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ARTICLE

PLESIADAPIDAE (MAMMALIA, PRIMATES) FROM THE LATE PALEOCENE FORT UNION FORMATION OF THE PICEANCE CREEK BASIN, COLORADO

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ABSTRACT—Utilizing the occurrence of plesiadapid mammals, we recognize both Tiffanian and Clarkforkian ages in the Fort Union Formation of the Piceance Creek Basin of Colorado. Five species of plesiadapids are described from eighteen fossil localities. The presence of *Nannodectes gazini*, *Plesiadapis fodinatus* and a new species *Chiromyoides gigas* indicate that at most eleven of the reported fossil localities are Tiffanian in age. The majority of the fossil specimens come from UCM locality 92177 (USGSD-2001) located 35.8 meters above the base of the Fort Union Formation, which we place in the Ti5 lineage zone. The occurrence of *Plesiadapis dubius* and *Chiromyoides caesor* in the Plateau Valley area suggests a younger Clarkforkian age for these stratigraphically higher localities. We are the first to recognize Tiffanian aged fossils in the Piceance Creek Basin, extending the mammalian record back to more than 58 million years ago.

INTRODUCTION

The Piceance Creek Basin in Northwestern Colorado (Fig. 1) is among the largest early Tertiary basins in the southern Rocky Mountains, yet very little has been published on its fossil vertebrate fauna. Bounded by the Grand Hogback, the Douglass Pass arch, the Sawatch and San Juan volcanic fields, and the Elks Springs arch; the Piceance Creek Basin encompasses 26,000 km^2 of terrain along the western slope of the Rocky Mountains. The basin preserves a thick sequence of Cretaceous, Paleocene and Eocene terrestrial sediments (see Peterson et al. 2003 and cited refs). Early expeditions led by Bryan Patterson for the Field Museum (Chicago) in the 1930s and 1940s resulted in discovery of both Paleocene and Eocene aged fossil vertebrates along the southwestern edge of the basin. More recent fossil collecting by the United States Geological Survey and the University of Colorado Museum over the last three decades along the northern edge of the basin has generated a sizable collection of fossil mammals. The purpose of this article is to describe the occurrence of late Paleocene Plesiadapidae, including a new species, and to use the occurrence of these fossils to refine the age of the rock units.

Plesiadapids bear mitten shaped, procumbent upper central incisors and molars with wide talonid basins. Plesiadapids are allied with the order Primates and researchers are particularly interested in determining the systematics and phylogeny of the group (Silcox, 2001; Bloch et al., 2007). Yet it is their common occurrence, morphological diversity, and high species turnover that also make plesiadapids particularly useful in determining the biostratigraphic age of late Paleocene rocks (Gingerich, 1976). The late Paleocene North American Land Mammal Ages (NALMA), the Tiffanian and Clarkforkian, are subdivided into species lineage zones of *Plesiadapis* (Gingerich, 1976; Lofgren et al., 2004; Secord et al., 2006). Although such small biostratigraphic subdivisions are somewhat controversial and problematic (Alroy, 1998; Holland and Patzkowsky, 2002; McKenna and Lillegraven, 2006), determination of the plesiadapid species present in the Piceance Creek Basin enables preliminary biostratigraphic correlation with other basins.

MATERIALS AND METHODS

Early Tertiary fossils were collected from beds informally referred to as the "DeBeque Formation" by Bryan Patterson (Wood et al., 1941, Kihm, 1984), although in this report we apply to the same beds the stratigraphic nomenclature advocated by Hale and Smith (1994); that is, Fort Union Formation overlain by Wasatch Formation. Eighteen fossil localities contain specimens of plesiadapids in the Piceance Creek Basin (Figs. 1 and 2). Twelve of these fossil localities are located between the Yampa and White Rivers along the northern edge of the Basin. Most of the specimens come from a single locality (USGSD-2001) located 35.8 meters above the base of the Fort Union Formation (Figs. 1 and 2; labeled 1). Initially discovered in 1977, the locality has produced a diverse mammalian fauna that includes multituberculates, condylarths, creodonts, paromomyoids, and a palaeanodont. Fossils were discovered in situ in white and maroon mudstones, concentrated at the base of a varicolored mudstone knoll, and from the surface of the surrounding white flats. Stratigraphically above USGSD-2001 are several productive localities among the low-lying hills of the valley floor, but fossil mammals are rare above 113 meters (Fig. 2). Two plesiadapid bearing localities, (UCM localities 78060 [Kihm, 1984] and 97018) are present on the eastern edge of the basin, north of the town of Meeker (Figs. 1.11 and 1.4). Six other plesiadapid-bearing localities in the extreme southwestern margin of the basin (Figs. 1.13-18 and 2.13-18) are part of the Plateau Valley fauna initially described by Patterson (1939) and Kihm (1984).

Stratigraphic sections were measured in the field using a Jacob staff and alidade, with units recorded to the nearest 0.1 m. A composite of the five measured stratigraphic sections is presented in Figure 2. Stratigraphic positions of the Plateau Valley localities were measured from the base of the Molina Sandstone, a widespread unit (Fig. 2). Fossil measurements were made to the nearest 0.01 mm using digital calipers and rounded to the nearest 0.1 mm. Measurements follow those of Gingerich (1976). For dental terminology, see Figure 3. Specimens were coated with magnesium dioxide and photographed using a SPOT Insight

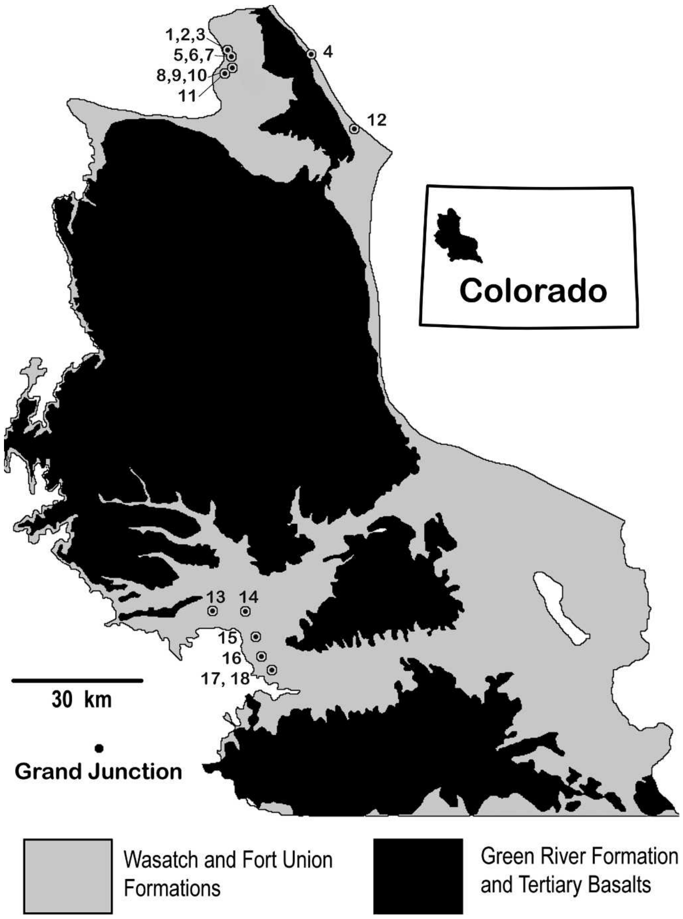

FIGURE 1. Geographic locations of the plesiadapid-bearing fossil localities discussed in the text. Detailed locality information is on file at the University of Colorado Museum. **Abbreviations**: **1**, USGSD-2001 UCM locality 92177; **2**, UCM locality 2004132; **3**, UCM locality 2004130; **4**, UCM locality 97018; **5**, UCM locality 98024; **6**, UCM locality 98054; **7**, UCM locality 98058; **8**, UCM locality 2004133; **9**, UCM locality 2003062; **10**, UCM locality 2004146; **11**, UCM locality 2005163; **12**, UCM locality 78060; **13**, FMNH locality 606-39; **14**, FMNH locality 7-37; **15**, FMNH locality 610-39; **16**, UCM locality 78009; **17**, UCM locality 78135; **18**, UCM locality 86097.

