EARLIEST EOCENE MAMMALIAN FAUNA FROM THE PALEOCENE-EOCENE THERMAL MAXIMUM AT SAND CREEK DIVIDE, SOUTHERN BIGHORN BASIN, WYOMING

KENNETH D. ROSE et al.

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Frontispiece: View looking east at Sand Creek Divide, southern Bighorn Basin, showing most of the PETM section. Prominent red band near the foot of the outcrop marks the base of the Eocene and the beginning of the PETM (see Figure 2B).

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ABSTRACT

An extensive earliest Eocene mammalian fauna is described from the PETM interval of Sand Creek Divide, about 17 km northeast of Worland, Wyoming. The assemblage, consisting of more than 1000 specimens representing 56 species, was collected over the last decade by surface prospecting, screen-washing, and limited excavation. Samples come from more than 40 localities spread throughout a 45-m section representing the entire PETM (~200 ka). Carbon isotope records from bulk sediment and from mammalian tooth enamel were compiled and used to delimit the PETM and to correlate the Sand Creek Divide section with the Polecat Bench section. The lowest 1-2 m of the PETM section at Sand Creek Divide appears to correspond to the Wa-M biozone at Polecat Bench, although the only taxon in common is the condylarth *Haplomylus zalmouti*. This narrow interval at Sand Creek Divide has also produced the lowest occurrence of *Diacodexis*, but has not yielded *Meniscotherium*, the index taxon for which the biozone was named. The remainder of the PETM section at Sand Creek Divide represents the Wa-0 biozone. About 15-20 m below the PETM faunas is a small sample of late Clarkforkian mammals. The upper boundary of the Wa-0 biozone is demarcated by the lowest occurrences of several Wa-1 taxa (*Hyracotherium grangeri*, *Cardiolophus radinskyi*, *Cantius ralstoni*, *Haplomylus speirianus*), which are found between 45 and 50 m. This is ~15-20 m higher than the lowest Wa-1 samples from the No Water Creek section of Bown (1979), indicating a thicker PETM section at Sand Creek Divide. An unexpected first occurrence at 50 m is the perissodactyl *Homogalax protapirinus*, otherwise unknown until Wa-3.

The Sand Creek Divide local fauna is similar in most regards to those previously described from Polecat Bench and Castle Gardens, corroborating the general character and composition of the Wa-0 fauna. However, due to its larger sample size, it is more speciose, with 30% more species than in the Polecat Bench or Castle Gardens Wa-0 assemblages. It is intermediate between Paleocene and other Eocene faunas in being dominated by phenacodontid condylarths, primarily the Wa-0 index taxa *Ectocion parvus* and *Copecion davisi*, occurring together with the typical Wasatchian genera *Hyopsodus*, *Hyracotherium*, *Diacodexis*, and *Cantius* (though less common than they are after the PETM), as well as hyaenodontid creodonts. As observed elsewhere, many PETM species are smaller than their close relatives from immediately before or after the PETM. Faunal records from Sand Creek Divide suggest that there may have been multiple waves of immigration during the PETM rather than a single event at the onset of the PETM. In particular, ungulates appear lower in the section than do euprimates, and omomyids appear earlier than do notharctids. The Wa-0 mammalian assemblage was more diverse than both late Clarkforkian and early Wasatchian (Wa-1) faunas. One new genus and five new species are named: the nyctitheriids *Leptacodon donkroni*, sp. nov., and *Plagioctenoides tombowni*, sp. nov., the ?microsyopid primate *Nanomomys thermophilus*, gen. et sp. nov., the omomyid primate *Teilhardina gingerichi*, sp. nov., and the cylindrodontid rodent *Tuscahomys worlandensis*, sp. nov. Several other probable new species are left unnamed because of inadequate material. The Sand Creek Divide local fauna has the oldest or first PETM records for six additional taxa, including *Esthonyx* (*E. spatularius* in Wa-M) and *Didelphodus* sp. (Wa-0).

I

INTRODUCTION

The boundary between the Paleocene and Eocene epochs of the Paleogene period is associated with a dramatic episode of global change in climate, geochemical cycles, and biology (e.g., Kennett and Stott, 1991; Zachos et al., 1993). Global temperature underwent a rapid rise of 5-9ºC, an event that has been termed the Paleocene-Eocene Thermal Maximum (PETM). Based on astronomical approaches, estimated time spans for the PETM have ranged from 150 ka to 220 ka (Norris and Röhl, 1999; Röhl et al., 2000, 2007). Using ^{3}He, Murphy et al. (2010) suggested a duration of ~200 ka. Coincident with this warming was a major perturbation of the global carbon cycle that resulted in a negative carbon isotope excursion (CIE) in sediment records from both marine and terrestrial environments. (For an overview of the PETM see Bowen et al., 2006; Zachos et al., 2008.) This disruption to the earth's climate system had far-ranging effects, including changes to atmospheric moisture transport, changes to global ocean circulation, triggering of inter-continental mammalian dispersal, mammalian dwarfing, extinction of 35-50% of deep-sea benthic foraminifera species, and significant northward range extensions of continental floras (see reviews by Bowen et al., 2006, and Gingerich, 2006).

The best terrestrial records of the CIE and associated PETM are preserved in the Bighorn Basin of Wyoming. At Polecat Bench, in the northern part of the basin, the CIE is recorded in both pedogenic carbonate nodules (e.g., Koch et al., 1992) and dispersed organic carbon from bulk sediment samples (Magioncalda et al., 2004). There the PETM interval is ~40 m thick and begins ~330 m above the contact with the underlying Fort Union Formation. Isotopic analyses of vertebrate fossil material (Fricke and Wing, 2004) and leaf margin data (Wing et al., 2005) indicate that PETM temperatures rose ~5°C, while studies of paleosols (Kraus and Riggins, 2007) and paleosol ichnofossils (Smith et al., 2008) demonstrate drier conditions at the beginning of the PETM interval and a return to more humid conditions by the end of it. At Cabin Fork in the southern part of the Bighorn Basin, the CIE has been recognized in various types of sedimentary organic matter (Wing et al., 2005; Smith et al., 2007). Paleofloral analysis of fossils from this area suggests a similar rise in MAT and transient drying (Wing et al., 2005). Finally, at the Honeycombs (Yans et al., 2006), which is ~6 km east of Cabin Fork, the CIE has also been identified, although associated records of environmental change have not been described.

In addition to records of the CIE and PETM, the Bighorn Basin preserves the best record of mammalian turnover associated with these events. The distinctive mammalian fauna from the interval of the PETM is best known from two parts of the Bighorn Basin (Figure 1): Polecat Bench in the northwestern part of the basin (Gingerich, 1989, 2001; Smith et al., 2002; Gingerich and Smith, 2006) and the Castle Gardens locality in the Honeycombs area of the southeast basin (Strait, 2001; Yans et al., 2006). At Polecat Bench, the PETM interval is distinguished by the Wasatchian-*Meniscotherium* (Wa-M) and Wasatchian-0 (Wa-0) biozones (e.g., Gingerich, 2001, 2003; Magioncalda et al., 2004, Gingerich and Smith, 2006). Wa-M is marked by the presence of *Meniscotherium* and several other distinctive taxa and starts several meters above the base of the CIE. About 10 m above the start of the CIE, Wa-M is succeeded by the Wa-0 biozone, as indicated by the disappearance of *Meniscotherium* and the first appearance of perissodactyls, artiodactyls, euprimates, and hyaenodontids. Toward the end of the CIE, the Wa-0 biozone is succeeded by the Wa-1 biozone, characterized by species-level changes in several taxa and the first appearance of the perissodactyl *Cardiolophus*. In the general Cabin Fork area (which includes the Castle Gardens locality and the Honeycombs section), Wing et al. (2009) have documented four different sections where the lowest Wa-0 fossils are associated with the first laterally continuous red paleosol containing pedogenic carbonate nodules. The fossils also coincide with a negative excursion of 3-4‰ in $\delta^{13}C_{org}$. At Cabin Fork, the earliest Wa-0 fossils have been found ~3 to 5 m above the base of the Willwood Formation (Wing et al., 2005). The lowest Wa-1 fossils appear ~37 m above the formation base and, similar to Polecat Bench, are found in the upper part of the CIE (Wing et al., 2005). Only a single specimen of *Meniscotherium* has been reported from the Cabin Fork–Honeycombs area (Yans et al., 2006), and that specimen came from ~4 m below where Wing et al. (2009) would place the base of the PETM. Wing et al. suggested that the specimen probably washed down from a higher stratigraphic level as a result of steep exposures.

In 2001 the Johns Hopkins University School of Medicine, in collaboration with researchers from several other institutions, initiated an exploration of the Sand Creek Divide area about 17 km north of Worland, Wyoming, for fossil mammals spanning the Paleocene-Eocene transition (Figure 2). This area includes the conformable contact between the Fort Union and Willwood formations, and continuous outcrops of these formations extend for several miles. An index fossil of the Wa-0 biozone, the phenacodontid condylarth *Copecion davisi*, had been reported from there by Gingerich (1989), but no further collecting was undertaken until this project. Now, after several seasons of intensive field efforts at Sand Creek Divide, together with detailed lithostratigraphic and chemostratigraphic studies, we report here a rich and stratigraphically well-documented assemblage that expands and clarifies our knowledge of the mammalian fauna during this pivotal interval. It contains substantially more species than reported for other Wa-0 local faunas, including a new genus and two new species of primates, several other new species, and the oldest or first PETM records for at least six additional species. Data presented here document the staggered first appearances of immigrant taxa, including the oldest North American primates, artiodactyls, and perissodactyls, though their relative abundances remained low and they were not to dominate until after the PETM. Nevertheless, the Wa-0 mammalian fauna was remarkably diverse—significantly more so than late Clarkforkian and other early Wasatchian faunas.

MATERIALS AND METHODS

Stratigraphy

In order to provide a paleoenvironmental context for the paleontological work taking place, a detailed sedimentological and stratigraphic study of the Paleocene-Eocene transition at Sand Creek Divide was undertaken. Because of limitations of the exposures, the lithostratigraphic and isotope sections were measured in two areas of the Sand Creek Divide. The North and South sections were correlated using the lowest persistent red paleosol (**Red 1**), which marks the base of the Willwood Formation, and the **Big Red** interval, which is easily traced throughout the Sand Creek area (Figure 3). The Fort Union Formation is only present in the North section, and samples for isotopic analysis of the lower part of the section were collected here. The stratigraphically highest isotope values from the North section are from the uppermost red paleosol in that section, above which exposures end. Consequently, the upper part of the isotope section was sampled from the South section. **Upper Purple 1** (UP1) in the South section is correlated to the uppermost red paleosol in the North section because both contain carbonate nodules and nodules end above UP1. The lowest reproducible isotope values in the South section are from the paleosol directly above **Upper Purple 2**, thus there is a slight gap in the isotope record. Lateral variations in thickness of various fluvial strata also produce thickness variations between the North and South sections (Figure 3). Stratigraphic sections were measured using a Jacob's staff and strike of 320° and dip of 3° SW. Lithologic details were described by digging ~1 meter wide trenches to expose fresh rock.

In an effort to identify the CIE associated with the Paleocene-Eocene boundary at Sand Creek Divide, and thus (1) identify the base of the Eocene section and (2) correlate these sections to others in the Bighorn Basin, samples of bulk sediment were collected for carbon isotope analysis, as were a limited number of samples of mammalian (*Coryphodon*) tooth enamel.

Bulk sediment samples were soaked in 0.1M HCl for three hours, rinsed in distilled water four times, and dried. Carbon isotope ratios were measured on a Finnigan Delta PlusXL continuous-flow gas-ratio mass spectrometer at the University of Arizona. Samples were combusted using a Costech elemental analyzer coupled to the mass spectrometer. Carbon isotope ratios are reported as $\delta^{13}C$, where $\delta = (R_{sample}/R_{standard} - 1)*1000$ ‰, and the standard is VPDB for carbon. Standardization is based on NBS-22 and USGS-24. Precision is better than ± 0.06 for $\delta^{13}C$ (1σ), based on repeated internal standards.

Most enamel samples were analyzed by Paul Koch at the Stable Isotope Laboratory of the University of California Santa Cruz. Enamel was removed from tooth fragments using a low speed dental drill under a binocular microscope. Following the protocol in Koch et al. (1997), all powders were soaked for 24 hours in 2% NaOCl to oxidize organic matter, rinsed five times with distilled water, soaked for 24 hours in 1 M calcium acetate-buffered/acetic acid to remove contaminating carbonate in non-lattice sites, rinsed five times with distilled water, and then freeze-dried. Approximately 1 mg of pretreated powder was analyzed using an Isocarb automated carbonate analysis system interfaced with a Micromass Optima gas source mass spectrometer. Samples were dissolved in 100% phosphoric acid at 90°C, with concurrent cryogenic trapping of CO_2 and H_2O. The CO_2 was then admitted to the mass spectrometer for analysis. The standards used in this study were Carrera Marble and NBS-19 and values are reported relative to V-PDB (for carbon) and V-SMOW (for oxygen). Precision, determined by repeated concurrent analysis of a modern elephant enamel standard, was 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{18}O$. Samples of enamel from the top of the Sand Creek Divide section were analyzed by Ross Secord, following the protocol of Koch et al. (1997), except that samples were oven-dried at 60ºC overnight (rather than freeze-dried). The samples were then reacted with phosphoric acid for 17 minutes at 77º ± 1ºC in a Finnigan MAT Kiel IV preparation device at the University of Michigan Stable Isotope Laboratory (UMSIL). Isotope ratios of the resulting CO_2 were measured with a Finnigan MAT 253 triple collector isotope ratio mass spectrometer. Analytical precision at UMSIL is better than ±0.1‰ (1 s.d.) for both δ18O and δ13C, based on international standards for carbonate (NBS-18, NBS-19).

Paleontology

Fossil specimens were collected mainly by surface prospecting. In contrast to much of the Willwood Formation, vertebrate fossils in the Wa-0 interval on Sand Creek Divide (McDermott's Butte Quadrangle) are relatively scarce and tend to be very fragmentary. Consequently, we are obligated to make use of isolated teeth to a much greater extent than in the rest of the formation. Many isolated teeth as well as micro-vertebrate remains were collected through screen-washing of in-situ sediment, as well as from anthills developed on Wa-0 strata, using mesh down to 0.5 mm. While it is impossible to know the exact source of anthill fossils, recent observations suggest that harvester ants usually forage within 20 m of the nest (Schoville et al., 2009). It is generally assumed that anthill samples, if taken from relatively flat areas, are quite limited in stratigraphic range and do not mix samples from significantly different levels. In addition to these methods, small-scale excavation was undertaken at a few localities (WW-74, 78, 80, and 186), where mammal fossils were found in situ.

Since the inception of our work in the Sand Creek Divide area in 2001, care has been taken to record the exact strata within the study area from which fossils were collected. Geographic

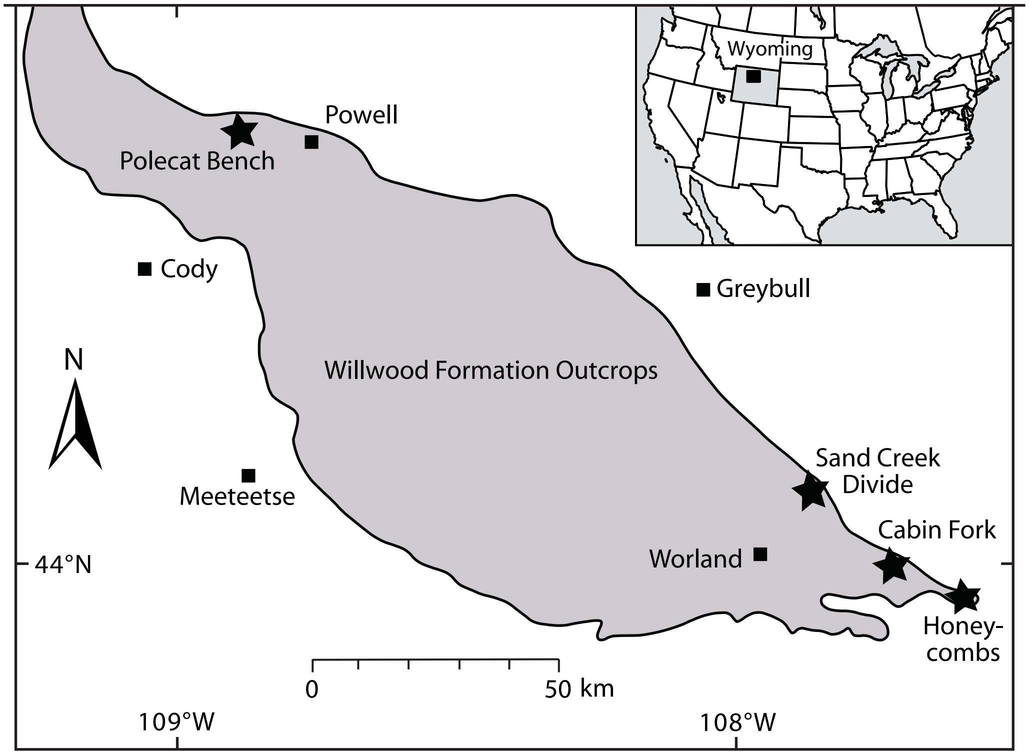

FIGURE 1 — Map of the Bighorn Basin, showing location of Sand Creek Divide and other PETM faunas (stars). Modified after Abdul Aziz et al., 2008.

coordinates of fossil occurrences have been marked with GPS units, and fossil localities have been situated in the field with respect to various marker beds that can be followed through much or all of the area. Even so, because of local variations in thickness, as well as discontinuity of many thinner mudstones and sandstones, it is difficult to be certain of the precise stratigraphic level of some localities. More than 40 numbered localities have been established, including one from the upper Clarkforkian, 39 spanning the PETM (three from Wa-M and 36 from Wa-0), and four from the Wa-1 interval. Locality numbers were not assigned to some individual specimens; however, those specimens were located by geographic coordinates and stratigraphic position.

More than 1000 mammalian specimens have been identified (the subject of this report), in addition to hundreds of remains of fish (*Lepisosteus* and *Amia*, s.l.), crocodilians, lizards, and turtles. Hundreds more unidentified teeth (mainly isolated antemolar teeth) and postcrania are not included in this number. As at other Wa-0 localities in the Bighorn Basin, many bones from the Wa-0 section at Sand Creek Divide are light yellow or orange, and tooth enamel tends to be light brown. However, this is not always the case. Some specimens are quite dark and have black enamel (e.g., all specimens from localities WW-80, 186; but also some from higher in the Wa-0 section).

Accurate species-level identification of isolated teeth can be very challenging and may be impossible for certain teeth that differ little or not at all between closely allied species (e.g., conservative molars in species that differ principally in premolar morphology). Hence taxonomic assignments based on isolated teeth should be regarded as tentative until more complete specimens are available. Some samples of isolated teeth from the same locality have been given the same catalogue number, although there is no evidence that they represent a single individual. Generally these specimens are designated below as “miscellaneous teeth” or “isolated teeth.”

Digital images of larger specimens were prepared using a Nikon digital camera mounted on a Nikon SMZ-1500 binocular microscope, or a Canon EOS digital camera fitted with a macro lens. Most of these specimens were coated with ammonium chloride to enhance visibility of surface details. Some postcranial elements were coated with a thin layer of Cover Girl® Foundation to even the surface, a technique developed by Chester Tarka at the American Museum of Natural History. Digital images were edited in Adobe Photoshop. Images of the smallest specimens were prepared by encasing them in flour inside gelcaps and scanning them in the OMNI-X HD600 High-Resolution Computed Tomography scanner in the Center for Quantitative Imaging at The Pennsylvania State University. Scans were collected using the X-TEK microfocus x-ray tube with source energy settings of 150kV, 0.11mA, a source-to-object distance of 27.65 mm, and a slice thickness and spacing of 0.0083 mm. Each gelcap was scanned with 2400 views and 3 samples averaged per view. Images were reconstructed with a 1024 x 1024

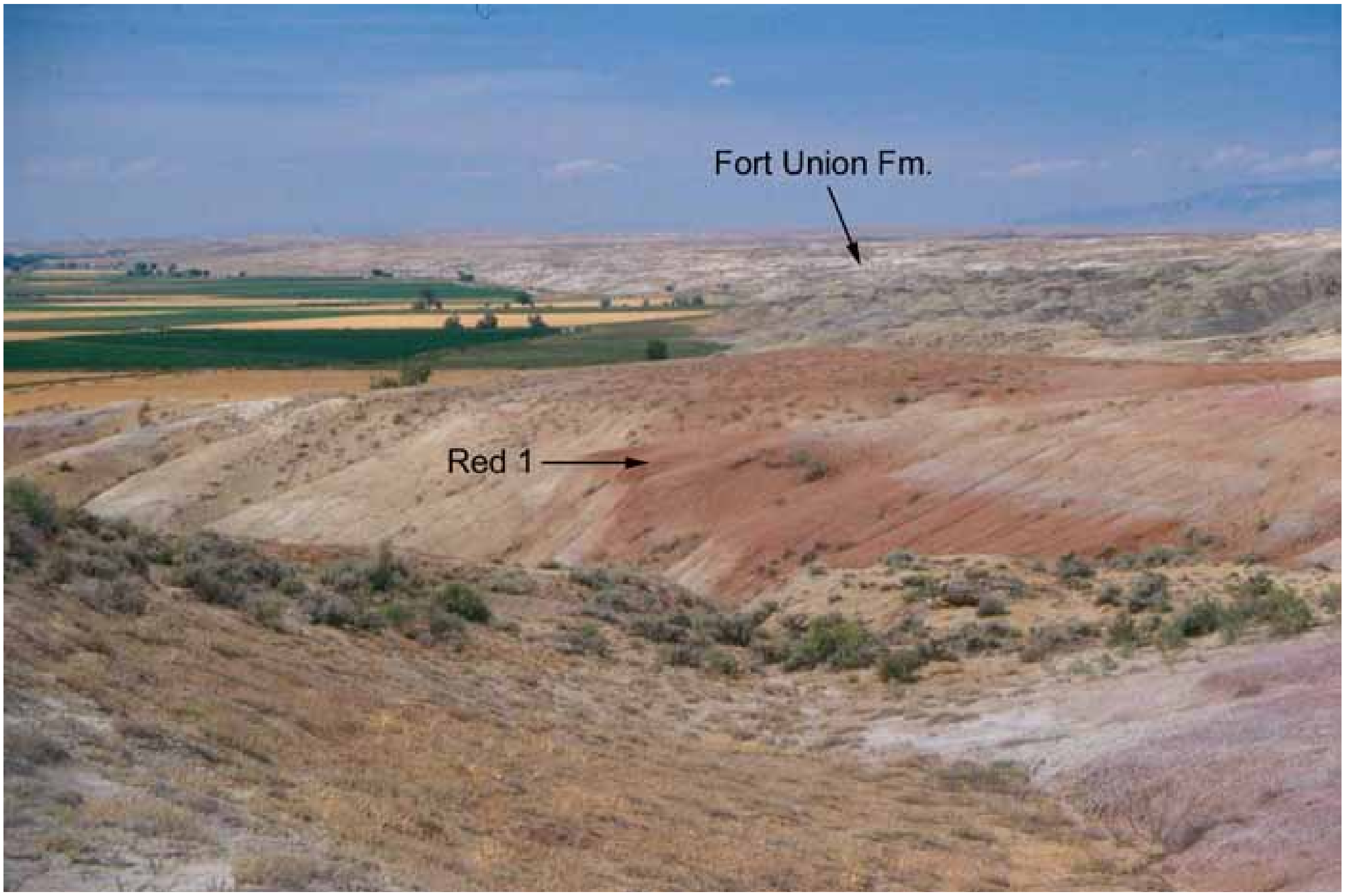

FIGURE 2A — Sand Creek Divide outcrops: Looking north, at lowest Eocene exposures in the foreground (Red 1), underlain by drab Paleocene Fort Union Formation, which is extensively exposed to the north (background).

pixel matrix using a field of view of 8.48 mm, resulting in a pixel size of 0.0083 mm. Resulting images were loaded into Amira 4.1.1 (Mercury Computer Systems, Inc.) and 3D surface models were generated using the Isosurface function. The snapshot tool was used to capture 2D images of the models which were then compiled into plates in Adobe Photoshop and Illustrator.

Measurements were made to the nearest 0.05 mm using a micrometer in the lens of a Nikon SMZ-10 binocular microscope or, for larger specimens, using digital calipers. Estimated measurements are indicated by *.

A small number of specimens collected in July 2010 and one in July 2011 (indicated by **) were not catalogued and accessible until after faunal analyses were completed. Consequently, they are not included in the specimen counts and faunal analyses; but they are listed among Referred Specimens below for completeness, and some are illustrated.

ABBREVIATIONS

D	depth
dist	distal
H	height
L	maximum length
ling	lingual
MNI	minimum number of individuals
prox	proximal
TNS	total number of specimens
W	maximum width
$\mathbf{W_a}$	trigonid width
$\mathbf{W_p}$	talonid width

INSTITUTIONAL ABBREVIATIONS

AMNH — Department of Vertebrate Paleontology, American Museum of Natural History, New York;
UCMP — University of California Museum of Paleontology, Berkeley, California;
UM — University of Michigan Museum of Paleontology, Ann Arbor, Michigan;
USGS — U.S. Geological Survey, Denver, collection transferred to USNM;

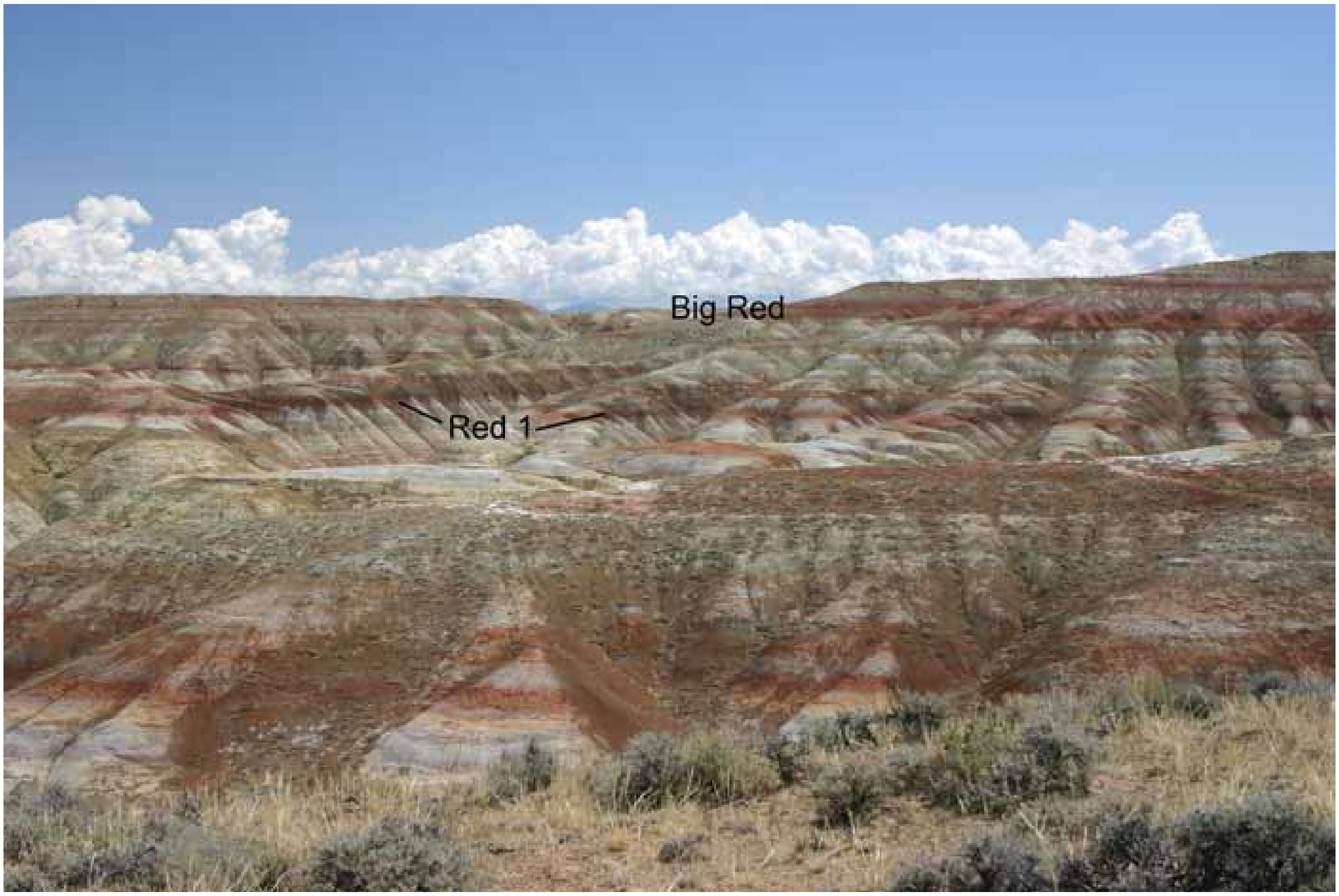

FIGURE 2B — Sand Creek Divide outcrops: Section to the northeast, showing the two principal marker beds of the PETM, which are persistent in the Sand Creek Divide area.

USNM — Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.;

UW — Department of Geology and Geophysics, University of Wyoming, Laramie, Wyoming;

WW — Willwood fossil locality, Johns Hopkins University School of Medicine (collection accessioned into USNM).

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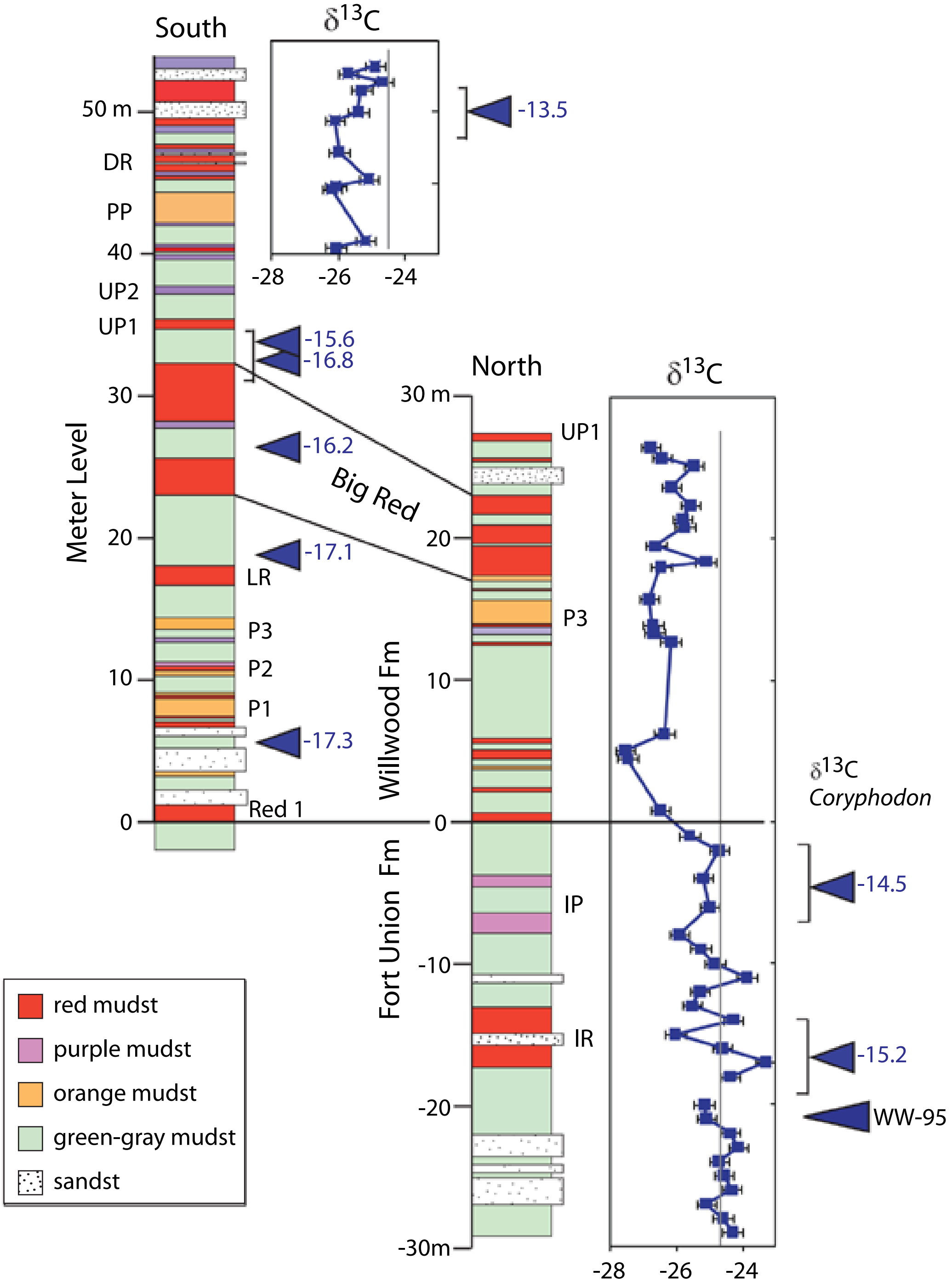


FIGURE 3 — Carbon isotope ratios of bulk sedimentary organic matter (=dispersed organic carbon, solid blue symbols and blue line) and of mammalian tooth enamel (large blue triangles) are plotted against the composite measured stratigraphic sections from the southern and northern parts of the Sand Creek Divide study area. (Biogenic isotopic data provided by Paul Koch and Ross Secord.) The lithologic section shows red, purple, and orange paleosols that alternate vertically with avulsion deposits consisting of green-gray mudstones and sandstones. The 0 m-level is placed at the base of the lowest continuous red paleosol (Red 1), which marks the contact between the Fort Union and Willwood formations. The north and south sections are correlated using Red 1 and the Big Red paleosol. From bottom to top of the section, bed abbreviations are: IR= intermittent red paleosol; IP= intermittent purple paleosol; P1 = Purple 1 paleosol; P2 = Purple 2 paleosol; P3 = Purple 3 paleosol; LR=Little Red paleosol; UP1 = Upper Purple 1 paleosol; UP2 = Upper Purple 2 paleosol; PP = Puffy Purple paleosol; DR = Double Red paleosols.

II

THE PALEOCENE-EOCENE BOUNDARY AT SAND CREEK DIVIDE

LOCATING THE PALEOCENE-EOCENE BOUNDARY

Carbon isotope ratios of bulk sedimentary organic matter (som, = dispersed organic carbon) and of mammalian tooth enamel are plotted against stratigraphic position in Figure 3. Relatively uniform $\delta^{13}C_{som}$ of ~-24.5 ‰ characterizes the section below the lowest red bed (Red 1), although variability in $\delta^{13}C_{som}$ increases upsection (see solid vertical line, Figure 3). $\delta^{13}C_{som}$ values begin to decrease ~1 to 2 m below the base of the Red 1 paleosol, reaching a low of ~-28 ‰, and then remain between -28 and -26 ‰ until the Big Red paleosol sequence. Above this sequence, $\delta^{13}C_{som}$ gradually increases to a value of ~-24 ‰.

The shift to lower $\delta^{13}C_{som}$ values that occurs just below the Red 1 paleosol is interpreted to represent the onset of the PETM carbon isotope excursion, while the return to higher values higher in the section is interpreted to record the end of the excursion. Support for this interpretation can be found by comparing the Sand Creek Divide isotopic record with that from Polecat Bench in the northern part of the basin (Figure 4). The remarkable similarity in both $\delta^{13}C_{som}$ and $\delta^{13}C_{enamel}$ indicates that the same changes to the carbon cycle are being recorded in both places. Because the $\delta^{13}C_{som}$ record from Polecat Bench is directly associated with the more obvious carbon isotope excursion in $\delta^{13}C$ of paleosol carbonate nodules that has been used to define the Paleocene-Eocene boundary in that area (Magnioncalda et al., 2004), we conclude that the CIE we observe at Sand Creek Divide is also the one associated with the PETM. Therefore we place the beginning of the Eocene epoch at approximately the same level as the base of the lowermost persistent red bed, Red 1, when $\delta^{13}C_{som}$ values drop below background levels (to ~-26 ‰). Because Red 1 also marks the boundary between the Willwood Formation and underlying Fort Union Formation, the base of that red bed is designated as the 0 m-level in the stratigraphic section.

SEDIMENTOLOGY OF THE PALEOCENE-EOCENE BOUNDARY INTERVAL

Both the Fort Union and Willwood formations are fluvial stratigraphic units that can be divided into two major kinds of deposits. Mudstones, on which moderately- to strongly-developed paleosols formed, alternate vertically with heterolithic deposits that consist of green-gray mudrocks, which show weak paleosol development, and small channel and thin sheet sandstones (Figure 5). The more strongly developed paleosols are floodplain deposits formed by annual overbank floods. The Fort Union Formation is characterized by gray and green-gray paleosols, whereas laterally persistent red, purple, and orange paleosols distinguish the Willwood Formation.

The heterolithic deposits have been interpreted as ancient avulsion belt deposits that formed on the floodplain as the main channels were episodically abandoned in favor of new channel courses (e.g., Kraus & Gwinn, 1997). This process of abandonment and channel initiation proceeds through crevassing of the old channel and deposition of both fine-grained deposits and sandstones on the floodplain. Crevasse channels are the conduits for the sediments, and they produce the small channel sandstones found in the heterolithic intervals. Although the small channel sandstones are part of the heterolithic intervals, they can scour down into the underlying mature paleosol. Consequently, paleosols can be locally cut out and replaced by sandstones and/or fine-grained channel-fill deposits.

Although the red and purple paleosols of the Willwood Formation vary in terms of their degree of pedogenic development, most of them represent at least several thousand years of time (e.g., Birkeland, 1999; Kraus, 1999). The weak pedogenesis of the avulsion deposits indicates that they accumulated rapidly compared to the mature paleosols. Similar deposits in the modern record can represent as little as several hundred years (e.g., Smith et al., 1989). Consequently, fossil accumulations found in the avulsion deposits between mature paleosols show little time averaging. Some of the most productive fossil localities in the Sand Creek Divide section are situated in these avulsion deposits (e.g., WW-74, WW-84).

In the uppermost ~15 m of the Fort Union Formation, gray paleosols grade laterally into areally restricted (~100 m wide) red and purple paleosols (Figure 3, IR and IP = **intermittent red** and **intermittent purple**). The absence of carbonate nodules in the Fort Union paleosols and their pervasive gray soil colors indicate generally poorly drained soil conditions. Yet, the local red and purple colors, representing the stratigraphically lowest evidence of such soil colors, suggest incipient improvement in soil drainage. Carbonate nodules first appear in **Red 1** at the base of the Willwood Formation (Kraus and Riggins, 2007). The presence of carbonate nodules and red soil colors indicates that soil drainage improved markedly at the start of the PETM. The paleosol change suggests that the climate became drier or that precipitation became more seasonal at the formation boundary.

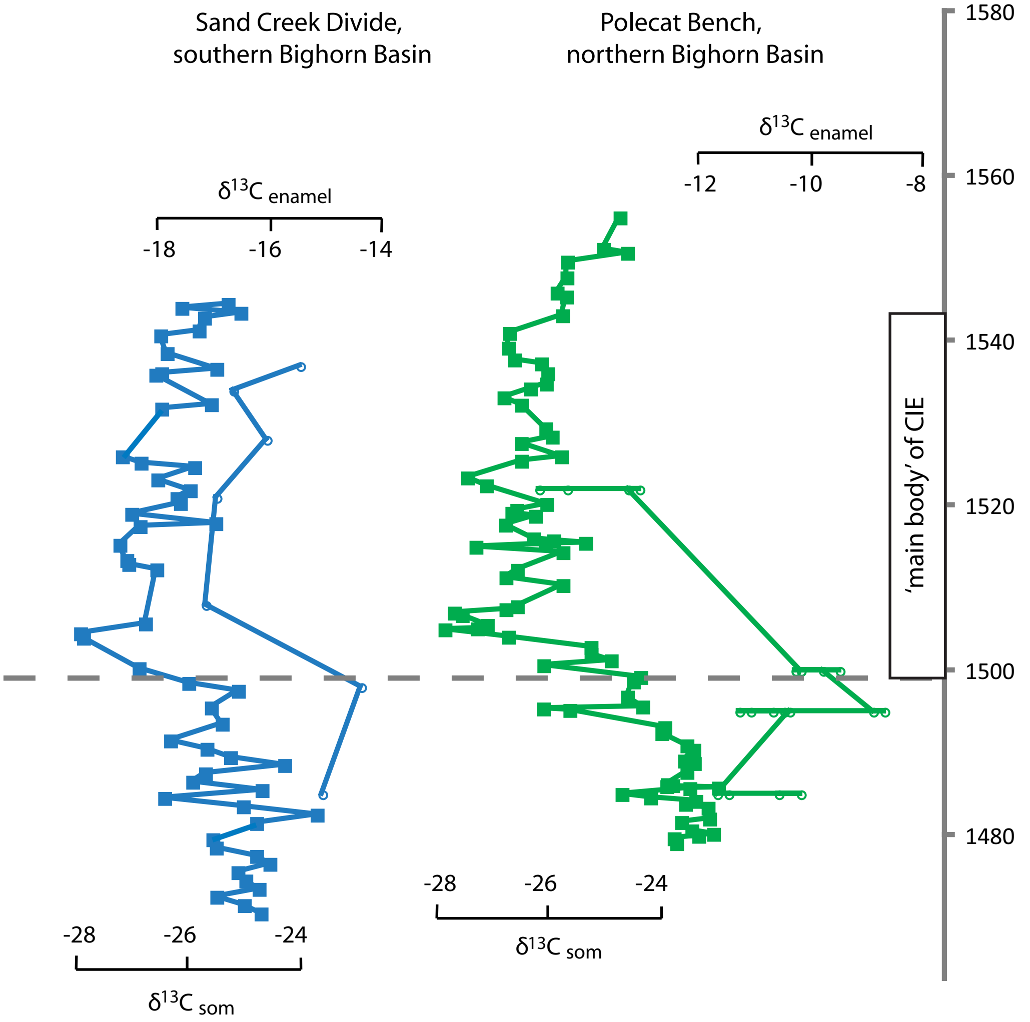


FIGURE 4 — Carbon isotope records of sedimentary organic matter (=dispersed organic carbon, solid symbols) and mammalian tooth enamel (open symbols) from Sand Creek Divide (blue) and Polecat Bench (green: Magioncalda et al., 2004; Secord et al., 2010). Meter levels are given for the Polecat Bench samples and reflect positions relative to the K/T boundary. The dashed horizontal line represents the approximate onset of the ~40 m thick 'main body' of the PETM CIE at Polecat Bench (Magioncalda et al., 2004). The carbon isotope records from Sand Creek Divide are correlated with the Polecat Bench records using the onset of the PETM CIE as a marker.

Four distinct and laterally traceable paleosols appear above Red 1 in the South section: **Purple 1** (P1), **Purple 2** (P2), **Purple 3** (P3), and **Little Red** (LR) (Figures 3, 5A). The matrix color of the three purple paleosols varies laterally between purple and red. P3 has a distinct yellow top, and this paleosol can be correlated to a yellow-purple couplet at ~15 m level in the North section. P1 and P2 are more difficult to correlate to the North section because a thick crevasse-splay interval (~6 to 12 m level) complicates the North section and a splay interval between Red 1 and P1 complicates the South section. LR has a consistent red matrix and is separated from the overlying Big Red interval by a thick (~5 m) avulsion deposit. The Big Red interval generally consists of two or three red or red/purple paleosols separated by avulsion deposits. Individual red paleosols can be over 2 m thick, which is considerably thicker than the typical mature paleosol in the PETM interval. The thickness of the entire Big Red interval varies depending on the local presence of avulsion deposits and lateral perturbations in the thickness of the avulsion deposits.

Upper Purple 1 and **Upper Purple 2** (UP1 and UP2) sit just above the Big Red interval in the South section (Figures 3, 5C). Both paleosols are thin (<1 m thick), and the matrix color varies laterally between red and purple. Above UP1, carbonate nodules are absent from the paleosols. The most distinctive paleosol in the upper part of the section — **Puffy Purple** (PP, above UP2) — is a complex paleosol that is divided into two purple paleosols by crevasse splay deposits. The presence of multiple paleosols is commonly obscured by surficial weathering that causes the beds to bleed together. The upper part of Puffy Purple is a laterally traceable gold

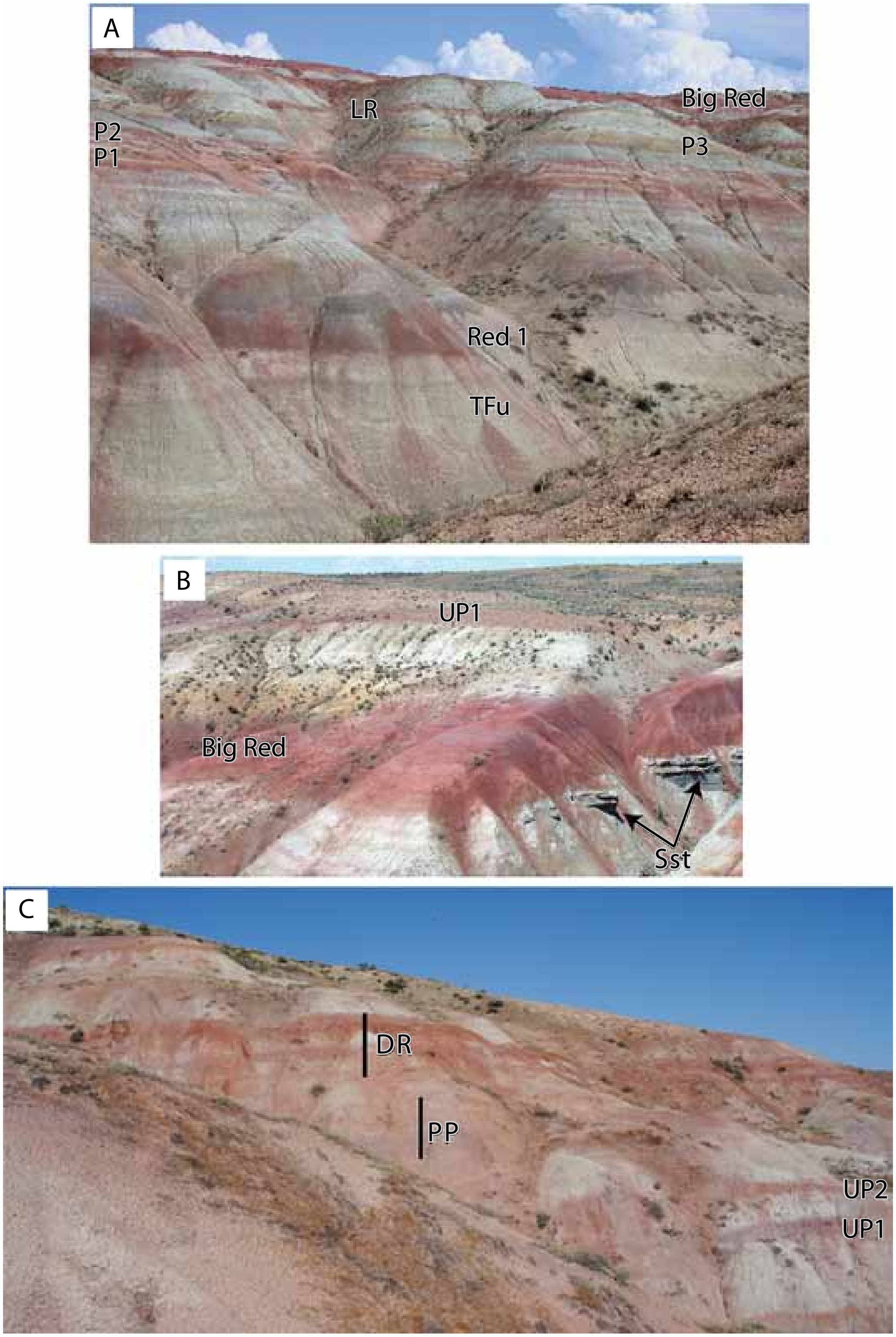


FIGURE 5 — Sand Creek Divide outcrops showing bright-colored paleosols interbedded with whitish avulsion deposits: A, stratigraphic interval from Red 1 through the Big Red paleosol; other laterally-traceable paleosols include Purple 1 (P1), Purple 2 (P2), Purple 3(P3) and Little Red (LR). Red 1 is underlain by drab beds of the uppermost Fort Union Formation. 44º 09.0567´N, 107º 51.8962´W, view to the southeast. B, Big Red paleosol, which is underlain and overlain by thick avulsion deposits that locally contain sandstone beds (Sst), 44º 08.769´N, 107º 50.912´W, view to the north. C, upper part of study interval showing Upper Purple 1 (UP1) and Upper Purple 2 (UP2) paleosols, Puffy Purple paleosol (PP), and Double Red (DR) paleosol interval. 44º 08.834´N, 107º 51.479´W, view to the northwest.

color because of abundant yellow-brown mottles and nodules within a purple or green-gray matrix. Above Puffy Purple is a series of densely spaced purple and red/purple paleosols. The disappearance of carbonate nodules and increase in purple mudstones with yellow-brown nodules above the Big Red interval indicate a return to more poorly drained soil conditions (Kraus and Riggins, 2007). The paleosols making up the **Double Red** (DR) interval near the top of the section suggest a return to wetter climates or less seasonal precipitation.

FOSSIL VERTEBRATE LOCALITIES AT SAND CREEK DIVIDE

We have established 44 numbered fossil vertebrate localities and numerous additional unnumbered sites, typically for a single specimen, in the study area; 39 numbered localities are in the PETM interval (Wa-M plus Wa-0; Figure 6). The Fort Union part of the section is relatively unfossiliferous and only one locality (WW-95) has produced multiple specimens. Four localities high in the section (WW-89, 173, 178, 184), above the marker bed designated Puffy Purple, have produced faunas of Wa-1 aspect, hence we draw the boundary between Wa-0 and Wa-1 in the South Section at about 44 m above the base of Red 1 (= the base of the Willwood Formation). The carbon isotope record in this section suggests that the Wa-0/Wa-1 boundary is near the end of the “main body” phase of the CIE where $\delta^{13}C$ values begin to increase gradually to pre-CIE values (similar to Polecat Bench).

Initial prospecting took place in the vicinity of UM locality BR-2 (SE¼, NE¼, section 11, T 48 N, R 92 W, Washakie County, Wyoming; McDermotts Butte Quadrangle), where *Copecion davisi* was found earlier (Gingerich, 1989), but exposures there are either poorly weathered or very steep, and little was found. Exposures 1-2 km west and southwest of BR-2 are less steep and proved to be more fossiliferous.

In the following summary of localities, approximate meter levels in the South Section at Sand Creek Divide are indicated. However, because the section varies in thickness in different parts of the study area, positions relative to the marker beds noted above are more important. Variations in thickness together with the intermittent occurrence or change in coloration of some of the beds make levels of some localities inexact. Unless otherwise noted, all localities are in the lower Willwood Formation, within Wa-0, and are situated in T 48 N, R 92 W, on McDermotts Butte Quadrangle, in Washakie County, Wyoming.

WW-71 (12 m): sandy cut between Purples 2 and 3. “Jon’s Hill;” discovered by Jonathan Bloch. SE¼, SE¼, section 3; 44.15611°N, 107.87000°W.

WW-72 (~6 m): in sandstone above Red 1. SE¼, SE¼, section 3; 44.15667°N, 107.87111°W.

WW-73 (13 m): in Purple 3. SE¼, SE¼, section 3; 44.15556°N, 107.87222°W.

WW-74 (12 m): white sandy mudstone above and cutting into Purple 2; same cut as WW-71. “Amy’s Hill;” discovered by Amy Chew. SE¼, SE¼, section 3; 44.15611°N, 107.87278° W. This is the most important and productive in situ screen-washing site in the section, which has produced an extensive micromammal assemblage.

WW-75 (~12 m): sandy mudstone and anthills; probably same cut as WW-71. SW¼, SW¼, section 2; 44.15556°N, 107.86528°W.

WW-76 (~19 m): in gray mudstone above Little Red. NW¼, NW¼, section 11; 44.15333°N, 107.86556°W.

WW-77 (14 m): in orange immediately above Purple 3 and in gray sandy silt overlying orange bed. SE¼, SE¼, section 3; 44.15500°N, 107.86778°W.

WW-78 (~3 m): in yellow/gray above Red 1. NE¼, NE¼, section 10; 44.15278°N, 107.86944°W.

WW-79 (~7 m): red mudstone, probably Purple 1. NE¼, NE¼, section 10; 44.15028°N, 107.87111°W.

WW-80 (1 m): mottled gray mudstone in Red 1. NE¼, SE¼, section 3; 44.15783°N, 107.87072°W. This layer has produced the only mammals suggestive of biozone Wa-M.

WW-83 (~12 m): anthills and gray flats between Purples 2 and 3; may be an extension of the cut in which WW-71 and 74 are developed. NE¼, NE¼, section 10; 44.15083°N, 107.86972°W.

WW-84 (~27m): in gray/yellow channel cut into the middle of Big Red, including anthills developed on this layer. SW¼, NW¼, section 11; 44.14958°N, 107.86469°W. Rich anthills at this site produced almost 300 identifiable mammal teeth.

WW-85 (~15 m): gray between two red beds (probably Purple 3 and Little Red). NE¼, NE¼, and SE¼, NE¼, section 10; 44.14917°N, 107.86852°W and 44.15015°N, 107.86890°W.

WW-86 (14 m): anthills and flats in gray/gold mottle above Purple 3. SW¼, SW¼, section 2; 44.15477°N, 107.86662°W.

WW-87 (14 m): in orange mudstone, anthills, and white sandy zone above Purple 3. NW¼, NW¼, section 11; 44.15222°N, 107.86750°W.

WW-88 (~27m): in gray mudstone within Big Red. NE¼, NW¼, section 11.

WW-89 (~45 m): anthills on drab sandy bed above an orange-purple band above Puffy Purple. SE¼, NW¼, section 11; 44.14750°N, 107.86028°W. Produces Wa-1 taxa (*Cantius ralstoni*, *Haplomylus speirianus*)

WW-90 (~32 m): in avulsion into Big Red. C of NW¼, section 11; 44.14956°N, 107.86300°W.

WW-91 (~6-9 m): in gray between two purples; probably between Purples 1 and 2, but possibly just below Purple 1. SE¼, NE¼, section 10; 44.14806°N, 107.86889°W.

WW-95 (~ -20m): drab mudstones in Fort Union Formation apparently below the intermittent red (IR), although IR is not present in this outcrop. SE¼, SW¼, section 2; 44.15403°N, 107.85878°W. Produces late Clarkforkian fauna.

WW-96 (~9 m): gray mudstone below deep red (probably Purple 2), thus probably between Purples 1 and 2. NE¼, NE¼, section 10; 44.15167°N, 107.87139°W.

WW-97 (~32 m): anthills and flats on avulsion into Big Red. NE¼, section 10; 44.14939°N, 107.87456°W to 44.15000°N, 107.87531°W, and extensions at the same level to the south and southeast.

WW-98 (~9 m): reddish brown mudstone capping purple

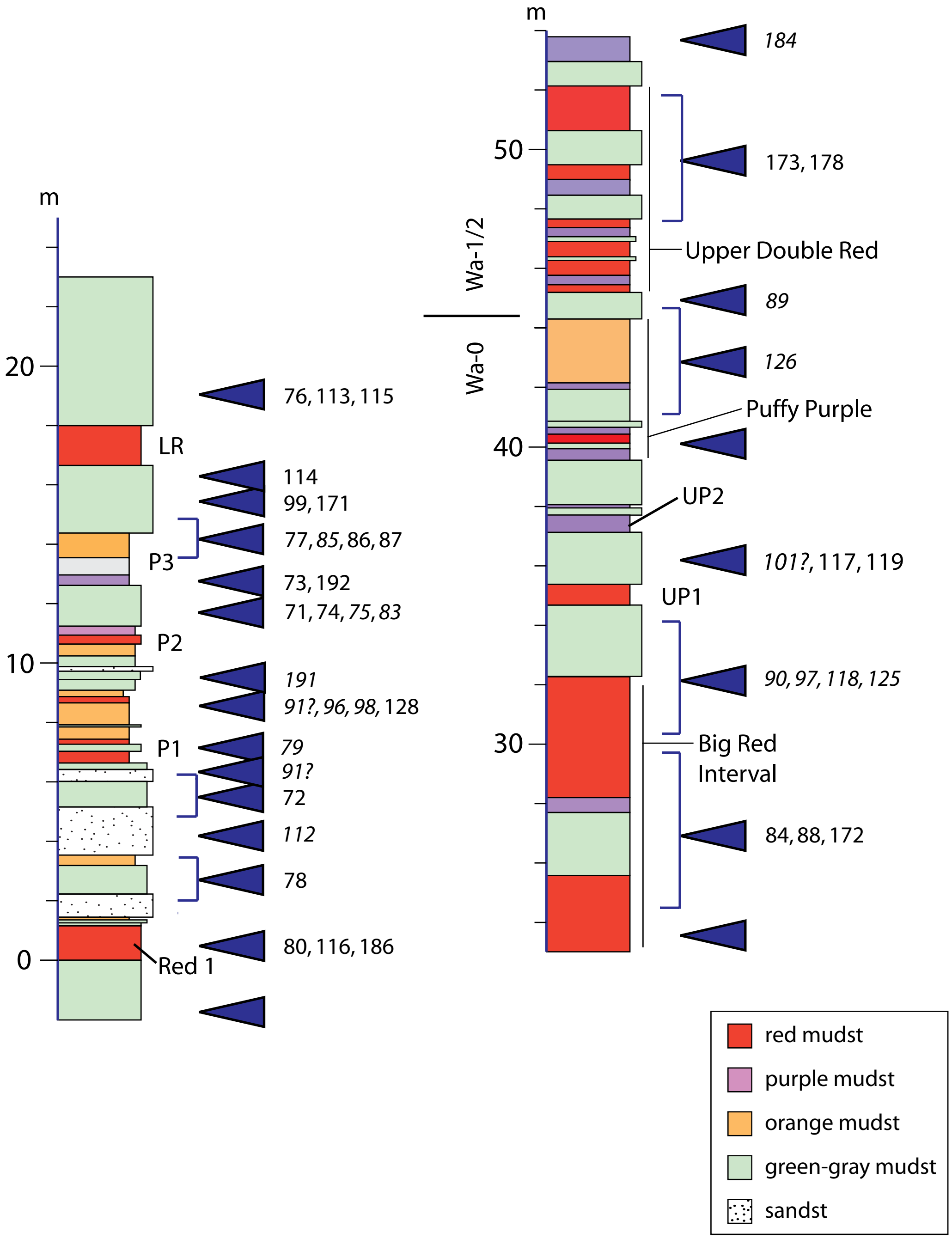


FIGURE 6 — Stratigraphic location of fossil vertebrate localities at Sand Creek Divide. Brackets indicate interval for specified localities. Italics and ? denote progressive degree of uncertainty of stratigraphic level for specified localities. Unlabeled triangles indicate unnumbered localities.

bed above WW-79, thus probably between Purples 1 and 2, but possibly between Purples 2 and 3. SE¼, NE¼, section 10, and SW¼, NW¼, section 11; 44.14972°N, 107.86972°W to 44.14861°N, 107.86889°W.

WW-99 (~16 m): in avulsion below Big Red, above Purple 3; probably between Purple 3 and Little Red. SW¼, NW¼, section 11; 44.14717°N, 107.86539°W.

WW-101 (~36 m): yellow and white sand and brownish-purple mudstone below bright red (probably Upper Purple 2), thus probably between Upper Purples 1 and 2. SW¼, NE¼, section 10; 44.14639°N, 107.87417°W.

WW-112 (~4 m): lowest mottled red and gray above Red

1; possibly =Purple 1, but more likely an intermittent red between Red 1 and Purple 1. SE¼, SE¼, section 3; 44.15550°N, 107.87258°W.

WW-113 (19 m): gray mudstone and anthills just above Little Red. SW¼, SW¼, section 2; 44.15475°N, 107.86614°W.

WW-114 (16 m): gray just below Little Red. SW¼, SW¼, section 2; 44.15472°N, 107.86392°W.

WW-115 (19 m): gray mudstone and anthills just above Little Red; same bed as WW-113. SW¼, SW¼, section 2, and NW¼, NW¼, section 11; 44.15356°N, 107.86556°W, and 44.15403°N, 107.86583°W.

WW-116 (1 m): yellow and drab mudstone within Red 1; same bed as WW-80. NE¼, SE¼, section 3; 44.15769°N, 107.87044°W. Probably correlates with Wa-M.

WW-117 (36 m): sandy white/gray immediately over Upper Purple 1. NE¼, SE¼, section 10; 44.14556°N, 107.87111°W.

WW-118 (~32 m): in avulsion cut into Big Red; level uncertain but probably below Upper Purple 1. SE¼, section 10; 44.14511°N, 107.87050°W.

WW-119 (~37 m): sandy white and gray just below Upper Purple 2; probably same bed as WW-101. NW¼, SE¼, section 10; 44.14664°N, 107.87325°W.

WW-125 (~32 m): white sandy bed and gray/orange mudstone just above or within Big Red, or possibly between Upper Purples 1 and 2. NW¼, SE¼, section 10; 44.14450°N, 107.87539°W, to 44.14367°N, 107.87475°W. McDermotts Butte and Rairden quadrangles.

WW-126 (~43 m): just above Puffy Purple, or possibly in Upper Purple sequence above Big Red. NE¼, NE¼, section 15; 44.13653°N, 107.87217°W.

WW-128 (8 m): in gray sandy bed between Purples 1 and 2. SE¼, SE¼, section 3; 44.15667°N, 107.86861°W.

WW-171 (15 m): orange and gray mudstone between Purple 3 and Little Red. SE¼, NE¼, section 10; 44.14889°N, 107.86917°W.

WW-172 (~28 m): in Big Red. Intersection of sections 10/11/14/15; 44.13909°N, 107.86735°W.

WW-173 (~48 m): in Upper Double Red above Puffy Purple. SW¼, NE¼, section 15, Rairden Quadrangle; 44.13497°N, 107.87642°W. Produces Wa-1 taxa (*Cantius ralstoni*, *Ectocion osbornianus*, *Hyracotherium grangeri*, *Homogalax protapirinus*).

WW-178 (~50 m): gray mudstone just above (or possibly within) Upper Double Red. SW¼ NE¼, section 15; 44.13621°N, 107.87734°W; 44.13214°N, 107.87485°W; 44.13363°N, 107.87369°W. Rairden and McDermotts Butte quadrangles. Produces Wa-1 taxa (*Ectocion osbornianus*, *Hyracotherium grangeri*, cf. *Cardiolophus radinskyi*).

WW-184 (~53 m): in purple above Upper Double Red. SE¼, NE¼, section 15; 44.13367°N, 107.87239°W. Produces Wa-1 taxa (*Hyracotherium grangeri*).

WW-186 (1 m): in Red 1. SW¼, SE¼, section 3; 44.15597°N, 107.87333°W.

WW-191 (~10 m): gray bed probably between Purples 1 and 2. SE¼, SE¼, section 3; 44.15714°N, 107.87006°W.

WW-192 (13 m): In Purple 3. SE¼, SE¼, section 3; 44.15625°N, 107.86922°W.

III

SYSTEMATIC PALEONTOLOGY OF THE SAND CREEK DIVIDE MAMMALIAN FAUNA

LATE PALEOCENE (CLARKFORKIAN) VERTEBRATES

A small number of fragmentary vertebrate fossils have been found in drab Fort Union sediments in or below the lowest intermittent red bed (IR in Figure 3), 16 m below the lowest definitive Wa-0 mammals. The significance of these fossils is that, together with the absence of any Wasatchian index fossils, they either indicate or strongly suggest the late Clarkforkian age (Cf-3) of the strata up to at least the intermittent red. A champsosaur vertebra (*Champsosaurus* sp., USNM 525383), considered diagnostic of Paleocene age, was found slightly below (probably < 20 m below) these mammal fossils. Mammals collected from this uppermost Paleocene interval (~the upper 30 m of Paleocene strata) are summarized below.

Order PHOLIDOTAMORPHA
Gaudin, Emry, and Wible, 2009
Suborder PALAEANODONTA Matthew, 1918
Family METACHEIROMYIDAE Wortman, 1903

PALAEANODON Matthew, 1918

Palaeanodon, cf. *P. parvulus* Matthew, 1918

Referred specimen.— USNM 525378 (left Mc IV), from WW-95.

This short, robust element (L=7.9 mm, prox W=3.3 mm, prox D=3.7 mm, dist W=4.6 mm, dist D=3.1 mm) is more expanded distally than proximally and is slightly bowed in the dorsoventral plane (its plantar aspect slightly concave), as is typical in palaeanodonts. It shows the characteristic palaeanodont distal metacarpal articulation for the proximal phalanx, directed distally and slightly toward the plantar surface. The median keel is small and restricted to the plantar half and is flanked by shallow depressions. This bone is of appropriate size to belong to *P. parvulus*, which is the only species of *Palaeanodon* that has been reported from the Clarkforkian. However, *P. nievelti*, from Wa-0, is only a little smaller, and in the absence of comparable elements, possible allocation to the latter cannot be excluded.

Order TAENIODONTA Cope, 1876
Family STYLINODONTIDAE Marsh, 1875

ECTOGANUS Cope, 1874

Ectoganus sp.

Referred specimen.— USNM 525380 (tooth fragments), from an unnumbered locality in the NE¼ sec. 26, T 49 N, R 92 W (44.19355°N, 107.86336°W, Big Horn County).

Several taeniodont tooth fragments come from much lower in the Fort Union Fm. than other specimens reported here. Although the exact level was not measured, proximity to the PETM makes a Clarkforkian age most probable. The fragments, including an incisor, leave no doubt that it represents *Ectoganus*, but the specimen is too damaged for useful description or more precise identification. According to Schoch (1986), the only species of *Ectoganus* known from the Clarkforkian is *E. lobdelli* (see discussion of this species in the section on Wa-0 mammals).

Order TILLODONTIA Marsh, 1875
Family ESTHONYCHIDAE Cope, 1883

AZYGONYX Gingerich, 1989

Azygonyx grangeri (Simpson, 1937)
Figure 7E-G

Referred specimens.— USNM 525375 (including a right I_2); USNM 521493 (RM_1 and incomplete P_4, M_2, and M_3). From an unnumbered locality (44.15944°N, 107.87278°W) in the the gray bed immediately below the intermittent red (IR).

These teeth are of appropriate size and morphology to belong to *A. grangeri*, which is known from the late Clarkforkian and early Wasatchian (Gingerich and Gunnell, 1979; Bown, 1979; Rose, 1981a). Measurements (mm) of the complete molar are: length = 11.8, trigonid width = 10.4, talonid width = 10.2 mm. This is about 10% larger than the holotype of *A. grangeri* (formerly placed in *Esthonyx*). The I_2 measures 5.05 mm wide x 9.90 mm buccolingually at the base of the crown. Apart from the late Wastachian (Lostcabinian) *Megalesthonyx hopsoni*, *A. grangeri* is the largest North American esthonychine tillodont. Both specimens reported here are from the same site in the gray bed below the intermittent red (IR), but differential wear suggests they are not from the same individual.

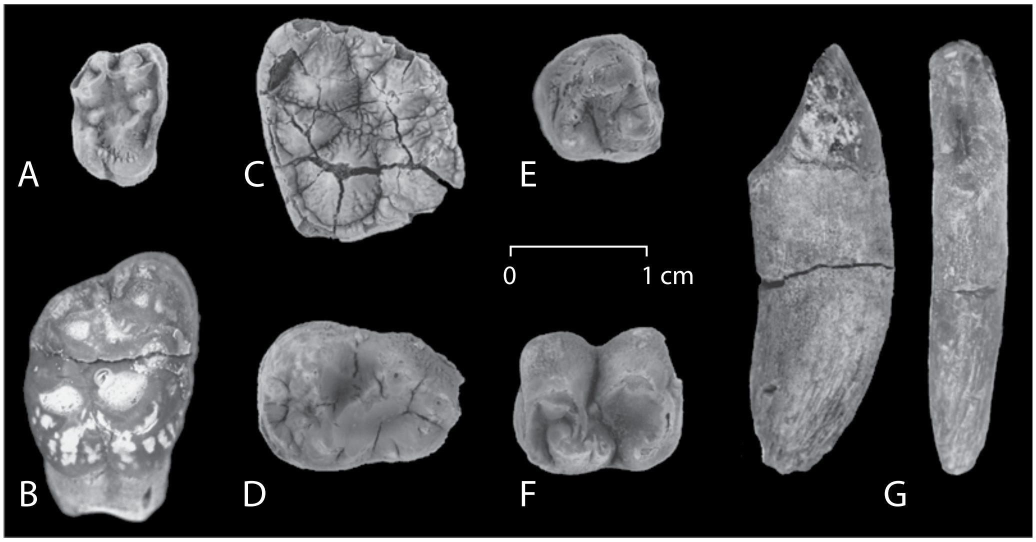


FIGURE 7 — Late Clarkforkian fossils. A, *Ectocion osbornianus*, RM^2, USNM 538280. B-D, *Phenacodus intermedius*: B, RM^2, USNM 538414; C, LM^3, USNM 525370; D, RM$_3$, USNM 525371. E-G, *Azygonyx grangeri*: E-F, RP$_4$ trigonid and RM$_1$, USNM 521493; G, RI$_2$, USNM 525375.

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

DIDYMICTIS Cope, 1875

Didymictis sp.

Referred specimen.— USNM 540589 (trigonid of LM$_1$), from the gray below the intermittent red (IR; same locality as *Azygonyx grangeri* above).

The carnassial trigonid (L=5.2 mm, W=5.4 mm) is essentially identical to that in other specimens of *Didymictis*, and is about 10-20% larger than specimens of *D. leptomylus* from Wa-0, reported below. This is consistent with Clarkforkian *D. proteus* (Polly, 1997). An incomplete right calcaneus (USNM 525376) is probably referable to *Didymictis*, although it is much smaller than most Wasatchian specimens compared. It is slightly larger than the calcaneus of *D. leptomylus* (USNM 527472) reported from Wa-0 below. The shape of the sustentacular facet, and the posterior articular process with a clear fibular facet, closely resemble those of *D. leptomylus* and *D. protenus* (USGS 27585).

Order CONDYLARTHRA Cope, 1881
Family APHELISCIDAE Matthew, 1918

HAPLOMYLUS Matthew, 1915

Haplomylus simpsoni Rose, 1981

Referred specimen.— USNM 525377 (RM^1), from slightly above WW-95.

This isolated tooth (L=3.1 mm, W=3.8 mm) is of appropriate size and morphology to represent this typical Clarkforkian species. Mean size of *Haplomylus* increased during the Clarkforkian (Rose, 1981a), and this very late Clarkforkian specimen fits that trend. Wa-0 *Haplomylus zalmouti* was dramatically smaller.

Family PHENACODONTIDAE Cope, 1881

ECTOCION Cope, 1882

Ectocion osbornianus Cope, 1882
Figure 7A

Referred specimens.— USNM 525374 (RM^1 or M^2 fragment, only slightly larger than *E. parvus*); USNM 525372 (RM^1 or M^2 fragment, size of *E. osbornianus*); USNM 525369 (LM$_3$; L=7.20 mm, W=4.85 mm); USNM 525373 (RM$_1$ or M$_2$ trigonid); USNM 538280 (RM^2; L=7.2 mm, W=9.0 mm); all from WW-95.

All specimens show the characteristic lophodont or subselenodont morphology of *Ectocion*, with bulging mesostyles on upper molars, and all are the size of *E. osbornianus* except 525374. Despite its smaller size, the latter tooth more likely represents the small end of the size range of *E. osbornianus* rather than *E. parvus*, which is otherwise restricted to Wa-0.

PHENACODUS Cope, 1873

Phenacodus intermedius Granger, 1915
Figure 7B-D

Referred specimens.— USNM 525379 (very heavily worn RM$_1$ and assoc. fragments); USNM 538414 (R maxilla with M^2); USNM 525370 (LM^3); USNM 525371 (RM$_3$). The last two specimens are from WW-95, the other two from drab strata ~10-20 m below the intermittent red (IR). USNM 540588 (RP^4, M^2 fragments, M^3); from slightly below WW-95.

According to Thewissen (1990), *Phenacodus intermedius* displays a broad size range and is the only large phenacodontid in late Clarkforkian strata. Thewissen indicated that it differs only in size from the larger *P. trilobatus*, although his size plots show substantial overlap in size between late Clarkforkian *P. intermedius* and Wasatchian *P. trilobatus*, making it difficult if not impossible to separate these two except by stratigraphic occurrence. Most of the specimens listed here fall within the published size range of both species. Based on stratigraphic occurrence we refer them to *P. intermedius*, although all except USNM 525379 are conspicuously larger than the Wa-0 specimens of *P. intermedius* described below.

Measurements (mm), following Thewissen (1990). —

USNM 525379: L=9.9, W=8.3 – size of Wa-0 *P. intermedius* (Gingerich, 1989, and specimens reported below) and within the range of Thewissen's early Wasatchian *P. intermedius*, but smaller than (outside the range of) Thewissen's Clarkforkian *P. intermedius* (nearly 70 specimens, n=15 from Cf-3).

USNM 538414: L=14.3, W=13.9 – near middle of the range of Cf-3 *P. intermedius* (Thewissen, 1990); longer than early Wasatchian *P. intermedius*; within the range of *P. trilobatus* but at the narrow end of the range.

USNM 525370: L=15.3, W=14.9 – within the range of both *P. intermedius* and *P. trilobatus*.

USNM 525371: L=14.2*, Wa=10.5 – at the large end of the range for Cf-3 *P. intermedius*. Also within the upper end of the range of *P. trilobatus*. 25-50% larger than Wa-0 *P. intermedius* reported by Gingerich (1989) and specimens listed below.

USNM 540588: P^4L=10.0*, W=11.5, M^2W=13.2, M^3L=12.1, W=11.8.

Order RODENTIA Bowdich, 1821
Family PARAMYIDAE Miller and Gidley, 1918

Paramyidae indet.

Referred specimen.— USNM 533608 (incisor), from the latest Clarkforkian intermittent red (IR).

This incisor fragment is slightly larger than most Wa-0 incisors and may belong to *Paramys annectens*.

Wa-0 FAUNA OF SAND CREEK DIVIDE

Order MULTITUBERCULATA Cope, 1884

Family NEOPLAGIAULACIDAE Ameghino, 1890

ECTYPODUS Matthew and Granger, 1921

Ectypodus tardus (Jepsen, 1930)
Figure 8

Referred specimens.— WW-74: USNM nos. 533589 (RP_4, RP^4, M_1 fragment), 540597 (LM_2, LM^1, RM^1), 541693 (P^3?).

Description.— Most of these teeth lie at or just below the low end of the size range of *E. tardus* reported by Krause (1982), as might be expected during this warm interval at the beginning of the Eocene. They are comparable in size to specimens referred to *E. tardus* from the Wa-0 fauna at Castle Gardens (Strait, 2001). P_4 is relatively low crowned and has nine serrations, rather than 10 or 11 as reported by Krause for the Bighorn Basin and Four Mile samples; however, Strait observed only 6-8 serrations on P_4s of *E. tardus* from Castle Gardens. The cusp count for P^4 is at the lower end of the range previously reported. Upper molar cusp formulae (see Measurements, below) are within the range reported by Krause (1982).

Measurements (mm).— P_4L=2.65, W=0.90, serrations=9; M_2L=0.95, W=0.90, cusp formula=4:2; P^3?L=1.1, W=0.6; P^4L=2.00, W=0.80, cusp formula=2:6; LM^1L=2.10, W=1.05, cusp formula=7:9:5; RM^1L=2.10, W=1.05, cusp formula=8:10:6.

Discussion.— Only one species of multituberculate has been found at Sand Creek Divide. Based on its morphology and small size, it is best referred to *Ectypodus tardus*. All specimens come from a single locality, and despite screen-washing, it remains rare. This contrasts with Castle Gardens, where *Ectypodus tardus* accounts for 6% of TNS and 11% of MNI (Strait, 2001). Gingerich (1989) reported only a single specimen of *E. tardus* from Polecat Bench, and no multituberculates have been reported from the Tuscahoma Formation of Mississippi (Beard and Dawson, 2009).

Hooker (2010) reported both *Ectypodus childei* and *Ectypodus*, cf. *E tardus*, from the early Ypresian Blackheath Formation at Abbey Wood, U.K. They have P_4s of similar size, and both have 11 serrations. Hooker distiguished *E.*, cf. *E. tardus*, by its lower-crowned P_4 which is mesially wider and has a lower first serration. He further suggested that Strait's (2001) figured specimen of *E. tardus* is more similar to *Ectypodus*, cf. *E. childei*, from the early Wasatchian Four Mile fauna. The Sand Creek Divide P_4 is relatively low crowned like *E. tardus*, but resembles the Abbey Wood *E. childei* specimens in being relatively narrow and having a somewhat higher first serration. It differs from the Abbey Wood specimens, however, in having fewer serrations. Larger samples are needed from Sand Creek Divide to determine if these specimens could represent *E.*, cf. *E. childei,* rather than *E. tardus*.

