Puercan mammalian systematics and biostratigraphy in the Denver Formation, Denver Basin, Colorado

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ABSTRACT

As a result of the Denver Basin Project, several more fossils of Puercan mammals are reported here from five areas in the Denver Formation: South Table Mountain, Greater Denver, the West Bijou Site, Big Gulch, and Corral Bluffs. Systematic description and discussion are provided for one multituberculate and 11 ungulate taxa, including a new species of *Baioconodon*. Some taxa represent extensions of previously recognized temporal and geographic ranges. Notably, the ungulate *Protungulatum donnae* from strata of early Puercan (Pu1) age in the Denver Formation represents the southernmost occurrence of the species, while *Oxyclaenus simplex*, in probable early Puercan strata of the Denver Formation, appears to represent both a temporal and geographic range extension from middle Puercan (Pu2) strata of the San Juan Basin, New Mexico. Additionally, I report the first occurrence in the Denver Basin of the arctocyonid *Loxolophus faulkneri*. Refined biostratigraphic interpretations, resulting from new discoveries and incorporating paleomagnetic, palynological, and radioisotopic analyses presented elsewhere, suggest that Puercan interval zones Pu1 and Pu2 are both represented by mammalian faunas in the Denver Formation. Localities at South Table Mountain, as well as the Denver Oxyclaenodon Site (DMNH loc. 299) and Nicole's Mammal Jaw locality (DMNH loc. 2557), are Pu1 correlatives. Discoveries reported here support previous interpretations that the Alexander and South Table Mountain localities are probably similar in age (i.e., Pu1) and are included here in the Littleton fauna. Based upon comparison to other Puercan faunas, the Littleton fauna may be temporally intermediate between typical Pu1 assemblages known north of the Denver Basin and earliest Pu2 assemblages from the Hanna Basin, Wyoming. Alternatively, faunal differences between the Littleton fauna and other Pu1 faunas may reflect ecological and biogeographic differences. The unusually high diversity of ungulates in the Littleton fauna suggests some of the diversification that elsewhere characterizes the onset of Pu2 may already have begun by Pu1 in the Denver Basin. The mammalian assemblage at Corral Bluffs is interpreted here as a probable Pu2 correlative, based upon occurrence of *Loxolophus faulkneri*, *Conacodon entoconus*, and *C. delphae*, and absence of Pu3 index taxa. Pu2/Pu3 correlatives (i.e., faunal assemblages that are either Pu2 or Pu3) also are reported here from the Big Gulch area, although more fossils are needed to refine their ages. The present study and others in this issue demonstrate that the Denver Basin is among the few places wherein correlation between Puercan mammalian biostratigraphy and paleomagnetic, palynological, and radioisotopic analyses is an attainable goal.

KEY WORDS: biostratigraphy, Paleocene, Puercan, Denver Formation, Denver Basin, Colorado, Eutheria, Multituberculata, Ungulata.

INTRODUCTION

The single most important evolutionary radiation amongst mammals, marked by rapid diversification and increase in body size, took place in the first million years after the Cretaceous-Tertiary (K-T) boundary (Alroy, 1999), a time interval coined by paleomammalogists as the Puercan North American Land Mammal "Age" (NALMA). Few places in North America preserve this explosive diversification wherein the roots of many modern mammalian orders were born. The Denver Basin, east of the Front Range in central Colorado, is one such place. Of the three Puercan interval-zones defined elsewhere (i.e., Pu1–Pu3; see Archibald et al., 1987 and Lofgren et al., in press), at least two are represented by mammalian faunal assemblages preserved in early Paleocene parts of the synorogenic, primarily fluvial, Late Cretaceous–Paleocene-spanning Denver Formation (D1 sequence of Raynolds, 2002).

While discoveries of dinosaurs and fossil leaves from the Denver Formation date back over a century (see Emmons et al., 1896 and Knowlton, 1896), the first early Paleocene mammals were discovered in 1939, from South Table Mountain, near Golden, and in the Corral Bluffs, east of Colorado Springs (Gazin, 1941a). Historically very important, South Table Mountain was the first site in North America where the K-T boundary was identified (Brown, 1943). In the late 1970s and early 1980s, early Paleocene mammals were discovered in Littleton (Alexander locality) and the West Bijou Creek area (eastern Denver Basin), and more specimens were recovered from Corral Bluffs and South Table Mountain, primarily by parties from the University of Colorado Museum (UCM). In his largely unpublished doctoral dissertation, Middleton (1983) described over 30 Puercan mammalian taxa, including several new species. While some of these new species have since been reported from the Hanna Basin of Wyoming by Eberle and Lillegraven (1998b), most remain unpublished. However, recent study of material from the Alexander locality by E. Dewar and M. Middleton offers promise that the new species will soon be published (Dewar, personal communication, 2002). Fieldwork in the 1990s through 2001, primarily associated with the Denver Museum of Nature & Science's Denver Basin Project, resulted in discovery of new mammal-bearing localities in the West Bijou and Big Gulch areas and recovery of more mammalian fossils from South Table Mountain and Corral Bluffs.

The principal objectives of this paper are to describe the Puercan mammalian fossils recovered subsequent to Middleton's (1983) study and to update and revise the early Paleocene mammalian biostratigraphy in the Denver Basin through comparison to other areas. Where available, data from palynology, paleomagnetics, and geochronology (see other papers in this issue) are incorporated here, as they provide independent means of dating and/or refining the dates of vertebrate fossil-bearing localities.

PUERCAN NORTH AMERICAN LAND MAMMAL AGE (NALMA)

The Puercan NALMA is an "age" in a provincial time scale, unique to North American nonmarine strata and based upon the occurrences of mammalian fossil taxa, that represents approximately the first million years of the Tertiary (Wood et al., 1941; Eberle and Lillegraven, 1998a; Swisher et al., 1993). The Puercan begins with the appearance of the ungulate *Protungulatum*, and ends with the appearance of the periptychid ungulate *Periptychus carinidens* (Archibald and Lofgren, 1990; Lofgren et al., in press).

Archibald et al. (1987) originally subdivided the Puercan into three interval zones (Pu1, Pu2, and Pu3, from oldest to youngest, respectively) based upon successive first appearances of mammalian taxa. Subsequently, Archibald and Lofgren (1990) suggested presence of a fourth interval zone, Pu0, preceding Pu1. However, where it was originally defined in northeastern Montana, Pu0 lacks index taxa and is differentiated from Pu1 by the absence of typical Pu1 taxa. Consequently, Pu0 and Pu1 faunas can be virtually identical (Lofgren, 1995). Furthermore, Pu0 cannot be recognized in the thickest, most complete Puercan section known (the Ferris Formation in the Hanna Basin of Wyoming), which preserves superposed mammalian assemblages representing Pu1 through Pu3 (Eberle and Lillegraven, 1998a; 1998b). This led Lofgren et al. (in press) to merge Pu0 and Pu1, and identify only three Puercan interval zones, the *Protungulatum/Ectoconus* Interval Zone (Pu1), *Ectoconus/Taeniolabis taoensis* Interval Zone (Pu2), and *Taeniolabis taoensis/Periptychus carinidens* Interval Zone (Pu3). Throughout the present paper, interval zones Pu1, Pu2, and Pu3 will be considered to equate with early, middle, and late Puercan time, respectively.

Where paleomagnetic analyses have been done on strata containing Puercan faunal assemblages, Pu1 faunas occur in strata of reversed polarity, correlated to C29r. Interval-zones Pu2 and Pu3 occur in strata of normal polarity, correlated to C29n (Lofgren et al., in press).

GEOGRAPHIC AND GEOLOGIC SETTING

The Denver Basin, an asymmetric structural basin whose axis lies near the Front Range, extends from Greeley southward to Colorado Springs, and from the mountain front eastward to Limon (Fig. 1). An estimated 915 m (3000 ft) of Late Cretaceous–

Eocene, synorogenic strata representing sediments eroded off the rising Front Range during the Laramide orogeny, infill the basin (Soister, 1978; Raynolds, 2002). The Late Cretaceous–Paleocene Denver Formation, named for the city of Denver as its "beds form the surface of the city" (Cross, 1888, p. 119), has an estimated maximum thickness of 460 m (Soister, 1978). In discussing the effects of the Laramide orogeny in the Denver Basin, Raynolds (2002) termed the two distinct pulses of synorogenic sedimentation the D1 and D2 sequences; the Denver Formation is contained within the older, D1 sequence. The formation is comprised primarily of fluvial strata that typically contain andesitic volcanic debris (Middleton, 1983; Soister, 1978). For details of the stratigraphy and sedimentology of the D1 sequence, including the Denver Formation, see Raynolds (2002). The age range for the Denver Formation is based upon fossil vertebrates (dinosaurs and mammals), pollen, magnetostratigraphy, and radioisotopic dating (Middleton, 1983; Nichols and Fleming, 2002; Obradovich, 2002; and Hicks et al., this issue).

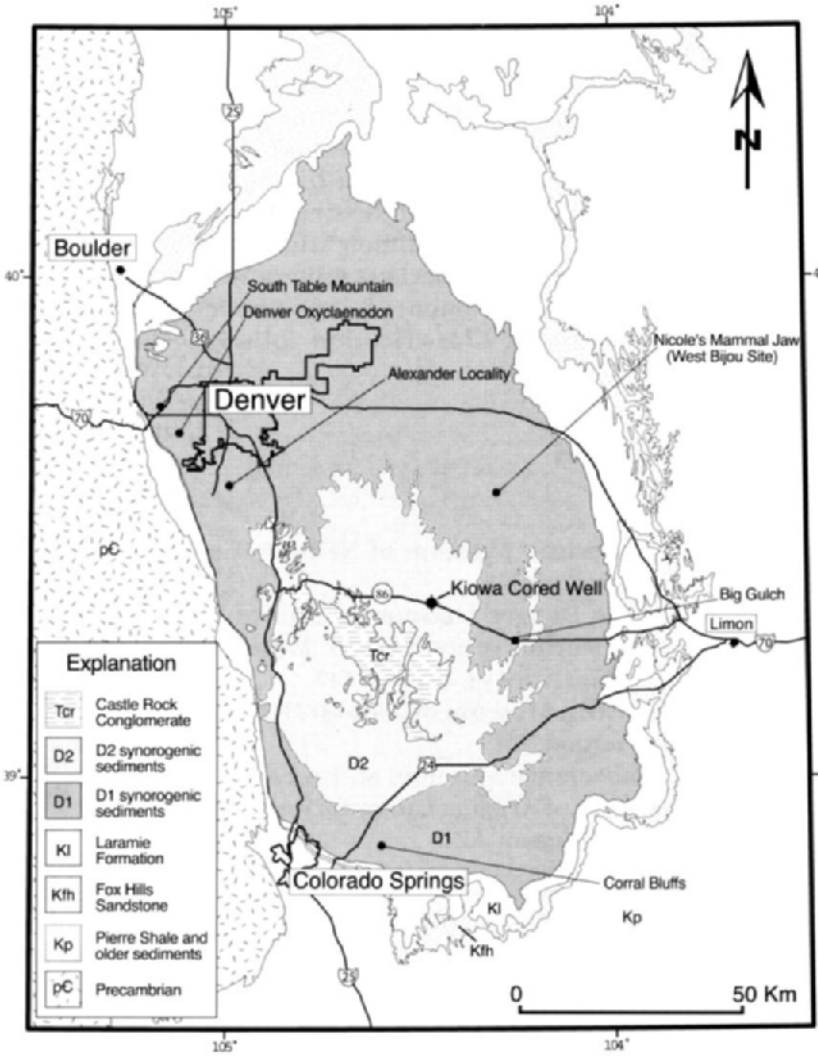

Figure 1. Map of Denver Basin, showing general location of study areas: South Table Mountain; greater Denver (which includes Alexander and Denver Oxyclaenodon localities); Corral Bluffs; West Bijou Site; and Big Gulch.

PALEONTOLOGICAL METHODS

Localities bearing fossil vertebrates were plotted on 1:50,000-scale topographic maps, and GPS coordinates were taken at each site. While some new localities resulted from the Denver Basin Project, several specimens also were recovered from sites originally discovered by Brown (South Table Mountain; see Gazin, 1941a) and the UCM (several localities at Corral Bluffs), reported by Middleton (1983). Steve Wallace, paleontologist for the Colorado Department of Transportation (CDOT), discovered DMNH 2563 and the Denver Crockies locality near Big Gulch.

Stratigraphic relationships of localities at South Table Mountain, Corral Bluffs, and Big Gulch were determined via detailed mapping and section measuring by R. Raynolds and other members of the Denver Basin Project. Nicole's Mammal Jaw locality (DMNH loc. 2557) is included in a stratigraphic section measured by Barclay et al. (this issue). For detailed locality information, qualified researchers are asked to contact collections managers at the DMNS in Denver and the UCM in Boulder.