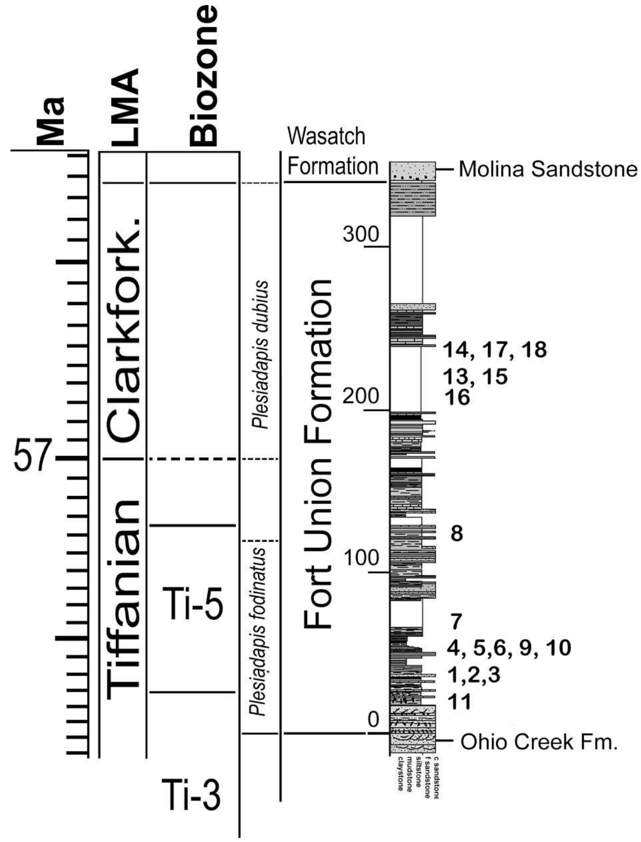

FIGURE 2. Stratigraphic locations of the plesiadapid-bearing fossil localities discussed in the text and listed in Figure 1. Units are in meters above base of the Fort Union Formation. Biozones are defined by Secord and colleagues (2006) from the Big Horn Basin and are correlated to the Piceance Creek Basin by the shared stratigraphic ranges of *Plesiadapis fodinatus* and *Plesiadapis dubius*. **Abbreviations**: **LMA**, land mammal age; **Ma**, million years ago.

camera (Diagnostic Instruments, Inc.) attached to a Leica MZ16 microscope.

Institutional Abbreviations—**FMNH**, Field Museum of Natural History; **UCM**, University of Colorado Museum; **UM**, The University of Michigan Museum of Paleontology; **USGS** and **USGSD**, U.S. Geological Survey, Denver; **UW**, The Geological Museum, University of Wyoming.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA
Order PRIMATES Linnaeus, 1758
Family PLESIADAPIDAE Trouessart, 1897
Genus *NANNODECTES* Gingerich, 1975
NANNODECTES GAZINI Gingerich, 1975
(Fig. 4A, B)

Referred Material—USGS 16872, P^4-M^2.

Locality—USGSD-2001 UCM locality 92177 (Figs. 1.1 and 2.1).

Known Occurrences—Tiffanian Saddle Locality, Bison Basin, Fremont County, Wyoming (Gazin, 1956).

Description

A right maxilla (USGS 16872) preserves P^4-M^2 from USGSD-2001 (Figs. 4A, 4B). As is typical for plesiadapids, the P^4 paracone and metacone are appressed; the worn metacone apparently was nearly as large as the paracone. A centrally positioned conule is prominent on the P^4. A worn parastyle is present but a metastyle, formed by an extension of the centrocrista crest, is absent. The preprotocrista and postprotocingulum extend from the parastyle and posterobuccal margin, respectively, and connect with the protocone apex. The margin of the P^4 is convex buccally, mainly due to an inflated paracone, and the ectocingulum is very weak.

The M^1 is slightly longer and wider than the M^2 and the paracone is slightly larger than the metacone, more so on the M^2. Wear has nearly eliminated the central conules and possibly the M^1 postprotocrista on USGS 16872. Although a small cuspule is present on the shelf-like ectocingulum opposite the valley between the paracone and metacone, this cuspule bears little resemblance to the mesostyle found in *Plesiadapis*, which is formed by an extension of the centrocrista crest (compare Fig. 4B with Fig. 4D). The shelf formed by the postprotocingulum is wide. Para- and metastyles are weak on M^1, but are absent on M^2. Unlike *Plesiadapis*, the enamel on all the teeth is smooth.

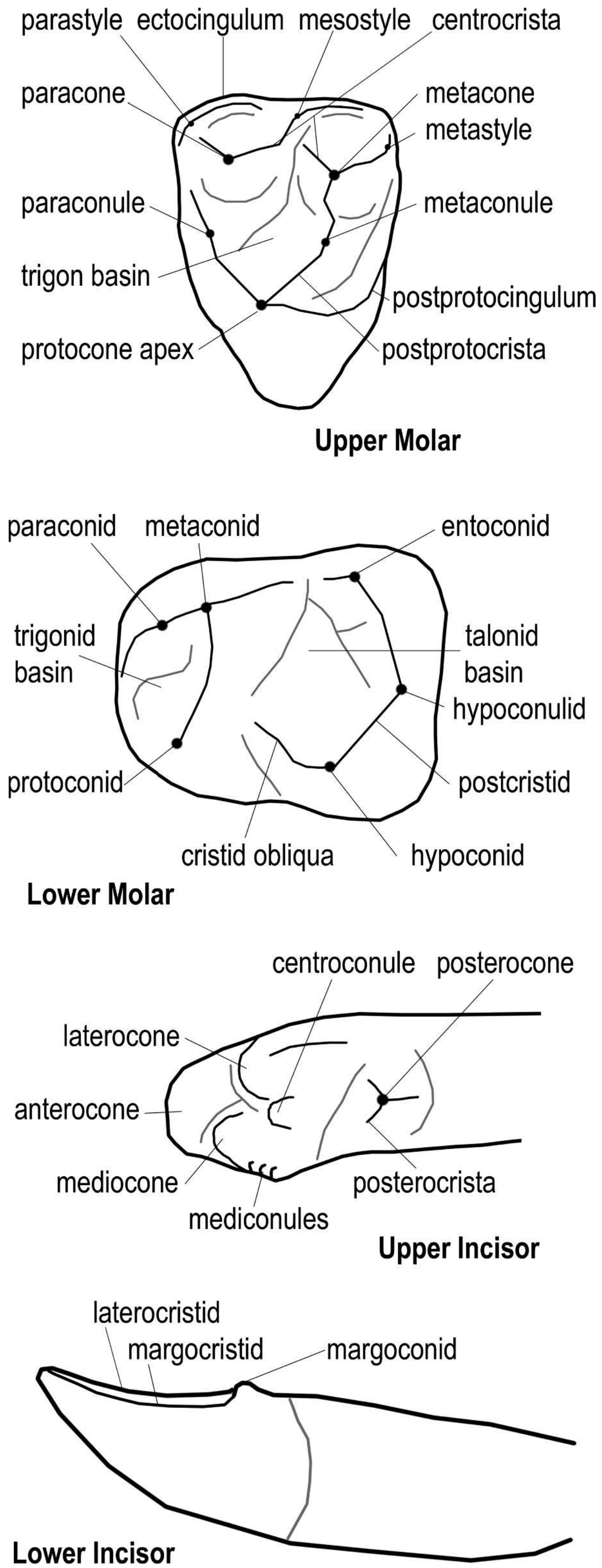

FIGURE 3. Terminology used in this article to describe dental anatomy. Anterior direction is to the left, posterior direction to the right (after Gingerich, 1976).

