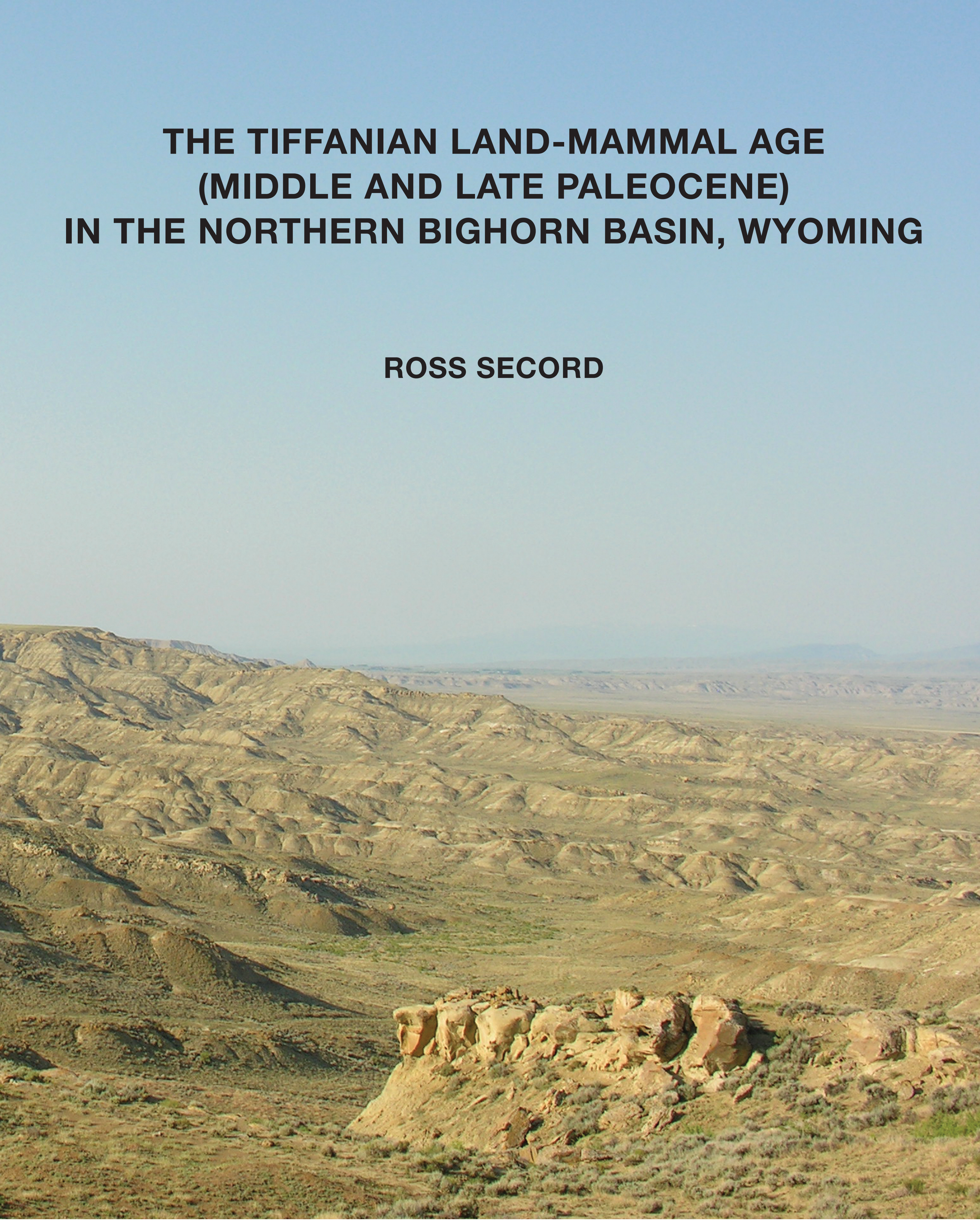
THE TIFFANIAN LAND-MAMMAL AGE (MIDDLE AND LATE PALEOCENE) IN THE NORTHERN BIGHORN BASIN, WYOMING

ROSS SECORD



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Frontispiece: View looking south-southwest across Silver Coulee on the west side of Polecat Bench, northern Bighorn Basin, Wyoming. Exposures are in the upper *Phenacolemur*, *Probathyopsis*, and *Plesiadapis simonsi* zones.

THE TIFFANIAN LAND-MAMMAL AGE (MIDDLE AND LATE PALEOCENE) IN THE NORTHERN BIGHORN BASIN, WYOMING

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Philip D. Gingerich, Director

To my wife Carole, for her unwavering love, support, patience, and optimism.

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ABSTRACT

The Tiffanian North American land-mammal age is an informal biochronologic unit that spans 4.5 myr of the middle and late Paleocene. It is preceded and succeeded by the Torrejonian and Clarkforkian land-mammal ages, respectively. The Tiffanian was initially based on a small collection of mammals from southern Colorado, but faunas of Tiffanian age are now known throughout the Rocky Mountain region. The richest and most complete sequence of middle and late Tiffanian faunas known occurs in the northern Bighorn Basin. These faunas are the primary basis for regional Tiffanian biochronology. The Bighorn Basin sequence is also important because it preserves the only known detailed record of faunal change across the Tiffanian-Clarkforkian boundary, which is marked by the first appearance of rodents in North America. Geomagnetic polarity reversals, a carbon isotope excursion marking the Paleocene-Eocene boundary, and a recent Ar^{40}/Ar^{39} age from a volcanic ash provide a strong geochronologic framework for the faunal sequence. Thus, this record affords a unique window into the evolution of North American mammals that can be compared globally with other biotic, paleoecological, and paleoclimatic records.

In spite of the importance of this Tiffanian record, numerous mammalian species represented by fossils collected over the last seventy-five years have not been described and the variability of many other species is poorly documented. This is especially true of small-bodied mammals. To remedy this, a compendium of Tiffanian and early Clarkforkian mammals that occur in the Bighorn Basin is presented. Most specimens are curated at the University of Michigan, but selected specimens curated at the Yale-Peabody Museum, originally collected by Princeton University crews, are also included. Seventeen new mammalian species are diagnosed and named, including two Leptictidae, two Pantolestidae, six Lipotyphla, one Plagiomenidae, four plesiadapiform Primates, and two Arctocyonidae. A new arctocyonid genus is also named. In addition, the size and morphologic variability of numerous others species is documented. The stratigraphic occurrences of all Tiffanian and early Clarkforkian species known from the Bighorn Basin are documented, and the faunal content of each biostratigraphic zone is summarized. This serves as the basis for a recently revised biostratigraphic zonation of the Tiffanian, and is intended to aid future studies of mammalian biochronology and evolution.

Changes in mammalian diversity (species richness) from the middle to the late Paleocene are compared with changes in global climate, inferred from the marine oxygen isotope record. The diversity record of the Bighorn Basin was combined with that of the Crazy Mountains Basin of Montana, since some temporal intervals are better represented in the latter. Localities were divided into clay-gall quarries, mudstone quarries, and surface collections. The number of individuals per species was estimated for each biozone or quarry, and the number of species was then normalized for sample size using rarefaction. Results indicate that species richness decreased from the Torrejonian to the early Tiffanian, reached a low point in the middle Tiffanian, and then began a steady increase to the middle Clarkforkian. The richness curve mirrors the marine temperature curve. Richness is significantly correlated with temperature suggesting that temperature had an important influence on the species diversity of Paleocene faunas.

I

INTRODUCTION

The Paleocene was an important time in mammal evolution. Eutherian mammals underwent a major adaptive radiation in the early Paleocene, following extinction of the dinosaurs, and rapidly became a prominent component of faunas. Paleocene faunas are composed mostly of archaic forms that were largely succeeded by members of modern orders in the early Eocene. The modernization of North American faunas happened abruptly in response to two immigration events in the late Paleocene. The first event included the first rodents to enter North America. Faunal composition did not change dramatically, but competition with rodents may have caused a decline in the diversity and abundance of multituberculates and plesiadapiformes, which were a major component of many Paleocene faunas (Krause, 1986; Maas et al., 1988). The second wave occurred at what is now the Paleocene-Eocene (P-E) boundary and included euprimates, perissodactyls, and artiodactyls. These immigrants quickly and dramatically changed the composition of North American faunas, as well as faunas on other Holarctic continents. The recent discovery that this dispersal, and other biotic events, coincided with a rapid increase in global temperature has resulted in a flurry of research (e.g., Gingerich, 1989; Koch et al., 1992, 1995; Clyde and Gingerich, 1998; Fricke et al., 1998; Dickens, 2001; Zachos et al., 2003; Bowen et al., 2004; Magioncalda et al., 2004; Wing et al., 2005; Zachos et al., 2005; Smith et al., 2006). Far less attention, however, has been given to faunas of middle and late Paleocene age.

The Tiffanian and Clarkforkian land-mammal ages span the middle to late Paleocene (Selandian and Thanetian marine stages). Land-mammal ages are informal biochronologic ages, typically divided into biochrons or zones used to correlate faunas regionally (e.g., Woodburne, 1987b; Lindsay, 2003; Woodburne, 2004b). The Tiffanian is the longest of the Paleocene land-mammal ages, and with a duration of about 4.5 myr, accounts for nearly half of the Paleocene (Secord et al., 2006). It is preceded and succeeded by the Clarkforkian and Torrejonian, respectively. The Torrejonian is about 3 myr in duration and is generally thought to have been a time of warm, subtropical climate (Rose, 1981a; Krause and Maas, 1990). The faunal composition of the type Torrejonian in the San Juan Basin, New Mexico, was recently revised and described in monographic fashion by Williamson (1996). The Clarkforkian is only about 1.2 myr in duration and is also generally thought to have been a time of warm, subtropical climate. The faunal content of the Clarkforkian was described in monographic fashion by Rose (1981a). The Tiffanian is thought to have been a time of cooler climate, and faunas and floras are typically less diverse (Hickey, 1980; Rose, 1981a; Wilf, 2000). The presence of thermophilic taxa such as crocodiles (Markwick, 1998), however, indicates that Tiffanian winters were warmer than today at mid-latitudes. Unlike the land-mammal ages bounding it, Tiffanian faunas have generally been treated in a piecemeal fashion until now.

The richest and most complete sequence of middle and late Tiffanian faunas known occurs in the northern Bighorn Basin. Consequently, the Bighorn Basin has become the reference section for the biostratigraphic zonation of the Tiffanian, as well as the Clarkforkian and much of the Wasatchian (Rose, 1980, 1981a; Gingerich, 1983b, 2001; Secord et al., 2006). Many of these biozones are, in turn, the basis for regional biochronologies (Archibald et al., 1987; Krishtalka et al., 1987; Lofgren et al., 2004; Robinson et al., 2004). Nevertheless, large parts of Tiffanian faunas collected by Princeton University crews as far back as 1928 have never been thoroughly studied. This is especially true of micromammals, which are often lumped together and identified only as "insectivores." These mammals were an important part of the ecosystem and their recognition and correct identification is important to any study that attempts to reconstruct Paleocene diversity or ecology.

The primary focus of this monograph is to review the content of Tiffanian and early Clarkforkian faunas from the northern Bighorn Basin, with a focus on describing new species, providing descriptions of variability, and describing the stratigraphic position of each taxon. This monograph is the companion publication to Secord et al. (2006), and includes the documentation of specimens that are the basis for the revised biostratigraphy presented therein. Descriptions emphasize specimens of late Tiffanian age (Ti-4, Ti-5, Ti-6) curated in the University of Michigan (UM) collections, but UM specimens of middle Tiffanian age (Ti-3) are also included. Specimens from the Yale Peabody Museum (YPM) were included, whenever possible, but the lists are not exhaustive and a considerable amount of Paleocene material at YPM merits further study. I diagnose 17 new mammalian species and describe numerous others that have become better known as a result of collecting by UM crews over the last few decades.

Chapter 2 provides an overview of Paleocene biostratigraphy in the Bighorn Basin. Chapter 3 presents a systematic treatment of Tiffanian and early Clarkforkian mammals. Chapter 4 explores the relationship between faunal change and climate change from the Torrejonian (To-2) to the late Clarkforkian (Cf-3), combining faunas from the Bighorn and Crazy Mountains basins. Recent revisions of the Paleocene geologic time scale (Luterbacher et al., 2004; Ogg and Smith, 2004), and

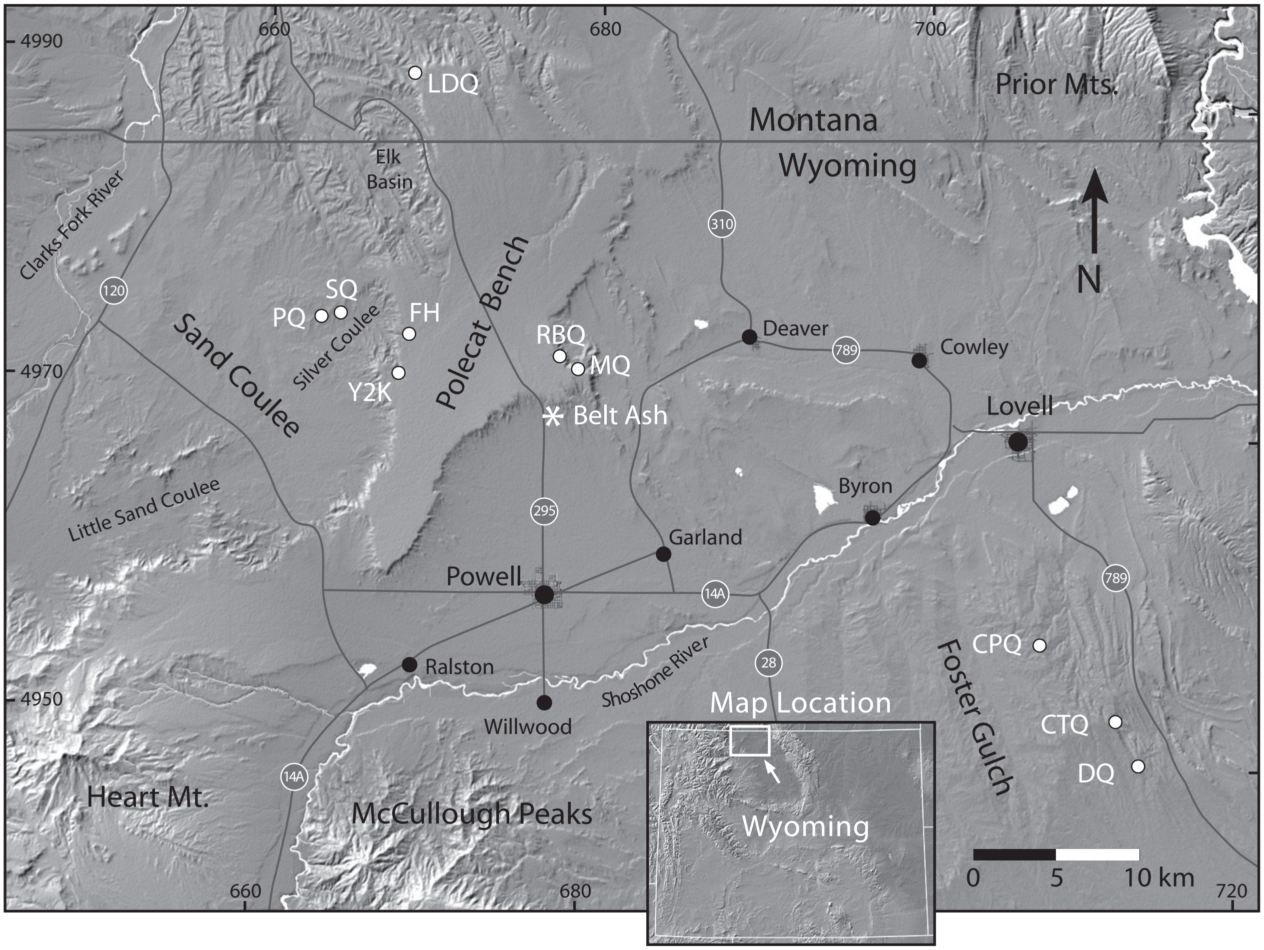

FIGURE 1 — Shaded-relief map showing location of important quarries and localities in the Polecat Bench and Foster Gulch areas of the northern Bighorn Basin, Wyoming. The Belt Ash is a volcanic ash that was recently dated at 59.00±0.3 Ma (Secord et al., 2006). Quarries: *CPQ*, Cedar Point; *CTQ*, Croc Tooth; *DQ*, Divide; *MQ*, Mantua; *PQ*, Princeton; *RBQ*, Rock Bench; *LDQ*, Long Draw; *SQ*, Schaff; *Y2K*, Y2K. *FH*, Fossil Hollow.

improvement of the marine temperature record (Zachos et al., 2001), coupled with the recognition of magnetic polarity zones in both basins (Butler et al., 1981, 1987) and refinement of biozone ages (Secord et al., 2006), allow for a higher resolution study of climate and diversity than was possible previously.

HISTORY OF BIGHORN BASIN COLLECTIONS

Gingerich (1980b) and Gingerich and Clyde (2001) provided overviews of the history of collecting fossil mammals in the Bighorn Basin. A summary follows, with emphasis on faunas pertinent to this study.

Tiffanian mammals were first found in the Bighorn Basin in 1928 around the margins of Polecat Bench by a Princeton University crew led by G. L. Jepsen. The following year Jepsen returned with W. J. Sinclair and three students, and discovered Mantua, Rock Bench, and Princeton quarries (Fig. 1). These quarries subsequently yielded large samples of Puercan, Torrejonian, and late Tiffanian aged mammals, respectively. The 1929 collections and additional material from 1928 formed the basis for Jepsen's doctoral dissertation (Gingerich, 1980b). Crews from Princeton University collected additional material in the 1930s, some of which has been studied and published in a piecemeal fashion, and some that is being described here for the first time.

Three additional quarries of Tiffanian age, Cedar Point, Divide, and Croc Tooth (or Witter), were discovered in the 1940s by R. V. Witter and A. C. Silberling in the Foster Gulch area east of Polecat Bench (Fig. 1; Gingerich, 1980b). Small collections were made from Divide and Croc Tooth quarries, but nearly 2000 specimens, many of which are jaws, were collected from Cedar Point Quarry in the 1950s, 1960s, and 1970s by Princeton crews, and in the 1970s and 1980s by UM crews. Schaff Quarry, a small but important late Tiffanian site, was discovered by C. R. Schaff in Silver Coulee on the west side of Polecat Bench in the 1960s (Fig. 1). A major effort to collect fossil mammals from restricted stratigraphic intervals in the badlands around Polecat Bench and in Sand Coulee to the west was initiated by P. D. Gingerich in 1975 for the University of Michigan. Collections made in the 1970s and 1980s by UM crews constitute the bulk of material described in this monograph.

Collecting by small UM crews from 1999 to 2003 added additional material to the late Tiffanian and early Clarkforkian collections. One important discovery made in 2000 was Y2K Quarry (Secord et al., 2002), which is late Tiffanian in age, and has yielded a diverse collection of micromammals. The discovery of mammal-bearing freshwater limestones in late Tiffanian beds is also important, but because the richest limestones were found near the end of this project, only a few specimens are included here. Skeletal remains of micromammals from similar limestones of Clarkforkian and Wasatchian age were the basis for a doctoral dissertation by Bloch (2001).

Princeton University collections are now curated at the Yale Peabody Museum (YPM). I devoted several weeks to studying the Princeton collection at YPM, focusing primarily on undescribed or poorly known small-bodied species from Cedar Point, Princeton, and Schaff quarries. I was able to borrow 89 key specimens for further study, but efforts were hampered by the absence of material on loan to others and by time constraints. Hence, this is not an exhaustive study of the Princeton collections. It does, however, include all identified Tiffanian and early Clarkforkian specimens in the UM collections.

Comprehensive faunal lists for Cedar Point and Princeton quarries were first published by Rose (1981a). Updated faunal lists for these, and also Divide, Croc Tooth, Schaff, and Y2K quarries are provided here in Appendix I.

MEASURING TECHNIQUES

Measurements for small mammals reported in this study were made using binocular microscopes with eyepiece reticles. An Olympus SZ40 microscope was used at YPM and a Leica SZ-4 was used at the University of Michigan. The reticules were calibrated using the same Mitutoyo digital caliper (Model No. CD-6"GS), which was checked for accuracy with an independent measure. The digital caliper was used directly for measuring larger specimens.

Length and width measurements for teeth in dentaries (measured under a microscope) were made in occlusal view with the lingual side of the dentary vertical at the M_1. Length measurements were checked with the dentary in lingual and buccal views. Insectivore teeth are often canted lingually, making width measurements especially sensitive to orientation. Compounding this problem is the tendency for some specimens to “flatten” parallel to bedding during post-depositional loading, resulting in teeth that are less canted. For these reasons the width measurements reported here for species with canted teeth should be regarded as estimates. Isolated teeth were oriented in the dentary position.

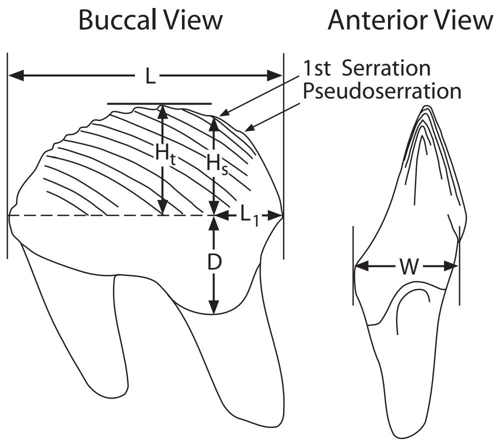

FIGURE 2 — Orientation and landmarks used for measurement of multituberculate lower fourth premolars. Modified from Krause (1987a). See also dental abbreviations.

Measurements are maximum tooth dimensions, unless otherwise indicated, and not the distance between interstitial facets. In some instances, such as in teeth of *Plesiadapis*, slightly different techniques were used so that measurements would be comparable to those of other authors. Measurements of upper teeth are Type 1 (my terminology), unless otherwise stated. Type 1 means that length was measured parallel to a line through the paracone and metacone. Expansions lingual of this line were not included in length. Width is maximum dimension measured perpendicular to length. Type 2 measurements are like Type 1, but include expansions lingual to the line through the paracone and metacone. Type 2 measurements are like those illustrated by Thewissen (1990), and were used here for the phenacodontids and *Litolestes*. Differences between these methods are minor in most cases but can be large for teeth that have expanded lingual regions, such as the M^3s of paromomyids or plesiadapids. In upper teeth, the practice of taking measurements parallel and perpendicular to the outer cusps, rather than relative to the palatal midline (e.g., Gingerich, 1976), can also result in significant differences in maxillae that are curved, especially for M^3. The advantage to this technique is that it requires no knowledge of the orientation of the maxillary, and can be easily applied to jaw fragments and isolated teeth.

Cusp nomenclature follows that of Van Valen (1966) for therians, and Krause (1977; 1982; 1987) for multituberculates. Figure 2 shows landmarks used for multituberculate fourth lower premolars.

INSTITUTIONAL ABBREVIATIONS

AMNH — American Museum of Natural History, New York, NY
BYU — Brigham Young University, Provo, UT
CM — Carnegie Museum of Natural History, Pittsburg, PA
FMNH — Chicago Field Museum of Natural History, Chicago, IL
MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, MA
PU — Princeton University, Princeton, NJ
SMM — Science Museum of Minnesota, St. Paul, MN
UALVP — Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton
UM — University of Michigan, Museum of Paleontology, Ann Arbor, MI
USGS — United States Geological Survey Collections, USNM, Washington, D.C.
USNM — United States National Museum, Smithsonian Institution, Washington, D.C.
UW — The University of Wyoming, Collection of Fossil Vertebrates, Laramie, WY
YPM-PU — Princeton University collections, Yale-Peabody Museum, New Haven, CT

DENTAL AND STATISTICAL ABBREVIATIONS

Alv.	alveolus or alveoli
C	number of cusps in multituberculate teeth
D (1)	multituberculates: distance from midline to base of exodaenodont lobe of P_4
D (2)	dentaries: distance from the buccal cervical margin of the M^1 crown above the anterior root to the base of the dentary
D (3)	plesiadapiform incisors: depth of root at cervical margin, perpendicular to long axis of root
H	height from base of enamel at cervical margin to apex of crown
HP	buccal crown height from base of posterior exodaenodont lobe to ultimate cusp
H_s	height from midline to first serration in P_4 of multituberculates
H_t	total height from midline to highest point in P_4 profile in multituberculates
L	length
L_1	length along midline to first serration in P_4 of multituberculates
Min.	minimum
Max.	maximum
Mlc	maximum lingual constriction
Mll	maximum lingual length
S	number of serrations in multituberculate P_4, excluding pseudoserrations (incipient serration on anterior of apical crest, lacking associated ridge; e.g., Scott, 2005)
SD	standard deviation
SE	standard error of mean
V	coefficient of variation
W	width
*****	estimated dimension due to incompleteness of specimen

ABBREVIATIONS IN REFERRED SPECIMEN LISTS

Ant.	anterior
Assoc.	associated
Dent.	dentary
FG	UM Foster Gulch locality
Frag.	fragment
Frags.	fragments
Iso.	isolated
L	left
Max.	maxilla
Misc.	miscellaneous
MP	UM McCullough Peaks locality
Post.	posterior
R	right
SC	UM Sand Coulee area locality
Tal.	talonid
Tals.	talonids
Tri.	trigonid
Tris.	trigonids
Unassoc.	unassociated

MISCELLANEOUS ABBREVIATIONS

BCM	Bighorn and Crazy Mountains basins
Indet.	indeterminate
NS	number of specimens
P-E	Paleocene-Eocene
Pers. comm.	personal communication

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II

MAMMALIAN BIOSTRATIGRAPHY

INTRODUCTION

The North American land-mammal ages were established as informal time units by the Wood Committee (1941). This was done because of difficulties correlating continental deposits in North America to the stratigraphic sequences in Europe upon which epochs and ages are based, and to alleviate confusion that had arisen by authors using the names of rock units interchangeably with time. Land-mammal ages and their subdivisions have proven to be useful aids in the correlation of continental strata and have facilitated communication among paleobiologists and geologists (Savage and Russell, 1983; Woodburne, 1987a, 2004a; Lindsay, 2003).

The North American land-mammal ages were initially defined as purely temporal units that were only loosely tied to stratigraphic sections. They were composites of regional faunas correlated on the basis of fossil content; and, because they did not meet standards for formal geochronologic units (e.g., NACSN, 1983; ISSC, 1994), have been regarded as informal ages. Improvements in the fossil record and in geochronologic correlation have, however, allowed many of the land-mammal ages to be brought more in line with stratigraphic standards (e.g., Woodburne, 1977, 1987b, 1996; Evander, 1986; Lindsay, 1995; Williamson, 1996). For example, the Clarkforkian land-mammal age now meets the criteria necessary to become a formal geochronologic age. Its stratigraphy, boundaries, and fossil content have been described in detail in the Clarks Fork Basin of Wyoming (Rose, 1980, 1981a; Gingerich, 2001; Gingerich and Clyde, 2001). Nevertheless, until this and other land-mammal ages are formally defined in publication, they remain informal ages.

The majority of fossils described in this monograph are Tiffanian in age. The Tiffanian land-mammal age is widely recognized as the temporal interval between the first occurrences of *Plesiadapis* and Rodentia (e.g., Archibald et al., 1987; Lofgren et al., 2004). The type Tiffanian is in Colorado (Simpson, 1935b,c,d; Wood et al., 1941), but the northern Bighorn Basin preserves a more complete record of Tiffanian faunas (Figs. 3, 4, 5) and has served for more than three decades as the primary reference area for the middle and late Tiffanian biozones (Ti-3 to Ti-6) (Gingerich, 1975, 1976, 1983b; Archibald et al., 1987; Lofgren et al., 2004; Secord et al., 2006). Many of the Bighorn Basin faunas occur in stratigraphic sequence, making them ideal for biostratigraphic studies (Fig. 6). Many other important Tiffanian faunas are known, including several large collections from Canada (e.g., Fox, 1990), but these faunas typically occur as isolated pockets and their temporal relationships are inferred from taxonomic content, rather than superpositional relationships (see Archibald et al., 1987, for an overview of Tiffanian localities). Late Tiffanian (Ti-5, Ti-6) faunas are poorly known outside the Bighorn Basin, and the Clarks Fork Basin contains the only detailed record of faunal change across the Tiffanian-Clarkforkian boundary.

The biozonation used here for the Tiffanian and Clarkforkian land-mammal ages is that of Secord et al. (2006) (Fig. 7). The descriptions of biozones, species, and localities presented here serve as the underlying basis for that zonation. The stratigraphic ranges for Tiffanian and early Clarkforkian species discussed in this document are summarized in Figure 8.

HISTORY OF BIOSTRATIGRAPHIC ZONES

The first biostratigraphic zonation for the Tiffanian and Clarkforkian land-mammal ages was developed by Gingerich (1975, 1976), based on evolutionary lineages of *Plesiadapis*, a common plesiadapiform mammal. These biozones allowed for much greater temporal resolution than was previously possible and supported the idea that the Clarkforkian was distinct from the underlying Tiffanian and overlying Wasatchian land-mammal ages. The biozonation was based mostly on a composite of stratigraphic sections in the Bighorn Basin and adjacent Crazy Mountains Basin in southern Montana. The superpositional relationships for species of *Plesiadapis* first outlined by Gingerich are still valid.

Rose (1980; 1981a) subsequently established two additional biozones for the Clarkforkian and latest Tiffanian, and demonstrated that the Clarkforkian was a distinct and valid land-mammal age. The older zone was based on the first occurrence of *Plesiadapis gingerichi* and straddled the Tiffanian-Clarkforkian boundary. Rose recognized the beginning of the Clarkforkian by the first appearance of rodents, but did not define a biozone to correspond with this appearance. He defined the last zone of the Clarkforkian (Cf-3), as an “acme” zone based on the abundance of *Ectocion* and *Phenacodus*. The zone was recognized, in practice, primarily by the absence of *Plesiadapis cookei*, which defined the preceding zone, and the absence of Wasatchian immigrants (e.g., perissodactyls, euprimates), which defined the suceeding zone. Rose’s zones were all based on measured stratigraphic sections and were in essence chronostratigraphic units, although never formally defined as such.

Archibald et al. (1987) followed the zonations proposed by Gingerich (1975, 1976, 1983b) and Rose (1980, 1981a), but

TABLE 1 — Stratigraphic levels and age calibrations for biozone and polarity zone boundaries from sections on the southeastern and western sides of Polecat Bench (SPB and WPB, respectively; Figs. 1, 3). All data are for base of zone. Biozone calibrations are from cubic spline interpolation (CSI). Ages for polarity chrons and Paleocene-Eocene boundary carbon isotope excursion (CIE) are from Ogg and Smith (2004). Hiatuses of 0.5 and 1.0 myr were modeled at base of C26r (see Secord et al., 2006). *Diff.* (*myr*), difference in million years; *m*, meters; *Ma*, age in million years before present; *NH*, no hiatus. Asterisk indicates that level is measured down from CIE.

Biozone or feature	SPB (m)	WPB (m)	CSI: no hiatus Ma	CSI: 0.5 myr hiatus Ma	Diff. (myr)	CSI: 1.0 myr hiatus Ma	Diff. (myr)
CIE	1475	0*	55.80	55.80	0.00	55.80	0.00
Cf-3	1290	-190*	56.22	56.22	0.00	56.22	0.00
Cf-2	1150	-340*	56.50	56.50	0.00	56.50	0.00
Cf-1	866	432	56.99	56.99	0.00	56.99	0.00
Ti-6	736	305	57.34	57.34	0.00	57.34	0.01
Ti-5b	640	215	57.69	57.69	0.01	57.68	0.02
Ti-5a	489	102	58.31	58.31	0.00	58.31	0.01
Ti-4b	350	—	58.85	58.84	0.01	58.83	0.02
Belt Ash	331	—	58.97	58.95	0.02	58.92	0.05
Ti-4a	265	—	59.50	59.39	0.11	59.29	0.21
Ti-3	194	—	60.29	60.04	0.24	59.80	0.49
Ti-2	139	—	60.95	60.58	0.37	60.21	0.73
To-Ti	89	—	61.57	61.09	0.49	60.60	0.97

split the *P. gingerichi* zone into two subzones, the *P. gingerichi* subzone (Ti-6) and the Rodentia subzone (Cf-1). The boundary separating these subzones was coincident with the Tiffanian-Clarkforkian boundary, defined by the first appearance of rodents. They treated the Paleocene biozones as biochronologic units (see Lindsay, 2003), rather than biostratigraphic units, extending them regionally on the basis of their fossil content.

Gingerich (2001) described the Bighorn Basin biozones with reference to their position in a composite measured section. He raised the ranks of the *P. gingerichi* and Rodentia subzones to zones. He also defined a new zone, the *Plesiadapis fodinatus* zone (Ti-5, revised), in the lower part of the interval that was previously occupied by the *Plesiadapis simonsi* zone, in recognition that *P. simonsi* may not extend as low in the section as previously thought. The *P. simonsi* zone was shortened considerably and was now concurrent with the upper part of the *P. fodinatus* zone. This revision was important because Princeton and Schaff quarries, as well as other localities in the Silver Coulee area on the northwest side of Polecat Bench (Figs. 1 and 4), were previously thought to occur in the *P. simonsi* zone, but were now in the *P. fodinatus* zone. The *P. fodinatus* and *P. simonsi* zones were given the symbols Ti-5a and Ti-5b, respectively, in a later publication (Gingerich, 2003).

Most recently, Secord et al. (2006) revised the Paleocene biostratigraphy of the Bighorn Basin (Fig. 7). They split the *Plesiadapis churchilli* zone (Ti-4) into two zones, the *P. churchilli* zone (Ti-4a) and the overlying *Phenacolemur* zone (Ti-4b). This split was based on the collection of new specimens, further study of museum collections, and the recognition that *P. churchilli* occurred stratigraphically lower on Polecat Bench than previously thought. They replaced the *P. fodinatus* zone (Ti-5a) with the *Probathyopsis* zone (Ti-5a revised), and the *Phenacodus-Ectocion* (Cf-3) zone with the *Copecion* zone (Cf-3 revised). The discovery of a volcanic ash, dated at 59.00±0.3 Ma, near the top of the *P. churchilli* zone, coupled with the position of magnetozones and revision of the geomagnetic polarity time scale (Luterbacher et al., 2004; Ogg and Smith, 2004), allowed the Bighorn Basin biozones to be placed in a more accurate geochronologic context than previously possible (Secord et al., 2006). When biozones were first defined in the Bighorn Basin (Gingerich, 1975), little was known about their durations, but now relatively accurate age estimates can be made for most boundaries above the base of the *P. churchilli* zone (Table 1; Fig. 7).

LITHOSTRATIGRAPHY

The lithostratigraphy pertinent to this study was described by Secord et al. (2006) and is summarized here. Paleocene fossils are found in two formations: the Fort Union Formation and the overlying Willwood Formation. The Willwood Formation is distinguished by the prevalence of brightly colored red beds (Van Houten, 1944) interpreted to be the B horizons of paleosols (Bown and Kraus, 1981; Kraus, 1997). The transition from drab beds to red beds coincides with the Clarkforkian-Wasatchian boundary in most of the Bighorn Basin, but occurs ~1.0 myr earlier on the west side of Polecat Bench in the early part of the Clarkforkian (Cf-1) (Rose, 1981a; Wing and Bown, 1985; Wing et al., 2000). Most fossils used in this study, except for a few Clarkforkian specimens, come from the Fort Union Formation.

Three informal members were recognized by Jepsen (1940) in the Fort Union Formation on and around Polecat Bench. In stratigraphic order these are: (1) the Mantua Lentil, (2) the Rock Bench quarry (RBQ) beds, and (3) the Silver Coulee beds

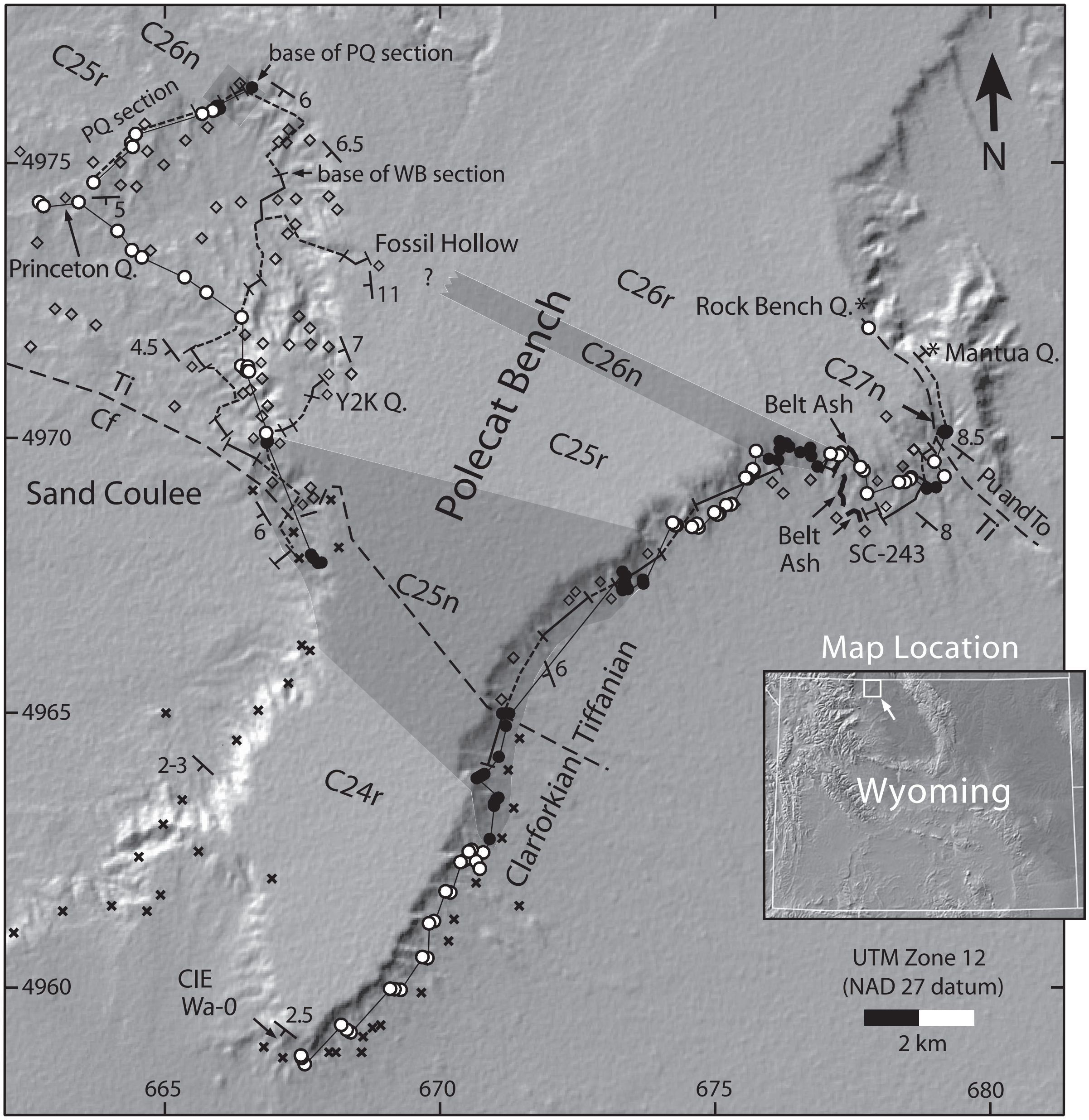


FIGURE 3 — Shaded-relief map of Polecat Bench in the northern Bighorn Basin, Wyoming, showing Paleocene mammal localities; locations of paleomagnetic samples collected by Butler et al. (1981, 1987) and Secord et al. (2006; Princeton Quarry section, upper left); projection of magnetic polarity zones (C27n-C24r); locations of measured sections used in Figure 6; location of the Belt Ash (UTM: 12T, E 677341, N 4969125, NAD 1927); and strike and dip symbols. Fossils were collected along the margins of Polecat Bench, in Sand Coulee, and in Foster Gulch (Fig. 1). Top of polarity zone C25n on the west side of Polecat Bench was estimated from stratigraphic thickness. Measured sections shown as thick solid lines; bed traces as short dashes; land-mammal age boundaries as long dashes; paleomagnetic sample sites connected by thin solid lines. Arrows point to outcrops containing the Belt Ash. UTM coordinates in kilometers. Symbols: *open circle*, normal polarity site; *solid circle*, reversed polarity site; *diamond*, Tiffanian fossil locality; *cross*, Clarkforkian fossil locality. Abbreviations: *Cf*, Clarkforkian; *PQ*, Princeton Quarry; *Pu*, Puercan; *Ti*, Tiffanian; *To*, Torrejonian; *Q*., Quarry.

(fluvial member of Hickey, 1980). Three additional informal members were recognized by Hickey (1980): the lacustrine, paludal, and conglomerate members, but only the lacustrine member, later formalized as the Belfry Member (Yuretich et al., 1984), is pertinent to this study. Nearly all the fossils described here are from the Silver Coulee beds, named by Jepsen for the area around Princeton Quarry that was called Silver Coulee by locals (Jepsen, 1940: p. 236).

The Silver Coulee beds are ~800 m thick on Polecat Bench and consist primarily of gray mudstones interbedded with yellow-gray to gray-orange fine- to medium-grained ribbon sandstones and carbonaceous shales. Shelf-forming beds of

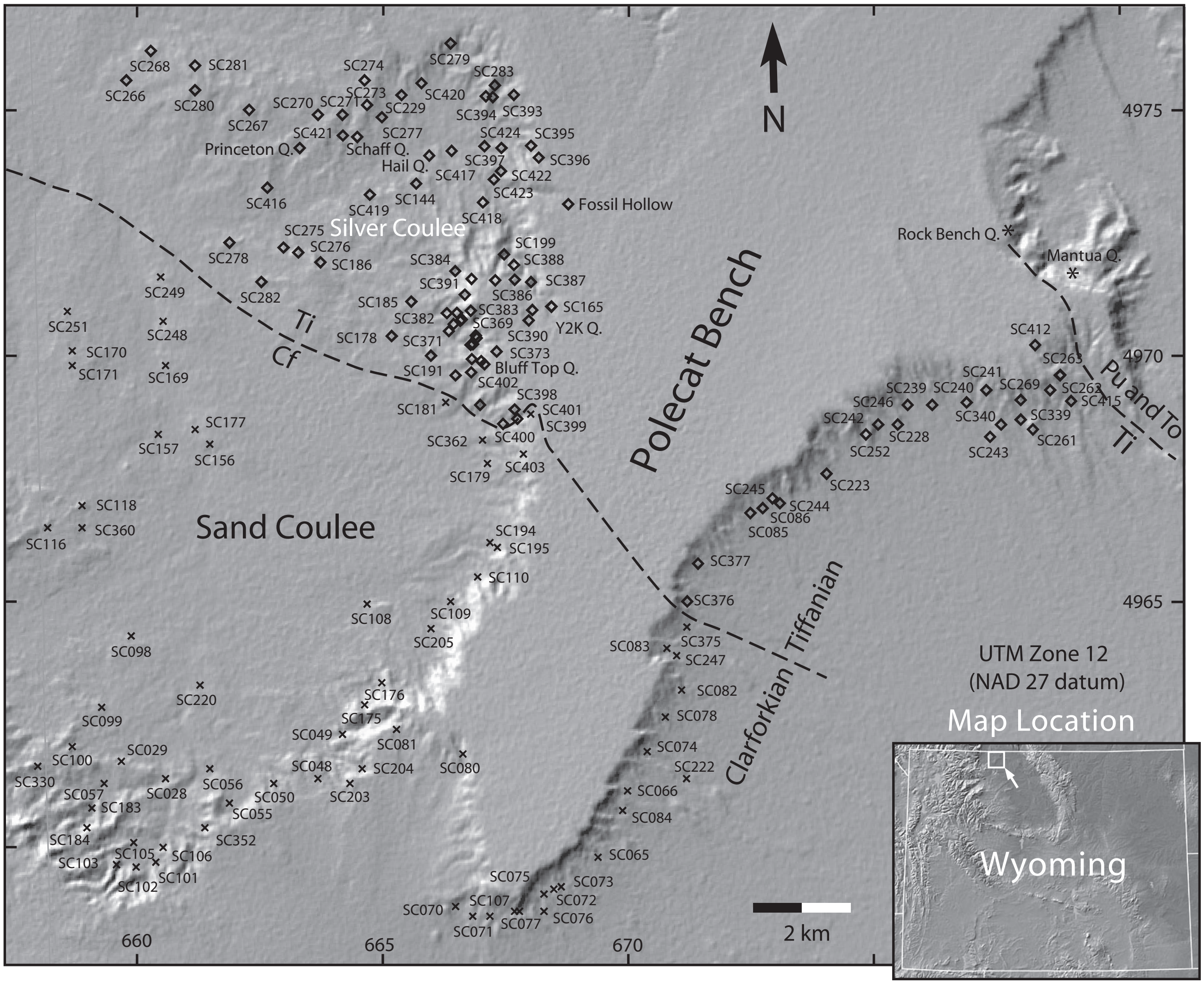


FIGURE 4 — Shaded relief map showing location of Tiffanian (open diamonds) and Clarkforkian (crosses) University of Michigan localities around Polecat Bench, and in Sand Coulee and Silver Coulee. UTM coordinates in kilometers (12T, NAD 1927). Symbols and abbreviations as in Figure 3.

intergradational argillaceous limestone lenses and nodules, calcareous siltstones, and fine-grained sandstones are also common. To my knowledge, there is no evidence for substantial unconformities or significant hiatuses in the Silver Coulee beds or lower Willwood Formation on Polecat Bench. The Silver Coulee beds are Tiffanian in age, except for the uppermost part, which is early Clarkforkian on Polecat Bench. Based on biostratigraphic continuity and on the completeness of the paleomagnetic record, the depositional record in the Silver Coulee beds is unusually complete.

The Rock Bench Quarry beds underlie the Silver Coulee beds on Polecat Bench (Fig. 6), and consist of a series of dark carbonaceous mudstones and shales, with subordinate sandstone ribbons and lignite. Rock Bench Quarry occurs in this unit and has yielded a large collection of Torrejonian mammals, a few of which are described or referenced below. The Rock Bench Quarry beds and Mantua Lentil were equated with the Lebo Member of the Fort Union Formation by Stow (1938), a correlation tentatively followed by Hickey (1980). A conglomeratic sandstone (the "quartzite conglomerate" of Jepsen, 1930b, p. 479 and Fig. 3) separates the Rock Bench Quarry beds from the Silver Coulee beds. It reaches a maximum thickness of 23 m and contains local lenses of dark, rounded pebbles of chert. I hereafter refer to it as the "chert conglomerate" to avoid confusion with other conglomeratic units, such as the Beartooth conglomerate. The conglomerates are granule- to pebble-size and primarily matrix-supported on Polecat Bench, but frequently clast-supported in exposures farther south. The upper part of this unit is either latest Torrejonian or early Tiffanian (Ti-1 or Ti-2) in age on Polecat Bench, based on the presence of a single specimen of *Phenacodus* (see *P.* cf. *P. grangeri* in Chapter 3).

The Belfry Member intergrades with the Silver Coulee beds along the northwest margin of Polecat Bench, but is better represented near Belfry, Montana, ~30 km to the northwest. Hickey and Yuretich (1997) described six cycles of tabular sandstone

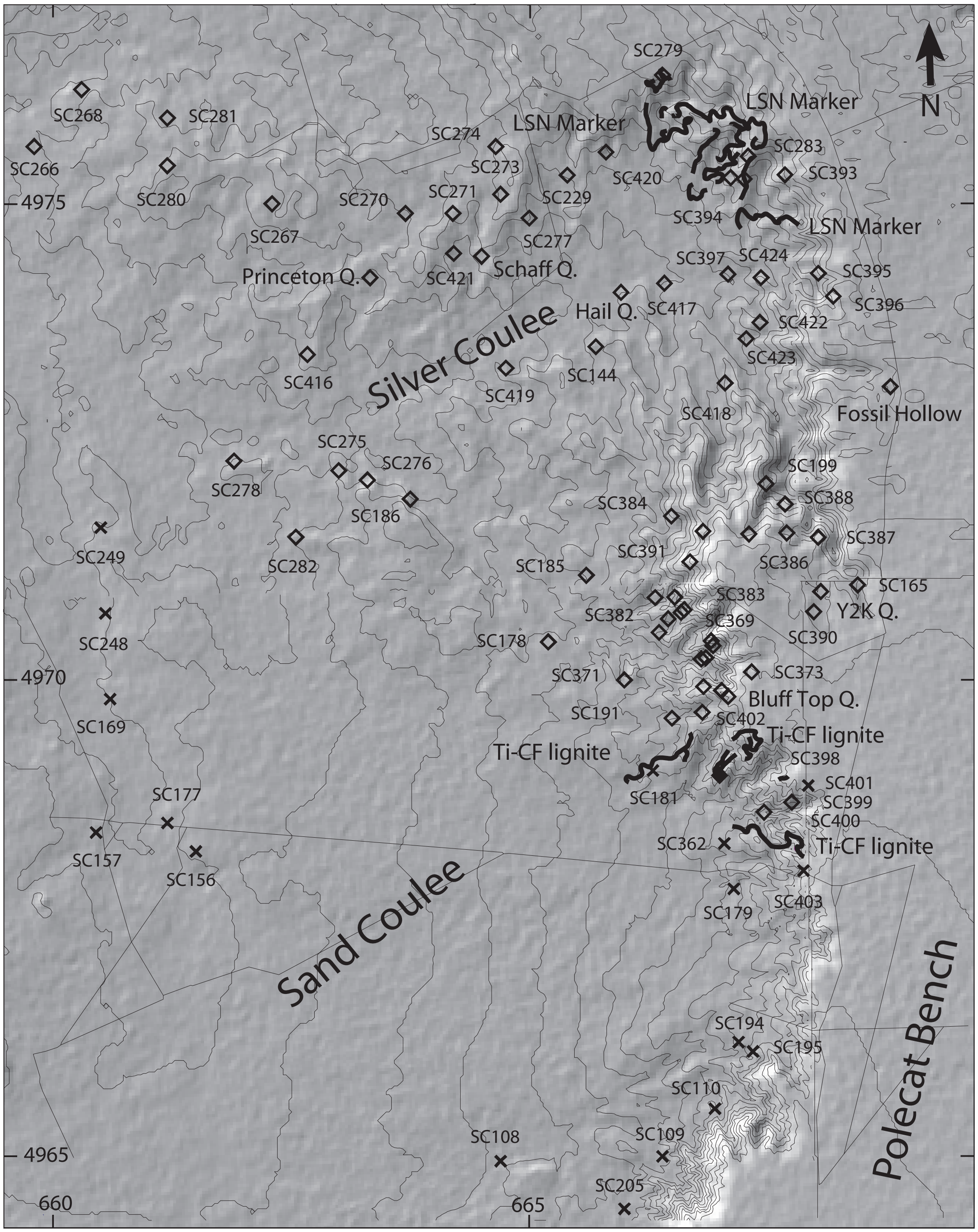


FIGURE 5 — Shaded relief map showing topographic lines (15 m intervals) in Silver Coulee area on west side of Polecat Bench. Solid lines in north show traces of limestone marker bed (LSN) in *Phenacolemur* zone (Ti-4b). Solid lines in south show traces of Tiffanian-Clarkforkian (Ti-Cf) boundary lignite at base of Rodentia zone. Open diamonds are Tiffanian mammal localities, and crosses are Clarkforkian mammal localities. UTM coordinates in kilometers (12T, NAD 1927).

and micrite that they interpreted as lake deposits in the Belfry Member. The sandstone-micrite couplets are intercalated with mudstones and lignites interpreted as fluvial floodplain deposits. We found that gar scales, and the remains of champsosaurs and pantodonts, were relatively common in the northern part of Silver Coulee where the Belfry Member intertongues with the Silver Coulee beds, suggesting a lake-margin or periodically flooded environment.

BIOZONE DEFINITIONS

The definitions and taxonomic content of the new and revised biozones described by Secord et al. (2006) were provided therein, and are augmented here with definitions for previously existing Tiffanian zones. Zone types (i.e., lineage or interval) follow guidelines and definitions of the North American Stratigraphic Code (NACSN, 2005) and International Stratigraphic Guide (ISSC, 1994). Note that the new zone definitions by NACSN (2005) are now in agreement with those by ISSC (1994), contrary to the previous version (NACSN, 1983). An asterisk after a species name indicates that it is part of a lineage with an evolutionary species known in the zone below (first occurrences) or above (last occurrences).

?Plesiadapis anceps lineage zone (Ti-2) — The *P. anceps* zone is the interval between the first occurrences of *P. anceps* and *P. rex*, its probable direct descendant (Gingerich, 1976). The presence of the *P. anceps* zone in the Bighorn Basin is suggested by a single specimen (YPM-PU 17816) identified as *P. anceps* by Gingerich (1976). As discussed in the *P. anceps* section, however, the stratigraphic level for this specimen is poorly constrained and no additional fossils have been found that corroborate a Ti-2 age.

Plesiadapis rex lineage zone (Ti-3) — The *P. rex* zone is the interval between the first occurrences of *P. rex* and *P. churchilli*, its probable direct descendant (Gingerich, 1976). A type fauna for Ti-3 has never been designated, but it is best represented in the Bighorn Basin by Cedar Point Quarry, a large sample of nearly 2000 specimens, many of which are jaws (Figs. 1 and 6, Appendix IA). The upper boundary of Ti-3 is best delineated on the southeast side of Polecat Bench, where Ti-3 reaches a thickness of ~70 m between fossiliferous levels at SC-263 and SC-261, the lowest Ti-4 locality. The lower boundary is very poorly constrained, however, and Ti-3 could be much thicker than 70 m. The upper boundary also occurs in Foster Gulch (Fig. 1) between Cedar Point and Divide quarries (Fig. 6), but because of the lack of fossils and the large geographic distance between the localities (9.5 km) it is also poorly constrained here. Ti-3 is the oldest Tiffanian biozone that is known with certainty in the Bighorn Basin.

Taxa of biostratigraphic value include: *Adunator meizon*, *Carpodaptes hazelae*, *Ignacius frugivorus*, *Neoplagiaulax hunteri*, *Neoplagiaulax jepi*, *Plesiadapis rex*, and *Ptilodus* sp. C. Lofgren et al. (2004) provided a regional list of genera in Ti-3.

Last occurrences (i.e., known only in the *P. rex* zone): *Adunator meizon*, *Aletodon quadravus*, *Aphanocyon amaurus* gen. et sp. nov., *Arctocyon* cf. *A. mumak**, *Bessoecetor* cf. *B. pilodontus**, *Bisonalveus holtzmani*, *Caenolambda jepseni*, *Carpodaptes hazelae*, *Cedrocherus ryani*, *Leptacodon acherontus* n. sp., *Chriacus oconostotae*, *Elphidotarsius elegans*, *Leptacodon* cf. *L. munusculum*, *Litocherus zygeus*, *Mimotricentes fremontensis*, *Myrmecoboides arenarius* n. sp., *Neoplagiaulax hunteri*, *N. jepi*, *Picrodus* cf. *P. silberlingi*, *Plesiadapis rex**, *Protictis agastor*, *P. paralus*, *Ptilodus* cf. *P. kummae**, *Ptilodus* sp. C., *Raphictis gausion*, *Titanoides* cf. *T. major*, and *Tytthaena parrisi*.

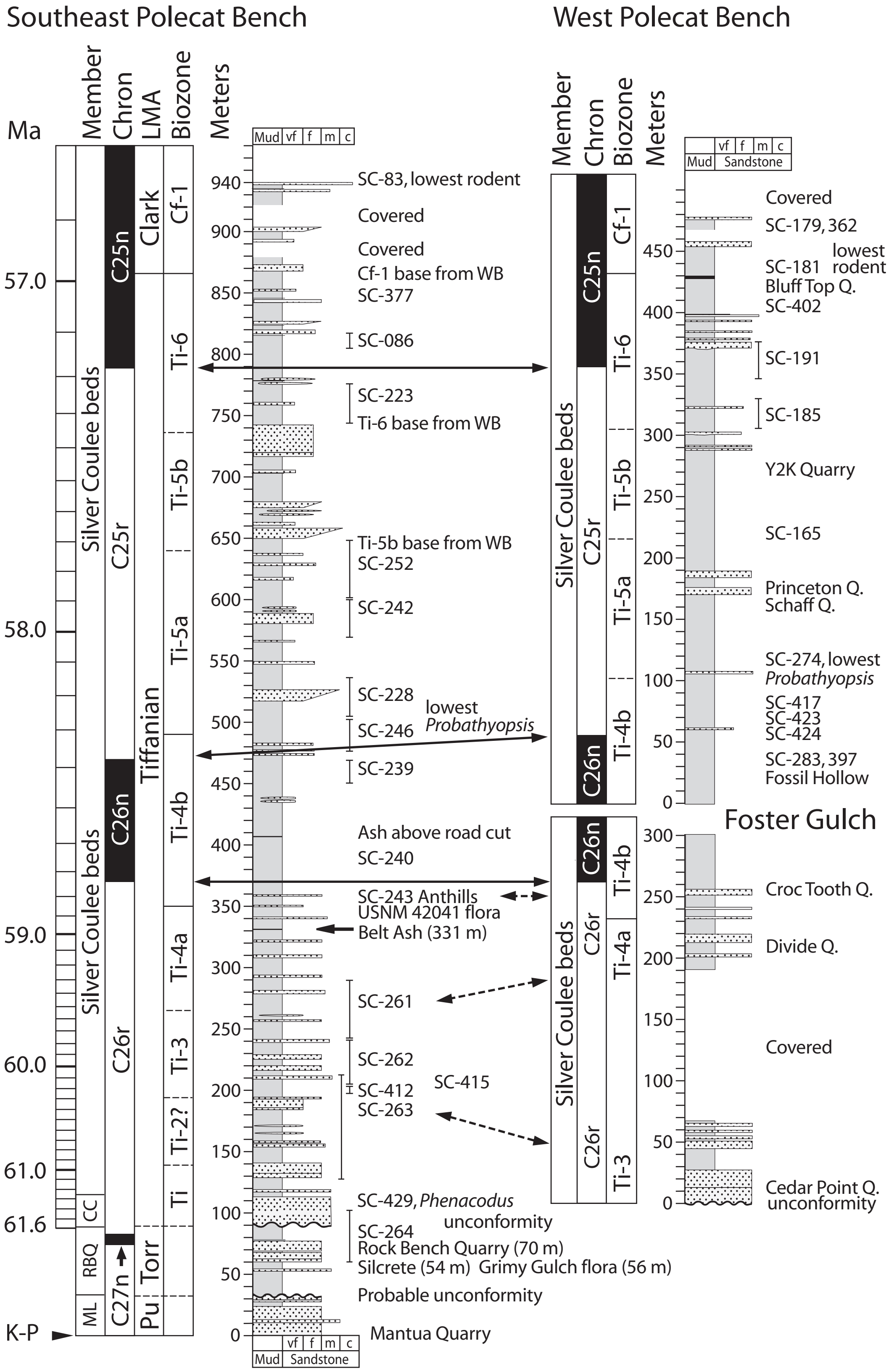
Additional species present: *Dissacus* cf. *D. navajovius*, *Ectocion cedrus*, *Ignacius frugivorus*, *Labidolemur soricoides*, *Leptonysson orthius* n. sp., *Palaeoryctes* sp., *Paleotomus radagasti*, *Peradectes elegans*, *Phenacodus grangeri*, and *Thryptacodon australis*. Possibly also *Aphanocyon codyensis* gen. et sp. nov.

Plesiadapis churchilli lineage zone (Ti-4a) — The *P. churchilli* zone is defined as the interval between the first occurrences of *Plesiadapis churchilli* and *Phenacolemur*. A type fauna for the zone has not been designated, but it is best represented in the Bighorn Basin by Divide Quarry, a moderate-sized sample from the Foster Gulch area (Figs. 1 and 6; Appendix IB). Long Draw Quarry in southern Montana (Fig. 1) is the type locality for *P. churchilli*, but has yielded a considerably smaller and less diverse sample. It is probably correlative with Divide Quarry and Ti-4a. The ranges of Ti-4a taxa are shown in Figure 8.

One of the most notable and potentially useful differences between Ti-3 and Ti-4a is the change from *Ptilodus* sp. C to *P. kummae*. *Ptilodus* sp. C is abundantly represented at Cedar Point Quarry (17% of total specimens), but it is not known at Divide Quarry, which is dominated by *Ptilodus kummae* (24% of total specimens). *Ptilodus kummae* is a rare element at Cedar Point Quarry, if it is present at all (see systematic section). Taxonomic abundance can be influenced by local ecologic factors, however, and these observations need to be compared with *Ptilodus* frequencies at localities outside the Bighorn Basin.

First occurrences are: *Aaptoryctes* (*A.* cf. *A. ivyi*), *Adunator minutus*, *Arctocyon mumak*, *Bessoecetor pilodontus* n. sp.*, *Chiromyoides caesor*, *Cyriacotherium* (*C.* cf. *C. argyreum**), *Didymictis* (*D.* cf. *D. dellensis*), *Haplolambda* cf. *H. quinni*, *Lambertocyon* (*L. gingerichi*), *Leptolambda churchilli*, *Litolestes* (*L.* cf. *L. ignotus*), *Neoplagiaulax mckennai*, *Palaeoryctes jepseni*, *Palaeosinopa* (*P. dorri*?), *Phenacodus magnus*, *Plesiadapis churchilli**, *Prochetodon* (*P. foxi*), *Ptilodus kummae*, *Titanoides gidleyi*, *Unuchinia* sp., and *Viverravus** (*V.* cf. *V. schaffi*).

FIGURE 6 — Correlation of West Polecat Bench and Foster Gulch sections to Southeast Polecat Bench section. Levels for Chron C26n, and Princeton and Schaff quarries in West Polecat Bench section are based on limestone marker-bed trace between Princeton Quarry and main WB section (Figs. 3 and 5; Appendix II). Meter levels are relative to Cretaceous-Paleogene boundary. Age scale is in 100 kyr intervals based on cubic spline interpolation between polarity zone boundaries calibrated to GPTS-04 (Secord et al., 2006). All rocks shown are Fort Union Formation. "Base from WB" refers to instances where a biozone boundary was better constrained in the West Bench Section and correlated to the Southeast Polecat Bench Section based on stratigraphic position. Solid and dashed arrows show magnetostratigraphic and biostratigraphic tie points, respectively, among sections. Magnetostratigraphy adapted from Butler et al. (1981, 1987) and Secord et al. (2006). Biozone symbols follow Figure 7. SC symbols denote University of Michigan vertebrate localities. Vertical bars show locality thicknesses. Abbreviations: *CC*, chert conglomerate; *ML*, Mantua Lentil; *RBQ*, Rock Bench Quarry beds; *LMA*, land-mammal age; *Clark*, Clarkforkian; *Pu*, Puercan; *Torr*, Torrejonian.


Southeast Polecat Bench
West Polecat Bench
Foster Gulch
Ma
Member
Chron
LMA
Biozone
Meters
Mud vf f m c
Mud Sandstone
57.0
58.0
59.0
60.0
61.0
61.6
K-P
Silver Coulee beds
CC
RBQ
ML
C25n
C25r
C26n
C26r
C27n
Clark
Tiffanian
Torr
Pu
Cf-1
Ti-6
Ti-5b
Ti-5a
Ti-4b
Ti-4a
Ti-3
Ti-2?
Ti
SC-83, lowest rodent
Covered
Covered
Cf-1 base from WB
SC-377
SC-086
SC-223
Ti-6 base from WB
Ti-5b base from WB
SC-252
SC-242
SC-228
lowest *Probathyopsis*
SC-246
SC-239
Ash above road cut
SC-240
SC-243 Anthills
USNM 42041 flora
Belt Ash (331 m)
SC-261
SC-262
SC-412
SC-415
SC-263
SC-429, *Phenacodus*
unconformity
SC-264
Rock Bench Quarry (70 m)
Silcrete (54 m) Grimy Gulch flora (56 m)
Probable unconformity
Mantua Quarry
Covered
SC-179, 362
lowest rodent
SC-181
Bluff Top Q.
SC-402
SC-191
SC-185
Y2K Quarry
SC-165
Princeton Q.
Schaff Q.
SC-274, lowest *Probathyopsis*
SC-417
SC-423
SC-424
SC-283, 397
Fossil Hollow
Croc Tooth Q.
Divide Q.
Covered
Cedar Point Q.
unconformity

Last occurrences: *Dissacus* cf. *D. navajovius*, *Leptonysson orthius* n. sp., and *Paleotomus radagasti*. Possibly also *Aphanocyon codyensis* gen. et sp. nov.

Known only in the *P. churchilli* zone: *Carpodaptes stonleyi*, *Carpomegodon jepseni*, cf. *Leptacodon choristus* n. sp., and *Nannodectes* sp.

Additional species present: *Ectocion cedrus*, *Ignacius frugivorus*, *Labidolemur soricoides*, *Peradectes* sp., and *Thryptacodon australis*.

Phenacolemur interval zone (Ti-4b) — The *Phenacolemur* zone is the interval between the first occurrences of *Phenacolemur* and *Probathyopsis*. Ti-4b is best represented by Croc Tooth Quarry in Foster Gulch, and by SC-243 and Fossil Hollow (SC-198) on the southeast and western sides of Polecat Bench (Figs. 3, 4, 5). It should be noted that Fossil Hollow was previously thought to be in the *P. simonsi* zone above Princeton Quarry (Ti-5, Gingerich, 2001, Fig. 2, p. 40). However, new measured sections clearly indicate that Fossil Hollow is well below Princeton Quarry (Fig. 6). Placement of Fossil Hollow above Princeton Quarry extended the ranges of several taxa into Ti-5 that last occur in Ti-4b.

The most common species of *Phenacolemur* in the *Phenacolemur* zone is *P. archus* n. sp. which is known from several localities, including the representative ones given above. The new species co-occurs with *P. pagei* at Fossil Hollow based on specimens in the YPM collections.

First occurrences: *Arctocyon* cf. *A. nexus*, *Carpolestes* (*C.* cf. *C. dubius*), *Cyriacotherium argyreum*, *Didymictis dellensis*, *Dipsalodon* (*D. churchillorum*), *Ectocion mediotuber**, *Ectoganus* (*E. lobdelli*), *Lambertocyon eximius**, *Phenacolemur pagei*, *Prochetodon cavus**, *Thryptacodon pseudarctos*, and *Viverravus schaffi*. *Carpolestes* and *Dipsalodon* are distinctive genera and their first occurrences may be especially useful. *Ectoganus* is a relatively rare taxon known only from floodplain deposits and may have been restricted to specialized environments.

Last occurrences: *Aaptoryctes* cf. *A. ivyi*, *Arctocyon mumak*, *Bessoecetor pilodontus* n. sp., *Chiromyoides caesor*, *Ectocion cedrus**, *Haplolambda* cf. *H. quinni*, *Ignacius frugivorus*, *Lambertocyon* (*L. eximius*), *Leptolambda churchilli*, *Neoplagiaulax mckennai*, *Ptilodus* (*P. kummae*), and *Titanoides gidleyi*. *Ptilodus* is one of the most common elements in many Ti-4 and older Tiffanian and Torrejonian zones, and its last occurrence in Ti-4b is an important biostratigraphic datum. *Neoplagiaulax mckennai* is an easily recognized Ti-4 index species.

Known only in the *Phenacolemur* zone: *Phenacolemur archus* n. sp. and *Plesiadapis* cf. *P. fodinatus**.

Additional species present: *Adunator minutus*, *Phenacodus grangeri*, *Phenacodus magnus*, and *Plesiadapis churchilli*.

Probathyopsis interval zone (Ti-5a) — The *Probathyopsis* zone is the interval between the first occurrences of *Probathyopsis* and *Plesiadapis simonsi*. The type area is on the west side of Polecat Bench. Princeton and Schaff quarries are representative faunas. *Phenacodus vortmani* is potentially useful for recognition or corroboration of Ti-5a. It first occurs at approximately the same level as *Probathyopsis* (Fig. 8) and does not appear to occur in earlier faunas outside the Bighorn Basin (Thewissen, 1990).

*Probathyopsis*s was recently synonymized with *Prodinoceras* by Lucas and Schoch (1998) following Schoch and Lucas (1985). I follow Thewissen and Gingerich (1987), however, and recognize *Probathyopsis* as a valid genus.

Placement of the base of Ti-5a on the southeast and west sides of Polecat Bench is based on locality data from specimen labels for YPM-PU 18342 (NW1/4, S10, T56N, R99W) and 18843 (SW1/4, S15, T57, R100), respectively. Both these specimens occur lower than any in the UM collections, but UM samples for localities at these levels are small. Although there is reason to be cautious of locality data associated with some YPM-PU specimens (e.g., Butler et al., 1981, p. 305), placement of the base of Ti-5a based on these specimens, relative to the top of Chron C26n, is in good agreement on both sides of Polecat Bench. YPM-PU 18342 and 18843 put the first occurrence of *Probathyopsis* at ~25 and 45 m above the top of C26n on the southeast and west sides of Polecat Bench, respectively (Fig. 6). The provenance of an additional specimen purportedly collected at a lower level is less certain. YPM-PU 18350 is labeled as coming from Fossil Hollow, which, if correct would lower the base of the *Probathyopsis* zone on the west side of Polecat Bench by ~85 m (~65 m in the composite section). Jepsen's 1937 unpublished field notes indicate that the tooth (in notes as *Titanoides*?) is from the "same level as Fossil Hollow." Fossil Hollow is geographically removed from other localities in the area, however, and there are few fossiliferous exposures nearby. Additionally, "Fossil Hollow level" is written on the labels of some specimens from localities that are actually 75 meters higher in the area near Schaff Quarry. Thus, the provenance of the purported Fossil Hollow specimen is in doubt. *Probathyopsis* is not known from any Ti-4 faunas outside the Bighorn Basin (Lofgren et al., 2004, Table 3.2, *Prodinoceras*) and, while its range may be extended downward with additional collecting, it seems unlikely that it will be found as low as the *P. churchilli* zone.

First occurrences: *Arctodontomys* sp., Arctostylopidae (*Arctostylops steini*), *Carpolestes dubius**, Dinocerata (*Probathyopsis harrisorum*), *Dissacus argenteus*, *Ectypodus powelli*, *Leptacodon packi*, *Litolestes ignotus*, *Microcosmodon conus*, *Neoliotomus conventus*, *Parectypodus laytoni*, *Phenacodaptes sabulosus*, *Phenacodus vortmani*, *Plesiadapis fodinatus**, *Princetonia* cf. *P. yalensis*, *Prodiacodon* cf. *P. tauricinerei*, *Unuchinia* cf. *U. dysmathes*, and *Viverravus laytoni*.

Last occurrences: *Dipsalodon churchillorum*, *Ectoganus* cf. *E. lobdelli**, *Peradectes elegans*, *Phenacodus magnus*, *Plesiadapis churchilli**, and *Thryptacodon australis*.

Known only in the *Probathyopsis* zone: *Adunator abditus* n. sp., *Micromomys gunnelli* n. sp., *Micromomys silvercouleei*, *Mimetodon churchilli*, *Neoplagiaulax hazeni*, *Paleotomus* cf. *P. radagasti*, *Pentacosmodon pronus*, *Prodiacodon paucus* n. sp., *Propalaeanodon schaffi*, *Wyonycteris microtis* n. sp., and *Wyonycteris galensis* n. sp.

Additional species present: *Adunator minutus*, *Aletodon* sp., *Arctocyon* cf. *A. nexus*, *Chiromyoides* cf. *C. caesor*, *Cyriacotherium argyreum*, *Didymictis dellensis*, *Ectocion mediotuber*, *Labidolemur soricoides*, *Palaeoryctes jepseni*, *Phenacolemur pagei*, *Phenacodus grangeri*, *Prochetodon cavus*, *Thryptacodon pseudarctos*, and *Viverravus schaffi*.

Plesiadapis simonsi lineage zone (Ti-5b) — The *P. simonsi* zone is defined as the interval between the first occurrences of *P. simonsi* and *P. gingerichi*. Y2K Quarry is the most representative sample, but there are few taxonomic differences between it and Princeton and Schaff quarries. *Plesiadapis simonsi* is an uncommon species that appears to be an evolutionary intermediate between *P. churchilli* and *P. gingerichi*. It is not well known dentally and is distinguished from closely related species primarily by size. The *P. simonsi* zone is best represented on the west side of Polecat Bench, although the type of *P. simonsi* (YPM-PU 17814) comes from Sand Draw in the Foster Gulch area (Fig. 1). For decades *Plesiadapis simonsi* was the defining "Ti-5" taxon and the base of the *P. simonsi* zone was placed below Princeton Quarry (e.g., Gingerich, 1976; Archibald et al., 1987). As discussed in Chapter 3, the identification of specimens of intermediate size between *P. simonsi* and *P. churchilli* makes recognition of a zone boundary somewhat arbitrary. Specimens that are well within the expected size range of *P. simonsi* do not occur until the SC-165 level above Princeton Quarry, which is where I place the boundary.

Plesiadapis simonsi has not been identified outside of the Bighorn Basin, presumably due to the paucity of fossiliferous deposits of this age.

First occurrences: *Plesiadapis* cf. *P. dubius**.

Last occurrences: *Adunator minutus*, *Arctodontomys* sp., *Carpolestes dubius**, *Labidolemur soricoides*, *Leptacodon packi*, *Litolestes ignotus*, *Microcosmodon conus**, *Palaeoryctes jepseni*, *Prochetodon cavus**, *Plesiadapis fodinatus**, *Unuchinia* (*U.* cf. *U. dysmathes*), and *Viverravus schaffi*.

Known only in the *P. simonsi* zone: cf. *Plagiomene zalmouti* n. sp., *Micromomys millennius* n. sp., *Mylanodon rosei*, and *Plesiadapis simonsi**.

Additional species present: *Arctocyon* cf. *A. nexus*, *Arctostylops steini*, *Cyriacotherium argyreum*, *Didymictis dellensis*, *Ectocion mediotuber*, *Ectypodus powelli*, *Parectypodus laytoni*, *Phenacodaptes sabulosus*, *Phenacodus grangeri*, *Phenacodus vortmani*, *Phenacolemur pagei*, *Princetonia* cf. *P. yalensis*, *Probathyopsis harrisorum*, *Prodiacodon* cf. *P. tauricinerei*, and *Thryptacodon pseudarctos*.

Plesiadapis gingerichi interval zone (Ti-6) — The *Plesiadapis gingerichi* zone is defined as the interval between the first occurrences of *Plesiadapis gingerichi* and Rodentia. The most representative area is on the western side of Polecat Bench. *Plesiadapis gingerichi* is an uncommon species. It is distinguished from *P. simonsi* primarily by its larger size. The lower boundary was placed at the first occurrence of a *Plesiadapis* molar (UM 110113) that was well within the expected size range of *P. gingerichi*.

Carpolestes nigridens first occurs at approximately the same time as *Plesiadapis gingerichi*, but a P^3 or a dentary preserving anterior teeth or alveoli is necessary to distinguish it from the earlier *C. dubius* (see systematic section), diminishing its biostratigraphic utility. Samples from Ti-6 are small and were mostly collected as lag weathering from mudstones, although a few specimens were quarried in the upper part of the zone (Bluff Top Quarry, SC-379). *Plesiadapis gingerichi* is not known outside the Bighorn Basin, with the exception of a single specimen

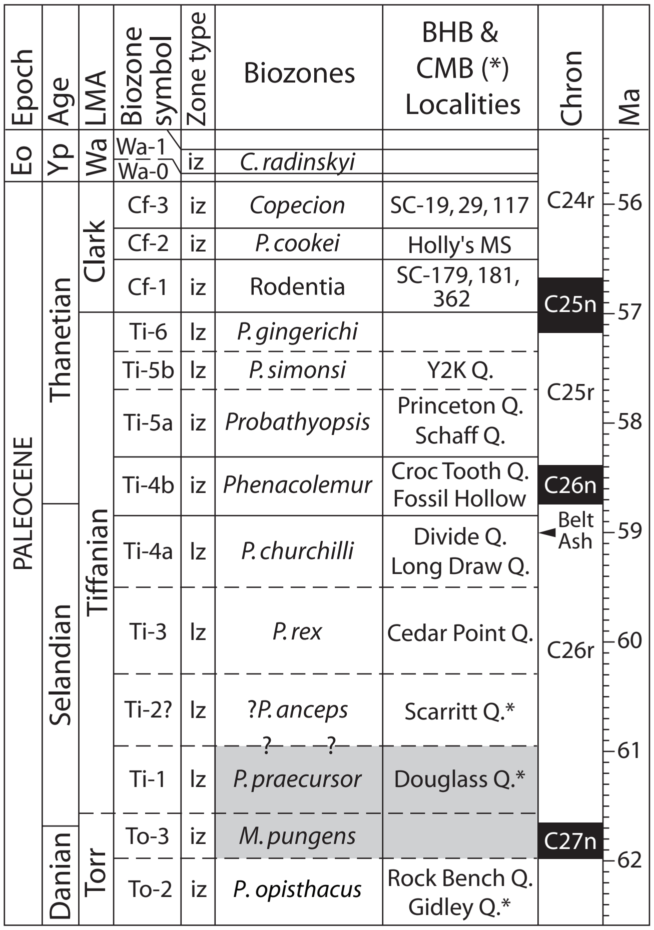


FIGURE 7 — Geochronologic chart showing middle to late Paleocene biozones and important fossil localities in the northern Bighorn and Crazy Mountains Basins. Biozones are named after taxon that defines base; succeeding taxon defines top. Revised biozone boundaries for Ti-2 to Cf-3 were calibrated by cubic spline interpolation (see Secord et al., 2006) between polarity chron reversal ages of Ogg and Smith (2004) and P-E boundary age (55.8 Ma) of Luterbacher et al. (2004). Localities with asterisks are in the Crazy Mountains Basin. Shaded intervals represent biozones in the San Juan Basin (*M. pungens*; Williamson, 1996; Lofgren et al., 2004) and Crazy Mountains Basin (*P. praecursor*; Gingerich, 1976, 1983; Hartman and Krause, 1993) that have not been recognized in the northern Bighorn Basin. Rock Bench and Gidley quarries have been correlated to the *P. opisthacus* zone based on faunal content (Lofgren et al., 2004), but *P. opisthacus* has not been found at these localities. Ages for bases of To-3 and Ti-1 were estimated from positions relative to magnetic polarity chrons in Williamson (1996) and Butler et al. (1987). Zone types follow ISSC (1994) and NACSN (2005): interval zones (iz) based on first occurrences of taxa not closely related to preceding or succeeding zone taxa; lineage zones (lz) based on evolutionary lineages of *Plesiadapis*; Abbreviations: *C.*, *Cardiolophus*; *Clark*, Clarkforkian; *Eo*, Eocene; *LMA*, land-mammal age; *M.*, *Mixodectes*; *MS*, microsite; *P.*, *Plesiadapis* for Ti zones, *Protoselene* for To-2; *Q.*, Quarry; *Torr*, Torrejonian; *Wa*, Wasatchian; *Yp*, Ypresian.

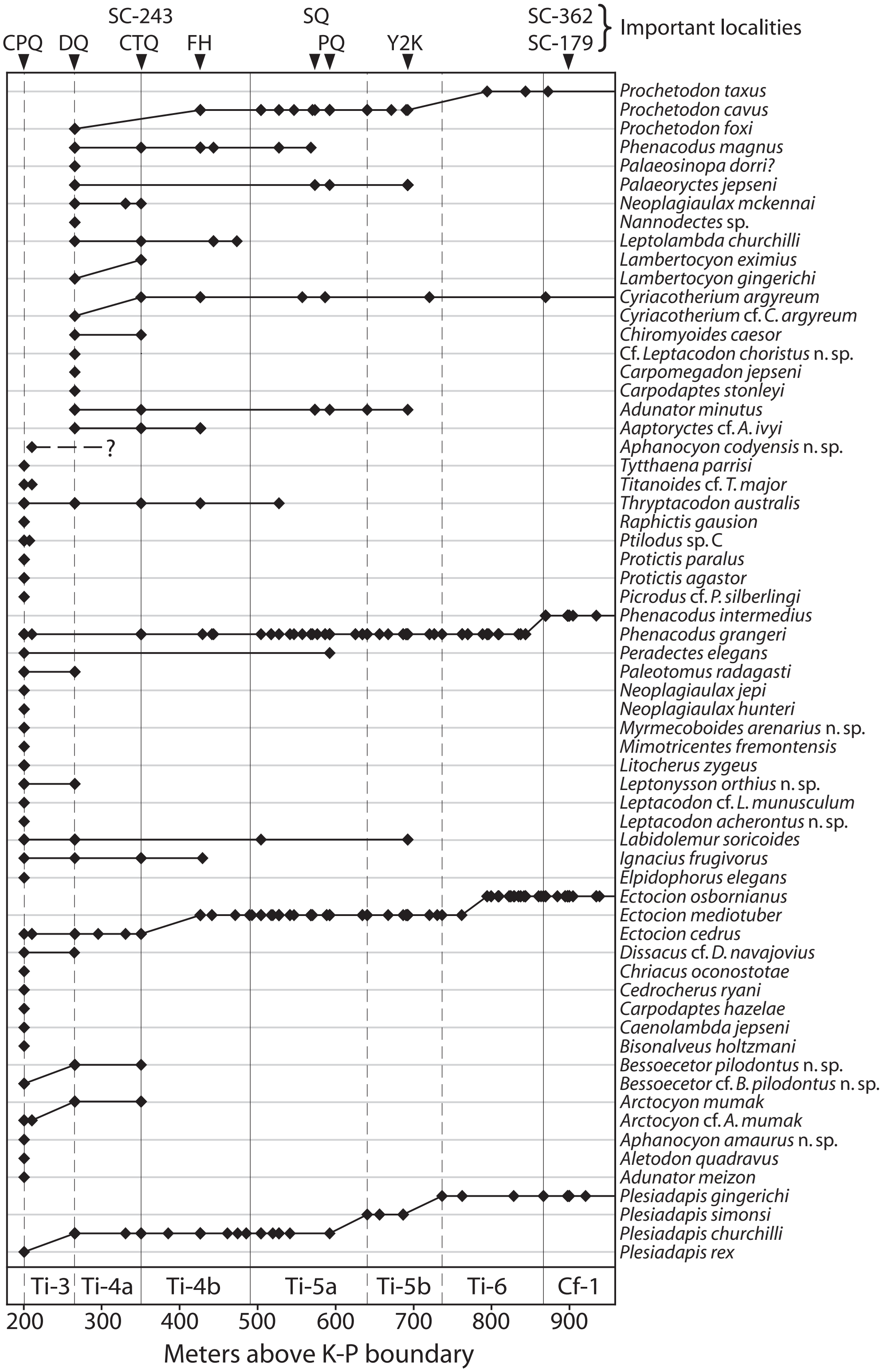
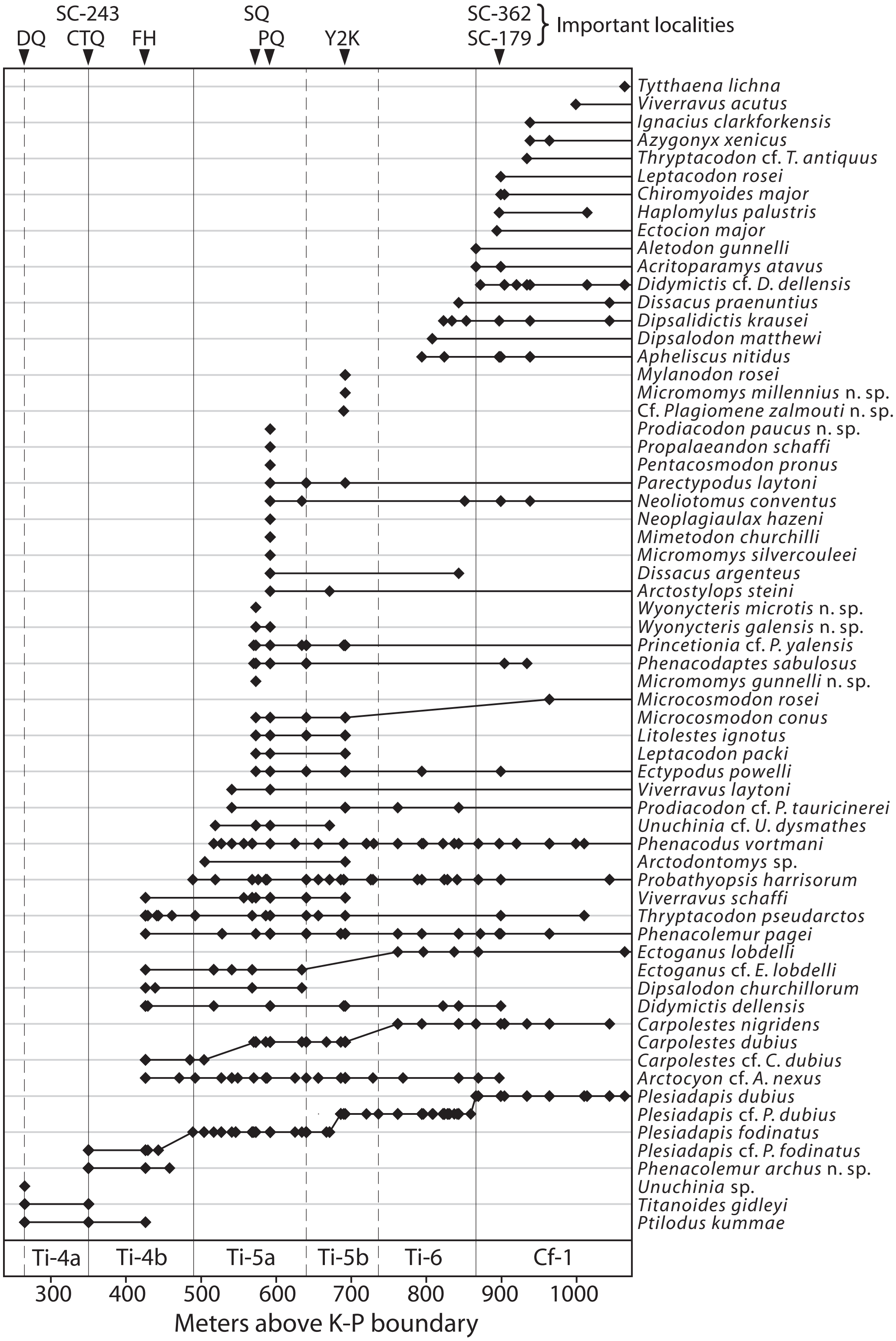


FIGURE 8 — Composite stratigraphic chart showing occurrences of middle Tiffanian to early Clarkforkian mammal species in the northern Bighorn Basin. Localities are in the Polecat Bench, Sand Coulee, and Foster Gulch areas (Figs. 1, 3, and 4). Data were compiled from sections in Figure 6. Meter levels for West Polecat Bench section were normalized to Southeast Polecat Bench section between top of C26n and base of C25n, resulting in minor adjustments. Bear Creek fauna in southern Montana is not shown but includes additional early



Clarkforkian (Cf-1) first occurrences of *Labidolemur kayi* and *Leipsanolestes* (*L. siegfriedti*), and singular occurrences of *Planetetherium mirabile* and *Protentomodon ursirivalis* (Simpson, 1928, 1929a, b; Gunnell and Bartels, 2001). *Chiromyoides gingerichi* n. sp. may also first occur at Bear Creek. Biozone abbreviations as in Figure 7. Connected lines show species in presumed evolutionary lineages. Quarries: *CPQ*, Cedar Point; *CT*, Croc Tooth; *DQ*, Divide; *PQ*, Princeton; *SQ*, Schaff; and *Y2K*, Y2K. *FH*, Fossil Hollow (SC-198).

(NMNH 170895) recently re-identified as *P. gingerichi* from the Wind River Basin of Wyoming (McKenna and Lillegraven, 2005; p. 38).

First occurrences: *Apheliscus nitidus*, *Carpolestes nigridens**, *Dipsalidictis krausei*, *Dipsalodon matthewi*, *Dissacus praenuntius*, *Ectocion osbornianus**, *Ectoganus lobdelli**, *Plesiadapis gingerichi**, and *Prochetodon taxus**.

Last occurrences: *Dissacus argenteus*, *Ectocion mediotuber**, *Phenacodus grangeri**, and *Plesiadapis* cf. *P. dubius**.

Additional species present: *Arctocyon* cf. *A. nexus*, *Didymictis dellensis*, *Ectypodus powelli*, *Neoliotomus conventus*, *Phenacodus vortmani*, *Phenacolemur pagei*, *Probathyopsis harrisorum*, and *Prodiacodon* cf. *P. tauricinerei*.

Rodentia interval zone (Cf-1) — The Rodentia zone is defined as the interval between the first occurrences of Rodentia and *Plesiadapis cookei*. The zone is best represented along the western margin of Polecat Bench. The earliest known rodent is represented by a single upper molar from a freshwater limestone from SC-181. At least two rodent species are present at SC-179, a large species, representing *Acritoparamys atavus* (see systematics), and an undescribed smaller species (see Bloch, 2001, pp. 111-112). The base of the Rodentia zone at SC-181 is ~3 m above a prominent marker-lignite that crops out over an area of ~2 km^2 (Fig. 5).

The base of the Rodentia zone is well exposed along the western margin of Polecat Bench, but most of the zone above this level is covered by vegetation. *Plesiadapis cookei*, is found just above the covered interval and defines the base of the succeeding zone (Cf-2). The largest sample from a single locality in the Rodentia zone in the Bighorn Basin is a surface collection from SC-179 consisting of 74 identified mammal teeth or jaws. A sequence of localities ~11 km northwest of Polecat Bench (e.g., SC-226 to SC-172) may preserve most of Cf-1, but fossil samples are small and correlation to the main sections is imprecise.

An important correlative of Cf-1 within the Bighorn Basin is the Bear Creek fauna from southern Montana (Simpson, 1928, 1929a,b; Rose, 1981a, Table 52), which was collected from the Eagle Coal Mine and represents a rarely sampled environment (Gunnell and Bartels, 2001, pp. 150-151). A potential correlative outside the Bighorn Basin is Big Multi Quarry in the Washakie Basin, which contains the most diverse sample of Clarkforkian mammals known from a single locality (Wilf et al., 1998). Although this sample contains some species that suggest equivalence to Cf-1, it also contains a large species of *Plesiadapis* that is almost certainly *P. cookei*. The combination of species suggests that it samples a temporal interval possibly equivalent to Paint Creek (SC-143, early Cf-2) or the upper part of Cf-1 in the Bighorn Basin.

First occurrences: *Acritoparamys atavus*, *Aletodon gunnelli*, *Chiromyoides major*, *Chiromyoides gingerichi* n. sp., *Didymictis* cf. *D. dellensis*, *Ectocion major*, *Azygonyx xenicus*, *Haplomylus palustris*, *Ignacius clarkforkensis*, *Labidolemur kayi*, *Leptacodon rosei*, *Leipsanolestes* (*L. siegfriedti*), *Microcosmodon rosei**, *Phenacodus intermedius**, *Plesiadapis dubius**, *Thryptacodon* cf. *T. antiquus*, *Tytthaena lichna*, and *Viverravus acutus*.

Last occurrences: *Arctocyon* (*A.* cf. *A. nexus*), *Carpolestes nigridens**, *Didymictis dellensis*, *Phenacodaptes sabulosus*, *Plesiadapis gingerichi**, and *Thryptacodon pseudarctos*.

Known only in the Rodentia zone: *Haplomylus palustris*, *Planetetherium mirabile*, and *Protentomodon ursirivalis*. The last two of these species are known only from Bear Creek and their presence is apparently controlled by environmental factors.

Additional species present: *Apheliscus nitidus*, *Cyriacotherium argyreum*, *Dipsalidictis krausei*, *Dissacus praenuntius*, *Ectocion osbornianus*, *Ectoganus lobdelli*, *Ectypodus powelli*, *Neoliotomus conventus*, *Phenacodus intermedius*, *Phenacodus vortmani*, *Phenacolemur pagei*, *Probathyopsis harrisorum*, and *Prochetodon taxus*.

Copecion interval zone (Cf-3) — The *Copecion* zone is the interval between the first occurrences of *Copecion* and *Meniscotherium* (see Gingerich, 2001, for discussion of *Meniscotherium* zone). Secord et al. (2006) replaced the *Phenacodus-Ectocion* acme zone of Rose (1980; 1981a) and Gingerich (2001) with the *Copecion* zone. The first occurrence of *Copecion* is slightly below (~15 m) the last appearance of *P. cookei*, and both taxa co-occur at SC-177. For this reason, reports before Secord et al. included *Copecion* in Cf-2 (Thewissen, 1990, p. 66; Lofgren et al., 2004). Additionally, several productive localities that were previously in the *P. cookei* range zone (SC-19, SC-62, SC-117, Rose, 1981a) are now in the *Copecion* zone. Faunal differences between the *Copecion* zone and the *Plesiadapis cooke*i zone are notably minor, in spite of large collections (> 1000 UM specimens).

First occurrences: *Copecion brachypternus*, *Dipsalidictis platypus*, *Dipsalidictis transiens*, *Hyopsodus* sp., and *Azygonyx grangeri**. *Mimoperadectes labrus* may also first occur in this interval but the only potentially referable specimen is too fragmentary for confident identification (Rose, 1981a, p. 36).

Last occurrences: *Aletodon* (*A. gunnelli*), *Apheliscus nitidus**, *Arctostylopidae* (*Arctostylops steini*), *Carpolestidae* (*Carpolestes simpsoni*), *Dipsalidictis aequidens*, *Dipsalidictis krausei*, *Dipsalodon* (*D. matthewi*), *Ectocion major*, *Ectypodus powelli*, *Azygonyx ancylion**, *Haplomylus simpsoni*, *Ignacius clarkforkensis**, *Microcosmodon* (*M. rosei*), *Palaeoryctes** (*P. punctatus*), *Plagiomene accola*, *Plesiadapidae* (*Chiromyoides major*, *Plesiadapis cookei*, *P. dubius*), *Probathyopsis* (*P. praecursor*), *Viverravus laytoni*, and *Worlandia* (*W. inusitata*).

Known only in *Copecion* zone: Cf. *Icaronycteris*, *Ceutholestes dolosus*, *Cyriacotherium psamminum*, *Limaconyssus habrus*, *Titanoides nanus*, and *Wyonycteris chalix*.

Additional species present: *Acritoparamys atavus*, *Acritoparamys atwateri*, *Adunator* cf. *A. minutus*, *Arctodontomys* cf. *A. wilsoni*, *Chriacus* sp., *Coryphodon proterus*, *Didymictis proteus*, *Dissacus praenuntius*, *Ectocion osbornianus*, *Ectoganus lobdelli*, *Labidolemur kayi*, *Leptacodon rosei*, *Microparamys cheradius*, *Neoliotomus* sp., *Niptomomys doreenae*, *Palaeanodon parvulus*, *Palaeonictis peloria*, *Palaeosinopa* sp., *Paramys taurus*, *Peradectes* sp., *Phenacodus intermedius*, *Phenacodus vortmani*, *Phenacolemur praecox*, *Plagioctenodon* sp., *Princetonia* sp., *Prodiacodon* cf. *P. tauricinerei*, *Thryptacodon* cf. *T. antiquus*, *Tinimomys graybulliensis*, *Uintacyon rudis*, *Viverravus acutus*, and *Viverravus politus*.

III

SYSTEMATIC MAMMALIAN PALEONTOLOGY

This section describes the systematic paleontology of specimens from localities of Tiffanian and early Clarkforkian age in the Polecat Bench stratigraphic sequence and from quarries in the Foster Gulch area, southeast of Polecat Bench (Fig. 1). Emphasis is on late Tiffanian (Ti-4a to Ti-6) species and not all species included in the faunal list for Cedar Point Quarry (Appendix IA) are discussed here. All cataloged specimens of this age in the UM collections are included here, as well as many specimens collected by Princeton crews that are now curated in the YPM collections (YPM-PU). Specimens from the middle and late Clarkforkian are usually not included in referred specimen lists, but most were reported by Rose (1981a). Higher level taxonomy and taxonomic organization generally follows McKenna and Bell (1997).

Class MAMMALIA Linnaeus, 1758
Order MULTITUBERCULATA Cope, 1884
Superfamily PTILODONTOIDEA Cope, 1887
Family PTILODONTIDAE Cope, 1887

PARECTYPODUS Jepsen, 1930a

Parectypodus laytoni (Jepsen, 1940)
Table 2

Ectypodus laytoni Jepsen, 1940, p. 296.
Parectypodus laytoni, Sloan, 1966, p. 310. Krause, 1980, p. 1173.

Holotype.— YPM-PU 14464, left and right maxillae with left P^2-M^3 and right P^{1-4}, and a right dentary with P_3-M_1, from Princeton Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a), *Plesiadapis simonsi* (Ti-5b), and *Plesiadapis cookei* (Cf-2) zones.

Description.— Detailed descriptions of *Parectypodus laytoni* were provided by Jepsen (1940) and Krause (1980).

Discussion.— *Parectypodus laytoni* was originally placed in *Ectypodus* by Jepsen (1940). Sloan (1966) later referred the species to *Parectypodus*, which has been followed by subsequent authors.

Parectypodus laytoni is a relatively rare species. The holotype from Princeton Quarry is by far the most complete specimen known. Two P_4s from SC-165, a locality slightly younger than Princeton Quarry, compare favorably with the holotype. The P_4s are distinguished from those of contemporary *E. powelli* by a greater distance between the anterior basal concavity and the first serration, a greater number of serrations, a straighter anterior margin, a steeper posterior margin, and a less distinct posterobuccal ledge. These characters were used by Krause (1980, p. 1173) to distinguish the species in Clarkforkian faunas. Precise serration counts for SC-165 specimens were not possible due to their condition, but UM 81699 appears to have had 13 or 14 serrations and UM 81700 probably had 12. Serration counts in the type sample of *P. laytoni* ranged from 12 to 14 with a mean of 12.4 (n = 8, Jepsen, 1940). The P_3 in UM 81699 is small compared with the size of the anterior basal concavity, as is P_3 in the holotype. UM 81699 has a slightly more curved posterior profile and a more arcuate lateral profile than the holotype, but these differences are presumably within intraspecific variability and I include both of the SC-165 specimens in *P. laytoni*.

It is not clear if isolated teeth of *Parectypodus laytoni*, other than upper fourth premolars, can be confidently distinguished from those of *Ectypodus powelli*. Nevertheless, I tentatively include a single P^4 (UM 109567) from Y2K Quarry in *P. laytoni*. The P^4 in the holotype of *P. laytoni* is longer and relatively narrower (higher length/width ratio) than that of *E. powelli*. Length/width ratios in the holotype and UM 109567 are 3.5 and 3.2, respectively, compared with a range of 2.6 to 3.0 (n = 8) in the Clarkforkian sample of *E. powelli* based on the measurements by Krause (1980, Table 4). UM 109567 differs further from most specimens of *E. powelli* in having eight cusps in the medial row and in having a buccal row of cusps that extends more than half the total P^4 length. Only one in eight specimens of *E. powelli* measured by Krause (1980, Table 4) had eight cusps. A more confident identification is not possible until P_4s of *P. laytoni* are recovered and the variability of *E. powelli* at Y2K Quarry is known.

Referred specimens.— **SC165** (wash): UM 81699, R dent. P_{3-4}; 81700, L P^4. **Y2K Q.** (SC389): UM 109567, R P^4.

NEOPLAGIAULAX Lemoine, 1882

Neoplagiaulax jepi Sloan, 1987
Table 3

Neoplagiaulax jepi Sloan, 1987, p. 192.

Holotype.— YPM-PU 21058, R P_4 from Cedar Point Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description.— A description of *Neoplagiaulax jepi* was provided by Sloan (1987).

Discussion.— Nine P_4s in the UM collections from Cedar Point Quarry compare favorably with the description and metric

TABLE 2 — Dental measurements for *Parectypodus laytoni* from the Clarks Fork Basin. *Y2K Q.*, Y2K Quarry. Measurements follow Figure 2.

		P^4 L	P^4 W	P^4 C	P_4 L	P_4 L_1	P_4 H_s	P_4 H_t	P_4 D	P_4 W
UM 81699	SC-165	—	—	—	3.17	0.57	1.20	1.43	1.40	1.28
UM 81700	SC-165	—	—	—	3.15	0.55	1.15	—	1.30	1.23
UM 109567	Y2K Q.	2.90	0.90	4:8:0	—	—	—	—	—	—
YPM-PU 14464 (type)		2.53	0.73	9:9:5	2.90	0.45	1.20	1.30	1.25	1.02

TABLE 3 — Dental statistics for *Neoplagiaulax jepi* from Cedar Point Quarry. Measurements follow Figure 2. Abbreviations: *max.*, maximum; *min.*, minimum; *n*, sample size; *SD*, standard deviation of sample; *SE*, standard error of mean; *V*, coefficient of variation.

		n	Min.	Max.	Mean	SE	SD	V
P_4	L	7	4.35	4.88	4.64	0.08	0.20	4.30
	W	6	1.65	2.13	1.88	0.06	0.15	7.79
	L_1	6	0.70	0.93	0.84	0.02	0.06	7.10
	H_s	6	1.50	1.70	1.58	0.02	0.06	3.54
	H_t	6	1.77	1.97	1.89	0.04	0.09	4.73
	D	6	1.75	2.40	2.21	1.10	0.25	11.16

data provided by Sloan (1987) for *N. jepi*. Sloan listed 12 serrations for all specimens. Four of five specimens in the UM collections for which cusp counts are possible also have 12 serrations, but UM 82062 has 13. The P_3 is preserved in UM 64423 and is little more than a short peg with a slight apical swelling. It appears to have no enamel.

Referred specimens.— **Cedar Point Q.**: UM 64423, R dent. I_1-P_4; 82050, L P_4; 82056, R P_4; 82057, L P_4; 82062, R P_4; 82098, R P_4; 83247, R P_4; 110938, L P_4; 110939, R P_4. Additional specimens listed by Sloan (1987): YPM-PU 21046, 21053, 21054, 21055, 21056, 21057a, 21057b, 21058.

Neoplagiaulax hunteri (Simpson, 1936)

Ectypodus hunteri Simpson, 1936, p. 6.

Holotype.— AMNH 33865, right dentary with incisor, P_4-M_2, from Scarritt Quarry (Ti-2), Crazy Mountains Basin, Montana.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description.— Descriptions of *Neoplagiaulax hunteri* were provided by Simpson (1939), Krause (1977), and Sloan (1987).

Discussion.— Three specimens in the YPM collections were referred to *Neoplagiaulax hunteri* by Rose (1981a, Table 40) from Cedar Point Quarry, but were not available for study. Two specimens in the UM collections from Cedar Point Quarry compare favorably with descriptions and illustrations of *N. hunteri*. UM 82097 (P_4) has 15 serrations and a distinctive break in slope after the eighth serration. It agrees well with the P_4s of *N. hunteri* illustrated by Krause (1977, Plate 5) and Sloan (1987, Fig. 11). UM 109627 from SC-262 is the anterior part of a P_4 that also compares favorably to *N. hunteri*. Although fragmentary, it is biostratigraphically important, as it is from one of the only localities at Polecat Bench that samples the *Plesiadapis rex* zone.

Referred specimens.— **Cedar Point Q.**: UM 82097, R P_4; 108835, L P_4 partial. **SC262**: UM 109627, R P_4 ant. half.

Neoplagiaulax mckennai Sloan, 1987

Neoplagiaulax mckennai Sloan, 1987, p. 192.

Holotype.— AMNH 86750, right dentary with $P_{3\text{-}4}$, M_1 alveolus, and M_2 crypt. From Love Quarry, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a) and *Phenacolemur* (Ti-4b) zones.

Description.— A description of *Neoplagiaulax mckennai* was provided by Sloan (1987).

Discussion.— Two P^4s from Divide Quarry compare favorably with the description, figures, and metric data provided by Sloan (1987) for *Neoplagiaulax mckennai* and are identified here as that species. The P^4 of *N. mckennai* differs from those of most other species of *Neoplagiaulax* in being wider, relative to length, and in lacking an external cusp or row of cusps. Both of the specimens from Divide Quarry lack an external cusp and have a low length/width ratio. P^4s of *N. hunteri* and *N. cimolodontoides* have a variably present external cusp (Krause, 1977; Scott, 2005) but are smaller and more anteroposteriorly elongate than the P_4 of *N. mckennai*. I have also include a P_4 from SC-340 at Polecat Bench in *N. mckennai*. UM 83561 has the distinctive break in slope along its posterior margin that is characteristic of *N. mckennai* (see Sloan, 1987). It is broken along the posterior margin, preventing precise measurement, but it is probably small for the species. I tentatively include YPM-PU 25031 (P_4) in *N. mckennai* because of general agreement in size and form to the holotype, although it could belong to an undescribed species. It has a very deep exodaenodont lobe and a relatively steep anterior profile. The posterior profile has a deep concavity from wear, but appears to have had the distinctive break in slope characteristic of *N. mckennai*.

More definite identifications cannot be made without knowing the variability in *N. mckennai*. A relatively large sample of *N. mckennai* was collected from Olive Quarry, Montana (Sloan, 1987), but is mostly undescribed. Sloan also indicated that *N. mckennai* was known from Long Draw and Croc Tooth quarries in the northern Bighorn Basin, but he cited no specimen numbers. Multituberculates from these localities curated at YPM were not available for study.

Dental measurements (mm).— UM 85306: P^4, L = 3.79, W = 2.00, C = 0:9:0. UM 110242: P^4, L = 3.75, W = 1.76, C = 0:7:0. YPM-PU 25031: P_4, L = 5.35, W = 2.20, H_t = 2.33, D = 2.70.

Referred specimens.— **Divide Q.** (FG046): UM 85306, L P^4; 110242, R P^4. **Sec. 5?**, **T54N**, **R95W** (PU field #574): YPM-PU

TABLE 4 — Dental measurements for *Neoplagiaulax hazeni* from Princeton Quarry (holotype and YPM-PU 14422; from casts) and for *N.* cf. *N. hazeni* from zones Ti-4a and Ti-4b. Measurements follow Figure 2. *Estimate.

		UM 73397	UM 73619	UM 77300	UM 77323	UM 85365	UM 86243	UM 91321	YPM-PU 14432 (type)	YPM-PU 14422
P^4	L	—	—	4.46	—	—	—	4.44	4.32	—
	W	—	—	1.67	—	—	—	1.48	1.35	—
	C	—	—	1:10:0	—	—	—	2:–:0	3:9?:0	—
P_4	L	5.25	5.05	—	4.82	4.65	5.28	—	—	5.03
	L_1	0.73	0.63	—	0.77	0.83	0.87	—	—	1.03
	H_s	1.90	1.70	—	1.78	1.80	1.90	—	—	1.90
	H_t	2.20	2.1*	—	2.13	2.30	2.30	—	—	2.2*
	D	2.2*	2.00	—	2.10	2.20	2.1*	—	—	2.00
	W	2.10	1.80	—	1.70	1.85	2.0*	—	—	1.90
	S	13	—	—	13	13	15	—	—	13

25031, L P_4. **SC340**: UM 83561, L P_4 partial. Sloan (1987) also reported *N. mckennai* from Croc Tooth and Long Draw quarries.

Neoplagiaulax hazeni (Jepsen, 1940)

Table 4

Ectypodus hazeni Jepsen, 1940, p. 304.
Neoplagiaulax hazeni, Sloan, 1987, p. 192.

Holotype.— YPM-PU 14432, a right maxilla with P^3 (part), and P^4-M^2, from Princeton Quarry, Wyoming, *Probathyopsis* zone.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* zone (Ti-5a).

Description.— A detailed description of *Neoplagiaulax hazeni* was provided by Jepsen (1940).

Discussion.— Jepsen (1940, p. 304) named *Ectypodus hazeni* based on a small sample of well-preserved specimens from Princeton Quarry. Sloan (1987) later referred the species to *Neoplagiaulax*, which has been followed by subsequent authors. The holotype, an additional P^4, a right lower dentary with I_1-M_1, and a second dentary fragment with $P_{3\text{-}4}$, and M_2, are the only described specimens from Princeton Quarry. No additional specimens that I am aware of have been collected at the Princeton Quarry level or higher. Several teeth from Divide Quarry and strata of approximately equivalent age on the south side of Polecat Bench are similar to those of *N. hazeni*, but may represent an unnamed species. I refer these to *Neoplagiaulax* cf. *N. hazeni* below.

Referred specimens.— **Princeton Q.**: YPM-PU 14323, R dent. I_1-M_1; 14340, L P^4; 14422, L dent. $P_{3\text{-}4}$, M_2; 14432 (holotype).

Neoplagiaulax cf. *N. hazeni*

Table 4

Biostratigraphic occurrences in Bighorn Basin.— ?*Plesiadapis rex* (Ti-3) and *Plesiadapis churchilli* (Ti-4a) zones.

Discussion.— Two P^4s from Divide Quarry (UM 77300 and 91321) are similar to those of *Neoplagiaulax hazeni* and *N. serrator*. However, they differ from *N. hazeni* in having fewer buccal cusps, in the position of the highest cusp, and in being about 10% longer. They have the same cusp count as some specimens of *N. serrator*, recently described by Scott (2005), but differ in being lower crowned, in the position of the highest cusp, and in being about 44% longer. The two P^4s of *N. hazeni* from Princeton Quarry have 3 to 4 buccal cusps and 9 medial cusps, while those from Divide Quarry have 1 or 2 buccal cusps, the most anterior being much smaller, and UM 77300 has 10 medial cusps (Table 4). Jepsen (1940) described the last cusp (ultimate) in P^4 of *N. hazeni* as being the highest (furthest from crown base), although Krause (1977, p. 18) pointed out that on YPM-PU 14340 the penultimate and ultimate cusps were subequal in stature. In UM 77300 the third and fourth cusps from the posterior end are the highest (posterior cusps in UM 91321 were lost to wear). In *N. serrator* the highest cusp can be the prepenultimate, penultimate, or penultimate and ultimate.

The lower blades from Divide Quarry included here differ from the P_4 in *N. hazeni* (YPM-PU 14422) in having a more arcuate lateral profile with a steeper posterior margin. However, two P_4s from SC-261, which is approximately the same age as Divide Quarry, have an arcuate profile comparable to that in the holotype, suggesting that the profile may be variable or that more than one species of this size may be present. The P_4s from Divide Quarry differ from those of *N. serrator* in having a considerably more arcuate lateral profile, lower cusp count (mode = 13; Table 4), and shorter length.

A large sample from Roche Percée was referred to *Neoplagiaulax* cf. *N. hazeni* by Krause (1977). P^4 buccal cusps vary from 1-3 and medial cusps from 8-10 (n = 35). Although the Divide Quarry form falls within this variability, P^4 length is above the range at Roche Percée and it does not appear to be the same species. Associations of upper and lower teeth are not known from Divide Quarry and it is possible that the P^4s represent a different species than the lower blades. Larger samples are needed for a confident identification.

Referred specimens.— **Divide Q.** (FG046): UM 46197, L P^4; 77278, L P_4 frag.; 77300, L P^4; 77323, R P_4; 85365, L dent. $P_{3\text{-}4}$; 86243, R P_4; 91321, L P^4; 108839, L P_4 ant half; 108850, R P_4 partial.; 108852, R P_4 ant. partial. **SC261**: UM 73421, 2 R P_4 frags.; 73619, L P_4. **SC262**: UM 73395, R P_4.

TABLE 5 — Dental statistics for *Ectypodus powelli* from Y2K Quarry. Measurements follow Figure 2. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
P^4	L	1	—	—	2.31	—	—	—
	W	2	0.70	0.80	0.75	—	—	—
M^1	L	2	2.36	2.38	2.37	—	—	—
	W	5	1.13	1.27	1.20	0.03	0.07	5.43
M^2	L	6	1.10	1.22	1.16	0.02	0.05	4.30
	W	6	1.13	1.33	1.24	0.03	0.08	6.10
P$_4$	L	6	2.92	3.57	3.20	0.09	0.22	6.99
	L$_1$	5	0.43	0.67	0.51	0.04	0.10	19.41
	H$_s$	5	1.00	1.12	1.07	0.02	0.05	4.86
	H$_t$	6	1.20	1.40	1.31	0.03	0.07	5.08
	D	5	1.10	1.75	1.32	0.11	0.26	19.45
	W	5	1.10	1.43	1.22	0.06	0.12	10.19
	S	6	10	11	—	—	—	—
M$_1$	L	9	1.70	2.22	1.99	0.06	0.17	8.36
	W	10	0.87	1.04	0.95	0.02	0.05	5.76
M$_2$	L	2	1.05	1.22	1.14	—	—	—
	W	2	1.02	1.17	1.10	—	—	—

ECTYPODUS Matthew and Granger, 1921

Ectypodus powelli Jepsen, 1940

Table 5

Ectypodus powelli Jepsen, 1940, p. 308. Krause, 1980, p. 1169.

Holotype.— YPM-PU 13979, a left dentary with P$_4$-M$_2$ from Princeton Quarry, northern Bighorn Basin.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a) through *Copecion* (Cf-3) zones.

Description.— Detailed descriptions of *Ectypodus powelli* were provided by Jepsen (1940) and Krause (1980).

Discussion.— When Jepsen described *Ectypodus powelli* it was known only from lower dentition. The subsequent discovery of associated upper and lower dentitions at Krause Quarry (SC-195; Cf-2) allowed upper teeth to be identified (Krause, 1980). Several associations of upper and lower teeth are now also known from Y2K Quarry (Ti-5b). Also noteworthy is a specimen (UM 99033) from SC-29 (Cf-3) collected in 1985 that is exceptionally complete and compares favorably with dentitions described by Krause (1980). It consists of a left dentary with I$_1$-M$_1$, and two right maxillae with P^3-M^2 and M$^{1-2}$. The practice at UM has been to catalog associated material under one number. Presumably these specimens were found in close proximity and represent two individuals, rather than three.

The size range in the Y2K Quarry sample of *Ectypodus powelli* is slightly higher than the range reported by Jepsen for Princeton Quarry but it is approximately equivalent to the sample from SC-188 (Holly's Microsite; Cf-2) (Krause, 1980). There appears to have been a progressive increase in the number of serrations on P$_4$ from the late Tiffanian to the middle Clarkforkian in the *E. powelli* lineage. Jepsen (1940) listed six specimens from Princeton Quarry, all with 10 serrations. At the slightly younger Y2K Quarry the P$_4$s are evenly divided between 10 and 11 serrations (n = 6). At SC-188 the P$_4$s have 11 (n = 11) or even 12 (n = 1) serrations (Krause, 1980). The high coefficient of variation in some P$_4$ measurements in the Y2K sample (Table 5) is largely due to a single large specimen (UM 109977). The coefficient of variation is sensitive to outliers, especially in small samples, and may diminish with a larger sample size.

It is not clear if teeth of *Parectypodus laytoni*, other than fourth premolars, can be confidently distinguished from those of *E. powelli*. Because *P. laytoni* is a rare species at Y2K Quarry I referred all isolated teeth that were within the expected variability of *E. powelli* to the latter. This could include a small number of *P. laytoni* specimens.

Referred specimens.— **SC165**: UM 81697, R P$_4$; 81701, R P$_4$. **SC179** (quarried): UM 110298, R M^1 post. half. **SC187**: UM 69296, L P$_4$. **SC191**: UM 68893, R P$_4$. **Y2K Q.** (SC389): UM 109215, R P^4; 109227, R P$_4$ partial; 109297, R P$_4$ ant. half; 109306, R P$_4$ ant. half; 109421, L M$_1$; 109428, L M$_1$; 109441, L M^1; 109476, L M^2; 109477, L P^4 ant. frag.; 109486, L P$_4$, M$_2$; 109487, R P$_4$; 109498, R P$_4$; 109504, L M$_2$; 109508, R M$_1$; 109514, R max. M$^{1-2}$; 109531, R M^1; 109586, R M$_1$; 109590, L M^2; 109871, L M$_1$; 109970, R M$_1$; 109971, L M$_1$; 109973, R M^2; 109974, P^2; 109976, L P$_4$ ant. frag.; 109977, L P$_4$; 109978, L M^1 partial; 109979, L dent. I$_1$, P$_4$; 109980, R M$_1$; 109981, L P^4; 109982, L M^2, assoc. R dent. frag. M$_{1-2}$; 109983, R P$_4$ frag.; 109984 R P$_4$ frag.; 109985, R M^2; 109986, R P^4 frag.; 109987, R M$_1$; 109989, R M^2; 109990, R P^4 ant. frag.; 109991, R M$_2$; 109992, L M^1 frag.; 110942, R M^2.

MIMETODON Jepsen, 1940

Mimetodon churchilli Jepsen, 1940

Mimetodon churchilli Jepsen, 1940, p. 317.

Holotype.— YPM-PU 14525, left dentary with I$_1$-M$_1$, from Princeton Quarry, northern Bighorn Basin.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* zone (Ti-5a).

Description.—A detailed description of *Mimetodon churchilli* was provided by Jepsen (1940, p. 317).

Discussion.— *Mimetodon churchilli* is known only from Princeton Quarry and lateral exposures of the Princeton Quarry horizon. The referred YPM specimens were described by Jepsen (1940, p. 317). Lower incisors of *Mimetodon* are easily distinguished from those of other ptilodontids by their lack of a mesial groove along the lower margin, and in having a long, planar, mesial interstitial facet. UM 110940 is similar to the incisor in the holotype but is considerably more laterally expanded near the base of the crown, almost to the degree of being semicircular. This is presumably within the variation of the species.

UM 108836 from Cedar Point Quarry is an anterior P$_4$ fragment that is very similar to *Mimetodon churchilli*. It is too fragmentary, however, for confident specific identification, and possibly could be a variant of *Neoplagiaulax hunteri*.

Referred specimens.— **Princeton Q.**: YPM-PU 14525 (holotype); 14533, R P$_4$. **SC187** (Princeton Q. bed): 110940, L lower incisor.

?*Mimetodon silberlingi*

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Discussion.— A single fragmentary P_4 from Divide Quarry compares closely to specimens of *Mimetodon silberlingi* figured by Krause (1977), from Roche Percée. It is too incomplete, however, for confident identification.

Referred Specimen.— **Divide Q.** (FG046): UM 82102, R P_4 ant. half.

Subfamily PTILODONTINAE Cope, 1887

PTILODUS Cope, 1881a

Ptilodus sp. C.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description.— A detailed description of *Ptilodus* sp. C was provided by Krause (1982).

Discussion.— *Ptilodus* "*cedrus*" was informally described by Krause (1982) as part of his doctoral thesis. He is currently preparing its description for publication (pers. comm.). The species was named for its type locality at Cedar Point Quarry. It is commonly listed in publications as *Ptilodus* sp. C., as I have done here. *Ptilodus* sp. C is best known from Cedar Point Quarry, where it is abundantly represented.

Two partial P_4s (UM 109629, 109645) from the lowest UM localities of Tiffanian age on Polecat Bench compare favorably with *Ptilodus* sp. C. Although fragmentary, these specimens are particularly important because *Ptilodus* sp. C. is not known from zones younger than the *Plesiadapis rex* zone and they help to constrain the age of these localities.

Descriptive P_4 statistics for UM specimens of Ptilodus *sp. C.*— Length: n = 12, Min = 8.12, Max = 9.63, Mean = 8.70, SE = 0.14, SD = 0.47, V = 5.42. Width: n = 11, Min = 2.60, Max = 3.45, Mean = 3.06, SE = 0.09, SD = 0.29, V = 9.40.

Referred specimens.— **Cedar Point Q.**: UM 63094, R dent. I_1-P_4; 63112, 5 R P_4s, (also includes other multituberculates); 64396, L dent. P_{3-4}; 64420, R dent. P_4-M_1; 64445, L dent. P_4; 64561, R dent. P_4; 71834, R P_4; 82063, R dent. P_4; 82091, R P_4; 83245, L P_4; 83246, L P_4. **SC263**: UM 109629, L P_4 half. **SC412**: UM 109645, R P_4 frag. Plus numerous specimens in the YPM from Cedar Point Quarry.

Ptilodus kummae Krause, 1977

Figure 9

Ptilodus kummae Krause, 1977, p. 6.

Holotype.— UALVP 9001, a nearly complete postcranial skeleton with associated left P^4, I^1, right P^{2-4}, P_4, and M_1, from Roche Percée local fauna, Saskatchewan, Canada.

Biostratigraphic occurrences in Bighorn Basin.— ?*Plesiadapis rex* (Ti-3), *Plesiadapis churchilli* (Ti-4a), and *Phenacolemur* (Ti-4b) zones.

Description.— A detailed description of *Ptilodus kummae* was provided by Krause (1977).

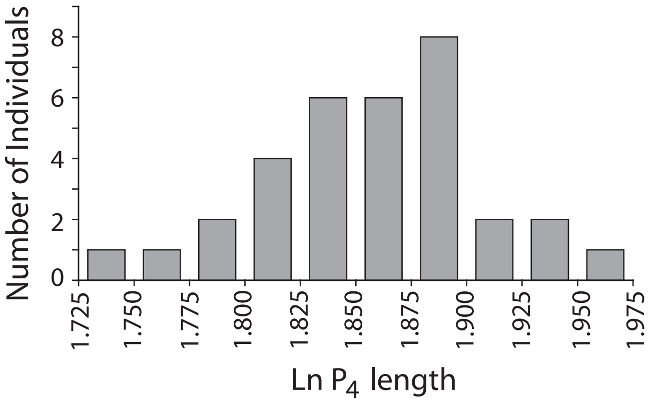


FIGURE 9 — Histogram of P_4 length of *Ptilodus kummae* from Divide Quarry, northern Bighorn Basin. Measurements transformed to natural logarithm.

Discussion.— Specimens of *Ptilodus kummae* from several localities in the northern Bighorn Basin were studied and described by Krause (1982) as part of his doctoral thesis. Subsequent collecting at Divide Quarry has more than tripled the number of specimens known from the Bighorn Basin. *Ptilodus kummae* differs from other species of *Ptilodus*, except *P. fractus*, in exhibiting a prominent break in slope along the anterior margin of the P_4 below the first serration, and in having a more erect anterior P_4 margin (Krause, 1982). It differs from *P. fractus* in being about 20% larger.

Krause (1982) noted that at several localities in the Bighorn Basin, *P. kummae* was slightly smaller than in the type sample. Measurements from Divide Quarry confirm Krause's observation. The mean P_4 length at Divide Quarry is 6.41 (n = 33, range 5.71-6.06 mm) compared with 6.84 at Roche Percée (n = 48, range 6.3-7.3 mm), the former being about 6% smaller. The mean P_4 width measurement is similar in both samples. This metric is highly sensitive to small differences in crown orientation, however, especially using isolated teeth, and may not be comparable between these samples. The frequency distribution of P_4 serration counts (S) is similar in both samples; i.e. the majority of specimens has 13 serrations while a smaller number have 12 and 14 (Divide Q.: S = 12, n = 5; S = 13, n = 14; S = 14, n = 4; Roche Percée: S = 12, n = 4; S = 13, n = 24; S = 14, n = 13; S = 15, n = 1). The mean number of serrations is slightly higher at Roche Percée (13.3) than at Divide Quarry (13.0). The distribution at Divide Quarry is approximately normal (Skew = -0.14; Fig. 9) and the P_4 coefficient of variation is relatively low (length = 4.84; width = 5.87). Thus, there is no suggestion of a second species. Although the Divide Quarry form is slightly smaller than in the type sample, it is about 15% larger than *P. fractus* (mean L = 5.56; n = 3). Given the small size difference and the lack of significant morphological differences between the Bighorn Basin and Roche Percée samples, I follow Krause (1982) and identify the Bighorn Basin specimens as *P. kummae*.

Ptilodus kummae was identified at Cedar Point Quarry by Krause (1982) based on a single uncataloged YPM-PU specimen. Four P_4s in the UM collections from Cedar Point Quarry exhibit a prominent break in slope below the first serration and an erect anterior margin, features that are comparable to those in *P. kummae*. These specimens are mostly larger than *P. kummae* from Roche Percée, however, with only a small amount of size overlap. They are smaller than teeth that are clearly referable to *Ptilodus* sp. C in the UM collections, which have a smoother anterior profile and more posteriorly inclined anterior margin. Two of the teeth in question were included in *Ptilodus* sp. C by Krause (one in UM 63112, and 64405). The differences in morphology seems great enough, however, to keep these specimens separate from *Ptilodus* sp. C, and I have tentatively referred them to *P.* cf. *P. kummae*. The larger YPM-PU collection of *Ptilodus* from Cedar Point Quarry was not available for study.