Most vertebrate fossils were recovered as float on the surface. Exceptions include DMNH loc. 2563 (= UCM loc. 91280), in which many mammalian fossils were recovered via screen-washing and sorting under the microscope, and Brown's *Baioconodon* locality (DMNH loc. 2387 = UCM loc. 77283) on South Table Mountain, in which quarrying resulted in several more specimens. Specimens are catalogued in paleontological collections at the DMNS and the UCM.

Only mammalian dental remains are described in this study. All dental measurements were done via a reticule in the eyepiece of a Nikon SMZ 1500 stereozoom microscope, and are in millimeters. Terminology and measurements of the single multituberculate tooth described here follow Middleton (1982). Cusp terminology for therians follows Van Valen (1966), while measurements follow Eberle and Lillegraven (1998b). Classification follows McKenna and Bell (1997).

ABBREVIATIONS

Institutions

AMNH The American Museum of Natural History, New York NY

DMNH/DMNS The Denver Museum of Nature & Science (formerly the Denver Museum of Natural History), Denver CO

NMMNH New Mexico Museum of Natural History, Albuquerque NM

SPSM St. Paul Science Museum, St. Paul MN

UALP University of Arizona Laboratory of Paleontology, Tucson AZ

UCM Museum, The University of Colorado, Boulder CO

UCMP Museum of Paleontology, University of California, Berkeley CA

USNM Department of Paleobiology, U.S. National Museum of Natural History, Smithsonian Institution, Washington DC

UW Collection of Fossil Vertebrates, Departmental Scientific Collections, Department of Geology and Geophysics, The University of Wyoming, Laramie WY

Dental Terminology and Measurements

Lowercase letters (e.g., m1) designate teeth from lower jaws

Uppercase letters (e.g., M1) designate teeth from upper jaws

L Left tooth (e.g., Lm1)

R Right tooth (e.g., Rm1)

Length Anteroposterior length

LTri Length of trigonid

LTal Length of talonid

WTri Width of trigonid

WTal Width of talonid

* Estimated measurement, required by breakage or wear

x Locus of tooth within dental series is uncertain (e.g., Rmx)

PUERCAN MAMMAL-BEARING LOCALITIES

Introduction

Fossils described in this report come from localities in five general regions (Fig. 1): South Table Mountain; Greater Denver (which includes sites in Littleton and Lakewood); Corral Bluffs; the West Bijou Site (see Barclay et al., this issue); and Big Gulch. Other Puercan localities in the Denver Basin were reported by Middleton (1983), but they were either not relocated or no additional fossils were recovered as a result of the Denver Basin Project, and consequently they are not discussed here.

South Table Mountain

Brown's Baioconodon locality (DMNH loc. 2387 = UCM loc. 77283)

This is the locality, along a ridge on the southeastern flank of South Table Mountain, at which Roland Brown (USGS) discovered Puercan mammals in 1939 and 1940 (see Gazin, 1941a, fig. 1). The locality, in exposures of the Denver Formation owned by Jefferson County Open Space, is in the NW1/4 of Section 31, T. 3 S., R. 69 W. From collections made by the University of Colorado Museum in the 1960s–1980s, Middleton (1983) described the South Table Mountain fauna in his study of Puercan vertebrates of the Denver Basin. Renewed collecting in the 1990s by DMNS resulted in several more specimens and a doubling in the recorded diversity. While most vertebrate fossils occurred as float, some were found in situ in light-colored, sandy mudstone and sandstone (Middleton, 1983; personal observation).

This site is the first in North America in which the K-T boundary was identified. Based upon the occurrence of dinosaur bones at the base of the ridge and earliest Tertiary plants and mammals at the top of the ridge, Brown (1943) surmised that the K-T boundary was within roughly a 49 ft (15 m) interval between the dinosaur-bearing strata and the mammal-bearing strata. Based upon palynology, Kauffman et al. (1990) refined the position of the K-T boundary to within an interval of about 16 ft (4.9 m; see Nichols and Fleming, 2002). As part of the Denver Basin Project, vertebrate fossils were recovered from a ten-meter interval in the vicinity of a channel sandstone coined the Alligator Sandstone;

this interval is approximately 49–82 ft (15–25 m) above the palynologically based K-T boundary of Kauffman et al. (1990). Brown's *Baioconodon* locality is approximately 59 ft (18 m) stratigraphically above the K-T boundary (Raynolds, personal communication, 2001).

Paleomagnetic analyses indicate that strata on both sides of the K-T boundary at South Table Mountain are of reversed polarity, correlated to C29R (R. Barclay, personal communication, 2002). Although relatively undiverse, the mammalian fauna at Brown's Baioconodon locality shares most of its taxa with the early Puercan (Pu1) Alexander locality in Littleton, Colorado (discussed below). The faunal similarity led Middleton (1983) to suggest that the sites are coeval and to include both in the Littleton local fauna. In addition to fossil turtles described by Hutchison and Holroyd (this issue), reptilian fossils recovered at or near Brown's Baioconodon locality include osteoderms and teeth referred to Alligatoroidea and a distal limb fragment of a lizard (X.-C. Wu, personal communication, 2001). *Lepisosteus* (gar) is rare. A pollen sample taken from the same strata that preserve the fossil mammals represents the lowermost Paleocene, palynomorph Zone P1 (Nichols and Fleming, 2002). A flora of fossil leaves, coined the Paleocene Piedmont flora by Johnson et al. (this issue), was discovered in the same channel deposit as Brown's Baioconodon locality.

Michon's Multi locality (DMNH loc. 2386)

Located on the west side of the same ridge that contains Brown's *Baioconodon* locality, Michon's Multi locality yielded a m2 of the multituberculate *Catopsalis alexanderi* and a crocodilian osteoderm as float. Michon's Multi locality is approximately two meters stratigraphically below Brown's *Baioconodon* locality (Raynolds, personal communication, 2000). However, as the fossils were found as float at Michon's Multi locality, they may have eroded from the same stratigraphic level as Brown's *Baioconodon* locality. *Catopsalis alexanderi* is also known from the Alexander locality, the Fort Union (= Polecat Bench) Formation in Wyoming, and the upper Hell Creek and lower Tullock Formations in Montana (Lofgren, 1995; Middleton, 1982), all early Puercan (Pu1) in age.

Greater Denver

Alexander locality (UCM loc. 77267)

Discovered in 1973 by Carl Alexander at a construction site in Littleton, the Alexander locality is the most productive fossil mammal site in the Denver Formation, where mammalian fossils outnumber their lower vertebrate counterparts (Middleton, 1983). The vertebrate fossils, described by Middleton (1983), were found as float over a large area, on nearly horizontal, fine-grained beds. Subsequently, Dewar (1996) analyzed mammalian paleoecology at the Alexander locality. Much of the site has since been covered over by an industrial park, and despite renewed prospecting associated with the Denver Basin Project, no new fossils were discovered. The Alexander locality's diverse vertebrate fauna comprised some 20 mammalian species-level taxa and 12 taxa of lower vertebrates. The fauna's age was interpreted by Middleton (1983) as early Puercan but temporally intermediate between the early Puercan Mantua Lentil local fauna in the Bighorn Basin, Wyoming and the middle Puercan fauna of the San Juan Basin, New Mexico. Paleomagnetic analyses indicate the site is in strata of reversed polarity, correlated to C29R (Hicks et al., this issue).

Denver Oxyclaenodon site (DMNH loc. 299)

In 1984, K. Don Lindsey discovered a sandstone nodule containing parts of a maxillary, dentary, and various postcranial elements of the oxyclaenid ungulate *Oxyclaenus simplex*. The specimens came from a road-cut exposure of the Denver Formation at the intersection of Florida Avenue and Kipling Street in Lakewood. No other vertebrate material has since been found at the site, although fossilized palm trunks have been recovered. The Denver Oxyclaenodon site is approximately 30 ft (9 m) stratigraphically above an in situ dinosaur rib (site coined Travis's Dino Site) discovered approximately 328 ft (100 m) south of the intersection of Kipling Street and Mississippi Avenue. *Oxyclaenus simplex* is known from Puercan, but not Lancian, time (Archibald et al., 1987; Williamson, 1996). Consequently, the Denver Oxyclaenodon Site is interpreted as Puercan in age; this locality and Travis's Dino Site help to bracket the K-T boundary to within 30 ft (9 m). Paleomagnetic analyses indicate the Denver Oxyclaenodon site is in strata of reversed polarity, correlated to C29R (Hicks et al., this issue).

West Bijou Site

Nicole's Mammal Jaw locality (DMNH loc. 2557)

This locality is nearly 12 miles (~ 19 km) south of Strasburg, Colorado, in exposures of the Denver

Formation owned by the West Arapahoe Soil Conservation District and operated by the Plains Conservation Center (PCC's West Bijou Site; see Barclay et al., this issue, for additional information on location and stratigraphy). DMNH loc. 2557 is located in the SW1/4 of Section 35, T. 5 S., R. 62 W., on the Strasburg SE Quadrangle map. One mammalian fossil, a jaw fragment of the ungulate *Protungulatum donnae*, was recovered as float, alongside fossils of turtle. Nicole's Mammal Jaw locality is approximately 39 ft (12 m) stratigraphically above the palynologically defined Cretaceous–Tertiary (K-T) boundary, which, in turn, is 16.4 ft (5 m) above the highest dinosaurian fossils (Barclay et al., this issue). Paleomagnetic sampling on both sides of the K-T boundary in this area indicate reversed polarity, interpreted as C29R (Hicks et al., this issue).

Big Gulch

DMNH loc. 2563 (= UCM loc. 91280)

Near Big Gulch, a tributary of West Bijou Creek, DMNH loc. 2563 was discovered by Steve Wallace, paleontologist for the Colorado Department of Transportation (CDOT), in a road cut along State Highway 86, about 11 miles (17.7 km) east of Kiowa, Colorado. DMNH loc. 2563 preserves a middle or late Puercan mammalian fauna (discussed below). Additionally, a diversity of lower vertebrates, including turtles (see Hutchison and Holroyd, this issue), *Lepisosteus* sp. (gar), champsosaur, and at least two crocodilians, is represented at DMNH loc. 2563. Large crocodilian teeth that lack striations are best referred to Crocodyloidea, while smaller, striated teeth probably represent Alligatoroidea. Additionally, osteoderms with two keels appear most similar to an undescribed species of Alligatoroidea from Upper Cretaceous strata of the Hell Creek Formation in Garfield County, Montana (UCMP 128400; X.-C. Wu, personal communication, 2001). Paleomagnetic analyses indicate that DMNH loc. 2563 is in strata of normal polarity, correlated to C29N (Hicks et al., this issue). This is consistent with age equivalents of either Pu2 or Pu3; as elsewhere, these interval zones occur in strata of normal polarity, interpreted as C29N (Lofgren et al., in press). A poor sample of Paleocene pollen was recovered near, but stratigraphically slightly below, DMNS loc. 2563 (Nichols and Fleming, 2002).

Denver Crockies locality (UCM loc. 91278)

Two road cuts to the east, and less than 10 m stratigraphically below DMNH loc. 2563, is the Denver Crockies locality, also discovered by Steve Wallace. The Denver Crockies locality has yielded fossils only of lower vertebrates (crocodilian and turtle). The site is approximately 250 ft (75 m) stratigraphically above the Cretaceous–Tertiary boundary, based upon projections to the Kiowa core (Raynolds, personal communication, 2001), and about 100 ft (30 m) below the Denver Basin paleosol (Farnham and Kraus, 2002). Importantly, a volcanic ash at Denver Crockies is dated at 65.03 ± 0.26 Ma (Obradovich, 2002). A fossil leaf flora in the vicinity of Denver Crockies yielded a low diversity, early Paleocene flora similar to those associated with Puercan faunas in Wyoming and elsewhere (Johnson et al., this issue).

Taeniodont site (DMNH loc. 510)

In 1999, amateur paleontologist George Robinson discovered a partial skull of a taeniodont in a road cut exposure of the Denver Formation along Highway 86, nearly 11 miles (17.7 km) east of Kiowa, Colorado. The specimen, most probably a stylinodontid taeniodont, requires further study and will be described elsewhere. The Taeniodont site is one road cut west, but at the same stratigraphic level as DMNH loc. 2563. The Taeniodont site preserves a diverse, early Paleocene pollen flora representing either palynomorph Zone P2 or P3 (Nichols and Fleming, 2002). The pollen assemblage is dominated by palm (*Arecipites* spp.; Nichols and Fleming, 2002), suggesting the taeniodont came to rest in a palm grove.

