Fossil Mammals of the Twelvemile Bonanza Local Fauna, Late Tiffanian of Southwestern Wyoming

By
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Abstract

Twelvemile Bonanza is a recently discovered Paleocene fossil mammal-bearing locality in southwestern Wyoming. The environment it preserves was most likely a relatively poorly drained, well-forested floodplain. The Twelvemile Bonanza Local Fauna is the only fauna that can be unambiguously assigned to the Ti5 interval outside of the Bighorn Basin; it therefore greatly adds to our knowledge of the mammals alive in North America during this time by providing additional geographic coverage of this poorly documented interval. The age of the fauna also puts the site in a prime position to test the effects of changing temperatures on the ranges, body sizes, and paleoecology of late Tiffanian mammals in Wyoming. The Twelvemile Bonanza local fauna is largely similar to the contemporary Princeton Quarry fauna in the Bighorn Basin. Where species differ, they differ most often among the smaller-bodied taxa of both sites, consistent with the modern observation that smaller species tend to have smaller ranges, suggesting they tend to become reproductively isolated more often when they do disperse. Taxa such as *Aletodon conardae* and Microsyopidae appear to have tracked warmer temperatures as their ranges expanded and contracted across Wyoming over the course of the late Paleocene. Furthermore, when comparing Twelvemile Bonanza to other sites in southwestern Wyoming immediately preceding it (Ti4) and following it (Cf1/Cf2) in time, two trends are noticeable: (1) carnivorous species decrease in body mass (a trend consistent with Bergman's Rule), and in diversity, as temperatures rise; (2) the body mass distributions of the fauna increasingly tend to cluster around a few peaks as temperatures rise, rather than being more evenly spread out. One explanation for the latter trend may be that the fauna become more specialized as temperatures increase, allowing species of similar body size to coexist in the same ecosystem.

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I. Introduction

Geology and Biostratigraphy of Twelvemile Bonanza

Twelvemile Bonanza is a relatively recently discovered Paleocene fossil mammal-bearing locality situated along the eastern flank of the Rock Springs Uplift in Sweetwater County, southwestern Wyoming. The fossil-bearing horizon is primarily green mudstone and lignite with virtually no paleosol development, most likely representing an overbank floodplain deposit that alternated often between poorly and moderately drained. The Twelvemile Bonanza Local Fauna contains *Probathyopsis harrisorum*, which is the index fossil for a stratigraphic interval called Ti5. This is the fifth interval in the North American Land Mammal Age known as the Tiffanian (Archibald et al. 1987), which encompasses the span of time approximately 61.5 to 57 million years ago, following the Torrejonian land mammal age and preceding the Clarkforkian. The Puercan precedes the Torrejonian, and together these four NALMAs encompass the Paleocene Epoch as it is exposed in North America (Figure 3). Ti5 itself encompasses the span of time between approximately 58.5 and 57.5 million years ago (Secord 2008). The presence of *Probathyopsis harrisorum* makes Twelvemile Bonanza the only definitive locality from Ti5 outside of the Bighorn Basin, in northern Wyoming. Other purported Ti5 localities such as Joe's Bone Bed in Big Bend, Texas and Dell Creek Quarry in west-central Wyoming are more likely to be late Ti4, given the presence of *Chiromyoides caesor* and *Nannodectes gidleyi* in the former (Schiebout 1974) and *Carpodaptes hobackensis* in the latter (Dorr 1952). More importantly, neither Joe's Bone Bed (Schiebout 1974) nor Dell Creek Quarry (Dorr 1952) contain any published specimens of Ti5 index fossils (namely *Probathyopsis*), so their temporal assignment remains uncertain. Additionally, the localities from southwestern Wyoming listed in Woodburne et al. (2004) as Ti5 are erroneously ascribed to this interval,

being located well within the *Plesiadapis churchilli* zone of Ti4. One purported Ti5 locality in Colorado, UCM 92177, contains an assemblage that is difficult to interpret (Burger and Honey 2008, Burger 2013), with *Plesiadapis fodinatus* and *Phenacodaptes sabulosus* (both characteristic but not necessarily diagnostic of Ti5) apparently coexisting with *Nannodectes gazini*, which is typical of Ti2 localities such as Saddle in southwestern Wyoming. To date, no definitive Ti5 index fossils have been reported in the published literature from UCM 92177.
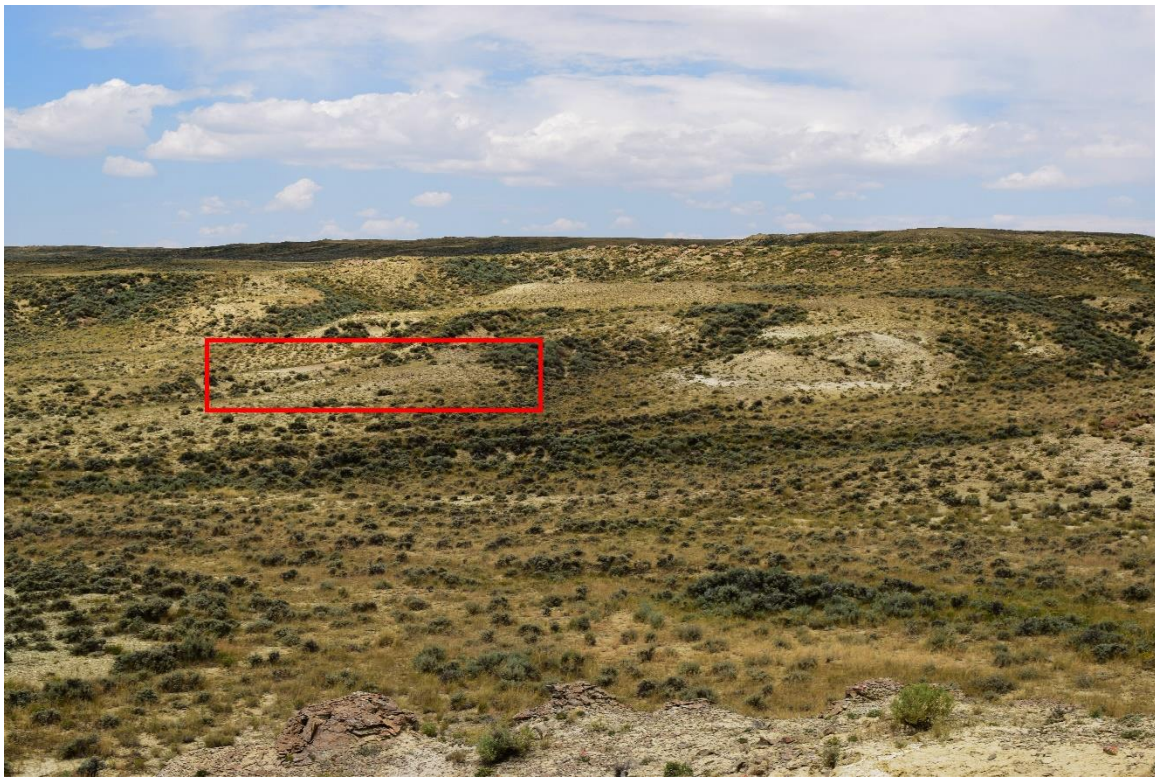
Figure 1. Twelvemile Bonanza, looking toward the northwest. The most fossiliferous zone is highlighted.

Figure 2. Twelvemile Bonanza. Close-up of a fossiliferous grey-green mudstone, looking approximately north.

Previous Research

Twelvemile Bonanza is located near Bitter Creek, Sweetwater County, Wyoming, along the eastern rim of the Rock Springs uplift in the upper portion of the Fort Union Formation (Love and Christiansen 1985). The Rock Springs uplift itself is located in the northwestern Washakie Basin, which is in turn situated in the greater Green River Basin (Roehler 1992). Wintefeld (1982) provided detailed information about the geology and systematic paleontology of various Ti4 localities near Bitter Creek. Wilf et al. (1998) provided extensive information about the geology, paleoecology, and systematic paleontology of the nearby Clarkforkian-age Big Multi Quarry; Dawson and Beard (1996) and Chester and Beard (2012) discussed additional

specimens. Likewise, Anemone and Dirks (2009) provided information about the geology and systematic paleontology of another nearby site called Mark's Locality, which is also Clarkforkian in age. The first taxon to be described from Twelvemile Bonanza was *Carpolestes twelvemilensis*, in Mattingly et al. (2017). Secord (2008) provided detailed information about the biostratigraphy and systematic paleontology of various contemporary Ti5 localities in the Bighorn Basin, including Princeton Quarry, Schaff Quarry, and Y2K Quarry.

The Twelvemile Bonanza locality was first prospected by Gus Winterfeld, Christopher Beard, and crew in the field season of 2001. Much of the material was collected that season, and subsequent fields seasons over the past seventeen years have augmented the original collection, as of this writing, to 192 readily-identifiable dental specimens representing at least 48 individuals.

Why Study the Twelvemile Bonanza Local Fauna?

The Twelvemile Bonanza Local Fauna is the only fauna that can be unambiguously assigned to the Ti5 interval outside of the Bighorn Basin; it therefore greatly adds to our knowledge of the mammals alive in North America during this time by providing additional geographic coverage of this poorly documented interval. The Ti5 interval takes place between two contrasting periods in the climate history of the Cenozoic: a mild but significant drop in temperature during the directly preceding Ti4, and the Paleocene-Eocene Thermal Maximum (PETM) at the end of the Clarkforkian (Zachos et al. 2001) (Fig. 3). Ti5 represents the beginning of the rebound in temperature that would culminate in the PETM. This puts the site in a prime

position to test the effects of a changing climate on the ranges and body sizes of late Tiffanian-age mammals in Wyoming, both because it fills a gap in knowledge that has been missing in southwestern Wyoming, and because it provides a more southerly point of comparison for the extensively sampled Ti5 sites in the northern Bighorn Basin.
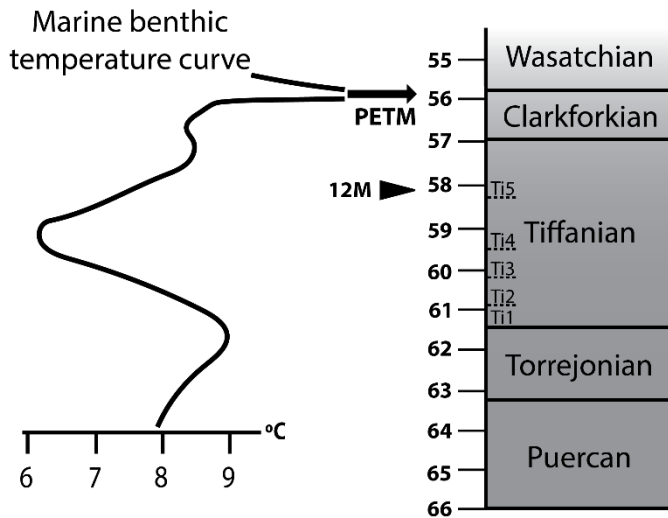
Figure 3. Estimated global temperature (adapted from Zachos et al. 2001) plotted against the North American Land Mammal Ages of the Paleocene Epoch. Twelvemile Bonanza (12M) is located near the base of the *Probathyopsis* zone, Ti5, approximately 58 million years ago.

Measuring Techniques

Dental specimens were examined through a Wild Heerbrugg binocular microscope and measured with a Unitron Z Series binocular microscope equipped with Mitutoyo calipers and stage, except in the case of specimens in the YPM-PU collections, which were measured by

applying measuring tools from the imaging software Fiji to photographs taken with a Nikon D3300 equipped with an Opteka High-Definition 10X Macro Lens 67 mm. Twelvemile Bonanza (and relevant Big Multi Quarry) specimens were imaged using an Olympus SZX16 ocular microscope equipped with an Olympus DP73 camera. Images were taken using the imaging software Olympus cellSens Standard and the stacking software CombineZP. All molar and premolar dental measurements were adapted as closely as possible to the general technique shown in Figure 4. Plesiadapid lower incisor lengths were measured from tip to margoconid, and widths were measured at the margoconid. Plesiadapid upper incisor lengths were measured from tip to posterocone, and widths were measured at the widest point formed by the mediocone and laterocone.
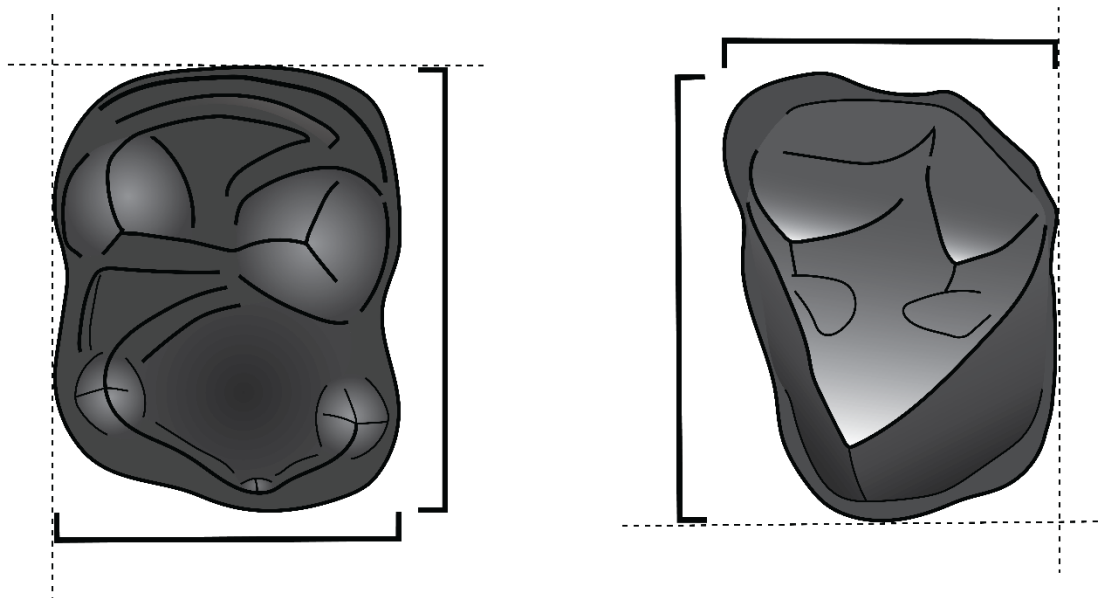
Figure 4. Generalized measurement techniques for upper and lower molars and premolars.

II.   Systematic Paleontology

Class MAMMALIA Linnaeus 1758

Infraclass EUTHERIA Huxley 1880

Order CARNIVORA Bowditch 1821

Family VIVERRAVIDAE Wortman and Matthew 1899

PROTICTIS Matthew 1937

Discussion. — The systematics of Paleocene viverravids have been outlined by Gingerich and Winkler (1985), with additional taxa incorporated by Meehan and Wilson (2002). In size and morphology, the Twelvemile Bonanza specimens most closely match *Protictis*. Polly (1997) suggests, on the basis of a stratocladistic analysis, that this taxon is synonymous with *Viverravus*. I would rather not commit to a position on the merits of stratocladistics, so I retain the traditional *Protictis* here. The Twelvemile Bonanza P_4 specimens lack the strongly tapered anterior of *Simpsonictis*; the anterior of the P_4 is instead more rounded at the base of the crown. In the P_4 of *Bryanictis*, the paraconid is much stronger relative to the metaconid, whereas the reverse is true in *Protictis* and the Twelvemile Bonanza specimens. Additionally, in *Bryanictis* the protoconid is relatively anteroposteriorly broad, whereas in *Protictis* and the Twelvemile Bonanza specimens it is less broad and more cuspate. In *Raphictis*, the P_3 protoconid seems to be considerably reduced, both in height and width at the base, compared to *Protictis* and the Twelvemile Bonanza specimens. In *Raphictis*, the P_4 is also more gracile in occlusal view, with a distinct

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notch in the center along the lingual edge, and the buccal edge of the talonid of M_1 is angular, almost parallel to the cristid obliqua.

Proctictis schaffi Gingerich and Winkler 1985

Figure 5, Table 1

Holotype. — YPM-PU 19365 (associated left dentary containing P_2-M_1, right dentary containing C_1, P_1, P_3-M_2) from Schaff Quarry.

Age and distribution. — Schaff Quarry, Bighorn Basin, northwestern Wyoming (*Probathyopsis* zone, Ti5a); Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a); UCM locality 92177, Colorado (Tiffanian).

Description. — The holotype and additional specimens were described in Gingerich and Winkler (1985).

Discussion. — The Twelvemile *Proctictis schaffi* material consists of a right dentary fragment containing P_3 and P_4 (CM 77144), associated left dentary fragments containing M_1 and P_3 (CM 86947), and an isolated P_4 (CM 89401).

The Twelvemile Bonanza *Proctictis* specimens fall comfortably within the range of variation in size and morphology of the contemporaneous Princeton and Schaff Quarry species *P. schaffi*. In most features, they are essentially identical to the holotype of *P. schaffi*. A few minor differences in M_1 can be seen: CM 86947, compared to the holotype, appears to have a slightly buccolingually narrower talonid, a lower lingual talonid notch, and the paraconid appears to connect with the protoconid slightly lower on the crown. However, inspection of multiple

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Yale Peabody specimens reveals that *P. schaffi* is variable in the latter two traits, and differences in the former trait can probably be attributed to the badly worn state of CM 86947.

Referred specimens.— CM 77144 (RP$_3$-P$_4$), CM 86947 (associated LP$_3$ and LM$_1$),CM 89401 (RP$_4$).
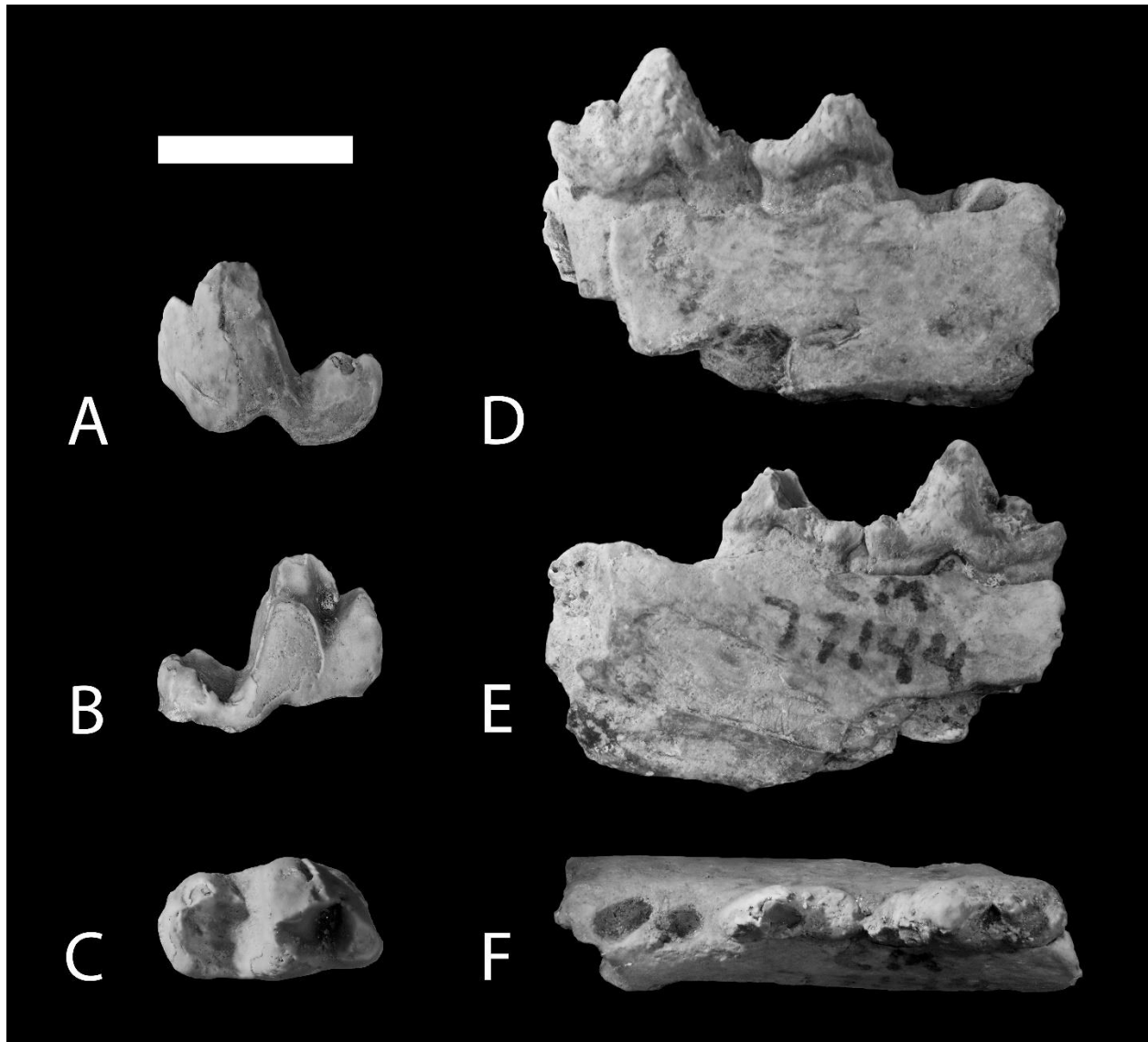
Figure 5. Dentition of *Proctictis schaffi* from Twelvemile Bonanza. CM 86947 LM$_1$ in (A) buccal, (B) lingual, and (C) occlusal views; CM 77144, RP$_3$-P$_4$ in (D) buccal, (E) lingual, and (F) occlusal views. Scale bar = 5 mm.

		length (mm)	width (mm)
CM 77144	Rp3	3.77	1.39
	Rp4	5.20	1.91
CM 86947	Lp3	3.38	1.40
	Lm1	5.78	3.27
CM 89401	Rp4	4.81	2.20

Table 1. Dental measurements for *Protictis schaffi* specimens from Twelvemile Bonanza.

Order CONDYLARTHRA Cope 1881

Family ARCTOCYONIDAE Murray 1866

ARCTOCYON Blainville 1841

Lambertocyon n. sp.

Figure 6, Table 2

Description and Diagnosis. —KU 156546 differs from other arctocyonids in possessing a remarkably flat lingual surface, which (as in other arctocyonids) is delineated by a sharp, prominent preprotocristid which runs from the anterolingual corner of the tooth to the tip of the protoconid, then connects at the protoconid tip to an equally sharp, prominent postprotocristid.

KU 156546 resembles *Lambertocyon* in that the entire surface of the tooth is highly and irregularly crenulated, and in that the talonid basin is extremely weak, reduced essentially to a ridge of tiny accessory cusps rimming the posterior of the protoconid. The posterior of the tooth is slightly wider than the protoconid, a condition intermediate between that of *Lambertocyon* and *Arctocyon.*

　　Discussion. — KU 156546 is close in size to the P_3 of YPM-PU 18757, *Arctocyon cf. A. nexus* from the contemporaneous Princeton Quarry, but significantly smaller than the P_3 of UW 68798, the specimen of *A. nexus* reported in Secord 2008. KU 156546 and YPM-PU 18757 share in common an array of tiny cusps along the anteroposterior crest. However, KU 156546 differs from *Arctocyon cf. A. nexus* from Princeton Quarry in possessing a broader, more rounded talonid that contours more closely with the posterior of the main cusp rather than jutting out posteriorly; as well as a weaker posterior talonid cusp, where instead the talonid is lined posteriorly with smaller, bulbous accessory cusps. KU 156546 is also somewhat shorter than YPM-PU 18757, but wider and higher-crowned. KU 156546 also compares somewhat favorably with the P_3 of AMNH 2462, *Colpoclaenus procyonides*, which is fairly similar to KU 156546 in length and possesses a similar row of blunt accessory cusps on the posterior talonid, but is noticeably thinner with a narrower, more posteriorly-tapering talonid. The protoconid of AMNH 2462 also seems to be a bit less anteroposteriorly broad. The anteroposterior crest of KU 156546 runs considerably closer to the lingual edge, terminating nearly at the posterolingual corner. The buccal ridge running posteriorly down from the main cusp is more defined in *C. procyonoides*. *C. procyonoides* also has a slightly more prominent paraconid. According to Gazin (1956), this taxon is known from the Saddle Locality in the Bison Basin of southwestern Wyoming, where it is referred to as *Claenodon procyonoides*. *Claenodon keeferi* from the Shotgun local fauna of

central Wyoming is described in Patterson and McGrew (1962). The P_3 of this taxon is not known, but comparing metrics reported in Patterson and McGrew (1962) for M_2 and M_3 of *C. keeferi* to those of AMNH 2462, the latter seems to be slightly smaller, implying KU 156546 is probably also slightly smaller.

In overall size and dimensions, KU 156546 compares less favorably with the P_3 and P_2 of *Lambertocyon*. However, KU 156546 compares far more favorably with this genus in two conspicuous ways: the tooth is highly crenulated, and the talonid basin itself is extremely weak. In the weakness of the talonid it compares especially favorably with the P_2 of *Lambertocyon*. For these reasons, I tentatively describe it as such. In talonid width relative to the protoconid, KU 156546 appears intermediate between the condition of *Lambertocyon* and that of the two other genera discussed above. KU 156546 appears to be considerably larger than any named species of *Lambertocyon*, including *L. gingerichi* from the Chappo Type Locality (Ti3), *L. eximius* from Foster Gulch in the Bighorn Basin (Ti4), and *L. ischyrus* from the Clarkforkian of Colorado (Gingerich 1979). If KU 156546 does indeed belong to *Lambertocyon*, it appears to buck the trend of decreasing size over time in *Lambertocyon* described by Gingerich (1979).

Referred specimens.— KU 156546 (LP$_2$).
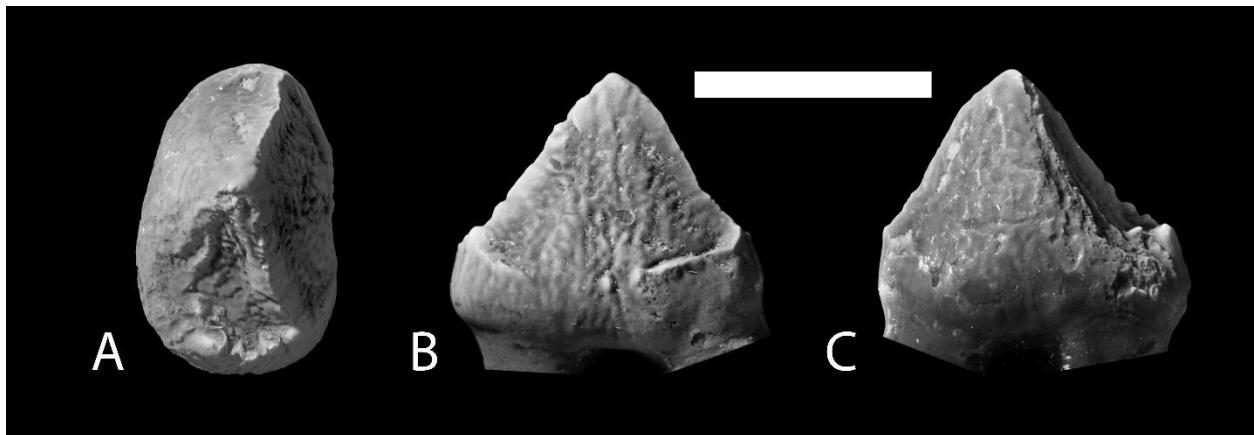
Figure 6. Dentition of *Lambertocyon n. sp.* KU 156546 (LP$_2$) in (A) occlusal, (B) buccal, and (C) lingual views. Scale bar = 5 mm.

		length (mm)	width (mm)
KU 15646	Lp2	6.60	4.27

Table 2. Dental measurements for *Lambertocyon n. sp.*

THRYPTACODON Matthew and Granger 1915

Discussion. — The Twelvemile *Thryptacodon* material consists of an isolated M^1 or M^2 (CM 72351), two dentary fragments each containing an M$_3$ and the talonid fragment of an M$_2$ (CM 72350 and CM 89400), an isolated M$_2$ (CM 77293) and an isolated M$_3$ (CM 77139). CM 72351 possesses a large hypocone whose base is situated more lingually than that of the protocone and hints at a cingulum wrapping around the tooth (the specimen is extremely worn), characteristic of *Thryptacodon*. The three M$_3$ specimens are quite distinctive. Not only is the talonid posterior strongly tapered, the hypoconulid itself projects as a spur well behind the entoconid/hypoconid rim, connected to the rim by a crest and a weak cuspule situated where the hypoconulid would normally be. The detailed morphology of the hypoconulid spur appears to be variable. In CM 89400, a crest projects buccally from the hypoconulid to form a shelf along the buccal posterior of the spur (this appears to be the condition of the holotype of *T. australis*; see

Simpson 1935b). In CM 72350, crests project from the hypoconulid on either side, and in CM 77139, the 'crests' are instead finely-spaced rows of neomorphic cuspules on either side. Along the entocristid between the entoconid and the base of the metaconid is a row of three to five cuspules (the posteriormost cuspule may be an entoconulid) [a similar row of cuspules occurs in a cast of the holotype of *T. loisi*; it's too hard to tell from the drawings in Matthew and Granger 1915 and Simpson 1935b whether this is a feature in the holotypes of *T. antiquus* and *T. australis*]. These are all characteristic of *Thryptacodon*. The paraconids are weak, but still more distinct and cusplike than those in a phenacodontid or many apheliscids. In CM 77139 and CM 89400, distinct crests connect the paraconid to the metaconid and protoconid, but such crests are absent in CM 72350; this appears to be a variable feature.

Thryptacodon pseudarctos Simpson 1928

Figure 7, Table 3

Holotype. — AMNH 22176, an isolated RM^2 from Bear Creak, northern Bighorn Basin, Montana.

Age and distribution. — See Secord (2008), p. 139; Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a).

Description. — The holotype was described by Simpson (1928), and additional specimens were referred to this taxon in Gingerich (1978), Rose (1981a), and Secord (2008).

Discussion. — The size and morphology of the M_3 specimens are more consistent with the late Tiffanian *T. australis* than with *T. antiquus*, the early Tiffanian *T. orthogonius*, or the Wasatchian *T. barae*. In the latter taxa, the M_3 talonid is more weakly posteriorly tapered and the hypoconulid spur less prominent and set-off; also, the latter taxa are significantly smaller. Direct comparison of the Twelvemile M_3 specimens to *T. pseudarctos* is difficult, as the holotype of *T. pseudoarctos* consists only of an isolated M^2; however, CM 72351 compares favorably (aside from the fact that the holotype of *T. pseudarctos* lacks a pericone, which according to Secord 2008 is a variable feature in this taxon). Secord (2008) refers a number of Tiffanian specimens to *T. pseudarctos* based on their larger size compared to *T. australis*. If this is indeed a valid distinction, then the Twelvemile Bonanza specimens can probably also be referred to *T. pseudarctos* based on their size, which would otherwise occupy the extreme upper range of *T. australis*. CM 72351, for example, is larger even than the type specimen of *T. pseudarctos*. It is possible that the specimens referred to *T. pseudarctos* here and in Secord (2008) may in fact comprise more than one species, but I have not been able to examine the relevant specimens and cannot make this determination here. The coefficient of variation in ln(length*width) of the Twelvemile Bonanza M_3 specimens is quite low (3.09), and these specimens fit the size profile of *T. pseudarctos*.