Referred specimens.— **Croc Tooth Q.** (FG028): UM 77073, R P^2; 77152, R P_4; 77161, R P_4; 110248, R P^4; 110249, L M_2; 110250, R P^2; YPM-PU 21076; 21078. **Divide Q.** (FG046): UM 45616, L P_4 partial; 77270, L P^2; 77276, L P_4; 77277, L P_4 frags.; 77280, L P^2, R P^4, L I_1 unassoc.; 77296, R P^4; 77299, L P_4 half; 77313, R P_4 half; 77316, L M_1; 77319, L M^1; 77322, L P_4; 80666, R P_4; 82071, L P_4; 83216, R P_4; 83219, R P_4; 83220, R P_4; 83223, L dent. I_1-P_4; 83235, R P_4; 83241, R P_4; 83265, R P_4; 85284, R P_4; 85285, L P_4; 85300, L P_4; 85301, R P_4; 85302, L P_4; 85310, R P_4; 85311, R P_4; 85366, R P_4; 85390, R max. P^{1-4}; 85391, R P_4; 85408, L P_4; 85442, R P_4; 85443, L P_4; 85916, R P_4; 85917, L P_4; 85925, L P_4; 86238, R max. M^1; 87038, L P_4; 87041, L P_4; 91323, R P_4; 91326, L P_4; 91329, L P_4; 91335, R dent. I_1, P_4; 92256, R P_4; 92266, R P^4; 108791, L P^4; 108792, R P^4; 108793, L P^4; 108794, R P^4; 108795, L P^4; 108796, R P^4; 108797, L P^4; 108798, L P^4; 108799, R P^4; 108800, L P^4; 108801, R P^4; 108802, R M^1; 108803, L M^1; 108804, L M^1; 108805, L M^2; 108806, R P^1; 108807, L P^1; 108808, L P^1; 108810, L P^2; 108811, L P^2; 108812, R P^2; 108813, R P^2; 108814, L P^2; 108815, R P^2; 108816, R P^2; 108817, R P^2; 108818, R P^2; 108819, R P^2; 108820, R P^2; 108821, R P^2; 108822, L P^2; 108823, R P^2; 108824, R P^2; 108825, R P^2; 108826, R P^2; 108827, R P^2; 108828, L P^3; 108829, L P^3; 108830, L P^3; 108831, L P^3; 108832, L P^3; 108833, L P^3; 108834, L P^3; 108840, R P_4 partial; 108841, L P_4 frags.; 108845, R P_4 partial; 108846, R P_4 partial; 108847, R P_4 half; 108849, R P_4 frag.; 108851, R P_4 partial; 108853, R P_4 frag.; 108854, L P_4 partial; 108855, L M_2; 108857, L P^3; 108859, R P_4 frag.; 110232, L P^2; 110233, L M_1; 110234, R P^3; 110235, L P_4; 110236, L P_4; 110237, R P^4; 110238, R P^1; 110239, L P^4; 110240, L P^1; 110245, P^2; 110246, L M^2; 110247, L M^2; 110257, L P_4 partial. **Fossil Hollow** (SC198): UM 69242, R P^4 partial; 79876, L P_4. **Long Draw Q.**: UM 45482, L P_4 half; 110251, R P_4 half; 110252, L P^2. **Seaboard Well**: YPM-PU 19153. **SC243**: UM 71761, L P_4; 77933, L P^4; 77934, R P^1; 77935, L P^1; 77936, R P^1; 77937, L P^2; 77938, L P^2; 77939, L P^2; 77940, R P^2; 77941, L P^2; 77942, R P^2; 77943, R P^2; 77944, P^3; 77945, P^3; 77946, P^3; 77947, L P^4; 77948, R P^4 frag.; 77949, L M_1; 77950, L M_1; 77951, L P^1; 77952, Tooth frags. (8). **SC261**: UM 73390, misc. tooth frags.; 110253, R P_4; 110254, R P_4; 110255, R P_4 frag.; 110256, L P_4 frag. (YPM-PU specimens from Krause, 1982).

Ptilodus cf. *P. kummae*

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Discussion.— Reasons for referring these specimens to *Ptilodus* cf. *P. kummae* were discussed in the *Ptilodus kummae* section.

Descriptive P_4 statistics for Ptilodus *cf.* P. kummae.— Length: n = 4, Min = 7.21, Max = 7.75, Mean = 7.54, SE = 0.11, SD = 0.23, V = 3.05. Width: n = 4, Min = 7.21, Max = 7.75, Mean = 7.54, SE = 0.11, SD = 0.23, V = 3.05.

Referred specimens.— **Cedar Point Q.**: UM 63112, R P_4 (also includes *Ptilodus* sp. C); 64405, R dent. I_1-P_4; 82060, L P_4; 83244, L P_4.

PROCHETODON Jepsen, 1940

Prochetodon foxi Krause, 1987b

Prochetodon foxi Krause, 1987b, p. 223.

Holotype.— YPM-PU 21223, right dentary with base of I_1 and $P_{3\text{-}4}$, from Long Draw Quarry, northern Bighorn Basin, Montana.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Description.— A detailed description of *Prochetodon foxi* was provided by Krause (1987b).

Discussion.— The holotype from Long Draw Quarry and a single P^3 from Divide Quarry were the only specimens known of *Prochetodon foxi* in the Bighorn Basin when Krause (1987b) described the species. Three additional specimens are now known from Divide Quarry. These specimens are within the variability described by Krause for *P. foxi* from localities outside the Bighorn Basin (primarily Roche Percée in Saskatchewan) and confirm its presence at Divide Quarry.

Dental measurements (mm).— UM 83221: P_4, L = 8.31, W = 2.24. UM 85921: M_1, L = 3.59, W = 1.65, C = 6.5:4.5.

Referred specimens.— **Divide Q.** (FG046): UM 77318, L P^3; 83221, L dent. P_4; 85921, L M_1. **Long Draw Q.**: YPM-PU 21223 (holotype).

Prochetodon cavus Jepsen, 1940

Prochetodon cavus Jepsen, 1940, p. 310. Krause, 1987, p. 228.

Holotype.— YPM-PU 13925, right dentary with base of I_1, P_3, and anterior part of P_4, from Princeton Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b), *Plesiadapis simonsi* (Ti-5b), and ?*Plesiadapis gingerichi* (Ti-6) zones.

Description.— Descriptions of *Prochetodon cavus* were provided by Jepsen (1940) and Krause (1987b).

Discussion.— Several new specimens of *Prochetodon cavus* have been collected since Krause (1987b) published his revision of *Prochetodon*. These specimens do not add significantly to knowledge of the species but help to better document its stratigraphic range.

Selected dental measurements (mm).— UM 79877: P^3, L = 3.54, W = 2.00, C = 4:4. UM 109860: P^4, L = 4.83, W = 1.48 (badly etched). UM 110282: P^4 partial, W = 1.58. UM 73384: P_4, L = 6.85, W = 2.16.

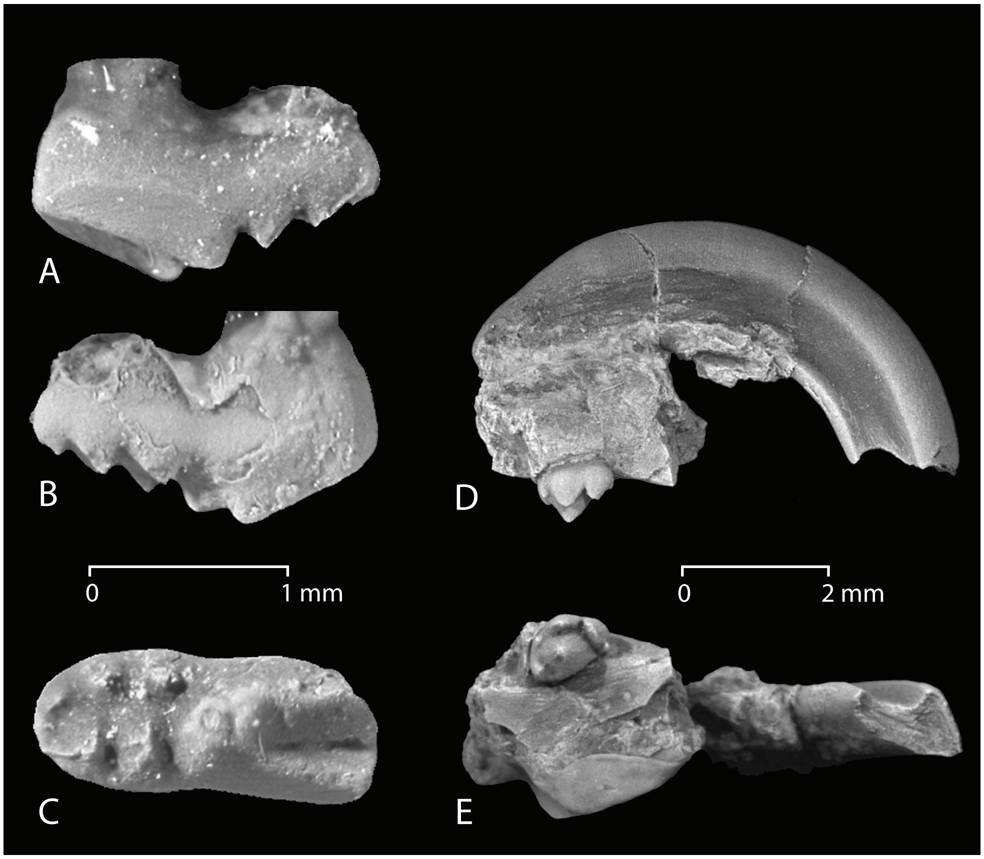


FIGURE 10 — Upper teeth of *Microcosmodon conus*. A–C, right P^4 (UM 109661, Y2K Quarry) in lingual (A), buccal (B), and occlusal (C) views. D–E, right R I^2, P^1 (UM 81696, SC-165) in distal (D) and occlusal (E) views.

Referred specimens.— **Fossil Hollow** (SC198): UM 69242, R P^1; 79869, L max. $P^{2\text{-}3}$; 79877, L P^3, L P_4 ant. half, R P_4 frag. **SC165**: UM 69256, R P^1; 77930, R P^3; 77931, L M_1; 77932, 9 iso. tooth frags. **SC187**: UM 76858, L P_4 frag.; 96368, R P_4; 110180, R P_4 frag. **SC228**: UM 71706, L P_4 frag. **SC229**: UM 110282, L P^4 ant. partial; 110284, L P^4 frag. **SC258**: UM 73384, R P_4. **SC266**: UM 73511, R P_4 frag. **SC277**: UM 73684, L P^3. **Schaff Q.**: UM 78893, 6 iso. tooth frags. **Y2K Q.** (SC389): UM 109860, L P^4.

Prochetodon taxus Krause, 1987b

Prochetodon taxus Krause, 1987b, p. 232.

Holotype.— UM 71311, partial skull with left P^1-M^2, right P^2-M^2, left dentary with $M_{1\text{-}2}$, and right dentary with P_4-M_2, from SC-226 in the northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis gingerichi* (Ti-6), Rodentia (Cf-1), and *Plesiadapis cookei* (Cf-1) zones.

Description.— A detailed description of *Prochetodon taxus* was provided by Krause (1987b).

Discussion.— *Prochetodon taxus* is a poorly represented taxon and is best known from the holotype. Its dental variability is not well-documented. Two specimens from the latest Tiffanian, an M^2 (UM 108267) and P_4 fragment (UM 108281) collected after Krause (1987b) described *P. taxus*, are close to the size of their counterparts in the holotype and I tentatively included these in the species. A P^3 from the earliest Clarkforkian (UM 108231) is smaller than the P^3s in the holotype, but is about the same size as UM 77555 from the middle Clarkforkian, identified as *P. taxus* by Krause (1987b, Table 6). It is larger than any included in *P. cavus* (Krause, 1987b, Table 4) and appears to be a small individual of *P. taxus*.

Dental measurements (mm).— UM 108267: M^2, L = 2.21, W = 2.15, C = 1:2.5:3. UM 108231: P^3, L = 3.97, W = 2.25, C = 5:4.

Referred specimens.— **SC191**: UM 108281, R P_4 partial. **SC226**: UM 71311, (holotype). **SC375**: UM 108231, L P^3. **Bluff Top Q.** (SC379): UM 108267, R M^2.

Superfamily TAENIOLABIDOIDEA
Granger and Simpson, 1929
Family MICROCOSMODONTIDAE
(Holtzman and Wolberg, 1977)

MICROCOSMODON Jepsen, 1930b

Microcosmodon conus Jepsen, 1930b
Figure 10, Table 6

Microcosmodon conus Jepsen, 1930b, p. 508.

Holotype.— YPM-PU 13331, a left dentary with I_1 and P_4 from "quarry level" in Big Sand Coulee, northern Bighorn Basin (presumably near Princeton Quarry).

TABLE 6 — Dental measurements for *Microcosmodon conus* and *Pentacosmodon pronus* from the Clarks Fork Basin. Measurements follow Figure 2. *JVQ*, Jepsen Valley Quarry; *Y2K Q*., Y2K Quarry.

		P. pronus		*M. conus*					
		MCZ 20066 JVQ	YPM-PU 19027 Sec. 21, T57N, R100W	UM 68266 SC-165	UM 68266 SC-165	UM 71657 SC-187	UM 81702 SC-165	UM 109661 Y2K Q.	UM 109972 Y2K Q.
P^4	L	—	—	—	—	—	—	1.69	—
	W	—	—	—	—	—	—	0.71	—
	C	—	—	—	—	—	—	3:4:0	—
M^1	L	—	—	2.60	—	—	—	—	—
	W	—	—	1.34	—	—	—	—	—
	C	—	—	6:7:4	—	—	—	—	—
P$_4$	L	1.80	2.03	—	1.66	1.72	1.80	—	—
	W	0.90	0.87	—	0.69	0.66	0.64	—	—
	L$_1$	0.40	0.53	—	—	0.46	0.50	—	—
	H$_s$	0.88	0.90	—	—	0.67	0.70	—	—
	H$_t$	1.17	1.03	—	—	0.78	0.85	—	—
	D	0.65	0.70	—	0.50	—	—	—	—
	S	5	5	—	—	5	5	—	—
M$_1$	L	2.25	—	—	—	2.96	—	—	—
	W	1.30	—	—	—	1.05	—	—	—
	C	4:3	—	—	—	7:4.5	—	—	—
M$_2$	L	1.37	—	—	—	1.30	—	—	—
	W	1.30	—	—	—	1.18	—	—	1.23
	C	3:2	—	—	—	3:2	—	—	—

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a) and *Plesiadapis simonsi* (Ti-5b) zones.

Description.— Descriptions of the lower dentition of *Microcosmodon conus* were provided by Jepsen (1930b) and Krause (1977). More recently, Fox (2005) provided descriptions of upper and lower dentitions, including some that were associated, and partial skulls.

Discussion.— The I^{2}s of *Microcosmodon* are the largest and most robust dental element. Because of their greater potential for preservation and discovery they are the only element known for eucosmodontids at many localities. Unfortunately, I^{2}s appear to be indistinguishable between *M. conus* and the younger *M. rosei*. Measurements of mesial-distal width made on the crown near the base of the enamel range from 0.90-1.04 mm (n = 4) in *M. conus* and 0.92-1.05 mm (n = 5) in *M. rosei*, with means of 0.97 mm in both. Dorsoventral depth ranges from 1.58-1.89 mm and 1.60-1.94 mm, respectively, with means of 1.76 and 1.74 mm. Upper cheek teeth of *M. rosei* are not known and it can be confidently distinguished from *M. conus* only by characteristics of the lower premolars (Krause, 1980). Thus, I have referred isolated I^{2}s from levels where P$_4$s are not known to Eucosmodontidae gen. and sp. indet.

UM 109661 is the first P^4 (Table 6, Figs. 10A-C) of *Microcosmodon conus* identified from the Bighorn Basin, which is the type area for the species. It appears to be within the variability of nine P^{4}s from the Gao Mine locality in Alberta, identified as *M. conus* by Fox (2005). Fox reported five cusps in the middle row, but noted that the posterior-most fifth cusp was small, and often lost to wear. UM 109661 has only four visible cusps. Fox also described a posterolingual cusp row developed on the ridge that descends from the ultimate cusp to the posterolingual corner. He reported two small cusps in this row, but again said that in most specimens the cusps had been lost to wear. There is no evidence of cusps on the posterolingual ridge in UM 109661. Presumably these small cusps and the fifth cusp in the middle row were lost to wear or were variably present in *M. conus* (although see below). These cusps appear to be minor, and UM 109661 compares favorably to Fox's description in all other aspects.

UM 68266 includes a right dentary fragment with P$_{3\text{-}4}$, and a left maxillary fragment with M^1. The specimens are labeled as being questionably associated. They were collected at SC-165 by R. G. Habetler, presumably at a wash site that later became known as "Habetler's concentration." The M^1 is within the variability of *M. conus* described by Krause (1977) from Saskatchewan and by Fox (2005) from Alberta, with the exception of number of cusps in the buccal and lingual rows. UM 68266 has only 6 visible buccal cusps and 3 or 4 lingual cusps (Table 6), while those described from Canada have 7 buccal and 5 to 9 lingual cusps. UM 68266 is in a medium state of wear and it is possible that a 7th small cusp on the anterior end of the buccal row was lost to wear. In the lingual row of Canadian specimens, Fox (2005) noted that the cusps were "poorly developed cuspules," which suggests that they would be easily lost to wear. Thus, it is possible that a cusp was lost to wear in UM 68266, although there is little room for additional cusps. Alternatively, there may have been fewer cusps in the Bighorn Basin form. The Canadian localities are probably correlative to one of the Ti-4 zones, and it may be that *M. conus* underwent a reduction in lingual cusps from Ti-4 to Ti-5. Krause (1980) suggested that *M. conus* and *M. rosei* were parts of an evolutionary lineage, ending with *M. rosei* in the Clarkforkian. The only two M^1s identified as *M. rosei* (UM 72039, 72667, Krause, 1980) both have fewer cusps than any of the M^1s of *M. conus* from Canada. Although the number of lingual cusps in UM 68266 may be the same as in *M. rosei*, the lingual row is shorter in the latter and terminates more posteriorly, based on UM 72667.

The possible differences in M^1 and P^4 cusps between *M. conus* in Canada and the Bighorn Basin are notable, but involve cusps that are probably best referred to as "cuspules." The counting of such cusps is somewhat subjective and these cusps may be variably present. Thus, these differences do not seem important enough to consider specific separation.

I tentatively include a maxillary fragment with I^2 and P^1 (UM 81696, Figs. 10D,E) in *Microcosmodon conus*. The I^2 of *Microcosmodon* may be indistinguishable from that of *Pentacosmodon*. Nevertheless, *Pentacosmodon* is much rarer than *Microcosmodon* and UM 81696 probably belongs to *M. conus*. The P^1 of *M. conus* does not appear to have occluded with lower teeth and is extremely variable in size and morphology (Fox, 2005). The P^1 in UM 81696 is similar to some described from Gao Mine, but still appears to differ in relative cusp size, and number and position of smaller cusps or cuspules. These differences are presumably due to high intraspecific variability.

Referred specimens.— **Princeton Q.**: YPM-PU 13331 (holotype); 13401, right dent. P_4-M_1; 14322, right dent. I_1, $M_{1\text{-}2}$; 14324, left dent. I_1, P_4-M_1, unerupted P_3; 14427, left dent. P_4-M_1; 14430, left dent. I_1, P_4-M_1; 14549, right dent. I_1, $P_{3\text{-}4}$. **SC165** (Habetler's concentration): UM 68266, R dent. P_4, and L max. M^1; 81696, L max., I^2, P^1; 81702, L P_4. **SC187**: UM 71657, R dent. I_1 (root), P_4-M_2. **Schaff Q.**: UM 110159, L I^2; YPM-PU 19393, P_4 (dent.?); 20728, L dent. I_1-M_2. **Y2K Q.** (SC389): UM 108534, R M_1; 109396, R I^2; 109435, L I^2; 109661, R P^4; 109972, L M_2.

Microcosmodon sp.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a), *Plesiadapis gingerichi* (Ti-6), and Rodentia (Cf-1) zones.

Discussion and description.— The I_1s listed below are included in *Microcosmodon* based on the lack of a longitudinal groove on the mesial face that is present in *Pentacosmodon* (Jepsen, 1940, p. 323), which is the only other eucosmodontid genus in this size range known from the late Paleocene of the northern Bighorn Basin.

Referred specimens.— **Divide Q.** (FG046): UM 77301, L I_1. **SC178**: UM 101822, I_1 frag. **SC179**: UM 108344, R I_1 frag. **SC226**: UM 71299, L I_1.

PENTACOSMODON Jepsen, 1940

Pentacosmodon pronus Jepsen, 1940

Table 6

Pentacosmodon pronus Jepsen, 1940, p. 322. Fox, 2005, p. 70.

Holotype.— YPM-PU 14085, a right dentary with the base of I_1, and P_4-M_2, from Princeton Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a) and *Plesiadapis simonsi* (Ti-5b) zones.

Description.— Lower dentition was described by Jepsen (1940) and Fox (2005). Upper molars were described by Fox (2005).

Discussion.— Very few specimens of *Pentacosmodon pronus* have been discovered in the Bighorn Basin since it was first described by Jepsen (1940). Important new material was recently described by Fox (2005), however, from the Gao Mine (Ti-4) in Alberta. In the Bighorn Basin, a dentary of *P. pronus* (MCZ 20066, Table 6) was reported by Schaff (1985) from Jepsen Valley Quarry and two uncataloged specimens were listed by Carlson and Krause (1985) from SC-165 (probably from Habetler's concentration). Additionally, an isolated P_4 (YPM-PU 19027) was collected by Princeton crews in 1965 from Sec. 21, T57N, R100W in the Silver Coulee area. Princeton Quarry is also in this section and the specimen is presumably from the *Probathyopsis* zone. As noted above, I^2s of *M. conus* and *P. pronus* may be indistinguishable. Thus, specimens of *P. pronus* could be present in the Eucosmodontidae gen. and sp. indet. material.

Referred specimens.— **Jepsen Valley Q.**: MCZ 20066 L dent., P_4-M_2. **Princeton Q.** (SC187): YPM-PU 14085 (holotype); 14426, L dent. I_1 base, P_4-M_2. **SC-165**: two uncataloged specimens, P_4 and M_1 (Carlson and Krause, 1985). **Princeton Q. area** (Sec. 21, T57N, R100W): YPM-PU 19027, R P_4.

Family EUCOSMODONTIDAE (Jepsen, 1940)

NEOLIOTOMUS Jepsen, 1930a

Neoliotomus conventus Jepsen, 1930a

Neoliotomus conventus Jepsen, 1930a, p. 122. Krause, 1980, p. 1176.

Holotype.— YPM-PU 13297, left dentary fragment with base of I_1, root of P_3, and anterior half of P_4, associated left M^1 and right maxillary fragment preserving a partial P^4; from Paint Creek (Cf-2), northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a), *Plesiadapis gingerichi* (Ti-6), and Clarkforkian zones.

Description.— Description were provided by Jepsen (1930a) and Krause (1980).

Discussion.— Krause (1980) identified three late Tiffanian specimens collected at or near Princeton Quarry (Ti-5a) as *Neoliotomus conventus* in his review of Clarkforkian multituberculates. He noted, however, that one fragmentary specimen (YPM-PU 19097) collected below Princeton Quarry appeared to be considerably larger than any other P_4 of the species and speculated that it might belong to a new species. An additional specimen collected (UM 73587) below Princeton Quarry after Krause's review also appears to be considerably larger than P_4s of *N. conventus*. UM 73587 is fragmentary but the spacing of ridges and height of the specimen indicate a larger size. A third P_4 (UM 110076) recently collected about 40 meters above Princeton Quarry is at least 14.4 mm long, which is larger than either of Krause's Clarkforkian length estimates and is intermediate in size between YPM-PU 19864 and Krause's estimate for YPM-PU 19097, from at and below the Princeton Quarry level, respectively (see Krause, 1980, Fig. 10). UM 110076 is partly encased in a nodule precluding additional description. It appears that there is a mean decrease in P_4 size in *N. conventus* from the late Tiffanian to the Clarkforkian and from the Clarkforkian to the Wasatchian, as suggested by Krause. The larger mean size of the late Tiffanian specimens may justify recognition of a new species, but I refrain from doing so pending the collection of a larger sample.

Juvenile specimens of *N. conventus* (UM 36192 and 101825) from early Clarkforkian limestones in the Clarks Fork Basin were recently reported by Bloch (2001, p. 46) in his unpublished dissertation.

The occurrences of *Neoliotomus* below Princeton Quarry in the lower *Probathyopsis* zone or possibly upper *Phenacolemur* zone (YPM-PU 19097) are the earliest known North American occurrences of this genus.

Referred specimens.— **SC083**: UM 66200, L P^4. **SC179**: UM 36192, L M_1; 68746, R P_4. **SC187**: UM 108388, R I_1 partial. **SC258**: UM 73346, R M_2, lower incisor frags. **SC271**: UM 73587, R P_4 frag. **SC280**: UM 73696, L I_1. **SC372**: UM 108247, L P^4, L P_4, R P_4, associated. **SC419**: UM 110076, P_4, I_1. From Krause (1980, pp. 1177-1178) **Near Princeton Q.**: YPM-PU 14466, 2 anterior premolars; 17855, I_1 frag. **Sec. 7**, **T57N**, **R100W**: YPM-PU 19097, P_4 partial.

Family EUCOSMODONTIDAE gen. and sp. indet.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a), *Phenacolemur* (Ti-4b), *Plesiadapis gingerichi* (Ti-6), and Rodentia zones.

Discussion and description.— The I^2s of *Microcosmodon conus*, *M. rosei*, and *Pentacosmodon pronus* may be indistinguishable, as noted above. At present the first two species can be confidently identified only with P_4s. Because of the rarity of *Pentacosmodon*, most or all of the I^2s included here probably belong to *Microcosmodon*. Eucosmodontid I^2s from Divide and Croc Tooth quarries differ from those at younger localities in having a deeper distal groove near the base of the crown and may belong to a species not yet recognized in the Bighorn Basin.

Referred specimens.— **Bluff Top Q.** (SC379): UM 108256, R I^2; 108257, L I^2. **Croc Tooth Q.** (FG028): UM 77154, L I^2. **Divide Q.** (FG046): UM 110143, R I^2; 110943, R I^2. **FG001**: UM 73972, I^2. **Fossil Hollow** (SC198): UM 110109, I^2 frag.; 110230, R I^2. **SC083**: UM 110190, 3 I^2s. **SC191**: UM 108292, R I^2.

Supercohort THERIA Parker and Haswell, 1897
Cohort MARSUPIALIA Illiger, 1811
Order DIDELPHIMORPHIA Gill, 1872
Family DIDELPHIDAE Gray, 1821

PERADECTES Matthew and Granger, 1921

Peradectes elegans Matthew and Granger, 1921

Peradectes elegans Matthew and Granger, 1921, p. 2.

Holotype.— AMNH 17376, dentaries with left P_2-M_4 and right P_1, P_3-M_4; from Mason Pocket in the northern San Juan Basin of southern Colorado.

Biostratigraphic occurrences.— *Plesiadapis rex* (Ti-3) and *Probathyopsis* (Ti-5a) zones.

Description and Discussion.— *Peradectes elegans* was described and figured by Simpson (1935b) and Krishtalka and Stucky (1983). Rose (1981a, pp. 152 and 156) included *P. elegans* in faunal lists from Cedar Point and Princeton quarries. Marsupials from these localities were not available for study.

Didelphidae gen. et. sp. indet.

?*Peratherium* sp., Rose, 1981a, p. 156.

Biostratigraphic occurrences.— *Probathyopsis* zone (Ti-5a).

Description and Discussion.— Rose (1981a, p. 156) identified YPM-PU 17810, reportedly a left dentary with P_1-M_4, as ?*Peratherium* sp. in a faunal list for Princeton Quarry. However, in their review of Paleocene and Eocene marsupials, Krishtalka and Stucky (1983, p. 232) stated that *Peratherium* was not known from the Paleocene of North America. McKenna and Bell (1997), and Lofgren et al. (2004) also do not list Paleocene occurrences of *Peratherium*. Rose noted that the specimen "almost surely represents a second species of marsupial at Princeton Quarry." Unfortunately, it was not available for study.

Referred specimen.— **Princeton Q.** (SC187): YPM-PU 17810, L dent. with P_1-M_4.

Cohort PLACENTALIA Owen, 1837
Superorder LEPTICTIDA McKenna, 1975
Family LEPTICTIDAE Gill, 1872

PRODIACODON Matthew, 1929

Prodiacodon paucus, new species

Figures 11–12, Table 7

Prodiacodon cf. *P. concordiarcensis*, Rose, 1981a, p. 156-157.
Prodiacodon n. sp., Secord et al., 2006, p. 229.

Holotype.— YPM-PU 14137, a left dentary with P_1-M_2 and associated M_3. Collected by G. L. Jepsen and R. Layton in 1934 at Princeton Quarry (Ti-5a), northern Bighorn Basin.

Biostratigraphic occurrences.— *Probathyopsis* zone (Ti-5a).

Diagnosis.— Differs from all other species of *Prodiacodon* in the combination of characters on P_3. Smaller than other species of *Prodiacodon*, except *P. concordiarcensis* and *P. pearcei*. Differs from *P. concordiarcensis* in: (1) being about 15% larger in most molar dimensions; (2) having an exodaenodont P_3 with an additional cusp on the posterior slope of the principal cusp and a greatly reduced talonid cusp; and (3) having $P_{2\text{-}3}$ with a more posteriorly positioned apex on the principal cusp and larger more separated paraconids. Molars differ in having a distinct mesoconid swelling on the cristid obliqua, and on $M_{1\text{-}2}$ an entoconid and hypoconulid that are larger, more distinct, and connate, rather than angular. Differs from *P. pearcei* in having a more trenchant and buccolingually compressed P_3 with an additional posterior cusp, a reduced talonid cusp, and a more acute, more posteriorly positioned principal cusp.

Further differs from *Prodiacodon tauricinerei* and *P. puercensis* in having narrower, more trenchant lower cheek teeth with

TABLE 7 — Dental measurements for *Prodiacodon paucus* n. sp. from Princeton Quarry, for the holotypes of *P. concordiarcensis* (Gidley Quarry) and *P. tauricinerei* (Gray Bull beds south of Dorsey Creek, Bighorn Basin), and for *P.* cf. *P. tauricinerei* from Y2K Quarry. *Estimate.

		P. paucus n. sp.		*P. concordiarcensis*	*P. tauricinerei*		*P.* cf. *P. tauricinerei*						
		YPM-PU 14137 (type)	YPM-PU 21162	AMNH 35693 (type)	YPM-PU 13104 (type)	YPM-PU 13104 (type)	UM 109240	UM 109312	UM 109336	UM 109358	UM 109432	UM 109575	UM 109662
P^1	L	—	2.0*	—	—	—	—	—	—	—	—	—	—
	W	—	0.77	—	—	—	—	—	—	—	—	—	—
P^2	L	—	1.60	—	—	—	—	—	—	—	—	—	—
	W	—	0.70	—	—	—	—	—	—	—	—	—	—
P^3	L	—	2.07	—	—	2.75	—	—	—	—	2.83	—	—
	W	—	1.47	—	—	2.20	—	—	1.87	—	2.30	—	—
P^4	L	—	2.25	—	—	—	—	—	2.50	—	—	—	—
	W	—	2.35	—	—	—	—	—	2.70	—	—	—	—
M^1	L	—	2.20	—	—	2.45	—	2.40	—	—	—	—	—
	W	—	2.97	—	—	3.45	—	—	—	—	—	—	—
M^2	L	—	2.1*	—	—	2.55	—	—	—	—	—	—	—
	W	—	—	—	—	3.80	—	—	—	—	—	—	—
P_3	L	1.80	—	1.70	2.75	—	2.77	—	—	—	—	2.75	—
	W	0.77	—	0.67	1.10	—	1.40	—	—	—	—	1.20	—
P_4	L	2.37	—	—	2.90	—	3.15	—	—	—	—	—	3.02
	W tri.	1.40	—	—	1.67	—	1.95	—	—	—	—	—	1.75
	W tal.	1.00	—	—	1.45	—	1.53	—	—	—	—	—	1.43
M_1	L	2.23	—	1.95	2.45	—	—	—	—	2.35	—	—	—
	W tri.	1.65	—	1.45	1.97	—	—	—	—	2.0*	—	—	—
	W tal.	1.25	—	1.15	1.67	—	—	—	—	1.55	—	—	—
M_2	L	2.25	—	1.85	2.35	—	—	—	—	—	—	—	—
	W tri.	1.87	—	1.63	1.97	—	—	—	—	—	—	—	—
	W tal.	1.30	—	1.15	1.73	—	—	—	—	—	—	—	—
M_3	L	2.0*	—	1.85	2.75	—	—	—	—	—	—	—	—
	W tri.	1.60	—	1.35	1.85	—	—	—	—	—	—	—	—
	W tal.	1.10	—	0.93	1.33	—	—	—	—	—	—	—	—

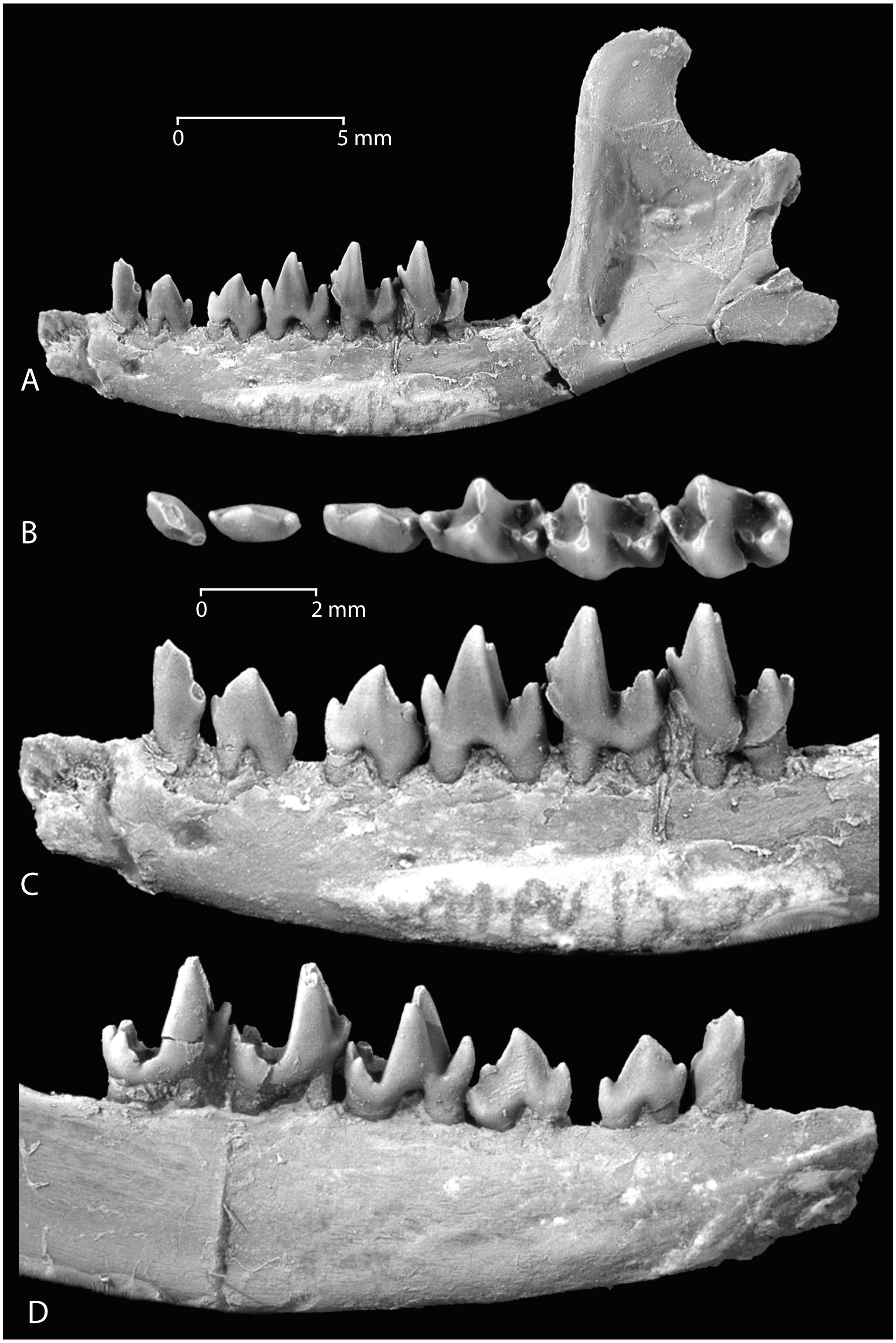


FIGURE 11 — Holotype of *Prodiacodon paucus* n. sp. from Princeton Quarry. Left dentary (YPM-PU 14137) with P_1-M_2 in buccal (A, C), occlusal (B), and lingual (D) views.

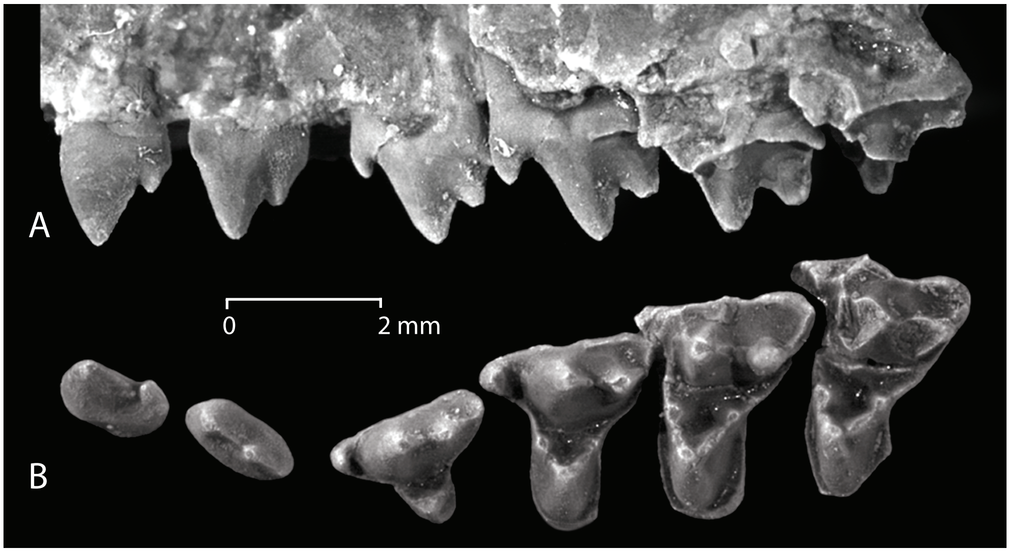


FIGURE 12 — Left maxilla (YPM-PU 21162) of *Prodiacodon paucus* n. sp. from Princeton Quarry, with P^1-M^2 in buccal (A) and occlusal (B) views.

higher P_4-M_3 trigonids, a lower crowned P_3, a shorter talonid on P_4, and a more medial M_3 paraconid. In upper teeth, P^3 has more trenchant buccal cusps, P^4 has a smaller metacone relative to the paracone, and molars have narrower cingula. M^1 lacks a hypocone (probably also M^2). Further differs from *P. tauricinerei* in having a smaller narrower P_4 paraconid and smaller P^2/P_2 relative to P^1/P_1.

Further differs from *Prodiacodon furor* in having an exodaenodont P_3 with an additional posterior cusp, a reduced talonid with sharper, more posterior principal cusps, and larger more separate paraconids. The P_4 paraconid is less anteriorly projecting and the talonid is shorter. Molars are higher crowned and more laterally compressed.

Further differs from *Prodiacodon crustulum*, based on Novacek's (1977) diagnosis and figures, in having a P_4 with a more posterior paraconid and a shorter talonid, and narrower lower molars. Upper molars differ in having no hypocone, narrower cingula, and no secondary cusp adjacent to the paraconule.

Etymology.— *Paucus* (L), few, little: in reference to the rarity of this species.

Description.— Teeth in the holotype (Fig. 11) are lightly worn or nearly unworn ($P_{2\text{-}3}$). P_1 is single-rooted, while P_2-M_3 are double-rooted. $P_{1\text{-}3}$ are trenchant. $P_{1\text{-}2}$ both have small anterior and posterior cusps, and a large central cusp. P_3 has a large central cusp with nearly equal anterior and posterior slopes and a large, separate, trenchant paraconid. Two cusps are developed on a sharp crest that descends from the principal cusp along the posterior margin; one at the base of the crest and one higher on the crown. The basal cusp is minute, while the higher cusp is larger and trenchant. P_4 narrows anteriorly to a prominent connate paraconid. P_4-M_2 have a large mesoconid developed on the cristid obliqua and a distinct entoconid, hypoconid, and hypoconulid on the talonid. Cristid obliquae contact the postvallid medially. Hypoconulids are large, project posteriorly, and are positioned posterior to the hypoconid and entoconid. Talonid basins are nearly open lingually, and have weak entocristids that are slightly more prominent on $M_{2\text{-}3}$. The hypoconulid on the associated M_3 lacks the posterior projection typical of most therians of this grade.

The dentary is shallow and has a depth of about 1.5 times the buccal height of M_1. The ascending ramus is high. Mental foramina are situated below the junction of $P_{1\text{-}2}$ and $P_{3\text{-}4}$. The C_1 alveolus indicates that C_1 was larger than P_1.

Upper teeth in YPM-PU 21162 (Fig. 12) are lightly worn or nearly unworn ($P^{2\text{-}3}$). P^4-M^2 have been anteroposteriorly compressed and rotated slightly due to post-depositional deformation. $P^{1\text{-}2}$ are subequal in size, trenchant, and double-rooted. Both have a high principal cusp and lower posterior cusp situated midway up the crown. P^3 has trenchant buccal cusps and a small protocone. A paracone, metacone, and posterior cusp are connected by a sharp crest, and decrease in height posteriorly. $P^{3\text{-}4}$ have distinct parastyles. The P^4 is molariform. The paracone is higher and larger than the metacone. Very narrow pre- and postcingula are connected around the protocone. Small para- and metaconules separate a shallow trigon basin.

The parastylar shelf is broken on $M^{1\text{-}2}$. The stylar shelf on M^1 is wide posteriorly, but narrow in the ectoflexus. Narrow pre- and postcingula are nearly confluent across the protocone on M_1. No hypocone is present. On M^1 the paracone is larger and higher than the metacone. These cusps are broken on M_2 but the paracone base is larger than the metacone base. Large distinct paraconules are separated from small metaconules by moderately deep trigon basins.

Discussion.— The holotype and referred specimens were included in a faunal list by Rose (1981a) as *Prodiacodon* cf. *P. concordiarcensis*. They do, however, almost certainly represent a distinct species. The most obvious differences are in the P_3, which is unlike the P_3 of any other species. It is similar to the P_3

of *P. concordiarcensis* in the degree of lateral compression and reduction of crown height, but differs in having an additional cusp along the posterior slope, an exodaenodont posterior buccal face, and a more posterior protocone. In contrast to the P_3 of *P. concordiarcensis*, which has a broad talonid area with a large cusp and small lingual basin, the talonid area in *P. paucus* is narrow with only a minute cusp and no sign of basining. An additional cusp along the posterior margin of P_3 is also found in *P. puercensis* and *P. tauricinerei*, but other features of the P_3 are very different, such as relative crown height and degree of lateral compression. Additional characters given in the diagnosis, such as size, also serve to distinguish *P. paucus* from other species.

Prodiacodon pearcei is similar in size to *P. paucus* but has a more inflated, less trenchant P_3 and lacks the additional cusp on the posterior slope. It was named by Gazin (1956b) based on a partial dentary from the Bison Basin in southern Wyoming. Gazin noted a close similarity to *P. concordiarcensis* but reported that the P_4 was about 14% longer and 27% wider. Novacek (1977) synonymized the species after re-measuring the teeth and concluding that differences were not of specific magnitude. Gazin's figure and measurements show the P_3 to be considerably more inflated and wider than in *P. concordiarcensis*. Using Novacek's data, the P_4 is 12% longer and nearly 30% wider than that of *P. concordiarcensis*. These differences may be of specific magnitude and I recognize *P. pearcei* as a valid species pending the description of larger samples and a better understanding of the variation in both species.

It is probable that the holotype and referred maxilla of *Prodiacodon paucus* belonged to the same individual. Both are left elements, exhibit the same degree of light wear, the same mode of preservation, agree well in size, and appear to be the only specimens of this species from Princeton Quarry. The orientations of P^4-M^2 are distorted from post depositional deformation but these teeth individually occlude well with their lower counterparts.

None of the premolars in either specimen appears to be deciduous, although this was clearly a young individual. The expectation in leptictids is that deciduous premolars erupt before M_1 and that permanent premolars erupt after all molars are in place (Slaughter et al., 1974). P_{2-3} show virtually no wear, while the cusps of M_{1-2} exhibit medium to light wear, the condition expected if P_{2-3} are permanent. P_4 exhibits about the same amount of wear as M_{1-2}, but it has the morphology expected for a permanent leptictid P_4. The P_1 is either moderately worn or broken. There is no replacement in this position in most mammals, and P_1/P^1 are nearly always the first permanent teeth to erupt and should show wear. This logic also follows in the maxilla where teeth show progressively greater wear from P^2-M^1, the opposite of what would be expected if the premolars were deciduous. P^1 has wear at the apex and along the posterolingual face. Although the slightly greater amount of wear on P^{2-3} could be evidence against the specimens belonging to one individual, the differences are small and wear is not necessarily distributed evenly between upper and lower opposing teeth.

UM 61585 is a lower molar from an anthill in the *Phenacolemur* zone. It compares favorably in size and structure with the M_3 associated with the holotype, but could possible be from another position. I have provisionally included it in *Prodiacodon paucus*.

Referred specimens.— **Princeton Q.** (SC187): YPM-PU 14137 (holotype); 21162, L max. C^1 frag., P^1-M^2. **SC243**: UM 61585, R M_3?

Prodiacodon cf. *P. tauricinerei*

Table 7

Prodiacodon sp., Secord, 2002, p. 105 A.

Biostratigraphic occurrences.— *Probathyopsis* (Ti-5a), *Plesiadapis simonsi* (Ti-5b) and *Plesiadapis gingerichi* (Ti-6) zones.

Description and discussion.— Fragmentary specimens from Y2K Quarry and other localities resemble teeth of both *Prodiacodon furor* from the late Torrejonian and *P. tauricinerei* from the early Eocene. Molars are easily within the size range of either species but are structurally closest to those of *P. furor* in having slightly less anteroposteriorly compressed trigonids than in *P. tauricinerei*. The P_4, however, is more similar to the latter in having a wider paraconid, relative to trigonid width. Novacek (1977, p. 30) noted that the metaconid in *P. furor* was larger and situated more posteriorly than in *P. concordiarcensis*, and he considered this an autapomorphy in *P. furor* (he notes on p. 30 that the metaconid on P_4 [= P_3 in homologies used here] is larger and posteriorly situated, but he apparently meant P_5 [= P_4], because P_4 [= P_3] has no metaconid and these characters are cited on P_5 in his diagnosis). However, only the base of the metaconid is preserved in the two P_4s in the typodigm. In the holotype (AMNH 35291) the break is at an oblique angle which could give the false appearance of a larger metaconid and in AMNH 35289 it is not obvious that the metaconid was significantly larger than in *P. concordiarcensis*. Furthermore, a P_4 (UM 108702) from Rock Bench Quarry is very similar to P_4 in the holotype of *P. furor* in size and structure, and may belong to *P. furor* but has a metaconid that is smaller than the protoconid. The validity of this character is in doubt pending the discovery of additional specimens of *P. furor* at Gidley Quarry.

One difference between *Prodiacodon furor* and *P. tauricinerei* is that the latter has a prominent additional cusp on the posterior slope of P_3. The P_3 in the Y2K form is similar to that in *Prodiacodon furor* in overall structure and in the absence of the additional cusp, but is considerably larger. It is close to the size of *P. tauricinerei* but has a smaller paraconid and a more trenchant talonid. The four P_3s included in the referred material all lack the additional cusp, suggesting that this feature is not variable. Upper teeth have not been described for *P. furor*. The P^3 in the Y2K form is within the variation of *P. tauricinerei*. The only P^4 (UM 109336) has the appearance of being etched, and may not be representative. It has only a trace of a postcingulum, in contrast to the well-developed postcingulum and small hypocone in *P. tauricinerei*, and its metaconid is smaller, relative to the paraconid. The Y2K specimens probably represent a new species but more complete material should be collected before establishing one.

A crushed snout (UM 68737) from the latest Tiffanian preserves at least P^3-M^3 and P_3-M_1 in occlusion, but is still partly encased in a concretion. Nevertheless, in the exposed parts no significant differences are apparent between it and the form at Y2K Quarry and it is included here in *P.* cf. *P. tauricinerei*. It is similar in size and the P_3 also lacks the additional large cusp on its posterior slope present in *P. tauricinerei*. Four fragmentary specimens from the Clarkforkian were referred to cf. *Prodiacodon tauricinerei* by Rose (1981a) and an additional one by Bloch (2001). These are about the same size as the late Tiffanian specimens and both samples may be part of a lineage leading to *P. tauricinerei* in the Eocene.

Referred specimens.— **Bluff Top Q.** (SC379): UM 108262, R M_2. **SC178**: UM 68737, crushed snout, L P^4-M^3, R P^3-M^2, L P_3-M_1. **SC273**: UM 73661, R $P_{3\text{-}4}$. **Y2K Q.** (SC389): UM 109139, R M_2; 109142, 3 premolars, probably assoc.; 109152, R M_3; 109240, R dent. P_3 (in crypt)-P_4 (erupting); 109312, L M^1 partial; 109314, L P_4; 109336, R max. $P^{3\text{-}4}$, assoc. C^1; 109358, L M_1; 109432, R P^3; 109575, L P_3; 109652, R P^3; 109655, L M_3; 109662, R P_4; 109848, L P^4 frag.; 110024, R M_1.

Cf. *Prodiacodon* sp.

Table 8

Biostratigraphic occurrences.— *Plesiadapis churchilli* zone (Ti-4a).

Description and discussion.— Isolated teeth from Divide Quarry and one from Long Draw Quarry appear to represent at least one undescribed species of *Prodiacodon*, or possibly a different leptictid genus. A P^3 (UM 109857) has a small, more lingually extended protocone than is typical in any described species of *Prodiacodon*. The specimens are closest to *P. tauricinerei* or *P. furor* in size but are slightly larger on average. The talonid on two P_4s (UM 87039, 110945) is considerably longer and slightly narrower than in either *P. tauricinerei* or *P. furor*, and the trigonid is higher. UM 110945 lacks enamel, presumably from crocodile predation (see Fisher, 1981).

Two lower molars from Divide Quarry (UM 85438, 92263) and one from Long Draw Quarry (YPM-PU 24573) have very anteroposteriorly compressed trigonids, to the degree seen is some palaeoryctids. Other features in these teeth are more typical of leptictids, however, such as wide talonid basins in UM 85438 and 92263, and well-separated hypoconid and hypoconulid cusps in YPM-PU 24573 (not preserved in UM specimens). The narrowness of the teeth, height of the trigonids, and degree of trigonid compression suggest a closer affinity to *Prodiacodon* than to *Palaeictops*, but the specimens do not agree with any described species.

I questionably include a fragmentary M_1 (UM 85920) that is similar in size to the other specimens but has a less anteroposteriorly compressed trigonid with a more rounded buccal margin than is typical of *Prodiacodon* and is more suggestive of *Palaeictops*. There may be more than one leptictid species in this sample, but if so, there is no discernable difference in size.

Referred specimens.— **Divide Q.** (FG046): UM 85438, R M_2?; 85920, L M_1 partial; 86234, R M_1; 87039, L P_4; 92263, L M_2?; 109857, R P^3; 110945, L P_4; 110947, L dent. frag. P_2. **Long Draw Q.**: YPM-PU 24573, R M_3.

TABLE 8 — Dental measurements for cf. *Prodiacodon* from Divide Quarry. *Estimate.

		UM 85438	UM 86234	UM 87039	UM 92263	UM 109857	UM 110947
P^3	L	—	—	—	—	—	—
	W	—	—	—	—	2.43	—
P_2	L	—	—	—	—	—	2.15
	W	—	—	—	—	—	0.85
P_4	L	—	—	3.33	—	—	—
	W tri.	—	—	1.80	—	—	—
	W tal.	—	—	1.35	—	—	—
M_1	L	—	2.35	—	—	—	—
	W tri.	—	2.05	—	—	—	—
	W tal.	—	1.67	—	—	—	—
M_2	L	—	—	—	2.47	—	—
	W tri.	2.25	—	—	2.0*	—	—
	W tal.	—	—	—	1.7*	—	—

Cf. *Palaeictops*

Palaeictops sp., Secord, 2002, p. 105A.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis simonsi* zone (Ti-5b).

Description and discussion.— A single fragmentary P^3 from Y2K Quarry appears to represent a leptictid about the size of *Palaeictops bicuspis*, known only from the Eocene. The P^3 is about 50% larger than those referred here to *Prodiacodon* cf. *P. tauricinerei* from Y2K Quarry. It is similar to the P^3 in the holotype of *P. bicuspis* but has a more lingually situated protocone and probably had a larger parastyle. More complete specimens of this species are necessary for a confident identification.

Three YPM-PU specimens from Princeton Quarry were questionably identified as *Palaeictops* by Rose (1981a, pp. 156-157), but these were not available for study. One specimen includes a skull and partial skeleton (YPM-PU 14526). A reconstruction of this individual was published by Case (1982, p. 433), who identified it as *Myrmecoboides*. As mentioned below in the *Myrmecoboides* section, however, it does not appear to belong to this genus.

Referred specimen.— **Y2K Q.**: UM 109256, R P^3.

MYRMECOBOIDES Gidley, 1915

Myrmecoboides arenarius, new species

Figure 13, Table 9

Myrmecoboides sp., Rose, 1981a, p. 152.
Myrmecoboides n. sp., Secord et al., 2006, p. 228.

Holotype.— YPM-PU 21301, a left dentary with $M_{1\text{-}3}$, preserving part of the horizontal ramus and angle. Collected by James Everhart on August 11, 1971, at Cedar Point Quarry in the Foster Gulch area of the northern Bighorn Basin, Wyoming.

TABLE 9 — Dental measurements for *Myrmecoboides arenarius* n. sp. from Cedar Point Quarry and for the holotype of *M. montanensis* (USNM 8037) from Gidley Quarry.

		USNM 8037 (type)	YPM-PU 21301 (type)	YPM-PU 21470
Dent. D		—	5.00	—
M_1	L	2.33	3.05	—
	W tri.	1.53	1.87	—
	W tal.	1.30	1.83	—
M_2	L	2.25	2.90	3.05
	W tri.	1.65	2.20	2.33
	W tal.	1.55	2.00	2.05
M_3	L	2.55	3.05	3.25
	W tri.	1.63	2.33	2.43
	W tal.	1.25	2.07	1.95

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Diagnosis.— The comparative descriptions that follow are based on a cast of the holotype of *Myrmecoboides montanensis* (USNM 8037) from Gidley Quarry, the only other described species in the genus. *Myrmecoboides arenarius* differs from *M. montanensis* in having: (1) larger molars; (2) lower and less anteroposteriorly compressed molar trigonids with a more open and more rounded trigonid notch; (3) more rounded molars; (4) a molar row oriented obliquely to the long axis of the dentary; (5) a shorter M_3 talonid with a less posteriorly projecting hypoconulid that is positioned closer to the hypocone; (6) an ascending ramus with a more gently sloping dorsal margin leaving more space behind M_3; and (7) absent or greatly reduced molar precingulids.

The M_1 is about 30% longer and 20% wider than the M_1 of *M. montanensis*. The degree of trigonid compression in the holotype is about 12%, 10%, and 18% less, relative to crown length, for M_1, M_2, and M_3, respectively, compared with trigonids in *M. montanensis*. Trigonid measurements were made from the point of contact between the cristid obliqua and postvallid, to the anterior-most point on the trigonid. There is a greater amount of lingual inclination in the molars of the holotype of *M. arenarius* than in those of *M. montanensis*, but this could have been influenced by post-depositional deformation. Because of this inclination, molars in *M. arenarius* are relatively wider if measured with the dentaries of both species in the same vertical orientation, but if molar width is measured parallel to the lingual surface of the molar trigonids, both species have the same relative width.

Etymology.— *Arenarius* (L), of sand: in reference to the sandstone deposits at Cedar Point Quarry, in which the holotype and other specimens were entombed.

Description.— The following description is based on the holotype unless otherwise indicated. Molars are lingually inclined to a moderate degree and have low trigonids relative to other leptictids. The molar row is moderately oblique to the long-axis of the dentary. Molars are subequal in length. Trigonids are anteriorly rounded, lack or have extremely reduced precingulids, and become progressively more anteroposteriorly compressed from M_1 to M_3. On all molars the paraconid is positioned anteriorly and slightly buccal of the metaconid. The M_1 paraconid is a relatively large, separate, and distinct cusp. The paraconid is highly variable in M_2. It is subequal in height and closely appressed to the metaconid in the holotype and YPM-PU 21490, but considerably lower and more anterobuccally positioned in YPM-PU 21305. The M_3 paraconid is also subequal in height and closely appressed to the metaconid in the first two specimens, but slightly lower and more anterior in the last. Talonid basins are shallow, rounded, and widely open lingually. All molars have a large hypoconid, a medium-sized entoconid, and a small- to medium-sized hypoconulid. The hypoconulid varies in position and is relatively close to the entoconid in M_{2-3} of YPM-PU 21490 and in M_1 of the holotype, but is farther apart and more centrally positioned in M_{2-3} of the holotype. Small metastylids are present anterior to the entoconid on M_{2-3} of YPM-PU 21490. Only slight metastylid swellings are visible in the other specimens, but these cusps may have been reduced by wear. In the holotype, the M_1 has a moderate amount of wear on the anterodorsal surface of the trigonid, but only light wear on the talonid, while M_{2-3} exhibit only light wear on the trigonid, but a significant amount of wear on the posterobuccal side of the talonid and in the talonid basin. The molars are generally rounded on the corners and margins, and the trigonid notch is open and rounded.

The dentary is deep relative to M_1 height and has a depth that is about 235% the height of the M_1 trigonid, measured below the buccal root of M_1. Relative to overall length, however, the dentary is relatively shallow compared with other mammals. A weak medial buttress is developed on the lingual surface of the dentary in the holotype and YPM-PU 21305. It begins below the talonid of M_3 and extends posteriorly to the dorsal edge of the mandibular foramen. The anterior margin of the ascending ramus slopes gently, leaving space behind the M_3. The mandibular fossa is ventrally deep.

Discussion.— *Myrmecoboides* is a rare taxon known primarily from quarry sites that have yielded large samples. It typically occurs at a frequency well below 1% (e.g., Rigby, 1980; Rose, 1981a, pp. 146, 149, 152). Its molars are highly unusual and I know of no other taxon from the Paleocene, except possibly the palaeanodont *Amelotabes* (Rose, 1978), that has teeth approaching this condition. Gidley (1915) originally placed *Myrmecoboides* in Marsupialia based on dental resemblance to *Myrmecobius*, an Australian anteater. Simpson (1937b), however, demonstrated that it was not a marsupial and was best placed in the Leptictidae. Leptictids are distinguished from other "insectivores" primarily by derived features of the P_4, and as Simpson noted, the P_4 of *M. montanensis* is structurally like those of leptictids. Simpson also noted, however, that *Myrmecoboides* was an aberrant member of the Leptictidae and does not belong with typical genera. I follow Simpson and other authors in placing *Myrmecoboides* in the Leptictidae (e.g., Novacek, 1977; McKenna and Bell, 1997) but note that it could alternatively be a member of the Escavadodontidae, a family provisionally placed in Palaeanodonta (Rose and Lucas, 2000).

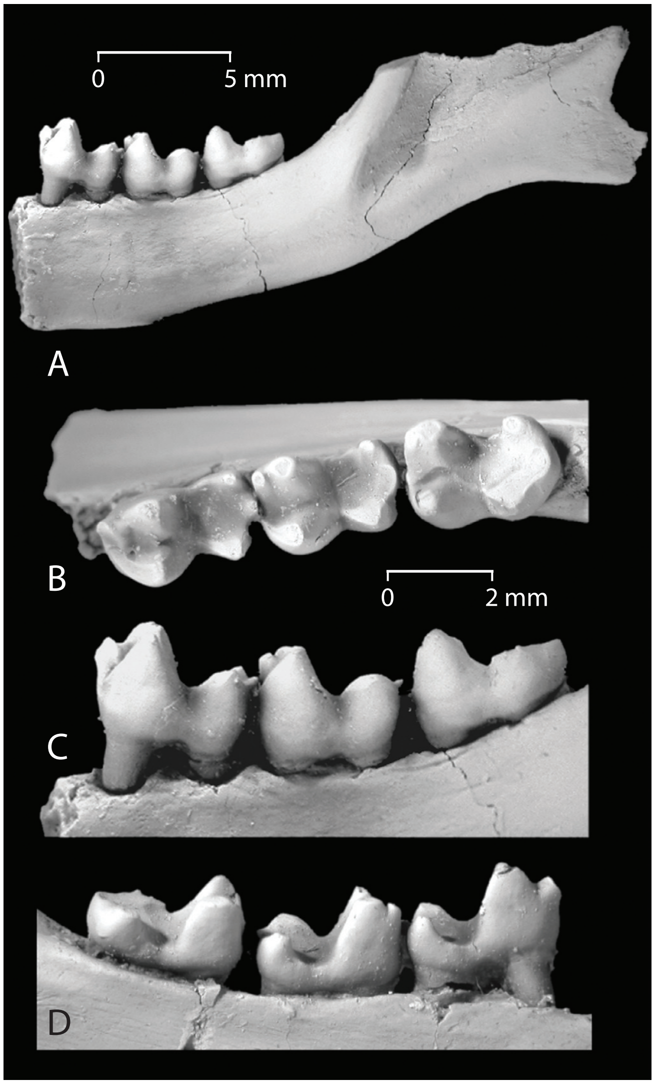


FIGURE 13 — Holotype of *Myrmecoboides arenarius* n. sp. from Cedar Point Quarry. Left dentary (YPM-PU 21301) in buccal (A, C), occlusal (B), and lingual (D) views.

Myrmecoboides arenarius is easily distinguished from *M. montanensis*, the type and only other described species in the genus. The holotype of *M. montanensis* was described and figured by Gidley (1915), Simpson (1937b), and Novacek (1977). *Myrmecoboides montanensis* is known from several localities of late Torrejonian (e.g., see Rigby, 1980; Rose, 1981a) and early Tiffanian age (Gingerich et al., 1983; Krause and Gingerich, 1983; Fox, 1990; Krause and Maas, 1990).

Variability in dental features in *Myrmecoboides arenarius* is high. Although this could suggest the presence of more than one species, the molars of *M. arenarius* lack indications of precise occlusion, as discussed below. Dental variability may be higher in mammals with poor occlusion and there is no appreciable difference in size among the specimens. Thus, there is no compelling evidence for the presence of more than one species.

A simplification in molar structure takes place in *Myrmecoboides* from the late Torrejonian to the middle Tiffanian. In molars of the younger *M. arenarius* trigonids are lower, the trigonid notch is more open and rounded, the M_3 talonid is shorter, and the anterior cingula are lost or greatly reduced. The postvallid is more rounded and lacks the flat shearing surface typical of leptictids. These features indicate less precise occlusion and a shift away from shearing. Additionally, the basal anterior margin of the ascending ramus is low and more gently sloping. These changes are indicative of a shift toward the condition seen in the earliest dental palaeanodonts, namely *Amelotabes simpsoni* (Rose, 1978), *Propalaeanodon schaffi* (Rose, 1979), and *Mylanodon rosei* (Secord et al., 2002), which first appear in the late Tiffanian after *M. arenarius*.

The earliest unequivocal palaeanodont is *Amelotabes simpsoni*, known from a single specimen reportedly collected at a level equivalent to Croc Tooth Quarry (Rose, 1978) in the *Phenacolemur* zone (Ti-4b). Rose (1978, p. 663) noted similarities between *Myrmecoboides* and *A. simpsoni* but suggested that these characters may be primitive. Rose was presumably referring to *M. montanensis*, the only species described at the time. It appears, however, that several features shared between *M. arenarius* and *A. simpsoni* may be synapomorphies. These are: (1) reduction of molar trigonid height; (2) an opening of the back of the molar talonid basin; (3) rounding of molar margins and cusps; (4) anteroposterior expansion of molar trigonids; (5) obliquity of the molar row; and (6) an ascending ramus with a low slope along the anterior dorsal margin. The unusual condition in *M. montanensis* of having significant diastemata between premolars is also present in *A. simpsoni* and was presumably retained in *M. arenarius*.

Derivation of *Amelotabes simpsoni* from *Myrmecoboides arenarius* or a closely related, shared ancestor, would require the addition of a more robust dentary, relative to M_1 size, a reduction in trigonid height, anteroposterior expansion of trigonids, reduction and rounding of cusps, and a lower basal slope on the anterior margin of the ascending ramus. All of these features might be expected, except perhaps the development of a more robust dentary, by the direction of character change noted above in the comparison of *M. arenarius* to *M. montanensis*. The suite of shared characters, the implied direction of character change, and the relative stratigraphic positions of these taxa, are compelling evidence that *M. arenarius* and *A. simpsoni* may have been sister taxa or species in an evolutionary lineage. The acquisition of more specimens of both species and of possibly related species will undoubtedly contribute to a better understanding of these taxa. A rigorous phylogenetic analysis including additional taxa is in order, but is beyond the scope of this section.

The Cedar Point Quarry (Ti-3) occurrence of *Myrmecoboides arenarius* is the youngest documented occurrence of *Myrmecoboides*. A younger specimen (YPM-PU 14526) from Princeton Quarry (Ti-5a), which includes a skull and postcrania, was reconstructed as *Myrmecoboides* by Case (1982, p. 433). The skull was not available for study but examination of the teeth by Douglas Boyer (pers. comm., 2003) indicated that the specimen does not belong to *Myrmecoboides*.

Referred specimens.— **Cedar Point Q.**: YPM-PU 21301 (holotype); 21305, dent. M_{1-3}. 21490, L dent. M_{2-3}.

Superorder PREPTOTHERIA McKenna, 1975
Grandorder ANAGALIDA Szalay and McKenna, 1971
Order RODENTIA Bowdich, 1821
Family ISCHYROMIDAE Alston, 1876

ACRITOPARAMYS Korth, 1984

Acritoparamys atavus (Jepsen, 1937)
Figure 14

Paramys atavus Jepsen, 1937, p. 297.
Acritoparamys atavus, Korth, 1984, p. 29. Ivy, 1990, p. 41.

Holotype.— YPM-PU 14200, R M_2 from Eagle Coal Mine, Bear Creek fauna; from the northern Bighorn Basin of Montana. Rodentia zone (Cf-1).

Biostratigraphic occurrences in Bighorn Basin.— Clarkforkian zones.

Description.— The holotype was described and figured by Jepsen (1937) and Korth (1984), and additional specimens were described and figured by Korth (1984) and Ivy (1990).

Discussion.— A single partial M^3 (UM 108587) etched from a freshwater limestone is the earliest occurrence of a rodent in the Bighorn Basin and probably in North America. It marks the beginning of the Clarkforkian on the west side of Polecat Bench. This is one of only two rodent molars known from early Clarkforkian localities in the Bighorn Basin that occur in a measured stratigraphic sequence. The second is an M^1 (UM 36190) from SC-179, about 35 meters higher in the section. It was also etched from a freshwater limestone and was informally recognized as a new species of *Acritoparamys* by Bloch (2001), based primarily on its small size. The M^1 is considerably smaller than those of *A. atavus*. The presence of two species close to the beginning of the Clarkforkian is especially important because it suggests that both immigrated into North America at approximately the same time, presumably as a result of the same causal mechanism.

The M^3 included here is similar to the M^3 in UM 73614 (Ivy, 1990, Figs. 7, 8C) from the middle Clarkforkian (Cf-2) identified as *Acritoparamys atavus* by Ivy. It differs, as far as can be compared, from this and other specimens included in the species only in having a paraconule that is situated slightly more anteriorly and that interrupts the confluence of the precingulum (Fig. 14). The precingulum is also slightly more constricted below the paraconule. UM 108587 is at the top of the size range for specimens of *A. atavus*. In this regard it is closer to the holotype of *A. atavus*, from the early Clarkforkian, than are most of the specimens that were included in *A. atavus* by Rose (1981a) and Ivy (1990), from the middle and late Clarkforkian. Korth (1984) placed middle and late Clarkforkian specimens in a separate species, *Apatosciuravus bifax*, in part because of their smaller size. Ivy (1990) pointed out, however, that specimens of *A. atavus* appear to follow a trend of decreasing size though time and that a large size might be expected for early Clarkforkian specimens. The larger size of UM 108587 is consistent with that prediction and it may be more representative of *A. atavus* than younger occurrences. The differences cited above do not seem great enough to warrant taxonomic separation of the younger Clarkforkian specimens referred to *A. atavus* by Ivy (1990) from UM 108587.

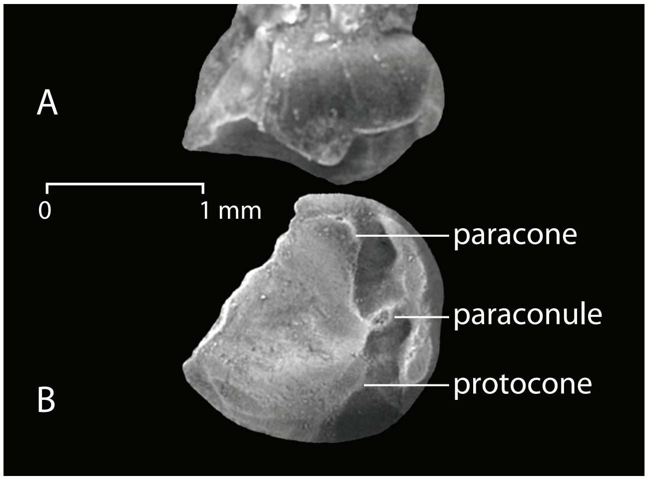


FIGURE 14 — Partial M^3 of *Acritoparamys atavus* (UM 108587) from SC-181 in buccal (A) and occlusal (B) views. This specimen marks the beginning of the Clarkforkian in the Polecat Bench-Sand Coulee sequence.

Numerous incisors are known from the early Clarkforkian but available comparative material is not adequate for even tentative identification.

Dental measurements (mm).— UM 108587: M^3, W = 1.7*.

Referred specimen.— **Bear Creek fauna**: AMNH 22195, L P^4; YPM-PU 14200; incisors included by Jepsen (1937) or Korth (1984): AMNH 22155; 22156; 22163; 22166; 22199; CM 11552, 11690; YPM-PU 14200c. **SC181**: UM 108587, R M^3 partial.

Grandorder FERAE Linnaeus, 1758
Order CIMOLESTA McKenna, 1975
Family PALAEORYCTIDAE Winge, 1917

PALAEORYCTES Matthew, 1913

Palaeoryctes jepseni Bloch et al., 2004
Figure 15

Palaeoryctes jepseni Bloch et al., 2004, p. 127.

Holotype.— UM 109156, right dentary with P_3-M_3 and alveoli for C_1 (posterior part) and P_2, from Y2K Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a), *Probathyopsis* (Ti-5a), and *Plesiadapis simonsi* (Ti-5b) zones.

Description and discussion.— A detailed description of *P. jepseni* was recently published by Bloch et al. (2004). Figure 15 shows the holotype from Y2K Quarry.

Referred specimens.— **Divide Q.** (FG046): UM 83232, R dent. $P_{3\text{-}4}$, C_1-P_2 alveoli; 83272, R M_2; 83273, L P_4; 87043, R dent. M_1. **Princeton Q.**: YPM-PU 13958, L max. P^3-M^1, partial M^2, R max. P^4-M^2, partial M^3; 14122, L max. P^4-M^3; 17806, L dent. P_4-M_1, $I_{2\text{-}3}$ roots, R dent. I_2, C_1 (base), P_3-M_3, I_3 alveolus; **Schaff Q.**: YPM-PU 19394, L dent. C_1 (partial), P_2-M_3. **Y2K Q.** (SC389): UM 109156 (holotype); 109319, L M^1; 109420, L M^1; 109434, L dent. C_1-M_1; 109458, R max. P^3-M^3, C^1-P^2 alveoli; 109506, L dP^4?; 109549, L M^2; 109584, R P^4; 109847, L M_1.

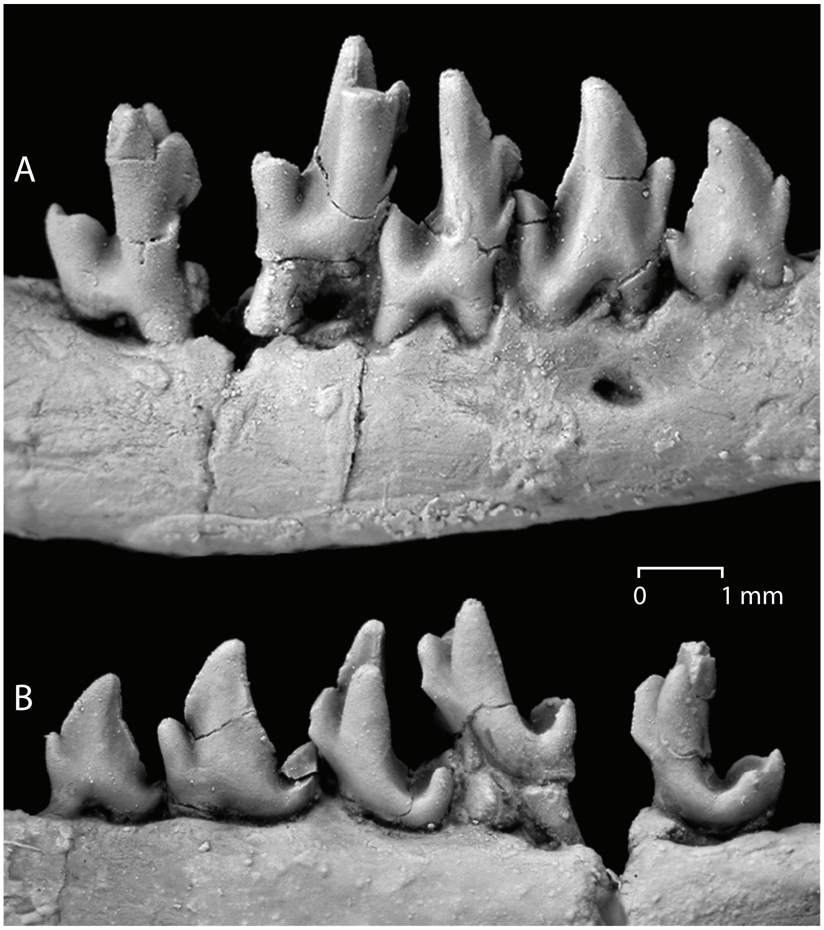


FIGURE 15 — Holotype of *Palaeoryctes jepseni* from Y2K Quarry. A–B, right dentary (UM 109156) with P_3-M_3 in buccal (A) and lingual (B) views.

AAPTORYCTES Gingerich,1982a

Aaptoryctes ivyi Gingerich, 1982a
Table 10

Aaptoryctes ivyi Gingerich, 1982a, p. 39.

Holotype.— UM 77291, crushed anterior portion of skull preserving left $P^{3\text{-}4}$ and right P^3-M^3, left dentary with C_1-M_3, and right dentary with P_2-M_3; from FG-047 in the Foster Gulch area, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences.— *Phenacolemur* (Ti-4b) or *Probathyopsis* (Ti-5a) zones.

Description and discussion.— The holotype of *Aaptoryctes ivyi* was described by Gingerich (1982a). Two specimens that were included in the hypodigm by Gingerich are referred by me to *A*. cf. *A*. *ivyi* below. I have not studied two additional specimens (CM 8802, CM 8890) included in the hypodigm from Dell Creek Quarry in southwestern Wyoming. No new specimens that are clearly referable to *A*. *ivyi* have been found in the Bighorn Basin or reported from elsewhere.

The exact age of the holotype is uncertain but it appears to be from either the *Phenacolemur* zone (Ti-4b) or lower part of the *Probathyopsis* zone (Ti-5a). Gingerich (1982a) identified an isolated molar of *Plesiadapis* (UM 77302), collected slightly higher than the type locality of *A*. *ivyi* (FG-047), as an M_1 of *P*. *simonsi* and concluded that the holotype was from the *P*. *simonsi* zone (then including strata now in Ti-5a and b). UM 77302 was re-identified here as an M_2 of *Plesiadapis churchilli* but a Ti-5a age assignment is still weakly supported by an unsubstantiated occurrence of *Probathyopsis* at a level that appears to be a slightly higher than FG-047. The occurrence is based on locality data from an unpublished areal photograph used by G. L. Jepsen. The occurrence of *P*. *churchilli* and *Phenacodus magnus* at FG-048 (Thewissen, 1990, UM 77304, 77305) and a partial skeleton of *Leptolambda churchilli* (YPM-PU 14879) at approximately the same level as FG-047 suggest, however, that FG-047 is correlative to the *Phenacolemur* zone. *Leptolambda churchilli* is not known from localities younger than the *Phenacolemur* zone and although the first two species are known from rare occurrences in the lower *Probathyopsis* zone they are common in the *Phenacolemur* zone. An earlier age is also supported by the fact that no specimens of *A*. *ivyi* or *A*. cf. *A*. *ivyi* have been found in the *Probathyopsis* zone on Polecat Bench, in spite of large microsamples from Princeton and Schaff quarries. If *Aaptoryctes ivyi* did range into the *Probathyopsis* zone it must have lived in a rarely sampled environment.

TABLE 10 — Dental measurements for the holotype of *Aaptoryctes ivyi* (UM 77291) and for *A.* cf. *A. ivy* from Divide Quarry (DQ), Fossil Hollow (FH), and Sand Coulee (SC) and Foster Gulch (FG) localities.

		UM 61591 SC-243	UM 61597 SC-243	UM 77291 (type) FG-47	UM 79875 FH	UM 79875 FH	UM 85288 DQ	UM 85927 DQ	UM 109856 DQ	UM 110229 FH	YPM-PU 20512 FH
M^1	L	—	—	2.85	—	2.65	—	—	2.80	—	—
	L lingual	—	—	1.45	—	1.25	—	—	1.20	—	—
	W	—	—	4.05	—	3.85	—	—	3.75	—	—
P_4	L	—	—	3.25	2.70	—	—	—	—	—	—
	W	—	—	2.25	1.80	—	—	—	—	—	—
M_1	L	—	2.55	2.80	—	—	—	2.65	—	—	—
	W	—	—	2.65	—	—	—	2.35	—	2.10	—
M_2	L	2.50	—	2.55	—	—	—	—	—	—	2.40
	W	2.40	—	2.70	—	—	2.50	—	—	—	2.45

Aaptoryctes cf. *A. ivyi*
Table 10

Aaptoryctes ivyi (in part), Gingerich, 1982a

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a) and *Phenacolemur* (Ti-4b) zones.

Description and discussion.— Isolated teeth from Divide Quarry, Fossil Hollow, and anthills at SC-243 appear to represent a new species of *Aaptoryctes*. However, I refrain from formally describing a new species because of the fragmentary nature of the material. The teeth are similar to those of *Aaptoryctes ivyi* (Gingerich, 1982a) in most respects, but are smaller and have a less inflated appearance. Subsequent references to *A. ivyi* refer only to the holotype. *Aaptoryctes ivyi* has enlarged premolars specialized for crushing (Gingerich, 1982a), which is a unique specialization in the Palaeoryctidae (as recognized by McKenna and Bell, 1997). The P_3 and P_4 of *A. ivyi* exhibit a high degree of buccolingual expansion, relative to other palaeoryctids, and have an inflated appearance. The M_1 also has an inflated appearance and the trigonid is less anteroposteriorly compressed than is typical of other palaeoryctids.

A P_4 (UM 79875) is probably the most diagnostic of the specimens identified here as *Aaptoryctes* cf. *A. ivyi*. It is highly inflated, but to a slightly lesser degree than in *A. ivyi*. It is smaller and the talonid basin is shallower, but in other respects it is very similar. It could possibly be a P_3 of *A. ivyi*, but the overall development and structure of the talonid agrees best with the P_4 in *A. ivyi*, which is basined, has a short cristid obliqua, and is rimmed by a crest along the posterior margin. The talonid of the P_3 consists of only a single cusp and a small lingual flat surface, and is considerably smaller relative to the overall size of the crown.

Two molars from Fossil Hollow (UM 77923 and YPM-PU 20512, in part) were included in the hypodigm of *Aaptoryctes ivyi* by Gingerich (1982a), but are here referred to *A.* cf. *A. ivyi*. UM 77923 is a dentary fragment preserving the trigonid of M_2. It has approximately the same amount of anteroposterior compression as the M_2 trigonid in *A. ivyi* but is buccolingually narrower. YPM-PU 20512 could be either an M_1 or an M_2 but is considerably smaller than either in *A. ivyi*.

Several of the molars I have included in *Aaptoryctes* cf. *A. ivyi* also bear a close resemblance to *Palaeoryctes cruoris* from the Chappo Type locality in southwestern Wyoming (Gunnell, 1994). The results of a stratocladistic analysis by Bloch et al. (2004) suggest that *P. cruoris* and *A. ivyi* were part of a single lineage beginning with *P. cruoris* in the middle Tiffanian and terminating with *A. ivyi* in the late Tiffanian. Characteristics in the referred molars are consistent with this hypothesis. Divide Quarry is closest in age to the Chappo Type locality but is slightly younger. The M_1 (UM 85927) from Divide Quarry is similar to that of *P. cruoris* but is larger, and has a less compressed and slightly shorter trigonid. It is, however, smaller than the M_1 in *A. ivyi* and is less inflated. The trigonid in the M_1 of *A. ivyi* is heavily worn and height cannot be measured, but based on the low height of M_2, it was almost certainly lower than the trigonid of UM 85927. The degree of trigonid compression in UM 85927 is similar to that in *A. ivyi*. M_1s from SC-243 and Fossil Hollow are close to UM 85927 but are more worn or less complete. The trigonids on these teeth are about 5% longer than those in *P. cruoris*, relative to total crown length, based on measurements made parallel to a vertically oriented postvallid, not including the precingulid. This is based on averages, however, and this character varies by about ±5% in *P. cruoris*.

The referred M_2 from Divide Quarry (UM 85288) is nearly identical to those of *Palaeoryctes cruoris* except for being larger, and it has a much higher trigonid than M_2 in *Aaptoryctes ivyi*. The referred M_2 (UM 77923) from Fossil Hollow, which is slightly younger, has a considerably lower trigonid that is about the same height as the M_2 in *A. ivyi*. This suggests that the younger Fossil Hollow specimens are closer to *A. ivyi*, as would be expected if both forms were part of the same evolving lineage. Of note, the M_2 figured by Gunnell (1994, UM 93117, Fig. 4) in a composite of *P. cruoris* differs from others in the Chappo sample that are more typical of *Palaeoryctes* in that its hypoconid and hypoconulid are spaced farther apart, the talonid is wider and squarer, and the paraconid is round, rather than blade-like. UM 93117 probably belongs to a leptictid.

The referred M^1s from Divide Quarry and Fossil Hollow are intermediate in size between those of *Aaptoryctes ivyi* and

TABLE 11 — Dental measurements for *Paleotomus radagasti* from Cedar Point (CPQ) and Divide (DQ) quarries, and for *P*. cf. *P. radagasti* from FG-1. *Estimate.

		UM 64504 CPQ	UM 64530 CPQ	UM 64530 CPQ	UM 66659 CPQ	UM 73968 FG-1	UM 83277 DQ	UM 85401 DQ	UM 108860 DQ	YPM-PU 21239 CPQ	YPM-PU 21416 (cast of type) CPQ
P^4	L	—	—	—	—	5.30	—	—	—	—	—
	W	—	—	—	—	4.65	—	—	—	—	—
M^1	L	—	—	—	—	—	—	—	—	—	—
	Mll	—	—	—	—	3.20	—	—	3.45	—	—
	W	—	—	—	—	6.20	—	—	6.85	—	—
	Mlc	—	—	—	—	2.60	—	—	3.20	—	—
M^2	L	—	—	—	—	6.00	—	—	—	—	—
	Mll	—	—	—	3.80	3.55	—	—	—	—	—
	W	—	—	—	9.25	7.85	—	—	—	—	—
	Mlc	—	—	—	3.25	2.75	—	—	—	—	—
M^3	L	—	—	5.95	—	—	—	—	—	—	—
	W	—	—	7.85	—	—	—	—	—	—	—
P_3	L	5.29	—	—	—	—	—	—	—	5.40	—
	W	2.57	—	—	—	—	—	—	—	2.50	—
P_4	L	—	—	—	—	—	6.57	—	—	6.50	5.40
	W	—	—	—	—	—	2.90	—	—	3.10	2.45
M_1	L	—	5.50	—	—	—	—	—	—	—	5.22
	W tri.	—	3.50	—	—	—	—	—	—	—	3.67
	W tal.	—	3.45	—	—	—	—	—	—	—	3.17
M_3	L	—	—	—	—	—	—	6.4*	—	—	—
	W tri.	—	—	—	—	—	—	4.8*	—	—	—
	W tal.	—	—	—	—	—	—	2.7*	—	—	—

Palaeoryctes cruoris. They differ further from the M^1 in *A. ivyi* in having relatively smaller and more buccolingually compressed paracones and metacones, and smaller and less rounded protocones. The anterior and posterior margins of the M^1 in *A. ivyi* expand lingually around the protocone but are nearly parallel in *P. cruoris*. The referred M^1s are also generally more gracile. They differ from those of *P. cruoris* in being larger and more buccolingually elongate. The M^1 (UM 109856) from Divide Quarry has a more buccally expanded parastylar area, as does that of *P. cruoris*, while the M^1 from Fossil Hollow (UM 110971) has a straighter buccal margin, as does that of *A. ivyi*. A distinct stylocone is present on UM 109856 and a swelling of the stylar shelf is present in this position in UM 110971. It is not clear if the M^1 in *A. ivyi* had a stylocone, due to wear, but one is present on M^2. It is also not clear because of wear if a stylocone was present in *P. cruoris*. An elongate paraconule is present in UM 110971 but a metaconule is barely discernable. The presence of conules in the M^1 of *A. ivyi* is uncertain but a prominent paraconule and smaller metaconule are present in specimens of *P. cruoris*. UM 110971 has incipient pre- and postcingula, and UM 110856 has an incipient precingulum, as does the M^1 of *A. ivyi*. Incipient pre- and postcingula are variably present in M^1s of *P. cruoris*.

The characteristics described above for the referred sample are consistent with those of a transitional species between *Palaeoryctes cruoris* and *Aaptoryctes ivyi*. The last two species are best distinguished using premolars, and based on the derived condition of the P_4 from Fossil Hollow (UM 79875), *Aaptoryctes* is the best identification for the specimens. Notably, all of the referred specimens may be older than the holotype of *A. ivyi* (see above) and it is possible that *A. ivyi* represents the final form in a lineage leading to greater premolar inflation. Alternatively, the teeth included here could belong to *A. ivyi* and the holotype represents an extreme variant of the species.

Referred specimens.— **Divide Q.** (FG046): UM 85288, L M_2; 85927, L M_1; 109856, R M^1. **Fossil Hollow** (SC198): UM 77923, R dent. partial M_2; 79875, L M^1, R P_4; 110229, L M_1 partial; 110331, R P_4 partial; 110971, L M^1; YPM-PU: 20512, R M_1 or M_2. **SC243**: UM 61591, R M_2; 61597, R M_1; 61598, R M_1.

Suborder DIDELPHODONTA McKenna, 1975
Family CIMOLESTIDAE Marsh, 1889

PALEOTOMUS Van Valen, 1967

Paleotomus radagasti (Van Valen, 1978)
Table 11

Niphredil radagasti Van Valen, 1978, p. 66.
Paleotomus radagasti, Krause and Gingerich, 1983, p. 172.

Holotype.— YPM-PU 21416, a left dentary with P_2, P_4-M_1, alveoli for P_1, P_3, and $M_{2\text{-}3}$, from Cedar Point Quarry. Also preserved are the lower part of the ascending ramus, the angle, and articular condyle.

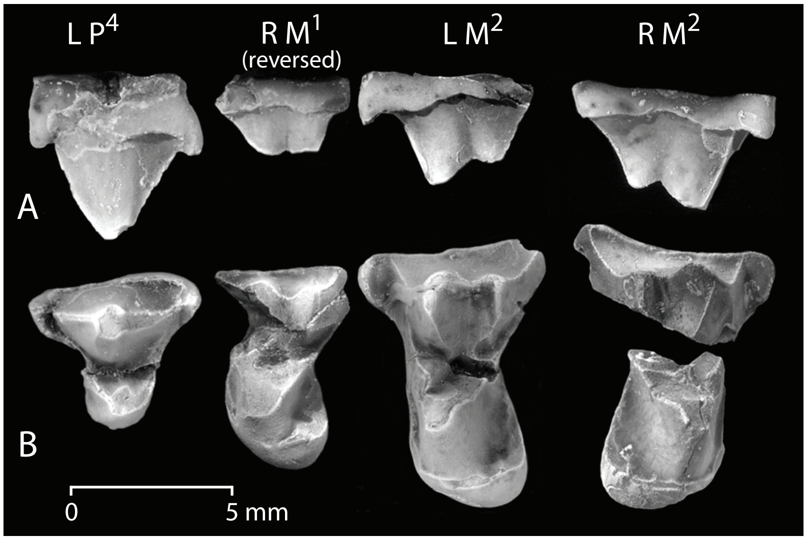


FIGURE 16 — Associated upper teeth (UM 73968) of *Paleotomus* cf. *P. radagasti* from FG-1. A–B, from left to right, left P^4, right M^1 (reversed image), left M^2, and right M^2 in buccal (A) and occlusal (B) views.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* (Ti-3) and *Plesiadapis churchilli* (Ti-4a) zones.

Description.— A brief description was provided by Van Valen (1978). To that description I add the following observations based on material from the type locality. Based on alveoli, C_1-P_1 were single-rooted. The C_1 alveolus is larger than any other. $P_{2\text{-}3}$ are double-rooted, trenchant, and have a single posterior "talonid" cusp separated from the protoconid by a "carnassial" notch. The posterior cusp is blade-like and bears a sharp crest that ascends the posterior face of the protoconid. Paraconids are incipient or absent on P_3. A weak discontinuous lingual cingulid is present on both P_3s. P_4 is double-rooted, trenchant, and has a distinct connate paraconid and single talonid cusp, both separated from the protoconid by "carnassial" notches. P_4 has a distinct posterolingual metaconid situated between the talonid cusp and protocone apex. The M_1 talonid bears three cusps and has a shallow basin. Based on three dentaries, mental foramina are present below the M_1 trigonid and below the P_1 or anterior root of P_2.

M^2 (UM 66659) has distinct para- and metaconules, while M^3 (UM 64530) has a distinct paraconule but indistinct metaconule. Two accessory cuspules are present along the parastylar wing on M^3, posterobuccally of a prominent parastyle. The posterior cuspule is at the anterior termination of a crenulated buccal cingulum. The M^2 has a wide postcingulum with a lingual hypoconular expansion, while the M^3 has a narrower postcingulum with a lingual expansion. Both molars have a narrow precingulum that is discontinuous with the postcingulum. Based on the M^1 (UM 108860) from Divide Quarry, the postcingulum becomes progressively narrower from M^1 to M^3, and hypoconular expansion is greatest on M^1.

Discussion.— The genus *Niphredil* and type species *N. radagasti* were established by Van Valen (1978) based on a dentary from Cedar Point Quarry. *Niphredil* was later synonymized with *Paleotomus* by Krause and Gingerich (1983, p. 172) after study of more complete material of *P. senior*, the type species for *Paleotomus*, indicated that generic separation was unwarranted. The most complete specimen of *P. radagasti* is still the holotype. Two additional dentaries preserve P_3 and the canine alveolus. Upper dentition is known only from isolated molars. UM 66659 (M^2) and 64530 (M^3) were figured by Gingerich (1980d, Fig. 3C).

The P_4 in YPM-PU 21239 from Cedar Point Quarry is 22% shorter than the P_4 in the holotype. It also differs in having a slightly smaller and more posteriorly situated metaconid. The P_3 in YPM-PU 21239 is indistinguishable from the P_3 of UM 64504 in both size and structure but the dentary in the latter is shallower. These three specimens encompass a considerable amount of variability.

Three specimens from Divide Quarry are here referred to *Paleotomus radagasti*. UM 85401 is a dentary preserving M_3 and alveoli for P_4-M_2. The enamel has been mostly removed from the M_3 by etching, possibly by crocodile ingestion (see Fisher, 1981), but the size does not appear to have been greatly reduced. The dentary is slightly smaller than any from Cedar Point Quarry. An isolated P_4 (UM 83277) is within the upper size range at Cedar Point Quarry, but slightly narrower. An M^1 (UM 108860) is within the size range expected for *P. radagasti*.

There appears to be a considerable amount of variability in size and proportion in *Paleotomus radagasti* at both Cedar Point and Divide quarries. This could be indicative of more than one species or of sexual dimorphism. The samples are too small, however, to adequately demonstrate either of these possibilities and I provisionally recognize a single highly variable species.

Referred specimens.— **Cedar Point Q.**: UM 64504, L dent. P_3, C_1-P_2 and P_4-M_3 alveoli; 64530, R M^3; 66659, L M^2; YPM-PU 20027, M^x; 21239, L dent. frag., $P_{3\text{-}4}$; 21416 (holotype); 24580 R M^1. **Divide Q.** (FG046): UM 83277, R P_4; 85401, R dent. M_3, P_4-M_2 alveoli; 108860, L M^1.

Paleotomus cf. *P. radagasti*

Figure 16, Table 11

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis simonsi* zone (Ti-5b).

Description.— P^4 has a distinct parastyle and metastyle. The principal cusp is singular and buccolingually compressed. There is no indication of a metacone. The protocone is small and connate, but well-developed and about half the height of the principal cusp. There is a weak discontinuous buccal cingulum. The P^4 has three roots. Important features of the molars are discussed below.

Discussion.— A fragmentary disarticulated palate (Fig. 16, UM 73968) preserving P^4-M^2 and fragments of other teeth was collected in the *Plesiadapis simonsi* zone in Foster Gulch. It is the most complete upper dentition of *Paleotomus* yet described and represents the youngest documented occurrence of this genus. The molars are broken to varying degrees. They are proportionally similar to molars identified as *Paleotomus radagasti* but are smaller and have a straighter buccal margin with a shallower ectoflexus. The M^1 and M^2 are about 10% and 15% smaller than UM 108860 and 66659, respectively, identified as *P. radagasti*. These teeth also differ in that the M^1 hypoconular expansion of the post cingulum is situated more lingually than in UM 108860 and the M^2 pre- and post cingula are connected across the protocone, rather than separate as in UM 66659.

Teeth are larger than those of *Paleotomus milleri* (Rigby, 1980), *P. junior* (Scott et al., 2002), and *P. carbonensis* (Secord, 1998) but are close in size to those of *Paleotomus senior* from Scarritt Quarry (see Gingerich, 1980c, Table 2). They differ, however, in having much wider post cingula with larger hypoconular expansions (e.g., compare Fig. 16 to Fig. 1 in Gingerich, 1980c) and a longer and more extended stylar shelf in M^2 that has a larger parastyle. Gingerich (1980d, Figs. 3D-F) referred an M_3 (UM 34759) from Dell Creek Quarry to cf. *Paleotomus* (then *Niphredil*) *radagasti* that was also about the size of *P. senior* and could belong to the same species as UM 73968. Dell Creek Quarry is probably a correlative of either the *Plesiadapis churchilli* or *Phenacolemur* zone, based on the co-occurrences of *Thryptacodon australis* (UM 27232) and *Neoplagiaulax mckennai* (UM 55129) (also see Dorr, 1958, 1978). Previous age estimates put Dell Creek Quarry in the *Plesiadapis simonsi* zone (~Ti-5a and Ti-5b here) based on the presence of *Plesiadapis fodinatus* (Gingerich, 1976; Archibald et al., 1987; Lofgren et al., 2004). However, the premolars in *Plesiadapis* from Dell Creek Quarry are more primitive than those of *P. fodinatus* (single talonid cusps on P_{3-4}, large metaconule on P^4) and the species may be *P. churchilli*.

The variability in *Paleotomus radagasti* is high, as noted in the discussion of the Cedar Point Quarry sample. UM 73968 bears the closest resemblance to *P. radagasti* and may represent a smaller descendant species or possibly a small individual of *P. radagasti*.

Referred specimens.— **FG001**: UM 73968, disarticulated palate, L P^4, M^2, R M^{1-2}.

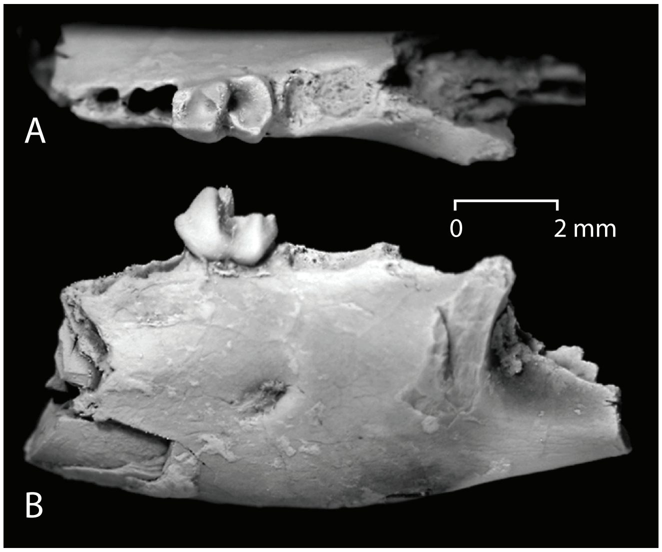


FIGURE 17 — Left dentary (UM 86237) of *Labidolemur soricoides* from Divide Quarry with M_1 in occlusal (A) and buccal views (B). Note incipiently divided P_4 alveoli.

Suborder APATOTHERIA Scott and Jepsen, 1936
Family APATEMYIDAE Matthew, 1909

LABIDOLEMUR Matthew and Granger, 1921

Labidolemur soricoides Matthew and Granger, 1921

Figure 17, Tables 12–13

Labidolemur soricoides Matthew and Granger, 1921, p. 4. McKenna, 1963, p. 18.
Apatemyidae indet., Secord, 2002, p. 105.

Holotype.— AMNH 17400, left and right dentaries preserving I_1 and M_1, from Mason Pocket, Colorado.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* (Ti-3), *Plesiadapis churchilli* (Ti-4a), *Phenacolemur* (Ti-4b), *Probathyopsis* (Ti-5a), and *Plesiadapis simonsi* (Ti-5b) zones.

Description.— A detailed description of the holotype was provided by McKenna (1963) and descriptions of the Cedar Point Quarry specimens were provided by West (1973). As an appendum to West's description, some specimens have two closely positioned mental foramina (e.g., UM 71833), rather than just one. The posterior foramen is the largest and is positioned below the anterior or posterior root of M_1. The anterior foramen is considerably smaller, is slightly lower, and about 1.0 mm more anterior.

Discussion.— Specimens included here in *Labidolemur soricoides* appear to represent a single lineage ranging from the middle to the late Tiffanian (Ti-3 to Ti-5a). There are probably two distinct species present in this lineage but I refrain from establishing a new species because of the fragmentary nature of the specimens available. Also problematic is the fragmentary condition of the holotype of *L. soricoides* from Mason Pocket (Ti-4a, Secord et al., 2006) in southern Colorado and it is not clear which of the Bighorn Basin Tiffanian forms should be placed

TABLE 12 — Dental measurements for *Labidolemur soricoides* and *L. kayi* from Mason Pocket, Divide (DQ) and Y2K quarries, from the *Probathyopsis* zone (Ti-5a), and from Sand Coulee (SC) localities. *Estimate.

		Labidolemur soricoides										*L. kayi*	
		AMNH 17400 (type) Mason Pocket	UM 77314 DQ	UM 80581 DQ	UM 85430 DQ	UM 86237 DQ	UM 109859 DQ	UM 109192 Y2K	UM 109282 Y2K	YPM-PU 19092 Ti-5	YPM-PU 20711 Ti-5	UM 73500 SC-188	UM 73616 SC-189
Dent. D		—	—	—	—	5.60	—	—	—	—	5.60	—	—
I^1	L	—	3.12	—	—	—	—	—	2.31	—	—	—	3.11
	W	—	1.49	—	—	—	—	—	1.22	—	—	—	1.37
I^2	L	—	—	—	—	—	—	2.38	—	—	—	—	—
	W	—	—	—	—	—	—	1.25	—	—	—	—	1.20
I_1	L	—	—	—	6.48	—	6.3*	—	—	—	—	6.40	—
	W	—	—	1.94	1.90	—	1.90	—	—	—	—	1.79	—
	D	—	—	2.90	2.80	—	2.95	—	—	—	2.85	2.70	—
P_2	L	—	—	—	—	—	—	—	—	—	—	2.10	—
	W	—	—	—	—	—	—	—	—	—	—	1.00	—
P_3	L alv.	—	—	—	—	0.70	—	—	—	—	0.75	0.60	—
	W alv.	—	—	—	—	0.70	—	—	—	—	0.70	0.55	—
P_4	L alv.	—	—	—	—	1.25	—	—	—	—	1.30	1.00	—
	W alv.	—	—	—	—	0.70	—	—	—	—	0.70	0.65	—
M_1	L	1.86	—	—	—	1.99	—	—	—	—	—	2.00	—
	W tri.	1.22	—	—	—	1.34	—	—	—	—	—	1.33	—
	W tal.	1.17	—	—	—	1.37	—	—	—	—	—	1.23	—
M_2	L	—	—	—	—	—	—	—	—	2.09	—	1.95	—
	W tri.	—	—	—	—	—	—	—	—	1.52	—	—	—
	W tal.	—	—	—	—	—	—	—	—	1.34	—	1.30	—

Table 13 — Dental statistics for *Labidolemur soricoides* from Cedar Point Quarry. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
Dent. D		3	4.60	5.30	4.93	0.20	0.35	7.12
I_1	L	2	5.50	5.70	5.60	—	—	—
	W	3	1.68	1.80	1.72	0.04	0.07	3.86
	D	3	2.41	2.57	2.46	0.05	0.09	3.75
P_3	L alv.	5	0.90	1.00	0.92	0.02	0.04	4.86
	W alv.	1	—	—	0.70	—	—	—
P_4	L alv.	6	1.05	1.35	1.14	0.05	0.12	10.72
	W alv.	5	0.55	0.70	0.65	0.03	0.06	9.58
M_1	L	4	1.73	1.82	1.77	0.02	0.04	2.29
	W tri.	2	1.13	1.15	1.14	—	—	—
	W tal.	4	1.20	1.26	1.22	0.01	0.03	2.36

this species. Differences between the Bighorn Basin forms are evident in the premolar alveoli, which are too poorly preserved in the holotype of *L. soricoides* for adequate comparison (tooth homologies used in this section follow Gingerich and Rose [1982]). There is also an increase in size of about 12% from Cedar Point Quarry (Ti-3) to Divide Quarry (Ti-4a), based on M_1 area, dentary depth below M_1, and I_1 depth. M_1 area in the holotype of *L. soricoides* is intermediate between these samples. Most Tiffanian specimens younger than Ti-4a are close to the size of the Divide Quarry form.

Seven dentaries of *Labidolemur* from Cedar Point Quarry preserving premolar alveoli were available for study. Unfortunately, none of these preserves premolars. YPM-PU 20837 was listed by West (1973) as having a crushed P_4, but it was not available for study. West listed the lengths of both the P_4 and M_1 in this specimen as 1.3 mm. The M_1 length is nearly 30% less than in other specimens and may be a measurement for a crushed tooth or a typographic error. Another specimen measured by West, YPM-PU 19938, lacks enamel and tooth size appears to have been significantly reduced from etching.

Comparison of the Cedar Point Quarry (Ti-3) specimens with two dentaries from younger localities (UM 86237, Divide Quarry; YPM-PU 20711, *Probathyopsis* zone) reveals changes in the *L. soricoides* lineage. P_3 alveoli in the former are anteroposteriorly elongate and slightly oblique, while those in the latter are shorter and rounder. A general change in the relative sizes of anterior and posterior P_4 roots also occurs through this interval. The anterior P_4 alveolus is smaller than the posterior one in most dentaries from Cedar Point Quarry, while the alveoli are subequal in UM 86237 and equal in the still younger YPM-PU 20711. There also appears to be a temporal trend toward fusion of P_4 roots, although this character is somewhat variable in younger forms. The P_4 alveoli are separated by a bony partition in all the Cedar Point Quarry specimens, except YPM-PU 19992. YPM-PU 19992, however, appears to have belonged to a juvenile based on longitudinal striations in the poorly preserved bone of the dentary and only light wear on M_1. The P_4 roots in UM 86237 from the younger Divide Quarry (Ti-4a) show an intermediate condition with vertical ridges on the walls between the alveoli incipiently dividing the roots (Fig. 17). The M_1 is lightly worn but no striations are visible in the bone, suggesting that it belonged to an adult. Fusion of P_4 roots is common in the younger *L. kayi*, which first occurs in the early Clarkforkian, but there is apparently some variability in this character (Rose, 1981a; Bown and Schankler, 1982). The P_4 roots in a specimen from the late Tiffanian (YPM-PU 20711, Ti-5a), tentatively included here in *L. soricoides*, were separated by a bony septum, suggesting variability in this form as well.

Gingerich (1982b) suggested that *Labidolemur kayi*, which first appears in the early Clarkforkian, may have been directly derived from *L. soricoides*. There is an increase in size of about 12% from the Cedar Point Quarry form to the late Tiffanian form of *L. soricoides* that is approximately the size of *L. kayi*. The general trend of P_3 reduction noted above in *L. soricoides* continues in *L. kayi* where the P_3 is reduced to a vestigial stub. Moreover, there has been a shortening of the anterior jaw region and a posterior shift in the position of I_1. This is readily apparent by the position of the enameled base of I_1 relative to the position of M_1, which has shifted posteriorly by 20-30%. These trends suggest that all these forms may indeed be part of a single evolving lineage.

A dentary fragment (YPM-PU 19092), probably from the *Probathyopsis* zone, appears to be from a juvenile *Labidolemur*. It preserves the root of I_1, the talonids of M_1 and M_2, and at least two alveoli anterior to M_1. The anterior region of the dentary is too short and shallow to have accommodated the adult premolars of *L. soricoides* or *L. kayi*. An alveolus directly anterior to M_1 appears to have held a single-rooted dP_4 with its root tightly appressed against the anterior root of M_1. The other alveolus is small and positioned directly above and parallel to the dorsal-buccal surface of I_1, like the orientation of the P_2 alveolus in adults. This presumably held a single-rooted dP_2 which was much smaller than the adult P_2. There may have been another small alveolus that held a single-rooted tooth positioned between the other two, but preservation in this area is poor.

Several anterior upper teeth in the UM collections probably belong to *Labidolemur soricoides*. UM 77314 and 110969 from Divide Quarry contain I^1s that are nearly identical in size and structure to those of *L. kayi* described by Gingerich and Rose (1982, Fig. 1B). The close agreement between other teeth of *L. soricoides* and *L. kayi* supports assignment of these teeth to the former. An I^1 from Y2K Quarry (UM 109282; Ti-5b) is considerably smaller than those from Divide Quarry. It further differs in having a gently rounded dorsal margin, compared with a more angular margin, and is relatively shorter. This tooth may belong to a smaller species or could possibly be from a different position. An I^2 from Y2K Quarry (UM 109192) is approximately the size expected for *Labidolemur soricoides*, based on the I^2 of *L. kayi* (Gingerich and Rose, 1982), and I refer it to that species. A partial dentary (UM 108607) from near the Tiffanian-Clarkforkian boundary is similar in size to those of both *L. soricoides* and *L. kayi*, but is too fragmentary for confident identification.

An unusually complete specimen of *L. kayi* was recently reported by Bloch and Boyer (2001) and Bloch (2001), including postcranial material, but has not been described in detail. This specimen will undoubtedly shed light on the phylogenetic position of the North American apatemyids and on the positional behavior of *Labidolemur*.

TABLE 14 — Dental measurements for *Unuchinia dysmathes*, *Unuchinia* cf. *U. dysmathes*, and *Unuchinia* sp. from Chappo Type Locality, Divide (DQ), Judson (JQ), Princeton (PQ) and Schaff (SQ) quarries, and Sand Coulee (SC) localities.

		Unuchinia dysmathes		*Unuchinia* cf. *U. dysmathes*					*Unuchinia* sp.		
		UM 81164 Chappo	SMM P77.6.31 (type) JQ	UM 110161 SC-274	YPM-PU 19390 SQ	YPM-PU 19520 SC-416	YPM-PU 24570 PQ	YPM-PU 25017 SQ	UM 83271 DQ	UM 110968 DQ	UM 110970 DQ
Dent. D		—	—	—	—	7.18	—	—	—	—	—
I^1?	L	—	—	—	—	—	—	—	—	—	—
	W	—	—	—	—	—	—	—	—	1.86	—
	D	—	—	—	—	—	—	—	—	3.17	—
I^2	L	3.61	—	—	—	—	—	—	—	—	—
	W	1.97	—	—	—	—	—	—	—	—	—
I_2?	L	—	—	4.15	—	—	—	—	—	6.25	—
	W	—	—	1.40	—	—	—	—	—	1.80	—
	D	—	—	2.68	—	—	—	—	—	3.06	—
P_2	L	—	—	—	—	—	—	—	—	—	3.80
	W	—	—	—	—	1.42	—	—	—	—	1.50
M_1	L	—	2.71	—	—	—	—	2.64	—	—	—
	W tri.	—	2.35	—	—	—	—	2.08	—	—	—
	W tal.	—	1.75	—	—	—	—	1.66	—	—	—
M_2	L	—	2.83	—	2.70	—	2.86	—	3.13	—	—
	W tri.	—	—	—	2.25	—	2.51	—	—	—	—
	W tal.	—	1.90	—	1.62	—	1.73	—	1.95	—	—
M_3	L	—	3.23	—	2.96	—	—	—	—	—	—
	W tri.	—	—	—	2.23	—	—	—	—	—	—
	W tal.	—	1.63	—	1.30	—	—	—	—	—	—

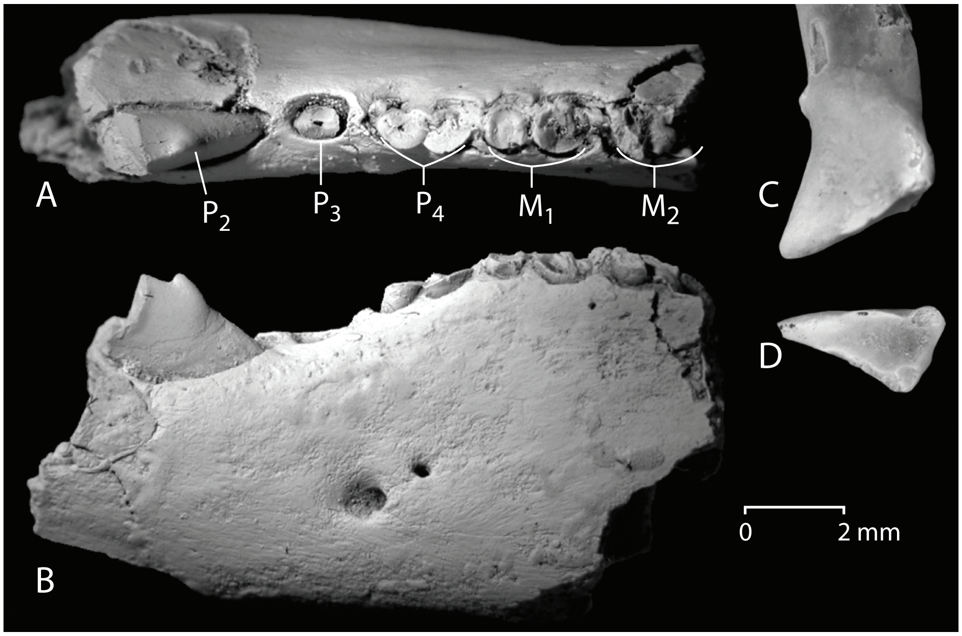


FIGURE 18 — Dentary and I^2 of *Unuchinia*. A–B, YPM-PU 19520, partial left dentary of *Unuchinia* cf. *U. dysmathes* with base of P_2 and roots of P_3-M_2 in occlusal (A) and buccal (B) views; collected near Princeton Quarry. C–D, UM 81164, I^2 tentatively referred to *Unuchinia* sp. in lateral (C) and occlusal (D) views; Chappo Type Locality, southwestern Wyoming.

Referred specimens.— **Cedar Point Q.**: UM 64517, L dent. M_1, alveoli for P_{3-4}, M_2; 71833, R dent. P_2-M_3 alveoli; 82088, L dent. frag., I_1 root, P_3-M_1 alveoli; YPM-PU 19938, R. dent., M_1, M_3, alveoli for P_{2-4}, M_2; 19992, R dent. I_1, M_1; 20054, L. dent., M_1, alveoli for P_4, M_{2-3}; 20614, L dent. I_1, alveoli P_2-M_3; 22018, R dent. I^1, alveoli P_2-M_3. **Divide Q.** (FG046): UM 77314, L I^1; 80581, R I_1; 85430, L I_1; 86237, L dent. M_1, alveoli for P_{2-4}, and M_2; 109859, L I_1; 110969, L and R I^1, probably not assoc. **SC419 area**: YPM-PU 20711, L dentary, I_1 root, P_2-M_3 alveoli. **Silver Coulee**, **S18**, **T57N**, **R100W**: 19092, R dent. frag., I_1 root, M_1 tal., M_2. **SC229**: UM 110321, R I_1 partial. **Y2K Q.** (SC389): UM 109192, L I^2; 109282, L I^1.

UNUCHINIA Simpson, 1937d

Unuchinia cf. *U. dysmathes*

Figures 18A,B; Table 14

Unuchinia sp., Rose, 1981a, p. 156.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a) and *Plesiadapis simonsi* (Ti-5b) zones.

Description.— The holotype of *Unuchinia dysmathes* was described in detail by Holtzman (1978). At least some of the specimens described here almost certainly belong to a new species. Homologies of anterior teeth are uncertain, but I provisionally follow the tooth homologies of Gunnell (1988).

I questionably identify an isolated tooth (UM 110161) as a right I_2. It has a prominent, buccally positioned margoconid, a well-developed margocristid, and lacks an interstitial facet. A short cristid is present on the mesioapical margin. A weak cristid crosses from the buccal to the mesial side of the anteroventral surface and continues apically, but remains external to the mesioapical cristid. A shallow trough on the dorsal surface follows the outer margin. The root is robust.

In YPM-PU 19520, a left dentary fragment (Fig. 18), most of the crown is missing from P_2, but it was procumbent, considerably smaller than the referred I_1, and has a centrally positioned margoconid. A crest originates from the margoconid and is deflected buccally. The P_2 is procumbent, and rests on the dorsal and lingual surfaces of the alveolus, which is slightly larger than the tooth. P_3 was single-rooted, and separated from the anterior and posterior alveoli by short diastemata (0.45 and 0.55 respectively). The root is smaller than the alveolus and P_3 was not procumbent. P_4 had two roots, the anterior root being smaller than the posterior one. The anterior root of M_1 was also smaller than its posterior root, and was smaller than the anterior root of M_2. The mandible reaches maximum thickness below M_1 and slopes steeply from M_1 to P_3. Two mental foramina are present, a large one below the intersection of P_3 and P_4, and a small one positioned higher and more posteriorly on the dentary below P_4. The mandibular symphysis extends to below the P_2 alveolus. Grooves that may be bite marks are present on the lingual surface of the dentary adjacent to the P_2 root.

Referred molars are similar to those of *Unuchinia dysmathes* but see below for a discussion of differences.

Discussion.— *Unuchinia* is a poorly known genus currently containing three species. Specimens from Princeton and Schaff quarries, and the surrounding area almost certainly represent an undescribed species. The most important specimen, YPM-PU 19520, is a partial dentary that preserves the base of P_2 but is otherwise edentulous (Fig. 18). It was collected from the area around Princeton and Schaff quarries in 1967 by R. Lambert. Of the described species, it compares most favorably to the holotype of *U. dysmathes* (SMM P77.6.31, Holtzman, 1978) from Judson Quarry in North Dakota that was recently correlated to the *P. churchilli* biochron (Ti-4, *sensu* Lofgren et al., 2004) by Kihm and Hartman (2004). YPM-PU 19520 differs from *U. dysmathes* in having: (1) a steeply sloping surface between the M_1 and P_3 alveoli, rather than a horizontal surface (see Figs. 7-10 in Holtzman, 1978); (2) a narrower anterior P_4 root and narrower P_2 and P_3 alveoli; and (3) diastemata on both sides of the P_3 alveolus. YPM-PU 19520 also has two mental foramina below $P_{3\text{-}4}$, as opposed to a single large one. The P_2 alveolus in both specimens is oblique to the long axis of the dentary, but is wider in *U. dysmathes*, suggesting a more robust P_2. The narrowing of alveoli in *Unuchinia* cf. *U. dysmathes* appears to correspond to a narrower dentary anterior to P_3, than in the holotype of *U. dysmathes*, and YPM-PU 19520 probably had a more gracile I_1 and I_2.

I have provisionally referred UM 110161 to *Unuchinia*. The root is approximately the right size and shape for an I_1 or I_2, based on the holotype of *U. dysmathes*, but because it lacks an interstitial facet it is more probably an I_2. It is considerably more arcuate along the anteroventral margin than the I_2 of *U. diaphanes* (Torrejonian; Gunnell, 1988), however, which suggests that it might be an upper tooth of *Unuchinia*. A less likely possibility is that it is a deciduous incisor of *Plesiadapis fodinatus*. No deciduous incisors of *Plesiadapis* are known with confidence, but Schlosser (1921, Plates 15, 8) and Gingerich (1976, p. 39) suggested that a lower incisor described by Russell (1964, Plates 3, 7a) was a dI_1 of *Plesiadapis tricuspidens*. UM 110161 differs considerably, however, and appears to have had a stout root, which is not the expectation for a deciduous tooth.

I have followed the dental homologies of Gunnell (1988), as noted above, who assumed that the first two large procumbent teeth in *Unuchinia diaphanes* are I_1 and I_2. It follows then that the first two procumbent teeth in *U. dysmathes* should also be I_1 and I_2. However, based on an examination of a cast of the holotype of *U. dysmathes*, the large anterior-most alveolus contains a secondary, smaller, more ventral alveolus on the buccal side. Matrix obscured the base of the secondary alveolus when the cast was made, but there is no indication of a separate socket in the exposed area. The confluent nature of the alveoli suggests that the secondary one held a deciduous incisor. It is also possible, however, that there were four procumbent permanent teeth in *U. dysmathes*, which would alter the interpretation of homology.

Molars referred here to *Unuchinia* cf. *U. dysmathes* are narrower than those in the holotype of *U. dysmathes* and have narrower talonids relative to trigonid width (Table 14). The molars in YPM-PU 19390 ($M_{2\text{-}3}$) are considerably narrower than in the holotype, especially in the talonids. Two isolated molars (YPM-PU 25017 and 24570) are closer to the holotype. All referred specimens are of approximately the same age.

The inclusion of *Unuchinia* in the Apatemyidae has been tentative at best because of the lack of convincing synapomorphies (e.g., McKenna, 1963; Van Valen, 1967; Holtzman, 1978). However, a previously undescribed I^2 from the Chappo Type locality (Ti-3) in southwestern Wyoming provides strong evidence that links *Unuchinia* to other apatemyids. No other upper teeth of *Unuchinia* have been described. UM 81164 was questionably identified as *Unuchinia dysmathes* by Gunnell (1994) and included in his published specimen count, but not discussed. It bears derived characters of the I^2 of *Labidolemur* and it undoubtedly belonged to an apatemyid. It has a wedge-shaped anteroventral surface (Fig. 18D) like the I^2 of *Labidolemur* (e.g., Gingerich, 1982b, Fig 2) but the anterior margin is double the width of the I^2 in *L. kayi* and 80% wider than that of *L. serus* (for measurements see Gingerich, 1982b; Gingerich and Rose, 1982). UM 81164 is double the expected size for I^2 of the contemporary *L. soricoides*, but its size is reasonable for *Unuchinia*. No other apatemyid this large is known from the Tiffanian. If UM 81164 is correctly identified as *Unuchinia* it provides strong evidence for inclusion of *Unuchinia* in Apatemyidae.

The specimens included here are the youngest reported occurrences of *Unuchinia*.

Referred specimens.— **Princeton Q.**: YPM-PU 24570, dent. frag., L M_2. **Schaff Q.**: YPM-PU 19390, R dent. $M_{2\text{-}3}$; 25017, L M_1. **SC274**: UM 110161, R I_2? **South of Princeton Q.**: (NE¼, S28, T57N, R100W): YPM-PU 19520, L dent. P_2 frag., $P_{3\text{-}4}$ and M_1 roots.

Unuchinia sp.

Figures 18C,D; Table 14

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Description.— The homologies for anterior teeth of *Unuchinia* are speculative, but I follow those of Gunnell (1988).

I provisionally identify UM 85416 as an I^1 of *Unuchinia*. It has a long stout root and a long crown with a strongly arcuate anterior margin as it approaches the apex. There is an interstitial wear facet on the mesial face that is interrupted where the tip is broken away. Enamel extends much farther down the root on the buccal face (3.3 mm) than on the mesial face. A ridge follows the buccal edge of the posterior surface and swells into a low cusp at the base of the crown. A low furrow follows the ridge internally. The crown is deflected mesially from the long axis of the root. It is slightly convex mesially. A weak crest begins medially on the anterodorsal face and extends to the mesial margin. The tip of the crown is missing.

UM 110970 (P_2?) has a small, but distinct margoconid positioned medially on the posterodorsal ("occlusal") surface near the base of the crown. A margocristid extends from the cusp to the apex of the crown and is deflected buccally forming a mesially concave curve. There is breakage along the anteroventral surface, but there was evidently a swelling about halfway up the crown on the ventral surface. The anteroventral margin is highly arcuate and convex, while the posterodorsal margin is concave.

Discussion.— The referred specimens are all isolated teeth from Divide Quarry. The M_2 (UM 83271) is virtually indistinguishable from that in the holotype of *Unuchinia dysmathes*, from Judson Quarry in North Dakota, which is approximately the same age (Kihm and Hartman, 2004). Although these teeth most probably belong to *U. dysmathes*, its molars are also similar to those of *U.* cf. *U. dysmathes*, as discussed above, and I refrain from making a specific identification. *Unuchinia dysmathes* is 10-20% larger than *U. asaphes* from Scarritt Quarry, but the molars are otherwise also very similar (Holtzman, 1978).

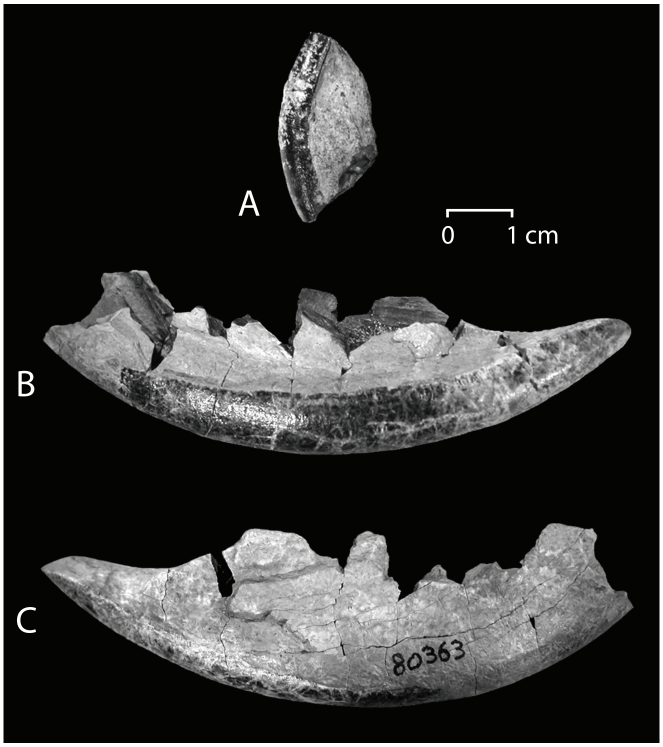


FIGURE 19 — Teeth of *Ectoganus*. A, UM 108316, I^3? of *Ectoganus lobdelli* in buccal view; SC-370 (Ti-6). B–C, UM 80363, right C_1 of *E*. cf. *E. lobdelli* in buccal (B) and lingual (C) views, from Fossil Hollow (Ti-4b).

Molars have not been described for *U. diaphanes* from Rock Bench Quarry (Gunnell, 1988), but the referred I_2 is considerably different (see *U*. cf. *U. dysmathes* discussion).

No upper teeth have been described for any species of *Unuchinia*. My identification of UM 85416 as an I^1 of *Unuchinia* is based on the presence of a mesial interstitial facet near the tip of the tooth, on resemblance to the I^1 of *Labidolemur*, and on size. It resembles the I^1 of *Labidolemur soricoides* in the degree the crown is deflected mesially from the root, in the pattern of enameling along the cervical margin, in the degree of curvature of the dorsal surface near the tip of the crown, and in the development and position of a dorsal crest. *Labidolemur* incisors have a distinctive crest that originates medially above the base of the crown on the dorsal surface, traverses the dorsal surface to the mesial edge, and terminates with a small cusp posterior to the crown's apex. A similar crest is present in UM 85416 but is interrupted along the mesial margin by a break and the presence of a terminal cusp is uncertain. UM 85416 could alternatively be an I_1, but this seems less likely because of the degree of curvature along the dorsal margin and its similarity to *Labidolemur* I^1s.

I questionably identify UM 110968 as an I_2 for the same reasons discussed in the *Unuchinia* cf. *U. dysmathes* section for UM 110161. It is notably larger than the latter, identified as an I_2 of *U*. cf. *U. dysmathes*.

I questionably identify UM 110970 as a P_2. Its base is quite similar to that of the P_2 in YPM-PU 19520, referred to *Unuchinia* cf. *U. dysmathes* above. In both, the basal cusp is medially positioned and a crest originates from it that is buccally deflected. The P_2 in YPM-PU 19520 rests on the dorsal and lingual surfaces of an alveolus that is larger than the tooth. The enamel is absent from the corresponding surfaces in UM 110970, as might be expected. Alternatively, UM 110970 could be an upper tooth of *Unuchinia*.

Referred specimens.— **Divide Q.** (FG046): UM 83271, R M_2; 85416, L I^1?; 110968, R I_2?; 110970, L P_2?

Suborder TAENIODONTA Cope, 1876
Family STYLINODONTIDAE Marsh, 1875

ECTOGANUS Cope, 1874

Ectoganus lobdelli (Simpson, 1929b)
Figure 19

?*Psittacotherium lobdelli* Simpson, 1929c, p. 11.
Cf. *Lampadophorus*, Rose, 1981a, p. 87.
Ectoganus gliriformis lobdelli, Schoch, 1986, p. 75.
Ectoganus lobdelli (in part), Gingerich, 1989, p. 30.
Ectoganus gliriformis (in part), Lucas et al. 1998, p. 265.

Holotype.— AMNH 22234, isolated right M^3 from the Bear Creek locality in the northern Bighorn Basin of southern Montana; Rodentia zone (Cf-1).

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis gingerichi* (Ti-6) and Clarkforkian zones.

Description.— The holotype was figured by Simpson (1929b) and Schoch (1986). Other specimens of *E. lobdelli* were described and figured by Schoch (1986) as *E. gliriformis lobdelli*.

Discussion.— The most recent revision of Taeniodonta was published by Schoch (1986) and a summary of Schoch's revision with minor changes was published by Lucas et al. (1998). Schoch (1986) recognized two subspecies in *Ectoganus gliriformis*, *E. gliriformis gliriformis* and *E. g. lobdelli*. Gingerich (1989), however, recognized these forms as separate species. Lucas et al. (1998) considered *E. lobdelli* a junior synonym of *E. gliriformis*. I agree with Gingerich (1989) that *E. g. lobdelli* merits specific status.