Corral Bluffs

East of Colorado Springs, numerous fossil vertebrate localities occur in an extensive amphitheater of cliffs and badlands of the Denver Formation coined Corral Bluffs (Middleton, 1983). Puercan mammals were first reported here by Gazin (1941a) and Brown (1943). Subsequently, Middleton (1983) reported several Puercan mammal localities spanning some 150 ft (46 m) of section. In 2001, as part of the Denver Basin Project, some of Middleton's (1983) localities were relocated and more fossil mammals were recovered, new localities were discovered, and the localities were tied into stratigraphic sections (Fig. 2). All sites from which fossil mammals were collected in 2001 span a 90 ft (27 m) interval. That interval is stratigraphically above an extensive, cliff-forming, channel sandstone informally coined the Bill Sandstone and below a prominent, white sandstone. The stratigraphy at Corral Bluffs is comprised of a series of fining-upward sequences; mammalian fossils are typically found as float in friable, fine-grained sandstone and siltstone on top of cliff-forming sandstone, which contains fossils of lower vertebrates. The finer-grained, mammal-bearing facies were interpreted as overbank deposits by Middleton (1983). The localities generally yield a low concentration of fossils; in several cases, one isolated mammalian fossil is the basis for recognition of a locality.

The mammal-bearing sequence at Corral Bluffs shares taxa with both Pu2 and Pu3 in the San Juan Basin, New Mexico. While Middleton (1983) suggested that the vertical distribution of ungulate taxa ("condylarths") at Corral Bluffs may provide some support for the superposition of Pu3 over Pu2, the absence of *Taeniolabis taoensis*, which defines the onset of Pu3 elsewhere, led others to conclude that Corral Bluffs cannot be assigned confidently to either interval zone (Archibald et al., 1987; Lofgren et al., in press). Paleomagnetic analyses indicate the mammal-bearing sequence at Corral Bluffs is in strata of normal polarity, correlated to C29N (Hicks et al., this issue), which is consistent with either Pu2 or Pu3.

In addition to some 12 mammalian taxa, several lower vertebrates, including turtles, champsosaur, fishes, and crocodilians, are known from Corral Bluffs (see Middleton, 1983; Hutchison and Holroyd, this issue). Notable reptilian fossils from the Alligator Rock locality (DMNS loc. 2548) include a partial skull of a crocodilian and a right dentary referred to Alligatoroidea (X.-C. Wu, personal communication).

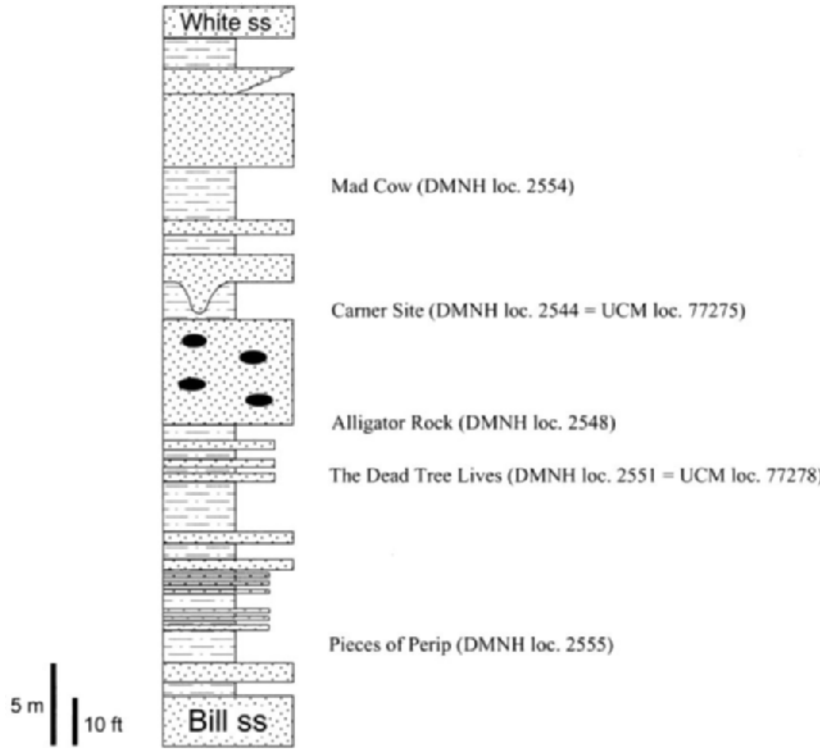

Figure 2. Composite stratigraphic section at Corral Bluffs showing relative positions of fossil mammal localities discussed in this report. Stippled pattern represents sandstone, while alternating dashes and stipples are sandy mudstone and siltstone. Black ovals represent ironstone concretions.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Subclass THERIIFORMES Rowe, 1988
Infraclass ALLOTHERIA Marsh, 1880
Order MULTITUBERCULATA Cope, 1884
Suborder PTILODONTOIDEA (Gregory and Simpson, 1926)
TAENIOLABIDIDAE Granger and Simpson, 1929
***Catopsalis* Cope, 1882a**
***Catopsalis alexanderi* Middleton, 1982**

Figure 3A

Catopsalis alexanderi Middleton, 1982, p. 1198.

Holotype.—UCM 34979, right dentary with i, p4, and m1–2.

Type locality.—UCM loc. 77267, in exposures of the Denver Formation at a construction site south of Littleton, Colorado (Middleton, 1982).

Referred specimen.—DMNH 43209, Rm2 from DMNH loc. 2386, South Table Mountain, Denver Formation, Denver Basin, Colorado (early Puercan).

Known distribution.—Denver Formation, Denver Basin, Colorado; Fort Union (= Polecat Bench) Formation, Wyoming; upper Hell Creek and lower Tullock Formations, Montana (all early Puercan).

Description and discussion.—DMNH 43209, a Rm2, is virtually identical to, although slightly longer than, m2s of *Catopsalis alexanderi* that Middleton (1982) described from the Alexander locality. DMNH 43209 is smaller than m2s of both *C. calgariensis* and *C. fissidens*, and it is distinctly larger than m2s of *C. joyneri* (see Lofgren, 1995).

Catopsalis alexanderi is differentiated from *C. foliatus* primarily by its smaller size (Middleton, 1982). From measurements of m2, however, the size difference is not that clear, as the single known m2 of *C. foliatus* is within the range of lengths of m2s of *C. alexanderi* but is considerably wider than the latter. As DMNH 43209 is within the range of widths for m2s of *C. alexanderi* and only 0.3 mm longer than the longest m2 measured by Middleton (1982), it probably represents a large individual of *C. alexanderi* rather than *C. foliatus*. DMNH 43209 supports Middleton's (1983) initial observation that each mammalian specimen from South Table Mountain differs slightly from its counterparts at the Alexander locality. The difference is not enough, however, to allow identification as a different species.

The wear on DMNH 43209, specifically the way in which the enamel (and not the dentine) has been removed, suggests that this specimen has passed through a crocodilian gut (Robinson, personal communication, 2000). Teeth that have been digested by crocodilians often look intact, except that they are missing their enamel, or they may bear small, interdental "islands" of enamel (Fisher, 1981). Several specimens of the condylarth *Baioconodon* from South Table Mountain also are enamel-free. On the lingual side of DMNH 43209, all of the enamel is gone, leaving behind a smooth, polished surface of dentine. Due to this wear, the width measured for DMNH 43209 is a minimal estimate.

DMNH 43209 represents the first occurrence of *Catopsalis alexanderi* at South Table Mountain. Measurements of the length and width of DMNH 43209, respectively, are 7.50 mm and 5.15 mm.

Grandorder UNGULATA Linnaeus, 1766
***Protungulatum* Sloan and Van Valen, 1965**
***Protungulatum donnae* Sloan and Van Valen, 1965**

Figure 3B–C; Table 1

Protungulatum donnae Sloan and Van Valen, 1965, p. 226.

Holotype.—SPSM 62-2028, left dentary with p2–m3.

Type locality.—Bug Creek Anthills, Hell Creek Formation, northeastern Montana (early Puercan).

Referred specimen and locality.—DMNH 44371, left dentary with p4–m2, from DMNH loc. 2557, Denver Formation, Denver Basin, Colorado (early Puercan).

Known distribution.—Upper Hell Creek Formation, Montana (early Puercan); possibly lower Tullock Formation, Montana (early or middle Puercan); possibly upper Frenchman and Ravenscrag Formations, Saskatchewan (Lancian and/or early Puercan); upper Ferris Formation, Hanna Basin, Wyoming (early, middle, and possibly late Puercan); and Denver Formation, Denver Basin, Colorado (early Puercan).

Description and discussion.—DMNS summer intern Nicole Boyle discovered DMNH 44371 in strata of the Denver Formation in the new Plains Conservation Centre south of Strasburg. While DMNH 44371 is worn (m1 in particular is worn flat and incomplete), nevertheless it can be confidently identified as *Protungulatum donnae*. The m2 on DMNH 44371 is virtually identical to m2s of *P. donnae* from the Bug Creek Anthills in northeastern Montana.

Its larger size is the easiest means of differentiating *Protungulatum donnae* from conspecific arctocyonids *Oxyprimus erikseni* and *O. galadrielae* (see Luo, 1991; Archibald, 1982). As is characteristic of *P. donnae*, p4 and m2 on DMNH 44371 are longer and wider than the p4s and m2s of *O. erikseni* and *O. galadrielae* reported by Lofgren (1995, table 47). While the length of m1 on DMNH 44371 is less than m1s of *P. donnae*, and it falls within the range of m1s of *O. erikseni* reported by Lofgren, this probably is due to wear and incompleteness; the length given for m1 on DMNH 44371 is a minimum estimate. Its width is considerably greater than those reported by Lofgren (1995) for *O. galadrielae* and *O. erikseni*,and well within the range for m1s of *P. donnae*.

While wear obscures the morphology of m1 on DMNH 44371, its m2 bears a paraconid that is lingual of the midline, as in *Protungulatum donnae*. It contrasts, however, with molars of *Oxyprimus erikseni*, in which the paraconid tends to be more medial, lining up with the groove between the proto- and metaconids (Luo, 1991).

DMNH 44371 represents the first documented occurrence of *Protungulatum donnae* in the Denver Basin and a geographic extension of the species' known range from Wyoming.

Table 1. Measurements of p4 and m1-2 on DMNH 44371, a left dentary fragment of *Protungulatum donnae* from DMNH loc. 2557, Denver Formation.

Element	Length	WTri	WTal
Lp4	3.50	2.20 = width	
Lm1	3.30*	-----	2.63
Lm2	3.80	3.20	3.05

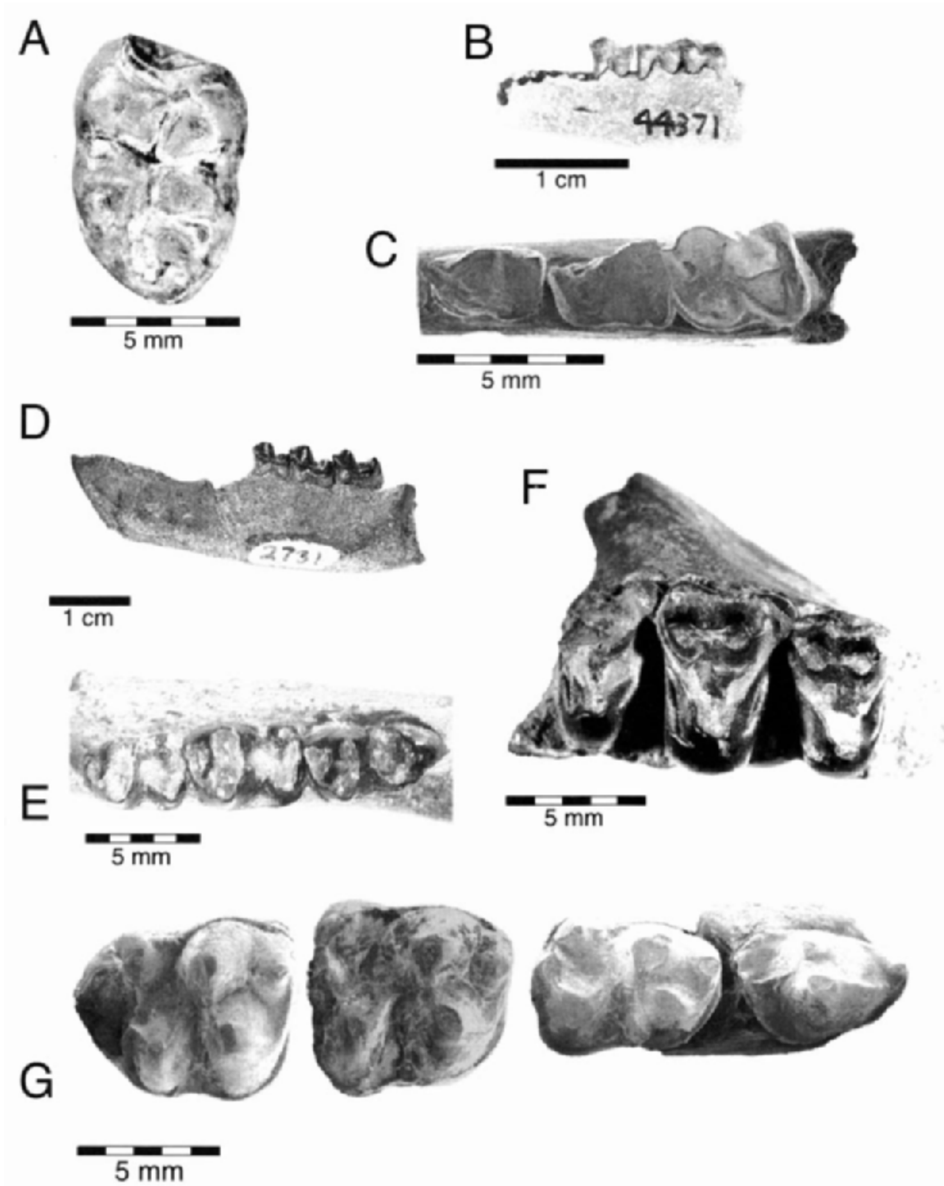

Figure 3. Photographs of selected specimens of multituberculates and arctocyonid ungulates from Denver Formation. ***A***, occlusal view of DMNH 43209, Rm2 of *Catopsalis alexanderi*; ***B***, labial view of DMNH 44371, left dentary with p4-m2 of *Protungulatum donnae*; ***C***, occlusal view SEM of teeth preserved on DMNH 44371, *P. donnae*; ***D*** and ***E***, labial and occlusal views, respectively, of teeth of DMNH 2731, left dentary with m1-3 of *Oxyclaenus simplex*; ***F***, occlusal view of right maxillary fragment with M1-3 also included in DMNH 2731, *O. simplex*; and ***G***, occlusal view (SEM) of DMNH 43208, holotype of *Baioconodon jeffersonensis* new species.