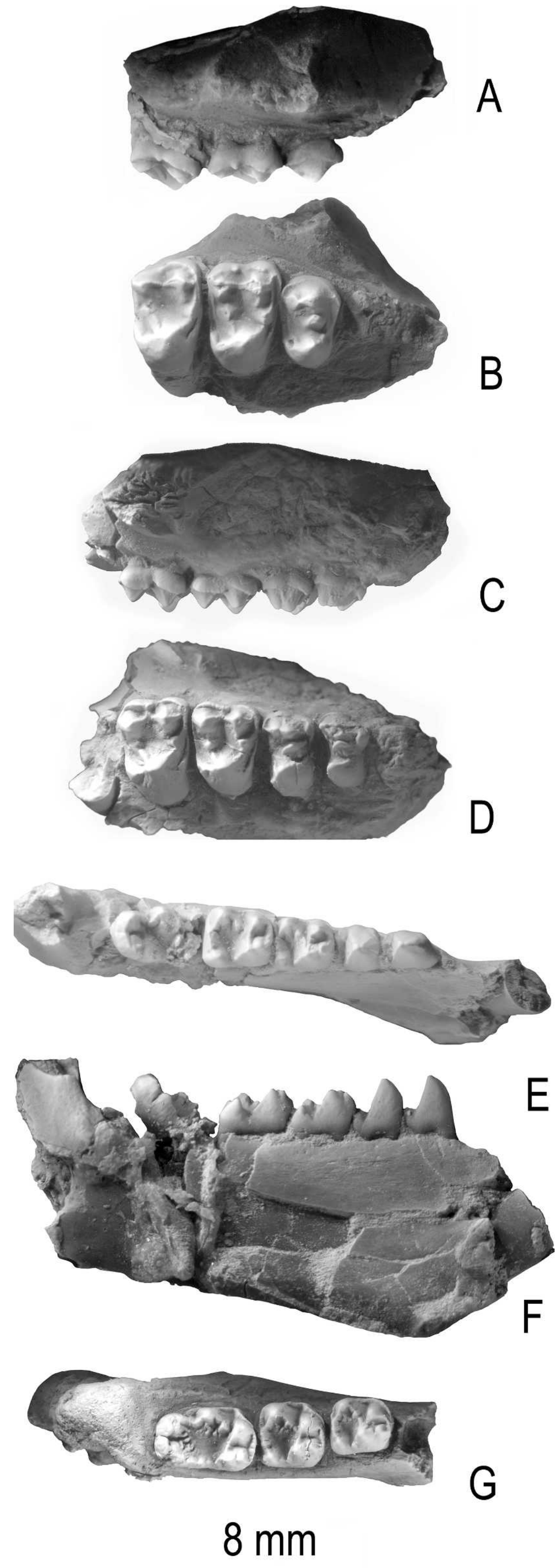

FIGURE 4. Plesiadapid fossil specimens from the Piceance Creek Basin. **A**, **B**, *Nannodectes gazini*, USGS 16872 P4-M2 buccal and occlusal views; **C**, **D**, *Plesiadapis fodinatus* USGS 2356 P3-M2 buccal and occlusal views; **E**, **F**, *P. fodinatus* UCM 98626 P3-M3 occlusal and buccal views; **G**, *P. fodinatus* USGS 2357 occlusal view.

TABLE 1. Measurements of USGS 16872 *Nannodectes gazini*.

P^4	Length	2.0
	Width	2.9
M^1	Length	2.5
	Width	3.7
M^2	Length	2.3
	Width	3.4

Length and width are anteroposterior and buccolingual diameters, respectively.

Comparison

This small plesiadapid closely resembles *Nannodectes gazini*. The specimen differs significantly from *Plesiadapis* in its smaller size, molars lacking mesostyles formed by an extension of the centrocrista, and in the relative proportions of the teeth, with the P^4 smaller relative to M^1, and the M^1 and M^2 subequal in size. The Piceance Creek Basin specimen differs in size from *Nannodectes simpsoni*, with M^2 nearly 25% smaller. Furthermore, the Piceance Creek Basin specimen differs significantly from *N. gidleyi* by its small size, absence of upper molar mesostyles, and weak central conules. Although significantly smaller than *N. intermedius*, the Piceance Creek Basin specimen shares a number of primitive traits with the species, including absence of a mesostyle flexure on the centrocrista and in apparently having the postcingulum slightly swollen where it joins the postprotocingulum. In comparing the Piceance Creek Basin specimen with UW 5433, a specimen of *N. gazini* preserving P^4-M^2 from the Bison Basin, Wyoming, we can find only a few distinguishable traits. USGS 16872 exhibits a slightly more convex P^4 buccal margin and slightly wider postprotocingulum on the upper molars. Nevertheless, these minor differences fail to provoke assignment to any other species. We conclude, therefore, that the Piceance Creek Basin specimen is referable to *N. gazini* on the basis of its near match in size and morphology.

TABLE 2. Summarized measurements of *Plesiadapis fodinatus* specimens from the Piceance Creek Basin.

		n	OR	Mean	DEV^2	VAR	STDEV
I^1	Depth	5	3.0–4.3	3.4	1.05	0.26	0.51
	Width	5	2.3–2.7	2.4	0.08	0.02	0.14
P^3	Length	1	2.4	2.4	—	—	—
	Width	1	3.5	3.5	—	—	—
P^4	Length	5	2.2–2.5	2.4	0.10	0.03	0.16
	Width	5	3.3–3.9	3.7	0.30	0.08	0.27
M^1	Length	8	2.9–3.5	3.2	0.16	0.02	0.15
	Width	8	4.0–4.7	4.3	0.33	0.05	0.22
M^2	Length	7	3.3–3.8	3.5	0.17	0.03	0.17
	Width	7	4.5–5.4	4.9	0.47	0.08	0.28
M^3	Length	6	3.0–3.6	3.2	0.20	0.04	0.20
	Width	6	4.1–5.0	4.5	0.62	0.12	0.35
I_1	Depth	11	3.2–4.3	3.9	1.04	0.09	0.31
	Width	11	1.9–2.6	2.3	0.33	0.03	0.17
P_3	Length	2	2.5–2.6	2.6	0.00	0.00	0.01
	Width	2	1.9–2.1	2.0	0.01	0.01	0.11
P_4	Length	10	2.2–3.1	2.7	0.74	0.08	0.27
	Width	10	2.0–2.3	2.1	0.11	0.01	0.11
M_1	Length	23	3.0–3.6	3.3	0.83	0.04	0.19
	Width	24	2.6–3.1	2.8	0.70	0.03	0.17
M_2	Length	31	3.0–4.0	3.5	2.06	0.07	0.26
	Width	31	2.4–3.4	3.0	2.00	0.06	0.25
M_3	Length	22	3.3–5.6	4.8	7.16	0.34	0.58
	Width	22	2.8–3.4	3.0	0.48	0.02	0.15

Length and width are anteroposterior and buccolingual diameters, respectively. Incisor depth is measured from the tip of the margoconid or posterocone to the opposite margin of the tooth. **Abbreviations**: **n**, number of specimens; **OR**, observed range, **DEV^2**, sum of square deviations from the mean; **VAR**, variance; **STDEV**, standard deviation. Units are in mm.

