 1963; Legendre and Legendre, 1998), such double-zeros contribute 0 distance to the dissimilarity measure 1—SM. In the context of examining individual species distributions, registering a distance of 0 in such cases seems more reasonable than treating such cases as missing data at a consequential loss in power. We omitted species that occur at only a single locality among the faunas considered here, and we could not analyze the presence and/or absence distribution of the metatherian *Didelphodon* across the landscape because this mammal occurs at every locality.

Most species distributions do not vary significantly with geographic distance within this data set (Table 11). This observation is true of most species of eutherians including all "palaeoryctoid" species (*Cimolestes* and *Batodon*), with the possible exception of *Cimolestes propalaeoryctes*. Even this species, however, shows only marginally significant spatial patterning in the presence and/or absence comparison, probably because of its absence from the Lance local fauna, and no significant spatial patterning in the abundance comparison. Therefore, there is little evidence for geographic patterning in the evolutionary radiation of palaeoryctoid eutherians in Lancian time. Three species (*Alostera saskatachewanensis, Paracimexomys priscus*, and *Pediomys florencae*) have distributions that varied significantly with geography in both comparisons (Table 11), *Alostera saskatachewanensis* and *Paracimexomys priscus* being characteristic of northern latitudes and *Pediomys florencae* being characteristic of southern latitudes during Lancian time (Tables 5 and 6). *Meniscoessus robustus* showed significant, geographically related variation in abundance, but not in occurrence (Table 11), being present at all latitudes (Table 6) but consistently more abundant at lower latitudes (Table 5). *Gypsonictops illuminatus* is more abundant (Table 5) and occurs more consistently (Table 6) at higher latitudes, and accordingly its distribution shows significant geographic patterning in the presence and/or absence data, although the correlation

TABLE 11. MATRIX CORRELATIONS BETWEEN INDIVIDUAL SPECIES DISTRIBUTIONS* AND GEOGRAPHIC DISTANCE (KM) BETWEEN FAUNAS

	Abundance data		Presence and/or absence data	
	r_M	p	r_M	p
Alostera saskatachewanensis	**0.6098**	**0.0179**	**0.70928**	**0.0082**
Alphadon jasoni	**0.2297**	**0.0661**	**0.30076**	**0.0344**
Alphadon marshi (incl. *wilsoni*)	−0.2915	0.9585	−0.13538	0.6243
Batodon tenuis	−0.0663	0.6229	−0.01266	0.3414
Cimolestes cerberoides	0.2793	0.2143	0.34310	0.1123
Cimolestes incisus	−0.0573	0.6033	−0.01655	0.3809
Cimolestes magnus	0.0614	0.2497	−0.08233	0.8485
Cimolestes propalaeoryctes	0.0176	0.3869	**0.16703**	**0.0815**
Cimolestes stirtoni	−0.0610	0.6006	−0.12367	0.8187
Cimolodon nitidus	−0.1813	0.7253	−0.20295	0.8996
Cimolomys gracilis	−0.1692	0.8622	−0.14550	0.8882
Didelphodon vorax	0.0848	0.3754	—	—
Essonodon browni	−0.1300	0.8143	−0.12367	0.8129
Glasbius twitchelli	−0.3252	0.9881	−0.16596	0.7925
Gypsonictops hypoconus	**0.3144**	**0.0625**	0.09502	0.1904
Gypsonictops illuminatus	**0.2914**	**0.0554**	**0.34681**	**0.0266**
Meniscoessus robustus	**0.7986**	**0.0005**	0.67589	0.1002
Mesodma formosa	−0.1873	0.7067	−0.13341	0.7157
Mesodma hensleighi	−0.2120	0.8985	−0.16000	0.9189
Mesodma thompsoni	−0.1586	0.7921	−0.12218	0.5012
Paracimexomys priscus	**0.4852**	**0.0119**	**0.61717**	**0.0048**
Pediomys cooki	0.0551	0.3988	0.06117	0.2759
Pediomys elegans	−0.1032	0.4850	−0.04566	0.4486
Pediomys florencae	**0.5915**	**0.0046**	**0.35848**	**0.0300**
Pediomys hatcheri	−0.1437	0.6680	−0.15972	0.7102
Pediomys krejcii	−0.2525	0.8899	−0.15972	0.7153
Protalphadon lulli	0.0813	0.3452	0.06117	0.2753
Turgidodon rhaister	−0.1463	0.8315	−0.06661	0.6924

*Species Distribution measured as either the Bray-Curtis distance (abundance data) or 1-simple matching coefficient (presence/absence data) between localities for each species individually (see text for explanation).

was only marginally significant in the abundance comparison (Table 11). Its congener, *G. hypoconus*, also shows marginally significant geographic patterning in the abundance comparison (Table 11), and these two species may have disjunct distributions (see following). *Alphadon jasoni* is also probably more abundant (Table 5) and occurs more frequently (Table 6) at northern latitudes, but its distribution shows significant geographic patterning only for the presence and/or absence data, the abundance comparison being only marginally significant (Table 11).