Order PROCREODI Matthew, 1915
OXYCLAENIDAE Scott, 1892
***Oxyclaenus* Scott, 1892**
***Oxyclaenus simplex* (Cope, 1884)**
Figure 3D–F; Tables 2 and 3

Holotype.—AMNH 3107, fragments of upper and lower jaws with RM1–3, LM1–2, and p4, m1–m2.

Type locality.—Nacimiento (= Puerco) Formation, San Juan Basin, New Mexico (middle Puercan).

Referred specimen and locality.—DMNH 2731 comprises a right maxillary fragment containing M1–2 and incomplete M3, L dentary with m1–m3, roots of premolars and base of canine, and postcranial elements entombed in matrix from DMNH loc. 299, Denver Formation, Denver Basin, Colorado (probably early Puercan).

Known distribution.—Nacimiento Formation, San Juan Basin, New Mexico (middle Puercan); Denver Formation, Denver Basin, Colorado (early Puercan).

Description and discussion.—DMNH 2731 comprises a maxillary fragment with RM1–M2 and most of M3, a left dentary with m1–m3 and roots of the other teeth, and matrix-entombed postcranial elements. The teeth are most similar in size and morphology to *Oxyclaenus simplex* from the Nacimiento Formation in the San Juan Basin, New Mexico. The upper molars on DMNH 2731 are virtually identical to those on AMNH 3107, the holotype *of O. simplex*. As in *O. simplex* (see Matthew, 1937), the upper molars of DMNH 2731 lack a hypocone and have relatively narrow anterior and posterior cingula that are not continuous around the lingual margin of the protocone. In contrast, upper molars of the closely related species *O. cuspidatus* are larger and more inflated, their anterior and posterior cingula are wider and better developed, a rudimentary hypocone may be present on M2, and the cingulum is continuous around the lingual margin of the crown on M3 (see Matthew, 1937; personal observation). Although worn down, para- and metaconules were present on upper molars of DMNH 2731.

The base of the canine exposed on the left dentary of DMNH 2731 suggests a large tooth with an ovate cross section. On the labial side of the dentary, a mental foramen occurs below a single-rooted p1, while a second, smaller mental foramen is below p3. While Matthew (1937) listed a p4 and m1 as part of the holotype of *O. simplex*, only Lm2 of the holotype was available for comparison. Although the cusps on m2 of DMNH 2731 appear slightly more worn than on the holotype, the specimens are virtually identical in all other respects. As is diagnostic for *Oxyclaenus* (see Matthew, 1937), the lower molars of DMNH 2731 bear a labial cingulid, the trigonid is noticeably taller than the talonid, the proto- and metaconids are subequal, and the smaller paraconid is lingual to the midline. On m1–m2, the hypoconulid is small, while on m3 it is large and projects posteriorly. As in *O. simplex*, the lower molars of DMNH 2731 appear smaller, narrower, and not so inflated as those of *O. cuspidatus*.

Table 2. Measurements of upper molars of DMNH 2731, *Oxyclaenus simplex* from DMNH loc. 299, Denver Formation.

Element	Length	Width
RM1	4.51	6.42
RM2	5.28	7.40
RM3	3.60*	6.40

Table 3. Measurements of lower molars of DMNH 2731, *Oxyclaenus simplex* from DMNH loc. 299, Denver Formation.

Element	Length	WTri	WTal
Lm1	4.50	3.13	3.44
Lm2	5.45	3.90	3.70
Lm3	6.30	3.37	2.90

Oxyclaenus sp. cf. *O. simplex*

Referred specimen and locality.—DMNH 43197, trigonid of Rm3 from DMNH loc. 2387, Denver Formation, Denver Basin, Colorado (early Puercan).

Description and discussion.—Due to its incompleteness, DMNH 43197, a Rm3 trigonid, is assigned only tentatively to *Oxyclaenus simplex*. However, as in *O. simplex*, DMNH 43197 bears tall, subequal proto- and metaconids, an anterior-projecting paraconid that is lingual of the midline, and a labial cingulid. DMNH 43197 is larger than the new, smaller species of *Oxyclaenus* that Middleton (1983) described from the Alexander locality, as well as arctocyonids *Protungulatum donnae* and species of *Oxyprimus*. DMNH 43197 appears narrower and not so inflated as m3 trigonids of *Oxyclaenus cuspidatus*.

The width of DMNH 43197 is 3.73 mm.

ARCTOCYONIDAE Giebel, 1855
LOXOLOPHINAE Van Valen, 1978
Baioconodon Gazin, 1941a
Baioconodon jeffersonensis new species

Figure 3G; Table 4

Holotype.—DMNH 43208, right dentary fragment with p4, with associated m1-m3.

Type locality.—DMNH loc. 2387 (= UCM loc. 77283 = South Table Mountain locality of Gazin, 1941a, fig. 1), Denver Basin, Colorado (early Puercan).

Hypodigm.—Holotype; DMNH 2501, dentary fragment containing Lm2-m3 and isolated Rm3; and DMNH 43193, right dentary fragment with worn m1-2, and associated incisor, all from type locality.

Etymology.—Named for Jefferson County, in which DMNH loc. 2387 resides, and in honor of Jefferson County Open Space, for acquiring the land and ensuring its protection from commercial development.

Diagnosis.—Most similar in size and morphology to *Baioconodon denverensis*; p4 larger and wider than *B. denverensis*, and possesses a small paraconid, large protoconid with appressed metaconid, and talonid with at least two cusps; molar talonids relatively wider than *B. denverensis*; m2 trigonid distinctly narrower than talonid, unlike *B. denverensis* but as in *Loxolophus*; molar paraconid slightly larger and more anterior-projecting than that of *B. denverensis*; m2 paraconid is medial, lining up with the groove separating the proto- and metaconids, as in most species of *Loxolophus* but unlike *B. denverensis*; fine, horizontal enamel striations are evident on cusps of unworn specimens.

Description and discussion.—The dentition of *Baioconodon*, the most primitive known loxolophine, is morphologically intermediate between *Protungulatum donnae* and later loxolophines, particularly *Loxolophus* (see Eberle and Lillegraven, 1998b). While *Baioconodon jeffersonensis* is most similar to *B. denverensis*, characters that differentiate the two species serve to ally the new species with the more derived *Loxolophus hyattianus* and *L. priscus*, which appear in middle Puercan time. The following description of *Baioconodon jeffersonensis* is based primarily on the holotype, DMNH 43208.

The p4 of *Baioconodon jeffersonensis* is morphologically very similar to, although larger and wider than, the p4s of *B. denverensis* reported by Middleton (1983). As in *B. denverensis* (see Middleton, 1983) and *Loxolophus hyattianus* (see Matthew, 1937), p4 of *B. jeffersonensis* has a small, circular paraconid on its anterior margin. The paraconid occurs just lingual to a ridge that extends anteriorly from the apex of the protoconid. A cingulid extends posterolabially from the paraconid and appears continuous around the labial margin of the tooth, albeit it is very narrow in the protoconid region. A weaker cingulid extends posterolingually from the paraconid but fades out in the region directly opposite the metaconid. As in *B. denverensis*, the metaconid on p4 of *B. jeffersonensis* is taller than the paraconid, although similar in circumference, and it is closely appressed to a much larger, taller, backwardly keeled protoconid. In contrast, most species of *Loxolophus* lack a paraconid on p4 (Eberle and Lillegraven, 1998b). On p4 of *B. jeffersonensis*, a short ridge runs from the protoconid to the metaconid. Another ridge extends down the posterior wall of the trigonid, roughly along the midline, and across the talonid. The posterior margin of p4 is missing, obscuring details of the talonid. Nevertheless, as on some specimens of *B. denverensis* (e.g., UCM 40151), at least two cusps occur on the p4 talonid of *B. jeffersonensis*; one is at the posterior extreme of the ridge extending down the back of the trigonid and the other is just lingual to it. In contrast, lower premolars of *Loxolophus* have small talonid heels and lack talonid cusps and cingulids (Matthew, 1937).

While molars of *Baioconodon jeffersonensis* appear very similar to *B. denverensis*, detailed comparisons reveal some important differences, particularly in m2. On all m2s of *Baioconodon jeffersonensis*, the trigonid is distinctly narrower than the talonid, as in *Loxolophus*, but unlike m2s of *B. denverensis* in which the trigonid is wider than, or subequal in width to, the talonid (see Middleton, 1983; Gazin, 1941a). The m1 of *B. jeffersonensis* also possesses a relatively wider talonid than m1s of *B. denverensis* measured by Middleton (1983, table 21). However, on m1–m2 of *Baioconodon jeffersonensis*, the trigonid is longer than the talonid, as in *B. denverensis*, but unlike *Loxolophus* in which the opposite is true (Eberle and Lillegraven, 1998b). As in *Loxolophus*, the trigonid is slightly taller than the talonid on molars of *Baioconodon jeffersonensis*. While this can also be true for worn molars of *B. denverensis*, on relatively unworn specimens (e.g., UCM 39552 and USNM 16621), the trigonid appears relatively taller than that of *Baioconodon jeffersonensis* and species of *Loxolophus*.

The paraconid on molars of *Baioconodon jeffersonensis* is slightly larger and projects more anteriorly than on *B. denverensis*. On m2, its apex is more medial in position, lining up with the groove separating the proto- and metaconids. On m1–m2 of *B. denverensis*, the paraconid is lingual to this groove (Middleton, 1983; personal observation). In most species of *Loxolophus*, the position of the paraconid typically is medial, although the larger, more derived *L. kimbetovius* and *L. faulkneri* possess a lingual paraconid (Eberle and Lillegraven, 1998b). The m3s of *Baioconodon jeffersonensis* and *B. denverensis* appear virtually indistinguishable, with exception of a relatively wider talonid on m3 of *Baioconodon jeffersonensis*, when compared with m3s of *B. denverensis* measured by Middleton (1983, table 21). As in *B. denverensis* but unlike *Loxolophus priscus* (see Matthew, 1937), the cingulids, particularly the anterior and labial ones, are well developed on DMNH specimens 43208 and 2501. However, on DMNH 43193, a considerably more worn specimen, cingulids are absent on m1 and weak on m2.

In addition to the vertical crenulations in the enamel that is typical of both *Loxolophus* and *Baioconodon*, DMNH specimens 43208 and 2501 (both relatively unworn specimens) bear delicate, horizontal enamel striations encircling each cusp; these striations are most noticeable on p4 and m3 of DMNH 43208. While the striations are not evident on DMNH 43193, their absence may be the result of wear. While Middleton (1983) noted the crenulate enamel on *B. denverensis*, he did not mention horizontal striations encircling the cusps. Furthermore, study of three specimens of *B. denverensis* from the Alexander locality (UCM specimens 34155, 39552, and 40151) at high magnification did not reveal these horizontal striations.