Cohort MARSUPIALIA Illiger, 1811

As at Polecat Bench and Castle Gardens, three species of marsupials are present, the larger *Mimoperadectes labrus* and two similar-sized much smaller species, here referred to *Peradectes protinnominatus* and *Herpetotherium innominatum*. The two smaller species are easily separated by their lower molars, but the upper molars are harder to differentiate because of conflicting characters, as discussed below. We also describe and illustrate here the first tarsal bones of marsupials from the Wa-0 interval.

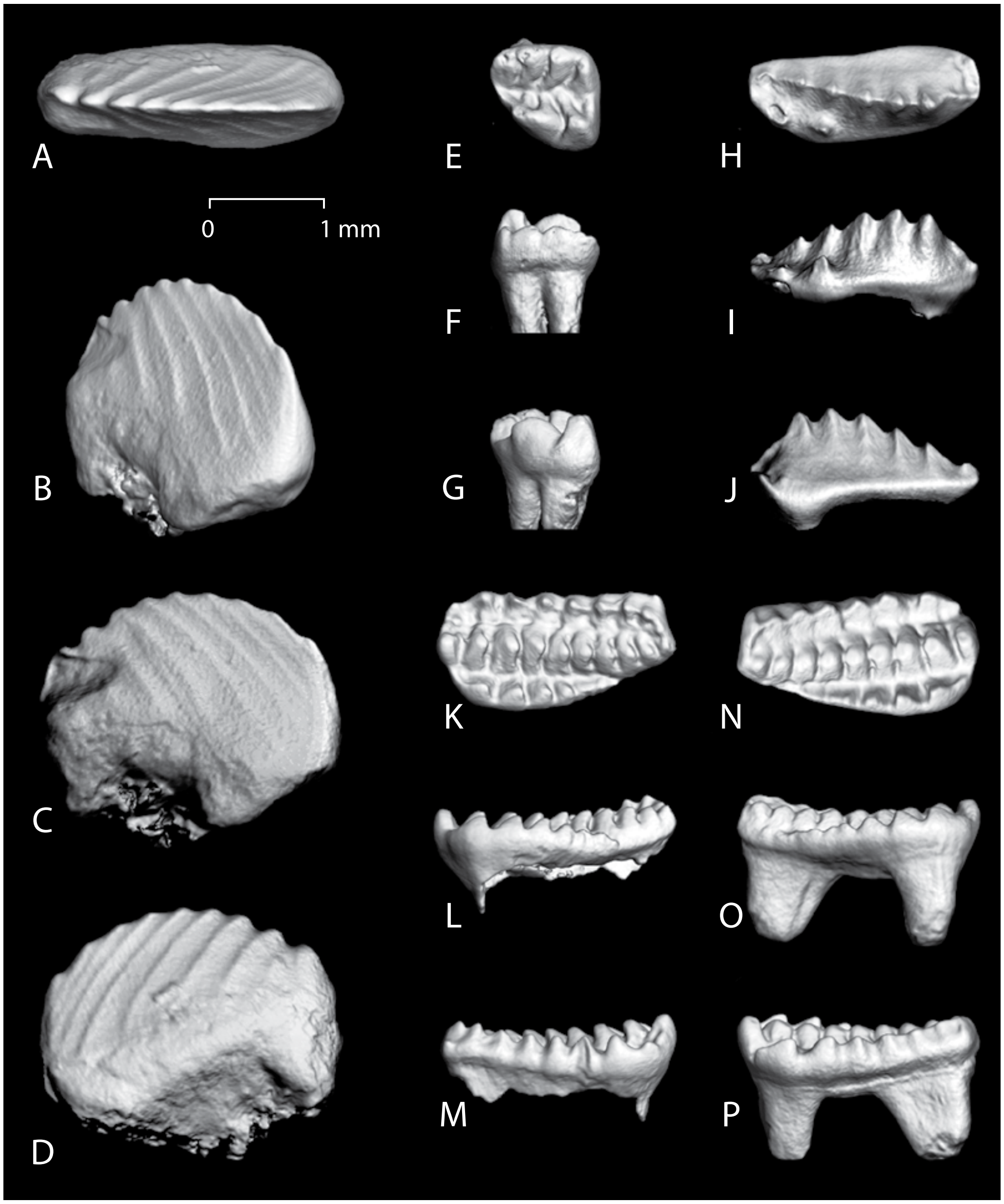


FIGURE 8 — *Ectypodus tardus*. A-D, RP_4, USNM 533589, in occlusal, anterior oblique, buccal, and lingual views; E-G, LM_2, USNM 540597, in occlusal, lingual, and buccal views; H-J, RP^4, USNM 533589, in occlusal, lingual, and buccal views; K-P, USNM 540597, RM^1 (K-M) in occlusal, lingual, and buccal views, and LM^1 (N-P) in occlusal, lingual, and buccal views.

Measurements of marsupial molars reported below and in Table 1 were taken following the procedure described by Clemens (1966).

Family HERPETOTHERIIDAE Trouessart, 1879

HERPETOTHERIUM Cope, 1873

Herpetotherium innominatum (Simpson, 1928)

Figures 9-10, 11I-L

Referred specimens.— WW-74: USNM nos. 527663 (L dentary with $M_{3\text{-}4}$), 538262 (RM_1, RM_2, RM^2?), 540347 (RM_2, RM^1?), and tentatively USNM 539480 (L astragalus).

Description.— Only two upper molars of this species have been found at Sand Creek Divide, and both are heavily abraded, leaving the relative sizes of stylar cusps ambiguous; however, both appear to be dilambdodont, and in both the remnant of cusp

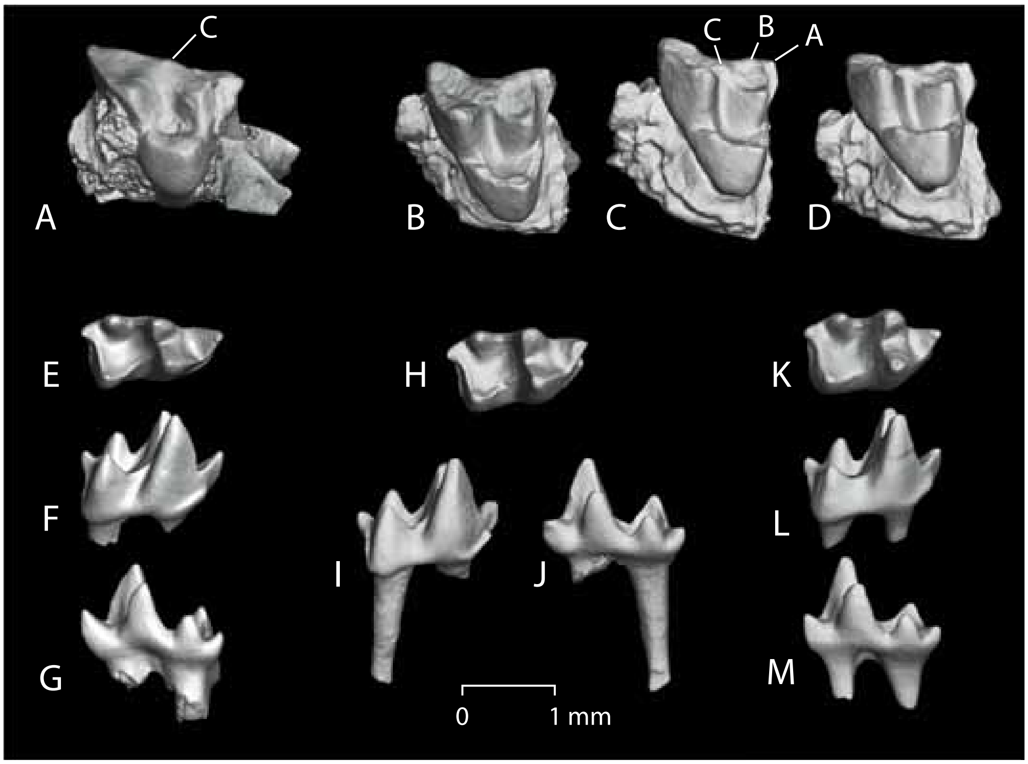


FIGURE 9 — *Herpetotherium innominatum*. A, RM^1, USNM 540347; B-D, RM^2?, USNM 538262; E-G, RM_1, USNM 538262; H-J, RM_2, USNM 538262; K-M, RM_2, USNM 540347. Lower molars in occlusal, buccal, and lingual views. Letters in A and C indicate stylar cusps.

C is the most obvious (Figure 9A-D). A strong cusp C or D is a hallmark of *Herpetotherium* (Korth, 1994, 2008). These teeth differ slightly from those of *Peratherium*, in which cusp B is largest, but abrasion may have accentuated the apparent differences. The lower teeth attributed here (Figures 9E-M, 10) are very similar to those of *Peratherium constans* from Dormaal, Belgium, but molars of different species of *Peratherium* and *Herpetotherium* differ little except in size (Korth, 1994). Like other *Herpetotherium* and *Peratherium*, they have a distinct hypocristid joining the hypoconid and hypoconulid. The hypoconulid projects posteriorly and is almost directly posterior to the entoconid, separated from it by a conspicuous notch; this feature distinguishes lower teeth of herpetotheriines from those of *Peradectes*. These teeth compare closely in size with those allocated to *H. innominatum* by Strait (2001) and Gingerich and Smith (2006).

A very small left astragalus (USNM 539480; Figure 11I-L) is tentatively referred to this species. The description follows terminology of Szalay (1994). It differs from the peradectid astragali described below in several key ways. The medial tibial facet (=tibial malleolar facet) is more nearly perpendicular to the dorsal surface of the trochlea, resulting in a deeper astragalar body and neck, in contrast to the flatter appearance of the two peradectid astragali. The trochlea, which is slightly grooved in contrast to that of peradectids, extends farther posteriorly and plantarly and has a tighter radius of curvature. In distal view, the navicular facet is deeper dorsoplantarly and wider transversely, with a sharp distal astragalar tuber ('adt' of Szalay, 1994: figure 6.12) on the dorsomedial corner of the astragalar head. The medial plantar tubercle is set in from the medial margin relative to that of peradectids, which is on the medial border. The ectal facet is relatively longer than in the astragalus tentatively attributed to *Peradectes* and is oriented plantolaterally at the proximal end and plantarly at the distal end. Although its medial portion is inclined slightly medially, the facet is not clearly divided into lateral and medial areas as it is in Oligocene *Herpetotherium* cf. *fugax* (Horovitz et al., 2008). The sustentacular facet is located on the distolateral part of the neck and is more convex transversely than in peradectids; however, a sustentacular bridge is present, as in *Peradectes*. The fossa between the sustentacular facet and the medial border of the astragalar neck is slightly larger than that in *Peradectes*, and the astragalar sulcus is deeper and broader than in *Peradectes*.

Measurements (mm).— USNM nos. 527663, M_3L=1.45, W=0.80, M_4L=1.40, W=0.80; 538262, M_1L=1.55, W=0.80, M_2L=1.55, W=0.90, M^2L=1.40, W=1.70; 540347, M_2L=1.50, W=0.85, M^1L=1.70, W=1.60. Astragalus, L= 2.10, W=1.70.

Discussion.— This species was long included in *Peratherium*, but recent studies suggest that the latter genus is restricted to Europe and that most North American species that had been included in *Peratherium* are more properly allocated to *Herpetotherium* (Korth, 1994, 2008), as first suggested by Crochet

TABLE 1 — Measurements (mm) of *Mimoperadectes labrus* from Sand Creek Divide.

Upper Teeth

Specimen	M^1L	M^1W	M^2L	M^2W	M^3L	M^3W	M^4L	M^4W
USNM 525601	3.00	3.10	3.10	3.70	3.10	3.10	—	—
USNM 538264	—	—	—	—	—	—	2.30	3.00
USNM 538267a	—	—	3.05	3.60	—	—	—	—
USNM 538267b	—	—	3.10	3.80	—	—	—	—
USNM 538267c	—	—	3.00	3.70	—	—	—	—
USNM 538267d	—	—	2.80	3.60	—	—	—	—
USNM 538269a	—	—	—	—	3.10	3.80	—	—
USNM 538269b	—	—	—	—	3.00	3.40	—	—
USNM 538271a	2.90	2.70	—	—	—	—	—	—
USNM 538271b	2.65	3.20	—	—	—	—	—	—
USNM 538271c	2.70	3.20	—	—	—	—	—	—
USNM 538271d	2.60	2.70	—	—	—	—	—	—
USNM 538271e	3.05	3.15	—	—	—	—	—	—
USNM 538271g	2.90	2.90	—	—	—	—	—	—
USNM 538271h	2.60	2.80	—	—	—	—	—	—
USNM 538271i	3.00	3.00	—	—	—	—	—	—
USNM 538309i	—	—	3.00	3.60	—	—	—	—
USNM 538313a	—	—	3.30	3.80	—	—	—	—
USNM 538313b	—	—	2.95	3.60	—	—	—	—
USNM 538313c	—	—	—	—	2.90	3.70	—	—
USNM 538318R	—	—	3.20	3.60	—	—	—	—
USNM 538318L	—	—	—	—	—	4.40	—	—
N	9	9	9	9	4	5	1	1
Mean	2.82	2.97	3.06	3.67	3.03	3.68	2.30	3.00
Std. deviation	0.18	0.21	0.15	0.09	0.10	0.49	—	—
Std. error	0.06	0.07	0.05	0.03	0.05	0.22	—	—
Minimum	2.60	2.70	2.80	3.60	2.90	3.10	—	—
Maximum	3.05	3.20	3.30	3.80	3.10	4.40	—	—

Lower Teeth

Specimen	M_1L	M_1W	M_2L	M_2W	M_3L	M_3W	M_4L	M_4W
USNM 521492	—	—	—	—	—	—	3.00	1.70
USNM 521505	3.15	1.70	3.40	1.90	—	—	—	—
USNM 521542	3.35	1.55	3.50	1.85	—	—	—	—
USNM 521676	—	—	—	—	3.10	1.70	—	—
USNM 527479	—	—	3.30	1.95	—	—	—	—
USNM 533571	—	—	—	—	3.05	1.90	3.00	1.70
USNM 538265a	3.30	1.70	—	—	—	—	—	—
USNM 538265b	3.30	1.65	—	—	—	—	—	—
USNM 538265c	3.10	1.10	—	—	—	—	—	—
USNM 538265d	3.10	1.65	—	—	—	—	—	—
USNM 538265e	3.20	1.65	—	—	—	—	—	—
USNM 538265f	3.15	1.00	—	—	—	—	—	—
USNM 538265g	3.20	1.65	—	—	—	—	—	—
USNM 538265h	3.20	1.60	—	—	—	—	—	—
USNM 538265i	3.15	1.10	—	—	—	—	—	—
USNM 538266a	—	—	3.60	1.70	—	—	—	—
USNM 538266b	—	—	3.30	1.90	—	—	—	—
USNM 538266c	—	—	3.10	1.75	—	—	—	—
USNM 538266d	—	—	3.10	1.60	—	—	—	—
USNM 538266e	—	—	3.20	1.70	—	—	—	—
USNM 538266f	—	—	2.90	1.50	—	—	—	—
USNM 538266g	—	—	3.20	1.90	—	—	—	—

TABLE 1 — Measurements (mm) of *Mimoperadectes labrus* (cont.)

Lower Teeth

Specimen	M_1L	M_1W	M_2L	M_2W	M_3L	M_3W	M_4L	M_4W
USNM 538266h	—	—	3.30	1.80	—	—	—	—
USNM 538266i	—	—	3.00	1.60	—	—	—	—
USNM 538266j	—	—	3.00	1.70	—	—	—	—
USNM 538266k	—	—	3.10	1.70	—	—	—	—
USNM 538266l	—	—	3.00	1.70	—	—	—	—
USNM 538270a	—	—	—	—	3.30	1.90	—	—
USNM 538270b	—	—	—	—	3.05	1.70	—	—
USNM 538270c	—	—	—	—	3.10	1.95	—	—
USNM 538309a	2.90	0.90	—	—	—	—	—	—
USNM 538309b	—	—	3.20	1.85	—	—	—	—
USNM 538309c	—	—	3.10	1.75	—	—	—	—
USNM 538309d	—	—	2.90	1.65	—	—	—	—
USNM 538309e	—	—	3.20	1.90	—	—	—	—
USNM 538309f	—	—	—	—	3.25	1.90	—	—
USNM 538309g	—	—	—	—	3.00	1.60	—	—
USNM 538309h	—	—	—	—	2.70	1.70	—	—
USNM 538314	—	—	—	—	3.20	1.80	—	—
USNM 539614	—	—	—	—	—	—	3.10	1.50
N	12	12	19	19	9	9	3	3
Mean	3.18	1.44	3.18	1.76	3.08	1.79	3.03	1.63
Std. deviation	0.12	0.31	0.19	0.13	0.18	0.12	0.06	0.12
Std. error	0.03	0.09	0.04	0.03	0.06	0.04	0.03	0.07
Minimum	2.90	0.90	2.90	1.50	2.70	1.60	3.00	1.50
Maximum	3.35	1.70	3.60	1.95	3.30	1.95	3.10	1.70

(1977). According to Korth (1994), *Herpetotherium* differs from *Peratherium* in having stylar cusp C or D most prominent on upper molars, whereas stylar cusp B is dominant in *Peratherium*. In 1994 Korth proposed the new genus *Copedelphys* and subsequently assigned several species formerly placed in *Peratherium*, including *P. innominatum*, to the new genus, which was said to differ by having equal-sized stylar cusps B, C, and D, and a more widely open M_1 trigonid. At least in the earliest Eocene marsupials reported here, the distinctions of *Copedelphys* seem negligible or do not apply; consequently we retain this species in *Herpetotherium*. Based on new cranial and postcranial fossils, Horovitz et al. (2009) recently concluded that *Herpetotherium* is the sister taxon of crown marsupials, consequently excluding it from Marsupialia. However, this conclusion was weakly supported, and relationships near the base of Marsupialia remain unstable. Pending a more robust assessment of the phylogenetic position of Herpetotheriidae, we tentatively retain the clade in Marsupialia.

The anatomy of the astragalus tentatively referred to *Herpetotherium innominatum* suggests a more stable ankle joint with more emphasis on flexion-extension than in peradectids. This is consistent with the growing body of research on fossil marsupial postcrania which suggests that peradectids, including *Peradectes* and *Mimoperadectes*, were arboreal and herpetotheriids were more terrestrial (Storch, 1990; Szalay, 1994; Kurz, 2005; Sánchez-Villagra et al., 2007; Horovitz et al., 2008, 2009).

Order DIDELPHIMORPHIA Gill, 1872
Family PERADECTIDAE Crochet, 1979

MIMOPERADECTES Bown and Rose, 1979

Mimoperadectes labrus Bown and Rose, 1979
Figures 11A-D, 12-13

Referred specimens.— WW-71: USNM 521542 (RM_1, RM_2); WW-74: USNM nos. 521505 (LM_1, LM_2), 538318 (RM^2, LM^3), 539483 (L astragalus), 539614 (RM_4); WW-75: 521676 (LM_3); WW-77: USNM 521492 (L dentary with $M_{3\text{-}4}$); WW-84: USNM nos. 538264 (LM^4), 538265 ($4LM_1$s, $5RM_1$s), 538266 ($5LM_2$s, $7RM_2$s), 538267 ($3LM^2$s, RM^2), 538269 (LM^3, RM^3), 538270 (LM_3, $3RM_3$s), 538271 ($2LM^1$s, $6RM^1$s); WW-87: USNM 527479 (L dentary with M_1 talonid-M_2); WW-97: USNM 538309 (LM^1, $4LM^2$s, LM^3, $2RM^3$s, LM^2); WW-98: USNM 525601 (R maxilla with $M^{1\text{-}3}$); WW-101: USNM 538314 (LM_3); WW-112: USNM 533571 (R dentary with $M_{3\text{-}4}$); WW-113: USNM 538313 (RM^2, LM^2, LM^3).

Description.— The specimens at hand represent all molar loci except RM^4 (Figure 12). They are essentially identical in size and morphology to the holotype and other specimens referred to

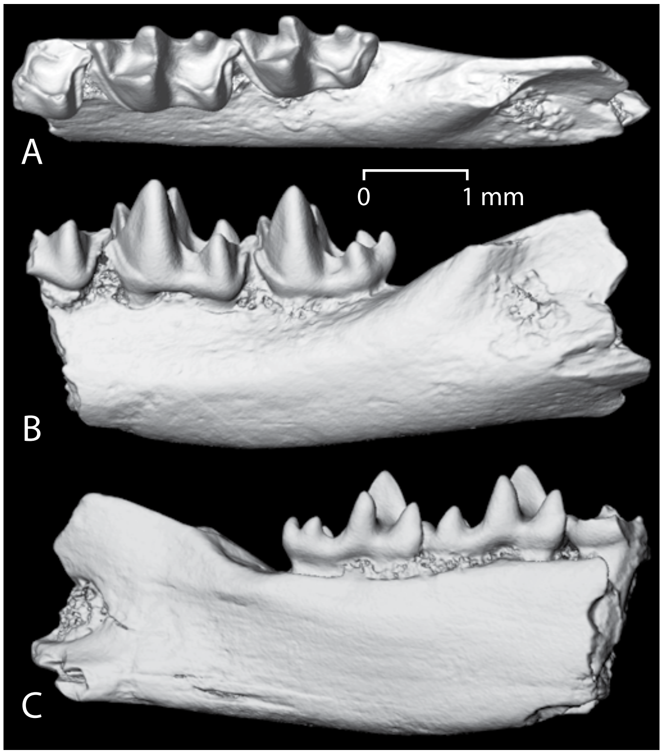


FIGURE 10 — *Herpetotherium innominatum*, L dentary with M_{3-4}, USNM 527663, in occlusal, buccal, and lingual views.

this species (Strait, 2001; Gingerich and Smith, 2006). The lower molars differ from those of *Herpetotherium* in lacking a distinct notch between the hypoconulid and entoconid and lacking a continuous hypocristid joining the hypoconid and hypoconulid. Instead, the latter two cusps are usually separated by a notch. USNM 538265F (Figure 12C) is relatively narrow and elongate, resembling M_1 in YPM 35149 but narrower and longer than M_1 in the holotype of *M. labrus*. It is possibly a dP_3 rather than M_1. The relative sizes of upper molar stylar cusps, best seen on M^{2-3}, are: B>D>C (Figure 12E-F). On M^1 and M^4, the stylar cusps are more reduced, and only cusp B is well developed. The metacone of M^4 is reduced, more so than in the holotype.

A marsupial astragalus (USNM 539483; Figure 11A-D) is attributed to *Mimoperadectes* based on its relatively large size, which is approximately three times longer than the other two marsupial astragali. Overall, it is fairly flat: the trochlea is weakly grooved, and the medial tibial facet slopes medially at an obtuse angle to the lateral tibial facet (=tibial trochlear facet) more distally and at a slightly sharper angle proximally. Consequently, the astragalus appears flatter distally. The lateral tibial facet extends onto the astragalar neck and is longer than the fibular facet. The neck is short. The navicular facet is dorsoplantarly deep laterally and tapers medially, forming a bridge of bone on the medial border of the astragalar neck which connects the navicular surface to the medial tibial facet. There is a deep pit between this bridge of bone and the dorsal surface of the neck. The sustentacular facet is positioned laterally on the plantar surface of the neck and is continuous with the ectal facet. The sustentacular facet lacks the small extension that links the facet with the medial plantar tubercle in most ameridelphians (Szalay, 1994). Instead, a deep arcuate fossa separates the medial border of the facet from the tubercle. The groove for the flexor fibularis is deep and wide. This astragalus is similar in size and most aspects of its morphology, including the arcuate fossa and absence of a sustentacular extension, to an astragalus (AMNH 89531) attributed to *Mimoperadectes* by Szalay (1994). It differs, however, in having a more gently sloping medial tibial facet and in having no evidence of an astragalar sulcus between the ectal and sustentacular facets. As *Mimoperadectes labrus* is the only "large" marsupial known from the Wa-0 interval, USNM 539483 can be confidently attributed to that species.

Measurements (mm).— Astragalus: L= 5.90, W=5.20. For tooth dimensions see Table 1.

Discussion.— *Mimoperadectes labrus* is the largest early Eocene peradectid in North America and one of the most characteristic Wa-0 taxa, although it is also known later in the Wasatchian (Bown and Rose, 1979). It is considerably more common at Sand Creek Divide than at either Polecat Bench or Castle Gardens (Gingerich, 1989, 2001; Strait, 2001), accounting for about 6% of the fauna by both TNS and MNI. The closely allied *M. sowasheensis*, from the Red Hot Local Fauna of Mississippi, has slightly weaker stylar cusps and is slightly smaller (Beard and Dawson, 2009; see Figure 13 herein). *M. houdei*, from slightly higher in the Willwood Formation, is of similar size to *M. labrus* and was distinguished from the latter by minor differences in upper molar proportions (longer and relatively larger M^1 compared to M^2, midline mesiodistal constriction) and a reduced metacone on M^4 (Horovitz et al., 2009). These distinctions should be reexamined, and the validity of *M. houdei* reassessed, when larger samples are available.

PERADECTES Matthew and Granger, 1921

Cf. *Peradectes protinnominatus* McKenna, 1960

Figures 11E-H, 14

Referred specimens.— WW-74: USNM nos. 521593 (LM^1), 538268 (three isolated right lower molars, probably M_2 or M_3, and isolated M^2 or M^3), 538312 (L maxilla with M^1, RM^1), USNM 539482 (L astragalus), 540320 (L maxilla with M^2 or M^3), and 540602 (RM^2 or M^3, LM^2 or M^3 fragment); WW-113: USNM 533583 (R dentary with M_{3-4}); WW-119: USNM 533582 (R dentary with M_2-M_3 trigonid).

Description.— The lower molars referred here are characterized by relatively broad talonids with buccally situated oblique crests and shallow hypoflexids. The hypoconulid is lower than and oriented just posterolateral to the entoconid, from which it is separated by a shallow notch; consequently the hypoconulid is less distinct than in *Herpetotherium* and *Peratherium*. The lower molars are very similar in size and morphology to UCMP 44767, which McKenna (1960) referred to *P. protinnominatus*. Interestingly, the Wa-0 molars have slightly wider talonids and shallower hypoflexids (with a straighter cristid obliqua), and are

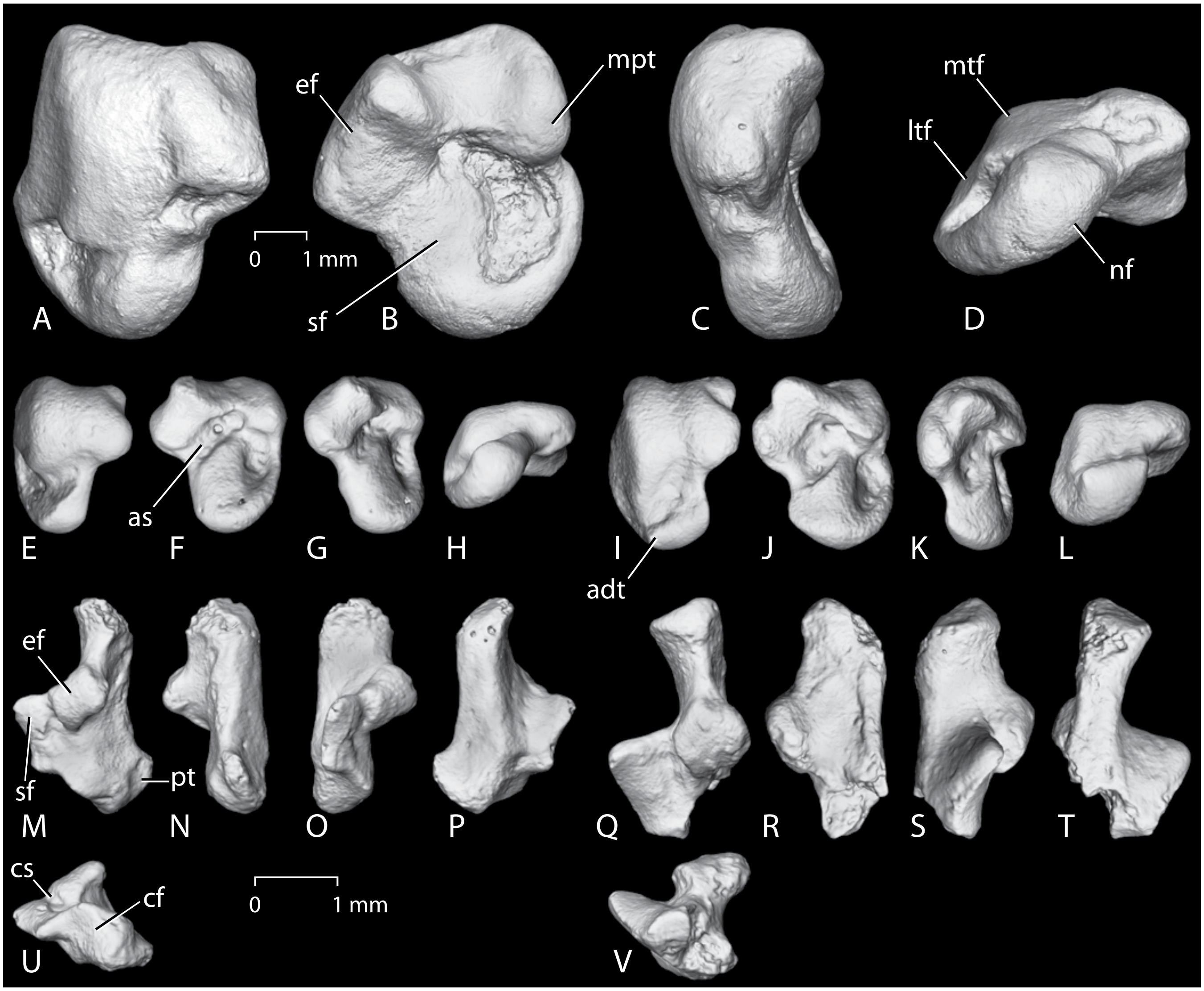


FIGURE 11 — Left tarsal elements of marsupials. A-D, USNM 539483, astragalus of *Mimoperadectes labrus* in dorsal, ventral, lateral, and distal views; E-H, USNM 539482, astragalus of cf. *Peradectes protinnominatus* in dorsal, ventral, oblique lateral, and distal views; I-L, USNM 539480, astragalus of cf. *Herpetotherium innominatum* in dorsal, ventral, lateral, and distal views; M-P, U, USNM 541910, marsupial calcaneus in dorsal, lateral, medial, ventral, and distal views; Q-T, V, USNM 540324, marsupial calcaneus, same views. Abbreviations: **adt**, distal astragalar tubercle; **as**, astragalar sulcus; **cf**, cuboid facet; **cs**, calcaneal sulcus; **ef**, ectal facet; **ltf**, lateral tibial facet; **mpt**, medial plantar tubercle; **mtf**, medial tibial facet; **nf**, navicular facet; **pt**, peroneal tubercle; **sf**, sustentacular facet. Scale at top applies to A-D; Scale at bottom applies to all other images.

very slightly larger, than specimens from the Clarkforkian (UM 71663) and early Wasatchian (UW 9605) of the Bighorn Basin, which were originally assigned to *P. chesteri* but were transferred to *P. protinnominatus* by Krishtalka and Stucky (1983b).

Five upper molars are assigned here because of their close resemblance to the holotype (UCMP 44077) and because they lack dilambdodonty (Figure 14A-C), the absence of which is characteristic of *Peradectes* (Krishtalka and Stucky, 1983b). However, they differ from the holotype in having a reduced paracone and a relatively larger stylar cusp B (these two cusps being subequal in size), and the M^{1}s have slightly more posteriorly expanded protocones—features that have been associated with *Herpetotherium* (=*Peratherium* in Krishtalka and Stucky, 1983a, b). Stylar cusps A, C, and D are distinct as well, but much smaller than cusp B.

A minute left astragalus (USNM 539482, Figure 11E-H) is included here because of its close resemblance to that of the peradectine *Mimoperadectes labrus*. Besides its much smaller size, it differs from that of *Mimoperadectes* in having a more gently sloping medial tibial facet, resulting in a more uniformly

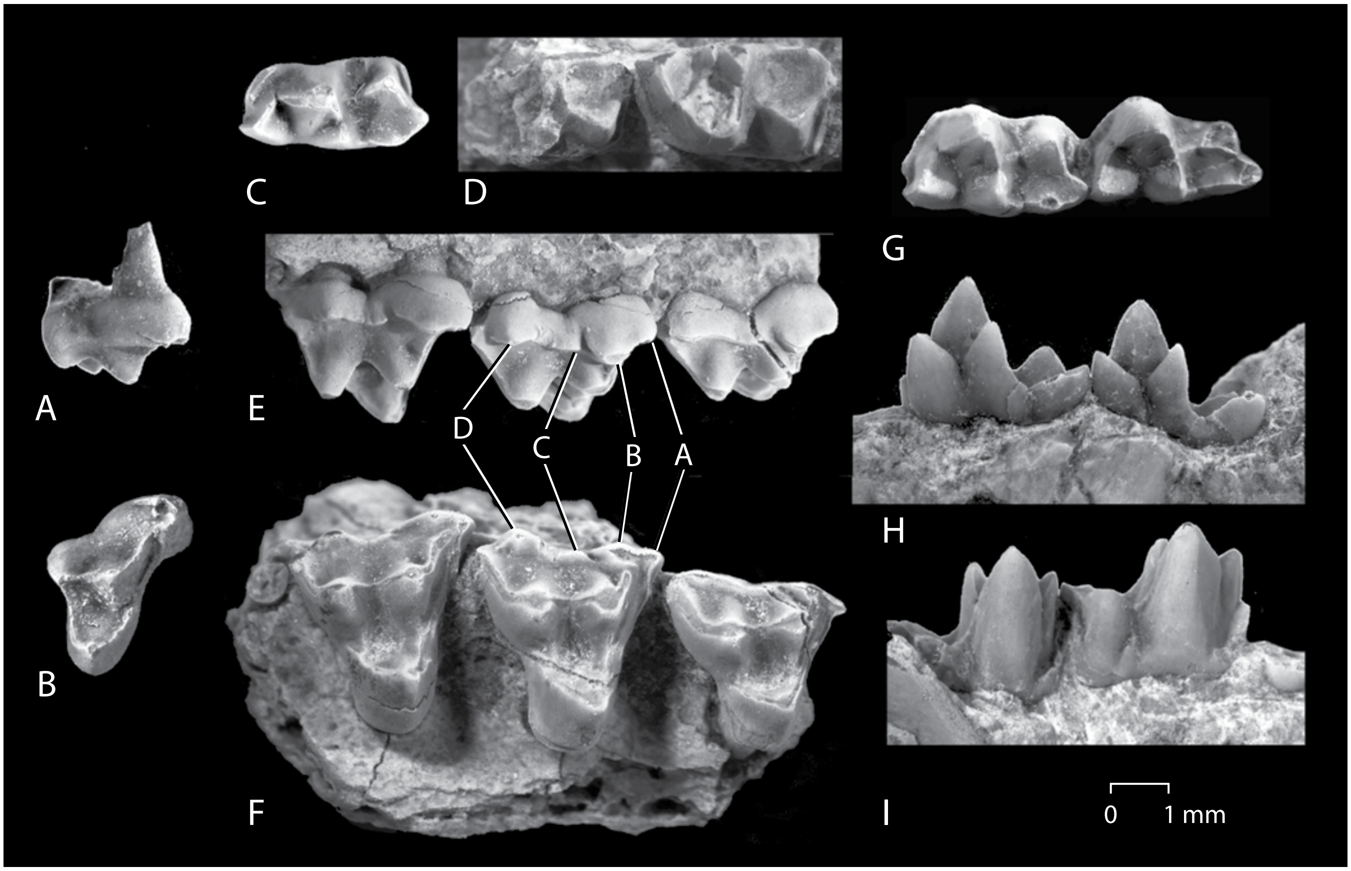


FIGURE 12 — *Mimoperadectes labrus*. A-B, LM^4 (reversed), USNM 538264, in buccal and occlusal views; C, RM$_1$, USNM 538265F, occlusal view; D, LM$_1$ talonid-M$_2$, USNM 527479, occlusal view; E-F, R maxilla with M$^{1-3}$, USNM 525601, in buccal and occlusal views, stylar cusps indicated; G-I, R dentary with M$_{3-4}$, USNM 533571, in occlusal, lingual, and buccal views.

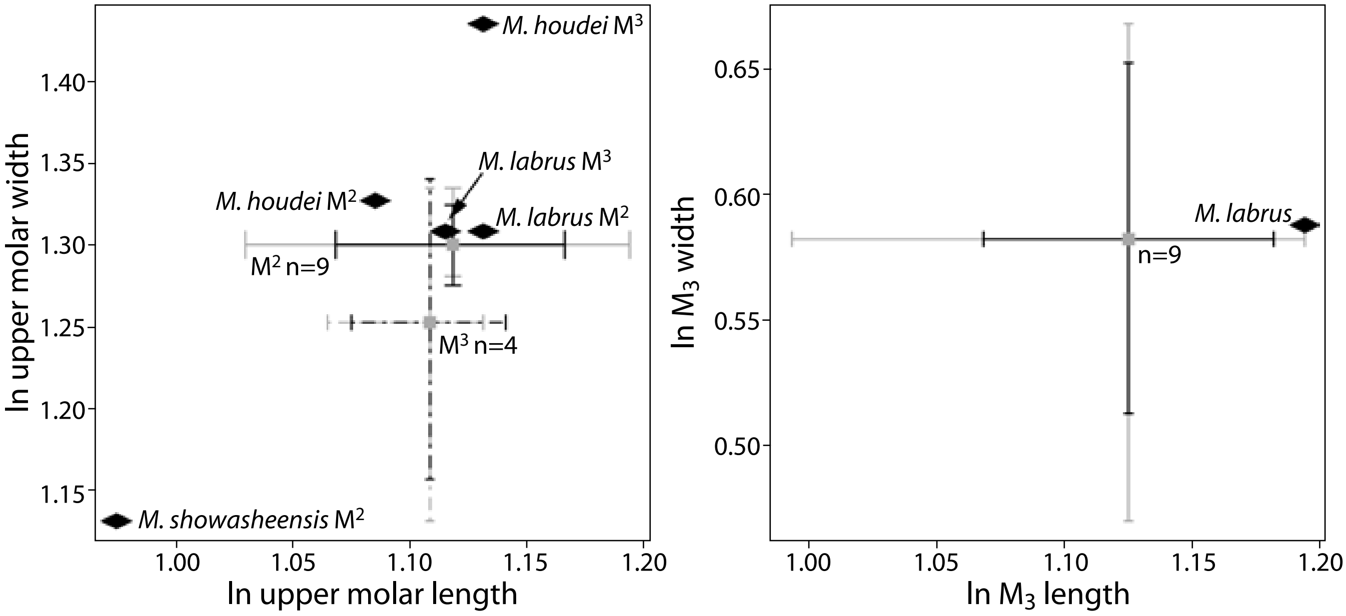


FIGURE 13 — *Mimoperadectes labrus*: Comparison of molar sizes in Sand Creek Divide sample with the holotypes of *M. labrus* and other species of *Mimoperadectes* (black diamonds). Range of Sand Creek Divide sample in gray; one standard deviation from the mean (gray square) in black. Upper molar plot (left) shows M^2 in solid lines, M^3 in dashed lines.

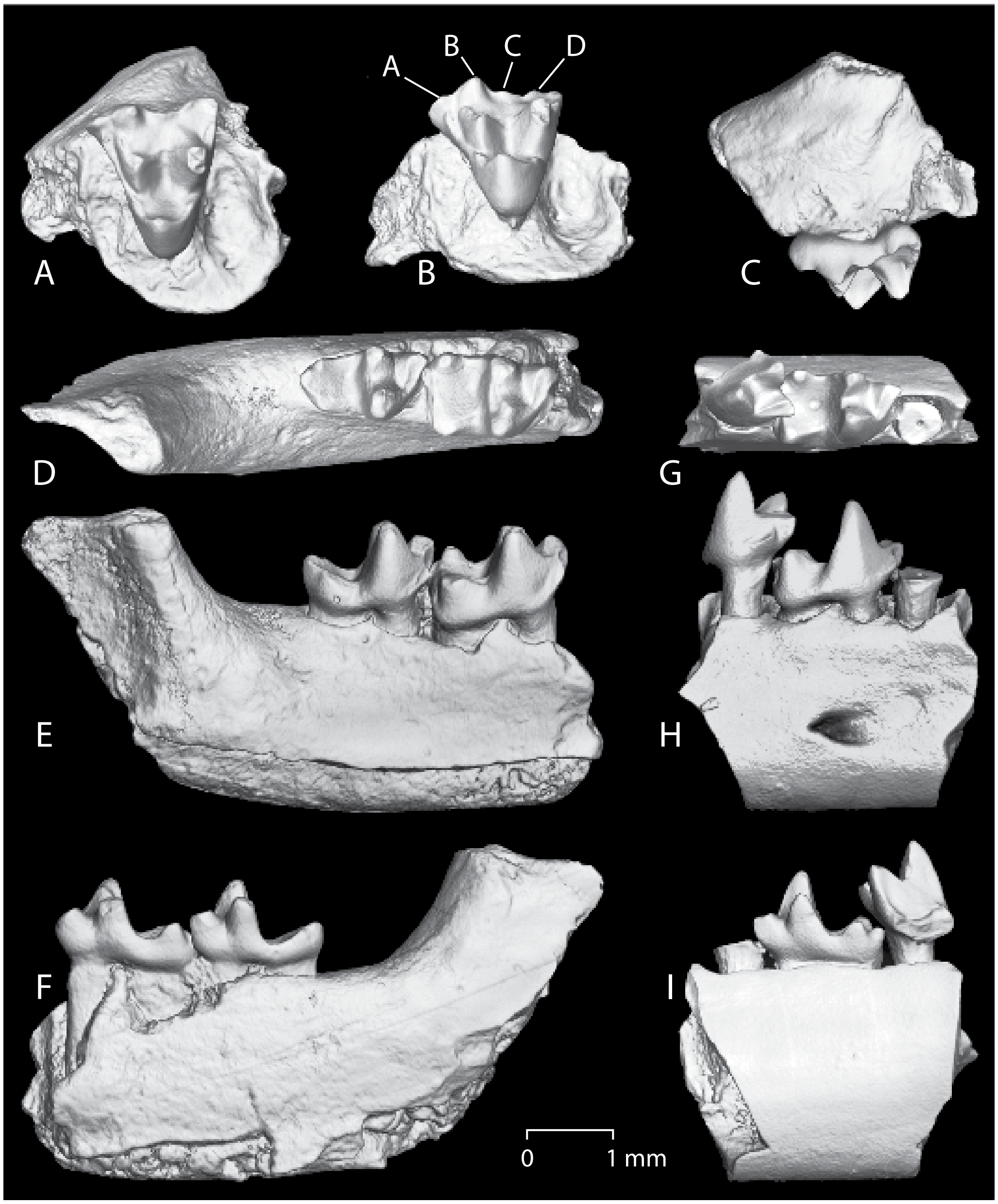


FIGURE 14 — Cf. *Peradectes protinnominatus*: A-C, L maxilla with M^2 or M^3, USNM 540320, in occlusal, oblique lingual, and buccal views; stylar cusps labeled in B. D-F, R dentary with M_{3-4}, USNM 533583, in occlusal, buccal, and lingual views; G-I, R dentary with M_2-M_3 trigonid, USNM 533582, in occlusal, buccal, and lingual views.

obtuse and rounded angle between the medial and lateral tibial facets. In addition, the lateral tibial facet does not extend as far onto the astragalar neck as in *Mimoperadectes*. The shape of the navicular facet resembles that of *Mimoperadectes*, but the pit between the extension of the navicular facet on the medial border of the neck and the dorsal surface of the neck is shallower. On the plantar surface, the sustentacular facet is more centrally situated, separated from the ectal facet by a narrow astragalar sulcus, and joined to the medial plantar tubercle by a narrow sustentacular extension. An ovoid fossa separates the sustentacular facet from the medial border of the astragalar neck, which is formed by the proximal extension of the navicular facet. This astragalus is generally similar to Wasatchian astragali allocated to Peradectinae by Szalay (1994).

Measurements (mm).— USNM 521593, M^1L=1.60, W=1.60; 533582, M_2L=1.50, W=0.90; 533583, M_3L=1.60, W=1.0, M_4L=1.50, W=0.90; 538268A, M_2 or M_3 L=1.65, W=1.05; 538268B, M_2?L=1.60, W=1.00; 538268C, M_3?L=1.60, W=0.95; 538268D, M^2 or M^3L=1.15, W=1.50; 538312, RM^1L=1.70, W=1.50, LM^1L=1.70, W=1.60; 540320, M^2 or M^3L=1.55, W=1.80; 540602 M^2 or M^3L=1.60, W=1.70. Astragalus (USNM 539482), L=1.85, W=1.50.

Discussion.— It is possible that the upper molars referred here are actually *Herpetotherium* molars that show little expression of dilambdodonty. We believe it is more likely, however, that they represent a new species, probably of *Peradectes*, but additional material and more complete specimens, especially maxillary dentitions, are desirable before proposing a new name.

MARSUPIALIA, unidentified

Figure 11M-V

Two left calcanei (USNM 540324, L=2.90 mm; USNM 541910, L=2.60 mm) from WW-74 belong to very small marsupials and perhaps represent *Peradectes* and *Herpetotherium*; however, neither calcaneus resembles that of Oligocene *Herpetotherium*. The larger calcaneus is broken distally, such that the shape of the calcaneo-cuboid facet and peroneal tubercle cannot be assessed. The sustentacular facet is ribbon-like and straight, being uniformly narrow throughout its length. The ectal facet is circular in dorsal view with no discernible separation into astragalar and fibular portions. The calcaneal tuber is medially inflected and short, making up less than half the length of the calcaneus. These features are similar to those seen in other ameridelphian tarsals (Szalay, 1994). However, the shape of the calcaneal tuber contrasts with the long, straight tuber of Oligocene *Herpetotherium* (Horovitz et al., 2008, 2009).

The smaller calcaneus is complete and differs from the larger in several ways. The calcaneal tuber is relatively shorter and less robust and is also medially inflected. In dorsal view, the ectal facet is rhomboid in shape rather than round as in the larger specimen and also lacks a distinct fibular facet. Medial to the ectal facet, the sustentaculum is also ribbon shaped (as in the larger calcaneus) and is separated from the ectal facet by a narrow, shallow calcaneal sulcus. This contrasts with the wider, deep calcaneal sulcus in the larger calcaneus. The peroneal tubercle on the smaller calcaneus is robust with a groove for the tendon of the fibularis (=peroneus) longus on its dorso-lateral surface. The calcaneo-cuboid facet is oriented oblique to the long axis of the calcaneus and is strongly concave. The smaller calcaneus does not closely resemble any fossil ameridelphian calcanei described by Szalay (1994), all of which have a longer, more robust tuber and a rounder ectal facet separated from the sustentaculum by a deep calcaneal sulcus.

In ectal facet shape and depth of the calcaneal sulcus the smaller calcaneus most closely resembles that of the modern didelphid *Caluromys* (Szalay, 1994). The larger calcaneus is generally similar to those of other ameridelphians allocated to the Peradectinae by Szalay (1994) and might be referable to *Peradectes*. However, the shorter, less robust calcaneal tuber in the smaller specimen, and its resemblance to *Caluromys*, may suggest more arboreal behavior, and thus would support allocation to *Peradectes* rather than to *Herpetotherium*. Alternatively, if the smaller calcaneus does belong with the *Herpetotherium*-like astragalus, it would suggest that at least some members of the genus may have been arboreal. In general, there is not enough information to assign either calcaneus confidently to a genus of marsupial; better associations are needed to resolve the issue.

Cohort EUTHERIA Huxley, 1880
Order CIMOLESTA McKenna, 1975
Family CIMOLESTIDAE Marsh, 1889

DIDELPHODUS Cope, 1882

Didelphodus sp.

Figure 15

Referred specimens.— WW-77: USNM nos. 521508 (L dentary with damaged M_2), 533501 (LM^2); WW-84: USNM nos. 533578 (RM_1 or M_2), 533580 (RM_1 or M_2), 538308 (LP_2); WW-113: USNM 540166 (LM_1 or M_2).

Description.— The six specimens representing *Didelphodus* are all at the small end of the size range for *D. absarokae* from higher in the Willwood Formation. The P_2 is simple and tall, dominated by the principal cusp (protoconid), followed by a simple, unicuspid talonid heel. The anterior crest from the protoconid is very steep, the posterior crest only slightly less steep. The lower molar trigonids are both longer and wider than the basined talonids. The prominent hypoconulid is separated from the hypoconid by a notch, but is joined to the entoconid by a crest that is higher than the hypoconid. The upper molar is relatively

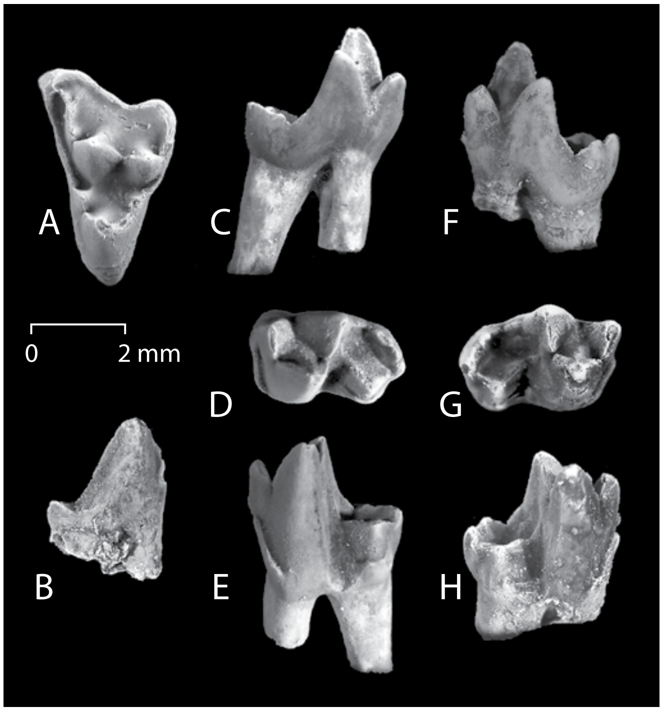


FIGURE 15 — *Didelphodus* sp.: A, LM^2, USNM 533501; B, LP_2, USNM 538308, in lingual view; C-E, $LM_{1/2}$, USNM 540166, in lingual, occlusal, and buccal views; F-H, $RM_{1/2}$, USNM 533578, in lingual, occlusal, and buccal views.

unworn. It is triangular (though slightly less transverse than in most *D. absarokae* compared), with a wide stylar shelf, well-marked ectoflexus, strong preparacrista, and larger parastylar than metastylar lobe. The metastylar lobe is less reduced than in M^3 of *D. absarokae*, hence it is identified as M^2. The paracone is conspicuously higher than the metacone. Well-developed conules are present, the paraconule larger than the metaconule. Except for their smaller size, these teeth closely resemble those of *D. absarokae*.

Measurements (mm).— USNM 521508, M$_2$L=3.25, W$_a$=2.2*, W$_p$=1.80; USNM 533501, M^{2}L=2.90, W=4.35; USNM 533578, M$_{1/2}$L=3.40, W$_a$=2.00, W$_p$=1.80; USNM 533580, M$_{1/2}$L=3.50, W$_a$=2.05, W$_p$=1.95; USNM 538308, P$_2$L=2.60, W=1.30, Hling=2.5*; USNM 540166, M$_{1/2}$L=3.35, W$_a$=1.90, W$_p$=1.70.

Discussion.— These specimens represent the oldest record of *Didelphodus* and the first reported from Wa-0. No obvious ancestor or sister taxon is known from the Clarkforkian, hence *Didelphodus* may be another immigrant taxon that arrived in North America at the beginning of the Eocene. The lower molars are smaller (ln area=1.85-1.97) than nearly all Willwood specimens of *Didelphodus* plotted by Bown and Schankler (1982: figures 2, 3), approximating only the smallest individuals from the late Wasatchian (Wa-6 and Wa-7 biozones), which was also a warm interval. Bown and Schankler showed that *Didelphodus* remained relatively large up to Biohorizon B, after which it gradually reduced in size into the Bridgerian. As in many other Wa-0 taxa, the teeth of *Didelphodus* from Sand Creek Divide are smaller than those of successive forms, suggesting it either belongs to a distinct (new) species or represents a population dwarfed in response to the warmer temperatures of the PETM. The two alternatives are not mutually exclusive. Neverthless, the few teeth known provide such a limited picture of this taxon that we consider it imprudent to propose a new species name until it is better known.

Order PANTOLESTA McKenna, 1975
Family PANTOLESTIDAE Cope, 1884

PALAEOSINOPA Matthew, 1901

Palaeosinopa lutreola Matthew, 1918
Figure 16

Referred specimens.— WW-74: USNM 521506 (LM$_2$); WW-84: USNM 538357 (R lower premolar and RM$_1$); WW-116: 538350 (damaged RM$_1$ and distal L calcaneus).

Description.— These few specimens represent the first record of the pantolestid *Palaeosinopa* in the basal Eocene of Wyoming. They are slightly larger than the holotype of *P. lutreola* but within the size range of that species as shown by Bown and Schankler (1982: figure 12). The molars show the distinctive characteristics of *Palaeosinopa*, including having metaconid and protoconid of equal height, paraconid well-developed and lower, M$_1$ trigonid cusps relatively conical with robust bases rather than being more "crestiform" (as in leptictids), talonid basins relatively wide (compared to palaeoryctoids; subequal in width or wider than the trigonid on M$_1$, but slightly narrower than the trigonid on M$_{2\text{-}3}$), trigonids relatively low (compared to palaeoryctids), and overall lower-crowned molars than other "proteutherians" (especially leptictids and palaeoryctids). The isolated M$_2$ shows characteristic heavy apical wear, in which the trigonid cusps wear completely away, leaving the trigonid flat—probably a reflection of a durophagous diet.

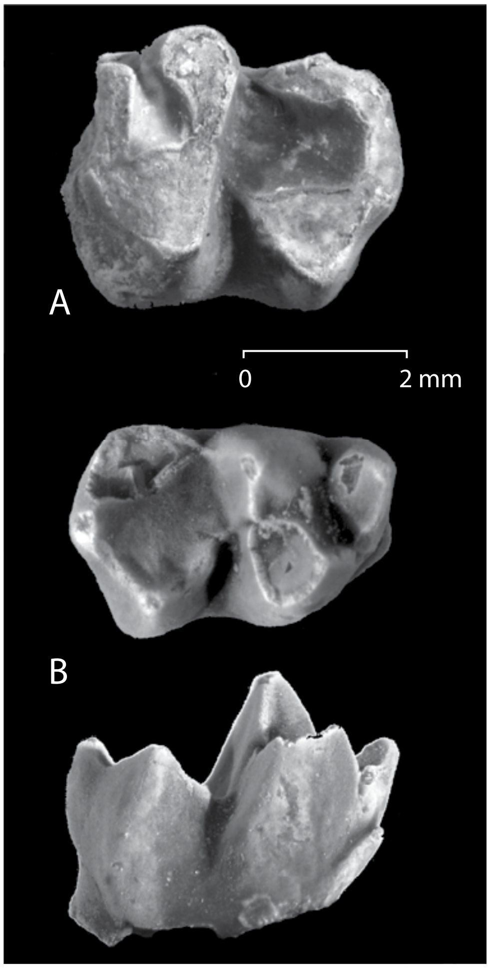


FIGURE 16 — *Palaeosinopa lutreola*: A, LM$_2$, USNM 521506, in occlusal view; B, RM$_1$, USNM 538357, in occlusal and buccal views.

The isolated lower premolar closely resembles P$_3$ and P$_4$ in *Palaeosinopa* in having a prominent primary cusp preceded by a distinct, slightly lingual anterobasal cusp and followed by a more prominent talonid cusp. There are no distinct cingula. Proportionally the tooth is more like P$_4$ in having a width:length index over 0.50, but its length is more consistent with P$_2$ or P$_3$. Based on these considerations it seems most likely to be P$_3$.

Measurements (mm).— USNM 538357: RP$_x$L=2.50, W=1.45; M$_1$L=4.0, W$_a$=2.35, W$_p$=2.55; 521506: M$_2$L=4.1*, W$_a$=2.90, W$_p$=2.70.

Discussion.— Two very small species of *Palaeosinopa* have been reported from basal Eocene strata elsewhere: *P. russelli*

Smith, 1997, from Dormaal, Belgium, and *P. aestuarium* Beard and Dawson, 2009, from the Red Hot local fauna of Mississippi. The teeth from Sand Creek Divide appear to be slightly larger than both of them. M_2 is about 15% larger than those of *P. aestuarium* and *P. russelli*, and M_1 is about 20% larger than that of *P. russelli*. According to Beard and Dawson (2009), *P. aestuarium* differs from *P. russelli* and *P. lutreola* in having a lower-crowned M_2 with more acute protoconid and hypoconid, and it differs from *P. lutreola* and resembles *P. russelli* in having an entoconulid and a large, posteriorly projecting hypoconulid. Damage or wear makes it impossible to judge most of these features in the Sand Creek Divide molars, although USNM 538357 has a projecting hypoconulid, as do several other specimens of *P. lutreola* (USGS 5971, 9120, 10512). The slightly worn M_2 of *P. russelli* has a slightly higher protoconid (relative to M_2 length) but a somewhat lower hypoconid than the less worn holotype of *P. aestuarium*, whereas values for protoconid and hypoconid heights in relatively unworn *P. lutreola* (USGS 5971, 9120, 10512) are comparable to those of *P. aestuarium*. Thus there do not seem to be significant crown-height differences among these species based on the small samples currently available. The presence of an entoconulid in *P. aestuarium* does not necessarily ally this species with *P. russelli*, as entoconulids are variably present in most if not all species of *Palaeosinopa*, including *P. lutreola* (Dunn and Rose, in prep.). *P. russelli* seems to have narrower talonid basins than either *P. aestuarium* or *P. lutreola* and may, therefore, be slightly more primitive. Hooker (2010) referred a somewhat larger lower jaw from the early Ypresian at Abbey Wood, U.K., to *Palaeosinopa*, cf. *P. osborni*. He described the teeth as similar in size to *P. lutreola*. The molars from Sand Creek Divide seem to conform in most details with the Abbey Wood specimen, although the M_1 from Sand Creek Divide is relatively narrower. These four small and primitive species of *Palaeosinopa*—two from Europe and two from North America—appear to be closely related, but more definitive assessment of their relationship will require larger samples and more complete specimens.

Order PHOLIDOTAMORPHA
Gaudin, Emry, and Wible, 2009
Suborder PALAEANODONTA Matthew, 1918
Family METACHEIROMYIDAE Wortman, 1903

PALAEANODON Matthew, 1918

Palaeanodon nievelti Gingerich, 1989
Figure 17

Referred specimens.— WW-73: USNM 533625 (R humeral midshaft); WW-74: USNM 533607 (incomplete L metacarpal III), USNM 538311 (R humeral midshaft and proximal radius, metacarpal IV?); WW-101: USNM 539501 (L metacarpal III missing distal epiphysis); and tentatively WW-73: USNM 538315 (L edentulous dentary); WW-78: USNM 527742 (partial skeleton including dentary fragment, vertebrae, fragmentary humerus, radius, ulna, pelvis, femora, tibiae, calcaneus, metapodials, phalanges).

Description.— Several specimens attest to the presence of at least one small species of *Palaeanodon* in the Sand Creek Divide fauna. A dentary fragment (USNM 538315), showing the characteristic medial buttress, is comparable in depth to those of *Palaeanodon nievelti* (UM 87335, holotype, and UM 83469) and Clarkforkian *P. ?parvulus* (UM 71431), but is decidedly thicker than *P. nievelti* across the medial buttress, as in *P. ?parvulus*. These characteristics of USNM 538315 may relate to sexual dimorphism or intraspecific variation, or could suggest presence of *P. parvulus* during the PETM. A humeral fragment (USNM 533625) from the same locality as the jaw, however, is very close in size to that of the holotype of *P. nievelti*, as are the few other fragments that can be compared. Two third metacarpals from other localities are markedly smaller than that of the holotype of *P. parvulus* (AMNH 15859). They are short and robust, with a distinct extensor tubercle on the radial side of the dorsal surface of the shaft.

USNM 527742 is a partial skeleton with a dentary fragment very similar to the holotype of *P. nievelti* but a slightly more gracile tibia than in *P. nievelti*. The fragmentary humerus of this specimen is smaller than in the holotype and has a shorter deltopectoral shelf. To the extent that they can be compared, these elements are conspicuously smaller than in the holotype of *P. parvulus*. Little information is available on intraspecific skeletal variation in palaeanodonts (and none at all for *P. nievelti*), but at present we assume that these differences can be reasonably encompassed within *P. nievelti*. The skeleton will be described in detail elsewhere.

Measurements (mm).— USNM 527742: dentary depth at last alveolus = 5.20, width 5mm posterior to alveoli =3.60; USNM 538315: dentary depth at last alveolus = 5.0, width 5 mm posterior to alveoli = 4.5, maximum width across medial buttress = 5.2. Comparable widths are 3.3 and 3.5 in *P. nievelti* (holotype), 4.2 and 5.0 in *P. ?parvulus* (UM 71431); USNM 538311: Mc IV? L=5.5, Wprox=2.3, Dprox=2.0, Wdist=2.9, Ddist=1.9.

Discussion.— *P. nievelti* is the smallest described species of *Palaeanodon*, being distinctly smaller (11-24%, according to Gingerich, 1989) than Clarkforkian *P. parvulus*. The presence of a dentary fragment the size of *P. parvulus* in the same Wa-0 locality at Sand Creek Divide as a humeral fragment resembling that of *P. nievelti* raises the question whether two species of *Palaeanodon* so close in size might have coexisted during the PETM, or if these Wa-0 specimens simply reflect the size range of a single species. Sexual (size) dimorphism in palaeanodonts, analogous with that of their inferred extant relatives, pangolins (Heath, 1992a, b), has been suspected but not yet demonstrated. *P. parvulus* is known from the Clarkforkian and also appears to have existed in the Clarks Fork Basin immediately after Wa-0 (Gingerich, 1989: figure 43), so its existence during Wa-0 would not be surprising. Until larger samples can demonstrate coexistence of two species, however, we prefer to be more conservative in assigning these few specimens to a single species, *P. nievelti*.

Order TAENIODONTA Cope, 1876
Family STYLINODONTIDAE Marsh, 1875

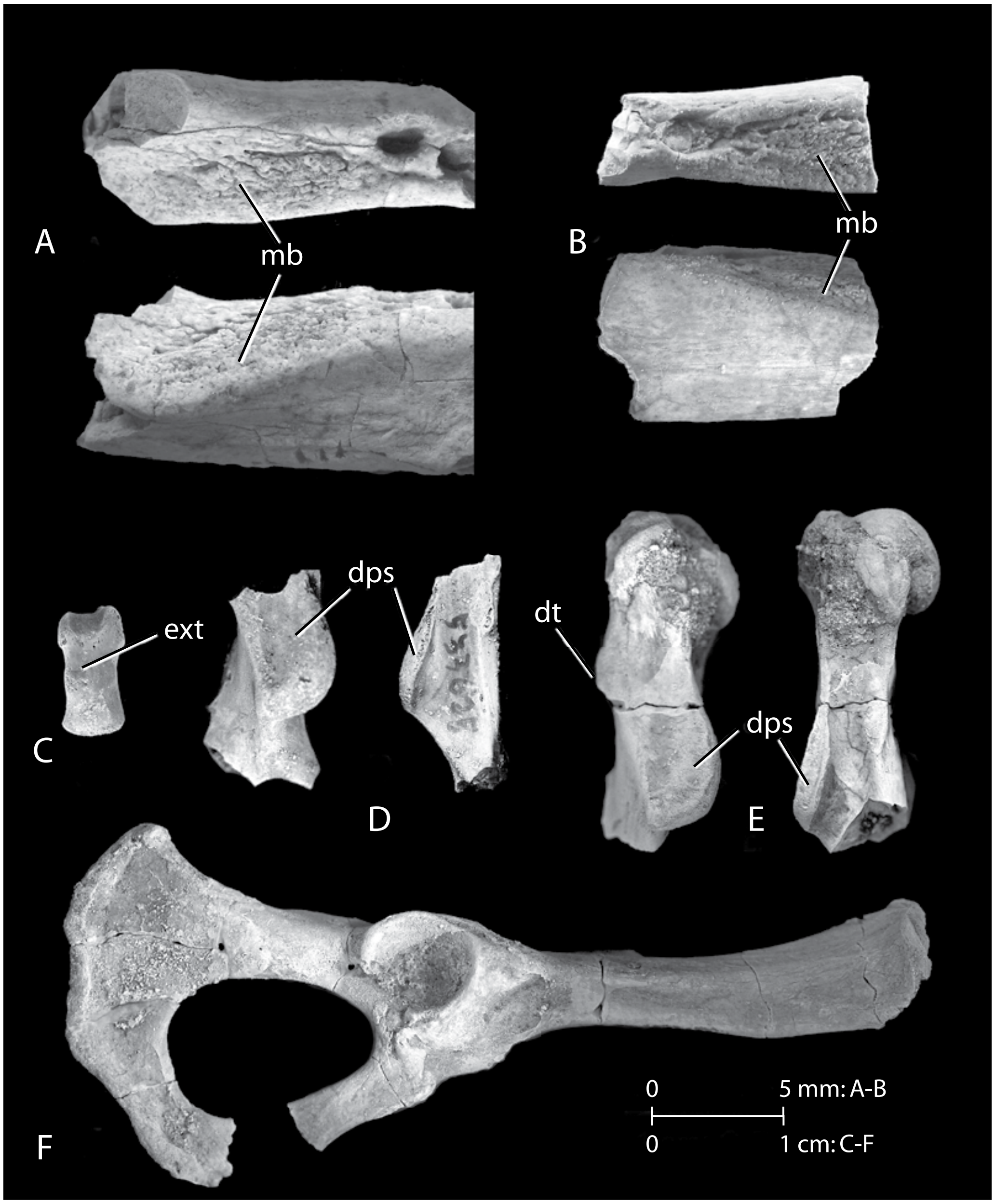


FIGURE 17 — *Palaeanodon nievelti*: A, left dentary fragment, USNM 538315, in dorsal and medial views (anterior to right); B, right dentary fragment, USNM 527742, in dorsal and medial views (anterior to left); C, left metacarpal III, USNM 539501, in dorsal view; D, right humeral shaft, USNM 533625, in anterior and medial views; E, right proximal humerus, USNM 527742, in anterior and medial views; F, right innominate, USNM 527742, in lateral view. Abbreviations: **dps**, deltopectoral shelf; **dt**, deltoid tubercle; **ext**, extensor tubercle; **mb**, medial buttress.

ECTOGANUS Cope, 1874

Ectoganus bighornensis Schoch, 1981

Figure 18B-E

Referred specimens.— WW-74: USNM 521518 (cheek tooth); WW-75: USNM 538319 (L M_2 or M_3); WW-84: USNM 533561 (RM_x); WW-98: USNM 538316 (intermediate phalanx); WW-186: USNM 527725 (subadult mandible with most of the teeth, several isolated upper teeth).

Description.— Several specimens are referable to the relatively small species *Ectoganus bighornensis*, which was regarded by Schoch (1986: 77) as a subspecies of *E. copei* characterized by "relatively low-crowned and shallow-rooted cheek teeth," unlike the "extremely hypsodont" teeth of *E. c. copei*. These Sand Creek Divide specimens compare well in size with *E. bighornensis* and are moderately low crowned and rooted, like Wa-0 specimens from Polecat Bench referred to this species by Gingerich (1989).

Taeniodont dental specimens are typically heavily worn, often leaving little more than a rim of enamel on cheek teeth. However, USNM 538319 shows relatively little wear, and USNM 527725 is a subadult specimen in which the M_3s are erupting and $P_{3\text{-}4}$ are in the crypt, unerupted. In the latter specimen enamel covers the entire molar crowns, which show high relief. USNM 527725 is the most complete known specimen of *E. bighornensis*, preserving most of the lower and upper dentition, including probable deciduous premolars (Figure 18B-E). It is thus substantially more complete than any other and merits description. Two incisors are preserved, one with the root, showing clearly that it is rooted and not evergrowing. They are probably upper incisors, because they are smaller than the broken roots of the two (left and right) lower incisors. The crowns are short, with a taller, worn, chisel-like labial cusp, and a lower, rounded lingual cusp. Enamel surrounds the crown except on a narrow part of the distal (posterior) surface. Crowns of one upper and one lower canine are preserved. The canines are typically gliriform and evergrowing, with bands of enamel restricted to the labial surface and extending both mesially and distally less than half the labiolingual thickness of the crown (slightly farther in the upper canine than in the lowers). The upper and lower canines are of roughly similar dimensions, but the upper differs from the lower in having a slightly wider band of enamel on the distal side, with a shallow groove near and parallel to the lingual enamel margin (see also Schoch, 1986: plates 36 and 43).

Both upper and lower cheek teeth of USNM 527725 have more or less vertical walls and lack cingula. P_1 and P_2 are essentially triangular in cross section; both are longer labially than lingually, but the disproportion is greater in P_1. Both teeth have a single large and high labial cusp, elongate on P_1, and a lower posterolingual cusp, which is pointed on P_2. Despite moderate wear on P_1 (less on P_2), which has obliterated any enamel that might have been present on the occlusal surface, enamel is more extensive than previously reported. Traces of thin enamel indicate its original presence on most of the anterior surface (as a thin band near the apex) as well as on the labial and posterolingual surfaces of P_1. A wider enamelless band separates the labial and lingual cusps posteriorly. Enamel surrounds most of P_2, although it is very thin on the anterior and middle of the posterior surfaces and in this area appears to be restricted to a narrow band near the cusp apices. Deciduous P_3 and P_4 are heavily worn but can be seen to be molariform, with slightly narrower trigonids than talonids and very thin enamel surrounding the crown. Part of the permanent P_3 is visible beneath the broken root of right dP_3. Both lower and upper molars are bilophodont in their unworn state, with tall but rounded (not acute) cusps at the four corners of each tooth. The lower molars lack any trace of a paraconid. They are rectangular but have wider trigonids than talonids. The protoconid and metaconid are joined by a high crest with only a shallow trigonid notch. Both cusps are twinned on M_2, each with either a single smaller cusp (RM_2) or a pair of smaller rounded cusps (LM_2) toward the midline of the tooth. The hypoconid and entoconid are joined by a similar but much lower crest. The cristid obliqua is very low and weakly developed, meeting the trigonid wall at the middle (M_1) or more buccally ($M_{2\text{-}3}$); consequently the lower molars are nearly bisected by a deep transverse groove separating trigonid and talonid. Nevertheless, the talonid notch (lingually) is deeper than the notch on the buccal side. A small hypoconulid is present on M_2 but is not evident on M_1. The anterior border of the ascending ramus of the dentary is even with the talonid of M_1. Unlike the antemolar teeth, the relatively unworn upper and lower molars are completely covered with enamel, and have no evident bands of restricted or thin enamel.

The upper teeth were found isolated rather than in the maxillae (except right P^1); nevertheless, nearly all cheek teeth are represented on one side or the other and most on both sides. They show slightly less relief than the lowers. The right P^1 approximates an obtuse triangle in cross section. It is dominated by a tall, elongate labial cusp, apparently consisting of a primary central cusp flanked by smaller and lower mesial and distal cusps, although this is difficult to verify due to wear. A lower posterolingual cusp was present but is broken in this specimen. Wide enamelless bands (wider toward the root) separate the labial and lingual cusps. Only the root of right P^2 remains, but a complete left P^2 is preserved. It is triangular and has two conical cusps, a tall buccal cusp and a lower lingual cusp. A broad enamelless band separates the cusps anteriorly, whereas on the posterior surface the enamelless band is much more restricted and extends only about halfway up the crown. Deciduous P^3 and P^4 are heavily worn triangular teeth with three main cusps, presumably the paracone, metacone, and protocone; dP^4 also has a small hypocone. Part of permanent P^3 is visible in the maxilla above the front of the left dP^3. P^4 is an ovoid tooth with a ring of rounded, peripheral cusps surrounding a moderate basin. The cusps are interpreted as a large, central paracone, small low metacone, and four smaller cusps along the lingual margin (probably the paraconule and protocone anteriorly and the metaconule and hypocone posteriorly). The upper molars are ovoid to quadrate, slightly wider transversely than anteroposteriorly. They are basined but open both lingually and buccally through deep notches between the protoloph (joining the paracone and protocone) and the metaloph (joining metacone and hypocone). The buccal notch is deeper. The paracone is distinctly larger and taller than the metacone, but the protocone and hypocone are more nearly equal in height. M^1 has a low, transversely elongate paraconule and a twinned metaconule, whereas M^2 has a twinned paraconule and a single metaconule. On both molars the preprotocrista is continuous with a steeply inclined anterior cingulum on the base of the paracone. The M^3s are not preserved.

USNM 538316 is a short, broad intermediate phalanx (L=15.4 mm, Wprox=16.3 mm, Wdist=14.4 mm) with a pair of shallow articular depressions proximally and a deeply grooved distal articulation. It is similar to the intermediate phalanx of *E. gliriformis* (USGS 16498) but considerably smaller, hence we refer it to *E. bighornensis*.

Several taeniodont specimens from the Wa-0 interval are too fragmentary to be certain which species they represent, but their robust features and specialized teeth show the unmistakable hallmarks of *Ectoganus*. Three come from in or near the base of Wa-0 (Red 1): USNM nos. 527724 (two caudal vertebrae,

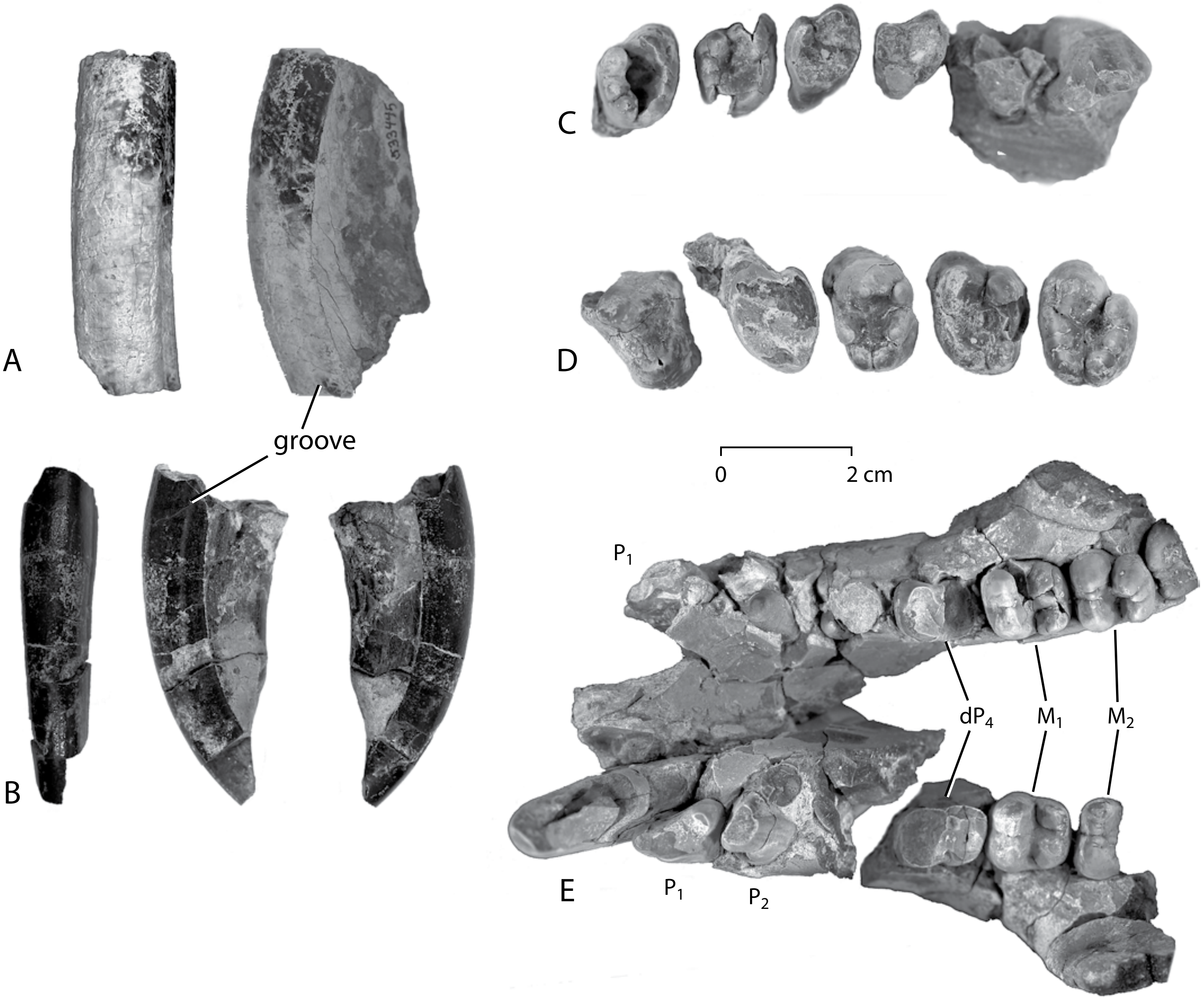


FIGURE 18 — Taeniodonts. A, *Ectoganus*, cf. *E. lobdelli*, fragmentary LC^1, USNM 533445, in labial and distal (lateral) views; B-E, *Ectoganus bighornensis*, USNM 527725: B, LC^1, in labial, distal, and mesial views; C, right upper dentition: P$^{1-2}$ in maxilla, dP$^{3-4}$, M$^{1-2}$; D, left upper dentition: P^2, dP$^{3-4}$, M$^{1-2}$; E, mandible with LC$_1$, P$_{1-2}$, dP$_4$-M$_2$ trigonid, and RP$_{1-3}$, dP$_4$, M$_1$-M$_3$ trigonid.

fragments of humerus and ulna, and associated fragments), 538281 (pisiform), and 538282 (associated tooth fragments). Two are from higher in the interval: USNM 538317 (incisor fragment, WW-86) and 539513 (fragments of edentulous left dentary and cranium, WW-84). These specimens provide further evidence that taeniodonts were common during the PETM.