TABLE 3. Measurements of *Plesiadapis dubius* specimens from the Piceance Creek Basin.

		n	OR	Mean	DEV^2	VAR	STDEV
I^1	Depth	1	3.1	3.1	—	—	—
	Width	1	2.1	2.1	—	—	—
P^3	Length	2	2.5–2.6	2.5	0.00	0.00	0.05
	Width	2	2.7–2.8	2.7	0.00	0.00	0.04
P^4	Length	1	2.5	2.5	—	—	—
	Width	1	2.0	2.0	—	—	—
M^1	Length	4	2.2–3.2	3.0	0.06	0.02	0.14
	Width	4	3.7–4.0	3.8	0.06	0.02	0.14
M^2	Length	2	3.3–3.4	3.4	0.02	0.02	0.13
	Width	2	4.6–4.7	4.7	0.03	0.03	0.18
M^3	Length	3	2.7–3.0	2.8	0.06	0.06	0.25
	Width	3	4.4–4.7	4.6	0.04	0.02	0.15
P_3	Length	2	1.9–2.1	2.0	0.02	0.02	0.14
	Width	2	1.7–2.0	1.8	0.03	0.03	0.18
P_4	Length	2	2.5–3.1	2.5	0.01	0.01	0.11
	Width	2	2.0–2.1	2.1	0.01	0.01	0.09
M_3	Length	2	4.4–4.5	4.5	0.00	0.00	0.04
	Width	2	2.7–2.8	2.8	0.00	0.00	0.07

Length and width are anteroposterior and buccolingual diameters, respectively. **Abbreviations**: **n**, number of specimens; **OR**, observed range, **DEV^2**, sum of square deviations from the mean; **VAR**, variance; **STDEV**, standard deviation. Units are in mm.

Genus *PLESIADAPIS* Gervais, 1877

PLESIADAPIS FODINATUS Jepsen, 1930
(Fig. 4C–G and Fig. 5A–D)

Referred Material—See Appendix 1.

Localities—USGSD-2001 UCM locality 92177 (Fig 1.1); UCM locality 2004132 (Fig. 1.2); UCM locality 2004130 (Fig. 1.3); UCM locality 97018 (Fig. 1.4); UCM locality 98024 (Fig. 1.5); UCM locality 98054 (Fig. 1.6); UCM locality 98058; (Fig. 1.7); UCM locality 2004133 (Fig. 1.8); UCM locality 2003062 (Fig. 1.9); UCM locality 2004146 (Fig. 1.10); UCM locality 2005163 (Fig. 1.11).

Description

The relatively narrow upper incisors exhibit small centroconule cusps and a short row of accessory cusps along the medial margin (mediconules). The upper incisor posterocrista and laterocone are more prominent (Fig. 5A, B). The P^2 is not preserved in any of the Piceance Creek Basin specimens, although P^3 and P^4 are well represented (Fig. 4D). These premolars display a distinct paraconule and paracone closely appressed against the metacone. Upper molars bear the diagnostic postprotocingulum, which extends from the protocone posteriorly. In several specimens, the postprotocristae are slightly bigger and rounded, extending the posterior ledge of the molar. True mesostyles occur on all three upper molars. The enamel is crenulated on the buccal side of the protocone and in the trigon basin, particularly on M^2 and M^3 (Fig. 4D).

The lower incisors exhibit a narrow occlusal surface with distinct margocristid and laterocristid ridges on each side. P_2 is absent, which creates a long diastema between the incisor and P_3. The P_3 is only slightly smaller than P_4. Both teeth in UCM 98626 lack a cristid obliqua crest and an entoconid cusp resulting in an undifferentiated posterior heel (Fig. 4E). However, from the same locality, isolated premolars (USGS 26574, UCM 73886) display entoconids and small crests, implying population variability in this trait. The M_1 and M_2 exhibit a reduced paraconid, with a low cristid obliqua extending half way between the meta- and protoconid cusps. The hypoconulid is weakly developed. Along the lingual edge of the lower molars the entoconid curves inward rather than projecting outward. Piceance Creek Basin M_3s are variable in enamel crenulations in the talonid basins

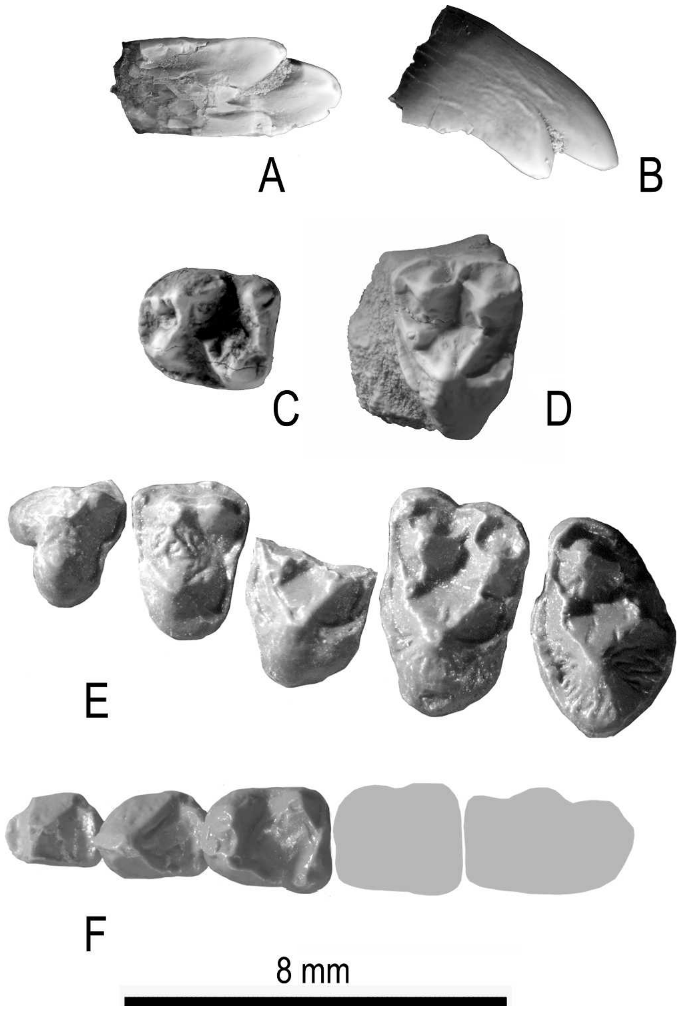

FIGURE 5. **A**, **B**, *Plesiadapis fodinatus* UCM 99409 right I1 buccal and occlusal views; **C**, *P. fodinatus* UCM 84112 M1 occlusal view; **D**, *P. fodinatus* UCM 42123 M1 occlusal view; **E**, *P. dubius* FMNH P26084 P3-M3 occlusal view. **F**, *P. dubius* FMNH P26112 P3-M1 occlusal view. [Planned for page column]

(compare Figs. 4E and 4G). We found no correlation between the size of the tooth and the degree of crenulation.