Since *Baioconodon jeffersonensis* is very similar to *B. denverensis*, it seems reasonable that *B. jeffersonensis* either descended from *B. denverensis* or that the two species shared a common ancestor (i.e., sister taxa). Moreover, given the characters that it shares with *Loxolophus hyattianus* and *L. priscus* (specifically a relatively shorter, narrower molar trigonid and more medially placed molar paraconid), *Baioconodon jeffersonensis* may be a plausible candidate for the ancestry of these two species, both of which appear in middle Puercan (Pu2) time. *Loxolophus hyattianus* is known from Corral Bluffs, a probable Pu2 correlative in the Denver Basin, as well as Pu2 and Pu3 in the San Juan Basin, New Mexico and, tentatively, in the Hanna Basin, south-central Wyoming (Eberle and Lillegraven, 1998b). While not documented from the Denver Basin, *L. priscus* is known from both Pu2 and Pu3 in the Hanna Basin and from Pu3 in the San Juan Basin (Eberle and Lillegraven, 1998b).

Baioconodon jeffersonensis co-occurs with *B. denverensis* at South Table Mountain, but it is not known from the nearby Alexander locality, where *B. denverensis* co-occurs with a larger species of *Baioconodon* (see Middleton, 1983).

***Baioconodon denverensis* Gazin, 1941**

Figure 4A; Table 5

Baioconodon denverensis Gazin, 1941a, p. 292.

Holotype.—USNM 16621, fragment of right dentary with m2–m3.

Type locality.—Exposures of Denver Formation on eastern Flank of South Table Mountain near Golden, Colorado (SW1/4 of NW1/4, Sec. 31, T. 3 S., R. 69 W.; Gazin, 1941a, fig. 1), early Puercan (Middleton, 1983).

Referred specimen and locality.—DMNH 43196, a Lm3, from DMNH loc. 2387 (= UCM loc. 77283 = South Table Mountain locality of Gazin, 1941a, fig. 1), Denver Basin, Colorado (early Puercan).

Known distribution.—Denver Formation, Colorado; and possibly the upper Ferris Formation, Wyoming and Ravenscrag Formation, Saskatchewan (all Puercan).

Description and discussion.—While isolated m3s of *B. denverensis* and *Baioconodon jeffersonensis* are morphologically very similar, m3s of *B. denverensis* have relatively narrower talonids than the latter. The talonid on DMNH 43196, a Lm3, is narrower than any of the known m3s of *Baioconodon jeffersonensis*, and it falls within the range of lengths, as well as trigonid and talonid widths, of m3s of *B. denverensis* reported by Middleton (1983, table 21).

Gazin (1941a) and Middleton (1983) provided thorough descriptions of lower molars of *B. denverensis*.

As on m3 of the holotype (USNM 16621), DMNH 43196 bears extra talonid cuspules; one occurs on the ridge between the entoconid and hypoconulid and the other is between the hypoconulid and hypoconid. While this feature is variable in *B. denverensis*, Middleton (1983) noted that any of the lower molars may have additional talonid cuspules.

Baioconodon sp. indet.

Referred specimen and locality.—DMNH 44362, dentary fragment with worn Lp4, from DMNH loc. 2387 (= UCM loc. 77283), Denver Formation, Denver Basin, Colorado (early Puercan).

Description and discussion.—Based upon its size, DMNH 44362, a dentary fragment containing a worn, poorly preserved Lp4, probably belongs to either *B. denverensis* or *Baioconodon jeffersonensis*, both of which occur at South Table Mountain. DMNH 44362 is missing all of its enamel, except for a small piece along its posterior margin. Several specimens of *B. denverensis* and one specimen of *Catopsalis alexanderi* from South Table Mountain show a similar, enamel-less condition, which suggests digestion by a crocodilian. Teeth that have passed through a crocodilian gut often appear intact, except for their lack of enamel (Fisher, 1981).

Estimates of length and width of the Lp4 on DMNH 44362 are, respectively, 6.0 and 3.5 mm.

Loxolophus Cope, 1885
Loxolophus faulkneri Eberle and Lillegraven, 1998b

Figure 4B–C; Table 6

Loxolophus faulkneri Eberle and Lillegraven, 1998b, p. 67.

Holotype.—UW 26491, right dentary fragment with associated p4, m2–3, and fragments of px and m1.

Type locality.—UW locality V-91003, upper Ferris Formation, Hanna Basin, Wyoming (middle Puercan).

Referred specimen.—USNM 16626, left dentary fragment with m1 and anterior root of m2, in exposures of Denver Formation in Corral Bluffs near Colorado Springs, Colorado (exact locality unknown; probably middle Puercan).

Description and discussion.—USNM 16626, figured by Brown (1943, pl. 2, figs. 8, 10), was initially identified as "Creodont, near *Eoconodon heilprinianus*" (Gazin, 1941a, p. 294). However, Middleton (1983) subsequently identified USNM 16626 as *Loxolophus* cf. *L. kimbetovius*, noting some differences between it and the holotype of *L. kimbetovius* from the San Juan Basin. Based upon comparisons with species of *Loxolophus* from the Hanna Basin, USNM 16626 is most similar in size and morphology to, and consequently identified as, *Loxolophus*

Table 4. Measurements of lower teeth of *Baioconodon jeffersonensis* new species from DMNH loc. 2387 (= UCM loc. 77283), Denver Formation.

DMNH Specimen Number	Element	Length	LTri	LTal	WTri or Width	WTal
43208	Rp4	6.20	-----	-----	4.80	-----
43208	Rm1	6.70	3.70	3.00	5.00	5.80
43193	Rm1	6.00*	3.50*	2.50*	4.80*	5.70*
43208	Rm2	7.60*	4.20	3.40*	6.45	6.90*
2501	Lm2	7.80	4.30	3.50	6.35	6.85
43193	Rm2	6.80*	3.80*	3.00*	5.90*	6.30*
43208	Rm3	7.90*	3.70	4.20*	5.85	5.30
2501	Lm3	7.80*	3.70	4.05*	5.75	5.20
2501	Rm3	8.00	3.80	4.20	6.05	5.20

Table 5. Measurements of DMNH 43196, a Lm3 of *Baioconodon denverensis* from DMNH loc. 2387 (= UCM loc. 77283), Denver Formation.

Element	Length	LTri	LTal	WTri	WTal
Lm3	8.30	3.70	4.60	5.50	4.60

faulkneri. The largest known species of *Loxolophus*, *L. faulkneri* is most similar to *L. kimbetovius* from middle Puercan strata of the San Juan Basin (Eberle and Lillegraven, 1998b).

While m1 of *Loxolophus faulkneri* has not been documented, the m1 on USNM 16626 nevertheless is comparable to m2–m3 of *L. faulkneri* in that it has a large, inflated trigonid with a relatively large, lingual paraconid that appears larger than that of *L. kimbetovius*. The molar paraconid is also lingual on *L. kimbetovius*, but labial on other species of *Loxolophus* (Eberle and Lillegraven, 1998b). As noted by Middleton (1983), the talonid on m1 of USNM 16626 is wider than its trigonid, as in most species of *Loxolophus*, except *L. kimbetovius*, in which the trigonid and talonid are of the same width (Matthew, 1937). The talonid morphology of m1 on USNM 16626 is comparable to m2 of *L. faulkneri* in that the hypoconulid is the smallest cusp, and its apex is closer to the entoconid than to the hypoconid. As is characteristic of *Loxolophus*, the enamel on USNM 16626 is rugose. As in *L. faulkneri*, a well-developed, rugose, crenulate cingulid encircles all but the lingual margin of the talonid on m1 of USNM 16626. I agree with Middleton (1983) that USNM 16626 is probably from a young individual; the virtually unworn m1 is most comparable to UW 26495, also from a young individual, as its m3 is only partially erupted (see Eberle and Lillegraven, 1998b, fig. 6*d*).

The diagnosis of *Loxolophus faulkneri*, which states "molar trigonid wider than talonid" (Eberle and Lillegraven, 1998b), was based solely on m2–m3, since m1 had not been documented. Similar relative proportions (trigonid wider than talonid) exist on m2–m3 of *L. kimbetovius*, some m2s in other species (*e.g.*, specimens of *L. hyattianus* and *L.* aff. *L. hyattianus* measured by Middleton, 1983), and m3s of all species of *Loxolophus* (see Matthew, 1937). Furthermore, most species of *Loxolophus* have an m1 trigonid that is narrower than the talonid; the exception is *L. kimbetovius*, whose m1 trigonid is similar in width to its talonid. Consequently, it is not surprising that *L. faulkneri* has an m1 in which the trigonid is narrower than its talonid.

PERIPTYCHIDAE Cope, 1882c
CONACODONTINAE Archibald et al., 1983
***Conacodon* Matthew, 1897**
***Conacodon entoconus* (Cope, 1882b)**

Figure 4D; Table 7

Haploconus entoconus Cope, 1882b, p. 686.
Anisonchus coniferus Cope, 1882c, p. 832.
Conacodon cf. *C. entoconus* Gazin, 1941a, p. 295.

Holotype.—AMNH 3462, right maxillary fragment with P3–M3.

Type locality.—Nacimiento (= Puerco) Formation, San Juan Basin, New Mexico (middle Puercan).

Referred specimen and locality.—DMNH 44369, right maxillary fragment with P4–M1 found in association with bone fragment and roots of lower posterior premolar or molar, from DMNH loc. 2548, in exposures of Denver Formation in the Corral Bluffs near Colorado Springs, Colorado (middle Puercan).

Known distribution.—Nacimiento Formation, San Juan Basin, New Mexico (middle Puercan); Denver Formation, Denver Basin, Colorado (middle Puercan).

Description and discussion.—DMNH 44369 is easily referred to *Conacodon entoconus*, based upon close similarity to specimens of *C. entoconus* from the Nacimiento Formation in the San Juan Basin, New Mexico. P4 and M1 are damaged and enamel-free, the latter observation of which suggests that this specimen passed through a crocodilian gut (Robinson, personal communication; Fisher, 1981). This condition is not uncommon in the Denver Basin, as several specimens of *Baioconodon denverensis* and a tooth of *Catopsalis alexanderi* from South Table Mountain also lack enamel. Incidentally, abundant crocodilian fossils, including a skull, were found at the same locality as DMNH 44369.

As noted by Matthew (1937) for *Conacodon entoconus*, P4 of DMNH 44369 is larger than M1, and it is comprised primarily of a large, conical, backwardly pitched cusp. While P4s of *C. entoconus* also bear a lingual cusp, this region of the P4 on DMNH 44369 is broken away. As in *C. entoconus*, M1 of DMNH 44369 is quite transverse due to lingual expansion of the hypocone. While the apex of the hypocone

Table 6. Measurements of m1 of *Loxolophus faulkneri* from Denver Formation.

Specimen number	Element	Length	LTri	LTal	WTri	WTal
USNM 16626	Lm1	10.20	6.40	3.80	7.40	8.60

is missing on M1 of DMNH 44369 (probably due to damage and lack of enamel), its base is expanded far more lingually than that of most periptychids, with exception of the much smaller *Oxyacodon*. Archibald et al. (1983) considered the hypocone's size and lingual expansion to be the most important character in uniting *Conacodon* and *Oxyacodon* into the subfamily Conacodontinae.

In the San Juan Basin, *Conacodon entoconus* is an index taxon for middle Puercan time (Pu2, or H-T Zone of Williamson, 1996). Matthew (1937) also noted its restriction to "the lower horizon of the Puerco . . . ." Middleton (1983) referred a single specimen (USNM 16625) from Corral Bluffs to *C. entoconus*. While its exact locality is unknown, Middleton (1983) suggested that USNM 16625, like specimens of *Conacodon* aff. *C. entoconus* from Corral Bluffs, was from lower in the stratigraphic section than the larger *Conacodon delphae*, known only from the stratigraphically highest localities at Corral Bluffs. This stratigraphic relationship, as well as the more derived morphology of *C. delphae*, suggested to Middleton (1983) that *C. delphae* descended from *C. entoconus* and replaced the latter in stratigraphically higher, younger strata at Corral Bluffs. While *C. entoconus* has not been documented north of Colorado, Eberle and Lillegraven (1998b) reported *C. delphae* from middle Puercan (Pu2) strata of the Ferris Formation in the Hanna Basin, suggesting that this species is contemporaneous with *C. entoconus*.

ANISONCHINAE Osborn and Earle, 1895
***Haploconus* Cope, 1882b**
***Haploconus* sp. indet.**
Figure 4E–F; Table 8

Referred specimens and locality.—UCM 87605, left dentary fragment with damaged m3 and posterior root of m2; DMNH 44394, right dentary fragment with p2–p3; both specimens from DMNH loc. 2563 (= UCM loc. 91280), a road-cut exposure of the Denver Formation along State Highway 86, 11 miles east of Kiowa, CO (middle or late Puercan).