Taeniodont teeth from Clarkforkian and latest Tiffanian localities appear to be indistinguishable from the type sample of *E. lobdelli* (see Gingerich, 1989, p. 30) and are included here in that species.

Dental measurements (mm).— UM 108316: I^3, W (enamel band) = 8.1-8.8.

Referred specimens.— **SC178**: UM 68730, C^1 frag. **SC250**: UM 71801, 3 assoc. cheek teeth. **SC257**: UM 73339, P^3?, canine frags. **SC370**: UM 108316, I^3 frag., P_x. **SC380**: UM 108237, L P_2?, R M_3?, partial M_x.

Ectoganus cf. *E. lobdelli*
Figure 19

Cf. *Lampadophorus*, Rose, 1981a, p. 156.
Ectoganus gliriformis lobdelli, Schoch, 1986, p. 75.
Ectoganus lobdelli (in part), Gingerich, 1989, p. 30.
Ectoganus gliriformis (in part), Lucas et al. 1998, p. 265.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b) and *Probathyopsis* (Ti-5a) zones.

Description.— Schoch (1986) provided descriptions and figures of some specimens included here that he identified as *Ectoganus g. lobdelli*.

Discussion.— Schoch (1986) diagnosed *Ectoganus g. gliriformis* (here recognized as *E. gliriformis*) as having extremely hypsodont teeth, and incisors and P^{1-2}/P_{1-2} that approach a totally rootless (evergrowing) condition. He characterized *E. g. lobdelli* (here recognized as *E. lobdelli*) as having moderately hypsodont teeth with second premolars only slightly more hypsodont than in *Psittacotherium*, which has rooted teeth. He did not mention the condition of the roots of incisors or P^{1-2}/P_{1-2} in *E. g. lobdelli*, but it is clear from his figures that its anterior premolars are rooted with a relatively short root, compared with the more derived long root in *E. g. gliriformis* (e.g., compare Plate 39, 4-6, with Plate 37, 13-14, or Plate 36, 5-6, Schoch, 1986). Schoch justified the recognition of subspecies because the diagnostic characters were variable and formed a seemingly continuous grade. *Ectoganus lobdelli* is a latest Tiffanian and Clarkforkian species, while *E. gliriformis* is a Wasatchian species. Both probably were parts of a single evolutionary lineage (Gingerich, 1989). The variability that Schoch referred to may have been from temporally intermediate specimens or from grouping taxa from localities of different ages.

Schoch (1986) referred five specimens now in the YPM collections (YPM-PU 18954, 18982, 18994, 20864, 21499) to *Ectoganus g. lobdelli*, stating that all were Clarkforkian in age. Using the coordinates he provided, however, four of these specimens are late Tiffanian in age and the fifth (YPM-PU 20864) is from an area in Foster Gulch that is temporally not well-constrained and could be either Tiffanian or Clarkforkian.

Of particular interest is UM 80363, a right C_1 from Fossil Hollow (Figs. 19B,C) in the *Phenacolemur* zone. One of the features Schoch (1986) used to distinguish *Ectoganus* from the more primitive *Psittacotherium* was that it had rootless, evergrowing canines, in contrast to deeply-rooted canines in *Psittacotherium*. In UM 80363, the proximal edge of enamel forms an uneven oblique margin that is ~2 cm closer to the base of the crown on the buccal side. This is contrary to what might be expected in an evergrowing tooth, such as a rodent incisor, in which the enamel forms a relatively even band across in base of the crown. In buccal view the enamel band narrows near the base. In ventral view the canine narrows slightly toward the apex, and although some narrowing may be due to wear or weathering of cementum along the mesial margin, the enamel band also appears to narrow slightly. Although this canine is close to an evergrowing condition, and not nearly as rooted as those of *Psittacotherium* figured by Schoch (1986), it appears to have been rooted to some degree.

A lower canine (CM 11560) of *Ectoganus lobdelli* from the type locality at Bear Creek was figured by Schoch (1986, Plate 32). The enamel appears to be in a band of equal thickness over the entire crown, although there may be a very slight narrowing near the base. It is not clear from the figure if the base of the enamel is preserved, but the length of enamel that is preserved is equivalent to that in UM 80363. CM 11560 also seems to differ from UM 80363 in having a slightly greater degree of curvature along the ventral margin. UM 80363 appears to represent a more primitive form than *E. lobdelli*. There is no evidence for the presence of more than one species in the late Tiffanian sample. Thus, I identify all specimens from the *Phenacolemur* and lower *Probathyopsis* zones as *E.* cf. *E. lobdelli*.

Identification of tooth homologies for YPM-PU specimens included here follow Schoch (1986). UM localities are listed for YPM-PU specimens that were collected at or near these localities based on coordinates provided by Schoch (1986).

Dental measurements (mm).— UM 80363: R C_1, mesial-distal W (at enamel base) = 16.7.

Referred specimens.— **Fossil Hollow** (SC198): UM 80363, R C_1. **MP054**: UM 91037, C^1 frag. **SC394** (near): YPM-PU 18994, R P^4?, R P_2?, R P_4, R M_1, L M_1. **SC419**: YPM-PU 21499, L P^2?, R P^{3-4}, L P^{3-4}, R M^1, L P_2?, R P_4, L P_4, R M_1, L M_3, incisor, canine tips. **SC267**: UM 73513, R P_2?, R M_x, 2 cheek teeth; YPM-PU 18954, R M_1, 2 rooted incisors (deciduous?); 18982, R P^3?, R P_4, L P_4. **SC270**: UM 98472, C^1 frag. **SC273**: UM 73665, P^3?, R P_2?, L M_x, other teeth.

Suborder TILLODONTIA Marsh, 1875
Family TILLOTHERIIDAE Marsh, 1875

AZYGONYX Gingerich, 1989

Azygonyx xenicus (Gingerich and Gunnell, 1979)

Esthonyx xenicus Gingerich and Gunnell, 1979, p. 135.
Azygonyx xenicus, Gingerich, 1989, p. 25.

Holotype.— UM 66166, left maxilla with dP^{3-4}, M^1, right maxilla with M^{1-2}, left and right dentaries, both with M_{1-2}; from SC-74, northern Bighorn Basin, Wyoming; *Plesiadapis cookei* zone (Cf-2).

Biostratigraphic occurrences in Bighorn Basin.— Rodentia (Cf-1) and *Plesiadapis cookei* (Cf-2) zones.

Description.— Descriptions and figures of the holotype and other specimens were provide by Gingerich and Gunnell (1979) and Rose (1981a).

Discussion.— *Azygonyx xenicus* is the oldest Tillodont known in North America and is presumably an intercontinental immigrant (Gingerich and Gunnell, 1979). Specimens included here were included in the hypodigm by Gingerich and Gunnell (1979). UM 71191, from SC-83 on the southeast side of Polecat Bench (Fig. 6), represents the earliest occurrence of *Azygonyx* at a locality that is temporally well-constrained. Although the Tiffanian-Clarkforkian boundary on the west side of Polecat Bench is not well-constrained by fossils, its position can be accurately estimated relative to the C26r-C25n polarity zone reversal (Fig. 6). Thus, SC-83 is in the lower part of the Rodentia zone about 70 m above the boundary. A second specimen was collected at SC-226 in an area west of Polecat Bench that is not as temporally well-constrained. A rodent incisor from a nearby locality (SC-215) that is slightly higher stratigraphically and the development of red paleosols suggest a Clarkforkian age for SC-226. This is supported by an estimate of stratigraphic position that places SC-226 in the Rodentia zone. Notably, *Azygonyx* has not been found at localities that are known to be earliest Clarkforkian in age (e.g., SC-179, 181, 362).

TABLE 15 — Measurements for upper dentition of *Titanoides* cf. *T. major* from Cedar Point Quarry (CPQ) and for *T. gidleyi* from Croc Tooth Quarry (CTQ). *Estimate. **Estimated tooth position.

		Titanoides cf. *T. major*			*T. gidleyi*						
		UM 63101 CPQ	UM 64529 CPQ	UM 110973 CPQ	UM 77193 CTQ	UM 110972 CTQ	YPM-PU 14974 CTQ	YPM-PU 16461 CTQ	YPM-PU 16463 CTQ	YPM-PU 16466 CTQ	YPM-PU 16473 CTQ
P^2	L	—	13.7	—	—	—	12.7	13.5**	—	—	—
	W	—	21.3	—	—	—	17.1	20.7**	—	—	—
P^3	L	—	—	—	—	—	14.4*	—	—	—	—
	W	—	—	—	—	—	19.5*	—	—	—	21.9**
P^4	L	—	—	—	—	15.0	16.1	—	—	—	—
	W	—	—	—	—	22.6	23.7	—	—	—	—
M^1	L	—	—	—	21.3**	—	18.3	—	21.0	—	—
	W	—	—	—	24.6**	—	19.8	—	25.0	—	—
M^2	L	26.2**	—	23.8**	—	—	20.9	—	—	—	—
	W	32.2**	—	32.3**	—	—	24.8	—	—	—	—
M^3	L	—	—	—	—	—	22.0	—	—	17.7	—
	W	—	—	—	—	—	31.5	—	—	31.0	—

Referred specimens from the Rodentia zone.— **SC083**: UM 71191, M^1? protocone. **SC226**: UM 71303, L M_2 partial.

Suborder PANTODONTA Cope, 1873
Family TITANOIDEIDAE Patterson, 1934

TITANOIDES Gidley, 1917

Titanoides major (Simons, 1960)

Titanoides majus Simons, 1960, p. 38.

Holotype.— YPM-PU 16447, a right dentary with $P_{2\text{-}3}$, part of P_4, alveoli or roots for C_1, P_1, and M_1; probably from SE¼, NE¼, Sec. 2, T56N, R99W, northern Bighorn Basin, Wyoming.

Description.— A description of the holotype was given by Simons (1960).

Biostratigraphic occurrences in Bighorn Basin.— latest Torrejonian or early Tiffanian.

Discussion.— Simons (1960) erected *Titanoides* "*majus*" for the holotype and only known specimen. The specific name was later amended to "*major*," however, to agree in gender with *Titanoides*, which is masculine (Gingerich, 1996a). Simons (1960) reported that the holotype was from the lowermost Silver Coulee beds near Sage Point on the northeast side of Polecat Bench, not far above Rock Bench Quarry, but provided no coordinates. Gingerich (1996a), however, reported that the holotype was from the SE¼, NE¼, Sec. 2, T56N, R99W, based on unpublished records. This is about 1.3 km southwest of the area Simons' specified and possibly slightly higher stratigraphically. In either event the most likely source for the specimen is the Chert conglomerate, described in the lithostratigraphic section in chapter 2, which crops out in both areas. The age of the Chert conglomerate is not well-constrained, but it is probably latest Torrejonian or early Tiffanian (Ti-1 or Ti-2) (Secord et al., 2006).

Gingerich and Childress (1983, p. 150) stated that a partial maxilla (YPM-PU 16446) from the area around SC-263, provisionally identified as *T. primaevus* by Simons (1960, p. 35), "is almost certainly the upper dentition of *T. major*." I have not seen this specimen. I identify several specimens as *Titanoides* cf. *T. major* below. No new specimens that can be confidently identified as *T. major* have been described.

Titanoides cf. *T. major*

Table 15

Titanoides gidleyi, Rose, 1981a, p. 152.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description and discussion.— The specimens included here represent a large species of *Titanoides*. Some or all may belong to *Titanoides major* but identification is hindered by two things. First, only $P_{2\text{-}3}$ and P_4 fragments are preserved in the holotype of *T. major* and no other specimens have been described. Second, it is often difficult to determine tooth homologies in isolated pantodont teeth and all of the specimens included here are isolated or associated teeth. Nevertheless, some generalizations can be made.

Simons (1960, p. 38) distinguished *Titanoides major* from *T. gidleyi* and *T. primaevus* in part by its larger size (premolars ~35-50% longer and 10-30% wider; my calculations). Size differences between *T. primaevus* and *T. gidleyi* appear to be minor, and as discussed below, it is probable that these species are conspecific. In any event, teeth from Cedar Point Quarry in the UM collections are larger than homologous teeth in the holotypes of either *T. gidleyi* or *T. primaevus*. A partial M_1 (UM 79985) from Cedar Point Quarry is 19.4 mm wide, which is almost 30% wider than M_1 in the holotype of *Titanoides gidleyi*. It also appears to have been relatively broader, with a shorter talonid and it had a higher entoconid, relative to metaconid height.

TABLE 16 — Measurements for lower dentition of *Titanoides gidleyi* from Croc Tooth Quarry (CTQ), Divide Quarry (DQ), and FG-007. **Estimated tooth position.

		UM 74026 FG007	UM 110144 CTQ	YPM-PU 16448 DQ	YPM-PU 16453 CTQ	YPM-PU 16460 CTQ	YPM-PU 16462 CTQ	YPM-PU 16467 CTQ	YPM-PU 16468 CTQ	YPM-PU 16471 CTQ
C_1	L	—	18.8	—	30.9	—	20.7*	—	—	18.0
	W	—	13.4	—	22.9	—	13.6	—	—	10.6
P_1	L	11.9	—	—	—	—	—	—	—	—
	W	—	—	—	—	—	—	—	—	—
P_2	L	12.9**	—	16.1	—	—	—	—	—	—
	W	11.2**	—	13.8	—	—	—	—	—	—
P_4	L	15.8**	—	—	—	—	—	—	—	—
	W	14.6**	—	—	—	—	—	—	—	—
M_1	L	19.3	—	—	—	—	—	—	21.2	—
	W	13.8	—	—	—	—	—	—	14.2	—
M_2	L	24.3	—	—	—	—	—	—	—	—
	W	14.8	—	—	—	—	—	—	—	—
M_3	L	32.7	—	—	—	32.7	—	27.8	—	—
	W	17.7	—	—	—	18.7	—	15.6	—	—

Two isolated upper molars included here could be either M^1s or M^2s. If these teeth are M^2s they are about 30% wider than those of *T. gidleyi* (YPM-PU 14974), and 15-25% longer. If they are M^1s they are about 60% wider and 30-45% longer. Both molars have damage along the buccal margin and were probably wider than the reported measurements (Table 15). In either case, these teeth are outside the size range expected for *T. gidleyi* or *T. primaevus* but may be closer to that of the larger *T. major*.

Simons (1960, p. 38) also distinguished *Titanoides major* from *T. gidleyi* and *T. primaevus* by smaller P_1 and P_2 metaconids (relative to *T. primaevus*), a more separate paraconid and metaconid on P_2, and a more quadrate P_3 at the base (relative to *T. gidleyi* and *T. primaevus*). A right P_4 (UM 82087) from Cedar Point Quarry and two lower premolars (UM 73394) from SC-262 agree with Simons' description of *Titanoides major* in being more quadrate than premolars of *T. gidleyi*. However, UM 82087 is ~20% smaller than the size expected for P_4 in *T. major* (based on scaling of premolars in other *Titanoides* species) but is probably too large to belong to *T. gidleyi*. The premolars in UM 73394 were found in association and are questionably identified as P_3 and P_4. They are too fragmentary for precise length measurements but the width of P_3 (~15 mm) is close to that of P_3 in the holotype of *T. major*, although length appears to be ~20% shorter. A small C_1 associated with the premolars indicates that these teeth belonged to a female (see discussion of *T. gidleyi*).

The specimens included here are intermediate in size between homologous teeth in *T. gidleyi* and *T. primaevus*, and the expected size of *T. major* teeth. They are proportionally closer to those of *T. major* and are conferred to that species.

Referred specimens.— **Cedar Point Q.**: UM 63101, L M^1 or M^2; 64529, L P^2, dP_x, unassoc.; 79985, M_1 partial; 82087, R P_4; 110973, L M^1 or M^2; 110974, L P_2?. **SC262**: UM 73394, R I_x, C_1, P_{3-4}?.

Titanoides gidleyi Jepsen, 1930b
Tables 15–16

Titanoides gidleyi Jepsen, 1930b, p. 506. Simons, 1960, p. 37.

Holotype.— YPM-PU 13235 left and right dentaries with left P_{2-4}, M_{2-3}, right P_{2-3}, M_{1-2}, two incisors, and fragmentary canines. From the southeast side of Polecat Bench, Sec. 11, T56N, R99W, Park County, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a) and *Phenacolemur* (Ti-4b) zones.

Description.— *Titanoides gidleyi* has been described by Jepsen (1930b) and Simons (1960).

Discussion.— The referred specimens are similar to teeth of both *Titanoides gidleyi* and *T. primaevus*. The holotype of *T. gidleyi* is from the Bighorn Basin (Jepsen, 1930b), while that of *T. primaevus* is from North Dakota (see Hartman and Kihm, 1991). Simons' (1960) distinguished *T. gidleyi* from *T. primaevus* by: (1) a more centrally placed protocone on P^3; (2) the posterior cingulum on M^3 forming a larger shelf; (3) a larger M^3/M_3 relative to the corresponding molar series; (4) a small posterior lobe on C_1, as opposed to an enlarged blade-like lobe; (5) smaller and lower premolar metaconids; and (6) tooth measurements about 10% smaller on average. Simons' noted that most of these differences were minor and might be attributed to individual variation by some researchers. He argued, however, that the development of the enlarged blade-like canine lobe in *T. primaevus* served a functional purpose and was the most significant difference between the species. He postulated that it was unlikely that the lobe was the result of sexual dimorphism or individual variation because it was part of an efficient dental mechanism.

Simons' (1960) observation that C_1 in *Titanoides primaevus* had an enlarged blade-like lobe was based on FMNH P 15520. This specimen appears, however, to represent a different species

(Gingerich, 1996a). It includes a nearly complete skeleton that was the holotype for *Sparactolambda looki*, a new genus and species named by Patterson (1939). It was collected from strata in Colorado that appear to be either late Tiffanian or Clarkforkian in age (Rose, 1981a; Gingerich and Childress, 1983; Archibald et al., 1987; Gingerich, 1996a) and may be significantly younger than the type locality of *T. primaevus* in North Dakota. Simons synonymized *S. looki* with *T. primaevus*, arguing that differences in comparable parts were not great enough to warrant generic or specific separation. Gingerich (1996a), however, revalidated the species as *T. looki* and suggested that it represented a species that was temporally intermediate between *T. primaevus* and *T. nanus*. Thus, FMNH P 15520 appears to represent a separate species and the blade-like lobe may be an apomorphy of *T. looki*. No lower canines of *T. primaevus* have been described from North Dakota and the specialized canine in FMNH P 15520 should not be considered representative of *T. primaevus*.

Simons' (1960) comparison of upper dental characters in *Titanoides gidleyi* and *T. primaevus* was based primarily on YPM-PU 14974, a maxilla with P^2-M^3 from Croc Tooth Quarry that he referred to *T. gidleyi*, and on PU 16490 that he assumed was part of the holotype of *T. primaevus*. With regard to (2) above, Simons was presumably referring to the metacingulum (in the terminology of Van Valen, 1966, p. 8) on M^3 as the posterior cingulum, because the postcingulum is very narrow and incomplete on both YPM-PU 14974 and 16466. Metacingular development on M^3 appears to be highly variable within the sample from Croc Tooth Quarry. The metacingulum flares posteriorly near the buccal margin forming a wide, rounded shelf in YPM-PU 14974 but it is considerably narrower in YPM-PU 16466. With regard to average size differences (6), M_1 is usually considered the least variable tooth position in most mammals (e.g., Gingerich and Smith, 1984). Based on original published measurements for these species (Gidley, 1917; Jepsen, 1930b) the M_1 in T. *primaevus* is only 4% longer and 3% wider than that in *T. gidleyi*, which is less than the variability expected in a single species. Specimens from Croc Tooth Quarry are too incomplete or too few to address (1), (3), and (5), but I note in regard to (3) that the M_3 in at least some mammals is the most variable molar position (Gingerich and Smith, 1984).

The holotypes of *Titanoides gidleyi* and *T. primaevus* appear to be approximately the same age. The holotype of *T. gidleyi* comes from the southeast side of Polecat Bench. Jepsen (1930b) reported that it came from Sec. 11, T56N, R99W and showed the locality on a map drawn at a small scale (his Fig. 1). Jepsen's map places the type locality of *T. gidleyi* in the area just north of a distinctive bend in the main road that crosses Polecat Bench. This is near the northwest corner of Sec. 11, which puts it either low in the *Phenacolemur* zone or high in the *P. churchilli* zone. The type locality of *T. primaevus* was relocated and correlated to the upper part of the *P. churchilli* zone by Hartman and Kihm (1991, 1995), implying that it occurs within the age range of *T. gidleyi* in the Bighorn Basin.

A revision of *Titanoides* and other pantodonts is in order (e.g., Gingerich and Childress, 1983; Lucas, 1998), although it is not clear if the material now known for *T. primaevus* and *T. gidleyi* is adequate to resolve the issues of intraspecific variation. Simons (1960, p. 33) points out that in pantodonts sometimes "slight differences in the dentition are associated with more radical differences in the rest of the skeleton." However, given the high variability in pantodont dentitions it seems most probable that the holotypes of *T. gidleyi* and *T. primaevus* are variants of a single species. I provisionally keep these species separate, however, pending a through study of known specimens and revision of the group.

Simons (1960, p. 37) reported in a footnote that *Titanoides gidleyi* was known from Cedar Point Quarry (Ti-3), based on YPM material, but did not cite any specimens. Rose (1981a, pp. 152-153) subsequently included *T. gidleyi* in a faunal list for the quarry, citing Simons' footnote. Specimens from Cedar Point Quarry in the UM collections are, however, considerably larger and have more quadrate premolars than those of *T. gidleyi* (or *T. primaevus*) and are identified here as *Titanoides* cf. *T. major*. I have not, however, studied the *Titanoides* specimens at YPM.

Sexual dimorphism is known in some pantodonts (e.g., Gingerich and Childress, 1983; Uhen and Gingerich, 1995; Gingerich, 1996a). Gingerich (1996a, p. 410) noted that lower canines of *Titanoides primaevus* (identified as *T. gidleyi* here) from Croc Tooth Quarry were strongly dimorphic, without further discussion. This does appear to be the case. Three small C_1s (UM 110144, YPM-PU 16462 and 16471) are probably from females, while a much larger one (YPM-PU 16453) is from a male. The last is slightly larger than C_1 in the holotype of *T. gidleyi* and is 50-70% longer and 70-115% wider than C_1s attributed to females here (Table 16). Simons (1960, p. 37) speculated that YPM-PU 16462 and 16471 might be canines of *T. zeuxis* or possibly deciduous teeth of *T. gidleyi*. *Titanoides zeuxis* has since been synonymized with *T. gidleyi* (Gingerich, 1996a), however, and the canine in UM 110144 has a thick, long root and is clearly a permanent tooth. Although none of the small canines has been found in association with other teeth of *T. gidleyi*, a small permanent C_1 (UM 73394) that is very similar to the small C_1s from Croc Tooth Quarry was found in association with premolars at SC-262 and identified here as *Titanoides* cf. *T. major*. It is within the size range of the small C_1s from Croc Tooth Quarry but the premolars are relatively larger. This specimen supports identification of the latter as belonging to females of *Titanoides*, rather than a smaller species. *Caenolambda jepseni*, which is about the size of *T. gidleyi* or slightly larger, is also present at Croc Tooth quarry, but is less abundant than *T. gidleyi* and is represented only by two teeth. The C_1 of *C. jepseni* has not been described but because of the relative rarity of the species and the close similarity of the small C_1s to those of *T.* cf. *T. major*, at least some of these are almost certainly those of *T. gidleyi*.

There also appears to be marked sexual dimorphism in *Titanoides primaevus*, as evidenced by a skull (FMNH P 8655) from the Riverdale Locality in North Dakota (Holtzman, 1978, pp. 60-61). Holtzman noted that the upper canines were small (inferred from alveoli) relative to those in the holotype. He also noted that the sagital and lambdoidal crests were "reduced," although he did not cite the specimen being compared.

The Divide Quarry collection contains only a few pantodont specimens of diagnostic value. YPM-PU 16449 (in part) contains a partial M_1 that agrees well in size and form to those of *Titanoides gidleyi*. Simons (1960, p. 28) suggested that it may belong to *Haplolambda quinni* but because it appears to be within the variability of *T. gidleyi* and no other specimens of *H. quinni* are known from Divide Quarry, I include it in *T. gidleyi*. UM 85307 is a saber-like C^1 that is badly crushed but was covered with enamel over about 85 mm of its length. It is similar to other C^1s described for *Titanoides* and I tentatively include it in *T. gidleyi*. Lastly, a partial dentary (YPM-PU 16448) preserves a large P_2 within the size range expected for *T. gidleyi*.

The referred specimen list below only includes specimens that I have examined. Other specimens identified by Simons (1960) in the YPM collections may also belong in *Titanoides gidleyi*.

Referred specimens.— **FG007**: UM 74026, $P_{1\text{-}2}$?, P_4-M_3, assoc. **Divide Q.** (FG046): UM 85307, C^1; 85403, R dP^4; 87037, L dP_4?. YPM-PU 16448, L dent. P_2; 16449, R M_1 partial; R dP_x, unassoc.; 16806, distal. phalanx. **SC261**: UM 73389, M^1 protocone. **Croc Tooth Q.** (FG028): UM 77193, L M^1; 110144, L C_1; 110972, R P^4. YPM-PU 16453, L C_1; 16454, R P_2; 16460, R M_3; 16461, L P^2?; 16462, R C_1; 16463, R M^1; 16466, R M^3; 16467, R M_3; 16468, R M_1; 16471, R C_1; 16473, L P^3 or P^4.

Family PANTOLAMBDIDAE Cope, 1883

CAENOLAMBDA Gazin, 1956a

Caenolambda jepseni Simons, 1960

Caenolambda jepseni Simons, 1960, p. 24.

Holotype.— YPM-PU 14863, left and right dentaries with I_1-M_3 (represented on at least one side), upper teeth including right incisor, C^1-P^4, M^2, and left P^3, M^2; partial postcranial skeleton; from NE¼, Sec. 18, T55N, R96W, in the Foster Gulch area of the northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* (Ti-3) and ?*Plesiadapis churchilli* (Ti-4a) zones.

Description.— The holotype of *Caenolambda jepseni* was described by Simons (1960).

Discussion.— When Simons (1960) described the locality of the holotype of *Caenolambda jepseni* he stated that its stratigraphic position was between Rock Bench Quarry and the lowermost Silver Coulee beds. He thought it was probably Torrejonian in age, noting that the associated fauna was known only from the Torrejonian, but he did not mention any taxa. The coordinates he provided for the holotype, however, place it in the Foster Gulch area where the oldest part of the Fort Union formation is correlative to the middle Tiffanian *Plesiadapis rex* zone and is underlain by strata of Cretaceous age. Apparently Simons' reference to stratigraphic position was based on a presumed age, because beds in Foster Gulch cannot be traced to Polecat Bench.

A specimen of *Picrodus* (YPM-PU 16476), a plesiadapiform, was also collected at or near the locality of the holotype. It is a partial dentary with M_1 and comparables favorably to specimens of *Picrodus* from Cedar Point Quarry. *Picrodus* is not known from zones younger than the *Plesiadapis rex* zone in the Bighorn Basin but is a rare species. It is known from the Olive Locality in Montana (Wolberg, 1979) and from the University of Wyoming locality V-77059 in southern Wyoming (Winterfeld, 1982). These localities are probably correlative to either the *P. churchilli* or *Phenacolemur* zones. *Caenolambda jepseni* has also been identified at Cedar Point Quarry (Rose, 1981a) but I have not studied these specimens. No specimens confidently referable to *C. jepseni* are known from zones younger then the *P. rex* zone, suggesting that this is the age of the holotype. A maxilla (YPM-PU 16662) discussed in the *Leptolambda churchilli* section from the slightly younger Seaboard Well locality could, however, possibly be a large individual of *C. jepseni*.

Family BARYLAMBDIDAE Patterson, 1937

LEPTOLAMBDA Patterson and Simons, 1958

Leptolambda churchilli (Gingerich and Childress, 1983)

Figure 20

Leptolambda schmidti (in part), Patterson and Simons, 1958, p. 3. Simons, 1960, p. 29.

Barylambda churchilli Gingerich and Childress, 1983, p. 145.

Holotype.— YPM-PU 14681, left and right dentaries with all teeth present except P_1; teeth are moderately to heavily worn; from NE¼, Sec. 9, T56N, R99W, along the southeast side of Polecat Bench, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a) and *Phenacolemur* (Ti-4b) zones.

Description.— The holotype of *Leptolambda churchilli* was described and figured by Gingerich and Childress (1983) as *Barylambda churchilli*. The hypodigm was described by Gingerich and Childress (1983). Some specimens were previously described by Patterson and Simons (1958) and Simons (1960; as *Leptolambda schmidti*).

Discussion.— Many specimens included here in *Leptolambda churchilli* were initially placed in *L. schmidti* by Patterson and Simons (1958, p. 4) (YPM-PU 14680, 14681, 14879, 14990, 14992, and 14996) based on a suite of dental and postcranial characters. Gingerich and Childress (1983) subsequently included most of the Bighorn Basin specimens in a new species, *Barylambda churchilli*, based on a 10-13% size difference, and considered *L. schmidti* a junior synonym of *Barylambda faberi*. Lucas (1998) revalidated *L. schmidti*, citing mostly postcranial differences between the taxa described by earlier authors that were not addressed by Gingerich and Childress. At the same time Lucas recognized *B. churchilli* as a distinct species without discussion. I also provisionally recognize *B. churchilli* as a distinct species but transfer it back to *Leptolambda*. The referral by Patterson and Simons of Bighorn Basin specimens to *Leptolambda* was based in part on the comparison of several partial skeletons from the Bighorn Basin with the holotype of *L. schmidti*. The many postcranial differences given by Simons were not addressed by Gingerich and Childress, nor did Lucas give reasons for keeping *B. churchilli* in *Barylambda*. I recognize, however, that a rigorous revision of the Pantodonta, including these specimens, is needed (e.g., Gingerich and Childress, 1983; Lucas, 1998).

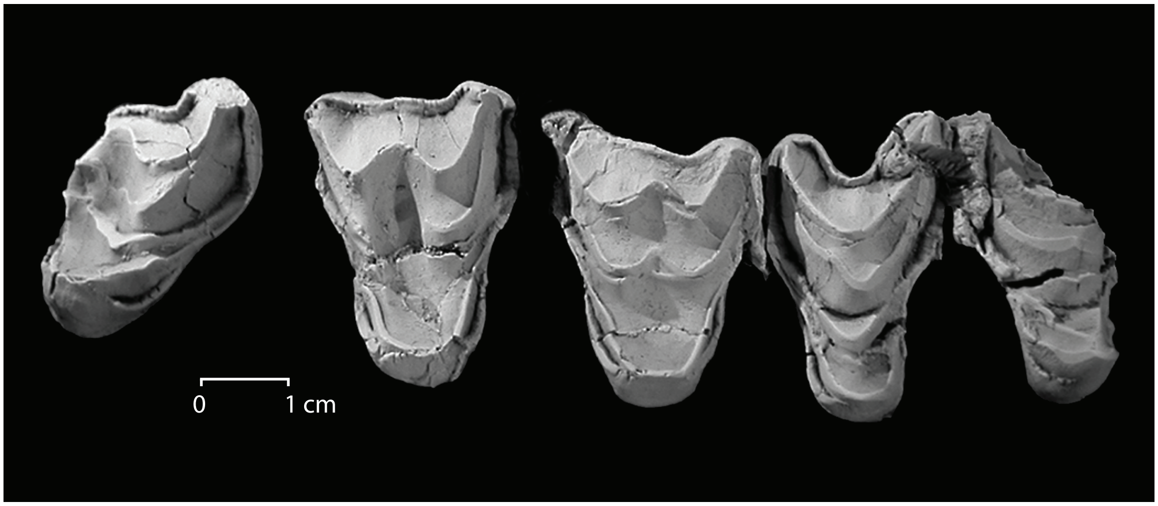


FIGURE 20 — Right maxilla of *Leptolambda churchilli* (UM 108480) with P^3-M^3 in occlusal view; from SC-397.

Three partial skeletons of *Leptolambda churchilli* are known from the Bighorn Basin, two from the Foster Gulch area (YPM-PU 14879 and 14996) and a third (YPM-PU 14680) from the southeastern side of Polecat Bench found near the holotype (Gingerich and Childress, 1983). A partial hind limb of a large pantodont (UM 108467), still in articulation, was recently collected on the west side of Polecat Bench from the *Phenacolemur* zone. It still needs preparation, but presumably belonged to *Leptolambda churchilli*. A partial maxilla (UM 108480, Fig. 20) identified here as *L. churchilli* was also collected at approximately the same level. It has slightly more anteroposteriorly compressed protocones on $M^{1\text{-}2}$ and more transversely elongate premolars than most specimens, but is presumably within variability of the species. The orientation of P^3 and M^3 have shifted from deformation, but P^4-M^1 occlude relatively well with the holotype dentary of *L. churchilli*. Both it and the holotype are from the *Phenacolemur* zone and are approximately the same age. A partial M^1 (UM 110098) from beds near the top of the *Phenacolemur* zone is notably large, with a length of 25.6 mm, and suggests an increase in body size near the end of this lineage in the Bighorn Basin.

YPM-PU 16662 is a partial maxilla from the Seaboard Well locality. It was initially identified as *Leptolambda schmidti* (= *L. churchilli* here) by Simons (1960), but Gingerich and Childress (1983, Fig. 5) noted that it could represent either *B. churchilli* or *Caenolambda jepseni*. YPM-PU 16662 is slightly atypical compared with other upper dentitions of *L. churchilli* (e.g., UM 108480 and YPM-PU 14996) in having: (1) slightly less anteroposteriorly compressed molar and premolar protocones; (2) a more quadrate, less triangular M^1 in occlusal view; (3) a narrower, steeper stylar shelf on M^1 (broken in $M^{2\text{-}3}$); and (5) a slightly smaller size. It is also similar to *C. jepseni* but differs in being about 10% larger and in having a more triangular P_2 and P_3 with more anteriorly placed protocones. The specimen could be within the variation of either species. Based on the presence of *Plesiadapis churchilli*, *Ptilodus kummae* (Krause, 1982) and *Phenacodus magnus* (Thewissen, 1990) the Seaboard Well locality is a correlative of either the *P. churchilli* or *Phenacolemur* zone.

Fragments of teeth and bones of large pantodonts are relatively common in the *Phenacolemur* zone in Silver Coulee on the west side of Polecat Bench. No teeth of *Titanoides* have been recovered from the area, and most specimens probably belong to *Leptolambda churchilli*. The species abruptly disappears with the appearance of uintatheres at the beginning of the *Probathyopsis* zone, however, presumably from competitive displacement or replacement.

Dental measurements (mm).— YPM-PU 16662: P^2, L = 16.9, W = 22.4; P^3, L = 17.2, W = 25.2; P^4, L = 16.8, W = 27.35; M^1, L = 21.0*, W = 29.0. UM 108480: P^3, W = 33.8*; P^4, L = 20.9, W = 34.2; M^1, L = 24.6, W = 32.8; M^2, L = 24.1, W = 35.8; M^3, L = 21.6*, W = 3.24*.

Referred specimens.— **Croc Tooth Q.** (FG028): UM 77155, R P_2, L M_1 (partial) unassoc. **Divide Q.** (FG046): UM 85308, L M_3 partial; 86240, L M_1. **Foster Gulch**: Sec. 5, T54N, R95W, YPM-PU 14996, partial skeleton, palate, R $P^{2\text{-}3}$, $M^{1\text{-}3}$, L M^3. **SC228**: YPM-PU 14681 (holotype). **SC283**: UM 73710, assoc. upper and lower tooth frags. **SC397**: UM 108480, L max. P^3-M^3 and R max. frags. **SC420**: UM 110098, R M^1 partial, frags. of other teeth.

Additional specimens referred by Gingerich and Childress (1983): **Foster Gulch**: YPM-PU 14879, skull and partial skeleton. YPM-PU 14990, L dent. L I_2, C_1-M_3, R dent. I_1-M_3. YPM-PU 14992, dent. P_3-M_3. YPM-PU 16485. Polecat Bench: **SC246**: YPM-PU 14680, dent., max. C^1, P^3-M^3.

HAPLOLAMBDA Patterson, 1939

Haplolambda cf. *H. quinni*

Haplolambda quinni (in part), Simons, 1960, p. 27. Gingerich and Childress, 1983, p. 146.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a) and *Phenacolemur* (Ti-4b) zones.

Description and discussion.— Simons (1960) referred a small dentary (YPM-PU 16445) from south of Divide Quarry to *Haplolambda quinni*, a taxon otherwise known only from the late Tiffanian or early Clarkforkian of Colorado. It was figured by Gingerich and Childress (1983, Figs. 2 and 3) who followed Simons' identification. Simons' referral to *H. quinni* was based on similarities in molar proportions to the holotype and on the shallowness of the dentary. Simons noted, however, that the molars were broader and the specimen was slightly larger. The M_1 is 10% longer than M_1 in the holotype and 20% wider. M_2, on the other hand, is about the same length but 18% wider. The M_3 is 10-20% longer, depending on which side of the holotype is compared, but about the same width. M_3 varies markedly in the holotype, based on casts. The differences in molar proportions and overall size between YPM-PU 16445 and the holotype of *Haplolambda quinni* are great enough to cast doubt on its identification as *H. quinni*.

Simons (1960) also questionably included a partial molar and a C_1? (YPM-PU 16449), as well as a tibia and associated calcaneum (YPM-PU 16481) from Divide Quarry in *Haplolambda quinni*. The molar differs in several respects from those of *H. quinni* but is inseparable from those of *Titanoides gidleyi*, to which I refer it. The canine is considerably larger than that in the holotype of *H. quinni* and differs further in having a sharp posterior (?) crest. Nevertheless, it is round like canines of *H. quinni*, is not referable to other taxa in the fauna, and could belong to *H.* cf. *H. quinni*. A small lower premolar grouped in the same number may also belong to this species. Simons described the tibia and calcaneum as being "extremely small" and probably belonging to *Haplolambda*. The posterior skeleton of *Haplolambda* is not known, however, and these bones could also represent the even smaller pantodont referred below to cf. *Haplolambda*.

I provisionally include two specimens from Croc Tooth Quarry, YPM-PU 16467 and 25032, in *Haplolambda* cf. *H. quinni*. The former is a heavily worn M^1 or M^2 that has a narrow and steep stylar shelf and would be very small for *Leptolambda churchilli* but is about the size of the M^2 in the holotype of *H. quinni*. The latter is probably a P^3 or P^4 that is transversely narrow and would also be small for *L. churchilli*.

Dental measurements (mm).— YPM-PU 16449: C_1?, L = 11.5, W = 10.3; R P_x, L = 15.4, W = 10.9. YPM-PU 16465: P^x, W = 24.8*. YPM-PU 25032: M^1 or M^2, L = 19.9*, W = 27.5*.

Referred specimens.— **Croc Tooth Q.** (FG028): YPM-PU 16465, R P^x; 25032, R M^1 or M^2. **SW¼**, **S22**, **T54N**, **R95W**: YPM-PU 16445, R dent. P_2-M_3; **Divide Q.**: YPM-PU 16449, C_1?, R P_x, unassoc.

Cf. *Haplolambda*

Figures 21A–D

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a) or *Phenacolemur* (Ti-4b) zone.

Description.— Determination of upper molar homologies in YPM-PU 18168 was based on the relative width of pre- and postcingula, the relative positions of the para- and metacones, the positions of the protocones, the degree, position, and style of cusp wear, and the form of the ectoloph near and around the metastyle. Other interpretations are possible but are less parsimonious.

The cingula on M^{1-2} and on a premolar protocone (P^3?) form a wide shelf that is continuous around the protocone and is widest posterolingually. Molar paracones and metacones are subequal. These cusps extend equally as far lingually in M^1 but the lingual base of the metacone is positioned more buccally than the paracone in M^2. The M^2 is shorter and is narrower than M^1 in preserved parts (the anterior half of the stylar shelf is missing in both). The M^1 has a large paraconule, but no distinct metaconule, whereas the M^2 has a very small paraconule and a small metaconule. There are prominent mesostyles on both molars positioned close to the buccal margin. The mesostyles rise steeply from narrow stylar shelves. The posterobuccal corner of M^2 is square, while both buccal corners in M^1 are rounded.

A C^1 fragment is saber-like. The mesial face is convex in occlusal view and lacks enamel. The buccal face has a very thin layer of enamel. Although this could be indicative of a deciduous tooth, the enamel of many pantodont canines is thin. A wide, flat, vertical wear facet is present along the anterior margin (Fig. 21D). A vertical ridge is present on the anterobuccal face.

A P_4? fragment has a short talonid extension that has no basin. A more anterior partial P_x has two prominent, almost vertical ridges that undoubtedly contacted a small talonid.

Discussion.— Associated teeth in YPM-PU 18168 probably represent an undescribed pantodont species. The general structure of M^1 and M^2 is close to that of *Pantolambda cavirictum* (changed from "*cavirictus*" by Rose, 1981a, p. 147, for gender agreement) but the M^2 is shorter than the M^1 and more transversely elongate. The shorter M^2 is an unusual trait that, among North American pantodonts, is apparently known only in *Haplolambda* (e.g., Simons, 1960). YPM-PU 18168 differs further from *Pantolambda* in the high degree of lateral compression in its saber-like C^1. *Pantolambda* has a more rounded C^1 in cross-section (Matthew, 1937; Simons, 1960). The C^1 in YPM-PU 18168 has a length width ratio of about 2:1, which is similar to a C^1 (UM 85307) referred here to *Titanoides gidleyi*, but differs in having a low ridge along the anterobuccal face.

Two species of *Haplolambda* are currently recognized in North America, *H. simpsoni* from Utah (Miller, 1986) and *H. quinni* from Colorado (Patterson, 1939). Miller (1986) identified the holotype (BYU 4508, maxilla with P^2-M^3) and only specimen of *H. simpsoni* as cf. *H. simpsoni* because of perceived taxonomic instability in Pantodonta. Lucas (1998), however, dropped the conferral in his review of the *Pantodonta*, without discussion. Two key characters of *Haplolambda*, based on the type species *H. quinni*, are an M^2 that is narrower than M^1 and a significantly reduced M^3 (Simons, 1960). The holotype of *H. simpsoni* lacks both these characters and has molar proportions comparable to those of *Leptolambda*. It differs from described species of *Leptolambda* in having longer and narrower premolars. This is especially true of P^4 that approaches a right triangle. *Haplolambda simpsoni* is probably best considered a species of *Leptolambda*, pending the discovery of more complete material.

The C^1 in the holotype of *Haplolambda quinni* is small and round, very unlike the C^1 in YPM-PU 18168. The small C^1 in *H. quinni* suggests that it is a female, however, and the condition of the male C^1 is unknown. The relatively large size of the C^1 in YPM-PU 18168 suggests that it was a male. The referred teeth differ further from those of *H. quinni* in being about 20% smaller in both length and width in M^1, in lacking an invaginated ectoflexus on M^2, in having narrower stylar shelves with more buccally positioned mesostyles on the molars, and in having much

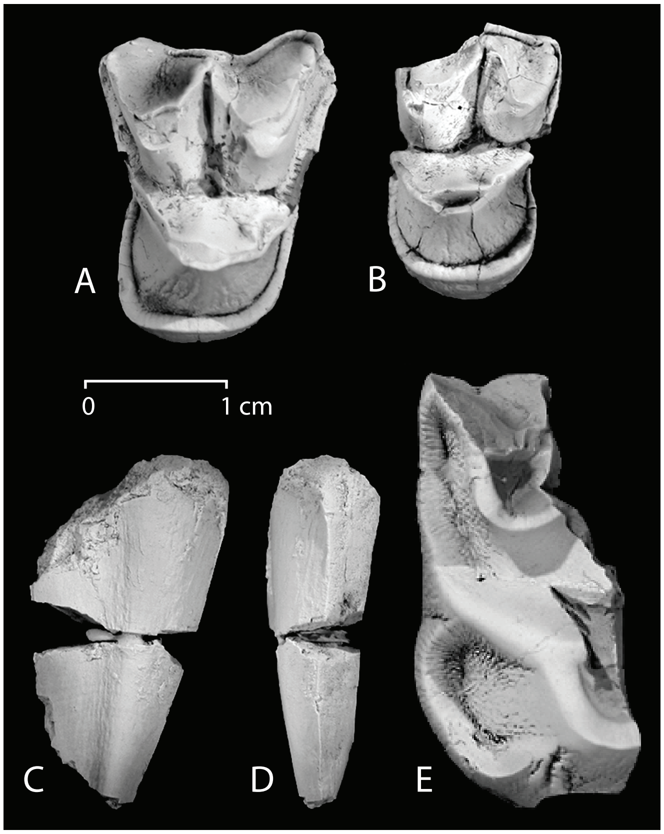


FIGURE 21 — Upper teeth of cf. *Haplolambda* (A-D) YPM-PU 18168 from NW 1/4, Section 11, T56N, R99W, Park Co., Wyoming; and Barylambdidae gen. et sp. indet. (E) from SC-187. A-B, cf. *Haplolambda* right M^1 (A) and left M^2 (B) in occlusal view; C-D, right partial C^1 in buccal (C) and anterior (D) views. E, partial upper molar of Barylambdidae gen. et sp. indet. (UM 73601) in occlusal view.

wider molar and premolar cingula that are continuous around the protocones. The only pantodonts I have seen with cingula this wide and continuous are *Pantolambda* and *Caenolambda* (see Simons, 1960). This is apparently a variable feature in individuals of *P. cavirictum* (e.g., AMNH 963, Fig. 43 in Matthew, 1937; USNM 21327, Fig. 10 in Simons, 1960), however, and possibly in *Caenolambda* as well. *Caenolambda pattersoni* (Gazin, 1956b) has a wide and continuous cingulum on M^2, while molar cingula in *C. jepseni* (Simons, 1960) are narrow and discontinuous. Considering the variability in the cingula of these taxa, it would not be surprising if it were also variable in other poorly known pantodonts, such as *Haplolambda*.

The associated teeth in YPM-PU 18168 do not fit well into any described pantodont genus. I confer them to *Haplolambda*, primarily because of the shorter M^2, relative to M^1, which is probably a derived feature in *Haplolambda*. The validity of this character relies entirely on the correct identification of molar homologies, however, and homologies assumed here will not be certain until teeth are found in a maxilla. I am aware of no record detailing the association of these specimens, and although it is clear that most of the teeth are from a single individual, it is possible that the unusual C^1 is the tip of a *Titanoides* C^1. Although the specimen probably represents a new and unusual taxon, I refrain from formally naming it because of the fragmentary and "associated" nature of the material.

YPM-PU 18168 was collected in the NW¼ of section 11, T56N, R99W by R. Wood in 1962, according to the specimen label. Strata in this area are in the *Phenacolemur* and *P. churchilli* zones, of late Tiffanian age, indicating that this species was a contemporary of several other pantodont species.

Dental measurements (mm).— YPM-PU 18168: M^1, L = 16.6, W = 22.5; M^2, W (min.) = 19.2.; M_2 trig. W (min.) = 11.5.

Referred specimen.— **NW¼**, **Sec. 11**, **T56N**, **R99W**: YPM-PU 18168, R C^1, M^1, M^2 fragments, L P^4 protocone, partial M^2, R partial P_x, P_4? frag., M_2 and M_3? trigonids, molar talonid, all assoc.

Genus and species indeterminate

Figure 21E

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* zone (Ti-5a).

Description and discussion.— A partial upper molar (UM 73601) collected near Princeton Quarry appears to represent a large barylambdid about the size of *Barylambda faberi*. It has a thick postcingulum that surrounds a relatively large basin (Fig. 21E) and in these respects differs from *Leptolambda*, *Barylambda*, *Haplolambda*, and *Caenolambda*. It compares more favorably with *Ignatiolambda*. In *I. barnesi*, the M^1 and the lingual half of M^3 are quadrate (Simons, 1960, Fig. 12) and M^3 has a heavy cingulum. UM 73601 is also quadrate but the postcingulum is much heavier. Also, because UM 73601 has a large metacingulum posterior to the metacone (Fig. 21E) it is probably not an M^3. It is larger than molars in the holotype of *I. barnesi*, based on Simons' description. It could represent an undescribed species of *Ignatiolambda* or be an extreme variant of another barylambdid.

This specimen is only slightly younger than the last occurrence of *Leptolambda churchilli* and represents the last occurrence of a barylambdid pantodont in the northern Bighorn Basin.

Referred Specimen.— **SC187**: UM 73601, partial R M^x.

Family CORYPHODONTIDAE Marsh, 1876

CORYPHODON Owen, 1845

Coryphodon?

Coryphodon sp. (in part), Rose, 1981a, p. 88.
Coryphodon proterus (in part), Uhen and Gingerich, 1995, p. 266.

Biostratigraphic occurrences in Bighorn Basin.— Rodentia zone (Cf-1).

Description and discussion.— The earliest occurrence of *Coryphodon* in North America is an important datum because *Coryphodon* is potentially an intercontinental immigrant. The earliest possible record of the family is an upper canine fragment from the early Clarkforkian that was identified as *Coryphodon* by previous authors (Rose, 1981a; Uhen and Gingerich, 1995). In my opinion, however, it is too fragmentary for confident identification. The first definite specimens of *Coryphodon* do not occur until the middle Clarkforkian, some 0.4 myr later, when they are a common component of the fauna.

TABLE 17 — Dental measurements for *Bessoecetor pilodontus* n. sp. from Divide and Croc Tooth quarries, for *B*. cf. *B*. *pilodontus* from Cedar Point Quarry, and for *B*. cf. *B*. *septentrionalis* from Croc Tooth Quarry. *Estimate.

		Bessoecetor pilodontus				*B*. cf. *B*. *pilodontus*				*B*. cf. *B*. *septentrionalis*
		UM 82099	UM 86242	UM 91332 (type)	UM 109855	UM 64523	UM 83257	YPM-MU 21493	YPM-PU 20081	YPM-PU 14965
M^1	L	—	—	—	2.95	—	—	—	—	—
	Mll	—	—	—	2.10	—	—	—	—	—
	W	—	—	—	3.60	—	—	—	—	—
	Mlc	—	—	—	2.00	—	—	—	—	—
P_3	L	—	—	—	—	—	—	2.23	—	—
	W	—	—	—	—	—	—	1.27	—	—
P_4	L	—	—	2.87	—	—	2.77	2.67	2.55	—
	W	—	—	1.65	—	—	1.30	1.60	1.43	—
M_1	L	—	2.75	2.53	—	—	2.66	2.55	2.40	—
	W tri.	—	2.27	2.15	—	—	1.83	2.10	2.0*	—
	W tal.	—	2.35	2.27	—	—	1.95	2.03	2.0*	—
M_2	L	3.10	—	2.70	—	2.95	2.57	2.53	2.50	2.40
	W tri.	2.60	—	2.65	—	2.35	2.05	2.30	2.33	1.95
	W tal.	2.35	—	2.40	—	2.20	1.87	2.00	2.05	1.70
M_3	L	3.47	—	3.25	—	3.20	—	2.97	2.70	2.60
	W tri.	2.57	—	2.55	—	2.35	—	1.70	2.25	2.10
	W tal.	1.90	—	1.75	—	1.77	—	2.23	1.70	1.37

The canine is similar in size, proportion, and enamel thickness to upper canines of *Coryphodon*, but other pantodonts such as *Titanoides*, and possibly *Leptolambda* and *Barylambda*, also have large saber-like upper canines. *Titanoides* is known from the Tiffanian and Clarkforkian of the Bighorn Basin (Gingerich, 1996a) but is rare in the Clarkforkian. The other taxa are not known in the Clarkforkian of the Bighorn Basin but *Barylambda* occurs in the Clarkforkian of Colorado and *Leptolambda* is a common taxon in the late Tiffanian. UM 71575 is heavily abraded and originated from a conglomerate composed of paleosol clasts. It potentially could be a reworked specimen of an earlier pantodont. Alternatively, it could be the earliest occurrence of *Coryphodon* in North America but a more diagnostic specimen is needed to confidently extend the range of this genus into the early Clarkforkian.

Referred specimen.— SC083: UM 71575, C^1 frag.

Suborder PANTOLESTA McKenna, 1975
Family PANTOLESTIDAE Cope, 1884

BESSOECETOR Simpson, 1936

Propalaeosinopa Simpson, 1927, p. 2.

Discussion.— Van Valen (1967) regarded *Propalaeosinopa albertensis*, *P*. *diluculi*, and *Bessoecetor thomsoni* to be conspecific, although he noted that populations were distinct. Subsequent authors followed Van Valen's synonymy of *P*. *diluculi* and *B*. *thomsoni*, but most have kept *P*. *albertensis* separate (e.g., Rigby, 1980; Rose, 1981a; Krause and Gingerich, 1983). Scott (2002) declared *P*. *albertensis*, which is the type species of *Propalaeosinopa*, to be a *nomen dubium*, asserting that the holotype has no characters of diagnostic value. The holotype of *P*. *albertensis* is a dentary preserving a worn P_4, alveoli for $M_{1\text{-}3}$, the posterior alveolus for P_3 (Simpson, 1927), and part of the ascending ramus. Although I disagree that the specimen has no characters of diagnostic value, it is less than adequate as the type for a genus. I suggest that its continued recognition would only serve to confuse the assignment of specimens to existing species. Collection of a larger sample from the type locality might remedy the problem but the collection of more specimens is unlikely since the holotype was recovered from a landslide and the productive bed was reportedly in a bluff (see Simpson, 1927).

Following the synonymies of Scott et al. (2002), other species contained in *Propalaeosinopa* are transferred to *Bessoecetor* and the type species for the genus becomes *B*. *septentrionalis*. The type specimen for the genus, however, remains the holotype of *B*. *thomsoni* (AMNH 33810) from Scarritt Quarry, upon which *Bessoecetor* was originally based, contrary to the assertion by Scott et al. that the holotype is that of *B*. *septentrionalis* (see ICZN, 1999).

Bessoecetor pilodontus, new species

Figure 22, Table 17

Bessoecetor n. sp., Secord et al., 2006, p. 228.

Holotype.— UM 91332, a right dentary with P_4-M_3 and alveoli for I_3-P_3; from Divide Quarry, northern Bighorn Basin.

Biostratigraphic occurrences.— *Plesiadapis churchilli* (Ti-4a) and ?*Phenacolemur* (Ti-4b) zones.

Diagnosis.— Larger than all other species of *Bessoecetor*. Differs further in having a wider more inflated P_4 with a less distinct paraconid that is less separate from the protoconid, and

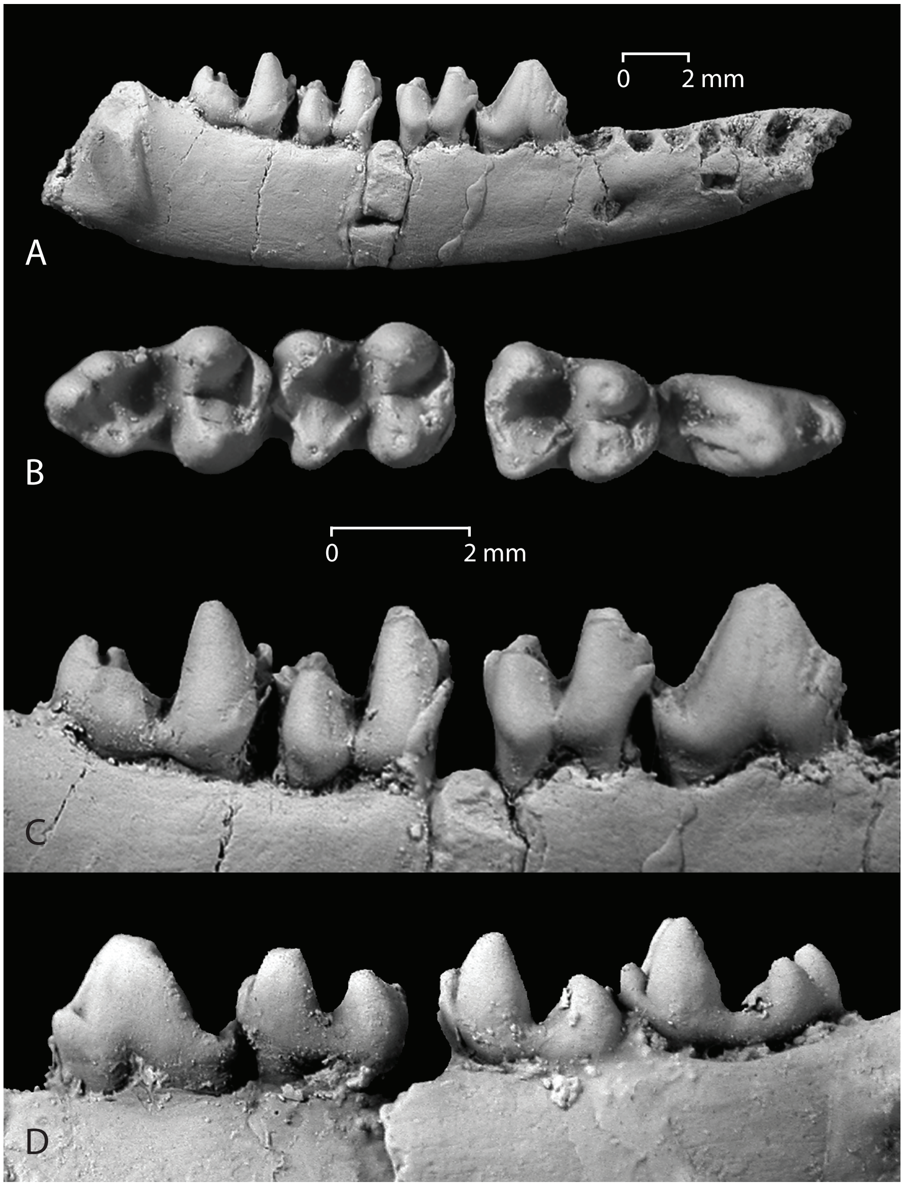


FIGURE 22 — Holotype (UM 91332) of *Bessoecetor pilodontus* n. sp. from Divide Quarry. A-C, right dentary preserving P_4-M_3 in buccal (A, C), occlusal (B), and lingual (D) views.

a shorter P_4 talonid. Further differs in having lower molar trigonids on M_{1-2}, an M_1 talonid that is wider than its trigonid, resulting in a lower M_1 length/talonid width ratio.

Description.— The P_4 paraconid is little more than a low bulge near the base of the crown. Anterior and posterior medial ridges ascend the protoconid. The talonid has a single medial cusp and a small lingual basin. There is no indication of a metaconid. Molar trigonids are subequal in height and relatively low. M_{1-2} paraconids are distinct cusps, moderately anteroposteriorly compressed, and are medially positioned between the protoconid and metaconid. Molar metaconids, protoconids, hypoconids, and entoconids are conical. The hypoconulid progressively shifts lingually from M_1, where it is slightly lingual of medial, to M_3, where it is adjacent to the entoconid. All molars have a short, but distinct, precingulid positioned well below the paraconid. The molar cristid obliqua contacts the postvallid at about one third of the distance from the buccal edge. The M_1 talonid is considerably wider than the trigonid, but these widths are subequal in M_2.

Dentary depth below the base to the M_1 trigonid is about 2.2 times the estimated height of M_1. Two mental foramina are present, one below the posterior alveolus for P_3 and the other below the intersection of M_1 and M_2. Alveoli indicate that C_1 and P_1 were single-rooted, while P_{2-3} were double-rooted. The alveolus for C_1 was much larger than other alveoli.

Discussion.— Scott et al. (2002) combined "*Diacodon*" *septentrionalis*, *Bessoecetor diluculi*, and *B. thomsoni* into a single species, *B. septentrionalis*, which has priority. They stated that

TABLE 18 — Dental measurements for *Leptonysson orthius* n. sp. from Cedar Point Quarry, the holotype of *L. basiliscus* from Gidley Quarry, *L.* cf. *L. basiliscus* from Rock Bench Quarry, *Leptonysson*? from Divide Quarry, and *Thelysia artemia* (holotype) from SC-167.

		Leptonysson orthius					*L. basiliscus*	*L.* cf. *L. basiliscus*	*Leptonysson*?	*Thelysia artemia*
		YPM-PU 14983	YPM-PU 17783	YPM-PU 20601 (type)	YPM-PU 20767	YPM-PU 20904	AMNH 35295 cast (type)	YPM-PU 14733	UM 91330	UM 68281 (type)
M^2	L	—	—	—	—	—	—	—	3.73	—
	Mll	—	—	—	—	—	—	—	2.57	—
	W	—	—	—	—	—	—	—	6.10	—
	Mlc	—	—	—	—	—	—	—	1.95	—
P$_3$	L	—	—	—	—	—	3.20	—	—	—
	W	—	—	—	—	—	1.20	—	—	—
P$_4$	L	4.20	4.15	3.95	—	4.40	3.83	—	—	—
	W	1.55	1.70	1.60	—	1.85	1.65	—	—	—
M$_1$	L	3.65	3.75	3.63	3.65	3.63	—	—	—	3.85
	W tri.	2.50	2.60	2.40	2.55	2.50	—	—	—	2.90
	W tal.	2.33	2.50	2.25	2.45	2.37	—	—	—	2.50
M$_2$	L	3.77	3.70	3.70	3.77	—	3.28	3.40	—	4.13
	W tri.	3.00	3.03	2.80	3.20	3.15	2.75	2.65	—	3.60
	W tal.	2.30	2.45	2.35	2.60	—	1.95	2.15	—	2.70
M$_3$	L	—	—	4.05	—	—	3.55	3.75	—	4.83
	W tri.	—	3.20	3.15	—	—	2.95	2.80	—	3.63
	W tal.	—	2.00	1.97	—	—	1.90	1.85	—	2.53
M$_4$	L	—	—	—	—	—	3.55	—	—	—
	W tri.	—	—	—	—	—	2.73	—	—	—
	W tal.	—	—	—	—	—	—	—	—	—

B. septentrionalis was virtually identical to *B. diluculi* and *B. thomsoni*, except for minor differences. I provisionally follow their synonymy.

Specimens of *Bessoecetor pilodontus* are larger in all dimensions when compared with casts of three dentaries of *B. septentrionalis* ("*diluculi*") from Gidley Quarry. Means of both M$_1$s from Divide Quarry are 15% greater in length, 25% greater in trigonid width, and 47% greater in talonid width than the M$_1$s from Gidley Quarry. Simpson's (1937b) data from Gidley and Silberling quarries suggest that with a larger sample there will be minor overlap in molar length between *B.* "*diluculi*" and *B. pilodontus*. There does not appear to be overlap in width, however, highlighting the more laterally expanded condition of teeth in *B. pilodontus*. Similarly, Simpson's (1937a) data for *B.* "*thomsoni*" from Scarritt Quarry suggest that there is minor size overlap in M$_1$ length but that M$_1$ width is outside that of *B. pilodontus*. There is more overlap with *B. pilodontus* in length measurements reported by Rigby (1980) for *B. diluculi* from Swain Quarry than in other populations. Rigby stated that the sample was indistinguishable from that at Gidley Quarry, however, and noted no size difference. It may be that Rigby's metric data are not comparable to Simpson's because of differences in measuring techniques. In any case, as with the other samples, width data for *B. pilodontus* are outside the reported range for Swain Quarry.

The holotype of *Bessoecetor* "*albertensis*" (AMNH 15543B) was declared a *nomen dubium* by Scott et al. (2002), as discussed above. Although I follow their recommendation, a brief comparison of *B. pilodontus* is warranted in the event that *B.* "*albertensis*" is resurrected. The P$_4$ of *B.* "*albertensis*" resembles those of *B. septentrionalis* (*sensu lato*) in probably having had a large, separate, prominent paraconid, unlike the indistinct paraconid of *B. pilodontus*. The P$_4$ appears to have been more inflated than is typical for *B. septentrionalis* but less than in *B. pilodontus*. The P$_4$ is ~20% narrower and the dentary ~20% shorter (based on distance between P$_4$ and M$_3$ roots) than in *B. pilodontus*. Thus, *B.* "*albertensis*" differs considerably from *B. pilodontus*.

I tentatively include an isolated M^1 from Croc Tooth Quarry in *Bessoecetor pilodontus*. The specimen is very similar to an M^1 of *B. septentrionalis* from Douglass Quarry (AMNH 3853) but is larger and more robust, as would be expected for *B. pilodontus*.

Hartman and Kihm (1995) noted that a specimen of *Bessoecetor* (then *Propalaeosinopa*) from the Riverdale Locality in North Dakota was significantly larger than comparable teeth of *Bessoecetor* from Judson and Brisbane reported by Holtzman (1978). The specimen (FMNH P 8663) is an M$_2$ with a length and width of 3.3 and 2.4 mm, respectively, which is close to the size of UM 82099 (Table 17) included here in *B. pilodontus*. Hence, *B. pilodontus* may also be present at the Riverdale Locality. Hartman and Kihm (1995) suggested that the Riverdale Locality was equivalent in age to the *Plesiadapis churchilli* zone (Ti-4 of Lofgren et al., 2004), and thus is roughly equivalent to Divide Quarry in age.

Referred specimens.— **Croc Tooth Q.** (FG028): UM 109855, L M^1. **Divide Q.** (FG046): UM 82099, L dent. M$_{2\text{-}3}$; 83274, L M^2 protocone; 86242, R M$_1$; 91332 (holotype).

TABLE 19 — Dental statistics for *Leptonysson orthius* n. sp. from Cedar Point Quarry. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
P$_4$	L	4	3.95	4.40	4.18	0.09	0.18	4.43
	W	4	1.55	1.85	1.68	0.07	0.13	7.90
M$_1$	L	5	3.36	3.75	3.66	0.02	0.05	1.37
	W tri.	5	2.40	2.60	2.51	0.03	0.07	2.95
	W tal.	5	2.25	2.50	2.38	0.04	0.10	4.14
M$_2$	L	4	3.70	3.77	3.74	0.02	0.04	1.08
	W tri.	5	2.80	3.20	3.04	0.07	0.16	5.13
	W tal.	4	2.30	2.60	2.43	0.07	0.13	5.46
M$_3$	L	1	—	—	4.05	—	—	—
	W tri.	2	3.15	3.20	3.18	—	—	—
	W tal.	2	1.97	2.00	1.99	—	—	—

Bessoecetor cf. *B. pilodontus*

Table 17

Propalaeosinopa cf. *diluculi*, Rose, 1981a, p. 152.
Bessoecetor septentrionalis (in part), Scott et al., 2002, p. 700.
Bessoecetor cf. n. sp., Secord et al., 2006, p. 228.

Biostratigraphic occurrences.— *Plesiadapis rex* zone (Ti-3).

Description and discussion.— Some specimens of *Bessoecetor* from Cedar Point Quarry compare favorably with *B. pilodontus*, while others exhibit an intermediate condition between *B. pilodontus* and *B. septentrionalis* ("*diluculi*"). YPM-PU 21493 and UM 64523 are close to *B. pilodontus* but have slightly narrower molars and the former is slightly smaller. The P$_4$ in the former is as inflated as in *B. pilodontus*, and has a similar paraconid and talonid. Two other specimens, YPM-PU 20881 and UM 83257, exhibit more of an intermediate condition between *B. pilodontus* n. sp. and *B. septentrionalis*. Both are smaller and have narrower P$_4$s than the first two dentaries, but are not as narrow as the three specimens of *B. septentrionalis* from Gidley Quarry that were available for comparison. The P$_4$ paraconids are small and reduced, as in *B. pilodontus*. The Cedar Point Quarry specimens could represent two species or more probably a single variable species that was part of an evolutionary lineage leading to *B. pilodontus*.

Referred specimens.— **Cedar Point Q.**: UM 64523, R dent. M$_{2-3}$, P$_1$-M$_1$ alveoli; 83257, L dent. P$_4$-M$_2$, P$_3$, and M$_3$ alveoli. YPM-PU 14590, R dent. P$_3$-M$_3$; 19600, R dent. M$_{2-3}$; 20881, R dent. P$_3$-M$_3$; 21411, R dent. M$_{2-3}$; 21412, L dent. M$_2$; 21493, R dent. P$_3$-M$_3$.

Cf. *Bessoecetor septentrionalis*

Table 17

Biostratigraphic occurrences.— *Phenacolemur* zone (Ti-4b).

Description and discussion.— A single dentary preserving M$_{2-3}$ from Croc Tooth Quarry probably represents an undescribed species of *Bessoecetor*. It is in the size range of *B. septentrionalis*, but based on comparison with three casts of dentaries from Gidley Quarry, differs in having narrower molars with slightly higher trigonids and more lingually positioned paraconids. Additionally, there is a large mental foramen below the M$_2$ talonid, a position that is more posterior than is typical for *B. septentrionalis*, which has the foramen below the M$_2$ trigonid or between M$_2$ and M$_1$. It differs from *Bessoecetor* cf. *B. pilodontus* in the same respects, only to a greater degree, and is smaller and has considerably more acute trigonid cusps. Collection of more complete specimens is desirable before establishing a new species.

Referred specimen.— **Croc Tooth Q.** (FG028): YPM-PU 14965, R dent. M$_{2-3}$.

PALAEOSINOPA Matthew, 1901

Palaeosinopa dorri?

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Description and discussion.— *Palaeosinopa* is a rare taxon in Paleocene localities in the northern Bighorn Basin (e.g., Rose, 1981a). A single M$_2$ from Divide Quarry is the only record of *Palaeosinopa* from localities of Tiffanian age. It is closest to the size expected for *P. dorri*, which is known only from a partial skull preserving most of the upper dentition (Gingerich, 1980c). The M$_2$ occludes reasonably well with molars in the holotype (UM 55122) but represents a slightly smaller individual. It is 30, 28, and 15% smaller (in length) than M$_2$ in the holotypes of *P. nunavutensis*, *P. veterrima*, and *P. didelphoides*, respectively, and 35% larger than M$_2$ in *P. lutreola*, all from the early Eocene. The type locality for *Palaeosinopa dorri* is Dell Creek Quarry in the Hoback Basin of western Wyoming, which is probably a correlative of the *P. churchilli* (Ti-4a) or *Phenacolemur* (Ti-4b) zones in the Bighorn Basin (see *Paleotomus* cf. *P. radagasti* section).

Dental measurements (mm).— UM 110948: L = 4.6, Tri. W = 3.6*, Tal. W = 3.6*

Referred specimen.— **Divide Q.** (FG046): UM 110948, L M$_2$.

LEPTONYSSON Van Valen, 1967

Leptonysson orthius, new species

Figures 23A–G, Tables 18–19

?*Propalaeosinopa* sp., Rose, 1981a, p. 152.
Leptonysson n. sp., Secord et al., 2006, p. 228.

Holotype.— YPM-PU 20601, a left dentary with P$_4$-M$_3$ and alveoli for P$_{1-3}$; from Cedar Point Quarry, northern Bighorn Basin.

Biostratigraphic occurrences.— *Plesiadapis rex* (Ti-3) and *Plesiadapis churchilli* (Ti-4a) zones.

Diagnosis.— The following comparison to *Leptonysson basiliscus*, the only other species in the genus, is based on a new interpretation of dental homologies in the holotype, discussed below. Differs from *L. basiliscus* in (1) being larger; (2) having a more posterior and more medially positioned P$_4$ metaconid and metaconid crest (a sharp crest connecting the metaconid and "carnassial" notch on the talonid); (3) having more rounded and less acute molar cusps; (4) having wider, heavier, and less vertical precingulids; and (5) having less posteriorly positioned M$_2$ hypoconulids. Differs from *Thelysia artemia* in (1) being smaller; (2) having smaller, less pillar-like molar hypoconids, especially on M$_3$; and (3) having relatively narrower M$_{1-2}$ trigonids (crown length/trigonid width ratios ~10% greater on average). The holotype is

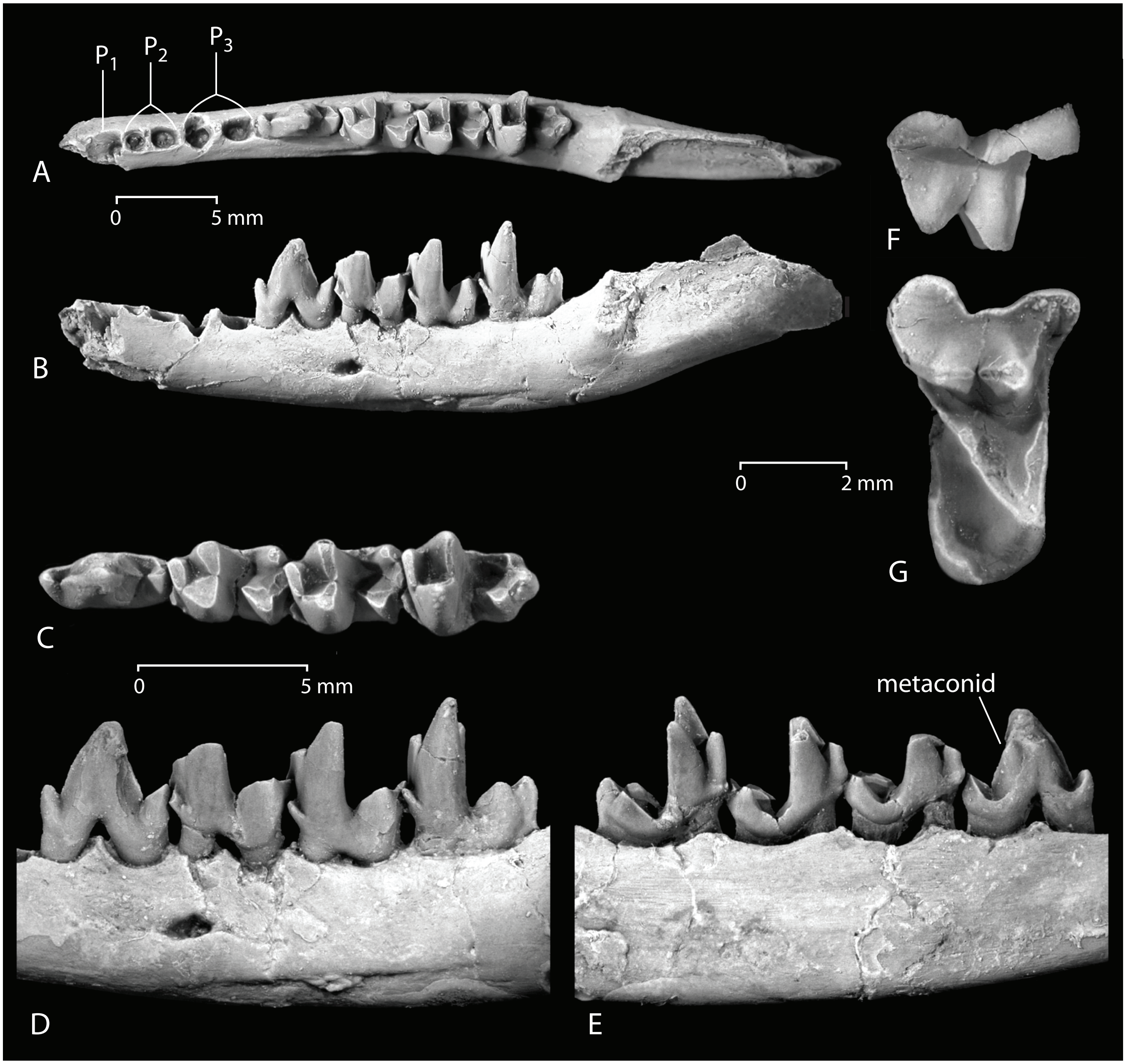


FIGURE 23 — Dentition of *Leptonysson orthius* n. sp. and *L. basiliscus*. A–E, left dentary with P_4-M_3 of *L. orthius* (YPM-PU 20601, holotype) in occlusal (A, C), buccal (B, D), and lingual (E) views; Cedar Point Quarry. F–G, right M^2 of *L. orthius* (UM 91330) in buccal (F) and occlusal (G) views; Divide Quarry. H–I (facing page), holotype of *L. basiliscus* in occlusal (H) and buccal (I) views, modified with permission from Van Valen (1967); Gidley Quarry.

the only described specimen of *T. artemia* and because its molar trigonids are more worn than most of *L. orthius*, relative trigonid width would probably be greater in unworn teeth.

Etymology.— *Orthios* (G), high, lofty, steep: in allusion to the high, steep molar trigonids of this species and genus.

Description.—The following designations for tooth positions follow the eutherian convention of $P_{1\text{-}4}$ and $M_{1\text{-}3}$. P_4 has a large acute paraconid separated from the protoconid by a "carnassial" notch. In a similar fashion, there is a single large acute talonid cusp also separated by a "carnassial" notch. Both notches are bounded by sharp crests on the cusps and on the protoconid. The crest on the posterior margin of the protoconid is confluent with a small, but distinct, metaconid situated slightly lingual of the protoconid apex, and well below it (the metaconid on the holotype was lost to wear and the protocone apex has been shifted slightly in a posterobuccal direction from deformation).

Trigonids are high on all molars but probably highest on M_3, although wear makes the relative heights of M_1 and M_2 difficult to assess. The M_1 trigonid is shorter than in M_{2-3}. Shallow "carnassial" notches are present in the paralophid and protolophid on some trigonids, and were probably present but lost to wear in others. All trigonids have strong anteriorly projecting precingulids, situated well below the paraconids. The M_1 talonid is approximately equal in width to the trigonid, but talonids on M_{2-3} become progressively narrower posteriorly. Talonid basins are relatively narrow and crowded by a large hypoconid. A vertical column extends buccally and ventrally from the hypoconid apex. The hypoconid apex is slightly higher than that of the entoconid. There is no entocristid anterior to the entoconid, leaving the talonid basins open lingually. The hypoconulid is large and subequal to the entoconid from which it is isolated by a wide notch. A large protostylid is present on the buccal base of the protoconid on M_1 in YPM-PU 17783, but absent on other molars and specimens. Small metastylids are present on M_1 and M_2 in some specimens but were lost to wear or were absent on others.

The dentary is relatively shallow and has a depth below the M_1 trigonid that is about 120% of the buccal height of the trigonid. There is a small mental foramen situated between the P_1 and C_1 alveoli, based on two dentaries. A larger mental foramen is situated below the M_1 trigonid or talonid. Alveoli indicate that C_1-P_1 were single-rooted, while P_2-M_3 were double-rooted. A partial alveolus, presumably for I_3, is present in YPM-20767 on the anterolingual tip of the dentary. It is about the size of the P_2 alveolus and slightly procumbent. The canine was quite large and the root was laterally compressed. P_1 was relatively large but much smaller than the canine, with a laterally compressed root that was slightly oblique to the long axis of the dentary.

Discussion.— The inclusion of this species in *Leptonysson* and the assignment of *Leptonysson* to Pantolestidae relies on the interpretation of dental homologies in the holotype of *L. basiliscus*, which was until now the only known specimen of *Leptonysson*. The holotype of *L. basiliscus* (AMNH 35295) is from Gidley Quarry in the Crazy Mountains Basin and is Torrejonian in age. It preserves two premolars and three molars separated by two alveoli that held a double-rooted tooth (Figs. 23H,I) (see also Van Valen, 1967, Text-fig. 4). Previous authors assumed that the molars were M_{1-3} and the premolars were P_{2-3} or dP_{2-3} (Van Valen, 1967; Clemens, 1973; Novacek, 1977; Gingerich, 1982a; Kellner and McKenna, 1996), using the traditional scheme of eutherian homologies (as opposed to those of McKenna, 1975). After comparing the holotype of *L. basiliscus* (epoxy cast) to specimens of *L. orthius* n. sp., however, it is readily apparent that the last molar in the former is a supernumerary M_4, and not an M_3. Thus, the teeth present are P_{3-4} and M_{2-4}, and the alveoli between these teeth held an M_1. This interpretation is supported by several lines of evidence.

First, the ultimate and penultimate molars in the holotype of *L. basiliscus* are both typical of M_3 in eutherian mammals of this grade. The talonid is long and narrow, and the hypoconulid is pointed and more posteriorly positioned than in the more anterior molars. A long pointed hypoconulid is not the design of a molar intended to interface with another molar posteriorly. The penultimate molar in *L. basiliscus* would be most unusual if it is an M_2, as in previous interpretations, but is ordinary as an M_3. Also, the ultimate molar is slightly smaller than the penultimate molar, which is a common condition in supernumerary M_4s, at least in humans and other primates (see Jungers and Gingerich, 1980; Kokten et al., 2003).

Second, the ultimate molar in the holotype of *L. basiliscus* is "impacted" in that the talonid extends into the ascending ramus and the molar would need to shift anteriorly by a considerable amount for the tooth to be fully functional (Figs. 23H,I) (also see Van Valen, 1967, Text-fig. 4). Eutherians of this grade typically have a space between the M_3 talonid and the ascending ramus. Indeed, if the ultimate molar were not present, the space between the ascending ramus and the talonid of the penultimate molar would be approximately equivalent to that in *Leptonysson orthius*. The "impacted" condition of the ultimate molar might be found in a juvenile that has not reached adult size, but this does not appear to be a juvenile dentary (see below).

Third, the alveoli between the premolars and molars in the holotype of *L. basiliscus* are closely spaced and the anterior alveolus is slightly anteroposteriorly compressed. Both of these features are typical of M_1 but atypical of P_4 in eutherians of this grade. The expectation for a P_4 is a laterally compressed or round anterior root, with a greater spacing between it and the posterior root. In light of this evidence there is no doubt that the ultimate molar in the holotype of *Leptonysson basiliscus* is a supernumerary M_4.

When first describing *Leptonysson basiliscus*, Van Valen (1967, pp. 235, 247) interpreted the teeth present as $dP_{2\text{-}3}$ and $M_{1\text{-}3}$. His interpretation of the premolars as deciduous was apparently based on the assumption that the ultimate molar was incompletely erupted. He noted, however, that there was no indication of a calcified permanent tooth in a hole in the mandible below dP_3. Clemens (1973) doubted Van Valen's interpretation of the premolars as deciduous for several reasons, including X-rays of the jaw, but did not question his homologies. Gingerich (1982a), as well as Kellner and McKenna (1996), also thought the premolars were permanent but followed Van Valen's interpretation of homologies. Using the homologies presented here, the very close structural similarity between the adult P_4 in *L. orthius* and that of *L. basiliscus* (Fig. 23) provide additional evidence that P_4 in the former is permanent.

Van Valen (1967, p. 247) reported five or six alveoli in front of the anterior-most premolar (P_3 here) in the holotype of *Leptonysson basiliscus*. He suggested that the posterior two probably held dP_1 and that there was a small deciduous canine in front of it. The anterior part of the dentary is badly damaged, however, and it is difficult to make a confident count of alveoli. Van Valen's Figure 4 (p. 247) shows four alveoli, and possibly the posterior part of a fifth, at the front of the jaw. Upon examination of a cast of the holotype, however, what is figured as a fourth alveolus appears to be a break in the dentary exposing cancellous bone. The two posterior-most alveoli are obliquely oriented and closely spaced, just like the P_2 alveoli in *L. orthius*. The alveolus anterior to these is consistent in size and orientation with the alveolus in *L. orthius* that held a single-rooted P_1. Thus, the number and relative size of alveoli in these species appears to have been the same. The P_2 of *L. basiliscus* was probably double-rooted, P_1 single-rooted, and there was a large permanent canine just anterior to the break at the front of the jaw.

An M_1 trigonid documents the presence of *Leptonysson orthius* at Divide Quarry and extends its range into Ti-4a. The size, trigonid height, relative positions of cusps, and distinctive mesially projecting precingulid, leave little doubt that it is correctly identified as *L. orthius*. More importantly, an isolated right M^2 (UM 91330) from Divide Quarry may also belong to *L. orthius*. No other proteutherian known from the middle or late Tiffanian of the Bighorn Basin is the proper size for this molar. It occludes reasonably well with a right M_2 (YPM-PU 20904) from Cedar Point Quarry but may be from a slightly smaller individual. The M^2 has a wide postcingulum with a large hypocone (Figs. 23F–G). Both these features preclude it from Palaeoryctidae *sensu stricto*, as recognized by Kellner and McKenna (1996). The M^2 is also similar to that of *Paleotomus* in size and structure but differs in having a more anteroposteriorly compressed protocone with a steeper lingual margin.

Gingerich (1982a) noted many similarities between *Thelysia artemia*, from the middle Clarkforkian, and *L. basiliscus*. *Leptonysson orthius* also exhibits many similarities to *T. artemia*, and is a structural and temporal intermediate between it and *L. basiliscus*. The differences between *L. orthius* and *T. artemia* appear to be no greater than between it and *L. basiliscus* and one could reasonably place *L. orthius* in *Thelysia*. I have placed it in *Leptonysson*, however, because it lacks the massive molar hypoconid on M_3, which may be a derived character in *Thelysia*. It should be noted that two of the differences Gingerich (1982a) used to distinguish *Thelysia* from *Leptonysson* (a larger P_4, based on alveoli, and a mental foramen below M_1) no longer hold using the dental homologies presented here. In light of this, differences may not be great enough to warrant generic separation of these species, but I refrain from synonymy pending the discovery of premolars of *Thelysia*. *Leptonysson basiliscus*, *L. orthius*, and *T. artemia* may represent members in a long, rarely sampled lineage.

The dental homologies in *Leptonysson basiliscus* presented here have important implications for taxonomic placement of *Leptonysson* and *Thelysia*. *Leptonysson* was described by Van Valen (1967) as a leptictid but transferred to Palaeoryctidae by Clemens (1973). Novacek (1977) also excluded it from Leptictidae, following Clemens. Kellner and McKenna (1996) reassigned *Leptonysson* to Leptictidae, however, citing the predicted semimolariform condition of what they interpreted as the ultimate premolar. It is now clear that the missing tooth was an M_1, however, and the tooth anterior to it is a P_4. The premolariform condition of the P_4 virtually excludes *Leptonysson* from Leptictidae. Kellner and McKenna (1996) used the position of the mental foramen below P_4 to exclude *Leptonysson* from Pantolestidae, noting that a mental foramen below M_1 was a synapomorphy of Pantolestidae. Using the homologies presented here, however, the mental foramen in *L. basiliscus* is below M_1. It is also below M_1 in *L. orthius* and in *Thelysia*. For this reason, and because of the morphology of M^2 (UM 91330), I provisionally place both genera in Pantolestidae pending a more rigorous phylogenetic analysis.

Referred specimens.— **Cedar Point Q.**: YPM-PU 14983, L dent. P_x frag., P_4-M_2; 17783, L dent. P_4-M_3, alveoli for C_1-P_3; 20601 (holotype); 20767, L dent. $M_{2\text{-}3}$, alveoli for I_3-P_4; 20904, R dent. P_4-M_2, M_3 tal. **Divide Q.** (FG046): UM 91330, R M^2; 109858, L M_1 tri.

Suborder ?PHOLIDOTA
Infraorder PALAEANODONTA Matthew, 1918
Family EPOICOTHERIIDAE Simpson, 1927

AMELOTABES Rose, 1978

Amelotabes simpsoni Rose, 1978

Amelotabes simpsoni Rose, 1978, p. 660.

Holotype.— YPM-PU 14855, right dentary with P_{2-3}, M_{1-2}, and alveoli for lateral incisor, C_1, P_1, P_4, and M_3. Reportedly from Croc Tooth Quarry level (Ti-4b) in Foster Gulch of the northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* zone (Ti-4b).

Description.— *Amelotabes simpsoni* was described in detail by Rose (1978).

Discussion.— *Amelotabes simpsoni* is known only from the holotype. Rose (1978) reported that the holotype was from the Croc Tooth Quarry level, although the specimen label only indicates that it is from south of Croc Tooth Quarry and gives coordinates that appear to be for the quarry.

I included a comparison of *Amelotabes simpsoni* and *Myrmecoboides arenarius* n. sp. in the *M. arenarius* discussion.

Family METACHEIROMYIDAE Wortman, 1903

PROPALAEANODON Rose, 1979

Propalaeanodon schaffi Rose, 1979

Propalaeanodon schaffi Rose, 1979, p. 2.

Holotype.— MCZ 20122, left dentary with P_{2-3} and alveoli for P_1, P_4, and M_{1-3}. From Jepsen Valley Quarry in the Silver Coulee area of the northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* zone (Ti-5a).

Description and discussion.— *Propalaeanodon schaffi* was described in detail by Rose (1979). It is still known only from the holotype and two tentatively referred humeri from Princeton Quarry.

Referred specimens.— **Jepsen Valley Q.** (NW¼, Sec. 27, T57N, R100W): MCZ 20122 (holotype). **Princeton Q.**: YPM-PU 13928, left humerus; 13929, distal end of left humerus.

MYLANODON Secord et al., 2002

Mylanodon rosei Secord et al., 2002

Metacheiromyid n. sp., Secord, 2002, p. 105.
Mylanodon rosei Secord et al., 2002, p. 388.

Holotype.— UM 109174, adult left dentary with partial P_4, M_1, and alveoli for P_{2-3}, and M_2; from Y2K Quarry (Ti-5b), on the west side of Polecat Bench, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis simonsi* zone (Ti-5b).

Description and discussion.— *Mylanodon rosei* was recently described by Secord et al. (2002). No new specimens have been discovered.

Referred specimens.— **Y2K Q.**: UM 109174 (holotype); 109530, L dent. of juvenile with unerupted P_4, base of unerupted P_3, an associated partial crown of P_3, and alveoli for dP_{3-4} and M_{1-2}; UM 110015, frag. of right humerus.

Order CREODONTA Cope, 1875
Family OXYAENIDAE Cope, 1877

DIPSALODON Jepsen, 1930b

Dipsalodon churchillorum Rose, 1981a

Dipsalodon churchillorum Rose, 1981a, p. 111.

Holotype.— YPM-PU 17846, left P^4, partial P_3, P_4-M_2, right P_3, C_1, and doubtfully associated right M_2; from Storm Quarry (Ti-5a) in the Silver Coulee area on the west side of Polecat Bench, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b) and *Probathyopsis* (Ti-5a) zones.

Description.— A description of the holotype and other specimens was provided by Rose (1981a).

Discussion.— Two species are currently recognized in *Dipsalodon*, *D. churchillorum*, known from the late Tiffanian and possibly Clarkforkian, and *D. matthewi*, known from the Clarkforkian and here provisionally extended into the latest Tiffanian. In his diagnosis, Rose (1981, p. 111) distinguished *D. churchillorum* from *D. matthewi* by its smaller size and shorter premolars. He also noted that its cheek teeth were narrower. Gunnell and Gingerich (1991, p. 145) added that M_2 is relatively smaller in *D. churchillorum*. The M_1 length and width in the holotype of *D. churchillorum* are about 15% and 20% less, respectively, than in *D. matthewi*.

When Rose (1981a) described *Dipsalodon churchillorum* it was known only from the holotype and two specimens from the Clarkforkian of Colorado (AMNH 56137, 86865). Gunnell and Gingerich (1991) subsequently included UM 67177, 71189, and FMNH P 26095 (erroneously reported as 2609) in the species. I include four additional specimens that are presumably within the variability of the species. YPM-PU 18961 is approximately the same age as the holotype. The M_1 is slightly smaller than in the holotype and proportionally narrower. The M_1 talonid is damaged on the holotype, but on YPM-PU 18961 a hypoconid and entoconid are distinguishable. The hypoconulid is little more than a crest separated from the entoconid by a shallow notch and from the hypoconid by a deeper one. A partial P_4 in YPM-PU 18961 is very similar to that of the holotype, as far as can be compared.

Teeth of *Dipsalodon churchillorum* from the *Phenacolemur* zone are larger than those in the holotype and in YPM-PU 18961. A P_3 and partial M_{1-2} trigonids (UM 108555) from approximately the same level as Fossil Hollow are proportionally similar to those in the holotype of *D. churchillorum* but are about 10% larger. A P_4 (UM 110302) talonid from Fossil Hollow and an M_2 trigonid (UM 98475) from a level between Fossil Hollow and the type locality are also larger than in the holotype of *D. churchillorum*. These teeth compare favorably with those of *D. churchillorum* but suggest a slightly larger mean size for the species in the *Phenacolemur* zone.

Relative size differences in canines of *Dipsalodon churchillorum* suggest sexual dimorphism. The C_1 in YPM-PU 18961 is about 5% longer and 20% wider than in UM 108555, even though the M_1 trigonid is 15% shorter. Greater extremes are seen between a canine of *D. churchillorum* (UM 108555) and one of *D. matthewi* (UM 66167, Cf-2). The former is about 40% shorter and 50% narrower at the enamel base. UM 108555 represents a large individual of *D. churchillorum* and although there is a 15-20% size difference between the species the slightly greater size of other teeth is not proportional to the much greater canine size. Canine dimorphism has also been recognized in hyaenodontid creodonts (Mellett, 1977).

The upper stratigraphic range of *Dipsalodon churchillorum* is not well-constrained in the Bighorn Basin. As noted above, Rose (1981a) referred specimens from the Clarkforkian of Colorado to the species, but no occurrences this young are known in the Bighorn Basin. Two specimens from the *P. gingerichi* zone (Ti-6), UM 67177 and 71189, were referred to *D. churchillorum* by Gunnell and Gingerich (1991). The size of the M_1 protocone in UM 67177 (P_2 or P_3, M^1 protocone, P^3? fragment), however, suggests an individual at least as large as specimens identified as *D. matthewi* (e.g., UM 82392, Gunnell and Gingerich, 1991, Fig. 1). It suggests the presence of *D. matthewi* in Ti-6, but it is too fragmentary for confident identification. UM 71189, an isolated P^3, is about 10% shorter than P^3 in UM 82392, but is about 25% narrower. It may belong to *D. churchillorum*, but in my opinion is not adequate for confident specific identification.

Dental measurements (mm).— UM 71189: P^3, L = 15.10, W = 9.65. UM 108555: C_1, L = 9.15, W = 6.25; P_3, L = 11.05,W = 7.25. UM 110302: P_4, W = 8.45. YPM-PU 18961: C_1, L = 9.55, W = 7.45; M_1, L = 11.95, W = 7.10.

Referred specimens.— **Fossil Hollow** (SC198): UM 110302, R P_4 partial. **Near Princeton Q.** (S½, Sec. 21, T57N, R100W): YPM-PU 18961, L P^{3-4} frags., R C^1, L C_1, R P_4 frag., L M_2. **SC270**: UM 98475, P_1?, R P_4 frag., R M_2 tri. **SC393**: UM 108555, R P^3 frag., M^1 frag., M^2 frag., L P_3, P_4 frag., M_2 frag., R C_1, M_1 frag. **SC419**: UM 110081, R P_2.

TYTTHAENA Gingerich, 1980d

Tytthaena parrisi Gingerich, 1980d

Tytthaena parrisi Gingerich, 1980d, p. 571.

Holotype.— YPM-PU 22352, left dentary with M_1 and posterior part of unerupted P_4 in crypt, from Cedar Point Quarry in Bighorn Basin.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description and Discussion.— A detailed description of the holotype and hypodigm was provided by Gingerich (1980d), and measurements were included in Gunnell and Gingerich (1991). No additional specimens of *Tytthaena parrisi* have been found in the Bighorn Basin since it was described. Only a single occurrence of *T. parrisi* is known outside the Bighorn Basin, from the Chappo Type Locality in the Green River Basin, Wyoming (Gunnell, 1994). The Chappo Type Locality is probably a correlative of the *Plesiadapis rex* zone (Gunnell, 1994; Lofgren et al., 2004). *Tytthaena parrisi* is the oldest known oxyaenid.

Referred specimens.— **Cedar Point Q.**: YPM-PU 21454, L max. P^4-M^2; 22352 (holotype); 22353, R M_2.

DIPSALIDICTIS Matthew, 1915b

Dipsalidictis krausei Gunnell and Gingerich, 1991

Dipsalidictis krausei Gunnell and Gingerich, 1991, p. 150.

Holotype.— UM 69331, skull with left and right I^3, P^2-M^2, alveoli for other teeth, left dentary with P_1-M_2, alveoli for I_x-C_1, right dentary with P_2-M_3, and associated postcranial elements; from Krause Quarry on the west side of Polecat Bench, northern Bighorn Basin, Wyoming; lower part of *P. cookei* zone (Cf-2).

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis gingerichi* (Ti-6) and Clarkforkian zones.

Description.— A detailed description of the holotype was provided by Gunnell and Gingerich (1991).

Discussion.— *Dipsalidictis krausei* is known from exceptionally well-preserved and complete material. When described by Gunnell and Gingerich (1991) it was known only from the Clarkforkian. Specimens included here document a slightly earlier occurrence of the species in the latest Tiffanian *P. gingerichi* zone. The most complete Tiffanian specimen is UM 108313. The P_4, and tooth and dentary fragments agree closely in size and structure with the holotype. An M_2 in UM 95845, from just above the Tiffanian-Clarkforkian boundary, is slightly larger and broader than in the holotype. In this regard it is similar to M_2 in the holotype of *D. aequidens*. The M_1 trigonid is considerably narrower than in *D. aequidens*, however, and overall these teeth are proportionally in better agreement with *D. krausei*. These species are best distinguished by differences in premolars and referral of fragmentary specimens is provisional pending the recovery of more complete material.

Referred specimens.— **SC083**: UM 66199, L M_1 tri. **SC171**: UM 71775, assoc. teeth. **SC245**: UM 71734, C_1, R P^4-M^2 frags. **SC362**: UM 95845, R M_2, L M_1 tri. **SC369**: UM 108313, R M^2 (part), L C_1, R P_4, L dent. frag. M_2 tal. **SC410**: UM 108928, L P^3.

Order CARNIVORA Bowdich, 1821
Family VIVERRAVIDAE Wortman and Matthew, 1899

VIVERRAVUS Marsh, 1872

Viverravus schaffi (Gingerich and Winkler, 1985)

Protictis schaffi Gingerich and Winkler, 1985, p. 110.
Viverravus politus (in part), Polly, 1997, p. 29.

Holotype.— YPM-PU 19365, associated left dentary with P_2-M_1 and right dentary with C_1, P_1, P_3-M_2, from Schaff Quarry in the Silver Coulee area on the west side of Polecat Bench, northern Bighorn Basin, Wyoming; *Probathyopsis* zone.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b), *Probathyopsis* (Ti-5a), and *Plesiadapis simonsi* (Ti-5b) zones.

Description.— Detailed descriptions of the holotype and other specimens were provided by Gingerich and Winkler (1985).

Discussion.— A relatively large sample of *Viverravus schaffi* is known from Schaff and Princeton quarries, including a partial skull (Gingerich and Winkler, 1985). Polly (1997) synonymized *Protictis schaffi* with *Viverravus politus* because he concluded that the two forms were part of a single evolutionary lineage. I follow Polly's inclusion of the species in *Viverravus*, but reject his synonymy with *V. politus*. *Viverravus schaffi* appears to be morphologically distinct from *V. politus* and merits specific status, regardless of whether or not it is part of the same lineage. Gingerich and Winkler (1985) did not include a comparison of *Viverravus* (*Protictis*) *schaffi* with *V. politus*.

Viverravus schaffi is most similar to the younger *V. politus*, the holotype of which is probably early Wasatchian in age (Rose, 1981a, p. 101). The most obvious difference between *Viverravus schaffi* and *V. politus* is a relatively longer M_1 trigonid with a more open basin. M_1 trigonid-length/total-length ratios distinguish the species (*V. schaffi*: mean = 0.58, range = 0.56-0.61, n = 4; *V. politus*: mean = 0.64, range = 0.62-0.65, n = 6) based on late Clarkforkian and early Wasatchian specimens in the UM collections. Trigonid length here is measured as the distance from near the base of the postvallid at the point where the slope changes, to the anterior-most point on the prevallid, measured perpendicular to the upper part of the postvallid. M_1 trigonid length averages 3.46 mm for *V. schaffi* (range = 3.30-3.70, n = 8) and 4.19 mm for *V. politus* (range = 3.95-4.65, n = 6; 4.0 in the holotype). M_1 length is also less in most specimens of *V. schaffi* (mean = 5.88, range = 5.65-6.40, n = 5) than in *V. politus* (mean = 6.58, range = 6.10-7.25, n = 6). *Viverravus schaffi* differs further in having a small to very reduced cusp directly behind the protoconid on P_3. This cusp is prominent on all specimens I have seen of *V. politus*. The M_1 talonid of *V. schaffi* typically has a squarer appearance in occlusal view than in *V. politus* and often has a reduced hypoconulid. The M_1 hypoconulid in *V. politus* is often prominent and the talonid has a more rounded or tapering appearance. Also, the M_2 paraconid is usually more internal in *V. schaffi*. Late Clarkforkian specimens of *V. politus* are generally smaller than those from the early Wasatchian (Polly, 1997, Fig. 7).

The first confident occurrence of *Viverravus schaffi* is at Fossil Hollow, near the base of the *Probathyopsis* zone. Fragmentary specimens from the earlier Divide Quarry (Ti-4a) are similar to *V. schaffi*, but referred to *V.* cf. *V. schaffi* below. Occurrences of *V. schaffi* above the *Probathyopsis* zone are uncertain due to the fragmentary condition of specimens. A fragmentary M_1 (UM 110311) from the latest Tiffanian is within the size range of *V. schaffi*, but may have had a more open trigonid. Rose (1981a) referred a P_4 and partial P^4 (UM 68748) from near the base of the Clarkforkian (SC-179) to *V. politus*, presumably based on size. I provisionally follow Rose.

Rose (1981a, pp. 100-101) identified a left dentary (UM 69336) from Krause Quarry (SC-195; Cf-2) as *Viverravus acutus*, noting that it was indistinguishable in comparable parts from the holotype. Subsequently, a right dentary (UM 102460) was collected at the quarry that may belong to the same individual. Polly (1997), however, referred both specimens to *V. politus* without discussion. The length of M_1 in UM 102460 is only 4.9 mm, which is close to the size of M_1 in the holotype of *V. acutus* but is shorter than any M_1s of *V. schaffi* or *V. politus* that I have measured. These dentaries do not appear to belong in *V. schaffi* or *V. politus*. I follow Rose in referring UM 69336 (and UM 102460) to *V. acutus*.

Referred specimens.— **Fossil Hollow** (SC198): UM 108902, R dent. M_2 (tal.); YPM-PU 19137, L P^4, R P^4. **SC165**: UM 68271, R M_1; 69538, L max. M^{1-2}; 81709, L P_4. **SC187**: UM 68855, L dent. M_1, alveoli C_1-P_4; 76857, L dent. M_1 frag., M_2; 80358, L dent. P_4-M_1. **SC270**: UM 73577, L M_1; 98476, R dent. P_4-M_1; 110155, R P_4. **SC271**: UM 110927, L dent. frag. M_1 tal., M_2. **Y2K Q.** (SC389): UM 109185, L M_1 partial; 109327, L M_2; 109484, R M_1. See Gingerich and Winkler (1985) for additional YPM specimens.

Viverravus cf. *V. schaffi*

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Description and discussion.— Several fragmentary specimens from Divide Quarry resemble *Viverravus schaffi* and *Protictis paralus*. *Protictis paralus* was named by Holtzman (1978) for specimens from the Judson Locality in North Dakota and additional specimens from Cedar Point Quarry were referred to the species by Gingerich and Winkler (1985). Gingerich and Winkler distinguished *P. paralus* from *V. schaffi* only by its smaller size. The partial P^4 from Divide Quarry is as large as specimens of *P. schaffi* (e.g., UM 16495), but other teeth are intermediate in size between *P. schaffi* and *P. paralus*. The only tooth complete enough to measure length and width is UM 110949, a P_4 (L = 4.47, W = 1.88 mm). Both dimensions are below the known range of *P. schaffi* (n = 5) and length is above the range of *P. paralus* (n = 2, Holtzman, 1978; n = 5, Gingerich and Winkler, 1985). The Divide Quarry specimens are too fragmentary for more confident identification.

Referred specimens.— **Divide Q.** (FG046): UM 85428, L M_1 tri.; 110949, R P_4; 110952, L M_1 partial; 110953, L P^4 partial.

Viverravus laytoni (Gingerich and Winkler, 1985)

Protictis laytoni Gingerich and Winkler, 1985, p. 107.
Viverravus laytoni, Polly, 1997, p. 18.

Holotype.— YPM-PU 16523, a right dentary with M_1, and alveoli for P_{1-4} and M_2; from Princeton Quarry (Ti-5a), northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a), Rodentia (Cf-1), and *Plesiadapis cookei* (Cf-2) zones.

Description.— A detailed description of the holotype was provided by Gingerich and Winkler (1985).

Discussion.— *Viverravus laytoni* was initially placed in *Protictis* by Gingerich and Winkler (1985), but subsequently transferred to *Viverravus* by Polly (1997), which I follow here. Polly synonymized *V. bowni* with *V. laytoni* and transferred the holotype of *V. bowni* (UM 76928) and a few other middle and late Clarkforkian specimens to *V. laytoni*. In an unpublished thesis, Bloch (2001) subsequently transferred the holotype of *V. bowni* and two other specimens (UM 76929, 76930) to *V. acutus*. The remaining Clarkforkian specimens are fragmentary, but a complete M_1 (UM 73654) compares favorably in size and morphology to those of *V. laytoni* from the Tiffanian. Thus, I follow Polly (1997) in identifying several Clarkforkian specimens as *V. laytoni*, including some that have not been previously published.

When *Viverravus laytoni* was first described it was known only from the holotype and an isolated M_1 from Princeton Quarry. The M_1 trigonid included here is the only additional specimen known from the Tiffanian of the Bighorn Basin. Some of the teeth included in *Raphictis*? below could belong to *V. laytoni* or a closely related form, but M_1s are absent in the sample.

Referred specimens.— **Princeton Q.**: YPM-PU 16523 (holotype); 17844, L M_1. **SC117**: UM 73654, L dent. M_1. **SC188**: UM 71578, L M_2; 71579, L C_1, P_3; 109679, R M_1 tri.; 109680, R P^4, missing protocone; 109691, L P^4, missing protocone; 109726, R P^4, missing protocone; 109775, L M_1 tri.; 109776, R P_3. **SC201**: UM 69270, R P_4, M_2 tal. **SC273**: UM 110154, R M_1 tri.

DIDYMICTIS Cope, 1875

Didymictis dellensis Dorr, 1952

Didymictis dellensis Dorr, 1952, p. 85.
Didymictis? sp. nov., Rose, 1981a, p. 156.
Protictis dellensis (in part), Gingerich and Winkler 1985, p. 117.
Didymictis proteus (in part), Polly, 1997, p. 34.

Holotype.— UM 27232, a right dentary with C_1-P_1, P_3-M_2, from Dell Creek Quarry in the Hoback Basin in southwestern Wyoming. The quarry is probably correlative to the *P. churchilli* or *Phenacolemur* zone, contrary to previous interpretations that placed it in Ti-5 (see *Paleotomus* cf. *P. radagasti* discussion).

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b) through Rodentia (Cf-1) zones.

Description.— The holotype was described by Dorr (1952) and Gingerich and Winkler (1985). Additional specimens were described by Gingerich and Winkler (1985).

Discussion.— Specimens of *Didymictis dellensis* from Princeton Quarry were initially referred to *Didymictis*? sp. nov. by Rose (1981a) but were later transferred to *Protictis dellensis* by Gingerich and Winkler (1985). Subsequently, Polly (1997) synonymized *P. dellensis* with *D. proteus*, hypothesizing that the two forms were part of the same evolutionary lineage. There are, however, significant morphological differences between the Princeton Quarry species and most of the Clarkforkian specimens included in *D. proteus* by Polly, and I do not follow his synonymy. Specimens from the middle Clarkforkian referred to *Didymictis proteus* by Polly (1997) are considerably larger than *D. dellensis*, and there appears to be little overlap in size (compare Gingerich and Winkler, 1985, Table 8; and Polly, 1997, Fig. 8). Other differences are discussed in the *Didymictis* cf. *D. dellensis* sp. 2 and cf. *Didymictis* sections below, in which I include most of the early Clarkforkian specimens of *Didymictis*.

UM 110139, a partial maxilla from the early Clarkforkian, is the youngest specimen complete enough to be confidently included in *Didymictis dellensis*. Like other specimens of *D. dellensis*, it has a small M^2 relative to M^1 (e.g., Gingerich and Winkler, 1985, Fig. 13). An M_1 (UM 108273) from just below the Tiffanian-Clarkforkian boundary, also included here in *D. dellensis*, is slightly smaller and slightly lower crowned than M_1 in the holotype, but not as low-crowned as most specimens referred to *D.* cf. *D. dellensis* sp. 2 or cf. *Didymictis*.

Didymictis dellensis appears to range at least as low as Fossil Hollow in the *Phenacolemur* zone, although identifications at this level are based on very fragmentary material. Gingerich and Winkler (1985) referred an M_1 to *D. dellensis* from the earlier *P. churchilli* zone, but it is included here in *Didymictis* cf. *D. dellensis* sp. 1.

Referred specimens.— **Bluff Top Q.** (SC379): UM 108273, L M_1. **FG041**: UM 77284, R M_2. **Fossil Hollow** (SC198): UM 69241, L dent. $M_{1\text{-}2}$ frags.; 80249, R M_2; 110196, R M_1 tri.; YPM-PU 24877, R M^2. **Princeton Q.**: YPM-PU 13937, R dent. P_1-M_2; 13961, R max. P^4; 14317, L M_1, probably same individual as 13937; 14319, R max. M^1; 14320, L P^4. **SC267** (vicinity): YPM-PU 18592, L dent. frag., P_4-M_1. **SC179**: UM 110139, L max. $M^{1\text{-}2}$. **SC187**: UM 96369, L M_1 tri., R M_1 tal. **SC386**: UM 108512, L M_1 tal.; 108547, R P_2. **SC389**: UM 108538, L P_4. **SC394**: UM 108551, R C_1, M_2. **SC407**: UM 108918, L M_2 tri.

Didymictis cf. *D. dellensis* sp. 1

Protictis dellensis (in part), Gingerich and Winkler 1985, p. 117.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Description and discussion.— Gingerich and Winkler (1985) referred a single M_1 (UM 63281) from Divide Quarry to *D. dellensis*. However, the trigonid on this specimen is noticeably higher (trigonid height = 9.8 mm) than those of *D. dellensis* and is above the range they reported from Princeton Quarry and vicinity, and Dell Creek Quarry (8.3-8.9 mm, n = 4). Other characters in the Divide Quarry form that may not be typical of *D. dellensis* are a large stylocone and high paracrista in UM 110951 (partial M^1) and the degree of transverse elongation of UM 85304 (M^1). A P_4 (or possibly P_3) from SC-261 may also belong to this species. It is shorter than P_4 in the holotype of *D. dellensis* and has relatively smaller and shorter posterior cusps. More complete specimens are needed for a confident identification.

Referred specimens.— **Divide Q.** (FG046): UM 63281, R M_1; 77269, L M^1; 85304, R M^2; 85439, L M^2; 110950, L P_3; 110951, L M^1 partial. **SC261**: UM 110291, R P_4.

Didymictis cf. *D. dellensis* sp. 2

Didymictis? undescribed species, Rose, 1981a, p. 99.
Didymictis proteus (in part), Polly, 1997, p. 34.

Biostratigraphic occurrences in Bighorn Basin.— Rodentia zone (Cf-1).

Description and discussion.— Rose (1981a) referred several specimens from the early and early middle Clarkforkian to *Didymictis*? undescribed species. UM 73714 is the most complete. He pointed out the close similarity between this form and *D. dellensis* at Princeton Quarry (then undescribed), but noted that the M_2 was much larger and broader, and the upper molars were slightly longer in the former. He thought that the larger M_2 may justify specific separation. Polly (1997) subsequently synonymized *P. dellensis* with *D. proteus* and included these

TABLE 20 — Dental statistics for *Litolestes ignotus* from Princeton Quarry. Measuring techniques Type 2 for upper teeth. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
P^3	L	1	—	—	1.66	—	—	—
	W	1	—	—	1.42	—	—	—
P^4	L	1	—	—	1.86	—	—	—
	W	1	—	—	1.96	—	—	—
M^1	L	1	—	—	1.67	—	—	—
	W	1	—	—	2.30	—	—	—
M^2	L	1	—	—	1.47	—	—	—
	W	—	—	—	—	—	—	—
P_2	L	1	—	—	1.23	—	—	—
	W	1	—	—	0.78	—	—	—
P_3	L	3	1.11	1.30	1.22	0.06	0.10	8.07
	W	3	0.84	0.96	0.90	0.03	0.06	6.67
P_4	L	9	1.58	1.95	1.76	0.04	0.11	6.49
	W	9	1.15	1.43	1.29	0.03	0.08	6.36
M_1	L	15	1.54	1.88	1.73	0.03	0.10	5.68
	W	13	1.25	1.58	1.37	0.02	0.09	6.47
M_2	L	13	1.28	1.61	1.45	0.03	0.11	7.31
	W	11	1.17	1.45	1.31	0.03	0.09	6.58
M_3	L	9	1.32	1.47	1.38	0.02	0.05	3.90
	W	8	0.90	1.12	0.98	0.02	0.07	7.15

TABLE 21 — Dental statistics for *Litolestes ignotus* from Schaff Quarry. Measuring techniques Type 2 for upper teeth. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
P^2	L	1	—	—	1.05	—	—	—
	W	1	—	—	0.70	—	—	—
P^3	L	2	1.55	1.66	1.61	—	—	—
	W	2	1.40	1.42	1.41	—	—	—
P^4	L	3	1.75	1.87	1.83	0.04	0.07	3.65
	W	3	1.82	2.05	1.94	0.07	0.12	5.96
M^1	L	2	1.67	1.70	1.69	—	—	—
	W	2	2.30	2.30	2.30	—	—	—
M^2	L	1	—	—	1.47	—	—	—
	W	—	—	—	—	—	—	—
P_2	L	3	1.07	1.25	1.18	0.06	0.10	8.34
	W	3	0.73	0.82	0.79	0.03	0.05	6.27
P_3	L	7	1.21	1.44	1.30	0.03	0.07	5.47
	W	7	0.82	0.93	0.89	0.01	0.04	4.17
P_4	L	15	1.67	1.90	1.76	0.02	0.06	3.64
	W	15	1.16	1.41	1.29	0.02	0.07	5.63
M_1	L	13	1.71	1.88	1.79	0.01	0.05	2.91
	W	13	1.31	1.57	1.43	0.02	0.07	5.08
M_2	L	11	1.40	1.63	1.49	0.02	0.08	5.27
	W	10	1.23	1.44	1.35	0.02	0.06	4.33
M_3	L	8	1.30	1.47	1.37	0.02	0.05	4.00
	W	8	0.93	1.18	1.04	0.02	0.07	6.79

specimens. I do not follow Polly's synonymy. The M_2 is consistently larger in early and early middle Clarkforkian specimens (i.e. UM 68432, 69907, 73381,101134), relative to M_1. Also of importance, M_1 trigonids are consistently lower crowned, relative to overall size, than in the holotype of *D. dellensis*. The protoconid is missing on some, but the distance in height between the carnassial notch in the protolophid and the point the cristid obliqua intersects the postvallid is noticeably less.

These specimens may represent an undescribed species, as noted by Rose (1981a). There appears to be a second undescribed viverravid in the early Clarkforkian, exemplified by UM 100363, that is still more distant from *D. dellensis* and is referred to cf. *Didymictis* below.

Referred specimens.— **SC083**: UM 66201, L M_1. **SC136**: UM 69907, L dent. $P_{3\text{-}4}$, R dent. P_3, M_1 tal., R M^1, L M_2 tal. **SC156**: UM 71589, L M_1, L M_1 tal., R M_1 tri. **SC173**: UM 68432, L $M^{1\text{-}2}$, L dent. C_1-M_2, R P^4, assoc. **SC217**: UM 101134, L dent. $P_{3\text{-}4}$, M_1 frag., M_2, L P_4, L M_1 frag., R M_1 tri., L P_4, L P_4 frag., at least 2 individuals. **SC248**: UM 71792, L M_1. **SC250**: UM 71802, L M_1. **SC260**: UM 73381, L M^1, P_4 frag.; 73714, R max. P^3-M^2. **SC375**: UM 108229, R M_2 tri.

Cf. *Didymictis*

Biostratigraphic occurrences in Bighorn Basin.— Rodentia zone (Cf-1).

Description and discussion.— Two specimens from adjacent localities that are probably early Clarkforkian in age, but are not precisely constrained temporally, may represent an undescribed species of *Didymictis* or possibly another genus. The most complete specimen is UM 100363, a right dentary preserving a partial P_4 talonid and $M_{1\text{-}2}$. It differs from the holotype of *D. dellensis* in having a narrower M_1 with a much lower trigonid and a more buccally positioned cristid obliqua-postvallid contact, and a relatively larger M_2 that is nearly as long as M_1. The M_2 is unusual in that the para- and metaconids are closer together and lower than in any specimens of *Didymictis* I have seen. The protocone of the M_1 trigonid is missing, but based on the para- and metacones, the trigonid is about 40% lower than in the holotype of *D. dellensis*. The M_1 is about 30% smaller in linear dimensions and the M_2 is about 5% larger.

The back part of the dentary of UM 100363 was discovered in a miscellaneous vial (UM 110979) that also contained other teeth, including the trigonid of a second right M_1 nearly identical to the other. The pieces of the dentary fit perfectly along an unweathered break and there is no doubt they belong together. A left P_2? (or P_3) from the same vial could also belong to one of these individuals. The premolar is most similar to P_2s of *Didymictis* but the protocone is positioned more posteriorly than is typical, and the anterior crest of the protocone is deflected lingually and terminates on the lingual side of the crown, rather than near the anterior base. It differs from the P_3 of contemporary *Didymictis* in being narrower, and in having no anterior accessory cuspule and only an incipient posterior one.

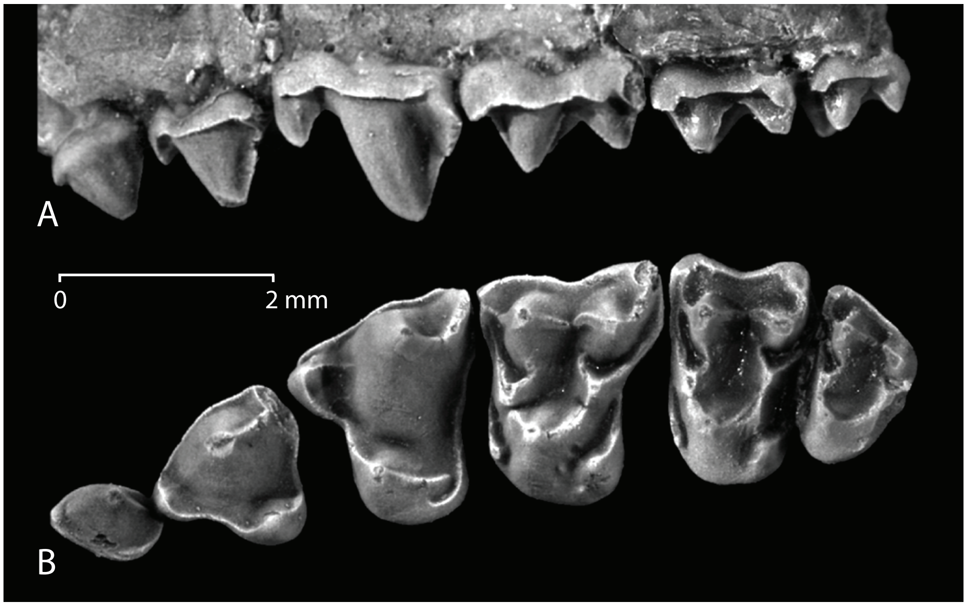


FIGURE 24 — Composite upper dentition of *Litolestes ignotus*. A–B, buccal and occlusal views of left maxilla with P^2-M^1 (YPM-PU 21193, Schaff Quarry) and left maxilla with M^{2-3} (UM 68261, SC-165). M^{2-3} are proportionally larger in most individuals, relative to M^1, than is depicted here.

These specimens are closest to teeth of *Didymictis* cf. *D. dellensis* sp. 2, and although they could be extreme variants of that form, they probably represent a new species.

Dental measurements (mm).— UM 100363: M_1, L = 7.40, tri. L = 4.35, W = 4.25; M_2, L = 6.5*, W = 4.15. UM 110979: P_3, L = 6.15, W = 2.25.

Referred specimens.— **SC217**: UM 100363, R dent. partial P_4 tal, M_{1-2}. **SC260**: UM 110979, R P_2?, M_1 tri., assoc.?

Raphictis?

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a) and *Phenacolemur* (Ti-4b) zones.

Description and discussion.— Three isolated teeth indicate the presence of at least one diminutive carnivore at Divide and Croc Tooth quarries, roughly the size of *Raphictis gausion* from Cedar Point Quarry. Gingerich and Winkler (1985) distinguished *R. gausion* from other viverravids by its narrower cheek teeth, higher and more needle-like trigonid cusps on M_1, and the angle of the M_1 talonid relative to the long axis of the dentary. No upper teeth have been described for the species. UM 110303 appears to be a P_4, but could be a P_3. It is smaller than the P_4 of *R. gausion*, is slightly less narrow, and it has a more lingual anterior accessory cuspule. It is about the size of the P_3 of *R. gausion*, but differs in being proportionally slightly wider and in having a strong anterior accessory cuspule and an additional accessory cuspule on the posterior slope of the protoconid. The P_3 of *R. gausion* (YPM-PU 19987) lacks an anterior accessory cuspule. One is also lacking or very small in the P_3 of some other diminutive species, such as *Viverravus laytoni* (UM 71579, but see below) and *V. acutus*. The protoconid cusp is especially high and pointed, which is suggestive of *Raphictis*.

An M^1 (UM 92270) is roughly the size expected for *Raphictis gausion* and is relatively narrow, a condition that might be expected in the M^1 of *Raphictis*. An M^2 (UM 85919) is large, relative to the size of the M^1 and could belong to a different taxon. It is probably too small to be included in *V.* cf. *V. schaffi* above. Some of these teeth may also be within the size range of the slightly younger *V. laytoni*, but no upper teeth or P_4s are known for the species.

Dental measurements (mm).— UM 85919: M^2, L = 1.85, W = 3.95. UM 92270: M^1, L = 2.90, W = 4.0. UM 110303: P_4, L = 2.95, W = 1.20. Landmarks follow Gingerich and Winkler (1985).

Referred specimens.— **Croc Tooth Q.** (FG028): UM 110303, L P_4. **Divide Q.** (FG046): UM 85919, L M^2; 92270, L M^1.

Grandorder LIPOTYPHLA Haeckel, 1866
Order ERINACEOMORPHA Gregory, 1910
Family ERINACEIDAE Fischer de Waldheim, 1817

LITOLESTES Jepsen, 1930b

Litolestes ignotus Jepsen, 1930b
Figures 24–25, Tables 20–21

Litolestes ignotus Jepsen, 1930b, p. 513.

Holotype.— YPM-PU 13352, a right dentary with P_4-M_3 and an associated incisor. Paratype: YPM-PU 13348, a right dentary with P_2, P_4-M_3. Both types are from Princeton Quarry, in the northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences.— *Probathyopsis* (Ti-5a) and *Plesiadapis simonsi* (Ti-5b) zones.

Description.— Description of lower dentitions were provided by Jepsen (1930b), Schwartz and Krishtalka (1976), Krishtalka (1976a), and Novacek et al. (1985). Krishtalka (1976a) described P^4-M^3.

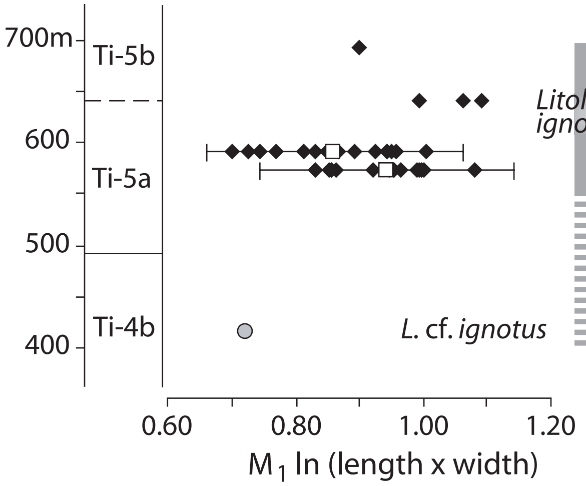


FIGURE 25 — Chart illustrating variability of M$_1$ area in *Litolestes ignotus* and *L.* cf. *L. ignotus* in Ti-4b and Ti-5, respectively. From lowest to highest, data are from Sand Draw, Schaff Quarry, Princeton Quarry, SC-165, and Y2K Quarry. Solid diamonds indicate Polecat Bench sequence; open squares show mean values. Solid gray bar corresponds to level for which *L. ignotus* is known with confidence; dashed bar indicates lack of data. Sand Draw specimen (gray circle) is poorly constrained stratigraphically, but is probably from Ti-4b. Error bars represent the range of expected variability in M$_1$ area of 0.4 natural log units, or about ± 2 SD (Gingerich, 1981).

Discussion.— *Litolestes ignotus* is a common species in late Tiffanian quarry sites, but is rarely found in surface collections, presumably because of its small size. Its lower dentition is well known and has been described in detail, including I$_{2-3}$, which are multi-lobed. A partial maxilla preserving P^2-M^1 was figured by Gingerich (1983a) and the morphology of P^4-M^3 was described by Krishtalka (1976a). Figure 24 shows a composite maxilla with P^2-M^3 based on two specimens. Tables 20 and 21 show the size variability for *L. ignotus* at Princeton Quarry, its type locality, and at Schaff Quarry, which is approximately the same age. M$_1$ and M$_2$ means are slightly higher at Schaff Quarry. Taken together, however, the combined size range of M$_1$ area from both quarries is ~0.4 natural log units (Fig. 25), which is approximately four standard deviations and is within the expected range of a single species (Gingerich, 1981). Although there may be minor taphonomic differences between the quarries, both exhibit the same morphologic variability and there appears to be only one species. The high coefficients of variation in some premolar dimensions may be the result of small sample sizes.

UM 109362 and 109460 from Y2K Quarry almost certainly are from the same individual. Both show the same degree of wear, the same quality of preservation, and are mirror images of one another. The upper parts of the P$_2$s are worn flat in a manner reminiscent of palaeanodonts, and suggest a coarse component in the diet of these "insectivores." These specimens differ from most specimens of *Litolestes ignotus* from Princeton and Schaff quarries in having less well-defined cusps and crests, especially on P$_4$, which lacks a distinct paraconid, but still appear to be within the variability of *L. ignotus*. The tooth surfaces have an etched appearance and the degree of tooth wear indicates a mature individual. The teeth have not lost their enamel, but wear or etching through predation may have caused some reduction in the definition of crests and cusps.