Of those species distributions that vary significantly with geography, three kinds of patterns are apparent, taking into account other information about these species. First, there are species without close relatives surviving into Lancian time, with restricted geographic distributions during the Lancian, but whose ancestors may have been more widespread at earlier times. In this first category are the eutherian *Alostera saskatachewanensis* and the multituberculate *Paracimexomys priscus*. A recent interpretation of *Alostera*, an unusual and problematic eutherian (Fox, 1989), places it among the "zhelestids," a primarily Asian group of mammals from which modern ungulates may have arisen (Nessov et al., 1998). Other possible North American zhelestids, according to Nessov et al. (1998), are *Avitotherium* and *Gallolestes*, which occurred in pre-Lancian time at more southern latitudes in Utah (Cifelli, 1990), Texas (Rowe et al., 1992; Cifelli, 1994), and Baja California, Mexico (Lillegraven, 1976; Clemens, 1980). If *Alostera* is part of a North American radiation of zhelestids, then its restricted northern distribution in Lancian time may be viewed as relict. Similarly, the restricted northern distribution of the multituberculate *P. priscus* in Lancian time may also be relict, because this species occurred at least in Wyoming in pre-Lancian time (Lillegraven and McKenna, 1986). Moreover, *P. priscus* appears to be a late surviving member of a group of multituberulates that radiated much earlier in the Cretaceous (Eaton and Nelson, 1991; Eaton, 1995).

A second category of species with restricted distributions includes those with close, contemporaneous relatives of similar size and morphology (and presumably similar ecology) present during Lancian time, but that occur, if not completely allopatrically, then at least in a disjunct way. In this second category are the metatherian *Alphadon jasoni* and the eutherian *Gypsonictops illuminatus. A. jasoni* is undoubtedly closely related to *A. marshi* and *A. wilsoni*, either of which can be easily confused with *A. jasoni*, particularly when only lower dentitions are compared. Moreover, the distribution of *A. jasoni* seems to be negatively associated with that of the pooled sample of *A. marshi* and *A. wilsoni*, i.e., *A. jasoni* seems to be abundant when *A. marshi* + *A. wilsoni* is rare and vice versa (Table 5). This negative association, however, is only marginally significant by an exact test ($r = -0.4148$, $p = 0.0746$, 7! permutations, excluding Muddy Tork, where neither taxon has been sampled [a double-zero]). Interpretation of the distribution of *Alphadon* species is further hampered by problems in their alpha taxonomy (Johanson, 1996). More systematic work is needed in order to gain confidence in estimates of the abundance of these species. Particular attention needs to be paid to identifying lower dentitions, which cannot at present be placed with confidence.

Likewise, the eutherian *Gypsonictops illuminatus* is also extremely similar to its congener *G. hypoconus*. These two species also appear to have a negative association in abundance (Table 5), but this difference is not significant by an exact test ($r = -0.3879$, $p = 0.1048$ from 7! permutations, excluding Muddy Tork [a double-zero]). Because *G. hypoconus* is well sampled only at the southern extreme of the area considered in these comparisons and because this species shows only marginally significant spatial patterning (Table 11), it is possible that failure to find a significant negative correlation is from geographically patchy sampling of *G. hypoconus*.

The third pattern is demonstrated by *Meniscoessus robustus*, by far the largest multituberculate and one of the two largest mammals (the other being the metatherian *Didelphodon*) known from the Lancian. Because of its large size and unique dental morphology, with highly crescentic molar cusps, it is unlikely that *Meniscoessus* was closely similar ecologically to other contemporaneous and sympatric mammals. The highly significant geographic patterning of *Meniscoessus* abundance (Table 11), abundant in the south and rare farther north (Table 5), in the absence of obvious competitors, suggests that the distribution of this taxon may have simply reflected its own intrinsic ecological tolerances.