Description and discussion.—UCM 87605 was damaged in transport between museums, and consequently the trigonid on m3 is broken away. However, prior to its being damaged, UCM 87605 was referred to *Haploconus* sp., based upon strong similarities to *Haploconus* from New Mexico and Utah. Specifically, the similarities include absence of a paraconid and presence of a large, posterior-projecting, lobate hypoconulid. The m3 on UCM 87605 is comparable in size and morphology to *Haploconus* sp. (i.e., UALP 11036 and 13223) from the Puercan Wagonroad locality in Utah and the holotype of *H. angustus* (AMNH 3477) from Torrejonian strata of the San Juan Basin, New Mexico.

When compared with all of the periptychids, p2–p3 on DMNH 44394 are most similar to, although smaller than, UCMP specimens of p2–p3 of *Haploconus angustus* from the San Juan Basin. While the holotype of *H. angustus* (AMNH 3477) does not preserve p2–p3, it nevertheless appears to be from a similar-sized individual as DMNH 44394, and it is noticeably smaller than the UCMP specimens. The p2–p3 on DMNH 44394 also are similar in size to *Conacodon cophater*, but while p3 of *C. cophater* has an anterior cusp (i.e., "paraconid"), p2–p3 on DMNH 44394 do not, as in *Haploconus*. Like *H. angustus*, p3 on DMNH 44394 is considerably larger than p2, and it bears a weak anterior cingulid; p2 lacks one altogether. Labial and lingual cingulids are absent on p2–p3 of DMNH 44394. Unlike p2 of *H. angustus*, which typically has a well-developed talonid heel (see Matthew, 1937), p2 on DMNH 44394 has a minute heel, lacking in cusps. However, p3 on DMNH 44394 has a large heel, comparable in relative size to that on p3s of *H. angustus*. Wear obscures the presence or absence of cusps on the heel of p3 on DMNH 44394. The wear pattern on p2–p3 of DMNH 44394 is virtually identical to that on specimens of *H. angustus* from the San Juan Basin. That is, p2 is unworn, with a tall, acute, slightly keeled central cusp (i.e., "protoconid"); p3 exhibits wear across the apex of the large, central cusp and extends posteriorly onto the heel.

Table 7. Measurements of P4 and M1 of DMNH 44369, *Conacodon entoconus* from DMNH loc. 2548, Denver Formation.

Element	Length	Width
RP4	6.2 mm	9.4 mm
RM1	4.5 mm	8.7 mm

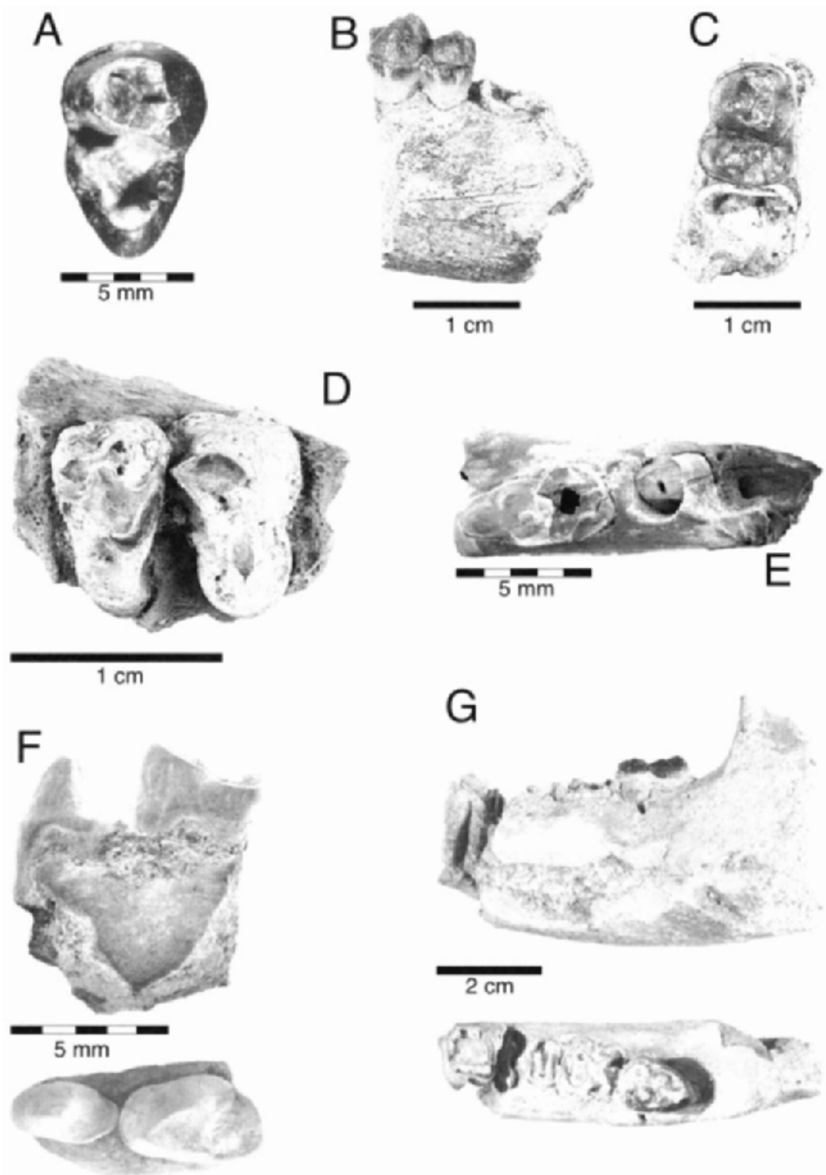

Figure 4. Photographs of selected arctocyonid and periptychid ungulates from Denver Formation. ***A***, occlusal view of DMNH 43196, Lm3 of *Baioconodon denverensis*; ***B*** and ***C***, labial and occlusal views, respectively, of USNM 16626, left dentary fragment with m1 of *Loxolophus faulkneri*; ***D***, occlusal view of DMNH 44369, right maxillary fragment with P4–P1 of *Conacodon entoconus*; ***E***, occlusal view of UCM 87605, left dentary fragment with partial m3 and root of m2 of *Haploconus* sp.; ***F***, labial (top) and occlusal views of DMNH 44394, dentary fragment with p2–p3 of *Haploconus* sp.; and ***G***, lingual (top) and occlusal views of DMNH 44374, right dentary fragment with m3 of *Ectoconus ditrigonus*.

Based upon size, it seems plausible that UCM 87605 and DMNH 44394 are from the same species. Both are comparable in size to *Haploconus* sp. from the Wagonroad locality in Utah and to the holotype of *H. angustus* (AMNH 3477). Incidentally, m3s of *Haploconus* sp. from the Wagonroad Locality (UALP specimens 11036 and 13223) are morphologically similar to, if not indistinguishable from, the m3 on AMNH 3477. Moreover, AMNH 3477 is considerably smaller than UCMP specimens of *H. angustus* (36613–36614), also from the San Juan Basin, suggesting that teeth of *H. angustus* are either highly variable in size or, alternatively, that more than one species is represented in the San Juan Basin. Matthew (1937) considered the latter to be the case, and he referred the larger specimens to Cope's (1888) *H. corniculatus*. However, based upon metrical analyses, Williamson (1996) concluded that there was no clear distinction between *H. corniculatus* and *H. angustus*; consequently, the former should be considered a junior synonym of the latter, as was first suggested by Simpson (1959). The Denver Basin specimens probably do not belong to *Haploconus elachistus*, a poorly known species from the middle or possibly late Puercan Gas Tank local fauna in Utah (see Gazin, 1941b; Robison, 1986). *H. elachistus* is smaller than *H. angustus*, and its p4 and lower molars bear a slight, medial paraconid (Gazin, 1941b). Earlier, Gazin (1939) described *Haploconus inopinatus* from the Dragon local fauna, but Williamson (1996) considered this species a junior synonym of *H. angustus*.

While specimens from the Denver Basin could belong either to *Haploconus* sp. or the smaller morph of *H. angustus*, their incompleteness, when considered alongside the size variation in *H. angustus* and close similarity of *Haploconus* sp. from Utah to the holotype of *H. angustus*, precludes placement in either taxon. Consequently, DMNH 44394 and UCM 87605 are identified as *Haploconus*, species indeterminate.

PERIPTYCHINAE Osborn and Earle, 1895
***Ectoconus ditrigonus* (Cope, 1882d)**
Figure 4G; Tables 9 and 10

Periptychus ditrigonus Cope, 1882d, p. 465.

Holotype.—AMNH 3798, fragment of right dentary with m2.

Type locality.—Nacimiento (= Puerco) Formation, San Juan Basin, New Mexico (middle Puercan).

Referred specimens and localities.—DMNH 44374, right dentary fragment with m3, base of m2, and roots of m1, from DMNH loc. 2554, in exposures of Denver Formation in Corral Bluffs near Colorado Springs, Colorado (middle Puercan); and DMNH 44393, LP4 from DMNH loc. 2563 (= UCM loc. 91280), in exposures of the Denver Formation along State Highway 86, 11 miles east of Kiowa, Colorado (middle or late Puercan).

Known distribution.—Upper Ferris Formation, western Hanna Basin, Wyoming (late Puercan); Denver Formation, Denver Basin, Colorado (middle and possibly late Puercan); North Horn Formation, Utah (middle Puercan); Nacimiento Formation, San Juan Basin, New Mexico (middle and late Puercan).

Description and discussion.—DMNH specimens 44374 and 44393 are virtually identical to specimens of *Ectoconus ditrigonus* from the Nacimiento Formation in the San Juan Basin, New Mexico. The m3 on DMNH 44374 bears a cusp lingual to the paraconid, as is diagnostic for *E. ditrigonus* (see Osborn and Earle, 1895; Robison, 1986). For a thorough description of m3 of *E. ditrigonus*, see Eberle and Lillegraven (1998b).

While Middleton (1983) noted that *Ectoconus ditrigonus* occurred only in the stratigraphically lowest localities at Corral Bluffs, DMNH 44374 was found very near the top of the bluffs, stratigraphically above all of Middleton's (1983) localities. Outside the Denver Basin, *E. ditrigonus* is known from both middle and late Puercan time (Eberle and Lillegraven, 1998b).

***Periptychus* Cope, 1881**
***Periptychus coarctatus* Cope, 1883**
Figure 5A–B, Table 11

Periptychus coarctatus Cope, 1883, p. 168.

Periptychus brabensis Cope, 1888, p. 354.

Holotype.—AMNH 3775, lower dentition.

Table 8. Measurements of p2–p3 and m3 of *Haploconus* sp. indet. from DMNH loc. 2563, Denver Formation.

Specimen Number	Element	Length	LTri	LTal	WTri or Width	WTal
DMNH 44394	Rp2	3.40	------	------	1.92	------
DMNH 44394	Rp3	4.50	------	------	2.90	------
UCM 87605	Lm3	4.80	2.00*	2.80*	3.15	2.65

Table 9. Measurements of DMNH 44393, an LP4 of *Ectoconus ditrigonus* from DMNH loc. 2563, Denver Formation.

Element	Length	Width
LP4	9.20	11.70

Table 10. Measurements of m3 on DMNH 44374, a right dentary fragment of *Ectoconus ditrigonus* from DMNH loc. 2554, Denver Formation.

Element	Length	LTri	LTal	WTri	WTal
Rm3	14.60	5.60	9.00	11.00	9.40

Type locality.—Nacimiento (= Puerco) Formation, San Juan Basin, New Mexico (middle or late Puercan).

Referred specimens and localities.—DMNH 44372, left and right dentary fragments with Lp2, Lp4, and Lm2-3 and Rm3, from DMNH loc. 2555; DMNH 44368, left dentary fragment with p3-m3 from DMNH loc. 2551 (= UCM loc. 77278), both localities in exposures of Denver Formation in Corral Bluffs near Colorado Springs, Colorado (middle Puercan); UCM 95666, a worn, incomplete Rm1; and DMNH 44395, a Lm2 trigonid, both from DMNH loc. 2563 (= UCM loc. 91280), in exposures of the Denver Formation along State Highway 86, 11 miles east of Kiowa, Colorado (middle or late Puercan).

Known distribution.—Nacimiento Formation, San Juan Basin, New Mexico (middle and late Puercan); Denver Formation, Denver Basin, Colorado (middle and possibly late Puercan); North Horn Formation, Utah (late Puercan); and upper Ferris Formation, western Hanna Basin, Wyoming (middle and late Puercan).

Description and discussion.—*Periptychus coarctatus* is the most abundant mammal known from the Denver Formation. The specimens reported here are comparable to other specimens of *Periptychus coarctatus* from the Denver Formation reported by Middleton (1983) and to *P. coarctatus* from the Nacimiento Formation in the San Juan Basin, New Mexico. The dentition of *P. coarctatus* (= *Plagioptychus matthewi*) was thoroughly described by Matthew (1897, 1937) and Simpson (1936), so only brief notes relevant to DMNH specimens are provided here.