Referred specimens.— CM 72350 (RM_2-M_3), CM 72351 (LM^1 or M^2), CM 77139 (RM_3), CM 77293 (LM_2), CM 89400 (LM_2-M_3).
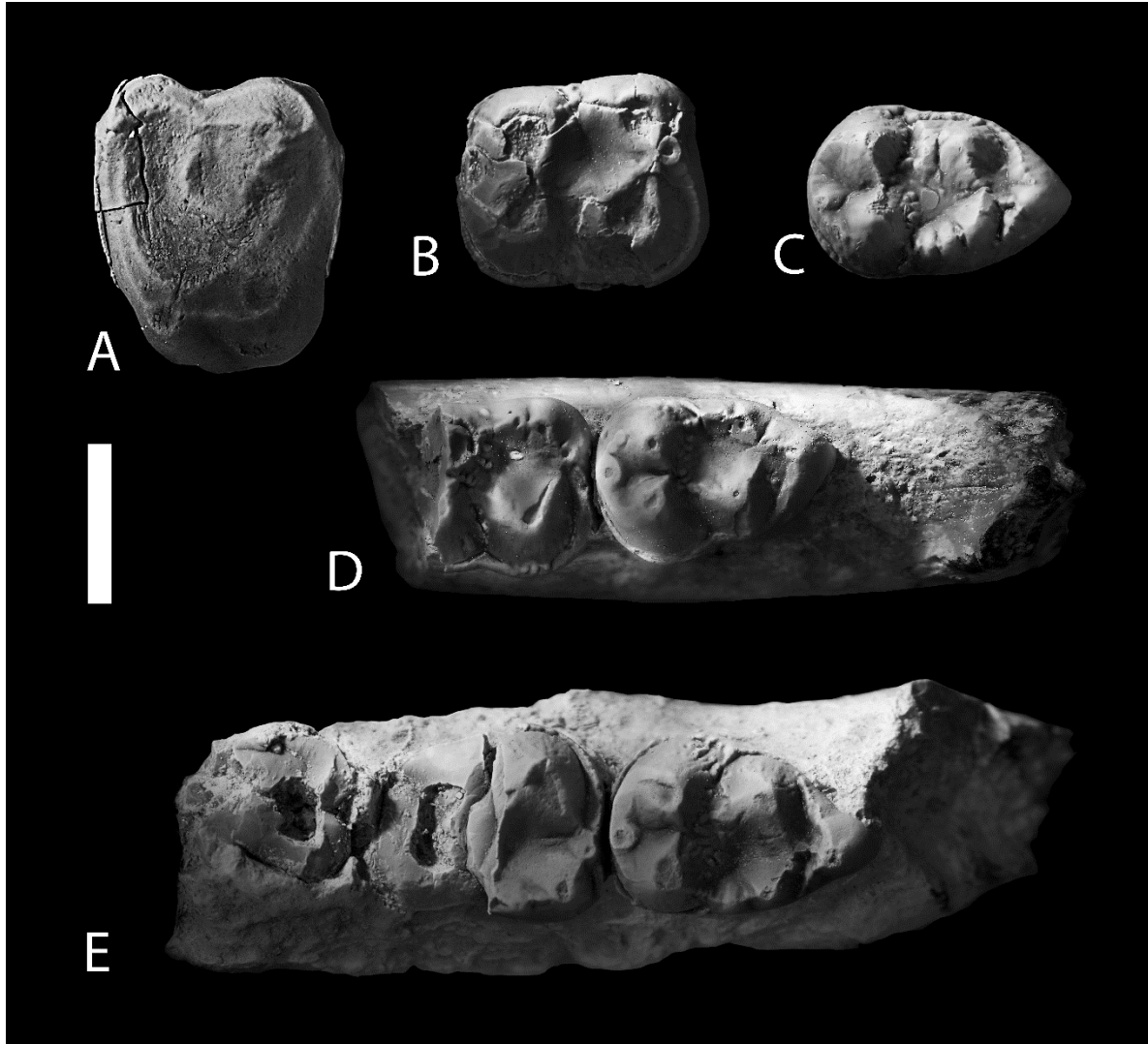
Figure 7. Dentition of *T. pseudarctos* from Twelvemile Bonanza. CM 72351 (LM^1 or M^2) in (A) occlusal view; CM 77293 (LM$_2$) in (B) occlusal view; CM 77139 (RM$_3$) in (C) occlusal view; CM 89400 (LM$_2$-M$_3$) in (D) occlusal view; and CM 72350 (RM$_2$-M$_3$) in (E) occlusal view. Scale bar = 5 mm.

		length (mm)	width (mm)
CM 72350	Rm2	frag.	frag.

	Rm3	8.60	6.06
CM 72351	LM1 or M2	7.71	9.09
	Rm3	8.33	6.02
CM 77293	Lm2	7.82	6.38
CM 89400	Lm2	frag.	frag.
	Lm3	7.62	5.47

Table 3. Dental measurements for *T. pseudarctos* specimens from Twelvemile Bonanza.

Family APHELISCIDAE Matthew 1918

ALETODON Gingerich 1977

Discussion. — *Aletodon* can be distinguished from closely-related apheliscids such as *Gingerichia*, *Phenacodaptes*, and *Apheliscus* by size (*Aletodon* is significantly larger) and by a number of features on P_4, which include:

(1) A well-developed hypoconid connected to a clear cristid obliqua running down the midline of the protoconid posterior. In *Phenacodaptes* all talonid cusps are weak or occasionally absent; in *Gingerichia geoteretes* and *G. hystrix*, the talonid is unicuspid or bicuspid, with all cusps compressed to the lingual side, and the cristid obliqua is absent or extremely faint;

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(2) The relative size of the talonid basin, which is reduced in *Aletodon*;

(3) A relatively well-defined paraconid flanked by anterior crests on each side with a connecting paracristid running along the midline of the tooth about halfway up the protoconid.

Aletodon gunnelli, the youngest known species of *Aletodon* and the type species for the genus, can be distinguished from the earlier *Litomylus* by a considerably weaker metaconid on P_4, as well as a P_4 talonid basin that is considerably smaller (see above). In *Litomylus* the metaconid is a clearly-defined cusp set off from the protoconid by what Simpson (1935) calls a "distinct pocket". The P_4 on the holotype of *Aletodon conardae*, a mid to late Tiffanian species, appears not to be fully erupted, but nevertheless a clear metaconid can be seen, a characteristic it shares with *Litomylus*. On the other hand, the size of *A. conardae* is very similar to *A. gunnelli* (the latter a bit larger), and these taxa share a relatively posteriorly oriented molar metaconid. Winterfeld (1982) noted additional features that make *A. conardae* appear transitional between *Litomylus* and *A. gunnelli*, most noticeably: (1) an M_1 with a narrower trigonid relative to talonid, as in *Litomylus*; (2) a relatively long anterior slope on P_4, as in *A. gunnelli*; and (3) an M_2 with a relatively wider trigonid relative to talonid, as in *A. gunnelli*.

Gingerich (1977) reports that the P_3 is almost as large as the P_4 in paratype specimens of *A. gunnelli*, and that is true for the Twelvemile P_3 specimens as well (it is also true for *Litomylus*, but not for closely related taxa such as *Phenacodaptes* where P_4 is the largest, or at least longest, tooth in the lower jaw).

Aletodon conardae Winterfeld 1982

Figures 8-9, Table 4

Holotype. — UW 13266 (left dentary containing P_4-M_2) from V-77059.

Age and distribution. — V-77059, Rock Springs Uplift, southwestern Wyoming (Ti4); Twelvemile Bonanza, southwestern Wyoming (*Probathyopsis* zone, Ti5a); Big Multi Quarry, Rock Springs Uplift, southwestern Wyoming (Cf1)?.

Description. — The holotype was described in Winterfeld (1982).

Discussion. — The Twelvemile Bonanza P_4, M_1, and M_2 specimens match *A. conardae* closely in morphology. CM 82428, an isolated P_4, possesses a sizeable metaconid, and CM 72356 (another isolated P_4) possesses two small cuspules in the usual position of a metaconid. The trigonid is narrower than the talonid in the M_1 specimens (KU 155869, CM 77106), and the trigonid is wider than the talonid in the M_2 specimens (CM 82427, CM 89410, KU 155869, CM 77106). Additionally, these specimens are all good size matches for *A. conardae*. The size of the P_3 in relation to P_4 is unknown in *A. conardae*, but an enlarged, elongated P_3 seems to be a general feature of the *Litomylus/Aletodon* clade, and the Twelvemile P_3 specimens (KU 155869, CM 77291, CM 77292) are consistent with this.

The Twelvemile specimens of upper dentition consist of a left maxillary fragment containing P^4 and M^1 (CM 77290), an isolated P^4 (CM 82424), and two isolated M^2 specimens (CM 82429, CM 89411). No upper dentition from *A. conardae* is known, but the Twelvemile specimens compare favorably with the suite of characters assigned to the genus *Aletodon* by

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Zack et al. (2005). The M^1 and M^2 specimens are comparable in size to those reported for *A. gunnelli* in Gingerich (1977), but a bit smaller, consistent with *A. conardae*. CM 82424 compares favorably with the P^4 associated with M^1 in CM 77290.

The sizeable presence of this taxon at Twelvemile Bonanza is particularly interesting, as Secord (2008) reports no specimens of *A. conardae* whatsoever in the far more extensively-sampled Tiffanian of the Bighorn and Crazy Mountain basins (see Figure 37). He reports what is possibly a new species of *Aletodon* in Ti4b–Ti5a of Bighorn Basin, describing a right dentary fragment containing M_2 and M_3, and referring an additional isolated P_3 and isolated M_3 to the same taxon. The potential type specimen is apparently within the size range of the mid-Tiffanian to Clarkforkian *A. quadravus*, but differs most noticeably from *A. quadravus*, *A. conardae*, and *A. gunnelli* in that the metaconid and protoconid are further apart, and the cristid obliqua/postvallid contact is more buccally-oriented. The Twelvemile specimens do not show this; they are definitely allied with *A. conardae* (and *A. quadravus*) in that the cristid obliqua/postvallid contact occurs right below the notch in the protocristid. It is difficult to judge the relative spacing between the metaconid and protoconid without seeing Secord's specimen, but it does not appear to be significantly different in the Twelvemile Bonanza specimens from any of the known species of *Aletodon*. The genus appears to have been far more common during Ti5 at Twelvemile Bonanza than the Bighorn Basin.

To shed light on how *Aletodon conardae* relates phylogenetically and biogeographically to other *Aletodon*, I undertook a tentative phylogenetic analysis of the genus in TNT v.1.5 using a character-taxon matrix of 18 dental characters, partially adapted from Gingerich (1977), Winterfeld (1982), and Gingerich (1983). I employed a branch-and-bound search for the most parsimonious tree, using *Litomylus* as the outgroup (see Appendix A and B). Phylogenetic

relationships within the genus appear to be in good agreement with the stratigraphic position of each species (see Figure 9).

 Referred specimens.— CM 72356 (RP$_4$), CM 77106 (RM$_1$-M$_2$), CM 77290 (LP^4-M^1), CM 77291 (RP$_3$), CM 77292 (RP$_3$), CM 82424 (LP^4), CM 82427 (RM$_2$), CM 82428 (LP$_4$), CM 82429 (LM^2), CM 89410 (RM$_2$), CM 89411 (LM^2), KU 155869 (associated RP$_3$, RM$_1$-M$_2$), KU 156538 (LP$_4$ jaw fragment). .
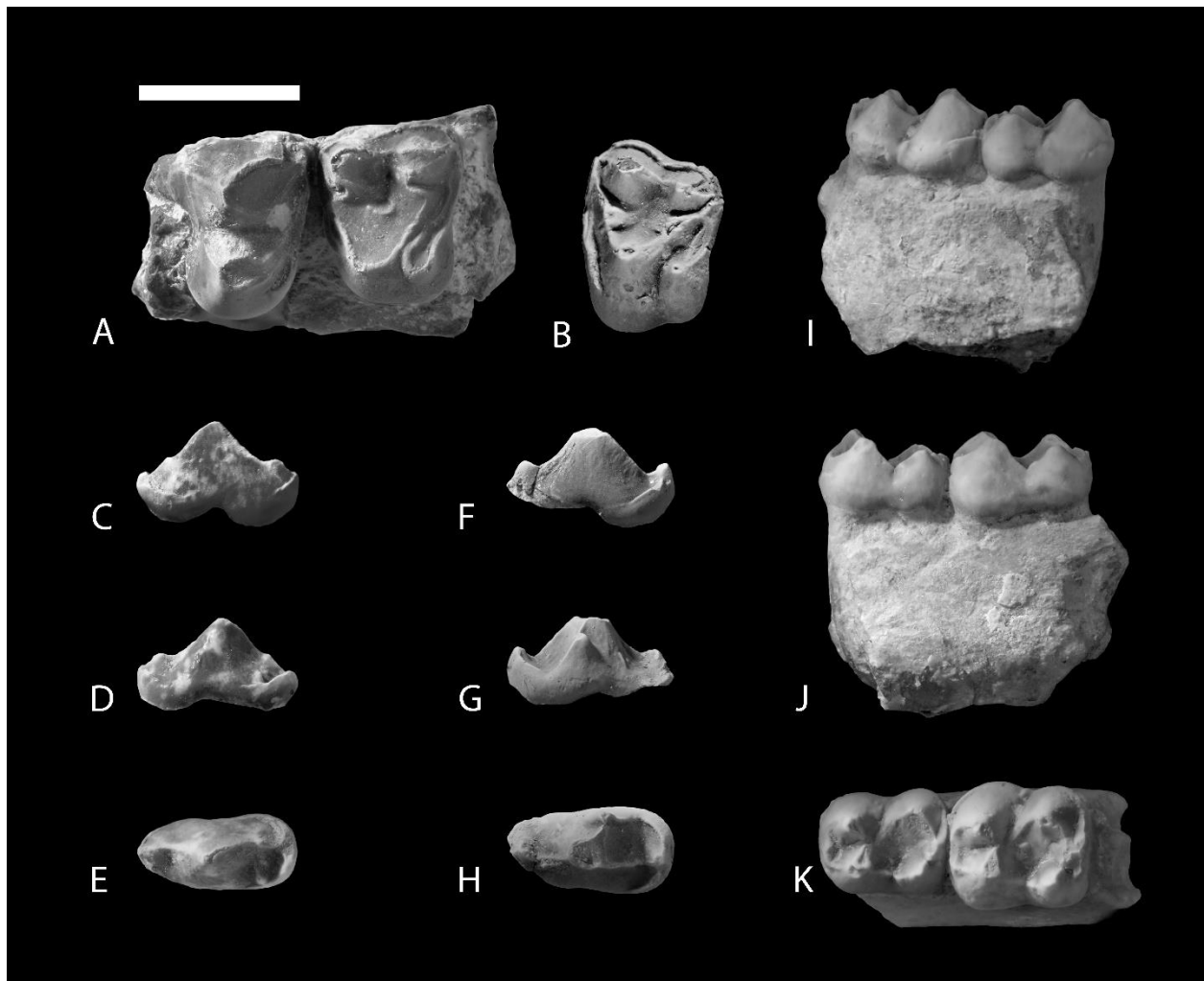
Figure 8. Dentition of *A. conardae* from Twelvemile Bonanza. CM 77290 (LP^4-M^1) in (A) occlusal view; CM 82429 (LM^2) in (B) occlusal view; KU 155869 (assoc. RP$_3$) in (C) buccal,

(D) lingual, and (E) occlusal views; CM 82428 (LP4) in (F) buccal, (G) lingual, and (H) occlusal views; KU 155869 (assoc. RM1-M2) in (I) buccal, (J) lingual, and (K) occlusal views. Scale bar = 5 mm.
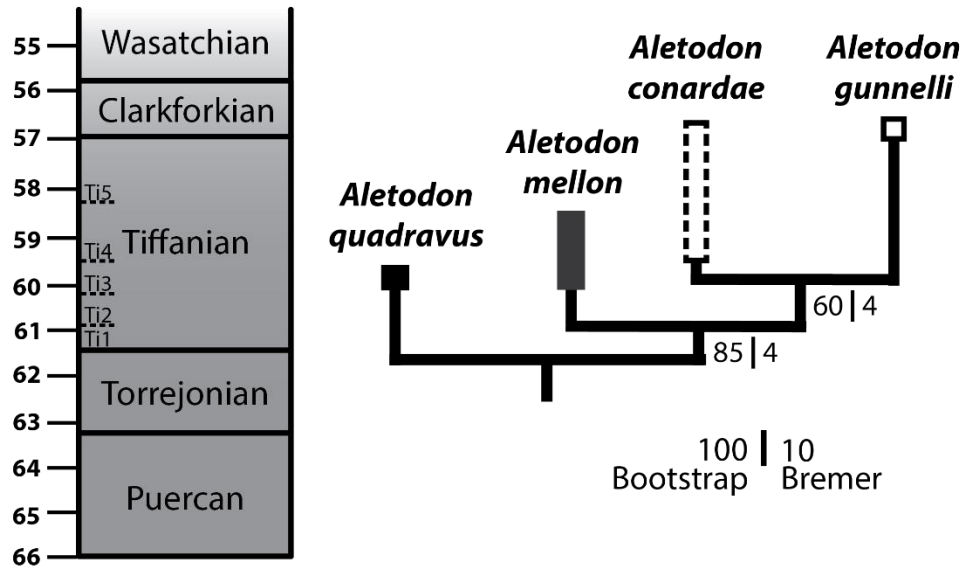
Figure 9. Phylogeny and temporal distribution of *Aletodon*.

		length (mm)	width (mm)
CM 72356	Rp4	5.12	2.98
CM 77106	Rm1	4.21	3.31
	Rm2	broken	broken
CM 77290	LP4	3.53	4.63
	LM1	3.54	4.52

CM 77291	Rp3	4.49	1.96
CM 77292	Rp3	5.12	2.32
CM 82424	LP4	4.10	4.65
CM 82427	Rm2	4.72	4.24
CM 82428	Lp4	5.21	2.87
CM 82429	LM2	4.24	5.41
CM 89410	Rm2	4.80	4.06
CM 89411	LM2	4.09	5.78
KU 155869	Rp3	4.97	2.41
	Rm1	4.03	3.11
	Rm2	4.34	3.89

Table 4. Dental measurements for *A. conardae* from Twelvemile Bonanza.

PHENACODAPTES Jepsen 1930

Type species. — *Phenacodaptes sabulosus,* YPM-PU 13302 (right dentary containing P_1-M_3) from Princeton Quarry.

Age and distribution. — Princeton and Schaff Quarries, Bighorn Basin, northwestern Wyoming (*Probathyopsis* zone, Ti5a); Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a).

Discussion. — According to Zack et al. (2005), *Gingerichia*, *Phenacodaptes*, and *Apheliscus* belong together in Apheliscinae, a clade nested within Apheliscidae. Synapomorphies of Apheliscinae include, among others, a P_4 larger or at least longer than any other tooth in the lower jaw with a large, tall protoconid, weak or absent paraconid and metaconid, and a relatively weak talonid basin. *Phenacodaptes* and *Apheliscus* differ from *Gingerichia* in having molar trigonids and talonids relatively closer in height, in having less developed molar paracristids, in possessing traces of posterior cingulids on P_4 and the lower molars, in the greater development of the hypoconulids on M_1 and M_2, and in having relatively quadrate upper molars. The differences between the late Tiffanian *Phenacodaptes* and the Clarkforkian and Wasatchian *Apheliscus* are more subtle, to the point that Zack et al. 2005 postulate the former is directly ancestral to the latter. *Phenacodaptes* possesses a slightly narrower M_3 trigonid relative to the M_2 trigonid; a P_4 with a more inflated protoconid and a cristid obliqua that contacts the post-vallid relatively lingually; and especially well-developed hypocones on M^1 and M^2.

Phenacodaptes n. sp.

Figures 10-11, Table 5

Description and Diagnosis. — The Twelvemile Bonanza specimens most closely resemble *P. sabulosus* and *Apheliscus* in the poor development of the molar paracristids, the presence of traces of posterior cingulids on the molars (especially M_2), and a number of features on P_4, including the presence of a hypoflexid cingulum; a talonid heel that tapers sharply into the midline of the P_4 on the buccal side in occlusal view; the presence of a (weak) paraconid; and a

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relatively low-crowned protoconid. Additionally, they possess the diagnostic features of *Phenacodaptes* laid out above, linking them more closely to *Phenacodaptes sabulosus* than to any other known apheliscine. *Phenacodaptes n. sp.* differs from *Phenacodaptes sabulosus* in possessing upper and lower third molars that are significantly larger relative to the remaining dentition (Figure 11).

Discussion. —The *Phenacodaptes* specimens from Schaff Quarry appear to belong to the same species as those from Twelvemile Bonanza, all of which differ from *Phenacodaptes sabulosus* from Princeton Quarry. Given the very close proximity in geography and time between Princeton Quarry and Schaff Quarry, this may imply sharp differences in the microenvironments of these two quarries. Schaff Quarry may share more in common environmentally with Twelvemile Bonanza than with Princeton Quarry, even though the former two sites are separated by larger distances and a greater amount of time. I measured the ratio of M_3 and M_2 area in the twenty-two YPM-PU Princeton Quarry *Phenacodaptes sabulosus* specimens for which it was possible to do so. I measured the same ratio in three Schaff Quarry specimens and two Twelvemile Bonanza specimens. The difference in mean ratio between the Princeton Quarry specimens and the combined Schaff Quarry + Twelvemile Bonanza specimens was highly significant ($p = 0.004$, significant at the 99.5% confidence level). The mean ratios are *not* significantly different between the Schaff Quarry and Twelvemile Bonanza specimens.

Referred specimens.— **Twelvemile Bonanza:** CM 72354 (RP_4, M_2, alveolus for M_1) CM 72355 (LM_2-M_3), CM 77104 (LP_4-M_3), CM 77105 (RM^1), CM 77141 (LM^2), CM 77142 (RM_3), CM 77143 (LM_3), CM 77288 (RM_1-M_2), CM 77289 (RM_2), CM 82420 (LP_3-P_4), CM 82421 (RP_4), CM 82422 (RM_2), CM 82423 (RM_1), CM 82425 (RM^2), CM 82426 (RM^2), KUVP 156540 (RM^2), KUVP 156543 (RM^2-M^3), KUVP 156544 (LP_4-M_1), KUVP 156547 (LM^1 or

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M^2), KUVP 156548 (LP$_2$). **Schaff Quarry:** YPM-PU 19382 (RdP$_4$,M$_1$), YPM-PU 19430 (LM$_2$-M$_3$), YPM-PU 19431 (LP$_4$-M$_2$), YPM-PU 19504 (LP$_2$-M$_3$, RP$_2$-M$_2$), YPM-PU 19505 (LM$_1$-M$_3$).
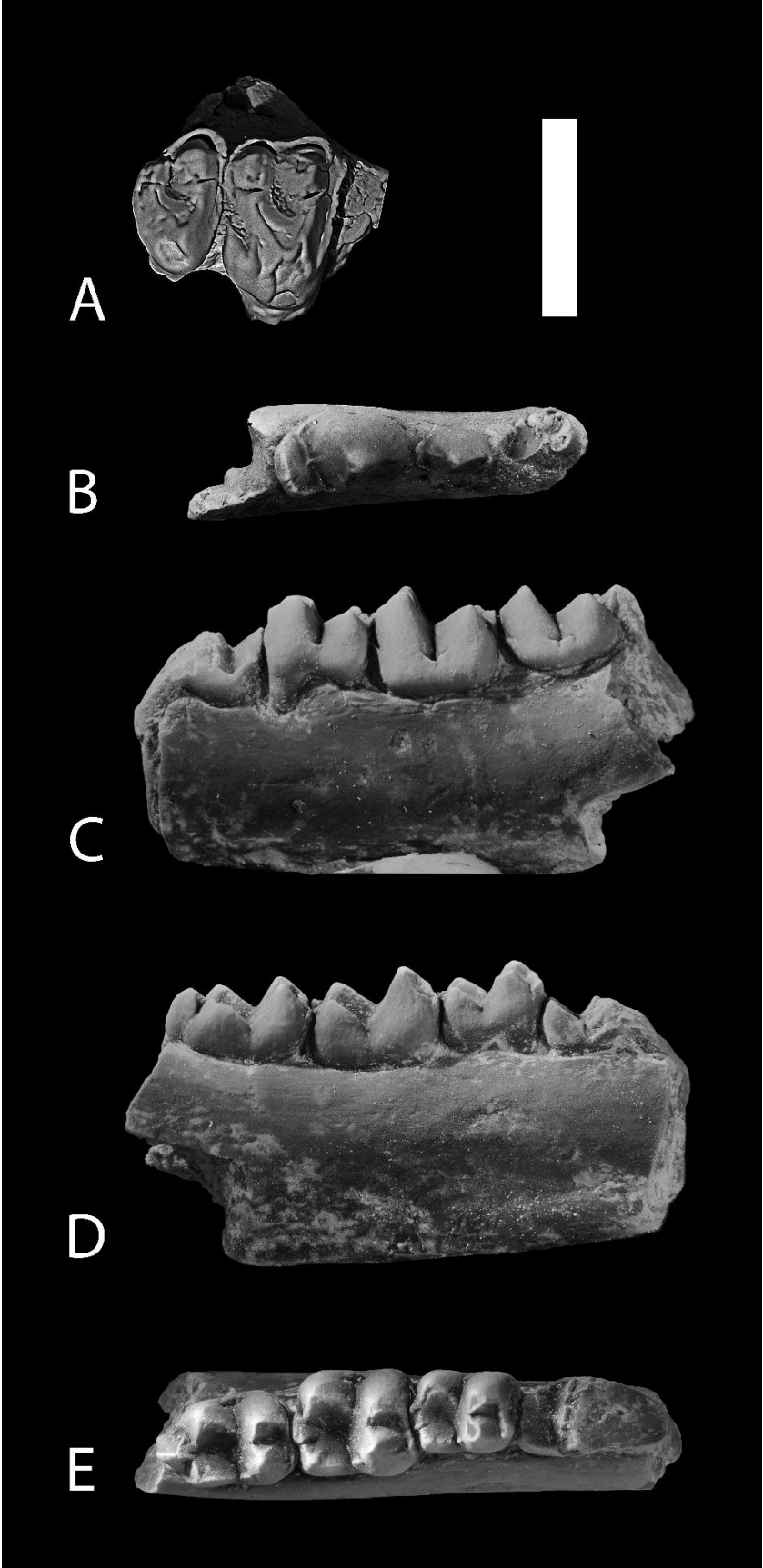
Figure 10. Dentition of *Phenacodaptes n. sp.* KU 156543 (RM^2-M^3) in (A) occlusal view; CM

82420 (LP$_3$-P$_4$) in (B) occlusal view; CM 77104, (LP$_4$-M$_3$) in (C) occlusal, (D) lingual, and (E)

occlusal views. Scale bar = 5 mm.
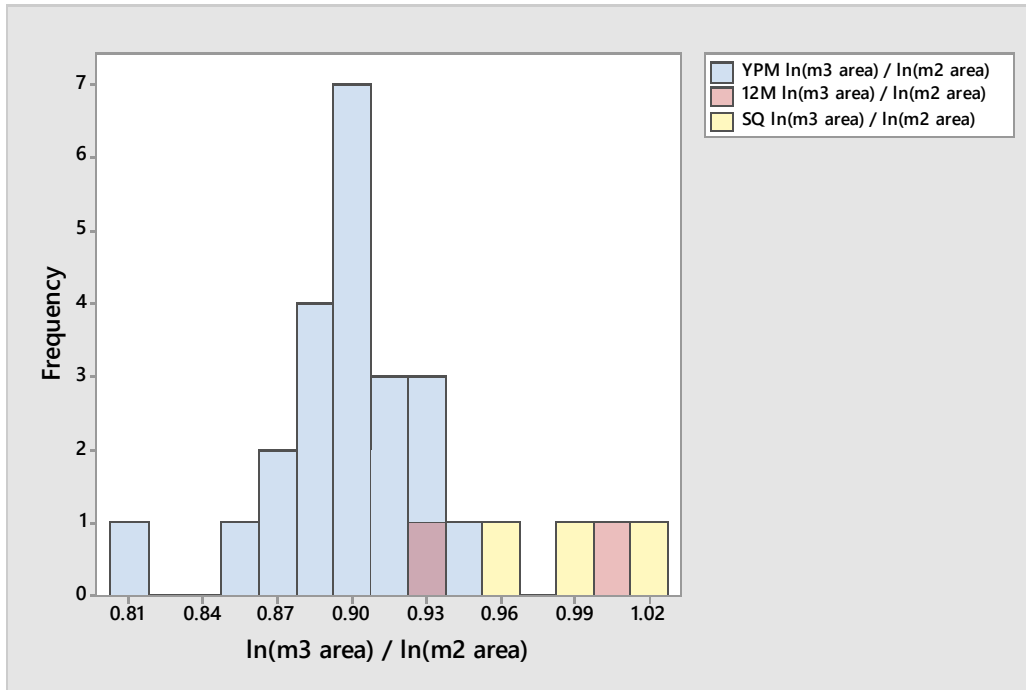
Figure 11. Natural log of M$_3$ area relative to M$_2$ area in *Phenacodaptes* specimens from

Princeton Quarry, Schaff Quarry, and Twelvemile Bonanza.

	P3 length	p3 width	p4 length	p4 width	m1 length	m1 width	m2 length	m2 width	m3 length	m3 width
CM 82420	2.02	1.18	3.36	2.31	n/a	n/a	n/a	n/a	n/a	n/a

CM										
82421	n/a	n/a	3.45	2.13	n/a	n/a	n/a	n/a	n/a	n/a
CM 72354	n/a	n/a	3.41	2.23	n/a	n/a	3.14	2.80	n/a	n/a
CM 77288	n/a	n/a	n/a	n/a	3.05	2.17	3.36	2.54	n/a	n/a
CM 77289	n/a	n/a	n/a	n/a	n/a	n/a	3.19	2.72	n/a	n/a
CM 82422	n/a	n/a	n/a	n/a	n/a	n/a	3.24	2.79	n/a	n/a
CM 72355	n/a	n/a	n/a	n/a	n/a	n/a	3.38	2.65	3.31	2.34
CM 77142	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	3.48	2.32
CM 77143	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	3.43	2.50
CM 77104	n/a	n/a	3.71	2.05	2.80	2.15	3.22	2.82	3.66	2.51

	M1 length	M1 width	M2 length	M2 width	M3 length	M3 width
CM 77105	3.13	3.62	n/a	n/a	n/a	n/a

CM 77141	n/a	n/a	3.55	4.34	n/a	n/a
CM 82425	n/a	n/a	3.34	4.12	n/a	n/a
CM 82426	n/a	n/a	3.47	4.28	n/a	n/a
KU 156543	n/a	n/a	3.27	4.35	2.31	3.66

Table 5. Dental measurements for *Phenacodaptes n. sp.* All measurements in millimeters.

Family PHENACODONTIDAE Cope 1881

ECTOCION Cope 1882

Discussion. — The Twelvemile *Ectocion* material consists entirely of molars and premolars, usually isolated but occasionally embedded in jaw fragments with other molars and premolars. The referred specimens are unmistakably phenacodont: the lower dentition bears reduced paraconids and pronounced hypoconulids and entoconulids, together with the characteristic metastylid cusp; the upper molars bear w-shaped ectolophs and prominent mesostyles consistent with *Ectocion*; and the upper premolars bear prominent ectolophs, likewise consistent with *Ectocion*. With the exception of CM 72369, all referred lower molars and

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premolars are consistent with *Ectocion*—the paracristid characteristically tapers out on the lingual side. All referred upper molars fit the size profile of Tiffanian species of *Ectocion*—only *Phenacodus bisonensis* and *P. vortmani* molars overlap these specimens in their observed widths, but *Phenacodus* molars have width/length ratios characteristically closer to one, and are typically more bunodont than these specimens, with less prominent ectolophs. All referred upper premolars bear prominent ectolophs consistent with *Ectocion*, and all fit the width/length profile of Tiffanian species of *Ectocion*.

Ectocion mediotuber Thewissen 1990

Figure 12, Table 6

Holotype. — YPM-PU 17718 (left dentary containing P_2-M_3) from Princeton Quarry.

Age and distribution. — See Thewissen (1990), p. 31; Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a).

Description. — See Thewissen (1990).

Discussion. — Different species of *Ectocion* are most consistently distinguished by absolute size and by differences in the morphology and relative size of P_3 (Thewissen 1990). The Twelvemile Bonanza specimens seem to be consistent in size with *E. mediotuber* and the Clarkforkian and early Wasatachian *E. osbornianus*. Though no specimens so far recovered from Twelvemile Bonanza preserve a P_3, the posterior fragment of an alveolus present in CM 72360 suggests a rather narrow P_3, characteristic of *E. mediotuber* (Figure 12). Given that *E. mediotuber* and *E. osbornianus* are closely matched in size and given the closer proximity in

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time of Twelvemile Bonanza to Princeton Quarry (the type locality for *E. mediotuber*), I provisionally refer the Twelvemile Bonanza specimens to *E. mediotuber*, pending the recovery of material preserving P_3.

The isolated M_1 and M_2 specimens are indistinguishable from one another and for statistical purposes were treated as equivalent and grouped together as M_1. The coefficient of variation among the lower M_1 and M_2 specimens is exceedingly low (1.73), and the specimens appear to follow a unimodal normal size distribution. CM 72352 appears slightly aberrant on the histogram, but this is almost certainly an artifact of low sample size. The coefficient of variation among the P_4 specimens is likewise very low (2.10), and given that the P_4 and M_1 are associated in CM 72360, all the P_4 and molar specimens probably belong to the same species. CM 72349 possesses a neomorphic lingual cusp on M^1 between the paracone and metacone, as does CM 89829. The coefficient of variation among the P^4 specimens is quite low (2.15), and the size distribution appears to be normal. Likewise, the coefficient of variation among the M^1 specimens is only 2.65 and they appear to follow a normal, unimodal distribution. Since P^4 and M^1 are associated in CM 72349, CM 72358, CM 72359, I conclude that the referred specimens probably belong to the same species. The upper molars and premolars lack sufficient features to distinguish them among *E. mediotuber and E. osbornianus*, and are referred here to *E. mediotuber* on the lack of evidence of separate species status from the lower dental specimens.