To summarize this comparison among Lancian mammalian faunas, it must be emphasized that all of these faunas are extremely similar in composition and do not vary greatly with distance, as evidenced by the nonsignificant correlations between χ^2 distance among the faunas and geographic distance (Table 10, upper half). Nevertheless, the variation among these faunas is associated with the geographic distance, as evidenced by the significant correlation between the distances between faunas in the reduced ordination space defined by correspondence analysis and geographic distance defined as either surface distance or latitudinal separation (Table 10, lower half). The partial correlation structure of each of these measures of geographic separation with faunal dissimilarity suggests that faunas differ in ways more closely related to simple geographic separation, than to latitude. Only a few species seem to show significant geographic patterning in their distributions, only two of these are eutherians, and neither of them is a palaeoryctoid (Table 11). Therefore, the hypothesis of geographic patterning to the evolutionary radiation of eutherians in the Lancian is not supported. Instead, certain species show geographic patterning that is understandable in terms of their replacement across the landscape by closely related and, presumably, ecologically similar species. Others show a pattern suggestive of contraction of a formerly more widespread distribution. Rather than historical effects, such as incomplete invasion of eutherian lineages into North America from Asia, simple spatial gradients can account for variation among mammalian faunas across this geographically small window into the latest Cretaceous.

CONCLUSIONS

The goals of this chapter have been to describe mammalian fossils recovered from the Hell Creek and Fort Union Formations of southwestern North Dakota and adjacent South Dakota, to report work in progress on the mammalian fauna of the Hell Creek Formation of southeastern Montana, and to reconsider geographic differentiation among Lancian mammalian faunas. Mammalian fossils occur throughout the vertical extent of the Hell Creek Formation in North Dakota, but at no one stratigraphic horizon are they yet exhaustively sampled. Although two well-sampled local faunas occur in the Hell Creek Formation of southeastern Montana, the distribution of fossil mammals there is geographically and stratigraphically irregular. The mammalian fauna recovered from these relatively new field areas is closely similar to other Lancian faunas, particularly those at more southern latitudes, such as the Lance fauna. We did not find evidence for geographic patterning of a latest Cretaceous evolutionary radiation of eutherians. Rather, simple spatial differences, and possibly replacement of ecologically similar species across the landscape, account for observed differences in composition among Lancian faunas. Separating the effects of geographic separation from those of time, however, may become possible in the future with more intense vertical sampling through the Hell Creek Formation and its lateral equivalents, to estimate a time factor, or by including faunas before and after the Lancian. Separating the effects of geographic separation from ecology may become possible with more explicit paleoenvironmental reconstruction to establish distances along paleoecological gradients. As these data become available, it should be possible to partition their effects by extending the partial matrix correspondence approach employed here.

ACKNOWLEDGMENTS

We thank Joseph Hartman, Kirk Johnson, and Douglas Nichols for inviting us to contribute to this volume, for providing invaluable assistance both in the field in North Dakota and in the laboratory, and for making their paleontologic, stratigraphic, and geologic data accessible. We thank the editors, Rich Cifelli and Bill Clemens, and an anonymous reader for reviews that pointed out ways to improve this manuscript. Kirk Johnson also provided the base map used to prepare Figure 1. We thank Dean Pearson, who found many of the localities reported here, collected many of the specimens described here, and has continued to supply logistical support to Hunter's field studies in southwestern North Dakota over the past several years. We also thank Robert Sokal and Michael Rosenberg for discussion of spatial statistics. Michael Rosenberg made available his spatial analysis program Passage (Rosenberg, 2000), which we used initially to calculate partial Mantel correlations, although we later replaced the significance tests with exact permutation tests using Matlab. A Geological Society of America research grant and a Patterson Award from the Society of Vertebrate Paleontology (to Hunter) supported field studies in southwestern North Dakota and South Dakota. National Science Foundation (NSF) grant EAR-84075507 (to Archibald) supported the original collection of the Ekalaka specimens and NSF grant EAR-9804771 (to Archibald) helped support their analysis.

APPENDIX: LOCALITY REGISTER

The person whose name follows each taxonomic assignment identified the fossil material. PTRM is Pioneer Trails Regional Museum.

PTRM locality V89004

Bowman County, North Dakota, Doaks Butte Quadrangle, 0.97 km south of Doaks Butte, sec. 33, T.129N, R.106W, 45°56′51″N, 103°56′46″W, elevation ~899 m. Hell Creek Formation, 81.68 m below top.