Three specimens referred to *Litolestes* cf. *L. ignotus* below are from older levels in the Bighorn Basin and are on the low end of the size range for *L. ignotus* from Princeton and Schaff quarries. YPM-PU 17823 is the only specimen that preserves an M$_1$ complete enough for precise measurement and is plotted in Figure 25 along with specimens of *Litolestes ignotus* from Princeton and Schaff quarries. It is approximately the same size as UM 80247 which is also from the *Phenacolemur* zone. The third specimen (UM 85410) is older than the first two and is from Divide Quarry. It has a dentary that is notably narrower and shallower than any from Princeton or Schaff quarries. Together these specimens suggest a progressive size increase in *Litolestes* from Divide Quarry, in the *Plesiadapis churchilli* zone, to Princeton and Schaff quarries in the *Probathyopsis* zone. Specimens from Habetler's Concentration at SC-165, which is in the succeeding *Plesiadapis simonsi* zone, suggest that the increasing trend continues. Three M$_1$s from Habetler's Concentration plot in the upper end of the range for *L. ignotus* (Fig. 25). There may, however, be a bias toward larger specimens at this locality and larger samples are needed to test this observation.

Referred specimens.— **Princeton Q.**: YPM-PU 13348 (paratype); 13352 (holotype); 13354, L dent. P$_4$-M$_2$; 13837, R dent. M$_{1-3}$; 13974, R dent. P$_4$-M$_3$; 13981, R dent. P$_4$-M$_2$; 14037, L dent. P$_4$-M$_3$; 14039, R dent. M$_{1-3}$; 14064, R dent. P$_3$-M$_2$; 14087, R dent. M$_{1-2}$ (juvenile); 14114, R max. P^4-M^2; 14127, R dent. P$_3$-M$_2$; 14164, L dent. P$_4$-M$_1$; 14168, L dent. P$_2$-M$_2$; 14326, L dent. M$_1$; 14384, L dent. M$_1$; 14385, R dent. M$_{1-3}$; 14386, L dent. M$_3$; 14513, R dent. P$_4$, M$_{2-3}$; 17679, R dent. P$_4$-M$_3$; 21188, R dent. (badly worn). **SC165** (Habetler's C.): UM 68261, L max. P^3-M^3 (M^1 damaged); 68265, R dent. P$_4$-M$_1$, R dent. P$_4$; 69539, R dent. P$_3$, M$_{1-2}$; 71505, R dent. P$_4$-M$_2$; 81704, R M$_1$; 81705, L P$_4$. **SC187**: UM 73519, L dent. P$_{2-3}$, M$_1$; 101910, R max. P^4-M^3. **Schaff Q.**: YPM-PU 17749, L dent. M$_{2-3}$; 19361, L dent. P$_2$-M$_3$; 19362, L dent. P$_3$-M$_3$; 19364, L dent. P$_2$, P$_4$-M$_3$; 19374, L dent. P$_2$-M$_3$; 19376, L dent. P$_4$-M$_2$; 19377, R max. P^3-M^2; 19378, R dent. P$_2$-M$_3$; 19380, R dent. P$_4$-M$_1$; 19381, R dent. P$_3$-M$_3$; 19434, L dent. P$_4$-M$_1$; 19470, L dent. P$_{3-4}$, M$_3$; 19477, L dent. P$_4$-M$_1$; 19491, L dent. M$_{2-3}$; 19501, L dent. P$_4$-M$_2$; 19506, R dent. P$_3$-M$_2$; 21181, L dent. P$_4$-M$_2$; 21182, R max. P^4; 21193, L max. P^2-M^1; UM 71045, R dent. P$_4$-M$_2$. **Y2K Q.** (SC389): UM 109362, L dent. P$_{2-4}$; 109410, L P^2, P^3 assoc.; 109460, R dent. P$_1$-M$_1$; 109518, R dent. P$_3$, P$_4$-M$_2$ roots.

Litolestes cf. *L. ignotus*

Figure 25

Biostratigraphic occurrences.— *Plesiadapis churchilli* (Ti-4a) and *Phenacolemur* (Ti-4b) zones.

Description and discussion.— Three specimens from Ti-4a and Ti-4b are on the lower end of the size range of *Litolestes ignotus*, as known from the type locality at Princeton Quarry. The most complete specimen is a dentary preserving P$_4$-M$_3$ (YPM-PU 17823). The specimen label indicates it is from the Sand

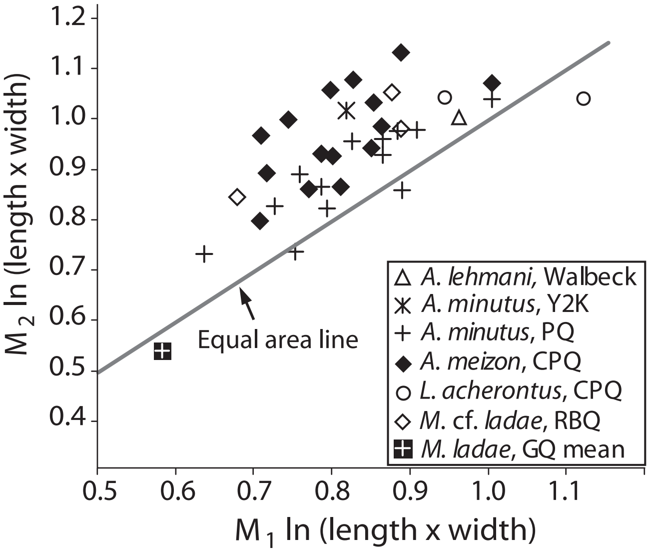


FIGURE 26 — Scatter plot of M_1 and M_2 area in *Adunator lehmani* (holotype cast), *A. minutus*, *A. meizon*, *Mckennatherium ladae*, *M.* cf. *M. ladae*, and *Leptacodon acherontus* n. sp. Data for Gidley Quarry from Simpson (1937b). Bighorn-Crazy Mountains Basin quarries: *PQ*, Princeton; *Y2K*, Y2K; *CPQ*, Cedar Point; *RBQ*, Rock Bench; *GQ*, Gidley. Walbeck refers to fissure filling in Germany.

Draw Anthill locality, a Princeton locality in the Foster Gulch area that has not been relocated. The locality appears to be in the *Phenacolemur* zone, although specimens from this locality could be from more than one level. The dentary is probably too large to have been collected by ants, and likely came from the surrounding area. A small bit of matrix still on the bone, and the pristine condition of the teeth, suggest that it was quarried from a tan-yellow sandstone. The P_4 is more anteroposteriorly elongate than are most of *L. ignotus*, but it is very similar to those of *L. ignotus* in other regards.

UM 80247 is a dentary fragment preserving $M_{1\text{-}2}$ from Fossil Hollow, also in the *Phenacolemur* zone. The molars are missing lingual cusps, but are close to the size of those in YPM-PU 17823. They are indistinguishable from those of *Litolestes ignotus* except for having a thinner, sharper, more anteroposteriorly compressed paraconid on M_2.

UM 85410 is a dentary fragment from Divide Quarry that preserves a single molar that is probably an M_2, but could possibly be an M_1. It is most similar to those of *Litolestes ignotus*, but like UM 80247, differs in having a thinner, sharper, more anteroposteriorly compressed paraconid than in either M_1 or M_2 of *L. ignotus*. If the molar is an M_1, it is below the size range of *L. ignotus*, and if it is an M_2, it is near the low end of the range. The dentary is about 25-30% shallower (dorsal-ventrally) and narrower than those of *L. ignotus*, and narrower than either of the other dentaries included here. It is possible that this individual was a juvenile that had not yet achieved full size.

The referred specimens appear to represent individuals in an evolving lineage of *Litolestes* that increases in size from the *Plesiadapis churchilli* zone to the *Phenacolemur* zone, as discussed in the *L. ignotus* section above.

Dental measurements (mm).— UM 85410: M_1 or M_2, L = 1.40, W = 1.22. YPM-PU 17823: P_4, L = 1.70, W = 1.13; M_1, L = 1.55, W = 1.33; M_2, L = 1.33, W = 1.32.

TABLE 22 — Dental measurements for *Adunator amplus* n. sp. from Rock Bench Quarry.

		YPM-PU 14738 (type)	YPM-PU 14746	YPM-PU 19483	YPM-PU 19641
P_4	L	2.32	2.50	—	2.45
	W	1.47	1.45	—	1.77
M_1	L	2.22	2.40	2.20	2.40
	W	1.79	1.70	1.90	1.83
M_2	L	2.33	—	2.38	2.53
	W	2.21	—	2.00	2.12

Referred specimens.— **Divide Q.** (FG046): UM 85410, R dent. frag. M_1 or M_2. **Fossil Hollow** (SC198): UM 80247, dent. P_4 frag., $M_{1\text{-}2}$. **Sand Draw Anthill**: YPM-PU 17823, L dent. P_4-M_3.

Order ERINACEOMORPHA *incertae sedis*

ADUNATOR Russell,1964

Adunator Russell, 1964, p. 47.
Diacocherus Gingerich, 1983a, p. 238.

Discussion.— Krishtalka (1976a) noted that the lower dentition of "*Diacodon*" *minutus* (Jepsen, 1930b) was "virtually identical" to that of *Adunator lehmani* from the Walbeck fauna of Germany and suggested they were congeneric. He also noted, however, that there were significant differences in the upper dentitions assigned to each taxon, suggesting that some material may not have been correctly identified. Recognizing that "*Diacodon*" *minutus* was not a valid taxon, Gingerich (1983a) placed "*D.*" *minutus* in a new genus, *Diacocherus*, but offered no comparison to *Adunator*. Subsequently, Novacek et al. (1985) considered *Diacocherus* a synonym of *Adunator*. Butler (1988, p. 127) also followed the synonymy, noting the leptictid-like nature of the upper molars referred to *A. lehmani*, and concluded that they were probably mistakenly included in the species. Other authors have continued to use *Diacocherus* (e.g., Fox, 1990; Kihm et al., 1993; Bloch, 2001), however, with little or no discussion. Based on comparison of casts of *A. lehmani*, I agree with Krishtalka and Novacek et al. (1985) that differences in the lower dentition between *Adunator* and *Diacocherus* do not warrant generic separation. Differences in the upper dentition cannot be adequately evaluated until upper teeth are found in association with lowers.

Novacek et al. (1985) also considered *Mckennatherium* a synonym of *Adunator*, but Krishtalka (1976a) recognized it as being distinct. One of the characteristics Krishtalka (1976a) and Gingerich (1983a) used to distinguished *Adunator minutus* from *Mckennatherium* was that M_2 was larger than M_1 in the former. Figure 26 shows that in the type sample of *M. ladae* from Gidley Quarry (mean data from Simpson, 1937b, n ranges from 6 to 9), M_1 area is larger than M_2 area, and the mean falls below the equality line. This is due more to molar width than to length. Bown and Schankler (1982) were unable to see a difference in

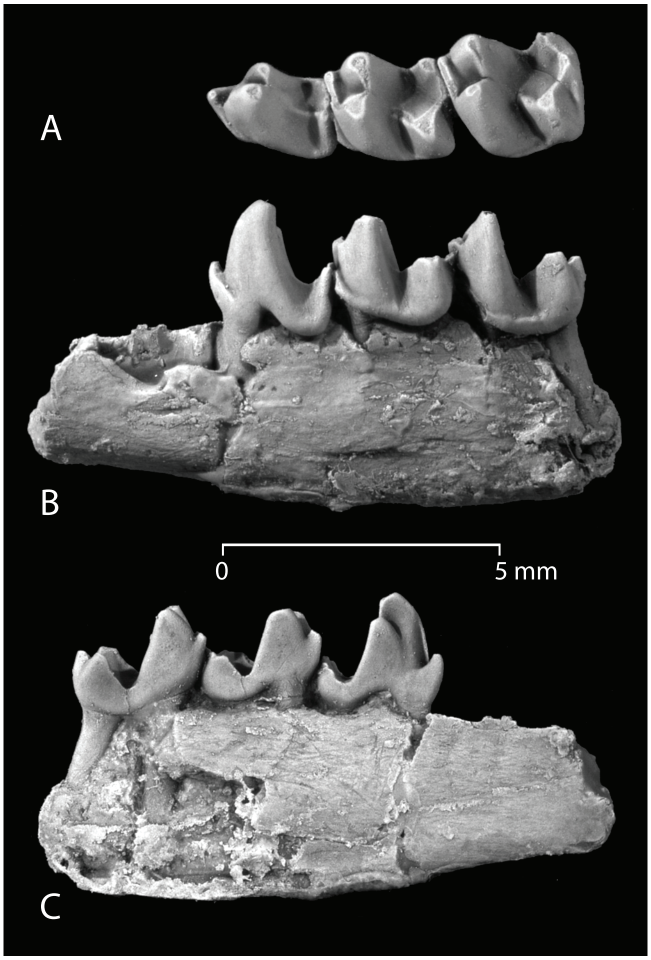


FIGURE 27 — Holotype of *Adunator amplus* n. sp. from Rock Bench Quarry. A–C, left dentary with P_4-M_2 (YPM-PU 14738) in occlusal (A), buccal (B), and lingual (C) views.

size, but perhaps did not take width into account. Specimens referred to *M.* cf. *M. ladae* from Rock Bench Quarry, however, plot above equality in the same area as *A. minutus*. The holotype of *A. lehmani* also plots in the area above equality.

Both *Mckennatherium ladae* and *M. cf. M. ladae* differ from *A. lehmani* in having a lower P_4 paraconid apical height, relative to apical metaconid height, and a narrower talonid basin, relative to P_4 total width, with a more obliquely oriented cristid obliqua. These differences plus the smaller M_2 in *M. ladae* seem great enough to continue to recognize *Mckennatherium*, although *M.* cf. *M. ladae* could arguably be placed in *Adunator* based on its larger M_2 size. I refrain from doing so, however, pending phylogenetic revision of the group.

Adunator amplus, new species

Figure 27, Table 22

Mckennatherium sp. nov., Rose, 1981a, p. 146.

Holotype.— YPM-PU 14738, a left dentary with P_4-M_1 from Rock Bench Quarry, in the northern Bighorn Basin.

Biostratigraphic occurrences.— *Pronothodectes jepi* zone (see Gingerich, 2001) (*Protoselene opisthacus* zone [To-2] of Lofgren et al. [2004]).

Diagnosis.— Differs from other species of *Adunator* and *Mckennatherium* in being significantly larger and in having more anteroposteriorly compressed molar trigonids. Further differs in having a lower P_4 paraconid apex relative to metaconid apical height. Further differs from other species of *Adunator*, except *Adunator abditus* n. sp., in having a narrower P_4 talonid basin, relative to total P_4 width. Further differs from of *Mckennatherium* and *Adunator abditus* n. sp. in having a less oblique cristid obliqua, nearly parallel to the longitudinal axis of the dentary. On average most dimensions of P_4-M_1 are 35-40% larger than in contemporary *M.* cf. *M. ladae*, also from Rock Bench Quarry.

Etymology.— *Amplus* (L), large: in allusion to the large size of this species.

Discussion.— The presence of this large species of *Adunator* at Rock Bench Quarry was reported by Krishtalka (1976a), and later included in a faunal list as *Mckennatherium* sp. nov. by Rose (1981a), but not formally described. My placement of this species in *Adunator*, rather than *Mckennatherium*, was based on its M_2 area being greater than M_1, and on a straighter P_4 cristid obliqua. It resembles *Mckennatherium*, however, in having a narrower P_4 talonid basin, relative to P_4 width, and a low P_4 paraconid. *Adunator amplus* was not included in Figure 26 because of its considerably larger size, but its relative M_{1-2} area is most similar to that of *A. meizon* in terms of distance above equality.

Referred specimens.— **Rock Bench Q.**: YPM-PU 14738 (holotype); 14746, L dent. P_4-M_1; 19483, R dent. M_{1-2}; 19641, R dent. P_4-M_2.

Adunator meizon (Gingerich, 1983a)

Figures 26 and 28, Table 23A

Mckennatherium cf. *ladae* (in part), Rose, 1981a, p. 152.
Diacocherus meizon Gingerich, 1983a, p. 241.

Holotype.— UM 82023, a right dentary with P_3-M_3, from Cedar Point Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description.— A description of *Adunator meizon* was provided by Gingerich (1983a).

Discussion.— Gingerich (1983a) distinguished *Adunator meizon* from *A. minutus* by its larger size, by more elevated paraconids on M_2 and M_3, and by having a more semimolariform P_4, rather than submolariform, with a paraconid usually positioned more anteriorly and well below the metaconid. His diagnosis was based largely on a small sample in the UM collections. Study of Cedar Point Quarry material at YPM reveals that *A. meizon* is actually slightly smaller than *A. minutus*, based on average M_1 area (Fig. 28, Table 23). It is, however, 3-4% larger in M_2 and M_3 length. As is often the case, the variability in large samples reveals some overlap of diagnostic traits among species. The variability is great enough in the position of premolar and molar paraconids in both *A. meizon* and *A. minutus*, that one can find exceptional specimens that will contradict the diagnosis. These characters hold for most specimens, however, and minor overlap does not preclude recognition of separate species.

TABLE 23 — Dental statistics for *Adunator meizon* and *A. minutus*. Abbreviations as in Table 3.

A. *Adunator meizon* from Cedar Point Quarry

		n	Min.	Max.	Mean	SE	SD	V
P_2	L	2	1.00	1.43	1.22	—	—	—
	W	2	0.49	0.53	0.51	—	—	—
P_3	L	2	1.60	1.65	1.63	—	—	—
	W	2	0.67	0.70	0.69	—	—	—
P_4	L	10	1.53	1.88	1.67	0.03	0.10	5.87
	W	12	0.80	1.15	0.95	0.03	0.11	11.58
M_1	L	17	1.65	2.10	1.80	0.02	0.10	5.45
	W	18	1.05	1.45	1.24	0.02	0.09	7.22
M_2	L	19	1.75	2.07	1.92	0.02	0.09	4.72
	W	20	1.27	1.53	1.39	0.02	0.08	6.08
M_3	L	13	1.47	1.87	1.71	0.03	0.12	6.97
	W	15	0.95	1.40	1.14	0.03	0.12	10.79

B. *Adunator minutus* from Princeton Quarry

		n	Min.	Max.	Mean	SE	SD	V
P_2	L	3	1.20	1.30	1.24	0.03	0.05	4.13
	W	5	0.51	0.60	0.55	0.02	0.04	6.68
P_3	L	10	1.30	1.65	1.52	0.03	0.10	6.88
	W	11	0.67	0.90	0.74	0.02	0.07	8.94
P_4	L	19	1.50	1.85	1.68	0.02	0.10	6.08
	W	20	0.82	1.30	1.00	0.03	0.14	13.99
M_1	L	23	1.65	2.05	1.83	0.02	0.09	5.05
	W	21	1.05	1.47	1.27	0.02	0.10	8.06
M_2	L	19	1.70	2.10	1.84	0.02	0.09	5.02
	W	19	1.21	1.67	1.37	0.03	0.12	8.85
M_3	L	15	1.46	1.90	1.65	0.03	0.12	6.98
	W	12	1.00	1.32	1.16	0.03	0.12	9.90

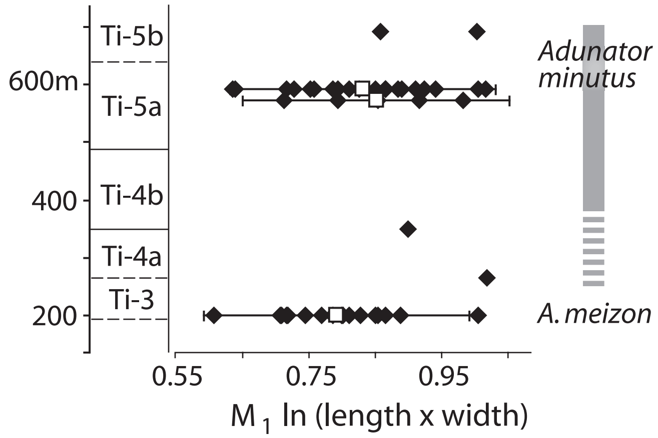


FIGURE 28 — Chart showing variability of M_1 area in *Adunator meizon* and *A. minutus* at various middle and late Tiffanian localities. From lowest to highest, data are from Cedar Point Quarry, Divide Quarry, SC-243 anthills, and Schaff, Princeton, and Y2K quarries. Solid gray bar corresponds to level for which *A. minutus* is known with confidence; dashed bar indicates lack of data. Error bars represent the range of expected variability in M_1 area of 0.4 natural log units, or about ± 2 SD (Gingerich, 1981).

Adunator meizon is further distinguished from *A. minutus* in features of the P_3. The P_3 paraconid in *A. meizon* is positioned well below the protoconid apex and connected to it by a paralophid that is convex in lateral view. This contrasts with the P_3 in *A. minutus* that has a higher paraconid, connected to a paralophid with a straighter margin. The P_3 in some specimens of *A. minutus* also has a small notch along the anterior edge of the paralophid, similar to the carnassial notch in carnivores.

A characteristic of *Adunator* (*sensu Diacocherus*) is that M_2 is larger than, or equal to M_1 in size (Gingerich, 1983a). This trait also helps to distinguish *Adunator meizon* from *A. minutus*, although there is some overlap. Specimens of *Adunator meizon* plot higher above equality on average than do those of *A. minutus*, two of which even fall below equality (Fig. 26).

Adunator meizon is also similar to *Leptacodon acherontus* n. sp. from Cedar Point Quarry. *Adunator meizon* differs in having a larger M_2 relative to M_1 (Fig. 26) and a reduced M_2 paraconid that is anteroposteriorly compressed and appressed to the metaconid, as opposed to one that is more connate and separate from the metaconid (see *L. acherontus*). Because there is some overlap in variability, the specific assignment of individuals with intermediate morphologies was somewhat arbitrary.

For both *Adunator meizon* and *A. minutus* coefficients of variation (V) are notably higher in width measurements than in length measurements for the same tooth position in nearly all cases (Tables 23A,B). This is probably due to small differences in tooth orientation, at least in part. Lingually canted teeth pose special problems. Nearly all measurements were made on teeth in dentaries, which I attempted to consistently orient in the same upright position for width measurement. However, post-depositional deformation of some specimens and possibly even primary differences in the degree of canting add additional complications. Nevertheless, although V may have been inflated by difficulties in orientation, in both *A. minutus* and *A. meizon* P_4 width has a consistently higher V than do other tooth positions. M_3 width has the next highest V. This reflects relatively high variability in these teeth that is also visible qualitatively.

Referred specimens.— **Cedar Point Q.**: UM 64566, L dent. P_4-M_1; 82023, L dent. P_3-M_3; 63115, R dent. $M_{1\text{-}3}$; 63117, R dent. M_2; 64571, L dent. P_4-M_1; YPM-PU 14988, R dent. P_2, $M_{1\text{-}2}$; 19959, L dent. P_4-M_3; 19999, R dent. P_4-M_3; 20012, L dent. P_4-M_3; 20022, R dent. $M_{1\text{-}3}$; 20023, R dent. $M_{2\text{-}3}$; 20053, L dent. P_4-M_3; 20057, L dent. P_4-M_2; 20072, R dent. P_2-M_2; 20646, L dent. P_4-M_2; 20847, L dent. $M_{2\text{-}3}$; 20874, L dent. $M_{1\text{-}3}$; 20887, L dent. $M_{2\text{-}3}$; 21288, L dent. P_4-M_3; 21388, L dent. P_4-M_2; 21396, L dent. P_4-M_3; 21429, R dent. $M_{1\text{-}3}$; 21435, R dent. P_4-M_3; 21853, R dent. P_2, P_4-M_3.

Adunator minutus (Jepsen, 1930b)

Figures 26, 28–29, Table 23B

Diacodon minutus Jepsen, 1930b, p. 511.
Palaeictops minutus, Gazin, 1956, p. 16.
Leptacodon minutus, McKenna, 1960, pp. 51, 53.
"*Diacodon minutus*" (in part), Krishtalka, 1976, p. 10.
Diacocherus minutus, Gingerich, 1983a, p. 239.
Diacocherus sp., Secord, 2002, p. 105.

Holotype.— YPM-PU 13360, a left dentary with M_{1-3}, from Princeton Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a), *Phenacolemur* (Ti-4b), *Probathyopsis* (Ti-5a), and *Plesiadapis simonsi* (Ti-5b) zones.

Description.— A description of *Adunator minutus* was provided by Gingerich (1983a).

Discussion.— Differences between *Adunator meizon* and *A. minutus* were discussed in the *A. meizon* section. Measurements for *A. minutus* from Princeton Quarry, its type locality, are presented in Table 23B. Coefficients of variation (V) are notably higher in width measurements than in length measurements for the same tooth position in nearly all cases. As discussed above, this is probably due partly to subtle differences in orientation of these lingually canted teeth.

I have tentatively referred a small sample from Divide Quarry, including a single dentary, to *Adunator minutus*. The relative area of M_1 to M_2 in UM 82101 plots in the overlap between *A. minutus* and *A. meizon* (Fig. 26, not shown). The P_4 paraconid is high on the crown, as is typical of *A. minutus*, but it is in an anterior position more typical of *A. meizon*. The paraconid in UM 80583 is positioned more posteriorly, but is lower on the crown. In both specimens the paraconid is high, with respect to the metaconid, and these are most similar to *A. minutus* in this regard. The M_2 paraconid height is lower than is typical of *A. meizon* and more like *A. minutus*. The Divide Quarry specimens fall in the upper range of size variation for both species. Divide Quarry is intermediate in stratigraphic position between the type localities of *A. meizon* and *A. minutus* and may represent an intermediate, although slightly larger form in a single lineage.

I also include specimens from Y2K Quarry in *Adunator minutus*. The sample is relatively small but is largely within the variability of *A. minutus* from Princeton and Schaff quarries. The Y2K Quarry form differs in the development and position of the P_4 metaconid and in having a slightly larger M_2 relative to M_1, more like *A. meizon* (Fig. 26). Most of the Y2K Quarry specimens have a P_4 metaconid that is smaller and lower on the trigonid than is typical for specimens of *A. minutus*. In fact the P_4 metaconids in UM 109577 and 109564 (Fig. 29) are more reduced and lower than any in the samples from Princeton and Schaff quarries, in spite of larger sample sizes. UM 109426 from Y2K Quarry, on the other hand, has a large metaconid positioned high on the crown, as is typical for *A. minutus*. The development and position of the P_4 metaconid appears to be variable in the Y2K Quarry sample, although this variability is somewhat different than at Princeton and Schaff quarries. The overall suite of characteristics is most similar to those of *A. minutus*, and these differences do not seem great enough to warrant recognition of a separate species.

Lower teeth anterior to P_2 in *Adunator minutus* have not been previously described. UM 109564 (Fig. 29) preserves five antemolar teeth and three closely spaced alveoli anterior to the most anterior tooth. Using traditional dental homologies for eutherian mammals, the anterior-most tooth would be a canine and the alveoli would have held I_{1-3}. It is noteworthy, however, that in this case the C_1 would be completely premolariform. There is no appreciable change in size from C_1 to P_1 and both teeth are single-rooted. This is atypical for early lipotyphlans. Alternatively, *Adunator* may have had five premolars, a scenario that has been proposed for early Lipotyphla by some authors (e.g., McKenna, 1968; Schwartz and Krishtalka, 1976). In this case the canine would have been lost, resulting in a the dental formula of 3.0.5.3. Nevertheless, I provisionally follow convention and call the fifth antemolar a canine.

YPM-PU 17632 preserves I_2 and P_{1-4} (Figs. 29D,E). The upper part of the crown of P_1 is missing. The I_2 is spatulate, and exhibits a high degree of labial-lingual compression. The alveoli for I_{2-3} are equal in size. The I_1 alveolus is partly obscured on YPM-PU 17632, but is visible on UM 109564 and appears to have been slightly smaller and slightly more mesial than the I_{2-3} alveoli. The spatulate condition of the I_2 contrasts with the I_2 in some lipotyphlans, such as *Litolestes* (Schwartz and Krishtalka, 1976) and nyctitheriids (Rose and Gingerich, 1987; Bloch, 2001), which are multi-lobed. Krishtalka (1976a) compared *A.* ("*Diacodon*") *minutus* with *Haplaletes*, a hyopsodontid condylarth, and suggested that they may be related. It is notable that in regard to incisor morphology, *A. minutus* is more similar to many condylarths, than to some lipotyphlans.

No specimens of *Adunator* have yet been found in the latest Tiffanian deposits above Y2K Quarry. However, several isolated teeth in a freshwater limestone from SC-179, just above the Tiffanian-Clarkforkian boundary, were informally referred to a new species of *Diacocherus* (= *Adunator*) by Bloch (2001), along with more complete specimens from the middle Clarkforkian. The species is larger than *A. minutus*, and may differ in other aspects as well.

Referred specimens.— **Divide Q.** (FG046): UM 80583, R P_4; 82101, L dent. P_4-M_3; 83233, R M_2; 85429, L M^1. **Princeton Q.**: YPM-PU 14118, R dent. M_{1-3}; 14146, R dent. P_{2-4}; 14233, L dent. P_4-M_3; 14248, R dent. P_4-M_2; 14327, L dent. M_{1-3}; 14328, R dent. P_{2-3}, M_{1-3}; 14331, R dent. P_4-M_1; 14439, R dent. P_4-M_3; 14529, R dent. P_{3-4}; 14530, L dent. P_4-M_3; 14534, R dent. P_3-M_1; 17631, L dent. P_3-M_1; 17632, L dent. I_2, P_{1-4}; 17633, L dent. P_2-M_2; 21184, L dent. M_{2-3}; 21185, L dent. P_4-M_3; 21189, L dent. M_2; 21190, L dent. M_3; 21191, L dent. M_1; 21192, L dent. M_3; 24814, R dent. P_3. **SC165** (Habetler's Concentration): UM 81711, L M_1 partial. **SC243**: UM 61586, L M_1. **Y2K Q.** (SC389): UM 109126, R M_1; 109232, L dent. P_{1-3}; 109338, R M_2; 109425, L dent. M_{2-3}; 109426, L dent. P_{2-4}; 109447, L M_1; 109564, L and R dents, R C_1, P_2-M_3, incisor alveoli; L P_3, M_{1-3}, P_2 alveoli; 109574, L dent. P_3?-M_1; 109577, L P_4; 109587, L dent. M_{2-3}; 109852, R M^1. **Schaff Q.**: YPM-PU 19425, L dent. P_2-M_2; 19426, R max. P^4-M^3; 19442, L dent. M_{1-2}; 19468, L dent. P_2, P_4-M_3; 19471, R dent. M_{1-3}; 20735, R dent. M_{1-2}; 21194, L dent. M_2.

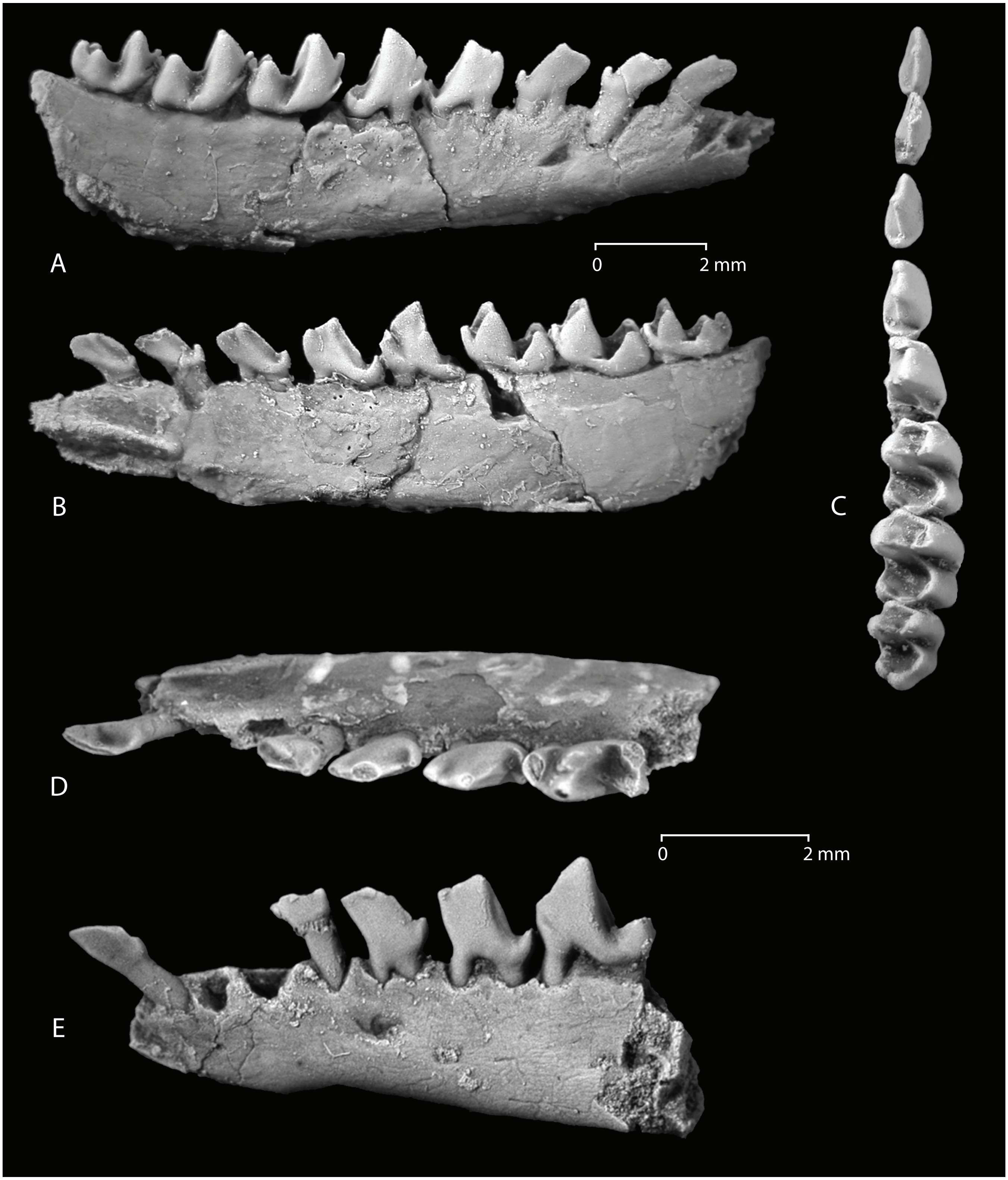


FIGURE 29 — Dentaries of *Adunator minutus*. A–C, right dentary with C_1-M_3 (UM 109564) in buccal (A), lingual (B), and occlusal (C) views, from Y2K Quarry. D–E, left dentary with I_2 and P_{1-4} (YPM-PU 17632) in occlusal (D) and buccal (E) views, from Princeton Quarry.

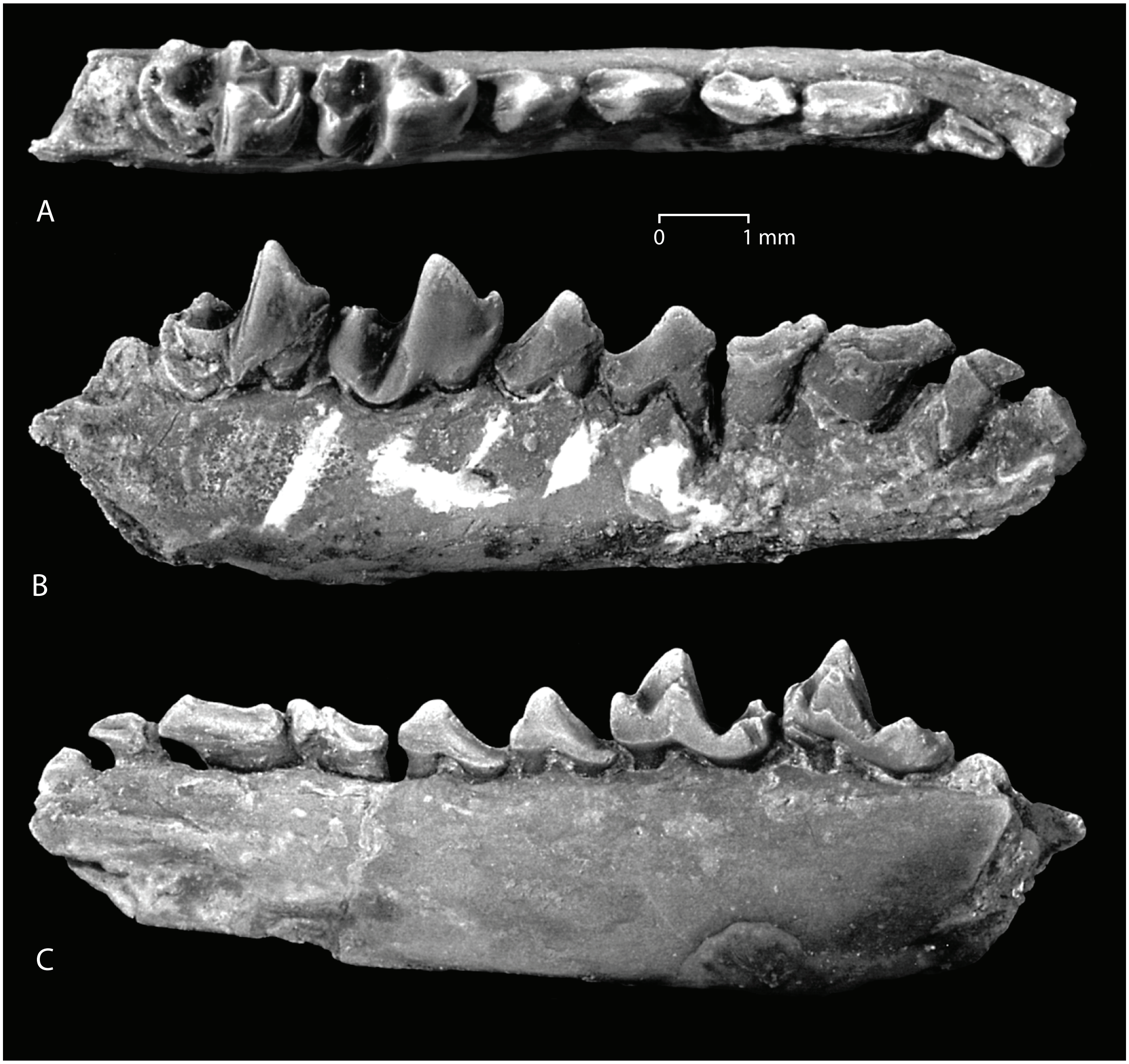


FIGURE 30 — Holotype of *Adunator abditus* n. sp. from Princeton Quarry. A–C, right dentary with I_2-M_1 (YPM-PU 14163) in occlusal (A), buccal (B), and lingual (C) views.

Adunator abditus, new species

Figure 30, Table 24

Adapisoricid or nyctithere indent. (in part), Rose, 1981a, p. 156.

Holotype.— YPM-PU 14163, a right dentary with I_2-M_1 from Princeton Quarry, in the northern Bighorn Basin.

Biostratigraphic occurrences.— *Probathyopsis* zone (Ti-5a).

Diagnosis.— Smaller than all other species of *Adunator* and *Mckennatherium*. Further differs from other species in these genera, in which anterior premolars are known, in having a P_3 that is shorter and lower relative to P_4, and in having a P_2 that is approximately equal to P_3 in size, as opposed to a P_3 that is larger than P_2 in other species. Further differs from *Mckennatherium* in having a higher P_4 paraconid with an apical height approximating that of the metaconid. Further differs from other species of *Adunator*, except possibly *A. lehmani*, in having a narrower P_4 talonid, relative to total P_4 width, that is less quadrate and has a more oblique cristid obliqua, and a more distal hypoconulid. Further differs from *A. minutus*, the only species in which teeth anterior to P_2 are known, in having a larger and more robust canine and P_1, in having a canine that is larger than P_1, and in having more closely spaced C_1-P_3 roots. The single roots of P_1 and C_1 are longer than those of *A. minutus*, in spite of its smaller size. C_1-P_3 also differ in having less mesial-dorsal projection.

TABLE 24 — Dental measurements for the holotype of *Adunator abditus* n. sp. (YPM-PU 14163) from Princeton Quarry. *Estimate. **Minimum length.

C_1	L	1.10
	W	0.43
P_1	L	—
	W	0.37
P_2	L	0.95
	W	0.43
P_3	L	0.90
	W	0.50
P_4	L	1.40
	W	0.95
M_1	L	1.43**
	W tri.	1.03*

Etymology.— *abditus* (L), hidden, concealed: in reference to the rarity and unrecognized presence of this species.

Description.— Nearly all of the enamel on the crowns of I_2-P_3 has been lost. Enamel remains on the buccal surface of P_4, on the P_4 talonid, and on the postvallid of the M_1 trigonid. Small longitudinal patches remain around the bases of the crowns on most teeth. The crowns of $I_{2\text{-}3}$ were largely lost to wear. The I_1 alveolus is mostly missing, but was anterior and mesial to I_2 and appears to have been smaller. The I_2 and I_3 roots are subequal. The I_2 root is more anteriorly inclined. The canine has shifted from its original position. Its crown was an elongate, anteriorly projecting wedge, with a long, robust root. There was a single medial posterior cusp. The P_1 is single-rooted and similar in form to the canine, but is slightly smaller. It too had a single posterior cusp. The tip appears to have been broken and re-cemented in a slightly incorrect orientation.

All teeth posterior to P_1 are double-rooted. $P_{2\text{-}3}$ have anterior protoconids confluent with long inclined posterior crests, single posterior cusps, and low paraconids. P_4 is submolariform. Its paraconid and metaconid are approximately equal in size and height on the crown. The talonid has three distinct cusps, including a small hypoconulid situated intermediately between the entoconid and hypoconid, but posterior to both cusps. The entoconid is partially broken.

The M_1 is obliquely oriented relative to the long axis of the dentary. Its paraconid is anteroposteriorly compressed and incorporated into a paralophid. The metaconid and protoconid were relatively low. The cristid obliqua contacted the postvallid medially and does not appear to have ascended it. The buccal half of the talonid is broken away and no other molars are preserved.

The dentary is deep, and is about 180% of the buccal height of the M_1 trigonid. Teeth form a straight row from C_1-M_1 that is deflected buccally anterior to C_1. A mental foramen is situated below the P_4 paraconid.

Discussion.— This specimen clearly represents an undescribed species, but its referral to *Adunator* is less certain. The relative size of M_1/M_2 and the condition of the M_2 paraconid are key in distinguishing *Adunator* from other genera, but M_2 is not known for this species. Nevertheless, other characters suggest affinities with *Adunator*. The general form of the M_1 and premolars agree well with *Adunator*. The approximately equal apical height of the P_4 paraconid and metaconid appears to be a derived condition shared with *Adunator minutus*. However, the narrowness of the P_4 talonid and obliquity of its cristid obliqua are more similar to *Mckennatherium ladae* and *A. amplus* n. sp. than to younger species of *Adunator*, and presumably represent a more primitive condition. An M_2 of *Adunator abditus* is needed for a more confident generic identification.

Enamel is missing or nearly absent over large areas of the teeth. Most enamel is gone from the lingual faces, except strips near the bases of the crowns, below the crown overhang (Fig. 30C). Buccal faces also underwent considerable loss of enamel, but to a lesser degree. Enamel is preserved on the postvallid of M_1. This etching pattern does not agree well with crocodilian etching, which should remove enamel to a greater degree and in a more homogeneous fashion. Nor does it agree with etching by falconiformes, which should also etch dentin and result in a more pitted pattern (Fisher, 1981). Most mammalian predators leave enamel intact. Thus, inorganic postmortem etching may be the most probable explanation.

I considered the condition of the holotype before deciding to establish a new species. Although the partial loss of enamel precludes comparison of some features, the unusual completeness of the specimen compensates for its poor condition. The degradation of enamel has probably not significantly reduced the size of most teeth. Even with the compromised condition of C_1 and P_1, it is evident that both teeth were considerably more robust than in the contemporary *A. minutus* (compare Figs. 29 and 30). The roots of C_1 and P_1 are more much gracile in *A. minutus*, and C_1-P_3 are separated by diastemata, contrasted with the closely appressed roots in *Adunator abditus*. It is difficult to determine how much of C_1 and P_1 are missing, but the retention of a small posterior cusp on each suggests that a large amount of the occlusal surfaces is still present.

M_1 in the holotype is similar in structure and overall size to M_1 in UM 92254 from Divide Quarry, described below as cf. *Adunator*. Cf. *Adunator* is clearly not the same species, but may be closely related to *Adunator abditus*.

Referred specimens.— **Princeton Q.**: YPM-PU 14136 (holotype).

Cf. *Adunator*

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Discussion and description.— A single dentary from Divide Quarry preserves M_1 a partial M_2, and alveoli for M_3, and C_1-P_4. Teeth are heavily worn. The overall resemblance is similar to species of *Adunator* and *Leptacodon*. It is about the same size as *Adunator abditus* n. sp. Its M_1 appears to have been longer than M_2, a trait not found in *Adunator* as described here, but present in some specimens of *Leptacodon* (e.g., Table 28). The M_1 morphology is, however, nearly identical to that of *Adunator abditus* n. sp. and differs from *Leptacodon* in having M_1 trigonid cusps that are lower, more rounded, and more conical. The P_4 was probably longer than

M_1 (based on alveoli), and clearly greater in size than that of *Adunator abditus* n. sp. The posterior dentary is shallower, relative to M_1 size, than in *A. minutus*, *A. meizon*, *A. abditus* n. sp. or *Leptacodon packi*, but is similar in depth to *Leptacodon tener*. M_1 is slightly larger than that of *L. tener*, as is the dentary. The dentary is similar, however, in relative depth and positioning of teeth. M_1 and M_2 hypoconulids appear to have been positioned lingually in close proximity to the entoconids, a trait found in *L. packi* and *L. munusculum*, but not in *L. tener*. All teeth posterior to P_1 were double-rooted while P_1 was single-rooted, a condition found in both *Leptacodon* and *Adunator*.

UM 92254 appears to represent an undescribed species with similarities to both *Leptacodon* and *Adunator*, and may belong in a separate genus. I am reluctant, however, to establish a new taxon based on this fragmentary and worn specimen.

Dental measurements (mm).— UM 92254: M_1, L = 1.55, W = 1.35*; M_2, L = 1.35*.

Referred specimen.— UM 92254, R dent. M_1, partial M_2, alveoli for C_1-P_4, and M_3.

LITOCHERUS Gingerich, 1983a

Litocherus zygeus Gingerich, 1983a

Litocherus zygeus Gingerich, 1983a, p. 232.

Holotype.— UM 64508, a right dentary with P_3-M_3, from Cedar Point Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* (Ti-3), ?*Plesiadapis churchilli* (Ti-4a), and ?*Phenacolemur* (Ti-4b) zones.

Description.— An adequate description was provided by Gingerich (1983a).

Discussion.— Two specimens in the YPM collections may represent late occurrences of *Litocherus zygeus* or possibly a slightly more progressive form. YPM-PU 17822 is a dentary preserving P_3-M_1, and according to the specimen label, is from the Sand Draw Anthill locality, anthill #1. This specimen is clearly too large to have been collected by ants, however, and must have come from the surrounding area. YPM-PU 17818 preserves P_2-M_3, and according to the label, was collected in 1951 by R. V. Witter in the area between Foster Gulch and Sand Draw. A large amount of matrix still on the specimen indicates that it originated from a fine-grained limonitic sandstone. UM localities in this area are in the *Phenacolemur* and *Probathyopsis* zones. The Sand Draw Anthills appear to be correlative to either the *Plesiadapis churchilli* or *Phenacolemur* zone, or may include fossils from both zones. In any event, these localities are probably younger than Cedar Point Quarry, the type locality for *L. zygeus*.

Both specimens have narrower premolars than is typical in the hypodigm. This character is variable, however, and some specimens in the hypodigm exhibit the same condition (e.g., YPM-PU PU 21387; R dent. $P_{2\text{-}3}$). Relative length-width dimensions are also variable in M_1, and some specimens have a considerably more elongate M_1 than others. The presence or absence of a P_4 metaconid is also variable, as well as the acuteness of cusps. Molars in YPM-PU 17818 are virtually identical to those in the hypodigm.

TABLE 25 — Dental measurements for holotype of *Wyonycteris galensis* n. sp. (YPM-PU 14138) from Princeton and Schaff quarries.

		YPM-PU 14138 (holotype)	YMP-PU 19493 (paratype)
P_4	L	1.40	—
	W	1.30	—
M_1	L	1.52	1.67
	W	1.33	1.25
M_2	L	1.47	1.63
	W	1.33	1.25
M_3	L	—	1.32
	W	—	—

The M_1 in UM 63107 was reduced to a flat horizontal plane from wear during the life of the animal. This degree and style of wear suggests a coarse component in the diet of this "insectivore."

Referred specimens.— **Cedar Point Q.**: UM 63106, L dent. P_4-M_3; 63107, R dent. M_1 (very worn); 64417, R dent. P_4-M_2; 64425, L dent. P_4 (juvenile); 64508, L dent.; 64516, R dent. P_4-M_2; 71831, L dent. P_4-M_3; 71835, R dent. P_4-M_1, M_3; 82026, L M^2; 82027, L dent. $P_{3\text{-}4}$; 83227, L dent. P_4; 83248, L dent. P_4-M_3; 83254, L dent. P_3-M_3. **Sand Draw Anthills**, **anthill #1**: YPM-PU 17822, right dent. P_3-M_1; SW¼, T55N, R96W, Divide between Sand Draw and Foster Gulch: YPM-PU 17818, L. dent. P_2-M_3. Plus numerous additional specimens from Cedar Point Quarry at YPM.

?*Litocherus lacunatus*

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* zone (Ti-4b).

Description and discussion.— Three teeth from anthills at SC-243 resemble teeth in UM 80803, referred to *Litocherus lacunatus* by Gingerich (1983a, Figs. 2C,D), and agree with descriptions of the holotype by Gazin (1956b). UM 61595 (M_2?) differs from the M_2 in UM 80803 only in having a slightly more reduce paralophid and a more centrally positioned hypoconulid. UM 61509 (M_1?) is similar in structure to the M_1 in UM 80803, but is about 15% longer and 23% wider. UM 61601 (M_1?) is structurally very similar to the M_1 in UM 80803 but is about 12% smaller. UM 61602 (P_4) is similar to the P_4 of the holotype as figured by Gazin (1956b, Plate 11-3), but is about 10% longer and 30% wider. A cast of the holotype was not available, but based on Gazin's (1956b) measurements, it is close to UM 80803 in size. There is probably more than one species included in the referred specimens. Although some of these teeth may belong to *L. lacunatus*, more complete specimens are needed for reliable identifications.

Dental measurements (mm).— UM 61590: M_1?, L = 3.15, W = 2.47. UM 61595: L M_2?, L = 2.37, W = 1.90. UM 61601: R M_1?, L = 2.35, W = 1.80. UM 61602: R P_4, L = 3.60, W = 2.50.

Referred specimens.— **SC243**: UM 61590, L M_1?; 61595, L M_2?; 61601, R M_1?; 61602, R P_4.

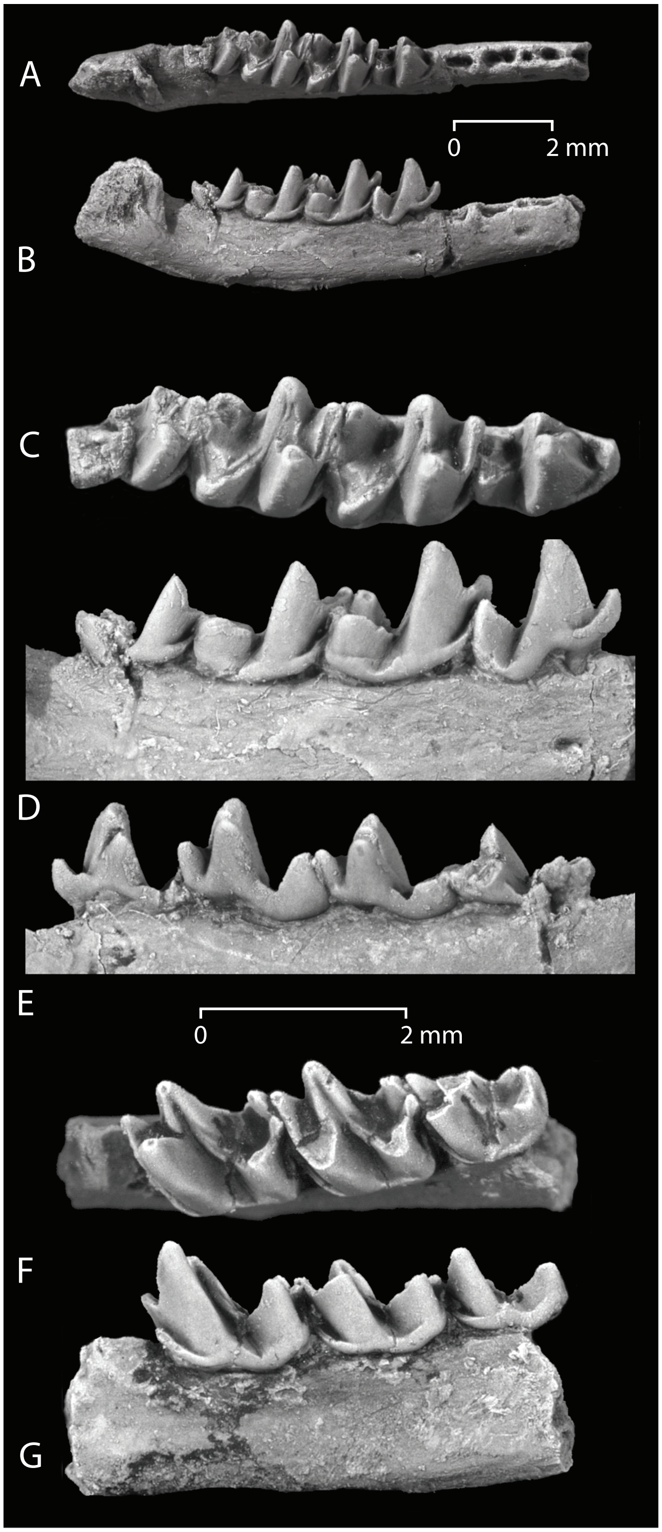


FIGURE 31 — Holotype and paratype of *Wyonycteris galensis* from Princeton and Schaff quarries, respectively. A–E, holotype right dentary with P_4-M_2 and partial M_3 (YPM-PU 14138) in occlusal (A, C), buccal (B, D), and lingual (E) views. F–G, paratype left dentary with M_{1-3} (YPM-PU 19493), in occlusal (F) and buccal (G) views.

Order SORICOMORPHA Gregory, 1910
Family NYCTITHERIIDAE Simpson, 1928

WYONYCTERIS Gingerich, 1987

Wyonycteris galensis, new species
Figure 31, Table 25

Adapisoricid or nyctithere indet. (in part), Rose, 1981a, p. 156.
Wyonycteris n. sp. B, Secord et al., 2006, p. 229.

Holotype.— YPM-PU 14138, a right dentary with P_4-M_2, and a partial M_3; from Princeton Quarry, northern Bighorn Basin, Wyoming.

Paratype.— YPM-PU 19493, left dentary with M_{1-3}, from Schaff Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences.— *Probathyopsis* (Ti-5a) and ?*Plesiadapis cookei* (Cf-2) zones.

Diagnosis.— Larger than *Wyonycteris chalix* and *W. richardi*. Further differs from *W. chalix* in having a P_4 with a longer, basined talonid, and a metaconid positioned lower on the crown. Further differs from *W. richardi* in having a double-rooted P_2, and a more anteriorly positioned anterior mental foramen.

Etymology.— *Gale* (G), polecat or skunk; *-ensis* denoting geographic name: in reference to Polecat Bench.

Description.— P_4 is submolariform with a prominent anteriorly projecting paraconid, situated low on the crown. The paraconid is confluent with a buccal cingulid that originates near the back of the anterior root. The metaconid is prominent and midway in height between the paraconid and protoconid. The P_4 talonid is broken lingually, but is long, and had a prominent hypoconid connected to a cristid obliqua that contacts the postvallid medially. The talonid slopes ventrally on both sides of the hypoconid. A second cusp may have been present lingual to the hypoconid. A small shallow basin is present lingual of the cristid obliqua.

P_4-M_3 are lingually canted, and molar trigonids are progressively more canted from M_1 to M_3. The molars become more obliquely oriented, relative to the longitudinal axis of the dentary, from M_1 to M_3. All molars have a prominent paraconid positioned buccolingually between the trigonid notch and metaconid. The molar cristid obliqua ascends to the apex of the metaconid creating a distinctive groove on the posterobuccal surface of the metaconid. The grooves are partly lost to wear on the holotype. A small notch is present on the cristid obliqua where the slope changes from descending to ascending. M_{1-2} talonids are "ncytalodont," in the sense described by Menu and Sigé (1971), meaning that the hypoconid and hypoconulid are connected by the postcristid, while the hypoconulid and entoconid are separated by a fissure, but closely approximated. The hypoconulid is situated lingual of median, posterior to the entoconid. Molar precingulids are strong and positioned below the paraconid. Incipient buccal cingulids are present on M_1 and M_2. On M_3 of the paratype the hypoconulid is directly behind the entoconid, and only slightly less lingual. This unusual condition results in nearly square corners on the talonid. The M_3 in the holotype is badly damaged, but appears to have had a similar condition.

The dentary is very shallow, and is only about 1.10 to 1.15% of the buccal height of M_1. The holotype preserves six alveoli

TABLE 26 — Dental measurements for holotype of *Wyonycteris microtis* n. sp. (YPM-PU 19479) from Schaff Quarry.

M^1	L	1.16
	W	1.17
M^2	L	1.02
	W	1.49
M^3	L	0.80
	W	1.22

anterior to P_4. $P_{2\text{-}3}$ were clearly double-rooted. P_1 was probably single-rooted. The two anterior alveoli are both elongate and longer than more posterior alveoli, which is typical of single-rooted teeth. They are separated, however, by a small rise of bone, a condition often found between the roots of double-rooted teeth. If P_1 were double-rooted it was considerably longer than P_2, which would be an unusual condition for a primitive lipotyphlan. A small mental foramen is positioned below the P_4 trigonid and a larger one below the anterior alveolus for P_2.

Discussion.— The referred specimens exhibit characteristic traits of *Wyonycteris* as outlined by Gingerich (1987), including a molar cristid obliqua that ascends the metaconid, obliquely oriented molars, and a "ncytalodont" talonid. These teeth also resemble those of *Eolestes simpsoni*, an erinaceomorph known only from the Wasatchian (Bown, 1979; Bown and Schankler, 1982). Based on comparison of a cast of YPM 35156 and descriptions of *E. simpsoni*, the P_4 of *W. galensis* is narrower than that of *E. simpsoni*, and has at least one distinct talonid cusp. Bown (1979) described the P_4 talonid of *E.* (*Leipsanolestes*) *simpsoni* as having no distinct talonid cusps. The talonid is obscured on the cast of YPM 35156. Additionally, the P_4 paraconid of *W. galensis* is confluent with a buccal cingulid, not positioned below it as in *E. simpsoni*. Molars are very similar, but may be less obliquely oriented in *E. simpsoni*. Differences in P_4 morphology are of at least specific magnitude, but an argument could be made for placing *W. galensis* in *Eolestes*. The taxa may be closely related, but they are currently placed in different orders (McKenna and Bell, 1997). Referral to *Wyonycteris* is tentative pending the discovery of upper molars, which have some of the key characters of *Wyonycteris*.

I tentatively refer YPM-PU 14088 from Princeton Quarry to *Wyonycteris galensis*. The molars are badly damaged but the dentary is very shallow and the preserved morphology agrees with other specimens.

UM 68288 is a left dentary fragment with an M_1 talonid and an M_2, from the Paint Creek locality (SC-143) of middle Clarkforkian age. The molars are slightly larger than those of *Wyonycteris galensis* or *Eolestes*, but are probably within the variability of either species. The M_2 paraconid differs in having a slight anterior deflection near the apex. The specimen may represent a late occurrence of *W. galensis*, or possibly an early occurrence of *Eolestes*.

The referred specimens represent the earliest known occurrences of *Wyonycteris*.

Referred specimens.— **Princeton Q.**: YPM-PU 14088, L dent. M_2 partial, M_3 partial; 14138 (holotype). **Schaff Q.**: YPM-PU 19493 (paratype).

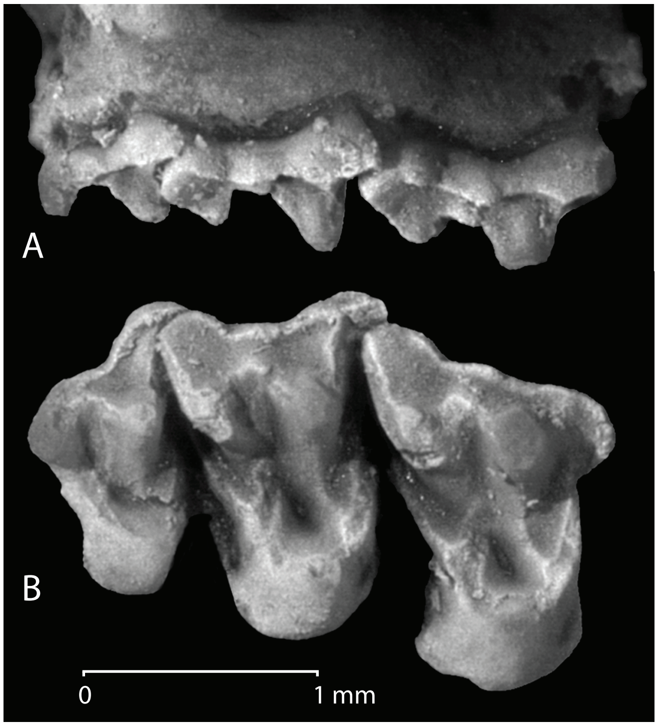


FIGURE 32 — Holotype of *Wyonycteris microtis* n. sp. from Schaff Quarry. Right maxilla with $M^{1\text{-}3}$ (YPM-PU 19479) in buccal (A) and occlusal (B) views.

Wyonycteris microtis, new species
Figure 32, Table 26

Wyonycteris n. sp. A, Secord et al., 2006, p. 229.

Holotype.— YPM-PU 19479, right maxilla with $M^{1\text{-}3}$ from Schaff Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences.— *Probathyopsis* zone (Ti-5a).

Diagnosis.— Differs from *Wyonycteris chalix* and *W. richardi* in having: (1) a crescentic metacone incorporated into the metacrista on $M^{1\text{-}2}$; (2) a more buccolingually elongate M^1; (3) a smaller or absent M^1 hypocone; (4) a small furrow between the mesostyle and the outer edge of the stylar shelf which bears an additional stylar cusp; and (5) a weaker ectoloph.

Etymology.— *mikrotes* (G), smallness: in reference to the extremely small size of this species.

Description.— All teeth show signs of wear and belonged to a mature adult. The paracone on all molars is larger than the metacone. On $M^{1\text{-}2}$ the metacone is reduced, anteroposteriorly compressed, and incorporated into the metacrista, to a greater degree on M^2 than on M^1. No parastyle is visible on M^1 or M^2, but could have been lost to wear. A small stylocone is visible on M^1 at the termination of the paracrista, but none is apparent on M^2. Ectolophs are present on $M^{1\text{-}2}$, but are weak, especially on M^2. Both $M^{1\text{-}2}$ have a mesostyle in the ectoloph that is separated from the outer margin of the stylar shelf by a furrow. A ridge is developed on the edge of the stylar shelf and a peak directly buccal of the mesostyle forms an accessory stylar cusp on both molars. Wear has partly obscured the condition of the molar conules, but they were distinct on $M^{1\text{-}2}$. There appears to have

TABLE 27 — Dental measurements for *Leptacodon acherontus* n. sp. from Cedar Point Quarry.

		YPM-PU 18466	YPM-PU 19957 (type)	YPM-PU 20811
P_3	L	—	1.13	—
	W	—	0.80	—
P_4	L	1.65	1.57	1.70
	W	1.18	1.20	1.10
M_1	L	1.80	—	2.05
	W	1.43	1.42	1.50
M_2	L	1.83	1.75	1.95
	W	1.55	1.55	1.45
M_3	L	1.83	1.80	1.90
	W	1.38	1.55	1.25

been a small metaconule on M^3. Trigon basins on M^{1-2} are very deep, but shallower on M^3. A short precingulum is present on the anterolingual face of the protocone on M^{1-2}. There is some damage to the posterolingual faces of M^{1-2}, but if a hypocone or postcingulum were present on either it was small and restricted. The molar protocones are anteriorly canted, M^3 exhibiting the greatest cant.

Discussion.— These molars are most similar to those included in *Wyonycteris* by Gingerich (1987), Smith (1995), and Bloch (2001). Differences between *W. microtis* and other species may be regarded by some authors as great enough to warrant generic separation. However, with no knowledge of the variability in *W. microtis*, and little knowledge of variability in other species, it may be premature. Bloch (2001) informally described two new species of *Wyonycteris*, *W.* "*gingerichi*" and *W.* "*acaradelphos*," both from the Wasatchian. The specimens were not available for study, but from descriptions and figures *W. microtis* differs from *W.* "*gingerichi*" in characters 1, 3, and 4 in my diagnosis, and in having a smaller mesostyle. No well-preserved upper molars of *W.* "*acaradelphos*" are known, but based on lower molar size, they would be smaller than those of *W. microtis*.

The molars in *Wyonycteris microtis* also share similarities with those of *Pontifactor* and *Nyctitherium*. Based on the description and figures provided by West (1974) and Krishtalka (1976b), and on casts of specimens, molars in *W. microtis* differ from those of *Pontifactor besteola*, the type species, in having: (1) smaller or no hypocones; (2) less well-defined ectolophs; (3) smaller mesostyles; (4) weaker para- and metaconules; (5) a less buccolingually elongate M^1; (6) a less crescentic metacone; and (7) a furrow between the mesostyle and the outer stylar shelf that is rimmed by a ridge. Based on the descriptions and figures provided by Robinson (1968) and Krishtalka (1976b) molars in YPM-PU 19479 differ from those of *Nyctitherium velox*, the type species, in characters 1, 2, 5, and 6, and in having an ectoloph.

No lower molars of *Wyonycteris microtis* have been identified. There are several isolated teeth from Y2K Quarry that are close to the expected size, but could potentially belong to other taxa. YPM-PU 19479 is too small to be the upper dentition of *W. galensis* n. sp., also known from Schaff Quarry.

Referred Specimen.— **Schaff Q.**: YPM-PU 19479 (holotype).

LEPTACODON Matthew and Granger, 1921

Leptacodon acherontus, new species

Figures 26 and 33, Table 27

Mckennatherium cf. *ladae* (in part), Rose, 1981a, p. 152.
Diacocherus meizon (in part), Gingerich, 1983a, p. 241.
Erinaceomorpha n. sp., Secord et al., 2006, p. 228.

Holotype.— YPM-PU 19957, a left dentary with $P_{3\text{-}4}$, an M_1 talonid, $M_{2\text{-}3}$, and alveoli for a double-rooted P_2 and single rooted P_1; from Cedar Point Quarry, in the northern Bighorn Basin.

Biostratigraphic occurrences.— *Plesiadapis rex* zone (Ti-3).

Diagnosis.— Larger than other species of *Leptacodon*, except cf. *L. choristus* n. sp. Differs from other species for which P_3 is known, except *L. rosei*, in having a shorter, more inflated P_3. Further differs from *L. munusculum* in having a wider, more inflated P_4. Further differs from *L. tener* in having a more posterior M_2 hypoconid, resulting in a squarer shaped talonid in occlusal view. Further differs from *L. catulus* in having strong P_4 and M_1 paraconids. Differs from cf. *L. choristus* n. sp. in being smaller, having a shorter P_3 with a weaker paraconid, a narrower, less exodaenodont P_4 with a larger talonid basin and lower paraconid, more rounded molar hypoconids, and a shorter M_3 talonid.

Etymology.— *Acherontos* (G), a river of the nether world: in allusion to the fluvial deposits at Cedar Point Quarry.

Description.— The following description is based on the holotype. The P_3 is short, rounded, and has a slightly inflated appearance. The protoconid is relatively low. A small, poorly developed paraconid is positioned low on the anterior face. The P_3 appears to have had a small, weakly developed talonid, bounded posteriorly by a low ridge, one broad talonid cusp, or possibly two cusps. The talonid had no real basin and was open buccally and lingually. A weak ridge begins at the paraconid, ascends the protoconid to its apex, and then descends to the talonid.

The P_4 is semimolariform, bearing three rounded trigonid cusps and a basined talonid. Like P_3, it has a slightly inflated appearance. The paraconid is large and situated low on the crown. The metaconid is well-developed and prominent, but smaller than the protoconid. The apex of the metaconid is above that of the paraconid but is still well below that of the protoconid. A distinct ridge begins at the paraconid and ascends to the protoconid apex. The talonid is long and well-developed. The basin is shallow, possibly due partly to wear around the periphery. Three talonid cusps can be distinguished. The hypoconid is the most prominent. The entoconid is small, poorly developed, and posteriorly positioned. The hypoconulid is little more than a ridge. All cusps are rounded. A strong cristid obliqua is present and contacts the postvallid medially. Both the trigonid and talonid are moderately exodaenodont.

The molars are lingually canted, as with most eutherians of this grade. The M_1 is badly damaged and missing the trigonid, the center of the talonid, and the talonid cusps. The hypoconid was large. The M_1 talonid is about 15% wider than the M_2 talonid.

The M_2 trigonid is relatively well-preserved, but the occlusal surface of the talonid is broken away. A strong precingulid follows the base of the crown and terminates buccally of medial, below the paralophid. There is some damage to the occlusal surface of the paraconid, but it was strong and separate from the metaconid. It is confluent with a strong paralophid that extends

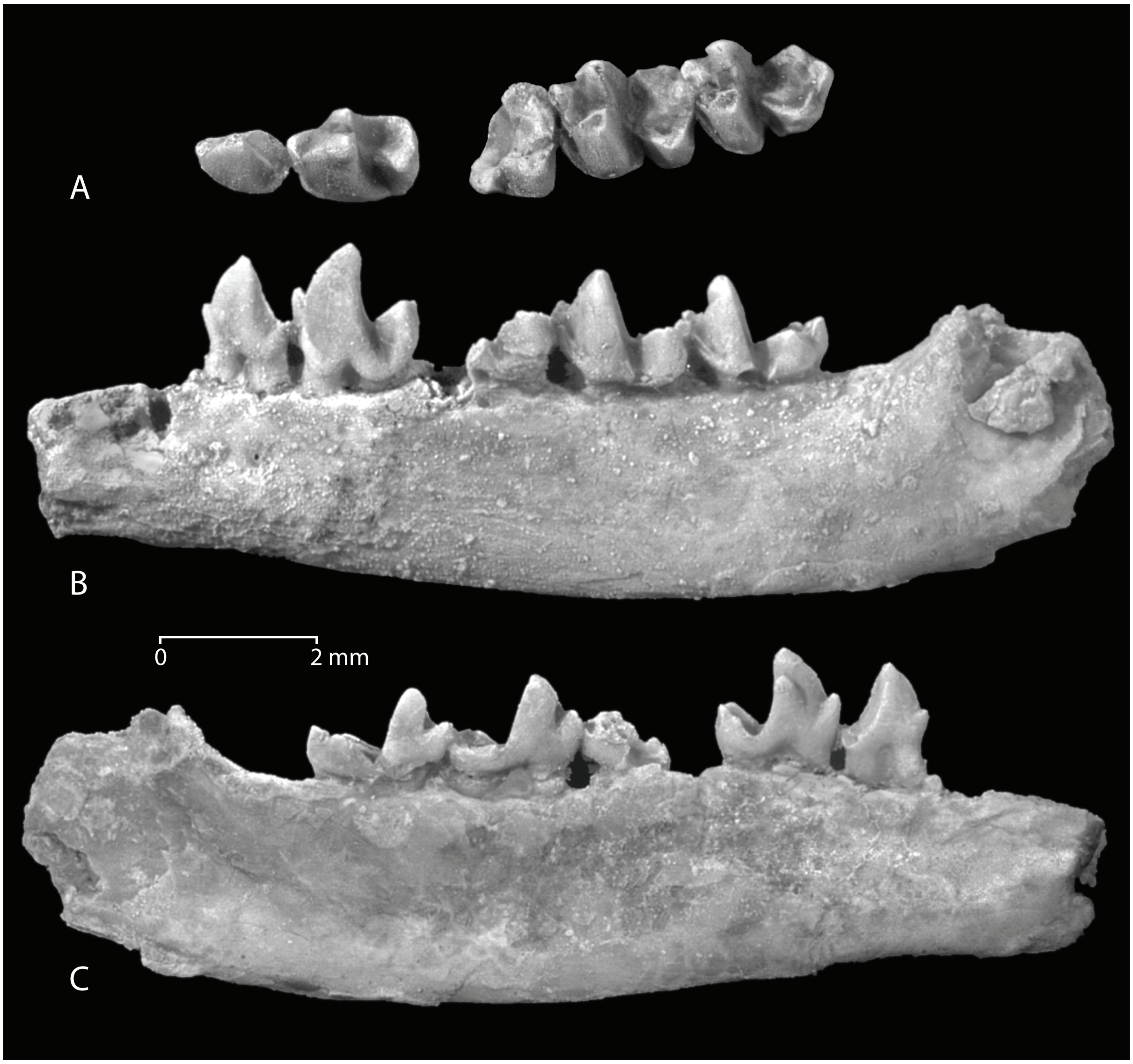


FIGURE 33 — Holotype of *Leptacodon acherontus* n. sp. (YPM-PU 19957) from Cedar Point Quarry. A-C, left dentary with P_3-P_4, $M_{2\text{-}3}$, and talonid of M_1 in occlusal (A), buccal (B), and lingual (C) views.

buccally and then weakens and ascends to the protocone apex. The paraconid is situated well below the other trigonid cusps. The protoconid and metaconid are subequal in size and height. A well-developed trigonid basin opens lingually. The cristid obliqua is mostly missing, but contacted the postvallid buccal of medial, slightly lingual of the protoconid apex.

The M_3 has a well-developed precingulid that follows the base of the crown and terminates buccally of medial, below the paralophid. The paralophid is largely broken away, but a strong one was present. The paraconid is large, well-separated from the metaconid, and situated below the other trigonid cusps. The metaconid appears to have been higher than the protoconid but the tip of the protoconid is missing. A well-developed trigonid basin opens lingually. The cristid obliqua contacts the postvallid near the midline, more lingually than in M_2. The M_3 talonid is heavily worn. The hypoconid is large and rounded. The entoconid and hypoconulid are well-developed and subequal in size. The hypoconulid is the most posterior cusp and is situated closer to the entoconid than the hypoconid. The hypoconulid and entoconid are separated by a small valley.

The dentary is moderately deep for a eutherian of this grade, with a depth below M_2 that is 172% of M_2 height. Three alveoli are preserved anterior to P_3, and probably held a single-rooted P_1 and double-rooted P_2.

Discussion.— Rose (1981a) referred 35 specimens from Cedar Point Quarry to *Mckennatherium* cf. *M. ladae*. He noted, however, that there may be as many as three species present in this sample. Rose reported that most specimens resembled *M.* cf. *M. ladae* from Rock Bench Quarry but that some resembled *Adunator* ("*Diacodon*") *minutus* from Princeton Quarry. Gingerich (1983a) later established "*Diacocherus*" *meizon*, based largely on a UM sample from Cedar Point Quarry, and included

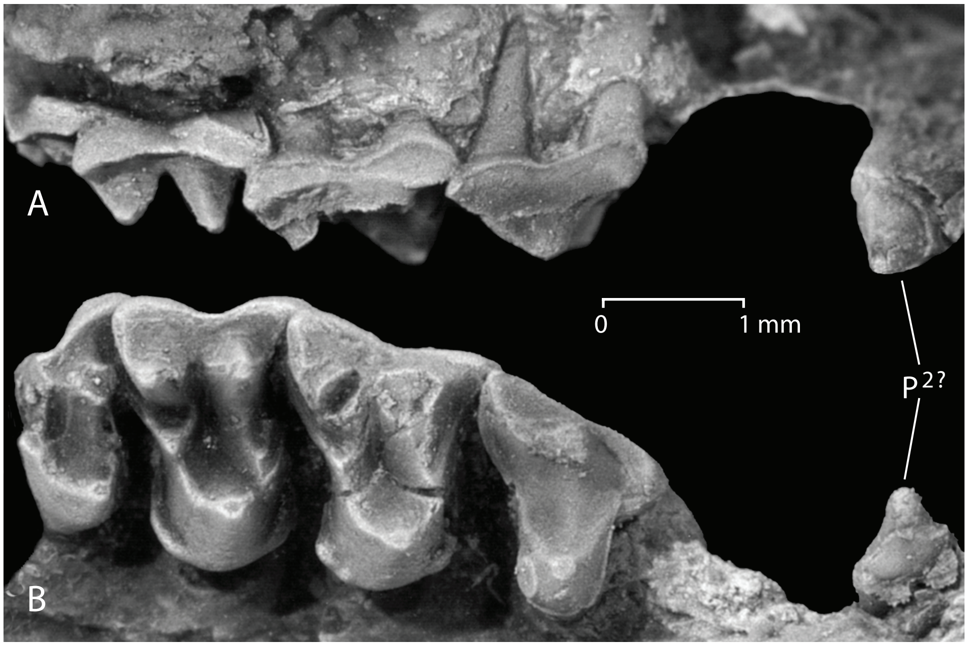


FIGURE 34 — Upper dentition of *Leptacodon packi* from Princeton Quarry. A–B, right maxilla with P^2?, P^4-M^3 (YPM-PU 14166) in buccal (A) and occlusal (B) views.

the YPM specimens referred by Rose. "*Diacocherus*" is here synonymized with *Adunator* (see *Adunator* above). Specimens in the YPM collections span a morphologic continuum from *A. meizon* to *Leptacodon acherontus*, making the species difficult to separate. It seems clear, however, that more than one species is present. The amount of morphologic variability in the Cedar Point Quarry collection is much greater than that exhibited by *A. minutus* at Princeton and Schaff Quarries. If the variability in *A. minutus* is comparable to that of *A. meizon*, which is a reasonable assumption, then there must be at least two species in the Cedar Point Quarry sample.

I distinguished *Leptacodon acherontus* from *Adunator meizon* based on the paraconid position in P_4 and $M_{2\text{-}3}$, on the development of the M_2 paraconid, on characteristics of P_4, and P_3, and on the relative size of molars. In particular, the M_2 paraconid in *Adunator* is reduced, anteroposteriorly compressed, and appressed to the metaconid (e.g., Krishtalka, 1976a; Novacek et al., 1985), while in *Leptacodon* the M_2 paraconid is more connate, better defined, and separate from the metaconid. M_2 is also larger than M_1 in most individuals of *Adunator* (Fig. 26). The specimens included in *Leptacodon acherontus* have distinct and separate M_2 paraconids, and M_2 is smaller than M_1 in YPM-PU 20811, which plots below the range in *A. meizon* (Fig. 26). Although only a partial M_1 talonid is preserved in the holotype of *L. acherontus*, it is approximately 15% wider than the M_2 talonid, suggesting that the holotype would have also plotted below equality. YPM-PU 18466 plots in the lower part of the range of *A. meizon* and is tentatively included in *L. acherontus*, although it could possibly belong to *A. meizon*, or even a third poorly represented species.

Leptacodon acherontus can also be quantitatively distinguished from *A. meizon* and *A. minutus* in having a longer M_3 with a more posterior hypoconulid. M_3/M_2 length ratios in *L. acherontus* exceed those in *A. meizon* and *A. minutus* in all but two specimens of *A. minutus* (YPM-PU 14118, 14439). Ratios range from 0.79-0.99 in *A. minutus* ($n = 17$), with a mean of 0.90±0.03 (±1.96 SE), from 0.82-0.96 in *A. meizon* ($n = 12$), with a mean of 0.89±0.03, and from 0.97-1.03 in *L. acherontus* ($n = 3$), with a mean of 1.00±0.02.

The P_3 in the holotype of *Leptacodon acherontus* is small, compared with P_4, and has a very short heel and relatively low paraconid. This contrasts with the P_3 in *A. meizon* (known only in the holotype and YPM-PU 20072), which is longer, more laterally compressed, and has a long posterior slope and longer heel. The P_3 in *Adunator abditus* n. sp. is also reduced relative to P_4, but is more elongate and narrower than that of *L. acherontus*. *Leptacodon acherontus* may also be slightly larger on average than *A. minutus*, but the type sample is small.

Referred specimens.— **Cedar Point Q.**: YPM-PU 18466, R dent., P_4-M_3; 19957 (holotype); 20811, R dent., P_4-M_3.

Leptacodon cf. *L. munusculum*

Leptacodon tener, Krishtalka, 1976b, p. 11.
Leptacodon munusculum, Krishtalka, 1976b, p. 11.
cf. *Leptacodon tener*, Rose, 1981a, p. 152.
cf. *Leptacodon munusculum*, Rose, 1981a, p. 152.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description.— Descriptions of *Leptacodon munusculum* were provided by Simpson (1935a; 1937b) and Krishtalka (1976b).

Discussion.— The holotype of *Leptacodon munusculum* (USNM 9819) is a fragmentary dentary preserving a somewhat damaged M_1 and M_3, from Gidley Quarry in the Crazy Mountains Basin, Montana. A second more complete dentary (AMNH

FIGURE 35 — Dentary of *Leptacodon packi* from Y2K Quarry. A–B, left P_2-M_3 (UM 109238) in buccal (A) and lingual (B) views. P_2 found in association.

35942) preserving P_4-M_3 from Gidley Quarry was later identified as *L. munusculum* by Krishtalka (1976b). Krishtalka also identified a single specimen from Cedar Point Quarry as *L. munusculum* (YPM-PU 20026), and two others as *L. tener*. Rose (1981a) later conferred eight specimens to *L. tener* and one to *L. munusculum* citing Krishtalka and communication with C. B. Wood, but expressing doubt as to the presence of more than one species. Krishtalka's identification of *L. munusculum* were based partly on comparison with the P_4 in AMNH 35942 from Gidley Quarry, which is distinguished from those of other species by a high degree of buccolingual compression and by talonid characters. The two specimens he referred to *L. tener*, however, consisted only of molars and were distinguished by details of the molar structure, with no discussion of variability of these features in other closely related species. There is no appreciable size difference in the *Leptacodon* specimens from Cedar Point Quarry, as noted by Rose (1981a), and many or all of the characters cited by Krishtalka appear to be variable in other species, such as *L. packi*. In the absence of more convincing evidence I consider these specimens to represent a single species near *L. munusculum*.

Referred specimens.— **Cedar Point Q.**: YPM-PU 14033, L dent. P_4-M_3; 14140, R P_3-M_3; 20026, R dent. P_4-M_2.

Leptacodon packi Jepsen, 1930b

Figures 34–35, Table 28

Leptacodon packi Jepsen, 1930b, p. 510. Krishtalka, 1976b, p. 13.
Cf. *Leptacodon* sp., Secord, 2002, p. 105.

Holotype.— YPM-PU 13296, a left dentary with P_4-M_3, from Princeton Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a) and *Plesiadapis simonsi* (Ti-5b) zones.

Description.— A description of the lower dentition of *Leptacodon packi* was given by Jepsen (1930b). Krishtalka (1976b) provided a photograph of YPM-PU 14140 (P_3-M_3) and a discussion of diagnostic characters.

Discussion.— The taxonomic position of *Leptacodon packi* has been questioned by numerous authors. McKenna (1960, p. 53) suggested that *L. packi* was a leptictid. Van Valen (1967p. 232) later placed the species in *Diacodon*, a leptictid. Krishtalka (1976b) placed *L. packi* back in *Leptacodon* but suggested that it may be more appropriately placed in *Nyctitherium*. Bown and Schankler (1982, p. 58) suggested that *L. packi* belonged in a group separate from *L. tener*, the type species for the genus. Despite the lack of agreement as to the taxonomic

TABLE 28 — Dental measurements for cf. *Leptacodon choristus* n. sp., *Leptacodon packi*, *L. packi*?, and *L. rosei*?, from Princeton (PQ), Schaff (SQ), Y2K, and Divide (DQ) quarries. *Estimate.

		Cf. *L. choristus*	*L. packi*							*L. packi*?			*L. rosei*?
		UM 80668 (type) DQ	YPM-PU 13296 (type) PQ	YPM-PU 14033 PQ	YPM-PU 14111 PQ	YPM-PU 14166 PQ	YPM-PU 14529 PQ	YPM-PU 19486 SQ	UM 109238 Y2K	YPM-PU 17668 PQ	YPM-PU 17809 PQ	YPM-PU 21196 SQ	YPM-PU 21198 SQ
P^2?	L	—	—	—	—	0.80	—	—	—	—	—	—	—
	W	—	—	—	—	0.45	—	—	—	—	—	—	—
P^4	L	—	—	—	—	1.36	—	—	—	—	—	—	—
	W	—	—	—	—	1.05	—	—	—	—	—	—	—
M^1	L	—	—	—	—	1.45	—	—	—	—	—	—	—
	W	—	—	—	—	1.77	—	—	—	—	—	—	—
M^2	L	—	—	—	—	1.30	—	—	—	—	—	—	—
	W	—	—	—	—	1.87	—	—	—	—	—	—	—
M^3	L	—	—	—	—	—	—	—	—	—	—	—	—
	W	—	—	—	—	1.45	—	—	—	—	—	—	—
P_2	L	—	—	—	—	—	—	0.95	—	—	—	—	0.97
	W	—	—	—	—	—	—	0.46	0.47	—	—	—	0.45
P_3	L	1.60	—	—	—	—	—	1.05	1.13	—	—	—	0.98
	W	0.86	—	—	—	—	—	0.64	0.56	—	—	—	0.54
P_4	L	1.66	1.31	1.45	1.43	—	—	1.20	1.28	1.45	—	—	—
	W	1.37	0.88	0.85	0.85	—	—	0.80	0.89	1.17	—	—	—
M_1	L	2.07	1.45	—	—	—	1.65	1.41	1.55	—	1.40	—	—
	W	1.73	0.99	—	1.13	—	0.98	1.05	0.98	—	1.32	—	—
M_2	L	1.97	1.43	1.55	1.50	—	1.50	1.40	1.42	1.45	1.42	1.40	—
	W	1.73	0.97	1.05	1.30	—	1.15	1.06	1.15	1.07	1.22	1.20	—
M_3	L	2.24	1.40	1.50	1.47	—	1.50	1.30	1.41	1.52	1.45	1.30	—
	W	1.67	0.98	0.9*	1.20	—	1.00	0.9*	0.96	1.05	1.15	0.90	—

position of *L. packi*, most subsequent workers have kept it in *Leptacodon*, as do I. A rigorous phylogenetic analysis of the genus is in order, but tangential to the focus of this study.

When Jepsen (1930b) described *Leptacodon packi* he included only the holotype in the species. Several additional specimens were subsequently collected at Princeton Quarry in the 1930s. In a comparison of the upper molar morphology of *L. packi*, Krishtalka (1973) considered YPM-PU 14166, a partial maxilla (Fig. 34), to be the upper dentition of *L. packi*. Krishtalka (1976b) later referred two additional dentaries from Princeton Quarry (YPM-PU 14033 and 14140) to the species but curiously did not include, nor mention YPM-PU 14166. YPM-PU 14166 is included here, and discussed below. An additional dentary was reported from Jepsen Valley Quarry (Schaff, 1985) but I have not seen this specimen.

YPM-PU 14033 and 21197 from Schaff Quarry, and UM 109238 from Y2K Quarry are very similar to the holotype of *L. packi*, and are easily within expected variability of the species. I have not seen YPM-PU 14140, but follow Krishtalka's identification. YPM 14111 and 14529, both from Princeton Quarry, probably also belong in *L. packi*, but are slightly more variable. The former has wider molars, relative to length, than in the holotype and the latter differs in having more rounded, less defined crests, and a less anteroposteriorly compressed M_3 trigonid. YPM-PU 17809 is still more variable, and has molars with rounded buccal corners, shallower hypoflexids, and lower crests, but could be a variant of *L. packi*. The holotype may be somewhat atypical for the species as it has sharper crests and talonids with more angular buccal corners than do most specimens.

The maxilla from Princeton Quarry (YPM-PU 14166; Fig. 34) appears to have lost its enamel from acid etching, presumable due to predation. The M_1 paracone and metacone are both broken, but an enamel-dentin junction is not visible. Furthermore, wear facets are absent on all teeth and the surfaces lack the luster typical of enamel. Enough general morphology is preserved, however, for comparison with the type species. The morphology of the upper dentition of *L. tener* was described in detail by McKenna (1968), although individual tooth measurements were not included. YPM-PU 14166 compares favorably with the holotype of *L. tener* in size and general morphology. Based on P^4-M^3 length, it is approximately equivalent in size to McKenna's reconstruction of *L. tener*. The P^4 in YPM-PU 14166 appears to have had no metacone, or a small metacone lost to etching. This contrasts with that in *L. tener*, which is large and distinct. The M^1 hypocone is quite small and there appears to have been no hypocone on M^2. This is similar to the condition in *L. tener*, which has tiny hypocones according to McKenna (1968). A small hypocone could have easily been lost on M^2 from etching. Both M^1 and M^2 clearly had strong conules, and pre- and postcingula that did not connect across the protocone. M^3 is notably smaller in *L. packi*, relative to M^2, than in *L. tener*.

Teeth in YPM-PU 14166 differ from those of *Leptacodon rosei* (Gingerich, 1987) in being generally smaller and less buccolingually elongate. The P^4 in *L. rosei* has a small metacone, which may have been comparable to that in YPM-PU 14166 before etching. The M^3 in *L. rosei* is larger relative to M^2, and M^1 and M^2 hypocones appear to be larger, but the hypocones in YPM-PU 14166 may have been significantly reduced from etching. Lower molars of *L. rosei* are on average wider and slightly smaller. The P_4 has a longer and wider talonid, and P_3 is lower and shorter, relative to P_4.

Referred specimens.— **Princeton Q.**: YPM-PU 13296 (holotype); 14033, L dent. P_4, $M_{2\text{-}3}$; 14111, R dent. P_4-M_1; 14140, R dent. P_3-M_3; 14166, R max. P^2?, P^4-M^3; 14529, R dent. $M_{1\text{-}3}$. **Schaff Q.**: YPM-PU 19486, R dent. P_2-M_3; 21197, L dent. **Y2K Q.** (SC389): UM 109238, L dent. P_2-M_3; 110020, R dent. P_4; 110944, L M^3.

Cf. **Leptacodon choristus**, new species

Figure 36, Table 28

Leptacodon n. sp., Secord et al., 2006, p. 228.

Holotype.— UM 80668, a right dentary with P_3-M_3, from Divide Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences.— *Plesiadapis churchilli* zone (Ti-4a).

Diagnosis.— Larger than all other described species of *Leptacodon*. Further differs from *L. proserpinae*, *L. munusculum*, *L. tener*, and *L. catulus* in having a considerably wider P_4, relative to length. Further differs from at least the last three species in having a paraconid higher on the crown. Further differs from *L. rosei* in having a much longer P_3 and a shorter P_4 talonid (relative to length). Further differs from *L. acherontus* n. sp. in having a longer P_3 with a larger paraconid, a broader, more exodaenodont P_4 with a shorter talonid, a larger P_4 paraconid with a higher apex, more angular molar hypoconids, and a longer M_3 talonid.

Etymology.— *Choristos* (G), separator: in reference to Divide Quarry, the type locality named after a divide or separation between drainages.

Description.— The P_3 has a prominent conical paraconid, moderately low on the crown, and lingual to the protoconid. The talonid has a single medial cusp and a small talonid basin anterior and lingual to the cusp.

P_4-M_3 are lingually canted, as is typical of eutherians of this grade. The P_4 has a large conical paraconid, situated moderately high on the crown, and slightly lower than the metaconid. It has a basined talonid and probably had two posterior cusps. The basin is situated on the lingual side of the crown and its width is equivalent to about 40% of the total width. The P_4 is strongly exodaenodont at the base of the postvallid.

The paraconids on $M_{1\text{-}3}$ are large and prominent, and separated from the metaconids by a deep troughs. Molar trigonid width is approximately equivalent to talonid width. The cristid obliqua on all molars contacts the postvallid at about one third of the trigonid width on the buccal side. It forms a weak ridge that continues up the postvallid toward the metaconid but terminates before reaching the trigonid notch. The distance between the metaconid apex and trigonid notch, relative to the equivalent distance in the protoconid, is approximately equal on M_1, but the metaconid becomes increasingly more dorsolingually extended on M_2 and M_3. Molar entoconids are higher than hypoconids. Hypoconulids are positioned lingually, close to the entoconids on $M_{1\text{-}2}$. The M_3 hypoconulid is slightly lingual of medial, and considerably more posterior than the entoconid forming a long pointed posterior extension.

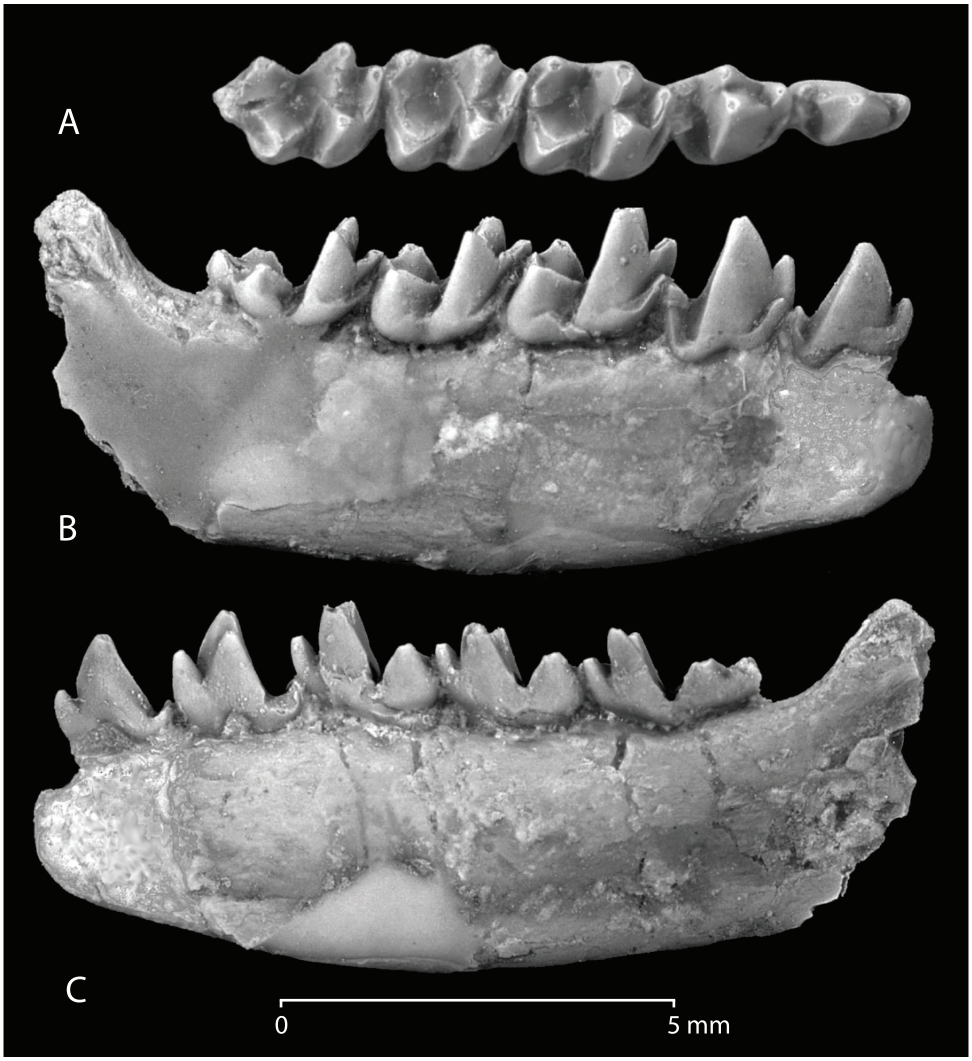


FIGURE 36 — Holotype of cf. *Leptacodon choristus* n. sp. from Divide Quarry. Right dentary with P_3-M_3 (UM 13360) in occlusal (A), buccal (B), and lingual (C) views.

The dentary is moderately deep for a therian of this grade, with a depth about 1.8 times the height of the M_1 trigonid.

Discussion.— My conferral of *Leptacodon choristus* to *Leptacodon* is based primarily on shared similarities with other species included in that genus: namely *L. packi*, *L. rosei*, and *L. acherontus* n. sp. However, it differs in important ways from *L. tener*, the the type species of *Leptacodon*, and may be more appropriately placed in a new genus. Notably, the inclusion of *L. packi* in *Leptacodon* has been questioned, as discussed in the *L. packi* section, and *L. acherontus* n. sp. may be more closely allied with cf. *L. choristus* than with *L. tener*. Nevertheless, a thorough revision of *Leptacodon* and closely related genera is beyond the scope of this monograph and I tentatively confer the Divide Quarry species to *Leptacodon*.

The P_4 in cf. *Leptacodon choristus* is considerably wider, relative to width, than in most species of *Leptacodon*. Although P_4 width in *Leptacodon* is highly variable, based on samples of *L. rosei* and *L. packi*, the degree of exodaenodonty in cf. *L. choristus* is probably outside that of most species. In the M_3 of *L. choristus*, the degree of metaconid elongation (distance from trigonid notch, see description above) is greater than in any other specimen of *Leptacodon* I have observed. This could be due in part to wear of the trigonid notch or the specimen could be an extreme variant. Nevertheless, the degree of elongation may be outside the variability in most species. The degree of metaconid elongation in M_2 is also high, but appears to be within the variation of *L. packi*. M_3 length and width, relative to M_2, are also high. M_3 dimensions are quite variable in other species, however, and additional specimens of cf. *L. choristus* are needed to determine if M_3 size is of diagnostic value.

Referred Specimen.— **Divide Q.**: UM 80668, R P_3-M_3.

Leptacodon rosei?

Figure 37, Table 28

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* zone (Ti-5a).

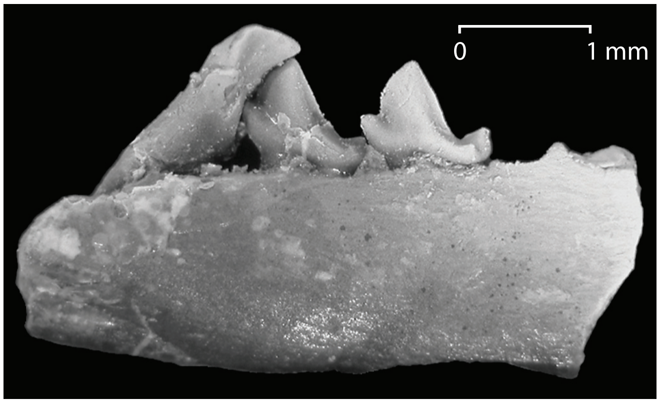


FIGURE 37 — Right dentary fragment (YPM-PU 21198) of *Leptacodon rosei*? with C_1, P_{2-3} in lingual view, from Schaff Quarry.

Description and discussion.— A single dentary fragment from Schaff Quarry appears to represent a second species of *Leptacodon* in the *Probathyopsis* zone. The P_2 and P_3 in YPM-PU 21198 are markedly different from those in specimens of *L. packi*, which have high, vertical protoconids (Fig. 37). Those in YPM-PU 21198 are low and convex along the anterior margin in lateral view. These premolars appear to be within the variation of *L. rosei*, which has similarly reduced P_{2-3}. The canine is very similar to that in UM 82389 of *L. rosei*. The canine for *L. packi* is not known. A confident identification cannot be made without more complete material.

Referred Specimen.— **Schaff Q.**: YPM-PU 21198, R dent. C_1, P_{2-3}.

Plagioctenodon sp.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis simonsi* zone (Ti-5b).

Description and discussion.— Several minute isolated teeth from Y2K Quarry most closely resemble those of specimens referred to cf. *Plagioctenodon krausae* by Rose (1981a) and Gingerich (1987) from the Clarkforkian. Bloch (2001) has included these and other specimens in an informal new species of *Plagioctenodon*. The hypodigm of the new species was not available for study. Comparison of the isolated teeth with UM 83931, included in the new species, suggests that there may be small differences between the Clarkforkian and the Y2K forms. However, more complete specimens are needed, as well as access to the hypodigm, before a more confident identification can be made.

Referred specimens.— **Y2K Q.** (SC389): UM 109346, L dent. frag. M_1 (tal.), M_2; 109663, L M_3; 109869, R P_3; 110021, R M_x.

Nyctitheriidae genus and species indet.

Discussion.— Krishtalka (1976b) described and figured a dentary (YPM-PU 14202) from Princeton Quarry preserving P_2, and P_4-M_3 as seemingly representing a new genus of nyctitheriid. He compared it to the lower dentition of *Pontifactor* and *Nyctitherium*. However, the specimen he considered to be *Pontifactor*, AMNH 15103, was later referred to cf. *Wyonycteris* by Gingerich (1987). In any case, based on his description and photographs YPM-PU 14202 does not appear to be a specimen of *W. galensis* n. sp. or of *Leptacodon packi*, and could represent a new genus. I have not seen this specimen.

Grandorder EUARCHONTA Waddell, 1999
Order ?DERMOPTERA (Illiger, 1811)
Family PLAGIOMENIDAE Matthew, 1918

Discussion.— MacPhee et al. (1989) argued against inclusion of Plagiomenidae in Dermoptera based on new cranial data. Many authors, however, have continued to questionably place plagiomenids in Dermoptera. Pending a rigorous phylogenetic analysis of these groups, I questionably place Cyriacotheriidae and Plagiomenidae in ?Dermoptera.

ELPIDOPHORUS Simpson, 1927

Elpidophorus elegans Simpson, 1927

Elpidophorus elegans Simpson, 1927, p. 5.

Holotype.— AMNH 15541, a right dentary with M_{1-2} and alveoli for P_{2-3}, and M_3; from a locality sometimes known as "Erickson's Landing" or "Red Deer River" in Alberta, Canada. The specimen was collected from a landslide.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description.— The holotype was adequately described by Simpson (1927).

Discussion.— UM 64565 was first identified as *Elpidophorus elegans* by Simons and Rose (1977) and later included in a faunal list for Cedar Point Quarry by Rose (1981a). It differs from the holotype in being slightly smaller, in having better developed cingulids, and in having a ridge on the internal face of the protocone in the trigonid basins. I attribute these differences to intraspecific variation, and follow the identification of previous authors. This is the only plagiomenid specimen known from Cedar Point Quarry, in spite of a sample size of nearly 2000 specimens (Appendix I-A).

Referred specimen.— **Cedar Point Q.**: UM 64565, L dent. M_{1-3}.

Cf. **Plagiomene zalmouti**, new species
Figure 38, Tables 29–30

Plagiomene n. sp., Secord et al., 2006, p. 229.

Holotype.— UM 108443, partial skull, left dentary, and associated postcrania. Upper dentition includes left C^1-M^3, alveoli for I^1 and I^3, and the root of I^2. The left dentary preserves C_1-M_3 and the roots of I_{1-3}. A partial crown of a right I_1 was found in association. The holotype was collected in SC-389 about 215 meters to the north of, and 4-5 meters stratigraphically below Y2K Quarry. It was preserved in a concretion that had weathered from gray siltstones and was broken into many pieces. No other fossils were found near the specimen.

Biostratigraphic occurrences.— *Plesiadapis simonsi* zone (Ti-5b).

Diagnosis.— Based on comparison with the hypodigm of *Plagiomene accola* and on numerous specimens of *P. multicuspis* in the UM collections, cf. *P. zalmouti* differs from species

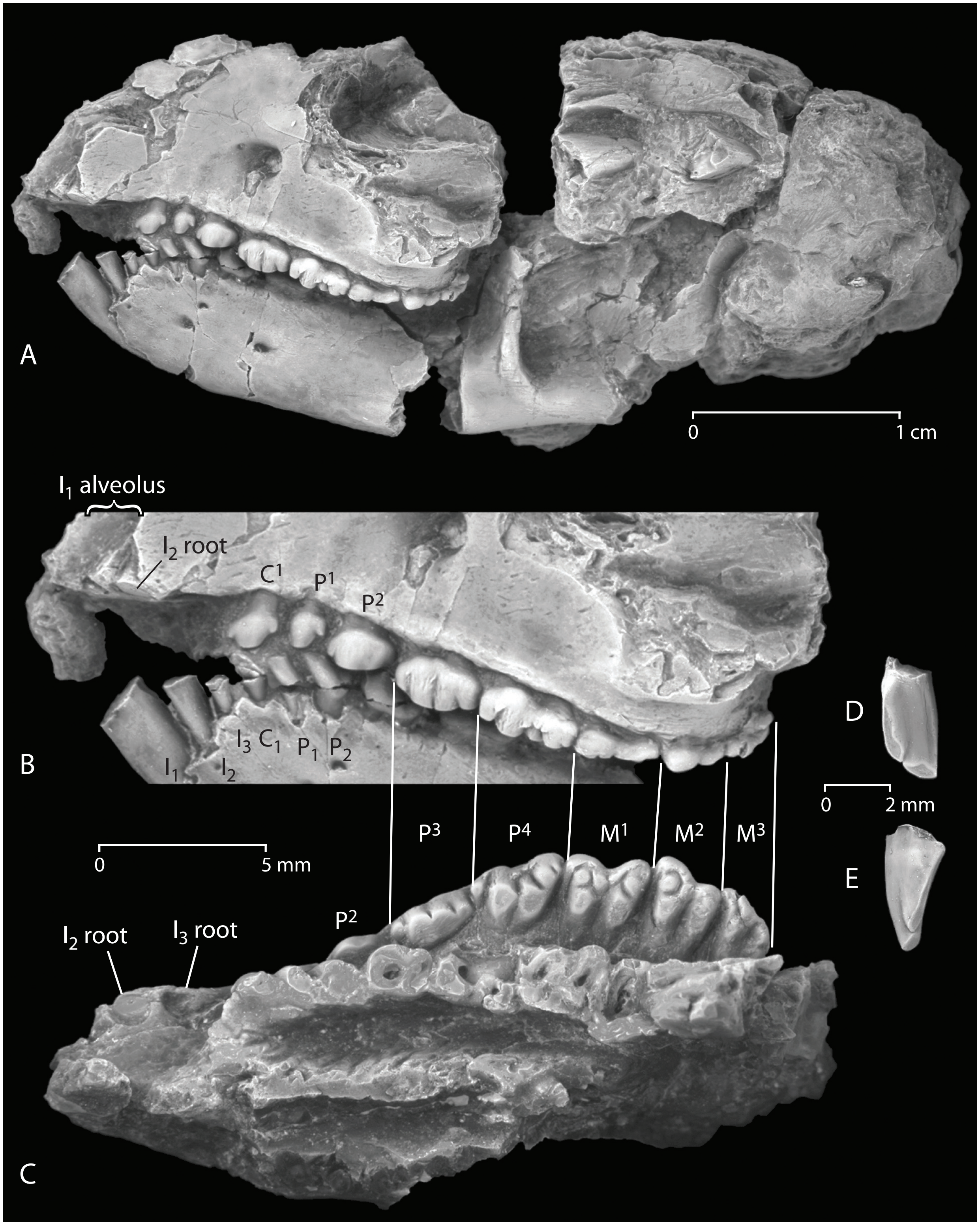


FIGURE 38 — Holotype of cf. *Plagiomene zalmouti* n. sp. (UM 108443). A, lateral view of partial skull and left dentary. B, buccal view of left C^1-M^3. C, partial occlusal views of P^2-M^3, lingual surfaces obscured. D-E, dorsal (D) and distal (E) views of associated R I_1.

TABLE 29 — Upper dental measurements for the holotype of cf. *Plagiomene zalmouti* n. sp., *P. accola*, and *Planetetherium mirabile* (cast). Measurements for P^4–M^1 of UM 98451 are from tooth impressions (molds) in concretion.

		Cf. *P. zalmouti*	*P. accola*		*P. mirabile*
		UM 108443 (type)	UM 98451	UM 71443 (type)	AMNH 22229
C^1	L	1.40	—	—	—
	W	—	—	—	—
P^1	L	1.15	—	—	—
	W	—	—	—	—
P^2	L	2.15	2.4	—	—
	W	—	1.5	—	—
P^3	L	2.65	3.3	—	—
	W	—	3.4	—	—
P^4	L	2.85	3.3	2.95	—
	W	—	—	4.45	—
M^1	L	2.55	2.8	2.70	2.30
	W	—	4.2	4.10	3.65
M^2	L	2.25	2.4	2.30	2.25
	W	—	3.6	3.55	3.30
M^3	L	1.85	2.2	—	—
	W	—	2.7	—	—

TABLE 30 — Lower dental measurements for the holotype of cf. *Plagiomene zalmouti* n. sp., *P. accola*, *Planetetherium mirabile* (casts), and *Elpidophorus elegans*. *Estimate. **Less reliable estimate.

		Cf. *P. zalmouti*	*P. accola*	*P. mirabile*		*E. elegans*
		UM 108443 (type)	UM 65636	AMNH 22162 (type)	AMNH 22205	UM 64565
Dent. D		5.80	6.5	—	—	—
I_1	W root	1.31	—	—	—	—
	D root	1.90	—	—	—	—
I_2	L root	1.03	—	—	—	—
	W root	1.02	—	—	—	—
I_3	L root	0.71	—	—	—	—
	W root	0.84	—	—	—	—
C_1	L root	0.82	—	—	—	—
	W root	0.88	—	—	—	—
C_1	L	1.3**	—	—	—	—
	W	0.80	—	—	—	—
P_1	L	1.2*	—	—	—	—
	W	0.90	—	—	—	—
P_2	L	1.7*	—	—	—	—
	W	1.15	—	—	—	—
P_3	L	2.2*	3.25	2.05	1.95	—
	W	1.60	1.95	1.35	1.65	—
P_4	L	3.0**	3.50	2.40	2.00	—
	W	2.10	2.80	2.00	2.20	—
M_1	L	2.6**	3.50	2.30	2.50	3.60
	W	2.20	2.95	2.25	2.55	3.10
M_2	L	2.6**	2.90	—	—	3.80
	W	—	2.70	—	—	3.30
M_3	L	2.2**	2.7*	—	—	4.50
	W	—	2.25	—	—	2.80

of *Plagiomene* in: (1) lacking twinned stylar cusps on the metastylar shelves of P^4-M^1; (2) having an anteroposteriorly shorter P^3, relative to M^1 length; (3) having a smaller, less prominent para- and metastyle on P^3; (4) having a shorter cheek tooth series (P_3-M_3) relative to the length of the anterior teeth (I_1-P_2 roots); and (5) having taller and equal entoconid and entoconulid cusps on M_3. It also appears to have a larger M_2 relative to M_1, but the teeth are not well enough exposed to be certain.

Cf. *Plagiomene zalmouti* differs further from *P. multicuspis* in: (6) being much smaller; (7) lacking large diastemata between C^1-P^1 and P^1-P^2; (8) having a relatively smaller C^1 and P^1; (9) having a larger I_1 (absolutely and relatively), with more mesiodistally constricted lobes; and (10) having a single-rooted, simpler P_2 with no paraconid.

Based on casts of *Planetetherium mirabile* from the type area at Bear Creek, cf. *Plagiomene zalmouti* differs from *Planetetherium* in having: (1) more buccolingually elongate upper molars, especially M^2; (2) a larger, better developed stylar area with well-defined twinned parastylar cusps on M^{1-2}; (3) a deeper ectoflexus on M^{1-2}; (4) a large diastema between I^3 and C^1; and (5) larger molars. The M_3 also appears to be larger, relative to M_2 than in *Planetetherium*. There may also be fewer anterior teeth in *Planetetherium*, as discussed below.

Based on comparison with numerous specimens from the type locality (SC-188) of *Worlandia inusitata*, cf. *Plagiomene zalmouti* differs from *Worlandia* in having: (1) much larger teeth: (2) smaller fourth premolars relative to first molars; (3) relatively smaller, less molariform third premolars; (4) a more triangular shaped P^4 with a well-developed metastylar wing; (5) more buccolingually elongate M^{1-2}; (6) a deeper ectoflexus on M^{1-2}; (7) eight antemolar lower teeth (as opposed to six); (8) a larger, more anteriorly projecting P_2; and (9) a closely positioned metaconid and paraconid on P_4 that are nearly equal in size and height.

Based on comparison with casts of AMNH 33856 and 55963 from Scaritt Quarry, cf. *Plagiomene zalmouti* differs from *Elpidophorus elegans* in having: (1) a more triangular shaped P^4 with a well-developed metastylar wing; (2) more anteriorly positioned molar protocones; (3) twinned stylar cusps on the parastylar wings of M^{1-2}; (4) more buccolingually elongate M^{1-2}; (5) a deeper ectoflexus on M^{1-2}; (6) absence of an ectoloph on upper molars; (7) a twinned entoconid and entoconulid on M_3 (and probably other molars); (8) a closely positioned metaconid and paraconid on P_4 that are nearly equal in size and height; and (9) much smaller teeth.

Etymology.— Named for Iyad S. Zalmout, who discovered the holotype, in recognition of his assistance with field work and his contributions to vertebrate paleontology.

Description.— The skull is crushed laterally. An infraorbital foramen is positioned above P^{2-3}. In the upper dentition, the crowns of C^1-M^3 are preserved, but all teeth are obscured to varying degrees by extremely hard matrix. The I^1 and I^3 alveoli and root of I^2 are preserved. C^1-P^1 are moderately worn while P^2-M^3 are more heavily worn. The I^1 alveolus is broken anteriorly, but the I^1 was clearly large, mesiodistally compressed, and slightly forward-facing. The I^2 root is nearly round and much smaller than the I^1 alveolus. The I^3 alveolus appears to be slightly smaller than the I^2 alveolus. There is a small diastema between the I^3 and C^1 alveoli, about 1 mm long.

C^1-P^1 have single roots and are separated by a small diastema, as are P^{1-2}. C^1 has a large central cusp, and small but distinct anterior and posterior cusps. The anterior cusp is situated relatively high on the crown. P^1 is slightly smaller than C^1, less laterally compressed, and has a rounded appearance. It has a large central cusp and a distinct posterior cusp. It lacks a distinct anterior cusp, and has only a very small anterior bulge. P^{2-4} also have a rounded appearance. The P^2 is much larger than P^1 and probably has two roots, although a division is not visible in the exposed area. The crown is heavily worn, but it probably had four bulbous, poorly defined cusps: two large central cusps, a small rounded anterior cusp (still present), and possibly a small elongate posterior cusp. P^3 has two visible buccal roots and, judging from the visible crown width, probably does not have a third lingual root. It has four bulbous cusps. The anterior cusp is low, rounded, and separate. The para- and metacones are subequal, closely appressed, large, and rounded. The posterior cusp is small and separate. The anterior and posterior cusps are more buccally situated than the middle cusps. P^4-M^3 are triple-rooted. P^4 is molariform. The paracone and metacone are subequal and buccolingually elongate, but less so than in the molars. There is no stylar shelf. There is a rounded, distinct parastyle. A large bulbous cusp is situated posterobuccally of the metacone on a metastylar wing and is incipiently divided into a smaller more buccally positioned cusp. An incipient buccal cingulum is positioned between the paracone and metacone. A narrow metacingulum is present. The P^4 almost certainly has a protocone, but this area of the tooth is obscured by the left dentary.

The M^1 is longer and wider than M^2. Both are transversely elongate and have transversely elongate para- and metacones. A moderately deep ectoflexus is present in both, and both have a well-developed paracingulum and narrower metacingulum. The paracingulum is continuous with a buccal cingulum that ends at the ectoflexus. Both molars have parastyles. Both also have a pair of twinned cusps positioned buccally of the paracone on the parastylar wing, that are round and equal in size. On M^1 there is a single large cusp positioned buccally of the metacone on the metastylar wing that may have had a smaller incipient cusp positioned buccally of it. The metastylar area is small and heavily worn on the M^2 and it is not clear if there were any distinct cusps positioned buccally of the metacone. There is progressively greater wear from M^1 to M^3 in the area lingual of the para- and metacones. The protocone is worn flat on M^1, is heavily worn on M^2, but still has considerable relief on M^3. Para- and metaconules are still visible on M^3 and almost certainly were present on all molars. There appear to have been two indistinct cusps on the parastylar wing of M^3, but the area is worn and fractured. A narrow paracingulum is present, but there is no metacingulum. The M^3 is the smallest molar.

In the lower dentition, the crowns of C_1-M_3 are preserved but are largely obscured. The roots of I_{1-3} are preserved. I_1-P_2 are single-rooted and P_3-M_3 are double-rooted. The I_1 was procumbent, much larger than the other incisors, and its root was moderately compressed mesiodistally. A partial crown of a right I_1 was found in association with the skull. An interstitial wear facet is present at the tip on the mesial surface. It is bilobed and has a large anterior cusp and a smaller, more proximally positioned lateral cusp on the distal margin of the crown. The dorsal surface is concave and the ventral one convex. The cusps are heavily worn but appear to have been relatively close together. I_2 has the most mesiodistally compressed root and was larger than I_3, which had a nearly round root. The C_1 root is rounded and slightly larger than the I_3 and P_1 roots. The crown is badly weathered, but appears to have been a single elongate, moderately procumbent cusp, like that of P_1. The P_2 is larger than the P_1 and is bilobed. The anterior cusp is moderately procumbent and elongate, much like the P_1 cusp, and the posterior cusp is smaller and lower. P_3 is much larger than P_2 and also appears to be bilobed. The anterior cusp is large and bulbous, and the posterior one is smaller and probably formed a heel. P_4 is largely obscured but was clearly molariform. Exposure along the lingual margin shows that the paraconid is supported by a large column and is about the same height as the metaconid, but moderately smaller. M_2 is the largest (at least in length) molar. The talonid of M_3 is exposed along the lingual margin revealing a twinned entoconid and entoconulid consisting of two tall cusps of equal size and height.

Three mental foramina are present in the dentary. The most anterior one is below P_2, followed by a slightly smaller one that is higher on the dentary below the P_{2-3} junction. The last is centered below P_4.

Several hand or foot elements are preserved in fragments of the same concretion that contained the holotype. There is no evidence to indicate the presence of any other mammal species or of another individual of cf. *Plagiomene zalmouti* at the type locality. Hence, the associated postcrania probably belong to the same individual as the holotype. The postcrania have not fully been prepared.

Discussion.— The holotype clearly represents a new plagiomenid species but assignment to *Plagiomene* is less certain. Although aspects of the upper dentition suggest affinities to *Plagiomene*, the lower dentition appears to be proportionately more similar to *Planetetherium*. A detailed comparison of dental morphology is not possible because teeth are encased in matrix that is equal in hardness to the enamel, which is degraded in places. The dentary was accidentally broken from the skull during preparation allowing a limited cross-sectional view of many lower teeth. It has not been possible to separate the occlusal surfaces of the upper and lower teeth. Nevertheless, a meaningful comparison can still be made based on exposed elements and proportions.

Features in the upper dentition shared with *Plagiomene*, such as twinned parastylar cusps and the transverse elongation of molars, appear to be derived characters in *Plagiomene* relative to older forms such as *Elpidophorus* and *Eudaemonema*. The lower cheek tooth series from P_3-M_3, is shorter, however, relative to the size of the more anterior teeth (or roots) than in species of *Plagiomene*. This is probably a primitive condition. The interesting mix of characters in the holotype suggests that it may belong in a new genus. However, without being able to make a detailed comparison of dental morphology the creation of a new genus may be unwise. Thus, I confer this species to *Plagiomene* based on assumed derivations shared in upper molars.

Among species of *Plagiomene*, cf. *P. zalmouti* is closest both morphologically and temporally to *P. accola*. The P^2 of *P. accola* has four outer cusps but no protocone, based on UM 98451, discovered after Rose's (1981a) description of the species. The para- and metacones are closely appressed and the styles are separate and distinct. The P^2 of cf. *P. zalmouti* is 10% shorter and differs further in having an indistinct parastyle and probably a less distinct metastyle if teeth were unworn. The central cones are too worn for adequate comparison. Although the P^2 of cf. *P. zalmouti* is shorter in absolute length than in *P. accola*, it is longer relative to P^3 length (P^2/P^3 lengths = 0.81, 0.73, respectively).

The P^3 of *Plagiomene accola* (UM 98451) is molariform in that it has para- and metacones, para- and metastyles, and possibly a small paraconule. The P^3 in cf. *P. zalmouti* is 20% shorter than in UM 98451 and the parastyle is smaller and not nearly as well-developed. The separation between the para- and metacones is also less distinct and the tooth is generally more rounded. The inner part of the tooth is obscured. The length of the P^3 relative to M^1 is about 15% less than in *P. accola* (P^3/M^1 lengths = 1.04, 1.18, respectively), resulting from a greater degree of molarization in the latter. This probably corresponds to a smaller P^3 protocone in cf. *P. zalmouti*, but this part of the tooth is obscured.

Teeth anterior to P^2 are not known for *Plagiomene accola*, but are known for the closely related but more progressive *P. multicuspis* of Wasatchian age. UM 76731, is a rostrum preserving C^1-P^3, and a partial M^1. There are large diastemata between C^1-P^1, and $P^{1\text{-}2}$, which contrast with much smaller diastemata in cf. *P. zalmouti*. The P^2 in *P. multicuspis* (UM 76731) shows a greater degree of molarization than in *P. accola* (UM 98451). The para- and metacones are more separate in *P. multicuspis* and the P^2 is about 8% longer relative to M^1 length. The P^3 of *P. multicuspis* is more molariform than in *P. accola* in that is has a larger protocone, more separated from the outer cusps, and a large metaconule (this area is obscured by matrix in UM 98451). Proportionally, however, the P^3/M^1 length ratios are about the same (1.14, 1.17, respectively).

The development of distinctive twinned stylar cusps in the parastylar and metastylar regions of $M^{1\text{-}2}$, and the metastylar region of P^4, are important synapomorphies in *Plagiomene accola* and *P. multicuspis* (e.g., Rose and Simons, 1977; Rose, 1981a). A similar condition is found in molars of *Worlandia* and *Planetetherium*, but these cusps are smaller, less distinct, and more variable in number. The development of distinctive twinned stylar cusps in the $M^{1\text{-}2}$ parastylar regions of cf. *P. zalmouti* is an important derived condition shared with species of *Plagiomene*. Unlike these species, however, cf. *P. zalmouti* lacks twinned stylar cusps in the parastylar region of P^4 and in the metastylar regions of $M^{1\text{-}2}$. The variability of these cusps cannot, or course, be assessed in cf. *P. zalmouti*, and upper molars of *P. accola* are known only from the holotype and UM 98451. Numerous upper dentitions of *P. multicuspis* are present in the UM collections, however, and they show almost no variability in the development of twinned stylar cusps in these positions. Of four M^1s and eight P^4s, all but one tooth have distinct twinned cusps in both the para- and metastylar regions. UM 68897 is the only exception and it has a single incipiently divided stylar cusp in the parastylar region of M^2, but the usual twinned cusps in the metastylar region.

Plagiomene accola is less derived, based on the holotype, than *P. multicuspis* in that it lacks twinned cusps in the parastylar region of P^4; but twins are present in both stylar regions of M^1 and in the parastylar region of M^2. The metastylar region in M^2 has two cusps, but one is incipiently developed. The only other upper molars known of *P. accola* are in UM 98451, which preserves part of M^2 and M^3. The metastylar area in the M^2 has distinct twinned cusps, demonstrating some variability in this feature. The development of twinned stylar cusps in cf. *P. zalmouti*, *P. accola*, and *P. multicuspis* occurs in a progressive temporal series, and corresponds to molarization of premolars. In the UM sample of *P. multicuspis* from the northern Bighorn Basin, none of six P^3s has twinned stylar cusps. A composite specimen figured by Rose and Simons (1977, YPM-PU 13272), however, has twinned para- and metastylar P^3 cusps. It is from the central Bighorn Basin and may be slightly younger in age, representing an even more progressive form, or could be an example of interpopulational variability in the species.

Teeth anterior to P_3 are not known in *P. accola*, but UM 71447 preserves roots of most or all anterior teeth. Rose (1981a) thought that all roots anterior to P_4 were present in UM 71447, but as he noted, the right dentary is in two pieces that do not fit together perfectly, and it is possible that a root is missing. In either case, the P_2 was probably single-rooted (contrary to Rose). Eight roots are preserved anterior to P_4, and P_3 was definitely double-rooted, so if all roots are present, P_2 would have to be single-rooted if *P. accola* retained the primitive formula of 3.1.4.3. It almost certainly did, given that the younger *P. multicuspis* retains this complement. Alternatively, P_2 could have been double-rooted if an additional root is missing in the break between dentary parts. If this were the case, however, the anterior root of P_2 would be larger than the posterior one, which would be highly unusual. The anterior root of P_2 in *P. multicuspis* is considerably smaller than the posterior one, as is the case in many mammals of this grade. Thus, *P. accola* probably had a single P_2 root, as does cf. *P. zalmouti*, and the double-rooted condition was developed later in *P. multicuspis*.

The number, size, and position of roots anterior to P_3 in cf. *Plagiomene zalmouti* is similar to that of *P. accola* (UM 71447). However, the posterior tooth row from P_3-M_3 is 15-20% longer in *P. accola*. The increase in the size of molars, relative to anterior teeth, appears to be a derived condition in *P. accola* shared with *P. multicuspis*.

Rose (1982) referred several lower incisors from Bear Creek to *Planetetherium mirabile*, based on their resemblance to the I_1 of *Worlandia inusitata* in UM 73788. Two of these, AMNH 22152 and 22153, were figured by Szalay (1972, Figs. 1-9) and by Simpson (1928, Fig. 12B), respectively. The partial incisor associated with the holotype of cf. *P. zalmouti* is indistinguishable from AMNH 22152, figured by Szalay, as far as can be compared. The lobes of these incisors are more restricted than those of *Plagiomene multicuspis*, which flare mesiodistally (see Rose, 1982), but are labiolingually shallower. The associated I_1 of *P. zalmouti* is larger than that of *P. multicuspis*, in spite of having smaller molars. This is consistent with the size of the I_1 root in *P. zalmouti*, which is larger than in *P. multicuspis* relative to the other incisor roots. The I_1 condition distinguishes cf. *P. zalmouti* from *P. multicuspis*, which presumably represents the derived form. The I_1 of *P. accola* is not known, but based on the root in UM 71447 it was larger than in *P. multicuspis*.