*Measurements (mm; L measured mesiodistally, W measured labiolingually; * denotes estimate).*— USNM nos. 521518: 12.4 x 10.7; 533561: L= 12.5, W=11.1; 538319: W=12.3 (length cannot be measured); 527725: LC$_1$L=11.8, W=18.7; LP$_1$L=12.1, Wpost=9.8; LP$_2$L=10.5, W=15*; LdP$_3$?L=10.8, W=8.3; LdP$_4$L=14.0*, W$_a$=9.2, W$_p$=9.0; LM$_1$L=12.3, W$_a$=11.9, W$_p$=10.5; LM$_2$W$_a$=12.5; RP$_1$L=11.9, Wpost=9.8; RP$_2$L=10.4*, W=15.4*; RdP$_4$L=11.8*, W$_a$=9.0; RM$_1$L=12.7, W$_a$=12.0*, W$_p$=11.2; RM$_2$L=12.4, W$_a$=12.2, W$_p$=10.0; RM$_3$W$_a$=11.4; LP^{2}L=10.4, W=14.0*; LdP^{3}L=9.85, W=14.0; LP^{4}L=9.5*, W=12.9; LM^{1}L=11.4, W=14.8; LM^{2}L=12.0, W=13.55; RC^{1}L=12.1, W=19.6; RP^{1}L=9.8, W=12.5*; RdP^{3}L=9.5, W=12.5*; RdP^{4}L=10.0, W=14.1; RM^{1}L=11.8, W=14.3; RM^{2}L=11.6, W=12.8. It should be noted that because of the unusual morphology of taeniodont teeth, it is difficult to orient and measure them consistently. All dimensions given here should therefore be taken as approximate.

Discussion.— Taeniodonts are surprisingly frequent in Wa-0 sediments, implying that climatic or environmental conditions during the PETM were more favorable to these animals than immediately before or afterwards, when they were much rarer (Rose, 1981a). Nevertheless, they are still relatively rare.

We follow Gingerich (1989) in recognizing *E. bighornensis* as the appropriate species (rather than subspecies) name for the small Wa-0 taeniodonts.

Ectoganus, cf. *E. lobdelli* Simpson, 1929

Figure 18A

Referred specimens.— WW-101: USNM 539514 (right unciform); WW-119: USNM 533445 (canine fragment); unnumbered locality just above Red 1: USNM 527722 (associated canine, incisor, cheek teeth, and bone fragments).

Description.— Two dental specimens are much larger than comparable teeth in USNM 527725 and probably represent the larger species *E. lobdelli*. A fragmentary canine, USNM 533445, has approximate dimensions (L=16.0 mm, labiolingual W=27.5* mm) exceeding those of *E. copei* and *E. bighornensis* and within the range of those of *Ectoganus gliriformis* and *E. lobdelli* (Schoch, 1986). Locality WW-119, which produced USNM 533445, is situated approximately 5 m above the top of the marker bed designated "Big Red," which places it no more than 7 m below the boundary between the Wa-0 and Wa-1 biozones. Thus, despite care taken in this area to ensure precise stratigraphic control, contamination from Wa-1 cannot be positively excluded. The second specimen, USNM 527722 (approximate canine dimensions: L=15.3 mm, W=27.5 mm) also is in the size range of *E. lobdelli* and *E. gliriformis*, and is unlikely to be a contaminant. It includes several heavily worn cheek teeth whose crowns consist of enamel rims surrounding dentine. They appear to be relatively low-crowned, like *E. lobdelli*, rather than higher crowned as in *E. gliriformis*. The specimen was found at the outset of our fieldwork, just above the lowest red bed more than 1 km east of the principal localities. This bed correlates with Red 1 in the principal study area, hence the specimen probably comes from the lowest 5 m of the PETM.

In addition, an isolated unciform from near the top of the Wa-0 section is tentatively allocated to *E. lobdelli* based on its size.

Discussion.— Schoch (1986) recognized *E. gliriformis* and *E. lobdelli* as subspecies of *E. gliriformis*: *E. gliriformis lobdelli* (Simpson, 1929) from late Tiffanian and Clarkforkian strata, and *E. g. gliriformis* from the Wasatchian (one questionable Clarkforkian specimen was included). He distinguished *E. gliriformis* from the other two Wasatchian species (*E. copei* and *E. bighornensis*) by its larger size. The Wasatchian subspecies was described as having more hypsodont cheek teeth than the Paleocene subspecies, but there is evidently no difference in their canines. Gingerich (1989) used these names as distinct species, and suggested that *E. lobdelli* existed in biozones Wa-1 and 2 as well as during the late Paleocene, whereas *E. gliriformis* comes from Wa-3 and later. We follow Gingerich in recognizing these taxa as species and, based on his determinations, we allocate USNM 533445 to *Ectoganus*, cf. *E. lobdelli*.

Order TILLODONTIA Marsh, 1875
Family ESTHONYCHIDAE Cope, 1883

At least two, and as many as four, species of tillodonts are present in the Sand Creek Divide local fauna. Two sizes each of *Azygonyx* and *Esthonyx* have been identified. Gingerich (1989, 2001) also acknowledged the possibility of two *Azygonyx* species in the Polecat Bench PETM section. However, in view of small sample sizes and poor understanding of intraspecific variation or the possibility of sexual dimorphism, the precise species diversity of tillodonts during the PETM remains uncertain.

AZYGONYX Gingerich, 1989

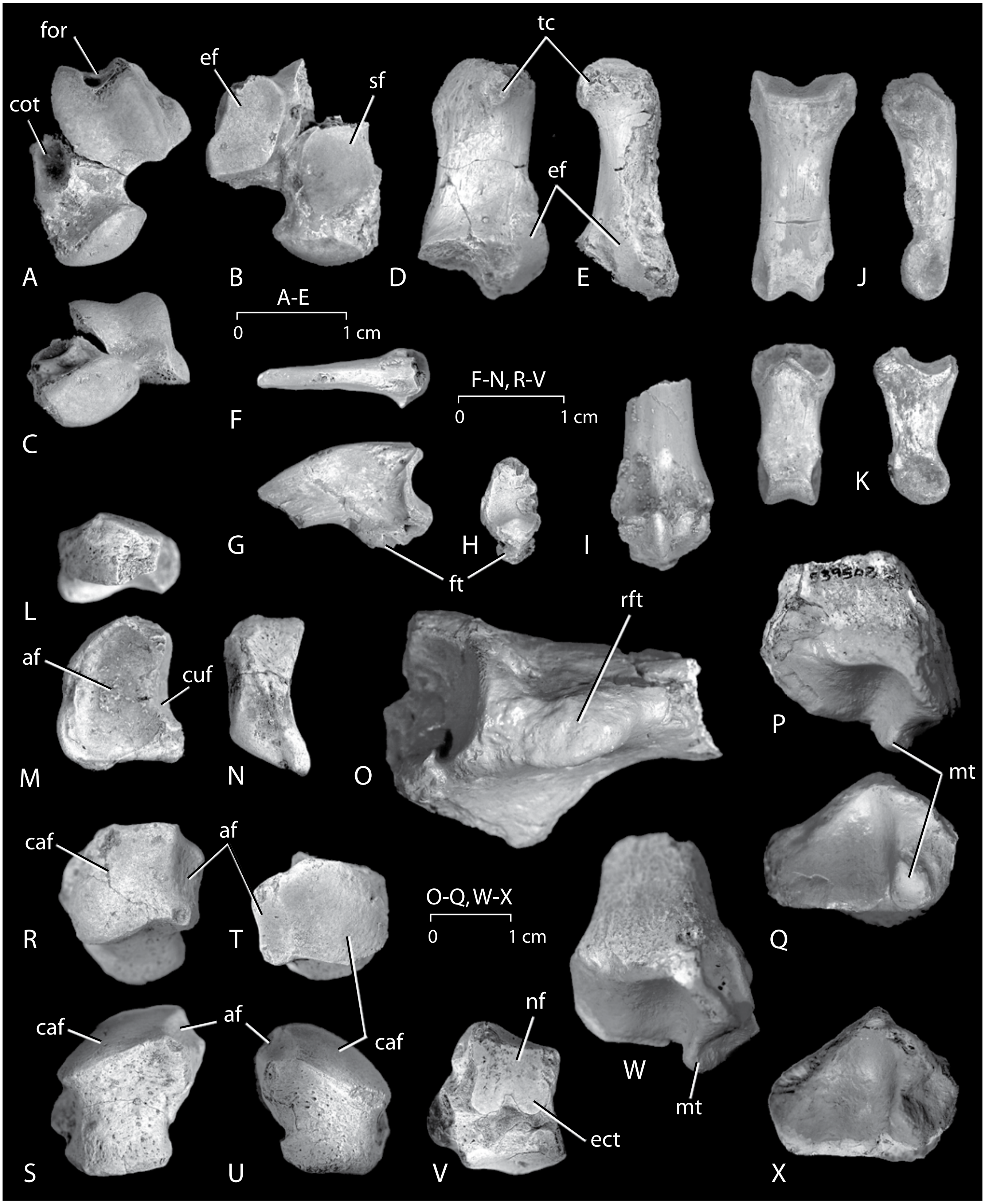
Azygonyx gunnelli Gingerich, 1989

Figure 19F-H, P-Q, T-V

Referred specimens.— Unnumbered localities: USNM 511054 (associated L foot bones including cuboid, fragmentary metatarsals, phalanges), from approximate level of Purple 3; 539508 (distal L tibia), from Big Red.

Description.— Most of the foot elements in USNM 511054 closely match those of the holotype (UM 83874: Gingerich, 1989) in size and morphology. The terminal phalanx is large, curved, and laterally compressed, and has a prominent flexor tubercle (missing due to damage in the holotype). The proximal articular surface of the cuboid resembles that of the holotype in having facets for both calcaneus and astragalus, as well as in the shape of those facets (calcaneal facet broad, almost quadrate, and slightly convex; astragalar facet narrow and slightly concave), but it is slightly smaller than the fragmentary cuboid of the holotype. The distal tibial articulation (USNM 539508) is relatively shallow, with a low ridge for the astragalar trochlea. It is anteroposteriorly wider on the medial side than laterally, and the tibial malleolus bears a tubercle anteriorly that was accommodated by a cotylar fossa on the astragalus. The specimen

FIGURE 19 — Tillodont postcrania. A-E, *Esthonyx spatularius*, USNM 538365: A-C, left astragalus in dorsal, ventral, and distal views; D-E, proximal part of left calcaneus in medial and dorsal views. F-H, *Azygonyx gunnelli*, USNM 511054, terminal phalanx in dorsal, lateral, and proximal views. I-N, *Azygonyx*, cf. *A. grangeri*, USNM 525633: I, distal metapodial (plantar view); J, proximal phalanx in dorsal and lateral views; K, intermediate phalanx in dorsal and lateral views; L-N, right navicular in dorsal, proximal, and medial views. O, *Azygonyx grangeri*?, USNM 539515, partial right ilium in lateral view. P-Q, *Azygonyx gunnelli*, USNM 539508, distal left tibia in oblique posterior and distal views. R-S, *Azygonyx grangeri*, cf. *A. grangeri*, USNM 525633, right cuboid in proximal and dorsal views. T-V, *Azygonyx gunnelli*, USNM 511054, left cuboid in proximal, dorsal, and medial views. W-X, *Azygonyx grangeri*?, USNM 539515, distal left tibia in oblique posterior and distal views. Abbreviations: **af**, astragalar facet; **caf**, calcaneal facet; **cot**, cotylar fossa; **cuf**, cuboid facet; **ect**, ectocuneiform facet; **ef**, ectal facet; **for**, astragalar foramen; **ft**, flexor tubercle; **mt**, malleolar tubercle; **nf**, navicular facet; **rft**, rectus femoris tuberosity; **sf**, sustentacular facet; **tc**, calcaneal tuber.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articulates reasonably well with the astragalus of the holotype.

Measurements (mm).— USNM 511054, cuboid maximum L (medially)=12.95, maximum W of proximal articulation=11.55, maximum W of distal articulation=9.1; intermediate phalanges (L x proximal W x distal W)=13.4 x 6.2 x 5.35, 14.8 x 7.25 x 5.65, 14.5 x 7.35 x 4.6; ungual phalanx, estimated total L=18.7, proximal W distal to articulation=3.0, articular W= 5.7, proximal dorsoplantar D=10.1 (including flexor tubercle). USNM 539508, distal tibia, maximum dimensions=23.7 x 16.7.

Discussion.— The laterally compressed ungual phalanx together with the moderately shallow distal tibia suggest scansorial habits and climbing ability. But the diplarthral (alternating or interlocking) articulations of the cuboid are more often associated with tarsal stability in terrestrial (especially cursorial or fossorial) mammals. Tillodonts are often considered to have been generalized terrestrial mammals that engaged in some digging and rooting, which is consistent with these very limited remains.

Azygonyx, cf. *A. grangeri* (Simpson, 1937)

Figure 19I-O, R-S, W-X

Referred specimen.— WW-117: USNM 525633 (RI^2, fragmentary RP^4, and associated bones including R cuboid, R navicular, metapodials, phalanges, caudal vertebrae).

Description.— Although few elements in this specimen are comparable to others known for *Azygonyx grangeri*, the two teeth found with the bones are unmistakably tillodont, and some of the other elements (metapodials and phalanges) are larger than those of the holotype of *A. gunnelli* or any other esthonychine except late Wasatchian *Megalesthonyx hopsoni*, suggesting that this specimen could represent *A. grangeri* (which is known both immediately before and immediately after the Wa-0 interval). However, the cuboid and navicular are very similar in size and morphology to those of the holotype of *A. gunnelli*. The cuboid (Figure 19R-S) is conspicuously larger and relatively longer than that of USNM 511054, referred above to *A. gunnelli*. Unfortunately, the cuboid of the holotype preserves only the proximal portion, so its relative length cannot be determined. Also associated with this specimen are a navicular (relatively wide, proximally concave, and proximodistally short; Figure 19L-N), complete proximal and intermediate phalanges (Figure 19J-K), a proximal ungual phalanx, and a few robust caudal vertebrae. The fragmentary ungual is similar to that associated with USNM 511054 but is larger, with a more prominent flexor tubercle.

A second specimen (USNM 539515) comes from about 10m higher (WW-126, near the boundary of Wa-0 and Wa-1) and consists of a distal tibia (Figure 19W-X), partial ilium (Figure 19O), and associated fragments. Comparison with other esthonychid remains indicates that these bones pertain to a large species of *Azygonyx*, probably *A. grangeri*. The distal tibia is very similar to that of *A. gunnelli* (USNM 539508) but slightly larger. The ilium is distinguished by a particularly prominent tuberosity for origin of the rectus femoris muscle.

Measurements (mm).— USNM 525633, cuboid maximum L (medially)=15.7, maximum W of proximal articulation=12.6, maximum W of distal articulation=9.65; navicular L=7.0, W=14.35; proximal phalanx L=21.3, proximal W=9.9, distal W=6.9; intermediate phalanx L=14.9, proximal W=7.8, distal W=6.0; ungual phalanx, proximal W distal to articulation=4.1, articular W=6.7, proximal dorsoplantar depth=11.6; caudal vertebrae (L x maximum centrum diameter)=26.3 x 15.5, 31.3 x 14.8. USNM 539515, distal tibia, maximum dimensions=23.7 x 17.9.

Discussion.— Samples of *Azygonyx grangeri* and *A. gunnelli* remain small, and intraspecific variation is poorly understood. Although the differences in size and relative proportions of the cuboid in the two Sand Creek Divide specimens suggest that two different species are represented, it is possible that these few specimens represent a single species, *A. gunnelli*. It is also possible that *A. gunnelli* is a slightly dwarfed form of *A. grangeri*, which is known from both earlier and later.

Those elements of USNM 525633 that can be compared (navicular, phalanges) are very similar in size and morphology to those of *Azygonyx*? sp., UM 66616, from the Wa-0 interval at Polecat Bench. *Azygonyx* foot elements, as well as the distal tibia, can be easily confused with those of oxyaenids. Compared to that of oxyaenids, the distal tibia of *Azygonyx* is not as wide anteroposteriorly and has a more distinct malleolar tubercle (which articulates with the cotylar fossa). The astragalar facet on the proximal cuboid is smaller in *Azygonyx*, and the terminal phalanges are more laterally compressed and lack the fissure present in unguals of oxyaenids.

ESTHONYX Cope, 1874

Esthonyx spatularius Cope, 1880

Figures 19A-E, 20A-I

Referred specimens.— WW-80 (=WW-116): USNM nos. 511098 (L maxilla with M$^{1\text{-}3}$), 533542 (associated teeth including L and RI^2 or I^3, RP^3, LM^2), 533591 (associated teeth including RI^2, RP^2?, RM^2, damaged RM$_1$ or M$_2$), 538365 (RM$_1$ trigonid, dentary fragments, and associated postcrania including damaged distal L tibia, astragalus and calcaneus, vertebrae), 539478 (damaged RM^x), 541962** (LP$_4$), 541963** (RM^1, and RM^3). Several of these specimens were found in different field seasons, but, based on location and stage of wear, probably represent the same individuals: USNM 511098, 533591, 538365, and 541962 are believed to represent one individual, and USNM 533542 and 541963 probably come from one individual.

Description.— Several specimens, all from the same locality at the base of the PETM/Wa-0 section, are allocated to *Esthonyx spatularius*, the smallest and earliest species of the genus, based on their comparable small size and (to the limited extent that they can be compared) close resemblance to the holotype, which consists of just a few associated teeth. Some of the specimens may represent the same individual, but at least two individuals were present. Most of the specimens referred here are upper teeth, which, aside from I^2, are not represented in the holotype. Like other *Esthonyx*, they have wide stylar shelves with prominent parastylar lobes on M$^{2\text{-}3}$, strong anterior and posterior cingula without a distinct hypocone, and a long, high lingual protocone

TABLE 2 — Measurements (mm) of calcaneus and astragalus of Wa-0 tillodonts. Measurements of *Azygonyx gunnelli* based on holotype, UM 83874. Tarsals of *Esthonyx spatularius* (USNM 538365) are damaged, and measurements should be regarded as approximate.

	A. gunnelli	*E. spatularius*
Astragalus		
L (measured medially)	24.9	17.0
Trochlea L (medial)	16.5	9.7
Midtrochlear L (from foramen)	9.9	8.0
Trochlea W at midpoint	13.0	8.5
Head W (maximum)	14.3	9.0
Head dorsoplantar height (maximum)	8.6	5.1
Calcaneus		
L (maximum, measured laterally)	37.3	28.9
Tuber L (to ectal facet)	20.4	14.0
Tuber proximal W	12.8	7.4
Tuber proximal depth (including plantar tubercle)	16.0	9.6
Tuber W (minimum)	7.3	4.8
Ectal facet L	13.2	10.2
Ectal facet W (maximum)	7.2	4.7
Sustentacular facet L	8.3	4.9
Sustentacular facet W	9.6	7.5
Cuboid facet, maximum diameter	11.3	7.3
Cuboid facet, minimum diameter	8.6	6.4
Distal W across sustentacular and ectal facets	21.5	14.1

slope. I^2 has enamel restricted mainly to the labial and lateral sides.

The postcranial fragments (USNM 538365) are notable in being the oldest known for *Esthonyx*. The distal tibia shows part of the astragalar facet, which is relatively shallow, and a small fibular facet. The tarsal elements closely resemble their counterparts in *Azygonyx gunnelli* but are 25-30% smaller and more gracile (see Table 2). The calcaneus is in two pieces that do not quite meet, a proximal part extending from tuber to ectal facet, and a distal section with sustentacular and cuboid facets. The calcaneal tuber of *E. spatularius* makes up approximately the same proportion of total calcaneal length as in *A. gunnelli*, but it is shallower and narrower. Both proximal and distal plantar tubercles are less prominent than in *A. gunnelli*. The ectal facet is the same relative length in both species but is narrower in *E. spatularius*. There is no evident fibular facet on the calcaneus. As in *Azygonyx*, the sustentacular facet of the calcaneus is wider than long and very shallowly concave. The cuboid facet is similarly almost flat. As in other esthonychines, the astragalar trochlea is shallowly grooved, and there is a deep notch at the proximal end of the trochlea occupied by the astragalar foramen. The astragalar body is deep, especially laterally, with a flaring lateral process at the distoplantar angle (formed by the distolateral margin of the ectal facet). The most distinctive astragalar feature is a deep, circular cotylar fossa on the distomedial side of the trochlea. The astragalar head is relatively flatter dorsoplantarly than in *A. gunnelli*. The ectal facet of the astragalus forms a gentle arc, while the sustentacular facet is convex proximodistally and almost flat transversely. A deep sulcus tali separates these two facets.

Measurements.— USNM 511098, M^1L=6.7*, M^1W=9.2*, M^2L=5.25, M^2W=10.2*, M^3L=5.1*, M^3W=9.2*; 533542, P^3L=6.45, P^3W=6.35, M^2L=6.80, M^2W=10.80; 533591, I^2 mesiodistal=5.40, labiolingual=6.30, P^2L=6.35, P^2W=5.30; 541962, P_4L=7.10, W_a=5.25; 541963, M^3L=4.70, W=7.80 (M^1 damaged). See Table 2 for tarsal measurements.

Discussion.— Small size is the principal criterion in the assignment of these specimens to *Esthonyx spatularius*. Gingerich and Gunnell (1979) observed that the smallest known *Esthonyx* specimens came from early Graybullian (i.e., biozones Wa-1 and 2). The precise provenance of the holotype of *E. spatularius* has long been in doubt, but it seems quite possible that it came from what is now known to be the Wa-0 section at the southern end of Polecat Bench. Gingerich (1989) subsequently reported another specimen of the species from this locality. However, the well-preserved lower dentition (AMNH 16065) illustrated and referred to *E. spatularius* by Gazin (1953: figure 5) has been shown to be of early Clarkforkian age and to belong to *Azygonyx xenicus* (Gingerich and Gunnell, 1979). It is possible that true *E. spatularius* is restricted to the earliest Wasatchian.

The five specimens here come from a very restricted site situated within basal Eocene Red 1. The same bed has produced the only records of *Haplomylus zalmouti* from the Sand Creek Divide area. *H. zalmouti* is regarded as an index fossil of the Wa-M interval, which is otherwise characterized by the condylarth *Meniscotherium* at Polecat Bench and one locality in the southeastern Bighorn Basin (Gingerich and Smith, 2006; Yans et al., 2006). Curiously, no specimens of *Meniscotherium* have been found at Sand Creek Divide.

Esthonyx sp.

Figure 20J-L

Referred specimens.— WW-78: USNM 533622 (RM^3), USNM 540590 (LP^4 and M^2 fragment, and associated cranial fragments); unnumbered locality: USNM 533597 (LI^2 or possibly RI_2), from in or just above Big Red.

Description.— These teeth appear to be too large to belong to *E. spatularius* and suggest the presence of a second species of *Esthonyx* during the PETM. M^3 (Figure 20J), the only comparable tooth, is conspicuously larger than that of *E. spatularius*. The isolated incisor, from the level of the Big Red paleosol, is slightly larger and more robust than those of *E. spatularius*. These specimens could represent the first appearance of *E. bisulcatus*, although they are slightly smaller than later Wasatchian specimens of that species. Though found several years apart, the two specimens from WW-78 may represent the same individual.

Measurements (mm).— USNM 533622, M^3L=5.20, W=10.20; 540590, P^4L=7.8*, P^4W=10.80, M^2W=7.75; 533597, mesiodistal=4.20, labiolingual=6.50.

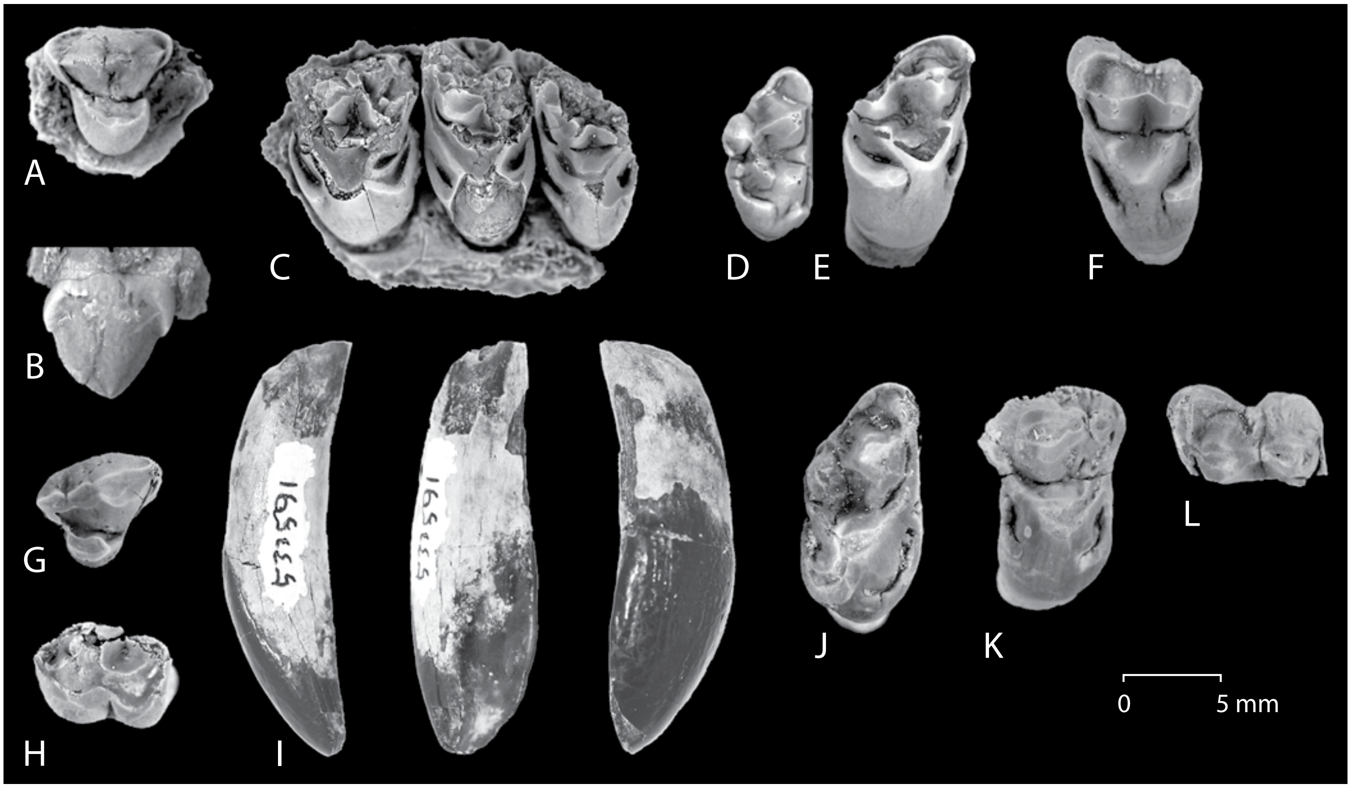


FIGURE 20 — A-I, *Esthonyx spatularius*: A-B, RP^3, USNM 533542, in occlusal and buccal views; C, L maxilla with M^{1-3}, USNM 511098; D-E, RM^3 and RM^1, USNM 541963; F, LM^2, USNM 533542; G, RP^2?, USNM 533591; H, LP_4, USNM 541962; I, RI^2, USNM 533591, in mesial, lingual, and distal (lateral) views. J-L, *Esthonyx* sp.: J, RM^3, USNM 533622; K-L, LP^4 and partial LM^2, USNM 540590.

Order PANTODONTA Cope, 1873
Family CORYPHODONTIDAE Marsh, 1876

Coryphodon Owen, 1845
Coryphodon sp.

Referred specimens.— WW-73: USNM 521679 (proximal phalanx); WW-75: USNM 538324 (intermediate phalanx); unnumbered localities: UM 110897 (maxilla?, top of Big Red), UM 110898 (partial skeleton, large species, just above Red 1). Uncatalogued tooth fragments were collected from localities WW-72, 88, 113, 118, and unnumbered localities, for isotope analysis.

Description.— The specimens referred here are of such large size and distinctive morphology that they cannot be confused with any other taxon known from the PETM. Most specimens collected consist of uncatalogued enamel fragments or isolated foot bones, but two substantially more complete specimens were collected by P.D. Gingerich and are housed at the University of Michigan.

Discussion.— Though common during the Clarkforkian and Wasatchian, *Coryphodon* is quite rare in the Wa-0 section at Sand Creek Divide, and is not particularly common at other Wa-0 localities. Tooth fragments of *Coryphodon* found at several levels within the Wa-0 section, as well as 5-15 m below the Fort Union-Willwood contact in the intervals of the intermittent red and purples, were analyzed for carbon isotope ($\delta^{13}C$) values by Paul Koch. An additional sample from high in the Sand Creek Divide section (~50 m, Wa-1) was analyzed by Ross Secord. The isotope values and stratigraphic positions of all these specimens are shown in Figure 3.

Order EULIPOTYPHLA Waddell, Okada, and Hasegawa, 1999
Suborder SORICOMORPHA Gregory, 1910
Family NYCTITHERIIDAE Simpson, 1928

LEPTACODON Matthew and Granger, 1921

Leptacodon donkroni, sp. nov.
Figures 21A-D, I-J, 22A-E

Holotype.— USNM 538087, R dentary with talonids of P_4 and M_1 and complete M_2.

Hypodigm.— Holotype and USNM nos. 538088 (LM^1), 538089 (LM^3), 538090 (RP^4), and tentatively 538091 (RI_2).

Locality and Horizon.— All known specimens are from locality WW-74 (SE¼ sec. 3, T 48 N, R 92 W, McDermott's Butte Quadrangle, Washakie County, Wyoming), lower Willwood

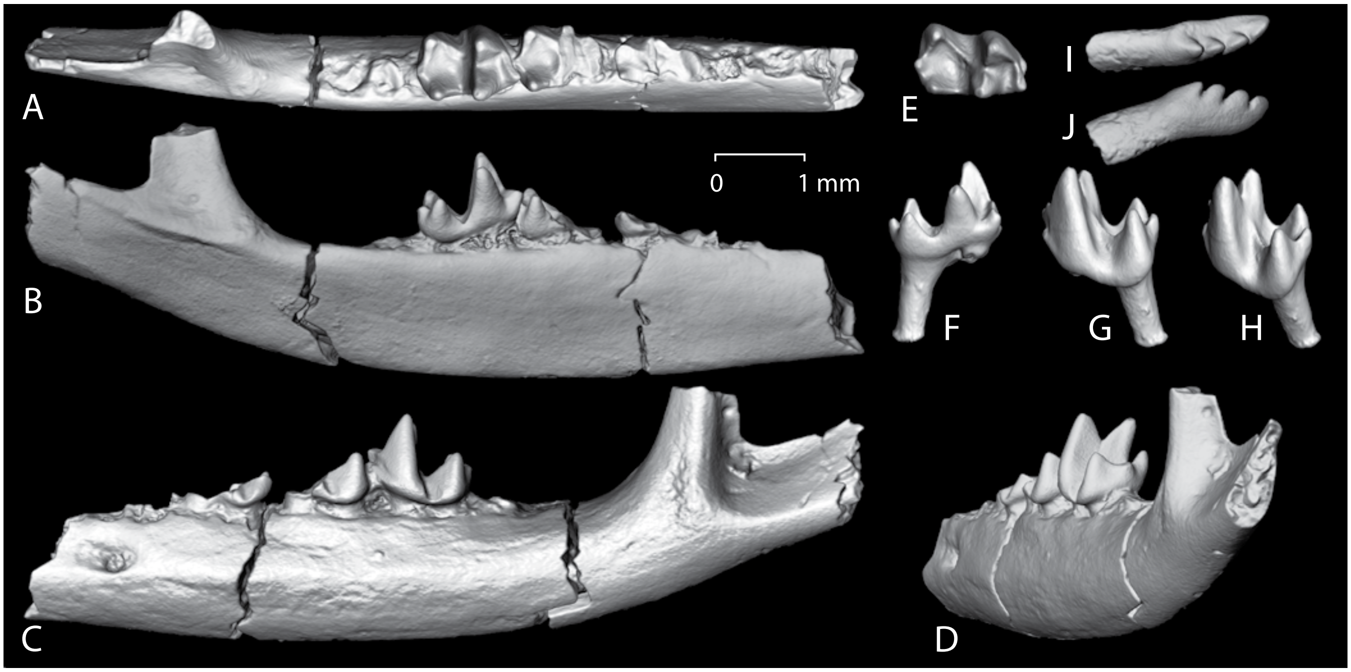


FIGURE 21 — *Leptacodon* lower teeth: A-D, *L. donkroni*, sp. nov., holotype, R dentary with M_2 and talonids of P_4-M_1, USNM 538087, in occlusal, lingual, buccal, and posterior oblique views. E-H, *Leptacodon* sp. 2, LM_1?, USNM 540402, in occlusal, lingual, buccal, and buccal oblique views. I-J, *L. donkroni*?, RI_2, USNM 538091, in dorsal and lateral views.

Formation, earliest Eocene (Wa-0 biozone).

Etymology.— In honor of the late Donald G. Kron, who served on our field crews for several field seasons, and who initiated and directed the superfine screen-washing program that resulted in discovery of these diminutive specimens.

Diagnosis.— Smallest species of *Leptacodon*; about 20% (or more) smaller than other species in most linear tooth dimensions. P^4 lacking distinct metacone; P^4 and M^1 more distinctly waisted than in other species. M^1 posterolingual lobe larger than in *L. munusculum*; differs from other species in lacking distinct hypocone.

Description.— A dentary and several isolated teeth represent a minute, new species of *Leptacodon* that is at least 20-25% smaller in most dimensions than reported samples of *L. catulus*, *L. dormaalensis*, *L. munusculum*, *L. nascimentoi, L. packi*, *L. proserpinae*, *L. rosei*, and *L. tener* (the type species). Among species of *Leptacodon* it is closest in size to the Torrejonian-Tiffanian species *L. munusculum*, which is only about 10% larger in some dimensions, but *L. donkroni* further differs from the Paleocene species in having a less developed P_4 talonid with only two distinct cusps (hypoconid and entoconid; a distinct hypoconulid is present in *L. munusculum*) and a better developed posterolingual shelf on M^1.

The dentary is very shallow (Figure 21A-D). Anterior to P_4 it preserves two complete alveoli, probably for P_3, which is clearly two-rooted in other species of the genus. The length of these two alveoli is about 0.90 mm, just slightly shorter than the estimated length of P_4, suggesting little reduction of P_3. A single mental foramen opens below the anterior root of P_3. Only the talonid of P_4 remains, but the base of the anterior part of the tooth is present, indicating an elongate trigonid as in other species. The cristid obliqua seems to be less oblique than in *L. tener* and *L. catulus*, in this regard resembling *L. munusculum*. The lower molars have broad talonid basins bounded posteriorly by moderately high and acute hypoconid and entoconid cusps and a lower, centrally positioned hypoconulid. The cristid obliqua and entocristid incline steeply toward the back of the trigonid. The cristid obliqua joins the back of the trigonid buccal to the trigonid notch, and the entocristid leads into a deep talonid notch. M_2 has a very low, crest-like paraconid, and tall and acute protoconid and metaconid cusps separated by a deep trigonid notch. The protoconid and metaconid are of approximately equal height. Although incomplete, M_1 seems to have been slightly shorter than M_2.

Several upper teeth (Figure 22A-E) are tentatively referred to this new species based on their diminutive size and close similarity to those of other *Leptacodon* species. P^4 (USNM 538090) has a smaller parastyle than in *L. tener*, *L. rosei*, and *L. dormaalensis*, but larger than in *L. munusculum*. A low metastyle is also present. A faint elevation on the postparacrista is the only indication of a metacone, in contrast to *L. tener*, *L. catulus*, *L. rosei*, and *L. dormaalensis*, all of which have a distinct metacone on P^4. *L. munusculum* is similar in lacking a metacone on P^4. M^1 (USNM 538088) is very similar to those of *L. tener*, *L. rosei*, and *L. dormaalensis* but much smaller. It differs in having a shallower ectoflexus, weaker conules that are closer to the protocone than in those species, and a slightly smaller posterolingual expansion without a distinct hypocone. A low cingulum is present on this lobe, unlike in those species. *L. munusculum* (AMNH 35951) differs in having a very constricted protocone lobe on M^{1-2} with almost no posterolingual expansion. Both P^4 and M^1 of *L. donkroni* are strongly waisted—much more so than in *L. tener*, *L. catulus*, *L. munusculum*, or *L. rosei*; but these teeth in the contemporaneous European species *L. dormaalensis* and *L. nascimentoi* are almost as waisted. M^1 of *L. nascimentoi* from Silveirinha, Portugal (Estravís, 1996), is slightly larger than that of *L. donkroni*, more transverse, and has a larger posterointernal lobe with a distinct hypocone. M^3 (USNM 538089) resembles those of *L. tener*, *L. rosei*, and *L. dormaalensis* in having a large parastyle, no metastyle, and no hypocone. As in those species, the paraconule is closer to the protocone than to the paracone, and the metaconule is midway between protocone and metacone.

A right I_2 of a nyctithere (USNM 538091, Figure 21I-J) probably represents *L. donkroni*, based on its diminutive size, but it could also represent *Leptacodon* sp. 2 below. It is very similar in morphology to its counterpart in *L. rosei* (USNM 539484, UM 82389), but differs in being about 15-20% smaller and having four apical lobes (cuspules) rather than five. The first lobe is largest, the other three noticeably smaller and roughly equal in size, but decreasing very slightly posteriorly. *L. rosei* has a fifth (posterior) cuspule which is acute rather than rounded like the others. Its anterior lobe also is largest, while the second through fourth are small, equal-sized, and more closely spaced than in USNM 538091. The molars of *L. rosei* are substantially larger than those of *Plagioctenoides microlestes*, and as this incisor is only slightly smaller than that of *L. rosei*, it is unlikely that it represents *P. microlestes*. The Wa-0 incisor is also similar to that of *Saturninia* (Sigé, 1976: figure 27) and slightly less so to *Amphidozotherium* (Sigé, 1976: figure 95), which appears to have a small, acute fifth cuspule as in *L. rosei*. These resemblances support its allocation to Nyctitheriidae.

Measurements (mm).— USNM 538087, P_4L (est.)=0.95, W_p=0.50, M_1L (est.)=1.00, W_p=0.70, M_2L=1.15, W_a=0.85, W_p=0.75, dentary depth (labial below M_1)=1.30; USNM 538088, M^1L=1.10, W=1.35; USNM 538089, M^3L=0.85, W=1.20; USNM 538090, P^4L=1.10, W=1.05; USNM 538091, I_2 crown L=1.10, W=0.50 (I_2 in *L. rosei*, USNM 539484, is 1.30 long x 0.60 wide).

Discussion.— These remarkable specimens, recovered in 0.5 mm-mesh screen, document the existence of a minute new species of *Leptacodon* during the PETM. They are much smaller than the isolated teeth from two Wa-M levels at SC-434 on Polecat Bench referred by Gingerich and Smith (2006) to *Leptacodon* sp. The Wa-M *Leptacodon* M^1 further differs from *L. donkroni* in having a larger posterolingual lobe with a distinct hypocone.

The new species is assigned to *Leptacodon* because of its close resemblance to other *Leptacodon* species, including the low, crest-like paraconid, central position of the hypoconulid, and absence of a mesostyle. These are arguably plesiomorphic traits; nonetheless, they link *L. donkroni* more closely with *Leptacodon* species than with *Pontifactor*, *Plagioctenoides*, *Wyonycteris*, or *Nyctitherium*. *Pontifactor*, *Plagioctenoides*, and *Wyonycteris* have upper molar mesostyles, and the latter two genera have acute hypoconulids twinned with the entoconid but separated by a notch. P_4 of *L. donkroni* further differs from those of *Plagioctenoides microlestes* and *Wyonycteris chalix* in having a wider, more basined talonid with a more distinct entoconid. The cristid obliqua of the lower molars of *L. donkroni* joins the back of the trigonid buccal to the trigonid notch, rather than lingual to the notch as in *W. chalix* and *Plagioctenoides microlestes*.

Bown (1979) named the new genus *Plagioctenodon* as an adapisoricid, but it was subsequently recognized to be a nyctitheriid (Bown and Schankler, 1982). Bown and Schankler (1982: 61) considered *Plagioctenodon* to have evolved from Paleocene *Leptacodon tener*, and differentiated it primarily on the basis of a higher P_4 paraconid than in *Leptacodon*. Their emended diagnosis also noted "P_{2-3} anteriorly inclined, P_2 larger than P_3, and no diastema separates these teeth." In most other respects there appears to be little difference between most species of *Leptacodon* and *Plagioctenodon*, and Smith (1996) synonymized them. Besides being larger, *P. krausae* differs from *L. donkroni* in having a tricuspid talonid on P_4, like *L. munusculum*. Two other issues complicate the question of whether *Plagioctenodon* should be synonymized with *Leptacodon*: the ambiguity of which species properly belong in *Leptacodon,* and the scarcity of specimens preserving the diagnostic anterior teeth. Beard and Dawson (2009) recently revisited this controversy, advocating retention of *Plagioctenodon* (to which they referred *L. rosei* and *L. dormaalensis*) based on its reduced P_3 with anteriorly canted protoconid and P_4 with a taller and less mesial paraconid than in *Leptacodon*. Although these minor differences do characterize many specimens, variation in these traits (and the inability to evaluate them in most specimens, including those reported by Beard and Dawson, as well as *L. donkroni*) renders questionable their utility as generic-level characters. For example, the holotype of *Plagioctenodon savagei* has a reduced P_3 but a more *Leptacodon*-like extended P_4 trigonid with a low paraconid. The crown of P_3 and the trigonid of P_4 are missing in the holotype of *L. donkroni*, but the apparently unreduced size of P_3 supports reference to *Leptacodon* even if *Plagioctenodon* is considered distinct. Resolution of these issues must await a thorough study and revision of North American nyctitheriids.

The equations provided by Bloch et al. (1998) yield a body mass estimate of ~4.8 g based on M^1, 3.1 g from M_1 (itself estimated, so a higher estimate is more likely). These estimates are only slightly higher than the masses of the smallest living shrews.

Leptacodon sp. 2, probably new
Figures 21E-H, 22F-H

Referred specimens.— WW-74: USNM 540350 (LM_2?), USNM 540402 (LM_1?); tentatively USNM 541783 (RM^1).

Description.— Two isolated lower molars resemble *Leptacodon* in having more open trigonids and more centrally situated hypoconulids than in *Plagioctenoides*. They are, however, larger than *L. donkroni* and are about the size of Torrejonian *L. munusculum*. They further differ from *L. donkroni* in having taller protoconids, and from both *L. donkroni* and *L. munusculum* in

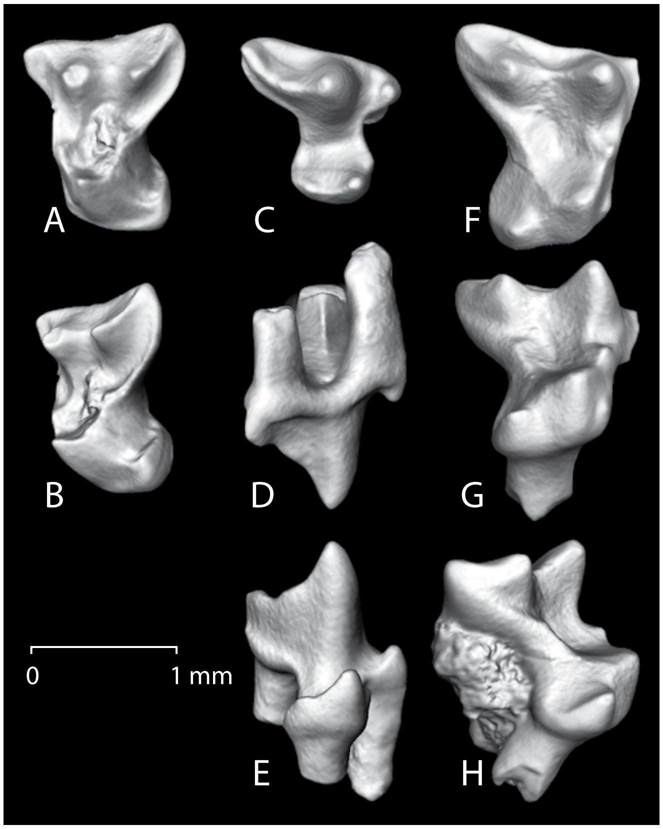


FIGURE 22 — *Leptacodon* upper teeth: A-B, *L. donkroni*, sp. nov., LM^1, USNM 538088, in occlusal and posterior oblique views; C-E, *L. donkroni*, sp. nov., RP^4, USNM 538090, in occlusal, buccal, and lingual views; F-H, *Leptacodon* sp. 2, RM^1, USNM 541783, in occlusal, lingual, and posterior views.

having relatively longer talonids and a more projecting hypoconulid that is set off from hypoconid and entoconid by deeper notches. The paraconid is low and crest-like, and the protoconid is slightly taller than the metaconid, in contrast to *L. donkroni*. The cristid obliqua is slightly stronger than in *L. donkroni* and joins the back of the trigonid low and near the middle. The hypoconid is more constricted and acute than in *L. donkroni*. The hypoflexid is a little deeper on USNM 540350 than on the other molar.

An upper molar (USNM 541783) is very similar to that of *L. donkroni* but is placed under this heading because it is slightly larger. It further differs from *L. donkroni* in having a more distinct hypocone with a slight lingual projection, a narrower stylar shelf, and more widely spaced paracone and metacone, the metacone lower compared to the paracone. Larger samples and more complete specimens are needed to determine whether this tooth belongs to *L. donkroni* or to another species of *Leptacodon.*

Measurements (mm).— USNM 540402, $M_{1?}$L=1.25, W_a=0.80, W_p=0.80; USNM 540350, $M_{2?}$L=1.25, W_a=0.75, W_p=0.70; USNM 541783, M^1L=1.20, W=1.40.

Discussion.— Based on the observed differences between these teeth and those of *Leptacodon donkroni*, it is probable that they represent a second new *Leptacodon* species from WW-74. In view of their fragmentary remains, however, we refrain from naming it pending additional evidence.

Using the M^1 regression equation of Bloch et al. (1998), the body mass of this animal was about 30% greater than that of *Leptacodon donkroni*, ~6.3 g.

PLAGIOCTENOIDES Bown, 1979

Plagioctenoides microlestes Bown, 1979

Figure 23M-P

Referred specimens.— WW-74: USNM 538093 (L dentary with P_4, M_1, and trigonid of M_2), USNM 538094 (R dentary with P_4, M_1 talonid-M_2).

Description.— Two lower jaw fragments (possibly representing the same individual) can be confidently allocated to the very diminutive nyctithere *Plagioctenoides microlestes*, one of the smallest known mammals, based on their size and P_4 morphology. As in the holotype, P_4 is semimolariform and relatively long and narrow, with a mesiodistally extended trigonid and a narrow, oblique talonid basin demarcated from the trigonid by a moderately deep hypoflexid. The tall protoconid dominates the tooth. A distinct paraconid is present anterolingual to the protoconid at the base of the crown; a small metaconid is situated lingual and very slightly posterior to the protoconid, a little more than halfway up the crown in lingual view. The prominent postmetacristid is continuous posteriorly with the low, strongly oblique cristid obliqua, which extends to the hypoconid, the strongest talonid cusp. The hypoconulid is weakly developed slightly posterolingual to the hypoconid, and the entoconid is indistinct, but a well-defined curved crest runs from the hypoconid to the lingual border of the back of the trigonid (below the metaconid), enclosing the talonid basin. These details of P_4 precisely duplicate those in the holotype, with a few minor exceptions (which we attribute to intraspecific variation): the Wa-0 P_4s are very slightly longer and narrower than in the holotype, and the postmetacristid is continuous with the cristid obliqua, whereas in the holotype the postmetacristid descends to the front of the talonid basin just lingual to the cristid obliqua but the two crests are not clearly joined. The disjunction of these crests in the holotype may be accentuated by wear. In addition, the holotype has a very faint entoconid. Notably, a second specimen of *P. microlestes* (UW 9707) from the same Wa-1/2 site as the holotype is virtually identical in its P_4 configuration to the two Wa-0 specimens.

USNM 538093 preserves two moderately large alveoli in front of P_4. Their combined length (0.85 mm) is as long as P_4, suggesting that they held single-rooted P_2 and P_3, as appears to be the case in *Plagioctenoides microlestes* (the P_3 root in the holotype is obscured by hematite, but P_3 is much smaller than P_4). Two mental foramina are present, one below P_4 and the other below the junction of the two alveoli anterior to P_4.

M_1 has a crest-like, low paraconid, and tall protoconid and metaconid, arranged approximately in an equilateral triangle. The metaconid is twinned and slightly smaller and lower than the protoconid. The cristid obliqua is well developed and continues up the back of the metaconid, as in *Wyonycteris* and *Nyctitherium* and occasionally *Plagioctenodon* (e.g., UW 9592), but not *Leptacodon*. The entoconid is tall and acute, higher than the hypoconid. The hypoconulid is joined to the hypoconid by a low hypocristid (called a postcristid by some authors), but it is closer to the entoconid than to the hypoconid, though not as close as in UW 10394 (the only specimen in the original hypodigm of *P. microlestes* that preserves molars); nevertheless, it is separated from the entoconid by a notch. This condition, which also characterizes both *Nyctitherium* and *Wyonycteris*, has been called nyctalodonty (Menu and Sigé, 1971; Gingerich, 1987), and is usually applied to bat molars. M_2 is similar to M_1 but the trigonid is more mesiodistally compressed, so the cusps form an isosceles triangle, the shortest side being lingual. M_2 appears to be slightly shorter than M_1, although neither jaw has both teeth complete. The molars are slightly exodaenodont and have deep hypoflexids. There is a low anterior cingulum but no buccal cingulum. The known cheek teeth incline slightly lingually.

Upper molars definitively referable to this species are not yet known, but diminutive dilambdodont nyctitheriid upper molars almost certainly attributable to *Plagioctenoides* have been found at the same locality as these lower jaws (see cf. *Plagioctenoides* sp., below).

Measurements (mm).— USNM 538093, P_4L=0.85, W=0.45, M_1L=1.10m W_a=0.70, W_p=0.75; dentary depth (labial below M_1)=0.90; 538094, P_4L=0.85, W=0.40, M_1 W_p=0.75, M_2L=1.10, W_a=0.70, W_p=0.75. Holotype (UW 9694) measures: P_3L=0.50, W=0.30; P_4L=0.80, W=0.50.

Discussion.— Although both Wa-0 specimens referred to *Plagioctenoides microlestes* contain only one tooth (P_4) in common with the holotype, which consists of a dentary with P_{3-4}, this tooth appears to be particularly important for distinguishing nyctithere species. The near identity in size and morphology with the holotype, which comes from slightly higher strata only about 25 km to the south, makes it highly probable that they represent the same species. *P. microlestes* is one of smallest Wasatchian mammals, with an estimated body mass of 3.7 g, based on the M_1 regression equation of Bloch et al. (1998). Among nyctitheres, it appears to be equaled in its small size only by *Leptacodon donkroni*, sp. nov., late Paleocene *Bayanulanius tenuis* Meng et al., 1998, from Mongolia, and late Tiffanian *Wyonycteris microtis* Secord, 2008, from North America. *P. microlestes* differs in molar structure from *L. donkroni*, as detailed above. It differs from *Bayanulanius* in having a much larger molar entoconid and in the nyctalodont condition of the talonid (evidently lacking from *Bayanulanius*). Comparable teeth of *W. microtis* and *P. microlestes* are not known, but their age difference supports their specific separation.

Plagioctenoides microlestes is remarkably similar to *Wyonycteris*, initially considered to be a chiropteran (Gingerich, 1987) and later an ?adapisoriculid (Smith, 1995; Hooker, 2010), but now usually regarded as a nyctitheriid (Gingerich and Smith, 2006; Secord, 2008; Beard and Dawson, 2009). Surprisingly, *Wyonycteris* has not previously been compared to *Plagioctenoides*. The type species, late Clarkforkian *W. chalix*, differs from *P. microlestes* in being at least 20% larger and having a relatively larger, more inflated P_4 trigonid and a smaller P_4 talonid. The cristid obliqua and entocristid are weaker than in *P. microlestes*, leaving the talonid unbasined. The trigonid cusps of a referred M_1 were described as forming an isosceles triangle (Gingerich, 1987), rather than an equilateral triangle as in the Wa-0 *P. microlestes*, but this distinction is not great. The molars of *W. chalix* are more exodaenodont than those of *P. microlestes*. In other respects, however, these specimens are nearly identical, including such features as the twinned metaconid, form of the cristid obliqua, and nyctalodont condition of the lower molars. Upper molars attributed to *W. chalix* are dilambdodont with well-developed mesostyles; they also have a small pericone and a weak hypocone. *W. richardi* Smith, 1995, from Dormaal, Belgium, is 10-15% larger than *P. microlestes*, and is almost identical in known features, including the shape of P_4. Like *W. chalix*, its upper molars are dilambdodont, with small pericones and hypocones. *W. richardi* appears to be very closely related to *P. microlestes*. *W. microtus* is weakly dilambdodont, and the pericone and hypocone are weak to absent. Tiffanian *W. galensis* Secord, 2008, has similar nyctalodont molars with strong oblique crests that rise to the metaconid, but the molar paraconids seem to be more acute than in *W. chalix* or *P. microlestes*, and the M_1 trigonid is more mesiodistally compressed. *W. primitivus* Beard and Dawson, 2009, from the Red Hot local fauna of Mississippi, differs from *P. microlestes* in being significantly larger (30-50% in comparable linear dimensions) and having a better developed talonid on P_4, lower molars with shallower hypoflexids and weaker oblique crests ascending to the metaconid, and upper molars with much weaker mesostyles. If all of these species are properly allocated to *Wyonycteris*, then the distinction between the latter and *Plagioctenoides* becomes moot, and *Plagioctenoides* would have priority as the valid generic name.

The Asian subfamily Asionyctiinae includes some of the smallest nyctitheres (e.g., *Bayanulanius*, noted above), some of which resemble *Plagioctenoides microlestes* in having the molar cristid obliqua extend to the apex of the metaconid (*Oedolius*, *Bayanulanius*). However, asionyctiines differ from *Plagioctenoides* in having an unbasined talonid on P_4 and lower molars with low entoconids, a relatively central hypoconulid, and lacking nyctalodonty (Russell and Dashzeveg, 1986; Meng et al., 1998; Missiaen and Smith, 2005). Where known, their upper molars are transversely wide and lack dilambdodonty.

Plagioctenoides tombowni, sp. nov.

Figure 23J-L, Q

Holotype.— USNM 538092, L dentary with P_4, M_{2-3}.

Hypodigm.— Holotype and USNM 540595 (LP_4).

Locality and Horizon.— WW-74 (SE¼ sec. 3, T 48 N, R 92 W, McDermott's Butte Quadrangle, Washakie County, Wyoming), lower Willwood Formation, earliest Eocene (Wa-0 biozone).

Etymology.— For Thomas M. Bown, in recognition of his

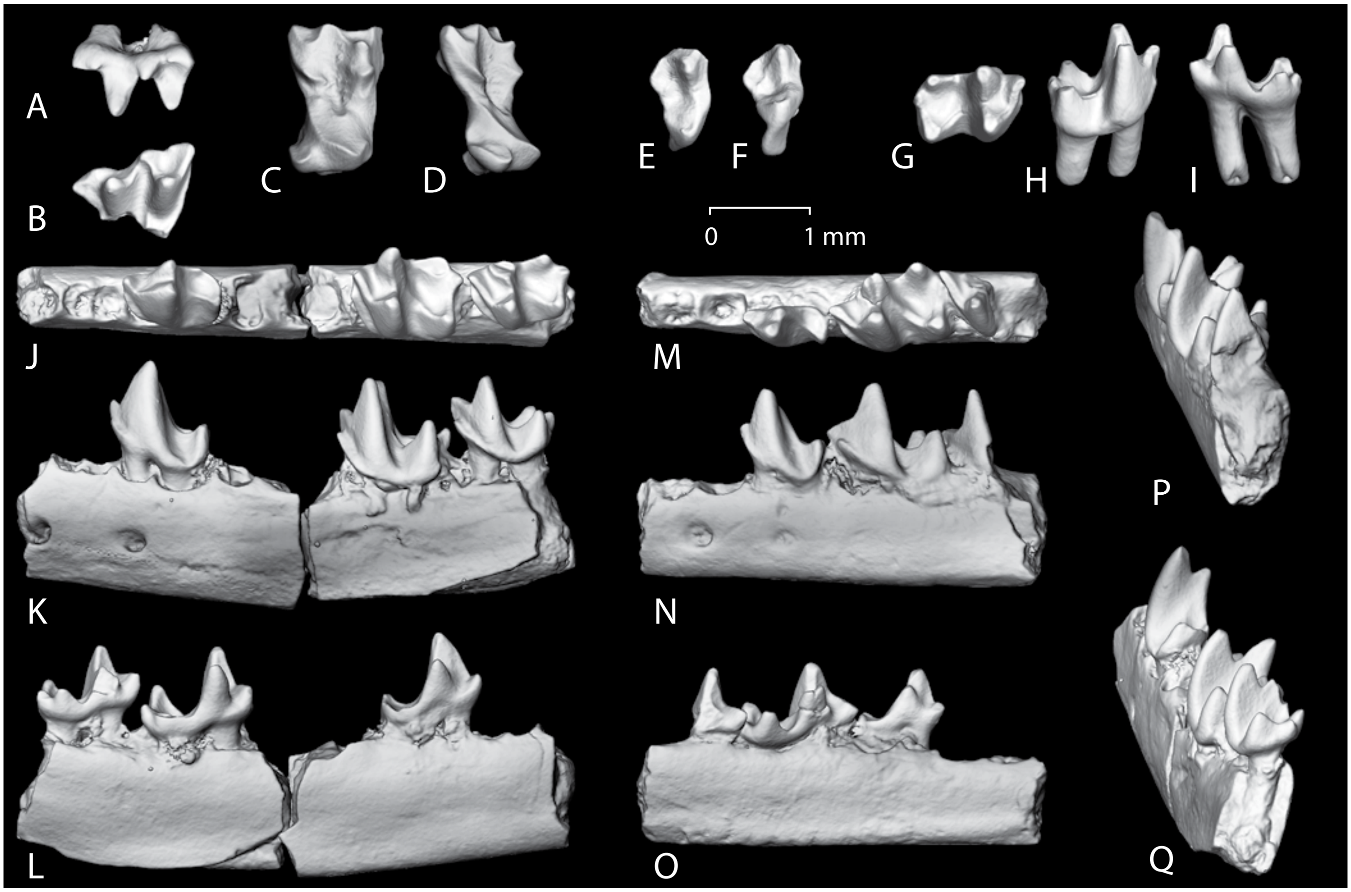


FIGURE 23 — *Plagioctenoides*. A-I, *Plagioctenoides* sp., USNM 540601: A-B, buccal part of LM^1in buccal and occlusal views; C-D, RM^2 in occlusal and posterior views; E-F, RM^3 in occlusal and oblique lingual views; G-I, RM_2 in occlusal, buccal, and lingual views. J-L, Q, *Plagioctenoides tombowni*, sp. nov., holotype, L dentary with P_4, M_{2-3}, USNM 538092, in occlusal, buccal, lingual, and oblique posterior views. M-P, *Plagioctenoides microlestes*, L dentary with P_4-M_1 and M_2 trigonid, USNM 538093, in occlusal, buccal, lingual, and oblique posterior views.

substantial contributions to the Willwood fauna in general and to fossil insectivores in particular.

Diagnosis.— Very small nyctithere; molars same size as in *P. microlestes* and with lingually shifted hypoconulid separated from entoconid by a notch, as in *P. microlestes* and *Wyonycteris chalix*. P_4 larger and relatively wider than in *P. microlestes*, with more distinct paraconid, larger metaconid situated medial to protoconid rather than posteromedial, and wider talonid basin with less oblique cristid obliqua. P_4 differing from that of *W. chalix* in having larger metaconid and wider talonid basin, differing from *W. primitivus* in being relatively shorter and narrower and about 30% smaller. Cristid obliqua on P_4 and molars less prominent on the postvallid than in both *P. microlestes* and *W. chalix*.

Description.— The holotype dentary contains three small, closely spaced alveoli in front of P_4, the more distal two (combined length=0.60) suggesting a two-rooted P_3, as in *Leptacodon rosei*, unlike the apparently single-rooted P_3 of *Plagioctenoides microlestes*. There are two mental foramina, one under P_4, the other under the third alveolus in front of P_4.

P_4 is larger than in *P. microlestes* and somewhat more molariform, with a more closed trigonid and a wider talonid basin. The metaconid is markedly more prominent than in *P. microlestes* (compare figure 23Q with figure 23P), and the cristid obliqua is more mesiodistally aligned, producing only a faint line to indicate its ascent on the postvallid toward the metaconid. The long axis of its talonid basin is more nearly mesiodistally oriented rather than oblique as in *P. microlestes*. The lingual wall of the talonid basin is higher and sharper than in *P. microlestes*, resulting in a better defined talonid basin. P_4 of *P. tombowni* is slightly shorter but distinctly narrower and more molarized than that of *Wyonycteris chalix*. The trigonid and talonid are almost equal in width, whereas in *W. chalix* the trigonid is wider than the talonid. The P_4 metaconid is larger than in *W. chalix* and the talonid is larger and clearly basined.

The molars are essentially identical to those in *P. microlestes*, except for having a weaker cristid obliqua. The metaconid of M_2 is slightly larger and taller than the protoconid, and is not twinned, in contrast to these features in M_1 in the only specimen of *P. microlestes* in which the metaconid is complete (the metaconid is broken on M_2 of USNM 538094). Whether these distinctions are real or simply reflect individual variation (or tooth locus) among the few known specimens should be reexamined when larger samples are known. The molars are slightly exodaenodont and show the same nyctalodont condition that characterizes *P. microlestes* and *Wyonycteris*.

Measurements (mm).— Holotype: P_4L=1.00, W=0.55, M_2L=1.10, W_a=0.75, W_p=0.70, M_3L=1.00, W_a=0.60, W_p=0.55; dentary depth (labial below M_1)=about 1.10. USNM 540595: P_4L=0.90, W=0.50.

Discussion.— *Plagioctenoides tombowni* is very similar to *P. microlestes*, differing principally in having a larger and more molarized P_4. These differences are comparable to those that distinguish other species of nyctitheriids (see discussion of *Wyonycteris* above).

Although it may seem unlikely that several similar-sized and dentally similar tiny insectivores would have coexisted in the same area during the PETM, present-day faunas suggest otherwise. Many extant shrew species—probably the closest living analogues for nyctitheres—have overlapping geographic ranges (e.g., Wilson and Ruff, 1999), and the number of coexisting soricid species in some central African habitats is particularly high (R. Hutterer, pers. comm.). Consequently it is plausible that several nyctithere species are present in the Sand Creek Divide fauna.

Plagioctenoides sp.

Figure 23A-I

Referred specimens.— WW-74: USNM nos. 538248 (L dentary with M_1), 538249 (isolated LM_2), 538250 (isolated R and LM^1 and three fragmentary upper molars), 538251 (isolated R and LM^2?), 538252 (isolated RM^2?), 540169 (L dentary with M_1, RM_1), 540601 (RM^1, RM^3, LM^x fragment, RM_1 or M_2), 541782 (LM_1 or M_2, M^x fragment), and tentatively USNM 541694 (LI_3 or I_1).

Description.— Several isolated teeth and fragmentary jaws are of appropriate size and morphology to belong to *Plagioctenoides* and must represent either *P. microlestes* or *P. tombowni*, but in the absence of direct association with P_4 they cannot be confidently assigned to species until differences between *P. microlestes* and *P. tombowni* are better understood. The lower molars assigned here are indistinguishable from those of *Plagioctenoides microlestes*, including having a low crestiform paraconid, a tall protoconid and slightly smaller metaconid (except USNM 538249, in which the metaconid is taller), a deep hypoflexid, a low cristid obliqua that rises part way up the trigonid wall toward the metaconid, an acute entoconid taller than the hypoconulid, and nyctalodonty. The crowns are slightly exodaenodont, and there is a low anterior cingulid but no ectocingulid. The upper molars assigned here are dilambdodont, with (where preserved) distinct mesostyle and less distinct parastyle, stylocone, and very small metastyle. The paracone is taller than the metacone, and the conules are very small with short pre- and post-conule cristae. The paraconule is more lingually situated than the metaconule. The hypocone is small but acute. A short anterolingual cingulum is variably present, but no pericone is developed.

Tentatively included here is an extremely small incisor (USNM 541694) with a bilobed crown and a very long, robust root almost three times as long as the crown height. The anterior lobe is much larger and taller, with a single cusp, from which a short, level crest extends mesially. Behind this cusp a crest descends almost vertically into a deep notch separating it from the much smaller and lower posterior cusp. The tooth is similar though not identical to I_3, and to a lesser extent I_1, of various nyctitheres, and its diminutive size is consistent with *Plagioctenoides*. It also resembles I_2 of *Oligoryctes* and might instead be an incisor of the very small parapternodontid from this local fauna (see below).

Measurements (mm).— USNM 538248, M_1L=1.10, W_a=0.70, W_p=0.75; USNM 538249, M_2L=1.05, W_a=0.80, W_p=0.70; USNM 538250, LM^1L=1.15, W=1.50, RM^1 damaged; USNM 538251, LM^2?L=0.90, W=1.30, RM^2?L=0.80, W=1.30; USNM 538252, RM^2?L=0.90, W=1.45; USNM 540169, RM_1L=1.20, W_a=0.80, W_p=0.85; LM_1L=1.20, W_a=0.80, W_p=0.80; USNM 540601, RM^1L=0.95, W=1.50, RM^3L=0.60, W=1.1 (est.), $RM_{1/2}$L=1.10, W_a=0.80, W_p=0.70; USNM 541694 (incisor), L=0.40, W=0.30, crown height=0.50; USNM 541782, $LM_{1/2}$L=1.15, W_a=0.70, W_p=0.80.

Discussion.— Lower molars in this sample could be tentatively assigned to either *Plagioctenoides microlestes* or *P. tombowni* based on cristid obliqua expression or metaconid height, but it seems more prudent to wait until these characters have been observed in more specimens with serially associated teeth. Apart from trivial differences (e.g., smaller size and weaker conules than in *W. chalix*), the upper molars described here are virtually indistinguishable from those of *Wyonycteris chalix* and *W. richardi*. They are more strongly dilambdodont than upper molars of *W. microtus* or *W. primitivus*.

This sample allows additional body mass estimates for *Plagioctenoides* (maximum of 5.8 g based on M_1 and 6.2 g based on M^1) based on the regression equations of Bloch et al. (1998).

Family PARAPTERNODONTIDAE Asher et al., 2002

PARAPTERNODUS Bown and Schankler, 1982

Cf. *Parapternodus* sp.

Figure 24

Referred specimens.— WW-74: USNM 533568 (incomplete R upper molar), USNM 540566 (RP^3).

Description.— Two very small isolated upper teeth are very similar in size and morphology to specimens (UM 81563 and 81558) referred to *Parapternodus antiquus* Bown and Schankler, 1982, by Asher et al. (2002), and at the same time are radically different from any other mammalian upper teeth from Sand Creek Divide. They also closely resemble their counterparts in the closely allied oligoryctid *Oligoryctes altitalonidus* (Asher et al., 2002: figure 46), known from the Uintan through Orellan NALMAs. The resemblances are sufficient to document the presence of Parapternodontidae at this locality. These teeth

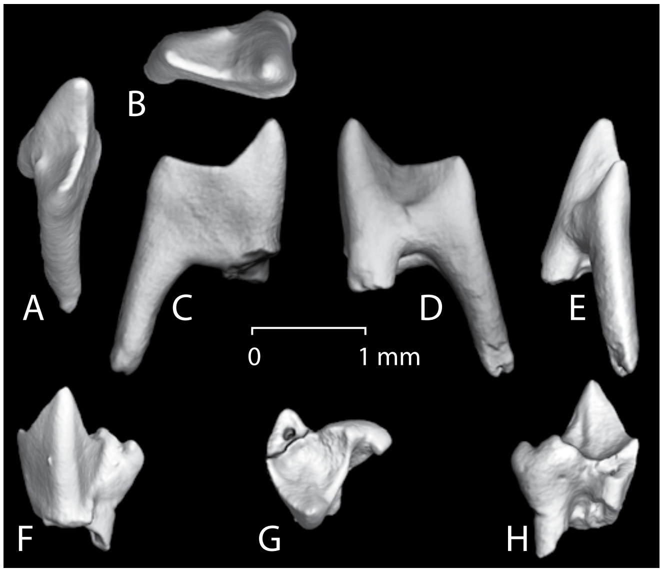


FIGURE 24 — Cf. *Parapternodus* sp.: A-E, RP^3, USNM 540566, in posterior oblique, occlusal, lingual, buccal, and posterior views; F-H, $RM^{1/2}$, USNM 533568, in lingual, occlusal, and buccal views.

represent one of the smallest mammals known from the PETM.

The fragmentary molar is characterized by a sharp V-shaped ectoloph whose vertex is a tall, sharp paracone. The tooth was therefore fully zalambdodont, although the crests of the ectoloph form a wider angle than that of the upper molars referred to *Parapternodus antiquus*. The anterior limb terminates buccally in a slightly raised stylocone, and a distinct, cuspate parastyle projects anterior to it. There is almost no indication of the basal precingulum that is well developed in UM 81563. The buccal side of the V-shaped ectoloph is deeply excavated. Although the posterobuccal margin is damaged, a deep ectoflexus can be inferred. The lingual margin of the tooth, which (based on UM 81563) would have had a small, low protocone, is missing. The isolated upper premolar, like the molar, is dominated by a tall, sharp paracone, but unlike the molar, the anterior surface of the paracone is nearly vertical and there is no preparacrista. No parastyle is present, in contrast to UM 81558, which has a small parastyle. The postparacrista extends to the posterobuccal margin of the tooth, forming a long, high shearing blade; it first descends steeply, then turns abruptly to form a level crest. The angle between the two parts of the crest (seen in profile, Figure 24C-D) is obtuse, rather than slightly acute as in UM 81558. In the latter specimen, a cusp (metastyle?) forms at the posterobuccal end of the postparacristid, but this cusp is not differentiated from the crest in USNM 540566. The buccal face of this crest is less deeply excavated than in UM 81558 and shows only a faint hint of the basal buccal cingulum seen in the latter.

Measurements (mm).— USNM 533568, L=1.10, W to base of paracone=1.05. Comparable measurements of UM 81563 (based on cast) are L=1.15, W to base of paracone=1.10, total W=1.65. USNM 540566, L=1.15, W=0.75. Comparable measurements of UM 81558 (based on cast) are L=1.25, W=0.90.

Discussion.— While it is difficult to gauge the significance of the minor differences outlined above, they suggest that the Sand Creek Divide teeth belong to a species different from *Parapternodus antiquus*. They might represent a new species, or could belong to the early Wasatchian parapternodontid *Koniaryctes paulus* Robinson and Kron, 1998, which was described from the Powder River Basin. Upper teeth of that taxon have not been reported. Yans et al. (2006) listed *P. antiquus* among mammals found by screen-washing at the Castle Gardens locality (UCMP locality V99019) in the southeastern Bighorn Basin.

Suborder ERINACEOMORPHA Gregory, 1910
Family AMPHILEMURIDAE Hill, 1953

MACROCRANION Weitzel, 1949

Macrocranion junnei Smith, Bloch, Strait, and Gingerich, 2002
Figures 25A-I, 26

Referred specimens.— WW-71: USNM 538297 (RM^2); WW-73: USNM 538310 (L dentary with P_4); WW-74: USNM nos. 538323 (RP^4, 3 isolated upper molars, 3 isolated lower molars), 540400 (isolated teeth: RM^1, RM^3, LM_3), 541795 (RM_1, LM_2, RM^2, LM^3), 542133 (RP_4), 542134 (RM^2); and tentatively USNM 540319 (L calcaneus), from WW-74.

Description.— The specimens assigned here (Figure 25A-I) are very similar to both *M. junnei* and *M. nitens*. They are slightly smaller than most specimens of *M. nitens* compared and within or very close to the size range previously reported for *M. junnei* (Figure 26; Strait, 2001; Smith et al., 2002). P_4 is similar to that of *M. nitens* from higher in the Willwood Formation: it widens posteriorly, has a moderately elongate and open trigonid, and a short, wide talonid consisting of a transverse ridge that is canted lingually (as is the whole tooth) so the lingual end is much higher. No discrete cusps are evident on the talonid ridge, which is demarcated from the trigonid by a transverse valley. The paraconid is very low, the metaconid larger and slightly higher and posterolingual to the protoconid, rather than directly lingual to it as in *M. nitens.* The more posterior position of the metaconid was considered a diagnostic trait of *M. junnei* (Strait, 2001; Smith et al., 2002). Lower molars referred here have wide talonid basins and are lingually canted and slightly exodaenodont, with the buccal side lower than the lingual side and high lingual cusps. M_1 is about 10% shorter and almost 20% narrower, on average, than a sample of *M. nitens* from higher in the Willwood Formation. This conforms well with Strait's (2001) larger sample of lower molars of *M. junnei*.

The upper teeth do not differ from the holotype in any significant way. P^4 is premolariform and lacks a metacone. A small parastyle is present anterior to the protocone; a poorly defined metastylar lobe connects to the paracone. The upper molars have paracones taller than metacones, and distinct hypocones. The parastylar and metastylar projections on M^{1-2} are demarcated by a moderate hypoflexus. M^2 is shorter than that of *M. nitens* but averages only slightly narrower. However, Strait's sample of M^2s has a much greater range of length, overlapping with that of *M. nitens*.

In their original description, Smith et al. (2002) clearly distinguished *M. junnei* from European *M. vandebroeki* but provided fewer distinguishing features from *M. nitens*, noting only that *M. junnei* "differs from later species of *Macrocranion* in having a deeper ectoflexus on the upper molars, a shorter M^2, and a more expanded parastylar lobe on M^3" (Smith et al., 2002: 375). They also noted that *M. junnei* has a narrower talonid on $M_{1\text{-}2}$. Our sample generally upholds these differences, but the deeper ectoflexus is accentuated by the shorter M^2 and is variable in our sample (the holotype has a particularly short and wide M^2); USNM 540400 (M^1) and 541795 (M^2) have a moderately deep ectoflexus, as in the holotype, whereas USNM 539481 and 538297 have a shallower ectoflexus indistinguishable from that of *M. nitens* (e.g., USNM 495248 from McNeil Quarry; Silcox and Rose, 2001).

Measurements (mm).— See Table 3.