As is characteristic of *Periptychus*, DMNH specimens 44372 and 44368 have strong vertical striations in their enamel, and their inflated premolars are larger than the molars. As is diagnostic of lower premolars of *P. coarctatus*, the premolars on DMNH 44372 and 44368 lack a cusp anterior to the large, conical, central cusp that takes up most of the tooth. In contrast, an antero-internal cusp is well developed on lower premolars of later species of *Periptychus* such as the Torrejonian *P. carinidens* (see Matthew, 1937). While Middleton (1983) noted that an anterior cingulid is usually present on p4 of *P. coarctatus*, the p4 on DMNH 44372 lacks one, as does its p2. An anterior cingulid is not evident on p3 or p4 of DMNH 44368, although the teeth are damaged, incomplete, and quite delicate; consequently, the matrix surrounding their bases has been left intact to help prevent further damage. The size and proportions of premolars and molars of *P. coarctatus* are quite variable (Matthew, 1937). Nevertheless, measurements of the DMNH specimens are within the ranges of length and width for other specimens of *P. coarctatus* from the Denver Basin (Middleton, 1983, table 26). The exception is the p3 on DMNH 44368, in which the estimated length is 0.2 mm longer than the longest p3 measured by Middleton.

Order CONDYLARTHRA Cope, 1881
MIOCLAENIDAE Osborn and Earle, 1895

Comments.—A Rm3 from the Denver Basin, referred below to Mioclaenidae indet., appears most similar to species of *Promioclaenus*. In light of recent revisions to this genus, a brief summary is given here.

Van Valen (1978) recognized five species of *Promioclaenus*: *P. vanderhoofi* (Simpson, 1936); *P. acolytus* (Cope, 1882c); *P. lemuroides* (Matthew, 1897); *P. pipiringosi* Gazin, 1956; and *P. wilsoni* Van Valen, 1978. Subsequently, Muizon and Cifelli (2000) regarded the differences between *P. wilsoni* and other species of *Promioclaenus* as indicative of different genera, and they erected the new genus *Valenia* to include "*Promioclaenus*" *wilsoni*. Muizon and Cifelli's diagnosis of *Valenia* primarily was based upon upper dentition of the holotype of "*P.*" *wilsoni* (KU 9446); the associated lower dentition was in poor condition, and the lower molars were not included in the diagnosis. Consequently, there is confusion as to whether lower molars previously assigned to "*P.*" *wilsoni* (e.g., Eberle and Lillegraven, 1998b, p. 100) belong in *Valenia*. Moreover, lower premolars and molars of "*P.*" *wilsoni* and *P. acolytus* are extremely similar in size and morphology; the only apparent differences are that lower molars of "*P.*" *wilsoni* appear relatively uninflated (Van Valen, 1978; Williamson, 1993) and narrower (Eberle, 1996) than *P. acolytus*. As a temporary solution to help reduce confusion, I retain "*P.*" *wilsoni* in reference to lower molars previously assigned to this taxon until such time as the systematics, and more specifically the differences among lower dentitions of *Promioclaenus*, "*P.*" *wilsoni*, and *Valenia*, are better understood and more thoroughly documented.

Mioclaenidae indet.

Figure 5C; Table 12

Referred specimen and locality.—UCM 87609, Rm3 from DMNH loc. 2563 (= UCM loc. 91280) in exposures of the Denver Formation along State Highway 86, 11 miles east of Kiowa, CO (middle or possibly late Puercan).

Description and discussion.—UCM 87609 is morphologically most similar to, although larger

Table 11. Measurements of DMNH specimens 44368, 44372, and 44395, as well as UCM 95666, lower teeth of *Periptychus coarctatus* from DMNH localities 2551, 2555, and 2563 (= UCM loc. 91280), Denver Formation.

Specimen Number	Element	Length	LTri	LTal	WTri or Width	WTal
44372	Lp2	9.80			7.90	
44368	Lp3	12.70*			9.10*	
44368	Lp4	12.30*			10.30*	
44372	Lp4	10.60			9.50	
UCM 95666	Rm1	10.00*	----	----	6.80*	6.10*
44372	Lm2	8.20	4.70	3.50	7.80	7.80
44368	Lm2	9.40*	5.00*	4.40*	8.00*	7.80*
44395	Lm2 trigonid	----	5.20*	----	7.60*	----
44368	Lm3	----	4.40*	----	7.80*	----
44372	Lm3	9.50	4.00	5.50	7.10	6.00
44372	Rm3	9.50	4.10	5.40	6.90	5.90

Figure 5, left. Photographs of selected periptychid and mioclaenid ungulates from Denver Formation. ***A*** and ***B***, labial (top) and occlusal views of left and right dentary fragments of *Periptychus coarctatus* included in DMNH 44372; and ***C***, occlusal view of UCM 87609, Rm3 of Mioclaenidae indet.

and more inflated than, m3s of *"Promioclaenus" wilsoni* and *Promioclaenus acolytus*. UCM 87609 is similar in size to *P. lemuroides*, which is about 20 percent larger than *P. acolytus* (see Williamson, 1993). However, UCM 87609 bears a distinct paraconid, unlike *P. lemuroides*, but like *"P." wilsoni* and *P. acolytus* (see Matthew, 1937; Simpson, 1937).

As is characteristic of *Promioclaenus*, the cusps on UCM 87609 are low, and the trigonid is slightly taller than the talonid. As in *"P." wilsoni* from the

Hanna Basin (see Eberle and Lillegraven, 1998b), UCM 87609 has a well-developed anterior cingulid, but it lacks a lingual cingulid. UCM 87609 bears a discontinuous, labial cingulid, present only in the hypoflexid region and between the hypoconid and hypoconulid. The small, but distinct, paraconid on UCM 87609 is lingual in placement, and it is appressed to the anterior margin of the metaconid, as in "*P.*" *wilsoni* (see Eberle and Lillegraven, 1998b) and *P. acolytus* (see Simpson, 1937). Also as in "*P.*" *wilsoni*, a paralophid is present on UCM 87609. Although the apices have been removed by wear, the proto- and metaconids appear subequal in size.

As in *Promioclaenus*, the talonid on UCM 87609 is longer and narrower than the trigonid, and it bears a large hypoconid, small entoconid, and large, posteriorly projecting hypoconulid. The apices are worn on all of the talonid cusps, obscuring details of cusp morphology. However, based upon its wear pattern, the entoconid may have been a ridge rather than a distinct cusp. A short, narrow diagonal ridge connects the entocristid to the posterior wall of the metaconid, essentially closing off the deep talonid basin. A narrow notch occurs lingual to the short, diagonal ridge. The cristid obliqua strikes the trigonid at its midline, directly below and posterior to the intersection of the proto- and metaconids.

While UCM 87609 is morphologically very similar to m3s of "*Promioclaenus*" *wilsoni* and *P. acolytus*, its larger size suggests that it belongs in another species. However, presence of a paraconid on UCM 87609 precludes its placement in the younger (i.e., Torrejonian) *P. lemuroides*. An even younger (i.e., Tiffanian) species, *P. pipiringosi* from the Bison Basin of Wyoming, is about the same size as *P. lemuroides*. The m3 of this species, however, has not been documented (Gazin, 1956). While UCM 87609 may belong to *P. pipiringosi* and consequently represents a temporal range extension into the Puercan, it is equally plausible that UCM 87609 is a new, large, Puercan species of *Promioclaenus*. Pending recovery of more specimens, and given the confusion surrounding the relationships of "*P.*" *wilsoni* to other species of *Promioclaenus* (discussed above), UCM 87609 is identified here only as Mioclaenidae indeterminate.

DISCUSSION

Puercan Mammalian Biostratigraphy in Denver Basin

At least two Puercan interval-zones, Pu1 and Pu2, are represented by faunas in the Denver Basin.

Pu1

Table 13 lists the mammalian taxa known from early Puercan (Pu1) localities in the Denver Basin. While no new specimens were recovered from the Alexander locality as a result of the Denver Basin Project, a faunal list based upon Middleton (1983) is included here as a basis for further discussion (below). It also allows comparison to the fauna from South Table Mountain, which includes both Brown's *Baioconodon* and Michon's Multi localities.

Nicole's Mammal Jaw locality (DMNH loc. 2557), in the West Bijou Site (see Barclay et al., this issue), represents the first occurrence in Colorado of the arctocyonid condylarth *Protungulatum donnae*. Its first appearance defines the onset of Puercan time (Archibald and Lofgren, 1990; Lofgren et al., in press). Fox (1990, 1997) reported *P.* cf. *P. donnae* from two localities in western Canada that he interpreted as representative of Late Cretaceous (i.e., Lancian) time on the basis of stratigraphy and palynology. That raises the possibility that *P. donnae* spanned the Cretaceous–Tertiary (K-T) boundary. However, Lofgren et al. (in press) maintained that *P. donnae*, the oldest known North American ungulate, still defines the advent of the Puercan land mammal "age." Furthermore, its purported Late Cretaceous appearance in Canada may suggest that the Lancian–Puercan boundary, defined by North American assemblages of terrestrial fossil mammals, is not precisely synchronous with the K-T boundary, which is based upon Old World marine invertebrates (see discussions by Lofgren et al., in press; Eberle and Lillegraven, 1998b).

While *Protungulatum donnae* is known from early and middle Puercan time (i.e., Pu1 and Pu2; Eberle and Lillegraven, 1998b), its occurrence in the Denver Basin appears to be within Pu1. The

Table 12. Measurements of UCM 87609, a rm3 of *Promioclaenus* from DMNH loc. 2563 (= UCM loc. 91280), Denver Formation.

Element	Length	LTri	LTal	WTri	WTal
Rm3	4.95	2.00	2.95	3.50	2.85

site is approximately 39 ft (12 m) above the palynologically defined K-T boundary (Barclay et al., this issue), and paleomagnetic sampling indicates that it is within strata of reversed polarity, interpreted as C29R (Hicks et al., this issue). That is consistent with a Pu1 age (Lofgren et al., in press). The occurrence of *P. donnae* in the Denver Basin is the most southerly record of the species, extended from the Hanna Basin in Wyoming.

While *Oxyclaenus simplex* is restricted to Pu2 in the San Juan Basin (Williamson, 1996), its occurrence at the Denver Oxyclaenodon site (DMNH loc. 299) appears to be within Pu1. The Denver Oxyclaenodon site is approximately 30 ft (9 m) stratigraphically above an in situ dinosaur rib coined "Travis's Dino Site" with no obvious unconformities between the two sites. Paleomagnetic analyses indicate the strata are of reversed polarity, correlated to C29R (Hicks et al., this issue), which is consistent with a Pu1 age (Lofgren et al., in press). Additionally, *Oxyclaenus* cf. *O. simplex* is known from Pu1 strata at South Table Mountain (this report). Presence of *O. simplex* in the Denver Basin represents a geographic range extension northward from the San Juan Basin and a probable temporal range extension from Pu2.

The mammalian fauna at South Table Mountain (Table 13) has doubled in recorded diversity since Middleton's (1983) study. *Baioconodon jeffersonensis*, *Oxyclaenus* cf. *O. simplex*, and *Catopsalis alexanderi* all are new occurrences at South Table Mountain. Middleton (1983) concluded that the South Table Mountain fauna was coeval with the early Puercan Alexander locality, since the few mammalian species that he reported from South Table Mountain were shared with the Alexander locality. Nevertheless, the sites could not be lithostratigraphically correlated to one another, due to distance and lack of exposures. The mammalian fossils at the Alexander locality were found as float on a leveled construction site in Littleton, with little stratigraphic section exposed (Middleton, 1983). Co-occurrence of *C. alexanderi* lends support to Middleton's hypothesis that the two localities are coeval. However, *Oxyclaenus* cf. *O. simplex* and *B. jeffersonensis* are not known from the Alexander locality. Instead, Middleton (1983) reported a new, smaller species of *Oxyclaenus* and a new, larger species of *Baioconodon* from the Alexander locality.

Despite some faunal differences, South Table Mountain and the Alexander locality are probably similar in age, as Middleton (1983) surmised. Paleomagnetic analyses indicate that both localities are in strata of reversed magnetic polarity, correlated to C29R (Hicks et al., this issue) and consistent with a Pu1 age (Lofgren et al., in press). However, Middleton's (1983) inclusion of South Table Mountain and the Alexander locality in the Littleton local fauna seems premature, given that a local fauna is defined as ". . . a localized fossil sample of a fauna . . . usually from a thickness of a meter or less of strata in one quarry or in a relatively small district" (Savage and Russell, 1983). I recommend a more cautious approach and refer to these localities together as the Littleton fauna, which, in a broad sense, means the total animal content, as based upon fossils (Savage and Russell, 1983), in the Littleton region.