Comparison

These plesiadapids are referred to *Plesiadapis*, and distinguished from *Nannodectes* by the presence of a centroconule on I^1, a squared and fissured heel on M_3 and their overall larger size (Gingerich, 1976). They differ from the early and middle Tiffanian *Plesiadapis praecursor, P. anceps*, and *P. rex* in their larger size, I^1 with centroconule, upper molars with prominent mesostyles, lower molars with more vertical buccal walls, and the M_3 with enamel frequently crenulated, and the heel strongly fissured. The late Tiffanian *P. simonsi*, late Tiffanian—early Clarkforkian *P. gingerichi*, and middle Clarkforkian *P. cookei* are all significantly larger.

The Clarkforkian—early Wasatchian *P. dubius* differs from the specimens in its small size, and narrower lower molars, absence of a centroconule on the I^1, and the lack of a pronounced paraconule on P^4.

These specimens are most similar to the late Tiffanian *Plesiadapis churchilli* and *P. fodinatus*, and compare closely in size and morphology to specimens of *P. fodinatus* and *P. churchilli* from the Rock Springs Uplift, Wyoming (Winterfeld, 1982). *P. fodinatus* has slightly smaller molars and incisors than *P. churchilli* (Gingerich, 1976; Winterfeld, 1982; Secord, 2004). Secondarily, *P. fodinatus* has P_{3-4}s with cristid obliqua crests and entoconid cusps, has curved rather than squared entoconids on M_{1-2}, and has more crenulated enamel than *P. churchilli*, all features considered to be derived (Gingerich, 1976). These traits are found to be variable in the Piceance Creek Basin material, but many specimens share the derived features of *P. fodinatus*.

Winterfield (1982) reported accessory medioconules in his sample of *Plesiadapis* sp. probably *P. churchilli*, and Secord (2004) additionally differentiated *P. churchilli* from *P. fodinatus* by the former "typically" (p. 202) having a row of small accessory cusps along the medial edge of the upper incisor posterior to the mediocone, versus *P. fodinatus* "typically" (p. 202) having only a single medioconule. Three of the upper incisors from the Piceance Creek Basin bear similar cusps, while the remaining three upper incisors completely lack medial accessory cusps. Secord (2004) additionally characterized *P. churchilli* as having a dorsoventrally deeper upper I^1 than *P. fodinatus*, but in the Piceance Basin sample, there appears to be no correlation between depth of the I^1 and the presence or absence of accessory medioconules. For example USGS 2376, which is within the size range of *P. fodinatus* and below that of *P. churchilli*, has the largest accessory cusps, but UCM 84115, which is the largest I^1, lacks accessory cusps. Measurements of Piceance Creek I^1 specimens are closer to the mean values of *P. fodinatus* than to *P. churchilli*. We think therefore that that the variation seen in the Piceance Creek Basin incisors is not indicative of species differences, but rather is variation within a single species, similar to the variation reported by Secord (2004) in the number of accessory medioconules for *Plesiadapis* cf. *dubius*. In addition, all the reported mean values of M_2 width and length for *P. churchilli* lay outside the observed range for the Piceance Creek Basin specimens (Fig. 6). Therefore the Piceance Creek specimens are best referred to *P. fodinatus*, based on size and the occurrence of derived features typically associated with *P. fodinatus*.

PLESIADAPIS DUBIUS (Matthew and Granger, 1915)
(Fig. 5E, F)

Referred Material—FMNH P26084 P^3-M^3; FMNH P26061 M^2-M^3; FMNH P26112 P_3-M_1; FMNH P26068 M_1, with partial M_2; UCM 41238 I^1; UCM 41240 P^3; UCM 42119 $M^{1;}$; UCM 42123 M^1; UCM 41239 M^1; UCM 41244 M^3; UCM 42122 M^3; UCM 41241 M_3; UCM 41237 M_3; UCM 42121 P_4.

Localities—FMNH locality 7-37 (Figs. 1.14, 2.14); FMNH locality 610-39 (Figs. 1.15, 2.15); FMNH locality 606-39 (Figs. 1.13, 2.13); UCM locality 78009 (Figs. 1.16, 2.16); UCM locality 86097 (Figs. 1.18, 2.18); UCM locality 78135 (Figs. 1.17, 2.17).

Description

P^3 and P^4 lack paraconules, having only three discrete cusps: the protocone, paracone, and metacone. The first upper molar is smaller then the second molar and both molars lack a hypocone along the postprotocingulum. Upper molars show significant crenulation of the enamel in the trigon basin (Fig. 5E). FMNH P26112, a lower dentary preserving P_3-M_1, has no alveolus for P_2 (Fig. 5F). The premolars and molars are small, with sharp crests. The M_3 talonid basin is well crenulated.

Comparison

The lower first molar exhibits a posterior basal cingulid continuous with the buccal extension of the entoconid crest, distobuccally (Fig. 5F). This feature has been used to distinguish *P. dubius* from *P. fodinatus* (Gingerich, 1976 p. 31). These speci-

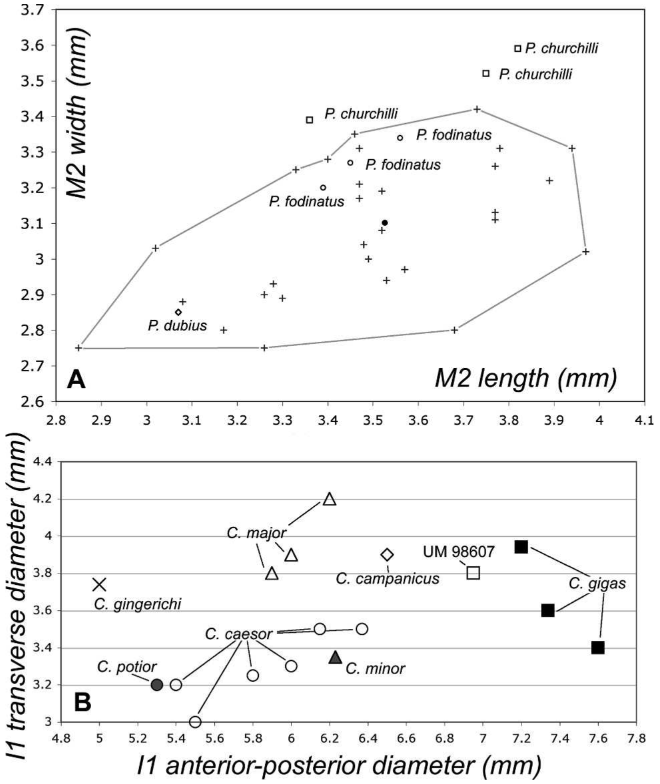

FIGURE 6. **A**, Bivariate plot of individual M2 width and length of *Plesiadapis* from the Piceance Creek Basin symbolized by plus symbols, the average symbolized by closed circles, and the polygon encircles observed range. Also plotted are reported averages of *P. dubius*, *P. churchilli* and *P. fodinatus* (Gingerich, 1976; Krause, 1978; Winterfield, 1982). **B**, Bivariate plot of individual I1 transverse and anterior-posterior diameters of *Chiromyoide*s (Gingerich, 1976; Winterfield, 1982; Secord, 2004).

mens are further attributed to *P. dubius* based on their smaller size, narrow lower molars, more angular cusps and crests in the lower molars, and the lack of a pronounced paraconule on the P^3 and P^4 (Fig. 5E). The specimens share with *P. fodinatus* the presence of mesostyles on the upper molars and the absence of P_2. *P. dubius* specimens are found in the Plateau Valley area from stratigraphically higher units than specimens of *P. fodinatus* from the north (Figs. 1 and 2). The FMNH specimens were previously referred to *P. dubius* by Kihm (1984).