Discussion.— *Macrocranion* is the most abundant small mammal from Castle Gardens (n=76) but is known from only a single definitive specimen from Polecat Bench (Strait, 2001; Smith et al., 2002) and possibly 2 isolated P^4s (Gingerich and Smith, 2006). While not rare in the Sand Creek Divide local fauna (n=18), *Macrocranion* is outnumbered by several other small mammal taxa, including *Mimoperadectes*, two primates (*Niptomomys* and *Teilhardina*), *Hyopsodus*, *Diacodexis*, and *Tuscahomys*. Its stratigraphic range at Sand Creek Divide is very limited (from ~10-14 m). Curiously, the prolific anthill locality at WW-84 produced no teeth of *Macrocranion* among hundreds of specimens. *Macrocranion nitens* has been shown to be a common constituent of micromammal accumulations higher in the Willwood Formation (Silcox and Rose, 2001). The close resemblance of these *Macrocranion* species suggests that *M. nitens* evolved anagenetically from *M. junnei*. Apart from size-sorting, the factors controlling the unusual distribution of *Macrocranion* during the early Eocene have yet to be determined.

cf. *Colpocherus* sp., probably new

Figure 25J-K

Referred specimens.— WW-74: USNM 521514 (R dentary with P_4-M_2); WW-75: USNM 521794 (R dentary with P_4); and tentatively, WW-74: USNM 539481 (isolated teeth: RM_1 or M_2, LM_1 or M_2); WW-75: USNM 521675 (isolated teeth: LM_1, 2 RM_1 or M_2).

Description.— Several specimens initially thought to represent *Macrocranion junnei* were found, on closer examination, to differ in some potentially significant features: P_4 is more molariform, with different proportions and a more basined talonid, and the lower molars are slightly narrower, with taller trigonids and higher protoconids and hypoconids. The lower molars are less lingually canted than in *Macrocranion*, hence buccal and lingual cusps are more nearly comparable in height. Although neither of the two P_4s is perfectly preserved, they are close enough in comparable details to be assigned to the same taxon and to allow description of P_4 morphology. In USNM 521514 the P_4 trigonid is moderately tall, dominated by the damaged protoconid, and is demarcated from the talonid lingually by a deep talonid notch. The paraconid is low and the metaconid much larger and higher and situated lingual to the protoconid. (The full extent of the metaconid is uncertain due to breakage, but it appears to have been prominent as in USNM 521794.) The postvallid is nearly vertical and is oriented almost transversely. The talonid is distinctly basined and about the same length and width as the trigonid. The hypoconid and entoconid are distinct, acute, and of equal height, and there is a small, centrally positioned hypoconulid. The cristid obliqua is low and slightly concave buccally, accentuating the hypoflexid; it meets the postvallid just lingual to the middle of the posterior trigonid wall, and ends near its base. The basin is closed lingually by a low entocristid. No cingula are evident. In USNM 521794 the paraconid of P_4 is even smaller and lower than in USNM 521514 and is situated near the mesial base of the crown. The hypoconid is distinct and acute; the entoconid is broken so its elevation cannot be ascertained, but it was probably similar to that in USNM 521514. A faint hint of a hypoconulid is present. In other respects it resembles P_4 in USNM 521514. The dentary of USNM 521794 has a large mental foramen below the middle of P_4.

Measurements (mm).— See Table 3.

Discussion.— The specimens considered under this heading have molars quite similar in size and morphology to those of *Macrocranion junnei* and were initially thought to represent that species. They differ in some subtle ways, however, and together with the more obvious contrasts in P_4 morphology, they suggest the presence of a second amphilemurid closely allied with *M. junnei*. Nevertheless, larger samples, and particularly, more complete specimens, are needed to detail the extent of variation in Wa-0 amphilemurids and to verify that two amphilemurids coexisted during the PETM.

P_4 differs from that of *Macrocranion* in ways that resemble P_4 of the recently described *Colpocherus mississippiensis* Beard and Dawson, 2009, from the Red Hot Local Fauna, Tuscahoma Formation of Mississippi. In particular, the basined talonid, stronger metaconid, and greatly reduced paraconid are similarities to *Colpocherus*. However, the premolar proportions in the Sand Creek Divide specimens differ from those in both *Macrocranion* and *C. mississippiensis*, and the lower molars differ from *Macrocranion* in features that are no closer to *C. mississippiensis*. Based on a single M_2 and a trigonid of M_1, lower molars of *C. mississippiensis* appear to be more bunodont and to have less lingual paraconids (Beard and Dawson, 2009) than either *Macrocranion* or the sample here referred to cf. *Colpocherus* sp.

Whether these specimens represent a new species of *Colpocherus* or *Macrocranion*, or could be variants of *M. junnei*, is difficult to ascertain based on present samples. The differences in P_4 morphology between these teeth and those of *M. junnei*, however, seem too great to be accommodated in a single species; and we have recognized this by assigning them to a different taxon.

A P_4 (UCMP 212662) referred to *Plagioctenodon savagei* by Strait (2001) closely resembles the P_4 in the two Sand Creek Divide specimens and may represent the same taxon. If the

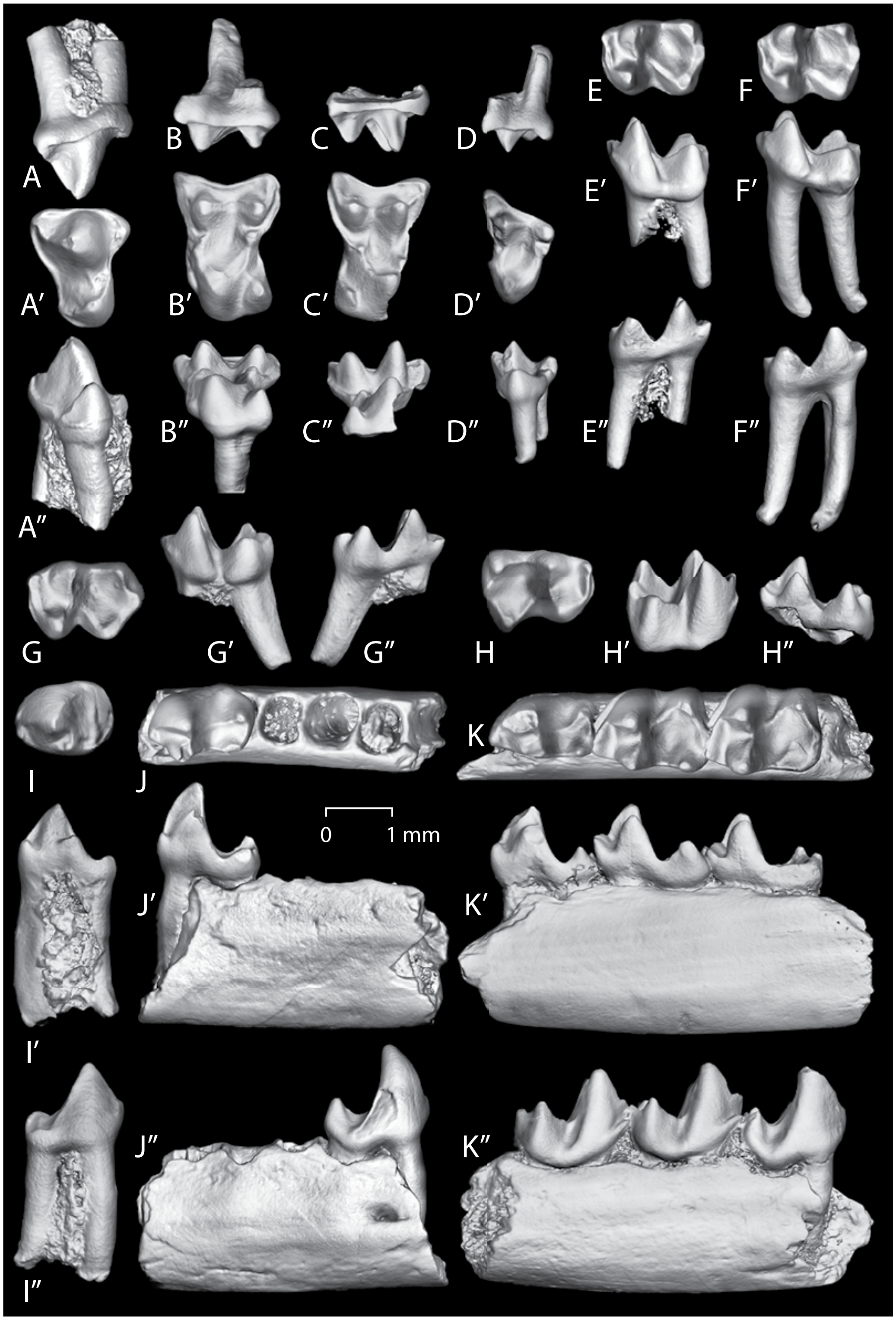


FIGURE 25 — Amphilemurids: A-I, *Macrocranion junnei*: A–A", RP^4, USNM 538323; B–B", LM^1, USNM 538323; C–C", RM^2, USNM 541795; D–D", LM^3, USNM 541795; A-D in buccal, occlusal, and lingual views. E–E", LM_1, USNM 538323; F–F", LM_2, USNM 538323; G–G", LM_2, USNM 541795; H–H", RM_1, USNM 541795; E-H in occlusal, buccal, and lingual views. I-I", RP_4, USNM 542133, in occlusal, lingual, and buccal views. J-K, cf. *Colpocherus* sp.: J-J", R dentary with P_4, USNM 521794; K-K", R dentary with P_4-M_2, USNM 521514; J-K in occlusal, lingual, and buccal views.

TABLE 3 — Measurements (mm) of amphilemurids from Sand Creek Divide (* = estimated).

Specimen	P^4L	P^4W	M^1L	M^1W	M^2L	M^2W	M^3L	M^3W	P_4L	P_4W	M_1L	M_1W_a	M_1W_p	M_2L	M_2W_a	M_2W_p	M_3L	M_3W
Macrocranion junnei																		
USNM 538297	—	—	—	—	1.50	2.05	—	—	—	—	—	—	—	—	—	—	—	—
USNM 538310	—	—	—	—	—	—	—	—	1.50	1.00	—	—	—	—	—	—	—	—
USNM 538323	1.50	1.75	1.3*	2.0*	1.60	2.25	—	—	—	—	1.55	1.25	1.10	1.50	1.20	1.15	—	—
USNM 538323	—	—	—	—	—	—	—	—	—	—	1.60	1.15	1.20	—	—	—	—	—
USNM 540400	—	—	1.65	2.05	—	—	1.00	1.60	—	—	—	—	—	—	—	—	1.70	1.05
USNM 541795	—	—	—	—	1.55	2.25	1.10	1.45	—	—	1.70	1.00	1.20	1.50	1.20	1.10	—	—
USNM 542133	—	—	—	—	—	—	—	—	1.50	1.05	—	—	—	—	—	—	—	—
USNM 542134	—	—	—	—	1.45	1.95	—	—	—	—	—	—	—	—	—	—	—	—
N	1	1	2	2	4	4	2	2	2	2	3	3	3	2	2	2	1	1
Mean	1.50	1.75	1.48	2.03	1.53	2.12	1.05	1.52	1.50	1.25	1.62	1.13	1.17	1.50	1.20	1.12	1.70	1.05
Std. deviation	—	—	—	—	0.07	0.15	—	—	—	—	0.08	0.13	0.06	—	—	—	—	—
Std. error	—	—	—	—	0.03	0.08	—	—	—	—	0.04	0.07	0.03	—	—	—	—	—
Minimum	—	—	1.3*	2.0*	1.45	1.95	1.00	1.45	1.50	1.00	1.55	1.00	1.10	1.50	1.20	1.10	—	—
Maximum	—	—	1.65	2.05	1.60	2.25	1.10	1.60	1.50	1.05	1.70	1.25	1.20	1.50	1.20	1.15	—	—
cf. *Colpocherus* sp.																		
USNM 521514	—	—	—	—	—	—	—	—	1.55	0.95	1.70	1.20	1.30	1.70	1.35	1.25	—	—
USNM 521675R	—	—	—	—	—	—	—	—	—	—	1.70	1.10	1.20	—	—	—	—	—
USNM 521675R	—	—	—	—	—	—	—	—	—	—	1.75	1.20	1.25	—	—	—	—	—
USNM 521675L	—	—	—	—	—	—	—	—	—	—	1.70	1.15	1.20	—	—	—	—	—
USNM 521794	—	—	—	—	—	—	—	—	1.65	1.00	—	—	—	—	—	—	—	—
USNM 539481	—	—	—	—	—	—	—	—	—	—	1.50	1.00	1.10	—	—	—	—	—
USNM 539481	—	—	—	—	—	—	—	—	—	—	1.65	1.15	1.15	—	—	—	—	—
N	—	—	—	—	—	—	—	—	2	2	6	6	6	1	1	1	—	—
Mean	—	—	—	—	—	—	—	—	1.60	0.98	1.67	1.13	1.20	1.70	1.35	1.25	—	—
Std. deviation	—	—	—	—	—	—	—	—	—	—	0.09	0.08	0.07	—	—	—	—	—
Std. error	—	—	—	—	—	—	—	—	—	—	0.04	0.03	0.03	—	—	—	—	—
Minimum	—	—	—	—	—	—	—	—	1.55	0.95	1.50	1.00	1.10	—	—	—	—	—
Maximum	—	—	—	—	—	—	—	—	1.65	1.00	1.75	1.20	1.30	—	—	—	—	—

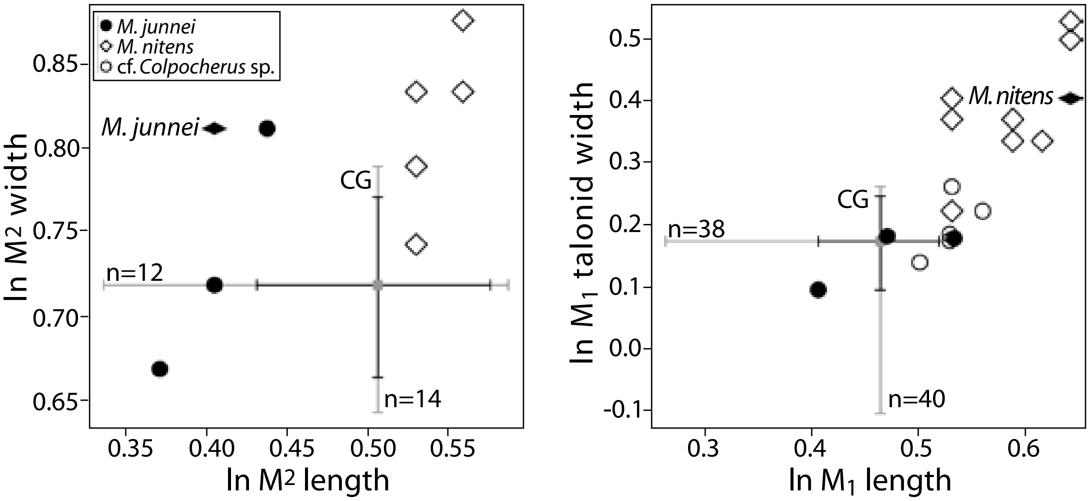


FIGURE 26 — Size distribution of M^2 and M_1 in *Macrocranion junnei*, *M. nitens*, and cf. *Colpocherus* sp. Black circles show Sand Creek Divide *Macrocranion*; open circles are cf. *Colpocherus*. Lines indicate range (gray) and one standard deviation from the mean (black) for Strait's (2001) samples of M^2s and undifferentiated M_1s and M_2s of *M. junnei* from Castle Gardens; means are indicated by gray squares. Open diamonds are *M. nitens* from USGS-USNM Willwood collection. Black diamonds indicate holotypes of *M. junnei* and *M. nitens*.

presence of two different amphilemurids is upheld by further study, the Castle Gardens sample of *Macrocranion junnei* should be reexamined to determine if it contains more than one species.

Order PRIMATES Linnaeus, 1758

With eight primate species representing four families, the Sand Creek Divide local fauna has the most diverse known Wa-0 primate assemblage. Five plesiadapiforms and three euprimates are present.

Family PAROMOMYIDAE Simpson, 1940

IGNACIUS Matthew and Granger, 1921

Ignacius graybullianus Bown and Rose, 1976
Figure 27A-C

Referred specimen.— WW-97S: USNM 538360 (LM_2).

Description.— A single lower molar (L=2.50 mm, W_a=1.90 mm, W_p=2.00 mm) records the presence of *Ignacius* during the PETM. The tooth is similar in size and morphology to specimens of this species from Clarkforkian and post-PETM early Wasatchian strata; there is no evidence of phyletic dwarfing. It has the rectangular outline and low relief characteristic of this species. The trigonid is low and mesially canted, resulting in a shallow, obtuse-angled talonid notch, in contrast to the right-angled or acute-angled notch seen in M_2 of *Phenacolemur*.

Discussion.— This is the first record of *Ignacius* from the PETM. The measurements of the single known specimen are close to the mean for *I. graybullianus* published by Silcox et al. (2008).

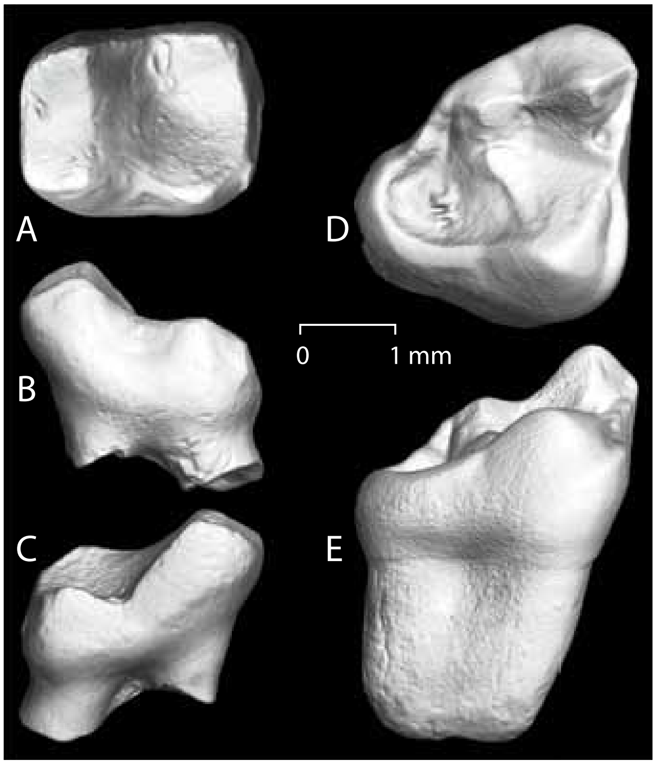


FIGURE 27 — Paromomyids: A-C, *Ignacius graybullianus*, LM_2, USNM 538360, in occlusal, buccal, and lingual views. D-E, *Phenacolemur praecox*, RM^3, USNM 538359, in occlusal and lingual views.

PHENACOLEMUR Matthew, 1915

Phenacolemur praecox Matthew, 1915
Figure 27D-E

Referred specimen.— WW-101: USNM 538359 (RM^3).

Description.— An isolated upper third molar (L=2.90 mm, W=2.70 mm) from near the top of the Wa-0 interval indicates that *Phenacolemur praecox* was present at least by the end of the PETM. Like its relative *Ignacius graybullianus*, *P. praecox* is the same size as representatives of this species from older and younger beds. The tooth shows the expanded posterior lobe typical of M^3 in paromomyids, and the relatively well-defined cusps, distinct metalophid, straight centrocrista, and excavated posterior lobe distinguish it from M^3 of *Ignacius*.

Discussion.— *Phenacolemur* remains very rare during Wa-0. Only three very fragmentary specimens of *P. praecox* have been reported from the Wa-0 interval at Polecat Bench (Gingerich, 1989; Gingerich and Smith, 2006). The species has not been reported from Castle Gardens. Measurements of the single M^3 from Sand Creek Divide match the mean measurements for *P. praecox* provided by Silcox et al. (2008).

Family MICROSYOPIDAE Osborn, 1892

ARCTODONTOMYS Gunnell, 1985

Arctodontomys wilsoni (Szalay, 1969)
Figure 28

Referred specimens.— WW-77: USNM 521525 (edentulous L dentary, questionably referred); WW-84: USNM nos. 538079 (R and L I$_1$), 538255 (RM^3, RM$_3$), 538355 (LP$_4$); WW-86: USNM 538354 (LP^4); WW-125: USNM 533569 (LM$_1$).

Description.— The two isolated lower incisors are about the same size as that in UM 80851 (*Arctodontomys*, cf. *A. wilsoni*; Gunnell, 1989: figure 32) and show the characteristic microsyopid lanceolate shape. The P$_4$ is virtually identical in size and morphology to that in *A. wilsoni*, UM 68321 (Gunnell, 1985), and approximates the mean dimensions of Bown's (1979) sample from the early Wasatchian of the No Water Creek area, southern Bighorn Basin. The trigonid consists of a tall protoconid and weak paracristid, without distinct paraconid or metaconid cusps. A small hypoconid and low peripheral crests define a shallow talonid basin, as in *A. wilsoni* but unlike Clarkforkian *A. simplicidens*. The other teeth, however, are slightly smaller to as much as 20% smaller in linear dimensions than the means for Gunnell's (1985) early Wasatchian sample of *A. wilsoni* from the Clark's Fork Basin. They more closely approximate dimensions in Bown's (1979) sample. Except in size, however, they are essentially identical to *A. wilsoni*. P^4 is relatively simple, with a large paracone, very small and low metacone, and moderate-sized, anteriorly placed protocone; there is no hypocone. The lower molars have reduced and buccally shifted paraconids, and large, lingually shifted hypoconulids set off from adjacent cusps by shallow notches.

Measurements (mm).— USNM 533569, LM$_1$L=2.75, W$_a$=1.90, W$_p$=2.00; USNM 538255, RM^{3}L=2.25, W=2.50; RM$_3$L=2.50, W$_a$=1.30, W$_p$=1.40; USNM 538354, LP^{4}L=2.20, W=2.95; USNM 538355, LP$_4$L=2.75, W=1.70.

Discussion.— *Arctodontomys wilsoni* was previously known during Wa-0 from a single isolated M$_1$ from Polecat Bench (Gingerich, 1989) and was not reported from Castle Gardens. We interpret the small sample reported here to confirm that *A. wilsoni* was present during this interval and that it was, on average, somewhat smaller than during Wa-1 and 2.

NIPTOMOMYS McKenna, 1960

Niptomomys, cf. *N. doreenae* McKenna, 1960
Figures 29-31

Referred specimens.— WW-74: USNM nos. 533573 (RM$_2$), 533574 (LM^1, RI$_1$), 533575 (RM^1, LM^2, LM^3, 2 fragmentary RI$_1$, RM$_2$), 533576 (LM^3), 533616 (R maxilla with M^2), 538358 (LM^3), 540318 (RM$_3$), 540344 (RM^2?), 540348 (RM^2 and molar fragment), 540399 (L maxilla with M^2, RM$_2$), 540568 (LI$_1$, LI$_1$ fragment), 540596 (isolated teeth: LM$_1$, LM$_2$, RM$_2$, RM$_3$, RM^2, LM^1 or M^2, incomplete LM^1), 541779 (LM$_1$, LM$_2$), 541780 (RM$_2$?, RM^1), 541794 (RM^1), 541909 (RM^1, LM^2), and questionably 533577 (LP$_4$), 541781 (LP$_4$); WW-84: 538081 (RM$_1$).

Description.— Nearly all of these specimens are isolated teeth (Figure 29) recovered by screen-washing in a single bed at WW-74. Most are slightly smaller, especially narrower, than the holotype and referred samples of the uintasoricine *Niptomomys doreenae* from the early Wasatchian of the Four Mile area, Colorado (McKenna, 1960; Szalay, 1969), and the No Water Creek area of the southern Bighorn Basin (Bown, 1979; see Figures 30-31 and Table 4 herein). In most other respects they closely resemble *Niptomomys* from those samples.

The upper molars are less transverse and more squared lingually than most previously described specimens of *N. doreenae*. The main cusps of the upper molars are peripheral, resulting in a large trigon basin, narrow stylar shelf, and short lingual protocone face. M^{1}s and M^{2}s have pre- and postcingula, the latter more prominent and terminating lingually in a tiny hypocone (Figure 29F) or hypoconal swelling, as in the Four Mile specimens (e.g., UCMP 44038, 47106) and Bighorn Basin samples of *N. doreenae* (Bown, 1979). The conules are situated closer to the paracone and metacone than to the protocone in about half the upper molars (Figure 29B, D), as observed by McKenna (1960) in the original description, but they are more centrally positioned in the others (Figure 29F).

The lower molars have short trigonids, narrower than the talonids, and expansive talonid basins with lingually shifted hypoconulids, characteristics of *Niptomomys*. As in the upper molars, the cusps are peripherally situated. The trigonids are longer than in the holotype of *N. doreenae*, however, often bearing small but distinct paraconids, in contrast to the holotype but not unlike many other specimens that have been referred to *N. doreenae*. Although Szalay (1969) discussed variation in the Four Mile and Bighorn Basin samples of *N. doreenae*, he did

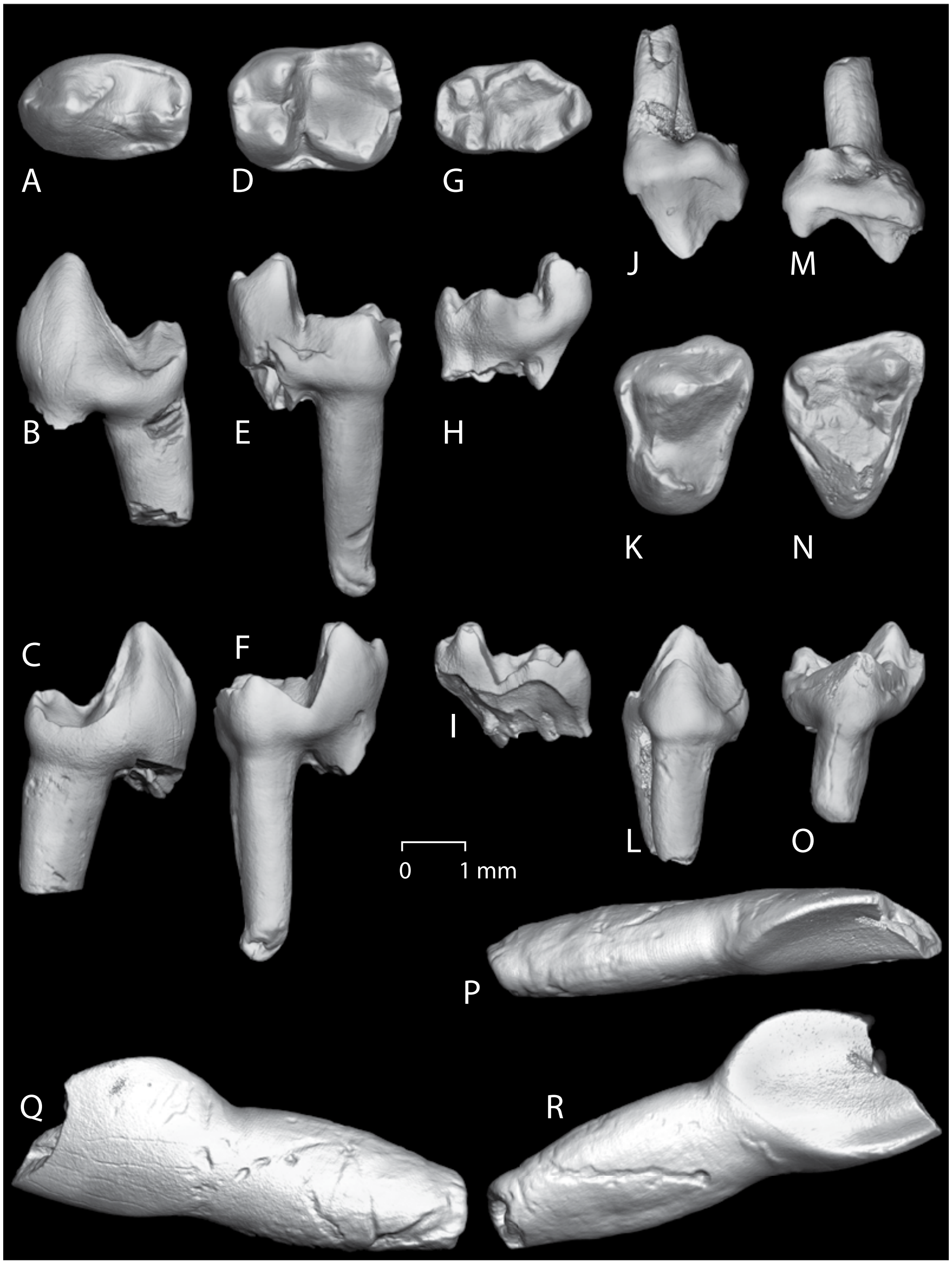


FIGURE 28 — *Arctodontomys wilsoni*, isolated teeth: A-C, LP_4, USNM 538355, in occlusal, buccal, and lingual views; D-F, LM_1, USNM 533569, in occlusal, buccal, and lingual views; G-I, RM_3, USNM 538255, in occlusal, lingual, and buccal views; J-L, LP^4, USNM 538354, in buccal, occlusal, and lingual views; M-O, RM^3, USNM 538255, in buccal, occlusal, and lingual views; P-R, LI_1 USNM 538079, in dorsal, lateral, and medial views.

not mention the rather variable condition of the molar trigonids. Bown (1979: 70) described the paraconid as "distinct on M_1… absent or connate with the metaconid [on M_2]." In the Sand Creek Divide sample the paraconid is variably present on all three lower molars and, when present, is noticeably buccal to the metaconid.

The isolated lower incisors in the Sand Creek Divide sample are lanceolate with a sharp dorsal margin (Figure 29X-

TABLE 4 — Measurements (mm) of *Niptomomys*, cf. *N. doreenae*, from Sand Creek Divide (SCD) and *Niptomomys* from other early Eocene localities.

Specimen	M^1L	M^1W	M^2L	M^2W	M^3L	M^3W	P_4L	P_4W	M_1L	M_1W_p	M_2L	M_2W_p	M_3L	M_3W_p
N. doreenae (SCD Wa-0)														
USNM 533573	—	—	—	—	—	—	—	—	—	—	1.15	0.85	—	—
USNM 533574	1.10	1.40	—	—	—	—	—	—	—	—	—	—	—	—
USNM 533575	1.10	1.40	1.10	1.40	0.80	1.00	—	—	—	—	1.20	0.90	—	—
USNM 533576	—	—	—	—	0.70	1.00	—	—	—	—	—	—	—	—
USNM 533577	—	—	—	—	—	—	1.20	0.75	—	—	—	—	—	—
USNM 533616	—	—	1.05	1.30	—	—	—	—	—	—	—	—	—	—
USNM 538081	—	—	—	—	—	—	—	—	1.25	1.00	—	—	—	—
USNM 538358	—	—	—	—	0.85	1.00	—	—	—	—	—	—	—	—
USNM 540318	—	—	—	—	—	—	—	—	—	—	—	—	1.10	0.70
USNM 540344	—	—	1.00	1.45	—	—	—	—	—	—	—	—	—	—
USNM 540348	—	—	1.00	1.35	—	—	—	—	—	—	—	—	—	—
USNM 540399	—	—	1.00	1.40	—	—	—	—	—	—	1.10	0.90	—	—
USNM 540596 R	—	—	0.90	1.30	—	—	—	—	—	—	1.10	0.95	1.10	0.75
USNM 540596 L	1.05	1.40	—	—	—	—	—	—	1.10	0.85	1.15	0.85	—	—
USNM 541779	—	—	—	—	—	—	—	—	1.20	0.85	1.10	0.85	—	—
USNM 541780	0.90	1.15	—	—	—	—	—	—	—	—	1.10	0.80	—	—
USNM 541781	—	—	—	—	—	—	1.20	0.85	—	—	—	—	—	—
USNM 541794	1.15	1.50	—	—	—	—	—	—	—	—	—	—	—	—
USNM 541909	1.10	1.30	—	—	—	—	—	—	—	—	—	—	—	—
N	6	6	6	6	3	3	2	2	3	3	7	7	2	2
Mean	1.07	1.36	1.01	1.37	0.78	1.00	1.20	0.80	1.18	0.90	1.13	0.87	1.10	0.73
Std. Deviation	0.09	0.12	0.07	0.06	0.08	—	—	—	0.08	0.09	0.04	0.05	—	—
Std. Error	0.04	0.05	0.03	0.02	0.04	—	—	—	0.04	0.05	0.01	0.02	—	—
Minimum	0.90	1.15	0.90	1.30	0.70	—	1.20	0.75	1.10	0.85	1.10	0.80	1.10	0.70
Maximum	1.15	1.50	1.10	1.45	0.85	—	1.20	0.85	1.25	1.00	1.20	0.95	1.10	0.75
N. doreenae (Four Mile)														
UCMP 44038	1.25	1.70	—	—	—	—	—	—	—	—	—	—	—	—
UCMP 44080	—	—	—	—	—	—	—	—	—	—	1.40	1.20	—	—
UCMP 44081 (holotype)	—	—	—	—	—	—	—	—	—	—	1.30	1.20	1.50	1.10
UCMP 44082	—	—	—	—	—	—	—	—	1.25	1.00	1.25	1.05	—	—
UCMP 46978	—	—	—	—	—	—	—	—	1.25	0.95	—	—	—	—
UCMP 47106	—	—	1.40	1.80	—	—	—	—	—	—	—	—	—	—
N	1	1	1	1	—	—	—	—	2	2	3	3	1	1
Mean	1.25	1.70	1.40	1.80	—	—	—	—	1.25	0.98	1.32	1.15	1.50	1.10
Std. Deviation	—	—	—	—	—	—	—	—	—	—	0.08	0.09	—	—
Std. Error	—	—	—	—	—	—	—	—	—	—	0.04	0.05	—	—
Minimum	—	—	—	—	—	—	—	—	1.25	0.95	1.25	1.05	—	—
Maximum	—	—	—	—	—	—	—	—	1.25	1.00	1.40	1.20	—	—

Y), features diagnostic of microsyopid incisors. They closely resemble I_1 in *N. doreenae* (USGS 6672) from D-1460 (Rose Quarry), much higher in the section. They are also similar to I_1 of *Niptomomys thelmae* (Bown and Gingerich, 1972; Gunnell and Gingerich, 1981) except for being smaller and more slender and having a gently concave rather than even superior margin.

Two P_4s from WW-74 (USNM 533577 and 541781; Figure 29R-W) are more similar to that of *Niptomomys* than to any other taxon from Sand Creek Divide and are tentatively included here. As in other *Niptomomys* specimens, there is no distinct paraconid, but the metaconid is prominent and situated lingual and slightly posterior to the protoconid. Although close in size and proportions to Szalay's (1969) and Bown's (1979) samples of *N. doreenae*, these specimens are narrower than Bighorn

TABLE 4 — Measurements (mm) of *Niptomomys*, cf. *N. doreenae*, from Sand Creek Divide (SCD) and *Niptomomys* from other early Eocene localities (cont.).

Specimen	M^1L	M^1W	M^2L	M^2W	M^3L	M^3W	P_4L	P_4W	M_1L	M_1W_p	M_2L	M_2W_p	M_3L	M_3W_p
N. doreenae (Bighorn Basin Wa-1/2)														
USGS 10520	—	—	—	—	—	—	1.20	0.90	1.30	1.05	1.20	1.00	1.20	0.80
USGS 25496	—	—	—	—	—	—	1.25	0.95	1.35	1.15	1.20	1.00	1.25	0.85
USGS 26547	—	—	—	—	—	—	1.30	0.95	1.30	1.05	1.20	1.00	—	—
USGS 9306	—	—	—	—	—	—	1.30	1.05	1.40	1.25	1.35	1.20	—	—
USNM 539495	—	—	—	—	—	—	1.20	0.85	1.30	1.10	1.35	1.10	—	—
UW 6898	1.20	1.65	1.15	1.60	0.90	1.25	—	—	—	—	—	—	—	—
UW 7125	—	—	—	—	—	—	1.30	0.90	1.30	1.15	1.25	1.15	—	—
N	1	1	1	1	1	1	6	6	6	6	6	6	2	2
Mean	1.20	1.65	1.15	1.60	0.90	1.25	1.26	0.93	1.33	1.13	1.26	1.08	1.23	0.83
Std. Deviation	—	—	—	—	—	—	0.05	0.07	0.04	0.08	0.07	0.09	—	—
Std. Error	—	—	—	—	—	—	0.02	0.03	0.02	0.03	0.03	0.04	—	—
Minimum	—	—	—	—	—	—	1.20	0.85	1.30	1.05	1.20	1.00	1.20	0.80
Maximum	—	—	—	—	—	—	1.30	1.05	1.40	1.25	1.35	1.20	1.25	0.85
N. thelmae														
AMNH 16829 (Was)	—	—	—	—	—	—	1.55	1.05	1.50	1.25	—	—	—	—
USGS 21867 (Wa-6)	—	—	—	—	—	—	—	—	1.55	1.30	1.40	1.25	1.60	1.10
USGS 26560 (Wa-6)	—	—	—	—	—	—	1.50	1.10	1.50	1.25	1.40	1.30	—	—
USGS 38066 (Wa-4-5)	—	—	—	—	—	—	—	—	—	—	1.75	1.35	—	—
YPM 27577 (holotype, Wa-6)	—	—	—	—	—	—	1.50	1.15	1.40	1.25	—	—	—	—
N	—	—	—	—	—	—	3	3	4	4	3	3	1	1
Mean	—	—	—	—	—	—	1.52	1.10	1.49	1.26	1.52	1.30	1.60	1.10
Std. Deviation	—	—	—	—	—	—	0.03	0.05	0.06	0.03	0.20	0.05	—	—
Std. Error	—	—	—	—	—	—	0.02	0.03	0.03	0.01	0.12	0.03	—	—
Minimum	—	—	—	—	—	—	1.50	1.05	1.40	1.25	1.40	1.25	—	—
Maximum	—	—	—	—	—	—	1.55	1.15	1.55	1.30	1.75	1.35	—	—
N. favorum (Castle Gardens)														
UCMP 212635 (holotype, Wa-0)	0.70	0.80	—	—	—	—	—	—	—	—	—	—	—	—

Basin *N. doreenae* measured in this study (Figure 30). They further differ from other P_4s referred to *Niptomomys* in having a slightly higher metaconid, a better developed talonid with distinct hypoconid and entoconid, and a low but well-defined cristid obliqua that continues part way up the postvallid. In the better preserved specimen (USNM 541781) the cristid obliqua closes a shallow talonid basin buccally (Figure 29R), whereas in *N. doreenae* a deep transverse valley, uninterrupted by the cristid obliqua, typically separates the talonid from the trigonid.

Measurements (mm).— For cheek teeth, see Table 4. Incisor dimensions: USNM 533574, crown L=2.4 (approximate), minimum B=0.60, proximal D=1.20; USNM 533575, minimum B=0.60, proximal D=1.10 (same for both fragments); USNM 540568, crown L=2.1, minimum B=0.60, proximal D=1.20.

Discussion.— *Niptomomys* is moderately common at WW-74 but is rare at other Wa-0 localities at Sand Creek Divide and elsewhere. Only two specimens of *Niptomomys*, an edentulous jaw and an isolated molar assigned to *N. doreenae*, are recorded from Wa-0 and Wa-M, respectively, at Polecat Bench (Gingerich, 1989; Gingerich and Smith, 2006). A single upper molar, which was assigned to a new species, *N. favorum* Strait, 2001, is the only representative of *Niptomomys* known from Wa-0 at Castle

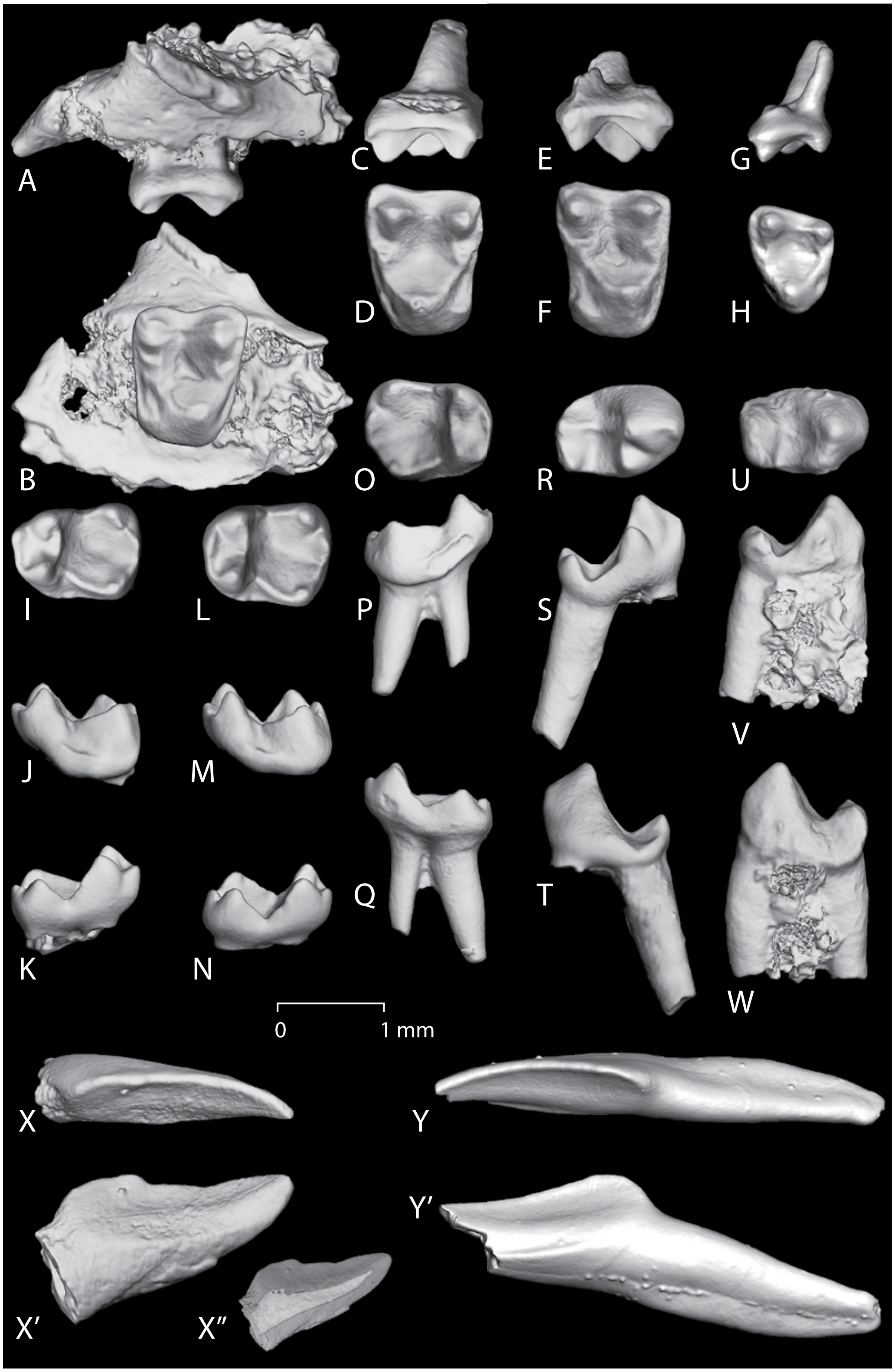


FIGURE 29 — *Niptomomys*, cf. *N. doreenae*. A-H, upper teeth in buccal and occlusal views: A-B, R maxilla with M^2, USNM 533616; C-D, LM^2, USNM 533575; E-F, RM^1, USNM 533575; G-H, LM^3, USNM 533575; I-K, LM_1, L-N, LM_2, both USNM 541779, in occlusal, buccal, and lingual views; O-Q, RM_2, USNM 533575, in occlusal, buccal, and lingual views; R-T, LP_4, USNM 541781, in occlusal, lingual, and buccal views; U-W, LP_4, USNM 533577, in occlusal, lingual, and buccal views; X-X´, LI_1, USNM 540568, in dorsal and medial views, X” is the same as X´(reduced), showing pulp cavity (lighter); Y-Y´, RI_1, USNM 533574, in dorsal and medial views.

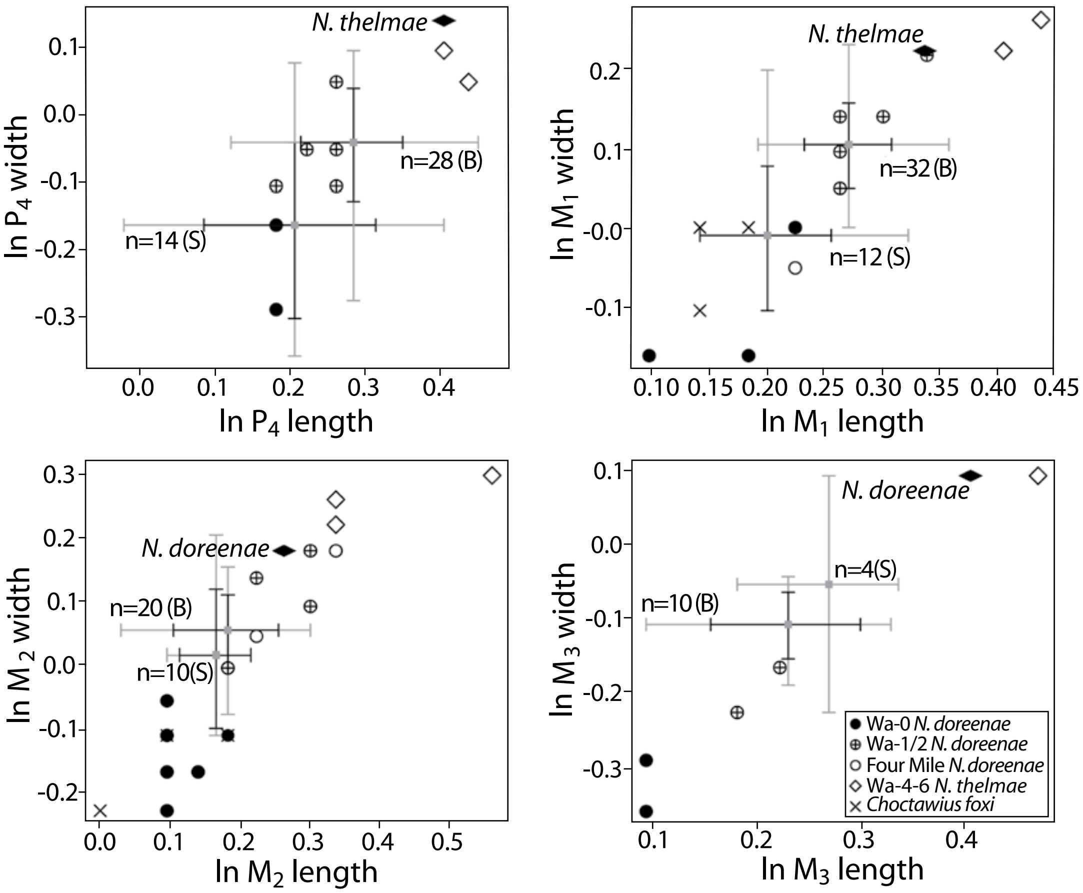


FIGURE 30 — Size distribution of *Niptomomys* lower cheek teeth. Points are individual specimens as indicated. Gray and black lines indicate observed range and one standard deviation from the mean (gray squares) of the predominantly Four Mile sample of *N. doreenae* reported by Szalay (1969), indicated by (S), and the early Wasatchian sample from the Willwood Formation reported by Bown (1979), indicated by (B). Note that our measurements of one Four Mile M_2 included in Szalay's sample are larger than Szalay's.

Gardens. Despite the similarity of most specimens in our sample to *N. doreenae*, the minor differences in size and morphology suggest that the Sand Creek Divide specimens may belong to a different though closely allied species. However, we prefer this more conservative allocation, pending more complete material that enables the sample to be unambiguously distinguished from *N. doreenae*. In addition, a more complete specimen than any now available would be preferable as a holotype, in view of the considerable size range of some teeth of *N. doreenae* and the ambiguities that already afflict uintasoricine taxonomy.

The P_4s described here are different enough from their counterpart in *N. doreenae* to indicate either that this sample represents a new species, or that the P_4s do not represent the same species as the other teeth. It is possible that they are P_4s of the new ?microsyopid described below; however, their larger size makes this unlikely.

Niptomomys remains poorly known, and characteristics distinguishing the three species, apart from size, are not well documented. Intraspecific variation of *N. doreenae* appears to be substantial, unless more than one species is involved. The Sand Creek Divide cheek teeth fall just below or within the lower part of the length range of *N. doreenae* reported by Szalay (1969) and Bown (1979) but tend to be narrower than in those samples (Figures 30-31). *N. favorum* (known only from the holotype molar, from Wa-0 at Castle Gardens) is much smaller than any other specimens of the genus and differs from all other *Niptomomys* in apparently lacking pre- and postcingula and any trace of a hypocone. Its reference to this genus is questionable. *N. thelmae* from higher in the Willwood Formation (Wa-4-6) is significantly larger than other species and has a more robust P_4. Most Willwood specimens of *Niptomomys*, from the early Wasatchian, are intermediate in size between the Wa-0 sample and *N. thelmae* and have been assigned to *N. doreenae*.

Beard and Dawson (2009) proposed a new uintasoricine genus, *Choctawius*, for the new species, *C. foxi*, from the Red Hot local fauna of Mississippi, and the enigmatic *C. mckennai* (formerly *Navajovius*? *mckennai*) from the San Juan Basin. *Choctawius* was said to differ from *Niptomomys* in being smaller, having taller and more nearly vertical molar trigonids and narrower talonids, lacking a talonid notch on the lower

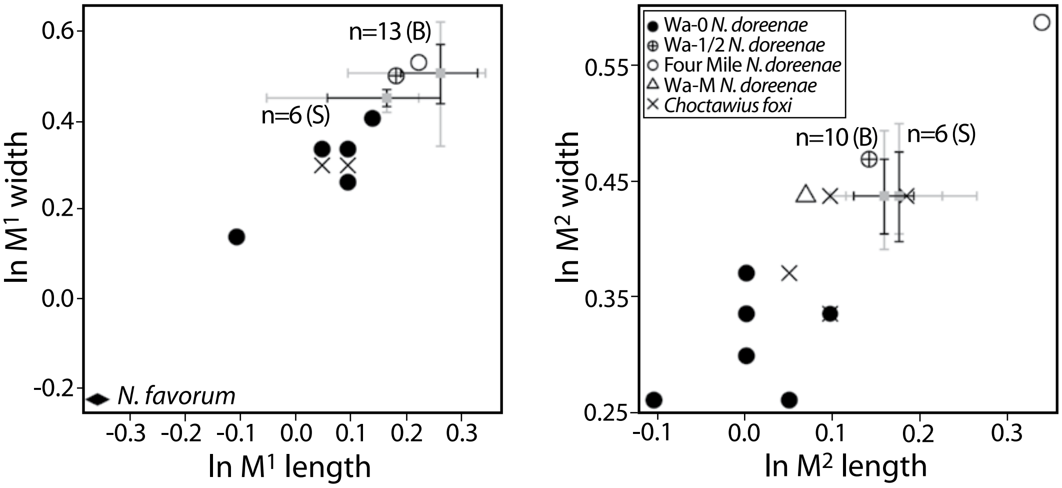


FIGURE 31 — Size distribution of *Niptomomys* and *Choctawius* upper molars. Points are individual specimens as indicated. Range and standard deviation bars refer to the same two samples of *N. doreenae* as in Figure 30; note that our measurements of Four Mile specimens included in Szalay's sample are larger than his. Triangle indicates Wa-M *N. doreenae* reported by Gingerich and Smith (2006).

molars, and having a less transverse M^1 and "less expansive trigon and weaker hypoparacrista" on the upper molars. Some of these traits also describe the Wa-0 sample which, as shown here, conforms closely with *Niptomomys* (except for P_4, which is unknown in *Choctawius*). *C. foxi* is slightly smaller than post-Wa-0 *N. doreenae* from the Bighorn Basin, but is very close in size to the Sand Creek Divide sample (Figures 30-31). We regard the other differences between *C. foxi* and *Niptomomys* to be trivial and doubtfully of generic significance. A thorough study based on larger samples and better material is clearly warranted to determine how many species and genera of Wasatchian uintasoricines are valid.

?MICROSYOPIDAE

Nanomomys thermophilus, gen. et sp. nov.

Figure 32

Holotype.— USNM 540567, LM$_1$.

Hypodigm.— Holotype and USNM 540167 (RM^1), USNM 541777 (RdP^4?), USNM 541778 (RM$_3$), and, tentatively, USNM 540345 (RI$_1$).

Locality and Horizon.— WW-74 (SE¼ sec. 3, T 48 N, R 92 W, McDermott's Butte Quadrangle, Washakie County, Wyoming), lower Willwood Formation, earliest Eocene (Wa-0 biozone).

Etymology.— Greek *nanos*, dwarf, small, and *omomys*, primate genus and ending used in other primate genera; in analogy with *Niptomomys* McKenna, 1960. Species name from Greek *therme*, heat, and *philos*, loving, in allusion to its occurrence during the PETM.

Diagnosis.— Very small primate, slightly smaller than *Niptomomys doreenae*, *Choctawius foxi*, and *Berruvius*, and comparable in size to *Choctawius mckennai*, *Uintasorex*, *Avenius*, and *Toliapina*. Lower molars relatively narrow and low crowned, with distinct and buccally-shifted paraconid, prominent hypoconulid, buccal cristid obliqua, and very shallow hypoflexid. M_1 trigonid mesiodistally elongate, with paraconid well separated from metaconid (in contrast to *Choctawius*); hypoconulid distinct and set off from hypoconid and entoconid by notches. Lower molar cusps peripheral; no cingula. M^1 triangular, more waisted than in *Niptomomys*, *Choctawius*, or *Uintasorex*; protocone lobe anteroposteriorly compressed; cusps peripheral, with almost no stylar shelf; metacone slightly smaller than paracone as in *Niptomomys*; protocone anteriorly canted and situated almost directly lingual to paracone; conules located midway between buccal cusps and protocone as in *Uintasorex*, not buccally shifted as in *Niptomomys*. Upper teeth differ from those of *Niptomomys, Choctawius*, and *Uintasorex* in lacking a precingulum and in having only very faint postcingulum; no evidence of a hypocone.

Description.— Five isolated teeth are assigned to this new taxon based on their extremely small size (equaling the smallest primates known: the microsyopids *Uintasorex parvulus* and *Choctawius mckennai*, the toliapinids *Avenius* and *Toliapina*, and the picromomyid *Picromomys petersonorum*), comparable morphology, and derivation from the same screen-wash site. Reference to Microsyopidae is based on resemblance of the molariform teeth and incisor to those of microsyopids such as *Niptomomys* and *Uintasorex*, but it is possible that *Nanomomys* is more closely related to Toliapinidae, if that family is valid.

The lower molar cusps are moderately acute, and the cuspate paraconid is buccally shifted and much smaller and lower than the other trigonid cusps. The M_1 trigonid is narrower than the talonid and elongate, as its paraconid is well anterior to the other cusps. The metaconid is large but slightly lower than the protoconid, and the entoconid is slightly higher than the hypoconid. The trigonid notch (between metaconid and

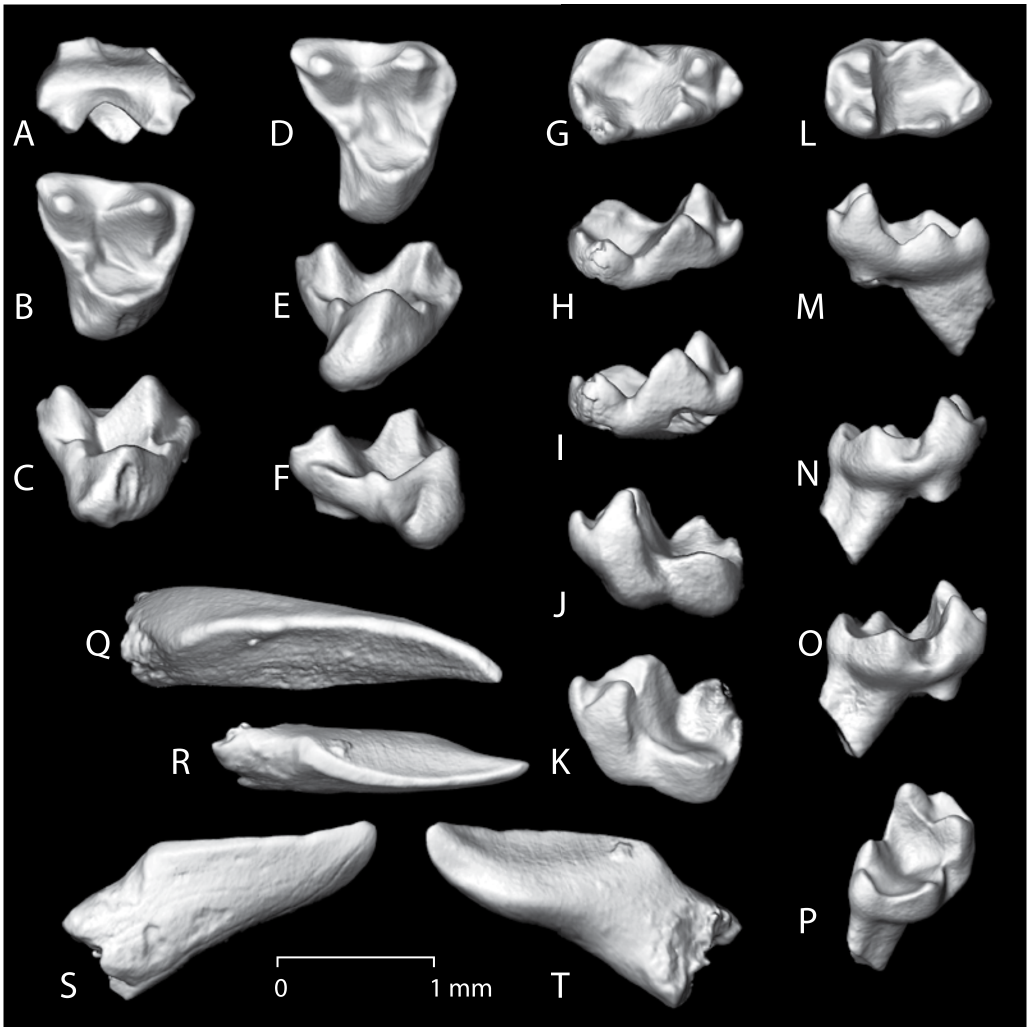


FIGURE 32 — *Nanomomys thermophilus*, gen. et sp. nov. (A-P, R-T) and *Niptomomys doreenae* (Q): A-C, RdP^4?, USNM 541777, in buccal, occlusal, and lingual views; D-F, RM^1, USNM 540167, in occlusal, lingual, and oblique posterior views; G-K, LM$_1$, USNM 540567, holotype, in occlusal (G), oblique occlusal (H, K), lingual (I), and buccal (J) views; L-P, RM$_3$, USNM 541778, in occlusal, lingual, buccal, oblique buccal, and oblique posterior views; Q, LI$_1$ of *Niptomomys*, USNM 540568, in dorsal view; R-T, RI$_1$, USNM 540345, in dorsal, lateral, and medial views.

protoconid) is relatively shallow. A shallow crease is visible inferior to the trigonid notch, but otherwise the posterior trigonid wall is smooth, not stepped by offset wear facets as in many early primates, because the cristid obliqua ends at the base of the protoconid and does not continue toward the metaconid. The talonid basin is large and wide, and the narrow talonid notch is not deep enough to open the basin lingually. The hypoconulid is slightly closer to the entoconid than to the hypoconid, and is demarcated from those cusps by notches. The talonid structure thus closely resembles that of *Arctodontomys*. The referred M$_3$ is similar to M$_1$ in nearly all details, except for having a more mesiodistally compressed trigonid, less buccally shifted paraconid, taller metaconid than protoconid, and an even more salient hypoconulid. The M$_3$ hypoconulid is distinctly lingual in position, and the hypoconulid lobe is extended posteriorly. A hint of an ectocingulid is present below the shallow hypoflexid, whereas no cingulids are present on M$_1$.

In addition to the upper molar characters listed in the diagnosis, it may be noted that the M^1 paracone inclines slightly buccally and its lateral wall is the most buccal part of the crown and lacks an ectocingulum. A low cingulum is restricted to the middle of the buccal margin. The postparacrista is longer than the premetacrista, as in *Niptomomys*. A tiny metastyle is present just posterior to the metacone; no parastyle is evident, but it is possible that it is broken off. The paraconule is slightly closer to the protocone than is the metaconule, and both cusps have short pre- and postconule cristae extending buccally. The trigon basin is deep. The tooth is distinctive in having a slight posterobuccal expansion of the base of the crown in the area where a hypocone or cingulum would develop, but neither is present. On the posterior face of the protocone a faint nannopithex fold extends down toward the base of the tooth (Figure 32F), as in some specimens of *Niptomomys* (e.g., UW 6898). It is met at its midpoint by a faint horizontal ridge extending forward from the base of the metaconule. The tooth identified as dP^4? (USNM 541777) is less transverse and less waisted than M^1, has a tiny parastyle, and has almost no posterior concavity, but otherwise it is virtually identical to M^1.

An isolated lower right I_1 (USNM 540345, Figure 32R-T), also from WW-74, is probably referable to this species. It is lanceolate, like that of *Niptomomys* (with the homolog of the lateral border in other plesiadapiforms rotated to be superior, and the crown essentially facing mediad); but it is shorter and smaller than I_1 of *Niptomomys* and lacks the basal expansion seen in *Niptomomys*.

Measurements (mm).— Holotype, USNM 540567, $M_1L=1.10$, $W_a=0.60$, $W_p=0.70$; USNM 541778, $M_3L=1.05$, $W_a=0.65$, $W_p=0.60$; USNM 541777, $dP^4L=1.00$, $W=1.05$; USNM 540167, $M^1L=1.05$, $W=1.20$; USNM 540345, $I_1L=1.45$, $B=0.40$, proximal depth=0.70.

Discussion.— These very diminutive teeth, recovered by screen-washing using 0.5 mm mesh, clearly represent a taxon distinct from any other in Wa-0, and different from any other known primate. Based on tooth size, it was smaller than all other known primates, living or extinct, except for the smallest uintasoricine microsyopids, picromomyids, and toliapinids, all of which have molars of about the same size. The body mass of *Nanomomys* was much less than that of the smallest extant primates, the mouse lemurs (*Microcebus*). Estimates based on M_1 area range from 8.0-9.5 g (using the all primate and prosimian regression equations of Conroy, 1987), to 22.0-23.7 g (using the all primate regression equations for M^1 and M_1 of Gingerich et al., 1982). The latter estimates are close to the lower end of the range of body mass in *Microcebus berthae*, the smallest living primate, but even the smallest reported M^1s in *M. berthae* are more than 30% longer than M^1 of *Nanomomys* (Rasoloarison et al., 2000). Consequently, we regard the lower estimates to be more accurate.

The compressed protocone lobe and absence of any trace of a hypocone or postcingulum give the upper teeth a very primitive appearance. The dental characteristics, including the molar features as well as the shape of the referred I_1, seem to accord best with uintasoricine Microsyopidae. Nevertheless, *Nanomomys* differs from known uintasoricines (*Uintasorex*, *Niptomomys*, and *Choctawius*) in several features noted in the diagnosis. The near absence of cingula on both upper and lower molars, the lack of any trace of a hypocone on M^1, the more waisted M^1, and the buccally and anteriorly shifted paraconid of M_1 distinguish *Nanomomys* from any other uintasoricine.

Picromomys petersonorum, though having lower molars of comparable size to *Nanomomys*, differs in being more bunodont and having a deeper talonid notch and a more lingual paraconid that is not mesially displaced on M_1. *Picromomys* is unique in having an accessory anterobuccal cusp on the trigonid. A close relationship between *Nanomomys* and *Picromomys* is unlikely.

Hooker et al. (1999) proposed the new family Toliapinidae to comprise five tiny, late Paleocene-early Eocene Old World genera: *Toliapina*, *Avenius*, *Berruvius*, *Altiatlasius*, and *Sarnacius*. They assigned the family to the Microsyopoidea. The relationships of *Altiatlasius* remain controversial and its inclusion in Toliapinidae is questionable, but the others seem likely to have microsyopoid affinities. Because of their diminutive size and the primitive appearance of their molars, especially the uppers, toliapinids invite comparison with *Nanomomys*. *Nanomomys* is smaller and lower crowned than *Sarnacius* and *Berruvius*, and similar in size to *Avenius* and *Toliapina* and slightly higher crowned. It resembles toliapinids in having the metaconid lower than the protoconid, although this is not a very unusual feature. However, *Nanomomys* differs from toliapinids in having a much larger metaconid, a more distinct hypoconulid, and a more open M_1 trigonid with a less lingual paraconid. M^1 of *Nanomomys* is waisted as in toliapinids, and triangular as in *Avenius* and *Toliapina*. It has a very reduced stylar shelf similar to that of *Toliapina vinealis*, but narrower than in all other toliapinids. *Nanomomys* differs from all toliapinids in having a more mesiodistally constricted protocone lobe and a straight buccal margin with no ectoflexus. It further differs from *Berruvius* and *Sarnacius* in having no hypocone and almost no posterolingual expansion. The resemblances to some toliapinids strengthen the probable microsyopid affinities of *Nanomomys*. Discovery of such a distinctive new primate at Sand Creek Divide is a reminder that we still have much to learn about early Eocene faunas.

Family OMOMYIDAE Trouessart, 1879

TEILHARDINA Simpson, 1940

Teilhardina brandti Gingerich, 1993

Figures 33, 34A-C

Referred specimens.— WW-74: USNM nos. 521825 (ungual phalanx), 533505 (RM_2), 533494 (R maxilla with P^4-M^3), 539466 (L maxilla with M^{2-3}), 539467 (L maxilla with P^4-M^3), 540329 (R talar body), 540587 (ungual phalanx), 540598 (RM^2), 542001 (ungual phalanx); WW-75: USNM 521795 (R dentary with M_2); WW-77: USNM 533554 (L dentary P_4-M_1); WW-84: USNM nos. 525543 (LP_4, LM_1, LM_2, RP^3), 525544 (RP_4, LM_2, LM_2 or M_3 trigonid), 538082 (LM_1, LM_2, RM_2), 538084 (LM_2), 539577 (L talus), 542002 (R navicular); WW-96: USNM nos. 525546 (R dentary with M_{2-3}), 525622 (L dentary with M_{2-3}), 538361 (L dentary with talonid of M_2); WW-97: USNM 525545 (LM_2); WW-125: USNM 525621 (R dentary with M_{1-3}).

Description.— Lower teeth of *Teilhardina brandti* were described by Gingerich (1993) and Smith et al. (2006). Upper teeth, a lower jaw with alveoli of all anterior teeth, and a few postcranial bones are described by Rose et al. (2011). Measurements are provided by these authors and are not repeated here.

Discussion.— *Teilhardina brandti* is the most common euprimate at Sand Creek Divide, being represented by 24 specimens, including nine jaws (Figures 33, 34). It first appears in the lower third of the Wa-0 section, about 7 meters below *Cantius*.

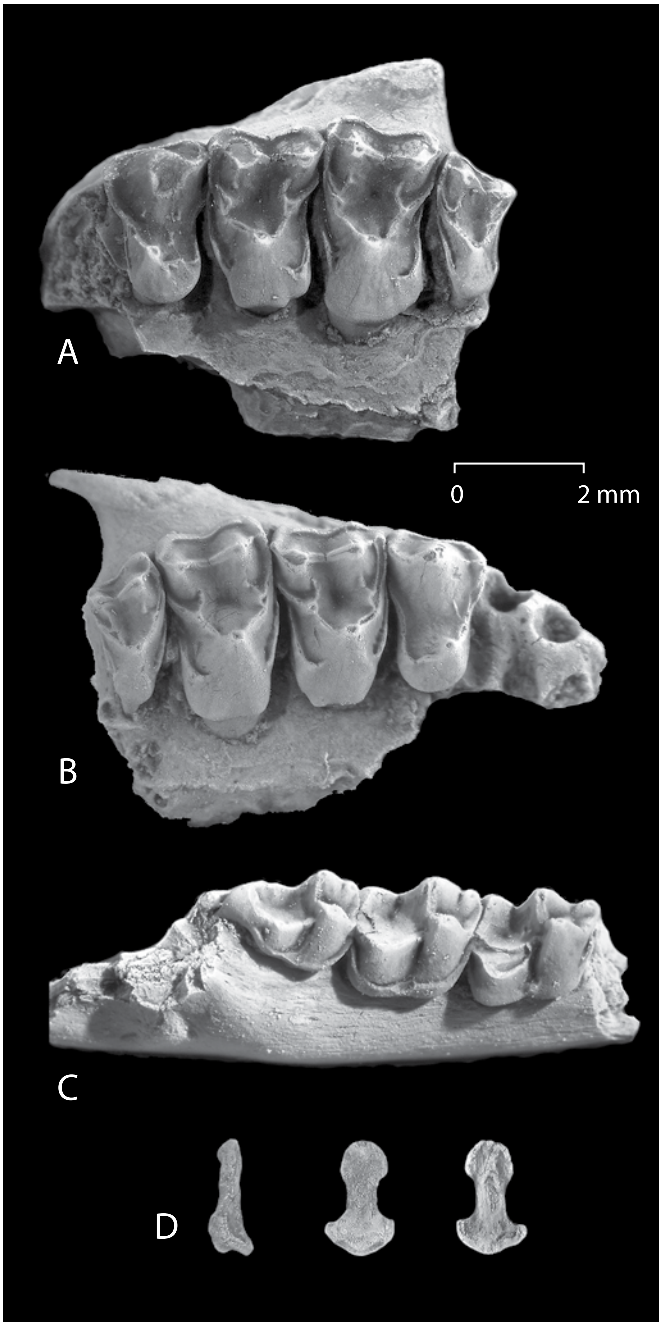


FIGURE 33 — *Teilhardina brandti*: A, L maxilla with P^4-M^3, USNM 539467; B, R maxilla with P^4-M^3, USNM533494; C, R dentary with $M_{1\text{-}3}$, USNM 525621; D, ungual phalanx, USNM 540587, in lateral, palmar, and dorsal views.

Only two specimens have been reported from Wa-0 at Polecat Bench, and none from Castle Gardens; however, several specimens of *T. brandti* have recently been collected in the Cabin Fork area adjacent to Castle Gardens (Rose et al., 2011), providing additional evidence that *Teilhardina* was an early immigrant and a relatively common constituent of the Wa-0 fauna.

Teilhardina gingerichi, sp. nov.

Figure 34D-G

Holotype.— USNM 527695, L dentary with P_3-M_1, collected by Paul Constantino, July 2004; only known specimen.

Locality and Horizon.— WW-117 (NE¼, SE¼, section 10, T 48 N, R 92 W, McDermott's Butte Quadrangle, Washakie County, Wyoming), lower Willwood Formation, earliest Eocene; ~5 m above the top of "Big Red," near the top of the Wa-0/PETM interval.

Etymology.— For Philip D. Gingerich, in recognition of his seminal contributions to knowledge of mammalian faunas during the PETM.

Diagnosis.— Largest species of *Teilhardina*: P_4-M_1 about 10% larger (linear dimensions) than *T. brandti* and similar in proportions; $\geq$ 10% longer than *T. americana* but similar in width. Differs from all other species of *Teilhardina* in having lower and less distinct metaconid on P_4. Further differs from *T. brandti* in having a smaller P_4 talonid.

Description.— The holotype is a jaw fragment with only P_3-M_1; however, these are probably the most diagnostic teeth among omomyids. The premolars are simple, each with a tall trigonid projecting slightly above the top of the M_1 trigonid, and a very small and short talonid. The trigonid of P_3 consists solely of the protoconid, with no trace of either paraconid or metaconid. A weak lingual cingulum continues anteriorly (where it is best developed) to the base of the protoconid; there is no buccal cingulum. The talonid has a centrally located cusp, the hypoconid, and a faint more lingual cusp (entoconid?) situated not quite at the lingual end of the postcristid. A low crest extends lingually from the lingual cusp and then anteriorly to become a faint lingual cingulum. A short and low cristid obliqua runs anteriorly from the hypoconid to the base of the protoconid. These weak crests define a shallow talonid basin that is about three times wider than its length.

P_4 is larger and wider than P_3 and has a somewhat better developed trigonid. The anterolingual cingulum is prominent and gives rise to a small paraconid. The metaconid is weakly developed, being little more than a swelling on the posterolingual aspect of the protoconid, just over halfway up the crown (metaconid height/protoconid height < 0.59; as the protoconid is slightly worn, original relative metaconid height was less). In comparison, mean metaconid height in *T. belgica* is 0.65, in *T. brandti* 0.68, and in *T. americana* 0.74 (Rose et al., 2011). Although P_4 is larger than P_3, its talonid basin is about the same length and narrower than that of P_3; it is similarly constructed, with faint talonid cusps and a very shallow basin. The cristid obliqua is slightly longer, extending part way up the back of the protoconid. Although P_4 is about as wide as in *T. americana*, it is longer, so its relative width is comparable to that of *T. brandti.* The buccal cingulum is very weak and is evident only at the anterior and posterior ends of the tooth.

M_1 is essentially identical to that in *Teilhardina brandti* but slightly larger. Wear on this tooth accentuates the stepped postvallid (i.e., offset wear facets 1 and 5), which is more typical of M_1 of *T. americana* (e.g., UM 75610, UW 7098) than of *T. brandti*. M_1 has a weak buccal cingulum.

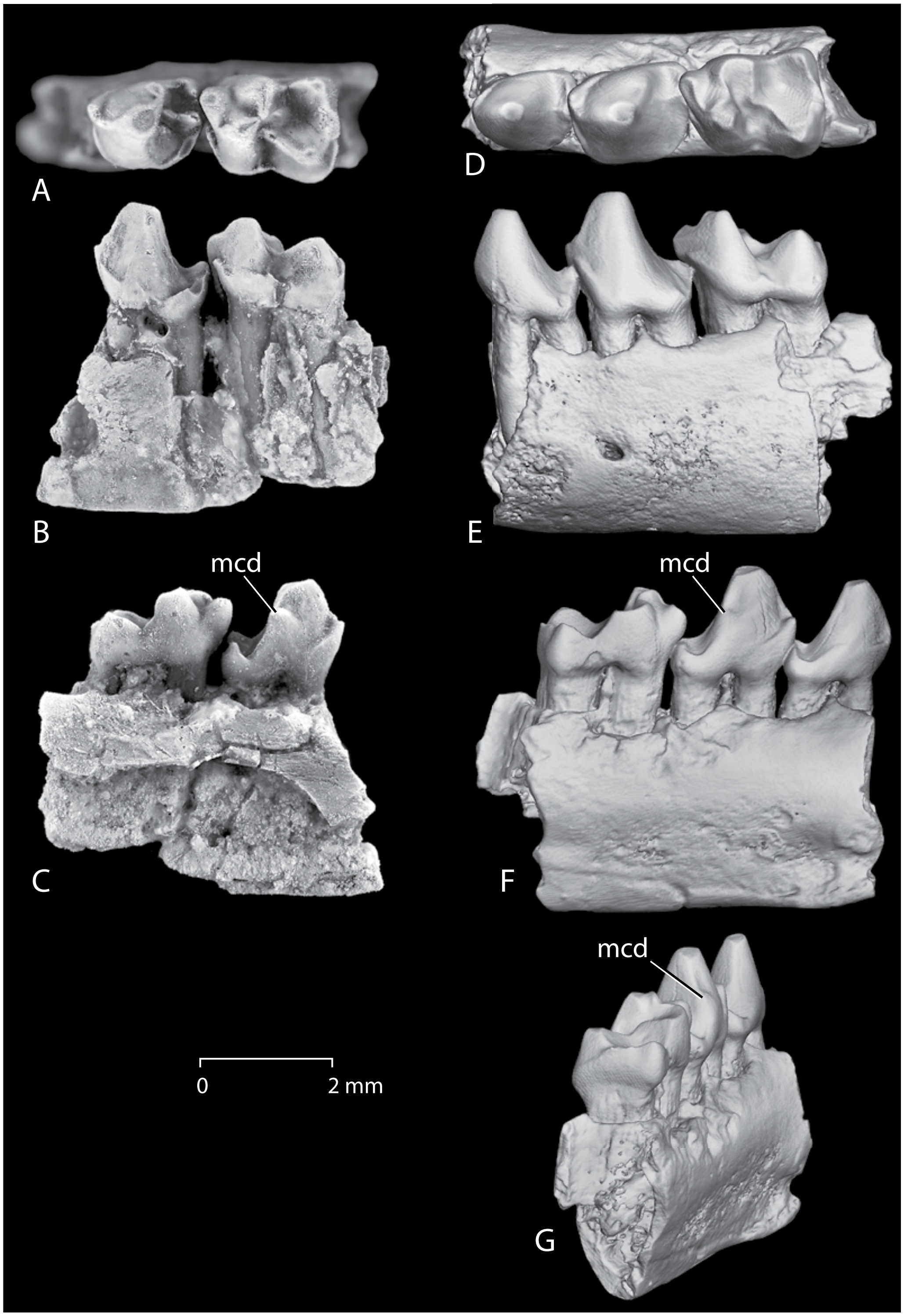


FIGURE 34 — A-C, *Teilhardina brandti*, L dentary with P_4-M_1, USNM 533554, in occlusal, buccal, and lingual views. D-G, *Teilhardina gingerichi*, sp. nov., L dentary with P_3-M_1, USNM 527695, holotype, in occlusal, buccal, lingual, and oblique posterior views. Note low P_4 metaconid (mcd) compared to *T. brandti*.