With at least 20 mammalian species represented, the Littleton fauna is arguably the most diverse Pu1 fauna. Taking into account taxa reworked from underlying Lancian strata, Lofgren (1995, table 11) reported 18 mammalian species from Pu1 faunal assemblages in northeastern Montana, while 13 species are documented from Mantua Lentil in the Bighorn Basin (Van Valen, 1978) and 11 from the Hanna Basin (Eberle and Lillegraven 1998a, b). While the Littleton fauna falls within the constraints of Pu1 (see Lofgren et al., in press), it is more similar, in terms of its faunal content and high diversity, to the earliest Pu2 faunal assemblage in the Hanna Basin than to any well-documented Pu1 fauna (Eberle, 1996). Several taxa are either shared with, or closely related to, taxa in earliest Pu2 of the Hanna Basin. As an example of the latter, *Procerberus grandis* may be the sister group to the largest known cimolestid, *Alveugena carbonensis* from earliest Pu2 in the Hanna Basin (Eberle, 1999). Also, *Baioconodon jeffersonensis* may be a sister taxon of Pu2 species of *Loxolophus* (this report), which is consistent with a pre-Pu2 age.

The Pu1 age of the Littleton fauna is based upon lack of characteristic Pu2 taxa, including *Ectoconus* (whose first appearance defines onset of Pu2), and the presence of a Pu1 index taxon (*Oxyprimus*) and other typical Pu1 taxa (Lofgren et al., in press). Furthermore, paleomagnetic analyses are consistent with a Pu1 age. Middleton (1983) concluded that the Littleton fauna is probably temporally intermediate between typical Pu1 and Pu2 faunas. That the Littleton fauna contains some 14 new mammalian species and two new genera (Middleton, 1983; this report), only a few of which have since been documented outside the Denver Basin, may suggest that it samples an interval of Pu1 time (i.e., late Pu1) that has not yet been documented elsewhere in North America. However, given that the Littleton fauna like other Pu1 faunas (see Lofgren et al., in press) lies within the Tertiary part of C29R (which has an estimated duration of only 270 ± 17 k.y., D'Hondt et al., 1996), any temporal difference would be relatively small on a geologic time scale.

Alternatively, ecological and biogeographical differences may account for faunal differences between the Littleton fauna and other Pu1 faunas. Specifically, with some 30 different leaf morphotypes represented, the flora in the vicinity of Brown's *Baioconodon* locality at South Table Mountain is considerably more diverse than earliest Paleocene floras found elsewhere, including the flora found in the vicinity of Pu1 DMNH loc. 2557 at the West Bijou Site and floras known outside the Denver Basin (Johnson et al., this issue). Additionally, from a biogeographic standpoint, the Littleton fauna is the southernmost known Pu1 fauna, and the Denver Basin is near the transition that has been suggested to divide northern and southern early Paleocene faunal provinces (Weil, 1999). While differences between the Littleton fauna and other Pu1 faunas may be due, in part, to small temporal differences, ecological and biogeographical differences may well have played a role too.

Puercan mammalian biostratigraphy in the Hanna Basin suggests that the first great Cenozoic radiation of mammals, marked by rapid diversification of ungulates and a trend towards increasing body size, was well underway by the onset of Pu2 (Lillegraven and Eberle, 1999). The Littleton fauna allows some refinement in that its unusually diverse ungulate fauna (Table 13) suggests that some diversification had already begun in Pu1. However, the mammals from the Littleton fauna are still of relatively smaller body size than their Pu2 counterparts. Body mass estimates range from 19–6.4 kg and fall within ranges typical of Pu1 faunas (Dewar, 1996).

Table 13. Mammalian faunal lists of early Puercan (PU1) localities in Denver Basin. Fauna of Alexander locality is from Middleton (1983); "*" indicates new species diagnosed by Middleton (1983) in his unpublished dissertation, while "" indicates names that have been published or changed since Middleton's (1983) study.**

ALEXANDER LOCALITY (UCM loc. 77267)

Order MULTITUBERCULATA
- *Mesodma* cf. *M. ambigua*
- *Xyronomys* new species*
- *Kimbetohia?* new species*
- *Catopsalis alexanderi*
- *Cimexomys minor*
- *Cimexomys* new species*

Order MARSUPIALIA
- *Peradectes pusillus*

Order CIMOLESTA
- *Procerberus grandis***
- *Procerberus* new species*
- *Proteutheria*, family indet.

Order CONDYLARTHRA
- *Oxyprimus* cf. *O. galadrielae*
- *Oxyclaenus* new species*
- *Baioconodon denverensis*
- *Baioconodon* new species*
- Arctocyonidae, genus and species indet.
- *Alticonus gazini***
- *Conacodon harbourae***
- *Conacodon* new species*
- *Ampliconus browni*
- *Oxyacodon* new species*
- *Periptychidae*, new genus and species*

SOUTH TABLE MOUNTAIN (DMNH locs. 2386 and 2387)

Order MULTITUBERCULATA
- *Catopsalis alexanderi*

Order CONDYLARTHRA
- *Baioconodon denverensis*
- *Baioconodon jeffersonensis* new species
- *Procerberus* new species 1*
- *Alticonus gazini*
- *Oxyclaenus* cf. *O. simplex*

NICOLE'S MAMMAL JAW (DMNH loc. 2557)

Order CONDYLARTHRA
- *Protungulatum donnae*

DENVER OXYCLAENODON (DMNH loc. 299)

Order CONDYLARTHRA
- *Oxyclaenus simplex*

Pu2/Pu3

Interval-zones Pu2 and Pu3 are faunally very similar; most differences relate to losses of Pu2 taxa in Pu3, and there are few index taxa for Pu3. Restriction of *Taeniolabis taoensis* to Pu3 is the primary means of differentiating these two interval-zones (Lofgren et al., in press). Since *T. taoensis* is not known from the Denver Basin, the mammalian assemblages at Corral Bluffs and near West Bijou Creek are difficult, if not impossible, to confidently assign to either Pu2 or Pu3.

Middleton (1983) noted that the vertical distribution of certain ungulate taxa may provide meager support for the superposition of Pu3 over Pu2 at Corral Bluffs. However, discoveries subsequent to Middleton's (1983) study suggest that while Pu2 is represented at Corral Bluffs, there is no evidence for an overlying Pu3. While Middleton (1983) reported that *Ectoconus ditrigonus*, most common in Pu2 in the San Juan Basin, occurred in the stratigraphically lowest localities at Corral Bluffs, it is reported here from the stratigraphically highest locality (DMNH loc. 2554), approximately 25 ft (7.6 m) higher than Middleton's (1983, fig. 3) highest locality, UCM loc. 77275. Middleton (1983) also noted that *Conacodon entoconus* (an index taxon for Pu2; see Williamson, 1996) was replaced by the larger, more derived *C. delphae* at the highest localities at Corral Bluffs. *C. entoconus* is reported here from the Alligator Rock locality (DMNH loc. 248), which is roughly the middle of the Puercan mammal-bearing section at Corral Bluffs (Fig. 2).

Outside the Denver Basin, the only documented occurrence of *Conacodon delphae* is from middle Puercan strata in the Hanna Basin (Eberle and Lillegraven, 1998b), suggesting that this species was contemporaneous with *C. entoconus*. Finally, Middleton (1983) noted that as in *Loxolophus kimbetovius* (which is restricted to Pu2 in the San Juan Basin), a specimen of *Loxolophus* cf. *L. kimbetovius* (USNM 16626) may be the stratigraphically lowest mammalian fossil at Corral Bluffs, based upon Brown's (1943) report, as the exact locality is unknown. While its stratigraphic interpretation is not questioned, upon further study, USNM 16626, a dentary fragment with m1 (see Fig. 4B-C), is referred to *Loxolophus faulkneri* (this report). This species also is known from the Hanna Basin, where it is restricted to Pu2 (Eberle and Lillegraven, 1998b).

Consequently, while *Loxolophus faulkneri*, *Conacodon entoconus*, and *C. delphae* corroborate presence of Pu2 at Corral Bluffs, the vertical distribution of ungulate taxa does not provide evidence for an overlying Pu3. In the absence of any index taxa for Pu3, including *Taeniolabis* (see Williamson, 1996; Lofgren et al., in press), Corral Bluffs is tentatively identified here as a Pu2 correlative. However, more fossils are needed to confirm this correlation. Corral Bluffs shares all of its taxa with Pu2 in the San Juan Basin, with exception of *Conacodon delphae* and *Loxolophus faulkneri*, both of which are restricted to Pu2 in the Hanna Basin (Eberle and Lillegraven, 1998b).

The mammalian fauna from DMNH loc. 2563 (Table 14) cannot be assigned confidently either to Pu2 or Pu3, as all of its mammalian taxa are known elsewhere from both interval zones (see Lofgren et al., in press). Fortunately, given the high abundance of vertebrate fossils recovered thus far, DMNH loc. 2563 offers considerable potential for recovering more Puercan mammals and further age refinement.

The Taeniodont site (DMNH loc. 510) is at the same stratigraphic level as DMNH loc. 2563, and also it cannot be confidently assigned to either Pu2 or Pu3. The only vertebrate fossil from the site, a partial skull of a taeniodont with most of the teeth broken off, requires further study before it can be confidently identified. However, as is characteristic for stylinodontid taeniodonts (Lucas et al., 1998), the specimen from the Denver Basin indicates a relatively large, though short and deep, skull, with a short, wide snout, prominent sagittal crest, and large canines. Stylinodontid taeniodonts are documented from strata no older than Pu2 (Williamson, 1996; Schoch, 1986).

The Denver Crockies locality (UCM loc. 91278) has yielded only lower vertebrate fossils to date. Nevertheless, it is a relevant site to discuss here, given: (1) its close geographic and stratigraphic proximity to DMNH loc. 2563; and (2) the presence of an ash dated at 65.03 ± 0.26 Ma (Obradovich, 2002). Since the mammalian fauna at DMNH loc. 2563 is no older than Pu2, the ash date at Denver Crockies seems anomalously old (see Obradovich, 2002). However, if Hicks et al.'s (2002) re-calibrated age of 65.51 ± 0.10 Ma for the K-T boundary is correct, a 65.03 Ma age for a Pu2/Pu3 correlative appears reasonable. Further radioisotopic analyses, and ideally a few mammalian fossils, probably would solve this dilemma.

Table 14. PU2 (Corral Bluffs) and PU2/PU3 correlatives (DMNH locs. 2563 and 510) in Denver Basin. Faunal list for Corral Bluffs based on Middleton (1983, table 35) and this report; "*" indicates name change from Middleton's (1983; table 35) faunal list (see discussion).

CORRAL BLUFFS LOCALITIES
Order MULTITUBERCULATA
Neoplagiaulacidae, genus and species indet.
Order CONDYLARTHRA
Oxyclaenus cf. *O. cuspidatus*
Loxolophus hyattianus
Loxolophus aff. *L. hyattianus*
*Loxolophus faulkneri**
Desmatoclaenus cf. *D. protogonioides*
Mioclaenidae genus and species indet.
Ectoconus ditrigonus
Periptychus coarctatus
Conacodon entoconus
Conacodon aff. *C. entoconus*
Conacodon delphae

DMNH LOC. 2563 (= UCM LOC. 91280)
Order MULTITUBERCULATA
Order CONDYLARTHRA
Periptychus coarctatus
Ectoconus ditrigonus
Haploconus sp.
Mioclaenidae indet.
Condylarthra, family indet.

TAENIODONT SITE (DMNH loc. 510)
Order CIMOLESTA
Stylinodontidae, genus and species as yet unidentified

FUTURE RESEARCH IN DENVER BASIN

An important future goal is simply intensified collection from known Puercan localities, as several hold considerable potential for recovery of more fossils. Increased mammalian diversity is needed to refine the ages of Pu2/Pu3 correlatives. Intensive prospecting in younger strata, along the top of the D1 sequence and just below the paleosol (see Raynolds, 2002), may help answer the question of whether Torrejonian mammals occur in the Denver Basin. To date, none has been documented. Nevertheless, pollen, magnetostratigraphy, and radiometric analyses indicate the presence of strata having radioisotopic ages that would be expected to yield Torrejonian mammals.

The importance and utility of the Denver Basin Project as a whole is magnified when all the data are integrated. In only one other sequence of rocks — the Hell Creek and Tullock Formations in northeastern Montana — are there magnetostratigraphic and radioisotopic analyses to go alongside Puercan mammalian biostratigraphy. Until the Denver Basin Project, these radioisotopic dates from Montana were the only ones associated with Paleocene mammal faunas in North America (Lofgren et al., in press). With the aid of these other geochronological tools, a future goal is to correlate the Puercan mammalian biostratigraphy of the Denver Basin to other areas north and south, with the ultimate goal of building a Western Interior-wide, mammal-based stratigraphic framework for the first million years of Tertiary time.

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