Mesodma thompsoni Clemens; Hunter
Cimolodon nitidus Marsh; Hunter
Meniscoessus robustus (Marsh); Hunter
Meniscoessus sp.; Hunter
?*Meniscoessus* sp.; Hunter
Multituberculata indet.; Hunter
Alphadon marshi Simpson; Hunter
Pediomys florencae Clemens; Hunter
Didelphodon vorax Marsh; Hunter
Marsupialia indet.; Hunter
Theria indet.; Hunter
Mammalia indet.; Hunter

PTRM locality V91007

Bowman County, North Dakota, Doaks Butte Quadrangle, 0.97 km south of Doaks Butte and 0.32 km east of V89004, sec. 33, T.129N, R.106W, 45°56′53″N, 103°56′29″W, elevation ~893 m. Hell Creek Formation, 80.16 m below top.

Mammalia indet.; Hunter
Theria indet.; Hunter

PTRM locality V92025

Harding County, South Dakota, Doaks Butte Quadrangle, 1.9 km southeast of Doaks Butte, sec. 30, T.23N, R.2 E., 45°55′47″N, 103°55′11″W, elevation ~905 m. Hell Creek Formation (lower one-third), 73 m below top.

Meniscoessus sp.; Hunter

PTRM locality V92002

Slope County, North Dakota, Pretty Butte Quadrangle, 2.7 km northeast of Pretty Butte, sec. 24, T.134N, R.106W, 46°23′47″N, 103°56′08″W, elevation ~823 m. Hell Creek Formation, 42.60 m below top.

Meniscoessus robustus (Marsh); Hunter
Multituberculata indet.; Hunter

PTRM locality V92067

Bowman County, North Dakota, Cedar Hills Quadrangle, 1.6 km southeast of Sunset Butte, sec. 27, T.131N, R.105W, 46°08′11″N, 103°47′49″W, elevation ~887 m (corrected from Hunter and Pearson, 1996). Hell Creek Formation, 37.18 m below top (corrected from Hunter and Pearson, 1996).

Mesodma thompsoni Clemens; Hunter
Cimolodon sp.; Hunter
Meniscoessus robustus (Marsh); Hunter
Meniscoessus sp.; Hunter
Multituberculata indet.; Hunter
?Multituberculata indet.; Hunter
Pediomys sp. cf. *P. florencae* Clemens; Hunter
Didelphodon vorax Marsh; Hunter
Didelphodon sp.; Hunter
Marsupialia indet.; Hunter
Gypsonictops illuminatus Lillegraven; Hunter
Theria indet.; Hunter
Mammalia indet.; Hunter
?Mammalia indet.; Hunter

PTRM locality V86003

Slope County, North Dakota, Pretty Butte Quadrangle, at base of Pretty Butte, sec. 35, T.134N, R.106W, 46°22′47″N, 103°56′53″W, elevation ~841 m. Hell Creek Formation, 35.05 m below top.

Meniscoessus sp.; Hunter
?*Meniscoessus* sp.; Hunter
Didelphodon sp.; Hunter

PTRM locality V87009

Slope County, North Dakota, Pretty Butte Quadrangle, sec. 35, T.134N, R.106W, 46°22′48″N, 103°56′53″W, elevation ~841 m. Hell Creek Formation, 31.43 m below top.

Meniscoessus robustus (Marsh); Hunter
?*Didelphodon* sp.; Hunter
Mammalia indet.; Hunter

PTRM locality V86002

Slope County, North Dakota, Marmarth Quadrangle, 2.9 km northeast of Marmarth, sec. 20, T.133N, R.105 W, 46°18′34″N, 103°53′33″W, elevation ~853 m. Hell Creek Formation, 29.18 m below top.

Cimolodon nitidus (Marsh); Hunter
Meniscoessus sp.; Hunter
Cimolestes magnus Clemens and Russell; Hunter
Theria indet.; Hunter

PTRM locality V93022

Bowman County, North Dakota, Cedar Hills Quadrangle, 1.9 km southeast of Sunset Butte, sec. 27, T.131N, R.105W, 46°08′04″N, 103°47′52″W, elevation ~893 m. Hell Creek Formation, 25.3 m below top.

Meniscoessus robustus (Marsh); Hunter
Theria indet.; Hunter
Mammalia indet.; Hunter

PTRM locality V88018

Bowman County, North Dakota, Mud Buttes Quadrangle, sec. 11, T.129N, R.105W, 46°01′00″N, 103°45′50″W, elevation ~945 m. Hell Creek Formation, 14.27 m below top.