Referred specimens.— CM 72349 (LP^4-M^2), CM 72352 (RM_1), CM 72358 (LP^4-M^3), CM 72359 (RP^4-M^1), CM 72360 (LP_4-M_1), CM 72361 (LP_4), CM 72362 (RM_1), CM 72363 (RM_2-M_3), CM 72365 (LM^1), CM 72366 (RP^4), CM 72367 (RM^2), CM 72368 (LP_4), CM 72369 (LM_2), CM 72370 (RM^2), CM 72371 (RM_1), CM 72372 (RM_3), CM 82430 (LP^4), CM 86945 (RM_1), CM 89412 (RP^3), CM 89413 (RM_2), CM 89829 (RM^1-M^2), KU 155865 (RM_2), KU

155866 (RM$_1$), KU 155867 (LM^3), KU 156530 (RM$_3$), KU 156531 (LM$_1$), KU 156536 (RM$_3$), 156550 (fragment with LM$_1$ talonid).
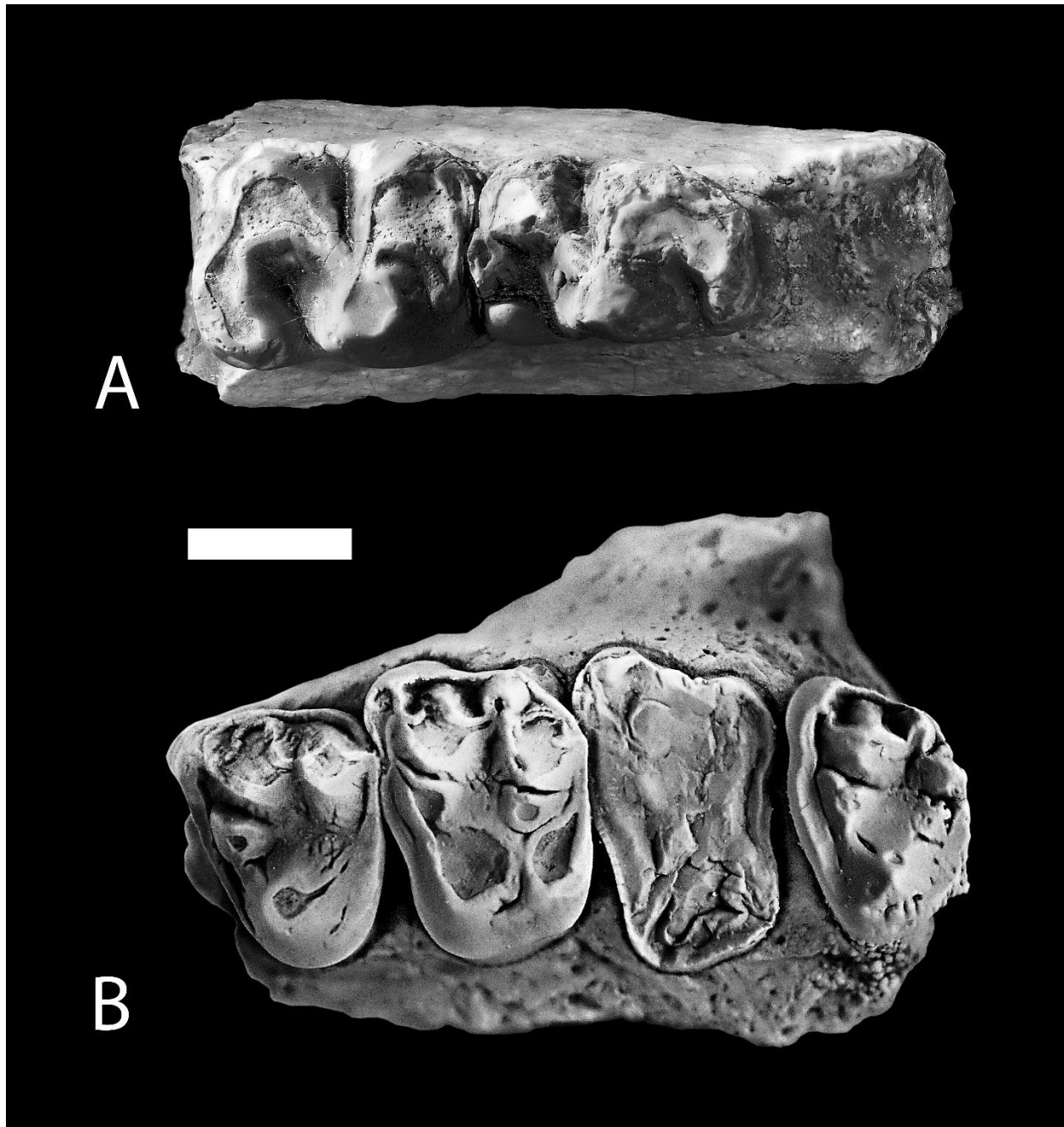
Figure 12. Dentition of *E. mediotuber* from Twelvemile Bonanza. CM 72360 (LP$_4$-M$_1$) in (A) occlusal view; CM 72358 (LP^4-M^3) in (B) occlusal view.

	width (mm)	length (mm)	l*w	ln(l*w)
CM 82430 (P4)	7.93	6.48	51.3864	3.939373546
CM 72358 (P4)	8.00	6.50	52	3.951243719
CM 72366 (P4)	8.22	6.56	53.9232	3.987560812
CM 72359 (P4)	7.93	5.88	46.6284	3.842209798
CM 72349 (P4)	7.30	6.04	44.092	3.78627836

Mean	7.876	6.292	49.606	3.901333247
Std Dev	0.343263747	0.309709541	4.08685618	0.083824999
CV (%)	4.358351282	4.922274974	8.23863279	2.148624421

	width (mm)	length (mm)	l*w	ln(l*w)
CM 72358 (M1)	8.88	6.39	56.7432	4.038535825
CM 72359 (M1)	8.68	6.39	55.4652	4.015755797
CM 72365 (M1)	7.78	6.62	51.5036	3.941651708
CM 89829 (M1)	9.72	6.74	65.5128	4.182245543
CM 72349 (M1)	8.41	5.92	49.7872	3.907757923

Mean	8.694	6.412	55.8024	4.017189359
Std Dev	0.707728762	0.313799299	6.122764676	0.106515781
CV	8.14042744	4.893937912	10.97222463	2.651500135

	width (mm)	length (mm)	l*w	ln(l*w)
CM 72370 (M2)	9.54	6.93	66.1122	4.191353299
CM 72367 (M2)	9.55	6.55	62.5525	4.136006204
CM 89829 (M2)	10.97	damaged		
CM 72349 (M2)	8.79	damaged		

	width (mm)	length (mm)	l*w	ln(l*w)
Mean	9.7125	6.74	64.33235	4.163679751
Std Dev	0.910764331	0.268700577	2.51708801	0.039136306
CV	9.377238929	3.986655443	3.91263184	0.939945149

	width (mm)	length (mm)	l*w	ln(l*w)
CM 72360 (p4)	4.73	6.91	32.6843	3.48689484
CM 72361 (p4)	5.22	7.01	36.5922	3.599835103
CM 72368 (p4)	4.48	7.11	31.8528	3.46112529
Mean	4.81	7.01	33.70976667	3.515951744
Std Dev	0.376430604	0.1	2.530645077	0.073778932
CV	7.826000093	1.426533524	7.507156907	2.098405703

	width (mm)	length (mm)	l*w	ln(l*w)
CM 72352 (m1 or m2)	6.29	7.50	47.175	3.853864091
CM 72360 (m1)	5.62	7.04	39.5648	3.677939834
CM 72362 (m1 or m2)	5.64	7.07	39.8748	3.685744545
CM 72371 (m1 or m2)	5.57	6.91	38.4887	3.650364692

CM 86945 (m1 or m2)	5.54	6.84	37.8936	3.634782232
KU 155866 (m1 or m2)	5.48	6.87	37.6476	3.628269207
CM 72363 (m2)	5.75	6.99	40.1925	3.693680411
CM 72369 (m1 or m2)	5.66	6.85	38.771	3.657672544
CM 89413 (m1 or m2)	5.61	6.96	39.0456	3.664730194
KU 155865 (m1 or m2)	5.67	6.99	39.6333	3.679669674

Mean	5.683	7.002	39.82869	3.682671743
Std Dev	0.225883451	0.191879592	2.71292806	0.063868356
CV	3.974721991	2.740354068	6.81149206	1.734294027

Table 6. Dental measurements for *E. mediotuber* from Twelvemile Bonanza.

PHENACODUS Cope 1873

Discussion. —The upper molars and premolar specimens of *Phenacodus* are distinguishable from *Ectocion* by their larger size, width/length ratios closer to one, and less prominent ectolophs. The lower molar specimens are distinguishable by their larger size, and the P_3 specimens can be distinguished by their larger size and strong metaconids. According to Thewissen (1990), the most reliable character for distinguishing among *Phenacodus* species is size.

Phenacodus grangeri Simpson 1935b

Figure 13, Table 7

Holotype. — AMNH 17185 (right maxilla containing M^1-M^2 and buccal fragment of M3) from the northeastern San Juan Basin, Colorado.

Age and distribution. — See Thewissen (1990) p. 50l; Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a).

Description. — See Thewissen (1990).

Discussion. — The P^4 is wider than long in the Twelvemile Bonanza *Phenacodus* specimens, characteristic of *P. grangeri* and unlike that of the similarly-sized Clarkforkian and early Eocene *P. intermedius*, whose P^4 width/length ratio is often nearly exactly one. The Twelvemile Bonanza *Phenacodus grangeri* specimens are essentially exactly what one would expect from an early Ti5 locality in light of the size trends delineated by Thewissen (1990). The mean size estimate I obtained from the Twelvemile Bonanza M_1 specimens falls between those calculated in Thewissen (1990) for the Cedar Point Quarry (Ti3) specimens and for the *Plesiadapis simonsi* zone (Ti5b) specimens.

Coefficients of variation for each type of tooth are quite low across the spectrum of measurements (width, length, width/length ratio and natural log length x width) and fall comfortably within the range of variation of *P. grangeri*; I therefore provisionally refer them all to this species.

Referred specimens.— CM 72374 (LP^4), CM 72375 (LP^4), CM 72376 (LM^1 or M^2), CM 72373, CM 86940, CM 72378, CM 72379, CM 72380, CM 77296, CM 82431, CM 82432, CM

72353, KU 155870, CM 72381, CM 77294 (LP^3), CM 77297 (LM^3), KU 156532 (LP$_4$), KU 156577 (RP$_3$).
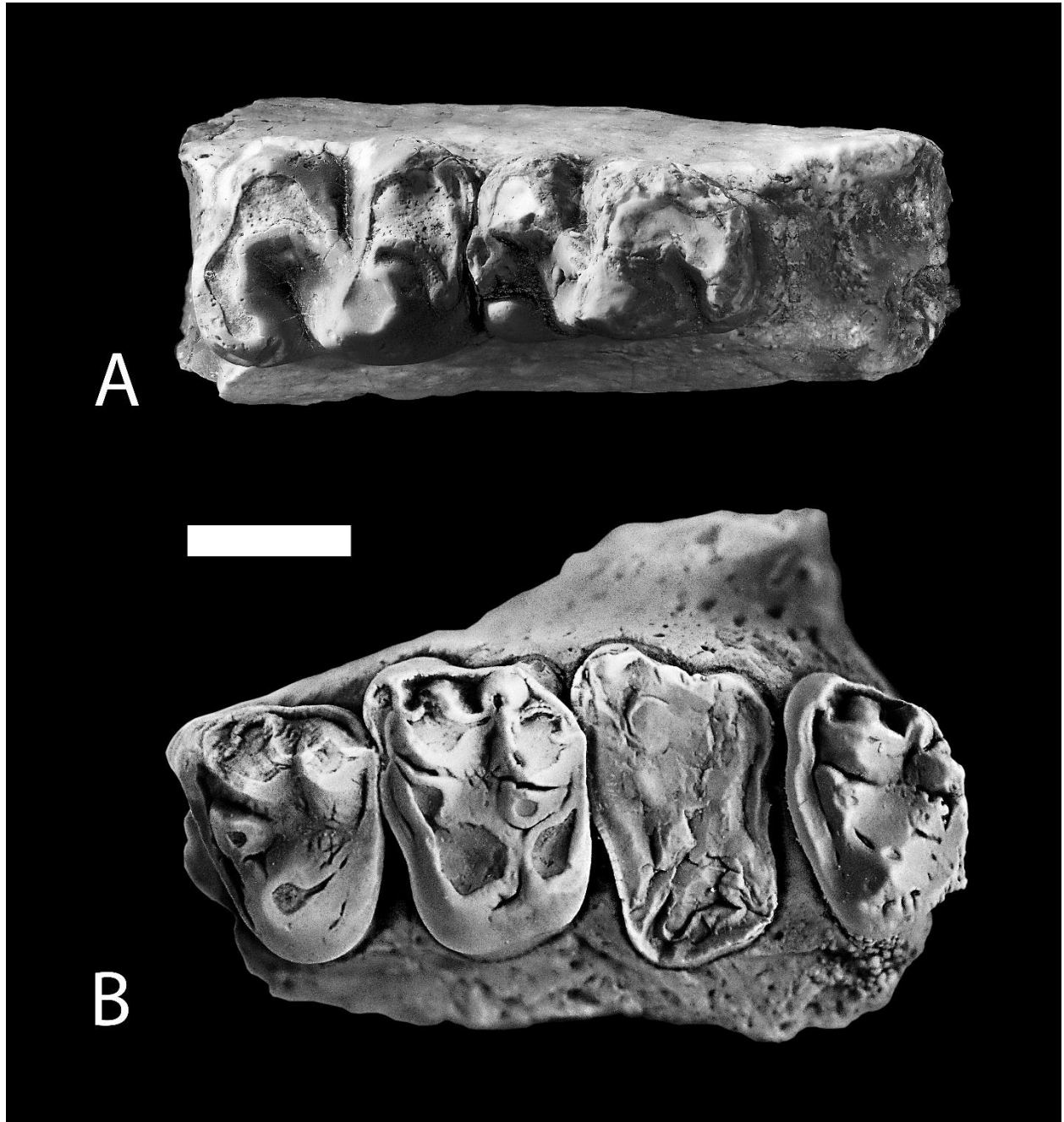
Figure 13. Dentition of *P. grangeri* from Twelvemile Bonanza. CM 77294 (LP^3)in (A) occlusal view; CM 72375 (LP^4) in (B) occlusal view; CM 72376 (LM^1 or M^2) in (D) occlusal view; CM 77297 (LM^3) in (D) occlusal view; CM 72373 (LP$_3$-M$_3$) in (E) occlusal view. Scale bar = 5 mm.

	width (mm)	length (mm)	l/w	l*w	ln(l*w)
CM 72373 (p3)	6.45	10.16	1.58	65.53	4.18
CM 72380 (p3)	5.87	8.41	1.43	49.37	3.90
CM 77296 (p3)	5.62	7.77	1.38	43.67	3.78
CM 86940 (p3)	6.59	9.97	1.51	65.70	4.19
OR					
Mean	6.13	9.08	1.48	56.07	4.01
Std Dev	0.46	1.17	0.09	11.27	0.21
CV	7.54	12.92	5.78	20.10	5.13

	width (mm)	length (mm)	l/w	l*w	ln(l*w)
CM 72373 (p4)	8.01	10.69	1.33	85.63	4.45
CM 72378 (p4)	8.19	10.35	1.26	84.77	4.44
CM 82431 (p4)	6.87	9.83	1.43	67.53	4.21
OR					
Mean	7.69	10.29	1.34	79.31	4.37
Std Dev	0.72	0.43	0.08	10.21	0.13
CV	9.31	4.21	6.25	12.87	3.07

	width (mm)	length (mm)	l/w	l*w	ln(l*w)
CM 72373 (m1)	10.15	11.67	1.15	118.45	4.77
CM 72379 (m1)	10.07	12.27	1.22	123.56	4.82
CM 82432 (m1)	8.58	10.48	1.22	89.92	4.50
OR					
Mean	9.60	11.47	1.20	110.64	4.70
Std Dev	0.88	0.91	0.04	18.13	0.17
CV	9.21	7.94	3.39	16.38	3.67

	width (mm)	length (mm)	l/w	l*w	ln(l*w)
CM 72373 (m2)	11.05	n/a	n/a	n/a	n/a

	width (mm)	length (mm)	l/w	l*w	ln(l*w)
CM 72353 (m3)	7.46	10.46	1.40	78.03	4.36
CM 72373 (m3)	9.59	12.01	1.25	115.18	4.75
CM 72381 (m3)	6.83	9.13	1.34	62.36	4.13
KU 155870 (m3)	7.43	10.37	1.40	77.05	4.34
OR					
Mean	7.83	10.49	1.35	83.15	4.40
Std Dev	1.21	1.18	0.07	22.52	0.26
CV	15.46	11.24	5.16	27.08	5.82

Length (mm)	Width (mm)

CM 72374	LP4	10.65	10.95
CM 72375	LP4	9.99	11.78
CM 72376	LM1 or M2	11.55	14.98
CM 77294	LP3	8.33	9.48
CM 77297	LM3	7.59	10.93

Table 7. Dental measurements for *P. grangeri* from Twelvemile Bonanza.

Order DINOCERATA Marsh 1873

Family PRODINOCERATIDAE Flerov 1952

PROBATHYOPSIS Simpson 1929

Discussion. — Dinoceratan dentition can immediately be distinguished from most other Paleocene taxa by its exceptionally large size—they were among the largest mammals living in Wyoming in the Paleocene. The talonid architecture is also distinctive. In prodinoceratids like *Probathyopsis*, the hypoconid and cristid obliqua are arranged in typical fashion, but the lingual portion of the talonid (everything on the lingual side of the cristid obliqua) takes the form of a low accessory shelf reminiscent of the hypocone shelf on an upper molar. The hypoconulid and entoconid are barely distinct among a posterolingual row of cuspules. In later uintatheres the

lower molars are bilophodont, and the cristid obliqua and protocristid together form a v-shaped crest.

The Twelvemile *Probathyopsis* material consists of an isolated fragment of an M_2 talonid (CM 89416).

Probathyopsis harrisorum Patterson 1939

Figure 14

Holotype. — FMNH P 15546 (left dentary containing P_3-P_4, M_2-M_3; right dentary containing M_2-M_3; fragments of I_1, I_2, C_1, and M_1 on both dentaries; associated postcrania) from "Plateau Valley beds…one mile north of the Douglas Harris ranch house," Colorado (Patterson 1939).

Age and distribution. — Bighorn Basin; Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a); the genus serves as an index fossil for Ti5 and later. The species is known from Ti5-Cf1.

Description. — The holotype was described by Patterson (1939). See Thewissen and Gingerich (1987) for descriptions and figures of additional material from the Bighorn Basin.

Discussion. — CM 89416 bears quite a close resemblance to the M_1 and M_2 talonids of the holotype of *P. "newbilli"* described and figured in Patterson (1939) and synonymized with *P. harrisorum* by Thewissen and Gingerich (1987). The width of CM 89416 is 13.5 mm, consistent with the observed range reported by Thewissen and Gingerich (1987).

Referred specimens.— CM 89416 (RM_2 talonid fragment).

Figure 14. M$_2$ talonid fragment of *Probathyopsis harrisorum* CM 89416 in occlusal view. Scale bar = 5 mm.

"INSECTIVORA" Bowdich 1821

Discussion. — "Insectivores" (Lipotyphla and Leptictida, plus various "archaic insectivores" which appear to ally more closely with modern Lipotyphla than with other dentally primitive mammals, per Novacek 1986) are traditionally distinguished from other Cenozoic mammal groups by how stereotypically tribosphenic and unmodified their teeth are relative to late Cretaceous eutherians (Butler 1972). In general, the higher-level systematics of Paleocene

"insectivores" (and many similar wastebasket taxa such as Proteutheria and Cimolesta) are poorly understood.

Order LIPOTYPHLA Haeckel 1866

Suborder ERINACEOMORPHA Gregory 1910

ADUNATOR Russell 1964

Discussion. — The earliest erinaceomorph groups to appear in the fossil record are Adapisoricidae and Erinaceidae, which first appear in the late Torrejonian and early Puercan, respectively. Krishtalka (1976) distinguished between Adapisoricidae and Erinaceidae by the following characteristics:

(1) Adapisoricids (or dormaaliids, if following the classification of Novacek et al. 1985) possess longer P_4 talonids, broader and more lophodont molar paraconids, more prominent molar hypoconulids, flat molar hypoconids, rounded molar talonid basins, and high molar entoconids lacking an entocristid. In addition, the talonid is wider than the trigonid on M_1, but the reverse is true on M_2; overall, however, M_1 and M_2 are of roughly equal size.

(2) Erinaceids possess shorter P_4 talonids, a more compressed and cusplike paraconid, significantly reduced hypoconulids, and an inversely conical talonid basin bearing a

strong entocristid. Additionally, there is a clear, stepwise reduction in the size of the molars from M_1 to M_3. The latter two features in particular seem to ally stem erinaceids more closely to the group that includes modern hedgehogs (Erinaceinae) than to Adapisoricidae or any other "insectivore" group.

The earliest erinaceomorph taxon to appear in the fossil record is *Adunator* in the Puercan (the second-earliest is *Litocherus* in the late Torrejonian). Like many Paleocene taxa, its dentition lies ambiguously between these two sets of characters. *Adunator*, for instance, possesses a relatively long P_4 talonid, a somewhat cusplike but still fairly broad molar paraconid, and fairly prominent molar hypoconulids (at least in the holotype for the genus, Wal 368), characteristic of adapisoricids. However, it also possesses a relatively deep molar talonid basin and a strong molar entocristid, characteristic of erinaceids. Additionally, there is no reduction from M_1 to M_2, but M_3 is clearly smaller than M_2. I refer *Adunator* to Erinaceomorpha out of convenience following Secord (2008), and do not attempt a formal classification of the genus. It certainly possesses the large, wide talonid basins characteristic of Erinaceomorpha.

Krishtalka (1976) synonymized *Adunator* and *"Diacodon" minutus* (Gingerich 1983 subsequently erected a new genus for *"Diacodon" minutus"* called *Diacocherus*; Novacek et al. 1985 in turn synonymized it with *Adunator*). Krishtalka (1976), however, distinguished *Adunator* from *Mckennatherium* by a number of features. I concur with Bown and Schankler (1982) that many of these are unrecognizable, but comparing the holotype of *Adunator* (Wal 368) with the holotype of *Mckennatherium ladae* (USNM 9640), two differences attributed to *Adunator* appear valid to me: the more molariform P_4, and a slight swelling of the metaconid on M_1 and M_2 in lingual view. I note that in *Adunator*, the P_4 talonid is less lingually compressed; in *Mckennatherium* all three cusps are aligned along the posterior and squeezed to the lingual half

of the talonid, and the cristid obliqua is oriented more or less at the median. In *Adunator* the three talonid cusps, along with the cristid obliqua, adopt a more typical tribosphenic arrangement. Additionally, on the P$_4$ of *Mckennatherium* there is a much more pronounced hypoflexid notch, and on the trigonid a more pronounced lingual dip of the paraconid surface where it conjoins with the metaconid. The paraconid itself is also much lower-crowned relative to the metaconid in *Adunator*, and *Adunator* possesses a stronger anterobuccal cingulum.

Given that the P$_4$ is not represented in the Twelvemile specimens, it is difficult to compare them meaningfully to *Adunator* and *Mckennatherium*. I tentatively ally them with *Adunator* on the basis of the metaconid on the M$_2$ of CM 82433, which appears to be swollen at the base more in accordance with Wal 368 than with USNM 9640. If anything, CM 82433 is *more* swollen than Wal 368, and is vaguely leaf-shaped in lingual view.

Adunator ?meizon Gingerich 1983

Figure 15, Table 8

Holotype. — UM 82023 (right dentary containing P$_3$-M$_3$) from Cedar Point Quarry, Wyoming.

Age and distribution. — Cedar Point Quarry (Ti3), northern Bighorn basin, Wyoming; Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a).

Description. — See Gingerich (1983).

Discussion. — The M$_2$ of CM 82433 is larger than that of *A. lehmani* (Wal 368), possesses a deeper, almost inversely conical talonid basin, and the hypoconulid is a bit stronger.

Compared to *A. amplus* (YPM-PU 14738), CM 82433 is smaller and more elongate, has a slightly more anteriorly-projecting paraconid, a weaker paracristid, a stronger hypoconulid, higher-crowned talonid cusps, and a metaconid that is shorter and more swollen at the base. Compared to *A. abditus*, the M_1 of CM 82433 is significantly larger, especially lengthwise.

CM 82433 is comparable to *A. meizon* (UM 82023, Gingerich 1983, known from Ti3, Cedar Point Quarry) in M_2 morphology, aside from the central portion of the M_2 being slightly pinched in CM 82433 and the talonid basin being slightly deeper and more inversely conical. It is within the observed size range of *A. meizon* both in the size of M_2 and in the ratio of M_2 to M_1, although there is enough overlap in these traits with *A. minutus* that CM 82433 also occupies the extreme upper range of that taxon. The paraconid is higher, more anteriorly-projecting, and more cusplike in CM 82433, more in accordance with the holotype of *A. meizon* (PU 13360, Jepsen 1930) than with the YPM *"Diacocherus" minutus* material, though there is a decent amount of variation in both taxa, as Secord (2008) notes.

Referred specimens.— CM 82433 (LM_2, M_1 fragment), CM 82434 (P_2, with fragments of P_3, P_1, and C_1).
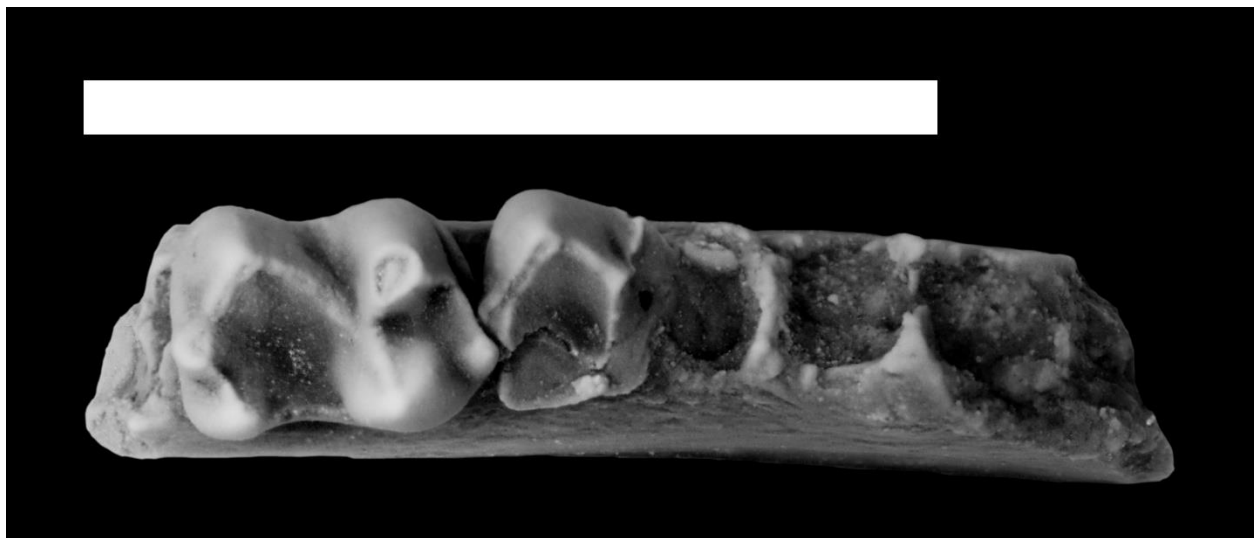
Figure 15. Dentition of *A. ?meizon* CM 82433 (LM$_2$, M$_1$ fragment). Scale bar = 5 mm.

	m1 length (mm)	m1 width (mm)	m2 length (mm)	m2 width (mm)
CM 82433	1.83*	1.24*	2.01	1.44

*estimated

Table 8. Dental measurements for *A. ?meizon* from Twelvemile Bonanza.

LITOLESTES Jepsen 1930

Litolestes ignotus Jepsen 1930

Figure 16, Table 9

Holotype. — YMP-PU 13352 (right dentary containing P$_4$-M$_3$ and associated incisor) from Princeton Quarry.

Age and distribution. — Various localities near Calgary, AB (Ti3-Ti4), Roche Percee, SK (Ti4); Princeton, Schaff, Y2K, and nearby quarries, northern Bighorn Basin, WY (Ti5); Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a).

Description. — The holotype was described by Jepsen (1930). Additional descriptions were provided by Krishtalka (1976), Schwartz and Krishtalka (1976), and Novacek et al. (1985).

Discussion. — The Twelvemile *Litolestes* material consists of a single isolated P_4 (CM 82435), which can be distinguished from *Adunator* most immediately by the short talonid, and less elongate dimensions overall. Currently, the sole recognized species is *L. ignotus*, known from Ti4 in Alberta and Ti5 in the Bighorn Basin. CM 82435 compares mostly favorably to the P_4 of the holotype (YPM-PU Jepsen 1930), though CM 82435 is less elongate and possesses a more lingually slanted paraconid (these features also distinguish it from PU 19387, figured in Novacek et al. 1985). Secord (2008) notes that measurements of length versus width in M_1 specimens of *L. ignotus* are highly but continuously variable, so unless given evidence otherwise, I assume the same is true of P_4. Secord also notes a high (but continuous) degree of variability in the development of the paraconid, some specimens apparently lacking a distinct paraconid altogether (Jepsen 1930 noted the same thing). I therefore tentatively refer this specimen to *L. ignotus*, despite the differences from the two specimens noted above.

Referred specimens.— CM 82435 (RP_4).
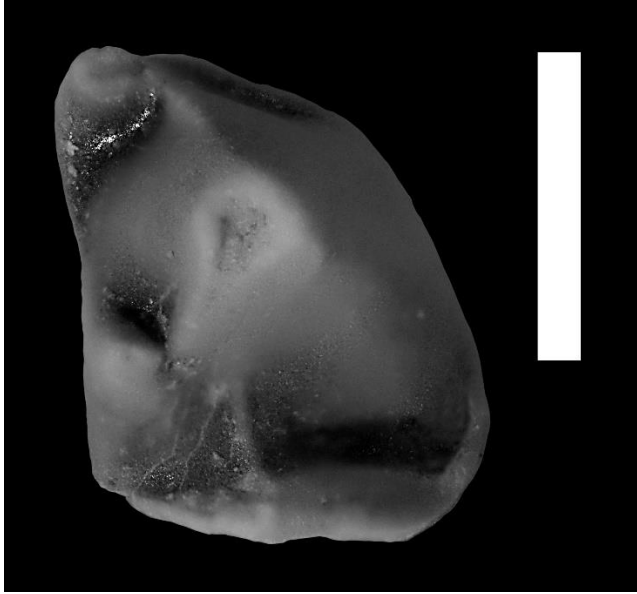
Figure 16. Dentition of *L. ignotus* CM 82435 (RP$_4$) from Twelvemile Bonanza. Scale bar = 1 mm.

	length (mm)	width (mm)
CM 82435 (p4)	1.62	1.34

Table 9. Dental measurements for *L. ignotus* from Twelvemile Bonanza.

Superorder FERAE Linnaeus 1758

Mirorder CIMOLESTA McKenna 1975

Family PALAEORYCTIDAE Winge 1917

Discussion. — Like "Insectivora", "Proteutheria" is a wastebasket group that encompasses many Paleocene mammals whose only feature in common is having relatively unmodified teeth more similar to Cretaceous eutherians than to more derived Paleocene eutherians. Palaeoryctids are relatively distinct, however, in possessing 'sub-zalambdodont' dentition in which the upper molars appear extremely broad buccolingually, and thinning considerably on the lingual side. The molar trigonids are similarly broad buccolingually, and the molar talonids are often miniscule and poorly-enclosed.

AAPTORYCTES Gingerich 1982

Type species. — *Aaptoryctes ivyi*, UM 77291 (articulated right maxilla containing P^3-M^3 and alveolus for P^2, right dentary containing C_1-M_3 and partial I_2) from UM locality FG-47.

Age and Distribution. — Dell Creek Quarry, Hoback Basin, western Wyoming (Ti4); UM locality FG-47, Bighorn Basin, northwestern Wyoming (*Plesiadapis simonsi* zone, Ti5b); SC-198/Fossil Hollow, Clark's Fork Basin, northwestern Wyoming (Ti5 or early Cf); Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a).

Discussion. — *Aaptoryctes* is distinctive among palaeoryctids in having large, bunodont upper fourth premolars (larger in area than the molars) with highly inflated paracone and protocone and otherwise very simplified topography with weak or indiscernible cingula and no (or very weak) additional cusps or crests.

?Aaptoryctes n. sp.

Figure 17, Table 10

Description and Diagnosis. — CM 77298 and KUVP 156542 are isolated right P^4 specimens. They are very similar in size and morphology to the P^4 of UM 77291, the holotype of *Aaptoryctes ivyi* and the only known specimen preserving the P^4. The Twelvemile Bonanza specimens differ from UM 77291 in having a less constricted waist between the paracone and protocone. UM 77291 also possesses vestigial parastylid and metastylid projections, whereas in the Twelvemile Bonanza specimens these structures are absent altogether.

Discussion. —The apical wear on the cusps are suggestive of a pantolestid. However, their morphology is much simpler than that of any known pantolestid or indeed any of the early, 'primitive' mammals. There are no cingula, not even a vestige of a stylar shelf, and no discernible metacone or any cusps other than the inflated paracone and a smaller protocone. CM 77298 is consistent in size with the P^4 of *Palaeosinopa dorri*, known from the late Tiffanian of Wyoming (Gingerich 1980), and is within the observed range of *P. reclusum*, known from Ti4 in Alberta (Rankin 2014). Otherwise, it is quite different in being much simpler, and in any case the holotype of *Aaptoryctes ivyi* also shows prominent apical wear.

The sole described species of *Aaptoryctes* is *A. ivyi*. Secord (2008) refers specimens from Croc Tooth Quarry (Ti4), Divide Quarry (Ti4), and the SC-243 anthills (Ti4?) to *Aaptoryctes* cf. *A. ivyi* (to which he also refers the Fossil Hollow specimens), but none of these specimens contain a P^4.