The P_4-M_2 series in cf. *Plagiomene zalmouti* is about 3-6% longer, than in *Planetetherium mirabile* (AMNH 22206; YPM-PU 17711) and about 15% shorter than in UM 65636 of *P. accola*. However, the length of P^4-M^2 is only 4% longer than in the holotype of *P. accola* (UM 71443). This suggests that the holotype of *P. accola* is from a small individual. Rose and Simons (1977) noted a high degree of size variability in *P. multicuspis* and size differences of 10% or more may not be meaningful when based on isolated specimens. Dental proportions are more useful. The M_2 in cf. *P. zalmouti* appears to be larger or equal in size to the M_1, which is similar to the proportions in *Planetetherium* and *Elpidophorus*. Precise measurement of these teeth is not possible but if M_2 is equal in size or larger than M_1 it is an important distinction between cf. *P. zalmouti* and species of *Plagiomene*, which have molars that decrease in size posteriorly.

A partial maxilla of *Planetetherium mirabile* preserving P^3-M^1 and five anterior alveoli was figured by Szalay (1969). The P^2 was almost certainly double-rooted, based on the relative sizes and orientations of the posterior two roots and the double-rooted condition in closely related species. The remaining three alveoli probably were for single-rooted teeth. It is improbable that any of these anterior teeth were double-rooted, because the general trend in late Paleocene plagiomenids is the addition of roots; but all younger forms have only single-rooted teeth anterior to P^2. Assuming teeth anterior to P^2 were single-rooted, there was no diastema between I^1 and C^1, as there is in cf. *Plagiomene zalmouti*.

Bown and Rose (1979) thought that the lower anterior dentition of *Planetetherium* probably had only six antemolar teeth, compared with the full complement of eight in *Plagiomene*. They based their conclusion on the holotype of *Planetetherium*, noting that it has three definite alveoli in front of P_3 and possibly a larger fourth alveolus where the jaw is broken. If the large alveolus is for I_1, as in other plagiomenids, then *Planetetherium* has two fewer teeth than *Plagiomene*. They also noted that the position of the symphyseal scar suggested that the fourth alveolus was the most anterior. They X-rayed the jaw and found that the third alveolus was anteriorly inclined and the second was only slightly inclined, similar to the anterior dentition in *Worlandia*, which also has only six antemolar teeth. If their supposition is correct, this is an important distinction between *Planetetherium* and cf. *P. zalmouti* that had eight antemolar lower teeth.

The holotype represents the only known plagiomenid of late Tiffanian age. It was found only 215 meters from Y2K Quarry, in a similar lithology (shaley mudstone). In spite of this, no teeth of cf. *Plagiomene zalmouti* have been identified at the quarry. Its absence there and at nearby Princeton and Schaff quarries leaves no doubt that cf. *P. zalmouti* lived in a habitat rarely sampled in the floodplain deposits of the Bighorn Basin.

Family CYRIACOTHERIIDAE Rose and Krause, 1982

Discussion.— Cyriacotheriidae was initially placed in Pantodonta by Rose and Krause (1982). They noted many similarities to Dermoptera (including Plagiomenidae) but concluded that the similarities were the result of dietary convergence. Lucas (1998), however, argued that cyriacotheriids shared more derived characters with Dermoptera (including Plagiomenidae) than with the Pantodonta, and were best allied with the former.

CYRIACOTHERIUM Rose and Krause, 1982

Cyriacotherium argyreum Rose and Krause, 1982

Cyriacotherium argyreum Rose and Krause, 1982, p. 28.

Holotype.— YPM-PU 18821, crushed snout with left P^1 (partial), P^2, right $P^{2\text{-}3}$, $M^{2\text{-}3}$, alveoli for left and right $I^{1\text{-}3}$, C^1, left P^4, right P^4-M^1, "Brice Canyon" locality, Sec. 8, T57N, R100W, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b), *Probathyopsis* (Ti-5a), *Plesiadapis simonsi* (Ti-5b), and Rodentia (Cf-1) zones.

Description.— A detailed description of *Cyriacotherium argyreum* was provided by Rose and Krause (1982).

Discussion.— Rose and Krause (1982) reported that the holotype and all referred specimens of *Cyriacotherium argyreum* were from the *Plesiadapis simonsi* zone. The *Plesiadapis simonsi* zone was thought at the time to extend below the Princeton Quarry level, but was recently restricted to a narrow interval above Princeton Quarry (Gingerich, 2001; Secord et al., 2006). The holotype is from "Brice Canyon," a Princeton University locality on the west side of Polecat Bench. This locality has not been precisely tied into measured sections, but based on structural tends in the area (Fig. 14, Gingerich, 1976) it probably lies below Princeton Quarry near the boundary between the *Probathyopsis* and *Phenacolemur* zones. Rose and Krause (1982) did not provide locality data for referred specimens, but based on revised biostratigraphy, some are from the *Phenacolemur* zone (e.g., YPM-PU 17847, UM 69239, 73586) and the early Clarkforkian (UM 73334, 73345).

I have not examined all the specimens in the YPM collection referred to *Cyriacotherium argyreum* by Rose and Krause (1982), but provisionally follow their identifications. Specimens in the UM collections from the *Phenacolemur* zone are very fragmentary, but agree with teeth of *C. argyreum* in size and form, with the exception of UM 77195 from Croc Tooth Quarry, included in *C.* cf. *C. argyreum* below.

Measurements of important specimens were provided by Rose and Krause (1982).

Referred specimens.— **Fossil Hollow** (SC198): UM 79873, L M^x partial; YPM-PU 17847, L M^1 or M^2, assoc. upper and lower frags. **Croc Tooth Q.** (FG028): YPM-PU 25033, L M_1 or

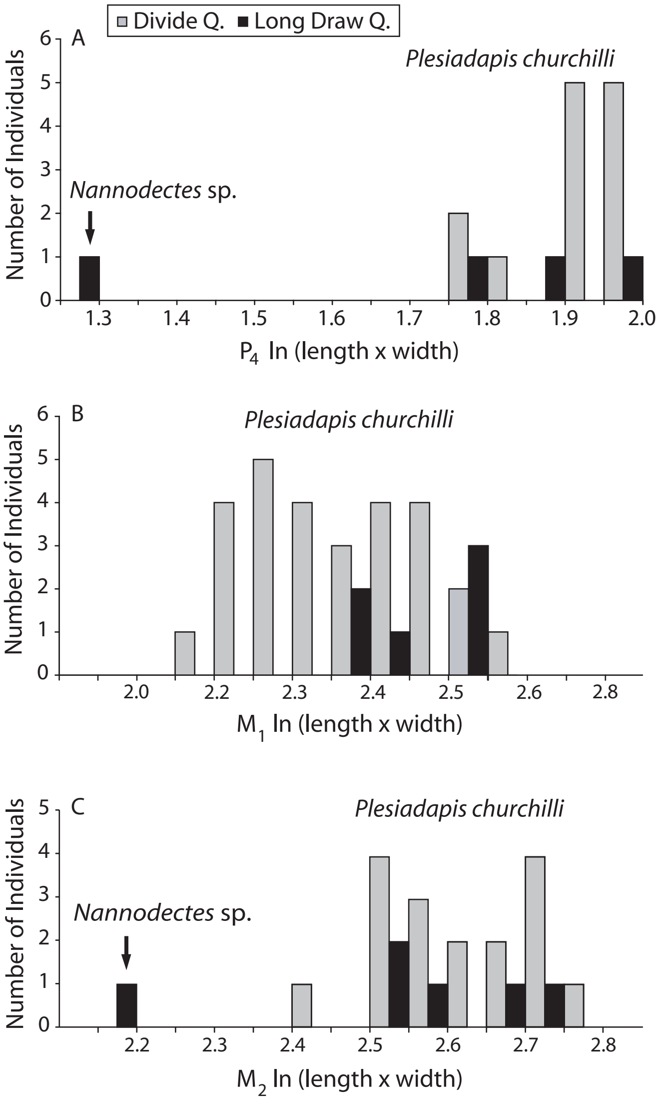


FIGURE 39 — Histograms of P_4 and M_2 tooth area in *Nannodectes* sp. and P_4, M_1, and M_2 tooth area in *Plesiadapis churchilli*, from Divide (gray bars) and Long Draw (black bars) quarries. Most data for Long Draw Quarry courtesy of P. D. Gingerich.

M_2. **SC144**: UM 63306, L max. M^2 frag., M^3 and assoc. frags. **SC257**: UM 73334, R dent. P_4. **SC258**: UM 73345, L M_x tri. **SC271**: UM 73586, R dent. M_1? partial. **SC275**: UM 73670, palate L I^{1-3}, P^4-M^2, R P^2-C^1.

Additional specimens referred by Rose and Krause (1982): YPM-PU 17311, L dent. P_2, R dent. P_2, dP_4; 18264, L dent. P_3, assoc. tooth frags; 18726, L dent. P_1-M_3, R dent. P_2, P_4; 18822, L max. M^{1-2}, I^1 frag, R max. P^{2-3}, M^{1-2}; L dent. P_{2-3}, R P_3; 18823, palate with L dP^3, P^4-M^2, R P^4-M^3, partial L P^{1-2}, M^3, and R dP^3? 18923, R max. M^{2-3}; 19059, R dent. P_{3-4}, M_3; 19060, dent. P_3; 19061, L P^3.

Cyriacotherium cf. *C. argyreum*

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Description and discussion.— UM 77195 is from Croc Tooth Quarry in the *Phenacolemur* zone and is considerably smaller than premolars of *Cyriacotherium argyreum*, if the tooth position is correctly identified as P^3 or P^4. The buccal edge is broken away, precluding precise measurement; but it is about the size of P^3 and P^4 in *C. psamminum*, which are 25-30% smaller than those in *C. argyreum* (Rose and Krause, 1982). An older specimen (UM 85441) from Divide Quarry in the *Plesiadapis churchilli* zone is a partial M_3 that is comparable in size to *C. argyreum* molars (talonid width = 6.0 mm), but may differ in having a better-developed anterior cingulid and entoconid. These specimens are too fragmentary for confident referral to *C. argyreum*.

Rose and Krause (1982) included YPM-PU 17819 from the Sand Draw Anthills in *Cyriacotherium* cf. *C. argyreum*, along with specimens from localities in Alberta correlative to the *Plesiadapis churchilli* zone. The Sand Draw Anthills may be slightly younger and are probably correlative to the *Phenacolemur* zone. I have not studied YPM-PU 17819, but it was tentatively identified as a dP^2 by Rose and Krause, who noted that it is nearly as molariform as the P^4 of *C. argyreum*, but was closer to the size of P^2. I tentatively include it here.

Referred specimens.— **Croc Tooth Q.**: UM 77195, L P^3 or P^4. **Divide Q.**: UM 85441, L M_3, partial. **Sand Draw Anthills**: YPM-PU 17819, dP^2?.

Order PRIMATES Linnaeus, 1758
Family PLESIADAPIDAE Trouessart, 1897

NANNODECTES Gingerich, 1975

Nannodectes sp.

Figures 39A,C

Description.— Descriptions of *Nannodectes simpsoni* were provided by Gazin (1956b) and Gingerich (1976). Descriptions of *Nannodectes gidleyi* were provided by Simpson (1935c,d) and Gingerich (1976).

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Discussion.— A right P_4 (YPM-PU 25016) and a left M_2 (YPM-PU 25015) from Long Draw Quarry most closely approximate teeth of *Nannodectes simpsoni* in size and morphology. The teeth are also similar to those of *N. gidleyi*. The P_4 is well below the size range of any known species of *Plesiadapis*. The M_2 falls in the extreme low end of the size range of *P. rex*, *P. fodinatus*, and *P. dubius*, but is well below the expected range of the contemporaneous *P. churchilli* (Figs. 39A,C). The P_4 differs further from those of *P. churchilli*, and older species of *Plesiadapis*, in being more anteroposteriorly elongate and in having a wider, more basined talonid.

Nannodectes gidleyi is distinguished from *N. simpsoni* primarily by its larger size and loss of the lower canine (Gingerich, 1976). The P_4 is within the size range of *N. simpsoni* reported by Gingerich (1976) and just below that of *N. gidleyi*. The M_2 is within the size range of both species. The depth and width of the P_4 talonid is most similar to that of *N. simpsoni* (USNM 20745; cast), which has a shallower and narrower basin than that of *N. gidleyi* (AMNH 17174, 17389; casts).

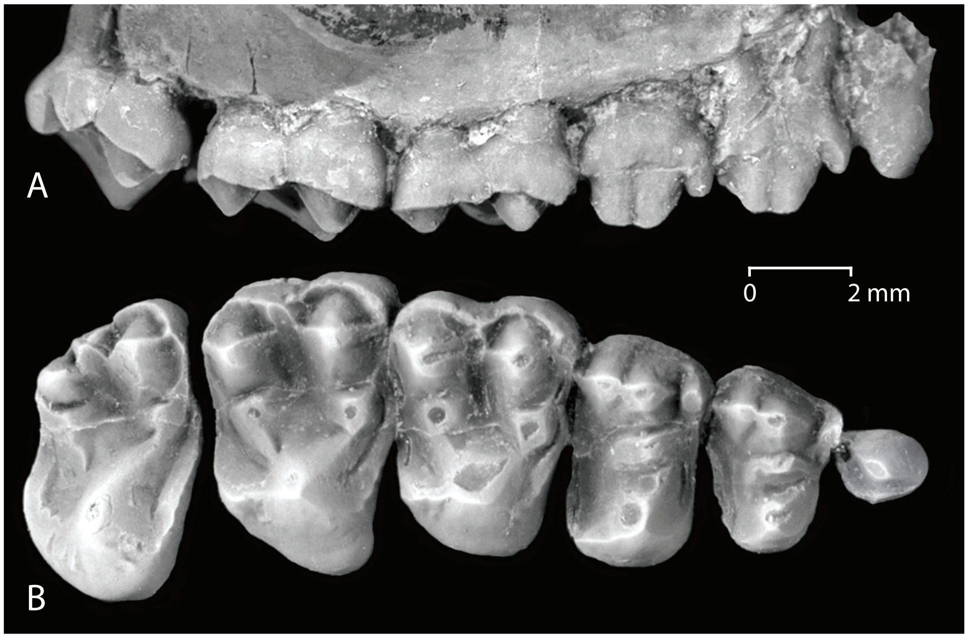


FIGURE 40 — Right maxilla (UM 83236) of *Plesiadapis churchilli* from Divide Quarry with P^2-M^3 in buccal (A) and occlusal (B) views.

Although these teeth most closely resemble *N. simpsoni*, I refrain from making a specific identification until more complete specimens are known.

These specimens represent the first record of *Nannodectes* in northern Wyoming.

Dental measurements (mm).— YPM 25016: P_4, L = 2.00, W = 1.79. YPM 25015: M_2, L = 3.10, W = 2.90.

Referred specimens.— **Long Draw Q.**: YPM 25015, L M_2; 25016 R P_4.

PLESIADAPIS Gervais, 1877

Plesiadapis anceps Simpson, 1936

Plesiadapis anceps Simpson, 1936, p. 19. Gingerich, 1976, p. 26.

Holotype.— AMNH 33822, left dentary with I_1, $M_{1\text{-}3}$, associated P_4, and maxillae with P^4, $M^{1\text{-}2}$, from Scarritt Quarry, Crazy Mountains Basin, Montana.

Biostratigraphic occurrences in Bighorn Basin.— ?*Plesiadapis anceps* zone (Ti-2).

Description.— A detailed description of *Plesiadapis anceps* was provided by Gingerich (1976).

Discussion.— A single dentary of *Plesiadapis* was collected by Princeton University crews, and later identified by Gingerich (1976) as *P. anceps*. I have not seen this specimen but tentatively follow his identification. This is the only specimen of *P. anceps* known from the Clarks Fork Basin and the only evidence for the presence of the *Plesiadapis anceps* zone. Gingerich reported that the specimen was collected in Sec. 2, T56N, R99W, approximately 500 feet (152 m) above Rock Bench Quarry. This would place it at about 170 m in the new South Bench Section (Fig. 6). I have prospected exposures at this level in Sec. 2, however, and found no indication of fossils. The first fossiliferous strata up and down section from this level are near the top of SC-263 in the *Plesiadapis rex* zone, and in the chert conglomerate at the base of the Silver Coulee beds (CC "member," Fig. 6), respectively. SC-263 should be too young to contain *P. anceps*. Thus, it may be more likely that YPM-PU 17816 came from the chert conglomerate.

Referred Specimen.— YPM-PU 17816, R dent. P_4-M_3.

Plesiadapis rex (Gidley, 1923)

Tetonius rex Gidley, 1923, p. 11.
Plesiadapis rex, Simpson, 1937b, p. 167. Gingerich, 1976, p. 27.

Holotype.— USNM 9828, a left M_2 from Locality 13, Crazy Mountains Basin, Montana.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description.— Detailed dental descriptions were provided by Gingerich (1976).

Discussion.— The morphology and variability in *Plesiadapis rex* was described by Gingerich (1976) who studied a large sample from Cedar Point Quarry. The specimens Gingerich studied are now curated at YPM. Additional specimens collected by UM crews from Cedar Point Quarry are listed below.

No definite occurrences of *Plesiadapis rex* are known from localities around Polecat Bench. Isolated teeth in UM 109619 and UM 73423, however, are within the variation and size range of both *P. rex* and *P. churchilli*, and could be teeth of either species. These specimens come from the lowest UM localities of Tiffanian age on Polecat Bench (SC-263 and SC-412). Most dimensions in these specimens are closest to the means for *P. churchilli* (Table 31), although the width of the P_3 in UM 73423 is at the mean for *P. rex* reported by Gingerich (1976). Larger samples are needed for a confident identification.

Dental measurements (mm).— UM 73423: P_3, L = 2.35, W = 2.01. UM 109619: L M^1, L = 3.35.

Referred specimens.— **Cedar Point Q.**: UM 64402, R dent. M_{1-2}; 63110, isolated teeth; 64404, L dent. P_3-M_1; 64406, L dent. P_4-M_2; 64409, L dent.; 64410, R dent. P_3-M_3; 64414, L dent. P_4-M_3; 64419, R dent. P_3-M_2; 64452, R dent.; 64453, R dent. M_2; 64454, L dent. I_1; 64455, R dent. M_{1-2}; 64456, R dent. P_4-M_3; 64457, R dent. P_4-M_3; 64502, R dent. M_{2-3}; 64507, R max.; 64514, R dent. P_4-M_2; 64519, L dent. I_1, P_3-M_3; 64520, R dent. P_3-M_3; 64521, R dent. I_1, P_3-M_3; 64524, L dent. M_2; 64525, isolated teeth; 64557, R dent. M_{1-2}; 64560, L max. P_3-M_1; 64573, L max. P_2-M_3; 64574, R dent. P_3-M_3; 64578, R dent. M_{1-3}; 64579, R dent. P_4-M_2; 71830, R dent. M_2; 82054, R dent. I_1, M_{1-2}; 82058, L dent. M_{1-3}; 82059, R dent. P_3-M_3; 82093, L dent. P_3-M_3; 83250, L dent. M_{1-2}; 83251, isolated teeth; 83253, R dent. M_{1-3}; 83255, R dent. M_{2-3}. Plus additional specimens listed by Gingerich (1976), now in the YPM collections.

Plesiadapis churchilli Gingerich, 1975

Figures 39–44, Table 31

Plesiadapis churchilli Gingerich, 1975, p. 142.
Plesiadapis fodinatus (in part), Gingerich, 1976, p. 29.
Plesiadapis simonsi (in part), Gingerich, 1982a, p. 39.

Holotype.— YPM-PU 21234, left dentary with I_1, P_{3-4}, M_{1-3}; from Long Draw Quarry, Bighorn Basin, Montana.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a), *Phenacolemur* (Ti-4b), and *Probathyopsis* (Ti-5a) zones.

Description.— Detailed dental descriptions were provided by Gingerich (1975; 1976). To those descriptions I add that *Plesiadapis churchilli* differs from *P. fodinatus* in having a dorsoventrally deeper I^1.

Discussion.— A previously undescribed sample of *P. churchilli* from Divide Quarry has greatly increased the number of specimens known of *P. churchilli* from the Bighorn Basin. The Divide Quarry sample is morphologically similar to the typodigm from Long Draw Quarry described by Gingerich (1975, 1976). It differs primarily in exhibiting a greater size range (Fig. 39, Table 31). The M_1 and M_2 size distributions display moderate bimodality (Fig. 39). Although the bimodality suggests the presence of two species, the size distributions are both within the 0.40 range expected for area in a single species of *Plesiadapis* in natural log space (e.g., Gingerich, 1981). The coefficient of variation is moderately high in some dimensions, compared with most of the large samples of *Plesiadapis* reported by Gingerich (1976), but I found no other evidence that suggests the presence of more than one species at Divide Quarry. However, both *P. churchilli* and a smaller species identified as *P.* cf. *P. fodinatus* (see below) appear to be present in younger populations in the *Phenacolemur* zone (SC-243 and Fossil Hollow).

Plesiadapis churchilli and *P. fodinatus* are most easily distinguished by characteristics of the upper incisors and lower premolars. Upper incisors of *P. churchilli* typically have a well-developed centroconule, several accessory cusps along the medial margin (medioconules), and are dorsoventrally deeper than in *P. fodinatus* (Fig. 42). *Plesiadapis fodinatus* lacks a strong centroconule and typically has only a single cusp along the medial margin. Figure 42 shows that there is no overlap in I_1 depth between the two species in the measured samples. The I^1s shown in Figure 42 from Fossil Hollow (upper Ti-4b) agree favorably with *P. fodinatus*, but were referred to *P.* cf. *P. fodinatus* because of differences in premolars from the same population. Three partial I^1s of *P. churchilli* (UM 80759, 110221, 110222) are also present at Fossil Hollow, but they are too fragmentary for depth measurement. These specimens are considerably larger than incisors of *P. fodinatus* and clearly would have plotted in the depth range for *P. churchilli*.

TABLE 31 — Dental statistics for *Plesiadapis churchilli* from Divide Quarry. Measuring techniques follow those of Gingerich (1976). Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
I^1	L	12	7.19	8.65	7.84	0.14	0.50	6.38
	W	15	2.48	3.18	2.74	0.05	0.20	7.30
	D	9	4.18	5.54	4.64	0.14	0.43	9.27
P^2	L	1	—	—	1.57	—	—	—
	W	1	—	—	1.33	—	—	—
P^3	L	3	2.42	2.73	2.59	0.09	0.16	6.18
	W	3	3.18	3.57	3.41	0.12	0.20	5.87
P^4	L	10	2.45	2.91	2.61	0.04	0.12	4.60
	W	10	3.82	4.62	4.23	0.08	0.25	5.91
M^1	L	6	3.18	3.52	3.36	0.05	0.13	3.87
	W	6	4.36	5.05	4.79	0.11	0.26	5.43
M^2	L	8	3.42	3.89	3.57	0.06	0.16	4.48
	W	8	5.00	5.71	5.34	0.07	0.21	3.93
M^3	L	13	3.14	3.84	3.47	0.05	0.19	5.48
	W	13	4.70	5.53	5.11	0.07	0.25	4.89
I_1	L	6	7.90	9.30	8.57	0.19	0.46	5.37
	W	6	2.30	2.86	2.58	0.09	0.22	8.53
	D	5	3.86	4.89	4.18	0.18	0.41	9.81
P_3	L	9	2.25	2.77	2.55	0.05	0.14	5.49
	W	9	1.84	2.32	2.11	0.05	0.16	7.58
P_4	L	13	2.43	2.86	2.64	0.04	0.13	4.92
	W	13	2.35	2.80	2.58	0.04	0.14	5.43
M_1	L	28	3.11	3.72	3.41	0.04	0.19	5.57
	W	28	2.81	3.61	3.13	0.04	0.21	6.71
M_2	L	17	3.42	4.07	3.82	0.04	0.18	4.71
	W	18	3.22	3.95	3.59	0.05	0.21	5.85
M_3	L	12	4.91	6.17	5.66	0.10	0.36	6.36
	W	12	3.01	4.04	3.46	0.08	0.29	8.38

The lower premolars of *Plesiadapis churchilli* are distinguished from those of *P. fodinatus* by greater width, by greater inflation resulting in more rounded corners, and by a shorter talonid. The premolar talonid of *P. churchilli* is typically dome-shaped around a medially positioned hypoconid and usually has an indistinct cristid obliqua. In contrast, *P. fodinatus* typically has premolars that are narrower, have more angular corners, and have longer talonids. Its premolars often have a well-developed entoconid and hypoconid resulting in a basined talonid, and a cristid obliqua that ascends the postvallid (Gingerich, 1976).

Figure 43 shows that the range of P_4 width in *P. churchilli* at Divide Quarry (Ti-4a) falls completely within that of *Plesiadapis*

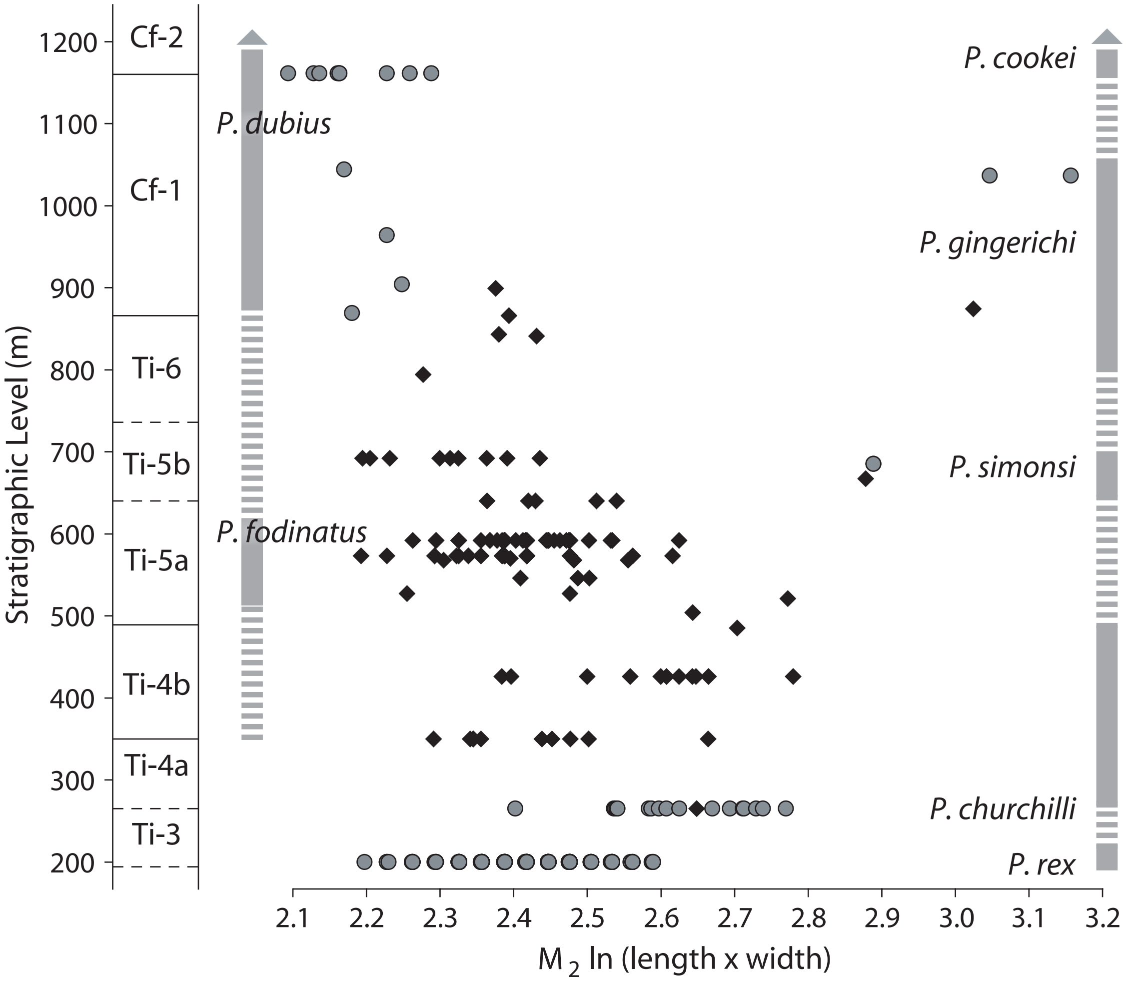


FIGURE 41 — Stratigraphic chart showing changes in *Plesiadapis* M_2 area from Ti-3 to Cf-2. Solid diamonds indicate specimens from the Polecat Bench sequence; gray circles indicate localities that were biostratigraphically correlated to the sequence. Solid gray bars correspond to levels for which a species is known with relative confidence; dashed bars indicate intermediate or conferred forms, or a lack of data. Expected range of variability for a species is about 0.4 ln units (Gingerich, 1981). Measurements for Cedar Point (200 m), Schaff (573 m), and Princeton quarries (592 m) courtesy of P. D. Gingerich, unpublished data.

rex from Cedar Point Quarry (Ti-3), although the mean is higher. A mean decrease in P_4 width occurs from Divide Quarry to Fossil Hollow (upper Ti-4b) and SC-243 (lower Ti-4b) in the *Phenacolemur* zone. Lower premolars in the *Phenacolemur* zone are either morphologically like those of *P. churchilli* or exhibit an intermediate condition between those of *P. churchilli* and *P. fodinatus* (see *P. fodinatus* section). The lack of larger P_4s at this level is probably due in part to size biases in the SC-243 sample, which was collected from anthills. It is clear from the Fossil Hollow sample that larger individuals of *Plesiadapis* were present at this time (Fig. 41, upper Ti-4b). The large M_2 from Fossil Hollow (UM 79868) and one of similar size in Ti-5a were identified as *P. churchilli* because they are close to the upper size range for the species from Divide Quarry. However, these specimens probably represent the beginning of a lineage leading to *P. simonsi*, which is thought to have been derived directly from *P. churchilli* (Gingerich, 1975, 1976, 1996b).

Referred specimens.— **Croc Tooth Q.** (FG028): UM 77169, R I^1; 77197, R max. M^{2-3}; 108787, L I_1; 108788, L P^3; 108789, L P^3; YPM-PU 14964, R dent. I_1-M_3; 17744, R M^2; 21584, R M_1; 21585, R I^1. **Divide Q.** (FG046): UM 45676, R P_4, R P^3 unassoc.; 77266, 3 I^1 frags.; 77272, R I_1; 77273, R I^1; 77297, R M^3; 77320, R M_2; 82073, R M_2; 82074, R dent. M_{1-3}; 82100, R dent. P_3-M_3; 83214, R dent. P_4-M_2; 83222, R M_1; 83236, R max. P^2-M^3; 83262, L M_3; 83269, R I_1; 85309, R dent. I_1-M_3; 85389, L M_1; 85411, R M_1; 85412, R dent. P_4-M_1; 85413, L M_1; 85426, R M_1; 85427, L M_1; 85440, R dent. M_{1-2}; 85913, R dent. M_{1-2}; 85922, R M_1; 85923, L M_1; 85928, L dent. M_{1-2}; 86244, L M_1; 86245, L M_1; 86248, R dent. I_1-M_3; 87042, R M^1; 91336, R I^1 tip; 92269, R M^1; 92275, R M_1; 92277, R M_2; 104979, R M_2; 108380, R M_2; 108382, R I_1; 108708, L M_1; 108709, R P^4; 108710, R P^4; 108711, R M^2; 108712, R M^3; 108713, L P_4; 108714, L I_1; 108715, R M_2; 108716, L M_1; 108717, L P_3; 108718, R M_3; 108719, L P_3; 108720, R I_1; 108721, L I_1; 108722, R I^1; 108723, L I^1; 108724, L I^1; 108725, R I^1; 108726, L I^1; 108727, R I^1; 108728, R I^1; 108729, L P^4; 108730, R P^4; 108731, L P^4; 108732, R P^3; 108733, R P^4; 108734, R P^4; 108735, R M^2; 108736, L M^2; 108737, L M^1; 108738, R M^3; 108739, R

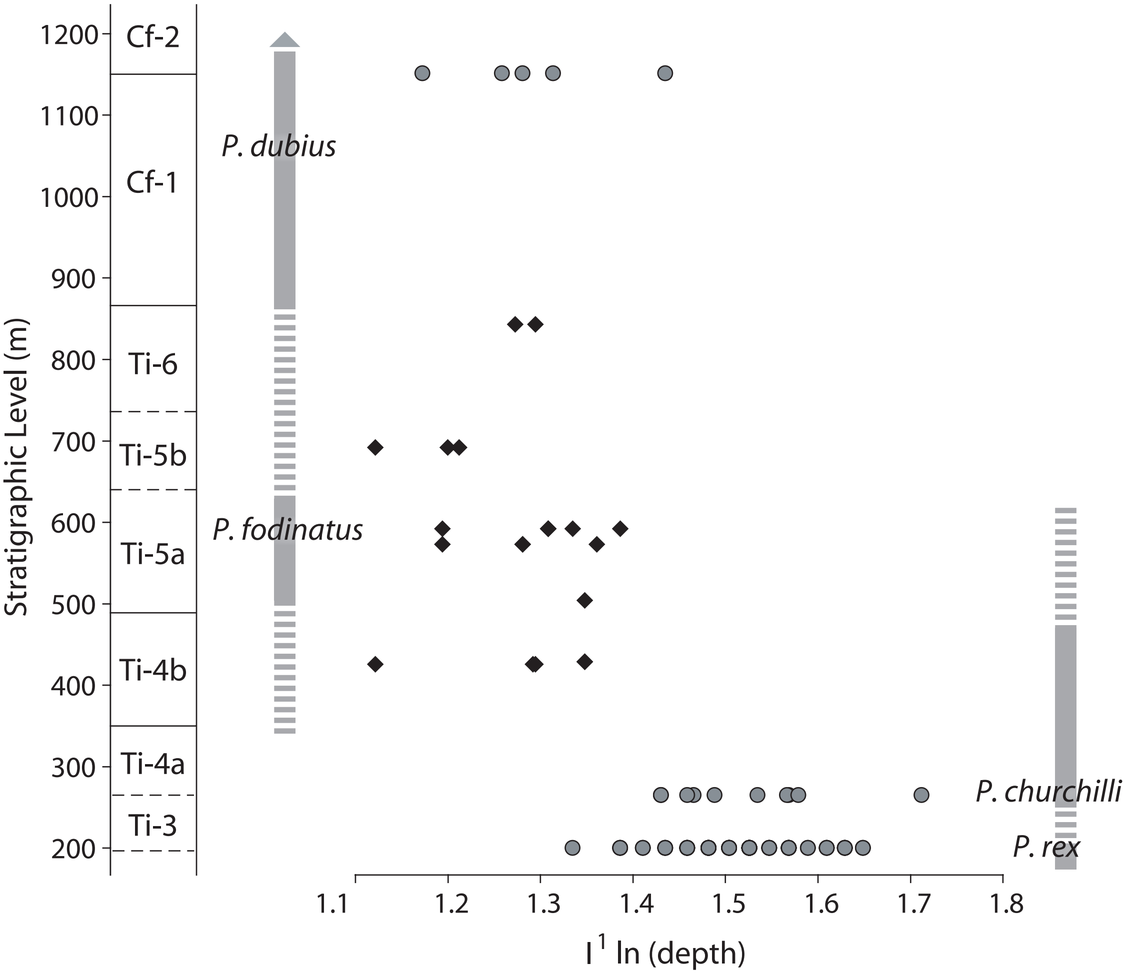


FIGURE 42 — Stratigraphic chart showing changes in *Plesiadapis* I^1 depth (depth of root at cervical margin) from Ti-3 to Cf-2. Expected range of variability for a species is about 0.2 ln units. Symbols and other comments as in Figure 41.

M^3; 108740, L M^3; 108741, R M^3; 108742, L M^3; 108743, L I^1; 108744, R P^4; 108745, L M^3; 108746, L P$_3$; 108747, R P$_4$; 108748, L M$_2$; 108749, L M$_1$; 108750, L M$_3$; 108751, R I$_1$; 108752, R P$_3$; 108753, L P$_4$; 108754, R P$_4$; 108755, R P$_4$; 108756, R P$_4$; 108757, R P$_4$; 108758, R P$_3$; 108759, L P$_2$; 108760, R M$_1$; 108761, R M$_2$; 108762, L M$_1$; 108763, R M$_2$; 108764, L M$_1$; 108765, R M$_3$; 108766, R M$_3$; 108767, L M$_3$; 108768, R M$_3$; 108769, R I^1; 108770, L I^1; 108771, L I^1; 108772, L I^1; 108773, R P$_4$; 108774, R M$_2$; 108775, L M$_2$; 108776, R M$_2$; 108777, L M$_2$; 108778, R M$_1$; 108779, L M$_1$; 108780, L M$_3$; 108781, R M$_3$; 108782, L M$_3$; 108783, L M$_3$; 108784, R M$_3$; 108785, L M^3; 108786, L M$_2$; 110215, L P^3. YPM-PU 17752, L dent. M$_1$; 17753, L dent. P$_4$-M$_3$; 17754, 3 I^{1}s. **FG048**: UM 77302, L dent. frag., M$_2$. **Fossil Hollow (SC198)**: UM 69236, R dent. M$_{2\text{-}3}$ tals.; 69245, L I$_1$ frag., L M$_2$, R M$_2$ assoc.; 69247, misc. unassoc. teeth; 79868, R M$_2$; 79870, R M$_{1\text{-}3}$ assoc.; 79879, L dent. M$_3$; 79882, R I$_1$; 80250, R I^1, L M^2; 80759, L M$_1$; 80760, R dent. P$_4$-M$_2$; 108898, L M$_3$; 108901, L dent. M$_1$ (tal.)-M$_3$, R dent. M$_{1\text{-}3}$, L M^3, assoc. teeth; 108904, L M$_3$; 108905, L P$_4$, M$_3$, phalanx frag. assoc.?; 110197, R dent. M$_1$ tri., M$_2$ tal., P$_2$ alveolus; 110200, L dent. M$_3$; 110201, L dent. M$_2$; 110210, L M$_2$; 110211, R P$_3$, P$_4$ assoc.; 110212, R M$_1$; 110213, R M$_1$, R M$_2$ assoc.?; 110214, R M$_1$; 110221, L I^1; 110222, R I^1; 110223, L M$_1$; 110224, L M^2; 110225, L and R I$_1$ frags., assoc.?; 110299, L M$_1$. **Long Draw Q**: UM 108377, R dent. P$_3$-M$_3$; YPM-PU 20845; 20846, R dent. I$_1$-M$_2$; 20858, L max. P^3-M^2; 20859, R dent. M$_1$ tal., M$_2$; 21234, L dent. I$_1$-M$_3$; 25012, R P$_3$; 25013, L M$_3$; and numerous YPM-PU uncataloged isolated teeth. **MP054**: UM 91040, R M$_2$; 91042, L I^1, M^3; 91043, R dent. M$_{1\text{-}3}$; 91044, L M$_3$; 92114, R M$_2$. **Silver Coulee Lower Level**: YPM-PU 18791, partial skull, R P$_2$-M$_3$, L C$_1$-M$_3$; 19019, R dent. P$_4$-M$_2$. 19158, R dent. **Sand Draw Anthills**: YPM-PU 17762, R M$_2$; 17787, R dent. P$_3$-M$_3$; plus numerous YPM-PU uncataloged isolated teeth. **SC187**: UM 80360, L M$_1$, R M$_3$ assoc. **SC228**: UM 71705, R dent. M$_{2\text{-}3}$; 110287, R M$_3$; 110288, L M$_3$; 110289, L I$_1$ tip. **SC229**: UM 71323, R dent. M$_{2\text{-}3}$. 110285, L M$_2$; 110320, R I$_1$. **SC239**: UM 110277, R I^1. **SC240**: UM 71652, R M$_{2\text{-}3}$. **SC243**: UM 61431, R P$_3$; 61436, L P$_3$ or P$_4$; 61438, L P$_4$; 61439, L P$_4$; 61442, L P^3; 61443, L P^3; 61453, L P^3; 61456, R P^3; 61461, R P$_3$; 61465, L P$_4$; 61476, L P$_3$ or P$_4$; 61477, L P^4; 61481, L P$_4$; 61482, R P$_4$; 61483, R P^4; 61487, R P$_3$; 61490, L P$_4$; 61491, L P^3; 61492, R P$_3$; 61494, R P$_3$; 61503, R I^1 partial; 61505, R P$_4$; 61509, R P$_3$; 61515, L P$_3$ or P$_4$; 61524, L P$_3$; 61525, R P$_3$ or P$_4$; 61528, L P$_3$ or P$_4$; 61545, R M^3; 61548, R P$_3$; 110216, L M$_2$. **SC261**: UM 73388, L M_2. **SC273**: UM 73658, L dent. M_1. **SC274**: UM 110926, R I_1 partial. **SC339**: UM 83559, R dent. M_2 tal., M_3. **SC417**: UM 110063, R M_2; 110064, L M^3; 110065, L dent. M_2 tal., M_3.

Plesiadapis fodinatus Jepsen, 1930b

Figures 41–44

Plesiadapis fodinatus Jepsen, 1930b, p. 515. Gingerich, 1976, p. 29.

Holotype.— YPM-PU 13278, right dentary with I_1, P_3, M_{1-2}, from Princeton Quarry in the Clarks Fork Basin, northern Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b), *Probathyopsis* (Ti-5a), *Plesiadapis simonsi* (Ti-5b), and *Plesiadapis gingerichi* (Ti-6) zones.

Description.— Detailed dental descriptions were provided by Gingerich (1975, 1976).

Discussion.— Differences between *Plesiadapis fodinatus* and *P. churchilli* were addressed in the *P. churchilli* discussion above. *Plesiadapis fodinatus* appears to be derived directly from *P. churchilli*, and represents the lower part of an evolutionary lineage ending with *P. dubius* in the Clarkforkian (Gingerich, 1975, 1976, 1996b). Several specimens from the *Phenacolemur* zone, which is stratigraphically between the type localities for *P. churchilli* and *P. fodinatus*, exhibit intermediate premolar morphology between these species. In recognition of this condition, I have referred these specimens to *P.* cf. *P. fodinatus* at the end of this section, along with molars from the same localities. *Plesiadapis churchilli*, or a large species close to it, is also present in the *Phenacolemur* zone and can be difficult to distinguish from *P.* cf. *P. fodinatus*. There is a great deal of size overlap between these species, but they can be distinguished using upper incisor morphology.

My identifications of upper incisors at Fossil Hollow were based on the presence and development of a centroconule, on the number of medial cusps, and on size, as discussed in the *P. churchilli* section. Three incisors from Fossil Hollow identified as *P.* cf. *P. fodinatus* are shown in Figure 42 (Ti-4b level). Three upper incisors of *P. churchilli* that are considerably larger are also present in the Fossil Hollow sample, but are too fragmentary for depth measurement. Figure 42 shows the marked decrease in I^1 depth between Divide Quarry (Ti-4a) and Fossil Hollow from *P. churchilli* to *P. fodinatus*. There is no overlap in size between these two samples. Although the sample from Fossil Hollow is small, the amount of variability is about the same as that seen in the *P. fodinatus* samples from Schaff and Princeton quarries (upper Ti-5a), and the combined variability of Fossil Hollow and Divide Quarry is probably too great for a single species. Even the highly variable sample of *P. rex* from Cedar Point Quarry (n = 62; unpublished data courtesy of P. D. Gingerich, lack of overlap due to rounding of measurements) is less variable than these combined samples. Upper incisor depth appears to be a useful in distinguishing *P. fodinatus* (including *P.* cf. *P. fodinatus*) from *P. churchilli*.

Figure 43 shows that lower premolars decrease in mean width from Divide Quarry (Ti-4a) to SC-243 (lower Ti-4b) and Fossil Hollow (upper Ti-4b), but mostly plot within the ranges of both *Plesiadapis churchilli* and *P. fodinatus*. Many of these teeth exhibit an intermediate morphologic condition between the two species. The talonids of P_3 and P_4 are mostly domed, as is typical of *P. churchilli*, but some are less inflated and more angular, as is typical of *P. fodinatus*. UM 61464 (L P_3 or P_4) has two talonid cusps and a cristid obliqua ascending the protoconid, as in *P. fodinatus*, but the talonid cusps are more closely approximated than is typical of *P. fodinatus*. The SC-243 sample was recovered from an anthill and is size biased, which probably accounts for the lack of larger P_4s.

Figure 41 shows that there is a decrease in mean M_2 size from Divide Quarry (Ti-4a) to SC-243 (lower Ti-4b) and an increase in the lower size range of *Plesiadapis*. Although size bias at SC-243 probably affected the mean, it probably did not greatly affect differences in the lower size range between the localities. Premolars of this size are relatively easy to spot while quarrying and should have been recovered in the Divide Quarry sample if present. Thus, the shift to a smaller size in the *Phenacolemur* zone appears to be real, reflecting the smaller size of *P.* cf. *P. fodinatus*.

Referred specimens of P. fodinatus.— **MP054**: UM 91041, R M^3; **SC165**: UM 68253, L dent. M_{1-3}; 68258, R dent. M_{2-3}; 68260, R M_1; 68262, L dent., assoc. L P_4, R I_1, R M_3; 68268, L max. P^{2-3}; 68269, L max. P^{2-3}; 68270, L dent. M_{1-2}; 71497, R max. P^{3-4}; 71500, R dent. P_3-M_2; 71503, R dent. P_4-M_1; 81715, R M^3; 81717, R P_4; 81720, R M_3; 81721, L M^3; 81722, L M^2; 81723, L P^3; 81724, L P^4; 108438, R dent. M_{1-2}; 108439, R M_3 tri.; 110166, R max. M^1, M^2 partial; 110167, R M_1; 110168, L I^1, R M^x, R P_4, M_3, assoc.?; 110169, R M_2; 110171, L M^2, M^3 assoc.?; 110173, R I^2, L M^2, assoc.? **SC187**: UM 73599, R dent. M_{2-3}; 77200, L M^2, R M^1, L M_2 unassoc.; 85238, L dent. P_3-M_3; 96367, L dent. M_{1-2}; 101909, L I_1, P_3-M_1; 108391, L M^2; 108392, L M^3; 108887, L I_1; 108894, R P_4; 109931, R dent. M_3; 110100, L dent. P_4-M_3; 110102, L I_1 frag., R M_3; 110226, L I_1; 110316, L M_{2-3} assoc. **SC199**: UM 69252, L dent. M_2 (partial), M^3. **SC228**: UM 71707, 2 L I_1s, L P_4, L M_3; 96365, R dent. M_{1-3}; 110290, L M_1. **SC229**: UM 110286, misc. teeth, L M^1, L M^2, R M^3, R M_2, and broken teeth, unassoc.?; 110342, R I^1 partial; 110343, L I^1 partial, L M^3, R P^4, R M^3, R P_4, L M_1, assoc.?. **SC246**: UM 71736, L I_1 frag., L M_3. **SC266**: UM 73505, L P^2, R P^3 assoc.; 73507, R dent. **SC267**: UM 73514, L M^1 or M^2. **SC270**: UM 73576, R max. M^{1-3}; 73578, L dent. M_{1-2}; 73582, L dent. I_1, P_4-M_2; 73583, R dent. frag., M_3; 73584, R dent. frag. P_4, M_2 and tooth frags; 110928, L I^1 partial. **SC273**: UM 110152, R dent. frags., M_1 tal., M_3. **SC277**: UM 73686, L dent. M_{2-3}; 73687, R dent. P_4-M_2. **SC281**: UM 110148, L I^1 frag. **SC388**: UM 108465, L M_3 tal. **SC416**: UM 110034, L M^3; 110035, L M_3. **SC419**: UM 110072, max. frag., M^{2-3}. **Schaff Q.**: 77424, L dent. M_{1-2}; 110157, R M_3; 110158, L M_2, I^1 frag; YPM-PU 19006; 19360; 19363; 19383; 19399; 19405; 19405; 19405; 19405; 19405; 19405; 19408; 19410; 19411; 19417; 19418; 19420; 19421; 19423; 19428; 19437; 19475; 19485; 19494; 19495; 19496; 19508; 19510; 19511; 19512; 19513; 20736; plus numerous uncataloged YPM-PU specimens. **Princeton Q.**: YPM-PU 13278, right dent. I_1, P_3, M_{1-2} (holotype); 13356; 13402; 13409; 13921; 13923; 13930; 13931; 13939; 13940; 13941; 13942; 13955; 13960; 13967; 13968; 13969; 13975; 14032; 14353; 14354; 14355; 14356; 14357; 14360; 14361; 14362; 14363; 14407; 17601; 17602; 17603; 17612; 17616; 17617; 17618; plus numerous uncataloged YPM-PU specimens. YPM numbers for Schaff and Princeton quarries courtesy of P. D. Gingerich.

TABLE 32 — Dental statistics for *Plesiadapis* cf. *P. dubius* from Y2K Quarry. Measuring techniques follow those of Gingerich (1976). Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
I^1	L	2	5.72	5.99	5.86	—	—	—
	W	2	2.12	2.23	2.18	—	—	—
	D	3	3.07	3.36	3.25	0.09	0.16	4.84
I^2	L	1	—	—	1.93	—	—	—
	W	1	—	—	1.37	—	—	—
P^2	L	1	—	—	1.72	—	—	—
	W	1	—	—	1.49	—	—	—
P^3	L	4	2.41	2.53	2.46	0.03	0.05	2.18
	W	4	3.33	3.53	3.44	0.05	0.10	2.84
P^4	L	8	2.35	2.54	2.44	0.02	0.06	2.32
	W	7	3.61	4.06	3.82	0.07	0.18	4.62
M^1	L	7	3.13	3.33	3.23	0.03	0.09	2.78
	W	7	4.16	4.38	4.27	0.04	0.10	2.37
M^2	L	6	3.24	3.45	3.35	0.04	0.09	2.64
	W	5	4.78	5.02	4.86	0.04	0.09	1.91
M^3	L	4	3.13	3.70	3.34	0.13	0.25	7.59
	W	4	4.16	4.63	4.46	0.10	0.21	4.66
I_1	L	4	6.30	7.03	6.67	0.15	0.30	4.50
	W	5	1.98	2.18	2.11	0.03	0.08	3.69
	D	5	2.77	3.03	2.90	0.04	0.10	3.39
P_3	L	3	2.40	2.72	2.59	0.10	0.17	6.50
	W	3	1.73	1.92	1.83	0.06	0.10	5.21
P_4	L	7	2.40	2.72	2.59	0.04	0.11	4.42
	W	8	1.98	2.29	2.15	0.04	0.12	5.35
M_1	L	5	2.95	3.30	3.11	0.06	0.13	4.25
	W	5	2.65	2.92	2.76	0.05	0.11	4.10
M_2	L	9	3.14	3.48	3.32	0.04	0.13	3.96
	W	9	2.77	3.30	3.03	0.06	0.18	5.89
M_3	L	6	4.80	5.41	5.01	0.10	0.26	5.10
	W	6	2.86	3.38	3.08	0.09	0.22	7.04

Referred specimens of Plesiadapis cf. *P. fodinatus*.— **Croc Tooth Q.** (FG028): 110183, R M^3. **Fossil Hollow** (SC198): UM 100359, R M^2; 108895, R I^1; 108897, R M^2, M^x; 108900, R M^2; 110198, L M$_1$; 110199, R I^1; 110220, R P$_3$. **Sand Draw Anthills**: uncataloged YPM-PU, L M^3. **SC243**: UM 61435, R M^3; 61440, L M^3; 61452, R P$_3$; 61460, R P^4; 61464, L P$_3$ or P$_4$; 61466, L P^4; 61467, R M^3; 61468, R M^3; 61472, L P$_3$; 61474, R P^3; 61480, R M^1; 61502, R P^4; 61508, R P^3; 61517, R M^2; 61526, R P$_3$; 61529, R P^3; 61538, L M^3; 61541, L M^1; 61542, L P^3; 61543, L P^4; 61546, L P$_3$. **SC394**: UM 108548, R I^1. **SC397**: UM 108575, L M^2; 108576, R M^1.

Plesiadapis cf. *P. dubius*

Figures 41–44; Table 32

Biostratigraphic occurrences in Bighorn Basin.— Probathyopsis (Ti-5a), *Plesiadapis simonsi* (Ti-5b), and *Plesiadapis gingerichi* (Ti-6) zones.

Discussion.— Plesiadapis dubius appears to be derived directly from *P. fodinatus* (Gingerich, 1975, 1976, 1996b; Rose, 1981a). The transition from *P. fodinatus* to *P. dubius* was most recently discussed by Rose (1981a). The species are quite similar, but *P. dubius* is distinguished by narrower cheek teeth and lower incisors, by the absence of P$_2$, by a smaller margoconid on I$_1$, and by features of the upper incisors. When *P. dubius* was reviewed by Gingerich (1976), only a single I^1 was known. It had two medioconules and no indication of a centroconule. When Rose reviewed *P. dubius* three additional specimens were known from the Paint Creek locality (SC-143) in the Clarks Fork Basin. Rose noted the presence of three small mediocones on each. Four additional I^{1}s are now known from Paint Creek. One has four mediocones (UM 102436), while another has only two (UM 75457), and the others have three (UM 87827 and 109911). No centroconule is present in any of the Paint Creek incisors. The number of mediocones and the presence a centroconule appear to be useful characteristics for distinguishing *P. dubius* from *P. fodinatus*, which typically has only a single mediocone, and has a centroconule in about half of the specimens in the hypodigm from Princeton Quarry (Gingerich, 1976).

Rose noted the intermediate nature of some specimens collected in the interval between SC-165 (base of Ti-5b in Figs. 41, 42, 43, and 44) and the early Clarkforkian. A new sample of *Plesiadapis* from Y2K Quarry confirms Rose's observations. A shift towards *P. dubius* is apparent in the mean decrease in P$_4$ width, shown in Figure 43, from Princeton and Schaff quarries (upper Ti-5a) to Y2K Quarry (upper Ti-5b), and is also suggested by a smaller mean M$_2$ size (Fig. 41). Both M$_1$ and M$_2$ are good proxies for body size (Gingerich et al., 1982; Gingerich and Smith, 1984).

One of four upper incisors from Y2K Quarry that preserve useful morphology, has a centroconule, which is poorly developed (UM 109383), while four of five have a single medial cusp. The fifth (UM 109861) has two or three incipiently developed medial cusps. UM 110168 from SC-165, about 50 meters below Y2K Quarry, has with 3 medial cusps and no centroconule. UM 108622 from the latest Tiffanian (SC-379) had at least two medial cusps and UM 110313 from the earliest Clarkforkian (SC-179) has three cusps. The presence of more than one medial cusp, and the absence of a centroconule are suggestive of an intermediate state between *P. fodinatus* and *P. dubius*. In recognition of the transitional position of the small species of *Plesiadapis* at Y2K Quarry and higher in the Tiffanian, I refer these specimens to *P.* cf. *P. dubius*.

Referred specimens.— **SC085**: UM 96147, R I$_1$, L M$_1$. **SC086**: UM 67175, P$_4$ tri. **SC178**: UM 101815, R M^3, R dent. M$_2$; 101818, L M$_1$; 101819, R I^1 frag.; 108308, R M^2, L I$_1$ frag.; 110193, R M$_3$. **SC185**: UM 68790, R P$_3$, L P^4. **SC186**: UM 68794, L P^4, L dent. P$_4$-M$_1$, M$_3$; R P$_4$, M$_1$, M$_3$ assoc.?; 68795, L dent. M$_{1-2}$; 110312, L I$_1$. **SC191**: UM 108282, L M$_{1-2}$, R M$_2$, M$_3$ tals., assoc.; 108285, R I^1 partial; 108336, L M$_3$ tal., R M$_1$ tal., not assoc.; 108337, R M^1; 108338, R M^2; 108339, L I^1 partial; 110278, iso. partial teeth, assoc.?. **SC193**: UM 108563, L M$_2$. **SC275**: UM 73671, R M$_1$, M$_3$. **SC370**: UM 108315, L max. M$^{1-3}$. **SC373**: UM 108246, R M^2, M^x, assoc. **Bluff Top Q.** (SC379): UM 108253, R P^4; 108258, I^1 partial; 108263, L M^3; 108264, L M$_2$ tal.; 108265, L M^2; 108268, R M$_1$; 108269,

TABLE 33 — Dental measurements for *Plesiadapis simonsi*. Measuring techniques follow those of Gingerich (1976). *SD*, Sand Draw; *ZQ*, Zalmout Quarry. *Estimate.

		UM 68796 SC-186	UM 73969 FG-1	UM 73981 FG-4	UM 74035 FG-9	UM 81719 SC-165	UM 92359 MP-115	UM 108450 ZQ	UM 108451 ZQ	UM 108959 ZQ	UM 109147 ZQ	YPM-PU 17814 SD (type)	YPM-PU 22010 FG-4
I^1	H	—	—	—	—	—	—	—	—	—	—	—	—
	W	—	—	—	—	—	3.0*	—	—	—	—	—	—
	D	—	—	—	—	—	—	—	—	—	—	—	—
P^3	L	—	—	—	3.00	—	—	—	—	—	—	—	—
	W	—	—	—	3.77	—	—	—	—	—	—	—	—
P^4	L	—	—	—	—	—	—	—	—	—	—	—	—
	W	—	5.1*	—	—	—	—	—	—	—	—	—	—
M^1	L	—	3.91	—	—	—	—	—	—	—	—	—	4.13
	W	—	5.38	—	—	—	—	—	—	—	—	—	5.49
M^2	L	4.25*	—	4.32	—	—	—	—	—	—	—	—	4.45
	W	—	—	6.16	—	—	—	—	—	—	—	—	6.21
M^3	L	4.16	—	—	—	—	—	—	—	—	—	—	—
	W	—	—	—	—	—	—	—	—	—	—	—	—
I_1	W	—	—	—	—	—	—	—	—	2.98	—	—	—
	D	—	—	—	—	—	—	—	—	—	—	—	—
P_4	L	—	—	—	—	—	3.05	—	—	—	—	—	—
	W	—	—	—	—	—	2.86	—	—	—	—	—	—
M_1	L	—	—	—	—	—	—	3.63	—	—	—	3.75*	—
	W	—	—	—	—	—	—	3.46	—	—	—	3.78	—
M_2	L	—	—	—	—	—	—	—	4.49	—	—	4.33	—
	W	—	—	—	—	—	—	—	3.96	—	—	4.36	—
M_3	L	—	—	—	—	5.88	—	—	—	—	7.02	—	—
	W	—	—	—	—	3.46	—	—	—	—	4.05	—	—

L M^3; 108272, dent. frag. L M_2; 108276, R M_1; 108615, L M^1; 108620, R M^3; 108622, L I^1. **SC380**: UM 108298, R molar tal. **SC386**: UM 108506, R M_2. **SC389**: UM 108539, R M^3; 109868, R dent. frag., M_2. **SC399**: UM 108595, R M^1; 108599, R P^3; 108600, L P^4; 108601, R M_x tal.; 108605, R max. frag., M^2 frag., M^3; 108609, R M_1. **SC400**: UM 108611, M^x partial. **SC401**: UM 109863, R dent. P_3-M_3. **SC402**: UM 108312, L molar tal. **SC407**: UM 108911, R M^1; 108919, R M^3 partial. **SC408**: UM 108942, L M_1. **Y2K Q.** (SC389): UM 108522, R max. I^1, P^4-M^2 assoc.; 108532, L I^1; 109134, L M_3; 109137, L I^1; 109140, R P_4, M_2, M_3 tri., assoc.; 109144, R M_3 tal.; 109151, L P^4; 109166, R M_2; 109175, R P_4; 109177, R max. M^{1-2}; 109181, R dent. P_4-M_2; 109203, L max. P^{2-3}; 109205, max. and R dent.; 109208, L I_1; 109218, L P^4; 109231, P^4 frag.; 109243, I^1 (part), M^1 (assoc.); 109253, L I^2; 109255, L M_2; 109303, R I_1, P_4 assoc.; 109318, L P_3; 109321, R max. I^2, P^3-M^3, cranial pieces; 109337, L M_2; 109343, R M^3; 109372, R I^1; 109383, L I^1; 109387, R I_1; 109388, R dent. P_4-M_3, assoc. R M^1; 109389, L M^3; 109398, L M^1; 109399, L P^4; 109438, L M^2; 109462, L M^1; 109465, R I_1; 109485, R M^2; 109517, L I^1; 109521, R dent. P_4, M_{2-3}; 109556, R P_3; 109560, R M_1; 109566, L M_1 tri.; 109576, L P^4; 109581, L dent. I_1, P_4-M_3; 109592, L M^2, frag.; 109656, R I^1 frag.; 109854, R dent. M_{1-2}; 109861, L I^1; 109993, R M_3; 109994, R M^3; 109995, R M^3; 109996, R M_2; 109997, R P^4; 109998, L M^3; 109999, R P^4; 110000, R P_4; 110001, R M_3; 110002, R P^3; 110018, R dent. P_3-M_1; 110019, R M^1.

Plesiadapis simonsi Gingerich, 1975

Figures 41, 43–44; Table 33

Plesiadapis simonsi Gingerich, 1975, p. 142. Gingerich, 1976, p. 32.

Holotype.— YPM-PU 17814, right dentary fragment with partial M_1 and M_2; from the Sand Draw area, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis simonsi* zone (Ti-5b).

Description.— Descriptions of the holotype and an edentulous dentary were provided by Gingerich (1975, 1976). Based on new specimens, I add that the P^3 lacks a metacone and paraconule in the only known specimen. The enamel of the upper molars is moderately wrinkled.

Discussion.— When *Plesiadapis simonsi* was described by Gingerich (1975) a dentary fragment with a partial M_1 and M_2, and an edentulous dentary were all that was known. Several isolated teeth and jaw fragments have been collected since then, including a few upper teeth, but the species is still poorly represented. Several new specimens of *P. simonsi* show important distinctions from older species. A left P^3 (UM 74035) has a large

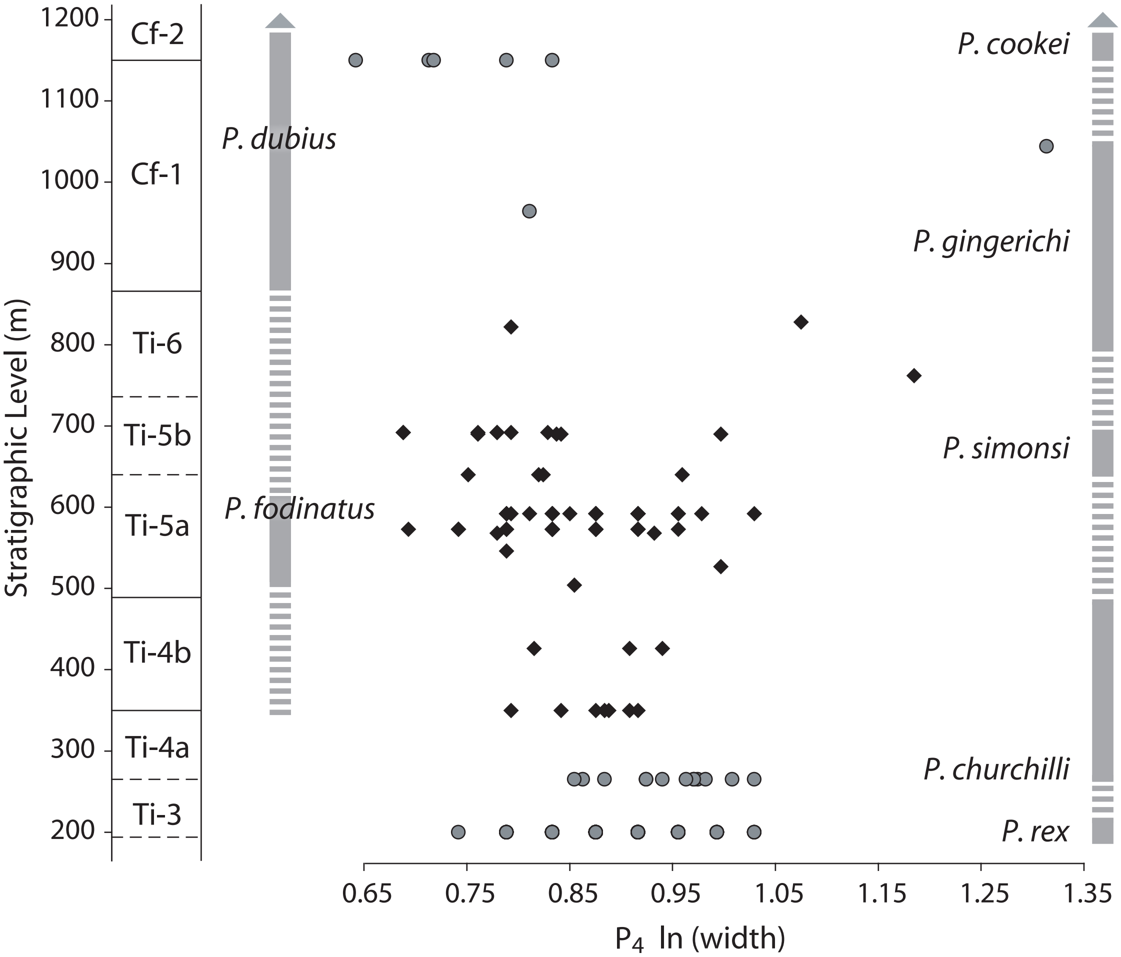


FIGURE 43 — Stratigraphic chart showing changes in *Plesiadapis* P_4 width from Ti-3 to Cf-2. Expected range of variability for a species is about 0.2 ln units. Symbols and other comments as in Figure 41.

paracone and protocone, but the metacone is virtually absent, demarcated only by a small swelling near the base of the metacrista. It also lacks a paraconule. This contrasts with the P^3 of *P. churchilli*, which consistently has a metacone positioned high on the crown and has a distinct paraconule. The P^3 of *P. gingerichi* is not known, but several undescribed specimens are known for *P. cookei*. These species appear to be part of an anagenetic lineage derived from *P. churchilli* that successively includes *P. simonsi*, *P. gingerichi*, and *P. cookei* (Rose, 1981a; Gingerich, 1996b). The P^3s of *P. cookei* consistently lack a metacone, or have a small swelling near the base of the metacrista, presumably a vestige of the metacone. All lack a paraconule. The absence of a metacone and paraconule in UM 74035 suggests that these cusps were lost in the transition from *P. churchilli* to *P. simonsi*, or were variably present.

Four specimens preserve upper molars of *Plesiadapis simonsi*, or represent small individuals of *P. gingerichi*. These teeth are virtually indistinguishable from molars of the holotype of *P. gingerichi* (UM 68409), except for their slightly smaller size. They differ from upper molars of *P. churchilli* in their larger size and in the greater degree of enamel wrinkling. A fragmentary I^1 tentatively referred here to *P. simonsi* (UM 92359) is larger than incisors of *P. fodinatus* and differs from those of *P. churchilli* in the absence of accessory cuspules and ornamentation. It had a reduced or absent centroconule and a single medial cusp. A round worn depression is present where a centroconule may have been, but if one were present it was small relative to those of *P. churchilli*. A P_4 and partial P_3 of *P. simonsi* cataloged with the I^1 (UM 92359) may belong to the same individual. The P_4 is wider than any of *P. churchilli* from Divide Quarry (Tables 31 and 33), but is considerably smaller than the holotype of *P. gingerichi* (UM 68409). It is anteroposteriorly short and transversely narrow, like UM 68409, and appears to have had only a single medial talonid cusp, much like lower premolars of *P. churchilli*. It has a squarer appearance in occlusal view and has squared corners, however, much like the P_4 of *P. gingerichi*, but unlike the more rounded P_4 of *P. churchilli*.

The oldest specimens that approach the size of the holotype of *P. simonsi* occur at SC-165 (UM 81719, M_3), and in the Y2K Quarry beds about 40 meters higher (Fig. 44, Ti-5b). These individuals probably represent a shift upward in body size in a lineage that was established at the Fossil Hollow level where there are clearly two species present. Based on an I_1 (UM 108959) from the Y2K Quarry level, *P. simonsi* appears to have had a

TABLE 34 — Dental measurements for *Plesiadapis gingerichi*. Measuring techniques follow those of Gingerich (1976). *Estimate; **tentatively identified.

		UM 68409 SC-171	UM 68421 SC-171	UM 68734 SC-178	UM 68741 SC-179	UM 68742 SC-179	UM 68743 SC-179	UM 71794 SC-248	UM 85252 FG-37	UM 96146 SC-85	UM 109279 SC-179	UM 110113 SC-185	UM 110125 SC-362	UM 110328** SC-85
P^4	L	—	—	3.2*	—	—	—	—	—	—	—	—	—	—
	W	—	—	—	—	—	—	—	—	—	—	—	—	—
M^1	L	4.75	—	—	4.73	—	—	—	—	—	—	—	—	—
	W	6.03	—	—	6.15	—	—	—	—	—	—	—	—	—
M^2	L	5.20	—	—	4.65	—	—	—	—	—	—	—	—	—
	W	7.11	—	—	—	—	—	—	—	—	—	—	—	—
M^3	L	5.01	—	—	—	—	—	—	—	4.13	—	—	—	—
	W	6.74	—	—	—	—	—	—	—	5.84	—	—	—	—
I_1	L	—	—	—	—	—	—	—	—	—	—	—	—	—
	W	—	—	—	—	—	—	—	—	—	2.92	—	—	—
P_3	L	—	—	—	—	—	—	3.87	—	—	—	—	—	—
	W	—	—	—	—	—	—	3.05	—	—	—	—	—	—
P_4	L	3.76	—	3.7*	—	—	—	—	—	—	—	—	—	3.42
	W	3.72	—	3.3*	—	—	—	—	—	—	—	—	—	2.93
M_1	L	4.60	—	—	4.33	4.75	4.9*	—	—	—	—	4.35	4.75	—
	W	4.27	—	—	4.08	4.34	—	—	—	3.9*	—	3.98	4.39	—
M_2	L	—	5.00	—	4.90	—	—	—	4.85	—	—	—	—	—
	W	—	4.70	—	4.20	4.71	—	—	4.34	—	—	—	—	—
M_3	L	—	—	—	—	7.54	—	—	—	—	—	—	—	—
	W	—	—	—	4.22	4.61	—	—	—	—	—	—	—	—

very reduced or absent margoconid, as does *P. cookei*, but a break in the critical area precludes certainty. Several teeth from the lower part of the *Probathyopsis* zone (e.g., Figs. 41 and 44, Ti-5a) are outside the size range of *P. fodinatus* documented by Gingerich (1976) at Princeton and Schaff quarries, and overlap with the expected size range of *P. simonsi* (±0.2 ln units for molar area, Gingerich, 1981). These specimens are indistinguishable from those of *P. churchilli*, however, and were included in that species pending the acquisition of larger samples.

Plesiadapis simonsi differs from *P. gingerichi* in having a smaller mean size (Rose, 1981a). No morphological criteria for distinguishing these species are known. There is about 25% size overlap between the species, assuming the holotypes are representative of mean size. Because sample sizes are small, the "boundary" between the *Plesiadapis simonsi* (Ti-5b) and *Plesiadapis gingerichi* (Ti-6) zones is somewhat arbitrary. UM 110113 is almost outside the expected size range of *P. simonsi*, but within that of *P. gingerichi*, and was therefore identified as *P. gingerichi*. This specimen marks the base of the *Plesiadapis gingerichi* zone (Fig. 44, Ti-6). Specimens above this level were referred to *P. gingerichi*, although some are closer to the size expected for *P. simonsi* (Fig. 43).

Referred specimens.— **FG001**: UM 73969, R max. P^4 (part), M^{1-2} (broken). **FG004**: UM 73981, R M^2. **FG009**: UM 74035, L P^3. **MP115**: UM 92359, R I^1 distal half, R P_3, R P_4. **Sand Draw Upper Beds**: YPM-PU 17814, R dent. M_{1-2}. **Sunday Locality** (FG004): YPM-PU 22010, L max. M^{1-2}. **SC165**: UM 81719, L M_3. **SC186**: UM 68796, R M^2 (part), M^3; 110322, R M_1 tri. **Zalmout Q.** (SC389): 108450, R M_1; 108451, R M_2; 108959, R I_1 base; 109147, dent. frag., R M_3.

Plesiadapis gingerichi Rose, 1981a

Figures 41, 43–44; Table 34

Plesiadapis gingerichi Rose, 1981a, p. 56.

Holotype.— UM 68409, right maxillary fragment with M^{1-3}, and left dentary fragment with P_4-M_1, M_2 trigonid; from SC-171 in the Clarks Fork Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis gingerichi* (Ti-6) and Rodentia (Cf-1) zones.

Description.— The dentition of *Plesiadapis gingerichi* was described by Rose (1981a).

Discussion.— *Plesiadapis gingerichi* appears to be part of an evolutionary lineage of large-bodied *Plesiadapis* (Rose, 1981a; Gingerich, 1996b). It occupies an intermediate temporal position between the older *P. simonsi* and the younger *P. cookei*, and is intermediate in size. The only known difference between *P. gingerichi* and *P. simonsi* is larger body size in the former, but representative samples for both species are small.

First lower molars of *Plesiadapis gingerichi* from the earliest Clarkforkian (Cf-1) are similar in size to M_1 in the holotype collected at a higher level (Fig. 44). Lower fourth premolars

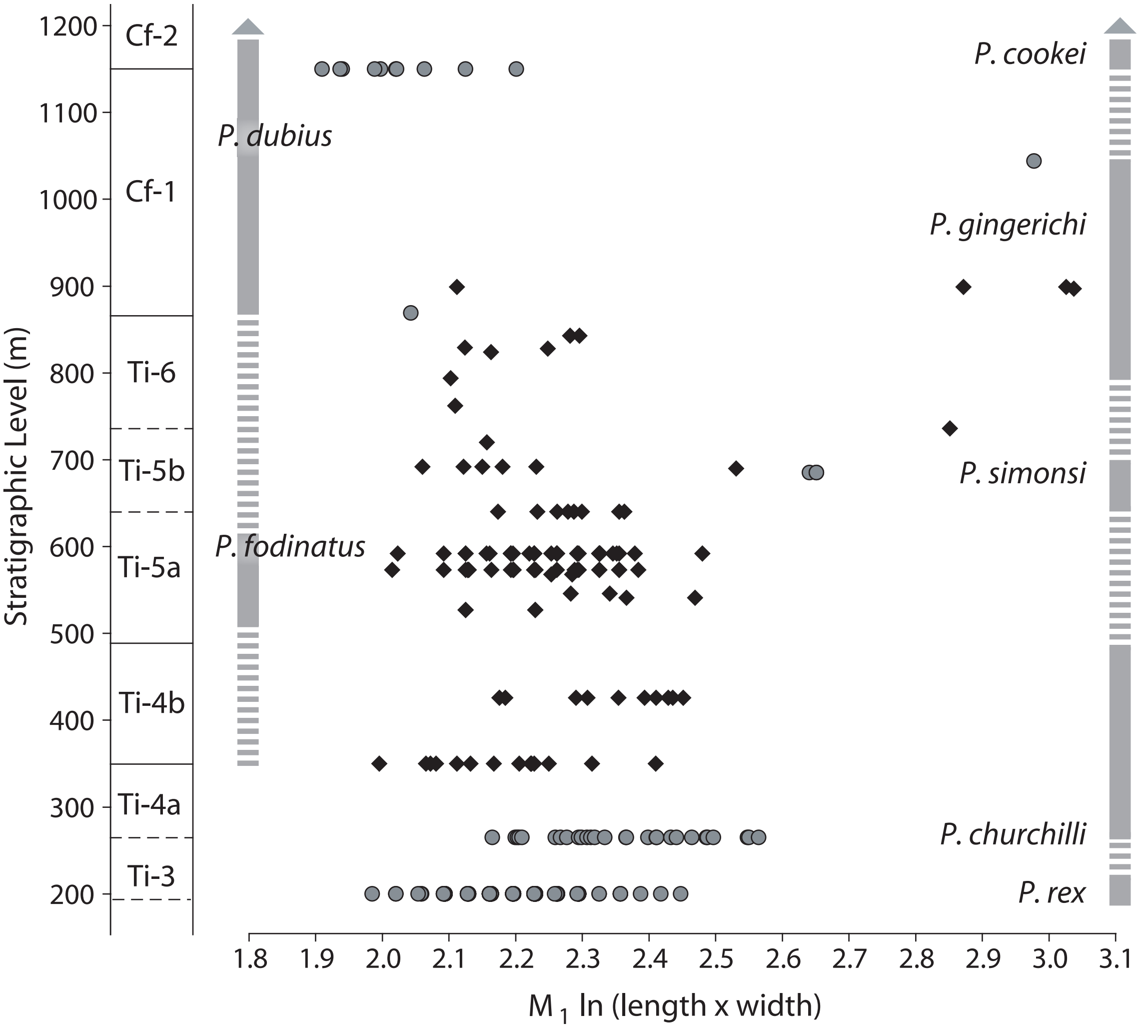


FIGURE 44 — Stratigraphic chart showing changes in *Plesiadapis* M_1 area from Ti-3 to Cf-2. Expected range of variability for a species is about 0.4 ln units (Gingerich, 1981). Symbols and other comments as in Figure 41.

from the underlying *Plesiadapis gingerichi* zone (Ti-6), however, do not agree well with that of the holotype (Fig. 43), and UM 110328 is near the size expected for *P. simonsi*. Also notable is an I_1 (UM 109279) from Cf-1 that is the same size as the only known I_1 of *P. simonsi* (UM 108959). These observations suggest two possibilities, that both *P. gingerichi* and *P. simonsi* are present in the latest Tiffanian, or that the form present differs from the holotype in having a considerably narrower P_4. The holotype of *P. gingerichi* was collected at SC-171, which is several kilometers from the main Polecat Bench sections and is not well-constrained stratigraphically. An I^1 (UM 71817) that is fully the size and has the morphology of *P. cookei* was collected from a locality just below SC-171 (Rose, 1981a), suggesting that SC-171 is stratigraphically close to the first occurrence of *P. cookei*, or possibly even above it. It may be that the holotype of *P. gingerichi* is morphologically closer to *P. cookei* than to the latest Tiffanian form. Pending the collection of larger samples, however, I have tentatively referred all the specimens in the *Plesiadapis gingerichi* zone to *P. gingerichi*.

The first occurrence of *Plesiadapis gingerichi* defines the base of *Plesiadapis gingerichi* zone. Unfortunately, because of the problems discussed above, the choice of this datum is somewhat arbitrary. First molar size has been shown to be less variable than premolar width (Gingerich and Smith, 1984). Accordingly, I used UM 110113, an M_1, which is closer to the mean M_1 size of *P. gingerichi* than to that of *P. simonsi*, to define the base (Fig. 44).

Referred specimens— **FG037**: UM 85252, L M_2. **SC085**: UM 96146, L M^3, R M_2 (part), M_3 tal.; 110328, R P_4. **SC171**: UM 68409 (holotype); 68421, R M_2. **SC178**: UM 68734, L P_4 (part), R P^4 (part). **SC179**: UM 68741, R dent. $M_{1\text{-}3}$, R max. $M^{1\text{-}2}$; 68742, L dent. $M_{1\text{-}3}$, claw and phalanx, assoc.?; 68743, R dent. M_1; 109279, L I^1. **SC181**: UM 71627, R I_1 frag.; 110202, L M_3 tal. **SC185**: UM 110113, L M_1. **SC226**: UM 71683, L I_1 tip. **SC248**: UM 71794, R P_3. **SC362**: UM 108320, R M^3 frag. **SC362 Q.**: UM 110125, L M_1.

TABLE 35 — Dental measurements for *Chiromyoides caesor* from the SC-243 anthills, Croc Tooth Quarry (CTQ), and Rock Springs Uplift (RSU), and for *C. minor* from Chappo Type Locality.

		Chiromyrides caesor									*Chiromyrides minor*		
		UM 61433 SC-243	UM 61451 SC-243	UM 61531 SC-243	UM 61532 SC-243	UM 61533 SC-243	UM 61535 SC-243	UM 61550 SC-243	UW 13063 RSU	YPM-PU 21575 CTQ	UM 68377 Chappo	UM 73999 Chappo	UM 93193 Chappo
I^1	H	—	—	—	—	—	—	—	—	6.90	—	6.20	—
	W base	—	—	—	—	—	—	—	—	3.32	—	3.19	—
	W apical	—	—	—	—	—	—	—	—	3.50	—	3.35	—
	D root	—	—	—	—	—	—	—	—	6.20	—	6.00	—
	D crown	—	—	—	—	—	—	—	—	6.37	—	6.23	—
M^2	L	—	—	—	—	2.30	—	—	—	—	—	—	—
	W	—	—	—	—	3.21	—	—	—	—	—	—	—
P_4	L	2.52	—	—	—	—	2.44	2.45	—	—	—	—	—
	W	2.47	—	—	—	—	2.52	2.46	—	—	—	—	—
M_1	L	—	—	2.41	—	—	—	—	2.43	—	1.90	—	2.36
	W	—	—	2.27	—	—	—	—	2.29	—	—	—	2.30
M_2	L	—	—	—	2.74	—	—	—	2.53	—	2.35	—	—
	W	—	—	—	2.76	—	—	—	2.43	—	2.26	—	—
M_3	L	—	3.60	—	—	—	—	—	—	—	3.26	—	—
	W	—	2.45	—	—	—	—	—	—	—	2.18	—	—

CHIROMYOIDES Stehlin, 1916

Chiromyoides caesor Gingerich, 1973

Figures 45A–D, Table 35

Chiromyoides caesor Gingerich, 1973, p. 517.

Holotype.— YPM-PU 21575, an isolated left I^1, from Croc Tooth Quarry in the Foster Gulch area of the Northern Bighorn Basin.

Biostratigraphic occurrences in Bighorn Basin.— ?*Plesiadapis churchilli* (Ti-4a) and *Phenacolemur* (Ti-4b) zones.

Description.— The holotype was described and figured by Gingerich (1973, 1976) and figured by Gingerich (1975).

The following descriptions are based on tentatively referred isolated teeth from the SC-243 anthills. In M^2? the paracone and metacone are nearly equal in size and connected by a centrocrista. Short anteroposteriorly oriented cristae travel from both outer cusps to the crown margins. A small mesostyle is present. The paraconule is low, rounded, and indistinct. The metaconule is an anteroposteriorly elongate ridge. The nannopithex fold is strong and bounds a relatively deep basin separated anteriorly by the postprotocrista. The trigon basin is relatively deep. The protocone is low and rounded. A strong precingulum begins below the paraconule and terminates on the anterolingual corner. No postcingulum is present.

P_4 has two closely spaced roots that may be partly fused in some individuals (e.g., UM 61550). The crown is broad and anteroposteriorly compressed. No distinct talonid cusps are present, but all talonids are worn and weathered. No talonid basin is present. A faint cristid obliqua begins on the posterior margin of the talonid and contacts the postvallid medially or slightly more buccal, and ascends the postvallid.

All lower molars are expanded along the basal buccal margin, but more so in M_2 and M_3 than M_1. M_2 and M_3 have short buccal cingulids, while M_1 has none. M_2 has a distinct paraconid, while M_1 has an indistinct one, and M_3 has none. The talonid basins are shallow on M_2 and M_3, but deeper on M_1. The entoconid and hypoconid are distinct on M_1 and M_2, and approximately equal in size on M_1. The hypoconid is the larger cusp on M_2. All molars lack a distinct hypoconulid, but have a large mesoconid.

Discussion.— Several isolated teeth from anthills at SC-243 along the southern side of Polecat Bench exhibit the morphology of *Chiromyoides* and are approximately the size expected for *C. caesor*. SC-243 is equivalent in age to Croc Tooth Quarry, the type locality of *C. caesor*, based on magneto- and biostratigraphy (Fig. 6) (Secord et al., 2006). I provisionally refer these teeth to *C. caesor* based on size, age, and similarity to molars in a dentary fragment (UW 13063) from southwestern Wyoming identified as *C. caesor* by Winterfeld (1982). UW 13063 appears to be within the size range of the SC-243 sample and several upper incisors included in Winterfeld's sample reportedly exhibited the narrower aspect that distinguishes *C. caesor* from *C. potior* and *C. major*. The specimens referred here are smaller than expected for *C. major*, and *Chiromyoides potior* is not known with certainty from the Bighorn Basin (see *C. gingerichi* n. sp. below).

Molars from SC-243 are morphologically close to those in UW 13063 (Winterfeld, 1982). The M_1 has a less distinct paraconid and the M_2 has a slightly greater degree of buccal expansion and has a buccal cingulid not present in UW 13063. These features are presumably within intraspecific variability. Based on a cast, the P_4 alveoli in UW 13063 are subequal in size and are close to the size of the M_1 alveoli. The roots were not fused. The posterior root of P_4 appears to have been appressed directly against the anterior root for M_1 or separated by a very

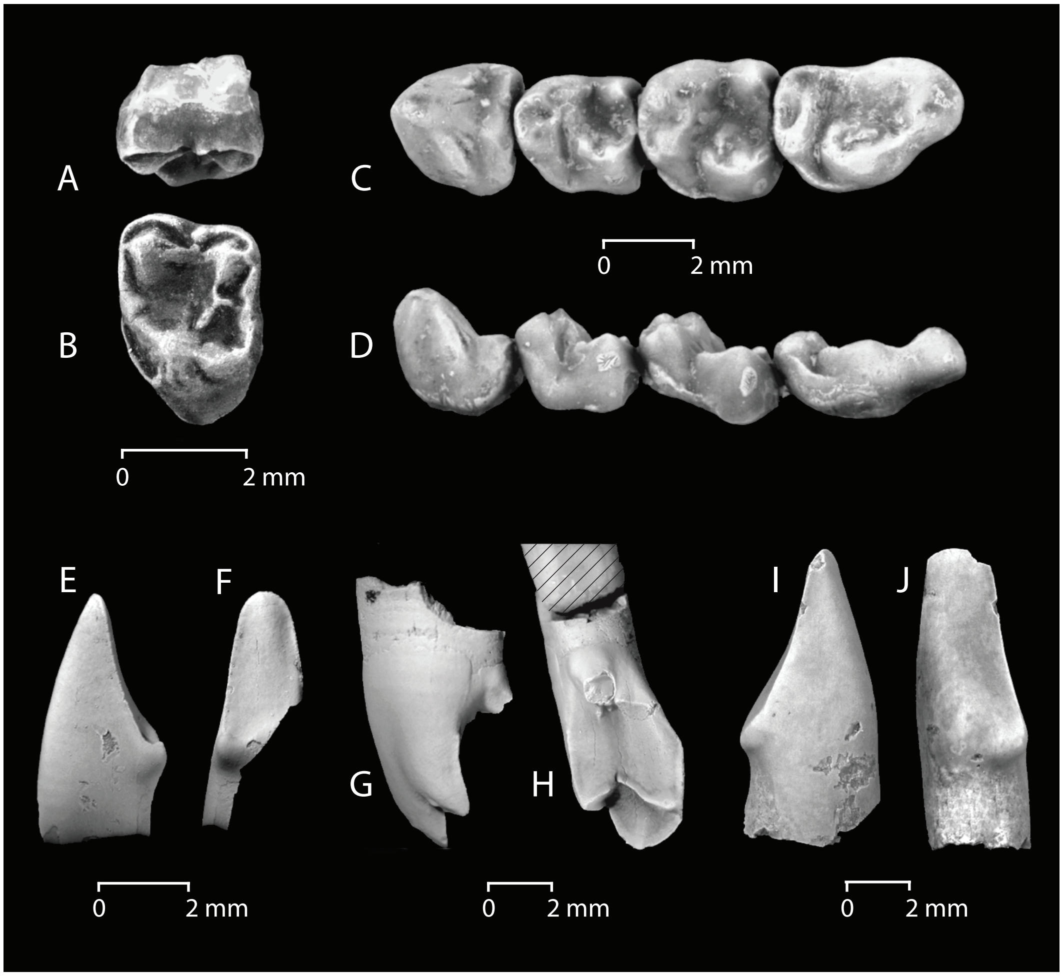


FIGURE 45 — Isolated teeth of *Chiromyoides*. A–D, *Chiromyoides caesor* from SC-243 anthills. A–B, UM 61533, left M^2 in buccal (A) and occlusal (B) views. C–D, left P_4-M_3 composite in occlusal (C) and buccal (D) views, (left to right: UM 61535, 61531, 61532, 61451). E–F, *Chiromyoides caesor*?, UM 110921, dI_1? or I_2? in lateral (E) and dorsal (F) views, from MP-115. G–H, holotype of *C. gingerichi* n. sp., UM 75671, left I^1 in lateral (G) and ventral (H) views, from FG-11. I–J, *Chiromyoides major*?, UM 102561, right dI_1? in lateral (I) and dorsal (J) views, from Paint Creek (SC-143).

thin partition. Based on the P_3 alveoli, the P_3 was considerably shorter and probably narrower than P_4. The anterior P_3 alveolus is much shorter than the posterior, and the alveoli were at least partly separated by a very thin partition of bone.

Molars from SC-243 are considerably larger and wider than those in a dentary fragment (UM 68377) of *Chiromyoides minor* from the Chappo Type Locality in southwestern Wyoming, described by Gingerich and Dorr (1979). The M_2 from SC-243 is 17% longer and 22% wider than the M_2 in the Chappo dentary. Both the M_2 and M_3 from SC-243 have a more expanded buccal margin. The I^1 holotype of *C. caesor* is 19% wider than the holotype of *C. minor*, based on data from Gingerich (1976), which appears to correspond to a widening of molars. An isolated M_1 from Chappo in the UM collections is slightly larger than the M_1 from SC-243, suggesting that there is also a larger species present at Chappo near the size of *C. caesor*.

A partial M_3 (YPM-PU 25014) from Long Draw Quarry probably also belongs to *Chiromyoides caesor*. It differs from the M_3 from SC-243 in having a less anteroposteriorly compressed trigonid with an indistinct paraconid, as opposed to no paraconid. It appears to have had a similar degree of buccal expansion and is about the same size. Both these features distinguish it from *C. minor* as represented by the Chappo dentary. UM 110955, a P^4 from Divide Quarry, may also belong to *C. caesor*, but more diagnostic specimens are needed to demonstrate the presence of the species.

Referred specimens.— **Croc Tooth Q.** (FG028): YPM-PU 21575, L I^1 (holotype). **Long Draw Q.**: YPM-PU 25014, L M_3. **SC243**: UM 61433, L P_4; 61451, L M_3; 61531, L M_1; 61532, L M_2; 61533, L M^2; 61535, L P_4; 61550, R P_4.

Chiromyoides cf. *C. caesor*

Figures 45E,F, Table 36

Biostratigraphic occurrences in Bighorn Basin.— ?*Phenacolemur* (Ti-4b), *Probathyopsis* (Ti-5a), and ?*Plesiadapis simonsi* (Ti-5b) zones.

TABLE 36 — Dental measurements for *Chiromyoides* cf. *C. caesor*, *C. gingerichi* n. sp., and *C. major*.

		C. cf. *C. caesor*		*C.* cf. *C. caesor*?	*C. gingerichi*					*C. major*			*C. major*?
		UM 92360 MP-115	UM 110150 SC-273	UM 110921 MP-115	UM 66135 SC-66	UM 67184 SC-136	UM 75671 (type) FG-11	YPM-PU 18348 Bear Creek	YPM-PU 19522 ~SC-209	Range n = 4 Paint Creek	UM 67247 Paint Creek	UM 109278 SC-179	UM 102561 Paint Creek
I^1	H	8.00	—	—	7.00	—	6.89	—	—	7.9–8.8	—	—	—
	W base	3.80	—	—	—	—	3.28	—	—	4.0–4.5	—	—	—
	W apical	—	—	—	—	—	3.74	—	—	4.5–4.9	—	—	—
	D root	6.40	—	—	4.80	—	4.76	—	—	5.9–6.5	—	—	—
	D crown	6.95	—	—	5.20	—	5.00	—	—	6.5–6.8	—	—	—
M^1?	L	2.59	—	—	—	—	—	—	—	—	—	—	—
	W	—	—	—	—	—	—	—	—	—	—	—	—
dI_2?	L	—	—	3.85	—	—	—	—	—	—	—	—	6.40
	W	—	—	—	—	—	—	—	—	—	—	—	2.67
	D	—	—	—	—	—	—	—	—	—	—	—	3.85
I_1	L	—	—	—	—	—	—	8.70	—	—	—	—	—
	W	—	—	—	—	2.97	—	2.70	—	—	—	—	—
	D	—	—	—	—	5.22	—	—	—	—	—	—	—
M_1	L	—	—	—	—	—	—	—	—	—	3.05	—	—
	W	—	—	—	—	—	—	—	—	—	2.91	—	—
M_3	L	—	4.10	—	—	—	—	—	3.74	—	—	4.07	—
	W	—	2.74	—	—	—	—	—	2.43	—	—	2.81	—

Description and discussion.— A partial left I^1 (UM 92360) from MP-115 in the McCullough Peaks area may be a large variant individual of *Chiromyoides caesor* or represent a slightly more progressive form. *Chiromyoides caesor* is distinguished from *C. major* by smaller size, and by a narrower I^1 crown (Gingerich, 1975, 1976) and mediocone. UM 92360 has the narrower aspect of *C. caesor* but it is similar in size to *C. major*. Its apical width is 15% greater than in the holotype of *C. caesor*. It has a maximum I^1 crown depth (dorsoventral) of 6.95 mm, which is slightly greater than I^1s of *C. major* (6.4-6.8 mm; n = 5; Paint Creek), but it is narrower (width = 3.8 mm, compared with 4.0-4.5, n = 4; mesiodistal just above posterocone). Its width/depth ratio is 0.55, which is closest to the holotype of *C. caesor* (0.52), but is less than in *C. major* (0.61-0.67, n = 4; mean = 0.65). The holotype of *C. potior* has a ratio of 0.66 and is dimensionally like *C. major* (Gingerich, 1976, demonstrated similar results with slightly different measurements).

UM 92360 has an additional basal cusp adjacent to the posterocone on the ventral-mesial side. This feature is not known in most species of *Chiromyoides* but is present in the holotype of *C. gingerichi* n. sp. and in *C. campanicus* from Europe. The cusp is large, prominent, and present on both the left and right I^1 in UM 92360. The area in which the cusp is situated receives heavy wear, however, and it may have been lost in some specimens. Samples of *Chiromyoides* are too small to determine if this cusp is of diagnostic value or is variably present.

A partial tooth (UM 110921) that may be a deciduous lower incisor of *Chiromyoides* was also found at MP-115 (Figs. 45E,F). It has the general form of a *Chiromyoides* I_1, but is more tapered in dorsal view. It is about half the length and depth of the expected size of an I_1 of *C. major* (Gingerich, 1976). An incisor (UM 102561, Figs. 45I,J) from Paint Creek (Cf-2) that is probably a dI_1 of *C. major* is considerably larger than UM 110921. If the Paint Creek specimen is a dI_1 of *C. major*, UM 110921 is too small to be a dI_1 of *C.* cf. *C. caesor* and may be a dI_2 without replacement or belong to a different taxon.

MP-115, is not well-constrained biostratigraphically. Teeth tentatively identified as *Plesiadapis simonsi* (UM 92359) from MP-115 suggest a Ti-5b age, but an M_3 (UM 92358) tentatively identified as *Arctocyon mumak* suggests correlation to the *Phenacolemur* zone. The additional presence of *Arctocyon* cf. *A. nexus*, which is common in the latter zone but scarce in the former, also suggests correlation to the *Phenacolemur* zone.

An isolated M_3 (UM 110150) of *Chiromyoides* from low in the *Probathyopsis* zone is nearly identical to M_3s of *C. major* (UM 109278) and *C. gingerichi* n. sp. (YPM-PU 19522), but neither of these species is known to range into the Tiffanian based on incisors. It differs markedly from the M_3 referred here to *C. caesor* (UM 61451). It is larger, the occlusal surface of the trigonid is much wider relative to the basal width, and the crown lacks the buccal expansion. The posterior lobe is larger and the crown is nearly bilaterally symmetrical, contrasted with greater asymmetry in UM 61451. Based on comparisons with other species, UM 110150 and 92360 (I^1) may belong to the same large species.

Referred specimens.— **MP115**: UM 92360, L I^1 partial, R I^1 frag., M^x frag. **SC273**: UM 110150, R M_x tri., M_3.

Chiromyoides gingerichi, new species

Figures 45G,H; Table 36

Chiromyoides potior (in part), Gingerich, 1976, p. 41. Rose, 1981a, p. 59.

Holotype.— UM 75671, a left I^1, from FG-11 in the Foster Gulch area of the northern Bighorn Basin.

Biostratigraphic occurrences in Bighorn Basin.— ?Rodentia (Cf-1) and *Plesiadapis cookei* (Cf-2) zones.

Diagnosis.— Differs from other species of *Chiromyoides* in having a shallower I^1 root depth at the base of the crown (anteroposteriorly at a right angle to the long axis of the tooth). Differs from other species of *Chiromyoides*, except *C. major* in having an I^1 mediocone that is mesiodistally wider than the laterocone. Further differs from *C. major* in having a smaller I^1 (crown is ~17% lower, 23% narrower [mesiodistally], and 23% shallower on average).

Etymology.— Named for professor Philip D. Gingerich in recognition of his outstanding contributions to our understanding of the Plesiadapidae and other Paleogene mammals.

Description.— The morphology of I^1 in *Chiromyoides gingerichi* is very close to that in *C. major*, described by Gingerich (1975, 1976). The holotype is very lightly worn. The apex of the anterocone is the highest on the crown, followed by those of the mediocone and the laterocone. The mediocone is flat on the occlusal surface and forms a shelf along its apex that contacts the laterocone distally about two thirds of the way across the occlusal surface of the crown. The laterocone is separated from the anterocone by a sharp notch. A cuspule is present on the anterior face of the laterocone. The posterocone is broken but was clearly prominent and projecting. A small, but distinct cusp was present adjacent to the ventral-mesial edge of the posterocone, but has largely been lost from wear. Several small cuspules are present along the ventral edge of the posterocone.

The crown of I_1 (YPM-PU 18348) has squared corners in occlusal view and tapers from the midsection to the base. It has a small margoconid at the base. The M_3 is like those described for *Chiromyoides* cf. *C. caesor* and *C. major* in the *C.* cf. *C. caesor* section.

Discussion.— Gingerich (1976) identified two upper central incisors (YPM-PU 17895, 21590) and a lower incisor (YPM-PU 81348) from the Clarkforkian of the Bighorn Basin as *Chiromyoides potior*. Subsequently, Rose (1981a) referred additional Clarkforkian specimens to the species, including a partial I^1 (UM 66135, Rose, 1981a, Fig. 29A). This specimen is missing the mesial half, however, and does not preserve some key diagnostic characters. The holotype of *C. gingerichi* was collected after these studies and reveals clear distinctions between it and *C. potior*, although it is similar in size. I have not been able to confirm the identification of *C. potior* by Gingerich (1976), which was based primarily on YPM-PU 17895, but there is nothing in the UM collections to suggest that more than one species of *Chiromyoides* in the size range of *C. gingerichi* is present. Thus, I provisionally refer all UM specimens previously identified as *C. potior* to *C. gingerichi*.

Chiromyoides gingerichi is distinguished from *C. potior* in having a mediocone that is considerably wider than the laterocone and more separate from it, contrasted with nearly equal, more closely approximated latero- and mediocones in *C. potior*. These cones are also more cuspate and more projecting in *C. potior*. The holotype of *C. gingerichi* is smaller than I^1s of *C. major*, but bears a similar cusp arrangement and is essentially a smaller version of *C. major*. It has a depth/width ratio of 0.68, which is close to I^1 ratios of *C. major* from the type locality that range from 0.61-0.67 (n = 4). Like *C. major*, the mediocone is considerably larger than the laterocone in mesiodistal breadth, but flatter and less projecting. The holotype also bears an additional basal cusp internal to the posterocone that has not been described in specimens of *C. major*. A similar cusp is present, however, in UM 92360, referred to *C.* cf. *C. caesor* above. This may be a variable feature in some species of *Chiromyoides*. The presumably derived state of I^1 found in both *Chiromyoides gingerichi* and *C. major* suggests that these species were closely related.

It is highly unlikely that the close resemblance of *Chiromyoides gingerichi* to *C. major* resulted from sexual dimorphism, because dimorphism has not been recognized in other plesiadapids (e.g., Gingerich, 1976). Further, if *C. gingerichi* represented females of *C. major* it would be expected to occur in approximately equal frequencies, but six I^1s of *C. major* are now known from the type locality at Paint Creek, and no specimens of *C. gingerichi* have been found there.

UM 67184, an I_1, almost certainly belongs in *Chiromyoides gingerichi* based on its small size and shallow depth. I have also identified YPM-PU 18348 as *C. gingerichi*, but with less confidence. It is from the Bear Creek fauna in southern Montana, which has been noted for its unusual faunal composition (e.g., Gunnell and Bartels, 2001). It is deeper (dorsoventrally) than UM 67184, but is slightly narrower. It is probably too small to belong to *C. major*, but could possibly belong to a different species.

Referred specimens.— **Bear Creek fauna**: YPM-PU 18348, L I_1. **FG011**: UM 75671 (holotype), L I^1. **SC209**: YPM-PU 19522, R M_3. **SC066**: UM 66135, L I^1 partial. **SC136**: UM 67184, L I_1.

Chiromyoides major Gingerich, 1975

Table 36

Chiromyoides major Gingerich, 1975, p. 143.

Holotype.— YPM-PU 21150, most of the crown of an isolated left I^1 from the Paint Creek locality (SC-143), in the northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— Rodentia (Cf-1), *Plesiadapis cookei* (Cf-2), and *Copecion* (Cf-3) zones.

Description.— *Chiromyoides major* was described and figured by Gingerich (1975, 1976) and by Rose (1981a).

Discussion.— The earliest occurrences of *Chiromyoides major* are in the Rodentia zone. UM 73527, a right I^1, bears the characteristic morphology of *Chiromyoides major*. The mediocone is larger than the laterocone, a characteristic of *C. major* (Gingerich, 1975, 1976) and *C. gingerichi* n. sp., although it is slightly less so than in most specimens of *C. major*. The crown is small for the species but it is considerably larger than that of *C. gingerichi* n. sp. A dentary (UM 73717) that preserves a partial I_1, still in the crypt, and the alveoli for P_3-M_1 (assuming permanent teeth were in place) was found at the same locality (SC-260). It is smaller than a partial dentary of *C. major* (UM 67245) figured by Rose (1981a) but it belonged to a juvenile that probably had not achieved full size. Both dentaries have a deep fossa just posterior to the symphysis about one third of the way above the base of the jaw. Two small mental foramina are present in both. Based on alveoli, the anterior roots of P_3 and P_4 were narrower than the posterior ones, especially in P_3, and P_3 was smaller than P_4. P_4 was notably shorter than M_1. Assignment of this specimen to a species is tentative because of the juvenile condition, but the dentary depth appears to be only slightly less than in UM 67245, suggesting that it belongs to *C. major*. An M_3 (UM 109278) from SC-179, which occurs low in the Rodentia zone, probably also belongs to *C. major*.

A lower incisor (UM 102561) from Paint Creek (Cf-2) probably is a dI_1 of *Chiromyoides major*, but could possibly represent an undescribed plesiadapid (Figs. 45I,J). It is too small to be a permanent incisor of any known species of *Chiromyoides*. It has a stout root that bears no indication of resorption, but the enamel appears to be thin. Like permanent I_1s of *Chiromyoides*, it is very deep (dorsoventrally) near the base of the crown, relative to crown width and height, and enamel along the cervical margin on the mesial face forms a "V" pattern pointing toward the apex of the crown. Enamel continues down the ventral face of the root much lower than on the dorsal margin. The margoconid is low, rounded, and indistinct. Most lower incisors of *Chiromyoides* have a weak margoconid, but one that is typically more distinct than in UM 102561. UM 110921, which was discussed in the *C.* cf. *C. caesor* section, may also be a deciduous lower incisor of *Chiromyoides*. However, it is considerably smaller than the Paint Creek incisor and could possibly be a dI_2 with no replacement or belong to a smaller species. Both incisors are wider near the margoconid than permanent incisors of *Chiromyoides*.

Referred specimens.— **FG006**: UM 79670, L M_3. **Paint Creek** (SC143): UM 67245, L dent. I_1-P_4 roots; 67247, R M_1; 75452, R I^1; 83014, L I^1; 83017, L I^1; YPM-PU 21150 R I^1, unassociated L I^1 (holotype); 21587, I^1. **Sand Draw Area**: YPM-PU 21588, I_1. **SC090**: UM 83431, R I^1. **SC179**: UM 109278, R M_3. **SC260**: UM 73527, R I^1; 73717, R dent. I_1 in crypt, P_3-M_1 alveoli.

Family MICROSYOPIDAE Osborn, 1892

ARCTODONTOMYS Gunnell, 1985

Arctodontomys sp.

Figure 46

Arctodontomys? n. sp., Secord et al., 2006, p. 229.

Biostratigraphic occurrences in Bighorn Basin.— upper *Phenacolemur* (Ti-4b) or lower *Probathyopsis* (Ti-5a) and *Plesiadapis simonsi* (Ti-5b) zones.

Description.— YPM-PU 17945 is the only definite specimen of this species known from the Bighorn Basin. It is a right dentary fragment that preserves M_{1-3}. The trigonids of M_1 and M_3, and the lingual talonids of M_2 and M_3 are badly damaged. The teeth also exhibit a moderately high degree of wear. M_2 is longer than M_1, while M_3 is much smaller than the other molars, especially in width. The talonid of M_1 was significantly wider than the trigonid, while the talonid on M_2 was probably only

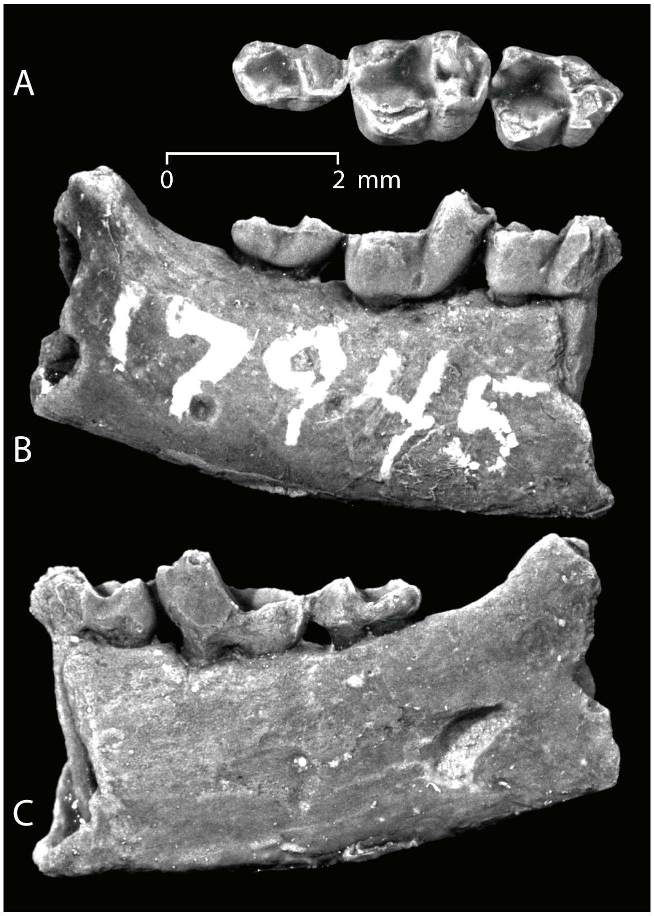


FIGURE 46 — Partial dentary of *Arctodontomys* n. sp. from Hail Quarry. A–C, right M_{1-3} (YPM-PU 17945) in occlusal (A), buccal (B), and lingual (C) views.

slightly wider. The M_1 is oriented obliquely to the long axis of the dentary, while M_{2-3} are nearly parallel. The trigonids are anteriorly inclined. The postvallids are offset from transverse. The M_1 postvallid is offset the most (~20 degrees), the M_2 less so, and the M_3 approaches transverse. No cingula are visible. The M_2 paraconid is low and distinguished from the paralophid only by a slight swelling.

The cristid obliqua contacts the postvallid buccally below the protoconid on all molars. The hypoconid is by far the largest talonid cusp on M_1 (and probably M_2), followed by the entoconid, and hypoconulid. The M_1 hypoconulid is distinct, cuspate, and anteroposteriorly compressed. It is more proximal to the entoconid than the hypoconid, and separated from the entoconid by a valley. The M_2 hypoconulid also appears to have been positioned close to the entoconid, but is worn and damaged. Molar talonid basins are relatively deep.

UM 110977 is a partial M^2 with the protocone broken away. Wear is moderately heavy. The paracone is larger than the metacone, and both cusps are low and rounded. The stylar shelf is narrow. There appears to have been a small parastyle connected to the paracone by a paracrista, but the area is worn. A curved, prominent metacrista contacts the posterobuccal corner. The outer cusps are connected by a nearly straight centrocrista. There is no mesostlye. The paraconule is heavily worn but appears to have been prominent. The metaconule is still prominent. The trigon basin is moderately deep.

Discussion.— The teeth in YPM-PU 17945 appear to belong to an undescribed species of *Arctodontomys*, best known from Big Multi Quarry in south-central Wyoming (Norejko and Beard, 1996; Wilf et al., 1998). The quarry is early or middle Clarkforkian in age. The species is also known from the late Tiffanian in the Washakie Basin (Beard, pers. comm., 2002). It has not been formally described, but casts were made available by Dr. C. Beard. One of the most distinctive features of this species is the very narrow and small M_3, relative to the size of other molars. As far as can be compared, YPM-PU 17945 differs from specimens from Big Multi Quarry in having a stronger hypoconulid on M_1 and probably M_2, that is separated from the entoconid by a distinct valley. The hypoconulid is indistinct on most of the specimens from Big Multi Quarry and is more a part of the postcristid. This difference is minor, however, and I provisionally regard the Bighorn Basin form as the same species, pending the discovery of more complete specimens.

The reasons for referring the Big Multi species to *Arctodontomys* have not been discussed, but I tentatively follow the identification of Wilf et al. (1998). I note, however, that this species also bears a close resemblance to *Navajovius kohlhaase* from Mason Pocket (Ti-4) in Colorado (Simpson, 1935d; Gunnell, 1989).

I also tentatively identify a partial M^2 (UM 110977) from Y2K Quarry as *Arctodontomys* sp. UM 110977 is near the size expected for an M^2 of this species, based on comparison with the M^2 of *Navajovius kohlhaase* (AMNH 17390) from Mason Pocket, and it is also similar in structure.

YPM-PU 17945 was collected in 1954 at Hail Quarry, which is in Sec. 23, T57N, R100W, 1.5 miles east of Princeton Quarry, according to the specimen label. Hail Quarry was plotted on areal photographs, presumably by G. L. Jepsen, in the SW1/4 of Sec. 23 between the slightly lower "PU anthills" locality (= SC-417) and the slightly higher "Horse Pasture" locality (= SC-144). I have not relocated Hail Quarry, but based on measured sections and on Jepsen's areal photograph, it lies near the base of the *Probathyopsis* zone.

Dental measurements (mm).— YPM-PU 17945: M_1, L = 1.60, talonid W = 1.25; M_2, L = 1.75, trig. W = 1.35.

Referred specimen.— **Hail Q.**: YPM-PU 17945, R dent. partial M_1, M_2, partial M_3. **Y2K Q.**: UM 110977, R M^2.

Family MICROMOMYIDAE Szalay, 1974

MICROMOMYS Szalay, 1973

Chalicomomys, Beard and Houde, 1989, p. 389.

Micromomys silvercouleei Szalay, 1973

Figures 47F,I and 48; Table 37

Micromomys silvercouleei Szalay, 1973, p. 77.

Holotype.— YPM-PU 17676, right dentary with P_4 and M_2, and five alveoli anterior to P_4; from Princeton Quarry in the northern Bighorn Basin, Wyoming.

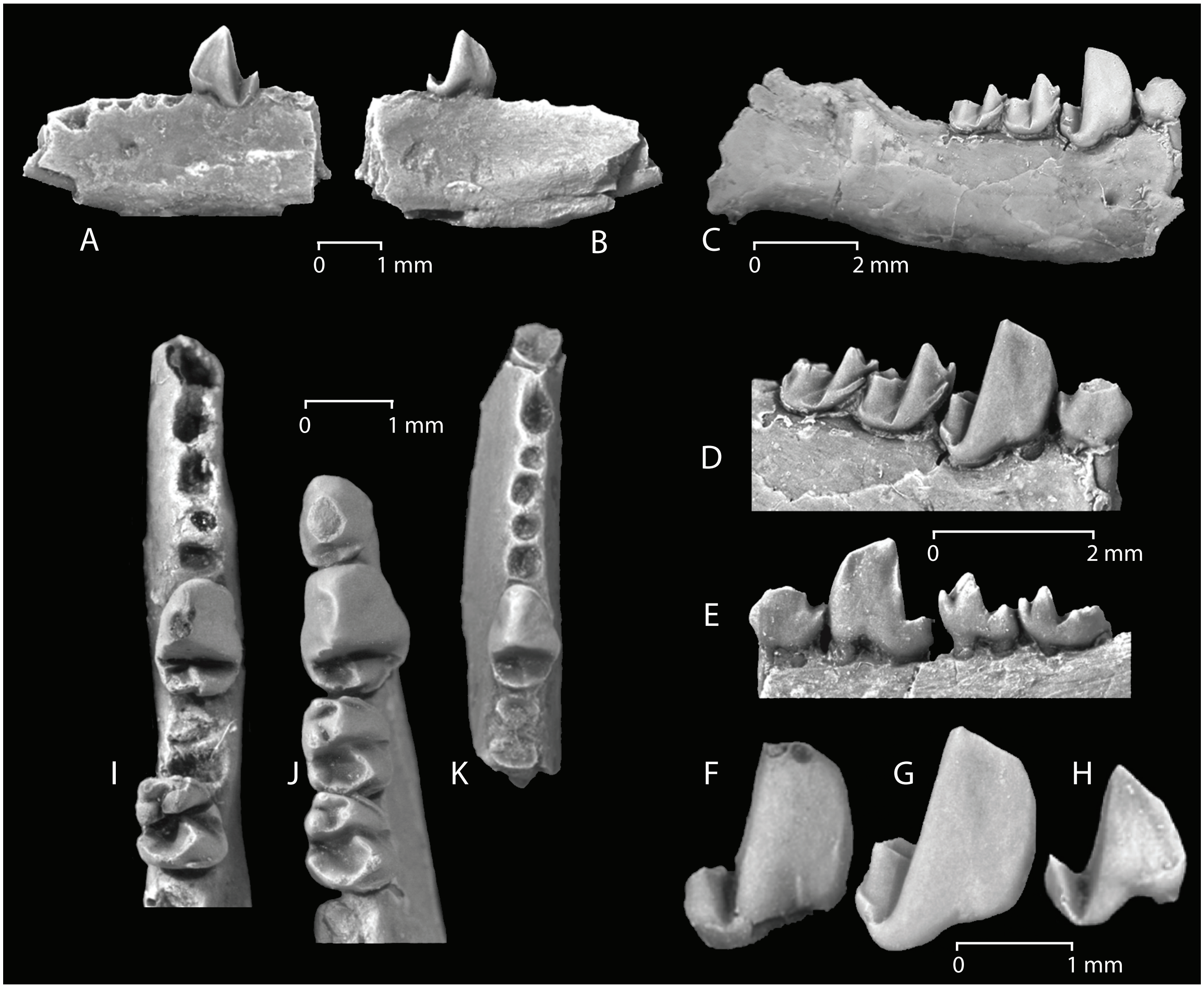


FIGURE 47 — Partial dentaries of *Micromomys* from the late Tiffanian. A–B, holotype of *M. gunnelli* n. sp. (UM 77528), left dentary with P_4 in buccal (A) and lingual (B) views, from Schaff Quarry. C–E, holotype of *M. millennius* n. sp. (UM 109659), right dentary with P_3-M_2 in buccal (C, D) and lingual (E) views, from Y2K Quarry. F–H and I–K, buccal and occlusal views of P_4 of *M. silvercouleei* (F, I), *M. millennius* (G, J), and *M. gunnelli* (H, K; reversed).

Biostratigraphic occurrence in Bighorn Basin.— *Probathyopsis* zone (Ti-5a).

Description.— The holotype was described and figured by Szalay (1973), Krause (1978), and Rose and Bown (1982), and figured in Szalay and Delson (1979, Fig. 25, p. 62). I have included photographs of a cast of the holotype (Figs. 47F,I) for comparison with other taxa.

Discussion.—The holotype of *Micromomys silvercouleei* is the only specimen of this species known with certainty. UM 77528, a left dentary preserving P_4 from Schaff Quarry, was referred to *M. silvercouleei* by Gunnell (1989), but is here designated as the holotype of *M. gunnelli* n. sp. *Micromomys silvercouleei* is the type species of *Micromomys*. Unfortunately, the holotype preserves only a P_4, a badly damaged M_2, and alveoli. Because *M. fremdi* is more complete, several authors have used it to represent the condition in *Micromomys* (e.g., Beard and Houde, 1989; Rose and Bown, 1996; Silcox and Gunnell, 2008). A comparison of the alveoli anterior to P_4 in the holotype of *M. silvercouleei*, however, indicates that it differs from *M. fremdi* in important ways. These differences have implications for the taxonomic position of *Micromomys* and particularly for the validity of "*Chalicomomys*" (Beard and Houde, 1989), a closely related species.

When Beard and Houde (1989) established "*Chalicomomys*," they noted the close phenetic similarity to *Micromomys*, but concluded that it was the result of symplesiomorphic characters. They asserted that because "*C*." *antelucanus*, the type species, shared some derived characters with *Tinimomys*, but differed in other aspects, that placing it in a new genus was the least objectionable option. Subsequently, Rose and Bown (1996) considered "*Chalicomomys*" a junior synonym of *Micromomys*. Silcox

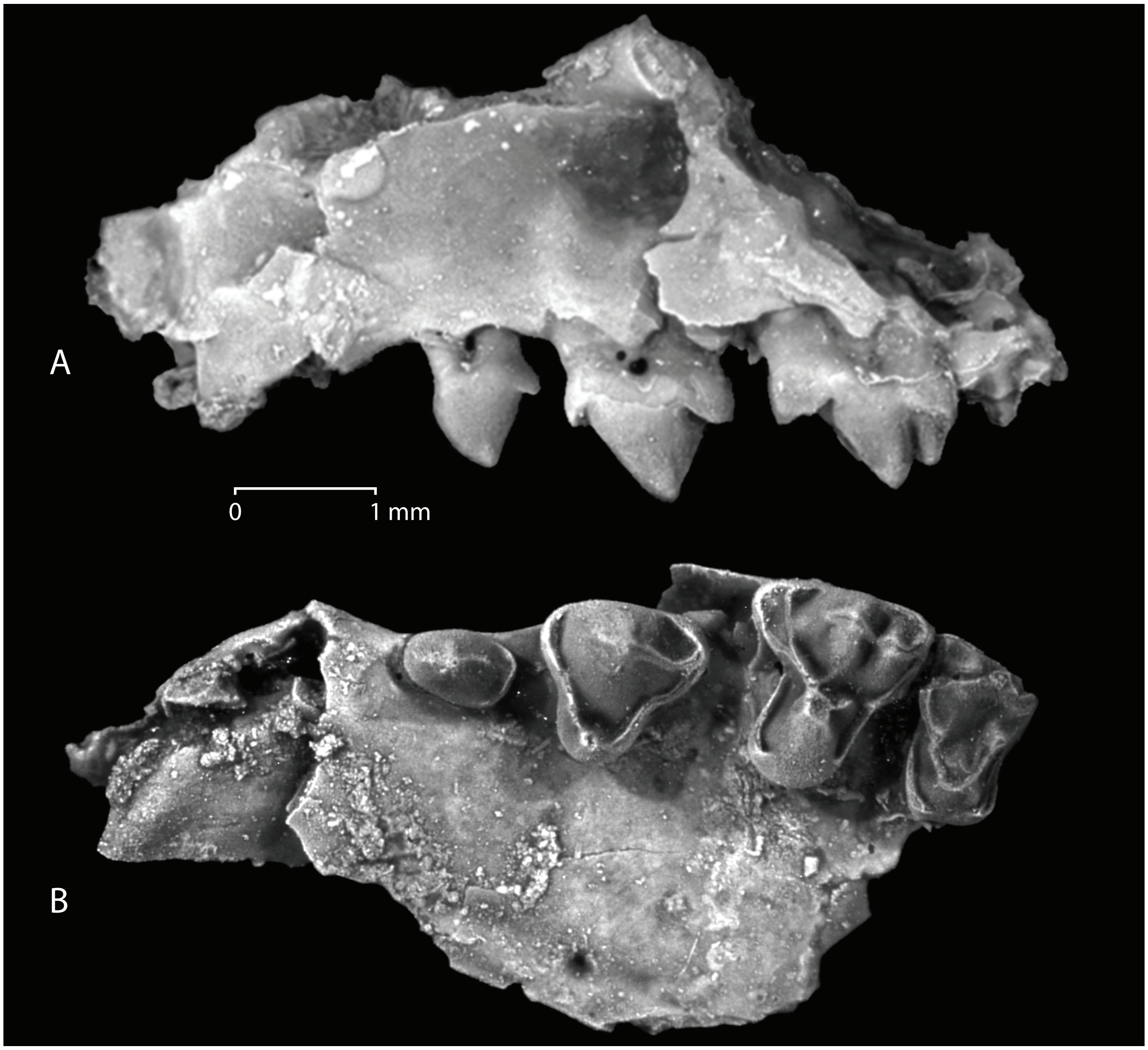


FIGURE 48 — Partial maxillary (UM 110140) of *Micromomys silvercouleei* or *M. millennius* from a late Tiffanian limestone (SC-278). A–B, left P^2-P^4 and partial M^1 (missing buccal cusps) in buccal (A) and occlusal (B) views.

and Gunnell (2008) have recognized "*Chalicomomys*" as a valid genus, however, for the same reasons as Beard and Houde, although Gunnell had a dissenting opinion. One of the characters Beard and Houde used to distinguish "*Chalicomomys*" from *Micromomys* was a double-rooted P_2 in the latter, but *M. silvercouleei* appears to have had a single-rooted P_2.

The alveoli anterior to P_4 in the holotype were discussed by Bown and Rose (1976) and by Krause (1978). Szalay (1973) did not discuss the alveoli directly, but inferred from them that *Micromomys silvercouleei* had a dental formula of 2.1.2.3. Bown and Rose (1976, pp. 132-133) noted that there were five or six alveoli anterior to P_4 and thought the most posterior ones held a double-rooted P_3. They concluded that the dental formula was probably 2.1.3.3. Upon further preparation of the holotype, however, Krause (1978) reported that there were only five alveoli preserved anterior to P_4 and that he saw no evidence for a sixth. He concluded that there were four teeth anterior to P_4 and that the dental formula was either 2.1.2.3 or 1.1.3.3. Although not explicitly stated, he presumably thought that P_3 was double-rooted and the rest of the teeth single-rooted. Of the five alveoli anterior to P_4, the two directly in front of P_4 are situated close to one another, and almost certainly held a double-rooted P_3, as concluded by Bown and Rose (1976). The two alveoli in front of the P_3 alveoli are larger than the P_3 alveoli, and are anteroposteriorly elongate. The anterior one is the largest and is posteriorly inclined, indicating that it probably held an anteriorly inclined single-rooted tooth, presumably like the C_1(?) in *M. fremdi* (Fox, 1984a). The posterior one held a single-root or two closely approximated roots. In the latter case the partition dividing the alveoli would have been obliterated. No indication of a patron has been reported by previous authors, however, nor is one evident in the holotype cast. Thus, the tooth directly in front of P_3, which was presumably a P_2, appears to have been single-rooted.

A single-rooted P_2 in *Micromomys silvercouleei* appears to be an apomorphy shared with "*Chalicomomys*" *antelucanus*, the

TABLE 37 — Dental measurements for the holotypes of *Micromomys silvercouleei*, *M. millennius* n. sp., *M. gunnelli* n. sp., *M. antelucanus* (cast), and *M. willwoodensis* (cast).

		M. gunnelli n. sp. UM 77528 Schaff Quarry	*M. silvercouleei* YPM-PU 17676 Princeton Quarry	*M. millennius* n. sp. UM 109659 Y2K Quarry	*M. willwoodensis* YPM-PU 17732 SC-2	*M. antelucanus* USNM 425589 SC-4
Dent. D		—	—	2.40	—	—
P^2	L	—	—	0.82	—	—
	W	—	—	0.57	—	—
P^3	L	—	—	1.23	—	—
	W	—	—	1.19	—	—
P^4	L	—	—	1.35	—	—
	W	—	—	1.51	—	—
P_3	L	—	—	1.02	—	—
	W	—	—	0.81	—	—
P_4	L	1.16	1.37	1.47	1.65	1.33
	W	0.80	0.98	1.28	1.32	1.07
	H	1.35	1.53	1.73	—	1.49
M_1	L	—	—	1.18	—	1.08
	W	—	—	0.99	—	1.00
M_2	L	—	—	1.16	—	1.04
	W	—	0.96	1.02	—	0.92

type species of "*Chalicomomys*," but contrasts with the double-rooted splayed roots in *M. fremdi*. The dorsal surface of the dentary is broken in the holotype of "*C.*" *antelucanus*, but the P_2 alveolus appears to have been relatively smaller, possibly representing a slightly more progressive condition.

Other characters that Beard and Houde (1989) assumed to be derived for "*Chalicomomys*" and *Tinimomys* to the exclusion of *Micromomys* include: (1) the absence of diastemata between I_1-C_1, and C_1-P_2; (2) a low crowned P_3 with a well developed heel; (3) a relatively wide and moderately exodaenodont P_4 (as used here, the degree to which enamel on the posterior root extends below enamel on the anterior root); (4) lower molars with metaconid and protoconid cusps of subequal height; and (5) a relatively long and high-crowned P^3 with a prominent and lingually situated protocone. With regard to (1), the anterior parts of the known dentaries in both *M. silvercouleei* and "*C.*" *antelucanus* are broken and the I_1-C_1 diastema cannot be adequately evaluated, but there is no appreciable diastema between C_1 and P_2 in *M. silvercouleei*. With regard to (2), the condition of P_3 is not known in *M. silvercouleei*, but it was probably close to the P_3 in *M. millennius* n. sp., for which the crown height and talonid development are about the same as in "*C.*" *antelucanus*. With regard to (3), according to my measurements based on epoxy casts of both holotypes, the P_4 in "*C.*" *antelucanus* is 9% wider, 3%, shorter, and the crown height is 3% lower, than in *M. silvercouleei*. The greater width may be a useful character, but there would probably be considerable overlap in intraspecific variability between the species. The buccal margin is more exodaenodont in *M. silvercouleei*, which is an important distinction. The utility of (4) cannot be assessed because only one molar of *M. silvercouleei* is known and individual variability is not known. With regard to (5), UM 110140 preserves P^3 (Fig. 48) and belongs to either *M. silvercouleei* or *M. millennius* n. sp. I provisionally refer it to the latter (see below), but if it belongs to *M. silvercouleei* or if the P^3 is representative of the genus, then there is essentially no difference between it and the P^3 of "*C.*" *antelucanus*. In summary, many of the derived characters used to distinguish "*Chalicomomys*" *antelucanus* from *Micromomys* also appear to be present in *M. silvercouleei*. Remaining differences do not warrant generic separation and I follow Rose and Bown in considering "*Chalicomomys*" a junior synonym of *Micromomys*.