Mammalia indet.; Hunter

PTRM locality V88004

Bowman County, North Dakota, Mud Buttes Quadrangle, sec. 2, T.129N, R.105W, 46°01′32″N, 103°45′54″W, elevation ~951 m. Hell Creek Formation, 10.61 m below top.

Theria indet.; Hunter

PTRM locality V87012

Bowman County, North Dakota, Mud Buttes Quadrangle, sec. 2, T.129N, R.105W, 46°01′08″N, 103°45′52″W, elevation ~945 m. Hell Creek Formation, 9.85 m below top. *Meniscoessus robustus* (Marsh); Hunter

Didelphodon sp.; Hunter
?*Didelphodon* sp.; Hunter
?Mammalia indet.; Hunter

PTRM locality V89003

Bowman County, North Dakota, Dogie Butte Quadrangle, sec. 13, T.129N, R.105W, 45°59′46″N, 103°45′29″W, elevation ~945 m. Hell Creek Formation, 8.4 m below top.

Cimolodon nitidus Marsh; Hunter
Meniscoessus robustus (Marsh); Hunter
Meniscoessus sp.; Hunter
Didelphodon sp.; Hunter
Mammalia indet.; Hunter

PTRM locality V98011

Slope County, North Dakota, Marmarth SE Quadrangle, sec. 16, T.133N, R.105W, 46°20′2″N, 103°52″37′W, elevation ~875 m. Hell Creek Formation, 5.90 m below top.

Mammalia indet.; Hunter

PTRM locality V88017

Bowman County, North Dakota, Mud Buttes Quadrangle, sec. 2, T.129N, R.105W, 46°01′08″N, 103°45′50″W, elevation ~951 m. Hell Creek Formation, 3.17 m below top.

Theria indet.; Hunter

UCMP locality V86081

Claw Butte Anthill No. 1. Carter County, MT, Blacktail Creek SW Quad, sec. 16, T.1 S., R.55 E., 45°45′43″N, 104°55′26″W, elevation ~1001 m. Hell Creek Formation, ~65 m below top.

Mesodma formosa (Marsh); Archibald
Mesodma? formosa (Marsh); Archibald
Mesodma thompsoni Clemens; Archibald
?*Mesodma thompsoni* Clemens; Archibald
Mesodma sp.; Archibald
?*Mesodma* sp.; Archibald
Cimolodon nitidus Marsh; Archibald
?*Essonodon browni* Simpson; Archibald
Meniscoessus robustus (Marsh); Archibald
Alphadon marshi Simpson; Archibald
Pediomys elegans Marsh; Archibald
Pediomys florencae Clemens; Archibald
Pediomys hatcheri Osborn; Archibald
Gypsonictops sp.; Archibald
Mammalia indet.; Archibald

UCMP locality V86082

Claw Butte Anthill No. 2. Carter County, MT, Blacktail Creek SW Quad, sec. 16, T.1 S., R.55 E., 45°45′43.5″N, 104°55′25″W, elevation ~1001 m. Hell Creek Formation, ~65 m below top.
Mesodma hensleighi Lillegraven; Archibald
Mesodma formosa (Marsh); Archibald

Mesodma thompsoni Clemens; Archibald
Mesodma sp.; Archibald
?*Mesodma* sp.; Archibald
Cimolodon nitidus Marsh; Archibald
Essonodon browni Simpson; Archibald
Meniscoessus robustus (Marsh); Archibald
Alphadon marshi Simpson; Archibald
Pediomys cooki Clemens; Archibald
Pediomys elegans Marsh; Archibald
Pediomys elegans Marsh or *P. cooki* Clemens; Archibald
Pediomys florencae Clemens; Archibald
Pediomys hatcheri Osborn; Archibald
Pediomys sp. cf. *P. hatcheri* Osborn; Archibald
Gypsonictops sp.; Archibald
Mammalia indet.; Archibald

UCMP locality V86083

Claw Butte Anthill No. 3. Carter County, MT, Blacktail Creek SW Quad, sec. 16, T.1 S., R.55 E., 45°45′43.5″N, 104°55′25″W, elevation ~1001 m. Hell Creek Formation, ~65 m below top.