Referred specimens.— CM 77298 (LP^4), KU 156542 (LP^4).
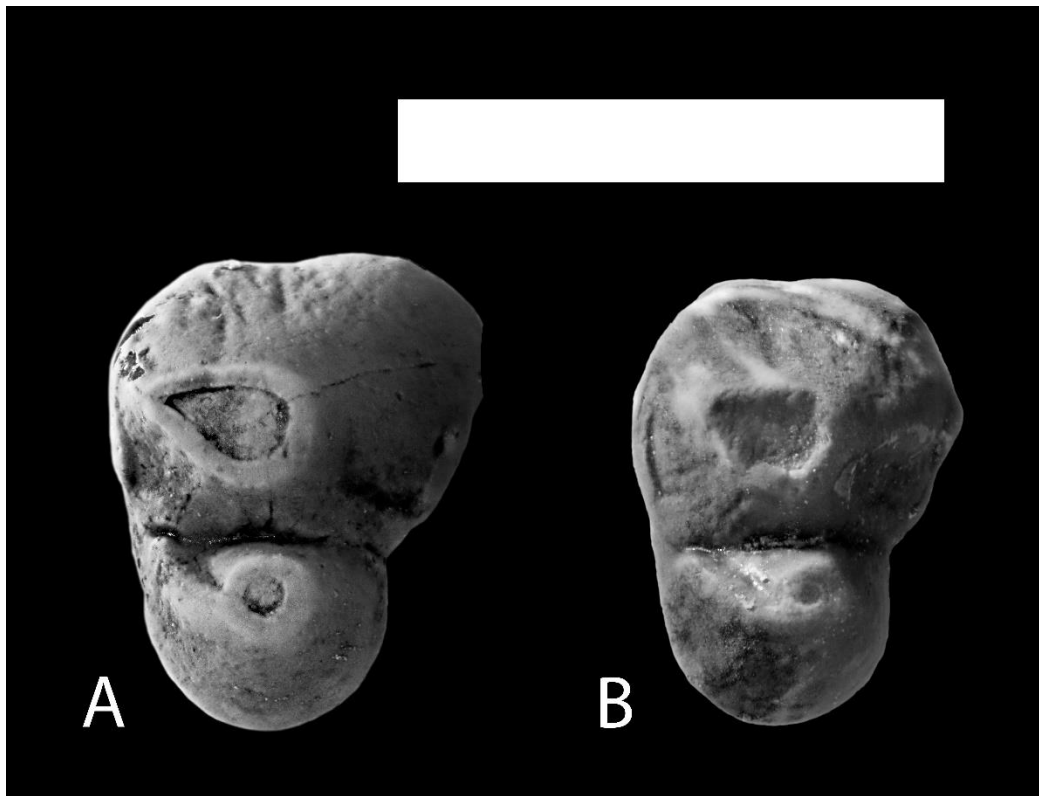
Figure 17. Dentition of *?Aaptoryctes n. sp.*, both in occlusal view. (A) CM 77298 (LP^4); (B) KU

156542 (LP^4). Scale bar = 5 mm.

	length (mm)	width (mm)
CM 77298	3.27	4.34
KUVP 156542	3.14	4.09

Table 10. Dental measurements for *?Aaptoryctes n. sp.*

Family PANTOLESTIDAE Winge 1917

Discussion. — Pantolestids known from relatively complete skeletal remains possess distinct features that make them well adapted to swimming and burrowing, rather like modern river otters and weasels. It is surprisingly difficult, however, to uniquely diagnose a pantolestid on dental and mandibular characters alone. The most commonly cited characters include a relatively abrupt mandibular angle and a posterior mental foramen below M_1 (Matthew 1909), with Matthew (1918) citing only the position of the posterior mental foramen. Subsequent authors have cited this feature as a synapomorphy of Pantolestidae (e.g. Kellner and McKenna 1996, Secord 2008). However, Paleocene and early Eocene taxa currently presumed to be pantolestids are variable in the exact placement of the posterior mental foramen; in some taxa it occurs below the anterior of P_4 and in others nearly as far back as the anterior of M_2. Also, many taxa referred to Apatemyidae, for example *Ottoryctes* and *Labidolemur*, also possess a posterior mental foramen below M_1. Another character sometimes cited is a deeply excavated masseteric fossa (e.g. Simpson 1927). However, other "proteutherian" taxa such as *Unuchinia dysmathes* and *Sinclairella dakotensis* (referred to Apatemyidae), *Aaptoryctes ivyi* (referred to Palaeoryctidae), and *Prodiacodon paucus* (referred to Leptictidae) also possess deeply excavated masseteric fossae. This feature is convergent across many groups of early and modern mammals; some species of the late Paleocene viverravid *Protictis*, for example, possess them as well. Matthew (1918), Van Valen (1966, 1967), and Gingerich (1980: 451) imply the diagnostic value of the height of the trigonid on M_3, which tends to be greater than that of M_1 and M_2 in taxa

assigned to Pantolestidae (although *Prodiacodon paucus*, referred to Leptictidae by Secord 2008, seems to share this feature).

Rather than possessing any unique dental or mandibular features, pantolestids instead seem to possess a unique *combination* of features that are otherwise plesiomorphic among many of the 'archaic' late Cretaceous and early Paleocene eutherian mammals or among eutherian mammals in general, including a posterior mental foramen below P_4 or M_1, deeply excavated masseteric fossa, stereotypically tribosphenic molars (which are slightly more specialized in many apatemyids), a primitive eutherian dental formula of 3.1.4.3 (reduced in apatemyids), a large M_3 with a trigonid higher than that of M_1 and M_2 (apparently also present in some leptictids), and extensive, even apical wear on the teeth.

PALAEOSINOPA Matthew 1901

Palaeosinopa sp.

Figures 18-19, Table 11

Discussion. — The Twelvemile Bonanza pantolestid material consists entirely of lower dentition. CM 77138 is an isolated lower molar, probably an M_1 based on the relatively expanded trigonid and the low paracristid. KU 156554 is a dentary fragment containing P_4-M_3. The apical wear on the molars of KU 156554 is extensive, especially M_1 and M_2, and the

posterior mental foramen is positioned below the posterior of P_4. M_3 is noticeably larger than M_1 and M_2, and likely higher-crowned.

To determine the systematic position of the Twelvemile Bonanza material within Pantolestidae and to assess the reliability of dental and mandibular characters for diagnosis, I undertook a branch-and-bound phylogenetic analysis in TNT v1.5 of various Paleocene and early Eocene taxa presumed to be pantolestids, using only dental and mandibular characters and taking the late Cretaceous taxon *Gypsonictops illuminatus* as the outgroup. The results of this analysis (Figure 18, Appendices C and D), which includes 56 original dental and mandibular characters, appear to show that there are no such characters capable of uniquely diagnosing any Paleocene genus of pantolestid, with the exception of two characters that differentiate all other pantolestid genera from *Propalaeosinopa*: (1) relatively large size and (2) relatively broad molar paraconids.

My diagnosis of the Twelvemile Bonanza material is therefore more phenetic than cladistic. The specimens possess a number of characters in common with *Palaeosinopa*, in contrast to *Leptonysson* and *Theylsia*, including (1) relatively weaker paracristds and protocristids on M_1; (2) relatively well-developed molar entocristids and well-enclosed talonids; (3) molar metaconids oriented posterior to (or subequal in anteroposterior position with) the protoconids, which constrict the anteroposterior extent of the lingual side of the molar talonids; (4) molar trigonids relatively anteroposteriorly uncompressed, occupying a greater portion of the tooth area; (5) molar hypoconids significantly lower than (or subequal in height to) the entoconids; and (6) a relatively deep dentary. All of these features apart from the well-developed molar entocristids, however, are shared with *Paleotomus*. Furthermore, the Twelvemile Bonanza specimens resemble *Paleotomus* (as well as *Propalaeosinopa*, *Leptonysson,* and *Thelysia*) in having a relatively gradual mandibular angle, and in possessing a posterior mental foramen close

to or below P$_4$ (though the precise position of the posterior mental foramen is highly variable among pantolestids even within genera). An equal case can probably be made for referring the Twelvemile Bonanza specimens to *Paleotomus*. I tentatively refer the material to *Palaeosinopa* on the grounds that the youngest known specimens of *Paleotomus* are from Cedar Point Quarry (Ti3), though I consider this a weak argument, and Gingerich (1980) mentions a lower molar from Dell Creek Quarry (Ti4) that could potentially belong to *Paleotomus*. The Twelvemile Bonanza specimens match the holotype of *Palaeosinopa dorri* (a taxon known only from maxillary remains; Gingerich 1980) reasonably well in size. Since no associated upper dentition has been recovered from Twelvemile Bonanza, I cannot rule out the possibility that these specimens do in fact belong to *P. dorri*.

Referred specimens.— CM 77138 (RM$_1$), KU 156554 (LP$_4$-M$_3$).
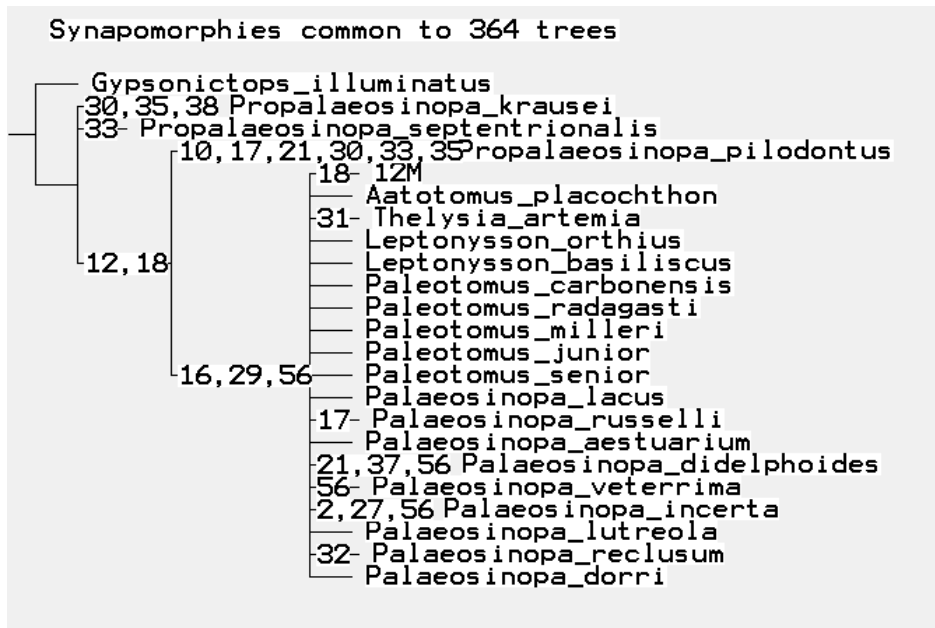
Figure 18. Results of a branch-and-bound phylogenetic analysis in TNT v1.5 of dental and mandibular features of Paleocene and early Eocene pantolestids. With the exception of *P.*

didelphoides, the included taxa are known only from dental, mandibular, and in rare cases partial maxillary remains. The middle Eocene genera *Pantolestes* and *Buxolestes*, known from more complete skeletal remains, are not included in this analysis.
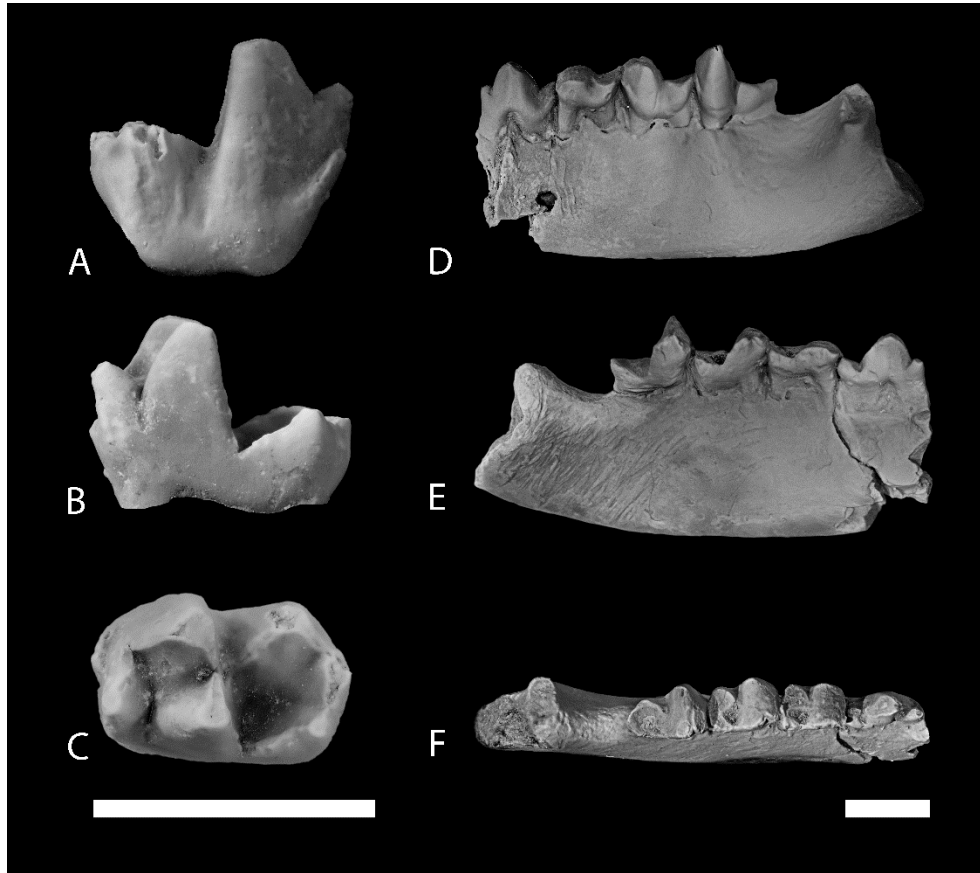
Figure 19. Dentition of *Palaeosinopa sp.* CM 77138 (LM$_1$) in (A) buccal, (B) lingual, and (C) occlusal views; KU 156554 left dentary fragment containing P$_4$-M$_3$ in (D) buccal, (E) lingual, and (F) occlusal views. Both scale bars = 5 mm; each pertains to the specimen in its respective column.

p4	m1	m2	m3

	length (mm)	width (mm)	length (mm)	width (mm)	length (mm)	width (mm)	length (mm)	width (mm)
KUVP 156554	4.60	2.21	4.02	2.72	4.59	3.13	4.79	3.29
CM 77138			4.65	2.90				

Table 11. Dental measurements for *Palaeosinopa sp.* from Twelvemile Bonanza.

PROPALAEOSINOPA Simpson 1927

Discussion. — *Propalaeosinopa* can be distinguished from later pantolestids most consistently by its smaller size and relatively narrow molar paraconids.

Propalaeosinopa septentrionalis

Figure 20, Table 12

Holotype. —AMNH 15543B (left dentary containg P_4 and alveoli for M_1-M_3) from the Paskapoo Formation, Alberta.

Age and distribution. — To2 (as far south as Gidley Quarry in Montana to as far north as the Bearspaw localities in Alberta) through Ti5 (Princeton and Schaff Quarries, WY); as far south as Swain Quarry, WY and the various Polecat Bench localities of Hartman (1986) during To3 and perhaps earliest Ti; possibly as far south as Cedar Point Quarry, WY during Ti3; consistent presence in Montana and Alberta from To2 through Ti4. Possibly present in the late Puercan, North Horn Formation, central Utah (Cifelli et al. 1995); Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a).

Description—Currently, *Propalaeosinopa septentrionalis* can be considered something of a wastebasket taxon for any *Propalaeosinopa* specimen not diagnosable as *P. pilodontus* (see Secord 2008) or *P. krausei* (see Rankin 2014). The Twelvemile Bonanza specimens are significantly larger than *P. krausei* and significantly smaller and less bunodont than *P. pilodontus*.

Discussion. — Fox (1990) proposed synonymizing *Diacodon septentrionalis* (Russell 1929) with *Propalaeosinopa albertensis* (Simpson 1927) to produce the novel combination *Propalaeosinopa septentrionalis*. Scott et al (2002) further proposed synonymizing *Propalaeosinopa septentrionalis* with all species classified by Simpson (1936) and (1937a,b) as *Bessoecetor* and declaring *Propalaeosinopa* to be a nomen dubium based on the type specimen (Simpson 1927) being of too poor quality to diagnosis the genus. I concur with Scott's decision to synonymize *Propalaeosinopa* and *Bessoecetor*, but do not necessarily agree with the logic behind suppressing the name *Propalaeosinopa*. I do not consider AMNH 15543B (Simpson 1927), the type specimen of the genus, to be any more or less diagnostic than many other specimens attributed to Pantolestidae. It possesses a large posterior mental foramen oriented under M_1, which has been the justification for assigning many specimens to that group (as in, for

example, *Thelysia artemia*, Kellner and McKenna 1996 and *Leptonysson basiliscus*, Secord 2008), as well as a deeply excavated masseteric fossa and extensive, even apical wear on the teeth. As I discussed above, these may not be the most reliable characters individually, but that is an issue that extends well beyond the nomenclatural status of *Propalaeosinopa*. Furthermore, the size of AMNH 15543B clearly links it with specimens attributed to *Bessoecetor*, at the expense of any other known pantolestid genera. If the type specimen of *P. albertensis* is diagnostic enough to synonymize with *Bessoecetor*, then by definition it is diagnostic enough to stand as the type for the genus, even if subjectively it isn't a particularly good type specimen. Many presumed pantolestid dental remains are not ideal for diagnosis. Under this nomenclatural regime, *P. septentrionalis*, *P. pilodontus*, and *P. krausei* are the three currently valid species of *Propalaeosinopa*. Given the enormous time span encompassed by the various specimens now under the umbrella of *P. septentrionalis*, I consider it likely that they do in fact represent multiple species, but I agree with Scott et al. (2002) that consistent evidence for separate species status is difficult to ascertain from the sparse dental remains currently published.

Referred specimens.— CM 72357 (RM$_3$, fragment of M$_2$), CM 89415 (LM$_2$-M$_3$).
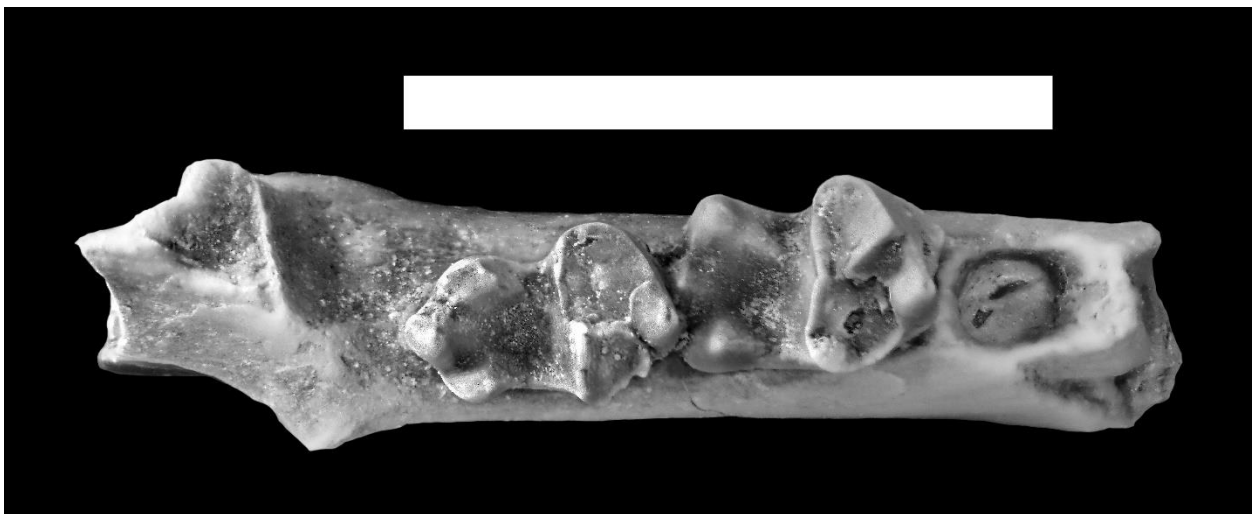
Figure 20. Dentition of *P. septentrionalis* CM 89415 (LM$_2$-M$_3$) in occlusal view. Scale bar = 5 mm.

		length (mm)	width (mm)
CM 72357	Rm3	2.45	1.61
CM 89415	Lm2	2.19	1.53
	Lm3	2.12	1.41

Table 12. Dental measurements of *P. septentrionalis* from Twelvemile Bonanza.

Order MULTITUBERCULATA Cope 1884

Superfamily PTILODONTOIDEA Cope 1887

Family PTILODONTIDAE Cope 1887

PROCHETODON Jepsen 1940

Type species. — *P. cavus*, YPM-PU 13925 (right dentary containing the base of I_1, P_3, and a fragment of P_4) from Princeton Quarry, northern Bighorn Basin, WY. The species comprising the genus *Prochetodon* are described in detail in Krause (1987) and Scott (2004).

Age and Distribution. — See Figure 22.

Discussion. — The Twelvemile *Prochetodon* material consists of an isolated P^3 (CM 72346), an isolated fragment of a P^3 (CM 89419), an isolated M^1 (CM 72347), an isolated P^4 (CM 77108), and a posterior P_4 fragment (CM 89418). All specimens of upper dentition possess the flat, untapered lateral profile, low crown, and lenticular cusps characteristic of *Prochetodon*. The P_4 specimen possesses the steep posterior angle, relatively shallow exodaenodont lobe, and relatively flat profile characteristic of *Prochetodon*.

Prochetodon n. sp.

Figures 21-23, Table 13

Description and Diagnosis. — CM 72346 is an RP^3 which possesses eight bunodont cusps, roughly equally developed and evenly apportioned into two rows of four. It is most similar in size and cusp formula to *Prochetodon cavus*. The lingual lobe and row of cusps in CM 72347 extends about two-thirds of the way up the tooth (between cusps three and four of the buccal and medial rows), and possesses a cusp formula of 9:9-10:10 (the presence of an anteriormost cusp in the medial row is ambiguous). It is most consistent with *P. cavus* in cusp formula and size. CM 77108 possesses nine medial cusps and one prominent anterobuccal cusp which is even with the anteriormost medial cusp, plus three tiny poorly-developed buccal cusps

extending about halfway down the tooth. It is most consistent with *P. cavus* in cusp formula, cusp position, and size.

In P^3 length, *Prochetodon n. sp.* is slightly less than two standard deviations lower than the mean of the YPM-PU *Prochetodon cavus* specimens (significance at the 95% level would entail a length for *P. n. sp.* of 3.04, which is two standard deviations from the mean). In width, it is a standard deviation and a half lower. *Prochetodon n. sp.* is nearly four standard deviations lower in the ratio of length to width than that of the YPM-PU *P. cavus* specimens, meaning the P^3 of *Prochetodon n. sp.* is significantly wider relative to its length than that of *P. cavus*. In P^4 length, *Prochetodon n. sp.* appears to be significantly smaller than *P. cavus*, but sample sizes are too low to attempt any statistics. No YPM-PU M1 specimens of *P. cavus* were available for direct comparison. If P^3 proves to be significantly smaller than *P. cavus* on a wider sampling, this preliminary data may indicate that *Prochetodon n. sp.* has a smaller P^3 compared to the remaining upper dentition, relative to *P. cavus*.
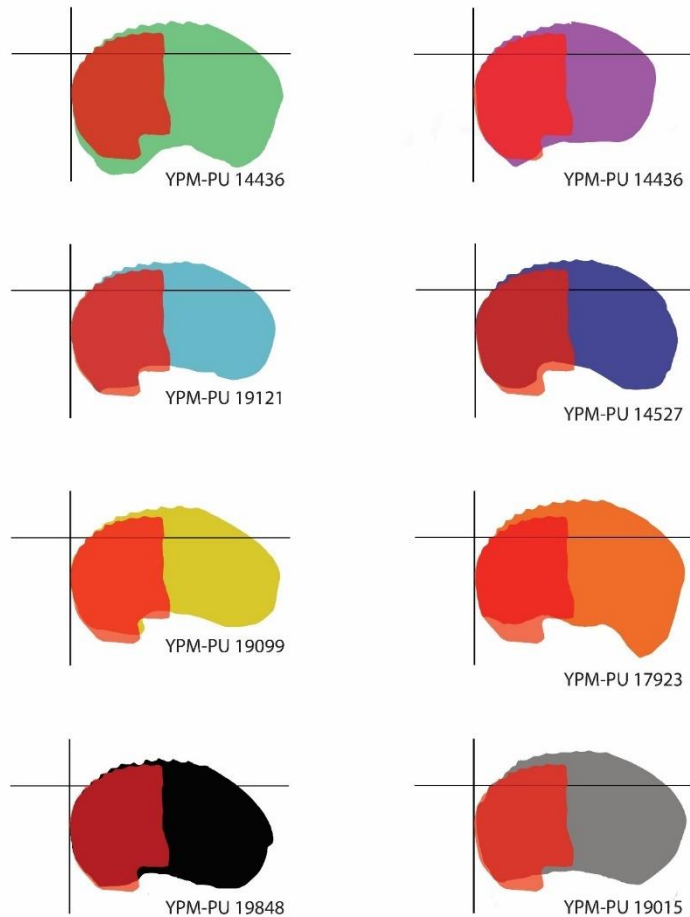
Figure 21. The P$_4$ of *Prochetodon n. sp.* CM 89418 (red insets) compared to P$_4$ specimens of *Prochetodon cavus* housed in the Yale Peabody collections.

CM 89418 consists of a posterior fragment of a P$_4$. The vaunted, steeply-arching, practically vertical posterior profile and distinctive posterior excavation on the buccal side makes it a good match for *Prochetodon*. However, it differs from *P. cavus*, *P. foxi*, and *P. taxus* in that the dorsal downslope of the blade appears to begin significantly earlier, at around the seventh or eighth cusp from the back (Figure 21). CM 89419 appears to be half of a P^3, containing two even rows

of cusps, one root which encompasses the whole area of the crown, and broken at the center. This is consistent with the P^3 of *P. cavus*, which in its entirety contains two roots and four rows of cusps in even rows. The specimen is also most consistent in size with *P. cavus*. It is nevertheless significantly smaller than *P. cavus*, making this taxon the smallest known species of *Prochetodon*.

To further assess the systematic position of *Prochetodon n. sp.*, I undertook a tentative phylogenetic analysis in TNT v1.5 based on 14 dental characters, employing a branch-and-bound search for the most parsimonious tree using *Baiotomeus douglassi* as the outgroup (see Appendices E and F). When characters 0,3,7,8,9, and 11 were treated as additive, the tree in Figure 22A was obtained.
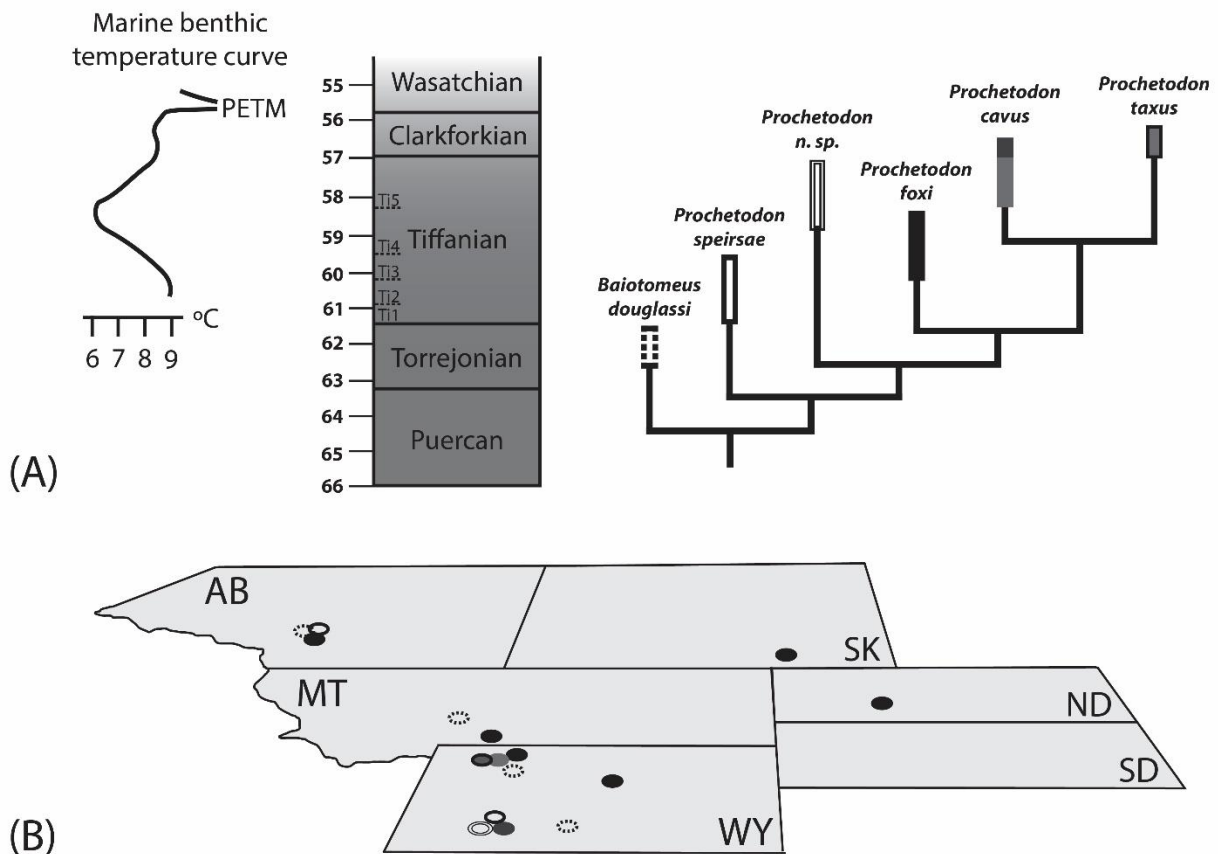
Figure 22. (A) Phylogeny, temporal distribution, and (B) geographic distribution of *Prochetodon* across North America during the Paleocene.

The oldest known species of *Prochetodon*, *P. speirsae*, is found at various localities near Calgary, Alberta (Scott 2004). The latitudinal range of the genus remained relatively stable in the Tiffanian and early Clarkforkian, apparently unaffected by shifts in global temperature. *Prochetodon cavus* appears in the Bighorn Basin at Ti5 (Krause 1987). *Prochetodon n. sp.* appears in southwestern WY in late Ti4 and Ti5 and disappears in the Clarkforkian. It appears to have been replaced at that time by *Prochetodon cavus*, previously only known as far south as the

Bighorn Basin. At the same time, *Prochetodon taxus* apparently replaced *Prochetodon cavus* in the Bighorn Basin (Krause 1987).

A few overriding phylogenetic trends can be discerned from the analysis:

1. P^4 cusps become increasingly gracile (*B. douglassi* → *P. speirsae* → *P. n. sp.* + *P.foxi* + *P. cavus* + *P. taxus*]

2. The dorsal downslope of P_4 begins further anteriorly in *P. foxi* + *P. cavus* + *P. taxus*

3. The P_4 exodaenodont lobe shallows (*B. douglassi* → *P. speirsae* → *P. n. sp.* + *P. foxi* + *P. cavus* + *P. taxus*]

4. P_4 serrations decrease in *P. cavus* + *P. taxus*

5. Buccal cusps on P^4 decrease in number (*P. speirsae, P. foxi* → *P. cavus* → *P. taxus*)

   (*P. n. sp.* appears to converge on the condition of *P. cavus*)

The anterior migration of the dorsal downslope of P_4 may perhaps have served to stabilize the degree of contact between P_4 and P^4 as the exodaenodont lobe shallowed, and both trends may have served to bring the locus of contact slightly forward. Similarly, a decrease in the number of P_4 serrations makes sense in combination with a reduction in the number of buccal cusps on P^4, against which the serrations would have occluded.

The apparently basal phylogenetic position of *Prochetodon n. sp.* relative to the stratigraphically earlier *P. foxi* suggests *P. n. sp.* may represent the northernmost member of a poorly-sampled southerly clade of *Prochetodon* that lies sister to the [*P. foxi* + *P. cavus* + *P. taxus*] clade.