TABLE 5 — Comparison of tooth dimensions (mm) of *Teilhardina gingerichi*, sp. nov., and *T. brandti*.

Species	P_4L	P_4W	M_1L	M_1W_a	M_1W_p
T. gingerichi, sp. nov.	1.95	1.40	2.20	1.50	1.65
T. brandti (mean)	1.74	1.26	1.99	1.34	1.49
Range	1.60–1.80	1.20–1.35	1.90–2.10	1.25–1.40	1.35–1.60
± 1 std. dev.	(1.66, 1.82)	(1.19, 1.33)	(1.92, 2.06)	(1.28, 1.41)	(1.41, 1.58)
± 2 std. dev.	(1.58, 1.90)	(1.13, 1.39)	(1.85, 2.13)	(1.22, 1.47)	(1.33, 1.66)
95% confidence limits	(1.67, 1.81)	(1.21, 1.31)	(1.94, 2.03)	(1.30, 1.39)	(1.44, 1.55)

Measurements (mm).— P_3L=1.60, W=1.20; P_4L=1.95, W=1.40; M_1L=2.20, W_a=1.50, W_p=1.65.

Discussion.— *Teilhardina gingerichi* is a primitive omomyid most similar to *T. brandti*. As noted above, it differs from all other *Teilhardina* species, including *T. brandti*, in being larger and having a weaker and lower metaconid. The holotype of *T. gingerichi* is outside the range and more than two standard deviations from the mean for all dimensions of *T. brandti* except M_1 talonid width (which is at about two standard deviations from the mean; see Table 5). Strength and position of the metaconid on P_4 are considered particularly decisive characters for interpreting evolutionary stage and taxonomy of *Teilhardina* (e.g., Bown and Rose, 1987; Rose et al., 2011). Though subtle, the differences between *T. gingerichi* and *T. brandti* are comparable in magnitude to those that distinguish other species of *Teilhardina*. Notably, the holotype comes from stratigraphically higher than any other *Teilhardina* specimen from the Sand Creek Divide section. The larger size and low metaconid, however, make it unlikely that *T. gingerichi* was a lineage segment leading to *T. americana*.

The new species also closely resembles early Eocene *Tetonius mckennai* from the Four Mile local fauna of northern Colorado, the smallest and most primitive species of *Tetonius*, which has been hypothesized to link the genus to *Teilhardina* (Bown and Rose, 1987). Though M_1 is almost the same size and morphology in both species, *Teil. gingerichi* differs from *Tet. mckennai* in having slightly longer and narrower premolars and a lower P_4 metaconid.

Family NOTHARCTIDAE Trouessart, 1879

CANTIUS Simons, 1962

Cantius torresi Gingerich, 1986

Figure 35A-B, D-G

Referred specimens.— WW-84: USNM 533614 (LM_3, LM^2, RM^2), 533615 (LM_3); WW-97: USNM 538362 (RP_4, LM^3); level of WW-114: USNM 521594 (LM^2); ~3 m below WW-119: USNM 527666 (L dentary with M_{1-2}).

Description.— Most but not all specimens referred here are distinctly smaller than *Cantius ralstoni*. As in *C. torresi*, the upper molars lack any trace of a mesostyle, and the M^2s have only a hint of a hypocone. USNM 538362 includes a right P_4 (Figure 35D) that is very similar to that in the holotype of *C. torresi*. It is short and wide, slightly more so than in the holotype and other *C. torresi* specimens compared, unlike the relatively more elongate P_4 of *C. ralstoni* (Figure 35C). The paraconid is small and very low, and the metaconid is prominent and almost as high as the protoconid, and situated lingual and slightly posterior to the protoconid. The paracristid and protocristid form a right angle. Gingerich (1986) regarded these features of P_4 to be diagnostic of the species. Notably, however, P_4 in USNM 538362 is larger than in *C. torresi* and compares well in overall size (but not proportions) with that of *C. ralstoni*. USNM 538362 also includes an unassociated left M^3 that is larger and anteroposteriorly longer than in UM 83475, part of the original sample of *C. torresi*, and larger even than in the holotype of *C. ralstoni*. It is the same size as in AMNH 16092 (*C. ralstoni*), and resembles both of these *C. ralstoni* specimens in having a complete lingual cingulum, unlike UM 83475. Nevertheless, it seems highly unlikely that two species of *Cantius* so similar in size and morphology would be present at the same horizon within Wa-0; consequently, we ascribe the differences observed to intraspecific variation and refer these teeth to *C. torresi*.

USNM 527666 (Figure 35F-G) is from a few meters above the top of Big Red and a few meters below WW-119, near the top of the Wa-0 interval. It is larger than the holotype and most specimens of *C. torresi* and is comparable in size to early Wasatchian specimens of *C. ralstoni*. We include it tentatively in *C. torresi* because of its stratigraphic occurrence within Wa-0, but without the crown of P_4 it is difficult to confirm this assignment, and it could represent the first appearance of *C. ralstoni*.

Measurements (mm).— USNM 521594, M^2L=3.20, W=4.70; USNM 527666, M_1L=3.70, W_a=2.85, W_p=3.20, M_2L=3.90, W_a=3.45, W_p=3.40; USNM 533614, RM^2L=3.20, W=5.00, LM^2L=3.00, W=4.60, M_3L=3.90, W_a=2.60, W_p=2.30; 533615, LM_3L=3.90, W_a=2.50, W_p=2.20; USNM 538362, RP_4L=3.20, W=2.65; LM^3L=3.05, W=4.65.

Measurements of the Wa-1 *C. ralstoni* specimens: USNM 538363, LP_4L=3.45, W=2.40, LP^4L=3.40, W=4.60, RM^2L=3.60, W=5.70; USNM 538364, RM^2L=3.70, W=6.00.

Discussion.— *Cantius* typically ranks among the three or four most abundant genera in Bighorn Basin Wasatchian faunas (Rose, 1981b; Bown et al., 1994), but it is surprisingly rare in the Sand Creek Divide fauna. *C. torresi* is better represented at Polecat Bench (Gingerich, 1989, and undescribed material) but has

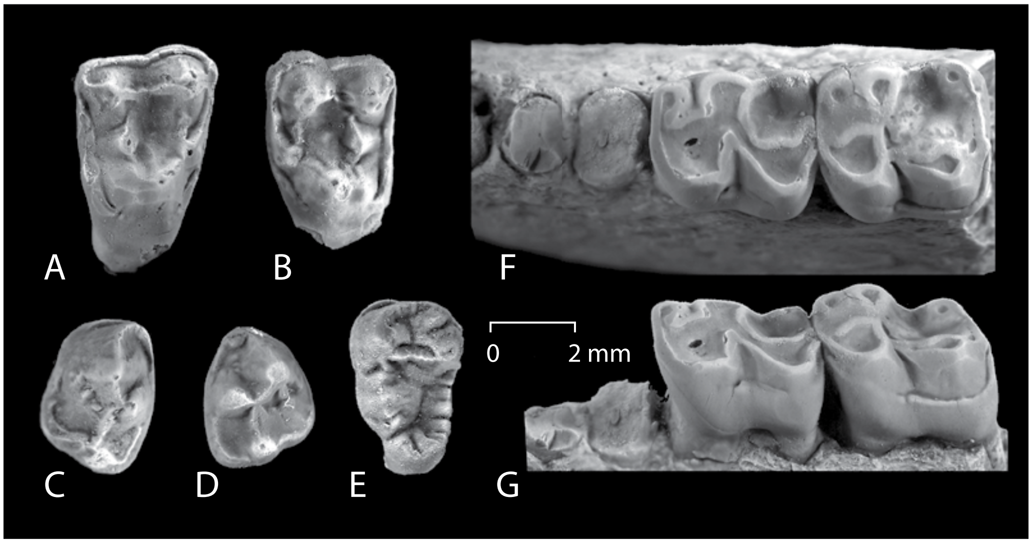


FIGURE 35 — *Cantius*: A-B, *C. torresi*, RM^2, LM^2, USNM 533614 from WW-84; C, *C. ralstoni*, LP_4, USNM 538363 from WW-89; D, *C. torresi*, RP_4, USNM 538362 from WW-97; E, *C. torresi*, LM_3, USNM 533615 from WW-84; F-G, *C. torresi*?, L dentary with M_{1-2}, USNM 527666 from level of WW-97.

not been reported from Castle Gardens (Strait, 2001; Yans et al., 2006). A single tooth from about 6 m below Big Red is the only record of *Cantius* from below this marker bed near the top of the Wa-0 section. *Cantius* has not been found in the relatively fossiliferous purple sequence below Little Red. The stratigraphic distribution of *Cantius* at Sand Creek Divide thus suggests that its arrival in the southern Bighorn Basin postdated that of the omomyid *Teilhardina*, though this must be regarded as tentative in view of the small sample size.

Several isolated teeth from WW-89 (about 12 m above the top of Big Red and immediately atop Puffy Purple) clearly represent *C. ralstoni*, and provide faunal evidence of a shift from Wa-0 to Wa-1. USNM 538363 (LP_4, LP^4, RM^2) and 538364 (RM^2, damaged left M^2) are slightly larger than the holotype of *C. ralstoni* (AMNH 16089) but the same size as AMNH 16092. As in the latter, the M^2s from WW-89 have a complete lingual cingulum and a stronger nannopithex fold than in *C. torresi*. P_4 is larger and relatively longer and narrower than in most *C. torresi* specimens, with a mesiodistally extended trigonid (Figure 35C). The metaconid is smaller and lower than is typical for *C. torresi*. A jaw fragment with P_4-M_3 (USNM 539499, WW-173), embedded in hematite (and not measurable accurately), also appears to be the same size and morphology as *C. ralstoni*. Nevertheless, the overlapping size and intermediate features of some of the specimens reported here suggest that *C. torresi* and *C. ralstoni* are lineage segments of *Cantius*.

Order CREODONTA Cope, 1875
Family OXYAENIDAE Cope, 1877

DIPSALIDICTIS Matthew, 1915

Dipsalidictis platypus Matthew, 1915
Figure 36A-E

Referred specimens.— WW-84: USNM 533562 (upper tooth fragments), 538345 (left astragalus).

Description.— Fragments of left P^4, M^1, M^2, and right M^1 (Figure 36A-D), almost certainly from the same individual, represent a very small oxyaenid and are essentially identical in size and morphology to the maxilla (UM 66137) referred to this species by Gingerich (1989). An isolated astragalus (USNM 538345, Figure 36E) from the same locality is similar in size to other astragali of *D. platypus* (maximum length=20.95 mm, width of trochlea=10.6 mm, maximum width of body=13.4 mm). It has a nearly flat tibial trochlea and a wide, dorsoventrally compressed head more similar to that of UM 66137 than to the holotype (Gingerich, 1989: figure 19); however, it appears to resemble the holotype more closely in having a shallow astragalar body (height=8.4 mm).

OXYAENIDAE, indet.
Figure 36F

Referred specimen.— WW-101: USNM 538344 (ungual phalanx).

Description.— An oxyaenid ungual phalanx measuring 16.3 mm long and 8.1 mm high x 7.7 mm wide (proximally) is probably too large to belong to *D. platypus* and is even bigger than isolated unguals associated with specimens of the significantly larger *Oxyaena gulo* (e.g., USGS 7186, 16485). It is moderately broad (not laterally compressed) and deeply fissured distally. The dorsal surface is strongly curved, and the plantar surface less so. The articular surface is almost as wide as it is deep dorsoplantarly, and there is a prominent, wide flexor tubercle.

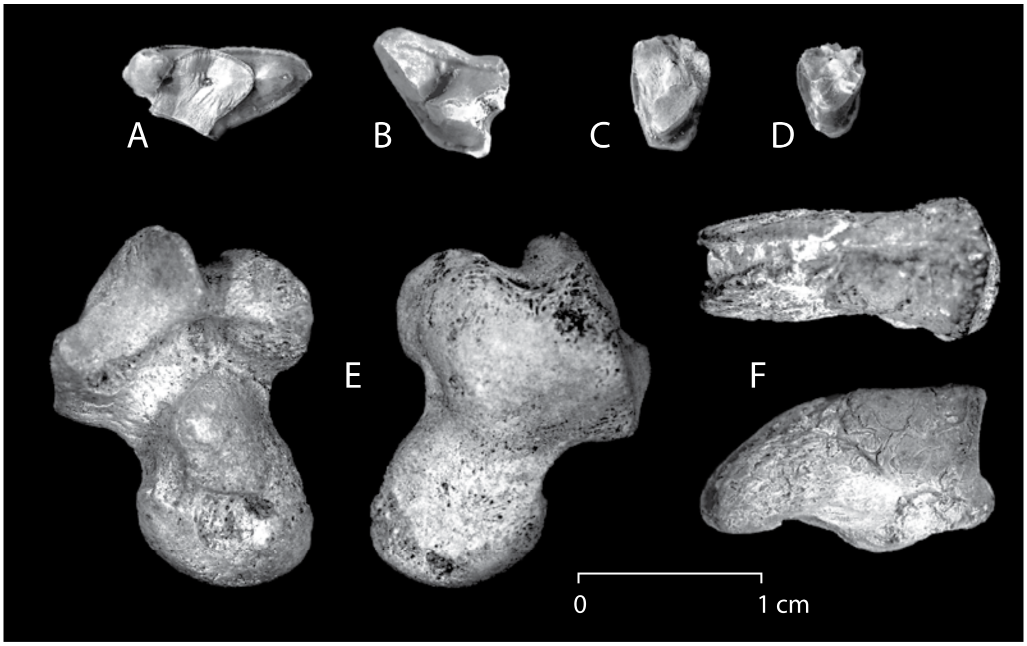


FIGURE 36 — Oxyaenids: A-E, *Dipsalidictis platypus*: A-D, USNM 533562, incomplete LP^4 (A), RM^1 buccal (B), LM^1 lingual (C), LM^2 lingual (D); E, L astragalus, USNM 538345, in ventral and dorsal views. F, oxyaenid ungual phalanx, USNM 538344, in dorsal and lateral views.

Discussion.— Only two other oxyaenids (besides *Dipsalidictis platypus)* have been reported from Wa-0, *Dipsalidictis transiens* and *Palaeonictis wingi* (Gingerich, 1989; Chester et al., 2010). This ungual may represent one of those species, or perhaps a species of *Oxyaena* otherwise unknown from this interval.

Family HYAENODONTIDAE Leidy, 1869

ARFIA Van Valen, 1965

Arfia junnei Gingerich, 1989

Figure 37A-F

Referred specimens.— WW-73: USNM 527664 (maxillae with damaged LM^{2-3} and RM^1); WW-74: USNM 511044 (R dentary with M_3 talonid); WW-77: USNM 511040 (L dentary with P_2-M_3, R dentary with P_2); WW-84: USNM nos. 493786 (RM_2), 538352 (LM_3 talonid), 538353 (LM_1, LP^4 and LM^1 frags.), and 540316 (LdP_4 trigonid); WW-96: USNM 533570 (LM_1); 2 m above WW-98: USNM 527476 (L maxilla with damaged M^{2-3}); WW-101: USNM 538351 (LP_4, LM^3), USNM 541912 (RdP_4); slightly below WW-119: USNM 527474 (LM_3 trigonid and associated fragments); WW-125: USNM 533595 (RM_3 talonid); WW-192: USNM 541970** (dentary fragments, LM_{1-2}, RP_3, and associated fragments including vertebrae and partial ulnae).

Description.— These specimens show typical features of *Arfia*, including an increase in molar size from M_1 to M_3, squared talonids with a prominent hypoconid and distinct hypoconulid which are joined by a moderately elevated postcristid, and a somewhat lower but still fairly tall entoconid. The enamel is weakly wrinkled, but much less so than in larger species such as *A. shoshoniensis*. The paraconid is smaller and lower than the metaconid on M_{1-2} but slightly larger than the metaconid on M_3. The M_1s in the sample have a weak entoconulid anterior to the entoconid, as in the holotype. USNM 511040 is a dentary containing most of the lower dentition, but the molars are heavily worn and badly weathered. P_{2-4}, however, are better preserved and, as in other specimens of *Arfia*, are simple, with a moderately tall protoconid and a small talonid cusp, somewhat smaller than in *A. shoshoniensis*. Only a hint of a small anterobasal cusp is present. As confirmed by isolated premolars in USNM 538351 and 541970, P_{2-3} have a slightly lower protoconid and a simpler unicuspid talonid than P_4. The talonid of P_4 has a narrow basin bounded by the short cristid obliqua laterally and a low crest lingually. A dP_4 (USNM 541912) is referred to *A. junnei* based on its size and talonid morphology. It is about the same length as M_1 but narrower. Its trigonid is elongate, with a prominent paraconid, and the talonid is basined and molar-like, though relatively narrower.

Early species of *Arfia* are mainly distinguished by size. These specimens compare closely in size with *A. junnei* (see Gingerich, 1989: table 9), the smallest North American species, and are smaller than early Wasatchian *A. zele*.

Measurements (mm).— USNM 493786, M_2L=6.80, W_a=3.45, W_p=3.25; USNM 511040, LP_2L=6.15, W=2.80, P_3L=6.90, W=2.90, P_4L=7.10, W=3.30, M_1L=6.30, W_a=3.40, W_p=3.60, M_2L=7.45, W_a=4.00, W_p=3.80, M_3L=8.85, W_a=4.0*, W_p=3.00, RP_2L=6.20; USNM 527474, M_3W_a=4.60; USNM 527476,

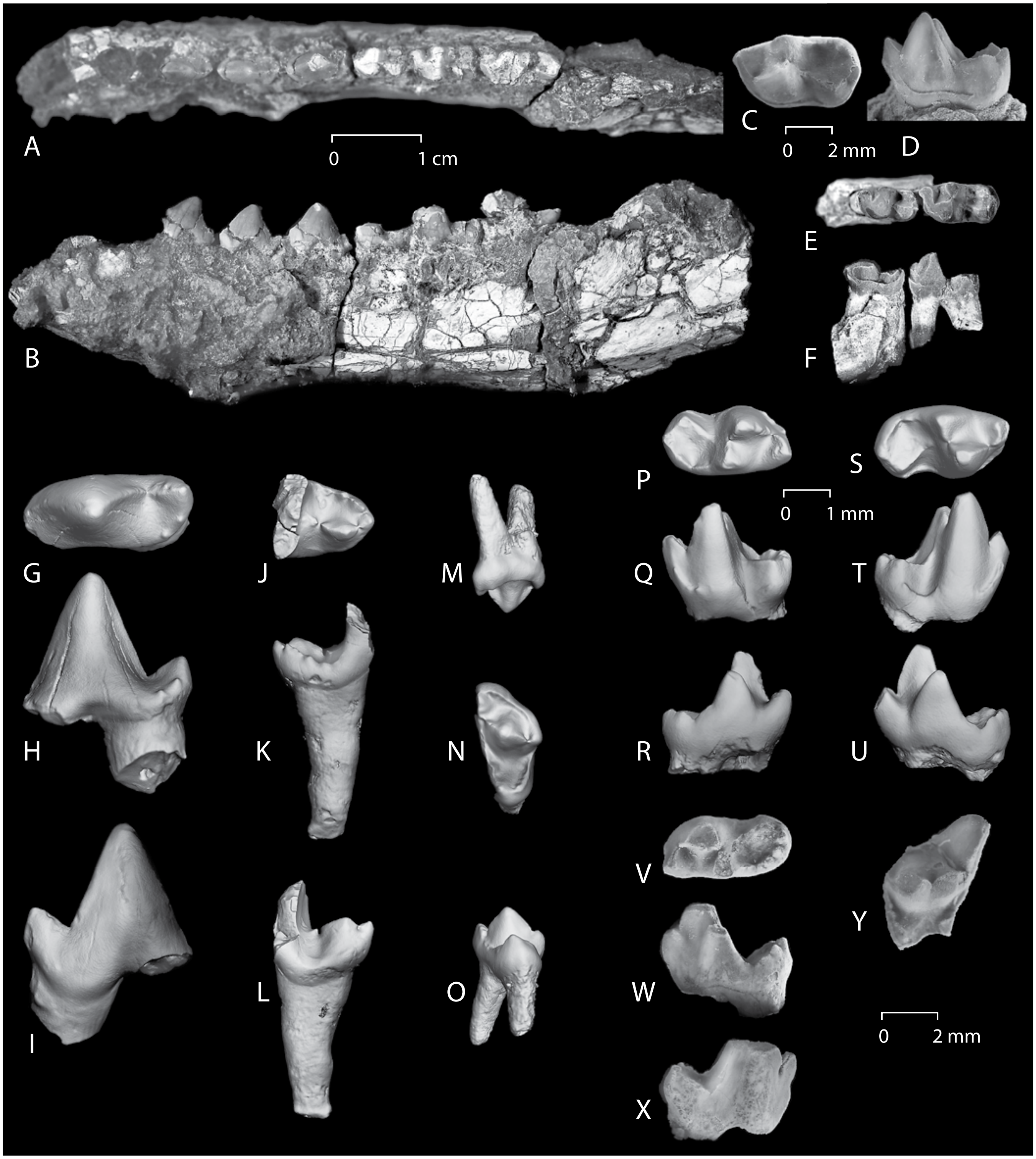


FIGURE 37 — Hyaenodontids: A-F, *Arfia junnei*. A-B, L dentary with P_2-M_3, USNM 511040; C-D, LM_1, USNM 533570; E-F, LM_{1-2}, USNM 541970; all in occlusal and buccal views. G-O, *Prolimnocyon eerius*. G-I, RP_4, USNM 540314, in occlusal, lingual and buccal views; J-L, LM_X talonid, USNM 540314, in occlusal, lingual and buccal views; M-O, LM^3, USNM 533579, in buccal, occlusal and lingual views. P-U, ?Hyaenodontid, new, LM_1 (P-R), RM_1 (S-U), USNM 541911, both teeth in occlusal, buccal and lingual views. V-Y, *Prototomus deimos*. V-X, RM_1, USNM 540165, in occlusal, lingual, and buccal views; Y, LM^2, USNM 540315, in occlusal view. A-B,E-F to scale in A; C-D to scale in C; G-U to scale in P; V-Y to scale in Y.

M^2L=7.40, M^3L=5.50; USNM 533570, M_1L=5.60, W_a=2.95, W_p=3.05; USNM 533595, M_3W_p=3.00; USNM 538351, P_4L=6.25, W=3.20; USNM 538352, M_3W_p=2.75; USNM 540316, P_4W_a=2.70; USNM 541912, dP_4L=5.70, W_a=2.60, W_p=2.70; USNM 541970, P_3L=6.10, W=2.90, M_1L=6.20, W_a=3.20, W_p=3.10, M_2L=7.65, W_a=3.70, W_p=3.60. Other specimens are damaged and cannot be accurately measured. For comparison, measurements of the original sample from Polecat Bench (from Gingerich, 1989) are: M_1L=5.6, W=3.2 (n=1); M_2L=6.8-7.5, W=4.0-4.5 (n=2); M_3L=7.3-7.5 (n=2), W=4.0-4.6 (n=5).

Discussion.— A. junnei is the largest and most common hyaenodontid in the Wa-0 fauna. In the Polecat Bench local fauna it is the most common carnivorous mammal (Gingerich, 1989). At Sand Creek Divide, *A. junnei* is slightly more common than *Uintacyon gingerichi* but much less common than *Didymictis*. A single specimen of *A. junnei* was reported from Castle Gardens (Strait, 2001), but it was not included in a subsequent faunal list (Yans et al., 2006), in which only *Galecyon* sp. was reported. The latter material was subsequently referred to *G. peregrinus* by Zack (2011). *A. junnei* is very slightly larger than *A. gingerichi* from Dormaal, Belgium (Smith and Smith, 2001).

PROTOTOMUS Cope, 1874

Prototomus deimos Gingerich and Deutsch, 1989

Figure 37V-Y

Referred specimens.— WW-84: USNM 538390 (L and R molar talonids), USNM 540315 (incomplete LM^2); WW-97: USNM 540165 (RM_1 and trigonid of LM_1).

Description.— A complete lower molar and four incomplete molars are the only definitive records of a hyaenodontid smaller than *Arfia junnei* and somewhat larger than *Prolimnocyon eerius*. The moderately open trigonid and narrow, elongate talonid basin closely approximate in size and morphology those of M_1 in the smallest North American species of *Prototomus*, *P. deimos*. The paraconid and metaconid are of equal height and much lower than the protoconid, but the metaconid is slightly the larger cusp. The hypoconulid is the tallest talonid cusp; the entoconid and the hypoconid are lower and of about the same height. A distinct entoconulid is situated anterior to the entoconid. These details correspond closely to those of M_1 in the holotype. The fragmentary M^2 is of appropriate size to go with the lower molar, and its connate paracone and metacone, and sharply angled, almost transverse metastylar blade, are characteristics of *Prototomus*.

Measurements (mm).— Only one specimen is complete enough to measure: USNM 540165, complete M_1L=4.50, W_a=2.15, W_p=2.05. M_1 in the holotype of *P. deimos* (from early Wasatchian strata above the PETM) is 4.4 mm long and 2.2 mm wide (Gingerich and Deutsch, 1989).

Discussion.— Prototomus deimos is rare at Sand Creek Divide; nevertheless, the close correspondence of these teeth with those of the holotype is evidence of the presence of a small species of *Prototomus* for which *P. deimos* is the most appropriate name. Gingerich (1989) reported four fragmentary teeth of *P. deimos* from the Wa-0 section at Polecat Bench. It should be mentioned that the isolated molar talonids from Sand Creek Divide (USNM 538390), which are slightly smaller than those of the holotype of *Prototomus deimos*, also closely resemble the poorly known hyaenodontid *Acarictis ryani*, which has been reported from Wa-0 based on very fragmentary specimens (Gingerich, 1989; Strait, 2001). The validity of *A. ryani* was challenged by Smith and Smith (2001), who suggested that the species is a synonym of either *Prolimnocyon* or *Prototomus*, most likely *Prolimnocyon haematus*. The matter cannot be convincingly resolved without better preserved fossils. We judge the meager available material described above to be closer to *Prototomus deimos* and await more definitive evidence that *A. ryani* was present at Sand Creek Divide.

PROLIMNOCYON Matthew, 1915

Prolimnocyon eerius Gingerich, 1989

Figure 37G-O

Referred specimens.— WW-84: USNM 533579 (LM^3), and tentatively USNM 540314 (RP_4 and four molar fragments).

Description.—An isolated M^3 (USNM 533579; Figure 37M-O) is slightly smaller than that of the holotype of *P. eerius* but is so close morphologically as to leave no doubt that it represents the same species. M^3 is more reduced in *Prolimnocyon* than in any other hyaenodontid, hence such a small M^3 could not belong to any other known hyaenodontid. As in the holotype, there is a single large buccal cusp (paracone) preceded by a prominent parastyle and followed by a much smaller metastyle. The stylar cusps are joined by a prominent ectocingulum. The protocone is much lower than the paracone, and a tiny paraconule is present on the preprotocrista. The P_4 and lower molar fragments (Figure 37G-L) closely resemble those of *Prolimnocyon atavus* but are much smaller and are therefore tentatively assigned to *P. eerius* (for which lower teeth have not been described). P_4 has a tall protoconid followed by a well-developed talonid heel. Though slightly damaged anteriorly, it appears to have lacked a paraconid, as in most *Prolimnocyon* specimens examined (*Prototomus* typically has a small paraconid). The molar talonids are narrow and basined. Such fragmentary material is difficult to allocate with confidence. Although these lower teeth probably represent *P. eerius*, it is possible that they belong to *Prototomus deimos* instead.

Measurements (mm).— USNM 533579, M^3L=1.50, W=2.80. M^3 in the holotype is 1.7 mm long and 3.3 mm wide (Gingerich, 1989). USNM 540314, P_4L=3.6, W=1.5; M_xW_p=1.8*, 1.9.

Discussion.— Prolimnocyon eerius is the oldest and smallest North American species of the genus. It remains exceedingly rare, being reported otherwise only from the holotype skull from Polecat Bench (Gingerich, 1989).

?Hyaenodontidae, unnamed sp. nov.?

Figure 37P-U

Referred specimens.— WW-84: 541911 (LM_1, RM_1).

Description.— Two very small molars appear to represent a new species of hyaenodontid. If so, they are the smallest hyaenodontid lower molars known from the Wa-0 interval. They are about 30% smaller than the referred lower teeth of *Acarictis ryani* (Gingerich, 1989; Strait, 2001) and differ from them in having shorter and wider talonid basins. They have open trigonids like *Prolimnocyon atavus*, and therefore might be the M_1s of *P. eerius*; but this seems unlikely, as the talonids differ from those of *P. atavus* and specimens tentatively assigned to *P. eerius* above in being much smaller and relatively shorter and wider, having a more elevated entocristid, and lacking the hypoconulid-hypoconid notch. The talonids are only slightly smaller than the trigonids and bear three distinct cusps. The talonid structure of these molars, while differing from that of most proviverrines, is similar to that of *Didelphodus*, and the teeth could easily be confused with that genus. However, compared to molars attributed above to *Didelphodus*, these teeth are smaller: 15-25% shorter and 25% narrower. In addition, the trigonids are relatively narrower, less elevated, and more extended mesiodistally, and the talonids are relatively shorter, than in any *Didelphodus* compared.

Measurements (mm).— $LM_1L=2.75$, $W_a=1.45$, $W_p=1.35$, $RM_1L=2.90$, $W_a=1.55$, $W_p=1.50$.

Discussion.— These two teeth appear to be different from any other taxon reported here, although their phylogenetic placement is ambiguous. They may represent a hyaenodontid or perhaps a cimolestid close to *Didelphodus*. They are more than 20% smaller than *Prototomus minimus*, the smallest hyaenodontid from Dormaal, Belgium (Smith and Smith, 2001).

Order CARNIVORA Bowdich, 1821

The name Carnivora (rather than Carnivoramorpha) is used here to include stem taxa as well as crown carnivorans. Carnivora are more diverse at Sand Creek Divide than in other Wa-0 local faunas. Measurements of carnivoran teeth follow Gingerich (1983: figure 1).

Family VIVERRAVIDAE Wortman and Matthew, 1899

DIDYMICTIS Cope, 1875

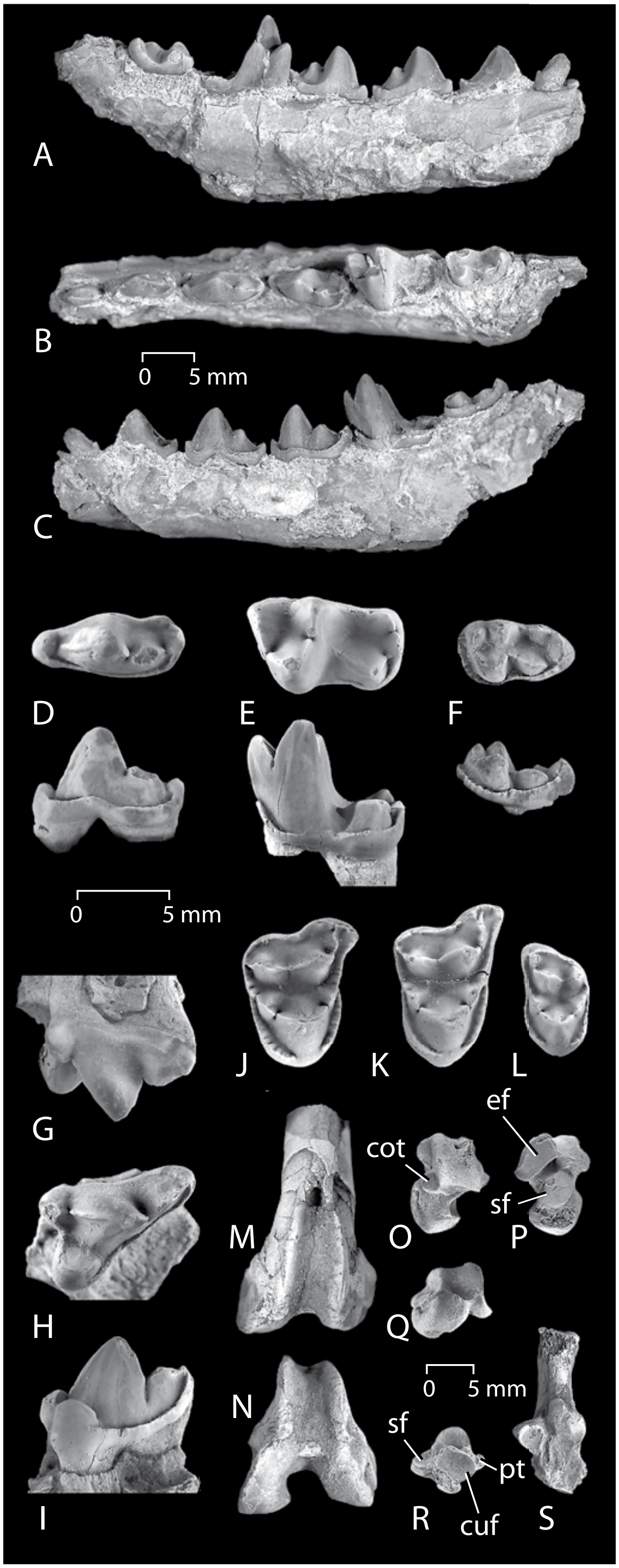
Didymictis leptomylus Cope, 1880

Figure 38

Referred specimens.— WW-71: USNM nos. 511043 (RM_2), 521672 (distal R tibia), 525664 (trigonids of LM_1 and RM_1, LP^4, RM^1), 525666 (RM_1 talonid), 527472 (associated postcrania including L distal femur, R distal tibia, R astragalus, L calcaneus, cuneiform, metatarsals, vertebrae), 538289 (L astragalus); WW-74: USNM nos. 511041 (RM^1, RM_1 talonid), 521509 (LM_2), 525661 (L dentary with M_1 talonid, RP^4, RM^1), 527652 (LM_2), 533547 (RM_1), 541775 (LM^1 and LM^1 fragment), 541914 (R astragalus and ?associated partial femur); WW-75: USNM nos. 527462 (L maxilla with P^4), 527463 (isolated teeth: LP_4, LM_1 trigonid, LM_2, RM_1, RM_2), 527464 (LM^1 and incomplete LP^4, RP^3, RM^1), 527465 (fragmentary LP_4, RM_1, LM^1), 527466 (RM_1 talonid), 527467 (talonids of RM_1 and LM_1), 533587 (L astragalus); WW-77: USNM nos.525667 (partial LP^4); WW-78: USNM 521503 (LP_3, LM_1, partial RP_4); WW-84: USNM 527471 (LM^2 and tooth fragments); WW-86: USNM 525663 (broken M^1); WW-96: USNM 525668 (incomplete RP^3 and RM^1); WW-97: USNM 527459 (LM_2, fragmentary RP_4 and RM^1), USNM 527460 (LM_2 talonid); WW-99: USNM 533602 (LM_1); WW-101: USNM 540168 (LM_1); unnumbered localities: USNM nos. 525660 (L dentary with P_3 talonid and M_1), 527468 (incomplete LP^3), 527469 (incomplete RM^1), 539474 (RM^2), 544685** (dentaries with LP_1-M_2, RP_3? and M_1); and questionably WW-74: USNM 527461 (RP^3, LM^2); WW-77: USNM 525665 (partial LP^4).

Description.— Specimens here referred to *Didymictis leptomylus* are slightly smaller than Clarkforkian *D. proteus* Simpson, 1937, and, where comparable ($M_{1\text{-}2}$; Figure 38A-C, E-F), are virtually identical to the holotype of *D. leptomylus*. M_1 (e.g., USNM nos. 521503, 527463, 540168) is identical in size and proportions to M_1 in the holotype of *D. leptomylus*, whereas the trigonid is shorter than in the holotype of *D. proteus* although the talonid is about the same length. M_2 (Figure 38F), in addition to being smaller than that in the holotype of *D. proteus*, has better defined and more widely separated paraconid and metaconid, as in *D. leptomylus* (see also Gingerich and Smith, 2006: figure 25) and unlike the connate paraconid-metaconid in the holotype of *D. proteus*. The paraconid is distinctly lower than the metaconid in some specimens, subequal in height in others. Polly (1997) described the trigonid cusps on M_2 of *D. proteus* as subequal in height. Bown (1979) assigned UW 9786, from the early Wasatchian No Water Creek fauna, to *D. protenus* "small variety," but it is the same size as *D. leptomylus* and closely resembles the Sand Creek Divide specimens in having discrete and separated trigonid cusps on M_2 (but of subequal height). It is probably better referred to *D. leptomylus*. Most M_2s in our sample are relatively shorter than those of both *D. leptomylus* and *D. proteus*, but some specimens (e.g., USNM 527463) are comparable in length to M_2 of *D. leptomylus*. The two complete P_4s in the sample (USNM 527463, 544685; Figure 38D) have the same dimensions as that in the holotype of *D. proteus*. P_4 is not preserved in the holotype of *D. leptomylus*; however, UW 9786 also has a P_4 of the same length.

M^2s in USNM nos. 527461 and 527471 (Figure 38L) compare well morphologically with (but are smaller than) some later Wasatchian specimens of *Didymictis* (e.g., USGS 25039). It is notable that they also resemble M^2 of *Vassacyon bowni* Heinrich et al., 2008, in having prominent parastyle, paracone, and conules; and it is possible that they represent that species. They differ from M^2 of *V. bowni*, however, in being less transverse and having the metaconule smaller and slightly more lingual than the paraconule. The Sand Creek Divide M^2s are larger than those of *Viverravus politus* and further differ in having prominent parastyles, relatively stronger paracones and conules, and a larger trigon basin. They differ from $M^2$of *Uintacyon* in having more widely separated paracone-metacone and a much larger trigon basin.



A small number of postcranial specimens, though not associated with teeth, can be confidently referred to this taxon as they show clear hallmarks of *Didymictis* (Heinrich and Rose, 1997). These Wa-0 elements are much smaller than representatives of this taxon from higher in the Willwood Formation. The femur bears a posteriorly-directed lesser trochanter. The small third trochanter is situated opposite the lower end of the lesser trochanter and extends a little farther distally. The distal femur (Figure 38M-N) is deeper anterioposteriorly than mediolaterally, with a well-defined and slightly elevated patellar groove. Even if the depth and boundaries of the groove have been slightly exaggerated by postmortem compression, the distal femur shows greater specialization of these features than in later *Didymictis*, implying that *D. leptomylus* was slightly more cursorially adapted (albeit incipiently) than later *Didymictis*. The astragalus (Figure 38O-Q) has a shallow trochlear groove, high lateral trochlear ridge with a nearly vertical lateral wall, an obliquely cylindrical head with a narrow calcaneal facet, and a distinct cotylar fossa for the tibial malleolus. The tibial articular surface extends onto the proximal neck, reflecting anterior contact during extreme dorsiflexion of the foot. The calcaneus (Figure 38R-S) is relatively narrow and has a distinct fibular facet and a distally placed peroneal tubercle.

Measurements (mm).— USNM 544685, P_1L= 3.10, W= 1.80, P_2L= 5.70, W=2.20, P_3L=7.45, W=3.10. See Table 6 for other dental measurements. Postcrania: USNM 521672, distal tibia W(m-l)=8.0, W(a-p)=6.2; 527472: distal femur W(m-l)=14.0,W(a-p, medial)=16.65, W(a-p, lateral)=15.55, distal tibia W(m-l)=8.35, astragalus L=10.5, W_{max}=7.75, trochlear W=5.1, calcaneus L=17.8, W=7.85; 533587, astragalus L=10.3, W_{max}=8.4, trochlear W=5.65; 538289, astragalus L=10.6, W_{max}=7.6, trochlear W=4.75; 541914, astragalus L=9.6, W_{max}=7.7, trochlear W=4.95. For comparison, an astragalus of *D. protenus* (USGS 27585) from 482 m in the Willwood Formation (biozone Wa-6) measures L=17.3, W_{max}=11.6, trochlear W=8.4.

Discussion.— *Didymictis leptomylus* is by far the most common mammalian carnivore in the Sand Creek Divide local fauna, outnumbering all other carnivorans combined. It is also the most common carnivoran in the Wa-0 faunas of both Polecat Bench and Castle Gardens (Gingerich, 2001; Strait, 2001). Heinrich et al. (2008) did not compare *Vassacyon bowni* (which is known only from two isolated M^2s) to *Didymictis*, but in view of the close resemblance to M^2 of *Didymictis* and the relative

FIGURE 38 — *Didymictis leptomylus*: A-C, L dentary with P_1-M_2, USNM 544685, in lingual, occlusal, and buccal views; D, LP_4, USNM 527463; E, LM_1, USNM 533602; F, LM_2, USNM 527463; D-F in occlusal and buccal views. G-I, maxilla fragment with LP^4, USNM 527462, in buccal, occlusal, and lingual views. J, RM^1, USNM 525664; K, RM^1, USNM 511041; L, LM^2, USNM 527461; all in occlusal view. M-N, L distal femur, USNM 527472, in anterior and distal views; O-Q, L astragalus, USNM 538289, in dorsal, ventral, and distal views; R-S, L calcaneus, USNM 527472, in distal and dorsal views. Abbreviations: **cot**, cotylar fossa; **cuf**, cuboid facet; **ef**, ectal facet; **ff**, fibular facet; **pt**, peroneal tubercle; **sf**, sustentacular facet.

TABLE 6 — Measurements (mm) of *Didymictis leptomylus* from Sand Creek Divide (* = estimated).

Upper Teeth

Specimen	P^3L	P^3W	P^4L	P^4W	M^1L	M^1W	M^2L	M^2W
USNM 511041	—	—	—	—	5.70	8.50	—	—
USNM 525661	—	—	7.65	—	6.0*	8.0*	—	—
USNM 525664 R	—	—	—	—	6.40	7.80	—	—
USNM 525664 L	—	—	7.90	6.05	—	—	—	—
USNM 527461	6.40	3.40	—	—	—	—	3.80	6.10
USNM 527462	—	—	8.20	5.50	—	—	—	—
USNM 527464	—	—	—	—	6.25	8.15	—	—
USNM 527471	—	—	—	—	—	—	3.60	6.00
USNM 539474	—	—	—	—	—	—	3.30	5.30
USNM 541775	—	—	—	—	5.50	7.90	—	—
N	1	1	3	2	5	5	3	3
Mean	6.40	3.40	7.92	5.78	5.97	8.07	3.57	5.80
Std. deviation	—	—	0.28	—	0.37	0.27	0.25	0.44
Std. error	—	—	0.16	—	0.17	0.12	0.15	0.25
Minimum	—	—	7.65	5.50	5.50	7.80	3.30	5.30
Maximum	—	—	8.20	6.05	6.40	8.50	3.80	6.10

Lower Teeth

Specimen	P_4L	P_4W	M_1L	M_1W_a	M_1W_p	M_2L	M_2W_a	M_2W_p
USNM 511041	—	—	—	4.00	—	—	—	—
USNM 511043	—	—	—	—	—	5.50	3.30	2.90
USNM 521503	—	3.40	8.40	—	4.35	—	—	—
USNM 521509	—	—	—	—	—	5.90	3.25	2.85
USNM 525660	—	—	—	5.60	—	—	—	—
USNM 525661	—	—	—		3.90	—	—	—
USNM 525664 R	—	—	—	4.55	—	—	—	—
USNM 525664 L	—	—	—	4.45	—	—	—	—
USNM 525666	—	—	—		4.20	—	—	—
USNM 527463R	—	—	8.20	4.85	3.95	6.40	3.40	3.00
USNM 527463L	7.95	3.40	—	4.90	—	6.20	3.50	3.00
USNM 527466	—	—	—	—	4.20	—	—	—
USNM 527467R	—	—	—	—	4.10	—	—	—
USNM 527467L	—	—	—	—	4.10	—	—	—
USNM 527652	—	—	—	—	—	—	3.50	—
USNM 533547	—	—	7.60	4.60	4.00	—	—	—
USNM 533602	—	—	8.25	4.90	4.10	—	—	—
USNM 540168	—	—	8.05	4.30	4.50	—	—	—
USNM 544685R	—	—	8.60	5.50	4.75	—	—	—
USNM 544685L	7.75	3.65	8.20	5.50	4.50	6.25	3.75	3.40
N	2	3	7	11	12	5	6	5
Mean	7.85	3.48	8.19	4.83	4.21	6.05	3.45	3.22
Std. deviation	—	0.14	0.31	0.52	0.26	0.36	0.18	0.22
Std. error	—	0.08	0.12	0.16	0.07	0.16	0.07	0.10
Minimum	7.95	3.65	7.60	4.00	3.90	5.50	3.25	2.85
Maximum	7.75	3.40	8.60	5.60	4.75	6.40	3.75	3.40

abundance of the latter in Wa-0, the possibility that *V. bowni* is based on M^2s of *D. leptomylus* should be considered.

The holotype of *D. leptomylus* is thought to derive from Wa-1-2 strata (although its exact provenance is unknown), whereas that of *D. proteus* is from the Clarkforkian. Polly (1997: 35) distinguished *D. proteus* from *D. leptomylus* by the "slightly larger" size of the former "(except in Wa-0)." However, his diagnosis of *D. leptomylus* states that it "differs from earliest Wasatchian

D. proteus in being slightly larger," implying that *D. proteus* encompassed the size range of *D. leptomylus*. No other distinguishing features were listed and, in fact, their ranges of tooth size overlap almost completely (except during Wa-0), which can be seen clearly in Polly's (1997) figure 8. Thus the morphological basis (if any) for separating these two species is unclear, and Polly evidently based taxonomic distinction solely on an inferred cladogenetic event. If they are synonymous, which seems likely, *D. leptomylus* has priority. Moreover, it is not clear why Polly assigned Wa-0 *Didymictis* to *D. proteus* rather than to *D. leptomylus*, which is closer in size. Indeed, M_1 of the holotype of *D. leptomylus* is within the size range of his sample of Wa-0 *D. proteus* (Polly, 1997: figure 8). Gingerich (1989) initially assigned his Wa-0 specimens to *D. leptomylus*, subsequently changed the assignment to *D. proteus* (Gingerich, 2001) following Polly, and more recently reverted to *D. leptomylus* (Gingerich and Smith, 2006). Besides closer size, the Sand Creek Divide specimens more closely resemble *D. leptomylus* in trigonid structure of M_2, although they differ from the holotypes of both *D. leptomylus* and *D. proteus* in having shorter M_2s.

VIVERRAVUS Marsh, 1872

Viverravus acutus Matthew, 1915

Figure 39A-F, J

Referred specimens.— WW-74: USNM 541964** (L dentary with M_1); WW-79: USNM 538337 (L dentary with M_{1-2} talonids); WW-84: USNM 538338 (LM_2, damaged LM_2, 2 fragmentary RP_4s); WW-85: USNM 527475 (R maxilla with P^{2-4}); WW-113: USNM 538396 (LM_2).

Description.— These specimens are very similar in morphology to the holotype of *Viverravus acutus*. An M_2 (USNM 538396) is the same size as that in the holotype, and the maxilla with premolars appears to be comparable in size. The other specimens are slightly smaller, close to the size of *V. bowni*, which was said to differ from *V. acutus* in being about 16-17% smaller (Gingerich, 1987). All are within the range of *V. acutus* as summarized by Polly (1997), however, and they show no notable differences from that species.

Measurements (mm).—USNM 541964, M_1L=3.70, W_a=2.00, W_p=1.60; USNM 538337, M_1L=3.9*, W=1.7*, M_2L=2.95*, W=1.30; USNM 538338, M_2L=2.45, W_a=1.5, W_p=1.15; USNM 527475, P^2L=2.00, W=0.90, P^3L=2.80, W=1.30, P^4L=4.20, W=2.45; USNM 538396, M_2L=2.95, W_a=1.60, W_p=1.30.

Discussion.— Gingerich (1989) attributed a specimen from Polecat Bench to *Viverravus bowni* but subsequently (Gingerich, 2001) referred it to *V. acutus*, following Polly (1997). Although Polly (1997) synonymized *V. bowni* with late Paleocene *V. laytoni* (originally *Protictis laytoni*), he referred the single Wa-0 specimen of *V. bowni* then known to *V. acutus*. He interpreted *V. acutus* to be sexually dimorphic and evidently considered the Wa-0 specimen to be a female *V. acutus*. More recently, Gingerich and Smith (2006) referred two isolated teeth from Wa-M to *V. bowni*, citing their smaller size. Some of the specimens reported here (USNM 541964, 538338) are even smaller than the holotype of *V. bowni*, and it is possible that one or both of them are large individuals of *V. rosei*. Another specimen is similar in size to the holotype of *V. acutus*, while at least one other is intermediate in size, raising doubt as to how many species are present in this small sample. We tentatively refer them all to *V. acutus*. *V. acutus* has also been reported from Castle Gardens (Yans et al., 2006), and is known both before and after Wa-0. Larger samples and more complete specimens are needed to determine if both *V. bowni* and *V. acutus* are valid, and if both were present during the PETM.

Viverravus rosei Polly, 1997

Figure 39L-Q

Referred specimen.— WW-84: USNM 538397 (partial RP_4, LM_1 trigonid).

Description.— Despite the fragmentary condition of these two teeth, they show characteristic features of *Viverravus*, including a posterior accessory cusp on P_4 between the protoconid and talonid cusp, and an open trigonid of M_1. They are much smaller than *V. acutus* and are very close in size and morphology to the holotype of *V. rosei*, the smallest species of *Viverravus*.

Measurements (mm).— M_1 trigonid L=2.0, W=2.0 (comparable measurements of the holotype are: L=2.0, W=1.7).

Discussion.— This is the first record of this diminutive species from Wa-0. Its occurrence during this temporal interval is not unexpected, as Polly (1997) reported it from the latest Clarkforkian as well as from biozones Wa-2 through Wa-4. Additional specimens of *V. rosei* extend its documented occurrence to Wa-1 (USGS 6622, R dentary with P_4-M_2) and Wa-6 (USNM 495295, R dentary with P_4-M_2).

Cf. *Viverravus politus* Matthew, 1915

Figure 39G-I, K

Referred specimens.— WW-85: USNM 538325 (LM_1, C^1, and associated fragments); WW-97: USNM 538356 (incomplete LP_4, LM^2).

Description.— An isolated M_1 compares most closely with *Viverravus politus* but has a slightly more closed trigonid and slightly narrower talonid, both of which are resemblances to M_2 of *Prototomus deimos*. Unlike the latter, however, the hypoflexid is shallower, the entoconid lower, and the hypoconulid less posteriorly projecting—all resemblances to *Viverravus*. It is slightly smaller than the holotype of *V. politus*. The P_4, though fragmentary, is unequivocally *Viverravus* based on its size and the presence of a prominent posterior accessory cusp between the protoconid and talonid. It is larger and more robust than P_4 of *Viverravus acutus* and compares closely with P_4 of *V. politus* (UM 65118; Rose, 1981a: figure 50). The referred M^2 is very transverse, with a nearly straight buccal margin lacking an ectoflexus. Although the anterobuccal margin is expanded, the parastyle and preparacrista are poorly developed; conules, if once present, are now worn away. In these features and size, the tooth is almost identical to M^2 of *V. politus* (UM 81942; Polly, 1997:

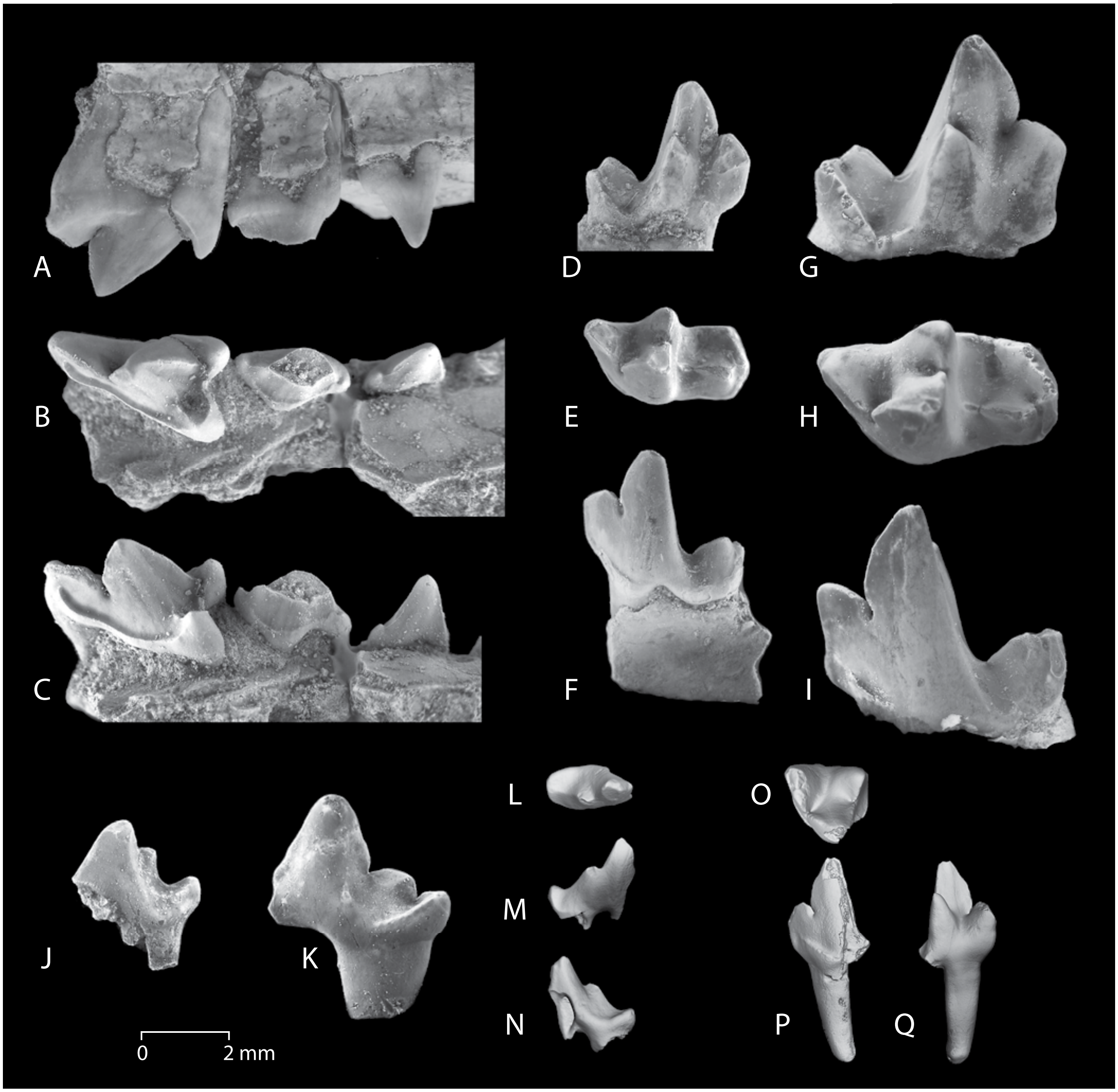


FIGURE 39 — *Viverravus*: A-C, *V. acutus*, R maxilla with $P^{2\text{-}4}$, USNM 527475, in buccal, occlusal, and lingual views; D-F, *V. acutus*, L dentary fragment with M_1, USNM 541964, in lingual, occlusal, and buccal views; G-I, cf. *V. politus*, LM_1, USNM 538325, in lingual, occlusal, and buccal views; J, *V. acutus*, RP_4, USNM 538338, lingual view; K, cf. *V. politus*, LP_4 (reversed for comparison), USNM 538356, lingual view; L-Q, *V. rosei*, partial RP_4 (L-N) and LM_1 trigonid (O-Q), USNM 538397, in occlusal, buccal, and lingual views. All to same scale.

figure 11), though slightly smaller than Polly's Wa-1 samples.

Measurements (mm).— USNM 538325, M_1L=5.80, W_a=3.10, W_p=2.45; USNM 538356, P_4W=2.1; M^2L=2.7, W=4.9.

Discussion.— These teeth provide evidence of at least a third species of *Viverravus* during the PETM and, like many other Wa-0 species, are slightly smaller than most older and younger conspecific specimens.

Family MIACIDAE Cope, 1880

UINTACYON Leidy, 1872

Uintacyon gingerichi Heinrich, Strait, and Houde, 2008
Figure 40A-E, G, J-L

Referred specimens.— WW-74: USNM 521550 (LM_3), 527662 (R dentary with P_4-M_2); WW-75: USNM 538394 (LP^4), 538405 (RM^1, LM^1); WW-80 (=WW-116): USNM 527549 (incomplete LM^1, fragments of tibia and astragalus), 527550 (RM_1 trigonid); WW-84: USNM 538343 (RM_1), 538391 (RM^1 fragment, RM^3); WW-97: USNM 538393 (RM^1, LM^1, LM^2); WW-113: USNM 538392 (RM^2); and questionably WW-79: USNM 527473 (RP^3, metastylar blade of RP^4, RM^3, LP^3, L calcaneus, and associated fragments).

Description.— These specimens are very similar to, but smaller than, Clarkforkian *Uintacyon rudis* and approximate the size of *U. gingerichi* reported by Heinrich et al. (2008).

The upper molars referred here (Figure 40K, L) closely resemble those of the holotype in being transverse with a salient parastylar lobe (elongate, with a transverse, sectorial preparacrista) and a conspicuous ectoflexus on M^1. Characteristics of *Uintacyon* include the metacone being much lower than, slightly buccal to, and closely appressed to the paracone, and the paraconule prominent (no distinct metaconule). The paraconule may be single or twinned (USNM 538405) and is separated from the preprotocrista by a carnassial notch, as in the holotype. M^1 has a well-developed stylar shelf with an incipient mesostyle on the ectocingulum, and prominent pre- and postcingula, which are not continuous lingually. M^2 and M^3 are successively smaller, and are generally similar to M^1 but have a narrower stylar shelf, shallower ectoflexus, and weaker cingula. USNM 538392 has a hint of a metaconule. The metacone of the diminutive M^3 is strongly reduced. P^4 has a tall paracone with steep preparacrista and a tiny parastyle (Figure 40J). A deep carnassial notch intervenes between the paracone and the well-developed, elevated metastylar blade. The protocone is small and anterolingually situated.

The lower molars have trenchant talonids with the entocristid very low, so the basin is not enclosed as in *Miacis*. Viewed from behind, the back of the talonid appears gabled (Figure 40G) with the cristid obliqua near the median axis of the talonid on M_2, slightly more buccal on M_1—forming a trenchant ridge with a gentle, weakly concave lingual slope and a steeper buccal slope.

Measurements (mm).— USNM 521550, M_3L=1.95, W=1.55; USNM 527662, P_4L=3.80, W=2.00, M_1L=4.65, W_a=3.40, W_p=2.25, M_2L=3.60, W_a=2.50, W_p=2.00; USNM 538343, M_1L=5.00, W_a=3.30, W_p=2.50; USNM 538391, M^1L=4.00, M^3L=1.70, W=3.30; USNM 538392, M^2L=2.70, W=4.70; USNM 538393, RM^1L=4.50, LM^1L=4.00, W=6.50; USNM 538394, P^4L=6.30, W=4.10; USNM 538405, LM^1W=5.45.

Discussion.— These specimens corroborate the presence of a small species of *Uintacyon* during the PETM. *Uintacyon gingerichi* is very similar in size and morphology to *Miacis winkleri* and *M. deutschi*, with which it could be easily confused. The principal difference in the lower teeth appears to be the slightly higher and sharper entocristid in *Miacis*, resulting in a slightly more basined talonid—the main feature that distinguishes these two closely allied genera. *U. gingerichi* further differs from *Miacis* in a few other subtle features: it has a relatively slightly lower trigonid, and the cristid obliqua is more centrally positioned on the talonid, resulting in a less steeply inclined lateral talonid wall on M_2. In addition, the cristid obliqua of M_2 remains level as it approaches the back of the trigonid, rather than inclining to form a slight notch as in *Miacis*.

MIACIS Cope, 1872

Cf. *Miacis deutschi* Gingerich, 1983
Figure 40F, H-I

Referred specimen.— WW-75: USNM 533586 (LM_2).

Description.— This isolated molar is virtually identical in size and shape to M_2 in the holotype. It is slightly larger and the trigonid wider and more inflated than that of *M. winkleri*. The tooth is also very similar to M_2 of *Uintacyon gingerichi*, and with no other specimens referable to *M. deutschi* it is tempting to conclude that it is simply a variant of *U. gingerichi*. However, like the holotype of *M. deutschi*, USNM 533586 has a higher trigonid and a more basined talonid, with a more distinct entoconid and higher entocristid, than in *U. gingerichi*, in which the talonid is more trenchant. These differences are typically used to distinguish these two closely allied miacid genera. In addition, the hypoconid is slightly more buccal, consequently the cristid obliqua is positioned slightly buccal to the middle of the talonid. The cristid obliqua inclines more steeply than in *U. gingerichi*, forming a shallow notch at the junction with the postvallid. The close similarity between these two species underscores the likelihood that *Miacis* and *Uintacyon* are sister taxa, and that *Miacis* diverged from *Uintacyon* in the late Paleocene.

Measurements (mm).— M_2L=3.65, W=2.5.

Discussion.— The stratigraphic range of *Miacis deutschi* was previously considered to include only upper Wa-2 and Wa-3 strata (Gingerich, 1983; Heinrich et al., 2008). Strait (2001) reported an isolated M_1 of *M. deutschi* from Castle Gardens, which was not mentioned by Heinrich et al. (2008).

Cf. *Miacis rosei* Heinrich, Strait, and Houde, 2008
Figure 40M-R

Referred specimen.— WW-84: USNM 538404 (RM_2, RM_3).

Description.— These carnivoran teeth are tentatively assigned to *Miacis rosei*, the smallest known miacid, based on their minute size. They are smaller than the comparable teeth of any known North American miacid except *M. rosei* and possibly *M. igniculus* Beard and Dawson, 2009. M_2 is about 20% shorter and 35% narrower than that in the holotype of *M. winkleri* (the smallest North American species of *Miacis*), whose dimensions are almost exactly the same as the mean for the small sample of *M. winkleri* reported by Gingerich (1983). M_3 is very close in size to the referred M_3 of *M.rosei* (Heinrich et al., 2008). They are identified as M_2 and M_3 based on trigonid height. The relative height of the protoconid of M_2 (H/W) is 1.44, at the high end of the range for M_2 of *M. winkleri* and well above that for *M. deutschi* (Gingerich, 1989). M_2 has not previously been known for *M. rosei*. The trigonid of both molars closely approaches an equilateral triangle, with the protoconid tallest, and the metaconid slightly taller than the paraconid. As is typical in *Miacis*, the talonids are obliquely ovoid basins, each surrounded by a well-defined crest bearing small but distinct hypoconid and hypoconulid and a low entocristid; on M_2 a small, lower entoconid is also present. M_3 is easily distinguished from that of *Uintacyon gingerichi* (USNM 521550) by its higher trigonid with more acute cusps and larger, more basined talonid.

Measurements (mm).— M_2L=3.0, W=1.8; protoconid H=2.6; M_3L=2.1, W=1.3.

Discussion.— The morphology of the two molars assigned here is most like that of *Miacis winkleri*, including having narrower talonid basins than in *M. exiguus* and *M. petilus*. Their size is consistent with that of the only two previously known teeth of *Miacis rosei*, M^1 and M_3 from the Wa-0 biozone of the Castle Gardens area (Heinrich et al., 2008). Like many other Wa-0 taxa, *Miacis rosei* is the smallest known species in its genus.

Miacis igniculus was based on an incomplete premolar (identified as P_4, but possibly an upper premolar) from the basal Eocene of Mississippi, whose referral to *Miacis* is questionable. Unfortunately, it cannot be directly compared with any of the teeth referred to *M. rosei*. Until more definitive evidence confirms that it indeed represents this genus, we regard *M. rosei* as the smallest species.

Smith and Smith (2010) recently proposed a new genus *Gracilocyon* for *Miacis winkleri*, *M. rosei*, and the new species *G. solei* from Dormaal, Belgium. However, the only diagnostic traits of *Gracilocyon* known in *M. rosei* pertain to M^1; and they are less well expressed in *M. rosei*, making its reference to the new genus equivocal. The two molars assigned here have narrow talonid basins comparable to those of *M. winkleri* and *G. solei*, which may prove to differentiate these species from other *Miacis*. However, the Sand Creek Divide molars differ from the latter two species in having more robust trigonids with lower paraconids. Until *M. rosei* is better known, and the distinctions between *Gracilocyon* and *Miacis are* better demonstrated, we retain this species in *Miacis*.

Hooker (2010) recently described a new species of very small *Miacis*, *M. rundlei*, from the early Ypresian Blackheath Formation at Abbey Wood, U.K. It is slightly larger than the Sand Creek Divide molars: M_2 is similar in length but 20-25% wider, whereas M_3 is both longer and relatively wider. Both species have relatively high trigonids; M_2 protoconid height compared to length is slightly less in cf. *M. rosei* than in *M. rundlei* (H/L = 0.87 vs. 0.91), but M_2 protoconid height compared to width is greater in cf. *M. rosei* (H/W = 1.44 vs. 1.31). A shallow notch separates the hypoconid and hypoconulid of M_2 and M_3 in both species. Cf. *M. rosei* differs from *M. rundlei*, however, in having narrower, more oblique talonid basins and more open trigonids. The precise interrelationships of these small, primitive species of *Miacis* remain to be deciphered when better samples are available.

“MIACOIDEA,” unidentified

Referred specimen.— WW-84: USNM 538395 (miscellaneous teeth).

Description.— These eight isolated teeth or tooth fragments represent at least three different taxa based on size differences. Included are an M^2 and several fragmentary premolars which cannot be confidently assigned to particular species but appear to represent taxa of miacids or viverravids described above.

Order CONDYLARTHRA Cope, 1881

This heading is used for convenience, with no implication of close relationship of all the taxa listed here. The precise phylogenetic position of several of the taxa included here is still very much in doubt, but this is not the appropriate venue for an exploration of their relationships.

Family ARCTOCYONIDAE Giebel, 1855

We use Arctocyonidae to include Oxyclaeninae, following Archibald (1998). Gingerich (1989) recognized three arctocyonids from the Wa-0 interval at Polecat Bench: *Thryptacodon barae*, *Chriacus badgleyi*, and *Princetonia yalensis*. *Thryptacodon* has not been found at Sand Creek Divide, but Strait (2001) reported it from Castle Gardens. Specimens very similar to *C. badgleyi* and *P. yalensis* are present at Sand Creek Divide, and all are here referred to *C. badgleyi*, as detailed below.

CHRIACUS Cope, 1883

Chriacus badgleyi Gingerich, 1989

Figure 41

Synonym.— *Princetonia yalensis* Gingerich, 1989.

Referred specimens.— WW-73: USNM 533555 (RM_2), USNM 538406 (RP^4?, RM^1), 538408 (LM_1, two molar fragments); WW-75: USNM 533605 (LM_1), 538413 (RM^1); WW-83: USNM 533564 (RM_3); WW-84: USNM 538379 (LdP^4, RM^1, RM^3), 538407 (RM_1, RM_3); WW-97: USNM 538388 (miscellaneous teeth); WW-101: USNM 533604 (LP_3, 2LM^1s, RM^2); WW-113: USNM 538385 (LP_4?); WW-119: USNM 539500 (L astragalus); WW-125: USNM 533594 (RM_1, LM_2 talonid), 538295 (RM^1); WW-171: USNM 533543 (dentaries with LM_{2-3}, RP_3-M_2), 542112** (LP_4, LM^1); unnumbered localities: USNM 539472 (RM^2), 539473 (LM_2), 539479 (R astragalus); and tentatively WW-71: USNM 538382 (LM_1), 538410 (L molar trigonid); WW-74: USNM 538342 (LM^2); WW-76: USNM 538411 (RP^4); WW-84: USNM 538369 (RP_2 or P_3); WW-113: USNM 538409 (LP^4 and 2 molar trigonids); WW-114: USNM 540306 (LM_1 trigonid).

Description.— The teeth assigned here bear the hallmarks of small arctocyonids, including lower premolars with tall trigonids and small, simple talonids, and moderately bunodont molars, the lowers with relatively low trigonids and broad talonid basins, and the uppers with a prominent posterolingual shelf continuous lingually with the precingulum. USNM 533543 (Figure 41I-J) contains simple premolars essentially

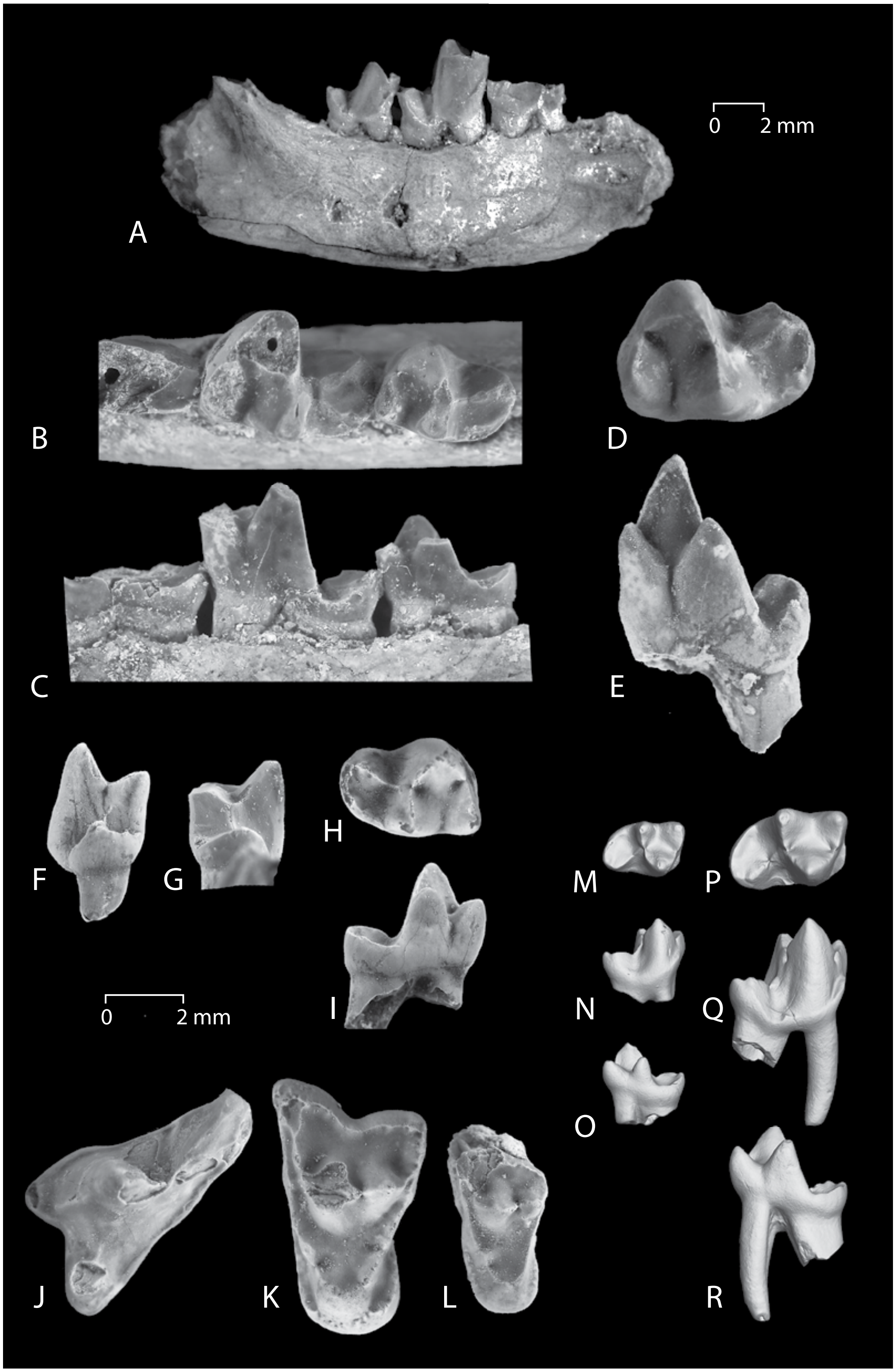


FIGURE 40 — Miacidae: A-C, G, *Uintacyon gingerichi*, R dentary with P_4-M_2, USNM 527662, in buccal (A), occlusal (B), and lingual (C) views; G, M_2 in posterior view. D-E, *U. gingerichi*, RM_1, USNM 538343, in occlusal and lingual views. F, H-I, cf. *Miacis deutschi*, LM_2, USNM 533586, in posterior, occlusal and lingual views. J-L, *U. gingerichi*, LP^4 (J, USNM 538394), LM^1 (K, USNM 538393), LM^2 (L, USNM 538393). M-R, cf. *Miacis rosei*, RM_2 (M-O), RM_1 (P-R), USNM 538404, in occlusal, buccal, and lingual views. Scale at upper right applies to A, scale at lower left to all others.

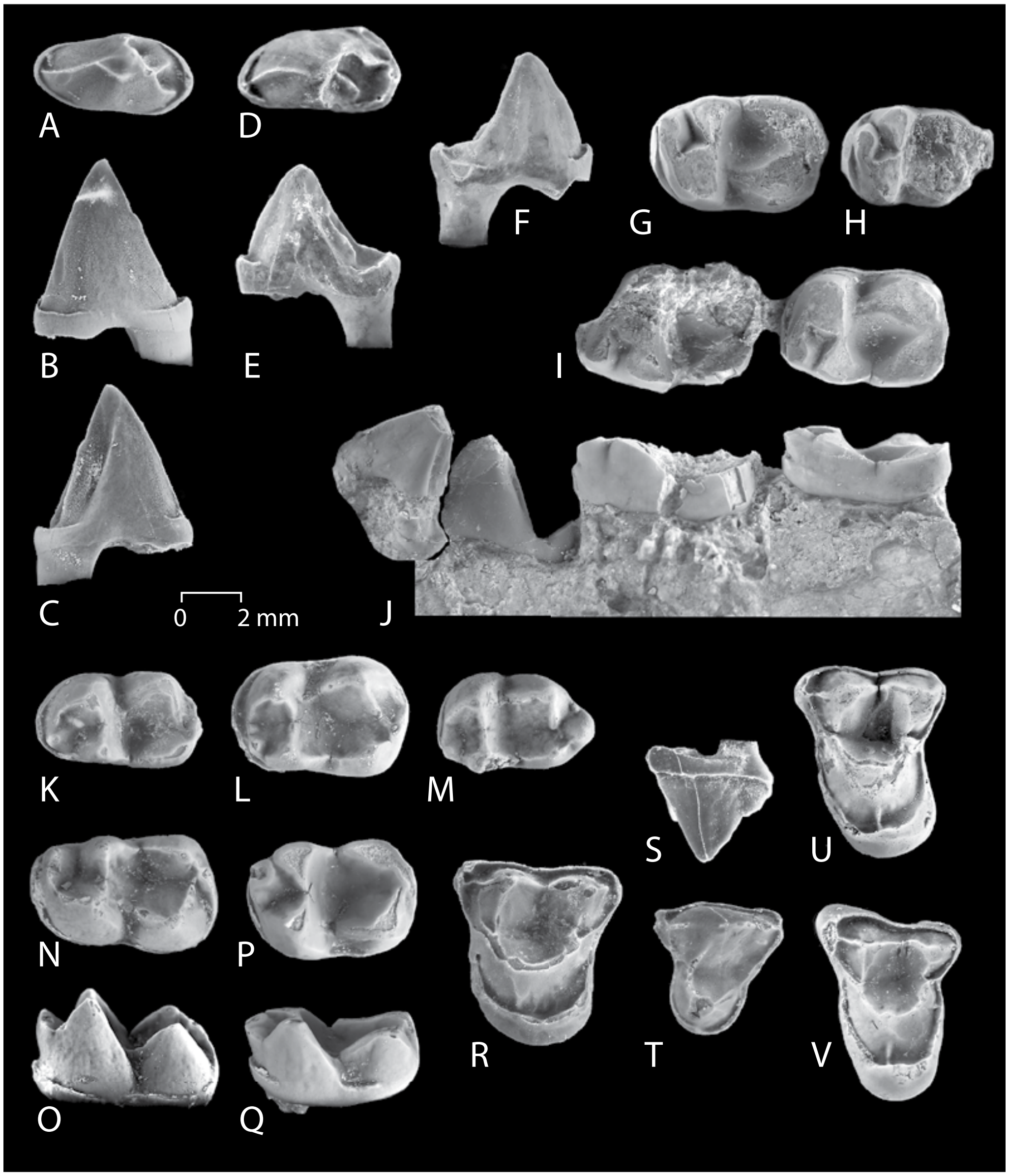


FIGURE 41 — *Chriacus badgleyi*: A-C, LP$_3$, USNM 533604, in occlusal, buccal, and lingual views; D-F, RP$_4$, USNM 538388, in occlusal, lingual, and buccal views; G-J, dentaries with LM$_2$ (G), LM$_3$ (H), RP$_3$-M$_2$ in occlusal (I) and lingual (J) views, USNM 533543; K, RM$_1$, USNM 538407; L, RM$_2$, USNM 533555; M, RM$_3$, USNM 538407; N-O, LM$_1$, USNM 533605, in occlusal and buccal views; P-Q, LM$_2$, USNM 539473, in occlusal and buccal views; R, LM^1, USNM 533604; S-T, cf. *C. badgleyi*, LP^4, USNM 538409; U, LM$^{1/2}$, USNM 538388; V, cf. *C. badgleyi*, LM^2, USNM 538342. All to same scale.

identical in size and morphology to those of the holotype of *Chriacus badgleyi* together with molars indistinguishable from those in the holotype of *Princetonia yalensis*, constituting strong evidence that these two similar and coexisting species are synonymous. In particular, P$_4$ lacks a metaconid and has only a slight enamel thickening where a metaconid would form (a diagnostic trait of *C. badgleyi*), and the lower molar talonids have a reduced hypoconulid situated at the lingual end of an inclined postcingulum and closer to the entoconid than to the hypoconid (characteristics of *P. yalensis*). In worn molars here referred to *C. badgleyi* (including USNM 533543), the hypoconulid may be almost indistinct, and the postcingulum continues almost uninterrupted to the entoconid, as in the holotype of *P. yalensis*. Relatively unworn molars reveal a distinct, low hypoconulid which is close to the entoconid but separated from it by a shallow notch and from the hypoconid by a deeper notch. The ectocingulum is weak and discontinuous or absent.