Mesodma formosa (Marsh); Archibald
Mesodma hensleighi Lillegraven; Archibald
Mesodma thompsoni Clemens; Archibald
Cimolodon nitidus Marsh; Archibald
Meniscoessus robustus (Marsh); Archibald
Protalphadon lulli (Clemens); Archibald
Alphadon marshi Simpson; Archibald
Glasbius twitchelli Archibald; Archibald
Glasbius sp. cf. *G. twitchelli* Archibald; Archibald
Pediomys cooki Clemens; Archibald
Pediomys florencae Clemens; Archibald
Pediomys hatcheri Osborn; Archibald
Pediomys krejcii Clemens; Archibald
Gypsonictops hypoconus Simpson; Archibald
Gypsonictops sp.; Archibald
Mammalia indet.; Archibald

UCMP locality V86084

Claw Butte Anthill No. 4. Carter County, MT, Blacktail Creek SW Quad, sec. 16, T.1 S., R.55 E., 45°45′44″N, 104°55′24″W, elevation ~1001 m. Hell Creek Formation, ~65 m below top.

Mesodma formosa (Marsh); Archibald
Mesodma hensleighi Lillegraven; Archibald
Mesodma thompsoni Clemens; Archibald
Cimolodon nitidus Marsh; Archibald
Essonodon browni Simpson; Archibald
Meniscoessus robustus (Marsh); Archibald
Alphadon? marshi Simpson; Archibald
Alphadon? wilsoni Lillegraven; Archibald
Protalphadon lulli (Clemens); Archibald
Alphadon marshi Simpson; Archibald
Glasbius twitchelli Archibald; Archibald
Pediomys sp. cf. *P. hatcheri* Osborn; Archibald
Pediomys cooki Clemens; Archibald
Pediomys elegans Marsh; Archibald
Pediomys florencae Clemens; Archibald
Pediomys hatcheri Osborn; Archibald
Turgidodon rhaister (Clemens); Archibald
Batodon tenuis Marsh; Archibald
Gypsonictops hypoconus Simpson; Archibald
Mammalia indet.; Archibald

UCMP locality V88007

Spigot-Bottle. Carter County, MT, Blacktail Creek SE Quad, sec. 3, T.1N, R.55 E., 45°51′29″N, 104°52′28″W, elevation ~939 m. Hell Creek Formation, ~61 m below top.

Mesodma formosa (Marsh); Archibald
Mesodma hensleighi Lillegraven; Archibald
Mesodma thompsoni Clemens; Archibald
Cimolodon nitidus Marsh; Archibald
Cimolomys gracilis Marsh; Archibald
Cimolodon nitidus Marsh; Archibald
Meniscoessus robustus (Marsh); Archibald
Protalphadon lulli (Clemens); Archibald
Alphadon marshi Simpson; Archibald
Alphadon wilsoni Lillegraven; Archibald
Pediomys cooki Clemens; Archibald
Pediomys elegans Marsh; Archibald
Pediomys florencae Clemens; Archibald
Pediomys hatcheri Osborn; Archibald
Pediomys sp. cf. *P. hatcheri* Osborn; Archibald
Pediomys krejcii Clemens; Archibald
Pediomys sp. cf. *P. krejcii* Clemens; Archibald
Pediomys sp.; Archibald
Turgidodon rhaister (Clemens); Archibald
Didelphodon vorax Marsh; Archibald
Metatheria indet.; Archibald
Batodon tenuis Marsh; Archibald
Cimolestes incisus Marsh; Archibald
Cimolestes propalaeoryctes Lillegraven; Archibald
Cimolestes stirtoni Clemens; Archibald
Gypsonictops sp.; Archibald
cf. *Paranyctoides* sp.; Archibald
“Insectivora” indet.; Archibald

PTRM locality V86005

PITA Flats locality, PTRM locality P86001, NM-4. Slope County North Dakota, Marmarth SE Quadrangle, sec. 10, T.133N, R.105W, 46°20′22″N, 103°51′36″W, elevation ~881 m. Fort Union Formation, Ludlow Member, ~~8 m above base.

Mesodma sp.; Hunter
Multituberculata indet.; Hunter
Oxyacodon priscilla Matthew; Hunter
?*Protungulatum* sp.; Hunter
Condylarthra indet.; Hunter
Mammalia indet.; Hunter

PTRM locality V97027

Slope County, North Dakota, Marmarth SE Quadrangle, sec. 9, T.133N, R.105 W, 46°20′55″N, 103°52′36″W, elevation ~860 m. Fort Union Formation, Ludlow Member, ~8 m above base.

Oxyprimus galadrielae Van Valen; Hunter

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MANUSCRIPT ACCEPTED BY THE SOCIETY SEPTEMBER 24, 2001

Printed in the U.S.A.