Referred specimens.— CM 72346 (RP^3), CM 72347 (RM^1), CM 77108 (LP^4), CM 89418 (RP_4 posterior fragment), CM 89419 (P^3 fragment).
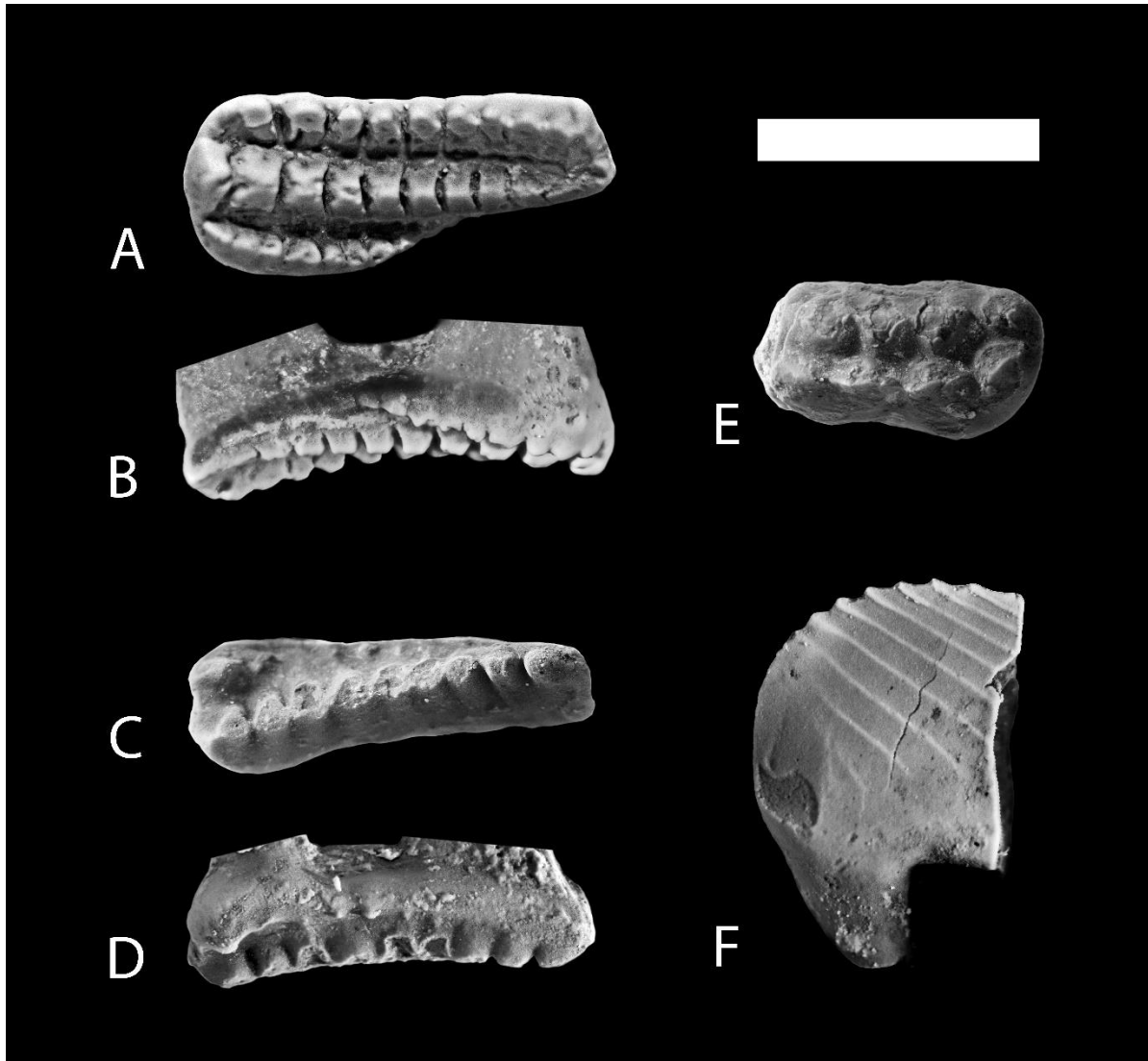
Figure 23. Dentition of *Prochetodon n. sp.* CM 72347, M^1 in (A) occlusal view and (B) buccal view; CM 77108, P^4 in (C) occlusal view and (D) buccal view; (E) CM 72346, P^3 in occlusal view;; (F) CM 89418, P_4 posterior fragment. Scale bar = 3 mm.

	P3			P4			P3/P4	M1		
	width	length	l/w	width	length	l/w	length	width	length	l/w
CM 72346	1.80	3.11	1.73							
CM 77108				1.43	4.36	3.05	0.71			

CM 72347								2.05	4.62	2.25
YPM-PU 14034	1.92	3.59	1.87							
YPM-PU 14336	1.89	3.61	1.91							
YPM-PU 19369	1.93	3.70	1.92	1.61	4.85	3.01	0.76			
YPM-PU 14433	2.06	3.77	1.83							
YPM-PU 14435				1.66	5.35	3.22				
YPM-PU average	1.95	3.67	1.88	1.64	5.10	3.12				
YPM-PU stdev	0.08	0.08	0.04	n/a	n/a	n/a				

p4	
length to peak 8th cusp	**height at peak 8th cusp**
2.35	3.63

Table 13. Dental measurements for *Prochetodon n. sp.* compared to *Prochetodon cavus* specimens housed in the Yale Peabody collections. All measurements in millimeters.

NEOPLAGIAULAX Lemoine 1882

Neoplagiaulax n. sp.

Figure 24

Holotype. — YPM-PU 14432 (right maxilla containing P^4-M^2 and a fragment of P^3), from Princeton Quarry, northern Bighorn Basin, WY.

Age and distribution. — Ti4 (Wannagan Creek Quarry, ND; Erickson 1991); Ti5 (Princeton Quarry, northern Bighorn Basin, WY); Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a).

Description and Diagnosis. — The Twelvemile Bonanza *Neoplagiaulax* material consists of an isolated LP^4 (CM 89417) which compares most favorably with *Neoplagiaulax hazeni*. The P^4 of *Neoplagiaulax hazeni* is characterized by nine medial cusps conjoined into a high ridge and increasing in height posteriorly such that the eighth cusp is the tallest; three or four anterobuccal cusps increasing in size posteriorly and occupying the anterior third of the tooth; and a cusp orientation such that the second anteriormost buccal cusp is even with the anteriormost medial cusp. CM 89417 matches all of these features, but differs from the holotype of *N. hazeni* in being about 20% smaller.

Referred specimens. — CM 89417 (LP^4).
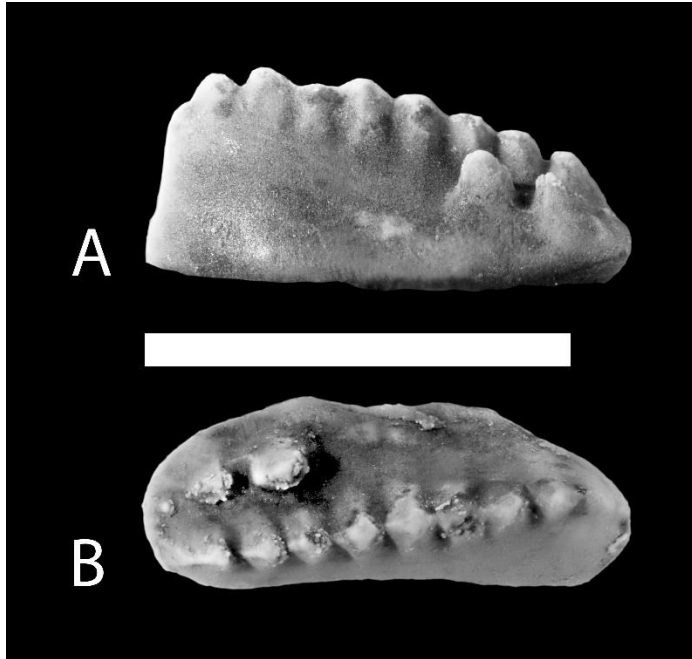
Figure 24. Dentition of *Neoplagiaulax n. sp.* L = 3.46 mm, W = 1.36 mm. Scale bar = 3 mm.

Order PLESIADAPIFORMES Simons and Tattersall 1972

Family CARPOLESTIDAE Simpson 1935

Carpolestes twelvemilensis Mattingly et al. 2017

Discussion. — Detailed descriptions and figures for *Carpolestes twelvemilensis* are provided in Mattingly et al. (2017).

Family MICROSYOPIDAE Osborn and Wortman 1892

?ARCTODONTOMYS Gunnell 1985

Discussion. — Rose (1981) distinguished *Microsyops simplicidens* from *Microsyops wilsoni* on the basis of its highly simplified P_4 compared to that of *M. wilsoni*. The paracristid of *M. simplicidens* is consistently weak or absent; the paraconid and metaconid are absent; and the talonid is simple, with a weak and discontinuous cristid obliqua, no ectocingulid, and only a single cusp. The trigonid of M_1 also differs slightly: in *M. simplicidens* the trigonid basin is a small circular point in the middle, whereas in *M. wilsoni* there is more open space between each cusp. Based on these characteristics, Gunnell (1985) erected the new genus *Arctodontomys*, with *A. simplicidens* as its type species. However, given that the P_4 of *M. wilsoni* is also less complex than that of most other microsyopid taxa (in which they are more nearly molariform), he also assigned *M. wilsoni* to *Arctodontomys*, yielding the new binomial combination *A. wilsoni*. Yet he also recruited, in part, *M. angustidens* into *Arctodontomys*, synonymizing the recruited specimens with *Diacodexis nuptus* to make *A. nuptus*. I find this a bit puzzling, as the P_4 of *M. angustidens* is practically molariform in its complexity. However, many specimens previously assigned to *M. angustidens* lack a P_4 metaconid (a feature that consistently distinguishes other *Arctodontomys*), and Gunnell found evidence of strong, stratum-dependent bimodality in this trait. He reported that "at UM locality SC-111, specimens of *Arctodontomys* have no trace of a

metaconid on P_4, while at UM locality SC-113, just 45 meters higher stratigraphically, specimens of *Microsyops* have a metaconid completely developed and distinct from the protoconid." The taxon *M. angustidens* had previously straddled this border. Therefore, those below were recruited into *A. nuptus*, and those above were retained as *M. angustidens*. In general, *Arctodontomys* occurs earlier than *Microsyops*. As of Gunnell (1985), the oldest known *Arctodontomys* taxon was *A. simplicidens*, which is Clarkforkian. Secord (2008) describes (but does not name) a new species in the Bighorn Basin, of which the only known specimen of lower dentition is YPM-PU 17945. This specimen was collected in Hail Quarry in 1954. The locality apparently cannot be relocated (Secord 2008) but is most likely Ti5, roughly coeval with Princeton Quarry. The P_4 is not present in this specimen, making a meaningful comparison with the Twelvemile specimens difficult. They are, at least, very similar in size to YPM-PU 17945, and similar in the morphology of M_1 and the small size of M_3.

?*Arctodontomys n.* sp. Secord 2008

Figures 25-31, Tables 14-18

Description. — The Twelvemile specimens consist of a left dentary fragment containing P_4 and M_1 (CM 72311) and a right dentary fragment containing P_4 and M_1 (CM 72312). The M_1 of CM 72312 is similar to that of *A. wilsoni*. The P_4 bears two talonid cusps and a strong internal cingulum, unlike *A. simplicidens*, but otherwise lacks any of the complexities of *A. wilsoni*. It is of comparable size to CM 72311, although the P_4 is a bit larger relative to the M_1.

The P_4 talonid of *?Arctodontomys n. sp.* is variable in how well it is enclosed; some specimens lack an external cingulid, resembling *A. simplicidens* in that regard; others more closely resemble *A. wilsoni*. CM 72311 allies in many ways with *A. wilsoni*. Like *A. wilsoni*, the P_4 is less complex than that of *Microsyops* or *A. nuptus* but more so than that of *A. simplicidens*. It bears two talonid cusps, a relatively strong cristid obliqua, an ectocingulid, and a paraconid and paracristid, although the latter two features are somewhat weak. It also possesses a fold of enamel running from protoconid to postvallid, though this too is rather weak. It is, however, a great deal smaller than *A. wilsoni* (less than a quarter of the size by crown surface area)—in fact it is virtually identical in size to *Navajovius kohlhaasae*. Additionally, unlike *A. wilsoni* and all other *Arctodontomys*, but like *Navajovius kohlhaasae*, CM 72311 possesses a clear trace of a metaconid (Figure 28C). CM 69336 also preserves an alveolus for what appears to be a tiny, vestigial canine, as in *Navajovius kohlhaasae* and the uintasoricines; the canine is completely lost in *Arctodontomys* and later microsyopines (Gunnell 1989). CM 69336 and other Big Multi Quarry specimens also show that this taxon retains a P_2 that is relatively small compared to P_3 (Figure 29, Table 18), a primitive trait among Microsyopidae in general (Bown and Gingerich 1972, Gunnell 1989).

Diagnosis. — *?Arctodontomys n. sp.* possesses highly reduced M_3 and M^3 relative to M_2 and M^2, respectively, compared to other microsyopids. *?Arctodontomys n. sp.* is smaller than any known species of *Arctodontomys*.

Discussion. — To gain insight into the systematic position of *?Arctodontomys n. sp.*, I undertook a branch-and-bound phylogenetic analysis in TNT v1.5 of several Paleocene and early Wasatchian microsyopids involving 37 dental and mandibular characters (see Appendix G and H). The analysis revealed two equally parsimonious trees, one with *?Arctodontomys n. sp.*

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nesting outside of a *Navajovius* + Microsyopine clade (Figure 25), and another with

?Arctodontomys n. sp. clustering in a polytomy with *Navajovius kohlhaasae* and *Choctawius*

mckennai (Figure 26).
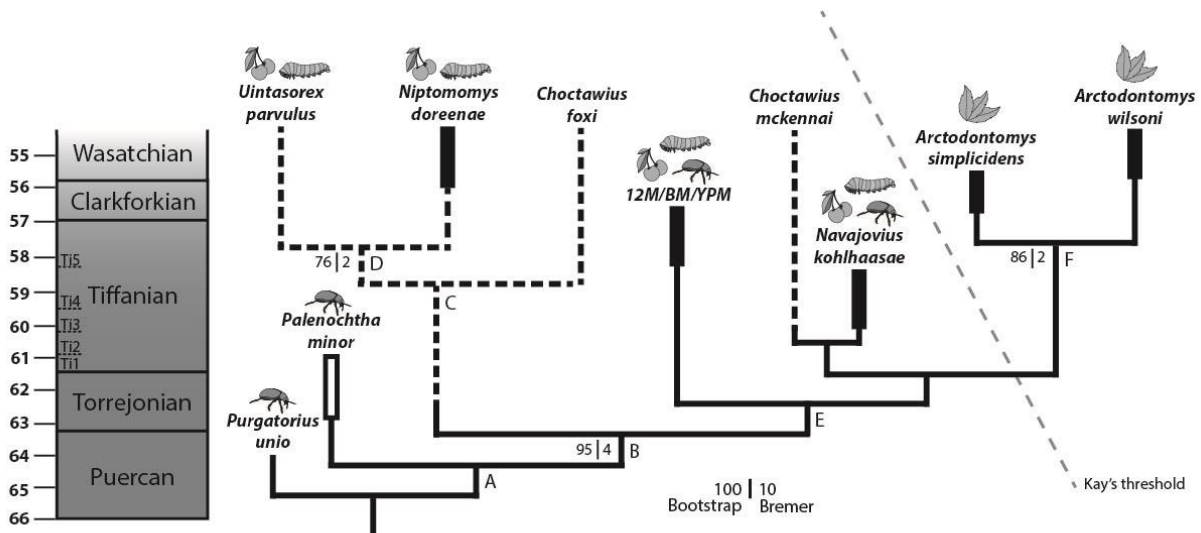
Figure 25. One of two equally parsimonious trees in a branch-and-bound phylogenetic analysis in TNT v1.5 of Paleocene and early Wasatchian microsyopids. *?Arctodontomys n. sp.* (12M/BM/YPM) nests just outside of a clade containing *Navajovius* and Microsyopinae. Dashed lines on the tree indicate taxa whose ranges occur past the earliest Wasatchian. Picture icons (insects with hard shells, soft larvae, berries, and leaves) indicate dietary inferences (see text).
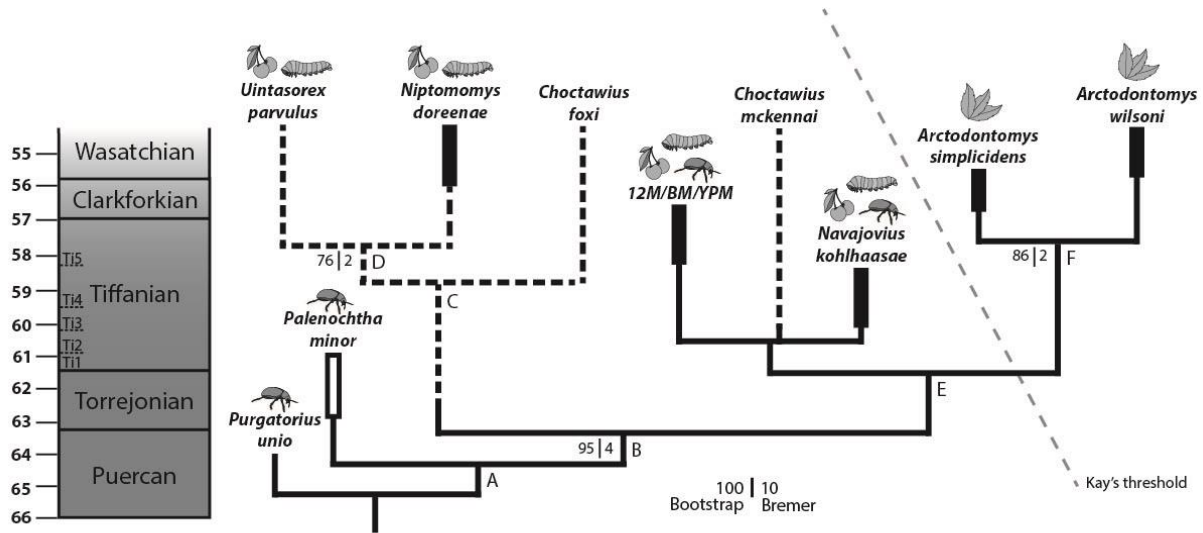
Figure 26. One of two equally parsimonious trees in a branch-and-bound phylogenetic analysis in TNT v1.5 of Paleocene and early Wasatchian microsyopids. *?Arctodontomys n. sp.* (12M/BM/YPM) clusters in a polytomy with *Navajovius kohlhaasae* and *Choctawius mckennai*, which appears just outside of Microsyopinae. Dashed lines on the tree indicate taxa whose ranges occur past the earliest Wasatchian. Picture icons (insects with hard shells, soft larvae, berries, and leaves) indicate dietary inferences (see text).

Clade	Synapomorphies
A	Lanceolate i1 where known; loss of i2; single-rooted p2; less anteriorly-projecting molar paraconids, paracristid prominent; diminutive size (*Arctodontomys* secondarily becomes much larger than *Purgatorius*)

B	p3 single-rooted (or roots variably appressed as in *N. kohlhaasae* and *?Arctodontomys n. sp.*); p3 reduced compared to p4; p4 metaconid weak or absent (secondarily regained in *N. doreenae*); dorsoventrally deep masseteric fossa and mandible (secondarily shallow in *N. kohlhaasae*); hypoconulid region twinned with entoconid, separated from hypoconid by notch; cristid obliqua contacts post-valled more buccally; buccal facies of hypoconid and protoconid less sharply columnar; cingulids of variable development distinctly underpin hypoflexid notch (often extend across much of buccal side of molar); hypocone shelf lingual to protocone and forms its own distinct lobe, especially on M1 (secondarily medial, smoothly contouring in *N. doreenae*); talonid relatively large compared to trigonid
C	Molar paraconids melded to base of metaconids, especially on m2 and m3; molar trigonids compressed, talonids especially large and bowl-shaped
D	Protoconids often reduced compared to metaconids; entocristids and entoconids often significantly higher than cristid obliqua and hypoconids; p4-m3 cusps particularly broad and blunt
E	Two small protocistids, anterior and posterior, form tiny secondary basin between protoconid and metaconid (secondarily absent in *A. simplicidens*); anterior molar trigonid basin relatively flat, ovulate, well-defined (least so in *A. simplicidens*)
F	Loss of canine; complete loss of p4 metaconid; large size

Table 14. Synapomorphies common to the phylogenetic trees shown in Figures 25 and 26. Clade labels correspond to those situated at the nodes in the figures.

In neither case does *?Arctodontomys n. sp.* nest clearly within *Arctodontomys*, but given the uncertainty in its position, additional material may yet demonstrate it to be the most basal member of that genus.

To gain insight into how *?Arctodontomys n. sp.* relates ecologically to other Paleocene and early Wasatchian microsyopids, I undertook a preliminary functional analysis (Table 15) of the same taxa by measuring "crushing potential" and "shearing potential", after Gunnell (1989) but modified as shown in Figure 27.

	m1		m2	
	"crushing" potential (trig. basin area + tal. basin area / total area)	"shearing" potential (sum of crest lengths / total perimeter)	"crushing" potential (trig. basin area + tal. basin area / total area)	"shearing" potential (sum of crest lengths / total perimeter)
UCMP 107406 (Purgatorius unio)	0.52	0.68	0.51	0.78
AMNH 35451 (Palenochtha minor)	0.54	0.77	0.57	0.81
UCMP 44081 (N. doreenae)	n/a	n/a	0.68	1.01
UCMP 44082 (N. doreenae)	n/a	n/a	0.59	0.91
UW 7125 (N. doreenae)	0.57	0.92	0.66	0.87

USGS 25496 (N. doreenae)	0.55	0.84	0.61	0.86
UCMP 96652 (U. parvus)	0.60	0.90	0.62	0.92
AMNH 55664 (U. parvus)	0.60	0.89	0.54	0.70
AMNH 17390 (Navajovius kohl.)	0.66	0.91	0.60	0.96
CM 72311 (12M)	0.62	0.85	n/a	n/a
CM 72312 (12M)	0.58	0.80	n/a	n/a
CM 69336 (BM)	0.60	0.92	0.62	0.99
CM 70723 (BM)	0.56	0.82	n/a	n/a
CM 71860 (BM)	0.55	0.94	0.58	0.89
UM 67214 (A. simplicidens)	entoconid broken off	entoconid broken off	n/a	n/a
UM 66178 (A. simplicidens)	0.55	0.76	entoconid broken off	entoconid broken off
KU 8520 (A. wilsoni)	0.59	0.79	0.58	0.82
UW 7194 (A. wilsoni)	0.51	0.88	0.52	0.83

Table 15. Analysis of crushing and shearing potential among selected specimens of microsyopids.
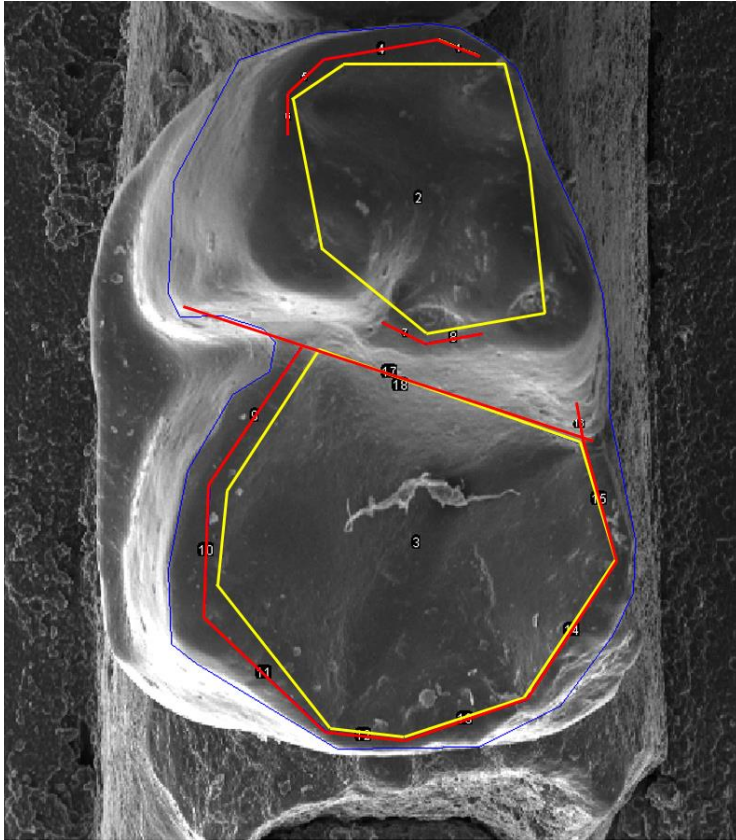
Figure 27. Measurement techniques for crushing and shearing potential in microsyopids. All dentition was measured in Fiji, using the landmarks shown in this figure or adapted as closely as possible. Measurements in red are for shearing potential (where the total combined length of the lines were calculated). Measurements in yellow are for crushing potential (where the area of the shape formed by the lines was calculated). Measurements in blue are for both total perimeter and total area (in the former, the total combined length of the lines were calculated; in the latter, the area of the shape formed by the lines was calculated).

Crushing potential remains largely the same across the board (a larger sample of *Purgatorius* and *Palenochtha* might show it to increase slightly in the microsyopids). The ratio of trigonid basin area to talonid basin area, however, decreases significantly in the uintasoricines, concentrating roughly the same total amount of crushing potential increasingly into the talonid (Table 16).

	m1		m2	
	[pr, met] / [hyp,ent] distance ratio	trigonid basin area / talonid basin area	[pr, met] / [hyp,ent] distance ratio	trigonid basin area / talonid basin area
UCMP 107406 (Purgatorius unio)	0.85	0.59	0.87	0.61
AMNH 35451 (Palenochtha minor)	1.02	0.68	0.68	0.48
UCMP 44081 (N. doreenae)	n/a	n/a	0.55	0.19
UCMP 44082 (N. doreenae)	n/a	n/a	0.60	0.28
UW 7125 (N. doreenae)	0.44	0.24	0.63	0.28
USGS 25496 (N. doreenae)	0.76	0.49	0.78	0.38
UCMP 96652 (U. parvus)	0.61	0.22	0.72	0.28
AMNH 55664 (U. parvus)	0.68	0.32	0.60	0.14
AMNH 17390 (Navajovius kohl.)	0.65	0.38	0.77	0.49
CM 72311 (12M)	0.61	0.43	n/a	n/a
CM 72312 (12M)	0.58	0.46	n/a	n/a
CM 69336 (BM)	0.56	0.43	0.71	0.39
CM 70723 (BM)	0.63	0.41	n/a	n/a

CM 71860 (BM)	0.62	0.47	0.73	0.44
UM 67214 (A. simplicidens)	entoconid broken off	entoconid broken off	n/a	n/a
UM 66178 (A. simplicidens)	0.70	0.52	entoconid broken off	entoconid broken off
KU 8520 (A. wilsoni)	0.65	0.50	0.65	0.31
UW 7194 (A. wilsoni)	0.62	0.38	0.68	0.33

Table 16. Analysis of talonid size versus trigonid size in selected specimens of microsyopids.

Likewise on the upper molars, the hypocone shelf contours more smoothly with the posterior edge of the trigon at least in *Niptomomys doreenae*, and hypocones are absent or considerably reduced, since there is no significant trigonid basin with which to occlude. The pre- and post-protocristae, however, are slightly more convex, approaching the protocone less sharply and linearly, seemingly to fit a larger talonid basin.

Uintasoricines reorganized their molar cristids to emphasize a long, relatively continuous shearing surface on the lingual side. This manifests in the melding of the paraconid to the protoconid and in the relatively high entocristid, which often exceeds the height of the cristid obliqua. Uintasoricines were also very small, among the smallest of all plesiadapiforms and indeed of all mammals. Taken together, these observations suggest a shift to a diet of more high-calorie, easy-to-obtain foods such as berries (to be processed by the loose cusp-in-fossa arrangement of the talonid) and larvae (to be processed by the long lingual shearing crest) (Strait 2001), and perhaps gum and sap as well. This would have been necessary to support the exceedingly high metabolism of such a small mammal.

Functionally, *Navajovius* and *?Arctodontomys n. sp.* appear to be similar, with a somewhat increased emphasis on crests rather than cusps compared to *Purgatorius unio* and *Palenochtha minor*. This may have allowed them to be more general in their diet, taking in occasional larvae and berries more efficiently; their smaller size compared to *P. unio* and *P. minor* is consistent with the need for this.

Arctodontomys passes Kay's threshold (Gunnell 1989), meaning its metabolic rate would have require it to emphasize leaves and larger fruit in its diet over insects. The slightly increased emphasis on shearing in the earlier, more generalist microsyopines may have been co-opted in the later ones from use in eating larvae to use in eating leaves or rind-heavy fruit. The broader trend of loss or reduction in anterior teeth is also consistent with this scenario. A shorter jaw would open and close more slowly but have increased leverage and a stronger bite force, more suitable for processing the tough cuticles of larvae; *Arctodontomys* continues this trend in the loss of the canine, and may again have co-opted such a shortening of the jaw for efficient processing of leaves. *Microsyops* and later, even larger taxa such as *Megadelphus* and *Craseops* emphasized shearing further still through the increasingly molariform P_4 (Gunnell 1989).

All known microsyopids appear to possess relatively dorsoventrally deep masseteric fossae and mandibles compared to *Purgatorius* and *Palenochtha*, except in *Navajovius* where they appear to be secondarily shallow (which *Navajovius* couples with autapomorphically high and sharp molar cristids, particularly the paracristid but also the entocristid).

In summary, the specimens at hand suggest that from relatively generalist late-Tiffanian microsyopid species such as *Navajovius* and *?Arctodontomys n. sp.*, two trends emerged: (1) *Arctodontomys* and *Microsyops* increased in size and co-opted the reduction in jaw length and the slight increase in shearing potential for use in eating leaves, and (2) uintasoricines, consistent

with a substantial decrease in size compared to other microsyopids, became increasingly specialized for eating small berries and larvae, and perhaps gum and sap.

If these dietary characterizations are correct, then the existence of generalist microsyopids coincides with a prominent dip in global temperatures around Ti4. Before that time, their closest relatives seem to have been species more dedicated to insectivory, such as *Purgatorius* and *Palenochtha*, and after that time, microsyopids were split between tiny-bodied berry/larvae specialists and larger-bodied leaf-eaters.

Referred specimens.— **From Twelvemile Bonanza:** CM 72311 (LP$_4$-M$_1$), CM 72312 (RP$_4$-M$_1$). **From Big Multi Quarry:** CM 69336 (LP$_4$-M$_2$, with fragments of the base of M$_3$ and complete or partial alveoli for P$_3$-P$_2$, C$_1$, and I$_1$), CM 69996 (RM^3), CM 70102 (LP$_3$-P$_4$, P$_4$ broken), CM 70705 (RM$_1$-M$_2$), CM 70713 (LM$_1$), CM 70723 (LP$_4$-M$_1$), CM 71269 (LM$_2$), CM 71820 (LM$_1$), CM 71860 (LP$_4$-M$_3$), CM 72196 (RP$_4$-M$_3$), CM 72254 (RM$_1$), CM 73770 (LM$_1$), CM 73830 (RP$_4$-M$_1$). **From Hail Quarry (1.5 miles east of Princeton Quarry)**: YPM-PU 17945 (RM$_1$-M$_3$).
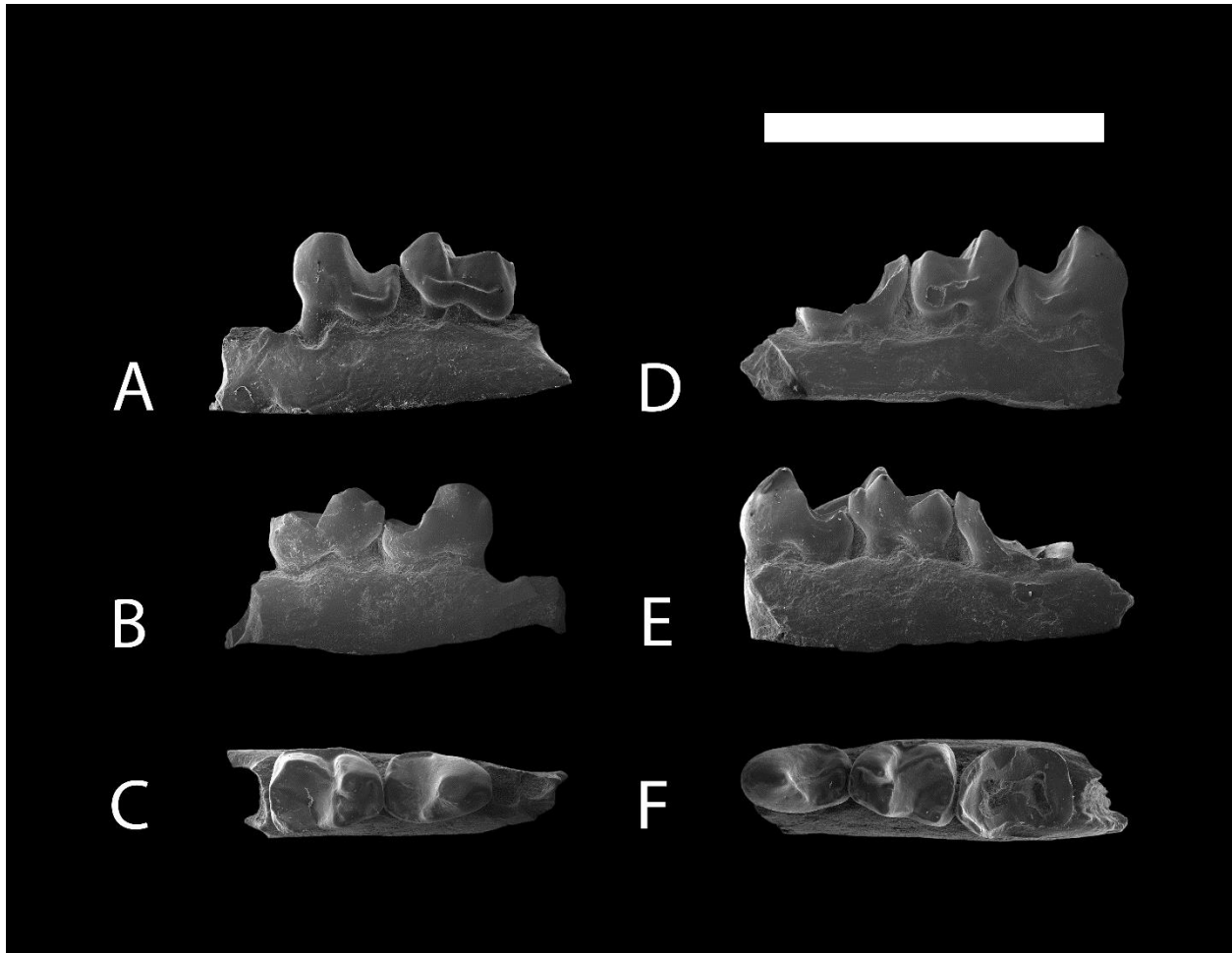
Figure 28. Dentition of *?Arctodontomys n. sp.* from Twelvemile Bonanza. CM 72311 (LP$_4$-M$_1$) in (A) buccal, (B) lingual, and (C) occlusal views; ; CM 72312 (RP$_4$-M$_1$) in (D) buccal, (E) lingual, and (F) occlusal views. Scale bar = 5 mm.