Genus *CHIROMYOIDES* Stehlin, 1916

CHIROMYOIDES GIGAS, sp. nov.
(Fig. 7A–I)

Types—Holotype UCM 98607 left I^1, Paratypes UCM 53514, I_1; UCM 51005, I^1; UCM 84106, I^1; UCM 84107, I^1.

Etymology—*gigas*, Greek for giant in allusion to the upper incisors.

Type Locality—USGSD-2001 UCM locality 92177 (Figs. 1.1, 2.1); 53.8 meters above the base of the Fort Union Formation.

Diagnosis—*Chiromyoides gigas* differs from *C. major, C. caesor, C. potior, C. gingerichi*, and *C. minor* in the larger size of upper incisors, measuring over 7 mm in anterior-posterior crown diameter, with anterior-posterior to transverse diameter ratios between 0.45 and 0.55.

Comparison

Chiromyoides gigas has a similar width with *C. major*, but the mediocone and laterocone are better developed and more appressed in *C. gigas*. Large and appressed mediocones and laterocones are also found on the upper incisors of *C. caesor*, but *C. gigas* can be distinguished from this species by its larger incisors.

Localities—USGSD-2001 UCM locality 92177 (Figs. 1.1, 2.1); UCM locality 98054 (Figs. 1.6, 2.1); UCM locality 98058 (Figs. 1.7, 2.7); UCM locality 86097 (Figs. 1.18, 2.18).

Description

All four upper incisors exceed 7 mm in anterior-posterior diameter of the crown, except UCM 84107, a highly worn and broken tooth. Transverse width measures between 3.4 and 3.9 mm. All incisors lack a centroconule (Fig. 7). The laterocone and mediocone are both well developed, with the mediocone placed more toward the apex of the incisor. The prominent posterocone curves inward, where it articulates with the lower incisor. There is no accessory cusp on the medial-dorsal side of the posterocone.

A lower right incisor (UCM 53514) is attributed to the same species based upon its large size (Fig. 7J). A prominent margoconid projects from the base of the tooth. A broad margocristid extends toward the apex of the incisor. UCM 53514 measures 4.7 mm and 2.7 mm in depth and width at the base of the enameled crown. Furthermore, the anteroposterior diameter of the crown measures 8.4 mm.

In delimiting species of *Chiromyoides*, authors have used the ratio of the anterior-posterior diameter to the transverse diameter of the upper incisors (Gingerich, 1976; Secord, 2004). *C. gingerichi* and *C. major* have the highest values ranging from 0.65 to 0.75, whereas *C. minor* and *C. caesor* have values ranging from 0.54 to 0.59. *C. potior* and *C. campanicus* have intermediate ratios of 0.60 to 0.64. The specimens from the Piceance Creek Basin have the lowest ratios, with values ranging from 0.45 to 0.55. These low ratios belie the fact that the total anterior-posterior diameter is nearly 15% longer than other species (Fig. 6B). Secord (2004) reported an upper incisor (UM 92360) from the Big Horn Basin that is similar in size to the *Chiromyoides* specimens from the Piceance Creek Basin. However, UM 92360 exhibits an additional cusp adjacent to the posterocone that is not found in the Piceance Creek Basin specimens. Aside from incisor size, the Piceance Creek Basin specimens are most similar to *C. caesor* from southwestern Wyoming (Winterfeld, 1982) and we consider *C. gigas* and *C. caesor* to be sister taxa.

CHIROMYOIDES CAESOR Gingerich, 1973
(Fig. 7J)

Referred Material—UCM 53515 I^1.

Locality—Hell's Half Acre (UCM locality 78009) Mesa County, Colorado (Figs. 1.16, 2.16).

Description

A single upper incisor from the *P. dubius* bearing UCM locality 78009 has anterior-posterior crown diameter of 5.7 mm and a transverse width of 3.3 mm (Fig. 7J). The ratio of 0.58 is well within the range for *C. caesor*. Morphologically the specimen is similar to *C. gigas* in having large and closely appressed mediocones and laterocones. Conceivably, the size difference between *C. caesor* and *C. gigas* is sexually dimorphic. However, the two species are currently known from localities at different stratigraphic levels within the Piceance Creek Basin.

CHIROMYOIDES sp. Stehlin, 1916
(Fig. 8)

Referred Material—UCM 41606, M_2.

Locality—UCM locality 78060 (Fig. 1.12).