Although many of the differences between "*Chalicomomys*" and *Micromomys* outlined by Beard and Houde (1989) are not valid for *Micromomys silvercouleei*, they are valid for *M. fremdi*. From the comparison above it appears that *M. silvercouleei* may share several synapomorphies with "*C.*" *antelucanus*, relative to *M. fremdi*, such as a single-rooted P_2, the lack of a diastema between C_1-P_2, and a relatively wider P_4. The longer P^3 and lower-crowned P_3 may also be derived characters shared by "*C.*" *antelucanus* and *Micromomys*. If the evidence presented here is affirmed by the discovery of new specimens of *M. silvercouleei*, it may be appropriate to place *M. fremdi*, and probably *M. gunnelli* n. sp., in a separate genus in recognition of the more derived condition in *M. silvercouleei*, *M. millennius* n. sp., and *M. antelucanus*.

Micromomys millennius, new species

Figures 47C–E,G,J and 48; Table 37

Micromomys n. sp., Secord, 2002, p. 105.
Micromomys n. sp. B, Secord et al., 2006, p. 229.

Holotype.— UM 109659, right dentary with P_3-M_2 and a partial alveolus for I_1; from Y2K Quarry in the northern Bighorn Basin.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis simonsi* zone (Ti-5b).

Diagnosis.— Differs from all other species of *Micromomys* in having a P_4 with a smaller length/width ratio. Differs further from other species, except *M. willwoodensis*, in having a larger P_4 with a narrower talonid basin relative to total width (measured from the cristid obliqua/postvallid contact to the lingual edge of the basin). Differs further from *M. antelucanus* and *M. willwoodensis* in having a more exodaenodont buccal lobe, extending well below the anterior base of the crown and below M_1.

In comparison to Paleocene species, *M. millennius* differs further from *M. fremdi* in having: (1) a wider, more rounded, slightly exodaenodont, and considerably more inflated P_3, with a longer, better developed talonid; and (2) a P_4 that has a marked break in slope in lateral view along the anterodorsal margin, a stronger anterior crest, and a cristid obliqua that does not ascend the postvallid.

Differs further from *M. vossae* in having: (1) a P_4 that is taller, lacks a hypoconulid, and has a cristid obliqua that does not ascend the postvallid; and (2) an M_1 talonid with a hypoconulid that is closer to the entoconid than to the hypoconid, and has no mesoconid.

Differs further from *M. silvercouleei* in having a P_4 that has a posterobuccal cingulum, is more inflated, and has a stronger vertical ridge on the anterolingual face. Differs further in having a mental foramen below the anterior root of P_4 (as opposed to the posterior root of P_3), and in having a relatively smaller M_2 paraconid.

Differs further from *M. gunnelli* n. sp. in having a P_4 that has: (1) an anterodorsal margin with a shallower slope, that has a marked break in slope in buccal view where the dorsal crest is deflected lingually; (2) a straighter anterior margin in occlusal view; (3) a stronger anterior crest; (4) a talonid with a deeper basin, a more posteriorly positioned entoconid, a more anteroposteriorly oriented cristid obliqua, and a more rounded posterior margin in occlusal view; (6) a posterobuccal cingulum; and (7) a cristid obliqua that does not ascend the postvallid.

Differs further from *Micromomys antelucanus* in being about 9% larger (M_1 length), in having a more obliquely oriented (less transverse) M_1 postvallid, and in having a posterobuccal cingulum on the P_4 talonid. The M_1 talonid is narrower, relative to trigonid width.

UM 110140 is an upper maxilla provisionally included in *Micromomys millennius*, although it could also belong to *M. silvercouleei*. Based on Fox's (1984a) description of *M. fremdi*, UM 110140 differs in having: (1) a much larger P^3, relative to P^4 or M^1, that more closely approximates an equilateral triangle in occlusal view, and has a better developed, more lingually situated protocone; (2) a P^4 with a narrower protocone; and (3) M^1 with a more quadrate outline in occlusal view. UM 110140 differs from *M. antelucanus* in having a P^3 with a larger, slightly more labial protocone, strong pre- and postcingula (as opposed to almost no cingula), and no parastyle. The P^3 of *M. antelucanus* is worn, however, which may exaggerate some differences. Upper teeth are not known for other species of *Micromomys*.

Etymology.— *Millennium* (L), thousand fold: in reference to Y2K Quarry, the type locality.

Description.— Detailed descriptions of the dentition of *Micromomys antelucanus* and *M. fremdi* were provided by Beard and Houde (1989) and Fox (1984a), respectively. The general structure of P_4 and of lower molars varies little among species of *Micromomys* and only pertinent features are described below. Dental homologies follow those of Fox (1984a).

UM 110140 preserves a left maxillary fragment with $P^{2\text{-}4}$, an M^1 with a broken buccal edge, and partial alveoli for C^1 (?). There appear to have been two closely spaced alveoli anterior to P^2 that were incompletely divided and were slightly larger than the P^2 alveoli. These alveoli presumably held a double-rooted C^1. A diastema about the length of P^2 separates the C^1 alveolus from the P^2. P^2 is double-rooted and bears only one large cusp. A crest along the posterior margin connects the apex of the cusp to a moderate cingulum that begins on the posterobuccal part of the crown and continues to the posterolingual face. P^3 approximates an equilateral triangle in occlusal view and has a large, acute buccal cusp and a much smaller and lower protocone. A paracingulum begins on the anterobuccal corner and is confluent with a strong preprotocrista that terminates at the protocone apex. A metacingulum begins near a weak metastyle and is confluent with a postprotocrista that also terminates at the protocone apex. A crest travels from the metastyle to the apex of the buccal cusp. The protocone is small, but distinct, and separated lingually from the buccal cusp by a narrow valley.

P^4 has a closely appressed paracone and metacone that are connected for most of their heights and separated only by a small valley, and buccal and lingual vertical trenches. There is a weak buccal cingulum that begins near the base of the metacone and is confluent with a metacrista that travels to the apex of the metacone. A weak metacingulum begins near the posterior base of the metacone and is confluent with a strong postcingulum. A large parastyle is positioned well anterior of the paracone on an anteriorly extended parastylar shelf, and has been reduced from wear. A precingulum begins about midway along the anterior face of the crown and continues to the base of the protocone. The pre- and postcingula are not connected across the protocone. A wide preprotocrista travels from the parastyle to the apex of the protocone. The protocone is anteroposteriorly compressed with steep anterior and posterior walls that are nearly vertical. A distinct vertical furrow is present along the posterior face of the protocone. A much shallower furrow is present in the same position on the anterior face of the protocone.

In M^1, all of the morphology buccal to the paracone and metacone apices was lost from breakage. Distinct para- and metaconules are connected to distinct pre- and postparaconule and metaconule wings. The trigon basin is shallow. Strong pre- and postcingula terminate at the lingual margin of the protocone in an incipient pericone and hypocone, respectively. The lingual margin of the crown is nearly quadrate in occlusal view.

In the holotype dentary, the alveolus for I_1 is mostly lost but the remaining part is oval in cross-section and extends at least as far back as M_1. P_3 and all teeth posterior to it are double-rooted. The P_3 crown has an inflated appearance and consists of a large central protoconid, and a small shelf-like talonid. The apex of the protoconid is broken. An anterior swelling is present about one third of the distance from the base of the crown. A small extension of enamel travels down the buccal side of the posterior root. The talonid consists of a flat lingually sloping shelf and a short cristid obliqua situated slightly buccal of the protocone apex. No basin is present, but a shallow one could have been lost from wear.

The anterior face of the P_4 trigonid is nearly flat and parallel to the postvallid. In buccal view the P_4 exhibits a distinct break in slope along the anterodorsal margin. The dorsal margin forms a secant ridge that begins at the protocone apex and descends the anterior face where it is confluent with a strong anterolingual ridge that is nearly vertical and does not reach the base of the crown. A strong exodaenodont lobe is developed on the buccal side of the posterior root. The base of the lobe extends well below the base of the enamel on the anterior root and below the base of the talonid. It extends buccally, overlapping the edge of the dentary. The postvallid is slightly oblique to the long axis of the dentary. The talonid basin is shallow and is bounded by two subparallel ridges on the buccal and lingual sides. The long axis of the basin is oblique to the long axis of the dentary. The buccal ridge (cristid obliqua) contacts an acute hypoconid. The lingual and posterior rims of the talonid basin meet posterolingually at a high point forming a kind of pseudocusp. No hypoconulid is present. A strong basal cingulum begins on the buccal side of the talonid and ends medially on the posterior side.

Molar trigonids are lingually canted. The M_1 protoconid is larger and appreciably higher than the metaconid. The paraconid is the smallest trigonid cusp and is slightly lower than the metaconid. On M_2 the protoconid and metaconid are equal in size and height, but the paraconid is smaller and slightly lower. On M_1, the hypoconulid is closer to the entoconid than to the hypoconid. On M_2, the hypoconulid is less developed and is little more than a high point in the rim of the talonid. It is also closer to the entoconid. The M_1 trigonid is about equal in width to the talonid, whereas the talonid in M_2 is wider than the trigonid.

Dentary depth is twice the height of the M_1 trigonid on the buccal side. A small mental foramen is present below the anterior root of the P_4.

Discussion.— The two specimens included here represent the most complete micromomyid specimens known from the late Tiffanian. The holotype was discovered in a small piece of matrix collected from Y2K Quarry for screenwashing. The break along the anterior margin exhibits abrasion and indicates that the anterior part of the dentary was detached before the sediment was lithified. Nevertheless, parts of other such dentaries that clearly belong together have been recovered from the quarry, and there is some hope of recovering more of the specimen. The maxilla (UM 110140) was preserved in a small piece of freshwater limestone and recovered by etching in formic acid. The preparation and taphonomy of similar Clarkforkian and Wasatchian age limestones were discussed by Bloch and Bowen (2001), Bloch and Boyer (2001), and Bowen and Bloch (2002).

The holotype most closely resembles *Micromomys silvercouleei* from the late Tiffanian, and *M. willwoodensis* and *M. antelucanus* from the early Wasatchian. *Micromomys antelucanus* was the type species for *Chalicomomys* (Beard and Houde, 1989), but I consider *Chalicomomys* a junior synonym of *Micromomys* for reasons discussed in the *M. silvercouleei* section. Y2K Quarry lies about 85 meters stratigraphically above Princeton Quarry, which yielded the holotype of *M. silvercouleei*. The holotype of *M. millennius* differs from that of *M. silvercouleei* primarily in relative width and degree of hypertrophy of P_4. The P_4 is 7% longer in the former, but about 30% wider. The degree of exodaenodonty is similar in both P_4s, but the buccal lobe of *M. millennius* extends buccally over the dentary wall to a greater degree. The distance between M_{1-3} alveoli is about 8% greater in *M. millennius*, indicating that it was slightly larger overall. The only known molar of *M. silvercouleei* is badly damaged and precise size comparisons are not possible. Nothing is known of the variability in *M. millennius* or *M. silvercouleei*, but P_4s in the closely related *M. fremdi* (Fox, 1984a) and *M. antelucanus* (Beard and Houde, 1989) do not exhibit variability this extreme.

The most obvious difference between *Micromomys millennius* and the Wasatchian species is the greater degree of P_4 exodaenodonty in the former. The base of the enamel on the posterior root of P_4 in *M. antelucanus* and *M. willwoodensis* is only slightly below that on the anterior root, while in *M. millennius* it is much lower. All of the Tiffanian species exhibit a greater degree of P_4 exodaenodonty than either *M. antelucanus* or *M. willwoodensis*. Additionally, *Micromomys millennius* has a P_4 length/width ratio of 1.15, compared with 1.24 in *M. antelucanus*, and 1.25 in *M. willwoodensis*. Ratios are higher in other species.

I have provisionally included UM 110140, a left maxilla, in *Micromomys millennius* because of the size of P^3 relative to other teeth. Based on relative width proportions of P^3 and P_{3-4} in *M. fremdi* and *M. antelucanus*, one might expect the P^3 of *M. millennius* to be slightly wider than that of *M. antelucanus*, which is the case in UM 110140. Alternatively, it could belong to *M. silvercouleei*. It is notable that differences between UM 110140 and the maxilla referred to *M. antelucanus* by Beard and Houde (1989) (CM 425588) are small enough that they may be attributed to individual variation if characters of the lower dentition did not support specific separation. As discussed in the *M. silvercouleei* section, several characters shared between these species, such as the expanded P^3, could be synapomorphies, suggesting close affinities.

Referred specimens.— **SC278**: UM 110140, L P^{2-4}, partial M^1, alveoli for C^1. **Y2K Q.**: UM 109659 (holotype).

Micromomys gunnelli, new species

Figures 47A–B,H,K; Table 37

Micromomys silvercouleei (UM 77528), Gunnell, 1989, p. 84.
Micromomys n. sp. A, Secord et al., 2006, p. 229.

Holotype.— UM 77528, left dentary with P_4, root of I_1, and alveoli for C_1-P_3, and M_1; from Schaff Quarry on the western side of Polecat Bench, in the northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* zone (Ti-5a).

Diagnosis.— Differs from other species of *Micromomys* in having a smaller P_4 (and probably smaller M_1). Differs further in having a steeper sloping anterodorsal margin on P_4 in buccal view, that lacks the sharp break in slope exhibited by other species, except *M. fremdi*.

Differs further from *Micromomys millennius* n. sp. and *M. willwoodensis* in having a P_4 that has: (1) a larger length/width ratio; (2) a wider talonid basin, relative to total width; (3) a talonid with the entoconid positioned along the posterior-most margin (as opposed to being more anterior); (4) a weaker vertical ridge on the anterolingual margin; and (5) a more rounded anterior margin in occlusal view (the anterior margins of *M. millennius* n. sp. and *M. willwoodensis* are nearly flat). Differs further from *M. silvercouleei* in having a mental foramen below the anterior root of P_4 (as opposed to the posterior root of P_3), and in (3), (4), and (5) above. Differs further from *M. antelucanus* in (1), (3), (4), and (5) above.

Differs further from *M. fremdi* in having smaller P_4 length/width ratio, and in lacking a significant diastema between C_1 and P_2. *Micromomys fremdi* and *M. vossae* may also differ in (3). Differs further from *M. silvercouleei* and *M. antelucanus* (and probably *M. millennius* n. sp., and *M. willwoodensis*) in having a double-rooted P_2. Differs further from *M. vossae* in having a P_4 with only one cusp (rather than three) and in (5).

Etymology.— Named for Dr. Gregg F. Gunnell, in recognition of his many contributions to our understanding of plesiadapiformes and other mammals.

Description.— The holotype was also figured in Gunnell (1989, Fig. 25, p. 84). I follow the dental homologies of Fox (1984a) for *Micromomys fremdi*, although other interpretations are possible.

The base of the root of I_1 is oval in cross-section and laterally compressed, as in other plesiadapiforms. Five alveoli anterior to P_4 are present. The most anterior one is anteroposteriorly elongate and much longer (~0.7 mm) than the other four. The root is posteriorly inclined, indicating that it held a single-rooted, anteriorly projecting crown. The remaining four alveoli are nearly round and appear to be close to vertical, but only the upper-most parts are visible. If viewed as pairs, the posterior alveolus is larger than the anterior one in both pairs, which is a pattern typical of double-rooted teeth, and the pairs are separated by a very short diastema. The alveoli probably held two double-rooted teeth, P_2 and P_3. There is a another very short diastema between the C_1 alveolus and the anterior alveolus for P_2, and a longer one would have been present between I_1 and C_1 (assuming there were no additional teeth).

The P_4 is lightly worn. It consists of a high protoconid and simple talonid. No paraconid or metaconid is present. A crest descends from the protocone apex along the anterior margin of the crown and is deflected lingually. In buccal view the anterior margin exhibits a slight change in slope where the crest is deflected. A buccal lobe on the posterior root extends well below the base of enamel on the anterior root and slightly overhangs the buccal side of the dentary. A weak buccal cingulum begins on the anterobuccal face of the crown and continues posteriorly to just past the anterior root. The postvallid is nearly transverse. The talonid is simple and has a shallow basin. The cristid obliqua is low, rounded, and indistinct. It is anteroposteriorly oriented and continues up the postvallid where it is deflected lingually forming a convex upward curve. The hypoconid is little more than a high point where the cristid obliqua contacts the posterior rim of the basin. No other talonid cusps are visible. The posterior margin of the talonid is rounded in occlusal view and the cristid obliqua reaches the margin near its posterior-most extremity.

A precise measure of the dentary below the M_1 root is not possible due to breakage along the ventral margin. Two small mental foramina are present, one below the posterior root of P_2 and one below the anterior root of P_4. The latter is positioned slightly lower.

Discussion.— The holotype of *Micromomys gunnelli* was initially identified as *M. silvercouleei* by Gunnell (1989), partly because it was from nearly the same stratigraphic level and the same geographic area as the holotype of the latter. Although there are similarities in the construction of P_4, other features indicate that the specimen belongs in a separate species. The P_4 is about 15% shorter and 20% narrower, lacks the distinctive break in slope along the anterodorsal margin, and has a simpler talonid than *M. silvercouleei*. Perhaps even more compelling is the difference in the spacing, size, and number of alveoli anterior to P_4. As discussed above, the holotype of *M. silvercouleei* probably had a single-rooted P_2, whereas *M. gunnelli* probably had a double-rooted P_2. Moreover, the size of the two alveoli anterior to the P_3 alveoli in M. silvercouleei are much larger and anteroposteriorly elongate. The pattern of alveoli in *M. gunnelli* is consistent with that in *M. fremdi* from the middle Tiffanian (Fox, 1984a), which had a single anteriorly projecting C_1, and double-rooted second and third premolars that are nearly equal in length. The only noticeable difference in alveoli is that *M. fremdi* has a longer diastema between C_1 and P_2.

The overall structure of P_4 in *Micromomys gunnelli* is also closest to that of *M. fremdi*, based on the description and figures provide by Fox (1984a). The P_4 of *M. gunnelli* differs from those of contemporary and younger species in having a steeper slope along the anterodorsal margin in buccal view, and in lacking the distinctive break in slope exhibited by other species (Figs. 47F-H). In species of *Micromomys*, the break in slope occurs where the dorsal crest is deflected lingually into a vertical ridge on the anterolingual face of the crown. Among other species of *Micromomys*, the break in slope is least apparent in *M. fremdi*. It is slightly more developed than in *M. gunnelli*, but this amount of difference may be within individual variation. The talonid basin also differs from other species (except *M. fremdi*) in shallowness, in having only a single weak cusp (hypoconid), and in having a cristid obliqua that ascends the postvallid of the trigonid. Although wear could have reduced the depth of the basin and removed cusps, other parts of the crown do not exhibit a high degree of wear. Most features shared with *M. fremdi* are presumably primitive (e.g., Fox, 1984a; Beard and Houde, 1989). The loss of a significant diastema between C_1 and P_2, and the widening of P_4 appear to be advanced traits, however, shared with younger species of *Micromomys*.

The co-occurrence of *Micromomys gunnelli* and *M. silvercouleei* in the same area and in the same biozone is important because it demonstrates that at least two micromomyid lineages were present in the late Tiffanian. Although *M. silvercouleei* and *M. millennius* n. sp. could have been part of a single lineage, *M. gunnelli* almost certainly represents a separate lineage.

Referred specimen.— **Schaff Q.**: UM 77528 (holotype).

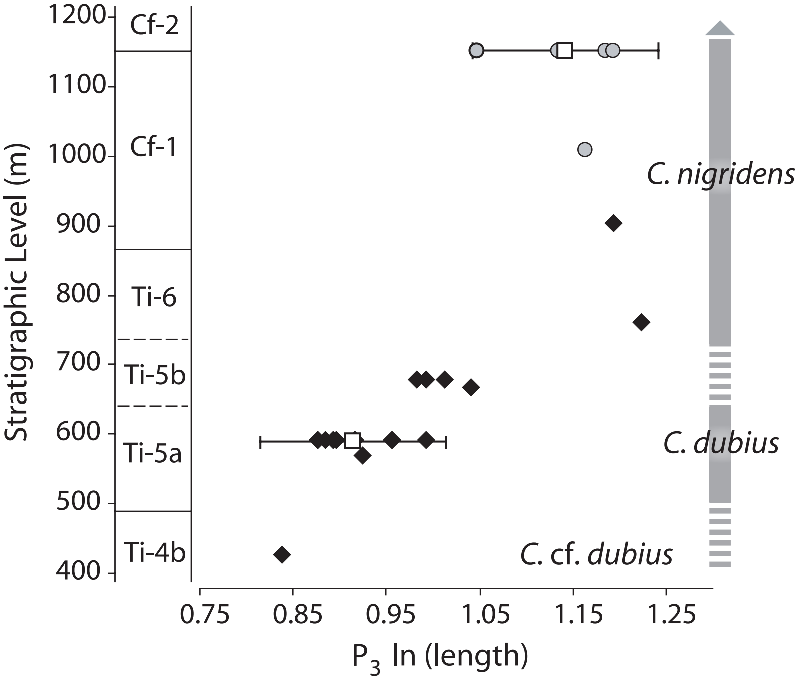


FIGURE 49 — Stratigraphic chart of P_3 length for *Carpolestes* cf. *C. dubius*, *C. dubius*, and *C. nigridens* through the late Tiffanian and early Clarkforkian. Solid diamonds indicate specimens from the Polecat Bench sequence; gray circles indicate localities that were biostratigraphically correlated to the sequence. Solid gray bars correspond to levels for which a species is known with relative confidence; dashed bars indicate intermediate or conferred forms. Squares show mean values for Princeton Quarry (592 m) and Paint Creek (1150 m); error bars show the expected range of variability for a species of 0.2 ln units. Data for Princeton Quarry, YPM 24614 from Paint Creek, and AMNH 22196 from Bear Creek (mid Cf-1) are from Rose (1975).

Family CARPOLESTIDAE Simpson, 1935

CARPODAPTES Matthew and Granger, 1921

Carpodaptes hazelae Simpson, 1936

Carpodaptes hazelae Simpson, 1936, p. 21. Rose, 1975, p. 21.

Holotype.— AMNH 33854, right dentary with P_4-M_3, from Scarritt Quarry, Crazy Mountains Basin, Montana.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description and discussion.— A description of the holotype of *Carpodaptes hazelae* was provided by Simpson (1936). A much larger sample of *C. hazelae* from Cedar Point Quarry was identified and described by Rose (1975). The sample is especially important because it provides an example of the dental variability in a carpolestid species. Additional specimens subsequently collected from Cedar Point Quarry by UM crews are within the variability described by Rose.

Referred specimens.— **Cedar Point Q.**: UM 64400, L dent. P_4-M_2; 64415, R dent. P_4-M_3; 64416, R dent. P_4-M_3; 64422, R dent. P_4-M_2; 64444, L dent. I_1, P_4-M_3; 64448, R dent. M_{1-2}; 64515, L dent. P_4-M_1; 64559, R dent. P_4-M_2; 82049, L dent. P_4, M_3; 82053, R dent. P_4-M_3; 82065, R dent. P_4-M_2; 82095, L dent. P_4, partial M_1; 83226, L dent. P_4-M_3. Plus additional YPM-PU specimens listed by Rose (1975).

Carpodaptes stonleyi Fox, 2002

Carpodaptes cygneus, Bloch, et al., 2001.
Carpodaptes stonleyi Fox, 2002, p. 870.

Holotype.— UALVP, 8744, a partial left dentary with P_4-M_2, and alveoli for I_{1-2}, C_1, and P_3; from locality UAR2, near Roche Percée, southeastern Saskatchewan. Reportedly late Tiffanian in age.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Description.— An exhaustive description of the holotype was provided by Fox (2002).

Discussion.— Several well-preserved dental specimens of *Carpodaptes* are known from Divide Quarry (Appendix IB). The specimens were recently described by Bloch et al. (2001) who identified them as *C. cygneus*. Fox (2002), however, included the Divide Quarry specimens in a new species, *C. stonleyi*, and restricted *C. cygneus* to its type locality in Alberta. *Carpodaptes stonleyi* appears to be a valid species, distinct from *C. cygneus*, and I provisionally follow Fox's inclusion of the Divide Quarry specimens in this species.

Referred specimens.— **Divide Q.** (FG046): UM 77295, L dent. P_4-M_3; 77321, R dent. P_4-M_3; 80669, R dent. P_4-M_2; 83237, L dent. P_4-M_2; 85236, L dent. P_4; 85283, L dent. P_4-M_1; 85286, L dent. I_{1-2}, P_4; 86236, L dent. P_4; 91324, L max. P^{2-4}, M^{2-3}.

CARPOMEGODON Bloch et al., 2001

Carpomegodon jepseni (Rose, 1975)

Carpodaptes jepseni Rose, 1975, p. 33. Szalay and Delson, 1979, p. 98. Gingerich, 1980a, p. 412.
Carpomegodon jepseni, Bloch et al., 2001, p. 120.

Holotype.— YPM-PU 20716, a right dentary with P_4-M_2 from Divide Quarry in the Foster Gulch area of the northern Bighorn Basin.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Description and discussion.— Descriptions of *Carpomegodon jepseni* were provided by Rose (1975) and Bloch et al. (2001). The species was initially placed in *Carpodaptes* by Rose (1975), who noted that it did not fit well into either *Carpodaptes* or *Carpolestes*. Additional specimens were subsequently collected from Divide Quarry by UM crews. Bloch et al. (2001) described these specimens and transferred the species to *Carpomegodon*, a new monotypic genus. No new specimens of *C. jepseni* have been reported. It is known only from Divide Quarry, with the exception of a fragmentary P_4 (YPM-PU 20852) from Long Draw Quarry that may belong to the species (Rose, 1975).

Referred specimens.— **Divide Q.** (FG046): UM 80575, R dent. P_4-M_3; 81290, R P_4; 83264, L P_4; 85282, R dent. P_4-M_2, R P^3, unassoc.; 85400, R dent. P_4-M_3; 85404, R M_2; 85918, L max. P^1-M^2; 86241, L max. P^3-M^2, alveoli for C^1-P^2; 92257, R max. $P^{2\text{-}3}$; 92261, R max. P^3-M^2; 92279, L dent. P_4-M_2; 110231, L M_1; YPM-PU 20716, R dent. P_4-M_2.

CARPOLESTES Simpson, 1928

Carpolestes dubius Jepsen, 1930b

Figures 49–50; Table 38

Carpolestes dubius Jepsen, 1930b, p. 520. Rose, 1975, p. 37.

Holotype.— YPM-PU 13275, right dentary with C_1, P_4-M_3, roots for I_1 and P_3, and alveolus for I_2; from Princeton Quarry, on the west side of Polecat Bench, the northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a) and *Plesiadapis simonsi* (Ti-5b) zones.

Description.— The holotype and partial upper dentition were described and illustrated by Jepsen (1930b). A larger sample of *C. dubius* was subsequently described and illustrated by Rose (1975). A reconstruction of the skull and left dentary was published in Szalay and Delson (1979, Fig. 44). Metric graphs including *C. dubius* were published by Rose (1975), Bloch and Gingerich (1998), and Bloch et al. (2001).

The I^1 of *Carpolestes dubius* has never been described. Based on specimens from Y2K Quarry, it has four principal cusps, an anterocone, a laterocone, and two basal cusps (a "doubled posterocone"). The crown is nearly straight along the distal margin in occlusal view, but swells mesially in the apical region near the anterocone. The laterocone is larger than the anterocone, and the lateral basal cusp is larger than the mesial one. A prominent crest on the mesial margin of the crown travels from the apex of the anterocone to near the base, where it

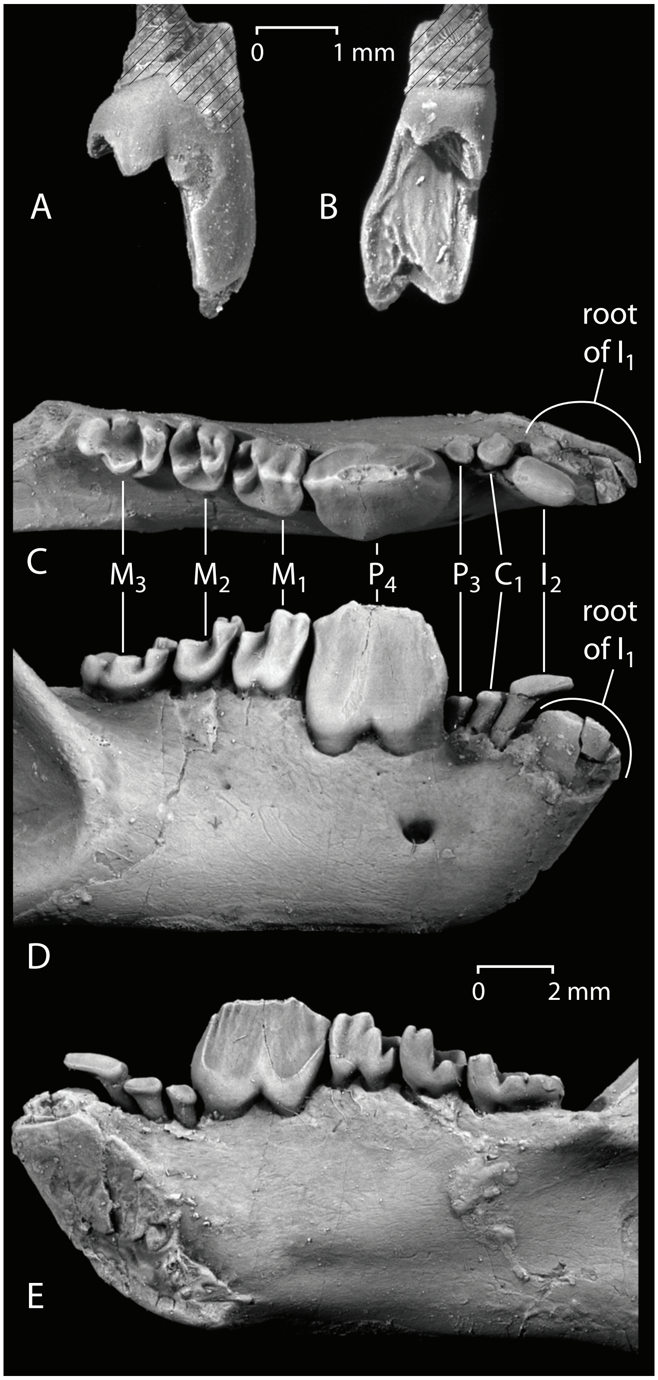


FIGURE 50 — Teeth of *Carpolestes dubius* and *C. nigridens*. A–B, right I^1 of *C. dubius* (109542) in lateral (A) and ventral (B) views, from Y2K Quarry. C–E, UM 109599, right dentary of *C. nigridens* with I_1-M_3 in occlusal (C), buccal (D), and lingual (E) views, from SC-181 limestone. Apex of P_4 truncated by weathering from limestone block.

TABLE 38 — Dental statistics for *Carpolestes dubius* from Y2K Quarry. HP = buccal crown height from base of posterior exodaenodont lobe to ultimate cusp. Abbreviations as in Table 3. *Estimate.

		n	Min.	Max.	Mean	SE	SD	V
I^1	H	1	—	—	3.0*	—	—	—
	W	2	1.00	1.10	1.05	—	—	—
	D	1	—	—	1.35	—	—	—
P^2	L	2	0.80	0.92	0.86	—	—	—
	W	2	0.75	0.75	0.75	—	—	—
P^3	L	3	2.67	2.75	2.71	0.02	0.04	1.49
	W	3	2.35	2.49	2.42	0.04	0.07	2.90
P^4	L	2	2.25	2.37	2.31	—	—	—
	W	2	2.26	2.35	2.31	—	—	—
M^1	L	1	—	—	1.70	—	—	—
	W	1	—	—	2.27	—	—	—
M^2	L	2	1.53	1.57	1.55	—	—	—
	W	2	2.20	2.45	2.33	—	—	—
M^3	L	3	1.30	1.40	1.36	0.03	0.05	3.78
	W	3	1.97	2.20	2.09	0.07	0.12	5.52
I_1	L	1	—	—	5.20	—	—	—
	W	3	1.02	1.11	1.06	0.03	0.05	4.47
	D	3	1.77	1.88	1.82	0.03	0.06	3.13
P_4	W	5	2.10	2.45	2.22	0.06	0.14	6.43
	HP	6	3.10	3.45	3.29	0.06	0.15	4.57
M_1	L	9	1.95	2.20	2.06	0.02	0.07	3.19
	W	9	1.55	1.85	1.71	0.03	0.10	6.11
M_2	L	6	1.65	1.90	1.77	0.03	0.08	4.71
	W	7	1.47	1.70	1.60	0.03	0.08	4.91
M_3	L	4	2.27	2.40	2.32	0.03	0.06	2.39
	W	4	1.33	1.47	1.43	0.03	0.06	4.49

may have been continuous with a shorter crest that mesially encloses a small basin. The latter crest is sharp, dorsoventrally oriented, and mesial of the mesial basal cusp. It creates a shallow basin bounded ventrally and laterally by posterocone cusps. The crest is rapidly reduced from wear. The enamel is wrinkled on unworn specimens.

Discussion.— When Jepsen (1930b) initially described *Carpolestes dubius* his diagnosis was based on a small sample of specimens from Princeton Quarry. Much larger samples were subsequently collected from Princeton and Schaff quarries, and other localities in the Silver Coulee area. After studying these samples, Rose (1975) concluded that *C. dubius* could only be differentiated from the younger *C. nigridens* (Simpson, 1928) by features in P^3. New, more complete specimens suggest, however, that dentaries of *C. nigridens* can be distinguished from those of *C. dubius* by a shortening of the dentary between I_1 and P_4 (see *C. nigridens* discussion below). The P^3 in *C. nigridens* has a better developed anterobuccal projection ("spur") and has five well-developed buccal cusps, compared with four in *C. dubius*. These features were illustrated by Rose (1975, Fig. 27) and P^3 dimensions for both species were compared in graphs by Rose (1975, Fig. 28), and Bloch and Gingerich (1998, Figs. 10 and 11). Rose (1975) speculated that a larger sample of *Carpolestes nigridens* might show overlap in the variability of the key characters in P^3 distinguishing it from *C. dubius*, which could render the latter invalid. Three additional P^3s of *C. nigridens*, however, all have the expanded anterobuccal lobe characteristic of the species, suggesting little, if any, overlap in the variability of this feature. Rose (1981a, p. 62) listed two additional P^3s of *C. nigridens*, but one (UM 71002) was subsequently included in *C. simpsoni* by Bloch and Gingerich (1998).

Figure 49 is a stratigraphic chart showing change in P^3 length in *Carpolestes* from the late Tiffanian to the middle Clarkforkian in the Clarks Fork Basin. Error bars are ±0.2 natural log length, which is approximately equivalent to four standard deviations (e.g., Gingerich, 1979b, 1980a). Note that there is no overlap in error bars between *C. dubius* and *C. nigridens*. Twelve P^3s are included from Princeton Quarry (592 m, Ti-5a), but because of rounding by Rose, fewer points are apparent. There appears to have been a relatively rapid expansion of the P^3 lobe between Princeton Quarry and the base of the *Plesiadapis gingerichi* zone (Ti-6, SC-178), and the fully developed P^3 of *C. nigridens* was already present in the latest Tiffanian.

Rose (1981a), described UM 69251 (isolated P^3) as an intermediate between *Carpolestes dubius* and *C. nigridens* in the degree of projection of the anteroexternal spur. The specimen plots directly below Y2K Quarry (692 m, Ti-5b) in Figure 49 and is longer than any from Princeton Quarry. Two of three P^3s recently collected at Y2K Quarry exhibit a similar degree of expansion of the anteroexternal spur, and confirm that UM 69251 is not an anomaly. Most of the P_3 data in Figure 49 were included in two graphs by Bloch and Gingerich (1998, Figs. 10 and 11). Their Figure 10 showed that the P^3s of *C. nigridens* plot in a discrete area, and are readily distinguished from those of *C. dubius* by length and width. However, new measured sections have changed the stratigraphic levels of some localities. Of importance is a P^3 from Fossil Hollow (UM 69240) which is their "760" point in Figure 10 and is also plotted in Figure 11 at the 760 meter level (note that many levels in these charts are not comparable to those presented here). Fossil Hollow was placed at about 60 meters above Princeton Quarry (e.g., Gingerich, 2001), but new sections indicate it is actually about 165 meters below it (Fig. 49, 426 m). I have referred UM 69240 to *C.* cf. *C. dubius*. It is smaller than any P^3 of *C. dubius* reported by Rose (1975) from Princeton Quarry, and P_4s of this from are lower crowned than in *C. dubius*. Also of note is UM 101821 from SC-178, which is the oldest specimen that can be confidently identified as *C. nigridens* (Fig. 49, base of Ti-6). It was plotted at the beginning of the Clarkforkian in Figure 11 by Bloch and Gingerich (1998). However, the beginning of the Clarkforkian is recognized here by the first occurrence of rodents, which have not been found as low as SC-178. Thus, SC-178 is latest Tiffanian in age.

When dealing with species in an evolutionary lineage, the referral of specimens with intermediate morphology collected at intermediate levels is somewhat arbitrary (e.g., Rose, 1981a). Specimens from Y2K Quarry and SC-199 do exhibit a somewhat intermediate condition, as discussed above, but I include them in *C. dubius* because they do not exhibit the extreme expansion of

TABLE 39 — Dental measurements for *Carpolestes* cf. *C. dubius*. All specimens are from Fossil Hollow, except UM 110062, from SC-417. HP = buccal crown height from base of posterior exodaenodont lobe to ultimate cusp. *Estimate.

		UM 69238	UM 69240	UM 79878	UM 80248	UM 100360	UM 104925	UM 110062	UM 110108
P^3	L	—	2.31	—	—	—	—	—	—
	W	—	2.14	—	—	—	—	—	—
M^1	L	—	—	—	1.51	—	—	—	—
	W	—	—	—	2.25	—	—	—	—
M^2	L	—	1.26	1.3*	1.42	—	—	—	—
	W	—	1.97	1.8*	2.05	—	—	—	—
M^3	L	—	1.10	1.10	—	—	—	—	—
	W	—	1.73	1.65	—	—	—	—	—
P$_4$	L	—	—	—	—	2.76	3.10	—	—
	W	—	—	—	—	1.87	1.75	—	—
	HP	—	—	—	—	2.70	2.2*	—	—
M$_1$	L	—	—	—	—	1.73	1.70	1.52	—
	W	—	—	—	—	1.56	1.50	1.41	—
M$_3$	L	1.97	—	—	—	—	—	—	1.95
	W	1.20	—	—	—	—	—	—	1.30

the P^3 anterobuccal lobe characteristic of *C. nigridens*. Additionally, the distance between I$_1$ and P$_4$ in UM 109111 is more than 30% greater than in *C. nigridens* (UM 109599) and the position of P$_3$ is not as posterolingual as in the dentaries of *C. nigridens* as discussed below. The P$_3$ position in the Ti-5b specimens is similar to that in *C. dubius* (YPM-PU 19409).

The upper incisors described here from Y2K Quarry are the first ones described for *Carpolestes dubius*. I^{1}s are unknown for *C. nigridens* but have been described for *C. simpsoni* (Gingerich, 1987; Bloch and Gingerich, 1998). Based on measurements and figures in Bloch and Gingerich (1998), the I^{1}s from Y2K Quarry are about 30% higher crowned (base of crown to apex) than those of *C. simpsoni*, and are deeper (dorsoventral depth, 1.80-1.85 mm in *C. dubius*). The incisors appear to be the same in other respects. They are also similar to those of *Carpodaptes stonleyi* (Fox, 2002), formerly identified by Krause (1978) and Rose et al. (1993) as *C. cygneus*. They are larger than those of *C. stonleyi* and *C. hazelae*, however, and differ further from *C. hazelae* in lacking a mediocone.

Fox (2002) questioned the validity of *Carpolestes dubius*, because it could be distinguished from *C. nigridens* only by features of the P^3, while its holotype is a dentary. Although this situation can be problematic for species with holotypes from isolated localities that have not produced additional specimens, this is not the case for *C. dubius*. Rose (1975) reported fourteen P^{3}s from Princeton Quarry, representing at least seven individuals. Associations of material from the same individual are common at the quarry and one or more of the P^{3}s may belong to the same individual as the holotype. More importantly, there is no evidence for there being any other species of *Carpolestes* present at Princeton Quarry, or at any of the other quarries in the lower part of the *Probathyopsis* zone. Thus, P^{3}s from Princeton Quarry can be confidently identified as *C. dubius*.

Referred specimens.— **SC144**: UM 67265, L dent. P$_4$-M$_1$ (part). **SC165**: UM 68264, L dent. M$_2$, R dent. frag.; 71007, L max. P$^{3-4}$ (frags.), M^2; 81710, L P$_4$; 108486, L dent. P$_4$-M$_2$; **SC187**: UM 68856, L dent. P$_4$-M$_2$; 68857, L dent. P$_4$; 68859, L max. P^3-M^2, R max. P$^{3-4}$; 69297, L dent. P$_4$-M$_1$; 73598, R max. P$^{3-4}$ (partial), P^2, assoc.; 80356, L P$_4$ dent. frag.; 80361, R dent. M$_1$; 110194, L P$_4$; 110293, L M^3; 110315, L dent. frag. M$_3$. **SC199**: UM 69251, R max. P^3. **SC266**: UM 73503, L max. P$^{3-4}$. **SC281**: UM 110923, L P$_4$ partial. **SC419**: UM 110075, L P$_4$. **Schaff Q.**: 68851, L dent. M$_{1-3}$; 77352, L P$_4$; 77353, R dent. M$_{1-2}$; 77423, R dent. P$_4$, M$_2$; 98479, R max. P^4-M^3. **Y2K Q.** (SC389): UM 108536, L dent. P$_4$-M$_1$, M$_2$ tal.; 109111, dent. I$_1$(root)-M$_2$; 109133, R max. P$_{2-3}$; 109167, I$_2$; 109182, R M$_3$; 109198, L dent. P$_4$-M$_3$; assoc. I$_1$; 109222, L M$_3$; 109229, L dent. P$_4$-M$_1$; 109230, L M$_2$; 109248, L M$_1$; 109263, L M$_1$; 109283, L dent. M$_{1-3}$; 109295, max. P^3-M^x; 109328, L dent. frag., I$_1$, P$_4$,; 109331, R M$_2$; 109361, R M$_1$; 109370, R M^3; 109459, L dent. I$_1$ (assoc.) P$_4$-M$_2$; 109479, R max. M$^{2-3}$; 109510, L dent. M$_{1-2}$; 109515, R M$_1$; 109542, R I^1; 109548, L max. P^2-M^3; 109568, L I^1; 109851, L I^1 base; 109870, R I$_1$; 110013, L M$_2$. **Zalmout Q.** (SC-389): UM 108962, L M$_1$. Plus additional PU (now YPM-PU) and MCZ specimens from Princeton, Schaff, and Fritz quarries listed by Rose (1975).

Carpolestes cf. *C. dubius*

Figure 49, Table 39

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b) zone.

Description and discussion.— Several specimens from Fossil Hollow (SC-198) and other localities in the *Phenacolemur* zone almost certainly represent an undescribed species of *Carpolestes*. The species is most similar to *C. dubius* and probably represents an older part of the *C. dubius–C. nigridens* lineage. Teeth of *C.* cf. *C. dubius* fall within or below the lower size range of *C. dubius*, as reported by Rose (1975) for Princeton Quarry. Mean tooth size is intermediate between that of *C. dubius* and

Carpodaptes hazelae, and close to that of *Carpolestes simpsoni* and *Carpodaptes aulacodon*. Only one P_4 (UM 100360) is unworn enough or complete enough for precise measurements of all dimensions. Nevertheless, it is apparent from several specimens that crown height is below that of specimens of *C. dubius* in the UM collections. I have not, however, compared the specimens to the larger sample in the YPM collections. The P_4 in UM 100360 had either eight or nine cusps and differs from P_4s of *C. dubius* only in being smaller.

The P^3 is the most diagnostic tooth in *Carpolestes* (Rose, 1975; Bloch and Gingerich, 1998). The degree of anterior expansion of the anterobuccal lobe distinguishes *C. dubius* from *C. nigridens* (Fig. 49), as discussed above. A single P^3 (UM 69240) from Fossil Hollow exhibits only a minor expansion of the anterobuccal lobe, less than in most specimens of *C. dubius*. Furthermore, as can be seen in Figure 49 (Ti-4b), it is shorter than any from Princeton Quarry (data from Rose, 1975), the type locality of *C. dubius*. It bears four large buccal cusps and a smaller fifth anterior-most cusp. *Carpolestes dubius* has four prominent cusps, and an incipient anterior-most fifth cusp (Rose, 1975). The anterior cusp in UM 69240 is better developed than is typical in *C. dubius*, but is probably within the variability of *C. dubius*.

Carpolestes cf. *C. dubius* is also similar to species of *Carpodaptes*, but is larger than *C. hazelae*, *C. cygneus*, and *C. stonleyi*. It differs further from these species in having a greater number of buccal cusps on P^3 and more cusps on P_4. It is about the same size as *C. aulacodon* and close to the same age. The P_4 of *C.* cf. *C. dubius* differs from that in the holotype of *C. aulacodon*, which is the only know specimen, in having more cusps, a less triangular shape in buccal view, and no distinct talonid. The P_4 of *C. aulacodon* has a wide base that tapers dorsally to a more acute apex, compared with the smoother dorsal margin in *Carpolestes*. It also has a distinct talonid composed of a single cusp, unlike the P_4 of *C.* cf. *C. dubius* and other species of *Carpolestes*, which lack a sharp break between the ultimate cusp and more anterior cusps.

Block and Gingerich (1998) suggested that *Carpomegodon* (then *Carpodaptes*) *jepseni* was ancestral to *Carpolestes dubius*. The stratocladistic analysis of Bloch et al. (2001), however, suggested that *C. jepseni* and *C. dubius* were derived from the smaller *Carpodaptes*. The observations presented here suggest that *C.* cf. *dubius* was the first form in the *Carpolestes* lineage, and was derived from a smaller carpolestid such as *Carpodaptes*. This is consistent with Bloch et al. (2001).

The specimens included here in *Carpolestes* cf. *C. dubius* almost certainly represent a new species. UM 100360 is, however, the only specimen suitable for a holotype and its P_4 appears to be somewhat unusual in having a high crown height and short length. A formal diagnosis is better done when a larger sample is available.

Referred specimens.— **Fossil Hollow** (SC198): UM 69238, L dent. M_3; 69240, L max. P^3, $M^{2\text{-}3}$; 69246, R dent. P_4; L max. $M^{2\text{-}3}$; 80248, L max. $M^{1\text{-}2}$; 100360, L dent. P_4-M_1; 104925, R dent. P_4-M_1; 110108, R dent. frag., M_3; 110334, R P_4. **SC229**: UM 110283, R P^4 partial. **SC417**: UM 110062, L dent. frag. w/ M_1.

Carpolestes nigridens Simpson, 1928

Figures 49–50

Carpolestes nigridens Simpson, 1928, p. 7. Rose, 1975, p. 36.

Holotype.— AMNH 22159, right dentary with P_4, $M_{1\text{-}2}$ from the Bear Creek coal mine.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis gingerichi* (Ti-6), Rodentia (Cf-1), and *Plesiadapis cookei* (Cf-2) zones.

Description.— The holotype was described by Simpson (1928) and by Rose (1975). Additional specimens were described by Rose (1975, 1981a). Graphs of specimens and statistics were included in Rose (1975). Additional graphs were published in Bloch and Gingerich (1998) and Bloch et al. (2001).

Discussion.— Comparisons of *Carpolestes nigridens* with *C. dubius* were made in the *C. dubius* section. As noted, the species are readily distinguished by the degree of projection of the anterobuccal lobe ("spur") in P^3, and the number of buccal cusps (Rose, 1975). The dentary length between P_4 and I_1 may also be of use in distinguishing *C. nigridens* from *C. dubius*, as discussed below. An increase in the degree of projection of the anterobuccal lobe in P^3, which corresponds to increased length, is seen in the transition from *C. dubius* to *C. nigridens* (Fig. 49) in the latest Tiffanian. The holotype of *C. nigridens* is from Bear Creek, which is correlative to the Rodentia zone, based on biostratigraphic evidence (e.g., Rose, 1981a; Archibald et al., 1987). A single P^3 is known from Bear Creek, which plots in the range of specimens identified as *C. nigridens* on Polecat Bench (Fig. 49).

Four P^3s of *Carpolestes* are known from the Paint Creek local fauna which appears to be correlative to the oldest part of the *Plesiadapis cookei* zone (e.g., Bloch and Gingerich, 1998). Bloch and Gingerich (1998) identified UM 81429 as *C. simpsoni* because of its smaller size, and the others as *C. nigridens*. Although their identification may be correct, a bimodal distribution cannot be demonstrated from the small sample size, and UM 81429 plots within the expected range of a single species (Fig. 49, Cf-2 level, far left). Thus, I provisionally include it in *C. nigridens*. If it is a specimen of *C. simpsoni* the mean length for *C. nigridens* at Paint Creek is greater than depicted in Figure 49.

Provisionally identifications of lower teeth and dentaries of *Carpolestes nigridens* were based on features of the dentary, and by their occurrences in or stratigraphically between localities yielding P^3s of *C. nigridens*. UM 109599 is the most complete dentary of *C. nigridens* yet described (Fig. 50). It was recovered from the same freshwater limestone as the earliest known rodent tooth (UM 108587), which marks the beginning of the Clarkforkian. It preserves the root of I_1, and I_2-M_3. Dentary length between P_4 and I_1 is 25-30% shorter than in specimens of *C. dubius* (UM 10911, YPM-PU 19409, 13275). The teeth in this area have a crowded appearance and the P_3 is shifted posterolingually, compared with most *C. dubius*. In buccal view, the posterior part of the P_3 crown and about half of the root are partially obscured by the P_4. The P_3 root is pressed against the anterolingual surface of the anterior root of P_4 and there is an opening between the alveoli. The I_2 appears to have been more tightly pressed against the buccal side of I_1 than in specimens of

TABLE 40 — Dental statistics for *Ignacius frugivorus* from Cedar Point Quarry. P_4 height is from base of enamel on anterobuccal root to crown apex. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
Dent. D		5	5.10	5.75	5.35	0.11	0.25	4.67
M^2	L	1	—	—	2.07	—	—	—
	W	1	—	—	3.08	—	—	—
M^3	L	1	—	—	1.41	—	—	—
	W	1	—	—	2.31	—	—	—
I_1	H	1	—	—	7.40	—	—	—
	W	4	0.96	1.20	1.10	0.06	0.12	11.30
	D	4	2.37	2.65	2.49	0.06	0.12	4.79
P_4	L	8	1.66	2.04	1.83	0.04	0.11	6.17
	W	6	1.03	1.25	1.15	0.03	0.08	7.16
	H	6	1.80	2.03	1.94	0.04	0.10	4.93
M_1	L	9	1.98	2.25	2.12	0.03	0.08	3.88
	W tri.	9	1.47	1.71	1.60	0.03	0.09	5.67
	W tal.	9	1.56	1.76	1.67	0.02	0.07	4.30
M_2	L	9	2.03	2.27	2.14	0.03	0.08	3.82
	W tri.	8	1.61	1.95	1.74	0.04	0.10	5.82
	W tal.	10	1.63	1.93	1.76	0.02	0.07	4.23
M_3	L	4	2.67	2.87	2.77	0.04	0.08	2.99
	W tri.	4	1.43	1.63	1.53	0.04	0.09	5.86
	W tal.	4	1.43	1.64	1.52	0.05	0.09	6.02

TABLE 41 — Dental statistics for *Ignacius frugivorus* from Divide Quarry. P_4 height is from base of enamel on anterobuccal root to crown apex. I^1 apical width is mesiodistal. Abbreviations as in Table 3.

		n	Min	Max	Mean	SE	SD	V
Dent. D		3	5.00	5.65	5.42	0.21	0.36	6.68
I^1	W apical	2	1.60	1.65	1.63	—	—	—
P^4	L	2	1.65	1.73	1.69	—	—	—
	W	2	2.10	2.17	2.14	—	—	—
M^1	L	3	1.90	2.05	1.97	0.04	0.08	3.88
	W	3	2.82	2.95	2.91	0.04	0.08	2.58
M^2	L	7	1.83	1.95	1.89	0.02	0.04	2.38
	W	5	2.73	3.07	2.93	0.06	0.12	4.21
M^3	L	1	—	—	1.30	—	—	—
	W	1	—	—	2.08	—	—	—
I_1	H	1	—	—	7.50	—	—	—
	W	5	1.14	1.30	1.23	0.03	0.07	5.71
	D	4	2.53	2.93	2.75	0.10	0.21	7.64
P_4	L	3	1.90	2.00	1.96	0.03	0.05	2.70
	W	3	1.30	1.42	1.34	0.04	0.07	5.17
	H	2	2.00	2.20	2.10	—	—	—
M_1	L	3	1.96	2.15	2.04	0.06	0.10	4.83
	W tri.	3	1.57	1.75	1.66	0.05	0.09	5.42
	W tal.	3	1.70	1.81	1.74	0.04	0.06	3.66
M_2	L	7	2.07	2.29	2.15	0.03	0.07	3.42
	W tri.	7.00	1.67	1.87	1.73	0.03	0.07	4.13
	W tal.	7.00	1.62	1.84	1.76	0.03	0.08	4.58

C. dubius. UM 108261 also exhibits crowding in this region, but is not as complete. The distance from the anterior crown of P_4 to the front of the I_2 alveolus is about 10-25% less than in dentaries of *C. dubius*, in spite of its larger size. UM 108261 is an exceptionally large specimen with a P_4 length 15-20% greater than in *C. dubius*. The shortening of the anterior dentary and the crowding of the I_2-P_3 in *C. nigridens* foreshadows the loss of P_3 in the younger *C. simpsoni* (Bloch and Gingerich, 1998; Bloch et al., 2001). The shorter anterior dentary appears to be a useful feature for distinguishing *C. nigridens* from *C. dubius*.

The position of the P_3 alveolus may also be of use in distinguishing *C. nigridens* from *C. dubius*. Four specimens (UM 95016, 101130, 108261, 109599) from the latest Tiffanian and early Clarkforkian referred to *C. nigridens* have a more posterolingually positioned P_3 alveolus than is typical of *C. dubius*. In these specimens, the lingual edge of the P_3 alveolus is nearly in line with a straight line parallel to the lingual edge of the P_4 (Fig. 50C). A fifth specimen (UM 73344), however, has a more medial alveolus in front of P_4, like that in *C. dubius*. This is presumably due to interspecific variation, or possibly the P_3 was lost and the alveolus is for C_1. There is variability in P_3 position in the Y2K Quarry sample of *C. dubius*, which exhibits some intermediacy between *C. dubius* and *C. nigridens* in P^3 length (Fig. 49), as discussed above. Two of these specimens (UM 109328, 109459) have a more medially positioned P_3 alveolus, while the alveolus in a third (UM 109459) is more lingual. Three dentaries (YPM-PU 13275, 19409, and UM 77423) of *C. dubius* from Princeton and Schaff quarries, all have more medially placed P_3 alveoli. Thus, with large enough samples the position of P_3 appears to be useful for distinguishing between these species.

P^3 measurements.— **Paint Creek**: UM 75459: P^3 L = 3.13. UM 67556: P^3 L = 3.27, W = 2.35. UM 81429: P^3 L = 2.85, W = 2.19. **SC178**: UM 101821: P^3 L = 3.40, W = 2.56. **SC260**: UM 73716: L P^3, L = 3.3*, W = 2.65.

Referred specimens.— **Bluff Top Q.** (SC379): UM 108260, R P_4; 108261, dent. R P_4; 108266, 3 P_4 frags. **FG037**: UM 85246, R dent. P_4. **Paint Creek** (SC143): UM 67556, R max. P^3; 68289, L max. M^2, L dent. M_1, unassoc.; 68292, R P^4, L M^1, R M^3, R M_1; 69943, R dent. M_{1-2}; 71006, L P^4, L P_4, unassoc.; 75459, I^2, P^3, P^4; 80562, R M_2; 80563, L dent. P_4 frag.; 80565, L dent. P_4-M_1; 81422, R P^3 partial; 81429, R P^3; 83021, L dent. M_2; 86544, L dent. M_{1-2}; 101879, L dent. P_4-M_1; 104035, L P_4, M_1; 109908, L dent. P_4-M_2; 109913, L P^4. **SC171**: UM 69540, max. R P^3-M^3?, R dent. R P_4-M_3, L dent., many teeth damaged. **SC178**: UM 68731, R M^1; 101821, R P^3. **SC179**: UM 108341, L dent. M_{1-2}. **SC181**: UM 109599, R dent. I_1-M_3; assoc. metatarsal; 110120, R M_1. **SC191**: UM 68885, R P_4 (part). **SC217**: UM 101130, L dent. P_4. **SC226**: UM 71306, R max. P^4 (partial), M^1; 71309, L dent. P_4. **SC258**: UM 73344, R dent. P_4; 73347, L P_4; 73351, L P_4. **SC260**: UM 73378, L M_1; 73379, R P_4 frag.; 73526, L dent. M_1; 73716, L P^3; 73719, R P_4; 87143, L dent. P_4 partial; 95016, L dent. P_4 roots, anterior alveoli. Plus additional AMNH, CM, YPM-PU specimens from Bear Creek and Paint Creek listed by Rose (1975).

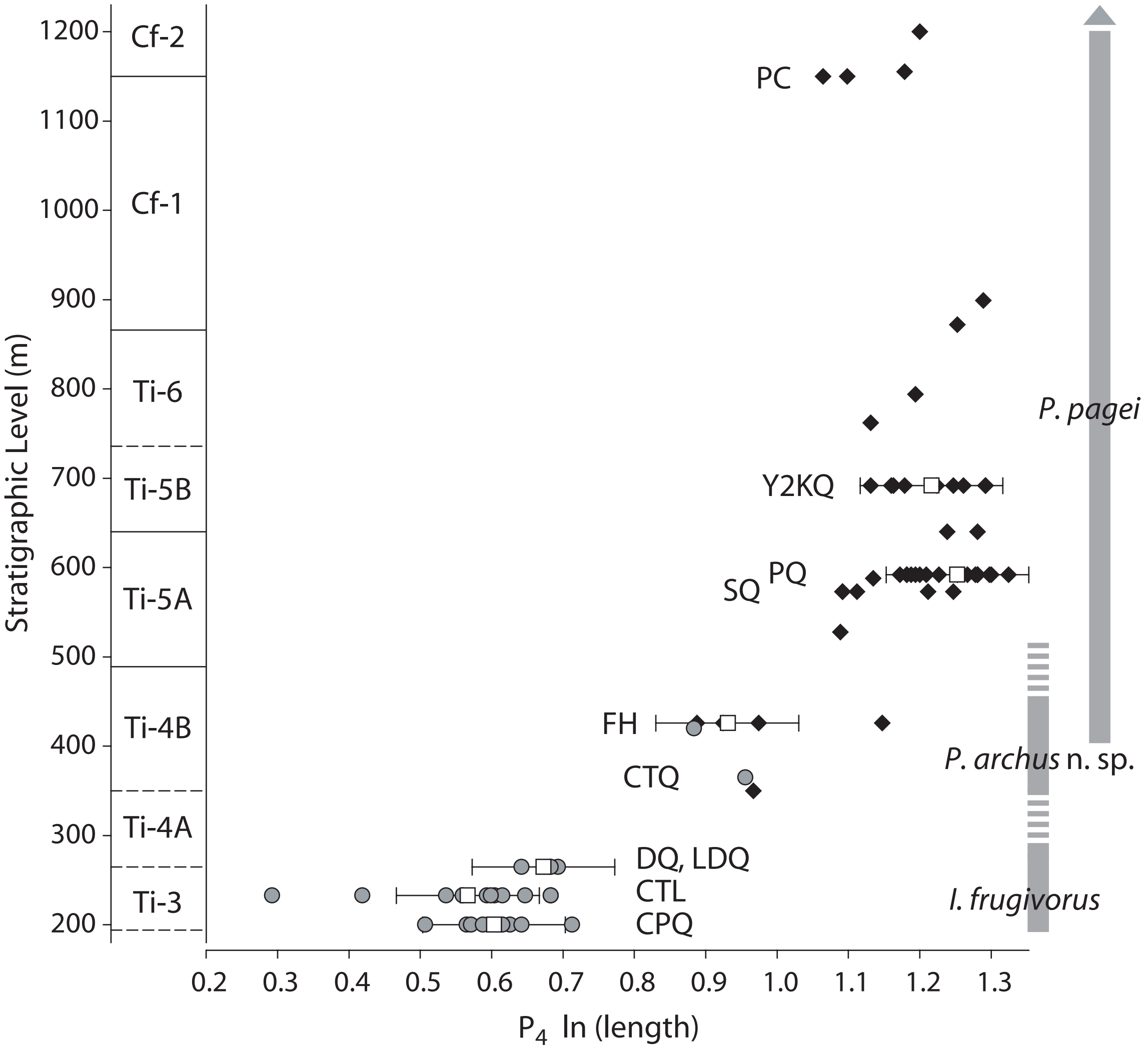


FIGURE 51 — Stratigraphic plot of *Ignacius* and *Phenacolemur* P_4 length from Ti-3 to Cf-2. All localities are in Bighorn Basin except Chappo Type Locality in southwestern Wyoming (Gunnell, 1994). Solid diamonds indicate specimens from the Polecat Bench sequence; gray circles indicate localities that were biostratigraphically correlated to the Polecat Bench sequence. Quarry (Q) and locality abbreviations: *CPQ*, Cedar Point; *CTL*, Chappo Type Locality; *CTQ*, Croc Tooth; *DQ*, Divide; *FH*, Fossil Hollow; *LDQ*, Long Draw; *PC*, Paint Creek; *PQ*, Princeton; *SQ*, Schaff.; *Y2KQ*, Y2K.

Family PAROMOMYIDAE

IGNACIUS Matthew and Granger, 1921

Ignacius frugivorus Matthew and Granger, 1921

Figures 51–53, Tables 40–41

Ignacius frugivorus Matthew and Granger, 1921, p. 5.

Holotype.— AMNH 17368, maxilla with P^2, P^4-M^2, and alveoli for P^3, from Mason Pocket in southern Colorado.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* (Ti-3), *Plesiadapis churchilli* (Ti-4a), and ?*Phenacolemur* (Ti-4b) zones.

Description.— The holotype was described and figured by Simpson (1935d) and by Bown and Rose (1976). The holotype was also figured by Szalay and Delson (1979, Fig. 19A, p. 53) and additional descriptions of the species were given by Matthew and Granger (1921), Simpson (1955), and Gunnell (1989). The posterior part of a dentary (YPM-PU 21405) included here in *I. frugivorus* was figured by Rose (1975, Fig. 35C, p. 55).

Discussion.— *Ignacius frugivorus* was first described by Matthew and Granger (1921) as the type and only species contained in the new genus *Ignacius*. *Ignacius* was subsequently synonymized with *Phenacolemur* by Simpson (1935d) who stated that teeth of *Ignacius* from Mason Pocket are "exactly like those of Gray Bull *Phenacolemur* in miniature." Simpson's analysis was, however, based on a small sample of incomplete specimens. After studying more complete material referred to *Ignacius* from other localities, Bown and Rose (1976) revalidated *Ignacius* arguing that differences between *Ignacius* and *Phenacolemur* were of sufficient magnitude to warrant generic distinction. All subsequent authors that I am aware of have followed revalidation of *Ignacius*, as do I. *Ignacius* is easily distin-

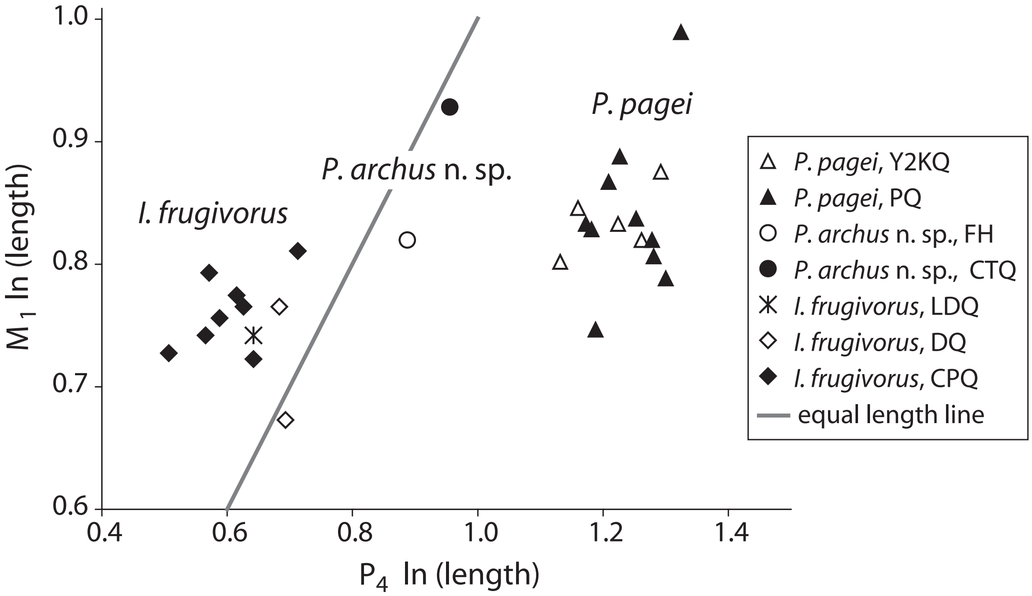


FIGURE 52 — Scatter plot of P_4 versus M_1 length for *Ignacius frugivorus*, *Phenacolemur archus* n. sp., and *P. pagei*, from various quarries and Fossil Hollow (FH). Abbreviations as in Figure 51.

guished from *Phenacolemur* by its smaller P_4, relative to molar size. $P^{2\text{-}4}$ are also smaller and less inflated in *Ignacius*, at least in species where these teeth can be compared.

Ignacius frugivorus can be distinguished from the older *I. fremontensis* by a larger P_4, slightly larger and proportionally wider molars (Gazin, 1971), and the absence or near absence a P_3. Bown and Rose (1976) stated that a double-rooted P_3 was variably present in *I. frugivorus* and cited two specimens as having a P_3: PU 14790 from Cedar Point Quarry and AMNH 33987 from Scaritt Quarry. Rose (1981a, pp. 146-147), however, re-identified PU 14790 as *I.* cf. *I. fremontensis*, noting that it was erroneously reported as being from Cedar Point Quarry by Bown and Rose (1976), and was actually from Rock Bench Quarry. Rose and Bown (1982, p. 68) later stated that P_3 was possibly present in some individuals of *I. frugivorus*, without further explanation. Subsequently, Bloch et al. (2002) stated that all species of *Ignacius* except *I. fremontensis* had lost P_3, but did not discuss AMNH 33987 from Scarritt Quarry.

Eight dentaries identified here as *Ignacius frugivorus* that have a well-preserved region anterior to P_4 were available for study, four from Cedar Point Quarry (YPM-PU 20062, 20798 20844, 21405), three from Divide Quarry (UM 77268, 85931, 92253), and one from Long Draw Quarry (YPM-PU 21222). None has alveoli for a P_3. All of these quarries are, however, younger than Scarritt Quarry, as is Mason Pocket, the type locality for *I. frugivorus* (Secord et al., 2006). Bown and Rose (1976) suggested that *I. fremontensis* and *I. frugivorus* were parts of a single evolutionary lineage. If this is correct, then the form at Scarritt Quarry may represent an intermediate condition between *I. fremontensis* and *I. frugivorus*. Of the three published specimens from Scarritt Quarry (AMNH 33896, 33987, 33988: Simpson, 1955) only AMNH 33987 is adequate for evaluation of alveoli anterior to P_4. If larger samples indicate that retention of P_3 is prevalent at Scarritt Quarry, this form may be best placed in a new species of *Ignacius*.

The presence of *Ignacius frugivorus* at Cedar Point Quarry was first reported by Bown and Rose (1976) and the species was included in a faunal list by Rose (1981a, p. 152). The Cedar Point Quarry form is very similar to the one from Divide and Long Draw Quarries, but differs in having a slightly shorter, less inflated, and more wedge shaped P_4. Figure 51 shows that the length of P_4s from Divide Quarry is in the upper range of the samples from Cedar Point Quarry and Chappo Type Locality. Figure 52 shows that P_4 length, relative to M_1 length, is also greater than in most specimens from Cedar Point Quarry. No dentaries preserving P_4 and M_1 of *Ignacius* are known from Chappo Type Locality. P_4 length in UM 77268 from Divide Quarry exceeds M_1 length (Fig. 52), a characteristic of *Phenacolemur*. The increasing size of P_4 in the *Ignacius* lineage may reflect an evolutionary trend that led to *Phenacolemur*, as discussed in the *P. archus* n. sp. section.

Differences in P_4 size and shape between the Divide Quarry form and older forms may be considered great enough to warrant specific separation by some authors. There is, however, overlap in these characters among the localities. Also, *I. frugivorus* is poorly known from the type locality and no dentaries preserve P_4 or M_1. Simpson (1955) reported a length of 1.6 mm for a P_4 from Mason Pocket, which, if equivalent to my measurements, is in the extreme low end of the size range of both the Cedar Point and Chappo samples. A comparison of P_4 length measurements for *Phenacolemur pagei* from Princeton Quarry, however, shows that Simpson's lengths are about 5% shorter on average. However, even with a 5% adjustment the Mason Pocket P_4 is still below the means of both samples. The short length suggests that the type sample is more similar to the Cedar Point and Chappo form, than to the Divide Quarry form, even though it appears to be temporally equivalent to Divide Quarry (Secord et al., 2006). Apparently the presence or absence of P_3

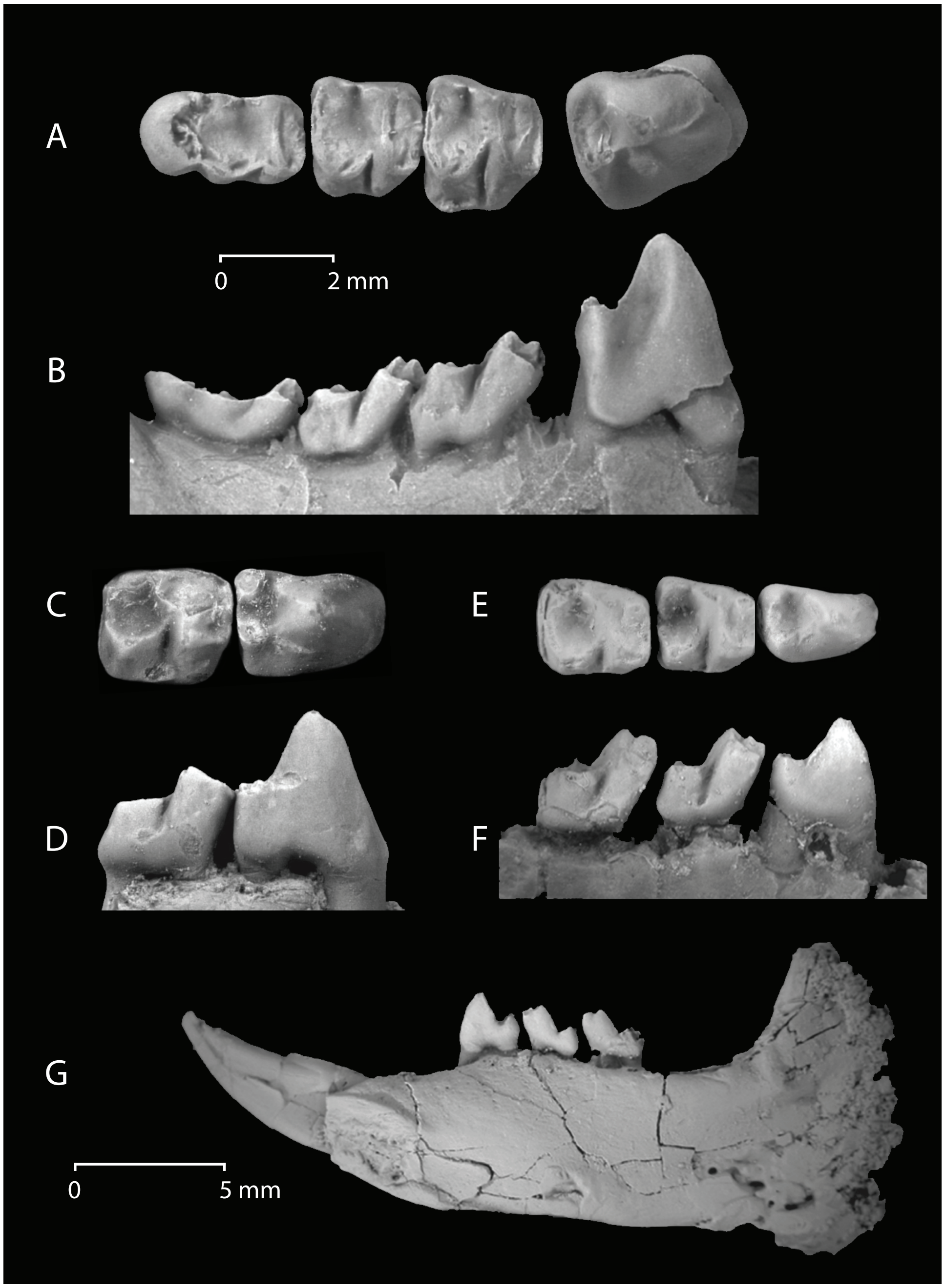


FIGURE 53 — Partial dentitions of *Phenacolemur and Ignacius*. A–B, right P_4-M_3 of *P. pagei* (YPM-PU 14030, cast) in occlusal (A) and buccal (B) views, from Princeton Quarry. C–D, right P_4-M_1 of *P. archus* n. sp. (UM 109601, holotype) in occlusal (C) and buccal (D) views, from Croc Tooth Quarry. E–G, right dentary with I_1, P_4-M_3 of *I. frugivorus* (UM 77268) in occlusal (E), buccal (F), and lingual (G) views, from Divide Quarry. H–M (facing page), from left to right, upper left I^1s of *I. frugivorus* (UM 110963), *P. archus* n. sp. (YPM-PU 25035), and *P. pagei*, respectively, in ventral (H, J, L) and lateral (I, K, M) views. N–O (facing page), right maxillary fragment (UM 69237) of *P. archus* n. sp. with P^4-M^1 in buccal (N) and occlusal (O) views.

cannot be ascertained from any of the dentary fragments from Mason Pocket. Because Mason Pocket appears to be younger than Cedar Point Quarry, and the P_3 was already lost or occurred infrequently in the latter, however, it is probable that the Mason Pocket form shared a similar condition. More teeth are needed from the type area before any firm conclusions can be made as to which of these samples is closest to the type sample.

I have tentatively included five specimens from the *Phenacolemur* zone (Ti-4b) in *Ignacius frugivorus*. Three specimens from the SC-243 anthills compare favorably with *I. frugivorus*, but *Phenacolemur archus* n. sp. also occurs at SC-243 and its variability is not well known. There is a marked shift from a relatively rare *I. frugivorus* in the *Plesiadapis churchilli* zone to a more abundant *Phenacolemur archus* n. sp. in the succeeding

Phenacolemur zone, and it is possible that some or all of these specimens belong to small variant individuals of *P. archus* n. sp. Nevertheless, UM 61555 (P^4) is quite similar to that of *I. frugivorus* (UM 83263) from Divide Quarry and lacks the buccal expansion seen in *P. archus* n. sp. (UM 61559, 69237) and other species of *Phenacolemur*. It is intermediate in size between P^4s of *P. archus* n. sp. and *I. frugivorus*. UM 61563 (M_2) is indistinguishable from the M_2 of *I. frugivorus* and lacks the buccal expansion typical of *P. archus* n. sp. UM 61562 (M^2) is more quadrate than is typical of upper molars of *Phenacolemur*, but is typical of *I. frugivorus*. I also tentatively refer two M_3s (YPM-PU 17745 and UM 108422) to *I. frugivorus* because of their small size. Discovery of a P_4 of *I. frugivorus* in the *Phenacolemur* zone is necessary before the presence of this species can be documented with certainty.

Additional specimens of *Ignacius frugivorus* from Cedar Point Quarry in the Princeton collection were reported by Rose (1981a, 152), but were not available for study.

Referred specimens.— **Croc Tooth Q.** (FG028): YPM-PU 17745, L M_3. **Cedar Point Q.**: YPM-PU 20062, L dent. I_1-M_2; 20073, R dent. P_4-M_3; 20690, R dent. P_4-M_3; 20797, R dent. P_4-M_2; 20798, R dent. I_1, alveoli for P_4-M_3; 20844, R dent. I_1-M_2; 20897, L dent. M_2 tal., M_3; 21248, R max. $M^{2\text{-}3}$; 21285, L dent. P_4-M_1; 21404, L dent. P_4-M_3; 21405, L dent. I_1 base, P_4-M_2; 21410, L dent. $M_{1\text{-}2}$. **Divide Q.** (FG046): UM 77268, R dent. I_1, P_4-M_2; 77275, R max. $M^{1\text{-}2}$; 83240, R max. $M^{1\text{-}2}$; 83263, L max. P^4-M^3; 83268, L M_2; 85388, dent. P_4-M_2 (loose teeth); 85924, L M_1; 85931, L dent. I_1; 92253, R dent. I_1, $M_{1\text{-}2}$; 92271, R M_2; 92276, R I_1; 110956, R I_1; 110957, L M_2; 110958, R M^2 partial; 110959, R P_4; 110960, L I_1; 110961, L P^4; 110962, L I^1; 110963, L I^1; 110964, L M^1 or M^2; 110965, R M^2; 110966, L M^2 partial; 110967, L M^2. **Long Draw Q.**: YPM-PU 21222, R dent. P_4-M_2. **SC243**: UM 61555, R P^4; 61562, R M^2; 61563, L M_2. **SC394**: UM 108422, L M_3.

Ignacius clarkforkensis Bloch et al., 2007

Ignacius graybullianus (in part), Rose, 1981a, p. 63. Bloch and Silcox (in part), p. 1159.
Ignacius cf. *graybullianus*, Secord, 2006, p. 229.
Ignacius clarkforkensis Bloch et al., 2007, p. 1159.

Holotype.— UM 108210, upper and lower dentitions preserving R I^1-C^1, P^3-M^3, L C^1-M^3, R I_1-M_3, L P_4-M_3, and an associated partial skeleton. The holotype was etched from a freshwater limestone collected at SC-62 (Cf-3) in the northern Bighorn Basin.

Biostratigraphic occurrences in Bighorn Basin.— Rodentia (Cf-1), *Plesiadapis cookei* (Cf-2), and *Copecion* (Cf-3) zones.

Description and discussion.— *Ignacius clarkforkensis* was named by Bloch et al. (2007), who included specimens of middle and late Clarkforkian age in the hypodigm. A right P^4 (UM 110184) collected from an anthill in the Rodentia zone compares favorably with *I. clarkforkensis* and I tentatively include it in the species. If correctly identified, UM 110184 represents the earliest occurrence of *I. clarkforkensis*. A few specimens from the late Tiffanian may also belong to *I. clarkforkensis* (i.e. UM 108452, partial P^4, Zalmout Quarry; UM 109184, M^1, Y2K Quarry; UM 77293, $P^{3\text{-}4}$ and M_2, FG-47), or a form close to it, but well-preserved premolars are necessary to confidently distinguish *Ignacius* from *Phenacolemur*. I included *Ignacius* in a preliminary faunal list for Y2K Quarry (Secord, 2002), but the acquisition of larger samples suggests that molars tentatively identified as *Ignacius* may represent variants of *Phenacolemur pagei*.

Referred specimens.— **SC062**: UM 108210 (holotype). **SC083**: UM 110184, R P^4. See Bloch et al. (2007) for additional Clarkforkian specimens.

PHENACOLEMUR Matthew, 1915

Phenacolemur Matthew, 1915, p. 479.
Simpsonlemur, Robinson and Ivy, 1994, p. 101.
Dillerlemur, Robinson and Ivy, 1994, p. 103.
Pulverflumen, Robinson and Ivy, 1994, p. 104.

Discussion.— Robinson and Ivy (1994) established several new paromomyid genera. I follow Silcox and Gunnell (2008) in considering these genera junior synonyms of *Phenacolemur*.

Phenacolemur pagei Jepsen, 1930b

Figures 51–53, Tables 42–43

Phenacolemur pagei Jepsen, 1930b, p. 514.

Holotype.— YPM-PU 13286, a right dentary with P_4-M_2, and alveoli for I_1 and M_3; from Princeton Quarry, on the west side of Polecat Bench, Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b), *Probathyopsis* (Ti-5a), *Plesiadapis simonsi* (Ti-5b), *Plesiadapis gingerichi* (Ti-6), Rodentia (Cf-1), and *Plesiadapis cookei* (Cf-2) zones.

Description.— The holotype was described and figured by Jepsen (1930b). Additional upper and lower dentitions from Princeton Quarry were described and figured by Simpson (1955), and figured by Szalay and Delson (1979, Figs. 22 and 23). Clarkforkian specimens of *Phenacolemur pagei* were described and figured by Rose (1981a), including statistical tables. Comparisons with other species were published by Bown and Rose (1976), Rose (1981a), and Rose and Bown (1982).

Discussion.— A relatively large sample of *Phenacolemur* was recently collected at Y2K Quarry in the *Plesiadapis simonsi* zone. This sample appears to be within the variability exhibited by *P. pagei* at Princeton Quarry, the type locality. *Phenacolemur pagei* is the second most abundant species at Y2K quarry in terms of number of specimens and only slightly less abundant than *Plesiadapis* cf. *P. dubius*. This contrasts with a proportionally greater abundance of *Plesiadapis fodinatus* at Princeton Quarry (Rose, 1981a). Simpson (1955) reported considerable variability in *P. pagei* from Princeton Quarry, noting that the upper teeth were "strikingly more variable" than the lowers. Rose (1981a) also noted variability in the Clarkforkian sample of *P. pagei*, especially in P_4. In my evaluation, the P_4 in the populations from Y2K and Princeton quarries is the most variable tooth. It varies in linear dimensions (especially width), in the degree of exodaenodonty, in the height of the talonid, and in the width of the talonid basin relative to total width.

TABLE 42 — Dental statistics for *Phenacolemur pagei* from Y2K Quarry. P_4 height is from base of enamel on anterobuccal root to crown apex. I^1 apical width is mesiodistal. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
I^1	H	2	4.50	4.90	4.70	—	—	—
	W base	5	1.16	1.36	1.28	0.04	0.08	6.49
	W apical	3	1.85	2.13	2.00	0.08	0.14	7.08
	D	5	1.92	2.09	2.00	0.03	0.07	3.54
P^2	L	5	2.24	2.44	2.33	0.04	0.09	3.86
	W	5	1.76	2.04	1.92	0.05	0.10	5.40
P^3	L	5	2.47	2.65	2.55	0.03	0.07	2.93
	W	5	2.05	2.25	2.11	0.04	0.09	4.09
P^4	L	12	2.12	2.51	2.27	0.04	0.14	5.99
	W	11	2.75	3.20	3.01	0.05	0.16	5.24
M^1	L	14	2.15	2.33	2.24	0.02	0.06	2.60
	W	11	3.06	3.45	3.26	0.04	0.13	4.08
M^2	L	9	1.73	2.10	1.90	0.04	0.12	6.09
	W	9	2.60	3.15	2.86	0.06	0.17	5.92
M^3	L	3	1.20	1.33	1.28	0.04	0.07	5.33
	W	3	2.05	2.25	2.18	0.06	0.11	5.06
I_1	W	1	—	—	1.36	—	—	—
	D	1	—	—	3.04	—	—	—
P_4	L	9	3.10	3.64	3.38	0.07	0.20	6.02
	W	9	2.09	2.57	2.41	0.06	0.17	6.92
	H	7	3.70	4.75	4.39	0.13	0.35	7.90
M_1	L	11	2.23	2.60	2.41	0.04	0.12	5.11
	W tri.	11	1.78	2.15	2.01	0.03	0.10	5.07
	W tal.	10	1.85	2.38	2.11	0.05	0.15	6.97
M_1	L	6	2.21	2.50	2.33	0.04	0.10	4.47
	W tri.	6	1.75	2.08	1.90	0.06	0.14	7.13
	W tal.	6	1.78	2.09	1.94	0.04	0.11	5.62
M_3	L	1	—	—	3.30	—	—	—
	W tri.	1	—	—	1.81	—	—	—
	W tal.	1	—	—	1.77	—	—	—

The M_1 mean length in the Y2K Quarry sample is about 5% greater than in Princeton Quarry (Tables 42 and 43). The inverse is true of P_4 length and width, which is slightly greater in the Princeton Quarry sample. Such minor differences do not warrant specific separation of the populations. Size difference between my data from Princeton Quarry and those of Simpson (1955) are undoubtedly due to slight differences in tooth orientation or landmarks.

Two complete medial upper incisors (UM 109478, 109502) and a third (UM 110012) preserving the upper part of the crown were recovered from Y2K Quarry. Based on the high frequency of *Phenacolemur pagei* and the lack of any definite specimens of *Ignacius* in the quarry, most or all of these teeth almost certainly belong to *P. pagei* (Fig. 53). Of described specimens (Bown, 1979; Godinot, 1984; Robinson and Ivy, 1994; Rose and Bown, 1996; Bloch et al., 2002), they are most similar in form to an I^1 identified as *P. simonsi* by Rose et al. (1993) and to the I^1 of *Acidomomys hebeticus* (Bloch et al., 2002). They differ from the I^1 of *P. simonsi* in having a mediocone and mediocrista that are lower on the crown (more proximally positioned) and in having a less projecting posterocone, based on Figure 3D in Rose et al.

TABLE 43 — Dental statistics for *Phenacolemur pagei* from Princeton Quarry. P_4 height is from base of enamel on anterobuccal root to crown apex. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
P_4	L	14	3.23	3.76	3.50	0.05	0.17	4.83
	W	14	1.96	2.84	2.53	0.06	0.21	8.26
	H	8	3.63	4.36	4.02	0.08	0.24	5.87
M_1	L	15	2.11	2.59	2.30	0.04	0.14	5.90
	W tri.	14	1.92	2.30	2.09	0.03	0.11	5.43
	W tal.	14	2.01	2.39	2.17	0.03	0.12	5.45

(1993). In the I^1s from Y2K Quarry, the apex of the laterocone is positioned more anteriorly than the mediocrista. The teeth are also much larger than in *P. simonsi*. They differ from the I^1 of *Acidomomys* in having a single posterocone that is more projecting, as opposed to a "doubled" posterocone, slightly lower crowns, and a slightly smaller laterocone. A crest along the distoventral margin is also better developed in the former, but there is considerable variability in this feature. The I^1s from Y2K Quarry also vary considerably in mesial-distal width across the apical cusps and in the distinctness of the mediocone.

An I^1 from the late Clarkforkian (Cf-3) was identified as *Phenacolemur* cf. *P. pagei* and figured by Rose et al. (1993). Based on a cast of the specimen (USGS 2216), the I^1s from Y2K Quarry differ in having a larger, better developed mediocone that flares medially toward the apex of the crown. This creates a convex medial margin along the crown, as opposed to a nearly straight margin in USGS 2216. The reduction of the mediocone in USGS 2216 appears to be an important distinction from the I^1 of *P. pagei*. Rose (1981a) placed a boundary between *P. pagei* and *P. praecox*, which appear to be sequential species in an evolutionary lineage, in the lower part of Cf-3. An analysis of Clarkforkian material in the UM collections, however, including new specimens collected since Rose's study, indicates that a marked shift in P_4 length/width ratios from *P. pagei* to *P. praecox* occurs in the underlying *Plesiadapis cookei* zone. Thus, USGS 2216 probably represents *P. praecox*.

Referred specimens.— **Bluff Top Q.** (SC379): UM 108270, R M^x partial; 108274, L M_1. **FG006**: UM 74070, R M^1; 77578, P^3; 77579, R M^2, R M_1 (unassoc.). **FG037**: UM 109602, R P_4. **Fossil Hollow** (SC198): YPM-PU 18351, R dent. frag., P_4-M_1; 24598 (in part), partial P_4. **SC109**: UM 69310, R max. M^1. **SC127**: UM 66908, R dent. P_4-M_3, edentulous; L dent. **SC136**: UM 67183, L P_4, I_1 frag.; 69905, R dent. edentulous. **SC143**: UM 67558, R max. $P^{2\text{-}3}$, R dent. P_4-M_1, M_3; 69944, R dent. P_4 (part)-M_1; 71167, R dent. I_1 (part), P_4-M_1; 81423, R M_3; 81428, R M_2; 87823, L M^2; 101877, R dent. P_4 (unassoc. R dent.); 102445, R P_4; 104931, R max. P^4-M^2; 109910, R M_1; 109914, R I_1 frag., L P_4 assoc.?; 109915, L M^1; 110203, R M^2, L P_4, M_3, R P_4 (part), M_3; 110207, L M_3. **SC165**: UM 68255, R dent. P_4; 68259, R P^4, L M_1 unassoc.; 69537, R max. $P^{2\text{-}4}$-M^1, I^1, M^2 assoc.; 108664, R P^4; 110204, R P_4; 71502, L max. $M^{2\text{-}3}$. **SC174**: UM 68438, R max. $M^{1\text{-}2}$. **SC176**: UM 68515, L $P^{3\text{-}4}$. **SC178**: UM 108307, R P_4. **SC179**: UM 108351, L P_4. **SC187**: UM 68858, L dent. P_4, R dent. P_4, M_2; 73597, L dent. P_4, I_1 root; 80354, R max. M^1; 110101, dent. frag., M_x frag. **SC191**: UM 108291, R dent. frag., P_4. **SC197**: UM 71024, L dent. P_4. **SC201**: UM 69269, R dent. P_4-M_2. **SC226**: UM 71304, L dent. P_4 tal.; 110133, L P_4-M_2, assoc. **SC258**: UM 73350, R dent. P_4. **SC268**: UM 73532, L dent. I_1, P_4; 110326, L M_1. **SC281**: UM 110149, R P^2. **SC362 Q.**: UM 110128, R P^3; 110136, L and R I^1s. **SC375**: UM 108226, L P_4. **Y2K Q.** (SC389): UM 108520, R P^4; 108521, R P^4; 109115, R I^1, C^1?; 109116, R P^4; 109117, L M_1; 109132, L dent. P_4-$M_{1\text{-}2}$; 109149, R max. frag. P^4-M^1; 109154, L dent. P_4-M_2; 109173, R M^1; 109180, R M^1; 109186, R I^1; 109224, R P^2; 109236, R dent. frag., P_4; 109242, L max. $M^{1\text{-}2}$; 109244, R dent. P_4-M_2; 109254, L dent. P_4-M_1; 109259, R max. P^4-M^2; 109260, L M^1; 109264, dent. M_1, P_4 roots; 109285, L I_1; 109351, R M_1; 109356, R M^2; 109366, R dent. $M_{1\text{-}2}$; 109375, R max. P^4-M^1; 109380, L max. P^4, $M^{1\text{-}2}$, dent. M_2; 109385, R M^1; 109391, R M_3; 109404, R M^2; 109405, R P^4; 109412, R M^1 partial; 109430, R max. $P^{3\text{-}4}$-M^3 (no M^2); 109440, L P_4; 109445, L I^1; 109452, R I_1; 109453, L P_4; 109468, R dent. P_4-M_2; 109474, R P^3; 109478, L I^1; 109481, L max. P^4-M^2; 109502, L I^1; 109523, L max. $P^{2\text{-}3}$; 109524, R dent. frag., $M_{1\text{-}2}$; 109538, R max. frag., P^2, P^1? alveolus; 109551, R P_4; 109654, L max. P^2-M^2; 109864, R dent. P_4-M_1; 109866, L I^1; 110004, R M_1; 110005, L M_3; 110006, R P_4; 110007, R P_4; 110008, R M^2; 110009, R M^2; 110010, L M^3; 110011, R P^3; 110012, R I^1; 110014, L max. frag., P^4-M^1. **Zalmout Q.** (SC389): UM 108448, R M_3; 109105, L M^2.

Phenacolemur archus, new species

Figures 51–53, Tables 44–45

Phenacolemur n. sp., Secord et al. 2006, p. 229.

Holotype.— UM 109601, right dentary fragment with P_4-M_1, from Croc Tooth Quarry in the Foster Gulch area of the northern Bighorn Basin.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b) and ?*Probathyopsis* (Ti-5a) zones.

Diagnosis.— Differs from other species of *Phenacolemur* (in which P_4 is known), except *P. simonsi* and *P. fortior*, in having a shorter P_4, both relative to M_1 length and in absolute dimensions. Differs from *P. simonsi* in having: (1) much larger molars; (2) a more expanded anterobuccal region on P^4; (3) more buccolingually elongated $M^{1\text{-}2}$ with squarer corners; (4) a buccally higher P_4 talonid relative to crown height; (5) a narrower P_4 talonid basin relative to total width; and (6) a basal buccal expansion in $M_{1\text{-}2}$. Differs from *P. fortior* in being about 20% smaller in molar dimensions, in having a narrower P_4, relative to length. The P_4 is about 15% shorter and 5% narrower than in *P. fortior*, based on published measurements (Robinson and Ivy, 1994).

Differs further from *P. praecox* (= *P. citatus*) in being smaller, and in (3), (5), and (6) above. Differs further from *P. pagei* and *P. jepseni* in having a buccolingually narrower P^4, relative to M^1 size, and a narrower, less bulbous P_4 with less exodaenodonty of the posterior root. Differs further from *P. pagei* in having a less expanded anterobuccal region on P^4. Also may differ in having larger, more robust upper and lower medial incisors that are lower crowned. I_1 has a stronger margoconid and is probably deeper. Differs further from *P. jepseni* in (3) above. Differs from *P. shifrae* in being much larger.

Etymology.— *Arche* (Gr.), beginning, chief, first cause, first place: alluding to *P. archus* being the earliest known species of

TABLE 44 — Dental measurements for *Phenacolemur archus* n. sp. and *P. pagei* (YPM-PU 18351). P_4 height is from base of enamel on anterobuccal root to crown apex. Apical width is mesiodistal. *Estimate.

		Phenacolemur archus										*P. Pagei*
		UM 61577 SC-243	UM 69237 Fossil Hollow	UM 77163 Croc Tooth Q.	UM 77165 Croc Tooth Q.	UM 109601 (type) Croc Tooth Q.	UM 109967 Fossil Hollow	YPM-PU 19163 Fossil Hollow level?	YPM-PU 24594 Fossil Hollow	YPM-PU 25034 Sand Draw	YPM-PU 25035 Sand Draw	YPM-PU 18351 Fossil Hollow
Dent. D		—	—	—	—	5.60	—	—	—	—	—	7.50
I^1	H	—	—	—	—	—	—	—	—	—	4.02	—
	W base	—	—	—	—	—	—	—	—	—	1.35	—
	W apical	—	—	—	—	—	—	—	—	—	1.93	—
P^4	L	—	2.10	—	—	—	—	—	—	—	—	—
	W	—	2.53	—	—	—	—	—	—	—	—	—
M^1	L	—	2.13	—	—	—	—	—	—	—	—	—
	W	—	3.01	—	—	—	—	—	—	—	—	—
M^2	L	—	—	—	1.87	—	—	—	—	—	—	—
	W	—	—	—	2.73	—	—	—	—	—	—	—
I_1	W	—	—	1.30	—	—	—	—	—	—	—	—
	D	—	—	3.00	—	—	—	—	—	—	—	—
P_4	L	2.63	2.95	—	—	2.60	2.53	2.43	2.65	2.42	—	3.15
	W	1.65	1.90	—	—	1.92	1.88	1.93	1.90	1.80	—	2.40
	H	2.58	—	—	—	3.05	—	—	3.23	—	—	—
M_1	L	—	—	2.45	—	2.53	—	2.27	—	—	—	2.30
	W tri.	—	—	1.98	—	2.07*	—	1.85	—	—	—	1.95
	W tal.	—	—	2.04	—	2.05*	—	2.05	—	—	—	2.16
M_2	L	—	—	2.25	—	—	—	2.20	—	—	—	—
	W tri.	—	—	1.97	—	—	—	1.80	—	—	—	—
	W tal.	—	—	1.95	—	—	—	2.00	—	—	—	—

TABLE 45 — Dental statistics for *Phenacolemur archus* n. sp. from SC-243 anthills. P_4 height is from base of enamel on anterobuccal root to apex. Apical width is mesiodistal. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
I^1	W apical	2	2.24	2.29	2.27	—	—	—
P^4	L	1	—	—	2.11	—	—	—
	W	1	—	—	2.76	—	—	—
M^1	L	2	2.02	2.16	2.09	—	—	—
	W	2	2.93	2.95	2.94	—	—	—
M^2	L	5	1.81	2.03	1.89	—	—	—
	W	5	2.61	3.22	2.87	—	—	—
M_1	L	5	2.18	2.38	2.26	0.04	0.08	3.48
	W tri.	5	1.68	1.86	1.78	0.03	0.07	3.86
	W tal.	5	1.82	2.03	1.89	0.04	0.08	4.48
M_2	L	9	2.04	2.25	2.12	0.02	0.07	3.53
	W tri.	9	1.68	1.99	1.82	0.03	0.09	4.70
	W tal.	8	1.67	1.95	1.79	0.04	0.10	5.63
M_3	L	1	—	—	2.70	—	—	—
	W tri.	1	—	—	1.58	—	—	—
	W tal.	1	—	—	1.50	—	—	—

Phenacolemur.

Description.— Figures and descriptions of *Phenacolemur* teeth were published by Jepsen (1930b), Simpson (1955), Szalay and Delson (1979), and Rose (1981a), and only pertinent structures are described here.

The I^1 (UM 61448, 61511, YPM-PU 25035) is robust, mesiodistally wide, and has a prominent mediocone, anterocone, and laterocone. The apex of the mediocone is well below that of the anterocone. The apex of the laterocone is near the base of the mediocone, but above the mediocrista. The mediocrista is strong, high, and robust. The posterocone is single, strong, and well-separated from the ventral surface of the crown.

The P^4 (UM 61559, 69237) is semimolariform and has a large paracone, but smaller metacone. The protocone is well-developed. The crown is expanded anterobuccally of the paracone. Weak, discontinuous post- and precingula are present. M^{1-2} are considerably wider than long and have rounded corners. M^1 is semi-rectangular.

The I_1 is large, deep, and robust. It has a strong margoconid (UM 77163). P_4 is slightly longer than M_1 and its apex is considerable higher than the M_1 trigonid. The P_4 is slightly exodaenodont, with enamel extending lower on the anterior root, than on the posterior root. The P_4 talonid basin width is about 55-60% of the total crown width. M_{1-2} have a buccal swelling at the base of the crown. In some specimens (e.g., UM 77163) an incipient buccal cingulid is present on the swelling. Weathering removed enamel from the lingual surface of M_1 in the holotype.

A small mental foramen is present on the dentary (UM 77163) below the P_4-M_1 junction and a larger one appears to have been present below the anterior face of P_4.

Discussion.— Bown and Rose (1976) and Rose (1981a) cited numerous characters that differentiate *Ignacius* from *Phenacolemur*. However, although these characters serve to differentiate the more derived species of *Ignacius* (i.e., *I. graybullianus* and *I. clarkforkensis*) from *P. pagei* or younger *Phenacolemur*, they do not work well to distinguish *I. frugivorus* from *P. archus*. In several respects *P. archus* is a morphological intermediate between *I. frugivorus* and *P. pagei*, including P_4 size (Fig. 51), relative P_4/M_1 size (Fig. 52), P^4/M^1 size, and degree of P_4 hypertrophy. This suggests that *P. archus* was derived from *I. frugivorus* or a form close to it in late Tiffanian, contrary to the suggestion that it was derived from *Paromomys maturus* in the middle Paleocene (Bown and Rose, 1976).

Phenacolemur archus is distinguished from *Ignacius* primarily by having a larger P_4 relative to M_1, greater degree of exodaenodonty in P_4, and a basal swelling on the buccal side of M_{1-2}. P^4 is also larger, relative to M^1, than in *Ignacius*. These characters appear to be derived for *Phenacodus*, and thus *P. archus* is best placed in that genus. Notably, the youngest specimens of *I. frugivorus*, which are from Divide Quarry, overlap with the P_4/M_1 length ratio in *P. archus*, but are smaller (Fig. 52). *Phenacolemur archus* is readily distinguished from *P. pagei* in having a shorter P_4 (Figs. 51 and 52) that lacks the bulbous lateral expansion and the extreme exodaenodonty found in most P_4s of *P. pagei* (e.g., Simpson, 1955). P^4 is also smaller, relative to M^1, than in *P. pagei*. M_1s are approximately the same length in both species but are slightly wider on average in *P. pagei* (Tables 42, 43, and 44). There is considerable variability in the P_4s of *Phenacolemur*, as discussed in the *P. pagei* section, but there appears to be little overlap between those of *P. pagei* and *P. archus*.

Phenacolemur pagei and *P. archus* appear to co-occur at Fossil Hollow. YPM-PU 18351, a right dentary with P_4-M_1 and a partial P_4 in YPM-PU 24598 resemble small individuals of *P. pagei*. Both are from Fossil Hollow according to specimen labels. In the former, the enamel on the anterior root of P_4 extends much lower than on the posterior root, which is typical of *P. pagei*. The dentary is also considerably more robust and about 35% deeper than in *P. archus* (UM 77163) (7.5 and 5.6 mm, respectively). The P_4 in YPM-PU 18351 is the largest P_4 from Ti-4b and is just below the range of *P. pagei* at Princeton Quarry, the type locality, but is within the range of specimens from Schaff and Y2K quarries (Fig. 51). YPM-PU 24598 is too fragmentary to measure. P_4s identified as *P. archus* from Fossil Hollow are close in size to that of the holotype (Fig. 51, gray circle). The distance between the largest and smallest P_4s at Fossil Hollow is 0.26, which is greater than the range exhibited at either Princeton or Y2K quarries, in spite of their much larger samples. Thus, two species appear to be present.

Two partial I^1s and a complete I^1 from anthills at SC-243 and in Sand Draw are identified as *Phenacolemur archus*. The identification is supported by the occurrence of two P_4s and one P^4 also referable to *P. archus* in the anthills. *Ignacius frugivorus* may also occur at SC-243 but the I^1s identified as *P. archus* are much larger and more robust than those of *I. frugivorus* from Divide Quarry (Fig. 53H-K). The three apical cusps in *P. archus* have the same configuration and relative sizes as those in *I. frugivorus*, based on fragmentary specimens from Divide Quarry (UM 110962, 110963), but those of *P. archus* are considerably larger (Fig. 53H-K). The incisors of *P. archus* are as deep and wide as those of *P. pagei* (Tables 42 and 44) but they are lower crowned, and the distance between the mediocone and the posterocone is less (Fig. 53J-M). The configuration of cusps is the same as in *P. pagei*, but the mediocone is larger, especially in YPM-PU 25035, and the mediocrista is stronger.

Of the paromomyid I^1s that have previously been figured (Bown, 1979; Godinot, 1984; Robinson and Ivy, 1994; Rose and Bown, 1996; Bloch et al., 2002) the I^1s of *Phenacolemur archus* are most similar to those of *P. simonsi* (Rose and Bown, 1996, Fig. 3D, p. 62) and *Acidomomys hebeticus* (Bloch et al., 2002). They differ from the I^1 of *P. simonsi* in having an anterocone that is slightly higher than the mediocone, a laterocone that is higher on the crown, and a mediocrista that is lower on the crown. The apex of the laterocone is higher than the mediocrista. They differ from the I^1 of *A. hebeticus* in being lower crowned, lacking a "double" posterocone, and in having a stronger mediocrista. The laterocone is also slightly smaller.

UM 77163 is the only specimen of *Phenacolemur archus* that preserves a significant part of the horizontal ramus. Although the P_4 has fallen out, the spacing and size of its roots leave little doubt that this specimen is correctly identified as *Phenacolemur*. It preserves I_1, and M_{1-2}. The lower incisor differs from those of *P. pagei* in having a distinct margoconid. Deformation has pushed the root of I_1 below the ventral surface of the dentary and lateral crushing may have increased its depth, but it appears to have been as deep as in *P. pagei*. The diastema between I_1 and P_4 is shorter than in specimens of *P. pagei*, but it could have been shortened from deformation.

YPM-PU 19163 is one of the most complete lower dentitions of *Phenacolemur archus*, preserving P_4-M_2. The specimen label indicates that it was collected in 1940 by crews from Princeton University at the "Fossil Hollow level," "1/2 mile SE of monument marking point where S.C.g. [Silver Coulee gray?] beds reach table top." I have not relocated the "monument" or the locality, but gray mudstones in this area that are exposed at the top of Polecat Bench are north of Fossil Hollow and stratigraphically slightly higher. These beds are also in the *Phenacolemur* zone (Ti-4b).

Hypodigm.— **Croc Tooth Q.** (FG028): UM 77163, R dent. I_1, M_{1-2}, P_4 and M_3 alveoli; 77165, L M^2; 109601 (holotype), R P_4-M_1. **Fossil Hollow** (SC198): UM 69237, R max. P^4-M^1; 109967, R P_4; YPM-PU 24594, L P_4. **Fossil Hollow level?**: YPM-PU 19163, R dent. frag., P_4-M_1. **Sand Draw anthills**: YPM-PU 25034, R P_4; 25035, L I^1. **SC243**: UM 61488, R I^1; 61511, L I^1; 61553, L M^2; 61554, R M_1; 61556, R M_1; 61557, L M_3; 61558, R M_2; 61559, R P^4; 61560, L M^1; 61561, R M_2; 61564, L M_2; 61565, L M^2; 61566, R M_1; 61567, L M^2; 61568, R M^2; 61569, L M^1; 61570, L M^1; 61571, R M_2; 61572, R M_2; 61573, L P_4; 61574, L M_2; 61575, R M_1; 61577, L P_4; 61578, L M_2; 61579, R M_2; 61580, L M_1; 61581, L M_1; 61584, L M_1 partial.

Family PICRODONTIDAE Simpson, 1937b

PICRODUS Douglass, 1908

Picrodus cf. *P. silberlingi* Douglass, 1908

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description.— Teeth and dentaries of *Picrodus silberlingi* have been described and figured by Simpson (1937b), Szalay (1968), and Gingerich et al. (1983).

Discussion.— Rose (1981a) identified four specimens from Cedar Point Quarry as *Picrodus* cf. *P. silberlingi* without discussion. Only one, YPM-PU 14989, was available for study. It is a right dentary preserving M_1 and alveoli for M_{2-3}. The holotype of *P. silberlingi* (CM 1670) is a right dentary with P_4-M_1 from Silberling Quarry in the Crazy Mountains Basin, and is late Torrejonian in age. The M_1 in YPM-PU 14989 is within the variability described by Szalay (1968) and bears no features that distinguish it from those described by him or by Simpson (1937b). It has a length and width of 2.35 and 1.2 mm, respectively, using Szalay's landmarks (OMD, Fig. 1) and a maximum length of 2.65 mm if the base of the tooth is included, as Simpson apparently did. It falls in the low end of the range reported by Simpson for M_1 length (2.6-2.9, n = 8) in *P. silberlingi* from the type area, but above the range reported by Szalay (1968) for Swain Quarry (1.75-2.13, n = 10). Szalay (p. 23) noted, however, that when the Crazy Mountains Basin sample was measured with his equipment its range was within that of the Swain Quarry sample. In any case, a direct comparison with casts of *P. silberlingi* (USNM 9622, 309875, CM 1670) from the Crazy Mountains Basin revealed no appreciable difference in size.

An additional dentary fragment (YPM-PU 16476) from a quarry at PU locality 106 in the Foster Gulch area preserves an M_1. The M_1 is about 2.5 mm in maximum length, and 1.25 mm wide. It is very similar to the Cedar Point Quarry specimen. *Picrodus* is not known from quarry sites above the *Plesiadapis rex* zone and suggests a Ti-3 age for PU locality 106.

I provisionally follow Rose (1981a) and refer these specimens to *P.* cf. *P. silberlingi*, pending examination of additional specimens from Cedar Point Quarry.

Referred specimens.— **Cedar Point Q.**: YPM-PU 14989, R dent. M_1, alveoli for M_{2-3}. **PU Locality 106** (Sec. 18, T55N, R96W): YPM-PU 16476, L dent. M_1.

Grandorder UNGULATA Linnaeus, 1766
Order DINOCERATA Marsh, 1873
Family UINTATHERIIDAE Flower, 1876

PROBATHYOPSIS Simpson, 1929b

Probathyopsis harrisorum (Patterson, 1939)

Bathyopsoides harrisorum Patterson, 1939, p. 374.
Probathyopsis harrisorum, Thewissen and Gingerich, 1987, p. 199.

Holotype.— FMNH P 15546, left dentary with P_{3-4}, M_{2-3}, right dentary with M_{2-3}, fragments of I_1, I_2, C_1, and M_1, on both dentaries, associated postcranial elements; from "Plateau Valley beds about 150 feet above the base of the horizon…one mile north of the Douglas Harris ranch house," Colorado (Patterson, 1939). Late Paleocene in age.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a), *Plesiadapis simonsi* (Ti-5b), *Plesiadapis gingerichi* (Ti-6), and Rodentia (Cf-1) zones.

Description.— The holotype was described by Patterson (1939). Additional material from the Bighorn Basin was described and figured by Thewissen and Gingerich (1987).

Discussion.— *Probathyopsis* was recently synonymized with *Prodinoceras* by Lucas and Schoch (1998) following Schoch and Lucas (1985). I follow Thewissen and Gingerich (1987, pp. 216-217), however, and recognize *Probathyopsis* as a valid genus for reasons cited therein.

Thewissen and Gingerich (1987) made a detailed study of *Probathyopsis* in the Bighorn Basin. Subsequent material collected from late Paleocene localities in this area is very fragmentary and adds little to our knowledge of the genus. Thewissen and Gingerich (1987) distinguished *P. harrisorum* from *P. praecursor* by its larger size (~10% in dentary length), retention of P_1, and by features of the astragalus. Because recognition of most of these characters requires unusually complete dental material or rare astragali, most specific identifications are based on size. The earliest occurrence of *P. praecursor* recognized by Thewissen and Gingerich (1987) was in the middle Clarkforkian. Early Clarkforkian specimens were identified as *P. praecursor* by Rose (1981a), but later identified as *P. harrisorum* by Thewissen and Gingerich (1987) presumably because of larger size. I provisionally follow their identifications.

The first occurrence of *Probathyopsis* is of interest biogeographically and biostratigraphically because it is the first member of Dinocerata to enter North America. It appears to be an intercontinental immigrant from Asia (e.g., Beard and Dawson, 1999) or South America (Gingerich, 1985). It is easily distinguished from other taxa, even with fragmentary teeth. The oldest verifiable occurrences of *Probathyopsis* are near SC-246 and SC-274, according to locality data from specimens in the YPM collections . These localities mark the base of the *Probathyopsis* zone. Its occurrence near this level is verified by UM 98470 from SC-270, which is only about 10 meters higher.

One specimen in the YPM collection, however, may be from a significantly lower level. The label on YPM-PU 18350 (M_3 talonid) indicates it is from Fossil Hollow, which is near the middle of the *Phenacolemur* zone (Fig. 6). However, Jepsen's 1937 unpublished field notes report that the tooth (recorded as ?*Titanoides* tooth) is from the "same level as Fossil Hollow." There are few fossiliferous exposures in the vicinity of Fossil Hollow. It is also clear from other specimen labels that Jepsen's crew though that some localities farther to the west, directly below Princeton Quarry, were approximately at the level of Fossil Hollow. They are if fact, about 100 meters higher. It is possible that YPM-PU 18350 was collected at a level they believed was equivalent to Fossil Hollow, but was actually significantly higher. The provenance of the specimen is in doubt and only additional collection can adequately resolve this problem.

Referred specimens.— **FG037**: UM 85250, L P_3, M_2. **Foster Gulch** (SW1/4, S5, T54N, R95W): YPM-PU 18846, R M_2 talonid. **SC085**: UM 66213, Upper tooth frags. **SC144**: YPM-PU 18849, R C_1, I^xs; 18866, R C_1, I^xs; 19344, L C_1, P_3 postcranial frags. **SC157**: UM 68030, M_x frags. **SC165**: UM 68257, max. frags.; YPM-PU 18842, C_1 and cheek tooth frags. **SC171**: UM 68419, M_3 tal.; 71776, R P^4?, R M^2 or M^3, assoc. bone. **SC174**: UM 68439, incisor. **SC179**: YPM-PU 21676, upper cheek tooth frag. **SC186**: UM 110310, R P_x frag., other tooth frags. **SC191**: UM 108284, R M^3. **SC193**: UM 108492, L M^1, partial, canine frag., tal., and cheek frags. **SC242**: YPM-PU 18840, P_x frag. **SC246**: YPM-PU 18342, L M_3, 2 I_1's **SC249**: UM 71796, L C^1, R C^1, assoc. postcrania. **SC257**: UM 73333, incisor. **SC270**: UM 98470, L dent. C_1, M_1 tal., M_2 tal., M_3, R dent. C_1, M_3. **SC274**: YPM-PU 18843, upper and lower tooth frags. **SC278**: UM 110040, M^x frags.; YPM-PU 19451, cheek tooth frags. **SC383**: UM 108425, I^x, C^1 frags., R P^4, R M^x, L M_x frag., pelvic frag., tooth frags. **SC384**: UM 108498, C frags., R max. P^{3-4}, M^{1-3}, L max. P^4 frag., M^2 partial, M^3 partial, R dent. P_{3-4}, R M_3 tal. **SC385**: UM 108484, L P^3, R tri. frag. **SC389**: UM 108446, M_1 frags.; 108545, M^x frags., C^1 frag.; UM 109109, M^x frags. **SC399**: UM 108592, L M^2, M^x frags. **SC416**: UM 110032, tooth frags. **SC421**: YPM-PU 19106, R C_1 partial. **NE¼, S12, T57N, R101 W**: YPM-PU 18869, premax. I^{2-3}, R I_1-C_1.

Order PROCREODI Matthew, 1915
Family OXYCLAENIDAE Scott, 1892

CHRIACUS Cope, 1883

Chriacus sp.

Figure 54, Table 46

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis gingerichi* (Ti-6), Rodentia (Cf-1), *Plesiadapis cookei* (Cf-2), and *Copecion* (Cf-3) zones.

Description.— Upper molars have a continuous cingulum present on the anterior, lingual, and buccal sides of the protocone. The cingulum is expanded slightly posterolingually into a low crest, but there is no distinct hypocone present. The trigon basin is deep, and cusps are high. The metaconule is large and distinct, but the paraconule varies from distinct (UM 109728) to small and indistinct (UM 71563).

The P_4 has a high trigonid with a distinct metaconid, well-separated from the protoconid, which is nearly as high. There is a continuous trough beginning low on the trigonid that goes over the trigonid between the metaconid and protoconid, and down the posterior wall. The P_4 has no paraconid. Its talonid is weakly basined and is pointed posteriorly. M_{1-2} have a rounded paraconid and metaconid, but a more acute protoconid. The hypoconid, hypoconulid, and entoconid are distinct and separate on M_1, but the first two cusps are less separate on M_2, and with wear the lingual and posterolingual margins of the talonid may be reduced to little more than a continuous crest.

Discussion.— *Chriacus* sp. is poorly represented in the northern Bighorn Basin. A P_4 of latest Tiffanian age from Bluff Top Quarry is the earliest record of the species. The most complete specimen in the UM collections is UM 86253, a right dentary with P_4-M_3 (M_2 trigonid missing), shown in Figure 54. A prominent P_4 metaconid, higher molar trigonids, a higher molar talonid/trigonid width ratio, and higher upper and lower molar cusps distinguish *Chriacus* sp. from *Princetonia*. UM 71563, an isolated M^1, was figured by Rose (1981a) who referred it to cf. *Tricentes* sp. It was later included in *Princetonia yalensis* by Gingerich (1989). However, based on new specimens from Y2K Quarry, upper molars of *Princetonia* have lower cusps and a larger and higher crested posterolingual expansion of the cingulum than those of *Chriacus*. UM 71563 has relatively high cusps and only a moderate posterolingual expansion of the cin-

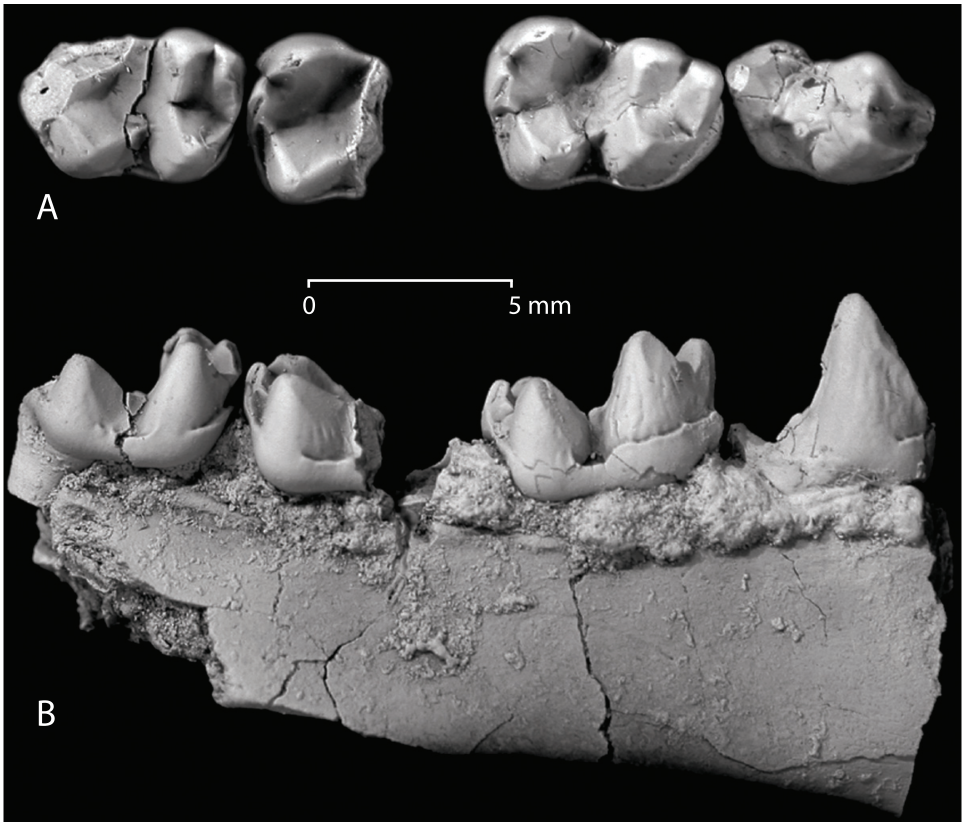


FIGURE 54 — Dentary of *Chriacus* sp. from the late Clarkforkian (UM 86253; SC-29). A–B, right P_4-M_1, M_2 talonid, and M_3 in occlusal (A) and buccal (B) views.

gulum, and thus probably belonged to *Chriacus* sp.

Defining characteristics of *Chriacus* are unclear and the genus appears to be a "waste basket" taxon. Nevertheless, I apply the name because it includes species similar to *Chriacus* sp. (e.g., *C. punitor*, *C. baldwini*). The specimens included here in *Chriacus* sp. may represent a new species, but I forego naming a new species pending taxonomic revision of the genus.

Referred specimens.— **SC179 Q.**: 110046, L M_1 tri. **SC193**: UM 110177, R M_1. **SC362 Q.**: UM 110126, L P^3. **Bluff Top Q.** (SC379): UM 108252, R P_4.

PRINCETONIA Gingerich, 1989

Princetonia cf. *P. yalensis*

Figure 55, Tables 46–47

Princetonia yalensis (in part) Gingerich, 1989.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a), *Plesiadapis simonsi* (Ti-5b), and ?*Plesiadapis gingerichi* (Ti-6) zones.

Description.— The following is based on unworn teeth from Y2K quarry except for P^4. The upper canine is long, saber-like, and buccolingually compressed with a sharp posterior edge. P^3 is triple-rooted and triangular in occlusal view. There is no protocone cusp above the lingual root. The P^4 has a high, acute protocone with a small, sharp crest that descends its lingual wall. Pre- and postcingula ascend lingually to meet the crest. The P^4 metacone is acute and secodont. There is no paracone. The base of the protocone is extended lingually. P^4 width exceeds length. There is no trigon basin. M^1 and M^2 have pre- and postcingula that merge with a very broad, high posterolingual crest separated from the protocone by a deep trench. There is no hypocone, but a small cusp is present on the crest lingually, and a little posterior of the protocone (more posterior in M^1), and is connected to the protocone by a small ridge. Upper molar cusps are relatively low. The P_4 does not have a paraconid or distinct metaconid, but has a strong, vertical "metaconid ridge" along the posterolingual wall. Lower molars match the description given by Gingerich (1989), except as noted below.

Discussion.— Lower molars included here in *Princetonia* cf. *P. yalensis* are similar in form to those in the holotype of *P. yalensis*, from the early Wasatchian, and also to those of *Chriacus* sp., from the latest Tiffanian and Clarkforkian. Molars of *Princetonia* differ from those of *Chriacus* in ways outlined by Gingerich (1989), especially in having more rectangular shaped $M_{2\text{-}3}$ and lower trigonids. Molar talonid cusps are also lower in *Princetonia*. Although $M_{1\text{-}2}$ trigonids are lower in *Princetonia*, the M_3 trigonid height is approximately equal to that in *Chriacus* sp. No premolars have been described for *P. yalensis* from the type locality or from the Wasatchian or Clarkforkian. Gingerich, however, included a dentary with P_2-M_3 (YPM-PU 13957) and other specimens in *P. yalensis* from the late Tiffanian Princeton Quarry, based on similari-

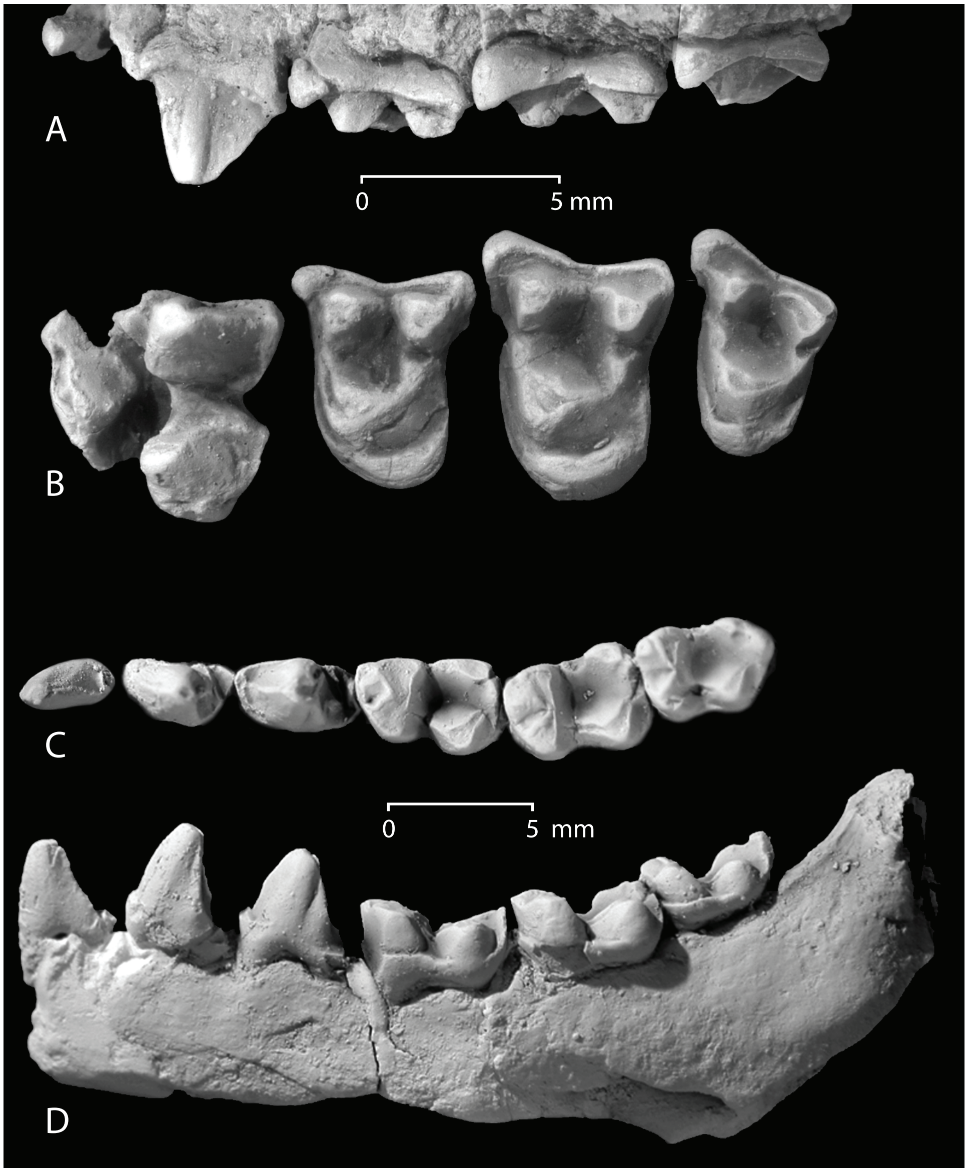


FIGURE 55 — Maxilla and dentary of *Princetonia* cf. *P. yalensis* from SC-419 and Princeton Quarry, respectively. A–B, UM 110070, left maxilla with partial P^4-M^3 in buccal (A) and occlusal (B) views. C–D, YPM-PU 13957, left dentary with P_2-M_3 in occlusal (C) and buccal (D) views.

ties to molars in the holotype (YPM-PU 23629, right dentary with M_{2-3}). The P_4s in late Tiffanian samples from Princeton and Y2K quarries lack a metaconid, distinguishing them from *Chriacus* sp., and other oxyclaenids.