Figure 29. Dentition of *?Arctodontomys n. sp.* from Big Multi Quarry. CM 69336 (LP$_4$-M$_2$) in (A) buccal, (B) occlusal, and (C) lingual views. Scale bar = 5 mm.
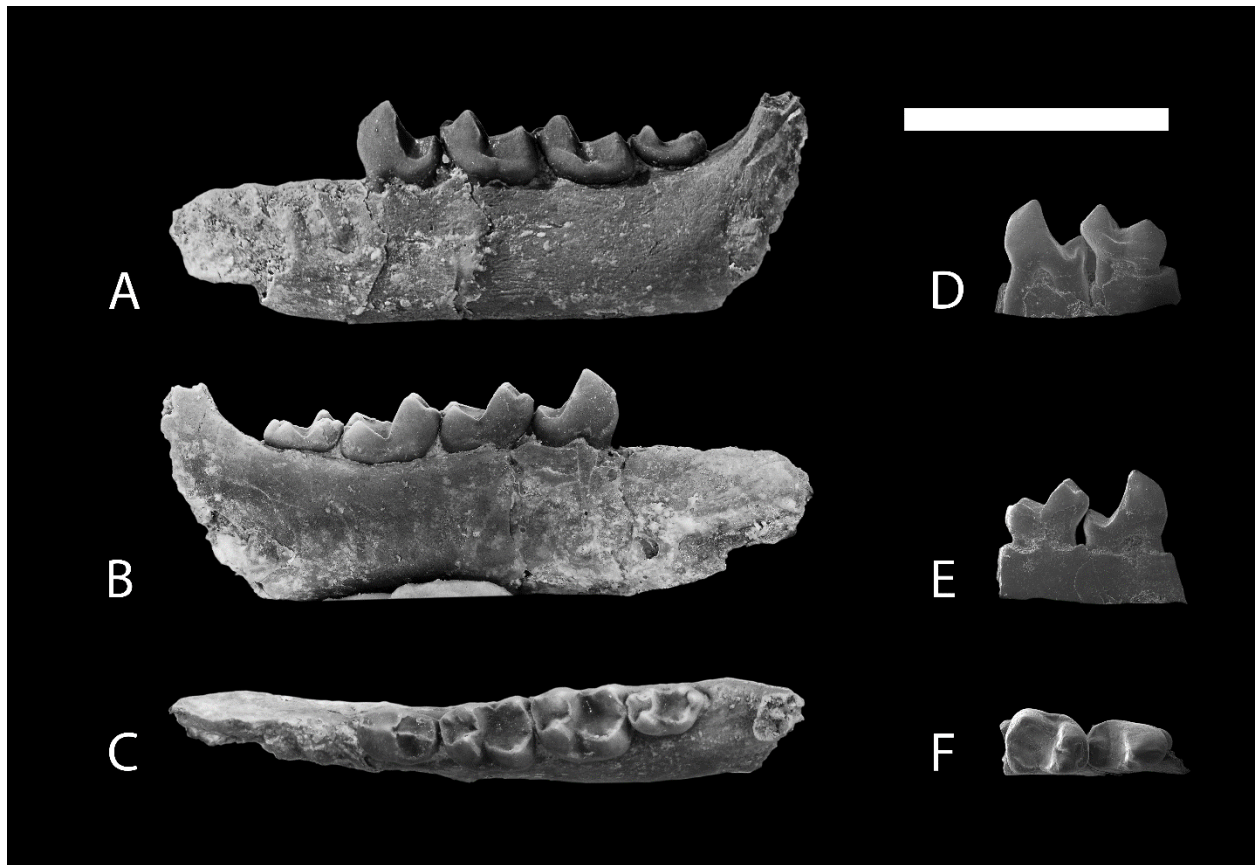
Figure 30. Dentition of *?Arctodontomys n. sp.* from Big Multi Quarry. CM 71860 (LP$_4$-M$_3$) in (A) buccal, (B) lingual, and (C) occlusal views; CM 70723 (LP$_4$-M$_1$) in (D) buccal, (E) lingual, and (F) occlusal views. Scale bar = 5 mm.
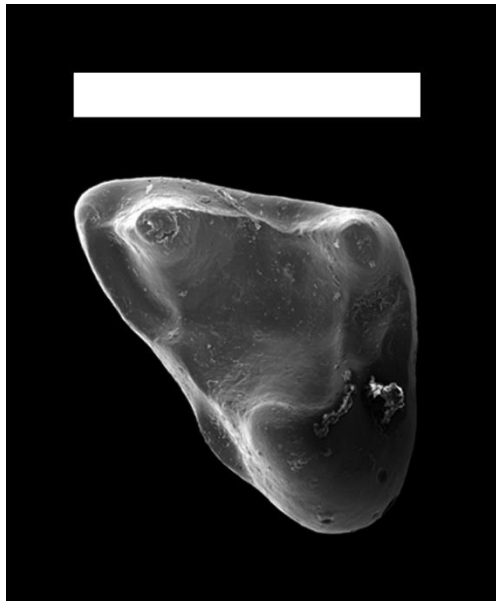
Figure 31. Dentition of *?Arctodontomys n. sp.* CM 69996 (RM^3) from Big Multi Quarry in occlusal view. Scale bar = 1 mm.

	p4 length	p4 width	m1 length	m1 width (trig)	m2 length	m2 width (trig)	m3 length	m3 width (trig)
CM 72311	1.60	1.01	1.70	1.02				
CM 72312	1.62	1.15	1.61	1.08				
CM 69336	1.68	1.04	1.82	1.19	1.90	1.38		
CM 70723	1.49	0.99	1.62	1.00				
CM 71860	1.61	0.99	1.78	1.21	1.90	1.35	1.50	0.91

	length	width
CM 69996 (M3)	1.18	1.03

Table 17. Dental measurements for *?Arctodontomys n. sp.* from Twelvemile Bonanza and Big Multi Quarry. All measurements in millimeters.

		p3/p4 length ratio		p2/p3 length ratio	
?A. n. sp.	CM 72311	0.59	p3 reduced	?	?
?A. n. sp.	CM 69336	0.57	p3 reduced	0.93	p3 ~larger to equal
?A. n. sp.	CM 71860	0.63	p3 reduced	0.89	p3 larger
?A. n. sp.	CM 73830	0.62	p3 reduced	0.72	p3 larger
?A. n. sp.	CM 70102	0.43	p3 reduced	0.99	p3 ~equal to p2
Purgatorius unio	UCMP 107406	0.80	p3, p4 close to equal	0.91	p3 ~larger to equal
Palenochtha minor	AMNH 35451	0.95	p3, p4 ~equal	0.54	p3 much larger
Niptomomys doreenae	USGS 25496	0.39	p3 reduced	?	p3 reduced*
Uintasorex parvulus	UCMP 96652	0.56	p3 reduced	1.04	p3 ~equal to p2
Navajovius kohlhaasae	AMNH 17390	0.34	p3 reduced	1.25	p3 reduced
A. simplicidens	UM 67214	0.48	p3 reduced	1.25	p3 reduced

A. wilsoni	UM 68321	0.39	p3 reduced	1.38	p3 reduced

Table 18. Premolar length ratios in selected specimens of microsyopids.

Family PAROMOMYIDAE Simpson 1940

PHENACOLEMUR Matthew 1915

Discussion. — The Twelvemile *Phenacolemur* material consists of one left dentary containing P_4–M_1 and an associated M_2 (CM 72344), one left dentary containing P_4–M_1 (CM 82419), and a right dentary containing P_4, alveoli for M_1, and the anterior alveolus for M_2 (72343). No upper dentition is represented.

Phenacolemur lower dentition is quite distinctive compared to other plesiadapiforms. The P_4 is triangularly tricuspid and enormously inflated in relation to M_1 and M_2 (almost twice as long and significantly wider at the talonid), with a very short but wide talonid (wider than the trigonid) and a tapered anterior, so that it resembles a bell (by contrast, the P_4 of *Ignacius* is puny). The M_1 and M_2 are short and practically square, in terms of length versus talonid width. The trigonid is highly reduced, being both shorter and narrower than the talonid (the latter being a general feature of plesiadapiforms). The paraconid and metaconid are highly reduced, compressed, and twinned on the lingual side, a feature it shares with some other plesiadapiforms but usually not to the same extreme. The molar talonid basins are quite deep, in contrast to the

shallower talonid basins of the closely-related paromomyid *Ignacius*. The M$_3$ of *Phenacolemur* is also distinctive, but no M$_3$ specimens are represented in this collection.

<div align="center">

Phenacolemur pagei Jepsen 1930

Figure 32, Table 19

</div>

Holotype. — YPM-PU 13286 (right dentary containing P$_4$-M$_2$ and alveoli for I$_1$ and M$_3$) from Princeton Quarry, northern Bighorn Basin, WY.

Age and distribution. — See Secord (2008) p. 126-127; Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a).

Description. — The holotype was described by Jepsen (1930). Additional material from Princeton Quarry was described by Simpson (1955) and Szalay and Delson (1979). Additional material from Clarkforkian localities was described by Rose (1981a).

Discussion. — The systematics of Eocene paromomyids were reviewed in Silcox et al. (2008). The Twelvemile specimens are significantly smaller than *P. praecox* and *P. fortior*, and the length/width ratios of M$_1$ and M$_2$ are closer to one. The P$_4$ is significantly more inflated compared to the M$_1$ than in *P. fortiori*, *P. simonsi*, *P. citatus,* or *P. willwoodensis*. *P. pagei* is one of only two *Phenacolemur* species known from the Paleocene, along with *P. archus* (Secord 2008). In the Twelvemile Bonanza specimens, the P$_4$ is much more inflated compared to M$_1$ than in *P. archus*. Overall, the size and morphology of P$_4$, M$_1$, and M$_2$ in the Twelvemile Bonanza specimens is consistent with *P. pagei*.

Referred specimens.— CM 72343 (LP$_4$), CM 72344 (RP$_4$-M$_2$), CM 82419 (LP$_4$-M$_1$), KU 156551 (RP$_4$-M$_1$).
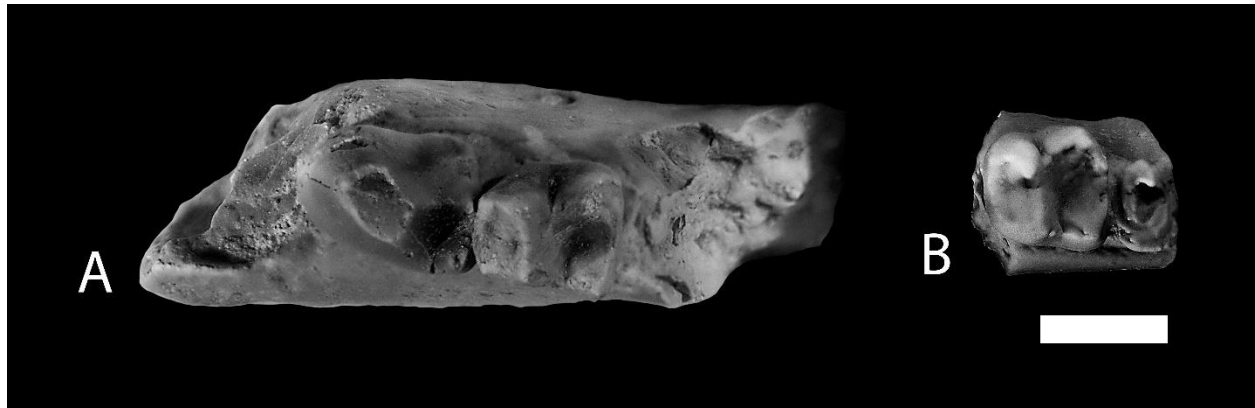
Figure 32. Dentition of *P. pagei* CM 72344 (A) RP$_4$-M$_1$ in occlusal view and (B) associated RM$_2$ in occlusal view. Scale bar = 2 mm.

		length (mm)	width (mm)
CM 72344	Rp4	2.67	2.03
	Rm1	2.33	2.01
	Rm2	2.25	1.94
CM 82419	Lp4	2.99	2.06
	Lm1	2.26	2.09
CM 72343	Rp4	3.18	2.21
KU 156551	Rp4	2.99	1.88
	Rm1	2.00	1.76

Table 19. Dental measurements for *P. pagei* from Twelvemile Bonanza.

Family PLESIADAPIDAE Trouessart 1897

PLESIADAPIS Gervais 1877

Plesiadapis fodinatus Jepsen 1930

Figure 33, Table 20

Holotype. — YPM-PU 13278 (right dentary containing I_1-, P_3, and M_1-M_2) from Princeton Quarry, northern Bighorn Basin, WY.

Age and distribution. — Ti4b and Ti5, various localities in Wyoming; apparently also present at UCM 92177, a locality in Colorado whose age is difficult to interpret.

Description. — Detailed descriptions were provided by Gingerich (1975, 1976).

Discussion. — The Twelvemile *P. fodinatus* material consists of various I^1, P^3, P^4, M^1, M^2, M^3, I_1, P_3, P_4, M_1, M_2, and M_3 specimens, usually isolated but often embedded in jaw fragments with other teeth. The upper incisors are unmistakably *P. fodinatus*, possessing two centroconules, a lateroconule, a secondarily reduced mediocone unmerged with the laterocone, a lenticular anterocone, and a bicusped posterocone. The lower incisors are plesiadapid, possessing a well-developed margoconid and margocristid. The P^3 is quite molarized and lacks a paraconule, and is most consistent in cusp formula and size with *P. fodinatus*. The M^3 bears a

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mesostyle and a high degree of crenulation characteristic of *P. fodinatus* and some later plesiadapids, and is most consistent in size with *P. fodinatus*. The M^2 and M^1 likewise bear mesostyles that distinguish them from earlier plesiadapids, and are most consistent in size with *P. fodinatus*. M_1 and an M_2 are highly crenulated, bear a mesoconid, and possess curved, triangular entoconid corners with the entoconid subsumed into the crest, characteristic of *P. fodinatus* and comparing favorably to the holotype. The M_3 is highly crenulated and possesses a large, squared, posterior lobe that is somewhat pinched in at the point where it connects with the hypoconid and entoconid, consistent with *P. fodinatus* and *P. dubius*. The size of the M_3 is consistent with *P. fodinatus*.

CM 72339 and CM 77279 each consist of an isolated P_4, and CM 77280 consists of a jaw fragment containing P_3 and P_4. These specimens possess clearly visible cristid obliqua and entoconids, in contrast to *P. churchilli*, but lack sufficient characteristics to distinguish them from *P. fodinatus* or *P. dubius*. However, given lack of evidence of separate species status from CM 72314 (a specimen containing P_3–P_4 and M_2–M_3) and given the low coefficient of variation of all P_4 material, I refer them to *P. fodinatus*. Only two P^3 specimens are represented in the current collection. One is part of a jaw fragment containing P^3–M^1 (CM 77281) and is little doubt *P. fodinatus*; the other is an isolated specimen and no evidence from the tooth itself suggests it belongs to a separate species from CM 77281. Likewise, only two P_3 specimens are represented in the current collection, one belonging to CM 77280 and another belonging to CM 72314. Again, no evidence suggests these two jaw fragments belong to separate species. Coefficients of variation for all upper molar specimens are quite low (3.03 for M^1, 2.42 for M^2, and 5.55 for M^3). The same is true for P_4–M_3 (4.57 for P_4, 5.20 for M_2, and 2.75 for M_3). The

highest coefficient comes from the P^4 specimens (7.72), but is probably an artifact of low sample size (only three).

Referred specimens.— CM 72313 (RP^4, M^3), CM 72314 (RP_3-M_3, no M_1), CM 72315 (LM^1-M^3), CM 72316 (RM_1-M_2), CM 72317 (RM_1-M_2), CM 72318 (RM_1-M_2), CM 72319 (RM_2-M_3), CM 72320 (LM_2-M_3), CM 72321 (LM_2-M_3), CM 72322 (LM_2), CM 72323 (RI^1), CM 72324 (RM^1), CM 72325 (RM^2), CM 72326 (RM^2), CM 72327 (RM^3), CM 72328 (LI^1), CM 72329 (LM^2), CM 72330 (RI_1), CM 72331 (RI_1), CM 72332 (RM_1), CM 72333 (RM_2), CM 72334 (RM_1), CM 72335 (RM_3), CM 72336 (RM_3), CM 72337 (RM_3 fragment), CM 72338 (LI_1), CM 72339 (LP_4), CM 72340 (LM_3), CM 72341 (LM_3), CM 77100 (LM^2), CM 77101 (LM^2), CM 77102 (RM^2), CM 77103 (RM^1), CM 77279 (RP_4), CM 77280 (LP_3-P_4), CM 77281 (RP^3-M^1), CM 77282 (RP^4), CM 77283 (LM^3), CM 77284 (RI^1), CM 77285 (RI^1), CM 82409 (RM^2), CM 82410 (LM^1, M^3), CM 82411 (RM^1), CM 82412 (RM^2), CM 82413 (RP^3), CM 82414 (RM_2 fragment), CM 82415 (RI_1), CM 82416 (RI_1), CM 82417 (LI_1), CM 86941 (RM_3), CM 86942 (LM_3), CM 86943 (LI_1), CM 89404 (LI^1), CM 89405 (RM^2), CM 89406 (RM^2), CM 89407 (RM^2), CM 89408 (RM_3 fragment), CM 89409 (LM^3), KU 155864 (RM_2), KU 156533 (RI^1), KU 156534 (RI_1), KU 156535 (RI_1), KU 156541 (RI^1), KU 156545 (LI_1), KU 156553 (RI^1), KU 156573 (LI_1), KU 156574 (LM^3).
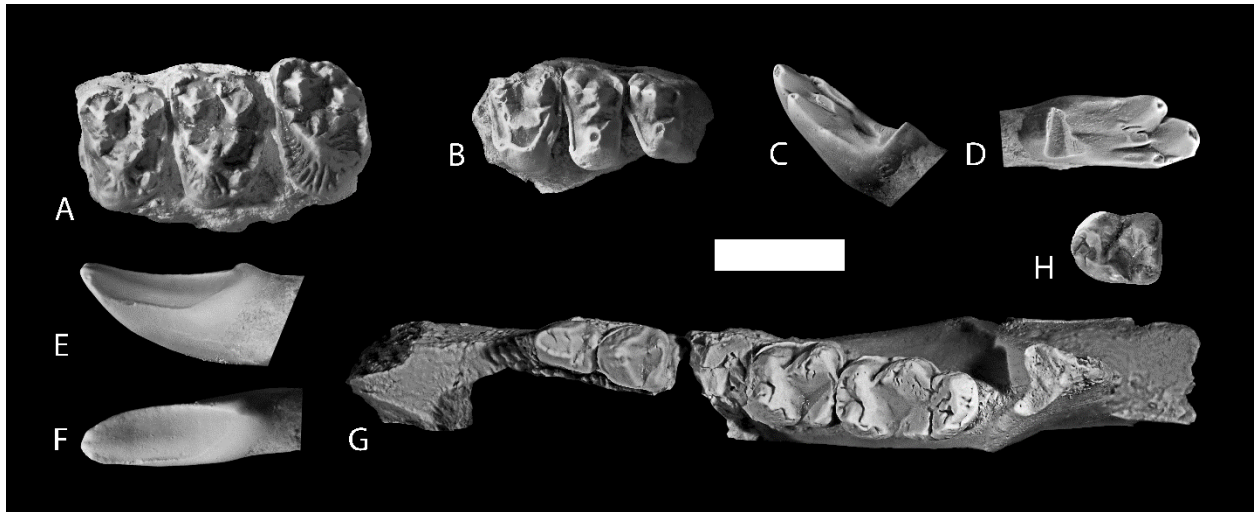
Figure 33. Dentition of *P. fodinatus* from Twelvemile Bonanza. (A) CM 72315 (LM$_1$-M$_3$) in occlusal view; (B) CM 77281 (RP$_3$-M$_1$) in occlusal view; CM 77284 (RI^1) in (C) buccal and (D) occlusal view; CM 82415 (RI$_1$) in (E) lingual and (F) occlusal view; (G) CM 72314 (RP$_3$-M$_3$, no M$_1$) in occlusal view; (H) CM 72334 (RM$_1$) in occlusal view. Scale bar = 5 mm.

	length (mm)	width (mm)
CM 77280 (p3)	2.64	2.11
CM 72314 (p3)	2.54	2.08
OR	2.54 - 2.64	2.08 - 2.11
Mean	2.59 ± 0.07	2.10 ± 0.02

	length (mm)	width (mm)	l*w	ln(l*w)

CM 77279 (p4)	3.24	2.31	7.48	2.01
CM 72314 (p4)	2.87	2.65	7.61	2.03
CM 72339 (p4)	2.77	2.29	6.34	1.85
CM 77280 (p4)	2.84	2.34	6.65	1.89
OR				
Mean	2.93	2.40	7.02	1.95
Std Dev	0.21	0.17	0.62	0.09
CV	7.20	7.07	8.85	4.57

	length (mm)	width (mm)	l*w	ln(l*w)
CM 72316 (m1)	3.34	3.05	10.19	2.32
CM 72317 (m1)	3.59	2.92	10.48	2.35
CM 72318 (m1)	3.50	2.71	9.49	2.25
CM 72332 (m1)	3.68	2.91	10.71	2.37
CM 72334 (m1)	3.51	2.75	9.65	2.27
OR				
Mean	3.52	2.87	10.10	2.31
Std Dev	0.13	0.14	0.53	0.05
CV	3.57	4.82	5.20	2.26

	length (mm)	width (mm)	l*w	ln(l*w)
CM 72314 (m2)	3.72	3.69	13.73	2.62
CM 72316 (m2)	4.06	3.56	14.45	2.67

CM 72317 (m2)	3.99	3.24	12.93	2.56
CM 72318 (m2)	3.63	2.95	10.71	2.37
CM 72319 (m2)	3.51	3.29	11.55	2.45
CM 72333 (m2)	3.93	3.44	13.52	2.60
KU 155864 (m2)	3.87	3.40	13.16	2.58
CM 72320 (m2)	3.25	3.12	10.14	2.32
CM 72321 (m2)	3.57	3.13	11.17	2.41
CM 72322 (m2)	4.18	3.55	14.84	2.70
OR				
Mean	3.77	3.34	12.62	2.53
Std Dev	0.29	0.23	1.62	0.13
CV	7.58	6.96	12.87	5.20

	length (mm)	width (mm)	l*w	ln(l*w)
CM 72314 (m3)	5.77	3.44	19.85	2.99
CM 72319 (m3)	5.43	3.15	17.10	2.84
CM 72335 (m3)	5.33	3.12	16.63	2.81
CM 72336 (m3)	5.02	3.17	15.91	2.77
CM 72337 (m3)	frag.	frag.	n/a	n/a
CM 77100 (m3)	5.50	3.35	18.43	2.91
CM 86941 (m3)	5.83	3.54	20.64	3.03
CM 89408 (m3)	frag.	frag.	n/a	n/a

CM 72320 (m3)	6.01	3.04	18.27	2.91
CM 72321 (m3)	5.54	3.31	18.34	2.91
CM 72340 (m3)	5.49	3.15	17.29	2.85
CM 72341 (m3)	5.22	3.30	17.23	2.85
CM 86942 (m3)	5.27	3.14	16.55	2.81
OR	5.02 - 6.01	3.04 - 3.54		
Mean	5.49	3.25	17.84	2.88
Std Dev	0.29	0.15	1.44	0.08
CV	5.27	4.72	8.07	2.75

	length (mm)	width (mm)
CM 82413 (P3)	2.67	3.65
CM 77281 (P3)	2.34	3.49
OR	2.34 - 2.67	3.49 - 3.65
Mean	2.51 ± 0.23	3.57 ± 0.11

	length (mm)	width (mm)	l*w	ln(l*w)
CM 77282 (P4)	3.12	4.36	13.60	2.61
CM 72313 (P4)	2.51	3.85	9.66	2.27
CM 77281 (P4)	2.49	4.07	10.13	2.32

OR				
Mean	2.71	4.09	11.13	2.40
Std Dev	0.36	0.26	2.15	0.19
CV	13.23	6.25	19.33	7.72

	length (mm)	width (mm)	l*w	ln(l*w)
CM 72315 (M1)	3.34	4.73	15.80	2.76
CM 72324 (M1)	3.35	4.52	15.14	2.72
CM 77103 (M1)	3.28	4.10	13.45	2.60
CM 77281 (M1)	3.05	4.35	13.27	2.59
CM 82410 (M1)	3.28	4.80	15.74	2.76
CM 82411 (M1)	3.34	4.71	15.73	2.76
OR				
Mean	3.27	4.54	14.86	2.70
Std Dev	0.11	0.27	1.19	0.08
CV	3.48	5.94	7.98	3.03

	length (mm)	width (mm)	l*w	ln(l*w)
CM 72325 (M2)	3.68	5.30	19.50	2.97
CM 72326 (M2)	3.58	5.48	19.62	2.98
CM 77102 (M2)	3.44	5.31	18.27	2.91

CM 82409 (M2)	3.49	5.01	17.48	2.86
CM 82412 (M2)	3.63	5.63	20.44	3.02
CM 89405 (M2)	3.53	5.74	20.26	3.01
CM 89406 (M2)	3.83	5.87	22.48	3.11
CM 89407 (M2)	3.39	5.23	17.73	2.88
CM 72315 (M2)	3.54	5.27	18.66	2.93
CM 72329 (M2)	3.65	5.18	18.91	2.94
CM 77101 (M2)	3.18	6.18	19.65	2.98
OR				
Mean	3.54	5.47	19.36	2.96
Std Dev	0.17	0.35	1.41	0.07
CV	4.81	6.36	7.30	2.42

	length (mm)	width (mm)	l*w	ln(l*w)
CM 72313 (M3)	3.38	4.94	16.70	2.82
CM 72327 (M3)	3.43	5.10	17.49	2.86
CM 72315 (M3)	3.37	5.34	18.00	2.89
CM 77283 (M3)	3.85	5.07	19.52	2.97
CM 82410 (M3)	3.54	5.62	19.89	2.99
CM 89409 (M3)	2.99	4.30	12.86	2.55
OR				
Mean	3.43	5.06	17.41	2.85

	length (mm)	width (mm)		
Std Dev	0.28	0.44	2.54	0.16
CV	8.13	8.77	14.58	5.55

	length (mm)	width (mm)
CM 82415 (i1)	7.53	2.37
KU 156545 (i1)	7.36	2.41

	length (mm)	width (mm)
CM 72323 (I1)	6.52	0.79
CM 77284(I1)	6.97	2.62

Table 20. Dental measurements for *P. fodinatus* from Twelvemile Bonanza.

Class MAMMALIA Linnaeus 1758

Infraclass METATHERIA Huxley 1880

Clade MARSUPALIA Illiger 1811

Order DIDELPHIMORPHIA Gill 1872

Family PERADECTIDAE Crochet 1979

PERADECTES Matthew and Granger 1921

Discussion. — Overall, the lower molars of Cretaceous and early Paleocene metatherians are quite similar to those of Cretaceous and many early Paleocene eutherians, in that they are fairly stereotypically tribosphenic. The most conspicuous differences typically include a hypoconulid strongly twinned to the entoconid, and strong, anteriorly-projecting paraconids equal in stature to the protoconids and metaconids.

Members of Didelphimorphia are distinguished from other "Ameridelphia" by rather subtle differences (Rose 2006, p. 81), and are contrasted with Australidelphia (Australian marsupials plus a relict South American sister group called microbiotheres). Australidelphia is distinguished mainly by features other than the lower molars, including limb morphology (Szalay 1982) and genome sequences. Marshall (1987) cites two distinguishing features of the lower molars that separate them from didelphids: trigonids narrower than talonids, and a reduced M_4.

Crochet (1979) distinguished didelphids and peradectids based on a number of features of the lower (and upper) molars. The lower molars of peradectids possess a twinned entoconulid and hypoconulid, where each cusp is of roughly equal size, relatively weak, and separated by a weak entoconid notch. Those of didelphids are less strongly twinned—the hypoconulid is very lingually oriented as in most metatheria, but it projects posterolingually and is separated from the entoconid by a strong entoconid notch. Further, in didelphids, the entoconid is much higher than the hypoconulid. Kristhalka and Stucky (1983) followed this distinction (though they classified Didelphini and Peradectini as subordinate tribes of Didelphidae) and provided descriptions and

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figures of *Peradectes* and several other taxa from these two groups. Horovitz (2009) offered additional fossil evidence supporting Peradectidae as a distinct clade that forms a sister relationship with Didelphidae.

<center>*Peradectes elegans* Matthew and Granger 1921</center>

<center>Figure 34, Table 21</center>

Holotype. — AMNH 17376 (left dentary containing P_2-M_4; right dentary containing P_1, P_3-M_4) from Mason Pocket, Colorado.

Age and distribution. — Ti2 (Saddle Locality, southwestern WY); Ti3 (various localities near Calgary, AB; Brisbane Locality, ND; Chappo Type Locality, southwestern WY: Cedar Point Quarry, northern Bighorn Basin, WY); Ti4 (Mason Pocket, CO); Ti5 (Princton Quarry and Jepsen Valley Quarry, northern Bighorn Basin, WY); Twelvemile Bonanza, Rock Springs Uplift, southwestern Wyoming (*Probathyopsis* zone, Ti5a); early Wasatchian (Sand Quarry, WY).

Description. — *Peradectes elegans* was described by Simpson (1935a) and Krishtalka and Stucky (1983).

Discussion. — The Twelvemile Bonanza *Peradectes* material consists of a single left dentary fragment (CM 89414) containing the talonids of M_3 and M_4, alveoli and partial remains of the respective trigonids, and the posterior alveolus of M_2. In their talonid morphology they ally with *Peradectes* rather than with the didelphids, and compare favorably with the type specimen of *P. elegans*, a species known from the Tiffanian and early Wasatchian of Colorado and Wyoming. The Twelvemile Bonanza specimen is consistent in M_4 talonid width with the

<center>106</center>

type specimen and UW 1104, both reported in Gazin (1956). However, the M_3 talonid seems to be narrower in the Twelvemile Bonanza specimen, in absolute value and relative to that of M_4. Additional and better preserved material is needed to determine whether this difference is meaningful, or whether other differences might be present. For now, I refer the material to *P. elegans*. The Twelvemile Bonanza specimen, like *P. elegans*, is larger than *P. pauli*, a species contemporary with *P. elegans* in the Tiffanian of Bison Basin. Other known species of *Peradectes* are generally smaller than *P. elegans*.

Referred specimens.— CM 89414 (LM$_3$-M$_4$).
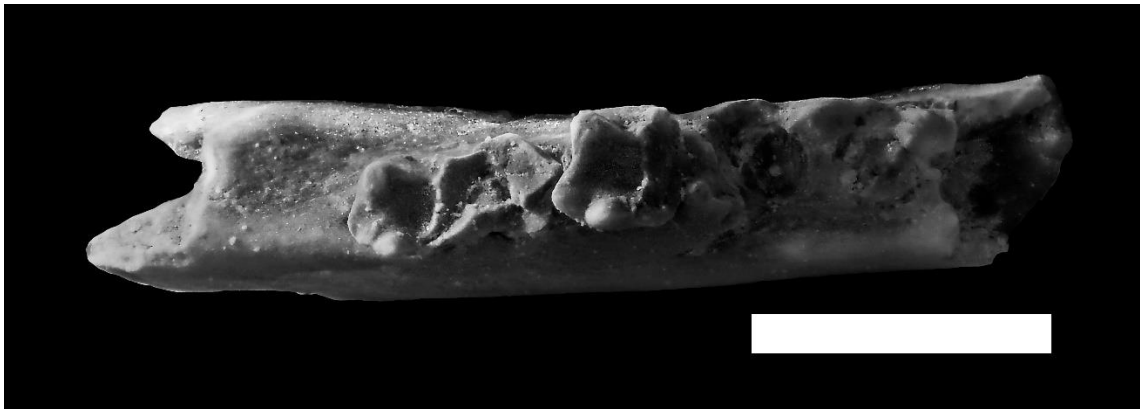
Figure 34. Dentition of *P. elegans* CM 89414 (LM$_3$-M$_4$).