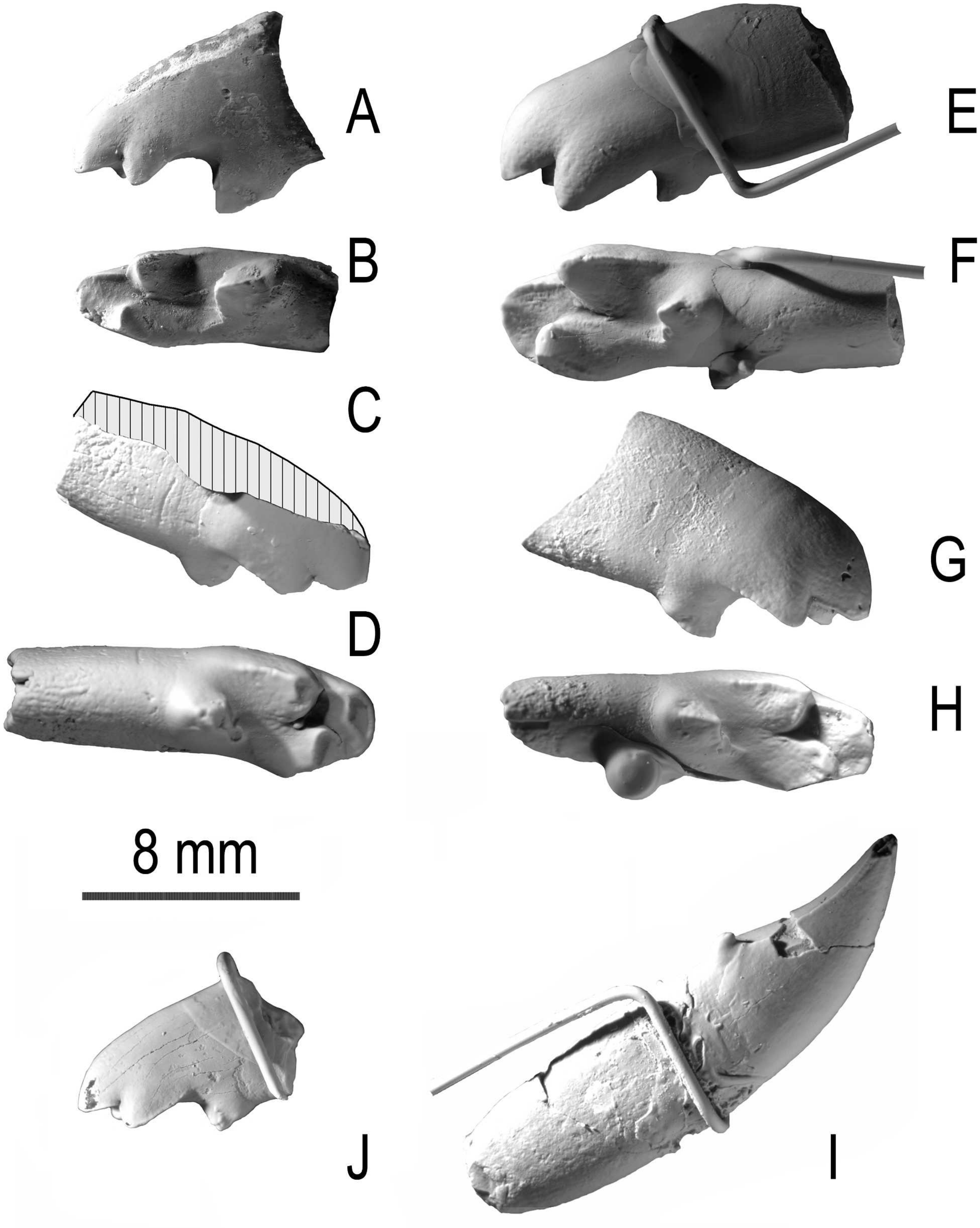

FIGURE 7. **A**, **B**, *Chiromyoides gigas* Holotype UCM 98607 left I1 buccal and occlusal views; **C**, **D**, *C. gigas* UCM 84107 I1 buccal and occlusal views; **E**, **F**, *C. gigas* UCM 51005 I1 buccal and occlusal views; **G**, **H**, *C. gigas* UCM 84106 I1 buccal and occlusal views; **I**, *C. gigas* UCM 53514 I1; **J**, *Chiromyoides caesor* UCM 53515 I1 buccal view.

TABLE 4. Measurements of *Chiromyoides gigas* specimens from the Piceance Creek Basin.

	Specimen	Anterposterior diameter	Transverse diameter	Depth	Width
I^1	UCM 51005	7.2	3.9	—	—
	UCM 84106	7.3	3.6	—	—
	UCM 84107	6.7	3.5	—	—
	UCM 98607	7.6	3.5	—	—
I_1	UCM 53514	—	—	4.7	2.7

Upper incisor diameters are measured across the crown of the tooth. Incisor depth is measured from the tip of the margoconid to the opposite margin of the tooth.

Description

A left M_2 (UCM 41606 from UCM locality 78060) exhibits a square occlusal surface peculiar to *Chiromyoides* (Fig. 8). The paraconid is absent, with a high metaconid on the trigonid. The postcristid extends transversely from the entoconid to the hypoconid, with no indication of a hypoconulid along its edge. The cristid obliqua contacts the trigonid proximal to the protoconid. UCM 41606 measures 2.9 mm in length and 2.8 mm in width.

BIOSTRATIGRAPHIC IMPLICATIONS

Our report is the first to recognize Tiffanian aged fossils in the Fort Union Formation of the Piceance Creek Basin. This study lengthens the mammalian fossil record in the Piceance Creek Basin back to more than 58 million years ago. The co-occurrence of *Plesiadapis fodinatus*, *Nannodectes gazini* and the new larger species *Chiromyoides gigas* reveals a biostratigraphic paradox. *P. fodinatus* occurs in the Ti5 lineage zone, whereas *N. gazini* is restricted to the Ti2 lineage zone (Lofgren et al., 2004; Secord et al., 2006). We suggest that the fauna from UGSD-2001 represents the Ti5 lineage zone because of the co-occurrence of other Ti5 mammalian genera such as *Ignacius*, and the absence of rodents. Furthermore, the underlying Ohio Creek Formation contains a mammalian fauna consistent with the Ti3 lineage zone (Burger, 2007). We also place the northern localities of the Piceance Creek Basin within the Ti5 lineage zone, because of the presence of *Plesiadapis fodinatus*. The *Chiromyoides* sp. bearing UCM locality 78060 is of a definite younger Clarkforkian age, because of the presence the fossil rodent *Franimys* (Kihm, 1984).

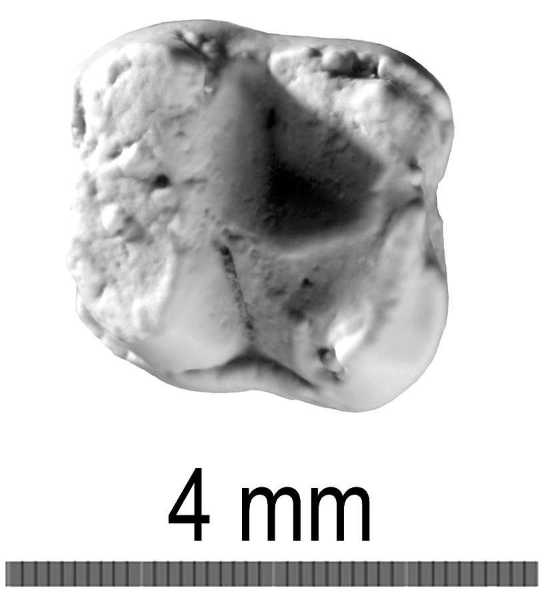

FIGURE 8. *Chiromyoides* sp. UCM 41606 M2 occlusal view.

The six Plateau Valley localities are Clarkforkian in age, because of the presence of the Clarkforkian species *P. dubius* and *C. caesor*. Strangely, the Plateau Valley fauna lacks rodents, tillodonts, coryphodontids, and larger *Plesiadapis* species that are characteristic of Clarkforkian faunas from Wyoming. Collecting efforts are underway to confirm these absences and to gain better insight into the makeup of Plateau Valley fauna.

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APPENDIX. Dental measurements of *Plesiadapis fodinatus*.