P^4 is preserved in three specimens (USNM 538406, 538409, 538411), which show slight differences. All three P^4s are triangular with a tall paracone and much lower protocone. The tooth is waisted, with a somewhat deeper constriction anteriorly. In USNM 538406 and 538409 (Figure 41S-T) P^4 has a small metacone, not present in the other specimen (USNM 538411), although its absence in the latter could be due to heavier wear. USNM 538406 and 538411 have strong parastyles, whereas the parastyle is weak in USNM 538409. Low cingula completely encircle the latter two teeth; USNM 538406 appears to have only a buccal cingulum, but the tooth margins are eroded. The upper molars allocated to *C. badgleyi* conform closely with those of *Chriacus*: they have rather narrow stylar shelves, distinct parastylar and metastylar projections and a shallow ectoflexus, and a prominent posterolingual cingulum, but a distinct hypocone was observed only in little-worn specimens (e.g., USNM 538342). When present there are multiple small cuspules on the cingulum in the area of the hypocone.

Measurements (mm).— See Table 7.

Discussion.— Gingerich (1989) distinguished the new genus *Princetonia* from other arctocyonids based on its having a long, narrow P_4 lacking a metaconid, together with broad, rectangular molars with lingual paraconids and broad, basined talonids. He further distinguished it from *Chriacus* by its low trigonids, rectangular M_{2-3}, and more rounded cusps and crests. Secord (2008) repeated some of these distinctions, but none has been demonstrated quantitatively. Because the holotype of *Princetonia yalensis* (the only original specimen from Wa-0) contained only molars, and that of *Chriacus badgleyi* only premolars, direct comparison of the types was impossible. USNM 533543 provides evidence that these two holotypes represent the same species, for which the name *C. badgleyi* has priority, following recommendation 69A.10 of the International Code of Zoological Nomenclature (ICZN, 1999).

Besides the holotype, Gingerich referred several specimens from the late Tiffanian Princeton Quarry to *P. yalensis*, and the absence of a metaconid on P_4 in this species was based on those referred specimens. However, the Princeton Quarry specimens differ in certain features from the holotype and may not be conspecific (Secord, 2008). For instance, Secord (2008) noted that the holotype lacks a distinct entoconid, which is present in the Princeton Quarry sample. The Sand Creek Divide sample shows that wear may result in a poorly defined entoconid, whereas unworn specimens have a distinct entoconid (e.g., USNM 533555). It also shows that the absence of a metaconid on P_4 is also characteristic of *C. badgleyi*, regardless of whether the Princeton Quarry sample represents the same species.

Chriacus and other small arctocyonids have long been in need of revision. The current concept of *Chriacus* (e.g., Archibald, 1998, based on Van Valen, 1978) probably contains multiple genera, but no comprehensive study has been undertaken to resolve its systematics. The type species, *C. pelvidens*, does indeed differ from *Princetonia yalensis* in having a distinct metaconid on P_4, as do specimens of "*Metachriacus punitor*" (now generally referred to *Chriacus*) and some individuals of *C. baldwini* we observed; but many specimens assigned to various species of *Chriacus* have a much less distinct P_4 metaconid or none at all. In particular, no specimen we examined of Wasatchian *Chriacus*, cf. *C. gallinae*, from the Bighorn Basin has a distinct metaconid on P_4, and all show little more than a slightly thickened vertical ridge ("metaconid ridge" of Secord, 2008) where a metaconid would be situated (e.g., USGS nos. 1957, 2353, 7386, 8358, 8595). The same is true for some individuals of *C. baldwini* (e.g., USNM nos. 15283 and 407522). Most importantly, the holotype of Wa-0 *C. badgleyi* lacks a distinct metaconid on P_4, an absence that was regarded as a diagnostic character of the species (Gingerich, 1989); instead it shows a similar "metaconid ridge" to that seen in at least one late Tiffanian specimen of *Princetonia yalensis* (YPM-PU 13957). Secord (2008) also reported this ridge in *Princetonia*. Thus metaconid expression on P_4 appears to be variable in *Chriacus* and does not separate it from *Princetonia*.

A possible difference that might still separate *P. yalensis* from *Chriacus* is the reduced hypoconulid in *Princetonia*. *Chriacus* sensu stricto (e.g., *C. pelvidens* and *C. gallinae*) is typically characterized by a prominent posteriorly-directed hypoconulid separated from the entoconid by a shallow notch. An inclined, shelf-like postcingulum rises from a low point on the buccal side to the hypoconulid in *Chriacus* (also seen in *C. punitor* and *C. baldwini*). Because of the reduced hypoconulid in *P. yalensis* (and the Sand Creek Divide specimens described here), the postcingulum continues essentially to the entoconid. However, not all *Chriacus* specimens have a prominent hypoconulid. Furthermore, at least two Princeton Quarry specimens (YPM-PU 13943 and 13957) referred to *Princetonia* by Gingerich (1989) have a stronger, posteriorly directed hypoconulid, as in *Chriacus*. These observations cast doubt on the utility of hypoconulid expression as a generic character in small arctocyonids.

The specimens described here confirm that *Chriacus* is by far the most abundant Wa-0 arctocyonid, while *Thryptacodon* (not known from Sand Creek Divide) is very rare, a pattern also apparent in the sample from Polecat Bench (Gingerich, 1989, 2001). Interestingly, this is the inverse of the pattern of relative abundance of these genera in the intervals preceding and succeeding Wa-0 in the Bighorn Basin. During the Clarkforkian, *Thryptacodon* is far more abundant than *Chriacus*-like taxa that have been variously referred to *Chriacus*, *Princetonia*, and *Tricentes* (Rose, 1981a; Secord, 2008). Similarly, Bown (1979) reported 73 specimens of *Thryptacodon* but only a single specimen of *Chriacus* from the early Wasatchian (Wa-1/2) of the No Water Creek area. *Chriacus* remains very rare and *Thryptacodon* abundant throughout the earlier Wasatchian. This pattern reverses during the Biohorizon B interval, when *Chriacus* becomes the dominant small arctocyonid, while *Thryptacodon* becomes uncommon. This inverse pattern of abundance of *Chriacus* and *Thryptacodon* during the Clarkforkian and Wasatchian suggests either shifting local habitats or ecological competition between these genera.

The absence of *Thryptacodon* in the Sand Creek Divide sample highlights a broader pattern in the distribution of condylarth genera that range across the Paleocene-Eocene boundary. Two other condylarths are relatively abundant before and after Wa-0 but rare or absent during this interval. *Haplomylus* was absent throughout Wa-0 but present in Wa-M (see below).

TABLE 7 — Measurements (mm) of *Chriacus badgleyi* from Sand Creek Divide (* = estimated).

Upper Teeth

Specimen	dP^4W	P^3L	P^3W	P^4L	P^4W	M^1L	M^1W	M^2L	M^2W	M^3L	M^3W
USNM 533604a	—	—	—	—	—	5.10	5.70	4.90	6.40	—	—
USNM 533604b	—	—	—	—	—	5.40	5.90	—	—	—	—
USNM 538342	—	—	—	—	—	—	—	4.60	6.50	—	—
USNM 538379	4.10	—	—	—	—	5.15	5.70	—	—	4.00	5.50
USNM 538388	4.00	—	—	—	—	—	—	4.90	6.45	—	—
USNM 538406	—	4.50	4.00	—	—	5.90	5.9*	—	—	—	—
USNM 538409	—	—	—	4.00	4.30	—	—	—	—	—	—
USNM 538411	—	—	—	4.50	5.00	—	—	—	—	—	—
USNM 539472	—	—	—	—	—	—	—	5.60	6.90	—	—
USNM 542112	—	—	—	—	—	5.60	5.95	—	—	—	—
N	2	1	1	2	2	5	5	4	4	1	1
Mean	4.05	4.50	4.00	4.25	4.65	5.43	5.83	5.00	6.56	4.00	5.50
Std. deviation	—	—	—	—	—	0.33	0.12	0.42	0.23	—	—
Std. error	—	—	—	—	—	0.15	0.05	0.21	0.11	—	—
Minimum	4.00	—	—	4.00	4.30	5.10	5.70	4.60	6.40	—	—
Maximum	4.10	—	—	4.50	5.00	5.90	5.95	5.60	6.90	—	—

Lower Teeth

Specimen	P_2L	P_2W	P_3L	P_3W	P_4L	P_4W	M_1L	M_1W_a	M_1W_p	M_2L	M_2W_a	M_2W_p	M_3L	M_3W_a	M_3W_p
USNM 533543R	—	—	4.8*	—	5.3*	—	5.8*	4.2*	3.9*	5.50	3.90	3.80	—	—	—
USNM 533543L	—	—	—	—	—	—	—	—	—	5.60	3.75	3.80	5.00	3.20	3.20
USNM 533555	—	—	—	—	—	—	—	—	—	5.70	3.50	3.90	—	—	—
USNM 533564	—	—	—	—	—	—	—	—	—	—	—	—	5.60	3.10	3.15
USNM 533594	—	—	—	—	—	—	5.60	3.00	3.45	—	—	4.20	—	—	—
USNM 533604	—	—	5.10	2.50	—	—	—	—	—	—	—	—	—	—	—
USNM 533605	—	—	—	—	—	—	6.05	3.40	3.75	—	—	—	—	—	—
USNM 538369	3.10	1.60	—	—	—	—	—	—	—	—	—	—	—	—	—
USNM 538382	—	—	—	—	—	—	4.5*	2.5*	2.8*	—	—	—	—	—	—
USNM 538385	—	—	—	—	5.20	2.20	—	—	—	—	—	—	—	—	—
USNM 538388	4.20	2.10	—	—	5.30	2.70	—	—	—	—	—	—	5.50	3.10	3.10
USNM 538407	—	—	—	—	—	—	5.30	3.10	3.20	—	—	—	5.10	3.10	3.00
USNM 538408	—	—	—	—	—	—	5.30	3.65	3.80	—	—	—	—	—	—
USNM 539473	—	—	—	—	—	—	—	—	—	5.50	3.55	3.60	—	—	—
USNM 542112	—	—	—	—	5.35	2.60	—	—	—	—	—	—	—	—	—
N	2	2	2	1	4	3	6	6	5	4	4	5	4	4	4
Mean	3.65	1.85	4.95	2.50	5.29	2.50	5.43	3.31	3.62	5.58	3.68	3.86	5.30	3.13	3.11
Std. deviation	—	—	—	—	0.06	0.27	0.54	0.59	0.29	0.10	0.19	0.22	0.29	0.05	0.09
Std. error	—	—	—	—	0.03	0.15	0.22	0.24	0.13	0.05	0.09	0.10	0.15	0.03	0.04
Minimum	3.10	1.60	4.80	—	5.20	2.20	4.50	2.50	3.20	5.50	3.50	3.60	5.00	3.10	3.00
Maximum	4.20	2.10	5.10	—	5.35	2.70	6.05	4.20	3.90	5.70	3.90	4.20	5.60	3.20	3.20

The distribution of *Apheliscus* is even more dramatic, as this genus is not recorded from either Wa-M or Wa-0, despite being relatively common in both Cf-3 and Wa-1/2 faunas (Bown, 1979; Rose, 1981a). These significant but transient changes in faunal composition highlight the distinctiveness of Wa-0 communities.

Family HYOPSODONTIDAE Trouessart, 1879

HYOPSODUS Leidy, 1870

Hyopsodus loomisi McKenna, 1960

Figures 42-43

Referred specimens.— WW-71: USNM 538327 (LP$_3$, LM^1); WW-73: USNM 539503 (RM^2); WW-74: USNM nos. 521510 (RM$_1$, RM$_3$, LM^2), 533548 (L dentary with M$_{2\text{-}3}$), 533549 (RdP$_4$), 533566 (RM^2); WW-75: USNM nos. 538258 (RM$_3$), 538261 (RM^2); WW-77: USNM 521519 (LM^1); 5m above WW-78: USNM 521549 (R dentary with M$_2$); WW-84: USNM nos. 538290-538293, 538328, 538331, 538333, 538335, 538336, 538340, 538341, 538381, 538384 (all miscellaneous isolated teeth), 541828 (LM$_2$); WW-87: USNM 527478 (R dentary with M$_{2\text{-}3}$); WW-96: USNM 525623 (dentaries with RM$_{2\text{-}3}$, LM$_3$); WW-97: USNM nos. 538329, 538330, 538334 (all miscellaneous isolated teeth); WW-113: USNM nos. 538332 (isolated teeth), 541829 (RP^4); WW-125: USNM 538326 (LM$_2$); WW-171: USNM nos. 533544 (L dentary with M$_3$), 533545 (L dentary with P$_4$-M$_3$), 538058 (L dentary with M$_{2\text{-}3}$), 538059 (L dentary with M$_2$), 538060 (L dentary with P$_3$-M$_3$), 538061 (R maxilla with P^4-M^2); unnumbered localities: USNM nos. 533565 (RP$_4$, RM$_2$), 539475 (RM^2).

Description.— The Sand Creek Divide specimens of *Hyopsodus* (Figures 42 and 43) closely approximate the holotype of *H. loomisi* and referred specimens from Polecat Bench (Gingerich, 1989) in size and morphology. They are slightly smaller overall and relatively narrower than the holotype and the Polecat Bench sample (Figure 43, Table 8). This is true for all teeth measured, but the difference is greater in the upper teeth than in lowers: about 5-8% shorter and 11-18% narrower (increasing from P^4 to M^3), compared to lower teeth (P$_4$-M$_3$) that are 1-3% shorter and 5-6% narrower. We ascribe the differences to intraspecific variation.

Measurements (mm).— See Table 8.

Discussion.— *Hyopsodus loomisi* is by far the most common mammal in the Sand Creek Divide local fauna by total number of specimens (17%) and ranks second by minimum number of individuals (8.5%). It ranks in the top three species at Polecat Bench (Gingerich, 1989, 2001), but curiously was not recorded in the initial study of the Castle Gardens fauna (though it has since been reported from there; Yans et al., 2006).

Hyopsodus wardi, from the early Ypresian at Abbey Wood, U.K., has been described as very similar to *H. loomisi*, differing only in being slightly smaller and having a relatively narrower M$_3$ (Hooker, 2010). The Sand Creek Divide sample generally upholds this distinction, although some of the upper teeth in our sample are slightly narrower than those from Abbey Wood. Nevertheless, the near identity of these samples implies a close relationship.

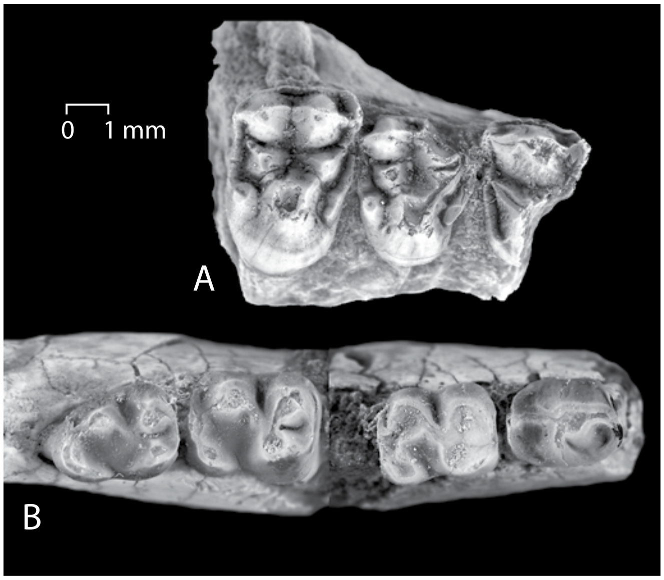


FIGURE 42 — *Hyopsodus loomisi*. A, R maxilla with P^4-M^2, USNM 538061; B, L dentary with P$_4$-M$_3$, USNM 533545.

Tong and Wang (2006) proposed the name *Asiohyopsodus confuciusi* for a new early Eocene species from Wutu, China, and referred *Hyopsodus loomisi* to this genus. In our judgment, *H. loomisi* is so close to other North American and European *Hyopsodus* that there can be little question that it is properly referred to this genus. Whether characters such as the relatively short and wide P$_{3\text{-}4}$ and reduced M$_3$ merit generic distinction of *A. confuciusi* from *Hyopsodus* should be reexamined in comparison with the large available samples of *Hyopsodus*.

Family APHELISCIDAE Matthew, 1918

HAPLOMYLUS Matthew, 1915

Haplomylus zalmouti Gingerich and Smith, 2006

Figure 44A-C

Referred specimens.— WW-80: USNM 525612 (L dentary with M$_{1\text{-}2}$), 525613 (L dentary with M$_1$ talonid-M$_2$); WW-116: USNM 539470 (LM$_2$).

Description.— These three fragmentary specimens have bunodont molars with reduced paraconids typical of *Haplomylus*. They are very similar to *H. speirianus* but are distinctly smaller, closely approximating the type sample of *H. zalmouti*. M$_1$ in USNM 525612 (Ln L x W=1.12) plots in the middle of the range of the type sample (Gingerich and Smith, 2006: figure 21). USNM 525612 is unworn and is higher crowned than the other two specimens, which are moderately worn.

TABLE 8 — Measurements (mm) of *Hyopsodus loomisi* from Sand Creek Divide.

Upper Teeth

Specimen	dP^{3}L	dP^{3}W	P^{3}L	P^{3}W	P^{4}L	P^{4}W	M^{1}L	M^{1}W	M^{2}L	M^{2}W	M^{3}L	M^{3}W
USNM 521510	—	—	—	—	—	—	—	—	2.80	3.50	—	—
USNM 521519	—	—	—	—	—	—	2.80	3.70	—	—	—	—
USNM 533566	—	—	—	—	—	—	—	—	3.20	4.30	—	—
USNM 538061	—	—	—	—	2.60	3.50	—	—	3.10	4.40	—	—
USNM 538261	—	—	—	—	—	—	—	—	3.10	4.30	—	—
USNM 538292R	—	—	—	—	2.75	3.60	2.90	3.40	—	—	2.20	2.95
USNM 538292L	—	—	—	—	—	3.40	—	—	—	—	—	—
USNM 538293	—	—	—	—	2.50	3.10	2.60	3.40	—	—	2.00	2.90
USNM 538327	—	—	—	—	—	—	2.90	3.90	—	—	—	—
USNM 538328R	—	—	2.40	2.60	2.70	3.70	2.70	3.50	3.15	4.60	2.30	3.10
USNM 538328L	—	—	—	—	2.70	3.55	2.80	3.40	3.20	4.40	—	—
USNM 538329R	—	—	—	—	2.60	3.50	2.80	3.70	3.20	4.30	—	—
USNM 538329L	—	—	—	—	2.85	3.50	—	—	2.80	3.60	—	—
USNM 538330R	—	—	—	—	2.60	3.70	2.90	3.50	2.90	3.90	2.70	3.10
USNM 538330L	—	—	—	—	3.00	3.30	2.90	3.30	3.10	4.20	—	—
USNM 538331R	2.60	2.30	2.90	2.70	2.40	3.25	3.00	3.70	3.10	4.30	2.20	3.20
USNM 538331L	—	—	2.70	2.90	2.80	3.60	2.70	3.60	3.00	4.30	2.40	2.90
USNM 538332	—	—	—	—	2.50	3.30	2.90	3.30	—	—	2.35	2.90
USNM 538334	—	—	—	—	—	—	2.60	3.60	—	—	—	—
USNM 538335	—	—	—	—	—	—	2.90	3.60	—	—	2.30	2.50
USNM 538341R	—	—	—	—	2.60	3.40	3.00	3.60	—	—	2.20	2.80
USNM 538341L	—	—	—	—	2.50	3.50	—	—	2.95	4.15	—	—
USNM 538381R	—	—	2.70	2.70	2.45	3.10	3.00	3.90	3.20	4.30	2.30	3.10
USNM 538381L	—	—	—	—	2.65	3.70	2.80	3.60	3.10	3.90	—	—
USNM 539475	—	—	—	—	—	—	—	—	3.10	4.00	—	—
USNM 539503	—	—	—	—	—	—	—	—	2.75	3.80	—	—
USNM 541829	—	—	—	—	2.60	3.50	—	—	—	—	—	—
N	1	1	4	4	17	18	17	17	17	17	10	10
Mean	2.60	2.30	2.68	2.73	2.64	3.46	2.84	3.57	3.04	4.13	2.30	2.95
Std. deviation	—	—	0.21	0.13	0.15	0.19	0.13	0.18	0.15	0.30	0.18	0.20
Std. error	—	—	0.10	0.06	0.04	0.04	0.03	0.04	0.04	0.07	0.06	0.06
Minimum	—	—	2.40	2.60	2.40	3.10	2.60	3.30	2.75	3.50	2.00	2.50
Maximum	—	—	2.90	2.90	3.00	3.70	3.00	3.90	3.20	4.60	2.70	3.20

Lower Teeth

Specimen	dP$_4$L	dP$_4$W	P$_3$L	P$_3$W	P$_4$L	P$_4$W	M$_1$L	M$_1$W$_a$	M$_1$W$_p$	M$_2$L	M$_2$W$_a$	M$_2$W$_p$	M$_3$L	M$_3$W$_a$	M$_3$W$_p$
USNM 521510	—	—	—	—	—	—	2.75	2.30	2.25	—	—	—	3.40	2.50	2.10
USNM 525623	—	—	—	—	—	—	—	—	—	3.40	2.80	2.45	3.20	2.35	2.00
USNM 527478	—	—	—	—	—	—	—	—	—	—	—	—	3.60	2.50	2.00
USNM 533544	—	—	—	—	—	—	—	—	—	—	—	—	3.10	2.30	1.95
USNM 533545	—	—	—	—	2.90	2.15	2.90	2.30	2.40	3.20	2.70	2.60	3.00	2.30	1.95
USNM 533548	—	—	—	—	—	—	—	—	—	3.50	2.90	2.70	3.20	2.50	2.15
USNM 533549	3.10	1.90	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 8 — Measurements (mm) of *Hyopsodus loomisi* (cont.).

Lower Teeth Specimen	dP$_4$L	dP$_4$W	P$_3$L	P$_3$W	P$_4$L	P$_4$W	M$_1$L	M$_1$W$_a$	M$_1$W$_p$	M$_2$L	M$_2$W$_a$	M$_2$W$_p$	M$_3$L	M$_3$W$_a$	M$_3$W$_p$
USNM 533565	—	—	—	—	2.80	2.10	—	—	—	3.30	2.50	2.50	—	—	—
USNM 538058	—	—	—	—	—	—	—	—	—	3.40	2.75	2.55	3.30	2.50	1.95
USNM 538059	—	—	—	—	—	—	—	—	—	3.30	2.80	2.60	—	—	—
USNM 538060	—	—	—	—	2.60	1.90	—	—	—	3.20	2.50	2.45	3.10	2.20	1.85
USNM 538258	—	—	—	—	—	—	—	—	—	—	—	—	3.10	2.35	1.90
USNM 538290R	—	—	2.60	1.80	2.70	1.95	3.10	2.20	2.20	—	—	—	3.20	2.30	1.85
USNM 538290L	—	—	—	—	3.00	2.00	3.20	2.40	2.45	3.25	2.70	2.50	—	—	—
USNM 538291R	—	—	2.50	1.70	2.80	2.20	—	—	—	2.90	2.40	2.30	3.25	2.50	2.00
USNM 538291L	—	—	—	—	2.90	2.20	3.20	2.30	2.10	3.60	2.90	2.70	3.20	2.35	1.90
USNM 538292	—	—	—	—	—	—	—	—	—	3.50	3.00	2.70	3.20	2.35	2.10
USNM 538326	—	—	—	—	—	—	—	—	—	3.60	2.90	2.80	—	—	—
USNM 538327	—	—	2.30	1.70	—	—	—	—	—	—	—	—	—	—	—
USNM 538328R	—	—	—	—	—	—	—	—	—	—	—	—	2.80	2.30	1.80
USNM 538328L	—	—	—	—	—	—	2.90	2.30	2.40	3.40	2.80	2.65	3.20	2.30	2.10
USNM 538329	—	—	—	—	—	—	—	—	—	3.40	2.70	2.70	3.20	2.60	2.10
USNM 538330R	3.30	2.20	2.40	1.85	2.60	1.90	—	—	—	—	—	—	3.20	2.50	2.20
USNM 538330L	—	—	2.70	1.90	3.00	2.30	3.20	2.40	2.40	3.30	2.70	2.70	3.20	2.60	2.10
USNM 538332	—	—	2.90	2.00	2.60	2.00	3.30	2.40	2.40	3.35	2.40	1.90	—	—	—
USNM 538333R	—	—	2.60	1.70	2.80	2.10	3.00	2.50	2.40	3.25	2.80	2.60	3.00	2.30	2.00
USNM 538333L	—	—	2.50	1.70	2.70	2.10	3.00	2.30	2.40	3.35	3.00	2.70	3.10	2.55	2.00
USNM 538334	—	—	—	—	—	—	—	—	—	3.56	2.90	2.70	—	—	—
USNM 538335R	—	—	2.50	1.80	2.70	2.10	3.10	2.30	2.25	—	—	—	3.45	2.55	2.20
USNM 538335L	—	—	—	—	2.95	2.10	2.90	2.20	2.25	3.40	2.90	2.55	3.10	2.40	2.10
USNM 538336R	—	—	—	—	—	—	—	—	—	—	—	—	3.30	2.40	2.00
USNM 538336L	—	—	—	—	—	—	—	—	—	3.30	2.60	2.60	2.80	2.15	1.80
USNM 538340R	—	—	2.40	1.60	2.80	2.10	3.10	2.35	2.40	3.30	2.50	2.50	3.40	2.40	2.10
USNM 538340L	—	—	2.60	1.60	3.00	2.30	3.00	2.20	2.25	3.40	2.85	2.80	3.10	2.45	2.00
USNM 538341R	—	—	—	—	—	—	—	—	—	—	—	—	3.30	2.50	—
USNM 538341L	—	—	—	—	—	—	3.25	2.45	2.30	3.45	2.80	2.65	3.20	2.40	2.10
USNM 538384R	—	—	—	—	2.70	1.90	2.90	2.50	2.40	—	—	—	3.20	2.20	1.95
USNM 538384L	—	—	—	—	2.90	2.30	3.10	2.30	2.40	3.50	2.90	2.60	3.20	2.40	2.20
USNM 541828	—	—	—	—	—	—	—	—	—	3.40	2.70	2.70	—	—	—
N	2	2	11	11	18	18	17	17	17	26	26	26	30	30	29
Mean	3.20	2.05	2.55	1.76	2.80	2.09	3.05	2.34	2.33	3.37	2.75	2.58	3.19	2.40	2.02
Std. deviation	—	—	0.16	0.12	0.14	0.13	0.15	0.09	0.10	0.15	0.17	0.18	0.17	0.12	0.12
Std. error	—	—	0.05	0.04	0.03	0.03	0.04	0.02	0.02	0.03	0.03	0.04	0.03	0.02	0.02
Minimum	3.10	1.90	2.30	1.60	2.60	1.90	2.75	2.20	2.10	2.90	2.40	1.90	2.80	2.15	1.80
Maximum	3.30	2.20	2.90	2.00	3.00	2.30	3.30	2.50	2.45	3.60	3.00	2.80	3.60	2.60	2.20

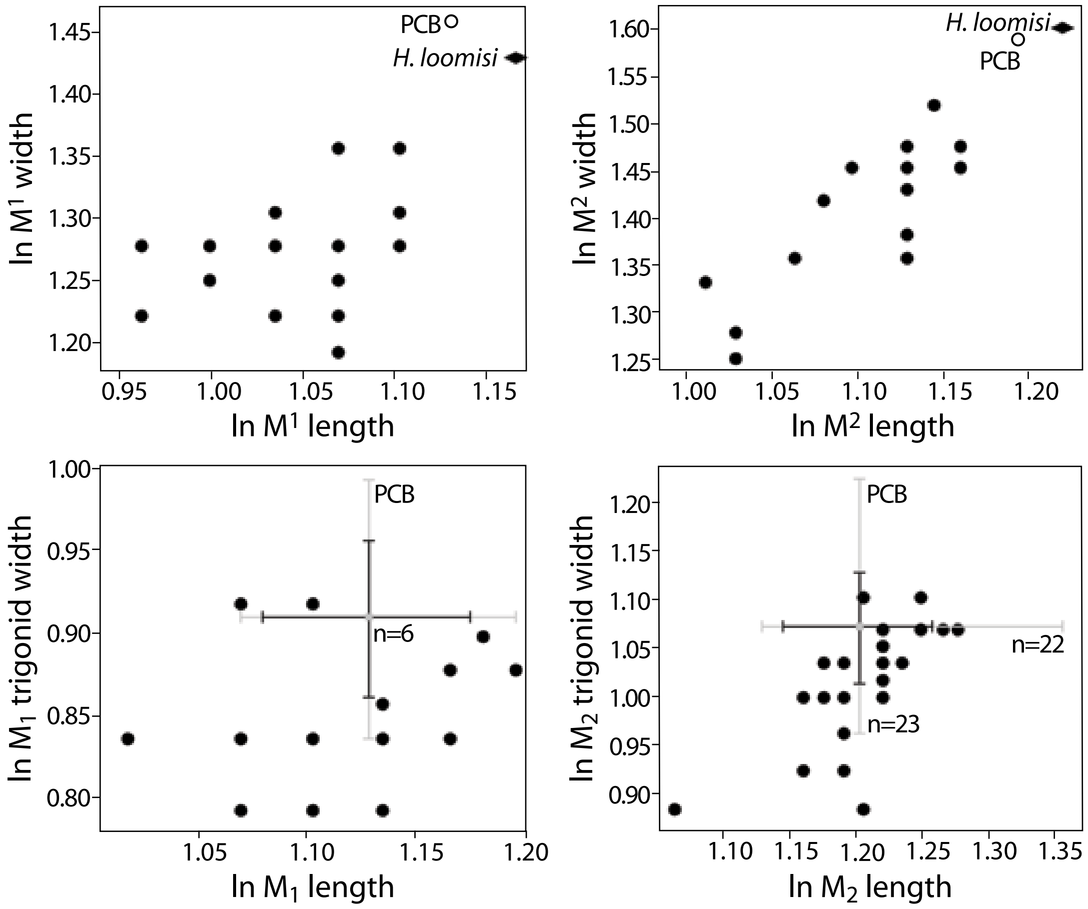


FIGURE 43 — Molar dimensions of Sand Creek Divide *Hyopsodus* (black circles), compared to holotype of *H. loomisi* (black diamond) and Polecat Bench sample (PCB) of Gingerich (1989). For PCB sample, gray lines indicate range; black lines indicate one standard deviation from the mean (gray square).

Discussion.— All three specimens of *Haplomylus zalmouti* are from Red 1, about 1 meter above the base of the PETM. *H. zalmouti* appears to be an index fossil of the Wa-M biozone, suggesting that localities 80 and 116 belong to that interval, although *Meniscotherium* has not been found there.

Haplomylus zalmouti is bracketed by larger species immediately below and above the PETM. As reported above, the much larger *H. simpsoni* has been found in late Clarkforkian strata about 20 m below the occurrence of *H. zalmouti*. The somewhat larger *H. speirianus* is a common taxon in the first several Wasatchian biozones above Wa-0. Four isolated teeth of *Haplomylus* (USNM 538303) found in anthills at locality WW-89 (~45 m level) are tentatively referred to the typical early Wasatchian species *H. speirianus*. These teeth are slightly larger than *H. zalmouti* (see Gingerich and Smith, 2006: table 3) but smaller than typical *H. speirianus*. Gingerich and Smith (2006) showed that post-Wa-0 earliest Wasatchian *Haplomylus* is smaller than later samples. If the teeth from WW-89 are correctly referred to *H. speirianus*, they add to evidence of a probable rapid but gradual (not punctuated) emergence of *H. speirianus* from *H. zalmouti*, and indicate (together with the presence of *Cantius ralstoni*) that the Wa-0/Wa-1 boundary has been crossed. It is notable that *Haplomylus* is absent between Red 1 and WW-89—that is, through the entire Wa-0 biozone—indicating that the specimens from WW-89 most likely are not the same as *H. zalmouti*.

Beard and Dawson (2009) named *Haplomylus meridionalis* as a small, low-crowned species from the Tuscahoma Formation of Mississippi. Although it is smaller than other species of *Haplomylus* except *H. zalmouti*, it is larger than the latter, nearly reaching the small end of the range of *H. speirianus* (Gingerich, 2010) like the teeth from WW-89. This could suggest that *H. meridionalis* postdates *H. zalmouti* and more likely dates from the beginning of Wa-1. The relative brachydonty of *H. meridionalis* is attributable in part to heavier wear than in the compared specimen of *H. zalmouti*.

Measurements (mm).— *H. zalmouti*: USNM 525612: M_1L=2.05, W_a=1.40, W_p=1.50, M_2L=2.10, W_a=1.65, W_p=1.70; USNM 525613: M_1W_p=1.55, M_2L=2.20, W_a=1.85, W_p=1.90; USNM 539470: M_2L=2.20, W_a=1.75, W_p=1.75. *H. speirianus*: USNM 538303: RP^{4}L=2.60, W=2.50; LM^1=2.40, W=3.10; LP$_3$L=2.6, W=1.15; LM$_2$L=2.30, W_a=1.90, W_p=1.90

?APHELISCIDAE, probably new

Figure 44D-F

Referred specimen.— WW-74 (USNM 540401, LM_3)

Description.— This diminutive, isolated third molar ($L=1.40$ mm, $W_a=0.95$ mm, $W_p=0.80$ mm) is distinctive in lacking any trace of a paraconid and having a wider trigonid than talonid. The trigonid is moderately high and consists of tall, subequal protoconid and metaconid joined by a very low paracristid. The two cusps are separated by a deep trigonid notch. The hypoconulid is close to the entoconid, separated by a shallow groove, and these two cusps are of equal height and slightly higher than the larger hypoconid. The entocristid descends into a deep talonid notch, making the talonid basin open lingually. The cristid obliqua is only slightly higher than the entocristid, and extends from the hypoconid to the base of the postvallid buccal to its midpoint, hence there is a moderately deep hypoflexid and the basin is almost as open buccally as lingually. A low cingulum is present only on the anterior aspect of the tooth.

Discussion.— The characters seen in this unusual tooth compare most closely with those of *Haplomylus* and *Apheliscus*, but it is about 30% smaller in linear dimensions than *H. zalmouti* (Gingerich and Smith, 2006). It also has a higher trigonid, shorter talonid, and less basal inflation than those genera. It cannot belong to any other taxon identified so far from the Wa-0 biozone. We conclude that this tooth probably represents a new genus and species of apheliscid, but we leave it unnamed until better known.

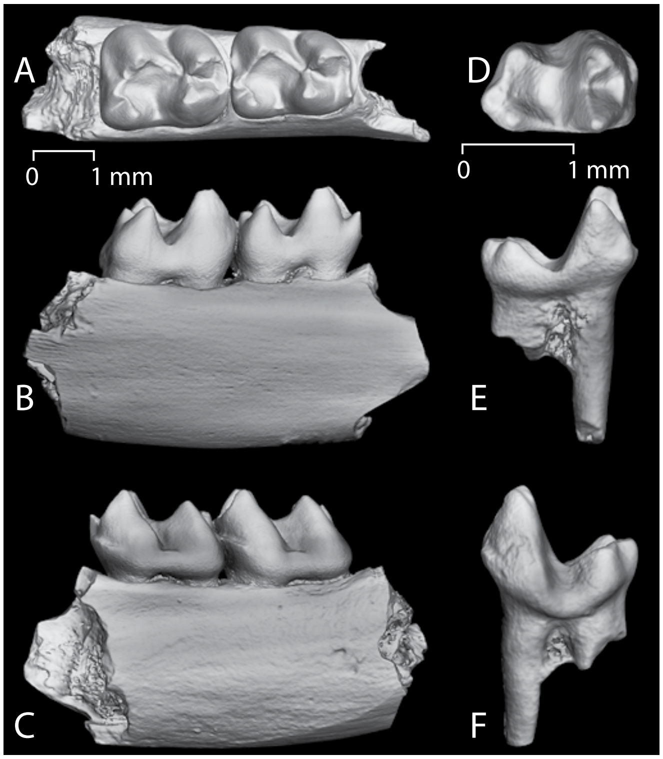


FIGURE 44 — A-C, *Haplomylus zalmouti*, L dentary with M_{1-2}, USNM 525612, in occlusal, lingual, and buccal views. D-F, new apheliscid?, LM_3, USNM 540401, in occlusal, lingual, and buccal views.

Family PHENACODONTIDAE Cope, 1881

PHENACODUS Cope, 1873

Phenacodus intermedius Granger, 1915

Figure 45A-B

Referred specimens.— WW-71: USNM 521496 (metacarpal II and phalanges); WW-75: USNM 539505 (incomplete RM_2); WW-77: USNM 533541 (L dentary with P_3, partial P_4, M_{2-3}); WW-84: USNM 533560 (L calcaneus); WW-86: USNM 538378 (incomplete M^2); WW-114: USNM 525625 (dentary fragments with LP_3-M_1, M_3, partial RP_4, LP^{3-4}); unnumbered locality: USNM 533558 (proximal humerus, astragalar trochlea, patella, distal metapodial, etc.).

Description.— These specimens are intermediate in size between *Phenacodus vortmani* and *P. trilobatus*, but are closer to the smaller species. Those that include teeth fall in the lower end of the size range of early Wasatchian *P. intermedius* as reported by Thewissen (1990). They are also in the upper part of the size range of *P. vortmani* from this interval. However, the jaws and teeth are more inflated than those of *P. vortmani*, resembling *P. intermedius* and *P. trilobatus* in this respect. Otherwise, they closely resemble other species of *Phenacodus*.

Measurements (mm).—USNM 525625, $LP_3L=8.80$, $W=5.80$, $LP_4L=10.3$*, $W=6.7$*, $LM_1L=10.50$, $W_a=8.60$, $W_p=8.50$, $M_3L=9.90$, $W_a=7.50$, $W_p=6.25$, $RP_4L=10.55$, $P^3L=8.00$, $W=8.40$, $P^4L=8.30$, $W=9.20$; USNM 533541, $P_3L=9.10$, $W=5.30$, $P_4L=9.1$*, $W_a=6.15$, $M_1L=10.65$*, $M_2L=10.40$, $W_a=9.40$, $W_p=8.7$*, $M_3L=10.85$, $W_a=8.40$, $W_p=6.50$; USNM 521496, Mc II L=44.5, proximal phalanx L=18.7, intermediate phalanx L=12.3; 533560, calcaneus L=52*.

Discussion.— Considering that species from the PETM tend to be smaller than their younger representatives or relatives, it is more likely that these specimens represent small individuals of *Phenacodus intermedius* than large ones of *P. vortmani*. In other respects they are typical for *Phenacodus*.

Phenacodus vortmani Cope, 1880

Figure 45C

Referred specimens.— WW-75: USNM 539507 (RP_3); WW-90: USNM 525616 (L dentary with P_{2-3}).

Description.— Two very fragmentary premolar specimens are closely comparable in size and morphology to *Phenacodus vortmani* (see Thewissen, 1990) and are sufficient to document the presence of this small species of *Phenacodus* during the PETM. They are very close to, or slightly smaller than, early Wasatchian samples of *P. vortmani* summarized by Thewissen. They are smaller, especially in width, than the specimens attributed to *P. intermedius* above.

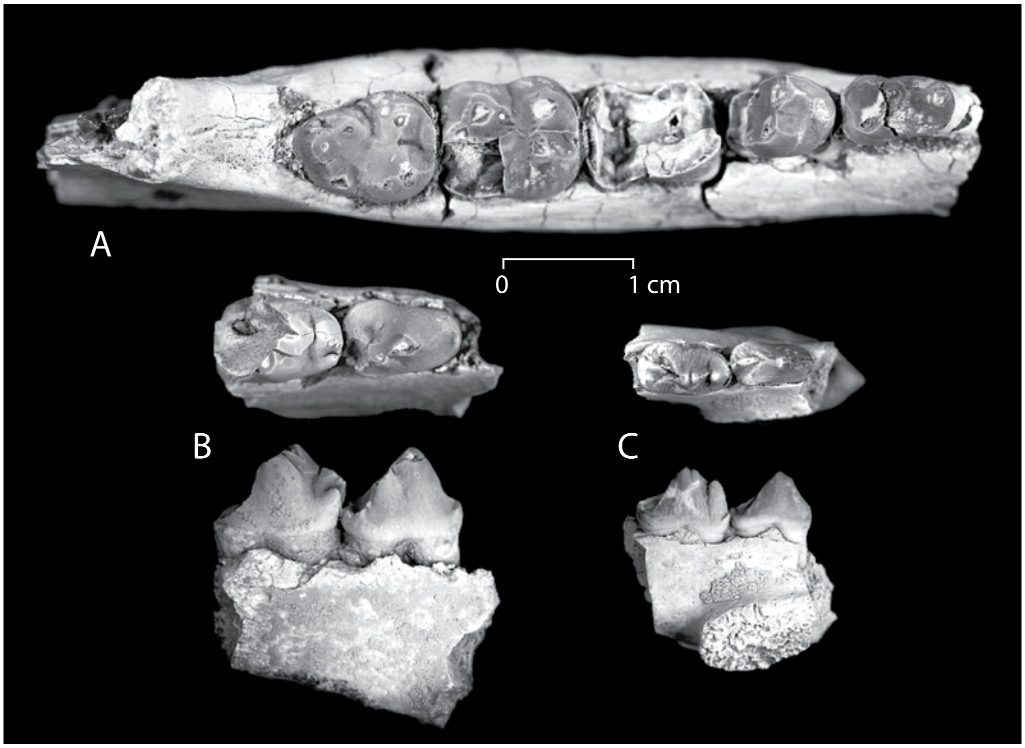


FIGURE 45 — *Phenacodus*. A, *P. intermedius*, L dentary with P_3-P_4 trigonid, M_{2-3}, USNM 533541, in occlusal view; B, *P. intermedius*, L dentary with P_3-P_4 trigonid, USNM 525625, in occlusal and lingual views; C, *P. vortmani*, L dentary with P_{2-3}, USNM 525616, in occlusal and lingual views.

Measurements (mm).— USNM 525616, P_2L=6.30, W=3.35, P_3L=7.05, W=3.90; USNM 539507, P_3L= 8.5*, W=4.45.

ECTOCION Cope, 1882

Ectocion parvus Granger, 1915

Figures 46-49

Referred specimens.— WW-71: USNM nos. 521494 (miscellaneous teeth), 521521 (miscellaneous teeth), 521544 (dentary fragments with broken molars), 525628 (R dentary with P_4-M_3), 538387 (miscellaneous teeth); WW-73: USNM 533592 (LM_2, LM^3), USNM 533623 (RM^2); WW-74: USNM nos. 521523 (dentaries with LP_3, RP_4-M_1, edentulous maxilla), 525599 (mandible with L and RP_3-M_3), 527650 (L dentary with partial M_{2-3}), 533504 (L maxilla with M^{1-3}), 533606 (miscellaneous teeth); WW-75: USNM nos. 521539 (L dentary with M_{1-2}), 521541 (R dentary with P_4), 521545 (miscellaneous teeth), 521548 (R dentary with M_{1-2}), 541827 (LM_3); WW-77: USNM 521515 (miscellaneous teeth); 2 m above WW-77: USNM 525600 (L dentary with P_2, P_4-M_3); WW-78: USNM 521673 (LP_4, RM^2); WW-79: USNM nos. 521677 (L dentary with P_3-M_1 trigonid), 533612 (L dentary with M_3), 538284 (R dentary with broken molar), 538348 (R dentary with M_{1-2}); WW-84: USNM nos. 525642 (R maxilla with M^{2-3}), 538080 (R dentary with P_4), 538294 (miscellaneous teeth), 538346 (miscellaneous teeth); WW-86: USNM 538349 (RM_1); WW-87: USNM 533596 (RM^1, LM^2, LM^3); WW-91: USNM 525631 (L dentary with M_{2-3}), USNM 533553 (R maxilla with P^4-M^1, dentary fragments with RM_3); WW-96: USNM nos. 527654 (mandible with LC, M_{1-2}, RM_3, associated bones), 527655 (R dentary with P_3-M_3), 527656 (L dentary with M_{1-3}), 527657 (L dentary with M_2 talonid-M_3), 527659 (R dentary with P_2, M_{2-3}); WW-97: USNM 538347 (miscellaneous teeth); WW-98: USNM nos. 525629 (R dentary with M_{1-2}), 533619 (maxillae with RP^{2-3}, LM^{1-2}, dentaries with RP_4-M_2, LP_4-M_1, associated bones), 538339 (dentaries with RdP_4-M_2, LP_4), 539504 (R dentary with M_{1-2}); WW-114: USNM 538305 (RM_3); WW-172: USNM 533631 (L dentary with M_{2-3}); unnumbered localities: USNM nos. 533478 (maxillae with R and LM^{1-3}, L dentary with M_3), 533557 (RM^1, M^2), 533600 (L dentary with M_2), 538300 (RdP_4, RM_2), 539477 (R dentary with M_3), 541959** (R dentary with P_3-M_1).

Ambiguous or currently indeterminate specimens assigned to *Ectocion*/*Copecion*— WW-71: USNM 538288 (isolated L astragalus, L and R calcanei) and 538299 (miscellaneous teeth); WW-74: USNM 521512 (miscellaneous teeth), 541776 (LM^2, RM^2); WW-75: USNM nos. 521540 (miscellaneous teeth), 538086 (miscellaneous teeth), 538257 (R calcaneus), and 539506 (miscellaneous teeth); WW-77: USNM 527660 (L maxilla with M^{1-2}); WW-84: USNM 538374 (isolated RdP_3, LM^3); WW-86: USNM 538366 (isolated RP_3, RdP_4).

FIGURE 46 — *Ectocion* and *Copecion* from Sand Creek Divide: A, *E. parvus*, L dentary with P_3-M_3, USNM 525599, in occlusal and buccal views; B, *E. parvus*, L dentary with P_2, P_4-M_3, USNM 525600, occlusal view; C, *C. davisi*, R dentary with P_2-M_3 trigonid, USNM 525598, occlusal view; D, *C. davisi*, L dentary with P_4-M_3, USNM 533546, occlusal view; E, *E. parvus*, L maxilla with $M^{1\text{-}3}$, USNM 533504, in occlusal and lingual views; F, *C. davisi*, L maxilla with P^4-M^3, USNM 527658, in occlusal and lingual views; G-H, LM^2 and RM^2 (unassociated, USNM 541776) in occlusal view; I, *E. parvus*?, L maxilla with $M^{1\text{-}2}$, USNM 527660, in occlusal and lingual views; J, *E. parvus*, R maxilla with $M^{2\text{-}3}$, USNM 525642, in occlusal and lingual views.

Description.— Most of these specimens closely resemble *Ectocion parvus* from Polecat Bench in having incipiently selenodont lower molars with metastylids and a low paracristid that does not join the metaconid, coupled with a shorter and wider P_4 than in *Copecion davisi* (Figure 46A-B); and upper molars with prominent parastyle and mesostyle, the latter often forming a bulge on the buccal margin, and a metaconule situated anterior to a line joining the well separated metacone

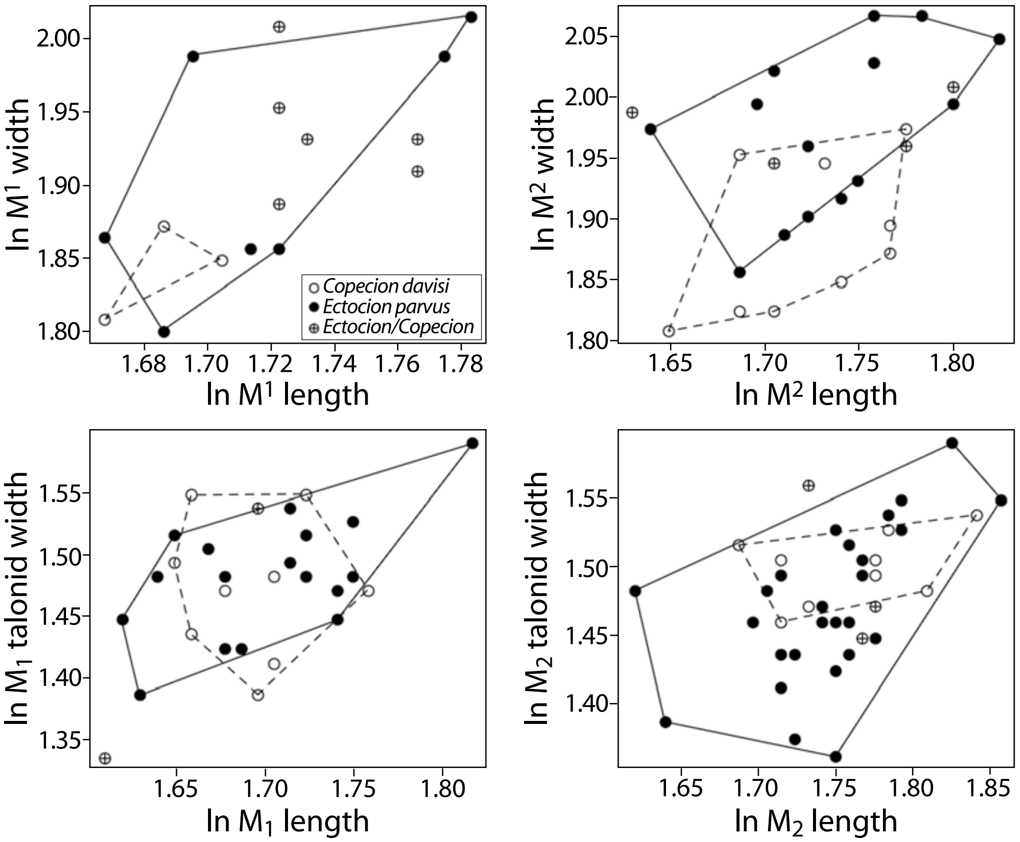


FIGURE 47 — Scatterplot of dimensions of molars of *Ectocion parvus* and *Copecion davisi* from Sand Creek Divide. Polygons circumscribe distribution of each species. Ambiguous specimens are indicated as *Ectocion/Copecion*.

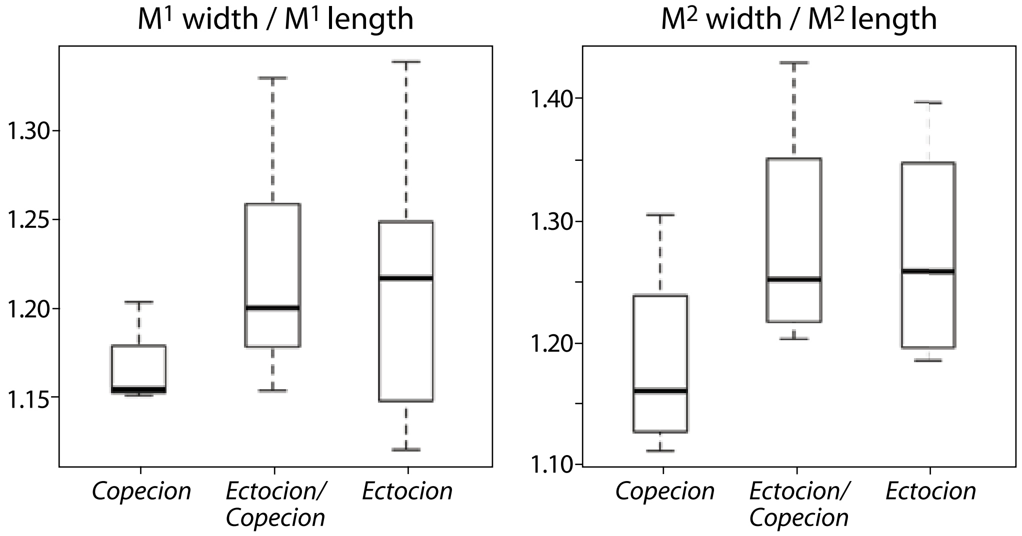


FIGURE 48 — Box plots of relative upper molar width in *Ectocion* and *Copecion* from the PETM at Sand Creek Divide. Bar in boxes indicates median, boxes indicate first and third quartiles (middle 50% of distribution), whiskers indicate range.

FIGURE 49 — *Ectocion* or *Copecion* tarsals: A, R calcaneus, USNM 538257, in dorsal and medial views; B, L astragalus, USNM 538288, in dorsal and ventral views.

and hypocone cusps. A well-developed lingual cingulum is sometimes present (Figure 46J) joining the hypocone to the base of the protocone, as described by Gingerich (1989); however, the cingulum is more often weakly developed (Figure 46E) or absent (Figure 46G-I) in the Sand Creek Divide sample. This leaves a conspicuous lingual furrow between the hypocone and protocone, which has been considered a hallmark of *Copecion*. In all other respects, however, these upper molars resemble those of *Ectocion*, as noted above. The upper molars of *E. parvus* are, on average, relatively wider than those of *C. davisi* (Figures 47, 48), but there is considerable overlap in size. A single damaged P^3 (USNM 533619) is preserved, which has a better separated paracone-metacone than in the Polecat Bench specimen described by Gingerich (1989).

The sample shows additional variation besides that mentioned above. Incipient entoconulids are variably present. When present, this cusp is situated on the entocristid immediately anterior to the entoconid, not on a lingual cingulum; it is therefore not a true entostylid, as previously described. A mesoconid is sometimes present on the cristid obliqua (e.g., USNM 525599, 538348). In some cases, the variation makes specimens difficult to identify with certainty as either *Ectocion parvus* or *Copecion davisi*. For example, the lower molar paracristid may be very low lingually and separated from the metaconid by a notch, as in *Ectocion*, but thereafter is continuous with a premetacristid on the anterior surface of the metaconid (USNM 521512, 538086), as in *Copecion*. Upper molars may have twinned metaconules; in one case (e.g., USNM 521540) one of the two cusps is aligned with the metacone-hypocone as in *Copecion*, while the other is anterior to that line as in *Ectocion*. In several specimens the position of the metaconule is ambiguous. In others, the metaconule is anterior to a line joining the well separated metacone-hypocone and there are prominent mesostyles—characteristics of *Ectocion*—but (as in *Copecion*) there is no lingual cingulum, and only a tiny cuspule is variably present at the base of a deep furrow between the protocone and hypocone (USNM 538086, 541776, Figure 46G-I). Most of the ambiguous upper molars have proportions closer to those of *E. parvus* than to those of *C. davisi* (Figure 48).

A few tarsal elements (Figure 49) are tentatively assigned here, but as the distinctions between *Ectocion parvus* and *Copecion davisi* have not been determined, it is not possible to assign them confidently to one taxon or the other.

Measurements (mm).— See Tables 9, 10.

Discussion.— *Ectocion parvus* was one of the most abundant mammals during the PETM at Sand Creek Divide, ranking first by minimum number of individuals and second by total number of specimens (behind *Hyopsodus*). Its close relative *Copecion davisi* ranks third or fourth by MNI and TNS, respectively. Consequently phenacodontids, though not as predominant as they were during the late Clarkforkian, were still very common animals during the PETM.

Although lower cheek teeth of *Ectocion parvus* can usually be readily distinguished from those of *Copecion davisi* (when not heavily worn) by shape of P_4 and structure of the molar trigonids, the upper teeth can be much more difficult to differentiate. As described above, some features initially considered diagnostic of one or the other taxon (Gingerich, 1989), including a lingual cingulum in *Ectocion* and a deep lingual groove separating protocone and hypocone in *Copecion*, are highly variable in the Sand Creek Divide sample, making assignment of some specimens ambiguous. Nevertheless, all ambiguous specimens surely belong to one of these two species.

COPECION Gingerich, 1989

Copecion davisi Gingerich, 1989

Figures 46-48

Referred specimens.— WW-71: USNM nos. 521495 (RP_4, LM_3), 521520 (incomplete LM_3), 538376 (miscellaneous teeth); WW-73: USNM 533556 (L dentary with M_1, distal tibia), USNM

TABLE 9 — Measurements (mm) of *Ectocion parvus* from Sand Creek Divide.

Upper Teeth

Specimen	P^2L	P^2W	P^3L	P^3W	P^4L	P^4W	M^1L	M^1W	M^2L	M^2W	M^3L	M^3W
USNM 521494	—	—	—	—	—	—	—	—	5.80	7.60	—	—
USNM 521515	—	—	—	—	—	—	—	—	—	—	6.60	4.85
USNM 521521	—	—	—	—	—	—	—	—	5.60	7.10	—	—
USNM 521545	—	—	—	—	5.35	6.55	—	—	—	—	—	—
USNM 521673	—	—	—	—	—	—	—	—	5.40	6.40	—	—
USNM 525642	—	—	—	—	—	—	—	—	5.80	7.90	4.90	6.70
USNM 533478R	—	—	—	—	—	—	5.45	7.30	5.45	7.35	4.20	5.50
USNM 533478L	—	—	—	—	—	—	—	—	5.50	7.55	4.10	5.45
USNM 533504	—	—	—	—	—	—	5.55	6.40	5.75	6.90	5.00	5.95
USNM 533553	—	—	—	—	—	5.95	5.60	6.40	—	—	—	—
USNM 533557	—	—	—	—	—	—	5.30	6.45	5.53	6.60	—	—
USNM 533592	—	—	—	—	—	—	—	—	4.85	6.40	—	—
USNM 533596	—	—	—	—	—	—	5.40	6.05	5.15	7.20	—	—
USNM 533606	—	—	—	—	—	—	—	—	5.70	6.80	5.15	7.15
USNM 533619R	3.95	2.70	4.90	5.10	—	—	—	—	—	—	—	—
USNM 533619L	—	—	—	—	—	—	5.90	7.30	6.20	7.75	—	—
USNM 533623	—	—	—	—	—	—	—	—	5.60	6.70	—	—
USNM 538294R	4.05	2.80	4.55	4.30	5.50	6.90	5.95	7.50	6.05	7.35	5.10	6.45
USNM 538294L	—	—	—	—	—	—	—	—	—	—	4.15	6.50
USNM 538346	—	—	—	—	—	—	—	—	5.95	7.90	5.20	6.90
USNM 538387	—	—	—	—	5.20	6.55	—	—	—	—	—	—
N	2	2	2	2	3	4	7	7	15	15	9	9
Mean	4.00	2.75	4.73	4.70	5.35	6.49	5.59	6.77	5.62	7.17	4.93	6.16
Std. deviation	—	—	—	—	0.15	0.39	0.25	0.58	0.34	0.52	0.77	0.77
Std. error	—	—	—	—	0.09	0.20	0.09	0.22	0.09	0.13	0.26	0.26
Minimum	3.95	2.70	4.55	4.30	5.20	5.95	5.30	6.05	4.85	6.40	4.10	4.85
Maximum	4.05	2.80	4.90	5.10	5.50	6.90	5.95	7.50	6.20	7.90	6.60	7.15

Lower Teeth

Specimen	dP_4L	dP_4W	C_1L	C_1W	P_2L	P_2W	P_3L	P_3W	P_4L	P_4W	M_1L	M_1W_a	M_1W_p	M_2L	M_2W_a	M_2W_p	M_3L	M_3W_a	M_3W_p
USNM 521494	—	—	—	—	—	—	—	—	5.65	3.75	—	—	—	5.70	4.45	4.30	—	—	—
USNM 521515R	—	—	—	—	—	—	—	—	—	—	—	—	—	5.75	4.80	4.60	—	—	—
USNM 521515L	—	—	—	—	—	—	—	—	—	—	5.30	4.15	4.50	—	—	—	—	—	—
USNM 521523R	—	—	—	—	—	—	—	—	5.50	3.95	5.05	3.90	4.25	—	—	—	—	—	—
USNM 521523L	—	—	—	—	—	—	5.35	3.30	—	—	—	—	—	—	—	—	—	—	—
USNM 521539	—	—	—	—	—	—	—	—	—	—	5.60	4.25	4.40	5.80	4.40	4.30	—	—	—
USNM 521541	—	—	—	—	—	—	—	—	5.80	4.30	—	—	—	5.80	4.50	4.20	—	—	—
USNM 521545R	—	—	—	—	—	—	—	—	—	—	5.40	4.10	4.15	5.90	4.45	4.25	—	—	—
USNM 521545L	—	—	—	—	—	—	—	—	—	—	5.55	4.35	4.45	—	—	—	6.60	4.55	3.70
USNM 521548	—	—	—	—	—	—	—	—	—	—	5.10	3.95	4.00	5.15	4.25	4.00	—	—	—
USNM 521673	—	—	—	—	—	—	—	—	5.60	3.60	—	—	—	—	—	—	—	—	—
USNM 521677	—	—	—	—	—	—	5.80	2.85	5.90	3.65	—	—	—	—	—	—	—	—	—
USNM 525599R	—	—	—	—	—	—	5.30	3.00	5.70	3.80	5.15	4.05	4.40	—	4.40	—	5.90	3.85	3.75

TABLE 9 — Measurements (mm) of *Ectocion parvus* (cont.).

Lower Teeth

Specimen	dP_4L	dP_4W	C_1L	C_1W	P_2L	P_2W	P_3L	P_3W	P_4L	P_4W	M_1L	M_1W_a	M_1W_p	M_2L	M_2W_a	M_2W_p	M_3L	M_3W_a	M_3W_p
USNM 525599L	—	—	—	—	—	—	5.30	3.10	5.55	3.85	5.20	4.10	4.55	5.45	4.50	4.30	6.00	3.90	3.75
USNM 525600	—	—	—	—	3.60	1.65	—	—	5.70	3.45	5.35	4.00	—	5.75	4.60	4.30	6.20	3.85	3.65
USNM 525628	—	—	—	—	—	—	—	—	6.10	4.10	—	—	—	5.85	4.60	4.45	5.50	3.70	3.40
USNM 525629	—	—	—	—	—	—	—	—	—	—	5.35	4.30	4.40	5.55	4.50	4.20	—	—	—
USNM 525631	—	—	—	—	—	—	—	—	—	—	—	—	—	5.55	4.45	4.45	5.70	3.50	—
USNM 527654R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.75	3.90	3.80
USNM 527654L	—	—	4.65	3.15	—	—	—	—	—	—	5.55	4.55	4.65	5.80	4.65	4.55	—	—	—
USNM 527655	—	—	—	—	—	—	5.90	3.15	6.05	4.00	5.70	4.10	4.25	5.55	4.45	4.10	5.90	3.70	3.30
USNM 527656	—	—	—	—	—	—	—	—	—	—	5.60	4.50	4.40	5.50	4.65	4.40	5.65	3.75	3.50
USNM 527657	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.50	3.60	3.15
USNM 527659	—	—	—	—	4.10	2.50	—	—	—	—	—	—	—	5.05	4.40	4.40	6.45	3.90	3.60
USNM 533478L	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.70	3.70	3.30
USNM 533553	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.50	3.40	3.05
USNM 533592	—	—	—	—	—	—	—	—	—	—	—	—	—	6.00	4.80	4.60	—	—	—
USNM 533600	—	—	—	—	—	—	—	—	—	—	—	—	—	5.75	4.15	3.90	—	—	—
USNM 533606R	—	—	—	—	—	—	—	—	—	—	5.75	4.65	4.60	—	—	—	—	—	—
USNM 533612	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.20	3.85	3.35
USNM 533619R	—	—	3.80	2.70	—	—	—	—	6.05	3.85	6.15	4.60	4.90	6.70	4.90	4.75	—	—	—
USNM 533619L	—	—	—	—	—	—	—	—	6.10	3.95	—	4.70	—	—	—	—	—	—	—
USNM 533631	—	—	—	—	—	—	—	—	—	—	—	—	—	5.85	5.05	4.50	6.20	—	3.60
USNM 538080	—	—	—	—	—	—	—	—	6.10	3.80	—	—	—	—	—	—	—	—	—
USNM 538294R	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
USNM 538294L	—	—	—	—	—	—	4.85	2.60	4.80	2.70	—	—	—	—	—	—	—	—	—
USNM 538300	6.60	3.70	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
USNM 538305	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.25	3.70	3.50
USNM 538339	6.50	3.60	—	—	—	—	—	—	—	—	5.60	4.15	4.55	5.95	4.85	4.65	—	—	—
USNM 538346R	—	—	—	—	—	—	5.60	2.95	—	—	—	—	—	5.75	4.60	4.15	5.55	3.55	3.55
USNM 538347R	—	—	—	—	—	—	—	—	—	—	—	—	—	6.15	5.25	5.00	—	—	—
USNM 538347L	—	—	—	—	4.60	2.30	—	—	—	—	—	—	—	5.70	4.70	4.35	—	—	—
USNM 538348	—	—	—	—	—	—	—	—	—	—	5.35	3.90	4.15	3.75	4.15	4.05	—	—	—
USNM 538349	—	—	—	—	—	—	—	—	—	—	5.70	4.05	4.35	—	—	—	—	—	—
USNM 538387R	—	—	—	—	—	—	5.80	3.20	5.55	3.60	—	—	—	—	—	—	—	—	—
USNM 538387L	—	—	—	—	—	—	—	—	—	—	—	—	—	5.60	4.40	4.20	—	—	—
USNM 539477	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.35	4.00	3.75
USNM 539504	—	—	—	—	—	—	—	—	—	—	5.75	4.00	4.40	6.00	4.15	4.70	—	—	—
USNM 541827	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.85	3.90	3.40
N	2	2	2	2	3	3	8	8	15	15	19	20	18	26	27	26	19	18	18
Mean	6.55	3.65	4.23	2.93	4.10	2.15	5.49	3.02	5.74	3.76	5.48	4.22	4.41	5.67	4.56	4.37	5.93	3.79	3.51
Std. deviation	—	—	—	—	0.50	0.44	0.35	0.22	0.34	0.36	0.27	0.26	0.21	0.50	0.27	0.25	0.35	0.25	0.22
Std. error	—	—	—	—	0.29	0.26	0.12	0.08	0.09	0.09	0.06	0.06	0.05	0.10	0.05	0.05	0.08	0.06	0.05
Minimum	6.50	3.60	3.80	2.70	3.60	1.65	4.85	2.60	4.80	2.70	5.05	3.90	4.00	3.75	4.15	3.90	5.50	3.40	3.05
Maximum	6.60	3.70	4.65	3.15	4.60	2.50	5.90	3.30	6.10	4.30	6.15	4.70	4.90	6.70	5.25	5.00	6.60	4.55	3.80

TABLE 10 — Measurements (mm) of *Ectocion/Copecion* from Sand Creek Divide.

Upper Teeth

Specimen	dP^4L	dP^4W	P^3L	P^3W	P^4L	P^4W	M^1L	M^1W	M^2L	M^2W	M^3L	M^3W
USNM 521512	—	—	—	—	5.00	5.15	5.60	7.05	—	—	—	—
USNM 521512	5.50	5.85	—	—	4.80	5.10	5.60	6.60	5.90	7.10	4.75	6.35
USNM 521540	—	—	—	—	—	—	5.85	6.75	—	—	—	—
USNM 527660	—	—	—	—	—	—	5.85	6.90	6.05	7.45	—	—
USNM 538086	—	—	—	—	5.50	5.85	5.60	7.45	5.50	7.00	—	—
USNM 538299	5.40	5.95	—	—	—	—	—	—	—	—	—	—
USNM 538374	—	—	—	—	—	—	—	—	—	—	3.85	4.50
USNM 539506	—	—	5.00	6.75	5.10	6.90	5.65	6.90	—	—	—	—
USNM 541776	—	—	—	—	—	—	—	—	5.10	7.30	—	—
N	2	2	1	1	4	4	6	6	4	4	2	2
Mean	5.45	5.90	5.00	6.75	5.10	5.75	5.69	6.94	5.64	7.21	4.30	5.42
Std. deviation	—	—	—	—	0.29	0.84	0.12	0.29	0.43	0.20	—	—
Std. error	—	—	—	—	0.15	0.42	0.05	0.12	0.21	0.10	—	—
Minimum	5.40	5.85	—	—	4.80	5.10	5.60	6.60	5.10	7.00	3.85	4.50
Maximum	5.50	5.95	—	—	5.50	6.90	5.85	7.45	6.05	7.45	4.75	6.35

Lower Teeth

Specimen	dP_3L	dP_3W	dP_4L	dP_4W	P_3L	P_3W	P_4L	P_4W	M_1L	M_1W_a	M_1W_p	M_2L	M_2W_a	M_2W_p	M_3L	M_3W_a	M_3W_p
USNM 521512R	—	—	6.50	3.95	—	—	—	—	—	—	—	5.90	4.70	4.35	—	—	—
USNM 521512L	—	—	—	—	—	—	5.80	3.85	5.00	3.90	3.80	5.55	4.50	4.45	5.90	3.95	3.60
USNM 521540	—	—	—	—	5.60	2.60	—	—	5.15	4.30	4.40	—	—	—	5.85	3.45	3.25
USNM 538086R	—	—	—	—	—	—	—	—	—	—	—	5.65	4.70	4.75	5.30	3.55	3.00
USNM 538086L	—	—	—	—	—	—	—	—	5.45	4.40	4.65	—	—	—	—	—	—
USNM 538299	—	—	—	—	—	—	—	—	—	—	—	5.85	4.60	4.25	—	—	—
USNM 538366	—	—	6.95	3.65	5.85	2.95	—	—	—	—	—	—	—	—	—	—	—
USNM 538374R	5.10	2.85	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
USNM 538374L	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
USNM 539506L	—	—	6.30	3.55	—	—	—	—	—	—	—	—	—	—	—	—	—
N	1	1	3	3	2	2	1	1	3	3	3	4	4	4	3	3	3
Mean	5.10	2.85	6.58	3.72	5.73	2.78	5.80	3.85	5.20	4.20	4.28	5.74	4.63	4.45	5.68	3.65	3.28
Std. deviation	—	—	0.33	0.21	—	—	—	—	0.23	0.26	0.44	0.17	0.10	0.22	0.33	0.26	0.30
Std. error	—	—	0.19	0.12	—	—	—	—	0.13	0.15	0.25	0.08	0.05	0.11	0.19	0.15	0.17
Minimum	—	—	6.30	3.55	5.60	2.60	—	—	5.00	3.90	3.80	5.55	4.50	4.25	5.30	3.45	3.00
Maximum	—	—	6.95	3.95	5.85	2.95	—	—	5.45	4.40	4.65	5.90	4.70	4.75	5.90	3.95	3.60

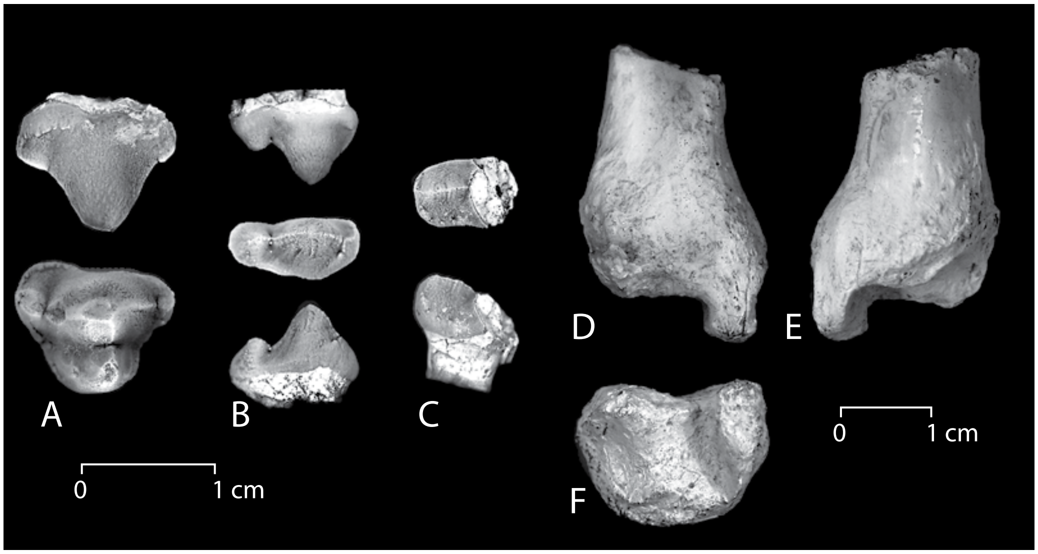


FIGURE 50 — *Dissacus praenuntius*. A, RP^4, USNM 538085, in buccal and occlusal views; B, LP^3?, USNM 521507, in buccal, occlusal, and lingual views; C, LP$_3$ talonid, USNM 521507, in occlusal and lingual views; D-F, distal R tibia, USNM 533618, in anterior, posterior, and distal views. Scale bar at A applies to A-C.

539502 (LP^4, RM^2); WW-74: USNM 521513 (LM$_2$), USNM 538368 (LdP^3, LM$_2$); WW-75: USNM 538260 (incomplete RM^1, LM$_x$ trigonid), USNM 538367 (LM^2); WW-77: USNM nos. 521524 (miscellaneous teeth), 525598 (R dentary with P$_2$-M$_3$ trigonid), 527661 (R dentary with M$_{1-3}$), 533552 (dentaries with LP$_3$-M$_2$, RM$_3$ talonid); WW-79: USNM 521678 (LM^2), USNM 541913 (RP$_3$); WW-83: USNM 533563 (miscellaneous teeth); WW-84: USNM 538083 (miscellaneous teeth); WW-86: USNM 525617 (R maxilla with P$^{3-4}$); WW-90: USNM 525615 (R dentary with P$_{2-3}$, M$_{2-3}$), USNM 538375 (RM$_2$); WW-91: USNM 525632 (R dentary with M$_2$); WW-97: USNM 538372 (miscellaneous teeth); WW-98: USNM 525630 (L dentary with M$_1$); WW-101: USNM 533603 (miscellaneous teeth), USNM 538370 (incomplete LM^x); WW-115: USNM 533585 (L dentary with dP$_4$-M$_1$); WW-118: USNM 533626 (L dentary with M$_{1-2}$, LM^2); WW-125: USNM 533581 (miscellanous teeth), 533611 (miscellaneous teeth); WW-128: USNM 527658 (L maxilla with P^4-M^3); WW-171: USNM 533546 (L dentary with P$_4$-M$_3$); unnumbered localities: USNM nos. 527665 (L dentary with M$_{2-3}$), 533610 (RM^2, canine), 539471 (RM$_1$).

Description.— Specimens assigned here differ from *Ectocion parvus* and resemble the sample of *Copecion davisi* from Polecat Bench in having more bunodont, bulbous cusps. The lower molars have an arcuate paracristid that joins the protoconid to the metaconid, and P$_4$ is narrow and elongate, with an anteriorly shifted paraconid, a more open trigonid, and a lower entoconid than in *E. parvus*. The upper molars are lingually hypsodont, with tall protocone and hypocone, no lingual cingulum, and a deep furrow dividing the protocone and hypocone. The metacone and hypocone are closer together than in *E. parvus*, and the metaconule is situated between these two cusps. In other respects—e.g., presence of metastylids, and variable entoconulids and mesoconids (e.g., USNM 521524, 527665) on lower molars, presence of distinct parastyle, mesostyle, and conules on upper molars—these specimens are similar to *E. parvus*.