There are several differences between molars in the late Tiffanian from and the holotype of *Princetonia yalensis*. The lingual margin of the M_2 talonid in the holotype is little more than an acute crest that is posteriorly confluent with the postcingulum, and there is no distinct entoconid. In contrast, M_2s in the late Tiffanian form all have a distinct entoconid, and most have an additional distinct cusp anterior to the entoconid, visible even in specimens with a high degree of wear. In this regard, *P. yalensis* is more similar to *Chriacus* sp., which lacks a distinct cusp anterior to the M_2 entoconid and has a more crest-like lingual margin. Molars in the late Tiffanian form are also slightly smaller than those in the holotype. For these reasons the Tiffanian specimens may represent a distinct species and I refer them to *P.* cf. *P. yalensis* pending the discovery of more specimens from the early Wasatchian.

An isolated lower incisor (UM 109333) from Y2K Quarry bears a close resemblance to incisors in the tooth comb of *Thryptacodon* (Gingerich and Rose, 1979; Rose et al., 1981) and those of lemuriform primates. These teeth have a distinctive crown with two dorsal furrows separated by a medial ridge, and a crown that is ventrally canted from the axis of the root, unlike those of plesiadapiforms in which the axes of the root and crown form a semi-confluent arc. No teeth of *Thryptacodon* are known from the quarry and the contemporary species, *T. pseudarctos*,

TABLE 46 — Dental measurements for *Chriacus* sp. and *Princetonia* from the northern Bighorn Basin. *BTQ*, Bluff Top Quarry; *PQ*, Princeton Quarry; *Y2K*, Y2K Quarry. *Estimate.

		Chriacus sp.				*P. yalensis*	*Princetonia* cf. *P. yalensis*									
		UM 73611 SC-188	UM 86253 SC-29	UM 108252 BTQ	UM 110177 SC-193	YPM-PU 23629 (type) SC-121(?)	UM 109123 Y2K	UM 109162 Y2K	UM 109214 Y2K	UM 109219 Y2K	UM 109246 Y2K	UM 109335 Y2K	UM 109345 Y2K	UM 110070 SC-419	YPM-PU 13943 PQ	YPM-PU 13957 PQ
P^2	L	—	—	—	—	—	—	—	—	4.00	—	—	—	—	—	—
	W	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P^3	L	—	—	—	—	—	—	4.00	—	—	4.40	—	—	—	—	—
	W	—	—	—	—	—	—	3.27	—	—	3.41	—	—	—	—	—
M^1	L	—	—	—	—	—	—	—	—	—	—	—	5.36	4.67	—	—
	W	—	—	—	—	—	—	—	—	—	—	—	6.34	5.54	—	—
M^2	L	—	—	—	—	—	5.64	—	5.50	—	—	5.06	—	4.87	—	—
	W	—	—	—	—	—	7.20	—	6.71	—	—	6.80	—	6.57	—	—
M^3	L	—	—	—	—	—	—	—	—	—	—	—	—	4.03	—	—
	W	—	—	—	—	—	—	—	—	—	—	—	—	5.10	—	—
P_2	L	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.39
	W	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.60
P_3	L	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.99
	W	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.21
P_4	L	—	5.29	5.23	—	—	—	—	—	—	—	—	—	—	—	4.51
	W	—	3.12	3.04	—	—	—	—	—	—	—	—	—	—	—	2.44
	H	—	4.90	—	—	—	—	—	—	—	—	—	—	—	—	—
M_1	L	5.62	6.00	—	5.4*	—	—	—	—	—	—	—	—	—	5.49	5.45
	W	3.73	4.27	—	3.35	—	—	—	—	—	—	—	—	—	3.77	3.45
M_2	L	—	—	—	—	5.56	—	—	—	—	—	—	—	—	5.30	5.25
	W	—	4.23	—	—	3.90	—	—	—	—	—	—	—	—	3.98	3.87
M_3	L	—	—	—	—	—	—	—	—	—	—	—	—	—	5.46	4.72
	W	—	3.96	—	—	3.50	—	—	—	—	—	—	—	—	3.35	3.15

TABLE 47 — Dental statistics for *Princetonia* cf. *P. yalensis* from Y2K Quarry. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
C^1	L	1	—	—	3.54	—	—	—
	W	1	—	—	2.58	—	—	—
	H	1	—	—	9.90	—	—	—
P^2	L	1	—	—	4.00	—	—	—
	W	—	—	—	—	—	—	—
P^3	L	2	4.00	4.40	4.20	—	—	—
	W	2	3.27	3.41	3.34	—	—	—
M^1	L	1	—	—	5.36	—	—	—
	W	1	—	—	6.34	—	—	—
M^2	L	3	5.06	5.64	5.40	0.13	0.30	5.60
	W	3	6.71	7.20	6.90	0.10	0.26	3.78
I$_3$	L	1	—	—	4.68	—	—	—
	W	1	—	—	1.65	—	—	—
	D	1	—	—	1.74	—	—	—
P$_3$	L	3	3.97	4.25	4.12	0.07	0.14	3.44
	W	2	2.18	2.34	2.26	—	—	—
P$_4$	L	2	4.95	5.14	5.05	—	—	—
	W	3	2.60	2.70	2.66	0.03	0.06	2.07
M$_1$	L	2	5.46	5.50	5.48	—	—	—
	W	2	3.55	3.88	3.72	—	—	—
M$_2$	L	1	—	—	5.27	—	—	—
	W	2	3.96	4.06	4.01	—	—	—
M$_3$	L	2	5.35	5.39	5.37	—	—	—
	W	2	3.40	3.80	3.60	—	—	—

TABLE 48 — Dental statistics for *Thryptacodon australis* from Cedar Point Quarry. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
P^4	L	4	4.90	5.66	5.29	0.18	0.35	6.71
	W	3	4.43	5.01	4.68	0.17	0.30	6.37
M^1	L	4	5.27	6.44	5.72	0.28	0.56	9.87
	W	4	5.99	6.86	6.45	0.21	0.42	6.53
M^2	L	2	6.10	6.25	6.18	—	—	—
	W	2	7.70	8.06	7.88	—	—	—
P$_4$	L	4	5.00	5.30	5.15	0.06	0.13	2.51
	W	4	2.70	2.84	2.75	0.03	0.07	2.43
M$_1$	L	7	6.26	6.94	6.55	0.10	0.27	4.19
	W	7	4.26	4.75	4.41	0.07	0.18	4.00
M$_2$	L	10	6.57	7.58	6.94	0.11	0.34	4.84
	W	10	5.34	6.26	5.64	0.08	0.26	4.67
M$_3$	L	3	6.30	7.40	6.76	0.33	0.57	8.43
	W	4	4.70	5.54	4.95	0.20	0.39	7.95

would be expected to have larger incisors. For this reason, and because of its abundance in the quarry, I tentatively include this incisor in *Princetonia* cf. *P. yalensis*.

UM 110070 preserves P^4-M^3 and is the only maxilla known for *Princetonia* cf. *P. yalensis* (Fig. 55A,B). This P^4 and two additional ones from Y2K Quarry (UM 110070, 81703) are similar to those of *Chriacus punitor* (AMNH 35665, Gidley Quarry) in having a large, lingually positioned protocone. The P^4 in UM 81703 differs from that of *C. punitor*, however, in having pre- and postcingula that ascend lingually to meet a sharp vertical ridge on the lingual wall of the protocone. The P^4 in UM 110070 is too worn to determine if this feature was present.

A maxillary fragment with P^4-M^1 (UM 83461) from the earliest Wasatchian was referred to *Chriacus badgleyi* by Gingerich (1989). Based on the new material from Y2K Quarry, upper molars of *Princetonia* have lower cusps and a larger and higher crested posterolingual expansion of the cingulum than those of *Chriacus* sp. from the Clarkforkian. UM 83461 has an expanded posterolingual crest, similar to that in *Princetonia* cf. *P. yalensis*, lacks a hypocone, and has relatively low cusps. These features suggest that this specimen may actually belong to *P. yalensis*.

Referred specimens.— **FG041**: UM 77289, L M$_3$. **Princeton Q.** (SC187): YPM-PU 13943, L dent. M$_{1-3}$; 13957, L dent. P$_2$-M$_3$. **SC165**: UM 81703, L P^4; 110176, L M$_1$. **SC193**: UM 108564, L M$_2$ tri. **SC266**: UM 110182, L P$_3$. **SC362**: UM 95863, R M^2. **SC389**: UM 108531, R M$_3$ trig. **SC419**: UM 110070, L max. P^4-M^3. **Schaff Q.**: YPM-PU 19398, 19467. **Y2K Q.** (SC389): UM 108533, R M$_1$ tri.; 109123, L M^2; 109130, C^1?; 109135, R dent. frag., M$_1$; 109145, L P$_4$; 109159, C^1; 109162, R P^3; 109169, L M$_1$; 109189, L P$_3$; 109214, L M^2; 109219, R P^2? partial; 109245, L M$_2$; 109246, L P^3; 109249, R M$_x$; 109333, R I$_3$?; 109335, L M^2; 109345, R M^1; 109355, R dent. P$_2$ (in crypt), P$_3$, L dent., radius, ulna, assoc.; 109409, R P$_4$; 109473, L M$_2$; 109490, R P$_4$; 109503, R P$_3$; 109651, L M$_3$; 110209, L M$_3$.

THRYPTACODON Matthew, 1915

Thryptacodon australis Simpson, 1935d

Figures 56–57, Table 48

Thryptacodon australis Simpson, 1935d, p. 20.

Holotype.—AMNH 17384, left and right dentaries with C$_1$-M$_3$ (except left P$_2$), and possibly associated M^2; from Mason Pocket (Ti-4) in the Animas Formation, San Juan Basin, Colorado.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* (Ti-3), *Plesiadapis churchilli* (Ti-4a), and *Phenacolemur* (Ti-4b) zones.

Description.— The lower dentition of *Thryptacodon australis* was described by Simpson (1935d).

Discussion.— Rose (1981a) included *Thryptacodon australis* in a faunal list for Cedar Point Quarry, based on 152 specimens, most of which are now in the YPM collections. A smaller sample from Cedar Point Quarry in the UM collections was available for study. The sample consists of 17 specimens, most of which are partial jaws. The holotype of *T. australis* appears to be within the variability of the UM sample, based on Simpson's (1935d) description. The variability in the Cedar Point Quarry sample is high, however, and it may include more than one species. Nevertheless, there is no clear bimodality and I provisionally identify all specimens as *T. australis*. I also refer small samples of isolated teeth to *T. australis* from Divide and Croc Tooth quarries

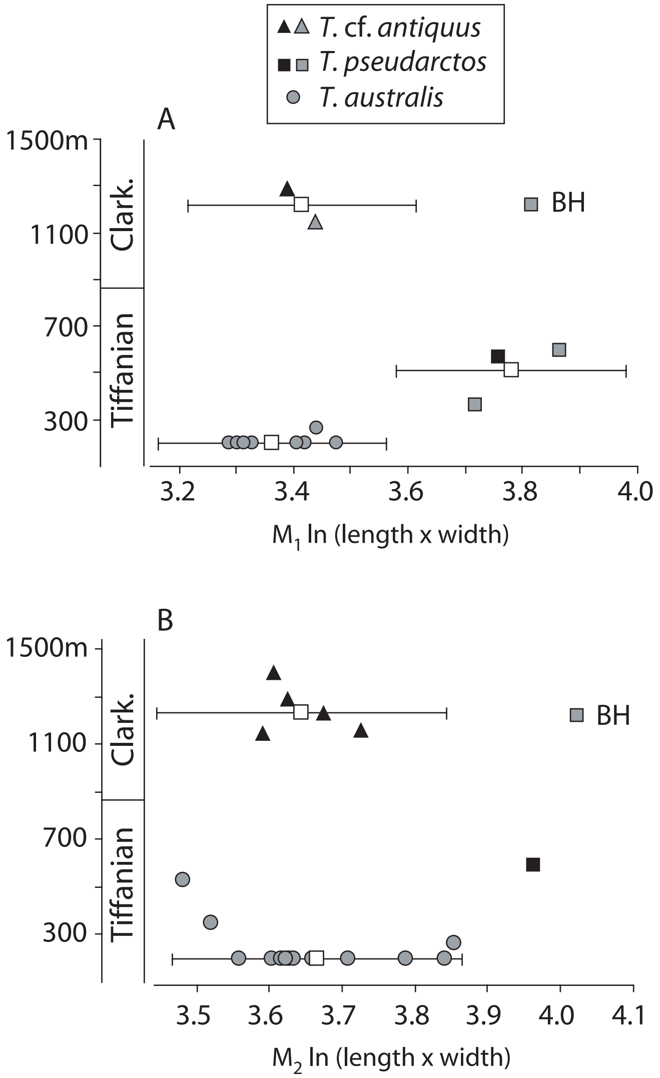


FIGURE 56 — Stratigraphic charts showing M_1 (A) and M_2 (B) size differences among *Thryptacodon australis*, *T. pseudarctos*, and *T.* cf. *T. antiquus*. All specimens are from the northern Bighorn Basin except two from Buckman Hollow (BH) in the Hoback Basin. Means shown as open boxes. Black symbols indicate specimens from the Polecat Bench sequence; gray symbols indicate specimens that were biostratigraphically correlated to the sequence. Error bars show expected range of variation of about 0.4 ln units for most individuals in a species (Gingerich, 1981).

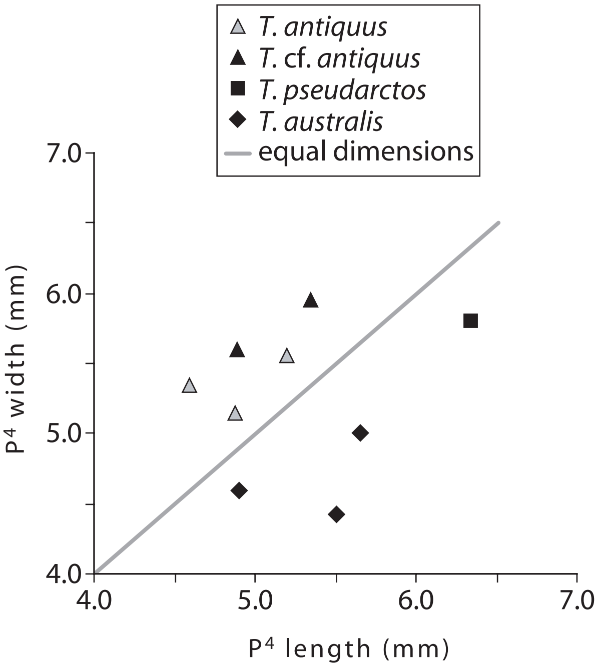


FIGURE 57 — Scatter plot of P^4 length and width in *Thryptacodon australis*, *T. pseudarctos*, *T.* cf. *T. antiquus*, and *T. antiquus* (early Wasatchian, Wa-2) from the northern Bighorn Basin.

that are within the variation exhibited at Cedar Point Quarry.

Thryptacodon australis is similar in size and molar morphology to *T. antiquus* from the Wasatchian and to *T.* cf. *T. antiquus* from the Clarkforkian (Rose, 1981a) (Fig. 56). The most conspicuous difference is in the P^4. In *T. australis* P^4 length exceeds width, while in *T. antiquus* width exceeds length (Fig. 57). The P^4 of *T. australis* has a very small anterolingually positioned protocone that varies from little more than a lingual expansion of the cingulum to a small low cusp. The protocone rises only slightly above the precingulum. The P^4 has a single, high acute buccal cusp, and a lingually convex metacrista. In contrast, the P^4 of *T. antiquus* is inflated with more rounded cusps, and has a much larger and higher protocone positioned more posteriorly. Its metacrista is relatively straight and the single buccal cusp is lower and more rounded that in *T. antiquus*. The P^4 is variable in both taxa, but the variation in the development of the protocone and in length/width ratios does not appear to overlap (Fig. 57).

Thryptacodon australis is also similar to *T. pseudarctos* described below. It differs in premolar characteristics and in being significantly smaller. Figure 56 shows the size distribution of teeth of *T. australis* from Cedar Point, Divide, and Croc Tooth quarries (gray circles in ascending order from bottom of 56B). Teeth from the last two localities are within the variability expected in the Cedar Point Quarry sample. Most teeth of *T. pseudarctos* are outside the size range of *T. australis*, but there is some overlap in M_3 and M^3 size. *Thryptacodon pseudarctos* first occurs in the *Phenacolemur* zone (Ti-4b) based on size, and appears to temporally overlap with *T. australis*. I have identified UM 79872 (M^1) and UM 110281 (M_2) as *T. australis* based on their small sizes. The former is from Fossil Hollow where several specimens of *T. pseudarctos* have been recovered, and the latter is from strata above Fossil Hollow (Fig. 56B, highest gray circle).

Referred specimens.— **Cedar Point Q.**: UM 63097, R dent. P_4-M_1; 63098, R dent. P_4 (frag.), M_{1-2}; 63099, L dent. P_4-M_1; 63108, 3 L P^4s, R M^1, R M^2, unassoc.; 64399, L dent. P_4-M_3; 64403, L dent. P_4-M_2; 64407, R dent.; 64424, R dent. M_{2-3}; 64446, L dent. M_2, C_1-M_3 alveoli; 64518, R dent. M_2; 64562, R dent. P_4-M_2; 64564, R dent. M_{1-3}; 64572, L dent. M_2; 64640, 2 R M^1s, L M^1, unassoc.; 71826, R max. P^4-M^2; 82061, R dent. M_{2-3}; 82090, R dent. frag. M_1. **Divide Q.** (FG046): UM 85312, R M_3; 92264, R M_2; 92278, R M^3; 110261, L M^1; 110263, R M^1; 110266, L M^3; 110275, R M^1; 110930, R M_3; 110931, R M_3; 110932, R M_1. **South of Divide Q.**: YPM-PU 23402, R M^1,

TABLE 49 — Dental measurements for *Thryptacodon pseudarctos*, *T. australis*, and *T.* cf. *T. antiquus* from the northern Bighorn Basin. *Estimate.

		T. pseudarctos								*T. australis*	*T.* cf. *T. antiquus*
		AMNH 22176 (type) Bear Creek	UM 68256 SC-165	UM 71762 SC-187	UM 74032 FG-8	UM 77028 SC-270	UM 79867 Fossil Hollow	UM 80355 SC-187	YPM-PU 19026 Sec. 7, T57N, R100W	UM 110281 SC-228	UM 71241 SC-195
P^4	L	—	—	—	6.35	—	—	—	6.50	—	4.95
	W	—	—	—	5.9*	—	—	—	3.60	—	5.0*
M^1	L	—	—	—	6.93	—	—	—	7.70	—	6.27
	W	—	—	—	7.59	—	—	—	6.20	—	7.00
M^2	L	6.92	7.33	—	—	—	6.90	6.78	—	—	6.22
	W	8.57	10.14	—	—	—	8.50	9.05	—	—	7.87
M^3	L	—	5.80	—	—	—	5.10	—	—	—	4.38
	W	—	—	—	—	—	6.20	—	—	—	5.40
P_4	L	—	—	5.35	—	—	—	—	—	—	—
	W	—	—	3.00	—	—	—	—	—	—	—
M_1	L	—	—	—	7.34	7.50	—	—	—	—	—
	W	—	—	—	5.7*	5.72	—	—	—	—	—
M_2	L	—	—	7.81	—	—	—	—	—	6.24	—
	W	—	—	6.74	—	—	—	—	—	5.21	—

M^3. **Fossil Hollow** (SC198): UM 79872, L M^1. **Long Draw Q.**: UM 108378, R M_2 tri. **MP054**: UM 110346, R M_1 tri. **Croc Tooth Q.** (FG028): YPM-PU 25023, R M^1 or M^2; 25024, R M_2. **SC228**: UM 110281, L M_2.

Thryptacodon pseudarctos Simpson, 1928

Figures 56–57, Table 49

Thryptacodon pseudarctos Simpson, 1928, p. 10.

Holotype.— AMNH 22176, isolated right M^2 from Bear Creek, northern Bighorn Basin, Montana.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b), *Probathyopsis* (Ti-5a), *Plesiadapis simonsi* (Ti-5b), and Rodentia (Cf-1) zones.

Description.— The holotype of *Thryptacodon pseudarctos* was described in detail by Simpson (1928). Additional specimens indicate that molars are similar to those of *T. australis*, but are larger on average. Based on UM 74032, P^4 length exceeds width (Fig. 57). The protocone is small and anterolingually positioned. The metacrista is slightly convex lingually. P_4 has a bulbous, inflated appearance. The metaconid varies from a distinct cusp to a large lingual bulge. A distinct cristid obliqua and hypoconid are present. The talonid basin varies from open to closed.

Mental foramina are present below P_1 and the posterior root of P_3. The posterior part of the symphysis is below P_2. P_1 was single-rooted, and $P_{2\text{-}4}$ double-rooted. P_1 was separated from P_2 by a short diastema, and from the canine by a longer diastema.

Discussion.— Simpson (1928) named *Thryptacodon pseudarctos* based on a single upper molar from the early Clarkforkian Bear Creek fauna in southern Montana. He noted similarities to the "Wasatch" species (i.e., *T. australis*) but thought differences were sufficient to merit specific separation. The species was later synonymized with *T. antiquus* by Van Valen and Sloan (1966), who argued that it was indistinguishable. Gingerich (1978) revalidated *T. pseudarctos* based on a specimen from Buckman Hollow of middle Clarkforkian age in southern Wyoming, which he argued was too large to be included in *T. antiquus*. Rose (1981a) provisionally recognized the species but only included specimens from the Bear Creek fauna in it. Krause (1986) referred two specimens from the middle Clarkforkian Paint Creek fauna to *T.* cf. *T. pseudarctos* without discussion.

This study indicates that there are at least three species of *Thryptacodon* present in the late Paleocene of the northern Bighorn Basin: *T. australis*, *T.* cf. *antiquus* (or *T. antiquus*; Rose, 1981a) and a large species identified here as *T. pseudarctos*. The large species can be distinguished by size, by premolar features, and possibly by pericone development in some specimens. Of these characters only size can be used in comparison with the holotype of *T. pseudarctos*. Nevertheless, it is similar in size to the upper molars identified here as *T. pseudarctos*, and there appears to be little overlap between it and *T. australis* or *T.* cf. *T. antiquus*. Figure 56 shows the temporal order of M_1 and M_2 size distributions for each species. The M_1s and M_2s of *T. pseudarctos* are well above the expected size ranges of the other species, but there appears to be some overlap in M^3s and M_3s (not shown).

Casts of CM specimens from Bear Creek indicate that both *Thryptacodon pseudarctos* and *T.* cf. *T. antiquus* are present at the type locality. CM 11682 (R M^1, L = 5.64, W = 6.32) and CM 11705 (R M^1, L = 5.95, W = 6.50) are easily within the size range of *T.* cf. *T. antiquus*, but are almost certainly too small to belong to *T. pseudarctos*. CM 11674 (L M^2, L = 6.22, W = 8.52), however, is similar in size to the holotype of *T. pseudarctos* and to specimens included here in the species. Both species are also present in the early Clarkforkian (Cf-1) in Sand Coulee, at approximately the same level (SC-413 and SC-217).

Gingerich (1978) indicated that *Thryptacodon pseudarctos*

TABLE 50 — Dental measurements of *Arctocyon mumak* from the northern Bighorn Basin. Measurements for holotype based on epoxy casts. *CTQ*, Croc Tooth Quarry; *DQ*, Divide Quarry. *Estimate.

		UM 77164 CTQ	UM 75814 FG-15	UM 83275 DQ	UM 85305 DQ	UM 91331 DQ	UM 110933 DQ	YPM-PU 17406 (type) near SC-243	YPM-PU 17746 CTQ	YPM-PU 18557 CTQ
P^4	L	—	13.4	—	—	—	—	—	—	—
	W	—	—	—	—	—	—	—	—	—
M^1	L	14.5	—	—	11.8	12.8	13.9	12.5*	—	—
	W	16.8	—	—	13.2	15.0	16.3	14.3*	—	—
M^2	L	—	—	15.0	—	—	—	14.0*	14.1	—
	W	—	—	19.4	—	—	—	18.3*	18.8	—
M^3	L	—	11.0	—	—	—	—	—	—	—
	W	—	—	—	—	—	—	—	—	—
P_4	L	—	—	—	—	—	—	18.5	—	—
	W	—	—	—	—	—	—	9.5	—	—
M_1	L	—	—	—	—	—	—	14.9	—	—
	W tri.	—	—	—	—	—	—	10.0	—	—
	W tal.	—	—	—	—	—	—	11.6	—	—
M_2	L	—	—	—	—	—	—	17.5	—	—
	W tri.	—	—	—	—	—	—	14.7	—	—
	W tal.	—	—	—	—	—	—	13.4	—	—
M_3	L	—	—	—	—	—	—	16.8	—	16.5
	W	—	—	—	—	—	—	11.3	—	11.4

could be distinguished from *T. antiquus* by its larger size, by the presence of a P_4 metaconid, by larger pericones on its upper molars, and by less labially compressed canines. The remarks were presumably made in reference to Buckman Hollow specimens and YPM-PU specimens. The degree of development of the P_4 metaconid and upper molar pericones is variable, as discussed below, but may still have some diagnostic value. Other characters useful in distinguishing *T. pseudarctos* from *T. australis* and *T.* cf. *T. antiquus* are features of the P^4, a more inflated P_4, and a proportionally wider M_1 with a lower length width ratio. M_1 length/width ratios vary from 1.43-1.60 (n = 7) in *T. australis*, 1.40-1.46 (n = 2) in *T.* cf. *T. antiquus*, and 1.24-1.34 (n = 4) in *T. pseudarctos*.

Pericone development is variable in *Thryptacodon pseudarctos* and *T.* cf. *T. antiquus* (Rose, 1981a). The M^2 pericones (cusp along the anterolingual cingulum) in UM 68256 and 80355, identified here as *T. pseudarctos*, are stronger than those in any of the specimens of *T. antiquus* that I have compared. However, no distinct pericone is present in UM 79867, also identified here as *T. pseudarctos* based on its large size. Nevertheless, the strong development of pericones in some specimens of *T. pseudarctos* may be taxonomically useful.

Figure 57 shows the P^4 size distribution of *Thryptacodon pseudarctos*, *T. australis*, and *T.* cf. *T. antiquus* from the northern Bighorn Basin. The morphology of P^4 in *T. pseudarctos* is most similar to that of *T. australis*. In both these species P^4 length exceeds width. The P^4 of *T. pseudarctos* differs, however, in being larger, in having a proportionally larger protocone, and in having less curvature in the metacrista. The protocone of *T. pseudarctos* is intermediate in size between that of *T. australis*, which is very small, and that of *T. antiquus*, which is a prominent feature. The protocone of *T. antiquus* is also positioned more posteriorly than in the other species.

P_4s in UM 71762 and YPM-PU 19026 are easily distinguishable from those of *T. australis* and *T.* cf. *T. antiquus* by their more inflated appearance and larger size. The former was not fully erupted from its crypt, and the base appears to be not fully formed. The top of the trigonid is transversely inflated, making it wider than the base. There is a large lingual "metaconid bulge" on the trigonid positioned midway between the talonid and trigonid apices, but there is no distinct metaconid. There is a long open talonid basin, a distinct cristid obliqua, and a hypoconid. Other talonid cusps are poorly developed. The P_4 in YPM-PU 19026 has a more distinct metaconid, a shorter talonid, and a higher lingual cingulum resulting in a closed talonid basin, than in UM 71762. It also has a prominent entoconid and a hint of a hypoconid. Thus, the development of the metaconid and features of the talonid are apparently quite variable in *T. pseudarctos*.

UM 87826 and 102434 from Paint Creek are presumably the specimens identified as *Thryptacodon* cf. *T. pseudarctos* by Krause (1986). They are within the size range of *T.* cf. *T. antiquus*, however, and identified here as that species. The specimens from Buckman Hollow shown in Figure 56 probably also belong to *T. pseudarctos*. They are slightly larger than any yet recovered from the Bighorn Basin, but are structurally indistinguishable. Buckman Hollow is considered middle Clarkforkian (Cf-2) in age (Archibald et al., 1987). No specimens of *T. pseudarctos* have been recovered from middle Clarkforkian strata in the Bighorn Basin, but UM 109615 (M_1 or M_2) was recently collected from an early Clarkforkian locality. It is incomplete, but was clearly close in size to the teeth of *T. pseudarctos* in Figure 56. UM 71620 (M^3, M_3) is also from the early Clarkforkian and tentatively identified as *T. pseudarctos*, although these teeth could conceivably be large individuals of *T.* cf. *T. antiquus*.

Referred specimens.— **Buckman Hollow**: UM 68355, R dent. M_{1-2}; 79857, R M^1; 79860, R dent. M_{1-2}. **FG004**: UM 73986, R dent. M_1; 110338, L M_3. **FG008**: UM 74031, L M_3; 74032, R max. P^4, M^{2-3}, L max. M^1, M^3, L dent. M_1. **Fossil Hollow** (SC198): UM 79867, L max. L M^{1-2}, R max. M^{1-2}; 108896, R M^3; 110332, R M_3; 110333, L M_3 tri.; 110337, R M_1 tal.; YPM-PU 25026, R M_2. **MP054**: UM 110920, L M^3 partial. **SC144**: UM 110227, R M^3. **SC165**: UM 68256, R max. M^{2-3}. **SC179**: UM 71620, R M^3, L M_3 assoc. **SC186**: UM 68793, R dent. M_3. **SC187**: UM 71762, R P_4, M_2; 80355, L M^2, R M^2. **SC239**: UM 110276, L M_3. **SC270**: UM 77028, L dent. M_1. **SC279**: UM 110924, R M_1 tri. **SC386**: UM 108435, L M^3. **SC394**: UM 108552, R M^1. **SC397**: UM 108572, L M^3. **SC413**: UM 109615, R dent. M_1 or M_2 partial. **SC422**: UM 110104, L M^3. **Silver Coulee**, **S7**, **T57N**, **R100W**: YPM-PU 19026, L dent. P_4-M_1, canine root, alveoli for P_{1-3}.

Family ARCTOCYONIDAE Giebel, 1855

ARCTOCYON de Blainville, 1841

Arctocyon mumak (Van Valen, 1978)

Table 50

Arctocyonides mumak Van Valen, 1978, p. 55.

Holotype.— YPM-PU 17406, left maxilla with M^{1-2}, right M^2, partial right and left P^4s, left dentary with P_4-M_3, and right M_3; reportedly from the southeast side of Polecat Bench, east border of S10, T56N, R99W (near SC-243).

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a) and *Phenacolemur* (Ti-4b) zones.

Description.— A cursory description of *Arctocyon mumak* was given by Van Valen (1978). To that I add that crests and cingula on upper teeth are highly crenulated. The P^3 has a massive principal cusp, lacks a protocone, has a prominent posterior cusp, and a posterolingual cingulum. No anterolingual or buccal cingula are present. P^4 also has a massive principal cusp. A small protocone is developed at the anterior end of a wide uneven postcingulum. A narrow discontinuous precingulum is present. Molar cusps are very low, and the hypocones are small. Para- and metaconules are present on all molars, but become smaller and less distinct posteriorly.

P_3 has a large principal cusp with anterior and posterior, medially positioned crenulated ridges, and no metaconid. The P_3 talonid has a distinct, medially placed, large central cusp separating a low narrow buccal cingulid, and a broader lingual cingulid. P_4 is similar to P_3, but differs in being larger and in having a wider talonid with a posterolingual cusp and more angular posterolingual corner. The lower molars have low crowns, and low and rounded cusps. The cristid obliqua is indistinct, low and rounded or absent. M_1 has a distinct, but low and rounded paraconid placed anterolingually on the protoconid. There is no paraconid on M_2 or M_3.

Discussion.— Several species of *Arctocyon* or closely related forms (i.e., *Aphanocyon* new genus) occur in middle and late Tiffanian strata of the Bighorn Basin. The variability in size and morphology is high, often making it difficult to objectively recognize species based on small samples. *Arctocyon mumak* is the largest known arctocyonid, and my identifications of it are based primarily on size. When Van Valen (1978) named *Arctocyon* (*Arctocyonides*) *mumak* he stated that he had seen specimens from eleven localities in the AMNH and YPM-PU (then PU) collections, but provided no locality or specimen numbers, except for the holotype. The coordinates he provided indicate that the type was collected in the vicinity of SC-243, and is probably from the *Phenacolemur* zone. Additional specimens included here from the *Phenacolemur* and *Plesiadapis churchilli* zones consist only of isolated and associated teeth.

Upper molars in the holotype of *Arctocyon mumak* are within the size range of *Arctocyon* upper molars from Divide and Croc Tooth quarries (Table 50). No other arctocyonid approaches the size of *A. mumak*, and because these teeth are from the type area they can be confidently identified as *A. mumak*. Van Valen (1978) noted that upper molars of *A. mumak* were more squarish, had lower cusps, and that the paracone and metacone were more closely approximated than those of *A. ferox*. The buccal cusps in UM 77164 and YPM-PU 17746 are more closely approximated than in *A. ferox*, but are higher, suggesting that cusp height may not be useful for distinguishing between these species. The size and positions of cusps are obscured due to heavy wear in many of the upper molars identified here as *A. mumak*, but most are more squarish than in *A. ferox* (AMNH 12456).

I have included two P^4s in *Arctocyon mumak* that exhibit a high degree of variability. The protocones are small to absent, and contrast with those *Arctocyon nexus* and *Aphanocyon*, which have a large well-developed protocone. UM 75814 is heavily built, while YPM-PU 17740 is more lightly built. The postcingulum varies from wide to nearly absent. Both teeth are approximately triangular in occlusal view. Variability of this magnitude could be indicative of the presence of more than one species or of sexual dimorphism.

An isolated M_2 trigonid (UM 110327) from near the base of the *Probathyopsis* zone is the youngest occurrence of a large *Arctocyon* in the UM collections. It is small for *A. mumak*, and has a distinct M_2 paraconid, a feature that is unusual or absent in *A. mumak* and *A.* cf. *mumak* from Cedar Point Quarry. For these reasons I have not included it in *A. mumak*.

A partial M_3 from the McCullough Peaks area (UM 92358) was tentatively identified as *Phenacodus magnus* by Thewissen (1990). However, it has a low trigonid, a shallow talonid basin, round wear pits, and lacks a well-defined cristid obliqua. These features are characteristic of *Arctocyon*. This specimen is the size expected for *A. mumak* and I tentatively identify it as that species.

Referred specimens.— **Croc Tooth Q.** (FG028): UM 77164, R M^1; YPM-PU 17740, L P^4. 18557, R M_3; 17746, L M^2. **Divide Q.** (FG046): UM 83275, R M^2; 85305, R M^1; 91331, L M^1; 110933, R M^1 or M^2. YPM-PU 17740, L P^4. **FG015**: UM 75814, L P^4, M^3. **MP115**: UM 92358, L M_3 part.

TABLE 51 — Dental measurements of *Arctocyon* cf. *A. mumak* from the northern Bighorn Basin. *CPQ*, Cedar Point Quarry; *JQ*, Jepsen Quarry. *Estimate.

		UM 63100 CPQ	UM 82084 CPQ	UM 108586 SC-262	UM 110327 SC-268	YPM-PU 14962 JQ
P^1	L	—	—	7.4	—	—
	W	—	—	—	—	—
P_3	L	—	—	—	—	—
	W	—	5.4	—	—	—
P_4	L	14.4	12.6	—	—	—
	W	7.9	7.1	—	—	—
M_1	L	11.8	11.9	—	—	13.0
	W tri.	8.8	8.2	—	—	—
	W tal.	10.7	9.2	9.9	—	10.2*
M_2	L	14.4	—	—	—	14.8*
	W tri.	12.3	—	—	11.5	11.7*
	W tal.	12.2	—	—	—	11.6*
M_3	L	14.4	—	—	—	—
	W	9.7	—	—	—	—

Arctocyon cf. *A. mumak*

Figure 58, Table 51

Claenodon cf. *acrogenius*, Rose, 1981a, p.152.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* (Ti-3) zone.

Description.— The P_4 has a large single principal cusp (protoconid) with anterior and posterior medially positioned crenulated ridges, and no metaconid. The P_4 talonid has a distinct medially placed, large central cusp (hypoconid?) separating a low narrow buccal cingulum, and a broader lingual cingular shelf bounded posteriorly by an entoconid. The lower molars have low crowns, and low and rounded cusps. The cristid obliqua is indistinct, low and rounded to absent. The M_1 has a distinct, but low and rounded paraconid placed anterolingually on the protoconid. There is no paraconid on M_2 or M_3.

Discussion.— The referred specimens represent a large *Arctocyon* that is morphologically close to *A. mumak*, but is smaller. All of the specimens measured (Table 51) are smaller than the holotype of *A. mumak*. Molar length is 15% to 22% greater in the holotype, and P_4 is 28% to 47% longer. This is greater size variability than is expected for a single species. It is conceivable, however, that *A. mumak* was sexually dimorphic and the holotype represents a large male, but this cannot be adequately addressed without a larger sample.

Rose (1981a) referred the Cedar Point Quarry specimens to *Arctocyon* cf. *A. acrogenius*, a species described by Gazin (1956b) from the Bison Basin in south-central Wyoming. This species is close to the size of the Cedar Point Quarry form, but UM 82084, which was subsequently collected from the quarry, differs in having a double-rooted P_2. As described by Gazin, the holotype of *A. acrogenius* has a long diastema between the P_3 and P_1. According to Gazin, there may have been a small single-rooted P_2 anterior to P_3 that was lost during the life of the animal, or P_2 may have been absent. UM 82084 from Cedar Point Quarry has two prominent alveoli directly in front of the P_3 that undoubtedly held a double-rooted P_2. Based on this difference, the Cedar Point Quarry specimens appear to represent a species distinct from *Arctocyon acrogenius*.

Referred specimens.— **Cedar Point Q.**: 63100, R dent. P_4-M_3; 82084, R dent. P_3-M_1. **Jepsen Q.**: YPM-PU 14962, R dent. M_{1-2}. **SC262**: UM 73398, R M^1 partial, R M_1 tal., M_2 tal., assoc.; 108586, R M_2 tri., M_1 tal., L P^1 partial, assoc.; 108684, R M_3. **SC263**: UM 99089, R M_1 and M_2 frags., R M^1 frag.

Arctocyon nexus (Gazin, 1956)

Anacodon? *nexus* Gazin, 1956c, p. 8.

Discussion.— see *Arctocyon* cf. *nexus* below.

Arctocyon cf. *A. nexus*

Figure 58, Table 52

Anacodon? *nexus*, Rose, 1981a, p.156.
Claenodon sp., Secord, 2002, p. 105.
Arctocyon cf. *A. nexus*, Secord, 2006, p. 240.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b), *Probathyopsis* (Ti-5a), *Plesiadapis simonsi* (Ti-5b), *Plesiadapis gingerichi* (Ti-6), and Rodentia (Cf-1) zones.

Description.— The P^3 is triple-rooted and narrow with a small lingual protocone bulge, but no distinct protocone. The P^4 is triangular in occlusal view, with a large acute metacone, a small or absent parastyle, and a small protocone. A small cusp is present in all specimens on a cingulum between the protocone and metacone. There is no P^4 trigon basin. Upper molars have distinct, but low cusps, including conules, and are highly crenulated before wear. The paracone and metacone are adjacent to one another.

The dentary tapers anteriorly at least to the base of the symphysis. P_3 and M_3 are reduced relative to P_4-M_2, effectively shortening the dental arcade. There is a significant diastema anterior to P_3. The P_4 has a single large secant cusp (protoconid), and no metaconid. Its talonid has a single prominent central cusp, and no basin. Molar trigonids are low and the cusps are indistinct. The talonid basins are wide. The cristid obliqua is indistinct and low. There is a small shallow basin (hypoflexid depression) on the molars between the cristid obliqua and a ridge connecting the protoconid and hypoconid. The M_1 hypoconulid is small, and the M_2 hypoconulid is indistinct or absent. The M_2 trigonid is wider than its talonid. The M_3 is shorter than the M_2.

The dP^4 is molariform and forms an equilateral triangle. It has a paracone, metacone, paraconule, metaconule, protocone, and hypocone. It has a distinct parastyle connected to the paracone by a crest. The dP_3 has a large, central, pointed cusp positioned midway up the protoconid, between a small posterior basal cusp and the protoconid apex. The dP_4 is typical of "condylarth" dP_4s with an anteroposteriorly elongate trigonid and a paraconid, metaconid, and protoconid. Its talonid basin is enclosed by a continuous peripheral ridge with no distinct talonid cusps. These deciduous teeth are all from Y2K Quarry. Although the teeth were

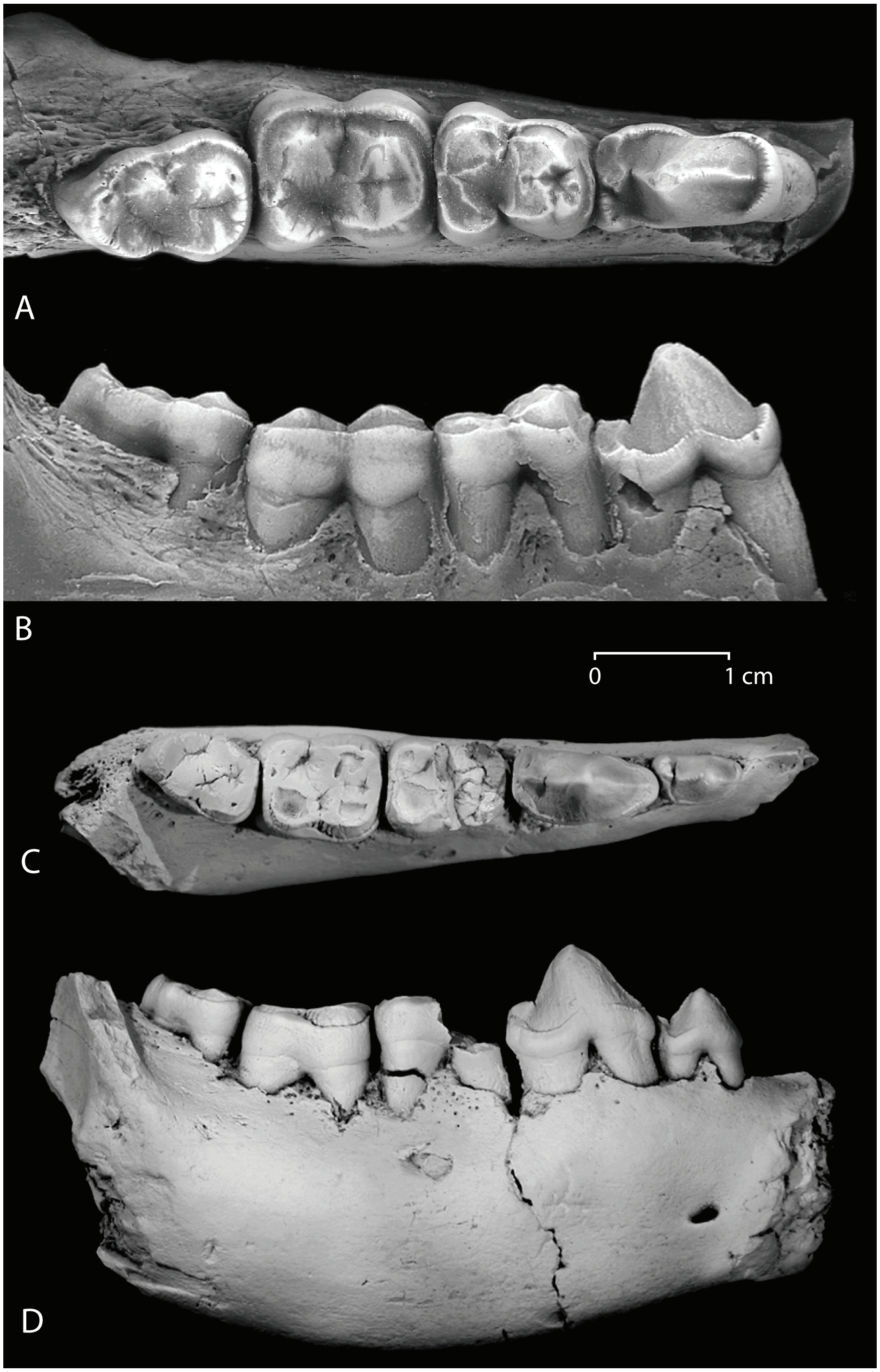


FIGURE 58 — Dentaries of *Arctocyon* cf. *A. mumak* (UM 63100) from Cedar Point Quarry and *Arctocyon* cf. *A. nexus* (YPM-PU 18757) from the *Probathyopsis* zone in Silver Coulee. A-B, UM 63100, right dentary with P_4-M_3 in occlusal (A) and buccal (B) views. C-D, YPM-PU 18757, right dentary with P_{3-4}, M_1 talonid, and M_{2-3} in occlusal (C) and buccal (D) views.

found separately and given different numbers, all are unworn and the left and right M_1s and dP_4s are nearly identical. Thus, all the deciduous teeth probably came from a single individual.

Discussion.— A small arctocyonid that most closely approximates *Arctocyon nexus* (Gazin, 1956c) from Buckman Hollow, of middle Clarkforkian age, is moderately represented in the late

TABLE 52 — Dental measurements of *Arctocyon* cf. *A. nexus* from the Bighorn Basin and the holotype of *Anacodon*? *nexus* from Buckman Hollow (BH), Wyoming. Y2K miscellaneous (misc.) is probably a single individual disarticulated after deposition and includes UM 109168, 109329, 109379, 109512, and 109569. *FH*, Fossil Hollow; *Y2K*, Y2K Quarry. *Estimate.

		Misc. Y2K	UM 68792 SC-186	UM 68798 SC-186	UM 69244 FH	UM 71710 SC-242	UM 79866 FH	UM 82106 FG-55	UM 108511 SC-386	UM 110067 SC-424	UM 110103 SC-422	USNM 21282 (type) BH	YPM-PU 18757 S22, T57N, 100W
P^3	L	—	—	—	—	6.3	—	—	—	—	—	—	—
	W	—	—	—	—	4.6	—	—	—	—	—	—	—
dP^4	L	8.0	—	—	—	—	—	—	—	—	—	—	—
	W	8.1	—	—	—	—	—	—	—	—	—	—	—
P^4	L	—	7.5	—	—	6.9	—	—	—	—	7.9	—	—
	W	—	8.0	—	—	7.4	—	—	—	—	7.5	—	—
M^1	L	—	8.8	—	—	—	—	—	—	—	8.6	—	—
	W	—	10.0	—	—	—	—	—	—	—	10.2	—	—
M^2	L	—	—	—	—	—	—	8.5	8.2	—	8.4	—	—
	W	—	—	—	—	—	—	11.4	11.7	—	12.1	—	—
M^3	L	—	—	—	—	—	—	6.4	—	—	6.0	—	—
	W	—	—	—	—	—	—	7.6	—	—	7.9	—	—
C_1	L	—	—	6.5	—	—	—	—	—	—	—	—	—
	W	—	—	3.4	—	—	—	—	—	—	—	—	—
P_3	L	—	—	8.0	—	—	—	—	—	—	—	—	6.8
	W	—	—	4.3	—	—	—	—	—	—	—	—	3.8
dP_4	L	8.6	—	—	—	—	—	—	—	—	—	—	—
	W	5.6	—	—	—	—	—	—	—	—	—	—	—
P_4	L	—	—	—	—	—	8.6	—	—	—	—	—	10.7
	W	—	—	—	—	—	4.9	—	—	—	—	—	5.4
M_1	L	8.9	—	—	9.0	9.0	8.5	—	9.2	8.8	—	9.5	8.5*
	W tri.	6.4	—	—	6.5	6.7	6.4	—	6.5	5.9	—	7.8	6.5
	W tal.	6.9	—	—	7.3	7.7	7.4	—	7.4	6.8	—	—	7.5
M_2	L	—	—	10.3	9.7	—	9.7	—	10.2	9.9*	—	10.7	9.6
	W tri.	—	—	9.0	7.8	—	8.4*	—	8.0	—	—	8.5	8.1
	W tal.	—	—	8.0	7.5	—	—	—	7.8	7.6	—	—	7.8
M_3	L	—	—	9.8	—	—	8.9	—	8.9	—	—	—	8.4
	W	—	—	7.3	—	—	6.4	—	6.4	—	—	—	—

Tiffanian and early Clarkforkian of the Bighorn Basin. It differs from *A. nexus* in being smaller and in having an M$_2$ trigonid that is wider than the talonid. Only M$_1$ and M$_2$ have been described for *A. nexus*, and other positions cannot be evaluated. The molars in the holotype of *Arctocyon nexus* are larger in nearly all cases than those in *A.* cf. *A. nexus* (Table 52). Apparently there is no temporal overlap between *A.* cf. *A. nexus*, which last occurs in the early Clarkforkian, and the Buckman Hollow fauna, which is middle Clarkforkian in age based on the presence of *Plesiadapis cookei* (Gazin, 1956c; Archibald et al., 1987).

Gazin (1956c) thought that the holotype and only specimen of *Arctocyon* (*Anacodon*?) *nexus* (USNM 21282, left dentary fragment with M$_{1\text{-}2}$) may represent a precursor species to *Anacodon* based on the lowness of its molar trigonids and the near loss of its cristid obliquae. He also noted the importance of several characters in *Anacodon*, even though they could not be assessed in USNM 21282, including the reduction of the premolars, a diastema anterior to P$_3$, and a deep flange on the distal end of the dentary. The flange was presumably to protect saber-like upper canines (see Matthew and Granger, 1915, for drawings). The most complete jaw included here in *A.* cf. *nexus* is YPM-PU 18757, which preserves much of the dentary (Figs. 58C,D). It has a reduced P$_3$ with a diastema anterior to it, as Gazin predicted for the precursor to *Anacodon*, but the P$_4$ is much larger than in *Anacodon* and it appears to lack a flange on the distal part of dentary. The dentary tapers anteriorly and there is no indication of an expansion to accommodate a flange. Moreover, some of these characters are also shared with other arctocyonids, such as *A. mumak*, which has low molar trigonids and faint cristid obliquae. Also, saber-like upper canines are found in other arctocyonids, such as *A. ferox*, and could be a sexually dimorphic feature common to large arctocyonids. Given the weak support for keeping *A. nexus* in the more derived *Anacodon*, I provisionally place it in *Arctocyon* pending a revision of the Arctocyonidae.

Variability in *Arctocyon* cf. *A. nexus* is notably constrained compared with other large arctocyonids (e.g., Rigby, 1980).

TABLE 53 — Dental statistics for *Lambertocyon* from Divide Quarry. *Estimate.

		n	Min.	Max.	Mean	SE	SD	V
C^1	L	1	—	—	7.7*	—	—	—
	W	1	—	—	4.9*	—	—	—
P^4	L	2	6.1	6.4	6.29	—	—	—
	W	3	7.0	7.2	7.08	0.04	0.08	1.07
M^1	L	2	7.7	7.7	7.72	—	—	—
	W	2	8.1	8.9	8.50	—	—	—
M^2	L	4	8.1	9.0	8.38	0.22	0.44	5.23
	W	4	10.1	11.5	10.77	0.29	0.59	5.45
M^3	L	4	6.2	7.3	6.74	0.26	0.51	7.59
	W	3	9.1	9.7	9.46	0.20	0.34	3.60
P_3	L	1	—	—	5.53	—	—	—
	W	1	—	—	4.27	—	—	—
P_4	L	1	—	—	6.57	—	—	—
	W	1	—	—	4.86	—	—	—
M_2	L	2	8.5	8.6	8.54	—	—	—
	W	2	6.1	6.3	6.18	—	—	—
M_3	L	6	8.8	9.8	9.27	0.17	0.42	4.51
	W	6	5.0	5.9	5.61	0.14	0.34	6.01

Coefficients of variation are low (e.g., V in M_1 L = 3.3, W = 3.8, n = 7; M_2 L = 2.78, W= 2.47, n = 7). High variability in some arctocyonids could be the result of sexual dimorphism.

In a comparison with other Bighorn Basin arctocyonids, *Arctocyon* cf. *A. nexus* differs from *Anacodon ursidens* in having molars with more distinct and higher cusps, higher trigonids, an M_2 trigonid that is wider than the talonid, and a proportionally larger P_4. *Arctocyon* cf. *A. nexus* differs from *Arctocyon* cf. *A. mumak* from Cedar Point Quarry in being much smaller and in having a diastema anterior to P_3. It differs from *Arctocyon ferox* and *A.* cf. *A. montanensis* from Scarritt Quarry in having: (1) a proportionally smaller P_3; (2) an M_3 that is shorter than M_2; (3) an M_2 trigonid that is wider than the talonid; (4) a larger P^4 protocone; (5) hypoflexid depressions on lower molars; (6) a large central talonid cusp on P_4; and (7) a slightly smaller size.

Several arctocyonid teeth from Divide and Croc Tooth quarries are similar to those of *Arctocyon* cf. *A. nexus*. However, they are slightly larger and exhibit some differences in morphology. Thus, I have not included them in *A.* cf. *A. nexus*. The P^4 (UM 91327) from Divide Quarry has a larger protocone than those of *A.* cf. *A. nexus*. Left and right associated molars from Croc Tooth Quarry (YPM-PU 200006) are intermediate in size between those of *A.* cf. *A. nexus* and *A.* cf. *A. mumak* from Cedar Point Quarry, and have a higher talonid/trigonid width ratio than any specimens of the former. Larger samples are needed from these localities before confident identifications can be made.

Referred specimens— **FG055**: UM 82106, L max. $M^{2\text{-}3}$; 110340, L P^4, M^1 frag. assoc. **Fossil Hollow** (SC198): UM 69244, R dent. M_1, L M_2 unassoc.; 79866, R dent. P_4-M_3; 110305, R M^2. **MP115**: UM 92357, R P^3 and tooth frags. **S22, T57N, R100W**: YPM-PU 18757, R dent. P_3-M_3 (M_1 broken), L M_1. **SC144**: UM 110086, astragalus, M^1 frag., assoc. **SC165**: UM 68276, R M_2 tal. **SC186**: UM 68792, L P^4, M^1; 68798, L dent. $M_{2\text{-}3}$, R P_3 assoc. **SC228**: UM 71708, L M^3. **SC242**: UM 71710, R max. $P^{3\text{-}4}$, L dent. M_1. **SC257**: UM 73363, L $M^{1\text{-}2}$. **SC258**: UM 73353, R M_1. **SC266**: UM 73504, L M_2. **SC273**: UM 73662, L max. $M^{2\text{-}3}$; 110151, R dent. edentulous. **SC362**: UM 108321, L P_4 protoconid. **SC382**: UM 108490, L P_4. **SC385**: UM 108502, L M^3. **SC386**: UM 108510, M^3; 108511, I^x, R dent. $M_{2\text{-}3}$, L M_1, R M^2, L M^2, assoc. **SC401**: UM 108590, L M^1 frag. **SC422**: UM 110103, maxillae, L P^4-M^3, R P^4-M^2. **SC424**: UM 110067, L M_1, M_2 assoc. **Y2K Q.** (SC389): UM 109168, L M_1; 109237, L dP_3; 109329, R M_1; 109379, R dP^4; 109393, M_x tal.; 109512, L dP_4; 109569, R dP_4; 109865, C^1? **Zalmout Q.** (SC389): UM 108956, L M_1 tal., M_3.

LAMBERTOCYON Gingerich, 1979a

Lambertocyon gingerichi Gunnell, 1994

Tables 53–55

Lambertocyon eximius (in part), Gingerich, 1979a, YPM-PU 17758, p. 528.
Lambertocyon gingerichi Gunnell, 1994, p. 86.

Holotype.— UM 81147, left M^1 from Chappo Type Locality.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Description.— The dentition of *Lambertocyon gingerichi* was described by Gunnell (1994), based on isolated teeth.

Development of upper molar mesostyles is highly variable, as is the openness of trigon basins. The P_3 of UM 77252 has an incipient talonid basin, forming a short posterolingual shelf. The P_4 of UM 77252 from Divide Quarry has a distinct metaconid and a sharp medial cristid obliqua that is confluent with a posterolingual postcristid forming a deep, lingually open basin on the talonid. A similar condition is seen in UM 85171 from the Chappo Type Locality.

Discussion.— When Gingerich (1979a) named *Lambertocyon* he referred specimens from the Chappo Type Locality to *Lambertocyon* sp., noting that they probably represented an unnamed larger species, but were not adequate for diagnosis. With the acquisition of a larger sample from Chappo, Gunnell (1994) later established *L. gingerichi*, based on isolated teeth. The new sample of *Lambertocyon* from Divide Quarry is equivalent in size to the Chappo sample, but it contains four partial jaws, and teeth are generally more complete. The Chappo and Divide Quarry samples are the largest known for *Lambertocyon*.

Teeth of *Lambertocyon* from Divide Quarry most closely resemble those of *L. gingerichi*, but are also similar to *L. eximius*. Little is known of the variability in *L. eximius*. The holotype of *L. eximius* (YPM-PU 19576) includes both upper and lower dentitions, but comes from a locality that yielded no other specimens (Gingerich, 1979a). Hence, it is not possible to evaluate if it is representative of the species, and comparisons are necessarily typological.

Study of the Divide Quarry material shows that many of the characteristics Gunnell (1994) used to distinguish *Lambertocyon gingerichi* from *L. eximius* are variable. Diagnostic features given by Gunnell for *L. gingerichi* included: (1) a heavier

TABLE 54 — Dental measurements for *Lambertocyon* from miscellaneous Bighorn Basin localities. *Estimate.

		UM 75818 FG-016	UM 91038 MP-054	UM 110219 SC-243	UM 110318 SC-261	YPM-PU 14970 Croc Tooth Q.	YPM-PU 19576 Coon Creek
P^3	L	—	—	—	—	—	5.0
	W	—	—	—	—	—	4.6
P^4	L	—	—	—	—	—	—
	W	—	—	—	—	—	6.2
M^1	L	—	—	—	—	—	7.6
	W	—	—	—	—	—	8.4
M^2	L	8.1	—	—	—	—	7.8
	W	9.8	—	—	—	—	10.5
M^3	L	—	—	6.0	—	—	5.7
	W	—	—	7.8	—	—	9.1
C_1	L	—	—	—	4.9*	5.1	—
	W	—	—	—	5.4*	5.4	—
P_2	L	—	—	—	—	—	4.7
	W	—	—	—	—	—	3.6
P_3	L	—	5.8	—	—	5.6	5.4
	W	—	4.5	—	—	4.8	4.0
P_4	L	—	6.2	—	—	6.3	5.7
	W	—	4.6	—	—	—	4.5
M_1	L	—	—	—	—	7.1	7.3
	W	—	5.5	—	—	5.7	5.3
M_2	L	—	7.8	—	—	7.5	8.3
	W	—	6.0	—	—	6.2	6.3
M_3	L	—	9.5	—	—	9.1	8.7
	W	—	5.4	—	—	5.9	5.5

cingulum and more distinct protocone on P^3; (2) a protocone more separate from the paracone on P^4 with a more gently sloping posterior protocone flank; (3) a stronger M^1 mesostyle; (4) a more closed M^2 trigon basin; (5) lack of a hypoflexid indentation on lower molars; and (6) larger size. P^3s are not present in the Divide Quarry sample, but P^4s agree with Gunnell's description of *L. gingerichi*. In regard to (3), however, mesostyles are highly variable. Development of the M^1 mesostyle is strong on UM 110259, but weak on UM 87040. The development of the M^2 mesostyle ranges from absent to extreme. In regard to (4), the development of M^2 basins is also variable. Most basins are less open than in the holotype of *L. eximius* (YPM-PU 19576), but the basin of UM 91320 is at least as open. In regard to (5), none of the lower molars has a hypoflexid indentation as deep as in YPM-PU 19576, but some have a small indentation.

Teeth in the Divide Quarry sample are larger than in the holotype of *Lambertocyon eximius* in nearly all dimensions, and larger than those from Chappo on average (compare Tables 53, 54, 55; specimens from Chappo were remeasured because of differences between my measuring techniques and those of Gunnell). All teeth from Divide Quarry exceed the length of those in the holotype of *L. eximius*, but there is overlap in width reflecting the generally narrower character of the Divide Quarry teeth. Thus, *L. gingerichi* may also differ from *L. eximius* in having narrower lower molars. It may also differ in having a more molariform P_4 with a better developed talonid basin.

Although there are differences between the holotype of *Lambertocyon eximius* and the hypodigm of *L. gingerichi*, larger samples are needed to conclusively demonstrate that more than one species is present. In particular, additional specimens of *L. eximius* are needed to show that the holotype is not an extreme variant of a single species. Nevertheless, the differences discussed above may be important and I tentatively recognize *L. gingerichi*.

Referred specimens.— **Divide Q.** (FG046): UM 77252, L dent. P_{3-4}; 80580, R C^1, P^4 unassoc.; 83242, L M^2; 83243, L max. M^{2-3}, broken; 85367, R M_3; 85414, L M_3; 87040, L M^1; 91320, R max. M^{2-3}; 91325, L M_2; 92255, L M_3; 92258, L M^2; 92265, L M^2; 92274, R M^2; 110258, L M^2; 110259, R M^1; 110260, R M^3; 110262, L M^1 partial; 110264, R M^3; 110265, R M^3; 110267, R M_3; 110268, R P^4; 110269, R M_3; 110270, R M_3; 110271, R P^4; 110272, R M^2 partial; 110273, R M^1 partial; 110274, L M^2 partial. YPM-PU 17758, R dent. M_{2-3}.

Lambertocyon eximius Gingerich, 1979a

Table 54

Lambertocyon eximius Gingerich, 1979a, p. 525.

Holotype.— YPM-PU 19576, crushed snout with P^3-M^3, right dentary with P_2-M_3, and left dentary with P_4-M_3.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* zone (Ti-4b).

Description.— *Lambertocyon eximius* was described in detail by Gingerich (1979a).

Discussion.— Comparisons of *Lambertocyon eximius* and *L. gingerichi* were made above. Gingerich (1979a) included dentaries from Croc Tooth Quarry and Divide Quarry in *L. eximius* when he described the species. The Divide Quarry specimen is identified here as *L. gingerichi*, along with the rest of the quarry sample. UM 91038 is the only new material from the Bighorn Basin that I identify as *L. eximius*. It consists of left and right dentaries preserving P_4, M_2, M_3, and the bases of P_3 and M_1. These teeth are very similar to those of the holotype of *L. eximius* in size and morphology. The molars differ, however, in lacking hypoflexid depressions and in having a more anteroposteriorly elongate M_3. Although the hypoflexid depressions were used by Gunnell (1994) to distinguish *L. eximius* from *L. gingerichi*, their development appears to be variable. YPM-PU 14970, identified as *L. eximius*, also lacks hypoflexid depressions. Casts show that these pits were also variably present in the closely related *Mimotricentes subtrigonus* from Swain Quarry.

The holotype of *L. eximius* was collected at a locality in the Foster Gulch area that yielded no other specimens (Gingerich, 1979a). Gingerich noted that although there was no associated fauna, the strike of the beds and known Tiffanian localities to the north and south indicated a late Tiffanian age. My placement of *L. eximius* in the *Phenacolemur* zone is based on YPM-PU 14970 from Croc Tooth Quarry.

Refined biostratigraphy suggests that *Lambertocyon* is restricted to the *Plesiadapis churchilli* and *Phenacolemur* zones, contrary to previous reports of occurrences in the *Plesiadapis simonsi* zone (Gingerich, 1979a; Gunnell, 1994).

Referred specimens— **MP054**: UM 91038, L dent. P_3-M_3, R dent. P_4, M_2. **Croc Tooth Q.** (FG028): YPM-PU 14970, L dent. C_1, P_3-M_3. **Coon Creek drainage**: YPM-PU 19576 (holotype).

Lambertocyon sp.
Table 54

Discussion.— The specimens below are too fragmentary for specific identification.

Referred specimens.— **FG016**: UM 75818, L M^2 and M^x frags. **SC243**: UM 110219, L M_3. **SC261**: UM 110318, R C_1.

APHANOCYON new genus

Type species.— *Aphanocyon codyensis* n. sp.

Included species.— *Aphanocyon codyensis* n. sp., and *Aphanocyon amaurus* n. sp.

Diagnosis.— *Aphanocyon* differs from other arctocyonids (following McKenna and Bell, 1997), except for *Desmatoclaenus*, in having a semi-molariform P_4 with a talonid basin and metaconid. Further differs from other arctocyonids, except *Anacodon*, in having lower molar trigonids with more transverse anterior and posterior walls (pre- and postvallids). Further differs from *Anacodon* in having higher trigonids, higher molar cusps, and proportionally larger fourth premolars. Further differs from *Desmatoclaenus* and other loxolophine arctocyonids in having indistinct or absent molar paraconids. Further differs from arctocyonine arctocyonids, except *Anacodon*, in having M_1 and M_2 metaconids and protoconids approximately equal in size, and better defined talonid cusps.

TABLE 55 — Dental statistics for *Lambertocyon* from Chappo Local Fauna. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
P^4	L	3	5.4	6.2	5.76	0.23	0.41	7.03
	W	3	6.3	7.5	6.83	0.36	0.63	9.15
M^1	L	1	—	—	7.45	—	—	—
	W	2	7.8	8.0	7.91	—	—	—
M^2	L	2	7.8	8.6	8.21	—	—	—
	W	2	9.6	10.7	10.13	—	—	—
P_3	L	1	—	—	5.50	—	—	—
	W	2	4.2	4.4	4.29	—	—	—
P_4	L	1	—	—	5.80	—	—	—
	W	1	—	—	4.23	—	—	—
M_2	L	1	—	—	8.44	—	—	—
	W	1	—	—	6.14	—	—	—

Etymology.— *Aphanos* (Gr.), unseen, invisible, obscure, and *kyon* (Gr., masc.), dog: in allusion to the rarity or unrecognized presence of this genus. The suffix follows that of *Arctocyon*.

Description.— Large arctocyonid. The P^4 has a single prominent buccal cusp (metacone) and a large, rounded, well-developed protocone. No trace of a paracone is present. It has a prominent metaconule and a parastyle. Pre- and postcingula are present.

Upper molars are bunodont with low cusps. There are distinct conules connected to the protocone by protocristae. The metaconule is isolated from the metacone, but the paraconule may be connected to the paracone by a minute ridge. Molars are crenulated.

The P_4 has a distinct metaconid separated from the protoconid by a posterior vertical trench. A vertical ridge (paralophid?) descends from the top of the protoconid to a precingulid or anterior basal cusp (paraconid?). A well-developed, basined talonid is present on P_4.

Lower molar paraconids are small and indistinct or absent. A crescentic paralophid connects the metaconid and protoconid. The metaconid and protoconid are approximately equal in size, causing the anterior and posterior walls of the trigonid to be nearly parallel.

Discussion.— *Aphanocyon* appears to be a derived arctocyonid that is in some respects convergent on the phenacodontid condylarth, *Phenacodus*. They both have a similar semi-molariform P_4 with a talonid basin and strong trigonid metaconid, have a large P^4 protocone, have bunodont upper and lower molars, and have a paralophid that connects the metaconid and protoconid on the lower molars. *Aphanocyon* and most arctocyonines differ from *Phenacodus*, however, in important characters such as their lack of upper molar mesostyles, the absence of a P^4 paracone, a weaker cristid obliqua on lower molars, and in having crenulated enamel.

Aphanocyon is also similar to *Desmatoclaenus*, which is best known from the Puercan. Its range was extended into

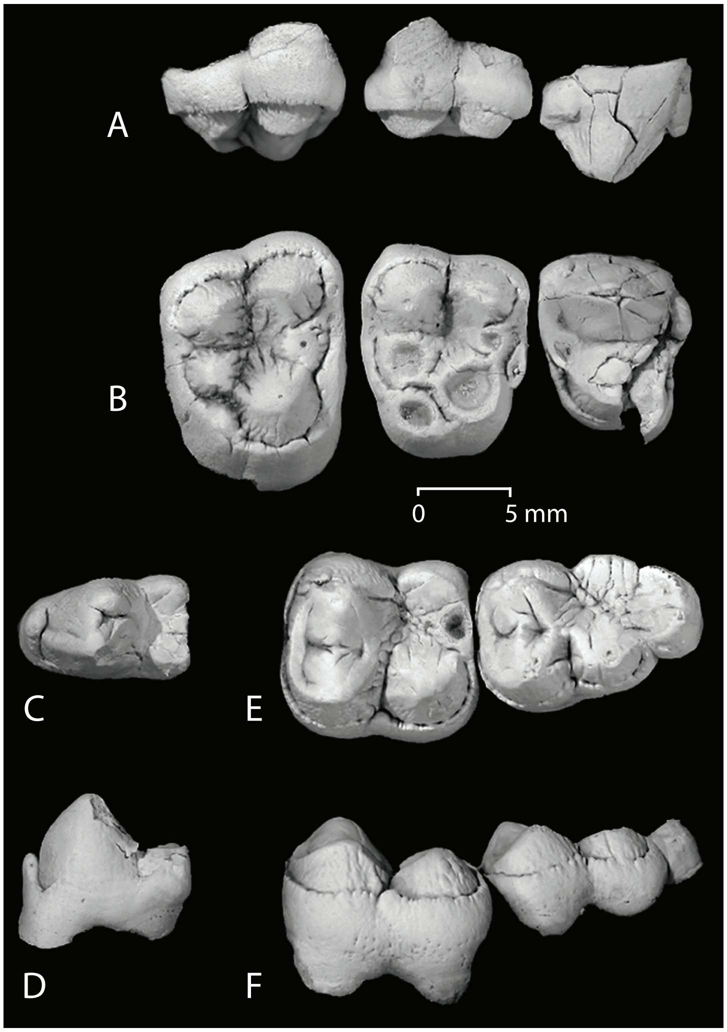


FIGURE 59 — Associated partial maxilla, dentary, and P_4 of *Aphanocyon codyensis* gen. et sp. n. (UM 92145, holotype; MP-94). A–B, right maxillary fragment with P^4-M^2 in buccal (A) and occlusal (B) views. C–D, left P_4 in occlusal (C) and buccal (D) views. E–F, left dentary fragment with M_{2-3} in occlusal (E) and buccal (F) views.

the Tiffanian when Van Valen (1978) based a new species, *D. mearae*, on an M^1 and M^2 from the Bison Basin. These teeth are very similar to *Aphanocyon amaurus* n. sp., but are about 30% smaller. Comparison to *Aphanocyon* is greatly hindered, however, without a fourth premolar. Specimens of *Desmatoclaenus* sp. (Fox, 1990) and *D. mearae* (Webb, 1996) have also been reported from the early and middle Tiffanian of Canada, respectively, but have not been described in publication.

Aphanocyon differs from the type species of *Desmatoclaenus*, *D. hermaeus* from the Puercan of Utah, in having more buccal-lingually oriented anterior and posterior trigonid walls, in the reduction or absence of its lower molar paraconids, and in having more basined P_4 talonids. The paraconids in *D. hermaeus* are large and prominent, and positioned well anterior of the metaconid, making for an asymmetrical wedge-shaped trigonid, in contrast to the nearly parallel anterior and posterior trigonid walls of *Aphanocyon*. *Desmatoclaenus* is not known from the middle or late Torrejonian, in spite of very large collections from the former over a wide geographic area (e.g., Lofgren et al., 2004). Its absence through most of the Torrejonian suggests that its resemblance to *Aphanocyon* is convergent.

Aphanocyon codyensis, new species

Figure 59, Table 56

Arctocyonidae n. sp. A, Secord et al., 2006, p. 228.

Holotype.— UM 92145, left and right maxillae with P^{3-4} and P^4-M^2, respectively, left and right dentaries both with M_{2-3}, and an associated left P_4. From MP094 in the McCullough Peaks area, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences.— *Plesiadapis churchilli* (Ti-4a) or *Phenacolemur* (Ti-4b) zone, and *Plesiadapis rex* (Ti-3) zone.

Diagnosis.— Differs from *Aphanocyon amaurus* n. sp. in its larger size, in the absence of a P^4 trigon basin, and in having a more anteroposteriorly elongate P_4 with a larger, more closed and more central talonid basin.

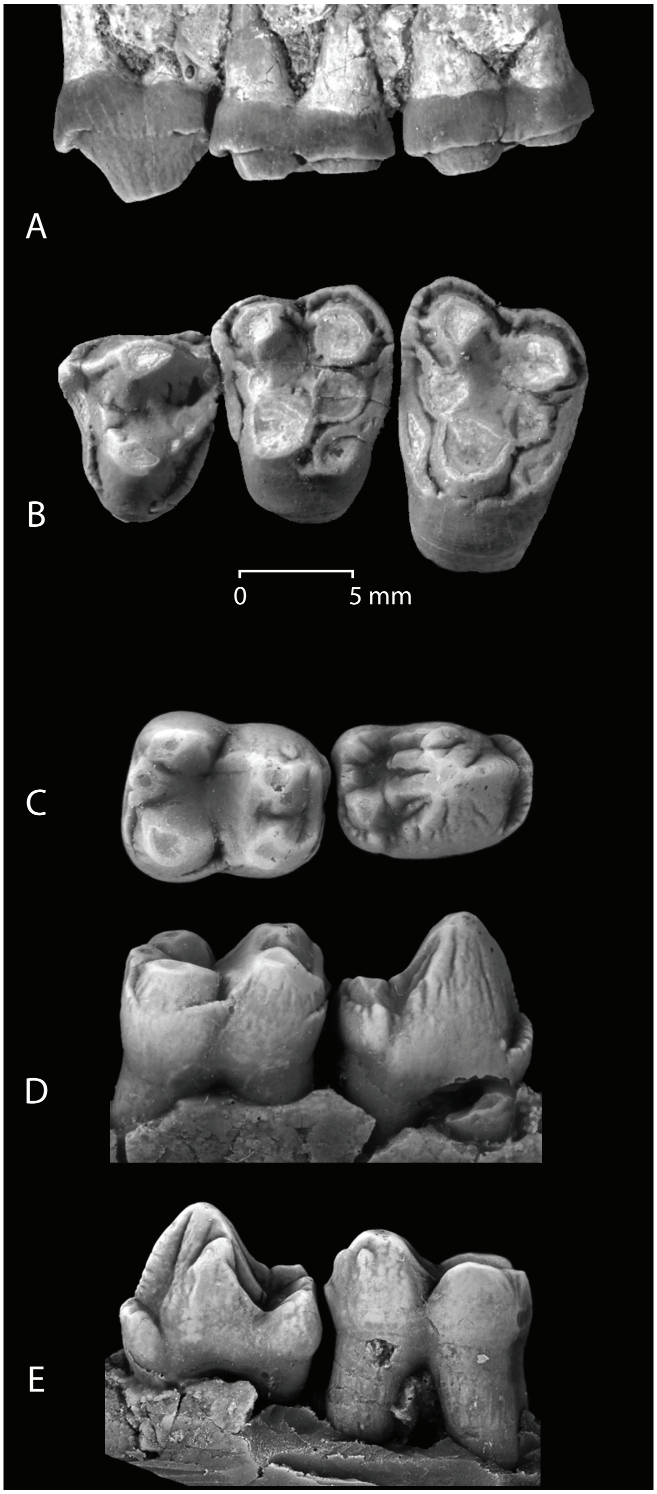


FIGURE 60 — Upper and lower dentition of *Aphanocyon amaurus* gen. et sp. n. from Cedar Point Quarry. A–B, left maxilla with P^4-M^2 (UM 64570) in buccal (A) and occlusal (B) views. C–E, right dentary with P_4-M_1 (UM 64394, holotype) in occlusal (C), buccal (D), and (E) lingual views.

Etymology.— In reference to the town of Cody, Wyoming, which is situated about 6 km to the west of the type locality.

Description.— The P^3 is simple and sub-triangular in occlusal view, and dominated by a single high and acute cusp (metacone). The anterior edge of the crown is broken, so it is not clear if a paraconule was present. A low, rounded metaconule is present posteriorly. The lingual side of the crown is damaged but a small shelf appears to have been present, possibly containing a very small, rudimentary protocone. The crown is about 5.5 mm high, and is about 1 mm lower than that of the P^4.

The P^4 protocone abuts against the metacone leaving no room for a trigon basin. A large rounded parastyle is present anteriorly and a prominent metaconule is present posteriorly. Pre- and postcingula are strong on the right P^4 and nearly continuous around the protocone, but less developed and more restricted on the left P^4. A wear pit in the enamel along an incipient postprotocrista suggests that a metaconule was present on the right P^4. The upper molars are typical of arctocyonids of this grade and may be morphologically indistinguishable from those of *A. amaurus* n. sp. or *Arctocyon*.

The P_4 has a large talonid with a large, central, closed talonid basin. A low cristid obliqua joins the trigonid buccally. The hypoconid and entoconid are distinct and large, and there was probably a small hypoconulid, but there is breakage at the back of the talonid.

The M_2 trigonid consists of a subequal metaconid and protoconid. There is no trace of a paraconid. The metaconid is slightly larger and higher than the protoconid. Transverse crests descend into the trigonid basin from the metaconid and protoconid, and are separated by an anteroposterior trench. The hypoconid is the largest talonid cusp, followed by the entoconid, and hypoconulid. Deep pits are worn into the hypoconulids on both M_2s. The cristid obliqua is very weak. The talonid basin is shallow and the enamel is crenulated. A cingulid begins anterolingually and is nearly continuous until it ends at the hypoconulid. It is strong around the talonid, but weaker around the trigonid. There are vertical furrows on the posterior walls of the metaconid and protoconid on $M_{2\text{-}3}$.

The M_3 is much longer and narrower than the M_2. The arrangement of trigonid cusps is like M_2. The talonid is deeply furrowed. The hypoconid is the largest talonid cusp. The entoconid is low and indistinct. There is no distinct hypoconulid, but rather a large posterior lobe that extends well past the other talonid cusps.

Discussion.— High variability in size and morphology has been documented in some arctocyonids (e.g., Godinot, 1980; Rigby, 1980). Even so, the differences between *Aphanocyon codyensis* and *A. amaurus* n. sp. are probably too extreme to be caused by variability in a single species. In M_1 dimensions, *A. codyensis* is about 15% larger. Differences in P_4 shape and P^4 basining are also probably too extreme for a single species. Differences between the holotypes of these species not noted in the diagnosis include in *A. amaurus* n. sp.: (1) a hypoflexid molar pit; (2) additional furrows on the posterior surface of the P_4 protoconid; (3) a precingulid on P_4; and (4) the absence of an anterior basal cusp on P_4. Some or all of these characters could be variable, however, and much larger samples are needed to test their utility.

TABLE 56 — Dental measurements of *Aphanocyon codyensis* gen. et sp. n. and *A. amaurus* n. sp. from the northern Bighorn Basin. *CPQ*, Cedar Point Quarry. *Estimate.

		Aphanocyon codyensis		*A. amaurus*		Cf. *Aphantocyon*
		UM 92145 (type) MP-94	UM 108684 SC-262	UM 64394 (type) CPQ	UM 64570 CPQ	UM 108472 SC-394
P^3	L	7.7*	—	—	—	—
	W	5.1	—	—	—	—
P^4	L	8.9*	—	—	7.3	—
	W	10.0	—	—	8.5	—
M^1	L	9.6	—	—	8.2	—
	W	12.6	—	—	10.3	—
M^2	L	10.5	—	—	8.5	—
	W	14.0	—	—	11.4	—
M^3	L	—	—	—	—	7.1
	W	—	—	—	—	8.9
P_3?	L	—	—	—	—	9.0*
	W	—	—	—	—	5.1
P_4	L	9.8*	—	8.9	—	—
	W	6.0	—	5.9	—	—
M_1	L	—	—	9.1	—	—
	W tri.	—	—	6.9	—	—
	W tal.	—	—	7.7	—	—
M_2	L	11.1	—	—	—	—
	W tri.	10.4	—	—	—	9.0*
	W tal.	10.3	—	—	—	—
M_3	L	12.1	13.9	—	—	—
	W	8.4	9.4	—	—	—

The holotype of *Aphanocyon codyensis* was collected at MP-094 in the McCullough Peaks area about 30 kilometers to the south of Polecat Bench. MP-094 is not tied into any sections but appears to be correlative to the *Plesiadapis churchilli* or *Phenacolemur* zone, based on the co-occurrence of *Phenacodus magnus* (UM 92146) and *Titanoides* (UM 92148). Identifications are tentative since UM 92146 is badly weathered and UM 92148 is very fragmentary.

UM 108684 is an isolated M_3 of *Aphanocyon codyensis* from a locality in the *Plesiadapis rex* zone. It is nearly identical to the M_3 in the holotype, and leaves little doubt that *Aphanocyon codyensis* also occurs in the Polecat Bench sequence.

Referred specimens.— **MP094**: UM 92145 (holotype). **SC262**: UM 108684, R M_3.

Aphanocyon amaurus, new species

Figure 60, Table 56

Claenodon ferox (in part), Rose, 1981a, p. 152.
Arctocyonidae n. sp. B, Secord et al., 2006, p. 228.

Holotype.— UM 64394, right dentary with P_4-M_1, P_3 alveoli, and a P_2 root. From Cedar Point Quarry in the northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences.— *Plesiadapis rex* zone (Ti-3).

Diagnosis.— See diagnosis for *Aphanocyon codyensis* n. sp.

Description.— The P^4 protocone is separated from the metacone by a shallow basin. The paraconule is small and poorly defined. A metaconule appears to have been present. On the upper molars, two small cusps that could arguably be called mesostyles are present. Like *A. codyensis*, the upper molars are typical of arctocyonids of this grade and may be difficult to distinguish from those of *Arctocyon*.

The P_4 has a distinct hypoconid, entoconid, and hypoconulid. The hypoconid is connected to a crest (cristid obliqua?) that ascends the posterior surface of the protoconid. Three deep furrows are present on the postvallid, one on the buccal side of the crest, and two on the lingual side. A precingulum is restricted to the anterior surface of the P_4.

The M_1 has a small, weak paraconid developed on a paralophid that connects the metaconid and protoconid. A pit is present in the hypoflexid, just buccal of an indistinct cristid obliqua. The talonid has a well-defined hypoconid, entoconid, and hypoconulid.

Etymology.— *Amauros* (Gr.), faint: in reference to the reduced molar paraconids.

Discussion.— See the discussion for *Aphanocyon codyensis* n. sp. for a comparison with that species. *Aphanocyon amaurus* is known only from Cedar Point Quarry. Its absence from other Ti-3 localities in the Bighorn Basin may be due to the paucity of localities of this age, rather than to rarity of the species.

The UM specimens included here in *Aphanocyon amaurus* were included in a faunal list by Rose (1981a, p. 152) as *Arctocyon* (*Claenodon*) *ferox*, presumably based on their size and on upper molar characters. Differences in fourth premolars, however, preclude identification as *Arctocyon*. Specimens in the YPM collections identified by Rose as *A. ferox* were not available for study, but presumably some or all of these belong to *A. amaurus*.

Referred specimens.— **Cedar Point Q.**: UM 64394, R dent. (holotype); 64570, L max. P^4-M^2.

Cf. *Aphanocyon*

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* zone (Ti-4b).

Description.— UM 108472 includes a P_3 or P_4 with a small lingual talonid basin, a hypoconid and an entoconid, but no hypoconulid or metaconid. It has a posterior ridge (cristid obliqua?) ascending the posterior surface of the protoconid from the hypoconid.

Discussion.— This premolar is similar in form to what might be expected for a P_3 of a species of *Aphanocyon* near the size of *A. amaurus* n. sp. The P_3 is not known for either species of *Aphanocyon* and this specimen could alternatively be an aberrant P_4 of *Arctocyon* cf. *A. nexus*. However, the associated M^3 is larger than any of the five specimens confidently identified as *Arctocyon* cf. *A. nexus* and I tentatively confer these teeth to *Aphanocyon*.

Referred specimen.— **SC394**: UM 108472, R M^3, L P_3?, R M_2 frag., assoc.

Order CONDYLARTHRA Cope, 1881
Family HYOPSODONTIDAE Trouessart, 1879

ALETODON Gingerich, 1977

Aletodon gunnelli Gingerich, 1977

Aletodon gunnelli Gingerich, 1977, p. 239.

Holotype.— UM 66301, a partial right dentary with P_4-M_1, M_3, and alveoli for M_2.

Biostratigraphic occurrences in Bighorn Basin.— Rodentia (Cf-1), *Plesiadapis cookei* (Cf-2), and *Copecion* (Cf-3) zones.

Description.— Descriptions and figures were provide by Gingerich (1977) and Rose (1981a), and metric data by Gingerich (1977).

Discussion.— A partial maxilla preserving M^1 and lingual parts of M^{2-3} (UM 108581) represents the oldest occurrence of *Aletodon gunnelli*. The teeth are heavily worn but compare closely in size and occlusal outline to those in UM 63307 figured in Rose (1981a, Fig. 35). M^2 differs in having pre- and postcingula that do not connect across the protocone. At least two other specimens of *A. gunnelli* (UM 65059, 67444) have separate cingula, however, indicating that cingular development is variable. UM 108581 is easily within the range of size and morphology exhibited by *A. gunnelli*, and although it is fragmentary, it does not compare favorably with other described taxa of this age.

Aletodon gunnelli was not previously known from the early Clarkforkian in the Bighorn Basin and the discovery of UM 108581 extends its range downward by ~500 kyr. UM 108581 was found at SC-181, which also yielded the oldest known rodent in North American and marks the beginning of the Clarkforkian. Its first occurrence at this level suggests that it too may have been an immigrant, although probably derived from a regional source area.

Referred specimens.— **SC021**: UM 65059, I^1, R M^2, R dent. M_{2-3}. **SC055**: UM 63297, L M_1, M_2; 65637, R P_4-M_1. **SC070**: UM 66850, R dP^4. **SC072**: UM 66159, R M_2. **SC074**: UM 71171, L M^2; 71233, R dent. P_3 (part), P_4. **SC076**: UM 66173, L P^3. **SC090**: UM 66290, R dent. M_1 (part), M_2; 66301, R dent. P_4-M_1, M_3. **SC092**: YPM-PU 19603; 21210; 22017. **SC107**: UM 97882, R dent. P_{3-4}, L M_2. **SC108**: UM 66629, R M_2. **SC136**: UM 67196, R dent. P_3-M_2 (P_4 partial); 67223, R M_2; YPM-PU 18087. **SC143**: UM 63280, L M_2; 67248, R M_2; 68285, R dent. P_4-M_1; 68291, R dent. P_4-M_3; 110053, L dent. M_1 tal., M_2, M_3 partial. **SC149**: UM 63307, R max. M^1(part)-M^3. **SC153**: UM 67444, R M^2. **SC155**: UM 67462, L M^1, R M_2; 67463, L M^2; 67464, R dent. P_4-M_1. **SC176**: UM 68509, L M_2. **SC181**: UM 108581, L max. M^{1-3} partials. **SC203**: UM 69290, R dent. M_2. **SC231**: UM 71430, R dent. M_{2-3}; L max. M^2. YPM-PU identifications from Gingerich (1977).

Aletodon sp.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b) and *Probathyopsis* (Ti-5a) zones.

Description and discussion.— A partial dentary (UM 73580) preserving M_{2-3} and two isolated teeth may represent a new species of *Aletodon*. The teeth in the dentary are within the size range of the older *A. quadravus* described by Gingerich (1983a), but the M_2 is proportionally narrower. The length of M_2 is above the mean (L = 4.15 mm, mean = 3.96 mm, n = 8), while its width is barely within the range (W = 3.53 mm, range = 3.5-4.0 mm, n = 8). Direct comparison with the holotype of *A. quadravus* reveals that the base of the crown is less expanded in UM 73580 and the metaconid and protoconid are further apart, relative to total width. The M_2 also differs in this way from those of *A. gunnelli* and *A. conardae*, and is much smaller. It differs further from the three species in having a cristid obliqua that contacts the postvallid more buccally. The cristid obliqua contacts the postvallid in *A. quadravus* and *A. conardae* directly below the trigonid notch in the holotypes, and slightly more lingual in most specimens of *A. gunnelli*. It contacts the postvallid buccally of the trigonid notch in UM 73580. The M_3 does not appear to differ significantly from those of the other species, except in size.

A fourth species of *Aletodon*, *A.* (*Platymastus*) *mellon* (Van Valen, 1978, p. 56), is known from only a partial M^1 or M^2. It was collected about 50 meters above Mason Pocket, according to Van Valen (1978), and may be close to the age of UM 73580. Gingerich (1983a) noted that the holotype of *A. mellon* was larger than an M^2 identified as *A. quadravus*, implying that it should also be larger than UM 73580. Although size comparisons with the holotype of *A. mellon* can be estimated, it is too fragmentary for accurate measurements and not adequate as a type specimen. I consider it a *nomen dubium*.

UM 73580 is also similar to the M_2 of *Litomylus*? *ishami* described by Gazin (1956a), based on a fragmentary dentary preserving only the talonid of M_1 and a complete M_2. The M_2 in UM 73580 is close to the size of M_2 in *L*? *ishami*, but the trigonid is slightly broader and extends laterally farther beyond the talonid. It also differs in having a distinct paraconid, in having a metaconid and protoconid that together form a more transverse line, and in having a less planar postvallid. It differs also in having a deep incision in the hypoflexid directly behind the postvallid. This last feature and the development of the paraconid are variable in *Aletodon gunnelli* and may not be significant.

An isolated P_3 and M_3 from anthills at SC-243 may also represent the same species as UM 73580. The P_3 is structurally similar to the P_3 of *Aletodon gunnelli* (e.g., UM 67196, 97882) but is more laterally compressed, which parallels the narrowness in UM 73580. The M_3 is the same size as in UM 73580, but the metaconid and protoconid are closer together, the hypoconulid and entoconid are further apart, and there is a peculiar prominent cusp in the center of the talonid basin.

Gingerich (1977) noted an M_2 (YPM-PU 18938) of *Aletodon* that is about the same age as UM 73580, and could potentially belong to the same species. I have not seen it.

I refrain from establishing a new species based on UM 73580 because of its fragmentary condition and the lack of knowledge of variability in this and other similar species.

Dental measurements (mm).— UM 61592: L P_3, L = 4.15, W = 1.74. UM 61599: R M_3, L = 4.25, W = 2.85*. UM 73580: M_2, L = 4.15, W = 3.53; M_3, L = 4.25, W = 3.05.

Referred specimens.— **SC243**: UM 61592, L P_3; 61599, R M_3. **SC-270**: UM 73580, R dent. $M_{2\text{-}3}$.

HAPLOMYLUS Matthew, 1915c

Haplomylus palustris Gingerich, 1994

Haplomylus palustris Gingerich, 1994, p. 123.

Holotype.— YPM-PU 18347, a right dentary with $M_{1\text{-}3}$, from Bear Creek, Montana, in the northern Bighorn Basin.

Biostratigraphic occurrences in Bighorn Basin.— Rodentia zone (Cf-1).

Description.— The holotype and other specimens were described by Gingerich (1994).

Discussion.— Fragmentary specimens of *Haplomylus* from Bear Creek were initially referred to *H.* cf. *H. simpsoni* by Rose (1981a, p. 128), who thought they might be small individuals of this species. Gingerich (1994) later established a new species, *H. palustris*, based on these specimens. He distinguished *H. palustris* from *H. simpsoni* by its small size and by less developed paraconid and metaconid cusps on P_4. In addition, the P_4 is also narrower than any of *H. simpsoni* measured by Rose (1981a) and has a less inflated appearance. The metaconid is expressed only as a vertical swelling on the posterolingual corner of the protocone. Besides the Bear Creek specimens, Gingerich also tentatively included a partial upper molar (UM 68434) from SC-173, an early Clarkforkian locality west of Polecat Bench.

TABLE 57 — Dental statistics for *Phenacodaptes sabulosus* from Habetler's Concentration wash site at SC-165. Abbreviations as in Table 3.

		n	Min.	Max.	Mean	SE	SD	V
P^3	L	1	—	—	1.97	—	—	—
	W	1	—	—	1.70	—	—	—
P^4	L	5	2.70	2.95	2.83	0.04	0.10	3.44
	W	6	3.47	3.67	3.60	0.03	0.08	2.22
M^1	L	6	2.43	2.70	2.61	0.05	0.12	4.45
	W	6	3.37	3.70	3.55	0.05	0.12	3.27
M^2	L	7	2.75	3.25	3.00	0.07	0.18	6.10
	W	7	4.00	4.45	4.29	0.06	0.15	3.40
M^3	L	2	2.30	2.55	2.43	—	—	—
	W	2	3.25	3.55	3.40	—	—	—
P_2	L	1	—	—	2.05	—	—	—
	W	1	—	—	1.08	—	—	—
P_3	L	2	1.91	1.93	1.92	—	—	—
	W	2	1.19	1.25	1.22	—	—	—
P_4	L	2	3.44	3.50	3.47	—	—	—
	W	2	2.01	2.10	2.06	—	—	—
M_1	L	1	—	—	3.02	—	—	—
	W	1	—	—	2.20	—	—	—
M_2	L	2	3.00	3.07	3.04	—	—	—
	W	2	2.57	2.65	2.61	—	—	—
M_3	L	4	2.90	3.35	3.07	0.10	0.20	6.44
	W	4	2.12	2.28	2.18	0.04	0.07	3.23

A dentary fragment with M_1 (UM 110178) recently collected near the base of the Clarkforkian is close in size to the holotype and is identified here as *Haplomylus palustris*. It lacks a well-defined paraconid, unlike specimens of *H. simpsoni*. The only M_1 available to Gingerich (1994) when he described *H. palustris* was in the holotype. He noted that "M_1 appears to retain a distinct paraconid," but based on his Figure 3, the holotype may be too worn to confidently evaluate the condition of the paraconid. The reduction of the paraconid on M_1 may parallel its reduction on P_4.

A second M_1 (UM 69233) collected near the base of the *Plesiadapis cookei* zone has a tiny paraconid that is barely distinguishable from the paralophid. Two other specimens from about the same level have small, but distinct paraconids. These specimens are all smaller than specimens of *H. simpsoni* from the late Clarkforkian and close to the size of *H. palustris*. Rose (1981a) provided a plot of M_1 and M_2 area for Clarkforkian and Wasatchian teeth of *Haplomylus*, documenting an increase in size through the Clarkforkian. If Clarkforkian specimens are part of a single lineage it appears that the paraconid in the early Clarkforkian form (*P. palustris*) was indistinct or variably present, but is consistently present and distinct in the late Clarkforkian form (*P. simpsoni*). Some specimens from the middle Clarkforkian placed in *H. simpsoni* by Rose (1981a) may be better allocated to *H. palustris*, but I refrain from including these specimens until *H. palustris* is better known.

Dental measurements (mm).— UM 110178: L M_1, interstitial L = 2.45, maximum L = 3.05, W = 2.10; dent. depth = 3.7.

Referred specimen.— **SC362**: UM 110178, dent. frag. L M_1.

PHENACODAPTES Jepsen, 1930b

Phenacodaptes sabulosus Jepsen, 1930b

Tables 57–58

Phenacodaptes sabulosus Jepsen, 1930b, p. 517.

Holotype.— YPM-PU 13302, a right dentary with P_1-M_3, from Princeton Quarry, northern Bighorn Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a) and *Plesiadapis simonsi* (Ti-5b) zones.

Description.— Descriptions and figures of *Phenacodaptes sabulosus* were provided by Jepsen (1930b) and Gazin (1959). A description and comparison to *Apheliscus* was provided by Rose (1981a) and Gazin (1959). Rose also included measurement statistics for specimens from the type locality.

Discussion.— *Phenacodaptes sabulosus* is a common fossil at some quarry and wash sites in the *Probathyopsis* and *Plesiadapis simonsi* zones. It is represented by over 100 specimens at Princeton Quarry and accounts for almost 20% of the total number (Rose, 1981a, p. 156). It is represented by seven jaws at Schaff Quarry, which is about 5% of the total number, but not by isolated teeth. It is curiously absent at Y2K Quarry, however, in spite of over 500 cataloged teeth. Y2K Quarry directly overlies Habetler's Concentration, a small wash site in SC-165 that is about 50 meters lower in the section. It has yielded 16 specimens of *P. sabulosus*, representing about 25% of the total. All these quarries preserve fossils in siltstone or mudstone, and the lithologies of Schaff and Y2K quarries are especially similar. Princeton, Schaff, and Y2K quarries have a similar taxonomic composition and the absence of *P. sabulosus* at Y2K Quarry suggests that it may have been sensitive to environmental conditions that other species were not.

Variation in the sample of *Phenacodaptes sabulosus* from Schaff Quarry mostly overlaps with that at Princeton Quarry, the type locality. Teeth are slightly smaller on average, however, and the only adult P_4 (YPM-PU 19431) is smaller than any in the Princeton Quarry sample. The size of M_2, relative to M_1, may also be lower on average, but there is considerable variability in size and degree of inflation of these teeth in the Princeton Quarry sample. I have provisionally included the Schaff Quarry specimens in *P. sabulosus*, but further study is warranted.

Rose (1981a) discussed differences between *Phenacodaptes sabulosus* from the late Tiffanian and *Apheliscus nitidus* from the Clarkforkian, noting morphologic intermediacy in some late Tiffanian and early Clarkforkian specimens. His Figure 39 shows two M_1s from the late Tiffanian (presumably UM 68732, 68890) that are intermediate in size between these species. Although there may be some intermediacy in these samples, the most diagnostic specimens from these levels, including material collected after Rose's study, bear the specializations of *A. nitidus* and appear to be much closer to it than to *P. sabulosus*. A similar conclusion was reached in an unpublished dissertation by Bloch (2001), based on UM 36193, a new specimen from a freshwater limestone collected in the early Clarkforkian. Bloch identified it as *Apheliscus nitidus* and noted that it was not particularly transitional in morphology but seemed to be most similar to the younger *A. nitidus*. It has not been described.

TABLE 58 — Dental measurements for *Phenacodaptes sabulosus*? and *Apheliscus nitidus* from the late Tiffanian and Clarkforkian of the Bighorn Basin. Summary measurements for *A. nitidus* from SC-143 (Paint Creek) include: UM 69941, 71047, 74054, 75453, 83016, 83020, and 98457. *n* is shown in parentheses. *Estimate.

		Phenacodaptes sabulosus?			*Apheliscus nitidus*							
		UM 68732 SC-178	UM 73380 SC-260	UM 101132 SC-217	Range SC-143	UM 66502 SC-48	UM 68744 SC-179	UM 68890 SC-191	UM 69938 SC-143	UM 108604 SC-399	UM 101827 SC-179	UM 110129 SC-362
P^4	L	—	—	—	—	—	2.20	—	2.50	—	—	—
	W	—	—	—	—	—	2.86	—	2.80	—	—	—
M^1	L	—	—	—	—	—	—	—	2.65	—	—	—
	W	—	—	—	—	—	—	—	2.81	—	—	—
P_3	L	—	—	—	—	2.11	—	—	—	—	—	—
	W	—	—	—	—	1.10	—	—	—	—	—	—
P_4	L	—	—	—	3.17–3.30 (2)	3.47	—	3.30	—	—	3.32	2.75*
	W	—	—	—	1.75–1.85 (2)	1.80	—	1.81	—	—	1.69	1.41
M_1	L	2.69	—	—	2.53–2.55 (2)	—	—	2.70	—	2.60	—	—
	W	2.09	—	—	1.88–1.90 (2)	—	—	2.00	—	2.02	—	—
M_2	L	—	3.30	3.45	3.01–3.41 (5)	—	—	—	—	3.25	—	—
	W	—	2.79	2.91	2.25–2.57 (5)	—	—	—	—	2.41	—	—
M_3	L	—	—	—	2.95–3.20 (3)	—	—	—	—	—	—	—
	W	—	—	—	2.06–2.25 (3)	—	—	—	—	—	—	—

The P_3-M_3 of *Apheliscus nitidus* are buccolingually narrower than those of *Phenacodaptes sabulosus*, are smaller on average, and have longer talonids. The last feature is especially exaggerated in the talonids of P_{3-4}, as exhibited by UM 66502, figured in Rose (1981a, Fig. 36D-E). Upper teeth can be distinguished by smaller, less developed hypocones in *A. nitidus* (Rose, 1981a), although this feature is somewhat variable. Upper molars are also less buccolingually elongate in *A. nitidus* (Tables 57 and 58) and often have a more rounded appearance.

UM 68890, a dentary with P_4-M_1, is the only specimen from the latest Tiffanian *Plesiadapis gingerichi* zone that preserves premolars. It compares closely with *Apheliscus nitidus* in form and is outside the variability of *P. sabulosus*. The teeth are narrower and the P_4 talonid is considerably longer than in *P. sabulosus*. It is as specialized as P_4s of *A. nitidus* from Paint Creek (e.g., UM 74054, 98457), but it is slightly larger. Another P_4 (UM 101827) from the earliest Clarkforkian, collected after Rose's study, is the size of *A. nitidus* and its talonid is as long as any in the UM collections. A third specimen (UM 110129) from the same level is also small, but the talonid is shorter, although not nearly as short as in *P. sabulosus*. These specimens bear the distinguishing features of *A. nitidus* and do not appear to be especially intermediate between it and *P. sabulosus*.

Two isolated M_2s (UM 73380, 101132) from an area west of the main measured sections lack the narrowness characteristic of *Apheliscus nitidus*, are large, and are inseparable from teeth of *Phenacodaptes sabulosus*. Based on the occurrence of rodent incisors from SC-215, which appears to be slightly higher stratigraphically, the M_2s are either early Clarkforkian or latest Tiffanian in age. These teeth may represent late occurrences of *P. sabulosus* and could be temporally equivalent to the specimens included here in *A. nitidus* from localities along Polecat Bench. Larger samples and better temporal resolution are necessary, however, to demonstrate temporal overlap in these species.

No specimens younger than Habetler's Concentration in the *Plesiadapis simonsi* zone can be unequivocally identified as *Phenacodaptes sabulosus*, but several teeth could belong to the species. Although there are several isolated hyopsodontid teeth from levels below the *Probathyopsis* zone, none appear to belong to *P. sabulosus*.

Referred specimens.— **SC165** (Habetler's Concentration - wash): UM 68267, L dent. M_{2-3}, M_1 assoc., L max. P^4-M^1; 69535, R max. P^3-M^3; 68272, R max. P^4(part)-M^2; 69536, R max. P^4-M^1; 71498, L max. P^4-M^1 (part), M^2; 71499, L max. M^{1-3}; 71501, R max. P^4-M^2; 71504, L dent. P_3-M_2; 71506, R dent. M_{2-3}; 71507, L max. P^4-M^2; 71508, L dent. P_2, P_4-M_3; 81706, R M^1; 81713, R P_3; 81714, R max. P^{3-4}; 110170, R M^2; 110172, L M^2. **SC187**: UM 108389, L M^2; 108891, L M_x tal.; 110294, R M_2. **SC217**: UM 101132, R dent. M_2. **SC260**: UM 73380, R M_2. **SC266**: UM 73506, L M_2, R M_2 assoc.? **Schaff Q.**: UM 77351, R dent. P_4-M_2; 110160, L M^1; YPM-PU 19431, L dent. P_4-M_2; 19382, L dent. dP_4-M_1; 19505, L dent. M_{1-3}; 19473, L dent. dP_4-M_1; 19430, L dent. M_{2-3}. Plus additional specimens in the YPM collections from Princeton Quarry and other localities in the *Probathyopsis* zone.

APHELISCUS Cope, 1875

Apheliscus nitidus Simpson, 1937c

Table 58

Apheliscus nitidus Simpson, 1937c, p. 4.

Holotype.— AMNH 15849, left maxillary fragment with P^4-M^1, from the Clarks Fork Basin, Wyoming.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis gingerichi* (Ti-6), Rodentia (Cf-1), *Plesiadapis cookei* (Cf-2), and *Copecion* (Cf-3) zones.

Description and discussion.— The holotype was figured by Matthew (1918) and described by Simpson (1937c). Rose (1981a) provided descriptions and figures of additional specimens, as well as metric data and statistics. Specimens from the late Tiffanian and early Clarkforkian included here were discussed in the *Phenacodaptes* section.

Referred specimens.— **FG041**: UM 77283, L M^2. **SC083**: UM 110188, R M_2; 110189, L M_3. **SC179**: UM 36193, rostrum, L and R dent., postcrania; 68744, R P^4; 101827, R P_4. **SC191**: UM 68890, L dent. P_4-M_1. **SC359**: UM 88325, L M^2; 88326, L M_1. **SC362 Q.**: UM 108326, L M_2; 110095, L P^4 partial; 110129, R P_4. **SC399**: UM 108604, L dent. M_{1-2}. **SC406**: UM 108334, R M^2 partial. Plus additional specimens from the middle and late Clarkforkian listed in Rose (1981a).

Cf. *Litomylus*? *ishami*

Biostratigraphic occurrences in Bighorn Basin.— ?*Plesiadapis churchilli* zone (Ti-4a).

Description and discussion.— A dentary fragment (YPM-PU 17751) preserving the talonid of M_1 and a nearly complete M_2 is similar to the holotype of *Litomylus*? *ishami* from Fossil Basin in southwestern Wyoming (Gazin, 1956a). It has a more oblique postvallid with a more posteriorly positioned metaconid, relative to the protoconid. Additionally, the entoconid and hypoconulid are more posteriorly positioned relative to the hypoconid, than in *L.*? *ishami*. In other regards it is nearly identical to the holotype. The dentary is laterally crushed, and the differences between it and the holotype of *L.*? *ishami* could have resulted from plastic deformation by subjecting it to lateral force with a component of anteroposterior shear. If the condition of YPM-PU 17751 is the result of deformation, it probably belongs to *Litomylus*? *ishami*. Nevertheless, an additional specimen is needed to establish the presence of the species in the Bighorn Basin.

YPM-PU 17751 is from an area about 2 km south of Divide Quarry that is not well-constrained biostratigraphically, but based on the strike of the beds is probably correlative to the *Plesiadapis churchilli* or *Phenacolemur* zone. A dentary (YPM-PU 16445) identified here as *Haplolambda* cf. *H. quinni* is also from the same quarter section.

Referred specimen.— **SW1/4**, **S22**, **T54N**, **R95W**: YPM-PU 17751, R dent. M_1 tal., M_2.

Hyopsodontidae genus and species indet.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* zone (Ti-4a).

Description and discussion.— Three isolated teeth from Divide Quarry are too fragmentary for reliable generic identification but are referable to the Hyopsodontidae. An M_2 is very similar to that of *Haplaletes disceptatrix* from Rock Bench Quarry and differs only in having a stronger hypoconulid. An M_3 is also similar, but is more elongate than in *H. disceptatrix* and more comparable to the M_3 of younger species of *Haplomylus*. Although these teeth are nearly indistinguishable from those of certain species, important diagnostic features such as relative molar size and P_4 morphology cannot be evaluated.

Referred specimens.— **Divide Q.** (FG046): UM 77271, R M_3; 83276, L M_2; 85915, R dP^4.

Family PHENACODONTIDAE Cope, 1881

PHENACODUS Cope, 1873

Phenacodus grangeri Simpson, 1935d

Phenacodus grangeri Simpson, 1935b, p. 23. Thewissen, 1990, p. 50.

Holotype.— AMNH 17185, right maxilla with $M^{1\text{-}2}$ and a partial M^3 from the “Tiffany beds” of the Animas formation, “2 miles N. of Arboles, Colorado” in the northern San Juan Basin (Thewissen, 1990). Late Tiffanian in age.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* (Ti-3), *Phenacolemur* (Ti-4b), *Probathyopsis* (Ti-5a), and *Plesiadapis simonsi* (Ti-5b) zones.

Description.— In the most recent revision of the *Phenacodontidae*, Thewissen (1990) provided descriptions and figures of *P. grangeri*, as well as references to previous work.

Discussion.— Thewissen (1990) reported that *Phenacodus grangeri* ranged from the *Plesiadapis rex* zone to the *Plesiadapis simonsi* zone. None of the specimens he identified, however, is from the intermediate *Plesiadapis churchilli* zone in the Bighorn Basin, as defined here. In spite of a relatively large sample from Divide Quarry, *Phenacodus magnus* is the only *Phenacodus* that has been confidently identified in the *Plesiadapis churchilli* zone.

Phenacodus grangeri appears to be part of a single lineage that includes the younger *P. intermedius* in the Clarkforkian. Thewissen (1990) placed the boundary between these species at the base of the Clarkforkian, which he thought was equivalent to the base of the *Plesiadapis gingerichi* zone. According to Thewissen, *Phenacodus grangeri* differs from *P. intermedius* only in having a relatively wider P^4. He summarized P^4 proportions (Table 5, p. 54) reporting a mean width/length ratio of 1.18 for *P. grangeri* (n = 28, SD = 0.09) and 1.07 for *P. intermedius* (n = 58, SD = 0.07). Thewissen’s standard deviations imply considerable overlap in P^4 proportion, however, and large samples are necessary to confidently distinguish between these species.

Width/length ratios of three P^4s from the upper part of the *Probathyopsis* zone range from 1.18-1.20 and have a mean of 1.9, which is close to the mean reported for *Phenacodus grangeri*. Higher in the section near the Tiffanian-Clarkforkian boundary, however, most P^4s yield intermediate values between the means of *P. grangeri* and *P. intermedius*. Two P^4s from latest Tiffanian localities have a mean of 1.12 and a range of 1.09-1.15. Five P^4s from the earliest Clarkforkian have a mean of 1.10 and range from 1.05-1.14. It appears that there was a gradual transition in the change of P^4 proportions from *P. grangeri* to *P. intermedius* and that latest Tiffanian and early Clarkforkian teeth represent an intermediate condition. Because at least two early Clarkforkian specimens (UM 68754 and 71612) exhibit the narrow P^4 characteristic of *P. intermedius*, I follow Thewissen in identifying Clarkforkian specimens as *P. intermedius*.

Measurements for P^4 (mm).— *Probathyopsis* zone — **SC275**, UM 73673: L = 9.6, W = 11.5. **SC386**, UM 108427: L = 9.4**, W = 11.1. **SC389**, UM 108528: L = 10.3, W= 12.36. *Plesiadapis gingerichi* zone — **SC185**, UM 68787, L = 10.02, W = 11.5. **SC370**, UM 108322, L = 10.69, W = 11.6. Measuring techniques follow those of Thewissen (1990).

Referred specimens.— **Bluff Top Q.** (SC379): UM 108259, R M_3; 108624, R M_3, dent. frag. **Cedar Point Q.**: UM 63095, L max. P^4-M^1; 63104, C_1, L M^1 or M^2; 63109, canine; 64395, L max. P^4-M^3; 64505, R dent. frag., M_3; 64509, R max. $M^{1\text{-}3}$; 64526, R M_2; 64558, L max. $M^{1\text{-}3}$; 82096, L dent. P_3-M_3; 108685, R P_4; 108705, L M_3; 108706, R M_3; 108707, R M^3; 109873, R P^4; 109875, L P_3; 109876, R P^3 partial. **Croc Tooth Q.** (FG028): UM 77153, L dent. P_3-M_3; 108687, R dP^4; 108688, R P^3; 108689, R P_3; 108690, L M^2; 108692, R M^1 or M^2; YPM-PU 25036, R M^1. **FG004**: UM 73979, I^1, C^1, R M^x, M^3; 73982, L M^1 or M^2, and frags.; 73988, R M^3. **FG037**: UM 77158, R M_1. **FG047**: UM 77294, R M^1 or M^2; 83231, R M^1 or M^2. **FG050**: UM 77310, L dP^3, M^1, M^3, R M^1, M^2 assoc. **SC086**: UM 66214, C^1, parts of R P^4, M^3. **SC144**: UM 67266, L P^4, R P^2, parts of L M^x, R P^4, C^1; 67267, L max. $M^{2\text{-}3}$. **SC165**: UM 68251, R dent. frag., L dent. frag. M_x frags.; 68252, L dent. $M_{1\text{-}2}$; 68254, L P_4, assoc. tooth frags.; 108668, R P_4. **SC178**: UM 68729, R P_4, M_3 assoc.; 68733, R P_3 tal., P_4; 68735, R dent. $M_{1\text{-}3}$, L P_3, M_1; 68736, L P_4-M_1, M_3; 101823, R M_3 tal.; 108557, R M^3 partial, M^x frags.; 108672, L M^3, R P_4. **SC185**: UM 68787, R P^3, M^3, M_x, M_3, L P^4, M_x; 110114, R P^4 frag. **SC186**: UM 68791, R M^3, M^x part. **SC187**: UM 73600, L dent. $P_{3\text{-}4}$, $M_{2\text{-}3}$; 80357, L M^2; 108885, L M^3; 108888, L M_2, R P^4 (frag.), assoc. bone. **SC191**: UM 68886, R M^x, M_3 assoc.; 68887, L dent. frag., P_4, R M_2 tri.; 68889, L M^1, L M_3 assoc.; 108290, L P^4 partial; 110279, R M^3. **SC199**: UM 69253, parts of L C^1, R C^1, R P^4. **SC228**: UM 96364, R M^1 or M^2. **SC229**: UM 71326, L dent. P_4, $M_{2\text{-}3}$, R dent. assoc. M_3. **SC243**: UM 108679, R M_3. **SC262**: UM 73396, I^1, C^1, L M^3. **SC263**: UM 110145, R M_3 tal. **SC266**: UM 110181, L M^3. **SC267**: UM 73515, L P_4 tal., M^3, R M^3; 73516, parts of R P^4, M^3, C^1. **SC270**: UM 73585, L M^2; 109968, L M^3. **SC271**: UM 73588, L P_4-M_2 assoc. **SC275**: UM 73673, palate, L P^4-M^3, R P^3-M^3. **SC277**: UM 73688, L M_3 partial. **SC278**: UM 73689, L P_4, M_3, R M_2 assoc.; 73690, R P_4, M_3. **SC279**: UM 73693, I^1, C^1, R M^3, L M_2 part, assoc. **SC284**: UM 82017, R dent. $M_{2\text{-}3}$. **SC370**: UM 108322, L P^4. **SC373**: UM 108250, M^x part. **SC379**: UM 108582, R P_4. **SC380**: UM 108239, dent. frags. L M_3; 108412, I_x, L M_3. **SC382**: UM 108417, M_x frag.; 108489, dent. frags., R M_2, R M^3 L M^3 frags.; 108491, R M^3 and upper frags. **SC383**: UM 108497, L P_4 frag. **SC384**: UM 108499, L M_3, P_x frag. **SC386**: UM 108427, L max. P^4 (part)-M^2, R max. frag., $P^{3\text{-}4}$ (part); 108428, L dent. M_2, R dent. frags., M_1; 108429, max. frag., M^x frags.; 108509, L M^x, frags. **SC388**: UM 108462, L P_3, M_x frag.; 108464, L M^3, petrosal? partial. **SC389**: UM 108442, R max. P^4 (part)-M^3; 108518, R M^2;

108528, R P^4; 109416, R M_2; 109417, L M_3. **SC394**: UM 108482, R M^x, L M^x, P^3 frags. **SC395**: UM 108577, R P^4 protocone, upper tooth frags. **SC410**: UM 108923, R M_3. **SC415**: UM 108938, L M_1 or M_2. **SC419**: UM 110080, L P^4; 110083, L P_3, M_3, M_x frags.; 110084, C^1, P^1, R P^2 assoc. **SC421**: UM 110099, R M_2. **Zalmout Q.** (SC389): UM 108447, L M^x frag., I^x, R P_3, bone and dent. frags., assoc.; 108449, P^1, L M^3, L M_2, M_3 tal., assoc. See Thewissen (1990) for a list of additional specimens in other museums.

Phenacodus cf. *P. grangeri*

Biostratigraphic occurrences in Bighorn Basin.— Late Torrejonian or early Tiffanian.

Description and discussion.— A *Phenacodus* M_2 (UM 112580) was recovered from the chert conglomeratic sandstone (CC "member," Fig. 6) above the Rock Bench Quarry beds in 2004. It is within the size range of *P. grangeri*, which ranges in age from the *Plesiadapis rex* (Ti-3) to the *Plesiadapis simonsi* (Ti-5b) zone. However, UM 112580 is longer and narrower than the average M_2 of *P. grangeri* from the *Plesiadapis rex* zone (UM 112580: L = 11.7, W = 9.3 mm; mean *P. grangeri* M_2: L = 10.82, W = 9.59 mm, Thewissen, 1990, Table A-18; L/W = 1.26 and 1.13 mm, respectively), suggesting that it may belong to another species. Notably, a P_4 of *Phenacodus* from The Breaks in southeastern Wyoming is also within the size range of *P. grangeri*, but may also be narrower (UW 28687: P_4, L = 10.5, W = 6.7 mm; unpublished data from dissertation, Higgins, 2000; *P. grangeri*: P_4, L = 10.54, W = 7.54; Thewissen, 1990, Table A-18; L/W = 1.57 and 1.40 mm, respectively). Biostratigraphy of The Breaks indicates that the P_4 is late Torrejonian in age (Higgins, 2003, Fig. 9). It is possible that both the Breaks specimens and UM 112580 represent an undescribed species of *Phenacodus* with narrower lower cheek teeth.

The age of the chert conglomerate is constrained by a partial dentary identified as *P. anceps* by Gingerich (1976) that was collected from the level of the conglomerate or higher (see *P. anceps* section), and by the underlying Rock Bench Quarry. This, coupled with the presence of *Phenacodus*, constrains the age to late Torrejonian or early Tiffanian (Ti-1 or Ti-2).

Referred specimen.— **SC429**: UM 112580, R dent. frag., M_2.

Phenacodus magnus Thewissen, 1990

Phenacodus magnus Thewissen, 1990, p. 55.

Holotype.— YPM-PU 20165, right P^4-M^2, left P_1 and P_2 fragments, right C_1, P_4-M_2, two incisors, and numerous bone fragments; from Sec. 14, T57N, R100W, the west side of Polecat Bench, in the Clarks Fork Basin, Wyoming. YPM-PU 21065 was erroneously reported by Thewissen (1990) as the holotype, but is actually a specimen of *Ptilodus* from Cedar Point Quarry (pers. comm. M.A. Turner, YPM, 2004).

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis churchilli* (Ti-4a), *Phenacolemur* (Ti-4b), and ?*Probathyopsis* (Ti-5a) zones.

Description.— Thewissen (1990) provided detailed descriptions and figures of the holotype and other specimens of *P. magnus*.

Discussion.— According to Thewissen (1990), *Phenacodus magnus* differs from other Paleocene phenacodontids primarily in being larger, but may also differ in having a narrower trigonid basin on P_4 and in having a more inflated appearance in tooth cusps. *Phenacodus magnus* is known mostly from isolated specimens recognized by their large size. There is considerable size overlap between *P. grangeri* and *P. magnus*, however, and it may not be possible to differentiate large specimens of *P. grangeri* from small specimens of *P. magnus*.

Thewissen (1990) reported that the holotype of *Phenacodus magnus* was from the 680 meter level in Sec. 14, T57N, R100W, in the *Plesiadapis simonsi* zone. The base of the zone, as it was recognized at the time, was below Princeton Quarry and is approximately equivalent to the base of the *Probathyopsis* zone used here. Section 14 spans about 100 meters of strata, however, probably sampling both the *Phenacolemur* zone and the base of the *Probathyopsis* zone. Nevertheless, all fossiliferous UM localities in Section 14 appear to be correlative to the *Phenacolemur* zone. The holotype was collected in 1964 by Princeton crews, and apparently, no more locality data than what Thewissen reported are associated with it (pers. comm., M.A. Turner, YPM, 2004). It is unclear how he arrived at the 680 meter level estimate. In any case, based on the range of *P. magnus* at other localities, the specimen is almost certainly from the *Phenacolemur* zone.

Thewissen (1990) reported other specimens of *Phenacodus magnus* from the *Plesiadapis simonsi* zone (~*Probathyopsis* zone). However, several of the specimens (i.e., UM 74037, 77304, 77305, 80357) are within the size range of *P. grangeri* and I transfer them to it. I have tentatively included two specimens (UM 98473, 71319) from the *Probathyopsis* zone in *P. magnus*, although they could conceivably be large individuals of *P. grangeri*. Others are too fragmentary for confident identification. *Phenacodus magnus* is a characteristic species of the *Plesiadapis churchilli* and *Phenacolemur* zones, and if it does range into the *Probathyopsis* zone, it is an uncommon species there.

Measurements reported by Thewissen (1990) are based on a composite of specimens reportedly from the *Plesiadapis simonsi* zone. Some of the specimens he measured were from Fossil Hollow, however, which was thought to be stratigraphically above Princeton Quarry at the time but is now known to be well below it in the *Phenacolemur* zone. Others specimens may be large individuals of *P. grangeri* or be from isolated localities in the *Phenacolemur* zone. The largest sample of *P. magnus* from a single locality is from Divide Quarry in the *Plesiadapis churchilli* zone. Several of these teeth are larger than those in the holotype and well outside the range of *P. grangeri* (compare measurements below to those for *P. grangeri* in Thewissen, 1990).

Thewissen (1990) suggested that *Phenacodus magnus* and *P. grangeri* were contemporaneous species that preferred poorly drained and well-drained environments, respectively. He noted however, that *P. magnus* occurred in both types of environments. The holotype and specimens from Fossil Hollow are from floodplain deposits while those from Divide and Croc Tooth quarries are from channel deposits. Additionally, Thewissen identified both species at Croc Tooth Quarry (UM 77153, 77198) even though he considered the quarry to represent a poorly drained environment not favorable to *P. grangeri*. At least two teeth from Croc Tooth Quarry (UM 77198, 108686) are outside the range for *Phenacodus grangeri* and may belong to *P. magnus*, while others are close to the size expected for *P. grangeri* (e.g., UM 77153). The differences that Thewissen attributed to facies could be the result of temporal differences. Divide Quarry is in the *Plesiadapis churchilli* zone where only *P. magnu*s occurs, while Croc Tooth Quarry is in the younger *Phenacolemur* zone. I provisionally follow Thewissen in recognizing both species, but note that it is not possible to convincingly demonstrate a bimodal distribution with the material in hand. Further study may show that that *P. magnus* and *P. grangeri* are species in a single evolutionary lineage.

Dental measurements for Divide Quarry (mm; Type 2).— UM 80582: P_4, L = 13.75, W = 10.40. UM 80667: M_2, L = 16.05, W = 14.40. UM 83218: P_3, L = 12.10, W = 8.10, P_4, L = 14.30, W = 10.55. UM 91319: M^3, L = 11.10, W = 11.80. UM 109961: M^3, L = 13.80, W = 13.60. Measuring techniques follow those of Thewissen (1990).

Referred specimens.— **Croc Tooth Q.** (FG028): UM 77198, M_1; 108686, L M^1. **Divide Q.** (FG046): UM 80582, L P_4; 80667, L M_2; 83218, R dent. P_{3-4}; 85930, R M^x, broken; 91319, R M^3; 109961, L M^3. **FG007**: UM 74028, L M_2. **Fossil Hollow** (SC198): UM 79881, R M_3; 83564, L max. P^4-M^2, R max. P^{3-4}, M^{2-3}, R P_4, parts of L C^1, R C^1, R M^1; 104924, R M_3, L M^x partial; 110301, L M_2 partial; 110306, L P_3. **MP094**: UM 92146, L dent. M_{1-2}. **SC228**: UM 71319, L M_3 tal. **SC270**: UM 98473, R dent. dP_4-M_1. **SC392**: UM 108474, R P_4. See Thewissen (1990) for additional specimens in the YPM collections.

Phenacodus vortmani (Cope, 1880)

Hyracotherium vortmani Cope, 1880, p. 747.
Phenacodus vortmani, Cope, 1882b, p. 199. Thewissen, 1990, p. 55.

Holotype.— AMNH 4824, left dentary with P_4, part of M_1, roots for P_3-M_3, and alveoli for P_{1-2}, from Wasatchian (*Lambdotherium* zone) age deposits in the Wind River Basin, Wyoming (Thewissen, 1990).

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a), *Plesiadapis simonsi* (Ti-5b), *Plesiadapis gingerichi* (Ti-6), and Clarkforkian and Wasatchian zones.

Description.— In the most recent revision of the Phenacodontidae, Thewissen (1990) provided descriptions and figures of *P. vortmani*, as well as references to previous work.

Discussion.— Teeth of *Phenacodus vortmani* are relatively common in the late Tiffanian of the Bighorn Basin. According to Thewissen (1990), *P. vortmani* differs from the contemporaneous *P. grangeri* only in being smaller. Size overlap between these species appears to be minimal. Using M_1 mean values reported by Thewissen, and assuming that 0.4 in natural log space is approximately equivalent to four standard deviations (e.g., Gingerich, 1979b, 1980a), expected overlap in M_1 area between these species should be small. Size overlap is probably greater, however, for other tooth positions.

Phenacodus vortmani is a long ranging species that first appears near the base of the *Probathyopsis* zone. Thewissen (1990) reported a single occurrence of *P. vortmani* in the *Plesiadapis churchilli* zone, based on UM 71703 from SC-228. However, this locality is now in the lowest part of the *Probathyopsis* zone. Interestingly, *P. vortmani* appears in the fossil record very close to the first occurrence of *Probathyopsis* (Fig. 8), which is almost certainly an intercontinental immigrant (e.g., Gingerich, 1985, 1999).

Referred specimens.— **FG004**: UM 73983, L max. P^4, M^2, M^1 part; 73985, R P^4, parts of L P^4, R M^2. **FG037**: UM 77157, iso. upper teeth. **SC178**: UM 101816, L dent. P_2, R dent. P_3, M_{1-3}. **SC186**: UM 68797, L dent. frag., P_4. **SC187**: UM 108892, R P^4 protocone. **SC191**: UM 68884, L P_4, M_2, M_3 assoc. **SC215**: UM 69928, R M_{1-3}, L M^3. **SC226**: UM 71300, L dent. M_{1-2}; 71302, L P_3, R M_3, L M_x frag.; 71313, L P^3, R P^4, R P_3 tri., unassoc. L M_3. **SC228**: UM 71703, L M_3. **SC248**: UM 71793, R M_{1-3}, assoc. **SC251**: UM 71819, L P_3, R M_{2-3}. **SC252**: UM 71417, L dent. P_4-M_2, assoc. M_3, R M_{1-2}; 71709, R dent. frag., P_4-M_1 assoc., R M^3. **SC257**: UM 73337, dent. crushed molars. **SC260**: UM 73529, L M_3, R M_3, astragalus, assoc.? **SC267**: UM 108693, R M^{1-2}. **SC270**: UM 73579, R dent. M_1; 98478, R M_3, L M_3; 109969, R M^3. **SC271**: UM 73589, L P^4. **SC273**: UM 73659, L M_3 tal.; 73663, R P_4, M_{2-3}, L M_3. **SC275**: UM 73672, parts of M_1, M_2; 73675, L M^1?, P^4 frag. **SC362 Q.**: UM 110094, L M^1. **SC370**: UM 108414, L M^3. **SC379**: UM 108583, L M^3. **SC380**: UM 110028, incisor, L M_3. **SC386**: UM 108504, L M^3; 108513, L M_3. **SC389**: UM 108519, L P^4, M^3; 108540, R P^4, M^x, R P_4, M_{2-3}, assoc. **SC390**: UM 108546, L M_2. **SC407**: UM 108913, R P_3 frag., P_4. See Thewissen (1990) for additional specimens in the YPM collections.