	AMNH 17376 (*P. elegans* type)	UW 1104	CM 89414
m3 tal. width (mm)	1.05	1.0	0.88
m4 tal. width (mm)	0.8	0.7	0.75

Table 21. Dental measurements for *P. elegans* from Twelvemile Bonanza.

III.   Paleoecology

I have summarized the Twelvemile Bonanza Local Fauna in Table 21. It is largely similar to the contemporary Princeton Quarry fauna in the Bighorn Basin. Where species differ, they differ most often among the smaller-bodied taxa of both sites, consistent with the modern observation that smaller species tend to have smaller ranges (Gaston 1996), suggesting they tend to become reproductively isolated more often when they do disperse. Taxa present at Princeton Quarry but not Twelvemile Bonanza are also very small (with the conspicuous exception of carnivores, see below). The Twelvemile Bonanza specimens were all obtained by surface collection (with the exception of a single *Carpolestes twelvemilensis* specimen obtained by preliminary screenwashing in the summer of 2017). Surface collecting is known to significantly bias against smaller specimens, which break easier, wear down faster, and are much harder to see (Rose 1981b). Fortunately, an assemblage like Twelvemile Bonanza can still be compared to other assemblages obtained by surface collection and deposited in similar conditions. As the same biases should be at play and therefore cancel out, we can at least obtain a picture of relative differences.

Twelvemile Bonanza Local Fauna							
	Species	TNS	Freq.	MNI	Freq.	Ecotype	Habitat

"Condylarths"	*Thryptacodon pseudarctos*	5	0.03	2	0.04	omnivore	? terrestrial
	Lambertocyon n. sp.	2	0.01	1	0.02	omnivore	? terrestrial
	Aletodon conardae	13	0.08	4	0.08	omnivore	? terrestrial
	Phenacodaptes n. sp.	15	0.09	4	0.08	omnivore	? terrestrial
	Ectocion mediotuber	32	0.20	4	0.08	omnivore/herbivore	terrestrial
	Phenacodus grangeri	21	0.13	3	0.06	omnivore/herbivore	terrestrial
Plesiadapiforms	*?Arctodontomys n. sp.*	2	0.01	1	0.02	omnivore	? arboreal
	Phenacolemur pagei	4	0.03	3	0.06	frugivore?	arboreal
	Plesiadapis fodinatus	67	0.42	8	0.17	omnivore	? arboreal
	Carpolestes twelvemilensis	9	0.06	4	0.08	omnivore	arboreal

Group	Species					Diet	Habitat
Multituberculates	*Prochetodon n. sp.*	6	0.0 4	2	0.0 4	omnivore	? arboreal
	Neoplagiaulax n. sp.	1	0.0 1	1	0.0 2	omnivore	? arboreal
Pantolestids	*?Palaeosinopa sp.*	3	0.0 2	2	0.0 4	omnivore/piscivore	semi-aquatic
	Propalaeosinopa septentrionalis	2	0.0 1	1	0.0 2	omnivore/piscivore	semi-aquatic
Palaeoryctids	*?Aaptoryctes n. sp.*	2	0.0 1	2	0.0 4	?omnivore/piscivore	?
"Insectivores"	*Adunator ?meizon*	2	0.0 1	1	0.0 2	insectivore	? terrestrial
	Litolestes ignotus	1	0.0 1	1	0.0 2	insectivore	? terrestrial
Carnivorans	*Protictis schaffi*	3	0.0 2	2	0.0 4	carnivore	? terrestrial
Marsupials	*Peradectes elegans*	1	0.0 1	1	0.0 2	insectivore	arboreal
Dinoceratans	*Probathyopsis harrisorum*	1	0.0 1	1	0.0 2	herbivore	terrestrial

		19					
Total	**20**	**2**	**48**				

Table 22. Faunal composition of Twelvemile Bonanza. TNS = Total Number of Specimens; MNI = Minimum Number of Individuals.

Apart from the way the fossils were collected, another factor that might confound direct comparisons of individual localities is whether they represented the same type of environment. I compared the Twelvemile Bonanza specimens directly to three other surface-collected grey-green mudstone localities in southwestern Wyoming. The first two, Interstate Locality and Hallelujah Hill Locality are situated within 4.5 miles of each other (Winterfeld 1982), and are Ti4 assemblages that directly precede Twelvemile Bonanza in time. In all analyses that follow I have pooled the fossil collections from these localities to form one representative Ti4 sample. I also compared Twelvemile Bonanza to Mark's Locality (Anemone and Dirks 2009), estimated to be a late Cf1 or transitional Cf1-Cf2 assemblage, slightly younger than Twelvemile Bonanza.

A strong correlation has been observed in modern ecosystems between a given biome (open forest, plain, desert, and so on) and the ranked distribution of body masses of mammals living in that biome (Gunnell 1994, Wilf et a. 1998, Gingerich 1989 and references therein); such a plot is known as a cenogram. To gain insight into whether the four localities above represent the same type of environment (at least in the broadest sense), I have plotted cenograms for each locality in Figure 32.
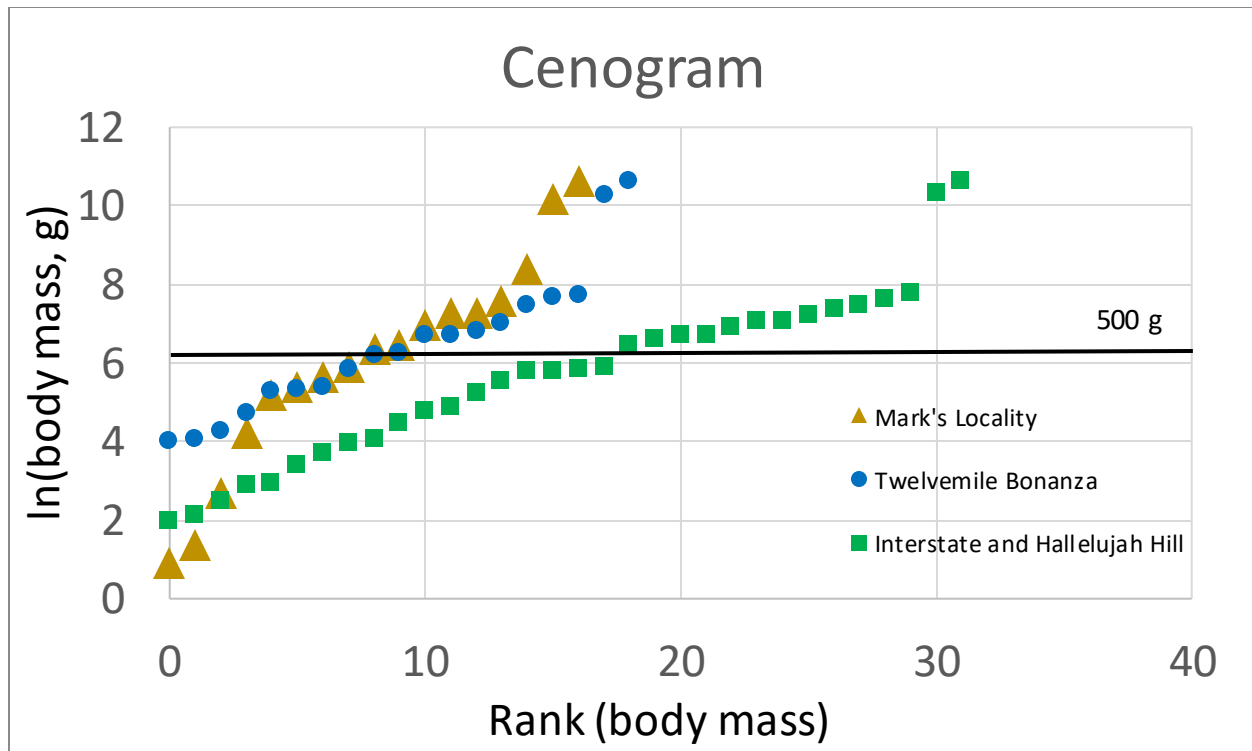
Figure 35. Cenogram plot for the Interstate and Hallelujah Hill localities, Twelvemile Bonanza, and Mark's Locality.

There are two important features to look for in a cenogram. The first is the behavior of each plot near 500 g (or an ln[body mass, g] of about 6.2), and the second is the slope of the line formed by medium-sized mammals (those between 500 g and 250 kg, which correspond to ln values between about 6.2 and 12.4) (Gingerich 1989). The value of the 500 g threshold corresponds to a similar one among primates called Kay's Threshold (Kay 1975). Below Kay's Threshold, primates are primarily insectivorous, or perhaps frugivorous, and herbivory is virtually non-existent. This is because small animals lose heat too quickly for a diet of leaves to support their metabolism. Herbivory becomes more and more common the further above Kay's Threshold a primate becomes, since bodies need proportionally fewer calories the larger they are. Cenogram analyses of modern ecosystems have revealed that more thickly-forested environments tend to

have high numbers of species in every size category (with the exception of very large animals, which are rare in every environment). The cenogram of a forest, therefore, will be relatively continuous, with no drastic vertical offsets near 500 g, and because there are many species in the "medium-sized" range, the slope within that range will be low. More open environments such as plains tend to have many fewer medium-sized species of mammals, especially between 500 and 600 g, perhaps because of the relative scarcity of plant mass. A cenogram will therefore show a drastic vertical offset between these values (since the x-axis is simply rank, there are no horizontal offsets) and a higher slope for medium-sized mammals.

The cenogram plots for each locality are largely similar with shallow slopes, particularly in the mid-range, and none contain any drastic vertical breaks at the 500 g threshold. This suggests they were probably all relatively well-forested floodplains and useful for direct comparison. Furthermore, their similar lithology (grey-green mudstone with little discernible paleosol development) indicates they probably all represented environments with frequent flooding and relatively poor drainage. During Ti4, global temperatures were lower compared to Ti5, the Clarkforkian, and much of the Eocene. This gives us a prime opportunity to test the influence of global temperatures on mammalian body mass and distribution in Wyoming during this time.

	Int + HH		Twelvemile Bonanza		Mark's Locality	
	TNS	MNI	TNS	MNI	TNS	MNI
Species Evenness (Whitaker Index)	16.03	26.58	10.95	22.15	11.57	25.75
Species Evenness (Shannon-Wiener Index)	2.59	3.07	2.41	2.78	2.17	2.67

Table 23. Species evenness calculations for Twelvemile Bonanza and Mark's Locality.

I compared species evenness among the localities by two measures. The Whitaker Index is a simple measure of the total sample size divided by the difference in log frequency between the most abundant and least abundant species. Lower evenness equals a greater difference, which equals a greater denominator and therefore a lower number. One shortcoming of the Whitaker Index is that it is only sensitive to unevenness between the high and low end of a frequency distribution. The Shannon-Wiener index is a bit more sophisticated: the frequency of each species in the fauna is multiplied by the natural log of that same frequency, and all of the natural log values are summed to obtain the final index. The Shannon-Wiener Index is therefore more sensitive to unevenness occurring at any point in a frequency distribution. Evenness in both the minimum number of individuals and the total number of specimens as measured by the Whitaker Index appears to be somewhat lower at Twelvemile Bonanza and can probably be attributed to the higher relative frequency of *Ectocion* and *Phenacodus*. Evenness in both the minimum number of individuals and the total number of specimens by Shannon-Weiner Index appears to decrease going from the Ti4 to the Cf1 localities. The apparent reason for this will be discussed later.

The average body masses of mammals in southwestern Wyoming seem to have been relatively stable throughout the span of time represented by these localities (Tables 23, 24, and 25). I have omitted *Probathyopsis harrisorum* from the Twelvemile Bonanza estimate and rodents from the Mark's Locality estimate, as these are immigrant taxa from Asia (Beard 1998, Beard and Dawson 1999, Bowen et al. 2002). The influence of immigration on Paleocene and early Eocene mammalian faunas is already well-documented and not what I wish to test here.

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The average body mass of the pooled Interstate and Hallelujah Hill localities appears to be significantly lower than those of Twelvemile Bonanza and Mark's Locality (between which there is no significant difference). I suspect, however, that this is due to the greater sample size and better representation of smaller taxa achieved by pooling the two localities together, which was necessary to obtain a comprehensive estimate of average body mass (the specimens in each individual locality would have been too fragmentary otherwise). When no M_1 of a taxon was available, I measured the closest available tooth and used proportions among the teeth in a more complete specimen (the holotype whenever possible) to reverse-calculate an estimated area for the M_1.

Int + HH pooled	avg ln [estimated body size (g)]	MNI	Freq. (MNI)	ln(body mass) * freq. MNI	Ecotype
Ptilodus sp.	5.22	4	0.04	0.23	small omnivore
Allocosmodon sp.	4.79	1	0.01	0.05	small omnivore
Ectypodus powelli	2.15	1	0.01	0.02	small omnivore
Ectypodus sp.	2.47	3	0.03	0.08	small omnivore
Mimetodon sp.	2.89	2	0.02	0.06	small omnivore
Mesodma sp.	3.39	1	0.01	0.04	small omnivore
Neoplagiaulax sp.	4.48	4	0.04	0.20	small omnivore
Dissacus sp.	7.64	2	0.02	0.17	Carnivore
Dipsalidictis sp.	6.46	1	0.01	0.07	Carnivore
Cyriacotherium	7.50	1	0.01	0.08	Herbivore
Litocherus lacunatus	4.88	6	0.07	0.33	Insectivore
Leptacodon sp.	2.92	1	0.01	0.03	Insectivore
Plagioctenodon sp.	3.69	1	0.01	0.04	Insectivore
Didymictis sp.	6.63	1	0.01	0.07	Carnivore
Protictis sp.	5.80	1	0.01	0.07	Carnivore
Propalaeosinopa sp.	5.79	3	0.03	0.20	Carnivore
Palaeosinopa sp.	6.70	1	0.01	0.08	Carnivore
Aaptoryctes sp.	5.85	1	0.01	0.07	Carnivore
Palaeoryctes cruoris	5.90	1	0.01	0.07	insectivore
Palaeoryctes sp.	4.08	2	0.02	0.09	insectivore

Labidolemur sp.	3.96	2	0.02	0.09	insectivore
Lambertocyon sp.	7.36	5	0.06	0.41	large omnivore
Thryptacodon sp.	7.23	5	0.06	0.41	large omnivore
Litomylus sp.	7.06	1	0.01	0.08	large omnivore
Aletodon conardae	6.91	4	0.04	0.31	large omnivore
Ectocion sp.	10.34	2	0.02	0.23	Herbivore
Phenacodus sp.	10.61	2	0.02	0.24	Herbivore
Carpocristes sp.	5.56	3	0.03	0.19	small omnivore
Ignacius frugivorus	6.70	3	0.03	0.23	Frugivore
Micromomys sp.	2.00	1	0.01	0.02	insectivore
Plesiadapis churchilli	7.79	16	0.18	1.40	large omnivore
Chiromyoides caesor	7.09	5	0.06	0.40	large omnivore
	32	87			

Average body mass	**6.07**
Std dev	**0.25**

Table 24. Body mass estimates for pooled taxa at the Interstate (Int) and Hallelujah Hill (HH) localities.

Twelvemile Bonanza	**avg ln [estimated body size (g)]**	**MNI**	**Freq. (MNI)**	**ln(body mass) * freq. MNI**

Phenacodus grangeri	10.64	3	0.06	0.68	herbivore
Ectocion mediotuber	10.28	4	0.09	0.87	herbivore
Plesiadapis fodinatus	7.74	8	0.17	1.32	large omnivore
Thryptacodon pseudarctos	7.50	2	0.04	0.32	large omnivore
Phenacolemur pagei	7.00	3	0.06	0.45	frugivore
Aletodon conardae	6.82	4	0.09	0.58	large omnivore
Phenacodaptes n. sp.	6.22	4	0.09	0.53	large omnivore
?Arctocyon sp.	7.67	1	0.02	0.16	large omnivore
Protictis schaffi	5.85	2	0.04	0.25	carnivore
Propalaeosinopa septentrionalis	5.32	1	0.02	0.11	carnivore
Palaeosinopa n. sp.	6.73	2	0.04	0.29	carnivore
Aaptoryctes sp.	6.72	2	0.04	0.29	carnivore
Carpolestes twelvemilensis	6.28	4	0.09	0.53	small omnivore
Microsyopid n. sp.	5.30	1	0.02	0.11	small omnivore
Prochetodon n. sp.	4.73	2	0.04	0.20	small omnivore
Neoplagiaulax n.sp.	4.25	1	0.02	0.09	small omnivore
Adunator ?meizon	3.99	1	0.02	0.08	insectivore
Litolestes ignotus	4.05	1	0.02	0.09	insectivore
Peradectes elegans	5.37	1	0.02	0.11	small omnivore
		47			

Average body mass	**7.07**
Std dev	**0.32**

Table 25. Body mass estimates for the taxa at Twelvemile Bonanza.

Mark's Locality (Cf1)	avg ln [estimated body mass (g)]	MNI	Freq. (MNI)	ln(body mass) * freq. MNI	
Phenacodus sp.	10.64	1	0.03	0.31	herbivore
Ectocion osbornianus	10.18	2	0.06	0.60	herbivore
Plesiadapis cookei	8.40	5	0.15	1.24	large omnivore
Plesiadapis dubius	7.58	4	0.12	0.89	large omnivore
Thryptacodon sp.	7.28	1	0.03	0.21	large omnivore
Phenacolemur pagei	6.95	2	0.06	0.41	frugivore

Carpolestes nigridens	6.48	4	0.12	0.76	large omnivore
Apheliscus nitidus	6.37	5	0.15	0.94	large omnivore
Didymictis sp.	5.92	1	0.03	0.17	carnivore
Palaeosinopa sp.	7.26	1	0.03	0.21	carnivore
Prochetodon cavus	5.19	2	0.06	0.31	small omnivore
Peradectes sp.	5.37	1	0.03	0.16	small omnivore
Diacocherus sp.	4.23	2	0.06	0.25	insectivore
Plagioctenodon sp.	2.67	1	0.03	0.08	insectivore
Parectypodus sp.	1.38	1	0.03	0.04	small omnivore
Nyctitheriidae	0.93	1	0.03	0.03	insectivore

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Average body mass	**6.61**
Stdev	0.36

Table 26. Body mass estimates for the taxa at Mark's Locality.

I further attempted to partition the taxa at each locality into six ecotypes: herbivore, large omnivore, carnivore, frugivore, small omnivore, and insectivore. As small taxa are poorly represented in surface collections and as the "frugivore" category consisted of a single taxon at all sites (*Ignacius* or *Phenacolemur*), I ignored the latter three categories to concentrate on the former three, testing for differences in average body mass between each site within ecotype. My criterion for placing an omnivore into the "large omnivore" category was an ln(body mass, g) value of five or more (approximately 150 grams). I chose this criterion based on the cenogram presented in Figure 6 of Wilf et al. (1998), where there seems to be a clean break in the plot of

estimated body masses at this value. Between the pooled Interstate/Hallelujah Hill localities and Twelvemile Bonanza, I found a significant difference in the distribution of carnivore body masses (p=0.04 when a two-sample t-test was applied). The average carnivore body mass at Mark's Locality is equal to that of Twelvemile Bonanza, so the same significant difference from the pooled localities applies. I doubt the difference can be attributed to greater sample size in the pooled localities, as collecting larger samples generally serves to *lower* average body masses through better representation of small taxa. The average body masses of the carnivores at each of the localities are presented in Tables 26, 27, and 28.

Int + HH pooled		MNI	Freq. (MNI) within ecotype	avg ln [estimated body mass (g)]	ln(body mass) * freq. MNI w.e.
carnivore	Dissacus sp.	2	0.40	7.64	3.06
	Dipsalidictis sp.	1	0.20	6.46	1.29
	Didymictis sp.	1	0.20	6.63	1.33
	Protictis sp.	1	0.20	5.80	1.16
Average					6.83
Std dev					0.90

Table 27. Body mass estimates for the pooled carnivore taxa at Interstate (Int) and Hallelujah Hill (HH).

Twelvemile bonanza		MNI	Freq. (MNI) within ecotype	avg ln [estimated body size (g)]	ln(body mass) * freq. MNI within ecotype
carnivore	Protictis schaffi	2	1.00	5.85	5.85
					5.85

Table 28. Body mass estimates for the taxa at Twelvemile Bonanza.

Mark's Locality		MNI	Freq. (MNI) within ecotype	avg ln [estimated body size (g)]	ln(body mass) * freq. MNI within ecotype
carnivore	Didymictis sp.	1	1.00	5.92	5.92
					5.92

Table 29. Body mass estimates for the taxa at Mark's Locality.

The pattern in body size is consistent with the basic premise of Bergmann's Rule: when temperatures decrease, body sizes increase. Relatively small, active carnivores may be especially susceptible to loss of body heat when temperatures are lower, compared to larger herbivores and omnivores. Carnivore diversity was also much higher in the pooled Interstate and Hallelujah Hill localities compared to Twelvemile Bonanza and Mark's Locality. It is also higher at Princeton Quarry.

There were no significant differences in either large omnivore or herbivore body masses among the localities. I have plotted the total body mass distributions of each locality together in Figure 32.
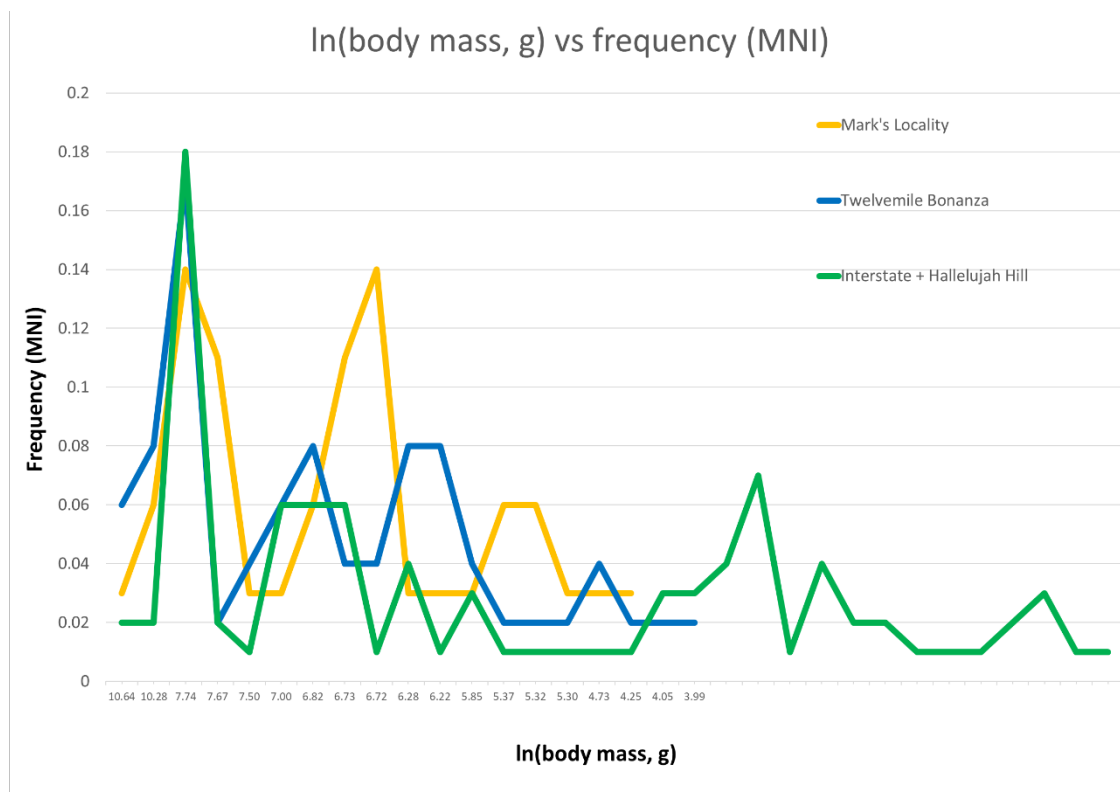
Figure 36. Body mass distributions for Interstate + Hallelujah Hill, Twelvemile Bonanza, and Mark's Locality.

The distributions themselves appear largely similar where they overlap; the relative frequency of larger species is uniformly a bit lower at the pooled Interstate and Hallelujah Hill localities, but that is probably because smaller species are better-sampled there. Four notable differences are (1) the blunting of the *Plesiadapis* peak at around 7.5-7.75 ln(body mass, g) going from Ti4 and Ti5 to Cf1; (2) the conspicuous second peak at around 6.5 ln(body mass, g) in the Mark's Locality distribution, corresponding to a body mass of about 665 g and specifically to the taxa *Carpolestes nigridens* and *Apheliscus nitidus*; (3) the higher relative frequency of taxa above 10 ln(body mass, g) at Twelvemile Bonanza, namely *Ectocion mediotuber* and *Phenacodus*

grangeri; and (4) a general increase in the tendency for body mass to cluster around a few peaks going from Ti4 to Cf1 (the most probable reason for the progressive decrease in species evenness previously discussed). One possible reason for this might be that there are more generalists at lower temperatures. This is also consistent with the dietary inferences I have made for the microsyopids (see discussion around Table 16).

The gradual decrease at these sites in the relative frequency of smaller-sized *Plesiadapis* over the course of the late Paleocene is consistent with a similar trend in the quarried and screenwashed localities of the Bighorn Basin (Secord 2008, appendices) (Table 29).

Locality	NALMA	*%Plesiadapis* (MNI)
Cedar Point Quarry	Ti3	25.7
Divide Quarry	Ti4	14.4
Princeton Quarry	Ti5	11.6
Y2K Quarry	Ti5	11.1
Holly's Microsite	Cf2	2.8

Table 30. Percentage of *Plesiadapis* from various localities in the Bighorn Basin, as determined from MNI.

The trend is also apparent in the more extensively quarried and screenwashed localities of southwestern Wyoming (Table 30).

Locality	NALMA	%Plesiadapis (MNI)
Chappo Type Loc.	Ti3	11.1

Big Multi Quarry	Cf1	0.8

Table 31. Percentage of *Plesiadapis* from Chappo Type Locality and Big Multi Quarry, as determined from MNI.

The trend makes sense if plesiadapids in general had an aversion to warmer temperatures. The lower absolute values at the more southerly localities further support this idea, as lower latitudes are always warmer on average than higher latitudes.

One factor complicates this interpretation. There are two species of *Plesiadapis* present at Mark's Locality: *Plesiadapis dubius* (MNI=4), at an ln(body mass, g) of around 7.6, and the larger *Plesiadapis cookei* (MNI=5), at an ln(body mass, g) of around 8.4. Only the smaller *Plesiadapis* reflects a decrease in relative frequency compared to Interstate, Hallelujah Hill, and Twelvemile Bonanza. The ecological partitioning of plesiadapids into smaller and larger forms is common in Clarkforkian localities, unlike Tiffanian localities (Gingerich 1976).

The high relative frequency of large herbivores at Twelvemile Bonanza, compared to the localities preceding and following it, is also difficult to interpret. *Ectocion* and *Phenacodus* are so common in late Tiffanian faunas that I felt it useful to broaden my comparisons of large herbivores beyond the four localities I have discussed so far. In order to compare the surface collections more directly with the quarried and screenwashed collections, I attempted to normalize them to each other by only including taxa in my percentage counts whose ln(body mass, g) values were greater than five. This was done to account for the low representation of small taxa in surface collections. Applying this method, I obtained very similar %herbivore values for Big Multi Quarry (12.50%), an extensively quarried and screenwashed locality, and Mark's Locality (11.11%), a surface collection located within 18 miles of the former and

representing the same period of time. This gives me some confidence that applying this method allows me to compare these two types of collections more directly. Table 31 contains %herbivore values for multiple late Paleocene localities in southwestern Wyoming and the Bighorn Basin in northern Wyoming.

NALMA	Locality (SW WY)	%herbivore	Locality (Bighorn Basin, WY/Carbon County, MT)	%herbivore
Ti4	Int + HH	8.6	Divide Quarry	14.1
Ti5	Twelvemile Bonanza	17.1	Princeton Quarry	5.7
Cf1	Big Multi Quarry	12.5	Bear Creek Quarry	3.7
	Mark's Locality	11.1	Rose (1981a) locs.	>60
Cf2	Buckman Hollow*	>60	Holly's Microsite (SC-188)	7.5
			Rose (1981a) locs.	>60
Cf3	███████████████		Rose (1981a) locs.	>60

*No comprehensive, up-to-date fauna list exists for Buckman's Hollow, a surface collection, but *Phenacodus* and *Ectocion* comprise a significant majority of the specimens described in Gazin (1956) and Holroyd and Rankin (2014).

Table 32. Percent herbivore values for multiple late Paleocene localities in southwestern Wyoming and the Bighorn Basin in northern Wyoming.

There is reason to think the relative frequency of large herbivores at Divide Quarry might be anomalously high: the taphonomic history of the deposits may bias them toward larger taxa in a way that is difficult to correct after the fact. Unlike all of the other localities analyzed here, which are mudstone deposits, Divide Quarry is a "clay-gall" deposit (Secord 2008). According to Bartels (1987), clay-gall deposits most likely formed when dried, abandoned river channels were suddenly reclaimed by the river. The high-energy flooding action would have ripped up any clay clasts and fossils that had accumulated in the channel, destroying smaller fossils and redepositing larger ones. The high relative frequency of herbivores at Divide Quarry might therefore be an artefact of preservation.

In any case, the numbers are difficult to interpret. The high relative frequency of herbivores at Twelvemile Bonanza, compared to the relatively low normalized frequency at Princeton Quarry and subsequent high relative frequency at the Rose (1981a) localities, might have been suggestive of a northward range expansion in response to increasing global temperatures. However, relative frequencies in southwestern Wyoming are subsequently low at Mark's Locality and Big Multi Quarry (even after normalization), inconsistent with the idea of a climate-driven range expansion. Herbivore relative frequency is also low (perhaps for taphonomic reasons) at Holly's Microsite.

The apheliscid "condylarth" *Aletodon* appears to have tracked warmer temperatures in a less ambiguous way throughout the late Paleocene, expanding and contracting its latitudinal range as temperatures rose and fell (Figure 33A-B).
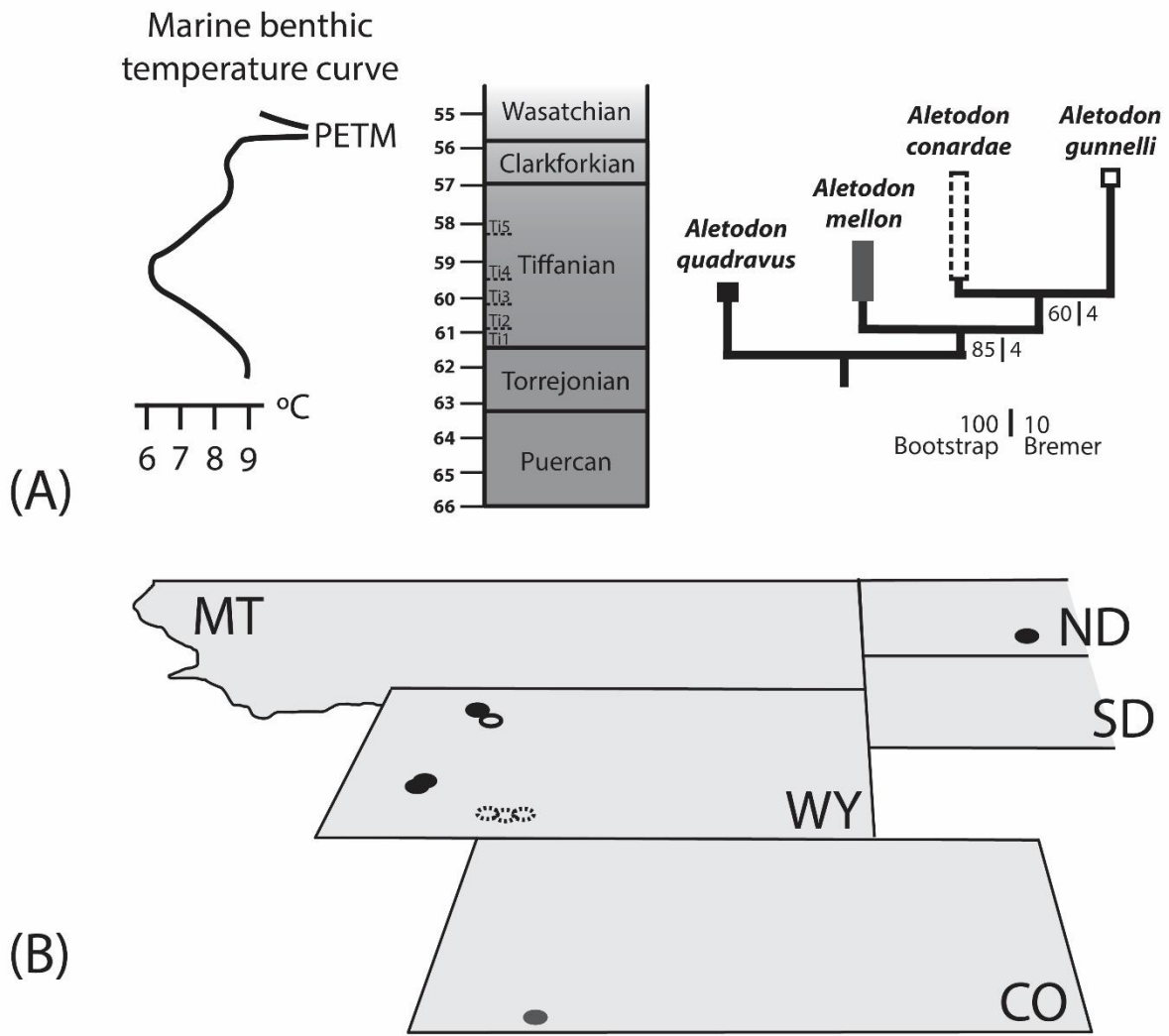
Figure 37. Phylogeny and distribution of *Aletodon* across North America during the Paleocene.