Measurements (mm).— See Tables 10, 11.

Discussion.— *Ectocion parvus* and *Copecion davisi* are closely related phenacodontids that coexisted during the PETM and were essentially limited to that interval. *C. davisi* is almost as common as *E. parvus* at Sand Creek Divide. As noted by Gingerich (1989), the two species overlap substantially in tooth size, although he observed that M^2 of *Copecion* is less transverse than *Ectocion* and therefore more nearly square (Figure 47). Our data indicate that both M^1 and M^2 of *C. davisi* are narrower than their counterparts in *E. parvus*. We note, however, that the holotype is more bunodont and squared and has smaller mesostyles than most specimens from Sand Creek Divide.

USNM 538306 is a left M$_3$ of *C. davisi* from approximately 5 m below Red 1 (the bed marking the start of Wa-0 and the PETM). Assuming it is not a contaminant from higher strata, it would constitute the oldest record of *C. davisi* and the first from the latest Paleocene. Although *C. brachypternus* has been reported from the Clarkforkian (Thewissen, 1990), the size of USNM 538306 (6.20 x 4.30 mm) is below the ranges for *C. brachypternus* reported by Thewissen and within the range of Sand Creek Divide *C. davisi*.

Family MESONYCHIDAE Cope, 1875

DISSACUS Cope, 1881

Dissacus praenuntius Matthew, 1915

Figure 50

Referred specimens.— WW-75: USNM 538085 (RP^4); and

TABLE 11 — Measurements (mm) of *Copecion davisi* from Sand Creek Divide.

Upper Teeth

Specimen	dP^{3}L	dP^{3}W	dP^{4}L	dP^{4}W	P^{3}L	P^{3}W	P^{4}L	P^{4}W	M^{1}L	M^{1}W	M^{2}L	M^{2}W	M^{3}L	M^{3}W
USNM 521524	—	—	—	—	—	—	—	—	—	—	5.65	7.00	—	—
USNM 521678	—	—	—	—	—	—	—	—	—	—	5.90	7.20	—	—
USNM 525617	—	—	—	—	5.70	4.60	4.95	5.70	—	—	—	—	—	—
USNM 527658R	—	—	—	—	—	—	5.25	6.05	—	—	—	—	—	—
USNM 527658L	—	—	—	—	—	—	5.25	6.30	5.40	6.50	5.10	6.55	4.35	5.85
USNM 533563R	—	—	—	—	—	—	—	—	—	—	—	—	4.95	6.00
USNM 533563L	—	—	—	—	—	—	—	—	5.50	6.35	—	—	5.05	6.65
USNM 533581	—	—	5.50	5.20	—	—	—	—	—	—	5.40	7.05	—	—
USNM 533603	—	—	—	—	—	—	5.15	5.90	—	6.85	—	—	—	—
USNM 533610	—	—	—	—	—	—	—	—	—	—	5.70	6.35	—	—
USNM 533611	—	—	6.25	6.05	—	—	—	—	—	—	—	—	—	—
USNM 533626	—	—	—	—	—	—	—	—	—	—	5.50	6.20	—	—
USNM 538083	—	—	—	—	—	—	—	—	5.05	5.15	5.40	6.20	—	—
USNM 538367	—	—	—	—	—	—	—	—	—	—	5.85	6.65	—	—
USNM 538368	6.20	3.55	—	—	—	—	—	—	—	—	—	—	—	—
USNM 538376	—	—	—	—	—	—	—	—	—	—	5.45	5.55	4.80	5.55
USNM 539502	—	—	—	—	—	—	5.25	5.85	—	—	5.85	6.50	—	—
N	1	1	2	2	1	1	5	5	3	4	10	10	4	4
Mean	6.20	3.55	5.88	5.63	5.70	4.60	5.19	5.96	5.32	6.21	5.58	6.53	4.79	6.01
Std. deviation	—	—	—	—	—	—	0.13	0.23	0.24	0.74	0.26	0.49	0.31	0.46
Std. error	—	—	—	—	—	—	0.06	0.10	0.14	0.37	0.08	0.16	0.15	0.23
Minimum	—	—	5.50	5.20	—	—	4.95	5.70	5.05	5.15	5.10	5.55	4.35	5.55
Maximum	—	—	6.25	6.05	—	—	5.25	6.30	5.50	6.85	5.90	7.20	5.05	6.65

Lower Teeth

Specimen	dP$_3$L	dP$_4$L	dP$_4$W	C$_1$L	C$_1$W	P$_2$L	P$_2$W	P$_3$L	P$_3$W	P$_4$L	P$_4$W	M$_1$L	M$_1$W$_a$	M$_1$W$_p$	M$_2$L	M$_2$W$_a$	M$_2$W$_p$	M$_3$L	M$_3$W$_a$	M$_3$W$_p$
USNM 521495	—	—	—	—	—	—	—	—	—	6.75	3.80	—	—	—	—	—	—	5.90	4.00	3.55
USNM 521513	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.95	4.55	4.60	—	—	—
USNM 521524	—	—	—	—	—	—	—	—	—	6.10	3.40	5.60	4.45	4.70	—	—	—	—	—	—
USNM 525598	—	—	—	—	—	—	—	6.00	3.40	5.90	3.70	5.25	4.60	4.70	5.40	4.90	4.55	—	—	—
USNM 525615	—	—	—	—	—	4.55	2.65	6.35	3.05	—	—	—	—	—	6.30	4.95	4.65	6.20	4.00	3.60
USNM 525630	—	—	—	—	—	—	—	—	—	—	—	5.20	4.30	4.45	—	—	—	—	—	—
USNM 525632	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.70	4.40	4.35	—	—	—
USNM 527661	—	—	—	—	—	—	—	—	—	—	—	5.30	4.35	4.50	5.40	4.60	4.55	5.60	—	3.55
USNM 527665	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.65	4.50	4.35	5.70	3.80	3.35
USNM 533546	—	—	—	—	—	—	—	—	—	6.30	3.30	—	4.50	4.15	5.55	4.70	4.30	5.60	3.90	3.40
USNM 533552	—	—	—	—	—	—	—	5.85	3.30	6.20	3.70	5.45	4.90	4.65	—	—	—	—	—	—
USNM 533556	—	—	—	—	—	—	—	—	—	—	—	5.50	4.05	4.10	—	—	—	—	—	—

TABLE 11 — Measurements (mm) of *Copecion davisi* (cont.).

Lower Teeth

Specimen	dP$_3$L	dP$_4$L	dP$_4$W	C$_1$L	C$_1$W	P$_2$L	P$_2$W	P$_3$L	P$_3$W	P$_4$L	P$_4$W	M$_1$L	M$_1$W$_a$	M$_1$W$_p$	M$_2$L	M$_2$W$_a$	M$_2$W$_p$	M$_3$L	M$_3$W$_a$	M$_3$W$_p$
USNM 533585	—	6.80	3.30	—	—	—	—	—	—	—	—	5.45	3.90	4.00	—	—	—	—	—	—
USNM 533603	—	6.80	4.45	—	—	—	—	6.60	3.10	7.15	3.85	—	—	—	—	—	—	—	—	—
USNM 533556	—	—	—	—	—	—	—	—	—	—	—	5.50	4.05	4.10	—	—	—	—	—	—
USNM 533563R	6.30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
USNM 533581R	—	—	—	—	—	5.10	2.50	—	—	6.50	3.80	5.50	4.35	4.40	6.10	4.80	4.40	—	—	—
USNM 533585	—	6.80	3.30	—	—	—	—	—	—	—	—	5.45	3.90	4.00	—	—	—	—	—	—
USNM 533603	—	6.80	4.45	—	—	—	—	6.60	3.10	7.15	3.85	—	—	—	—	—	—	—	—	—
USNM 533610	—	—	—	4.10	2.50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
USNM 533611	—	—	—	—	—	—	—	—	—	—	—	5.35	4.55	4.35	—	—	—	—	—	—
USNM 533626	—	—	—	—	—	—	—	—	—	—	—	5.80	4.15	4.35	5.90	4.80	4.45	—	—	—
USNM 538083	—	—	—	—	—	—	—	5.50	3.05	—	—	—	—	—	—	—	—	—	—	—
USNM 538306	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.30	4.35	3.90
USNM 538368L	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.55	4.90	4.50	—	—	—
USNM 538372R	—	—	—	—	—	—	—	—	—	5.50	3.30	—	—	—	5.90	4.80	4.50	5.65	3.90	3.55
USNM 538372L	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.35	3.70
USNM 538375	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.10	—	—	—	—
USNM 538376R	—	—	—	—	—	—	—	6.30	3.35	—	—	—	—	—	—	—	—	5.65	3.85	3.25
USNM 539471	—	—	—	—	—	—	—	—	—	—	—	5.25	4.05	4.20	—	—	—	—	—	—
USNM 541913	—	—	—	—	—	—	—	5.25	2.45	—	—	—	—	—	—	—	—	—	—	—
N	1	2	2	1	1	2	2	7	7	8	8	11	12	12	11	12	11	8	8	9
Mean	6.30	6.80	3.88	4.10	2.50	4.83	2.58	5.98	3.10	6.30	3.61	5.42	4.35	4.38	5.76	4.75	4.47	5.83	4.14	3.54
Std. deviation	—	—	—	—	—	—	—	0.48	0.32	0.51	0.23	0.18	0.28	0.23	0.29	0.21	0.11	0.28	0.52	0.19
Std. error	—	—	—	—	—	—	—	0.18	0.12	0.18	0.08	0.05	0.08	0.07	0.09	0.06	0.03	0.10	0.18	0.06
Minimum	—	6.80	3.30	—	—	4.55	2.50	5.25	2.45	5.50	3.30	5.20	3.90	4.00	5.40	4.40	4.30	5.60	3.80	3.25
Maximum	—	6.80	4.45	—	—	5.10	2.65	6.60	3.40	7.15	3.85	5.80	4.90	4.70	6.30	5.10	4.65	6.30	5.35	3.90

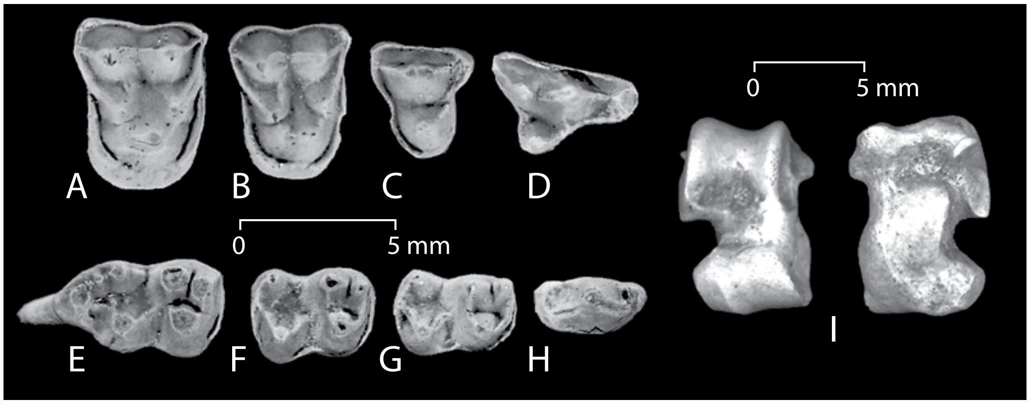


FIGURE 51 — *Diacodexis ilicis*: A, RM^2, USNM 538412; B, RM^1, USNM 521546; C, RP^4, USNM 538412; D, RP^3, USNM 538398; E, RM$_3$, USNM 538438; F, RM$_2$, USNM 538438; G, RM$_1$, USNM 538371; H, RP$_4$, USNM 538403; I, R astragalus, USNM 538301, in dorsal and ventral views.

tentatively WW-73: USNM nos. 527477 (partial R astragalus), 533618 (distal R tibia and associated fragments), WW-74: USNM 521507 (LP$_3$ talonid, LP^3?).

Description.— These very fragmentary specimens do little more than demonstrate the presence of at least one species of *Dissacus* during Wa-0 at Sand Creek Divide. The P^4 is essentially identical to that in *D. praenuntius* (YPM-PU 13295; O'Leary and Rose, 1995: figure 5) and about 20% larger than that of *D. willwoodensis*. It has a large, blunt paracone, lower protocone, a prominent metastyle, and a hint of a parastyle. A slight, abraded swelling (not a wear facet) at the base of the postparacrista is the only indication of a metacone. The other teeth (USNM 521507) include the talonid of P$_3$, comparable in size to that of *D. praenuntius*, and an associated P^3? that is slightly smaller than that of *D. willwoodensis* and more than 25% smaller than that of *D. praenuntius*. It may indicate the presence of a second mesonychid species in this fauna, but until more definitive evidence is forthcoming we tentatively include it here.

The two postcranial specimens, though also very fragmentary, bear hallmarks of the Mesonychidae. A fragmentary astragalus (USNM 527477) has an incomplete trochlea but preserves a prominent squatting facet at the junction of trochlea and neck, as seen in an astragalus questionably referred to *Dissacus* by Thewissen (1991: figure 2K). The astragalar head has a shallowly grooved navicular facet and a narrow cuboid facet, whereas the distal tibia is moderately grooved with a prominent anteromedial process. The tibia differs from that of *Pachyaena* in having a distinct anterior process as an extension of the median ridge that divides the two parts of the astragalar facet, and a more steeply inclined lateral astragalar facet. The size of these elements is consistent with assignment to *D. praenuntius*, but little is known of variation in size or morphology among species of *Dissacus*.

Measurements (mm).— USNM 521507, P^3?L=9.7, W=4.8; USNM 527477, astragalar head W=10.6, dorsoplantar depth=12; USNM 533618, distal tibia W=22, maximum A-P dimension=16.3; USNM 538085, P^{4}L=11.9, W=9.4.

Discussion.— Unlike many species during the PETM, *Dissacus praenuntius* continued from the late Clarkforkian into the Wasatchian with no apparent decrease in size. The smaller *D. willwoodensis* comes from somewhat higher in the formation.

Order ARTIODACTYLA Owen, 1848
Family DIACODEXEIDAE Gazin, 1955

DIACODEXIS Cope, 1882

Diacodexis ilicis Gingerich, 1989
Figures 51-52

Referred specimens.— WW-71: USNM nos. 521543 (RM^1), 538287 (R astragalus), 538371 (RM$_1$); WW-73: USNM 533593 (R calcaneus); WW-75: USNM nos. 521546 (RM^1, LM^1), 533588 (R dentary with M$_3$), 538438 (RM$_2$, RM$_3$); WW-80: USNM 541960** (L dentary with M$_{1-2}$); WW-84: USNM nos. 538398 (isolated teeth: LM$_1$, RP$_4$, LP^4, LM^1, RP^3, RM^2), 538399 (LM$_1$, LM^1, RP^3), 538403 (isolated teeth: LP$_4$, LM$_1$, LM$_2$, LM$_3$, RP$_4$, RM$_3$), WW-86: USNM 538400 (LM^1); WW-96: USNM 538301 (R astragalus); WW-97: USNM nos. 533590 (L astragalus), 538402 (isolated teeth: LP$_4$, LP^4, RM$_2$ and fragments); WW-101: USNM 538412 (RP^4, RM^2); WW-113: USNM 538401 (LM$_3$, RM$_1$); WW-117: USNM 538298 (L dentary with M$_3$ erupting); WW-171: USNM 538050 (L dentary with M$_3$), USNM 542111** (R calcaneus); unnumbered locality: USNM 533601 (R astragalus).

Description.— Although a few jaw fragments and tarsals of *Diacodexis* have been found at Sand Creek Divide, most of the specimens referred to *D. ilicis* are isolated teeth (Figure 51). These specimens are very similar morphologically to *D. ilicis* described from Polecat Bench, which itself differs only trivially from the *D. secans* complex (including *D. metsiacus*). However, lower teeth from the Sand Creek Divide sample, while similar in length to those from Polecat Bench, are distinctly narrower (Figure 52). Sample sizes for each locus are small, however, and it seems unlikely that multiple species coexisted in different

TABLE 12 — Measurements (mm) of *Diacodexis ilicis* from Sand Creek Divide (* = estimated).

Upper Teeth

Specimen	P^{4}L	P^{4}W	M^{1}L	M^{1}W	M^{2}L	M^{2}W
USNM 521543	—	—	3.50	3.90	—	—
USNM 521546R	—	—	3.90	5.05	—	—
USNM 521546L	—	—	3.30	4.50	—	—
USNM 538399	—	—	3.40	4.30	—	—
USNM 538398R	—	—	—	—	3.60	4.80
USNM 538398L	3.00	3.30	3.40	4.35	—	—
USNM 538400	—	—	3.90	4.90	—	—
USNM 538402	3.30	3.70	—	—	—	—
USNM 538412	3.30	3.60	—	—	4.30	5.40
N	3	3	6	6	2	2
Mean	3.20	3.53	3.57	4.50	3.95	5.10
Std. deviation	0.17	0.21	0.27	0.42	—	—
Std. error	0.10	0.12	0.11	0.17	—	—
Minimum	3.00	3.30	3.30	3.90	3.60	4.80
Maximum	3.30	3.70	3.90	5.05	4.30	5.40

Lower Teeth

Specimen	P$_4$L	P$_4$W	M$_1$L	M$_1$Wa	M$_1$W$_p$	M$_2$L	M$_2$W$_p$	M$_2$W$_p$	M$_3$L	M$_3$W$_a$	M$_3$W$_p$
USNM 521543	—	—	—	—	—	—	—	—	—	—	—
USNM 521546R	—	—	—	—	—	—	—	—	—	—	—
USNM 521546L	—	—	—	—	—	—	—	—	—	—	—
USNM 533588	—	—	—	—	—	—	—	—	5.10	2.85	2.60
USNM 538050	—	—	—	—	—	—	—	—	6.00	5.70	3.10
USNM 538371	—	—	4.00	2.40	2.65	—	—	—	—	—	—
USNM 538398R	3.60	1.50	—	—	—	—	—	—	—	—	—
USNM 538398L	—	—	3.70	2.40	2.60	—	—	—	—	—	—
USNM 538399R	—	—	—	—	—	—	—	—	—	—	—
USNM 538399L	—	—	3.80	2.30	2.60	—	—	—	—	—	—
USNM 538400	—	—	—	—	—	—	—	—	—	—	—
USNM 538401R	—	—	3.90	2.40	2.50	—	—	—	5.10	3.10	2.80
USNM 538401L	—	—	—	—	—	—	—	—	—	—	—
USNM 538402R	—	—	—	—	—	4.30	3.00	—	—	—	—
USNM 538402L	3.80	2.00	—	—	—	—	—	—	—	—	—
USNM 538403R	3.60	1.80	—	—	—	—	—	—	5.25	2.80	2.80
USNM 538403L	3.30	1.70	4.10	2.40	2.60	4.10	2.90	2.85	5.50	3.30	3.00
USNM 538412	—	—	—	—	—	—	—	—	—	—	—
USNM 538438	—	—	—	—	—	3.90	2.85	2.75	5.50	3.10	2.85
USNM 541960	—	—	4.0*	2.4*	2.5*	4.5*	2.8*	3.2*	—	—	—
N	4	4	6	6	6	4	4	3	6	6	6
Mean	3.58	1.75	3.92	2.38	2.58	4.20	2.89	2.93	5.41	3.48	2.86
Std. deviation	0.21	0.21	0.15	0.04	0.06	0.26	0.09	0.24	0.34	1.11	0.17
Std. error	0.10	0.10	0.06	0.02	0.03	0.13	0.04	0.14	0.14	0.45	0.07
Minimum	3.30	1.50	3.70	2.30	2.50	3.90	2.80	2.75	5.10	2.80	2.60
Maximum	3.80	2.00	4.10	2.40	2.65	4.50	3.00	3.20	6.00	5.70	3.10

parts of the Bighorn Basin during the PETM. Consequently, we ascribe this difference to intraspecific variation and small sample size.

The Sand Creek Divide sample of *D. ilicis* confirms Gingerich's (1989) description of the species, including the presence of distinct molar paraconids, a centrally positioned hypoconulid that is not twinned with the entoconid, absence of a hypolophid joining hypoconid and entoconid, and absence of a buccal cingulum (except in the hypoflexid). The hypoconulid lobe of M$_3$ is variably developed; it is usually long, and in two specimens (USNM 538050 and 538438) bears an accessory cuspule between the hypoconulid and the entoconid.

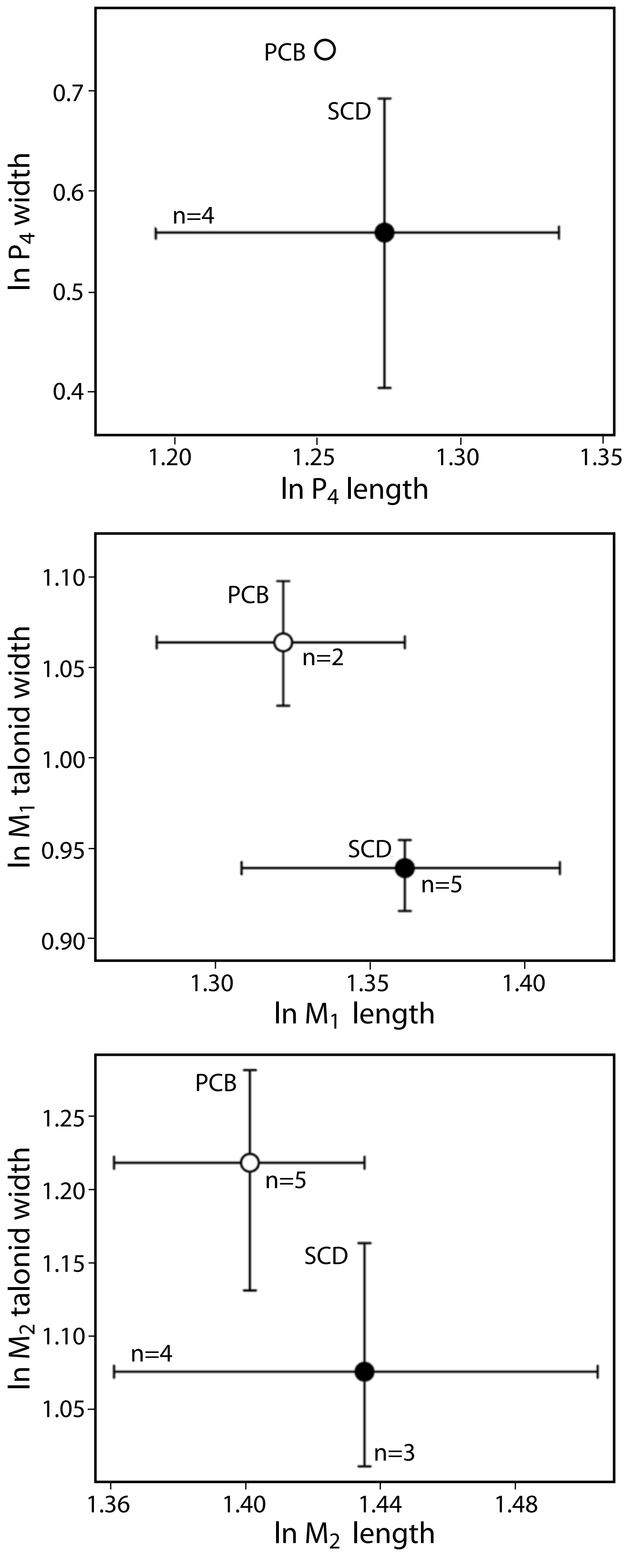


FIGURE 52 — *Diacodexis ilicis*, scatterplots of P_4-M_2 size in Sand Creek Divide sample (SCD, filled circles show means), compared to type sample from Polecat Bench (PCB, from Gingerich, 1989; open circles show means, lines show ranges).

Upper teeth of *D. ilicis* are reported here for the first time. P^3 is known from two specimens, both of which have a higher paracone and a more distinct protocone lobe than in later *Diacodexis* specimens compared. Otherwise the upper teeth are similar in detail to those of later species of *Diacodexis* from the Willwood Formation, with the possible exception of having somewhat more lingually extensive pre- and postcingula.

Measurements (mm).— See Table 12.

Discussion.— Gingerich (1989) considered the principal distinction of *D. ilicis* from other species of *Diacodexis* to be its relatively shorter lower premolars, with P_4 slightly shorter than M_1. The few isolated P_4s in our sample are consistent with that observation (Table 12). Comparison with *Diacodexis* samples from higher in the Willwood Formation suggests that *D. ilicis* was also slightly smaller than later species, as indicated by slightly narrower cheek teeth and smaller, mainly shorter, calcaneus and astragalus (see Kumar et al., 2010: figure 14).

A dentary with two eroded molars (USNM 541960) was found at WW-80 in July 2010. Despite its poor preservation, there is little question that it represents *Diacodexis*. WW-80 is the highest outcrop on its ridge, making contamination from younger strata very unlikely. This evidence suggests that the first appearance of *Diacodexis* coincided with the onset of the CIE. The next lowest occurrence of *Diacodexis* is at 12 meters.

Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821

HYRACOTHERIUM Owen, 1840

Hyracotherium sandrae Gingerich, 1989
Figures 53A-F, 54

Referred specimens.— WW-71: USNM nos. 521497 (miscellaneous teeth, unassociated), 521516 (LdP^3, RdP^3, RdP^4, unassociated), 538286 (L astragalus); WW-73: USNM nos. 521498 (L dentary with M$_3$), 525655 (L dentary with M$_{1\text{-}2}$), 525656 (LP^4, LM^3, LM$_1$, unassociated), 533624 (RM^2); WW-74: USNM nos. 521511 (miscellaneous teeth, unassociated), 527649 (R maxilla with dP^3, L dentary with M$_1$ and erupting M$_3$, associated bones), 533567 (LP^4, RP^4, RM^3), 541774 (RM^1); WW-75: USNM 521547 (LM$^{1/2}$, LM^3); WW-77: USNM nos. 533502 (LM$^{2/3}$), 533613 (L maxilla with M^1, associated proximal radius-ulna, distal tibia, scapular glenoid, foot bones); 5 m above WW-78: USNM nos. 511099 (R maxilla with P$^{2\text{-}4}$, LM^1, partial LM^2, L dentary with M$_{1\text{-}3}$, associated vertebrae and limb fragments), 525627 (L dentary with LdP$_{3\text{-}4}$M$_{1\text{-}2}$), 525657 (dentaries with LP$_{3\text{-}4}$, RP$_2$, M$_1$, RM^1); WW-79: USNM nos. 525641 (associated distal femur, proximal and distal tibia, cuboid, navicular), 525658 (R maxilla with P^4, LP^4), 525659 (RM^3); WW-85: USNM 533617 (dentaries with R and LP$_{3\text{-}4}$, R astragalus, associated bones); WW-90: USNM 538377 (RM^2, LM^3); WW-91: USNM 538383 (LM$^{1/2}$), USNM 538389 (RM$^{1/2}$); WW-96: USNM 527653 (L dentary with M$_{1\text{-}3}$), USNM 533572 (RM^1, RM^2, associated bones including cuboid); WW-97: USNM 538386 (LM^x); WW-98: USNM nos. 525602 (dentaries with LM$_3$, RM$_{1\text{-}2}$, associated bones including L calcaneus and astrag-

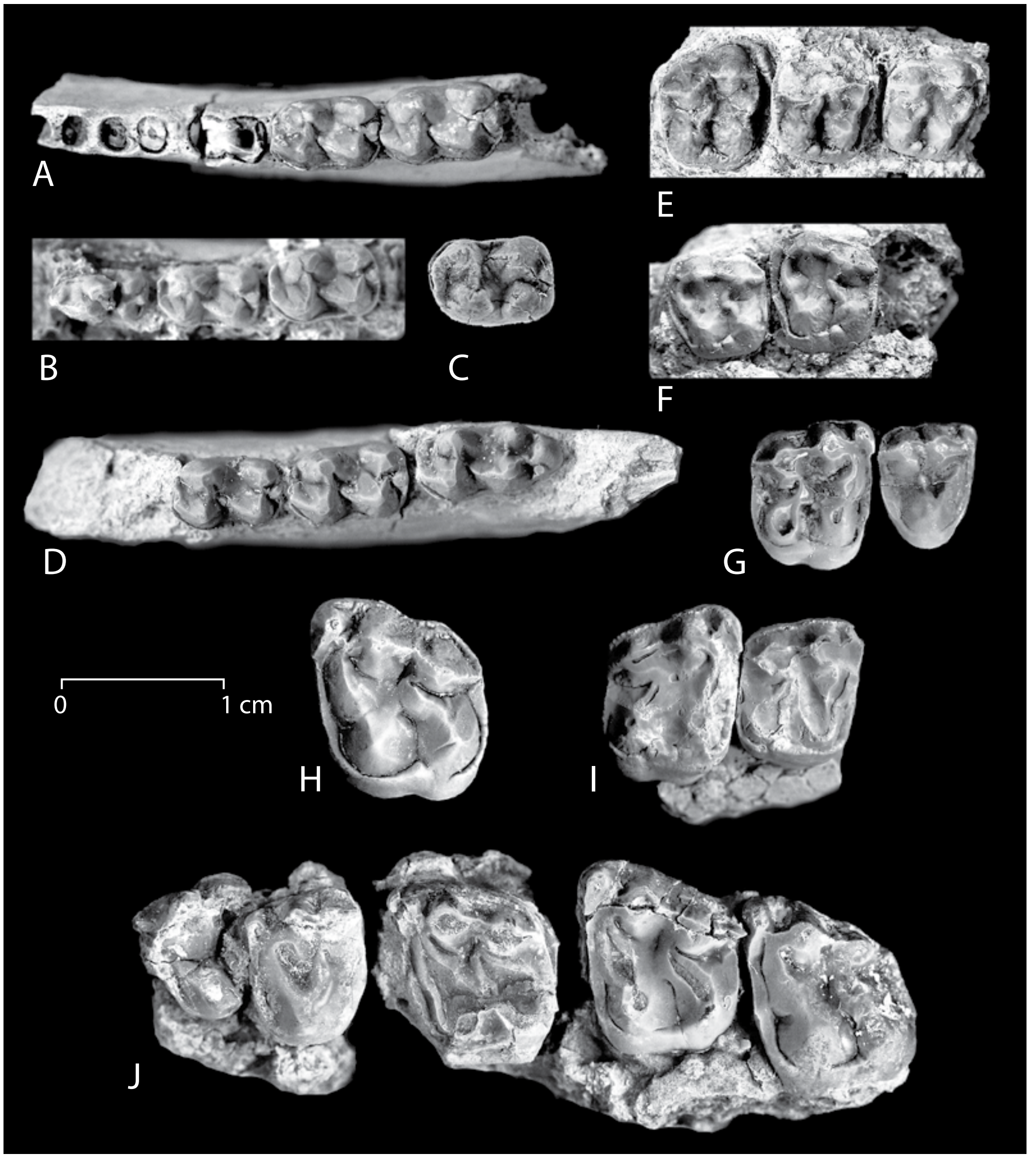


FIGURE 53 — Sand Creek Divide perissodactyls, all in occlusal view. A-F, *Hyracotherium sandrae*, Wa-0: A, L dentary with M_{1-2}, USNM 525655; B-C, L dentary with dP_{3-4}-M_1, RM_2, USNM 525626; D, L dentary with M_{1-3}, USNM 527653; E-F, R maxilla with dP^4-M^1(part)-M^2, L maxilla with dP^4-M^1, USNM 525626; G, *Hyracotherium grangeri*, R maxilla with P^4-M^1, USNM 539516 (locality WW-178, Wa-1); H, *Cardiolophus radinskyi*, LM^1 or M^2, USNM 539517 (locality WW-178, Wa-1); I, *H. grangeri*, R maxilla with M^{1-2}, USNM 541918 (locality WW-173, Wa-1); J, *Homogalax protapirinus*, L maxilla with P^3-M^3 (locality WW-173, Wa-1). All to same scale.

alus), 525624 (R dentary with M_1, M_3, associated tarsal fragments), 525626 (maxillae with RdP^4-M^2, LdP^3-M^1, dentaries with RdP_{2-4}, M_{1-2}, LdP_3-M_1, associated postcrania); WW-101: 538373 (miscellaneous teeth, unassociated); WW-117: USNM 538380 (RM_3); WW-118: USNM 533598 (L dentary with P_4-M_1); WW-119: USNM 533584 (LP^4, M^3); unnumbered localities: USNM nos. 521502 (R dentary with P_4, M_1 talonid-M_2, and ?associated canine), 533599 (R dentary with P_4, M_2), 538013 (R maxilla with M^{2-3}), 538283 (distal femur and distal tibia; Red 1).

Description.— The small equid *Hyracotherium sandrae* is common at Sand Creek Divide. Although some specimens show the paracristid continuous with a weak premetacristid, creating a small anterior fovea on the trigonid (the hallmark of *H. sandrae* according to Gingerich, 1989, and Froehlich, 2002), this feature is less well developed and less consistent in the Sand Creek Divide sample, making some individuals even more similar to later Wasatchian species. The teeth are otherwise indistinguishable in size and morphology from the type sample from Polecat Bench.

Measurements (mm).— See Table 13.

Discussion.— Hooker (1994) and Froehlich (2002) advocated restriction of the name *Hyracotherium* to the type species, *H.*

TABLE 13 — Measurements (mm) of *Hyracotherium sandrae* from Sand Creek Divide.

Upper Teeth

Specimen	Meter	dP^{3}L	dP^{3}W	dP^{4}L	dP^{4}W	P^{2}L	P^{2}W	P^{3}L	P^{3}W	P^{4}L	P^{4}W	M^{1}L	M^{1}W	M^{2}L	M^{2}W	M^{3}L	M^{3}L	M^{X}L	M^{X}W
USNM 511099	8.0	—	—	—	—	—	—	5.20	—	5.20	6.80	6.80	8.00	—	—	—	—	—	—
USNM 521497R	11.5	—	—	—	—	—	—	—	—	5.50	6.90	5.70	6.20	7.20	8.00	—	—	—	—
USNM 521497L	11.5	—	—	—	—	—	—	—	—	—	—	—	—	6.65	8.45	—	—	—	—
USNM 521511	11.5	—	—	—	—	4.90	4.70	—	—	—	—	—	—	—	—	6.50	7.50	—	—
USNM 521516	8.5	5.50	4.95	5.50	5.95	—	—	—	—	—	—	—	—	—	—	—	—	—	—
USNM 521547	11.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.25	7.30	—	—
USNM 525626R	8.5	—	—	6.40	7.10	—	—	—	—	—	—	—	—	7.30	8.40	—	—	—	—
USNM 525626L	8.5	—	—	6.35	6.70	—	—	—	—	—	—	7.05	7.70	—	—	—	—	—	—
USNM 525656	13.0	—	—	—	—	—	—	—	—	5.35	6.10	—	—	—	—	—	—	—	—
USNM 525658R	7.0	—	—	—	—	—	—	—	—	5.40	6.90	—	—	—	—	—	—	—	—
USNM 525658L	7.0	—	—	—	—	—	—	—	—	5.60	6.60	—	—	—	—	—	—	—	—
USNM 525859	7.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.90	7.80	—	—
USNM 527649	11.5	5.65	5.35	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
USNM 533502	14.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.60	7.40
USNM 533567R	11.5	—	—	—	—	—	—	—	—	5.50	6.70	—	—	—	—	6.80	7.25	—	—
USNM 533567L	11.5	—	—	—	—	—	—	—	—	5.10	6.30	—	—	—	—	—	—	—	—
USNM 533572	8.5	—	—	—	—	—	—	—	—	—	—	6.80	7.90	7.45	8.80	—	—	—	—
USNM 533584	37.5	—	—	—	—	—	—	—	—	5.20	6.00	—	—	—	—	6.60	7.20	—	—
USNM 533613	14.0	—	—	—	—	—	—	—	—	—	—	6.00	6.60	—	—	—	—	—	—
USNM 533624	13.0	—	—	—	—	—	—	—	—	—	—	—	—	7.50	8.80	—	—	—	—
USNM 538013	7.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.00	7.40	—	—
USNM 538373	37.5	—	—	—	—	—	—	—	—	5.50	6.30	6.90	—	—	—	7.00	8.10	—	—
USNM 538373	37.5	—	—	—	—	—	—	—	—	5.80	6.40	—	—	—	—	—	—	—	—
USNM 538377	32.0	—	—	—	—	—	—	—	—	—	—	—	—	7.20	7.95	6.90	7.80	—	—
USNM 538383	8.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.80
USNM 538386	32.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.20	6.90
USNM 538389	8.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.10	6.40
USNM 541774	11.5	—	—	—	—	—	—	—	—	—	—	6.30	6.50	—	—	—	—	—	—
N		2	2	3	3	1	1	1		10	10	7	6	6	6	8	8	3	4
Mean		5.58	5.15	6.08	6.58	4.90	4.70	5.20	—	5.42	6.50	6.51	7.15	7.22	8.40	6.62	7.54	6.30	6.88
Std. deviation		—	—	0.51	0.58	—	—	—	—	0.21	0.33	0.51	0.80	0.30	0.37	0.35	0.32	0.26	0.41
Std. error		—	—	0.29	0.34	—	—	—	—	0.07	0.10	0.19	0.33	0.12	0.15	0.12	0.11	0.15	0.21
Minimum		5.50	4.95	5.50	5.95	—	—	—	—	5.10	6.00	5.70	6.20	6.65	7.95	6.00	7.20	6.10	6.40
Maximum		5.65	5.35	6.40	7.10	—	—	—	—	5.80	6.90	7.05	8.00	7.50	8.80	7.00	8.10	6.60	7.40

TABLE 13 — Measurements (mm) of *Hyracotherium sandrae* (cont.).

Lower Teeth

Specimen	Meter	dP_2L	dP_2W	dP_3L	dP_3W	dP_4L	dP_4W_a	dP_4W_p	P_2L	P_2W	P_3L	P_3W	P_4L	P_4W	M_1L	M_1W_a	M_1W_p	M_2L	M_2W_a	M_2W_p	M_3L	M_3W_a	M_3W_p
USNM 511099	8.0	—	—	—	—	—	—	—	—	—	—	—	—	—	6.50	4.50	4.50	7.50	4.85	4.55	8.45	4.90	4.60
USNM 521497	11.5	—	—	—	—	—	—	—	—	—	—	—	—	—	6.80	4.50	4.20	—	—	—	9.05	4.95	4.60
USNM 521498	13.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8.60	4.30	4.20
USNM 521511	11.5	—	—	—	—	6.30	3.70	4.00	—	—	5.75	3.30	—	—	—	—	—	—	—	—	—	—	—
USNM 525602	8.5	—	—	—	—	—	—	—	—	—	—	—	—	—	6.50	3.90	4.20	7.20	4.40	4.55	8.10	4.10	3.95
USNM 525624	8.5	—	—	—	—	—	—	—	—	—	—	—	—	—	5.95	4.20	4.30	—	—	—	8.70	4.65	4.30
USNM 525626R	8.5	4.60	2.05	6.00	3.30	6.50	3.80	4.30	—	—	—	—	—	—	6.90	4.30	4.40	7.60	5.30	5.20	—	—	—
USNM 525626L	8.5	—	—	6.00	3.10	6.30	3.70	3.90	—	—	—	—	—	—	6.80	4.40	4.40	—	—	—	—	—	—
USNM 525627	2.0	—	—	5.90	2.90	—	—	—	—	—	—	—	—	—	6.80	4.30	4.40	—	4.40	—	—	—	—
USNM 525655	13.0	—	—	—	—	—	—	—	—	—	—	—	—	—	6.60	4.35	4.40	7.40	4.75	4.80	—	—	—
USNM 525656	13.0	—	—	—	—	—	—	—	—	—	—	—	—	—	6.50	4.20	4.15	—	—	—	—	—	—
USNM 525657	2.0	—	—	—	—	—	—	—	4.40	2.50	5.30	3.30	5.60	4.00	6.50	4.80	4.60	—	—	—	—	—	—
USNM 527649	11.5	—	—	—	—	—	—	—	—	—	—	—	—	—	7.10	4.45	4.35	—	—	—	—	—	—
USNM 527653	8.5	—	—	—	—	—	—	—	—	—	—	—	—	—	6.80	4.50	4.30	7.40	4.80	4.65	9.00	4.50	4.20
USNM 533598	32.0	—	—	—	—	—	—	—	—	—	—	—	5.50	3.50	6.60	4.00	4.20	—	—	—	—	—	—
USNM 533599	5.0	—	—	—	—	—	—	—	—	—	—	—	5.50	3.70	—	—	—	7.05	4.60	4.80	—	—	—
USNM 533617	14.0	—	—	—	—	—	—	—	—	—	5.80	3.15	5.60	3.90	—	—	—	—	—	—	—	—	—
USNM 538373	37.5	—	—	—	—	—	—	—	—	—	—	—	—	—	6.20	3.90	3.90	7.35	4.40	4.60	—	—	—
USNM 538380	37.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9.10	4.60	4.60
N		1	1	3	3	3	3	3	1	1	3	3	4	4	14	14	14	7	8	7	7	7	7
Mean		4.60	2.05	5.97	3.10	6.37	3.73	4.07	4.40	2.50	5.62	3.25	5.55	3.78	6.61	4.31	4.31	7.36	4.69	4.74	8.71	4.57	4.35
Std. deviation		—	—	0.06	0.20	0.12	0.06	0.21	—	—	0.28	0.09	0.06	0.22	0.29	0.25	0.17	0.18	0.31	0.23	0.37	0.31	0.26
Std. error		—	—	0.03	0.12	0.07	0.03	0.12	—	—	0.16	0.05	0.03	0.11	0.08	0.07	0.05	0.07	0.11	0.09	0.14	0.12	0.10
Minimum		—	—	5.90	2.90	6.30	3.70	3.90	—	—	5.30	3.15	5.50	3.50	5.95	3.90	3.90	7.05	4.40	4.55	8.10	4.10	3.95
Maximum		—	—	6.00	3.30	6.50	3.80	4.30	—	—	5.80	3.30	5.60	4.00	7.10	4.80	4.60	7.60	5.30	5.20	9.10	4.95	4.60

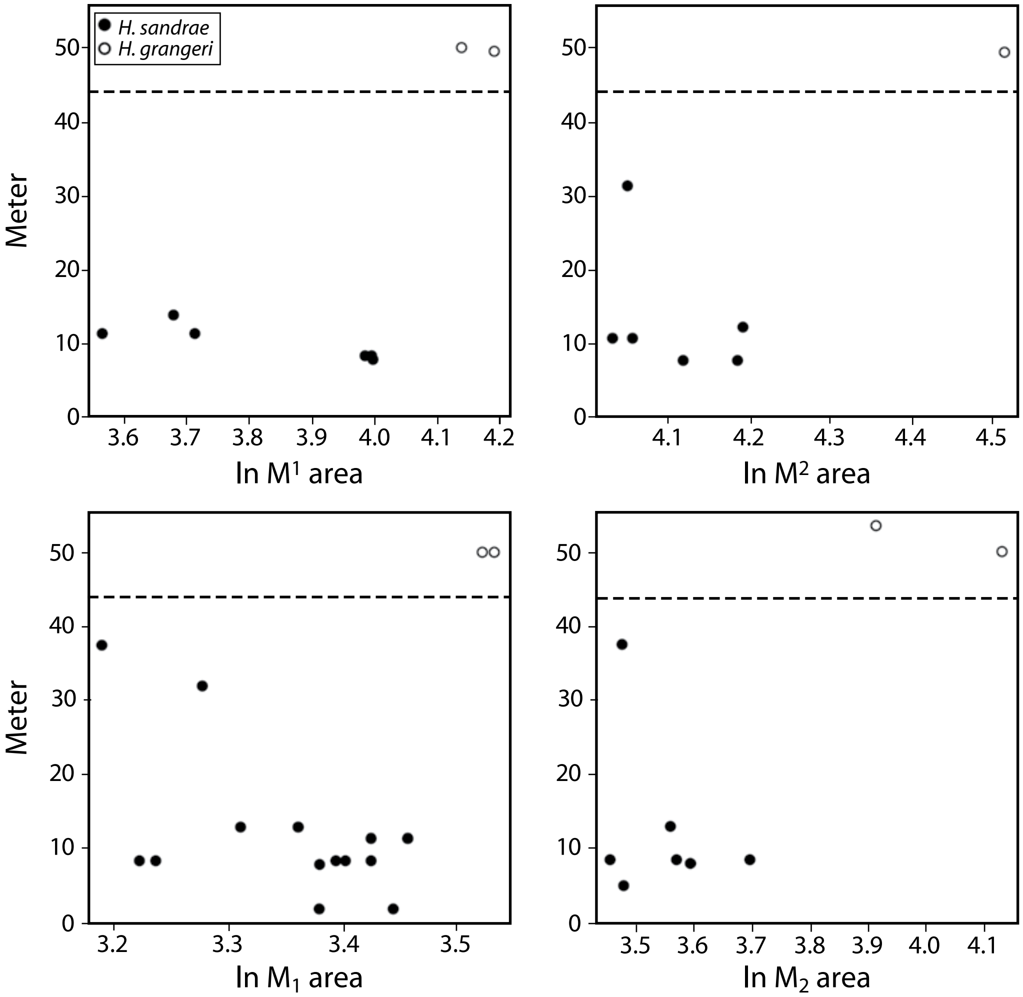


FIGURE 54 — Molar size in *Hyracotherium* from the Sand Creek Divide section shown by stratigraphic level from the base of the Willwood Formation. Solid circles are *H. sandrae*, open circles *H. grangeri*. Dashed line at 44 m shows inferred Wa-0/Wa-1 boundary.

leporinum, which now appears to be a palaeotheriid. Froehlich (2002) further advocated the application of multiple generic names for samples long attributed to *Hyracotherium*, including the new, monotypic genus *Sifrhippus* for *H. sandrae*. However, *H. sandrae* differs only in minor dental features from later species that have been placed in *Hyracotherium* (Gingerich, 1989, 1991). The name has been applied to most North American early Eocene equids for more than a century and therefore is arguably justifiable on the grounds of stability. We follow current usage of the genus *Hyracotherium* for *H. sandrae* (e.g., Yans et al., 2006; Secord et al., 2008; Gingerich, 2001, 2010).

All dental specimens of *Hyracotherium* collected from the Wa-0 interval at Sand Creek Divide appear to represent *H. sandrae*. Samples are not large enough to establish clear trends but are consistent with a slight reduction in size through the PETM (e.g., M_1 area, Figure 54). Secord et al. (2008) reported a zone of abundant equids near the base of the PETM section at Cabin Fork, southeast of Sand Creek Divide, and further observed that they were larger than later samples of *H. sandrae* and possibly included *H. grangeri*. Although no zone of equid abundance has been found near the base of the section at Sand Creek Divide, the lowest dental specimens are among the largest; and two specimens of postcranial elements without associated teeth (USNM 525641 from WW-79, and USNM 538283 from an unnumbered locality in Red 1) are slightly larger than most other *H. sandrae* associations and could belong to a larger population or to *H. grangeri*. Specimens attributed to *H. grangeri* have been found in strata just above the Wa-0 interval at Sand Creek Divide (see below, Upper Boundary of the Wa-0 Biozone).

Order RODENTIA Bowdich, 1821
Family PARAMYIDAE Miller and Gidley, 1918

PARAMYS Leidy, 1871

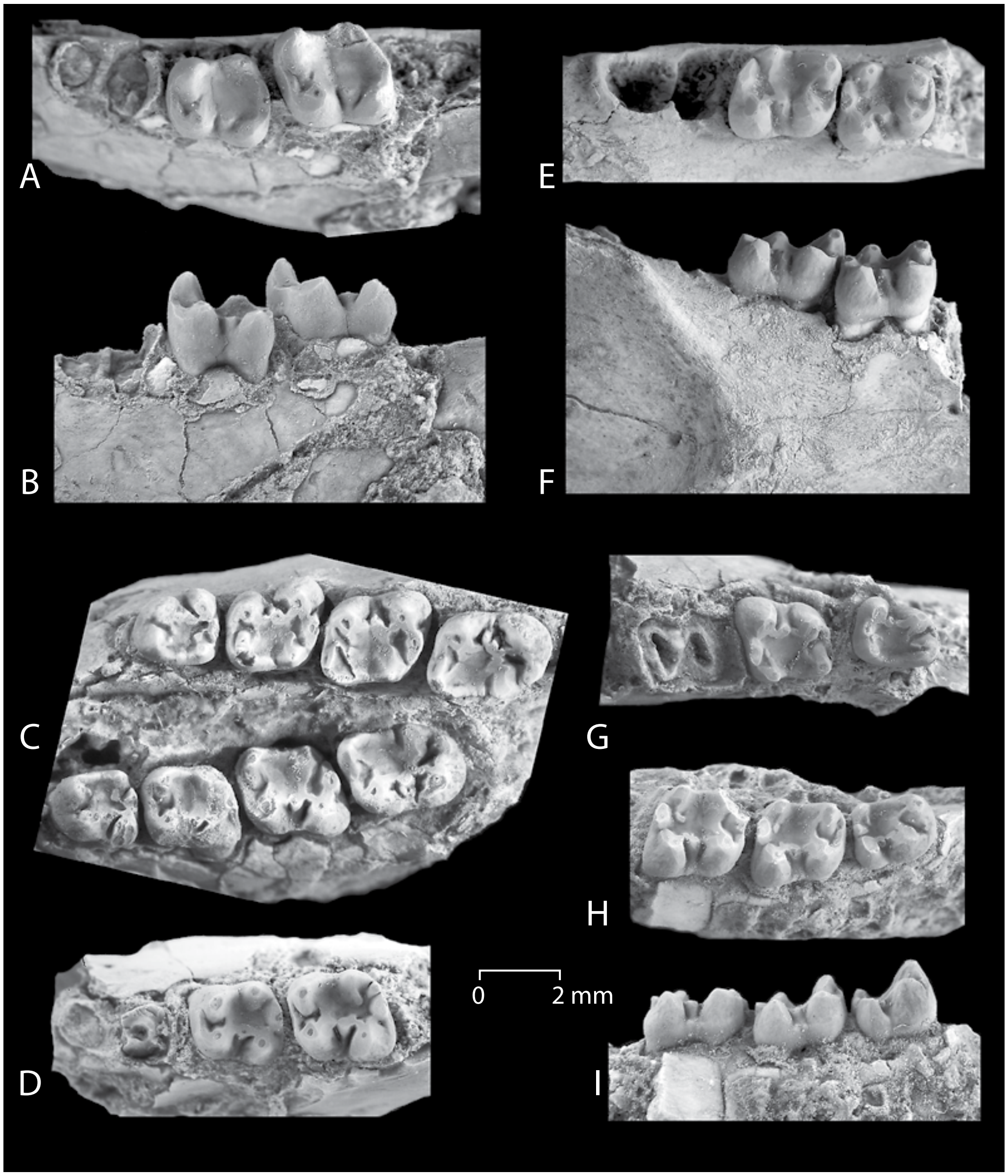


FIGURE 55 — Lower dentitions of rodents: A-B, *Paramys taurus,* L dentary with $M_{1\text{-}2}$, USNM 525634, in occlusal and buccal views. C-I, *Tuscahomys*, cf. *T. major*: C, mandible with L and RP_4-M_3, USNM 525635, in occlusal view; D, L dentary with $M_{1\text{-}2}$, USNM 533551, in occlusal view**;** E-F, R dentary with $M_{1\text{-}2}$, USNM 541961, in occlusal and buccal views; G, L dentary with P_4-M_1, USNM 525637, in occlusal view; H-I, R dentary with P_4-M_2, USNM 525640, in occlusal and buccal views.

Paramys taurus Wood, 1962
Figure 55A-B

Referred specimens.— WW-74 level: USNM 525634 (dentaries, $LM_{1\text{-}2}$, RM_2, I_1); WW-84: USNM 540591 (LM_1, LM_2), 540592 (LM_1, RM_3).

Description.— A small number of specimens show the primitive rhomboidal molars typical of this small species of *Paramys*. The talonids are wider than the trigonids on all three molars, but the condition is most pronounced on M_1. The trigonids are very short, consisting of a prominent tall and acute metaconid and a much lower protoconid, the two cusps joined anteriorly by a low, arcuate anterolophid or anterior cingulum (=para-cristid of non-rodents); there is no paraconid. The talonids are substantially wider than long and are deeply basined, lacking any features within the basin. The talonid cusps are peripheral and there is little basal inflation of the crowns. The hypoconid is slightly larger than the entoconid and the two cusps are of about the same height. The posterolophid forms the posterior margin of the molars and bears a much smaller

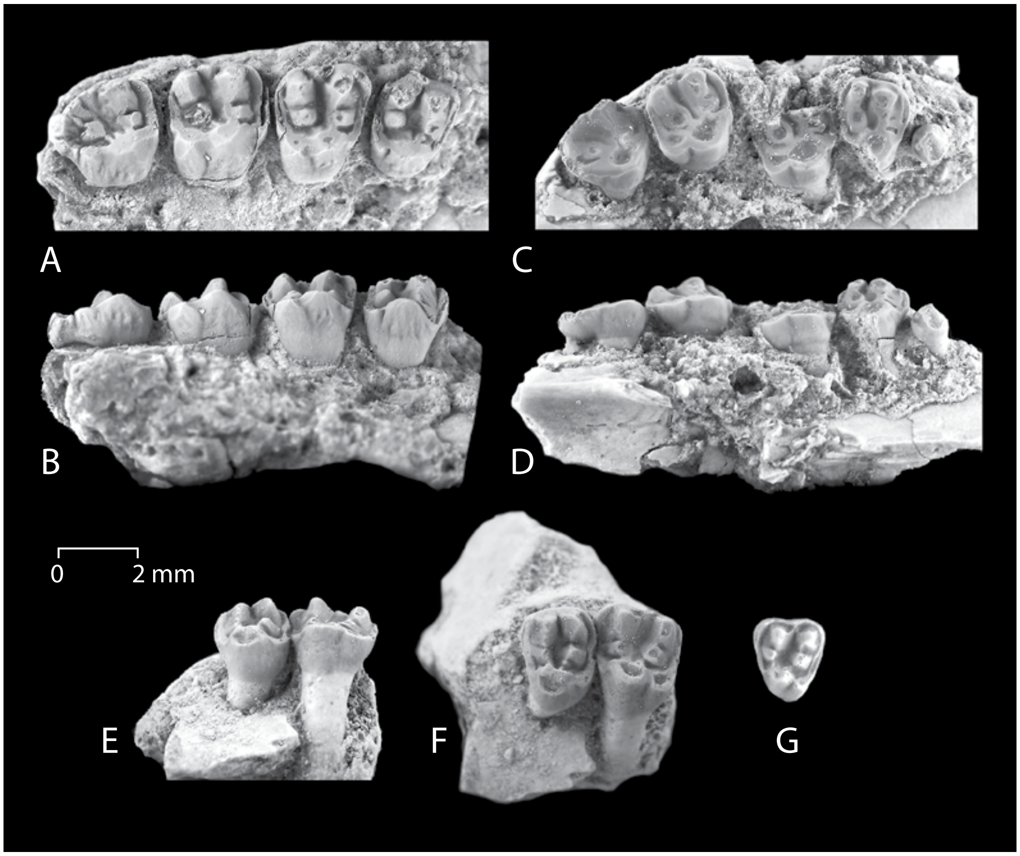


FIGURE 56 — Upper dentitions of *Tuscahomys*: A-B, *Tuscahomys*, cf. *T. major*, R maxilla with P^4-M^3, USNM 521504, in occlusal and lingual views; note moderate lingual hypsodonty. C-G, *T. worlandensis*, sp. nov.: C-D, R maxilla with P^3-M^3, USNM 538322, in occlusal and lingual views; E-F, L maxilla with P^4-M^1, holotype, USNM 527651, in lingual and occlusal views; G,?*T. worlandensis*, LdP^4, USNM 521674, occlusal view. Note slightly stronger lophodonty, relative brachydonty, and absence of distinct P^4 hypocone in *T. worlandensis*.

hypoconulid just buccal to the midline axis of each molar. A prominent mesoconid is situated anterolingual to the hypoconid.

Measurements (mm).— USNM 525634: LM$_1$L=2.60, W$_a$=2.00, W$_p$=2.35, LM$_2$L=2.80, W$_a$=2.50, W$_p$=2.70, RM$_2$L=2.80, W$_a$=2.50, W$_p$=2.70; USNM 540591: M$_1$L=2.40, W$_a$=1.90, W$_p$=2.15, M$_{1/2}$L=2.60, W$_a$=2.10, W$_p$=2.30; USNM 540592: M$_1$L=2.25, W$_a$=1.90, W$_p$=2.10, M$_3$L=2.70, W$_a$=2.10, W$_p$=2.35.

Discussion.— These specimens conform to the morphology of *Paramys taurus* (e.g., Wood, 1962; Ivy, 1990) but are at the small end of the size range or slightly smaller than samples described from before and after the PETM. *P. taurus* is known from both Polecat Bench and Castle Gardens.

Family CYLINDRODONTIDAE Miller and Gidley, 1918

TUSCAHOMYS Dawson and Beard, 2007

Tuscahomys, cf. *T. major* Dawson and Beard, 2007

Figures 55C-I, 56A-B, 57-59

Referred specimens.— WW-71: USNM 540593 (LM$_1$ or M$_2$); WW-74: USNM 538296 (LM$_2$); WW-75: USNM 538259 (RM^2); WW-77:USNM 533551 (L dentary with M$_{1\text{-}2}$); WW-79: USNM 521504 (R maxilla with P^4-M^3), USNM 525637 (L dentary with P$_4$-M$_1$, RM$_1$?, premaxillae with L and R I^1); WW-84: USNM nos. 540603-540605 (isolated LM^{1}s), 540606-540608 (isolated LM^{2}s), 540609-540612 (isolated M^{3}s), 540613-540615 (isolated RM^1 or M^2), 540616-540617 (isolated RM^{1}s), 540618-540619 (isolated RP^{4}s), 540620-540623 (isolated LM$_3$s), 540624-540625 (isolated LM$_1$ or M$_2$), 540626 (LM$_2$), 540627-540629 (isolated LM$_1$ or M$_2$), 540630 (LP$_4$), 540631 (RM$_3$), 540632-540634 (RM$_1$ or M$_2$); WW-91: USNM 538307 (R dentary with M$_2$); WW-96: USNM 525638 (R dentary with I$_1$, M$_2$), USNM 525640 (R dentary with P$_4$-M$_2$); WW-97: USNM nos. 540594 (LdP^4), 540599 (RM$_1$, LM$_3$), 540600 (RM$_3$?); WW-97 level: USNM 525636 (L dentary with M$_3$, M^2); WW-112: USNM 525635 (mandible with L and R P$_4$-M$_3$); 4 m below WW-112: USNM 525639 (L dentary with M$_2$); WW-116: USNM 540317 (LM$_1$ or M$_2$); unnumbered locality: USNM 538285 (R dentary with M$_2$); WW-191: USNM 541961** (R dentary with M$_{1\text{-}2}$).

Description.— Several jaws and 40 isolated teeth (Figures 55-58) closely resemble those of the cylindrodontid *Tuscahomys*,

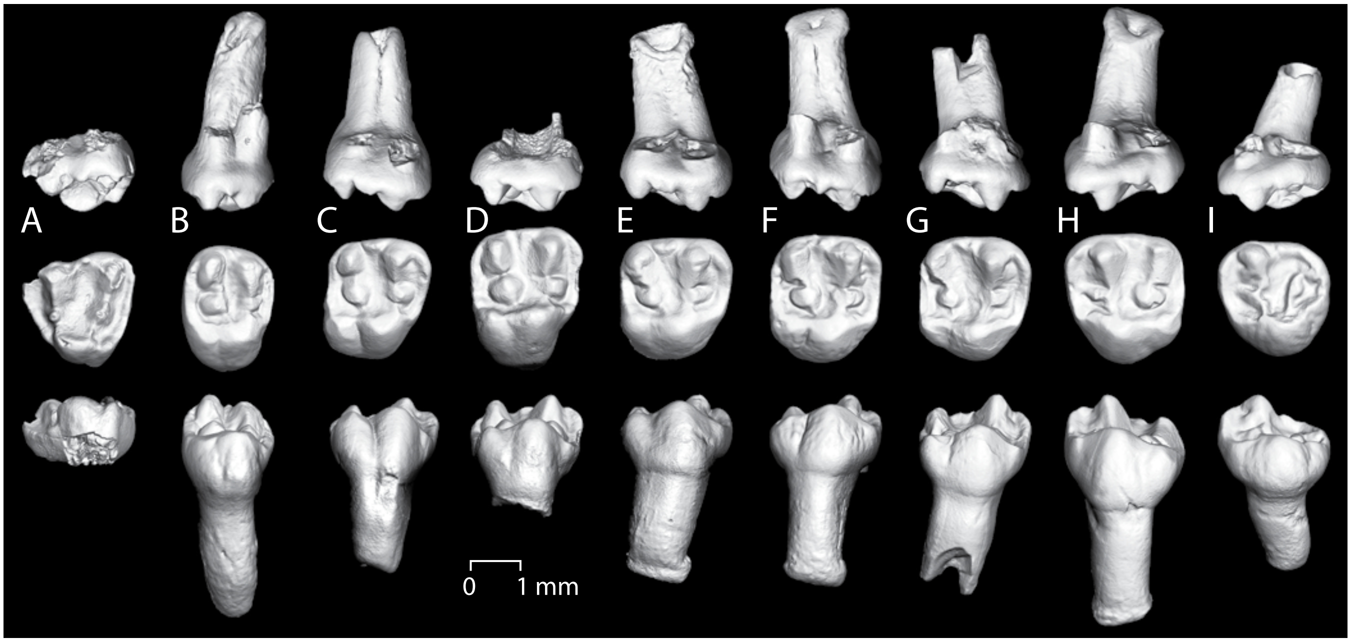


FIGURE 57 — Upper teeth of *Tuscahomys*, cf. *T. major*, in buccal (top row), occlusal (middle), and lingual (bottom) views: A, LdP^4, USNM 540594; B, RP^4, USNM 540619; C, RM^1, USNM 540617; D, RM^1, USNM 540616; E, RM$^{1/2}$, USNM 540615; F, RM$^{1/2}$, USNM 540613; G, RM$^{1/2}$, USNM 540614; H, LM^2, USNM 540608; I, LM^3, USNM 540609.

recently described from the basal Eocene Red Hot local fauna, Tuscahoma Formation of Mississippi (Dawson and Beard, 2007). Close comparison of the Sand Creek Divide specimens with the sample from Mississippi shows that the Wyoming specimens overlap in size with *T. major* (Figure 59).

P^4 is smaller than the molars and relatively shorter, with paracone and metacone closer together. A very small mesostyle is present in two of the specimens (USNM 521504, 540619; Figures 56A-B, 57B), whereas there is no mesostyle in the other (USNM 540618), as in *T. major*. A distinct protoloph is developed but the metaloph is weak or absent (USNM 521504). The protoconule (=paraconule) is variable in size but smaller than the metaconule. A distinct, small hypocone is present on all three P^{4}s. Well-developed anterior and posterior cingula are present, the posterior cingulum longer than the anterior. USNM 540594 is a dP^4 (Figure 57A) of appropriate size and morphology to represent the same species. It is fully molariform and triangular in shape, with well separated paracone and metacone and expansive anterior and posterior cingula. The protoloph and metaloph are well developed, with distinct protoconule and metaconule. The ectoloph is weakly dilambdodont and bears a well-developed mesostyle on the buccal margin. A low hypocone is present at the lingual end of the postcingulum and is linked to the protocone by a short crest.

M^1 and M^2 are rectangular and slightly wider (transversely) than long, whereas M^3 has nearly equal diameters and is nearly round. However, relative breadth (compared to length) decreases from M^1 to M^3. M$^{1\text{-}2}$, in general, seem to be slightly longer anteroposteriorly than in *T. major* (Figure 59) from Mississippi. The molars, as well as P^4, are moderately hypsodont lingually, but there is variation in this trait. Some specimens (e.g., USNM 521504, 540616; Figure 57D) are as lingually hypsodont as *T. major* or more so, but most are somewhat less hypsodont. In particular, the hypocone in the Sand Creek Divide sample is distinctly smaller and lower than the protocone (especially viewed lingually), whereas in *T. major* the hypocone is almost as large and high as the protocone. The paracone and metacone are well separated, the paracone larger and taller than the metacone. A variable mesostyle is situated between the two cusps on the buccal margin; it may be a prominent anteroposteriorly elongate cusp (Figure 57C, E), a much smaller cusp (Figure 57D, H), or something in between (Figures 56A-B, 57F). The conules are prominent, the metaconule usually slightly more so, and the protoconule projects anterior to the protoloph. The cross-lophs are not particularly well developed, though the protoloph is somewhat stronger than the metaloph, which may not become evident until the tooth is worn. The protocone is large and is situated more or less lingual to the paracone. It is joined to the hypocone by an anteroposterior crest which forms a sharp ridge in unworn teeth (e.g., Figure 57D, G). In lingual view the crest forms a moderately high wall, or mure, joining the two cusps, with only a shallow valley between them. Anterior and posterior cingula are well developed, the posterior cingulum lingually joining the hypocone, and the anterior either curving up to the protocone or variably (mainly on M^2?) giving rise to a small lingual cusp before joining the protocone (Figure 57G, H). M^3 (Figures 56A-B, 57I) is a nearly round tooth characterized by a prominent paracone and virtually no metacone. The conules and hypocone are small, and the anterior and posterior cingula are broad. The cross-lophs are slightly better developed than on M$^{1\text{-}2}$.

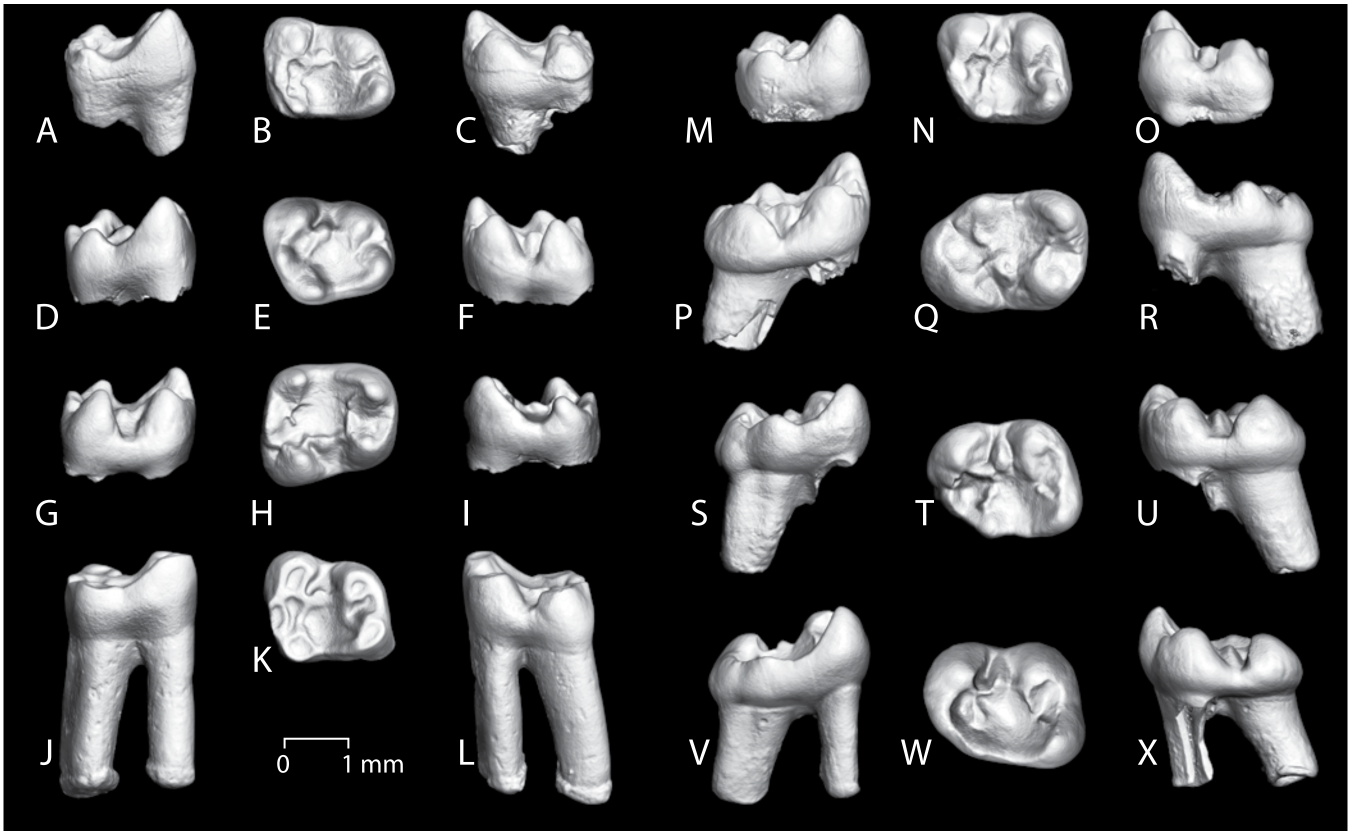


FIGURE 58 — Lower teeth of *Tuscahomys*, cf. *T. major*: A-C, LP_4, USNM 540630, in lingual, occlusal, and buccal views; D-F, LP_4, USNM 540629, in lingual, occlusal, and buccal views; G-I, RM_1, USNM 540599, in buccal, occlusal, and lingual views; J-L, L$M_{1/2}$, USNM 540593, in lingual, occlusal, and buccal views; M-O, LM_2, USNM 540626, in lingual, occlusal, and buccal views; P-R, RM_3, USNM 540631, in buccal, occlusal, and lingual views; S-U, LM_3, USNM 540621, in lingual, occlusal, and buccal views; V-X, LM_3, USNM 540622, in lingual, occlusal, and buccal views.

The lower cheek teeth are rhomboidal in occlusal view. P_4 has a narrower trigonid and shorter talonid than the molars, and M_3 differs from $M_{1\text{-}2}$ in having a longer talonid. The trigonids are progressively wider from P_4 to M_3 and, as in *Paramys*, they consist of a tall metaconid set anterolingual to the lower protoconid, joined by an arcuate anterolophid. A very low and weakly developed metalophid is interrupted by a deep trigonid notch. The talonids are broad and basined, bounded buccally by the hypoconid and prominent mesoconid, the latter with deep buccal creases separating it from the protoconid and hypoconid. The entoconid is usually slightly higher than the hypoconid and is situated lingual (on P_4) or increasingly anterolingual to the hypoconid (molars). A large, transversely extended hypoconulid, sometimes twinned (e.g., USNM 533551, Figure 55D), is present on the posterolophid approximately midway between hypoconid and entoconid. The hypoconulid is set off from those cusps by a notch, which tends to be deeper between entoconid and hypoconulid. The most distinctive feature of the lower molars is the presence of a hypolophid extending from the entoconid buccally into the talonid basin. On M_1 this crest typically curves back toward the hypoconulid; it may also bifurcate, with a low crest also joining the mesoconid. On the posterior molars the hypolophid crosses the basin to approach (on M_3) or join (M_2) the back of the mesoconid, enclosing a small, deeper basin between it and the posterolophid (e.g., Figure 58K, N, Q, T). The exact configuration of these hypolophids varies considerably in our sample, but all specimens have some development of these crests (perhaps weakest in USNM 533551). M_3 in the Sand Creek Divide sample, unlike that of *T. major*, lacks a metastylid.

Measurements (mm).— USNM 540594, dP^4 L=2.20, W=2.15; for all other measurements see Table 14. Our measurement of a cast of the holotype $M^{1/2}$ of *T. major* (L=2.05 mm, W=2.65 mm) is outside the range for this species published by Dawson and Beard (2007) and within the range of M^1 in the Sand Creek Divide sample, suggesting that *T. major* may actually be closer in size to the Sand Creek Divide sample than is indicated by Dawson and Beard's original measurements. Subsequently, Beard and Dawson (2009) reported a new, larger upper molar of *T. major* that closely conforms to the size of the sample reported here (see Figure 59).

Discussion.— *Tuscahomys*, cf. *T. major*, is by far the most common rodent species during the PETM at Sand Creek Divide. These teeth are immediately separable from those of *Paramys* and its close relatives by the greater complexity of the lower

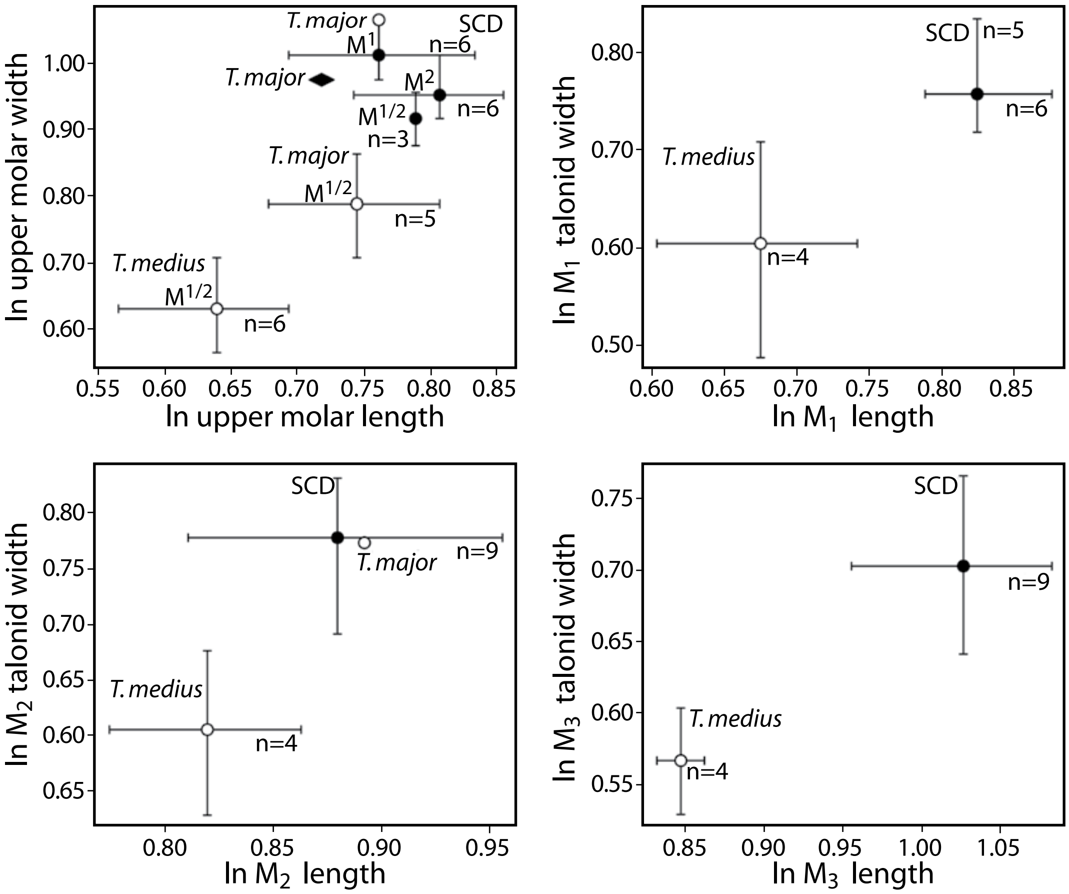


FIGURE 59 — Molar dimensions of the Sand Creek Divide sample of *Tuscahomys* (SCD, means indicated by black circles, ranges indicated by lines), compared with ranges for *T. major* and *T. medius* samples from the Red Hot Local Fauna in Mississippi (means or single occurrences indicated by open circles; data from Dawson and Beard, 2007). In upper left plot, our measurement of the holotype of *T. major* is indicated by the black diamond, and a new, larger specimen of *T. major* reported by Beard and Dawson (2009) is plotted at the top of the graph.

teeth and the distinctive upper molar morphology, characterized particularly by isolated conules, weak lophodonty, and moderate lingual hypsodonty.

In nearly every regard, the Sand Creek Divide teeth duplicate characteristics seen in the Mississippi sample of *T. major*. There is a tendency for upper molars in our sample to be less lingually hypsodont and to have slightly weaker hypocones and mesostyles than in the Mississippi sample; however, these features vary considerably in both samples. Indeed, some teeth in the Sand Creek Divide sample (e.g., USNM nos. 540599, 540617, 540626; see Figures 57C, 58G-I, M-O) are virtually indistinguishable in size and morphology from specimens in the Mississippi sample. The inability to identify consistent differences between our sample and that of *T. major* from the Red Hot local fauna (even though their geographic separation makes it likely that they are not conspecific) leads us to defer proposing a new species name until the two samples can be more clearly distinguished.