Phenacodus intermedius Granger, 1915

Phenacodus intermedius Granger, 1915, p. 340. Thewissen, 1990, p. 59.

Holotype.— AMNH 15761, palate with left M^{2-3}, right P^4-M^2, left dentary with P_3-M_2, M_3 fragment, right dentary with P_4-M_3, from "Gray Bull beds, Five Mile Creek, Bighorn basin," Wyoming (Granger, 1915). Probably from the *Haplomylus-Ectocion* zone of the Wasatchian (Thewissen, 1990).

Biostratigraphic occurrences in Bighorn Basin.— Clarkforkian and Wasatchian zones.

Description and discussion.— In the most recent revision of the Phenacodontidae, Thewissen (1990) provided descriptions and figures of *Phenacodus intermedius*, as well as references to previous work. Differences between *P. intermedius* and *P. grangeri* were discussed in the *P. grangeri* section. This section summarizes specimens in the UM collections currently known from the Rodentia zone.

Measurements for P^4 (mm).— Rodentia zone — **SC179**, UM 68754: L = 10.7, W = 11.3. UM 71612: L = 9.8, W = 10.6. **SC362**, UM 95844: L = 10.5, W = 11.6. **SC250**, UM 71805: L = 11.4, W = 12.8. Measuring techniques follow those of Thewissen (1990).

Referred specimens from the Rodentia zone.— **FG041**: UM 77287, L M^1 or M^2; 85273, R M_3. **SC082**: UM 66198, L M_3. **SC169**: UM 68404, R P^4, M^x frag., crushed M_x; 68405, L P^4. **SC171**: UM 68408, L dent. M_2; 68416, L M^{1-2}, parts of R P^4, M^2; 68422, R dent. P_4-M_2. **SC172**: UM 71373, R M_3 tal. **SC173**: UM 68431, L M_3, R M_x part; 68433, R M^3. **SC177**:

UM 68727, L P_4, R M_3, dent. frags. **SC179**: UM 68749, R M_3, and M_x frags.; 68753, L M_{1-2}, R P_4, M_{2-3}; 68754, L max. C^1-P^1, P^3-M^1, R max. P^4-M^3; 68755, R P^3; 71612, P^4, M_3 tal. frag.; 71619, L dent. P_4-M_1 tri. **SC215**: UM 69929, L M_3 tal. **SC217**: UM 101136, R M_x tal. **SC226**: UM 71297, L dent. P_4-M_2, R dent. M_{1-2}; 71301, L dent. M_{1-3}, R P_3, M_3 tal.; 71313, L M_3 tal. **SC249**: UM 71797, L M^3, M_{1-3}; 71798, M^x frags. **SC250**: UM 71800, R M^{2-3} partial; 71805, L max. P^4-M^1, R M^1; 71807, R P_4, M_{1-2} (heavy wear), L P_4 tri.; 71809, R M^3 partial. **SC251**: UM 71822, R dent. M_{2-3}. **SC257**: UM 73330, L P^4, L M^3, L M^3, phalanges, metapodials, vertebrae, 2 assoc. individuals; 73336, L dent. M_1 tri., M_2; 73338, R M^3, M^x frag.; 73340, R dent. P_{3-4}; 73361, R M_2 tal., M_3. **SC260**: UM 73720, R P_4 frag. **SC285**: UM 73721, L P_3-M_3, R P_3, M_{2-3}. **SC286**: UM 73724, R C_1. **SC358**: UM 88228, L dent. M_x. **SC362**: UM 95842, L P_4, M_2, M_3 tal., assoc.; 95844, R M^3, L P^4, L P_4; 95846, L M_3 tal.; 101913, P^4, R P_3, M_3, assoc.?; 108330, L M^1 or M^2, R P^4 frag.; 109268, R M_2; 110091, L P_4; 110096, L dP^4; 110142, R M^3. **SC403**: UM 108232, R M^2.

ECTOCION Cope, 1882

Ectocion collinus Russell, 1929

Ectocion collinus Russell 1929, p. 177.
Ectocion collinus (in part), Thewissen, 1990, p. 25.

Holotype.— UALVP 118, a partial right M^3 from the Cochrane I locality, Alberta, Canada; earliest Tiffanian in age.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description.— Descriptions and figures of the holotype and other specimens, and references to previous work were provide by Thewissen (1990).

Discussion.— Three specimens (UM 58125; YPM-PU 14961, 20856) from the Bighorn Basin were identified as *Ectocion collinus* by Thewissen (1990). According to him, lower teeth of *E. collinus* can be distinguished from those of *E. cedrus* by their larger size and by the consistent lack of a metaconid on P_3. Both species were identified by Thewissen at Jepsen Quarry in Foster Gulch (not to be confused with Jepsen Valley Quarry in Silver Coulee), which appears to be correlative to the *Plesiadapis rex* zone (Gingerich, 1976). YPM-PU 14961 (Thewissen, 1990, Fig. 6) from Jepsen Quarry has molars that are slightly wider, and a P_4 that is longer than any of *E. cedrus* from Cedar Point Quarry (Thewissen, 1990, Table A-5). The P_3 also lacks a metaconid, but so do some specimens of *E. cedrus*. The size of YPM-PU 14961 is easily within the range of *E. collinus*, and I provisionally follow Thewissen's identification.

UM 58125 is identified below as cf. *Ectocion*. I have not seen YPM-PU 20856.

Dental measurements (mm).— YPM-PU 14961 (cast): P_2, L = 3.65, W = 3.35; P_3, L = 5.20, W = 3.35; P_4, L = 7.35, W = 4.2*; M_1, L = 6.35, tri. W = 5.2; M_2, L = 7.10, tri. W = 5.95; M^3, L = 7.60, tri. W = 5.15.

Referred specimen.— **Jepsen Q.**: YPM-PU 14961, R dent. P_2-M_3.

Ectocion cedrus Thewissen, 1990

Ectocion cedrus Thewissen, 1990, p. 29.

Holotype.— UM 82085, a left dentary with P_2-M_3, and alveoli for C_1, and P_1, from Cedar Point Quarry in the northern Bighorn Basin.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* (Ti-3) and *Plesiadapis churchilli* (Ti-4a) zones.

Description.— Descriptions and figures of the holotype and other specimens were provide by Thewissen (1990), as well as references to previous work.

Discussion.— *Ectocion cedrus* from the Bighorn Basin and elsewhere was described in detail by Thewissen (1990). Additional material included here is mostly fragmentary and adds little to our knowledge of the species. According to Thewissen, *E. cedrus* differs from the younger *E. mediotuber* in being smaller, in having smaller premolars relative to molar size, and in having a weaker hypoconid and higher paraconid on P_3. Unfortunately, the size ranges of *E. cedrus* and *E. mediotuber* largely overlap and identifications are difficult to make using small samples. I follow Thewissen in identifying teeth from Croc Tooth Quarry as *E. cedrus*, but I identify other teeth from the *Phenacolemur* zone as *E. mediotuber*. Croc Tooth Quarry is slightly older than other *Ectocion* bearing localities in the *Phenacolemur* zone. Many teeth from the other localities are too fragmentary for confident identification, however, and some could represent late occurrences of *E. cedrus* or an intermediate form.

Referred specimens.— **Cedar Point Q.**: UM 63096, R dent. M_{2-3}; 63103, M^2, M^2 unassoc.; 64397, R dent. C_1 root, P_1-M_3; 64398, R dent. M_{2-3}; 64401, R dent. P_{3-4}; 64408, L dent. frags., M_{1-3}; 64418, R dent. M_2; 64447, L dent. frag., M_{2-3}; 64450, R dent. P_3-M_2; 64451, R dent. M_3; 64506, L dent. dP_{3-4}; 64511, L dent. M_3; 64512, L dent. M_{1-3}; 64522, R dent. M_{2-3} (M_3 erupting); 64527, iso. teeth; 64556, R max. P^3-M^3; 64563, R dent. frag., P_4-M_1; 64633, L dent. M_{1-3}; 71827, R dent. M_1 or M_2; 71829, L dent. M_{2-3}; 82064, L dent. dP_4-M_2; 82089, R dent. M_{2-3}; 82094, R dent. P_3-M_1; 83225, R dent. P_2-M_3; 83258, L max. P^4-M^3; 109874, L M_3; 109877, L M^3; 109878, L P^3; 109879, R P_4; 109880, L M^3; 109881, R P_3; 109964, R M^3. **Croc Tooth Q.** (FG028): UM 77038, R dP_4, R M_1, R M_2 unassoc.; 109953, R P_4; 109954, L P_4. **Divide Q.** (FG046): UM 77267, L M^2, L M_2, L M_1 part, unassoc.; 77279, R M_2; 80584, R P^3, R dP_4, R M^2 unassoc.; 83215, R dent. M_{2-3}; 83217, R dent. C_1, dP_{2-4}, M_{1-2}; 83238, L dent. M_3; 83270, L P^3, L M^1, R M^1, L M^2, R M^2, R M^2, R M_1, R M_2, unassoc.; 85271, R dent. dP_4-M_2; 85402, R max. P^3-M^3; 85409, R max. M^{1-2}; 85415, R M_1; 85814, R P_3; 85914, R lower; 85926, R dent. M_{1-3}; 86246, R dent. P_2, dP_4-M_1; 91322, R M_1; 91328, L M_2; 91333, L max. dP^{2-4}; 91334, L dent. M_{1-3}; 92260, L M^1; 92262, R M_1; 92267, L M^2; 92268, L P^3; 104980, L P^4; 108381, L M^1; 109882, R M_3; 109883, R M_3; 109948, R M_3; 109949, R P_4; 109950, L P^4; 109951, L M^3; 109952, L M^3; 109955, R M_3; 109956, L M_3; 109957, L M_3; 109958, L M_3; 109959, R M^3; 109960, R P^4; 109962, L P_3; 109963, L P^3. **Long Draw Q.**: UM 63277, L M^3, R dP_4, R M_1 tri. **SC241**: UM 110164, R M_3. **SC261**: UM 73706, R P^3; 110292, R M_3. **SC262**: UM 73397, L dent. P_4-M_1, M_3; 73399, L dent. M_1, M_3, R dent.

P_3. **SC263**: UM 109624, R M^3 partial. **SC269**: UM 110162, L M_3. **SC424**: UM 110934, L dent. M_1 tal. See Thewissen (1990) for additional specimens in other collections.

Ectocion mediotuber Thewissen, 1990

Ectocion mediotuber Thewissen, 1990, p. 31.

Holotype.— YPM-PU 17718, a left dentary with P_2-M_3, from Princeton Quarry in the northern Bighorn Basin.

Biostratigraphic occurrences in Bighorn Basin.— *Phenacolemur* (Ti-4b), *Probathyopsis* (Ti-5a), *Plesiadapis simonsi* (Ti-5b), and *Plesiadapis gingerichi* (Ti-6) zones.

Description.— Thewissen (1990) provided descriptions and figures of the holotype and other specimens, as well as references to previous work.

Discussion.— *Ectocion mediotuber* from the Bighorn Basin and elsewhere was described in detail by Thewissen (1990). Additional material included here is mostly fragmentary and adds little to our knowledge of the species. I have included all specimens from the *Phenacolemur* zone in *Ectocion mediotuber*, except those from Croc Tooth Quarry, following Thewissen (1990). Croc Tooth Quarry is slightly older than other *Ectocion* bearing localities in Ti-4b and appears to contain *E. cedrus*. Some specimens from the *Phenacolemur* zone, such as UM 71325, dP^{3-4}, are probably also within the variation of *E. cedrus*. Although both species could be present in this interval, this observation may simply reflect an overlap in variability between the species.

Differences between *E. mediotuber* and the younger *E. osbornianus* are discussed in the *E. osbornianus* section.

Referred specimens.— **FG004**: UM 73984, L P^4, R M^3, assoc. **FG009**: UM 74036, R M^2. **FG048**: UM 77303, R dent. M_2. **Fossil Hollow** (SC198): UM 69243, R P^4, M^x, L M_3 assoc.; 79865, R max. dP^3, dP^4 frag., M^x frag.; 79880, R M^{2-3}; 108899, M^x; 110324, L M_2; 110325, R P_2. **SC165**: UM 108410, C, L P^4, L M^3, L M_3; 108440, L M_3 tal. **SC187**: UM 68854, L M^x, M^3 assoc.; 80359, L dent. P_4, M_1 tal., M_2 tri.; 85239, L dent. M_1 tal., M_2. **SC199**: UM 69250, R dent. M_{1-2}. **SC228**: UM 71320, M_3; 71704, R max. M^2; 83110, L dent. M_{2-3}; 110280, L P^4, P_4 partials; 110295, L dP^4, M_x frags. **SC242**: UM 71711, R M_x; 71712, R M_3. **SC246**: UM 71737, L M_2 (part), L M_3. **SC266**: UM 73508, R dent. M_{1-2}. **SC270**: UM 73574, L M^1 (part), M^2, R M^2; 73581, L M^{2-3} assoc.; 73676, palate L M^{1-3}, R P^4-M^3, L dent. M_{1-2}; 98471, R dent. P_4, M^x frag.; 98474, R max. M^{1-2} crushed; 98478, L P^4. **SC273**: UM 73657, L dent. P_4-M_1; 73664, L max. I^x, P^3-M^3; 73666, L max. P^3-M^2. **SC274**: UM 73668, L dent. M_{1-2}. **SC275**: UM 73674, L dent. P_4-M_1. **SC277**: UM 73683, R P^4, M^1 (part), M_2. **SC384**: UM 108501, R M^3. **SC389**: UM 109267, R and L dent. frags.; 109414, R M_1?; 109415, R M_2?. **SC390**: UM 108461, L M_1, M_x frags. **SC419**: UM 110071, L max. M^{1-3}; 110082, R M_3 partial. **Y2K Q.** (SC389): UM 108523, M_2 tal.; 108524, R M^3; 108525, L dP_4 tri.; 109164, L P^3 frag.; 109247, L M^3; 109390, L max. P^3-M^3; 110003, L P_3 partial; 110017, R M_1; 110025, L M_3. **Zalmout Q.** (SC389): UM 109650, R M_2.

Ectocion osbornianus (Cope, 1882)

Oligotomus osbornianus Cope, 1882a, p. 182.
Ectocion osbornianus, Thewissen, 1990, p. 35.

Holotype.— AMNH 4409, partial dentaries and maxillae with left P^3 fragment, P^4-M^2, P_3, and right P^4, M^1 fragment, and M_2, from the "Gray Bull beds" of the Bighorn Basin, Wyoming (Granger, 1915, p. 352).

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis gingerichi* (Ti-6), and Clarkforkian and Wasatchian zones.

Description.— Rose (1981a) and Thewissen (1990) provided descriptions and figures of *E. osbornianus*, *sensu* Thewissen (1990). West (1971, 1976) also provided descriptions and figures of deciduous and permanent dentitions, but some specimens were later transferred to *E. mediotuber* by Thewissen (1990).

Discussion.— New material collected in the Bighorn Basin since Thewissen's (1990) revision of the Phenacodontidae extends the range of *Ectocion osbornianus* downward into the late Tiffanian. As defined by Thewissen (1990), *E. osbornianus* differs from the older *E. mediotuber* in having a larger P_3 with a larger, more developed protoconid and hypoconid, and a P_4 with a wider trigonid basin and a paraconid that is typically larger than in *E. mediotuber*. Based on his measurements, P_4s of *E. osbornianus* from the *Plesiadapis gingerichi* zone are also about 14% longer and wider on average than those of *E. mediotuber*. However, the size difference is only about 7% greater for P_4s from the younger *Plesiadapis cookei* zone.

A single P_3 of *Ectocion* from Y2K Quarry is the only one known from the *Plesiadapis simonsi* zone. UM 110003 is partial but has a weak hypoconid and compares favorably in size with *E. mediotuber*. It is outside the size range of most, if not all *E. osbornianus*. Two P_3s from SC-191 in the *Plesiadapis gingerichi* zone represent the lowest confident occurrences of *E. osbornianus*. They are larger than any of *E. mediotuber* reported by Thewissen (n = 7) and the hypoconids are high and well-developed. The new teeth from SC-191 extend the range of *E. osbornianus* downward by about 105 m, or ~200 kyr into the late Tiffanian (based on an accumulation rate of 546 m/myr, Table 1).

Measurements for P_3 (mm).— **SC-179**, UM 71621: L = 7.15, W = 4.20. UM 101828: L = 6.95, W = 4.10. UM 108347: L = 7.05, W = 4.05. UM 108352: L = 6.95, W = 4.30. **SC-191**, UM 108286: L = 7.25, W = 4.55. UM 108293: L = 6.70, W = 4.00. **SC-215**, UM 69924: L = 6.65, W = 4.15. **SC-217**, UM 101135: L = 7.25, W = 4.30. **SC-226**, UM 101134: L = 6.75, W = 3.95. **SC-259**, UM 73373: L = 7.65, W = 4.65. **SC-380**, UM 108299: L = 6.45, W = 3.95. **SC-411**, UM 108943: L = 6.70, W = 3.95. Measuring techniques follow those of Thewissen (1990).

Referred specimens from the Plesiadapis gingerichi *and Rodentia zones*.— **Bluff Top Q.** (SC379): UM 108254, L M^2; 108275, L M_2; 108616, M^x frag.; 108617, L P^4, partial; 108618, L M^3; 108621, L M^3. **FG037**: UM 85247, L max. M^{1-2}; 85248, R dent. M_2. **FG041**: UM 77290, R M^1 or M^2. **SC082**: UM 66197, L max. M^{1-3}, R P_3; 108475, R P_4. **SC083**: UM 108665, M_x tri. **SC085**: UM 96148, L max. P^3, M^3. **SC086**: UM 66215, C^1, L dP^4-M^2, R M^2, R dP_4; 66216, R dent. M_{1-2}; 83184, L dent. M_{2-3}.

SC156: UM 68026, L P^4, M^2, R M^3. **SC171**: UM 68410, L max. M^{1-2}, R max. M^{2-3}; 68412, R dent. P_4, M_2, R M^2; 68413, L dent. P_4-M_2; 68415, L dent. P_3 (part), P_4-M_1; 68418, L dent. P_4-M_1, R M_3; 71773, R dent. M_{2-3}; 71777, R dent. M_{2-3}. **SC172**: UM 68424, R max. P^{3-4}, L dent. C_1-M_3, R dent. P_1-M_3; 68425, L dent. M_{1-3}, R M_3; 68427, R dent. P_4-M_2; 71372, R dent. M_{1-3}; 83162, L P^4, M^3, assoc.; 83164, L dP_4, L P_4, L M^1, unassoc. **SC173**: UM 68433, R dent. ?P_{1-2}, P_4-M_1, in concretion; 68435, R M^3, L dent. M_{1-3}. **SC179**: UM 68750, L dent. M_{1-3}, L max. M^3; 68751, L max. M^{1-2}; 68752, L max. P^4-M^3, R M^{2-3}; 71613, R dent. M_{2-3}; 71616, L dent. P_4, R P^3; 71617, L dent. dP_4-M_2, R M_3; 71618, L dent. M_{1-3}; 71621, R dent. P_{3-4}, M_1 tri.; 71622, L M_2; 71623, R M_3; 95847, R dent. M_{1-2}; 95848, R dent. P_4-M_3; 101828, R P_3, M_1; 101829, L dent. M_{2-3}; 101830, L dent. M_{1-2}; 101832, R P^4, L M^x, M_2, L M_3; 102426, L max. M^{2-3}; 102427, L M^3; 108343, R M^x; 108345, L dent. P_4, M_{1-2}; 108346, L P_4, M_{2-3}, assoc.; 108347, R P_3, R P^3, R M^3, assoc.; 108350, L M_3; 108352, R P_3; 109272, R max. M^{2-3}; 109273, L M_2; 109274, L M_3; 109276, R M_2; 109277, R P^4; 110050, R M_3. **SC180**: UM 68757, R M^2, L M_3. **SC181**: UM 71625, R dent. M_2 partial; 71626, L max. dP^{3-4}, M^1; 108663, L M^2; 109600, R M_2; 110119, R M^3 partial. **SC191**: UM 68891, L dent. P_4 tri., M_1, M_3; 108283, R M^x frag.; 108286, R P_3; 108293, R dent. P_{3-4}. **SC193**: UM 108418, R dent. M_1, P^3. **SC215**: UM 69921, L max. P^4-M^2; 69922, L max. M^{1-3}; 69924, L dent. P_3-M_2; 69926, R max. M^{2-3}; 69927, R max. P^4-M^3, R M^1. **SC217**: UM 100364, R M^{2-3}; 100366, R dent. M_2; 100367, L dent. M_{1-2}; 101135, L dent. P_{3-4}. **SC226**: UM 71296, L dent. M_2, R P^4; 71298, L dent. P_4-M_1; 71308, L dent. M_1 tal., M_{2-3}; 110134, R P_3, M_x frags. **SC227**: UM 71314, R dent. P_4-M_2; 71315, R dent. M_{2-3}; 71358, L max. M^{1-3}; 73705, R M^x, M^3 assoc. **SC247**: UM 71790, R P_4. **SC250**: UM 71804, R dent. P_1-M_3, I_2-C_1 roots, postcrania; 71806, L M^x, R P^4, M_3; 71814, R dent. P_4, M_{2-3}, L dent. M_2; 71815, L dent. M_{1-3}, R dent. M_1. **SC251**: UM 71818, L dent. M_{1-2}, R dent. dP_4-M_2. **SC257**: UM 73335, L M_2 (part), M_3; 73341, L dent. M_2; 73359, L dent. M_{2-3}; 73362, L max. M^1, M^2 partial. **SC259**: UM 73373, L dent. P_4-M_1, M_3, R dent. P_3-M_2; 73374, L P_4 (part), assoc. frags. **SC260**: UM 73525, R dP^4, L M^2, assoc.; 73715, L max. M^{1-2}; 73718, L dent. M_1, M_2 (part). **SC286**: UM 73723, R P^4, M^2, L M^3, L M_1, M_3, assoc. **SC362 Q.**: UM 101912, R dent. M_{1-2}; 108325, L M_{1-3}, dent. frags.; 108327, R M^3; 108328, L M_2; 108331, R M^3; 108332, R M_2; 110089, L dent. frag., M_2; 110090, R dent. P_4-M_2, M_3 tal.; 110092, L M^x; 110093, R M_2. **SC373**: UM 108243, L M^1; 108244, L P^4. **SC376**: UM 108233, R M^2, M^3 frags.; 108234, L P^4, M^1, P_4. **SC380**: UM 108236, L P^4; 108299, R dent. P_{3-4}, M_{1-2}; L P_3, M_2; 108301, L M_2; 108302, M_x frags. **SC399**: UM 108593, canine, L dP_4, M_1, M_2 tal., assoc.; 108596, L dent. frag., P_4 tal., M_1; 108602, L P^4; 108603, L max. M^{1-2}, P^4 and M^3 roots; 108606, R P_4; 108608, L M_2. **SC407**: UM 108910, R dent. frag., P_4 tal., M_1; 108914, L dent. M_{1-3}; 108920, L dent. frags.; 108921, R dent. M_1 tri., M_2. **SC408**: UM 108941, R M^3. **SC410**: UM 108924, R P^3; 108925, L M^x. **SC411**: UM 108943, R max. P^3-M^2, P_3, M_2, L M_3; 108945, L M^1; 108949, L M_2. **SC413**: UM 109611, L M_2; 109614, M^x frag.; 109616, L dent. frags., M_{1-2}. **SC414**: UM 109610, L M^1. See Thewissen (1990) for additional specimens from the Clarkforkian and Wasatchian.

Cf. *Ectocion*

Ectocion collinus (in part), Thewissen, 1990, p. 29.

Biostratigraphic occurrences in Bighorn Basin.— Early Tiffanian?

Description and discussion.— Two specimens from a chert pebble conglomerate in the lower part of the Fort Union Formation (Fig. 6) may represent a new species of *Ectocion* or another phenacodontid. UM 58125, a right dentary preserving P_4-M_3, was identified as *Ectocion collinus* by Thewissen (1990). Although it is similar to specimens of *E. collinus* from Douglass Quarry (e.g., YPM-PU 14603), the M_2 trigonid is wider than the talonid and the crown has an inflated appearance. These features are more typical of *Tetraclaenodon* and *Phenacodus*. The molars are within the uppermost size range of *E. collinus* from Douglass Quarry (Thewissen, 1990, Table A-4). An additional specimen (UM 95331) collected after Thewissen's study, however, is above the size range reported for *E. collinus*. Both specimens are just below the size ranges of *T. puercensis* from Rock Bench Quarry (Thewissen, 1990, Table A-1) and are smaller than those of *P. matthewi* (AMNH 17191) from southern Colorado (see Thewissen, 1990).

The chert pebble conglomerate also yielded a specimen identified as *Phenacodus* cf. *P. grangeri* and is latest Torrejonian or early Tiffanian in age, as discussed above.

Dental measurements (mm).— UM 58125: P_4, L = 6.85, W = 4.55; M_1, L = 6.73, tri. W = 5.30; M_2, L = 7.00, tri. W = 5.90; UM 95331, M_2, L = 7.60, tri. W = 5.90.

Referred specimens.— **SC337**: UM 58125, R dent. P_4-M_3; 95331, L M_2 tri., R M_2.

Order ARCTOSTYLOPIDA
Cifelli, Schaff, and McKenna, 1989

Family ARCTOSTYLOPIDAE Schlosser, 1923

ARCTOSTYLOPS Matthew, 1915a

Arctostylops steini Matthew, 1915a

Arctostylops steini Matthew, 1915a, p. 429.

Holotype.— AMNH 16830, left dentary with P_3-M_3; probably from the *Copecion* zone (Cf-3) (Rose, 1981a, p. 97).

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a), *Plesiadapis simonsi* (Ti-5b), *Plesiadapis cookei* (Cf-2), and *Copecion* (Cf-3) zones.

Description and discussion.— One of the most interesting and enigmatic late Paleocene species is *Arctostylops steini*. Descriptions of *A. steini* were provided by Matthew (1915a), Rose (1981a), and Cifelli et al. (1989). The species is known from only two specimens of Tiffanian age, both of which include partial skulls and dentaries (Jepsen and Woodburne, 1969; Cifelli et al., 1989). The origin and taxonomic position of *Arctostylops* has been controversial. *Arctostylops* has traditionally been allied with the South American Notoungulata (e.g., Matthew, 1915a; Gingerich, 1985). Cifelli et al. (1989), however, argued that *Arctostylops* was most closely related to Asian arctostylopids and that its resemblance to Notoungulata was secondarily derived. More recently, Bloch (2001), and Kondrashov and Lucas (2004) considered *Arctostylops* a notoungulate, which I follow here. The most complete specimens of *Arctostylops steini* yet known, including a partial skeleton and juvenile dentitions, were recently recovered from freshwater limestones of late Clarkforkian age, but have not been described in publication (see dissertation by Bloch, 2001, pp. 100-105, Fig. 10).

Referred specimens.— **Five meters from Princeton Q.** (SC187): MCZ 20004, anterior part of skull and associated left and right dentaries with nearly complete dentition (I^{2-3}, partial, C^1-M^3, I_2-M_3). **Near SC144**: YPM-PU 20397, skull and dentary frags., poor preservation.

Order MESONYCHIA Van Valen, 1969
Family MESONYCHIDAE Cope, 1875

DISSACUS Cope, 1881b

Dissacus argenteus O'Leary and Rose, 1995

Dissacus argenteus O'Leary and Rose, 1995, p. 152.

Holotype.— YPM-PU 16135, left dentary with C_1, P_4-M_1, right dentary with C_1, P_2, P_4-M_3, and alveoli for P_1 and P_3, left C^1, and right M^1; from Princeton Quarry, northern Bighorn Basin, Wyoming. Late Tiffanian, *Probathyopsis* zone.

Biostratigraphic occurrences in Bighorn Basin.— *Probathyopsis* (Ti-5a) and Rodentia (Cf-1) zones.

Description.— A description of the holotype was provided by O'Leary and Rose (1995).

Discussion.— O'Leary and Rose (1995) distinguished *Dissacus argenteus* from *D. praenuntius* by its smaller size (~15%) and shorter P_2 that has a convex, rather than flat, mesial border. Variability in *D. argenteus* has not been documented. Specimens included here are identified based on their size relative to *D. praenuntius* of Clarkforkian age. *Dissacus argenteus* is known with confidence only from Princeton Quarry and the surrounding area (SC-187), but two molars of latest Tiffanian and early Clarkforkian age (UM 108255 and 73343, respectively) appear to be younger occurrences of the species. The teeth are very similar to one another in size and form, and are either first or second molars. Both are below the size ranges for M_1 or M_2 reported for *D. praenuntius* by O'Leary and Rose (1995) and Rose (1981a), and are about 20% smaller than the means reported by Rose. The teeth are about 10% shorter than in the holotype of *D. argenteus* and proportionally wider, based on data from O'Leary and Rose (1995). Although these teeth are smaller than the holotype, they are presumably within the size variability of *D. argenteus*. If these teeth are correctly identified, *Dissacus argenteus* overlaps temporally with *D. praenuntius* in the latest Tiffanian and early Clarkforkian. Both species occur together at Bluff Top Quarry.

Dental measurements (mm).— UM 73343: M_1 or M_2, L = 11.60, tri. W = 6.05. UM 73712: M^1 or M^2, L = 11.50. UM 108255: M_1 or M_2, L = 11.85, tri. W = 6.35. UM 110317: M_3, L = 9.75, tri. W = 4.70.

Referred specimens.— **Bluff Top Q.** (SC379): UM 108255, R M_1 or M_2. **SC187**: UM 110317, L M_3. **SC258**: UM 73343, L C_1, M_1 or M_2. **SC284**: UM 73712, R C_1, M^1 or M^2. **Princeton Q.**: YPM-PU 13924, R M^1?, and three additional uncataloged isolated teeth (O'Leary and Rose, 1995).

Dissacus praenuntius Matthew, 1915b

Dissacus praenuntius Matthew, 1915b, p. 87.

Holotype.— AMNH 16069, partial left M^1, P_4, partial right and left lower molars, distal humerus, patella, and two phalanges; from the head of Big Sand Coulee, late Clarkforkian in age (Rose, 1981a).

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis gingerichi* (Ti-6) and Clarkforkian zones.

Description.— The holotype was briefly described by Matthew (1915b) and the M^1 and P_4 were illustrated by Simpson (1937c). Additional specimens were described by Rose (1981a), Gingerich (1989), and O'Leary and Rose (1995).

Discussion.— O'Leary and Rose (1995) distinguished *Dissacus praenuntius* from *D. argenteus* by its larger size and longer P_2 that has a flat, rather than convex, mesial border. *Dissacus argenteus* is about 15% smaller. Clarkforkian specimens were described by Rose (1981a) and I included this section to document an early occurrence of the species. UM 108619 is an M_1 or M_2 from the latest Tiffanian and is close to the mean length (M_{1-2}, L = 14.31, n = 9; W = 6.73, n = 8) reported by Rose for M_{1-2}, but is wider than most. It compares closely to other specimens in the UM collections and is probably too large to be *D. argenteus*.

Dental measurements (mm).— UM 71789: P_3, L = 12.25, W = 6.35. UM 108619: M_1 or M_2, L = 14.35, tri. W = 6.80.

Referred specimens from the Plesiadapis gingerichi and Rodentia zones.— **Bluff Top Q.** (SC379): UM 108619, L M_1 or M_2. **SC247**: UM 71789, L dent., L P_3, M_1 (part), M_2, R P_3, parts of other teeth. See Rose (1981a) for additional specimens from the Clarkforkian.

Dissacus cf. *D. navajovius*

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* (Ti-3) and *Plesiadapis churchilli* (Ti-4a) zones.

Description and discussion.— Two P^4s, one from Divide Quarry and one from Cedar Point Quarry, are structurally close to those of *Dissacus navajovius*, but are slightly larger. The P^4s are probably within the size range of *D. praenuntius*, but differ in having a deeper valley between the protocone and paracone, a smaller metacone that is positioned lower on the crown, and a posteriorly inclined paracone. UM 83224 is probably a P_2 and is the size of P_2s of *D. praenuntius*. It differs in being slightly narrower and in having a higher, more acute crown. These teeth are probably too large to belong to *D. argenteus* but may be within the upper size range of *D. navajovius*. Better material is needed for a confident identification.

Dental measurements (mm).— UM 83224: P_2, L = 12.50, W = 5.00. UM 83230: P^4, L = 12.6*, W = 9.1*. UM 86239: P^4, L = 12.1, W = 9.75.

Referred specimens.— **Cedar Point Q.**: UM 83230, R P^4. **Divide Q.** (FG046): UM 83224, R P_2; 86239, R P^4.

Pachyaena?

Dissacus sp., Rose, 1981a, p. 152.

Biostratigraphic occurrences in Bighorn Basin.— *Plesiadapis rex* zone (Ti-3).

Description and discussion.— UM 64510 was first noted by Rose (1981a) who suggested that it could belong to a species of *Dissacus* near *saurognathus* (now in *Ankalagon*) or to an early species of *Pachyaena*. UM 64510 is virtually indistinguishable from upper molars of *Pachyaena ossifraga* in the UM collections (e.g., UM 94783), but is slightly smaller. It is also about the size expected for *A*. *saurognathus*, as Rose pointed out. *Ankalagon* is known only from the Torrejonian of the San Juan Basin and *Pachyaena* is known only from the Eocene. This tooth is clearly not adequate to extend the ranges of either, but is important because it documents the presence of a large mesonychid that coexisted with the smaller *D*. cf. *D*. *praenuntius*.

Dental measurements (mm).— UM 64510: P^4, L = 19*, W = 20.9.

Referred specimen.— **Cedar Point Q.**: UM 64510, L M^1 or M^2.

IV

MAMMALIAN DIVERSITY AND CLIMATE CHANGE

INTRODUCTION

The idea that climate influences, or even drives mammalian evolution has been a popular theme in paleobiology (e.g., Vrba, 1992, 1993; Barnosky et al., 2003). Climate may affect a variety of faunal attributes, including the relative abundance of species, taxonomic composition, mean body size, and species diversity. This chapter focuses on the last of these and investigates the relationship between mammalian diversity (species richness) and climate from the middle to the end Paleocene (Torrejonian to late Clarkforkian; Fig. 7). I focus exclusively on changes in alpha diversity in faunas from the Bighorn and Crazy Mountains basins (BCM), which together form a long northwest-southeast trending syncline between northwestern Wyoming and south-central Montana (Gingerich, 1983b).

Several authors have noted a decline in mammalian diversity and evenness in the Tiffanian followed by increased diversity and evenness in the Clarkforkian or Wasatchian, and suggested that this may follow cooling and warming trends (Rose, 1981a, b; Krause and Maas, 1990; Maas et al., 1995). They cautioned, however, that diversity estimates may be biased by factors such as sample size and differences in depositional environment. Others have raised similar concerns, noting higher diversity in some Canadian faunas of Tiffanian age (e.g., Scott, 2005). Regression of species diversity (number of species) on sample size (number of specimens) in BCM faunas shows that these variables are highly correlated ($p = 0.02$) and suggests that about 40% ($r^2 = 0.40$) of the variance in diversity can be explained by differences in sample size (Fig. 61). I attempt to correct for this bias by standardizing sample size using rarefaction and by applying different methods for counting the number of individuals in each sample based on collecting methods and taphonomy.

There is general agreement that the early Paleocene (Danian; Puercan and Torrejonian) climate was subtropical or warm temperate at mid-latitudes, while cooler, more temperate conditions prevailed in the middle Paleocene (Selandian, Ti-1 to Ti-4a). This was followed by a warming trend in the late Paleocene (Thanetian; late Tiffanian and Clarkforkian). These interpretations are based on stable oxygen isotopes in marine carbonates, paleobotanical data, and other evidence such as the presence of alligators (Wolfe and Hopkins, 1967; Hickey, 1980; Wing et al., 1991; Markwick, 1998, 1999; Wilf, 2000; Zachos et al., 2001; Johnson and Ellis, 2002). A few Torrejonian and Tiffanian floras have been studied but these are not adequate for estimating temperatures zone by zone. Thus, I use the marine benthic oxygen isotope record compiled by Zachos et al. (2001) as a proxy for continental climate change. The temperatures derived from benthic carbonates reflect surface water temperatures at high latitudes where water descends as it cools. Although this may not be a good proxy for absolute continental temperature, it should accurately reflect relative changes in global temperature. I correlate the marine record to the Bighorn Basin using recently calibrated geochronologic ages for biozone boundaries (Secord et al., 2006).

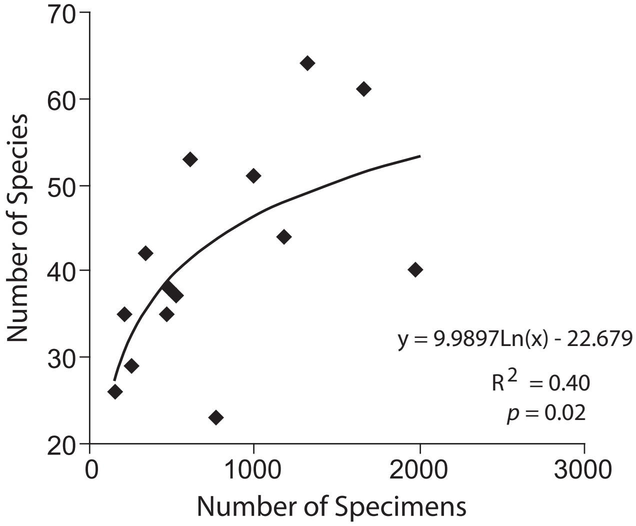


FIGURE 61 — Scatter plot of number of specimens versus number of species from quarries and surface collections in the Bighorn and Crazy Mountains basins. Logarithmic trend line fit to points. Approximately 40% of variance in species diversity is explained by sample size.

This chapter begins with a discussion of previous studies of Paleocene mammalian diversity. I then present the methodology used for grouping faunas into three depositional environments, counting individuals in these environments, and standardizing for sample size. A discussion of statistical methods follows. Results are presented next, followed by a discussion of interpretations, and then conclusions.

PREVIOUS DIVERSITY STUDIES

Rose (1981a,b) published the first detailed studies of mammalian diversity in the Paleocene. The work reported here relies in large part on his faunal lists and specimen counts, as well as those of Krause and Maas (1990). Rose included only BCM faunas in his analysis. He excluded samples from Scarritt and Princeton quarries (Fig. 7), however, because of a bias for small-bodied species. Both quarries occur in mudstone or fine-grained sandstone and tend to preserve teeth from shrew- to rabbit-sized mammals, contrasted with the coarser-grained clay-gall quarries that tend to preserve larger teeth (Krause and Maas, 1990, Fig. 5). He considered clay-gall samples from Gidley (To-2), Rock Bench (To-2), and Cedar Point (Ti-3) quarries to be relatively unbiased. Rose also excluded Douglass Quarry (Ti-1) because of its small sample size, but a much large sample is now available (Krause and Maas, 1990). Taphonomic differences among these quarries are discussed below.

Rose (1981a,b) calculated various diversity indices (Simpson, Shannon, Whittaker, rank-abundance plots) to investigate species richness and evenness. His results generally show a drop in richness and evenness from the Torrejonian to the Tiffanian continuing into the Clarkforkian, followed by increased richness, but relatively low evenness, in the early Wasatchian. He noted, however, that caution should be used in interpreting measures of diversity between the Paleocene quarries, and Clarkforkian and Wasatchian surface collections because of sorting and sampling differences. He suggested that if sampling were more complete in the Clarkforkian, an increase in richness might result. No direct correction was made for sample size. Rose (1981b) proposed that the general pattern of diversity change was partly due to changes in climate. He suggested that high diversity in the Torrejonian and Wasatchian coincided with warm equable conditions, while lower Tiffanian and Clarkforkian diversity was probably related to cooler temperatures. He noted that diversity closely paralleled mean annual temperature (MAT) estimates from leaf-margin analyses.

In a follow up to Rose's (1981a,b) work, Krause and Maas (1990) preformed a similar analysis using additional data. In particular, they had considerably larger samples from Douglass and Scaritt quarries of early Tiffanian age (Ti-1 and Ti-2, Fig. 7). They also included additional material from Holly's Microsite (SC-188), a quarry and wash site of middle Clarkforkian age. Like Scarritt and Princeton quarries, Holly's Microsite is also biased toward smaller tooth size. Krause and Maas (1990) concluded that the Torrejonian (Rock Bench Quarry) and the earliest Tiffanian (Douglass Quarry) had equally high diversity, based on diversity indices (Simpson, Shannon, Whittaker). They surmised that high species evenness at Douglass Quarry was representative of ecological stability, suggesting that the most pronounced Paleocene cooling occurred later. They suggested that because Cedar Point Quarry (Ti-3) was probably not strongly biased taphonomically, and exhibited very low diversity, cooling probably occurred between Ti-1 and Ti-3. Their Clarkforkian diversity estimates varied widely, but they found that when species from Holly's Microsite (Cf-2), Paint Creek (Cf-2), and surface collections were combined, Clarkforkian diversity was higher than was apparent in the data available to Rose (1981a,b). Higher diversity for the Clarkforkian was more consistent with Rose's suggestion of the influence of temperature on diversity.

The most recent diversity analyses that included Paleocene mammals were published by Alroy (2000a,b) and Alroy et al. (2000). Data were compiled from publications and standardized for sample size by subsampling faunal lists. The faunas were ordered by an algorithm called "maximum likelihood appearance event ordination" that reorders first and last appearances until a likelihood function using overlapping age ranges is maximized (Alroy, 2000a). This relative time scale was then calibrated with radioisotopic ages, although few were available for the Paleogene. A list showing the faunal ordering and bin content has never been published, although raw data are available online (Paleobiology Database: http://paleodb.org/). The database is continually evolving as new data are added, however, and a direct comparison of the faunal chronology used in these studies with more traditional chronologies may not be possible. In general, Alroy's diversity curves indicate an increasing diversity trend from the early to the middle Paleocene, followed by a decreasing tend reaching a low point in the late Paleocene. An increasing tend is then established in the late Paleocene that persists into the Eocene. Although it is not evident from their charts, Alroy et al. (2000) described a "crash" in diversity near the Tiffanian-Clarkforkian boundary, accompanied by the highest extinction rate of the dataset, which spanned most of the Cenozoic.

FOSSIL QUARRIES AND SURFACE COLLECTIONS

Data acquisition

Primary faunal lists and specimen counts for Gidley, Rock Bench, Cedar Point, and Princeton quarries are from Rose (1981a), Douglass and Scarritt quarries from Krause and Maas (1990), and Holly's Microsite from Krause (1986). Numerous subsequent amendments to these lists, including new species and taxonomic changes described here for Cedar Point and Princeton quarries were taken into account, but do not appreciably alter specimen counts. Revised faunal lists for Cedar Point Quarry, Princeton Quarry, and Holly's Microsite are given in Appendix I. *Phenacodus*, *Coryphodon*, and *Dipsalidictis* (*Oxyaena*) *aequidens* appeared in a faunal list for Holly's Microsite published by Krause (1986) but are excluded here because they appear to have been surface collected from the surrounding area (SC-188), based on museum records. Faunal lists for Divide Quarry, and Tiffanian and early Clarkforkian surface collections were compiled from specimens described here. Specimen counts for middle and late Clarkforkian surface collections are mostly from the UM paleontological database, provided courtesy of P. D. Gingerich.

Specimens included in this analysis consisted only of teeth and jaws, with the exception of two humeri of *Propalaeanodon* from Princeton Quarry (Rose, 1981a). Published specimen counts undoubtedly also consisted nearly entirely of dental material. Although postcranial material is present in all the quarry samples, associated teeth and postcrania are known for only a few Paleocene species. Postcrania could be sorted into taxonomic groups and assigned to species based on known dental material from the same quarry, but such a procedure has not been attempted for these quarries, and many identifications would be tenuous.

Changes in continental temperature were approximated using the marine benthic oxygen stable isotope record compiled by

Zachos et al. (2001). The geochronologic ages provided were based on Cande and Kent (1992, 1995). I recalibrated the age for each sample to the geomagnetic polarity time scale of Ogg and Smith (2004) by interpolating between magnetic polarity reversals using a cubic spline function (PetroPlot freeware, by Su, Y., Langmuir, C. H., and Asimow, P. D., 1999-2002). Temperatures were calculated using the calcite-water equation of Friedman and O'Neil (1977) and a mean δ^{18}O ocean composition of -1.2‰ for an ice-free world. It should be noted, however, that the analysis presented here is not dependent on the choice of equations or mean δ^{18}O ocean value.

Taphonomy and collecting bias

The fossils used in this study can be divided into three general groups reflecting their taphonomic and collection histories. I treat each of these as an "isotaphonomic" group (e.g., Clyde and Gingerich, 1998; Behrensmeyer et al., 2000), although some caveats follow. I refer to these groups as clay-gall quarries, mudstone quarries, and surface collections. Gidley, Rock Bench, Douglass, Cedar Point, and Divide quarries are clay-gall quarries (Fig. 7). In this type of quarry, fossils typically occur as a lag deposit, at or near the base of a channel sandstone. Fossils are preserved in a sandstone matrix, intimately associated with "clay galls." The term refers to curled clasts of clay derived from the drying and cracking of mud, and later embedded in a sand stratum (Bates and Jackson, 1984). Clasts of carbon and plant debris are also common occurrences in these deposits.

In his unpublished dissertation, Bartels (1987) studied quarry assemblages in the Bighorn Basin and concluded that bones and teeth in the clay-gall deposits probably accumulated in abandoned river channels. The bones and teeth were later mobilized during episodes of river avulsion when the river reclaimed the channel. The vertebrate remains were deposited as lag along with plant debris and clasts of clay that were ripped up from dried mud in the channels. This scenario is consistent with available evidence. Whether or not it is accepted, it is clear from fossil abrasion and the depositional settings that vertebrate material has undergone some transport. Associated material in the clay-gall quarries is rare or nonexistent (e.g., Gidley Quarry, Simpson, 1937b).

The mudstone quarries include Scarritt, Schaff, Princeton, Y2K, and Holly's Microsite. In contrast to the clay-gall deposits, the mudstone quarries show little or no evidence of water transport, and associated dental material is not uncommon. A partial leptictid skeleton was recovered from Princeton Quarry (Case, 1982, Fig. 42-1, p. 433) and even articulated postcranial remains have been reported (Bartels, 1987). At Y2K Quarry several jaws were recovered in pieces, separated by several centimeters of sediment, that fit together—indicating that some specimens were more complete when they entered the site. This is probably typical of the mudstone quarries. Y2K and Schaff quarries were not, however, included in the diversity analysis due to small sample size.

Bartels (1987) concluded that vertebrate remains at Princeton Quarry appeared to have accumulated in and at the margins of a small pond, possibly through the actions of a predator. He made a similar conclusion for Holly's Microsite: bones and teeth accumulated around a small pond, only though attrition and possibly the actions of a predator. He noted, however, the lack of evidence for predation in both sites. The only reason to infer predation is a bias for small body size, but this could be attributed to other processes such as low energy water transport. All of the mudstone quarries have a bias for small body-size, relative to the clay-gall quarries and surface collections (e.g., Krause and Maas, 1990, Fig. 5). A possible difference between Princeton Quarry and the other mudstone quarries is a lack of snail shells. Snail shells are common in the other quarries, but are not present in the few small samples of matrix I have seen from Princeton Quarry. One explanation is dissolution of shell due to slightly different geochemistry. Alternatively, Princeton Quarry may have a slightly different taphonomic history.

Lithologic differences between Scarritt Quarry and the other mudstone quarries are the greatest. The fossiliferous horizon at Scarritt Quarry is marked by a shell bed that ranges up to about 10 cm in thickness and is almost entirely composed of shell fragments (Simpson, 1937b). Bones and teeth occur in the shell bed and in claystone above and below the bed, along with more complete shells. Shell concentrations of this sort have not been reported from the other quarries. The fragmentary nature of the shells suggests that the bed formed by the winnowing of mud, which may have also attributed to mixing of vertebrate material into the shell bed. In spite of this lithologic difference, however, the processes responsible for bringing mammalian material into Scarritt Quarry did not necessarily differ appreciably from those of the other mudstone quarries. Simpson (1937b) noted a much higher frequency of association of upper and lower jaws at Scarritt Quarry than at Gidley Quarry (4 of 50 jaws [227 specimens], compared with 1 in >1000 specimens at Gidley), an attribute similar to the other mudstone quarries. I tentatively include Scarritt Quarry with the other mudstone quarries but note that because of its unusual lithology, diversity estimates could be less reliable.

The surface collections consist primarily of teeth and jaws that weathered from mudstones deposited by overbank flooding on ancient river floodplains. Because of the nature of surface collecting, these are probably the most biased samples included in the analysis. Unlike quarry samples where nearly all of the material in a concentration is recovered, regardless of size, surface collections are biased toward what is readily visible to the collector. As fossils work their way through the weathering horizon of a mudstone, small jaws are commonly fragmented into even smaller pieces that may never be exposed on the surface or may be too small to be easily seen. Plots of tooth size for surface collections and quarries illustrate the considerable bias toward large tooth-size in surface collections from the Bighorn Basin (Krause and Maas, 1990, Fig. 5).

The Bear Creek fauna (Cf-1), which contains several rare species (e.g., Rose, 1981a), was excluded from this analysis because of its unusual occurrence in a coal mine. Vertebrate fossils reportedly were found in an "argillaceous" layer directly above a coal seam (Simpson, 1928), a depositional environment that is quite different from the other quarries and appears to represent a rarely sampled environment (e.g., Gunnell and Bartels, 2001).

TABLE 59 — Rarefied species diversity and estimated mean temperature for quarries and surface collections from the Bighorn-Crazy Mountains basin sequence. Data are rarefied to 105 individuals. 95% confidence intervals (CI) are ±1.96 standard error of mean. Abbreviations: *CG*, clay-gall; *MS*, mudstone; *n*, number of individuals; *Q.*, Quarry; *RD*, rarefied species diversity; *Temp*, mean benthic marine temperature correlated to biozone (see Data acquisition section). Rarefaction done using Analytic Rarefaction (2001 version) software by Steve Holland (http://www.uga.edu/~strata/software/Software.html).

Quarry	Quarry Type	Biozone	Mean Age Ma	Mean Temp (°C)	95% CI ±	Quarry RD n=105	95% CI ±	Surface RD n=105	95% CI ±
—		Cf-3	56.01	9.33	0.37	—	—	27.3	5.55
Holly's Microsite	MS	Cf-2	56.36	8.62	0.65	34.7	0.94	29.4	5.17
—		Cf-1	56.75	8.83	0.36	—	—	26.2	4.84
—		Ti-5b	57.34	8.37	0.32	—	—	20.8	3.70
Princeton Q.	MS	Ti-5a	58.00	7.60	0.26	29.6	3.92	26.7	3.98
—		Ti-4b	58.58	7.45	0.43	—	—	23.4	2.61
Divide Q.	CG	Ti-4a	59.18	6.93	0.39	21.7	4.44	—	—
Cedar Point Q.	CG	Ti-3	59.90	7.14	0.60	17.2	4.47	—	—
Scarritt Q.	MS	Ti-2	60.62	7.63	0.68	20.0	2.79	—	—
Douglass Q.	CG	Ti-1	61.26	8.40	0.73	24.8	4.55	—	—
Rock Bench Q.	CG	To-2	62.54	8.17	0.53	29.0	5.02	—	—
Gidley Q.	CG	To-2	62.54	8.17	0.53	29.3	4.84	—	—

METHODS

Rarefaction and Specimen Counting

Sample size was standardized with rarefaction using Analytic Rarefaction 1.3 software (Holland, 2003). Rarefaction allows for comparison of species diversity among samples of disparate sizes (Raup, 1975). It provides an estimate of the number of species expected in a fauna if the sample size were smaller than the actual size. Thus, species diversity can be compared at the size of the smallest sample. Rarefied diversity estimates are probabilistic estimates based on the relative abundance of each species in a sample. For this study, species abundance was calculated from the estimated number of individuals in each sample. Different criteria were used for estimating the number of individuals from the three taphonomies.

Minimum number of individual (MNI) counts were used to estimate individuals in the mudstone quarries. MNI is the minimum number of individuals possible when all fossil elements are considered. This approach is justified by the relatively high number of associated teeth and jaws found at the mudstone quarries. Clearly, many specimens were more complete when they entered these sites and were later disassociated. The opposite appears to be the case for the clay-gall quarries. As discussed above, fossils in the clay-galls are water-transported and the occurrence of associated left and right jaws is rare or nonexistent. For these reasons, I assumed that number of specimens (NS) gave the best estimate of the number of individuals.

The NS count was also used for surface collections. This is justified in part by the collecting procedures followed by UM crews. When two specimens appear to be from the same individual or show evidence of association, they are given a single number. Repeated collecting at a locality can still result in jaws or teeth of the same individual receiving separate catalog numbers as new material is exposed. This appears to be uncommon in the UM collections, however, judging from the rarity of jaw fragments with different catalog numbers that fit together, or even exhibit the same degree of wear and preservation. The disarticulation and scattering of jaws and teeth before burial can result in elements of the same individual weathering from mudstones many meters apart, also resulting in parts being cataloged separately. During several summers of collecting, however, I never found teeth or parts of a single jaw that were more than a meter apart and clearly fit together. Thus, an NS count for surface collections appears to be most appropriate.

It should be noted that MNI counts will invariably underestimate the number of individuals actually present, since it would be highly unusual if all specimens entered a quarry site as complete upper and lower dentitions. Inversely, using NS counts will probably overestimate the number of species, since a few elements from single individuals are probably present, even if their association is not obvious. These problems are tempered by the fact that a large portion of the specimens used in this study are dentaries (Rock Bench = 42%, Cedar Point = 39%, Princeton = 56%, Bartels, 1987) and the frequency of maxillae is much lower. Since dentaries can only be assigned to left or right, the difference between an MNI and the number of specimen estimates is much smaller than the difference using isolated teeth or postcrania. The choice of a counting method does not greatly affect a comparison of diversity among isotaphonomic samples, but does matter when comparing samples with different taphonomic histories.

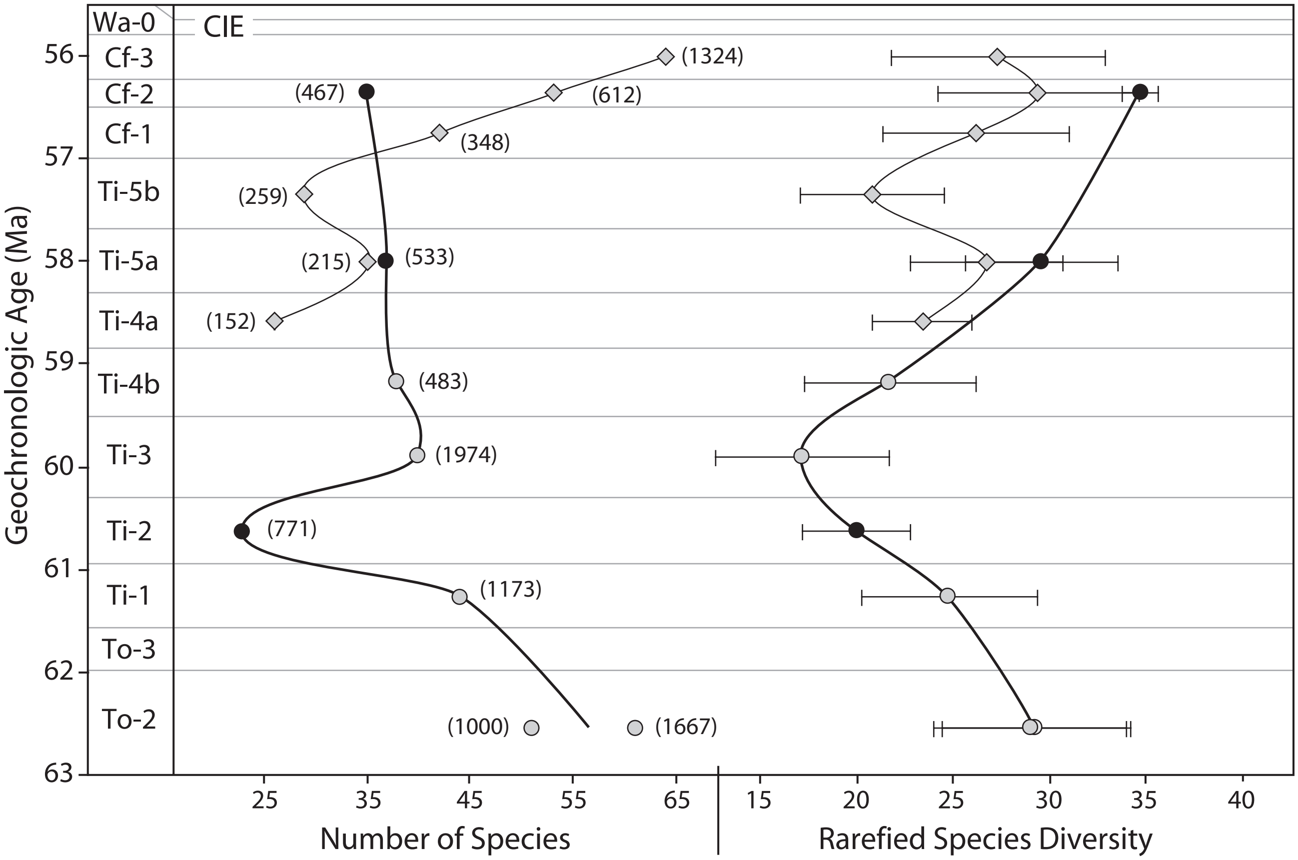


FIGURE 62 — Curves showing species diversity before (left) and after rarefaction (right). Rarefied curves are standardized to 105 individuals. Surface collections (gray diamonds), clay-gall quarries (gray circles), and mudstone quarries (black circles) are shown. Total number of specimens in each sample is shown in parentheses. Ti-6 was combined with Ti-5b due to paucity of fossils in Ti-6.

Statistical Analysis

Correlations between rarefied richness and temperature were tested for statistical significance using ordinary least squares regression (LSR) and Spearman's rank correlation (SRC). The question being tested is whether or not species richness was positively correlated with temperature in the Paleocene. Thus, correlation tests were one-tailed. This hypothesis is based on the positive spatial correlation that exists today between richness and temperature (e.g., McCoy and Connor, 1980; Rosenzweig, 1995), only here changes in richness and temperature are being compared through time.

Ordinary least squares regression determines the slope and intercept of a best-fit line through a scatter of points based on a dependent variable and one or more independent variables. In this case, rarefied richness is the dependent variable and temperature is the independent variable. If the probability (p-value) that the slope is equal to zero is ≤ 0.05, then the regression can be said to be significant with 95% confidence. The assumptions underlying the regression are that richness and temperature are internally independent, are normally distributed, and are homoscedastic (variance is homogeneous). The last two of these are difficult to determine with certainty when dealing with small sample sizes, however, and it is desirable to also perform a nonparametric test, such as Spearman's rank correlation.

Spearman's rank correlation (SRC) requires no assumption of normality or constancy of variance. Using this test, values are numbered from smallest to largest, and a test of correlation is applied to these ranks (e.g., Sokal and Rohlf, 1997, p. 598). In this case, temperature and richness were ranked. Because SRC relies solely on ranks, however, it is less powerful than least squares regression.

Variables in a time series are sometimes serially correlated (or autocorrelated; e.g., Shumway, 1988; McKinney, 1990; Shumway and Stoffer, 2000; Commandeur and Koopman, 2007). That is, the regression errors (residuals) are correlated with themselves lagged by one or more units. Serial correlation violates the assumption of independence necessary to accurately test the significance of a regression. In the case of positive serial correlation, the error variance for standard statistical tests is underestimated, resulting in a lower probability estimate and an overly optimistic conclusion. Negative serial correlation will tend to overestimate the error variance, but positive correlation is more common (e.g., Commandeur and Koopman, 2007, pp. 3-7).

To test for first order serial correlation in the regression residuals, I used the Durbin-Watson statistic (DW). The Durbin-Watson test uses the difference between successive regression residuals to approximate the amount of serial correlation present

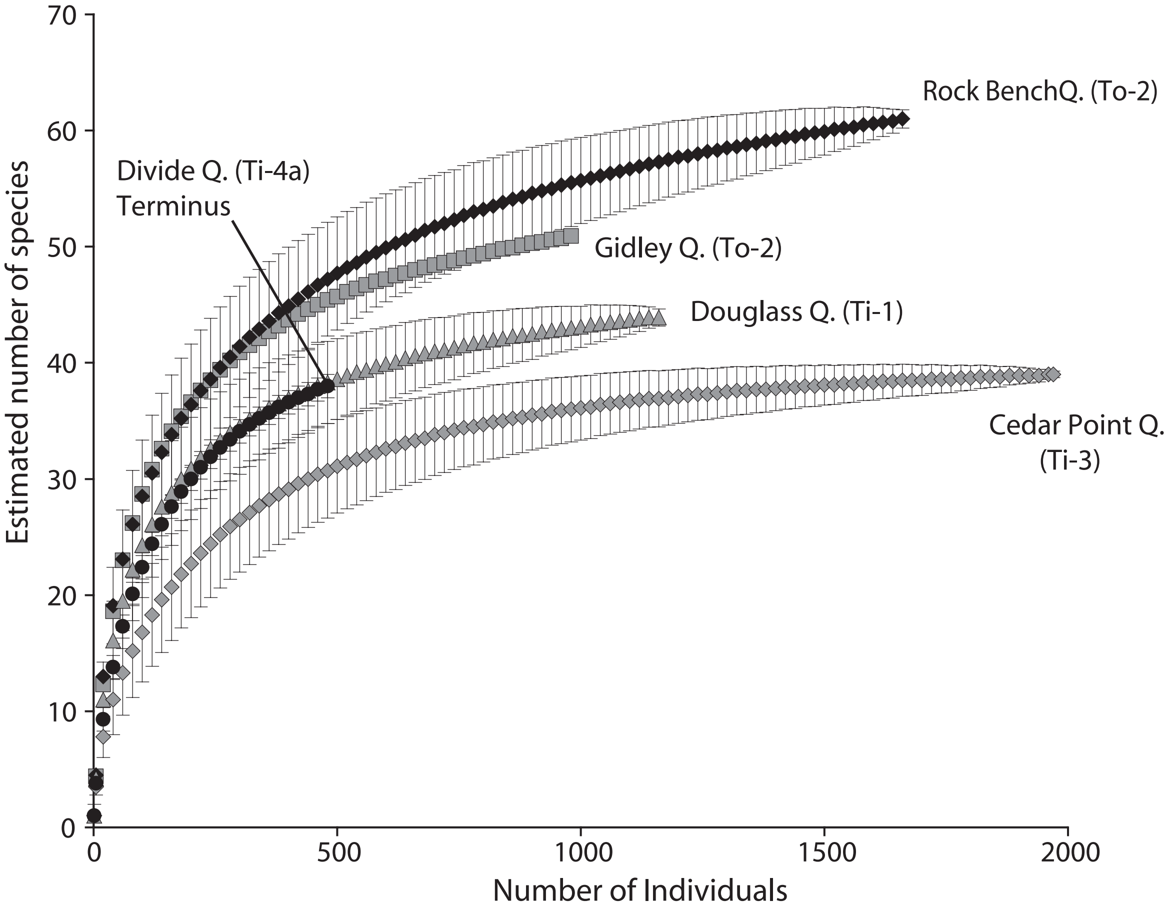


FIGURE 63 — Rarefaction curves for clay-gall quarries from the Bighorn and Crazy Mountains basins. Divide Quarry follows same trajectory as Douglass Quarry. Note good separation of Rock Bench-Gidley, Douglass-Divide, and Cedar Point quarries. Number of individuals is equivalent to number of specimens. Bars show 95% confidence intervals (1.96 SE).

(e.g., Wonnacott and Wonnacott, 1977; Andersen et al., 1987). DW values range from 0 to 4. A value of about 2 indicates the absence of serial correlation, while values of 0 and 4 indicate strong positive and negative serial correlation, respectively. Upper and lower critical values have been calculated for the Durbin-Watson statistic based on sample size and the number of independent variables in the regression (e.g., Shumway and Stoffer, 2000). If DW is greater than the upper critical value, the null hypothesis of serial correlation can be rejected. If it is below the lower critical value, serial correlation is probably present. If it falls between critical values, the presence of serial correlation is uncertain. For sample sizes tested here, DW lower and upper critical values at 95% confidence are: n = 12: 0.971, 1.331; n = 8: 0.763, 1.332, n = 7: 0.700, 1.356; n = 6, 0.610, 1.400 (Savin and White, 1977).

Tests of serial correlation assume that values are evenly spaced in time (e.g., McKinney, 1990; Commandeur and Koopman, 2007), but the temporal spacing of the richness estimates used here is somewhat uneven (Fig. 62, Table 59). To correct for this I calculated an even distribution of the same number of points in time, and then interpolated richness among the points using a cubic spline function. Results were nearly identical to those from linear interpolation. Temperature was not interpolated, but rather new estimates were made for each new time point by averaging values over 0.25 myr on either side of the point using the Zachos et al. (2001) dataset (see above). Even distributions were not calculated for the mudstone quarries due to small sample size (n = 3) or for the surface collections, which were only weakly correlated with temperature ($r^2 = 0.13$).

In cases where the possibility of serial correlation could not be rejected using the Durbin-Watson statistic, I used first and generalized differencing in an attempt to remedy the potential problems caused by serial correlation (e.g., Wonnacott and Wonnacott, 1977, p. 629; Andersen et al., 1987, p. 358; McKinney, 1990, p. 53). The results of generalized differencing were not substantially different from first differencing, so only the latter are reported. First differencing is merely the difference between each value and the value that precedes it, and was done with both dependent (richness) and independent (temperature) variables. Because the first value has no predecessor, a degree of freedom is lost. First differencing removes the linear temporal trend, and provides a bin by bin comparison of changes in richness and temperature. It may, however, also degrade the signal of interest, i.e., the long-term correspondence of temperature

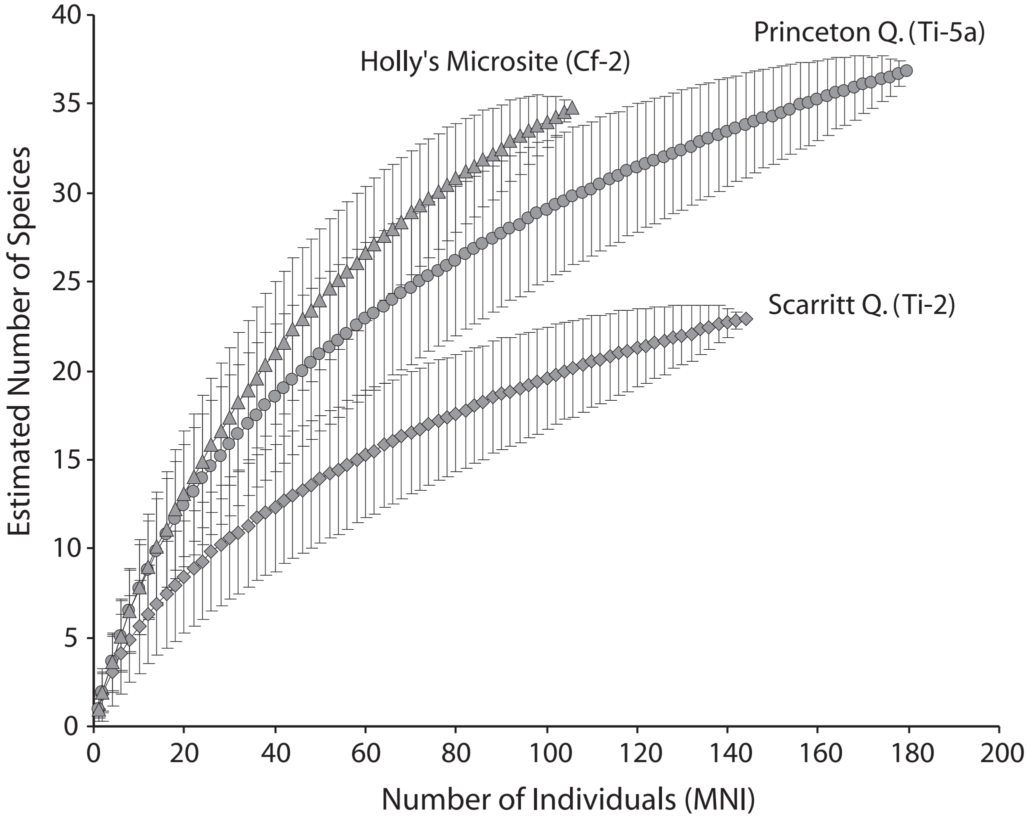


FIGURE 64 — Rarefaction curves for mudstone quarries from the Bighorn Basin. Note good separation between Scarritt and Princeton quarries. Number of individuals based on Minimum Number of Individuals (MNI; see text). Bars show 95% confidence intervals (1.96 SE).

and richness. Nevertheless, if temperature and richness covary though the Paleocene, a positive correlation should still exist.

Lastly, I tried leading and lagging temperature relative to rarefied richness in case there was a systematic offset in the correlation of marine temperature to the Bighorn Basin biozones. Temperature was led or lagged by one biozone for the raw richness values and by 0.5 myr for evenly spaced values. Lagging temperature by one biozone for the entire dataset puts anomalously high values from the Paleocene-Eocene Thermal Maximum into Cf-3 (Zachos et al., 2001). Thus Cf-3 was not included, reducing the sample size to eleven. A temperature lead for Gidley and Rock Bench quarries in the raw dataset was calculated using a lead of 0.65 myr, which is the average duration among bins.

RESULTS

Figure 62 compares un-rarified species diversity to rarefied diversity standardized to 105 individuals. Rarefaction substantially changed the shapes of the diversity curves. Figures 63 and 64 show the rarefaction curves for clay-gall and mudstone quarries, respectively. The clay-gall curves are relatively steep up to about 500 individuals but then shallow between 500 and 1000 individuals, suggesting that estimates are asymptotically approaching the quarry's "actual" diversity. In contrast, the slopes for the mudstone quarries remain relatively steep, suggesting that "actual" diversity may be considerably higher, especially for Holly's Microsite. This is probably due to the smaller samples sizes of the mudstone quarries (Fig. 62).

The clay-gall quarries fall into three groups (Fig. 63). Rock Bench and Gidley quarries have the highest richness, while Divide and Douglass quarries have intermediate values, and Cedar Point Quarry has the lowest. These groups are well separated at the sample size of Douglass Quarry (n = 1173) and 95% confidence intervals do not overlap. The sample size for Gidley Quarry (n = 1000) is just below the confidence interval for Rock Bench Quarry, suggesting that it may be slightly less diverse. The curve for Divide Quarry follows the same trend as Douglass Quarry, suggesting equivalent richness. When considered in temporal sequence these data indicate a decrease in richness from the Torrejonian (To-2) to the early Tiffanian (Ti-1), followed by another decrease from the early to middle Tiffanian (Ti-3), and then by an increase in the late Tiffanian (Ti-4b) (Fig. 62B).

The three mudstone quarries have non-overlapping confidence intervals at the sample size of Holly's Microsite (n = 467). Scarritt Quarry has the lowest richness and is well below Princeton Quarry and Holly's Microsite. Holly's Microsite appears to be slightly richer than Princeton Quarry. In temporal sequence this implies a large increase in richness from the middle to the late Tiffanian (Ti-3 to Ti-5a), and another increase in the middle Clarkforkian (Cf-2) (Fig. 62B). Considered together, the mudstone and clay-gall estimates suggest that richness reached a low point in Ti-2 or Ti-3 and then began to gradually increase into

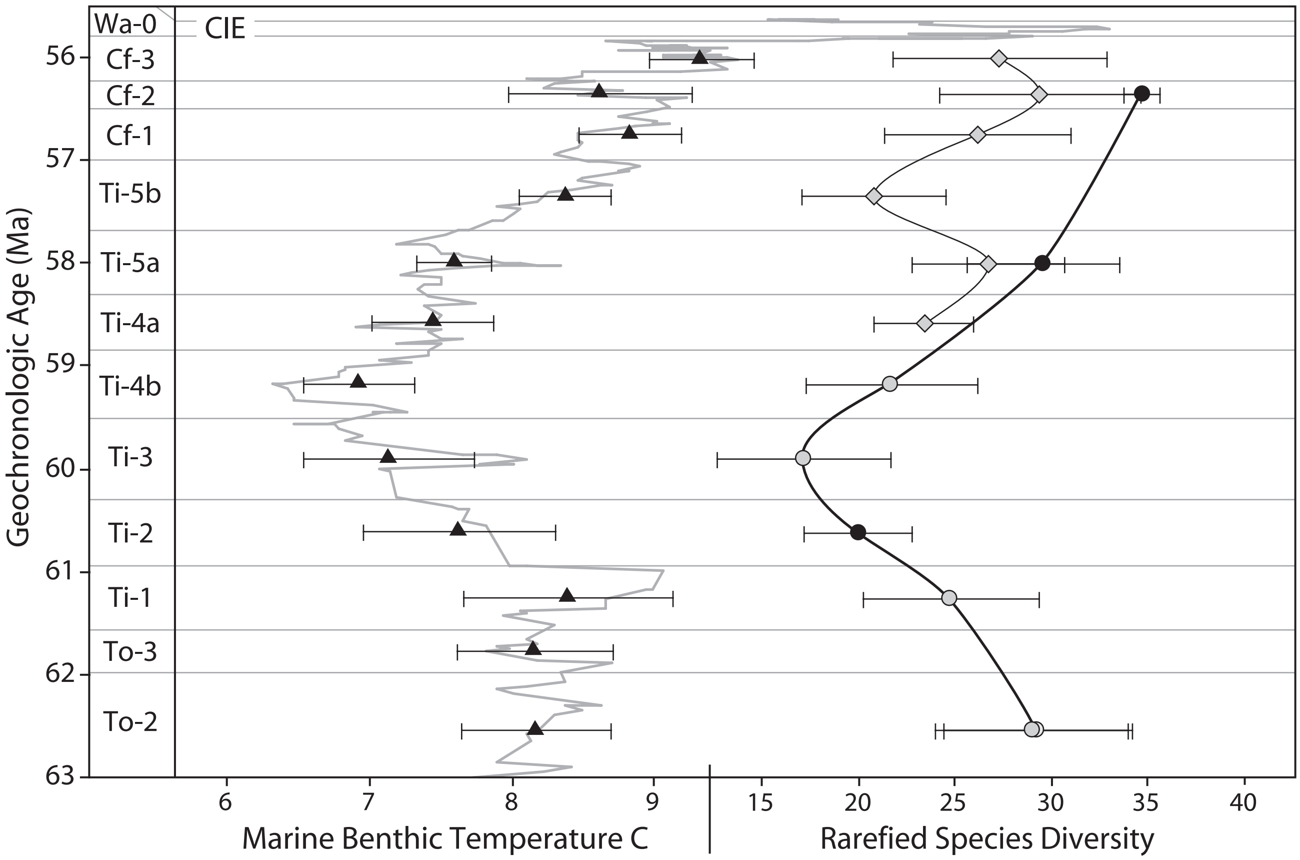


FIGURE 65 — Comparison of curves for marine temperature (left), calculated from Zachos et al. (2001), and rarefied species diversity (right). For temperature curve, gray line shows 5-point moving averages and solid triangles show mean temperature for each biozone. The marine record was correlated to the Bighorn Basin using ages for paleomagnetic reversals, calibrated to the geomagnetic polarity time scale of Ogg and Smith (2004) (see text). Bars show 95% confidence of mean (1.96 SE). For diversity curves, gray diamonds indicate surface collections; solid gray circles indicate clay-gall quarries; solid black circles indicate mudstone quarries. Ti-6 was combined with Ti-5b due to paucity of fossils in Ti-6. Rarefied number of species shown for a sample size of 105 individuals.

the late Tiffanian and Clarkforkian.

Richness estimates for surface collections suggest a decrease in the latest Tiffanian (Ti-5b and Ti-6 combined), followed by an increase in the Clarkforkian (Fig. 65). When comparing surface collections and mudstone quarries from the same intervals, the surface collections are less rich in both cases. This suggests underestimation of the number of individuals in the former, or overestimation in the latter, or both. Nevertheless, both taphonomies suggest an increase in richness from Ti-5a to Cf-2.

Figure 65 compares the marine temperature record to rarefied richness. Least squares regression indicates that rarified richness is significantly correlated with temperature at 95% confidence for All Localities, All Quarries, and for either of these with temperature lagged (Table 60). Using Spearman's rank correlation, All Localities and All Quarries are slightly below 95% significance, but are significant when temperature is lagged. The Durbin-Watson statistic, calculated on evenly spaced richness, indicates that the null hypothesis of first order serial correlation can be rejected for All Quarries, for Clay-gall Quarries, and for All Localities or All Quarries lagged. All of the combinations that were significant before being evenly spaced, remain significant, but Clay-gall Quarries are now also significant using regression and All Quarries is significant using Spearman's test. All Quarries remain significant after first differencing using either test. Notably, correlation is strongest and significance is highest in the lagged datasets.

DISCUSSION

Rarefied mammalian richness is significantly correlated with marine temperature for All Localities and for All Quarries using least squares regression, but slightly below 95% significance using Spearman's rank correlation (Table 60). When temperature is lagged for All Localities or for All Quarries the correlations become stronger, and are significant at 99% confidence with LSR and 95% with SRC. The correlation between All Quarries and temperature is astonishingly high when lagged by one biozone (r = 0.98). The Durbin-Watson test strongly suggests that this strength is not due to first order serial correlation. The Durbin-Watson statistic is ambiguous for All Quarries, but when richness and temperature are differenced to remove possible serial correlation, All Quarries remains significant with

TABLE 60 — Statistics for rarefied species richness regressed on benthic marine temperature. *P*-values in bold indicate that species diversity is significantly correlated to temperature with 95% confidence ($p \leq 0.05$). Durbin-Watson (DW) values in bold indicate that the null hypothesis of serial correlation can be rejected with 95% confidence. See Methods for explanation of tests. Temperature (temp.) lead and lag indicate that temperature has been moved up or down in time by one biozone (raw values) or by 0.5 myr (other columns, after even distribution), except for Cf-2 temperature, which lags by only 0.3 myr to avoid including values from the Paleocene-Eocene Thermal Maximum. *LSR*, ordinary linear least-squares regression; *n*, number of samples; *p*, probability; r^2, coefficient of determination; *Q*., quarry; *SRC*, Spearman's Rank Correlation nonparametric test; *temp*., mean benthic marine temperature calculated from Zachos et al. (2001), recalibrated to Ogg and Smith (2005).

	Raw Values				Even Distribution				First Differences				
	n	LSR r^2	LSR *p*	SRC *p*	r^2	DW	LSR *p*	SRC *p*	n	r^2	DW	LSR *p*	SRC *p*
All localities	12	0.32	**0.027**	0.060	0.29	**1.61**	**0.035**	0.168	—	—	—	—	—
All quarries	8	0.56	**0.016**	0.063	0.64	0.99	**0.009**	**0.038**	7	0.46	0.97	**0.047**	**0.020**
Clay-gall Quarries	5	0.62	0.057	0.161	0.70	**1.70**	**0.037**	0.276	—	—	—	—	—
Mudstone Quarries	3	0.56	—	—	—	—	—	—	—	—	—	—	—
Surface	6	0.13	0.129	0.078	—	—	—	—	—	—	—	—	—
All loc.: temp. lead	12	0.21	0.068	0.135	0.13	1.23	0.127	0.198	7	0.21	0.84	0.153	0.252
All loc.: temp. lag	11	0.58	**0.003**	**0.010**	0.49	**1.58**	**0.008**	**0.036**	—	—	—	—	—
All Q.: temp. lead	8	0.26	0.096	0.122	0.13	0.86	0.196	0.166	7	0.03	1.14	0.350	0.485
All Q.: temp. lag	8	0.98	**<0.001**	**0.001**	0.82	**1.61**	**0.001**	**0.006**	—	—	—	—	—

95% confidence. Thus, the probability that these correlations occurred at random or as an artifact of serial correlation is small and there appears to be an underling relationship between temperature and species richness.

The stronger correlation of richness with lagged temperature suggests that there may be a systematic offset in the geochronologic correlation of marine temperature to the BCM biozones. Correlation is strongest when temperature is lagged by one biozone (Raw Values, Table 60). In general, biozone duration decreases from the Torrejonian to the end Clarkforkian (Table 59), resulting in greater temperature lags for the older zones. Two possible reasons for a systematic offset of this nature come to mind. First, paleomagnetism is unknown for many Paleogene marine cores, so the composite oxygen isotope record compiled by Zachos et al. (2001) is presumably based largely on biostratigraphic correlation. This is far less precise than using paleomagnetic reversals and adds unknown error to their reported Ma ages. Because many of the cores preserve the PETM, correlation error should be lowest closest to this event, but may increase with increasing age. Second, uncertainties in the calibration of BCM biozones below C26n are moderately large due to either a slower depositional rate or a possible hiatus near the base of the Polecat Bench section (Secord et al., 2006). The biozone age calibrations used here assume no hiatus, but if one were present it would have resulted in older calculated ages for biozones below C26n and could account for a systematic offset similar to the one hypothesized here. The effects of a 0.5 and 1.0 myr hiatuses on age calibration were modeled by Secord et al. (2006, Table 1, Fig. 6).

Species richness in the quarry samples is more strongly correlated to temperature than in the surface collections (Table 60), and the significant correlation in the All Localities regression is largely driven by quarry samples. Notably, there appears to be an anomalously low estimate of richness of 20.8 in the surface collections from Ti-5b (which includes Ti-6). The late Tiffanian surface collections are the smallest in the entire dataset (Fig. 62) and are presumably the least reliable. The Ti-5b sample falls out as a major outlier in the regression of All Localities lagged and when removed r^2 increases from 0.58 to 0.90, and the *p*-values decrease from 0.003 and 0.010 to <0.001 for both LSR and SRC (n = 11). For All Localities r^2 increases from 0.32 to 0.42, and the *p*-value decreases from 0.027 to 0.016 for LSR, and from 0.060 to 0.034 for SRC when Ti-5b is removed (n = 11).

Rarefaction probably provides better approximations of relative diversity than the diversity indices (Simpson, Shannon, Whittaker) used in previous studies (Rose, 1981a; Krause and Maas, 1990), which do not account for differences in sample size. The richness pattern in Figure 65 shares some similarities with the results of these studies, such as a general decrease in diversity from the Torrejonian to Ti-2 or Ti-3, but it differs in other important aspects. This study suggests a decrease in diversity in the earliest Tiffanian (Ti-1, Douglass Quarry), while Krause and Maas found essentially no change in diversity until Ti-2. This study also suggests a steady increase in diversity from the middle Tiffanian (Ti-3, Cedar Point Quarry) to the middle Clarkforkian, based on quarry data. In contrast, the results of Krause and Maas (1990) suggested higher diversity in the late Tiffanian (Ti-5a, Princeton Quarry) than in many Clarkforkian localities (e.g., Holly's Microsite), although their Clarkforkian diversity estimates differed greatly.

There is no compelling evidence to support the diversity "crash" that Alroy et al. (2000) described near the Tiffanian-Clarkforkian (Ti-Cf) boundary. There is an implied drop in rarefied richness in the surface collections from Ti-5b, but as discussed above, the late Tiffanian surface collections are the smallest samples in the dataset and may not be reliable. Moreover, there is overlap in 95% confidence intervals between the Ti-5b sample and bounding samples. Even if the Ti-5b sample does indicate a real drop in diversity, it would be of a much smaller magnitude than the one implied by Alroy et al. (2000). Thus, their diversity crash must be an artifact of their data or their methodology, or of both. This appears to be the same conclusion that Alroy has reached (pers. com., May 2007). Using improved methods of sampling standardization, their late Paleocene drop in diversity is reportedly no longer present in this dataset (Paleobiology Database: http://paleodb.org/).

The significant correlation between marine temperature and mammalian diversity in the entire dataset and in the combined quarries suggests that mammalian diversity is strongly dependant on MAT. This conclusion is based on a small number of faunas and needs to be tested further using larger datasets. The much larger dataset compiled by Alroy (2000b,a), however, may not have been adequate for testing the climate-diversity question. Although their study represents an important attempt, no corrections were made for taphonomic or method-of-collection biases. It also seems clear that the most accurate results will be based on actual specimen counts and not on sampling published faunal lists. Although the subsampling of faunal lists does provide a relative estimate of the number of specimens, a more accurate count may be needed to demonstrate significance. Assuming that MAT is not the only factor controlling species diversity, a highly accurate count of specimens may be needed to identify a correlation through the scatter created by the other factors.

CONCLUSIONS

Results indicate that mammalian species richness in the Bighorn-Crazy Mountains basins sequence decreased from the Torrejonian to the early Tiffanian, reached a low point in the middle Tiffanian, and then began a steady increase to the middle Clarkforkian. Species richness is significantly correlated with marine temperature. The correlation is driven largely by quarry samples, and smaller surface collections are only weakly correlated. The correlation is strengthened when temperature is lagged, suggesting that a systematic offset may exist in the geochronologic correlation of marine temperature to the Bighorn-Crazy Mountains basins sequence. A large part of the variance in richness is explained by dependence on MAT, suggesting that MAT is an important factor controlling mammalian diversity. Future work should focus on testing these results by compiling larger, more regional datasets using specimen-based counts and associated taphonomic information, and a refined paleoclimate record as new data become available.

V

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VI

APPENDICES

APPENDIX I: FAUNAL LISTS

Mammalian faunal lists for Cedar Point and Princeton quarries are updated lists from Rose (1981a). Counts of specimens and minimum number of individuals (MNI) for these quarries are mostly from Rose (1981a), but modifications were made when necessary. Asterisks indicate identifications reported by other authors that I have not confirmed.

APPENDIX I-A: Cedar Point Quarry

Taxon	Total/MNI
MULTITUBERCULATA	
Family PTILODONTIDAE	
Neoplagiaulax jepi	17/2
Neoplagiaulax hunteri	3/2
Cf. *Ectypodus powelli**	4/3
Ptilodus sp. C.	329/89
Ptilodus cf. *P. kummae*	5/2
DIDELPHIMORPHIA	
Family DIDELPHIDAE	
*Peradectes elegans**	5/3
LEPTICTIDA	
Family LEPTICTIDAE	
Myrmecoboides arenarius n. sp.	3/2
CIMOLESTA	
Family PALAEORYCTIDAE	
Palaeoryctes sp.	7/2
DIDELPHODONTA	
Family CIMOLESTIDAE	
Paleotomus radagasti	7/3
APATOTHERIA	
Family APATEMYIDAE	
Labidolemur soricoides	10/4
PANTODONTA	
Family PANTOLAMBDIDAE	
*Caenolambda jepseni**	5/1
Family TITANOIDEIDAE	
Titanoides cf. *T. major*	20/4
PANTOLESTA	
Family PANTOLESTIDAE	
Bisonalveus holtzmani	1/1
Bessoecetor cf. *B. pilodontus*	12/5

Taxon	Total/MNI
ERINACEOMORPHA	
Family ERINACEIDAE	
Cedrocherus ryani	1/1
ERINACEOMORPHA incertae sedis	
Adunator meizon	23/14
Litocherus zygeus	68/31
Erinaceomorpha gen. et. sp. indet.	2/2
SORICOMORPHA	
Family NYCTITHERIIDAE	
Leptacodon acherontus n. sp.	3/2
Leptacodon cf. *L. munusculum*	9/5
?DERMOPTERA	
Family PLAGIOMENIDAE	
Elpidophorus elegans	1/1
PRIMATES	
Family PLESIADAPIDAE	
Plesiadapis rex	811/128
Family CARPOLESTIDAE	
Carpodaptes hazelae	77/40
Family PAROMOMYIDAE	
Ignacius frugivorus	20/8
Family PICRODONTIDAE	
Picrodus cf. *P. silberlingi*	4/3
PROCREODI	
Family OXYCLAENIDAE	
*Chriacus oconostotae**	3/2
Thryptacodon australis	152/30
Family ARCTOCYONIDAE	
*Mimotricentes fremontensis**	2/2
Arctocyon cf. *A. mumak*	6/3
Aphanocyon amaurus gen. et sp. n.	14/4

APPENDIX I-A: (Cont.)

Taxon	Total/MNI
CONDYLARTHRA	
Leptonysson orthius n. sp.	7/4
CREODONTA	
Family OXYAENIDAE	
Tytthaena parrisi	3/1
CARNIVORA	
Family VIVERRAVIDAE	
Protictis agastor	10/4
Protictis paralus	20/7
Raphictis gausion	12/6
Family HYOPSODONTIDAE	
Aletodon quadravus	14/5
Family PHENACODONTIDAE	
Phenacodus grangeri	99/18
Ectocion cedrus	181/52
MESONYCHIA	
Family MESONYCHIDAE	
Dissacus cf. *D. navajovius*	3/1
Pachyaena?	1/1

APPENDIX I-B: Divide Quarry

Taxon	Total/MNI
MULTITUBERCULATA	
Family PTILODONTIDAE	
Neoplagiaulax mckennai	2/2
Neoplagiaulax cf. *N. hazeni*	10/5
?*Mimetodon silberlingi*	1/1
Ptilodus kummae	117/27
Prochetodon foxi	3/1
Family EUCOSMODONTIDAE	
Genus and sp. indet.	3/2
LEPTICTIDA	
Family LEPTICTIDAE	
Cf. *Prodiacodon* sp.	7/2
CIMOLESTA	
Family PALAEORYCTIDAE	
Palaeoryctes jepseni	4/2
Aaptoryctes cf. *A. ivyi*	3/1
DIDELPHODONTA	
Family CIMOLESTIDAE	
Paleotomus radagasti	3/1
APATOTHERIA	
Family APATEMYIDAE	
Labidolemur soricoides	7/2
Unuchinia sp.	4/1
PANTODONTA	
Family TITANOIDEIDAE	
Titanoides gidleyi	6/1
Family BARYLAMBDIDAE	
Leptolambda churchilli	2/1
Haplolambda cf. *H. quinni*	2/1
PANTOLESTA	
Family PANTOLESTIDAE	
Bessoecetor pilodontus n. sp.	4/2
Palaeosinopa dorri?	1/1
Leptonysson orthius n. sp.	2/1
CARNIVORA	
Family VIVERRAVIDAE	
Viverravus cf. *V. schaffi*	4/2
Didymictis cf. *D. dellensis*	6/2
Raphictis?	2/1
ERINACEOMORPHA	
Family ERINACEIDAE	
Litolestes sp.	1/1
ERINACEOMORPHA incertae sedis	
Adunator minutus	4/1
Cf. *Adunator*	1/1
SORICOMORPHA	
Family NYCTITHERIIDAE	
Cf. *Leptacodon choristus* n. sp.	1/1
?DERMOPTERA	
Family CYRIACOTHERIIDAE	
Cyriacotherium cf. *C. argyreum*	1/1
PRIMATES	
Family PLESIADAPIDAE	
Plesiadapis churchilli	119/14
Family CARPOLESTIDAE	
Carpodaptes stonleyi	9/6
Carpomegodon jepseni	13/5
Family PAROMOMYIDAE	
Ignacius frugivorus	23/6
PROCREODI	
Family OXYCLAENIDAE	
Thryptacodon australis	10/2
Family ARCTOCYONIDAE	
Arctocyon mumak	5/2
Arctocyon small sp.	1/1
Lambertocyon gingerichi	29/6

APPENDIX I-B: (Cont.)

Taxon	Total/MNI
CONDYLARTHRA	
Family HYOPSODONTIDAE	
Hyopsodontidae gen. et. sp. indet.	3/1
Family PHENACODONTIDAE	
Phenacodus magnus	6/1
Ectocion cedrus	62/8
MESONYCHIA	
Family MESONYCHIDAE	
Dissacus cf. *D. navajovius*	2/1

APPENDIX I-C: Croc Tooth Quarry

Taxon	Total/MNI
MULTITUBERCULATA	
Family PTILODONTIDAE	
*Neoplagiaulax mckennai** (reported by Sloan, 1978)	?
Ptilodus kummae	8/2
Family EUCOSMODONTIDAE	
Genus and sp. indet.	1/1
PANTODONTA	
Family TITANOIDEIDAE	
Titanoides gidleyi	14/2
Family BARYLAMBDIDAE	
Leptolambda churchilli	1/1
Haplolambda cf. *H. quinni*	2/1
PANTOLESTA	
Family PANTOLESTIDAE	
Bessoecetor pilodontus n. sp.	1/1
Cf. *Bessoecetor septentrionalis*	1/1
CARNIVORA	
Family VIVERRAVIDAE	
Raphictis?	1/1
?DERMOPTERA	
Family CYRIACOTHERIIDAE	
Cyriacotherium argyreum	1/1
PRIMATES	
Family PLESIADAPIDAE	
Plesiadapis churchilli	9/2
Plesiadapis cf. *P. fodinatus*	3/2
Chiromyoides caesor	1/1
Family PAROMOMYIDAE	
Ignacius frugivorus	1/1
Phenacolemur archus n. sp.	4/2
PROCREODI	
Family OXYCLAENIDAE	
Thryptacodon australis	2/1
Family ARCTOCYONIDAE	
Arctocyon mumak	3/1
Arctocyon small sp.	3/1
Lambertocyon eximius	1/1
CONDYLARTHRA	
Family PHENACODONTIDAE	
Phenacodus grangeri	7/2
Phenacodus magnus	2/1
Ectocion cedrus	3/2

APPENDIX I-D: Princeton Quarry

Taxon	Total/MNI
MULTITUBERCULATA	
Family PTILODONTIDAE	
Parectypodus laytoni	9/5
Neoplagiaulax hazeni	4/1
Ectypodus powelli	10/8
Mimetodon churchilli	2/1
Prochetodon cavus	12/3
Family EUCOSMODONTIDAE	
Microcosmodon conus	7/4
Pentacosmodon pronus	2/1
Neoliotomus conventus	4/1
DIDELPHIMORPHIA	
*Peradectes elegans**	4/3
Didelphidae gen. et. sp. indet.*	1/1
LEPTICTIDA	
Family LEPTICTIDAE	
Prodiacodon paucus n. sp.	2/1
?*Palaeictops**	3/3
CIMOLESTA	
Family PALAEORYCTIDAE	
Palaeoryctes jepseni	11/4
APATOTHERIA	
Family APATEMYIDAE	
Unuchinia cf. *U. dysmathes*	3/2
?PHOLIDOTA	
Family METACHEIROMYIDAE	
Propalaeanodon schaffi	2/2

APPENDIX I-D: (Cont.)

Taxon	Total/MNI
CARNIVORA	
Family VIVERRAVIDAE	
Viverravus schaffi	12/4
Viverravus laytoni	2/2
Didymictis dellensis	5/1
ERINACEOMORPHA	
Family ERINACEIDAE	
Litolestes ignotus	25/14
ERINACEOMORPHA incertae sedis	
Adunator minutus	43/17
Adunator abditus n. sp.	1/1
SORICOMORPHA	
Family NYCTITHERIIDAE	
Wyonycteris galensis n. sp.	2/2
Leptacodon packi	8/5
Nyctitheriidae genus and species indet.	1/1
LIPOTYPHLA or CIMOLESTA	
Apternodus like sp. A	1/1
Apternodus like sp. B	1/1
PRIMATES	
Family PLESIADAPIDAE	
Plesiadapis fodinatus	112/19
Family MICROMOMYIDAE	
Micromomys silvercouleei	1/1
Family CARPOLESTIDAE	
Carpolestes dubius	48/13
Family PAROMOMYIDAE	
Phenacolemur pagei	51/17
PROCREODI	
Family OXYCLAENIDAE	
Princetonia cf. *P. yalensis*	14/5
Thryptacodon sp.	3/2
Family ARCTOCYONIDAE	
Arctocyon sp.	1/1
Order CONDYLARTHRA	
Family HYOPSODONTIDAE	
Phenacodaptes sabulosus	103/27
Family PHENACODONTIDAE	
Phenacodus grangeri	3/1
Ectocion mediotuber	15/5
MESONYCHIA	
Family MESONYCHIDAE	
Dissacus argenteus	5/2

APPENDIX I-E: Y2K Quarry

Taxon	Total/MNI
MULTITUBERCULATA	
Family PTILODONTIDAE	
Parectypodus laytoni	1/1
Ectypodus powelli	46/11
Prochetodon cavus	1/1
Family EUCOSMODONTIDAE	
Microcosmodon sp.	5/1
LEPTICTIDA	
Family LEPTICTIDAE	
Prodiacodon cf. *P. tauricinerei*	15/4
Cf. *Palaeictops*	1/1
CIMOLESTA	
Family PALAEORYCTIDAE	
Palaeoryctes jepseni n. sp.	9/2
APATOTHERIA	
Family APATEMYIDAE	
Labidolemur soricoides	2/1
?PHOLIDOTA	
Family METACHEIROMYIDAE	
Mylanodon rosei	2/2
CARNIVORA	
Family VIVERRAVIDAE	
Viverravus schaffi	3/1
ERINACEOMORPHA	
Family ERINACEIDAE	
Litolestes ignotus	4/2
ERINACEOMORPHA incertae sedis	
Adunator minutus	15/4
SORICOMORPHA	
Family NYCTITHERIIDAE	
Leptacodon packi	3/2
Plagioctenodon sp.	3/1
PRIMATES	
Family PLESIADAPIDAE	
Plesiadapis cf. *P. dubius*	59/7
Family MICROSYOPIDAE	
Arctodontomys sp.	1/1
Family MICROMOMYIDAE	
Micromomys millennius n. sp.	1/1
Family CARPOLESTIDAE	
Carpolestes dubius	28/5
Family PAROMOMYIDAE	
Phenacolemur pagei	54/8

APPENDIX I-D: (Cont.)

Taxon	Total/MNI
PROCREODI	
Family OXYCLAENIDAE	
Princetonia cf. *P. yalensis*	24/3
Family ARCTOCYONIDAE	
Arctocyon cf. *A. nexus*	9/1

Taxon	Total/MNI
CONDYLARTHRA	
Family PHENACODONTIDAE	
Ectocion mediotuber	7/3

APPENDIX I-F: Holly's Microsite (SC-188)

Phenacodus, *Coryphodon*, and *Dipsalidictis* (*Oxyaena*) *aequidens* were included in a faunal list published by Krause (1986), but are excluded here because they appear to be taxa from the surrounding locality (SC-188) not known from the quarry.

Taxon	Total/MNI
MULTITUBERCULATA	
Family EUCOSMODONTIDAE	
Ectypodus powelli	92/24
Microcosmodon rosei	16/2
DIDELPHIMORPHIA	
Family DIDELPHIDAE	
Peradectes protinnominatus	21/4
LEPTICTIDA	
Family LEPTICTIDAE	
Prodiacodon cf. *P. tauricinerei*	3/1
RODENTIA	
Family ISCHYROMIDAE	
Acritoparamys atavus	32/4
Acritoparamys atwateri	8/2
Microparamys cheradius	19/3
Microparamys cf. *M. minutus*	1/1
Paramys taurus	7/2
Family REITHROPARAMYIDAE	
Reithroparamys sp. indet.	3/2
CIMOLESTA	
Family PALAEORYCTIDAE	
Palaeoryctes punctatus	2/1
APATOTHERIA	
Family APATEMYIDAE	
Labidolemur kayi	8/3
TILLODONTIA	
Family TILLOTHERIIDAE	
Azygonyx ancylion	1/1
CARNIVORA	
Family VIVERRAVIDAE	
Didymictis proteus	3/2
Viverravus cf. *V. laytoni*	8/2
Family MIACIDAE	
Uintacyon rudis	1/1
CREODONTA	
Family OXYAENIDAE	
Cf. *Tytthaena*	1/1

Taxon	Total/MNI
ERINACEOMORPHA	
Family ERINACEIDAE	
Leipsanolestes cf. *L. siegfriedti*	5/2
ERINACEOMORPHA incertae sedis	
Adunator cf. *A. minutus*	18/4
SORICOMORPHA	
Family NYCTITHERIIDAE	
Leptacodon rosei	27/7
Plagioctenodon cf. *P. krausae*	8/2
?DERMOPTERA	
Family PLAGIOMENIDAE	
Worlandia inusitata	87/11
PRIMATES	
Family PLESIADAPIDAE	
Plesiadapis cookei	17/3
Family MICROMOMYIDAE	
Niptomomys doreenae	2/1
Family MICROSYOPIDAE	
Tinimomys graybulliensis	3/1
Family CARPOLESTIDAE	
Carpolestes simpsoni	31/6
Family PAROMOMYIDAE	
Ignacius graybullianus	7/2
Phenacolemur cf. *P. praecox*	17/3
Phenacolemur cf. *P. simonsi*	1/1
PROCREODI	
Family OXYCLAENIDAE	
Chriacus sp.	2/1
Princetonia sp.	4/1
Thryptacodon sp.	1/1
CONDYLARTHRA	
Family HYOPSODONTIDAE	
Haplomylus simpsoni	1/1
Family PHENACODONTIDAE	
Ectocion osbornianus	9/3
ARCTOSTYLOPIDA	
Family ARCTOSTYLOPIDAE	
Arctostylops steini	1/1

APPENDIX II: UTM DATA FOR STRATIGRAPHIC SECTIONS

Locations here define the traces of stratigraphic sections and important marker beds in the stratigraphic sections and maps in Chapter 2. UTM data are relative to NAD 27 CONUS, 12T. Abbreviations: *BTQ*, Bluff Top Quarry; *CS*, carbonaceous shale; *LSN*, limestone nodule bed; *MS*, mudstone; *WB*, West Polecat Bench. Correlations are usually across small canyons.

APPENDIX II-A: Bed trace from Princeton Quarry section to West Bench section

UTM Easting	UTM Northing	Section	Meter Level (WB)
666478	4976295	Trace LSN	22
666481	4976445	Trace LSN	22
667103	4975998	Trace LSN	22
667343	4975869	Trace LSN	22
667538	4975753	Trace LSN	22
667238	4975420	Trace LSN	33
667218	4975267	Trace LSN	33
667123	4974784	Trace LSN	33
666907	4974618	Trace LSN	33

APPENDIX II-B: Fossil Hollow section and bed trace to West Bench section

UTM Easting	UTM Northing	Section	Meter Level (WB)
668827	4973029	Fossil Hollow section	15
668628	4972945	Fossil Hollow section	51
668418	4973076	Fossil Hollow section	66
668372	4972969	Fossil Hollow section	81
667424	4973754	Fossil Hollow trace	62
667011	4973642	Fossil Hollow trace	62
667680	4973329	Fossil Hollow trace	62

APPENDIX II-C: West Bench stratigraphic section

UTM Easting	UTM Northing	Section	Bed	Meter Level (WB)
667361	4974440	WB Main	—	30
667429	4974230	WB Main	Trace	49
666997	4974006	WB Main	Trace	49
667434	4974225	WB Main	LSN	51
667019	4973959	WB Main	Correlation	68
667011	4973686	WB Main	Correlation	68
666933	4973616	WB Main	Ridge top, trace, correlation	100
666965	4973253	WB Main	Trace, correlation	106
667069	4973096	WB Main	Trace, correlation	131
666985	4972804	WB Main	Trace, correlation	137
667009	4972685	WB Main	CS, trace	153
666833	4972535	WB Main	Lignite	219
666800	4972532	WB Main	LSN	228
666694	4972209	WB Main	Trace to SC185 (LT-2)	275
666601	4971831	WB Main	Trace to SC185 (LT-2)	275
666222	4971619	WB Main	Trace to SC185 (LT-2)	275
666218	4971643	WB Main	Trace to SC185 (LT-2)	275
665838	4971481	WB Main	Trace to SC185 (LT-2)	275
665994	4971252	WB Main	*P. gingerichi*	305
666082	4971149	WB Main	Trace marker 1	312
666221	4971148	WB Main	Trace marker 1	312

APPENDIX II-C: West Bench Section (Cont.)

UTM Easting	UTM Northing	Section	Bed	Meter Level (WB)
666266	4971111	WB Main	Trace marker 2	325
666527	4970853	WB Main	Trace marker 2	325
666569	4970809	WB Main	Trace marker 3	345
666602	4970634	WB Main	Trace marker 3	345
666282	4970472	WB Main	Trace marker 3	345
666215	4970282	WB Main	Trace marker 3	345
666355	4970166	WB Main	Trace marker 4	345
666429	4970010	WB Main	Trace	359
666633	4970603	WB Main	LSN shelves	370
666438	4970046	WB Main	Mid shelf SC-191	374
666453	4969851	WB Main	CS trace	395
666804	4969683	WB Main	CS trace	395
666939	4969608	WB Main	BTQ level CS	410
667657	4968987	WB Main	Ti-Cf Lignite trace 1	423
667325	4968457	WB Main	Ti-Cf Lignite trace 1	423
667542	4968039	WB Main	Ti-Cf Lignite trace 1	423
667264	4967812	WB Main	SC-179 top	471

APPENDIX II-D: Y2K Quarry trace

UTM Easting	UTM Northing	Section	Bed	Meter Level
668000	4970900	Y2K Quarry	—	264
668001	4970728	Y2K Quarry	Trace - CS	291
667886	4970651	Y2K Quarry	Trace - Bench Mark (est. strat. thickness)	314
667612	4970421	Y2K Quarry	Trace	350
667586	4970318	Y2K Quarry	Trace	355
667544	4970377	Y2K Quarry	Trace	355
667550	4970162	Y2K Quarry	Trace	360
667386	4970089	Y2K Quarry	Trace	388
667386	4970089	Y2K Quarry	Trace	388
667042	4969904	Y2K Quarry	Y2K - BTQ trace	395
667106	4970062	Y2K Quarry	Y2K - BTQ trace	395
667175	4970176	Y2K Quarry	Y2K - BTQ trace	395
667395	4970075	Y2K Quarry	Y2K - BTQ trace	395

APPENDIX II-E: Ti-Cf boundary marker lignite

UTM Easting	UTM Northing	Bed Trace	Segment	Meter Level (WB)
667701	4968969	Ti-Cf Marker lignite	1	429
667674	4968957	Ti-Cf Marker lignite	1	429
667653	4968954	Ti-Cf Marker lignite	1	429
667002	4968983	Ti-Cf Marker lignite	2	429
666979	4968984	Ti-Cf Marker lignite	2	429
666963	4969069	Ti-Cf Marker lignite	2	429
666988	4969105	Ti-Cf Marker lignite	2	429
667035	4969133	Ti-Cf Marker lignite	2	429
667062	4969152	Ti-Cf Marker lignite	2	429
667044	4969173	Ti-Cf Marker lignite	2	429
667122	4969169	Ti-Cf Marker lignite	2	429
667092	4969241	Ti-Cf Marker lignite	2	429
667172	4969225	Ti-Cf Marker lignite	2	429
667282	4969262	Ti-Cf Marker lignite	2	429
667268	4969305	Ti-Cf Marker lignite	2	429
667327	4969337	Ti-Cf Marker lignite	2	429
667377	4969401	Ti-Cf Marker lignite	2	429
667312	4969397	Ti-Cf Marker lignite	2	429
667374	4969451	Ti-Cf Marker lignite	2	429
667277	4969463	Ti-Cf Marker lignite	2	429
667261	4969456	Ti-Cf Marker lignite	2	429
667212	4969438	Ti-Cf Marker lignite	2	429
667148	4969457	Ti-Cf Marker lignite	2	429
667139	4969448	Ti-Cf Marker lignite	2	429
667143	4969370	Ti-Cf Marker lignite	2	429
667176	4969396	Ti-Cf Marker lignite	2	429
667208	4969436	Ti-Cf Marker lignite	2	429
667432	4969374	Ti-Cf Marker lignite	2	429
667405	4969309	Ti-Cf Marker lignite	2	429
667381	4969263	Ti-Cf Marker lignite	2	429
667327	4969187	Ti-Cf Marker lignite	2	429
667275	4969170	Ti-Cf Marker lignite	2	429
667305	4969217	Ti-Cf Marker lignite	2	429
667348	4969272	Ti-Cf Marker lignite	2	429
667283	4969271	Ti-Cf Marker lignite	2	429
667165	4969218	Ti-Cf Marker lignite	2	429
667102	4969157	Ti-Cf Marker lignite	2	429
667046	4969093	Ti-Cf Marker lignite	2	429
667018	4969047	Ti-Cf Marker lignite	2	429
666699	4969441	Ti-Cf Marker lignite	3	429
666711	4969394	Ti-Cf Marker lignite	3	429
666694	4969349	Ti-Cf Marker lignite	3	429
666670	4969302	Ti-Cf Marker lignite	3	429
666664	4969232	Ti-Cf Marker lignite	3	429
666652	4969194	Ti-Cf Marker lignite	3	429
666655	4969178	Ti-Cf Marker lignite	3	429
666635	4969150	Ti-Cf Marker lignite	3	429
666629	4969186	Ti-Cf Marker lignite	3	429
666621	4969251	Ti-Cf Marker lignite	3B	429
666556	4969220	Ti-Cf Marker lignite	3B	429
666537	4969181	Ti-Cf Marker lignite	3C	429
666497	4969172	Ti-Cf Marker lignite	3C	429
666468	4969177	Ti-Cf Marker lignite	3D	429
666357	4969174	Ti-Cf Marker lignite	3D	429
666310	4969155	Ti-Cf Marker lignite	3D	429
666271	4969092	Ti-Cf Marker lignite	3D	429
666222	4969102	Ti-Cf Marker lignite	3D	429
666175	4969078	Ti-Cf Marker lignite	3D	429
666180	4969024	Ti-Cf Marker lignite	3D	429
666150	4968980	Ti-Cf Marker lignite	3D	429
666084	4968981	Ti-Cf Marker lignite	3D	429
666035	4968970	Ti-Cf Marker lignite	3D	429
666050	4968924	Ti-Cf Marker lignite	3D	429
667143	4968452	Ti-Cf Marker lignite	4	429
667228	4968437	Ti-Cf Marker lignite	4	429
667286	4968403	Ti-Cf Marker lignite	4	429
667295	4968428	Ti-Cf Marker lignite	4	429
667358	4968464	Ti-Cf Marker lignite	4	429
667418	4968397	Ti-Cf Marker lignite	4	429
667448	4968361	Ti-Cf Marker lignite	4	429
667554	4968254	Ti-Cf Marker lignite	4	429
667654	4968240	Ti-Cf Marker lignite	4	429
667870	4968151	Ti-Cf Marker lignite	4	429
667867	4968163	Ti-Cf Marker lignite	4	429
667817	4968232	Ti-Cf Marker lignite	4	429
667861	4968260	Ti-Cf Marker lignite	4	429
667846	4968270	Ti-Cf Marker lignite	4	429
667817	4968289	Ti-Cf Marker lignite	4	429
667758	4968270	Ti-Cf Marker lignite	4	429
667731	4968277	Ti-Cf Marker lignite	4	429
667733	4968308	Ti-Cf Marker lignite	4	429
667709	4968362	Ti-Cf Marker lignite	4	429
667757	4968359	Ti-Cf Marker lignite	4	429
667821	4968337	Ti-Cf Marker lignite	4	429
667867	4968305	Ti-Cf Marker lignite	4	429

APPENDIX II-F: South Bench main stratigraphic section

UTM Easting	UTM Northing	Section	Bed	Meter Level (WB)
678820	4971562	SB	Mantua Quarry	0
678706	4971452	SB	Lateral trace	28
678757	4971348	SB	Lateral trace	28
678684	4971311	SB	Lateral trace - LT-1	52
679044	4971014	SB	Lateral trace - LT-1	52
679103	4970617	SB	Lateral trace - LT-2	56
679211	4970227	SB	Lateral trace - LT-2	56
679229	4969988	SB	Lateral trace - LT-2	56
679075	4970184	SB	Black chert	102
678981	4969806	SB	—	102
678798	4969685	SB	—	185
678304	4970246	SB	Lateral trace - LT-3	208
678761	4969456	SB	Lateral trace - LT-3	208
678795	4969356	SB	Lateral trace - LT-3	208
678674	4968976	SB	Lateral trace - LT-3	208
678659	4968890	SB	Cross canyon correlation	211
678307	4968661	SB	Near hilltop	279
678084	4968508	SB	Cross canyon correlation	285
677963	4968700	SB	Lateral trace CS	291
677435	4969077	SB	LT-4, Belt ash	331
677524	4968820	SB	LT-4, Belt ash	331
677613	4968824	SB	LT-4, Belt ash	331
677657	4968684	SB	LT-4, Belt ash	331
677368	4968085	SB	LT-4, Belt ash	331
677616	4968641	SB	LT-4, Belt ash	331
677649	4968596	SB	LT-4, Belt ash	331
677368	4969085	SB	LT-4, Belt ash	331
677361	4969348	SB	LT-4, Belt ash	331
677185	4969389	SB	LT-4, Belt ash	331
677158	4969342	SB	LT-4, Belt ash	331
677097	4969299	SB	LT-4, Belt ash	331
677049	4969422	SB	Red-yellow LSN pods	336
676999	4969493	SB	Lignite	342
676594	4969836	SB	Lateral trace	366
676840	4969658	SB	Lateral trace	366
676560	4969819	SB	Bentonite above road cut	371
676393	4969790	SB	Correlation across road cut	371
676214	4969478	SB	Sandstone	478
674673	4968772	SB	Top of Bench correlation	742
674062	4967881	SB	—	742
673392	4967457	Ridge Crest	Correlation	819
672793	4967134	Ridge Crest	Correlation	819
671979	4966450	—	Sandstone at top of ridge	849
671498	4965765	—	Bluff capping sandstone	849
671168	4964920	Eagle's Nest	Top of sandstone	872
670800	4964050	SB	—	938

APPENDIX III: LOCALITIES

List of meter levels and coordinates for localities included in this study. All Universal Transverse Mercator (UTM) coordinates are in Grid Zone 12T, are reported using the NAD 27 CONUS datum, and are rounded to the nearest 100 meters. More precise coordinates are available to qualified researchers by contacting the University of Michigan Museum of Paleontology. Composite levels are based primarily on magnetostratigraphic correlation of West Bench (WB) and Foster Gulch sections to South Bench Section (Fig. 6) (see Secord et al., 2006). Abbreviations: *Comp PDG 2001*, composite meter levels from Gingerich (2001) and Gingerich and Clyde (2001); *Comp this paper*, composite meter levels used in this study.

Locality	Biozone	WB (m)	Comp PDG 2001 (m)	Comp this paper (m)	UTM Easting	UTM Northing
Bear Creek (Eagle Mine)	Cf-1	—	0	0	643900	5000900
Bluff Top Q. (SC379)	Ti-6	379	0	843	667100	4969800
Cedar Point Q.	Ti-3	—	215	200	707700	4955400
Croc Tooth Q. (FG028)	Ti-4b	—	415	365	712400	4950900
Divide Q. (FG046)	Ti-4a	—	0	265	713900	4948200
FG001	Ti-5	—	0	0	693600	4954100
FG002	Ti-5	—	0	0	693700	4954300
FG003	Ti-?	—	0	0	695100	4952500
FG004	Ti-5	—	0	0	690000	4955800
FG005	Ti-5	—	0	0	689400	4954900
FG007	Ti-4	—	0	0	700600	4955600
FG008	Ti-4	—	0	0	701000	4955300
FG009	Ti-5	—	0	0	700600	4954500
FG010	Cf-?	—	0	0	684300	4956000
FG012	Cf-?	—	0	0	688100	4953400
FG013	Ti-5	—	0	0	692600	4956100
FG014	Ti-?	—	0	0	692600	4956200
FG015	Ti-4?	—	0	0	692900	4955900
FG016	Ti-4	—	0	0	692900	4956100
FG021	Cf-?	—	0	0	694200	4949000
FG036	Ti-6/Cf-1	—	0	0	711000	4950300
FG037	Ti-6/Cf-1	—	0	0	711100	4950400
FG038	Ti-6/Cf-1	—	0	0	713300	4947800
FG041	Cf-1/Cf-2	—	0	0	710000	4950900
FG044	Ti-4	—	0	0	711500	4951700
FG045	Ti-?	—	0	0	710500	4952800
FG047	Ti-5	—	0	0	709600	4952100
FG048	Ti-5	—	0	0	709300	4951800
FG049	Ti-5	—	0	0	708600	4952200
FG050	Ti-5	—	0	0	708100	4952300
FG053	Ti-?	—	0	0	707500	4954100
FG054	Ti-?	—	0	0	705500	4953500
FG055	Ti-4b	—	0	0	701300	4952400
FG063	Cf-?	—	0	0	703800	4948300
FG064	Cf-?	—	0	0	710800	4949000
FG069	Cf-?	—	0	0	707700	4948300
FG071	Cf-?	—	0	0	700000	4947600
FG093	Cf-?	—	0	0	723400	4936100
FG096	Cf-?	—	0	0	728600	4930600
FG099	Cf-?	—	0	0	701900	4949100
FG101	Cf-?	—	0	0	699300	4949000
Fossil Hollow (SC198)	Ti-4b	-15	655	426	668800	4973100
Hail Q.	Ti-5a	59	0	505	666000	4974100
Jepsen Q.	Ti-3	—	0	0	709000	4954300
Long Draw Q.	Ti-4a	—	0	265	668500	4989200
MP010	Cf-?	—	0	0	663100	4936900
MP054	Ti-4b	—	0	0	668900	4930800
MP093	Ti-5	—	0	0	668200	4931900
MP094	Ti-4b?	—	0	0	662300	4932700
MP115	Ti-4b	—	0	0	662000	4933300
Princeton Q. (SC187)	Ti-5a	—	530	592	663300	4974200
SC078	Cf-1	—	1145	0	670800	4962700
SC082	Cf-1	—	1025	0	671100	4963200
SC083	Cf-1	—	965	938	670800	4964100
SC085	Ti-6	—	860	828	672500	4966800
SC086	Ti-6	—	840	808	673100	4967000
SC134	Cf-1	—	1160	0	652300	4971400
SC135	Cf-1	—	1160	0	650500	4971700
SC144	Ti-5a	135	655	586	665700	4973500
SC156	Cf-1/2	—	1030	0	661500	4968200
SC165	Ti-5b	185	710	640	668500	4971000
SC169	Cf-1	—	985	0	660600	4969800
SC170	Cf-1	581	1020	1045	658700	4970100

APPENDIX III: (Cont.)

Locality	Biozone	WB (m)	Comp PDG 2001 (m)	Comp this paper (m)	UTM Easting	UTM Northing
SC171	Cf-1	580	1030	1044	658700	4969800
SC172	Cf-1	580	1030	1044	655800	4972100
SC173	Cf-1	550	1000	1014	655900	4972600
SC174	Cf-1	550	1000	1014	657500	4971400
SC177	Cf-1	—	1020	0	661200	4968500
SC178	Ti-6	300	820	762	665200	4970400
SC179	Cf-1	435	885	899	667200	4967800
SC180	Ti-6	399	855	863	667000	4969000
SC181	Cf-1	402	865	866	666300	4969100
SC185	Ti-6	275	805	736	665600	4971100
SC186	Ti-5b	200	730	656	663800	4971900
SC187	Ti-5a	—	530	592	663300	4974200
SC191	Ti-6	330	835	794	666000	4970000
SC193	Ti-6	377	855	841	666500	4969600
SC194	Cf-1	—	1135	0	667200	4966200
SC199	Ti-5b	211	730	667	667500	4972100
SC208	Cf-1	650	1100	1114	649800	4972600
SC215	Cf-1	535	985	999	654600	4974000
SC216	Cf-1?	470	920	934	655400	4974500
SC217	Cf-1?	470	920	934	656500	4973500
SC223	Ti-6	—	780	761	674100	4967600
SC226	Cf-1?	500	950	964	654100	4975100
SC227	Cf-1?	430	880	894	656000	4974800
SC228	Ti-5a	—	585	527	675500	4968600
SC229	Ti-5a	—	510	504	665400	4975300
SC239	Ti-4b	—	490	461	676200	4969000
SC240	Ti-4b	—	415	385	676900	4969100
SC241	Ti-4a	—	395	330	677300	4969300
SC242	Ti-5a	—	635	588	675100	4968600
SC243	Ti-4b	—	415	350	677400	4968400
SC244	Ti-6	—	860	828	672800	4966900
SC245	Ti-6	—	855	823	673000	4967100
SC246	Ti-5a	—	540	489	675700	4969000
SC247	Cf-1	—	1025	0	671000	4963900
SC248	Cf-1	456	895	920	660600	4970700
SC249	Cf-1	—	895	0	660500	4971600
SC250	Cf-1	600	1050	1064	658000	4970100
SC251	Cf-1	546	985	1010	658600	4970900
SC252	Ti-5b	—	695	625	674900	4968400
SC257	Cf-1?	405	855	869	656900	4975000
SC258	Cf-1?	—	0	0	656900	4980000
SC259	Cf-1?	420	870	884	656900	4974500
SC260	Cf-1?	440	890	904	656800	4973900
SC261	Ti-4a	—	300	265	678300	4968500
SC262	Ti-3	—	215	210	678600	4969300
SC263	Ti-3	—	155	200	678800	4969600
SC266	Ti-5a	—	510	570	659800	4975600
SC267	Ti-5a	—	510	517	662300	4975000
SC268	Ti-5a	—	510	528	660300	4976200
SC269	Ti-4a	—	335	295	678000	4969100
SC270	Ti-5a	—	510	568	663700	4974900
SC271	Ti-5a	—	510	557	664200	4974900
SC273	Ti-5a	—	510	541	664700	4975100
SC274	Ti-5a	—	510	519	664700	4975600
SC275	Ti-5b	260	690	720	663000	4972200
SC276	Ti-6	280	690	741	663300	4972100
SC277	Ti-5a	—	510	546	665000	4974900
SC278	Ti-5b	266	690	726	661900	4972300
SC279	Ti-4b	—	510	441	666400	4976400
SC280	Ti-5a	—	510	517	661200	4975400
SC281	Ti-4b?	—	510	0	661200	4975900
SC282	Ti-6	300	710	762	662600	4971500
SC283	Ti-4b	1	490	443	667300	4975500
SC285	Cf-1?	500	950	964	656000	4973300
SC286	Cf-1	540	990	1004	655000	4973500
SC337	Ti-2?	—	0	0	683200	4964800
SC338	Cf-1	—	0	0	650000	4977000
SC339	Ti-3	—	0	0	678000	4968700
SC340	Ti-4a	—	0	330	677600	4968600
SC358	Cf-1?	—	0	0	649800	4945100
SC359	Cf-1	—	0	0	656200	4942300
SC362	Cf-1	433	875	897	667100	4968300
SC369	Ti-6	389	—	853	666800	4970900
SC370	Ti-6	332	—	796	666500	4970900
SC371	Ti-6	321	—	785	666500	4970600
SC372	Ti-6	387	—	851	666800	4969900
SC373	Ti-6	345	—	809	667300	4970100
SC374	Ti-6	351	—	815	666600	4970700
SC375	Cf-1	—	—	872	671200	4964500
SC376	Ti-6	—	—	860	671200	4965000

APPENDIX III: (Cont.)

Locality	Biozone	WB (m)	Comp PDG 2001 (m)	Comp this paper (m)	UTM Easting	UTM Northing
SC377	Ti-6	—	—	842	671400	4965800
SC379	Ti-6	379	—	843	667000	4969900
SC380	Ti-6	373	—	837	666600	4970700
SC382	Ti-6	306	—	769	666300	4970900
SC383	Ti-6	324	—	788	666700	4971200
SC384	Ti-5b	185	—	640	666500	4971700
SC385	Ti-5b	269	—	729	667300	4971500
SC386	Ti-5b	234	—	692	667700	4971500
SC387	Ti-5b	202	—	658	668000	4971500
SC388	Ti-5a	171	—	625	667700	4971800
SC389	Ti-5b	232	—	690	668100	4970900
SC390	Ti-5b	270	—	730	668000	4970700
SC391	Ti-6	290	—	752	666800	4971600
SC392	Ti-4b	1	—	443	667100	4975300
SC393	Ti-4b	-3	—	439	667700	4975300
SC394	Ti-4b	-12	—	429	667300	4975300
SC395	Ti-4b	1	—	443	668000	4974300
SC396	Ti-4b	15	—	458	668200	4974000
SC397	Ti-4b	1	—	443	667100	4974300
SC398	Cf-1	—	—	0	667700	4968900
SC399	Ti-6	360	—	824	667800	4968700
SC400	Ti-6	395	—	859	667500	4968600
SC401	Ti-6	379	—	843	667700	4968900
SC402	Ti-6	367	—	831	666800	4969700
SC403	Cf-1	—	—	0	667900	4968000
SC406	Cf-1	—	—	872	671200	4965400
SC407	Ti-6	358	—	822	666800	4970200
SC408	Ti-6	365	—	829	666900	4970400
SC409	Ti-6	340	—	804	666400	4970500
SC410	Ti-6	370	—	834	666900	4970200
SC411	Ti-6	335	—	799	666900	4970400
SC412	Ti-3	—	—	207	678300	4970200
SC413	Cf-1	546	—	1010	653900	4974000
SC414	Cf-1	546	—	1010	654300	4974400
SC415	Ti-3	—	—	200	679000	4969100
SC416	Ti-5b	—	—	671	662700	4973400
SC417	Ti-4b	40	—	485	666400	4974200
SC418	Ti-5a	99	—	548	667100	4973100
SC419	Ti-5a	180	—	634	664800	4973300
SC420	Ti-4b	—	—	473	665800	4975500
SC421	Ti-5a	125	—	576	664200	4974500
SC422	Ti-5a	47	—	492	667400	4973800
SC423	Ti-4b	30	—	474	667300	4973600
SC424	Ti-4b	27	—	471	667400	4974200
SC429	Ti	—	—	110	678900	4970100
Schaff Q.	Ti-5a	—	530	573	664500	4974500
Seaboard Well	Ti-4	—	0	0	662500	4982900
Storm Q.	Ti-5a	150	530	602	—	—
Y2K Quarry (SC389)	Ti-5b	234	—	692	668100	4970900
Zalmout Q. (SC389)	Ti-5b	228	—	686	—	—