At Ti3, *Aletodon quadravus* appears in the Bighorn Basin and in southwestern Wyoming. During Ti3 and Ti4, *Aletodon* appears to have contracted its range southward, appearing only as far north as southwestern Wyoming (e.g. Winterfeld 1982). This corresponds to a significant drop in global temperature. At the end of Ti4, global temperature rebounds and *Aletodon conardae*

appears at multiple sites in southwestern Wyoming, including Twelvemile Bonanza at the beginning of Ti5, where it has a sizeable presence. In the far more extensively-sampled Bighorn Basin, only two specimens can potentially be attributed to *Aletodon* during this time (Secord 2008). At Cf1, *Aletodon gunnelli* appears unambiguously in the Bighorn Basin. The body size of *Aletodon* increases over time.

The distribution of microsyopids over the course of the Paleocene reflect a similar pattern (no microsyopids appear as far north as the Bighorn Basin until the Clarkforkian; Secord 2008). Greater sampling of southerly localities coeval with Mason Pocket, Ray's Bone Bed, and Joe's Bone Bed seems likely to reveal a larger radiation of southern microsyopids, with 12M/YPM/BMQ perhaps representing the northernmost extent of this southerly radiation. The discovery of such a radiation may shed more light on the uintasoricine/microsyopine split.

IV. Appendices

Appendix A: List of characters and scoring employed in phylogenetic analysis of *Aletodon*

P_4

Metaconid

  0. Relatively small
  1. Relatively large

Anterior slope

  0. Relatively short
  1. Relatively long

Length relative to M_1

  0. Relatively short
  1. Intermediate
  2. Relatively long

M_1

Trigonid/talonid width ratio

  0. Trigonid narrower than talonid
  1. Trigonid roughly equal to talonid

M_2

Trigonid/talonid width ratio

  0. Trigonid roughly equal to talonid
  1. Talonid narrower than talonid

Trigonid basin

  0. Relatively small
  1. Relatively large

M_1, M_2

Protoconid, metaconid alignment

0. Less posteriorly-oriented metaconid, less post-vallid tilt
1. Much more posteriorly-oriented metaconid, conspicuous post-vallid tilt

Cristid obliqua post-vallid contact

0. Medial
1. Buccal

Anterior slope

0. Relatively short
1. Relatively long

Rugose enamel

0. Absent
1. Present

P$_4$ and lower molars

Width:length ratio

0. Relatively high (premolars and molars relatively wide)
1. Relatively low (premolars and molars relatively narrow)

Upper molars

Morphology

0. Relatively broad
1. Relatively narrow

Paracone, metacone

0. Widely spaced
1. Narrowly spaced

Protocone compared to hypocone

0. Relatively small
1. Relatively large

Paraconule cingulid

0. Present
1. Absent

Metaconule

0. Relatively posteriorly-oriented
1. Relatively anteriorly-oriented

Hypocone shelf

0. Contours relatively smoothly with trigon
1. Bulges posteriorly around metaconule

All teeth

Overall size

0. Relatively small
1. Intermediate
2. Relatively large

Appendix B: Character-taxon matrix constructed for phylogenetic analysis of *Aletodon*

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Litomylus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aletodon quadravus	1	?	0	0	0	0	0	0	?	1	0	0	1	0	0	0	0	0
Aletodon mellon	?	?	?	?	?	?	?	?	?	?	?	0	0	2	1	1	1	1
Aletodon conardae	0	0	1	0	1	0	1	0	0	1	0	1	?	?	?	?	?	1
Aletodon gunnelli	1	1	2	1	1	1	1	1	1	1	1	1	0	1	0	0	1	2

Appendix C: List of characters and scoring employed in phylogenetic analysis of selected pantolestid taxa

Anterior lower dentition

0. I_3 relative size

    0. Relatively large
    1. Relatively tiny

1. Canine relative size

    0. Diameter of alveolus slightly shorter or subequal to length of P_2
    1. Relatively tiny, closely appressed to P_1

2. P_1 relative size

    0. Relatively small; alveolus smaller than the anterior alveolus of P_2, closely wedged between P_2 and the canine
    1. Relatively large (alveolus roughly equal to the posterior alveolus of P_2, or larger)
    2. Double-rooted

3. P_4-P_2 height gradient

    0. P_3 and/or P_2 lower than P_4
    1. P_3 and/or P_2 much lower than P_4, in some cases barely half the height

4. P_2 talonid basin

    0. Unenclosed, no distinct basin
    1. Talonid basin distinct, relatively well-enclosed by an entocristid

5. P_3 talonid basin

    0. Unenclosed, no distinct basin
    1. Talonid basin distinct, relatively well-enclosed by an entocristid

6. P_3 hypoconid development

    0. Hypoconid is relatively low-crowned; no distinct 'carnassiform' notch between hypoconid and protoconid
    1. Hypoconid is relatively higher-crowned, with a relatively distinct 'carnassiform' notch between the hypoconid and protoconid

P₄

7. Paraconid morphology/orientation

    0. Relatively small; forms a thin cingulid along the anterior of the P_4 rather than a distinct cusp

    1. Relatively small, generally restricted to the lingual side; base less distinct from protoconid

    2. Relatively large with a well-developed 'carnassiform' notch between paraconid and protoconid on the lingual side

8. Protoconid morphology

    0. Somewhat bladelike, relatively elongated

    1. Relatively short and blunt

9. Metaconid

    0. Absent or present only as a weak enamel fold

    1. Distinct, cuspate

10. Talonid anteroposterior crest

    0. Well-developed; sharp and raised high above the entocristid

    1. Relatively poorly developed, even in height with the entocristid

11. Talonid basin

    0. Relatively lingually restricted, narrow

    1. Relatively wide, occupying at least half of the talonid

12. Talonid lingual excavation

    0. Relatively well-excavated on the lingual side

    1. Relatively poorly excavated on the lingual side

Lower molars

13. Entocristid orientation

    0. Oriented anteroposteriorly or in a direction opposite to the cristid obliqua

    1. Oriented nearly parallel to the cristid obliqua

14. Buccolingual orientation of paraconid

    0. Relatively lingual, anteriorly projecting

    1. Relatively medial, dorsally projecting, especially on M_1 and M_2

15. Anteroposterior orientation of paraconid

    0. Relatively dorsally projecting, significantly anteroposteriorly shorter at the base than the protoconid and metaconid, especially M_2, M_3

    1. Relatively anteriorly projecting, subequal in anteroposterior breadth at the base with the protoconid and metaconid, especially M_2, M_3

16. Width of paraconid at base relative to protoconid, metaconid

    0. Paraconid significantly narrower at the base than the protoconid and metaconid

    1. Paraconid width at the base subequal to that of the protoconid and metaconid

17. M_1 trigonid basin morphology

    0. The notch separating the paraconid from the protoconid/metaconid is transverse, and there is a clear transverse slope leading up to the notch between the protoconid and metaconid; the notch between the paraconid and protoconid is much less developed

    1. The notch between the paraconid and protoconid is much higher; the notch between the protoconid and metaconid is roughly equal in height to the trigonid basin floor

18. M_2, M_3 trigonid compression

    0. Relatively anteroposteriorly uncompressed, forms relatively obtuse angle where the protoconid is the vertex (especially M_1, where there is also marked buccolingual compression)

    1. Intermediate; M_2 relatively uncompressed, M_3 relatively compressed

    2. Relatively anteroposteriorly compressed, especially M_2, M_3

19. Trigonid orientation relative to talonid

    0. Relatively anteriorly slanted, forming a more obtuse lateral angle with the talonid cusps and making the talonid basin anteroposteriorly broader

    1. Relatively dorsally-oriented; talonid basin anteroposteriorly narrower

20. Protoconid/metaconid orientation

    0. The metaconid is posterior to or roughly even with the protoconid

    1. The protoconid is posterior to the metaconid, making the talonid broader on the lingual side, at least on M_2, M_3 and often on all lower molars

21. M_1, M_2 trigonid height relative to talonid height

    0. Trigonid at least 2x the height of the talonid

    1. Relatively bunodont; trigonid ~1.5x the height of the talonid

22. M_1 paraconid lingual secondary bulge

    0. Absent

    1. Present

23. Entocristid

    0. Relatively prominent entocristid, forming a more enclosed talonid basin
    1. Relatively weak entocristid; talonid dips down to the crown base on the lingual side

24. Hypoconid orientation

    0. Buccally oriented
    1. Relatively medially oriented

25. Hypoconid morphology

    0. Relatively cuspate; apical wear
    1. Relatively lophate wear occurs along the slope of the trigonid basin, especially on M_2, M_3

26. Entoconid height

    0. Entoconid significantly higher than hypoconid
    1. Entoconid slightly higher than or subequal to hypoconid
    2. Hypoconid significantly higher than entoconid

27. Entoconid proximity to hypoconulid

    0. Entoconid migrates closer to hypoconulid going from $M_1 \rightarrow M_3$
    1. Entoconid position remains relatively stable going from $M_1 \rightarrow M_3$

28. Hypoconulid projection

    0. Relatively blunt, gradual projection with apical wear on the cusp
    1. Relatively sharp projection, especially on M_3 and to varying degrees on M_2, with wear along the diagonal slant of the trigonid basin

29. Talonid basins

    0. Relatively shallow
    1. Relatively deep

30. M_3 hypoconulid size

    0. Relatively narrow
    1. Relatively broad and bulbous

Dentary

31. Position of posterior mental foramen

    0. Below P_4 anterior
    1. Below P_4 posterior
    2. Below M_1 trigonid
    3. Below M_1 talonid

32. Size of posterior mental foramen

    0. Relatively large
    1. Relatively small

33. Position of anterior mental foramen

    0. Anterior to P_2 or absent
    1. Below P_2
    2. Between P_2, P_3
    3. Below P_3

34. Thickness of dentary bone relative to tooth crown at M_3

    0. Exceeds crown height of M_3 by 1.5-2x
    1. Roughly equal to or less than M_3 crown height

35. Thickness of dentary bone relative to tooth crown at P_4

    0. Exceeds crown height of P_4 by 1.5-2x
    1. Roughly equal to or less than P_4 crown height

36. Anterior buccalward arc of dentary bone

    0. Absent; dentary relatively anteroposteriorly straight
    1. Present

37. Mandibular angle

    2. Relatively gradual
    3. Relatively abrupt

38. Anteriorward ventral arc of dentary bone

    0. Base of arc located below M_3 or just posterior to it, if the jaw is oriented so that an imaginary line across the base of the molar crowns is horizontal
    1. Base of arc located below M_2 posterior or at M_2/M_3 juncture
    2. Base of arc located at the M_1/M_2 juncture or below M_1 posterior

P^4

39. Parastyle

    0. Cuspate
    1. Lobate

40. Metacone

    0. Cuspate

    1. Weak or subsumed into metastyle crest

Upper molars

41. Parastyle, metastyle development

    0. Relatively well-developed with sharp projection

    1. Relatively poorly developed

42. Paracone, metacone separation

    0. Relatively compressed at the tips, melded at the base, with the metacone and often the paracone tilted posteriorly

    1. Relatively broad at the tips, distinct at the base, with the metacone and paracone oriented relatively dorsally

43. Protocone anteroposterior orientation

    0. Projects relatively anteriorly relative to paracone, metacone

    1. Projects relatively medially relative to paracone, metacone

44. Protocone cusp tip morphology and wear orientation

    0. Relatively lophate, wears along the slope of the trigon basin

    1. Relatively cuspate, wears apically

45. Paraconule orientation

    0. Oriented relatively lingually, closer to protocone, compared to the metaconule

    1. Oriented relatively buccally, so that the paraconule-metaconule axis is parallel to the paracone-metacone axis

46. Hypocone development

    0. Hypocone relatively weak or absent as a distinct cusp

    1. Hypocone relatively strong

47. Hypocone shelf orientation

    0. Relatively lingual

    1. Relatively medial

48. Protocristae

    0. Approach protocone tip at a relatively obtuse angle

    1. Approach protocone tip at a relatively acute angle

49. Lingual lobe

0. Relatively narrow compared to [paracone, metacone + parastyle, metastyle]
1. Relatively broad

50. Paracone, metacone buccolingual morphology

   0. Paracone and metacone at least as wide as long, possessing well-defined bases with a convex buccolingual profile
   1. Paracone and metacone possess a relatively concave buccolingual profile, with no clear break between the buccal side of the cusp and the stylar shelf

51. Development of preparacrista

   0. Relatively raised, thick, runs continuously with the perimeter of the parastyle
   1. Relatively low (dips near to the base of the crown), loph indistinct, terminates near the base of the paracone on the lingual side

52. Angular continuity of metacrista and postprotocrista

   0. The metacrista curves more strongly than the postprotocrista, creating an abrupt change of direction at the metaconule
   1. The metacrista and the postprotocrista are angularly aligned, forming a common line or convex curve

53. Paraconule, metaconule cusp development

   0. The conules are either subsumed into the corresponding trigon crests and poorly developed as distinct cusps, or take on a relatively flat, zig-zagged 'sub-zalambdodont' form
   1. Relatively well-developed bunodont cusps

M^3

54. M^3 size relative to M^2, M^1

   0. Relatively large (equal in width to M2), owing to a buccally expanded parastyle
   1. Relatively small

Overall

55. Absolute size

   0. Largest
   1. Larger
   2. Medium
   3. Smaller
   4. Smallest

Appendix D: Character-taxon matrix constructed for phylogenetic analysis of selected pantolestid taxa

Taxon	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Gypsonictops illuminatus	0	?	?	?	?	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	1	0	0	0	?	?	?	?
Propalaeosinopa septentrionalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0
Propalaeosinopa krausei	1	0	0	0	0	0	0	1	?	?	?	?	0	0	0	0	0	0	2	0	1	0	0	0	0	1	0	0
Propalaeosinopa pilodontus	?	0	1	?	0	?	?	1	0	1	1	1	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0
Palaeosinopa dorri	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	0	0	?	0	?	?	?	0	?
Palaeosinopa reclusum	1	?	1	0	1	?	?	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1
Palaeosinopa lutreola	1	0	1	0	1	1	1	2	0	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Palaeosinopa incerta	?	0	1	0	?	1	1	1	0	1	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1
Palaeosinopa veterrima	0	0	2	0	?	1	1	1	0	1	0	1	1	?	?	0	1	0	0	0	1	0	1	0	0	0	?	0
Palaeosinopa didelphoides	0	1	0	?	1	1	1	?	0	0	0	1	1	?	?	1	1	?	0	?	0	1	0	0	0	0	?	1
Palaeosinopa aestuarium	?	?	?	?	?	1	1	1	0	1	0	1	1	?	?	0	1	1	0	1	0	0	0	0	0	0	?	?
Palaeosinopa russelli	?	?	1	?	?	1	?	1	0	0	0	1	?	0	0	1	?	1	0	0	1	1	0	0	0	0	0	0
Palaeosinopa lacus	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	1	?	0	0	0	0	0	?	0	?	?	?	?
Paleotomus senior	?	?	1	1	0	0	1	2	0	1	0	1	1	1	1	1	1	0	0	1	0	?	0	0	1	1	0	1
Paleotomus junior	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	1	0	0	0	?	1	0	0	1	1	?	?	1
Paleotomus milleri	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	?	?	?	?	?	0	0	?	?	?	?	?
Paleotomus radagasti	?	?	?	?	?	?	?	2	0	1	0	?	1	0	?	1	1	0	0	?	?	?	0	1	?	?	0	?
Paleotomus carbonensis	?	?	?	?	?	?	1	?	?	1	?	?	1	0	?	0	?	1	?	?	?	?	0	1	?	?	?	?
Leptonysson basiliscus	?	1	1	1	?	0	1	2	0	1	0	1	1	0	0	0	1	1	0	1	1	?	0	1	1	1	2	1
Leptonysson orthius	0	?	0	?	?	?	?	2	?	1	?	0	0	0	1	0	1	1	2	1	1	0	0	1	1	1	2	1
Thelysia artemia	?	?	?	1	?	?	0	?	?	0	0	1	?	0	0	1	1	0	2	0	1	0	0	1	0	1	2	0
Aatotomus placochthon	?	?	1	?	?	0	0	2	0	0	0	1	1	?	?	1	1	0	1	0	0	0	1	1	0	0	0	1
12M	?	?	?	1	?	0	0	2	0	?	0	0	1	0	0	?	?	0	1	0	0	0	0	0	?	1	?	?

Taxon	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
Gypsonictops illuminatus	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	5
Propalaeosinopa septentrionalis	0	1	0	4	0	2	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	0	5
Propalaeosinopa krausei	0	1	1	4	0	1	0	1	0	0	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	5
Propalaeosinopa pilodontus	0	1	1	4	1	3	0	1	0	0	0	?	?	?	?	1	1	1	1	?	?	?	?	?	?	?	?	5
Palaeosinopa dorri	?	?	?	?	?	?	?	?	?	0	?	1	?	1	1	1	1	1	1	1	1	1	0	0	0	1	0	3
Palaeosinopa reclusum	0	0	1	3	0	1	0	0	0	0	2	1	0	1	1	1	1	1	1	1	1	1	0	0	0	1	0	3
Palaeosinopa lutreola	0	0	0	4	1	1	0	0	0	1	0	1	?	1	1	1	1	1	0	1	1	1	0	0	1	1	1	3
Palaeosinopa incerta	0	0	0	4	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1
Palaeosinopa veterrima	0	0	0	2	1	0	0	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	0
Palaeosinopa didelphoides	0	0	0	2	1	1	0	0	0	1	0	?	?	1	1	1	1	1	?	1	1	1	0	0	1	0	1	1
Palaeosinopa aestuarium	0	0	?	?	?	?	?	?	?	1	?	1	1	1	?	1	1	1	?	1	1	1	0	0	1	1	?	3
Palaeosinopa russelli	0	?	0	2	1	2	1	1	1	0	?	?	?	1	?	1	1	1	?	1	1	0	0	0	1	0	4	3
Palaeosinopa lacus	1	1	0	1	1	0	0	?	1	0	1	1	?	0	?	0	0	1	1	0	1	0	1	0	1	0	?	3
Paleotomus senior	0	1	0	2	?	1	0	0	?	?	0	?	?	0	?	0	0	?	?	?	?	?	1	0	1	1	?	2
Paleotomus junior	?	1	0	?	?	?	?	?	?	1	?	?	?	?	?	0	0	?	1	?	?	?	0	?	?	1	?	4
Paleotomus milleri	?	?	?	2	?	0	?	?	?	?	?	1	1	0	0	0	0	1	0	0	1	0	1	1	1	0	?	3
Paleotomus radagasti	?	?	?	?	?	?	?	?	?	?	?	1	?	1	0	0	0	?	0	0	0	0	1	1	1	0	?	0
Paleotomus carbonensis	?	1	0	2	1	2	1	1	?	0	?	?	?	0	0	0	0	1	?	0	?	1	1	1	1	1	?	2
Leptonysson basiliscus	1	1	0	2	1	2	1	1	1	0	1	1	?	1	?	0	?	1	?	1	1	0	0	1	1	0	?	4
Leptonysson orthius	1	1	0	4	1	0	1	1	0	0	1	?	?	0	?	0	0	0	0	0	0	0	1	1	1	0	?	3
Thelysia artemia	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3
Aatotomus placochthon	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3
12M	0	0	?	1	1	?	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2

Appendix E: List of characters and scoring employed in phylogenetic analysis of *Prochetodon*

P$_4$

0. Dorsal slope

  0. Lacks vaunted posterior typical of Prochetodon; anterior dorsal downslope only begins anterior to cusps
  1. Anterior dorsal downslope begins at 7th or 8th cusp from the back
  2. Anterior dorsal downslope begins at 10th cusp from the back
  3. Anterior dorsal downslope begins at 11th cusp from the back

1. Angle of dorsoanterior margin

  0. Relatively acute, sharp
  1. Relatively obtuse, blunt

2. Length:height ratio

  0. Relatively high at least in some specimens
  1. Relatively low

3. Exodaenodont lobe

  0. Relatively deep, set off from rest of crown by a prominent peak on anterior of crown
  1. Intermediate depth, set off from rest of crown by a prominent peak on anterior of crown
  2. Relatively shallow, grading smoothly into the crown anterior or only weakly set off

4. Number of serrations

  0. Relatively many (12-16)
  1. Relatively few (10-12)

5. Size compared to P^3, P^4

  0. Relatively small
  1. Relatively large

P^3

6. Number of cusps

  0. 6 cusps
  1. 9 cusps
  2. 8-9 cusps

7. Length:width ratio

0. Low (~1.4)
1. Intermediate (~1.7)
2. High (~1.8-1.9)

P^4

8. Number of cusps in buccal row

   0. 6.5-8 cusps, buccal shelf extends well past midline
   1. 2.5-5 cusps, buccal shelf extends ~mid-length
   2. 1 cusp, buccal shelf extends ~mid-length

9. Cusp morphology

   0. Medial and buccal cusps relatively robust, enamel coarsely crenulated
   1. Buccal cusps relatively robust, no crenulation
   2. Medial and buccal cusps relatively gracile, no crenulation

10. Mesiodistal height differential

   0. Relatively flat
   1. Mesial relatively low compared to distal

11. Length:width ratio

   0. Relatively low (~2.25)
   1. Intermediate low (~3.0)
   2. Intermediate high (~3.3)
   3. Relatively high (~3.5-3.6)

All teeth

12. Cusp morphology

   0. Conical
   1. Lenticular

13. Absolute size

   0. Relatively small
   1. Intermediate small
   2. Intermediate large
   3. Relatively large

Appendix F: Character-taxon matrix constructed for phylogenetic analysis of *Prochetodon*

	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Baiotomeus douglassi	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prochetodon speirsae	0	0	0	1	0	1	1	2	0	1	0	3	1	3
Prochetodon foxi	2	1	0	2	0	0	1	1	0	2	1	1	1	2
Prochetodon n. sp.	1	1	0	2	0	0	2	1	1	2	0	1	1	0
Prochetodon cavus	2	0	1	2	1	0	2	2	1	2	0	1	1	1
Prochetodon taxus	3	1	?	2	1	0	1	2	2	2	0	2	1	2

Appendix G: List of characters and scoring employed in phylogenetic analysis of Paleocene and early Wasatchian microsyopids

0. Shape of I_1

    0. Lanceolate but buccally tilted
    1. Lanceolate

1. Presence of I_2

    0. Absent
    1. Present

2. Presence of lower canine

    0. Present
    1. Absent

3. P_2 roots

    0. Double-rooted
    1. Single-rooted

4. P_3 size relative to P_2

    0. Larger or subequal
    1. Smaller

5. P_3 roots

    0. Double-rooted
    1. Double-rooted but roots are appressed
    2. Single-rooted

6. P_3 morphology

    0. Relatively molariform
    1. Talonid basin still present
    2. Nubbin

7. P_4 paraconid

    0. Absent or a weak infolding of an anterior dorsoventral ridge
    1. Variable presence of a relatively distinct cusp
    2. Relatively distinct cusp

8. P_4 metaconid

0. Absent
1. Variable presence of a weak metaconid
2. Relatively strong

9. P_4 talonid cusps

    0. Zero or one cusp
    1. Variable presence of a weak second cusp
    2. Two cusps
    3. Lobate ridge

10. P_4 talonid basin

    0. Unenclosed or variably enclosed on lingual side; instead, tapers sharply downward, interrupted by a cingulum only near the crown
    1. Enclosed basin

11. P_4 size relative to P_3

    0. Subequal
    1. Relatively large

12. Lower molar mesoconids

    0. Absent
    1. Present on one or more molars

13. Lower molar paraconids

    0. Sharp, anteriorly-projecting cusp
    1. Cusp reduced and positioned more lingually, paracristid more dominant
    2. Paraconid nearly melded with metaconid, especially on M_2, M_3

14. Lower molar talonid basins

    0. Enclosed by high, sharp entocristid
    1. Strongly notched entocristid, more open talonid in at least some specimens

15. M_1, M_2 hypoconulids

    0. Absent, ridgelike, or only vaguely cuspate
    1. Distinctly cuspate, separated from entoconid by stronger notch

16. Size of M_3 relative to M_2, M_1

    0. Subequal
    1. Reduced
    2. Highly reduced

17. Lower molar hypoconulid regions

   0. Not twinned with entoconid or separated from hypoconid by notch
   1. Twinned with entoconid, separated from hypoconid by prominent notch

18. Lower molar cristid obliqua

   0. Contacts post-vallid medially
   1. Contacts post-vallid relatively buccally

19. Lower molar protoconids and hypoconids

   0. Buccal facies relatively columnar
   1. Buccal facies relatively less columnar

20. Lower molar protoconids

   0. Relatively equal in height to metaconid
   1. Reduced in height compared to metaconid

21. Lower molar hypoflexid

   0. Openly extends to the base of the crown, generally more medially intrusive
   1. Distinctly underpinned by cingulids of variable development, often extending across the buccal side of the molar

22. Lower molar protocristids

   0. No or a single protocristid
   1. Two nubbin protocristids, an anterior and posterior, which form a tiny secondary basin between the protoconid and metaconid

23. Lower molar trigonid basins

   0. Either a single oblique slit or a trifecta of poorly-defined slits between cusps
   1. Relatively flat, open central basins

CM 69336 CM 71860 CM 70723 CM 72311 CM 72312 Palenochtha minor AMNH 35451

A. wilsoni KU 8520 A. wilsoni UW 7194 A. simplicidens UM 66178 A. simplicidens UM 67214 Purgatorius unio UCMP 107406

Navajovius kohlhaasae AMNH 17390 N. doreenae USGS 25496 N. doreenae UCMP 44082 N. doreenae UW 7125 Uintasorex parvulus AMNH 55664

1   0

Buccal ⟷ Lingual
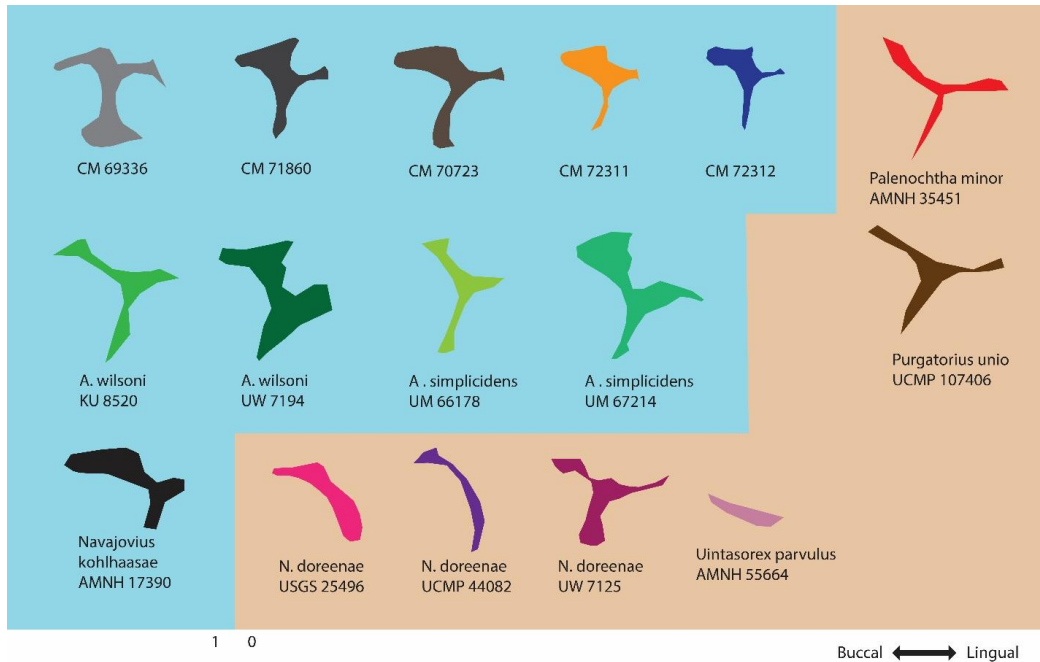
24. Lower molar entoconids, entocristids

   0. Lower or equal in height with cristid obliqua
   1. Higher, often substantially, than cristid obliqua

25. Lower molar trigonid compression

   0. Relatively uncompressed
   1. Relatively compressed, talonid generally relatively large
   2. Extremely compressed, talonid particularly large and bowl-shaped

26. P_4-M_3 cusps

   0. Relatively acute
   1. Relatively broad, low-crowned

27. Masseteric fossa

   0. Shallow
   1. Deep

28. P^4 parastyle cusp

   0. Absent
   1. Present

29. P^4 metacone

   0. Absent

1. Present

30. P^4 basin

    0. Poorly-basined between and posterior to paracone and protocone; tapers down to the base of the crown
    1. Well-basined between and posterior to paracone and protocone; enclosed by a cingulum

31. Upper molar stylar shelves

    0. Relatively well-developed
    1. Relatively poorly-developed

32. M^1, M^2 hypocones

    0. Absent
    1. Present on one or more molars

33. M^1, M^2 hypocone shelves

    0. Relatively symmetrical compared to pre-protocingulum
    1. Asymmetrically bulges, often lingually to protocone compare to pre-protocingulum; forms its own distinct lobe

34. M^1, M^2 trigon wall

    0. Trigon wall approaches protocone relatively convexly, slope of wall relatively shallow
    1. Trigon wall more steeply and linearly set off from hypocone shelf

35. M^3 parastyle

    0. Weak
    1. Prominent, strongly bulged out buccally to paracone

36. All teeth – absolute size

    0. Relatively large
    1. Intermediate
    2. Diminutive

Appendix H: Character-taxon matrix constructed for phylogenetic analysis of Paleocene and early Wasatchian microsyopids

	0	1	2	3	4	5	6	7	8	9	10	11
Purgatorius unio	?	1	1	0	0	0	0	2	0	2	1	0
Palenochtha minor	?	0	1	1	0	0	?	0	0	2	1	0
Navajovius kohlhaasae	0	0	1	1	2	1	?	0	1	2	1	1
12M/BM/YPM	?	0	1	1	1	1	?	0	1	1	0	1
Arctodontomys simplicidens	?	0	0	1	2	2	1	0	0	0	0	1
Arctodontomys wilsoni	1	0	0	1	2	2	?	0	0	1	1	1
Niptomomys doreenae	1	0	1	1	2	2	2	1	2	3	1	1
Uintasorex parvulus	1	0	1	1	0	2	?	0	2	2	1	1
Choctawius mckennai	?	?	?	?	?	?	?	?	?	?	?	?
Choctawius foxi	?	?	?	?	?	?	?	?	?	?	?	?

	12	13	14	15	16	17	18	19	20	21	22	23
Purgatorius unio	0	0	0	0	0	0	0	0	0	0	0	0
Palenochtha minor	1	1	1	0	0	0	0	0	0	0	0	0
Navajovius kohlhaasae	0	1	0	1	1	1	1	1	0	1	1	1
12M/BM/YPM	1	1	1	0	2	1	1	1	0	1	1	1
Arctodontomys simplicidens	1	1	1	1	?	1	1	1	0	1	1	1
Arctodontomys wilsoni	0	1	1	1	0	1	1	1	0	1	1	1
Niptomomys doreenae	0	2	1	0	1	1	1	1	1	1	0	0
Uintasorex parvulus	0	2	1	0	0	1	1	1	1	1	0	0
Choctawius mckennai	?	?	?	?	?	?	?	?	?	?	?	?
Choctawius foxi	0	2	1	0	?	1	1	1	0	1	0	0

	24	25	26	27	28	29	30	31	32	33	34	35	36
Purgatorius unio	0	0	0	?	0	0	0	0	0	0	0	?	1
Palenochtha minor	0	0	0	0	?	?	?	0	0	0	0	0	2
Navajovius kohlhaasae	0	0	0	0	1	0	1	0	1	1	1	1	2
12M/BM/YPM	0	0	0	1	?	?	?	?	?	?	?	0	2
Arctodontomys simplicidens	0	0	0	1	?	?	?	?	?	?	?	?	0
Arctodontomys wilsoni	0	0	0	1	0	1	0	0	1	1	1	1	0
Niptomomys doreenae	1	1	1	1	1	1	0	1	0	0	0	0	2
Uintasorex parvulus	1	1	1	1	?	?	?	0	0	1	0	?	2
Choctawius mckennai	?	?	?	?	0	0	1	1	1	1	1	?	2
Choctawius foxi	0	1	0	?	?	?	?	1	1	1	0	0	2

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