Previous authors have identified the prevalent rodent taxon from the PETM in the Bighorn Basin as either *Acritoparamys atwateri* (Gingerich, 1989, 2001; Strait, 2001) or a new species of cf. *Reithroparamys* (Gingerich and Smith, 2006), or both (Yans et al., 2006); and the Bighorn Basin samples closely approximate these taxa, at least following published descriptions. Although it is possible that several taxa are present, it would not be surprising if the most common species were the same in the Polecat Bench, Castle Gardens, and Sand Creek Divide samples. What is much less certain is the appropriate name for this rodent, in part because of ambiguity surrounding previously named taxa. The Sand Creek Divide sample resembles *A. atwateri* (which Wood [1962] assigned to *Reithroparamys*) in having a prominent transversely extended hypoconulid, but differs in having a hypolophid extending from the entoconid into the talonid basin, which is absent in *Acritoparamys* (Korth, 1984). This greatly diminishes the possibility that the lower teeth in the sample, at least, represent *A. atwateri*. The moderate hypsodonty and wall-like crest (mure) joining protocone and hypocone seem to differ from the condition in *A. atwateri*, thus reducing the likelihood that the upper teeth belong to *A. atwateri*.

It is more difficult to reject affinity with *Reithroparamys*, in

TABLE 14 — Measurements (mm) of *Tuscahomys*, cf. *T. major*, from Sand Creek Divide (* = estimated).

Upper Teeth

Specimen	P^{4}L	P^{4}W	M^{1}L	M^{1}W	M^{2}L	M^{2}W	M$^{1/2}$L	M$^{1/2}$W	M^{3}L	M^{3}W
USNM 521504	1.95	2.65	2.30	2.90	2.30	2.75	—	—	2.60	2.45
USNM 525636	—	—	—	—	2.10	2.60	—	—	—	—
USNM 538259	—	—	—	—	2.30	2.50	—	—	—	—
USNM 540603	—	—	2.0*	2.80	—	—	—	—	—	—
USNM 540604	—	—	2.05	2.70	—	—	—	—	—	—
USNM 540605	—	—	2.20	2.70	—	—	—	—	—	—
USNM 540606	—	—	—	—	2.20	2.50	—	—	—	—
USNM 540607	—	—	—	—	2.20	2.50	—	—	—	—
USNM 540608	—	—	—	—	2.35	2.70	—	—	—	—
USNM 540609	—	—	—	—	—	—	—	—	2.20	2.30
USNM 540610	—	—	—	—	—	—	—	—	2.40	2.30
USNM 540611	—	—	—	—	—	—	—	—	2.40	2.45
USNM 540612	—	—	—	—	—	—	—	—	2.45	2.45
USNM 540613	—	—	—	—	—	—	2.20	2.60	—	—
USNM 540614	—	—	—	—	—	—	2.20	2.50	—	—
USNM 540615	—	—	—	—	—	—	2.20	2.40	—	—
USNM 540616	—	—	2.20	2.75	—	—	—	—	—	—
USNM 540617	—	—	2.10	2.65	—	—	—	—	—	—
USNM 540618	1.75	2.40	—	—	—	—	—	—	—	—
USNM 540619	1.80	2.45	—	—	—	—	—	—	—	—
N	3	3	6	6	6	6	3	3	5	5
Mean	1.83	2.50	2.14	2.75	2.24	2.59	2.20	2.50	2.41	2.39
Std. Deviation	0.10	0.13	0.11	0.09	0.09	0.11	0.00	0.10	0.14	0.08
Std. Error	0.06	0.08	0.05	0.04	0.04	0.05	0.00	0.06	0.06	0.04
Minimum	1.75	2.40	2.00	2.65	2.10	2.50	2.20	2.40	2.20	2.30
Maximum	1.95	2.65	2.30	2.90	2.35	2.75	2.20	2.60	2.60	2.45

part because it is unclear exactly what constitutes this genus. There is considerable disagreement concerning which species properly belong to *Reithroparamys* (compare, for example, Wood [1962], Korth [1984], and Dawson and Beard [2007]). Ultimately, identification of the genus reverts to the type species, but the holotype of the type species, Bridgerian *R. delicatissimus* (Leidy, 1871), was lost long ago, and the prevailing concepts of this species and the genus are based primarily on a well-preserved skeleton (AMNH 12561; Matthew, 1920; Wood, 1962) whose identity with the holotype is problematic. Wood's (1962) diagnosis of *Reithroparamys* includes dental traits in common with the Sand Creek Divide sample (e.g., protoconule and metaconule round, hypolophid extending from entoconid into talonid basin) together with gnathic and cranial characters that cannot be assessed in any known PETM specimens. The only conflicting character is the tendency for the metaconule to be twinned, which, although a common variation in primitive rodents, was not observed in any specimen from Sand Creek Divide. In his description of *Reithroparamys*, Wood (1962) further noted the distinctly bilophodont condition of P^4-M^3 and "little suggestion of lingual hypsodonty in the upper cheek teeth" (p. 122)—the first a derived trait, and the second presumably plesiomorphic—which together would seem to separate the Sand Creek Divide sample from *Reithroparamys*. The contrasts are a matter of degree, however, and the differences are subtle. In fact, the upper dentition of AMNH 12561 shows about the same degree of hypsodonty as most of the Sand Creek Divide sample.

The presence of a hypolophid on lower molars of *Reithroparamys* is a derived character shared with *Tuscahomys* and other primitive cylindrodontids such as Bridgerian *Mysops*, but it is not restricted to these genera. Increasing hypsodonty is a derived trait particularly characteristic of cylindrodonts (M. Dawson, pers. comm., 2010). Significantly, the species of *Reithroparamys* most similar to the Wa-0 rodents, *R. ctenodactylops*, was recently reassigned to *Tuscahomys* (Dawson and Beard, 2007) partly based on these two features. Gingerich and Smith's (2006) illustrations and description of cf. *Reithroparamys* from Wa-M of Polecat Bench make it clear that these teeth represent the same or a very closely allied species to the Sand Creek Divide sample.

Thus *Tuscahomys* and *Reithroparamys* appear to be dentally very similar, but whether this reflects close relationship (or even synonymy) or homoplasy is uncertain. A thorough and comprehensive review of primitive rodents that includes all of the contentious taxa and examines intraspecific as well as interspecific variation is sorely needed to resolve the validity and interrelationships of these forms.

TABLE 14 — Measurements (mm) of *Tuscahomys*, cf. *T. major* (cont.).

Lower Teeth

Specimen	P_4L	P_4W_a	P_4W_p	M_1L	M_1W_a	M_1W_p	M_2L	M_2W_a	M_2W_p	$M_{1/2}L$	$M_{1/2}W_a$	$M_{1/2}W_p$	M_3L	M_3W_a	M_3W_p
USNM 525635R	2.15	1.60	1.90	2.40	2.00	2.30	2.60	2.05	2.20	—	—	—	2.90	2.10	2.10
USNM 525635L	2.10	1.60	—	2.35	—	—	2.60	2.05	2.20	—	—	—	2.95	2.15	2.10
USNM 525636	—	—	—	—	—	—	—	—	—	—	—	—	2.70	2.20	1.95
USNM 525637	2.15	1.55	1.65	2.20	1.80	2.10	—	—	—	—	—	—	—	—	—
USNM 525638	—	—	—	—	—	—	2.45	2.10	2.30	—	—	—	—	—	—
USNM 525639	—	—	—	—	—	—	2.35	—	2.20	—	—	—	—	—	—
USNM 525640	2.05	1.55	1.60	2.20	1.85	2.10	2.40	—	2.20	—	—	—	—	—	—
USNM 533551	—	—	—	2.25	1.80	2.05	2.40	2.15	2.30	—	—	—	—	—	—
USNM 538296	—	—	—	—	—	—	2.35	2.00	2.15	—	—	—	—	—	—
USNM 538307	—	—	—	—	—	—	2.30	2.05	2.10	—	—	—	—	—	—
USNM 540317	—	—	—	—	—	—	—	—	—	2.40	—	2.35	—	—	—
USNM 540593	—	—	—	—	—	—	—	—	—	2.20	1.70	1.95	—	—	—
USNM 540599	—	—	—	2.30	1.80	2.10	—	—	—	—	—	—	2.85	1.90	2.00
USNM 540620	—	—	—	—	—	—	—	—	—	—	—	—	2.90	2.20	2.10
USNM 540621	—	—	—	—	—	—	—	—	—	—	—	—	2.60	1.95	1.90
USNM 540622	—	—	—	—	—	—	—	—	—	—	—	—	2.70	2.15	2.00
USNM 540623	—	—	—	—	—	—	—	—	—	—	—	—	2.75	2.10	2.15
USNM 540624	—	—	—	—	—	—	—	—	—	2.35	2.10	2.15	—	—	—
USNM 540625	—	—	—	—	—	—	—	—	—	2.40	2.10	2.25	—	—	—
USNM 540626	—	—	—	—	—	—	2.25	2.05	2.00	—	—	—	—	—	—
USNM 540627	—	—	—	—	—	—	—	—	—	2.20	1.95	2.20	—	—	—
USNM 540629	—	—	—	—	—	—	—	—	—	2.20	1.70	2.00	—	—	—
USNM 540630	2.20	1.60	1.75	—	—	—	—	—	—	—	—	—	—	—	—
USNM 540631	—	—	—	—	—	—	—	—	—	—	—	—	2.80	1.95	1.90
USNM 540632	—	—	—	—	—	—	—	—	—	2.20	1.90	2.15	—	—	—
USNM 540633	—	—	—	—	—	—	—	—	—	2.25	2.20	2.20	—	—	—
USNM 540634	—	—	—	—	—	—	—	—	—	2.30	2.20	2.25	—	—	—
N	5	5	4	6	5	5	9	7	9	9	8	9	9	9	9
Mean	2.13	1.58	1.73	2.28	1.85	2.13	2.41	2.06	2.18	2.28	1.98	2.17	2.79	2.08	2.02
Std. Deviation	0.06	0.03	0.13	0.08	0.09	0.10	0.12	0.05	0.09	0.09	0.20	0.13	0.12	0.11	0.09
Std. Error	0.03	0.01	0.07	0.03	0.04	0.04	0.04	0.02	0.03	0.03	0.07	0.04	0.04	0.04	0.03
Minimum	2.05	1.55	1.60	2.20	1.80	2.05	2.25	2.00	2.00	2.20	1.70	1.95	2.60	1.90	1.90
Maximum	2.20	1.60	1.90	2.40	2.00	2.30	2.60	2.15	2.30	2.40	2.20	2.35	2.95	2.20	2.15

Tuscahomys worlandensis, sp. nov.

Figure 56C-G

Holotype.— USNM 527651, L maxilla with P^4-M^1, from WW-74.

Hypodigm.— Holotype; and from WW-79: USNM 538322 (R maxilla with P^3-M^3, P^4-M^1 incomplete), and tentatively WW-75: USNM 521674 (LdP^4).

Locality and Horizon.— Holotype from WW-74 (SE¼ sec. 3, T 48 N, R 92 W), referred specimens from WW-75 and WW-79, all McDermott's Butte Quadrangle, Washakie County, Bighorn Basin, Wyoming; lower Willwood Formation, earliest Eocene (Wa-0 biozone).

Etymology.— For Worland, Wyoming.

Diagnosis.— Less lingually hypsodont than other species of *Tuscahomys*. P^4 with paracone and metacone close together and no mesostyle, as in *T. major*. P^4 differs from other species of *Tuscahomys* in lacking a hypocone, and having a more lophodont metaloph. Molars more lophodont, with smaller conules and mesostyle than in other species.

Description.— Two maxillae (Figure 56C-F) differ from the rest of the Sand Creek Divide sample of *Tuscahomys* in being slightly smaller and having subtle but significant morphological differences. Most evident is the more anteroposteriorly compressed P^4, with paracone and metacone more closely approximated and without a mesostyle—features said to characterize *T. medius* and *T. major* as well (Dawson and Beard, 2007). Unlike those species, however, there is no indication of a hypocone on P^4. Another notable difference is the lack of lingual hypsodonty, the presence of which Dawson and Beard (2007) considered diagnostic of the genus. In addition, the molars of *T. worlandensis* have slightly weaker protoconule, metaconule, and mesostyle, and slightly stronger cross-lophs, than in other *Tuscahomys* specimens compared. In other respects, they are very similar to *Tuscahomys,* cf. *T. major*. P^3, as in other primitive rodents, is a small, round, one-rooted tooth. It is worn in USNM 538322, obscuring crown details.

A dP^4 (USNM 521674; Figure 56G) is tentatively referred to the new species because it is slightly smaller, and its paracone and metacone are closer together than in a dP^4 (USNM 540594) referred to *Tuscahomys*, cf. *T. major*. However, the tooth is somewhat more bunodont and less lophodont than USNM 540594, in contrast to the molars.

Measurements (mm).— Holotype: P^4L= 1.75, W=2.5, M^1L=2.20, W=2.65; USNM 538322: P^3L=0.90, W=1.00, P^4L=1.70, M^2L=2.00, W=2.45, M^3L=2.20, W=2.30; USNM 521674: LdP^4? L=1.70, W=2.00.

Discussion.— The two maxillae referred to the new species are very similar to the Mississippi species of *Tuscahomys*, as well as to the sample referred above to *Tuscahomys*, cf. *T. major*, and to *T. ctenodactylops* from the very early Eocene of Sweetwater County, Wyoming. *T. ctenodactylops* was initially assigned to *Reithroparamys* (Korth, 1984) but was transferred to *Tuscahomys* by Dawson and Beard (2007) based on its lingual hypsodonty, prominent conules, anteroposterior crest joining protocone and hypocone, and other features. *T. worlandensis*, sp. nov., differs particularly in being less hypsodont than other species and in lacking a hypocone on P^4, but these seem to be minor differences and it is very probable that these species are closely related. If further study shows that *Reithroparamys* and *Tuscahomys* are related and differ primarily in relative hypsodonty, then *T. worlandensis* might be better placed in *Reithroparamys*. At present, the similarity in other aspects of crown morphology to various species of *Tuscahomys* supports allocation to that genus.

The maxillae of *T. worlandensis* are not associated with lower teeth, so it is unknown how or if the lower dentition differs from that of *Tuscahomys*, cf. *T major*. It is possible, if not likely, that some of the lower teeth here referred to the latter species actually belong to *T. worlandensis*.

RODENTIA, indeterminate

Referred specimens.— WW-77: USNM 533550 (distal R tibia and astragalar body), USNM 538320 (distal L tibia); WW-84: about 30 uncatalogued isolated teeth; WW-97: USNM 538321 (9 isolated teeth); WW-172: USNM 533632 (incisor); unnumbered locality: USNM 539476 (R astragalus).

Description.— These specimens show diagnostic features of rodents, but cannot be more precisely assigned at this time. When postcranial differences are better understood it may be possible to assign the postcranial elements. Most of the teeth listed here are either incisors or heavily worn cheek teeth whose diagnostic details are ambiguous or obliterated. Two samples (USNM 538321 and the uncatalogued teeth from WW-84) include a few upper molars that are more lophodont and have smaller conules than those attributed to *Tuscahomys*; they may belong to *Paramys taurus*. Size differences among these unassigned teeth suggest the presence of a smaller form not otherwise recognized in the assemblage.

IV

DISCUSSION

FIRST APPEARANCES DURING THE PETM

The data from Sand Creek Divide suggest that immigrant taxa did not all arrive in the southern Bighorn Basin concurrently, but rather that they may have appeared sequentially during the PETM. Specimens of *Hyracotherium* and *Diacodexis* are known from the top of Red 1, within 1-2 m of the base of the Willwood Formation (and the start of the CIE), documenting their presence at the very beginning of the Eocene (Figure 60). Also first appearing at (or restricted to) this level are *Haplomylus zalmouti* and *Esthonyx spatularius*. All of these taxa are smaller than their early Wasatchian successors. It is notable, however, that larger individuals of *Hyracotherium*, perhaps *H. grangeri*, were reported from near the base of the PETM at Cabin Fork (Secord et al., 2008). Euprimates do not appear in the Sand Creek Divide section until tens of thousands of years later, the omomyid *Teilhardina* first appearing at about 8-9 meters above the base of the Willwood Formation (see also Smith et al., 2006; Rose et al., 2011), and the notharctid *Cantius* not until about 16 m. Two other important immigrants, the condylarth *Hyopsodus* and the hyaenodontid *Arfia*, make their first appearances together with *Teilhardina*. Other hyaenodontids are not recorded until substantially higher in the PETM section. While these data imply a multiphase mammalian turnover during the PETM, it should be realized that sampling remains inadequate at some levels (especially near the base of the PETM) and new discoveries can easily alter the current view. For example, until July 2010, the lowest occurrence of *Diacodexis* was at 12 m. Thus we cannot rule out the possibility that all immigrants *did* arrive synchronously near the beginning of the PETM; but current evidence does not support this in the Sand Creek Divide section.

UPPER BOUNDARY OF THE WA-0 BIOZONE

Several specimens of *Hyracotherium* larger than *H. sandrae* (USNM 533633, 541915-541919, tentatively assigned to *H. grangeri*; Figure 53G, I) were found at WW-173 and WW-178, at about 50 m in the Sand Creek Divide section and about 5-10 m above the Puffy Purple (see Figure 6). The upper teeth closely match the holotype of *H. grangeri* in morphology and are slightly larger. In that narrow interval they are associated with larger, more lophodont basal perissodactyls that seem to represent both *Cardiolophus* and *Homogalax*, indicators of biozone Wa-1 or later. Measurements of all these specimens are given in Table 15.

USNM 539517 (LM^1 or M^2, Figure 53H) is identified as *Cardiolophus radinskyi* rather than *Hyracotherium grangeri* based on its larger size, stronger lophodonty despite retention of small conules, and relatively squared (actually rhomboid) outline (W/L=1.10, compared with 1.10-1.15 in M^1 and M^2 of the holotype, based on measurements of Gingerich, 1991). USNM 539509 (L maxilla with P3-M^3, Figure 53J) is identified as *Homogalax protapirinus* based on having slightly stronger crosslophs and wider premolars and molars than in *Cardiolophus* (W/L of M^1=1.26, of M^2=1.20, of M^3=1.29). The co-occurrence of *Cardiolophus radinskyi* and *Homogalax protapirinus* is unexpected and significant, for although *Cardiolophus* has been known from Wa-1 (and its first appearance used an an indicator of that biozone), the first appearance of *H. protapirinus* has been used to define Wa-3 (Gingerich, 1991; Chew, 2005). If this specimen is correctly identified, it represents a substantial range extension for *Homogalax*. In any case, the occurrence of either of these genera is a strong indication that the upper boundary of Wa-0 has been crossed.

The latter interpretation is supported by the occurrence at WW-173 of *Ectocion osbornianus* (USNM 541937). *E. osbornianus* is typical of strata below and above the PETM but has not been found in the PETM interval at Sand Creek Divide (though Gingerich, 1989, reported two specimens from the Wa-0 interval at Polecat Bench). Isotopic evidence from the south section at Sand Creek Divide corroborates the transition to the post-PETM Wa-1 biozone. *Coryphodon* dental remains yielding a $\delta^{13}C$ value of -13.5‰, and the increase of $\delta^{13}C$ ratios of bulk sedimentary organic matter to pre-CIE levels, are both considered to indicate the end of the CIE/PETM (see Figure 3). Also present at WW-173 is the taxon *Cantius ralstoni*, first known from Wa-1. The first appearance of *C. ralstoni*, however, is a few meters lower than these perissodactyls, at WW-89 (45 m). In addition, the assemblage from WW-89 includes teeth tentatively attributed to the taxon *Haplomylus speirianus*, also first known from Wa-1. These two records constitute the lowest occurrence of probable Wa-1 mammals in the Sand Creek Divide section.

FAUNAL COMPOSITION AND DIVERSITY

The rapid and severe environmental changes of the PETM had serious consequences for existing biotas. In the Bighorn Basin alone, the PETM marks the first appearance of euprimates, artiodactyls, perissodactyls, and hyaenodontid creodonts (Bowen et al., 2002; Smith et al., 2006) as well as the apparent transient dwarfing of mammal species and ichnofaunas (Clyde and Gingerich, 1998; Gingerich, 2003; Smith et al., 2009). Also corresponding to the PETM were a brief increase in the

Table 15 — Measurements (mm) of perissodactyls from above Wa-0 at Sand Creek Divide (* = estimated).

Upper Teeth

Specimen		Meter	P^3L	P^3W	P^4L	P^4W	M^1L	M^1W	M^2L	M^2W	M^3L	M^3W
Cardiolophus radinskyi	USNM 539517	49.5	—	—	—	—	—	—	10.75	11.80	—	—
Homogalax protapirinus	USNM 539509	50.0	7.65	8.50	7.15	9.20	8.90	11.20	10.0*	12.00	9.60	12.40
Hyracotherium grangeri	USNM 539516	49.5	—	—	5.95	7.40	7.50	9.05	—	—	—	—
Hyracotherium grangeri	USNM 541918	50.0	—	—	—	—	7.20	8.85	8.20	9.80	—	—
Hyracotherium grangeri	USNM 541919	50.0	—	—	—	—	—	—	—	—	7.65	9.80

Lower Teeth

Specimen		Meter	dP_3L	dP_3W	dP_4L	dP_4W_a	dP_4W_p	M_1L	M_1W_a	M_1W_p	M_2L	M_2W_a	M_2W_p	M_3L	M_3W_a	M_3W_p
Hyracotherium grangeri	USNM 533633	53.5	—	—	—	—	—	—	—	—	8.70	5.75	5.65	—	—	—
Hyracotherium grangeri	USNM 539516	49.5	—	—	—	—	—	—	—	—	—	—	—	11.20	5.80	5.35
Hyracotherium grangeri	USNM 539518	49.5	—	—	—	—	—	—	—	—	—	—	—	11.00	5.65	5.30
Hyracotherium grangeri	USNM 541915L	50.0	—	—	—	—	—	7.10	4.80	4.85	—	—	—	—	—	—
Hyracotherium grangeri	USNM 541915R	50.0	—	—	—	—	—	7.10	4.75	4.85	—	—	—	10.50	5.45	5.10
Hyracotherium grangeri	USNM 541916	50.0	5.80	3.20	6.85	4.00	4.25	—	—	—	—	—	—	—	—	—
Hyracotherium grangeri	USNM 541917	50.0	—	—	—	—	—	—	—	—	9.35	6.15	6.25	11.35	5.80	5.70

proportion of digging mammals, potential long-term increases in standing richness and turnover (Clyde and Gingerich, 1998; Gingerich, 2003), and floral range extensions of 600-1500 km northwards (Wing et al., 2005). The Sand Creek Divide local fauna adds to our knowledge of faunal response to the conditions of the PETM and allows us to examine more closely a number of aspects of this response, including spatial variation in the composition and diversity of the known Wa-0 faunas, and temporal variation from faunas immediately preceding and immediately following the PETM.

All known Bighorn Basin Wa-0 local faunas (Table 16) are from fluvial floodplain settings and were collected by surface prospecting, quarrying and/or screen-washing. In addition, much of the specimen identification was done by just a few workers with similar species definitions. This makes the faunas amenable to comparisons of composition, diversity, and turnover (in the case of chronological comparisons). Although turnover is often expressed as standardized, instantaneous per-taxon rates of first and last appearances (Alroy, 2000; Foote, 2000; Chew, 2009), these rates require precise estimates of temporal duration that would introduce more uncertainty in this case than a simple discussion of proportions of new taxa per land-mammal biochron. Composition is readily quantified by the relative abundance of orders, genera and species, with 95% confidence intervals estimated using the multinomial distribution (Moore et al., 2007, eqn. 2). Diversity is more difficult to describe as it contains two interrelated components: richness and evenness. Richness (S) is the number of species in a community, whereas evenness refers to the distribution of species abundances. Evenness affects the richness of *samples* (a community with high evenness will yield *samples* with higher richness than a community with low evenness, even if both communities have the same total number of species), thus both aspects of diversity must be quantified.

Richness can be compared among samples by rarefaction, which charts cumulative species richness as a function of the number of individuals (e.g., Hurlburt, 1971; Foote, 1992). Most rarefaction software packages (e.g., Holland, 2003) provide 95% confidence intervals for rarefaction curves although the variance estimates are conditional (they do not take into account the uncertainty of sampling; Colwell et al., 2004). Thus 95% confidence intervals invariably approach the final values of expected species richness and are not appropriate for comparison near the high end of a rarefaction curve. The Probability of Interspecific Encounter (PIE) index (Hurlburt, 1971) is used to quantify evenness. PIE is the probability that any two specimens drawn at random from the community will belong to different taxa (it is the inverse of Simpson's Index of Dominance). As it cannot be tested for statistically significant variation, evenness is further assessed graphically using Whittaker (rank-abundance) plots, in which species abundances are plotted in $\log_{10}$ format on the y-axis against species rank (from most to least abundant) on the x-axis (Magurran, 2004). A steep Whittaker curve reflects a sample with low evenness whereas a nearly horizontal curve reflects a sample with high evenness. Although the log-transformation

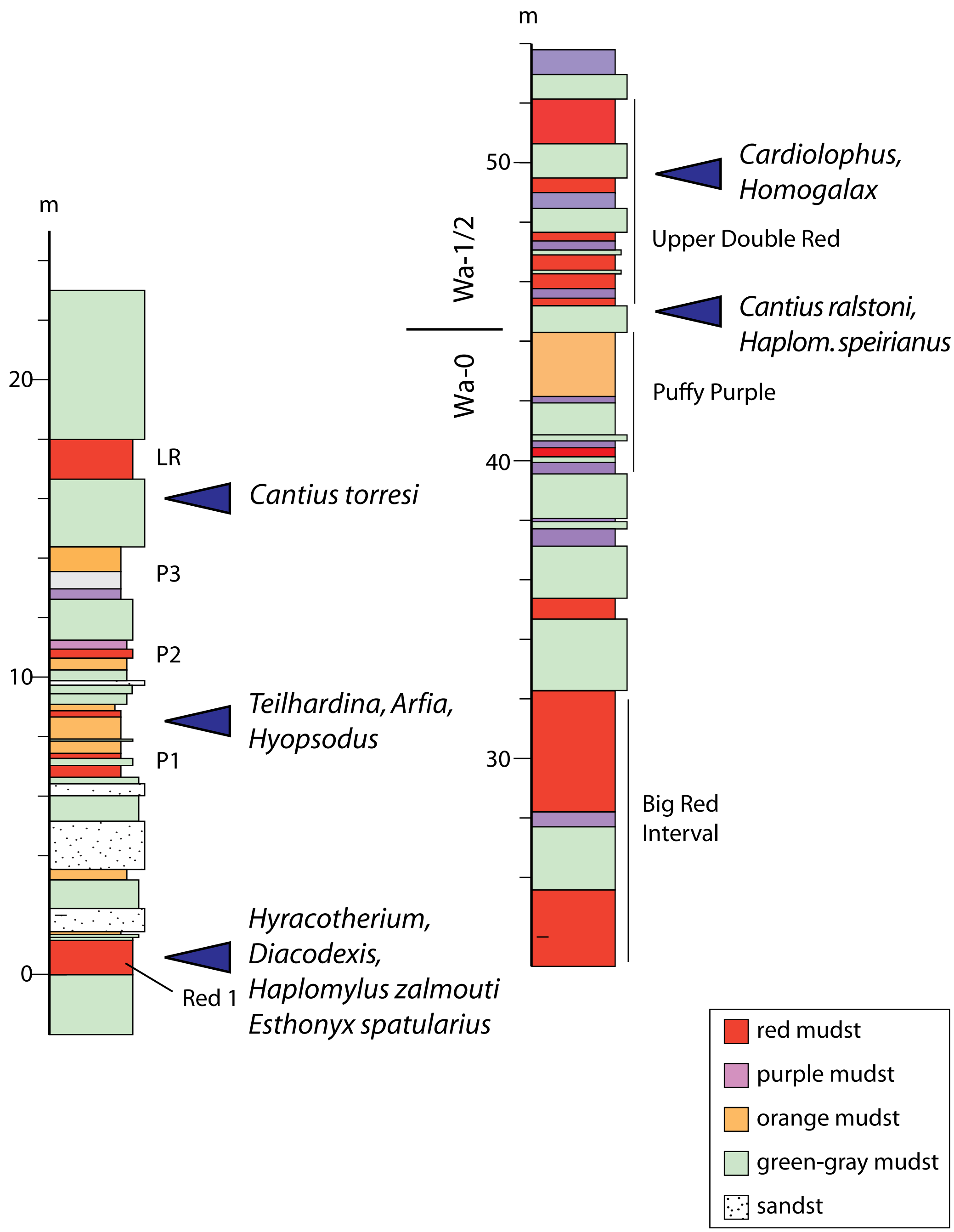


FIGURE 60 — Significant first occurrences of mammalian taxa in the Sand Creek Divide section. Compare with Figures 3 and 6.

of abundances can mask variation (Magurran, 2004), the Whittaker plots provide context for the interpretation of PIE.

The parameters discussed above are relatively independent of sample size, but they can be influenced by other factors unique to fossil samples, including method of fossil collection, method of counting individuals, and time-averaging. Most of the samples analyzed here were found by surface prospecting (Table 16), but at a few sites quarrying and/or screen-washing was also employed. The latter processes capture the small species that are otherwise under-sampled at surface-prospected sites (Winkler, 1983; Silcox and Rose, 2001). Samples that *combine* surface prospecting and quarrying/screen-washing have higher measures of diversity and different compositions than samples that were only surface-prospected or only quarried/screen-washed. Similarly, samples that accumulated over longer periods of time have higher diversity measures than those that were deposited

TABLE 16 — Bighorn Basin fossil mammal faunas from the late Clarkforkian and early Wasatchian. L: number of localities; BhB: Bighorn Basin; SP: surface prospecting; SW: screen washing; Q: quarrying. ^{1}includes Castle Gardens; ^{2}includes Polecat Bench.

LAND MAMMAL AGE		LOCATION	L	SAMPLING METHOD	REFERENCE
Wasatchian	Wa-3	Elk Creek	55	SP	(Chew, 2009)
	Wa-1/2	No Water Creek	35	SP, some SW, Q	(Chew, 2009)
	Wa-0	Castle Gardens	1	SW	(Strait, 2001)
		Honeycombs^1	5	SW, some SP	(Yans et al., 2006)
		Northern BhB^2	20	SP	(Gingerich, 1989)
		Polecat Bench	4	SP, some SW	(Gingerich, 2001a)
		Sand Creek Divide	36	SP, some SW, Q	This paper
	Wa-M	Honeycombs	1	SP	(Yans et al., 2006)
		Polecat Bench	1	SP, SW	(Gingerich and Smith, 2006)
		Sand Creek Divide	3	SP, Q, and SW	This paper
Clark-forkian	Cf-3	Northern BhB	50	SP	(Rose, 1981a)
	Cf-2	Northern BhB	21	SP, some Q	(Rose, 1981a)

more quickly. Time-averaging is an important consideration for the chronological comparisons made here, as the samples used in these comparisons incorporate different amounts of time. Finally, many of the samples analyzed here include two different counts of individuals: total numbers of specimens (TNS) and minimum number of individuals (MNI). TNS counts every specimen as an individual, assuming little or no association between specimens within a sample. MNI usually counts the largest number of specimens of the same element and assumes a high degree of association between specimens (Badgley, 1986). The two counts produce similar patterns of variation in composition, diversity and turnover, but MNI overestimates rare species (Badgley, 1986) and has not been calculated for several of the samples compared herein. Thus, TNS is used in all of the following comparisons.

Comparison with other Wa-0 faunas

Although PETM sections have been identified outside of northern Wyoming (e.g., Wing et al., 2003; Bowen and Bowen, 2008; Beard and Dawson, 2009), the most extensively studied PETM faunas come from the Bighorn Basin (Table 16). Only here are data sufficient to allow comparisons of faunal structure and composition. The type Wa-0 fauna was initially described from 20 localities across the northern Bighorn Basin (Gingerich, 1989). However, most of the specimens come from four main localities at the southern end of Polecat Bench (Gingerich, 2001a). The fauna includes 40-41 species found primarily by surface prospecting. A second large Wa-0 fauna comes from the Honeycombs area in the southern Bighorn Basin (Strait, 2001, 2003; Yans et al., 2006). Most of the species here were recovered by screen-washing at the Castle Gardens locality (29 species in Strait, 2001; 38 in Yans et al., 2006). In comparison, the Sand Creek Divide fauna includes 56 species from 40 localities that were mainly surface prospected, although a few sites were successfully quarried or screen-washed. Table 17 presents Sand Creek Divide species data and relative abundances with 95% confidence intervals.

The Polecat Bench area has also yielded a significant sample of 18-19 species from a wash site in a 4-5 meter-thick zone at the base of the Wasatchian (Gingerich and Smith, 2006). Although the sample contains three typical Wasatchian genera (*Macrocranion*, *Meniscotherium* and cf. *Reithroparamys*), it also has three unique species (*Meniscotherium priscum*, *Amphigyion straitae*, and *Haplomylus zalmouti*) and lacks the artiodactyls, perissodactyls, and primates typical of Wa-0. This led the authors to designate it as a new biozone, Wa-M (for the distinctive genus *Meniscotherium*; see also Magioncalda et al., 2004; Yans et al., 2006). Though common in the Wasatchian of southern Wyoming and New Mexico, *Meniscotherium* is known only from the Wa-M interval in the Bighorn Basin. It has been suggested that the Wa-M fauna existed for a brief period just before and during the maximum excursion of the CIE and was then replaced by the Wa-0 fauna. However, samples from the Honeycombs area and Sand Creek Divide cast doubt on the uniqueness of this interval. In the Honeycombs area, a single Wa-M locality has been reported (Yans et al., 2006), which produced

TABLE 17 — Mammalian fauna from the PETM at Sand Creek Divide, with relative abundances. Numbers in parentheses include questionably attributed specimens. CI: confidence interval; MNI: minimum number of individuals; TNS: total number of specimens.

	TNS	95% CI	MNI	95% CI	%TNS	%MNI
MULTITUBERCULATA						
Ectypodus tardus	7	3.39, 10.61	1	0, 7.15	0.7	0.3
MARSUPIALIA						
Herpetotherium innominatum	6	2.39, 9.61	2	0, 8.15	0.6	0.6
Mimoperadectes labrus	66	62.39, 69.61	20	13.85, 26.15	6.5	5.7
Cf. *Peradectes protinnominatus*	13	9.39, 16.61	4	0, 10.15	1.3	1.1
CIMOLESTA						
Didelphodus sp.	6	2.39, 9.61	4	0, 10.15	0.6	1.1
PANTOLESTA						
Palaeosinopa lutreola	5	1.39, 8.61	3	0, 9.15	0.5	0.8
PHOLIDOTAMORPHA						
Palaeanodon nievelti	6	2.39, 9.61	4	0, 10.15	0.6	1.1
TAENIODONTA						
Ectoganus bighornensis	5	1.39, 8.61	5	0, 11.15	0.5	1.4
Ectoganus, cf. *E. lobdelli*	3	0, 6.61	3	0, 9.15	0.3	0.8
Ectoganus sp. [one of the above spp.]	5		5		0.5	1.4
TILLODONTIA						
Azygonyx gunnelli	2	0, 5.61	2	0, 8.15	0.2	0.6
Azygonyx, cf. *A. grangeri*	1	0, 4.61	1	0, 7.15	0.1	0.3
Esthonyx spatularius	5	1.39, 8.61	2	0, 8.15	0.5	0.6
Esthonyx sp. [prob. not *E. spatularius*]	2	0, 5.61	1	0, 7.15	0.2	0.3
PANTODONTA						
Coryphodon sp.	7	3.39, 10.61	7	0.85, 13.15	0.7	2
EULIPOTYPHLA						
Leptacodon donkroni, sp. nov.	5	1.39, 8.61	1	0, 7.15	0.5	0.3
Leptacodon sp. 2, probably new	3	0, 6.61	1	0, 7.15	0.3	0.3
Plagioctenoides microlestes	2	0, 5.61	1	0, 7.15	0.2	0.3
Plagioctenoides tombowni, sp. nov.	2	0, 5.61	2	0, 8.15	0.2	0.6
Plagioctenoides sp. indet.	19		2		1.9	0.6
Cf. *Parapternodus* sp.	2	0, 5.61	1	0, 7.15	0.2	0.3
Macrocranion junnei	18	14.39, 21.61	5	0, 11.15	1.8	1.4
Cf. *Colpocherus* sp., probably new	2 (7)	0, 5.61	2 (3)	0, 8.15	0.2	0.6
PRIMATES						
Ignacius graybullianus	1	0, 4.61	1	0, 7.15	0.1	0.3
Phenacolemur praecox	1	0, 4.61	1	0, 7.15	0.1	0.3
Arctodontomys wilsoni	8	4.39, 11.61	4	0, 10.15	0.8	1.1
Niptomomys, cf. *N. doreenae*	36 (38)	32.39, 39.61	6	0, 12.15	3.5	1.7
Nanomomys thermophilus, gen.et sp. nov.	5	1.39, 8.61	1	0, 7.15	0.5	0.3
Teilhardina brandti	24	20.39, 27.61	12	5.85, 18.15	2.4	3.4
Teilhardina gingerichi, sp. nov.	1	0, 4.61	1	0, 7.15	0.1	0.3
Cantius torresi	8	4.39, 11.61	5	0, 11.15	0.8	1.4
CREODONTA: Oxyaenidae						
Dipsalidictis platypus	2	0, 5.61	1	0, 7.15	0.2	0.3
Oxyaenid, indet. [prob. not *D. platypus*]	1	0, 4.61	1	0, 7.15	0.1	0.3

TABLE 17 — Mammalian fauna from the PETM (cont.).

	TNS	95% CI	MNI	95% CI	%TNS	%MNI
CREODONTA: Hyaenodontidae						
Arfia junnei	16	12.39, 19.61	9	2.85, 15.15	1.6	2.5
Prototomus deimos	5	1.39, 8.61	2	0, 8.15	0.5	0.6
Prolimnocyon eerius	6	2.39, 9.61	1	0, 7.17	0.6	0.3
?Hyaenodontid, unnamed sp. nov.?	2	0, 5.61	1	0, 7.18	0.2	0.3
CARNIVORA						
Didymictis leptomylus	52 (55)	48.39, 55.61	19 (20)	12.85, 25.15	5.1	5.4
Viverravus acutus	7	3.39, 10.61	5	0, 11.15	0.7	1.4
Viverravus rosei	2	0, 5.61	1	0, 7.18	0.2	0.3
Cf. *Viverravus politus*	3	0, 6.61	2	0, 8.15	0.3	0.6
Uintacyon gingerichi	14 (15)	10.39, 17.61	6 (7)	0, 12.15	1.4	1.7
Cf. *Miacis deutschi*	1	0, 4.61	1	0, 7.18	0.1	0.3
Cf. *Miacis rosei*	2	0, 5.61	1	0, 7.18	0.2	0.3
Unidentified "miacoids"	8		4		0.8	1.1
CONDYLARTHRA						
Chriacus badgleyi	31 (40)	27.39, 34.61	13 (17)	6.85, 19.15	3.1	3.7
Hyopsodus loomisi	177	173.39, 180.61	30	23.85, 36.15	17.4	8.5
Haplomylus zalmouti	3	0, 6.61	3	0, 9.15	0.3	0.8
?Apheliscidae, unnamed sp. nov.	1	0, 4.61	1	0, 7.15	0.1	0.3
Phenacodus intermedius	7	3.39, 10.61	7	0.85, 13.15	0.7	2
Phenacodus vortmani	2	0, 5.61	2	0, 8.15	0.2	0.6
Ectocion parvus	76	72.39, 79.61	35	28.85, 41.15	7.5	9.9
Copecion davisi	65	61.39, 68.61	27	20.85, 33.15	6.4	7.6
Ectocion parvus/Copecion davisi	44		9		4.3	2.5
MESONYCHIA						
Dissacus praenuntius	5	1.39, 8.61	3	0, 9.15	0.5	0.8
ARTIODACTYLA						
Diacodexis ilicis	45	41.39, 48.61	14	7.85, 20.15	4.4	4
PERISSODACTYLA						
Hyracotherium sandrae	62	58.39, 65.61	22	15.85, 28.15	6.1	6.2
RODENTIA						
Paramys taurus	5	1.39, 8.61	3	0, 9.15	0.5	0.8
Tuscahomys, cf. *T. major*	50	46.39, 53.61	18	11.85, 24.15	4.9	5.1
Tuscahomys worlandensis, sp. nov.	2 (3)	0, 5.61	2 (3)	0, 8.15	0.2	0.6
Unidentified	43		—		4.2	
TOTAL	1015 (1036)		353 (361)			

three mammal specimens (*Meniscotherium* sp, a rodent, and a perissodactyl; Yans et al., 2006). In the Sand Creek Divide area, the Wa-M interval has yielded 6 mammalian taxa, including the artiodactyl *Diacodexis ilicis*, but *Meniscotherium* has not been recovered. The other taxa identified from this interval at Sand Creek Divide are *Palaeosinopa lutreola*, *Ectoganus bighornensis*, *Esthonyx spatularius*, *Haplomylus zalmouti*, and *Uintacyon gingerichi*. Notably, only two taxa, *E. spatularius* and *H. zalmouti* are restricted to the Wa-M interval at Sand Creek Divide, and the only species shared with any other Wa-M assemblage is *H. zalmouti*. The presence of perissodactyls and artiodactyls in Wa-M samples from Castle Gardens and Sand Creek Divide (and possibly the absence of *Meniscotherium* from Sand Creek Divide) suggest that this interval may not warrant a separate biozone designation.

To determine whether there was significant spatial variation in community structure across the region during this critical interval, the Sand Creek Divide fauna can be compared with the

TABLE 18 — Bighorn Basin Wa-0 and Wa-M samples compared with the Sand Creek Divide Wa-0 sample. S: number of species; TNS: total number of specimens. [1]Total sample size reduced (from TNS=1015) because the following taxa have been excluded: unidentified rodents (TNS=43), unidentified "miacoids" (TNS=8), indeterminate *Ectoganus* (TNS=5), indeterminate *Plagioctenoides* (TNS=19), *Ectocion parvus/Copecion davisi* (TNS=44).

Biozone	Samples (Reference)		TNS	S
Wa-0	CG:	Castle Gardens (Strait, 2001)	314	29
Wa-0+Wa-M	PCB:	Polecat Bench (Gingerich, 2001a; Gingerich and Smith, 2006)	464	57
	SCD:	Sand Creek Divide (this paper)	896[1]	56

contemporary faunas from the northern and southern parts of the Bighorn Basin. The samples for these comparisons are summarized in Table 18. Because it is short and has produced few fossils, the Wa-M interval has been combined with the Wa-0 interval in the Sand Creek Divide (SCD) and northern Bighorn Basin (Polecat Bench, PCB) samples. The PCB and SCD samples each capture most of the PETM event and are approximately equivalent in terms of time-averaging (~200 ka). Both also consist of approximately 25% screen-washed specimens. The Castle Gardens (CG) sample from the southern Bighorn Basin is quite different from the others: it does not include specimens from the Wa-M interval, it represents a shorter amount of time (<200 ka), and it is composed almost entirely of screen-washed specimens. In addition, the CG sample is under-reported. The 314 specimens and 29 species included in the initial Castle Gardens faunal list (Strait, 2001) represent only 12% of the total specimens and 76% of the species now known from the Castle Gardens site (Yans et al., 2006). However, there is no published up-to-date faunal list currently available for this area. The CG sample is included here for completeness despite its limitations and differences from the other samples.

Figure 61 compares the composition and diversity of the Sand Creek Divide assemblage to the other Bighorn Basin PETM samples. There is a high degree of similarity between the SCD and the PCB samples. Although the PCB sample has slightly higher richness and evenness than the SCD sample, these differences are not significant. Minor compositional differences between the SCD and PCB samples include a relatively high proportion of creodonts (9%, primarily *Arfia junnei*) in the latter, whereas the former has a relatively high proportion of primates (9%, primarily *Niptomomys doreenae* and *Teilhardina brandti*) and carnivores (9%, primarily *Didymictis leptomylus* and *Uintacyon gingerichi*). Again, none of these differences is statistically significant. In contrast, the CG sample from the southern Bighorn Basin has significantly lower richness than the other two and correspondingly low evenness. There are also significant compositional differences between the CG sample and the others, including a high proportion of rodents (13%, primarily *Acritoparamys atwateri*), marsupials (14%,

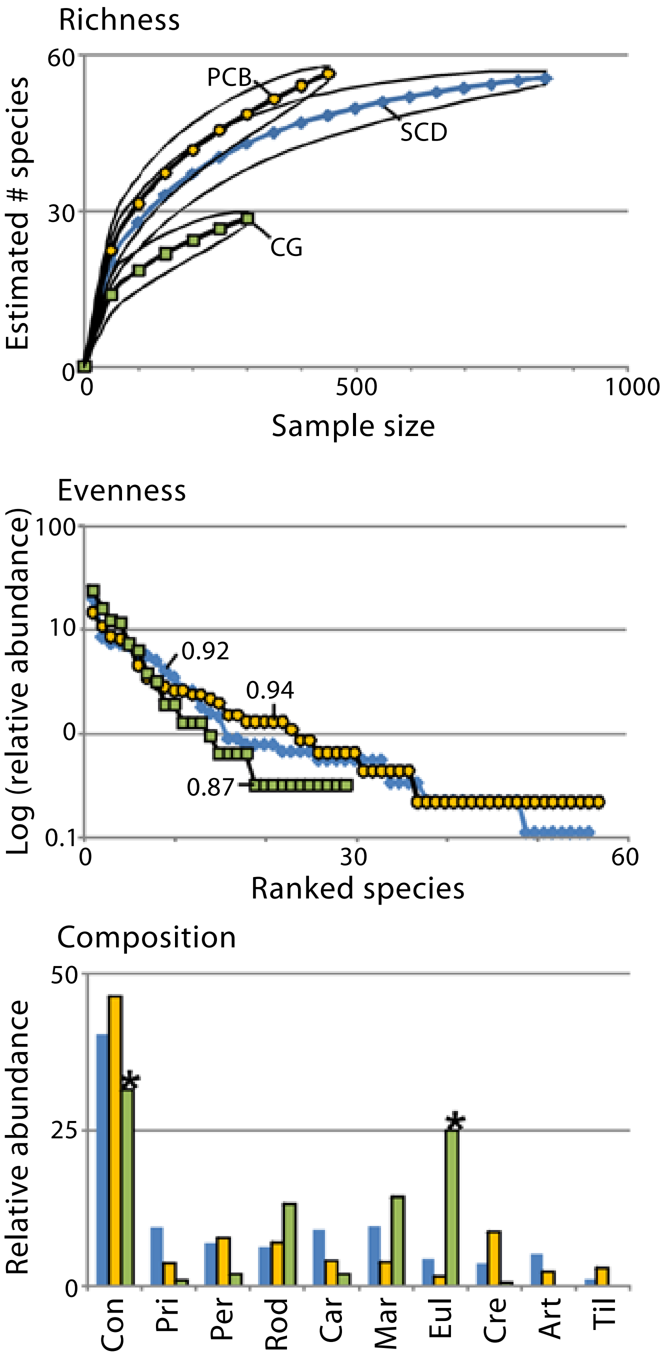


FIGURE 61 — Comparison of diversity and composition, based on TNS, in the Castle Gardens (CG), Polecat Bench (PCB), and Sand Creek Divide (SCD) samples. Richness: thin, black lines surrounding curves indicate 95% confidence intervals. Evenness: PIE estimates are included on the Whittaker (rank abundance) plots. Composition: *=significant difference at the 0.05 alpha level, determined by non-overlapping confidence intervals. Graph compares relative abundances of the ten most common orders. In all graphs green=CG, yellow=PCB, and blue=SCD. Ordinal abbreviations—Art: Artiodactyla; Car: Carnivora; Con: Condylarthra; Cre: Creodonta; Eul: Eulipotyphla; Mar: Marsupialia; Per: Perissodactyla; Pri: Primates; Rod: Rodentia; Til: Tillodontia.

TABLE 19 — Bighorn Basin late Clarkforkian (Cf-2 and Cf-3) and early Wasatchian (Wa-1/2 and Wa-3) samples compared with the Sand Creek Divide Wa-0 sample. BhB: Bighorn Basin; S: number of species; TNS: total number of specimens. [1]Total sample size reduced (from TNS=1015) as noted in Table 18.

Biozone	Samples (Reference)	TNS	S
Wa-3	Elk Creek (Chew, 2009)	1724	56
Wa-1/2	No Water Creek (Chew, 2009)	2336	59
Wa-0	Sand Creek Divide (this paper)	896[1]	56
Cf-3	Northern BhB (Rose, 1981a)	1032	50
Cf-2	Northern BhB (Rose, 1981a)	1296	50

several taxa), and lipotyphlans (25%, primarily *Macrocranion junnei* and *Plagioctenodon* sp.). Multituberculates (not included in Figure 61) are also unusually abundant in the CG sample (13%, primarily *Ectypodus tardus*). The high proportion of lipotyphlans and low proportion of condylarths in the CG sample are statistically significantly different from the other two samples.

The low richness and evenness of the CG sample in comparison with the other Bighorn Basin samples is most likely related to under-reporting and possibly less time-averaging in the CG sample. The compositional differences most likely relate to the fact that the CG sample is composed almost entirely of screen-washed specimens. Screen-washing results in samples with a high proportion of small taxa (such as multituberculates, marsupials, and lipotyphlans; Silcox and Rose, 2001). Thus, it is probable that the Castle Gardens fauna is not so different from other Wa-0 faunas in the Bighorn Basin.

In summary, minor differences between the Sand Creek Divide and northern Bighorn Basin Wa-0 faunas are likely due to small differences in preservation and/or random sampling effects. Larger differences between those two assemblages and the one from Castle Gardens are probably related to sampling effects and variation in the primary method of fossil collection in the latter. These results suggest that the various Bighorn Basin Wa-0 samples come from a single, basin-wide PETM fauna. Real community variation (beta diversity) appears to have been minimal across the region during the PETM. There is little evidence of a distinctive Wa-M fauna at Sand Creek Divide.

Comparison with other land-mammal biozones

Some of the best known and most extensively described faunas immediately bracketing the PETM come from the Bighorn Basin (Table 16). Samples from the late Clarkforkian Land-Mammal Age are best represented in the northern Bighorn Basin (Rose, 1981a, b), where stratigraphic sections are relatively thick. Most of the Clarkforkian samples were obtained by surface prospecting, but one locality in the Cf-2 biozone (=*Plesiadapis cookei* zone of Rose, 1981a) was quarried and contributed 23% of the total specimens from that interval. The early Wasatchian Land-Mammal Age is well-represented in the central and southern parts of the Bighorn Basin (Bown et al., 1994), where stratigraphic sections are thinner. The Wa-1 and Wa-2 biozones are combined here, following Chew (2009), as the first appearance of the index taxon for Wa-2 (*Arfia shoshoniensis*) occurs only 6 m above the first appearance of the index taxon for Wa-1 (*Cardiolophus radinskyi*). It is likely that few (if any)

TABLE 20 — Relative abundance (%) of the 10 most common orders in late Clarkforkian and early Wasatchian samples. Note that Artiodactyla is within the 10 most common orders by total number of specimens (TNS) while Multituberculata is within the 10 most common orders by minimum number of individuals (MNI). Wa-0 sample percentages are based on the Sand Creek Divide sample, modified as indicated in Tables 18–19.

Order	Cf-2		Cf-3		Wa-0		Wa-1/2	Wa-3
	TNS	MNI	TNS	MNI	TNS	MNI	TNS	TNS
Condylarthra	50	42	70	55	40	35	35	37
Primates	14	13	2	4	9	9	31	15
Perissodactyla	0	0	0	0	7	7	14	30
Rodentia	11	10	9	10	6	7	1	1
Carnivora	6	8	8	12	9	11	4	2
Marsupialia	1	2	0	0	9	8	3	0
Eulipotyphla	2	2	0	1	5	4	0	0
Creodonta	2	4	1	2	4	5	1	4
Artiodactyla	0	0	0	0	5	4	6	7
Tillodontia	3	3	3	5	1	2	1	2
Multituberculata	2	2	0	0	1	0	1	0

quarried/screen-washed specimens were included in Chew's combined Wa-1/2 sample, while the Wa-3 sample contains no quarried/screen-washed specimens.

The samples for the chronological comparisons are summarized in Tables 19 and 20. The Sand Creek Divide sample alone is used to represent Wa-0 to avoid errors related to taxonomic uncertainty in the combination of the various Bighorn Basin Wa-0 samples. Method of collection varies across the samples, from Cf-3, Wa-1/2 and Wa-3 with few or no quarried or screen-washed specimens, to Cf-2 and Wa-0 with about 25% quarried or screen-washed specimens. Time averaging is also of concern, as the Clarkforkian and Wasatchian biozones were probably longer than the ~200 ka Wa-0 interval. A recent Paleocene geochronology suggests that the Cf-2 biozone spanned 280 ka and the Cf-3 biozone spanned 420 ka (Secord et al., 2006). Even if the samples do not cover the entire length of each of these biozones, they likely incorporate more time than Wa-0. The duration of the Wa-1/2 and Wa-3 biozones is ~430 ka, based on average sediment accumulation rates between the end of the PETM and a geomagnetic reversal in the central Bighorn Basin (Clyde et al., 2007; Chew, 2009). Average sediment accumulation rates are not entirely accurate, as the stratigraphic section is thinner in the No Water Creek area than in the Elk Creek and Sand Creek areas (e.g., Wa-0 spans ~45m at Sand Creek Divide but only ~25m in the No Water Creek area), which suggests that Wa-3 is probably <430 ka. However, both are likely much longer than Wa-0.

Figure 62 compares the composition and diversity of the late Clarkforkian biozones with Wa-0 from Sand Creek Divide. Richness and evenness are lowest in Cf-3, intermediate in Cf-2, and highest in Wa-0. The difference between Clarkforkian richness and Wa-0 richness may be statistically significant, although the 95% confidence intervals of the Wa-0 and Cf-2 richness curves overlap extensively. There are statistically significant differences in composition between Wa-0 and the late Clarkforkian. The proportion of condylarths is significantly higher in the Clarkforkian (50-70%, primarily *Ectocion osbornianus* and *Phenacodus primaevus*) than in Wa-0 (40%), while the proportion of marsupials is significantly higher in Wa-0 (9%, primarily *Mimoperadectes labrus*) than in the Clarkforkian (0-1%). Perissodactyls and artiodactyls first appear in Wa-0 as well. Ordinal relative abundances are otherwise similar except for an unexpectedly low (but not significantly low) proportion of primates in Cf-3 (2% versus 9% in Wa-0 and14% in Cf-2).

A similar pattern of composition and diversity variation is apparent in the comparison of Wa-0 with the early Wasatchian biozones (Figure 63). Richness is highest in Wa-0 and lower in Wa-1/2 and Wa-3. This difference may be significant, although there is extensive overlap of the 95% confidence intervals. Evenness is more difficult to quantify. PIE is high and nearly equal in Wa-0 and Wa-1/2 and lower in Wa-3. As the inverse of Simpson's Index of Dominance, PIE reflects the evenness of the relative abundances of the most common species (those ranked highest in the Whittaker graph). The Wa-0 and Wa-1/2 samples have nearly the same Whittaker curves at the beginning, but the Wa-1/2 curve departs from the Wa-0 curve in the lower-ranked species (species ranked 21-59). Here, the Wa-1/2 curve is steeper than that of Wa-0 and more similar to that of Wa-3.

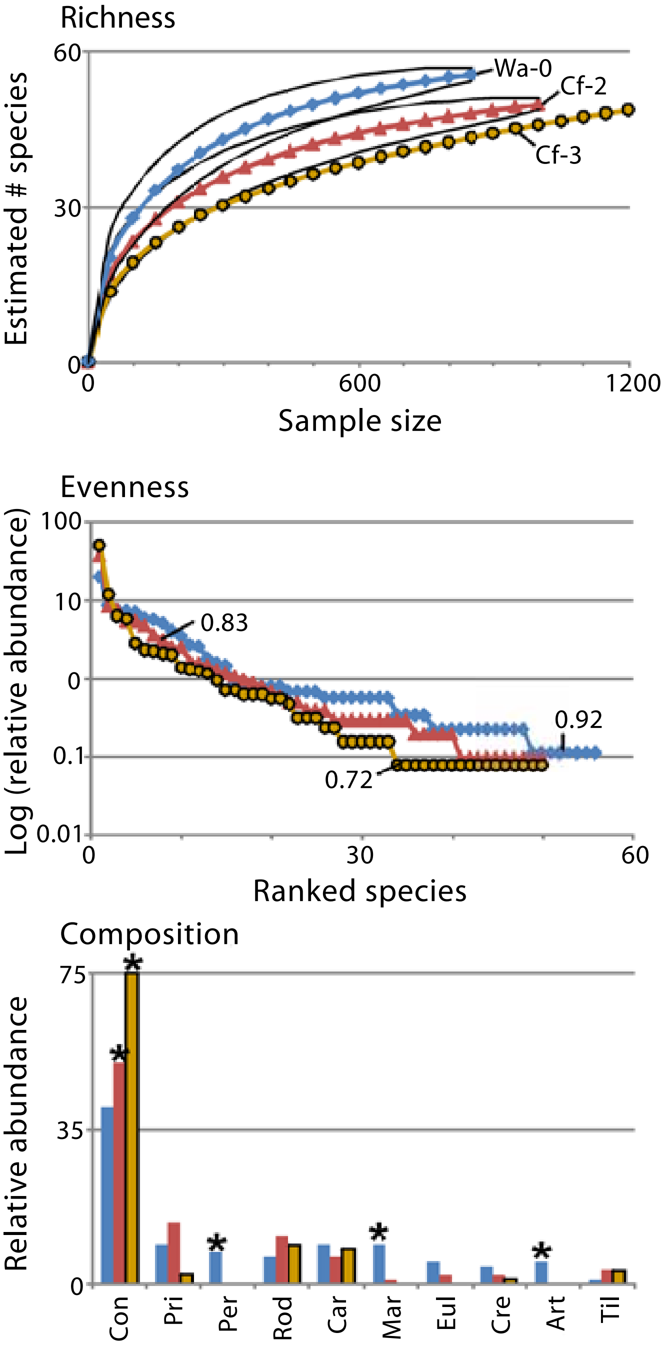


FIGURE 62 — Comparison of diversity and composition, based on TNS, in the late Clarkforkian (Cf-2 and Cf-3) and Wa-0 (Sand Creek Divide) samples. Richness: thin, black lines surrounding curves indicate 95% confidence intervals. Evenness: PIE estimates are included on the Whittaker (rank abundance) plots. Composition: *=significant difference at the 0.05 alpha level, determined by non-overlapping confidence intervals. Graph compares relative abundances of the ten most common orders. In all graphs blue=Sand Creek Divide, red=Cf-2, and brown=Cf-3. Ordinal abbreviations as in Figure 61.

In this example, the Whittaker curve refines the PIE evenness pattern. Evenness among the most abundant species is similar in Wa-0 and Wa-1/2, but overall evenness is higher in Wa-0 than in Wa-1/2 and Wa-3. There are important compositional differences between the early Wasatchian biozones and Wa-0 as well. Primates (15-31% in the post Wa-0 biozones, primarily *Phenacolemur praecox* and *Cantius* spp.) and perissodactyls (14-30% in the post Wa-0 biozones, primarily *Hyracotherium grangeri*) are significantly more common in Wa-1/2 and Wa-3 than in Wa-0 (when they made up 9% and 7%, respectively), although primates are not quite significantly higher in Wa-3 (Figure 63). Again, marsupials are significantly higher (9% versus 0-3%) and carnivores are also higher (9% versus 2-4%, primarily *Didymictis leptomylus*) in Wa-0.

The variation in diversity between Wa-0 and the late Clarkforkian and early Wasatchian biozones is the opposite of expectation given the potential for the inflation of diversity through time-averaging. The late Clarkforkian and early Wasatchian biozones were probably longer than the ~200 ka duration of Wa-0, and this should have inflated their diversity measures relative to Wa-0. Yet richness and evenness are lower (richness is probably significantly lower) in late Clarkforkian and early Wasatchian biozones than in Wa-0. The slightly higher richness and evenness of Cf-2 relative to Cf-3 may be related to the high proportion of quarried specimens in the former. But even this combined with time-averaging did not raise the diversity of Cf-2 above that of Wa-0. This suggests that Wa-0 was unusually diverse for the time. Most of the compositional differences are probably related to the first appearance of perissodactyls, artiodactyls and euprimates at the beginning of the Wasatchian. The high proportion of marsupials in the Sand Creek Divide Wa-0 sample and the high proportions of Wa-0 carnivorans relative to Wa-1/2 and Wa-3 may be sampling anomalies.

Species are ordered by rank abundance in Table 21. The changing abundance of phenacodontid condylarths across the Paleocene-Eocene boundary is particularly interesting. Throughout the Clarkforkian, three species of phenacodontids accounted for more than 60% of specimens in seven of eight successive intervals (54% in the other interval; 40-50% by MNI), with *Ectocion osbornianus* alone making up 41-58% of specimens (Rose, 1981a). In early Wasatchian samples, however, the proportion of phenacodontids (2-4 species) was markedly lower, and continued to decline precipitously (2-16%, with the higher abundances occurring earlier). The proportion of phenacodontids (4 species) at Sand Creek Divide is 19%, higher than at any other time in the early Eocene, but conspicuously lower than during the latest Paleocene. The relative abundance of phenacodontids during the PETM contributes to the intermediate aspect of the Wa-0 fauna first recognized by Gingerich (1989).

There are a total of 83 genera and 133 species represented in the two late Clarkforkian and three early Wasatchian biozone samples. (To reduce taxonomic uncertainty, 16 groups of specimens that were identified as “sp.” in multi-species genera are omitted from the following comparisons). Seven of the species span the entire interval: *Viverravus acutus*, *V. politus*, *Didymictis proteus* (probably =*D. leptomylus*), *Phenacodus vortmani*, *P. intermedius*, *Ectocion osbornianus* (reported at Polecat Bench),

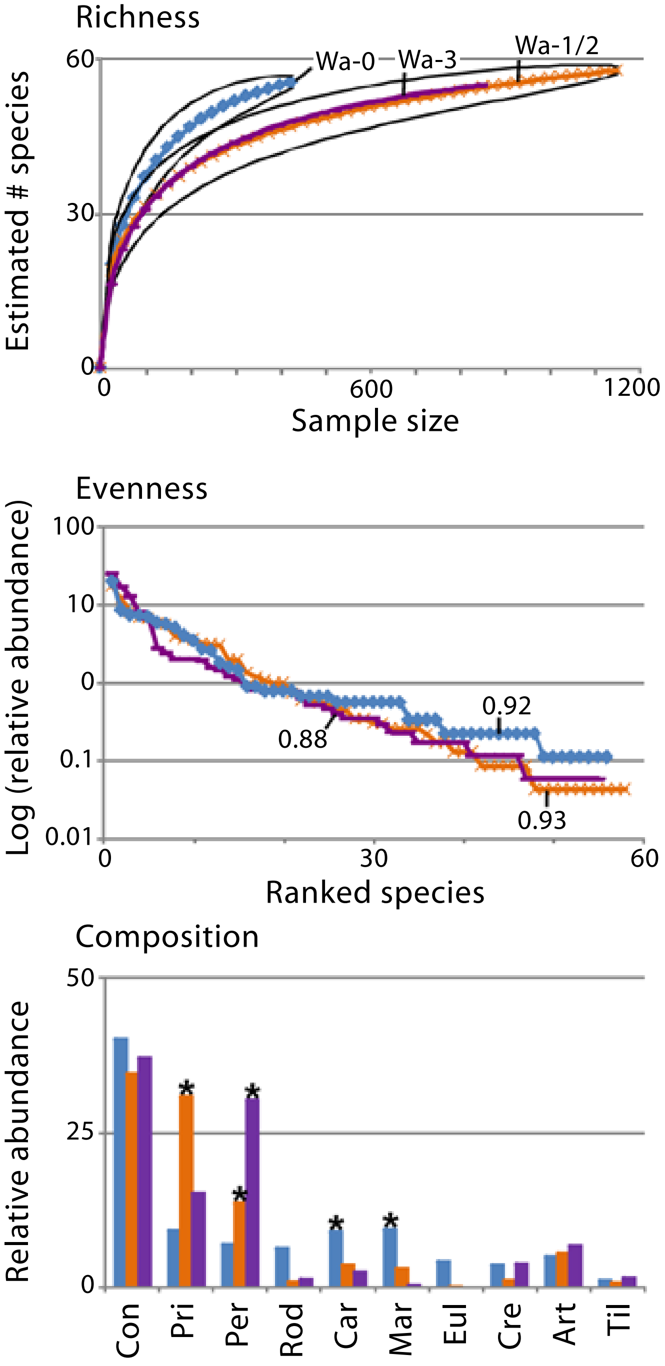


FIGURE 63 — Comparison of diversity and composition, based on TNS, in the early Wasatchian (Wa-1/2 and Wa-3) and Wa-0 (Sand Creek Divide) samples. Richness: thin, black lines=95% confidence intervals. Evenness: PIE estimates are included on the Whittaker (rank abundance) plots. Composition: *=significant difference at the 0.05 alpha level, determined by non-overlapping confidence intervals. Graph compares relative abundances of the ten most common orders. In all graphs blue=Wa-0, orange=Wa-1/2, purple=Wa-3. Ordinal abbreviations as in Figure 61.

TABLE 21 — Faunal list for Sand Creek Divide Wa-0 sample ordered by TNS relative abundance. MNI: minimum number of individuals; TNS: total number of specimens.

Rank TNS	Taxon	TNS	MNI	%TNS	%MNI	Rank MNI
1	*Hyopsodus loomisi*	177	30	17.4	8.5	2
2	*Ectocion parvus*	76	35	7.5	9.9	1
3	*Mimoperadectes labrus*	66	20	6.5	5.7	5
4	*Copecion davisi*	65	27	6.4	7.6	3
5	*Hyracotherium sandrae*	62	22	6.1	6.2	4
6	*Didymictis leptomylus*	52	19	5.1	5.4	6
7	*Tuscahomys,* cf. *T. major*	50	18	4.9	5.1	7
8	*Diacodexis ilicis*	45	14	4.4	4.0	8
9	*Ectocion parvus/Copecion davisi*	44	9	4.3	2.5	11
10	Unidentified rodents	43	—	4.2	—	—
11	*Niptomomys,* cf. *N. doreenae*	36	6	3.5	1.7	13
12	*Chriacus badgleyi*	31	13	3.1	3.7	9
13	*Teilhardina brandti*	24	12	2.4	3.4	10
14	*Plagioctenoides* sp. indet.	19	2	1.9	0.6	17
15	*Macrocranion junnei*	18	5	1.8	1.4	14
16	*Arfia junnei*	16	9	1.6	2.5	11
17	*Uintacyon gingerichi*	14	6	1.4	1.7	13
18	Cf. *Peradectes protinnominatus*	13	4	1.3	1.1	15
19	*Cantius torresi*	8	5	0.8	1.4	14
19	*Arctodontomys wilsoni*	8	4	0.8	1.1	15
19	Unidentified "miacoids"	8	4	0.8	1.1	15
20	*Coryphodon* sp.	7	7	0.7	2.0	12
20	*Phenacodus intermedius*	7	7	0.7	2.0	12
20	*Viverravus acutus*	7	5	0.7	1.4	14
20	*Ectypodus tardus*	7	1	0.7	0.3	18
21	*Didelphodus* sp.	6	4	0.6	1.1	15
21	*Palaeanodon nievelti*	6	4	0.6	1.1	15
21	*Herpetotherium innominatum*	6	2	0.6	0.6	17
21	*Prolimnocyon eerius*	6	1	0.6	0.3	18
22	*Ectoganus bighornensis*	5	5	0.5	1.4	14
22	*Ectoganus* sp.	5	5	0.5	1.4	14
22	*Dissacus praenuntius*	5	3	0.5	0.8	16
22	*Palaeosinopa lutreola*	5	3	0.5	0.8	16
22	*Paramys taurus*	5	3	0.5	0.8	16
22	*Esthonyx spatularius*	5	2	0.5	0.6	17
22	*Prototomus deimos*	5	2	0.5	0.6	17
22	*Leptacodon donkroni,* sp. nov.	5	1	0.5	0.3	18
22	*Nanomomys thermophilus,* gen. et sp. nov.	5	1	0.5	0.3	18
23	*Ectoganus,* cf. *E. lobdelli*	3	3	0.3	0.8	16
23	*Haplomylus zalmouti*	3	3	0.3	0.8	16
23	Cf. *Viverravus politus*	3	2	0.3	0.6	17
23	*Leptacodon* sp. 2, probably new	3	1	0.3	0.3	18
24	*Azygonyx gunnelli*	2	2	0.2	0.6	17
24	Cf. *Colpocherus* sp., probably new	2	2	0.2	0.6	17
24	*Phenacodus vortmani*	2	2	0.2	0.6	17
24	*Plagioctenoides tombowni,* sp. nov.	2	2	0.2	0.6	17
24	*Tuscahomys worlandensis,* sp. nov.	2	2	0.2	0.6	17
24	?Hyaenodontid, unnamed sp. nov.?	2	1	0.2	0.3	18
24	Cf. *Miacis rosei*	2	1	0.2	0.3	18
24	Cf. *Parapternodus* sp.	2	1	0.2	0.3	18
24	*Dipsalidictis platypus*	2	1	0.2	0.3	18
24	*Esthonyx* sp.	2	1	0.2	0.3	18
24	*Plagioctenoides microlestes*	2	1	0.2	0.3	18
24	*Viverravus rosei*	2	1	0.2	0.3	18
25	?Apheliscidae, unnamed sp. nov.	1	1	0.1	0.3	18
25	*Azygonyx,* cf. *A. grangeri*	1	1	0.1	0.3	18
25	Cf. *Miacis deutschi*	1	1	0.1	0.3	18
25	*Ignacius graybullianus*	1	1	0.1	0.3	18
25	Oxyaenid, indet.	1	1	0.1	0.3	18
25	*Phenacolemur praecox*	1	1	0.1	0.3	18
25	*Teilhardina gingerichi,* sp. nov.	1	1	0.1	0.3	18

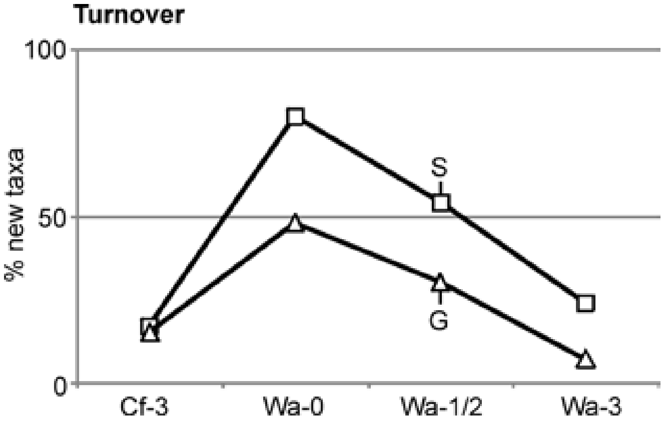


FIGURE 64 — Proportions of new species (S) and genera (G) in the late Clarkforkian (Cf-3) and early Wasatchian (Wa-0, Wa-1/2 and Wa-3) biozones.

and *Niptomomys doreenae*. Five more—*Ignacius graybullianus*, *Phenacolemur praecox*, *Paramys taurus*, *Azygonyx grangeri*, and *Tinimomys graybulliensis*—probably also span the entire interval but have gaps in their sampling distribution. Fifteen genera span the entire interval from Cf-2 to Wa-3, and 10 more probably also span the entire interval but have gaps in their sampling distribution. In summary, 9% of the species and 30% of the genera in the chronological samples are found throughout the late Clarkforkian and early Wasatchian, implying that 91% of the species and 70% of the genera present either disappeared or first appeared during this time. It is clear that the Bighorn Basin mammal fauna during the late Clarkforkian and early Wasatchian underwent tremendous change.

The pattern of first and last appearances of taxa suggests that most of this faunal change was concentrated in the Wa-0 interval. The proportion of new species and genera, those not seen in any previous biozone, is extremely high (80% and 48%, respectively) in Wa-0 (Figure 64). Nearly one-quarter of the total species (29/133) are found only in Wa-0, whereas singleton species in the other biozones range from 5-10% of the total. In addition, three species are found throughout the late Clarkforkian and early Wasatchian but are missing from Wa-0, including the Castle Gardens and Polecat Bench areas (*Uintacyon rudis*, *Thryptacodon antiquus*, and *Prodiacodon tauricinerei*). The proportion of new species and genera in the Cf-3 and Wa-3 biozones is comparatively low and nearly equal, while the same proportions are somewhat elevated in Wa-1/2 (Figure 64). These results suggest that the Wa-0 fauna was compositionally unique. Most Wa-0 species were different from those that had been there previously and many of them had disappeared by the end of the PETM, as nearly half of the Wa-1/2 species were also new (there is no apparent increase in Wa-1/2 diversity). Gingerich (2003) suggested that both diversity and turnover were set at a higher level following the Wa-0 interval, but these results do not indicate such an increase in the nearly 1 Ma immediately following Wa-0. In the later part of the Wasatchian, however, mammalian faunas in the Bighorn Basin and neighboring basins do exhibit high diversity and turnover, possibly related to rising temperatures at the beginning of the Early Eocene Climatic Optimum (Schankler, 1980; Chew, 2009; Woodburne et al., 2009).

SUMMARY AND CONCLUSIONS

The Sand Creek Divide local fauna adds significantly to our understanding of the mammalian fauna during the PETM. It is the largest local fauna described from this interval, with more than 1000 mammalian specimens from 40 localities spaced throughout the interval. The 40 localities are placed within the 45-meter PETM interval by relation to marker beds and to carbon isotope stratigraphy (which defines the interval), producing a detailed biostratigraphic record. Available evidence suggests waves of immigration during the PETM, rather than a single immigration event at the onset of the PETM. Modern ungulates seem to have arrived very near the beginning of the PETM, and before euprimates, or at least prior to adapoids. Additional sampling will test whether these patterns hold up. The end of the PETM, as indicated by a return to late Paleocene δC^{13} values, coincides approximately to the Wa-0/Wa-1 boundary. This boundary is recognized at Sand Creek Divide by the occurrence of several biostratigraphically important taxa: *Cantius ralstoni*, *Cardiolophus radinskyi*, *Homogalax protapirinus*, *Haplomylus speirianus*, and *Ectocion osbornianus*.

Like other PETM local faunas from the Bighorn Basin, the Sand Creek Divide assemblage is dominated by the phenacodontid condylarths *Ectocion parvus* and *Copecion davisi*. *Hyopsodus loomisi* and *Hyracotherium sandrae* are also common, as at Polecat Bench. The most common carnivorous mammals were *Didymictis leptomylus* and *Arfia junnei*, as at Polecat Bench, with *Uintacyon gingerichi* almost as common. Other common small mammals include *Tuscahomys*, cf. *T. major*, *Mimoperadectes labrus*, *Diacodexis ilicis*, *Niptomomys*, cf. *N. doreenae*, *Teilhardina brandti*, and *Macrocranion junnei*. The fauna includes a new genus and species of ?microsyopid primate, *Nanomomys thermophilus*, whose teeth are similar in size to those of the smallest known primates. Four other new species named herein (two nyctitheriids, an omomyid primate, and a rodent) and four unnamed but probably new species were also identified. In addition to taxa already known to make their first appearance during the PETM, we report here the oldest records of *Esthonyx* (Wa-M) and *Didelphodus* (Wa-0). Evidence presented here suggests that *Wyonycteris* is a probable synonym of the nyctitheriid *Plagioctenoides*, and *Princetonia yalensis* is a probable synonym of *Chriacus badgleyi*.

With 56 species identified, the Sand Creek Divide local fauna (Wa-M + Wa-0) is comparable in species richness to the combined Wa-M and Wa-0 local faunas from Polecat Bench. However, the Wa-0 fauna from Sand Creek Divide, taken alone, is richer than any other from this biozone, with 54 species recorded. The fauna demonstrates strong similarities with other Wa-0 samples described from the Bighorn Basin and strong differences from faunas immediately preceding and following it.

The Wa-0 fauna was compositionally unique and unusually diverse for the time. With high relative abundance of phenacodontid condylarths (though lower than in the Clarkforkian) coupled with the earliest appearances (but relatively low abundances) of euprimates, artiodactyls, and perissodactyls, it is intermediate in character between Clarkforkian and other Wasatchian faunas. Euprimates and perissodactyls, in particular, show a marked increase in relative abundance after the Wa-0 interval. The PETM does not appear to have heralded an era of higher standing diversity and turnover in the Wasatchian. Instead, the Wa-0 fauna indicates a short-term response to a brief period of remarkable climatic and environmental change.

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