Number	Locality	Tooth	Depth	Width	Length
USGS 26573	L. 92177	I^1	3.00	2.33	—
UCM 99409	L. 92177	I^1	3.08	2.37	—
USGS 2376	L. 92177	I^1	3.19	2.32	—
USGS 16886	L. 92177	I^1	3.37	2.40	—
UCM 84115	L. 98058	I^1	4.26	2.67	—
USGS 2356	L. 92177	P^3	—	3.49	2.36
USGS 2356	L. 92177	P^4	—	3.86	2.15
UCM 99404	L. 92177	P^4	—	3.61	2.46
USGS 2375	L. 92177	P^4	—	3.92	2.51
UCM 99434	L. 92177	P^4	—	3.29	2.52
UCM 77019	L. 97018	P^4	—	3.93	2.53
USGS 2375	L. 92177	M^1	—	4.27	3.17
UCM 99404	L. 92177	M^1	—	4.30	3.08
USGS 16891	L. 92177	M^1	—	4.01	2.92
USGS 26570	L. 92177	M^1	—	4.09	3.16
USGS 16888	L. 92177	M^1	—	4.65	3.17
USGS 16871	L. 92177	M^1	—	4.22	3.25
UCM 99444	L. 2005163	M^1	—	4.54	3.26
USGS 16883	L. 92177	M^1	—	4.19	3.45
USGS 2356	L. 92177	M^2	—	4.74	3.25
USGS 26570	L. 92177	M^2	—	4.53	3.76
USGS 16883	L. 92177	M^2	—	5.00	3.52
USGS 16889	L. 92177	M^2	—	4.97	3.32
UCM 73884	L. 92177	M^2	—	4.96	3.50
UCM 88518	L. 92177	M^2	—	4.83	3.50
UCM 84114	L. 92177	M^2	—	5.44	3.58
UCM 73884	L. 92177	M^3	—	4.62	3.15
USGS 16894	L. 92177	M^3	—	4.56	2.98
UCM 88511	L. 92177	M^3	—	4.13	3.09
UCM 88513	L. 92177	M^3	—	4.64	3.15
UCM 81484	L. 98024	M^3	—	4.08	3.16
UCM 77020	L. 97018	M^3	—	5.02	3.57
UCM 84111	L. 98054	I_1	3.19	1.91	—
UCM 92482	L. 92177	I_1	3.52	2.31	—
UCM 73885	L. 92177	I_1	3.69	2.33	—
USGS 26575	L. 92177	I_1	3.73	2.25	—
UCM 99403	L. 92177	I_1	3.75	2.43	—
USGS 16873	L. 92177	I_1	3.83	2.49	—
UCM 81191	L. 92177	I_1	3.86	2.40	—
UCM 92483	L. 92177	I_1	4.06	2.43	—
UCM 99408	L. 92177	I_1	4.06	2.23	—
UCM 81189	L. 92177	I_1	4.08	2.42	—
UCM 73883	L. 92177	I_1	4.19	2.30	—
UCM 84113	L. 92177	I_1	4.28	2.61	—
UCM 98626	L. 92177	P_3	—	1.89	2.54
UCM 73886	L. 92177	P_3	—	2.05	2.56
USGS 16867	L. 92177	P_4	—	2.13	2.22
UCM 73887	L. 92177	P_4	—	1.99	2.46
UCM 98626	L. 92177	P_4	—	2.27	2.50
UCM 77023	L. 97018	P_4	—	2.21	2.50
USGS 16885	L. 92177	P_4	—	2.16	2.57
UCM 98552	L. 2004133	P_4	—	2.02	2.64
UCM 81482	L. 98024	P_4	—	2.02	2.75
UCM 100696	L. 2004146	P_4	—	2.27	2.84
USGS 26574	L. 92177	P_4	—	2.23	2.93
UCM 81190	L. 92177	P_4	—	2.01	3.00
USGS 26565	L. 92177	M_1	—	2.76	—
UCM 98625	L. 92177	M_1	—	2.67	2.96
UCM 98626	L. 92177	M_1	—	2.61	3.01
UCM 73881	L. 97018	M_1	—	2.70	3.05
USGS 2360	L. 92177	M_1	—	3.02	3.06
USGS 16867	L. 92177	M_1	—	3.05	3.11
USGS 26572	L. 92177	M_1	—	2.79	3.11
UCM 88509	L. 92177	M_1	—	2.75	3.16
USGS 26569	L. 92177	M_1	—	2.68	3.19
USGS 26568	L. 92177	M_1	—	2.73	3.19
UCM 84112	L. 98054	M_1	—	2.78	3.23
USGS 2361	L. 92177	M_1	—	2.92	3.24
UCM 88519	L. 92177	M_1	—	2.81	3.24
USGS 2364	L. 92177	M_1	—	2.73	3.29
UCM 81481	L. 92177	M_1	—	3.03	3.29
UCM 100694	L. 2004146	M_1	—	2.67	3.30
UCM 98566	L. 2004133	M_1	—	2.89	3.30
USGS 2369	L. 92177	M_1	—	2.77	3.33
USGS 2357	L. 92177	M_1	—	2.81	3.35
USGS 16876	L. 92177	M_1	—	3.08	3.40
UCM 99407	L. 92177	M_1	—	2.79	3.40
USGS 2363	L. 92177	M_1	—	2.93	3.42
USGS 2372	L. 92177	M_1	—	2.97	3.54
USGS 16893	L. 92177	M_1	—	3.33	3.54
UCM 84110	L. 98054	M_1	—	2.67	3.57
USGS 16895	L. 92177	M_1	—	2.75	3.58
USGS 26571	L. 92177	M_1	—	2.72	3.59
UCM 73882	L. 97018	M_1	—	2.38	2.98
UCM 98626	L. 92177	M_2	—	3.03	3.02
USGS 2358	L. 92177	M_2	—	2.88	3.08
UCM 98575	L. 2003062	M_2	—	2.47	3.14
UCM 77021	L. 97018	M_2	—	2.75	3.26
UCM 99438	L. 2004130	M_2	—	2.90	3.26
UCM 81479	L. 98024	M_2	—	2.93	3.28
UCM 88520	L. 92177	M_2	—	2.89	3.30
USGS 16879	L. 92177	M_2	—	2.52	3.30
USGS 2365	L. 92177	M_2	—	3.25	3.33
USGS 2370	L. 92177	M_2	—	3.28	3.40
USGS 2360	L. 92177	M_2	—	3.35	3.46
USGS 2357	L. 92177	M_2	—	3.17	3.47
USGS 16864	L. 92177	M_2	—	3.31	3.47
UCM 98606	L. 92177	M_2	—	3.21	3.47
USGS 16866	L. 92177	M_2	—	3.01	3.47
USGS 16875	L. 92177	M_2	—	3.04	3.48
USGS 16874	L. 92177	M_2	—	3.00	3.49
UCM 73881	L. 97018	M_2	—	3.08	3.52
UCM 77018	L. 97018	M_2	—	3.19	3.52
USGS 16878	L. 92177	M_2	—	2.94	3.53
UCM 99402	L. 92177	M_2	—	2.97	3.57
UCM 100695	L.2004146	M_2	—	3.03	3.59
USGS 2371	L. 92177	M_2	—	2.80	3.68
USGS 16877	L. 92177	M_2	—	3.42	3.73
USGS 26565	L. 92177	M_2	—	3.13	3.77
USGS 26569	L. 92177	M_2	—	3.26	3.77
USGS 2368	L. 92177	M_2	—	3.11	3.77
USGS 2367	L. 92177	M_2	—	3.31	3.78
USGS 2359	L. 92177	M_2	—	3.22	3.89
USGS 2361	L. 92177	M_2	—	3.31	3.94
USGS 2366	L. 92177	M_2	—	3.02	3.97
UCM 98575	L. 2003062	M_3	—	2.78	3.34
UCM 73882	L. 97018	M_3	—	2.79	3.39
USGS 16865	L. 92177	M_3	—	2.92	4.26
UCM 99438	L. 2004130	M_3	—	2.74	4.28

Number	Locality	Tooth	Depth	Width	Length
UCM 98626	L. 92177	M_3	—	3.07	4.50
USGS 2373	L. 92177	M_3	—	2.96	4.52
UCM 99443	L. 2005163	M_3	—	3.03	4.63
USGS 16868	L. 92177	M_3	—	2.81	4.92
USGS 2368	L. 92177	M_3	—	2.93	4.98
USGS 2358	L. 92177	M_3	—	3.11	4.99
USGS 16869	L. 92177	M_3	—	2.94	5.03
USGS 16882	L. 92177	M_3	—	2.82	5.03
USGS 2357	L. 92177	M_3	—	3.07	5.04
USGS 2371	L. 92177	M_3	—	2.91	5.05
USGS 2359	L. 92177	M_3	—	3.07	5.05
USGS 26566	L. 92177	M_3	—	3.00	5.06
USGS 2372	L. 92177	M_3	—	3.06	5.16
UCM 81487	L. 92177	M_3	—	2.94	5.20
USGS 16870	L. 92177	M_3	—	3.07	5.22
USGS 2374	L. 92177	M_3	—	3.11	5.41
USGS 16880	L. 92177	M_3	—	3.14	5.46
USGS 26567	L. 92177	M_3	—	3.40	5.56